

The Fish Community of an East African Mangrove: Effects of Turbidity and Distance from the Sea

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Abstract—Mangroves are often reported as nursery grounds for fish. Fish may enter mangroves in order to avoid predators, but may not need to do so if turbidity provides a sufficient predator refuge outside the forest. This study assessed the effects of turbidity in the field and laboratory on mangrove fish community structure and behaviour. The extent to which fish penetrate into mangroves has received little attention. This study also looked at differences in fish community structure at mangrove sites near (6m) and far (200m) from the mangrove/sea boundary.

Twelve field samples were taken at approximately monthly intervals from replicate 25m² landward and seaward plots, in a *Sonneratia alba* stand at Gazi Bay, Kenya. A total of 25 species of fish were caught, 15 in seaward plots and 13 in landward ones. Mean abundance for all plots and sampling times was 2.15 (equivalent to 0.09 m⁻²). Seaward plots had a total mean abundance more than twice that of landward plots (2.75 ± 1.9 S.D. vs. 1.23 ± 0.33 S.D. respectively). There was no relationship between abundance and turbidity. Laboratory experiments showed no significant changes in behaviour of three common species in response to turbidity. The low density of fish recorded concurs with previous work, and probably reflects conditions in Gazi Bay as a whole, rather than unusual features of the mangrove environment there.

INTRODUCTION

Many studies have shown that mangrove habitats can support high abundances and diversities of juvenile fish, suggesting that they can be important nursery sites (e.g. Chong *et al.*, 1990; Robertson & Duke, 1990; Williamson *et al.*, 1994; Sheaves, 1995; Vance *et al.*, 1996; Nagelkerken *et al.*, 2000a; Lugendo *et al.*, 2005). The two leading explanations for the nursery role of mangroves are: 1) the predation risk hypothesis – juveniles can reduce the risk of predation by larger fish by entering the spatially complex environment of the mangrove forest, 2) the food availability hypothesis – there is greater availability of food in mangroves compared with adjacent habitats (Laegdsgaard & Johnson, 2001). The hypotheses are not mutually

exclusive; for example, food availability within mangroves may be enhanced because foraging efficiency is higher compared with habitats that require greater anti-predator vigilance (Boyer *et al.*, 2004). Whilst some studies do suggest that the enhanced abundance of food in mangroves might attract some species (e.g. Laegdsgaard & Johnson, 2001), the weight of evidence now favours the importance of predator-avoidance. For example, Mumby *et al.* (2004) showed that mangroves allowed juvenile fish to grow to larger (and thus less vulnerable) sizes before risking the migration to adult habitats; they suggest that mangroves ‘alleviate a predatory bottleneck’ during early ontogeny of coral reef fishes.

Mangroves may afford protection against predation in at least two ways: by providing literal

refuges against predators, such as narrow spaces between pneumatophores, and by obscuring the visibility of the prey species. The fact that some species are attracted to shaded areas, regardless of habitat complexity, supports the idea that they are hiding from view (Cocheret de la Moriniere *et al.*, 2004). Reductions in visibility can also be caused by turbidity, which decreases the visibility of distant objects comparatively more than those that are only visible at short distances, and hence is likely to have a bigger impact on the feeding abilities of piscivores compared with planktivores (De Robertis *et al.*, 2003). Since the juveniles of most fish species that utilise mangroves at the current field site, Gazi Bay, are planktivorous or benthic feeders (Kimani *et al.*, 1996; Huxham *et al.*, 2004), and are preyed upon by larger piscivores, this differential effect of turbidity should provide an advantage in turbid habitats. It has long been argued that turbidity attracts juvenile fish because of the potential predator refuge it provides (Blaber & Blaber, 1980; Abrahams & Kattenfeld, 1997; Maes *et al.*, 1998). Hence the attraction of mangroves might be explained by the high turbidity of the waters in which many are found.

In the absence of predation risk, fish seeking refuge might be expected to forsake the mangroves. For example, species may move from mangroves to mudflats or seagrass beds as they grow larger, the concomitant reduction in predation risk allowing them to exploit the greater abundance or suitability of prey in these habitats (Laegdsgaard & Johnson, 2001; Lugendo *et al.*, 2005). Similarly, fish may leave the mangroves during night-time to forage in adjacent seagrass beds (Nagelkerken *et al.* 2000b). Both these phenomena suggest that predator refuge, rather than food availability, explains the use of mangroves by the species involved. Increased turbidity in non-mangrove habitats will reduce the risks from visual predators in those habitats, allowing fish to leave the cover of the mangroves to forage. Hence mangroves may be less important to juvenile fish during periods, or in locations, with high adjacent turbidity. This may explain the higher densities of fish in clear, as opposed to turbid, mangrove areas reported by Thayer *et al.* (1987). During previous work at Gazi Bay, Huxham *et al.* (2004) found relatively low densities of fish within the mangroves, and speculated that this could be

due to relatively high turbidity in the Bay. The main objective of the current work was to explore this possibility further by examining the relationships between turbidity and fish density and diversity in the field, and to complement this with behavioural work in the laboratory with three relevant species. The null hypotheses were those of no relationship between turbidity and fish communities, and of no behavioural response of individual fish to different turbidity treatments.

A secondary objective of the current work was to determine whether fish community structure differed between landward and seaward areas of mangroves. Sampling fish within mangroves is difficult, since the vegetation prevents the use of conventional techniques such as seine nets. A growing literature reports studies using block or stake nets operated within the forests, which unequivocally establish the presence of fish in the habitat and provide density estimates. However, much remains unknown about fish use of mangroves. For example, only one study (Vance *et al.*, 1996) has measured the extent to which fish penetrate into the forest. Whilst most work reports single or replicate nets set at or close to the mangrove/sea boundary, Vance *et al.* (1996) compared a site some 50 m from the sea with sites 23 m away and contiguous with the mangrove creek boundary, and reported lower densities at the most inland site. However, their inland site was un-replicated and contained a different species of mangrove compared with their seaward sites, hence it is difficult to generalise from their work. The current study used replicated plots set in a monospecific stand of trees to examine the effects of distance from the sea.

MATERIALS AND METHODS

Study area

This work was conducted at Gazi Bay, on the southern Kenyan coast some 60 km south of Mombasa at 4°25'S and 39°50'E (Figure 1). The Bay covers approximately 1.5 km² and is sheltered from the Indian Ocean by Chale Peninsula. A small, permanent river, the Kindongoweni, flows into the bay from the north. Maximum tidal range is approximately 3.8 m, with salinities in the Bay

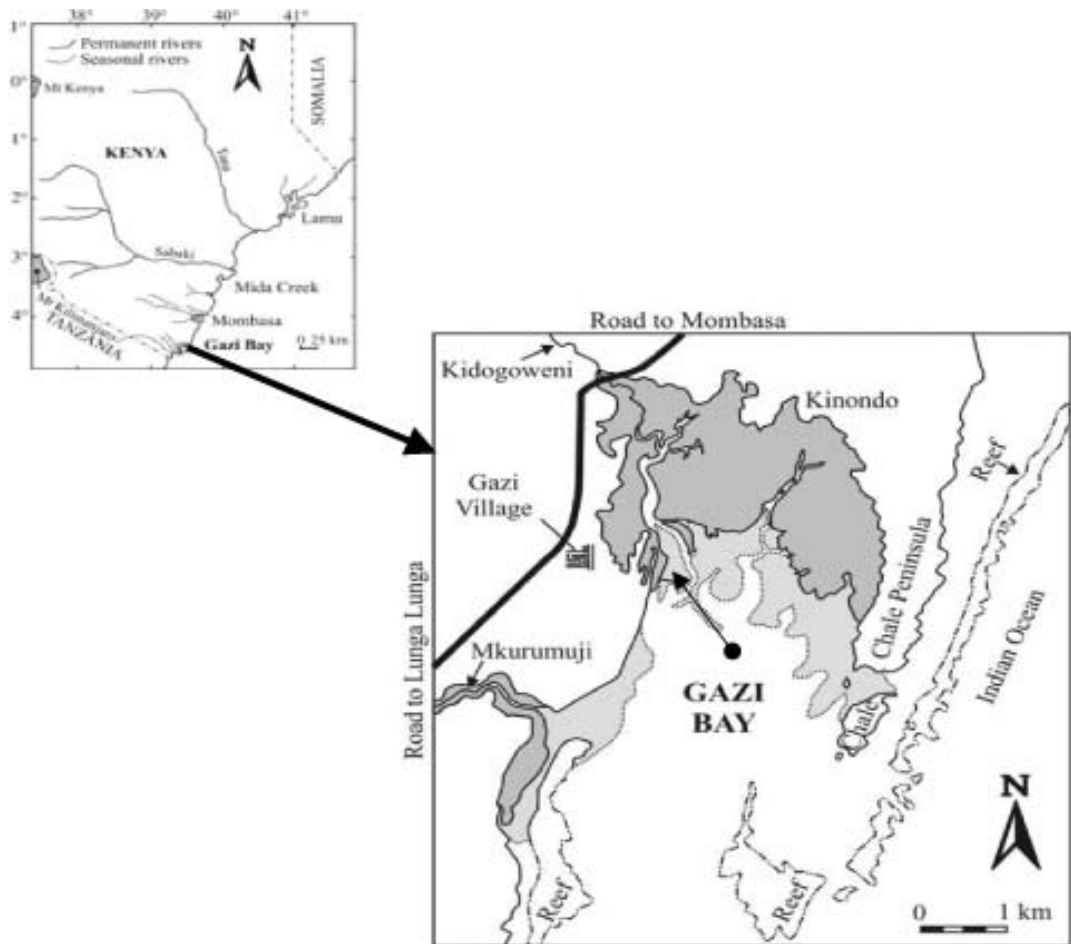


Fig. 1. Map of the study area (re-drawn from Bosire *et al.* 2003). The location of the study site is indicated by the arrow. Dark shading shows mangrove areas, light shading sea-grass beds

ranging from 24 ppt. during the SE Monsoon (Kitheka, 1997) to 34 ppt. (pers. obs.). The more exposed, southerly shores of the Bay are lined with fringing *Sonneratia alba* mangrove stands. The current study was conducted in one of these stands, a mostly natural *Sonneratia* forest which also had some deliberately planted trees (established in 1994). The site is approximately 250 m wide (from seaward to landward edge) with a maximum water depth of 1.8 m at spring high tide; the semi-diurnal tidal regime exposes all trees at the site twice a day. It is characterised by a muddy sand substrate (with 6 % silt content) and experiences the same salinity regime as does the Bay as a whole. Further details are provided by Crona & Rönnbäck (2005), who refer to this area as their 'integrated plantation' site.

Field sampling

Six plots were established in August 2005 in two distinct areas within the stand; three close to the landward and three to the seaward fringe of the mangroves. Each plot was a 5×5 m square area, with approximately 40 m between plots in the same area and approximately 200 m between areas; seaward plots were all within 6 m of the seaward fringe, whilst landward plots were all at least 200 m from the sea, and within 10 m of the landward fringe. Mean pneumatophore density in the plots was 193 (± 79 s.d.) per m². Stake nets were used to catch fish, as described in Crona & Rönnbäck (2005) and Huxham *et al.* (2004). Plots were enclosed with 22 m long × 2.5 m high nets of 2 mm stretch mesh size. On the day before fishing, the bottoms of the

nets were buried in the substrate, and they were rolled down to be flush with the substrate surface. At high tide the following day, nets were carefully raised by hand, and the tops secured on stakes or branches, thus enclosing 25 m² of water; captured fish were recovered at the subsequent low tide. All fishing was conducted at spring high tides at or shortly after 08.00 hours (i.e. approximately 2 hours after daybreak). The first samples were taken on 21 August 2005, and eleven more sets of samples were taken at approximately monthly intervals over a year. On the sixth sampling date (6 March 2006) an additional replicate plot was added to seaward and landward areas, giving a total of four replicates in each area.

The species, weight and standard length of all fish recovered from the plots were recorded. A 20 ml sample of water was taken at 1 m height above the ground adjacent to and seaward of each of the plots immediately before raising the nets at each sampling date. Turbidity was measured in these samples using a Hach DR 890 handheld colorimeter, which gives readings in Formazin Attenuation Units (FAU), which are equivalent to Nephelometric Turbidity Units (NTU).

Laboratory experiments

The laboratory work was completed at the KMFRI Gazi field station. The bottoms of two circular plastic tanks (1 m diameter) were covered in ~ 5 cm of coral sand. Half of each tank was designated as a simulated mangrove habitat, created by using *Avicennia marina* pneumatophores pushed firmly into the sand at a density of 38 m⁻², equivalent to a low natural density in *Avicennia* stands at Gazi. The other half represented bare sediment.

150 l of fresh, unfiltered, seawater were placed in each tank, giving a depth of approximately 20 cm. This depth of water allowed the turbidity to be raised while still allowing the observer to see the fish. One tank was used as a clear control and had seawater only. Kaolin (~7 g) was stirred into the water in the other tank to increase turbidity; sufficient Kaolin was added to raise turbidity to high ambient levels (~ 30 FAU). Water turbidity was recorded at the end of each observation period in each treatment using the colorimeter; pilot testing had shown little change in turbidity levels over 30

minutes using this set-up. A single fluorescent tube directly above both tanks provided light. The tanks were placed side by side in close proximity to allow each to be observed simultaneously.

Juveniles of two species, *Lutjanus fulviflamma* and *Lethrinus harak*, and adults of one other, *Sphaeramia orbicularis* were used in the experiment; the size ranges of the juveniles were 80-103 mm and 60-120 mm for each species respectively. *L. fulviflamma* and *L. harak* are known to use the mangroves before migrating offshore (Huxham *et al.*, 2004, Huxham pers. obs.). *S. orbicularis* is a lifetime resident of the mangrove areas in Gazi Bay (Kimani *et al.*, 1996; Huxham *et al.*, 2004). Fish were caught by local fishermen in mangrove creeks and brought to the field station for observations. The fish were left in a holding tank until observation, and placed in a second holding tank after observations. After all observations were completed, fish were returned to the sea as close to the capture site as possible and were held at the field station for less than 48 hours.

Observations were carried out on two fish (one fish per tank) simultaneously. Each fish was placed first in either the control (clear) or treatment (turbid) tank, left to acclimatise for 30 minutes and then observed for a further 30 minutes. During the observation period, the locations of the fish (either pneumatophore or bare sediment) were recorded once each minute for 30 minutes. Fish were then swapped between tanks, and a further round of acclimatisation and observations was carried out on two fish simultaneously. After each acclimatisation and observation period, the water in the high turbidity treatment was vigorously stirred to re-suspend any kaolin that may have settled out of the water column.

Statistical analyses

The effects of turbidity on abundance of fish were explored by regressing the number of fish caught per plot against the turbidity measured for that plot, and also the summed abundance per date against the mean turbidity, measured at all plots, for that date. Mean species richness and abundance of fish were compared between landward and seaward areas using repeated-measures ANOVA, with time as the within-subject and area the between subject factors,

following transformations for heteroscedasticity where necessary. Mean size (summed across dates) was compared between sites for species caught in sufficient numbers using t-tests. Fish community structure was compared between landward and seaward areas using Shannon-Weiner (with log e) diversity and Pielou's evenness measures, and Multi-Dimensional Scaling, based on Bray-Curtis similarity measures following transformation, on community data summed over all sampling dates. One way Analysis of Similarity (ANOSIM) was performed to test for significant differences between communities. Differences in behaviour shown in the laboratory experiment were analysed

factor, also showed no significant differences, and there were no obvious trends in abundance over time (Figure 2a). Mean (\pm S.D.) number of species for all plots across all sampling times was 0.85 ± 0.49 . Whilst mean and total number of species caught was higher in the seaward plots (Table 1), repeated measures ANOVA on square-root transformed data showed no significant differences in mean number of species in landward and seaward plots, and there were no significant differences in Shannon-Weiner diversity or Pielou's evenness (t-tests, Table 1). Only two species, *Gerres oyena* and *Lutjanus fulviflamma*, were caught in sufficient numbers at both landward and seaward plots to

Table 1. Summary data for seaward ('sea') and landward ('land') plots. Means are \pm S.D. Abundance, species and turbidity are means for unpooled data. Shannon-Weiner (H') and Pielou's evenness (J') are means for data pooled across dates

	Mean Abundance	Mean Species H'	Mean J'	Mean	Total count	Total sp.	Mean Turbidity
Sea	2.75 ± 1.9	0.99 ± 0.48	1.29 ± 0.38	0.71 ± 0.16	125	15	12.7 ± 18
Land	1.23 ± 0.33	0.72 ± 0.49	1.19 ± 0.68	0.75 ± 0.19	53	13	11.3 ± 10

by comparing the mean times spent by each species of fish in the pneumatophore habitat in turbid and clear treatments, using paired t-tests. Statistical analyses were performed using SPSS v14 and PRIMER 5 software.

RESULTS

Field sampling

A total of 25 species of fish were caught over the 12 sampling dates. 15 species were recorded in seaward plots and 13 in landward ones (Table 1). Three species were found in both areas – these were three of the four most abundant species caught. Most of the species were recorded only in low numbers, with 13 represented as only a single individual (Table 2). Mean abundance for all plots and sampling times was 2.15 (equivalent to 0.086 m^{-2}). Seaward plots had a mean abundance more than twice that of landward plots (Table 1); however the large variance meant this difference was non-significant (t-test after $\log_{10} x+1$ transformation). Repeated measures ANOVA on square-root transformed abundance data, with time as the within subject

Table 2. All species caught over the twelve sampling dates, with total numbers for individuals caught in seaward and landward plots

Species	Seaward	Landward
<i>Anchoviella commersonii</i>	38	
<i>Amblygobius phalaena</i>		1
<i>Apogon fraenatus</i>	1	
<i>Archamia fucata</i>	1	
<i>Corythoichthys amplexus</i>	1	
<i>Gerres oyena</i>	34	23
<i>Hepsetia penguis</i>		1
<i>Lutjanus fulviflamma</i>	9	12
<i>Lutjanus ehrenbergi</i>		3
<i>Gobius nebulosus</i>		1
<i>Periophthalmus koelreuteri</i>	8	3
<i>Ostracion cubicus</i>		1
<i>Pseudopeneus barberinus</i>		1
<i>Platycephalus crocodilus</i>	1	
<i>Parapriacanthus guentheri</i>	6	
<i>Pelates quadrilineatus</i>	3	
<i>Saurida undosquamis</i>	1	
<i>Sardinella melanura</i>		2
<i>Sphaeramia orbicularis</i>	1	
<i>Sphyrnaea barracuda</i>		3
<i>Sphyrnaea jello</i>	4	
<i>Spratelloides gracilis</i>	11	
<i>Sygnathidae</i> sp.		1
<i>Synchiropus stelatus</i>		1
<i>Terapon jarbua</i>	6	

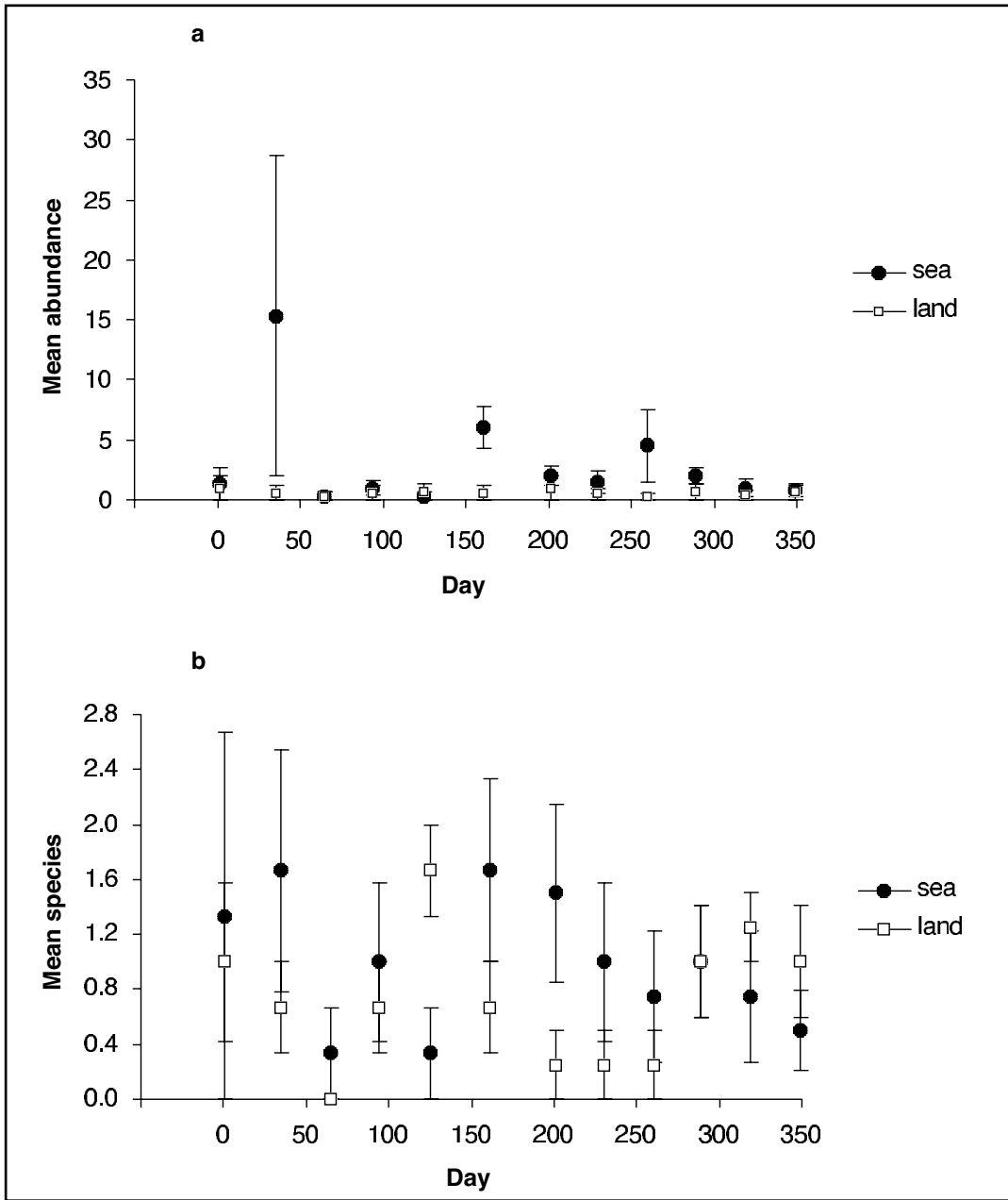


Fig. 2. Mean (\pm S.E.) abundance (a) and species number (b) of fish caught at the seaward and landward plots on each of twelve sampling occasions; day 1, the first sampling time, was 28th August 2005. N = 3 for the first 6 samples, and 4 for the last 6

allow statistical comparisons of their mean sizes; because crab predation (of fish caught in nets before collection) made weight measurements unreliable only length was used. *G. oyena* individuals caught in the landward plots were significantly larger than those in the seaward plots (t-test, $t = 2.9$, d.f. = 29, P

= 0.008), whilst there was no significant difference between *L. fulviflamma* size in the two areas.

Abundances of individual species were highly variable. For example, on the only occasion *Anchoviella commersonii* was encountered, 38 individuals were caught (making by far the largest

single catch). To reduce the influence of such abundant species, 4th root transformed data were used to construct the MDS plot, which showed a tendency for the landward and seaward sites to separate (Figure 3). However, ANOSIM analysis of landward compared to seaward data showed a non-significant difference.

Turbidity measurements over the year were very variable and ranged from 0 – 109 FAU, with no significant differences between seaward and landward plots (Table 1). Highest values were recorded in the months of June, July and August, suggesting some seasonality in turbidity. There was no significant relationship between turbidity and fish abundance, either for individual plots (Figure 4a) or for mean values per date (Figure 4b).

Laboratory experiments

All three species showed a strong preference for the pneumatophore over the bare half of the tank, regardless of the clarity of the water (Figure 5). Large and significant differences in turbidity were maintained between clear and turbid treatments – mean turbidity (FA units) for turbid treatments was 32, compared with 6.3 for clear treatments.

However, there were no significant differences in the time spent in the pneumatophore half of the tank for any of the three species investigated (Figure 5).

A striking behaviour of *L. harak* may explain the lower time it spent in pneumatophores in clear water compared to turbid water: some of the individuals buried themselves in the sediment on their sides with only a single eye visible at the sediment surface. This burial behaviour may provide a predator refuge, thus reducing the refuge value of the mangroves to this species.

DISCUSSION AND CONCLUSION

Field sampling

Huxham *et al.* (2004) reported low densities of fish within mangrove habitats at Gazi, a finding repeated in the current work. The overall mean density of 0.09 m⁻² is almost two orders of magnitude less than the highest densities reported from mangrove sites (Thayer *et al.*, 1987) and amongst the lowest reported in the literature (see Table 4 in Huxham *et al.*, 2004). Methodological differences are unlikely

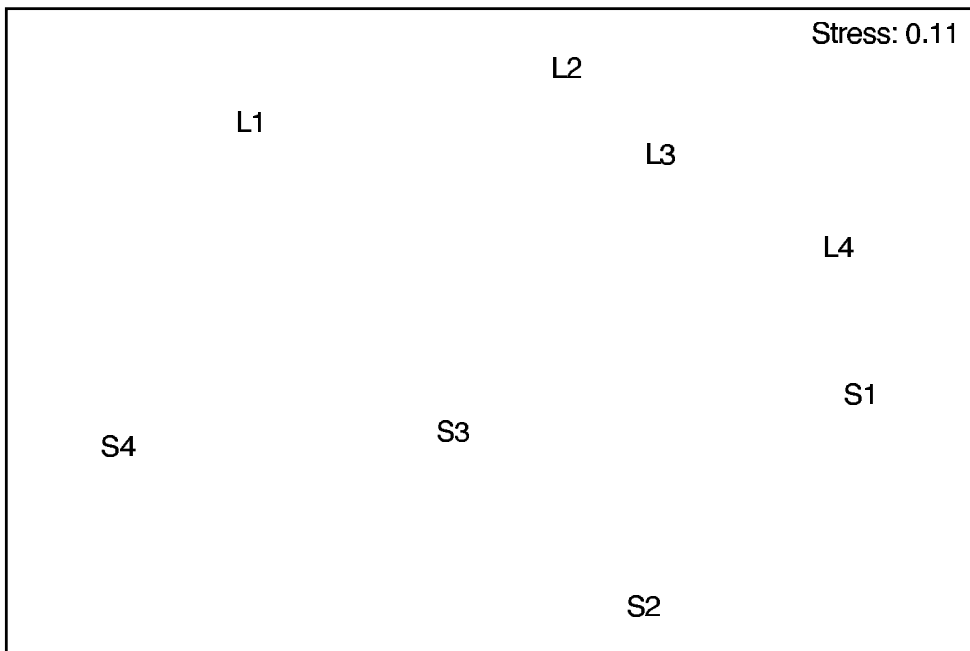


Fig. 3. Multidimensional scaling plot of summed data for landward (L) and seaward (S) sites, using 4th root transformed data

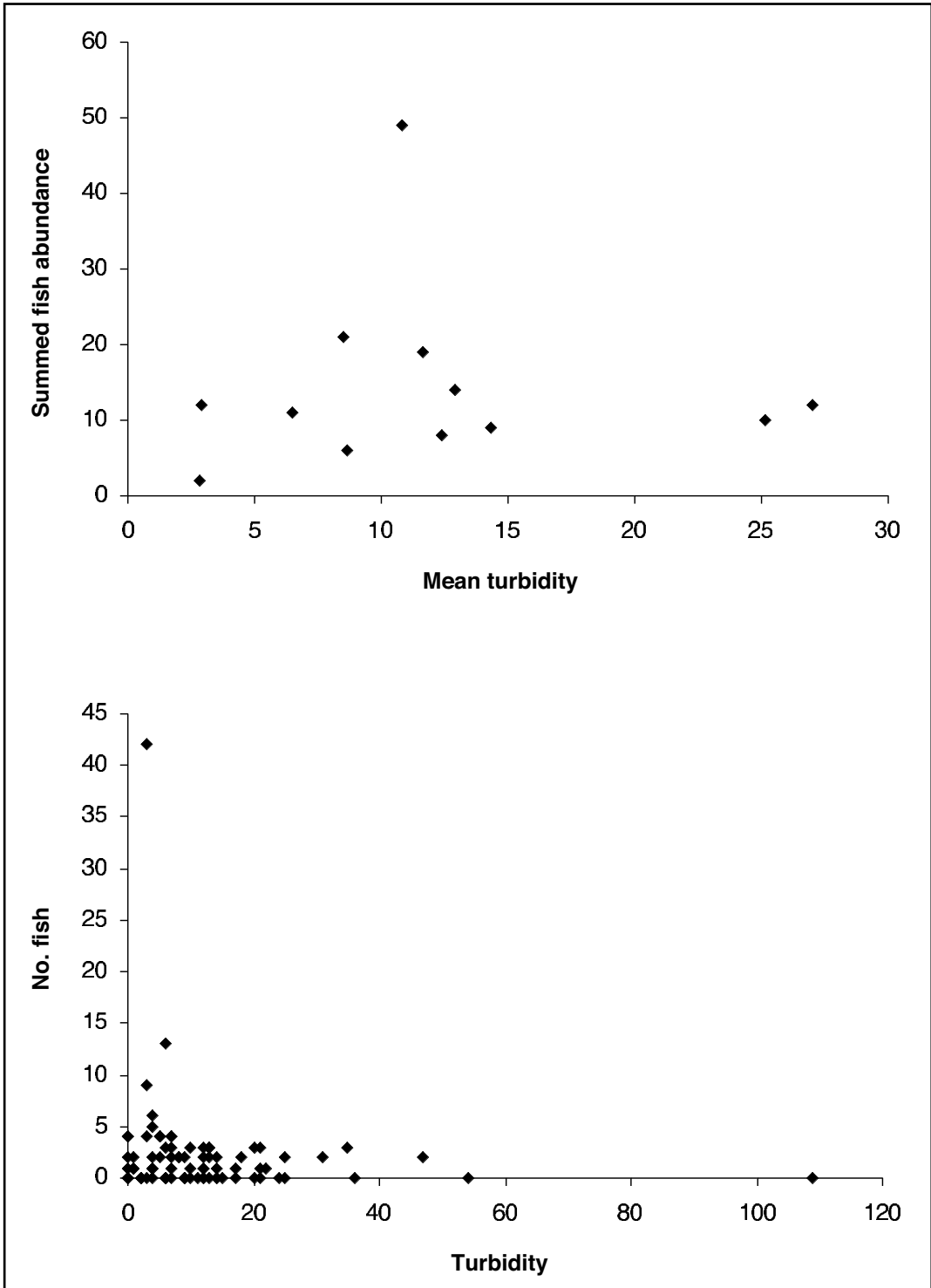


Fig. 4. Number of fish caught against turbidity (in FAU); a) shows data summed for each sampling date, against the mean turbidity for all plots, b) shows data for each plot and date separately

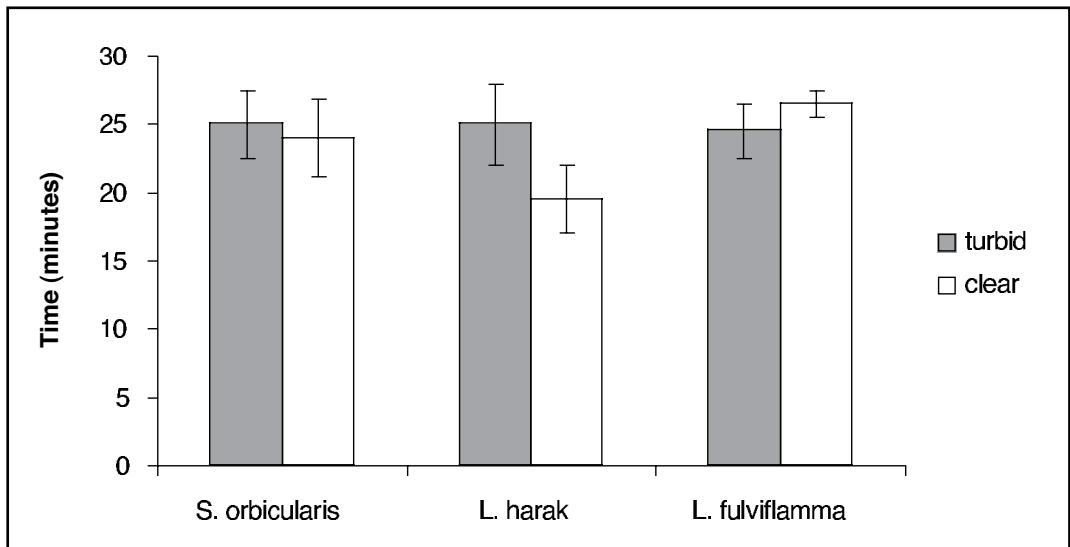


Fig. 5. Mean (\pm S.D.) minutes spent in the pneumatophore half of the behavioural experiment tank during 30 minute trials under turbid and clear conditions using three species of fish. N = 12, 15, 13 for *S. orbicularis*, *L. harak* and *L. fulviflamma* respectively

to be the cause of this relative scarcity. Fishing by the current authors using three different methods (described here and in Huxham *et al.*, 2004) has given low fish densities, as have incidental catches in work focused on prawns at the same site (Crona & Rönnbäck (2005), Crona pers. comm.). Lugendo *et al.* (2007) found evidence that fringing mangroves in Tanzania that are exposed at low tide are less valuable feeding areas than mangrove-lined creeks that retain water. The current site was a fringing mangrove, hence may be less important fish habitat than other nearby mangroves; however low densities of fish have been found in a range of mangrove habitats at Gazi (Huxham *et al.*, 2004). The current results provide no support for the suggestion that these low densities are related to turbidity; there was no relationship between fish numbers and turbidity in the field, and the short-term behavioural experiments also showed no effects of turbidity. These results are consistent with those of Lugendo *et al.* (2005), who found no significant positive relationships between the densities of a range of species in Chwaka Bay, Zanzibar and the turbidities of the habitats sampled. Their mean density of 0.24 fish per m² in mangrove creeks is not directly comparable to the present work, since they did not sample within the forest, but does suggest that densities at Gazi may be atypically low within

the East African region. Hence the reasons for the relative scarcity of fish within Gazi mangroves remain unknown. Sheridan & Hays (2003) reviewed the literature on mangroves as fish nurseries. Their work supported the notion of mangroves as predator refuges for some species. It did not, however, report a strong general trend of increased density of fish within mangroves in the relatively few studies that allow comparison with relevant adjacent habitat. Huxham *et al.* (2004) found similar densities of fish in mangrove and adjacent habitat in Gazi, suggesting that the densities found within the forests may reflect relatively low densities in the Bay as a whole, possibly as a result of high fishing pressure on the adjacent reef.

The current work suggests that differences do exist between the communities of fish found at the seaward and landward fringes of the mangrove. Only three species were found in both areas, and the multivariate analysis suggests a separation of sites (although this was non-significant). The low numbers of most species encountered makes interpreting the data harder. The four most abundant species caught included the three found at both areas (along with a single large catch of the schooling species *Anchoviella commersonii*). Hence the overlap between areas in these species, and not in others, might result in part simply from different

numbers of individuals. However, it probably also represents genuine ecological differences. For example, the two species of goby *Amblygobius phalaena* and *Gobius nebulosus* were both found only in landward sites, consistent with observations of these fish as high tidal species (MH pers. obs.). The pelagic schooling species *A. commersonii* and *Spratelloides gracilis* were found only in seaward plots, consistent with their being essentially open water species, possibly straying accidentally into the mangrove fringe. However, *Gerres oyena*, the most abundant species overall, also occurs in schools and was found at landward sites; it was previously found in a number of other mangrove sites at Gazi (Huxham *et al.*, 2004) and is thus a regular, non-accidental, part of the mangrove fauna here. *G. oyena* and *Lutjanus fulviflamma* were the two species found most regularly at both areas and Lugendo *et al.* (2005) also found these species to be common in a range of shallow habitats in Zanzibar, and classified them as habitat generalists. Vance *et al.* (1996) reported densities at their site 43 m from the mangrove creek four times lower than those reported from their plot adjacent to the creek. The current work supports their suggestion that numbers of both individuals and species of fish are likely to decline with distance from the seaward fringe; the landward plots had lower diversity and abundance, although neither measure differed significantly. However, much smaller relative differences were recorded at Gazi compared with those found by Vance *et al.* (1996), despite the landward plots in the current study being ~150 m further from the sea than the one fished by Vance *et al.* (1996). Hence part of the large difference they report was probably caused by differences between mangrove species (*Rhizophora stylosa* and *Ceriops tagal* at seaward and landward sites respectively) as well as differences in location. They also found that the sizes of fish were generally smaller at their landward site. This was not reflected in the present study, but size differences could not be explored for most species because of the low numbers caught.

Laboratory experiments

All three species showed a strong preference for the pneumatophore habitat. However, neither the juveniles (*Lutjanus fulviflamma* and

Lethrinus harak) nor the mangrove resident adults (*Sphaeramia orbicularis*) showed changed preferences under turbid versus clear conditions. Hence the null hypothesis of no effect of turbidity on behaviour cannot be rejected, and the laboratory and field results are consistent with recent fieldwork from Australia showing no effects of turbidity on estuarine fish (Johnston *et al.*, 2007). Our experiments were conducted over short periods of time in artificial conditions. Abrahams & Kattenfeld (1997) conducted laboratory trials with freshwater minnows over even shorter periods (20 minutes) and found significant effects of turbidity on anti-predator behaviour. However they used food as an incentive for fish to leave the 'safe' habitat, and involved a real predator. Hence the behaviour of these species may respond to turbidity under less stressful, more natural or more sophisticated conditions than those used in the present study.

In conclusion, no relationships were found between fish behaviour and turbidity, either in the field or the laboratory, suggesting that water clarity cannot explain the low densities of fish reported here and previously from Gazi mangroves. The current work supports the idea that fish communities within mangroves will change with distance from the seaward fringe, with a general reduction in diversity and abundance, but could not test the effects of distance on the average size within species because of the low numbers found.

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