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Mangrove fish: A comparison of community structure between forested and cleared habitats

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Keywords

Mangrove, fish, nursery, clearing, stake net, East Africa

Absract

The fish communities of mangrove and cleared sites were investigated in Gazi Bay, Kenya. Five forested sites were compared with paired sites that had been cleared of mangroves by human activity. Forested sites included plantations and natural stands of *Sonneratia alba* and natural *Rhizophora mucronata* stands. Two methods of stake netting were used to take quantitative samples; method one used a single 100m long, 18mm mesh net, method two used paired 24m, 1mm mesh nets – samples were taken during 7 different months in 2002. Mean abundances of fish found in mangrove and cleared sites respectively were 0.004m^2 and 0.014m^2 (method 1) and 0.21 m^2 and 0.25 m^2 (method 2). Thirty species were sampled, 12 of which were found exclusively in mangrove habitats and 10 of which were limited to cleared sites. The most abundant species in mangrove plots was *Atherina afra* (although it was only found in two, large catches); the most abundant in cleared plots was *Gerres oyena* (found frequently). Mean abundance (using data pooled for all sites) was significantly higher in cleared, compared with forested, sites, and multivariate analysis showed significantly different community structures in the two habitat types. There was large variation in catch rates between dates and sites, with one forested site recording no catches at all.These results do not support the predator-refuge hypothesis (which predicts higher abundance of juvenile fish inside mangroves). The low abundance of fish recorded in the mangrove sites may have been due to site-specific factors determining fish abundance within mangrove forests, to the sampling techniques used or to relatively high turbidities at these sites.

Introduction

Mangals (mangrove trees and shrubs and their associated faunal communities) are often cited as providing important habitat for species utilised in commercial and subsistence fisheries, and this ecosystem service provides a powerful argument for mangrove conservation (Chong *et al*, 1990, Lee 1999). The two main hypotheses proposed to explain why mangroves may be attractive to fish are:

1) the predator-refuge hypothesis, which suggests that prey species can avoid predators by migrating into mangals when the trees are inundated by tides (Laegsdgaard & Johnson, 2001). This could be because the structural complexity provided by the aboveground parts of mangroves may reduce predator efficiency by impeding movement or restricting predator vision. Similarly, high turbidity within mangroves may also reduce predator efficiency (Abraham & Kattenfeld, 1997).

2) The feeding hypothesis, which suggests that there is a greater abundance of food, due to the claimed high productivity of the mangroves and the associated epi- and benthic fauna and, hence, greater abundances and diversity of fish (Laegsdgaard & Johnson, 2001).

These hypotheses are not mutually exclusive; a species may favour mangals due to a combination of increased food availability and a reduction in predation pressure. However, they do make different predictions. In particular, the predator refuge hypothesis assumes a more intimate relationship between fish and mangroves – fish must be entering into the mangrove forest at high tide and sheltering among roots and pneumatophores. In contrast, it is possible that fish could benefit from mangrove productivity by feeding on the fringes and in the creeks of a forest, without

necessarily entering the mangrove area itself; carbon produced in mangroves is known to transfer to nearby habitats (Hemminga et al., 1994).

Many studies have provided evidence that mangroves may act as nursery habitat for juveniles of commercially important fish species (e.g. Chong et al., 1990, Robertson & Duke, 1990, Williamson et al., 1994, Sheaves, 1995, Vance et al., 1996, Al-Khayat & Jones 1999, Lee, 1999, Nagelkerken et al., 2000). A smaller number of studies have compared fish communities in mangroves with adjacent habitats, such as mudflats (Chong et al., 1990), seagrass beds and shallow coral reefs (Nagelkerken et al., 2000) and sandy beaches (Williamson et al., 1994). However, despite the importance of this topic for both mangrove conservation and for commercial/artisanal fisheries a recent review has concluded that current evidence is not sufficient to support the idea that mangroves are better nurseries than comparable ecosystems and that more research is needed (cited in Beck et al., 2003).

It is difficult or impossible to use many traditional methods of fishing, such as trawling and seining, within mangroves. For this reason, the majority of studies on mangrove fish communities have caught fish in the habitat immediately adjacent to the mangroves, or in mangrove creeks. One danger of sampling adjacent to mangroves is that small-scale habitat differences may have large effects on fish communities. For example Nagelkerken et al. (2000) found different fish communities within mangroves and in seagrass beds adjacent to them. Hence samples from creeks and adjacent habitat may not be representative of the fish community actually entering mangrove forests at high tide. Relatively few studies, (Thayer et al., 1987, Morton, 1990, Ley et al., 1994,1999, Halliday & Young, 1996, Vance et al., 1996 and Rönnbäck et al., 1999) have reported sampling quantitatively among mangrove trees.

Only two of these (Morton, 1990 and Thayer et al., 1987) made comparisons with adjacent habitats, and these two studies used different methods for sampling outside and within mangroves. The variety of methods used to sample fish communities makes comparisons between mangroves and other coastal habitats difficult.

Quantitative sampling inside mangroves can be achieved using stake-nets (Vance et al., 1996, Rönnbäck et al., 1999). This method encloses a known area of water, and thus allows quantitative comparisons between sites differing in location and habitat. While both the studies by Vance et al. (1999) and Rönnbäck et al. (1999) quantitatively sampled inside mangals, neither provided a comparison with different habitat types near-by. Both studies sampled over relatively short time periods; for seven nights over a period of a fortnight (Rönnbäck et al., 1999) and for six and eight days in November and March respectively (Vance et al., 1996). Seasonal variation in the utilisation of mangroves by fish, which is known to occur at some sites (Halliday & Young, 1996, Ley et al., 1999), and is likely to be the norm rather than the exception, means that longer sampling periods may give different results.

An ideal experimental test (ignoring ethical and logistic implications) of the importance of mangroves to fish would be to compare large replicate pristine mangrove stands with adjacent areas experimentally cleared of mangroves. Such a study has, to our knowledge, never been attempted. The present study uses sites cleared by human activity, for timber, fuel wood and beach access, as ‘treatments’ in such an experiment. The field site is Gazi bay, Kenya. Despite the many publications describing work carried out in Gazi bay, there is little information on the fish communities within the mangroves in this system; although Kimani et al. (1996) found 128 species of fish in the Bay, they did not sample within the mangrove forests. Gazi bay is ideal for carrying out this work, as it has a mixture of relatively

undisturbed and replanted mangrove areas and areas completely cleared of trees. A comparison of fish communities inside mangals and on substrate cleared of trees is described here, using a modified version of Vance et al.'s (1996) stake netting technique. The null hypothesis is that fish abundances, biomass and other measures of community structure are the same in mangals and in areas cleared of mangroves.

Materials and Methods

Site description

Gazi Bay lies 50km south of Mombasa, Kenya (Figure 1). It covers approximately 1.5km^2 and is sheltered from the Indian Ocean by Chale Peninsula. A small, permanent river, the Kindongoweni, flows into the bay from the north. Tidal range is approximately 3.5m and at low water, the mangrove forests and large areas of sand are exposed.

The bay is fringed by approximately 6 ha. of mangrove forests (Kimani et al, 1996), dominated by *Sonneratia alba* and *Rhizophora mucronata*, with *Ceriops tagal*, *Avicennia marina*, *Luminitzera racemosa*, *Bruguiera gymnorrhiza* and *Pemphis acidula* also present. The mangroves exhibit zonation, with the small stands of forest to the south having *Sonneratia* as the most seaward species, and the forests to the north *Rhizophora* as the most seaward species. The landward edge of the mangroves at Gazi is characterised by a zone of *Avicennia marina* and *Pemphis acidula*.

Local people have cleared several areas of mangroves along the intertidal zone at Gazi Bay, mostly for fuel wood. This clearance has created open areas (e.g. Mwamsangaza in Figure 1) that are used by fishermen as landing points, for mooring boats etc. Plots on two of these open areas were selected as cleared sites, for comparison with forested sites. Cleared and forested sites were chosen to allow paired comparisons to be made (that is, they were close or contiguous), and to reflect a range of different types of woodland. The cleared sites used are shown in maps drawn in 1993 (Schrijvers et al., 1995), and so have been open since at least then. They are subject to low level disturbance from local fishermen landing canoes, and there is no natural regeneration occurring.

The sites sampled are shown in Figure 1. Sites 1-5 are forested sites (details in Table 1), and sites 1a-5a are the relevant unforested paired sites. Pore water salinity measurements taken close to our most southerly (Fondo & Martens, 1998) and northerly (Matthijs et al., 1999) sites gave sea water salinity; since all sites were close to the tidal creek (Table 1) salinity levels were unlikely to differ between them. The inter-tidal sand flats and creeks adjacent to all the study sites (Figure 1) support dense seagrass beds that are coupled with the mangroves by fluxes of organic material (Hemminga et al., 1994).

Stake netting

Two different methods were used to sample fish:

Method 1: A 100m long ×3m wide net, of mesh size 18mm and enclosing an area of 625 m^2, was deployed at sites 2, 2a, 5, 5a and 4 during February and March 2002. At forested sites (2, 4 and 5), a rectangular path was cleared of prop roots and pneumatophores. The net was deployed at low tide along the cleared path. The lead line of the net had a chain (10mm) sewn into it; this was buried in the sediment and held in place with wooden pegs. The net was rolled down to the level of the sediment and left until high water. At high water, the top of the net was lifted onto wooden stakes, placed at approximately 3m intervals, such that it cleared the water. This method is a modified version of Vance et al (1996), differing from their approach principally in having the base buried into the sediment, thus preventing any fish from escaping underneath the net.

Samples were taken at four consecutive high waters at each site, giving four samples for each site. Two people walked around the perimeter of the net once each at low

tide, and any fish caught were returned to the laboratory and placed in a freezer. Samples taken at night were collected by torch light. The net was then lowered until the next high water. The consecutive high water sampling ensured that two samples were collected by daylight and two samples were collected by torch light at each site, to ensure equal sampling effort and efficiency for all sites. Since it was not logistically possible to deploy more than one net at a time, paired sites were not sampled simultaneously. Instead, sampling at any given forested site was followed immediately by sampling at the appropriate cleared site.

Method 2: The sampling method was modified in the light of the initial results. Given the relatively small numbers of fish caught, and the logistical problems involved in deploying a 100m net, a method that would catch smaller fish and that would allow simultaneous sampling of paired sites was adopted. Fish were caught during July, August, September, October and November 2002 with two 24m (+1m overlap to seal) long nets of mesh size 1mm (approx) at full stretch (each enclosing an area of 36 m^2). At forested sites (1, 2, 3, 4 and 5), the same procedure for method 1 was followed: a path was cleared to allow placement of the net. The lead line of the net had a rope attached that was buried in the sediment to prevent the bottom of the net lifting up at high tide. Two nets were deployed simultaneously, one at a mangrove site and the other at the relevant paired non-mangrove site.

The nets were deployed at low tide in the same fashion as the larger net in method 1. However, for method 2, each pair of sites was sampled only once before moving the nets to the next pair. Hence, each round of sampling consisted of fishing for five consecutive days, with two samples (from paired forested and cleared sites) taken

each day. Thirty paired samples were taken in total, with one sampling period in July, August, October and November, and two in September.

All fish caught were returned to the laboratory where length, wet weight and species were recorded. Species were classified into broad trophic groups, based on information about feeding habits available from the literature.

Analyses

Results from the netting using method one were used to compile total species lists and to estimate the effects of consecutive sampling in a single site, but were not analysed further. To examine the completeness of the species lists obtained, cumulative species richness curves were produced for mangrove and non-mangrove sites taken with method 2. After correcting for non-normality and heteroscedasticity where necessary, mean total abundance, species richness (i.e. numbers of species) and biomass of fish in mangrove and non-mangrove sites were compared, using paired t-tests (giving eighteen tests in total). The power of these tests was established using the minimum detectable difference procedure described in Zar (1984, p111). Data from all the sampling periods were pooled and used in a split plot ANOVA and in multivariate analyses. The split plot (or semi-nested) ANOVA was conducted as described by Quinn & Keough (2002, p313), with the 'within plot' factor the six sampling rounds. The PRIMER (Plymouth routines in Multivariate Ecological Research) package was used to perform hierarchical clustering with group average linking with the Bray-Curtis similarity measure, followed by Analysis of Similarity (ANOSIM), to assess

for any significant differences between site types, and SIMPER to identify the key species driving any differences detected.

Results

A total of 30 species of fish were caught (using data from both fishing methods). Twelve of these species were found only in mangrove sites, 10 only in cleared sites (Table 2). There was no obvious distinction between trophic groups found in the two habitat types (Table 2). Mean densities of all fish species were $0.004m^2$ and $0.014m^2$ in mangrove and cleared areas respectively, based on method 1, and $0.21\ m^2$ and $0.25\ m^2$ in mangrove and cleared areas, respectively, based on method 2. There were large standard errors around these means (Figures 2a and 2b), with many individual counts of zero and a few large catches of schooling species such as *Atherina afra*. The effects of taking consecutive samples from the same site were examined by plotting abundance against sample number for catches using method one (Figure 3). The most abundant species found in mangrove plots was *Atherina afra* (although it was only found in two, large catches); the most abundant in cleared plots was *Gerres oyena* (found frequently, Table 2). Cumulative species curves (Figure 4) based on catches using method 2 suggest that many species remain to be caught; the fact that eight of the species caught using method 1 were not captured using method 2 supports this conclusion.

To examine temporal variation, mean abundance, biomass and species richness, based on data pooled across sites recorded using method 2 for all dates sampled, are shown in Figure 2a. Late September sampling had the highest abundance and species

richness recorded in both mangrove and non-mangrove sites. There was also considerable spatial variation between sites, revealed by pooling across times to show mean values for individual sites (Figure 2b). Site 1, a *S. alba* plantation, recorded the highest mean abundance, biomass and species richness of the mangrove sites; its paired site, 1a, recorded the highest or second highest variables from the cleared sites. No fish were caught at site 4, a mature, undegraded stand of *R. mucronata* and *A. marina*. Total species richness at all sites was (mangrove/cleared pair) 1: 11/10, 2: 13/9, 3: 7/4, 4: 0/2, 5: 4/9 (Table 2). Hence site 2, a natural *R. mucronata* stand, recorded the highest total number of species, whilst site 4 (also natural *R. mucronata*) recorded the lowest. Sites 1 and 5 were perhaps the most similar, in that both were monospecific plantations of *S. alba*. Despite this, their mean (Figure 2b) univariate measures and total species richness counts were very different.

Because data recorded from the same site at different times may not be independent, results from each sampling round were initially kept separate. After ln (x+1) transformation paired t-tests were performed to test for significant differences in abundance, biomass and species richness. Three of the six sampling rounds recorded higher mean abundance in the cleared sites, but none of these comparisons were significant. Four of the sampling rounds recorded higher biomasses at cleared sites, with one significant difference, and three showed higher species richness at cleared sites, although there were no significant differences. Using the highest variances recorded for each of the three variables, power analyses were conducted to find the minimum detectable differences, assuming 10% chance of type 2 error. These gave the following values (data are ln transformed, with actual maximum differences found in any of the six tests in parentheses): abundance, 3.76 (1.16); biomass, 4.18 (2.37);

species richness, 1.66 (0.55). Hence the large variability in the data, combined with the small sample size of only 6 site pairs, rendered the power of individual tests low. Data were therefore pooled between sampling dates. As suggested above, this procedure may compromise the independence of samples, hence the results of analyses on pooled data need to be treated with some caution. Split plot ANOVAs, with treatment as a fixed factor and plots (paired sites) and times (sampling rounds) as random factors, showed significantly higher abundance in cleared plots, along with significant differences between plots for all the dependent variables (Table 2). The significant treatment × time interaction for biomass means further caution should be exercised in interpreting these results.

Cluster analysis was performed on fourth root transformed data; this corrected for the influence of a single very large catch of *Atherina afra*, and zero catches at site 4. There was a separation of mangrove and cleared sites (Figure 5). Site 4 was distinct since no fish were caught at this site. Site 1 was clustered amongst the cleared sites, reflecting the larger mean abundance of fish caught here, and the fact that 7 of the 8 species found in both types of site were recorded at site 1 (Table 2). Analysis of Similarity gave a global R value of 0.39, and a P value of 0.016; hence there was a significant difference between fish communities from the two types of site. SIMPER analysis identified three species as responsible for 10% or more of the total dissimilarity found: *Gobius nebulosus* (15%), *Gerres oyena* (13.6%) and *Chanos chanos* (11%). Although none of these dominant species were exclusive to cleared sites, they were all more abundant in these sites than within mangroves (Table 2).

Discussion

The aim of the current work was to compare fish communities between forested and cleared sites, with a null hypothesis that there are no differences between site types. This can be rejected; the multivariate analyses show a significant difference in community structure, with the univariate analyses based on pooled data revealing significantly higher mean species richness and abundance at cleared sites. However, total species richness was higher in mangrove sites; 20 compared with 18 in cleared sites. Site 1, a planted *S. alba* stand, had the highest mean abundance, biomass and species richness of the mangrove sites (Figure 2b), along with the second highest total number of species. It also supported many of the species found only in mangroves (Table 2). This suggests that plantations are able to provide suitable (or possibly superior) habitat for fish. Whilst this site is structurally very similar to site 5 (another, older *S. alba* plantation), its fish communities are quite distinct, clustering instead with the contiguous cleared sites (Figure 4). The mangrove sites were more widely dispersed geographically than the cleared sites, which perhaps explains their lower level of similarity (Figure 4). Hence location may be more important that species mix in determining fish use of mangroves.

The densities of fish recorded in the current study were much lower than those reported in most comparable work (Table 4). Only the study by Halliday & Young (1996) found lower densities, but they used an 18mm mesh net, the same as that used in method one. Hence the most appropriate comparison is with densities found using method one, which gave a mean density some 10 times lower than that observed by Halliday & Young (1996). Method one involved the consecutive sampling of the

same habitat, which facilitated sampling logistics with this large net. Halliday & Young (1996), Vance et al. (1996) and Rönnbäck et al. (1999) all report reduced catches on subsequent days when consecutive sampling was used. The present study concurs with this (Figure 3), suggesting that mangrove fish may be territorial or that they avoid areas where capture has recently occurred. Note that this effect is the opposite of that predicted if the initial establishment of stake nets in mangroves, with the associated disturbance of cutting roots and digging, had deterred fish. In that case, catches should increase with time after the first disturbance – there is no evidence of this in the current study (Figures 2a and 3).

Because of the effects of consecutive sampling at the same site, Halliday & Young (1996) give only the densities of their first days' catches. Excluding data from the second of the two consecutive days at each sampling site using method one gives mean densities of 0.01 and 0.022 m^{-2} for mangrove and cleared sites respectively. This is still four times lower than that reported by Halliday & Young (1996). The surprisingly low densities found initially were one of the main incentives for changing fishing method, but despite the use of a 1mm mesh net recorded densities remained amongst the lowest in the literature.

There are at least five possible explanations for this low fish density. First, the current study may have sampled with an unusually low efficiency. Mark-recapture estimates of recovery efficiency in stake netting range from 38% (Ley et al., 1999) to 75% (Thayer et al., 1987). Many stake netting studies (eg Morton, 1990; Vance et al., 1996) used nets with weighted leadlines deployed at high tide. Pilot surveys at Gazi showed that gaps remained under the leadline unless it was buried in the sediment;

hence all samples in the current study were taken after burying the leadlines and removing any possibility of escape underneath the net. Sampling was thus at least as efficient as that reported in most other studies (although studies using a combination of netting and rotenone, such as Ley et al. (1999), may achieve higher efficiencies).

Second, the mangrove habitats and fisheries resources at Gazi have been heavily exploited by cutting and fishing, with a large fishery exploiting the reef some 2km offshore. Whilst fishing pressure could explain the low densities of commercially important, migratory fish species, there were many species that are not exploited offshore which were also found in low densities. Habitat degradation may play a role on a large scale, but cannot explain small scale, between site differences; site 4 is a virtually untouched stand of mature *Rhizophora* and *Avicennia* trees, and yet no fish were ever found here. Highest densities in mangroves were found at site 1, a *Sonneratia* plantation.

Third, to our knowledge this is the first time stake netting has been used in African mangroves, hence all the comparisons in Table 2 are with mangrove systems in other continents. It is possible that the densities recorded are typical of African (or at least East African) mangroves. This seems unlikely, however, since fish diversity in Gazi Bay is comparable to that in similar tropical estuaries (Kimani et al., 1996).

Fourth, the exact positioning and timing of stake netting within a mangrove may affect the densities of fish found. Rönnbäck et al. (1999) compared four sites differing in elevation above sea level (classified as inland or seaward) and mangrove species (*Rhizophora* or *Avicennia*). They found highest fish abundance in their most inland

site, and higher abundances in pneumatophore (*Avicennia*) than in prop root (*Rhizophora*) sites. They speculated that their highest site provided a better predator refuge – being further away from the main channel - than the lower ones, thus supporting more fish. Since Rönnbäck et al. (1999) had no replication for each of their site types, it is not possible to say whether distance from the creek was the genuine causal factor. Although varying in elevation, all of the current sites were close to the main creek (Table 1) thus this effect cannot be tested for. The current results concur with those of Rönnbäck et al. (1999) in finding the lowest densities at a prop root site (site 4). However, this site also differs from the others in many other ways (for example, it is inside a bend in the creek, thus possibly having lower larval supply). Mangrove sites within 75m of each other, at the same tidal level and with the same species of tree, can show consistent differences in fish abundance (Halliday & Young, 1996), and the reasons for these differences are poorly understood. It is possible, therefore, that the sample sites at Gazi happened to have low densities compared with similar sites at Gazi. Untangling the main causal factors for inter-site differences within mangrove systems will require properly replicated experimental studies.

Fifth, there is evidence that the predator refuge function of mangrove forests interacts with water clarity. In experimental manipulations, Laegdsgaard & Johnson (2001) found that some fish that were attracted to artificial mangrove habitats in the presence of predators avoided them when predators were absent; the habitat was therefore attractive as a refuge but was sub optimal as a feeding site. Fish may reduce or eliminate their anti-predator behaviour in turbid waters (Abrahams & Kattenfeld, 1997), since the turbidity itself may provide adequate protection from predators (Cyrus & Blaber, 1992; Maes et al., 1998). Thus in sites with high turbidity (such as

those sampled in Gazi – pers. obs.) fish may not need to enter mangroves in order to gain the advantages of a predator refuge. Information on turbidity is generally unavailable in the papers listed in Table 3. However, it is interesting to note that the highest densities of fish reported within mangroves are from low turbidity sites. Ley et al. (1999) used visual censuses at their sites, which implies high water clarity, and Thayer et al (1987) report a maximum mean density of fish, at a site with high water clarity, some 7-8 times greater than mean densities recorded in more turbid sites. The idea that turbidity may help determine the utility of mangroves as a predator-refuge deserves further study.

The higher mean densities and species richness found in cleared, compared with forested, sites were unexpected. Previous work has reported higher densities inside mangroves compared with adjacent habitats (Table 4). In contrast to these studies, the cleared sites at Gazi are artificial, disturbed habitats, and it is possible that this may affect fish abundance and community structure, hence comparisons with previous work need to be made with caution. However, these results are the opposite of those predicted by the predator-refuge hypothesis, which would imply that fish should enter mangrove stands at high tide in order to hide from predators among prop roots and pneumatophores. A related prediction is that the mean size of fish inside, compared with outside, mangroves should be less, since the vulnerable juveniles seek shelter whilst larger fish move outside to richer foraging grounds (Laegdsgaard & Johnson, 2001). Of the species that were found in both habitat types in sufficient numbers, there were no significant differences in mean length. Only *Chanos chanos* showed a significant difference in mean weight between habitat types (t-test, $t = 7.6$, d.f. = 85, $P < 0.001$); fish caught at mangrove sites were smaller on average (mean biomass, g, ±

S.E.: mangrove sites 0.02 (0.002), cleared sites 0.15 (0.007)). With this exception, therefore, these results do not support the predator refuge hypothesis. This does not imply, of course, that mangroves are unimportant for fish (although it may imply that small patches of mangrove can be removed at Gazi without damaging fish communities). Research in the Caribbean (Nagelkerken et al., 2001) and Australia (Williamson et al., 1994) has shown differences in fish community structure between bays with and without mangroves. Hence mangroves may be exerting an effect on a larger scale than that investigated in the present study, for example by enhancing food supply in contiguous seagrass beds through carbon outwelling (Hemminga et al., 1994), thus affecting fish communities in Gazi Bay as a whole. Intensive sampling at Gazi, mostly using beach seines and benthic trawls, has to date recovered a total of 346 species of fish (Wakwabi, pers. comm). This is higher than that recorded in other tropical, mangrove-fringed bays (e.g. Robertson & Duke, 1987; Williamson et al., 1994; Tongnunui et al., 2002), suggesting that the Bay as a whole is not depauperate in fish.

The small sample sizes recorded mean that any assertions about the dependence of particular species on mangroves must be tentative. However, the commonest of the species found exclusively in mangrove sites, *Sphaeramia orbicularis*, has previously been identified as a true mangrove resident (Mees et al., 1999). Ninety six percent of 1351 individuals caught by fyke nets in mangrove creeks at Gazi belonged to this species (Mees et al., 1999). Because fyke nets sample mangrove habitat indirectly (by fishing the creeks draining from it), it is possible that fish caught using this method are utilising creeks but not mangroves. The current results support the suggestion that *S. orbicularis* is a true mangrove specialist, as does the failure of. Kimani et al. (1996)

to find *S. orbicularis* during intensive seine net fishing of Gazi creeks and the open bay. Seven of the 12 species found only in mangrove sites in the current study were not recorded amongst the 128 species reported by Kimani et al. (1996). This compares with 3 of the 8 species found in both habitat types, and 2 of the 10 species found only in cleared sites. These data support the idea of a distinct mangrove community of fish, consisting of species closely associated with mangroves and thus unlikely to be caught in open water. In contrast, the species found in cleared sites and in both types are likely to be moving more freely between inshore habitats such as creeks, sandflats and seagrass beds.

In conclusion, very low densities of fish were found in both mangrove and cleared habitats, a result which may be specific to Gazi Bay and which could only be fully explained with much more extensive work. The current work provides no support for the predator-refuge theory, which would predict small scale increases in fish abundance in mangrove sites. This could result from the relatively high turbidity at this site obviating this putative function of mangroves.

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TABLE 1. Characteristics of mangrove sites. Fringe width refers to the minimum distance from the sampling site to the seaward fringe of mangroves. Status: P = planted (with age in years), N = natural, D = degraded (obvious signs of cutting).

Site	Species	Max. tree height (m)	Fringe width (m)	Status	Substrate type	% C*
1	*S. alba*	5	10	P (6 yr)	Muddy sand	n.a
2	*R. mucronata* (dominant), *B. gymnorrhiza, C. tagal, A. marina*	10	7	N (D)	Muddy sand	4.7
3	*S. alba* (dominant), *C. tagal*	8	6	N (D)	Mud	7
4	*R. mucronata* (dominant), *A. marina*	12-15	15	N	Muddy sand	3.4
5	*S. alba*	8	20	P (15 yr)	Muddy sand	0.35

* of sediment, by loss of weight on ignition. Note that these data were not collected in the present study, but are taken, where possible, from sites close to the present ones described in Schrijvers et al. (1995) and Middelburg et al. (1996).

TABLE 2 –Total catches using both methods at all mangrove and cleared sites. Feeding types (from the literature and some gut content analyses) refer to major food groups taken by appropriate size classes: B = zoobenthos, Z = zooplankton, D = detritivore, H = macroalgae and phytoplankton, N = fish/predator, N/A = not available.

Species (family)	**Total captures**	**Percent in mangroves**	**Feeding type (B, Z, C, H)**	**Sites found**
Both site types				
Atherina afra (Atherinidae)	166	98	B Z	1,1a, 2a
Gerres oyena (Gerreidae)	157	8	B Z	1,1a,2,2a,3a,4a,5,5a
Chanos chanos (Chanidae)	101	12	B Z H D	1,1a,2a,3,3a,5a
Gobius nebulosus (Gobiidae)	57	21	N/A	1,1a,2a,3a
Engraulis japonicus (Engraulidae)	25	56	B Z H	1,2,2a,3a
Lutjanus ehrenbergi (Lutjanidae)	24	63	B N	1,1a,2,2a,3,5,5a
Sphyraena jello (Sphyraenidae)	7	71	N Z	1,2,5,5a
Valamugil seheli (Mugilidae)	6	17	D H Z	2,2a
Mangroves only				
Sphaeraemia orbicularis (Apogonidae)	5	100	B Z N	1,3,5
Saurida undosquamis (Synodontidae)	4	100	B Z N	2, 3
Hemiramphus far (Hemiramphidae)	4	100	Z H	1,2,3
Monodactylus argenteus (Monodactylidae)	3	100	D Z H	2,3
Lutjanus bohar (Lutjanidae)	1	100	B N	2
Lutjanus argentimaculatus (Lutjanidae)	1	100	B Z N	2
Callogobius maculipinnis (Gobiidae)	1	100	N/A	2
Upeneus sulphurous (Mullidae)	1	100	B	1
Narke capensis (Narkidae)	1	100	B	1
Sphyraena putnamiae (Sphyraenidae)	1	100	N	2
Antennablennius australis (Bleniidae)	1	100	N/A	2
Sorsogona prionata (Platychepalidae)	1	100	N/A	3
Cleared sites only				
Caranx sexfasciatus (Carangidae)	10	0	B Z N	4a,5a
Lethrinus harak (Lethrinidae)	7	0	B N	1a,2a
Gerres filamentosus (Gerreidea)	5	0	D B	1a
Caranx ignobilis (Carangidae)	4	0	N B	5a
Terapon jarbua (Teraponidae)	3	0	D B Z H	1a,5a
Sillago sihama (Sillaginidae)	3	0	B Z H	5a
Sphyraena barracuda (Sphyranidae)	2	0	N	1a
Gnathanodon speciosus (Carangidae)	2	0	B N	1a
Sardinella melanura (Clupeidae)	1	0	Z H	2a
Leiognathus equulus (Leiognathidae)	1	0	D N B Z	5a

TABLE 3 – Split plot ANOVA results for pooled, ln (x+1) transformed data from method 2, with paired sites treated as plots and treatment (wooded or cleared) as the only fixed factor. F values are calculated as described in Quinn & Keough (2002, p317).

Abundance

Factor	Df	MS	F	P
Treatment	1	8.2	12.5	0.017
Plot	4	7.1	5.7	0.003
Time	5	3.6	3.9	0.11
Trt×time	5	0.66	0.7	0.66
Plot×time	20	1.26	1.3	0.29
Error	24	0.99		
Total	59			

Biomass

Factor	Df	MS	F	P
Treatment	1	2.5	0.4	0.54
Plot	4	6.3	3.5	0.04
Time	5	2.9	0.5	0.79
Trt×time	5	5.9	3.7	0.01
Plot×time	20	2.1	1.3	0.28
Error	24	1.6		
Total	59			

Species richness

Factor	Df	MS	F	P
Treatment	1	1.2	5.8	0.06
Plot	4	1.3	4.5	0.01
Time	5	1.2	3.7	0.06
Trt×time	5	0.2	1.1	0.38
Plot×time	20	0.3	1.7	0.12
Error	44	0.2		
Total	59			

TABLE 4 –Comparison of mean densities found in the current study with comparable studies from the literature. Stake net refers to studies where an area is entirely enclosed; block netting involves enclosing two or three sides of an area with net.

Study	Mean density (fish m^{-2}) in mangroves	Mean density (fish m^{-2}) in adjacent habitats	Fishing gear used
Current	0.004 (method 1) 0.21 (method 2)	0.014m^2 (method 1) 0.25 m^2 (method 2)	Stake net (18 and 1 mm mesh)
Halliday and Young (1996)	0.04	NR	Block net (18mm mesh)
Ley et al (1999)	6.5	NR	Block net (6mm mesh) with rotenone, and visual estimation
Morton (1990)	0.27	0.15	Block net (18mm mesh) in mangroves. Beach seine (150mm mesh) in adjacent habitat
Robertson and Duke (1990)	3.5	NR	Block net (3mm mesh)
Rönnbäck et al (1999)	5.1	NR	Stake net (2-3mm mesh size)
Thayer et al (1987)	8.0	0.22	Block net (3mm mesh) and rotenone in mangroves. Otter trawl (3mm mesh tail bag) in adjacent habitat
Vance et al. (1996)	0.83	NR	Stake net (2mm mesh)

FIGURE 1. Map of Gazi Bay showing the sampling sites (adapted with permission from deTroch et al., 2001).

FIGURE 2 (a) Mean (± SE) abundance, biomass and species richness of all fish taken from mangrove (black) and cleared (open) sites using method two during six separate rounds of sampling (starting dates shown). Each bar represents a mean of n=5 sites * significant difference ($P<0.05$).

FIGURE 2 (b) Mean (± SE) abundance, biomass and species richness of all fish taken from the five mangrove (black) and cleared (open) sites; data pooled across all sampling dates.

FIGURE 3. Effects of consecutive sampling using method one. Each graph shows total numbers caught at the same site at four sampling times each separated by 12 hours. Site 4 is not shown because no fish were caught.

FIGURE 4. Cumulative species curve for fish caught at all mangrove and cleared sites using method two.

FIGURE 5. Dendrogram showing cluster analysis (average linkage with fourth root transformed data of Bray Curtis similarity) of pooled fish data collected from all mangrove (1-5) and paired, cleared (1a-5a) sites.

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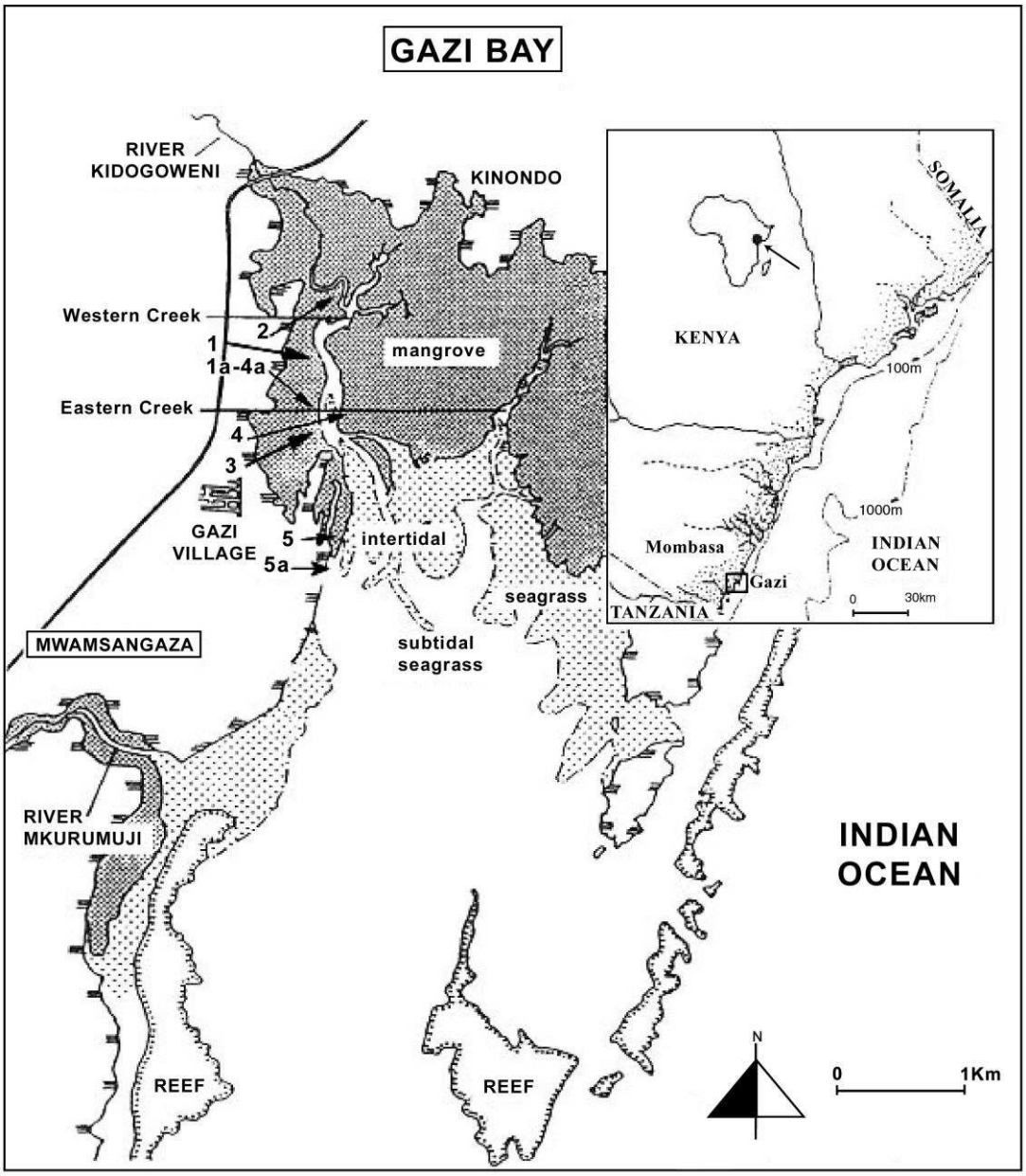

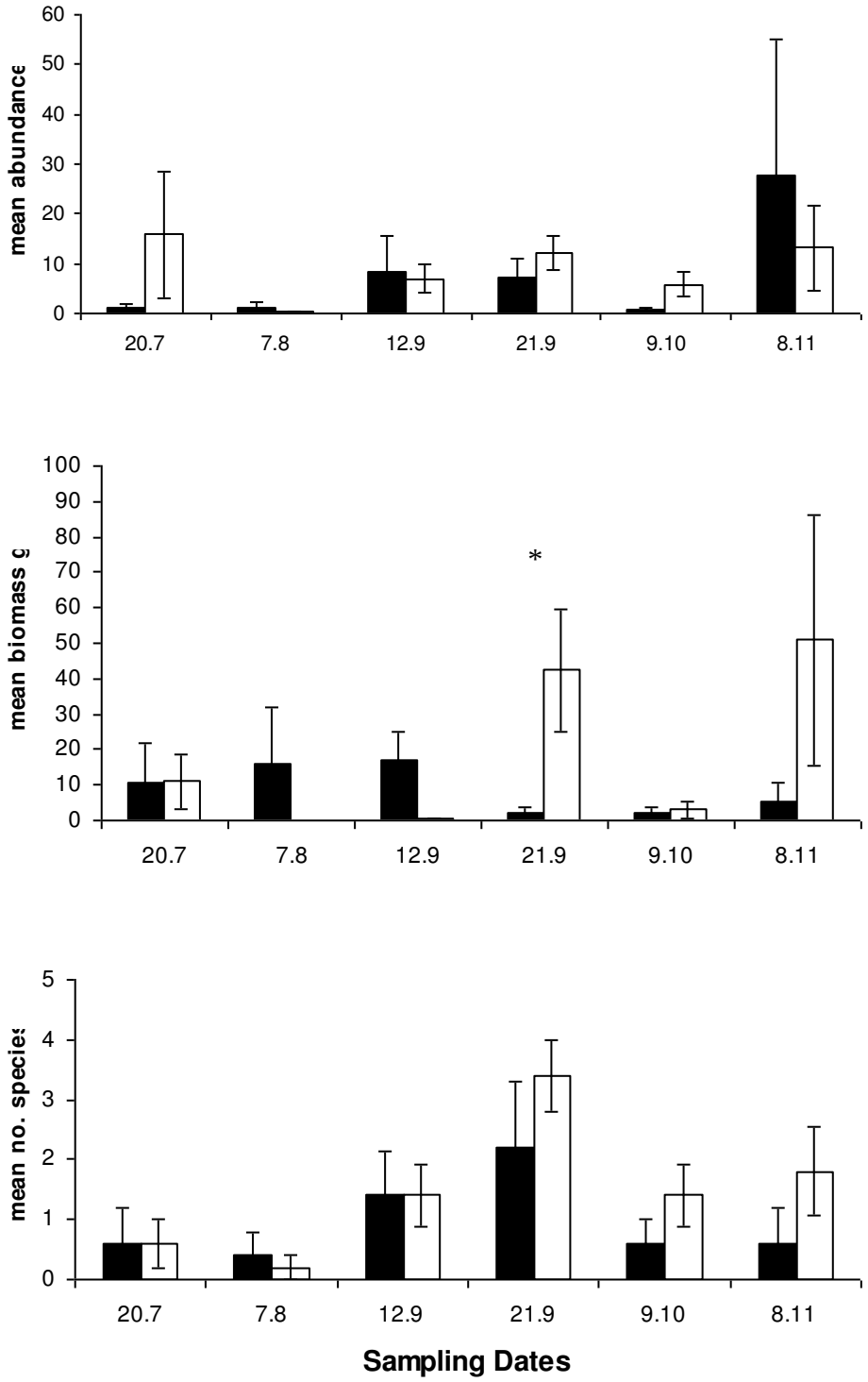
mean abundance
60
50
40
30
20
10
0
20.7
7.8
12.9
21.9
9.10
8.11
mean biomass g
100
90
80
70
60
50
40
30
20
10
0
*
20.7
7.8
12.9
21.9
9.10
8.11
mean no. species
5
4
3
2
1
0
20.7
7.8
12.9
21.9
9.10
8.11
Sampling Dates

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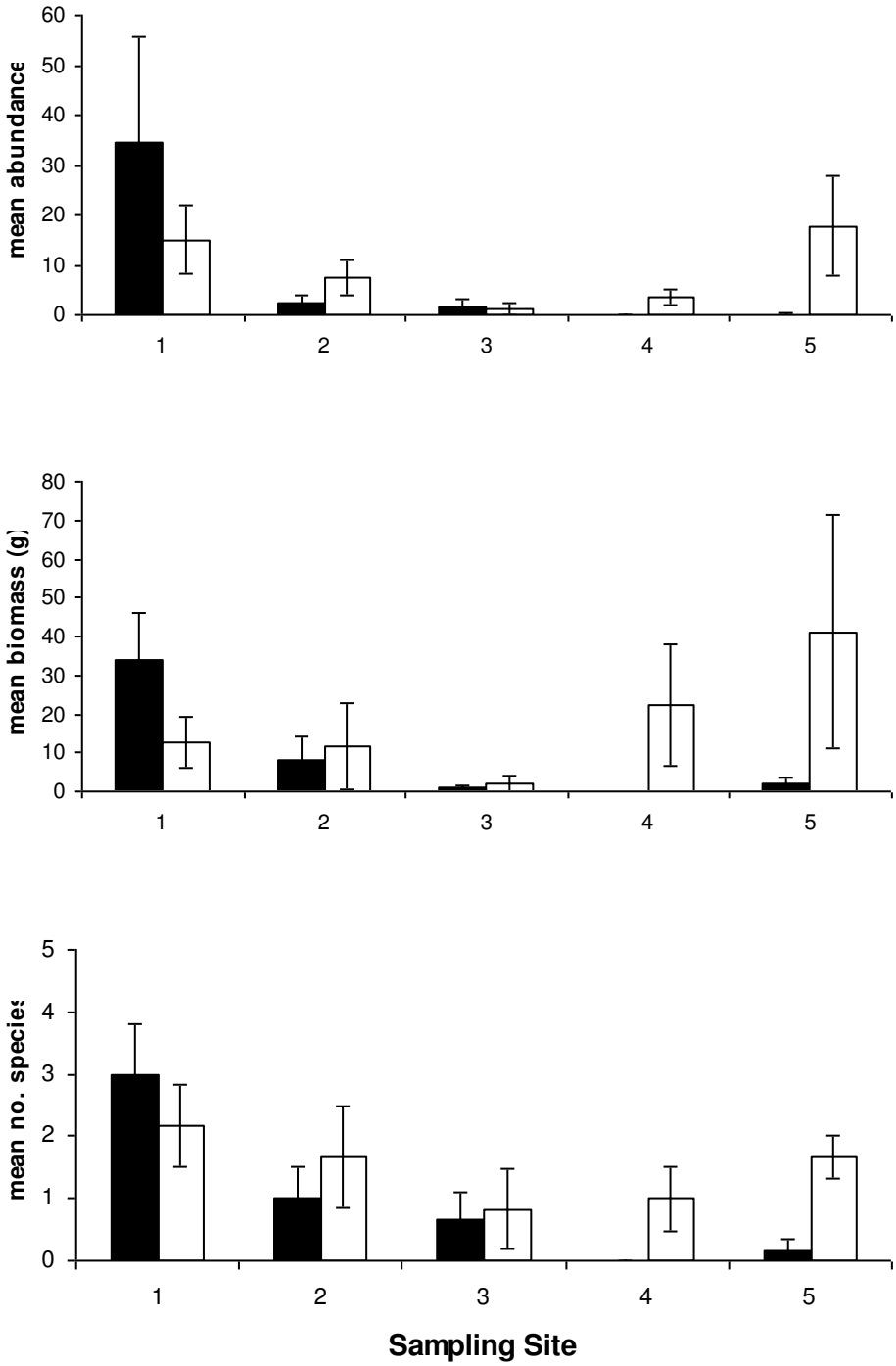

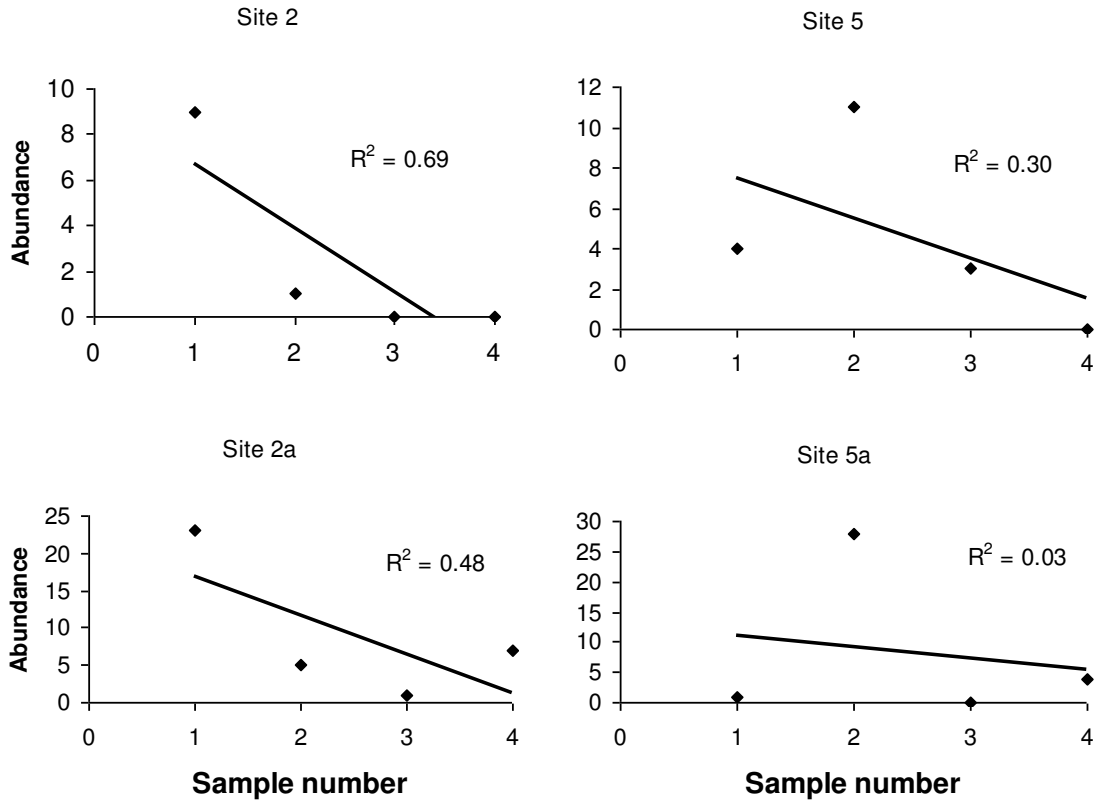
Site 2
Site 5
Site 2a
Site 5a
Abundance
Abundance
R^2 = 0.69
R^2 = 0.30
R^2 = 0.48
R^2 = 0.03
Sample number
Sample number

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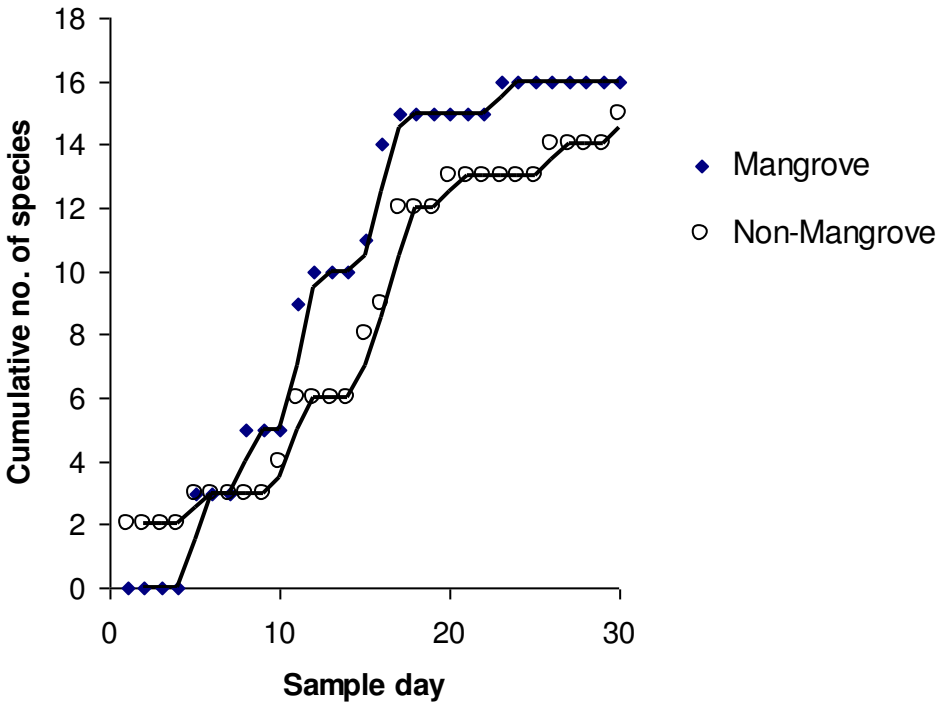

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