

ORIGINAL ARTICLE

# The influence of reef type and seasonality on population structure of coral-reef fishes within Malindi Marine Park, Kenya

Gamoe A. Locham<sup>1,2</sup>, Boaz Kaunda-Arara<sup>2</sup> & Chrisestom M. Mlewa<sup>3</sup>

<sup>1</sup> Kenya Wildlife Service, Watamu Marine National Park, Kenya

<sup>2</sup> Department of Fisheries and Aquatic Sciences, Moi University, Eldoret, Kenya

<sup>3</sup> Pwani University College, Kilifi, Kenya

## Keywords

Coral-reef fishes; fringing and patch reefs; monsoons; trophic and assemblage structures.

## Correspondence

Boaz Kaunda-Arara, Department of Fisheries and Aquatic Sciences, Moi University, PO Box 1125, Eldoret, Kenya.  
E-mail: b\_kaunda@yahoo.com

Accepted: 4 January 2010

doi:10.1111/j.1439-0485.2010.00363.x

## Abstract

Effective conservation requires knowledge of the effects of habitat on distribution and abundance of organisms. Although the structure of coral reef fish assemblages is strongly correlated with attributes of reef structure, data relating reef types to fish assemblages are scarce. In this study we describe the influence of gross habitat characteristics and seasonality on coral reef fish assemblages of fringing and patch reefs in Kenya. Results showed that total fish abundance was not significantly different between the reefs; however, the fringing reef had higher species diversity during both the northeast (42 spp.) and southeast (36 spp.) monsoon seasons when compared to the patch reef. The more fished species (e.g. *Siganus sutor* and *Lethrinus mahsena*) were more abundant on the patch reef in both seasons. Statistical analysis indicated common species between the reefs were more abundant on the fringing reef. Seasons affected abundance of the more vagile species (*S. sutor*), whereas the reef-attached sky emperor, *L. mahsena* was affected more by reef type than by seasons. No significant interaction effects of habitat and seasons were found, indicating independence of habitat and environmental variability in affecting fish assemblages on the reefs. Smaller sized fish dominated the fringing reef more than the patch reef, whereas the skewness index (Sk) indicated a normal-sized frequency distribution on the patch reef. Trophic structure of the fishes varied more within than between reefs, whereas fish assemblage structure was affected more by seasons on the fringing reef. These results suggest that conservation measures such as marine protected area (MPA) design and setting should consider effects of reef morphology and environmental variability on coral-reef fish assemblage structure.

## Problem

The structure of coral reef fish assemblages is usually strongly correlated with attributes of reef structure. Fish-habitat interaction influences abundance, diversity and breeding population size (Roberts & Ormond 1987; Jones 1988), and forms the basis of the so-called declining population paradigm in ecology (Coughley 1994). Understanding spatial variations in the dimensions of coral reef

fish diversity (e.g.  $\alpha$   $\beta$   $\gamma$  diversities) as well as both local community and regional metacommunity structures is critical for conservation of coral reef ecosystems (Mellin *et al.* 2009). Most coral reef fishes are known to be highly sedentary, inhabiting a limited section of a reef profile (Sale 1980), and therefore the spatial extent and distribution of habitat niches are important in regulating their populations. Local distribution and abundance of coral reef fishes are influenced by features such as reef height,

depth, and topographic complexity (Thresher 1983; Hixon & Beets 1993). The close relationship between fishes and reef attributes such as complexity is thought to mediate the high species diversity in coral reefs (Randall *et al.* 1990; McCormick 1995). Furthermore, within-reef differences in coral cover and microhabitat juxtaposition are known to affect fish abundance and predator–prey relationships (Hixon & Beets 1993; Weaver *et al.* 2001). There are many geomorphological types of reefs with different sub-classes within a reef complex (Andréfouët *et al.* 2006). Although these reefs have similar habitat profiles, often the diversity and abundance of functional groups vary along the profiles (Galzin 1987; Mellin *et al.* 2009).

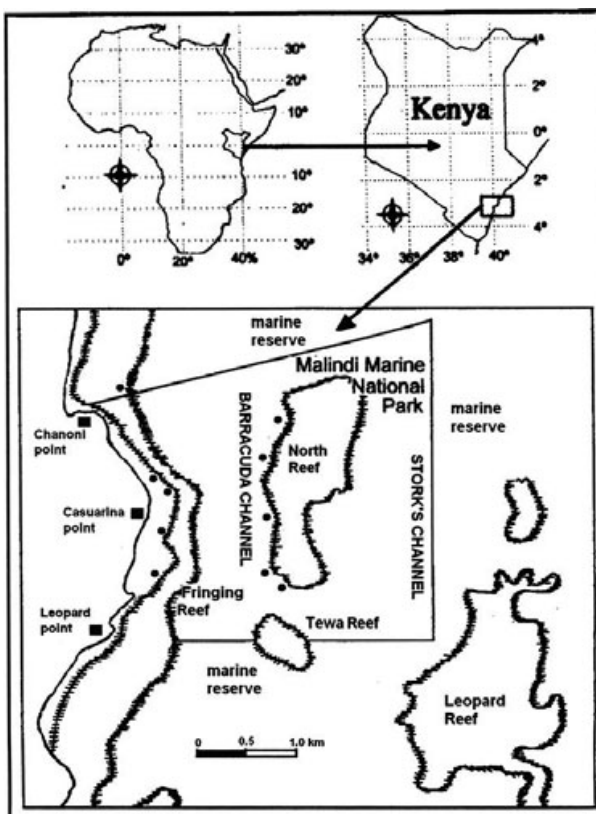
Studies of living reefs have shown that fish assemblage structure shows a high degree of variability at small spatial scales (Doherty 1983; Galzin 1987; Sale *et al.* 1994). Relatively fewer large spatial scale studies on fish assemblage structure exist and they have mostly focused on within-reef effects (Goldman & Talbot 1976; Williams 1991; Connell & Kingsford 1998). However, there is a need to study assemblages and processes across seascapes and reefs, especially those of different geomorphologic origin (Harborne *et al.* 2006). These studies may be important for ecosystem conservation and in explaining hierarchical effects on reefs (Sale 1998; Pandolfi 2002; MacNeil *et al.* 2009).

Coastal East Africa is dominated by fringing reefs with scattered lagoonal patch reef systems (Hamilton & Brakel 1984). The coast experiences seasonality caused by both northeasterly and southeasterly monsoon winds (McClanahan 1988). The northeast monsoon season (NEM, November–March) is a period of calm weather, elevated temperatures and lower salinities, whereas the southeast monsoon (SEM, April–October) is characterized by rough seas, cool weather, and high salinities. The influence of this seasonality on biological and physical parameters is well documented for the East African coast (Nzioka 1979; Hamilton & Brakel 1984; McClanahan 1988; Kaunda-Arara *et al.* 2009); however, little is known about the effects of seasonality and its interactions with habitat on reef fish assemblage structure in the Western Indian Ocean (WIO). In this study, we tested for the first time in coastal Eastern Africa the hypothesis that reef structure based on geomorphology and seasonality has an effect on assemblages of trappable coral reef fishes. The Malindi Marine Park in Kenya has a system of patch and fringing reefs and therefore offered a rare opportunity to test this hypothesis.

## Materials and Methods

### Study sites

This study was carried out in Malindi Marine Park (6.3 km<sup>2</sup>, created in 1968), coastal Kenya (Fig. 1). Like



**Fig. 1.** A map of Malindi Marine Park, Kenya, showing the nearshore fringing reef spanning the park boundaries, a system of patch reefs inside and outside the park. Sampling was done on the west slopes of Fringing and North Reef sites (●). Areas designated as reserves surround the park and are fished.

other marine parks in Kenya, the park receives total protection from extractive exploitation, whereas adjacent areas designated as ‘reserve’ receive limited protection as fishing with traditional gear, mostly traps, is allowed. Kenyan reefs are typified by a fringing reef located 100–2000 m from shore, the fringing reefs on the north coast often as bound patch or rock island reefs within lagoons (Hamilton & Brakel 1984).

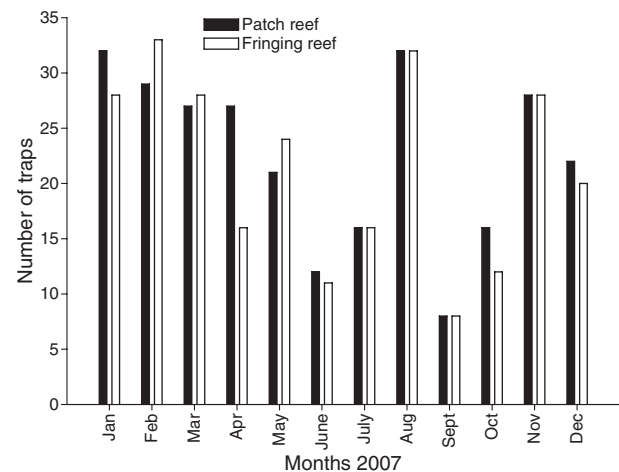
The park includes both a continuous fringing fossil reef located about 200 m off the high water mark and extending several kilometers from the southern edge of park boundary, and a patch reef system located about 1 km from shore (Fig. 1). During low tide, the platform of the fringing reef becomes exposed, revealing a bottom substrate consisting mostly of benthic algae and coral rubble, with sparse living coral cover (Kaunda-Arara & Rose 2004a; Kaunda-Arara *et al.* 2009). The slopes of the platform descend to depths of up to 7 m at high tides. The park also includes a system of small discrete reefs – the North, Tewa and Leopard Reefs (Fig. 1). These reefs are located 1–1.5 km from the shore with their flats descending into a lagoon. Except for the

submerged Tewa Reef, the other reefs have their platforms exposed at low tides. We consider these reefs to be 'coastal patch reefs' following the classification of Hamilton & Brakel (1984), Andréfouët & Guzman (2005) and Andréfouët *et al.* (2006). Sampling on these coastal patch reefs was done on the west slopes of the larger (2 × 1 km) North Reef (Nr, Fig. 1). This reef is topographically more complex than the fringing reef, with a higher biodiversity. It comprises a reef flat of semi-fossilized coral rock that is exposed at low tides. Beds of the seagrass *Thalassondendron ciliatum* and isolated live coral heads dominated by massive *Porites* and *Galaxea* spp. occur on the upper edges of the east and south-west slopes of the reef (Kaunda-Arara & Rose 2004a,b). The North Reef is circled by two channels on the east and west sides, the Stork's passage and Barracuda channel, respectively (Fig. 1). The east and north-east side of this reef is exposed to heavy surf; however, the south-west slopes are well protected with rich coral gardens popular for tourist activities.

#### Field sampling

Fish assemblages of the reefs were sampled using local traditional traps on the west slopes of both the fringing and patch reef (Fig. 1). Trapping of juvenile and adult fish at the patch and fringing reef sites was done from January to December 2007 using traditional Dema traps. The traps, modified from Kaunda-Arara & Rose (2004a) are pentagonal in shape, measuring approximately 1.5 × 1.3 × 0.6 m high. They were constructed of metal frames and covered with a wire mesh of 1 cm stretch length. Each trap had a single topside funnel door made of bamboo reeds through which the fish enter and an underside aperture for removing the catch. On each sampling day, 3–7 Dema traps were deployed simultaneously on the patch and fringing reefs in a straight line at intervals of about 20 m between traps. The actual number of traps deployed on any sampling day depended largely on the number of non-defective or lost traps. Prior to deployment, the traps were baited with approximately 0.5 kg of a mixture of green and brown benthic algae and mashed tissues of the mangrove gastropod, *Terebralia palustris*. The traps were deployed from a motor boat during low tide, and retrieved during the subsequent low tide period of the following day, having fished for about 12 h. Trap placement ranged from 1 to 4 m (on the fringing reef) and from 1 to 5 m (on the patch reef) at low tides. Monthly distribution of traps ranged from 8 to 32 (patch reef) and 8 to 33 (fringing reef) (Fig. 2). There was no significant difference in the number of traps that fished on both reefs ( $\chi^2 = 3.897$ ,  $P = 0.973$ ).

During retrieval, traps were hauled up and the catch emptied into a plastic basin containing ambient tempera-



**Fig. 2.** Monthly distribution of Dema traps on the patch and fringing reefs during the study period. A total of 1559 and 737 fish were caught by 270 and 256 traps on the patch and fringing reefs, respectively.

ture seawater. All fish were identified to the lowest taxonomic level possible using field guides by Randall (1992), Leiske & Myers (1994), and Allen (1997). The total length (cm) of each identified fish was measured on a fish board, and body depth was taken using a tape measure to the nearest 0.1 cm. The fish were then released alive at the capture site. The Dema traps were then cleaned, baited and re-deployed at other selected sites on the patch and fringing reefs. Traps were deployed so as not to fish the same site to avoid auto-correlation of catches and local depletion effects.

#### Data analysis

The daily trap catch data were pooled to derive monthly mean abundance of fishes as catch per trap per day. The catch data collected from January–March and November–December were pooled to represent catches for the NEM season, whereas data collected between April and October represented the SEM season. The species seasonal abundance was then compared between and within reefs using a two sample *t*-test with unequal variances following log transformation ( $\log_e x + 1$ ). Mean sizes of fish between reefs were compared using a two-sample *t*-test. The interaction between season and reef type in influencing catches was tested using 2-way ANOVA. Seasonal size frequency distributions were examined using graphical plots for the two dominant commercial species (the sky emperor, *Lethrinus mahsena* and the whitespotted rabbitfish, *Siganus sutor*). The size frequency distributions were then examined for skewness using the skewness index (Sk) derived from the difference between the median (Md) and mean ( $\mu$ ) of the size frequencies weighted by the median (Zar

1996). To examine the trophic structure of fishes on the reefs, species were grouped into four main trophic categories (Algal grazers, Invertebrate feeders, Piscivores, and Planktivores) based on records in Fishbase and the literature, and percentage numerical abundance of the categories derived. A multivariate simple correspondence analysis (CA) was used to explore associations of species with respect to reef type and seasons. CA was first completed on the total species dataset, but the large number of species ( $n = 47$ ) made it difficult to identify the important patterns and hence, for ease of interpreting the plots, analysis was based on the 16 most abundant species that had a mean catch rate of  $\geq 0.03$  per trap per day.

## Results

### Species composition and abundance on reefs

During the NEM season, a total of 47 species were caught, of which 22 were common to both the fringing and patch reefs, 20 were specific to the fringing reef and 5 were specific to the patch reef (Table 1). Of the 22 species common to both reefs, the Labridae (*Chelinus chlorourus*, *Cheilinus trilobatus*), Lethrinidae (*Lethrinus miniatus*, *Lethrinus nebulosus*), Lutjanidae (*Lutjanus bohar*, *Lutjanus gibbus*) and Balistidae (*Suflammen fraenatus*) had significantly higher catch rates on the fringing reef ( $P < 0.05$ , Table 1). However, the commercially important species *Lethrinus mahsena* (sky emperor) and *Siganus sutor* (whitespotted rabbitfish) had significantly higher catches on the patch reef ( $P < 0.05$ , Table 1). During the SEM season, 40 species were caught in the park, of which 20 were common to both reef types (Table 2). Some families (e.g. Fistulariidae, Tetraodontidae, Apogonidae, Pomacentridae and Soleidae) sampled during the NEM season were not caught during this season (Tables 1 and 2). Among the species that were common to both reefs, *Calotomus spinidens*, *Leptoscarus vaigiensis*, *L. miniatus*, *L. nebulosus* and *Lutjanus fulviflamma* had significantly higher catch rates on the fringing reef than on the patch reef ( $P < 0.05$ , Table 2). However, four species, *Cheilios inermis*, *L. mahsena*, *Parupeneus barberinus* and *S. sutor*, had significantly higher catch rates on the patch reef than on the fringing reef ( $P < 0.05$ , Table 2). Total fish catch between the reefs did not show significant differences either in the NEM or the SEM seasons ( $t_{\text{stat}} = -0.52$  and  $0.53$ , respectively,  $P = 0.30$ ) (Tables 1 and 2).

### Seasonal variation in relative abundance of commercial species

During the NEM season there was a high species richness on the fringing reef ( $n = 42$ ) compared to the patch reef

( $n = 27$ ) (Fig. 3a). However, of the 42 species, only five (*Siganus sutor*, *Lethrinus mahsena*, *Lethrinus nebulosus*, *Lethrinus miniatus* and *Chelinus chlorourus*) dominated the fringing reef, with relative abundances of  $>5\%$ , whereas the patch reef was dominated by only two of the 27 species (*S. sutor* and *L. mahsena*), with relative abundances  $>5\%$  (Fig. 3b). The two most common commercial species in the park and coastal East Africa (*S. sutor* and *L. mahsena*) showed significantly higher relative abundances on the patch reef (*S. sutor* 45%; *L. mahsena* 42%) than on the fringing reef (relative abundances  $<30\%$ ) (Fig. 2). During the SEM season, the fringing reef maintained higher species richness (Fig. 4A); however, the two dominant commercial species maintained a higher abundance in the catch on the patch reef [*S. sutor* (65%) and *L. mahsena* (28%)] than on the fringing reef (Fig. 4B).

### Interaction of reefs and seasons

The total catch of coral reef fishes in the park is influenced by both the season and the reef type (2-way ANOVA,  $P < 0.05$ , Table 3). However, there were species-specific variations on the effects of season and reef type on fish abundance. The abundance of the whitespotted rabbitfish, *Siganus sutor*, was affected by both seasons and reef type. However, abundance of emperors, including the commercially important sky emperor, *Lethrinus mahsena*, was affected significantly more by reef type than by seasons (Table 3). A similar influence was observed on 'other' categories, consisting mostly of the wrasses (*Cheilinus* spp. and *Chlorourus* spp.). The seagrass parrot fish, *Leptoscarus vaigiensis*, common in lagoonal East African reefs, showed no significant response to either factors (Table 3). No significant interaction effect between reef type and seasons was observed for the common fish species, indicating that effects of the two factors on fish abundance are not conditional on each other.

### Seasonal size frequency distribution of dominant species on reefs

During the rough SEM season, there were more small-sized sky emperors (TL  $< 10$  cm) on the fringing reef compared to the patch reef (Fig. 5A). The frequency distribution of the species on the fringing reef was more positively skewed on the patch reef ( $Sk = 2.23$ ) than on the fringing reef ( $Sk = 1.63$ ), indicating a non-normalized distribution on the patch reef. The modal size of the sky emperors on the fringing and patch reefs was 13 and 15 cm, respectively. There were more large-sized sky emperors (TL  $> 20$  cm) on the patch reef compared to the fringing reef (Fig. 4A) during the SEM season. During

families/species	fringing reef	patch reef	t-test	
	No/trap/day $\pm$ SD	No/trap/day $\pm$ SD	t	P
<b>Acanthuridae</b>				
<i>Acanthurus blochii</i>	0.11 $\pm$ 0.29	–	–	–
<i>Acanthurus nubilus</i>	0.02 $\pm$ 0.07	–	–	–
<i>Ctenochaetus striatus</i>	0.01 $\pm$ 0.05	0.01 $\pm$ 0.04	1.00	0.16
<b>Fistulariidae</b>				
<i>Aulostomus chinensis</i>	0.01 $\pm$ 0.04	–	–	–
<b>Balistidae</b>				
<i>Balistapus undulatus</i>	0.02 $\pm$ 0.08	0.01 $\pm$ 0.06	0.55	0.29
<i>Sufflamen fraenatus</i>	0.07 $\pm$ 0.12	0.02 $\pm$ 0.08	2.13	0.02
<b>Scaridae</b>				
<i>Calotomus carolinus</i>	0.18 $\pm$ 0.55	0.05 $\pm$ 0.10	1.52	0.07
<i>Calotomus spinidens</i>	0.01 $\pm$ 0.05	0.01 $\pm$ 0.05	0.00	0.50
<i>Leptoscarus vaigiensis</i>	0.24 $\pm$ 0.75	0.06 $\pm$ 0.17	1.53	0.07
<b>Monacanthidae</b>				
<i>Cantherhines fronticinctus</i>	–	0.01 $\pm$ 0.04	–	–
<i>Paraluteres prionurus</i>	0.01 $\pm$ 0.05	–	–	–
<b>Tetraodontidae</b>				
<i>Canthigaster solandri</i>	0.01 $\pm$ 0.05	–	–	–
<b>Chaetodontidae</b>				
<i>Chaetodon auriga</i>	–	0.01 $\pm$ 0.04	–	–
<i>Chaetodon trifasciatus</i>	0.01 $\pm$ 0.05	–	–	–
<b>Labridae</b>				
<i>Cheilinus chlorourus</i>	0.27 $\pm$ 0.40	0.08 $\pm$ 0.14	3.03	0.00
<i>Cheilinus trilobatus</i>	0.07 $\pm$ 0.14	0.01 $\pm$ 0.06	2.79	0.00
<i>Cheilio inermis</i>	0.10 $\pm$ 0.27	0.06 $\pm$ 0.12	1.08	0.14
<i>Coris caudimacula</i>	–	0.01 $\pm$ 0.06	–	–
<i>Halichoeres dussumieri</i>	0.03 $\pm$ 0.10	–	–	–
<i>Novaculichthys macrolepidotus</i>	–	0.02 $\pm$ 0.09	–	–
<i>Novaculichthys taeniurus</i>	0.02 $\pm$ 0.09	0.01 $\pm$ 0.04	0.81	0.21
<i>Thalassoma hebraicum</i>	0.02 $\pm$ 0.07	0.03 $\pm$ 0.10	–0.33	0.37
<i>Thalassoma lunare</i>	0.04 $\pm$ 0.13	0.03 $\pm$ 0.10	0.63	0.26
<b>Apogonidae</b>				
<i>Cheilodipterus quinquelineatus</i>	0.01 $\pm$ 0.04	–	–	–
<b>Pomacentridae</b>				
<i>Dascyllus trimaculatus</i>	–	0.04 $\pm$ 0.17	–	–
<i>Pomacentrus chrysurus</i>	0.01 $\pm$ 0.04	–	–	–
<i>Pomacentrus pavo</i>	0.01 $\pm$ 0.04	–	–	–
<b>Serranidae</b>				
<i>Epinephelus coioides</i>	0.02 $\pm$ 0.08	–	–	–
<i>Epinephelus longispinis</i>	0.01 $\pm$ 0.04	–	–	–
<i>Epinephelus merra</i>	0.05 $\pm$ 0.15	0.02 $\pm$ 0.09	1.13	0.13
<i>Epinephelus strictus</i>	0.01 $\pm$ 0.04	–	–	–
<i>Epinephelus tauvina</i>	0.02 $\pm$ 0.08	0.01 $\pm$ 0.04	1.07	0.15
<b>Lethrinidae</b>				
<i>Lethrinus mahsena</i>	0.76 $\pm$ 0.72	2.64 $\pm$ 2.30	–5.10	0.00
<i>Lethrinus miniatus</i>	0.36 $\pm$ 0.45	0.20 $\pm$ 0.33	1.67	0.05
<i>Lethrinus nebulosus</i>	0.42 $\pm$ 0.62	0.07 $\pm$ 0.22	3.82	0.00
<i>Lethrinus olivaceus</i>	0.01 $\pm$ 0.08	–	–	–
<b>Lutjanidae</b>				
<i>Lutjanus bohar</i>	0.08 $\pm$ 0.16	0.02 $\pm$ 0.07	1.98	0.03
<i>Lutjanus ehrenbergi</i>	0.01 $\pm$ 0.06	–	–	–
<i>Lutjanus fulviflamma</i>	0.02 $\pm$ 0.09	0.02 $\pm$ 0.07	0.00	0.50
<i>Lutjanus gibbus</i>	0.12 $\pm$ 0.27	0.01 $\pm$ 0.04	2.61	0.01
<b>Mullidae</b>				
<i>Parupeneus barberinus</i>	0.04 $\pm$ 0.13	–	–	–

**Table 1.** Mean catch rates (number per trap per day) of trappable species of reef fish on the fringing and patch reefs of Malindi Marine Park, Kenya, during the northeast monsoon season (NEM). SD denotes standard deviation of the mean. Dash (–) denotes absence of data.

Table 1. (Continued)

families/species	fringing reef	patch reef	t-test	
	No/trap/day $\pm$ SD	No/trap/day $\pm$ SD	t	P
Pinguipedidae				
<i>Parapercis hexophthalma</i>	0.01 $\pm$ 0.04	–	–	–
Haemulidae				
<i>Plectorhinchus flavomaculatus</i>	0.01 $\pm$ 0.04	0.01 $\pm$ 0.04	1.00	0.50
<i>Plectorhinchus gaterinus</i>	0.02 $\pm$ 0.08	–	–	–
Soleidae				
<i>Pardachirus marmoratus</i>	0.01 $\pm$ 0.05	–	–	–
Siganidae				
<i>Siganus stellatus</i>	0.01 $\pm$ 0.04	–	–	–
<i>Siganus sutor</i>	1.25 $\pm$ 1.36	2.83 $\pm$ 3.16	-2.93	0.00
Total catch	4.60 $\pm$ 8.45	6.33 $\pm$ 8.03	-0.52	0.30

the calm NEM season, the size frequency distribution of the species did not differ significantly between the fringing ( $Sk = 1.93$ ) and patch ( $Sk = 1.64$ ) reefs (Fig. 4B), indicating uniform size distribution between the reefs. However, smaller-sized fish ( $Tl < 15$  cm) were more frequent on the fringing reef, whereas large-sized sky emperors ( $Tl > 20$  cm) dominated the patch reef (Fig. 5b).

For the whitespotted rabbitfish, *Siganus sutor*, the size frequency distribution of individuals did not vary greatly between the reefs (Fringing  $Sk = 1.29$ ; Patch  $Sk = 1.84$ ) during the SEM season (Fig. 6A). However, during the calm NEM season the rabbitfish showed a more normal distribution on the fringing reef ( $Sk = 0.54$ ) compared to the patch reef, which had a higher frequency of small-sized individuals ( $Sk = 1.89$ ).

### Trophic and assemblage structures

Analysis of trophic structure by numbers of species indicated seasonal differences between rather than within reefs (Fig. 7). During the NEM season, algal grazers and invertebrate feeders dominated both reefs (35–48%, Fig. 7A). The invertebrate feeders (primarily feeders on motile invertebrates) mostly consisted of Lethrinidae, whereas Siganidae dominated algal grazers. The piscivores (mostly Lutjanidae and Serranidae) were more numerous (~20%) on the fringing reef (Fig. 7A). During the SEM season, both reefs were dominated by algae grazers (Fig. 7B). The invertebrate feeders and piscivores constituted ~20% of total numbers in this season. Planktivores were virtually absent in the samples from both reefs.

Multivariate analysis of association of the fishes based on their catch rates separated the species composition on the basis of reef type more than seasons (Fig. 8). The monsoon seasons seemed to affect assemblage structures within reefs rather than between reefs. The CA plot revealed an association of five species with the fringing reef during the NEM and nine species during the SEM

season. During the NEM season, the fringing reef was characterised by *Chelinus chlorourus*, *Lutjanus gibbus*, *Epinephelus merra*, *Lethrinus nebulosus* and *Thalossoma lunare*. During the SEM, this reef was characterised by *Lutjanus bohar*, *Acanthurus blochii*, *Leptoscarus vaigiensis*, *Lethrinus miniatus*, *Thalossoma hebraicum*, *Epinephelus tauvina*, *Leptoscarus vaigiensis*, *Cheilinus trilobatus*, *Lutjanus fulviflamma* and *Calotomus spinidens*. The patch reef was associated more with the two commercially important species, *L. mahsena* during the NEM and *S. sutor* during the SEM season, forming a seasonal assemblage distinct from that of the fringing reef (Fig. 8).

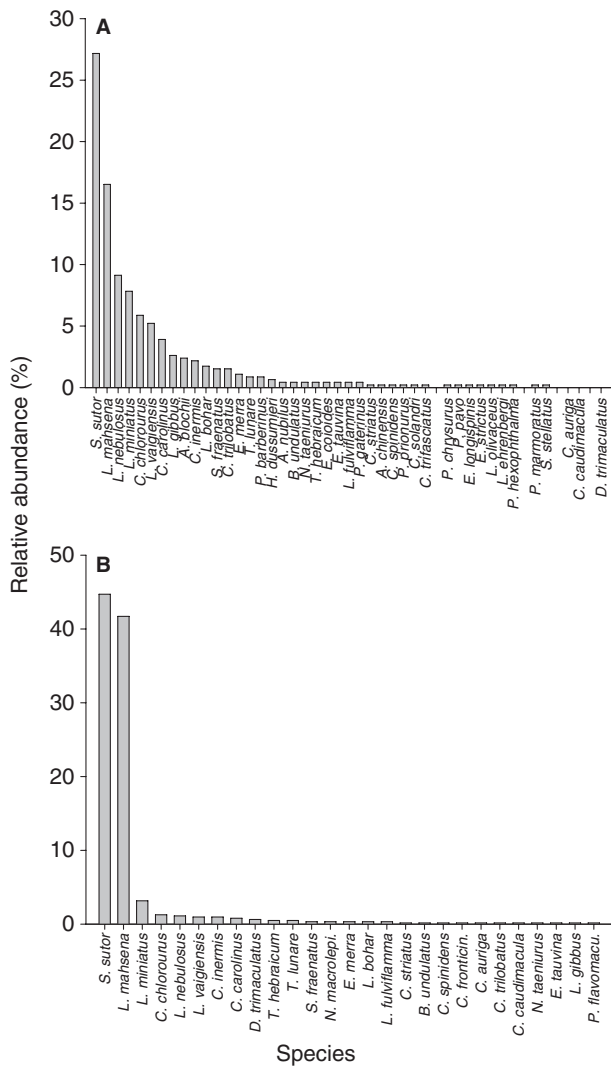
### Discussion

The overall fish abundance was not significantly different between reefs; however, the fringing reef had higher species diversity both during the NEM (42 spp.) and the SEM (36 spp.) season compared to the patch reef. Statistical analysis indicated that most of the common species dominated the fringing reef. The fringing reef is a fossil reef and has high benthic algal cover (Hamilton & Brakel 1984); it is likely that the enhanced primary production on this reef together with protection afforded by its nearshore location facilitates higher species diversity. The observed high seasonal abundance of algal grazers on this reef seems to support the notion that primary production may be mediating the observed diversity. Other factors such as spatial variability in recruitment can contribute to differences in diversity between habitats (Roughgarden *et al.* 1988; Letourneur 1996; Gutierrez 1998; Kaunda-Arara *et al.* 2009). However, more focused studies on aging and age structure of the fishes are required for useful comparison of recruitment effects between the reefs. Age validation studies in *Siganus sutor* (Ntiba & Jaccarini 1988) and *Lethrinus mahsena* (Pilling *et al.* 2000) therefore represent a useful first step.

The commercially important species (*S. sutor* and *L. mahsena*) were more abundant on the patch reef in

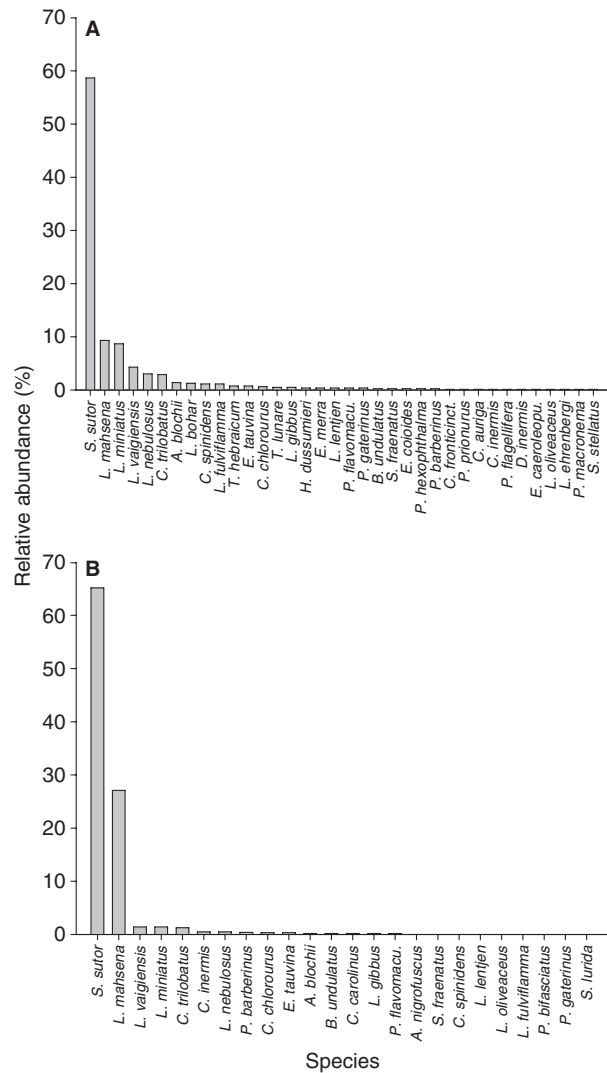
families/species	fringing reef	patch reef	t-test	
	No./trap/day $\pm$ SD	No./trap/day $\pm$ SD	t	P
<b>Acanthuridae</b>				
<i>Acanthurus blochii</i>	0.11 $\pm$ 0.45	0.02 $\pm$ 0.10	1.05	0.15
<i>Acanthurus nigrofuscus</i>	–	0.01 $\pm$ 0.06	–	–
<b>Balistidae</b>				
<i>Balistapus undulatus</i>	0.02 $\pm$ 0.08	0.02 $\pm$ 0.06	0.28	0.39
<i>Sufflamen fraenatus</i>	0.02 $\pm$ 0.08	0.01 $\pm$ 0.05	0.72	0.24
<b>Scaridae</b>				
<i>Calotomus carolinus</i>	–	0.02 $\pm$ 0.09	–	–
<i>Calotomus spinidens</i>	0.09 $\pm$ 0.19	0.01 $\pm$ 0.04	2.31	0.01
<i>Leptoscarus vaigiensis</i>	0.34 $\pm$ 0.53	0.18 $\pm$ 0.29	1.79	0.04
<b>Monacanthidae</b>				
<i>Cantherhines fronticinctus</i>	0.01 $\pm$ 0.04	–	–	–
<i>Paraluteres prionurus</i>	0.01 $\pm$ 0.04	–	–	–
<b>Chaetodontidae</b>				
<i>Chaetodon auriga</i>	0.01 $\pm$ 0.04	–	–	–
<b>Labridae</b>				
<i>Cheilinus chlorourus</i>	0.05 $\pm$ 0.14	0.04 $\pm$ 0.10	0.75	0.23
<i>Cheilinus trilobatus</i>	0.23 $\pm$ 0.36	0.16 $\pm$ 0.23	0.79	0.22
<i>Cheilio inermis</i>	0.01 $\pm$ 0.04	0.06 $\pm$ 0.18	–1.88	0.03
<i>Halichoeres dussumieri</i>	0.03 $\pm$ 0.09	–	–	–
<i>Pteragogus flagellifera</i>	0.01 $\pm$ 0.04	–	–	–
<i>Thalassoma hebraicum</i>	0.06 $\pm$ 0.11	–	–	–
<i>Thalassoma lunare</i>	0.04 $\pm$ 0.15	–	–	–
<b>Serranidae</b>				
<i>Dermatolepis inermis</i>	0.01 $\pm$ 0.04	–	–	–
<i>Epinephelus caeruleopuntatus</i>	0.01 $\pm$ 0.06	–	–	–
<i>Epinephelus coioides</i>	0.02 $\pm$ 0.08	–	–	–
<i>Epinephelus merra</i>	0.03 $\pm$ 0.09	–	–	–
<i>Epinephelus tauvina</i>	0.06 $\pm$ 0.14	0.04 $\pm$ 0.09	0.68	0.25
<b>Lethrinidae</b>				
<i>Lethrinus lentjen</i>	0.03 $\pm$ 0.11	0.01 $\pm$ 0.04	1.14	0.13
<i>Lethrinus mahsena</i>	0.74 $\pm$ 1.04	3.47 $\pm$ 3.05	–5.13	0.00
<i>Lethrinus miniatus</i>	0.69 $\pm$ 0.91	0.18 $\pm$ 0.29	3.10	0.00
<i>Lethrinus nebulosus</i>	0.24 $\pm$ 0.34	0.06 $\pm$ 0.16	2.92	0.00
<i>Lethrinus oliveaceus</i>	0.01 $\pm$ 0.04	0.01 $\pm$ 0.06	–0.19	0.42
<b>Lutjanidae</b>				
<i>Lutjanus bohar</i>	0.10 $\pm$ 0.21	–	–	–
<i>Lutjanus ehrenbergi</i>	0.01 $\pm$ 0.06	–	–	–
<i>Lutjanus fulviflamma</i>	0.09 $\pm$ 0.24	0.01 $\pm$ 0.04	1.90	0.03
<i>Lutjanus gibbus</i>	0.04 $\pm$ 0.12	0.02 $\pm$ 0.09	0.97	0.17
<b>Pinguipedidae</b>				
<i>Parapercis hexophthalma</i>	0.02 $\pm$ 0.06	–	–	–
<b>Mullidae</b>				
<i>Parupeneus barberinus</i>	0.02 $\pm$ 0.06	0.05 $\pm$ 0.10	–1.87	0.04
<i>Parupeneus bifasciatus</i>	–	0.01 $\pm$ 0.04	–	–
<i>Parupeneus macronema</i>	0.01 $\pm$ 0.04	–	–	–
<b>Haemulidae</b>				
<i>Plectorhinchus flavomaculatus</i>	0.03 $\pm$ 0.14	0.02 $\pm$ 0.07	0.30	0.38
<i>Plectorhinchus gaterinus</i>	0.03 $\pm$ 0.09	0.01 $\pm$ 0.05	1.09	0.14
<b>Siganidae</b>				
<i>Siganus lurida</i>	–	0.01 $\pm$ 0.04	–	–
<i>Siganus stellatus</i>	0.01 $\pm$ 0.04	–	–	–
<i>Siganus sutor</i>	4.66 $\pm$ 4.60	8.35 $\pm$ 6.02	–2.71	0.01
Total catch	7.94 $\pm$ 11.14	12.81 $\pm$ 11.52	–0.53	0.30

**Table 2.** Mean catch rates (number per trap per day) of trappable species of reef fish on the fringing and patch reefs of Malindi Marine Park, Kenya, during the southeast monsoon season (SEM). SD denotes standard deviation of the mean. Dash (–) denotes lack of data.



**Fig. 3.** Percentage relative abundance of trappable coral reef fishes on the (A) fringing reef and (B) patch reef within Malindi Marine Park, Kenya, during the northeast monsoon season (NEM). The generic names are as shown in Tables 1 and 2.

both seasons. These species are heavily fished in the adjacent fisheries and form the bulk of artisanal fish catches in Kenya (Kaunda-Arara *et al.* 2003; McClanahan & Mangi 2004). It is likely that spatial connectivity to the adjacent fisheries afforded by the fringing reef contributes to the lower abundance of these species on this reef. The fringing reef is continuous with the adjacent fisheries and this likely affects fish abundance in the park through spillover effects (McClanahan & Kaunda-Arara 1996; Kaunda-Arara & Rose 2004b). These results reinforce the proposal that a marine park design should consider the proportion of habitat types enclosed within its boundaries (Russ 2002; Botsford *et al.* 2009). If the main objective is to enhance adjacent fisheries through spillover, then parks



**Fig. 4.** Percentage relative abundance of trappable coral reef fishes on the (A) fringing reef and (B) patch reef within Malindi Marine Park, Kenya, during the southeast monsoon season (SEM). The generic names are as shown in Tables 1 and 2.

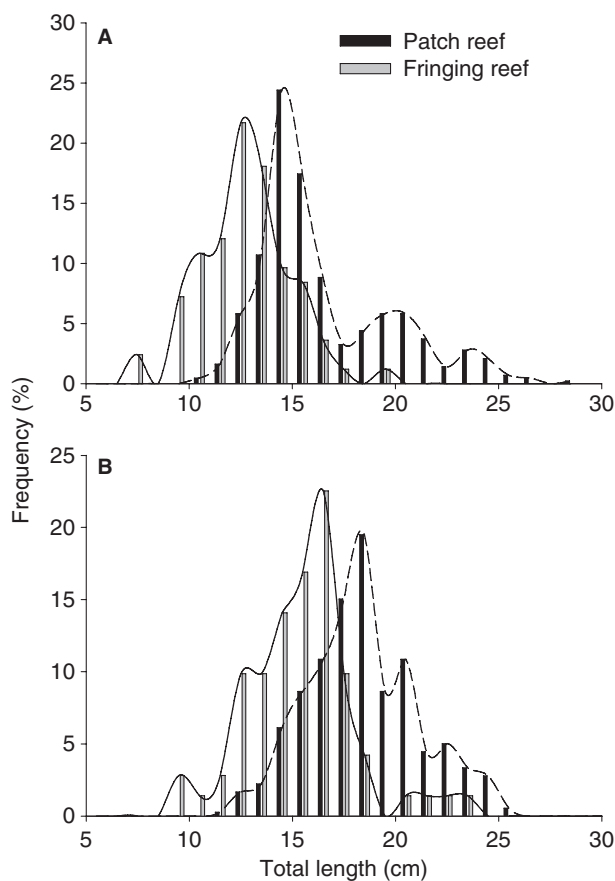
should enclose smaller proportions of fringing reefs contiguous with adjacent fisheries. The smaller proportion of enclosed fringing reef will likely provide a higher probability of out-migration especially to short-distance dispersers (Botsford *et al.* 2001; Kaunda-Arara & Rose 2004c). Parks with higher proportions of patch reefs will likely enhance conservation objectives, by affording limited connectivity with adjacent fisheries, thereby providing spatial refuge to exploited species. Malindi fishers intensely fish the fringing reef edge of the park during the NEM season (Kaunda-Arara & Rose 2004a,b); this observation seem to validate the notion of higher out-migration on the fringing reef and hence lower relative abundance of the exploited species on this reef.



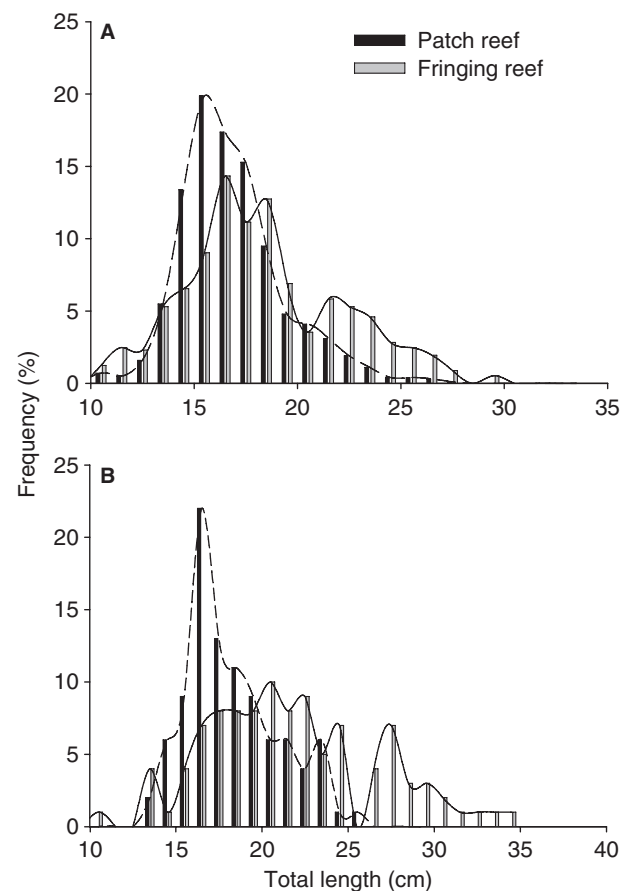
**Table 3.** Two-way ANOVA results on the influence of reef type, season and interaction between reef and season on the abundance (number per trap per day) of the common coral reef fishes within Malindi Marine Park, Kenya. MS, df and F are test parameters.

species	season			reef type			season × reef		
	MS	df	F	MS	df	F	MS	df	F
<i>Leptoscarus vaigensis</i>	9.30E-02	1	0.884	0.360	1	3.425	4.172E-02	1	0.397
<i>Siganus sutor</i>	104.2	1	4.85 *	98.00	1	4.562*	5.10	1	0.237
<i>Lethrinus mahsena</i>	3.57	1	1.34	66.3	1	24.88*	0.65	1	0.245
<i>Lethrinus nebulosus</i>	4.48E-02	1	0.15	1.86	1	6.225*	0.125	1	0.418
<i>Lethrinus miniatus</i>	0.387	1	3.02	3.64E-02	1	0.284	0.192	1	0.237
'Others'	0.000	1	0.000	2.972	1	10.69*	0.00	1	0.000
Total catch	176.81	1	17.692*	0.344	1	7.039*	23.136	1	0.144

\*Significant at P < 0.05.



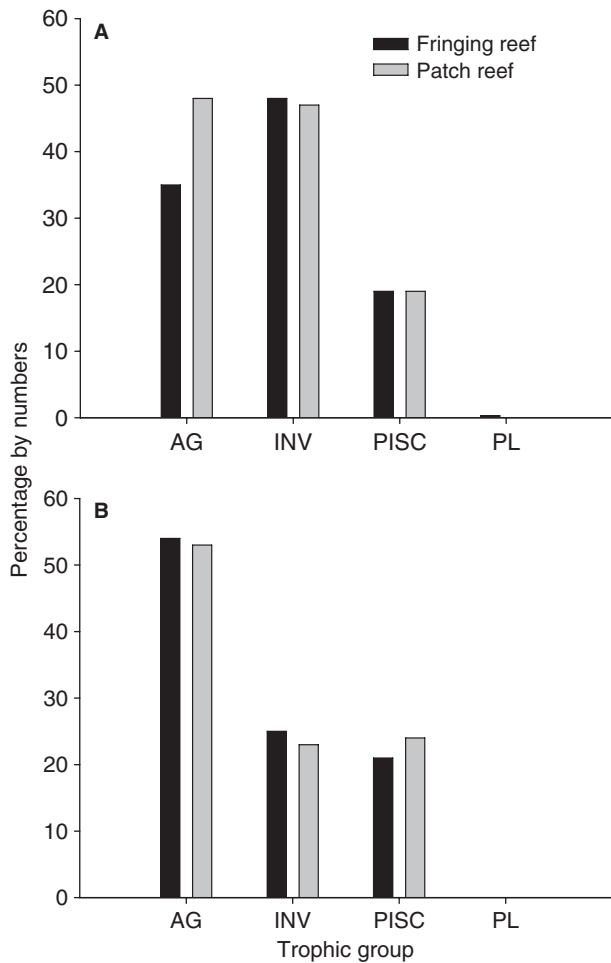
**Fig. 5.** Size-frequency distribution of the sky emperor, *Lethrinus mahsena*, on the fringing and patch reefs within Malindi Park, Kenya, during (A) the southeast monsoon (SEM) and (B) the northeast monsoon (NEM) seasons.



**Fig. 6.** Size-frequency distribution of the whitespotted rabbitfish, *Siganus sutor*, on the fringing and patch reefs within Malindi Park, Kenya, during (A) the southeast monsoon (SEM) and (B) the northeast monsoon seasons (NEM).

The abundance of the commercially important *S. sutor* was influenced more by seasons than by reef structure; however, the more sedentary sky emperor, *L. mahsena*, was affected more by reef type. These results suggest that conservation measures such as marine protected area

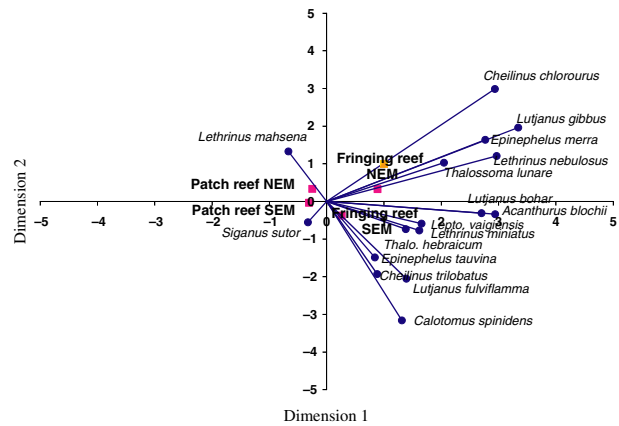
(MPA) design and setting should consider the influence of habitat types and environmental variability on fish assemblages. Moreover, the lack of significant interaction effects indicates that the influence of reef type and seasons on fish abundance is not conditional on each



**Fig. 7.** Trophic structure of fish assemblages expressed as a proportion of total numbers of fish sampled on each reef during (A) the northeast (NEM) and (B) the southeast monsoon (SEM) seasons. Trophic groups: AG, Algal grazers; INV, Invertebrate feeders; PISC, Piscivores; PL, Planktivores.

other. Conservation measures of the vagile *S. sutor* would therefore likely hinge on park management regulations (e.g. poacher control, fisher movements) that take into account seasonal distribution of the species.

Smaller-sized sky emperors dominated the fringing reef during the rough SEM season, with the larger sizes occurring on the patch reef during this season. The species had uniform size distribution between the reefs during the NEM season. For the more mobile rabbitfish, size frequency distribution did not differ between the reefs during the SEM season. However, during the calm NEM season, smaller-sized rabbitfish dominated the patch reef. These results may indicate site differences in recruitment between the species or that the nearshore fringing reef provides more physical protection to the juveniles of the sedentary emperors compared to the vagile rabbitfishes.



**Fig. 8.** Multivariate analysis (CA) of the association of trap catches with the reefs and seasons in Malindi Marine Park, Kenya, for species with catch rates  $\geq 0.03$ . ■ reef-type; • fish species.

The rabbitfish is known to spawn during the NEM season on the East African coast (Ntiba & Jaccarini 1990), and it is likely that dominance of juveniles on the patch reef in this season reflects site-specific settlement.

Multivariate analysis showed assemblage structure separated more by reef than by seasons, with seasonal effects being stronger within the fringing reef. The patch reef is dominated by the two commercial species in both seasons, whereas assemblage structure on the fringing reef seems to vary with season. The trophic structure of the reefs is mostly dominated by algal grazers and invertebrate feeders. These observations seem to support the thinking that reef fish assemblages are open systems, with non-constant dynamics and structure (Sale 1991), which seem to be influenced by reef geomorphology. However, a more pluralistic sampling approach is needed to make unequivocal conclusions on the dynamics of assemblage structure of these reefs.

Coral reef fish assemblage structures are often assessed using underwater visual census (UVC) techniques. However, visual census has been criticized on a number of grounds, including visibility, detectability and species-specific behavioural responses, which generate biases (Harmelin-Vivien *et al.* 1985; Samoily & Carlos 2000; McClanahan *et al.* 2007). In addition, UVC methods suffer from biases associated with target, cryptic and sparsely distributed species (Jennings & Polunin 1995; Edgar *et al.* 2004). In this work, we assessed assemblage structure using local traps. Although traps and other fisheries-dependent methods have biases associated with selectivity and catchability (Connell & Kingsford 1998; Wolff *et al.* 1999) and may be difficult to standardize in time and space (McClanahan & Mangi 2004), they are pervasive and easy to deploy, and can easily be used to sample exploited populations across park boundaries.

Studies on assemblage variability between reefs are lacking in the WIO; however, fisheries-dependent methods have been shown to produce some similarities to visual census methods but are likely to underestimate the degree of site separation and changes in fish communities across parks associated with fishing (McClanahan & Mangi 2004; McClanahan *et al.* 2010). These results therefore provide baseline data for comparing assemblage structure between reefs in the WIO region using other sampling methods including UVC.

In conclusion, the results indicate higher diversity of fishes on the fringing reef type, small-sized individuals dominate this reef and there is greater spatial homogeneity in fish sizes within the park during the calm NEM season. There is no significant seasonal variability in trophic structure within reefs and assemblage structure seems to be influenced more by reef type than by seasonal features. These results provide a basis for understanding tropical reef fish ecology across habitats, and are important in evaluating the role of reef type in conservation, especially in coastal East Africa, which has a mix of fringing and patch reefs.

### Acknowledgements

We thank the director of Kenya Wildlife Service for permission to work within the park, and the park warden Mr D. Mwakio and his rangers for logistical support. We are grateful to Michael Kazungu, Anthony Nzioka, Bakari Faiz and Massoud Zamu for field assistance. Mr Julius Manyala assisted with data analysis. We thank the two anonymous reviewers for constructive criticism and useful suggestions. This work was supported by WIOMSA (MASMA/AG/04/03) and the Wildlife Conservation Society-RFP Grants to BKA.

### References

- Allen G. (1997) *Marine Fishes of the Great Barrier Reef and South-East Asia – A Field Guide for Anglers and Divers*. Western Australia Museum, Perth: 292 pp.
- Andréfouët S., Guzman H.M. (2005) Coral reef distribution, status and geomorphology-biodiversity relationship in Kuna Yala (San Blas) archipelago, Caribbean Panama. *Coral Reefs*, **24**, 31–42.
- Andréfouët S., Muller-Karger F.E., Robinson J.A., Kranenburg C.J., Torres-Pulliza D., Spraggins S.A., Murch B. (2006) Global assessment of modern coral reef extent and diversity for regional science and management applications: a view from space. *Proceedings of the 10th International Coral Reef Symposium*, **1**, 1732–1745.
- Botsford L.W., Hastings A., Gaines S.D. (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters*, **4**, 144–150.
- Botsford L.W., Brumbaugh D.R., Churchill G., Kellner J.B., John L., Farrell M.R.O., Ralston S., Soulanille E., Weststad V. (2009) Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Reviews in Fish Biology and Fisheries*, **19**, 69–95.
- Connell S.D., Kingsford M.J. (1998) Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. *Coral Reefs*, **17**, 49–57.
- Coughley G. (1994) Direction in conservation biology. *Journal of Animal Ecology*, **63**, 215–244.
- Doherty P.J. (1983) Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology*, **64**, 176–190.
- Edgar G.J., Barrett N.S., Morton A.J. (2004) Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. *Journal of Experimental Marine Biology and Ecology*, **308**, 269–290.
- Galzin R. (1987) Structure of fish communities of French Polynesian coral reefs. I. Spatial scales. *Marine Ecology Progress Series*, **41**, 137–1987.
- Goldman B., Talbot F.H. (1976) Aspects of the ecology of coral reef fishes. In: Jones O.A., Endean R. (Eds), *Biology and Geology of Coral Reefs*, Vol. IV. Academic Press, New York: 124–125.
- Gutierrez L. (1998) Habitat selection by recruits establishes local patterns of adult distribution in two species of damselfishes: *Stegastes dorsopunicans* and *S. planifrons*. *Oecologia*, **115**, 268–277.
- Hamilton G.H., Brakel W.H. (1984) Structure and coral fauna of East African Reef. *Bulletin of Marine Science*, **34**, 248–266.
- Harborne A.R., Mumby P.J., Micheli F., Perry C.T., Dahlgren C.P., Holmes K.E., Brumbaugh D.R. (2006) The functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes. *Advances in Marine Biology*, **50**, 57–189.
- Harmelin-Vivien M., Harmelin J.G., Chauvet C., Duval C., Galzin R., Lejeune P., Barnabé G., Blanc F., Chevalier R., Duclerc J., Lasserre G. (1985) Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes. *Revue Ecologie (Terre Vie)*, **40**, 467–539.
- Hixon M.A., Beets J.P. (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, **63**, 77–101.
- Jennings S., Polunin N.V.C. (1995) Biased underwater visual census biomass estimates for target-species in tropical reef fisheries. *Journal of Fish Biology*, **47**, 733–736.
- Jones G.P. (1988) Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral fishes. *Journal of Experimental Marine Biology and Ecology*, **123**, 115–126.
- Kaunda-Arara B., Rose G.A. (2004a) Effects of marine reef national parks on fishery CPUE in coastal Kenya. *Biological Conservation*, **118**, 1–13.

- Kaunda-Arara B., Rose G.A. (2004b) Out-migration of tagged fishes from marine reef National Parks to fisheries in coastal Kenya. *Environmental Biology of Fishes*, **70**, 363–372.
- Kaunda-Arara B., Rose G.A. (2004c) Long-distance movements of coral reef fishes. *Coral Reefs*, **23**, 410–412.
- Kaunda-Arara B., Rose G.A., Muchiri M.S., Kaka R. (2003) Long-term trends in coral reef fish yields and exploitation rates of commercial species from coastal Kenya. *Western Indian Ocean Journal of Marine Science*, **2**, 105–116.
- Kaunda-Arara B., Mwaluma J.M., Gamoe A.L., Øresland V., Osore K.M. (2009) Temporal variability in fish larval supply to Malindi Marine Park, coastal Kenya. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **19**, S10–S18.
- Leiske E., Myers R. (1994) *Collins Pocket Guide to Coral Reef Fishes: Indo-pacific and Caribbean*. Herper Collins Publishers, London: 400 pp.
- Letourneur Y. (1996) Dynamics of fish communities of Reunion fringing reefs, Indian Ocean. 2. Patterns of temporal fluctuations. *Journal of Experimental Marine Biology and Ecology*, **195**, 31–52.
- MacNeil M.A., Graham N.A., Polunin N.V., Kulbicki M., Galzin R., Harmelin-Vivien M., Rushton S.P. (2009) Hierarchical drivers of reef-fish metacommunity structure. *Ecology*, **90**, 252–264.
- McClanahan T.R. (1988) Seasonality in East Africa's coastal waters. *Marine Ecology Progress Series*, **44**, 191–199.
- McClanahan T.R., Kaunda-Arara B. (1996) Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conservation Biology*, **10**, 1187–1199.
- McClanahan T.R., Mangi S. (2004) Gear-based management of a tropical artisanal fishery based on species selectivity and capture size. *Fisheries Management and Ecology*, **11**, 51–60.
- McClanahan T.R., Graham N.A.J., Maina J., Chabanet P., Bruggemann J.H., Polunin N. (2007) Influence of instantaneous variation on estimates of coral reef fish populations and communities. *Marine Ecology Progress Series*, **340**, 221–234.
- McClanahan T.R., Kaunda-Arara B., Omukoto J. (2010) Composition and diversity of fish and fish catches in closures and open-access fisheries of Kenya. *Fisheries Management and Ecology*, **17**, 63–76.
- McCormick M.I. (1995) Fish feeding on mobile benthic invertebrates: influences of spatial variability in habitat associations. *Marine Biology*, **121**, 627–637.
- Mellin C., Andréfouët S., Kulbicki M., Dalleau M., Vigliola L. (2009) Remote sensing and fish-habitat relationships in coral reef ecosystems: review and pathways for multi-scale hierarchical research. *Marine Pollution Bulletin*, **58**, 11–19.
- Ntiba M.J., Jaccarini V. (1988) Age and growth parameters of *Siganus sutor* in Kenyan marine waters, derived from numbers of otolith microbands and fish lengths. *Journal of Fish Biology*, **33**, 465–470.
- Ntiba M.J., Jaccarini V. (1990) Gonad maturation and spawning times of *Siganus sutor* off the Kenya coast. Evidence for definite spawning seasons in a tropical fish. *Journal of Fish Biology*, **37**, 315–325.
- Nzioka R.M. (1979) Observations on the spawning seasons of East African reef fishes. *Journal of Fish Biology*, **14**, 239–342.
- Pandolfi J.M. (2002) Coral community dynamics at multiple scales. *Coral Reefs*, **21**, 13–23.
- Pilling G.M., Millner R.S., Easey M.W., Mees C.C., Rathacharen S., Azemia R. (2000) Validation of annual growth increments in the otoliths of the lethriniid *Lethrinus mahsena* and the lutjanid *Aprion virescens* from sites in the tropical Indian Ocean, with notes on the nature of growth increments in *Pristipomoides filamentosus*. *Fishery Bulletin*, **98**, 600–611.
- Randall J.E. (1992) *Divers Guide to Fishes of Maldives*. Immel Publishing, London: 193 pp.
- Randall J.E., Allan G.R., Steene R.C. (1990) *Fishes of the Great Barrier Reef and Coral Sea*. Crawford House, Bathurst, Australia.
- Roberts C.M., Ormond R.F.G. (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series*, **41**, 1–8.
- Roughgarden J., Gaine S., Possingham H. (1988) Recruitment dynamics in complex life cycles. *Science*, **241**, 1460–1466.
- Russ G.R. (2002). Yet another review of marine reserves as reef fishery management tools. In: Sale P.F. (Ed.), *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press, San Diego: 421–443.
- Sale P.F. (1980) The ecology of fishes on coral reefs. *Oceanography and Marine Biology: An annual review*, **18**, 367–421.
- Sale P.F. (1991) Reef fish communities: Open non equilibrium systems. In: Sale P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego: 564–598.
- Sale P.F. (1998) Appropriate scales for studies of reef-fish ecology. *Australian Journal of Ecology*, **23**, 202–208.
- Sale P.F., Guy J.A., Steel W.J. (1994) Ecological structure of assemblages of coral reef fishes on isolated patch reefs. *Oecologia*, **98**, 83–99.
- Samoilys M.A., Carlos G. (2000) Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Environmental Biology of Fishes*, **57**, 289–304.
- Thresher R.E. (1983) Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef lagoon. *Marine Ecology Progress Series*, **10**, 137–145.
- Weaver D.C., Gilliam D.S., Andregg D., Dodge R.E. (2001) *Community Structure and Habitat Association of Reef Fishes on Staghorn Coral (Acropora cervicornis)*. Reef. 9th International Coral Reef Symposium, Bali.
- Williams D.Mc.B. (1991) Patterns and process in the distribution of coral reef fishes. In: Sale P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego: 437–474.
- Wolff N., Grober-Dunsmore R., Rogers C.S., Beets J. (1999) Management implications of fish trap effectiveness in adjacent coral reef and gorgonian habitats. *Environmental Biology of Fishes*, **55**, 81–90.
- Zar J.H. (1996) *Biostatistical Analysis* (3rd edn). Prentice Hall, Upper Saddle River, NJ.