

MARINE RESERVES AND THEIR INFLUENCE ON
ADJACENT FISHERIES IN COASTAL KENYA

CENTRE FOR NEWFOUNDLAND STUDIES

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**Marine reserves and their influence on adjacent
fisheries in coastal Kenya**

by

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**A thesis submitted to the
School of Graduate Studies
in partial fulfillment of the
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Abstract

Analysis of more than two decades (1978 to 2001) of commercial fish catch data collected by the Kenya Fisheries Department indicates that a rapid overall decline in landings occurred in coastal Kenya during the last decade. The decline was most severe in the most populated Mombasa district. Amongst the commercial families, the groupers (family Serranidae) showed the steepest decline in landings and forecasts indicated a gradual decline in yields for the next decade (2002-2011). This thesis reports on the results of experiments to test the efficacy of two of the oldest marine parks in Kenya (Malindi, 6.3 km² and Watamu, 10 km², created in 1968) to restore such over-fished stocks and their potential to sustain adjacent sites through a spillover effect. A comparison of catch per unit effort (CPUE) and sizes of fish species across the park boundaries showed that species are orders of magnitude more abundant and larger inside the parks than the adjacent fished sites. However, higher seasonal abundance and even larger sizes of some species (e.g., the whitespotted rabbitfish, *Siganus sutor* and the seagrass parrotfish, *Leptoscarus vaigensis*) occur outside the parks (especially at Watamu). Results suggest that yields of some species in adjacent fished sites and perhaps beyond may have been sustained by a spillover effect from the parks. However, this effect appears to be species and site specific and affected by season and reef types. Size frequency distribution of commercial species showed a high proportion of small sized fish inside the parks, suggesting the parks additionally function as nursery grounds.

A logistic decay model fit to species abundance (CPUE and #/500 m²) data across the park boundaries showed steep gradients of fish abundance (especially for the sky emperor, *Lethrinus mahsena*) across a patch reef at Malindi, indicating limited dispersal across this reef type. However, the locally abundant whitespotted rabbitfish, *Siganus sutor*, had a shallow gradient of abundance across this reef indicating ability for dispersal. Inter-annual variations in patterns of abundance were evident. For example, *S. sutor* was more abundant outside Malindi Park during the SE monsoon of 2000/2001 but was more abundant during the NE monsoon in 2001/2002.

Tagging experiments showed higher spillover rates of commercial species, mostly of *S. sutor* and the emperors along fringing reefs at Malindi and Watamu Parks. Little spillover was suggested off the patch reef at Malindi. Most of tagged fish showed little out-migration from the parks and had multiple recaptures within the parks. Large-scale (30-180 km) movements were reported in three species (*Gaterin flavomaculatus*, *S. sutor* and *L. mahsena*) that were generally believed to be sedentary on home reefs.

Reduction of fishing mortality within the parks may interact with species behavior to enhance conservation potential of the parks. For example, results of acoustic telemetry studies within Malindi Park, showed site fidelity and homing tendency in a commercial grouper (*Epinephelus tauvina*: Serranidae) displaced to multiple

sites (0.5-2.6 km) within the park. Homing in this species is thought to be linked to tidal factors amongst others and to play a role in the preservation of spawning stock biomass within the parks.

Estimates of demographic parameters (growth, mortality and survival rates) of some commercial reef fishes necessary for stock assessment and management are provided. These rates are largely unknown for most species, thus making cross-regional comparisons difficult. However, where data exist for other geographical areas, growth parameters (e.g., instantaneous annual growth rate, K, and absolute growth rates) were higher, especially for *Siganus sutor* and *Lethrinus mahsena*, on the Kenyan coast suggesting superior conditions for growth.

The overall implication of these results to species conservation, and the function and design of marine parks are discussed in the thesis.

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Chapter 1

General Introduction and Overview

Increasing fishing pressure in coastal zones from recreational, subsistence and commercial harvesters has led to biologically important declines in the stocks of inshore fisheries (FAO, 1995). This decline is even more pronounced in developing countries where the scarcity of resources has complicated the inherent difficulties of managing multi-species stocks (McManus, 1997).

Conventional fisheries management strategies and single species models have proved difficult to apply in these countries, and may be problematic in tropical ecosystems (Jennings and Kaiser, 1998). Effort is being made to find socially and ecologically acceptable alternatives. One such alternative that is gaining popularity worldwide is the establishment of marine protected areas (MPAs) or reserves. Reserves are increasingly being considered as a viable means of allowing depleted stocks to recover and as cost-effective alternatives to conventional fisheries management (Bohnsack, 1992; Jennings, 2001). Overall empirical data suggest that area protection can help restore depleted stocks.

Differences in fish abundance between fished and unfished sites have been reported in many places and attributed to the effects of fishing (see reviews in Roberts and Polunin, 1991; Jennings, 2001). However, conclusive validation of

these differences has often been hampered by a lack of historical data, particularly before protection was instated (Crowder et al., 2000).

Reef fishes are singularly vulnerable to overfishing because many species have high natural mortality rates as a consequence of exploitation by predatory species (Johannes, 1978; Ursin, 1982). Hence, even moderate levels of fishing can lead to a rapid decline in productivity. Such overfishing is believed to have caused stock decline in many developing countries (Pauly et al., 1998). In coastal East Africa, some reef lagoons are believed to have been fished beyond sustainable levels. For example, in Kenya, the disparity in fish biomass between protected (≈ 1000 kg/ha) and unprotected reefs (≈ 100 kg/ha) has been attributed to fishing pressure (McClanahan and Obura, 1995). Although reserves have the potential to restore overfished sites, their effectiveness will depend on many factors including the spatial-scale of protection, design and effective regulation (Jennings, 2001).

Marine reserves have been established for a variety of purposes throughout the world and have both ecological and economic benefits. The potential ecological benefits are many (e.g., Bohnsack, 1998), and the promise of replenishing fished sites with dispersing larvae (Carr and Reed, 1993) and emigrating juvenile and adult stages (Alcala and Russ, 1990), have made reserves attractive to management. Recent interest has focused on testing their efficacy in achieving

these goals and in particular on their potential as management tools in tropical multi-species ecosystems (Roberts and Polunin, 1991). By increasing the number, diversity and size of fish, reserves may increase the abundance of larval, juvenile and adult fish beyond their boundaries (Dugan and Davis, 1993; Roberts, 1997). This so-called “spillover” effect (*sensu* Rowley, 1994), although predicted by theoretical considerations such as the frequency dependent movements of the Ideal Free Distribution model (Fretwell and Lucas, 1970) and modeling (Polacheck, 1990; DeMartini, 1993; Man et al., 1995; Nowlis and Roberts, 1997) studies, has not been tested adequately in the field (e.g., Sale, 1998; Murray et al., 1999).

Previous studies that have examined the influence of marine reserves on species recovery and their potential to enhance adjacent fisheries yields have had several shortcomings. These include limited reserve size, lack of appropriate replicate sites, inadequate temporal and spatial scales (Dugan and Davis, 1993), inappropriate methodologies and lack of historical data to assess any before and after effects. There is therefore a need for more empirical tests of the efficacy of reserves as fisheries management tools (Crowder et al., 2000).

Several studies have reported variable results with respect to catch per unit effort in fishing grounds adjacent to marine reserves. Alcala and Russ (1990) reported a 54% decline in the total catch associated with the elimination of a protected

area that covered just 10% of the total area. Another study found a 35% decrease in total catch with the creation of a reserve that occupied 65% of the fishing grounds (McClanahan and Kaunda-Arara, 1996). Consequently, the area of reserve to exploited area, the edge/area relationships (Stamps et al., 1987), the transfer or emigration rates of fish across the boundary (Polacheck, 1990; DeMartini, 1993), edge permeability (Stamps et al., 1987), the age (Nowlis and Roberts, 1997) and size of the reserve (Walters, 2000) may all affect the ability of reserves to function effectively.

The creation of a reserve has the immediate consequence of changing the allocation of harvesting opportunities or other uses between groups (Rosenberg, 2001). Hence, there is often widespread resentment among fishers over displacement from traditional fishing grounds. Furthermore, if desired species do not spillover, then fishers will not benefit and may not be receptive to reserves, thus making management difficult and perhaps jeopardizing the long-term sustainability of the reserves. Field studies aimed at testing spillover may therefore be useful in designing reserves to maximize both species conservation (increased survivorship and sustainable exploitation) and the ability to sustain yields in adjacent fisheries.

Modeling studies suggest that reserves will only maintain or increase yields when fishing occurs at high levels, above maximum sustainable yields (Polacheck,

1990; Nowlis and Roberts, 1997). Moreover, spillover depends on fish abundance and transfer rates from reserves to fishing grounds, which is a function of fish movements (DeMartini, 1993) and reserve shape and edge permeability (Stamps et al., 1987). The model of DeMartini (1993) developed for coral reef fishes suggests that movement rates are critical to determining the optimal size of reserves. Reserves are most likely to benefit fisheries relying on species with moderate mobility. Low-mobility fish do not move enough to significantly contribute to spillover, while highly mobile fish abundance is not greatly increased in reserves. If population density is higher inside a reserve than in adjacent fished areas, random movement is expected to produce net emigration from the reserve. If net emigration is an important factor determining the distribution of fishes, then the abundance of fish should be maximal in the center of the reserve decreasing gradually away from that center. Fishes with their home ranges centered in the reserve but close to the boundary are more likely to spillover than those with their home ranges in the center of the reserve. Highly mobile fish could easily relocate from the reserve to areas outside. Thus mobile fish should exhibit a shallower gradient of abundance across reserve boundaries than do sedentary fish, while moderately mobile species will yield greater benefits to fishing areas closer to the reserve. These predictions suggest that reserves will function differently in terms of supplying fish to adjacent areas according to behavioral traits (e.g. mobility) of the species. Although these

predictions are expected by logic and theoretical considerations (e.g., Kramer and Chapman, 1999), little data exist to validate them.

Studies monitoring coral reef fish movements often depend on visual re-sightings, however, this method may underestimate the spatial-scale of movements (Appeldoorn, 1997) and hence the potential of reserves to restock adjacent sites through post-larval emigration. There is need for more direct experimental tests (e.g., through tagging) of fish movements from reserves that include fisheries recaptures in estimating the scale of emigration from reserves.

In subsequent chapters of this thesis I present data aimed at testing the efficacy of two of the oldest marine protected areas in Kenya, the Malindi and Watamu National Parks (created in 1968), as conservation and fisheries management tools. The specific objectives of the research were:

- to investigate the role of Kenya's marine parks on fisheries conservation by comparing catch per unit effort and fish densities across park boundaries,
- to determine the potential influence of two of the oldest marine parks in Kenya on the adjacent fisheries using a spillover model and by examining site and species specific variations in patterns of spillover,
- to investigate the potential interaction of zero fishing mortality within the parks and species traits (e.g., site fidelity and homing) in the conservation of exploited species and,

- to estimate demographic rates (e.g., growth, mortality and survival rates) of some of the most important exploited fish species in coastal Kenya, necessary for stock assessment and management.

The results of my two years of fieldwork in coastal Kenya are presented in subsequent chapters. The chapters are organized as a series of stand-alone papers. In Chapter 3, I examine the long-term trends in commercial fish landings using historical landing data from the Kenya Fisheries Department. Additionally, I determine the exploitation and fishing mortality rates of commercial reef fishes and a long-term forecast of landings. The potential of Malindi and Watamu Marine National Parks (created in 1968) to conserve fish stocks and sustain adjacent fish landings through a spillover effect is examined in Chapter 4 by comparing fish densities across park boundaries. A spillover model (logistic decay function) is used to describe the pattern of fish abundance from the center of the parks across the park boundaries. Movements of fish from the marine parks are further assessed using tagging experiments inside and across the park boundaries in Chapter 5 and 6.

The interaction of zero fishing mortality inside the parks and species behavioral traits in species conservation is studied by experimental testing of site fidelity and homing tendency in a commercial grouper (*Epinephelus tauvina*: Serranidae) within Malindi Park using acoustic telemetry (Chapter 7). Finally, in Chapter 8, I

present results on the demographic rates (e.g., growth, mortality and survival rates) of some exploited marine fish species in coastal Kenya useful for scientific management of stocks. Chapter 9 summarizes the major thesis of my work and underscores the contribution of my work to assessing the potential role of marine reserves in the conservation of fishes and in sustaining yields in adjacent fishing grounds.

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Chapter 2

Co-authorship statement

2.1 General

All major intellectual and practical contributions to this work were my own. I conceived the idea, designed the research project proposal and carried out all aspects of the research including data gathering and analysis and manuscript preparation. I am the lead author on all manuscripts included in this thesis. My supervisor, Dr. George A. Rose is junior author on all manuscripts. He was responsible for valuable insights and editorial comments on the manuscripts and assisted with the fieldwork and the provision of funding. All those who provided advice, field assistance and funding are acknowledged at the end of each chapter.

2.2 Chapter 3 co-authorship

The data used to analyze the long-term trends of Kenya's coastal fisheries are archived at the Kenya Fisheries Department. The data were gathered and collated by S.M. Mucai and R. Kaka. I consequently analyzed the data and interpreted the results with insight and editorial input from G. A. Rose. Data used to derive exploitation rates and population parameters were generated in another part of my research (Chapter 4).

Chapter 3

Long-term trends in coral reef fish yields and exploitation rates of commercial species from coastal Kenya

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3.1 Abstract

Analysis of long-term (1978-2001) marine fisheries data showed that Kenyan coral-reefs produced an estimated 2-4 metric t/km²/year of demersal fish. A rapid overall decline in landings occurred during the 1990's. Yields (t/km²/year) showed bimodal peaks in 1982 (2.98) and 1991 (2.90). The average total landings dropped by 55% during the last decade following peak landings in 1982.

Landings of the commercially important families (e.g., Siganidae, Lethrinidae, Lutjanidae and Serranidae) declined by about 40% during the last decade, with the groupers (Serranidae) showing the steepest (72%) decline. Analysis of landings per administrative district showed a 78% decline in the densely populated Mombasa district between the periods 1983-91 and 1992-2001. The less populated districts have registered stable (e.g., Kilifi) to increasing (e.g., Kwale) catches over time. An AutoRegressive Moving Average (ARIMA) model forecast of landings predicted a gradual decline in catches during the next decade (2002-211) with a trend slope of -0.01t/km². Length-frequency analysis

for the commercially important species indicated above optimum exploitation (E) and fishing mortality (year^{-1}) rates for the sky emperor, *Lethrinus mahsena* (E = 0.64; F = 2.48) and lower but strong rates for the emperor, *L. sanguineus* (E=0.51; F=0.93). The more abundant and commercially important whitespotted rabbitfish, *Siganus sutor*, showed equally strong rates (E= 0.56; F = 1.44 yr^{-1}). A precautionary approach in the management of Kenya's coral-reef fisheries is recommended.

3.2 Introduction

Fishing is the dominant extractive activity in Oceania and an important source of income and sustenance in coastal communities worldwide. However, in the past decade many marine fisheries resources have been declining (FAO, 1995).

Although ocean climate variation has likely played an important role in many regional declines (e.g., Lauck et al., 1998; Drinkwater, 2002), the most important factor has been overfishing (Pauly and Christensen, 1995; Hutchings, 2000; Rose et al., 2000). The effects of fishing have been the subject of recent reviews (Jennings and Polunin, 1996; Jennings and Kaiser, 1998). Growth overfishing reduces the size and yield of target species (Koslow et al., 1988; Russ, 1991; Munro, 1983), recruitment overfishing reduces the recruitment success of populations (Jennings and Lock, 1996) while ecosystem overfishing alters species interactions and habitat quality (McClanahan, 1995). Marine fishes have been thought to be resilient to these effects (Musick, 1999), but such resilience has likely been overstated, and will depend on the degree and frequency of

impact and the life history traits of target species (Sadovy, 2001). In developing countries, the effects of fishing are exacerbated by inadequate resources available to management agencies and increasing human populations (McManus, 1997). The outdated notion that fisheries resources are unlimited, often reinforced by increasing annual catches, has led to overfishing of many tropical fisheries resources (Pauly et al., 2002).

In East Africa, coral reef fisheries have a long history (Brochman, 1984). In Kenya, reef fisheries are exploited by approximately 8000 artisanal fishermen. These fishermen mostly use traditional dug-out canoes on grounds that include most of the lagoons between shore and the fringing reefs (Brochman, 1984). East African reefs have been thought to be exploited at sustainable levels or to be somewhat over-fished (McClanahan and Obura, 1995). However, there are no estimates of yields or exploitation rates for these fisheries, largely as a consequence of inadequate landing statistics (UNEP, 1998). In other tropical reef systems, few estimates of long-term yields of coral reef fisheries have been reported (Dalzel, 1996; Mapya et al., 2002), but cross-regional comparisons may be problematic because of local variations in reef areas and types, depth and fishing effort (Russ, 1991). Recent increases in human population in coastal East Africa (e.g., 4.2% per year in Kenya) have likely increased the demand for marine food fish. However, the effects of any such increased demand on reef fish resources have not been quantified.

Studies on long-term yields of coral reef fisheries are few (Mapya et al., 2002) but can provide important information for management on the state of stocks. In this paper, we document long-term trends in the yields of coral reef associated fish families in Kenyan waters of the Western Indian Ocean. We also provide estimates of exploitation and fishing mortality rates for the principal commercial species, and develop a time series model of landings with long-term projections.

3.3 Materials and Methods

The Kenya Fisheries Department routinely collects fish landing statistics along the approximately 600 km long coastline (Fig. 3-1). Fish Scouts who are supervised by Fisheries Assistants record landed weight of fish by taxonomic families at designated landing beaches. The data from all landing sites within the administrative units or districts (e.g., Mombasa, Kilifi, Kwale and Lamu) are compiled into a national annual statistical bulletin. Landing data contained in the annual statistical bulletins from 1978 to 2001 were analyzed in this study for reef associated families (Lethrinidae, Lutjanidae, Siganidae, Scaridae, Acanthuridae, Serranidae, and an "others" category). Non-reef pelagic families (mostly Clupeidae and Carangidae) are highly variable in the catches and were excluded. Exploitation levels and fishing mortality rates were derived from length-frequency data obtained from commercial trap landings. Trained assistants sampled trap fish landings at four active fish landing sites adjacent to Watamu and Malindi Marine National Parks (Fig. 3-1) at bi-weekly intervals from May 2000 to April 2002. Total length (nearest mm) of random samples of landed fish species,

number of traps per fisherman, fishing ground and fisherman's name was recorded. Length-frequency data of the commercially important fish species (the whitespotted rabbitfish, *Siganus sutor*, the sky emperor, *Lethrinus mahsena* and the emperor *L. sanguineus*) were used to estimate exploitation and fishing mortality rates and population growth parameters.

3.3.1 Data analyses

It is estimated that artisanal fishermen in coastal Kenya operate within an area of approximately 800 km² of lagoons that extend between the shore and continuous fringing reefs at depths less than 5 m at low tide (McClanahan and Obura, 1995; UNEP, 1998). This reef area was used to standardize catches (tonnes/km²). Time series of landings, metric tonnes, (t / km²/ year) were used to analyze temporal trends in catches of the major demersal families of coral reef fish (e.g., Siganidae, Lethrinidae, Lutjanidae, Scaridae, Acanthuridae, Serranidae and "others").

A locally-weighted scatterplot smoother (LOWESS) (Cleveland, 1979) was used to fit smoothed trend lines to the full data series using the MINITAB package. The LOWESS, is based on a weighted least squares algorithm that gives local weights the most influence while minimizing the effects of outliers (see Cleveland, 1979 for details). A smoothness parameter (f) of 0.2 was found to adequately smooth the data without distorting the main temporal patterns. Additionally, an AutoRegressive Integrated Moving Average (ARIMA) model (Box and Jenkins,

1976) was used to forecast landings for the next decade (2002-2011). An ARIMA (111) model that integrates first order Autoregressive (AR) and Moving Average (MA) model parameters with first differencing of the annual catches (Rothschild, 1996; O'Donovan, 1983) was used to forecast catches as:

$$y_t = \theta_0 + \phi_1 y_{t-1} + a_t - \theta a_{t-1} \quad (1)$$

where, y_t is the first difference of the catches at time t , ϕ and θ are AR and MA parameters, respectively, a_t is a random error term and θ_0 is the model constant. The model assumes stationarity and homogeneity of means and variances, respectively. The means and variances of the output series (catches) were made stationary and homogeneous by first differencing and \log_e transformation of the data, respectively. The slope (s) of the forecast trend in landings during the next ten years (2002-2011) was derived following O'Donovan (1983) formula:

$$s = \theta_0 / (1 - \phi_1) \quad (2)$$

The ARIMA model is considered parsimonious in analyzing data whose underlying structure is unknown and with individual observations that are prone to error (Box and Jenkins, 1976). The long-term landing data was divided into 3 time intervals (1978-82, 1983-91 and, 1993-2001) based on a preliminary assessment of the temporal pattern of landings. A one-way ANOVA was used to test for significant differences in landings (metric t) between the 3 time periods. All data were first tested for normality and homoscedasticity using Kolmogorov's test and Levene's test, respectively, (Zar, 1975). Where variances were significantly different within the families (e.g., Serranidae and Scaridae) and in

the districts (e.g., Mombasa), the catch was first \log_e transformed before ANOVA was performed. Where the mean catch between the time periods were found to be different (ANOVA, $p < 0.05$), a Bonferroni test was used for *post hoc* analysis. Exploitation level (E) and fishing mortality rate (F) and growth parameters (e.g., instantaneous annual growth rate, K, and the asymptotic length, L_∞) were estimated for the three major commercial species using length-frequency analysis (LFA). LFA was carried out using length-based routines in the FiSAT package (Gayanilo et al., 1995). In order to increase the modal sizes, length-frequency data were pooled tri-monthly for the sky emperor and the emperor *L. sanguineus* for the period May 2000 to January 2002. Monthly length-frequency (June 2000 to March 2002) data were analyzed for the more abundant whitespotted rabbitfish. Having obtained estimates of the growth parameters (K and L_∞) from ELEFAN I sub-package in FiSAT, ELEFAN II was used to estimate instantaneous total (Z) and natural mortality (M at 27°C) rates from linearized length-converted catch curve and Pauly's empirical formula (Pauly, 1980, 1984):

$$\ln M = -0.0152 - 0.279 \ln L_\infty + 0.6543 \ln K + 0.463 \ln T \quad (3)$$

T is the annual sea surface temperature (27°C). F was then obtained from the difference between Z and M. The exploitation rate (E) for each of the three species was derived from the ratio, F/Z, (Gulland, 1971). The exploitation rate indicates whether the stock is lightly ($E < 0.5$) or strongly ($E > 0.5$) exploited, based on the assumption that the fish are optimally exploited when $F = M$ or $E = 0.5$ (see Gulland, 1971).

3.4 Results

3.4.1 Total catch

The long-term total landings of demersal coral reef fishes averaged 2.11 ± 0.49 t/km²/year. Annual landings peaked in 1982 (2.98 t/km²/year) and 1991 (2.90 t/km²/year) (Fig. 3-2a). Following the peak in 1982 the catches dropped by 23% to 2.3 in 1984 and remained relatively stable during 1983-91 when landings averaged 2.53 ± 0.20 t/km²/year (Table 3-1 and Fig. 3-2a). Following this period of relative stability, annual landings declined by 30% from 1991 to 1992 (2.03), with a further 25% decline in subsequent years to lowest levels observed in 2000 (1.3). The average landings for the period 1992-2001 (1.65 ± 0.21 t/km²/year) were significantly lower than landings from 1978-82 (29%) and 1983-91 (35%) (Table 3-1).

3.4.2 Catch by taxonomic group

The fish families landed showed differences in trends (Fig. 3-2). The rabbitfishes (family Siganidae) showed increasing landings during 1978-82 (0.71 ± 0.09 t/km²/year) that stabilized during 1983-91 (0.75 ± 0.07 t/km²/year). However, the 1992-2001 average landings (0.45 ± 0.09) were significantly lower (ANOVA, $P < 0.05$, Table 3-1) than for the earlier periods, with the lowest catches in 2000 (0.32 t/km²/year) (Fig. 3-3b). The emperors (family Lethrinidae), had peak landings in 1982 (0.90 t/km²/year) and 1991 (0.83 t/km²/year) (Fig. 3-3c). Average landings of emperors did not differ between 1978-82 (0.74 ± 0.13 t/km²/year) and

1983-91 (0.78 ± 0.03 t/km²/year), however, the landings during the last decade, 1992-2001 (0.48 ± 0.08 t/km²/year), were significantly lower than for the earlier periods (Table 3-1).

The groupers (family Serranidae), had one prominent peak during 1982-83 (0.32 t/km²/year), however, unlike the other families, catches subsequently declined steeply (72%) to an average of 0.09 ± 0.01 t/km²/year during the period 1992-2001, which was significantly lower (ANOVA, $p < 0.05$) than earlier periods (Fig. 3d and Table 3-1). The snappers (family Lutjanidae), had peak landings in 1982 (0.36) and 1991 (0.30), with a subsequent decline to low levels in 2000 (0.12 t/km²/year) (Fig. 3-1e). The other families, which are less important in commercial catches (e.g., Scaridae and Acanthuridae) showed rising catches (1978-84) followed by a general decline during the 1990's, however, the landings for the Scaridae showed a rising trend in recent years as did the "others" (e.g. Labridae, Gaterinidae, Holocentridae etc) category (Fig. 2g and h).

3.4.3 Landings per district

Landings categorized according to administrative districts showed variable trends (Fig. 3-3). The densely populated Mombasa district (≈ 280 persons/km², UNEP, 1998) registered peak landings in 1986 (908) followed by a consistent decline in subsequent years to the lowest levels observed in 1997 (118 t/km²) (Fig. 3-3a). The average landings during 1992-2001 (159 ± 31 t/km²) were significantly lower

(78%) than during 1983-91 ($722 \pm 156 \text{ t/km}^2$) (Table 3-2). Kilifi district ($\approx 57 \text{ persons/km}^2$), had an isolated peak landings in 1982 (571 t/km^2), after which landings dropped (69%) to a low in 1985 (175), followed by relative stability (1985-1997) and a decline in the late 1990's (Fig. 3-3b). Overall there were no significant differences in quantities landed at Kilifi between periods (ANOVA, $p > 0.05$, Table 3-2). The less populated Lamu district ($\approx 33 \text{ persons/km}^2$) showed an erratic trend in landings that generally declined over time following a peak in 1983 (Fig. 3-3c). The average quantities landed at Lamu during 1978-82 ($763.8 \pm 150 \text{ t/km}^2$) were significantly higher than the rest of the periods (Table 3-2). In contrast, the more populated Kwale district ($\approx 53 \text{ persons/km}^2$) showed an initial increase in landings (1978-82) followed by a gradual drop to lowest level in 1991. The district registered increased catches during the 1990's (Fig. 3-3d).

3.4.4 Forecast landings (2002-2011)

Based on ARIMA (111) model, the combined catches of all the families were used to forecast total landings for the next decade following the last recorded landings in 2001 (Fig. 3-4). The model generated for this forecast was:

$$y_t = -0.007 - 0.058y_{t-1} + a_t + 0.950a_{t-1} \quad (3)$$

The model output indicated increased landings in 2002 following the recorded catches in 2001 ($1.3 \text{ t/km}^2/\text{year}$). Subsequent forecasts predicted a consistent decline in catches to the year 2011 with a shallow slope of -0.01 t/km^2 (equation 2) (Fig. 3-4). The 95% prediction limits indicated greater confidence in the

forecasts during the next 4 years (2002-2005), with decreasing confidence (increasing confidence interval) in subsequent years.

3.4.5 Exploitation and fishing mortality rates

Analysis of length-frequency data (Fig. 3-5) for the three commercially important species yielded a higher asymptotic total length (L_{∞}) for the emperor (*L. sanguineus*) (46.2 cm) than for the sky emperor (*L. mahsena*) (37.8 cm) and the whitespotted rabbitfish (*S. sutor*) (39.9 cm) (Table 3-3). Length-converted catch curves and Pauly's empirical formula yielded high total (Z /year) and natural mortality (M /year) rates for the sky emperor ($Z=3.84$, $M=1.36$) and the whitespotted rabbitfish ($Z=2.59$, $M=1.15$) (Fig. 3-6). The emperor *L. sanguineus* had the lowest mortality rates ($Z=1.83$, $M=0.90$). Of the three species, the sky emperor had the highest exploitation ($E=0.64$) and fishing mortality ($F=2.59$) rates. The emperor, *L. sanguineus* had lower rates ($E=0.51$, $F=0.93$), as did the whitespotted rabbitfish, *S. sutor* ($E=0.56$, $F=1.44$).

3.5 Discussion

The data indicate that a rapid overall decline in landings occurred in coastal Kenya during the 1990's. The decline was most severe at Mombasa (78%) which contributes > 40% of coastal landings and was less evident in some districts (e.g., Kwale). Environmental conditions could play a role in declining catches, but there is little evidence of large-scale change in climate along the East African coast in recent times. Annual human population growth rate in Kenya is

estimated at 4.2% and the rate is thought to be higher for the coastal towns (UNEP, 1998). Population driven demand for food and employment, coupled with destructive fishing activities (McClanahan et al., 1997) has likely played a role in the recent decline in coastal landings.

The Siganidae and the Lethrinidae form the bulk (~40%) of the artisanal landings in coastal Kenya, and it is noteworthy that their landings declined by 40% during the 1990's. The overall decline in landings is likely influenced greatly by the decline in the yield of the two groups. However, declines in all the major demersal fish families (e.g., Siganidae, Lethrinidae, Lutjanidae and Serranidae) have occurred over the last decade. Fishing and exploitation rates are above optimum levels for the commercially exploited species in these families. It is likely that sustainable yield levels have been exceeded. However, estimation of sustainable yields is likely to be difficult due to the many landing sites, many gears and inappropriate records, a problem that is common for most tropical stocks (Russ, 1991). It is noteworthy that the landings of the "others" category is showing an increasing trend in recent years (Fig. 3-2h), and this has likely been caused by increased marketing of species formerly considered less valuable.

Amongst the families studied, the groupers (family Serranidae) showed an earlier and a steeper decline (~72%) in catches compared to the other groups. The groupers may have suffered high fishing mortality due to their sedentary life and

the tendency to form spawning aggregations in some species (Thomson and Munro, 1983) which makes them highly vulnerable to exploitation. It is likely that some serranids have suffered spawning collapse because of reduced population levels. Furthermore, fishing may skew sex ratios in protogynous (maturing as females) groups such as the Serranidae (Thomson and Munro, 1983), thereby causing spawning failure. Elsewhere, the Nassau grouper, *Epinephelus striatus*, is commercially extinct in the Bermuda fishery (Luckhurst, 1996). The gonochoristic (separate sex) families (e.g., Lutjanidae, Lethrinidae, Siganidae) are likely to be more resilient under high fishing effort and the different reproductive ecology and behaviour may have allowed these groups to maintain stock levels without suffering dramatic declines as in the Serranidae.

Earlier reviews of coral reef fish yields (e.g., Marshall, 1980) concluded that yields range from 0.8-5 metric t /km²/year. However, studies of reef-fish yields from American Samoa and the Philippines (Wass, 1982; Dalzel, 1996; Mapya et al., 2002) have documented yields in the range of 8-27 t /km²/year. Our analysis of reef fish landings indicate that Kenyan reef-fish yields averaged 2.1 t /km²/year. However, this figure is likely conservative given that about 40% of the landings may not be reported (FAO, 1985). Therefore, potential yields may actually average 3-4 t/km²/year. Yield estimates from different regions may not be strictly comparable because of the variations in reef area and type, depths, fishing intensity (Russ, 1991) and fish assemblages.

The continued decline in marine fisheries production may have been downplayed by the relatively small role of the marine fishery in national fisheries production. Of Kenyan total annual fishery production, only 7.4% comes from marine waters (UNEP, 1998). There are a number of physical, climatic and economic factors that combine to constrain the marine fishery in Kenya. Firstly, the area of the continental shelf, to a depth of 200m, is only about 8500 km², less than 10% of the fishable area of Lake Victoria (the largest freshwater lake in the country). Secondly, the South-East Monsoon which is prevalent from March to October is associated with very strong winds and rough currents. These conditions constrain the use of small dug-out canoes which are the main fishing craft. Thirdly, the East African coast does not have high productivity due to the oceanic origin of the coastal currents and lack of major upwelling areas (Hamilton and Brakel, 1984). Despite these constraints and the low contribution to national production, marine fishery resources are locally important sources of livelihood and protein for coastal communities.

The conventional methods of regulating a fishery are often difficult to enforce in developing countries (McManus, 1997). Marine protected areas are straightforward and cost effective tools for managing over utilized resources in these countries. Kenya has four national marine parks, and although these comprise less than 5% of the total reef area, they have been found to effectively conserve biodiversity and local fish biomass (McClanahan and Kaunda-Arara, 1996). Additionally, the parks may form important sources of larval recruits of exploited

species, and export adults of certain species to the adjacent fished sites (see Chapter 3 and 4). Marine parks in Kenya therefore likely play an important role in sustaining adjacent fisheries. However, there is still a need for robust validation of the effects of marine protected areas on fisheries through experimentation in order to optimize their potential as conservation tools (Crowder et al., 2000).

In conclusion, the trend analysis has shown that demersal coral-reef fish production has declined by over 30% for the total catches and 78% in the densely populated district (Mombasa) during the last decade. The principal commercial species are being exploited beyond optimal levels, and our forecast predicts a gradual decline in landings during the next decade. However, model forecasts are probably only instructive in terms of the direction of change while absolute forecast values are likely unreliable over a long term (J. Wroblewski, personal communication). The causes of the declining trends cannot be determined from the present data, but human population driven increase in fishing effort as a result of increased demand for food may have played an important role. More detailed analysis will require improvement of the data collection system to include species records, catch per gear and the associated fishing effort. In order to ensure sustained production and conservation of Kenya's marine fisheries resources, a precautionary approach to management is recommended, perhaps utilizing an expanded system of reserves.

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Table 3-1. Mean catch of coral reef fish families and total catch (t / km²/ year) between years (1978-82, 1983-91 and 1992-2001) in coastal Kenya, n=24 data points.

Families	Mean catch ± s.d.			ANOVA		Bonferroni post hoc
	78/82	83/91	92/2001	F	P	
Siganidae	0.71 ± 0.09	0.75 ± 0.07	0.45 ± 0.09	35.16	0.00	78/82=83/91>92/2001
Lethrinidae	0.74 ± 0.13	0.78 ± 0.03	0.48 ± 0.08	38.18	0.00	78/82=83/91>92/2001
Lutjanidae	0.27 ± 0.06	0.24 ± 0.04	0.15 ± 0.03	13.93	0.00	78/82=83/91>92/2001
Scaridae	0.14 ± 0.05	0.29 ± 0.06	0.21 ± 0.04	16.16	0.00	83/91>92/2001>78/82
Acanthuridae	0.05 ± 0.02	0.07 ± 0.01	0.06 ± 0.02	2.87	0.08	78/82=83/91=92/2001
Serranidae	0.19 ± 0.07	0.15 ± 0.04	0.09 ± 0.01	12.35	0.00	78/82=83/91>92/2001
Others	0.21 ± 0.06	0.25 ± 0.04	0.20 ± 0.03	4.12	0.03	83/91>92/2001=78/82
Total	2.31 ± 0.46	2.53 ± 0.20	1.65 ± 0.24	24.43	0.00	78/82=83/91>92/2001

Table 3-2. Mean annual landings (t / year) of demersal coral reef fish in the administrative districts of coastal Kenya during the periods 1978-82, 1983-91 and 1992-2001.

District	Mean catch \pm s.d.			ANOVA		Bonferroni <i>post hoc</i>
	1978/82	1983/91	1992/2001	F	P	
Mombasa	496.4 \pm 42.2	722.4 \pm 155.6	158.8 \pm 31.2	154.49	0.00	83/91>78/82>92/2001
Kilifi	283.4 \pm 163.6	269.7 \pm 91.0	200.4 \pm 115.5	1.17	0.33	78/82=83/91=92/2001
Lamu	762.8 \pm 155.5	666.8 \pm 92.4	583.1 \pm 123.6	3.84	0.04	78/82>83/91=92/2001
Kwale	374.6 \pm 68.5	353.0 \pm 79.2	378.4 \pm 81.5	0.27	0.77	78/82=83/91=92/2001

Table 3-3. Exploitation (E) and mortality (Z,M,F) rates and population growth parameters (L_{∞} and K) of three commercially important coral reef fish species from coastal Kenya derived from length-frequency modal progression analysis of fisheries landing data from May 2000 to January 2002. Parameters are explained in the text.

Species	L_{∞} (cm)	K/year	Z/year	M/year	F/year	E
<i>Siganus sutor</i>	39.90	0.52	2.59	1.15	1.44	0.56
<i>Lethrinus mahsena</i>	37.80	0.75	3.84	1.36	2.48	0.64
<i>Lethrinus sanguineus</i>	46.20	0.43	1.83	0.90	0.93	0.51

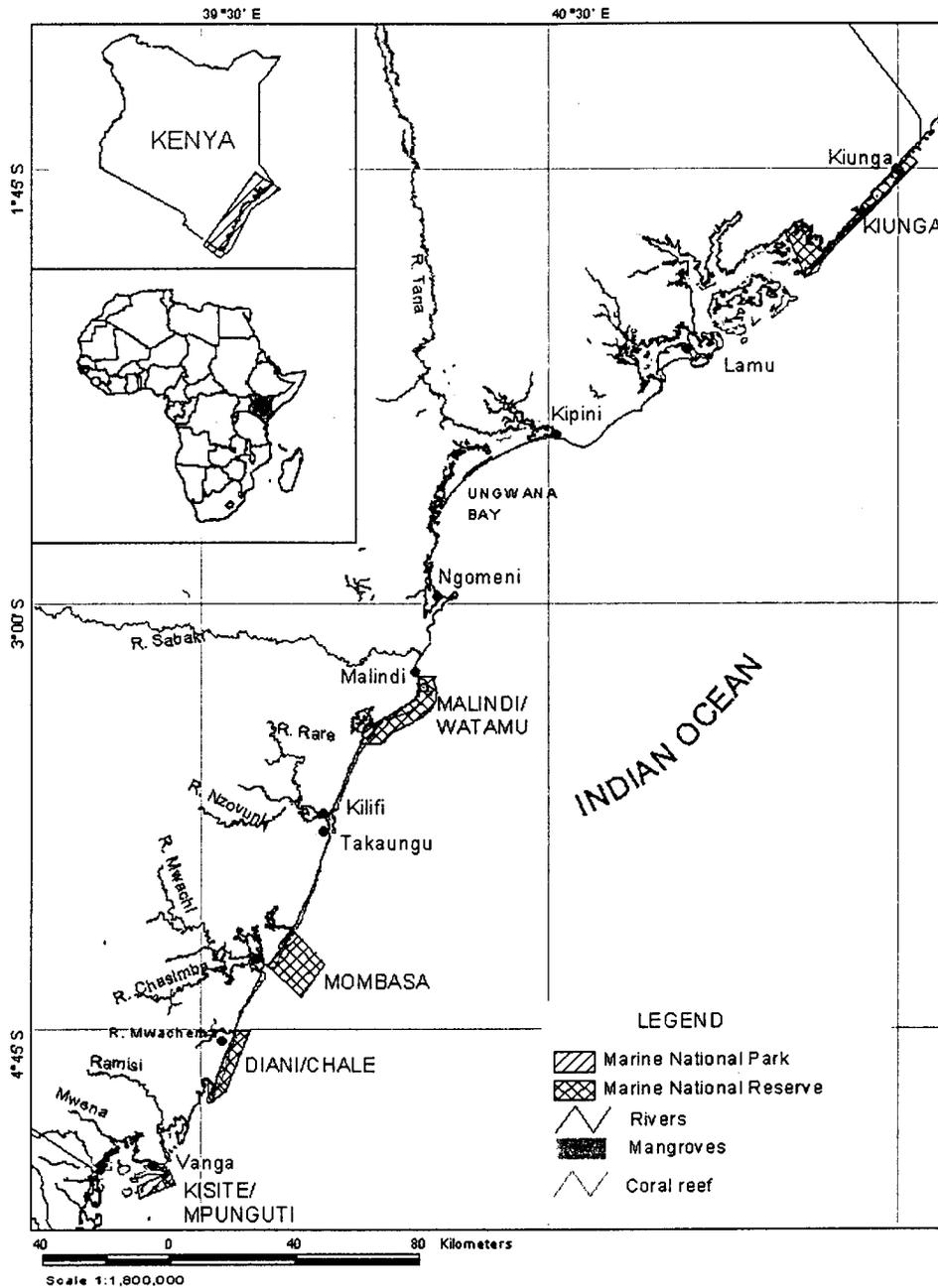


Figure 3-1: Kenyan coastline showing the major fish landing sites (●), the associated coastal habitats and the marine national parks and reserves.

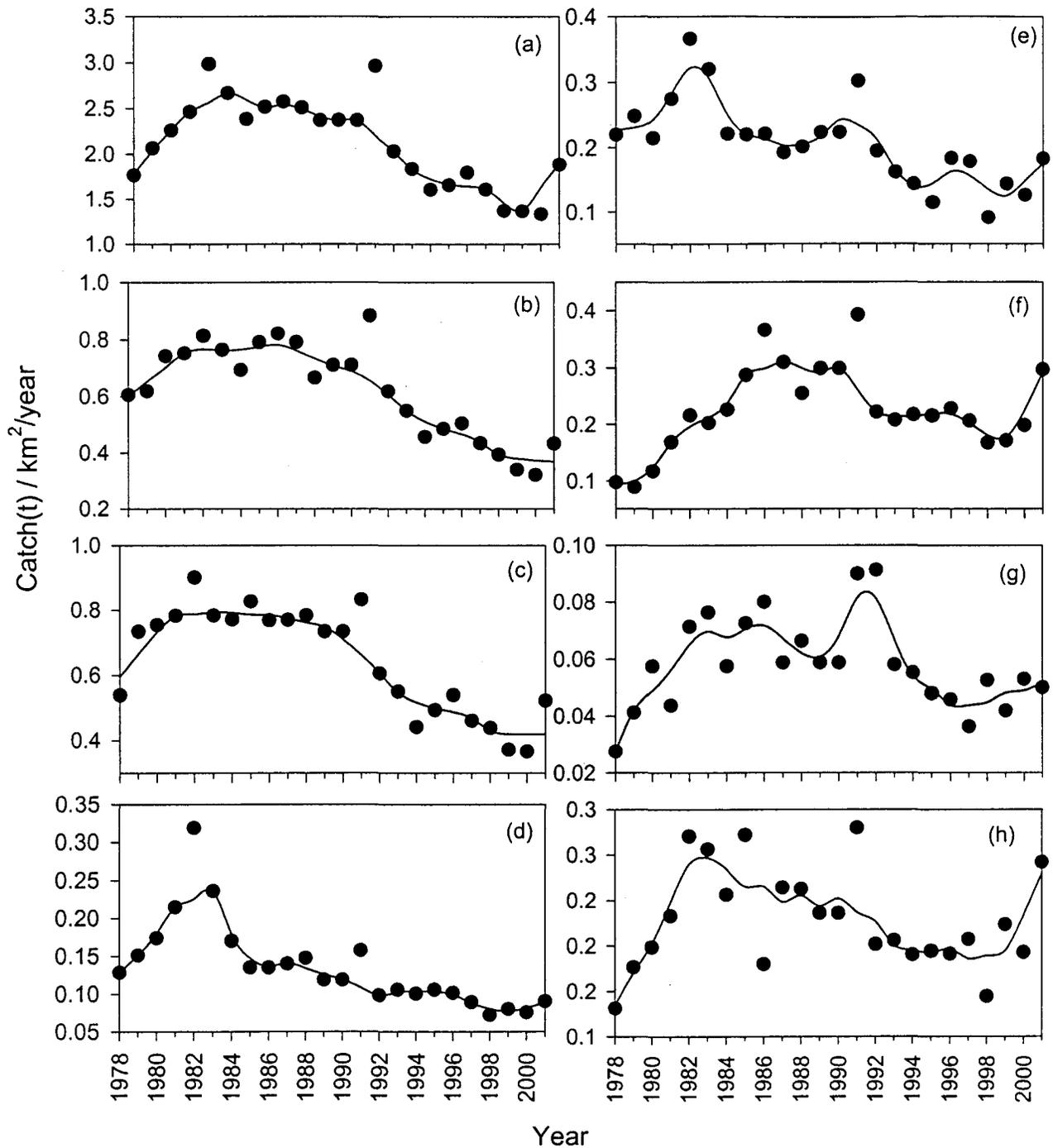


Figure 3-2: Long-term trends in annual landings (t /km²/year) of demersal coral reef fish families from 1978 to 2001 in coastal Kenya. Continuous lines show the LOWESS trend fit to landings, while (•), show the actual landings. (a) All families (b) Siganidae (c) Lethrinidae (d) Serranidae (e) Lutjanidae (f) Scaridae (g) Acanthuridae (h) others.

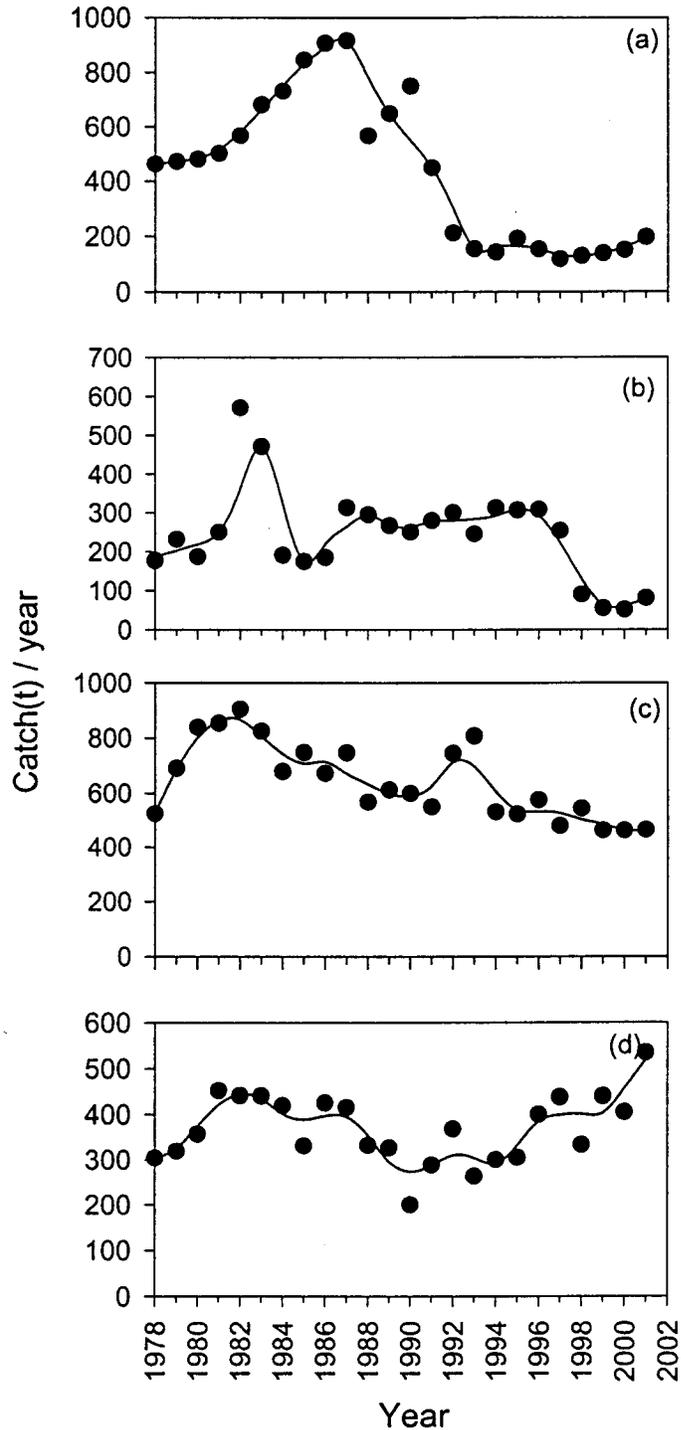


Figure 3-3: Long-term trends in the annual landings (t / year) of demersal coral reef fish in the active fish landing districts in coastal Kenya. Continuous lines show the LOWESS trend fit to landings, while (•), show the actual landings. (a) Mombasa, (b) Kilifi, (c) Lamu, (d) Kwale.

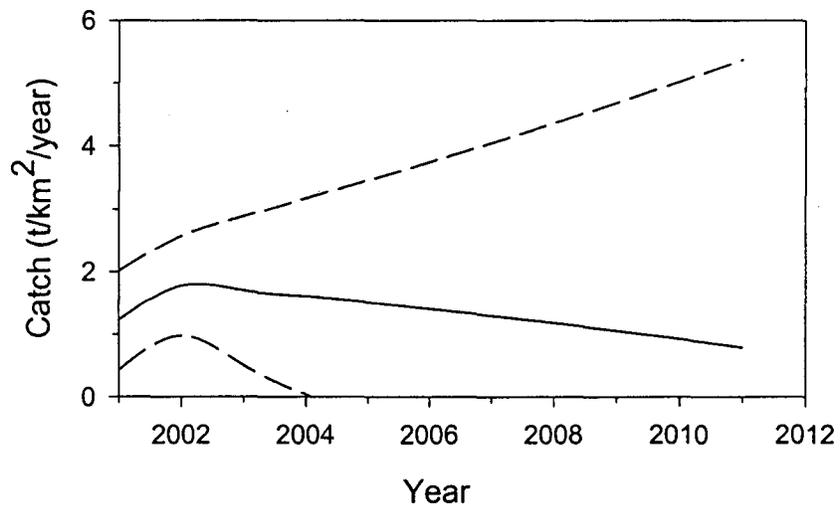
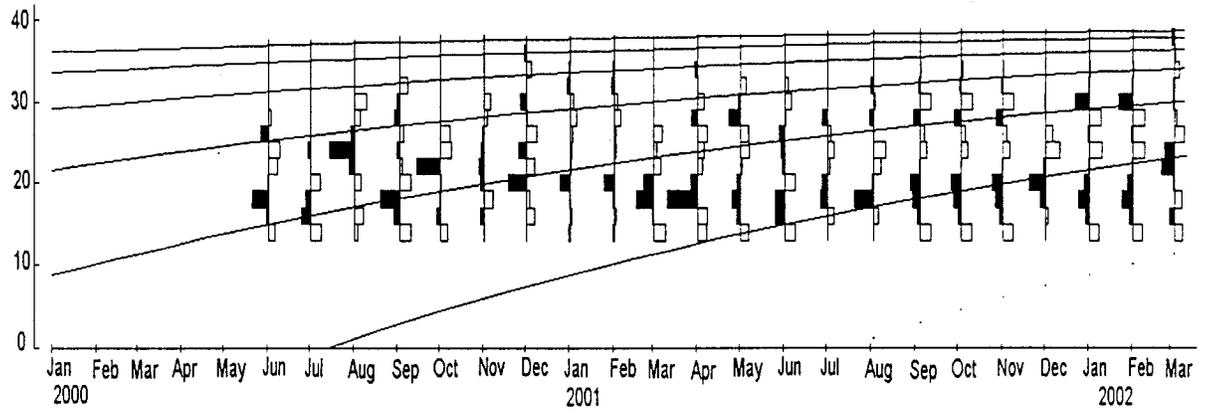
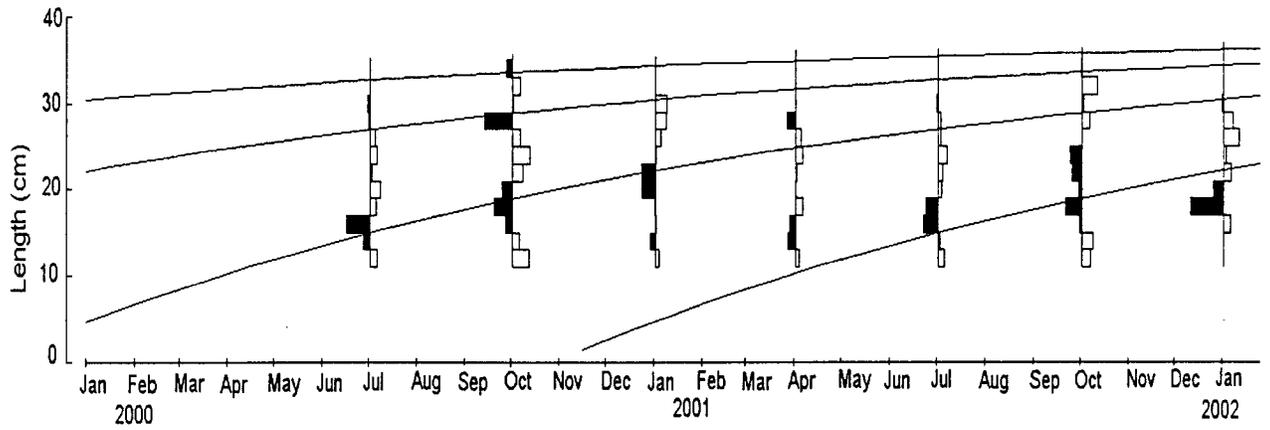


Figure 3-4: Forecast landings of demersal coral reef fish in coastal Kenya for the next ten years (2002-2011). The middle line represents the mean forecast values while the upper and lower dashed lines are the corresponding 95% confidence intervals.

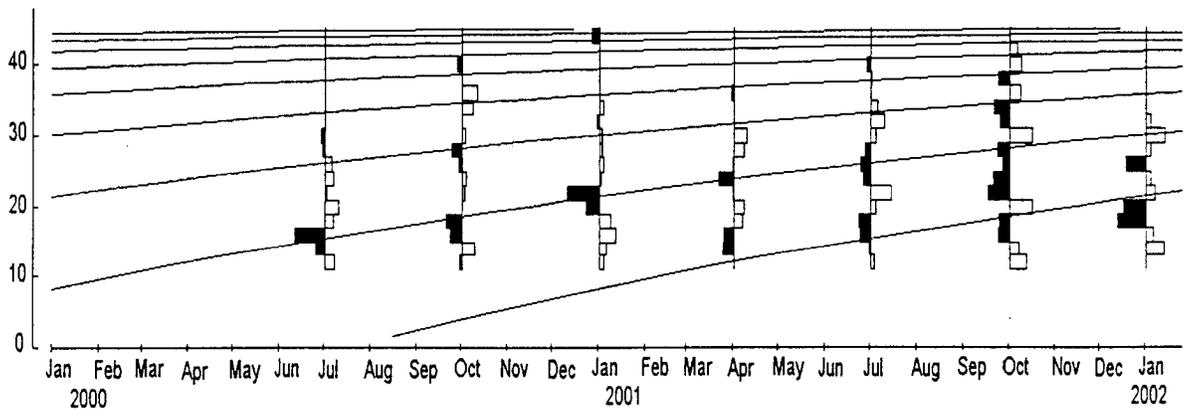
(a) *Siganus sutor*

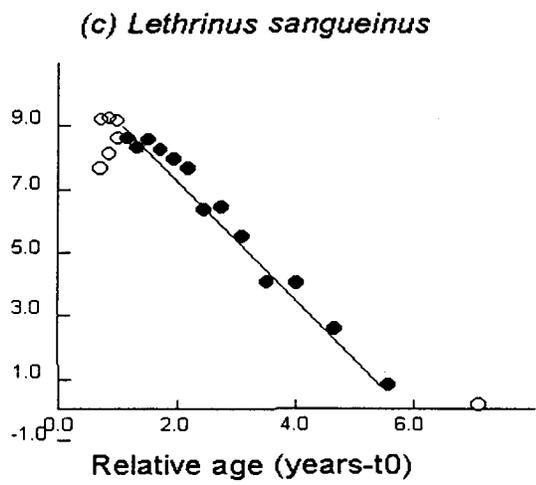
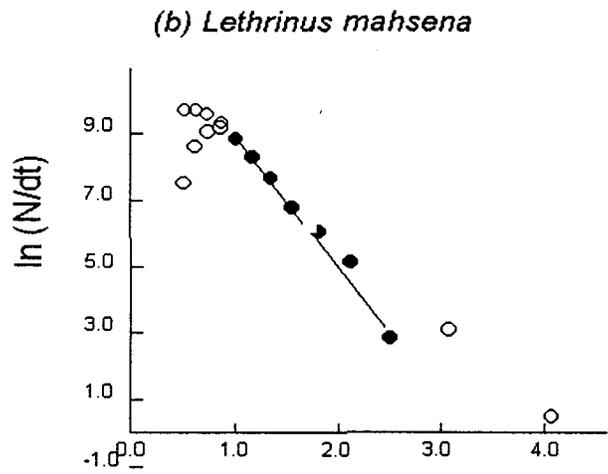
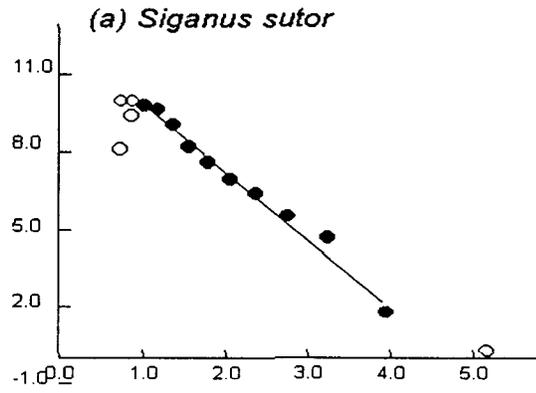


(b) *Lethrinus mahsena*



(c) *Lethrinus sanguineus*





Chapter 4

Effects of marine reef National Parks on fishery CPUE and fish densities in coastal Kenya

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4.1 Abstract

The role of marine protected areas in conserving fish stocks and their potential influence on adjacent fisheries was studied at Malindi and Watamu Marine National Parks, Kenya (established in 1968). For most species fish densities (#/500 m²) along visual transects and catch per unit effort (CPUE) in traditional *Dema* traps fished across park boundaries was higher within the parks (up to an order of magnitude). However, a few species (e.g., the seagrass parrotfish, *Leptoscarus vaigensis* and the whitespotted rabbitfish, *Siganus sutor*) had higher seasonal CPUE outside the parks. Potential spillover of fishes from the parks to adjacent fished areas was tested with a logistic “decay” model of density gradients (CPUE and #/500 m²) across park borders from fringing and patch reefs during the NE and SE monsoon seasons. A steep decay in fish densities and CPUE off the Malindi patch reef suggested little spillover of most species in either season (p 's < 0.05). However, greater spillover was suggested off fringing reefs, especially at Watamu during the NE monsoon from the pattern of CPUE. Species differences were evident. Considering the two most important

commercial species, sky emperor, *Lethrinus mahsena*, densities declined consistently and abruptly at park borders (Type III decay), whereas *S. sutor* densities did not (Type II curve indicating moderate decay). Patterns of density change analyzed for visual transects indicated a more rapid decay of density with distance from the park centers than revealed by the CPUE data. Size frequencies compared between the parks and adjacent areas suggested a fishing down of larger *L. mahsena* outside the parks but the effect of fishing on *S. sutor* was less definite. Species diversity declined at both park boundaries (p 's <0.05).

We conclude that although spillover of most species from the parks is limited, the most important commercial species (*S.sutor*), exhibits significant spillover to adjacent fisheries and the parks likely comprise important nursery and growth areas for other species.

4.2 Introduction

Marine protected areas have been thought to hold potential to enhance fisheries production in adjacent waters (Bohnsack, 1992; Ayling and Ayling, 1986; Alcala, 1988). Enhancement might occur through dispersal of larvae from protected spawning grounds (Carr and Reed, 1993; Bohnsack, 1998), migration of juveniles and adults (Shepherd and Brown, 1993; Russ and Alcala, 1996; McClanahan and Kaunda-Arara, 1997; Chapman and Kramer, 2000;

McClanahan and Mangi, 2000), and by providing a buffer against genetic change, altered sex ratios and other potential outcomes of selective fishing mortality (Bohnsack, 1992). Protected areas could also decrease the likelihood of stock collapse from unanticipated fishing mortalities, management errors, and environmental changes (Roberts, 1997; Dayton, 1998; Lauck et al., 1998). However, many putative benefits derived from modeling studies (e.g., Polachek, 1990; DeMartini, 1993; Man et al., 1995), have not been validated (Roberts and Polunin, 1991; Towns and Ballantine, 1993; Murray et al., 1999). Validation has been hampered by a lack of protected areas, especially of appropriate sizes and ecological composition, an inability to replicate sites and a general absence of baseline and long-term data to describe biological and ecological states both prior to and after the implementation of protection (Murray et al., 1999; Allison et al., 1998).

The use of marine area protection in fisheries management has developed only recently (Roberts and Polunin, 1991; Dugan and Davis, 1993; Rowley, 1994). Historically, the primary objective of most marine area protection has not been to enhance fisheries, but rather to assist conservation or non-fisheries use of the area or resource. Where fisheries were a concern, area protection has been typically used not to enhance but to control fishing and other extractive effort in cases in which enforcement by conventional methods was difficult (Bohnsack, 1998), or in areas where the potential effects of a fishery and environmental

variability on the ecosystem could not be determined (Roberts, 1997). At most, reserves have been thought to benefit successful co-existence of fishing and tourism that rely on a shared resource base (Jennings et al., 1995). However, area protection may constrict the area available for fishing, and support for such conservation measures may be lacking if there is little perceived or real spill-over of benefits to adjacent fishing communities (Johannes, 1978; Roberts and Polunin, 1991). Reserves may not realize their objectives if the legitimate needs of local communities are not considered (Allison, 1998; McClanahan, 1999).

In East Africa, reef fish comprise a major resource and form the basis of artisanal coastal fisheries in Kenya and Tanzania. Marine reserves were established in this region over 30 years ago, and National Marine Parks were first gazetted in Kenya in 1968 to protect some of the most spectacular reefs (and fishing grounds) on the East African coast (Fig. 3-1). The adjacent fisheries are virtually unmanaged and little is known about the impact of exploitation except that overall fish biomass typically declines on exploited reefs (McClanahan and Muthiga, 1988; McClanahan and Shafir, 1990). In particular, the relative densities, composition and movements of reef fishes in and across management boundaries are unknown, although recent studies have hypothesized that spill-over of fishes may be occurring from Kenyan marine parks to adjacent fished regions (McClanahan and Kaunda-Arara, 1997; McClanahan and Mangi, 2000). In the present study, we use trap catches and fish densities along visual

transects to examine the spill-over hypothesis by comparing fish numbers, catches and community structure inside, outside and across the boundaries of the two oldest marine parks in coastal Kenya. We also examine the dependence of gradients in fish density across park boundaries and into fished zones on reef structure and size, seasonal oceanographic characteristics and fishing intensity outside park boundaries.

4.3 Methods

4.3.1 Study sites

Kenyan marine parks provide coral reefs with total protection from extractive exploitation while adjacent areas designated as “reserves” receive limited protection and allow fishing, but only with “traditional” gear, mostly traps. The present research was done in Malindi (6.3 km²) and Watamu (10 km²) National Marine Parks, both created in 1968, and their adjacent fished reserves (Fig. 4-1). (Note that some jurisdictions use “reserve” to describe no-fishing areas, but we prefer the East African usage in which reserve implies controlled extraction). Malindi Park contains part of a continuous near-shore fringing reef and several patch reefs. The fringing reef is an erosional fossil located about 200 m from the high water mark that extends several kilometers from the park boundaries. A patch reef system is located within the park approximately 1 km from shore. The North reef, a flat of semi-fossil coral rock that is exposed at low tides, is the largest (2 x 1 km) patch reef within the park. Beds of the seagrass *Thalassondendron ciliatum* and isolated coral heads dominated by massive

Porites and *Galaxea spp.* occur on the upper edges of the east and south west-slopes of the North reef forming sites popular for tourist activities (Blom et al., 1985). The park also includes a submerged patch reef (Tewa Reef) on the south-eastern side of North Reef. In 1998, local lobbying by fishermen resulted in relaxation of the total fishing ban in this area of the park with some trap fishing being allowed up to 500 m inside the southern border particularly during the SE monsoon season. Malindi Park is surrounded by a marine reserve that has been fished for many years.

Watamu Marine Park is situated about 25 km south of Malindi Marine Park (Fig. 4-1). For much of the coast between the parks there is a fringing reef that occurs near-shore near Malindi and Watamu but is over 1 km from shore in the central region. This reef continues to bound Watamu Park, making the park a massive lagoon with conspicuous islands surrounded by patches of flat eroded inner reef. The shallow lagoon areas of the park are carpeted by seagrasses. The northern park border is located where the fringing reef meets the shore and forms a raised platform about 1 m above sea level. The park is bordered by two reserves to the south that include the Mida Creek tidal lagoon fringed by mangrove trees.

The two parks are extensively carpeted with seagrass beds that extend to adjacent fished sites. However, patches of sand and coral rubble break the continuity of these beds at various points. The water within the parks is generally

shallow at most places (~ 5 m at low tide), however, deep water patches (> 10 m at low tide) occur especially at Malindi Park that is traversed by a surge channel.

Coastal East Africa experiences two distinct meteorological and oceanographic seasons caused by the movement of the Inter-Tropical Convergence Zone (ITCZ) and the associated northeast (NE) and southeast (SE) monsoons (McClanahan, 1988). The SE monsoon season typically prevails from April to October and is characterized by high cloud cover, high wind energy and low solar insolation and temperatures. Oceanographic conditions during this season are characterized by cool water, a deep thermocline, high water-column mixing and wave energy, strong currents and low salinity. In contrast, the NE monsoon (November-March) brings warmer waters, a shallow thermocline, calm conditions and high salinity (McClanahan, 1988). This study covered the two monsoon seasons.

4.3.2 Fish trap catches

Traditional pentagonal shaped *Dema* traps commonly used in East African coastal fisheries were used in this study (e.g., Kaunda-Arara and Ntiba, 1997). *Dema* traps typically measure approximately 1.5 x 1.3 x 0.6 m high and are constructed of wooden frames meshed with bamboo rods and reeds and weighted with stones. The traps commonly used in Kenya have a maximum mesh size of approximately 4.5 cm, a single top-side funnel door through which

the fish enters, and an underside aperture for removing the catch. Traps are a popular fishing gear in the tropics because of their low cost, ease of maintenance and minimum labor requirements (Munro, 1983; Burnett-Herkes et al., 1988).

Trap fishing was conducted during the SE monsoon at Malindi from June to August, 2000 and at Watamu Marine Park from August to October, 2000. During the NE monsoon trap fishing was undertaken from December to February 2001 in both parks. The traps were laid along transects located at geometric intervals (0, 0.2, 0.4, 0.8, 1.6 and 3.2 km) from and parallel to the southern border of the parks. Traps were also fished on transects located approximately 1.4 and 5.8 km inside the Malindi and Watamu Park boundaries, respectively. At Malindi, traps were fished on the North and Fringing Reefs adjacent to the fished reserve to the south (Fig. 4-1). Traps were not fished north of either park because of the presence of raised reef platforms, few lagoons, and hence few fishable grounds. Sampling effort ranged from 7-18 days per transect during each season, the variability being caused by loss of traps to occasional rough seas or theft and the relative inaccessibility of some sites.

In order to assess annual variation in patterns of CPUE, a second year of trapping was done but only across the Malindi Patch reef. During the second year, trap fishing was carried out from June to August 2001 during the SE

monsoon season and from November to February 2002 during the NE monsoon season. Sampling effort ranged from 10-18 days per transect.

Each fishing event consisted of 2 transects fished with 4-6 traps for 3-4 days. Each trap was baited with approximately 1 kg of a mixture of green and brown benthic algae and mashed tissues of the mangrove gastropod *Terebralia palustris*, and fished for 24 h. Transect and trap positions were located using a Garmin GPS. The initial trap placement design was systematic with stations 20 to 30 m apart along each transect. However, preliminary trials showed a general decline of daily catches per trap, perhaps as a consequence of trap avoidance or local depletion (Fig. 4-2). Catches furthest from the park boundary declined the fastest. Subsequently, a random component was introduced into the systematic design. Station intervals were maintained at 20-30 m but the starting point for each fishing day was chosen haphazardly. This quasi-randomization of fishing location enhanced the likelihood that daily catches were independent samples without auto-correlation. During each fishing event, traps were hauled and catch emptied into a basin containing ambient temperature sea-water. All fish were identified to the lowest taxonomic level possible using field guides from Bock (1978), Randall (1992), Allen (1997), Lieske and Myers (1994), with difficult specimens confirmed using Smith and Heemstra (1998). The total length (cm) and body depth (mm) of each identified fish was estimated with a measuring board and a caliper, respectively. The minimum trappable sizes of 21 species of

fish were derived from a regression of body depth on total length. A body depth of 4.5 cm corresponding to the maximum mesh diameter of the *Dema* traps was used to estimate the minimum trappable length for each species. All fish were released alive with the exception of a few specimens that were taken to the laboratory for assessment of reproductive status and weight measurements.

Indices of relative density (RDD) and relative size (RSD) differences were derived for species caught both in the parks and the fished reserves as:

$$\text{RDD} = (\bar{C}_{\text{park}} - \bar{C}_{\text{Reserve}}) / (\bar{C}_{\text{park}} + \bar{C}_{\text{Reserve}}); \text{ and}$$

$$\text{RSD} = (\bar{S}_{\text{park}} - \bar{S}_{\text{Reserve}}) / (\bar{S}_{\text{park}} + \bar{S}_{\text{Reserve}})$$

where, \bar{C}_{park} and \bar{S}_{park} and \bar{C}_{Reserve} and \bar{S}_{Reserve} are the mean catch rates and sizes in the park and the reserve (Lechowicz, 1982; Chapman and Kramer, 1999). Index values range from -1 to $+1$, where positive values indicate higher park densities or greater relative size.

4.3.3 Fish visual census

Fish census inside the parks and in the reserves was done using a visual census technique (Sale and Douglas, 1981). Fish were normally counted along the trap transect lines. In order to avoid disturbance to traps, counts were normally conducted when traps were not fishing. Fish were counted from December 2000 to February 2001 (NE monsoon) along 8 and 7 transects at Watamu and Malindi, respectively. Sampling was alternated at bi-weekly intervals between the two

parks during each season and each transect was sampled once a month. During fish counting, an observer laid a 100-meter nylon twine weighted with lead weights on the reef substrate. Transect width was diver estimated at 2.5 m either side of the line, two reference markers placed at about 20 m interval from the starting point aided in estimation of correct transect width. The observer swam slowly within the 5 x 100 m belt carefully checking the recesses and overhangs, and recording individual fish to the family level and estimating fish size to the nearest 10-cm interval. Fish < 5 cm were not recorded. Due to high fish density and diversity within the parks, a discrete group censusing technique (Sale and Douglas, 1981) was used to count fish inside the parks, in which fish were counted in sequence starting with the more abundant family (e.g., Pomacentridae) and finishing with the less abundant group (e.g., Lethrinidae). Once the 100-m belt transect was counted, the transect line was rolled up and a starting point for a replicate line chosen randomly. No attempt was made to standardize time taken to sample each transect. A minimum of three replicate counts were carried per site during each sampling.

4.3.4 Fish trapability

The formulae of Miller and Hunte (1987) that estimates the “effective area fished” or catchability index was used to estimate the trappability or vulnerability of the species commonly caught in the *Dema* trap. This index (E) is derived as:

$$E \text{ (m}^2 \text{ haul}^{-1}\text{)} = c/f / D,$$

Where, c/f is the catch per trap haul and D is the density ($\#/500\text{m}^2$) of fish > 12 cm total length (average minimum trappable size of fishes) estimated by visual transects.

4.3.5 Habitat characteristics

Topographic complexity and substrate composition are known to affect fish abundance and distribution (Luckhurst and Luckhurst, 1978; Roberts and Ormond, 1987). Hence, we measured the substrate composition along the fished transects using a method modified from McClanahan and Mangi (2000). Starting at a point on one end of each transect, a concrete slab (20 X 20 cm) attached to a buoy was randomly dropped at approximately 10-20 positions around the point, for each drop, the substrate type (sand, rubble, algae, seagrass bed and corals) on which the slab fell was scored. A second focal point was then selected at an interval of about 20-30 m and the procedure repeated; sampling was stopped at a point on the furthest limit of the traps along the transect.

4.3.6 Fish Landing statistics

We also monitored and compared catch rates of fishermen operating at different sites from the two parks. Trained field assistants recorded daily fish landings at 4 sites (Watamu, Uyombo, Silversands and Mayungu) located at different distances from the two parks (Fig. 4-1). The total weight of fish landed, total length of each fish caught (or a random sample of each species landed), gear

type and fishing grounds were recorded for two weeks of each month from June 2000 to June 2001.

4.3.6 Model fit

Hypothetical relationships describing gradients in densities (CPUE) of commercially fished species across park boundaries under different dispersal conditions and near uniform fishing intensities are illustrated in Figure 4-3. We used a logistic decay function to describe how the proportion of mid-park mean fish density changes with distance across the park centers. The function can be written as:

$$Y = 1/(1 + \text{Exp}(\beta_0(\beta_1 - x))) \quad (1)$$

where, Y is the proportion of the mid-park densities (CPUE), β_0 and β_1 are the slope and the inflexion point of the curve, respectively, and "x" is the distance (km) from the park center. In order to estimate the standard error of the predicted values, Equation (1) was linearized (Neter et al., 1985) as:

$$Z = b + mx \quad (2)$$

where the parameters b and m represent $\beta_0\beta_1$ and $-\beta_0$ respectively, and Z is:

$$\ln [(1-Y)Y^{-1}] \quad (3)$$

The slope (β_0) of the density gradient from the center of the parks outward was used to test for spill-over. An assumption is that any density gradient results from rate of removals exceeding replacement from spill-over or emigration. In cases of fast spill-over and near-instantaneous re-dispersal over fished and non-

fished areas to a single density, no gradient results ($\beta_0 = 0$) and density equilibrium is attained (dispersal type I). A medium spill-over with moderate relative fishing mortality in the reserves would result in a gradient of catch rates from the border with slope > 1 (dispersal type II). In cases of slow spill-over relative to fishing mortality, this slope would increase and ultimately reach negative infinity (dispersal type III). These constructs are used to test for evidence of spill-over from the protected to fished regions under near constant fishing effort. The position of the inflexion point (β_1) relative to the park boundaries was also tested. If $\beta_1 \pm 2$ s.e.'s did not include the park boundary, the inflexion point was considered to differ significantly from the boundary. In cases in which the fitted model slopes were significant, the model was also fit at least 5 times to data in which densities were re-assigned to distances randomly to test if the results could have been determined by chance, given the low sample sizes. In no case did the results support a possibility that the reported results could have occurred by chance. As the model will likely be more meaningful with more spatial spread of fish densities within the parks (as in Watamu), the average of the two innermost fish density (CPUE and $\#/500 \text{ m}^2$) data in Malindi Park was used to interpolate the model inward to approximately a kilometer from the park center and used as the model intercept.

4.4 Results

4.4.1 Trap catches during 2000/2001 period at Watamu and Malindi Parks

4.4.2 Watamu Park

At Watamu during the NE monsoon, a total of 32 species were caught, of which thirteen (41%) were common to both park and reserve (Table 4-1). Of these thirteen species, 9 had higher CPUE inside the park. In contrast, the commercially important whitespotted rabbitfish, *Siganus sutor*, had higher CPUE in the reserve. The dominant species both inside and outside the park were the commercially important emperors (*Lethrinus sanguenius* and the sky emperor *L. mahsena*), and *S. sutor* that together comprised >80% of the catch by number. During the SE monsoon season, 21 species were caught at Watamu of which 9 (43%) were common to park and reserve (Table 4-2). Of these nine species, five had higher CPUE inside the park, including the goldspotted sweetlip, *Gaterin flavomaculatus* and *S. sutor*. Four species had higher CPUE in the reserve (Table 4-2).

4.4.3 Malindi Park

At Malindi during the NE monsoon, a total of 28 species were caught, of which 17 (68%) were common to the park and reserve (Table 4-3). For 10 of these seventeen species, CPUE did not differ significantly across the park boundary. However, five species, including the abundant (>80% of catch) *L. mahsena* and *S. sutor* had significantly higher CPUE inside the park. The seagrass parrotfish,

Leptoscarus vaigiensis, and the black spot snapper, *Lutjanus fulviflamma*, had significantly higher CPUE outside the park (Table 4-3). During the SE monsoon, 21 species were caught in Malindi, of which 16 (76%) were common to park and reserve (Table 4-4). *S. sutor* was the predominant catch. Only 2 species (*Leptoscarus vaigiensis* and *Parupeneus barberinus*) had higher CPUE outside the park while 14 species, including *S. sutor* had higher CPUE inside the park (Table 4-4).

4.4.4 CPUE gradients

In Watamu Park, total catch declined outside the park boundary in both seasons (slopes β_0 of -0.7 and -1.2 , $p < 0.05$, during the NE and SE monsoon seasons respectively, Table 4-5 and Fig.4-4e), which fits an overall model of medium to low fish spillover (Type II and III) across the park boundary. Catches were higher in the NE monsoon season (Fig.4-4e). However, these results masked the different results for various species. Of the 3 dominant species in both the research catch and commercial fishery, *S. sutor* showed a Type III response during the SE monsoon ($\beta_0 = -0.84$, Table 5 and Fig.4-4a), However, the species had higher abundance in the reserve during the NE monsoon and there was no evidence of density decay at the boundary. The emperors had higher densities within the park during the NE monsoon with more even densities across the reserve during this season (Fig. 4-4bandc). *L. sanguineus* showed a particularly steep Type III gradient during the NE monsoon ($\beta_0 = -1.61$, Fig. 4-4c).

Models of total catch at Watamu had inflexion points during the NE (at 6.4 km) and SE (at 4.6 km) monsoons that did not differ from the park boundary (at 5.8 km; $p's > 0.05$) (Fig. 4-4e and Table 4-5). All species with significant decay slopes had inflexion points that did not differ from the park boundary.

At Malindi, the decline in CPUE for all species combined indicated a weak Type III gradient during both seasons from the patch reefs (NE monsoon, β_0 : -0.78; SE monsoon, β_0 : -0.88; Fig. 4-5f) and a similar gradient during the SE monsoon for the fringing reef (β_0 : -0.84 Table 4-5 and Fig. 4-5g). Of the commercially important species, *S. sutor* showed a Type II response during both seasons with high CPUE outside the park during the SE monsoon (NE monsoon, β_0 : -0.45; SE monsoon, β_0 : -0.53; Fig. 4-5d and Table 4-5), while, *L. mahsena* showed a more truncated (Type III decay) CPUE across the park (β_0 : -1.05, Fig. 4-5a). Models of total catch of all species in Malindi patch reef had inflexion points that differed from the park boundary in both seasons. The inflexion point of *S. sutor* density was less distinct but inside the park during the NE monsoon and at the park boundary in the SE monsoon (Fig. 4-5d and Table 4-5). A comparison of total catch at the edge of both reef types showed that CPUE was significantly greater at the fringing reef border (12 fish /trap/day \pm 7.02) than at the border of the patch reef portion of the park (3.9 fish/trap/day \pm 1.0; Fig. 5) during the NE monsoon.

4.4.5 Trapability

Trapability ($\text{m}^2 \text{ haul}^{-1}$) of species showed differences between seasons, however, overall mean trappability did not differ significantly between seasons (Mann-Whitney $U=85.5$, $d.f.=12,12$, $p>0.05$, Table 4-6). Of the twelve species for which trapability could be compared between seasons, 9(75%) had higher trapability during the NE monsoon. *L. mahsena* had a particularly high trapability (2.594) during the NE monsoon, while the commercially important *S. sutor* had a higher trapability (0.153) during the SE monsoon season (Table 4-6).

4.4.6 Species Diversity

The diversity (\approx richness) of trappable species shows a general decline from within the parks into the reserves in both parks (Fig. 4-6). At Watamu, the decline in diversity indicated weak Type I and II gradients during the NE and SE monsoons respectively (β_0 : -0.41, NE and -0.64, SE), with indistinct inflexion points. At Malindi, diversity showed a sharp decline (Type III) off the fringing reef border during both seasons (β_0 : -1.52, NE and -3.75, SE, Fig.4-6b) and a medium decline off the patch reef that was significant during the NE monsoon (β_0 : -0.32, Fig.4-6c). At both Malindi reef types, diversity was greater during the NE monsoon at most sites. However, at Watamu, there was no significant difference in diversity between seasons within the park, but a higher diversity outside the park during the NE monsoon.

4.4.7 Fish Size

The mean length of several species was greater inside than outside the parks (Table 4-7). Of the twelve species occurring across the boundary at Malindi, five (42%) had greater mean sizes on the patch reef inside the park (model p 's < 0.05). However, the seagrass parrotfish and *S. sutor* were larger outside the park (p 's < 0.05), although *S. sutor* caught on the fringing reef inside the park were larger than those caught outside the park off this reef ($p < 0.05$). At Watamu, three (33%) of the nine species occurring across the boundary were significantly larger inside the park. *S. sutor*, *L. mahsena* and the seagrass parrotfish (*Leptoscarus vaigiensis*) had greater mean lengths outside the park but the differences were not significant ($p > 0.05$).

The size frequency distributions of *S. sutor* compared between the parks and reserves show different seasonal patterns (Fig. 4-7). At Malindi patch reef, *S. sutor* size frequency distribution differed between the park and the reserve during the NE monsoon season ($\chi^2 = 80.7$, $\chi^2_{(0.05) 8, 1} = 15.5$, $p < 0.05$) when more small-sized fish (< 19 cm) were found inside the park (Fig. 3-7c). However, large fish (> 20 cm) were also common in the reserve. Size frequency distribution across the fringing reef border differed only during the SE monsoon ($\chi^2 = 25.3$, $\chi^2_{(0.05) 6, 1} = 12.1$, $p < 0.05$) when more large fish (> 23 cm) were found inside the park (Fig. 4-7b). In Watamu there were no consistent differences in size frequencies between the park and reserve in both seasons ($p > 0.05$), although more large fish

(> 26 cm) were found outside the park during the SE monsoon (Fig. 4-7f) and there were more small fish (< 19 cm) outside the park during the NE monsoon (Fig. 4-7e).

L. mahsena had a greater proportion (> 60%) of small-sized individuals (<19 cm) outside both parks (Fig. 4-8). Most fish outside the parks were immature (≥ 20 cm).

The mean minimum trappable sizes of *S. sutor* and *L. mahsena* are 12.9 ± 1.2 and 13.4 ± 0.8 cm, respectively, which is slightly higher than the derived mean trappable size (12.7 ± 2.2 cm) for all species trapped by the *Dema* (Table 4-8). *Leptoscarus vaigiensis*, *Parupeneus barberinus*, *Acanthurus nigrofuscus* and *Gaterin flavomaculatus* had higher minimum trappable sizes.

4.4.8 Trap catches during 2001/2002 period at Malindi Park

During the second year of sampling across the Malindi patch reef, CPUE for the total catch was higher during the NE monsoon (Fig. 4-9f). However, the gradient of the CPUE for the total catch was shallower (but not significant) during the NE monsoon ($\beta_0 = -0.07$) but more steep and significant during the SE monsoon ($\beta_0 = -0.9$, $P < 0.05$) (type III dispersal pattern, Table 4-9). The pattern of total catch from the park center had inflexion points during the NE (0.79 km) and SE (0.48 km) monsoons that did not differ from the park boundary (1.4 km from park

center, $p > 0.05$). Of the commercially important species, *S. sutor* showed higher catches during the NE monsoon season (Fig. 4-9a), however, CPUE gradient was more truncated (but not significant) during the SE season ($\beta_0 = -0.89$, Table 4-9) but shallower and significant during the NE monsoon ($\beta_0 = -0.40$, $p < 0.05$) corresponding to type II dispersal pattern. *L. mahsena* exhibited CPUE gradients that were more truncated (type III dispersal pattern) but not significant during both seasons (Fig. 4-9b). Other species, in particular the seagrass parrotfish *Leptoscarus vaigensis*, had CPUE that appeared to be higher outside the park especially during the NE monsoon.

4.4.9 Fish visual census

A comparison of fish densities censused across the park boundaries showed higher densities inside the parks for most families (Tables 4-10 and 4-11). At Watamu Park, densities were orders of magnitude higher inside the park in both seasons except for the Labridae and Siganidae during the NE monsoon season (Table 4-10). Relative density differences were positive and highest for the Lethrinidae during both seasons. At Malindi Park, families showed significantly higher densities within the park during both seasons. For the more commercial families, densities were significantly higher inside the park during both seasons for the Siganidae, while the Lethrinidae had significantly high densities inside the park during the SE monsoon (Table 4-11).

Densities of most families showed a sharp decline at the park boundaries indicating a type III response of density gradient with distance (Fig. 4-10 and 11). At Watamu Park, the gradient in densities of all families counted was steep in both seasons (NE, $\beta_0 = -0.77$; SE, $\beta_0 = -0.75$) and the inflexion point of the pattern of change of density occurred significantly inside the park in both seasons (NE=1.64 km, and 1.31km, Table 4-12 and Fig. 4-10). Family specific patterns were also evident. The Siganidae had a density gradient that was not significant in both seasons. However, higher densities occurred inside the park and in the reserve during the SE and NE monsoons, respectively. In contrast, the Lethrinidae, had a significant but more truncated density gradient (type III dispersal) during the SE monsoon (Table 4-12 and Fig.4-10c). The Labridae and Pomacentridae showed a pattern that was less truncated at the boundary especially during the NE monsoon.

At Malindi Park, total density gradients across the patch reef was steep and significant in both seasons (NE, $\beta_0 = -0.88$; SE, $\beta_0 = -0.76$, Table 4-12). The inflexion point of the pattern of change of total densities was significantly inside the park in both seasons (NE = 0.83 km and SE=0.42 km from park center). Among the families counted, the Siganidae showed a density gradient that was steep in both seasons (Type III dispersal) with the inflexion point significantly inside the park during the SE monsoon ($\beta_1 = 0.41$ km from park center). The densities of the Lethrinidae decreased more abruptly at the park boundary

especially during the SE monsoon indicating a Type III dispersal pattern (Fig. 4-11c). Similarly, the Labridae had a significant density gradient corresponding to type III dispersal pattern during the SE monsoon.

4.5.0 Habitat characteristics

The Malindi and Watamu Marine Parks enclose lagoons with low and uniform topographic complexity dominated by a mosaic of seagrass beds interspersed with sand, algae, live corals and coral rubble of varying cover (Table 4-13).

There was no evidence of a trend or pattern in benthic cover categories with distance from either park. However, live corals are concentrated within the parks and have only patchy distribution outside the parks.

4.5.1 Commercial fish landings

Although there were significant differences in CPUE among sites (ANOVA, $p < 0.05$) for all gear types except spear fishing (Table 4-14), there was no significant correlation between CPUE and mean distance from the parks for any gear type (Spearman's (r_s) range 0-0.03, all $p > 0.05$). Fishermen south of the parks tended to have higher landings than those to the north using the same gear. For example, trap fishermen just south of the Watamu Park boundary (Uyombo, Fig. 4-1) landed equal quantities of fish (5.1kg/trap) as those that fished 3-4 km south of Malindi Park (Mayungu site, Fig. 4-1). Both these sites had higher landings than at Watamu landing that is close to Watamu Park but to

the north. Interestingly, net and line fishermen at Watamu landing, who tend to be more mobile, landed more fish (23 kg / fisherman) than all the fishermen at other sites. No significant correlations were found between catch of different gear types among sites except for lines and nets (Spearman's (r_s) = 1.00, $p < 0.05$).

4.6 Discussion

Our data indicated that the density of most fish species was higher inside than outside both the Malindi and Watamu Parks. For some species, such as the emperors (*Lethrinus spp.*) and grunts (*Gaterin flavomaculatus*), especially at Watamu, density differences were large, up to an order of magnitude. These differences are thought to result from increased protection from fishing and also perhaps habitat protection within the Parks. We noted that live corals were concentrated within the parks. It was not possible to directly test whether these differences were attributed to the existence of the parks (historical data is lacking for a before-after comparison). However, the somewhat larger density differences at Watamu, where no fishing is allowed within the park boundaries, in contrast to Malindi where some fishing is allowed within the south-east border, supports the notion that the protection afforded by the parks is the primary cause of the observed differences. It is important to note that the densities of some species were higher outside than inside the parks, and there were differences between the areas. In the case of *S. sutor*, catch rates were much higher outside

the park at Watamu especially during the NE monsoon, but not at Malindi. We are uncertain of the cause of this difference, but it likely relates to the mobility and habitat preferences of this species. However, in most cases where CPUE outside the parks was equal to or greater than inside the parks, the differences were not great, and in some cases may be spurious. For example, the CPUE of the seagrass parrotfish did not differ inside and outside either park, but this species may be able to squeeze out of traps like the *Dema* (Robichaud et al., 1998). In general, but not for all species, our results are consistent with earlier reports that fish densities are higher within these parks than in adjacent areas (McClanahan and Muthiga, 1988; Watson and Ormond, 1996).

Seasonal differences were important to the observed variation in CPUE for some species. In particular, *S. sutor* CPUE was 3 times as high at Malindi within the park than in the reserve in both seasons, but CPUE was twice as high during the SE than NE monsoon within each site. However, we cannot generalize this observation, because at Watamu, CPUE was higher within the park during the SE monsoon, but higher outside the park during the NE season, and overall CPUE did not differ inside and outside the park. It is apparent that local interactions between seasonal oceanographic influences, local reef effects, and species differences must be considered to understand the impacts of protected areas on fisheries.

The shape of the fish density gradient from within the parks and across the boundaries to the adjacent reserves was overall consistent with Type II (moderate spillover) and III (minimal spillover) models for Watamu and Malindi respectively. The inflexion points include the park border at Watamu but occurred within the park at Malindi, with higher CPUE during the NE monsoon. This result is further evidence that park protection is a cause of the differences between the densities observed inside and outside the parks, because fishing has been allowed 500 m inside the southern boundary of Malindi. However, it is also important to point out that the densities of some species did not exhibit any decay across the boundary, and fit a Type I model (zero slope), while other species like the emperors exhibited a very steep Type III decay at the park boundaries. In particular, the case of the *S. sutor* is of interest, as this is the most important commercial species in the region (Kenya Fish. Dept., 1999). At Malindi, the slope of the density gradient for *S. sutor* was significant but shallow during both seasons, indicating a Type I decay pattern. The inflexion point was within the park in the NE season but at the park border during the SE season. At Watamu, the densities outside the park were actually higher and there was no decay across the border during the NE season (if anything, a negative decay). There was a significant decay at Watamu during the SE season. These seasonal differences suggest high mobility in this species, and densities may at times be as high or higher outside the parks than inside as a result of fish movements. In contrast, our data for the other key commercial species, the

emperors, suggest less mobility and steeper and more seasonally constant density gradients corresponding to the park boundaries at both Watamu and Malindi.

Fishing pressure may be expected to influence density gradients. However, the shallow gradient in CPUE of *S. sutor* across the Malindi Park during the SE monsoon, when the southern border is heavily fished (Kaunda-Arara, pers. obs.), further supports the notion that this species is highly mobile and is potentially capable of spilling over. Modeling studies have suggested that indications of spill-over from marine protected areas is likely to be higher under conditions of high fishing pressure (Polacheck, 1990; Nowlis and Roberts, 1997). Our data are inadequate to test this prediction, but any effect appears to be species specific and also perhaps dependent on season and reef topography.

Although most species (75%) had higher trappability during the SE monsoon, overall there was no seasonal difference in mean trappability. However, trappability is likely to be affected by species behaviour and may not reflect the true vulnerability or differences in abundance between species. Determination of trappability is relatively easy for resident and easily observable species, however, for wide ranging species or species that are difficult to observe (e.g., *Leptoscarus vaigiensis* and most Serranidae) trapability indices are difficult to estimate and can be biased.

Species diversity decayed sharply at the borders of the Watamu Park and the fringing reef in Malindi in both seasons (factor of 5 within a few km), and less sharply at the patch reef border of Malindi Park. Inflexion point was more distinct on the patch reef at Malindi. Interestingly, there were some species caught outside the parks that were not caught inside the parks. However, there was no evidence that fundamental habitat differences could account for either these differences or more importantly the decline in species diversity outside the parks. There was also an increasing number of low trophic level species such as *Arothron spp.*, *Canthigaster spp.*, *Epibulus sp.*, *Heniochus spp.*, and *Pomacentrus spp* in the fished site adjacent to Watamu Park, especially during the NE monsoon season. Fishing pressure is intense during the calm NE monsoon season, and most fishers increase the number of traps and boats and fishing effort. We suggest that the presence of a higher proportion of low trophic level planktivores and algeavores may be a result of local overfishing of higher trophic level species. Similar results showing changes in community structure attributed to fishing have been found for fished reefs in Jamaica (Koslow et al., 1988) and the Seychelles (Jenning et al., 1995). These may be local cases of fished down food webs (Pauly et al., 1998).

Our data indicated that for many species, larger individuals and larger mean sizes occurred inside than outside the parks. This result suggests an additional effect of the parks, most likely on fish survivorship and resultant size (there is no

evidence of or reason to suspect increased growth rates within the parks). However, for the most important commercial species, *S. sutor*, this general result did not hold at either of the parks. One other species, the seagrass parrotfish, was larger outside than inside the parks. These results are not intuitive given that these species are relatively heavily exploited and fishing has typically been thought to result in decreases in size of such fishes in other areas (e.g., Koslow et al., 1988; Jennings et al., 1995) and in Kenya (McClanahan and Muthiga, 1988; Watson and Ormond, 1996). However, our results indicate a significant proportion of smaller *S. sutor* within the parks during both seasons. The most likely explanation for these findings is that the parks provide protection for this species and delay recruitment to the adjacent fisheries. An alternative hypothesis that there is selective cropping of smaller fish seems unlikely (it is typically the opposite in most fisheries). The occurrence of high proportions of small sized *L. mahsena* in the reserves is consistent with the effects of fishing on population structure.

The commercial landings data indicate that CPUE differed among gear types and landing sites but was not dependent on landing site distance from the park. If we compare only the commercial traps, that were identical to our research traps (we employed local fishers to build and assist in the deployment of the research traps to lessen any bias), we found no difference in CPUE with distance of landing sites from park boundaries. This result appears to be at odds with the results of

the research traps. The simplest explanation for this is that the commercial landing sites did not represent the fishing sites in terms of distance from the parks (a common bias in commercial fisheries landing statistics). The interpretation of these data is also confounded by direction, as it appears that fixed gear landings are higher south of the parks independent of distance. Perhaps the most important aspect of these data is that all of these very active landing sites are close to the parks (within 4 km). We do not have data at further distances from the parks.

During the second year of sampling across the Malindi patch reef, the overall CPUE was higher during the NE monsoon as was in the first year, however, the gradient of the pattern of total CPUE was only significant during the SE monsoon as opposed to the first year when both seasons had significant trends. CPUE was more truncated at the park boundary during the SE monsoon (Type III dispersal), compared to the first year when catches were equal in the reserve in both seasons. *S. sutor* had higher CPUE across the park boundary in the NE monsoon during the second year as opposed to the SE monsoon in the first year. Fishing intensity remained the same between years (Kaunda-Arara, pers. obs) and although the reasons between inter-annual seasonal variations are not apparent, differences in recruitment patterns may be significant between years. *L. mahsena* maintained a sharp decline in CPUE at the park boundary during the second year, reflecting a consistent type III dispersal pattern in this species.

Fish densities as determined by visual census were significantly higher within the parks and the density gradients across park boundaries were more truncated than reflected by the CPUE data. The large differences between fish counted in and out of the parks can be attributed to fishing mortality outside the parks, however, the shy and jittery nature of fishes (increased flight distance) in the reserve may also have biased the differences between the sites. Despite this potential bias, some families (e.g., Labridae and Pomacentridae) had high seasonal abundance in the reserves, especially at Watamu, thus supporting the lack of significant difference in CPUE of some species of these families across the park boundaries. Furthermore, the higher visual counts of *S. sutor* in the reserves especially during the NE monsoon is consistent with the trap catches.

Our findings are instructive to the design of areas to be protected from fishing or other extractive activities. Park design relative to reef structure had a major influence on fish spill-over to the adjacent fished reserve. More spill-over was suggested at the fringing reefs at Malindi and Watamu than from the patch reef at Malindi. The discontinuity in habitat type caused by the largely patchy nature of the reefs at Malindi may contribute to more restricted movements of fish there. Studies elsewhere have also shown limited movement of fish from patch reefs (Ratikin and Kramer, 1999; Chapman and Kramer, 2000; Munro, 2000). However, such discontinuity may not be perceived in the same way by all species (Wiens et al., 1985), and more mobile species could potentially traverse

the sand and deep water habitats that separate reef patches (Stamps et al., 1987; Beinstein et al., 1991; Ratikin and Kramer, 1999). The best example at Malindi and Watamu is *S. sutor*.

Spillover was species specific. Many species showed little evidence of spillover from either Park or reef type in either season. For the two most important commercial fishes, *L. mahsena* and *S. sutor*, very different patterns were evident. The emperors (particularly *L. mahsena*) exhibited little evidence of dispersal, with very low CPUE outside the parks and a steep Type III density decay at the park borders. In contrast, the Type I model that appeared to best fit *S. sutor*, especially during the NE monsoon season in Watamu, suggests that this species disperses from the parks sufficiently rapidly to equalize densities across fished and non-fished areas. Hence spill-over from a protected area will depend on species specific behaviour, particularly with respect to home range and seasonal migration patterns. The importance of *S. sutor* to the commercial fisheries may be dependent on its distributional behaviour and resultant availability to the fisheries as well as its abundance and favour as an edible species.

It is also noteworthy that reef structure and topography may influence spillover from marine protected areas. The raised reed platform at northern border of Watamu Park precludes fishing for more than a km from the border. However, the southern border is fished heavily. Catch rates to the south reserve that is

contiguous with the park (Uyombo beach, Table 3-14) are correspondingly higher than to the north (Watamu beach). A similar result was found at Mombasa Marine Park south of Watamu on the Kenya coast (McClanahan and Mangi, 2000).

In conclusion, we have shown that in the two oldest marine parks in coastal Kenya (established in 1968), densities of most species and species diversity is much higher inside the parks than in adjacent fished reserves. The spill-over of adult fish is limited for most species from the patch reefs, higher from fringing reefs. However, there are important exceptions to these generalities. Seasonality influences spillover. Most importantly, some species may spill-over consistently as fishable adults (e.g., *S. sutor*), and protection of even small areas of patch reefs may sustain productivity in these species. Hence, given that the *S. sutor* is the most important commercial fish in the area, the direct effects of the parks on sustaining adjacent fisheries by spill-over of adults may be considerable.

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Table 4-1: Mean catch rates (#/trap/day) and relative density differences (RDD) of trappable species of reef fish in Watamu Marine Park and the adjacent fished reserve during the NE monsoon season. $RDD = (density_{PARK} - density_{RESERVE}) / (density_{PARK} + density_{RESERVE})$; t : two tailed t-test ($t_{0.05(2), df}$) for means with unequal variance, p : test probability. (-) denotes species not trapped at site.

	Park	Reserve			
Species	Catch (\pm s.d.)	Catch (\pm s.d.)	RDD	t	p
<i>Abudefduf sexfasciatus</i>	0.02 (0.07)	0.08 (0.22)	-0.56	-0.91	0.38
<i>Acanthurus dussumieri</i>	0.26 (0.33)	0.15 (0.39)	0.25	0.37	0.71
<i>Calotomus carolinus</i>	0.16 (0.32)	0.08 (0.22)	0.33	1.40	0.17
<i>Leptoscarus vaigiensis</i>	0.09 (0.19)	0.97 (0.94)	-0.82	-2.01	0.03
<i>Gaterin flavomaculatus</i>	0.90 (1.26)	0.02 (0.07)	0.95	2.87	0.01
<i>Cantherhines pardalis</i>	0.09 (0.19)	0.15 (0.18)	-0.27	-0.79	0.43
<i>Lethrinus mahsena</i>	2.68 (0.68)	1.09 (2.05)	0.42	2.16	0.04
<i>Lethrinus nebulosus</i>	0.42 (0.56)	0.04 (0.09)	0.84	2.81	0.01
<i>Lethrinus sanguineus</i>	3.10 (2.74)	0.18 (0.36)	0.89	5.33	0.001
<i>Lutjanus fulviflamma</i>	0.08 (0.12)	0.06 (0.22)	0.14	0.29	0.77
<i>Parupeneus barberinus</i>	0.22 (0.43)	0.06 (0.16)	0.56	0.56	0.58
<i>Scarus ghobban</i>	0.51 (1.62)	0.12 (0.07)	0.62	1.28	0.02
<i>Siganus sutor</i>	0.70 (0.57)	2.83 (2.42)	-0.60	-3.54	0.002
<i>Macolor niger</i>	0.03 (0.12)	-	-		
<i>Parupeneus rubescens</i>	0.09 (0.24)	-	-		
<i>Sufflamen fraenatus</i>	0.10 (0.16)	-	-		
<i>Acanthurus nigrofuscus</i>	0.01 (0.04)	-	-		
<i>Acanthurus leucosternon</i>	0.02 (0.07)	-	-		
<i>Balistapus undulatus</i>	0.29 (0.36)	-	-		
<i>Calotomus viridescens</i>	0.09 (0.30)	-	-		
<i>Cheatodon auriga</i>	0.05 (0.11)	-	-		
<i>Cheilinus chlorourus</i>	0.26 (0.59)	-	-		
<i>Cheilinus trilobatus</i>	0.03 (0.09)	-	-		
<i>Halichoeres hortulanus</i>	0.07 (0.14)	-	-		
<i>Lethrinus ramak</i>	0.08 (0.24)	-	-		
<i>Arothron sp</i>	-	0.05 (0.17)	-		
<i>Canthigaster sp</i>	-	0.06 (0.20)	-		
<i>Diodon sp</i>	-	0.04 (0.09)	-		
<i>Epibulus sp</i>	-	0.02 (0.05)	-		
<i>Heniochus sp</i>	-	0.04 (0.05)	-		
<i>Pomacanthus sp</i>	-	0.12 (0.30)	-		
<i>Pomacentrus sp</i>	-	0.04 (0.14)	-		

Table 4-2: Mean catch rates (catch/trap/day) and relative densities differences (RDD) of trappable species of reef fish in Watamu Marine Park and the adjacent fished reserve during the SE monsoon season. $RDD = (density_{PARK} - density_{RESERVE}) / (density_{PARK} + density_{RESERVE})$; t: two tailed t-test ($t_{0.05(2) df}$) for means with unequal variance, p: test probability. (-) denotes species not trapped at the site.

Species	Park	Reserve	RDD	t	p
	Catch (\pm s.d.)	Catch (\pm s.d.)			
<i>Acanthurus dussumieri</i>	0.06 (0.15)	0.13 (0.18)	- 0.38	-1.01	0.32
<i>Calotomus carolinus</i>	0.07 (0.21)	0.09 (0.17)	- 0.14	-2.29	0.77
<i>Cantherhines pardalis</i>	0.11 (0.14)	0.26 (0.52)	- 0.39	-0.87	0.40
<i>Gaterin flavomaculatus</i>	0.65 (0.80)	0.10 (0.23)	0.73	0.48	0.02
<i>Lutjanus fulviflamma</i>	0.06 (0.15)	0.07 (0.13)	- 0.09	-0.24	0.81
<i>Leptoscarus vaigiensis</i>	0.06 (0.13)	0.03 (0.11)	0.32	0.65	0.52
<i>Lethrinus mahsena</i>	0.14 (0.27)	0.06 (0.21)	0.34	0.70	0.49
<i>Lethrinus sanguineus</i>	0.85 (0.89)	0.44 (0.60)	0.32	1.36	0.19
<i>Siganus sutor</i>	2.76 (1.92)	1.25 (1.24)	0.38	2.32	0.02
<i>Lethrinus nebulosus</i>	0.06 (0.15)	-	-		
<i>Scarus sordidus</i>	0.02 (0.08)	-	-		
<i>Sufflamen fraenatus</i>	0.13 (0.28)	-	-		
<i>Abudefduf sexfasciatus</i>	0.01 (0.05)	-	-		
<i>Cheilinus trilobatus</i>	0.13 (0.25)	-	-		
<i>Cheilinus chlorourus</i>	0.29 (0.35)	-	-		
<i>Canthigaster sp</i>	0.02 (0.08)	-	-		
<i>Balistaphus undulatus</i>	0.06 (0.15)	-	-		
<i>Naso hexacanthus</i>	-	0.02 (0.06)	-		
<i>Pomacanthus sp</i>	-	0.02 (0.04)	-		
<i>Siganus luridus</i>	-	0.03 (0.08)	-		
<i>Heniochus sp</i>	-	0.02 (0.06)	-		

Table 4-3: Mean catch rates (catch/trap/day) and relative density differences (RDD) of trappable species of reef fish in Malindi Marine Park and the fished adjacent reserve during the NE monsoon season. $RDD = (\text{density}_{\text{PARK}} - \text{density}_{\text{RESERVE}}) / (\text{density}_{\text{PARK}} + \text{density}_{\text{RESERVE}})$; t: two tailed t-test ($t_{0.05(2) \text{ df}}$) for means with unequal variance, p: test probability. (-) denotes species not trapped at the site.

Species	Park	Reserve	RDD	t	p
	Catch (\pm s.d.)	Catch (\pm s.d.)			
<i>Acanthurus dussumieri</i>	0.41 (0.49)	0.33 (0.89)	0.11	0.36	0.72
<i>Balistapus undulatus</i>	0.51 (0.49)	0.02 (0.26)	0.94	4.72	0.001
<i>Calotomus carolinus</i>	0.18 (0.19)	0.20 (0.06)	-0.06	-0.33	0.74
<i>Leptoscarus vaigiensis</i>	0.10 (0.18)	0.71 (0.89)	-0.75	-3.19	0.004
<i>Scarus ghoban</i>	0.01 (0.05)	0.15 (0.34)	-0.86	-1.87	0.07
<i>Cheatodon auriga</i>	0.04 (0.15)	0.11 (0.32)	-0.46	-0.95	0.35
<i>Cheilinus chlorourus</i>	0.23 (0.41)	0.01 (0.05)	0.91	2.48	0.02
<i>Cheilinus trilobatus</i>	0.01 (0.02)	0.02 (0.08)	-0.66	-1.07	0.29
<i>Epinephelus tauvina</i>	0.09 (0.13)	0.02 (0.08)	0.60	2.22	0.03
<i>Gaterin flavomaculatus</i>	0.26 (0.12)	0.12 (0.21)	0.37	1.40	0.17
<i>Lethrinus mahsena</i>	4.07 (4.85)	0.83 (1.22)	0.66	3.04	0.005
<i>Lethrinus sanguienus</i>	0.10 (0.29)	0.16 (0.31)	-0.23	-0.67	0.50
<i>Lutjanus fulviflamma</i>	0.02 (0.08)	0.11 (0.18)	-0.73	-2.26	0.03
<i>Naso hexacanthus</i>	0.13 (0.24)	0.22 (0.52)	-0.24	-0.68	0.49
<i>Parupeneus macronema</i>	0.03 (0.08)	0.03 (0.16)	-0.05	-0.08	0.93
<i>Siganus luridus</i>	0.04 (0.10)	0.11 (0.23)	-0.46	-1.29	0.20
<i>Siganus sutor</i>	4.22 (4.30)	1.62 (1.19)	0.44	2.73	0.01
<i>Cephalopholis argus</i>	0.16 (0.20)	-	-	-	-
<i>Epinephelus longispinus</i>	0.01 (0.05)	-	-	-	-
<i>Epinephelus merra</i>	0.07 (0.13)	-	-	-	-
<i>Gaterin gaterinus</i>	0.06 (0.27)	-	-	-	-
<i>Halichoeres hortulanus</i>	0.03 (0.08)	-	-	-	-
<i>Lutjanus bohar</i>	0.01 (0.05)	-	-	-	-
<i>Acanthurus nigrofuscus</i>	0.05 (0.12)	-	-	-	-
<i>Siganus stellatus</i>	0.02 (0.09)	-	-	-	-
<i>Scarus strongylocephalus</i>	0.01 (0.03)	-	-	-	-
<i>Calotomus viridescens</i>	0.07 (0.17)	-	-	-	-
<i>Cephalopholis argus</i>	0.16 (0.21)	-	-	-	-

Table 4-4: Mean catch rates (catch/trap/day) and relative densities differences (RDD) of trappable species of reef fish in Malindi Marine Park and the fished adjacent Reserve during the SE monsoon season. $RDD = (\text{density}_{\text{PARK}} - \text{density}_{\text{RESERVE}}) / (\text{density}_{\text{PARK}} + \text{density}_{\text{RESERVE}})$; t: two tailed t-test ($t_{0.05(2) \text{ df}}$) for means with unequal variance, p: test probability. (-) denotes species not trapped at the site.

Species	Park	Reserve	RDD	t	p
	Catch (\pm s.d.)	Catch (\pm s.d.)			
<i>Acanthurus nigrofuscus</i>	0.04 (0.10)	0.03 (0.12)	0.07	0.11	0.91
<i>Balistapus undulatus</i>	0.21 (0.25)	0.01 (0.04)	0.94	2.01	0.01
<i>Calotomus carolinus</i>	0.04 (0.10)	0.03 (0.15)	0.16	0.25	0.81
<i>Leptoscarus vaigiensis</i>	0.21 (0.40)	0.34 (0.46)	-0.24	-0.77	0.47
<i>Scarus ghobban</i>	0.04 (0.10)	0.03 (0.15)	0.16	0.25	0.81
<i>Chaetodon auriga</i>	0.08 (0.20)	0.03 (0.09)	0.47	0.63	0.56
<i>Cheilinus trilobatus</i>	0.13 (0.21)	0.02 (0.09)	0.68	1.17	0.29
<i>Cheilinus chlorourus</i>	0.08 (0.20)	0.04 (0.14)	0.39	0.54	0.60
<i>Chelio inermis</i>	0.04 (0.10)	0.02 (0.08)	0.40	0.55	0.60
<i>Gaterin flavomaculatus</i>	1.13 (1.61)	0.18 (0.32)	0.72	1.43	0.02
<i>Lethrinus elongatus</i>	0.08 (0.20)	0.004 (0.03)	0.89	0.94	0.38
<i>Lethrinus mahsena</i>	0.58 (0.63)	0.01 (0.06)	0.97	2.25	0.04
<i>Lethrinus sanguineus</i>	0.42 (0.72)	0.02 (0.10)	0.92	1.36	0.02
<i>Parupeneus barberinus</i>	0.04 (0.10)	0.06 (0.14)	-0.14	-0.31	0.77
<i>Siganus luridus</i>	0.08 (0.20)	0.02 (0.14)	0.55	0.69	0.51
<i>Siganus sutor</i>	9.50 (6.30)	2.75 (2.83)	0.55	1.55	0.01
<i>Thalossoma spp</i>	0.04 (0.10)	-	-		
<i>Cephalopholis argus</i>	0.04 (0.10)	-	-		
<i>Naso hexacanthus</i>	-	0.07 (0.24)	-		
<i>Cantherhines pardalis</i>	-	0.01 (0.06)	-		
<i>Heniochus spp</i>	-	0.02 (0.08)	-		

Table 4-5. Summary of the gradient (β_0) and inflexion point (β_1) of proportion of within park CPUE (y) of the reef fish caught across two marine reserves in coastal Kenya. $y = 1/(1+\text{EXP}(\beta_0(\beta_1 - x)))$. ** $p < 0.01$, * $p < 0.05$, (-) inadequate sample size. Error bars are \pm s.e. β_1 significance is indicated if ± 2 s.e.'s does not include park boundaries (5.8 and 1.4 km from park center at Watamu and Malindi, respectively).

Species	NE monsoon		SE Monsoon	
	β_0	β_1	β_0	β_1
(a) Watamu				
<i>Siganus sutor</i>	0.50 \pm 0.4	6.20 \pm 1.92	-0.80 \pm 0.34*	2.20 \pm 1.9*
<i>Lethrinus mahsena</i>	-0.20 \pm 0.3	2.90 \pm 2.1	-0.10 \pm 0.47	2.60 \pm 2.1
<i>Lethrinus sanguineus</i>	-1.60 \pm 0.3**	4.30 \pm 1.4	-0.10 \pm 0.26	∞
Others	-0.30 \pm 0.20*	3.80 \pm 0.20	-0.10 \pm 0.16	3.40 \pm 1.0
Total catch	-0.70 \pm 0.3*	6.40 \pm 1.8*	-1.20 \pm 0.26**	4.60 \pm 1.6
(b) Malindi				
<i>Lethrinus mahsena</i>	-1.05 \pm 0.3*	0.80 \pm 2.3	-	-
<i>Leptoscarus vaigiensis</i>	-0.01 \pm 4.2	∞	-0.40 \pm 0.30	3.60 \pm 1.0
<i>Gaterin flavomaculatus</i>	1.40 \pm 0.5	2.30 \pm 0.8*	-	-
<i>Siganus sutor</i>	-0.45 \pm 0.2*	0.51 \pm 0.2*	-0.53 \pm 0.1*	0.88 \pm 0.3
Others	-1.30 \pm 1.5	2.90 \pm 2.6	-0.14 \pm 0.2	2.50 \pm 0.5
Total catch patch reef	-0.78 \pm 0.1*	0.95 \pm 0.2*	-0.88 \pm 0.2*	0.42 \pm 0.3*
Total catch fringing	-0.32 \pm 0.8	1.43 \pm 2.1	-0.84 \pm 0.2*	0.61 \pm 1.4

Table 4-6: Seasonal differences in trappability (T_b) of 12 species of reef fish trapped by the *Dema* in coastal Kenya. ∂T_b denotes difference in trappability between NE and SE monsoons.

Species	NE monsoon season			SE monsoon season			∂T_b
	Catch/ Trap	# / 500 m ²	T_b	Catch/ trap	# / 500 m ²	T_b	
<i>Acanthurus negrofuscus</i>	0.045	30.00	0.002	0.042	14.8	0.003	-0.001
<i>Balistapus undulatus</i>	0.511	1.57	0.325	0.208	1.00	0.208	0.117
<i>Calotomus carolinus</i>	4.86	0.18	0.037	0.042	2.2	0.019	0.018
<i>Cheatodon auriga</i>	0.041	2.714	0.015	0.083	1.7	0.049	-0.034
<i>Cheilinus chlorourus</i>	0.233	1.857	0.125	0.083	0.7	0.119	0.006
<i>Gaterin flavomaculatus</i>	0.263	1.857	0.142	1.125	2.70	0.417	-0.275
<i>Leptoscarus vaigiensis</i>	0.101	3.43	0.030	0.208	6.00	0.035	-0.005
<i>Lethrinus mahsena</i>	4.08	1.571	2.594	0.583	6.75	0.086	2.508
<i>Lutjanus fulviflamma</i>	0.017	2.714	0.006	0.041	1.10	0.038	-0.032
<i>Parupeneus macronema</i>	0.031	3.286	0.009	0.042	2.80	0.015	-0.006
<i>Scarus ghobban</i>	0.011	4.570	0.002	0.042	1.00	0.042	-0.04
<i>Siganus sutor</i>	4.220	63.428	0.067	9.50	62.00	0.153	-0.086
Means \pm (s.d.)	1.20 (1.93)	9.76 (18.71)	0.27 (0.73)	0.99 (2.69)	8.56 (17.29)	0.099 (0.12)	0.18

Mann-Whitney test, $U=85.5$, $U_{0.05(2), 12, 12} = 102$, $p>0.05$

Table 4-7: Mean difference in length between species inside (a) Malindi and (b) Watamu Marine Parks and their adjacent fished reserves. Data analysed using two-tailed t-test for means with unequal variance, p: t-test probability. d_i = length difference between sites.

Species	Park			Reserve			d_i	p
	Mean length (cm)	(range)	n	Mean length (cm)	(range)	n		
(a) Malindi								
<i>Acanthurus dussumieri</i>	19.5	(12.2 - 26.0)	25	18.0	(12.5 - 23.6)	29	1.5	0.12
<i>Calotomus carolinus</i>	28.0	(18.5 - 36.7)	32	19.2	(15.0 - 24.5)	18	8.8	0.01
<i>Cheilinus chlorourus</i>	23.8	(21.4 - 30.0)	17	20.5	(14.2 - 39.4)	28	3.3	0.02
<i>Gaterin flavomaculatus</i>	26.8	(17.5 - 36.2)	17	26.1	(18.5 - 41.0)	19	0.7	0.55
<i>Leptoscarus vaigiensis</i>	23.5	(20.5 - 26.0)	28	25.0	(19.0 - 29.0)	36	-1.5	0.01
<i>Lethrinus mahsena</i>	20.8	(15.2 - 29.8)	210	18.3	(13.5 - 28.5)	106	2.5	0.01
<i>Lethrinus sanguienus</i>	22.6	(19.2 - 29.8)	12	21.9	(15.3 - 29.0)	17	0.7	0.55
<i>Lutjanus fulviflamma</i>	21.3	(19.0 - 21.7)	17	23.1	(17.5 - 28.3)	11	-1.8	0.25
<i>Naso hexacanthus</i>	30.2	(21.5 - 33.7)	12	18.9	(15.0 - 31.5)	24	11.3	0.01
<i>Parupeneus barberinus</i>	30.8	(22.0 - 40.4)	18	27.4	(19.5 - 35.4)	21	2.4	0.45
<i>Scarus ghobban</i>	45.9	(23.7 - 49.0)	15	27.9	(21.4 - 37.2)	10	18.0	0.02
<i>Siganus sutor</i>	19.8	(10.6 - 34.0)	310	21.5	(11.5 - 36.0)	381	-1.7	0.01
<i>Siganus sutor</i> *	18.2	(12.3 - 31.1)	121	14.3	(14.0 - 26.5)	101	3.4	0.04
(b) Watamu								
<i>Acanthurus dussumieri</i>	24.8	(15.7 - 38.7)	18	19.2	(16.5 - 25.7)	14	5.6	0.01
<i>Calotomus carolinus</i>	26.6	(17.7 - 35.8)	60	22.7	(19.5 - 25.0)	7	3.9	0.01
<i>Gaterin flavomaculatus</i>	30.8	(17.9 - 42.0)	106	26.4	(21.5 - 30.0)	6	4.4	0.01
<i>Leptoscarus vaigiensis</i>	24.5	(20.5 - 28.5)	24	25.3	(15.7 - 30.0)	48	-0.8	0.21
<i>Lethrinus mahsena</i>	18.3	(11.2 - 33.0)	309	17.7	(13.5 - 26.0)	53	0.6	0.11
<i>Lethrinus sanguienus</i>	22.9	(12.5 - 44.0)	406	20.4	(12.6 - 30.2)	18	2.5	0.09
<i>Parupeneus barberinus</i>	27.7	(17.6 - 41.5)	37	27.8	(21.5 - 40.0)	8	-0.1	0.98
<i>Cantharhines pardalis</i>	16.7	(15.5 - 18.0)	26	16.2	(14.0 - 18.5)	14	0.5	0.20
<i>Siganus sutor</i>	20.4	(13.2 - 28.0)	224	20.9	(11.0 - 34.5)	161	-0.5	0.19

* fish caught on the fringing reef portion of Malindi Marine Park

Table 4-8: Minimum trappable sizes of 21 species of coral reef fishes trapped by the traditional *Dema* in Kenyan lagoonal reefs, derived from a regression of total length (TL) on body depth (D): $TL = \alpha D + \beta$ and the average mesh size of the traps (≈ 4.5 cm). $S_{y,x}$ is standard error of regression.

Species	n	Intercept	X variable	Adjusted r^2	Minimum trappable size (cm) $\pm S_{y,x}$
<i>Acanthurus dussumieri</i>	16	4.21	1.79	0.47	12.5 \pm 2.1
<i>Acanthurus negrofuscus</i>	15	9.74	1.33	0.66	15.7 \pm 1.1
<i>Acanthurus mata</i>	14	- 1.37	2.44	0.98	9.61 \pm 0.7
<i>Naso hexacanthus</i>	20	- 3.54	3.06	0.91	10.2 \pm 1.2
<i>Leptoscarus vaigiensis</i>	34	13.15	1.45	0.45	19.7 \pm 1.4
<i>Siganus sutor</i>	281	0.73	2.7	0.88	12.9 \pm 1.2
<i>Epinephelus merra</i>	17	- 1.38	3.23	0.9	13.2 \pm 4.1
<i>Gaterin flavomaculatus</i>	40	5.15	2.4	0.91	15.9 \pm 1.3
<i>Lutjanus fulviflamma</i>	18	4.35	2.34	0.73	14.9 \pm 1.9
<i>Cheilinus trilobatus</i>	16	- 1.32	2.67	0.93	10.7 \pm 1.6
<i>Cheilinus chlorourus</i>	18	0.23	2.52	0.80	11.6 \pm 1.4
<i>Lethrinus mahsena</i>	70	3.07	2.29	0.90	13.4 \pm 0.8
<i>Lethrinus sanguineus</i>	68	2.25	2.36	0.90	12.9 \pm 1.6
<i>Lethrinus rubroviolaceus</i>	14	- 0.62	2.96	0.96	12.7 \pm 0.7
<i>Cheatodon auriga</i>	17	4.22	0.99	0.83	8.7 \pm 0.4
<i>Parupeneus barberinus</i>	18	- 3.89	4.27	0.93	15.3 \pm 2.2
<i>Scarus ghobban</i>	11	- 0.16	2.82	0.89	12.5 \pm 1.8
<i>Sufflamen fraenatus</i>	19	3.31	1.69	0.89	10.9 \pm 0.8
<i>Balistapus undulatus</i>	18	5.05	1.49	0.65	11.8 \pm 2.1
<i>Calotomus carolinus</i>	23	2.46	2.39	0.95	13.2 \pm 1.3
<i>Cantherhines pardalis</i>	17	8.07	1.05	0.46	12.8 \pm 0.9

Table 4-9: Summary of the gradient (β_0) and inflexion point (β_1) of proportion of within park CPUE (y) of the reef fish caught across the patch reef at Malindi Park into the adjacent fished reserve during the second year (2001/2002) of sampling. $y = 1/(1+\text{EXP}(\beta_0(\beta_1 - x)))$. * $p < 0.05$, error bars are \pm s.e. β_1 significance is indicated if ± 2 s.e.'s does not include park boundary (1.4 km from the park center).

Species	NE monsoon		SE Monsoon	
	β_0	β_1	β_0	β_1
<i>Lethrinus mahsena</i>	-0.62 \pm 0.23	0.23 \pm 0.27	0.81 \pm 0.63	0.91 \pm 0.57
<i>Leptoscarus vaigiensis</i>	0.53 \pm 0.23	2.48 \pm 2.14	-0.30 \pm 0.11	0.36 \pm 0.62
<i>Gaterin flavomaculatus</i>	-0.08 \pm 0.07	2.15 \pm 2.12	-0.34 \pm 0.21	0.65 \pm 1.18
<i>Siganus sutor</i>	-0.40 \pm 0.07*	1.91 \pm 0.28	-0.89 \pm 0.15	0.68 \pm 1.19
Others	-0.05 \pm 0.14	5.40 \pm 2.04	-0.29 \pm 0.16	1.72 \pm 2.12
Total catch	-0.07 \pm 0.05	0.79 \pm 1.62	-0.91 \pm 0.17*	0.48 \pm 1.62

Table 4-10: Mean densities (#/500m²) and relative density differences (RDD) of common families of reef fish censused across Watamu Marine Park into adjacent reserve. $RDD = (density_{PARK} - density_{RESERVE}) / (density_{PARK} + density_{RESERVE})$; t : two tailed t-test ($t_{0.05(2), df}$) for means with unequal variance, p: test probability.

Family	Park	Reserve	RDD	t	p
	#/500m ² (± s.d.)	#/500m ² (± s.d.)			
(a) NE monsoon					
Siganidae	41.1 ± 31.07	21.5 ± 17.46	0.3	0.98	0.39
Lethrinidae	4.4 ± 1.53	0.4 ± 0.52	0.82	4.33	0.04
Pomacentridae	21.1 ± 7.31	3.3 ± 4.27	0.73	3.77	0.03
Labridae	8.1 ± 7.60	5.4 ± 6.26	0.21	0.45	0.69
Acanthuridae	32.0 ± 20.50	4.9 ± 10.01	0.73	12.7	0.001
Totals	112.6 ± 60.3	48.2 ± 50.48	0.40	4.3	0.02
(b) SE monsoon					
Siganidae	52.9 ± 22.37	7.83 ± 1.92	0.74	4.0	0.03
Lethrinidae	7.3 ± 6.36	0.2 ± 0.45	0.95	5.92	0.03
Pomacentridae	26.4 ± 9.74	7.7 ± 4.35	0.55	1.24	0.30
Labridae	13.7 ± 8.75	3.5 ± 7.8	0.59	2.7	0.02
Acanthuridae	26.7 ± 0.47	5.5 ± 8.7	0.66	4.8	0.009
Totals	145.5 ± 97.4	45.3 ± 52.9	0.53	3.2	0.04

Table 4-11: Mean densities (#/500m²) and relative density differences (RDD) of the families of reef fish censured at Malindi Marine Park and the adjacent reserve. $RDD = (density_{PARK} - density_{RESERVE}) / (density_{PARK} + density_{RESERVE})$, t : two tailed t-test ($t_{0.05(2), df}$) for means with unequal variance, p : test probability.

Family	Park	Reserve	RDD	t	p
	#/500m ² (± s.d.)	#/500m ² (± s.d.)			
(a) NE monsoon					
Siganidae	91.5 ± 7.78	28.0 ± 16.39	0.53	6.92	0.002
Lethrinidae	3.0 ± 0.70	2.1 ± 1.64	0.18	1.02	0.35
Scaridae	13.3 ± 2.41	0.2 ± 0.45	0.97	7.41	0.04
Labridae	15.1 ± 1.87	1.5 ± 1.87	0.82	14.53	0.00
Totals	220.1 ± 20.39	38.0 ± 21.5	0.71	10.30	0.01
(b) SE monsoon					
Siganidae	66.4 ± 31.79	10.4 ± 12.14	0.73	2.46	0.02
Lethrinidae	6.75 ± 1.06	0.1 ± 0.22	0.97	8.79	0.04
Scaridae	10.17 ± 5.89	1.0 ± 1.0	0.82	2.18	0.03
Labridae	8.0 ± 7.78	1.8 ± 4.80	0.63	1.11	0.02
Totals	127.9 ± 39.19	43.7 ± 19.79	7.49	2.8	0.02

Table 4-12. Summary of the gradient (β_0) and inflexion point (β_1) of the proportion of within park densities (y) of the reef fish censused across two marine parks in coastal Kenya. $y = 1/(1+\text{EXP}(\beta_0(\beta_1 - x)))$. * $p < 0.05$, (-) indeterminate. Error bars are \pm s.e. β_1 significance is indicated if ± 2 s.e.'s does not include park boundaries (3.3 and 1.4 km at Watamu and Malindi, respectively)

Group	NE monsoon		SE Monsoon	
	β_0	β_1	β_0	β_1
(a) Watamu				
Acanthuridae	-0.69 \pm 0.45	0.97 \pm 1.29	-3.62 \pm 5.3	2.81 \pm 2.29
Pomacentridae	-1.56 \pm 2.49*	1.54 \pm 1.29*	-22.8 \pm 25.0	0.41 \pm 0.69
Lethrinidae	-0.65 \pm 0.21	1.01 \pm 1.61	-0.99 \pm 0.08*	1.09 \pm 0.17*
Siganidae	-0.34 \pm 0.32	1.19 \pm 1.05	-0.67 \pm 0.21	0.42 \pm 0.69
Labridae	0.42 \pm 0.23	∞	-0.39 \pm 0.22	0.35 \pm 0.51
Totals	-0.77 \pm 0.08*	1.64 \pm 0.26*	-0.75 \pm 0.14*	1.31 \pm 0.44*
(b) Malindi				
Labridae	-0.73 \pm 0.34	0.78 \pm 0.45	-0.78 \pm 0.27*	0.23 \pm 0.38*
Siganidae	-0.84 \pm 0.15*	0.91 \pm 0.26	-0.92 \pm 0.19*	0.41 \pm 0.31*
Lethrinidae	-1.08 \pm 1.97	2.86 \pm 1.77	∞	-
Scaridae				
Totals	-0.88 \pm 0.15*	0.83 \pm 0.25*	-0.76 \pm 0.16*	0.42 \pm 0.26*

Table 4-13: The variation of % benthic cover with distance in (a) Malindi and (b) Watamu Marine Parks. r^2 = coefficient of determination, ns= not significant ($p > 0.05$)

% Benthic Cover					
Distance (km)	Sand	Seagrass	Algae	Corals	Rubble
a) Malindi					
-1.4	3.8	24.2	22.8	12.4	36.8
-1.0	24.3	27.0	24.3	4.1	20.3
0.0	33.3	44.4	2.8	0.0	19.4
0.2	21.2	45.5	4.6	0.0	28.8
0.4	4.1	32.7	6.1	0.0	57.1
0.8	21.8	34.6	5.4	0.0	38.2
1.6	8.8	12.3	26.3	10.5	42.1
r ²	0.0	0.4	0.05	0.04	0.17
p	ns	ns	ns	ns	ns
b) Watamu					
-3.3	12.0	26.0	38.0	16.0	8.0
-1.96	32.7	53.1	14.3	0.0	0.0
0.0	0.0	50.9	13.2	7.5	28.4
0.2	19.7	34.4	16.4	9.8	19.7
0.4	29.1	47.3	9.1	1.8	12.7
0.8	27.5	30.4	11.6	0.0	30.4
1.6	12.3	58.5	16.9	0.0	12.3
r ²	0.0	0.15	0.5	0.4	0.3
p	ns	ns	ns	ns	ns

Table 4-14: Catch landing statistics of fishers landing catches at beaches located at different distances from the parks. Distances are estimated from the nearest park. n; number of fishing days.

Site	Distance from park (km)	Catch per fisher (kg) / day \pm s.d.				n
		Trap	Net	Line	Spear	
Mayungu	3.0 - 4.0	5.1 \pm 3.4	6.8 \pm 5.8	4.4 \pm 2.9	10.0 \pm 6.0	35
Watamu	1.0 - 2.0	2.0 \pm 1.2	23 \pm 11.0	23 \pm 7.0	10.1 \pm 8.3	30
Uyombo	0.5 - 1.0	5.1 \pm 2.4	5.6 \pm 3.2	3.8 \pm 2.2	10.1 \pm 6.6	60
Mida creek	0.5 - 3.0	2.7 \pm 1.9	3.1 \pm 1.8	3.3 \pm 2.5	2.0 \pm 0.7	24
Silversands	0.5 - 1.0	3.4 \pm 2.6	-	-	-	18
ANOVA; F	-	6.9	21.5	88.3	0.82	
F _{crit}	-	2.40	2.7	2.7	3.0	
p	-	<0.05	<0.05	<0.05	>0.05	

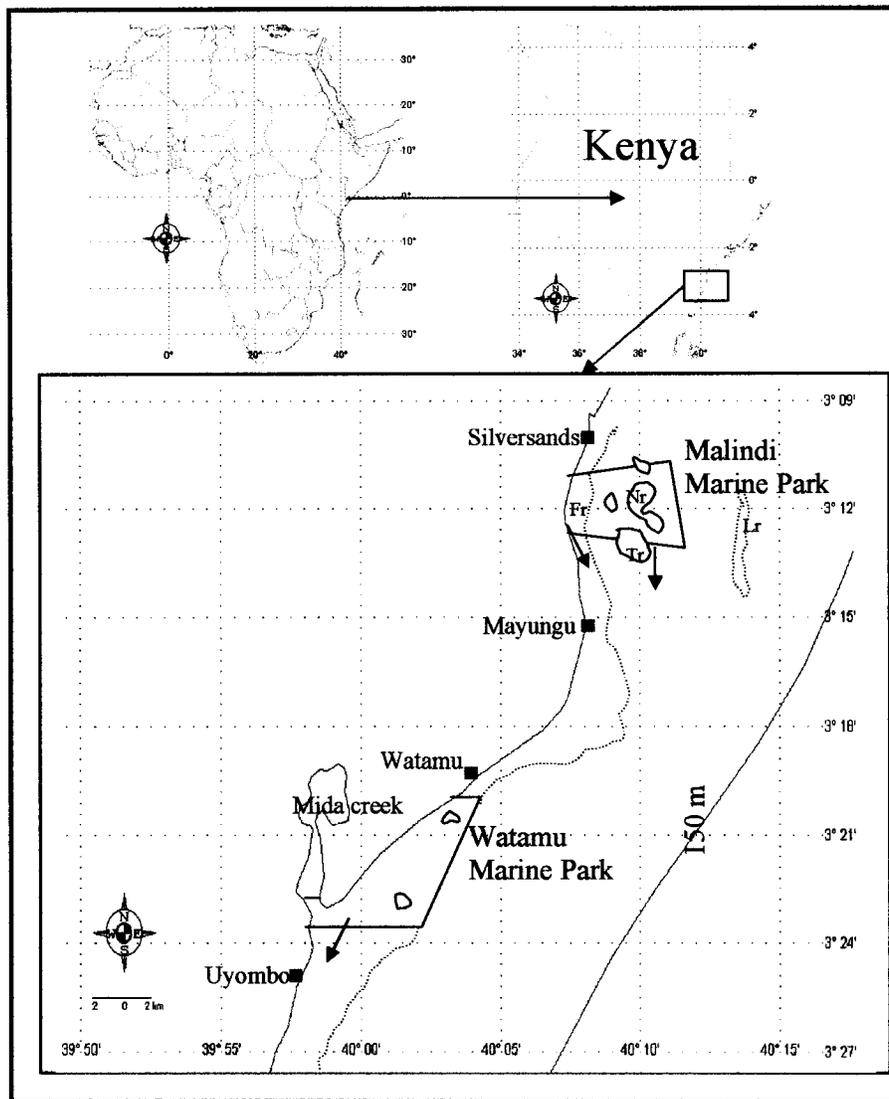


Figure 4-1: Map of the studied parks showing the reefs, the adjacent fished reserves and the fish landing sites (▪). The arrows show the trap transect directions from the park boundaries. Nr-North reef, Fr-Fringing reef, and Tr-Tewa reef, Lr- Leopard reef.

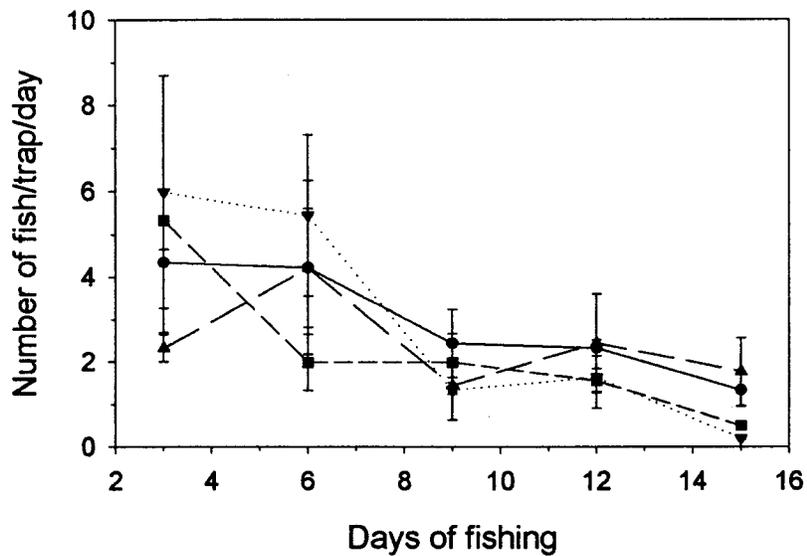


Figure 4-2: The variation of mean catch rates of traps fishing at same position during systematic sampling on transect lines over a two week period. Transects 1-4 are placed at distances of 0, 0.2, 0.4 and 0.8 km from the park border of the Malindi patch reef. Error bars indicate \pm s.d.
 ● -transect 1, ◆ -transect 2, ■ -transect 3, ▲ -transect 4

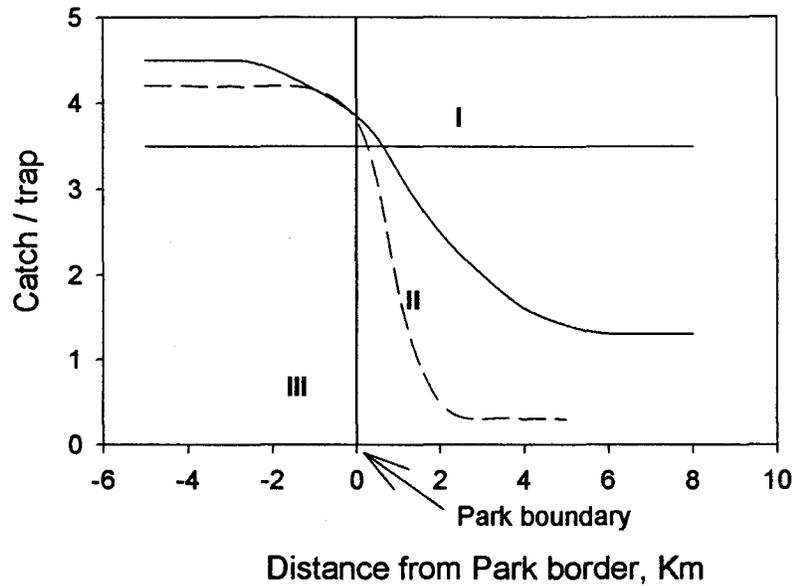


Figure 4-3: A hypothetical model of dispersal patterns of exploited fish species from a marine Park under conditions of equal catchability. Highly mobile species (I) show a CPUE gradient of near zero outside the Park boundary. Moderately mobile species (II) show gradients that are less steep while species with low mobility have increasingly negative gradient approaching ∞ (III).

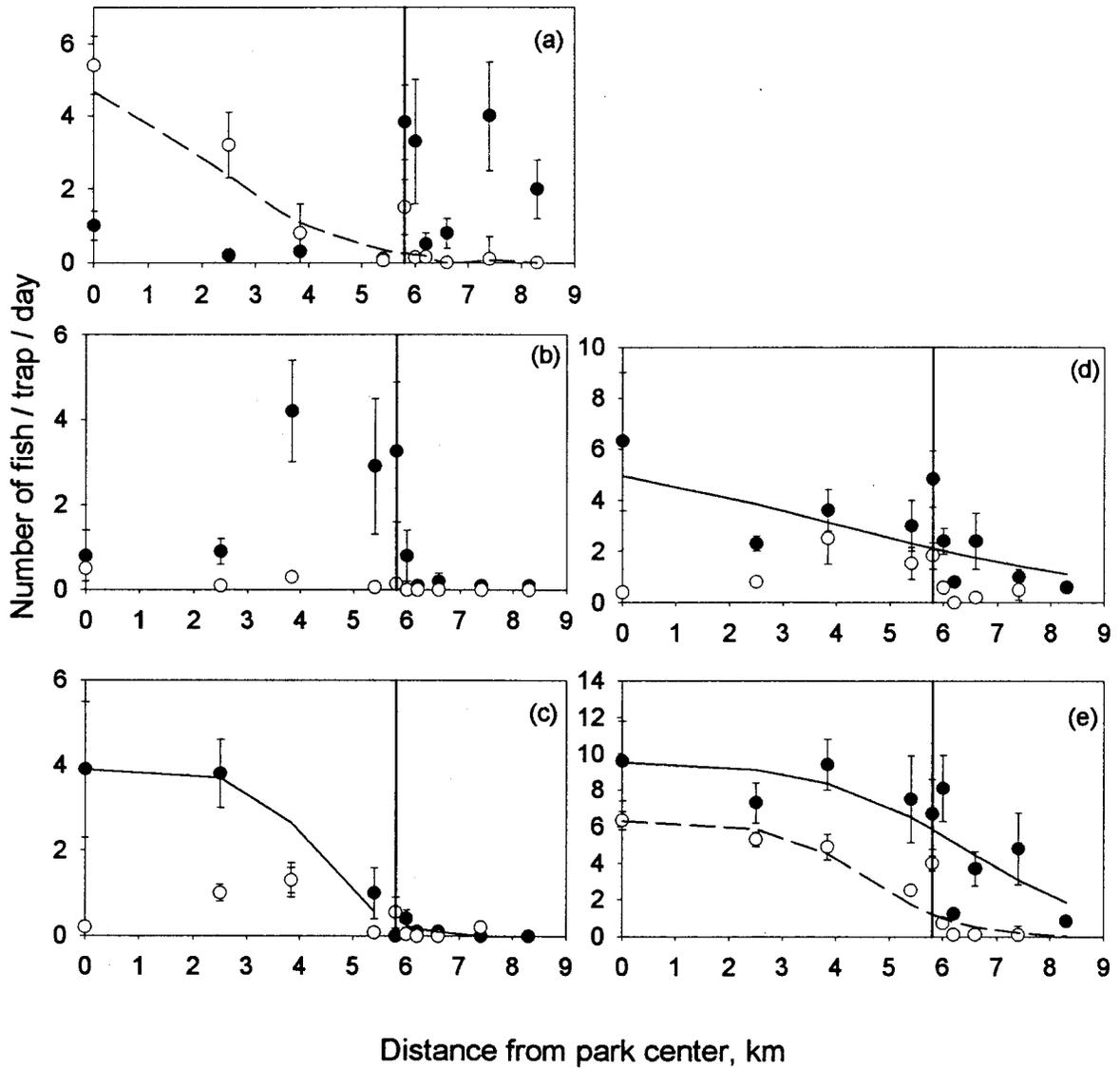


Figure 4-4: Seasonal gradients in mean CPUE of the common species of fish across Watamu Marine Park into adjacent reserve in coastal Kenya. Error bars are \pm s.e.m. Vertical line mark park boundary, continuous line and (●) indicate NE Monsoon, dashed line and (○) indicate SE monsoon. Models: (a) *Siganus sutor*, $y = 1/(1+\exp(-0.84*(2.2-x)))$, (b) *Lethrinus mahsena* (c) *L. sanguineus*, $y = 1/(1+\exp(-1.61*(4.3-x))$, (d). Others, $y = 1/(1+\exp(-0.34*(3.8-x))$ (e). Total catch, $y = 1/(1+\exp(-0.75*(6.4-x))$, $y = 1/(1+\exp(-1.2*(4.6-x))$

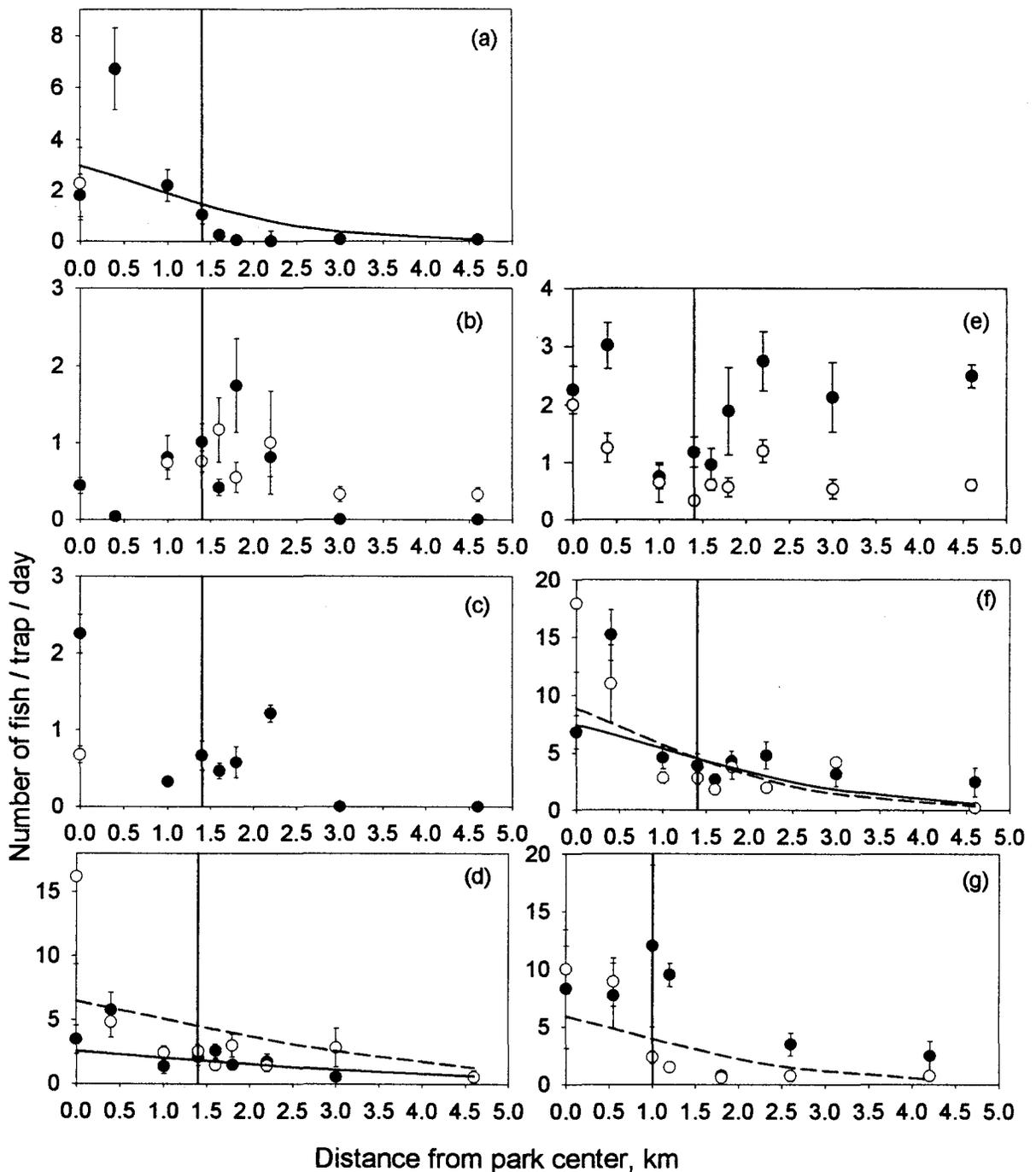


Figure 4-5: Seasonal gradients in mean CPUE of the common species of fish across Malindi Marine Park into adjacent reserve in coastal Kenya. Data analyzed for the patch reef (a-f) and for the fringing reef (g), error bars are \pm s.e.m. Vertical line mark park boundary, continuous line and (●) indicate NE monsoon, dashed line and (○) indicate SE Monsoon. Models; (a) *Lethrinus mahsena*, $\bullet y=1/(1+\exp(-1.05*(0.79 - x)$ (b)*Leptoscarus vaigensis*, (c) *Gaterin flavomaculatus* (d) *Siganus sutor*, $\bullet y=1/(1+\exp(-0.45*(0.51 - x)$, $\circ y = 1/(1+\exp(-0.53*(0.88 - x)$ (e) Others (f) Total catch patch reef, $\bullet y=1/(1+\exp(-0.78*(0.95 - x)$, $\circ y = 1/(1+\exp(-0.88*(0.42 - x)$ (g) Total catch fringing reef, $\circ y = 1/(1+\exp(-0.84*(0.61 - x)$,

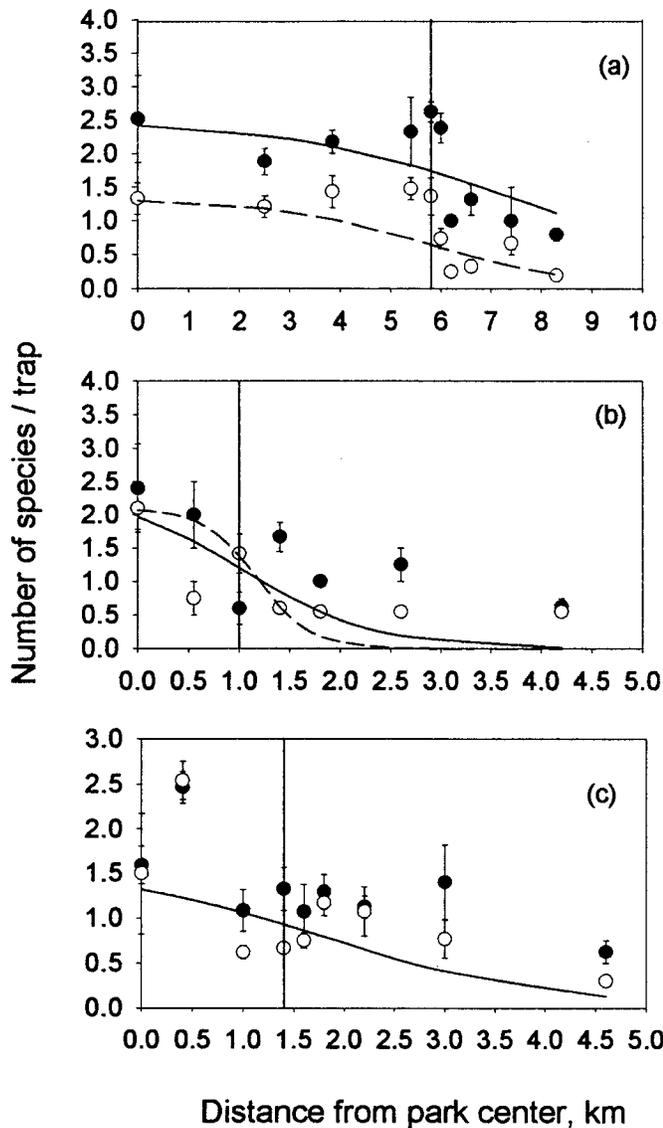


Figure 4-6: The seasonal trend in diversity of trappable fish across (a) Watamu Marine Park, (b) Malindi Marine Park fringing reef, and (c) Malindi Patch reef, into adjacent reserves in coastal Kenya. Error bars are \pm s.e.m. Vertical line mark park boundary, continuous line and (●) indicate NE monsoon, dashed line and (○) indicate SE Monsoon. Models: (a) ● $y = 1/(1+\exp(-0.41*(7.75-x)))$, ○ $y = 1/(1+\exp(-0.64*(5.71-x)))$ (b) ● $y = 1/(1+\exp(-1.52*(1.0 - x)))$, ○ $y = 1/(1+\exp(-3.75*(1.17 - x)))$

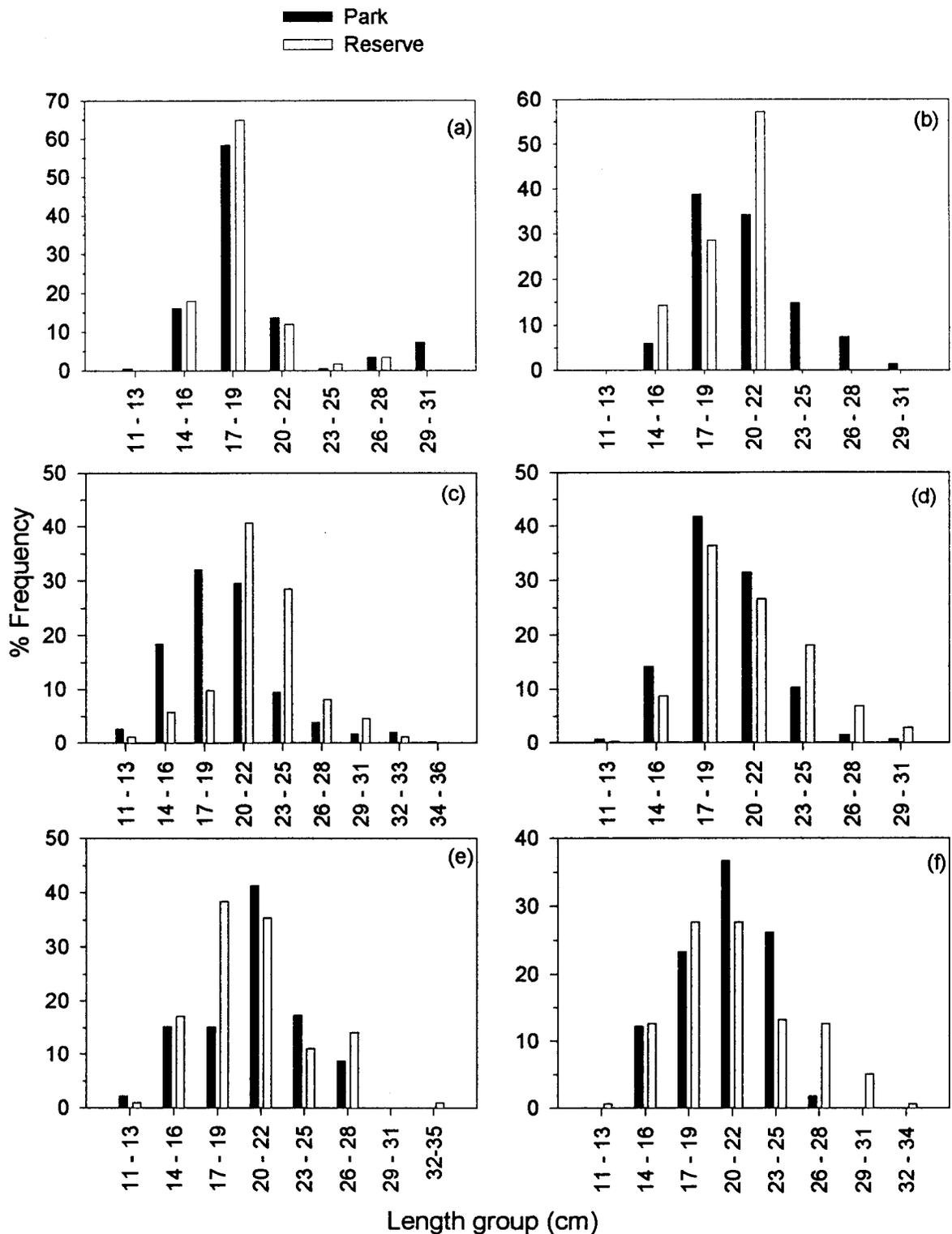


Figure 4-7: Seasonal size frequency distribution of commercially important whitespotted rabbitfish, *iganus sutor*, inside and outside marine national parks in coastal Kenya. (a) Fringing reef Malindi NE, (b) Fringing reef Malindi SE, (c) Patch reef Malindi NE, (d) Patch reef Malindi SE, (e) Watamu NE, (f) Watamu SE.

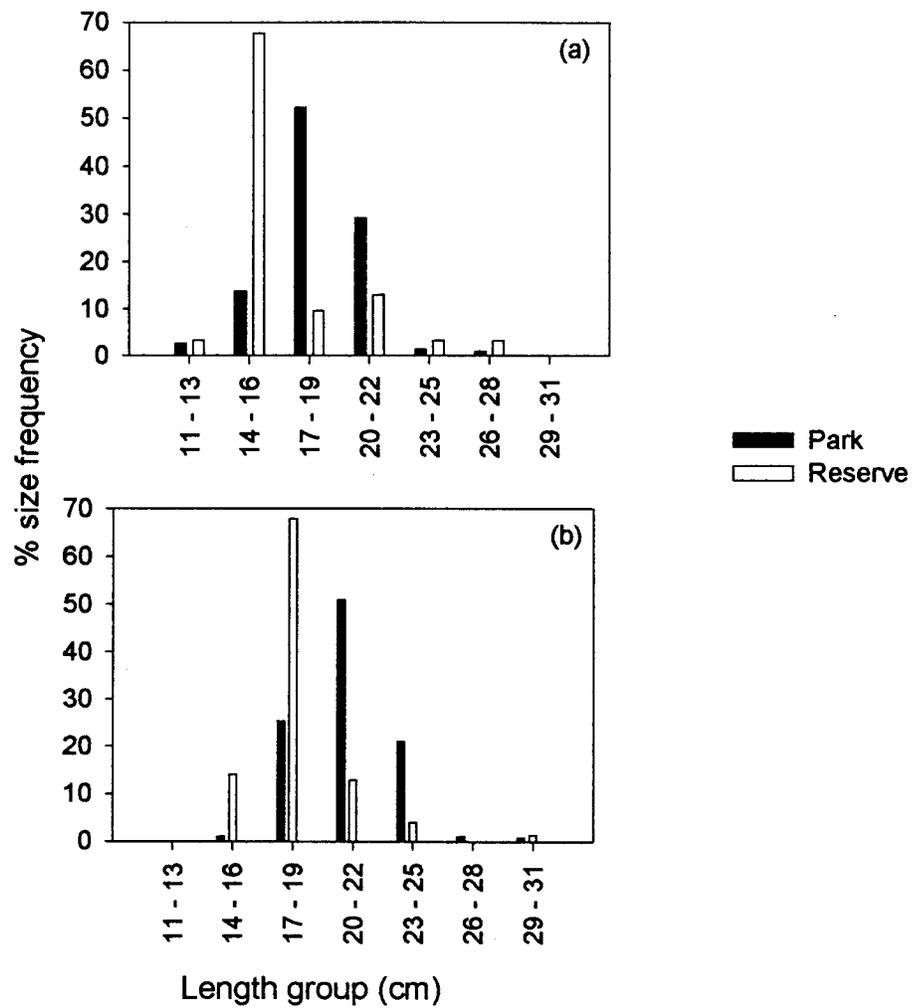


Figure 4-8: Seasonal size frequency distribution of commercially important sky emperor, *Lethrinus mahsena*, inside and outside (a) Watamu and (b) Malindi Marine National Parks in coastal Kenya during the NE monsoon season.

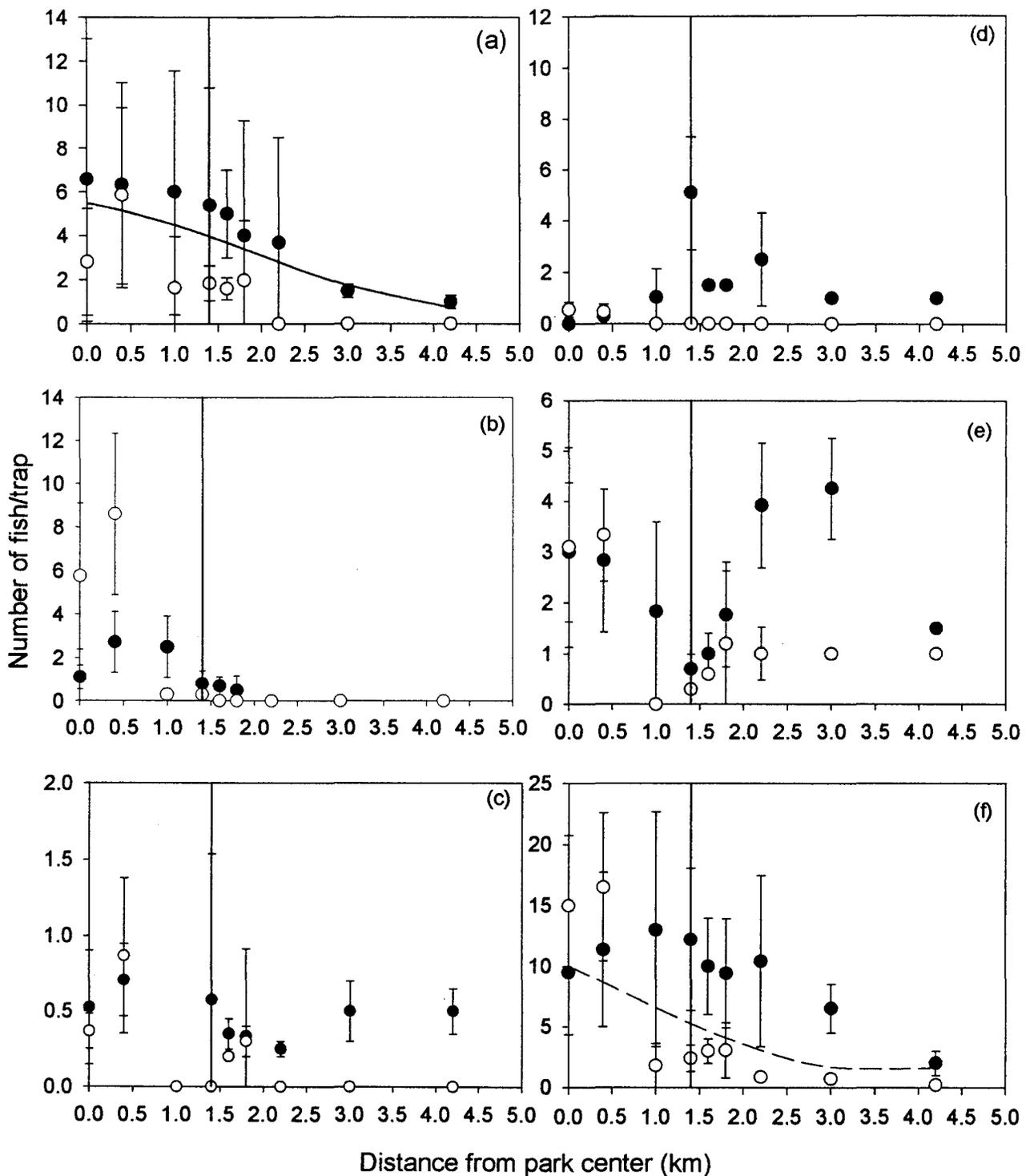


Figure 4-9: Seasonal gradients in mean CPUE of the common species of fish across Malindi patch reef into adjacent reserve in coastal Kenya during 2001/2002 period. Error bars are \pm s.e.m. Vertical line mark park boundary, continuous line and (●) indicate NE monsoon, dashed line and (○) indicate SE Monsoon. Models; (a) *Siganus sutor*, $\bullet y = 1/(1+\exp(-1.40*(1.91-x)))$, (b) *Lethrinus mahsena* (c) *Gaterin flavomaculatus* (d) *Leptoscarus vaigensis* (e) Others (f) Total catch, $\circ y = 1/(1+\exp(-0.91*(0.48-x)))$.

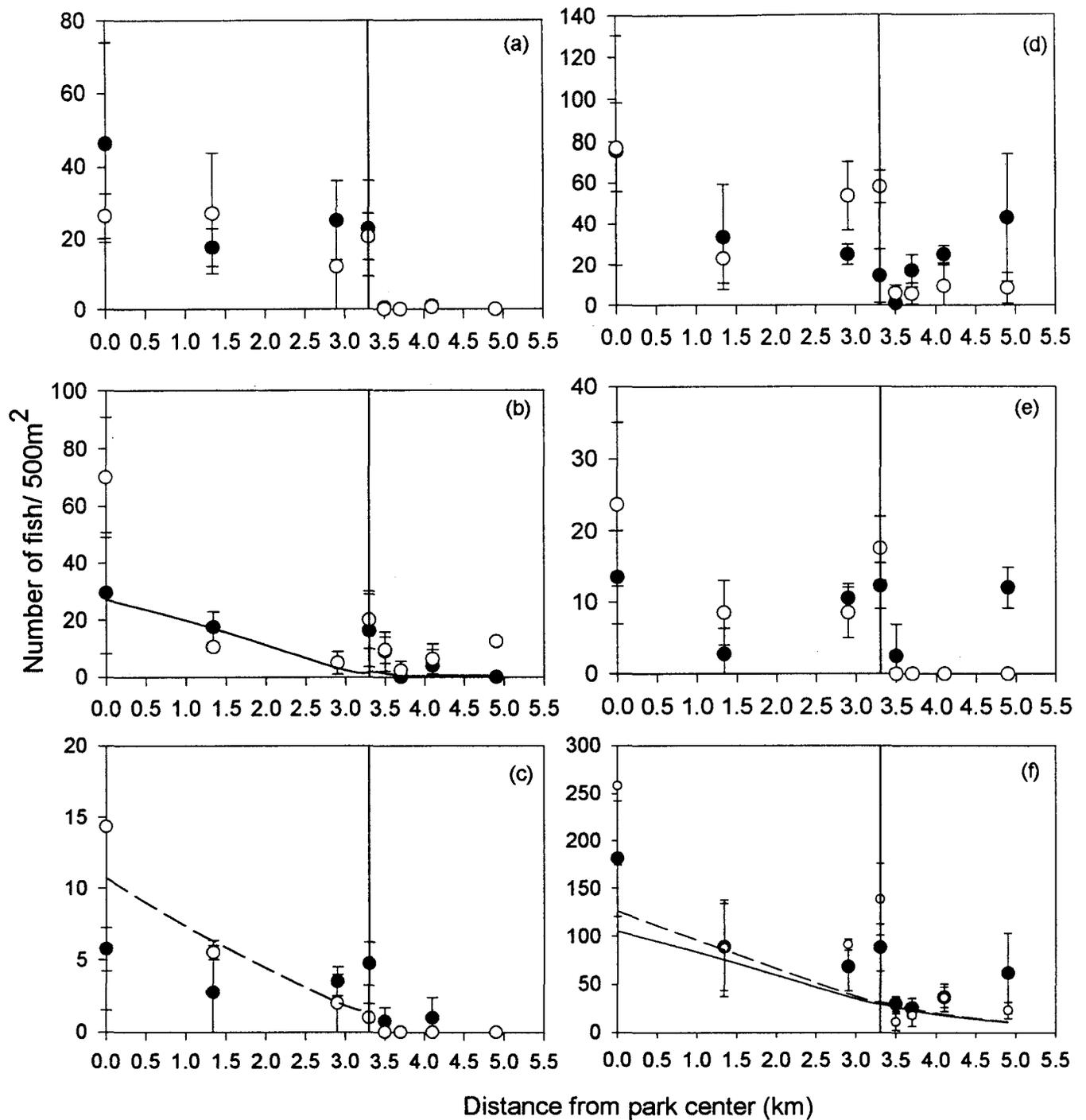


Figure 4-10: Seasonal gradients in mean densities ($\#/500\text{ m}^2$) of the families of coral reef fish censused across Watamu Marine Park into adjacent reserve in coastal Kenya. Error bars are \pm s.e.m. Vertical lines mark park boundary, continuous line and (●) indicate NE monsoon, dashed line and (○) indicate SE Monsoon. Models; (a) Acanthuridae (b) Pomacentridae, ● $y = 1/(1+\exp(-1.56*(1.54-x))$ (c) Lethrinidae ○ $y = 1/(1+\exp(-0.99*(1.09-x))$ (d) Siganidae (e) Labridae (f) Totals, ● $y = 1/(1+\exp(-0.77*(1.64-x))$, ○ $y = 1/(1+\exp(-0.75*(1.31-x))$

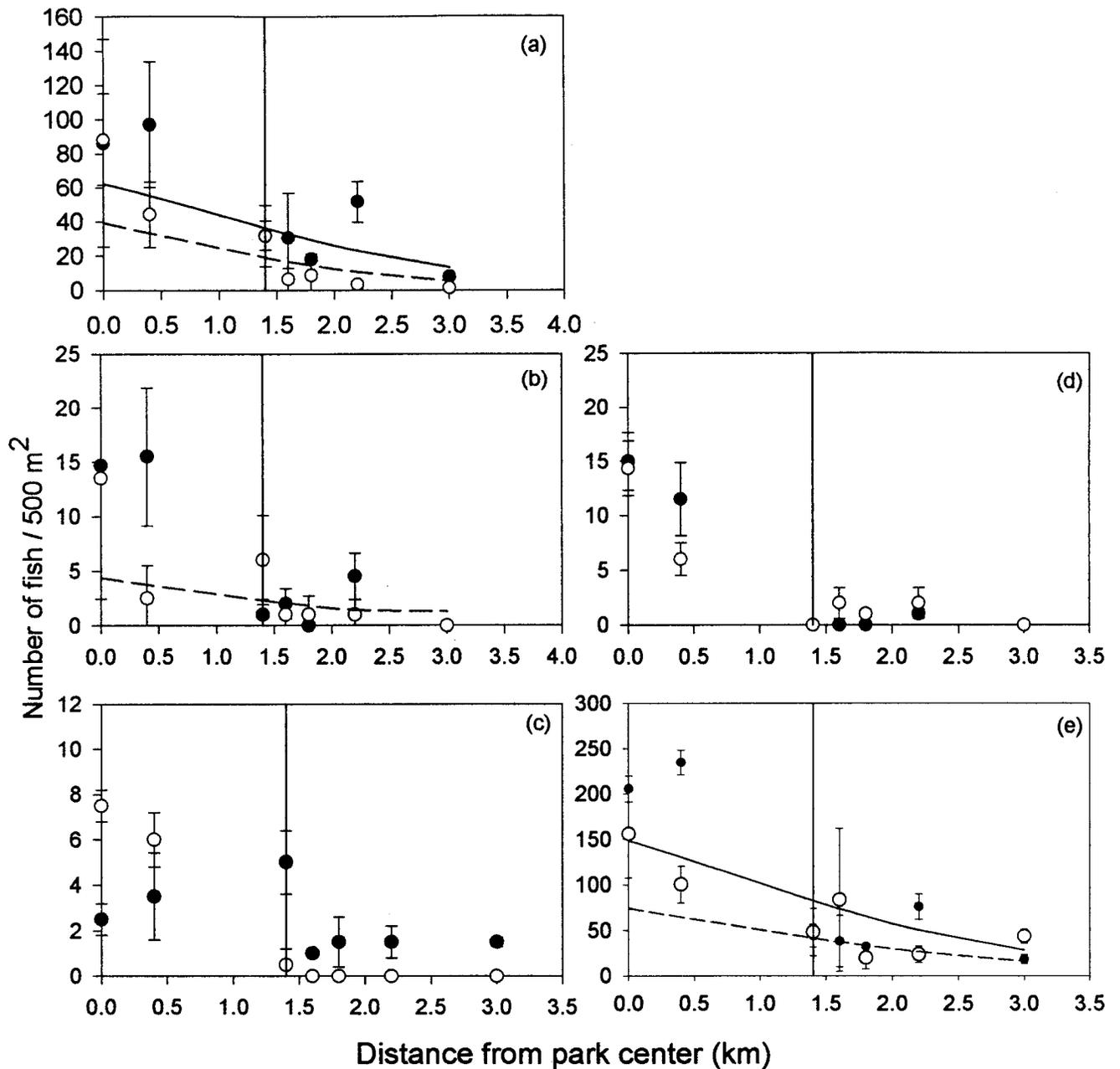


Figure 4-11: Seasonal gradients in mean densities (#/500 m²) of the families of coral reef fish censused across Malindi Marine Park into adjacent reserve in coastal Kenya. Error bars are \pm s.e.m. Vertical line mark park boundary, continuous line and (●) indicate NE monsoon, dashed line and (○) indicate SE Monsoon. Models; (a) Siganidae, ● $y = 1/(1+\exp(-0.84*(0.91-x)))$, ○ $y = 1/(1+\exp(-0.92*(0.41-x)))$, (b) Labridae, ○ $y = 1/(1+\exp(-0.78*(0.23-x)))$ (c) Lethrinidae (d) Scaridae (e) Totals, ● $y = 1/(1+\exp(-0.88*(0.83-x)))$, ○ $y = 1/(1+\exp(-0.76*(0.42-x)))$

Chapter 5

Out-migration of tagged fishes from marine reef National Parks to fisheries in coastal Kenya

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5.1 Abstract

Movements of 25 species of coral reef fish from Malindi and Watamu Marine National Parks (created 1968) in coastal Kenya were evaluated from 3911 fish tagged inside the parks from February 2001 to March 2002. Only 3 species, the commercially important whitespotted rabbitfish, *Siganus sutor*, the sky emperor, *Lethrinus mahsena*, and the emperor, *L. sanguineus*, exhibited consistent movements from the parks. At Malindi Park, more fish (6.9%) were recaptured by fishermen off a fringing reef than off a patch reef (1.4%). *S. sutor* had a higher monthly spillover rate (0.25) from the fringing reef than from the patch reef (0.07). In contrast, *L. mahsena* had low monthly spillover rates from both reefs (patch; 0.04, fringing; 0.004). *S. sutor* moved greater distances off the fringing reef (1.6 ± 1.07 km) than off the patch reef (0.67 ± 0.51 km; $p < 0.05$). At Watamu Park, *L. mahsena*, *L. sanguineus* and the gold-spotted sweetlips, *Gaterin flavomaculatus*, had equal monthly spillover rates (0.01). In contrast, *S. sutor* had a lower monthly rate (0.003). The emperors showed no difference in net distance moved

from the park boundary, however, *L. sanguineus* traveled significantly longer distances (4.27 ± 2.7 km) than did *L. mahsena* (1.96 ± 1.43 km; t-test, $p < 0.05$). Distances between release and capture sites were either random (*L. mahsena*), increasing (*L. sanguineus*), or decreasing (*S. sutor*) with respect to time at liberty.

5.2 Introduction

Marine reserves are widely recognized for their potential to conserve fish species and communities through local increases in biomass and diversity (Roberts and Polunin, 1991), and may be particularly effective tools for management of over-utilized stocks in tropical coral reefs (Bohnsack, 1998). Reserves may enhance local diversity and biomass because coral reef fishes are typically site attached and remain within small home ranges during their lifetime (Ehrlich, 1975; Sale 1991). In many tropical countries, coral reef fishes are heavily exploited (Munro, 1983; Russ, 1991) and alternative and conventional fisheries management methods are either unsuitable or difficult to apply and enforce (McManus, 1997).

Some reef fishes may have ranges with dimensions greater than their reserves. Their movements may be associated with spawning (Warner, 1995), feeding (Holland et al., 1993), or ontogenetic shifts in habitat and home range expansion (Robertson et al., 1979; Bartels, 1984; Kramer and Chapman, 1999) and may take them into fished areas adjacent to reserves. However, the effectiveness of reserves in enhancing adjacent fisheries through spillover (*sensu* Rowley, 1994),

and in conserving reef fishes, may be affected by species or site differences in fish mobility (Attwood and Bennet, 1994; Jennings, 2001; Griffiths and Wilke, 2002) and habitat structure (Appeldoorn, 1997; Murray et al., 1999).

Spillover from marine reef reserves has typically been assessed using indirect methods such as trapping (Russ and Alcala, 1996; Ratikin and Kramer, 1996, McClanahan and Kaunda-Arara, 1996; McClanahan and Mangi, 2000).

However, the results of these studies can only be inferential. A limited number of studies have employed direct methods such as tagging to assess fish movements, primarily in Caribbean (Corless et al., 1997; Chapman and Kramer 2000; Munro, 2000) and Hawaiian waters (Holland et al., 1993), and on the Great Barrier Reef, Australia (Samoilys, 1997; Zeller and Russ, 2000). However, most tagging studies have relied solely on visual sightings to assess movements.

Although resightings are valuable for examining short-term habitat use and daily random movements, they are likely to underestimate the spatial-scale of movements (Appeldoorn, 1997).

In this study, recaptures from tagging experiments are used to quantify spillover of several species of commercial reef fishes from two national marine parks in Kenyan waters of the Western Indian Ocean into adjacent fisheries. Recaptures are based on directed research trapping inside the parks and commercial reef fisheries operating outside the parks and up to 200 km from them, along the East

African coast. The movement patterns of fish tagged on different reef types (patch and continuous reefs) within the parks are examined.

5.3 Materials and Methods

5.3.1 Study sites

Kenya's coral reefs experience two levels of protection. Marine parks receive total protection from extractive exploitation while areas adjacent to the parks designated as reserves receive limited protection and allow fishing with "traditional" gear. This work was done at Malindi and Watamu Marine National Parks and the adjacent fished reserves (Fig. 5-1). Malindi and Watamu parks were both created in 1968 and cover areas of 6.3 km² and 10 km², respectively. Malindi Park has both a continuous fringing reef (erosional fossil) located about 200 m off the high water mark and running through the park for several kilometers (Hamilton and Brakel, 1988) and a patch reef system located about 1 kilometer from shore. Notable among the patch reefs are the North reef and the submerged Tewa reef. The larger North reef (2 x 1 km) includes a reef flat of semi-fossil coral rock that is exposed at low tides. Beds of the seagrass *Thalassondendron ciliatum* and isolated coral heads dominated by massive *Porites* and *Galaxea* spp. occur on the upper edges of the east and south-west slopes of the North reef. In 1998, local lobbying by fishermen resulted in trap fishing being allowed 500 m inside the south-east boundary, off the North reef.

Consequently, fish tagged or recaptured in this part of the park were treated as being outside the park.

Watamu Park is situated about 25 km south of Malindi Park (Fig. 5-1). For much of the coast between the parks there is a fringing reef that occurs near-shore near Malindi and Watamu but is over 1 km from shore in the central region. Watamu Park itself is bounded by a linear fringing reef located 1-2 km from shore. Inside the fringing reef, the park is a large lagoon carpeted by seagrass beds. The northern park border is located where the fringing reef meets the shore and forms a raised platform about 1 m above sea level. The park is bordered by two reserves to the south that include the Mida Creek tidal lagoon fringed by mangrove trees.

5.3.2 Fish trapping

Traditional pentagonal shaped *Dema* traps commonly used in East African coastal fisheries were used to trap fish for tagging (e.g., Kaunda-Arara and Ntiba, 1997). *Dema* traps typically measure approximately 1.5 x 1.3 x 0.6 m high and are constructed of wooden frames meshed with bamboo rods and reeds and weighted with stones. The traps commonly used in Kenya have a mesh size of approximately 4.5 cm maximum dimensions, a single top-side funnel door through which the fish enters, and an underside aperture for removing the catch. Traps were fished on fixed transects spaced at geometric intervals from inside

the parks across the borders into adjacent sites. They were inspected after soaking for 24 hrs. The trapped fish were emptied into a basin containing ambient temperature seawater. All fish were identified to the species level using field guides from Bock (1978), Randall (1992), Allen (1997), and Lieske and Myers (1994), with difficult species confirmed using Smith and Heemstra (1998).

5.3.3 Fish tagging

A total of 3911 fish were tagged inside the two parks (Table 5-1). For each fish to be tagged, total length was measured (nearest mm) and a serially numbered lock-on spaghetti tag (Floy FD-94, 6 cm long, orange) inserted into the musculature below the dorsal fin using a tagging gun. The tag number was recorded and fish released at the capture point. Fish were double tagged at random intervals in order to estimate rate of tag loss. Fish less than 14 cm in total length or species unsuitable for tagging (e.g., muraenids, chaetodontids) were released immediately without tagging. Fish were first tagged in both parks from February to June 2001 and from January to March 2002 when tags were mostly put on the commercially important species that had shown greater movements outside the parks. At Malindi, fish were tagged along transects at both the patch and continuous fringing reefs, while at Watamu fish were tagged at various locations within the park (Fig.5 -1). Each tag carried "reward" and "return to park" messages. Fishermen fishing in waters adjacent to the parks were informed of the tagging program in advance and a reward (Ksh. 100)

advertised as an incentive to report recapture information. Enthusiasm and participation in the program were periodically reinforced during meetings with local fishermen's associations. Tag number, total length (nearest mm), date of recapture, recapture location, fisherman's name and gear type, were recorded for each recaptured fish. Fishermen fish at distinct reef sites that are identified using traditional local names generally derived from prominent seascape or adjacent onshore features. These sites were located with the help of experienced fishermen and their positions marked using a GPS. These positions were then used to estimate the direct distance between release and recapture sites.

5.3.4 Data analyses

Gross (from point of tagging) and net (from park boundary) distances moved and times at liberty were \log_e -transformed to correct for unequal variances prior to comparison among species and sites using t-tests. Non-parametric tests were used to test associations between days at liberty and distances traveled as well as fish size and movement. Parametric regression methods were used to further examine significant non-parametric correlations.

Where sample sizes were adequate, spillover (rates of dispersal relative to distance) was derived from the slopes of plots of natural log of returns against distance moved (Appeldoorn, 1997). As returns were limited for most species,

rates of spillover from the parks were mostly calculated from the ratio of recaptures by traps inside and outside the parks weighted by the respective fishing intensity, thus:

$$S = (R_o / R_i) * (E_i / E_o) \quad (1)$$

where, S is spillover rate(month⁻¹), R_o is mean number of fish recaptured outside the park by trap fishermen each month, R_i is mean number of fish recaptured inside the parks each month excluding multiple recaptures, E_i and E_o are number of traps/km² inside and outside the parks, respectively. The determination of spillover rate assumes, (a) equal tag loss inside and outside the parks and, (b) equal natural mortality rate of tagged fish inside and outside the parks.

The number of research traps fished inside the parks averaged 7.5 ± 2.3 and 6.3 ± 2.9 traps per month at Malindi patch and fringing reefs, respectively and 12.0 ± 2.7 traps per month at Watamu. Fishermen fish an average of 26 days a month (Kaunda-Arara personal observations; McClanahan and Kaunda-Arara, 1997) with an average of 6 traps per fisherman off the Malindi patch reef and 4 traps per fisherman off both the Malindi fringing reef and Watamu Park. The positions of fishermen's traps outside the parks were marked using a GPS and the areas fished estimated using Mapinfo 4.1 software (Mapinfo corporation). Reef areas fished by trap fishermen were estimated at 5.0 and 2.5 km² off the Malindi patch and fringing reefs, respectively, and 4.5 km² outside Watamu Park.

5.4 Results

5.4.1 Recaptures and spillover rates

5.4.2 Malindi Park

A total of 1605 (17 species) and 653 (14 species) fish were tagged on the patch and fringing reef portions of Malindi Park, respectively, (Table 5-2), while 386 fish were tagged outside this park. Tagging effort was unevenly distributed between months ($\chi^2 = 372.1$, d.f. = 7, $p < 0.001$), with most fish being tagged in February of 2001 and 2002 (Table 5-1). Tag returns were unevenly distributed between months ($\chi^2 = 189$, d.f. = 7, $p < 0.001$) with a higher proportion (11.2%) of returns coming from fish tagged in April 2002. Traps, gill nets and handlines were the major gear used by fishermen in adjacent grounds (Table 5-3). Trap fishermen recaptured significantly more fish than fishermen using other gear ($\chi^2 = 64.84$, d.f. = 3, $p < 0.05$). Of the 1605 fish tagged on the patch reef, 159 (9.8%) were recaptured within the reef, while 22 (1.4%) were recaptured in adjacent fisheries (Table 5-2). Seventy-two (11.0%) of the 653 fish tagged on the fringing reef were recaptured within the reef, while 45 (6.9%) were recaptured in adjacent fisheries outside this reef. Trap-effort within the park averaged 24.3 ± 22 and 21 ± 8.2 sets per month (a trap-set \approx one trap hauled per day of fishing) on the patch and fringing reefs, respectively, while fishermen on adjacent patch and fringing reefs averaged 2496 and 2288 trap-sets per month, respectively.

At Malindi Park, only one species, the Whitespotted rabbitfish, *Siganus sutor*, exhibited consistent movements from the park. At the patch reef, only 12 (1.6%) and 8 (1.5%) of the tagged *S. sutor* and sky emperor, *Lethrinus mahsena*, respectively, moved from the reef into adjacent fisheries (Table 5-2). In contrast, 41 *S. sutor* (9.4%) and 1 *L. mahsena* (2.4%) moved from the fringing reef into adjacent fisheries. Monthly spillover rates (equation 1) were calculated for 3 species (Table 5-4). Spillover rates were higher for *S. sutor* tagged on the fringing reef (0.25) than on the patch reef (0.07). For *L. mahsena*, spillover was much lower but somewhat higher from the patch reef (0.04) than from the fringing reef (0.004) (Table 5-4). Additionally, a higher dispersal rate by *S. sutor* on the fringing reef was suggested by the shallow slope (0.41/km, $p < 0.05$) of the frequency distribution of displacement with distance (Fig. 5-2). The limited dispersal range prohibited a similar analysis on the patch reef.

5.4.3 Watamu Park

A total of 1653 (20 species) and 297 (5 species) fish were tagged inside and outside Watamu Park, respectively. Of the fish tagged inside the park, 242 (14.6%) were recaptured in research traps within the park, while 40 (2.4%) were recaptured by fishermen in adjacent fisheries (Table 5-2). The spangled emperor, *Lethrinus nebulosus*, gibbus sweetlips, *Plectorhincus gibbosus*, and the bridled triggerfish, *Sufflamen fraenatus*, had the most recaptures within the park. Trap-

effort within the park averaged 41.4 ± 33.3 sets per month, while that of fishermen adjacent to the park was estimated at 1872 trap-sets per month.

Tagging effort was unevenly distributed between months ($\chi^2 = 485.6$, d.f. = 4, $p < 0.001$), with most fish being tagged in March (Table 5-1). Tag returns were also unevenly distributed between months ($\chi^2 = 162$, d.f. = 4, $p < 0.001$). Trap fishermen in adjacent fisheries recaptured significantly more fish than fishermen using other gear ($\chi^2 = 11.52$, d.f. = 3, $p < 0.05$, Table 5-3).

Only the emperors (*L. nebulosus*, *L. mahsena* and *L. sanguieunus*) exhibited consistent movements to the fishing grounds outside the park (Table 5-2).

Monthly rates of spillover (equation 1) were calculated for three species (Table 5-4). *L. mahsena*, *L. sanguieunus* and gold-spotted sweetlips, *Gaterin flavomaculatus*, all had spillover rates of 0.01. Fifteen *L. mahsena* (3.5%) were recaptured by fishermen in adjacent fisheries, while 32 (7.6%) were recaptured in research traps within the park (Table 5-2). Eleven *L. sanguieunus* (3.3%) moved into the adjacent fisheries while 89 (26.4%) were recaptured within the park. *S. sutor* had a low spillover rate (0.003) from the park with only 1.2% of the 340 fish tagged within the park being recaptured outside (Tables 5-2 and 5-4).

5.4.4 Time at liberty and movements

At Malindi Park, *S. sutor* exhibited the largest range of movements. Gross distances traveled by this species did not differ between fish tagged on the patch (1.74 ± 5.1 km) and on the fringing reefs (2.01 ± 1.21 km) ($t = 1.02$, d.f. = 32, $p > 0.05$; Fig. 5-3a and c). However, the species on average traveled further from the park boundary (net distance) off the fringing reef (1.59 ± 1.07 km) than off the patch reef (0.67 ± 0.51 km) ($t = 3.73$, d.f. = 27, $p < 0.001$; Fig. 5-3b and d). Of the species at Malindi that showed lesser degrees of mobility, *L. mahsena* and three other species (the blackspot emperor, *Lethrinus harak*, the dory snapper, *Lutjanus fulviflamma*, and the redlip parrotfish, *Scarus rubroviolaceus*) had mean gross movements of 1.35 ± 0.54 km. Of these species, the blackspot emperor and the dory snapper traveled longer distances (~ 2.0 km) from the patch reef, however, these species traveled only limited net distances outside the park boundary (0.53 ± 0.07 km).

For *S. sutor*, the distances of recapture from Malindi Park appeared to be negatively associated with times at liberty on both reefs (Fig. 5-3). However, correlations between distance and time at liberty were significant for movements from the fringing reef (gross: Spearman rank correlation, $r_s = -0.42$; net: $r_s = -0.37$, $p < 0.05$; Fig. 5-3c and d) but not from the patch reef (gross: $r_s = -0.39$; net: $r_s = -0.61$, $p > 0.05$; Fig. 5-3a and b). There was no relationship between the initial

tagged lengths of recaptured *S. sutor* and distance moved ($r_s = 0.147$, $n = 62$, $p > 0.05$, range: 15.6-33.2 cm total length).

For fishes tagged at Watamu Park, only two emperors, *L. mahsena* and *L. sanguineus*, were consistently caught outside the park boundary (Fig. 5-4). On average, *L. sanguineus* traveled longer gross distances (4.27 ± 2.7 km) than did the *L. mahsena* (1.96 ± 1.43 km) ($t = 2.412$, d.f. = 11, $p < 0.05$) (Fig. 5-4a and c). However, mean net distances traveled from the park boundary did not differ between the species (*L. mahsena*: 1.11 ± 0.69 km, *L. sanguineus* : 1.69 ± 1.39 km) ($t = 1.149$, d.f. = 10, $p > 0.05$, Fig. 5-4bandd). For *L. mahsena*, associations between days at liberty and distance moved were negative but not significant (gross: $r_s = -0.40$; net: $r_s = -0.07$, $p > 0.05$). In contrast, for *L. sanguineus*, days at liberty and distance were strongly positive (gross: $r_s = 0.61$, $p = 0.05$, net: $r_s = 0.60$, $p = 0.06$). Other species that traveled outside Watamu Park but in lesser numbers were the bluebarred parrotfish, *Scarus ghobban*, and the spangled emperor, *L. nebulosus*. These species exhibited mean net movements outside the park boundary of 0.7 ± 0.3 km. None of *S. sutor* tagged inside the park were recaptured in the adjacent fisheries except for individuals tagged near the border. There was no relationship between the initial tagged total lengths and distances moved for recaptured *L. mahsena* ($r_s = 0.37$, $p = 0.241$; range: 15.2-20.7 cm) and *L. sanguineus* ($r_s = 0.61$, $p = 0.058$; range: 15.0-23.9 cm).

The species tagged outside the two parks moved shorter distances before capture compared to those tagged inside the parks (Fig. 5-5). For the dominant species tagged outside both parks, *S. sutor*, distance moved before capture outside Watamu Park (0.54 ± 0.44 km) did not differ from that outside Malindi Park (0.48 ± 0.77 km) ($t = 0.388$, d.f. = 68, $p > 0.05$) (Fig. 5-5a and c).

5.4.5 Tag Loss

A total of 210 and 109 fish were double tagged at Malindi and Watamu, respectively. At Malindi, 55 (7.7%) of *S. sutor* were double tagged during the period February 2001/2002. Four of these were recaptured in the research traps inside the park and one had a missing tag at the end of the period, an additional two double tagged fish with missing tags were reported by fishermen after 348 days at liberty. This represented a tag loss rate of 5.5% per year by *S. sutor* tagged at Malindi. At Watamu, 19 (22%) *S. sutor* were double tagged in 2001/2002 period, of which 3 double tagged fish were recaptured in research traps within the park with no tags missing. However, one fish returned by fishermen after 367 days of liberty had a missing tag. This represented a tag loss of ~5.3% per year for *S. sutor* in Watamu. During the period January-April 2002 an additional 108 (27.7%) *S. sutor* were double tagged in Malindi, with no recaptures within the period. However, of the 37 (34.9%) *L. mahsena* double tagged in Malindi during this period, six were recaptured in research traps and

three were found to have lost tags within 4 months. This represented an 8.1% tag loss over 4 months or an annualized tag loss of 24.3% by *L. mahsena*.

5.5 Discussion

Although many species were tagged within the parks, only the whitespotted rabbitfish and the emperors exhibited consistent out-migration from the parks, while a limited number of species, in particular the orangestriped triggerfish, *Balistapus undulatus*, the peacock grouper, *Cephalopholis argus*, and the spangled emperor, *Lethrinus nebulosus*, had recapture rates within the parks sufficiently high to indicate very localized movements in these species.

For *S. sutor* and *L. mahsena*, spillover rates varied between the parks and reef types. The relatively low spillover rates from the patch reef at Malindi Park may be caused by unwillingness of fishes to cross sand and mostly deep-water habitat patches surrounding this reef. In addition, the extra fishing permitted within a portion of this park may have provided an added barrier to spillover from the patch reef. In contrast, *S. sutor* tagged on the continuous fringing reef in this park had a much higher spillover rate and traveled greater distances from the park boundary. These results are in general agreement with earlier findings that many coral reef fishes are highly sedentary, especially from patch reefs. For example, only one parrotfish, *Sparisoma chrysopteron*, seemed to perform significant movements outside the patch reefs in Jamaica (Munro, 2000), while

Chapman and Kramer (2000), found limited movements of reef fish species between fringing reefs in Barbados. Our data suggest that greater spillover of reef fishes is to be expected along habitats that provide continuity (Appeldoorn, 1997; Murray et al., 1999). The fringing reef seems to provide such continuity for *S. sutor* at Malindi. Although continuous habitats may facilitate movements, other factors may determine direction and rates of movement (Wiens et al., 1985). For example, most species showed very limited movement from the fringing reef at Malindi, except for *S. sutor*. In contrast, at Watamu, movements of this species outside the park were minimal and the emperors exhibited greater out-migration. In addition, virtually all recaptures occurred to the south of the tagging locations, indicating unidirectional movements. We conclude that rates of spillover are likely to be species and site specific, and directional.

There were three patterns evident in the relationship between distance from the tagging site to the recapture site outside the park boundaries and days at liberty. *L. mahsena* at Watamu showed no relationship, which suggests that movements from release sites have a random component. The emperor *L. sanguineus* were recaptured further away as time at liberty increased which suggests a directional dispersal with all recaptures to the south. A very different pattern was evident with *S. sutor* which were recaptured closer to the release site and park boundary as time at liberty increased. Such a negative relationship suggests that movements away from the park occur shortly after release and then either fish

are caught (the likelihood of capture increases with distance and time at large in the fished zone), or move out of the capture zone. Rapid dispersal of reef fish from tagging sites has also been reported by Corless et al. (1997) and Cole et al. (2000).

These results suggest that marine reserve design should be based on species-specific behavior as it relates to available reef and habitat types. Marine reserves whose objectives include conservation of species should include a contiguous habitat sufficiently large to span movement ranges. Reserves that enclose patch reefs are more likely to achieve that goal. However, spillover to adjacent grounds will be enhanced by including continuous reefs and having reserves somewhat smaller than the median distance moved by the target species. For example, where median distances fall within the reserve, as is likely at Malindi patch reef, little spillover should be expected. Additionally, reserves that have seaward boundaries closer to the shore (as at Watamu) may facilitate greater offshore-onshore dispersal and lateral spillover may be minimal for some species. *S. sutor* may have dispersed this way at Watamu Park, and thus was not subject to high exploitation in adjacent fisheries.

The exclusive use of trap recaptures in this study in the calculation of spillover reduced the sample size of recaptures from outside the parks substantially, and could result in spillover rates being underestimated. However, as only trapping

was conducted within the parks, we thought it inappropriate to use all recaptures from other gear outside the parks. Furthermore, lack of within park recaptures of fish tagged outside the parks made it difficult to estimate net spillover (Russ, 2002), other than to consider immigration as zero, which is possible. The high fishing effort outside the parks may have reduced the likelihood of within park recaptures.

Tag loss rate is likely to be a function of body form and habitat structure. For example, *S. sutor* has a low average rate of annual tag loss (5.5%). Although comparative data are lacking for reef species in the region, such a low rate could result from living in less structurally complex habitats (e.g., seagrass beds). In contrast, *L. mahsena* typically occupies more rugose habitats (e.g., within coral heads and rubbles) and was found to have a higher tag loss rate (24.3%), perhaps as a result of frequent contact with reef surface. Also, the emperors have softer bodies than the whitespotted rabbitfish making tag loss more likely.

In conclusion, this study shows that spillover of most exploited coral reef fishes is limited from patch reefs, although certain species such as *S. sutor* may exhibit limited movements. However, protection of these reefs is likely to result in a substantial build up of local fish densities. In contrast, marine reserves that are contiguous with adjacent sites (e.g., through fringing reefs) may result in higher spillover rates particularly for more mobile species such as *S. sutor* and the

emperors. If the objective of a marine reserve is to enhance adjacent fisheries through spillover, then habitat and reef types and movement patterns of potential commercial species should be foremost in reserve design.

5.6 Acknowledgments

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Table 5-1. Monthly distribution of tagging and proportion of tagged fish returned by fishermen in reserves adjacent to (a) Malindi and (b) Watamu Marine National Parks in coastal Kenya.

Month	2001												2002		Totals
	F	M	A	M	J	J	A	S	O	N	D	J	F	M	
(a) Malindi															
Number tagged	596	238	313	313	132	-	-	-	-	36	-	107	865	89	2689
Number recaptured	11	5	35	8	13	-	-	-	-	0	-	1	66	5	144
% recaptured	1.8	2.1	11.2	2.6	9.8	-	-	-	-	0	-	0.9	7.6	5.6	5.4
(b) Watamu															
Number tagged	156	794	361	-	-	-	-	-	-	-	-	468	171	-	1950
Number recaptured	6	25	68	-	-	-	-	-	-	-	-	2	0	-	101
% recaptured	3.8	3.1	18.8	-	-	-	-	-	-	-	-	0.4	0	-	5.2

Table 5-2: Species of fish tagged and recaptured within and outside Malindi (patch and fringing reefs) and Watamu Marine parks, Kenya. Brackets indicate % recapture. N_t is number of fish tagged, R_i is number recaptured within parks, R_o is number recaptured by fishermen outside parks.

Species	Malindi patch reef			Malindi fringing reef			Watamu		
	(N_t)	(R_i)	(R_o)	N_t	R_i	R_o	(N_t)	(R_i)	(R_o)
<i>Acanthurus dussumieri</i>	34	6 (17.6)	0	36	9 (25.0)	0	19	1 (5.3)	0
<i>Balistapus undulatus</i>	75	34 (45.3)	0	13	12 (92.3)	0	24	8 (33.3)	0
<i>Calotomus carolinus</i>	20	0	1 (5.0)	7	1 (14.3)	0	31	0	0
<i>Cephalopholis argus</i>	17	14 (82.4)	0	7	1 (14.3)	0	7	0	0
<i>Cheilinus chlororufus</i>	24	3 (12.5)	0	14	5 (35.7)	0	25	4 (16.0)	0
<i>Epinephelus tauvina</i>	24	2 (8.3)	0	15	13 (86.7)	0	-	-	-
<i>Gaterin flavomaculatus</i>	35	6 (17.1)	0	34	7 (20.6)	3 (8.8)	112	12 (10.7)	4 (3.6)
<i>Leptoscarus vaigiensis</i>	19	0	0	15	0	0	37	0	0
<i>Lethrinus mahsena</i>	524	41 (7.8)	8 (1.5)	41	11 (26.8)	1 (2.4)	423	32 (7.6)	15 (3.5)
<i>Lethrinus sanguineus</i>	11	0	0	-	-	-	337	89 (26.4)	11 (3.3)
<i>Lutjanus fulviflamma</i>	6	0	0	-	-	-	7	0	0
<i>Parupeneus barberinus</i>	6	0	0	-	-	-	52	3 (5.8)	0
<i>Siganus sutor</i>	760	38 (5)	12 (1.6)	437	7 (1.6)	41(9.4)	340	39 (11.5)	4 (1.2)
<i>Siganus luridus</i>	8	0	0	-	-	-	38	0	1 (2.6)
<i>Scarus rubroviolaceus</i>	11	0	1 (9.1)	-	-	-	-	-	-
<i>Epinephelus fasciatus</i>	13	1 (0.1)	0	-	-	-	-	-	-
<i>Naso hexacanthus</i>	18	12 (66.7)	0	-	-	-	-	-	-
<i>Lutjanus bohar</i>	-	-	-	8	4 (50.0)	0	19	0	0
<i>Lethrinus harak</i>	-	-	-	3	0	0	-	-	-
<i>Lethrinus nebulosus</i>	-	-	-	16	0	0	77	47 (61.0)	5 (6.5)
<i>Epinephelus merra</i>	-	-	-	7	2 (28.6)	0	11	0	0
<i>Lethrinus ramak</i>	-	-	-	-	-	-	15	3 (20.0)	0
<i>Scarus ghoban</i>	-	-	-	-	-	-	49	0	0
<i>Parupeneus rubescens</i>	-	-	-	-	-	-	9	0	0
<i>Sufflamen fraenatus</i>	-	-	-	-	-	-	21	4 (19.0)	0

Table 5-3. Distribution of recaptured fish among gear used by fishermen adjacent to (a) Malindi and (b) Watamu Marine Parks in Kenya. (χ^2 -chi square test of the distribution of tag returns amongst gear)

Gear	Number of Fishermen*	Number of tags returned per gear	% returned per gear
(a)Malindi			
Trap	38	88	65.2
Line	14	15	11.1
Nets	13	32	23.7
Spear	-	0	0.0
$\chi^2 = 64.84, p < 0.05$			
(c)Watamu			
Trap	18	45	45.9
Line	32	32	32.7
Nets	14	18	18.4
Spear	-	3	3.1
$\chi^2 = 11.52, p < 0.05$			

* Data from Kenya Fisheries Department records and research fish landings database.

Table 5-4. Monthly spillover rates(S) of tagged commercially important reef species based on recaptures outside (R_o) and inside (R_i) Malindi and Watamu Marine Parks in coastal Kenya. (\pm s.d. of monthly recaptures, $S=(R_o/R_i)*(E_i / E_o)$, where E_i and E_o are number of traps/km² inside and outside the parks, respectively).

Species	Malindi Park						Watamu Park		
	Patch reef			Fringing reef			R_o	R_i	S
	R_o	R_i	S	R_o	R_i	S			
<i>Siganus sutor</i>	0.8±1.6	2.2±4.7	0.07	4.2±5.5	1.0±1.9	0.25	0.3±1.1	0.5±1.4	0.003
<i>Lethrinus mahsena</i>	0.4±0.5	2.4±2.9	0.04	0.1±0.3	1.3±2.2	0.004	1.3±2.4	8.4±8.2	0.01
<i>Lethrinus sanguineus</i>	-	-	-	-	-	-	1.2±1.2	16.0±20.2	0.01
<i>Gaterin flavomaculatus</i>	-	-	-	0.3±0.6	0.8±0.9	0.01	0.3±0.6	2.6±2.8	0.01

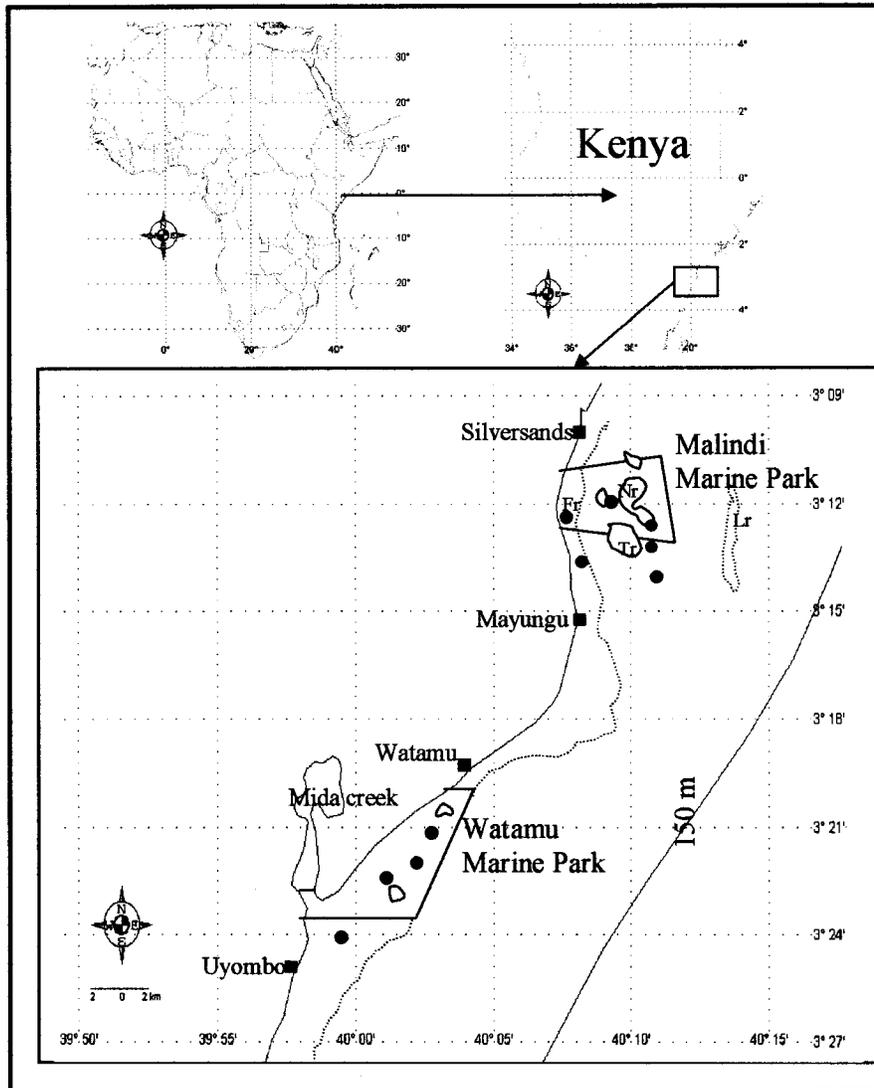


Figure 5-1: Map of Malindi and Watamu Marine Parks showing the reefs, Fish tagging sites (●), the adjacent fished reserves and the fish landing sites (■).Nr-North reef, Fr-Fringing reef, Tr-Tewa reef, Lr- Leopard reef.

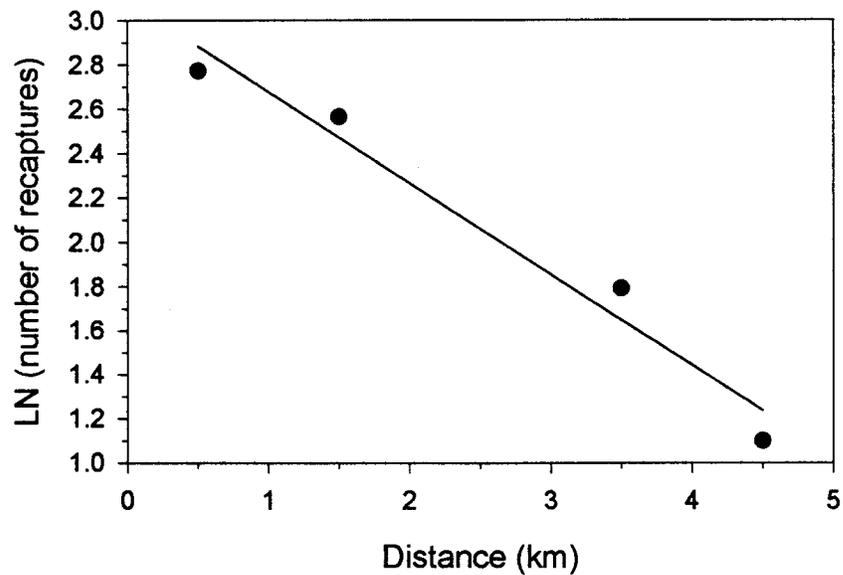


Figure 5-2. The relationship between number of recaptures and distance traveled for the whitespotted rabbitfish, *Siganus sutor*, on the fringing reef at Malindi Marine Park, coastal Kenya. Model: $\ln y = 3.09 - 0.412x$, $r^2 = 0.96$, $p < 0.05$

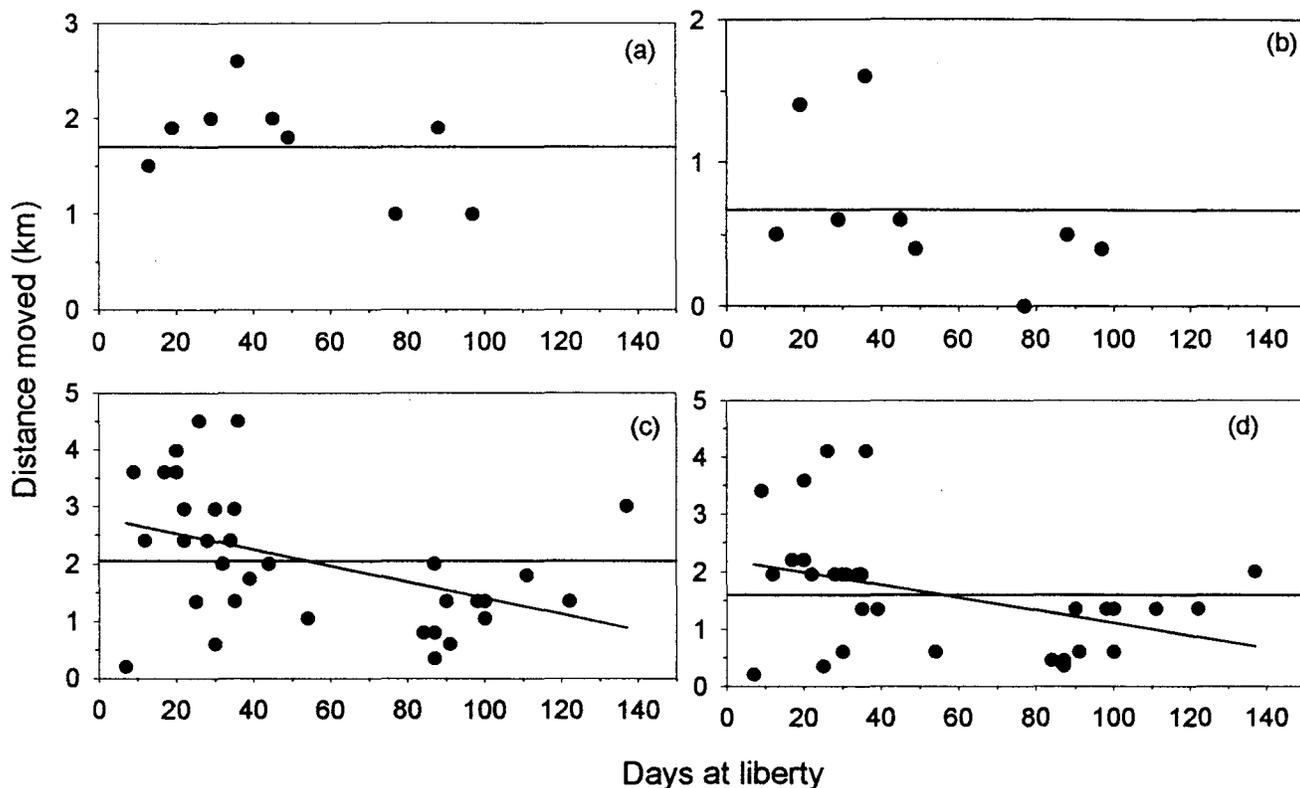


Figure 5-3. The relationship between gross and net distance moved and time at liberty for *Siganus sutor* tagged on the patch and fringing reefs of Malindi Marine Park, Kenya (a) Gross movements-patch reef ($r_s = -0.39$, $p > 0.05$) (b) Net movements-patch reef ($r_s = -0.61$, $p > 0.05$), (c) Gross movements-fringing reef, ($r_s = -0.42$, $y = 2.81 - 0.014x$, $p < 0.05$) (d) net movements-fringing reef ($r_s = -0.37$, $y = 2.21 - 0.011x$, $p < 0.05$). Horizontal line is mean distance moved.

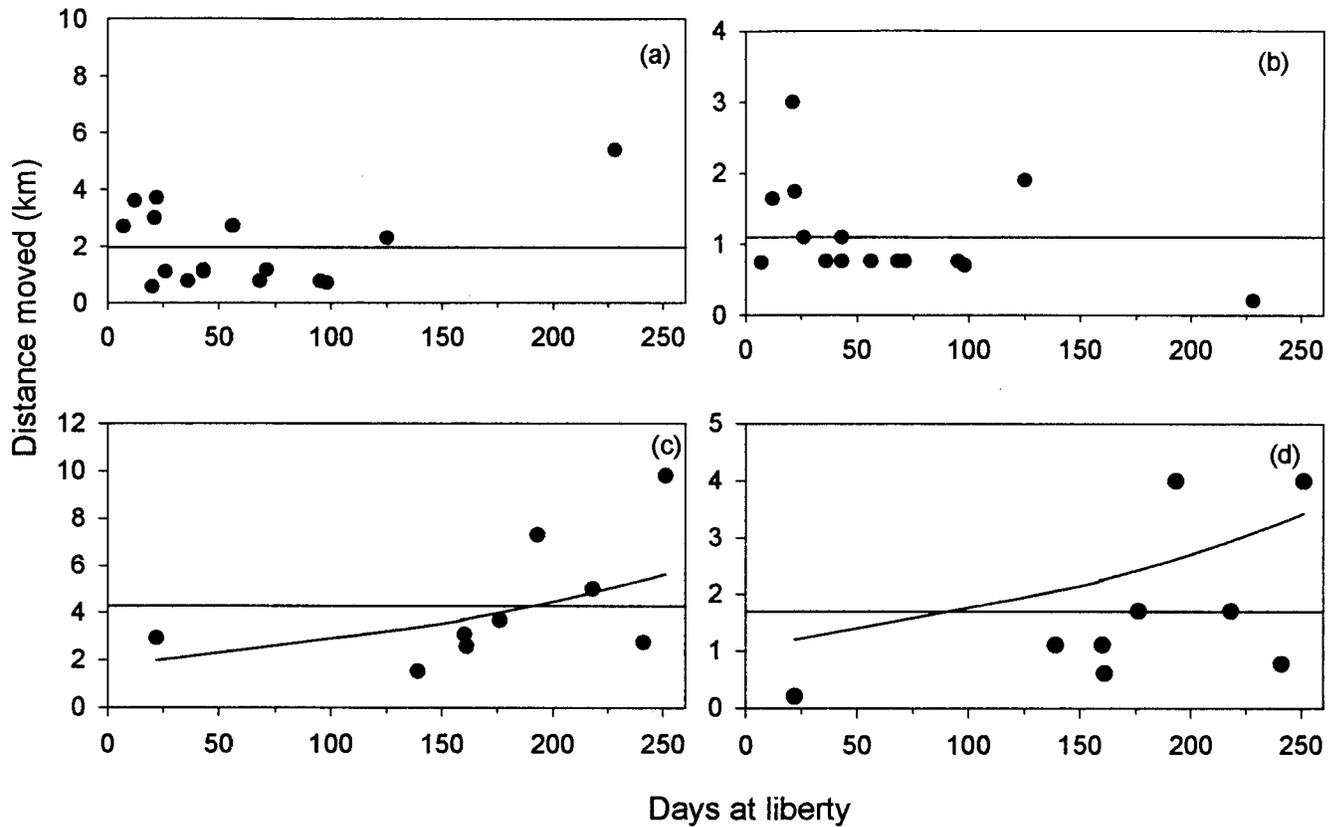


Figure 5-4. The relationship between gross and net distances moved and time at liberty of emperors tagged at Watamu Marine Park. (a). Gross movement, *Lethrinus mahsena* ($r_s=-0.07, p>0.05$) (b) Net movement, *L. mahsena* ($r_s=-0.40, p>0.05$) (c) Gross movements, *L. sanguineus* ($r_s=0.61, \log y=0.002x+0.034, p=0.051$) (d), Net movements, *L. sanguineus* ($r_s=0.60, \log y=0.002x+0.249, p=0.06$). Horizontal line is mean distance moved.

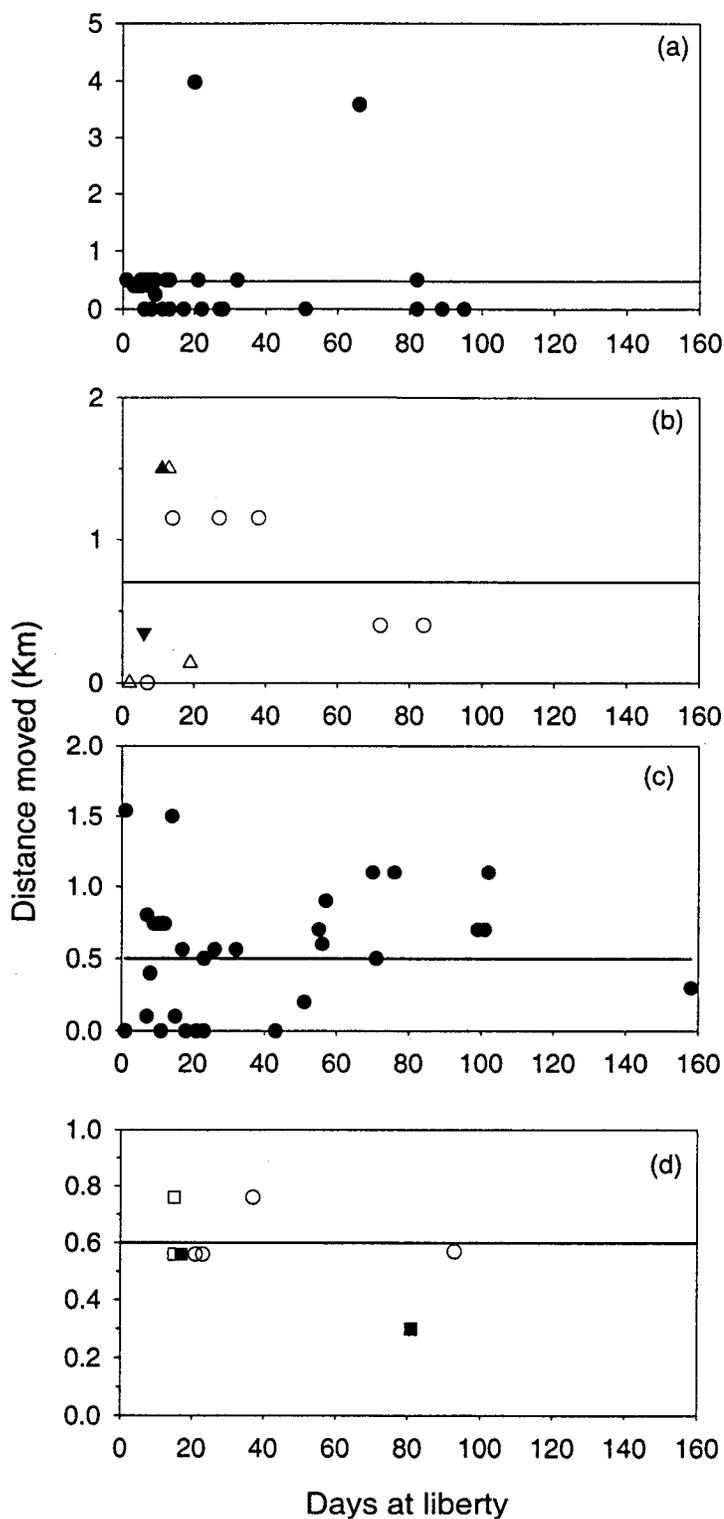


Figure 5-5. The relationship between distance moved and time at liberty for fish tagged outside the parks at Malindi (a & b) and Watamu (c & d). (a) *Siganus sutor*, (b) Other species, (c) *S. sutor* (d) Other species. (●) *Siganus sutor*; ▲ *Lethrinus nebulosus*; ▼ *Leptoscarus vaigensis*; ○ *Siganus luridus*; Acanthurus dussimieri; ■ *Lethrinus sanguineus*; Δ *Lethrinus rubroviolaceus*). In no case was there a significant relationship between distance moved and days at liberty (all r_s $p > 0.05$). Horizontal line is mean distance moved.

Chapter 6

Long distance movements of coral reef fishes

Boaz Kaunda-Arara and George A. Rose

Submitted to: Coral Reefs- Notes

6.1 Introduction

Most coral reef fishes are thought to be highly sedentary with movements limited to a few kilometers for even the most mobile species (Bardach, 1958; Holland et al., 1993). Reports of longer distance movements in coral reef fishes are rare.

The hind grouper, *Epinephelus guttatus*, was reported to move 10's of Kilometers between patch reefs in Bermuda (Bardach, 1958), however, returns to the home reef were also evident and supported the notion of site fidelity in reef fishes (Sale, 1980). Other reports on large spatial-scale movements in tropical fishes have been limited to pelagic and non-typical reef species like the blue runner, *Caranx fuses* (155 km) (Beaumariage, 1964) and the blue trevally, *Caranx melampygus* (72 km) (Holland et al., 1996). Large spatial-scale movements (100's km) associated with spawning migrations have been reported for warm temperate reef fishes (Griffiths and Wilke, 2002). Movements are demanding in energy requirements (Bernstein et al., 1991) and are not without functional role. Among coral reef fishes, local movements have been associated with feeding, spawning and ontogenetic shifts in habitat requirements (Sale, 2002).

Additionally, movements may ensure connectivity between stocks. However a major unanswered question in marine ecology is the degree of connectedness between populations (Robert et al., 2000). In coral reef environments, the open nature of reproduction in most fishes has made pelagic larval dispersal the dominant linkage between reef fish populations (Doherty and Williams, 1988). However, active adult dispersal between source and sink populations (Crowder et al., 2000) may complement larval dispersal in maintaining connectivity between populations and is thought to be a more stable mechanism evolutionarily (Holt, 1996). In this paper we report on long-distance movements in three species of coral reef fishes that have been considered sedentary on home reefs.

6.2 Materials and Methods

A total of 3916 coral reef fish of 26 species with lengths greater than 14 cm were trapped and tagged inside Watamu and Malindi Marine Parks, coastal Kenya (Fig. 4-1) from February 2000 to April 2002. For each tagged fish, total length was measured (nearest mm) and a serially numbered lock-on spaghetti tag (Floy FD- 94, 6 cm long, orange) inserted into the dorsal musculature below the dorsal fin using a tagging gun. Fish were released at the capture point. Each tag carried “reward” and “return to park” messages. Fishermen fishing in waters adjacent to the parks were informed of the tagging program prior to the exercise and of the reward (Ksh. 100) to enhance the likelihood of full reporting of

recapture information. Enthusiasm and participation in the exercise were periodically reinforced during meetings with local fishermen's associations. Tag number, total length (nearest mm), date of recapture, recapture location, fisherman's name and gear, were recorded for each recaptured fish. Along the East African coast, fishermen fish at distinct reef sites identified using traditional local names that generally have been derived from prominent seascape or adjacent onshore features. These sites were located with the help of experienced fishermen and their positions marked using a GPS. Reef positions were then used to estimate the direct distance between release and recapture sites.

6.3 Results and Discussion

Tagging experiments in the Watamu and Malindi Marine National Parks in Kenya indicated that although most species and individuals traveled relatively short distances (< 5 km, Table 6-1), individuals of some species migrate long distances between reefs (Table 6-1 and Fig. 6-1). Four gold-spotted sweetlips (*Gaterin flavomaculatus*: Haemulidae) tagged inside Watamu during March 2001 moved more than 138 km (maximum 180 km) within 34 to 340 days (mean minimal straightline distance of 1.9 ± 1.5 km/day). A Sky emperor (*Lethrinus mahsena*: Lethrinidae) tagged at Watamu was recovered 148 km from the tagging site after 63 days at liberty, an average movement rate of 2.3 km/day (Fig. 6-1). Two whitespotted rabbitfish (*Siganus sutor*: Siganidae) tagged at Malindi were

recaptured 30 km away after 33 and 47 days at liberty (mean movements of 0.6 and 0.9 km/day), respectively. All movements were southward along the coast.

Long distance movements of coral reef fishes may lead to enhancement of genetic homogeneity among spatially separated reef populations (Doherty et al., 1994), influence metapopulation structure, and be significant to reserve design. The gold-spotted sweetlips, sky emperors and whitespotted rabbitfish are tropical coral reef fish described as sedentary on a home reef (Smith and Heemstra, 1998). However, long distance movements were evident in individuals of all three species. Fishermen recaptured 5% of tagged gold-spotted sweetlips at distances from 138-180 km from tagging sites along the Kenyan coast (Table 6-1 and Fig. 6-1). Although grunts (related to sweetlips) are known to perform diel migration between sites over mid-range distances of tens of kilometers (Ogden and Ehrlich, 1977), the present study indicates that the sweetlips can move much longer distances within one to twelve months. There are no previous reports of substantial movements in these species. Indeed, most tagged rabbitfish and emperors moved within a range of a few kilometers (Table 6-1), however, some individuals moved long distances. It is important to note that although tagging return rates cannot be quantified at long distances from the release sites, it is almost certain the return rates would be lower with increasing distance from the tagging site as a consequence of lack of knowledge of the nature of the study

and the reward. Hence the numbers of fish undertaking long distance migrations is likely underestimated.

Methodologies of previous studies may have limited the detection range of large-scale movements. Few tagging studies have been conducted, and most of those involved visual “recaptures” in which detection range was limited to a small reef area (Appeldoorn, 1997). Studies conducted using traditional knowledge coupled with tagging experiments increase the likelihood of detecting longer distance movements, and indeed this study indicates that such movements occur. During local knowledge meetings, fishermen asserted that “new” fish would appear on the reefs at certain times of the year. Such immigration implies medium to long distance movements. The movements could be attributed to a group that differs in migratory behavior from resident stocks, or the migrating fish could be resident fish that become migratory at certain times of the year. Movements consume time and energy resources (Bernstein et al., 1991) and imply some functional adaptation. Elsewhere a small proportion (7%) of temperate sparids have been found to migrate long distances (200-1000 km) towards adult spawning aggregations (Griffiths and Wilke, 2002). In an environment like the coastal East African ocean that has seasonal hydrodynamic changes caused by strong monsoon winds (McClanahan, 1988), it may be advantageous to have resident and non-resident individuals as a bet-hedging strategy. Additionally, such large-scale spatial movements may serve to maintain genetic homogeneity among reef

populations (Doherty et al., 1994; Soule and Simberloff, 1986). Better knowledge of fish movement patterns is required to optimize the size and spacing of marine reserves in coastal oceans and to better understand connectivity of marine populations.

6.4 Acknowledgements

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Table 6-1: Medium to large spatial-scale movements of individuals of tagged coral reef fish species a long coastal Kenya. N is species sample size at tagging site from February to June 2001. Recapture information derived from fishermen returns, sites are shown in Figure 6-1.

Individuals	N	Total length (cm)	Site tagged	Site captured	Distance Moved (Km)	Days taken	Movement rate (Km/day)	% range movement (Km)		
								<5,	5-20	20-180
<i>Gaterin flavomaculatus</i>	82	34.6	Watamu	Gazi	138	34	4.1	0	0	4.9
<i>Gaterin flavomaculatus</i>	-	36.8	Watamu	Vanga	180	90	2.0	-	-	-
<i>Gaterin flavomaculatus</i>	-	39.4	Watamu	Gazi	138	120	1.2	-	-	-
<i>Gaterin flavomaculatus</i>	-	38.3	Watamu	Vanga	180	340	0.5	-	-	-
<i>Lethrinus mahsena</i>	313	21.2	Watamu	Msambweni	148	63	2.3	4.5	0	0.3
<i>Siganus sutor</i>	523	19.5	Malindi	Watamu	30	33	0.9	6.3	0	0.4
<i>Siganus sutor</i>	-	20.6	Malindi	Watamu	30	47	0.6	-	-	-

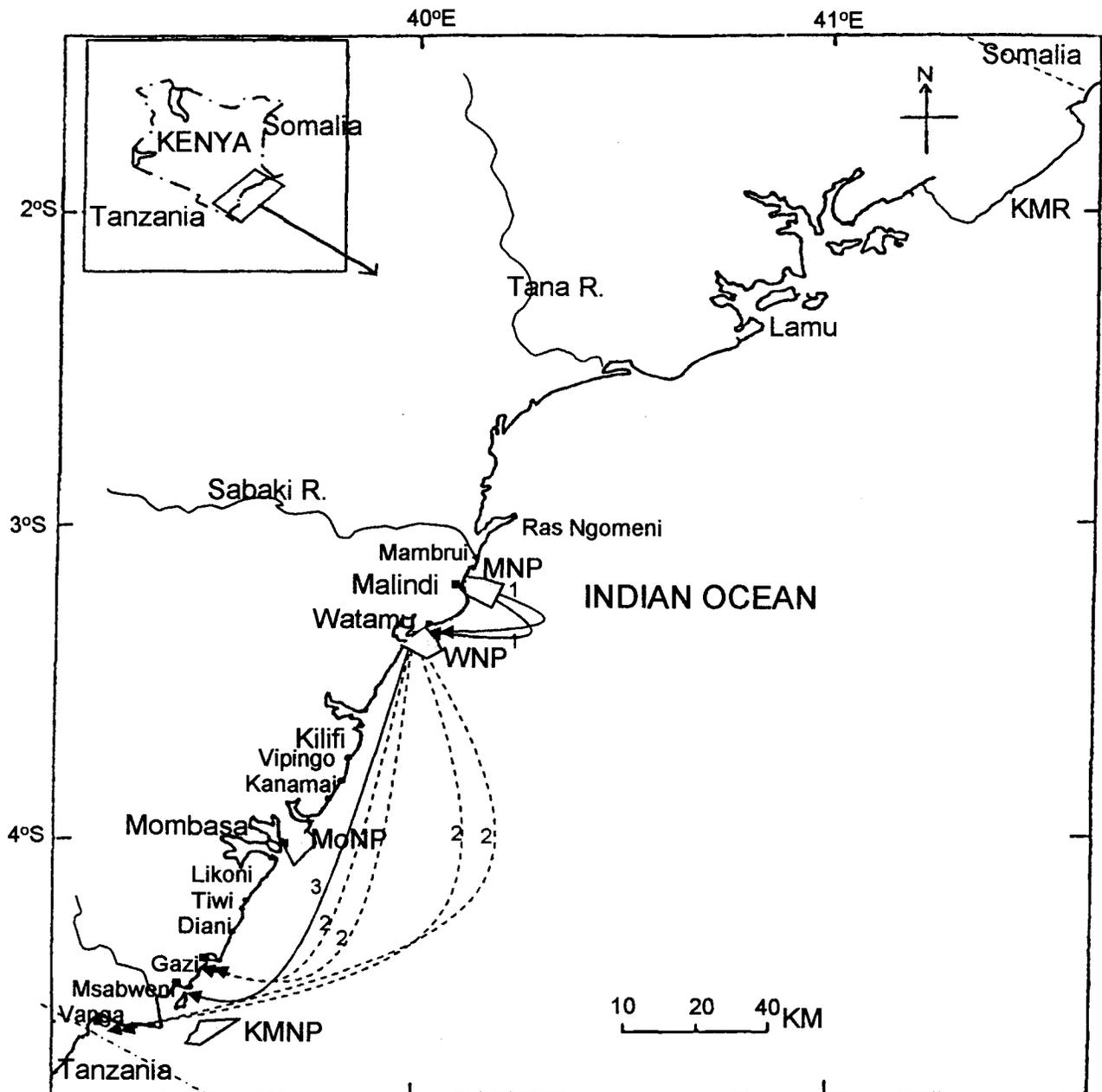


Figure 6-1: Medium to large-scale movements of tagged coral reef fish species along Kenyan coastline. 1- whitespotted rabbitfish, *Siganus sutor*, 2- gold-spotted sweetlips, *Gaterin flavomaculatus*, 3- sky emperor, *Lethrinus mahsena*. MNP- Malindi National Park, WNP- Watamu National Park, MoNP- Mombasa National Park, KMNP- Kisite Mpunguti National Park and, KMR- Kiunga Marine Reserve.

Chapter 7

Homing and site fidelity in the greasy grouper (*Epinephelus tauvina*: Serranidae) within a marine protected area in coastal Kenya

Boaz Kaunda-Arara and George A. Rose

Submitted to: Marine Ecology Progress Series

7.1 Abstract

Homing ability and site fidelity in the greasy grouper (*Epinephelus tauvina*: Serranidae) were studied at Malindi Marine Park (6.3 km² created 1968) in coastal Kenya from January to April 2002 using acoustic telemetry.

Displacement experiments involving 12 groupers (mean size, 57.9 ± 8.8 cm) from multiple capture sites resulted in a 67% homing success. Upon release at displacement sites, most movements were small scale and non-directional.

Neither the tidal range nor time of day influenced the magnitude of these daily movements (2-way ANOVA, $p > 0.05$). Returns to the capture sites were sudden, and occurred predominantly (88%) on spring tide dates. Fish displaced at spring tidal phase returned to capture sites faster (7.3 ± 3.9 days) than those displaced at neap tidal phase (13.5 ± 3.1 days) (Mann-Whitney $U = 17$, d.f. = 3,5, $p < 0.05$).

Time taken to return to capture sites ranged from 4 to 16 days (mean 10.4 ± 4.7

days) and was not correlated with distance of displacement (spearman rank correlation, $r_s = 0.185$, $p > 0.05$). However, time taken to home was negatively correlated with tidal range at displacement ($r_s = -0.51$, $p < 0.05$). Home ranges established after homing (0.07 - 0.73 km^2) were stable and negatively correlated with fish size ($r^2 = 0.63$, $p < 0.05$), suggesting an ontogenetic shift in home range development. Malindi Park likely provides habitat for 50-100 adult greasy groupers.

7.2 Introduction

Homing may be defined as the return of an animal to a place formerly occupied rather than to equally probable places (Gerking, 1959), and has been documented in many species (Papi, 1992). Among the teleost fishes, homing is best documented in the salmonids (Ditman and Quinn, 1996) and has also been reported in several coastal marine fishes (Green, 1971; Robichaud and Rose, 2001). Homing influences community structure and recruitment variability and may result in energy and nutrient transfer between habitats (Papi, 1992). The mechanisms by which fish home are not well known. Laboratory studies have documented the ability of fish to detect visual and olfactory cues (Schmidt-Koenig, 1975; Ditman and Quinn, 1996) and other stimuli such as electric and magnetic fields (Quinn and Ditman, 1992). Familiarity with the physical environment (currents, tides and bathymetry) and learning have also been postulated as mechanisms of homing (Helfman et al., 1982; Rose, 1993).

However, the multiplicity of factors operating in nature often obscures the exact mechanism of homing in different fishes.

In coral reef habitats, many fishes show restricted movements within small home ranges (Sale, 1991). Although site fidelity may be expected in these habitats (Switzer, 1993), the ability to home has been demonstrated in only a few coral reef species (Bardach, 1958; Ogden and Ehrlich, 1977; Marnane, 2000).

Evidence for homing in coral reef fishes has mostly been limited to incidental observations of fish returning to feeding, shelter or spawning sites (Switzer, 1993) and to medium sized species with limited ranges (Ogden and Ehrlich, 1977; Marnane, 2000). Constraints imposed by the methods of capture and visual re-sighting have largely precluded studies of larger fish and home ranges. However, recent developments in ultrasonic telemetry (e.g., Holland et al., 1993; Zeller, 1997) enable larger scale home range studies suitable for studying larger and less easily observed fish.

Coral reef habitats are typically of small scale and the orientation mechanisms thought to be used in large-scale migration (e.g., magnetic fields and celestial cues) (Papi, 1992) may not apply. Reef habitats are highly dynamic environments characterized by tidal currents and changes in water level, temperature and salinity. In coastal East Africa, tidal amplitudes are large (~ 4 m

in Kenya, McClanahan, 1988), and such tidal activity could provide directional information.

The groupers (family Serranidae) are relatively large-sized commercial reef fishes with worldwide distribution in tropical oceans. Groupers are long-lived and protogynous pelagic spawners within reef crevice habitats (Shapiro, 1987). Their typically sedentary habits lead to high vulnerability to overfishing and local extinction (Luckhurst, 1996). Within marine reserves, site fidelity may enhance the likelihood of sustaining locally reproducing populations that could provide sources of dispersing larval recruits for adjacent areas. However, there have been few studies of the abilities of groupers to home to specific sites or of the extent of their home ranges. In this study, we use telemetric methods to assess homing behavior of greasy groupers (*Epinephelus tauvina*) of various sizes (large groupers of this species are up to 75 cm in length and > 5 kg in weight). We also examine the hypotheses that home ranges are size-dependent and that homing abilities relate to fish size and to tidal conditions.

7.3 Materials and Methods

7.3.1 Study site

Kenyan marine parks provide coral reefs with total protection from extractive exploitation. Adjacent areas designated as “reserves” receive limited protection and allow fishing with “traditional” gear, mostly traps. The present research was

done at Malindi National Marine Park (6.3 km²), created in 1968 (see Fig. 4-1). The park contains part of a continuous near-shore fringing reef and several patch reefs. The fringing reef is an erosional fossil located about 200 m from the high water mark, spans the park, and extends several kilometers outside park boundaries. A major patch reef system is located within the park approximately 1 km from shore. The North reef, a flat of semi-fossil coral rock that is exposed at low tides, is the largest (2 x 1 km) patch reef within the park. Beds of the seagrass *Thalassondendron ciliatum* and isolated coral heads dominated by massive *Porites* and *Galaxea* genera occur on the upper edges of the east and south west-slopes of the North reef. The park also includes a submerged patch reef (Tewa Reef) on the south-eastern side of North Reef. Malindi Marine Park is surrounded by a marine reserve that has been fished for many years.

7.3.2 Fish tagging

Groupers were captured at three sites distributed between the fringing and the North reefs (Fig. 4-1) using traditional *Dema* traps (described in Kaunda-Arara and Ntiba, 1997). Individual fish were selected for tagging based on criteria of minimum size (30 cm total length) and good body condition. All other fish were released after tagging with an external "T-anchor" tag (Floytag, Seattle, WA). Groupers to be tagged were placed in a 50-liter basin containing about 10 liters of seawater. Small quantities of anesthesia (MS222, Argent Ltd., Seattle, USA) were then incrementally added to the seawater until the fish lost equilibrium and

was calm. No attempt was made to standardize the concentration of the anaesthetic solution as the effective dosage varied between individuals and with ambient temperature (25-35°C). In order to minimize stress, surgery was conducted with the fish held ventro-dorsally with the opercular slit immersed in seawater. A longitudinal incision (~1 cm and just large enough to insert the tag) was made in the abdominal wall slightly above the central line posterior to the ventral fins. A ultrasonic transmitter tag (3.2 x 0.85 cm, Lotek, St. John's, Canada) was inserted into the abdominal cavity through the incision which was then closed with 3-4 gut sutures. The surgery and tag implantation took approximately 2-3 minutes. Each tag transmitted a distinct electronic numeric identification code on a frequency of 77 kHz every five seconds. Transmitters had an estimated longevity (battery-life) of six months.

Following surgery, total length was measured (nearest mm) and an external tag (Floy FD-94, 6cm long, orange) inserted into the dorsal musculature. The fish was then transferred to a 100 liter basin containing fresh seawater and revived through repeated mechanical aeration of the water. Fish normally revived and became active within 5-15 minutes. Visual observations on two recaptured fish indicated that the incisions healed completely within 1-2 weeks.

7.3.3 Displacement experiments and tracking

Fourteen groupers were tagged, including 12 translocated fish and 2 controls released at the capture site (Table 7-1). Fish were translocated under anesthesia to release sites by boat (0.5-2.6 kms away) and released only after apparent full recovery from the anesthesia. Displacement sites were randomly selected but had similar gross topographic complexity as the capture sites. The initial movements of most fish were usually monitored underwater soon after release by a diver. Most fish visited different coral heads upon release before settling down within a reef crevice with no subsequent movements. Tracking began immediately after release from a 5.5 m open boat with a manually operated portable receiver (Lotek, SRX_400) and omnidirectional hydrophone (Lotek, St. John's). Preliminary underwater observations and tracking indicated that most fish typically settled within reef crevasses and moved infrequently, but once moving traveled relatively long distances. Consequently, the tracking routine was restricted to a daily single location of each tagged fish.

Displacement sites were visited daily following tagging. During a tracking session, the SRX receiver was initially set at the highest possible gain that did not overload detection circuits. When a signal was detected, the boat was maneuvered in the apparent direction of the signal whilst the gain was gradually reduced to zero. As this reduction of the gain effectively reduced the detectable range of the tag, most fish were located to within a few meters, and their position

logged using a hand-held Garmin GPS receiver. Whenever a fish was not detected at the displacement site, the capture site was visited to check for the possibility of a return. If the fish was not at the capture site, the boat was let to drift along transects over the site of last location, with the number of drifts and drift area increased whenever the fish was not located. Daily tracking periods averaged 4hrs and were distributed at random over the 12 hours of daylight. No tracking was done at night.

Signal detection range was determined using a tag placed on the seafloor near a coral head. The positions from which the tag could be detected were marked using the GPS as the boat was allowed to drift along several transects beginning and ending with zero detections and passing the tag location at various minimal ranges. Results showed that acoustic signals could be detected only from distances ranging up to 35 m from the tag even at maximum gain and that signal strength could be asymmetrical about the tag position depending on bottom topography. Signal strength varied greatly even with the hydrophone stationary and on top of a known tagged fish with receiver gain set low. Such variability was associated with movements of fish in and out of a crevice (Fig. 7-1). Signals detected with low receiver gains almost certainly indicated that the fish was very close (within a few meters) to the boat.

7.3.4 Habitat characteristics

As the greasy grouper typically sheltered in crevasses within coral heads on the reef, the positions of the major coral heads at the study site, especially on the fringing reef, were mapped using the GPS. Additionally, the height and surface width and length of the coral heads were recorded.

7.3.5 Data analyses

The minimum polygon area (Winter and Ross, 1982), which represents a non-statistical measure of dispersion over the total area used by an individual, was used as a measure of home range size. All position fixes for a given fish were plotted using Mapinfo 4.1 software (Mapinfo corporation) onto a map of the park, and the outer-most positions connected by straight lines to form a polygon. Positions that were considered anomalous GPS records (outside the possible range) resulting from unknown sources were excluded from the polygon. The Aspect ratio (AR), a ratio of the maximum linear dimension (largest diagonal) to the minimum linear dimension (largest width) of the home range area, was used to describe the shape of the home range. Oblong and circular shapes have AR values greater and less than 2, respectively (Winter, 1977). Observation-area curves (number of observations Vs total area covered, Odum and Kuenzler, 1955) were used to examine the stability of the home ranges demarcated for each fish. Linearity ratios (LR) (Danielson and Swihart, 1987) were used to test for randomness of movements of individuals at sites of displacement. LR, the

ratio of the distance between an individual's first and last positions and the total distance moved by an individual during the complete tracking period, is a measure of the directedness of movements, with values tending to zero if movements are random, and unity if movements are unidirectional. Statistical analyses followed Zar (1975).

7.4 Results

Of the 12 groupers displaced within the park, 8(67%) homed to their capture sites within 4-16 days (mean 10.4 ± 4.7 days) (Table 7-1, Fig. 7-2). The other 4 fish did not return to the sites of capture. Of these 4 non-homers, code 133 was recaptured by fishermen outside the park 10 days after translocation. Codes 56 and 83 could not be relocated after 1 and 7 days, respectively, while code 152 stayed near the site of displacement throughout the study. Among the fish that homed, code 155 was not detected at the displacement site for seven days prior to being detected at the capture site.

Seven (88%) homing fish returned on spring tidal phase (new and full moon lunar phases) (Table 7-1 and Fig. 7-3). Fish that were displaced on dates that coincided with spring tides returned to the capture site more quickly (mean days: 7.3 ± 3.9), than did fish displaced on neap tides (half moon lunar phase) (mean days: 13.5 ± 3.1) (Mann-Whitney $U=17$, $d.f.=3,5$, $p<0.05$). The number of days taken to home was inversely related to tidal range at displacement (Spearman

rank correlation, $r_s = -0.51$, $p < 0.05$). There was no correlation ($r_s = 0.185$, $p > 0.05$) between distance of displacement and the time taken to return to capture site (Fig. 7-4), with fish displaced the shortest distance (e.g., codes 155 and 84, 0.5 km) taking as many days to home as those displaced the longest distance (e.g., code 116, 2.6 km) (Table 7-1 and Fig. 7-2).

Movements of most groupers at displacement sites tended to be haphazard and non-directional with low linear ratios (Table 7-2). However, code 37 exhibited a more directed movement ($LR = 0.92$, Table 7-2 and Fig. 7-2). Neither tidal state (spring vs neap tides) nor time of the day of observation (morning vs afternoon) had any effect on the magnitude of daily movements of the fish (2-way ANOVA: tide, $p = 0.608$; time, $p = 0.452$; tide*time, $p = 0.970$).

Home range size on return to capture locations ranged from 0.07 to 0.73 km² (mean: 0.344 ± 0.23 km², Fig. 7-2). Cumulative area occupied tended to reach an asymptote after approximately 1 week (Fig. 7-5). The shapes of the home ranges determined from the aspect ratios (AR) varied from oblong ($AR > 2$) to circular ($AR < 2$). Most fish were located at least every second day throughout the study, mostly near coral heads (Table 7-1). Fish that were not displaced (controls: codes 96 and 160), remained near their capture sites throughout the experiment (~ 4 months), although code 160 suddenly disappeared from its home range after a long period (105 days) of residence.

Home range was significantly and negatively related to fish length ($r^2 = 0.63$, $P < 0.05$; Fig. 7-6). The smallest fish tagged (34 and 49 cm) for which home range could be estimated had much larger ranges than the larger fish suggesting either a non-linear relationship between size and home range or a size threshold above which the home range declines.

7.5 Discussion

Sixty-seven percent of transplanted groupers homed back to their release site, or 88% of transplanted fish whose fate was known. There was no evidence of directionality to the homing behavior observed. Fish captured on opposite sides of the same reef (e.g., the north reef) and released on the other side returned to their side in opposing directions. Most fish appeared to stay near the release site and move short non-directional distances until some cue spurred them to return to their capture sites, and once cued they returned very quickly (most within a day or between relocations). This notion is supported by the low values of LR that indicate random movements around the release sites. The cue to move appears to be related to oceanographic conditions, in particular spring tides. Nearly all (88%) homing groupers returned on spring tidal phase, and fish transplanted on spring tides returned more quickly. The maximum tidal amplitudes along the Kenyan coast are approximately 4 m (McClanahan, 1988), and such tides could effectively provide not only a timing cue but also directional clues to homing fish.

Only the smallest transplanted fish (code 152, 34 cm) remained near the new site. It could be that the larger fish tagged (most > 50 cm) were more familiar with the park topography and hence homed more quickly. However, juvenile groupers (mostly *E. merra* but also greasy groupers) are widely distributed within Malindi Park (Kaunda-Arara, personal observation), and their knowledge of the reefs is likely to be established as juveniles. Hence, larger adult fish should not necessarily be expected to home with greater success. In addition, the lack of a relationship between displacement distance and time of return suggests that familiarity with the environment is not the sole determinant of homing success. An alternative hypothesis for a size basis for homing, and thought to be more likely, is an ontogenetic development of home range as fish mature (Lirman, 1994). Immature fish may not yet have become firmly attached to a home range. Code 152 was considerably smaller than the other tagged fish, perhaps the only juvenile tagged, and did not return to the capture site. Greasy groupers are known to mature as females (protogynous hermaphrodites) in the size range 45-50 cm, whilst transforming to males in the larger size groups (James et al., 1996). Code 152 was the only tagged fish < 45 cm in length.

Home ranges appeared to remain stable once established, and to overlap considerably. It is likely that each fish had a core area within which only that grouper lived and a larger range that overlapped with the ranges of other fish. Our data also suggest that home range declines as fish grow larger. This finding

is contrary to the general relationship between range and size for animals (Gaston and Blackburn, 1996). However, if home range is subject to ontogenetic development then smaller (presumably younger) fish may roam more prior to developing a relatively small home range. Alternatively, there may be a sex-related change in home range size. The larger females (< 50 cm) may have larger home ranges compared to the supposedly more territorial males.

In Kenyan fisheries, commercial landings of groupers have declined steadily over the past two decades (Kenya Fish. Dept. unpubl. data; Chapter 3). Worldwide, groupers have been over-fished in many coastal areas (Russ, 1991). The demonstrated homing behavior and establishment of home ranges indicates that marine protected areas have strong conservation potential for these fishes. The density and numbers of greasy groupers within Malindi Park are not known precisely, but the present estimates of home range suggest that the numbers are not large, and in the order of 50-100 fish. Spawning by these fish could result in dispersal of larvae and juveniles to adjacent fishing grounds outside the park, but this remains speculative and requires further study.

7.6 Acknowledgements

We are grateful to the Head of the wetland program of the Kenya Wildlife Service, Dr. N. A. Muthiga, for granting permission to work within the Park. We thank, M. Ndegwa, for assistance in the field and A. Simms for assistance with

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Table 7-1: Summary statistics of tagging, homing conditions and dates (day/month) for greasy groupers tagged and displaced to multiple sites within Malindi National Marine Park, coastal Kenya during January to April 2002.

Fish ID (codes)	Total length (cm)	Distance displaced (km)	Dates		Days taken to home	Tide on transloc- ation	Tide on homing	Number of days tracked	Number of days located	% fixes	Maximum days between locations
			trans.	return							
37	49.0	1.5	26/2	4/3	6	Spring	Spring	53	38	71.7	102
36	65.0	1.2	9/1	18/1	9	Neap	Spring	53	17	32.1	85
128	66.0	1.6	5/3	19/3	14	Neap	Spring	23	18	78.3	40
155	68.0	0.5	24/2	11/3	15	Neap	Spring	32	24	75.0	58
84	57.5	1.2	27/3	10/4	13	Spring	Spring	18	16	88.9	34
140	64.0	1.0	28/2	6/3	6	Spring	Neap	28	19	67.9	45
122	55.3	1.2	12/4	16/4	4	Spring	Spring	5	5	100	5
116*	64.0	2.6	24/2	12/3	16	Neap	Spring	24	16	66.7	38
152	34.0	1.5	24/2	-	-	Neap	-	34	26	76.5	58
56*	54.0	1.0	2/1	-	-	Spring	-	53	1	1.9	-
83*	60.0	1.2	23/2	-	-	Neap	-	32	7	21.9	9
133*	54.5	2.6	24/2	-	-	Neap	-	14	1	7.1	-
Controls											
96	65.3	-	-	-	-	-	-	63	17	27.0	94
160*	54	-	-	-	-	-	-	53	31	58.5	105

*fish disappeared from site during study or captured by fishermen

Table 7-2: Home range characteristics for individuals of greasy groupers (*Epinephelus tauvina*) tracked within Malindi Marine Park coastal Kenya.

Fish ID (code)	Home range area (Km ²)	Aspect ratio (length/width)	Linear ratio(LR)*
37	0.726	2.7	0.92
36	0.394	2.3	0.21
155	0.168	1.6	0.48
116	0.212	1.4	0.05
128	0.222	2.01	0.21
84	0.241	1.5	0.37
140	0.065	1.6	0.03
152	0.274	1.3	0.05
Controls			
96	-	-	-
160	0.389	2.7	0.01

* LR for movement at displacement sites

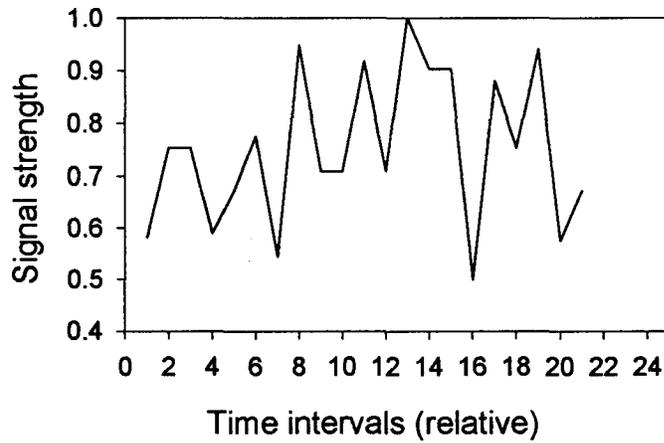
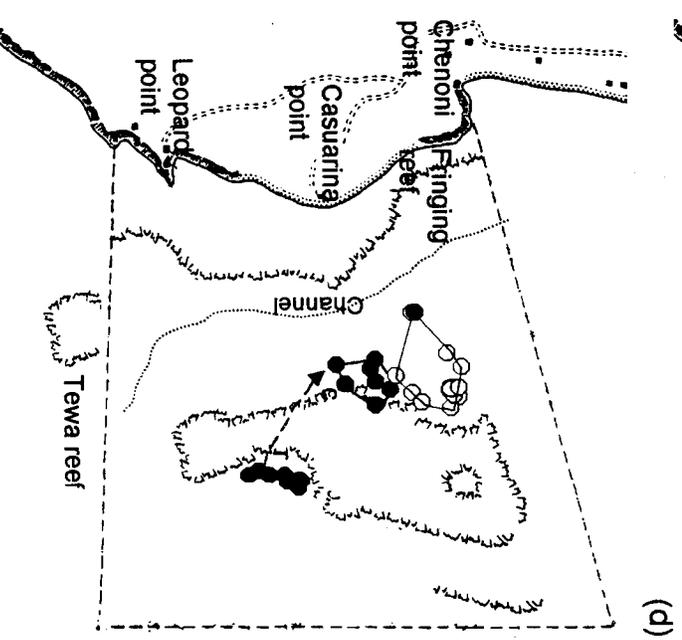
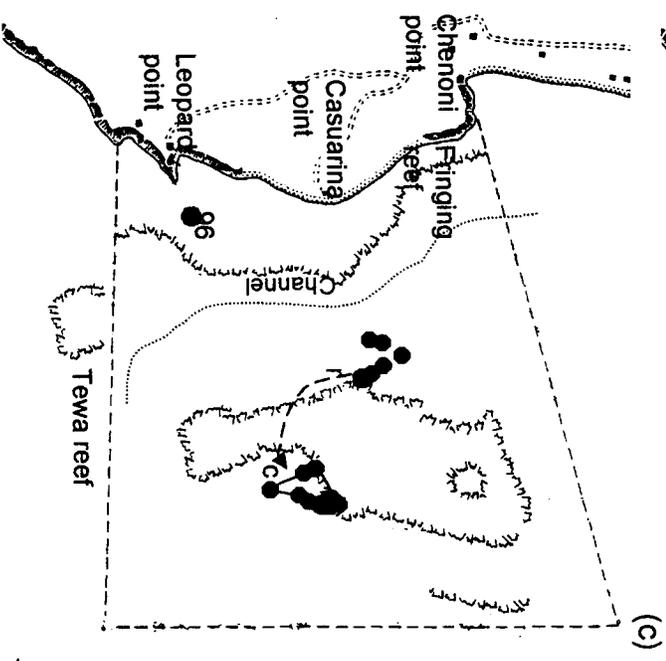
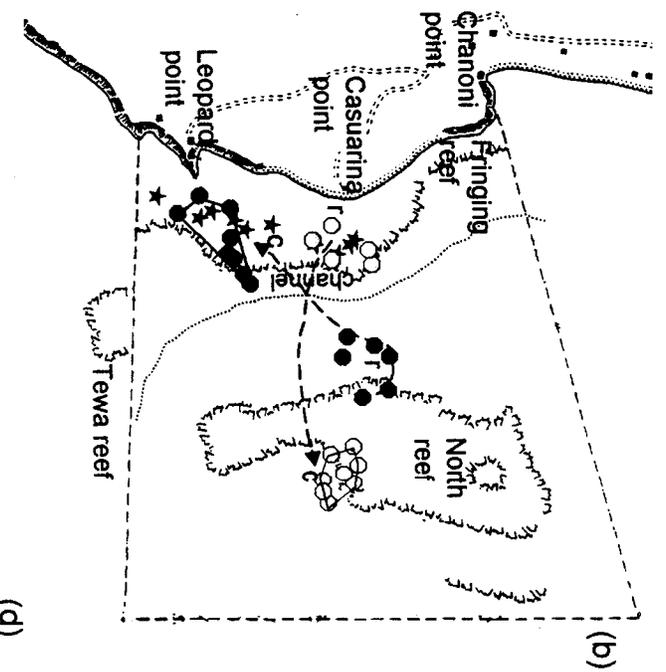
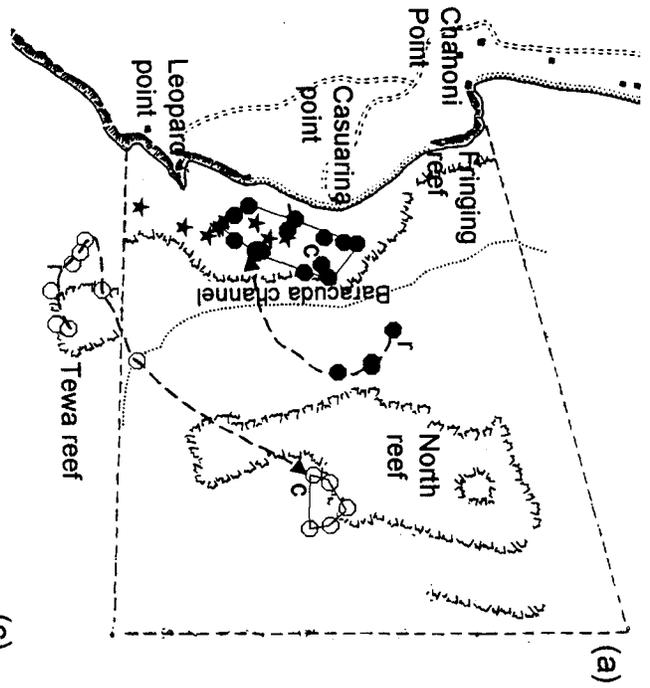


Figure 7-1: The variation of signal strength with time (relative units) monitored from fish in a reef crevice with the hydrophone positioned stationary above the fish and the receiver gain set constant at a low level.



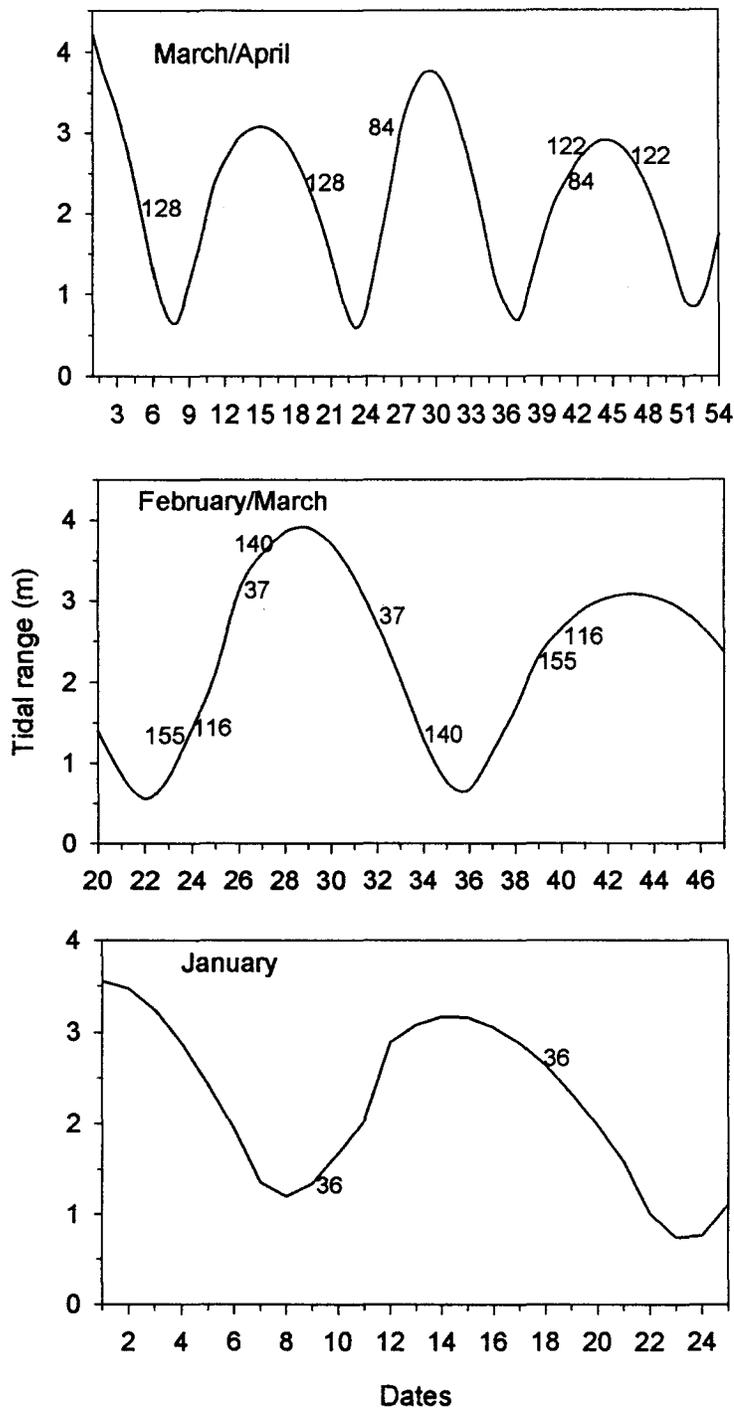


Figure 7-3: Diel tidal range on displacement and return to capture sites by greasy groupers (*Epinephelus tauvina*) homing within Malindi Marine Park, Kenya during January to April 2002. Figures show positions of individually coded fish at displacement and on homing. Dates are sequential (see Table 7-1). Tide data from Kenya Ports Authority tide table.

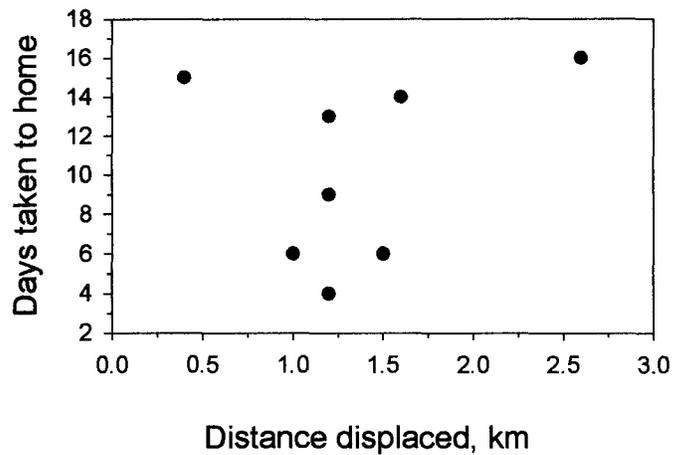


Figure 7-4: The relationship between days taken to return to capture sites by greasy groupers and distance of displacement within Malindi Marine Park, Kenya. ($r^2=0.185$, $p>0.05$)

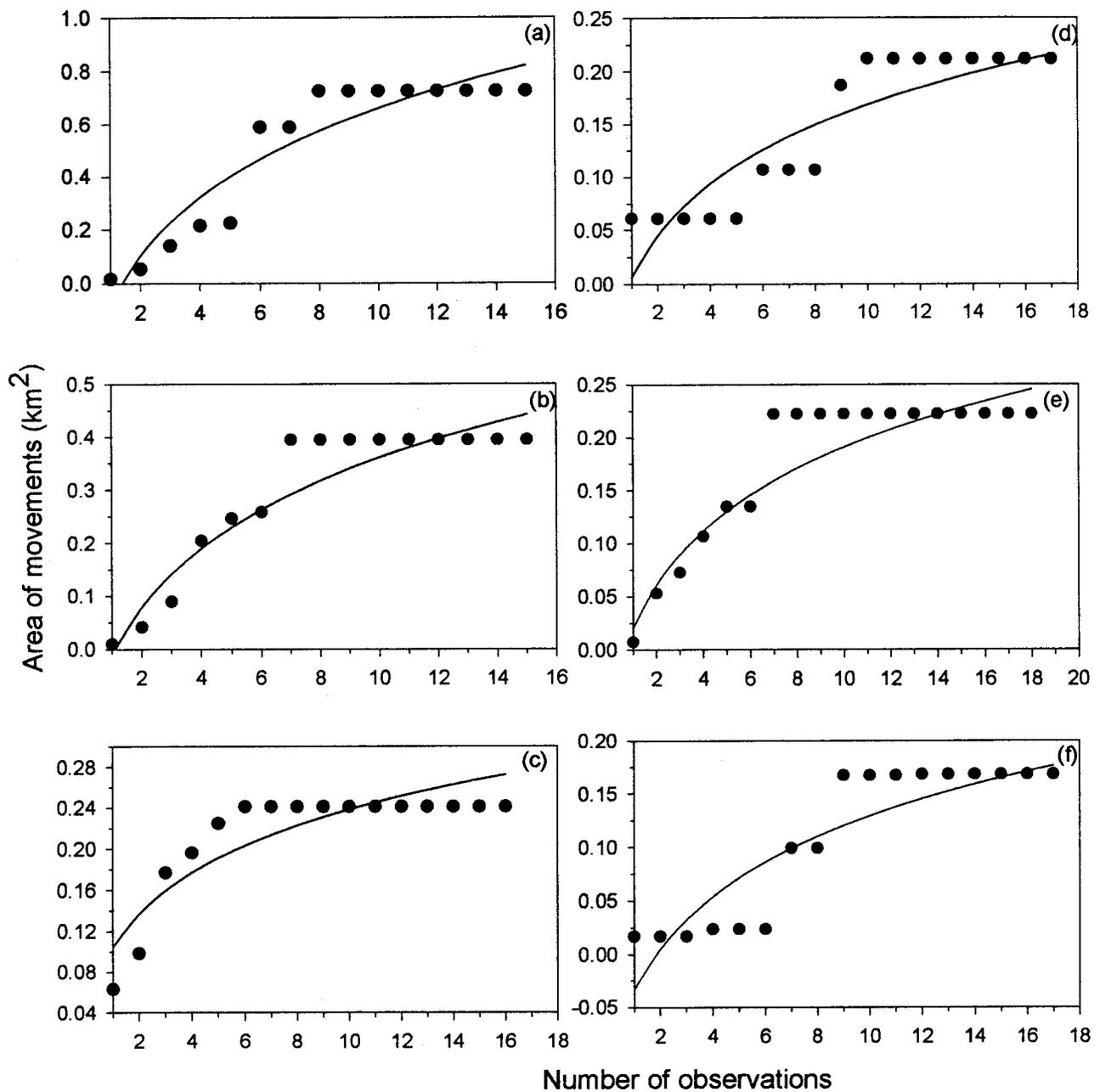


Figure 7-5: Observation-area curves for individuals of the greasy grouper upon return to capture sites following displacement from multiple sites within Malindi Park, Kenya, all curves show an asymptote. (a- code 37 $y=0.99\log x-0.37$, $r^2=0.88$; b-code 36 $y=0.50\log x-0.16$, $r^2=0.90$; c-code 84 $y=0.18\log x+0.051$ $r^2=0.78$; d-code 116 $y=0.22\log x-0.06$ $r^2=0.80$; e-code 128 $y=0.23\log x-0.049$ $r^2=0.87$; f-code 155 $y=0.22\log x-0.10$, $r^2=0.80$)

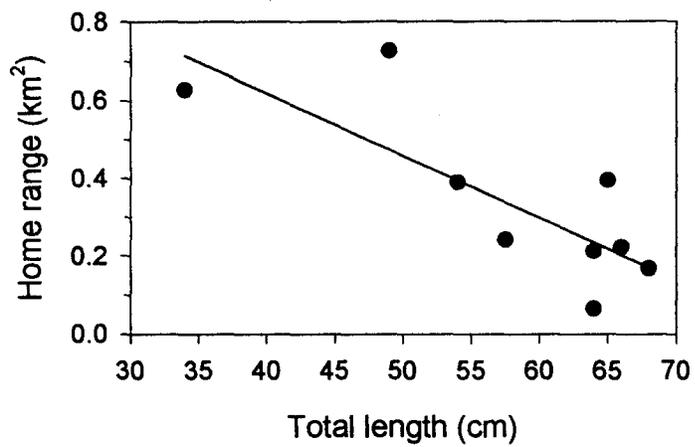


Figure 7-6: The relationship between home range size (km²) and total length (cm) of greasy groupers tracked within Malindi Marine National Park, Kenya. Model: $y=1.26-0.016x$, $r^2=0.63$, $p<0.05$

Chapter 8

Growth and survival rates of exploited coral reef fishes in Kenyan Marine Parks derived from tagging and length-frequency data

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Submitted to: Journal of Fish Biology

8.1 Abstract

Absolute growth rates and parameters were derived for 11 and 7 species of exploited coral reef fishes, respectively, using mark-recapture data from 3916 fish tagged within Malindi and Watamu National Marine Parks, Kenya, in 2001 and 2002. Growth rates ranged over an order of magnitude among species. Of the dominant commercial species, the whitespotted rabbitfish, *Siganus sutor*, had both the highest absolute growth rate (21.9 ± 14.6 cm/year) and growth coefficient ($K = 1.2/\text{year}$), whereas emperors (*Lethrinus spp.*) had somewhat lower rates (overall mean 10.95 ± 3.65 cm/year; maximum for *L. nebulosus*, 14.6 ± 7.3 cm/year; $K = 0.92/\text{year}$). In contrast, the orangestriped triggerfish, *Balistapus undulatus*, had an average annual growth rate of only 2.0 ± 1.9 cm. Growth coefficient (K) estimated for *S. sutor* and the sky emperor, *Lethrinus mahsena*, using length-frequency analysis (LFA) indicated a lower growth rate

($K=0.54/\text{year}$) for *S. sutor* than derived from tagging, but for *L. mahsena* the LFA-derived growth rate ($K=0.64/\text{year}$) was comparable to the K derived from tagging ($0.57/\text{year}$). Growth rates derived here for most but not all species (*L. mahsena* in particular) were similar to those reported from other coral reef regions. Catch-curve determined annual survival rate (S) was higher for *S. sutor* (0.145) than for *L. mahsena* (0.029), whereas, natural annual mortality rates (M) were comparable (*S. sutor*, 1.12 ; *L. mahsena*, 1.25), suggesting higher predation or emigration rates for *L. mahsena*.

8.2 Introduction

Demographic rates are fundamental to fisheries stock assessments and estimation of potential yields (King, 1995; Gallucci et al., 1996). In temperate waters, these rates can be estimated from changes on various parameters over time intervals determined from regular seasonal patterns of skeletal deposits (Weatherley and Gill, 1987). However, in tropical waters, lack of distinct seasonality has made such analyses less useful (Sparre and Venema, 1998), although some ageing techniques using otolith microstructures have been developed (Williams et al., 1995).

Many coral reef fishes support fisheries in the tropical oceans. However, demographic rates have been estimated for only a few of these species (Pauly, 1980; Buesa, 1987), in particular in the Caribbean (Munro, 1983) and French

Polynesian waters (Ariaz-Gonzalez et al., 1993). In these studies, age and growth have typically been determined by length-frequency analyses (Munro, 1983). However, the influence of environmental factors on growth rates, and the year-round spawning that typifies many tropical species, indicates that independent validation using more than one method of growth estimation would be beneficial (Weatherley and Gill, 1987; Sparre and Venema, 1998).

Demographic rates of commercial coral reef species in the Western Indian Ocean are mostly unknown (but see Ntiba and Jaccarini, 1988), and estimates from other regions having different environments may not be applicable (Pauly, 1980). The chief objective of this paper is to estimate growth parameters for several important commercially exploited species in the Western Indian Ocean. Apparent survival rates of these species within Marine National Parks was also determined. The estimates were based on both mark-recapture experiments and length frequency analyses of coral reef fishes in coastal Kenya. Reef fisheries in Kenya support approximately 8000 artisanal fishermen who fish between the fringing reefs and shore.

8.3 Materials and Methods

8.3.1 Study sites

This work was undertaken in Malindi (6.3 km²) and Watamu (10 km²) Marine National Parks on the Kenyan coast, both created in 1968 (see Fig. 4-1). Malindi Marine Park encloses a continuous fringing reef and patch reef habitats.

Watamu Marine Park is located approximately 25 kms south of Malindi and is bounded by a linear fringing reef located 1-2 km from the shore. Inside the fringing reef is a large lagoon (10 km²) with islands surrounded by patches of flat eroded inner reef.

8.3.2 Fish tagging

Traditional pentagonal shaped *Dema* traps (Kaunda-Arara and Ntiba, 1997) commonly used in East African coastal fisheries were used to trap fish for tagging. Trapped fish were identified to the species level possible using field guides from Bock (1978) and Lieske and Myers (1994), with difficult species confirmed using Smith and Heemstra (1998). Fish less than 14 cm in total length or species unsuitable for tagging (e.g., muraenids and chaetodontids) were released immediately. For each fish to be tagged, a serially numbered lock-on spaghetti tag (Floy FD-94, 6 cm long, orange) was inserted into the dorsal musculature below the dorsal fin using a tagging gun. The tag number was recorded, total length (nearest millimeter) measured and the fish released at the capture point. Fishermen fishing in waters adjacent to the parks were informed of the tagging program prior to its start and a reward (Ksh. 100) advertised as an incentive to report recapture information. Enthusiasm and participation in the exercise were periodically reviewed during meetings with local fishermen's associations. Tag number, total length (nearest millimeter), date of recapture, recapture location, fisherman's name and gear type, were recorded for each

recaptured fish. For the whitespotted rabbitfish, *Siganus sutor*, which is the most important commercial species in the adjacent fisheries, weight (g) was also recorded for recaptured fish. A total of 3911 fish (25 species) were tagged in the parks between February 2001 and March 2002.

Research fishing with *Dema* traps was conducted both inside and outside the two marine parks. Traps in fished sites adjacent the parks were set along transects located at geometric intervals (0, 0.2, 0.4, 0.8, 1.6 and 3.2 km) from and parallel to the southern border of the parks (Fig. 4-1). Each fishing event consisted of 2 transects fished with 4-6 traps for 3-4 days. Sampling effort ranged from 7-18 days per transect.

8.3.5 Data analyses

Growth increment data for seven species of fish including the commercially important *S. sutor*, and emperors (*Lethrinus spp.*) were used to derive growth parameters using the FiSAT package (Gayaniilo et al., 1994). To reduce bias caused by handling stress and time-dependent measurement error, only fish at liberty for more than 30 days were utilized for calculation of growth rates. The few fish that had been free for long periods but had not grown at all were considered to be affected by the tagging and excluded from analysis. Both fish recaptured in research traps within the parks and those returned by fishermen from outside the parks were utilized in growth estimates. The growth parameters

were derived using analytical methods based on the von Bertalanffy growth model:

$$L_t = L_\infty[1 - \exp -(K(t-t_0))] \quad (1)$$

Where L_t = length at time t (years), L_∞ = asymptotic length (cm), K = growth coefficient (yr^{-1}) and t_0 = hypothetical age when length would be zero. L_∞ was initially estimated from; $L_\infty = 0.95L_{\text{max}}$ (Pauly and Murphy, 1982), where L_{max} is the size of the largest fish caught. Fabens routine in FiSAT was then used to obtain a further estimate of L_∞ and the growth coefficient (K) and to help identify any anomalous data (Munro, 1999). In cases for which resulting estimates of L_∞ were markedly larger than both the initial estimate and known values from the literature, Appeldoorn's methods was subsequently used to derive K with fixed values of L_∞ . Munro's method was used to derive the parameters if sample size was small. In most cases there was convergence of L_∞ with initial estimates. The methods are all incorporated as routines in the FiSAT package.

The Phi-prime index, ϕ' , (Munro and Pauly, 1983), was used to compare growth performance of species for which previous estimates had been made and were available in "Fishbase 98" (Froese and Pauly, 1998) or the literature.

Further estimates of growth parameters were made for *S. sutor* and the sky emperor, *Lethrinus mahsena*, (the two most important commercial reef species along the East African coast) using length frequency analysis (LFA) on fish caught within the parks. To increase modal definition for LFA, samples were

pooled tri-monthly without weighting and assigned a single collection date.

Estimates of the growth coefficient K (yr^{-1}) and asymptotic size L_{∞} (cm) were made on the restructured length frequency data using the surface response option in ELEFAN I subpackage in FiSAT and the parameter combination with the highest index of fit (R_n , range 0-1) selected. In ELEFAN 1, data are reconstructed to generate “peaks” and “troughs”, and the goodness of fit index (R_n) is defined by:

$$R_n = 10\text{ESP}/\text{ASP}/10 \quad (2)$$

Where, the ASP (Available Sum of Peaks) is computed by adding the best values of the available “peaks” and the ESP (Explained Sum of Peaks) is computed by summing all the peaks and troughs of the Length-frequency modal progression “hit” by the growth curve. Details of the ELEFAN procedures are given in Pauly (1987).

The instantaneous annual total mortality rate (Z) for *S. sutor* and *L. mahsena* were calculated using linearized length-converted catch curves, derived from the linearized catch equation as:

$$\ln N_t = \ln N_0 - Zt, \quad (3)$$

In the equation, N_t (number at age) is replaced with the frequency, F , between two size classes L_1 and L_2 , and t becomes the age at the class interval mid-point. The equation therefore becomes (Pauly, 1984):

$$\ln(N_i / dt_i) = a + b.t_i \quad (4)$$

where N is number of fish in length class i , dt is the time needed for the fish to grow through the length class, t is the relative age (computed with $t_0 = 0$) corresponding to the mid-length of class i . A regression line was fit to points immediately to the right of the highest point on the curve. The slope of the line, b , is an estimate of $-Z$. Since fishing is not allowed inside the parks, estimates of Z should reflect natural mortality plus emigration rates (Pinto, 1986). Having derived the growth coefficients (K) and asymptotic lengths (L_∞), natural mortality rates (M) for *S. sutor* and *L. mahsena* were then estimated following Pauly's (1980) empirical equation;

$$\ln M = -0.0152 - 0.279 \ln L_\infty + 0.6543 \ln K + 0.463 \ln T \quad (5)$$

Where T (the annual average sea surface temperature) is 27 °C on the Kenyan coast (Brakel, 1984). As Z is confounded by emigration rates from the parks, estimates of apparent annual survival rates (S) may better reflect population changes within the Parks. S was calculated for *S. sutor* and *L. mahsena* as:

$$S = \exp(-Z), \quad (6)$$

following the derivation in Sparre and Venema (1998).

8.4 Results

Growth rates derived from length changes between tagging and recaptures for fish that had been at large for more than 30 days ranged over an order of magnitude for the different species (Table 8-1). The orangestriped triggerfish, *Balistapus undulatus*, peacock grouper, *Cephalopholis argus*, and blacktip

grouper, *Epinephelus fasciatus*, had the slowest growth rates (0.005 ± 0.003 cm/day). *S. sutor* showed the fastest growth rate (0.06 ± 0.04 cm/day; 21.9 ± 14.6 cm/year) amongst all the species. The three species of emperors (*Lethrinus spp*) had a mean growth rate of 10.95 ± 3.65 cm/year, with the spangled emperor, *L. nebulosus*, exhibiting the fastest rate of 0.04 ± 0.02 cm/day (14.6 ± 7.3 cm/year).

Length and weight data for *S. sutor* were obtained at capture from 48 fish released without tagging, and from 26 tagged fish at the time of recapture after being at liberty for more than 30 days. Length-weight relationships for these fish are described by the equations:

Tagged fish: $W = 0.0187 \cdot L^{2.88}$ (7) and,

Untagged fish: $W = 0.032 \cdot L^{2.73}$ (8)

the two relationships are similar (Fig. 8-1), and the length coefficients do not differ significantly ($t_{0.05(2), 70} = 1.994$, $t = 0.28$, $p > 0.05$).

Both the Fabens and Appeldoorn methods in FiSAT indicated a seasonal growth amplitude $C = 0$ and hence lack of seasonal variation in growth for all species. *S. sutor* had the highest growth coefficient ($K = 1.20$ / year) with a fixed L_{∞} of 36.3 cm total length. The estimate of K for *S. sutor* using LFA in ELEFAN I (Fig. 8-2a) was lower (0.54 /year). However, LFA indicated an L_{∞} of 35.7 cm for this species, comparable to that initially estimated from L_{max} (36.3 cm, Table 8-2).

The emperors had moderate growth rates, with the spangled emperor, *Lethrinus nebulosus*, having the highest K (0.92/year, Table 8-2). The growth coefficient of *L. mahsena* derived from tagging data was 0.57/year, while LFA (Fig. 8-2b) in ELEFAN I generated a higher but comparable coefficient (K= 0.64/year) for this species. L_{∞} estimates of 35.2 and 29.5 cm were estimated for *L. mahsena* using length-frequency analysis in ELEFAN I and tagging data, respectively. The growth curves used to generate the growth parameters (Table 8-2) for the seven species of reef fish using mark-recapture data are shown in Figure 8-3. The annual survival rate (S, equation 6) calculated from the slope of the linearized length-converted catch curve (annual Z) (Fig. 8-4) was lower for the sky emperor (S= 0.029, Z=3.52) than for the whitespotted rabbitfish (S= 0.145, Z=1.93). Given that fishing is not permitted in the parks (i.e., fishing mortality $F = 0$), the present estimates of S will depend on natural mortality (M) plus emigration from the parks. Annual natural mortality rates (M) of 1.12 and 1.25 were calculated for *S. sutor* and *L. mahsena*, respectively.

8.5 Discussion

The growth coefficient (K) estimated in this study for *S. sutor* averaged 1.2/year and was similar to rates estimated for East African waters by Ntiba and Jaccarini (0.9/year) based on otolith microstructure and by Woodland (1984) using LFA (1.5/year). Growth performance indices for *S. sutor* from the present and these earlier studies were also similar. However, the K estimated in this study from LFA

(0.54/year) was much lower and likely unreliable because of a poor fit of the growth curve to the length-frequency progressions. The better match between the otolith microstructure and tagging-based estimates of K supports the notion that these methods are superior to LFA in determinations of growth rates (King, 1995). LFA-based estimates may be biased by the difficulty in separating length modes in fishes that spawn near year-round in the tropical regions (Sparre and Venema, 1998) and are often believed to underestimate K (Isaac, 1990).

The K values estimated for *L. mahsena* from both tagging (0.57/year) and LFA (0.64/year) were greater than and outside the range (0.1-0.3) previously reported for this species (Froese and Pauly, 1996). The similarity of K estimated by 2 independent methods adds credence to these values. Higher rates in the emperors (the spangled emperor, *Lethrinus nebulosus*, had even a higher rate) than reported from other areas suggest superior conditions for growth in the Kenyan coastal region. There was a paucity of data in the literature on most other species for comparison to presently determined growth parameters.

However, the similarity of K and L_{∞} values derived for *L. mahsena* and *S. sutor* in this chapter using LFA to those derived in chapter 3 (see Table 3-3) for specimens obtained outside the parks, seem to validate the results of ELEFAN.

Estimates of Z/K and M/K, that describe the ratio of mortality rate to the growth coefficient, can be made from tagging and LFA analyses and may prove useful to

fisheries management (Gallucci et al., 1996). In this study Z includes both M and the rate of emigration. The present data suggest a higher Z/K for *L. mahsena* (5.5) than for *S. sutor* (3.6), which in turn suggests that *S. sutor* has a broader length composition than *L. mahsena* in Malindi and Watamu Parks (see, e.g., Gallucci et al., 1996). This result is in keeping with higher “spill-over” or out-migration of *S. sutor* in all size ranges than *L. mahsena*. The M/K ratios for *L. mahsena* (1.95) and *S. sutor* (2.07) using the LFA determinations of K, lie within the range (1.5-2.5) expected for most species (Beverton and Holt, 1959), although for *S. sutor* a somewhat lower (0.9) estimate is derived using tagging data.

For fishes, tagging success will often depend to some extent on the body, skin and scale type of the species. In this study, *S. sutor* was an ideal candidate for tagging, with a low rate of tag loss (see Chapter 5) and little evidence of any effect on growth as suggested by length-weight comparisons (Fig. 8-1).

Emperors appeared to be more prone to tag loss, but our data are insufficient to assess the potential effect of tagging on growth of this and the several other species. However, the similarity of the K values assessed by tagging and LFA is consistent with the notion that for *L. mahsena*, as for *S. sutor*, tagging had little to no effect on growth. However, there were a few exceptional fish that had not grown at all over a period of more than 30 days, and these were deemed to have been affected by the tagging and were not included in the analyses. This might

have eliminated some slow growing individuals. Nevertheless, the close fit of the data to the general growth curve of most species suggests that the curves are an accurate reflection of growth in the population.

Finally, our data suggest that apparent survival rates (S) of the two most important species in coastal East African fisheries, *S. sutor* and *L. mahsena*, were quite low within the Malindi and Watamu Marine Parks. There is no evidence that tagging had any effect on S; there are no fisheries within the parks and expected natural mortality based on growth characteristics and temperature was similar for the two species. However, there is strong evidence that emigration of both species occur from both Parks (see chapter 5) and may contribute to the low survival rates. *S. sutor* has a low emigration rate from Watamu Park, while *L. mahsena* emigrates from both parks. This disparity in movements could perhaps explain the lower apparent survival rate of *L. mahsena* relative to *S. sutor*, particularly since natural mortality rates were comparable between the two species. There is also some evidence that fish predation rates within these parks may be elevated (McClanahan, 1995). In conclusion, this study confirms the usefulness of tagging as a means to better determine demographic rates of commercial fishes that form the basis for stock assessments of many tropical small-scale fisheries (Gallucci et al., 1996).

8.6 Acknowledgments

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Table 8-1: Absolute growth rates of 11 species of coral reef fishes in coastal Kenya derived from lengths at capture and recapture for fish that had been at liberty for more than 30 days.

Species	n	Mean size at capture (cm) \pm s.d.	Mean size at recapture (cm) \pm s.d.	Mean days free \pm s.d.	Growth rate (cm day ⁻¹ \pm s.d)
<i>Gaterin flavomaculatus</i>	6	26.4 \pm 1.84	29.2 \pm 3.89	100.6 \pm 52.4	0.03 \pm 0.02
<i>Gaterin gaterinus</i>	1	26.8	26.8	134	0.01
<i>Lethrinus mahsena</i>	16	18.9 \pm 3.20	19.6 \pm 1.83	108.8 \pm 76.6	0.03 \pm 0.03
<i>Lethrinus sanguineus</i>	6	20.7 \pm 1.96	23.3 \pm 3.37	138.2 \pm 109.7	0.02 \pm 0.01
<i>Lethrinus nebulosus</i>	6	25.8 \pm 6.3	28.9 \pm 4.97	70.3 \pm 85.7	0.04 \pm 0.02
<i>Siganus sutor</i>	32	19.2 \pm 3.95	22.2 \pm 4.26	61.5 \pm 35.9	0.06 \pm 0.04
<i>Siganus luridus</i>	1	14.6	16.3	37.0	0.05
<i>Naso hexacanthus</i>	3	23.2 \pm 1.85	26.9 \pm 3.0	148.0 \pm 67.0	0.025 \pm 0.003
<i>Balistapus undulatus</i>	6	24.3 \pm 4.1	25.3 \pm 3.3	223.2 \pm 94.8	0.005 \pm 0.003
<i>Cephalopholis argus</i>	4	38.7 \pm 6.8	40.2 \pm 6.3	231.0 \pm 0.0	0.01 \pm 0.002
<i>Epinephelus fasciatus</i>	1	27.6	28.0	46.0	0.01

Table 8-2: Summary of growth parameter estimates for seven species of tagged coral reef fish sampled from Watamu and Malindi Marine Parks, coastal Kenya. K is annual instantaneous growth rate, ϕ' (phi-prime), is a growth performance index, N is sample size, L_∞ in brackets are fixed values initially derived from $L_\infty = 0.95L_{\max}$

Species	Published values					Current estimates					
	L_{\max}	L_∞	K	ϕ''	S	L_{\max}	L_∞	K	N	ϕ''	Method
<i>Siganus sutor</i>	45	36.2	1.5	3.06	1	38.2	(36.3)	1.20	32	3.19	A
<i>Lethrinus mahsena</i>	65	28.3	0.3	2.60	2	29.5	(28.0)	0.57	16	2.65	A
<i>Lethrinus nebulosus</i>	86	58.5	0.7	3.41	2	36.1	39.7	0.92	6	3.16	M
<i>Lethrinus sanguineus</i>	-	-	-	-	3	44.0	(41.8)	0.77	6	3.13	F
<i>Gaterin flavomaculatus</i>	60	-	-	-	2	41.2	(39.1)	0.78	6	3.07	M
<i>Naso hexacanthus</i>	-	-	-	-	4	38.8	32.9	1.32	3	3.20	M
<i>Balistapus undulatus</i>	30	-	-	-	5	29.7	28.4	0.54	6	2.64	M

1. Woodland, (1990); 2. Carpenre and Allen (1989); 3. Masuda et al. (1984); 4. Myers (1991), 5. Matsuura (1979).
Methods; A, Appeldoorn, M, Munro, and F, Faben.

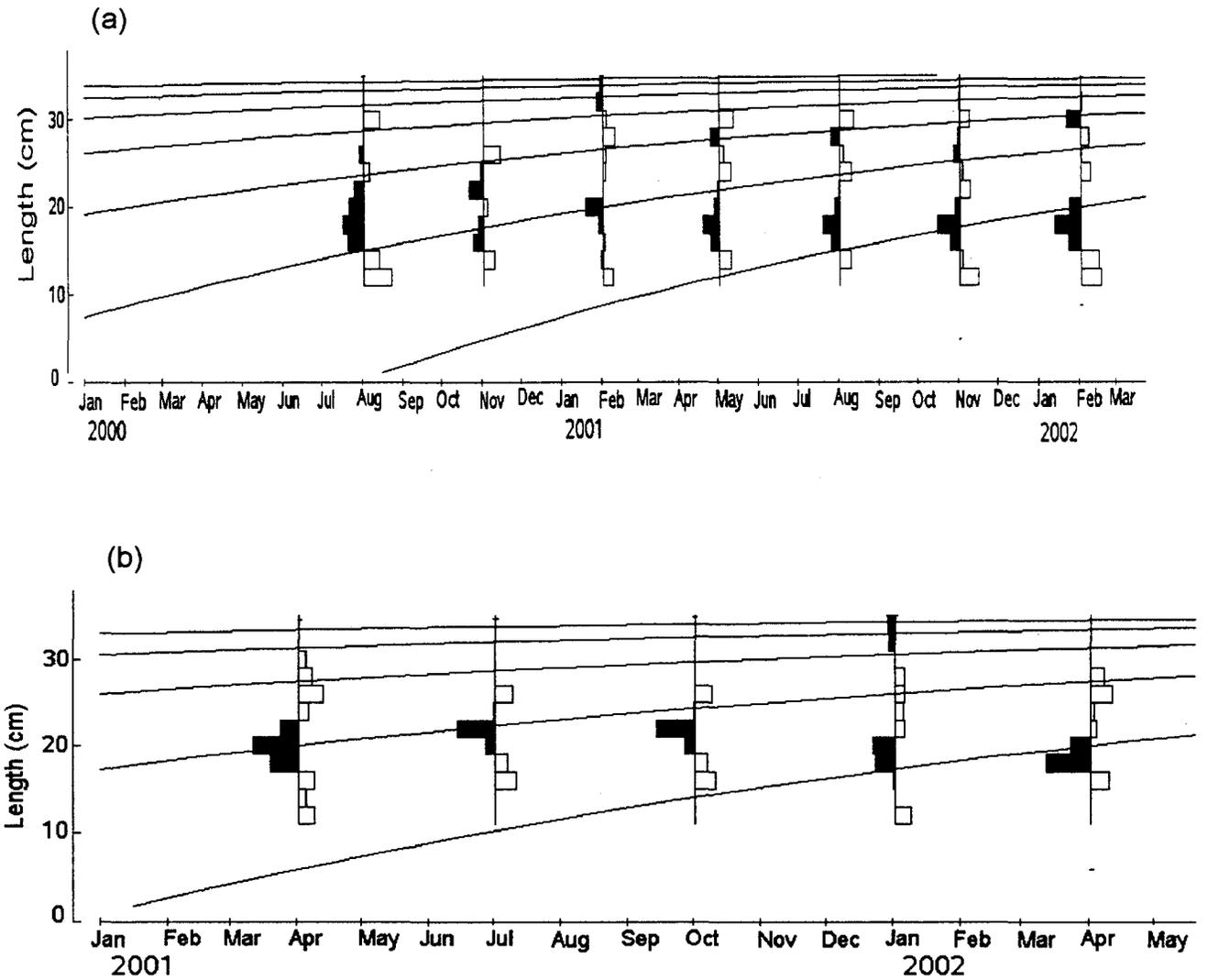


Figure 8-2: The growth curves (continuous lines) of cohorts of (a) whitespotted rabbitfish, *Siganus sutor*, (b) sky emperor, *Lethrinus mahsena*, in coastal Kenya superimposed over restructured length frequency data. Peaks (black) are positive points and troughs (white) are negative points. *Siganus Sutor*; $n=2253$, $R_n = 0.34$, $L_\infty = 35.7$ cm, $K = 0.54/\text{year}$. *Lethrinus mahsena*; $n=1232$, $R_n = 0.42$, $L_\infty = 35.2$ cm, $K = 0.64/\text{year}$. Parameters are explained in text.

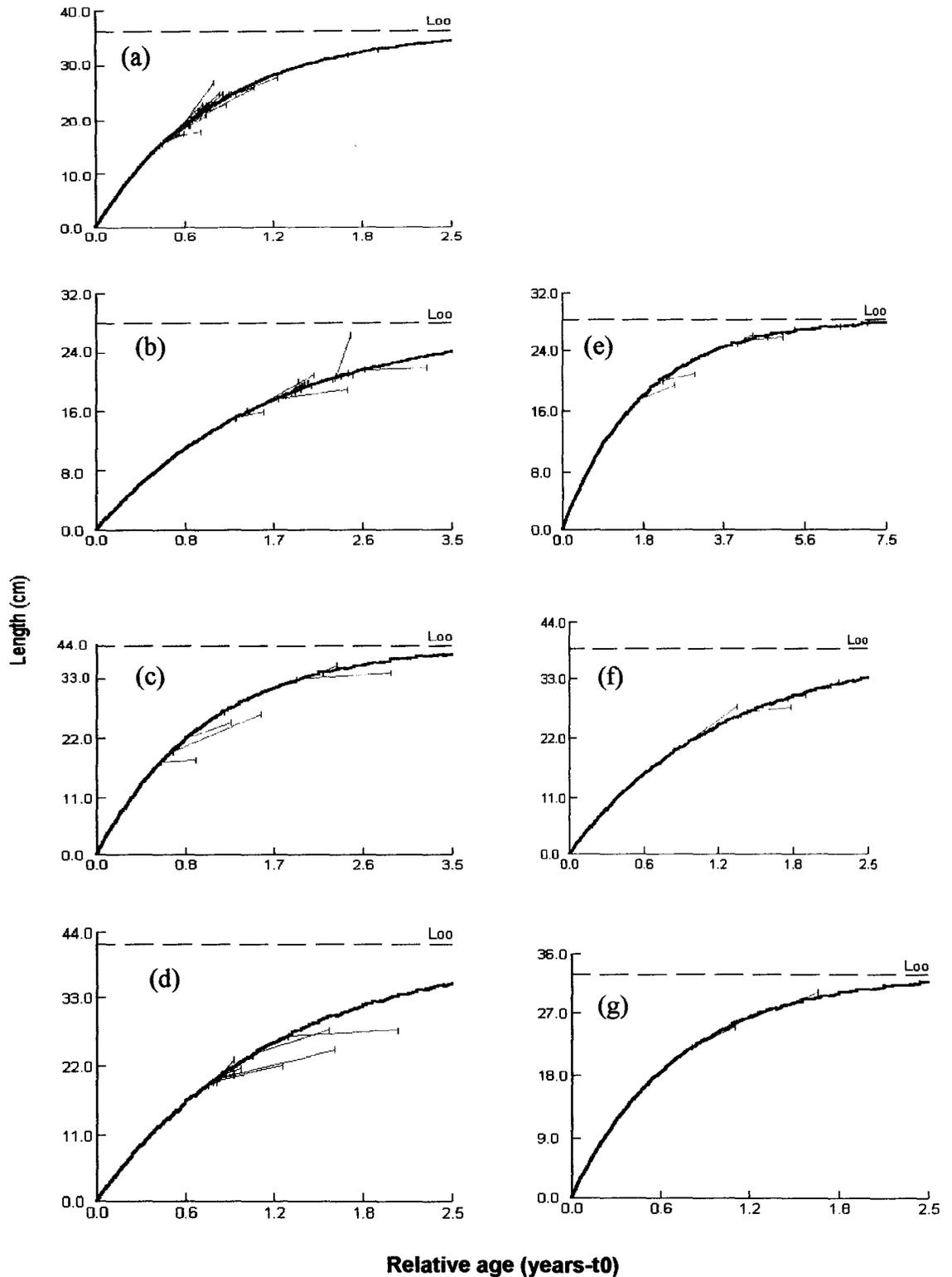


Figure 8-3: Growth curves of seven species of exploited coral reef fish based on mark-recapture data from coastal Kenya. Sidelines show deviation of individual growth from the average population growth curve. L_{∞} is asymptotic length approached by the growth curves for (a) *Siganus sutor*, (b) *Lethrinus mahsena*, (c) *Lethrinus nebulosus*, (d) *Lethrinus sanguineus*, (e) *Balistapus undulatus*, (f) *Gaterin flavomaculatus*, and (g) *Naso hexacanthus*. Growth parameters are given in Table 8-2.

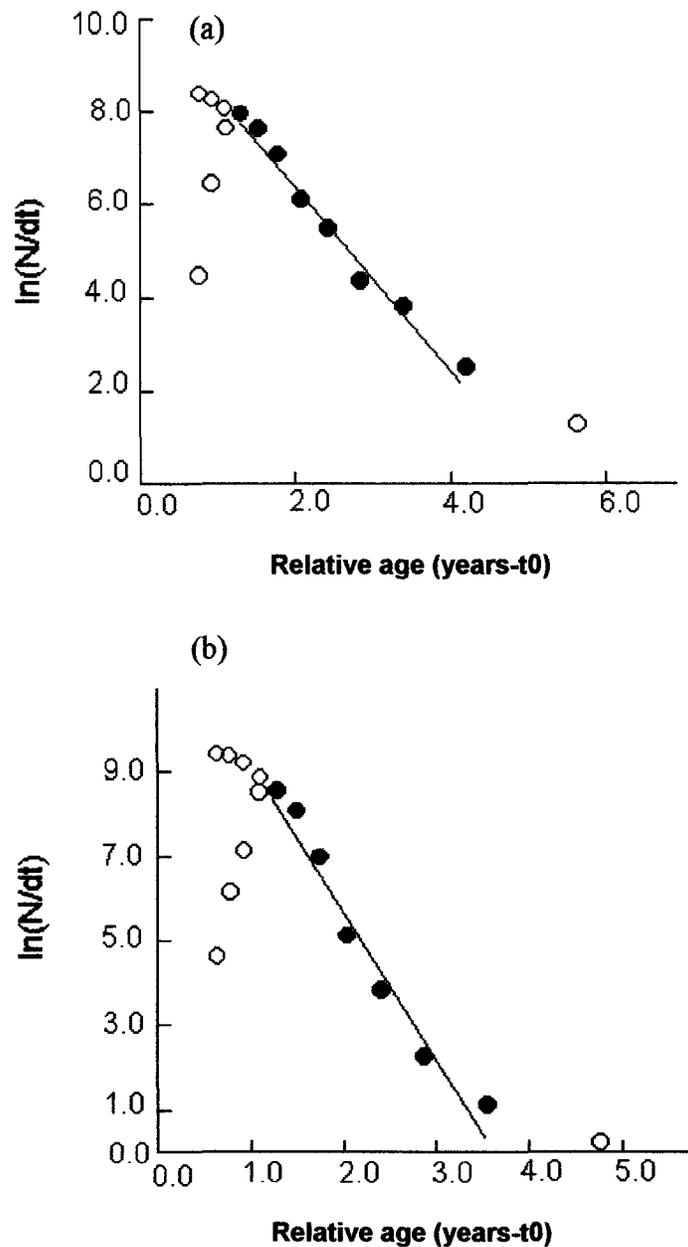


Figure 8-4: Linearized length-converted catch curves used to estimate annual survival rates (S) from the slopes (Z) of the curves in (a) *Siganus sutor* and (b) *Lethrinus mahsena* inside Malindi and Watamu Marine Parks, Kenya. Curves are fitted using ELEFAN II package. N is number of fish in length class i and dt is time needed for fish to grow through the length class. Closed cycles (●) were used in the regression, yellow cycles were not. Mortality (Z) and survival (S) rates; *S. sutor* $Z=1.93/\text{year}$, $S=0.145/\text{year}$; *L. mahsena*, $Z=3.52/\text{year}$, $S=0.029/\text{year}$.

Chapter 9

Summary

There is increasing evidence that marine reserves are effective in restoring overfished stocks (Jennings, 2001) and interest in their potential role in fisheries management is now mounting (Roberts and Polunin, 1991). Reserves are considered an effective management option particularly in the tropics where conventional fisheries management methods that regulate input and output parameters are difficult to apply and enforce. An additional advantage of reserves is their potential to sustain adjacent fisheries through a spillover effect of adult, juvenile and larval fish (Rowley, 1994). The spatial-scale of reserves, their design with respect to local conditions, and species behavior, will all affect the effectiveness of the reserves in enhancing fish abundance both within and outside its boundaries. Since most reserves are allocative in nature, conflict will often arise on resource use allocation between fisheries management and fishermen. In order to mitigate potential conflicts, reserves need to provide economic as well as ecological spillover benefits to local communities.

In this thesis I examined evidence of the role of two of the oldest marine reserves in coastal Kenya (Malindi and Watamu Parks, both created 1968) in conserving fish stocks and maintaining adjacent fisheries production through a spillover effect. Historical data on Kenya's coastal fisheries (Chapter 3) indicate that landings of commercial fish families have declined sharply in the last decade.

The large drop (78%) in fish landings in the densely populated district of Mombasa together with the high exploitation ($E > 0.5$) and fishing mortality rates of commercial species (e.g., *Lethrinus mahsena* and *L. sanguineus*) imply that fishing pressure is largely responsible for the decline in landings. Although data on fishing pressure is lacking, this notion is reinforced by the steepest decline (72%) in landings of the most vulnerable group to fishing pressure, the groupers (family Serranidae). There may also have been some related loss of productive habitat.

Comparisons of catch per unit effort (CPUE) and fish densities (#/500 m²) across the park boundaries (Chapter 4) indicated that the abundance of most species is orders of magnitude higher inside the parks. This suggests that the parks do provide effective refugia from fishing. However, some species (e.g., *Leptoscarus vaigensis*, *Siganus sutor* and the Labridae) have higher seasonal abundance outside the parks. Hence, the role of the parks in reducing fishing mortality may vary between species and season. Fish sizes are also larger inside the parks for most but not all species, and length-frequency analysis indicates a wide size structure of exploited species within the parks. The parks therefore likely serve as important nursery grounds and may help maintain genetic structures of exploited species.

Spillover of fishes from marine reserves will depend on species, home range size and location, and mobility. Species with home ranges centered inside the parks

will likely spillover little and will be more protected from fishing mortality. However, highly mobile species are likely to be less conserved by the reserves and any spillover-effect to adjacent fisheries will be minimal. Greater spillover is expected for the moderately mobile species. Densities may be expected to peak inside the parks and decrease with distance from their centers but not to zero levels (Kramer and Chapman, 1999). I tested these predictions by fitting CPUE and fish density data to the logistic decay function ($Y = 1/(1 + \text{Exp}(\beta_0(\beta_1 - x)))$). The influence of habitat structure on spillover was also evaluated by comparing density gradients across patch and fringing reefs. Results showed steep density (number of fish/trap and #/500 m²) gradients from patch reefs for most species suggesting little spillover from this reef type except for *S. sutor*. The two most important commercial species (*S. sutor* and *L. mahsena*) showed seasonal and site-specific differences in patterns of density gradients across reserve boundaries. For *L. mahsena*, densities declined abruptly at the park borders in both seasons (NE and SE monsoons), indicating little dispersal, while *S. sutor* had a shallower density gradients suggesting greater dispersal from the parks especially during the SE and NE monsoons at Malindi and Watamu, respectively. Inter-annual variation in patterns of CPUE was noted for *S. sutor* across the patch reef at Malindi.

Habitat structure may interact with species mobility to determine the magnitude and direction of movements of fish from reserves (Wiens et al., 1985). In this thesis I show that movements are more pronounced on continuous fringing than

on patch reefs (Chapter 5). Tagging experiments showed out-migration of only a few (12%) of the species tagged inside the parks with multiple recaptures of most species within the parks. Movements from the parks were mostly attributable to three species (*S. sutor*, *L. mahsena* and *L. sanguineus*). At Malindi Park, more fish (6.9%) were recaptured by fishermen adjacent to a fringing reef than a patch reef (1.4%) within the park. A greater range of movements was exhibited by *S. sutor* tagged on a fringing reef that spans the park. The species traveled greater average distance from the fringing reef (1.6 ± 1.07 km) than the patch reef (0.67 ± 0.51 km). Similarly, other species moved shorter average distance (<0.5 km) from the patch reef. At Watamu Park (a park bounded by a fringing reef), only the emperors (Lethrinidae) consistently moved outside the park. Few tagged *S. sutor* were caught outside Watamu Park, although this species constitutes the bulk of the catches in adjacent fisheries. Movement rates are therefore judged to be site and species specific.

These results have implications for the design and function of marine reserves. Home ranges and median distance of movements most likely fall within the park at the Malindi patch reef, thus parks enclosing patch reefs will likely conserve fish densities even within a small area. The commercially preferred species in the fisheries (*S. sutor*) migrates mostly from the fringing reef portion of Malindi Park. Thus designs that include a small portion of reefs contiguous with adjacent sites will facilitate greater spillover (e.g., *S. sutor* at Malindi), while designs that include a greater portion of these reefs within the park will likely lead to greater local

retention of the species with minimal spillover. The geometry of a reserve will also influence spillover rates and direction. Watamu Park, which has greater along-shore than cross-shore dimensions, appears to have a greater lateral spillover of the emperors than of *S. sutor*. It may be that *S. sutor* performs a more onshore-offshore movements as opposed to along-shore movements (the data are insufficient to confirm this). Hence it is likely that catch rates of *S. sutor* outside Watamu Park are sustained more by a offshore source of adults perhaps supplemented by a within park source of larval recruits.

The design criteria will obviously depend on the park objectives. Presently, the major objective of Kenya's marine parks is to conserve biodiversity with a focus on tourism. As most species don't seem to emigrate from the parks and biomass is higher inside the parks, this suggests that the conservation (increased survivorship of species and their sustainable utilization) objective is being met. However, design strategy that takes into account movement patterns in relation to park size, shape and habitat distribution may ensure greater spillover.

In this thesis, I also demonstrated that the parks may play a role in conserving populations of commercial groupers (Chapter 7) that have been heavily overfished outside the parks. Homing by greasy groupers, *Epinephelus tauvina*, (67% homing success) may interact with zero fishing mortality within the parks to conserve a strong local spawning stock biomass. Although studies show that homing tendency is strong in some teleosts (Papi, 1992), such evidence is

scarce for coral reef fishes and in particular for large sized commercial species like the groupers. I have used ultrasonic telemetry to document homing and site fidelity in large sized groupers within Malindi Marine Park. The homing mechanism used by this species is unknown, but tidal factors (in particular spring tidal phase) may play an important role. More research will be needed to determine the homing mechanism in this species.

Scientific management of fisheries requires knowledge of population parameters. For example, growth parameters are necessary in assessing stocks and modeling populations. However, such parameters are lacking for most exploited tropical species. Part of this paucity of data has to do with the difficulty of ageing tropical fish and the extra effort and resources needed to validate results often derived from length-based methods (Pauly, 1982). In this thesis, I provide data on growth rates and parameters for some exploited reef fishes from Kenyan waters of the Western Indian Ocean (WIO) (Chapter 8). Population parameters (e.g., K , L_{∞} , θ' , Z and M) are derived using tagging data and length-frequency analysis (LFA) based on the von Bertalanffy growth model. Overall growth rate (K /year) seems to be higher for species on the Kenyan coast suggesting a superior environment for growth. Tagging and LFA yielded different estimates of K for *S. sutor*, but K derived for *L. mahsena* was comparable for both methods. The results demonstrate the use of tagging data to validate results of LFA analysis.

I believe my thesis provides empirical data that will be useful in designing marine reserves both in Kenya and in other parts of the world. The data supports the efficacy of reserves as fisheries management tools and further provides additional data necessary for stock assessment and modeling.

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