Fisheries Management and Ecology

Fisheries Management and Ecology, 2011, 18, 50–60

Changes in life history and ecological characteristics of coral reef fish catch composition with increasing fishery management

T. R. MCCLANAHAN

Wildlife Conservation Society, Marine Programs, Bronx, NY, USA

C. C. HICKS

Coral Reef Conservation Project, Mombasa, Kenya and ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Australia

Abstract Length, life history and ecological characteristics of landed fish communities were studied over a 10-year period to test theories of fishing disturbance during a time of increased gear and closure management in heavily utilised fisheries. It was predicted that with greater management restrictions: (1) the earliest and fastest responses in the fishery will be seen in those species with faster turnovers, or relatively lower vulnerabilities to fishing; (2) the fishery would transition to a landed catch with higher mean trophic levels, and greater mean body lengths. In addition, the removal of a non-selective, small-mesh seine nets should benefit the catch of gears that previously had the greatest species selectivity overlap with the seine net. Many predictions were supported, although maximum lengths and lengths at maturity responded more rapidly than anticipated. The response to eliminating the non-selective seine net was a more rapid increase in sizes caught by gears with a larger overlap in size (hook and lines) than species selectivity (gill nets). The simultaneous comparison of management systems over time indicates that open-access fishing grounds can benefit from restrictions imposed in adjacent fishing grounds. The study indicated that multi-species coral reef fisheries management objectives of maximising yields, as well as maintaining the fish community's life-history diversity, require management trade-offs that balance local socio-economic and biodiversity needs.

KEYWORDS: community structure, competition, fisheries closures, fisheries exploitation, growth rates, marine protected areas, portfolio.

Introduction

Fishing is a strong selective force influencing the ecology and evolution of aquatic ecosystems (Tegner & Dayton 1999; Worm *et al.* 2006). Many of these changes are unforeseen and difficult to predict, especially in complex and species-rich ecosystems such as coral reefs (McClanahan 1995; Bascompte *et al.* 2005). There are, however, predictable changes in coral reef fish communities with ecological disturbances (Pratchett *et al.* 2008), fishing intensity (McClanahan *et al.* 2008) and time since closures (McClanahan *et al.* 2007). Similarly, changes in fishing intensity and management are expected to have a number of ecological and evolutionary consequences (Jennings & Kaiser 1998). The role of fisheries science should seek generalisations concerning fishing impacts and management such that the full consequences of human resource extraction are better understood and used to inform management (Jennings & Blanchard 2004; Beddington *et al.* 2007). Understanding the outcomes and distinctions of alternative management options, their interaction with the bio-physical environment and climate change are areas of fisheries science in need of further development (Cheung *et al.* 2008; Cinner *et al.* 2009).

Theoretical and empirical analyses suggest that fishing has the greatest impact on slow growing and

Correspondence: Tim McClanahan, Wildlife Conservation Society, Marine Programs, Bronx, NY 10460, USA (e-mail: tmcclanahan@wcs.org)

doi: 10.1111/j.1365-2400.2010.00768.x

larger species, with late maturity, low rates of population increase, higher trophic levels, large sizes at sexual maturity (Jennings *et al.* 1999; Rochet *et al.* 2000) and low rates of natural mortality (Russ & Alcala 1998; Cheung *et al.* 2005). Consequently, it is thought that effective management should allow the recovery of species with life histories that reflect slower turnovers (Jennings & Kaiser 1998; Kaplan 2009). However, the majority of coral reef fisheries in the tropics, even with management, will continue to be heavily exploited even after implementing management restrictions. It is therefore unclear what recovery trajectories may be expected in these areas and over what time scales. In addition, the complexity of coral reefs and the poverty of management institutions in the tropics, largely preclude the efficacy of species- and even site-specific management and data evaluation efforts (Johannes 1998). Case studies that use intrinsic characteristics of the entire fish communities to seek generalisations and patterns above the species-specific responses are therefore required to evaluate effects of different management strategies. Without efforts to generalise, the vast majority of coral reef fisheries will lack a common understanding of fishing impacts and subsequent principles for management. Therefore, adopted management options evaluated by intrinsic measures, such as life history and ecological criteria, will help to provide a basis for empirically testing and developing these general principles.

This study evaluates aspects of species life history and ecological characteristics in three systems of management. Efforts to restore a highly exploited fishery have developed different approaches to management, specifically through fisheries closures and gear restrictions (McClanahan *et al.* 2008). Changes in length, life history and ecology were evaluated to seek general patterns and better understand the full consequences of these changes in management. It was hypothesised that as restrictions increase from fully unrestricted to gear (seine net removal) and fishery closure management that the relative composition of species within the fishery should change. The hypothesised changes were: (1) the fastest recovery responses within species with faster turnovers, or relatively lower vulnerabilities to fishing (Jennings & Kaiser 1998; Jennings *et al.* 1999; Kaplan 2009); (2) a transition to species with higher trophic levels (Pauly *et al.* 1998); and (3) that the body lengths of landed fish should increase (Ault *et al.* 2008). In addition, (4) the elimination of the seine gear should benefit the catch of gears with the most overlap in terms of species and size selectivity (McClanahan & Mangi 2004). These hypotheses are evaluated over a 10-year period where a seine net removal programme was instigated in a portion of the fisheries monitoring sites and where selected sites lie either in close proximity to or at a distance from an effectively enforced no-take closure.

Methods

Study sites

Eleven fish landing sites were sampled over a 10-year time period along a ~ 75-km stretch of the southern Kenyan coastline. There has been a gradual movement towards greater area and gear management in this area, but the specific response has differed among the studied landing sites. Differences among these closely associated landing sites were used to evaluate the difference in management treatments, and this study evaluated the effects on the fish catch over time. Sites were selected to be representative of the shallow-water, multi-gear, multi-species, coral reef and artisanal fisheries of this region. Five study sites were located to the north of Mombasa city and within 5 km of the Mombasa Marine National Park, an effectively enforced no-take, or fisheries closure zone since 1991. A further six sites were south of Mombasa city and over 25 km from the nearest fisheries closure (McClanahan *et al.* 2008). The 11 study sites fall within two marine reserves, where gear restrictions apply to prohibit the use of beach seines. However, enforcement has been variable. Of the sites close to the Mombasa Marine National Park, only Kenyatta had eliminated the use of beach seines at the time of this study. Beach seine use was prevalent in the remaining four sites – Marina, Msanakani, Nyali and Reef. All six sites south of Mombasa city have been successful in eliminating beach seine use, although this has been a process that occurred gradually over 20 years, but with most of the change occurring between 2001 and 2004 (McClanahan *et al.* 2007, 2008).

Fishing is typically conducted from the beach to the fringing reef within the sand, coral and seagrass habitats of the fringing reef lagoon using five active gears (McClanahan & Mangi 2001). The five main gear types include trap, line, net, spear and beach seine, and have been previously described (McClanahan & Mangi 2004; Mangi & Roberts 2006). Minor variation exists within gear type as gears are modified based on local conditions. Nonetheless, gears were easily identified and placed within the above five categories. Beach seine and spear guns have been illegal in all Kenyan marine waters since 2001 (Kenya Gazette Notice No. 7565), but enforcement was variable and these gears were still commonly used (McClanahan *et al.* 2005).

Design and sampling

This study was designed to test the effects of fisheries closures and gear restrictions on: (1) the life-history characteristics; (2) the ecological traits; and (3) the lengths of the landed fish community. Collected over a 10-year time period, from February 1998 to August 2007, the analysis builds on a similar 10-year study (1994–2005) along the same coastline. The previous study focused on changes in the catch rates and trophic levels of landed catch based on analysis of the family groupings (McClanahan *et al.* 2008). This parallel study, collected data less frequently, but identified catch to the sub-genus level and investigated changes in fish lengths and species composition.

Management classification

Landing sites were classified into three distinct areas based on gear use composition at each site (McClanahan *et al.* 2008). These were: (1) South coast sites (Tradewinds, Mwaepe, Mvuleni, Mwyanza, Mgwani and Chale), situated at a great distance from the nearest no-take zone but where gear restrictions were successfully enforced beginning in 2001 and completed in 2004; (2) North coast sites (Nyali, Msanakani, Reef and Marina), situated adjacent to an effective and enforced fisheries closure of ~ 6 km^2 but where gear restrictions were never enforced; and (3) Kenyatta, situated adjacent to an effectively enforced no-take zone where gear restrictions were effectively enforced.

Field methods

At each landing site, standard methods were used to record gear use by the fishers and landed fish catch. Landed fish were identified to species level (Smith & Heemestra 1986; Lieske & Myers 1994), counted and the standard length was measured to the nearest centimetre using a fixed marker ruler on a flat board (McClanahan & Mangi 2004). Where possible the whole catch was measured whether the catch was for market or home use. For large catches of small fish, as is common with beach seine, a random stratified subsample was measured to ensure that each gear was sampled and a good representation of species and sizes landed were recorded (McClanahan & Mangi 2004). A total of 134 fishing days and five gear types were sampled in six sampling years over a 10-year time period, recording 27 095 fish (Table 1). This represented 152 species of fish, although 90% of the catch comprised only 15 species, which were the focus of this study.

Taxonomic classification

Species identification and length data were collected by four persons over the study period. These persons overlapped for at least 1 year to enable training and thus ensure consistency in sampling and species identification. A species photograph library was compiled to cross check species identification over time. Where data were misidentified, for example species that did not occur in the region, or entered incorrectly, for example lengths that exceeded known maximum lengths, these were removed prior to analysis (<2% of the data). There were some problems with consistent identification to the species level that caused some pooling of a few similar species. For example, *Lethrinus lentjan* (Lacepède) has been known by the incorrect synonym *Lethrinus mahsenoides* (Valenciennes) and *Lethrinus obsoletus* (Forsskål) by the incorrect syno-

Table 1. Description of the 11 studied landing sites including number of sampling days, fish sampled, proximity to a marine protected area and history of beach seine management in Kenya

Management group	Landing site	Number of sampling days	Number of fish sampled	No take zone <5 km to site	Year of beach seine exclusion
North	Marina	14	4981	Mombasa MNP	No exclusion
North	Msanakani	7	462	Mombasa MNP	No exclusion
North	Nyali	3	220	Mombasa MNP	No exclusion
North	Reef	7	894	Mombasa MNP	No exclusion
Kenyatta	Kenyatta	38	4608	Mombasa MNP	1998–2002
South	Chale	9	1010	None	2001
South	Mgwani	9	1538	None	1999
South	Mvuleni	16	3658	None	>20 years ago
South	Mwanyaza	12	3697	None	>20 years ago
South	Mwaepe	11	1591	None	2001
South	Tradewinds	8	4396	None	2005

nym *Lethrinus ramak* (Forsskål). The nomenclature of Smith and Heemestra (1986) for *L. lentjan and L. obsoletus* was used throughout.

Data analyses

Effect on length of catch

Differences in lengths of landed catch between years, gears and management status were assessed with three-way, crossed fixed-effects orthogonal analysis of variances (ANOVAS). Homogeneity of variances was assessed with Levene's test and normality of the data with normal probability plots of the residuals and Shapiro–Wilks test. Normality and homogeneity significance levels were set at $P < 0.01$. Change in length was plotted against time for management and gear and the best-fit linear relation plotted. Length frequency distributions were plotted for each management group and the first and last year of catch for each management group. Differences in lengths between the first and last years were tested for each management group individually, using an ANOVA.

Life-history analysis

Information about eight life-history characteristics was taken from FishBase (http://www.fishbase.org/) for the most abundant 15 species. These were intrinsic growth rate, life span, generation time, natural mortality, age at maturity, maximum length, length at maturity and length to achieve optimum yield. Mean life-history characteristics of the catch were calculated by management grouping for each year (k) as;

$$LH_k = \frac{\sum_{i=1}^{m} Y_{ik} LH}{\sum Y_{ik}} \tag{1}$$

Y_{ik} is the relative abundance in the catch of species i in year k, LH is the life-history characteristic for species i of m species. Changes over time in the life-history characteristics of each management grouping were analysed using a redundancy analysis (RDA) to examine the relationship between life-history characteristics and (1) spatial variation of the study sites through time and (2) species composition. Life-history characteristics were assigned as predictors and the species abundance as the response variables (Ter Braak 1995; Quinn & Keough 2002).

Ecological characteristics

Five characteristics of the ecology of the catch were calculated; diversity, trophic level and three functional groupings. Diversity was calculated as a variation of Simpson's diversity index using the following equation:

$$D_k = 1 - \sum_{i=1}^{m} \left(\frac{Y_{ik}}{\sum Y_{ik}} \right)^2 \tag{2}$$

The 15 species were assigned to one of three functional groupings based on information on their food using classifications from FishBase (http://www.fishbase.org/). The relative abundance of each functional group was calculated by management category for each year. Additionally, trophic level designations were taken from FishBase for the most abundant 15 species (http://www.fishbase.org/). The mean trophic level of the catch was calculated by management grouping for each year (k) as (eqn 1). Changes over time in the ecological characteristics for each management grouping were analysed using RDA to examine how they related to: (1) spatial variation of the study sites through time and (2) species composition. Ecological characteristics were assigned as predictors and species abundance as response variables (Ter Braak 1995; Quinn & Keough 2002).

Results

Changes in body lengths

The length of the most abundant target fishes increased over the study period, and 73% of those differences were statistically significant (Table 2; $P < 0.01$). The greatest increase in mean length over time (6.8 cm) was shown by two herbivorous species, *Siganus sutor* (Valenciennes) and *Scarus psittacus (Forsskal)*. *Leptoscarus vaigiensis* (Quoy & Gaimard) and *Lethrinus harak* (Forsskål) had the smallest increases (0.6 and 0.7 cm respectively), which were driven by changes in the south coast sites. Four species were not statistically different or lacked sufficient degrees of freedom for testing. Ninety-three percent of species differed significantly ($P < 0.01$) in their body lengths, as landed by different gears and 73% of species differed significantly ($P < 0.01$) in their lengths, as landed by management groups.

When pooling all species, the length of fish in all three management groupings increased over time. South coast sites showed the greatest increase (5.2 cm), followed by Kenyatta (3.9 cm) and north coast sites (3.5 cm) (Fig. 1a). Differences in the rates of increase accounted for the significant interactions between management and time ($P < 0.0001$; Table 2). Apart from 2004, the largest fish were consistently landed at Kenyatta, while the smallest fish were consistently landed at the north coast sites (Fig. 1a).

Table 2. Change in fish lengths from the beginning to the end of the study. Results of significance tests for univariate 3-factor crossed analysis of variance (*f*) for the entire catch and 15 most abundant species in the landed catch

	d.f.	SL (cm) 1998	SL (cm) 2007	Trend (cm)	Year (*f*)	Gear (*f*)	Management (*f*)	Year × Management (*f*)
All[†]	$(5,4,2,10)_{24\,345}$	13.9	18.4	+ 4.5	226.8**	227.8**	69.7**	17.2**
Acanthurus triostegus	$(1,4,1,6)_{691}$	12.3	15.5	+ 3.2	9.2*	1.0	7.2*	0.8
Acanthurus nigrofuscus	$(1,4,1,6)_{363}$	11.6	15.1	+ 3.5	0.06	6.1**	8.1*	1.1
Calotomus carolinus[‡]	$(4,4,2,9)_{1378}$	13.4	19.1	+ 5.7	25.1**	24.3**	84.7**	2.9*
Cheilinus chlorourus.	$(2,4,1,6)_{349}$	16.3	18.2	+ 1.9	5.5*	7.1**	3.6	2.6
Cheilio inermis[§]	$(3,4,2,8)_{577}$	20.6	22.3	+ 1.7	2.4	9.4**	5.6*	5.1**
Geres oyena[¶]	$(0,2,2,4)_{300}$	10.1	13.5	+ 3.4	Lost df	9.2**	39.6**	14.7**
Leptoscarus vaigiensis[††]	$(5,4,2,10)_{4995}$	16.1	16.7	+ 0.6	17.5**	3.4*	18.3**	13.9**
Lethrinius harak[‡‡]	$(4,4,2,9)_{1134}$	19.9	20.6	+ 0.7	12.9**	60.3**	27.6**	16.3**
Lethrinius obsoletus[§§]	$(1,4,1,5)_{407}$	14.6	16.0	+ 1.4	48.4**	12.9**	0.2	15.1**
Lethrinus lentjan[¶¶]	$(5,4,2,10)_{6045}$	11.6	15.2	+ 3.6	39.8**	51.9**	25.8**	15.7**
Lutjanus fulviflamma[†††]	$(5,4,2,10)_{775}$	14.7	15.6	+ 0.9	9.4**	26.7**	17.9**	4.6**
Parupeneus barberinus[‡‡‡]	$(3,4,1,8)_{436}$	16.3	22.0	+ 5.7	1.3	16.8**	4.5	3.1*
Parupeneus macronema[§§§]	$(4,4,2,8)_{596}$	15.0	17.9	+ 2.9	16.2**	22.1**	4.4	8.6**
Scarus psittcus	$(1,3,1,3)_{437}$	14.7	21.5	+ 6.8	58.5**	8.9**	13.6*	9.8**
Siganus sutor[¶¶¶]	$(5,4,2,10)_{5834}$	13.6	20.4	+ 6.8	158**	136**	26**	24**

$^{*}P < 0.01$; $^{**}P < 0.0001$.

[†] Interaction as south coast increasing fastest then Kenyatta, north coast stable. [‡] Interaction as south coast increases at a faster rate than Kenyatta from 2000 to 2004. [§] Interaction as south coast steady while north coast variable. [¶] Interaction as Kenyatta and north coast spike in 2004. [††] Interaction as south coast increases at a faster rate than Kenyatta or north coast. [‡‡] Interaction as south coast increases at a faster rate than Kenyatta or north coast with a peak in 2004. [§§] Interaction as Kenyatta decreases, south coast stable, north coast decreases. [¶¶] Interaction as south coast increases faster than Kenyatta or north coast. [†††] Interaction as north coast declined, Kenyatta and south coast increased. [‡‡‡] Interaction as north coast declined till 2004 then a rapid recovery. [§§§] Interaction as south coast recovers faster than Kenyatta, north coast always high. [¶¶¶] Interaction as large variance in north coast lengths over time.

Evaluation of interactions at the species level found that 80% of species showed significant time and management interactions ($P < 0.01$). Of these interactions, 61% were attributable to south coast sites increasing at a greater rate than north coast or Kenyatta sites, 8% were attributable to south coast, and Kenyatta sites increasing at a greater rate than north coast sites, and 31% were attributable to high variability between years in the length of landed catch in the north coast (Table 2).

The lengths of fish in the landed catch increased for all fishing gears over the study period (Fig. 1b). The largest fish were caught by spears and gill nets, the smallest fish were caught by beach seines and lines. The greatest increases in the lengths of landed fish were found in the trap and line landings (6.4 and 4.1 cm), while the smallest increases in lengths of landed fish were found in the beach seine, net, and spear landings (2.8, 1.9, 1.8 cm). By the end of the study, there were no differences in the size of fish found in the trap, spear or net landings, and the fish landed by beach seine represented the smallest sized fish (Fig. 1b).

Frequency distributions of standard lengths for all species combined indicated that the largest fish were captured in Kenyatta and smallest in the north coast (Fig. 2a). The size frequency data were near to normal distribution with a slight positive tail for all management categories, across all years and individually for the first to last years (Fig 2a–d). The increases in mean length were also represented by the size-frequency distributions (Fig 2a–d). There was a significant shift ($P < 0.001$) in the size frequency distributions from the first to the last years across all management categories, greatest in the south coast (Fig. 2c) and least in the north coast (Fig. 2d).

Life-history ordinations

Ordination of sites and species by their weighted average life-history characteristics indicated differences based on the three management categories (Fig. 3). The greatest variation in species abundances and life-history characteristics occurred along the first canonical axis, which separate sites based on gear management, while the second axis separate the sites based on area or closure management The north coast sites were characterised by a longer generation time, longer life span and older fish at first maturity. Two of the three most dominant species in the catch of all three management systems have short life spans (*S. sutor* = 5.6 year and

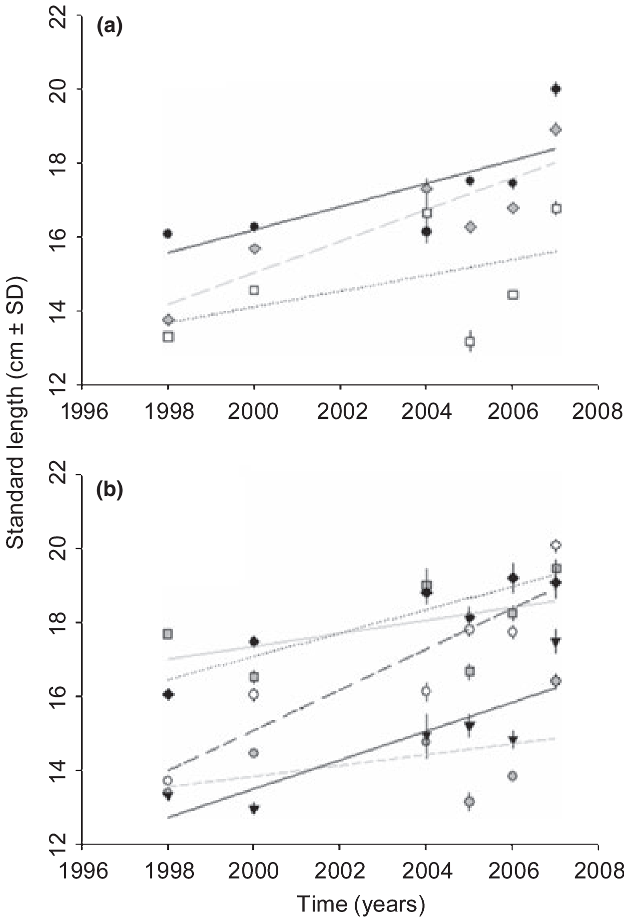

Figure 1. Lengths (mean ± SD) of landed fish catch over study period by (a) management grouping (●– Kenyatta with gear/closure restrictions; ◇– south coast with gear restrictions and □– north coast sites with no restrictions) and (b) gear type (◎– beach seine, ▼– line, ▣– net, ♦– spear and ○–trap).

L. lentjan = 5.9 year) and the third most dominant species in all systems but the most dominant species in the north coast management has an intermediate life span (*L. vaigiensis* = 7.7 year). Therefore, this separation is based largely on *L. vaigiensis* dominance and the subdominant members of the catch with long life spans, largely *Chelio inermis* (Forsskål) (21.9 year) and *Gerres oyena* (Forsskål) (12.4 year). South coast (gear management present) and Kenyatta (both gear and area management present) were separated by the second canonical axis. Kenyatta was characterised by a faster rate of intrinsic growth (*K*), longer maximum lengths and higher rates of natural mortality. This is largely driven by a dominance *of S. sutor* in the Kenyatta catch with its high intrinsic growth rates ($K = 0.51$). South coast sites were characterised by shorter lengths at first maturity and shorter lengths at optimum yield, although they also displayed faster rates of intrinsic growth, longer maximum length and higher rates of natural mortality. The dominance of *L. lentjan* in the south coast and its shorter lengths at maturity and optimum yield largely drive this small difference between the two restrictive management fisheries.

There were notable changes in weighted-average life-history characteristics over time (Fig. 3). South coast and Kenyatta fish showed movements towards greater maximum lengths, intrinsic growth rates and rates of natural mortality. South coast fish followed a similar trajectory to Kenyatta but with a lag or delayed response. North coast sites showed less directional movement in the life-history characteristics of landed fish over the study period.

Ecological ordinations

Multivariate ordinations of sites through time, based on ecological characteristics, found patterns similar to those observed with life-history characteristics (Fig. 4). The greatest distinction was observed for the north coast, which was characterised by a lower trophic level and higher proportions of invertivores and herbivores than the other two management groups. South coast sites were characterised by high diversity and a higher proportion of piscivores/invertivores fishes. Over time, the relative composition of the 15 most abundant species of the landed catch in both Kenyatta and south coast sites decreased in the diversity or higher dominance and to a lesser extent increased in trophic level. South coast site changed at a slower rate than Kenyatta. North coast sites showed variation with time in the species composition of the landed catch, but the changes lacked a clear direction, and the landings were always characterised by herbivores and low diversity.

Discussion

These study sites clustered into distinct management groupings based on the composition of fish species (McClanahan *et al.* 2008). These differences reflected distinct life history and ecological characteristics at the sub-genus level that changed over time. In addition, fish lengths increased in all management categories, even sites with no restrictions, albeit at a slower rate than the two areas with active management. There were directional changes in relative life history and ecological characteristics over time in the two areas with active management (gear restrictions and closure), while no clear directional change in these characteristics was evident where there were no fishing

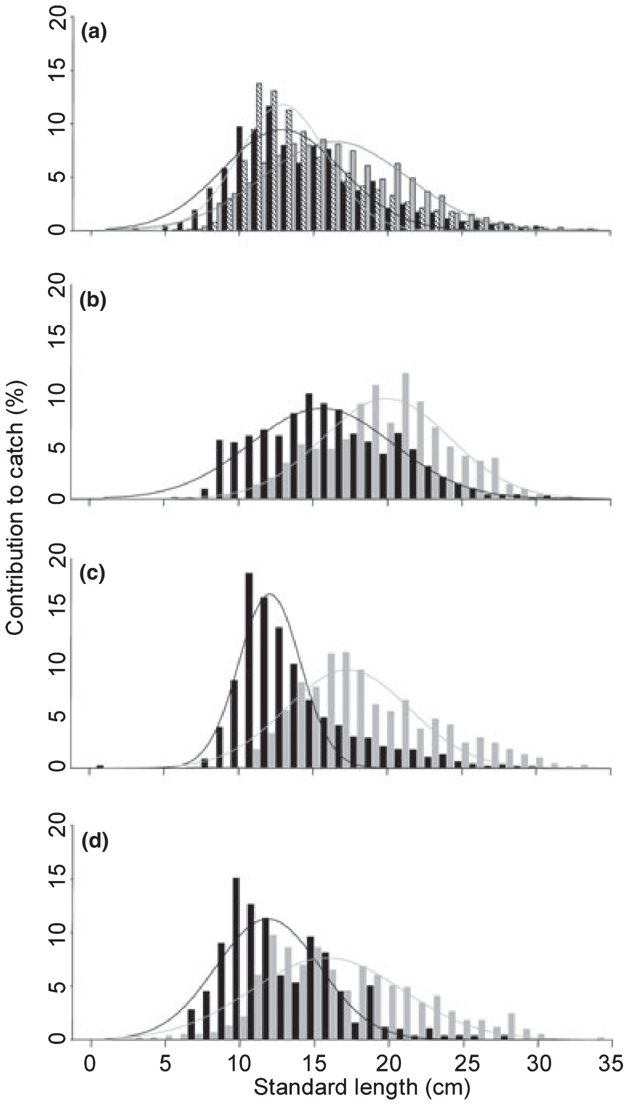

Figure 2. Size frequency distributions for (a) the whole landed catch by management grouping (▭– Kenyatta with gear/closure restrictions, ▨– south coast with gear and ■– north with no restrictions, restrictions), (b) Kenyatta with gear/closure restrictions (■– 1998, ▭– 2007), (c) south coast with gear restrictions (■– 1998, ▭– 2007) and (d) north coast with no restrictions (■– 1998, ▭– 2007).

restrictions. Consequently, management restrictions are the expected cause of the changes in size, life history and ecological characteristics of the fish community. Some observed changes, such as increases in size, trophic level, relative rates of natural mortality and growth were predictable from theories of fishing impacts or disturbances (Jennings *et al.* 1999). Other responses, such as increases in the relative contribution of species with larger maximum attainable length had not been expected to respond so rapidly and the longer life spans of fish in the unmanaged fishery were unexpected.

An increase in body size and associated life-history characteristics is expected with increasing management restrictions and the basis for length-based management of fisheries (Ault *et al.* 2008). Fish lengths are expected to increase as gears are managed for larger mesh or selectivity of larger fishes. Here, as beach seines caught the smallest fish, elimination of this gear resulted in an increase in lengths caught by other gear. Specifically, landed fish around the south coast in 1998 had similar mean lengths to those landed fish around the north coast. However, by 2007 landed fish around the south coast had increased to a similar mean length as landed fish around Kenyatta. Catches from traps and lines responded most to the elimination of the beach seine, as measured by the rate of rise in mean fish length. By the end of the study, differences in the size of fish caught between gears were small, with most gear catching fish of around 17–20 cm, whereas beach seines, lines and traps caught fish < 14 cm at the start of the study. Consequently, the gear that caught the smallest sized fish prior to its elimination had the fastest rises. Gill nets and spears, which initially caught the largest size fish, had the smaller changes over time.

Beach seine is a gear with weak selectivity that captures a high diversity of species (Gell & Whittington 2002) creating an overlap in selectivity with most gears. A previous study of gear selectivity in Kenya found greatest similarity in species caught by beach seines, traps and gill nets, and weaker similarity with lines (McClanahan & Mangi 2004). It was therefore predicted that the elimination of beach seines would produce the largest responses among traps and gill nets. A greater response for traps was confirmed by this study, but the fast and slow rates of increase for lines and gill nets, respectively, were contrary to predictions. Consequently, similarities in species selectivity may be less important than similarities in size selectivity among gear. Here, removing the gear with selectivity for the smallest individuals resulted in the fastest body length increases among gears that also selected for small sizes.

Patterns in life-history characteristics among management groups largely supported the predictions, but with some complications where trophic level and life history interacted in unexpected ways. For example, the overall abundances as estimated by CPUE were lower in the north coast, the fishery with the least management restrictions (McClanahan *et al.* 2008). Despite this higher fishing impact, the relative composition of the landed catch had a high proportion of species with high vulnerability characteristics, such as low growth and natural mortality rates and older age at maturity, life span and generation time. In addition,

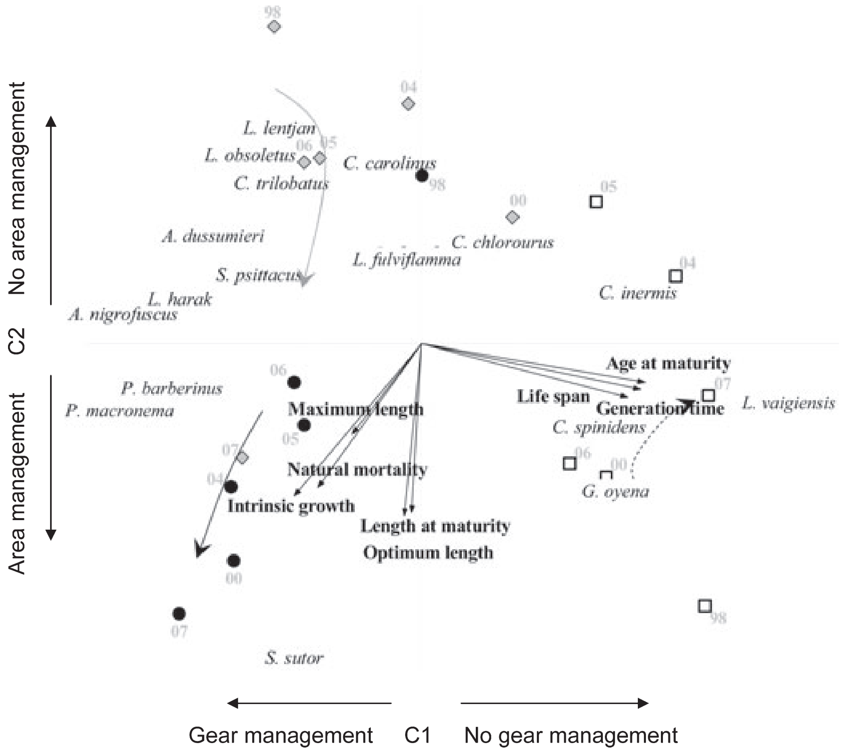

Figure 3. Redundancy analysis showing spatial distribution of management groupings over the study period and the associated life-history characteristics of the species driving differences in distribution. (C1 = 51.1%, C2 = 33.4%, $F = 31.72$, $P = 0.002$). ● – Kenyatta with gear/closure restrictions; ◇ – south coast with gear restrictions and □ – north coast sites with no restrictions, ——► – life-history characteristics, general direction of change with time for ↗ – Kenyatta, ↗ – north coast, ↗ – south coast sites.

these sites had the lowest mean trophic levels, with the catch sustained predominantly by herbivores. This pattern occurs because *L. vaigiensis* is the dominant herbivore caught and has an intermediate life span, and because two subdominant carnivores in the catch, *C. inermis* and *G. oyena*, have long life spans. The reasons for the longer life spans is unclear and unexpected, but may be that populations outside of the fishery help maintain the populations in the fishery or that they may have specific morphologies that allow them to slip through nets and persist in this small mesh net fishery. For example, *C. inermis* manages to persist in this fishery possibly because of its long and slender body, allowing it to escape nets until later in life. The low diversity of species in the north coast fisheries is probably because so few species can persist at such high fishing intensity.

Conversely, the sites that had experienced active gear, area management and highest CPUE, i.e. south coast and Kenyatta, had a greater proportion of species with reduced vulnerabilities, such as shorter generation times, greater rates of natural mortality, greater rates of growth, shorter life spans and fish that were younger at first maturity. Although these sites had greater proportions of species with low vulnerabilities, which had undergone the fastest rates of recovery after restrictions, they also experienced the recovery of species with high vulnerability to fishing, albeit at a slower rate. The sites with greater management also had higher mean trophic levels and a greater diversity of species and a greater proportion of piscivore–invertivores than their less managed counterparts. The managed sites showed a shift in life history indicators over time towards a greater proportion of species with higher trophic levels and relatively lower vulnerabilities to fishing.

There were no discernable differences in the lengths at first maturity and lengths to achieve optimum yield of the landed catch between managed or unmanaged sites overall. However, over time, the lengths at first maturity and lengths to achieve optimum yield of the landed catch within managed sites increased. In addition, species that achieved greater maximum lengths were landed at managed sites. This suggests that responses to fishing in body size life-history characteristics are complex and can have different

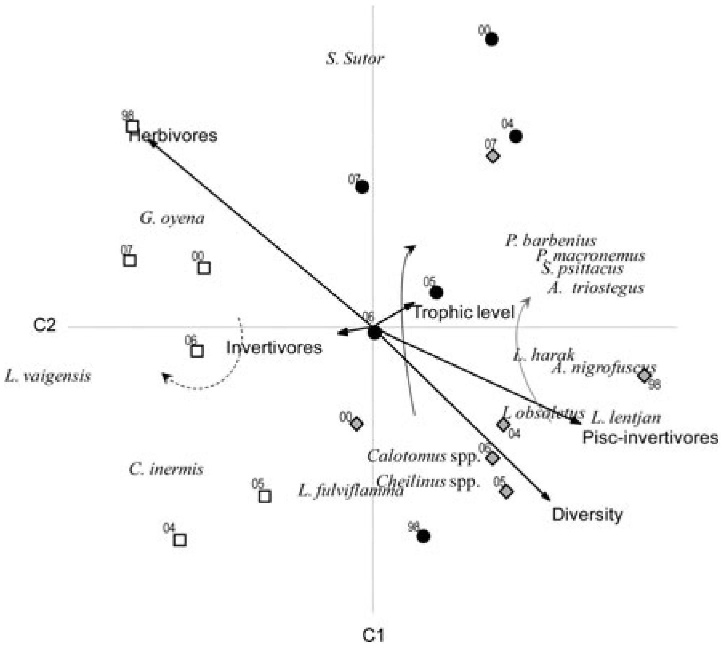

Figure 4. Redundancy analysis showing spatial distribution of management groupings over the study period and the associated ecology characteristics of the species driving differences in distribution. (C1 = 55.0, C2 = 31.3, F = 9.64, P = 0.002). ● – Kenyatta with gear/closure restrictions; ◇ – south coast with gear restrictions and □ – north coast sites with no restrictions, ⟶ – ecological characteristics, general direction of change with time for ↗ – Kenyatta, ↗ – north coast, ↗ – south coast sites.

rates and directions of response to management (Cheung *et al.* 2008). However, while management may effectively increase the abundance of fish species with both high and low vulnerabilities to fishing depending on fishing pressure, the recovery of species most vulnerable to fishing is expected when fishing stops or is reduced to very low levels (Jennings *et al.* 1999; Dulvy *et al.* 2004). The challenge remains to find if there are levels of exploitation and recovery that can sustain valuable and vulnerable target species.

This study suggests that there are trade offs in management that make it difficult to achieve protection for all species and their life histories through large scale open access combined with small closures and even standard fisheries restrictions. Maximising sustainable yield from large species, as well as maintaining vulnerable species and high biodiversity of the fish community in high dependence and fishing pressure countries, such as in Kenya, may require spatial heterogeneity in management (Jennings 2007). These life-history characteristics and their changes may appear to be an arcane interest of fisheries biologists and conservationists but the prices of fish can be associated with these characteristics and influence the incomes from fisheries (McClanahan 2010).

It is possible that, in Kenya, gear management has increased the size of fish landed and decreased the proportion of vulnerable life-history characteristics targeted. While the maintenance of the trophic level of the catch and the supply of species with large body size characteristics has resulted from fisheries closures or offshore unfished areas that ensure that recruitment originates from outside the fishing grounds (McClanahan *et al.* 2008; McClanahan 2010). For example, the rabbitfish *S. sutor*, appeared resilient to heavy fishing in north coast sites, despite its relatively large maximum length, optimal harvesting size and size at sexual maturity compared with the majority of the landed catch. Other explanations do, however, exist. For example, body size life-history characteristics (e.g. maximum length, length at first maturity, optimal harvesting length and age at first maturity) may be less vulnerable to fishing than predicted or be specific to gear types. An example of this is body shape; *C. inermis*, has large body size characteristics (maximum attainable length, length at maturity), but has a long narrow body shape that may allow it to escape nets and maintain populations under heavy fishing pressure. Alternatively, all dominant species in this management group were strongly associated with seagrass and sand ecosystems, which persist and may even benefit from heavy fishing (McClanahan & Kurtis 1991). Consequently, the considerable resilience of seagrass and associated fauna (Heck & Valentine 2007) appears to give this fishery considerable resilience and high yields (McClanahan *et al.* 2008).

In short, predicting life-history characteristics from management intensity is neither simple nor straightforward when based only on simple body size, species and ecological turnover considerations. Regardless, there were spatial and temporal patterns that suggest that fishing does influence these characteristics, albeit in ways that are not always easily predicted. It is therefore critical that management considers a broad spectrum of ecological, life history and productivity indicators to assess effectiveness (Jennings *et al.* 2001). More comparative work is needed to determine if the patterns observed here are common to other coral reef fisheries. Additional studies may reveal other fish species characteristics that provide resilience to fishing and can be predicted by theories of human stress and disturbance (Odum 1985; Clark 1996; Rapport & Whitford 1999; Cheung *et al.* 2008). Such analyses could develop a general theory of disturbance effects that are hard to detect from single-region studies.

The general rise in fish size in all management groups over time is a provocative finding. This is best explained by either a broad-scale response to increased closures and gear management that then influences all landing sites, or some slowly changing environmental factor that is increasing the production and size of caught fish in this region. The first option remains the most likely, as gear selectivity and heavy fishing pressure is expected to maintain constant sizes of captured fish even if production increases. If true, the implication is that open-access fishing grounds can benefit from management in adjacent fishing grounds. This might produce an interest in supporting large-scale national fisheries restriction policies, but could also result in free loading and supporting increased management in distant but not local fishing grounds. Nevertheless, in terms of coral reef fisheries, a combination and heterogeneous use of gear and area management produces the most risk-spreading results, enabling multiple, mutually beneficial but sometimes conflicting objectives to be achieved.

Acknowledgements

The Wildlife Conservation Society, through grants from the Eppley, McBean, Tiffany Foundations and the Pew Fellows Program in Marine Conservation, supported the co-management and research in southern Kenya. Research clearance was provided by Kenya's Ministry of Science and Technology and data collection and management efforts by Kenya's Fisheries Department and Kenya Wildlife Services. S. Mangi, J. Maina, Kitema and P. Mutisya assisted with the fisheries data collection. We are grateful to the many fishers and fisheries officers of southern Kenya for their cooperation. This paper was improved by the comments of the anonymous reviewers.

References

Ault J.S., Smith S.G., Luo J., Monaco M.E. & Appeldoorn R.S. (2008) Length-based assessment of sustainability benchmarks for coral reef fishes in Puerto Rico. *Environmental Conservation* **35,** 221–231.

Bascompte J., Melian C. & Sala E. (2005) Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences* **102,** 5443–5447.

Beddington J.R., Agnew D.J. & Clark C.W. (2007) Current problems in the management of marine fisheries. *Science* **316,** 1713–1716.

Cheung W.W.L., Pitcher T.J. & Pauly D. (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation* **124,** 97–111.

Cheung W.W.L., Close C., Lam V. & Pauly D. (2008) Application of macroecological theory to predict effects of climate change on global fisheries potential. *Marine Ecology Progress Series* **365,** 187–197.

Cinner J.E., McClanahan T.R., Graham N.A.J., Pratchett M.S. & Wilson S. (2009) Gear-based fisheries management as a potential adaptive response to coral bleaching. *Journal of Applied Ecology* **46,** 724–732.

Clark J.S. (1996) Testing disturbance theory with long-term data: alternative life-history solutions to the distribution of events. *American Naturalist* **148,** 976–996.

Dulvy N.K., Freckleton R.P. & Polunin N.V.C. (2004) Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters* **7,** 410–416.

Gell F.R. & Whittington M.W. (2002) Diversity of fishes in seagrass beds in the Quirimba Archipelago, northern Mozambique. *Marine & Freshwater Research* **53,** 115–121.

Heck K.L. & Valentine J.F. (2007) The primacy of top-down effects in shallow benthic systems. *Estuaries and Coasts* **30,** 371–381.

Jennings S. (2007) Reporting and advising on the effects of fishing. *Fish & Fisheries* **8,** 269–276.

Jennings S. & Blanchard J.L. (2004) Fish abundance with no fishing: predictions based on macroecological theory. *Journal of Animal Ecology* **73,** 632–642.

Jennings S. & Kaiser M.J. (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology* **34,** 202–352.

Jennings S., Greenstreet S.P.R. & Reynolds J.D. (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology* **68,** 617–627.

Jennings S., Kaiser M. & Reynolds J.D.. (2001) *Marine Fisheries Ecology*. Oxford: Blackwell Science, 417 pp.

Johannes R.E. (1998) The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends in Ecology & Evolution* **13,** 243–246.

Kaplan D.M. (2009) Fish life histories and marine protected areas: an odd couple? *Marine Ecology Progress Series*, **377,** 213–225.

Lieske E. & Myers R. (1994) *Collins Pocket Guide. Coral Reef Fishes. Indo-Pacific & Caribbean including the Red Sea*. London: Harper Collins, 400 pp.

Mangi S.C. & Roberts C.M. (2006) Quantifying the environmental impacts of artisanal fishing gear on Kenya's coral reef ecosystems. *Marine Pollution Bulletin* **52,** 1646–1660.

McClanahan T.R. (1995) Harvesting in an uncertain world: impact of resource competition on harvesting dynamics. *Ecological Modelling* **80,** 21–26.

McClanahan T.R.(2010) Effects of fisheries closures and gear restrictions on fishing income in a Kenyan coral reef. *Conservation Biology*, doi: 10.1111/j.1523-1739.2010.01530.x.

McClanahan T.R. & Kurtis J.D. (1991) Population regulation of the rock-boring sea urchin Echinometra mathaei (de Blainville). *Journal of Experimental Marine Biology & Ecology* **147,** 121–146.

McClanahan T.R. & Mangi S. (2001) The effect of closed area and beach seine exclusion on coral reef fish catches. *Fisheries Management & Ecology* **8,** 107–121.

McClanahan T.R. & Mangi S. (2004) Gear-based management of a tropical artisanal fishery based on species selectivity and capture size. *Fisheries Management & Ecology* **11,** 51–60.

McClanahan T.R., Maina J. & Davies J. (2005) Perceptions of resource users and managers towards fisheries management options in Kenyan coral reefs. *Fisheries Management & Ecology* **12,** 105–112.

McClanahan T.R., Graham N.A.J., Calnan J.M. & MacNeil M.A. (2007) Towards pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Applications* **17,** 1055–1067.

McClanahan T.R., Hicks C.C. & Darling E.S. (2008) Malthusian overfishing and efforts to overcome it on Kenyan coral reefs. *Ecological Applications* **18,** 1516–1529.

Odum E.P. (1985) Trends expected in stressed ecosystems. *BioScience* **35,** 419–422.

Pauly D., Christensen V., Dalsgaard J., Froese R. & Torres Jr F. (1998) Fishing down marine food webs. *Science* **279,** 861–863.

Pratchett M., Munday P., Wilson S., Graham N., Cinner J., Bellwood D., Jones G., Polunin N. & McClanahan T. (2008) Effects of climate-induced coral bleaching on coral-reef fishes - Ecological and economic consequences. *Oceanography & Marine Biology Annual Review* **46,** 251–296.

Quinn G.P. & Keough M.J. (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press, 537 pp.

Rapport D.J. & Whitford W.G. (1999) How ecosystems respond to stress. *BioScience* **49,** 193–203.

Rochet M.J., Cornillon P.A., Sabatier R. & Pontier D. (2000) Comparative analysis of phylogenetic and fishing effects in life history patterns of Teleost fishes. *Oikos* **91,** 255–270.

Russ G.R. & Alcala A.C. (1998) Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family response*s*. *Coral Reefs* **17,** 383–397.

Smith M.M. & Heemestra P.C. (1986) *Smith*'s Sea Fishes. Berlin: Springer Verlag, 1047 pp.

Tegner M.J. & Dayton P.K. (1999) Ecosystem effects of fishing. *Trends in Ecology & Evolution* **14,** 261–263.

Ter Braak C.J.F. (1995) Ordination. In: R.H.G. Jongman, C.J.F. Ter Braak & O.F.R. van Tongeren (eds) *Data Analysis in Community and Landscape Ecology*. Cambridge: Cambridge University Press, pp. 91–73.

Worm B., Barbier E.B., Beaumont N., Duffy J.E., Folke C., Halpern B.S., Jackson J.B.C., Lotze H.K., Micheli F., Palumbi S.R., Sala E., Selkoe K.A., Stachowicz J.J. & Watson R. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* **314,** 789–790.