

Use of replanted mangroves as nursery grounds by shrimp communities in Gazi Bay, Kenya

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Abstract

This study quantitatively assessed the distribution of postlarval and juvenile shrimps in natural, degraded and replanted stands of *Sonneratia alba* mangroves in Gazi Bay, Kenya in 2002–2003. Two plantations (matrix and integrated) differing in historical status and planting strategy were studied. Sampling was conducted using stake nets (2 mm mesh), each net enclosing 9 m² of intertidal microhabitat. A total of 615 shrimps from 19 species/taxa were caught, including several penaeid species of major commercial importance. Penaeids dominated the catch (66%) followed by *Macrobrachium* spp. (16%) and *Acetes* sp. (6%). Shrimp abundance ranged from 0.42 to 10.0 ind. per net (9 m²) for individual sites across spring tides and significant differences were detected between sites and over time ($p < 0.001$). Results showed no significant difference in diversity of species/taxa between sites. However, multivariate analysis revealed significant differences in community assemblages between sites, except for the natural stand and integrated plantation. These two sites harbored higher abundances of the majority of all taxa caught. The observed distribution patterns are discussed with regard to measured environmental parameters such as elevation, structural complexity and sediment characteristics.

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1. Introduction

Increasing pressure on the world's mangrove resources by a number of anthropogenic activities has led to a worldwide up-surge of the number of reforestation programs initiated in the last decades (Field, 1996). Field (1998) lists three main reasons behind the majority of mangrove rehabilitation initiatives: conservation and landscaping, multiple use systems for high and sustainable yield and protection of coastal areas. However, regardless of primary motives, the progress of any mangrove rehabilitation scheme will ultimately depend on the successful re-establishment of essential ecological

functions, underpinning the provision of goods and services from these ecosystems. Monitoring of the tree component, although a conspicuous and vital element in the mangrove ecosystem, is not enough to provide estimates of such functional diversity. To date, very few studies have focused on the return of ecosystem functions other than those directly associated with the trees (Al-Khayat and Jones, 1999; Macintosh, 2002; Morrisey et al., 2003). Apart from some information in Rönnbäck et al. (1999), no studies have, to our knowledge, provided quantitative data on the utilization of these rehabilitated habitats by larval or juvenile fish and shrimp.

The nursery role of mangroves is well established (e.g. Robertson and Duke, 1987; Vance et al., 1996; Primavera, 1998; Rönnbäck et al., 2002) and the proposed reasons why juveniles of many commercially

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important fish and penaeid shrimp species utilize these coastal forests have been food abundance, shelter from predation and the hydrodynamic ability of mangroves to retain immigrating larvae and juveniles (Robertson et al., 1992; Robertson and Blaber, 1992; Rönnbäck, 1999; Chong et al., 2001).

Studies on shrimp distributional pattern in mangrove systems have almost exclusively focused on penaeid shrimps, likely due to their immense importance as a commercial fishery resource in tropical and sub-tropical regions (Rönnbäck, 1999; Mwatha, 2002). Most studies have, however, been conducted in the open water habitats of the mangrove system, such as creeks, channels and adjacent mudflats. These studies have compiled an impressive amount of information on the population dynamics of several penaeid species, yet quantitative estimates of their distribution inside the forested mangrove habitat remain few and isolated (Vance et al., 1996, 2002; Rönnbäck et al., 1999, 2002; Meager et al., 2003). Despite abundant evidence in favor of the nursery function of mangroves for early life stages of many penaeid shrimp species, questions remain as to the amount of support different mangroves provide to commercial shrimp fisheries. Riverine, fringing and basin mangrove ecosystems may differ significantly in their supportive role for commercial stocks (Rönnbäck et al., 2002) and such issues need to be taken into account when planning and implementing rehabilitation programs.

The present study was conducted with the aim of quantitatively investigating the distribution of shrimp postlarvae and juveniles in two replanted, fringing monostands of *Sonneratia alba* in southern Kenya. The plantations differed with respect to the status of the area prior to planting as well as the density and structure of the plantation effort. The study also included comparisons of the plantations to a natural stand of *S. alba* and a previously forested, but since clear-cut area. Although the main focus of this paper is on penaeid shrimps, diversity of other shrimp taxa and differences in community assemblages associated with natural, replanted and deforested areas are also described and discussed.

2. Materials and methods

2.1. Study area

This study was conducted in fringing *Sonneratia alba* stands of differing age and status along the north western shore of Gazi Bay, Kenya (Fig. 1). 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. Seasonal rains dominate the climate with two pronounced rainy seasons; a period of heavy rains from April to June (South East monsoon) and a period of lighter rains from

October to November (North East monsoon). Total annual rainfall ranges between 1000 and 1600 mm and the salinity in the study area ranges from 24 to 26.5 during the SE monsoon (Kitheka, 1997). Gazi Bay has a semi-diurnal tidal regime with a tidal height at spring high tide ranging from approximately 2.0 to 4.0 m. Tidal currents vary and although currents of up to 0.6 m s⁻¹ have been recorded current speed in the open areas of the bay are generally less than 0.25 m s⁻¹ (Kitheka, 1997).

2.2. Sampling schedule and fishing methods

The field sampling was carried out on three spring tides; April–May 2002 (one spring tide) and April–May 2003 (two spring tides). The method of using stake nets to obtain quantitative measurements of shrimp density in mangrove habitats was first developed by Vance et al. (1996) (with reference to block net sampling of fish by Thayer et al. (1987)) and later modified by Rönnbäck et al. (1999, 2002). The method employed in this study is the one described in Rönnbäck et al. (2002). Net pens measuring 3 × 3 m, thus enclosing 9 m², were set using four corner poles and the lower end of the net was secured in the mud. At high tide the nets were raised and catch was collected the following low tide. All nets had a stretched mesh size of 2 mm. Four different sites were included in the investigation; a natural stand, site N, a clear-cut, degraded area, site D, and two different areas of planted mangroves, site MP and site IP (Fig. 1). The size of the individual sites ranged from 1700 (MP) to 10,800 (N) m² (Table 1). The two plantations differed with respect to the method of planting used. Site MP (matrix plantation) was planted on a clear-cut strip of fringing mangrove in a 1 × 1 m matrix, which has resulted in a dense monostand of *S. alba* with a relatively high degree of canopy cover and a more homogenous root complexity throughout the site than plantation IP. The latter site (integrated plantation (IP)) was planted in a degraded but partly forested area adjacent to a natural stand of *S. alba*. Consequently, this site had a more heterogeneous appearance with natural canopy gaps and a higher variability in root complexity due to the diversity in age of the existing trees. Both plantations were initiated in 1994.

Penaeid shrimp larvae are reported to enter coastal areas through diurnal vertical migration coupled to inshore currents, while postlarval migration is closely linked to lunar phases and tidal amplitudes (reviewed in Garcia and Le Reste, 1981; Dall et al., 1990). Furthermore, it has been shown by Staples and Vance (1979) and Stoner (1991) that shrimp catchability significantly increases with night sampling due to a more active behavior, possibly as a result of feeding (Vance, 1992; Primavera and Lebata, 1995). Sampling was therefore conducted on spring tides, all nets deployed at night, around maximum high tide, and catch collected at dawn

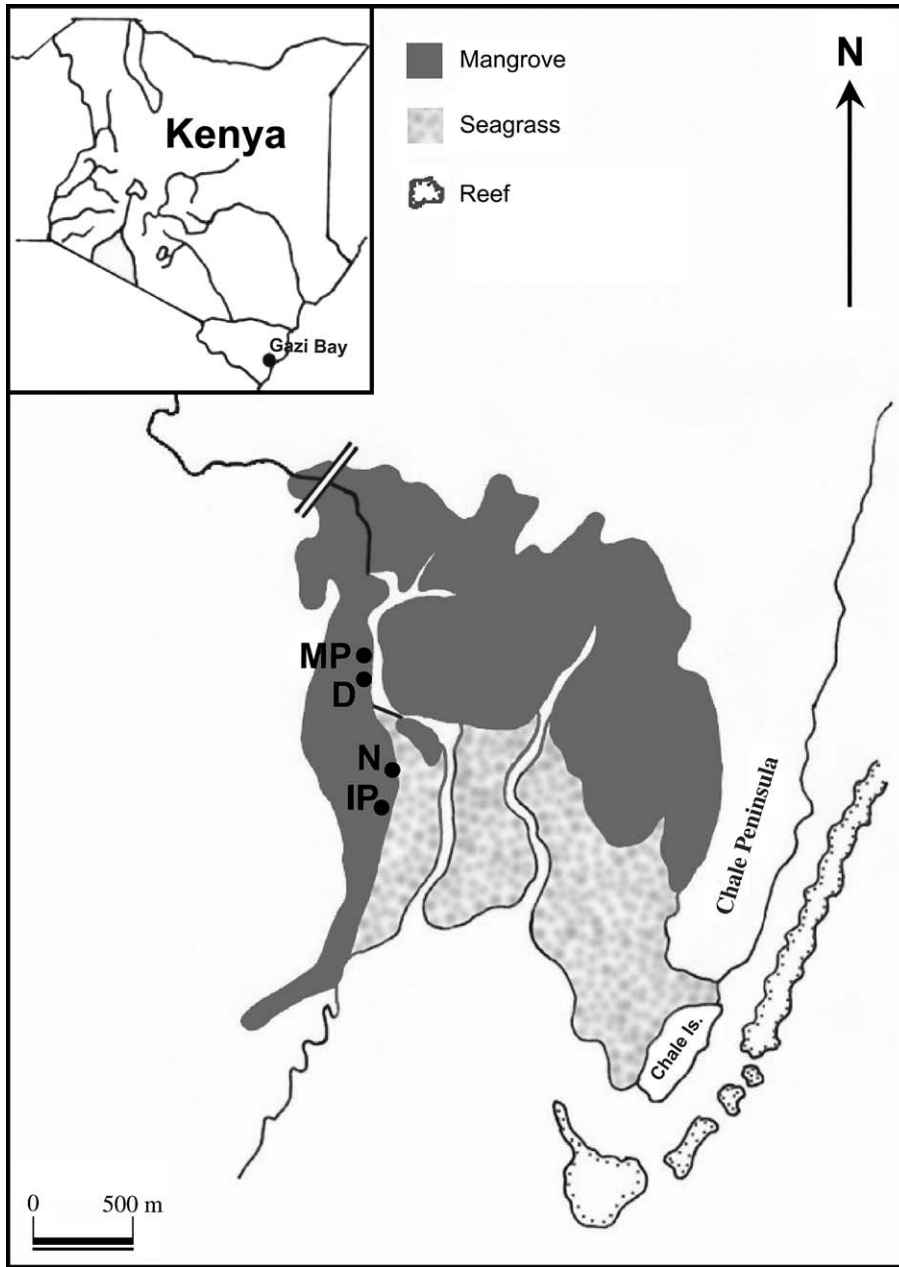


Fig. 1. Map of study area, Gazi Bay, Kenya. The area is located on the southern Kenyan coast at 4°25'S and 39°50'E. N=natural stand, IP=integrated plantation, MP=matrix plantation and D=denuded plot.

Table 1

Physical parameters of mangrove habitats sampled in Gazi Bay, Kenya. Area, relative site elevation, structural complexity (ratio of mangrove root surface to sediment area), organic content, percent finest fraction of sediment (<0.075 mm), sediment chl *a* content, and range of water depth at high tide for each studied site; N, natural; IP, integrated plantation; MP, matrix plantation; D, deforested site (mean ± SE)

Site	Total area (m ²)	Elevation (m)	Water depth at high tide (m)	Structural complexity	Sediment organic content (%)	Fine sediment content (%)	Chl <i>a</i> sediment content (mg m ⁻²)
N	10800	0.14	1.16–1.51	0.44 ± 0.14	7.9 ± 1.6	3.7 ± 0.5	66.4 ± 8.7
IP	7900	0	1.30–1.65	0.27 ± 0.10	14.3 ± 1.1	5.7 ± 0.7	77.1 ± 7.9
MP	1700	0.37	0.80–1.45	0.23 ± 0.09	9.2 ± 1.8	9.6 ± 0.7	94.6 ± 7.4
D	3700	0.37	0.80–1.45	0	1.6 ± 0.3	2.2 ± 0.3	62.0 ± 8.3

as the tide receded. Two sites were always sampled simultaneously with four nets deployed in each site. The same two sites were sampled for two or three consecutive nights resulting in a total of eight or 12 nets per site and spring tide. All sites were sampled on each spring tide, and when consecutive spring tides were sampled the order in which the sites were sampled was switched for the second sampling occasion so as to avoid any bias from two sites always being sampled on the first days of the rising spring tide. Shrimps were sorted from other crustaceans, fish and detritus and preserved in 8% seawater-formalin. All individuals were then identified to species or lowest taxonomic group using Joubert (1965) and Kensley (1972).

2.3. Sampling of environmental parameters

Relative site elevation was measured by simultaneously measuring tidal height of all sites at a given time. Ten sediment samples were taken randomly within each site using a glass test tube in order to establish chlorophyll *a* content of the sediment. The upper 5 mm of the core were transferred to a clean glass test tube wrapped in aluminum foil and a fixed volume of 90% acetone was added. The samples were transported to the laboratory and analyzed for chlorophyll *a* content using Standardized Swedish Methods (Svensk Standard SS028146). Another ten randomly selected samples were taken with a plastic corer (26.7 mm diameter) dried and analyzed to determine mean grain size according to Morgans (1956) and sediments were classified based on the Wentworth scale as described in Boggs (2001). Within each area enclosed by a net, four cores (26.7 mm diameter, 1.5 cm depth) were taken for analysis of sediment organic content. Cores were dried at 60 °C to constant weight, ashed in a muffle furnace at 550 °C for 5 h and weighed again. Organic content is expressed as percentage of the initial dry weight.

Structural complexity of the forested habitats was calculated as a ratio between root surface area and sediment surface area. These measurements were obtained by measuring the base and height of roots in a sub-sample (1 m²) of the area enclosed by each net and then treating each root as a perfect cone for which the surface area was computed.

2.4. Statistical analysis

Biotic data similarity matrices were constructed using the Bray–Curtis similarity coefficient on non-standardized 4th root transformed data. Formal significance tests were conducted using ANOSIM permutation tests for multivariate data (Clarke and Green, 1988) and two-way Anova for univariate comparisons of selected species. All shrimp data was tested statistically for the effect of consecutive sampling, but as there was no trend or

significant differences between catches per net and day, nets were pooled within sites and individual spring-tide periods served as temporal units. Data for individual nets was also checked to eliminate the possibility that crab predation consistently lowered the catches in certain nets due to the order of catch collection. No such trend was detected. For two-way crossed ANOSIM, as well as two-way Anova, factors time and site were used for analysis of species assemblages and individual species distribution, respectively. Univariate analysis was preceded by $(x + 0.01)^{0.1}$ transformation of abundance data. Further exploration of species responsible for similarities between sites was conducted through a similarities procedure (SIMPER; Warwick et al., 1990). Multivariate analyses were run using the PRIMER 5 software and Canoco 4.5. Environmental data were tested for significant differences between sites using parametric and non-parametric Anova and Mann–Whitney *U*-tests or Tukey's test for post-hoc unplanned comparisons. For multiple comparisons significance levels were adjusted using the Bonferroni method (Rice, 1989). Univariate statistics were computed with STATISTICA 6.0.

3. Results

3.1. Habitat characteristics

The integrated plantation (IP) had the lowest elevation followed by the adjacent natural stand (N). These habitats thus had the largest water depth at high tide (Table 1). Depth differences of up to 0.20 m on consecutive nights were common. The higher elevation of sites MP and D and their position approximately 500 m further up the creek resulted in these sites being inundated approximately 80 min less every tidal cycle. The clear-cut area was characterized by coarser sediments, predominantly sand, while the forested sites had a higher percentage of the fine sediment fraction (<0.075 mm) with highest values found in the matrix plantation (Table 1). A Kruskal–Wallis ANOVA showed significant differences between sites with respect to this parameter ($p < 0.001$) and post-hoc comparisons with Mann–Whitney *U*-test showed significant differences ($p < 0.05$) between all sites except sites IP and N. Sediment organic content also varied between sites (1.6–14.3%) with the largest mean values in the integrated plantation (IP) (Table 1). This variable, along with chlorophyll *a* levels in surface sediments, was found to differ significantly between study areas ($p < 0.001$). Post-hoc tests showed that all pair-wise between site comparisons were significant ($p < 0.05$) except for MP and N for sediment organic content, while chlorophyll *a* levels were significantly higher in the matrix plantation ($p < 0.05$). Structural complexity ($p = 0.38$) did not differ significantly between forested sites although a trend

could be seen with the highest structural complexity found in the natural stand (N), and the lowest in the matrix plantation (MP). Fewer but markedly larger pneumatophores, associated with a few large trees, in site IP and N contributed to the higher values of structural complexity compared to MP. The latter had smaller but more numerous pneumatophores, creating a different, yet possibly just as complex micro-environment. Worth noting is that additional structural complexity provided by debris such as fallen twigs, logs and branches were not included in the complexity measure. Occurrence of such elements was higher in the natural stand likely resulting in an underestimation of microhabitat complexity in this site compared to the plantations. No pneumatophores or other structural components existed in the clear-cut area.

3.2. Shrimp abundance and species richness

A total of 615 shrimps from 19 different species/taxa were caught. Penaeid shrimps dominated the catch (66%), followed by *Macrobrachium* spp. (16%), *Acetes* sp. (6%) and other carideans (11%) (Fig. 2). The

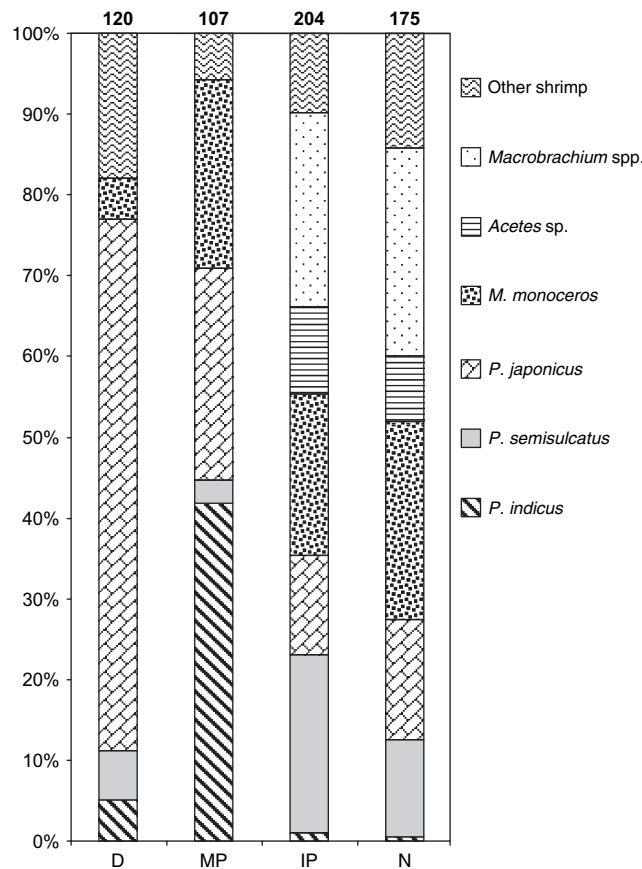


Fig. 2. Percentage contribution of shrimp species to total shrimp abundance in *Sonneratia alba*, Gazi Bay. Values are averaged over all sampling occasions. Number of shrimps upon which calculations were made are indicated at the top of each site column. N=natural stand, IP=integrated plantation, MP=matrix plantation and D=deforested area.

penaeid shrimp community was dominated by post-larval and juvenile life stages.

No pronounced differences in species richness among sites were found. Instead diversity measures seemingly differed more between years (Table 2). The total number of shrimp species/taxa encountered at each site was also lower in the matrix plantation (eight taxa) compared to the other sites (10–13 taxa). In addition, the natural stand and integrated plantation had a more even relative distribution by species/taxa to total abundance (Fig. 2).

The variability of shrimp abundance within sites was consistently high in each spring tide, and mean daily shrimp abundance ranged from 0.42 (site D) to 10 (site MP) ind per net (9 m²) (Table 3). There were also significantly lower total shrimp abundances in 2002, particularly in sites MP and D (Table 3). These low values are the main factor responsible for the significant difference in total shrimp abundance between sites and over time (Table 4). The same trend generally applies for individual penaeid shrimp species as well as *Acetes* sp. and *Macrobrachium* spp. in 2003 (Table 3). Two species deviate from the above pattern; *Penaeus indicus* and *P. japonicus*, which in 2003 were found in higher numbers in sites MP and D, respectively.

Results from a two-way Anova of abundance values for six selected species are presented in Table 4 and showed that for all tested species sites differed significantly in abundance while difference in abundance over time was significant for all species except *Metapenaeus monoceros* and *Acetes* sp. Only *P. indicus* and *P. japonicus* showed a significant interaction between time and site. Tukey post-hoc comparisons showed abundance of *P. indicus* in site MP to be significant higher ($p < 0.05$) than all other sites while there were also differences in *P. indicus* abundance of MP between years due to increasing values in 2003. Similarly, abundance of *P. japonicus* was significantly higher in site D ($p < 0.05$) than all other plots while increasing abundance values in 2003 at this site resulted in a significant time \times site interaction (Table 4).

Table 2
Species richness (Margalef's index R) and Shannon–Wiener diversity index (H') for juvenile shrimps caught in fringing *Sonneratia alba* mangrove stands in Gazi Bay, Kenya. Values are averaged over sites and years. Natural (site N), replanted (site MP and IP) and denuded (site D)

	R		H'	
	Avg	SE	Avg	SE
Site				
N	1.24	0.11	0.74	0.10
IP	1.06	0.10	0.73	0.09
MP	0.67	0.11	0.74	0.10
D	1.03	0.13	0.63	0.11
Year				
2002	0.84	0.12	0.46	0.08
2003	1.10	0.07	0.73	0.06

Table 3

Mean abundance (\pm SE) per net (9 m²) of shrimps sampled in fringing mangroves in Gazi Bay, Kenya, over three sampling seasons in 2002 and 2003 (spring tide 1 and 2). Replanted (IP and MP), natural (N) and clear-cut (D) sites of *Sonneratia alba*. $n = 12$

Shrimp species	N	IP	MP	D
<i>Penaeus indicus</i>				
2002	0	0	0	0.08 \pm 0.08
2003(1)	0.08 \pm 0.08	0.17 \pm 0.11	0.50 \pm 0.23	0.08 \pm 0.08
2003(2) ^a	0	0	4.63 \pm 2.35	0.50 \pm 0.33
<i>P. japonicus</i>				
2002	0.67 \pm 0.28	0.67 \pm 0.28	0.08 \pm 0.08	0
2003(1)	1.00 \pm 0.65	1.00 \pm 0.30	0.08 \pm 0.08	4.08 \pm 1.08
2003(2) ^a	0.75 \pm 0.41	0.63 \pm 0.42	3.13 \pm 1.44	3.50 \pm 0.78
<i>P. semisulcatus</i>				
2002	0.08 \pm 0.08	1.50 \pm 0.88	0	0
2003(1)	1.25 \pm 0.92	1.33 \pm 0.51	0.17 \pm 0.11	0.25 \pm 0.18
2003(2) ^a	0.63 \pm 0.18	1.38 \pm 0.63	0.13 \pm 0.13	0.50 \pm 0.27
<i>Metapenaeus monoceros</i>				
2002	0.17 \pm 0.11	2.00 \pm 1.15	0.33 \pm 0.26	0.17 \pm 0.11
2003(1)	1.75 \pm 1.10	0.50 \pm 0.19	0.58 \pm 0.29	0.25 \pm 0.13
2003(2) ^a	2.38 \pm 1.50	1.38 \pm 0.46	1.63 \pm 0.56	0.13 \pm 0.13
Total Penaeid				
2002	2.08 \pm 0.48	4.17 \pm 1.47	0.42 \pm 0.26	0.25 \pm 0.18
2003(1)	4.33 \pm 2.69	3.08 \pm 0.65	1.33 \pm 0.45	4.92 \pm 1.12
2003(2) ^a	3.75 \pm 1.49	3.63 \pm 0.91	9.50 \pm 3.63	4.63 \pm 0.94
<i>Acetes</i> sp.				
2002	0.08 \pm 0.08	0.25 \pm 0.18	0	0
2003(1)	0.83 \pm 0.46	1.33 \pm 0.58	0	0
2003(2) ^a	0.38 \pm 0.18	0.38 \pm 0.26	0	0
<i>Macrobrachium</i> spp.				
2002	1.00 \pm 0.35	2.08 \pm 0.68	0.17 \pm 0.17	0.17 \pm 0.11
2003(1)	0.67 \pm 0.43	0.42 \pm 0.34	0	0
2003(2) ^a	3.13 \pm 1.51	2.38 \pm 1.22	0	0
Total shrimp community				
2002	2.08 \pm 0.48	6.58 \pm 1.66	0.58 \pm 0.29	0.42 \pm 0.26
2003(1)	6.92 \pm 4.43	5.50 \pm 1.10	1.67 \pm 0.45	5.92 \pm 1.36
2003(2) ^a	8.50 \pm 3.01	7.75 \pm 2.38	10.0 \pm 3.82	5.75 \pm 1.18

^a $n = 8$.

Post-hoc comparisons for *Macrobrachium* spp. and *Acetes* sp. showed a general pattern where sites IP and N had significantly higher abundances ($p < 0.05$) compared to D and MP over both years.

3.3. Multivariate analysis of species assemblages

An ANOSIM (analysis of similarities) for a two-way crossed design was performed. The factors were time of sampling and site. Global tests showed weak differences among sites ($R = 0.187$, $p < 0.001$) with sites IP and N being similar in terms of shrimp species composition and abundance, while site D and MP differed from both IP and N ($p < 0.05$). Site MP and D also differ from each other ($p < 0.01$). SIMPER analysis showed *Macrobrachium* spp. to be relatively strongly associated with the integrated plantation and natural stand as this species, together with *Acetes* sp. were essentially only

found in these sites (Tables 3 and 5). *Penaeus japonicus* characterized the species assemblage for the denuded area, while *Metapenaeus monoceros* showed affinity to forested sites and *P. semisulcatus* was found predominantly in site IP and N (Tables 3 and 5). Comparisons between sampling occasions showed no significant differences. The low values of global R are most likely due to the highly variable and patchy presence of species such as *P. indicus*, which is also the reason this species does not appear in Table 5.

3.4. Species distributions and environmental parameters

A canonical correspondence analysis (CCA) with unrestrained permutations was run and inter-species relationships plotted against percentage sediment organic content, mg chlorophyll a m⁻² as well as percentage fine fraction of total sediment (< 0.075 mm) (Fig. 3).

Table 4
ANOVA test summary for total shrimp abundance as well as abundance of *P. indicus*, *P. semisulcatus*, *P. japonicus*, *M. monoceros*, *Macrobrachium* spp. and *Acetes* sp. with spring tide (time) and site as factors

Source of variation	df	SS	MS	F	p
Total shrimp abundance					
Time	2	1.407	0.704	18.860	<0.001
Site	3	0.725	0.242	6.476	<0.001
Time × site	6	0.772	0.129	3.447	0.004
Error term	116	4.328	0.037		
<i>Penaeus indicus</i>					
Time	2	0.178	0.89	4.997	0.008
Site	3	0.335	0.112	6.268	<0.001
Time × site	6	0.310	0.052	2.899	0.011
Error term	116	2.069	0.018		
<i>P. semisulcatus</i>					
Time	2	0.310	0.155	4.980	0.008
Site	3	0.597	0.199	6.392	<0.001
Time × site	6	0.067	0.011	0.360	0.902
Error term	116	3.610	0.031		
<i>P. japonicus</i>					
Time	2	0.718	0.359	10.702	<0.001
Site	3	0.601	0.202	6.021	<0.001
Time × site	6	1.494	0.249	7.427	<0.001
Error term	116	3.889	0.034		
<i>Metapenaeus monoceros</i>					
Time	2	0.255	0.127	3.043	0.052
Site	3	0.347	0.116	2.760	0.045
Time × site	6	0.233	0.039	0.927	0.478
Error term	116	4.860	0.042		
<i>Macrobrachium</i> spp.					
Time	2	0.351	0.176	5.941	0.003
Site	3	1.305	0.435	14.715	<0.001
Time × site	6	0.280	0.047	1.576	0.160
Error term	116	3.430	0.030		
<i>Acetes</i> sp.					
Time	2	0.100	0.050	2.400	0.095
Site	3	0.277	0.092	4.409	0.006
Time × site	6	0.133	0.019	0.899	0.498
Error term	116	2.432	0.021		

The 1st and 2nd axis of the CCA explained 81.8% of the total variance in distribution of species and environmental variables. The CCA reinforces the pattern observed above, with *Acetes* sp., *Macrobrachium* spp. and *Penaeus semisulcatus* being associated with the natural stand and integrated plantation, *Penaeus indicus* with the matrix plantation, *Metapenaeus monoceros* with all forested sites and *Penaeus japonicus* with the deforested site.

4. Discussion

The variability in shrimp catches among nets at any given site was quite large. Certain nets yielded consistently higher catches of shrimp, a phenomena also observed by Vance et al. (2002), which they attributed to several parameters including local topography and

substrate elevation resulting in highly localized water currents in the mangrove creeks. Vance et al. (2002) also noted a certain degree of predation on shrimps caught in the nets by fish and suggested this to be a possible source of underestimation of shrimp abundance. Predation on shrimps by fish and crabs, which are abundant at all sites in the present study, was observed. Hence this may have led to a similar overall underestimation of shrimp abundance although the method of catch collection was designed to minimize such predation.

Shrimp catches were considerably lower in 2002 compared to 2003 samples. Such natural yearly fluctuations in shrimp abundance have also been observed for penaeids in both Australia and Malaysia (Vance et al., 1998; Ahmad Adnan et al., 2002). In both 2002 and 2003 a similar pattern of shrimp abundance emerged, however, with higher abundances of certain species in certain sites indicating reoccurring preference for these sites over time by a particular species.

Comparisons of individual species abundances showed that some species such as *Penaeus japonicus* and *P. indicus* exhibited a selective preference for the denuded site and the matrix plantation respectively. This pattern is also supported by analysis of similarities showing differences (although weak) in species composition between study areas. The low average similarity values within sites reflect the variance in species occurrence and abundance. Worth noting is that for all forested sites (IP, N and MP) at least three species of shrimps are responsible for 80% of the similarity within sites, whereas for the clear-cut site only one species, *P. japonicus*, accounts for 80% similarity (Table 5, Fig. 2). Many juvenile penaeid species are known to prefer structurally complex micro-habitats as shelter from predation (Primavera and Leбата, 1995; Primavera, 1997; Macia et al., 2003) and this may explain the preference for these forested sites. In all comparisons including the denuded site, *P. japonicus* ranked as the most important characterizing species. In site comparisons including the natural stand, *Macrobrachium* spp. ranked high and could be considered a potential characterizing species.

Penaeus semisulcatus, *Acetes* sp. and *Macrobrachium* spp. were found to be strongly associated with the integrated plantation and the natural stand (Fig 2) and univariate results further support this. *P. semisulcatus* is a penaeid species whose juveniles are known to occur primarily in seagrass beds (de Freitas, 1986; Loneragan et al., 1994; Macia, 2005). The close proximity to adjacent seagrass beds in Gazi may thus explain the higher numbers and more regular occurrence of the species at these sites. To our knowledge no studies exist on habitat preferences and behavioral ecology for *Acetes* sp. and *Macrobrachium* spp. in mangrove environments. Meager et al. (2003) did, however, study other species of these genera and found them in higher abundances in sites with lower elevation, i.e. at greater water depths,

Table 5

Shrimp species responsible for similarities within and dissimilarities between sites of *Sonneratia alba* mangroves in Gazi Bay, Kenya based on shrimp abundance. Natural (site N), replanted (site IP and MP) and denuded (site D)

Site	Species	$\delta_i/SD(\delta_i)$	Contribution (%)	Cumulative contribution (%)	Average similarities
<i>Species responsible for observed similarity between sites</i>					
N	<i>Macrobrachium</i> spp.	0.66	41.63	41.63	30.50
	<i>P. japonicus</i>	0.50	25.63	67.26	
	<i>M. monoceros</i>	0.42	15.63	83.19	
IP	<i>M. monoceros</i>	0.48	24.60	24.60	29.48
	<i>P. semisulcatus</i>	0.51	22.98	47.57	
	<i>Macrobrachium</i> spp.	0.42	20.79	68.36	
	<i>P. japonicus</i>	0.47	20.13	88.49	
MP	<i>M. monoceros</i>	0.60	55.31	55.31	26.86
	<i>P. indicus</i>	0.41	24.64	79.95	
	<i>P. japonicus</i>	0.35	16.87	96.83	
D	<i>P. japonicus</i>	1.39 ^a	82.35	82.35	39.88
		Dissimilarities/SD	Contribution (%)	Cumulative contribution (%)	Average dissimilarities
<i>Species responsible for observed dissimilarity between sites</i>					
IP, N	<i>Macrobrachium</i> spp.	1.02	18.79	18.79	69,71
	<i>M. monoceros</i>	0.96	16.48	35.27	
	<i>P. japonicus</i>	0.94	15.55	50.82	
IP, MP	<i>M. monoceros</i>	0.99	17.95	17.95	78,20
	<i>P. japonicus</i>	0.95	15.57	33.53	
	<i>Macrobrachium</i> spp.	0.76	14.60	48.12	
N, MP	<i>Macrobrachium</i> spp.	1.03 ^b	18.25	18.25	80,22
	<i>M. monoceros</i>	1.00	18.02	36.28	
	<i>P. japonicus</i>	0.98	16.22	52.49	
IP, D	<i>P. japonicus</i>	1.11 ^b	21.56	21.56	74,87
	<i>M. monoceros</i>	0.87	14.37	35.93	
	<i>P. semisulcatus</i>	0.93	14.00	49.94	
N, D	<i>P. japonicus</i>	1.12 ^b	21.64	21.64	73,83
	<i>Macrobrachium</i> spp.	1.02 ^b	17.51	39.15	
	<i>M. monoceros</i>	0.87	13.39	52.54	
MP, D	<i>P. japonicus</i>	1.28 ^b	27.76	27.76	75,15
	<i>M. monoceros</i>	0.96	18.89	46.65	
	<i>P. indicus</i>	0.84	15.60	62.25	

^a The species potentially characterizes the species assemblage within a site.

^b A possible discriminating species between sites.

which also distinguishes the natural stand and integrated plantation in Gazi Bay.

Most individuals of *Penaeus indicus* were caught in the matrix plantation. This species has been shown to have an almost absolute preference for mangroves over unvegetated habitats (Rönnbäck et al., 2001), which may explain its low abundance in the deforested site, but not the extreme low densities in the natural stand and integrated plantation. Differences in sediment properties among forested sites are also unlikely to solely explain this pattern (Fig. 3), as *P. indicus* has previously been found not to select for mangrove microhabitats differing in organic content or proportion of fine sediment (Rönnbäck et al., 2001). The distribution patterns of

Penaeus japonicus has not been extensively investigated in natural environments but studies conducted show this species to have a preference for primarily bare, sandy areas (de Freitas, 1986; Macia, 2005). The same author found that juveniles of this species were able to bury themselves very efficiently in the substratum and possibly able to tolerate quite high temperatures on the exposed sandflats due to this fact. This reported behavior combined with pigmentation providing good camouflage in the sand (personal observation) supports the distribution pattern of *P. japonicus* as the only penaeid species found in significant numbers in the deforested site. This observed distribution pattern may be linked to a preference for sandier substrates (in this

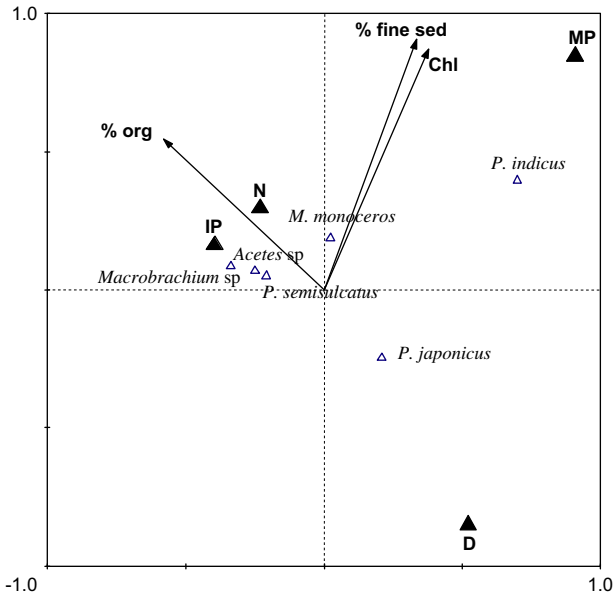


Fig. 3. Canonical Correspondence Analysis (CCA) of shrimp abundance and environmental variables. Biplot with 1st and 2nd axis accounting for 81.8% of total variance of species distribution. Sites are plotted as nominal variables; N=natural stand, IP=integrated plantation, MP=matrix plantation and D=deforested area.

case a direct result of deforestation) rather than active selection of unvegetated areas.

Metapenaeus monoceros has been found to be widespread, occurring in a variety of habitats (Hughes, 1966; de Freitas, 1986; Rönnbäck et al., 2002). However, postlarvae of this species have been reported to have a selective preference for unvegetated shallows while juveniles and subadults were equally distributed among mangroves and adjacent sandflats in Mozambique (Rönnbäck et al., 2002). The present study found *M. monoceros* to be moderately represented in all sites, although with a preference for forested areas. These sites all have a higher degree of fine sediments and organic content compared to the denuded site. Macia (2005) also found this species to prefer fine sediments (muddy), which may be one determinant for habitat choice.

The pattern of distribution of different species of shrimp among the studied sites may be a result of selective preferences of species for certain habitats as suggested by some authors (Hughes, 1966; de Freitas, 1986). However, it is also possible that the observed pattern is a result of survival rather than active habitat selection, in this case indicating a higher level of survival for a larger number of species in the replanted and natural stands of mangroves in Gazi Bay as compared to the deforested area.

5. Conclusions

Slightly higher abundances of the majority of shrimp species/taxa were caught in the integrated and natural stand of *Sonneratia alba* studied. Although there were

no noticeable differences in species diversity between areas these two sites also had a more even distribution of species in terms of percentage composition of catch. They also harbored a higher diversity of penaeid species likely due to greater heterogeneity in terms of structural complexity as well as longer inundation time. There were significant differences in overall shrimp abundance between forested and unvegetated sites, however, catches were also highly variable within microhabitats, which means only modest conclusions should be drawn from this. This suggests that detecting differences in microhabitat preferences for shrimps and evaluating replanted habitat use in the field may call for an even larger number of samples or investigations focusing on larger spatial scales than in this study. However, increasing the spatial scale of investigation often results in variations in physical factors confounding the sampling design. Hence, ideally, future mangrove planting projects should take such aspects into account in order to increase the possibilities of evaluating the return of related ecological functions.

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