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Interactions between epifauna and infauna in a Kenyan mangrove forest: an experimental approach

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Jan Schrijvers

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Verhandeling voorgelegd tot het behalen van de graad van Doctor in de Wetenschappen, Groep Biologie

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Voor mijn ouders ...
aan wie ik het allemaal te danken heb.

En wat de primaire wonderen betreft (...) die moet je voor jezelf veroveren, in zweet gebaad, onder zonnestralen, veel lachen, in stof en regen, met slechts weinig metgezellen.

Nancy Newhall, 1960

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PREFACE

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FOREWORD

Although the study of the Gazi mangrove ecosystem at the Kenyan coast is only some nine years old, it can be characterized as stirring and varied.

In 1985, the Kenya-Belgium Project in Marine Sciences (KBP) was launched as an active cooperation between several Belgian oceanographical laboratories of the Free University of Brussels and the University of Gent on the one hand, and the Kenya Marine and Fisheries Research Institute at Mombasa on the other hand. Ever since the start of the project, it has been financed by the Belgian General Bureau of Developmental Cooperation (ABOS), with Prof. Dr. P. Polk as intermediary. The main objectives of the project were (1) to provide basic equipment for qualitative oceanographical research, (2) to educate Kenyan oceanographers, and (3) to advise Kenyan oceanographers during their PhD research. It was not until 1987, however, that the pristine and well accessible mangroves of Gazi Bay, about 60 km south of Mombasa, were chosen as one of the important work terrains for the KBP.

As a consequence, the Laboratories of Morphology, Systematics, and Ecology of Plants and Animals (Marine Biology section) of the University of Gent (represented by Prof. Dr. E. Coppejans, Prof. Dr. A. Coomans and Prof. Dr. M. Vincx), and the Laboratory of Ecology and Systematics of the Free University of Brussels (represented by Prof. Dr. P. Polk) joined in project 2.0043.88 of the Belgian National Fund for Scientific Research in order to develop a scientific in-depth study of these Gazi mangroves. This project of "Floristics, Faunistics, and Ecology of Kenyan Coastal Biotopes" ran from 1988 to 1991 and gave a first insight in the systematics, inventarisation, autecology, and spatial and temporal patterns of primary producers (mangroves, seagrasses, algae, and phytoplankton) and of secondary producers (zooplankton, zooendobenthos, phytal communities, and mangrove oysters). In turn, this project offered the direct inducement for the pioneering community ecological study of the mangrove meiobenthos and macrobenthos at Gazi Bay carried out by Drs. S. Vanhove and myself.

The next step was the extension of the structural ecological study to a more process-orientated analysis of the Gazi mangrove ecosystem in order to outline a rational management of Kenyan mangroves in general. With this in mind, the EC research programme TS2-0240-C (GDF) "Dynamics and Assessment of Kenyan Mangrove Ecosystems" was started within the EC domain of Science and Technology for Development (DG XII), running from the end of 1989 to the end of 1992. Four Belgian oceanographical laboratories (the Laboratories of Analytical Chemistry and of Ecology and Systematics of the Free University of Brussels and the Laboratories of Morphology, Systematics, and Ecology of Plants and Animals (Marine Biology section) of the University of Gent), two Dutch marine institutes (the Delta Institute for Hydrobiological Research at Yerseke and the Laboratory for Aquatic Ecology of the Catholic University of Nijmegen), and two Kenyan marine research groups (the Kenya Marine and Fisheries Research Institute and the Department of Zoology of the University of Nairobi) participated as EC partners with the intention to achieve (1) a description, an inventarisation, and an estimation of material and energy fluxes, (2) an integration of this information in a mathematical model, and (3) the development of ecological expertise in Kenya. With the assistance of both FKFO and EC projects, the structural ecology of the Gazi mangroves' endobenthos was further unraveled. In addition, the Delta Institute for Hydrobiological Research of the Netherlands and the University of Nairobi in Kenya started the research on resident and natant epibenthos as tertiary producers.

In 1992, a second FKFO project was started. Project G.20009.92 "Systematics, Ecology, and Biogeography of Marine Organisms in the Indian Ocean" of the Belgian National Fund for Scientific Research now also welcomed the Laboratory of Ecology and Aquaculture of the Catholic University of Leuven (Prof. Dr. F. Ollevier), the Research Group of Zoology of the University of Limburg (Prof. Dr. E. Schockaert), and the Laboratory of Analytical Chemistry of the Free University of Brussels (Prof. Dr. F. Dehairs). The project differed from its predecessor as the result of its extension in two research

directions. On the one hand, systematic inventarisation and structural, spatial ecological study, of primary producers and turbellarians in particular, were carried out on the Indian Ocean scale. On the other hand, the basic ecological information of the mangrove benthos at Gazi Bay, which had been gathered in previous projects, was used to make an in-depth analysis of such dynamical processes as material and energy pathways, feeding ecology, temporal patterns with secondary production and respiration estimates, parasitology, decompositional processes, and fluxes among adjacent biotopes. As the Marine Biology section of the University of Gent eventually also joined in the study of the natant epibenthos in terms of structural patterns, the research reached a stage in which the endobenthos could be unraveled in terms of its functionality and role in the mangrove ecosystem and its interaction with the epibenthos. The PhD research that is here presented especially fits in the latter objective (the term 'benthos' therefore always indicates zoobenthos unless stated otherwise). Since the second FKFO project came to a stop at the end of 1995, however, the presented study intends to be more than a doctoral work. It also wants to be a broader reflection on the structural and dynamical endobenthos research in the scientifically most discussed mangrove bay of eastern Africa.

The evaluation of this research is by no means the final curtain, however. Its findings, for instance, have just begun to be confirmed in recently published scientific papers. Moreover, this merely foreshadows an era in which local, Kenyan experts in endo- and epibenthology (Ms. D. Anyona, Ms. E. Fondo, Mr. E. Kimani, Mrs. A. Muthumbi, Mr. G. Mwatha, Mr. J. Ntiba, Mr. J. Okondo, Mrs. B. Okoth, Mr. R. Ruwa, and Mr. E. Wakwabi) carry on the search for knowledge of this important compartment in one of their country's most valuable ecosystems, the mangroves.

SAMENVATTING

Mangrovewouden kunnen voorkomen in de getijdenzone van tropische gebieden die aan een aantal basisvoorwaarden voldoen. Die voorwaarden zijn vooral gekoppeld aan een warme watertemperatuur (> 15° C), ondiep water en een bescherming tegen een hevige golfslag zodat een geschikte, slibbige sedimentsamenstelling ontstaat. Het mangrove-ecosysteem kent zowel een intrinsieke als een extrinsieke ecologische waarde. Het vormt een bufferzone waar de output van het continent naar de open oceaan aan belangrijke biogeochemische transformaties onderworpen wordt. Op regionaal vlak vormen mangrovegebieden belangrijke schakels in de koolstof- en stikstofkringloop tussen continent en oceaan. Ze spelen daarbij een belangrijke rol als bron van nutriënten voor de ondersteuning van de voedselketen in de eigenlijke kustzone met inbegrip van de koraalriffen. Economisch profileert dit ecosysteem zich voornamelijk als kraamgebied voor mariene en commercieel belangrijke vissen, als producent van mangrovehout en als belangrijke visgrond.
Het is dan ook de alsmaar groeiende bevolking en de ermee gepaard gaande mangrovekaalslag, die een bedreiging vormen voor deze gebieden.
Allerlei procesgerichte fundamentele onderzoeksterreinen die noodzakelijk zijn in de bescherming en het beheer van mangroves, werden reeds voorgesteld als noodzakelijk in de bescherming en het beheer van mangroves. Hiertoe behoren o.a. het onderzoek naar het voedsel dat mangroves bieden aan zwemmende, epibenthische dieren, die het mangrovegebied opzoeken tijdens vloed, en het aandeel van de bodemdieren in een geïsoleerde detritusvoedselketen van het ecosysteem. In beide domeinen staat het onderzoek van het endobenthos centraal zowel als voedsel voor hogere trofische niveaus als hun aandeel in de regeneratie van organisch materiaal in de mangrovebodem. Het is duidelijk dat dit endobenthologisch luik nood heeft aan meer dan structureel onderzoek. Dynamische processen zoals het zoeken naar de functie van dit endobenthos en dus de interactie met het epibenthos, vragen om een experimentele aanpak zoals het gebruik van kooien.
Het meio- en macrobenthos van mangrovebodems werden tot nu toe echter vooral bestudeerd in het kader van ruimtelijke en temporele patronen. Slechts één studie beschrijft het gebruik van kooien om de trofische relatie tussen het epi- en endobenthos van mangroves te achterhalen. Kooiexperimenten werden echter vooral uitgevoerd in gematigde streken. Een gedetailleerde studie van de historische achtergrond van, en de vraagstelling en hypothesevorming tijdens die kooiexperimenten, leidt echter tot een steeds weerkerende hiaat. De vraagstelling reikt meestal niet verder dan die van de detectie van predatiedruk door epibenthos op endobenthos. Onverwachte of ongewone resultaten worden daarbij meestal stiefmoederlijk behandeld zonder andere interactieve componenten in overweging te nemen. De feitelijke interactie is nl. een resultaat van specifieke predatorische, voedselcompetitieve, temporele en ruimtelijke, proceduregebonden en indirecte, zoals bioturbatiegebonden, effecten. Het is dus zeker nodig om tijdens de experimentele uitvoering de niet gewilde effecten onder controle te houden. Zoniet, moeten ze zeker in rekening genomen worden tijdens de interpretatie van de experimentele resultaten.
De bedoeling van het voorgestelde onderzoek was de rol van het endobenthos in de mangrovegebieden te achterhalen door zijn interactie, vooral in termen van voedselcompetitie en predatie, met het epibenthos te onderzoeken. Daarbij werd algemeen aangenomen dat een predatiedruk zou wijzen op het belang als prooi, daar waar een voedselcompetitieve druk eerder de sterke band met het regeneratiesysteem in de bodem zou benadrukken. Daarom werd een kooiexperiment gebruikt om het epibenthos volledig te verwijderen en op die manier de reactie van het endobenthos na te gaan. Rekening houdend met het voorgaande, dienden de doelstellingen en de concrete uitvoering echter nauwlettend te worden opgesteld.
Eerst en vooral moest er nagegaan worden of bepaalde endobenthische groepen inderdaad gestructureerd werden door het epibenthos. Indien die impact bestond, moest zijn oorzaak achterhaald worden. Meer nog, de impact en de drijfveer achter die impact moesten tussen twee verschillende zones in het

mangrovewoud vergeleken worden. De bekomen informatie moest dan gebruikt worden in een voorlopig trofodynamisch benthisch schema om op die manier de rol van het endobenthos in Oostafrikaanse mangrovewouden te onthullen.

De mangroves rond Gazi Bay, ongeveer 60 km ten zuiden van Mombasa in Kenya, werden uitgekozen als onderzoeksterrein omwille van hun bereikbaarheid en hun typische Oostafrikaanse morfologie. Kooien met een maaswijdte van 2 mm zorgden voor het uitsluiten van het epibenthos. Temporele en proceduregebonden effecten werden opgevangen door de kooibehandeling aan te vullen met respectievelijk een 'niet' behandeling (blank) en een 'halve' behandeling (halve kooi die identiek is aan de kooi maar waarvan één zijde open is om het epibenthos toch toegang te verlenen). Die drie behandelingen werden verdeeld over drie units (1 x 1 m) en de bekomen negen 'units' werden gerangschikt volgens een 'randomized block design'. Dat ontwerp zorgde voor een maximale randomizatie en interspersie tussen de units onderling. Gedurende zes maanden tot één jaar werden de negen 'units' maandelijks bemonsterd voor meiobenthos- en macrobenthosgegevens en geanalyseerd op omgevingsfactoren. De meiobenthosgegevens bestonden uit densiteiten van hogere taxa (waaronder vnl. nematoden aangevuld met oligochaeten, rotiferen, ostracoden, copepoden, polychaeten, turbellariën en anderen). De nematoden werden geïdentificeerd tot op genusniveau en gerangschikt volgens voedingstype. De macrobenthosgegevens bestonden uit densiteiten van hogere taxa (oligochaeten, polychaeten, amphipoden, insektelarven, gastropoden, nematoden en ev. cnidariën). Oligochaeten en insektelarven werden geïdentificeerd tot op familieniveau en de polychaeten, amphipoden en nematoden werden op genusnaam gebracht. De lengte van de amphipoden werd vervolgens gemeten. De omgevingsfactoren waren onder te brengen in granulometrische gegevens (aandeel van de verschillende korrelgrootten en mediaan, spreiding en scheefheid van het sediment) en fysicochemische metingen (organisch materiaal, temperatuur, saliniteit, pH, redox potentiaal, opgeloste zuurstof, concentratie van chlorophyl *a* en fucoxanthine). Om een zowel kwalitatief als kwantitatief beeld te krijgen van het aanwezige epibenthos werden ook krabben, gastropoden en heremietskreeften geïdentificeerd en geteld. Het zwemmende deel van het epibenthos, dat de mangroves opzoekt tijdens vloed, bleef echter een onbekende factor.

De gegevens van het experiment werden statistisch behandeld om per periode en per variabele een uitspraak te doen omtrent een significant exclusie-effect of proceduregebonden effect. Hiertoe werden twee ANOVA (variantie analyse) ontwerpen gebruikt. Het 2-wegs factoriële ontwerp beschouwde zowel de 3 verschillende 'exclusie' behandelingen als de verschillende perioden, als onafhankelijke groepen. Het gemengde ontwerp echter beschouwde de perioden als groepen, maar dan wel als duidelijk afhankelijk in de tijd. Een significant exclusie-effect werd aanvaard als voor minstens één van beide ANOVA ontwerpen de gegevens van de blanks en halve kooien onderling niet verschilden maar wel afweken van de kooiresultaten. Een significant proceduregebonden effect werd aanvaard als voor minstens één van beide ontwerpen de gegevens van de halve en hele kooien onderling niet verschilden maar wel afweken van de resultaten in de blanks. De kans dat de statistische analyse geen significant effect aantoonde, terwijl het wel aanwezig was (type II fout), werd acherhaald via poweranalyse.

De controle van alle andere interactieve componenten zorgde ervoor dat het relatieve belang van epibenthische voedselcompetitie en predatie in de relatie met het endobenthos, getest kon worden. Om ook de ruimtelijke invloed te bepalen, werd het voorgestelde experiment uitgevoerd in twee verschillende vegetatiezones van het Gazi mangrovewoud : de hoger gelegen en dichtbegroeide *Avicennia marina* zone en de lager gelegen en meer open *Ceriops tagal* zone.

Dit onderzoek werd automatisch opgesplitst in 4 deelaspecten. Hoofdstuk IV beschrijft het kooiexperiment voor de exclusie van het epibenthos van de *Ceriops tagal* zone met het oog op het nagaan van zijn interacties met het meiobenthos (in termen van predatie en voedselcompetitie). Er werd een significant exclusie-effect gevonden in de bovenste sedimentlaag (0-2 cm) voor het totale meiobenthos, de nematoden en de oligochaeten tijdens de eertse twee maanden, en voor de copepoden tijdens de laatste

zes maanden van het experiment. De densiteiten van de meest voorkomende predatorische en microalgen-etende nematoden hadden de neiging te stijgen in de oppervlaktelaag samen met een significante verhoging van het percentage slibbige detritus en de concentratie van pigmenten. Voedselcompetitie met het epibenthos leek doorslaggevend in de structurering van de nematodengemeenschap. Dat werd vooral duidelijk door de ermee gepaard gaande positieve exclusie-effecten op het slibbige detritus, de pigmentconcentratie en de nematodensamenstelling, en de afwezigheid van enige opwaartse migratie van nematoden in het kooisediment tijdens het experiment. Hetzelfde kon worden besloten voor de oligochaeten. De copepoden, daarentegen, werden vooral door predatie gecontroleerd. Die bevindingen wezen erop dat de meiofaunagemeenschap in het *Ceriops tagal* sediment (die voor ongeveer 95 % was samengesteld uit nematoden en oligochaeten) eerder deel uitmaakten van een geïsoleerd, detritus-voedselweb met slechts minieme predator-prooi interacties met het epibenthos.

Hoofdstuk V tracht die stelling over meiofauna/macro-epifauna interacties ook te bevestigen voor de *Avicennia marina* zone in hetzelfde gebied. Het exclusie-experiment werd hier dan ook gebruikt voor het natrekken van de dominante biologische interacties die het meiobenthos in dit mangrovewoud structureren. Significante exclusie-effecten werden aangetoond voor de oligochaeten en voor één van de dominante microalgen-etende nematodengenera (*Ethmolaimus*). Deze effecten werden bediscussieerd in het kader van epibenthische samenstelling en densiteiten, van voedingsgedrag, van voedselbronnen en van de omgevingsvariabelen. Er werd besloten dat het meiobenthos (vooral samengesteld uit nematoden en oligochaeten) hoofdzakelijk onder invloed staat van voedselcompetitie met het epibenthos. Daarmee werden de bevindingen voor het *Ceriops tagal* meiobenthos ook bevestigd voor de *Avicennia* zone. Het slibbige detritus en de microalgen konden beschouwd worden als de gemeenschappelijke voedselbron. De afwezigheid van een effect op de predatorische nematoden toonde aan dat de drijvende kracht achter een interne regulatie nog diende gevonden te worden. De impact van het epibenthos op het meiobenthos zou zelfs gecompliceerd kunnen zijn door een bijkomende interactie met het infaunale macrobenthos.

Daarom beschrijft Hoofdstuk VI het gebruik van het kooiexperiment om de interactie tussen het epibenthos en het macro-endobenthos van de *Avicennia marina* zone te onderzoeken. Een significante stijging van de densiteiten van amphipoden (*Grandidierella* spec.) en insektelarven (familie Dolichopodidae) duidde op een positief exclusie-effect, terwijl zulk een effect niet werd waargenomen voor de oligochaeten (vooral de tubificiden), de polychaeten (*Namalycastis* spec.) en de macro-nematoden (*Oncholaimus*). Voedselcompetitieve interacties werden gegeven als meest voor de hand liggende structurerende factor van de amphipodengemeenschap. Die verklaring werd verder ondersteund door de aanwezigheid van een ermee gepaard gaand positief exclusie-effect op de densiteit van microalgen. Er werd daarom voorgesteld dat de competitie voor microalgen en gesedimenteerd organisch materiaal (detritus) als voedsel, de bepalende regulerende factor is die het epibenthos uitoefent op het macro-endobenthos van dit mangrovesediment. De aanwezigheid van epibenthische predatie kon echter niet worden uitgesloten. De vraag of predatiedruk op het macrobenthos in de bodem van een Oostafrikaans mangrovewoud volledig afwezig is, bleef daarom nog onbeantwoord.

Hoofdstuk VII wil dan ook de nadruk leggen op de interacties tussen het epibenthos en het macro-endobenthos van de lager gelegen *Ceriops tagal* zone. De hypothese dat predatiedruk toeneemt bij afnemende hoogte in het intergetijdengebied, ten koste van de epibenthische competitieve invloed, werd op die manier getest. Het kooiexperiment werd gebruikt om het epibenthos te verwijderen van de *Ceriops tagal* zone. Een significante stijging van de dominante tubificidenpopulatie en de polychaet *Namalycastis* spec. in de kooien, duidde op een positief exclusie-effect. Epibenthische predatie bleek een iets grotere invloed te hebben in de *Ceriops tagal* zone dan in de hoger gelegen *Avicennia marina* zone. Toch werd de voedselcompetitie voor het slibbige detritus nog steeds gezien als de doorslaggevende structurerende kracht achter de oligochaeten. Het merendeel van het bestudeerde macro-endobenthos werd daarom ook eerder beschouwd als een trofisch doodlopend systeem met een slechts minieme trofische interactieve

plaats in het mangrove voedselweb.

Hoofdstuk VIII geeft een synthese. De gegevens van het meio- en macrobenthos in de *Avicennia marina* en de *Ceriops tagal* zones werden gecombineerd om zo een algemeen overzicht en besluit te geven, en om te kunnen beantwoorden aan de doelstellingen die door deze studie werden vooropgesteld.

Beide vegetatiezones vertoonden typische mangrovekarakteristieken, weerspiegeld in een hoog gehalte aan slibbig detritus en hoge nematodendensiteiten. Bovendien waren beide zones vrij hoog in het intergetijdengebied gelegen, waarvan de hoge anorganische zandfractie, de hoge saliniteit en de dominante microalgen-etende nematoden een bewijs waren. Het verschil tussen beide zones was tweeledig. Enerzijds was het een gevolg van het verschil in ligging in het intergetijdengebied, gekoppeld aan een lichte verandering in de endobenthos- en epibenthosgemeenschap. Anderzijds veroorzaakte de eerder dunbegroeide en meer open *Ceriops* vegetatie een lagere hoeveelheid organisch materiaal en een hogere microalgendensiteit dan de *Avicennia* zone.

Slechts enkele studies vermeldden het voorkomen van proceduregebonden effecten op omgevingsfactoren en hun impact op de biotische experimentele respons. Onze studie was echter in staat significante proceduregebonden effecten op macrobenthische oligochaeten en meiobenthische nematoden in de *Avicennia marina* zone en op macrobenthische nematoden in de *Ceriops tagal* zone, statistisch te detecteren. Die effecten zouden ev. veroorzaakt kunnen zijn door veranderingen in saliniteit, anorganisch slib, kooischaduw en vochtigheid. Maar, eerder dan de concrete interpretatie van proceduregebonden effecten, zorgde de mogelijkheid tot een statistische detectie van die effecten, voor een grotere betrouwbaarheid van gevonden significante exclusie-effecten.

De interpretatie van die exclusie-effecten leidde tot de volgende stellingen. De bestudeerde benthosgemeenschap van het Oostafrikaans hoog gelegen mangrovesediment was duidelijk betrokken in twee verstrengelde recyclagesystemen. Die systemen werden duidelijker waargenomen naarmate de voedselbron beperkt en de voedselaanvoer laag was. Die beperking leidde nl. tot een voedselcompetitie die sterker werd naarmate meer consumenten aanwezig waren. (1) Het microalgen systeem was gecentralizeerd rond microalgen als voedsel, en microalgen-etende nematoden, de amphipood *Grandidierella* spec. en het microalgen-etende epibenthos als consumenten. Dat systeem was het meest zichtbaar in de *Avicennia marina* zone. (2) Het detritus systeem was gecentralizeerd rond het slibbige detritus als voedsel, en de meio- en macrobenthische oligochaeten en het detritus-etende epibenthos als consumenten. Dat systeem was het meest duidelijk in de *Ceriops tagal* zone.

De experimentele resultaten bevestigden duidelijk het bestaan van beide systemen met de amphipoden en het grootste deel van de nematoden als vooral microalgen-etend, en de oligochaeten als vooral detritus-etend. Het voedsel was een regulerende factor voor de gemeenschapsstructuur van de consumenten, vooral in die gebieden waar het aanbod beperkt was. Daarenboven werd het duidelijk dat de voedselcompetitie veel belangrijker was dan de epibenthische predatie in het structureren en reguleren van de globale endobenthische gemeenschap. Deze studie geeft dan ook een inzicht in de beslissende rol van het endobenthos in dit Oostafrikaanse mangrovewoud als regenerator van mangrovemateriaal en zijn eerder zwak aandeel in het prooiaanbod voor het demersale en pelagische deel van het mangrovesysteem.

I. INTRODUCTION

A. CHALLENGE

Mangroves are littoral plant formations which can frequently be found along tropical coastlines that are protected from intensive wave action by coral reefs. They have variously been described as coastal woodland, mangal, tidal forest or mangrove forest. Mangrove trees belong to many different genera and families, and are not always closely related phylogenetically. Their common characteristic, however, is a morphological, physiological, and reproductive adaptation that enables them to grow in an unstable, difficult environment (Hutchings & Saenger 1987). The existence of extensive mangrove communities is dependent on the following basic requirements (Chapman 1977):

(1) warm air and ocean temperature (> 15 °C)
(2) muddy substrate
(3) protection from intensive wave action
(4) salt water
(5) large tidal range on a gently sloping shore
(6) favourable ocean currents
(7) shallow water

Their ecological value is intrinsic as well as extrinsic. They are used as feeding grounds, nursery areas, and shelters by a variety of animal species (Sasekumar *et al.* 1992). Moreover, mangrove areas also function as buffer sites with important biogeochemical transformations and a constant flow of living and non-living matter in and out the system. As such, they can be regarded as an important link in the flux between land and ocean (Hutchings & Saenger 1987).

Exploitation of mangroves has always been successfully managed in the past (Hatcher *et al.* 1989). For centuries, locals have used mangroves as an important source of different products for their traditional societies. The most wanted products are fire wood, fuel, charcoal, food, timber or construction material, and tannin or dye (Kokwaro 1986). Mangrove areas are also used for aquaculture and fisheries. The mangrove ecosystem is an important economic resource for the entire coastal economy of Kenya. One of the most important direct economic functions of mangroves at the Kenyan coast is the use of the wood in the production process of the local cement industry. Other economic functions are the direct use as fuel wood and building poles by the population living in the direct surroundings of the mangrove areas. Apart from tourism, the commercial and subsistence fishery is one of the main sources of employment and income in the area. This marine stock depends to a large extent on the mangrove ecosystem. Tourists have not been attracted in great numbers to Kenyan mangrove forests. However, the coastal protection and the buffer and nutrient source for the coral reefs, means that the indirect value of the mangroves to the tourist sector is of significance. The presence of these forests assures that the coastal zone maintains its natural beauty (Hirsh & Mauser, personal communication).

Mangroves, however, are being decimated by an ever increasing population close to the coastlines (Alongi 1989). Anthropogenic effects are mainly linked with clear felling of the forest for woodchip production, farming, aquaculture, salt mining, tin mining, housing, tourism, port and airport facilities, and industrial sites (Hatcher *et al.* 1989). Kenyan mangrove forests in particular, are increasingly becoming subject to uncontrolled dumping of domestic and industrial waste (Ruwa & Polk 1986) and to exploitation for salt mining and tourist facilities (personal observation).

Process orientated fundamental research on mangrove systems has lagged behind that on coral reefs. Until the 60s most developed countries considered mangroves as wasteland. More recently, however, there has been a surge of interest in the factors that control the structure and function of mangrove ecosystems.

Several key areas of research, most relevant to conservation and imperative for proper management of mangroves, were reported by Hatcher *et al.* (1989). Two of them can be considered as a direct inducement to the present research:

(1) The mangrove forest and its surroundings have always been considered as important feeding grounds for natant organisms coming from adjacent waters (Sasekumar *et al.* 1992). The endobenthos of the mangrove floor *e.g.* is believed to be an important prey item (Chong & Sasekumar 1981; Robertson 1987; Sasekumar *et al.* 1992). The relative importance of mangrove areas as feeding grounds, nursery areas or shelters in attracting crabs, prawns, shrimps, and fishes still needs further research, though.

(2) The fate of the mangrove primary production is another interesting research topic. Part of this production may be exported to adjacent waters, due to outwelling or migration of natant herbivores and detritivores (Hemminga *et al.* 1994; Lee 1995). The other part of the primary production is retained in the forest and is mediated by the benthos which consists of resident epibenthos, endobenthos, and a bacterial community. In this retention system, bacteria, and particulated and dissolved organic matter (POM and DOM) are closely linked (Rao *et al.* 1994; Middelburg *et al.*, submitted personal communication). They have already been indicated to recycle matter at an enormous rate, implying an energy and carbon sink for this system (Alongi 1989). On the other hand, however, the microbial community may easily be ingested by protozoans, meiofauna, and macrofauna. The latter might be preyed upon by visiting organisms, again leading to an energy and carbon transfer. Research on how many bacteria are consumed by this endobenthos should be stimulated to try and find out if a real carbon sink exists (Alongi 1989).

The trophodynamics of the endobenthos clearly is a central theme in both key areas. The entire microbial/meiofaunal/macrofaunal food chain model could, indeed, be looked upon as a sink, raising the following question: to what extent are meiofauna and macrofauna consumed by higher trophic groups or linked with the carbon system ? It is therefore of vital importance to study the mangrove endobenthic system (Robertson 1987). The study of the interaction between the mangrove endobenthos and epibenthos, in particular, will partly cover both research interests. It will therefore, however, have to go beyond detailed lists of species and analysis of spatial and temporal patterns. Functional analysis of interactions between and within benthic groups needs to be approached by means of experimental techniques such as cages.

Mangrove trophodynamical studies, especially in terms of epibenthos/endobenthos interactions, are mainly limited to the New World (Florida and the Carribean) (Odum & Heald 1972; Robertson 1987) and to some parts of the Old World such as South-east Asia (Malley 1978; Leh & Sasekumar 1985; Robertson 1986; Smith 1987) and Australia (Robertson 1987; Alongi 1989; Robertson & Daniel 1989). The Indian Ocean mangrove systems, and in particular those of East Africa, have not been studied to the same extent as those of the other Indo-West Pacific regions. Until recently, literature on mangrove benthic systems, as on most tropical benthic studies, was rare, scattered and mainly published by congresses, and in monographs and journals of developing countries.

B. BENTHIC MANGROVE RESEARCH

1. Meiobenthos

Gerlach (1957) was one of the first to give a systematic account of the meiobenthos (nematodes) in a Brasilian mangrove sediment. Only during the last two decades, the meiobenthic ecology of mangroves received more interest.

Community structure, species composition and diversity were first emphasized in detail by Decraemer & Coomans (1978) during a Belgian expedition in Australian mangroves. From then onwards, most of the attention has been focussed on the spatial and temporal variation of the meiobenthic community structure and composition by means of community analysis techniques. The influence of the mangrove forest's intertidal position and zonation on the meiofauna has been analysed in South Africa (Dye & Furstenberg 1978; Dye 1983a,1983b), East Africa (Vanhove *et al.* 1992; Vanhove 1993; Olafsson 1995; Schrijvers, in press), Australia (Hodda & Nicholas 1985; Alongi 1987a, 1987b; Nicholas *et al.* 1991; Nicholas & Stewart 1993), India (Kondalarao & Ramana Murty 1988; Sarma & Wilsanand 1994) and Malaysia (Sasekumar 1994). Research on seasonal influence, mainly in terms of monsoonal rain, is limited to India (Sultan Ali *et al.* 1983; Krishnamurthy *et al.* 1984), Australia (Alongi 1987a; Alongi 1988a; Alongi 1990), and Malaysia (Sasekumar 1994). Okondo (in preparation) are the first to follow the monthly meiofaunal variation in an East African mangrove sediment. The role of the meiobenthos in the trophic and detrital web of mangroves has also gained attention (Krishnamurthy *et al.* 1984; Dye & Lasiak 1986).

Only recently, the vertical distribution of the meiobenthos along a sediment depth profile started getting some more attention (Vanhove *et al.* 1992; Ansari *et al.* 1993; Vermeulen, in preparation; Okondo, in preparation).

Meiobenthic densities in mangroves are now known to be dominated by nematodes and are considered to be very variable. From the studies investigating nematode assemblage structure at the genus or species level, it is clear that no distinct assemblages can be confined to mangrove areas (Olafsson 1995). The important impact of human activities, such as tree felling, on densities and composition has recently been proved (Schrijvers, in press).

2. Macrobenthos

Although mangrove macrobenthos has been studied more than meiobenthos, it has mainly been approached in terms of species composition, diversity, and zonation with little quantitative information. Data are skewed and limited because of research problems such as the choice of study season and site, and the use of different sieve sizes, different preservation and extraction techniques, varying sample depths, and different counting techniques. Nevertheless, overall macrobenthic densities are regarded to be lower in mangroves than on unvegetated flats or reefs (Alongi 1989).

Like for meiobenthos, ecological studies on the macrobenthos in and on mangrove sediments are mainly concerned with the community structure and its change in time, space and environment. Literature ranges from seasonal and monsoonal influence (Sasekumar 1974; Kurian 1984; Kumar 1995) to intertidal gradient (Day 1974; Frith *et al.* 1976; Frith 1977; Murty & Balaparameswara 1977; Broom 1982; Wells 1983; Kurian 1984; Nateewathana & Tantichodok 1984) and tannin impact (Poovachiranon *et al.* 1986; Giddins *et al.* 1986).

In general, a distinction can be made between the endo- and epifaunal macrobenthos. It is mainly the epibenthos (gastropods and crustaceans such as hermit crabs and crabs) and the larger or surface dwelling endobenthos that have received most of the attention (in Schrijvers *et al.* 1995).

3. Biological interactions

Research on interactions between the endobenthos (meio- and macrofauna) and the epibenthos (resident and natant) in mangrove forests, as a next important step in ecological analysis, is scarce. These are the two main fields:

a) Bioturbation

Epibenthic bioturbation of mangrove sediments is broad and complex. Nevertheless, only the production of burrows and pellets by crabs and the formation of mounds by thalassanid shrimps together with the feeding activity of crabs, hermit crabs, and gastropods have been regarded as important in terms of disturbance (Alongi 1989). This bioturbation modifies the sediment texture and topography directly (McNae 1968; Malley 1977; Warren & Underwood 1986) and influences the endobenthic structure indirectly (Dye & Lasiak 1986; Dittmann 1993).

b) Trophic relationships

Since the baseline study of Odum & Heald (1972), trophic chain models on and, especially, in tropical mangrove sediments have not been studied in more detail. This is also true for ecological processes in most other soft tropical sediments such as tidal flats (Vargas 1988).

Epibenthos-microbenthos relationships are mainly concerned with the feeding ecology of molluscs, pelagic and benthic crustaceans (prawns and crabs), and fishes in mangroves. In general, the microbenthos, *i.e.* bacteria associated with detritus, fungi, microalgae, cyanobacteria, and protozoans turned out to be more or less important food items for this epibenthos, (Robertson 1987) such as crabs (McIntosh 1984; Leh & Sasekumar 1985; Dye & Lasiak 1986; Giddins *et al.* 1986; Robertson 1986; Dye & Lasiak 1987; McIntosh 1988; Wolcott & O'Connor 1992), fishes (Ong & Sasekumar 1984), gastropods (Branch & Branch 1980; Dye & Lasiak 1987) and amphipods (Poovachiranon *et al.* 1986).

Epibenthos-endobenthos relationships concentrate especially on meiobenthos and small macrobenthos (< 1 mm), although its function remains vague due to taxonomic and manipulative problems. As in most temperate intertidal studies, the role of the endobenthos as food for the epibenthos is the central theme. This theme is approached by means of gut analysis (Leh & Sasekumar 1985; Dye & Lasiak 1986; Dahdouh-Guebas, personal communication), correlations of prey and predator densities (McIntyre 1968; Robertson & Duke 1990), observation of feeding behaviour (McIntosh 1984; McIntosh 1988), and only one manipulative cage experiment (Dye & Lasiak 1986). The latter is also the only study dealing with the impact of the resident mangrove epibenthos. The competitive interaction between fiddler crabs and meiobenthos in this study is stated to be more important than predation or ingestion. The most comprehensive literature in tropical benthos, however, is on the natant epifauna visiting Malayan mangrove forests for food. Penaeid prawns are believed to either ingest smaller benthos non-selectively (nematodes and protozoans) or use it as a supplementary food item (Chong & Sasekumar 1981; Robertson 1987; Sasekumar *et al.* 1992). Many fishes are also found to be benthic feeders, preying on surface feeding crabs, amphipods and polychaetes, and encrusting bivalves as a major food source (Robertson 1987). The role of the infauna as selected fish and prawn food, however, is not as clear (Alongi 1989), and most of this research is carried out in subtidal inlets near the mangrove edge instead of in the forest itself (Robertson & Duke 1990; McIntosh 1988; Sasekumar *et al.* 1992). The question: 'Do these natant organisms key-in on mangrove forest floors as sites of high food abundance or as sites of shelter from predators ?', still remains to be answered. This problem has already been studied for salt marshes (Minello & Zimmerman 1992).

The presence of a structuring epibenthic force on the endobenthos and the driving force behind this impact, is far from known for mangrove forest sediments. That knowledge though, could eventually give an insight in the role of the endobenthos in the sediment (Kennedy 1993). Manipulative field techniques, such as cage experiments, are needed to further unravel these benthic interactive pathways (Alongi 1989). Before applying these techniques, a comparison between the present concepts and the methods mainly borrowed from temperate regions has to be made.

C. CAGE EXPERIMENTS IN TEMPERATE REGIONS

The detection of biological interactions between epibenthos and endobenthos in temperate coastal regions has a long tradition. This research made use of a wide range of methods going from direct field observations and stomach or gut analyses to laboratory, natural, or field experimental work.

The experimental approach in benthic ecology was especially stimulated by Platt (1964). Dayton (1973), Woodin (1974) and Peterson (1979) were the ones to really emphasize causality. They thought correlation (method of agreement) was not sufficient and therefore promoted experimental work to test hypotheses using the method of difference (i.e. analysis of variance). Nowadays, biological experiments are believed to be indispensable to focus on relatively simple cycles of causality (Zolman 1993). It soon became obvious that the exclusion or inclusion of epibenthos via cage experiments was the best way to tackle the problem of epibenthos/endobenthos interactions.

1. Cage experiments

a) Rocky bottoms

The use of cage manipulative techniques was first reported as far back as 1927 and 1928 by Blegvad in the Danish Limfjord. Most of the pioneering usage of cage experiments, however, was applied on rocky intertidal areas. Relations between macro-epifauna (sessile, surface dwelling, and natant) were studied in terms of physical or predatory disturbance and competitive exclusion (Connell 1961; Paine 1966; Connell 1970; Dayton 1971; Paine 1974; Menge & Sutherland 1976).

b) Macrofauna in soft bottoms

It was not until 1968 that Naqvi tried to use these cage methods to detect the influence of the epibenthos on the macro-infauna in soft bottoms. Whereas epibenthic exclusion on rocky shores promoted some taxa to increase which resulted in the decrease in overall diversity due to competitive exclusion, the opposite seemed to be true for soft bottoms. It was believed that epibenthic predation kept the macro-infaunal densities under its carrying capacity since there was more space and food than in rocky habitats. Tests on this predation hypothesis resulted in a wide range of cage experiments in subtidal regions (Virnstein 1977; Virnstein 1979; Holland *et al.* 1980; Hurlberg & Oliver 1980; Berge & Valderhaug 1983; Federle *et al.* 1983; Hall *et al.* 1990a; Hines *et al.* 1990), on intertidal, unvegetated flats (Reise 1977; Reise 1978; Peterson 1979; Berge & Hesthagen 1981; Scherer & Reise 1981; Woodin 1981; Kalejta 1993; Kent & Day 1983; Ambrose 1984; Quammen 1984; Fitzhugh & Fleeger 1985; Gee *et al.* 1985; Raffaelli & Milne 1987; Raffaelli *et al.* 1989; Trush *et al.* 1994), in zones covered by seagrass (Young *et al.* 1976; Reise 1977; Reise 1978; Nelson 1981; Summerson & Peterson 1984), and in salt marshes (Vince *et al.* 1976; Van Dolah 1978; Kneib & Stiven 1982; Ward & Fitzgerald 1983; Frid & James 1988; Kneib 1988; Haase 1993). Some studies see the increase in predatory infauna after epibenthic exclusion as an evidence for epibenthic predatory control (Commito 1982; Kent & Day 1983; Ambrose 1984; Gee *et al.* 1985; Kennedy 1993). In most studies, however, the epibenthic structuring impact on the macro-endobenthos remained a controversial issue.

c) Meiofauna in soft bottoms

Due to problems of logistics, difficulties in handling and manipulating, the experimental approach to epibenthos/meiobenthos relationships was initiated much later (Coull & Palmer 1984). It soon became clear that meiobenthos, with its short generation time and benthic larval stages, was very useful in cage experiments (Bell 1980). Although some of the early field experiments on meiobenthos have to be mentioned (Boaden 1962; Nair & Govindarhutty 1972 in Coull & Palmer 1984; Bleakley & Boaden 1974 in Coull & Palmer 1984), the bulk of meiobenthic studies in the 60s and 70s was mainly concerned with enumeration, identification, and correlation. A general debate developed. On the one hand, meiobenthos was generally believed to play an important role in the nutrient regeneration within the detrital foodweb (Gerlach 1978). On the other hand, this meiobenthos was gradually found to be food for higher trophic levels such as juvenile fishes, shrimp, crabs, and gastropods especially in muddy habitats where deposit feeding and predatory macrofauna are most abundant (Robertson & Newell 1982a; Coull & Wells 1983; Hicks & Coull 1983; de Morais & Bodiou 1984; Pihl & Rosenberg 1984; Gee 1989). This debate asked for the detection of a possible epibenthic predatory control of the meiobenthos via cage experiments. Until then, previous theories on meiofaunal population control were mainly linked with intra-meiofaunal predation (Heip & Smol 1975) or with the physical environment (Hulings & Gray 1976).

Similar to macro-infaunal studies, these cage experiments were, and still are, carried out in a wide range of coastal habitats such as subtidal flats (Buzas 1978; Olafsson & Moore 1990; Olafsson & Moore 1992), intertidal, unvegetated flats (Reise 1979; Sherman & Coull 1980; Berge & Hesthagen 1981; Scherer & Reise 1981; Warwick *et al.* 1982; Fitzhugh & Fleeger 1985; Gee *et al.* 1985; Gee 1987; Smith & Coull 1987), zones covered by seagrass (Webb & Parsons 1991), and salt marshes (Bell & Coull 1978; Bell 1980; Fleeger *et al.* 1982; Hoffman *et al.* 1984; Ellis & Coull 1989). Only a limited number of experimental results did not conceive the epibenthic predation as a structuring force for the meiobenthic community (Berge & Hesthagen 1981; Fleeger *et al.* 1982; Gee *et al.* 1985; Gee 1987; Webb & Parsons 1991).

2. Problems

These cage experiments of temperate regions are a simplistic approach to tackle the problem of the complex epibenthos/endobenthos interaction. Most studies emphasize a predatory control. Thus, they expect the prey densities to increase after exclusion of large mobile epibenthic predators. Moreover, they predict an eventual infaunal predator increase followed by an equilibrium or stabilization.

Nevertheless, many unexpected and counterintuitive results were found (Quammen 1984; Sih *et al.* 1985; Service *et al.* 1992), let alone the unsuccessful experiments which were not published (Hurlberg & Oliver 1980; Connell 1983; Hurlbert 1984). Profound evaluation does reveal a possible explanation. Firstly, prey evidence does not automatically lead to functional evidence such as predation pressure on the prey structure and dynamics (Hall *et al.* 1990b). Secondly, other interactive components beside predation might be compensating, skewing or even replacing a possible predation pressure.
Other interactive components could be:

(1) Specific predatory effects (Young *et al.* 1976; Virnstein 1977; Woodin 1978)
(2) Competition for food sources (trophic amensalism)
(3) Temporal and spatial effects (in terms of habitat, season, succession phase, and reproduction cycle) (Holland *et al.* 1980; Haase 1993; Kalejta 1993; Trush *et al.* 1994)
(4) Procedural effects (see later)
(5) Indirect effects caused by four main factors (Kneib 1991):

- Complex community organization with multitrophic, larval/adult, and intracompetitive interactions (Kneib & Stiven 1982; Kent & Day 1983; Kneib 1988; Kneib 1991; Posey & Hines 1991; Olafsson & Moore 1992; Wootton 1994; Minello & Zimmerman 1992). This approach goes beyond the simple cycles of causality.
- Animals providing *e.g.* shell refuges (Kuhlmann 1994)
- Plants leading to reduced foraging activity (Vince *et al.* 1976; Heck & Thoman 1981; Minello & Zimmerman 1992), but also causing increased refuge possibility and augmentation of food supply such as epiphytes for grazers (Kneib 1991)
- Bioturbation (see later)

Two of the most conspicuous and frequently confounding effects in cage studies will be explained in more detail:

a) Procedural effects

The building and use of cages for field experiments, automatically leads to unwanted environmental modifications (Peterson 1979; Reise 1985; Hairston 1990; Hall *et al.* 1990b; Wilson 1991) such as sediment and physico-chemical modifications (Virnstein 1977; Hurlberg & Oliver 1980), algal growth on the cage mesh known as fouling (Reise 1978), and invasion of juveniles (Virnstein 1977; Buzas 1978; Reise 1978; Bell 1980; Kneib 1988).

Yet, Hall *et al.* (1990b) promote the use of cages as a useful and necessary tool provided that careful considerations are made. The sediment in and outside the cages is to be compared during the experiment and treatment control becomes indispensable (Hurlbert 1984; Hairston 1990; Wilson 1991). A partial cage will control the procedural effects and assures an almost natural epibenthic abundance on the sediment. Conclusions can only be made when the experimental output is augmented with observational data, gut contents analysis, or laboratory experiments (Virnstein 1977; Virnstein 1979; Olafsson & Moore 1992).

Enclosures have advantages when focussing on specific predator effects over short time scales (Hall *et al.* 1990c). Abnormal intraspecific interactions, however, may affect normal behaviour when enclosing very high abundances (Ward & Fitzgerald 1983; Raffaelli *et al.* 1989; Hall *et al.* 1990c; Webb & Parsons 1991). Exclosures, on the other hand, are especially useful when asking for the global epibenthic impact on an endobenthic community without specifically referring to a predatory hypothesis. This kind of experiment does make treatment controls a necessity, though (Hall *et al.* 1990c).

b) Bioturbational effects

Exclusion or inclusion of the epibenthos during cage experiments may also alter the bioturbational impact leading to indirect effects. According to the nature of this impact, these indirect effects might be positive, negative, or neutral.

Tube structures may provide refuge possibilities from predation or facilitate larval settlement and thereby diminish a possible predatory control (Woodin 1978; Woodin 1981; Bell & Woodin 1984). This is especially obvious during cage inclusion treatments.

Also burrows and mounds, created by several epibenthic animals, might influence the endobenthic structure. The invasion of burrow associates (Bright 1977), the passive deposition of meiobenthos in the burrows (DePatra & Levin 1989), the oxygenation of the sediment surface (Katz 1980), the spatial refuge from predators (Hoffman *et al.* 1984), and the provision of suitable microhabitats in sediment depth (Dittmann, in press) result in increases in abundance of some endobenthic groups around burrows. Nevertheless, infaunal abundances can be reduced in assemblages of burrowing organisms, an effect often also attributed to bioturbation (Dittmann, in press).

The bioturbational consequences of the epibenthic feeding activity in terms of sediment disturbance and production of feeding and faecal pellets in particular, are also considered important (Bell & Coull 1978; Reise 1979; Bell 1980; Sherman & Coull 1980; Kneib & Stiven 1982; Hoffman *et al.* 1984; Gee *et al.* 1985; Webb & Parsons 1991; Olafsson & Moore 1990; Olafsson & Elmgren 1991; Olafsson & Moore 1992). This activity is proved to lead to positive (Bell & Coull 1978; Reise 1979; Gee *et al.* 1985; Webb & Parsons 1991; Olafsson & Moore 1992) as well as negative effects (Sherman & Coull 1980) on meiobenthic taxa.

In general, both burrow and feeding activities are believed to increase after inclusion and decrease or even disappear after exclusion of the epibenthic community. This will eventually lead to indirect effects on the target endobenthic community.

D. CAGE EXPERIMENTS IN SALT MARSHES

Salt marshes are known to be the equivalent of mangroves in temperate regions (figure 1.1) (Adam 1990). A detailed review of the marsh cage studies will give an even better insight in typical problems concerning both substance and methodology. This might be needed before application on tropical mangrove forests. Coastal marshes can be defined as areas, vegetated by herbs, grasses, or low shrubs that border saline water bodies. They are exposed to air for the majority of the time though subjected to periodic flooding as a result of fluctuations (tidal or non-tidal) in the level of the adjacent water body (Adam 1990). The tidal pools in the low and high intertidal zones and the channels, ditches, inlets, and creeks of the low intertidal region of salt marshes can be considered as subtidal.

During high tides and especially when the tide recedes, the natant macro-epifauna increase in density in salt marshes. These animals, mainly larval, juvenile and adult fishes, shrimps, crabs, and mysids, are believed to use marshes as shelter, nursery, and feeding grounds. At low tide, this natant epi- and hyperbenthos is restricted to tidal pools, embayments, and creeks with concentrated densities (Ward & Fitzgerald 1983; Kneib 1987). The exposed marsh sediment surface then becomes inhabited by resident macro-epifauna like fiddler crabs, gastropods, bivalves, and insects. They are mainly bottom dwelling deposit feeders (Nichols & Robertson 1979; Weisberg & Lotrich 1982; Adam 1990).

As mentioned before, the impact of this epibenthic community (resident and natant) on the marsh endobenthos has been studied by a limited number of cage experiments (table 1.1). These experiments have mainly been applied on North American marshes while only few have been carried out in Europe (Frid & James 1988; Haase 1993). Most of them hypothesize an epibenthic predatory impact, expecting a prey density increase after exclusion and a decrease after inclusion. And again, most studies find predation/disturbance to be of main importance for regulation of the endobenthic community. As stated above, a simplistic approach to this biological issue of epibenthos/endobenthos interactions might, however, have skewed the general experimental output and interpretation.

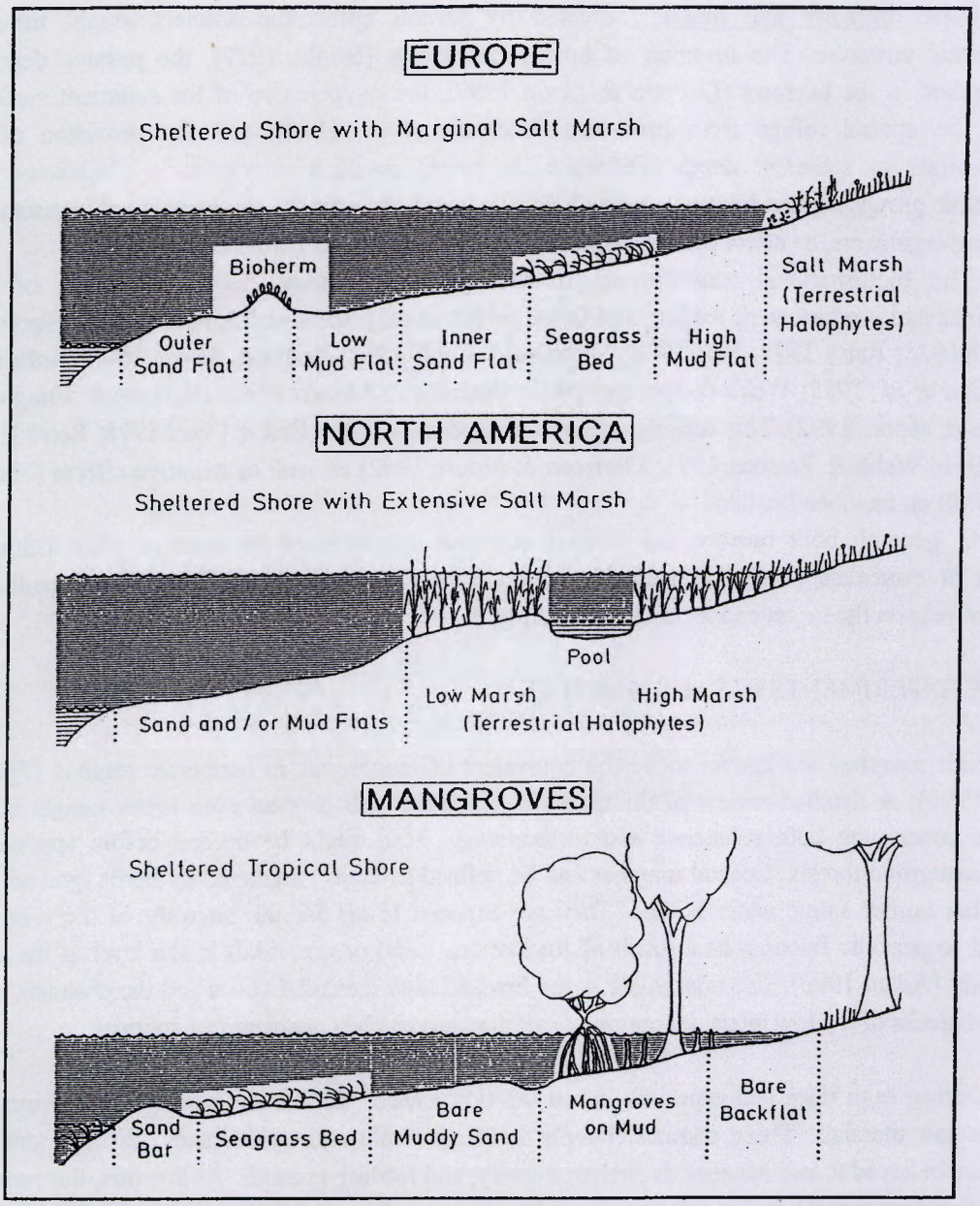


Figure 1.1: Zonation of habitats on three types of sedimentary shores between low and high tide line *(after Reise 1985)*.

1. Specific predatory effects

a) Endobenthos

Predation pressure only seemed to have an impact on the most susceptable, available, visible and therefore vulnerable endobenthic taxa. This includes the epibenthic part of the meiobenthos, mainly restricted to the top 2 mm such as harpacticoid copepods, nauplii, and polychaetes (Bell 1980; Ellis & Coull 1989). Also for the macro-endobenthos, the surface or subsurface dwelling groups, were the only groups believed to be affected by predation. They are mainly amphipods (Vince *et al.* 1976; Van Dolah 1978), annelids (Haase 1993), and surface deposit feeding gastropods (Frid & James 1988). It indicates that other groups (such as the dominant nematodes) will be regulated by other factors.

b) Epibenthos

Only one study deals with the impact of resident epifauna (Hoffman *et al.* 1984). Bell (1980) even refers to this part of the epibenthos as not that important. It is striking that most of the studies that find the predatory effect to be evident, use enclosure experiments (Bell & Coull 1978; Ellis & Coull 1989) or specifically exclude certain natant animals, believed or even known to be predators (Vince *et al.* 1976; Bell 1980; Haase 1993). An overall epibenthic impact via cage exclusion has rarely been studied.

It is true that the visiting, natant epifauna outnumber the resident inhabitants, but an influence on the underlying sediment by the latter may not be neglected, especially during low tide.

There is indeed evidence that several visiting animals use the marsh surface as feeding ground (Weisberg & Lotrich 1982; Frid 1988 in Frid & James 1988; Minello & Zimmerman 1992; Minello *et al.* 1994), but also as shelter (Minello & Zimmerman 1992). Together with the indirect disturbance by predation (Kneib 1985), this could indeed provoke the presence of a predation pressure and explain the predation hypothesis.

The influence of the resident epifauna is also relevant. On the one hand, this part of the marsh epifauna acts as a bioturbating agent while feeding and building biogenic structures (burrows). This causes the production of feeding and faecal pellets, an aeration of the top 5 mm, a sediment oxygenation and modification, and a change in nutrient profiles, eventually leading to an endobenthic response (Bell *et al.* 1978; Katz 1980; Montague 1980; DePatra & Levin 1989). On the other hand, selective, non-selective, and even accidental ingestion of meio- and macrobenthos may occur, though only weak evidence exists (Teal 1962; Montague 1980; Robertson & Newell 1982b; Reise 1985). Other possible impacts such as resource competition between the permanent epibenthos and the endobenthos, could be of equal importance, although they were never mentioned for salt marshes.

2. Resource competition

As mentioned above, the exposed marsh sediment surface becomes inhabited mainly by resident macro-epifauna like fiddler crabs, gastropods, bivalves, and insects, which are in general bottom dwelling deposit feeders. Therefore, other possible impacts such as resource competition between this permanent epibenthos and the endobenthos could be of equal importance. That kind of impact was never mentioned for salt marshes. The study of Hoffman *et al.* (1984) is the only cage experiment in which resident fiddler crabs were excluded. Instead of resource competition, predation pressure was put forward as the main impact since these crabs were believed to ingest the meiobenthos.

Author (date)	Locality	Epibenthos	Endobenthos	Hypothesis	Method	Evaluation
Cage experiments in salt marshes						
Vince *et al.*(1976)	high & low intertidal marsh (Massachusetts, USA)	fish (different sizes)	epibenthic small invertebrates (snails, amphipods)	predation pressure	exclusion fences	fish predation pressure = dominant but not only regulating factor
Bell & Coull (1978)	high marsh substrate in microecosystems (USA)	grass shrimp and other large natant forms (> 2 mm)	meiobenthos	predation pressure and/or disturbance	cage exclusion and reintroduction	macrofaunal control via predation on esp. nematodes, oligochaetes and copepods
Van Dolah (1978)	intertidal marsh (Maryland, USA)	fish and shrimp	amphipod *Gammarus* spec.	predation pressure because prey evidence	cage exclusion	predation pressure = major source of mortality
Bell (1980)	high intertidal marsh (South Carolina, USA)	natant macroepifauna (> 2 mm)	meiobenthos	predation pressure and/or disturbance	cage exclusion	predation pressure
Fleeger *et al.* (1982)	intertidal marsh (Louisiana, USA)	natant macroepifauna	meiobenthos	regulation	cage exclusion (among others)	predation pressure is only partial answer
Kneib & Stiven (1982)	intermediate intertidal marsh (North Carolina, USA)	fish	macro-endobenthos (> O.5 mm)	predation pressure	cage exclusion/inclusion	unknown interactive component (unexpected result)
Ward & Fitzgerald (1983)	tidal pool in intermediate marsh (Canada)	sticklebacks	macro-endobenthos (> 0.5 mm)	predation pressure	cage exclusion/inclusion	procedural effects
Hoffman *et al.* (1984)	low intertidal marsh (Rhode Island, USA)	fiddler crab *Uca pugnax*	meiobenthos	regulation	cage exclusion	predation pressure
Frid & James (1988)	intertidal marsh (England)	birds and tidally feeding natant forms	macro-endobenthos	predation pressure	cage exclusion (2 mesh sizes)	unexpected result, range of possible interactions discussed
Kneib (1988)	intertidal marsh (Georgia, USA)	grass shrimp and fish	macro-endobenthos (> 0.5 mm)	indirect positive effect	cage exclusion	unexpected result, different scenarios discussed

Author (date)	Locality	Epibenthos	Endobenthos	Hypothesis	Method	Evaluation
Ellis & Coull (1989)	intertidal/subtidal mudflat (South Carolina, USA)	juvenile fish	meiobenthos	regulation	cage exclusion/inclusion	predation pressure
Haase (1993)	tidal pools and ditches in high marsh (North Sea)	natant 'predators' (> 1 mm)	macro-endobenthos (> 5 mm)	predation pressure	cage exclusion	predation pressure by shore crab in tidal pools
Cage experiments in mangroves						
Dye & Lasiak (1986)	mudbank in intermediate mangroves (NE Australia)	fiddler crabs *Uca* spec.	meiobenthos	none (diet ?)	cage exclusion	no predation, maybe exploitative competition?
Vargas (1988)	intertidal mudflat surrounded by mangroves (Costa Rica)	'macropredators'	macro-endobenthos (> 0.5 mm)	predation pressure	cage exclusion	predation pressure = relatively unimportant
Dittman (1993)	tidal flat close to mangroves (NE Australia)	soldier crabs	meiobenthos and small macrobenthos (> 0.5 mm)	regulation ?	cage exclusion	predation

Table 1.1 : A review on the use of cage experiments in salt marshes and mangroves in the study of endobenthos/epibenthos interactions.

3. Temporal and spatial effects

a) Temporal

Most marsh studies apply a satisfactory temporal control. It is Bell (1980), especially, who indicates that the lack of any nematode response might be attributed to a sampling interval that is too long.

b) Spatial

The general gradient hypothesis for rocky bottoms (Connell 1972 in Virnstein 1977) was formulated by Virnstein (1977) for soft bottoms. He expected predation pressure to reduce in shifting from subtidal to intertidal zones, causing spatial effects. This was believed to be a logic consequence of a decreasing inundation time which reduced the foraging time for the natant macro-epifauna. In addition, Olafsson & Moore (1990) even stressed the absence of any biological control for the endobenthic structure in intertidal regions due to extreme changes in the abiotic environment. They believe that only in stable subtidal habitats, biological structuring forces might become more obvious.

Since the bulk of salt marsh studies concentrates on the predatory impact of the natant epifauna, this intertidal gradient in terms of macro-epifaunal exposure becomes obvious. North American marshes are much lower and therefore more frequently flooded than those found in Europe (figure 1.1) (Reise 1985). Consequently, in contrast with most American studies, Frid & James (1988) and Haase (1993) did not detect any evidence of predation pressure on a European intertidal marsh. One study only reports on the nekton use (epibenthos and hyperbenthos) of a European salt marsh but deals only with the low intertidal to subtidal creek communities (Cattrijsse *et al.* 1994). Studies in the more extensive North American marshes frequently mention the changing predatory impact along the intertidal gradient (Bell & Coull 1978; Bell 1980; Fleeger *et al.* 1982). Nevertheless, Weisberg & Lotrich (1982) stated the opposite, detecting an increased fish feeding activity at high tides to maximize the intake of marsh surface prey. Whether a reduced impact of the natant epibenthos from low to high marshes is gradually replaced by a biological control, now provided by the epibenthic residents of the salt marsh, is still not clear.

4. Procedural effects

These effects have already been discussed in detail for temperate cage studies in general. Most marsh studies report that procedural effects were avoided, although some studies use only a subjective field comparison of the environment in and outside the cages as procedural control (Kneib & Stiven 1982; Ellis & Coull 1989). Only a number of studies used an accurate control treatment and mention the presence of artefacts. These artefacts mainly were a change in feeding behaviour of fishes in enclosures and a larval attraction to cages (Bell 1980; Ward & Fitgerald 1983; Kneib 1988). Control of salinity and sedimentary modification is rarely detected or even mentioned.

5. Indirect effects

a) Complex community organization

Multitrophic interactions are rarely taken into account. A restricted number of studies tried to get some insight in these systems for marsh areas (Kneib & Stiven 1982; Kneib 1988). Their unexpected results were also explained in terms of possible intracompetitive and larval/adult interactions.

Intracompetitive interactions in particular, however, are not expected to be important for major taxa but rather on species level (Bell 1980).

b) Refuges

Dealing with marshes, the possibility for the vegetation to be a mediating agent becomes more pronounced. The thick root mat and the above ground vegetation might reduce foraging activity or increase refuge possibilities (Vince *et al.* 1976; Fleeger *et al.* 1982).

c) Bioturbation

Bioturbational agents have rarely been mentioned as the main epibenthic impact on the endobenthos. Hoffman *et al.* (1984) observed a negative meiobenthic response to epibenthic inclusion. They were convinced that the decrease in density due to predation was much stronger than the increase due to spatial refuge in burrows. The feeding activity of the epibenthos is also frequently mentioned as a possible explanation for indirect effects after exclusion (Bell & Coull 1978; Bell 1980; Kneib & Stiven 1982; Hoffman *et al.* 1984). Bioturbational effects have already been discussed in detail for temperate cage studies.

E. CAGE EXPERIMENTS IN MANGROVE FORESTS

Mangroves differ from salt marshes in their domination by trees (Adam 1990). They require warm air and ocean temperatures (> 15° C), shallow water, and a protection from strong wave action to develop appropriate sedimentary conditions (reefs) (Chapman 1977). Mangrove forests are generally formed in low, mid, and high intertidal zones. Like the marshes, mangroves are inhabited by resident as well as natant macro-epifauna. The permanent resident forms, however, are much more pronounced than those in the temperate marshes. They consist of a wide range of crustaceans (brachyurans and anomurans) and gastropods like detritivores, vegetarians, grazers, and deposit feeders (Alongi 1989).

In an overview of benthic mangrove research, only one study (Dye & Lasiak 1986) was found to be dealing with cage experiments in order to detect an epibenthos/endobenthos interaction on the mangrove forest floor (table 1.1). The experiment was carried out on a flat, closely surrounded by mangroves. Two other comparable studies were made by Vargas (1988) and Dittmann (1993), although they were clearly limited to tidal flats rather than real mangrove sediment. Dye & Lasiak (1986) are the first to refer to exploitative competition between meiobenthos and fiddler crabs (*Uca* spp.) as a driving structuring force. This reference clearly sheds new light on the interaction concept, though it has to be considered with caution. The study specifically excluded the genus *Uca*, concentrated only on the meiobenthos of the top 2 mm, and lacked any temporal control.

It is obvious that benthic mangrove research needs to study the complex epibenthos-endobenthos interaction on the forest floor in order to elucidate the role of the endobenthos in this soil. As mentioned above the trophodynamics of the endobenthos is a central theme in important key areas of mangrove research. The entire infaunal food chain might be a sink for carbon and that then raises the question: to what extent are these meio- and macrofauna consumed by higher trophic groups or linked with the carbon sink system ?

Research on temperate and, especially, salt marsh regions learns that the best way to answer this question, is the use of cage experiments. The direct application of the epibenthic predation pressure hypothesis, however, is too simplistic.

Therefore, the final evaluation of the experimental output asks for a much broader approach that takes other interactive components into account. Cage experiments will show if the global endobenthos or specific endobenthic taxa are regulated, impacted, and structured by the overall epibenthos under mangroves. An accurate and detailed experiment might even reveal the underlying cause of this impact in terms of predation or resource competition. This way, the global endobenthic role in a mangrove forest could be clarified in terms of energy transfer to higher trophic levels or linkage with the detrital foodweb. Warwick (1987) found that nematodes compete with epibenthic shrimps for detrital food and therefore concluded that the energy sink is more pronounced than the energy transfer up the food chain. It is difficult, though, to manipulate entire benthic populations and to develop an adequate experimental design to discern interactions within complex assemblages in nature (Alongi & Tenore 1985). And in order to emphasize predation/competition, it is necessary to control or avoid the other possible interactive components, as seen in temperate regions (Kneib 1991).
These components are:

(1) Specific predatory effects
(2) Temporal and spatial effects
(3) Procedural effects
(4) Indirect effects

The objectives of the present research and the implementation of its experimental design, taking all the previous in account, are stated in the following chapters (II and III).

II. OBJECTIVES

1. Does the epibenthos (resident and visiting) have a regulating and structuring influence on the meio- and macrofaunal endobenthos of an East African mangrove forest ?

2. If this impact exists, is it caused by predatory or competitive interactions between the endobenthos and the epibenthos ?

3. Do impact and cause of impact differ between a high intertidal *Avicennia marina* forest and a low intertidal *Ceriops tagal* forest ? If yes, to what extent and for what reason ?

4. How can this information be used to construct a preliminary trophodynamical benthic scheme and to trace the endobenthic role in East African mangrove forests ?

III. IMPLEMENTATION

A. STUDY SITE

Gazi Bay (4°25'S and 39°50'E) is situated on the Kenyan coast, about 60 km south of Mombasa and 50 km north of the Tanzanian border (figure 3.1). The sampling sites were chosen along the western creek of the bay in the Gazi mangroves.

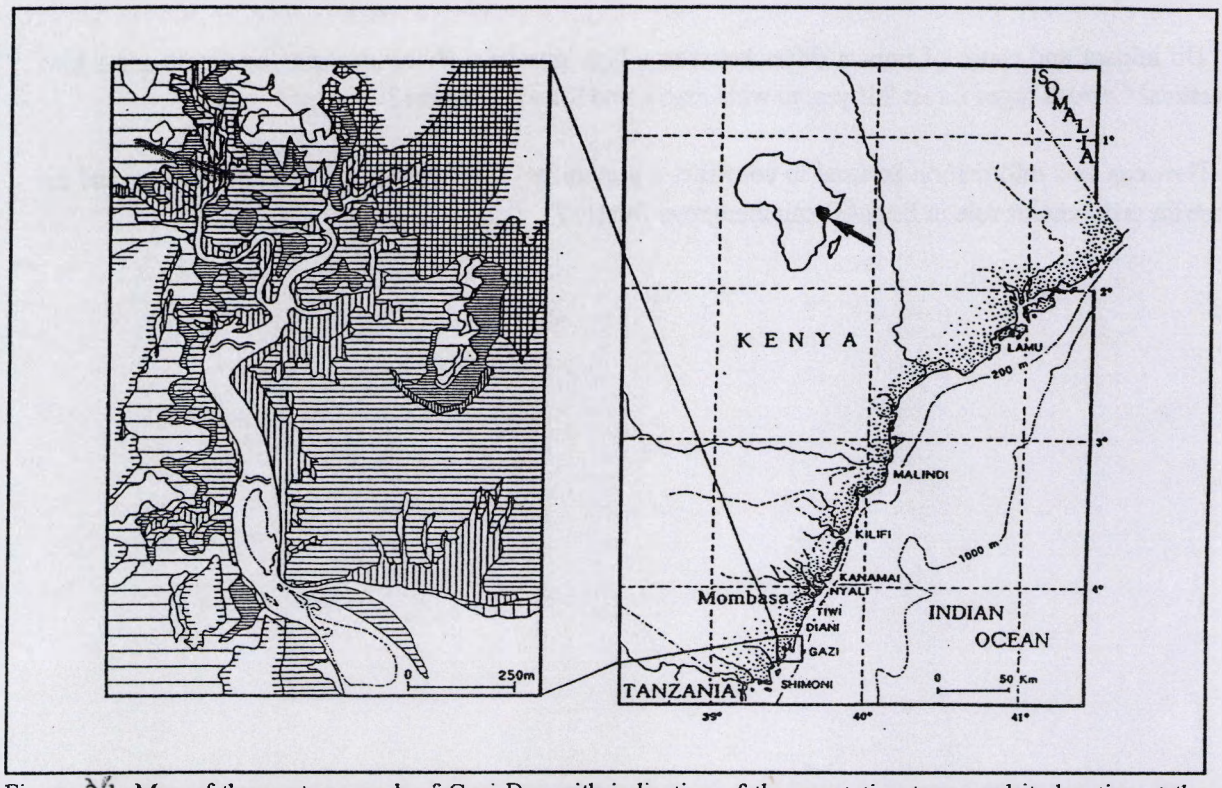


Figure 3.1: Map of the western creek of Gazi Bay with indication of the vegetation types and its location at the Kenyan coast *(drawing by Bruyneel 1995).*

The Gazi mangrove forest has a typically East African morphology that is rather low in height because of the seasonal rainfall (McNae 1968). Vast mangrove areas in Kenya are mostly associated with creeks and islands. Gallin *et al.* (1989) and Beeckman *et al.* (1990) give detailed accounts of the Gazi mangrove vegetation. The zonation greatly corresponds to Chapman's description. He gives a clear outline of the mangrove zonation around Tanga and the Rufiji mouth in northern Tanzania which is representative for East African mangroves (after Walter & Steiner 1936 in Chapman 1977) (figure 3.2). The intertidal can go from low to high over:

(1) A pioneer zone with *Sonneratia alba* at the open coast and *Rhizophora mucronata* along the river mouth and upstream. Where the soil is rather sandy and firm, however, both types are replaced by few frontal isolated *Avicennia marina* trees.

(2) An *Avicennia marina* zone, behind *Sonneratia alba*, on less muddy soils

(3) A *Rhizophora mucronata* zone up the river

(4) A *Ceriops tagal* zone with isolated *Bruguiera gymnorrhiza* trees

(5) A landward belt dominated by *Avicennia marina* progressively getting smaller and finally disappearing at the edge of a sandy salina

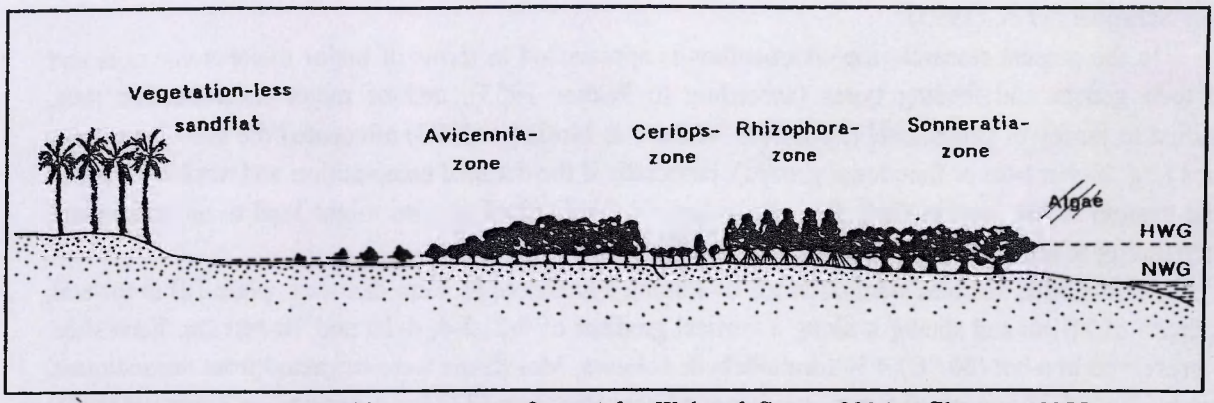


Figure 3.2: Zonation of an East African mangrove forest *(after Walter & Steiner 1936 in Chapman 1977).*

Gazi mangroves are riverine rather than basin (Twilley *et al.* 1986), but they are not directly influenced by freshwater. The two small rivers (Kidogoweni and Mkurumu) are seasonal and seepage is restricted to a few sites only. The inferior and median parts are inundated at each high tide, the superior parts only at spring high tide (Gallin *et al.* 1989). The Gazi forests, as most Kenyan mangroves, are commercially exploited, but are not used for export (Chapman 1977).

B. GLOBAL EPIBENTHIC IMPACT

1. Epibenthos

There are no quantitative studies on the resident, bottom dwelling epifauna of Gazi mangroves. Only some qualitative results and my personal observation can give an insight in their occurrence and composition (epifauna in general: Ruwa, personal communication; hermit crabs: Reay & Haig 1990; crabs: Vannini, personal communication; gastropods: Slim *et al.*, submitted personal communication; plates 1a and 1b). The present study is the first to offer quantitative results of the resident epifauna under Gazi mangroves. The following quantitative estimation was made near the experimental sampling sites. This estimation was established during the low and high waters of both the spring and neap tides:
The slow moving adult and juvenile gastropods and hermit crabs were counted in three quadrats (0.5 x 0.5 m) around a tree and in three similar quadrats in between the trees (plate 1c).
The fast moving adult and juvenile crabs and their burrows were observed and counted in three quadrats (0.5 x 0.5 m) around a tree and in one quadrat (2 x 2 m) in between the trees. The counting only started after 15 minutes to avoid escape behaviour.
The average of the data gave an overall number of individuals per m^2 and per species.

Until now, only one study on the natant epifauna (fishes) visiting Gazi mangrove forests has been published (van der Velde *et al.* 1995). This study, however, did not emphasize fishes that visit the high intertidal regions during flood. It therefore leaves this part of the epibenthos as an unknown factor.

2. Endobenthos

The meiobenthos of the Gazi mangrove forest floor has been studied extensively in terms of nematode taxonomy (Verschelde & Vincx 1993; Verschelde *et al.* 1995). Its ecology has received some attention regarding vertical distribution (Vanhove *et al.* 1992, Vanhove 1993; Vermeulen, in preparation; Okondo, in preparation) and human impact (Schrijvers, in press). Okondo (in preparation) are the first to follow the monthly meiofaunal variation in a Gazi mangrove sediment.

The only known taxonomic and ecological study on mangrove macro-endobenthos in the Gazi area is the one by Schrijvers *et al.* (1995).

In the present research, the endobenthos is approached in terms of major meiobenthic taxa and nematode genera and feeding types (according to Wieser 1953), and of major macrobenthic taxa, identified to family or genus level if possible. Walters & Moriarty (1993) advocated the use of amalgam groups (*e.g.* higher taxa or functional groups), especially if the detailed composition and trophic structure of the system is not known. Only the manipulation of individual species might lead to an incomplete understanding of the community trophic structure (Kneib 1991).

Meiobenthic samples were obtained by forcing a handcore (3.6 cm diameter; plate 1d) in the soil to a depth of 20 cm and slicing it along a vertical gradient of 0-2, 2-4, 4-10 and 10-rest cm. Each slice was preserved in a hot (60 °C) 4 % formaldehyde solution. Meiofauna were extracted from the sediment (sieve meshes of 38 µm and 0.5 mm) by means of centrifugation (2734 x g during 3 x 3 minutes) with $MgSO_4$ with a 1.28 density. This method allows for a fast and easy separation of the target fauna from mangrove roots and detritus. The nematodes and other meiofaunal taxa were counted. The nematodes were randomly picked out (120 individuals per sampled slice) and identified to genus level. They were then classified in trophic groups following the commonly used feeding types 1A (selective deposit feeders), 2A (epistratum feeders), 1B (non-selective deposit feeders) and 2B (omnivores/predators) (Wieser 1953).

Macrobenthic samples were obtained by means of a large handcore (12.5 cm diameter; plate 1d). The long handle permitted sampling the sediment of the experimental treatments (see later) without disturbing the surrounding sediment. The core was forced into the sediment to a depth of 20 cm and the sampled soil was then divided in two subsamples (the top 2 cm and the rest). Before sieving, both parts were preserved in a cold 8 % neutralized formaldehyde solution. Macrofauna were extracted from the sediment by sieving with mesh sizes of 0.5, 1, and 2 mm. All the taxa (Oligochaeta, Amphipoda, Polychaeta, Insecta larvae, Nematoda, Gastropoda, and Cnidaria) were counted. The oligochaetes and all the insect larvae were identified to family level and the amphipods, polychaetes, and nematodes to genus level. Amphipod length (from antennal peduncle to telson) was measured with a *camera lucida* under a stereoscopic microscope. The average individual amphipod length per sample was calculated in order to test for adult invasion or reproduction in the experimental treatments (see later).

The detailed profile of the meiobenthos was useful to control vertical migration movements. The depth profiles of meio- and macrobenthos were chosen in order to avoid excessive slicing (*e.g.* upper mm's) or bulk results (*e.g.* 10 cm). Excessive slicing gives skewed results in impact studies because it mainly concentrates on the epibenthic or surface related groups and overestimates predator/disturbance effects (Vince *et al.* 1976; Van Dolah 1978; Bell 1980; Ellis & Coull 1989; Haase 1993). Bulky samples would result in underestimating possible effects by including deeper layers (Warwick *et al.* 1990). Only the upper 2 cm is emphasized, basically because the effect was expected to occur in this area. And especially for macrobenthos, preliminary counts revealed > 90 % of the density in this layer.

The lower sieve mesh limit for meiobenthos was chosen to be 38 µm. Studying the dynamics of nematode populations asks for a minimum mesh size of 40 µm. At certain times > 30 % of the meiofauna was detected to pass through a 50 µm screen (personal observation). For the macrobenthos, a 0.5 mm sieve replaced the traditional 1 mm mesh size (Gee *et al.* 1985; Dittmann 1995). This mesh was found to be used in most marsh cage studies on macro-endobenthos (table 1.1).

3. Environmental factors

A 6 cm diameter core sample was taken to a varying depth of > 10 cm (plate 1d). The soil water in the sample holes was analysed for bulk values of pH, salinity, and dissolved oxygen (DO_2) respectively measured with a combined, calibrated electrode with consolidated cover (in a Jenway 3405 electrochemical analyser), an ATAGO refractometer (0-100 psu), and an electrode type 737 Clark (Jenway). Other measurements were performed on vertical slices of the core (0-2/2-4/4-10/10-rest cm). Temperature and redox potential were determined in the three uppermost slices, respectively using a bar thermometer sensitive to 0.01°C (Jenway) and a combination Hamilton electrode (Jenway). The % of particulate organic matter (POM) and some granulometric variables were determined for all slices. After drying at 100 °C, the POM was quantified taking in account the loss in weight after a 4 hour 600 °C combustion. The very low carbonate content of the sediment permitted the use of this method. A Coulter^R LS 100 Particle Size Analyser was used to characterize the granulometry of the sediment. This analysis was done both before and after a 600 °C combustion. Before grain size analysis, the gravel fraction (> 1 mm) was mechanically separated by sieves. It mainly held root material. The median grain size of the sediment was an important granulometric characteristic. This is a measure for the general grain size tendency of the sediment, and corresponds to the 50 % line of the cumulative distribution curve (Holme & McIntyre 1984). The lower this median, the siltier the sediment (negatively correlated with the % of mud). A 1 cm diameter core was used to estimate the % of organic carbon in the slices 0-2, 2-4, and 4-10 cm by means of a Carbon-Nitrogen analyser NA 1500 Carlo Erba. The two uppermost slices were analysed for chlorophyll *a* and fucoxanthin pigment concentration. A Gilson HPLC-chain was used following the method of Mantoura & Llewellyn (1983), but the time of the linear gradient elevation and the isocratic hold were slightly modified.

4. Exclusion cages

To detect a global epibenthic impact, all epibenthos (> 2 mm), natant as well as resident, was to be excluded. Exclusion cages were placed and the influence on the meio- and macro-endobenthic structure and on the environmental factors (as described in the previous chapters) in these constructions, was followed through time. The experiment was carried out over six months to one year (from July 1992 to July 1993) with a monthly sampling. Coull & Palmer (1984) pointed out that the determination of an equilibrium in meiobenthic assemblages may, indeed, require months.

The cage (1 m²) (figure 3.3; plate 1e) had a lower and upper part. The lower part was composed of four 0.3 m high, perforated PVC plates which were completely buried in the sediment to inhibit entry to burrowing epibenthos. The upper part was composed of an aluminium frame (0.7 m high) that was covered by a plastic screen with a 2 mm mesh. The permanent cover was detachable to facilitate sampling.

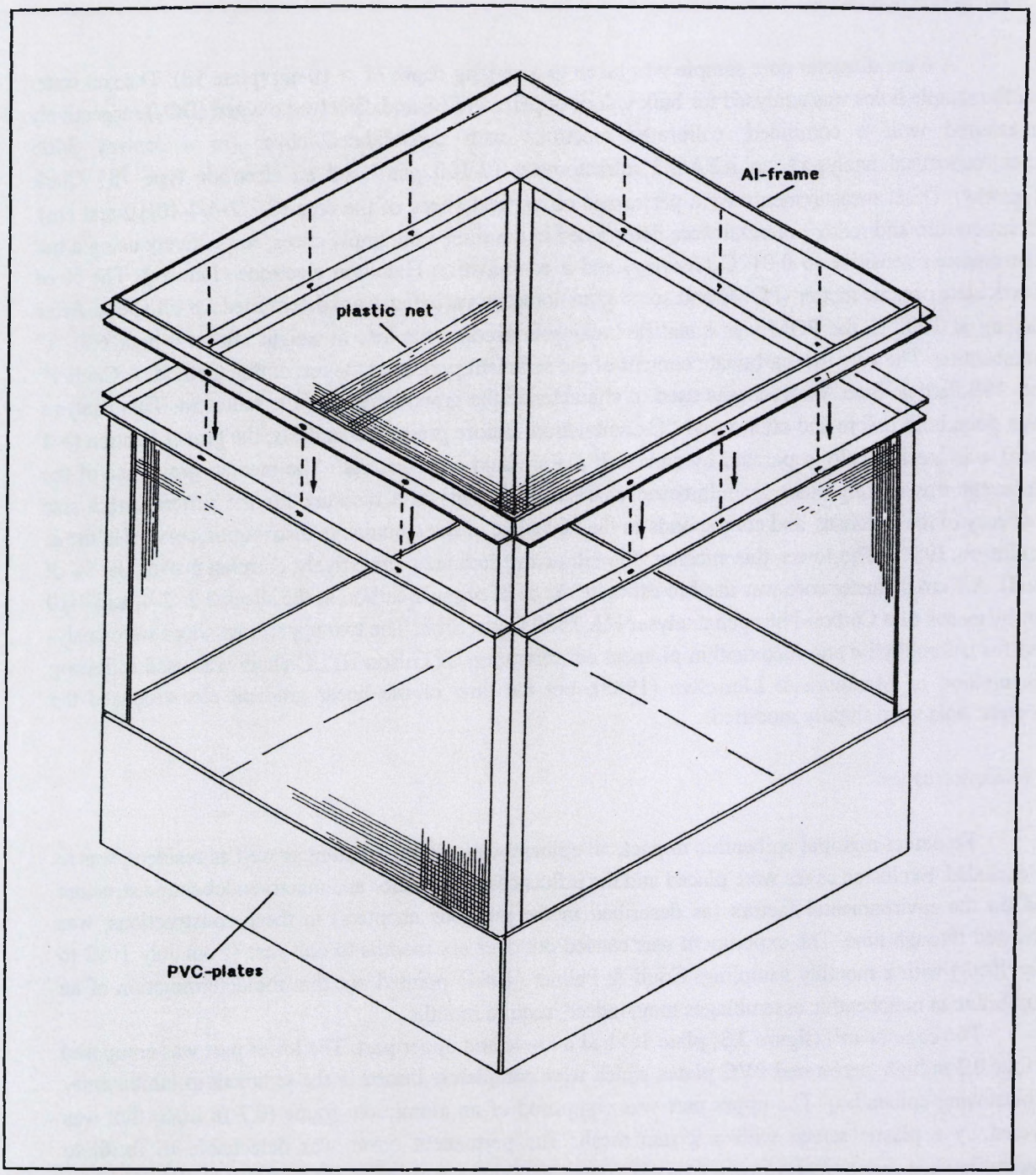


Figure 3.3: Model of the cage construction used in the exclusion experiment. It consisted of a lower and upper part. The lower part was composed of four 0.3 m high and 1 m long perforated PVC plates which were completely buried in the sediment. The upper part was composed of an aluminium frame (0.7 m high) that was covered by a plastic net with 2 mm mesh. The top was detachable to facilitate sampling *(drawing by Bruyneel 1995)*.

The use of a 2 mm mesh made it possible to non-selectively exclude the epibenthos > 2 mm. The most conspicuous effects were believed to result from the removal of the dominant epifauna. A mesh size of > 2 mm was expected to reduce the exclusion effect (Reise 1977; Reise 1978; Kneib & Stiven 1982). A screen of < 2 mm might have advanced fouling (procedural effect). The resident epibenthos was manually removed within the first five hours of the experiment.

Large sesarmid crabs were caught using mouse traps. A continuous removal of the juveniles was carried out during the experiment. The cage cover was set in place to avoid immigration of resident epifauna during low tide and of natant epifauna during high tide. Most cages in marsh or previous mangrove studies were either topless (Bell 1980; Fleeger *et al.* 1982; Dittmann 1993) or were provided with a flashing border or strip (Hoffman *et al.* 1984) or a cover during floodings only (Ward & Fitzgerald 1983).

5. Temporal control

Experiments need proper controls. This consideration is absent in many studies (Kuhlmann 1994). One of these are temporal controls. In experimentations with biological systems, temporal controls are required because the natural environment and the biological factors exhibit temporal change (Hurlbert 1984). As mentioned above, the detection of effects is dependent on succession phase, sediment modification, and season (Bell 1980; Dye & Lasiak 1986; Holland *et al.* 1980). Since a treatment cannot be confounded with these time related nuisance variables, an 'untreated' treatment should be used (Hurlbert 1984; Zolman 1993). Imposing no experimental variables allows to follow the natural temporal variation of the system. In this study, blank and natural sites with a surface of 1 m^2 (marked with a rope) were used as temporal controls (plate 1f).

6. Procedural control

Besides 'untreated' treatments, controls also have a second function. They need to allow for the separation of the effects of several aspects of the experimental procedure (= 'caging' in this study) on environmental and biotic factors (Hurlbert 1984).

Therefore, partial cages were applied. They were identical to full cages but one of their sides stayed open to avoid exclusion of epibenthos (plate 1g). This method controlled procedural effects such as fouling of the cage mesh, sedimentary and humidity changes, light/shadow effects and absence of leaf fall. A field comparison of these effects in and outside the cages was carried out as an extra procedural control (Wilson 1991). The possible attraction of epibenthos by the partial cages as a shelter, was also checked. At least weekly, the number of epifauna was counted in each unit.

7. Replication, randomization and interspersion control

a) Replication

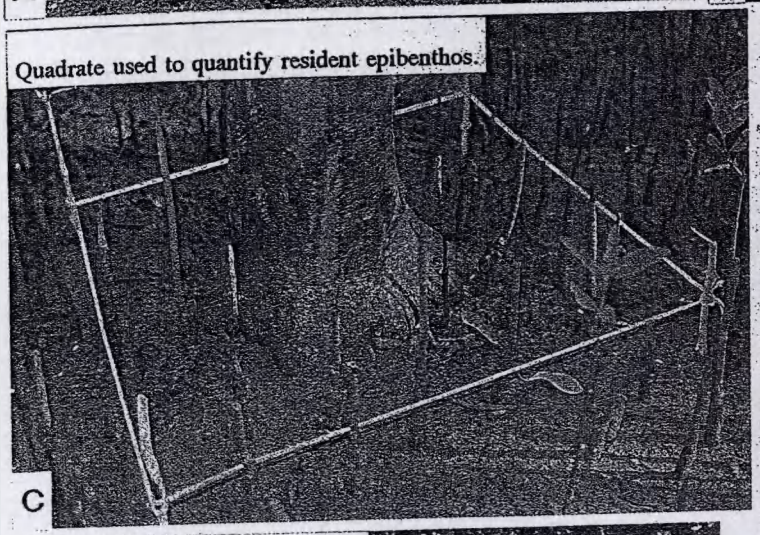
Replication controls the stochastic factor i.e. the among-replicates variability due to aggregation (Hurlbert 1984). Each of the treatments (cage, blank, and partial cage) were therefore appointed to three units of each 1 m^2. Macrobenthos, meiobenthos, and environmental factors were, however, sampled only once per month in each unit. The within-unit replication was eliminated to prevent any disturbance caused by sampling (Frid & James 1988). Influence on the surrounding sediment in the same unit, that was to be sampled afterwards (*e.g.* in terms of meiofaunal refuge), was avoided by filling the sample holes with silicon plugs or sediment bags (Marinelli & Coull 1987; Ellis & Coull 1989). Samples were taken in the same unit coordinates for each sampling period and within 10 cm from the cage edges, to avoid potential effects of the cage structure (Bell & Woodin 1984; Ellis & Coull 1989).

Uca lactea annulipes 'flock', *Ceriops tagal* zone.

A

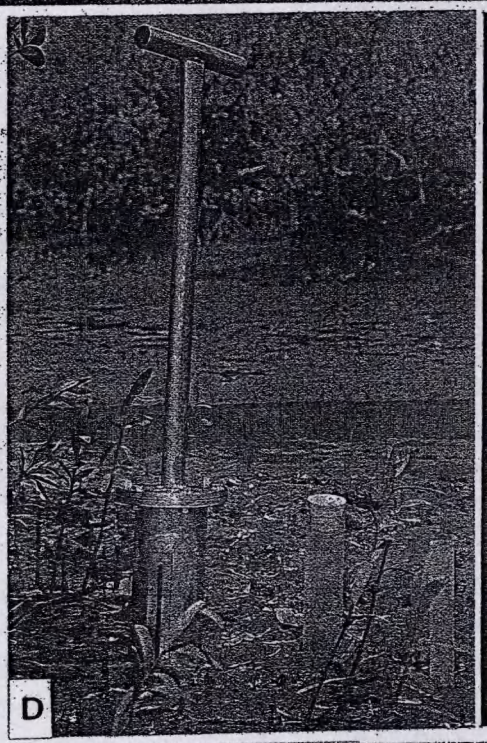
Terebralia palustris, *Ceriops tagal* zone.

B



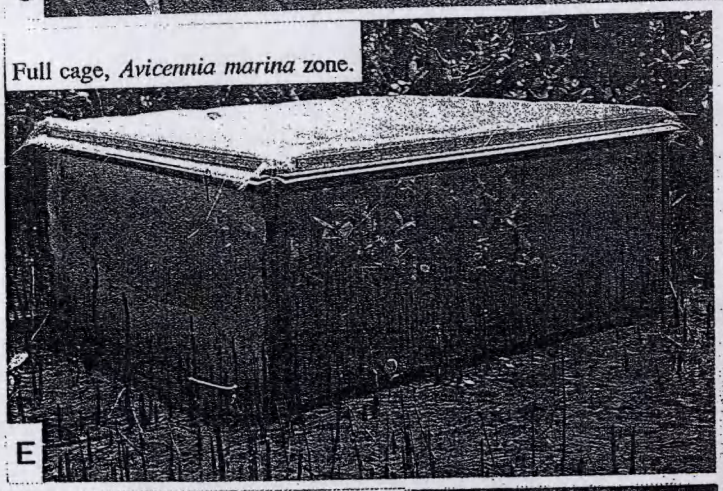
Quadrate used to quantify resident epibenthos.

C



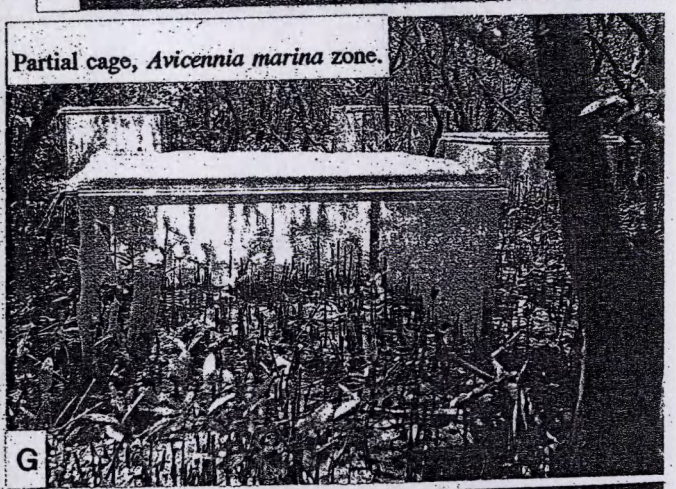
D

Sampling gear (fltr: macrobenthos, sediment, meiobenthos).



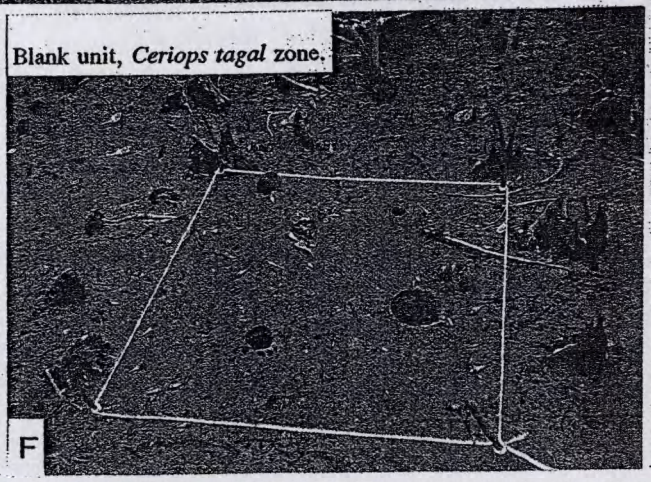
Full cage, *Avicennia marina* zone.

E



Partial cage, *Avicennia marina* zone.

G

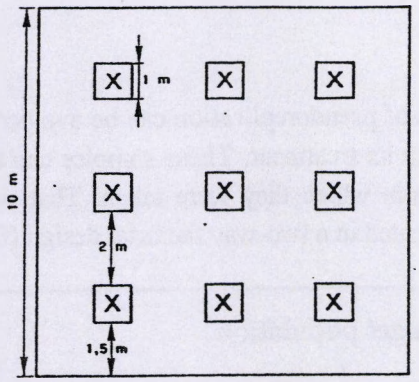


Blank unit, *Ceriops tagal* zone.

F

b) Randomization

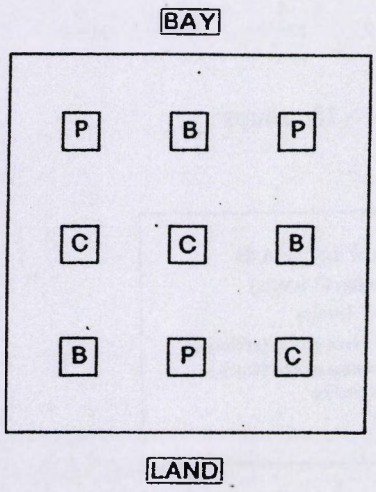
Randomization reduces the potential bias of the experimenter in the assignment of treatments to units (Hurlbert 1984). Each of the three treatments was randomly assigned to three units. The result was a 10 x 10 m square with the nine units 1 to 2 m apart:



c) Interspersion

Interspersion controls a regular spatial variation in the properties of the different units and, thereby reduces the probability of chance segregation of treatments (Hurlbert 1984). The initial similarity of the units is an important condition for the dependent variables. Rerandomization of the units results in a maximum interspersion and an optimal randomization/interspersion ratio. And any chance segregation of the treatments along a possible spatial gradient (such as the intertidal) will be reduced. This study did go further, however. Three blocks were chosen. Three different treatments were randomly appointed to the three units of each block. Possible segregation was checked for. Rerandomization within each block produced maximum interspersion. This type of field design is known as a 'randomized block design' (Hurlbert 1984; Zolman 1993).

It resulted in:



with B = blank, P = partial cage, and C = cage.

8. Experimental and statistical design

This 'randomized block design' makes control during the experimental execution very reliable, but it was not used, however, during the statistical analysis. If so, the analysis would have led to pseudoreplication because of lack of replication within each unit per month. In addition, blocks were not believed to be very different since they were perpendicularly positioned on the intertidal gradient which was believed to be most pronounced. Two other statistical approaches were chosen.

a) Factorial design

With this design, the problem of pseudoreplication can be avoided. Sampling in benthic ecology in fact means, loosing a sample due to its treatment. These samples can therefore be treated as entities that not directly represent the unit from which they were taken. That way, monthly samples become independent samples that have to be treated in a two-way factorial design (figure 3.4 and table 3.1).

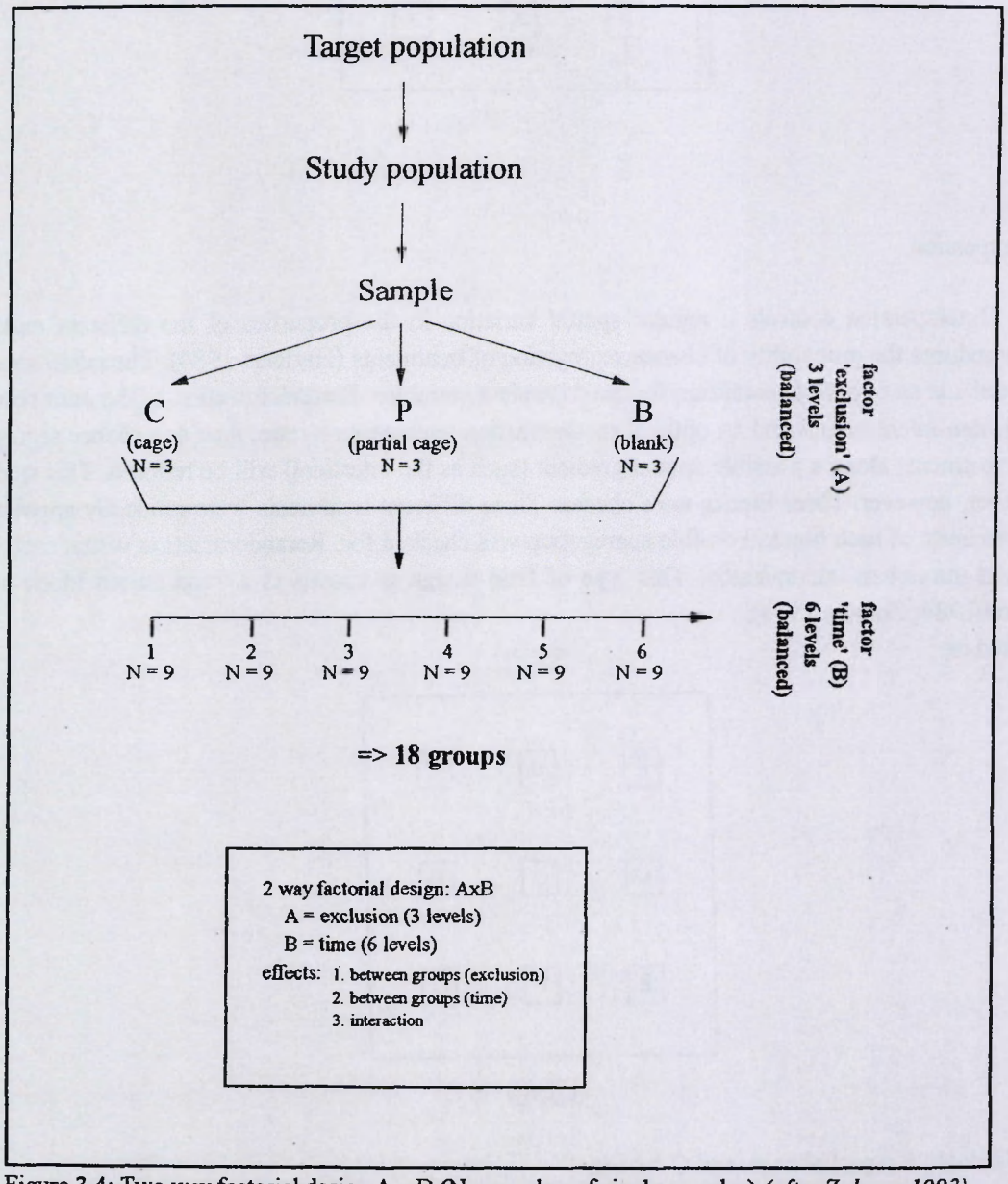


Figure 3.4: Two way factorial design A x B (N = number of single samples) *(after Zolman 1993).*

Source	df	F-ratio
A(exclusion)	2	A / (S/AB)error
B(time)	5*	B / (S/AB)error
A(exclusion) x B(time)	10	AxB / (S/AB)error
(S/AB)error	36	
Total	53	

Total # of entities = 54
Total # of independent observations = 54
Total degrees of freedom = 53
* in case of # of periods = 6

Table 3.1 : The 3 (exclusion) x 6 (time) factorial analysis of variance (ANOVA) table (A x B) *(after Zolman 1993).*

Disadvantages to this design:

(1) Time cannot entirely be regarded as an independent variable, since different groups are not randomly assigned. Samples through time are indeed linked to a certain structure (= the unit).

(2) The statistical generalization (figure 3.5) from the sample entity to the study population is much weaker than when using a unit as the entity

(3) The factorial design has a tendency to overdesign and therefore becoming too complex. An increase of the number of groups (the treatment is split in time) will produce an increase in the F-ratio (A/(S/AB)). This leads to a higher probability in detecting a non-significant effect.

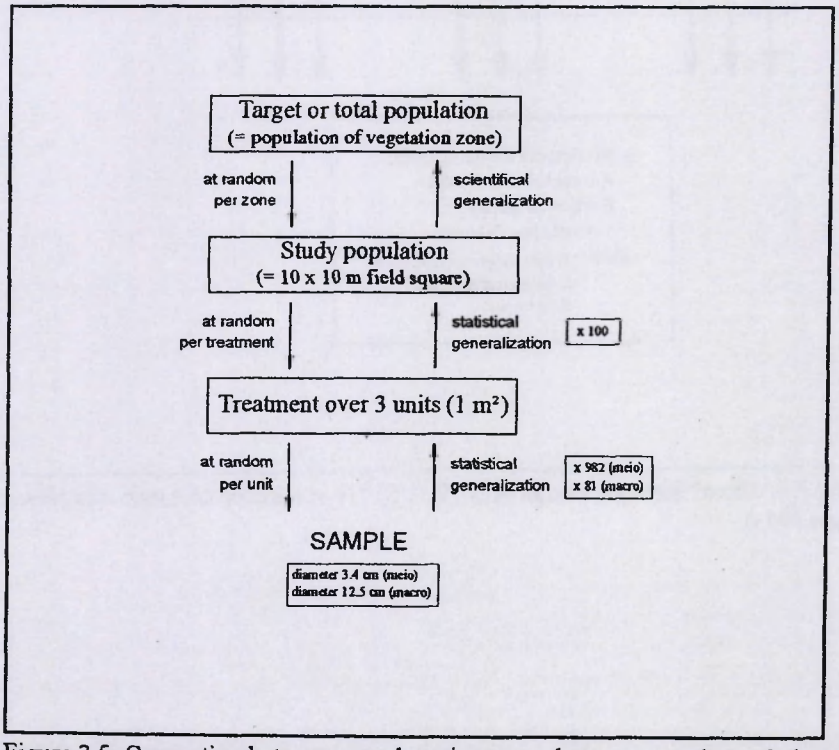


Figure 3.5: Connection between sample estimates and target or total population via generalizations *(after Zolman 1993).*

b) Mixed factorial design

In assuming the unit as an entity, it becomes possible to use the time variable as a repeated measure within the same subject and strengthens the statistical generalization about the study population. Moreover, the sensitivity to a treatment effect is higher for the mixed than for the factorial design. The F-ratio for the treatment effect is A/(S/AB) (for factorial) compared to A/(S/A) (for mixed design) (figure 3.6 and table 3.2).

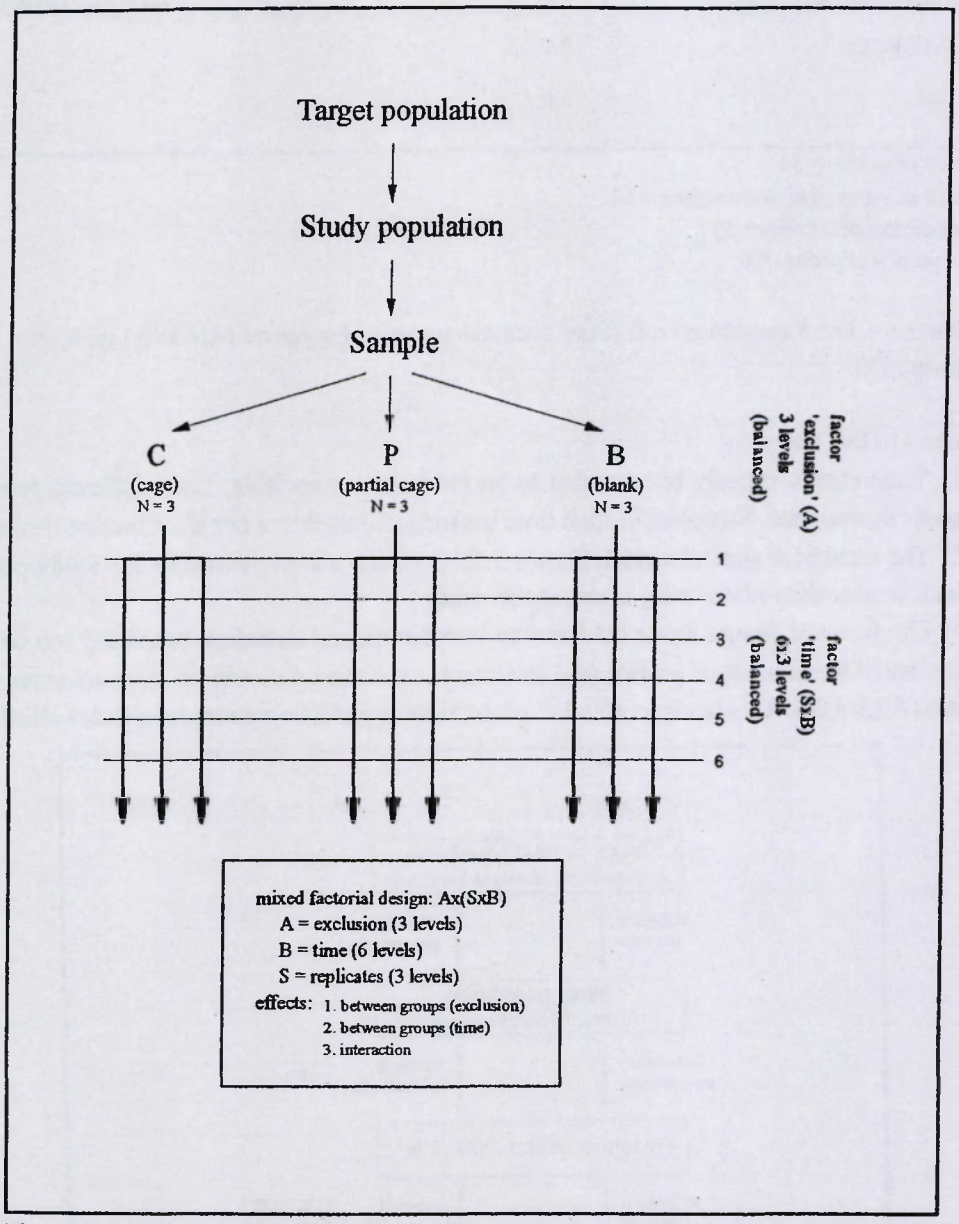


Figure 3.6: Mixed factorial design A x (B x S) (N = number of single samples *(after Zolman 1993)*.

Source	df	F-ratio
A(exclusion)	2	A / (S/A)error
(S/A)error	6	
B(time)	5*	B / Bx(S/A)error
A(exclusion) x B(time)	10	AxB / Bx(S/A)error
Bx(S/A)error	30	
Total	53	

Total # of entities = 9
Total # of independent observations = 9
Total degrees of freedom = 53
* in case of # of periods = 6

Table 3.2: The 3 (exclusion) x 6 (time) mixed factorial analysis of variance (ANOVA) table (A x (BxS)) *(after Zolman 1993).*

Disadvantages to this design:

(1) The sensitivity to a time effect (and an interaction effect) is higher for the factorial than for the mixed design. The variability within the exclusion treatments for the mixed design is taken over time periods and therefore reduces, due to a better temporal control. The F-ratio for the time effect is B/(S/AB) (for factorial design) compared to B/(B x S/A) (for mixed design).

(2) The sample is accepted as representative for the unit, though no replication is carried out. This pseudoreplication ignores a possible aggregation of biotic factors.

9. Algorithm of analysis

The interpretation and evaluation of the experimental output of both designs made it necessary to construct an algorithm as to make final decisions (figure 3.7). In order to meet the three assumptions for the analysis of variance (ANOVA), the density data were root-root transformed and the % values of the environmental factors were transformed angularly. Whenever these assumptions were not met, the non-parametric Kruskal Wallis and Median tests were applied. When finding a global 'interaction' or 'exclusion treatment' effect, detailed comparison between groups was done by a contrast analysis (within the CSS: Statistica software programme). A significant exclusion effect was accepted if C was significantly different ($p < 0.05$) from both B and P, with B and P similar. A significant procedural effect was accepted if B was significantly different ($p < 0.05$) from both P and C, with P and C equal. Moreover, these effects could only be accepted if they occurred for one or both designs and if the initial period (before the experiment) showed no effect.

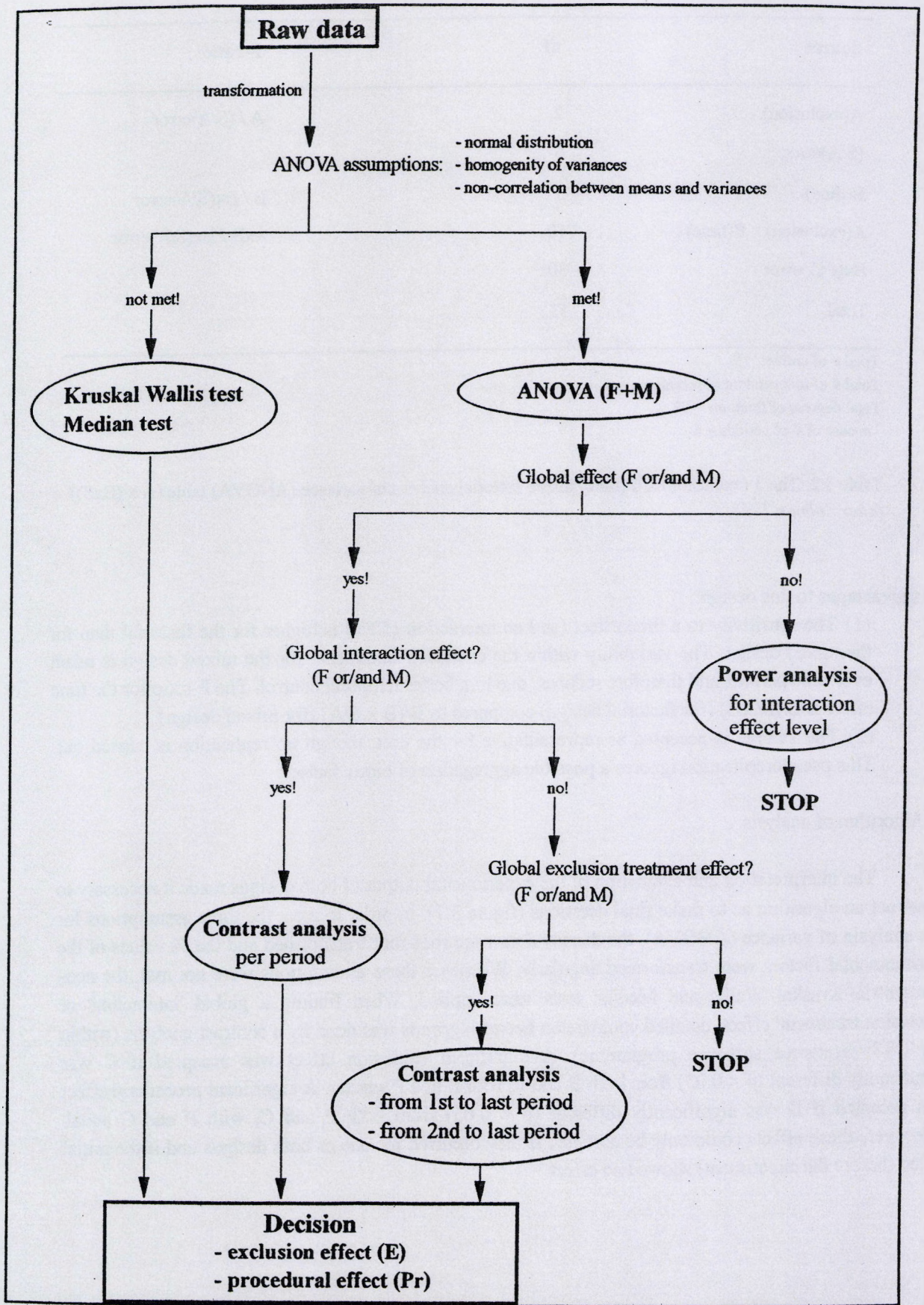


Figure 3.7: The algorithm used to make final decisions (F = factorial design; M = mixed design; E = exclusion effect; Pr = procedural effect).

10. Power analysis

Power is defined as the probability of rejecting the null hypothesis when it is false and therefore gives an idea of the test sensitivity. The power is (1 - β) in which β is type II error. This error is more frequent than type I error α. A 4 to 1 ratio of type II to type I error is a reasonable target. This means that having an α of 0.05 should provide a β of 0.2 or a power of 0.8 (80 %) (Zolman 1993).

The determination of power, after an experiment has been executed (*post hoc* or *a posteriori*), can provide very useful information regarding the importance of non-significant findings. When we are unable to demonstrate an effect, it is important to question whether our experimental design had sufficient power to detect these specific effects (Hall *et al.* 1990b) or whether the design was too weak to detect anything but large differences (Toft & Shea 1983). *Post hoc* power analysis can only be meaningfully applied to non-significant results. It should not be used to justify *post hoc* elevation of non-significant data to pseudosignificance, but rather to direct to a better design for future studies (Andrew & Mapstone 1987). It is a very unexploited technique in ecological research because of the preoccupation with type I error and a lack of awareness of type II error and its importance (Toft & Shea 1983).

Four parameters and the power tables provided by Cohen (1977) are needed to calculate the power:

(1) α = significance criterion of type I error

(2) u = degrees of freedom of the numerator of the interaction F-ratio

(3) n = sample size (# of replicates per sample)

(4) f = effect size

Most studies predict the effect size and wonder if the power of the design was adequate enough to indicate this effect as significant (Raffaelli & Milne 1987; Raffaelli *et al.* 1989; Hall *et al.* 1990c). In this study, however, no effect size predictions were made. The power values for the actual effect size were calculated via Cohen tables (1977) and the four parameters:

(1) $\alpha = 0.05$

(2) u = (3 - 1) x (# of periods - 1)

(3) n = 3

(4) f = effect size calculated via methods provided by Gray (personal communication) using MS_{effect} (= A x B), MS_{error} (S/AB for factorial and B x (S/A) for mixed design), η^2 and Cohen tables (1977). The effect size is derived from η^2. η^2 is calculated as follows:

$$\eta^2 = \sigma^2_{S/A} \times (\sigma^2_{S/A} + \sigma^2_{S/AB})$$

with $\sigma^2_{S/AB} = MS_{error}$

$$\sigma^2_{S/A} = u \times (MS_{effect} - MS_{error}) / n.a$$

with a = # of treatment groups (3 x # of periods)

As mentioned before, the sensitivity of the mixed design to an interaction effect is lower than that of the factorial design. This will be reflected in a higher power value.

C. CAUSE OF IMPACT

1. Bioturbation

In general, the present experiment does not test explicitely for bioturbational effects. Moreover, only few cage studies in salt marshes mention bioturbation to be of a main importance in the biological interaction (Kneib & Stiven 1982).

Tube structures are possible refuges that are mainly built by large polychaetes. Similar tubes were not found in the sediment studied. If they were present, they would have been inhabited by macro-endobenthos which was not excluded from the cages.

Burrows possibly have positive effects on the meiobenthos, but they were found to persist for years (DePatra & Levin 1989). This study indeed revealed that old biogenic structures persisted throughout the experiment so that the effect of physical modification and bioturbation could not be assessed. All samples were taken at about 10 cm from the burrows to avoid skewed density results. In addition the use of cages small enough to fit between existing burrows was avoided (Dye & Lasiak 1986).

Disturbance caused by feeding activity is another possible bioturbational agent. The manual removal of the epibenthos throughout the experiment and the sampling activity, however, led to an artificial disturbance of the sediment. This kind of disturbance mainly affects the upper mm's. That is why the upper 2 cm was studied as a whole.

2. Predation/competition

This study avoids the usual predation and predation pressure hypothesis of most cage experiments that deal with the impact of epibenthos on endobenthos.

This research wants to find the relative importance of predation and/or exploitative competition as structuring force on the global endo-, meio-, and macrobenthos or specific endobenthic taxa. The exclusion of all epibenthic animals (> 2 mm) and the follow-up of all endobenthic taxa (> 38 µm), the control of temporal, procedural, and bioturbational effects, and the minimal refuge and plant constraints did indeed avoid most other interactive components. Only the complex multitrophic, intracompetitive, and larval/adult interactions might bring unexpected and unexplicable results. The experimental output will be used as a base for this evaluation. It will, however, be complemented with data on the epibenthic composition, feeding ecology, and behaviour from literature, the general tendencies in both meio- and macrobenthic densities, the environmental changes throughout the experiment, and the general knowledge of the trophic community structure in mangroves.

A possible indication for predatory control is a proportionate increase of the prey densities after exclusion (Bell & Coull 1978) although this is not always believed to be true (Ellis & Coull 1989). The detection of a vertical upward migration in the sediment can also be expected when predatory disturbers are excluded (Dye & Lasiak 1986; Alongi 1989).

On the other hand, exploitative competition is only to be expected if food sources are limited and food supply is low (Branch & Branch 1980; Evans 1983). In that case, one can predict to observe a significant increase in the common food source after exclusion of the epibenthos. Moreover, when this effect runs parallel with that on specific endobenthic taxa, an exploitative competition will seem to be present.

D. INTERTIDAL GRADIENT EFFECT

The degree of epibenthic influence is known to be spatially dependent (Kneib 1991). The interaction between epibenthic and endobenthic communities might change according to habitat and intertidal position. The present research and experiment was therefore applied to two different mangrove vegetation zones at Gazi Bay (figures 3.8 and 3.9).

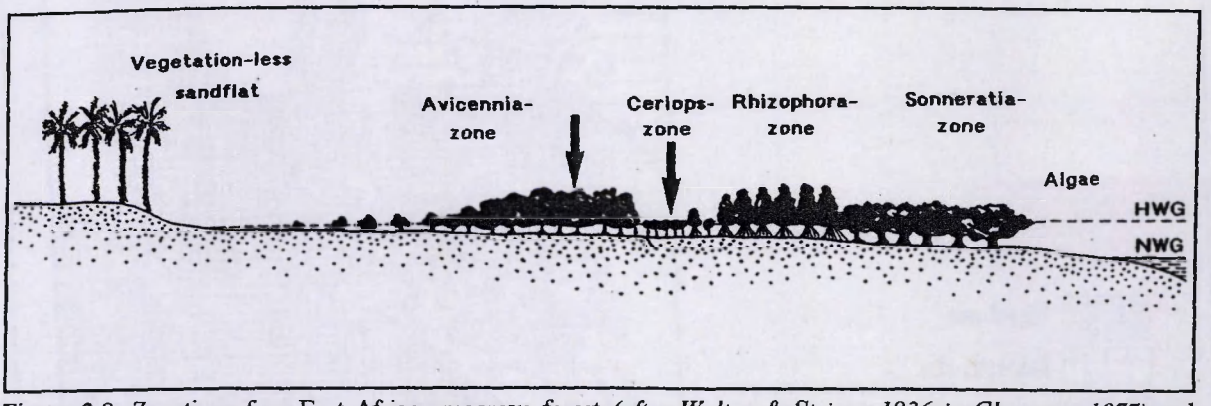


Figure 3.8: Zonation of an East African magrove forest *(after Walter & Steiner 1936 in Chapman 1977)* and indication of the position of the experimental sites in the *Avicennia marina* and the *Ceriops tagal* vegetation zones (arrows).

The *Ceriops tagal* zone covers about 0.5 km². It is a non-exploited and patchy area that borders the westbank of the western creek of the bay. The study site in this vegetation was situated about 2.8 m aboveMLWS (= intermediate in the intertidal zone), and inundated only during about 65 % of the high tides (Slim, personal communication). The *Ceriops tagal* forest and tree morphology is quite patchy, low, and sometimes even shrubby. The restricted fresh water supply and the salty soil might be the explanation for shrubby growth, as this species seems to be most sensitive to high soil salinity (Gallin *et al.* 1989). It is used for construction material, tannins, firewood, and charcoal (Kokwaro 1986).

The *Avicennia marina* zone extends over at least 0.5 km², has not been denuded and is therefore still virgin. It borders the westbank of the western creek of the bay and flanks the *Ceriops tagal* vegetation, separating it from the land. The study site in this vegetation was situated more than 3 m above MLWS (higher than *Ceriops tagal*) and was flooded only during spring tides (Slim, personal communication). The *Avicennia marina* forest and tree morphology produces a denser canopy. The forest floor is muddier and richer in detritus than that of *Ceriops tagal*. *Avicennia marina* vegetation is used for dyes, tannins, dhow and mast material, and medicines (Kokwaro 1986).

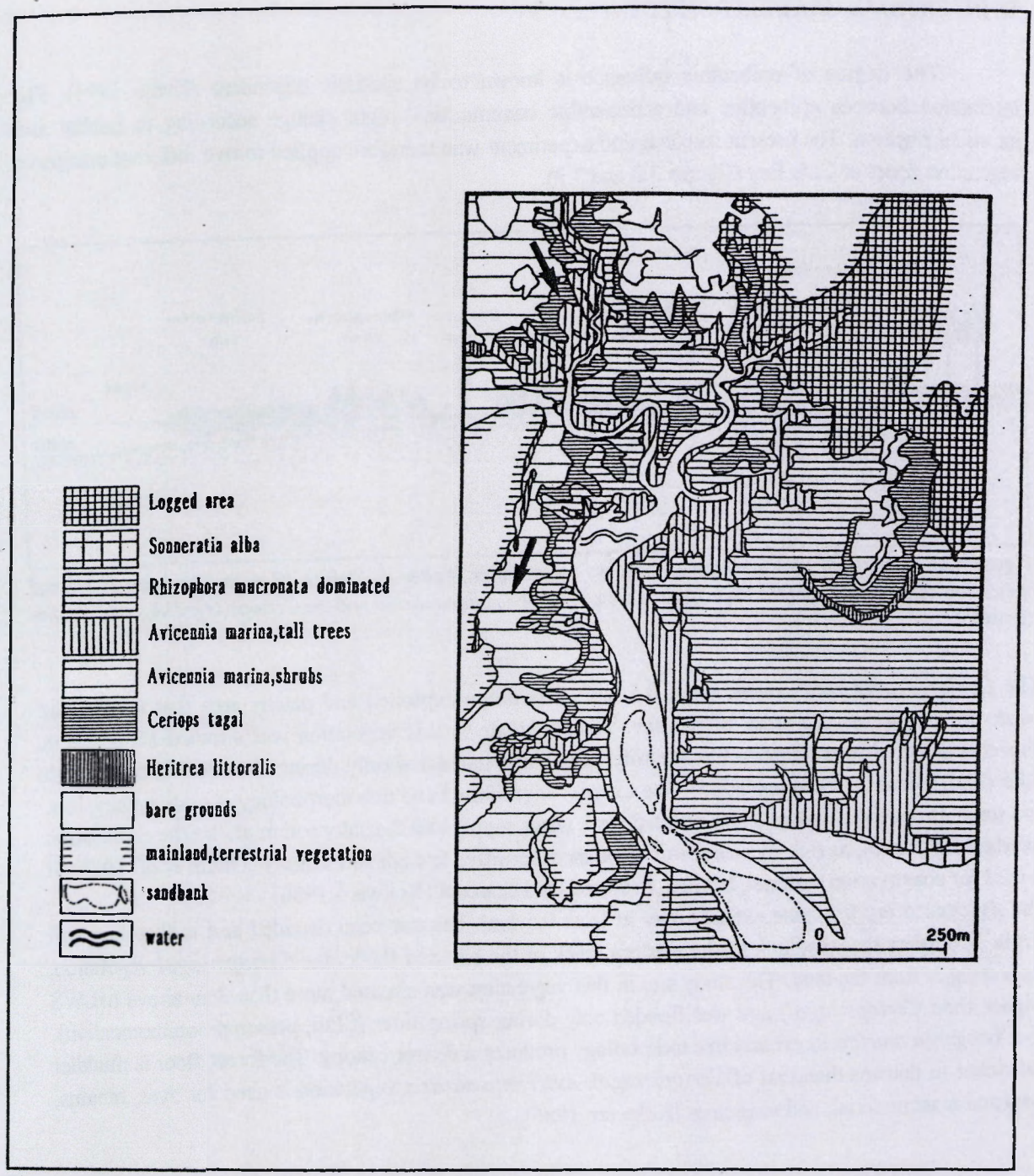


Figure 3.9: Map of the western creek of Gazi Bay with indication of the vegetation types and the position of the experimental sites in the *Avicennia marina* and the *Ceriops tagal* zones (arrows).

The difference in the intertidal position for both zones makes the *Avicennia marina* study site less frequently inundated. It therefore receives less natant epibenthic visitors than the *Ceriops tagal* site. As mentioned above, this will make it possible to test the intertidal gradient hypothesis (Virnstein 1977). It is hypothesized that the relative importance of predation/competition in the epibenthos/endobenthos interaction of the mangrove forest will change according to intertidal position and vegetation type.

The proposed research automatically led to four connected research topics. These specific topics were eventually summarized with the aim of providing a general overview and conclusion along with answers regarding the proposed objectives of this study.

Chapter IV reports on the cage experiment as used to exclude the epibenthos from the *Ceriops tagal* mangrove sediment in order to study the interactions with the meiobenthos (in terms of predation, food competition, and food enhancement). The density of the meiobenthic taxa and nematode genera and a broad range of environmental variables were followed in a depth profile over one year of caging. There was a significant exclusion effect in the upper sediment layer for total meiofauna, nematodes, and oligochaetes during the first two months and for copepods during the last six months of caging. The density of the most common predatory and microalgae feeding nematodes in particular tended to increase in the surface layers along with the percentage of muddy detritus and pigment concentration. Food competition with the epibenthos seemed to be most important in structuring the nematode community. This was suggested by the parallel exclusion effect on muddy detritus, pigments, and nematode composition and the lack of evidence for upward nematode migration in the cage during the experiment. The same could be concluded for the oligochaetes, whereas copepod densities were believed to be more controlled by predation. These findings indicated that the meiofaunal community of the *Ceriops tagal* mangrove sediment (comprising about 95 % of nematodes and oligochaetes) was part of a rather isolated, detrital food web with only minor predator-prey interactions with the epibenthos.

Chapter V attempts to prove the previous statement, concerning meiofauna/macro-epifauna interactions, for the *Avicennia marina* vegetation zone of the same area. The manipulative exclusion technique was used to trace the dominant biological interactions that structure the meiobenthos of an East African *Avicennia marina* mangrove forest. The densities of the major meiobenthic taxa and nematode genera, and a broad range of environmental factors were monitored in a depth profile established during one year of caging. Significant exclusion effects were indicated for oligochaetes and for one of the dominant epistrate feeding nematodes. They are discussed in terms of epibenthic composition and density, feeding behaviour, food resources, and the abiotic environment. The conclusion is that the observed meiobenthos (especially oligochaetes and nematodes) is mainly under exploitative or resource competitive influence of the epibenthos. This indeed confirms the findings concerning the *Ceriops tagal* meiobenthos of the same region. The common food source was shown to be muddy detritus and microalgae. The absence of any effect on the predatory nematodes (2B) showed that the driving force for an internal regulation still had to be found. The impact of epibenthos on meiofauna might be complicated by multilevel interactions with the infaunal macrobenthos.

Hence, ***Chapter VI*** describes the use of the cage exclusion experiment in examining the interaction between the epibenthos (permanent and visiting) and the macro-infauna of the high intertidal Kenyan *Avicennia marina* mangrove sediment. Densities of Oligochaeta (families Tubificidae and Enchytraeidae), Amphipoda, Insecta larvae, Polychaeta, and macro-Nematoda, and a broad range of environmental factors were followed over five months of caging. A significant increase of amphipod and insect larvae densities in the cages indicated a positive exclusion effect, while no such effect was observed for oligochaetes (Tubificidae in particular), polychaetes, and macro-nematodes. Resource competitive interactions were a plausible explanation for the status of the amphipod community. This was also supported by the parallel positive exclusion effect detected for microalgal densities. It is therefore hypothesized that competition for microalgae and deposited food sources is the determining structuring force exhibited by the epibenthos on the macrobenthic infauna of this mangrove sediment. The presence of epibenthic predation, however, cannot be excluded. The question of whether predation pressure on the macrobenthos of the East African mangrove forest floor is entirely absent, still had to be answered.

Therefore, ***Chapter VII*** emphasizes the interactions between macrobenthic in- and epifauna of the mid-intertidal *Ceriops tagal* stand in order to test the hypothesis that predation pressure increases, at the expense of a diminishing epibenthic competitive influence, when going downward in the intertidal zone. The cage experiment was used to exclude permanent and visiting epibenthos. Densities of the macrobenthic taxa Oligochaeta (families Tubificidae and Enchytraeidae), Amphipoda (*Grandidierella* spec. and *Ampelisca* spec.), Insecta larvae (family Dolichopodidae), Polychaeta (families Nereidae and Terebellidae), macro-Nematoda (family Oncholaimidae) and Gastropoda, and a broad range of environmental factors were followed over five months of caging. A significant increase in the dominant tubificid population and the polychaete *Namalycastis* spec. in the cages indicated a positive exclusion effect. Epibenthic predation seemed to be more important in the *Ceriops tagal* mangrove forest than in the high intertidal *Avicennia marina* zone. Nevertheless, resource competition for muddy detritus was still believed to be the major structuring force for oligochaetes. The bulk of the studied macrobenthic infauna is therefore suggested to be a trophic dead end and to have only a minor interactive position in the mangrove foodweb.

Since these four connected research topics stand quite independently, ***Chapter VIII*** gives a synthesis. The data for both meio- and macrobenthos in *Avicennia marina* and *Ceriops tagal* zones were combined in order to reveal answers to the general objectives of this study. This eventually made it possible to apply the information in constructing a preliminary trophodynamical benthic scheme and in tracing the endobenthic role in East African mangrove forests.

Chapters IV, V, VI, and VII have been derived from scientific papers and manuscripts from which the general and overlapping part and the discussion of Material and Methods have been removed. These parts have been collectively explained in this chapter. Only those elements that are specific for the different research topics will be stated separately in the corresponding chapters.

Chapter IV is derived from:
Schrijvers J., Okondo J., Steyaert M. & Vincx M. (1995). Influence of epibenthos on meiobenthos of the Ceriops tagal mangrove sediment at Gazi Bay, Kenya. Marine Ecology Progress Series 128: 247-259.

Chapter V is taken from:
Schrijvers J., Schallier R., Silence J., Okondo J. & Vincx M. Interactions between epibenthos and meiobenthos in a high intertidal Avicennia marina mangrove forest. submitted to Oecologia

Chapter VI used as baseline:
Schrijvers J., Fermon, H. & Vincx M. Resource competition between macrobenthic epi- and infauna of a Kenyan Avicennia marina mangrove forest. Marine Ecology Progress Series, in press

Chapter VII is derived from:
Schrijvers J., Camargo M., Pratiwi R. & Vincx M. Macrobenthic infauna under a Kenyan Ceriops tagal mangrove impacted by epibenthos. submitted to Marine Biology

IV. INFLUENCE OF EPIBENTHOS ON MEIOBENTHOS IN THE *CERIOPS TAGAL* FOREST

A. INTRODUCTION

The *Ceriops tagal* mangroves are one of the most extensive and economically important vegetation zones along the coast of Kenya (Kokwaro 1986). A rational management of Kenyan mangroves can be achieved only by analysing structure, function and energy fluxes of the mangrove system and its relation with other ecosystems. Ecological studies on the meiobenthos in East African mangrove systems are few (Dye & Furstenberg 1978; Dye 1983a, 1983b; Dye & Lasiak 1986; Vanhove *et al.* 1992; Vanhove 1993; Schrijvers, in press). In the present study, the interactions between the epibenthos (consisting mainly of crabs, gastropods, hermit crabs and - to a lesser extent - of shrimps and demersal fishes) and the meiofauna were examined. This could reveal some insight in the role of the meiobenthos in *Ceriops tagal* mangrove soils.

The role of the meiobenthos (comprising about 90 % of nematodes in general) in the trophic dynamics of an overall benthic ecosystem has been hypothesized to be twofold.

(1) The meiobenthos may play an important role in the detrital food web as a self-contained energy sink with an internal predator regulation (Gerlach 1978; Reise 1979; Heip 1980; Connell 1983; Gee *et al.* 1985; Olafsson & Moore 1992; Alkemade *et al.* 1993; Giere 1993; Walters & Moriarty 1993). If this is the case, the meiobenthos depends on, or competes with, the other benthic subsystems (such as the epibenthos) for detrital food.

(2) On the other hand, several trophic links with the epibenthos have been recognized, mainly in temperate areas. Predation on meiofauna is either selective or non-selective (Bell & Coull 1978; Reise 1979; Tenore & Rice 1980; Gee *et al.* 1985; Marinelli & Coull 1987; Gee 1989; Hall *et al.* 1990c; McLachlan & Romer 1990; Castel 1992; Olafsson & Moore 1992; Giere 1993).

For mangrove sediments, as for salt marshes, the potential influence of the mangrove epibenthos in structuring the meiofauna is broad. One can expect that internally regulated meiofaunal communities are mainly affected by competition with, and food enhancement by, the epibenthos (Sultan Ali *et al.* 1983; Dye & Lasiak 1986; Alongi 1989; Tietjen & Alongi 1990; Alongi & Christoffersen 1992), whereas meiofauna that are consumed by this epibenthos would be more predator controlled (Bell 1980; Hoffman *et al.* 1984; Alongi 1989; Dittmann 1993). Moreover, the physical disturbance and modification of the mangrove sediment by the epibenthos (mainly through tube digging and feeding activities) may also be of importance (Bright 1977; Bell & Coull 1978; Alongi & Tietjen 1980; Bell 1980; Sherman & Coull 1980; Hoffman *et al.* 1984; Dye & Lasiak 1986; Marinelli & Coull 1987; Alongi 1989; DePatra & Levin 1989; Dittmann 1993).

B. MATERIAL AND METHODS

The study area, the quantification of environmental and biotic factors, the experimental and statistical design, and the statistical analysis have been accurately described in Chapter III.

For this subresearch in particular, seven series of samples were taken over time in the three treatments of the *Ceriops tagal* experimental site:

- period 1: before caging (6/8/92) (env/meio)
- period 2: after 22 caging days (28/8/92) (env/meio)
- period 3: after 52 caging days (27/9/92) (env/meio)
- period 4: after 84 caging days (29/10/92) (env)
- period 5: after 111 caging days (25/11/92) (env)
- period 6: after 139 caging days (23/12/92) (env/meio)
- period end: after 358 caging days (30/7/93) (meio)

Correlation : Non-parametric Spearman rank correlation coefficients were calculated ($p < 0.05$) to determine a relationship between biotic and environmental variables along the depth gradient and along the horizontal gradient within the upper layer.

Major meiobenthic taxa: These biotic factors were analysed using a 3 x 4 x 5 (between groups) factorial ANOVA design with treatments (3), slices (4), and periods (5) as groups. Additionally, a 3 (between groups) x 5 (within subjects) mixed ANOVA design was applied with treatments (3) as groups and periods (5) as subjects repeated over time. The mixed design analysed only the upper 2 cm layer, since significant effects were found to be restricted to this slice.

Environmental factors: Effects on environmental factors were detected using a 3 x 4 x 6 (between groups) factorial ANOVA design with treatments (3), slices (4), and periods (6) as groups. In addition, a 3 (between groups) x 6 (within subjects) mixed ANOVA design with treatments (3) as groups and periods (6) as subjects repeated over time. The mixed design analysed only the upper 2 cm layer.

Nematode genera: Nematode genera were identified only for the cage treatments of periods 1 and 3. Therefore, no ANOVA was used but the general evolution of the different genera and feeding type densities provided a help during the interpretation.

C. RESULTS

1. Spatial distribution patterns

a) Depth profile

The ANOVA for the total slice effect indicated a significant ($p < 0.05$) depth gradient in the sediment for both environmental and biotic factors. Figure 4.1 shows the existence of a prominent gradient from sandy, well oxygenated, warm, and pigment-rich surface layers to muddy, less oxygenated, colder, and pigment-poor deeper layers.

Most meiofauna taxa (*e.g.* nematodes, oligochaetes and copepods) had significantly higher densities in the upper layers. On the contrary, the halacaroids did not follow this pattern: they were significantly more abundant in slice 4-10 cm (figure 4.1). Other meiofauna taxa did not show a prominent depth pattern.

b) Horizontal pattern in the upper layer

To exclude the overriding vertical pattern, the Spearman rank correlation coefficients were calculated for all 0-2 cm layers (table 4.1). A clear division could be made between muddy and sandy patches. The former were positively correlated with detritus and pigments, while the latter were characterized by higher temperatures. Copepods, kinorhynchs, oligochaetes, and polychaetes occurred in higher densities in the first habitat. These taxa, together with ostracods, also showed a tendency to *avoid* high temperatures but *preferred* high salinities and chlorophyll *a* concentrations.

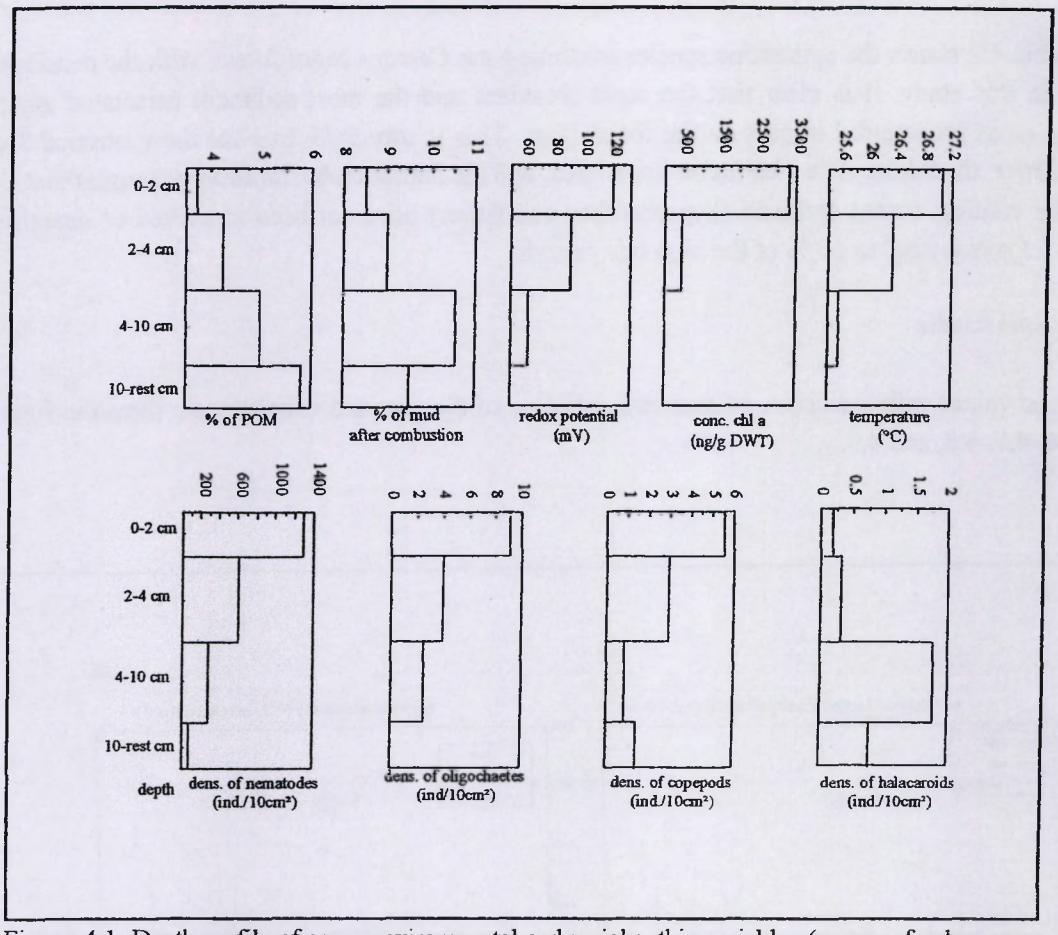


Figure 4.1: Depth profile of some environmental and meiobenthic variables (means of values over one year) *(Ceriops tagal)*.

	cope	**kino**	**olig**	**poly**	**ostr**	**hala**	**temp**	**chl *a***	**POM**
% of mud before combustion	+	+		+			-	+	
% of mud after combustion			+	+				+	+
% of sand before combustion				-	-		+	-	-
% of sand after combustion			-	-				-	-
salinity (ppt)	+				+		-		-
temperature (°C)	-	-			-				
chlorophyll a (ng/g DWT)	+	+	+		+			+	+
fucoxanthine (ng/g DWT)						-	+	+	
% of POM								+	+

Table 4.1: Significant positive and negative Spearman rank correlations ($p < 0.05$) for some environmental and meiobenthic variables *(Ceriops tagal)*.

2. Epibenthic composition

Table 4.2 shows the epibenthic species inhabiting the *Ceriops tagal* forest, with the densities as estimated in this study. It is clear that the most abundant and the most sediment orientated animals exhibit the most pronounced impact on the forest floor. This is especially true for the gastropod *Terebralia palustris*, the fiddler crab *Uca lactea annulipes*, and the hermit crab *Clibanarius longitarsus*.

The visiting, natant epifauna (hyperbenthos and fishes) have not been identified or quantified, but its impact is restricted to 65 % of the high tide periods.

3. Experimental results

Mean values with indication of standard deviation of the reported variables are shown in figures 4.2, 4.5, 4.6, 4.7, 4.8, and 4.9.

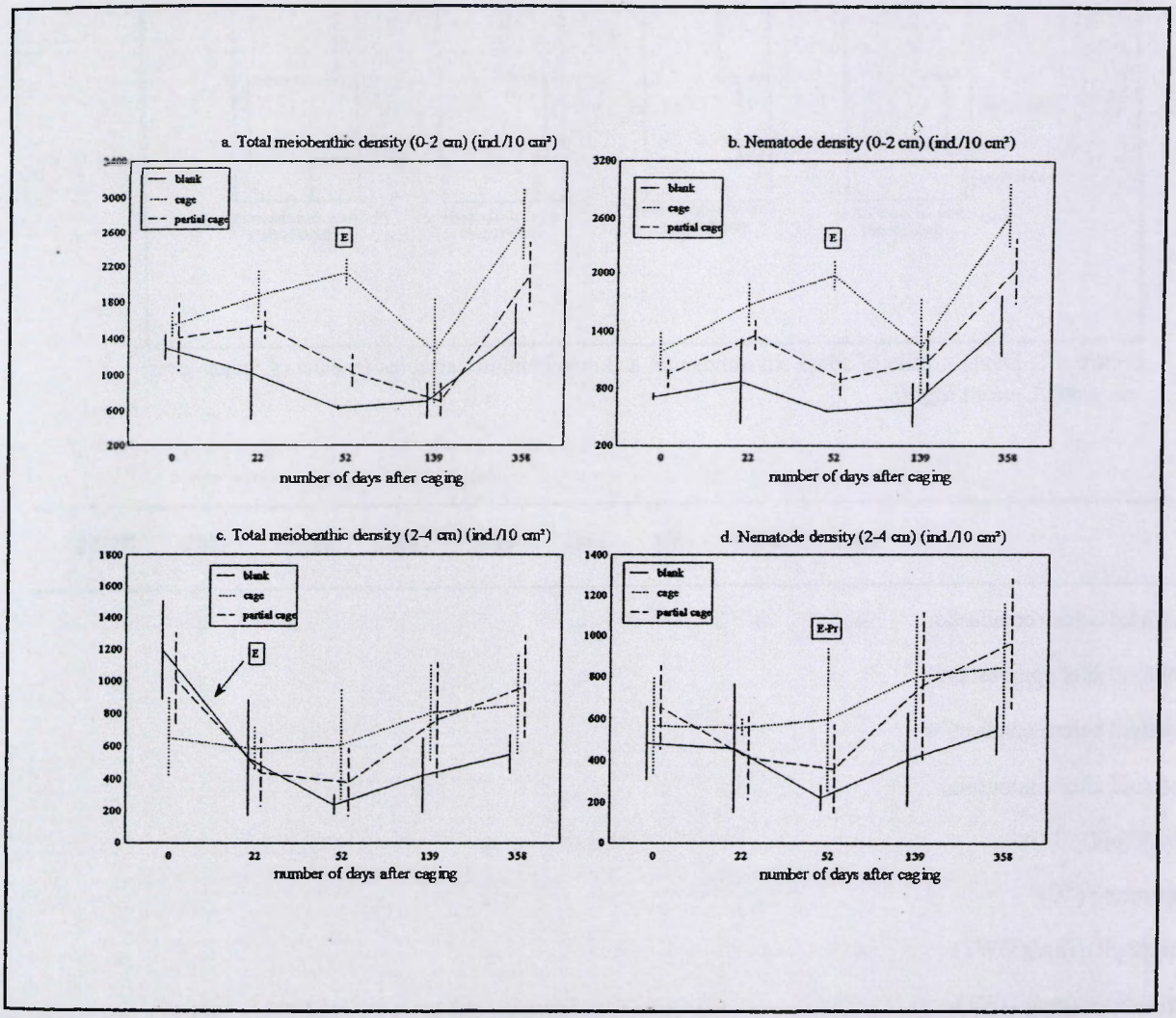


Figure 4.2: Total meiofauna and nematode densities (ind./10cm²) in the cage, partial cage, and blanck treatments: mean values and standard deviations in the two upper layers over time (E = significant exclusion effect with $p < 0.05$; Pr = significant procedural effect with $p < 0.05$) *(Ceriops tagal)*.

epibenthic species	author	feeding behaviour	habitat	average density (ind./m²) (this study)
Cerithidea decollata	Brown 1971 McIntosh 1984 Dye & Lasiak 1987	non-selective deposit feeding (detritus)	frequently on trees	11
Terebralia palustris	Dye & Lasiak 1987	non-selective deposit feeding (inorganic parts, microalgae, bacteria, protozoans)	sediment dwelling	65
	Slim *et al.* (submitted pers. comm.) pers. obs.	*Ceriops tagal* leaves		
Sesarma guttatum	Dahdouh-Guebas (pers. comm.) Leh & Sasekumar 1985	omnivorous with preference for mangrove plant matter (83-97 % of diet) with brachyuran remains, inorganic particles, micro-algae, diatoms, meiofauna and insects	sediment dwelling	rare
Metopograpsus thukuhar	Dahdouh-Guebas (pers. comm.) McIntosh 1988	omnivorous with preference for macroalgae and animal items (sometimes fresh leaves, seedlings, leaf litter and detritus)	forest dweller (trunk, roots, floor)	0.5 (adult) 1 (juv.)
Uca lactea annulipes	Crane 1975 McIntosh 1984 Dye & Lasiak 1986 Wolcott & O'Connor 1992	selective deposit feeding (microheterotrophs, microalgae, detritus)	sediment dweller	6 (adult) 3.5 (juv.)
Clibanarius longitarsus	Reay & Haig 1990 Gherardi & Vannini 1993 Vannini (pers. comm.)	muddy detritus (never leaves)	mangrove mud dweller	12
visiting fauna (unknown)	?	herbivorous or carnivorous?	high tidal (only during 65? % of high tides)	

Table 4.2 : Description of permanent and visiting epibenthos excluded from the cages in the studied *Ceriops tagal* zone (in terms of average densities, feeding behaviour, and habitat).

a) Biotic factors

Exclusion effect: Exclusion effects were observed for nematode and total meiofauna densities in slices 0-2 and 2-4 cm (figure 4.2). It showed an increase of 1.5 to 2x in the cages as compared to control treatments.

The nematode increase in the surface layer of the cage after two months was not accompanied by a clear decrease in the deeper layers (figure 4.3) which indicated that upward vertical migration could not explain the observations.

After three months and one year, the exclusion effect was no longer detectable, density differences between treatments having fallen back to their original levels.

Concerning nematode feeding guilds two parallel (though non-significant) trends were observed in the cages over time (figure 4.4). There was a general increase of feeding type 2B (omnivores/predators) in slice 0-2 cm at the expense of type 1B (non-selective deposit feeders) and an *ex aequo* for type 2A (epistrate feeders). In the deepest layer an opposite change in feeding types occurred with a decrease of 2B and an increase of 1B.

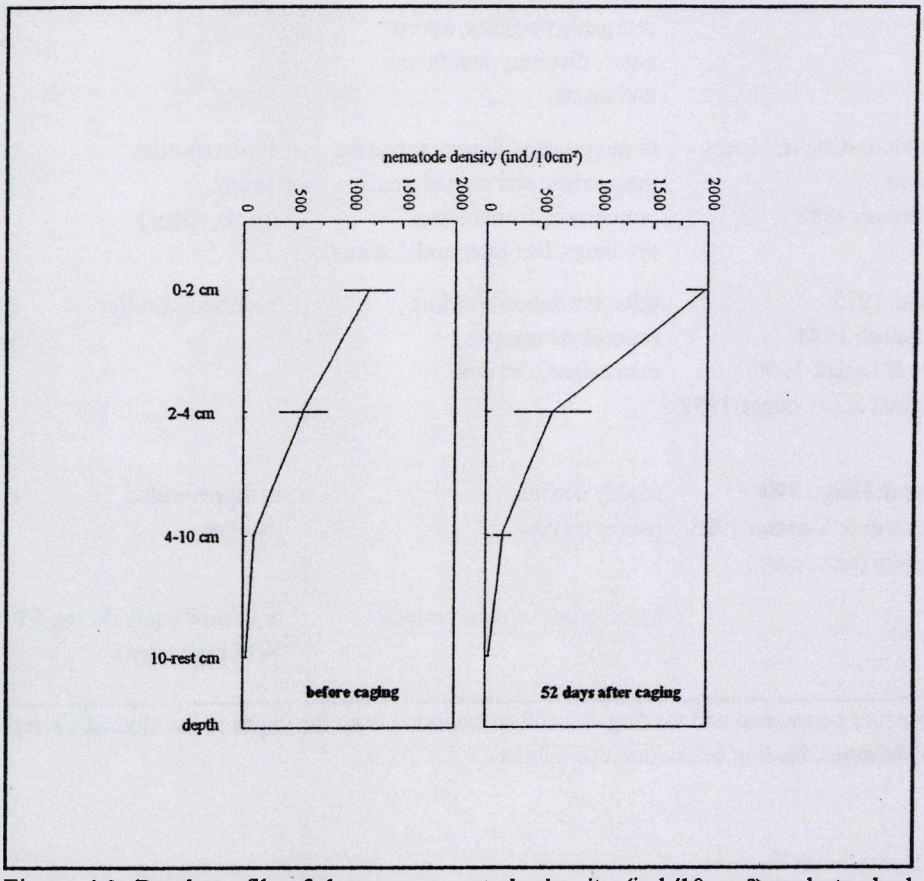


Figure 4.3: Depth profile of the mean nematode density (ind./10 cm²) and standard deviation in the cage over two periods *(Ceriops tagal)*.

As for the most common nematode genera, *Chromaspirina* and *Sphaerolaimus* (type 2B) and *Ptycholaimellus* and *Spirinia* (type 2A) increased conspicuously in the surface layer, whereas *Daptonema* (type 1B) increased in the deepest layer (table 4.3).

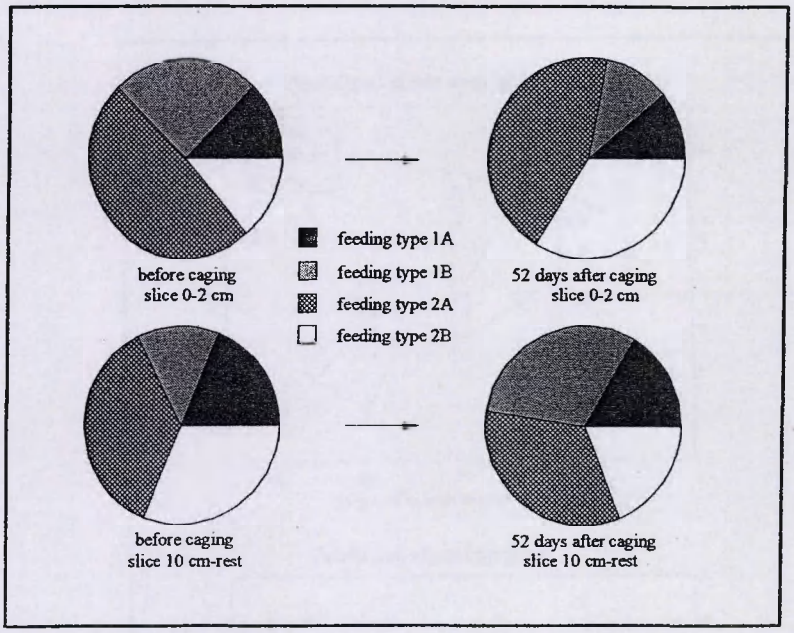


Figure 4.4: Mean relative composition (%) of the nematode feeding types (Wieser 1953) of the surface (0-2 cm) and deepest layer (10-rest cm) of the cage over two periods *(Ceriops tagal)*.

		slice 0-2 cm		slice 10-rest cm	
ind./10 cm²		**period 1**	**period 3**	**period 1**	**period 3**
Chromaspirina	2B	43.4	294.2	98.7	95.1
Microlaimus	2A	43.5	185.5	246.7	268.8
Daptonema	1B	154.1	64.0	33.0	116.0
Ptycholaimellus	2A/2B	158.1	179.1	32.9	-
Sphaerolaimus	2B	71.1	95.9	-	-
Spirinia	2A	71.1	121.5	16.4	-
Desmodora	2A	142.3	179.1	82.3	54.5
Terschellingia	1A	98.8	44.8	16.5	-

Table 4.3 : Mean density values (ind./10 cm²) of the most common nematode genera of the surface (0-2 cm) and deepest layer (10-rest cm) in the cage over two periods *(Ceriops tagal)*.

As for the other meiofauna taxa, exclusion effects were demonstrated for copepod and oligochaete densities in the upper layer (figure 4.5). The oligochaete response was observed as a density increase in the upper slice of the cage after two months (10x). Copepod densities showed a general decline over one year. ANOVA showed only a significant exclusion effect during the last half year of caging. The upward trend during this period was significantly stronger in cages (4x) than in partial cages and blanks.

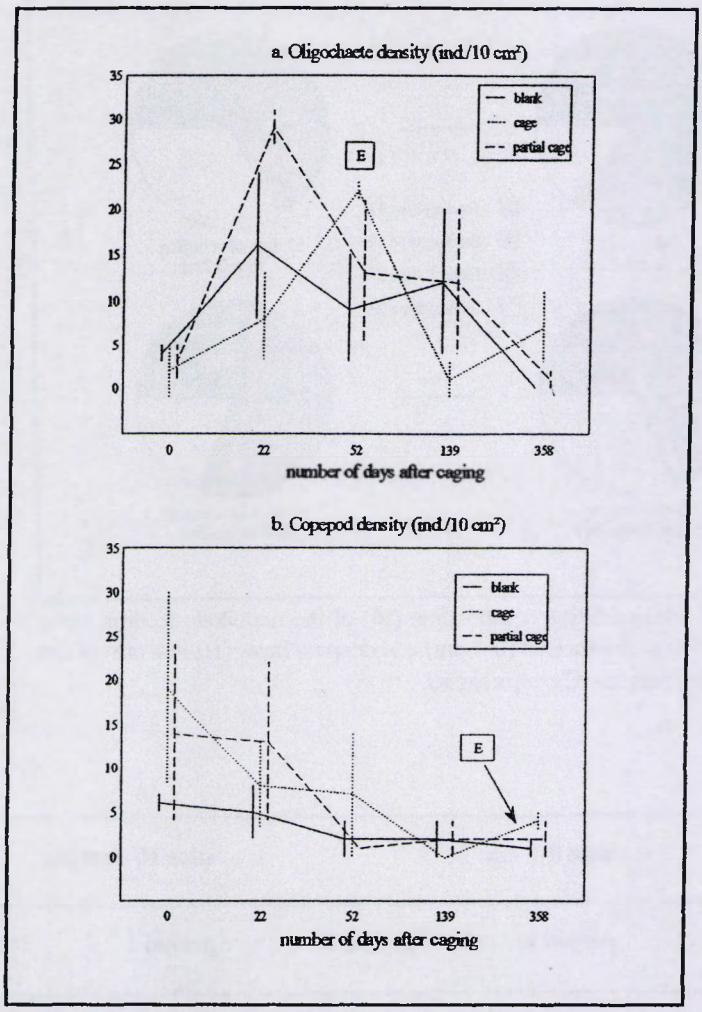


Figure 4.5: Oligochaete and copepod densities (ind./10 cm²) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper layer over time (E = significant exclusion effect with $p < 0.05$) *(Ceriops tagal)*.

No effect: No procedural effect could be demonstrated for the patterns in nematode, oligochaete, or copepod densities. Neither procedural nor exclusion effects could be detected for polychaetes, ostracods, halacaroids, and kinorhynchs.

b) Environmental factors

Exclusion effect: Highly significant exclusion effects ($p < 0.01$) were demonstrated for chlorophyll *a* and fucoxanthin concentration in the surface layer (figure 4.6).

A significant exclusion effect ($p < 0.05$) on % of mud before combustion was also notable in slice 0-2 cm (figure 4.7).

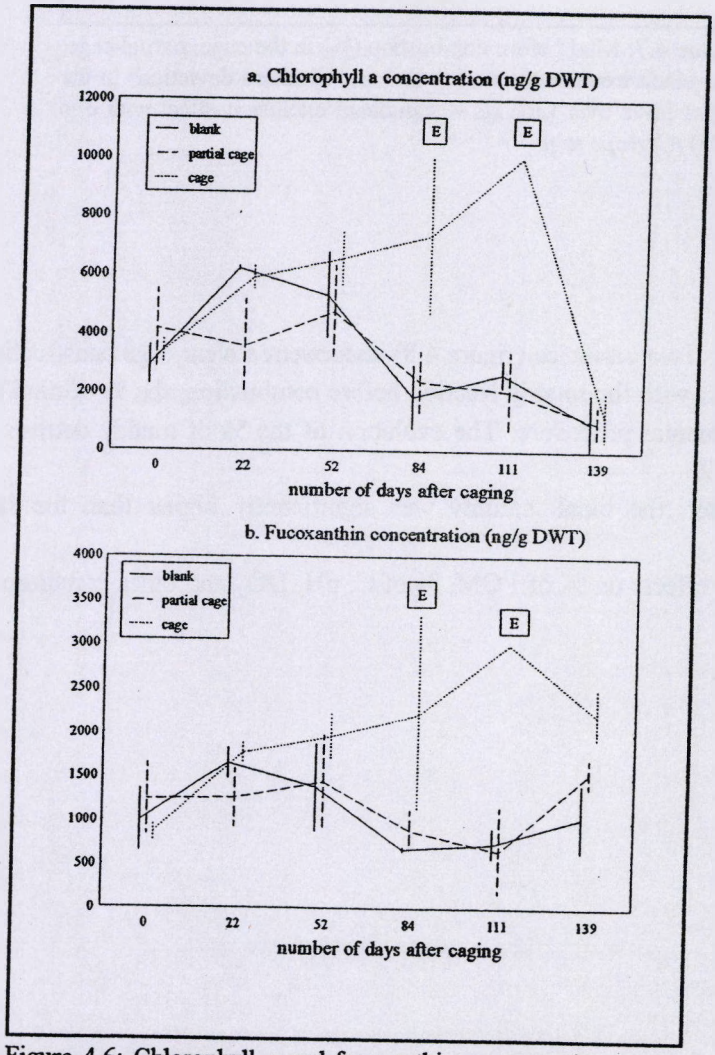


Figure 4.6: Chlorophyll *a* and fucoxanthin concentrations (ng/g DWT) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper layer over time (E = significant exclusion effect with $p < 0.05$) *(Ceriops tagal)*.

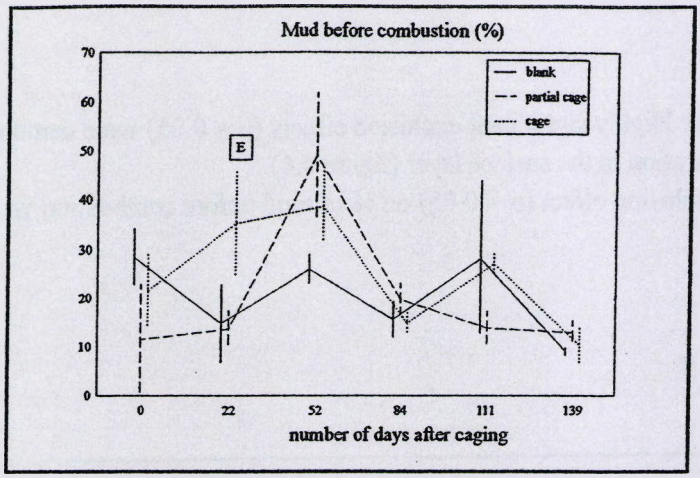


Figure 4.7: Mud before combustion (%) in the cage, partial cage, and blank treatments: mean value and standard deviations in the upper layer over time (E = significant exclusion effect with $p < 0.05$) *(Ceriops tagal)*.

Procedural effect: Two variables (figure 4.8) underwent a clear cage construction effect in the upper slice (0-2 cm). In contrast with the muddy fraction before combustion, the % of mud after combustion was influenced by the experimental procedure. The evolution of the % of muddy detritus (from 0 to 22 days) becomes clear in figure 4.9.

Two months later, the blank salinity was significantly higher than the salinity in both other treatments.

No effect: Clear effects on % of POM, % of C, pH, DO_2 and other granulometric factors were not detected.

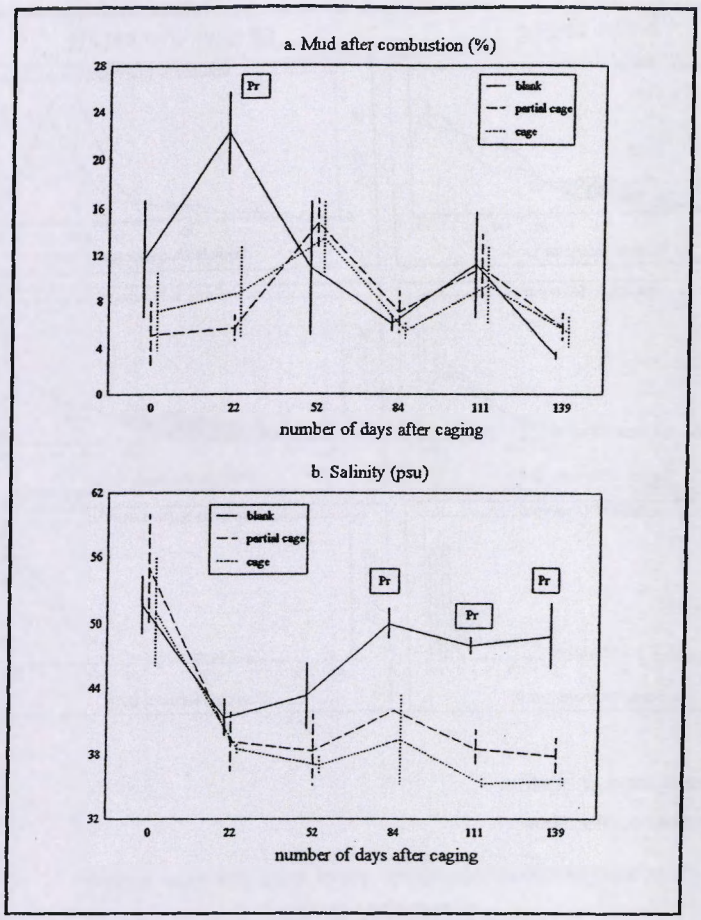


Figure 4.8: Mud after combustion (%) and salinity (psu) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper layer over time (Pr = significant procedural effect with $p < 0.05$) *(Ceriops tagal).*

D. DISCUSSION

1. Experimental material and methods

The evaluation and discussion of the used material and methods concerning study site, quantification of environmental and biotic factors, experimental and statistical design, and statistical analysis have been accurately expounded in Chapter III.

2. Spatial distribution patterns

This study shows a correlation of the meiobenthic community structure with physical gradients in the sediment. This may reflect a typical rigid system of environmental factors regulating infaunal community structure in extreme eulittoral habitats (Hulings & Gray 1976). Especially in mangrove sediments the pigment gradient is very conspicuous (Alongi 1989; Ming-Yi *et al.* 1994). Most meiofauna taxa have been shown to prefer subsurface O_2 rich layers (Dye 1983a; Alongi & Sasekumar 1992). It is therefore not surprising that they are found to be positively correlated to characteristics such as the chlorophyll *a* concentration that are typical for these layers.

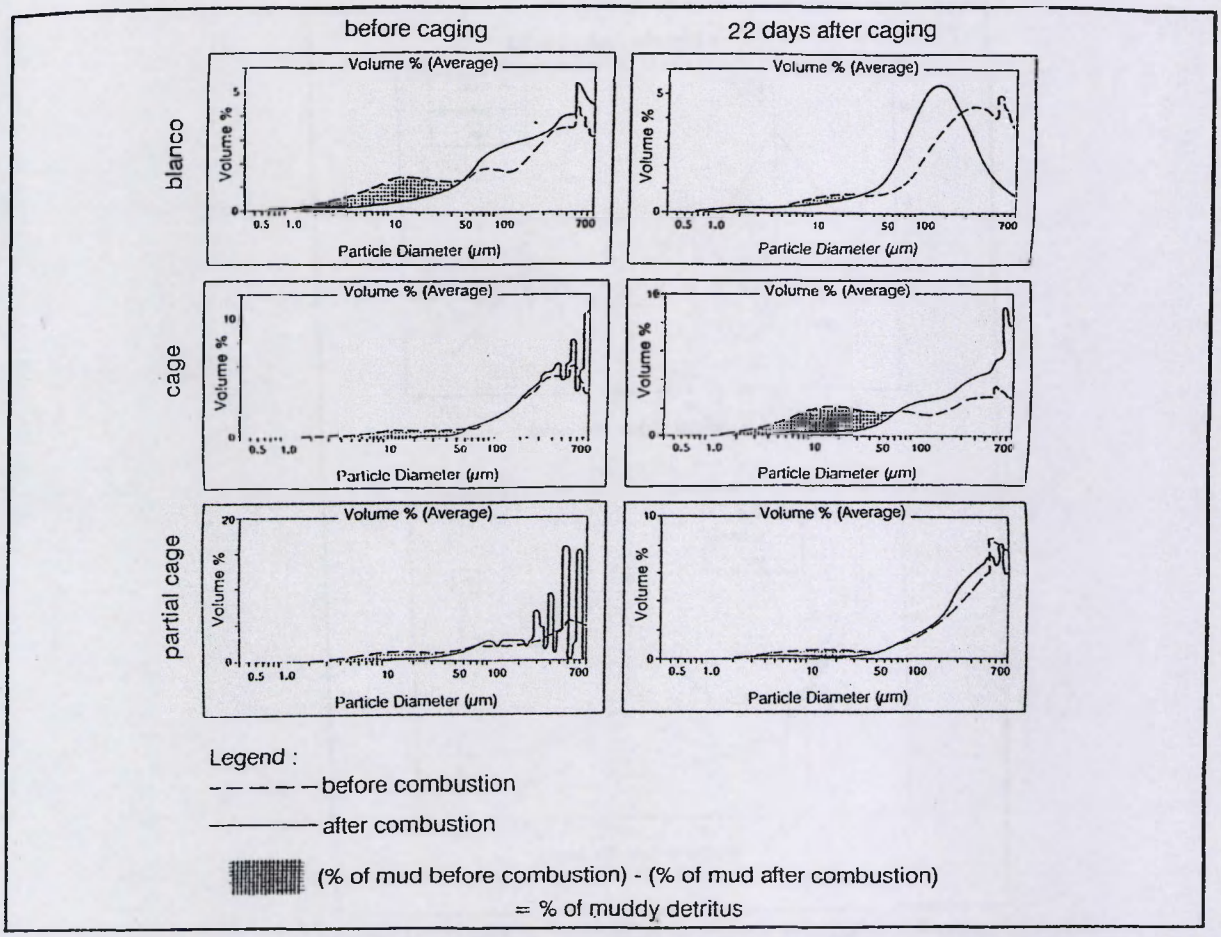


Figure 4.9: Grain size composition (volume %), before and after combustion, of the surface layer in the cage, partial cage, and blank treatments over two periods (with indication of the % of muddy detritus) *(Ceriops tagal)*.

3. Experimental results

a) Environmental factors

Exclusion effect: Some sediment characteristics (% of mud before combustion) and the pigment concentration showed an exclusion effect in the upper layer. In general, there was an evolution in the cages to a muddier and pigment-richer sediment after 22 and 84 days respectively. The increase of the % of mud was owing to detritus accumulation since the % of mud after combustion did not show a parallel increase. As the total organic material (% of POM and C) in the sediment did not change, this detrital increase was most probably restricted to the muddy fraction of the detritus (figure 4.9).

Effects on the pigment concentration (chlorophyll *a* in particular) are correlated with changes in microalgae and diatoms (Gerdol & Hughes 1994a).

Procedural effect: It is obvious that the sediment of the partial cage and cage treatments became more humid through time than that of the blank treatment as a result of the cage construction (table 4.4). This resulted in lower salinities.

	after 1 month of caging			after 5 months of caging			evaluation
	B	C	P	B	C	P	
fouling	-	-	-	-	-	-	OK
shading	-	+	±	-	+	±	± procedural
sedimentation	-	-	-	-	-	-	OK
moisture	-	-	-	-	+	+	procedural
litter fall	+	-	±	+	-	±	± OK
epibenthos	+	-	+	+	-	+	OK

Table 4.4 : Qualitative observations (- = absent, + = present and ± = intermediate) of possible artefacts in the three reatments (B, P and C) after one and five months of caging with procedural evaluation *(Ceriops tagal)*.

b) Nematode and total meiofauna density

An exclusion effect on nematode and total density was also reported by Dye & Lasiak (1986) (an increase of 2x to even 5x), by Hoffman *et al.* (1984) (10x) and by Dittmann (1993) (5x). Bell (1980) found only an exclusion effect for total meiofauna density.

Competition: No quantitative studies on the resident, bottom dwelling epifauna of Gazi mangroves are found. Some qualitative results and personal observation give an insight in the occurrence and composition. Only Slim *et al.* (submitted personal communication) found the gastropod *Terebralia palustris* of the same *Ceriops tagal* zone to be represented by 33 ind./m². This is much lower than found in the present study (65 ind./m²). This study gives therefore the first quantitative results of the resident epifauna under *Ceriops* mangroves of Gazi. Until now, only one quantitative study on the natant epifauna visiting Gazi mangrove forests has been published (van der Velde *et al.* 1995). This part of the epibenthos is a quite unknown factor.

The epibenthos in the *Ceriops tagal* vegetation was dominated by the crab *Uca lactea annulipes* (9.5 ind./m²), the gastropod *Terebralia palustris* (65 ind./m²) and the hermit crab *Clibanarius longitarsus* (12 ind./m²) (table 4.2). According to Dye & Lasiak (1986) competition with the nematodes is the driving force: the dominant epibenthos and pelagic fauna are thought to be important grazers on detritus and the associated bacteria, protozoans, and fungi (Gerlach 1978; Alongi 1989). Stomach content analyses of *Uca polita* and *Uca vocans* and fiddler crabs in general revealed bacteria, microalgae, and protozoans to be the dominant dietary items (Dye & Lasiak 1986). The diet of gastropods in mangroves is limited to microalgae, bacteria, and fungi (Branch & Pringle 1987 in Alongi 1989). As in the present study, caging and exclusion of gastropods has been shown to cause an increase of chlorophyll *a* in a study of Branch & Branch (1980). The hermit crab *Clibanarius longitarsus* mainly feeds on muddy detritus (never on leaves) (table 4.2).

Consequently, the exclusion effect as a conspicuous increase of pigment concentration and muddy detritus could not have been entirely caused by the cage construction. Moreover, the exclusion effect (especially for muddy detritus) was parallel to that on nematodes and total meiofauna (*i.e.* after 52 days of caging). Therefore the nematodes and the epibenthos in this study are believed to compete for food.

Predation: Concerning the predation hypothesis, *Uca pugnax* and juvenile crabs in general have been shown to ingest nematodes (Bell 1980; Hoffman *et al.* 1984). Dittmann (1993) was convinced that consumption of, and predation on, the meiofauna by the dominant crab *Mictyris longicarpus* was the structuring factor.

But, Dye & Lasiak (1986) stressed that exclusion of predation as a driving force would lead to an upward vertical migration of nematodes. No evidence for this was found in this study, stressing the lack of predatory control (Alongi 1989).

Bioturbation: A third interaction possibility is disturbance through bioturbation (Alongi 1989) by burrowing (Bright 1977; DePatra & Levin 1989) or feeding activities and by the production of (pseudo)fecal pellets (Sherman & Coull 1980; Hoffman *et al.* 1984; Dye & Lasiak 1986; Dittmann 1993). As mentioned before, exclusion of bioturbational effects was probably not detected in our experiments (Chapter III).

Procedure: In this study, the effect of the cage construction itself was reflected in a decrease of the muddy fraction (after combustion) and salinity in the cages and partial cages. The potential effect of these changes is believed to be marginal as compared to the obvious exclusion effect on nematodes. Bell (1980) found no experimental effect on the muddy fraction, whereás Virnstein (1977) and Alongi (1989) found an increase due to water stagnation.

c) Nematode genera composition

A disproportionate increase of the nematode genera as found in this study, is not expected when predation would have been the driving force behind the nematode community. This seems to be an extra evidence for the lack of predation pressure.

Although the overall 2A type % did not change, the increase of the most common type 2A nematode genera (epistratal microalgae feeders) and an overall increase of type 2B (omnivores/predators) in the upper layer was evident. It was followed by a new equilibrium in nematode density. Epistrate feeders might be reacting to the microalgal abundance and could be rapidly grazed down by nematode predators that were partly coming from deeper layers. The presence of type 2B could also be a reason for the decrease of type 1B nematodes which were not or only slightly affected by competition. These findings support the competition hypothesis. Unfortunately, we did not compare these data with the evolution of feeding types in partial cage and blank treatments. A comparison would probably indicate possible significant exclusion and procedural effects on genus composition and trophic structure of the nematode community.

Though indications for the food competitive process, seem to be present, some trends remain unclear. A reaction to the muddy detritus increase would have led to a positive response of especially the 1A/1B feeding types. This was not so. On the other hand, a reaction to the microalgal increase would have led to a positive response of 2A genera. Although these genera indeed showed a positive exclusion effect, it was evidenced only before that on the chlorophyll *a* concentration. Further and more detailed research is needed to confirm the resource competition with the nematodes.

d) Oligochaete density

Hoffman *et al.* (1984) too found a 4 fold increase of annelids in general while Dittmann (1993) showed a 5 fold increase of oligochaetes.

Competition: From the five food categories for oligochaetes (Giere & Pfannkuche 1982) the most important dietary item for interstitial tubificids and enchytraeids is believed to be organic matter enriched with bacteria rather than microalgae which were found to be most important for nematodes (Giere 1975). Organic matter is particularly plentiful in littoral sands and muds. Indeed, it was this muddy detritus that showed a conspicuous exclusion effect in the experiment, indicating that the removal of epibenthos turned out to favour the oligochaetes in terms of competition for food.

Predation: Nevertheless, a decrease of predation by crabs (Dittmann 1993) or by juvenile fishes can also be a possible factor. In temperate regions, there is evidence that young demersal fishes (*e.g.* gobiids) prey upon oligochaetes (Giere & Pfannkuche 1982). Virnstein (1977) on the other hand showed with a cage experiment in a temperate shallow estuarine bottom that the dominant tubificid was largely unaffected by predation of crabs or fishes.

Bioturbation: It is known that the production of burrows and food and fecal pellets by crustaceans may have a positive effect on oligochaete numbers (Bell & Coull 1978; Reise & Ax 1979; Alongi & Tietjen 1980; Dittmann 1993). Indeed, the exclusion could possibly lead to a decrease of oligochaetes in the cages. This kind of effect, however, was not observed in this experiment.

Procedure: As mentioned above, the two environmental factors influenced by the cage construction were % of mud (after combustion) (after one month of caging) and salinity (after three months of caging). The detailed composition of the oligochaete fauna is not known which makes it difficult to analyse the response to changes in the abiotic environment.

e) Copepod density

Bell (1980), Hoffman *et al.* (1984), and Dittmann (1993) showed a similar exclusion effect on harpacticoid copepods.

Competition: Concerning competition regulation, only juvenile crabs were mentioned to be possible competitors of copepods (Bell 1980). Their food is assumed to consist mainly of detritus, but selective grazing on single food particles has also been observed (Marcotte 1984 in Hicks & Coull 1983).

Predation: Reise (1979) and Webb & Parsons (1991) believed that predation has little or no influence. Still, Hoffman *et al.* (1984) and Dittmann (1993) proposed that it was mainly predation by epibenthos (such as crabs) that influenced the copepod numbers. The late effect in this study (only after one year) accords with the study of Bell (1980) who found only an effect on copepods after an exclusion during nine months. Hicks & Coull (1983) thought that, especially for muddy or detrital substrata, juvenile fishes are primary predators on harpacticoids. They were also excluded in this experiment. Hicks & Coull (1983), Gee (1989), and Giere (1993) mentioned that, whereas nematodes and oligochaetes are certainly important in remineralization of organic matter and may be food items for epibenthic deposit-feeders, copepods seem to be the major taxon in terms of fish food and/or biomass transfer to the demersal-pelagic realm.

Bioturbation: Sediment reworking activities (Bell & Coull 1978; Reise 1979; Webb & Parsons 1991; Olafsson & Moore 1992) were postulated to be an alternative structuring force. This experiment did not reveal this kind of effects.

f) Other taxa densities

In contrast with this study where there is no effect on polychaetes, Bell (1980) and Hoffman *et al.* (1984) mentioned a significant increase. The absence of an effect on polychaetes led to the question whether our experimental design was adequate to detect possible effects in the first place. Therefore, the techniques of power analysis (Cohen 1977) were employed for a *post hoc* determination of the sensitivity of our experiment. The α significance level (0.05), the degrees of freedom of the numerator of the interaction F-ratio (8), the sample size (3), and the effect size (f) permitted to estimate the power level of 6 % (average value of factorial and mixed design) via power tables provided by Cohen (1977) (table 4.5). Such a low power value was also common in subtidal caging experiments and it severly limits the detection power of effects on polychaetes (Hall *et al.* 1990c). The same can be concluded for effects on ostracod (13.5 %), halacaroid (9 %), and kinorhynch (11 %) numbers (average value of factorial and mixed design) (table 4.5).

taxon		MS_{effect}	MS_{error}	η^2	f	power
Halacaroidea	factorial	0.203772	0.193047	0.01	0.101	6 %
	mixed	0.203772	0.134060	0.08	0.295	12 %
Kinorhyncha	factorial	52.1420	40.53983	0.05	0.229	10 %
	mixed	52.1420	32.96264	0.09	0.314	12 %
Ostracoda	factorial	1465.412	959.209	0.09	0.314	12 %
	mixed	1465.412	900.486	0.1	0.333	15 %
Polychaeta	factorial	3.115584	2.917173	0.01	0.101	6 %
	mixed	3.115584	2.772387	0.02	0.143	6 %

Table 4.5 : The power and the effect size (f) per meiobenthic taxon with the 'interaction' variance (MS_{effect}), the 'error' variance (MS_{error}) and the estimated magnitude of treatments (η^2) *(calculated via tables and formulas provided by Cohen 1977) (Ceriops tagal).*

g) Conclusion

Exclusion of all epibenthos from a *Ceriops tagal* mangrove sediment clearly influenced the nematode, oligochaete, and copepod densities, *i.e.* the dominant part of the total meiobenthos. The excluded permanent epibenthos was dominated by detritivores. The absence of this epibenthos led to an increase of muddy detritus and microalgae in the surface layer. This was accompanied by a higher abundance of diatom feeding nematodes (type 2A) and oligochaetes and a subsequent increase of predatory nematodes (type 2B). Eventually, it brought the system to a new equilibrium. The structure of the meiofaunal community is not only regulated by the physical environment, but mainly by biological, competitive interactions with the epibenthos. These findings indicate the meiofaunal community of mangrove sediments to be part of an isolated, detrital food web with only minor predator-prey interactions with the epibenthos. In order to further generalize this statement for other zones, the same research was carried out in the *Avicennia marina* forest.

V. INFLUENCE OF EPIBENTHOS ON MEIOBENTHOS IN THE *AVICENNIA MARINA* FOREST

A. INTRODUCTION

The role of the meiobenthos in a Kenyan *Ceriops tagal* mangrove vegetation zone was the subject of Chapter IV. The manipulative exclusion experiment allowed to trace possible interactions between the epibenthos on the one hand and the total or specific meiofauna on the other hand. It was expected that isolated and internally regulated meiofaunal communities would be mainly affected by competition with the epibenthos (Dye & Lasiak 1986; Alongi 1989). Meiofauna that are consumed by this epibenthos, however, were believed to be more predator controlled (Bell 1980; Hoffman *et al.* 1984; Alongi 1989; Dittmann 1993). The experimental results indicated the studied meiofaunal community to be rather part of a detrital food web with only minor predator-prey interactions with the epibenthos. This contrasted with most experiments performed in the intertidal zone of temperate areas, indicating that meiofaunal communities are mainly structured by predation and disturbance by the macro-epifauna (Bell & Coull 1978; Buzas 1978; Nichols & Robertson 1979; Reise 1979; Scherer & Reise 1981; Warwick *et al.* 1982; Fitzhugh & Fleeger 1985; Smith & Coull 1987; Palmer 1988; Wilson 1991).

The present study attempts to affirm this statement on meiofauna/macro-epifauna interactions for the *Avicennia marina* vegetation zone of the same area. The *Avicennia marina* vegetation zone differs significantly from *Ceriops tagal*. It is situated much higher in the intertidal zone and flooded only during spring tide (invaded by less visiting fauna). The forest floor is richer in detritus. The forest and tree morphology is denser. Moreover, in the epifaunal crab community *Uca lactea annulipes* (deposit feeding) is entirely replaced by *Sesarma meinerti* (vegetarian). The crab *Sesarma guttatum* and the hermit crab *Clibanarius longitarsus* are totally absent.

By means of the exclusion experiment, this study attempts to answer the following questions: Is the epibenthos structurally controlling the meiofauna in an *Avicennia marina* vegetation zone ? If this control exists, is it competitive, predatory, or bioturbational ? And to what extent can this control be distinguished from the one detected for the *Ceriops tagal* vegetation zone ?

B. MATERIAL AND METHODS

The study area, the quantification of environmental and biotic factors, the experimental and statistical design, and the statistical analysis have been accurately described in Chapter III.
For this subresearch in particular, seven series of samples were taken over time in the three treatments of the *Avicennia marina* experimental station:

- period 1: before caging (6/8/92) (env/meio/nema)
- period 2: after 22 caging days (28/8/92) (env/meio)
- period 3: after 50 caging days (25/9/92) (env/meio/nema)
- period 4: after 85 caging days (30/10/92) (env)
- period 5: after 112 caging days (26/11/92) (env)
- period 6: after 139 caging days (23/12/92) (env/meio/nema)
- period end: after 358 caging days (30/7/93) (meio/nema)

Major meiobenthic taxa: These biotic factors were analysed using a 3 x 5 (between groups) factorial ANOVA design with treatments (3) and periods (5) as groups. Additionally, a 3 (between groups) x 5 (within subjects) mixed ANOVA design was applied with treatments (3) as groups and periods (5) as subjects repeated over time.

Both designs analysed only the upper 2 cm layer, since significant effects in Chapter IV were found to be restricted to this slice. Ostracods and kinorhynchs were treated in the nonparametric Kruskal Wallis and Median tests since the ANOVA assumptions were not met.

Environmental factors: Effects on environmental factors in the upper sediment layer were detected using a 3 x 6 (between groups) factorial ANOVA design and a 3 (between groups) x 6 (within subjects) mixed ANOVA design with treatments (3) as groups and periods (6) as subjects repeated over time.

Nematode genera: Significant effects on the nematode genera were analysed via a 3 x 4 (between groups) factorial ANOVA design and a 3 (between groups) x 4 (within subjects) mixed ANOVA design with treatments (3) as groups and periods (4) as subjects repeated over time. The analysis was limited to the upper sediment layer.

C. RESULTS

1. Meiofaunal composition

Figure 5.1 presents the relative abundance of the major meiobenthic taxa, the nematode feeding types, and the dominant and significantly affected nematode genera for the blank sites. The dominant Nematoda (93 %) were followed by Oligochaeta (2 %), Rotifera (2 %), Copepoda (1 %), Turbellaria (1 %) and Halacaroidea (1 %). The other taxa were very rare (< 1 %). The nematodes consisted mainly of epistrate feeders (2A) (59 %) and omnivores/predators (2B) (29 %). The different feeding types (1A, 1B, 2A, and 2B) were respectively dominated by the genera *Haliplectus* (55 %), *Daptonema* (28 %), *Desmodora* (59 %) and *Chromaspirina* (44 %).

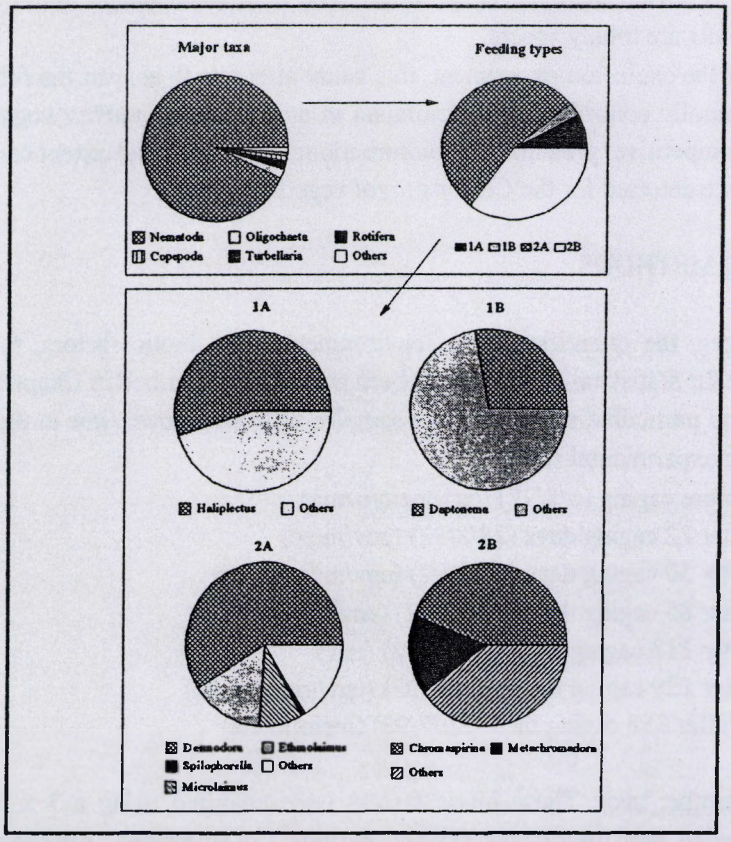


Figure 5.1: Relative abundance (%) of the major meiobenthic taxa and the nematode feeding types, and the dominant and significantly affected genera in the blank sites *(Avicennia marina)*.

2. Epibenthic composition

Four different resident epibenthic animals have been identified in the studied mangrove zone (table 5.1). The non-selective deposit feeding gastropods *Terebralia palustris* and *Cerithidea decollata* were dominant. It is especially
Terebralia palustris that exhibits a conspicuous influence due to its high abundance and its sediment dwelling behaviour. The crab *Sesarma meinerti*, more than *Metopograpsus thukuhar*, is expected to show a great impact. It continuously feeds on *Avicennia* leaves and never occurs on trunks or roots.

The visiting, natant epifauna (hyperbenthos and fishes) have not been identified or quantified, but are believed not to be abundant in this mangrove zone.

epibenthic species	**author**	**feeding behaviour**	**habitat**	**average density (ind./m²) (this study)**
Cerithidea decollata	Brown 1971 McIntosh 1984 Dye & Lasiak 1987	non-selective deposit feeding (detritus)	frequently on trees	57
Terebralia p-alustris	Dye & Lasiak 1987	non-selective deposit feeding (inorganic parts, microalgae, bacteria, protozoans)	sediment dwelling	36
Sesarma meinerti	Cott 1929	vegetarian	sediment dwelling	0.25 (1 burrow per m²)
	Emmerson & M-cGwynne 1992 Steinke *et al.* 1993 Micheli *et al.* 1991	omnivorous with preference for leaves (75% of diet)		
Metopograpsus thukuhar	Dahdouh-Guebas (pers. comm.) McIntosh 1988	omnivorous with preference for macroalgae and animal items (sometimes fresh leaves, seedlings, leaf litter and detritus)	forest dweller (trunk, roots, floor)	1
visiting fauna (unknown)	?	herbivorous or carnivorous ?	high tidal (only during spring tides)	?

Table 5.1: Description of permanent and visiting epibenthos excluded from the cages in the studied *Avicennia marina* zone (in terms of average densities, feeding behaviour, and habitat).

3. Experimental results

Mean values with indication of standard deviation of the reported variables are shown in figures 5.2, 5.3, 5.4, 5.5, 5.6, and 5.7.

a) Major meiobenthic taxa

Exclusion effect: The oligochaete density was subjected to a clear significant exclusion effect after five months and one whole year of caging (figure 5.2). The increase of the density of this taxon was about 4 x more for the cages compared to the other treatments. It was the only biotic exclusion effect on larger taxa detected in this study.

Procedural effect: A significant global procedural effect was observed for the nematode density (figure 5.2). This density showed an increase of about 2-3 x in the partial cage and cage treatments as compared to the blank units after five months.

No effect: The copepods, polychaetes, ostracods, halacaroids, turbellarians, and kinorhynchs did not show any effects for the upper slice. Since the ostracod and kinorhynch densities did not meet the ANOVA assumptions, they were analysed using the non-parametric Kruskal Wallis and Median tests. The copepod numbers are presented in figure 5.2.

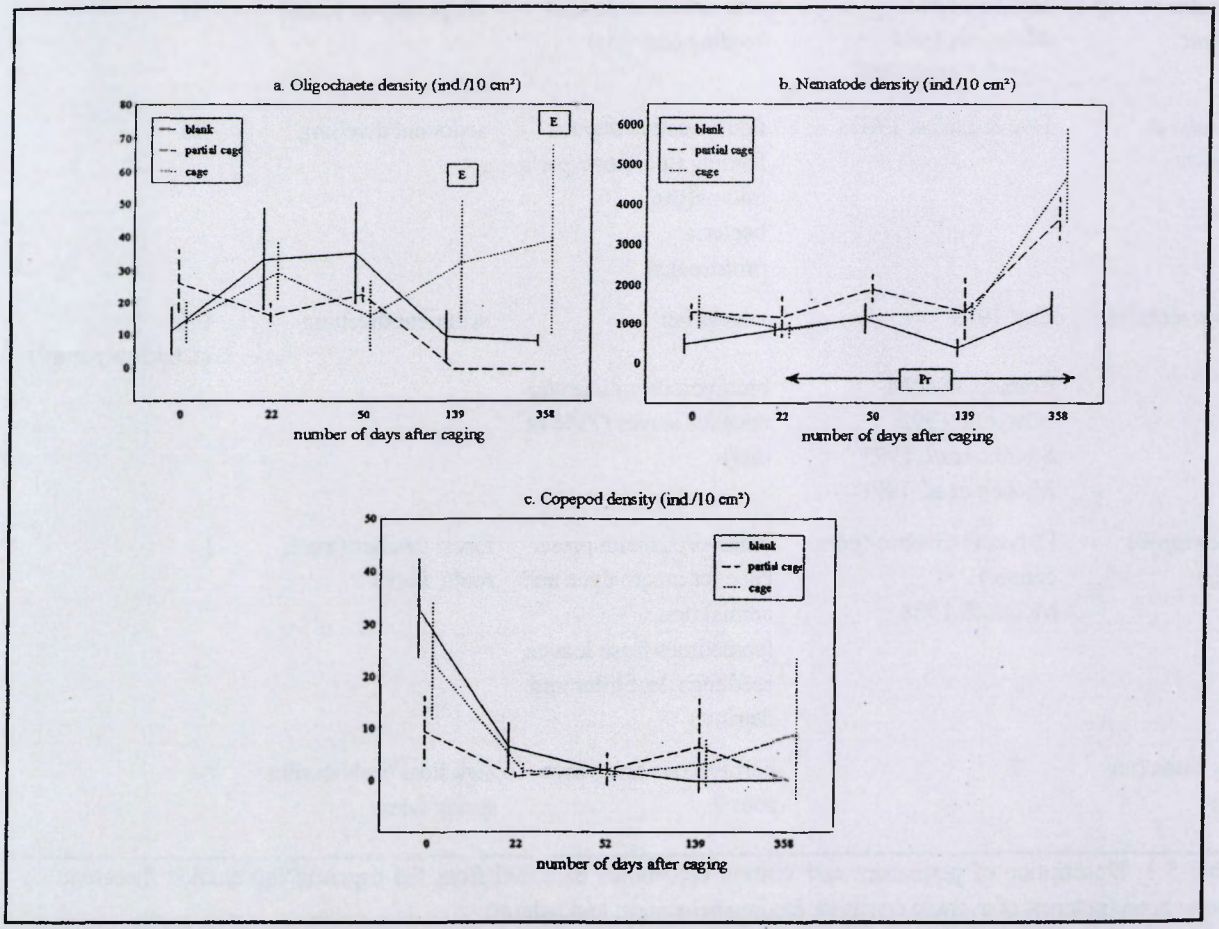


Figure 5.2: Oligochaete, nematode, and copepod densities (ind./10 cm²) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper slice over time (E = significant exclusion effect with $p < 0.05$; Pr = significant procedural effect with $p < 0.05$) *(Avicennia marina)*.

b) Nematode genera and feeding guilds

Selective (1A) and non-selective (1B) deposit feeders: Neither the feeding guilds as a whole nor the specific 1A and 1B genera showed an effect. Their contribution to the total nematode density, however, was only minor (figure 5.1).

Epistrate feeders (2A) (figure 5.3): The microalgae grazing nematodes as a group indicated a conspicuous, significant procedural effect over the whole experimental period. This coincided with a similar effect on the global nematode community. It is probably linked with the procedural effect as detected for the genera *Microlaimus* and *Spilophorella*. *Microlaimus* is one of the dominant 2A genera (figure 5.1). Another dominant 2A genus (*Ethmolaimus*) (figure 5.1), however, revealed an underlying important impact. It was forced to undergo a significant ($p < 0.01$) exclusion effect after two months of caging. Its density increased particularly in the cage when compared to the others. This followed the same trend than was found for the concentration of chlorophyll *a*.

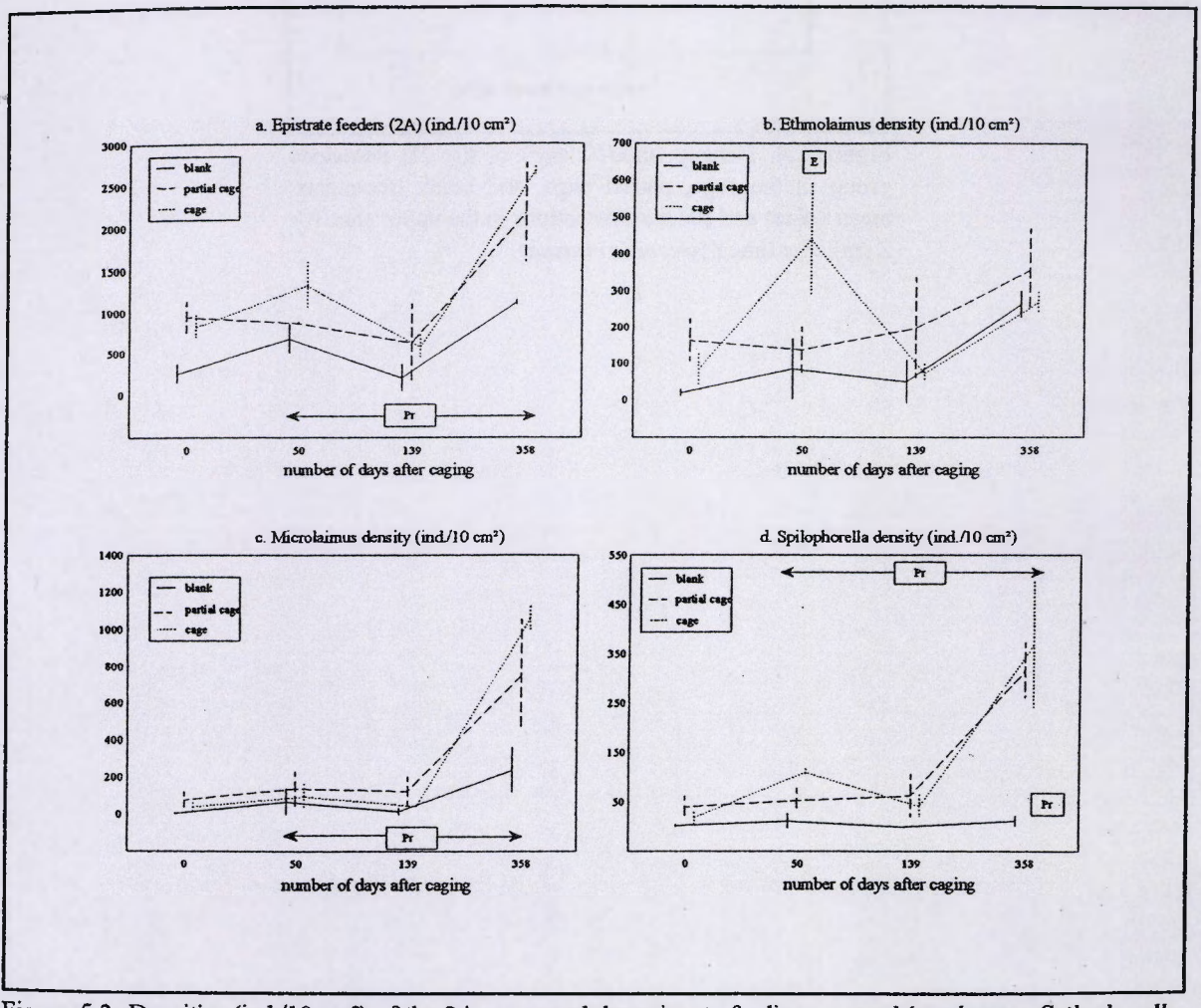


Figure 5.3: Densities (ind./10 cm²) of the 2A group and the epistrate feeding genera *Microlaimus*, *Spilophorella*, and *Ethmolaimus* in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper slice (0-2 cm) over time (E = significant effect with $p < 0.05$; Pr = procedural effect with $p < 0.05$) *(Avicennia marina)*.

Omnivores and predators (2B) (figure 5.4): Neither the feeding guild as a whole nor the specific 2B genera showed an effect. Nevertheless, this group appeared to be the second most abundant (figure 5.1).

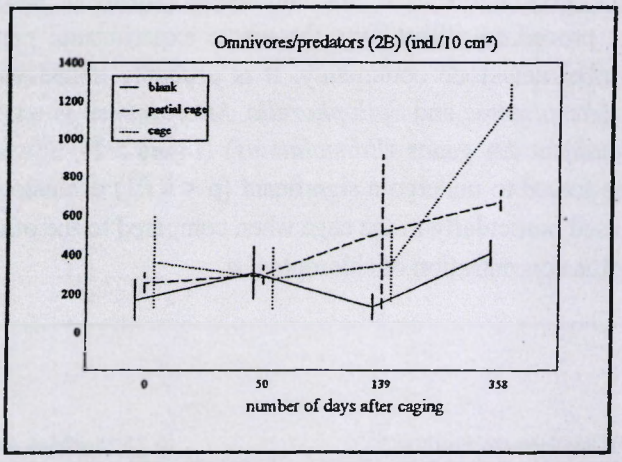


Figure 5.4: Density (ind./10 cm²) of the 2B nematode group in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper slice (0-2 cm) over time *(Avicennia marina)*.

c) Environmental factors

Exclusion effect: The median grain size before combustion (negatively correlated with the % of mud before combustion) underwent a slight significant exclusion effect after 112 days of caging, showing a 1.5 x decrease in the cages compared to the partial cage and blank treatments (figure 5.5). This reveals a slight increase of the muddy detrital fraction since a decrease of the median after combustion was significantly evidenced for both the cages and partial cages in the same period.
The concentration of chlorophyll *a* indicated a highly significant ($p < 0.01$) exclusion effect after 50 days of caging. The increase was 5 x higher in the cage compared to the other treatments (figure 5.5).

Procedural effect: As a result of the cage and partial cage construction, the treated sediment experienced a salinity decrease reflected as a procedural effect after 22 days of caging (figure 5.6).
Both statistical designs (factorial and mixed) indicated a procedural treatment effect for pH, with a more acidic sediment in the blank units throughout the experiment (figure 5.6).

The median grain size after combustion (which is in general negatively correlated with the inorganic muddy fraction) showed a decrease in the cages and partial cages as compared to the blanks. This led to a procedural effect after 112 days (figure 5.7).

A possible procedural impact on redox potential could not be detected since practical problems made it impossible to measure this variable during the first two periods.

No effect: No clear effect on all other factors was detected (including the % of POM and the % of organicarbon).

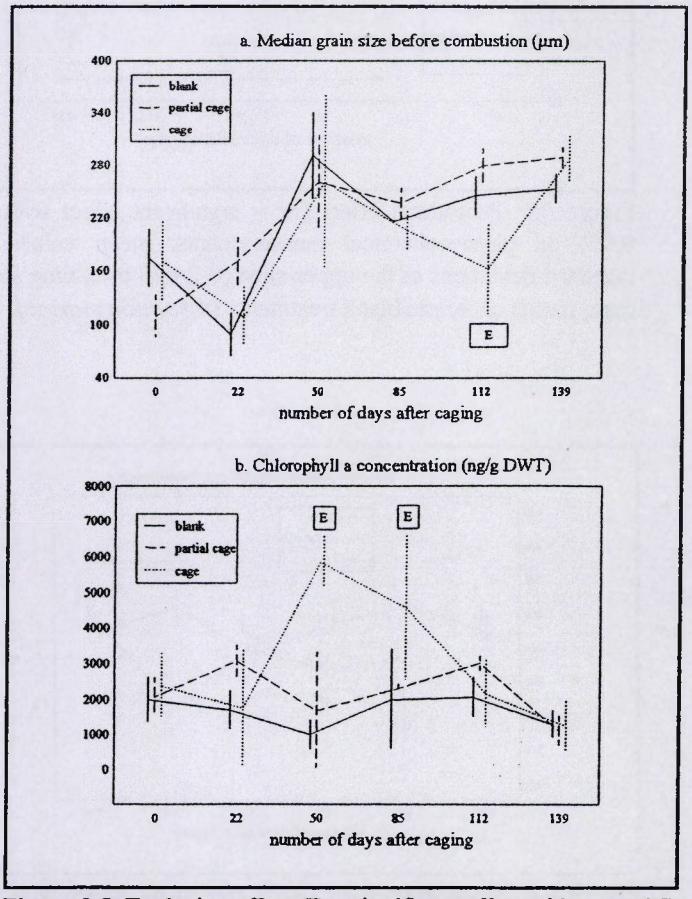


Figure 5.5: Exclusion effect (E = significant effect with $p < 0.05$) on environmental measurements: mean values and standard deviations in the upper slice (0-2 cm) over time for the cage, partial cage, and blank treatments *(Avicennia marina)*.

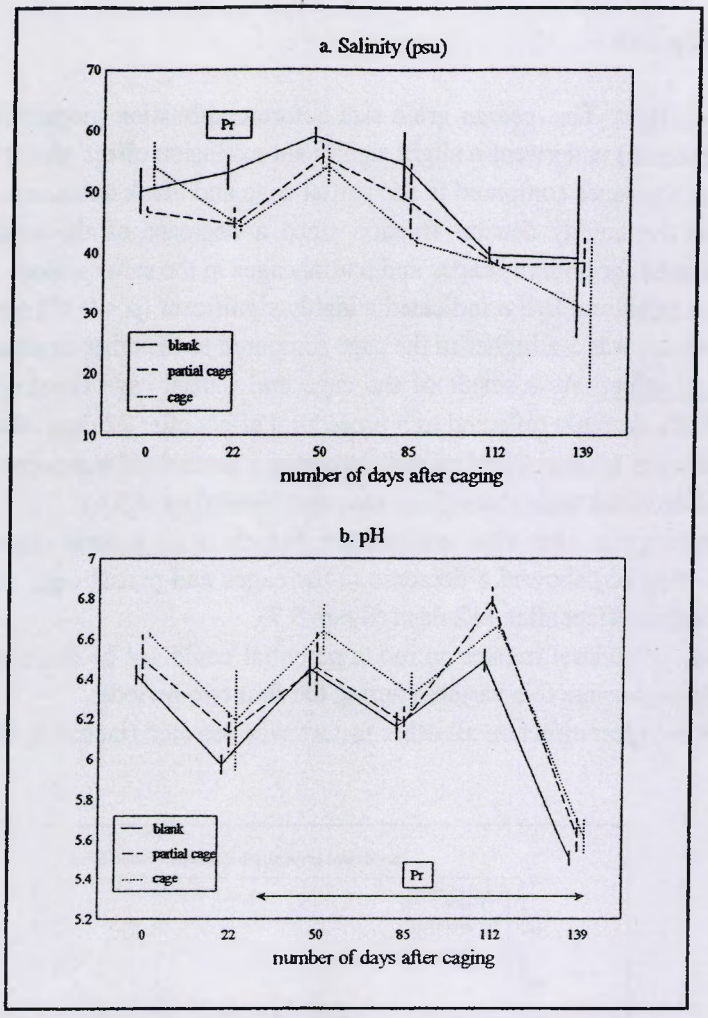


Figure 5.6: Procedural effect (Pr = significant effect with $p < 0.05$) on physicochemical measurements: mean values and standard deviations of the upper slice (0-2 cm) over time for the cage, partial cage, and blank treatments *(Avicennia marina)*.

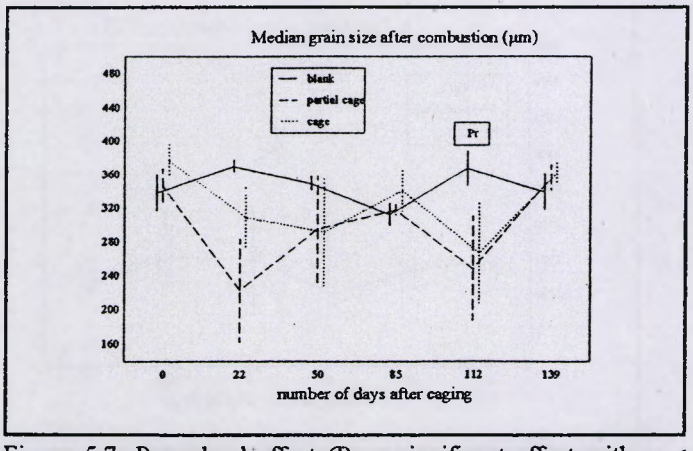


Figure 5.7: Procedural effect (Pr = significant effect with $p < 0.05$) on granulometric measurements: mean values and standard deviations in the upper slice (0-2 cm) over time for the cage, partial cage, and blank treatments *(Avicennia marina)*.

D. DISCUSSION

1. Experimental material and methods

The evaluation and discussion of the used material and methods concerning study site, quantification of environmental and biotic factors, experimental and statistical design, and statistical analysis have been accurately expounded in Chapter III.

2. Experimental results

a) Procedural effects

Possible artefacts and procedural effects (Hairston 1990) were taken into account by a detailed protocol in the field (table 5.2) and by using a randomized block design with procedure controls (Hurlbert 1984). The most obvious procedural effect in this study was displayed by the nematodes. However, this was probably due to the effect on *Spilophorella* and *Microlaimus* of which the latter is one of the dominant 2A genera.

	after 1 month of caging			**after 5 months of caging**			**evaluation**
	B	**C**	**P**	**B**	**C**	**P**	
fouling	-	-	-	-	-	-	OK
shading	-	+	±	-	+	±	± procedural
sedimentation	-	-	-	-	-	-	OK
moisture	-	+	+	-	+	+	procedural
litter fall	+	-	-	+	-	-	OK
epibenthos	+	-	+	+	-	+	OK

Table 5.2 : Qualitative observations (- = absent, + = present, and ± = intermediate) after one and five months of caging with an evaluation of the procedure (*(Avicennia marina)*.

Only the salinity and the median after combustion underwent an underlying environmental procedural influence. A decrease of salinity due to the cage construction might have been caused by the PVC plates anchoring the cage to the soil or by shading effects (cage top). Both kept the sediment less dry as compared to the blank units. Several studies showed that mud and detritus deposition can be due to procedural effects in exclusion cages (Virnstein 1977; Hulberg & Oliver 1980; Woodin 1981; Menge *et al.* 1986), probably as a result of increased water stagnation. This effect can possibly attract or repel certain infaunal species (Hulberg & Oliver 1980; Heip *et al.* 1985). In this study, a decrease of the median grain size of the inorganic sediment fraction indicated a shift to a slightly siltier condition due to the cage construction (after 112 days).

b) Resource competition

No quantitative studies on the resident, bottom-dwelling epifauna of Gazi mangroves are available. Only some qualitative results and personal observation give an insight in the occurrence and composition. This study thus offers the first quantitative results of the resident epifauna under *Avicennia* mangroves of Gazi. Until now, only one quantitative study on the natant epifauna visiting Gazi mangrove forests has been published (van der Velde *et al.* 1995). This part of the epibenthos therefore remains an unknown factor.

The dominant epibenthos of the *Avicennia marina* mangal forest floor (table 5.1) was found to comprise mainly detritivorous, non-selective deposit feeding gastropods (*Cerithidea decollata* and *Terebralia palustris*), and almost exclusively vegetarian crabs (*Sesarma meinerti* and *Metopograpsus thukuhar*). In the studied area, these species were represented by 57, 36, 0.25, and 1 ind./m^2 respectively. As mentioned before, the demersal and hyperbenthic fauna are not abundant in this mangrove zone. Any effects of the epibenthos on meiobenthic community structure (especially oligochaetes and nematodes) are therefore likely to result mainly from modifications in the food resources on which the meiofauna also depend (Cameron 1966 in Warwick *et al.* 1990). The only comparable study mentioning this resource competition as a possible control was conducted by Dye & Lasiak (1986).

Also for this study, there is evidence of a competitive rather than a predatory control by the epibenthos. The exclusion effect on oligochaetes responded, with a time lag of about one month, to the slight increase on muddy detritus, normally fed on by gastropods and crabs. Giere & Pfannkuche (1982) indicated this detritus and its associated bacterial community to be an important food source for oligochaetes.

Concerning nematodes, the specific and strong exclusion effect on the dominant epistrate feeding nematode genus *Ethmolaimus* coincided with the conspicuous increase of chlorophyll *a*. As mentioned above similar exclusion effects on other 2A genera might have been suppressed by a global procedural effect (figure 5.3). The increase of *Ethmolaimus* can most probably be ascribed to the exclusion of microalgae feeding gastropods. The lack of any effect on other 2A genera was likely due to possible artefacts and procedural effects during the experiment. They might have compensated or covered an underlying exclusion effect. Between 50 and 85 days after caging, a sudden decline in the concentration of chlorophyll *a* and the density of *Ethmolaimus* to their former level was observed.

c) Predation

Does this mean that epibenthic predation exhibits no regulating effect on the studied meiofaunal community at all ?

Until now, most comparable studies (Bell 1980; Hoffman *et al.* 1984; Dittmann 1993) mentioned the meiobenthic structure to be mainly influenced by predation from the macro-epifauna. No evidence for this, however, is provided here. Although the oligochaete community experienced a global increase due to exclusion, this is believed not to be caused by the absence of predation. Oligochaetes were mentioned by Giere (1993) to be prey of small fishes. As the *Avicennia marina* zone is situated in the upper intertidal zone and not frequently flooded, the impact of these animals is not believed to be of major importance. Moreover, the observed densities of demersal and hyperbenthic animals appeared to be very low during high tide (personal observation). The more abundant resident epibenthic animals have not been reported to feed on oligochaetes (table 5.1).

The low hyperbenthic and demersal impact might also be an explanation for the lack of any effect on copepods. Indeed, this was precisely the sole taxon believed to be under predatory influence in Chapter IV.

It is the motility, visibility, and epibenthic lifestyle in muddy sediments (Giere 1993; Nelson & Coull 1989) that makes copepods a selective prey of shrimp (Reise 1979; Pihl & Rosenberg 1984; Gee *et al.* 1985) and juvenile fishes (Gee 1989; Nelson & Coull 1989).

Passive or active predation on nematodes would lead to a global exclusion effect (Hoffman *et al.* 1984; Bell & Coull 1978; Dittmann 1993). Any disproportionate increase in some genera would indicate a rather competitive release (Grassle & Sander 1973 in Hall *et al.* 1991). The procedural effect on nematodes was indeed a combination of procedural and exclusion effects on different genera or groups of genera. This makes the predatory influence to be of minor importance for nematodes as well.

d) No effect

Besides copepods, polychaetes, kinorhynchs, halacaroids, turbellarians and ostracods did not show any effect either. The α significance level (0.05), the degrees of freedom of the numerator of the interaction F-ratio (8), the sample size (3), and the effect size (f) resulted in power levels of 8 % for turbellarians, 7.5 % for polychaetes and ostracods, and 7 % for halacaroids (average power for factorial and mixed design) (Hall *et al.* 1990c). The effect size per taxon was calculated via the ANOVA-variances, the number of degrees of freedom (8), of interaction groups (15) and of replicates within a group (3) (table 5.3). The power levels point to the chance of avoiding a type II error ($1-\beta$) and were calculated via the power table provided by Cohen (1977) (Chapter III). The power could not be calculated for copepods and kinorhynchs because these taxa were analysed via nonparametric tests. The low level for polychaetes could possibly explain an undetectable predatory influence. Olafsson & Moore (1990) stated that polychaetes are mainly preyed on by larger animals. This could indicate that effects become perceptable only after separate exclusion of the larger epibenthos.

taxon		MS_{effect}	MS_{error}	η^2	f	power
Turbellaria	factorial	0.615209	0.479607	0.01	0.101	6 %
	mixed	0.615209	0.488495	0.05	0.229	10 %
Polychaeta	facorial	0.105525	0.135925	0.0008	0.05	5 %
	mixed	0.105525	0.151205	0.05	0.229	10 %
Ostracoda	factorial	0.070451	0.119511	0.0011	0.05	5 %
	mixed	0.072451	0.118765	0.07	0.274	10 %
Halacaroidea	factorial	0.424692	0.596024	0.02	0.143	6 %
	mixed	0.424692	0.572790	0.04	0.204	8 %

Table 5.3 : The power and the effect size (f) per taxon with the 'interaction' variance (MS_{effect}), the 'error' variance (MS_{error}) and the estimated magnitude of treatments (η^2) *(calculated via tables and formulas provided by Cohen 1977) (Avicennia marina).*

e) Conclusion

One can conclude that this study indicates that the *Avicennia marina* meiobenthos is mainly under exploitative or resource competitive influence of the epibenthos (for detritus and microalgae). This was also concluded for the *Ceriops tagal* meiobenthos of the same region (Chapter IV). The use of the meiobenthos as prey for epibenthic predators, however, is not touched upon. A slight predation pressure, exhibited by natant epibenthic predators, might be present, albeit covered by the stronger food competitive forces caused by the resident epifauna.

Consequently, it can be stated that the role of the meiobenthos in these East African mangrove sediments is mainly situated in an isolated, detrital and microalgal food web with only minor energy fluxes to the epibenthos. The absence of any effect on the predatory nematodes (2B) shows that the driving force for an internal regulation still has to be found. The impact of epibenthos on meiofauna might indeed be further complicated by multilevel interactions with the infaunal macrobenthos.

VI. INFLUENCE OF EPIBENTHOS ON MACROBENTHOS IN THE *AVICENNIA MARINA* FOREST

A. INTRODUCTION

Exclusion experiments are a valuable tool to detect the influence of epibenthic animals on macroendobenthic communities. Most studies have been conducted in temperate intertidal, soft, and unvegetated areas (Reise 1977; Reise 1978; Scherer & Reise 1981; Kent & Day 1983; Ambrose 1984; Fitzhugh & Fleeger 1985; Raffaelli *et al.* 1989; Trush *et al.* 1994), soft seagrass covered coastal zones (Young *et al.* 1976; Reise 1977; Reise 1978; Nelson 1981; Summerson & Peterson 1984), or salt marshes (Vince *et al.* 1976; Van Dolah 1978; Kneib & Stiven 1982; Ward & Fitzgerald 1983; Frid & James 1988; Kneib 1988; Haase 1993). In general, predation was accepted as the obvious epibenthic influence on the macro and meiofauna. About half of the studies excluding large epibenthic predators, mentioned an at least twofold increase in total endobenthic prey abundance (Reise 1985).

Mangrove areas are soft vegetation-covered zones characteristic for tropical coasts. They are frequently mentioned to be intensively used by epibenthic animals as feeding grounds, nursery areas, and shelters (Hutchings & Saenger 1987). In order to assess the importance of the endobenthic community under the mangrove trees as a food source, exclusion experiments were conducted in a Kenyan *Avicennia marina* stand. Detection of epibenthic predation in such a high intertidal zone would indicate the mangrove forest floor, and not only the creeks and flats surrounding it, to be of importance as feeding ground for the epibenthos.

The few exclusion studies that have been conducted in mangroves mainly focussed on the meiobenthos (Dye & Lasiak 1986; Alongi 1989; Dittmann 1993; Chapters IV and V) leaving the macrobenthos as an interesting endobenthic category to be studied.

When dealing with high intertidal *Avicennia* sediments, the impact of the permanent epibenthos can be expected to be more important than that of the visiting fauna. These resident organisms are mainly leaf shredders and selective or non-selective deposit feeders (crabs and gastropods). It is hypothesized that exclusion of the epibenthos would therefore rather result in:

(1) Leaf accumulation, favouring infaunal leaf shredders

(2) Accumulation of detritus, bacteria, protozoans, and microalgae favouring infaunal deposit feeders

B. MATERIAL AND METHODS

The study area, the quantification of environmental and biotic factors, the experimental and statistical design, and the statistical analysis have been accurately described in Chapter III.
For this subresearch in particular, six series of samples were taken over time in the three treatments of the *Avicennia marina* experimental site:

- period 1: before caging (6/8/92) (env/macro)
- period 2: after 22 caging days (28/8/92) (env/macro)
- period 3: after 50 caging days (25/9/92) (env/macro)
- period 4: after 85 caging days (30/10/92) (env/macro)
- period 5: after 112 caging days (26/11/92) (env/macro)
- period 6: after 139 caging days (23/12/92) (env/macro)

Macrobenthic taxa: These biotic factors were analysed using a 3 x 6 (between groups) factorial ANOVA design with treatments (3) and periods (6) as groups. Additionally, a 3 (between groups) x 6 (within subjects) mixed ANOVA design was applied with treatments (3) as groups and periods (6) as subjects repeated over time. Only the upper 2 cm layer was analysed.

Since the oligochaete families Tubificidae and Enchytraeidae did not meet the ANOVA assumptions, the non-parametric Kruskal Wallis and Median tests were used.

At one occasion, the Least Significant Difference test (LSD) (Sokal & Rohlf 1995) was used in order to detect initial unit differences for amphipods.

Environmental factors: Effects on environmental factors of the upper sediment layer were detected using a 3 x 6 (between groups) factorial ANOVA design and a 3 (between groups) x 6 (within subjects) mixed ANOVA design with treatments (3) as groups and periods (6) as subjects repeated over time.

C. RESULTS

1. Endobenthic composition

The endobenthos was composed of the following taxa:

Oligochaeta: families Tubificidae (mainly *Ainudrilus* spec.) and Enchytraeidae (mainly *Marionina* spec.) (Erseus, personal communication)

Insect larvae: mainly family Dolichopodidae (Goddeeris, personal communication)

Amphipoda: family Grandidierellidae (*Grandidierella* spec.) (De Grave, personal communication)

Polychaeta: families Nereidae (*Namalycastis* spec.) and Opheliidae (*Armandia* spec.) (Day 1967)

Nematoda: family Oncholaimidae (mainly *Oncholaimus* spec.) (Platt & Warwick 1988)

Gastropoda

Cnidaria

While comparisons between temperate and tropical regions usually reveal a higher benthic diversity in the latter, the number of taxa in this mangrove study was low. This probably reflects the high intertidal position of the sampling site, resulting in extreme anaerobic conditions with abrupt changes in salinity, temperature, redox, and DO_2 (Tietjen & Alongi 1990).

The overall macrobenthic density was 23361 ind./m². Figure 6.1 shows the relative abundance (average of all blank units over all periods) of the macrobenthic taxa. It is clear that the oligochaetes (78 % tubificids and 22 % enchytraeids) made up the largest part of the macrobenthic infauna (94 %). Within the remaining 6 %, the amphipod *Grandidierella* spec. (56 %) dominated. It was followed by the polychaete genus *Namalycastis* spec. (21 %), gastropods (10.7 %), macrobenthic nematodes (7 %), insect larvae (5 %), and cnidarians (0.3 %). The polychaete *Armandia* spec. was found only in the sediment of a single cage unit after 112 days.

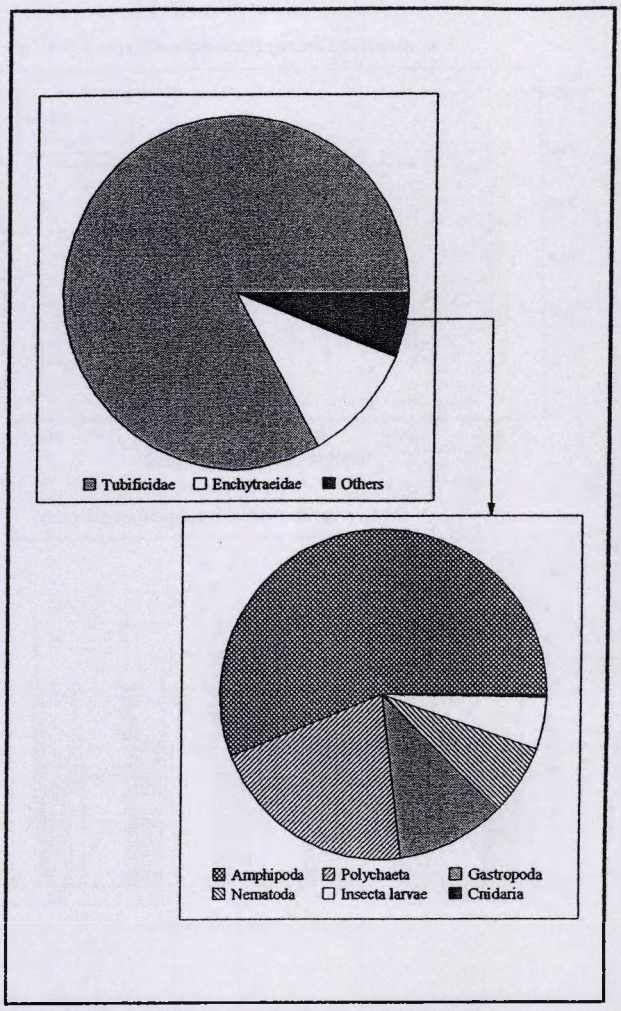


Figure 6.1: Relative abundance (%) of the major macrobenthic infaunal taxa and oligochaete families (average of blank sites over all periods) *(Avicennia marina)*.

2. Epibenthic composition (see table 5.1)

3. Experimental results

a) Biotic factors

Exclusion effect: Cage amphipod densities exceeded those of partial cage and blank sediment from the 85th day of the experiment onwards (with a factor of 4 to 5). This increase was confirmed by an overall significant exclusion effect (figure 6.2). The average individual amphipod length did not differ significantly among treatments (figure 6.2).

The density of insect larvae increased significantly after 85 days. A significant exclusion effect was detected after 85 and 139 days, cage densities reaching 5 to 6 x higher levels than in the other treatments (figure 6.3).

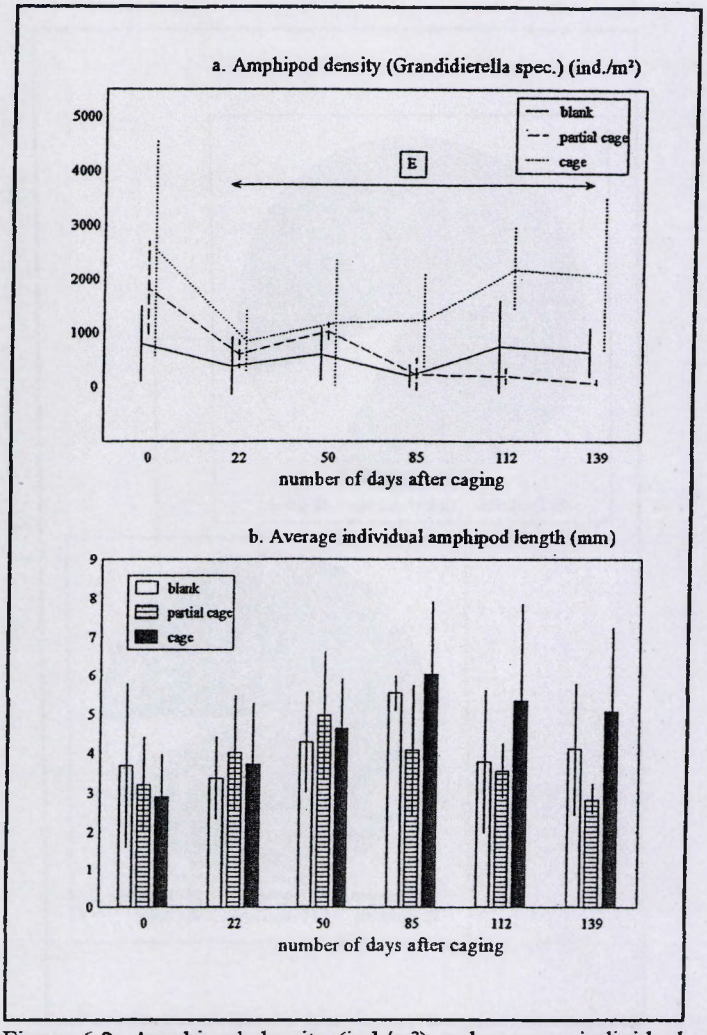


Figure 6.2: Amphipod density (ind./m²) and average individual amphipod length (mm) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper slice (0-2 cm) over time (E = significant exclusion effect with $p < 0.05$) *(Avicennia marina)*.

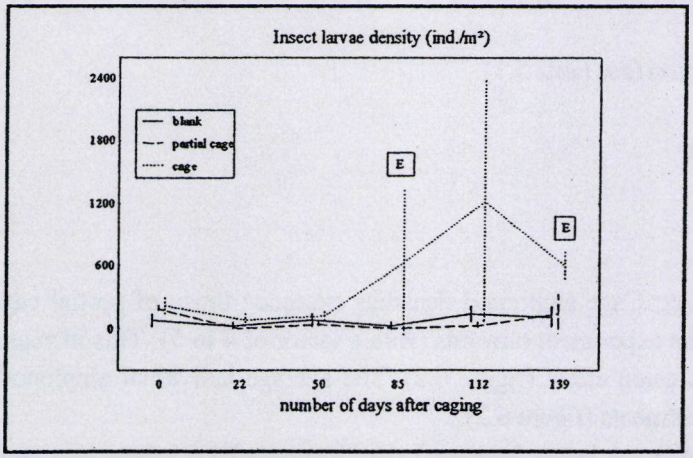


Figure 6.3: Insect larvae density (ind./m²) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper slice (0-2 cm) over time (E = significant exclusion effect with $p < 0.05$) *(Avicennia marina)*.

Procedural effect: Already after 22 days, a significant procedural effect was detected for oligochaete densities. This effect was repeated after 2 months. The cage and partial cage densities slightly surpassed the blank density (figure 6.4).

Table 6.1 shows the results of the Kruskal Wallis and Median tests on the Tubificidae and Enchytraeidae densities for periods 1, 2, and 5. Both tests did not detect any effect. Nevertheless, the Median test was suggestive of a procedural effect for the Tubificidae after 112 caging days: a significant difference ($p < 0.05$) was observed between the blank and partial cage treatment which was not detected before this period. As the oligochaetes made up 94 % of the total macro-infaunal density, trends in the total community were inextricably linked with oligochaete trends (figure 6.4).

No effect: Neither procedural nor exclusion effects were detected for polychaetes (figure 6.5), macro-nematodes (figure 6.5), gastropods or cnidarians.

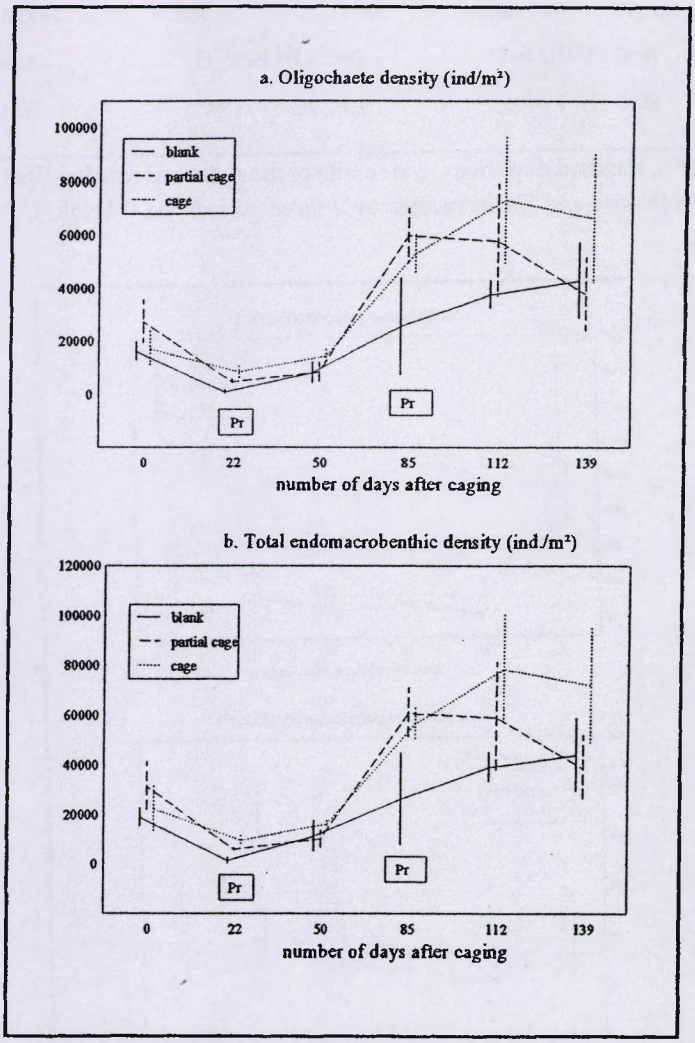


Figure 6.4: Oligochaete and total macrobenthic densities (ind./m²) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper slice (0-2 cm) over time (Pr = procedural effect with $p < 0.05$) *(Avicennia marina)*.

		before caging		22 days after caging		112 days after caging	
		mean	**stdv**	**mean**	**stdv**	**mean**	**stdv**
Tubificidae	blank	13040	2508	379	379	31928	4403
	cage	20421	828	6749	4517	52202	10322
	partial	26067	10581	2390	557	48962	10263
	Kruskal	B=C / B=P / P=C		B=C / B=P / P=C		B=C / B=P / P=C	
	Median	B≠C / B=P / P=C		B≠C / B=P / P=C		B≠C / **B≠P** / P=C	
Enchytraeidae	blank	2733	1965	800	719	9455	3834
	cage	1287	1287	1548	1432	6132	3459
	partial	2714	663	2271	738	14128	14128
	Kruskal	B=C / B=P / P=C		B=C / B=P / P=C		B=C / B=P / P=C	
	Median	B=C / B=P / P=C		B=C / B=P / P=C		B=C / B=P / P=C	

Table 6.1 : Densities (ind./m²), standard deviations, and results of the statistical Kruskal Wallis and Median tests for the oligochaete families Tubificidae and Enchytraeidae over three periods (B = blank, C = cage and P = partial cage) *(Avicennia marina)*.

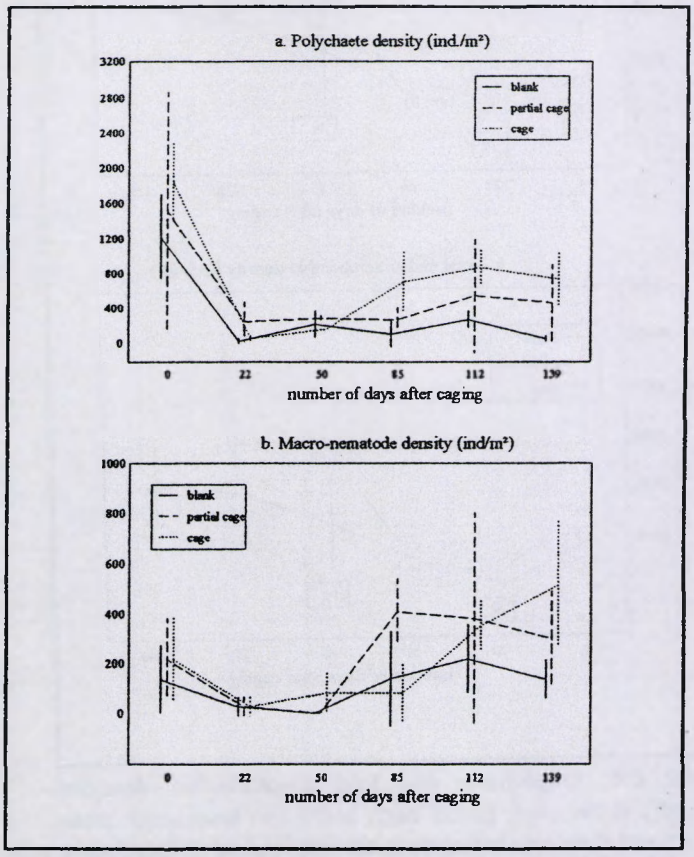


Figure 6.5: Polychaete and nematode densities (ind./m²) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper slice (0-2 cm) over time *(Avicennia marina)*.

b) Environmental factors

Exclusion effect: A highly significant exclusion effect after 50 and 85 days of caging was demonstrated for the concentration of chlorophyll *a*. It showed an increase of about 5 x in the cage as compared to the other treatments (figure 6.6).

Also, the median grain size before combustion (negatively correlated with the % of mud before combustion) underwent a significant exclusion effect after 112 days of caging, showing a 1.5 x decrease in the cages compared to the partial cage and blank treatments (figure 6.6). This effect was not found for the median after combustion and was therefore related to the muddy detritus fraction.

Procedural effect: As a result of the cage and partial cage construction, the sediment underwent a salinity decrease after 22 days of caging (figure 6.7).

ANOVA indicated a procedural treatment effect for pH, with a more acidic sediment in the blank units throughout the experiment (figure 6.7).

The median grain size after combustion (which is in general negatively correlated with the inorganic muddy fraction) showed a decrease in the cages and partial cages as compared to the blanks. This led to a procedural effect after 112 days (figure 6.8).

A possible procedural impact on the redox potential could not be detected since practical problems made it impossible to measure this variable during the first two periods.

No effect: No clear effect was detected for all other variables (including the % of POM).

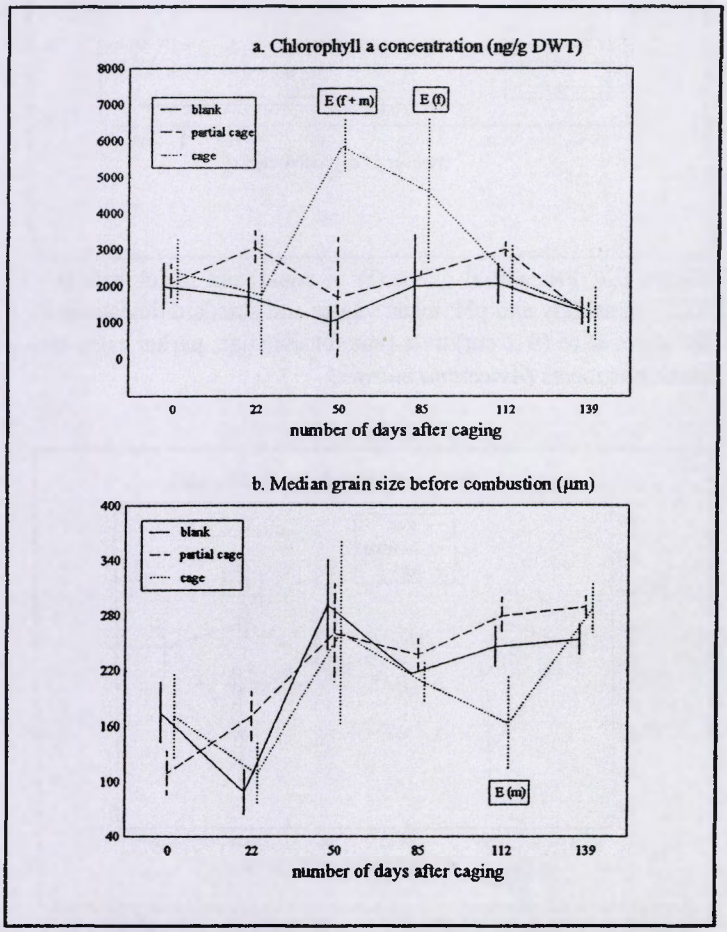


Figure 6.6: Exclusion effect (E = significant effect with $p < 0.05$) on environmental factors: mean values and standard deviations in the upper slice (0-2 cm) over time for the cage, partial cage, and blank treatments *(Avicennia marina)*.

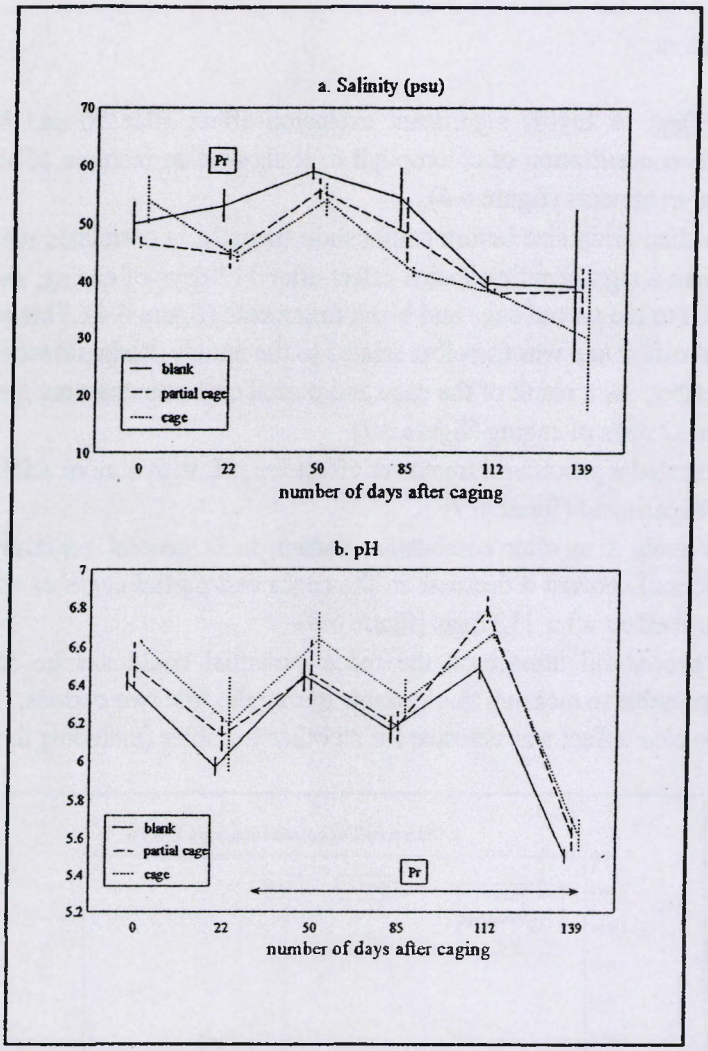


Figure 6.7: Procedural effect (Pr = significant effect with $p < 0.05$) on salinity and pH: mean values and standard deviations in the upper slice (0-2 cm) over time for the cage, partial cage, and blank treatments *(Avicennia marina)*.

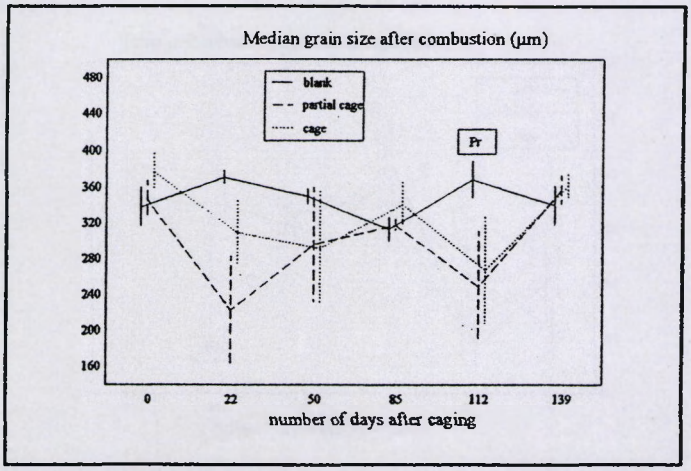


Figure 6.8: Procedural effect (Pr = significant effect with $p < 0.05$) on median after combustion: mean values and standard deviations in the upper slice (0-2 cm) over time for the cage, partial cage, and blank treatments *(Avicennia marina)*.

D. DISCUSSION

1. Experimental material and methods

The evaluation and discussion of the used material and methods concerning study site, quantification of environmental and biotic factors, experimental and statistical design, and statistical analysis have been accurately expounded in Chapter III.

2. Experimental results

a) Environmental factors

Microalgae: The clear exclusion effect on the chlorophyll *a* concentration is correlated with the density of microalgae in the sediment (Admiraal 1977; Gerdol & Hughes 1994a). The increase possibly results from the exclusion of the microalgae feeding epibenthos (see table 5.1). Microalgal growth can also be a response to a release of nutrients from previously deposited mud. This was, however, not evident from our study.

Sediment texture and detritus: Several studies showed that mud and detritus deposition can be due to procedural effects in exclusion cages (Virnstein 1977; Hulberg & Oliver 1980; Woodin 1981; Menge *et al.* 1986), probably as a result of increased water stagnation. This effect can possibly attract or repel certain infaunal species (Hulberg & Oliver 1980; Heip *et al.* 1985). In this study, a decrease of the median grain size of the inorganic sediment fraction indicated a shift to a slightly siltier condition due to the cage construction (after 112 days).

The exclusion effect on the median grain size before combustion (which is negatively correlated with the percentage of mud before combustion) suggests, however, the muddy detritus to be marginally influenced by the exclusion.

Physicochemical factors: It is obvious that the sediment of the cage and partial cage treatments became more humid through time than that of the blank treatment as a result of cage construction (PVC plates and cover) (see table 5.2). This resulted in lower salinities.

b) Biotic factors

Amphipod density: Gut content analysis of several individuals (N=10) of *Grandidierella* spec. revealed detritus and small leaf particles, originating from the mangrove sediment, to be dominant in the diet. The mangrove amphipod *Parhyale hawaiensis* was shown to consume large quantities of decomposing mangrove leaves (Poovachiranon *et al.* 1986). In general, crabs, amphipods, capitellid polychaetes, and isopods seem to be breaking down mangrove leaves in small particles, egesting it as plant detritus which thus becomes a food source for other species (Poovachiranon *et al.* 1986; Camilleri 1992).

No microalgae were observed in the stomach of *Grandidierella* spec. Gerdol & Hughes (1994b) found that microalgae were not detectable in the gut of *Corophium volutator*, although this amphipod was shown to ingest 4000 cells/h and to significantly reduce diatom densities. Moreover, Pinckney & Sandulli (1990) refer to diatoms as an important food source for many amphipods.

The exclusion effect on this genus can possibly be related to three types of interactions:

(1) Predation on amphipods: Stomach analysis of the permanent epibenthos revealed little predatory evidence (see table 5.1). Possible predation by the visiting fauna might have been minor compared with the competitive influence of the permanent epifauna.

(2) Competition for leaf material: The amphipod gut content analysis and the findings of Poovachiranon *et al.* (1986) and Camilleri (1992) suggest resource competition for leaves to be an acceptable explanation. The exclusion of *Sesarma meinerti*, which mainly feeds on mangrove leaves (see table 5.1), could have been the direct inducement. On the other hand, Camilleri (1989) argued that this resource competition for leaves and leaf particles may be facilitated by the availability of different particle sizes. *Sesarma meinerti* takes whole leaves and large particles while small shredders like amphipods are restricted to rather small particles. Moreover, the role of direct bacterial decomposition of the leaves could also have gained in importance (Robertson & Daniel 1989).

(3) Competition for microalgae and deposited food: The excluded epibenthos was dominated by deposit and microalgae feeders (see table 5.1). In spite of the absence of microalgae in their stomachs, the exclusion effect on amphipods was detected one month after the clear exclusion effect on the concentration of chlorophyll *a*. As soon as amphipod cage densities increased, the microalgal peak started to decrease back to its former level. Also the indirect exclusion effect on muddy detritus ran parallel with that on amphipods and the amphipods stomach contained a clear detrital fraction.
This kind of competition is believed to be the determining factor.

Insect larvae density: According to O'Meara (1976), marine insect larvae are basically omnivores (mainly browsers and filter feeders). The resource competition hypothesis (as discussed for amphipods) would be supported if most insect larvae found were browsers abrading solid material and manipulating and breaking down leaf and detritus particles. Most of the larvae in this study, however, belonged to the family of the Dolichopodidae (Goddeeris, personal communication) which are predaceous and are frequently found in damp soil, sand, and rotting wood in the intertidal zone (Smith 1989). Examination of gut contents of the Dolichopodidae found in this study revealed a lot of oligochaete setae.

O'Meara (1976) mentioned fishes and other insects to be the main predators on insect larvae. Still, no larvivorous fishes have been described for the studied area (Mees, personal communication).

Oligochaete and total densities: Both densities were closely linked since oligochaetes made up the largest part of the total infaunal macrobenthos.
Procedural effects on oligochaetes have been documented before and are thought to be a result of sediment modification caused by the cage construction (Hulberg & Oliver 1980; Hall *et al.* 1990a). The procedural effect in our study could possibly be linked with changes of environmental factors due to cage construction:

(1) Salinity: This factor has been stated to be crucial in determining oligochaete distribution (Giere 1980; Giere & Pfannkuche 1982). This holds especially for salinity of tropical, intertidal areas where 40 psu is the upper tolerance limit for oligochaetes (Giere & Pfannkuche 1982).

(2) pH: Tolerance experiments (Giere 1977 in Giere & Pfannkuche 1982) showed that extreme alkalinities (exceeding 9) in combination with high salinities and temperatures could cause a deterioration of viability in interstitial tubificids. No such conditions were found in this experiment.

(3) Light intensity: The shadow caused by the construction cover could possibly have induced an upward vertical migration of littoral, negatively phototactic oligochaetes (Giere & Pfannkuche 1982).

(4) Mud: The decreased grain size could have influenced habitat selection. This is, however, more relevant in mesopsammic forms for which interstitial space is a crucial condition for life (Giere & Pfannkuche 1982).

Nevertheless, most studies concentrating on oligochaete densities in temperate areas found successful exclusion effects. These effects were usually concluded to be a result of predation exclusion (Reise 1977; Reise 1978; Kneib & Stiven 1982; Connell 1983; Gee *et al.* 1985). The only experimental studies dealing with oligochaetes of mangrove sediments are those presented in Chapters IV and V, indicating that meiobenthic oligochaetes are influenced by competition with the deposit feeding epibenthos rather than by predation. The slight increase of the oligochaete density in the cage after 112 days (which was not statistically evidenced) could as well be a response to the indirect exclusion effect on the muddy detritus. The most important dietary item for interstitial tubificids and enchytraeids is believed to be organic matter (detritus) enriched with bacteria (Giere & Pfannkuche 1982).

Polychaete and nematode densities: As found for meiobenthic polychaetes in a *Ceriops tagal* and an *Avicennia marina* mangrove sediment (Chapter IV and V), macro-polychaetes did not show an exclusion effect. However, in other experimental studies in seagrass beds (Reise 1978; Reise 1979) and in mudflats (Reise 1978) polychaetes reacted positively to epibenthic exclusion.

Some studies have shown the number of meiobenthic nematodes to double in the cage sediment in contrast with the control cages after two months of epibenthic exclusion (Reise 1979; Chapter IV). The macro-nematodes in our study all belonged to the family of Oncholaimidae. These are believed to be scavengers with a very broad diet that stimulate bacterial and fungal metabolism by decomposing organic matter (Lopez *et al.* 1979; Jensen 1987). This alternative feeding behaviour could possibly have kept this group from being influenced by resource competition.

The absence of significant effects for polychaetes and nematodes possibly results from the efficiency of the experimental design to detect effects. The α significance level (0.05), the degrees of freedom of the numerator of the interaction F-ratio (10), the sample size (3), and the effect size (f) resulted in power levels of 8 % for polychaetes and 5 % for nematodes (average power for factorial and mixed design) (Hall *et al.* 1990c). The effect size (f) per taxon (table 6.2) was calculated via the ANOVA-variances, the number of degrees of freedom (10), of interaction groups (18), and of replicates within a group (3). The power levels point to the chance of avoiding a type II error ($1-\beta$) and were calculated via the power table provided by Cohen (1977). The low levels could possibly result in an undetectable influence.

taxon	design	MS_{effect}	MS_{error}	η^2	f	power
Polychaeta	factorial	3.48393	2.506394	0.07	0.274	11 %
	mixed	3.48393	2.845246	0.04	0.05	5 %
Nematoda	factorial	1.98072	1.930757	0.005	0.05	5 %
	mixed	1.98072	2.601394	0.04	0.05	5 %

Table 6.2: The power and the effect size (f) per macrobenthic taxon with the 'interaction' variance (MS_{effect}), the 'error' variance (MS_{error}) and the estimated magnitude of treatments (η^2) *(calculated via tables and formulas provided by Cohen 1977) (Avicennia marina).*

c) Conclusion

Oligochaete, polychaete, and macro-nematode densities were not positively affected after epibenthic exclusion. The positive exclusion effect on the amphipod community seems to point to a resource competition with the dominant epibenthos for microalgae, muddy detritus and, possibly, for leaves. No driving force for the conspicuous positive exclusion effect on insect larvae could be found. However, in this case too, predatory exclusion is believed to be unimportant.

Therefore, the predation hypothesis is thought to be minor as an interaction between the epibenthos and macrobenthic infauna under the studied *Avicennia marina* stand. A resource competitive effect of the permanent epibenthos is found to be more conspicuous. The question whether epibenthic predation on endobenthos of this high intertidal mangrove forest floor is absent remains to be answered.

VII. INFLUENCE OF EPIBENTHOS ON MACROBENTHOS IN THE *CERIOPS TAGAL* FOREST

A. INTRODUCTION

Studies on trophic relationships in mangroves generally assume larval, juvenile, and adult stages of shrimp, penaeid prawns, and fishes to be predators on zooplankton and meio- and macrobenthic food sources (among which small benthic crustaceans and worms) (Poovachiranon *et al.* 1986; Sasekumar *et al.* 1992). Beside food, mangals are also believed to offer shelter and nursery sites to the visiting epibenthos (Hutchings & Saenger 1987). However, spatial partitioning in the epibenthic distribution (over mudflats, inlets or creeks, seagrass beds, subtidal adjacent waters, and mangrove forest floors) in terms of feeding is pronounced. Sasekumar *et al.* (1992) even believed the mangrove forest itself to be invaded for shelter rather than for food during high tides, leaving only the surrounding areas as feeding grounds.

In general, cage exclusion studies in the tropics expected predation pressure to be dominant in structuring the endobenthos (Vargas 1988 for macrobenthos; Dittmann 1993 for meiobenthos). Chapter VI, however, reported the macrobenthic infauna of a high intertidal *Avicennia marina* mangrove floor to be structured by an exploitative competition with the permanent epibenthos rather than by predation from the epibenthos coming from adjacent waters. The question whether predation pressure on the macrobenthos of this East African mangrove forest floor is entirely absent, remains to be answered. Moreover, Virnstein (1977) mentioned a possible gradient of increasing predation from high to low intertidal zones in temperate regions due to increasing density of visiting predators.

A parallel research was therefore carried out in a mid-intertidal *Ceriops tagal* forest of the same region. This *Ceriops tagal* vegetation zone differed significantly from *Avicennia marina*. Because of its intertidal position it was more frequently flooded (65 % of the high tides) and therefore invaded by more visiting fauna. The forest floor was poorer in detritus and the forest and tree morphology was more shrub like. In the permanent epifaunal community, the crab *Sesarma meinerti* was absent and replaced by the hermit crab *Clibanarius longitarsus* and the crabs *Uca lactea annulipes* and *Sesarma guttatum*. Moreover, the infaunal composition was slightly different. The cage experiment was now used to exclude the permanent and visiting epibenthos from the *Ceriops tagal* forest floor. The detailed macrobenthic response was predicted to offer some insight in the role of the infaunal community in the decomposition and interactive pathways of mangroves (Kennedy 1993).

B. MATERIAL AND METHODS

The study area, the quantification of environmental and biotic factors, the experimental and statistical design, and the statistical analysis have been accurately described in Chapter III.
For this subresearch in particular, six series of samples were taken over time in the three treatments of the *Ceriops tagal* experimental site:

- period 1: before caging (6/8/92) (env/macro)
- period 2: after 22 caging days (28/8/92) (env/macro)
- period 3: after 52 caging days (27/9/92) (env/macro)
- period 4: after 84 caging days (29/10/92) (env/macro)
- period 5: after 111 caging days (25/11/92) (env/macro)
- period 6: after 139 caging days (23/12/92) (env/macro)

Macrobenthic taxa: These biotic factors were analysed using a 3 x 6 (between groups) factorial ANOVA design with treatments (3) and periods (6) as groups. Additionally, a 3 (between groups) x 6 (within subjects) mixed design was applied with treatments (3) as groups and periods (6) as subjects repeated over time. Only the upper 2 cm layer was analysed.

Environmental factors: Effects on environmental factors of the upper sediment layer were detected using a 3 x 6 (between groups) factorial ANOVA design and a 3 (between groups) x 6 (within subjects) mixed ANOVA design with treatments (3) as groups and periods (6) as subjects repeated over time. Since some environmental factors (*e.g.* skewness before combustion, % of POM, and % of total carbon) did not meet the ANOVA assumptions, the non-parametric Kruskal Wallis and Median tests were used.

C. RESULTS

1. Endobenthic composition

The overall macrobenthic density was 23058 ind./m². It consisted mainly of oligochaetes (94 %) in turn dominated by the family Tubificidae (98.4 %). The family Enchytraeidae comprised only 1.6 % of the oligochaete density (figure 7.1). Almost half of the rest 6 % was composed of polychaetes (47 %) with the family Terebellidae (33 %) and the nereid *Namalycastis* spec. (14 %). These polychaetes were followed by the macro-nematode *Oncholaimus* spec. (21.5 %), gastropods (17 %), and amphipods (13 %) dominated by *Grandidierella* spec. (making up 11.5 %) with a small fraction of *Ampelisca* spec. The insect larvae (mainly represented by the family Dolichopodidae) made up only about 1.5 % of this rest fraction (or 0.08 % of the total macrobenthic infauna).

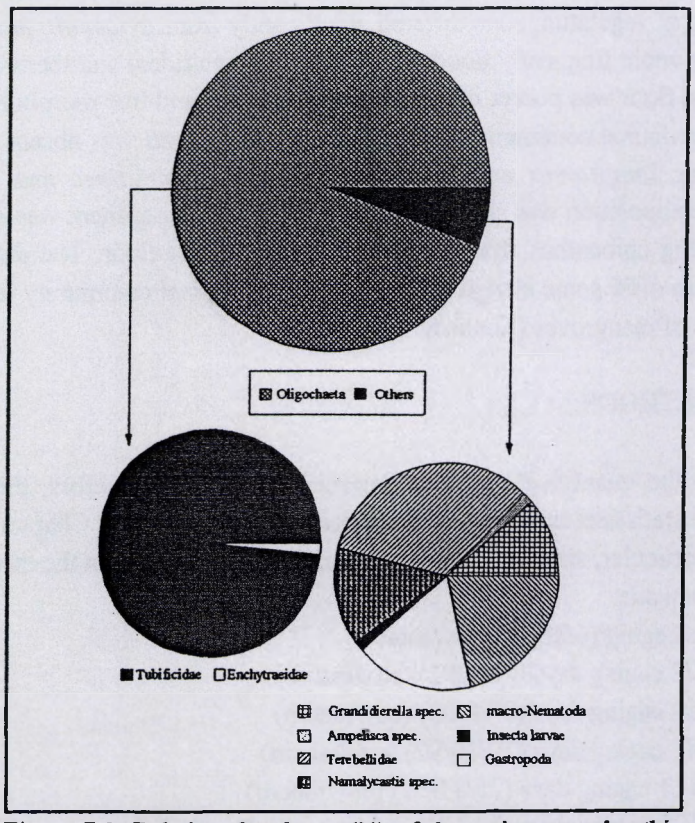


Figure 7.1: Relative abundance (%) of the major macrobenthic taxa, families, and genera (average of blank sites over all periods) *(Ceriops tagal)*.

2. Epibenthic composition (see table 4.2)

3. Experimental results

a) Biotic factors

Exclusion effect: A clear exclusion effect was observed for the oligochaete family Tubificidae after three and four months of caging (figure 7.2). Densities tripled in the cage sediment in contrast with the other treatments. The family of Enchytraeidae was not affected by the experiment (figure 7.2). The polychaetes too showed a significant higher density in the cage than in the partial cage and blank units after five months, although this exclusion effect was not as conspicuous as for oligochaetes (figure 7.3). This effect, however, was mainly due to a very clear exclusion effect on *Namalycastis* spec. from the 52nd day after the start of the experiment onwards (figure 7.3). The terebellids, being the dominant polychaetes (figure 7.1), were not affected. The amphipods (mainly consisting of *Grandidierella* spec.) were statistically evidenced to undergo an exclusion effect after one month (figure 7.4). This effect, however, was questionable, since the density of the cage sediment before the start of the experiment was already significantly higher than that of the other treatments (LSD $p < 0.05$).

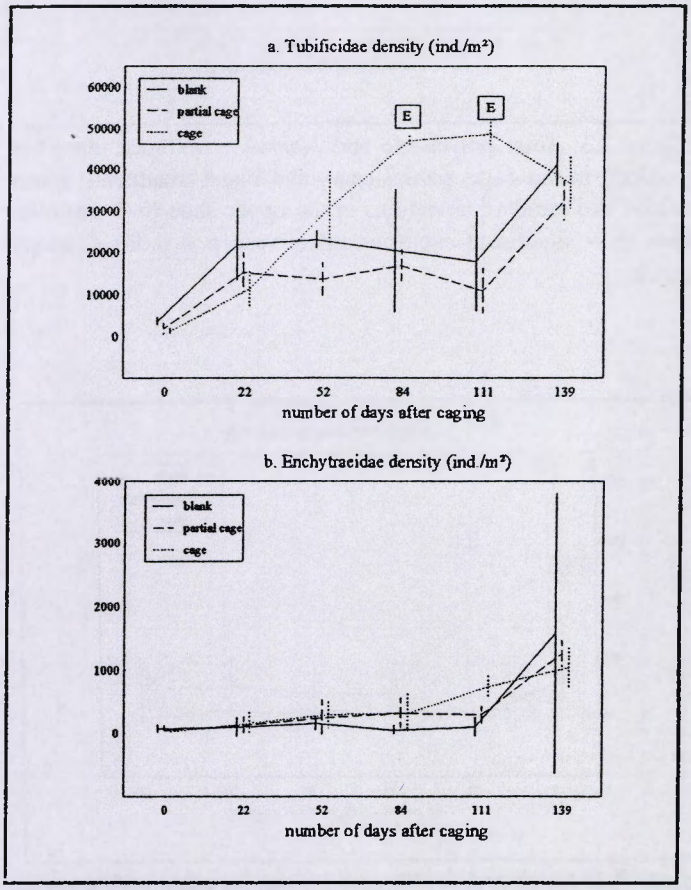


Figure 7.2: Tubificid and enchytraeid densities (ind./m²) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper slice (0-2 cm) over time (E = significant exclusion effect with $p < 0.05$) *(Ceriops tagal)*.

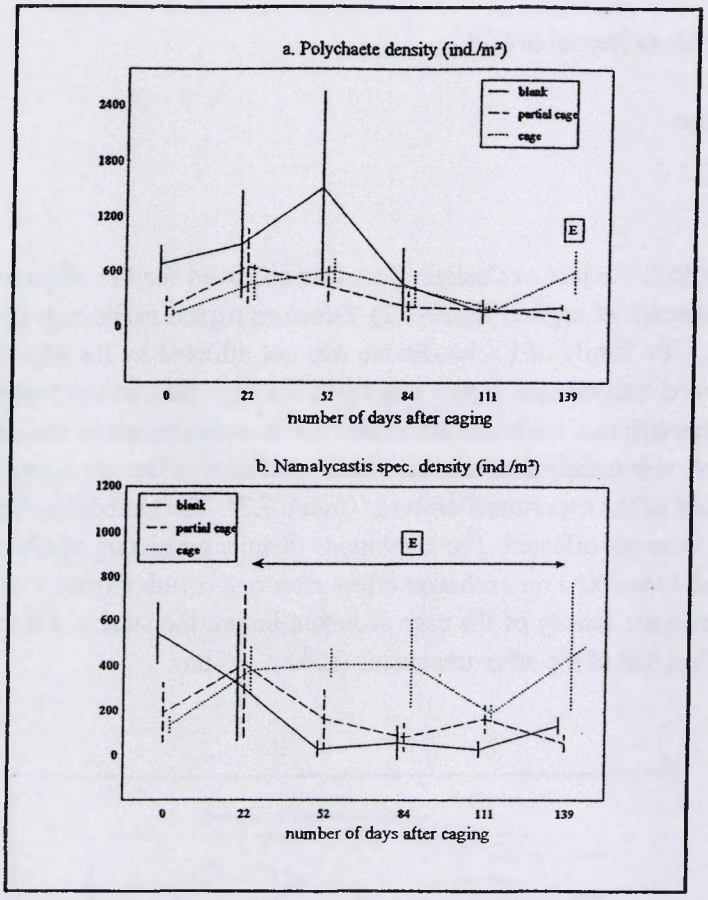


Figure 7.3: Total polychaete and *Namalycastis* spec. densities (ind./m²) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper slice (0-2 cm) over time (E = significant exclusion effect with $p < 0.05$) *(Ceriops tagal)*.

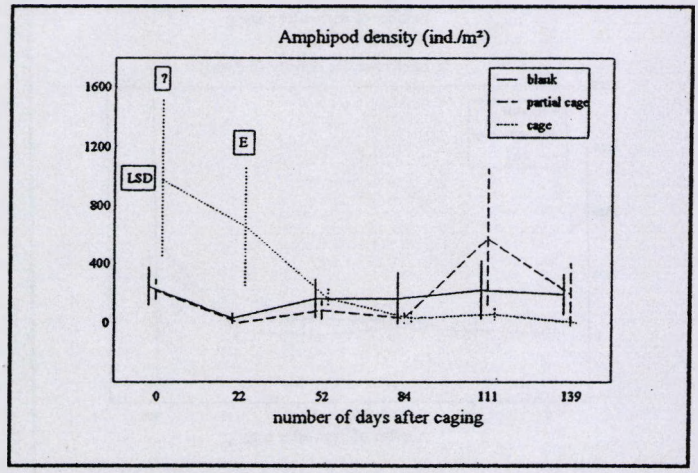


Figure 7.4: Amphipod density (ind./m²) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper slice (0-2 cm) over time (E = significant exclusion effect with $p < 0.05$) *(Ceriops tagal)*.

Procedural effect: Only the macro-nematode density showed a conspicuous and significant procedural effect after one month (figure 7.5). The density of this group seemed to be suppressed by the cage and partial cage construction.

No effect: Neither the insect larvae nor the gastropods indicated to be affected by the experiment.

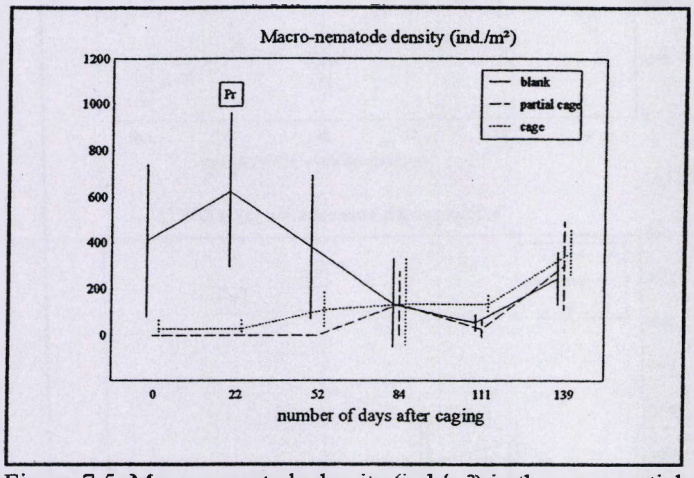


Figure 7.5: Macro-nematode density (ind./m²) in the cage, partial cage, and blank treatments: mean values and standard deviations in the upper slice (0-2 cm) over time (Pr = significant procedural effect with $p < 0.05$) *(Ceriops tagal)*.

b) Environmental factors

Exclusion effect: Both pigments, chlorophyll *a* and fucoxanthin, showed quite a parallel course during the experiment, with a highly significant ($p < 0.01$) exclusion effect after 84 and 111 days of caging (figure 7.6) Both cage concentrations increased to a level of about 4 x that of the other two treatments. These concentrations again decreased at the end of the experiment (after 139 days).

After one month already, a significant exclusion effect became clear for the % of muddy detritus (= % of mud before combustion - % of mud after combustion). It doubled in the cage as compared with blank and partial cage (figure 7.7). This effect, however, disappeared again after the second month.

Procedural effect: From the 84th day of caging onwards, the salinity of the cage and partial cage sediment started to decrease compared with that of the blank units (figure 7.8).
In contrast with the muddy detrital fraction, the % of mud after combustion was influenced by the experimental procedure after 22 days (figure 7.8).

No effect: Clear effects on the % of POM, % of C, pH, DO_2, temperature, and other granulometric factors were not detected.

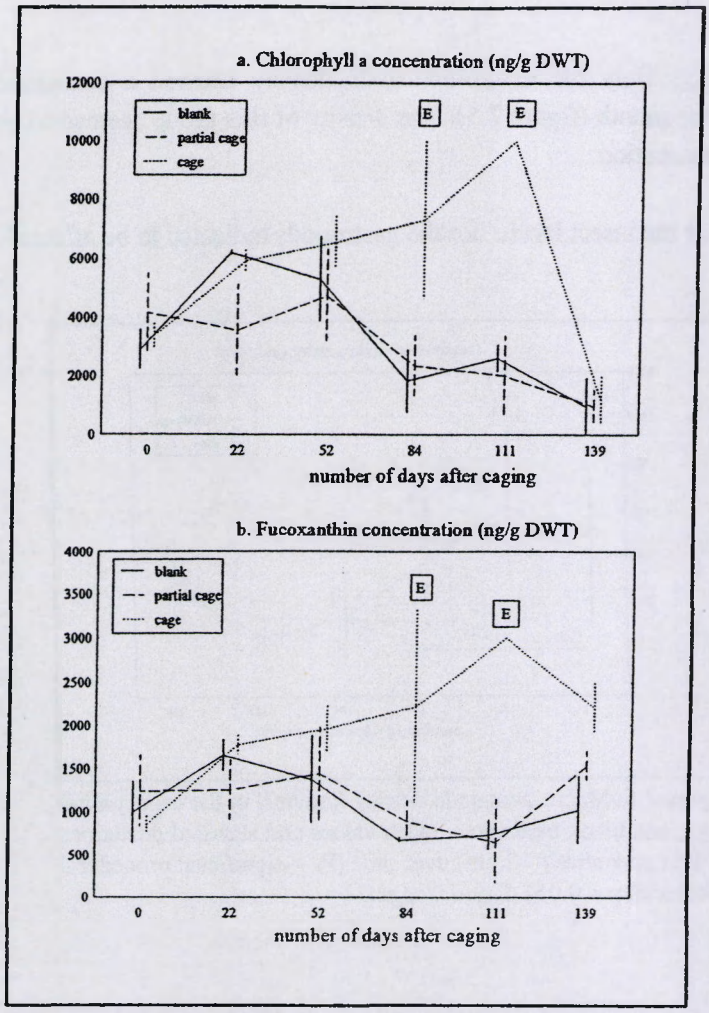


Figure 7.6: Exclusion effect (E = significant effect with $p < 0.05$) on the pigment concentrations: mean values and standard deviations in the upper slice (0-2 cm) over time for the cage, partial cage, and blank treatments *(Ceriops tagal)*.

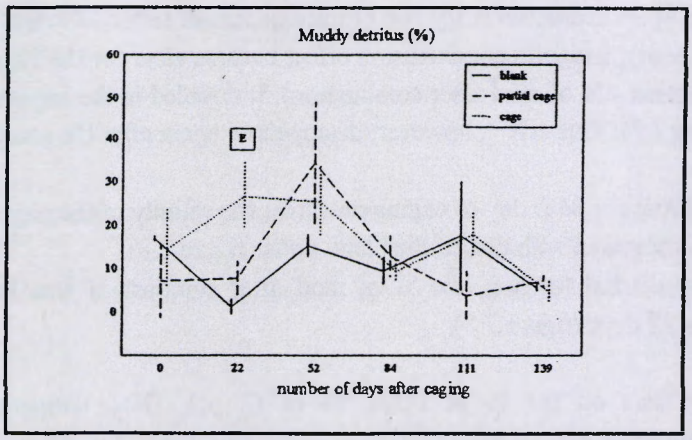


Figure 7.7: Exclusion effect (E = significant effect with $p < 0.05$) on the % of muddy detritus: mean values and standard deviations in the upper slice (0-2 cm) over time for the cage, partial cage, and blank treatments *(Ceriops tagal)*.

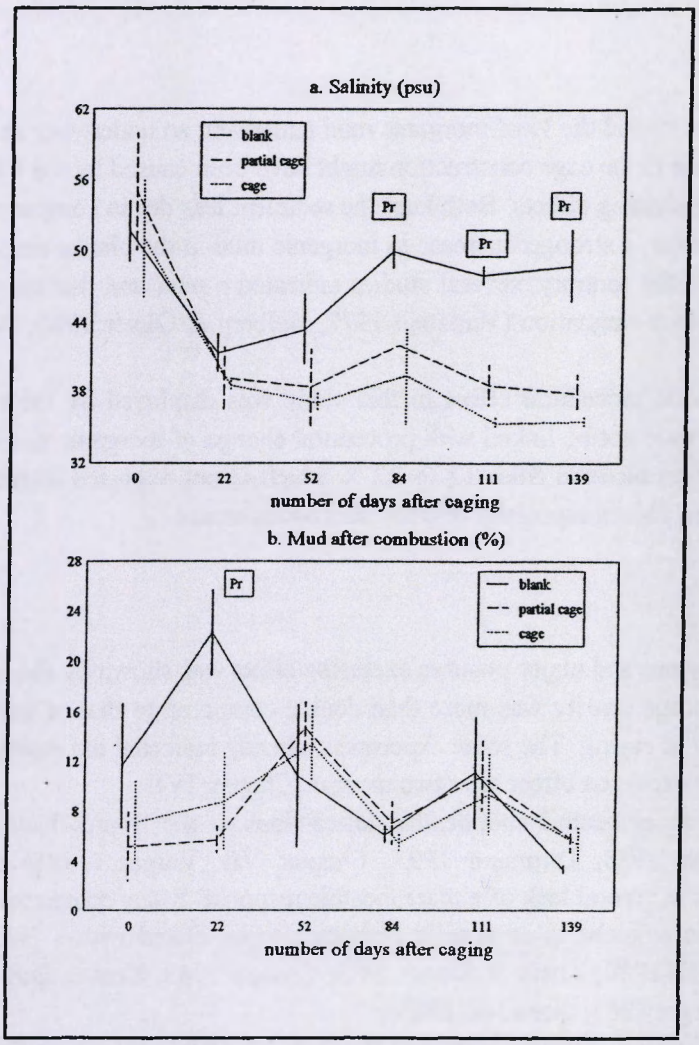


Figure 7.8: Procedural effect (Pr = significant effect with $p < 0.05$) on environmental factors: mean values and standard deviations in the upper slice (0-2 cm) over time for the cage, partial cage, and blank treatments *(Ceriops tagal)*.

D. DISCUSSION

1. Experimental material and methods

The evaluation and discussion of the used material and methods concerning study site, quantification of environmental and biotic factors, experimental and statistical design, and statistical analysis have been accurately expounded in Chapter III.

2. Experimental results

a) Procedural effects

Only the salinity and the % of inorganic mud underwent an underlying abiotic procedural impact. A salinity decrease due to the cage construction might have been caused by the PVC plates anchoring the cage to the soil or by shading effects. Both kept the sediment less dry in comparison with the blank units (see table 4.4). However, a stronger increase in inorganic mud in the blanks than in the other treatments was not expected. On the contrary, several studies indicated a mud and detritus deposition in the cages owing to increased water stagnation (Virnstein 1977; Hulberg & Oliver 1980; Woodin 1981; Menge *et al.* 1986).

The only biotic procedural effect in this study was displayed by the macro-nematodes. This response, however, could not be linked with procedural change of inorganic mud. The inorganic muddy fraction showed only an increase from 12 to 22 % which is not expected to have an influence on the nematode composition. This is especially true for macro-nematodes.

b) Oligochaeta

The most obvious and major positive exclusion effect was shown by the oligochaetes (especially the tubificids). Their cage density was more than double compared to that of the other treatments after three and four months of caging. The same experiment already indicated the meiobenthic oligochaetes to show an even stronger exclusion effect after two months (Chapter IV).

Few studies on epibenthic-endobenthic interactions in the tropics have dealt with effects on macrobenthos (Vargas 1988; Dittmann 1993; Chapter VI). Vargas (1988) and Dittmann (1993) explicitely pointed to the general lack of a macrobenthic response. Many comparable studies in temperate regions found specific oligochaete or annelid responses to be linked with a predatory absence (Reise 1977; Reise 1978; Bell 1980; Kneib & Stiven 1982; Connell 1983; Kent & Day 1983; Hoffman *et al.* 1984; Fitzhugh & Fleeger 1985; Gee *et al.* 1985).

Table 4.2, however, already indicated the lack of permanent epibenthic predators (such as carnivorous crabs) in the studied vegetation zone. Omnivores or odd-job predators are believed to be able to swallow oligochaetes only by chance. This was indicated for *Littorina littorea* (Reise 1985). Concerning the visiting epibenthos (hyperbenthos and fishes), Giere & Pfannkuche (1982) and Giere (1993) described oligochaetes as possible food for young demersal fishes (*e.g.* gobiids), shore crabs, and shrimps in temperate regions. In tropical mangrove studies, however, the importance of this taxon in terms of food in inlets, creeks, and mudflats has not been mentioned (Vargas 1988; Sasekumar *et al.* 1992). Also, Virnstein (1977) indicated that the tubificids, although dominant, were not affected by predation of crabs or fishes in a temperate shallow estuarine bottom.

An exploitative competition between epibenthos and infauna is expected only if food sources are limited and food supply is low (Evans 1983). As a matter of fact, the deposit feeding nature of most of the permanent epibenthos (see table 4.2) is believed to keep this food limited and low. Moreover, McIntosh (1988) mentioned that fiddler and sesarmid crabs of salt marshes are food-limited themselves. It was therefore predicted for this study that a significant food increase would be observed after epibenthic exclusion.

An important food source, the muddy detritus, indeed showed this positive exclusion effect. This detritus is thought to be produced by sloppy feeding and faecal pellets of shredders such as crabs leading to an accumulation of smaller (between 0.45 and 350 µm) POM fractions (Camilleri 1992).

It might be that the uptake of the muddy detrital fractions (< 63 µm) by both oligochaetes and epibenthos leads to a resource competition. Oligochaetes are frequently indicated to be macrofaunal deposit feeders living on detritus associated with bacteria and fungi (Giere & Pfannkuche 1982; Reise 1985; Hedlund & Augustsson 1995). The positive macro-oligochaete response came one month after that of the meio-oligochaetes (Chapter IV). The earlier meiofaunal response could be due to a higher P/B ratio and turnover rate (Bell 1980).

The chlorophyll *a* and fucoxanthin concentrations underwent this positive exclusion effect as well. This can be correlated with an increase in the microalgal and diatom food sources (Admiraal *et al.* 1983; Burford *et al.* 1994; Gerdol & Hughes 1994a) as observed after gastropod exclusion in salt marshes (Pace *et al.* 1979). Although Giere (1975) described microalgae (especially diatoms) to be less important in the diet of oligochaetes, a parallel, positively affected trend became clear between the pigment concentrations and the oligochaete abundance in this study.

In general, oligochaetes seem to take over the role of the most important detritivores during the exclusion. These detritivores are believed to belong mainly to the permanent epibenthos (see table 4.2).

c) Polychaeta

The positive exclusion effect on the polychaete *Namalycastis* spec. might be an indication of resource competition as well. As is the case for most Indian mangrove polychaetes (Kumar 1995), this group too seems to be detritivorous. Fauchald & Jumars (1979) mentioned nereids with eversible pharynx and jaws but without paragnaths, as found in this study, to be mainly feeding on plant food, detritus, and microalgae.

The salt marsh polychaete *Namalycastis abiuma*, however, was observed not to feed on detritus and algae but rather on decaying wood on the surface (Rasmussen 1994). This could point to a higher vulnerability to predation. Virnstein (1979) found that the polychaete *Nereis succinea* underwent a positive exclusion effect after one exclusion month due to the absence of predators. Two facts, however, might not support the predatory impact:

- Dittmann (1993) did not observe a significant increase in polychaetes after epibenthic exclusion. She, however, worked on an unvegetated mudflat surrounded by mangroves. Data from studies under the mangroves themselves are not known.
- The dominant polychaete family Terebellidae is deposit feeding and therefore lives near the sediment surface. Still, it was not affected by exclusion.

This could have been caused, however, by a protective tube. Tubes were indeed reported to be efficient in avoiding predation on amphipods. Furthermore, the dominance of terebellids could have been caused by this protective advantage (Nelson 1979).

Only an insight in the feeding behaviour of *Namalycastis* spec. in this study might reveal a more reliable interpretation of the experimental outcome.

In general, polychaetes are believed to be of more relevance than oligochaetes as a trophic component in marine biota (Giere & Pfannkuche 1982).

d) Amphipoda

Grandidierella spec. showed only a slight increase in the cage after one month. Moreover, this happened before the increase in chlorophyll *a* and muddy detritus. Muddy detritus and microalgae might not be an important food source for these animals after all. Poovachiranon *et al.* (1986) and Camilleri (1992) suggested leaves to be directly fed on by mangrove amphipods. Since these leaves did not really accumulate in the cages (see table 4.4), the lack of an effect could be explainable.

e) Insecta larvae

In this study, the insect larvae (mainly represented by the family Dolichopodidae) did not respond to the significant exclusion effect of their tubificid prey. A positive exclusion effect on the insect larvae of *Avicennia marina* (Chapter VI) might not have been a response to a food increase (believed to be oligochaetes as observed during gut analysis). Yasuda (1995) rather found that the developmental time from first instar to adult emergence decreased with increasing prey densities. Thus, this cannot be reflected as a larval density increase. Moreover, O'Meara (1976) and Székely & Bamberger (1992) indicated insect larvae to be structured by predators. The more terrestrial *Avicennia marina* vegetation zone is believed to be more under influence of insects which are possible predators on the insect larvae. This could be a reason for the larvae to stay unaffected in the *Ceriops tagal* area. A power level of 19 % (average value for factorial and mixed design), however, points to a quite high type II error (Cohen 1977; table 7.1). This means that the non-significant output might be false.

f) Gastropoda

The absence of any significant effect on the gastropods in our study might be attributed to a statistically undetectable influence. A power level of 14 % is quite weak for avoiding a type II error (1-β) (Cohen 1977; table 7.1).

taxon	design	MS_{effect}	MS_{error}	η^2	f	power
Insect larvae	factorial	2.54	1.48	0.12	0.333	17 %
	mixed	0.38	1.71	0.13	0.42	21 %
Gastropoda	factorial	4.88	3.51	0.07	0.274	11 %
	mixed	4.88	2.9	0.11	0.333	17 %

Table 7.1 : The power and the effect size (f) per macrobenthic taxon with the 'interaction' variance (MS_{effect}), the 'error' variance (MS_{error}), and the estimated magnitude of treatments (η^2) *(calculated via tables and formulas provided by Cohen 1977) (Ceriops tagal).*

g) Conclusion

The dominant part (about 93 %) of the macrobenthic infauna (tubificid oligochaetes and polychaete *Namalycastis* spec.) under the mid-intertidal *Ceriops tagal* mangroves showed a positive epibenthic exclusion effect. On the other hand, the polychaete family Terebellidae, the amphipods, the insect larvae, and the gastropods were not affected by epibenthic exclusion. The predatory impact of the visiting epibenthos is thought to be more important as structuring force for the *Ceriops tagal* than for the *Avicennia marina* zone of the same region. It is, however, still believed to be minor compared to the exploitative competition with the permanent epibenthos for muddy detritus and microalgae. Oligochaetes seem to take over the role of the most important detritivores during exclusion. The macrobenthic infauna are to be situated as a trophic dead end in the mangrove soil and are hypothesized to have only a minor role as interactive or non-interactive component in the mangrove foodweb.

VIII. SYNTHESIS

A. NON-MANIPULATED SITUATION

Both vegetation zones (*Avicennia marina* and *Ceriops tagal*) were non-exploited and situated along the westbank of the western creek of Gazi Bay. However, whereas *Avicennia marina* was inundated only during the high water of the spring tides, *Ceriops tagal* was flooded during about 65 % of all high water periods (Slim, personal communication). This was a result of the difference in height above MLWS (> 3 m and 2.8 m respectively). Moreover, the *Avicennia marina* forest and tree morphology formed a higher and more dense canopy than that associated with *Ceriops tagal*. The latter was more patchy, low and sometimes even shrub like. The restricted fresh water supply and the salty soil might be an explanation for the shrub growth as this species seems to be most sensitive to high soil salinity (Gallin *et al.* 1989).

Consequently, both sites showed a different environmental character linked with a specific benthic community. The non-manipulated character of the studied sediments is discussed with data from the top 2 cm of the sediment, averaged over all blanks for all periods.

1. Environment

The percentage of mud and organic matter in the soil is associated with slow moving water. It is therefore linked with geomorphology, tides, roots, trees, and the age and maturity of the mangroves (Frith *et al.* 1976). Mangrove sediments in general contain a high content of mud and organic matter trapped by roots and stems (McNae 1968). The sites studied in this research showed a quite high (30 % for *Avicennia marina* and 20 % for *Ceriops tagal* respectively) mud content mainly consisting of muddy detritus (figure 8.1). The average mud content of 25 different Zanzibarian mangrove sites was only about 12 % (1-60 %) (Olafsson 1995). Still, the values in the present study are lower than those found by Schrijvers *et al.* (1995) for the Gazi area. This difference might be due to an increasing organic content with increasing sediment depth (see figure 4.1). Since the present study concentrated on the top 2 cm, whereas Schrijvers *et al.* (1995) considered a 20 cm sediment core, relatively low values were estimated. The retention of mud and POM by stems and roots of the mangrove forest is believed to be less pronounced when going from low to high intertidal zones (McNae 1968). Since both zones were situated quite high intertidally, the inorganic part of the studied sediments was conspicuously sandy (87 and 86 % for *Avicennia marina* and *Ceriops tagal* respectively) (figure 8.1). The average proportion of sand for the 25 mangrove stations in Zanzibar was only about 34 % (1-79 %) (Olafsson 1995). The muddy consistency of both sites in this study, and of *Avicennia marina* in particular (personal observation), is therefore believed to be rather due to the high detrital content (21 and 9 % for *Avicennia marina* and *Ceriops tagal* respectively). The concentration of chlorophyll *a* (1674 and 3139 ng/g DWT for *Avicennia marina* and *Ceriops tagal* respectively) (table 8.1) was quite similar to that in the top 2 cm of mangrove sediments in India and Australia (Alongi 1989). In general, mangrove chlorophyll *a* concentrations are thought to be limited due to shading produced by the forest canopy (Robertson 1987; Alongi 1989). Also the inhibition of the diatom and microalgal growth by the sedimentary dissolved carbon could be a causal factor (Alongi 1989). The higher salinities (47-49 psu) for the studied sites as compared to lower stations of the same region (Schrijvers *et al.* 1995) are supposed to be due to a longer desiccation following a less frequent inundation (table 8.1).

The difference in intertidal height between the *Avicennia marina* and *Ceriops tagal* zone was predicted to be reflected in a higher inorganic and organic muddy fraction, a higher POM fraction, and a lower salinity and temperature for the lower intertidal *Ceriops tagal* site.

The microalgal density (chlorophyll *a* concentration) was not expected to change among the studied intertidal zones in line with the comparisons between low and high intertidal Australian mangroves (Alongi 1988a). However, besides a different tidal height, the tree and forest morphology of both zones also contrasted. The less dense, low and sometimes even shrub like *Ceriops tagal* vegetation caused a better light penetration and a stronger desiccation than that found in the *Avicennia marina* forest. Whereas the inorganic mud fraction indeed increased towards the lower *Ceriops* zone, the organic fractions clearly decreased (figure 8.1). The open canopy additionally avoided a pronounced decrease in salinity and temperature. The twofold increase in the chlorophyll *a* concentration (1674 and 3139 ng/g DWT for *Avicennia* and *Ceriops* respectively) was thought to be linked with a less heavy shading under the *Ceriops tagal* canopy (table 8.1). In addition, the lower POM content could possibly have resulted in a lower concentration of dissolved organic matter (DOM), weakening the inhibition of diatom and microalgal growth (Alongi 1989).

Environmental variable	*Avicennia marina*	*Ceriops tagal*
% of muddy detritus	21.05	9.05
% of POM	5.14	3.62
concentration of chlorophyll a (ng/g DWT)	1674.20	3139.18
concentration of fucoxanthin (ng/g DWT)	621.64	1046.00
salinity (psu)	49	47
temperature (°C)	30	30
redox potential (mV)	141	79

Table 8.1: Environmental factors in both studied zones.

2. Meiobenthos

The total meiofaunal density in the top layer (0-2 cm) was similar in both zones (983 and 1023 ind./10 cm^2 for *Avicennia marina* and *Ceriops tagal* respectively). The nematode dominance (respectively 93 and 83 % of the total density) was also found for other mangrove studies in Australia (Hodda & Nicholas 1985; Nicholas *et al.* 1991), India (Sarma & Wilsanand 1994), South Africa (Dye 1983a, 1983b) and East Africa (Vanhove *et al.* 1992; Olafsson 1995; Schrijvers, in press; table 8.2). Besides nematodes, also oligochaetes, turbellarians, copepods, rotifers, ostracods, and nauplii were numerically important for both zones (> 1 % of the total meiofauna) (figure 8.2). Other mangrove studies indeed mention oligochaetes to be one of the more abundant meiofaunal taxa (Hodda & Nicholas 1985; Olafsson 1995). The role of the meiobenthic oligochaetes in mangroves was put forward as one of deposit feeding and browsing and of acting as prey for polychaetes and turbellarians (McIntyre 1968). The first ecological study on turbellarians from tropical coasts in the southern hemisphere reported a turbellarian proportion of 3-11 % near mangroves (Dittmann 1991). This was indicated to be lower than the overall world value (7-25 %) and totally insignificant against the 90 % dominance as reported in an Australian mangrove study (Alongi 1987a). It was believed that the extraction technique in most studies underestimates the turbellarian densities (Alongi 1989).

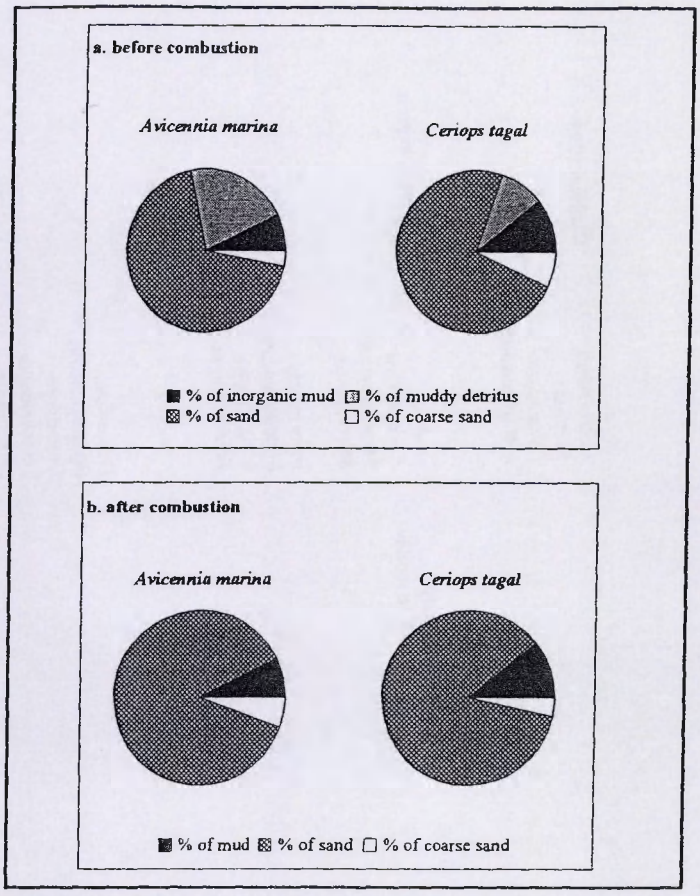


Figure 8.1: Proportions (volume %) of the grain fractions in the upper layer (0-2 cm) of the studied sediments (before and after combustion).

Anyway, the muddy character of mangroves was mentioned as a factor in the promotion of the turbellarian presence that might be of importance in establishing internal predatory links (Dittmann 1991). Only the *Avicennia marina* meiobenthic community consisted of more than 1 % of copepods being lower than the oligochaete proportion (figure 8.2). Similarly, only minor copepod densities were recorded by most other mangrove studies (Dye 1983a, 1983b; Hodda & Nicholas 1985; Alongi 1987a, 1987b). However, in a study by Kondalarao & Ramana Murty (1988), copepods made up about 5 % of the total mangrove meiofauna. They were even estimated to be the second most abundant major meiofaunal taxon in Zanzibarian mangroves (Olafsson 1995).

The nematode community of both zones consisted of more than 50 % of genera belonging to the 2A feeding type (epistrate or epigrowth feeders) (figure 8.2). This was not expected since some detailed nematode studies in Australian mangroves reported a dominance (50-60 %) of deposit feeding genera (1A and 1B) and an equal proportion of about 25 % consisting of epistrate feeding and predatory/omnivorous genera respectively (Alongi 1987b; Warwick 1987; Nicholas *et al.* 1991). Only Nicholas & Stewart (1993) reported proportions of 75 % consisting of epistrate feeders followed by deposit feeders (25 %) and omnivore/predators (2.4 %). Deposit feeding nematodes are supposed to have an important role in the detrital decomposition, stimulating bacterial activity (Odum & Heald 1972) although this role has lately been questioned for mangrove detritus (Tietjen & Alongi 1990). An increasing 2A density was reported only along a decreasing intertidal height (Nicholas *et al.* 1991) or an increasing sand gradient (Kennedy 1993). The dominance of epistrate feeders in mangrove sediments has recently been linked with a sandy environment (Olafsson 1995).

Location	Mean total meiofaunal density (ind./10cm²)	Mean nematode proportion (%)	Second most important taxa	Number of other taxa	Dominant nematode feeding type	Dominant nematode genera (> 5 %)	Author
Gazi, East Africa low/mid intertidal different mangrove vegetations	1976-6707 (0-20 cm)	95	copepods turbellarians oligochaetes polychaetes ostracods rotifers	3	-	-	Vanhove et al. 1992
Zanzibar, East Africa low/mid/high intertidal different mangrove vegetations	205-5263 (0-5 cm)	64-99	copepods oligochaetes polychaetes turbellarians kinorhynchs chironomids	8	2A	*Microlaimus* *Spirinia* *Desmodora* *Metachromadora*	Olafsson 1995
Gazi, East Africa low/mid intertidal *Ceriops* and *Rhizophora* mangroves denuded and virgin	1439-6101 (0-20 cm)	79-92	turbellarians oligochaetes copepods ostracods polychaetes	11	2B/2A when sandy 1A/1B when more muddy	sandy : *Chromadora* *Metachromadora* *Microlaimus* more muddy : *Metalinhomoeus* *Molgolaimus* *Terschellingia*	Schrijvers, in press
Gazi, East Africa							this study
Ceriops tagal mangroves	1023 (0-2 cm)	83	ostracods nauplii oligochaetes rotifers	8	2A	*Daptonema* *Ptycholaimellus* *Desmodora* *Terschellingia* *Linhomoeus* *Spirinia* *Sphaerolaimus*	
Avicennia marina mangroves	983 (0-2 cm)	93	copepods turbellarians oligochaetes rotifers	8	2A	*Desmodora* *Microlaimus* *Ethmolaimus* *Chromaspirina* *Metachromadora* *Haliplectus*	

Table 8.2: A review of studies on the meiobenthos in East African mangrove sediments.

Nematode feeding type *(after Wieser 1953)*	*Avicennia marina*	*Ceriops tagal*
1A (selective deposit feeders)	*Haliplectus*	*Terschellingia*
1B (non-selective deposit feeders)	-	*Linhomoeus*
2A (epistrate feeders)	*Desmodora* *Ethmolaimus* *Microlaimus*	*Ptycholaimellus* *Desmodora* *Daptonema* *Spirinia*
2B (omnivores/predators)	*Chromaspirina* *Metachromadora*	*Sphaerolaimus*

Table 8.3: The most common nematode genera (> 5% of the total nematode density) arranged according to feeding type for both studied zones.

This is a possible explanation for the 2A dominance in our higher intertidal stations which were indicated to be rather sandy. As mentioned before, the microalgal availability was not conspicuously higher than that for other mangrove sediments. In general, the food availability for meiofauna (especially POM, bacteria and/or microphytobenthos) is said to have a supporting and only minor structuring role whereas environmental parameters are thought to be more important for meiofaunal dispersion (Ansari *et al.* 1993). The most common nematode genera (> 5 % of the total nematode density) for both zones are indicated in table 8.3.

No real differences between both zones were observed for the total meiofaunal, the nematode or the 2A group densities. The total meiofaunal density variation along an intertidal gradient in an Indian mangrove sediment was explained by an overall positive correlation between meiofauna and the POM fraction (Sarma & Wilsanand 1994). However, a reaction of the nematodes to the food availability would predict an increase in the 2A group in the *Ceriops tagal* zone containing a higher microalgal density (table 8.1). This was not observed (figure 8.2). It might again point to the physical environment rather than the food availability as a structuring force for the meiofaunal community. The increase in the relative numerical importance of deposit feeders (1A + 1B = 36 %) at the expense of omnivores/predators (13 %) for *Ceriops tagal* in contrast with *Avicennia marina* cannot be explained in terms of food sources either (figure 8.2). This trend is generally believed to occur when going to a sediment which is richer in muddy detritus (Kennedy 1994), which is not so for the *Ceriops tagal* soil (figure 8.1).

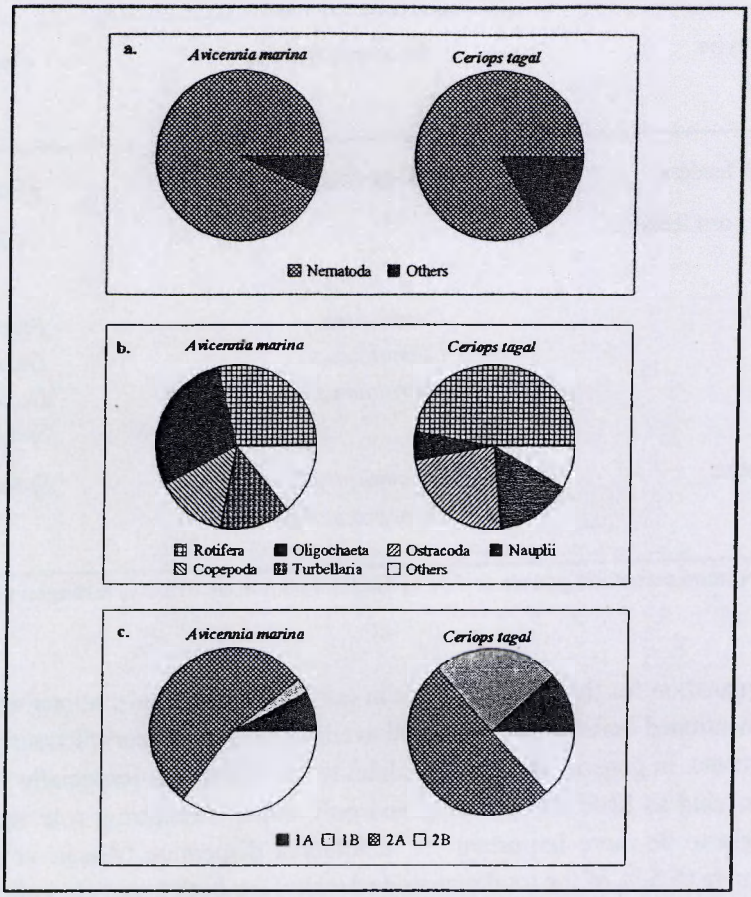


Figure 8.2: Relative abundances of the major meiobenthic taxa (> 1% of the total density) and the nematode feeding types in the upper layer (0-2 cm) of the studied sediments.

3. Macrobenthos

The similar total macro-endobenthic densities of 23361 and 23058 ind./m² for *Avicennia marina* and *Ceriops tagal* respectively (in 0-2 cm), are much higher than reported for most other studies (table 8.4). This considerable difference is due to varying sampling and counting techniques. Most studies used a sieve mesh size of 1 mm or only counted those animals which are visible without magnification. By doing so, taxa such as polychaetes, oligochaetes, nemerteans, sipunculids, isopods, amphipods, and cirripeds were easily underestimated while emphasis was rather laid on infaunal burrowing crabs, thalassinid shrimp, and surface dwelling gastropods and crustaceans. However, these latter taxa were considered to be epifaunal in our study. In addition, a 0.5 mm sieve mesh was used and counting was carried out under magnification. Moreover, oligochaetes were regarded to be macrobenthos when retained in this sieve mesh. Comparing our densities with a similar study (with a sieve mesh of 1 mm) in the same region, it becomes clear that most of the macrobenthic animals in the present study occur within the 0.5-1 mm range (especially oligochaetes) (Schrijvers *et al.* 1995). Though 85 % of the tropical benthic density consists of polychaetes (Longhurst & Pauly 1987), oligochaetes become more important in mangrove sediments.

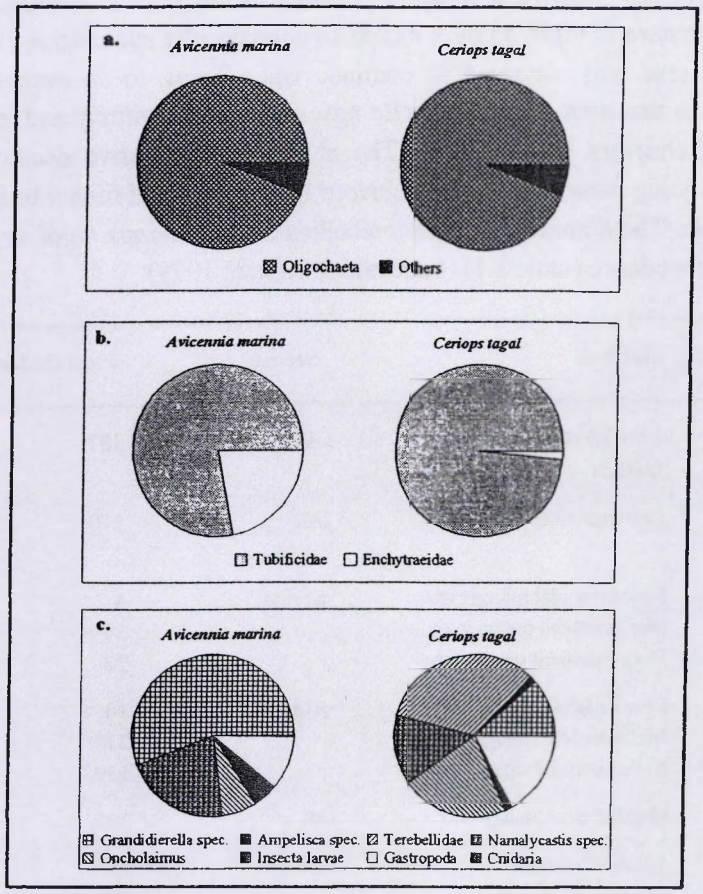


Figure 8.3: Relative abundances of all macro-endobenthic taxa in the upper layer (0-2 cm) of the studied sediments.

Organically enriched fine to medium sands and mud around and under mangroves are especially attractive (Giere & Pfannkuche 1982; Diaz & Erseus 1994; Schrijvers *et al.* 1995; Erseus, personal communication).

Primarily for macro-oligochaetes, detritus is the decisive factor because the particle size, and thus the interstitial pores, have no influence (Giere & Pfannkuche 1982). An oligochaete dominance (94 %) in the studied mangrove soil, characterized by sandy but detritus rich sediments, is therefore evident (figure 8.3). The role of the meiobenthic oligochaetes in mangrove sediments as mentioned before (McIntyre 1968) might be generalized for the entire oligochaete community. The slightly higher density of oligochaetes in the *Avicennia* zone might be due to the positive correlation with organic matter (figure 8.3).

The macro-endobenthic community overall had a low diversity with a monotonous composition of mainly oligochaetes (families Tubificidae and Enchytraeidae), polychaetes (*Namalycastis* spec. and family Terebellidae), and amphipods (*Grandidierella* spec. and *Ampelisca* spec.). This could possibly have been caused by the high intertidal position of the sampling site resulting in extreme anaerobic conditions with abrupt changes in salinity, temperature, redox, and DO_2 as found for mangrove nematode communities (Tietjen & Alongi 1990; Olafsson 1995). Such a low diversity was also found for sediments of other mangroves (Kumar 1995) and of salt marshes (Haase 1993). Most macrobenthic representatives in our study were found to be detritivorous and therefore well adapted to the detrital mangrove habitat. The same was reported for an Indian mangrove soil (Kumar 1995). An increase in the number of polychaete and amphipod families towards the lower *Ceriops* zone was clear (figure 8.3).

While the absolute and relative amphipod densities decrease, the monospecific *Grandidierella* spec. community of *Avicennia* is replaced by a mixed *Grandidierella* spec./*Ampelisca* aff. *stenopus* community in *Ceriops*. The trend was observed to continue when going to an even lower intertidal *Rhizophora mucronata* zone. In that area, *Grandidierella* spec. disappears entirely and is replaced by *Ampelisca* aff. *stenopus* alone (Schrijvers *et al.* 1995). The absolute and relative density and diversity increase in polychaetes, when going from *Avicennia* to *Ceriops* (figure 8.3) and further to *Rhizophora* (Schrijvers *et al.* 1995), is noticeable. The dominance of the terebellids in the *Ceriops tagal* zone might be related with the higher microalgal abundance (table 8.1) (Fauchald & Jumars 1979).

Location	Habitat	Season	Total (ind./m²)	Author
Selangor, Malaysia	Low intertidal mangroves Infauna	All	137	Sasekumar (1974)
Morrumbere Estuary, Mozambique	Low intertidal mangroves	All	170	Day (1974)
Surin Island, Thailand	Low intertidal mangroves Mid intertidal mangroves High intertidal mangroves	Spring	4 10 28	Frith *et al.* (1976)
Phuket Island, Thailand	Low intertidal mangroves Mid intertidal mangroves High intertidal mangroves	Autumn	80 218 129	Frith (1977)
Kuala Lumpur, Malaysia	Mudflat near mangroves	All	304	Broom (1982)
Northwest Cape, Western Australia	*Avicennia* forest *Rhizophora* forest	Spring	257 473	Wells (1983)
Cochin Estuary, India	Low intertidal mangroves	Premonsoon Monsoon	5872 420	Kurian (1984)
Ka Yao Thai, Thailand	Low intertidal mangroves Mid intertidal mangroves High intertidal mangroves	All	49 107 142-178	Nateewathana & Tantichodok (1984)
Cochin Estuary, India	Mangroves	All	8970	Kumar (1995)
Gazi Bay, Kenya	Low to mid intertidal mangroves	Premonsoon	265-4125	Schrijvers *et al.* (1995)
Gazi Bay, Kenya	Mid to high intertidal mangroves	All	23058-23360	Schrijvers (this study)

Table 8.4: A review of studies on the macrobenthos in and on mangrove sediments.

4. Epibenthos

As generally reported for Indo-West Pacific mangrove forests, the epibenthos in the mangrove sites studied, mainly consisted of a large number of residents such as crabs, hermit crabs and gastropods. The resident epibenthic community showed a composition that is typical for an East African high intertidal mangrove zone (table 8.5) (Emmerson & McGwynne 1992; Micheli *et al.* 1991; Steinke *et al.* 1993).

The important resident leaf shredding crab *Sesarma meinerti* of the *Avicennia* zone (Emmerson & McGwynne 1992; Steinke *et al.* 1993) is entirely replaced by the leaf shredding gastropod *Terebralia palustris* in the *Ceriops tagal* zone.

Sesarma guttatum also feeds on leaves and other plant parts in the *Ceriops tagal* forest although its contribution is supposed to be minor. The *Sesarma meinerti* density in southern African *Avicennia* forests was estimated to be about 4 ind./m² (Emmerson & McGwynne 1992) which is higher than reported for this study. The epibenthic deposit feeding guild in *Avicennia* is composed of *Cerithidea decollata*, *Terebralia palustris* and *Metopograpsus thukuhar*. The same guild consists of *Clibanarius longitarsus*, *Cerithidea decollata*, *Metopograpsus thukuhar* and *Uca lactea annulipes* in the *Ceriops* zone (tables 8.5 and 8.6).

It is obvious that the most abundant and most sediment-orientated epifauna have the most pronounced impact on the forest floor. The visiting and natant organisms are unknown but are nevertheless expected to be less important in the *Avicennia* than in the *Ceriops* forest due to a different inundation frequency. For the resident epifauna, *Terebralia palustris*, *Uca lactea annulipes* and *Clibanarius longitarsus* are most pronounced in the *Ceriops* forest while *Terebralia palustris* and *Sesarma meinerti* are prominent in the *Avicennia* forest (tables 8.5 and 8.6).

Epibenthic species	***Avicennia marina***	***Ceriops tagal***
Cerithidea decollata	57	11
Terebralia palustris	36	65
Sesarma guttatum	-	rare
Sesarma meinerti	0.25 1 burrow per m²	-
Metopograpsus thukuhar	1 (adult)	0.5 (adult) 1 (juv.)
Uca lactea annulipes	-	6 (adult) 3.5 (juv.)
Clibanarius laevimanus	-	12
visiting fauna (unknown)	?	?

Table 8.5: Estimates of the densities (ind./m²) of the different epibenthic species occuring in both studied zones.

epibenthic species	author	feeding behaviour	habitat	this study (see also table 8.5)
Cerithidea decollata	Brown 1971 McIntosh 1984 Dye & Lasiak 1987	non-selective deposit feeding (detritus)	frequently on trees	*Avicennia marina* and *Ceriops tagal*
Terebralia palustris	Dye & Lasiak 1987	non-selective deposit feeding (inorganic parts, microalgae, bacteria, protozoans) *Ceriops tagal* leaves	sediment dwelling	*Avicennia marina* and *Ceriops tagal*
	Slim *et al.* (unpublished) pers. obs.			
Sesarma guttatum	Dahdouh-Guebas *et al.* (pers. comm.) Leh & Sasekumar 1985	omnivorous with preference for mangrove plant matter (83-97 % of diet) with brachyuran remains, inorganic particles, microalgae, diatoms, meiofauna and insects	sediment dwelling	*Ceriops tagal*
Sesarma meinerti	Cott 1929	vegetarian	sediment dwelling	*Avicennia marina*
	Emmerson & McGwynne 1992 Steinke *et al.* 1993 Micheli *et al.* 1991	omnivorous with preference for leaves (75% of diet)		
Metopograpsus thukuhar	Dahdouh-Guebas *et al.* (pers. comm.) McIntosh 1988	omnivorous with preference for macroalgae and animal items (sometimes fresh leaves, seedlings, leaf litter and detritus)	forest dweller (trunk, roots, floor)	*Avicennia marina* and *Ceriops tagal*
Uca lactea annulipes	Crane 1975 Robertson *et al.* 1980 McIntosh 1984 Dye & Lasiak 1986 Wolcott & O'Connor 1992	selective deposit feeding (microheterotrophs, microalgae, detritus)	sediment dweller	*Cerops tagal*
Clibanarius longitarsus	Reay & Haig 1990 Gherardi & Vannini 1993 Vannini (pers. comm.)	muddy detritus (never leaves)	mangrove mud dweller	*Ceriops tagal*
visiting fauna (unknown)	?	herbivorous or carnivorous ?	during high tides	only during spring tides for *Avicennia marina*; only during 65 % of high tides for *Ceriops tagal*

Table 8.6 : Description of permanent and visiting epibenthos excluded from the cages in the studied mangrove vegetation zones (in terms of feeding behaviour and habitat)

5. Summary

The studied *Avicennia marina* as well as the *Ceriops tagal* vegetation zones showed typical mangrove characteristics reflected by high muddy detritus and POM fractions and high nematode and oligochaete densities. Moreover, both sites are typical high intertidal mangrove areas showing high inorganic sandy fractions and a high salinity. The dominance of epigrowth feeding nematode genera is linked with the exceptionally high sandy fraction.

The difference between the *Avicennia marina* and the *Ceriops tagal* sediments is twofold. On the one hand, it is a consequence of the different tidal height leading to a higher inorganic sand fraction, a lower endobenthic diversity and a change in the epifaunal community towards the higher *Avicennia marina* zone. On the other hand, the less dense and more open *Ceriops tagal* forest canopy causes a lower detrital content and a higher pigment concentration as compared to those of the *Avicennia marina* forest. Both zones are inhabited by a typical East African resident epibenthic community consisting of a leaf shredding and a deposit feeding guild.

B. PROCEDURAL EFFECTS

In order to control the experimental procedure and to separate the effects of several aspects of this procedure on environmental and biotic factors, partial cages were used. They were identical to full cages but had one side open to avoid the exclusion of epibenthos. An observational field comparison of these effects was carried out as an extra control in and outside the cages. In many other comparable studies this subjective field comparison (Virnstein 1977; Hurlberg & Oliver 1980; Kneib & Stiven 1982; Ellis & Coull 1989) or the short term experiment (Bell & Woodin 1984) were thought to be sufficient for controlling or avoiding procedural impacts. This frequently led to vague interpretations, though.

Chapters IV, V, VI, and VII mentioned several environmental and biotic factors as significantly influenced by the experimental procedure. Summarizing these effects gives the opportunity to link them with certain experimental constructions.

1. Environmental factors

a) Lower part of the cage construction

The lower part of the cage consisted of four 30 cm high perforated PVC plates which were completely buried in the sediment to anchor the cage to the soil. This lower part avoided the immigration of burrowing epibenthos. The plates were perforated in order to permit a natural, horizontal water flow.

Placement: The initial placement and burying of the lower cage wall in the sediment did not cause a major disturbance. It was gradually pushed down into man-made grooves between the roots, without influencing the caged area.

Salinity: The underground part is believed to have increased the humidity of the cage sediment, eventually leading to a lower salinity in the partial cage and cage sediment. The perforations were able to reduce, but not eliminate, this effect. Several aspects support this explanation:

(1) The field tables (table 8.7) for both zones indeed report an increase in the humidity in the caged sediment

(2) Comparing the humidity change and the salinity graphs (figure 8.4) of both zones, clearly reflects a more conspicuous effect for the *Ceriops tagal* site. An artefact during the experimental execution could explain this, *i.e.* most plates of the *Ceriops* cages were not perforated which led to a reduced water flow and a weaker desiccation during low water.

(3) The weaker but significant salinity decrease for the *Avicennia* cages (figure 8.4) occurred much earlier than in the *Ceriops* constructions (figure 8.4). The first samples after placing the cage in the *Avicennia* site were taken during receding water of a spring tide. Since this high intertidal zone is only flooded during spring tides, this might have led to the local and early effect (table 8.7).

Many other studies, however, applied a cage with a solid bottom (10-30 cm high, without perforations) which was buried in the sediment and where no salinity detections were reported (Fleeger *et al.* 1982; Dye & Lasiak 1986; Ellis & Coull 1989). The use of an underground mesh extension (Bell 1980; Kneib & Stiven 1982; Hoffman *et al.* 1984; Kneib 1988) could be the solution for this artefact. Large mesh sizes might, however, reduce cage stability and epibenthic exclusion.

b) Upper part of the cage construction

The upper part consisted of an aluminium frame (70 cm high) that was covered by a plastic screen with a 2 mm mesh size. These walls prevented the invasion of resident and visiting epifauna.

Current flow: The inducement of a physical structure (such as a cage) is believed to change sedimentation and erosion agents. In general, an increased water stagnation leads to a higher mud deposition (Virnstein 1977; Virnstein 1978; Hurlberg & Oliver 1980). Although the field tables (table 8.7) do not show procedural effects in terms of sedimentation, grain size measurements did detect an inorganic mud change in both zones. A decrease in the median of the inorganic sediment fraction (after combustion) reflects an increase in the inorganic mud in the cage and partial cage constructions in *Avicennia marina* (figure 8.5). That increase was to be expected. The early, abrupt and opposite procedural effect in the *Ceriops* zone, however, might be due to a rather blank artefact (figure 8.5).

Many studies did not report on procedural sedimentary effects (Bell 1980; Kneib & Stiven 1982; Hoffman *et al.* 1984; Dye & Lasiak 1986; Ellis & Coull 1989). Moreover, the choice of a high marsh site was generally believed to reduce these effects significantly. Artefacts are only expected to be numerous near open mud flats or high energy beaches with great sediment transport (Bell 1980; Kneib & Stiven 1982). Still, the observed sedimentary modification in our mangrove experiment suggests that an insufficient control treatment or a subjective observation in the field might result in inaccurate detections of these common cage artefacts.

Fouling: Fouling exists in the growth of organisms (such as algae) on the cage wall impeding the normal current flow and leading to a juvenile attraction (settlement change) and a local food and nutrient level augmentation (Woodin 1974; Reise 1978; Virnstein 1978; Frid & James 1988). In our study, the fouling agents were accurately followed throughout the experiment but no modification of the cage wall was observed (table 8.7). A screen of < 2 mm might have advanced fouling. However, many other studies using a smaller mesh were not hindered by fouling (Kneib & Stiven 1982; Fleeger *et al.* 1982; Dye & Lasiak 1986). It is the juvenile attraction in particular, that frequently complicates the interpretation of experimental results (Virnstein 1977; Buzas 1978; Reise 1978; Virnstein 1978; Bell 1980; Kneib 1988). The retained larvae and juveniles may prey on, or compete with, other (adult) organisms. In our study, juveniles of crabs and gastropods were continous removed from the cages.

Shelter attraction: Several studies have reported on a possible unnatural movement, recruitment, or colonization into cages by macrofauna.

These animals were believed to use the cages as artificial reef structures (Virnstein 1978; Bell 1980). This artefact did not occur, however, in the present study. The mesh size of 2 mm was much too small to permit epifaunal immigration into the cages. The open side of the partial cages could have been used as shelter entrance, though. Even then, field counts of epifauna on partial cage and blank sediment did not detect any differences (table 8.7). Moreover, the shelter attraction is especially evident on intertidal and subtidal mudflats where no natural structures are present (Virnstein 1978). This is not true for mangroves.

Shading: see Cover

c) Cover

A permanent cover (2 mm mesh) prevented invasion of resident and visiting epibenthos and avoided leaf accumulation in the cages. This cover was detachable to facilitate sampling. Many other studies were mainly concerned with the impact of the natant organisms and therefore used open cages with walls higher than high water levels or covered the cage only during floodings (Bell 1980; Kneib & Stiven 1982; Fleeger *et al.* 1982; Ward & Fitzgerald 1983; Hoffman *et al.* 1984; Ellis & Coull 1989). In general, the impact of resident epifauna was not considered to be important (Bell 1980) and was therefore only sporadically hindered using flashing (Hoffman *et al.* 1984). The problem of leaf accumulation in the cage, however, becomes especially evident in mangroves where cage covers then become a necessity (Dye & Lasiak 1986).

Shading: Besides the buried cage part, the shade of the cage walls and cover might also have caused a humidity increase and a salinity decrease in the cage soil. This shading was slightly less pronounced in the partial cages due to one open side (table 8.7). Nevertheless, the influence of shading is believed to be of minor importance in detecting the different procedural impacts on salinity for both zones (figure 8.4). A different, natural shading, linked with the canopy density, already existed.

Leaf fall: Natural leaf fall is expected to be partly exported by the tides and partly retained by epibenthos. The use of a cover totally eliminated leaf fall on the cage sediment. This was even more pronounced by removing the fallen leaves from the cover in order to avoid leaching in the cage. From the moment the cages were placed, the leaf fall was considered none. The retention of the leaves, initially trapped in the cage, replaced the amount of leaves that would have been taken by epibenthos without the cage. The situation in the partial cage treatments could more or less be considered natural (table 8.7).

	after 1 month of caging			after 5 months of caging			evaluation
	B	**C**	**P**	**B**	**C**	**P**	
a. *Avicennia marina*							
fouling	-	-	-	-	-	-	OK
shading	-	+	±	-	+	±	± procedural
sedimentation	-	-	-	-	-	-	OK
moisture	-	+	+	-	+	+	procedural
litter fall	+	-	-	+	-	-	OK
epibenthos	+	-	+	+	-	+	OK
b. *Ceriops tagal*							
fouling	-	-	-	-	-	-	OK
shading	-	+	±	-	+	±	± procedural
sedimentation	-	-	-	-	-	-	OK
moisture	-	-	-	-	+	+	procedural
litter fall	+	-	±	+	-	±	± OK
epibenthos	+	-	+	+	-	+	OK

Table 8.7 : Qualitative observations (- = absent, + = present and ± = intermediate) of possible artefacts in the three treatments (B, P and C) after one and five months of caging with procedural evaluation.

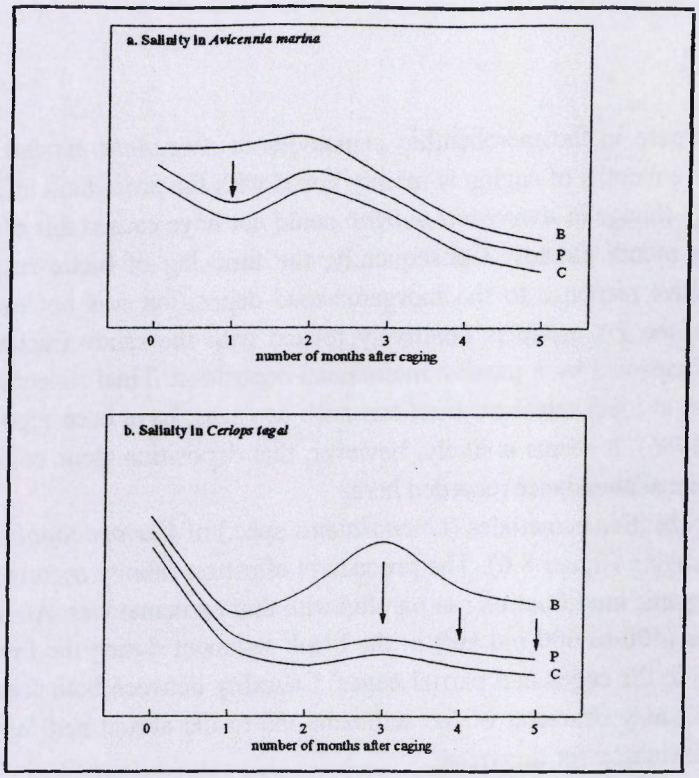


Figure 8.4: Procedural effects on salinity during the experiment in both studied zone (schematic representation) (B = blank; P = partial cage; C = cage).

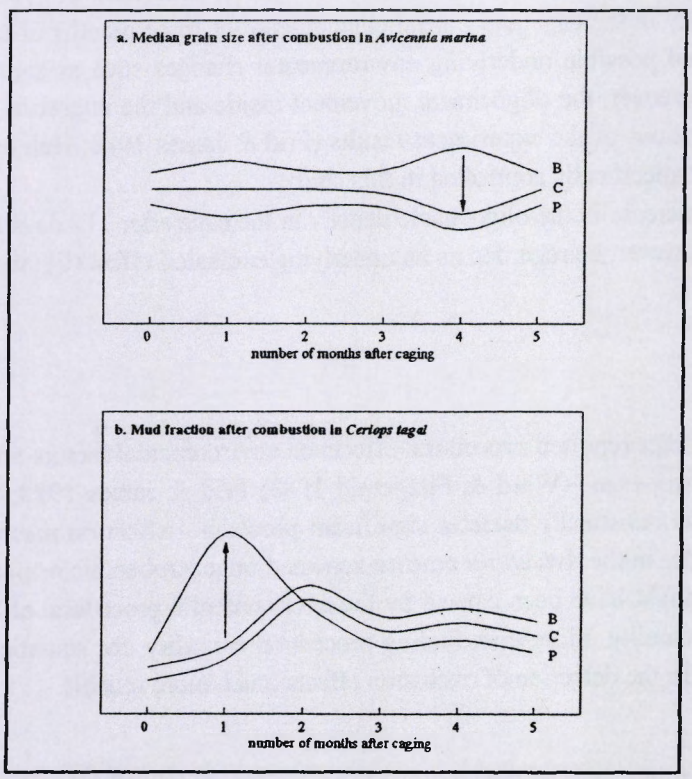


Figure 8.5: Procedural; effects on the grain size composition during the experiment in both studied zones (schematic representation) (B = blank; P = partial cage; C = cage).

2. Biotic factors

a) Nematodes

The increase in the meiobenthic nematodes of *Avicennia marina* in the cage and partial cage sediment after five months of caging is mainly linked with the procedural effect on some 2A genera (figure 8.6). The salinity change in *Avicennia marina* could not have caused this effect, however. It was showing after one caging month already. Consequently, the time lag of biotic response would be too long (4 months). A positive response to the inorganic mud deposition was not expected. As mentioned in the previous chapter, the 2A group is positively related with the sandy fraction. A mud deposition might, however, be accompanied by a passive meiofaunal deposition. Tidal suspension, transport and deposition of meiofauna due to mechanical obstructions such as cages, have been reported by a number of workers (Dye & Lasiak 1986). It seems unlikely, however, that deposition alone could account for the substantial increase in meiofaunal abundance recorded here.

The macrobenthic nematodes (*Oncholaimus* spec.) of *Ceriops tagal* underwent a procedural effect after 1 month of caging (figure 8.6). The procedural effect on salinity occurred much later. The procedural effect on the inorganic mud fraction ran parallel with that on nematodes. An increase in both mud (8 to 20 %) and nematodes (400 to 600 ind./m²) in the blank sediment during the first 22 days of the experiment was not observed in the cages and partial cages. Causality between both factors, however, is not evident due to the overall sandy character of the sediment and to the abrupt and fast change. An intrinsic blank artefact could be the reason for this result.

b) Oligochaetes

The macrobenthic oligochaetes of *Avicennia marina* underwent a significant procedural effect with an increase in density in the cage and partial cage units after three months of caging (figure 8.7). Chapter VI already discussed possible underlying environmental changes such as salinity, pH, light intensity, or mud deposition. Moreover, the oligochaete movement inside and the migration in and out the cages could lead to misinterpretations of the experiment results (Frid & James 1988; Hall *et al.* 1990b; Wilson 1991). This impact was not specifically controlled in this study.

The slight increase in the oligochaete density in the cage after 112 days (which was not statistically evidenced) might, however, be regarded as an underlying exclusion effect (figure 8.7).

3. Summary

Only few studies reported procedural effects on environmental factors and their possible impact on biotic experimental responses (Ward & Fitzgerald 1983; Frid & James 1988; Kneib 1988). This study, however, was able to statistically detect a significant procedural effect on macrobenthic oligochaetes and meiobenthic nematodes in the *Avicennia marina* zone and on macrobenthic nematodes in the *Ceriops tagal* zone. These effects might have been caused by the environmental procedural effects on salinity, inorganic mud, shading, and humidity. More than finding procedural causality, the statistical detection of procedural impacts as such, makes the detection of exclusion effects much more reliable.

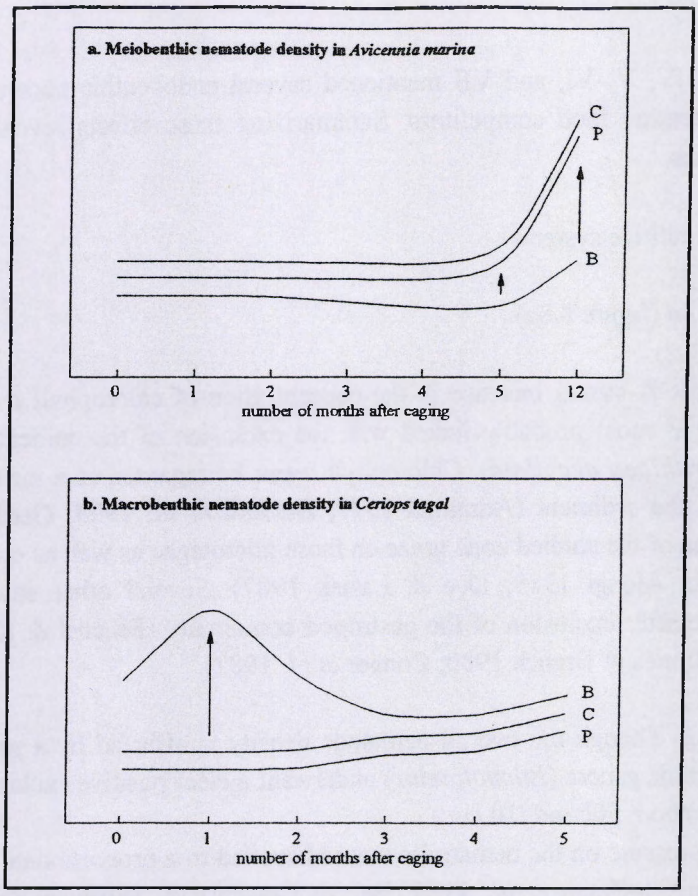


Figure 8.6: Procedural effects on the nematode densities during the experiment in both studied zones (schematic representation) (B = blank; P = partial; C = cage).

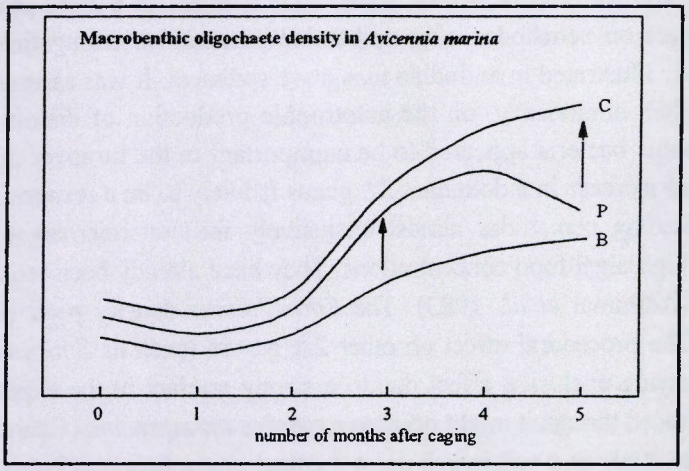


Figure 8.7: Procedural effect on the macrobenthic oligochaete density during the experiment in the *Avicennia marina* zone (B = blank; P = partial cage; C = cage).

C. COMPETITION

Chapters IV, V, VI, and VII mentioned several endobenthic taxa as positively affected by the exclusion of epibenthic food competitors. Summarizing these effects reveals two different exploitative competitive systems.

1. Microalgal competitive system

a) *Avicennia marina* (figure 8.8a)

Microalgae: A strong increase in the concentration of chlorophyll *a* (from about 2000 to about 6000 ng/g DWT) is most probably linked with the exclusion of the epibenthic gastropods (*Terebralia palustris* and *Cerithidea decollata*). Chlorophyll *a* can be regarded as a measure for the microalgal and diatom density in the sediment (Admiraal 1977; Burford *et al.* 1994; Gerdol & Hughes 1994a). The gastropod epifauna of the studied zone graze on these microalgae as well as on bacteria and fungi (Branch & Pringle 1987 in Alongi 1989; Dye & Lasiak 1987). Several other studies found a characteristic microalgal increase after exclusion of the gastropod community (Fenchel & Kofoed 1976; Nicotri 1977; Pace *et al.* 1979; Branch & Branch 1980; Connor *et al.* 1982).

Nematodes: Though the overall nematode density is affected by a procedural effect, one of the dominant 2A nematode genera (*Ethmolaimus*) underwent a clear positive exclusion effect after two months (from about 100 to about 500 ind./10 cm^2).

Predation pressure on the nematodes would have led to a proportionate increase in all genera after predatory exclusion (Hoffman *et al.* 1984; Bell & Coull 1978; Dittmann 1993). The selection of the nematodes as prey is suppressed by a lower availability, a smaller body size, and a weaker escape behaviour into the water column as is usually found for copepods (Warwick 1987; Ellis & Coull 1989). In general, nematodes are less important in gut analyses than copepods, though this might be due to the lack of an exoskeleton and to faster digestion (Warwick 1987).

Exploitative competition for benthic microalgae is given as a more plausible explanation for the disproportionate impact on nematodes after epibenthic removal. A strong link between nematodes and microalgae was already illustrated in an Indian mangrove sediment. It was assumed that nematodes depend, energetically rather than numerically, on the autotrophic production of diatoms since the production of aerobic and heterotrophic bacteria appeared to be unimportant in the turnover of carbon (Sultan Ali *et al.* 1983). The significant increase in a dominant 2A genus is likely to be a response to the microalgal density increase. Epistrate feeding nematodes almost exclusively feed on microalgae (bacteria are much less important) and need high algal food concentrations. They have already been reported to positively react to algal density peaks (Admiraal *et al.* 1983). The *Ethmolaimus* density peak coincides exactly with the chlorophyll *a* peak. The procedural effect on other 2A genera (such as *Spilophorella* and *Microlaimus*) might mask an underlying exclusion effect due to a strong artefact in the experiment. The cause of this artefact could not be traced though it might point to a passive resuspension (Chapter VIIB).

A comparable study in a salt marsh did not detect an exclusion effect on nematodes (Bell 1980). Predation pressure was thought to be present though not detectable due to a depth refuge, to specific predatory interactions, or to too long sampling intervals. From our findings, however, it is evident that this lack of effect might be ascribed to the insufficient exclusion of resident epifauna competing for food with the nematodes.

A peak density of *Ethmolaimus* was observed leading to density stabilization at the pre-experimental level (100 ind./10 cm²). Internal predation or possible intracompetitive forces might have caused this sudden decline.

Amphipods: The amphipod *Grandidierella* spec. underwent a positive exclusion effect with a density increasing towards an asymptotic level (from about 1000 to about 2000 ind./m²).
Some marsh studies have described a predatory influence of natant epibenthos on amphipods (Vince *et al.* 1976; Van Dolah 1978). However, the exclusion of resident crabs on a tropical mangrove flat did not indicate a predatory effect on the amphipods (Dittmann 1993). In our study, no amphipod prey evidence (table 8.6) and no possible prey size selectivity (Chapter VI) was observed. These factors led us to believe that a structuring force other than predation was acting on the amphipod community.

Again, exploitative competition is a plausible explanation for the behaviour of the amphipod *Grandidierella* spec. after exclusion. Although several mangrove studies describe amphipods as either leaf shredding or detritivorous (Kostalos & Seymour 1976; Boonruang 1978; Poovachiranon *et al.* 1986; Camilleri 1989; Camilleri 1992), microalgae and diatoms might also be an important food enrichment (Hargrave 1970; Pinckney & Sandulli 1990). Although these microalgae may be heavily ingested, they are not always visible in the gut tract (Gerdol & Hughes 1994b). In this study, the exclusion effect on *Grandidierella* spec. was observed one month after the incline in the concentration of chlorophyll *a*. Moreover, the asymptotic increase in the amphipod genus was followed by a sudden decline in chlorophyll *a* and the 2A nematode genus *Ethmolaimus*. Whereas detritus, small leaf particles and whole leaves, possibly culturing a microalgal growth, might be of importance to the amphipods, it is believed that 2A nematodes and *Grandidierella* spec. are rather involved in a food competitive system around the limited microalgal community in this vegetation zone.

b) *Ceriops tagal* (figure 8.8b)

Microalgae: The increase in the concentration of chlorophyll *a* (from about 4000 to about 10000 ng/g DWT) in the *Ceriops* zone is gradual and peaks only after four months of caging. The high pigment concentration and the late and gradual positive exclusion effect, as compared with that of the *Avicennia* zone, is probably due to the open vegetation and the difference in epifaunal composition. The gastropod *Terebralia palustris* which is the most important microalgae feeder in *Avicennia*, primarily feeds on *Ceriops* leaves in this zone. The only possible microalgae feeding candidates in *Ceriops tagal* are therefore the gastropod *Cerithidea decollata*, the crabs *Uca lactea annulipes* and *Metopograpsus thukuhar*, and the hermit crab *Clibanarius longitarsus*. However, these epifaunal species are not very abundant. The most abundant animals such as *Uca* and *Cerithidea* prefer bacteria to microalgae (Dye & Lasiak 1986; Dye & Lasiak 1987). Moreover, *Cerithidea* and *Metopograpsus* are frequently found on the trees exhibiting no heavy impact on the sediment (table 8.6).

Nematodes: The significant exclusion effect on the total nematode density (from about 1000 to about 2000 ind./10 cm²) occurred before the significant increase in the chlorophyll *a* concentration (after two months of caging). In this mangrove zone, exploitative competition for microalgae is therefore not evident. A fast positive response of nematodes after a specific *Uca* exclusion was also reported by Dye & Lasiak (1986). Since *Uca* predation pressure was not believed to be important (the *Uca* flotation feeding technique avoids ingestion of larger particles such as nematodes), other reasons for their results have been mentioned. Inhibited *Uca* foraging and thus the increase in sediment stability could possibly have led to a vertical upward migration of nematodes in the soil.

Moreover, the increase in the *Uca* food, detritus and bacteria in particular, was believed to have stimulated the total meiofauna and nematode community via exploitative competition. In Australian studies especially, mangrove nematodes are mentioned to be dominated by selective deposit feeders, which have an important role in the decomposition of detritus and the stimulation of bacterial production (Odum & Heald 1972; Alongi 1987b; Warwick 1987; Nicholas *et al.* 1991). However, in this study, the dominance of 2A nematode genera (about 50 % of the total nematodes) indicates that oligochaetes are the important detritivores. An effect on the entire nematode community, in terms of food competition with the epibenthos, is therefore predicted only to be mediated by microalgal density changes. As a matter of fact, the significant increase in nematodes (and thus 2A genera in particular), during the first two months, might be a reaction to the weak and non-significant microalgal stimulation. This is similar to what has been found for the 2A genus *Ethmolaimus* in *Avicennia marina*. After this period, however, the concentration of chlorophyll *a* surpassed 6000 ng/g DWT, a level above which no food limitation is probably occurring. The driving competitive force behind nematodes in the *Avicennia marina* zone is then probably replaced by another, maybe more physical, structuring force. Complex interactions (internal predation and intracompetitive or larval-adult interactions) within the infauna are also important in structuring soft bottom marine communities (Ambrose 1984). An infaunal predation might point to the nematode decline. The only predatory infaunal organisms in this study are believed to be the 2B nematode genera (both meio- and macrobenthic). Although they are numerically not dominant, they were shown to be able to play an important role in the carbon flow model and small food web. A significant proportion of their diet was reported to consist of metazoans (Kennedy 1994). However, these multilevel interactions have been frequently stated as not existent in tropical tidal flats and especially not in mangrove sediments due to a low endobenthic diversity.

Amphipods: No exclusion effects were detected for the amphipod community consisting of *Grandidierella* spec. and *Ampelisca* spec. Moreover, the low amphipod density was unexpected since microalgal food concentrations were noticeably high. Again, this might be explained by other unknown physical or complex biological interactions causing the amphipod community to be kept under its food carrying capacity. Amphipod variations are therefore probably not induced by the same microalgal competitive system as the one described for *Avicennia marina*. This, however, does not reject the amphipods' important role in, and strong liaison with, the microalgal system. The strong decline in microalgae after 5 months of caging is probably linked with a not registered natural variation.

2. Detrital competitive system

a) *Avicennia marina* (figure 8.8c)

Muddy detritus: The significant decrease in the median grain size (before combustion) after 4 months reflected a very slight increase in the muddy detritus. This positive exclusion effect was late and very weak (a muddy detrital proportion of about 13 % in the cages against about 10 % in the other treatments). The only abundant epibenthic animals feeding on this fraction are the gastropods *Cerithidea decollata* and *Terebralia palustris* (which does not feed on *Avicennia* leaves). These gastropods exhibit rather non-selective deposit feeding behaviour and do not, therefore, specifically select the muddy detritus (table 8.6). It is therefore clear that the observed evolution of the muddy detritus in the cages is not influenced by the absence of epibenthos but rather mediated by a natural variation.

Oligochaetes: For the oligochaete densities also, the positive exclusion effect occurred quite late and was only reached gradually. The slight non-significant positive effect on the macrobenthic oligochaetes was covered by a much stronger procedural effect. The most important dietary item for interstitial tubificids and enchytraeids is organic matter and detritus associated with bacteria and fungi (Giere 1975; Giere & Pfannkuche 1982; Reise 1985; Giere 1993; Hedlund & Augustsson 1995). Microalgae are not important as food for tubificids but might be grazed upon by smaller enchytraeids (Giere 1975). However, a detrital competitive system between the oligochaetes and the epibenthos seems to be revealed only slightly at the end of the experiment. It is probably suppressed by the high initial amount of muddy detritus (about 30 %) and the low presence of detritus feeding epifauna. This keeps the oligochaetes in the *Avicennia marina* soil from being food limited. However, the involvement in, and the monopolization of, the detrital decomposition by oligochaetes in this zone seems to be obvious. The natural decrease in muddy detritus in the cages, which was not induced by epibenthic exclusion, seems to be caused by the oligochaete increase, feeding on this detrital pool. In *Avicennia marina*, the muddy detrital pool is therefore believed to be controlled by its oligochaete consumers. However, this is only speculative since it is based on a method of agreement among the non-manipulated variations of detritus and the meio- and macrobenthic oligochaete densities.

b) *Ceriops tagal* (figure 8.8d)

Muddy detritus: The muddy detrital fraction of the cage sediment increased after one month of caging (from about 10 to about 25 %) in contrast with the stable and lower proportion of the blank sediments (about 9 %). The detritus is produced by either 'sloppy' feeding or by faecal pellets of leaf shredders such as the gastropod *Terebralia palustris* and the crabs *Sesarma guttatum* and *Metopograpsus thukuhar* (table 8.6). The mangrove leaves are thereby transformed to smaller POM fractions (0.45-350 µm) (Camilleri 1992). This detritus is then ingested by selective and non-selective deposit feeders such as the epifaunal crab *Uca lactea annulipes*, the hermit crab *Clibanarius longitarsus* and the gastropod *Cerithidea decollata* (table 8.6). An increase in this small detrital fraction is therefore probably due to the exclusion of these detritivores. Moreover, other mangrove studies mentioned *Uca* to be food limited leading to a strong pressure on the amount of detritus (McIntosh 1988; Camilleri 1989).

Oligochaetes: Both meio- and macrobenthic oligochaetes indicated a positive exclusion effect. Whereas the meiobenthic part showed a peak density with a decline (from about 5 to 20 and back to 5 ind./10 cm^2), the macrobenthic oligochaetes increased to an exceptionally high level (from about 2500 to about 45000 ind./m^2).

A reaction to predatory exclusion was not thought to be the driving force behind the impact on oligochaetes in this high intertidal tropical region. Firstly, the resident and permanent epifauna were not described as carnivorous (table 8.6). If they would have been found to be predatory in nature, a relation would have been expected with an omnivorous or odd-job predatory behaviour (Reise 1985). Firstly, other studies were not convinced that predation by resident crabs is the structuring factor for oligochaetes (Dye & Lasiak 1986; Dittmann 1993). Secondly, though oligochaetes have been mentioned as the common food source for young demersal fish, shore crabs, shrimps, and birds of temperate regions (Giere & Pfannkuche 1982; Giere 1993), a lot of studies that predicted a predation pressure by natant organisms on oligochaetes, did not detect effects after exclusion (Virnstein 1977; Fleeger *et al.* 1982; Kneib & Stiven 1982; Ward & Fitzgerald 1983; Frid & James 1988). For tropical regions too, no predation pressure on oligochaetes by natant epibenthos was reported (Vargas 1988; Sasekumar *et al.* 1992).

In this study, several elements confirm a strong oligochaete competitive system around the common detrital food source. In the first place, the average natural muddy detrital content of the *Ceriops tagal* sediment is low (about 9 %). Like oligochaetes, several deposit feeding crabs (such as *Uca*) and gastropods (such as *Cerithidea*) also feed on detritus associated with bacteria, fungi, and protozoans (Dye & Lasiak 1986; Branch & Pringle 1987 in Alongi 1989; table 8.6). The oligochaetes and the deposit feeding epibenthos do not only depend on the same food but are also both food limited too. In salt marshes and mangroves, the deposit feeding epifaunal *Littorina*, *Sesarma*, and *Uca* were reported to be food limited (Genoni 1985; McIntosh 1988; Camilleri 1989). An artificial increase in the detritus was only answered by a moderate increase in the *Uca* density. This automatically pointed to an exploitative competition from other consumers (Genoni 1985). Also oligochaete populations were observed to be food limited. Although, at first sight, they all seem to be ingesting the same food, an underlying trophic specialization could biologically accomodate the oligochaete community (Giere 1975).

Therefore, this *Ceriops tagal* sediment is believed to contain a competitive system for detritus. An increase in the muddy detritus is answered by an increase in the meiobenthic and macrobenthic oligochaetes which eventually leads to a sudden decline in the meio-oligochaetes and the muddy detritus. The positive exclusion effect on meio- and macrobenthic oligochaetes occurred respectively one and two months after the muddy detrital increase. The faster response of the meiobenthic animals might be linked with a higher turnover rate and P/B ratio (Bell 1980; Vargas 1988). Competition between meio- and macrobenthic oligochaetes for detritus promotes the larger oligochaetes at the expense of the meiobenthic fraction. In excluding the abundant deposit feeding epifauna, the macrobenthic oligochaetes eventually take over this role. This detrital competitive system thus confirms the important role of oligochaetes in the detrital decomposition and the natural variation as found in *Avicennia marina*. The oligochaete community in *Ceriops tagal* is believed to be controlled by its limited detrital food source whereas the opposite was suggested for the *Avicennia* vegetation zone.

3. Summary

The studied East African high intertidal mangrove benthic community is involved in two intermixed decompositional systems. These systems become more obvious when food sources are limited and food supply is low, leading to food competition (Evans 1983). Exploitative competition will get even stronger when consumers are abundant, food limited and therefore food structured. Deposit feeding communities, as opposed to suspension feeders, are mainly structured according to food competition since their densities and species composition remain relatively stable through space and time (Levinton 1972).

(1) The microalgal system centers around the microalgae as food, and the 2A nematodes, *Grandidierella* spec., and the microalgal deposit feeding epibenthos as consumers. The fate of the considerable microalgal production in sediments, especially in the tropics, has long been an unanswered question. A relatively small fraction was reported as food for macrobenthic deposit feeders (*e.g.* amphipods). However, it is generally accepted now that the meiofauna could also be major consumers of edaphic microalgae (Montagna 1984). This indeed makes the proposed competitive system plausible.

Applied to *Avicennia*:

- Low chlorophyll *a* concentration and pronounced microalgae feeding epibenthic community
- Strong and fast increase in chlorophyll *a* after epibenthic exclusion
- Positive reaction of the densities of 2A nematode genera and of the amphipod genus *Grandidierella* spec.
- Decline in the chlorophyll *a* concentration and the 2A nematode density
- Higher density level of *Grandidierella* spec. taking over the role of the microalgae feeding epibenthos

Applied to *Ceriops*:

- Higher chlorophyll *a* concentration and less pronounced microalgae feeding epibenthic community
- Strong but slow and gradual increase in chlorophyll *a* after epibenthic exclusion
- Initial positive reaction of the density of 2A nematode genera up to a certain chlorophyll *a* level
- No *Grandidierella* spec. response

(2) The detrital system centers around the muddy detritus as food, and the oligochaetes (meio- and macrobenthic) and the detrital deposit feeding epibenthos as consumers. Meiofauna are known to affect the availability and usage of detritus by macrofauna (Alongi & Tenore 1985). The competition between meiobenthos and macrobenthos for food and space as possible force behind this influence, has largely been ignored, however. This is, in part, due to the inherent difficulties to demonstrate competition, especially for food, in nature.

Applied to *Avicennia*:

- High detrital content and very small detritus feeding epibenthic community
- No response of muddy detritus to epibenthic exclusion
- Non-manipulated increase in oligochaete densities coinciding with a decrease in muddy detritus fraction

Applied to *Ceriops*:

- Lower detrital content and pronounced detritus feeding epibenthic community
- Strong and fast increase in muddy detritus after epibenthic exclusion
- Positive reaction of the meiobenthic oligochaete densities (with time lag)
- Positive reaction of the macrobenthic oligochaete densities (with time lag)
- Decline in the muddy detrital content and the meiobenthic oligochaete density
- Higher density level of the macrobenthic oligochaetes taking over the role of the detritus feeding epibenthos

These results clearly confirm the existence of the two food systems, with the amphipod *Grandidierella* spec. and the bulk of the nematodes predominantly feeding on microalgae, and the oligochaetes specifically feeding on detritus. This food seems to be structuring and regulating the endobenthic community, especially in those regions where it is limited.

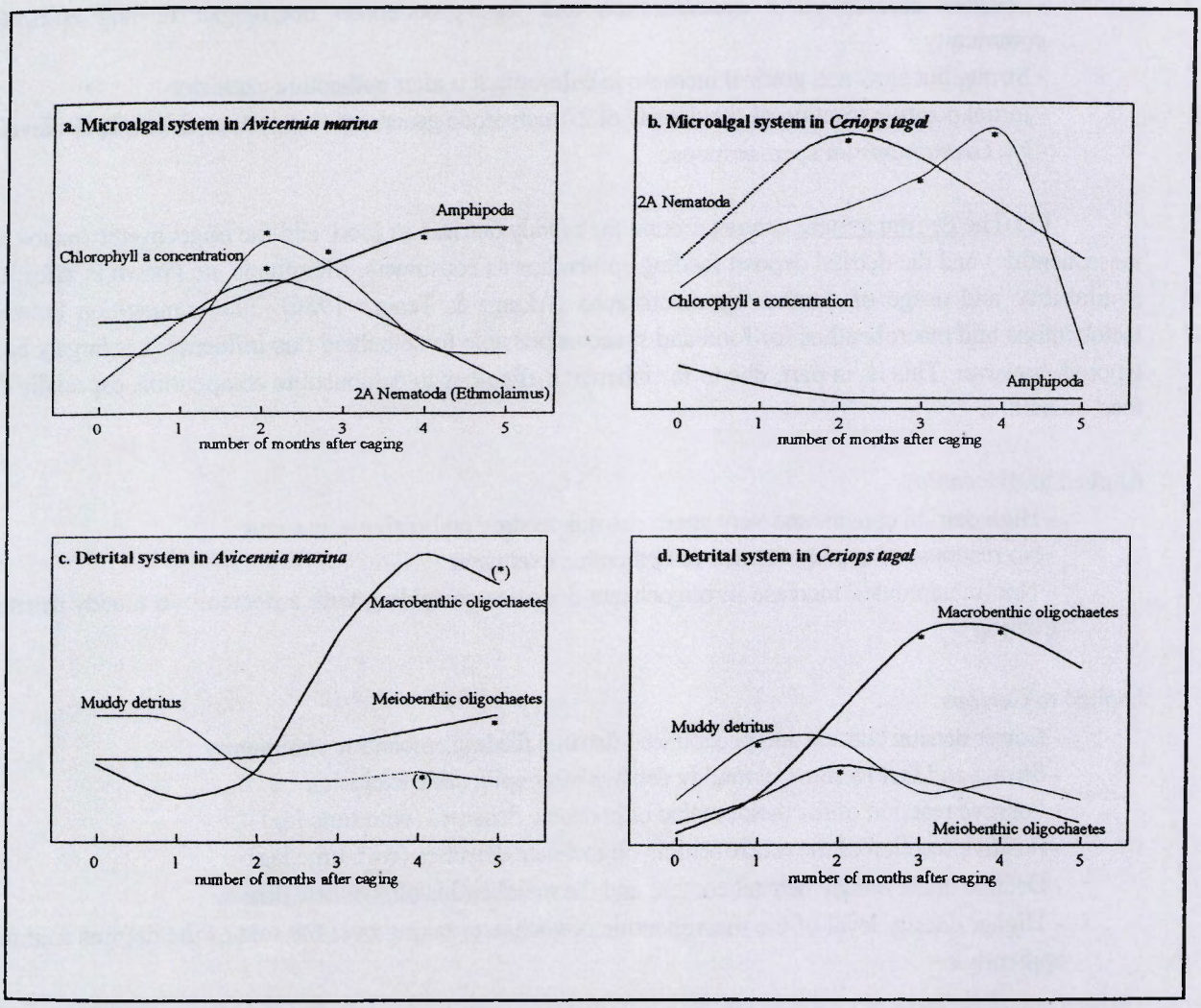


Figure 8.8: The two decompositional systems linked with microalgae and muddy detritus and their evolution during the exclusion experiment in both studied zones (schematic representation) (* = positive and significant exclusion effect).

D. PREDATION

Chapters IV, V, VI, and VII mention only copepods, insect larvae, and the polychaete *Namalycastis* spec. to be regulated by an epibenthic predation.

1. Copepoda

a) Prey evidence

In general, benthic copepods (harpacticoids) form an important prey for several natant organisms. Especially juvenile fishes prey on copepods (Hicks & Coull 1983; Coull & Palmer 1984; Warwick 1987; Gee 1989; Nelson & Coull 1989). The earliest evidence for this interaction was given by Smidt (1954) (in Coull & Palmer 1984). Although thought to be less important than fishes (Reise 1979), shrimps were reported to feed on harpacticoids too (Reise 1979; Pihl & Rosenberg 1984; Gee *et al.* 1985). The transfer to the resident epibenthic realm, as in marshes and mangroves, is not so evident. Some resident crabs are thought to ingest copepods (Hoffman *et al.* 1984; Dittmann 1993). The flotation feeding technique of several crabs (*i.e.* fiddler crabs), however, avoids the uptake of larger particles such as microalgae and meiobenthos (Dye & Lasiak 1986; Dye & Lasiak 1987).

The resident, deposit feeding epifauna in the studied area use this flotation technique (*Uca* spec., *Sesarma guttatum*) or nonselectively 'ingest' or 'graze on' the sediment (gastropods) (table 8.6). A specific uptake of copepods, if present at all, is therefore believed to be due to natant, visiting organisms which possibly lead to an intertidal impact gradient (Virnstein 1977).

b) Functional, predatory evidence

Though prey evidence is not necessarily causing predation pressure, harpacticoids were frequently found to be numerically stimulated after exclusion of predatory epibenthos (Bell & Coull 1978; Bell 1980; Fleeger *et al.* 1982; Hicks & Coull 1983; Ellis & Coull 1989). In this study, the benthic copepods have undergone a significant, but very weak exclusion impact after one year of caging in the *Ceriops tagal* zone (figure 8.9). We are also inclined to assign this impact to natant predatory forces. The absence of a similar effect in the *Avicennia marina* zone could indeed point to the intertidal gradient (figure 8.9) (Virnstein 1977). This upper intertidal zone is less frequently flooded. Moreover, during high water at spring tide, the observed densities of epibenthos, visiting the *Avicennia marina* zone, were quite low (personal observation). Also for temperate salt marshes, there was a lack of evidence for predatory control of the harpacticoid community in upper regions (Fleeger *et al.* 1982). The increase in the total copepod density in the lower intertidal *Ceriops tagal* zone especially during the last half year of caging, was similar to that found in experiments by Bell (1980). Predation was the driving force behind this late effect.

c) Prey selectivity

Why are the copepods the only meiobenthic taxon affected by predation in this study ?
Copepods are generally stated to be the major meiobenthic taxon in terms of food and/or biomass transfer to the demersal/pelagic realm (Hicks & Coull 1983). Selective predation on copepods was reported by several salt marsh cage studies (Bell & Coull 1978; Fleeger *et al.* 1982; Ellis & Coull 1989). One of the reasons for this prey selectivity is the more pronounced availability and vulnerability of copepods, due to their high mobility, activity, and visibility (Warwick 1987; Nelson & Coull 1989; McCall & Fleeger 1993).

This is especially true for muddy sediments in which copepods tend to become surface dwelling (Nelson & Coull 1989; Giere 1993). Sandy communities were found to be less or not at all affected by predation (Reise 1979; Webb & Parsons 1991). The rather sandy character of the studied zones could therefore be a reason for the overall weak impact. This was additionally reflected upon, due to a lack of surface accumulation in the vertical gradient of the copepod community in the *Ceriops tagal* sediment (Chapter IV).

Other possible forces behind the selection of prey were mentioned to be those based on size and emergence behaviour (Warwick 1987; McCall 1992). The selection of copepods as prey due to their larger size would predict an even stronger predatory impact on oligochaetes and polychaetes for this study. But that did not happen. The higher emergence behaviour of copepods might advance predation efficiency, if the predators are not biting into the sediment but rather striking at objects in the water column. An upward migration of copepods and the presence of natant predators during high water would result in an ideal predator-prey interaction. Harris (1972) (in Hicks & Coull 1983) found no significant change in vertical copepod distribution at different stages of the tide. This could be due though, to the sample site on a beach that was always saturated by water. However, harpacticoids in general are thought to migrate down at ebb and upwards at flood (McLachlan *et al.* 1977 in Hicks & Coull 1983).

d) Competition

The positive exclusion effect on copepods in a mangrove study by Dye & Lasiak (1986) was thought to be caused by a food competitive interaction between these copepods and the fiddler crabs. Juvenile crabs in particular, are possible competitors with copepods (Bell 1980). Their common food consists of detritus and single particles such as diatoms and fungi (Hicks & Coull 1983). The impact of juvenile crabs in this study is minimal since the immigration in the cages during the experiment was partly compensated by a continual removal. Consequently, possible food competition is believed to be minor compared to the predatory structuring impact exhibited on the harpacticoids.

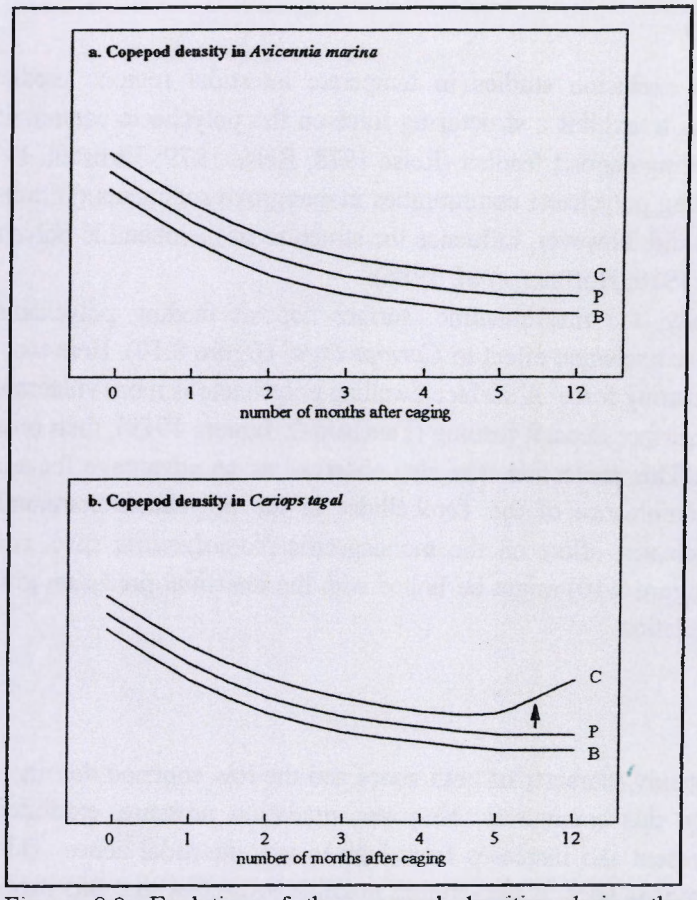


Figure 8.9: Evolution of the copepod densities during the experiment in both studied zones (schematic representation) (B = blank; P = partial cage; C = cage).

2. Polychaeta

a) Competition

Namalycastis spec. is a nereid polychaete genus with an eversible pharynx and jaws but without paragnaths. Nereids are generally described as omnivores although most species have a relatively limited diet, consisting of detritus, algae and diatoms (Fauchald & Jumars 1979). Few are carnivorous and some are real omnivores. The *Namalycastis* spec. in this study is considered as detritivorous. Most polychaetes in mangrove sediments were described as detritivorous (Kumar 1995) and *Namalycastis abiuma*, a common polychaete from salt marshes, was observed to feed on decaying wood on the surface (Rasmussen 1994). This feeding behaviour and the lack of an exclusion effect in *Avicennia marina* (figure 8.11), might refer to a polychaete role within the described detrital competitive system of *Ceriops tagal*. However, food competition might play a minor role in structuring the polychaete community and explaining the positive response in the *Ceriops tagal* forest (figure 8.10). It is certainly not the driving force, however, since macrobenthic oligochaetes are so abundant that it is hard to believe that they would not be outcompeting the polychaetes.

b) Predation

Most cage exclusion studies in temperate intertidal regions predicted and confirmed natant epibenthic predators to exhibit a structuring force on the polychaete community. These polychaetes were mainly surface dwelling deposit feeders (Reise 1978; Reise 1979; Virnstein 1979; Haase 1993). Resident crabs are not affecting polychaete communities in mangrove sediments (Dittmann 1993). Both natant and resident epibenthos did, however, influence the structure of meiobenthic polychaetes in salt marshes (Bell & Coull 1978; Bell 1980; Hoffman *et al.* 1984).

In this study, the macrobenthic, surface deposit feeding polychaete *Namalycastis* spec. has undergone a positive exclusion effect in *Ceriops tagal* (figure 8.10). Here too, predation is believed to be the underlying structuring force. A surface dwelling polychaete is more vulnerable to predation. Though the terebellids are also surface deposit feeding (Fauchald & Jumars 1979), their protective tube might be a way to avoid predation. This protection was also observed as an advantage for amphipods (Nelson 1979). It could explain the dominance of the Terebellidae in the polychaete community of *Ceriops tagal*. The absence of any exclusion effect on the monospecific *Namalycastis* spec. community in the *Avicennia marina* sediment (figure 8.10) might be linked with the intertidal predation gradient as already mentioned for the copepod regulation.

3. Summary

The quite sandy character of both zones and the low copepod density made it difficult to detect a structuring force on this community. However, predation pressure, exhibited by natant organisms on harpacticoids, is present and increases from high to low intertidal zones. This is also confirmed for the polychaete *Namalycastis* spec. It is therefore possible to predict that this predation pressure will become more pronounced in low intertidal zones such as *Rhizophora mucronata* which are more frequently flooded and contain more mud. It might even affect other and more abundant endobenthic taxa in those zones.

For the high intertidal zones studied it is clear, however, that exploitative competition is much more decisive in regulating and structuring the endobenthic community, than epibenthic predation.

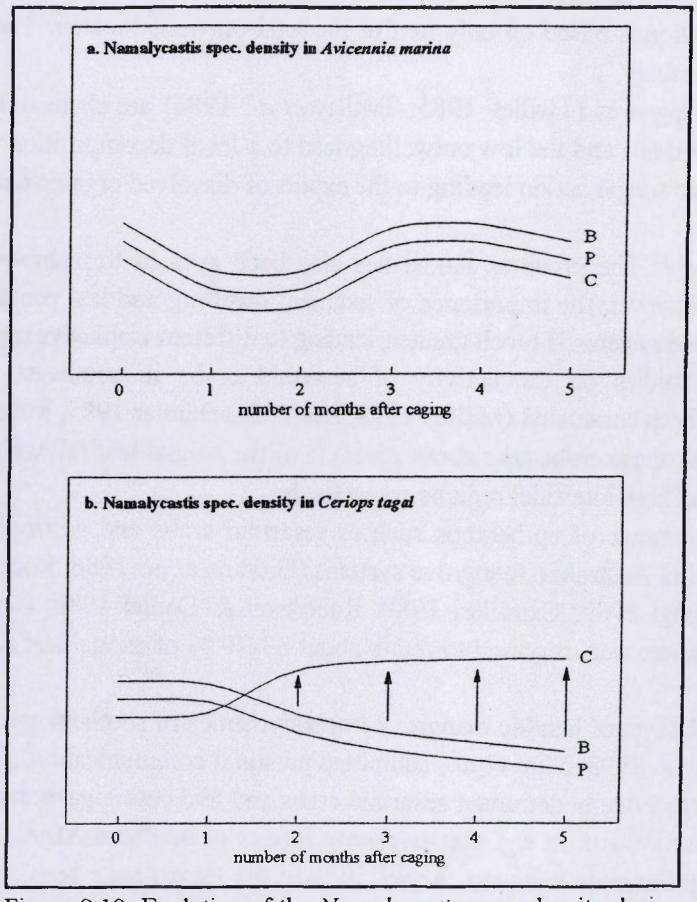


Figure 8.10: Evolution of the *Namalycastis* spec. density during the experiment in both studied zones (schematic representation) (B = blank; P = partial cage; C = cage).

E. CONCLUSION

1. General trophodynamics of mangroves

a) Strategies

Before going into specific pathways it is necessary to give an outline of two different trophodynamical mangrove strategies that occur in the New World and the Old World respectively.

New World: The earliest and most extensive research on mangrove trophodynamics has been carried out in Florida and the Carribean region. These mangroves are generally characterized by the unimportant role of leaf consuming crabs in the initial processing of litter.

For riverine and fringing mangrove forests (Odum & Heald 1972; Lugo & Snedaker 1974; Cundell *et al.* 1979; Flores-Verdugo *et al.* 1987; Robertson 1987), this involves a large (> 80 %) outwelling of litter fall, phytoplankton, benthic algae, and seagrasses to the subtidal estuary. Only there will fragmentation of the material be carried out by crabs or smaller detritivores such as amphipods. Consequently, the importance of litter processing by invertebrates decreases with tidal height. Processing, thereby, initiates a subtidal decomposition made up from bacterial, fungal, and saprophytic decay, and a utilization and reutilization by invertebrates via pellet production.

Finally, these animals themselves are a source of energy transfer to the carnivores. The nearshore, estuarine secondary production is based on only half of the total outwelled matter. The other part is exported much further from the estuary.

Basin mangroves (Twilley 1985; Twilley *et al.* 1986) are characterized by a low water turnover. The minor role of crabs and the low outwelling lead to a local decomposition which is primarily effected by direct bacterial and fungal action leading to the export of dissolved organic matter and leachates.

Old World: The previous model has also been applied to mangrove systems of the Indo-West Pacific region. However, the importance of sediment dwelling and leaf consuming crabs on the mangrove forest floor in these systems is much greater, leading to different trophodynamical channels.

Several studies on the activity of sesarmid crabs in southeast Asian riverine and fringing mangroves have been conducted (Malley 1978; Leh & Sasekumar 1985; Robertson 1986; Smith 1987; Lee 1989). In general, these crabs take about 25-30 % of the annual leaf fall with a removal of 9 % and 20-30 % for low/mid and high intertidal regions respectively.

The importance of epibenthos such as sesarmid crabs and gastropods in litter retention is even more pronounced in Australian mangrove systems (Giddins *et al.* 1986; Robertson 1986; Robertson 1987; Smith 1987; Alongi 1989; Camilleri 1989; Robertson & Daniel 1989; Camilleri 1992; Micheli 1993). These leaf consumers were reported to retain about 33-70 % of annual leaf fall leading to a very low litter accumulation.

Little is known of benthic mangrove trophodynamics of southern and eastern Africa (Micheli *et al.* 1991; Steinke *et al.* 1993; Slim *et al.*, submitted personal communication). It is evident however, that the presence of the numerically dominant sesarmid crabs and leaf eating gastropods (as in this study) points to the same retention system. In *e.g.* the *Avicennia* forests of southern Africa, the leaves are predominantly eaten by the crab *Sesarma meinerti*. About 50 % of the leaves have been reported to be removed by this crab (Emmerson & McGwynne 1992). Gut contents revealed that these leaves make up about 75 % of the crab's diet (Steinke *et al.* 1993).

For Indo-West Pacific areas, it is generally held that (Robertson 1987; Robertson & Daniel 1989):

(1) an increase in the turnover rate of the leaves will make them less available to higher consumers
(2) leaf retention will increase with decreasing tidal export
(3) primary and secondary production are more tightly coupled in space as well as in time
(4) litter processing by resident mangrove invertebrates will increase with tidal height

b) Pathways of a mangrove-estuarine system involving crabs (figure 8.11)

Herbivory: The above-ground herbivory consists mainly of leaf damage by insects and crabs thereby leading to a direct consumption of the primary production. Only 2 % of the leaves are processed via this direct pathway (Robertson & Duke 1987). For mangroves, the energy and material dominantly flows through the decomposition pathways rather than through a typical plant/herbivore/carnivore food chain. This was also reported for other important tropical systems such as open savannahs and tropical rainforests.

Source of detritus: The mangrove standing stock consists of 22-50 % of wood (detritus, branches, trunks, and above-ground dead parts) and of 50-78 % of litter (leaves, stipules, propagules, and twigs). The amount of below-ground biomass (roots) is unknown. Litter fall and detritus are mainly composed of autochthonous mangrove material. The leaves frequently make up more than 50 % (98 % of all leaves eventually reach the forest floor) coupled with branches, propagules, and twigs. In some forests, a high biomass of dead wood is maintained (Robertson 1987).

It is further supplemented by benthic algae and epiphytes on logs, branches, lower trunks, and prop roots (Hoffman & Dawes 1980). The contribution of benthic microalgae is small since shading is severe under most forest canopies. Zero net algal primary production was estimated for low, mid, and high intertidal mangrove zones in Australia in contrast with unshaded intertidal flats (Robertson 1987; Alongi 1989). The allochthonous contribution to the litter accumulation mainly originates from deposited phytoplankton and seagrasses (Hoffman & Dawes 1980). It is obvious that the amount of detritus greatly exceeds that which is consumed by herbivores in mangroves.

Detrital export: The way and the amount of leaf, litter, detritus, and DOM export from mangroves is still an open question. The migration of animals feeding in or near mangroves during part of their life cycle, contributes to this export. This was reported for penaeid prawns (Staples 1980 in Robertson 1987). The most important loss, however, is thought to be attributed to the direct transport known as 'outwelling' (Hemminga *et al.* 1994 for Gazi; Lee 1995 for review). Van der Valk & Attiwill (1984) reported that about 40 % of the mangrove litter was exported each summer. Root litter was not believed to be exported. Recently, the contribution of DOM to outwelling has gained in importance possibly leading to even higher export amounts (Lee 1995). The dynamics of the detrital movement is complex and dependent on estuarine geomorphology, tidal flux, and type of detritus (*e.g.* buoyancy). Leaves were found to be exported much further than refractory detritus.

Leaf shredding: Whole leaves, the most important part of the litter fall, can be subject to direct microbially affected processes. However, most freshly fallen leaves and propagules are first processed by large organisms such as crabs. These leaf shredders thereby initialize the decomposition process before the litter is removed by tides. They were estimated to eat > 50 % of the retained leaves (Robertson & Daniel 1989). Leaf shredding by crabs transforms the litter in three ways. The largest part of the processed leaves is directly consumed (86 %) and transformed into faecal pellets. These pellets contain POM fractions (between 100 and 1600 µm) (Malley 1978). During this consumption, 'sloppy' feeding also produces small fractions which are lost to the shredder. However, the remaining part (14 %) of the leaves is first plastered to the burrow walls. Aging of this material will lead to a decrease in tannin and flavolan concentrations eventually leading to a preferred consumption. Only a small fraction of the buried litter gets lost to the food web (Robertson & Daniel 1989). Besides crabs, other possible leaf shredders are gastropods, juvenile crabs, isopods, amphipods, insects, shrimps, and capitellid polychaetes (Boonruang 1978; Beever *et al.* 1979; Poovachiranon *et al.* 1986; Robertson & Duke 1990; Robertson & Daniel 1989; Camilleri 1992; Proffitt *et al.* 1993; for Gazi: Slim *et al.*, submitted personal communication). Most of them must consume additional food (such as bacteria and other invertebrates) in order to maintain their minimum nitrogen requirements (Giddins *et al.* 1986; Robertson 1986). Sesarmid crabs were indeed observed to be partly carnivorous (McIntosh 1984).

Detrital processing: The presence of POM in the mangrove soil is therefore mainly derived from the activity of these leaf shredders. The POM pool is, however, also replenished by microalgal accumulation and via DOM transformation (Camilleri & Ribi 1986). The POM fractions vary from coarse (about 1.5 mm) to fine (< 600 µm). In general, the most abundant fraction is smaller than 84 µm whereas only 1-4 % of the sediments are composed of 84 µm - 1 mm POM particles (Camilleri 1992). Also dissolved organic matter (DOM) is believed to be an important 'detrital' element comprising leachates and lignocellulosic components such as tannins, flavolans, and phenolics. Bacterial attack is able to transform this DOM into POM leading to an alternative pathway (Benner *et al.* 1986 in Alongi 1989; Camilleri & Ribi 1986).

Whole litter, POM, and DOM are gradually reworked by bacteria (for Gazi: Rao *et al.* 1994; Middelburg *et al.*, submitted personal communication). The formation of small POM fractions facilitates bacterial production and thereby reduces the decomposition time by 60 % (Lugo & Snedaker 1974; Robertson & Daniel 1989). The microbial community eventually channels the majority of the primary production before making it available to higher consumers (Robertson 1987). The fate of the high bacterial productivity itself is questionable (Alongi 1988a, 1988b). However, the structuring regulation of the bacterial community is believed to be mainly a result of the nutrient conditions and other environmental factors whereas predatory influence is of minor importance. This predatory impact might get more pronounced in aerobic layers where more benthic organisms are available. Nevertheless, the role of bacteria in mangrove soils can be seen in terms of prey for invertebrates or of nutrient regeneration (Alongi 1988b).

Detritivores: Several selective and non-selective deposit feeders use the mangrove detritus as their dominant diet. This detritivorous community consists of endobenthos such as amphipods, nematodes, copepods, isopods, oligochaetes, polychaetes, and sipunculids (Poovachiranon *et al.* 1986; McIntosh 1988), resident as well as natant epibenthos such as ocypodid crabs, gastropods, hermit crabs, shrimps, prawns, and fishes (McIntosh 1988; Vannini, personal communication) and zooplankton (Poovachiranon *et al.* 1986). The ingestion, digestion, and excretion of the detritus stimulates the detrital processing and accelerates the mineralization as mentioned previously. This then promotes bacterial production and enriches the food by decreasing the C/N ratio and accumulating N, P, and trace metals (Webster & Benfield 1986).

Secondary production values for meio- and macrofauna of mangroves remain questionable since most studies have used P/B ratios from subtidal temperate regions (Sultan Ali *et al.* 1983 ; McIntosh 1984). No valid estimates of secondary production in mangrove sediments have been reported until now. However, tropical species are generally reported to have a greater activity, faster growth rates, shorter life spans, higher mortality rates, and a greater production per unit biomass (Alongi 1989).

Predation: Even if secondary producers did reflect a small biomass and low productivity, they still might be an important food source for carnivores (Evans 1983). Predation is believed to be twofold. Infaunal predation has not been mentioned for mangrove sediments but predaceous macroinfauna and meiofauna (such as annelids, turbellarians, copepods, and nauplii) were reported to be important in temperate sediments (Kennedy 1993). Epibenthic predation is regarded to be the most important predatory pathway in mangroves. These epibenthic predators could be large terrestrial carnivores (monkeys, raccoons,...), resident epibenthic predators and omnivores (sesarmid crabs,...), and aquatic, visiting epibenthic predators (larvae, juveniles and adults of shrimp, prawns, fish, crabs, large zooplankters,...) (Evans 1983). The swimming crab *Scylla serrata* was indeed observed to be an important predator in some mangroves (Hill 1979).

2. Benthic trophodynamics applied to the studied East African mangroves

a) *Avicennia marina* (figure 8.12)

The litter fall in this zone is dominated by *Avicennia marina* leaves. The most important epibenthic leaf shredder is the crab *Sesarma meinerti* (Cott 1929; Emmerson & McGwynne 1992; Micheli *et al.* 1991; Steinke *et al.* 1993; table 8.6). This crab might, however, be assisted in this activity by the less abundant crab *Metopograpsus thukuhar* (McIntosh 1988; Dahdouh-Guebas, personal communication). *Terebralia palustris* has not been reported to feed on *Avicennia* leaves (Slim *et al.*, submitted personal communication).

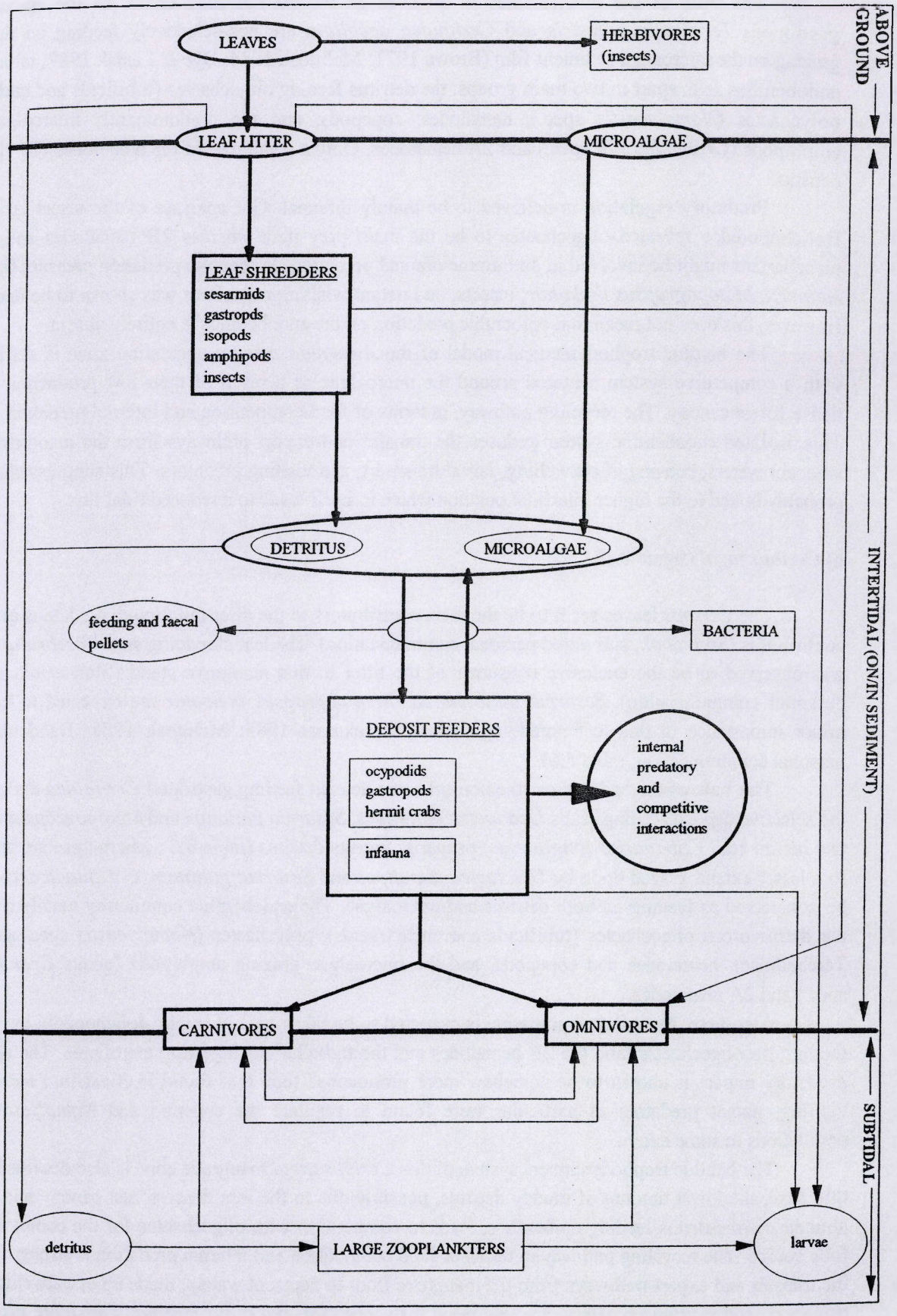


Figure 8.11: Pathways of a mangrove-estuarine system involving crabs *(after McIntosh 1988)*.

The bulk of the invertebrates is involved in the detrital food chain. In the epibenthos, the gastropods *Terebralia palustris* and *Cerithidea decollata* are non-selectively feeding on detritus and grazing on the microalgal sediment film (Brown 1971; McIntosh 1984; Dye & Lasiak 1987; table 8.6). The endobenthos falls apart in two main groups: the detritus feeding oligochaetes (tubificids and enchytraeids), polychaetes (*Namalycastis* spec.), nematodes, copepods, and the predominantly microalgae feeding amphipods (*Grandidierella* spec.) and 2A nematodes. Only a small part of the nematodes (11 %) feeds on detritus.

Predatory regulation is believed to be mainly infaunal. Gut analyses of the insect larvae family Dolichopodidae revealed oligochaetes to be the main prey item whereas 2B nematodes and, possibly, turbellarians might be involved in an intrameiofaunal predation. Epibenthic predation pressure by *Sesarma meinerti*, *Metopograpsus thukuhar*, insects, and natant, visiting organisms was shown to be non-existent. However, this does not mean that epibenthic predation on the endobenthos is entirely absent.

The benthic trophodynamical model of the *Avicennia marina* vegetation zone is detritus based with a competitive system centered around the microalgae as a result of their low production under the dense forest canopy. The recycling pathway, in terms of food competition and internal predation, is strong. This isolated endobenthic system reduces the transfer and export pathways from the mangrove floor to adjacent waters, consing of outwelling, larval transport, and visiting predators. This suppressed transfer is probably linked to the higher intertidal position which in itself leads to a reduced tidal flux.

b) *Ceriops tagal* (figure 8.13)

The *Ceriops* leaves seem to be the main contributors to the litter fall though no data is available to confirm this (Slim *et al.*, submitted personal communication). The leaf shredding snail *Terebralia palustris* was observed to be the exclusive consumer of the litter in this mangrove stand (Slim *et al.*, submitted personal communication). *Sesarma guttatum* and *Metopograpsus thukuhar* are expected to be of only minor importance in this leaf shredding (Leh & Sasekumar 1985; McIntosh 1988; Dahdouh-Guebas, personal communication; table 8.6).

The bulk of the epibenthos (the non-selective deposit feeding gastropod *Cerithidea decollata* and the selective deposit feeding crabs *Uca lactea annulipes*, *Sesarma guttatum* and *Metopograpsus thukuhar* and hermit crab *Clibanarius longitarsus*) primarily ingests detritus (table 8.6). Microalgae are also, albeit to a lesser extent, grazed upon by *Uca lactea annulipes* and *Sesarma guttatum*. *Cerithidea decollata* can be considered as feeding on both detritus and microalgae. The endobenthic community mainly consists of the detritivorous oligochaetes (tubificids and enchytraeids), polychaetes (*Namalycastis* spec. and family Terebellidae), nematodes and copepods, and the microalgae grazing amphipods (genus *Grandidierella* spec.) and 2A nematodes.

Also here, the infaunal predation is expected to be taken care of by the dolichopodid insect larvae feeding on oligochaetes, and the 2B nematodes and the turbellarians ingesting meiofauna. The epibenthic predatory impact is shown to be somehow more pronounced than that found in *Avicennia marina*. The visiting, natant predators in particular were found to regulate the copepod and *Namalycastis* spec. populations to some extent.

The benthic trophodynamical system of this *Ceriops tagal* mangrove zone is also detritus based. In this case, the lower amount of muddy detritus, possibly due to the less dense forest canopy and the high abundance of detritus feeding epibenthos, leads to competition with oligochaetes for the common detrital food source. The recycling pathway in terms of food competition and internal predation is strong. However, the transfer and export pathways from the mangrove floor to adjacent waters, made up of outwelling, larval transport, and visiting predators, are less weak than these for *Avicennia marina*. This more pronounced transfer is probably linked with the lower intertidal position which results in a higher tidal flux.

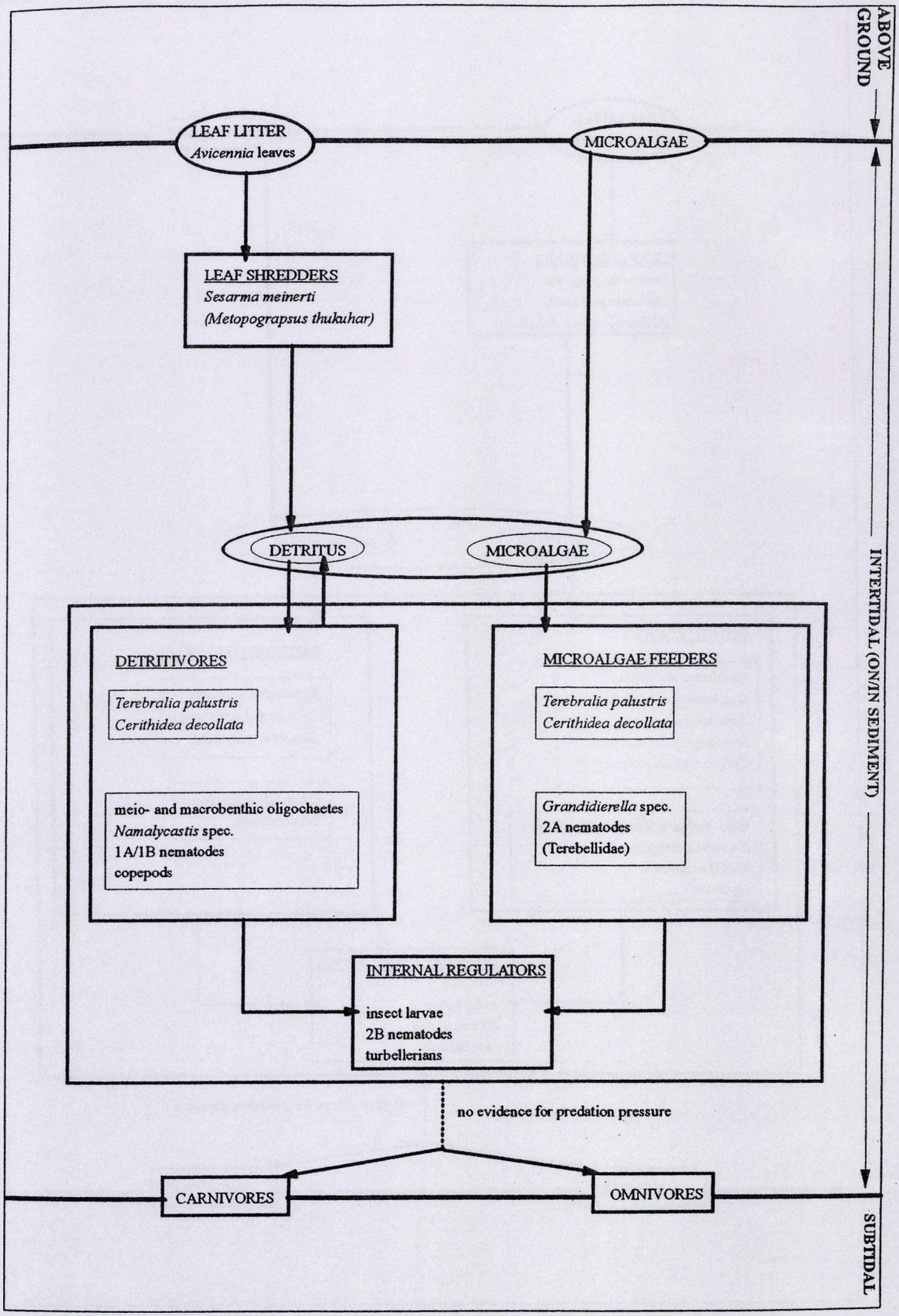


Figure 8.12: Preliminary benthic trophodynamics applied to an East African *Avicennia marina* mangrove vegetation zone using data gathered in this study.

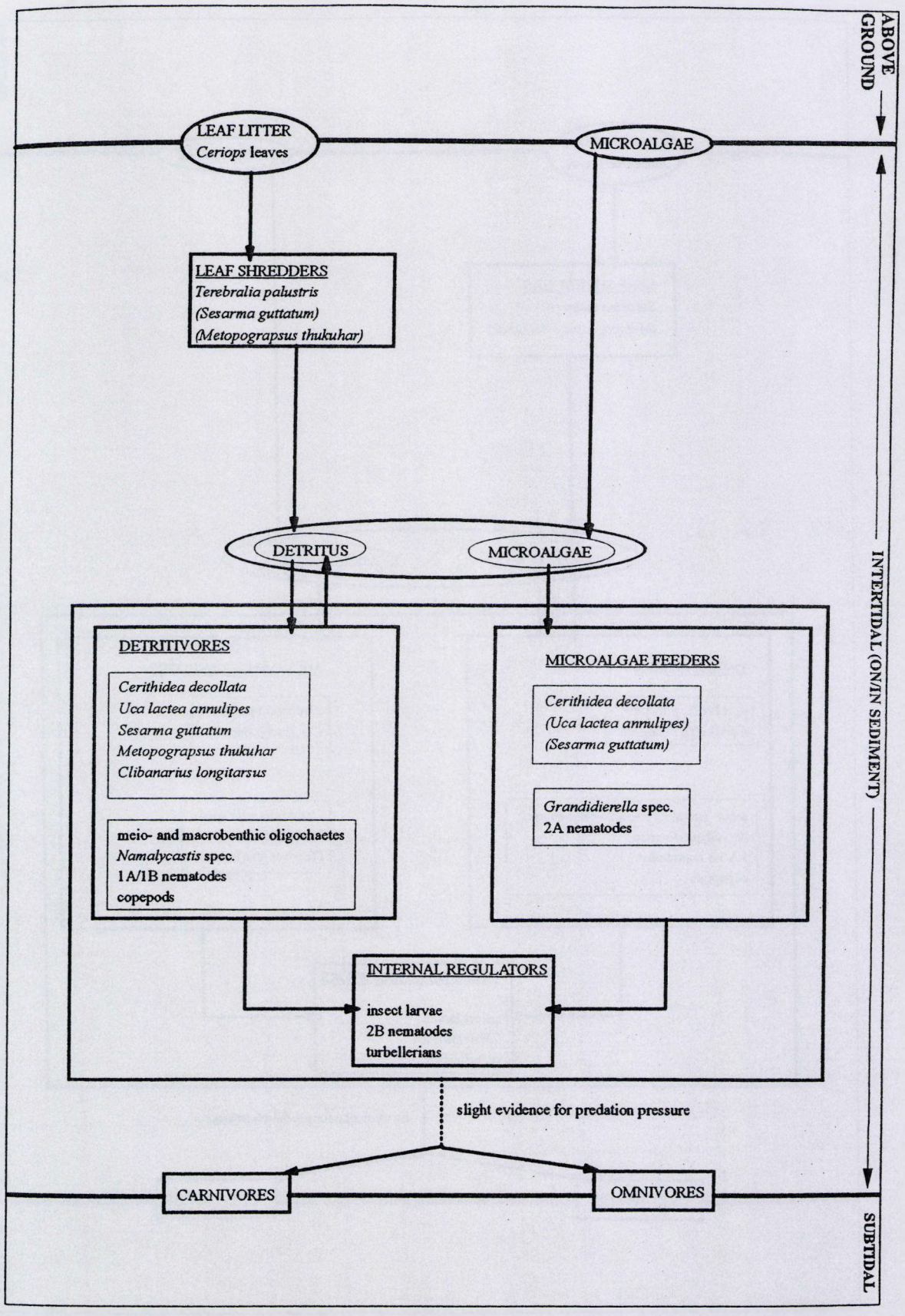


Figure 8.13: Preliminary benthic trophodynamics applied to an East African *Ceriops tagal* mangrove vegetation zone using data gathered in this study.

c) Generalization

The main objective of the proposed study was to gain an understanding of the role of the endobenthos of an East African mangrove sediment as a carbon sink in the soil or as an energy transfer to higher trophic levels. This objective was achieved by analysing the regulation of the endobenthic community structure in terms of competitive systems within the community and of predatory impacts from outside the community.

Predation: The studied mangrove vegetation zones can both be considered as high intertidal. Epibenthic predatory regulation was found to be minimal since it was mainly linked with natant organisms coming from adjacent waters. This predation pressure was mainly evident for some rare taxa such as copepods and the polychaete *Namalycastis* spec. It is only detected, although still weakly, in the *Ceriops* zone. The lower position of *Ceriops tagal* probably causes this higher natant, predatory influence.

Exploitative competition: An indication of a food competition among benthic organisms, points to a strong involvement in the regeneration of material in the soil. However, this competition is only evident when food is limited.

The status of the studied mangrove zones gave the ideal opportunity to find two competitive systems. *Avicennia marina* reflected a typical mangrove system with a high muddy detrital content and a low microalgal density. Epibenthic exclusion therefore uncovered an exploitative competitive system centered around benthic microalgae and diatoms. *Ceriops tagal*, however, had a considerably lower muddy detritus proportion but a higher microalgal concentration. Exclusion of epibenthos was therefore able to reveal an exploitative system with the detritus as common food source. These systems confirm a strong involvement of the majority of the endobenthos in an isolated decompositional pathway in the mangrove sediment. It points to a carbon sink with only minor energy fluxes to higher trophic levels.

This study, therefore, gives an insight into the decisive role of the endobenthos as regenerators of mangrove material and its rather weak contribution to the prey for the mangrove demersal or pelagic realm.

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APPENDICES

Contents

* Frequently used terms

meiobenthos/meiofauna: animal community in the sediment with size range 38 µm-0.5 mm
macrobenthos/macrofauna: animal community in the sediment with size range > 0.5 mm
endobenthos/infauna: animal community living in the sediment
epibenthos/epifauna: animal community living on or in contact with the bottom
hyperbenthos: animal community living in close contact with the bottom (lowest 1 m of water column)
resident epibenthos: animal community staying in the studied zone (during flood and ebb)
natant, visiting epibenthos: animal community visting the studied zone during flood (also consisting of hyperbenthos)
macro-endobenthos: macrobenthic community living in the bottom
macro-epibenthos/macro-epifauna: macrobenthic part of the epibenthos (to differentiate from the endobenthos)
macro-polychaetes: macrobenthic polychaetes
macro-nematodes: macrobenthic nematodes
macro-oligochaetes: macrobenthic oligochaetes
meio-polychaetes: meiobenthic polychaetes
meio-nematodes (= nematodes): meiobenthic nematodes
meio-oligochaetes: meiobenthic oligochaetes
microbenthos: organisms of microscopic size living in the bottom

Ceriops
blanco
period 1

0-2 cm
6-8-92

	11.31 am A	11.38 am B	2.30 pm C	mean	std
% mud after	16.65		6.61	11.63	5.02
% mud before	34.37		22.74	28.56	5.82
% sand after	78.47		88.46	83.47	4.99
% sand before	62.12		72.02	67.07	4.95
% coarse sand after	4.88		4.93	4.91	0.02
% coarse sand before	3.51		5.24	4.38	0.86
median after	239.30		327.90	283.60	44.30
median before	166.40		275.40	220.90	54.50
kurtosis after	2.26		6.18	4.22	1.96
kurtosis before	-0.54		0.35	-0.10	0.44
skewness after	-1.36		-2.03	-1.70	0.33
skewness before	-0.68		-1.10	-0.89	0.21
POM (%)	2.50		1.79	2.14	0.36
total carbon (%)	1.42	1.06	0.71	1.06	0.29
pH	7.09	7.58	5.87	6.85	0.72
salinity (ppt)	48.00	53.00	54.00	51.67	2.62
redox (mV)					
dissolved oxygen (mg/l)	32.00	9.00	11.00	17.33	10.40
temperature (°C)	25.00	21.20	20.90	22.37	1.87
chlorophyll a (ng/g DWT)	3582.27	3182.19	1966.40	2910.29	687.12
fucoxanthine (ng/g DWT)	1404.12	1056.59	536.73	999.15	356.43

2-4 cm
6-8-92

11.31 am A	11.38 am B	2.30 pm C	mean	std
16.65	10.70	9.84	12.40	3.03
11.19	23.50	17.72	17.47	5.03
79.50	86.10	86.42	84.01	3.19
84.37	71.53	78.49	78.13	5.25
3.85	3.20	3.74	3.60	0.28
4.44	4.97	3.79	4.40	0.48
203.30	292.70	234.40	243.47	37.06
327.10	249.00	272.50	282.87	32.72
2.34	3.38	4.24	3.32	0.77
3.28	0.17	1.05	1.50	1.31
-1.40	-1.57	-1.66	-1.54	0.11
-1.81	-1.07	-1.31	-1.40	0.31
4.34	2.84	4.71	3.96	0.81
1.43	2.51	1.48	1.81	0.50
7.09	7.58	5.87	6.85	0.72
48.00	53.00	54.00	51.67	2.62
32.00	9.00	11.00	17.33	10.40
24.40	20.90	20.50	21.93	1.75
0.00	544.97	0.00	181.66	256.90
0.00	121.69	0.00	40.56	57.37

Ceriops
blanco
period 1

4-10 cm
6-8-92

	11.31 am A	11.38 am B	2.30 pm C	mean	std
% mud after	20.79	20.19	15.93	18.97	2.16
% mud before	21.87	20.39	13.03	18.43	3.87
% sand after	76.10	86.84	83.40	82.11	4.48
% sand before	73.77	74.98	83.83	77.53	4.48
% coarse sand after	3.11	2.97	0.67	2.25	1.12
% coarse sand before	4.36	4.63	3.14	4.04	0.65
median after	166.20	263.30	189.50	206.33	41.39
median before	265.00	253.20	289.00	269.07	14.90
kurtosis after	1.78	4.17	3.73	3.23	1.04
kurtosis before	0.67	0.87	2.72	1.42	0.92
skewness after	-1.17	-1.67	-1.69	-1.51	0.24
skewness before	-1.17	-1.24	-1.68	-1.36	0.23
POM (%)	5.40	3.64	5.04	4.69	0.76
total carbon (%)	3.03	2.79	6.35	4.06	1.62
pH	7.09	7.58	5.87	6.85	0.72
salinity (ppt)	48.00	53.00	54.00	51.67	2.62
redox (mV)					
dissolved oxygen (mg/l)	32.00	9.00	11.00	17.33	10.40
temperature (°C)	22.40	20.40	19.80	20.87	1.11
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00

10-rest cm
6-8-92

11.31 am A	11.38 am B	2.30 pm C	mean	std
12.79	15.36	1.34	9.83	6.09
22.73	22.29	9.73	18.25	6.03
83.22	80.86	79.42	81.17	1.57
72.60	73.20	74.67	73.49	0.87
3.99	3.78	19.25	9.01	7.24
4.67	4.51	15.60	8.26	5.19
281.00	245.20	211.60	245.93	28.34
285.80	249.60	337.20	290.87	35.94
3.27	2.45	2.38	2.70	0.40
0.68	0.86	1.93	1.16	0.55
-1.59	-1.40	-1.50	-1.50	0.08
-1.20	-1.23	-1.53	-1.32	0.15
9.11	5.05	5.98	6.71	1.74
7.09	7.58	5.87	6.85	0.72
48.00	53.00	54.00	51.67	2.62
32.00	9.00	11.00	17.33	10.40
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00

Ceriops blanco period 2 — 0-2 cm, 28-8-92

	11.25 am A	9.55 am B	11.10 am C	mean	std
% mud after	19.91	27.18	19.68	22.26	
% mud before	3.95	16.91	23.50	14.79	8.12
% sand after	79.37	80.97	80.14	80.16	0.65
% sand before	79.31	68.16	47.15	64.87	13.33
% coarse sand after	0.72	2.12	0.18	1.01	0.82
% coarse sand before	3.95	4.66	2.35	3.65	0.97
median after	143.80	217.40	145.20	168.80	34.37
median before	256.80	161.50	208.00	208.77	38.91
kurtosis after	3.29	-0.07	3.82	2.35	1.72
kurtosis before	1.43	3.03	0.53	1.66	1.03
skewness after	-1.59	-0.91	-1.72	-1.41	0.36
skewness before	-1.33	-1.34	-1.07	-1.25	0.12
POM (%)	3.81	2.21	3.35	3.12	0.67
total carbon (%)	2.02	1.07	0.75	1.28	0.54
pH	6.01	6.13	6.09	6.08	0.05
salinity (ppt)	42.00	39.00	43.00	41.33	1.70
redox (mV)					
dissolved oxygen (mg/l)	15.00	14.00	14.00	14.33	0.47
temperature (°C)	34.30	29.90	28.20	30.80	2.57
chlorophyll a (ng/g DWT)	6102.96	6295.84		6199.40	96.44
fucoxanthine (ng/g DWT)	1830.89	1467.56		1649.23	181.66

Ceriops blanco period 2 — 2-4 cm, 28-8-92

	11.25 am A	9.55 am B	10.10 am C	mean	std
	13.71	22.96	22.13	19.60	4.18
	14.65	27.94	16.79	19.79	5.83
	83.97	76.50	77.73	79.40	3.27
	80.63	68.51	79.35	76.16	5.44
	2.32	0.54	0.14	1.00	0.95
	4.72	3.55	3.88	4.05	0.49
	197.20	132.80	141.50	157.17	28.53
	311.70	196.10	279.50	262.43	48.71
	3.53	2.63	2.97	3.04	0.37
	1.98	-0.01	1.45	1.14	0.84
	-1.58	-1.42	-1.63	-1.54	0.09
	-1.50	-0.91	-1.36	-1.26	0.25
	5.75	2.57	5.05	4.46	1.36
	2.20	1.79	2.14	2.04	0.18
	6.01	6.13	6.09	6.08	0.05
	42.00	39.00	43.00	41.33	1.70
	15.00	14.00	14.00	14.33	0.47
	32.00	28.10	26.20	28.77	2.41
	1369.38			1369.38	0.00
	404.93			404.93	0.00

Ceriops blanco period 2 — 4-10 cm, 28-8-92

	11.25 am A	9.55 am B	10.10 am C	mean	std
% mud after	17.78	24.85	15.15	19.26	4.10
% mud before	15.53	15.48	17.96	16.32	1.16
% sand after	81.07	74.74	84.11	79.97	3.90
% sand before	80.72	80.06	78.94	79.91	0.73
% coarse sand after	1.15	0.68	0.74	0.86	0.21
% coarse sand before	3.75	4.46	3.10	3.77	0.56
median after	177.90	125.20	178.40	160.50	24.96
median before	285.80	248.30	257.90	264.00	15.91
kurtosis after	2.83	2.21	4.03	3.02	0.76
kurtosis before	1.99	1.86	1.47	1.77	0.22
skewness after	-1.45	-1.30	-1.72	-1.49	0.17
skewness before	-1.50	-1.48	-1.36	-1.45	0.06
POM (%)	5.37	3.12	3.27	3.92	1.03
total carbon (%)	3.64	2.14	6.35	4.04	1.74
pH	6.01	6.13	6.09	6.08	0.05
salinity (ppt)	42.00	39.00	43.00	41.33	1.70
redox (mV)					
dissolved oxygen (mg/l)	15.00	14.00	14.00	14.33	0.47
temperature (°C)	28.30	26.00	24.90	26.40	1.42
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00

Ceriops blanco period 2 — 10-rest cm, 28-8-92

	11.25 am A	9.55 am B	10.10 am C	mean	std
	24.28	16.22	25.38	21.96	4.08
	19.41	23.54	23.79	22.25	2.01
	71.38	81.04	73.82	75.41	4.10
	76.34	72.42	72.58	73.78	1.81
	2.34	2.74	0.80	1.96	0.84
	4.25	4.04	3.63	3.97	0.26
	168.60	210.30	148.30	175.73	25.81
	294.40	234.20	244.00	257.53	26.37
	0.94	2.45	1.71	1.70	0.62
	1.30	0.65	0.66	0.87	0.30
	-1.05	-1.35	-1.19	-1.20	0.12
	-1.40	-1.14	-1.16	-1.23	0.12
	5.35	4.46	4.79	4.87	0.37
	6.01	6.13	6.09	6.08	0.05
	42.00	39.00	43.00	41.33	1.70
	15.00	14.00	14.00	14.33	0.47
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00

Ceriops
blanco
period 3

0-2 cm
27-9-92

	8.58 am A	9.02 am B	10.02 am C	mean	std
% mud after	5.04	18.69	8.80	10.84	
% mud before	23.04	30.32	24.81	26.06	3.10
% sand after	81.12	78.64	87.84	82.53	3.89
% sand before	71.17	65.73	71.18	69.36	2.57
% coarse sand after	3.48	2.67	3.36	3.17	0.36
% coarse sand before	5.09	3.95	4.01	4.35	0.52
median after	301.70	189.00	277.60	256.10	48.46
median before	282.00	189.70	236.60	236.10	37.68
kurtosis after	2.66	1.95	5.44	3.35	1.51
kurtosis before	0.55	-0.06	0.47	0.32	0.27
skewness after	-1.54	-1.22	-1.89	-1.55	0.27
skewness before	-1.19	-0.88	-1.09	-1.05	0.13
POM (%)	10.68	10.21	4.93	8.60	2.61
total carbon (%)	1.31	0.71	14.39	5.47	6.31
pH	6.79	6.18	6.45	6.47	0.25
salinity (ppt)	39.00	45.00	46.00	43.33	3.09
redox (mV)	101.00	167.00	77.00	115.00	38.05
dissolved oxygen (mg/l)	30.00	18.00	13.00	20.33	7.13
temperature (°C)	27.30	27.00	28.70	27.67	0.74
chlorophyll a (ng/g DWT)	3437.93	5511.16	6973.74	5307.61	1450.65
fucoxanthine (ng/g DWT)	1015.33	1023.42	2092.12	1376.96	505.71

2-4 cm
27-9-92

8.58 am A	9.02 am B	10.02 am C	mean	std
17.72	18.81	12.21	16.25	2.89
23.98	26.70	22.80	24.49	1.63
78.40	78.42	85.69	80.84	3.43
71.48	68.99	73.85	71.44	1.98
3.88	2.77	2.10	2.92	0.73
4.54	4.31	3.35	4.07	0.52
280.30	194.10	228.70	234.37	35.42
276.20	217.20	228.80	240.73	25.52
1.89	1.89	4.08	2.62	1.03
0.64	0.27	0.81	0.57	0.22
-1.36	-1.24	-1.71	-1.43	0.20
-1.18	-1.02	-1.17	-1.12	0.07
12.39	-2.19	4.39	4.86	5.96
1.89	1.25	2.12	1.75	0.37
6.79	6.18	6.45	6.47	0.25
39.00	45.00	46.00	43.33	3.09
87.00	173.00	45.00	101.67	53.27
30.00	18.00	13.00	20.33	7.13
27.00	26.80	28.20	27.33	0.62
886.98	1012.60	0.00	633.19	450.66
0.00	0.00	0.00	0.00	0.00

Ceriops
blanco
period 3

4-10 cm
27-9-92

	8.58 am A	9.02 am B	10.02 am C	mean	std
% mud after	16.67	10.23	13.64	13.51	2.63
% mud before	26.85	18.87	20.07	21.93	3.51
% sand after	80.36	86.74	84.12	83.74	2.62
% sand before	69.40	77.18	76.51	74.36	3.52
% coarse sand after	2.97	3.03	2.24	2.75	0.36
% coarse sand before	3.75	3.95	3.42	3.71	0.22
median after	240.80	260.40	213.60	238.27	19.19
median before	220.90	238.40	245.20	234.83	10.24
kurtosis after	2.23	4.07	3.54	3.28	0.78
kurtosis before	0.22	1.41	1.05	0.89	0.50
skewness after	-1.38	-1.63	-1582.00	-528.34	745.05
skewness before	-1.01	-1.30	-1.25	-1.18	0.12
POM (%)	7.66	3.74	4.34	5.25	1.72
total carbon (%)	2.02	1.41	3.32	2.25	0.80
pH	6.79	6.18	6.45	6.47	0.25
salinity (ppt)	39.00	45.00	46.00	43.33	3.09
redox (mV)	61.00	178.00	60.00	99.67	55.39
dissolved oxygen (mg/l)	30.00	18.00	13.00	20.33	7.13
temperature (°C)	26.80	26.80	27.10	26.90	0.14
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00

10-rest cm
27-9-92

8.58 am A	9.02 am B	10.10 am C	mean	std
12.17	7.60	11.84	10.54	2.08
21.16	22.36	27.61	23.71	2.80
84.51	88.43	85.61	86.18	1.65
75.05	73.81	70.34	73.07	1.99
3.32	3.97	2.55	3.28	0.58
3.79	3.83	2.05	3.22	0.83
225.50	264.50	196.80	228.93	27.74
241.20	223.40	166.00	210.20	32.09
3.50	5.32	4.05	4.29	0.76
0.92	0.71	0.23	0.62	0.29
-1.49	-1.75	-1.57	-1.60	0.11
-1.22	-1.15	-0.91	-1.09	0.13
5.79	3.59	3.97	4.45	0.96
6.79	6.18	6.45	6.47	0.25
39.00	45.00	46.00	43.33	3.09
30.00	18.00	13.00	20.33	7.13
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00

Ceriops
blanco
period 4

0-2 cm
29-10-92

	10.29 am A	11.11 am B	12.44 am C	mean	std
% mud after	7.04	5.97	5.37	6.13	
% mud before	20.05	16.09	10.66	15.60	3.85
% sand after	89.15	89.07	89.98	89.40	0.41
% sand before	76.19	79.96	84.73	80.29	3.49
% coarse sand after	3.81	4.96	4.65	4.47	0.49
% coarse sand before	3.76	3.95	4.61	4.11	0.36
median after	259.30	301.70	290.00	283.67	17.88
median before	250.10	270.40	323.50	281.33	30.95
kurtosis after	6.05	5.95	6.80	6.26	0.38
kurtosis before	0.70	1.38	3.11	1.73	1.01
skewness after	-1.87	-1.83	-1.93	-1.88	0.04
skewness before	-1.18	-1.33	-1.69	-1.40	0.21
POM (%)	3.09	1.95	2.22	2.42	0.49
total carbon (%)	0.92	1.19	1.24	1.12	0.14
pH	6.08	6.18	6.04	6.10	0.06
salinity (ppt)	48.00	51.00	51.00	50.00	1.41
redox (mV)	-17.00	-17.00	75.00	13.67	43.37
dissolved oxygen (mg/l)					
temperature (°C)	34.60	34.10	34.40	34.37	0.21
chlorophyll a (ng/g DWT)	367.13	2211.50	2945.85	1841.49	1084.78
fucoxanthine (ng/g DWT)	708.35	632.99	698.88	680.07	33.52

2-4 cm
29-10-92

10.29 am A	11.11 am B	12.44 am C	mean	std
9.24	7.88	8.70	8.61	0.56
9.02	20.16	12.80	13.99	4.63
87.50	88.83	89.19	88.51	0.73
83.31	75.70	82.92	80.64	3.50
3.26	3.29	2.11	2.89	0.55
6.77	4.14	4.28	5.06	1.21
235.80	224.00	218.20	226.00	7.32
379.70	252.60	310.40	314.23	51.96
5.15	5.23	5.92	5.43	0.34
3.58	0.62	2.41	2.20	1.22
-1.79	-1.65	-1.86	-1.76	0.08
-1.86	-1.14	-1.59	-1.53	0.30
5.34	3.22	5.19	4.58	0.97
1.62	2.52	2.22	2.12	0.37
6.08	6.18	6.04	6.10	0.06
48.00	51.00	51.00	50.00	1.41
-12.00	-42.00	-110.00	-54.67	41.00
32.70	32.30	32.30	32.43	0.19
617.28	468.70	419.72	501.90	84.00
165.18	0.00		82.59	82.59

Ceriops
blanco
period 4

4-10 cm
29-10-92

	10.29 am A	11.11 am B	12.44 am C	mean	std
% mud after	9.46	9.57	8.57	9.20	0.45
% mud before	16.05	14.05	13.02	14.37	1.26
% sand after	77.13	87.71	89.47	84.77	5.45
% sand before	78.67	81.25	82.92	80.95	1.75
% coarse sand after	3.41	2.72	1.96	2.70	0.59
% coarse sand before	5.28	4.70	4.06	4.68	0.50
median after	265.20	228.40	241.00	244.87	15.27
median before	332.70	314.80	298.90	315.47	13.81
kurtosis after	4.73	4.55	6.02	5.10	0.65
kurtosis before	1.46	2.32	2.59	2.12	0.48
skewness after	-1.78	-1.62	-1.92	-1.77	0.12
skewness before	-1.43	-1.60	-1.61	-1.55	0.08
POM (%)	6.10	3.52	4.00	4.54	1.12
total carbon (%)	1.75	3.19	2.36	2.43	0.59
pH	6.08	6.18	6.04	6.10	0.06
salinity (ppt)	48.00	51.00	51.00	50.00	1.41
redox (mV)	-121.00	-30.00	-115.00	-88.67	41.56
dissolved oxygen (mg/l)					
temperature (°C)	29.70	29.90	30.40	30.00	0.29
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00

10-rest cm
29-10-92

10.29 am A	11.11 am B	12.44 am C	mean	std
10.58	9.86	8.79	9.74	0.74
21.76	18.83	13.19	17.93	3.56
85.64	87.25	87.90	86.93	0.95
72.94	77.20	82.54	77.56	3.93
3.78	2.89	2.31	2.99	0.60
5.30	3.97	4.27	4.51	0.57
288.00	238.40	257.60	261.33	20.42
306.80	274.60	312.80	298.07	16.77
4.28	4.34	5.29	4.64	0.46
0.52	1.10	2.72	1.44	0.93
-1.78	-1.61	-1.90	-1.76	0.12
-1.18	-1.30	-1.67	-1.38	0.21
9.75	7.32	4.36	7.14	2.20
6.08	6.18	6.04	6.10	0.06
48.00	51.00	51.00	50.00	1.41
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00

Ceriops
blanco
period 5

0-2 cm
25-11-92

	11.41 am A	11.22 am B	9.28 am C	mean	std
% mud after	2.88	5.14	1.78	3.27	
% mud before	1.11	2.32	0.70	1.38	0.69
% sand after	95.48	93.92	98.22	95.87	1.78
% sand before	91.93	96.82	94.59	94.45	2.00
% coarse sand after	1.64	0.94	0.00	0.86	0.67
% coarse sand before	6.96	0.86	4.71	4.18	2.52
median after	147.90	76.82	189.80	138.17	46.63
median before	306.90	154.30	321.20	260.80	75.53
kurtosis after	0.09	-0.72	7.20	2.19	3.56
kurtosis before	5.81	3.47	4.28	4.52	0.97
skewness after	-0.85	-0.39	-2.24	-1.16	0.79
skewness before	-1.90	-1.53	-1.84	-1.76	0.16
POM (%)	3.60	2.20	2.67	2.82	0.58
total carbon (%)	4.78	0.69	0.89	2.12	1.88
pH	6.37	6.32	6.22	6.30	0.06
salinity (ppt)	49.00	47.00	48.00	48.00	0.82
redox (mV)	92.00	103.00	-20.00	58.33	55.57
dissolved oxygen (mg/l)	7.00	22.00	6.00	11.67	7.32
temperature (°C)	34.90	33.10	28.70	32.23	2.60
chlorophyll a (ng/g DWT)	2176.53	2416.08	3287.35	2626.65	477.31
fucoxanthine (ng/g DWT)	529.24	739.96	955.85	741.68	174.17

2-4 cm
25-11-92

	11.41 am A	11.22 am B	9.28 am C	mean	std
	2.73	3.67	2.58	2.99	0.48
	2.02	2.52	0.91	1.82	0.67
	93.83	94.20	97.20	95.08	1.51
	95.39	97.25	94.44	95.69	1.17
	3.44	2.13	0.22	1.93	1.32
	2.59	0.23	4.65	2.49	1.81
	207.90	134.20	160.00	167.37	30.54
	198.10	137.80	308.60	214.83	70.73
	0.73	-0.23	5.95	2.15	2.72
	4.40	4.04	1.95	3.46	1.08
	-1.12	-0.73	-2.12	-1.33	0.58
	-1.73	-1.70	-1.44	-1.62	0.13
	4.83	3.49	5.64	4.65	0.89
	2.04	1.59	2.66	2.10	0.44
	6.37	6.32	6.22	6.30	0.06
	49.00	47.00	48.00	48.00	0.82
	-2.00	3.00	-25.00	-8.00	12.19
	7.00	22.00	6.00	11.67	7.32
	33.40	30.60	28.60	30.87	1.97
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	198.54	66.18	93.59

Ceriops
blanco
period 5

4-10 cm
25-11-92

	11.41 am A	11.22 am B	9.28 am C	mean	std
% mud after	2.17	4.10	1.95	2.74	0.97
% mud before	3.19	3.49	0.95	2.54	1.13
% sand after	95.00	93.56	97.97	95.51	1.84
% sand before	96.41	84.59	94.59	91.86	5.20
% coarse sand after	2.83	2.33	0.08	1.75	1.20
% coarse sand before	0.40	0.47	4.46	1.78	1.90
median after	216.20	141.10	182.40	179.90	30.71
median before	126.60	139.40	319.60	195.20	88.12
kurtosis after	1.92	-0.02	4.59	2.16	1.89
kurtosis before	2.00	3.17	4.29	3.15	0.94
skewness after	-1.38	-0.82	-1.86	-1.36	0.42
skewness before	-1.30	-1.63	-1.86	-1.60	0.23
POM (%)	5.01	4.77	3.99	4.59	0.44
total carbon (%)	0.59	1.41	1.57	1.19	0.43
pH	6.37	6.32	6.22	6.30	0.06
salinity (ppt)	49.00	47.00	48.00	48.00	0.82
redox (mV)	-20.00	-12.00	-25.00	-19.00	5.35
dissolved oxygen (mg/l)	7.00	22.00	6.00	11.67	7.32
temperature (°C)	30.30	28.90	28.30	29.17	0.84
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00

10-rest cm
25-11-90

	11.41 am A	11.22 am B	9.28 am C	mean	std
	3.16	5.23	2.37	3.59	1.21
	3.53	1.23	1.66	2.14	1.00
	93.63	92.01	97.58	94.41	2.34
	96.00	95.11	95.27	95.46	0.39
	3.21	2.76	0.05	2.01	1.40
	0.47	3.66	3.07	2.40	1.39
	183.90	162.80	176.30	174.33	8.73
	119.60	305.00	242.70	222.43	77.03
	0.45	-0.27	5.32	1.83	2.48
	1.26	4.28	1.09	2.21	1.46
	-0.97	-0.81	-2.00	-1.26	0.53
	-1.10	-1.80	-1.22	-1.38	0.31
	7.83	8.07	4.17	6.69	1.78
	6.37	6.32	6.22	6.30	0.06
	49.00	47.00	48.00	48.00	0.82
	7.00	22.00	6.00	11.67	7.32
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00

Ceriops
blanco
period 6

0-2 cm
23-12-92

	11.05 am A	10.45 am B	9.15 am C	mean	std
% mud after	0.49	0.30	0.42	0.40	
% mud before	1.03	0.95	0.89	0.96	0.06
% sand after	96.33	92.36	94.77	94.49	1.63
% sand before	93.71	92.97	94.40	93.69	0.58
% coarse sand after	3.18	7.34	4.81	5.11	1.71
% coarse sand before	5.26	6.08	4.71	5.35	0.56
median after	305.30	395.90	326.80	342.67	38.65
median before	327.40	353.50	312.40	331.10	16.98
kurtosis after	7.78	5.83	6.10	6.57	0.86
kurtosis before	5.20	3.56	3.86	4.21	0.72
skewness after	-1.89	-1.74	-1.75	-1.79	0.07
skewness before	-2.02	-1.74	-1.76	-1.84	0.13
POM (%)	1.66	1.40	3.35	2.14	0.86
total carbon (%)	0.57	0.65	1.50	0.91	0.42
pH	5.56	5.15	5.05	5.25	0.22
salinity (ppt)	49.00	45.00	52.50	48.83	3.06
redox (mV)	140.00	119.00	128.00	129.00	8.60
dissolved oxygen (mg/l)	6.00	7.00	6.00	6.33	0.47
temperature (°C)	33.40	31.10	28.40	30.97	2.04
chlorophyll a (ng/g DWT)	161.94	381.58	2365.56	969.69	991.09
fucoxanthine (ng/g DWT)	1203.55	489.92	1396.52	1030.00	389.93

2-4 cm
23-12-92

11.05 am A	10.45 am B	9.15 am C	mean	std
0.92	0.41	0.87	0.73	0.23
0.95	1.29	0.82	1.02	0.20
96.73	93.81	96.64	95.73	1.36
94.02	93.98	94.82	94.27	0.39
2.35	5.78	2.49	3.54	1.58
5.03	4.73	4.36	4.71	0.27
259.10	344.20	231.30	278.20	48.03
330.40	301.70	306.40	312.83	12.57
6.24	5.56	5.56	5.79	0.32
4.15	2.66	5.01	3.94	0.97
-1.85	-1.69	-1.67	-1.74	0.08
-1.81	-1.57	-1.89	-1.76	0.13
4.49	3.18	5.94	4.54	1.13
1.95	1.11	2.08	1.71	0.43
5.56	5.15	5.05	5.25	0.22
49.00	45.00	52.50	48.83	3.06
96.00	68.00	85.00	83.00	11.52
6.00	7.00	6.00	6.33	0.47
30.70	29.80	27.80	29.43	1.21
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00

Ceriops
blanco
period 6

4-10 cm
23-12-92

	11.05 am A	10.45 am B	9.15 am C	mean	std
% mud after	0.77	0.59	0.82	0.73	0.10
% mud before	2.39	1.35	1.44	1.73	0.47
% sand after	93.58	93.51	97.13	94.74	1.69
% sand before	92.82	91.70	94.29	92.94	1.06
% coarse sand after	5.65	5.90	2.05	4.53	1.76
% coarse sand before	4.79	6.95	4.27	5.34	1.16
median after	353.00	340.40	255.60	316.33	43.25
median before	301.30	354.30	317.10	324.23	22.22
kurtosis after	5.98	5.12	5.84	5.65	0.38
kurtosis before	1.65	3.01	3.80	2.82	0.89
skewness after	-1.94	-1.70	-1.86	-1.83	0.10
skewness before	-1.44	-1.70	-1.86	-1.67	0.17
POM (%)	4.69	3.68	5.81	4.73	0.87
total carbon (%)	1.95	1.29		1.62	0.33
pH	5.56	5.15	5.05	5.25	0.22
salinity (ppt)	49.00	45.00	52.50	48.83	3.06
redox (mV)	57.00	68.00	50.00	58.33	7.41
dissolved oxygen (mg/l)	6.00	7.00	6.00	6.33	0.47
temperature (°C)	28.90	29.80	27.50	28.73	0.95
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00

10-rest cm
23-12-92

11.05 am A	10.45 am B	9.15 am C	mean	std
0.91	1.02	0.97	0.97	0.04
2.71	2.73	2.55	2.66	0.08
94.32	94.32	96.41	95.02	0.99
92.62	92.11	94.03	92.92	0.81
4.77	4.66	2.62	4.02	0.99
4.67	5.16	3.42	4.42	0.73
363.70	324.40	266.80	318.30	39.79
285.30	315.10	269.10	289.83	19.05
4.74	5.24	4.77	4.92	0.23
0.98	1.52	1.24	1.25	0.22
-1.90	-1.89	-1.79	-1.86	0.05
-1.28	-1.43	-1.35	-1.35	0.06
10.35	7.76	10.30	9.47	1.21
5.56	5.15	5.05	5.25	0.22
49.00	45.00	52.50	48.83	3.06
6.00	7.00	6.00	6.33	0.47
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00

Ceriops
partial cage
period 1

	0-2 cm 6-8-92					2-4 cm 6-8-92				
	12.08 am A	11.10 am B	2.15 pm C	mean	std	12.08 am A	11.10 am B	2.15 pm C	mean	std
% mud after	5.14	8.65	1.76	5.18		4.18	4.18	9.51	5.96	2.51
% mud before	2.66	27.83	4.03	11.51	11.56	4.70	4.70	12.51	7.30	3.68
% sand after	85.63	89.75	90.22	88.53	2.06	83.67	89.56	87.15	86.79	2.42
% sand before	64.27	67.15	82.53	71.32	8.02	72.05	72.76	81.95	75.59	4.51
% coarse sand after	1.76	1.50	8.02	3.76	3.01	12.15	1.17	3.34	5.55	4.75
% coarse sand before	4.03	5.02	13.44	7.50	4.22	23.25	5.17	5.54	11.32	8.44
median after	303.80	331.20	233.30	289.43	41.24	255.90	300.70	255.10	270.57	21.31
median before	151.30	221.30	279.20	217.27	52.29	275.30	255.30	352.60	294.40	41.96
kurtosis after	3.96	3.68	5.87	4.50	0.97	3.14	4.14	4.56	3.95	0.59
kurtosis before	-0.43	-0.24	2.35	0.56	1.27	0.34	0.33	2.92	1.20	1.22
skewness after	-1.60	-1.62	-1.86	-1.69	0.12	-1.50	-1.67	-1.70	-1.62	0.09
skewness before	-0.71	-0.85	-1.58	-1.05	0.38	-1.13	-1.07	-1.73	-1.31	0.30
POM (%)	1.86	1.38	2.93	2.06	0.65	5.61	2.12	4.32	4.02	1.44
total carbon (%)										
pH	6.79	5.39	5.10	5.76	0.74	6.79	5.39	5.10	5.76	0.74
salinity (ppt)	48.00	58.00	59.00	55.00	4.97	48.00	58.00	59.00	55.00	4.97
redox (mV)										
dissolved oxygen (mg/l)	11.00	27.00	24.00	20.67	6.94					
temperature (°C)	24.00	21.70	23.90	23.20	1.06	24.00	20.90	23.60	22.83	1.38
chlorophyll a (ng/g DWT)	6064.47	3211.70	3225.05	4167.07	1341.67	370.94	896.59	0.00	422.51	367.84
fucoxanthine (ng/g DWT)	1819.34	900.44	993.15	1237.64	413.06	0.00	160.94	0.00	53.65	75.87

Ceriops
partial cage
period 1

	4-10 cm 6-8-92					10-rest cm 6-8-92				
	12.08 am A	11.10 am B	2.15 pm C	mean	std	12.08 am A	11.10 am B	2.15 pm C	mean	std
% mud after	13.58	11.30	10.45	11.78	1.32	12.03	12.65	13.63	12.77	0.66
% mud before	24.58	24.54	20.72	23.28	1.81	31.71	26.66	20.82	26.40	4.45
% sand after	82.86	85.22	86.29	84.79	1.43	87.38	84.03	84.05	85.15	1.57
% sand before	70.41	71.21	74.54	72.05	1.79	65.02	67.94	73.77	68.91	3.64
% coarse sand after	3.56	3.48	3.26	3.43	0.13	0.59	3.32	2.32	2.08	1.13
% coarse sand before	5.00	4.25	4.74	4.66	0.31	3.27	5.40	5.41	4.69	1.01
median after	248.60	259.10	272.80	260.17	9.91	242.50	244.70	228.30	238.50	7.27
median before	296.40	227.20	287.70	270.43	30.78	192.20	264.30	306.20	254.23	47.08
kurtosis after	2.80	3.45	4.35	3.53	0.64	2.98	3.63	3.30	3.30	0.26
kurtosis before	0.21	0.20	0.87	0.43	0.32	-0.42	0.03	0.80	0.14	0.51
skewness after	-1.42	-1.48	-1.75	-1.55	0.14	-1.40	-1.60	-1.51	-1.50	0.08
skewness before	-1.09	-1.03	-1.27	-1.13	0.10	-0.81	-1.01	-1.27	-1.03	0.19
POM (%)	5.26	3.09	4.32	4.22	0.89	4.52	5.18	6.20	5.30	0.69
total carbon (%)										
pH	6.79	5.39	5.10	5.76	0.74	6.79	5.39	5.10	5.76	0.74
salinity (ppt)	48.00	58.00	59.00	55.00	4.97	48.00	58.00	59.00	55.00	4.97
redox (mV)										
dissolved oxygen (mg/l)										
temperature (°C)	23.20	19.60	22.40	21.73	1.54					
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Ceriops
partial cage
period 2

0-2 cm
28-8-92

	10.55 am A	11.45 am B	8.50 am C	mean	std
% mud after	6.16	4.18	6.86	5.73	
% mud before	19.19	11.37	10.26	13.61	3.97
% sand after	89.39	89.01	92.18	90.19	1.41
% sand before	76.22	80.18	82.03	79.48	2.42
% coarse sand after	4.45	6.81	4.09	5.12	1.21
% coarse sand before	4.59	8.45	7.69	6.91	1.67
median after	315.00	406.50	301.80	341.10	46.56
median before	279.10	414.00	325.00	339.37	56.00
kurtosis after	5.86	6.86	4.40	5.70	1.01
kurtosis before	0.84	2.95	3.89	2.56	1.28
skewness after	-1.88	-2.06	-1.60	-1.85	0.19
skewness before	-1.22	-1.78	-1.79	-1.60	0.27
POM (%)	1.97	0.87	2.11	1.65	0.55
total carbon (%)		0.64	0.65	0.65	0.00
pH	6.04	6.01	6.24	6.10	0.10
salinity (ppt)	40.00	42.00	35.50	39.17	2.72
redox (mV)					
dissolved oxygen (mg/l)	15.00	18.00	14.00	15.67	1.70
temperature (°C)	26.70	31.90	24.10	27.57	3.24
chlorophyll a (ng/g DWT)	2760.59	5788.38	2203.64	3584.20	1575.09
fucoxanthine (ng/g DWT)	1010.83	1736.51	1015.90	1254.41	340.90

2-4 cm
28-8-92

10.55 am A	11.45 am B	8.50 am C	mean	std
8.97	6.81	8.12	7.97	0.89
14.78	22.39	20.94	19.37	3.30
87.05	87.66	88.62	87.78	0.65
80.44	70.62	75.05	75.37	4.02
3.98	5.53	3.26	4.26	0.95
4.78	6.99	4.01	5.26	1.26
279.50	353.90	272.00	301.80	36.97
313.50	304.90	266.00	294.80	20.67
5.04	4.93	5.31	5.09	0.16
1.83	0.34	0.62	0.93	0.65
-1.91	-1.80	-1.80	-1.84	0.05
-1.53	-1.12	-1.17	-1.28	0.18
9.27	1.85	4.03	5.05	3.11
4.23	1.83	1.33	2.46	1.27
6.04	6.01	6.24	6.10	0.10
40.00	42.00	35.50	39.17	2.72
25.90	29.90	23.90	26.57	2.49
0.00	526.12	3929.85	1485.32	1741.83
0.00	0.00	1566.39	522.13	738.40

Ceriops
partial cage
period 2

4-10 cm
28-8-92

	10.55 am A	11.45 am B	8.50 am C	mean	std
% mud after	15.02	8.88	9.61	11.17	2.74
% mud before	21.31	22.75	17.81	20.62	2.07
% sand after	81.43	86.52	85.84	84.60	2.26
% sand before	73.24	71.43	76.83	73.83	2.24
% coarse sand after	3.55	4.60	4.55	4.23	0.48
% coarse sand before	5.46	5.82	5.36	5.55	0.20
median after	238.30	306.40	321.10	288.60	36.07
median before	322.30	277.90	316.70	305.63	19.74
kurtosis after	2.48	4.47	4.64	3.86	0.98
kurtosis before	0.71	0.43	1.23	0.79	0.33
skewness after	-1.38	-1.72	-1.86	-1.65	0.20
skewness before	-1.25	-1.12	-1.37	-1.25	0.10
POM (%)	9.64	3.37	6.39	6.47	2.56
total carbon (%)	16.94	1.75	3.71	7.47	6.75
pH	6.04	6.01	6.24	6.10	0.10
salinity (ppt)	40.00	42.00	35.50	39.17	2.72
redox (mV)					
dissolved oxygen (mg/l)					
temperature (°C)	24.60	27.50	24.30	25.47	1.44
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00

10-rest cm
28-8-92

10.55 am A	11.45 am B	8.50 am C	mean	std
12.33	10.61	11.49	11.48	0.70
39.50	25.68	16.76	27.31	9.36
84.43	86.14	84.72	85.10	0.75
57.07	69.96	77.07	68.03	8.28
3.24	3.25	3.79	3.43	0.26
3.43	4.36	6.17	4.65	1.14
244.30	271.70	292.20	269.40	19.62
124.00	237.20	353.00	238.07	93.49
2.58	3.97	3.60	3.38	0.59
-0.86	0.61	1.65	0.47	1.03
-1.52	-1.66	-1.65	-1.61	0.06
-0.52	-1.14	-1.49	-1.05	0.40
8.16	5.91	7.59	7.22	0.95
6.04	6.01	6.24	6.10	0.10
40.00	42.00	35.50	39.17	2.72
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00

Ceriops
partial cage
period 3

	0-2 cm 27-9-92					2-4 cm 27-9-92				
	8.30 am A	8.42 am B	10.25 am C	mean	std	8.30 am A	8.42 am B	10.25 am C	mean	std
% mud after	14.87	12.09	17.22	14.73		12.33	11.82	14.69	12.95	1.25
% mud before	56.20	60.00	30.96	49.05	12.89	26.93	54.95	25.96	35.95	13.44
% sand after	82.55	84.47	80.03	82.35	1.82	84.25	85.50	82.27	84.01	1.33
% sand before	42.12	39.18	65.31	48.87	11.69	69.51	43.87	69.34	60.91	12.05
% coarse sand after	2.58	3.44	2.75	2.92	0.37	3.42	2.68	3.04	3.05	0.30
% coarse sand before	1.68	0.82	3.73	2.08	1.22	3.56	1.18	4.70	3.15	1.47
median after	210.90	221.70	230.40	221.00	7.98	328.40	216.20	265.20	269.93	45.93
median before	42.18	37.93	195.10	91.74	73.11	223.00	47.18	265.30	178.49	94.44
kurtosis after	2.99	3.32	2.33	2.88	0.41	2.91	3.48	2.86	3.08	0.28
kurtosis before	-0.95	-0.59	-0.19	-0.57	0.31	0.32	-0.87	0.27	-0.09	0.55
skewness after	-1.43	-1.43	-1.38	-1.41	0.02	-1.57	-1.43	-1.52	-1.51	0.06
skewness before	-0.08	-0.11	-0.87	-0.35	0.37	-1.04	-0.14	-1.09	-0.76	0.44
POM (%)	5.57	5.04	10.08	6.90	2.26	3.97	3.79	7.38	5.05	1.65
total carbon (%)	0.83	0.44	1.48	0.92	0.43	2.06	0.54	2.22	1.61	0.76
pH	6.31	6.55	6.42	6.43	0.10	6.31	6.55	6.42	6.43	0.10
salinity (ppt)	36.00	43.00	36.00	38.33	3.30	36.00	43.00	36.00	38.33	3.30
redox (mV)	117.00	114.00	132.00	121.00	7.87	103.00	78.00	150.00	110.33	29.85
dissolved oxygen (mg/l)	22.00	19.00	14.00	18.33	3.30					
temperature (°C)	27.30	27.00	32.20	28.83	2.38	26.70	26.80	31.00	28.17	2.00
chlorophyll a (ng/g DWT)	2931.28	4579.99	6732.65	4747.97	1556.44	0.00	976.05	0.00	325.35	460.11
fucoxanthine (ng/g DWT)	720.81	1583.74	2019.79	1441.45	539.77	0.00	225.12	0.00	75.04	106.12

Ceriops
partial cage
period 3

	4-10 cm 27-9-92					10-rest cm 27-9-92				
	8.30 am A	8.42 am B	10.25 am C	mean	std	8.30 am A	8.42 am B	10.25 am C	mean	std
% mud after	14.21	11.13	12.77	12.70	1.26	10.08	9.62	38.85	19.52	13.67
% mud before	26.74	56.39	28.05	37.06	13.68	23.09	49.71	9.25	27.35	16.79
% sand after	81.05	85.86	83.67	83.53	1.97	85.55	82.62	60.22	76.13	11.31
% sand before	69.66	42.33	68.71	60.23	12.67	72.74	48.72	85.58	69.01	15.28
% coarse sand after	4.74	3.01	3.56	3.77	0.72	4.37	7.76	0.93	4.35	2.79
% coarse sand before	3.60	1.28	3.24	2.71	1.02	4.17	1.56	5.17	3.63	1.52
median after	279.60	228.80	262.10	256.83	21.07	276.20	339.80	112.40	242.80	95.79
median before	202.10	42.81	192.90	145.94	73.02	255.50	64.00	265.60	195.03	92.75
kurtosis after	2.40	3.52	3.19	3.03	0.47	3.93	3.69	-0.36	2.42	1.97
kurtosis before	0.29	-0.90	0.12	-0.16	0.52	0.48	-0.78	3.83	1.17	1.95
skewness after	-1.37	-1.45	-1.55	-1.46	0.07	-1.58	-1.58	-0.64	-1.27	0.44
skewness before	-1.01	-0.04	-0.96	-0.67	0.44	-1.13	-0.78	-1.52	-1.14	0.30
POM (%)	4.91	3.07	5.37	4.45	0.99	5.04	2.19	3.76	3.67	1.17
total carbon (%)	2.25	1.69	2.54	2.16	0.35					
pH	6.31	6.55	6.42	6.43	0.10	6.31	6.55	6.42	6.43	0.10
salinity (ppt)	36.00	43.00	36.00	38.33	3.30	36.00	43.00	36.00	38.33	3.30
redox (mV)	93.00	33.00	85.00	70.33	26.60					
dissolved oxygen (mg/l)										
temperature (°C)	26.70	26.80	27.90	27.13	0.54					
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Ceriops
partial cage
period 4

0-2 cm
29-10-92

	10.08 am A	10.53 am B	1.07 pm C	mean	std
% mud after	7.26	4.79	9.12	7.06	
% mud before	22.74	21.54	15.19	19.82	3.31
% sand after	88.52	89.69	88.58	88.93	0.54
% sand before	73.09	74.18	80.56	75.94	3.29
% coarse sand after	4.22	5.52	2.30	4.01	1.32
% coarse sand before	4.17	4.28	4.25	4.23	0.05
median after	277.80	322.70	224.30	274.93	40.22
median before	244.80	236.60	292.70	258.03	24.74
kurtosis after	4.84	5.37	5.42	5.21	0.26
kurtosis before	0.34	0.48	1.65	0.82	0.59
skewness after	-1.65	-1.68	-1.76	-1.70	0.05
skewness before	-1.04	-1.05	-1.40	-1.16	0.17
POM (%)	3.13	1.22	4.27	2.87	1.26
total carbon (%)	1.54	0.67	1.28	1.16	0.36
pH		6.26	6.36	6.31	0.05
salinity (ppt)		42.00	42.00	42.00	0.00
redox (mV)	-48.00	13.00	-60.00	-31.67	31.96
dissolved oxygen (mg/l)	42.00	16.00		29.00	13.00
temperature (°C)	31.70	35.50	36.10	34.43	1.95
chlorophyll a (ng/g DWT)	2864.07	3333.68	892.49	2363.41	1057.62
fucoxanthine (ng/g DWT)	977.56	1137.41	578.64	897.87	234.97

2-4 cm
29-10-92

10.08 am A	10.53 am B	1.07 pm C	mean	std
8.42	8.59	10.20	9.07	0.80
40.86	23.27	14.65	26.26	10.91
87.98	87.42	86.63	87.34	0.55
57.22	71.78	80.72	69.91	9.68
3.60	3.99	3.17	3.59	0.33
1.92	4.95	4.63	3.83	1.36
245.00	236.30	252.20	244.50	6.50
95.02	249.40	321.60	222.01	94.51
4.22	4.42	4.43	4.36	0.10
-0.72	0.20	1.89	0.46	1.08
-1.46	-1.49	-1.69	-1.55	0.10
-0.45	-1.03	-1.53	-1.00	0.44
5.59	3.07	4.27	4.31	1.03
2.31	1.34	1.87	1.84	0.40
	6.26	6.36	6.31	0.05
	42.00	42.00	42.00	0.00
-53.00	-59.00	-40.00	-50.67	7.93
42.00	16.00		29.00	13.00
30.80	33.50	34.60	32.97	1.60
	698.60		698.60	0.00
127.48	202.54		165.01	37.53

Ceriops
partial cage
period 4

4-10 cm
29-10-92

	10.08 am A	10.53 am B	1.07 pm C	mean	std
% mud after	9.32	9.71	10.11	9.71	0.32
% mud before	26.43	31.66	17.95	25.35	5.65
% sand after	86.47	86.81	86.76	86.68	0.15
% sand before	69.34	65.44	79.44	71.41	5.90
% coarse sand after	4.21	3.48	3.13	3.61	0.45
% coarse sand before	4.23	2.90	4.61	3.91	0.73
median after	288.80	223.10	260.70	257.53	26.92
median before	237.40	153.40	303.10	231.30	61.27
kurtosis after	4.22	4.16	4.35	4.24	0.08
kurtosis before	-0.04	-0.39	1.20	0.26	0.68
skewness after	-1.63	-1.46	-1.68	-1.59	0.09
skewness before	-0.94	-0.76	-1.34	-1.01	0.24
POM (%)	4.95	2.85	5.70	4.50	1.21
total carbon (%)	2.10	2.10	2.56	2.25	0.22
pH		6.26	6.36	6.31	0.05
salinity (ppt)		42.00	42.00	42.00	0.00
redox (mV)	-92.00	-100.00	-37.00	-76.33	28.00
dissolved oxygen (mg/l)	42.00	16.00		29.00	13.00
temperature (°C)	29.60	30.60	32.20	30.80	1.07
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00

10-rest cm
29-10-92

10.08 am A	10.53 am B	1.07 pm C	mean	std
9.62	11.73	10.40	10.58	0.87
31.29	18.68	20.22	23.40	5.62
87.47	86.50	87.28	87.08	0.42
65.96	76.57	75.61	72.71	4.79
2.91	1.87	2.52	2.43	0.43
2.75	4.75	4.17	3.89	0.84
249.90	203.20	244.90	232.67	20.94
179.00	301.60	291.20	257.27	55.51
4.46	4.21	4.47	4.38	0.12
-0.35	1.17	1.03	0.62	0.69
-1.62	-1.62	-1.65	-1.63	0.01
-0.79	-1.35	-1.31	-1.15	0.25
5.56	9.09	5.20	6.62	1.76
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00

Ceriops
partial cage
period 5

0-2 cm
25-11-92

	8.43 am A	12.05 am B	10.30 am C	mean	std
% mud after	2.11	2.11	0.94	1.72	
% mud before	1.07	0.83	1.34	1.08	0.21
% sand after	97.04	95.48	96.26	96.26	0.64
% sand before	93.73	92.41	94.09	93.41	0.72
% coarse sand after	0.85	2.41	2.80	2.02	0.84
% coarse sand before	5.20	6.76	4.57	5.51	0.92
median after	162.00	226.70	290.00	226.23	52.26
median before	320.10	406.30	273.30	333.23	55.09
kurtosis after	4.65	4.49	6.73	5.29	1.02
kurtosis before	2.22	3.37	0.90	2.16	1.01
skewness after	-1.72	-1.75	-2.02	-1.83	0.14
skewness before	-1.49	-1.83	-1.21	-1.51	0.25
POM (%)	2.61	0.90	2.46	1.99	0.77
total carbon (%)	1.18	0.49	1.12	0.93	0.31
pH	6.32	6.56	6.46	6.45	0.10
salinity (ppt)	37.00	41.00	37.50	38.50	1.78
redox (mV)	20.00	-73.00	-30.00	-27.67	38.00
dissolved oxygen (mg/l)	2.00	14.00	21.00	12.33	7.85
temperature (°C)	28.70	31.50	30.60	30.27	1.17
chlorophyll a (ng/g DWT)	1647.98	3877.64	557.51	2027.71	1381.78
fucoxanthine (ng/g DWT)	781.74	1197.26	0.00	659.67	496.34

2-4 cm
25-11-92

8.43 am A	12.05 am B	10.30 am C	mean	std
3.19	1.07	1.20	1.82	0.97
0.93	1.18	0.88	1.00	0.13
95.72	92.05	94.79	94.19	1.56
91.90	93.71	94.32	93.31	1.03
1.08	6.88	4.01	3.99	2.37
7.17	5.11	4.80	5.69	1.05
152.20	343.90	272.00	256.03	79.07
401.40	313.50	326.80	347.23	38.68
2.63	5.16	5.87	4.55	1.39
3.86	1.15	2.24	2.42	1.12
-1.47	-1.82	-1.91	-1.74	0.19
-1.93	-1.30	-1.58	-1.60	0.26
6.33	1.62	4.41	4.12	1.93
3.41	0.76	1.34	1.84	1.14
6.32	6.56	6.46	6.45	0.10
37.00	41.00	37.50	38.50	1.78
-39.00	-79.00	-107.00	-75.00	27.90
2.00	14.00	21.00	12.33	7.85
28.50	30.90	29.80	29.73	0.98
	760.40		760.40	0.00
0.00	185.56		92.78	92.78

Ceriops
partial cage
period 5

4-10 cm
25-11-92

	8.43 am A	12.05 am B	10.30 am C	mean	std
% mud after	3.13	1.29	1.21	1.88	0.89
% mud before	1.55	3.29	1.27	2.04	0.89
% sand after	95.92	91.95	94.76	94.21	1.67
% sand before	92.34	92.07	94.03	92.81	0.87
% coarse sand after	0.95	6.76	4.03	3.91	2.37
% coarse sand before	6.11	4.64	4.70	5.15	0.68
median after	124.60	327.40	305.20	252.40	90.82
median before	380.40	204.20	323.70	302.77	73.44
kurtosis after	1.99	3.69	6.56	4.08	1.89
kurtosis before	3.36	-0.08	1.63	1.64	1.40
skewness after	-1.23	-1.63	-2.08	-1.65	0.35
skewness before	-1.83	-0.90	-1.45	-1.39	0.38
POM (%)	4.48	2.99	3.64	3.70	0.61
total carbon (%)	2.76	1.62	1.87	2.08	0.49
pH	6.32	6.56	6.46	6.45	0.10
salinity (ppt)	37.00	41.00	37.50	38.50	1.78
redox (mV)	-61.00	-129.00	-178.00	-122.67	47.97
dissolved oxygen (mg/l)	2.00	14.00	21.00	12.33	7.85
temperature (°C)	28.30	29.90	29.20	29.13	0.65
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00

10-rest cm
25-11-92

8.43 am A	12.05 am B	10.30 am C	mean	std
3.01	1.85	1.97	2.28	0.52
1.74	1.92	1.63	1.76	0.12
96.01	95.23	94.73	95.32	0.53
93.60	93.39	93.21	93.40	0.16
0.98	2.93	3.30	2.40	1.02
4.76	4.69	5.16	4.87	0.21
136.30	265.30	291.80	231.13	67.92
299.20	295.10	327.60	307.30	14.45
2.67	4.57	4.67	3.97	0.92
2.09	1.90	1.43	1.81	0.28
-1.39	-1.83	-1.93	-1.72	0.24
-1.51	-1.47	-1.41	-1.46	0.04
5.15	6.27	8.73	6.72	1.50
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00

Ceriops
partial cage
period 6

0-2 cm
23-12-92

	9.23 am A	11.27 am B	10.00 am C	mean	std
% mud after	0.47	0.46	0.97	0.63	
% mud before	1.17	0.95	1.52	1.21	0.23
% sand after	92.23	90.70	94.20	92.38	1.43
% sand before	93.18	90.34	95.07	92.86	1.94
% coarse sand after	7.30	8.84	4.83	6.99	1.65
% coarse sand before	5.65	8.71	3.41	5.92	2.17
median after	376.40	390.30	302.70	356.47	38.44
median before	332.70	362.80	245.10	313.53	49.93
kurtosis after	4.51	4.58	5.09	4.72	0.26
kurtosis before	2.47	2.87	1.98	2.44	0.37
skewness after	-1.66	-1.64	-1.75	-1.69	0.05
skewness before	-1.53	-1.60	-1.35	-1.49	0.10
POM (%)	3.20	2.30	4.00	3.17	0.69
total carbon (%)	1.20	0.83	1.32	1.12	0.21
pH	5.42	5.72	5.60	5.58	0.12
salinity (ppt)	36.00	40.00	37.50	37.83	1.65
redox (mV)	136.00	83.00	150.00	123.00	28.86
dissolved oxygen (mg/l)	7.00	8.00	8.00	7.67	0.47
temperature (°C)	27.70	33.60	31.90	31.07	2.48
chlorophyll a (ng/g DWT)	1281.84	184.40	1480.96	982.40	570.10
fucoxanthine (ng/g DWT)	1647.55	1658.13	1293.68	1533.12	169.36

2-4 cm
23-12-92

9.23 am A	11.27 am B	10.00 am C	mean	std
0.62	0.48	0.66	0.59	0.08
0.91	1.93	1.10	1.31	0.44
91.62	91.38	94.61	92.54	1.47
93.63	92.36	94.86	93.62	1.02
7.76	8.14	4.73	6.88	1.53
5.64	5.71	4.04	5.13	0.77
357.40	369.90	290.90	339.40	34.67
349.00	271.90	295.20	305.37	32.29
5.29	3.68	4.17	4.38	0.67
3.89	0.71	3.18	2.59	1.36
-1.76	-1.50	-1.55	-1.60	0.11
-1.78	-1.14	-1.62	-1.51	0.27
3.07	3.19	5.69	3.98	1.21
1.71	0.79	2.86	1.79	0.85
5.42	5.72	5.60	5.58	0.12
36.00	40.00	37.50	37.83	1.65
113.00	-19.00	32.00	42.00	54.35
7.00	8.00	8.00	7.67	0.47
27.20	32.00	30.20	29.80	1.98

Ceriops
partial cage
period 6

4-10 cm
23-12-92

	9.23 am A	11.27 am B	10.00 am C	mean	std
% mud after	0.85	0.61	0.59	0.68	0.12
% mud before	1.80	1.85	1.25	1.63	0.27
% sand after	94.42	93.10	95.16	94.23	0.85
% sand before	93.41	92.79	94.23	93.48	0.59
% coarse sand after	4.73	6.29	4.25	5.09	0.87
% coarse sand before	4.79	5.36	4.52	4.89	0.35
median after	294.10	328.90	304.80	309.27	14.55
median before	334.90	302.80	332.40	323.37	14.58
kurtosis after	4.13	3.91	4.96	4.33	0.46
kurtosis before	2.87	1.65	3.58	2.70	0.80
skewness after	-1.60	-1.50	-1.67	-1.59	0.07
skewness before	-1.72	-1.42	-1.80	-1.65	0.17
POM (%)	7.13	3.49	4.13	4.92	1.59
total carbon (%)	2.03	1.20	2.24	1.82	0.45
pH	5.42	5.72	5.60	5.58	0.12
salinity (ppt)	36.00	40.00	37.50	37.83	1.65
redox (mV)	44.00	-40.00	71.00	25.00	47.27
dissolved oxygen (mg/l)	7.00	8.00	8.00	7.67	0.47
temperature (°C)	27.50	29.60	28.90	28.67	0.87
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00

10-rest cm
23-12-92

9.23 am A	11.27 am B	10.00 am C	mean	std
0.62	0.65	0.79	0.69	0.07
1.57	2.21	0.94	1.57	0.52
97.18	94.63	95.43	95.75	1.06
94.28	92.49	93.31	93.36	0.73
2.20	4.72	3.78	3.57	1.04
4.15	5.30	5.75	5.07	0.67
334.40	326.70	317.20	326.10	7.03
351.60	332.80	377.60	354.00	18.37
5.79	4.61	6.28	5.56	0.70
3.55	1.79	4.68	3.34	1.19
-1.90	-1.67	-2.01	-1.86	0.14
-1.91	-1.51	-2.01	-1.81	0.22
3.74	4.41	8.22	5.46	1.97
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00

Ceriops
cage
period 1

	0-2 cm 6-8-92					2-4 cm 6-8-92				
	1.00 pm A	1.21 pm B	1.50 pm C	mean	std	1.00 pm A	1.21 pm B	1.50 pm C	mean	std
% mud after	11.73	4.01	5.59	7.11		14.46	5.92	8.43	9.60	3.58
% mud before	16.74	15.93	32.32	21.66	7.54	15.76	35.03	35.22	28.67	9.13
% sand after	84.54	84.95	90.08	86.52	2.52	83.06	87.61	87.69	86.12	2.16
% sand before	77.00	79.80	66.73	74.51	5.62	78.45	62.44	62.46	67.78	7.54
% coarse sand after	3.73	11.04	4.33	6.37	3.31	2.48	6.47	3.88	4.28	1.65
% coarse sand before	6.26	4.27	0.95	3.83	2.19	5.79	2.53	2.32	3.55	1.59
median after	246.90	391.80	326.80	321.83	59.26	191.00	333.20	260.50	261.57	58.06
median before	347.30	308.80	136.50	264.20	91.66	334.30	147.20	125.00	202.17	93.87
kurtosis after	3.70	6.61	6.07	5.46	1.26	3.22	5.73	5.19	4.71	1.08
kurtosis before	1.39	1.59	-0.12	0.95	0.76	1.65	-0.54	-0.53	0.19	1.03
skewness after	-1.58	-1.97	-1.89	-1.81	0.17	-1.48	-1.86	-1.77	-1.70	0.16
skewness before	-1.45	-1.44	-0.81	-1.24	0.30	-1.50	-0.65	-0.53	-0.89	0.43
POM (%)	1.55	1.17	1.77	1.50	0.25	3.18	3.56	2.67	3.13	0.36
total carbon (%)										
pH	6.48	6.77	4.55	5.93	0.99	6.48	6.77	4.55	5.93	0.99
salinity (ppt)	47.00	48.00	58.00	51.00	4.97	47.00	48.00	58.00	51.00	4.97
redox (mV)										
dissolved oxygen (mg/l)	9.00	23.00	11.00	14.33	6.18					
temperature (°C)	24.60	23.20	23.20	23.67	0.66	24.30	23.00	23.00	23.43	0.61
chlorophyll a (ng/g DWT)	2773.43	3618.38	3737.87	3376.56	429.26	0.00	775.34	658.27	477.87	341.27
fucoxanthine (ng/g DWT)	967.60	872.96	742.44	861.00	92.31	0.00	0.00	167.18	55.73	78.81

Ceriops
cage
period 1

	4-10 cm 6-8-92					10-rest cm 6-8-92				
	1.00 pm A	1.21 pm B	1.50 pm C	mean	std	1.00 pm A	1.21 pm B	1.50 pm C	mean	std
% mud after	20.24	7.48		13.86	6.38	9.83	10.69	13.97	11.50	1.78
% mud before	20.51	38.43		29.47	8.96	19.98	32.51	37.09	29.86	7.23
% sand after	78.24	87.09		82.66	4.42	85.66	85.65	82.19	84.50	1.63
% sand before	74.71	59.40		67.06	7.65	74.90	64.73	60.41	66.68	6.07
% coarse sand after	1.52	5.43		3.48	1.96	4.51	3.66	3.84	4.00	0.37
% coarse sand before	4.78	2.17		3.48	1.31	5.12	2.76	2.50	3.46	1.18
median after	161.80	322.20		242.00	80.20	308.30	305.00	256.40	289.90	23.73
median before	299.70	123.80		211.75	87.95	315.90	162.80	114.50	197.73	85.85
kurtosis after	2.44	4.57		3.51	1.06	4.82	4.28	3.08	4.06	0.73
kurtosis before	0.74	-0.73		0.01	0.74	1.08	-0.27	-0.54	0.09	0.71
skewness after	-1.32	-1.70		-1.51	0.19	-1.92	-1.80	-1.56	-1.76	0.15
skewness before	-1.27	-0.58		-0.93	0.34	-1.36	-0.81	-0.65	-0.94	0.30
POM (%)	8.13	3.51	10.65	7.43	2.96	7.62	8.49	6.06	7.39	1.00
total carbon (%)										
pH	6.48	6.77		6.63	0.15	6.48	6.77	4.55	5.93	0.99
salinity (ppt)	47.00	48.00		47.50	0.50	47.00	48.00	58.00	51.00	4.97
redox (mV)										
dissolved oxygen (mg/l)										
temperature (°C)	23.70	22.10		22.90	0.80					
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Ceriops
cage
period 2

0-2 cm
28-8-92

	10.30 am A	9.20 am B	8.30 am C	mean	std
% mud after	3.73	9.19	13.35	8.76	
% mud before	20.82	45.46	39.67	35.32	10.52
% sand after	87.31	82.13	80.62	83.35	2.86
% sand before	73.35	51.54	56.59	60.49	9.32
% coarse sand after	8.96	8.68	6.03	7.89	1.32
% coarse sand before	5.83	3.00	3.74	4.19	1.20
median after	399.90	341.20	293.50	344.87	43.51
median before	299.00	83.06	113.30	165.12	95.47
kurtosis after	7.09	3.56	2.74	4.47	1.89
kurtosis before	0.61	-0.97	-0.82	-0.39	0.71
skewness after	-2.02	-1.57	-1.41	-1.67	0.26
skewness before	-1.17	-0.30	-0.50	-0.66	0.37
POM (%)	1.80	3.39	2.82	2.67	0.66
total carbon (%)		1.44	1.68	1.56	0.12
pH	6.24	6.00	5.92	6.05	0.14
salinity (ppt)	38.50	38.00	39.00	38.50	0.41
redox (mV)					
dissolved oxygen (mg/l)	16.00	15.00	15.00	15.33	0.47
temperature (°C)	27.70	24.90	24.10	25.57	1.54
chlorophyll a (ng/g DWT)	5361.93	6177.99	6170.17	5903.36	382.86
fucoxanthine (ng/g DWT)	1608.58	1853.41	1851.05	1771.01	114.86

2-4 cm
28-8-92

10.30 am A	9.20 am B	8.30 am C	mean	std
8.61	11.12	8.68	9.47	1.17
23.97	41.02	43.27	36.09	8.62
84.49	84.17	82.34	83.67	0.95
72.43	55.93	53.50	60.62	8.41
6.90	4.71	8.98	6.86	1.74
3.60	3.05	3.23	3.29	0.23
318.40	262.80	375.00	318.73	45.81
233.80	106.90	95.18	145.29	62.77
4.17	3.44	3.81	3.80	0.30
0.13	-0.84	-0.98	-0.56	0.49
-1.66	-0.50	-1.64	-1.27	0.54
-1.03	-0.84	-0.38	-0.75	0.27
4.17	3.48	3.22	3.62	0.40
2.47	1.73		2.10	0.37
6.24	6.00	5.92	6.05	0.14
38.50	38.00	39.00	38.50	0.41
26.60	24.70	24.10	25.13	1.07
183.63	0.00	6562.33	2248.65	3051.15
183.63	0.00	1431.90	538.51	636.15

Ceriops
cage
period 2

4-10 cm
28-8-92

	10.30 am A	9.20 am B	8.30 am C	mean	std
% mud after	10.52	11.26	9.70	10.49	0.64
% mud before	16.07	17.64	30.38	21.36	6.41
% sand after	85.74	82.33	84.34	84.14	1.40
% sand before	80.83	78.02	66.26	75.04	6.31
% coarse sand after	3.70	6.41	5.96	5.36	1.19
% coarse sand before	3.55	4.34	3.36	3.75	0.42
median after	265.60	309.50	323.90	299.67	24.80
median before	274.60	276.50	185.10	245.40	42.65
kurtosis after	4.17	3.25	4.27	3.90	0.46
kurtosis before	1.83	1.34	-0.25	0.97	0.89
skewness after	-1.65	-1.56	-1.73	-1.65	0.07
skewness before	-1.47	-1.37	-0.83	-1.22	0.28
POM (%)	3.64	2.60	3.71	3.32	0.51
total carbon (%)	1.47	2.06	0.96	1.50	0.45
pH	6.24	6.00	5.29	5.84	0.40
salinity (ppt)	38.50	38.00	39.00	38.50	0.41
redox (mV)					
dissolved oxygen (mg/l)					
temperature (°C)	24.90	24.70	24.50	24.70	0.16
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00

10-rest cm
28-8-92

10.30 am A	9.20 am B	8.30 am C	mean	std
9.20	12.87	11.31	11.13	1.50
28.77	28.71	24.95	27.48	1.79
87.31	83.71	83.66	84.89	1.71
75.63	67.52	71.54	71.56	3.31
3.49	3.42	5.03	3.98	0.74
4.40	3.77	3.51	3.89	0.37
285.10	279.60	306.10	290.27	11.42
276.80	222.20	222.60	240.53	25.64
5.09	3.30	3.61	4.00	0.78
1.11	0.04	0.40	0.52	0.44
-1.86	-1.60	-1.64	-1.70	0.11
-1.29	-0.97	-1.07	-1.11	0.13
5.09	5.42	3.05	4.52	1.05
6.24	6.00	5.92	6.05	0.14
38.50	38.00	39.00	38.50	0.41
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00

Ceriops
cage
period 3

	0-2 cm 27-9-92					2-4 cm 27-9-92				
	9.25 am A	9.48 am B	10.43 am C	mean	std	9.25 am A	9.48 am B	10.43 am C	mean	std
% mud after	9.64	13.42	17.22	13.43		10.00	10.86	15.65	12.17	2.49
% mud before	45.25	28.69	42.10	38.68	7.18	29.99	22.45	38.48	30.31	6.55
% sand after	83.08	79.70	79.06	80.61	1.76	82.12	83.42	79.69	81.74	1.55
% sand before	52.73	67.48	55.51	58.57	6.40	76.66	73.63	59.06	69.78	7.68
% coarse sand after	7.28	6.88	3.72	5.96	1.59	7.88	5.72	4.66	6.09	1.34
% coarse sand before	2.02	3.83	2.39	2.75	0.78	3.35	3.92	2.46	3.24	0.60
median after	312.20	281.60	215.00	269.60	40.58	286.60	328.90	230.30	281.93	40.39
median before	77.87	209.00	102.20	129.69	56.95	168.60	246.80	125.80	180.40	50.10
kurtosis after	3.15	2.90	2.37	2.81	0.33	3.83	3.56	2.52	3.31	0.57
kurtosis before	-0.66	0.11	-0.72	-0.42	0.38	-0.20	0.81	-0.63	-0.00	0.60
skewness after	-1.43	-1.54	-1.34	-1.44	0.08	-1.56	-1.70	-1.38	-1.55	0.13
skewness before	-0.36	-0.95	-0.53	-0.62	0.25	-0.80	-1.22	-0.63	-0.88	0.25
POM (%)	3.69	6.17	11.01	6.96	3.04	2.43	3.54	6.68	4.22	1.80
total carbon (%)	1.88	1.58	0.90	1.45	0.41	1.78	3.08	1.35	2.07	0.74
pH	6.34	6.54	6.25	6.38	0.12	6.34	6.54	6.25	6.38	0.12
salinity (ppt)	38.00	36.00	37.00	37.00	0.82	38.00	36.00	37.00	37.00	0.82
redox (mV)	143.00	144.00	62.00	116.33	38.42	145.00	130.00	127.00	134.00	7.87
dissolved oxygen (mg/l)	11.00	8.00	12.00	10.33	1.70	0.00			0.00	0.00
temperature (°C)	27.80	29.60	27.60	28.33	0.90	27.40	28.50	27.30	27.73	0.54
chlorophyll a (ng/g DWT)	7731.26	6298.62	5573.20	6534.36	896.66	0.00	515.53	1213.85	576.46	497.42
fucoxanthine (ng/g DWT)	2319.38	1889.59	1671.96	1960.31	269.00	0.00	0.00	260.08	86.69	122.60

Ceriops
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period 3

	4-10 cm 27-9-92					10-rest cm 27-9-92				
	9.25 am A	9.48 am B	10.43 am C	mean	std	9.25 am A	9.48 am B	10.43 am C	mean	std
% mud after	9.22	10.36	13.93	11.17	2.01	9.39	12.68	11.41	11.16	1.35
% mud before	18.98	44.49	34.97	32.81	10.53	20.69	31.97	42.58	31.75	8.94
% sand after	86.62	83.16	81.68	83.82	2.07	88.56	77.21	84.20	83.32	4.67
% sand before	76.97	53.13	62.53	64.21	9.80	75.04	65.01	36.33	58.79	16.40
% coarse sand after	4.16	6.48	4.39	5.01	1.04	2.05	10.11	4.39	5.52	3.39
% coarse sand before	4.05	2.38	2.50	2.98	0.76	4.27	3.02	1.09	2.79	1.31
median after	279.40	315.80	245.60	280.27	28.67	252.50	281.80	256.00	263.43	13.07
median before	258.60	91.74	127.10	159.15	71.79	261.10	164.10	87.26	170.82	71.13
kurtosis after	4.48	3.79	3.13	3.80	0.55	5.55	2.79	3.81	4.05	1.14
kurtosis before	1.45	-0.92	-0.28	0.08	1.00	0.99	-0.27	-0.47	0.08	0.64
skewness after	-1.70	-1.66	-1.53	-1.63	0.07	-1.92	-1.42	-1.60	-1.65	0.21
skewness before	-1.38	-0.38	-0.70	-0.82	0.41	-1.25	-0.76	-0.50	-0.84	0.31
POM (%)	4.50	6.69	4.79	5.33	0.97	4.18	4.40	2.61	3.73	0.80
total carbon (%)	1.09	1.65	3.31	2.02	0.94					
pH	6.34	6.54	6.25	6.38	0.12	6.34	6.54	6.25	6.38	0.12
salinity (ppt)	38.00	36.00	37.00	37.00	0.82	38.00	36.00	37.00	37.00	0.82
redox (mV)	137.00	92.00	67.00	98.67	28.96					
dissolved oxygen (mg/l)										
temperature (°C)	27.10	27.30	26.80	27.07	0.21					
chlorophyll a (ng/g DWT)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
fucoxanthine (ng/g DWT)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

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period 4

	0-2 cm 29-10-92					2-4 cm 29-10-92				
	12.11 am A	11.48 am B	1.30 pm C	mean	std	12.11 am A	11.48 am B	1.30 pm C	mean	std
% mud after	6.46	4.98	5.13	5.52		10.76	9.45	8.81	9.67	0.81
% mud before	13.00	13.66	18.02	14.89	2.23	11.80	12.97	18.77	14.51	3.05
% sand after	89.77	91.19	90.57	90.51	0.58	87.31	88.85	88.66	88.27	0.69
% sand before	81.97	82.16	78.32	80.82	1.77	83.09	82.98	77.66	81.24	2.53
% coarse sand after	3.77	3.83	4.30	3.97	0.24	1.93	1.70	2.53	2.05	0.35
% coarse sand before	5.03	4.18	3.66	4.29	0.56	5.11	4.05	3.57	4.24	0.64
median after	256.60	310.40	289.10	285.37	22.12	206.30	200.60	222.40	209.77	9.23
median before	318.20	294.20	255.00	289.13	26.05	337.80	295.80	246.30	293.30	37.40
kurtosis after	5.95	7.22	5.84	6.33	0.63	5.26	5.95	5.24	5.48	0.33
kurtosis before	2.21	2.08	1.15	1.81	0.47	2.84	2.42	0.99	2.09	0.79
skewness after	-1.78	-2.01	-1.72	-1.83	0.12	-1.83	-1.83	-1.64	-1.76	0.09
skewness before	-1.55	-1.48	-1.26	-1.43	0.12	-1.73	-1.60	-1.22	-1.52	0.22
POM (%)	3.31	1.63	1.76	2.23	0.76	9.08	4.61	3.43	5.71	2.43
total carbon (%)	1.85	1.19	0.87	1.30	0.41	3.85	1.90	1.18	2.31	1.13
pH	6.28	6.44	6.58	6.43	0.12	6.28	6.44	6.58	6.43	0.12
salinity (ppt)	35.50	37.50	45.00	39.33	4.09	35.50	37.50	45.00	39.33	4.09
redox (mV)	-47.00	-47.00	36.00	-19.33	39.13	-23.00	-80.00	-85.00	-62.67	28.12
dissolved oxygen (mg/l)	5.00	10.00	18.00	11.00	5.35	5.00	10.00	18.00	11.00	5.35
temperature (°C)	33.70	34.90	32.90	33.83	0.82	32.50	33.70	32.00	32.73	0.71
chlorophyll a (ng/g DWT)		10000.00	4628.37	7314.19	2685.82		0.00	1790.30	895.15	895.15
fucoxanthine (ng/g DWT)	658.92	3000.00	3000.00	2219.64	1103.60	0.00	0.00	169.28	56.43	79.80

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period 4

	4-10 cm 29-10-92					10-rest cm 29-10-92				
	12.11 am A	11.48 am B	1.30 pm C	mean	std	12.11 am A	11.48 am B	1.30 pm C	mean	std
% mud after	8.13	8.88	8.71	8.57	0.32	10.14	10.53	9.71	10.13	0.33
% mud before	17.94	12.26	24.19	18.13	4.87	12.71	13.56	25.32	17.20	5.75
% sand after	88.87	88.95	87.97	88.60	0.44	87.69	87.11	87.26	87.35	0.25
% sand before	77.67	83.19	71.96	77.61	4.58	82.63	81.15	71.08	78.29	5.13
% coarse sand after	3.00	2.17	3.32	2.83	0.48	2.17	2.36	3.03	2.52	0.37
% coarse sand before	4.93	4.55	3.85	4.44	0.45	4.67	5.29	3.60	4.52	0.70
median after	258.10	232.90	260.40	250.47	12.46	243.50	253.00	282.60	259.70	16.65
median before	300.50	334.70	246.80	294.00	36.18	324.60	360.00	245.90	310.17	47.69
kurtosis after	5.64	5.42	4.82	5.29	0.35	4.98	4.67	4.64	4.76	0.15
kurtosis before	1.12	2.98	0.33	1.48	1.11	2.92	2.70	0.32	1.98	1.18
skewness after	-1.85	-1.79	-1.67	-1.77	0.08	-1.81	-1.79	-1.77	-1.79	0.02
skewness before	-1.34	-1.75	-1.08	-1.39	0.28	-1.74	-1.75	-1.11	-1.53	0.30
POM (%)	4.46	2.80	3.43	3.56	0.68	8.48	5.61	6.90	7.00	1.17
total carbon (%)	6.86	2.55	2.32	3.91	2.09					
pH	6.28	6.44	6.58	6.43	0.12					
salinity (ppt)	35.50	37.50	45.00	39.33	4.09					
redox (mV)	-37.00	-98.00	-142.00	-92.33	43.05					
dissolved oxygen (mg/l)	5.00	10.00	18.00	11.00	5.35					
temperature (°C)	30.40	30.90	29.70	30.33	0.49					
chlorophyll a (ng/g DWT)										
fucoxanthine (ng/g DWT)										

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period 5

0-2 cm
25-11-92

	9.09 am A	11.05 am B	9.57 am C	mean	std
% mud after	2.29	2.34	2.49	2.37	
% mud before	1.69	1.08	0.59	1.12	0.45
% sand after	91.87	92.47	92.77	92.37	0.37
% sand before	97.33	92.99	88.03	92.78	3.80
% coarse sand after	5.84	5.19	4.74	5.26	0.45
% coarse sand before	0.98	5.93	11.38	6.10	4.25
median after	259.50	258.30	207.10	241.63	24.42
median before	172.40	313.50	376.60	287.50	85.37
kurtosis after	-0.13	0.17	-0.33	-0.10	0.21
kurtosis before	4.66	3.93	5.16	4.59	0.50
skewness after	-0.91	-1.02	-0.78	-0.90	0.10
skewness before	-1.65	-1.65	-1.78	-1.69	0.06
POM (%)	2.02	3.53	1.08	2.21	1.01
total carbon (%)	1.91	1.23	1.17	1.44	0.34
pH	6.39	6.43	6.34	6.39	0.04
salinity (ppt)	35.00	35.00	36.00	35.33	0.47
redox (mV)	-17.00	-83.00	-31.00	-43.67	28.39
dissolved oxygen (mg/l)	7.00	10.00	4.00	7.00	2.45
temperature (°C)	28.60	34.50	28.20	30.43	2.88
chlorophyll a (ng/g DWT)	10000.00	10000.00	10000.00	10000.00	0.00
fucoxanthine (ng/g DWT)	3000.00	3000.00	3000.00	3000.00	0.00

2-4 cm
25-11-92

9.09 am A	11.05 am B	9.57 am C	mean	std
1.87	1.97	2.17	2.00	0.12
2.27	1.30	0.84	1.47	0.60
92.33	92.72	92.94	92.66	0.25
97.43	95.42	93.17	95.34	1.74
5.60	5.31	4.89	5.27	0.29
0.30	3.28	5.99	3.19	2.32
317.60	287.30	252.40	285.77	26.64
128.80	225.50	308.10	220.80	73.27
1.63	0.70	0.22	0.85	0.58
3.79	4.32	5.28	4.47	0.62
-1.44	-1.20	-1.03	-1.22	0.17
-1.56	-1.59	-1.74	-1.63	0.08
4.07	3.15	2.36	3.19	0.70
1.00	0.89	1.11	1.00	0.09
6.39	6.43	6.34	6.39	0.04
35.00	35.00	36.00	35.33	0.47
-25.00	-75.00	-64.00	-54.67	21.45
7.00	10.00	4.00	7.00	2.45
28.40	32.40	28.00	29.60	1.99
3208.05	964.97	1754.38	1975.80	929.02
993.05	144.83	297.53	478.47	369.16

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period 5

4-10 cm
25-11-92

	9.09 am A	11.05 am B	9.57 am C	mean	std
% mud after	1.61	1.67	2.33	1.87	0.33
% mud before	1.75	1.90	1.24	1.63	0.28
% sand after	93.58	93.50	93.11	93.40	0.21
% sand before	98.24	96.09	95.37	96.57	1.22
% coarse sand after	4.81	4.83	4.56	4.73	0.12
% coarse sand before	0.01	2.01	3.39	1.80	1.39
median after	319.30	315.10	284.60	306.33	15.46
median before	169.70	182.80	257.50	203.33	38.67
kurtosis after	3.14	2.64	1.57	2.45	0.65
kurtosis before	4.09	3.16	4.96	4.07	0.74
skewness after	-1.74	-1.64	-1.42	-1.60	0.13
skewness before	-1.76	-1.45	-1.74	-1.65	0.14
POM (%)	3.76	5.24	2.50	3.83	1.12
total carbon (%)	2.34	1.63	1.90	1.96	0.29
pH	6.39	6.43	6.34	6.39	0.04
salinity (ppt)	35.00	35.00	36.00	35.33	0.47
redox (mV)	-59.00	-34.00	-43.00	-45.33	10.34
dissolved oxygen (mg/l)	7.00	10.00	4.00	7.00	2.45
temperature (°C)	28.40	29.40	28.00	28.60	0.59
chlorophyll a (ng/g DWT)					
fucoxanthine (ng/g DWT)					

10-rest cm
25-11-92

9.09 am A	11.05 am B	9.57 am C	mean	std
1.34	3.26	6.05	3.55	1.93
2.44	1.99	1.24	1.89	0.49
92.80	91.87	91.50	92.06	0.55
97.35	96.04	95.54	96.31	0.76
5.86	4.87	2.45	4.39	1.43
0.21	1.97	3.22	1.80	1.23
358.50	320.40	116.10	265.00	106.43
172.10	221.70	264.50	219.43	37.76
2.97	1.62	-0.58	1.34	1.46
3.00	2.59	3.74	3.11	0.47
-1.74	-1.50	-0.60	-1.28	0.49
-1.61	-1.48	-1.62	-1.57	0.07
6.39	5.11	5.51	5.67	0.53

Ceriops
cage
period 6

0-2 cm
23-12-92

	8.50 am A	9.30 am B	10.25 am C	mean	std
% mud after	0.82	0.43	0.39	0.55	
% mud before	1.62	0.84	0.65	1.04	0.42
% sand after	96.62	92.45	92.62	93.90	1.93
% sand before	96.34	92.72	93.03	94.03	1.64
% coarse sand after	2.56	7.12	6.99	5.56	2.12
% coarse sand before	2.04	6.44	6.32	4.93	2.05
median after	266.70	371.10	376.40	338.07	50.51
median before	268.00	349.50	346.50	321.33	37.73
kurtosis after	5.85	5.19	4.87	5.30	0.41
kurtosis before	2.24	4.06	4.83	3.71	1.09
skewness after	-1.85	-1.72	-1.67	-1.75	0.08
skewness before	-1.50	-1.75	-1.80	-1.68	0.13
POM (%)	6.05	2.47	1.74	3.42	1.88
total carbon (%)	2.10	0.81	0.68	1.20	0.64
pH	5.52	5.78	5.47	5.59	0.14
salinity (ppt)	35.00	36.00	35.50	35.50	0.41
redox (mV)	103.00	102.00	101.00	102.00	0.82
dissolved oxygen (mg/l)	8.00	6.00	5.00	6.33	1.25
temperature (°C)	29.10	29.00	29.00	29.03	0.05
chlorophyll a (ng/g DWT)	2239.72	1084.45	205.25	1176.47	833.11
fucoxanthine (ng/g DWT)	1800.09	2344.02	2469.75	2204.62	290.61

2-4 cm
23-12-92

8.50 am A	9.30 am B	10.25 am C	mean	std
0.60	0.65	0.37	0.54	0.12
1.11	2.99	0.62	1.57	1.02
96.58	92.84	93.26	94.23	1.67
96.47	93.75	91.89	94.04	1.88
2.82	6.51	6.37	5.23	1.71
2.42	3.26	7.49	4.39	2.22
273.40	322.60	355.70	317.23	33.81
279.90	182.30	367.20	276.47	75.52
5.59	3.84	4.83	4.76	0.71
3.54	0.38	5.17	3.03	1.99
-1.75	-1.53	-1.59	-1.62	0.09
-1.69	-0.96	-1.97	-1.54	0.42
4.76	4.58	2.23	3.86	1.15
1.15	3.50	1.64	2.10	1.01
5.52	5.78	5.47	5.59	0.14
35.00	36.00	35.50	35.50	0.41
71.00	85.00	102.00	86.00	12.68
8.00	6.00	5.00	6.33	1.25
28.70	28.30	28.50	28.50	0.16

Ceriops
cage
period 6

4-10 cm
23-12-92

	8.50 am A	9.30 am B	10.25 am C	mean	std
% mud after	0.83	0.79	0.66	0.76	0.07
% mud before	0.69	1.88	2.50	1.69	0.75
% sand after	96.19	94.47	93.65	94.77	1.06
% sand before	93.57	94.40	93.65	93.87	0.37
% coarse sand after	2.98	4.74	5.69	4.47	1.12
% coarse sand before	5.74	3.72	3.85	4.44	0.92
median after	275.70	291.70	313.00	293.47	15.28
median before	354.60	246.40	244.90	281.97	51.36
kurtosis after	5.91	4.63	3.64	4.73	0.93
kurtosis before	6.50	1.13	1.28	2.97	2.50
skewness after	-1.90	-1.62	-1.50	-1.67	0.17
skewness before	-2.15	-1.20	-1.28	-1.54	0.43
POM (%)	6.76	4.00	6.17	5.64	1.19
total carbon (%)	1.95	2.83	2.07	2.28	0.39
pH	5.52	5.78	5.47	5.59	0.14
salinity (ppt)	35.00	36.00	35.50	35.50	0.41
redox (mV)	15.00	-3.00	28.00	13.33	12.71
dissolved oxygen (mg/l)	8.00	6.00	5.00	6.33	1.25
temperature (°C)	27.80	27.90	27.90	27.87	0.05
chlorophyll a (ng/g DWT)					
fucoxanthine (ng/g DWT)					

10-rest cm
23-12-92

8.50 am A	9.30 am B	10.25 am C	mean	std
0.76	0.84	0.71	0.77	0.05
1.21	1.64	1.45	1.43	0.18
93.70	95.06	95.47	94.74	0.76
93.31	93.85	94.53	93.90	0.50
5.54	4.10	3.82	4.49	0.75
5.48	4.51	4.02	4.67	0.61
299.90	300.40	287.70	296.00	5.87
311.60	310.20	267.60	296.47	20.42
4.26	4.79	4.59	4.55	0.22
2.40	2.30	2.55	2.41	0.10
-1.58	-1.73	-1.62	-1.64	0.06
-1.44	-1.55	-1.49	-1.49	0.04
5.06	6.65	5.43	5.71	0.68

Avicennia
blanco
0-2 cm

	period 1 6-8-92					period 2 28-8-92				
	2.00 pm A	2.40 pm B	3.45 pm C	mean	std	11.40 am A	12.25 am B	2.35 pm C	mean	std
% mud after	6.13	7.69	10.15	7.99	1.65	5.82	8.99	5.77	6.86	1.51
% mud before	31.03	33.87	41.12	35.34	4.25	51.95	44.20	39.66	45.27	5.07
% sand after	89.40	88.66	84.44	87.50	2.18	73.75	86.01	88.59	82.78	6.47
% sand before	65.98	63.13	56.83	61.98	3.82	47.78	53.80	58.63	53.40	4.44
% coarse sand after	4.47	3.65	5.41	4.51	0.72	20.43	5.00	5.64	10.36	7.13
% coarse sand before	2.99	3.00	2.05	2.68	0.45	0.27	2.00	1.71	1.33	0.76
median after	345.00	307.00	360.00	337.33	22.31	373.00	359.00	378.00	370.00	8.04
median before	215.00	175.00	133.00	174.33	33.48	57.00	91.00	118.00	88.67	24.96
kurtosis after	6.83	5.72	4.76	5.77	0.85	4.13	4.90	7.30	5.44	1.35
kurtosis before	-0.45	-0.60	-0.98	-0.68	0.22	-0.87	-0.91	-0.67	-0.82	0.10
skewness after	-2.15	-1.99	-2.04	-2.06	0.07	-1.63	-1.94	-2.25	-1.94	0.25
skewness before	-0.81	-0.70	-0.50	-0.67	0.13	-0.19	-0.41	-0.53	-0.38	0.14
POM (%)	3.60	5.27	4.40	4.42	0.68	4.52	4.18	4.03	4.24	0.20
total carbon (%)	3.79	5.44	2.06	3.76	1.38	2.33	2.92	1.40	2.22	0.63
muddy detritus (%)	24.90	26.18	30.97	27.35	2.61	46.13	35.21	33.89	38.41	5.49
pH	6.35	6.45	6.46	6.42	0.05	6.04	5.95	5.93	5.97	0.05
salinity (ppt)	49.00	46.00	55.00	50.00	3.74	49.00	55.00	55.00	53.00	2.83
redox (mV)										
dissolved oxygen (mg/l)	7.00	13.00	19.00	13.00	4.90	18.00	15.00	14.00	15.67	1.70
temperature (°C)	27.60	28.10	27.20	27.63	0.37	28.80	29.50	30.80	29.70	0.83
chlorophyll a (ng/g DWT)	2549.36	2335.30	1079.59	1988.08	648.32	1986.56	2184.43	922.18	1697.72	554.31
fucoxanthine (ng/g DWT)	723.18	645.04	291.51	553.24	187.80	710.35	861.52	400.01	657.29	192.11

Avicennia
blanco
0-2 cm

	period 3 25-9-92					period 4 30-10-92				
	11.30 am A	12.25 am B	12.35 am C	mean	std	10.17 am A	10.47 am B	11.52 am C	mean	std
% mud after	8.24	11.12	11.65	10.34	1.50	6.10	6.25	6.75	6.37	0.28
% mud before	28.71	17.42	27.85	24.66	5.13	25.59	24.88	23.51	24.66	0.86
% sand after	86.95	81.89	82.98	83.94	2.17	90.28	90.90	89.12	90.10	0.74
% sand before	67.05	75.98	67.07	70.03	4.20	71.46	72.01	73.71	72.39	0.96
% coarse sand after	4.81	6.99	5.37	5.72	0.92	3.62	2.85	4.13	3.53	0.53
% coarse sand before	4.24	6.60	5.08	5.31	0.98	2.95	3.11	2.78	2.95	0.13
median after	341.00	361.00	346.00	349.33	8.50	320.00	292.00	324.00	312.00	14.24
median before	237.00	357.00	278.00	290.67	49.80	216.00	218.00	215.00	216.33	1.25
kurtosis after	5.39	3.47	3.73	4.20	0.85	7.37	7.18	6.95	7.17	0.17
kurtosis before	-0.43	1.46	-0.14	0.30	0.83	0.09	0.09	0.37	0.18	0.13
skewness after	-1.98	-1.71	-1.78	-1.82	0.11	-2.21	-2.15	-2.21	-2.19	0.03
skewness before	-0.87	-1.49	-0.99	-1.12	0.27	-0.99	-1.00	-1.05	-1.01	0.03
POM (%)	5.60	2.71	5.67	4.66	1.38	3.89	5.20	7.12	5.40	1.33
total carbon (%)	2.20	1.73	3.73	2.55	0.85	2.31	2.44	1.61	2.12	0.36
muddy detritus (%)	20.47	6.30	16.20	14.32	5.94	19.49	18.63	16.76	18.29	1.14
pH	6.43	6.57	6.35	6.45	0.09	6.11	6.25	6.11	6.16	0.07
salinity (ppt)	60.00	60.00	57.00	59.00	1.41	57.00	47.00	59.00	54.33	5.25
redox (mV)	254.00	313.00	272.00	279.67	24.69	51.00	21.00	76.00	49.33	22.48
dissolved oxygen (mg/l)	9.00	13.00	7.00	9.67	2.49					
temperature (°C)	30.50	31.30	34.80	32.20	1.87	32.80	33.40	30.20	32.13	1.39
chlorophyll a (ng/g DWT)	1387.48	408.31	1199.49	998.43	424.27	824.60	1170.32	3991.17	1995.36	1418.29
fucoxanthine (ng/g DWT)	453.96	837.20	499.00	596.72	171.04	745.22	334.38	2049.83	1043.14	731.33

Avicennia
blanco
0-2 cm

	period 5 26-11-92					period 6 23-12-92				
	9.10 am A	9.54 am B	11.07 am C	mean	std	10.35 am A	9.50 am B	8.35 am C	mean	std
% mud after		6.18	9.55	7.87	1.69	6.58	5.19	5.91	5.89	0.57
% mud before		17.46	23.15	20.31	2.85	18.75	17.40	16.29	17.48	1.01
% sand after		90.76	85.61	88.19	2.58	88.22	91.55	90.34	90.04	1.38
% sand before		78.55	72.83	75.69	2.86	76.87	79.93	81.32	79.37	1.86
% coarse sand after		3.06	4.84	3.95	0.89	5.20	3.26	3.75	4.07	0.82
% coarse sand before		3.99	4.02	4.00	0.01	4.38	2.67	2.39	3.15	0.88
median after		345.00	388.00	366.50	21.50	369.00	319.00	328.00	338.67	21.76
median before		268.00	223.00	245.50	22.50	277.00	245.00	237.00	253.00	17.28
kurtosis after		7.32	5.00	6.16	1.16	5.97	6.42	5.71	6.03	0.29
kurtosis before		1.16	0.32	0.74	0.42	1.07	1.55	1.81	1.48	0.31
skewness after		-2.27	-2.10	-2.19	0.09	-2.03	-1.94	-1.89	-1.95	0.06
skewness before		-1.26	-0.99	-1.13	0.14	-1.27	-1.36	-1.38	-1.34	0.05
POM (%)		5.00	7.17	6.09	1.09	6.00	6.00	7.00	6.33	0.47
total carbon (%)	1.35	1.30	3.67	2.11	1.11	1.45	2.14	3.76	2.45	0.97
muddy detritus (%)		11.28	13.60	12.44	1.16	12.17	12.21	10.38	11.59	0.85
pH	6.41	6.55	6.50	6.49	0.06	5.48	5.47	5.56	5.50	0.04
salinity (ppt)	41.00	38.00	40.00	39.67	1.25	46.00	20.50	51.00	39.17	13.36
redox (mV)	90.00	90.00	79.00	86.33	5.19	150.00	147.00	147.00	148.00	1.41
dissolved oxygen (mg/l)	10.00	11.00	6.00	9.00	2.16	13.00	9.00	11.00	11.00	1.63
temperature (°C)	28.10	30.50	32.70	30.43	1.88	28.30	27.70	27.30	27.77	0.41
chlorophyll a (ng/g DWT)	2064.66	1368.28	2766.11	2066.35	570.66	1762.91	1333.33	801.42	1299.22	393.27
fucoxanthine (ng/g DWT)	718.97	658.91	1260.50	879.46	270.55	0.00	0.00	0.00	0.00	0.00

Avicennia
partial cage
0-2 cm

	period 1 6-8-92					period 2 28-8-92				
	1.40 pm A	2.30 pm B	4.00 pm C	mean	std	11.30 am A	12.00 am B	2.50 pm C	mean	std
% mud after	7.49	7.13	8.41	7.68	0.54	11.66	19.90	23.02	18.19	4.79
% mud before	48.11	43.34	40.89	44.11	3.00	37.96	33.62	35.89	35.82	1.77
% sand after	85.01	92.20	57.42	78.21	14.99	84.75	77.38	75.87	79.33	3.88
% sand before	49.47	52.44	55.79	52.57	2.58	58.95	62.26	60.93	60.71	1.36
% coarse sand after	7.50	0.67	34.17	14.11	14.45	3.59	2.72	1.11	2.47	1.03
% coarse sand before	2.42	4.22	3.32	3.32	0.73	3.09	4.12	3.18	3.46	0.47
median after	370.00	349.00	319.00	346.00	20.93	301.00	212.00	153.00	222.00	60.83
median before	75.00	122.00	131.00	109.33	24.55	145.00	208.00	159.00	170.67	27.01
kurtosis after	5.94	5.42	5.40	5.59	0.25	3.93	1.99	1.80	2.57	0.96
kurtosis before	-1.18	-1.13	-1.01	-1.11	0.07	-0.80	-0.52	-0.67	-0.66	0.11
skewness after	-2.12	-2.03	-1.97	-2.04	0.06	-1.80	-1.36	-1.24	-1.47	0.24
skewness before	-0.26	-0.41	-0.46	-0.38	0.08	-0.55	-0.77	-0.62	-0.65	0.09
POM (%)	6.06	6.10	6.21	6.12	0.06	5.61	7.08	6.90	6.53	0.65
total carbon (%)						3.33	2.94	3.26	3.18	0.17
muddy detritus (%)	40.62	36.21	32.48		3.33	26.30	13.72	12.87	17.63	6.14
pH	6.47	6.37	6.66	6.50	0.12	6.07	6.05	6.28	6.13	0.10
salinity (ppt)	48.00	46.00	46.00	46.67	0.94	47.00	46.00	41.00	44.67	2.62
redox (mV)										
dissolved oxygen (mg/l)	18.00	20.00	17.00	18.33	1.25	18.00	20.00		19.00	1.00
temperature (°C)	29.60	27.60	27.00	28.07	1.11	29.10	27.50	27.80	28.13	0.69
chlorophyll a (ng/g DWT)	2840.01	1608.17	1741.26	2063.15	552.01	3402.53	3374.75	2426.65	3067.98	453.63
fucoxanthine (ng/g DWT)	771.98	805.78	480.16	685.97	146.18	1034.43	1825.50	1205.84	1355.26	339.80

Avicennia
partial cage
0-2 cm

	period 3 25-9-92					period 4 30-10-92				
	11.20 am A	11.45 am B	2.20 pm C	mean	std	10.00 am A	10.30 am B	12.13 pm C	mean	std
% mud after	7.23	12.60	18.58	12.80	4.64	7.31	7.50	7.01	7.27	0.20
% mud before	33.19	25.00	20.80	26.33	5.14	25.65	29.73	22.54	25.97	2.94
% sand after	88.57	83.74	77.96	83.42	4.34	88.84	88.58	89.42	88.95	0.35
% sand before	63.22	70.95	74.08	69.42	4.56	70.12	66.56	74.35	70.34	3.18
% coarse sand after	4.20	3.66	3.46	3.77	0.31	3.85	3.92	3.57	3.78	0.15
% coarse sand before	3.59	4.05	5.12	4.25	0.64	4.23	3.71	3.11	3.68	0.46
median after	381.00	277.00	227.00	295.00	64.15	325.00	320.00	308.00	317.67	7.13
median before	192.00	266.00	324.00	260.67	54.02	257.00	214.00	240.00	237.00	17.68
kurtosis after	6.21	3.39	1.84	3.81	1.81	6.50	6.19	6.40	6.36	0.13
kurtosis before	-0.57	0.04	1.02	0.16	0.65	0.07	-0.39	0.48	0.05	0.36
skewness after	-2.15	-1.66	1.83	-0.66	1.77	-2.14	-2.10	-2.07	-2.10	0.03
skewness before	-0.72	-1.03	-1.83	-1.19	0.47	-1.00	-0.81	-1.14	-0.98	0.14
POM (%)	4.85	4.21	4.19	4.42	0.31	5.57	6.31	5.10	5.66	0.50
total carbon (%)	1.93	4.47	2.89	3.10	1.05	3.87	2.12	2.59	2.86	0.74
muddy detritus (%)	25.96	12.40	2.22	13.53	9.72	18.34	22.23	15.53	18.70	2.75
pH	6.22	6.52	6.63	6.46	0.17	6.11	6.29	6.13	6.18	0.08
salinity (ppt)	58.00	53.00	56.00	55.67	2.05	57.00	44.00	44.00	48.33	6.13
redox (mV)	257.00	142.00	286.00	228.33	62.18	51.00	44.00	7.00	34.00	19.30
dissolved oxygen (mg/l)		5.00	8.00	6.50	1.50		15.00	17.00	16.00	1.00
temperature (°C)	29.80	29.70	30.20	29.90	0.22	32.80	33.00	32.50	32.77	0.21
chlorophyll a (ng/g DWT)	0.00	1114.23	3939.60	1684.61	1658.13	2213.76	2187.36	2479.72	2293.61	132.04
fucoxanthine (ng/g DWT)	0.00	475.57	1694.92	723.50	713.81	1189.02	983.95	1677.42	1283.46	290.88

Avicennia
partial cage
0-2 cm

	period 5 26-11-92					period 6 23-12-92				
	8.43 am A	9.30 am B	11.28 am C	mean	std	7.45 am A	10.10 am B	9.08 am C	mean	std
% mud after	11.51	16.61	5.65	11.26	4.48	8.04	6.97	6.26	7.09	0.73
% mud before	16.73	24.27	16.04	19.01	3.73	21.01	15.71	15.53	17.42	2.54
% sand after	86.92	82.40	91.18	86.83	3.58	86.63	87.26	89.91	87.93	1.42
% sand before	78.63	71.70	79.99	76.77	3.63	74.12	79.52	80.52	78.05	2.81
% coarse sand after	1.57	0.99	3.17	1.91	0.92	5.33	5.77	3.83	4.98	0.83
% coarse sand before	4.64	4.03	3.97	4.21	0.30	4.87	4.77	3.95	4.53	0.41
median after	218.00	192.00	335.00	248.33	62.20	367.00	367.00	333.00	355.67	16.03
median before	302.00	253.00	282.00	279.00	20.12	291.00	301.00	272.00	288.00	12.03
kurtosis after	4.75	3.08	7.20	5.01	1.69	6.62	5.36	5.24	5.74	0.62
kurtosis before	1.18	0.17	1.45	0.93	0.55	2.64	2.04	1.88	2.19	0.33
skewness after	-1.85	-1.62	-2.14	-1.87	0.21	-2.03	-1.93	-1.82	-1.93	0.09
skewness before	-1.28	-1.05	-1.34	-1.22	0.12	-1.55	-1.43	-1.35	-1.44	0.08
POM (%)	3.44		4.81	4.13	0.69	6.00	7.00	7.00	6.67	0.47
total carbon (%)	2.40	2.78	3.98	3.05	0.67	2.40	4.41	4.40	3.74	0.95
muddy detritus (%)	5.22	7.66	10.39	7.76	2.11	12.97	8.74	9.27	10.33	1.88
pH	6.81	6.86	6.69	6.79	0.07	5.75	5.57	5.54	5.62	0.09
salinity (ppt)	37.00	38.00	39.00	38.00	0.82	35.00	36.00	44.00	38.33	4.03
redox (mV)	67.00	48.00	32.00	49.00	14.31	215.00	245.00	270.00	243.33	22.48
dissolved oxygen (mg/l)	0.12	0.11	0.06	0.10	0.03	7.00	12.00	17.00	12.00	4.08
temperature (°C)	27.80	28.70	32.10	29.53	1.85	26.70	27.90	27.20	27.27	0.49
chlorophyll a (ng/g DWT)	2709.62	3165.29	3155.45	3010.12	212.52	1692.50	948.22	696.39	1112.37	422.90
fucoxanthine (ng/g DWT)	1387.08	1254.11	1420.13	1353.77	71.75	0.00	0.00	0.00	0.00	0.00

Avicennia
cage
0-2 cm

	period 1 6-8-92					period 2 28-8-92				
	3.30 pm A	3.15 pm B	4.20 pm C	mean	std	2.00 pm A	0.35 pm B	3.05 pm C	mean	std
% mud after	6.05	7.47	9.46	7.66	1.40	5.88	11.21	14.46	10.52	3.54
% mud before	40.91	32.23	41.42	38.19	4.22	47.99	44.58	36.18	42.92	4.96
% sand after	88.17	84.04	84.57	85.59	1.83	88.78	84.66	81.50	84.98	2.98
% sand before	55.64	64.02	55.69	58.45	3.94	52.62	53.98	60.54	55.71	3.46
% coarse sand after	5.78	8.49	5.97	6.75	1.24	5.34	4.13	4.04	4.50	0.59
% coarse sand before	3.45	3.75	2.89	3.36	0.36	-0.61	1.44	3.28	1.37	1.59
median after	378.00	401.00	352.00	377.00	20.02	353.00	307.00	265.00	308.33	35.94
median before	147.00	235.00	130.10	170.70	45.99	81.00	89.00	156.00	108.67	33.63
kurtosis after	6.75	5.31	4.71	5.59	0.86	6.93	3.88	2.66	4.49	1.80
kurtosis before	-1.06	-0.57	-1.04	-0.89	0.23	-0.85	-0.80	-0.73	-0.79	0.05
skewness after	-2.18	-2.00	-1.94	-2.04	0.10	-2.15	-1.76	-1.50	-1.80	0.27
skewness before	-0.46	-0.80	-0.46	-0.57	0.16	-0.34	-0.41	-0.61	-0.45	0.11
POM (%)	5.64	5.47	5.21	5.44	0.18	4.67	4.66	9.03	6.12	2.06
total carbon (%)						1.46	1.90	5.05	2.80	1.60
muddy detritus (%)	34.86	24.76	31.96	30.53	4.25	42.11	33.37	21.72	32.40	8.35
pH		6.61	6.63	6.62	0.01	6.02	6.00	6.54	6.19	0.25
salinity (ppt)		50.00	58.00	54.00	4.00	45.00	43.00	44.50	44.17	0.85
redox (mV)										
dissolved oxygen (mg/l)	17.00	15.00	23.00	18.33	3.40	13.00	20.00		16.50	3.50
temperature (°C)	29.10	28.10	26.50	27.90	1.07	30.50	31.50	32.51	31.50	0.82
chlorophyll a (ng/g DWT)	3680.89	1767.45	1683.90	2377.41	922.33	1297.88	0.00	3924.38	1740.75	1632.44
fucoxanthine (ng/g DWT)	1206.66	767.12	935.33	969.70	181.08	687.78	0.00	1035.57	574.45	430.30

Avicennia
cage
0-2 cm

	period 3 25-9-92					period 4 30-10-92				
	12.00 am A	12.15 am B	2.30 pm C	mean	std	11.39 am A	11.20 am B	12.27 am C	mean	std
% mud after	11.43	21.11	9.76	14.10	5.00		5.52	7.68	6.60	1.08
% mud before	20.42	22.06	40.80	27.76	9.24		25.77	32.77	29.27	3.50
% sand after	82.96	75.84	86.25	81.68	4.34		89.65	88.54	89.10	0.56
% sand before	73.98	72.80	56.04	67.61	8.19		71.03	64.02	67.52	3.51
% coarse sand after	5.61	3.05	3.99	4.22	1.06		4.83	3.78	4.30	0.53
% coarse sand before	5.60	5.14	3.16	4.63	1.06		3.20	3.21	3.20	0.01
median after	361.00	206.00	308.00	291.67	64.32	350.00	364.00	305.00	339.67	25.17
median before	332.00	330.00	120.00	260.67	99.47	225.00	219.00	175.00	206.33	22.29
kurtosis after	3.75	1.65	4.79	3.40	1.31	7.28	7.91	5.87	7.02	0.85
kurtosis before	0.99	0.67	-0.95	0.24	0.85	0.24	0.10	-0.57	-0.08	0.35
skewness after	-1.77	-1.27	-1.91	-1.65	0.27	-2.24	-2.33	-2.01	-2.19	0.13
skewness before	-1.36	-1.29	-0.45	-1.03	0.41	-0.98	-0.97	-0.69	-0.88	0.13
POM (%)	4.15	4.11	7.67	5.31	1.67	5.68	5.02	6.69	5.80	0.69
total carbon (%)	3.27	1.65	0.90	1.94	0.99	3.36	3.06	5.96	4.13	1.30
muddy detritus (%)	8.99	0.95	31.04	13.66	12.72		20.25	25.09	22.67	2.42
pH	6.69	6.77	6.47	6.64	0.13	6.18	6.43	6.36	6.32	0.11
salinity (ppt)	51.00	53.00	58.00	54.00	2.94	40.50	42.00	42.50	41.67	0.85
redox (mV)	253.00	268.00	257.00	259.33	6.34	38.00	59.00	66.00	54.33	11.90
dissolved oxygen (mg/l)	9.00		7.00	8.00	1.00		60.00	7.00	33.50	26.50
temperature (°C)	34.30	31.50	30.60	32.13	1.58	34.60	32.10	31.30	32.67	1.41
chlorophyll a (ng/g DWT)	6121.26	6565.55	4855.21	5847.34	724.61	5049.82	1873.62	6737.86	4553.77	2016.56
fucoxanthine (ng/g DWT)	1391.98	1402.08	936.22	1243.43	217.27	1609.74	449.15	2926.99	1661.96	1012.25

Avicennia
cage
0-2 cm

	period 5 26-11-92					period 6 23-12-92				
	10.36 am A	10.15 am B	11.48 am C	mean	std	8.10 am A	10.50 am B	9.30 am C	mean	std
% mud after	10.74	7.65	20.36	12.92	5.41	5.78	5.24	6.83	5.95	0.66
% mud before	30.48	28.30	20.37	26.38	4.34	13.50	16.03	12.36	13.96	1.53
% sand after	85.78	87.86	77.50	83.71	4.47	89.60	90.71	87.56	89.29	1.30
% sand before	66.38	68.28	77.20	70.62	4.72	81.78	80.68	82.66	81.71	0.81
% coarse sand after	3.48	4.49	2.14	3.37	0.96	4.62	4.05	5.61	4.76	0.64
% coarse sand before	3.14	3.42	2.43	3.00	0.42	4.72	3.29	4.98	4.33	0.74
median after	277.00	334.00	189.00	266.67	59.65	346.00	359.00	379.00	361.33	13.57
median before	191.00	204.00	91.00	162.00	50.48	296.00	250.00	314.00	286.67	26.95
kurtosis after	4.33	5.63	1.90	3.95	1.55	5.33	6.26	4.75	5.45	0.62
kurtosis before	-0.36	-0.13	-0.87	-0.45	0.31	2.66	1.94	2.94	2.51	0.42
skewness after	-1.83	-2.01	-1.36	-1.73	0.27	-1.81	-1.98	-1.83	-1.87	0.08
skewness before	-0.78	-0.86	-0.37	-0.67	0.21	-1.51	-1.39	-1.55	-1.48	0.07
POM (%)						7.00	6.00	8.00	7.00	0.82
total carbon (%)	3.64	1.91	11.80	5.78	4.31	4.61	2.71	2.10	3.14	1.07
muddy detritus (%)	19.74	20.65	0.01	13.47	9.52	7.72	10.79	5.53	8.01	2.16
pH	6.62	6.68	6.72	6.67	0.04	5.73	5.58	5.52	5.61	0.09
salinity (ppt)	38.00	37.00	38.00	37.67	0.47	21.00	47.50	21.00	29.83	12.49
redox (mV)	14.00	34.00	14.00	20.67	9.43	148.00	169.00	129.00	148.67	16.34
dissolved oxygen (mg/l)	12.00	6.00	5.00	7.67	3.09	18.00	13.00	12.00	14.33	2.62
temperature (°C)	30.30	29.40	32.50	30.73	1.30	27.00	29.70	27.30	28.00	1.21
chlorophyll a (ng/g DWT)	1436.38	1553.15	3494.98	2161.50	944.11	917.69	2236.79	554.58	1236.35	722.78
fucoxanthine (ng/g DWT)	729.34	552.68	2353.67	1211.90	810.57	0.00	0.00	0.00	0.00	0.00

Cerlops blanco period 1

0-2 cm 6-8-92

ind./10 cm²	11.31 am A	11.38 am B	2.30 pm C	mean	std
Amphipoda	0.00	0.00	3.93	1.31	1.85
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	4.91	5.89	6.88	5.89	0.80
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.98	0.00	0.98	0.65	0.46
Kinorhyncha	4.91	2.95	10.81	6.22	3.34
Nauplii	20.63	58.95	148.35	75.98	53.51
Nematoda	753.55	660.22	725.06	712.94	39.06
Oligochaeta	4.91	2.95	4.91	4.26	0.93
Ostracoda	81.54	98.25	91.37	90.39	6.85
Polychaeta	5.89	2.95	0.00	2.95	2.41
Rotifera	239.72	438.18	482.39	386.76	105.53
Tardigrada	0.98	0.98	0.00	0.65	0.46
Turbellaria	8.84	4.91	15.72	9.82	4.47
Total	1126.89	1276.22	1490.40	1297.84	149.19

2-4 cm 6-8-92

ind./10 cm²	11.31 am A	11.38 am B	2.30 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	4.91	7.86	14.74	9.17	4.12
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.98	0.33	0.46
Nauplii	34.39	52.07	83.51	56.66	20.31
Nematoda	310.46	727.03	404.78	480.75	178.35
Oligochaeta	0.98	2.95	1.96	1.96	0.80
Ostracoda	16.70	6.88	13.75	12.44	4.12
Polychaeta	0.00	2.95	0.98	1.31	1.23
Rotifera	438.18	407.72	1043.38	629.76	292.74
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	2.95	5.89	2.95	2.41
Total	805.62	1210.40	1569.98	1195.33	312.23

Cerlops blanco period 1

4-10 cm 6-8-92

ind./10 cm²	11.31 am A	11.38 am B	2.30 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	4.91	1.96	2.95	3.27	1.23
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	1.96	0.65	0.93
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	39.30	8.84	33.40	27.18	13.19
Nematoda	79.58	737.83	241.69	353.03	280.03
Oligochaeta	2.95	15.72	6.88	8.51	5.34
Ostracoda	8.84	5.89	2.95	5.89	2.41
Polychaeta	0.98	0.00	0.00	0.33	0.46
Rotifera	126.74	254.46	199.44	193.55	52.31
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	3.93	2.95	2.29	1.67
Total	263.30	1028.64	492.22	594.72	320.75

10-rest cm 6-8-92

ind./10 cm²	11.31 am A	11.38 am B	2.30 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	5.89	3.93	5.89	5.24	0.93
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	0.00	0.98	0.33	0.46
Nematoda	56.00	15.72	29.47	33.73	16.72
Oligochaeta	62.88	84.49	41.26	62.88	17.65
Ostracoda	0.00	0.98	0.98	0.65	0.46
Polychaeta	8.84	0.98	3.93	4.58	3.24
Rotifera	0.00	0.00	0.00	0.00	0.00
Tardigrada	185.69	108.07	125.76	139.84	33.21
Turbellaria	0.00	0.00	0.00	0.00	0.00
Total	319.30	214.18	208.28	247.25	51.00

Ceriops blanco period 2

0-2 cm 28-8-92

ind./10 cm²	11.25 am A	9.55 am B	11.10 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	6.88	0.00	7.86	4.91	3.50
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	1.96	0.00	0.65	0.93
Insecta larvae	0.00	0.00	0.98	0.33	0.46
Kinorhyncha	3.93	0.00	11.79	5.24	4.90
Nauplii	81.54	9.82	24.56	38.64	30.93
Nematoda	1140.64	244.63	1233.00	872.76	445.75
Oligochaeta	24.56	4.91	19.65	16.37	8.35
Ostracoda	64.84	0.00	85.47	50.11	36.42
Polychaeta	0.00	0.98	0.98	0.65	0.46
Rotifera	18.67	5.89	9.82	11.46	5.34
Tardigrada	0.00	0.00	0.98	0.33	0.46
Turbellaria	41.26	0.00	9.82	17.03	17.60
Total	1382.33	268.21	1404.93	1018.49	530.61

2-4 cm 28-8-92

	11.25 am A	9.55 am B	10.10 am C	mean	std
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	2.95	3.93	0.00	2.29	1.67
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	4.91	0.00	1.64	2.32
	17.68	19.65	12.77	16.70	2.89
	108.07	860.64	405.76	458.16	309.46
	2.95	10.81	14.74	9.50	4.90
	0.00	67.79	0.00	22.60	31.96
	0.98	1.96	0.00	0.98	0.80
	0.98	10.81	5.89	5.89	4.01
	0.00	0.00	0.00	0.00	0.00
	0.00	21.61	4.91	8.84	9.25
	133.62	1002.12	444.08	526.60	359.33

Ceriops blanco period 2

4-10 cm 28-8-92

ind./10 cm²	11.25 am A	9.55 am B	10.10 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.98	2.95	0.98	1.64	0.93
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.98	0.00	0.33	0.46
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.98	0.00	0.00	0.33	0.46
Nauplii	38.32	26.53	9.82	24.89	11.69
Nematoda	118.88	157.19	166.04	147.37	20.47
Oligochaeta	2.95	0.00	1.96	1.64	1.23
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	10.81	18.67	0.98	10.15	7.23
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	0.00	0.00	0.00	0.00
Total	172.91	206.32	179.79	186.34	14.40

10-rest cm 28-8-92

	11.25 am A	9.55 am B	10.10 am C	mean	std
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.98	0.00	0.00	0.33	0.46
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	2.95	0.00	0.98	1.39
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	67.79	18.67	18.67	35.04	23.16
	68.77	35.37	35.37	46.50	15.75
	0.98	0.00	0.00	0.33	0.46
	0.98	0.00	0.00	0.33	0.46
	0.00	0.00	0.00	0.00	0.00
	7.86	7.86	5.89	7.20	0.93
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	147.37	64.84	59.93	90.71	40.11

Ceriops blanco period 3

0-2 cm 27-9-92

ind./10 cm²	8.58 am A	9.02 am B	10.02 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.98	0.00	3.93	1.64	1.67
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.98	0.00	0.33	0.46
Insecta larvae	0.00	0.98	0.00	0.33	0.46
Kinorhyncha	6.88	0.98	9.82	5.89	3.68
Nauplii	7.86	10.81	6.88	8.51	1.67
Nematoda	572.78	566.88	547.23	562.30	10.92
Oligochaeta	17.68	4.91	4.91	9.17	6.02
Ostracoda	30.46	36.35	0.00	22.27	15.93
Polychaeta	0.00	0.98	0.98	0.65	0.46
Rotifera	1.96	16.70	0.98	6.55	7.19
Tardigrada	0.00	1.96	0.00	0.65	0.93
Turbellaria	7.86	0.98	6.88	5.24	3.04
Total	646.46	642.53	581.62	623.54	29.68

2-4 cm 27-9-92

	8.58 am A	9.02 am B	10.02 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.98	0.00	0.00	0.33	0.46
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.98	0.00	0.33	0.46
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	6.88	7.86	7.86	7.53	0.46
Nematoda	132.63	264.28	266.25	221.06	62.53
Oligochaeta	1.96	5.89	3.93	3.93	1.60
Ostracoda	0.00	1.96	0.00	0.65	0.93
Polychaeta	0.00	0.00	0.98	0.33	0.46
Rotifera	7.86	5.89	5.89	6.55	0.93
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.98	0.98	0.00	0.65	0.46
Total	151.30	287.86	284.92	241.36	63.69

Ceriops blanco period 3

4-10 cm 27-9-92

ind./10 cm²	8.58 am A	9.02 am B	10.02 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.00	0.00	0.00	0.00
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.98	0.00	0.00	0.33	0.46
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	1.96	0.98	0.98	1.31	0.46
Nematoda	123.79	198.46	267.23	196.49	58.58
Oligochaeta	1.96	0.00	3.93	1.96	1.60
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.98	0.33	0.46
Rotifera	4.91	4.91	1.96	3.93	1.39
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	3.93	0.00	0.00	1.31	1.85
Total	137.55	204.35	275.09	205.66	56.16

10-rest cm 27-9-92

	8.58 am A	9.02 am B	10.10 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	1.96	0.98	0.00	0.98	0.80
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	2.95	3.93	0.00	2.29	1.67
Nematoda	48.14	59.93	60.91	56.33	5.80
Oligochaeta	0.00	0.00	0.00	0.00	0.00
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.98	0.98	0.00	0.65	0.46
Rotifera	1.96	0.98	0.98	1.31	0.46
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	0.00	0.00	0.00	0.00
Total	56.00	66.81	61.90	61.57	4.42

Ceriops blanco period 6

0-2 cm 23-12-92

ind./10 cm²	11.05 am A	10.45 am B	9.15 am C	mean	std
Amphipoda	1.96	0.00	2.95	1.64	1.23
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.00	4.91	1.64	2.32
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.98	0.00	0.33	0.46
Insecta larvae	2.95	0.00	3.93	2.29	1.67
Kinorhyncha	0.00	0.98	2.95	1.31	1.23
Nauplii	0.00	1.96	0.00	0.65	0.93
Nematoda	601.27	918.61	362.53	627.47	227.77
Oligochaeta	1.96	21.61	12.77	12.12	8.04
Ostracoda	12.77	21.61	93.33	42.57	36.07
Polychaeta	0.00	0.98	0.00	0.33	0.46
Rotifera	0.00	0.00	0.00	0.00	0.00
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	5.89	13.75	9.82	9.82	3.21
Total	626.81	980.50	493.20	700.17	205.59

2-4 cm 23-12-92

11.05 am A	10.45 am B	9.15 am C	mean	std
0.00	0.00	0.98	0.33	0.46
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.98	1.96	0.98	0.80
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.98	0.33	0.46
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
312.42	711.31	185.69	403.14	223.97
2.95	20.63	9.82	11.13	7.28
0.00	1.96	1.96	1.31	0.93
1.96	0.00	0.98	0.98	0.80
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.98	2.95	1.96	1.96	0.80
318.32	737.83	204.35	420.17	229.39

Ceriops blanco period 6

4-10 cm 23-12-92

ind./10 cm²	11.05 am A	10.45 am B	9.15 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.00	1.96	0.65	0.93
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	0.00	0.00	0.00	0.00
Nematoda	107.09	119.86	200.42	142.46	41.32
Oligochaeta	0.00	0.00	2.95	0.98	1.39
Ostracoda	0.00	0.00	0.98	0.33	0.46
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	0.00	0.00	0.00	0.00	0.00
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.98	0.00	1.96	0.98	0.80
Total	108.07	119.86	208.28	145.41	44.72

10-rest cm 23-12-92

11.05 am A	10.45 am B	9.15 am C	mean	std
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	1.96	0.98	0.98	0.80
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
79.58	29.47	114.95	74.67	35.07
0.00	0.00	0.98	0.33	0.46
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
79.58	31.44	116.91	75.98	34.99

Ceriops blanco period end

0-2 cm 30-7-93

ind./10 cm²	11.45 am A	1.00 pm B	12.20 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	2.95	13.75	5.57	5.91
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.00	1.96	0.65	0.93
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	0.98	0.00	0.33	0.46
Kinorhyncha	0.00	5.89	4.91	3.60	2.58
Nauplii	0.98	2.95	1.96	1.96	0.80
Nematoda	1876.51	1110.19	1365.63	1450.78	318.59
Oligochaeta	0.98	0.00	0.00	0.33	0.46
Ostracoda	0.00	10.81	10.81	7.20	5.09
Polychaeta	0.00	0.00	1.96	0.65	0.93
Rotifera	0.00	0.00	0.00	0.00	0.00
Tardigrada	0.00	1.96	0.00	0.65	0.93
Turbellaria	0.00	5.89	5.89	3.93	2.78
Total	1878.48	1141.63	1406.89	1475.67	304.72

2-4 cm 30-7-93

	11.45 am A	1.00 pm B	12.20 am C	mean	std
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.98	0.00	0.98	0.65	0.46
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	520.71	412.64	697.55	543.63	117.44
	0.98	0.98	2.95	1.64	0.93
	0.00	0.00	0.98	0.33	0.46
	0.00	0.00	0.00	0.00	0.00
	0.00	0.98	0.98	0.65	0.46
	0.00	0.00	0.00	0.00	0.00
	0.00	0.98	1.96	0.98	0.80
	522.67	415.58	705.41	547.89	119.66

Ceriops blanco period end

4-10 cm 30-7-93

ind./10 cm²	11.45 am A	1.00 pm B	12.20 am C	mean	std
Amphipoda			0.00	0.00	0.00
Bivalvia			0.00	0.00	0.00
Ciliata			0.00	0.00	0.00
Cladocera			0.00	0.00	0.00
Copepoda			1.96	1.96	0.00
Decapoda larvae			0.00	0.00	0.00
Gastropoda			0.00	0.00	0.00
Halacaroidea			0.00	0.00	0.00
Insecta larvae			0.00	0.00	0.00
Kinorhyncha			0.00	0.00	0.00
Nauplii			5.89	5.89	0.00
Nematoda			365.48	365.48	0.00
Oligochaeta			1.96	1.96	0.00
Ostracoda			0.00	0.00	0.00
Polychaeta			0.00	0.00	0.00
Rotifera			5.89	5.89	0.00
Tardigrada			0.00	0.00	0.00
Turbellaria			1.96	1.96	0.00
Total			383.16	383.16	180.62

10-rest cm 30-7-93

	11.45 am A	1.00 pm B	12.20 am C	mean	std
			0.00	0.00	0.00
			0.00	0.00	0.00
			0.00	0.00	0.00
			0.00	0.00	0.00
			1.96	1.96	0.00
			0.00	0.00	0.00
			0.00	0.00	0.00
			1.96	1.96	0.00
			0.00	0.00	0.00
			0.00	0.00	0.00
			0.00	0.00	0.00
			117.90	117.90	0.00
			0.00	0.00	0.00
			0.00	0.00	0.00
			0.00	0.00	0.00
			31.44	31.44	0.00
			0.00	0.00	0.00
			0.00	0.00	0.00
			153.26	153.26	72.25

Ceriops
partial cage
period 1

0-2 cm
6-8-92

ind./10cm²	12.08 am A	11.10 am B	2.15 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	26.53	3.93	5.89	12.12	10.22
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	18.67	23.58	0.00	14.08	10.16
Decapoda larvae	0.98	0.00	0.00	0.33	0.46
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.98	0.33	0.46
Insecta larvae	0.00	0.98	0.98	0.65	0.46
Kinorhyncha	23.58	27.51	10.81	20.63	7.13
Nauplii	289.82	271.15	34.39	198.45	116.26
Nematoda	1175.00	930.37	750.58	951.98	173.94
Oligochaeta	5.89	0.00	3.93	3.27	2.45
Ostracoda	99.23	89.40	34.39	74.34	28.53
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	52.07	68.77	4.91	41.92	27.04
Tardigrada	7.86	0.00	0.98	2.95	3.50
Turbellaria	33.40	38.32	9.82	27.18	12.44
Total	1733.02	1454.01	857.67	1348.23	365.10

2-4 cm
6-8-92

	12.08 am A	11.10 am B	2.15 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	4.91	0.98	1.96	2.62	1.67
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	3.93	7.86	8.84	6.88	2.12
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	37.33	53.05	36.35	42.25	7.65
Nematoda	432.29	926.47	598.32	652.36	205.33
Oligochaeta	3.93	7.86	4.91	5.57	1.67
Ostracoda	0.98	1.96	8.84	3.93	3.50
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	138.53	63.86	25.54	75.98	46.91
Tardigrada	0.98	0.00	0.00	0.33	0.46
Turbellaria	0.98	1.96	0.00	0.98	0.80
Total	623.87	1064.01	684.78	790.89	194.72

Ceriops
partial cage
period 1

4-10 cm
6-8-92

ind./10cm²	12.08 am A	11.10 am B	2.15 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.98	0.98	0.65	0.46
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	3.93	1.96	3.93	3.27	0.93
Insecta larvae	0.00	2.95	0.00	0.98	1.39
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	15.72	21.61	19.65	18.99	2.45
Nematoda	69.76	216.14	57.97	114.62	71.95
Oligochaeta	0.98	5.89	0.98	2.62	2.32
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	8.84	1.96	6.88	5.89	2.89
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.98	0.00	0.98	0.65	0.46
Total	100.21	251.51	91.37	147.70	73.50

10-rest cm
6-8-92

	1.00 pm A	1.21 pm B	1.50 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.98	0.33	0.46
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	2.95	0.98	3.93	2.62	1.23
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.98	0.00	5.89	2.29	2.58
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	28.49	0.00	42.25	23.58	17.59
Nematoda	25.54	46.18	64.84	45.52	16.05
Oligochaeta	0.00	0.00	0.00	0.00	0.00
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.98	0.33	0.46
Rotifera	12.77	4.91	18.67	12.12	5.63
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	0.00	0.00	0.00	0.00
Total	70.74	52.07	137.55	86.78	36.69

Ceriops
partial cage
period 2

0-2 cm
28-8-92

ind./120cm²	10.55 am A	11.45 am B	8.50 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	10.81	4.91	2.95	6.22	3.34
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	25.54	7.86	4.91	12.77	9.11
Decapoda larvae	4.91	0.00	1.96	2.29	2.02
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	0.98	0.00	0.33	0.46
Kinorhyncha	13.75	22.60	22.60	19.65	4.17
Nauplii	5.89	5.89	3.93	5.24	0.93
Nematoda	1178.96	1287.03	1595.53	1353.84	176.50
Oligochaeta	27.51	27.51	32.42	29.15	2.32
Ostracoda	92.35	114.95	72.70	93.33	17.26
Polychaeta	1.96	0.00	0.00	0.65	0.93
Rotifera	1.96	7.86	0.98	3.60	3.04
Tardigrada	0.00	0.98	0.00	0.33	0.46
Turbellaria	26.53	3.93	11.79	14.08	9.37
Total	1390.19	1484.51	1749.77	1541.49	152.23

2-4 cm
28-8-92

	10.55 am A	11.45 am B	8.50 am C	mean	std
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.98	3.93	0.00	1.64	1.67
	0.00	0.00	0.00	0.00	0.00
	0.98	3.93	1.96	2.29	1.23
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	5.89	0.00	1.96	2.78
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.98	0.00	0.33	0.46
	161.12	418.53	650.39	410.02	199.83
	5.89	3.93	12.77	7.53	3.79
	0.98	1.96	2.95	1.96	0.80
	0.00	0.00	0.00	0.00	0.00
	0.98	7.86	4.91	4.58	2.82
	0.00	0.98	0.00	0.33	0.46
	0.98	3.93	11.79	5.57	4.56
	171.93	451.93	684.78	436.22	209.66

Ceriops
partial cage
period 2

4-10 cm
28-8-92

ind./10cm²	10.55 am A	11.45 am B	8.50 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.98	0.98	0.98	0.98	0.00
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	16.70	0.98	0.00	5.89	7.65
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	0.00	1.96	0.65	0.93
Nematoda	145.41	127.72	354.67	209.27	103.07
Oligochaeta	0.98	0.98	3.93	1.96	1.39
Ostracoda	0.00	0.00	0.98	0.33	0.46
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	0.98	1.96	1.96	1.64	0.46
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.98	0.00	0.00	0.33	0.46
Total	166.04	132.63	364.50	221.06	102.34

10-rest cm
28-8-92

	10.55 am A	11.45 am B	8.50 am C	mean	std
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.98	0.00	0.98	0.65	0.46
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	7.86	0.00	0.00	2.62	3.71
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	51.09	26.53	131.65	69.76	44.90
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.98	0.98	0.00	0.65	0.46
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	60.91	27.51	132.63	73.69	43.86

Ceriops
partial cage
period 3

0-2 cm
27-9-92

ind./10cm²	8.30 am A	8.42 am B	10.25 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	19.65	15.72	1.96	12.44	7.58
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.98	1.96	0.98	1.31	0.46
Decapoda larvae	1.96	0.00	0.00	0.65	0.93
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	1.96	0.00	0.65	0.93
Kinorhyncha	12.77	8.84	7.86	9.82	2.12
Nauplii	1.96	0.98	0.98	1.31	0.46
Nematoda	1176.01	719.17	785.97	893.72	201.47
Oligochaeta	23.58	6.88	7.86	12.77	7.65
Ostracoda	58.95	130.67	33.40	74.34	41.17
Polychaeta	0.98	0.00	0.00	0.33	0.46
Rotifera	4.91	11.79	9.82	8.84	2.89
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	11.79	10.81	0.98	7.86	4.88
Total	1313.56	908.78	849.83	1024.06	206.12

2-4 cm
27-9-92

ind./10cm²	8.30 am A	8.42 am B	10.25 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	3.93	0.00	1.31	1.85
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.98	0.00	0.00	0.33	0.46
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.98	0.98	0.00	0.65	0.46
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.98	0.00	0.33	0.46
Nauplii	0.98	0.00	0.00	0.33	0.46
Nematoda	214.18	657.27	206.32	359.26	210.75
Oligochaeta	14.74	2.95	0.98	6.22	6.07
Ostracoda	0.98	4.91	1.96	2.62	1.67
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	0.98	2.95	5.89	3.27	2.02
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	1.96	0.98	0.00	0.98	0.80
Total	235.79	674.95	215.16	375.30	212.05

Ceriops
partial cage
period 3

4-10 cm
27-9-92

ind./10cm²	8.30 am A	8.42 am B	10.25 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	1.96	0.00	0.65	0.93
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.00	0.00	0.00	0.00
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	3.93	0.00	3.93	2.62	1.85
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	0.00	1.96	0.65	0.93
Nematoda	27.51	150.32	48.14	75.32	53.69
Oligochaeta	1.96	0.98	0.00	0.98	0.80
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	0.00	4.91	3.93	2.95	2.12
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	0.00	0.98	0.33	0.46
Total	33.40	158.18	58.95	83.51	53.82

10-rest cm
27-9-92

ind./10cm²	8.30 am A	8.42 am B	10.25 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.98	0.98	0.00	0.65	0.46
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.98	0.98	0.00	0.65	0.46
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	1.96	1.96	0.00	1.31	0.93
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	0.00	0.00	0.00	0.00
Nematoda	16.70	146.39	0.00	54.36	65.43
Oligochaeta	0.00	0.00	0.00	0.00	0.00
Ostracoda	0.00	2.95	0.00	0.98	1.39
Polychaeta	0.98	0.00	0.00	0.33	0.46
Rotifera	0.98	2.95	0.00	1.31	1.23
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	0.00	0.00	0.00	0.00
Total	22.60	156.21	0.00	59.60	68.93

Ceriops
partial cage
period 6

0-2 cm
23-12-92

ind./10cm²	8.50 am A	9.30 am B	10.25 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	1.96	0.65	0.93
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.00	0.00	0.00	0.00
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.98	1.96	0.98	1.31	0.46
Nauplii	0.00	1.96	0.98	0.98	0.80
Nematoda	648.43	1562.12	1041.41	1083.99	374.23
Oligochaeta	2.95	1.96	0.98	1.96	0.80
Ostracoda	3.93	5.89	1.96	3.93	1.60
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	0.00	0.00	0.00	0.00	0.00
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	1.96	0.98	3.93	2.29	1.23
Total	658.25	1574.89	1052.22	1095.12	375.44

2-4 cm
23-12-92

8.50 am A	9.30 am B	10.25 am C	mean	std
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.98	0.33	0.46
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
461.76	550.18	1257.56	756.50	356.14
1.96	0.00	0.98	0.98	0.80
1.96	0.00	0.00	0.65	0.93
0.00	0.00	0.00	0.00	0.00
0.00	0.00	1.96	0.65	0.93
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
465.69	550.18	1261.49	759.12	356.90

Ceriops
partial cage
period 6

4-10 cm
23-12-92

ind./10cm²	8.50 am A	9.30 am B	10.25 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	1.96	0.65	0.93
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.00	0.00	0.00	0.00
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	1.96	0.00	1.96	1.31	0.93
Insecta larvae	1.96	0.00	0.00	0.65	0.93
Kinorhyncha	1.96	0.00	0.00	0.65	0.93
Nauplii	0.00	0.00	0.00	0.00	0.00
Nematoda	196.49	294.74	237.76	243.00	40.28
Oligochaeta	0.00	0.00	0.00	0.00	0.00
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	0.00	3.93	7.86	3.93	3.21
Tardigrada	0.00	1.96	0.00	0.65	0.93
Turbellaria	0.00	1.96	0.00	0.65	0.93
Total	202.39	302.60	249.55	251.51	40.93

10-rest cm
23-12-92

8.50 am A	9.30 am B	10.25 am C	mean	std
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
1.96	0.00	0.00	0.65	0.93
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
64.84	94.32	80.56	79.91	12.04
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
1.96	13.75	11.79	9.17	5.16
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
68.77	108.07	92.35	89.73	16.15

Ceriops
partial cage
period end

ind./10cm²	0-2 cm 30-7-93					2-4 cm 30-7-93				
	12.15 am A	12.30 am B	12.55 am C	mean	std	12.15 am A	12.30 am B	12.55 am C	mean	std
Amphipoda	2.95	2.95	0.00	1.96	1.39	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ciliata	2.95	0.00	0.98	1.31	1.23	0.00	0.00	0.98	0.33	0.46
Cladocera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.00	4.91	1.64	2.32	0.00	0.00	0.00	0.00	0.00
Decapoda larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.98	2.95	11.79	5.24	4.70	0.00	0.00	0.00	0.00	0.00
Nauplii	2.95	0.00	109.05	37.33	50.73	0.00	0.00	0.00	0.00	0.00
Nematoda	1670.19	2603.54	1807.74	2027.16	411.41	1070.89	530.53	1287.03	962.82	318.15
Oligochaeta	0.00	2.95	0.98	1.31	1.23	0.00	0.00	0.00	0.00	0.00
Ostracoda	0.00	3.93	21.61	8.51	9.40	0.00	0.98	0.00	0.33	0.46
Polychaeta	0.00	1.96	0.98	0.98	0.80	0.00	0.00	0.00	0.00	0.00
Rotifera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.96	0.65	0.93
Tardigrada	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.33	0.46
Turbellaria	2.95	1.96	5.89	3.60	1.67	0.00	1.96	0.00	0.65	0.93
Total	1682.97	2620.24	1963.95	2089.05	392.73	1070.89	533.48	1290.96	965.11	318.16

Ceriops
partial cage
period end

ind./10cm²	4-10 cm 30-7-93					10-rest cm 30-7-93				
	12.15 am A	12.30 am B	12.55 am C	mean	std	12.15 am A	12.30 am B	12.55 am C	mean	std
Amphipoda		0.00		0.00	0.00		0.00		0.00	0.00
Bivalvia		0.00		0.00	0.00		0.00		0.00	0.00
Ciliata		0.00		0.00	0.00		0.00		0.00	0.00
Cladocera		0.00		0.00	0.00		0.00		0.00	0.00
Copepoda		0.00		0.00	0.00		0.00		0.00	0.00
Decapoda larvae		0.00		0.00	0.00		0.00		0.00	0.00
Gastropoda		0.00		0.00	0.00		0.00		0.00	0.00
Halacaroidea		5.89		5.89	0.00		0.00		0.00	0.00
Insecta larvae		0.98		0.98	0.00		0.00		0.00	0.00
Kinorhyncha		0.00		0.00	0.00		0.00		0.00	0.00
Nauplii		1.96		1.96	0.00		1.96		1.96	0.00
Nematoda		440.15		440.15	0.00		92.35		92.35	0.00
Oligochaeta		0.00		0.00	0.00		0.00		0.00	0.00
Ostracoda		0.98		0.98	0.00		0.00		0.00	0.00
Polychaeta		0.00		0.00	0.00		0.00		0.00	0.00
Rotifera		13.75		13.75	0.00		15.72		15.72	0.00
Tardigrada		0.00		0.00	0.00		0.00		0.00	0.00
Turbellaria		0.00		0.00	0.00		0.00		0.00	0.00
Total		463.72		463.72	218.60		110.04		110.04	51.87

Ceriops
cage
period 1

0-2 cm
6-8-92

ind./10cm²	1.00 pm A	1.21 pm B	1.50 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.98	0.00	0.98	0.65	0.46
Cladocera	0.00	0.00	1.96	0.65	0.93
Copepoda	29.47	3.93	24.56	19.32	11.07
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.98	0.98	0.00	0.65	0.46
Insecta larvae	0.98	0.98	0.00	0.65	0.46
Kinorhyncha	14.74	19.65	5.89	13.43	5.69
Nauplii	166.04	0.98	201.41	122.81	87.35
Nematoda	984.43	1513.00	1048.29	1181.91	235.56
Oligochaeta	5.89	0.00	0.98	2.29	2.58
Ostracoda	79.58	59.93	56.98	65.50	10.03
Polychaeta	2.95	0.00	0.98	1.31	1.23
Rotifera	1.96	16.70	0.00	6.22	7.45
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	27.51	3.93	0.00	10.48	12.15
Total	1315.52	1620.09	1342.05	1425.89	137.75

2-4 cm
6-8-92

ind./10cm²	1.00 pm A	1.21 pm B	1.50 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.98	0.33	0.46
Copepoda	0.00	0.98	55.02	18.67	25.71
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	42.25	30.46	99.23	57.31	30.03
Nematoda	821.34	260.35	611.09	564.26	231.40
Oligochaeta	9.82	0.98	0.00	3.60	4.42
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	2.95	0.00	0.98	1.39
Rotifera	0.98	0.00	0.00	0.33	0.46
Tardigrada	0.00	0.00	0.98	0.33	0.46
Turbellaria	0.00	0.00	0.00	0.00	0.00
Total	874.40	295.72	767.31	645.81	251.38

Ceriops
cage
period 1

4-10 cm
6-8-92

ind./10cm²	1.00 pm A	1.21 pm B	1.50 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	5.89	1.96	2.78
Copepoda	0.98	0.00	2.95	1.31	1.23
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.98	0.33	0.46
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.98	0.33	0.46
Nauplii	0.00	0.00	10.81	3.60	5.09
Nematoda	86.46	110.04	119.86	105.45	14.02
Oligochaeta	2.95	0.98	2.95	2.29	0.93
Ostracoda	0.00	0.00	1.96	0.65	0.93
Polychaeta	0.00	0.00	4.91	1.64	2.32
Rotifera	0.98	0.00	0.00	0.33	0.46
Tardigrada	0.00	0.00	1.96	0.65	0.93
Turbellaria	0.00	0.00	0.00	0.00	0.00
Total	91.37	111.02	153.26	118.55	25.82

10-rest cm
6-8-92

ind./10cm²	1.00 pm A	1.21 pm B	1.50 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.98	0.33	0.46
Copepoda	4.91	5.89	0.98	3.93	2.12
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.98	0.00	0.33	0.46
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	16.70	0.98	24.56	14.08	9.80
Nematoda	14.74	45.19	40.28	33.40	13.35
Oligochaeta	0.00	0.00	0.00	0.00	0.00
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	1.96	0.98	0.00	0.98	0.80
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	0.00	0.00	0.00	0.00
Total	38.32	54.04	66.81	53.05	11.65

Ceriops
cage
period 2

0-2 cm
28-8-92

ind./120cm²

	10.30 am A	9.20 am B	8.30 am C	mean	std
Amphipoda	1.96	0.00	1.96	1.31	0.93
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.98	2.95	0.98	1.64	0.93
Cladocera	0.00	0.00	3.93	1.31	1.85
Copepoda	14.74	3.93	4.91	7.86	4.88
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	2.95	0.00	0.00	0.98	1.39
Kinorhyncha	27.51	23.58	6.88	19.32	8.94
Nauplii	23.58	10.81	10.81	15.06	6.02
Nematoda	1765.49	1908.93	1315.52	1663.32	252.80
Oligochaeta	7.86	1.96	13.75	7.86	4.81
Ostracoda	173.90	67.79	62.88	101.52	51.22
Polychaeta	3.93	0.00	0.98	1.64	1.67
Rotifera	0.00	0.00	0.00	0.00	0.00
Tardigrada	3.93	0.00	0.98	1.64	1.67
Turbellaria	46.18	8.84	2.95	19.32	19.14
Total	2073.01	2028.79	1426.54	1842.78	294.88

2-4 cm
28-8-92

	10.30 am A	9.20 am B	8.30 am C	mean	std
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	1.96	0.00	0.00	0.65	0.93
	0.00	0.00	0.00	0.00	0.00
	1.96	1.96	0.00	1.31	0.93
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.98	0.33	0.46
	0.98	0.98	0.98	0.98	0.00
	393.97	742.74	525.62	554.11	143.81
	3.93	0.98	7.86	4.26	2.82
	3.93	0.00	0.98	1.64	1.67
	2.95	0.00	1.96	1.64	1.23
	10.81	8.84	0.00	6.55	4.70
	0.00	0.00	0.00	0.00	0.00
	14.74	5.89	0.00	6.88	6.06
	435.23	761.41	538.39	578.35	136.13

Ceriops
cage
period 2

4-10 cm
28-8-92

ind./10cm²

	10.30 am A	9.20 am B	8.30 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	1.96	0.00	0.00	0.65	0.93
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	1.96	0.00	0.65	0.93
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	47.16	0.00	0.00	15.72	22.23
Nematoda	93.33	650.39	282.95	342.23	231.25
Oligochaeta	0.98	2.95	1.96	1.96	0.80
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	7.86	13.75	0.00	7.20	5.63
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	0.00	0.00	0.00	0.00
Total	151.30	669.06	284.92	368.43	219.47

10-rest cm
28-8-92

	10.30 am A	9.20 am B	8.30 am C	mean	std
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.98	0.00	0.33	0.46
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.98	0.00	0.00	0.33	0.46
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.98	0.00	0.00	0.33	0.46
	38.32	269.20	180.77	162.76	95.11
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.98	0.00	0.33	0.46
	10.81	24.56	7.86	14.41	7.28
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	51.09	295.72	188.63	178.48	100.13

Ceriops
cage
period 3

0-2 cm
27-9-92

ind./10cm²	9.25 am A	9.48 am B	10.43 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	15.72	0.00	4.91	6.88	6.57
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.98	0.00	2.95	1.31	1.23
Kinorhyncha	25.54	23.58	4.91	18.01	9.30
Nauplii	26.53	21.61	0.98	16.37	11.07
Nematoda	2196.80	1761.56	1957.07	1971.81	177.99
Oligochaeta	23.58	21.61	21.61	22.27	0.93
Ostracoda	27.51	91.37	29.47	49.45	29.65
Polychaeta	1.96	0.00	8.84	3.60	3.79
Rotifera	10.81	9.82	0.98	7.20	4.42
Tardigrada	0.00	0.00	0.98	0.33	0.46
Turbellaria	8.84	56.98	1.96	22.60	24.48
Total	2338.27	1986.55	2034.69	2119.84	155.70

2-4 cm
27-9-92

9.25 am A	9.48 am B	10.43 am C	mean	std
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
1.96	3.93	0.00	1.96	1.60
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	1.96	0.00	0.65	0.93
329.13	379.23	1079.73	596.03	342.64
4.91	2.95	1.96	3.27	1.23
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
7.86	2.95	2.95	4.58	2.32
0.00	0.00	0.00	0.00	0.00
1.96	1.96	0.00	1.31	0.93
345.83	392.99	1084.64	607.82	337.71

Ceriops
cage
period 3

4-10 cm
27-9-92

ind./10cm²	9.25 am A	9.48 am B	10.43 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	1.96	0.00	0.65	0.93
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	1.96	0.00	0.00	0.65	0.93
Nematoda	99.23	87.44	261.34	149.33	79.34
Oligochaeta	0.00	0.00	0.00	0.00	0.00
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	9.82	10.81	3.93	8.19	3.04
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	0.98	0.00	0.33	0.46
Total	111.02	101.19	265.27	159.16	75.14

10-rest cm
27-9-92

9.25 am A	9.48 am B	10.43 am C	mean	std
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.98	0.00	0.00	0.33	0.46
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
1.96	0.00	0.00	0.65	0.93
0.00	0.00	0.00	0.00	0.00
0.98	0.00	0.00	0.33	0.46
0.00	0.00	0.00	0.00	0.00
22.60	28.49	37.33	29.47	6.06
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
12.77	13.75	0.98	9.17	5.80
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
39.30	42.25	38.32	39.95	1.67

Ceriops
cage
period 6

0-2 cm
23-12-92

ind./10cm²	8.50 am A	9.30 am B	10.25 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.00	0.00	0.00	0.00
Decapoda larvae	0.00	0.00	0.98	0.33	0.46
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.98	0.00	0.00	0.33	0.46
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	11.79	3.93	5.56
Nauplii	0.98	0.00	0.98	0.65	0.46
Nematoda	1277.21	510.88	1915.81	1234.63	574.35
Oligochaeta	0.00	0.00	3.93	1.31	1.85
Ostracoda	25.54	1.96	7.86	11.79	10.02
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	0.98	0.00	0.98	0.65	0.46
Tardigrada	0.00	0.00	1.96	0.65	0.93
Turbellaria	0.00	2.95	0.00	0.98	1.39
Total	1305.70	515.80	1944.30	1255.27	584.27

2-4 cm
23-12-92

	8.50 am A	9.30 am B	10.25 am C	mean	std
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.98	0.00	0.33	0.46
	0.00	0.00	0.00	0.00	0.00
	0.00	0.98	0.00	0.33	0.46
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.98	0.00	0.33	0.46
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	383.16	1051.24	962.82	799.07	296.30
	0.00	0.98	0.98	0.65	0.46
	0.00	1.96	0.98	0.98	0.80
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	383.16	1057.13	964.78	801.69	298.34

Ceriops
cage
period 6

4-10 cm
23-12-92

ind./10cm²	8.50 am A	9.30 am B	10.25 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.00	0.00	0.00	0.00
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.98	7.86	3.93	4.26	2.82
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	0.00	0.00	0.00	0.00
Nematoda	24.56	245.62	208.28	159.49	96.62
Oligochaeta	0.00	3.93	3.93	2.62	1.85
Ostracoda	0.00	0.00	3.93	1.31	1.85
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	0.98	0.00	0.00	0.33	0.46
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	0.00	0.00	0.00	0.00
Total	26.53	257.41	220.07	168.00	101.19

10-rest cm
23-12-92

	8.50 am A	9.30 am B	10.25 am C	mean	std
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	3.93	1.31	1.85
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	1.96	62.88	68.77	44.54	30.20
	0.00	0.00	1.96	0.65	0.93
	0.00	0.00	1.96	0.65	0.93
	0.00	0.00	0.00	0.00	0.00
	1.96	0.00	0.00	0.65	0.93
	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00
	3.93	62.88	76.63	47.81	31.53

Ceriops cage period end	0-2 cm 30-7-93					2-4 cm 30-7-93				
ind./10cm²	12.15 am A	12.30 am B	12.55 am C	mean	std	12.15 am A	12.30 am B	12.55 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ciliata	6.88	0.00	0.00	2.29	3.24	0.98	0.00	0.98	0.65	0.46
Cladocera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Copepoda	4.91	1.96	3.93	3.60	1.23	0.00	0.98	0.00	0.33	0.46
Decapoda larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.33	0.46
Insecta larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	12.77	11.79	1.96	8.84	4.88	0.00	0.00	0.00	0.00	0.00
Nauplii	5.89	18.67	5.89	10.15	6.02	0.00	0.00	0.00	0.00	0.00
Nematoda	3183.19	2426.69	2249.85	2619.91	404.79	1287.03	618.95	628.78	844.92	312.64
Oligochaeta	9.82	10.81	0.98	7.20	4.42	0.00	0.00	0.00	0.00	0.00
Ostracoda	17.68	25.54	10.81	18.01	6.02	0.00	1.96	0.00	0.65	0.93
Polychaeta	0.98	0.00	2.95	1.31	1.23	0.00	0.00	0.00	0.00	0.00
Rotifera	0.98	0.98	1.96	1.31	0.46	1.96	0.98	0.00	0.98	0.80
Tardigrada	2.95	1.96	0.98	1.96	0.80	0.98	0.00	0.00	0.33	0.46
Turbellaria	2.95	1.96	0.00	1.64	1.23	0.00	0.98	0.98	0.65	0.46
Total	3249.02	2500.38	2279.32	2676.24	414.95	1290.96	623.87	631.73	848.85	312.64

Ceriops cage period end	4-10 cm 30-7-93					10-rest cm 30-7-93				
ind./10cm²	12.15 am A	12.30 am B	12.55 am C	mean	std	12.15 am A	12.30 am B	12.55 am C	mean	std
Amphipoda	0.00			0.00	0.00	0.00			0.00	0.00
Bivalvia	0.00			0.00	0.00	0.00			0.00	0.00
Ciliata	0.00			0.00	0.00	0.00			0.00	0.00
Cladocera	0.00			0.00	0.00	0.00			0.00	0.00
Copepoda	3.93			3.93	0.00	0.00			0.00	0.00
Decapoda larvae	0.00			0.00	0.00	0.00			0.00	0.00
Gastropoda	0.00			0.00	0.00	0.00			0.00	0.00
Halacaroidea	0.00			0.00	0.00	0.00			0.00	0.00
Insecta larvae	0.00			0.00	0.00	0.00			0.00	0.00
Kinorhyncha	0.00			0.00	0.00	0.00			0.00	0.00
Nauplii	1.96			1.96	0.00	0.00			0.00	0.00
Nematoda	768.29			768.29	0.00	137.55			137.55	0.00
Oligochaeta	7.86			7.86	0.00	0.00			0.00	0.00
Ostracoda	0.98			0.98	0.00	0.00			0.00	0.00
Polychaeta	0.00			0.00	0.00	0.00			0.00	0.00
Rotifera	15.72			15.72	0.00	19.65			19.65	0.00
Tardigrada	0.00			0.00	0.00	0.00			0.00	0.00
Turbellaria	5.89			5.89	0.00	1.96			1.96	0.00
Total	804.64			804.64	379.31	159.16			159.16	75.03

Avicennia
blanco
0-2 cm

ind./10 cm²	period 1 6-8-92 2.00 pm A	2.40 pm B	3.45 pm C	mean	std	period 2 28-8-92 11.40 am A	12.25 am B	2.35 am C	mean	std
Amphipoda	0.98	0.00	0.00	0.33	0.46	2.94	0.00	0.00	0.98	1.39
Bivalvia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.96	0.65	0.92
Ciliata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cladocera	0.98	0.00	1.96	0.98	0.80	0.00	0.98	0.00	0.33	0.46
Copepoda	19.60	40.31	39.33	33.08	9.54	10.78	0.00	8.82	6.53	4.69
Decapoda larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halacaroidea	1.96	0.00	2.94	1.63	1.22	6.76	4.90	4.90	5.52	0.88
Insecta larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	0.00	0.00	0.00	0.00	0.98	1.96	0.98	1.31	0.46
Nematoda	558.51	129.79	757.13	481.81	261.79	992.13	601.77	932.15	842.02	171.64
Oligochaeta	18.68	0.98	14.70	11.45	7.58	54.08	16.72	29.50	33.43	15.50
Ostracoda	0.98	0.00	0.00	0.33	0.46	0.00	0.98	0.00	0.33	0.46
Polychaeta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rotifera	26.55	4.90	39.33	23.59	14.21	25.57	32.45	48.18	35.40	9.46
Tardigrada	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Turbellaria	15.73	0.00	4.90	6.88	6.57	12.74	5.88	7.87	8.83	2.88
Total	643.97	175.98	860.29	560.08	285.60	1105.98	665.64	1034.36	935.33	192.93

Avicennia
blanco
0-2 cm

ind./10 cm²	period 3 25-9-92 11.30 am A	12.25 am B	12.35 am C	mean	std	period 6 23-12-92 10.35 am A	9.50 am B	8.35 am C	mean	std
Amphipoda	0.98	0.00	0.00	0.33	0.46	0.00	19.60	0.00	6.53	9.24
Bivalvia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Copepoda	0.98	2.94	2.94	2.29	0.92	0.98	0.00	0.00	0.33	0.46
Decapoda larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halacaroidea	5.88	3.92	1.96	3.92	1.60	2.94	1.96	0.00	1.63	1.22
Insecta larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	4.90	5.88	3.59	2.57	0.00	0.00	0.00	0.00	0.00
Nematoda	1693.22	927.24	806.29	1142.25	392.71	270.48	700.70	173.46	381.55	229.12
Oligochaeta	57.03	21.63	27.53	35.40	15.49	11.76	19.60	0.98	10.78	7.63
Ostracoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.33	0.46
Rotifera	28.52	13.77	20.65	20.98	6.03	0.00	0.00	0.00	0.00	0.00
Tardigrada	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Turbellaria	21.63	6.86	9.80	12.76	6.38	4.90	39.20	4.90	16.33	16.17
Total	1808.24	981.26	875.05	1221.52	417.14	291.06	781.06	180.32	417.48	261.03

Avicennia
blanco
0-2 cm

period end
30-7-93

ind./10 cm²	A	12.50 am B	12.40 am C	mean	std
Amphipoda		0.00	0.00	0.00	0.00
Bivalvia		0.00	0.00	0.00	0.00
Ciliata		0.00	0.00	0.00	0.00
Cladocera		0.00	0.00	0.00	0.00
Copepoda		0.00	0.00	0.00	0.00
Decapoda larvae		0.00	0.00	0.00	0.00
Gastropoda		0.00	0.00	0.00	0.00
Halacaroidea		9.00	11.00	10.00	1.00
Insecta larvae		1.00	19.00	10.00	9.00
Kinorhyncha		0.00	0.00	0.00	0.00
Nauplii		0.00	0.00	0.00	0.00
Nematoda		1791.00	1729.00	1760.00	31.00
Oligochaeta		11.00	9.00	10.00	1.00
Ostracoda		0.00	0.00	0.00	0.00
Polychaeta		0.00	0.00	0.00	0.00
Rotifera		11.00	19.00	15.00	4.00
Tardigrada		0.00	0.00	0.00	0.00
Turbellaria		0.00	0.00	0.00	0.00
Total		1823.00	1787.00	1805.00	851.01

Avicennia
partial cage
0-2 cm

period 1
6-8-92

ind./10cm²	1.40 pm A	2.30 pm B	4.00 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	3.93	1.31	1.85
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	9.83	17.69	0.98	9.50	6.83
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.98	1.97	5.90	2.95	2.12
Insecta larvae	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	61.93	106.16	58.89	75.66	21.60
Nematoda	1008.56	1437.15	1478.43	1308.05	212.44
Oligochaeta	27.52	38.34	13.76	26.54	10.06
Ostracoda	0.98	0.98	0.00	0.65	0.46
Polychaeta	0.00	0.00	0.98	0.33	0.46
Rotifera	0.00	16.71	10.81	9.17	6.92
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	47.18	33.42	40.30	40.30	5.62
Total	1156.98	1652.42	1613.98	1474.46	225.04

period 2
28-8-92

11.30 am A	12.00 zm B	2.50 pm C	mean	std
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
0.00	0.98	0.00	0.33	0.46
0.00	0.00	0.00	0.00	0.00
1.97	0.00	0.98	0.98	0.80
0.00	0.00	0.98	0.33	0.46
0.98	0.00	0.00	0.33	0.46
8.85	6.88	2.95	6.23	2.45
0.00	1.97	0.98	0.98	0.80
0.00	0.00	0.98	0.33	0.46
2.95	0.00	0.98	1.31	1.23
1923.73	646.81	971.20	1180.58	541.92
12.78	21.63	14.75	16.39	3.79
0.00	0.98	0.00	0.33	0.46
0.00	0.00	0.00	0.00	0.00
9.83	0.98	0.98	3.93	4.17
0.00	0.00	0.00	0.00	0.00
14.75	4.92	3.93	7.87	4.88
1975.84	685.15	998.71	1219.90	549.64

Avicennia
partial cage
0-2 cm

period 3
25-9-92

ind./10cm²	11.20 am A	11.45 am B	2.20 pm C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	3.93	6.88	3.60	2.82
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	6.88	0.00	2.29	3.24
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	1.97	4.92	2.30	2.02
Insecta larvae	8.85	0.98	2.95	4.26	3.34
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	0.98	0.00	0.33	0.46
Nematoda	2338.56	1446.98	1938.48	1908.01	364.62
Oligochaeta	25.56	23.59	19.66	22.94	2.45
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	4.92	12.78	2.95	6.88	4.25
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	40.30	14.75	13.76	22.94	12.28
Total	2418.19	1512.84	1989.60	1973.54	369.78

period 6
23-12-92

7.45 am A	10.10 am B	9.08 am C	mean	std
2.00	0.00	0.00	0.67	0.94
0.00	0.00	0.00	0.00	0.00
1.00	0.00	0.00	0.33	0.47
0.00	0.00	0.00	0.00	0.00
4.00	0.00	19.00	7.67	8.18
0.00	0.00	0.00	0.00	0.00
1.00	0.00	0.00	0.33	0.47
8.00	49.00	0.00	19.00	21.46
4.00	0.00	0.00	1.33	1.89
0.00	0.00	0.00	0.00	0.00
7.00	0.00	0.00	2.33	3.30
2134.00	1271.00	1999.00	1801.33	379.03
1.00	0.00	0.00	0.33	0.47
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
12.00	0.00	19.00	10.33	7.85
0.00	0.00	0.00	0.00	0.00
21.00	0.00	79.00	33.33	33.41
2195.00	1320.00	2116.00	1877.00	395.18

Avicennia
partial cage
0-2 cm

period end
30-7-93

ind./10cm²	1.20 pm A	12.45 am B	12.00 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	1.00	9.00	3.33	4.03
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	0.00	0.00	0.00	0.00	0.00
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	9.00	0.00	1.00	3.33	4.03
Insecta larvae	19.00	0.00	0.00	6.33	8.96
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	0.00	0.00	0.00	0.00
Nematoda	3150.00	3548.00	4501.00	3733.00	566.84
Oligochaeta	0.00	0.00	0.00	0.00	0.00
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	11.00	0.00	3.67	5.19
Rotifera	0.00	19.00	21.00	13.33	9.46
Tardigrada	0.00	0.00	0.00	0.00	0.00
Turbellaria	0.00	9.00	1.00	3.33	4.03
Total	3178.00	3588.00	4533.00	3766.33	567.37

Avicennia
cage
0-2 cm

ind./10cm²	period 1 6-8-92 3.30 pm A	 3.15 pm B	 4.20 pm C	 mean	 std	period 2 28-8-92 2.00 pm A	 12.35 am B	 3.05 pm C	 mean	 std
Amphipoda	0.00	0.98	0.98	0.65	0.46	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.93	1.31	1.85
Cladocera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Copepoda	8.84	36.35	23.58	22.92	11.24	0.00	2.95	2.95	1.97	1.39
Decapoda larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.98	0.33	0.46	0.00	0.00	0.00	0.00	0.00
Halacaroidea	4.91	2.95	0.98	2.95	1.60	0.98	0.98	2.95	1.64	0.93
Insecta larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nauplii	62.88	242.67	57.97	121.17	85.93	0.00	0.00	0.00	0.00	0.00
Nematoda	1910.90	1072.85	939.24	1307.66	430.03	1065.98	852.78	578.67	832.48	199.46
Oligochaeta	12.77	22.60	6.88	14.08	6.48	35.37	36.35	16.70	29.47	9.04
Ostracoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.96	0.65	0.92
Polychaeta	0.00	0.00	0.98	0.33	0.46	0.00	0.98	0.00	0.33	0.46
Rotifera	3.93	6.88	0.98	3.93	2.41	7.86	34.39	13.75	18.67	11.38
Tardigrada	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Turbellaria	19.65	23.58	13.75	18.99	4.04	9.82	16.70	2.95	9.82	5.61
Total	2023.88	1408.86	1046.32	1493.02	403.50	1120.01	945.13	623.86	896.33	205.47

Avicennia
cage
0-2 cm

ind./10cm²	period 3 25-9-92 12.00 pm A	 12.15 am B	 2.30 pm C	 mean	 std	period 6 23-12-92 8.10 am A	 10.50 am B	 9.30 am C	 mean	 std
Amphipoda	6.88	0.00	0.00	2.29	3.24	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ciliata	0.00	0.98	1.96	0.98	0.80	0.00	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Copepoda	2.95	0.00	0.98	1.31	1.23	1.00	9.00	0.00	3.33	4.03
Decapoda larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	3.93	0.98	1.64	1.67	0.00	10.00	0.00	3.33	4.71
Insecta larvae	3.93	2.95	4.91	3.93	0.80	0.00	0.00	0.00	0.00	0.00
Kinorhyncha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	3.33	4.71
Nematoda	1256.58	1194.68	1302.75	1251.34	44.27	1209.00	1682.00	1159.00	1350.00	235.65
Oligochaeta	31.44	5.89	10.81	16.05	11.07	9.00	59.00	22.00	30.00	21.18
Ostracoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rotifera	1.96	0.98	1.96	1.63	0.46	0.00	0.00	0.00	0.00	0.00
Tardigrada	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Turbellaria	21.61	9.82	4.91	12.11	7.01	19.00	0.00	31.00	16.67	12.76
Total	1325.35	1219.23	1329.26	1291.28	50.97	1238.00	1770.00	1212.00	1406.67	257.13

Avicennia
cage
0-2 cm

period end
30-7-93

ind./10cm²	1.35 pm A	12.30 am B	11.30 am C	mean	std
Amphipoda	0.00	0.00	0.00	0.00	0.00
Bivalvia	0.00	0.00	0.00	0.00	0.00
Ciliata	1.00	0.00	8.00	3.00	3.56
Cladocera	0.00	0.00	0.00	0.00	0.00
Copepoda	32.00	0.00	1.00	11.00	14.85
Decapoda larvae	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00
Halacaroidea	0.00	29.00	2.00	10.33	13.22
Insecta larvae	11.00	18.00	10.00	13.00	3.56
Kinorhyncha	0.00	0.00	0.00	0.00	0.00
Nauplii	0.00	0.00	0.00	0.00	0.00
Nematoda	4102.00	6548.00	3811.00	4820.33	1227.41
Oligochaeta	30.00	80.00	10.00	40.00	29.44
Ostracoda	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.00	0.00	0.00	0.00	0.00
Rotifera	0.00	49.00	0.00	16.33	23.10
Tardigrada	0.00	0.00	9.00	3.00	4.24
Turbellaria	0.00	0.00	0.00	0.00	0.00
Total	4176.00	6724.00	3851.00	4917.00	1284.61

Ceriops
cage
period 1

ind./10 cm²	0-2 cm 6-8-92 A	B	C	mean	std	2-4 cm 6-8-92 A	B	C	mean	std
Adoncholaimus	30.76	15.13	20.36	22.08	6.50	0.00	0.00	21.84	7.28	10.30
Anoplostoma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bathylaimus	41.02	0.00	20.36	20.46	16.75	0.00	0.00	0.00	0.00	0.00
Belondira	0.00	0.00	0.00	0.00	0.00	10.94	0.00	0.00	3.65	5.16
Camacolaimus	0.00	15.13	0.00	5.04	7.13	0.00	0.00	10.92	3.64	5.15
Chromadora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chromadorita	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chromaspirina	92.29	30.26	0.00	40.85	38.41	43.75	64.58	10.92	39.75	22.09
Cyatholaimidae	0.00	0.00	10.18	3.39	4.80	0.00	0.00	0.00	0.00	0.00
Daptonema	194.84	166.43	91.60	150.96	43.54	0.00	0.00	32.76	10.92	15.44
Desmodora	92.29	196.69	142.49	143.82	42.63	32.81	46.13	54.60	44.51	8.97
Dorylaimidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dorylaimopsis	10.25	0.00	10.18	6.81	4.82	0.00	0.00	0.00	0.00	0.00
Ethmolaimus	0.00	0.00	0.00	0.00	0.00	10.94	0.00	0.00	3.65	5.16
Eubostrichus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halalaimus	20.51	15.13	0.00	11.88	8.68	10.94	9.23	0.00	6.72	4.81
Halichoanolaimus	0.00	0.00	0.00	0.00	0.00	32.81	55.35	10.92	33.03	18.14
Haliplectus	51.27	0.00	0.00	17.09	24.17	65.63	18.45	10.92	31.67	24.21
Leptonemella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Linhomoeus	10.25	136.17	132.31	92.91	58.47	10.94	18.45	185.63	71.67	80.64
Linhystera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Metachromadora	10.25	0.00	0.00	3.42	4.83	0.00	0.00	10.92	3.64	5.15
Metadesmolaimus	0.00	0.00	10.18	3.39	4.80	0.00	0.00	0.00	0.00	0.00
Metalinhomoeus	0.00	15.13	122.13	45.75	54.36	0.00	9.23	87.36	32.20	39.19
Microlaimus	71.78	15.13	30.53	39.15	23.92	240.64	18.45	32.76	97.28	101.54
Molgolaimus	0.00	15.13	30.53	15.22	12.46	10.94	0.00	0.00	3.65	5.16
Monhystera	0.00	0.00	0.00	0.00	0.00	0.00	9.23	10.92	6.72	4.80
Neochromadora	0.00	15.13	10.18	8.44	6.30	0.00	0.00	0.00	0.00	0.00
Odontophora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.92	3.64	5.15
Oxystomina	0.00	0.00	0.00	0.00	0.00	65.63	0.00	0.00	21.88	30.94
Paracanthonchus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paralinhomoeus	0.00	0.00	0.00	0.00	0.00	0.00	18.45	0.00	6.15	8.70
Paramonhystera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paradontophora	0.00	15.13	20.36	11.83	8.63	0.00	9.23	10.92	6.72	4.80
Plectus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pomponema	0.00	0.00	0.00	0.00	0.00	0.00	9.23	0.00	3.08	4.35
Prochromadorella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ptycholaimellus	143.56	272.34	81.42	165.77	79.51	328.14	415.15	163.80	302.36	104.22
Sabatieria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sigmophoranema	10.25	0.00	30.53	13.59	12.69	0.00	0.00	0.00	0.00	0.00
Siphonolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sphaerolaimus	51.27	30.26	111.95	64.49	34.64	0.00	0.00	0.00	0.00	0.00
Spilophorella	30.76	45.39	0.00	25.38	18.92	0.00	0.00	0.00	0.00	0.00
Spirinia	41.02	196.69	10.18	82.63	81.63	0.00	516.63	87.36	201.33	225.79
Synonchiella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Syringolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.92	3.64	5.15
Terschellingia	10.25	242.08	81.42	111.25	96.97	21.88	221.41	43.68	95.66	89.37
Theristus	10.25	75.65	30.53	38.81	27.33	65.63	36.90	131.04	77.86	39.39
unknown	61.53	0.00	50.89	37.47	26.85	32.81	36.90	109.20	59.64	35.09
Total	984.40	1513.00	1048.31	1181.90	235.57	984.43	1513.00	1048.31	1181.91	235.56

Ceriops
cage
period 1

ind./10 cm²	4-10 cm 6-8-92 A	B	C	mean	std	10-rest cm 6-8-92 A	B	C	mean	std
Adoncholaimus	0.00	15.93	0.00	5.31	7.51	0.00	0.00	0.00	0.00	0.00
Anoplostoma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bathylaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Belondira	49.84	0.00	0.00	16.61	23.49	656.29	0.00	0.00	218.76	309.38
Camacolaimus	0.00	0.00	11.91	3.97	5.61	0.00	0.00	0.00	0.00	0.00
Chromadora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chromadorita	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30.83	10.28	14.53
Chromaspirina	0.00	111.48	11.91	41.13	49.98	0.00	70.37	123.33	64.57	50.52
Cyatholaimidae	37.38	0.00	23.82	20.40	15.45	0.00	0.00	0.00	0.00	0.00
Daptonema	0.00	47.78	11.91	19.90	20.31	0.00	0.00	61.66	20.55	29.07
Desmodora	0.00	31.85	59.56	30.47	24.33	0.00	140.74	30.83	57.19	60.40
Dorylaimidae	0.00	0.00	83.39	27.80	39.31	0.00	0.00	154.16	51.39	72.67
Dorylaimopsis	0.00	15.93	0.00	5.31	7.51	0.00	0.00	0.00	0.00	0.00
Ethmolaimus	174.46	15.93	0.00	63.46	78.76	82.04	0.00	30.83	37.62	33.84
Eubostrichus	12.46	0.00	11.91	8.12	5.75	0.00	0.00	0.00	0.00	0.00
Halalaimus	24.92	0.00	0.00	8.31	11.75	0.00	0.00	0.00	0.00	0.00
Halichoanolaimus	37.38	31.85	0.00	23.08	16.47	0.00	35.19	0.00	11.73	16.59
Haliplectus	161.99	334.45	71.47	189.30	109.08	0.00	281.49	30.83	104.11	126.06
Leptonemella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Linhomoeus	0.00	47.78	71.47	39.75	29.72	0.00	0.00	0.00	0.00	0.00
Linhystera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Metachromadora	12.46	15.93	11.91	13.43	1.78	0.00	0.00	30.83	10.28	14.53
Metadesmolaimus	12.46	0.00	0.00	4.15	5.87	0.00	0.00	0.00	0.00	0.00
Metalinhomoeus	0.00	127.41	35.74	54.38	53.66	0.00	70.37	30.83	33.73	28.80
Microlaimus	186.92	143.34	71.47	133.91	47.60	82.04	316.67	154.16	184.29	98.13
Molgolaimus	0.00	0.00	11.91	3.97	5.61	0.00	0.00	0.00	0.00	0.00
Monhystera	0.00	270.75	23.82	98.19	122.41	0.00	35.19	0.00	11.73	16.59
Neochromadora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Odontophora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oxystomina	112.15	0.00	11.91	41.35	50.30	0.00	35.19	30.83	22.01	15.66
Paracanthonchus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paralinhomoeus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paramonhystera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paradontophora	0.00	0.00	11.91	3.97	5.61	0.00	0.00	0.00	0.00	0.00
Plectus	37.38	0.00	0.00	12.46	17.62	164.07	0.00	0.00	54.69	77.34
Pomponema	0.00	0.00	0.00	0.00	0.00	0.00	0.00	92.50	30.83	43.60
Prochromadorella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30.83	10.28	14.53
Ptycholaimellus	12.46	47.78	11.91	24.05	16.78	0.00	0.00	61.66	20.55	29.07
Sabatieria	0.00	0.00	11.91	3.97	5.61	0.00	0.00	0.00	0.00	0.00
Sigmophoranema	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Siphonolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sphaerolaimus	0.00	15.93	11.91	9.28	6.76	0.00	0.00	0.00	0.00	0.00
Spilophorella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spirinia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Synonchiella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30.83	10.28	14.53
Syringolaimus	0.00	79.63	23.82	34.48	33.37	0.00	0.00	0.00	0.00	0.00
Terschellingia	0.00	63.71	71.47	45.06	32.02	0.00	211.12	0.00	70.37	99.52
Theristus	62.31	47.78	297.81	135.97	114.59	0.00	0.00	30.83	10.28	14.53
unknown	49.84	47.78	83.39	60.34	16.32	0.00	140.74	30.83	57.19	60.40
						0.00	175.93	61.66	79.20	72.89
Total	984.41	1513.02	1048.24	1181.89	235.59	984.44	1513.00	1048.26	1181.90	235.57

Ceriops cage period 3	0-2 cm 27-9-92					2-4 cm 27-9-92				
ind./10 cm²	A	B	C	mean	std	A	B	C	mean	std
Adoncholaimus	113.24	69.76	34.95	72.65	32.03	142.65	18.74	0.00	53.80	63.29
Anoplostoma	0.00	17.44	0.00	5.81	8.22	0.00	0.00	0.00	0.00	0.00
Bathylaimus	22.65	104.65	104.84	77.38	38.70	0.00	0.00	0.00	0.00	0.00
Belondira	0.00	0.00	0.00	0.00	0.00	57.06	0.00	0.00	19.02	26.90
Camacolaimus	0.00	34.88	17.47	17.45	14.24	0.00	0.00	19.38	6.46	9.14
Chromadora	0.00	0.00	17.47	5.82	8.24	0.00	0.00	0.00	0.00	0.00
Chromadorita	0.00	0.00	17.47	5.82	8.24	0.00	0.00	0.00	0.00	0.00
Chromaspirina	158.53	279.06	401.90	279.83	99.36	85.59	187.40	251.90	174.96	68.46
Cytholaimidae	0.00	0.00	17.47	5.82	8.24	0.00	0.00	0.00	0.00	0.00
Daptonema	45.29	69.76	69.90	61.65	11.57	0.00	18.74	0.00	6.25	8.83
Desmodora	203.83	191.85	139.79	178.49	27.80	85.59	431.02	96.88	204.50	160.24
Dorylaimidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dorylaimopsis	22.65	17.44	34.95	25.01	7.34	0.00	0.00	0.00	0.00	0.00
Ethmolaimus	0.00	34.88	0.00	11.63	16.44	114.12	18.74	38.75	57.20	41.07
Eubostrichus	0.00	87.21	17.47	34.89	37.67	0.00	0.00	19.38	6.46	9.14
Halalaimus	45.29	174.41	17.47	79.06	68.37	0.00	18.74	0.00	6.25	8.83
Halichoanolaimus	0.00	17.44	17.47	11.64	8.23	28.53	0.00	19.38	15.97	11.89
Haliplectus	0.00	0.00	0.00	0.00	0.00	342.36	112.44	135.64	196.81	103.35
Leptonemella	0.00	0.00	0.00	0.00	0.00	0.00	18.74	0.00	6.25	8.83
Linhomoeus	0.00	0.00	87.37	29.12	41.19	0.00	37.48	96.88	44.79	39.89
Linhystera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Metachromadora	45.29	34.88	52.42	44.20	7.20	0.00	0.00	0.00	0.00	0.00
Metadesmolaimus	0.00	0.00	0.00	0.00	0.00	85.59	18.74	0.00	34.78	36.74
Metalinhomoeus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	174.39	58.13	82.21
Microlaimus	362.36	174.41	52.42	196.40	127.48	485.01	281.10	736.32	500.81	186.18
Molgolaimus	90.59	0.00	0.00	30.20	42.70	0.00	0.00	0.00	0.00	0.00
Monhystera	181.18	17.44	69.90	89.51	68.27	28.53	18.74	19.38	22.22	4.47
Neochromadora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Odontophora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oxystomina	0.00	17.44	0.00	5.81	8.22	0.00	18.74	38.75	19.16	15.82
Paracanthonchus	0.00	0.00	34.95	11.65	16.48	0.00	0.00	0.00	0.00	0.00
Paralinhomoeus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paramonhystera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paradontophora	90.59	0.00	17.47	36.02	39.24	28.53	37.48	0.00	22.00	15.98
Plectus	22.65	0.00	0.00	7.55	10.68	28.53	0.00	0.00	9.51	13.45
Pomponema	45.29	0.00	17.47	20.92	18.65	0.00	0.00	19.38	6.46	9.14
Prochromadorella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ptycholaimellus	181.18	34.88	314.53	176.86	114.21	0.00	37.48	19.38	18.95	15.30
Sabatieria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sigmophoranema	45.29	0.00	0.00	15.10	21.35	0.00	0.00	0.00	0.00	0.00
Siphonolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sphaerolaimus	158.53	87.21	52.42	99.39	44.17	0.00	37.48	0.00	12.49	17.67
Spilophorella	181.18	34.88	0.00	72.02	78.49	28.53	0.00	0.00	9.51	13.45
Spirinia	0.00	156.97	174.74	110.57	78.52	57.06	187.40	38.75	94.40	66.18
Synonchiella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Syringolaimus	22.65	17.44	0.00	13.36	9.69	0.00	18.74	19.38	12.71	8.99
Terschellingia	22.65	17.44	104.84	48.31	40.03	0.00	0.00	77.51	25.84	36.54
Theristus	45.29	17.44	17.47	26.73	13.12	142.65	112.44	77.51	110.87	26.62
unknown	90.59	52.32	52.42	65.11	18.02	456.48	131.18	58.13	215.26	173.15
Total	2196.79	1761.53	1957.04	1971.79	178.00	2196.81	1761.56	1957.07	1971.81	178.00

Ceriops
cage
period 3

ind./10 cm²	4-10 cm 27-9-92 A	B	C	mean	std	10-rest cm 27-9-92 A	B	C	mean	std
Adoncholaimus	28.53	41.94	0.00	23.49	17.49	0.00	0.00	0.00	0.00	0.00
Anoplostoma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bathylaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Belondira	0.00	62.91	0.00	20.97	29.66	0.00	0.00	0.00	0.00	0.00
Camacolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	75.27	25.09	35.48
Chromadora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chromadorita	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chromaspirina	0.00	83.88	279.58	121.15	117.14	122.04	88.08	75.27	95.13	19.73
Cyatholaimidae	0.00	41.94	0.00	13.98	19.77	0.00	0.00	0.00	0.00	0.00
Daptonema	0.00	20.97	0.00	6.99	9.89	122.04	0.00	225.82	115.95	92.29
Desmodora	28.53	0.00	74.56	34.36	30.72	0.00	88.08	75.27	54.45	38.86
Dorylaimidae	85.59	0.00	0.00	28.53	40.35	0.00	0.00	75.27	25.09	35.48
Dorylaimopsis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ethmolaimus	228.24	41.94	279.58	183.25	102.10	0.00	88.08	0.00	29.36	41.52
Eubostrichus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halalaimus	28.53	0.00	0.00	9.51	13.45	0.00	0.00	0.00	0.00	0.00
Halichoanolaimus	0.00	62.91	37.28	33.40	25.83	0.00	0.00	0.00	0.00	0.00
Haliplectus	256.77	251.65	577.80	362.07	152.56	122.04	0.00	301.09	141.04	123.65
Leptonemella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Linhomoeus	0.00	62.91	0.00	20.97	29.66	0.00	176.16	225.82	133.99	96.89
Linhystera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Metachromadora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Metadesmolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Metalinhomoeus	0.00	0.00	18.64	6.21	8.79	0.00	0.00	301.09	100.36	141.94
Microlaimus	342.36	398.45	205.03	315.28	81.25	366.13	440.39	0.00	268.84	192.50
Molgolaimus	57.06	0.00	0.00	19.02	26.90	244.09	0.00	0.00	81.36	115.07
Monhystera	114.12	104.85	130.47	116.48	10.59	0.00	88.08	75.27	54.45	38.86
Neochromadora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Odontophora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oxystomina	28.53	62.91	55.92	49.12	14.84	0.00	88.08	0.00	29.36	41.52
Paracanthonchus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paralinhomoeus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paramonhystera	0.00	146.80	0.00	48.93	69.20	0.00	0.00	0.00	0.00	0.00
Paradontophora	0.00	20.97	0.00	6.99	9.89	0.00	0.00	0.00	0.00	0.00
Plectus	0.00	41.94	37.28	26.41	18.77	0.00	0.00	0.00	0.00	0.00
Pomponema	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Prochromadorella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ptycholaimellus	28.53	0.00	0.00	9.51	13.45	0.00	0.00	0.00	0.00	0.00
Sabatieria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sigmophoranema	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Siphonolaimus	28.53	0.00	0.00	9.51	13.45	0.00	0.00	0.00	0.00	0.00
Sphaerolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spilophorella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spirinia	28.53	62.91	0.00	30.48	25.72	0.00	0.00	0.00	0.00	0.00
Synonchiella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Syringolaimus	342.36	0.00	37.28	126.55	153.36	0.00	264.23	75.27	113.17	111.15
Terschellingia	0.00	20.97	18.64	13.20	9.38	0.00	0.00	0.00	0.00	0.00
Theristus	285.30	167.77	55.92	169.66	93.65	366.13	176.16	225.82	256.04	80.44
unknown	285.30	62.91	149.11	165.77	91.55	854.31	264.23	225.82	448.12	287.65
Total	2196.81	1761.53	1957.09	1971.81	178.01	2196.78	1761.57	1957.08	1971.81	177.98

Avicennia
0-2 cm
ind./10 cm²

	period 1 6-8-92 blanco					period 1 6-8-92 cage				
	A	B	C	mean	std	A	B	C	mean	std
Adoncholaimus	6.08	0.00	10.97	5.68	4.49	79.63	52.34	15.92	49.29	26.10
Bathylaimus	0.00	0.00	0.00	0.00	0.00	53.08	0.00	7.96	20.35	23.37
Belondira	12.15	1.55	0.00	4.57	5.40	0.00	13.09	7.96	7.01	5.38
Camacolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chromaspirina	66.84	1.55	54.86	41.08	28.38	451.21	39.26	47.75	179.40	192.23
Daptonema	0.00	0.00	10.97	3.66	5.17	0.00	52.34	23.87	25.40	21.40
Desmodora	206.59	52.60	285.25	181.48	96.62	822.79	601.93	517.25	647.32	128.80
Diplolaimelloides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dorylaimopsis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ethmolaimus	18.23	6.19	32.91	19.11	10.93	132.71	26.17	87.53	82.14	43.66
Eubostrichus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	23.87	7.96	11.25
Greeffiella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halalaimus	0.00	0.00	0.00	0.00	0.00	79.63	0.00	0.00	26.54	37.54
Halichoanolaimus	0.00	0.00	0.00	0.00	0.00	26.54	13.09	7.96	15.86	7.84
Haliplectus	12.15	10.83	98.74	40.57	41.13	0.00	0.00	47.75	15.92	22.51
Linhomoeus	0.00	1.55	0.00	0.52	0.73	0.00	0.00	7.96	2.65	3.75
Metachromadora	12.15	0.00	32.91	15.02	13.59	106.17	52.34	55.70	71.40	24.62
Metacyatholaimus	6.08	18.57	21.94	15.53	6.82	0.00	0.00	0.00	0.00	0.00
Metalinhomoeus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.96	2.65	3.75
Microlaimus	6.08	0.00	10.97	5.68	4.49	53.08	65.43	7.96	42.16	24.70
Monhystera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nemanema	0.00	0.00	10.97	3.66	5.17	0.00	0.00	0.00	0.00	0.00
Neochromadora	0.00	0.00	21.94	7.31	10.34	0.00	0.00	0.00	0.00	0.00
Oncholaimellus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oncholaimus	48.61	13.92	32.91	31.82	14.18	0.00	0.00	0.00	0.00	0.00
Paracanthonchus	24.30	20.11	0.00	14.81	10.61	0.00	0.00	7.96	2.65	3.75
Paradesmodora	18.23	0.00	10.97	9.73	7.49	0.00	39.26	7.96	15.74	16.94
Ptycholaimellus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhabditis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sigmophoranema	115.45	0.00	98.74	71.39	50.94	26.54	78.51	23.87	42.98	25.15
Sphaerolaimus	0.00	0.00	10.97	3.66	5.17	0.00	0.00	0.00	0.00	0.00
Spilophorella	6.08	0.00	0.00	2.03	2.86	26.54	26.17	0.00	17.57	12.43
Spirinia	0.00	1.55	0.00	0.52	0.73	0.00	0.00	23.87	7.96	11.25
Syringolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Terschellingia	0.00	1.55	10.97	4.17	4.85	26.54	0.00	0.00	8.85	12.51
Theristus	0.00	0.00	0.00	0.00	0.00	26.54	13.09	0.00	13.21	10.84
Thoracostoma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.96	2.65	3.75
1A	12.15	12.38	120.68	48.40	51.11	106.17	0.00	71.62	59.26	44.21
1B	0.00	0.00	10.97	3.66	5.17	79.63	65.43	39.79	61.61	16.49
2A	285.58	100.57	383.99	256.71	117.49	1035.13	758.95	668.44	820.84	155.96
2B	249.12	15.47	241.36	168.65	108.36	690.08	235.54	151.19	358.94	236.67
parasitic	12.15	1.55	0.00	4.57	5.40	0.00	13.09	7.96	7.01	5.38
Total	1118.00	259.93	1514.00	963.98	523.43	3822.00	2146.00	1878.00	2615.33	860.23

Avicennia
0-2 cm
ind./10 cm²

	period 1 6-8-92 partial cage					period 3 25-9-92 blanco				
	A	B	C	mean	std	A	B	C	mean	std
Adoncholaimus	12.16	16.15	0.00	9.43	6.87	0.00	0.00	0.00	0.00	0.00
Bathylaimus	0.00	48.44	0.00	16.15	22.83	0.00	0.00	0.00	0.00	0.00
Belondira	0.00	0.00	0.00	0.00	0.00	33.20	0.00	0.00	11.07	15.65
Camacolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chromaspirina	133.72	80.73	15.08	76.51	48.53	265.60	78.91	109.95	151.49	81.68
Daptonema	0.00	16.15	15.08	10.41	7.37	66.40	0.00	18.32	28.24	28.00
Desmodora	328.23	597.40	799.33	574.99	192.98	232.40	591.86	329.85	384.70	151.79
Diplolaimelloides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dorylaimopsis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ethmolaimus	243.13	96.88	150.82	163.61	60.39	199.20	0.00	54.97	84.73	84.00
Eubostrichus	0.00	0.00	0.00	0.00	0.00	0.00	19.73	0.00	6.58	9.30
Greeffiella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halalaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halichoanolaimus	12.16	16.15	15.08	14.46	1.69	0.00	0.00	0.00	0.00	0.00
Haliplectus	24.31	0.00	120.65	48.32	52.10	166.00	39.46	54.97	86.81	56.35
Linhomoeus	0.00	48.44	0.00	16.15	22.83	66.40	0.00	18.32	28.24	28.00
Metachromadora	60.78	32.29	120.65	71.24	36.82	0.00	78.91	36.65	38.52	32.24
Metacyatholaimus	0.00	0.00	0.00	0.00	0.00	33.20	0.00	0.00	11.07	15.65
Metalinhomoeus	12.16	0.00	0.00	4.05	5.73	0.00	0.00	0.00	0.00	0.00
Microlaimus	24.31	80.73	135.73	80.26	45.49	166.00	0.00	36.65	67.55	71.21
Monhystera	0.00	16.15	0.00	5.38	7.61	0.00	0.00	0.00	0.00	0.00
Nemanema	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Neochromadora	24.31	16.15	0.00	13.49	10.10	0.00	0.00	0.00	0.00	0.00
Oncholaimellus	48.63	64.58	0.00	37.74	27.47	0.00	0.00	0.00	0.00	0.00
Oncholaimus	0.00	16.15	0.00	5.38	7.61	99.60	39.46	36.65	58.57	29.04
Paracanthonchus	12.16	0.00	0.00	4.05	5.73	33.20	19.73	18.32	23.75	6.71
Paradesmodora	0.00	0.00	0.00	0.00	0.00	166.00	0.00	36.65	67.55	71.21
Ptycholaimellus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhabditis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sigmophoranema	12.16	48.44	0.00	20.20	20.58	132.80	0.00	36.65	56.48	56.00
Sphaerolaimus	0.00	16.15	30.16	15.44	12.32	0.00	0.00	0.00	0.00	0.00
Spilophorella	12.16	64.58	45.24	40.66	21.65	33.20	0.00	0.00	11.07	15.65
Spirinia	48.63	64.58	30.16	47.79	14.06	0.00	0.00	0.00	0.00	0.00
Syringolaimus	0.00	16.15	0.00	5.38	7.61	0.00	0.00	0.00	0.00	0.00
Terschellingia	0.00	0.00	0.00	0.00	0.00	0.00	19.73	0.00	6.58	9.30
Theristus	0.00	80.73	0.00	26.91	38.06	0.00	39.46	18.32	19.26	16.12
Thoracostoma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1A	24.31	0.00	120.65	48.32	52.10	166.00	78.91	54.97	99.96	47.71
1B	12.16	161.46	15.08	62.90	69.70	66.40	39.46	36.65	47.50	13.41
2A	692.93	968.76	1161.29	940.99	192.21	929.61	611.58	494.77	678.65	183.75
2B	279.60	306.78	180.98	255.79	54.05	498.01	197.29	219.90	305.06	136.74
parasitic	0.00	0.00	0.00	0.00	0.00	33.20	0.00	0.00	11.07	15.65
Total	2018.00	2874.00	2956.00	2616.00	424.17	3386.44	1854.48	1612.58	2284.50	785.42

Avicennia
0-2 cm
ind./10 cm²

	period 3 25-9-92 cage					period 3 25-9-92 partial cage				
	A	B	C	mean	std	A	B	C	mean	std
Adoncholaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bathylaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Belondira	0.00	21.92	0.00	7.31	10.34	0.00	12.58	0.00	4.19	5.93
Camacolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chromaspirina	100.58	0.00	0.00	33.53	47.42	158.49	150.91	162.84	157.41	4.93
Daptonema	25.15	0.00	0.00	8.38	11.85	0.00	25.15	0.00	8.38	11.86
Desmodora	1030.98	306.94	286.77	541.56	346.17	566.03	326.97	556.38	483.12	110.49
Diplolaimelloides	0.00	0.00	23.90	7.97	11.27	0.00	0.00	0.00	0.00	0.00
Dorylaimopsis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ethmolaimus	276.60	394.63	645.23	438.82	153.70	226.41	75.45	108.56	136.81	64.78
Eubostrichus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Greeffiella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halalaimus	0.00	0.00	0.00	0.00	0.00	11.32	12.58	0.00	7.97	5.66
Halichoanolaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Haliplectus	50.29	21.92	47.79	40.00	12.82	45.28	0.00	27.14	24.14	18.61
Linhomoeus	0.00	0.00	47.79	15.93	22.53	0.00	50.30	0.00	16.77	23.71
Metachromadora	176.02	43.85	119.49	113.12	54.15	90.56	62.88	122.13	91.86	24.21
Metacyatholaimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Metalinhomoeus	25.15	21.92	0.00	15.69	11.17	0.00	0.00	0.00	0.00	0.00
Microlaimus	176.02	109.62	0.00	95.21	72.58	33.96	264.09	122.13	140.06	94.80
Monhystera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nemanema	25.15	0.00	0.00	8.38	11.85	11.32	0.00	0.00	3.77	5.34
Neochromadora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oncholaimellus	25.15	0.00	0.00	8.38	11.85	0.00	12.58	0.00	4.19	5.93
Oncholaimus	0.00	21.92	71.69	31.21	29.99	11.32	0.00	13.57	8.30	5.94
Paracanthonchus	0.00	65.77	167.28	77.68	68.81	22.64	0.00	13.57	12.07	9.30
Paradesmodora	100.58	0.00	23.90	41.49	42.91	0.00	0.00	13.57	4.52	6.40
Ptycholaimellus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhabditis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sigmophoranema	100.58	0.00	0.00	33.53	47.42	11.32	12.58	13.57	12.49	0.92
Sphaerolaimus	25.15	0.00	23.90	16.35	11.57	0.00	12.58	0.00	4.19	5.93
Spilophorella	100.58	109.62	119.49	109.90	7.72	33.96	88.03	40.71	54.23	24.06
Spirinia	0.00	0.00	0.00	0.00	0.00	11.32	0.00	13.57	8.30	5.94
Syringolaimus	25.15	0.00	95.59	40.25	40.46	0.00	0.00	54.28	18.09	25.59
Terschellingia	50.29	328.86	286.77	221.97	122.61	22.64	37.73	40.71	33.69	7.91
Theristus	25.15	0.00	23.90	16.35	11.57	0.00	12.58	0.00	4.19	5.93
Thoracostoma	0.00	0.00	0.00	0.00	0.00	0.00	37.73	0.00	12.58	17.78
1A	125.73	350.78	334.56	270.36	102.48	90.56	50.30	67.85	69.57	16.48
1B	75.44	21.92	47.79	48.39	21.85	0.00	37.73	0.00	12.58	17.78
2A	1684.77	986.58	1290.46	1320.60	285.83	894.32	842.56	868.50	868.46	21.13
2B	452.62	65.77	310.67	276.35	159.78	271.69	251.51	366.40	296.53	50.08
parasitic	0.00	21.92	0.00	7.31	10.34	0.00	12.58	0.00	4.19	5.93
Total	4677.12	2893.96	3966.96	3846.01	732.98	2513.16	2389.36	2605.50	2502.67	88.55

Avicennia
0-2 cm
ind./10 cm²

period 6
23-12-92
blanco

	A	B	C	mean	std
Adoncholaimus	0.00	0.00	0.00	0.00	0.00
Bathylaimus	0.00	24.17	0.00	8.06	11.39
Belondira	0.00	0.00	0.00	0.00	0.00
Camacolaimus	0.00	0.00	0.00	0.00	0.00
Chromaspirina	154.29	72.52	15.93	80.91	56.79
Daptonema	0.00	24.17	0.00	8.06	11.39
Desmodora	77.14	229.64	77.39	128.06	71.83
Diplolaimelloides	0.00	0.00	6.83	2.28	3.22
Dorylaimopsis	0.00	0.00	0.00	0.00	0.00
Ethmolaimus	0.00	132.95	15.93	49.63	59.27
Eubostrichus	0.00	0.00	0.00	0.00	0.00
Greeffiella	0.00	0.00	0.00	0.00	0.00
Halalaimus	0.00	0.00	0.00	0.00	0.00
Halichoanolaimus	0.00	0.00	0.00	0.00	0.00
Haliplectus	12.86	0.00	2.28	5.04	5.60
Linhomoeus	0.00	0.00	0.00	0.00	0.00
Metachromadora	0.00	84.60	11.38	32.00	37.49
Metacyatholaimus	0.00	0.00	0.00	0.00	0.00
Metalinhomoeus	0.00	0.00	0.00	0.00	0.00
Microlaimus	0.00	48.34	2.28	16.87	22.27
Monhystera	0.00	0.00	4.55	1.52	2.15
Nemanema	0.00	0.00	0.00	0.00	0.00
Neochromadora	0.00	0.00	0.00	0.00	0.00
Oncholaimellus	0.00	0.00	0.00	0.00	0.00
Oncholaimus	0.00	12.09	4.55	5.55	4.98
Paracanthonchus	12.86	0.00	0.00	4.29	6.06
Paradesmodora	0.00	24.17	0.00	8.06	11.39
Ptycholaimellus	0.00	0.00	0.00	0.00	0.00
Rhabditis	0.00	0.00	0.00	0.00	0.00
Sigmophoranema	0.00	0.00	0.00	0.00	0.00
Sphaerolaimus	0.00	12.09	4.55	5.55	4.98
Spilophorella	0.00	0.00	0.00	0.00	0.00
Spirinia	0.00	0.00	4.55	1.52	2.15
Syringolaimus	0.00	24.17	0.00	8.06	11.39
Terschellingia	12.86	12.09	20.49	15.14	3.79
Theristus	0.00	0.00	2.28	0.76	1.07
Thoracostoma	0.00	0.00	0.00	0.00	0.00
1A	25.71	12.09	22.76	20.19	5.85
1B	0.00	48.34	13.66	20.67	20.35
2A	90.00	435.10	100.16	208.42	160.34
2B	154.29	205.47	36.42	132.06	70.78
parasitic	0.00	0.00	0.00	0.00	0.00
Total	540.00	1402.00	346.00	762.67	458.96

period 6
23-12-92
cage

A	B	C	mean	std
13.63	0.00	0.00	4.54	6.43
68.16	93.52	49.16	70.28	18.17
0.00	0.00	0.00	0.00	0.00
0.00	37.41	12.29	16.57	15.57
81.79	205.75	36.87	108.14	71.42
0.00	0.00	0.00	0.00	0.00
163.59	505.02	405.53	358.05	143.38
0.00	0.00	0.00	0.00	0.00
0.00	0.00	24.58	8.19	11.59
95.43	37.41	86.02	72.95	25.42
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
13.63	0.00	12.29	8.64	6.13
0.00	0.00	0.00	0.00	0.00
27.26	0.00	36.87	21.38	15.62
0.00	18.70	12.29	10.33	7.76
81.79	280.57	49.16	137.17	102.27
0.00	0.00	0.00	0.00	0.00
13.63	0.00	0.00	4.54	6.43
40.90	56.11	36.87	44.63	8.29
0.00	0.00	0.00	0.00	0.00
27.26	0.00	0.00	9.09	12.85
13.63	0.00	0.00	4.54	6.43
0.00	0.00	0.00	0.00	0.00
81.79	18.70	24.58	41.69	28.46
0.00	18.70	0.00	6.23	8.82
27.26	0.00	0.00	9.09	12.85
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00
27.26	0.00	0.00	9.09	12.85
54.53	93.52	12.29	53.45	33.17
27.26	74.82	24.58	42.22	23.08
13.63	37.41	12.29	21.11	11.54
0.00	0.00	0.00	0.00	0.00
149.95	93.52	12.29	85.26	56.50
0.00	56.11	0.00	18.70	26.45
0.00	0.00	0.00	0.00	0.00
218.11	93.52	61.44	124.36	67.58
81.79	149.64	49.16	93.53	41.85
381.70	748.18	602.15	577.35	150.64
340.80	598.55	122.89	354.08	194.41
0.00	0.00	0.00	0.00	0.00
2044.83	3217.18	1683.58	2315.19	654.63

Avicennia
0-2 cm
ind./10 cm²

	period end 30-7-93 cage					period end 30-7-93 partial cage				
	A	B	C	mean	std	A	B	C	mean	std
Adoncholaimus	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bathylaimus	99.21	80.24		89.72	9.49	120.27	45.18	56.54	74.00	33.05
Belondira	0.00	0.00		0.00	0.00	0.00	0.00	113.08	37.69	53.30
Camacolaimus	0.00	0.00		0.00	0.00	0.00	90.36	0.00	30.12	42.60
Chromaspirina	248.02	240.71		244.37	3.66	200.45	135.55	339.23	225.08	84.96
Daptonema	0.00	0.00		0.00	0.00	40.09	45.18	0.00	28.42	20.21
Desmodora	694.47	882.61		788.54	94.07	400.91	451.82	621.92	491.55	94.50
Diplolaimelloides	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dorylaimopsis	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ethmolaimus	297.63	240.71		269.17	28.46	240.55	316.27	508.85	355.22	112.94
Eubostrichus	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
Greeffiella	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halalaimus	0.00	240.71		120.36	120.36	40.09	45.18	0.00	28.42	20.21
Halichoanolaimus	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
Haliplectus	198.42	160.48		179.45	18.97	0.00	271.09	0.00	90.36	127.79
Linhomoeus	148.81	80.24		114.53	34.29	0.00	45.18	0.00	15.06	21.30
Metachromadora	347.23	641.90		494.57	147.33	200.45	90.36	169.62	153.48	46.37
Metacyatholaimus	0.00	0.00		0.00	0.00	40.09	0.00	56.54	32.21	23.74
Metalinhomoeus	0.00	80.24		40.12	40.12	40.09	90.36	56.54	62.33	20.93
Microlaimus	992.10	1123.33		1057.71	65.61	320.73	903.64	1017.69	747.35	305.24
Monhystera	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nemanema	0.00	80.24		40.12	40.12	0.00	0.00	0.00	0.00	0.00
Neochromadora	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oncholaimellus	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oncholaimus	0.00	0.00		0.00	0.00	0.00	90.36	0.00	30.12	42.60
Paracanthonchus	0.00	0.00		0.00	0.00	0.00	0.00	56.54	18.85	26.65
Paradesmodora	0.00	160.48		80.24	80.24	80.18	180.73	0.00	86.97	73.94
Ptycholaimellus	0.00	0.00		0.00	0.00	0.00	45.18	0.00	15.06	21.30
Rhabditis	0.00	80.24		40.12	40.12	0.00	0.00	0.00	0.00	0.00
Sigmophoranema	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sphaerolaimus	148.81	0.00		74.41	74.41	40.09	90.36	113.08	81.18	30.50
Spilophorella	496.05	240.71		368.38	127.67	280.64	271.09	395.77	315.83	56.66
Spirinia	0.00	0.00		0.00	0.00	80.18	0.00	226.15	102.11	93.62
Syringolaimus	347.23	401.19		374.21	26.98	240.55	180.73	113.08	178.12	52.07
Terschellingia	0.00	1684.99		842.49	842.49	721.64	0.00	565.38	429.01	309.99
Theristus	0.00	0.00		0.00	0.00	0.00	90.36	0.00	30.12	42.60
Thoracostoma	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
1A	198.42	2246.65		1222.53	1024.12	761.73	316.27	565.38	547.79	182.28
1B	99.21	160.48		129.84	30.63	200.45	271.09	113.08	194.87	64.63
2A	2629.06	2728.08		2678.57	49.51	1443.27	2213.91	2883.46	2180.21	588.44
2B	1091.31	1283.80		1187.55	96.25	681.55	587.36	735.00	667.97	61.03
parasitic	0.00	0.00		0.00	0.00	0.00	0.00	113.08	37.69	53.30
Total	8036.00	12838.00		6958.00	5296.23	6174.00	6867.64	8820.00	7287.21	1120.23

Ceriops blanco 0-2 cm

	period 1 6-8-92					period 2 28-8-92					period 3 27-9-92				
	11.31 am A	11.38 am B	2.30 pm C	mean	std	11.25 am A	9.55 am B	11.10 am C	mean	std	8.58 am A	9.02 am B	10.02 am C	mean	std
Oligochaeta															
Enchytraeidae	0	163	81	81	67	0	0	326	109	154	244	244	0	163	115
Tubificidae	4971	2689	3015	3558	1008	18335	13364	33900	21866	8748	22084	20943	26158	23062	2239
Polychaeta															
Armandia spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Namalycastis spec.	733	407	489	543	139	0	652	326	326	266	81	0	0	27	38
Terebellidae	0	0	407	136	192	326	0	1385	570	591	1304	326	2852	1494	1040
Amphipoda															
Grandidierella spec.	81	244	407	244	133	0	0	81	27	38	163	0	326	163	133
Ampelisca spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	163	326	489	326	133	244	489	326	353	102	407	326	570	435	102
Insecta larvae	0	81	0	27	38	0	0	0	0	0	0	0	0	0	0
Nematoda															
Oncholaimus spec.	815	0	407	407	333	570	244	1059	625	335	244	81	815	380	314
Cnidaria															
Total	12549	7416	9697	9887	2100	38137	28766	73422	46775	19227	48405	43434	60058	50632	6967

Ceriops blanco 0-2 cm

	period 4 29-10-92					period 5 25-11-92					period 6 23-12-92				
	10.29 am A	11.11 am B	12.44 am C	mean	std	11.41 am A	11.22 am B	9.28 am C	mean	std	11.05 am A	10.45 am B	9.15 am C	mean	std
Oligochaeta															
Enchytraeidae	0	163	0	54	77	0	0	326	109	154	0	4726	0	1575	2228
Tubificidae	6764	13446	40989	20400	14813	4075	16054	33329	17819	12008	34633	47672	41315	41207	5323
Polychaeta															
Armandia spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Namalycastis spec.	0	0	163	54	77	0	0	81	27	38	163	81	163	136	38
Terebellidae	407	0	815	407	333	0	163	244	136	102	81	81	81	81	0
Amphipoda															
Grandidierella spec.	0	81	244	109	102	0	163	489	217	203	326	244	0	190	139
Ampelisca spec.	0	0	163	54	77	0	0	0	0	0	0	0	0	0	0
Gastropoda	163	163	81	136	38	81	0	244	109	102	0	0	244	81	115
Insecta larvae	0	0	0	0	0	163	0	0	54	77	0	0	81	27	38
Nematoda															
Oncholaimus spec.	0	0	407	136	192	0	81	81	54	38	163	407	163	244	115
Cnidaria															
Total	14505	27544	85239	42429	30735	8393	32840	69267	36833	25011	70570	106018	83609	86733	14639

Ceriops partial cage 0-2 cm	period 1 6-8-92					period 2 28-8-92					period 3 27-9-92				
	12.08 am A	11.10 am B	2.15 pm C	mean	std	10.55 am A	11.45 am B	8.50 am C	mean	std	8.30 am A	8.42 am B	10.25 am C	mean	std
Oligochaeta															
Enchytraeidae	0	163	0	54	77	0	326	81	136	139	652	81	0	244	290
Tubificidae	1222	244	3667	1711	1439	8556	19069	17928	15184	4710	8068	17357	15320	13582	3987
Polychaeta															
Armandia spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Namalycastis spec.	0	326	244	190	139	244	81	896	407	352	0	163	326	163	133
Terebellidae	0	0	0	0	0	570	0	163	244	240	244	163	407	272	102
Amphipoda															
Grandidierella spec.	163	163	326	217	77	0	0	0	0	0	163	0	81	81	67
Ampelisca spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	0	570	0	190	269	0	326	81	136	139	0	0	81	27	38
Insecta larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nematoda															
Oncholaimus spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cnidaria															
Total	2771	2363	8475	4536	2790	18743	39278	38219	32080	9441	18254	35530	32352	28712	7508

Ceriops partial cage 0-2 cm	period 4 29-10-92					period 5 25-11-92					period 6 23-12-92				
	10.08 am A	10.53 am B	1.07 pm C	mean	std	8.43 am A	12.05 am B	10.30 am C	mean	std	9.23 am A	11.27 am B	10.00 am C	mean	std
Oligochaeta															
Enchytraeidae	407	570	0	326	240	489	163	244	299	139	1548	1141	1059	1250	214
Tubificidae	11490	18987	20128	16868	3831	11979	3586	16787	10784	5455	38626	32026	26566	32406	4931
Polychaeta															
Armandia spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Namalycastis spec.	0	81	163	81	67	163	81	244	163	67	0	81	81	54	38
Terebellidae	0	163	244	136	102	0	81	0	27	38	163	0	0	54	77
Amphipoda															
Grandidierella spec.	0	81	0	27	38	1222	407	81	570	480	407	81	0	163	176
Ampelisca spec.	0	0	0	0	0	0	0	0	0	0	81	0	0	27	38
Gastropoda	733	81	0	272	328	326	244	0	190	139	81	81	81	81	0
Insecta larvae	0	0	0	0	0	0	81	0	27	38	0	0	0	0	0
Nematoda															
Oncholaimus spec.	326	0	81	136	139	0	81	0	27	38	163	570	163	299	192
Cnidaria															
Total	24854	39849	41152	35285	7395	28033	9045	34715	23931	10873	81897	67311	55658	68289	10735

Ceriops
cage
0-2 cm

	period 1 6-8-92					period 2 28-8-92					period 3 27-9-92				
	1.00 pm A	1.21 pm B	1.50 pm C	mean	std	10.30 am A	9.20 am B	8.30 am C	mean	std	9.25 am A	9.48 am B	10.43 am C	mean	std
Oligochaeta															
Enchytraeidae	0	81	0	27	38	407	0	81	163	176	489	407	0	299	214
Tubificidae	1467	2037	163	1222	784	16461	11164	6030	11218	4258	35285	38463	18172	30640	8911
Polychaeta															
Armandia spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Namalycastis spec.	163	163	81	136	38	489	407	244	380	102	407	489	326	407	67
Terebellidae	0	0	0	0	0	244	0	0	81	115	326	163	81	190	102
Amphipoda															
Grandidierella spec.	326	896	1548	924	499	326	1222	407	652	405	244	163	81	163	67
Ampelisca spec.	0	81	81	54	38	0	0	0	0	0	0	0	0	0	0
Gastropoda	570	815	0	462	341	489	81	163	244	176	326	244	0	190	139
Insecta larvae	0	81	0	27	38	0	0	0	0	0	0	0	0	0	0
Nematoda															
Oncholaimus spec.	0	81	0	27	38	81	0	0	27	38	0	163	163	109	77
Cnidaria															
Total	4482	7497	3749	5243	1622	36426	25669	13690	25262	9286	73830	79779	37485	63698	18694

Ceriops
cage
0-2 cm

	period 4 29-10-92					period 5 25-11-92					period 6 23-12-92				
	12.11 am A	11.48 am B	1.30 pm C	mean	std	9.09 am A	11.05 am B	9.57 am C	mean	std	8.50 am A	9.30 am B	10.25 am C	mean	std
Oligochaeta															
Enchytraeidae	0	733	244	326	305	570	652	978	733	176	1467	896	733	1032	314
Tubificidae	45308	47835	47753	46965	1172	44901	48161	52480	48514	3104	35448	29907	44982	36779	6226
Polychaeta															
Armandia spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Namalycastis spec.	652	163	407	407	200	163	244	163	190	38	244	896	326	489	290
Terebellidae	0	0	0	0	0	0	0	0	0	0	81	0	244	109	102
Amphipoda															
Grandidierella spec.	0	0	0	0	0	81	0	81	54	38	0	0	0	0	0
Ampelisca spec.	81	0	0	27	38	0	0	0	0	0	0	0	0	0	0
Gastropoda	244	0	0	81	115	489	815	1059	788	234	163	163	0	109	77
Insecta larvae	81	0	0	27	38	81	81	0	54	38	0	0	163	54	77
Nematoda															
Oncholaimus spec.	0	407	0	136	192	163	163	81	136	38	244	326	489	353	102
Cnidaria															
Total	92410	97869	96810	95696	2364	92165	99173	108545	99961	6710	74889	63888	93225	77334	12101

Avicennia
blanco
0-2 cm

ind./m²	period 1 6-8-92					period 2 28-8-92					period 3 25-9-92				
	2.00 pm A	2.40 pm B	3.45 pm C	mean	std	11.40 am A	12.25 am B	2.35 pm C	mean	std	11.30 am A	12.25 am B	12.35 am C	mean	std
Oligochaeta	20244	11301	16911	16152	3690	2276	81	0	786	1054	12683	8943	2520	8049	4197
Polychaeta															
Armandia spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Namalycastis spec.	1382	1707	569	1220	479	0	81	0	27	38	325	325	0	217	153
Terebellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda															
Grandidierella spec.	1707	650	0	786	704	1138	0	0	379	537	6016	1220	0	2412	2597
Ampelisca spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	163	325	894	461	314	0	0	0	0	0	0	0	650	217	307
Insecta larvae	0	81	163	81	66	0	81	0	27	38	0	81	163	81	66
Nematoda															
Oncholaimus spec.	325	0	81	136	138	0	0	81	27	38	0	0	0	0	0
Cnidaria	0	0	0	0	0	0	0	0	0	0	81	0	0	27	38
Total	23821	14065	18618	18835	3986	3415	244	81	1247	1534	19106	10569	3333	11003	6446
Amphipod length (mm)	4	3		3	0	3			3	0	4	4		4	0

Avicennia
blanco
0-2 cm

ind./m²	period 4 30-10-92					period 5 26-11-92					period 6 23-12-92				
	10.17 am A	10.47 am B	11.52 am C	mean	std	9.10 am A	9.54 am B	11.07 am C	mean	std	10.35 am A	9.50 am B	8.35 am C	mean	std
Oligochaeta	813	45122	30894	25610	18471	41951	40813	29919	37561	5424	63089	35285	30244	42873	14443
Polychaeta															
Armandia spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Namalycastis spec.	0	325	0	108	153	244	407	163	271	101	81	0	81	54	38
Terebellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda															
Grandidierella spec.	0	488	81	190	213	1951	244	0	732	868	813	1057	0	623	452
Ampelisca spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	0	0	0	0	0	81	81	244	136	77	81	244	163	163	66
Insecta larvae	0	0	81	27	38	81	81	244	136	77	244	0	81	108	101
Nematoda															
Oncholaimus spec.	0	0	407	136	192	407	81	163	217	138	244	81	81	136	77
Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	813	45935	31463	26070	18812	44715	41707	30732	39051	6010	64553	36667	30650	43957	14769
Amphipod length (mm)		5	6	6	0	4	3		4	0	3	5		4	1

Avicennia
partial cage
0-2 cm

ind./m²	period 1 6-8-92 1.40 pm A	2.30 pm B	4.00 pm C	mean	std	period 2 28-8-92 11.30 am A	12.00 am B	2.50 pm C	mean	std	period 3 25-9-92 11.20 am A	11.45 am B	2.20 pm C	mean	std
Oligochaeta	38699	18862	24472	27344	8349	5772	5366	2846	4661	1295	3902	13008	8455	8455	3717
Polychaeta															
Armandia spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Namalycastis spec.	3415	813	325	1518	1356	81	81	569	244	230	325	244	285	285	33
Terebellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda															
Grandidierella spec.	2358	569	2520	1816	884	244	894	650	596	268	813	1220	1016	1016	166
Ampelisca spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	81	325	81	163	115	81	81	81	81	0	0	0	0	0	0
Insecta larvae	163	244	163	190	38	0	0	0	0	0	81	0	41	41	33
Nematoda															
Oncholaimus spec.	407	244	0	217	167	81	0	0	27	38	0	0	0	0	0
Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	45122	21057	27561	31247	10164	6260	6423	4146	5610	1037	5122	14472	9797	9797	3817
Amphipod length (mm)	4	3	3	3	0	3	5	4	4	1	6	3	5	4	1

Avicennia
partial cage
0-2 cm

ind./m²	period 4 30-10-92 10.00 am A	10.30 am B	12.13 pm C	mean	std	period 5 26-11-92 8.43 am A	9.30 am B	11.28 am C	mean	std	period 6 23-12-92 7.45 am A	10.10 am B	9.08 am C	mean	std
Oligochaeta	60569	46585	72114	59756	10438	38699	87480	47642	57940	21204	41382	18943	52683	37669	14022
Polychaeta															
Armandia spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Namalycastis spec.	325	407	81	271	138	163	1463	0	542	655	325	1057	0	461	442
Terebellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda															
Grandidierella spec.	650	0	0	217	307	81	407	81	190	153	163	0	0	54	77
Ampelisca spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	81	0	81	54	38	0	0	163	54	77	0	0	81	27	38
Insecta larvae	0	0	0	0	0	81	0	0	27	38	407	0	0	136	192
Nematoda															
Oncholaimus spec.	569	407	244	407	133	81	976	81	379	422	163	569	163	298	192
Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	62195	47398	72520	60705	10310	39106	90325	47967	59133	22351	42439	20569	52927	38645	13480
Amphipod length (mm)	4			4	0	4	3	4	3	0	3			3	0

Avicennia
cage
0-2 cm

ind./m²	period 1 6-8-92 3.30 pm A	3.15 pm B	4.20 pm C	mean	std	period 2 28-8-92 2.00 pm A	0.35 pm B	3.05 pm C	mean	std	period 3 25-9-92 12.00 am A	12.15 am B	2.30 pm C	mean	std
Oligochaeta	19593	23821	8130	17182	6629	11382	5203	8293	8293	2523	17073	11545		14309	2764
Polychaeta															
Armandia spec.	0	0	0	0	0	0	0	0	0	0	0	0		0	0
Namalycastis spec.	1707	2439	1382	1843	442	81	0	81	54	38	163	163		163	0
Terebellidae	0	0	0	0	0	0	0	0	0	0	0	0		0	0
Amphipoda															
Grandidierella spec.	2764	4878	0	2547	1997	163	1545	813	840	565	0	2358		1179	1179
Ampelisca spec.	0	0	0	0	0	0	0	0	0	0	0	0		0	0
Gastropoda	163	325	0	163	133	0	0	0	0	0	244	0		122	122
Insecta larvae	325	163	163	217	77	163	0	81	81	66	81	163		122	41
Nematoda															
Oncholaimus spec.	244	407	0	217	167	81	0	0	27	38	0	163		81	81
Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0		0	0
Total	24797	32033	9675	22168	9315	11870	6748	9268	9295	2091	17561	14390		15976	1585
Amphipod length (mm)	3	3		3	0	2	4	3	3	1		5		5	0

Avicennia
cage
0-2 cm

ind./m²	period 4 30-10-92 11.39 am A	11.20 am B	12.27 am C	mean	std	period 5 26-11-92 10.36 am A	10.15 am B	11.48 am C	mean	std	period 6 23-12-92 8.10 am A	10.50 am B	9.30 am C	mean	std
Oligochaeta	48618	63171	47073	52954	7252	72114	44553	102358	73008	23607	58780	98862	40894	66179	24236
Polychaeta															
Armandia spec.	0	0	0	0	0	163	0	0	54	77	0	0	0	0	0
Namalycastis spec.	813	244	1057	705	341	650	813	1138	867	203	1057	325	813	732	304
Terebellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda															
Grandidierella spec.	1951	1707	0	1220	868	3252	1870	1382	2168	792	4065	732	1382	2060	1443
Ampelisca spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	244	325	2033	867	825	325	1138	813	759	334	325	1626	2846	1599	1029
Insecta larvae	163	81	1626	623	710	569	2846	244	1220	1157	650	407	732	596	138
Nematoda															
Oncholaimus spec.	0	244	0	81	115	325	488	244	352	101	650	732	163	515	251
Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	51789	65772	51789	56450	6592	77398	51707	106179	78428	22250	65528	102683	46829	71680	23213
Amphipod length (mm)	6	5		6	1	6	5	5	5	0	5	5	5	5	0

Avicennia blanco 0-2 cm — period 1

	A	B	avg	std
Tubificidae	15547	10532	13040	2508
Enchytraeidae	4696	768	2732	1964

Avicennia partial cage 0-2 cm — period 1

	A	B	avg	std
Tubificidae	36648	15485	26067	10582
Enchytraeidae	2051	3376	2714	663

Avicennia cage 0-2 cm — period 1

	A	B	avg	std
Tubificidae	19593	21248	20421	828
Enchytraeidae	0	2572	1286	1286

Avicennia blanco 0-2 cm — period 2

	A	B	avg	std
Tubificidae	758	0	379	379
Enchytraeidae	1518	81	800	719

Avicennia partial cage 0-2 cm — period 2

	A	B	avg	std
Tubificidae	2840	2725	2783	58
Enchytraeidae	2932	2640	2786	146

Avicennia cage 0-2 cm — period 2

	A	B	avg	std
Tubificidae	11262	2232	6747	4515
Enchytraeidae	125	2971	1548	1423

Avicennia blanco 0-2 cm — period 5

	A	B	avg	std
Tubificidae	36329	27525	31927	4402
Enchytraeidae	5621	13287	9454	3833

Avicennia partial cage 0-2 cm — period 5

	A	B	avg	std
Tubificidae	38699	59223	48961	10262
Enchytraeidae	0	28255	14128	14128

Avicennia cage 0-2 cm — period 5

	A	B	avg	std
Tubificidae	62522	41879	52201	10322
Enchytraeidae	9591	2673	6132	3459

HIGH WATER — KILINDINI

		Time a.m.	Ht. m.	Time p.m.	Ht. m.	
Wed.	1	0443	3.0	1656	3.7	Sp.
Thu.	2	0526	3.2	1739	3.7	
Fri.	3	0609	3.2	1822	3.6	
Sat.	4	0652	3.3	1905	3.4	
Sun.	5	0737	3.3	1951	3.2	
Mon.	6	0825	3.2	2040	2.9	
Tue.	7	0919	3.1	2137	2.6	
Wed.	8	1023	2.9	2249	2.4	
Thu.	9	1138	2.9	–	–	Np.
Fri.	10	0018	2.3	1257	2.9	
Sat.	11	0142	2.3	1405	3.0	
Sun.	12	0246	2.4	1458	3.1	
Mon.	13	0334	2.6	1542	3.2	
Tue.	14	0413	2.7	1619	3.2	
Wed.	15	0447	2.8	1652	3.3	
Thu.	16	0519	2.9	1723	3.3	Sp.
Fri.	17	0548	3.0	1752	3.3	
Sat.	18	0617	3.0	1820	3.2	
Sun.	19	0646	3.0	1849	3.1	
Mon.	20	0717	3.0	1920	3.0	
Tue.	21	0751	2.9	1954	2.8	
Wed.	22	0830	2.9	2034	2.6	
Thu.	23	0919	2.8	2126	2.3	
Fri.	24	1024	2.7	2243	2.1	Np.
Sat.	25	1151	2.7	–	–	
Sun.	26	0032	2.1	1319	2.9	
Mon.	27	0202	2.3	1425	3.1	
Tue.	28	0302	2.5	1518	3.4	
Wed.	29	0349	2.8	1604	3.6	
Thu.	30	0432	3.1	1647	3.7	
Fri.	31	0513	3.3	1728	3.7	Sp.

LOW WATER — JULY, 1992

		Time a.m.	Ht. m.	Time p.m.	Ht. m.	
Wed.	1	1030	0.5	2316	0.2	
Thu.	2	1116	0.4	2356	0.2	
Fri.	3	1201	0.4	–	–	
Sat.	4	0036	0.2	1248	0.5	
Sun.	5	0118	0.3	1337	0.6	
Mon.	6	0201	0.5	1431	0.8	
Tue.	7	0247	0.7	1533	1.0	
Wed.	8	0340	0.9	1649	1.1	
Thu.	9	0446	1.1	1820	1.2	
Fri.	10	0605	1.2	1941	1.1	
Sat.	11	0723	1.1	2042	0.9	
Sun.	12	0825	1.0	2128	0.7	
Mon.	13	0915	0.9	2206	0.6	
Tue.	14	0956	0.8	2239	0.5	○
Wed.	15	1033	0.7	2310	0.5	
Thu.	16	1106	0.7	2338	0.4	
Fri.	17	1138	0.6	–	–	
Sat.	18	0006	0.4	1209	0.7	
Sun.	19	0034	0.5	1241	0.7	
Mon.	20	0102	0.5	1315	0.8	
Tue.	21	0131	0.6	1352	0.9	
Wed.	22	0204	0.8	1437	1.1	
Thu.	23	0243	0.9	1535	1.2	
Fri.	24	0333	1.0	1658	1.3	
Sat.	25	0446	1.2	1843	1.2	
Sun.	26	0620	1.2	2003	1.0	
Mon.	27	0743	1.0	2059	0.7	
Tue.	28	0846	0.8	2143	0.4	
Wed.	29	0937	0.5	2223	0.2	●
Thu.	30	1024	0.3	2301	0.1	
Fri.	31	1108	0.2	2338	0.0	

HIGH WATER — KILINDINI

		Time a.m.	Ht. m.	Time p.m.	Ht. m.	
Sat.	1	0552	3.5	1807	3.7	
Sun.	2	0632	3.5	1847	3.5	
Mon.	3	0712	3.5	1926	3.2	
Tue.	4	0754	3.3	2008	2.9	
Wed.	5	0840	3.1	2054	2.6	
Thu.	6	0935	2.9	2155	2.2	
Fri.	7	1050	2.7	2335	2.0	Np.
Sat.	8	1231	2.6	–	–	
Sun.	9	0130	2.1	1355	2.7	
Mon.	10	0240	2.3	1451	2.9	
Tue.	11	0325	2.5	1533	3.0	
Wed.	12	0400	2.7	1606	3.1	
Thu.	13	0430	2.9	1636	3.2	
Fri.	14	0457	3.0	1703	3.3	
Sat.	15	0524	3.1	1730	3.3	Sp.
Sun.	16	0550	3.2	1756	3.3	
Mon.	17	0616	3.2	1822	3.2	
Tue.	18	0644	3.2	1851	3.0	
Wed.	19	0715	3.1	1922	2.8	
Thu.	20	0750	3.0	1957	2.6	
Fri.	21	0834	2.9	2043	2.3	
Sat.	22	0935	2.7	2157	2.1	
Sun.	23	1111	2.6	–	–	Np.
Mon.	24	0007	2.0	1300	2.7	
Tue.	25	0150	2.3	1412	3.0	
Wed.	26	0248	2.6	1505	3.3	
Thu.	27	0333	3.0	1550	3.5	
Fri.	28	0413	3.3	1631	3.7	
Sat.	29	0452	3.6	1709	3.7	
Sun.	30	0530	3.7	1747	3.6	
Mon.	31	0607	3.7	1824	3.4	Sp.

AUGUST 1992 — LOW WATER

		Time a.m.	Ht. m.	Time p.m.	Ht. m.	
Sat	1	1150	0.1	–	–	
Sun.	2	0015	0.0	1233	0.2	
Mon	3	0053	0.1	1317	0.4	
Tue	4	0130	0.3	1403	0.6	
Wed.	5	0210	0.5	1454	0.9	
Thu.	6	0254	0.8	1601	1.1	
Fri.	7	0351	1.1	1740	1.3	
Sat.	8	0521	1.3	1927	1.2	
Sun.	9	0707	1.3	2034	1.0	
Mon.	10	0820	1.1	2118	0.8	
Tue	11	0909	0.9	2152	0.7	
Wed	12	0947	0.8	2221	0.5	
Thu.	13	1020	0.6	2248	0.4	○
Fri.	14	1050	0.5	2314	0.4	
Sat.	15	1118	0.5	2338	0.3	
Sun.	16	1146	0.5	–	–	
Mon.	17	0003	0.3	1216	0.5	
Tue.	18	0029	0.4	1247	0.6	
Wed.	19	0056	0.5	1321	0.7	
Thu	20	0125	0.6	1401	0.9	
Fri.	21	0200	0.8	1453	1.1	
Sat.	22	0245	1.0	1611	1.3	
Sun.	23	0358	1.2	1813	1.3	
Mon.	24	0554	1.2	1945	1.0	
Tue.	25	0734	1.0	2041	0.7	
Wed.	26	0838	0.7	2124	0.4	
Thu	27	0928	0.4	2202	0.2	
Fri.	28	1012	0.2	2238	0.0	●
Sat.	29	1054	0.0	2313	0.0	
Sun.	30	1134	0.0	2348	0.0	
Mon.	31	1214	0.1	–	–	

HIGH WATER						KILINDINI	SEPTEMBER, 1992						LOW WATER	
		Time a.m.	Ht. m.	Time p.m.	Ht. m.				Time a.m.	Ht. m.	Time p.m.	Ht. m.	
Tue.	1	0644	3.6	1901	3.2		Tue.	1	0023	0.1	1254	0.3	
Wed.	2	0723	3.4	1938	2.8		Wed.	2	0059	0.3	1335	0.5	
Thu.	3	0804	3.2	2020	2.5		Thu.	3	0135	0.6	1421	0.8	
Fri.	4	0851	2.8	2113	2.2		Fri.	4	0215	0.9	1519	1.1	
Sat.	5	0959	2.6	2257	2.0	Np.	Sat.	5	0306	1.2	1654	1.4	
Sun.	6	1157	2.4	–	–		Sun.	6	0440	1.4	1859	1.3	
Mon.	7	0114	2.1	1335	2.5		Mon.	7	0654	1.4	2009	1.1	
Tue.	8	0221	2.3	1431	2.7		Tue.	8	0808	1.2	2051	0.9	
Wed.	9	0302	2.6	1510	2.9		Wed.	9	0854	1.0	2123	0.7	
Thu.	10	0334	2.8	1542	3.0		Thu.	10	0929	0.8	2151	0.6	
Fri.	11	0401	3.0	1610	3.2		Fri.	11	0959	0.6	2217	0.5	
Sat.	12	0428	3.2	1637	3.2		Sat.	12	1027	0.5	2241	0.4	○
Sun.	13	0454	3.3	1704	3.3	Sp.	Sun.	13	1055	0.4	2308	0.3	
Mon.	14	0520	3.4	1730	3.2		Mon.	14	1123	0.3	2330	0.3	
Tue.	15	0547	3.4	1758	3.1		Tue.	15	1153	0.4	2358	0.4	
Wed.	16	0615	3.4	1827	3.0		Wed.	16	1224	0.4	–	–	
Thu.	17	0646	3.3	1859	2.8		Thu.	17	0023	0.5	1259	0.6	
Fri.	18	0721	3.2	1936	2.6		Fri.	18	0054	0.6	1339	0.8	
Sat.	19	0805	3.0	2025	2.3		Sat.	19	0131	0.8	1430	1.0	
Sun.	20	0906	2.7	2145	2.1		Sun.	20	0219	1.0	1546	1.2	
Mon.	21	1043	2.6	2357	2.2	Np.	Mon.	21	0339	1.3	1743	1.3	
Tue.	22	1237	2.7	–	–		Tue.	22	0547	1.3	1915	1.0	
Wed.	23	0130	2.5	1352	2.9		Wed.	23	0724	1.1	2011	0.8	
Thu.	24	0226	2.9	1445	3.2		Thu.	24	0826	0.7	2054	0.5	
Fri.	25	0310	3.2	1530	3.4		Fri.	25	0914	0.4	2133	0.3	
Sat.	26	0350	3.5	1610	3.5		Sat.	26	0957	0.2	2210	0.1	●
Sun.	27	0428	3.8	1648	3.5		Sun.	27	1037	0.0	2245	0.1	
Mon.	28	0505	3.9	1726	3.4	Sp.	Mon.	28	1116	0.0	2320	0.1	
Tue.	29	0542	3.8	1802	3.3		Tue.	29	1154	0.1	2355	0.2	
Wed.	30	0618	3.7	1838	3.0		Wed.	30	1232	0.3	–	–	

HIGH WATER						KILINDINI	OCTOBER, 1992						LOW WATER	
		Time a.m.	Ht. m.	Time p.m.	Ht. m.				Time a.m.	Ht. m.	Time p.m.	Ht. m.	
Thu.	1	0654	3.5	1915	2.8		Thu.	1	0029	0.4	1312	0.5	
Fri.	2	0732	3.2	1958	2.5		Fri.	2	0106	0.7	1354	0.8	
Sat.	3	0814	2.8	2048	2.3		Sat.	3	0145	1.0	1446	1.1	
Sun.	4	0912	2.5	2223	2.1		Sun.	4	0235	1.3	1802	1.3	
Mon.	5	1058	2.3	–	–	Np.	Mon.	5	0403	1.5	1756	1.4	
Tue.	6	0032	2.2	1249	2.4		Tue.	6	0620	1.5	1918	1.2	
Wed.	7	0142	2.4	1352	2.5		Wed.	7	0738	1.3	2005	1.0	
Thu.	8	0224	2.7	1434	2.7		Thu.	8	0825	1.1	2040	0.9	
Fri.	9	0257	2.9	1508	2.9		Fri.	9	0901	0.9	2111	0.7	
Sat.	10	0327	3.1	1539	3.0		Sat.	10	0933	0.7	2139	0.6	
Sun.	11	0356	3.3	1608	3.1		Sun.	11	1003	0.5	2206	0.5	○
Mon.	12	0423	3.4	1639	3.1		Mon.	12	1033	0.4	2233	0.4	
Tue.	13	0451	3.5	1707	3.1		Tue.	13	1103	0.3	2300	0.4	
Wed.	14	0520	3.6	1738	3.0	Sp.	Wed.	14	1134	0.3	2329	0.4	
Thu.	15	0552	3.5	1811	2.9		Thu.	15	1208	0.4	–	–	
Fri.	16	0625	3.4	1847	2.8		Fri.	16	0000	0.5	1245	0.5	
Sat.	17	0704	3.3	1928	2.6		Sat.	17	0036	0.7	1328	0.7	
Sun.	18	0750	3.0	2025	2.4		Sun.	18	0110	0.9	1420	0.9	
Mon.	19	0851	2.8	2148	2.3		Mon.	19	0214	1.1	1531	1.1	
Tue.	20	1022	2.6	2338	2.4		Tue.	20	0340	1.3	1705	1.1	
Wed.	21	1206	2.6	–	–	Np.	Wed.	21	0536	1.3	1831	1.0	
Thu.	22	0059	2.7	1323	2.8		Thu.	22	0707	1.0	1932	0.8	
Fri.	23	0157	3.0	1420	3.0		Fri.	23	0809	0.7	2021	0.6	
Sat.	24	0244	3.4	1507	3.1		Sat.	24	0858	0.4	2103	0.4	
Sun.	25	0328	3.6	1550	3.2		Sun.	25	0941	0.2	2142	0.3	●
Mon.	26	0405	3.8	1628	3.2		Mon.	26	1022	0.1	2220	0.2	
Tue.	27	0443	3.8	1707	3.2	Sp.	Tue.	27	1100	0.1	2258	0.3	
Wed.	28	0520	3.8	1744	3.1		Wed.	28	1138	0.2	2332	0.4	
Thu.	29	0558	3.6	1821	2.9		Thu.	29	1215	0.3	–	–	
Fri.	30	0631	3.4	1858	2.7		Fri.	30	0007	0.5	1253	0.5	
Sat.	31	0707	32.	1940	2.6		Sat.	31	0046	0.8	1333	0.7	

HIGH WATER — KILINDINI — NOVEMBER, 1992 — LOW WATER

		HIGH WATER Time a.m.	Ht. m.	Time p.m.	Ht. m.		LOW WATER Time a.m.	Ht. m.	Time p.m.	Ht. m.	
Sun.	1	0746	2.9	2029	2.4		0125	1.0	1417	1.0	
Mon.	2	0833	2.6	2140	2.3		0214	1.3	1513	1.2	
Tue.	3	0942	2.4	2316	2.3	Np.	0325	1.5	1630	1.3	
Wed.	4	1123	2.3	–	–		0511	1.5	1755	1.3	
Thu.	5	0038	2.5	1248	2.4		0645	1.4	1900	1.1	
Fri.	6	0132	2.7	1345	2.5		0744	1.2	1947	1.0	
Sat.	7	0213	2.9	1429	2.6		0828	1.0	2025	0.8	
Sun.	8	0249	3.1	1506	2.7		0905	0.7	2100	0.7	
Mon.	9	0322	3.3	1541	2.8		0939	0.5	2132	0.6	
Tue.	10	0354	3.4	1616	2.9		1013	0.4	2204	0.5	○
Wed.	11	0427	3.6	1650	2.9	Sp.	1047	0.3	2237	0.5	
Thu.	12	0501	3.6	1726	2.9		1122	0.3	2312	0.5	
Fri.	13	0537	3.6	1803	2.9		1158	0.3	2349	0.5	
Sat.	14	0615	3.5	1844	2.8		1237	0.4	–	–	
Sun.	15	0656	3.3	1930	2.7		0030	0.7	1321	0.6	
Mon.	16	0743	3.1	2026	2.6		0118	0.8	1410	0.7	
Tue.	17	0841	2.9	2136	2.6		0216	1.0	1509	0.9	
Wed.	18	0956	2.6	2300	2.6		0334	1.2	1622	1.0	
Thu.	19	1126	2.5	–	–	Np.	0511	1.2	1741	1.0	
Fri.	20	0021	2.8	1250	2.6		0642	1.0	1850	0.9	
Sat.	21	0126	3.1	1355	2.7		0750	0.8	1948	0.7	
Sun.	22	0219	3.3	1448	2.8		0844	0.6	2037	0.6	
Mon.	23	0305	3.5	1534	2.9		0929	0.4	2120	0.5	
Tue.	24	0348	3.6	1616	2.9		1010	0.2	2201	0.4	●
Wed.	25	0427	3.6	1655	2.9	Np.	1049	0.2	2240	0.4	
Thu.	26	0504	3.6	1732	2.9		1125	0.2	2317	0.5	
Fri.	17	0539	3.5	1809	2.9		1200	0.3	2353	0.5	
Sat.	28	0614	3.3	1845	2.8		1235	0.4	–	–	
Sun.	29	0647	3.1	1922	2.7		0030	0.7	1310	0.6	
Mon.	30	0722	2.9	2003	2.6		0109	0.9	1347	0.7	

HIGH WATER — KILINDINI — DECEMBER, 1992 — LOW WATER

		HIGH WATER Time a.m.	Ht. m.	Time p.m.	Ht. m.		LOW WATER Time a.m.	Ht. m.	Time p.m.	Ht. m.	
Tue.	1	0800	2.7	2052	2.5		0151	1.1	1428	0.9	
Wed.	2	0847	2.5	2153	2.4		0243	1.3	1516	1.1	
Thu.	3	0949	2.3	2308	2.5	Np.	0353	1.4	1619	1.2	
Fri.	4	1115	2.2	–	–		0523	1.4	1732	1.2	
Sat.	5	0022	2.6	1241	2.2		0648	1.3	1841	1.1	
Sun.	6	0122	2.8	1346	2.3		0750	1.1	1937	1.0	
Mon.	7	0210	3.0	1437	2.5		0839	0.8	2024	0.9	
Tue.	8	0252	3.2	1520	2.6		0920	0.6	2105	0.7	
Wed.	9	0332	3.4	1600	2.7		0958	0.4	2145	0.5	○
Thu.	10	0411	3.5	1639	2.9		1035	0.2	2224	0.4	
Fri.	11	0449	3.6	1718	2.9		1112	0.2	2304	0.4	
Sat.	12	0528	3.6	1757	3.0	Sp.	1149	0.1	2345	0.4	
Sun.	13	0608	3.6	1839	3.0		1227	0.2	–	–	
Mon.	14	0649	3.4	1923	3.0		0028	0.5	1308	0.3	
Tue.	15	0734	3.2	2012	2.9		0116	0.6	1351	0.5	
Wed.	16	0824	2.9	2109	2.8		0209	0.8	1440	0.6	
Thu.	17	0925	2.6	2218	2.8		0314	1.0	1537	0.8	
Fri.	18	1043	2.4	2338	2.8		0437	1.1	1647	1.0	
Sat.	19	1214	2.3	–	–	Np.	0612	1.1	1807	1.0	
Sun.	20	0055	2.9	1336	2.3		0734	0.9	1920	0.8	
Mon.	21	0200	3.1	1438	2.5		0835	0.7	2020	0.6	
Tue.	22	0252	3.2	1528	2.6		0923	0.5	2110	0.5	
Wed.	23	0337	3.4	1610	2.7		1003	0.3	2153	0.6	
Thu.	24	0417	3.4	1648	2.8		1040	0.3	2231	0.5	●
Fri.	25	0453	3.4	1722	2.9	Sp.	1113	0.2	2307	0.5	
Sat.	26	0528	3.4	1755	2.9		1144	0.2	2342	0.5	
Sun.	27	0557	3.3	1826	2.9		1214	0.3	–	–	
Mon.	28	0627	3.2	1857	2.9		0015	0.6	1244	0.4	
Tue.	29	0657	3.0	1929	2.8		0049	0.7	1313	0.5	
Wed.	30	0728	2.8	2005	2.7		0124	0.9	1345	0.7	
Thu.	31	0803	2.6	2048	2.6		0204	1.0	1415	0.8	