

## Status of Coral Reef Fish Communities within the Mombasa Marine Protected Area, Kenya, more than a Decade after Establishment

Cosmas N. Munga<sup>1,4,6</sup>, Mohamed O.S. Mohamed<sup>2</sup>, Nassir Amiyo<sup>2</sup>,  
Farid Dahdouh-Guebas<sup>3,4</sup>, David O. Obura<sup>5</sup> and Ann Vanreusel<sup>6</sup>

<sup>1</sup>Kenya Marine and Fisheries Research Institute (KMFRI), PO Box 81651 – 80100 Mombasa, Kenya; <sup>2</sup>Kenya Wildlife Service, PO Box 82144 - 80100 Mombasa, Kenya; <sup>3</sup>Laboratory of Systems Ecology and Resource Management, Département de Biologie des Organismes, Faculté des Sciences, Université Libre de Bruxelles - ULB, Avenue Franklin D. Roosevelt 50, B-1050 Brussels, Belgium; <sup>4</sup>Laboratory of Plant Biology and Nature Management, Mangrove Management Group, Faculty of Sciences and Bio-Engineering Sciences, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium; <sup>5</sup>Coastal Oceans Research and Development – Indian Ocean, PO Box 10135– 80101, Bamburi, Kenya; <sup>6</sup>Gent University, Marine Biology Group, Krijgslaan 281 – S8, 9000 Gent, Belgium.

**Keywords:** Ecological monitoring, no-take area, partially-protected area, Marine Protected Area, Kenya.

**Abstract**—The abundance, trophic composition and diversity of fish were investigated in the Mombasa Marine Protected Area (MPA) on the Kenya coast over a period of four years (2004-2007) sixteen years after its establishment to determine its effectiveness. Fish monitoring data collected using belt transects revealed significant differences in fish abundance, distribution and composition between the MPA's no-take area and a partially-protected area with controlled exploitation. Although seasonal variation was apparent in the trophic composition, annual differences over the four year study period were not significant. Results indicated that differences in fish composition within the MPA were due to a greater abundance of haemulids (nocturnal carnivores) and acanthurids (herbivores) in the no-take area than in the partially-protected area. Fish diversity also varied between the no-take area and the partially-protected area with a higher Shannon-Wiener diversity index associated with the no-take area. Dominance was higher in the partially-protected area than in the no-take area and was also higher during the southeast (SE) monsoon season. These results support the claim of greater effectiveness of the fully protected no-take area, compared to the partially-protected area in sustaining the rich fish community found in previous studies.

## INTRODUCTION

Marine Protected Areas (MPAs) provide an important strategy for the conservation of marine biodiversity and productivity, particularly in the maintenance of fish stocks. MPAs are considered a scientific benchmark for fishery management and biodiversity conservation (McClanahan *et al.*, 1999; Botsford *et al.*, 2006; Louis *et al.*, 2007; Wells *et al.*, 2007). During the 1992 Convention on Biological Diversity (CBD), a global target was set to establish an effectively managed, representative system of MPAs covering 10% of all marine ecoregions (Wells *et al.*, 2007).

The Mombasa Marine Protected Area was gazetted in 1986 but only implemented in 1991 in an urban and tourism development area. There were reports of overfishing and conflicts among resource users before the MPA was established, especially between fishermen and boat operators who take tourists out to snorkel. This led to over-exploitation of fishery resources, degradation of coral and sea grass ecosystems, and an exponential increase in sea urchin populations (McClanahan & Kaunda-Arara, 1996; UNEP/FAO/PAP/CDA, 2000). By the time the MPA was established, conditions within no-take areas and those zoned for controlled exploitation were similar; although the coral cover was slightly higher in the no-take area than in the partially-protected area (McClanahan & Kaunda-Arara, 1996; Muthiga *et al.*, 2008). This indicated that the no-take area was already more diverse than the partially-protected area within the MPA. Three years after promulgation of the MPA, the diversity and abundance of finfish species, especially the heavily-fished triggerfish (*Balistapus undulatus*), increased dramatically and resulted in spillover of adult fish that were caught by the fishermen around the no-take area boundary (McClanahan & Mangi, 2000; 2001). This was also positively correlated with increased coral cover (45%), fleshy algae, coralline algae and soft corals that formed a more diverse and robust coral reef community in the no-take area (McClanahan

& Kaunda-Arara, 1996). However, results of studies by McClanahan and Mangi (2000; 2001) showed that the overall total catch by fishermen in the area still remained low. This was primarily due to the 63% reduction of the fishing grounds and the exclusion of about 70 fishermen from the no-take area when it was established (McClanahan & Mangi, 2000; 2001).

The Mombasa Marine Protected Area, like other MPAs in the Western Indian Ocean (WIO) region, suffered substantial coral mortality as a result of the 1998 El Niño-induced coral bleaching event (Arthur, 2000; Obura, 2001). Initial analysis by McClanahan *et al.* (2002) of the Mombasa MPA one year after the bleaching event indicated that there was little detectable effect on fish abundance and composition, despite the changes in reef complexity (i.e. a significant reduction in coral cover and an increased cover of fleshy algae). However, McClanahan *et al.* (2002) found that, in the no-take area, the abundance of parrotfishes (Scaridae), goatfishes (Mullidae), wrasses (Labridae) and butterflyfishes (Chaetodontidae) declined three years after the bleaching event. In the partially-protected area of the MPA, the abundance of Chaetodontidae and surgeonfishes (Acanthuridae) decreased during the bleaching period, while angelfishes (Pomacanthidae) increased in density. The successional change in reef complexity in the MPA was in part attributable to these changes in fish abundance and species composition, and also due to the continued impact of fishing in its partially-protected area. Fishing has an impact on the abundance of mobile species, especially Scaridae and Mullidae that are likely to move beyond the boundaries of the no-take area (McClanahan *et al.*, 2002).

This study examined the effectiveness of the Mombasa MPA six years after the bleaching event and 16 years after the MPA's establishment, using Kenya Wildlife Service's (KWS) underwater visual census standardized fish monitoring data (from 2004 to 2007). The study addressed the following questions on coral fishes:

1. Are there significant differences in fish species composition and diversity between the no-take area and the partially-protected area within the MPA?
2. Are there significant seasonal or annual differences in fish community composition in the no-take and partially-protected areas?
3. Which fish taxa are primarily responsible for the differences observed? Comparison of the fish communities in the no-take area and the partially-protected area will provide an evaluation of the management effectiveness of the MPA and enable development of future directions and conservation.

## METHODS

### Study area

The Mombasa Marine Protected Area is located within the Nyali-Bamburi-Shanzu area lying between Mtwapa and Tudor Creeks, north of Mombasa in the Coast Province of Kenya in the Indian Ocean (Fig. 1). The MPA located between  $3^{\circ}57'S - 4^{\circ}9'S$  and  $39^{\circ}42'E - 39^{\circ}51'E$  is zoned into two distinct areas: an inner no-take zone (fully protected) with an area of  $10 \text{ km}^2$  and a surrounding partially protected zone with an area of  $200 \text{ km}^2$  that nearly fully encompasses the no-take zone. Public access and controlled use of marine resources, e.g. by artisanal fishing from dugout canoes, is permitted in the partially protected zone. Climatic conditions in the area are primarily determined by the reversing monsoon winds: the dry northeast monsoon

(NEM) season occurs between October and March, and the wet southeast monsoon (SEM) season between April and September (McClanahan, 1988). Four sampling stations were selected, two within the no-take area (Coral Garden and Starfish) and two within the partially-protected area (Nyali and Ras Watene). Previous studies have indicated differences in reef complexity (notably Coral Garden) between the sampling stations within the no-take and partially-protected areas, despite being similar in water depth (McClanahan & Kaunda-Arara, 1996).

### Sampling

The belt transect sampling technique described by English *et al.* (1997) was used for the fish surveys. These were undertaken by KWS trained observers using randomly deployed transects (at most six replicate belt

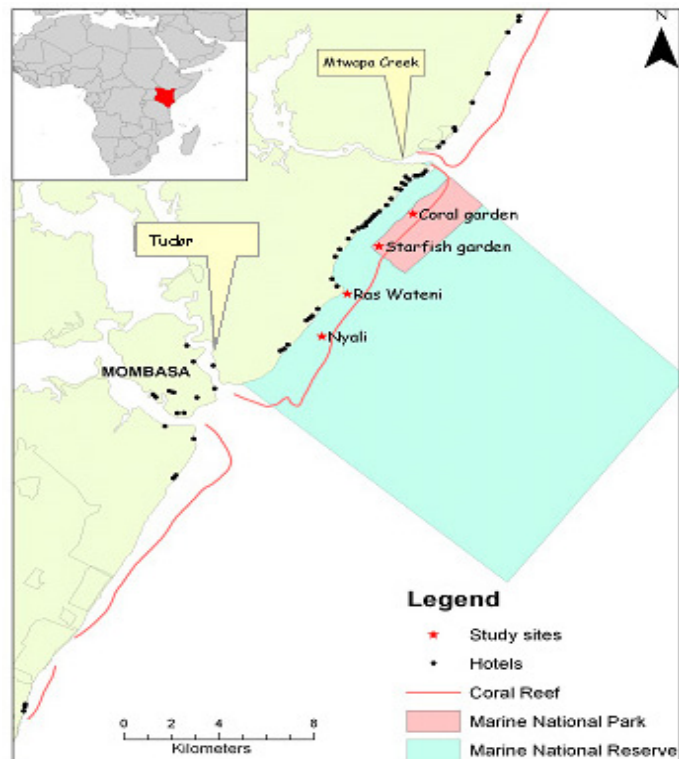


Figure 1. Mombasa Marine Protected Area with its no-take (Marine National Park) and partially-protected areas (Marine National Reserve) and the sampling stations.

transects of 50 x 5 m per sampling station). In the no-take area, totals of 41 transects were completed in the NEM (24 at Starfish and 17 at Coral Garden) and 42 in the SEM (18 transects at Starfish and 24 at Coral Garden). In the partially-protected area, totals of 20 transects were undertaken in the NEM (12 transects at Ras Iwatine and 8 at Nyali) and 36 transects in the SEM (18 transects each at Ras Iwatine and Nyali). A total of 13 fish families were monitored for abundance: Labridae (wrasses), Acanthuridae (surgeonfishes), Haemulidae (grunts/sweetlips), Scaridae (parrotfishes), Lutjanidae (snappers), Chaetodontidae (butterflyfishes), Siganidae (rabbitfishes), Mullidae (goatfishes), Lethrinidae (emperors), Pomacanthidae (angelfishes), Balistidae (triggerfishes), Carangidae (jacks) and Serranidae (groupers). At least two observers were used during each sampling session: one laid the transect line, and the other snorkelled while counting and identified fish sighted directly ahead within the 2.5 m water column on either side of the line). Fish were identified using keys by Richmond (1997), Smith and Heemstra (1998), and Lieske and Myers (1994). Sampling was undertaken twice per year in the dry NEM and wet SEM as consistently as possible, using the same members of the monitoring team at all sampling stations during each sampling session. All sampling was conducted during the low tide at an average depth of 2 m.

### Data analysis

Replicate data from the visual fish census were used to calculate fish family abundances per 250 m<sup>2</sup> in the no-take and partially-protected areas, per sampling station (Coral Garden, Starfish, Ras Iwatine and Nyali), per season (NEM and SEM), and per year (2004, 2005, 2006 and 2007). Unfortunately, fish monitoring at Ras Iwatine and Nyali was not accomplished in all four years and data for 2004 are not available. Similarities or dissimilarities in fish abundance and composition were presented in non-metric Multidimensional Scaling (MDS) plots using PRIMER statistical software. Two-

way Analysis of Similarity (ANOSIM) was applied to establish significant differences in fish abundance and composition between stations, seasons and years. Where differences existed, Similarity Percentage Breakdown (SIMPER) was used to identify which fish taxon or taxa contributed to the difference. Fish biomass could not be calculated as fish lengths were not estimated. Fish taxa were also classified into trophic guilds according to Durville *et al.* (2003) and analysed in a similar manner. Further, as an indication of ecosystem health (Pillans *et al.*, 2007), measures of fish diversity were calculated using the Shannon-Wiener diversity index ( $H'$ ), and dominance index ( $N_{inf}$ ) according to Hill (1973) ( $N_{inf} = 1 / \max \{p_i\}$  with  $p_i$  being the proportion of the  $i$ th taxa). Differences were determined using Two-way Analysis of Variance (ANOVA), combining stations and seasons after testing for homogeneity of variances by Levene's test. *Post hoc* pair-wise comparison using the Tukey HSD Test was applied to establish differences between groups.

## RESULTS

### Fish abundance and trophic guild composition

Results of the non-metric MDS-plots based on fish densities showed a distinct difference in species composition between the protection types (Fig. 2a), i.e. the no-take area and the partially-protected area (2-way ANOSIM:  $R = 0.478$ ;  $P = 0.001$ ). The same test indicated that there was no significant difference between the seasons (2-way ANOSIM:  $R = 0.124$ ;  $p = 0.096$ ) (Fig. 2b). There was a significant difference between sampling stations (2-way ANOSIM:  $R = 0.338$ ;  $p = 0.001$ ; Fig. 3a), the results of pair-wise comparison tests indicating differences between Starfish and Ras Iwatine, Starfish and Nyali, Coral Garden and Ras Iwatine, and Coral Garden and Nyali ( $p < 0.05$  in all cases). There was, however, no significant difference between the years sampled (2-way ANOSIM:  $R = -0.055$ ,  $p = 0.676$ ; Fig. 3b). Results of the 2-way SIMPER analysis indicated that there were higher abundances of Haemulidae and

Acanthuridae in the no-take area than in the partially-protected area (Tables 1 and 2). While Labridae comprised the most abundant family in both the partially-protected (22.7%) and the no-take (13.4%) areas, the families Serranidae and Carangidae were the least abundant in both these areas. Fish abundances were more or less uniformly distributed between the seasons, with the Labridae being slightly more abundant in the SEM than in the NEM.

Results of the non-metric MDS-plots based on fish trophic guild composition indicated significant difference between the protection types (Fig. 4a) and between the seasons (Fig. 4b) (2-way ANOSIM:  $R = 0.380$ ;  $P = 0.001$  and  $R = 0.174$ ;  $p = 0.045$  respectively). There was no significant difference between the sampling stations (2-way ANOSIM:  $R = 0.188$ ;  $p = 0.053$ ; Fig. 5a); however, results of pair-wise comparison

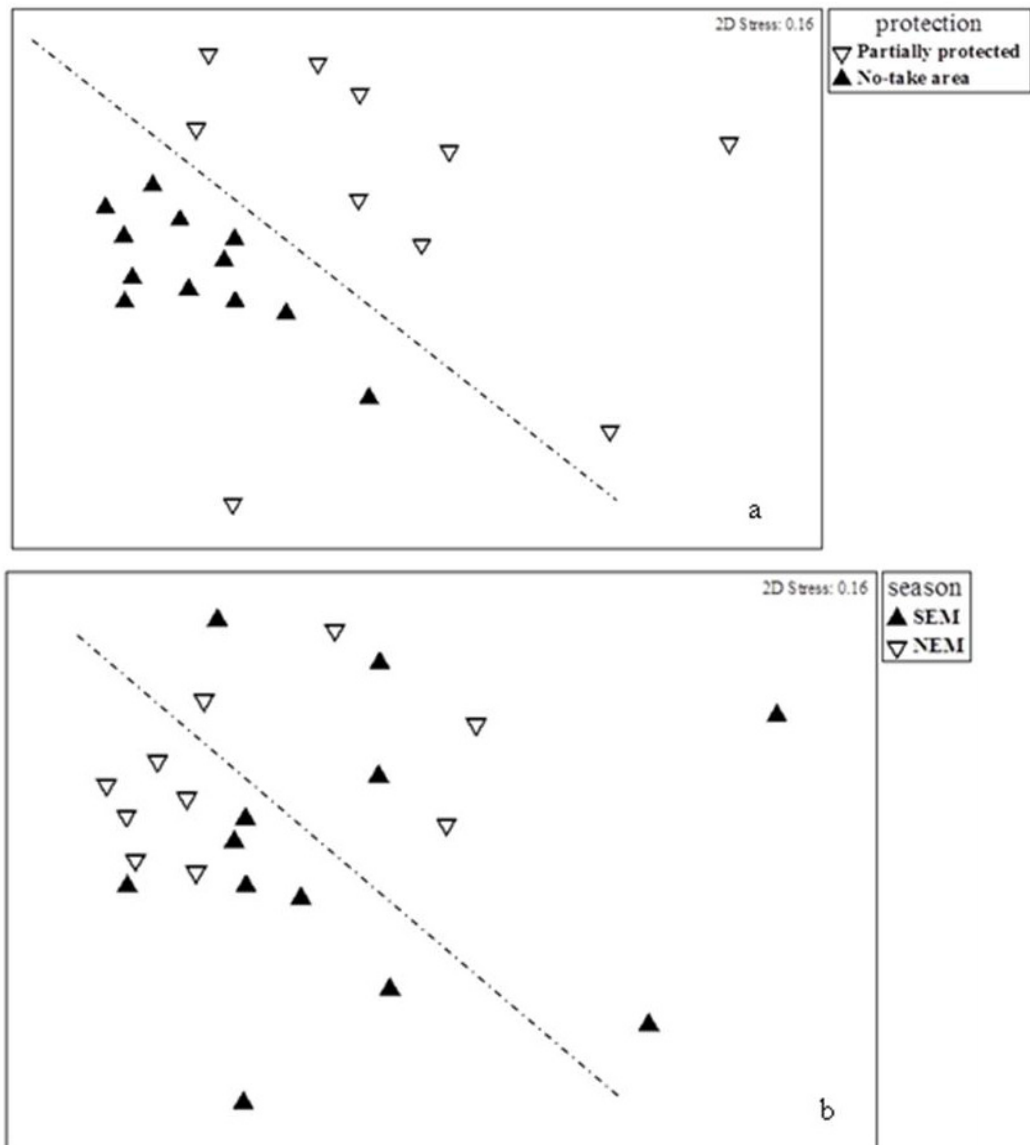


Figure 2. Non-metric MDS of fish densities in terms of a) protection type and b) season with a dotted line separating the no-take area from the partially-protected area.

Table 1. Two-way SIMPER analysis of fish abundance per 250 m<sup>2</sup> in the no-take and partially-protected areas.

Fish families	No-take area	Partially-protected area	Average dissimilarity	Contribution (%)
	Abundance	Abundance		
Labridae	13.89	22.72	5.07	15.67
Haemulidae	11.39	2.54	4.85	15.00
Acanthuridae	12.38	8.64	2.78	8.60
Lutjanidae	8.41	5.63	2.64	8.15
Siganidae	6.49	9.13	2.63	8.13
Lethrinidae	5.74	5.76	2.52	7.80
Mullidae	6.91	9.15	2.41	7.46
Carangidae	3.42	4.31	2.08	6.43
Balistidae	4.87	4.82	1.80	5.55
Pomacentridae	5.20	6.05	1.65	5.11
Serranidae	2.49	2.79	1.44	4.45
Scaridae	10.88	11.49	1.36	4.20
Chaetodontidae	7.93	6.9	1.11	3.45

Table 2. Two-way SIMPER analysis of fish abundance per 250 m<sup>2</sup> in the NEM and SEM.

Fish families	SEM	NEM	Average dissimilarity	Contribution (%)
	Abundance	Abundance		
Labridae	19.77	15.67	3.45	13.25
Carangidae	2.70	5.18	2.45	9.45
Haemulidae	8.01	6.60	2.24	8.66
Siganidae	7.61	7.78	2.23	8.62
Lutjanidae	7.96	6.17	2.16	8.34
Lethrinidae	5.11	6.51	2.13	8.24
Acanthuridae	10.83	10.50	2.08	8.04
Mullidae	8.13	7.69	1.88	7.25
Serranidae	1.68	3.75	1.70	6.58
Pomacentridae	4.48	6.92	1.66	6.40
Balistidae	5.35	4.25	1.55	6.00
Scaridae	11.25	11.05	1.44	5.55
Chaetodontidae	7.12	7.93	0.94	3.64

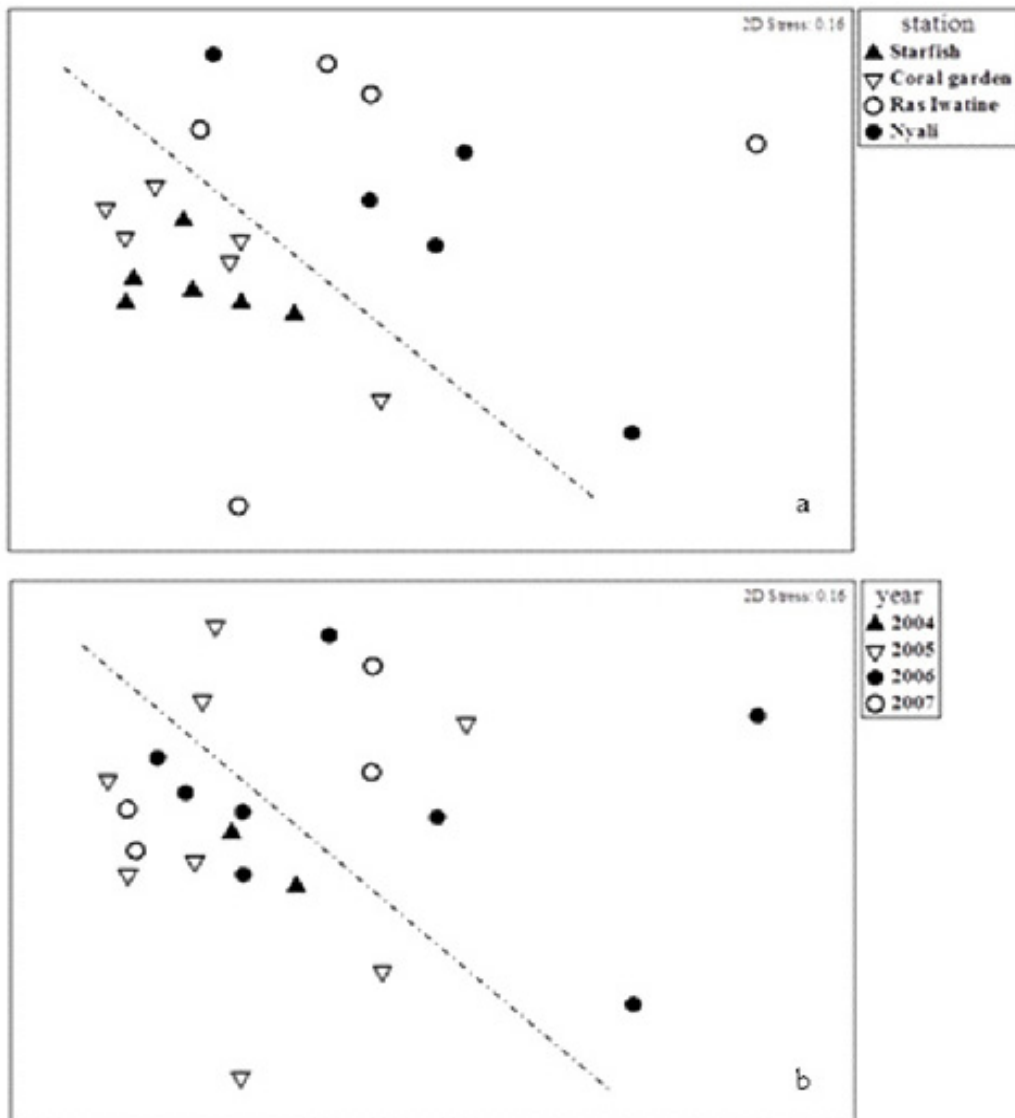


Figure 3. Non-metric MDS of fish densities in terms of a) sampling stations and b) years with a dotted line separating the no-take area from the partially-protected area.

tests indicated differences between Starfish and Ras Iwatine, and between Starfish and Nyali ( $p < 0.05$  in both cases). The same test yielded no significant difference between the years sampled (2-way ANOSIM:  $R = -0.267$ ;  $p = 0.091$ ; Fig. 5b). This difference between the protection types in fish trophic guild composition was attributable to more abundant diurnal carnivores (e.g. Mullidae, Labridae, Scaridae and Balistidae), while the piscivores (e.g. carangids and serranids)

were the least abundant both in the no-take area and the partially-protected area (Table 3). Seasonal differences in fish guild composition were due to more abundant piscivores in the NEM and more abundant diurnal carnivores in the SEM (Table 4).

### Fish diversity

Seasonally, Shannon-Wiener diversity indices were generally higher during the NEM than the SEM at all the sampling stations except

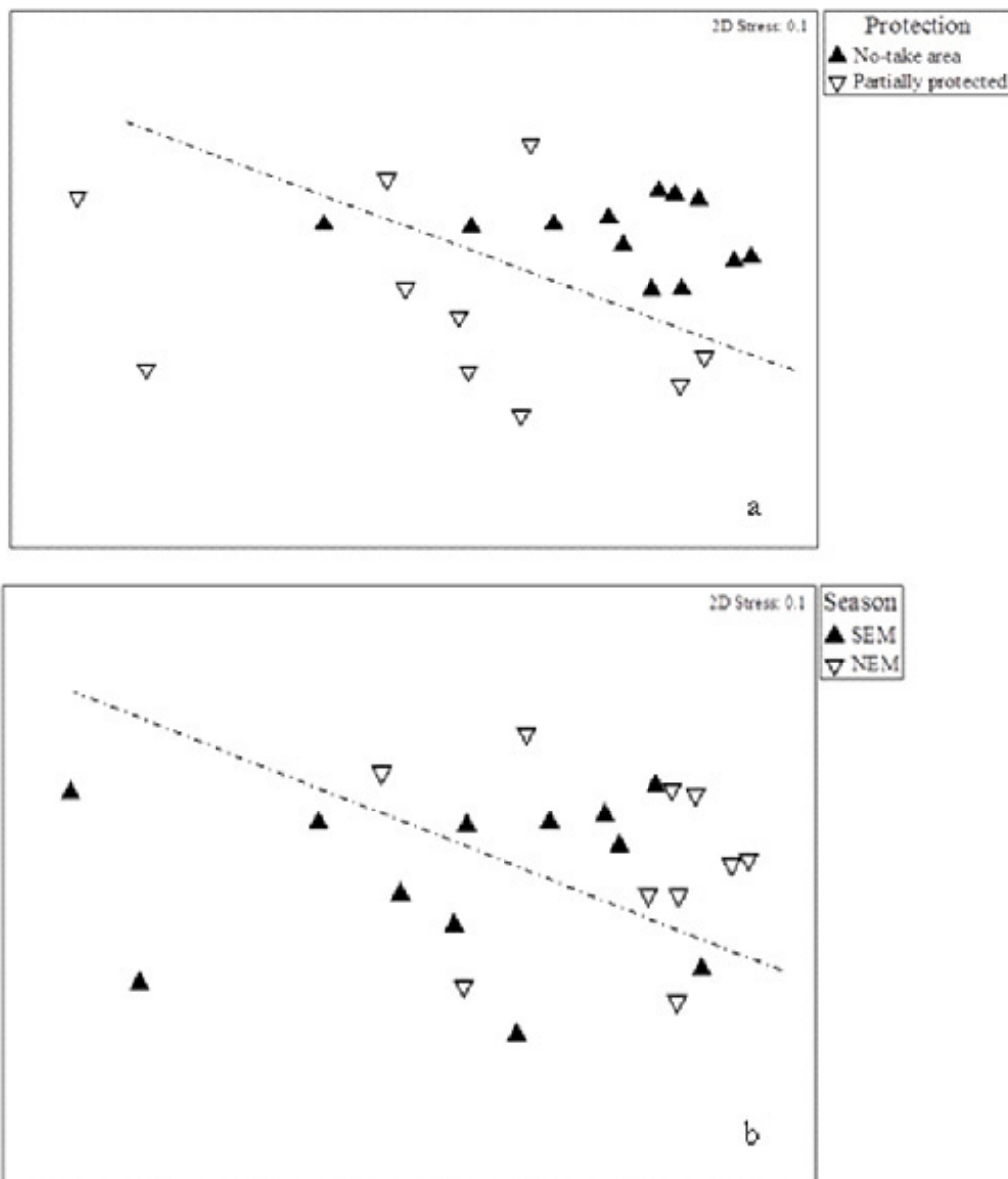


Figure 4. Non-metric MDS of fish densities of trophic guilds in terms a) protection type and b) season with a dotted line separating the no-take area from the partially-protected area.

Nyali (Fig. 6a). Results of a *post hoc* pair-wise Tukey HSD test showed that the no-take area differed significantly during the NEM from the partially-protected area during the SEM ( $p < 0.05$ ). The Coral Garden and the Starfish sampling stations in the no-take area yielded increasingly higher Shannon-Wiener diversity indices ( $H'$ ); the values at Ras Iwatine and Nyali in the partially-protected area were lower, the lowest occurring in 2006 (Fig.

6b). Two-way ANOVA indicated significant differences in the Shannon-Wiener diversity index between the protection types and between the seasons ( $Df = 1$ ; Err  $Df = 134$ ;  $f = 26.148$ ;  $p = 0.000001$  and  $Df = 1$ ; Err  $Df = 134$ ;  $f = 21.339$ ;  $p = 0.00001$  respectively). The same test indicated that there was no significant effect due to the interaction of season and protection type ( $Df = 1$ ; Err  $Df = 134$ ;  $f = 0.120$ ;  $p = 0.730$ ).



Table 3. Two-way SIMPER analysis of fish guild abundance in the no-take and partially-protected areas.

Trophic guilds	No-take area		Partially-protected area	
	Abundance	Abundance	Average dissimilarity	Contribution (%)
Diurnal carnivore	22.16	30.16	5.19	29.33
Piscivore	7.22	7.34	3.24	18.32
Browser of sessile invert	12.46	8.54	2.55	14.43
Omnivore	8.01	7.75	2.54	14.36
Nocturnal carnivore	24.67	21.59	2.46	13.89
Herbivore	25.48	24.61	1.71	9.68

Table 4. Two-way SIMPER analysis of fish guild abundance in the SEM and NEM.

Trophic guilds	SEM		NEM	
	Abundance	Abundance	Average dissimilarity	Contribution (%)
Piscivore	4.74	10.32	4.38	25.18
Diurnal carnivore	28.58	22.45	4.11	23.61
Omnivore	6.05	10.11	2.70	15.52
Nocturnal carnivore	24.69	21.57	2.46	14.15
Herbivore	26.27	23.66	2.06	11.86
Browser of sessile invert	9.67	11.89	1.68	9.68

With the exception of Nyali, the dominance index was seasonally higher in the SEM (lower values) than in the NEM (higher values) (Fig. 7a). Results of a *post hoc* pair-wise Tukey HSD test showed that the partially-protected area in both the NEM and SEM and the no-take area in the SEM were significantly different from that of the no-take area in the NEM ( $p < 0.05$ ). Higher dominance indices ( $N_{inf}$ ) signifying lower dominance were associated with the Coral Garden and the Starfish point in the no-take area; the indices at Ras Iwatine and Nyali in the partially-protected area were again lower, the lowest occurring in 2006 (Fig. 7b). Two way ANOVA indicated a significant difference in dominance index between the protection

types (Df = 1; Err Df = 134;  $f = 19.68$ ;  $p = 0.00002$ ) and between the seasons (Df = 1; Err Df = 134;  $f = 9.591$ ;  $p = 0.0024$ ) but no significant effect due to season and protection type interactions (Df = 1; Err Df = 134;  $f = 1.439$ ;  $p = 0.232$ ).

## DISCUSSION

A clear difference in fish composition was found between the no-take and the partially-protected areas within the Mombasa MPA, attributable to higher abundances of the Haemulidae and Acanthuridae in the former area. The Acanthuridae was one of the most dominant fish families in the no-take area of the Mombasa MPA in an earlier study,

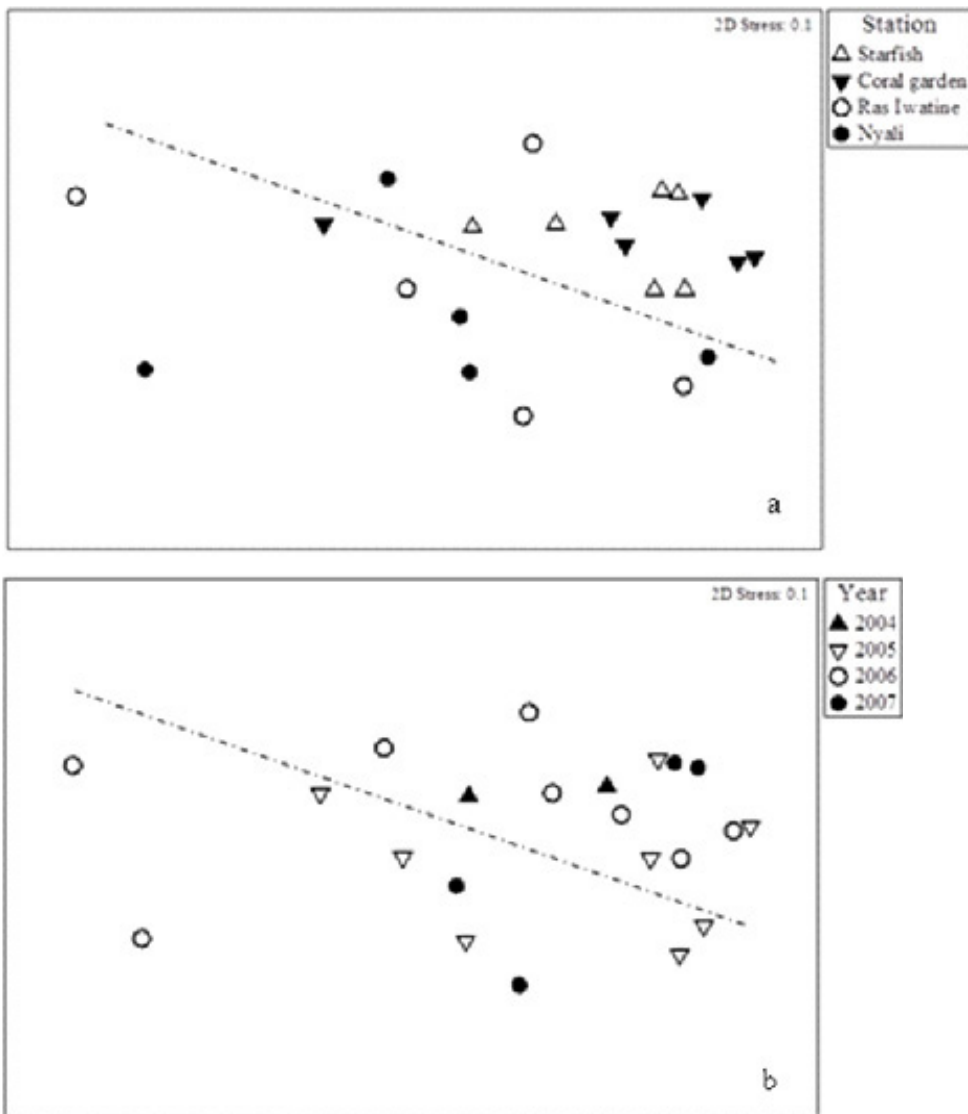


Figure 5. Non-metric MDS of fish densities of trophic guilds in terms of a) sampling stations and b) years with a dotted line separating the no-take area from the partially-protected area.

its biomass being estimated to be more than 100 kg/ha in the year 2001 (Muthiga *et al.*, 2003). McClanahan *et al.* (2007) described the success of this fish family in the no-take area over other herbivorous fish families such as the Scaridae (parrotfishes), as being due to their longevity, giving them a competitive advantage in the no-take area. Our study showed that Haemulidae were similarly high in abundance in the no-take area, relative to the partially-protected area.

High abundances of carnivorous fish families, especially the nocturnal carnivores (Haemulidae, Serranidae, Lutjanidae and Lethrinidae), surpassed other fish families and are typical of coral reef environments in MPAs or areas with minimal fishing pressure. Similar findings derived from visual fish censuses in the Mozambique Channel were recorded in the naturally protected area of the Glorieuses Islands by Durville *et al.* (2003) and in the Juan de Nova's natural no-take area by

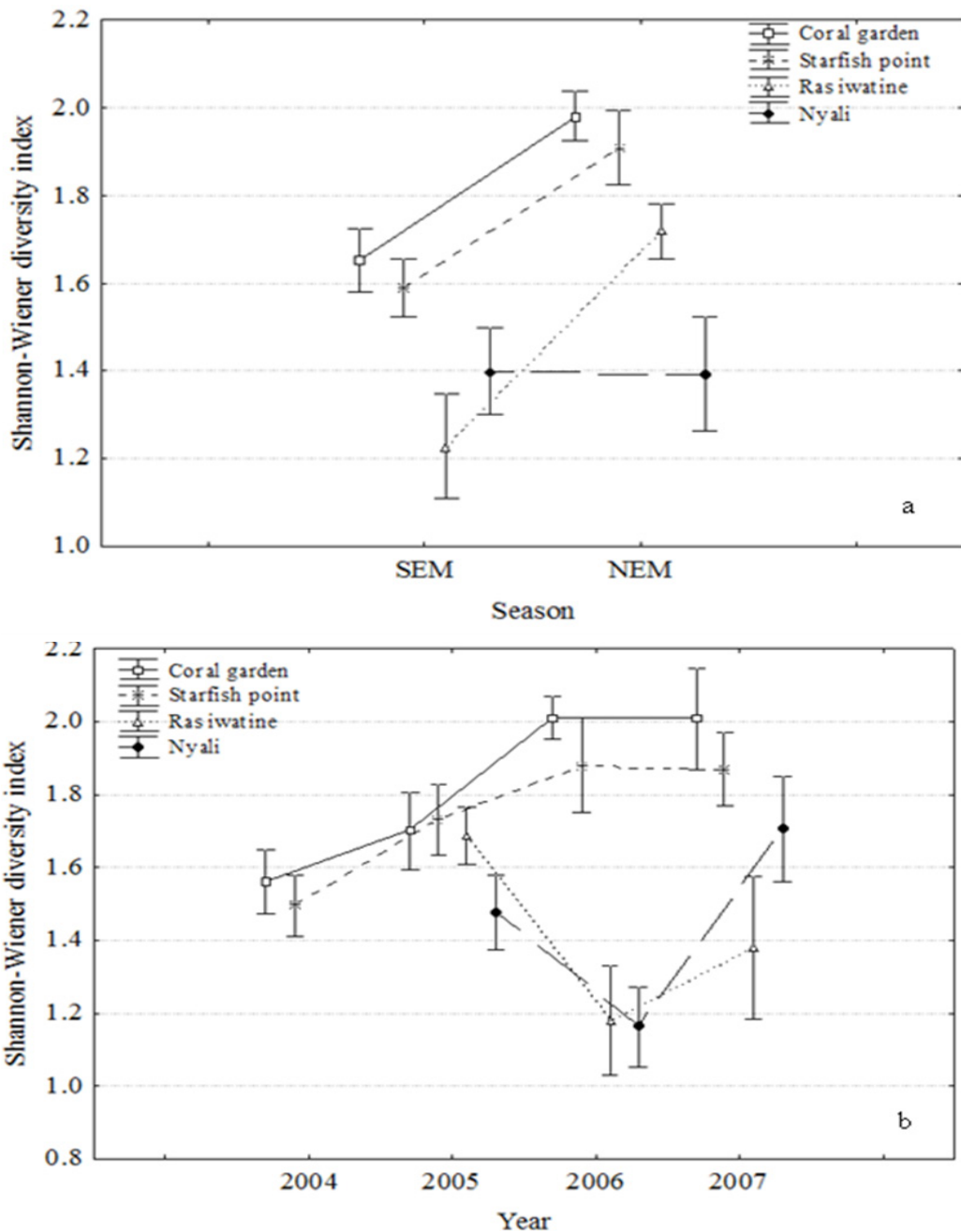


Figure 6. Mean  $\pm$  SE Shannon-Wiener indices of fish diversity at the sampling stations in a) seasons and b) years.

Chabanet and Durville (2005). The presence of such large populations can be related to the absence of fishing pressure in these no-take areas, since carnivores are in general the fish species most targeted by artisanal fishermen outside these no-take areas.

A higher abundance of herbivores (Acanthuridae, Scaridae and Siganidae) and browsers of sessile invertebrates (e.g. Chaetodontidae) can also be partly attributed to a lack of fishing pressure in the no-take area. McClanahan and Kaunda-Arara (1996)

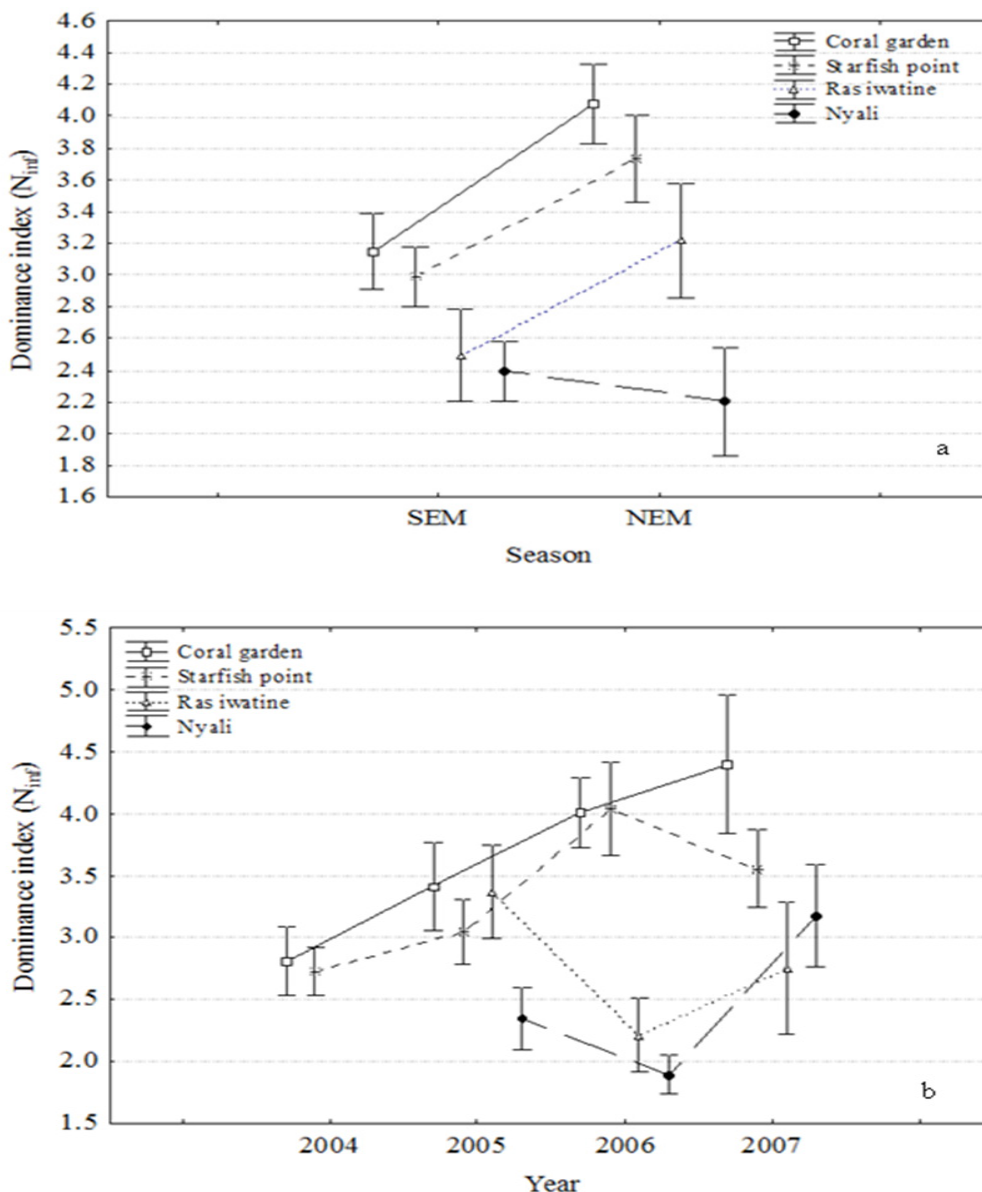


Figure 7. Mean ± SE of fish dominance indices at the sampling stations in a) seasons and b) years.

noted that populations of acanthurids were very low on Kenyan unprotected reefs as were the chaetodonts. Chaetodonts live in association with coral reefs and are considered as bio-indicators of reef health. A study by Pereira and Videira (2005) on the community structure of chaetodonts in Southern Mozambique revealed that reefs with relatively high hard coral cover had higher chaetodon abundances. A higher

reef topographic complexity is found at Coral Garden within the Mombasa Marine no-take area, and this possibly accounted for the higher populations of chaetodonts in the no-take area (McClanahan & Kaunda-Arara, 2006).

Piscivores (e.g. Serranidae and Carangidae) are often slow-growing and late-maturing species that are vulnerable to overfishing, explaining their low abundance both in the no-

take area and the partially-protected area (Table 2). The Carangidae are also highly variable and mostly non-reef pelagics (Kaunda-Arara *et al.*, 2003) making them largely absent in most coral reef environments. Carangids in the Mombasa Marine no-take area and partially-protected area also exhibited the greatest seasonality with a higher abundance encountered in the warmer temperatures during the NEM than in the colder temperatures of the SEM (Table 2). This is in agreement with findings by Munro *et al.* (1973) who found that the elevated capture of ripe black trevallies (*Caranx lugubris*) in the Caribbean coincides with the period between February and September when spawning reaches a peak during these warmer summer months. This species also has a circumtropical distribution in the Pacific and Indian Oceans.

The lower fish diversity in the partially-protected area confirmed that artisanal fishing is having an effect on the fish community. The dominant fishes in the partially-protected area were labrids (wrasses) which are diurnal carnivores. Pillans *et al.* (2007) showed that commercial fishing in an unprotected marine area can cause a dramatic decline in evenness and dominance of a few fish species over others. Conversely, the higher fish diversity in the no-take area, especially at Coral Garden (Fig. 6a), is a sign of its previously noted effectiveness in conserving biodiversity (McClanahan & Kaunda-Arara, 1996; McClanahan, 1997) since its promulgation in 1991 when it was also associated with higher coral cover (McClanahan, 1994; McClanahan & Kaunda-Arara, 1996). The higher fish diversity in the no-take area compared to the partially-protected area was again reported more recently by Muthiga *et al.* (2003). This is associated with a reduced dominance by fish taxa in the no-take area relative to its higher habitat complexity, further evidence that it is successful in protecting this aspect of marine biodiversity.

The higher diversity of fish taxa during the warmer NEM corroborates the results of a long-term fisheries-independent monitoring programme in the northern Indian River Lagoon of Florida in which

higher species richness and diversity are correlated with warmer water temperatures during summer (Tremain & Adams, 1995). Regular fluctuations in temperature with other environmental factors such as salinity and dissolved oxygen levels (Ernesto *et al.*, 2009; Larry and Michael, 1975) have been found to contribute to changes in the composition and relative abundance of fish species. The influx of juvenile fish during the warmer NEM may also account for the higher diversity of fish sampled during this season. Similar findings in a study on Georgia estuarine fish populations revealed that seasonal changes in fish diversity resulted primarily from an influx of juveniles in warm summer seasons (Michael & Eugene, 1970). The higher fish diversity recorded during the NEM in this study may also have been partially attributable to favourable and calm weather conditions that enabled better sampling compared to the rainy and rough SEM when sampling is difficult.

The results of this study thus confirm that the Mombasa MPA no-take area, especially the Coral Garden, continues to be richer in fish diversity than the partially-protected area. This difference in fish diversity is in part linked to the level of protection, status of the fish community before promulgation of the MPA and its recovery after the 1998 El Niño-induced coral bleaching event. Acanthuridae and Haemulidae were found to be more abundant in the no-take area and Labridae dominated the partially-protected area and merit further monitoring.

**Acknowledgements** - We are greatly indebted to Kenya Wildlife Service – Coast and the Kenya Wildlife Service monitoring team for monitoring data, and the opportunity they gave to the first author to participate in some of the monitoring campaigns in the Mombasa MPA. We thank Jan Vanaverbeke, Gent University Marine Biology Group for assistance with the statistical analyses. We also thank one anonymous reviewer for constructive comments on the first version of this manuscript. The study was made possible by a VLIR UOS (Belgium) scholarship awarded to the first author.

## REFERENCES

- Arthur R (2000) Coral bleaching and mortality in three Indian Ocean reef regions during an *El Niño* southern oscillation event. *Current Science*, 79: 1723-1729
- Botsford LW, Hastings A (2006) Conservation dynamics of marine metapopulations with dispersing larvae. In: Sale P, Kritzer J (eds) *Marine Metapopulations*. Academic Press, San Diego, pp 411-429
- Chabanet P, Durville P (2005) Reef fish inventory of Juan de Nova's natural no-take area (Western Indian Ocean). *Western Indian Ocean Journal of Marine Science* 4: 145-162
- Durville P, Chabanet P, Quod JP (2003) Visual census of the reef fishes in the natural partially protected area of the Glorieuses Islands. *Indian Ocean Journal of Marine Science* 2: 95-104
- English S, Wilkinson C, Baker V (eds) (1997) *Survey manual for tropical marine resources*, 2nd edition. ASEAN-Australia marine science project: Living coastal resources, Australian Institute of Marine Science, PMP No 3, Townsville, Australia, 390 pp
- Ernesto M, Manuel CR, Rocio ZH, Selene OB (2009) Seasonal variations in the diversity, abundance and composition of species in an estuarine fish community in the Tropical Eastern Pacific, Mexico. *The Ichthyological Society of Japan* 56: 330-339
- Hill MO (1973) Diversity and evenness: A unifying notation and its consequences. *Ecology* 54: 427-432
- Kaunda-Arara B, Rose AG, Muchiri MS, Kaka R (2003) Long-term trends in coral reef fish yields and exploitation rates of commercial species from coastal Kenya. *Indian Ocean Journal of Marine Science* 2: 105-116
- Larry GA, Michael HH (1975) Abundance, diversity and seasonality of fishes in Colorado lagoon, Alamitos bay, California. *Estuarine and Coastal Marine Science* 3: 371-380
- Lieske E, Myers R (1994) *Collins pocket guide to coral reef fishes: Indo-pacific and Caribbean*. Herper Collins, London, 400 pp
- Louis WB, Fiorenza M, Ana MP (2007) Biological and Ecological Considerations in the Design, Implementation and Success of Marine Protected Areas. In: *FAO report and documentation of the expert workshop on Marine Protected Areas and fisheries management: Review of issues and considerations*. Rome, 12-14 June 2006. *FAO Fisheries report No. 825*, FAO, Rome, 332 pp
- McClanahan TR, Graham NAJ, Calnan JM, MacNeil MA (2007) Toward pristine biomass: Reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Applications* 17: 1055-1067
- McClanahan TR, Marnane MJ, Cinner JE, Kiene WE (2006) A comparison of marine protected areas and alternative approaches to coral reef management. *Current Biology* 16: 1408-1413
- McClanahan TR, Mwanguni S, Muthiga NA (2005) Management of the Kenyan coast. *Ocean and Coastal Management* 48: 901-931
- McClanahan TR (2002) The near future of coral reefs. *Environmental conservation*, 29: 460-483
- McClanahan TR, Maina J, Pet-Soede L (2002) Effects of the 1998 coral mortality event on Kenyan coral reefs and fisheries. *Ambio* 31: 7-8
- McClanahan TR, Mangi S (2001) The effect of a closed area and beach seine exclusion on coral reef fish catches. *Fisheries Management and Ecology* 8: 107-121

- McClanahan TR, Mangi S (2000) Spillover of exploitable fishes from a marine no-take area and its effect on the adjacent fishery. *Ecological Applications* 10: 1792-1805.
- McClanahan TR, Glaesel H (1997) The effects of traditional fisheries management on fisheries yields and the coral reef ecosystems of Southern Kenya. *Environmental Conservation* 24: 105-120
- McClanahan TR, Kaunda-Arara (1996) Fishery recovery in a coral reef marine no-take area and its effect on adjacent fishery. *Conservation Biology* 10: 1187-1199
- McClanahan TR (1988) Seasonality of East Africa's Coastal Waters. *Marine Ecology Progress Series* 44: 191-199
- Michael D, Eugene P (1970) Annual cycles of species occurrence, abundance and diversity in Georgia estuarine fish populations. *American Midland Naturalist* 83: 382-392
- Munro JL, Gaut VC, Thompson R (1973) Spawning seasons of Caribbean reef fishes. *Journal of Fish Biology* 5: 69-84
- Muthiga N, Costa A, Motta H, Muhando C, Mwaipopo R, Schleyer M (2008) Status of coral reefs in East Africa: Kenya, Tanzania, Mozambique and South Africa. *Status of Coral Reefs of the World: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville, Australia*, pp 91-104
- Muthiga N, Maina J, McClanahan T (2003) The effectiveness of management of marine protected areas in Kenya. A report prepared for the international tropical marine environment management symposium, Manila, Philippines, 10 pp
- Obura DO (2001) Kenya – Review of coastal marine environment and pollution issues. In: Sheppard C (ed) *Special supplement to Seas at the Millennium. Marine Pollution Bulletin* 42: 1264-1278
- Pereira MAM, Videira EJS (2005) Distribution and community structure of butterflyfishes (Pisces: Chaetodontidae) in Southern Mozambique. *Western Indian Ocean Journal of Marine Science* 4: 39-46
- Pillans S, Ortiz JC, Pillans RD, Possingham HP (2007) The impact of marine reserves on nekton diversity and community composition in subtropical eastern Australia. *Biological Conservation* 136: 455-469
- Richmond MD (1997) *A guide to the seashores of Eastern Africa and the Western Indian Ocean islands*. Sida, SAREC, Sweden, 448 pp
- Smith JLB, Heemstra R (1998) *Smith's sea fishes*, fourth ed. Valiant Publishing Sandton, South Africa, 578 pp
- Tremain DM, Adams DH (1995) Seasonal variations in species diversity, abundance and composition of fish communities in the northern Indian River Lagoon, Florida. *Bulletin of Marine Science* 57: 171-192
- UNEP/FAO/PAP/CDA (2000) *Progress in Integrated Coastal Management for Sustainable Development of Kenya's Coast. The Case of Nyali-Bamburi-Shanzu Area. Report Prepared within the Project "Protection and Management of the Marine and Coastal Areas in the Eastern African Region" – EAF/5-II. East African Regional Seas Technical Reports Series No. 6*, 66 pp
- Wells S, Burgess N, Ngusuru A (2007) Towards the 2012 marine protected area targets in Eastern Africa. *Ocean and Coastal Management* 50: 67-83