Available online at www.sciencedirect.com
SCIENCE DIRECT®

Biological Conservation 118 (2004) 1–13

BIOLOGICAL CONSERVATION

www.elsevier.com/locate/biocon

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

Boaz Kaunda-Arara [a,*], George A. Rose [b]

[a] Department of Fisheries, Moi University, P.O. Box 1125, Eldoret, Kenya
[b] Fisheries Conservation Chair, Marine Institute of Memorial University, P.O. Box 4920, St. John's, Nfld, Canada A1C 5R3

Received 28 August 2002; received in revised form 1 May 2003; accepted 21 June 2003

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 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*, WSR) 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) across park borders from fringing and patch reefs. A steep decay in CPUE off the Malindi patch reef suggested little spillover of most species. However, greater spillover was suggested off fringing reefs. Species differences were evident. The two most important commercial species showed different density gradients. Species diversity declined more abruptly off the fringing reefs. We conclude that although spillover of most species from the parks is limited, the most important commercial species exhibits significant spillover to adjacent fisheries and the Parks likely comprise important nursery and growth areas for other species.

Keywords: Fish yields; Marine protected areas; Monsoons; Patch reefs; Spillover-model; *Siganus sutor*; *Lethrinus mahsena*

1. Introduction

Marine protected areas hold potential to sustain fisheries production in adjacent waters (Bohnsack, 1992; 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, 1996; 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). Additionally, reserves may select for short dispersers and may skew sex ratios in species with differential mobility rates between sexes. However, many putative effects derived from modeling studies (e.g., Polachek, 1990; DeMartini, 1993; Man et al., 1995), have not been validated (Roberts and Polunin, 1991; Sale, 1998; Murray et al., 1999). Validation has been hampered by a lack of reserves, 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 reserves (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 sustain fisheries, but rather to assist conservation or non-fisheries use of the area or resource. Where fisheries were a concern, area

* Corresponding author.
E-mail addresses: b_kaunda@yahoo.com (B. Kaunda-Arara), grose@caribou.mi.mun.ca (G.A. Rose).

0006-3207/$ - see front matter © 2003 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2003.06.001

protections have been used 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 cannot 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 available area for fishing, and support for such conservation measures may be lacking if there is little perceived or real spillover of benefits to adjacent fishing communities (Johannes, 1978; Roberts and Polunin, 1991). Reserves may not therefore realize their objectives if the legitimate needs of local communities are not considered (Allison et al., 1998; McClanahan, 1999).

In East Africa, reef fish comprise a major resource and form the basis of artisanal coastal fisheries in Kenya and Tanzania (e.g., Kaunda-Arara, 1997). Marine reserves were established in this region over 30 years ago, and National Marine Parks were first gazetted in Kenya in 1968 to protect reefs (and fishing grounds) on the East African coast (Fig. 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). In particular, the relative densities, composition and movements of reef fishes in and across management boundaries are unknown, although recent studies have hypothesized that spillover of fishes may be occurring from Kenyan marine parks to adjacent fished regions (McClanahan and Kaunda-Arara, 1996; McClanahan and Mangi, 2000). In the present study, we use trap catches to examine the spillover hypothesis by comparing catches and community structure inside, outside and across the boundaries of the two oldest marine parks in

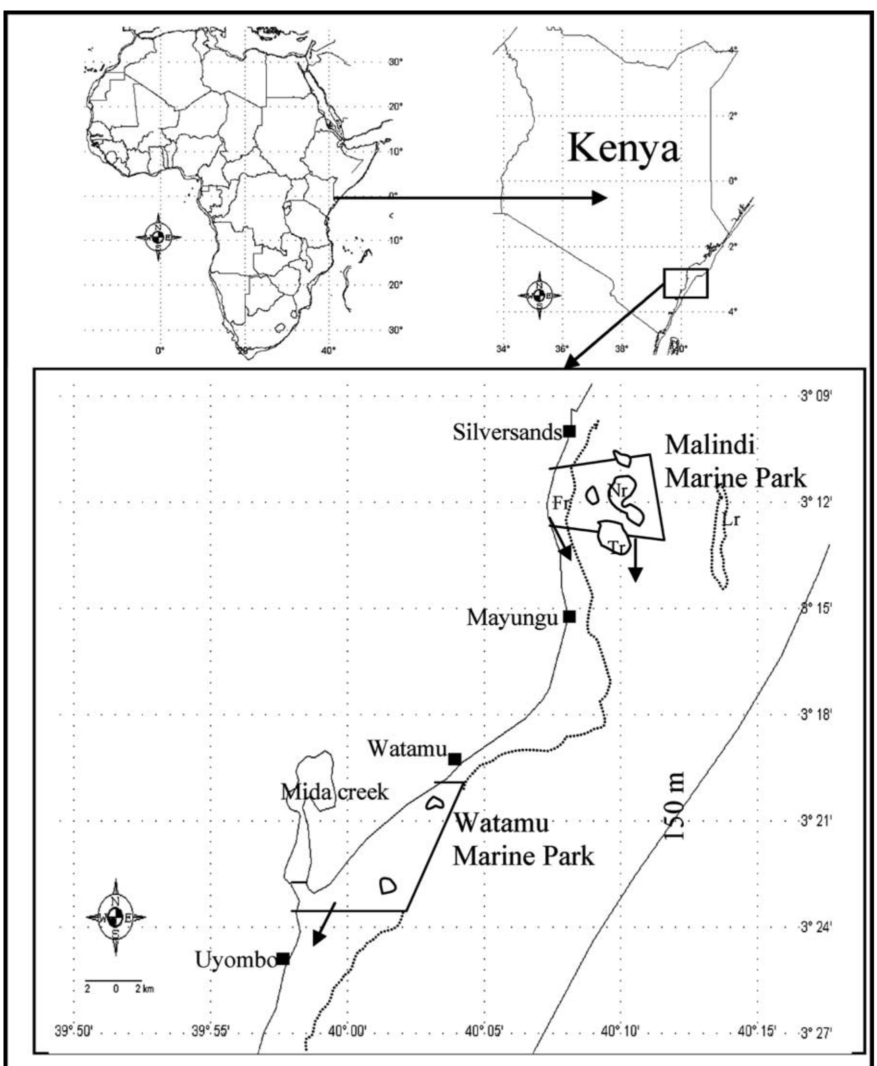

Fig. 1. Map of the studied parks showing the reefs, the adjacent fished reserves and the fish landing sites. The arrows show the trap transect directions from the park boundaries. NR, North reef; FR, Fringing reef; TR, Tewa reef; LR, Leopard reef.

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.

2. Methods

2.1. 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, with "traditional" gear, mostly traps. The present research was done in Malindi (6.3 km^2) and Watamu (10 km^2) National Marine Parks, both created in 1968, and their adjacent fished reserves (Fig. 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.) Both parks enclose lagoons with low and uniform topography dominated by a mosaic of seagrass beds interspersed with sand, algae, live corals and coral rubbles of varying cover. 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 parks.

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 (2×1 km) patch reef within the park. Beds of the seagrass *Thalassondendron ciliatum* and isolated coral heads dominated by massive *Porites* and *Galaxea* occur on the upper edges of the east and south west-slopes of the North reef forming sites popular for tourist activities. The park also includes a submerged patch reef (Tewa Reef) to the south 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. 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.

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 was designed to cover the two monsoon seasons.

2.2. 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 $1.5 \times 1.3 \times 0.6$ 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.

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 km inside the Malindi Park boundary and across the entire length of Watamu Park. At Malindi, traps were fished on the North and Fringing Reefs adjacent to the fished reserve to the south (Fig. 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 to 18 days per transect, the variability being caused by loss of traps to occasional rough seas or theft and the relative inaccessibility of some sites.

Each fishing event consisted of two 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 receiver. The initial trap placement design was systematic with stations 20–30 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. 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, and the fish released alive at the capture site.

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

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

and

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

where $\bar{C}_{\mathrm{park}}$ and $\bar{S}_{\mathrm{park}}$ and $\bar{C}_{\mathrm{Reserve}}$ and $\bar{S}_{\mathrm{Reserve}}$ 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.

2.3. 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 Fig. 3. We used a logistic decay function to describe how the proportion of mid-park CPUE changes with distance across the park boundaries. The function can be written as:

$$Y = 1/(1 + \exp(\beta_0(\beta_1 - x))), \tag{1}$$

where Y is the proportion of the mid-park densities (CPUE), β_0 and β_1 are the slope (i,e, mean change in CPUE per unit change in distance from park center) and the inflexion point (i,e, distance at which mid-park biomass is halved) 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, Eq. (1) was linearized (Neter et al., 1985) as

$$Z = b + mx \tag{2}$$

where the parameters b and m represent $\beta_0\beta_1$ and $-\beta_0$, respectively, and Z is: ln $[(1 - Y)Y^{-1}]$.

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

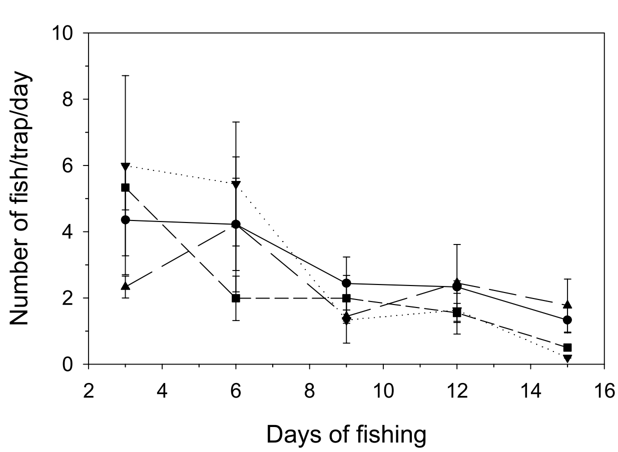

Fig. 2. The variation of mean catch rates of traps fishing at same position during systematic sampling on transect lines over a two week period. Transects 1–4 are placed at distances of 0, 0.2, 0.4 and 0.8 km from the park border of the Malindi patch reef. Error bars indicate ±s.d. ●-transect (1); ▲-transect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

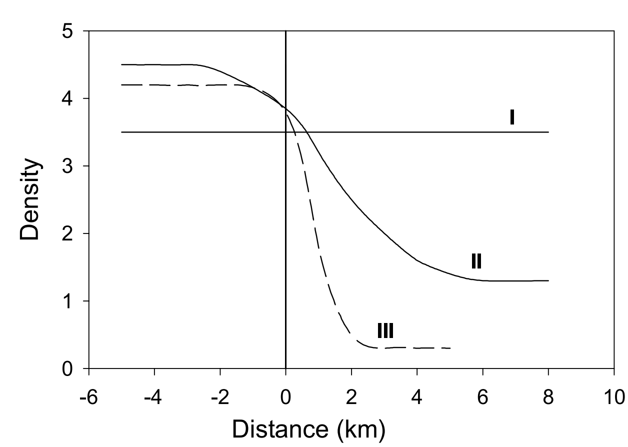

Fig. 3. A hypothetical model of density (CPUE) of exploited fish species across the boundary of a marine reserve under conditions of equal catchability. Highly mobile species (high-spillover, I) show a density gradient of near zero outside the reserve boundary. Moderately mobile species (moderate-spillover, II) show gradients that are less steep while species with low mobility have increasingly negative gradient approaching ∞ and more truncated at the boundaries (low-spillover, III). Vertical line indicates park boundary.

single density, no gradient results ($\beta_0 = 0$) and density equilibrium is attained (high- spillover, model I, Fig. 3). A medium spillover with moderate relative fishing mortality in the reserves would result in a gradient of catch rates from the border with slope > 1 (moderate-spillover, model II). In cases of slow spillover relative to fishing mortality, this slope would increase and ultimately reach infinity (low-spillover, model III). These constructs are used to test for evidence of spillover from the protected to fished sites 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 five times to data in which densities were re-assigned to distance 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 CPUE within the parks (as in Watamu), the average of the two innermost CPUE data in Malindi Park was used to interpolate the model inward to approximately one kilometer from the park center and used as the model intercept.

3. Results

3.1. Watamu

At Watamu during the NE monsoon, a total of 32 species were caught, of which 13 (41%) were common to both park and reserve (Table 1). Of these 13 species, nine had higher CPUE inside the park. In contrast, the commercially important whitespotted rabbitfish (WSR), *Siganus sutor*, had higher CPUE in the reserve. The dominant species both inside and outside the park were the commercially important emperors (*Lethrinus miniatus*, *Lethrinus mahsena*, sky emperor, SEM), and WSR 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 1). Of these nine species, five had higher CPUE inside the park, including the goldspotted sweetlip, *Gaterin flavomaculatus* and the WSR. Four species had higher CPUE in the reserve (Table 1).

3.2. Malindi

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 2). For 10 of these 17

Table 1
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 NE and SE monsoon seasons

Species	Park catch (± s.d.)	Reserve catch (± s.d.)	RDD	*t*	*p*
(a) NE monsoon					
Abudefduf sexfasciatus	0.02 (0.07)	0.08 (0.22)	−0.56	−0.91	0.38
Acanthurus dussumieri	0.26 (0.33)	0.15 (0.39)	0.25	0.37	0.71
Calotomus carolinus	0.16 (0.32)	0.08 (0.22)	0.33	1.40	0.17
Leptoscarus vaigiensis	0.09 (0.19)	0.97 (0.94)	−0.82	−2.01	0.03
Gaterin flavomaculatus	0.90 (1.26)	0.02 (0.07)	0.95	2.87	0.01
Cantherhines pardalis	0.09 (0.19)	0.15 (0.18)	−0.27	−0.79	0.43
Lethrinus mahsena	2.68 (0.68)	1.09 (2.05)	0.42	2.16	0.04
Lethrinus nebulosus	0.42 (0.56)	0.04 (0.09)	0.84	2.81	0.01
Lethrinus miniatus	3.10 (2.74)	0.18 (0.36)	0.89	5.33	0.001
Lutjanus fulviflamma	0.08 (0.12)	0.06 (0.22)	0.14	0.29	0.77
Parupeneus barberinus	0.22 (0.43)	0.06 (0.16)	0.56	0.56	0.58
Scarus ghobban	0.51 (1.62)	0.12 (0.07)	0.62	1.28	0.02
Siganus sutor	0.70 (0.57)	2.83 (2.42)	−0.60	−3.54	0.002
(b) SE monsoon					
Acanthurus dussumieri	0.06 (0.15)	0.13 (0.18)	−0.38	−1.01	0.32
Calotomus carolinus	0.07 (0.21)	0.09 (0.17)	−0.14	−2.29	0.77
Cantherhines pardalis	0.11 (0.14)	0.26 (0.52)	−0.39	−0.87	0.40
Gaterin flavomaculatus	0.65 (0.80)	0.10 (0.23)	0.73	0.48	0.02
Lutjanus fulviflamma	0.06 (0.15)	0.07 (0.13)	−0.09	−0.24	0.81
Leptoscarus vaigiensis	0.06 (0.13)	0.03 (0.11)	0.32	0.65	0.52
Lethrinus mahsena	0.14 (0.27)	0.06 (0.21)	0.34	0.70	0.49
Lethrinus miniatus	0.85 (0.89)	0.44 (0.60)	0.32	1.36	0.19
Siganus sutor	2.76 (1.92)	1.25 (1.24)	0.38	2.32	0.02

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 site.

Table 2
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 NE and SE monsoon seasons

Species	Park catch (± s.d.)	Reserve catch (± s.d.)	RDD	t	p
(a) NE monsoon					
Acanthurus dussumieri	0.41 (0.49)	0.33 (0.89)	0.11	0.36	0.72
Balistapus undulatus	0.51 (0.49)	0.02 (0.26)	0.94	4.72	0.001
Calotomus carolinus	0.18 (0.19)	0.20 (0.06)	−0.06	−0.33	0.74
Leptoscarus vaigiensis	0.10 (0.18)	0.71 (0.89)	−0.75	−3.19	0.004
Scarus ghobban	0.01 (0.05)	0.15 (0.34)	−0.86	−1.87	0.07
Cheatodon auriga	0.04 (0.15)	0.11 (0.32)	−0.46	−0.95	0.35
Cheilinus chlorourus	0.23 (0.41)	0.01 (0.05)	0.91	2.48	0.02
Cheilinus trilobatus	0.01 (0.02)	0.02 (0.08)	−0.66	−1.07	0.29
Epinephelus tauvina	0.09 (0.13)	0.02 (0.08)	0.60	2.22	0.03
Gaterin flavomaculatus	0.26 (0.12)	0.12 (0.21)	0.37	1.40	0.17
Lethrinus mahsena	4.07 (4.85)	0.83 (1.22)	0.66	3.04	0.005
Lethrinus miniatus	0.10 (0.29)	0.16 (0.31)	−0.23	−0.67	0.50
Lutjanus fulviflamma	0.02 (0.08)	0.11 (0.18)	−0.73	−2.26	0.03
Naso hexacanthus	0.13 (0.24)	0.22 (0.52)	−0.24	−0.68	0.49
Parupeneus macronema	0.03 (0.08)	0.03 (0.16)	−0.05	−0.08	0.93
Siganus luridus	0.04 (0.10)	0.11 (0.23)	−0.46	−1.29	0.20
Siganus sutor	4.22 (4.30)	1.62 (1.19)	0.44	2.73	0.01
(b) SE monsoon					
Acanthurus nigrofuscus	0.04 (0.10)	0.03 (0.12)	0.07	0.11	0.91
Balistapus undulatus	0.21 (0.25)	0.01 (0.04)	0.94	2.01	0.01
Calotomus carolinus	0.04 (0.10)	0.03 (0.15)	0.16	0.25	0.81
Leptoscarus vaigiensis	0.21 (0.40)	0.34 (0.46)	−0.24	−0.77	0.47
Scarus ghobban	0.04 (0.10)	0.03 (0.15)	0.16	0.25	0.81
Chaetodon auriga	0.08 (0.20)	0.03 (0.09)	0.47	0.63	0.56
Cheilinus trilobatus	0.13 (0.21)	0.02 (0.09)	0.68	1.17	0.29
Cheilinus chlorourus	0.08 (0.20)	0.04 (0.14)	0.39	0.54	0.60
Chelio inermis	0.04 (0.10)	0.02 (0.08)	0.40	0.55	0.60
Gaterin flavomaculatus	1.13 (1.61)	0.18 (0.32)	0.72	1.43	0.02
Lethrinus elongatus	0.08 (0.20)	0.004 (0.03)	0.89	0.94	0.38
Lethrinus mahsena	0.58 (0.63)	0.01 (0.06)	0.97	2.25	0.04
Lethrinus miniatus	0.42 (0.72)	0.02 (0.10)	0.92	1.36	0.02
Parupeneus barberinus	0.04 (0.10)	0.06 (0.14)	−0.14	−0.31	0.77
Siganus luridus	0.08 (0.20)	0.02 (0.14)	0.55	0.69	0.51
Siganus sutor	9.50 (6.30)	2.75 (2.83)	0.55	1.55	0.01

Parameters are as in Table 1.

species, CPUE did not differ significantly across the park boundary. However, five species, including the abundant (>80% of catch) SEM and WSR had significantly higher CPUE inside the park. The seagrass parrotfish, *Leptoscarus vaigensis*, and the black spot snapper, *Lutjanus fulviflamma*, had significantly higher CPUE outside the park. During the SE monsoon, 21 species were caught in Malindi, of which 16 (76%) were common to park and reserve (Table 2). The WSR was the predominant catch. Only two species (*L. vaigensis* and *Parupeneus barberinus*) had higher CPUE outside the park while 14 species, including WSR had higher CPUE inside the park (Table 2).

3.3. CPUE gradients

In Watamu Park, total catch declined outside the park boundary in both seasons (slopes of −0.7 and −1.2, $p < 0.05$, during the NE and SE monsoon seasons respectively, Table 3 and Fig. 4(e)), which fits a overall model of moderate to low fish spillover (Fig. 3) across the park boundary. Catches were higher in the NE monsoon season (Fig. 4(e)). However, these results masked the different results for various species. Of the three dominant species in both the research catch and commercial fishery, the WSR showed a low-spillover response during the SE monsoon (β_0: −0.84, Table 3 and Fig. 4(a)), However, the WSR 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 (Figs. 4(b) and (c)). *L. miniatus* showed a particularly steep gradient of CPUE (low-spillover) during the NE monsoon (β_0: −1.61, Fig. 4(c)). 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;

Table 3
Summary of the gradient (β_0) and inflexion point (β_I) of proportion of within park CPUE (y) of the reef fish caught across two marine reserves in coastal Kenya

Species	NE monsoon		SE Monsoon	
	β_0	β_I	β_0	β_I
(a) Watamu				
Siganus sutor	0.47 ± 0.4	6.21 ± 1.9	$-0.84 \pm 0.3^*$	2.22 ± 1.9
Lethrinus mahsena	-0.17 ± 0.3	2.94 ± 2.1	-0.14 ± 0.5	2.60 ± 2.1
Lethrinus miniatus	$-1.61 \pm 0.3^{**}$	4.30 ± 1.4	-0.07 ± 0.3	∞
Others	$-0.34 \pm 0.2^*$	3.82 ± 0.2	-0.06 ± 0.16	3.40 ± 1.0
Total catch	$-0.69 \pm 0.3^*$	6.41 ± 1.8	$-1.2 \pm 0.26^{**}$	4.61 ± 1.6
(b) Malindi				
Lethrinus mahsena	$-1.05 \pm 0.3^*$	$0.79 \pm 0.2^*$	–	–
Leptoscarus vaigiensis	-0.01 ± 4.2	∞	-0.432 ± 0.3	3.60 ± 1.0
Gaterin flavomaculatus	1.40 ± 0.5	2.30 ± 0.8	–	–
Siganus sutor	$-0.45 \pm 0.2^*$	$0.51 \pm 0.2^*$	$-0.53 \pm 0.1^*$	0.88 ± 0.3
Others	-1.30 ± 1.5	2.90 ± 2.6	-0.14 ± 0.2	2.50 ± 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 ± 0.8	1.43 ± 2.1	$-0.84 \pm 0.2^*$	0.61 ± 0.3

$y = 1/(1 + \exp(\beta_0(\beta_I - x)$; (–), inadequate sample size. Error bars are ±s.e. β_I significance is indicated if ±2s.e's does not include parks boundary (5.8 and 1.4 km from park center at Watamu and Malindi, respectively).

$^*p < 0.05$.

$^{**}p < 0.01$.

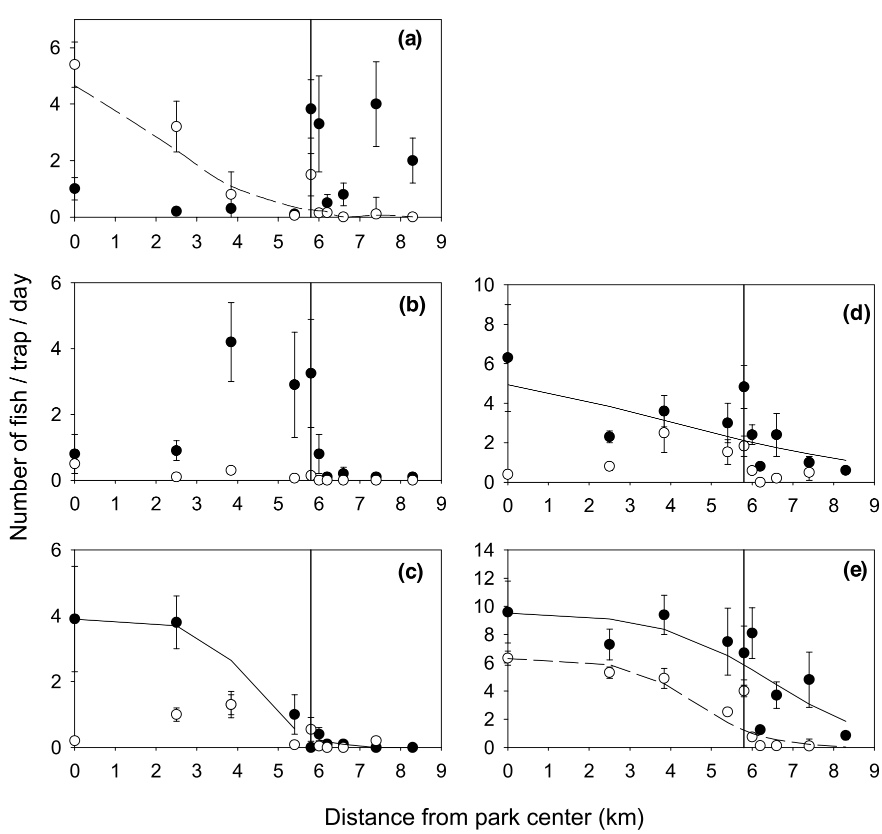

Fig. 4. Seasonal gradients in mean CPUE of the common species of fish across Watamu Marine Park into adjacent reserve in coastal Kenya. Error bars indicate ±s.e.m. Vertical line mark park boundary, continuous line and λ indicate Northeast monsoon, dashed line and μ indicate Southeast monsoon. Models: (a) *Siganus sutor* (○) $y = 1/(1 + \exp(-0.84^*(2.2 - x)))$; (b) *Lethrinus mahsena*; (c) *Lethrinus miniatus* (●) $y = 1/(1 + \exp(-1.61^*(4.3 - x)))$; (d) others (●) $y = 1/(1 + \exp(-0.34^*(3.8 - x)))$; and (e) total catch (●) $y = 1/(1 + \exp(-0.75^*(6.4 - x)))$ and (○) $y = 1/(1 + \exp(-1.2^*(4.6 - x)))$.

p's > 0.05) (Fig. 4(e) and Table 3). 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 low-spillover response (Fig. 3) during both seasons from the patch reefs (NE monsoon, β_0: −0.78; SE monsoon, po: −0.88; Fig. 5(f)) and a moderate-spillover during the SE monsoon for the fringing reef (β_0: −0.61 Table 3 and Fig. 5(g)). Of the commercially important species, WSR showed a moderate-spillover 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. 5(d) and Table 3), while, the SEM showed a more truncated (low-spillover) CPUE across the park (β_0: −1.05, Fig. 5(a)). Models of total catch of all species in Malindi patch reef had inflexion points that were significantly inside the park in both seasons. The inflexion point of the WSR density was less distinct but inside the park during the NE monsoon and at the park boundary in the SE monsoon (Fig. 5(d) and Table 3). 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 ± 7.02) than at the border of the patch reef portion of the park (3.9 fish/trap/day ±1.0; Fig. 5(f) and (g)) during the NE monsoon.

3.4. Species diversity

The diversity of trappable species showed a general decline from within the parks into the reserves in both parks (Fig. 6). At Watamu, the decline in diversity from

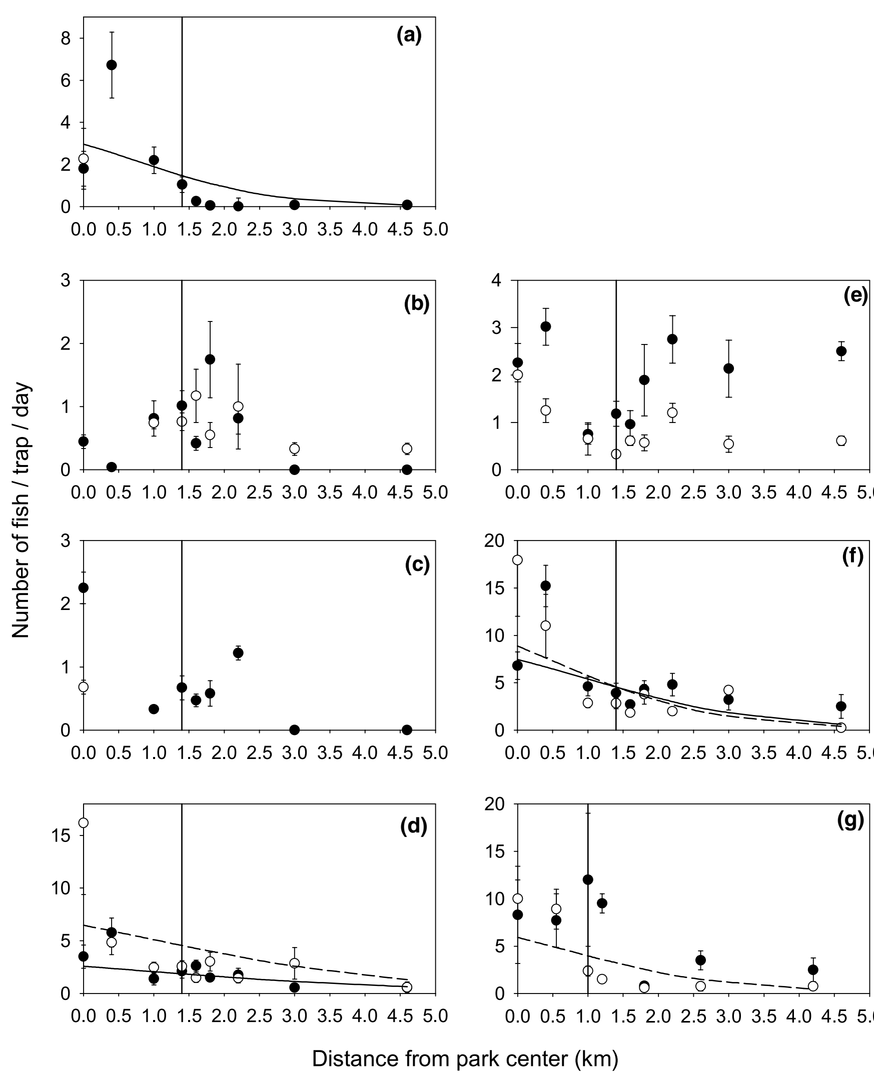

Fig. 5. Seasonal gradients in mean CPUE of common species of fish from Malindi Marine Park into adjacent reserve in coastal Kenya. Data analyzed for the patch reef (a)–(f) and for the fringing reef (g), error bars indicate ±s.e.m. Vertical line mark park boundary, continuous line and λ indicate Northeast monsoon, dashed line and μ indicate Southeast monsoon. Models: (a) *Lethrinus mahsena* (•) $y = 1/(1+\exp(-3.3^*(0.87-x)))$; (b) *Leptoscarus vaigensis*; (c) *Gaterin flavomaculatus*; (d) *Siganus sutor* (•) $y = 1/(1+\exp(-2.47^*(0.92-x)))$ and (○) $y = 1/(1+\exp(-22.8^*(0.32-x)))$; (e) others; (f) total catch patch reef (○) $y = 1/(1+\exp(-0.81^*(0.15-x)))$; and (g) total catch fringing reef (•) $y = 1/(1+\exp(-0.72^*(1.9-x)))$.

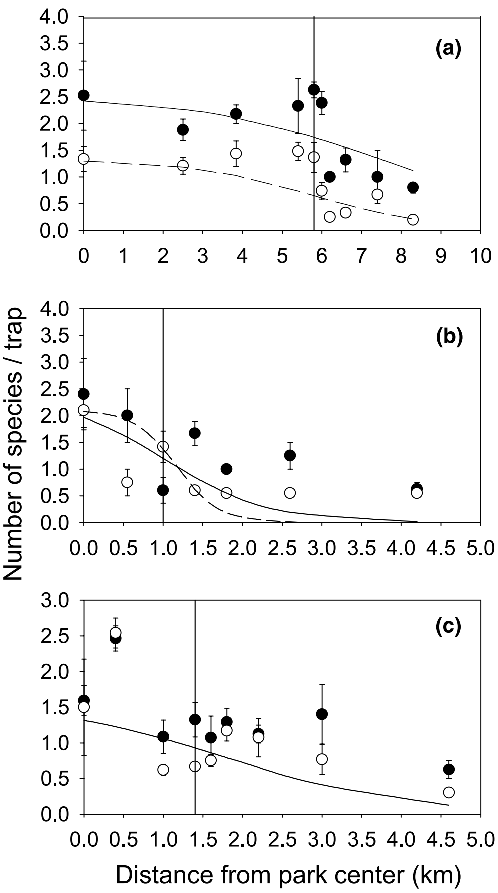

Fig. 6. The seasonal trend in diversity of trappable fish across: (a) Watamu Marine Park; (b) Malindi Marine Park fringing reef; (c) Malindi patch reef, into adjacent reserves in coastal Kenya. Error bars indicate ±s.e.m. Vertical line mark park boundary, continuous line and λ indicate Northeast monsoon, dashed line and μ indicate Southeast monsoon. Models: (a) (•) $y = 1/(1 + \exp(-0.41^{*}(7.75 - x)))$ and (○) $y = 1/(1 + \exp(-0.64^{*}(5.71 - x)))$.

the park center showed shallow and medium 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 off the fringing reef border during both seasons (β_0: −1.52, NE and −3.75, SE, Fig. 6(b)) and a medium decline off the patch reef that was significant during the NE monsoon (β_0: −0.32, Fig. 6(c)). 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 (Fig. 6(a)).

3.5. Fish size

The mean length of several species was greater inside than outside the parks (Table 4). Of the twelve species occurring across the boundary at Malindi, five (42%) had significantly greater mean sizes on the patch reef inside the park (p's < 0.05). However, the seagrass parrotfish and the WSR were larger outside the park (p's < 0.05), although WSR caught on the fringing reef inside the park were larger than those caught outside the park off this reef ($p < 0.05$). At Watamu, four (44%) of the nine species occurring across the boundary were significantly larger inside the park. The WSR, SEM and the seagrass parrotfish had greater mean lengths outside the park but the differences were not significant ($p > 0.05$).

The size frequency distributions of WSR compared between the parks and reserves show different seasonal patterns (Fig. 7). At Malindi patch reef, the WSR showed significant difference in size frequency distribution between the park and the reserve during the NE monsoon season ($\chi^2 = 80.7$, $\chi^2_{(0.05)8,1} = 15.5$) when more small sized fish (<19 cm) were found inside the park (Fig. 7(c)). However, large fish (>20 cm) were also common in the reserve. Size frequency distribution across the fringing reef border was different only during the SE monsoon ($\chi^2 = 25.3$, $\chi^2_{(0.05)6,1} = 12.1$ when more large (>23 cm) were found inside the park (Fig. 7(b)). In Watamu there were no 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. 7(f)) as there were more small fish (<19 cm) outside the park during the NE monsoon (Fig. 7(e)).

4. Discussion

Our data indicate that the density of most fish species is 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 note that live corals are concentrated within the parks. It is not possible to directly test whether these differences may be 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 causes 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 the WSR, 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

Table 4
Mean difference in length between species inside (a). Malindi and (b) Watamu Marine Parks and their adjacent fished reserves

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

Data analyzed using two-tailed *t*-test for means with unequal variance, *p* is *t*-test probability, d_I = length difference between sites.
[a] Fish caught on the fringing reef portion of Malindi Marine Park.

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).

The shape of the fish density gradient from within the park and across the boundaries to the adjacent reserves was overall consistent with moderate- and low-spillover models for Watamu and Malindi, respectively. The inflexion point confidence interval included the park border at Watamu but occurred within the park at Malindi, suggesting greater dispersal from Watamu than Malindi Park. 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 is allowed within 500 m of 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 high-spillover model (zero slope), while other species like the emperors exhibited a very steep decay (low-spillover) at the park boundaries. In particular, the case of the WSR is of interest, as this is the most important commercial species in the region (Kenya Fisheries Department, 1999). At Malindi, the slope of the density gradient for WSR was significant but shallow during both seasons, indicating high-spillover. The inflexion point was within the park in the NE season but at the park border during the SE season, further suggesting seasonality in the dispersal pattern. 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 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 WSR 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 spillover from marine protected areas is likely to be higher under conditions of high fishing pressure (Polachek, 1990; Nowlis and Roberts, 1997). Our data are

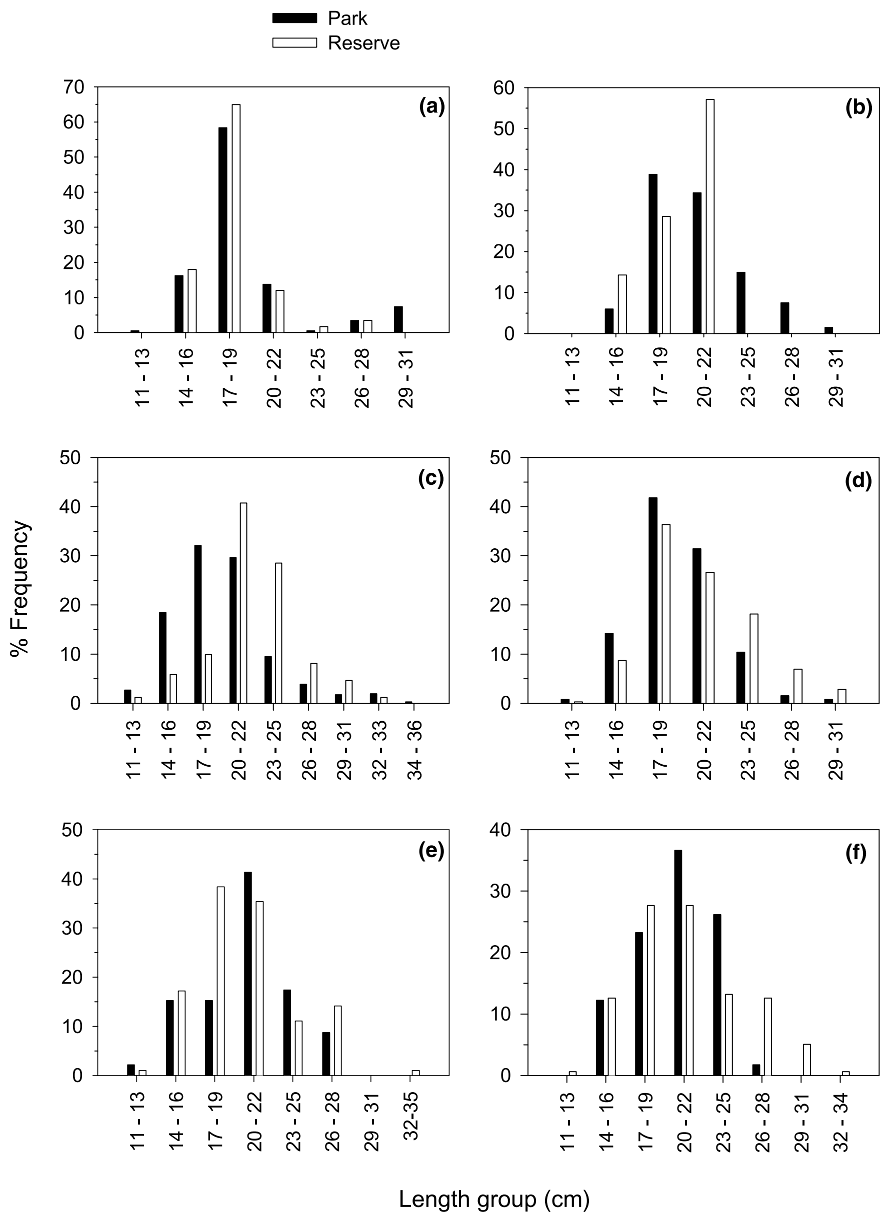

Fig. 7. Seasonal size frequency distribution of commercially important whitespotted rabbitfish, *Siganus sutor*, inside and outside marine National Parks in coastal Kenya: (a) Fringing reef Malindi, Northeast monsoon; (b) Fringing reef Malindi, Southeast monsoon; (c) Patch reef Malindi, Northeast monsoon; (d) Patch reef Malindi, Southeast monsoon; (e) Watamu, Northeast monsoon; and (f) Watamu, Southeast monsoon.

inadequate to test this prediction, but any effect appears to be species specific and also perhaps dependent on season and reef topography.

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. The 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 *Arothrion* spp., *Canthigaster* spp., *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 depletion 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 (Jennings et al., 1995). These communities may be local cases of fished down food webs (Pauly et al., 1998).

Our data indicate that many species included larger individuals, and had larger mean sizes, 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, the WSR, fish were larger outside than inside both parks. The seagrass parrotfish was also 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 decrease 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 WSR 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 SEM (the second most important commercial species) outside the Parks is more consistent with the typical effects of fishing on population structure, and with SEM being less mobile than the WSR.

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 spillover to the adjacent fished reserve. More spillover 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, 1996; 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, deep-water and seagrass beds that separate reef patches (Stamps et al., 1987; Bernstein et al., 1991; Ratikin and Kramer, 1996). The best example at Malindi and Watamu is the WSR.

Spillover was strongly 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, the emperors and WSR, very different patterns were evident. The emperors (particularly the SEM) exhibited little evidence of dispersal, with very low CPUE outside the parks and a steep density decay at the park borders. In contrast, the high-spillover model that appeared to best fit the WSR, 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 spillover from a protected area will depend on species specific behaviour, particularly with respect to home range and seasonal migration patterns.

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 spillover of adult fish from the patch reefs is limited for most species, but higher from fringing reefs. However, there are important exceptions to these generalities. Bathymetry and seasonality influence spillover. Most importantly, some species may spillover consistently as fishable adults (e.g., the WSR), and protection of even small areas of patch reefs may enhance productivity in these species. Hence, given that the WSR is the most important commercial fish in the area, the direct effects of the parks on enhancing adjacent fisheries by spillover of adults may be considerable.

Acknowledgements

We are grateful to the Head of the Wetland program of the Kenya Wildlife Service, Dr. Nyawira Muthiga, for granting us permission to work within the Marine Parks. A number of people assisted with the labour intensive trap work and we thank; M. Ndegwa, S. Mangi, C. Morris, J. Green, C. Mwatete, R. Anam, A. Shaibu, and the fishermen of Malindi–Watamu reserves. T.R. McClanahan provided useful advice on sampling design and made useful comments on the manuscript. We are grateful to the Wardens of the Parks (Messrs. R. Njue and G. Wakaba) and the rangers of the parks for the generous support without which this work would have been impossible to accomplish. Funding was received from the Wildlife Conservation Society (N.Y.), the International Foundation for Science (IFS, Sweden), the Fisheries Conservation Chair of Memorial University, Canada, and a Memorial-Canadian Development Agency fellowship to B.K.A.

References

Alcala, A.C., 1988. Effects of marine reserves on coral fish abundances and yields of Philippines coral reefs. Ambio 17, 194–199.

Allen, G., 1997. Marine Fishes of the Great Barrier Reef and South-East Asia – A Field Guide for Anglers and Divers. Western Australia Museum, Perth. 292 pp..

Allison, G.W., Lubchenco, J., Carr, M.H., 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecol. Appl. 8, 79–92.

Bernstein, C., Kacelnik, A., Krebs, J.R., 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. J. Anim. Ecol. 60, 205–225.

Bock, K., 1978. A Guide to Common Reef Fishes of the Western Indian Ocean and Kenya Coast. Macmillan Press Ltd., London. 118 pp..

Bohnsack, J.A, 1992. Reef resource habitat protection: the forgotten factor. Mar. Recreational Fish. 14, 117–129.

Bohnsack, J.A., 1998. Application of marine reserves to reef fisheries management. Aust. J. Ecol. 23, 298–304.

Carr, M.H., Reed, D.C., 1993. Conceptual issues relevant to marine harvest refuges. Examples from temperate reef fishes. Can. J. Fish. Aquat. Sci. 50, 2019–2028.

Chapman, R.M., Kramer, D.L., 1999. Gradients in coral reef fish diversity and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. Mar. Ecol. Prog. Ser. 181, 81–96.

Chapman, R.M., Kramer, D.L., 2000. Movements of fishes within and among fringing coral reefs in Barbados. Environ. Biol. Fish. 57, 11–24.

Dayton, P.K., 1998. Reversal of the burden of proof in fisheries management. Science 279, 821–822.

DeMartini, E.E., 1993. Modelling the potential of fishery reserves for managing Pacific coral reef fishes. U.S. Fish. Bull. 91, 414–427.

Dugan, J.E., Davis, G.E., 1993. Applications of marine refugia to coastal to coastal fisheries management. Can. J. Fish. Aquat. Sci. 50, 2029–2042.

Jennings, E.M., Grandcourt, N., Polunin, N.V.C., 1995. The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. Coral Reefs 14, 25–235.

Johannes, R.E., 1978. Traditional marine conservation methods in Oceania and their demise. Ann. Rev. Ecol. Syst. 9, 349–364.

Kaunda-Arara, B., 1997. Analysis of fish catch data from 1985 to 1994 in the Kenyan inshore marine waters. Afr. J. Trop. Hydrobiol., Fish. 7, 17–21.

Kaunda-Arara, B., Ntiba, M.J., 1997. The reproductive biology of *Lutjanus fulviflamma* (Pisces: Lutjanidae) from Kenyan inshore marine waters. Hydrobiologia 353, 153–160.

Kenya Fisheries Department, Ministry of Regional Development, 1999. Annual Statistical Bulletin. Nairobi, Kenya, 25 pp.

Koslow, J.A., Hanley, F., Wicklund, R., 1988. Effects of fishing on reef fish communities at Pedro Bank and Port Royal Cays, Jamaica. Mar. Ecol. Prog. Ser. 43, 201–212.

Lauck, T., Clark, C.W., Mangel, M., Munro, G.R., 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecol. Appl. 8, 72–78.

Lechowicz, M.J., 1982. The sampling characteristics of electivity indices. Oecologia 52, 22–30.

Lieske, E., Myers, R., 1994. Collins Pocket Guide to Coral Reef Fishes: Indo-Pacific and Caribbean. Herper Collins Publishers, London. 400 pp..

Man, A., Law, R., Polunin, N.V.C., 1995. Role of marine reserves in recruitment to reef fisheries: A metapopulation model. Biol. Conserv. 71, 97–204.

McClanahan, T.R., 1988. Seasonality in East Africa's coastal waters. Mar. Ecol. Prog. Ser. 44, 191–199.

McClanahan, T.R., Muthiga, N.A., 1988. Changes in Kenyan coral reef community structure and functions due to exploitation. Hydrobiologia 166, 269–276.

McClanahan, T.R., Kaunda-Arara, B., 1996. Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. Conserv. Biol. 10, 1187–1199.

McClanahan, T.R., 1999. Is there a future for coral reef parks in poor tropical countries? Coral Reefs 18, 321–325.

McClanahan, T.R., Mangi, S., 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. Ecol. Appl. 10, 1792–1805.

Munro, J.L., 2000. Outmigration and movement of tagged coral reef fish in a Marine Fishery Reserve in Jamaica. In: Proceedings of the 51st Gulf and Caribbean Fisheries Institute, pp. 557–568.

Murray, S.N., Ambrose, R.F., Bohnsack, J.A, Botsford, L.W., Carr, M.H., Davis, G.A., Dayton, P.K., Gotshall, D., Gunderson, D.R., Hixon, M.A., Lubchenco, J., Mangel, M., MacCall, A., McArdle, D.A., Ogden, J.C., Roughgarden, J., Starr, R.M., Tegner, M.J., Yoklavich, M.M., 1999. No take reserve networks: Sustaining fishery populations and marine ecosystems. Fish. Manage. 24, 11–25.

Neter, J., Wasserman, W., Kutner, M.H., 1985. Applied Linear Statistical Models. Regression Analysis of Variance and Experimental Designs. Rochard D. Irvin Inc., Homewood, IL. 1127 pp..

Nowlis, J.S., Roberts, C.M., 1997. You can have your fish and eat it, too: theoretical approaches to marine reserve design. In: Proceedings of the 8th International Coral Reef Symposium 2, pp. 1907–1910.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing Down Marine Food Webs. Science 279, 860–863.

Polachek, T., 1990. Year round closed areas as a management tool. Nat. Res. Model 4, 327–354.

Randall, J.E., 1992. Divers Guide to Fishes of Maldives. Immel Publishing Ltd., London. 193 pp..

Ratikin, A., Kramer, D.L., 1996. Effect of a marine reserve on the distribution of coral reef fish in Barbados. Mar. Ecol. Prog. Ser. 131, 97–113.

Roberts, C.M., Polunin, N.V.C., 1991. Are reserves effective in management of reef fisheries. Rev. Fish Biol. Fish. 1, 65–91.

Roberts, C.M., 1997. Ecological advice for the global fisheries crisis. Trends Ecol. Evol. 12, 35–38.

Robichaud, D.R., Hunte, W., Oxenford, H.A., 1998. Effects of increased mesh size on catch and fishing power of coral reef fish traps. Fish. Res. 39, 275–294.

Rowley, R.J., 1994. Marine reserves in fishery management. Aquat. Conserv. Mar. Freshw. Ecosyst. 4, 233–254.

Russ, G.R., Alcala, A.C., 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island. Mar. Ecol. Prog. Ser. 132, 1–9.

Sale, P., 1998. A promise not yet fulfilled. Trends Ecol. Evol. 13, 125.

Shepherd, S.A., Brown, L.D., 1993. What is an Abalone Stock: implications for the role of refugia in Conservation. Can. J. Fish. Aquat. Sci. 50, 2001–2009.

Smith, J.L.B., Heemstra, P.C., 1998. Smith's Sea Fishes, fourth ed. Valiant Publishing Santom, South Africa. 578 pp..

Stamps, J.A., Buechner, M., Krishnan, V.V., 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. Am. Nat. 4, 533–552.

Watson, M., Ormond, R.F.G., 1996. Effect of artisanal fishery on the fish and urchin populations of a Kenyan coral reef. Mar. Ecol. Prog. Ser. 109, 115–129.

Wiens, J.A., Crawford, C.S., Gosz, J.R., 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45, 421–427.