# Kenyan coral reef lagoon fish:
# effects of fishing, substrate complexity, and sea urchins

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**Abstract.** Population density, number of species, diversity, and species-area relationships of fish species in eight common coral reef-associated families were studied in three marine parks receiving total protection from fishing, four sites with unregulated fishing, and one reef which recently received protection from fishing (referred to as a transition reef). Data on coral cover, reef topographic complexity, and sea urchin abundance were collected and correlated with fish abundance and species richness. The most striking result of this survey is a consistent and large reduction in the population density and species richness of 5 families (surgeonfish, triggerfish, butterflyfish, angelfish, and parrotfish). Poor recovery of parrotfish in the transition reef, relative to other fish families, is interpreted as evidence for competitive exclusion of parrotfish by sea urchins. Reef substrate complexity is significantly associated with fish abundance and diversity, but data suggest different responses for protected versus fished reefs, protected reefs having higher species richness and numbers of individuals than unprotected reefs for the same reef complexity. Sea urchin abundance is negatively associated with numbers of fish and fish species but the interrelationship between sea urchins, substrate complexity, coral cover, and management make it difficult to attribute a set percent of variance to each factor – although fishing versus no fishing appears to be the strongest variable in predicting numbers of individuals and species of fish, and their community similarity. Localized species extirpation is evident for many species on fished reefs (for the sampled area of 1.0 ha). Fifty-two of 110 species found on protected reefs were not found on unprotected reefs.

## Introduction

Despite advances in our knowledge of the ecology of coral reef fishes (Sale 1991a), efforts to quantify the direct and indirect impacts of fish harvesting have been limited to few studies (Russ 1991; Roberts and Polunin 1991; Grigg 1994). Previous research has produced variable results and impacts may depend on ecological characteristics of fished locations, the degree of fishing effort, and fishing methods (Goeden 1982; Koslow et al. 1988; Samoilys 1988; Russ and Alcala 1989; Russ 1991). Fisheries management plans rely on an understanding of how these factors interact to affect coral reef fish abundance and species diversity. In principle, this knowledge can be used to develop fisheries management plans which preserve high productivity and species diversity of coral reefs. However, the present state of knowledge is still meager, relying mostly on species surveys in areas experiencing different levels and types of fishing. Before a general and predictive model of fish harvesting impacts can be developed, many more comparisons between reefs which differ in reef fishing intensity, ecological zones, and biogeographic regions are needed.

Questions of interest include (1) are patterns of fish assemblage structure predictable depending on human resource use; (2) which species are most (or least) affected by fishing impacts; (3) does compensation occur between species of high and low food preference or ability to escape capture; and (4) do localized, regional or global species extinctions occur? This study addresses these questions through a comparative survey of eight common coral reef fish families found in three categories of reef management, fully protected from fishing, unprotected and one reef in transition from no protection to full protection. The reefs are representative of leeward shallow ($<1.5$ m deep at low spring tides) hard substrate areas of Kenya's southern fringing reef lagoons. Reefs are similar in their depth and shelter from waves but differ in the time since protection from fishing, coral and shell collecting, reef topographic complexity (sometimes related to water depth), water flow, and abundance and species composition of sea urchins (McClanahan and Shafir 1990). Fishing methods in unprotected reefs include spear-fishing, line-fishing, baited fish traps, collection for the tropical-fish aquarium trade, beat seining in the coral-dominated areas, and pull seining in adjacent seagrass beds.

## Materials and methods

Replicate (5–9 per site) belt transects (5 m × 100 m) were haphazardly conducted in shallow lagoonal areas in three protected reefs [Malindi, Watamu and Kisite Marine National Parks (MNP)], four unprotected reefs (Vipingo, Kanamai, Ras Iwatine and Diani) and one recently protected reef (Mombasa MNP excluded fishermen in 1990) during December 1991 and October and December 1992 (Fig. 1). Ras Iwatine, adjacent the Mombasa MNP, was declared a reserve along with Mombasa MNP but, unlike the park, it had not experienced protective management before this study.

Fish counts were made using a discrete-group sampling technique (DGS) in which individuals, from related families, or species with similar body shapes or behaviors, are counted during separate passes along belt transects (Greene 1990). This census method reduces confusion associated with sampling diverse groups and improves sampling accuracy (Greene 1990), but increases the effort per replicate. Fish within eight families [Acanthuridae (surgeonfish), Scaridae (parrotfish), Pomacentridae (damselfish), Chaetodontidae (butterflyfish), Pomacanthidae (angelfish), Balistidae (triggerfish), Diodontidae (pufferfish) and Labridae (wrasses)] were identified to species (Fischer and Bianchi 1984; Smith and Heemstra 1986; Allen

Fig. 1. a Map of Kenya's southern coast and b location of study sites in relationship to the coast and fringing reef. *MNP*, Marine National Park

1985, 1991) and counted. The eight families were combined into four groups with similar numbers of species per group (group 1, Pomacentridae; group 2, Chaetodontidae; Pomacanthidae and Diodontidae; group 3, Labridae, and group 4, Acanthuridae, Balistidae, and Scaridae). Transects were placed in areas dominated by coral rubble or living coral; extensive seagrass beds were avoided. At the beginning of each transect, an observer would measure a 5 m distance perpendicular to the transect line and then would slowly snorkel parallel to the transect line at ~2.5 m from the line, identifying and counting all individuals 2.5 m on either side of the observer. All species identifications and counts were conducted by a single observer. A potential source of fish count error is avoidance of the transect area while placing the line transect (Fowler 1987) and during the transect counts (Lincoln-Smith 1988). In fished areas, it is possible that some fish will avoid humans until they habituate to their presence. In order to reduce this source of error, the order of the censusing was from group 1 to 4 or species least to most affected by this problem.

Line-transects 10 m long were conducted to estimate coral cover and topographic complexity (rugosity = straight line distance/bottom contour distance, see McClanahan and Shafir 1990 for sampling details). Fish transects ($n = 18$ to 54/site) were placed over the same hard substrate areas. Sea urchin population density was estimated by counting urchins in 10 m$^2$ circular quadrats haphazardly placed on the bottom, ($n = 18$ to 54/site, McClanahan and Shafir 1990). Data were analyzed to determine fish abundance, species-area relationships, and diversity (Simpson's Index, $D = 1 - \Sigma pi^2$). The raw transect data were not normally distributed and logarithmic transformation seldom increased normality (see McClanahan and Muthiga 1992 for a more thorough treatment of this problem). Therefore, Wilcoxin nonparametric signed rank tests were used on the fish count data to compare species abundance differences between the protected and unprotected reefs. Parametric statistics (ANOVA) were used on data for family density, species per transect, and diversity was analyzed by the management groupings rather than transects (i.e. data based on sites rather than transects are normally distributed; Sokal and Rohlf 1981).

Cluster analysis was performed on abundance data using the Bray-Curtis Index of Similarity $[S = 2\Sigma |\min x_i; x_j|/\Sigma(x_i + x_j)$; Bray and Curtis (1957)] and average between-group linkages (Ludwig and Reynolds 1988). Data were analyzed by fish family to determine numbers of species per area, total population densities, and species per transect (500 m$^2$). Single and multiple correlation analysis, and ANCOVA tests were performed on total abundance (eight families combined) and species per transect with substrate characteristics of rugosity, coral cover, and sea urchin density (Sokal and Rohlf 1981).

## Results

The data indicate high spatial variability within and between reefs. This is exemplified by the high variation in fish population density within the three categories of reef (Table 1), and the medium to low community similarity between reefs (Fig. 2). Nevertheless, several clear and predictable associations between the fauna and reef management categories are evident. Cluster analysis, for combined families and most individual families (Fig. 2), indicates that protected and unprotected reefs are distinct communities – sharing only ~25% "community similarity". The transition reef is more variable, clustering with protected and unprotected reefs depending on the family and census date. The fish community on the transition reef was a unique subset of the protected reefs with the Acanthuridae, Pomacanthidae and Pomacentridae, and the last census (December 1992) of the Balistidae and Chaetodontidae being most similar to protected reefs (Fig. 2). On the
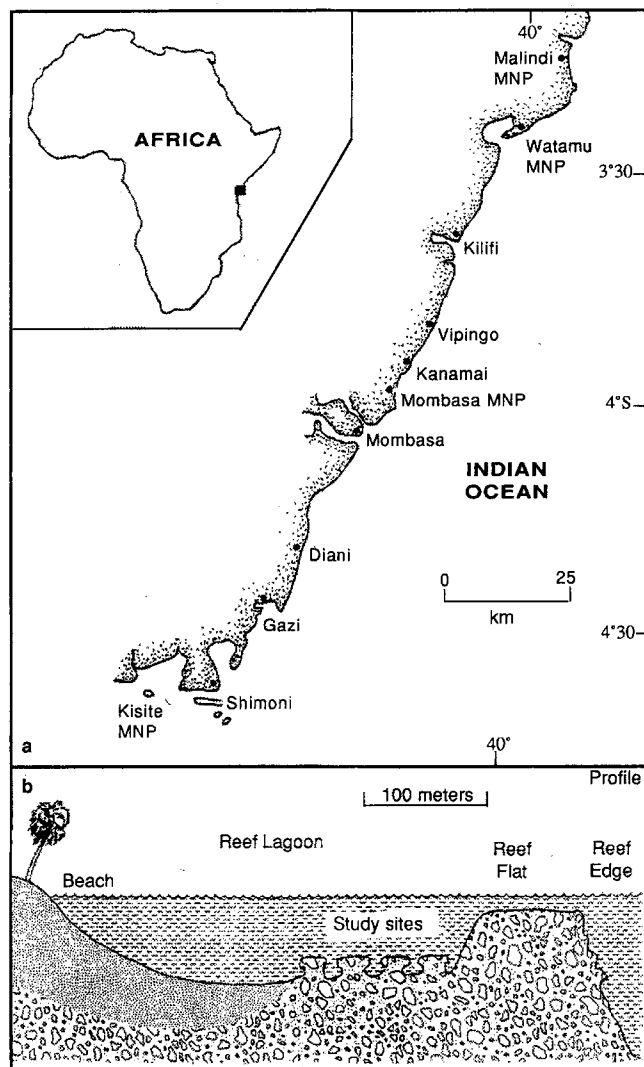
**Table 1.** Sample size, coral reef characteristics, and population density ($\bar{x} \pm$ SEM, #/500 m² (variation based on sites)) of fish in the three reef categories

| | Protected | Transition | Unprotected | Di | Rank |
|---|---|---|---|---|---|
| Sites | 3 | 1 | 4 | | |
| Transects | 14 | 19 | 20 | | |
| Sampled area, m² | 7000 | 9500 | 10000 | | |
| Topographic complexity, m/m | 1.23 + 0.03 | 1.30 + 0.03 | 1.17 + 0.02 | − | |
| Coral cover, % | 21.40 + 4.35 | 31.75 + 0.74 | 13.30 + 2.70 | − | |
| Sea urchins, number/10 m² | 2.65 + 0.90 | 34.75 + 3.24 | 107.80 + 66.65 | + | |
| **Acanthuridae** | | | | | |
| Ctenochaetus striatus | 26.68 ± 17.36 | 1.54 ± 0.88 | 0.00 ± 0.00 | − | ** |
| Acanthurus nigrofuscus | 15.82 ± 5.20 | 12.57 ± 1.69 | 0.90 ± 0.83 | − | ** |
| Acanthurus leucosternon | 7.33 ± 3.83 | 0.27 ± 0.27 | 0.00 ± 0.00 | − | ** |
| Naso annulatus | 4.93 ± 4.44 | 0.14 ± 0.07 | 0.25 ± 0.15 | − | NS |
| Zebrasoma scopas | 3.53 ± 2.94 | 0.84 ± 0.58 | 0.00 ± 0.00 | − | * |
| Ctenochaetus strigosus | 3.33 ± 2.40 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | * |
| Acanthurus triostegus | 3.20 ± 3.20 | 1.04 ± 0.43 | 1.45 ± 0.60 | − | NS |
| Acanthurus tennenti | 1.53 ± 1.53 | 0.04 ± 0.04 | 0.00 ± 0.00 | − | + |
| Acanthurus dussumieri | 0.83 ± 0.83 | 0.82 ± 0.41 | 0.00 ± 0.00 | − | + |
| Acanthurus nigricauda | 0.57 ± 0.35 | 0.81 ± 0.39 | 0.00 ± 0.00 | − | + |
| Zebrasoma veliferum | 0.28 ± 0.17 | 0.24 ± 0.12 | 0.00 ± 0.00 | − | NS |
| Paracanthurus hepatus | 0.13 ± 0.13 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | NS |
| Acanthurus mata | 0.08 ± 0.08 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | NS |
| Naso francolina | 0.07 ± 0.07 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | NS |
| Acanthurus xanthopterus | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.30 ± 0.19 | − | + |
| Naso lituratus | 0.00 ± 0.00 | 0.13 ± 0.13 | 0.00 ± 0.00 | 0 | NS |
| Naso unicornis | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.05 ± 0.05 | − | NS |
| **Balistidae** | | | | | |
| Balistapus undulatus | 1.43 ± 0.46 | 0.24 ± 0.18 | 0.00 ± 0.00 | − | ** |
| Sufflamen chrysopterus | 1.13 ± 0.64 | 0.04 ± 0.04 | 0.00 ± 0.00 | − | * |
| Rhinecanthus aculeatus | 0.33 ± 0.33 | 0.36 ± 0.16 | 0.45 ± 0.39 | + | NS |
| Pseudobalistes fuscus | 0.13 ± 0.13 | 0.04 ± 0.04 | 0.00 ± 0.00 | − | NS |
| **Chaetodontidae** | | | | | |
| Chaetodon auriga | 2.88 ± 1.19 | 1.55 ± 0.24 | 0.75 ± 0.10 | − | ** |
| Chaetodon trifasciatus | 2.47 ± 0.74 | 0.04 ± 0.04 | 0.30 ± 0.19 | − | ** |
| Chaetodon trifascialis | 0.87 ± 0.68 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | * |
| Chaetodon xanthocephalus | 0.53 ± 0.27 | 0.21 ± 0.13 | 0.05 ± 0.05 | − | NS |
| Chaetodon falcula | 0.27 ± 0.27 | 0.67 ± 0.67 | 0.00 ± 0.00 | − | NS |
| Chaetodon lunula | 0.22 ± 0.12 | 0.73 ± 0.40 | 0.05 ± 0.05 | − | NS |
| Chaetodon guttatissimus | 0.13 ± 0.13 | 0.15 ± 0.15 | 0.00 ± 0.00 | − | NS |
| Chaetodon kleinii | 0.13 ± 0.13 | 0.38 ± 0.02 | 0.00 ± 0.00 | − | NS |
| Chaetodon lineolatus | 0.07 ± 0.07 | 0.00 ± 0.00 | 0.10 ± 0.10 | + | NS |
| Chaetodon melannotus | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.05 ± 0.05 | + | NS |
| **Diodontidae** | | | | | |
| Diodon hystrix | 0.20 ± 0.12 | 0.42 ± 0.14 | 0.25 ± 0.19 | + | NS |
| Diodon liturosus | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.05 ± 0.05 | + | NS |
| Diodon holocanthus | 0.00 ± 0.00 | 0.33 ± 0.18 | 1.00 ± 0.45 | + | ** |
| **Labridae** | | | | | |
| Thalassoma hebraicum | 17.40 ± 1.36 | 24.59 ± 5.03 | 27.05 ± 9.01 | + | NS |
| Thalassoma hardwicke | 17.18 ± 11.99 | 1.30 ± 0.78 | 3.10 ± 1.86 | − | ** |
| Diprotacanthus xanthurus | 8.47 ± 8.27 | 6.73 ± 1.60 | 0.25 ± 0.25 | − | * |
| Gomphosus caeruleus | 8.47 ± 0.74 | 4.79 ± 1.75 | 5.50 ± 2.82 | − | * |
| Halichoeres hortulanus | 6.82 ± 2.33 | 6.67 ± 1.24 | 0.95 ± 0.33 | − | ** |
| Labroides dimidiatus | 6.65 ± 3.08 | 2.95 ± 1.58 | 1.15 ± 0.67 | − | ** |
| Stethojulis albovittata | 5.42 ± 1.96 | 3.27 ± 1.91 | 5.35 ± 1.15 | − | NS |
| Thalassoma lunare | 4.52 ± 2.33 | 0.30 ± 0.30 | 0.75 ± 0.30 | − | * |
| Cheilio inermis | 0.83 ± 0.83 | 0.44 ± 0.18 | 1.30 ± 0.33 | + | + |
| Thelassoma amblycephalum | 0.67 ± 0.67 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | NS |
| Labrichthys unilineatus | 0.62 ± 0.36 | 0.07 ± 0.07 | 0.05 ± 0.05 | − | NS |
| Coris caudimacula | 0.48 ± 0.39 | 0.76 ± 0.46 | 0.55 ± 0.30 | + | NS |
| Bodianus axillaris | 0.47 ± 0.29 | 1.18 ± 0.55 | 0.00 ± 0.00 | − | NS |
| Cheilinus trilobatus | 0.47 ± 0.29 | 0.10 ± 0.06 | 0.00 ± 0.00 | − | * |
| Cheilinus digrammus | 0.42 ± 0.42 | 0.07 ± 0.07 | 0.00 ± 0.00 | − | NS |
| Novaculichthys taeniourus | 0.40 ± 0.40 | 0.14 ± 0.07 | 0.05 ± 0.05 | − | NS |
| Anampses caeruleopunctatus | 0.38 ± 0.22 | 0.99 ± 0.49 | 0.05 ± 0.05 | − | NS |
| Anampses twistii | 0.38 ± 0.22 | 0.13 ± 0.07 | 0.05 ± 0.05 | − | NS |
| Cheilinus fasciatus | 0.38 ± 0.22 | 0.27 ± 0.13 | 1.20 ± 0.45 | + | NS |
| Coris gaimard africana | 0.33 ± 0.24 | 0.07 ± 0.07 | 0.05 ± 0.05 | − | NS |

**Table 1.** (continued)

| | Protected | Transition | Unprotected | Di | Rank |
|---|---|---|---|---|---|
| *Hemigymnus melapterus* | 0.27 ± 0.18 | 0.00 ± 0.00 | 0.45 ± 0.39 | + | NS |
| *Labroides bicolor* | 0.27 ± 0.13 | 2.80 ± 2.80 | 0.00 ± 0.00 | − | NS |
| *Hologymnosus doliatus* | 0.20 ± 0.12 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | NS |
| *Coris aygula* | 0.15 ± 0.08 | 0.13 ± 0.07 | 0.00 ± 0.00 | − | NS |
| *Anampses meleagrides* | 0.13 ± 0.13 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | NS |
| *Coris formosa* | 0.13 ± 0.07 | 0.39 ± 0.19 | 0.05 ± 0.05 | − | NS |
| *Hemigymnus fasciatus* | 0.13 ± 0.13 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | NS |
| *Pseudocheilinus hexataenia* | 0.07 ± 0.07 | 0.91 ± 0.45 | 0.20 ± 0.08 | + | NS |
| *Halichoeres nebulosus* | 0.00 ± 0.00 | 0.11 ± 0.11 | 0.35 ± 0.13 | + | + |
| *Halichoeres scapularis* | 0.00 ± 0.00 | 1.87 ± 0.76 | 7.55 ± 2.61 | + | + |
| *Stethojulis strigiventer* | 0.00 ± 0.00 | 2.05 ± 1.76 | 0.55 ± 0.34 | + | NS |
| *Macropharyngodon bipartitus* | 0.00 ± 0.00 | 0.07 ± 0.07 | 0.00 ± 0.00 | 0 | NS |
| *Pteragogus pelycus* | 0.00 ± 0.00 | 0.07 ± 0.07 | 0.00 ± 0.00 | 0 | NS |
| Pomacanthidae | | | | | |
| *Centropyge multispinis* | 1.45 ± 0.49 | 2.80 ± 0.80 | 0.00 ± 0.00 | − | ** |
| *Pomacanthus chrysurus* | 0.37 ± 0.19 | 0.07 ± 0.07 | 0.00 ± 0.00 | − | * |
| *Pomacanthus semicirculatus* | 0.22 ± 0.12 | 0.63 ± 0.22 | 0.10 ± 0.06 | − | NS |
| Pomacentridae | | | | | |
| *Chromis nigrura* | 33.78 ± 32.91 | 4.15 ± 3.01 | 0.50 ± 0.50 | − | * |
| *Chromis dimidiata* | 28.40 ± 22.41 | 20.66 ± 5.09 | 1.25 ± 1.12 | − | ** |
| *Plectroglyphidodon lacrymatus* | 22.27 ± 3.18 | 19.66 ± 4.87 | 3.15 ± 0.86 | − | ** |
| *Neopomacentrus azysron* | 15.50 ± 7.26 | 0.40 ± 0.20 | 0.00 ± 0.00 | − | NS |
| *Abudefduf sexfasciatus* | 12.28 ± 7.80 | 29.03 ± 9.48 | 4.80 ± 0.48 | − | NS |
| *Pomacentrus sulfureus* | 11.38 ± 6.39 | 0.76 ± 0.09 | 0.00 ± 0.00 | − | ** |
| *Chromis viridis* | 8.98 ± 2.13 | 0.81 ± 0.81 | 6.90 ± 3.98 | − | * |
| *Chrysiptera unimaculata* | 7.70 ± 2.67 | 8.77 ± 2.57 | 20.80 ± 5.72 | + | * |
| *Dascyllus aruanus* | 7.58 ± 7.11 | 0.07 ± 0.07 | 31.40 ± 17.80 | + | NS |
| *Stegastes nigricans* | 6.27 ± 5.87 | 0.26 ± 0.26 | 4.35 ± 1.65 | − | NS |
| *Chromis weberi* | 4.35 ± 3.95 | 32.57 ± 9.68 | 0.65 ± 0.65 | − | * |
| *Plectroglyphidodon dickii* | 3.93 ± 1.22 | 11.69 ± 1.26 | 0.05 ± 0.05 | − | ** |
| *Dascyllus carneus* | 2.38 ± 1.21 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | * |
| *Dascyllus trimaculatus* | 2.20 ± 2.20 | 4.83 ± 0.50 | 4.45 ± 1.75 | + | NS |
| *Abudefduf vaigiensis* | 1.68 ± 1.56 | 15.69 ± 8.41 | 9.08 ± 8.22 | + | NS |
| *Pomacentrus caeruleus* | 1.48 ± 0.16 | 4.41 ± 1.09 | 0.25 ± 0.19 | − | * |
| *Neoglyphidodon melas* | 0.80 ± 0.80 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | NS |
| *Amphiprion akallopisos* | 0.73 ± 0.47 | 0.07 ± 0.07 | 0.00 ± 0.00 | − | * |
| *Plectroglyphidodon johnstonian* | 0.58 ± 0.58 | 0.33 ± 0.18 | 0.00 ± 0.00 | − | NS |
| *Chromis ternatensis* | 0.55 ± 0.37 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | NS |
| *Amphiprion allardi* | 0.38 ± 0.22 | 2.21 ± 0.40 | 0.80 ± 0.49 | + | NS |
| *Abudefduf sparoides* | 0.32 ± 0.22 | 0.54 ± 0.36 | 5.75 ± 4.49 | + | * |
| *Pomacentrus pavo* | 0.27 ± 0.27 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | NS |
| *Amblyglyphidodon leucogaster* | 0.08 ± 0.08 | 0.00 ± 0.00 | 0.10 ± 0.10 | + | NS |
| *Neoglyphidodon melas* | 0.07 ± 0.07 | 1.97 ± 1.19 | 0.45 ± 0.29 | + | NS |
| *Pomacentrus baenschi* | 0.07 ± 0.07 | 0.89 ± 0.16 | 0.00 ± 0.00 | − | NS |
| *Chrysiptera annulata* | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.25 ± 0.25 | + | NS |
| *Chrysiptera glauca* | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.10 ± 0.06 | + | NS |
| *Chrysiptera leucopoma* | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.45 ± 0.45 | + | NS |
| *Chrysiptera biocellata* | 0.00 ± 0.00 | 0.00 ± 0.00 | 3.15 ± 2.11 | + | * |
| *Chromis pembae* | 0.00 ± 0.00 | 0.07 ± 0.07 | 0.00 ± 0.00 | − | NS |
| *Neopomacentrus cyanomos* | 0.00 ± 0.00 | 2.42 ± 2.10 | 0.15 ± 0.15 | + | NS |
| *Stegastes fasciolatus* | 0.00 ± 0.00 | 0.52 ± 0.29 | 0.00 ± 0.00 | − | NS |
| Scaridae | | | | | |
| *Scarus sordidus* | 18.25 ± 7.70 | 0.07 ± 0.07 | 0.00 ± 0.00 | − | ** |
| *Scarus rubroviolaceus* | 5.90 ± 1.71 | 1.13 ± 1.13 | 0.15 ± 0.10 | − | ** |
| *Scarus viridifucatus* | 3.33 ± 3.33 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | * |
| *Calotomus carolinus* | 3.12 ± 2.82 | 2.15 ± 0.73 | 0.75 ± 0.68 | − | * |
| *Scarus scaber* | 1.80 ± 1.80 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | * |
| *Scarus niger* | 1.67 ± 0.71 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | ** |
| *Scarus frenatus* | 1.17 ± 0.20 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | ** |
| *Scarus gibbus* | 0.87 ± 0.24 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | * |
| *Hipposcarus harid* | 0.75 ± 0.63 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | * |
| *Scarus russelii* | 0.63 ± 0.19 | 0.43 ± 0.26 | 0.10 ± 0.06 | − | * |
| *Scarus ghobban* | 0.53 ± 0.29 | 0.50 ± 0.32 | 1.05 ± 0.43 | + | NS |
| *Scarus atrilunula* | 0.27 ± 0.27 | 0.00 ± 0.00 | 0.00 ± 0.00 | − | NS |
| *Leptoscarus vaigiensis* | 0.23 ± 0.15 | 0.13 ± 0.07 | 2.00 ± 0.89 | + | * |
| *Scarus falcipinnis* | 0.13 ± 0.13 | 0.07 ± 0.07 | 0.00 ± 0.00 | − | NS |
| *Cetoscarus bicolor* | 0.07 ± 0.07 | 0.00 ± 0.00 | 0.05 ± 0.05 | − | NS |

$^+ P < 0.10$; $^* P < 0.05$; $^{**} P < 0.01$
Significance level of Wilcoxon signed rank test based on transect counts. Di indicates sign of the difference in population density between protected and unprotected reefs

transition reef, Scaridae, Labridae, and the first two censuses of the Balistidae and Chaetodontidae clustered with unprotected reefs.

Summing species abundance into family abundance (Table 2) and total censused fish abundance (Fig. 3) analyzed by reef category, indicates a pattern of fish abundance and species richness dependent on reef management (Figs. 2 and 3 and Table 2). In contrast, species diversity (using the most sensitive indicator of diversity, Routledge 1979) did not differ for combined (Fig. 3) and individual families (Table 2, at $P < 0.05$). Five of eight families showed a significant decrease in fish abundance in unprotected versus protected reefs (Table 2, Fig. 3). Analysis of the combined data for all censused species indicates approximately a 50% reduction in abundance, numbers of species per transect, and total numbers of species in fished reefs (Figs. 3 and 4). Reduced species richness is evident for all families except Labridae and Diodontidae (Fig. 4). In contrast, for Diodontidae there were more species per transect ($P < 0.05$) on fished than protected reefs.

At the species level, differences based on reef categories are less evident, being largely attributable to the high population variation of some species among reef management categories (Table 1). A total of 118 species were identified in the eight families of which 100 were found in protected reefs, 86 in the transition, and 66 on fished reefs. For the protected and transition reefs combined, 110 species were counted indicating that eight species are unique to fished reefs, 44 species are unique to protected reefs and 52 species are unique to both the protected and transition reefs. Eighty-nine of the population differences between protected and fished reefs were negative (i.e. parks had more individuals than unprotected reefs), 29 positive

and three neutral. Most of the positive differences (86%) were found among the Diodontidae, Labridae, and Pomacentridae.

Nonparametric statistical analysis of species populations counts indicated that there were 45 significant differences for the 118 censused fish species (at $P < 0.05$) between protected and fished reefs. Six of the 45 differences resulted from species showing increased population densities outside parks (1 Labridae, 3 Pomacentridae, 1 Diodontidae (*Diodon holocanthus*), and 1 Scaridae (*Leptoscarus vaigensis*). Statistical tests must be considered in the context that 52 of the 118 censused species were not found in unprotected reefs and, therefore, population estimates and subsequent statistical analysis of these rare species may be inaccurate.
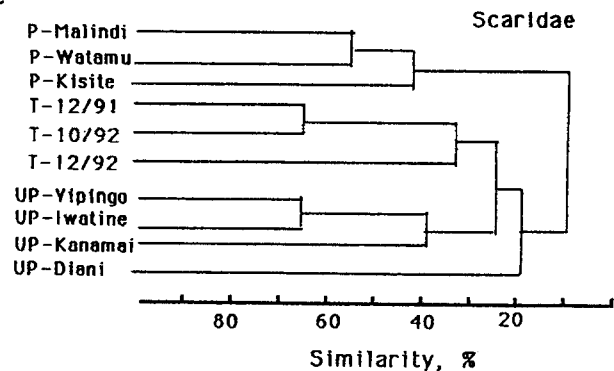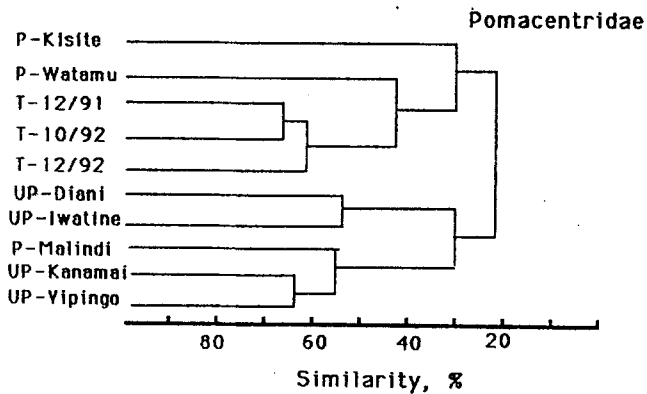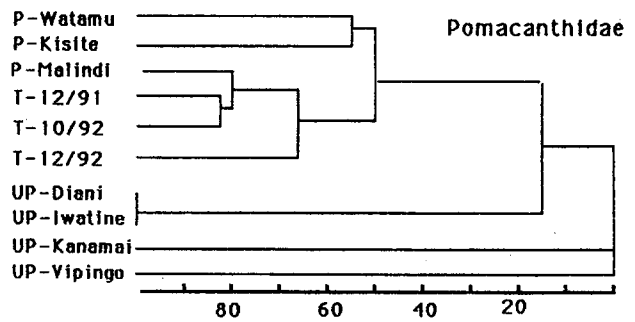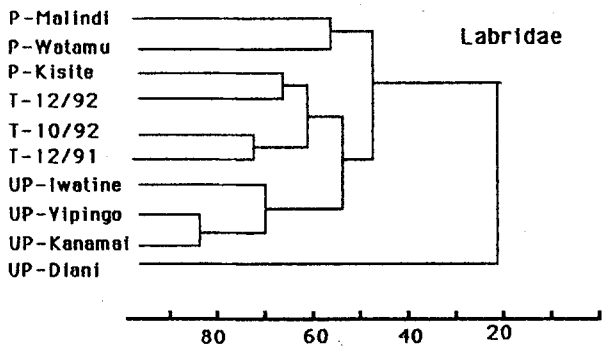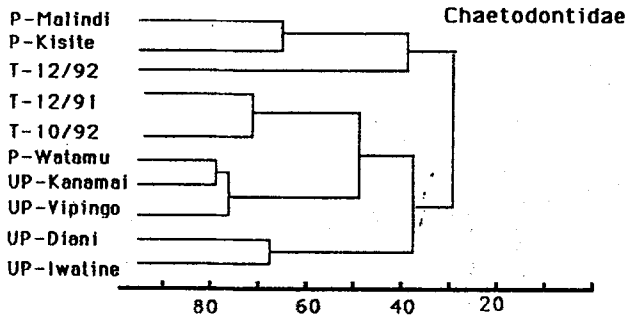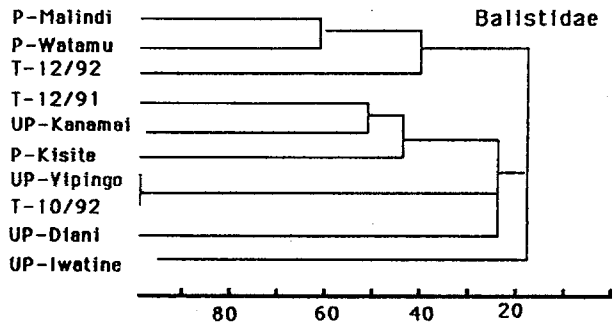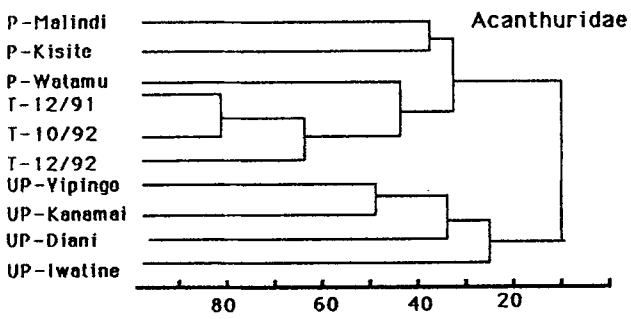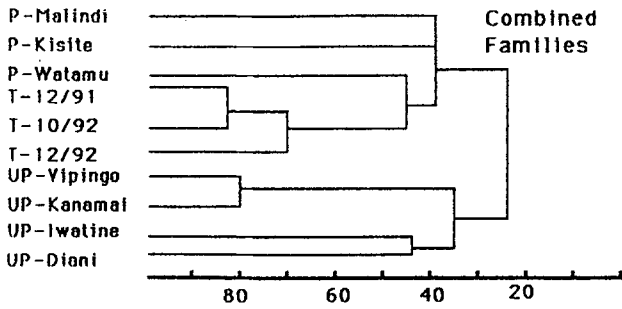
Reef characteristics of coral cover, reef topographic complexity (rugosity), and sea urchin abundance indicate statistically significant associations with both numbers of fish and species abundance (Figs. 5 and 6). In the figures, correlations are for the eight sites combined, but, in some instances, it may be more appropriate to consider reef categories separately. ANCOVA analysis with protection as a category and rugosity and sea urchin abundance as covariants indicated that reef protection was the only significant variable ($P < 0.008$) for the number of species, but no factors were significant for fish numbers (protection $P < 0.12$). However, the small numbers of replicates in reefs categories and the existence of a "transition reef" under the protection category may weaken this test in determining sources of variance.

Differences between Mombasa MNP and Ras Iwatine sites are instructive as these two sites are close together ($< 2$ km), but differ in their management and sea urchin

**Table 2.** Numbers of individuals, species ($\bar{x} \pm$ SEM), and diversity (Simpson's Index) of eight fish families on three protected reefs, four unprotected reefs, and three sampling dates on the transition reef

F values ANOVA tests and levels of significance $^+ P < 0.10$; $* P < 0.05$; $** P < 0.01$

| Fish family | Protected | Transition | Unprotected | F-Test p |
|---|---|---|---|---|
| Density, number/500 m$^2$ | | | | |
| Acanthuridae | 68.30 ± 12.91 | 18.50 ± 4.40 | 2.95 ± 1.00 | 23.8 ** |
| Balistidae | 3.03 ± 0.80 | 0.67 ± 0.24 | 0.45 ± 0.39 | 7.7 * |
| Chaetodontidae | 7.57 ± 3.04 | 3.72 ± 0.47 | 1.30 ± 0.24 | 4.12 + |
| Diodontidae | 0.20 ± 0.12 | 0.76 ± 0.12 | 1.30 ± 0.37 | 4.03 + |
| Labridae | 82.10 ± 7.67 | 63.20 ± 12.42 | 56.50 ± 16.36 | 0.9 NS |
| Pomacanthidae | 2.03 ± 0.69 | 3.50 ± 0.89 | 0.10 ± 0.06 | 9.34 ** |
| Pomacentridae | 174.00 ± 15.04 | 162.80 ± 23.30 | 98.83 ± 29.65 | 2.73 NS |
| Scaridae | 38.72 ± 5.51 | 4.49 ± 1.72 | 4.10 ± 1.54 | 38.15 ** |
| Species/500 m$^2$ | | | | |
| Acanthuridae | 5.71 ± 0.35 | 3.63 ± 0.27 | 1.30 ± 0.22 | 31.83 ** |
| Balistidae | 1.64 ± 0.22 | 3.05 ± 0.33 | 0.30 ± 0.11 | 9.45 * |
| Chaetodontidae | 2.93 ± 0.41 | 1.95 ± 0.24 | 0.80 ± 0.24 | 7.04 * |
| Diodontidae | 0.14 ± 0.10 | 0.63 ± 0.11 | 0.85 ± 0.15 | 7.72 * |
| Labridae | 11.00 ± 0.62 | 10.53 ± 0.57 | 8.50 ± 0.49 | 2.49 NS |
| Pomacanthidae | 1.14 ± 0.25 | 1.58 ± 0.19 | 0.10 ± 0.07 | 14.57 ** |
| Pomacentridae | 11.86 ± 0.82 | 12.68 ± 0.43 | 8.00 ± 0.40 | 13.25 ** |
| Scaridae | 6.71 ± 0.47 | 1.84 ± 0.24 | 1.60 ± 0.34 | 28.54 ** |
| Diversity, D | | | | |
| Acanthuridae | 0.68 ± 0.10 | 0.47 ± 0.09 | 0.46 ± 0.01 | 2.54 NS |
| Balistidae | 0.37 ± 0.19 | 0.30 ± 0.15 | 0.00 ± 0.00 | 2.63 NS |
| Chaetodontidae | 0.68 ± 0.05 | 0.67 ± 0.06 | 0.56 ± 0.08 | 0.99 NS |
| Labridae | 0.81 ± 0.03 | 0.82 ± 0.04 | 0.75 ± 0.06 | 0.67 NS |
| Pomacanthidae | 0.36 ± 0.18 | 0.31 ± 0.10 | 0.00 ± 0.00 | 3.59 + |
| Pomacentridae | 0.77 ± 0.08 | 0.86 ± 0.01 | 0.79 ± 0.04 | 0.7 NS |
| Scaridae | 0.69 ± 0.09 | 0.58 ± 0.07 | 0.50 ± 0.10 | 1.04 NS |

Combined Families

Acanthuridae

Balistidae

Chaetodontidae

Diodontidae

Labridae

Pomacanthidae
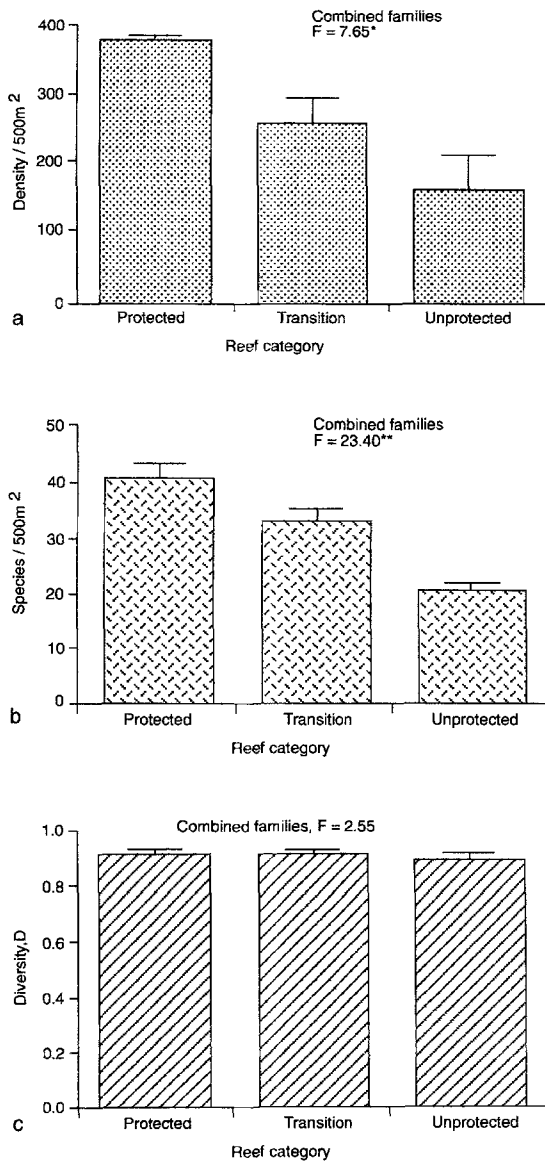
Pomacentridae

Scaridae

Similarity, %

Fig. 3a–c. Number of fish, fish species (per 500 m²), and diversity ($x \pm$ SEM, Simpson's Index) for eight families in the protected, transition and unprotected reefs. $F$ values and level of significance indicated; * $P < 0.05$; ** $P < 0.01$

population densities. Whereas most fished reefs had high sea urchin population density ($140.7 \pm 81.9$ urchins/10 m², $x \pm$ SEM without Ras Iwatine) relative to protected reefs, Ras Iwatine had relatively low sea urchin population densities ($9.2 \pm 1.0$ urchins/10 m², $\pm$ SEM) compared to Mombasa MNP ($34.8 \pm 3.2$ urchins/10 m²). However, the Ras Iwatine site also had lower rugosity than Mombasa MNP. Comparisons indicate that reef protection is more important than sea urchin population numbers in predicting numbers of fish and species (Fig. 6).

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Fig. 2. Cluster analysis diagrams for eight families at all study sites. Similarity based on the Bray-Curtis measure and clustering on average between-group linkages. P, protected reefs; T, transition reef (three sampling dates in the Mombasa MNP); UP unprotected reefs
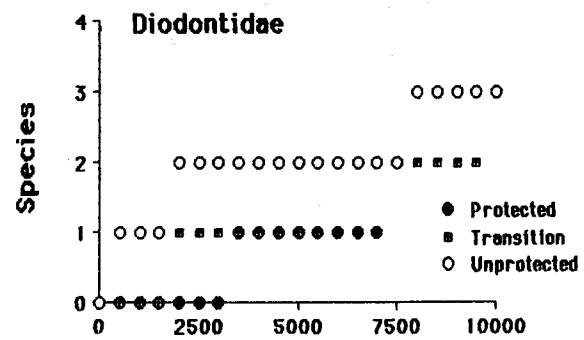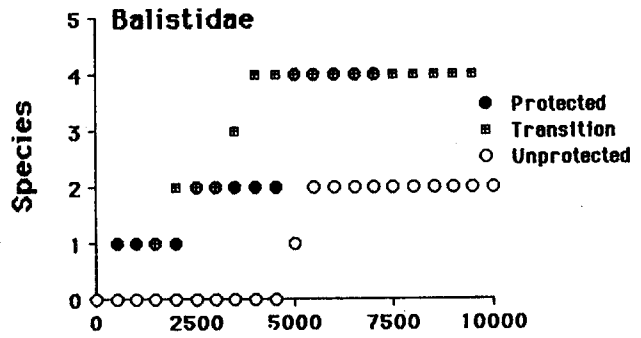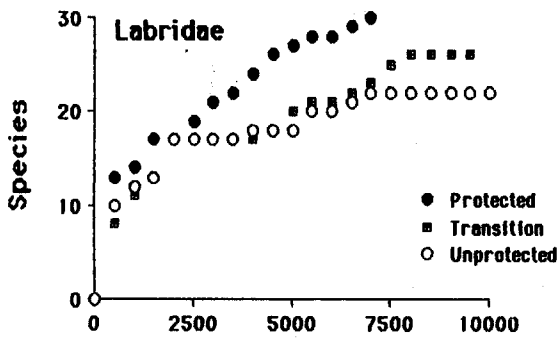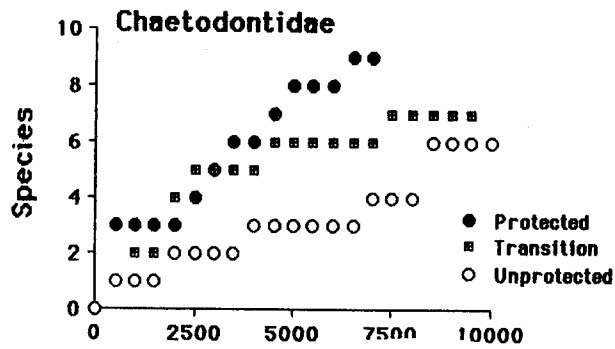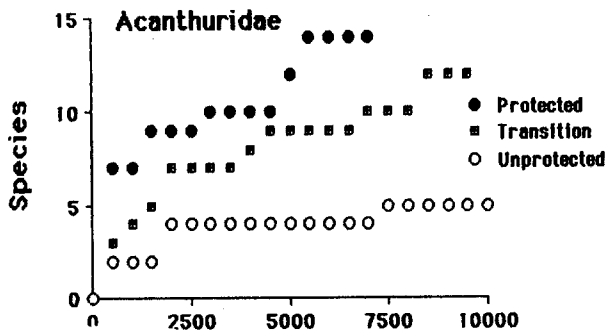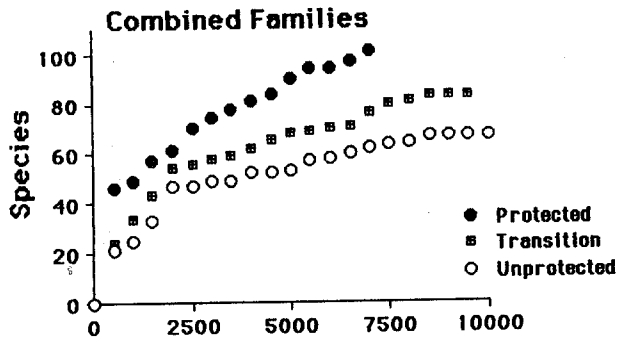
Rugosity and coral cover were closely correlated ($r^2 = 0.94$, $P < 0.0001$) but multiple regression analysis of fish numbers and species did not increase by considering both coral cover and rugosity as independent variables. Consequently, only the analyses based on rugosity are presented. The overall relationship between rugosity and fish numbers is not statistically significant and is particularly non-evident within protected reefs (Fig. 5). However, average numbers of species per transect are positively correlated with rugosity but data may exhibit two different responses to rugosity with protected reefs lying above the fished and transition reefs.

Numbers of fish and fish species are both negatively associated with the natural logarithm of sea urchin numbers (Fig. 6). In the case of fish numbers, the relationship was negative with most data, regardless of the management category, lying near the best-fit line. Ras Iwatine, which had both low sea urchin and fish numbers, was an exception. Numbers of species may indicate two responses to sea urchin abundance based on the reef's management category, protected reefs having greater species numbers than unprotected reefs regardless of sea urchin abundance. The overall effect (based on slopes and intercepts of correlations based on management categories) is that the logarithm of sea urchin numbers explain $\sim 25\%$ and protection $\sim 75\%$ of the variation in numbers of fish species, assuming no other interactive effects. Since rugosity and ln urchin abundance are negatively associated ($28\%$ in this data set) the actual effect of sea urchin abundance on numbers of species may be somewhat less than the above prediction. Based on this analysis, protection from fishing is the strongest predictor for numbers of fish species followed by reef rugosity, and sea urchin abundance. Erosion of the substrate by sea urchin grazing activities may make urchins partly responsible for lowered rugosity in unprotected reefs (McClanahan and Kurtis 1991).

## Discussion

Sources of variation in the data include observer bias, time of day, tides, and other sampling factors (Fowler 1987; Lincoln-Smith 1988). Observer bias, by the DGS technique, is estimated to be about 10% (Greene 1990). Consecutive censuses in the Mombasa MNP fringing reef had $\sim 75\%$ similarity between censuses [in contrast to 50% similarity found for small patch reefs (Sale and Guy 1991)]. Considering that 10% of the community variation is associated with sampling error, the 75% similarity in community composition between censuses seems high for reefs in a transition from no regulation to full protection. This suggests relative stability over a one year interval. However, the community composition of the last census had more similarity with older parks than the initial census, suggesting further recovery from fishing over this time period. From these data and personal observations, before and after park protection, I propose that rapid changes in the fish fauna occurred within the first year of the park's establishment.

High spatial variability and patchiness of the fish fauna have implications to the designation and design of protected

Figures showing Species vs Area (m²) for Combined Families, Acanthuridae, Balistidae, Chaetodontidae, Diodontidae, Labridae, Pomacanthidae, Pomacentridae, and Scaridae, each with Protected, Transition, and Unprotected data series.
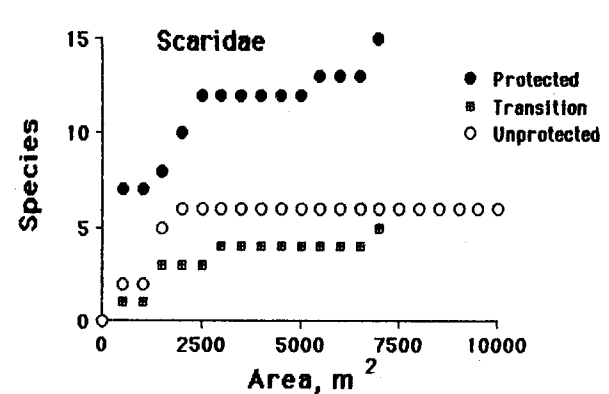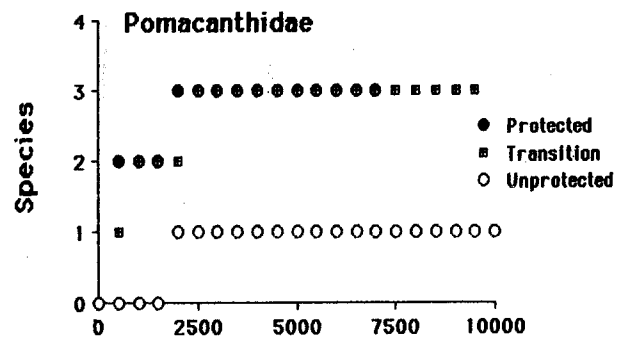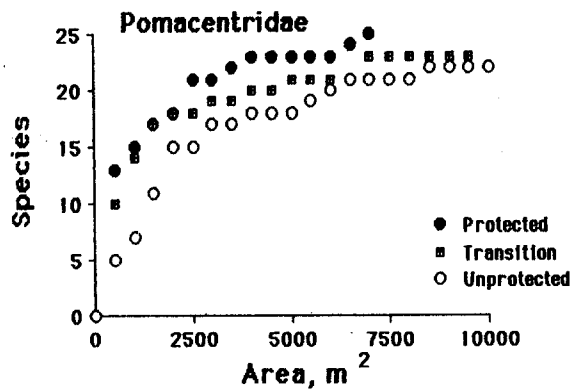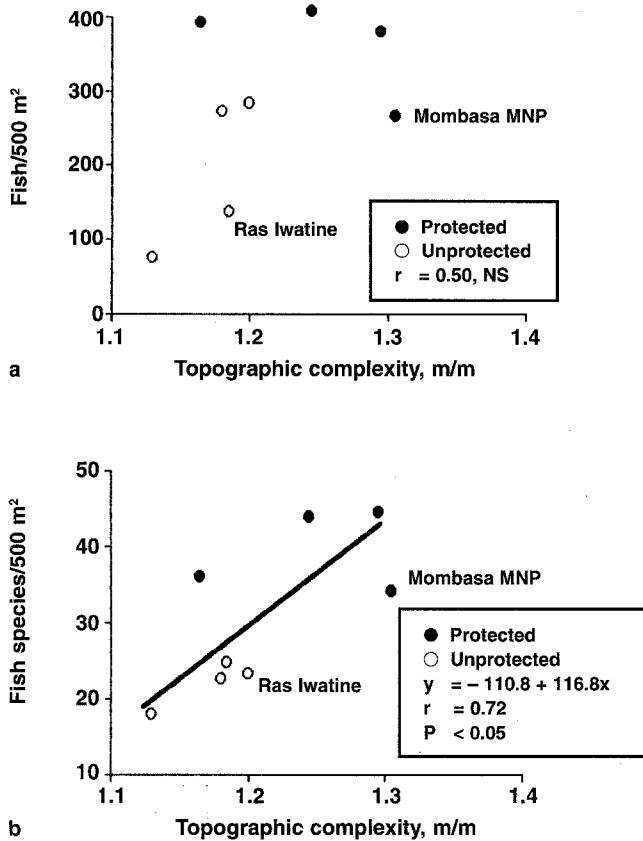
Fig. 5. Relationship between fish abundance for eight families **a** and fish species number **b** as a function of reef topographic complexity (rugosity)
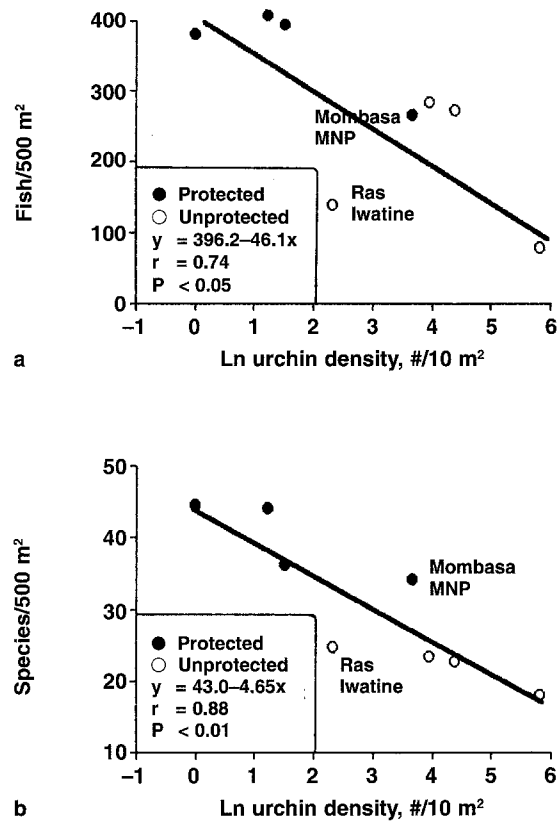


Fig. 6. Relationship between fish abundance for eight families **a** and fish species per transect **b** as a function of the natural logarithm of sea urchin population density

areas. Some groups such as parrotfish often display differences in dominant species among different protected areas (e.g. *Scarus viridifucatus*). This suggests that protection of significant populations of as many species as possible requires the protection of a variety of coral reef habitats. This can be achieved by protecting areas which contain many patchy or varying habitats or by the protection of many small areas with unique faunal or habitat characteristics. Given the possible unimportance of dispersal restrictions, and high within-site genetic diversity of coral reef organisms (Stoddart 1984; Watts et al. 1990), some of the arguments for large protected areas might not apply in coral reef ecosystems.

The community structure of fish is fairly consistent and predictable depending on management category. Levels of similarity, however, among protected and unprotected reefs were variable and family dependent. Overall, protected and unprotected reefs were distinct sharing only ~25% similarity. This result suggests that ~75% of the variance in community composition is attributable to site differences. These include differences in reef management, reef substrate complexity, coral cover, water depth, abiotic factors, recruitment variability, and fishing intensity. It has been suggested from surveys and experiments with gastropods

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Fig. 4. Number of species shown as a function of area sampled in protected, transition (Mombasa MNP), and unprotected reefs. Plots show the total for eight fish families combined and for each eight individual families

(McClanahan 1989, 1990b), sea urchins (McClanahan and Muthiga 1988), and reef substrate variables (McClanahan and Shafir 1990), that low levels of similarity between protected and unprotected sites is evidence that human resource use is responsible for producing major faunal variations in coral reef ecosystems.

Fish censuses in the Mombasa MNP prior to and after park establishment (McClanahan 1990a; McClanahan unpublished report) indicate slightly greater than ~100% increase in fish numbers. Species belonging to the families Labridae, Diodontidae, Pomacanthidae, Lutjanidae, Lethrinidae, Gaterinidae, Scaridae, and Acanthuridae displayed increases in population numbers of >100% over the four year interval. Unfortunately, detailed information at the species level was not recorded; however, my subjective impression is that an increase in species density occurred over this period (also see Russ and Alcala 1989). Assuming fish removal and associated indirect effects (McClanahan and Shafir 1990) were having the greatest impact on the fauna, further population and species richness increases, would be expected in the transition reef, with continued reef protection.

Species increases, in the transition reef, may occur in many families, but low scarid species richness and population numbers suggest that this family is most likely to experience additional species and population increases. The transition reef census lacked many of the scarid species which excavate and scrape dead coral surfaces (Bellwood 1990). The most commonly censused scarid, *Calotomus carolinus*, largely feeds on seagrass and fleshy

algae rather than algal and coralline turfs (McClanahan, personal observation). High sea urchin abundance (~4000 kg/ha; McClanahan and Mutere 1994) in the transition reef may be depressing populations and species richness of scarids which feed directly on hard substrate (Hay and Taylor 1985; Carpenter 1990; Robertson 1991; McClanahan 1992). A recent review of the competitive relationship between coral-reef inhabiting sea urchins and herbivorous fishes (McClanahan 1992) suggests that sea urchins are superior resource competitors but are less tolerant of predation than herbivorous fishes. It remains to be seen whether sea urchin abundance will be further reduced as predicted (McClanahan and Shafir 1990; McClanahan 1990a, 1992).

Data on Balistid populations in the transition reef (Balistidae being perhaps the most important daytime predators of sea urchins (McClanahan and Shafir 1990)), still indicate a low abundance of *Balistapus undulatus* relative to *Rhinecanthus aculeatus* (which largely feeds on juvenile sea urchins). Large female and terminal male wrass, such as *Coris formosa*, *C. aygula* and *Cheilinus trilobatus* feed on adult sea urchins and are more abundant than before park designation. Scavengers such as *Lethrinus harak*, *L. mahsena*, *L. lentjan* and *Lutjanus fulviflamma* have also increased since protection, but appear to feed mostly on juveniles or injured sea urchins. Further tests are in progress to determine various aspects of triggerfish-sea-urchin-parrotfish interrelationships.

Ecological compensation among fish species, attributable to fishing, appears restricted to diodontids and small-bodied species of the Labridae and Pomacentridae. In the Caribbean, diodonts have increased as a percentage of the fish catch over time (Koslow et al. 1988) and may somehow benefit from reduced predation, competition or increased food such as gastropods and sea urchins (McClanahan 1990b). A mass recruitment of *Diodon holocanthus* and associated juvenile mortality occurred on Kenya's southern reef during the 1992 northeast monsoons. Juveniles largely occupied seagrass beds and were not included in the coral reef census described in the paper. Observations suggest that juvenile *D. holocanthus* experienced lower mortality in unprotected than protected reefs, perhaps due to a reduction in their predators or lowered levels of starvation. Fishing with seine nets may be a primary source of mortality in unprotected reefs.

Wrass seemed only moderately affected by fishing with reductions of *Coris formosa*, *C. gaimard africana*, *C. aygula* and *Cheilimus trilobatus* adult females and terminal males being evident. Reduced population densities of fish parasite cleaners such as *Labroides dimidiatus* and *Diprotacanthus xanthurus* were also evident. Some small fusiform species such as *Thalassoma hebraicum*, *Halichoeres scapularis*, *Cheilio inermis* and *Halichoeres nebulosus* had somewhat larger populations in unprotected reefs. Perhaps these species are able to escape through existing fishing nets (2 to 4 cm diagonal length) and experience lower mortality in unprotected reefs. Pomacentrids also appeared to be only moderately affected by protection from fishing, and observed differences in species between protected and unprotected reefs may result from the direct and indirect interaction of substrate, recruitment, and mortality.

Despite increased population densities of some species on fished reefs, none of the censused fish exhibited high dominance [in contrast to gastropods (McClanahan 1990b), sea urchins (McClanahan and Shafir 1990) and coral (McClanahan and Mutere 1994)]. Consequently, diversity indices were similar among reef management categories. Whether low dominance is a property of the fish community (e.g. lottery competition, Sale 1991b) or a result of fishing (e.g. compensatory mortality, McClanahan and Shafir 1990) requires further study. (Clearly, further experimental manipulation of sea urchins and reef complexity is required to determine their various effects on reef fish species diversity and abundance under various management regulations.)

This study indicates that localized extirpations of fish species, due to fishing and associated community structure changes, are common in shallow-water reefs (Russ and Alcala 1989). Fifty-two of the 110 species found in protected reefs were not found on the fished reefs on a scale of 1.0 ha. The low population and species density of all Pomacanthidae species, and some species of Chaetodontidae, Pomacentridae, Acanthuridae, and Scaridae (see Table 1) on fished reefs is of environmental concern. However, many species may be abundant in deeper and less heavily fished reef edge sites (Samoilys 1988). Future coral reef research needs to identify species of extinction concern on a spatial scale larger than measured in this study (1 ha), and to determine which species have sufficient refuge from human impacts. In the future, species extirpations caused by fishing will depend on the intensity of fishing effort and the establishment and maintenance of marine protected areas.

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