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Re-establishment of epibiotic communities in reforested mangroves of Gazi Bay, Kenya

B. I. Crona · S. Holmgren · P. Rönnbäck

Abstract Recolonization of epibiotic flora and fauna in two fringing *Sonneratia alba* reforestation plots was investigated and compared to a natural mangrove stand and a denuded site in Gazi Bay, Kenya. The reforested sites differed with respect to land history and planting density. Habitat availability in the form of pneumatophore surface differed among forested sites ($P<0.001$), and between landward and seaward zones ($P<0.05$). Eighteen algal species were found in the natural area compared to 23 and 10 in replanted sites. Only one species was encountered in the denuded area. SIMPER analysis distinguished *Enteromorpha ramulosa, Polysiphonia* sp., *Hypnea* sp. and *Caloglossa leprieuri* as the main algal species responsible for differences between sites. Algal biomass was positively correlated to pneumatophores area ($P<0.001$). Total algal biomass differed markedly between forested sites: 1.4 (matrix replantation), 28.6 (natural stand) and 44.3 g m^{-2} (integrated replantation) in the seaward zones. The matrix replantation showed strong differences in algal community assemblages compared to the other forested sites, and this site also had significantly lower biomass of sessile benthic fauna ($P<0.001$). Statistical differences in algal ($P<0.01$) and sponge ($P<0.05$) community composition between landward and seaward zones were observed in all sites and trunk fouling fauna was distinctly different between sites. Reasons for the above patterns are discussed and it is suggested that zonation patterns affecting pneumatophore surface and inundation time, in combination with proximity of sites to natural seeding areas, are the most likely explanations for observed patterns of epibiotic community distribution in this study.

Keywords *Sonneratia alba* · Algae · Epibiotic communities · Recolonization · Replanted mangroves · Sponges

Introduction

In response to the increasing decimation of mangroves forests several re- and afforestation programs have been initiated world wide (Imbert et al. 2000; Kairo et al. 2001) and the need for mangrove rehabilitation has become recognized as a high priority in local coastal management plans for many developing countries (Lindén and Lundin 1996). Earlier mangrove restoration goals have ranged from supply of quality wood for logging to shore-line stabilization, often overlooking the role of mangroves as habitats for a diverse flora and fauna (Field 1996). Still today the majority of rehabilitation programs focus mainly on structural aspects of reforestation (Ellison 2000),

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thus neglecting important issues such as the recolonization of associated flora and fauna, which is essential if the ecological functions of a replanted mangrove forest are to be restored.

The role of epibiotic communities of both flora and fauna in mangroves has received only limited scientific attention to date. Ellison and Farnsworth (1990; 1992) and Ellison et al. (1996) demonstrated the role of root fouling communities, both directly and indirectly, on the growth of mangrove roots. The fouling community effectively prevents isopod colonization which can otherwise reduce root growth by more than 50% and facultative mutualism has been reported to occur between massive sponges and mangroves thus potentially enhancing mangrove productivity (Ellison et al. 1996). Proches et al. (2001) also showed that pneumatophores and their associated epibiota provide a unique structural feature to the physical environment of mudflats resulting in increased microhabitat complexity and giving rise to arthropod assemblages distinctly different from those of surrounding sediments.

Sponges and filamentous algae may constitute food for fish foraging in the mangroves at high tide. Several species of angelfish of the genus *Pomacanthus*, butterflyfish (*Chaetodon*) and some filefish (*Cantherines*) have a large sponge component in their diet (Randall and Hartman 1968). Although adults of these species are mainly reef-associated, some have been documented to enter mangroves (de Troch et al. 1998). Many juveniles of reef-bound species, such as Tetradontidae, Ostraciidae and Chaetodontidae occur in mangroves and are known to feed on filamentous algae and benthic invertebrates (Randall and Hartman 1968; Dunlap and Pawlik 1996; de Troch et al. 1998).

Substrate availability as a limiting resource is a factor affecting most epibiotic communities (Osman 1977) in combination with variable complexity in habitat structure attributable to absolute abundance of individual structural components such as pneumatophores (Beck 2000). Since little information has been published on the return of ecosystem functions in rehabilitated mangroves the objective of this study was to investigate recolonization of the epibiotic flora and fauna on pneumatophores and tree trunks in replanted mangroves, *Sonneratia alba*, in Gazi Bay, Kenya, and compare the findings with epibiotic communities in adjacent natural mangroves and a denuded stand (currently a sandflat). This is valuable

baseline information needed as the interest for mangrove rehabilitation increases world wide.

Methods

Study area

Gazi Bay is located on the southern Kenyan coast at 4°25′ S and 39°50′ E. The inner estuary is sheltered from intense wave impact by shallow reefs at the mouth of the bay (Fig. 1). Seasonal monsoons dominate the climate with two pronounced rainy seasons; a period of heavy rains from April–June (SE monsoon) and a period of lighter rains from October–November (NE monsoon). Total annual rainfall ranges from 1000 to 1600 mm and the salinity in the study area ranges from 24 to 26.5 ppt during the SE monsoon (Kitheka 1997). High flushing rates are coupled with low water residence times (3 to 4 h) and result in high rates of exchange between inshore and offshore waters (60–90% of the volume per tidal cycle) (Kitheka 1997).

Site description

Four sites were investigated between March and June 2002; one natural stand of *Sonneratia alba* (N) and two replanted sites of the same species (MP and IP) of equal age (8 years) but differing planting density, and one denuded site (D) included for comparison. Site IP (Integrated Plantation) was replanted in a degraded stand of *S. alba* with a planting density of approximately 4330 trees ha^{-1} (Kairo 1995). This site thus contained a certain amount of forest cover at the time of planting which distinguishes it from MP. Site MP (Matrix Plantation) was planted on denuded ground which had been clear-felled under commercial logging practices in the 1970's (Kairo 1995) and where no natural regeneration of mangroves had occurred. This site was planted in a 1.0×1.0 m matrix with a planting density of approximately 10,250 trees ha^{-1} (Kairo 1995). Since their establishment pruning has been carried out twice but no thinning has been done in either of the plantations (Kairo personal communication). Site (D), adjacent to MP, was also logged in the 1970's. Each site was subdivided into two zones, a landward zone (ZI) and a seaward zone

Fig. 1 Map of the study area, Gazi Bay, Kenya. The area is located on the southern Kenyan coast at 4°25′ S and 39°50′ E. N=natural stand, IP=integrated plantation, MP=matrix plantation and D=denuded site
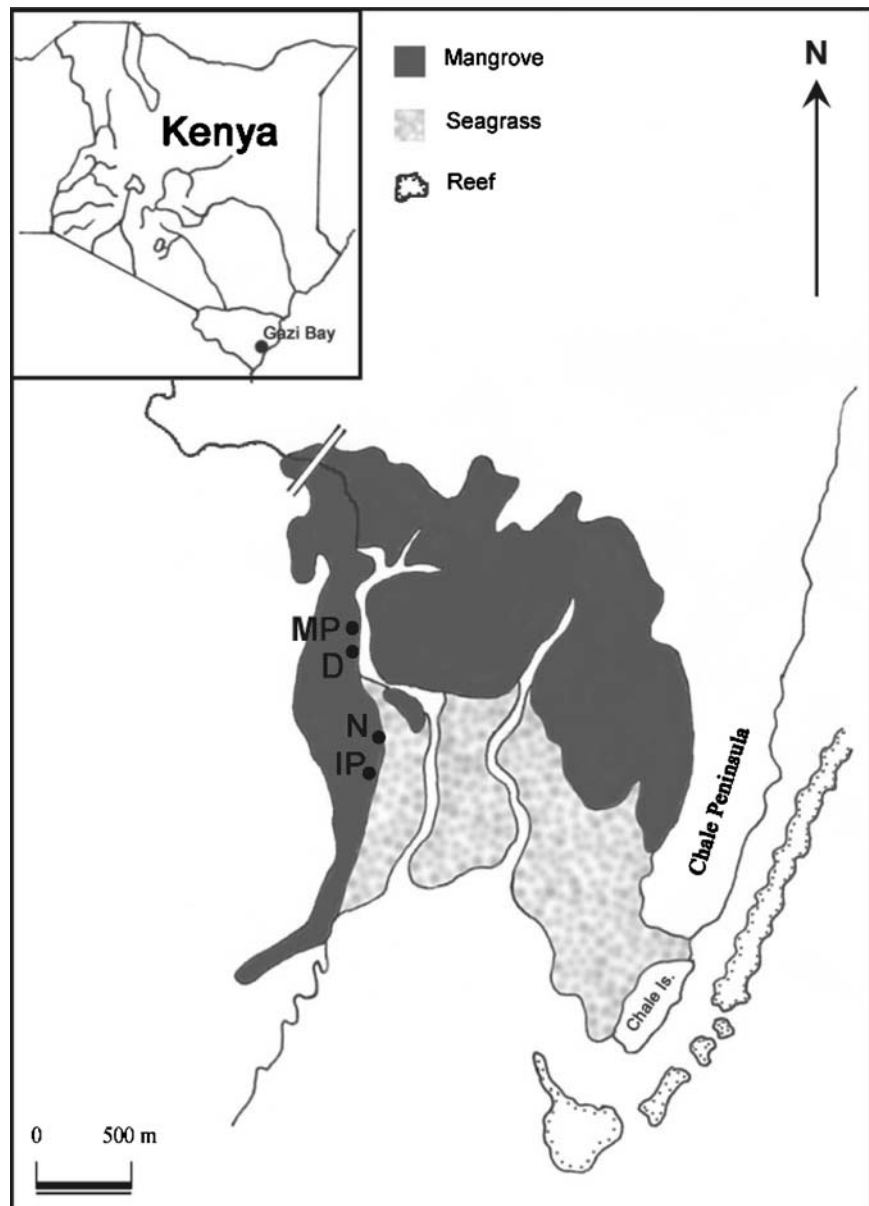
(ZII) based on visual observations of a natural epifaunal gradient and inundation patterns. Zones were approximately 25 meters deep and elevation differences between them ranged between 0.61 to 0.96 meters resulting in a slope around 2°, resulting in differences in inundation, between zones, of approximately 60 min per tide. All sites were located along a tidal channel (Fig. 1) and belong to inundation class I as described by Watson (1928), with inundation approx 12 h day^{-1}. The size of the sites ranged from 1,715 m^2 (MP) to 10,845 m^2 (N).

Relevant site characteristics are summarized in Table 1.

Sampling design

Sampling was done using 0.5×0.5 m wood frames. Ten replicates were taken in each zone and were selected by randomly paired coordinates, giving a total of 80 samples for all four sites. A sub-sample of roots in each frame were measured and counted. The base diameter and height of each pneumatophore was

Table 1 Summary of features (range or mean ± SE) characterizing the *Sonneratia alba* sites studied in Gazi Bay, Kenya

Site	Natural (N)	Integrated plantation (IP)	Matrix plantation (MP)	Denuded (D)
Feature				
Site area (m^2)	10,845	7,931	1,715	3,741
Planting density[a] (# ha^{-1})	–	4330	10,250	–
Current stand density[b] (# ha^{-1})	4300±1221	–	7640±600	–
Energy exposure	High	High	Low	Low
Relative site elevation (m)	0.14	0	0.37	0.37
Sediment type[c]	ZI: mud	ZI: mud	ZI: muddy sand	ZI: sand
	ZII: muddy sand	ZII: mud	ZII: mud	ZII: muddy sand
Sediment organic content[c]	7.9±1.6	14.3±1.1	9.2±1.8	1.6±0.3
Pore water salinity*	ZI: 34.6±0.3	ZI: 34.4±0.2	ZI: 34.0±0.8	ZI: 35.9±1.1
	ZII: 34.5±0.3	ZII: 34.2±0.1	ZII: 34.6±0.2	ZII: 27.4±5.8
Water column salinity	36.5–38.0	36.5–38.0	36.0–37.5	36.0–37.5
Canopy cover	50–75%	50–75%	100%	0%
Pneumatophore density (# m^{-2})*	ZI: 174±21	ZI: 424±24	ZI: 380±41	–
	ZII: 280±37	ZII: 322±35	ZII: 400±26	
Pneumatophore area (m^2 per m^2 forest)*	ZI: 0.30±0.03	ZI: 0.41±0.06	ZI: 0.16±0.01	–
	ZII: 0.55±0.07	ZII: 0.55±0.6	ZII: 0.24±0.03	
Average trunk area (cm^2 per m^2 forest)*	ZI: 1.2±0.2	ZI: 0.4±0.1	ZI: 1.3±0.4	–
	ZII: 0.7±0.2	ZII: 0.8±0.1	ZII: 1.0±0.1	
Trunk diameter range (cm)*	Min: 4.3	Min: 2.5	Min: 1.2	–
	Max: 93.5	Max: 48.0	Max: 8.6	

Data from [a] Kairo (1995), [b] Bosire et al. (2003), [c] Crona and Rönnbäck (2005). ZI=landward zone, ZII=seaward zone, *n=10

determined and used to calculate root surface area available for epifaunal colonization. For ease of surface computation pneumatophores were treated as perfect cones. Pore water samples were randomly collected in each site by digging a hole in the sediment 10–15 cm deep, and poor water and water column salinity was measured using an optical refractometer (Atago brand). All epibiota on both roots and sediment within the frame was removed and dried at 60°C to constant weight. Sessile fauna growing on the roots was determined to the taxonomic level of phyla. Although a detailed account of the diversity of the sponges and ascidians would have been preferable, the poorly documented taxonomy of these organisms in East African waters made this difficult. As a result they were grouped into respective phyla both representing the functional group of sessile filter feeders on pneumatophores. The potential benefits of such grouping when studying stability and persistence of marine benthic communities has been reviewed by Steneck and Dethier (1994). Algae were determined to genus and species wherever possible (Jaasund 1976; Richmond 1997). For each site ten random trees were also selected in each zone (a total of 60 trees) and the circumference was measured and used to calculate trunk area available

for colonization, from the sediment surface and one meter up (Table 1). All sessile organisms found growing on the lowest meter of each tree trunk were counted and determined to genus, and species level wherever possible.

Statistical analysis

Species abundance, biomass and frequency data were double square root transformed and subjected to non-metric multi-dimensional scaling ordination (nMDS) using the Bray–Curtis similarity coefficient (Field et al. 1982). The nMDS is a method based on a non-parametric regression of distance on dissimilarity of samples. The goodness-of-fit of the regression line is evaluated by calculating a stress value which is a measure of how well the MDS succeeded in fitting the multidimensional data onto a 2-dimesional plane. An alternative assessment of the dimensionality of the dataset is presented by non-parametrically correlating the original sample similarity matrix with that representing distance between samples in ordination space. Biomass data for both flora and fauna was tested for significant differences using analysis of similarity randomization tests (ANOSIM, Clarke and Green 1988; Clarke and Warwick 2001). Algal species

responsible for differences in sites observed in nMDS plots were identified with a dissimilarity percentage program (SIMPER, Warwick et al. 1990). Data on root complexity and trunk area were analysed using nested, one-way ANOVA. When conditions for use of parametric statistics were not met Kruskal–Wallis and Mann–Whitney U tests as well as Spearman rank correlation were applied. For multiple comparisons significance levels were adjusted using the Bonferroni method (Rice 1989). All statistical analysis were performed using Primer 5 (version 5.2.1) or Statistica 6.0.

Results

Surface available for colonization

Results from a hierarchically nested ANOVA (zones nested in sites) performed on number of pneumatophores and total pneumatophore area (Table 1) reveal significant differences between sites ($P<0.001$) and zones ($P<0.05$), which supports the sub-division of each site into zones in the analysis of biological data that follows.

Average trunk area m^{-2} available for colonization by sessile fauna was compared for sites N, IP and MP (Table 1). Results of a one way hierarchically nested ANOVA (zones nested in sites) show a highly significant difference in available trunk area between sites ($P<0.001$).

Species richness of epibiotic communities

The algal species encountered in each zone and site are shown in Table 2. Site D had only one species of algae, *Enteromorpha ramulosa*. This algae was found growing both on hard substrate and freely on the sediment surface. Site MP had a total of ten algal species, all of which were found in zone II, while only four species were found in zone I. In sites IP and N a total of 23 and 18 species were found respectively. For all forested sites the algae found belong to classes Rhodophyta and Chlorophyta. Several different taxa of both ascidians and poriferans were found growing on the pneumatophores of *Sonneratia alba* stands in Gazi Bay. *Tedania digitata vulcanis*, which could be positively identified to species, dominated the poriferan community.

Algal biomass and total epibiotic biomass on roots and sediment

For all sites, algal biomass and combined epibiotic biomass (algae, sponges and ascidians) were measured. Biomass was consistantly higher in the seaward zone (ZII) for all sites and the natural (N) and replanted site (IP) had the highest total biomass of algae and sessile fauna (Table 2). The replanted site (MP) had lower algal biomass in the seaward zone (ZII) than the adjacent denuded plot which was a result of the high presence of *Enteromorpha ramulosa* in the cleared area, a green algae favoured by intense sunlight and growing directly on the sediment. nMDS ordination revealed a high similarity between sites IP and N for both algal and total epibiotic biomass (Fig. 2a, b) expressed by the small distance between sites in the plot. Sites D and MP differed markedly from all sites except for combined epibiotic biomass where sites MP and D showed slightly higher resemblance (Fig. 2a, b). This similarity was due, in part, to a common lack of poriferans and ascidians among MP and D samples. The low stress of the nMDS plot (<0.05) suggests a very good fit of the multidimensional data onto the 2-dimensional plot (Clarke 1993). The dimensionality of the datasets for both algae and total biomass was further assessed through non-parametric Spearman correlation between distance in the ordination space and distance in the original p-dimensional space ($r_{algae}=1.0$, $r_{tot\ bio}=1.0$) for both nMDS plots presented in Fig. 2. To test the relationship between algal biomass and pneumatophore area a Spearman rank order correlation was conducted, resulting in a positive relationship ($r_{algae}=0.55$, $P<0.001$). A similar correlation was also run to test differences between zones in terms of biomass of algae and sponges ($r_{algae}=0.39$, $P<0.01$; $r_{sponge}=0.22$, $P=0.046$).

Analysis of similarities (ANOSIM) between sites for algal biomass and combined epibiotic biomass ($R=0.422$ and $R=0.407$ respectively, $P<0.001$) indicates dissimilarity between sites. Furthermore, the results reveal a high degree of dissimilarity between all pair wise between-site comparisons ($P<0.001$) except for sites IP and N which were similar for algal biomass but not for average combined epibiotic biomass ($P=0.015$). To explore why, Mann–Whitney U tests were used to test differences in average sponge and algal biomass between and within the natural

Table 2 List of organisms encountered at each studied site of *Sonneratia alba* in Gazi Bay, Kenya

	Zone I				Zone II			
	N	IP	MP	D	N	IP	MP	D
Biomass of organisms on pneumatophores								
Rhodophyta (Algae)								
Catenella nipae	1.8 (1.8)	6.2 (5.4)	–	–	329 (217)	19.9 (19.9)	46.8 (23.3)	–
Ceramium brevizonatum var. caraibicum	41.0 (23.4)	68.0 (20.7)	–	–	10.4 (8.3)	29.2 (24.9)	–	–
Ceramium sp.		9.8 (9.8)	–	–	–	–	–	–
Coelothrix irregularis	0.8 (0.8)	–	–	–	–	2.1 (2.1)	–	–
Gelidiopsis intricata	–	0.3 (0.3)	–	–	–	2.7 (2.7)	–	–
Gracilaria crassa	–	–	–	–	–	6.4 (6.4)	–	–
Gracilaria salicornia	321 (300)	352. (266)	–	–	1503 (821)	3294 (1537)	–	–
Heterosiphonia sp.	–	–	–	–	0.9 (0.9)	–	–	–
Hypnea sp.	5.6 (3.5)	107 (70.1)	–	–	325 (190)	160 (50.2)	–	–
Laurencia perforate	–	5.0 (5.0)	–	–	12.8 (12.1)	–	–	–
Polysiphonia sp.	180 (71.9)	177 (173)	–	–	451 (284)	675 (432)	80.6 (35.2)	–
Unidentified red algae. T1	–	30.5 (26.9)	–	–	36.6 (32.6)	–	–	–
Unidentified red algae. T2	–	1.2 (1.2)	–	–	–	–	–	–
Phaeophyta (Algae)								
Bostrychia binderi	0.6 (0.6)	–	–	–	–	–	–	–
Bostrychia radicans	–	20.1 (11.2)	–	–	38.6 (21.5)	5.9 (4.2)	2.6 (2.6)	–
Caloglossa leprieuri	90.1 (48.1)	139 (35.7)	1.7 (1.7)	–	140 (47.1)	140 (44.3)	7.5 (7.4)	–
Endosiphonia clavigera	–	–	–	–	–	12.4 (12.4)	–	–
Chlorophyta (Algae)								
Chaetomorpha crassa	–	5.8 (4.3)	–	–	–	2.0 (1.3)	–	–
Cladophora patentiranea	5.2 (4.2)	9.6 (6.2)	3.5 (2.4)	–	10.9 (8.4)	2.8 (2.8)	1.6 (1.6)	–
Enteromorpha kylinii	–	1.3 (0.9)	–	–	0.7 (0.7)	–	–	–
Enteromorpha ramulosa	0.4 (0.4)	–	–	–	–	73.9 (49.9)	–	688 (407)
Ulva pertusa	–	–	–	–	–	–	–	–
Unidentified green algae	–	0.7 (0.7)	–	–	–	–	–	–
Cyanophyta unidentified	12.4 (8.4)	1.5 (1.5)	–	–	64.9 (63.5)	16.3 (14.7)	27.2 (15.1)	–
Diatoms	–	12.7 (12.7)	–	–	39.2 (23.4)	77.0 (53.1)	–	–
Hydrozoans	21.6 (21.6)	14.3 (12.4)	–	–	–	–	0.8 (0.8)	–
Total algal biomass	681.0	961.9	5.2	0	2963	4519	167.0	688.8
Chordata								
Ascidians	0.26 (0.2)	0.4 (0.2)	–	–	–	1.5 (0.7)	–	–
Porifera								
Poriferans	20.7 (8.3)	20.0 (9.1)	–	–	43.8 (9.1)	75.9 (14.7)	–	–
Total combined biomass	21.65	21.32	0.005	0	46.73	81.88	0.169	0.689

Table 2 Continued

	Zone I				Zone II			
	N	IP	MP	D	N	IP	MP	D
Abundance of organisms on tree trunks								
Gastropoda								
Cerithidea decollata	2 (2)	–	2 (2)	–	–	–	2 (2)	–
Clypeomorus bifasciatus	4 (3)	9 (8)	–	–	4 (3)	2 (2)	–	–
Nerita sp.	4 (3)	–	02 (2)	–	2 (2)	–	17 (7)	–
Patellid (unidentified)	6 (3)	–	–	–	53 (45)	2 (2)	2 (2)	–
Terebralia palustris	–	2 (2)	–	–	–	–	–	–
Cirripedia (Crustacea)								
Balanus amphitrite	4 (3)	17 (17)	125 (44)	–	45 (19)	4 (3)	179 (50)	–
Chirona tenuis	132 (50)	–	115 (70)	–	436 (247)	4 (3)	62 (19)	–
Chthalamus dentatus	404 (139)	2 (2)	3.3 (1.1)[a]	–	574 (215)	40 (12)	389 (162)	–
Bivalvia								
Brachidontes variabilis	28 (28)	–	11 (11)	–	109 (76)	2 (2)	547 (198)	–

Mean (SE) dry weight (mg m^{-2}) for algae, (g m^{-2}) for ascidians and poriferans on pneumatophores (n=10). Mean (SE) abundance (# m^{-2} trunk area) of trunk epifauna (n=10). Total combined biomass (algae, ascidians and poriferans) expressed in g m^{-2}. Natural stand (N), replanted (IP and MP) and denuded (D)

stand and integrated plantation. Tests between sites proved non-significant (p_{sponge}=0.516; p_{algae}=0.250) while Zone I and II of the integrated plantation differed significantly (p_{sponge}=0.008; p_{algae}=0.041) and Zone I and II of the natural stand showed somewhat weaker trends (p_{sponge}=0.059; p_{algae}=0.049).

Analysis of similarity percentages (SIMPER) of algal species distributions was done to reveal the main species responsible for observed dissimilarities among sites (Table 3). *Enteromorpha ramulosa* was the sole species responsible for characterizing site D as it was the only species of algae found in this habitat. Consequently it also played a dominant role in distinguishing this site from all other areas sampled. Two species of algae contributed to over 80% of total algal biomass in site MP as compared to four and three species in the natural stand and the integrated plantation, respectively (Table 2). *Polysiphonia* sp. was responsible for over 50% of the biomass in the matrix plantation, but was also present as a potential characterizing species in both the natural stand and integrated plantation. Three out of four species characterizing sites N and IP were the same despite differences in their percentage contribution.

Epibiotic communities of trunks

A total of nine animal species from three phyla were recorded (Table 2). No sponges, ascidians or algae were found on the trunks and the majority of specimens recorded were found around the upper limits of the 1 m range of trunk area investigated. There is a clear separation between sites although some interspersion of samples from site N and IP is found (Fig. 3). No correlation was found between the number of species of sessile fauna present and available trunk area. Correlation between trunk area and abundance of the three most common fouling species was done revealing no correlation for *Chirona tenuis*, a positive correlation for *Chthalamus dentatus* (r=0.29, P<0.05) and a negative correlation for *Balanus amphitrite* (r=0.35, P<0.01).

Discussion

Patterns of biomass distribution

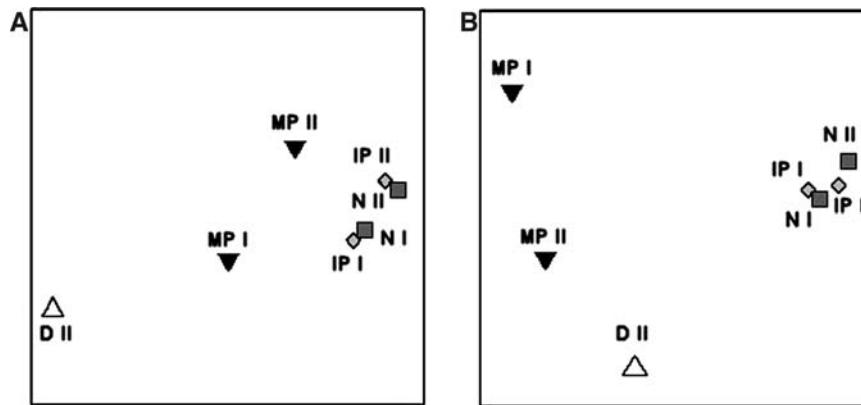When examining community composition of the investigated sites in terms of algal biomass two

Fig. 2 (**a**) nMDS plots of total algal biomass per mangrove site and zone in Gazi Bay, Kenya. Each symbol represents the average value of that zone (*n*=10). Stress=0 (**b**) nMDS plots of combined epibiotic biomass per site and zone. Stress=0 N=natural stand, IP=integrated plantation, MP=matrix planta-

tion, D=denuded site, I=landward zone, II=seaward zone. For site D, ZI contained no epibiotic biomass and consequently was not included in the MDS analysis. For both nMDS plots distances between points are represented as equal distances in all dimensions of the plot

Table 3 Algal species responsible for similarities within and dissimilarities among sites of *Sonneratia alba* mangroves in Gazi Bay, Kenya

Site	Species	$\delta_i/SD(\delta_i)$	Contrib %	Cum contrib %	Avg sim
Species responsible for observed similarity within sites					
IP	*Caloglossa leprieuri*	1.64[a]	28.60	28.60	40.61
	Hypnea sp.	1.22[a]	24.80	53.40	
N	*Polysiphonia* sp.	0.85[a]	45.36	45.36	36.13
	Caloglossa leprieuri	0.84[a]	26.85	72.21	
MP	*Polysiphonia* sp.	0.47	51.45	51.45	26.03
	Catenella nipae	0.36[a]	30.83	82.28	
D	*Enteromorpha ramulosa*	#####	100.00	100.00	100.00

Sites	Species	Dissim/SD	Contrib %	Cum contrib %	Avg dissim
Species responsible for observed dissimilarity between sites					
D, MP	*Enteromorpha ramulosa*	6.87[b]	45.00	45.00	100.00
D, IP	*Enteromorpha ramulosa*	3.87[b]	26.51	26.51	100.00
	Caloglossa leprieuri	1.92[b]	12.38	38.88	
	Hypnea sp.	1.17[b]	12.27	51.16	
MP, IP	*Polysiphonia* sp.	1.22[b]	13.66	13.66	84.77
	Hypnea sp.	1.19[b]	13.53	27.18	
	Caloglossa leprieuri	1.59[b]	13.20	40.38	
D, N	*Enteromorpha ramulosa*	3.25[b]	31.63	31.63	99.37
	Polysiphonia sp.	1.21[b]	19.05	50.69	
	Caloglossa leprieuri	1.06[b]	13.20	63.89	
MP, N	*Polysiphonia* sp.	1.07[b]	19.53	19.53	75.50
	Caloglossa leprieuri	1.07[b]	16.47	36.01	
IP, N	*Polysiphonia* sp.	1.17[b]	14.19	14.19	63.58
	Gracilaria salicornia	1.01[b]	13.59	27.77	
	Hypnea sp.	1.07[b]	11.86	39.63	
	Caloglossa leprieuri	1.10[b]	10.88	50.51	
	Ceramium brevizonatum var caraibicum	1.03[b]	9.62	60.13	

[a] indicates that the species potentially characterizes the species assemblage of a site and [b] indicates a possible discriminating species between sites. Analysis is based on algal biomass m^{-2}
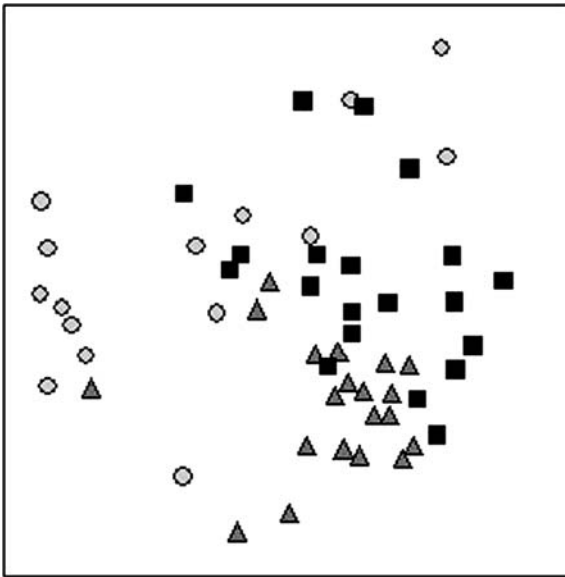
Natural (N), replanted (IP and MP) and denuded (D)

Fig. 3 nMDS of epibiotic trunk fauna based on species abundance per standardized available mangrove trunk area (m²) in Gazi Bay, Kenya. N=natural stand (squares), IP=integrated plantation (circles), MP=matrix plantation (triangles). Stress=0.16

distinct patterns emerge (Fig. 2a). For algal biomass there is a clear gradient with algal biomass of the denuded site being markedly lower than replanted site IP and the natural site (N), while replanted site MP has intermediate biomass values. This is also supported by a positive correlation between algal biomass and total pneumatophore area. Pneumatophore area in the matrix plantation (MP) is half of that in both the replanted site IP and the natural stand (N) (Table 1). Although no causal relation can be determined with certainty the lower root area is surely important in determining the colonization efficiency and recruitment possibilities of algae. If algal recruitment follows the lottery model proposed for epibiota (Sutherland 1980), lower pneumatophore area available would certainly reduce chance recruitment of algal spores from the water column. A higher level of canopy cover observed in the matrix plantation as opposed to the natural and integrated stands, and consequently lower solar radiation in the former plot, could also affect the abundance, biomass and composition of algal species present. This is likely the main reason for observed higher algal biomass values in the seaward zone of the cleared compared to the replanted area (MP), since the only

species present in the former was *E. ramulosa*, a green algae thriving in sun exposed environments (Oliveira et al. 2005) and consequently lacking in the adjacent shaded habitat.

If biomass of sponges and ascidians is included in the nMDS analysis the pattern and spatial relationship between sites change (Fig. 2b). While sites IP and N remain tightly clustered site MP is now found positioned far from N, IP and D. The reason for this is the lack of sponges and ascidians in all but one sample from site MP. Since both of these organism groups require hard substrate for their growth and survival none were present in site D. Studies of sponge assemblages suggest a number of factors responsible for species distributions including water flow rate (Maldonado and Young 1996), sedimentation and nutrient levels (Bell and Barnes 2003), depth (Alvarez et al. 1990), light (Cheshire and Wilkinson 1991), and habitat availability (Barthel and Tendal 1993). Sedimentation and nutrient levels were not investigated in this study but are assumed to be similar due to the close proximity and fringing position of all sites in the bay as well as the thorough mixing of the waters entering the bay (Kitheka 1997; Mwashote and Jumba 2002). Lower root surface availability was significant in site MP, but the lack of pneumatophore surface may not provide a sole satisfactory explanation. Several investigations on factors affecting distribution and composition of mangrove epibiotic communities have concluded that larval behaviour and longevity may affect recruitment patterns (e.g. Sutherland 1980; Bingham and Young 1995). New colonists seem to recruit primarily from local sources and sponge colonization has been suggested to occur from root to root (Farnsworth and Ellison 1996) or through fragmentation of adult colonies (Bingham and Young 1995). Ascidian larvae are known to swim short distances (2–15 m) (Davis and Butler 1989) and many have developed swimming behaviours promoting settlement in close proximity to parental colonies (Bingham and Young 1991). The location of site MP up-stream along the creek from sites N and IP may thus be another reason why larval recruitment or entrapment of colonial fragments has not occurred.

Maldonado and Young (1996) showed that distribution of four tropical demosponges, including *Tedania ignis*, a close relative to the dominant sponge

in this study (*Tedania digitata vulcani*), was likely affected by post-settlement mortality of larvae due to suboptimal habitat conditions. This resulted in adult populations strongly associated with both high and low irradiance, but always with a high level of water movement. Since sites IP and N have a higher wave energy exposure and presumable higher levels of water movement this may explain their abundant sponge communities compared to site MP. Differences in canopy cover may thus play a subordinate role in determining the presence of sponges.

Observed differences in combined epibiotic biomass at the zone level for IP and N was a result of much higher total biomass values for sponges and algae found in zone II of IP as compared to zone II of N (Table 2). Correlation values also support this and suggest that the main difference in terms of both sponge and algal biomass is at the zone level, linked to inundation, rather than differences in vegetation structure and habitat availability between the natural and replanted site.

Algal species assemblages

A few studies have described mangrove associated algal communities (Burkholder and Almodovar 1974; Beanland and Woelkerling 1983; Davey and Woelkerling 1985; Rodriguez and Stoner 1990) with focus on algal communities in *Rhizophora* and *Avicennia* stands. To our knowledge none have dealt with epibiotic assemblages associated with *Sonneratia* sp. The dominating algal species in this study were *Polysiphonia* sp., *Catenella nipae*, *Hypnea* sp. and *Caloglossa leprieuri*. Apart from *Hypnea* sp., these species have all been found as dominant components among the studies mentioned above. Their respective dominance within the different sites of this study varies however. Relatively low values of average similarity within all sites are likely due to the marked zonation pattern described earlier. Algal diversity of forested sites was in the upper range of values reported previously (Beanland and Woelkerling 1983; Davey and Woelkerling 1985; Rodriguez and Stoner 1990). However, while replanted site IP and the natural stand (N) had a high diversity, replanted site MP counted approximately half the number of species and the denuded site grew only one species, growing freely on the sediment and known to thrive

in extreme ecological conditions (Oliveira et al. 2005). Average dissimilarity values between sites reinforce the pattern and provide further evidence that site MP has a distinctly different community composition in terms of epiphytic algae as compared to the other forested sites (Table 3). Davey and Woelkerling (1985) observed fluctuating frequency of colonizing red algae over time and related this to grazing, competition for substratum and sloughing off of pneumatophore bark. De Troch et al. (1998) reported that between 6 and 7% of the fish community sampled in Gazi Bay consist of herbivores, but effects of grazing on newly established algae in the area is unknown. Hence it is difficult to speculate on the importance of herbivory to the lack of algal coverage in site MP. It is possible that the less diverse algal community in site MP is stable and may not reach the higher species diversity of N and IP. Similarly altered community assemblages were observed after disturbance by Davey and Woelkerling (1985) and in colonization experiments by Eston et al. (1992). Another explanation is that since replanting in plot IP was integrated with sparse but existing forest cover the existence of epibiotic communities on remaining root structures at the time of planting may have facilitated the ease and speed of recolonization. Closer proximity of site IP to the natural site (N) compared with site MP is also plausible, although a difference in proximity of approximately 500 meters seems unlikely to account entirely for the low diversity and recruitment after eight years.

Fouling fauna of mangrove tree trunks

The fouling community of mangrove tree trunks differs entirely from that of pneumatophores. The primary reason behind the distinct difference in communities is likely a higher tolerance to wave exposure and dessication by the barnacles dominating the trunk fouling community. Patterns of species abundance of sessile fauna on tree trunks reveal a clear separation between sites (Fig. 3). Despite the lack of correlation between species richness and available trunk area, species assemblages between the sites apparently differ. Negative correlation for *Balanus amphitrite* appears because of the highly localized presence of this species in the matrix plantation (MP) where trunk diameters are smaller than the

other forested sites (Table 1). Barnacle larvae are known to exhibit patchy distributions in the water column (Grosberg 1982) and availability of suitable substrata, competition from other species and presence of sexually mature conspecifics have been suggested to influence their settlement and consequent distribution (Bayliss 1993; Coates and McKillup 1995; Satumanatpan and Keough 2001). Bayliss (1993) observed highly aggregated distributions of *Balanus amphitrite* on pneumatophores of *Avicennia marina* and suggested that mechanisms responsible may be settling behaviour of cyprid larvae, post-settlement mortality, selective predation among others. Furthermore, Satumanatpan et al. (1999) have shown that settlement determines large scale distributions such as along shore variations in abundance observed in this study while post-settlement mortality, in combination with settlement cues mentioned above, is responsible for small scale vertical distribution. This may explain the distinct pattern in barnacle species distribution and composition between studied sites in Gazi Bay.

Conclusion

Results presented indicate that after eight years, marked differences in epibiotic biomass exist between replanted stands of *Sonneratia alba* and consequently also between the replanted and natural stands studied. Differences among replanted sites as well as between replanted and natural sites also exist with regard to algal species assemblages. As both reforestation plots were initiated in the same year the effect of time cannot solely account for the discrepancies in epibiotic communities between these two sites nor are the physical parameters investigated significantly different between sites. Instead, clear zonation patterns of pneumatophore surface and inundation time, in combination with proximity of sites to natural seeding areas, seem more plausible explanations for the observed patterns of epibiotic community distribution in this study. Due to lack of replication at the level of planting strategy and history of sites prior to planting it is risky to draw too strong conclusions from this study with respect to these factors. It would, nonetheless, be interesting to investigate how such aspects as planting density, location and pre-planting history of sites may affect the return of associated flora and fauna such as those studied in Gazi Bay.

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