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TOWARD PRISTINE BIOMASS: REEF FISH RECOVERY IN CORAL REEF MARINE PROTECTED AREAS IN KENYA

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Abstract. Identifying the rates of recovery of fish in no-take areas is fundamental to designing protected area networks, managing fisheries, estimating yields, identifying ecological interactions, and informing stakeholders about the outcomes of this management. Here we study the recovery of coral reef fishes through 37 years of protection using a space-for-time chronosequence of four marine national parks in Kenya. Using AIC model selection techniques, we assessed recovery trends using five ecologically meaningful production models: asymptotic, Ricker, logistic, linear, and exponential. There were clear recovery trends with time for species richness, total and size class density, and wet masses at the level of the taxonomic family. Species richness recovered rapidly to an asymptote at 10 years. The two main herbivorous families displayed differing responses to protection, scarids recovering rapidly, but then exhibiting some decline while acanthurids recovered more slowly and steadily throughout the study. Recovery of the two invertebrate-eating groups suggested competitive interactions over resources, with the labrids recovering more rapidly before a decline and the balistids demonstrating a slower logistic recovery. Remaining families displayed differing trends with time, with a general pattern of decline in smaller size classes or small-bodied species after an initial recovery, which suggests that some species- and size-related competitive and predatory control occurs in older closures. There appears to be an ecological succession of dominance with an initial rapid rise in labrids and scarids, followed by a slower rise in balistids and acanthurids, an associated decline in sea urchins, and an ultimate dominance in calcifying algae. Our results indicate that the unfished "equilibrium" biomass of the fish assemblage >10 cm is 1100–1200 kg/ha, but these small parks (<10 km^2) are likely to underestimate pre-human influence values due to edge effects and the rarity of taxa with large area requirement, such as apex predators, including sharks.

Key words: coral reef ecology; ecological interactions; ecological succession; fisheries closures; fisheries production; fisheries yields; indirect effects; marine reserves; marine protected areas; maximum sustained yield; MSY; spillover.

INTRODUCTION

The recovery rate of fish in no-take areas has important implications for the design and management of protected area networks and the management of fisheries (Halpern and Warner 2002*a*, Roberts et al. 2003, Gaylord et al. 2005). Recovery rate information provides a basis for determining the usefulness and timing of permanent, periodic, or rotational closures. It also gives estimates of net production and identifies life-history and time-dependent ecological responses and interactions in ecosystems following disturbance. The use of recovery data has, however, been hindered by the inability to study well-enforced closed areas over sufficiently long and undisturbed periods in conjunction with suitable control sites (McClanahan and Graham 2005, Sale et al. 2005).

There are good examples of recovery rates in single full-closure areas over time (McClanahan and Kaunda-Arara 1996, Christie 2004, Russ and Alcala 2004, Abesamis and Russ 2005), but with one exception (McClanahan and Graham 2005), these studies have not exceeded 20 years; results indicate time scales were insufficient to detect the full trajectory of change (McClanahan 2000, Russ and Alcala 2004). Consequently, most efforts to model recovery have either been based on meta-analysis of disparate studies using reserves in different regions and ecosystems or used space-for-time substitutions (McClanahan 2000, Mosquera et al. 2000, Côté et al. 2001, Halpern and Warner 2002*b*, Halpern 2003, Micheli et al. 2004, McClanahan and Graham 2005). Russ et al. (2005) compared the direct vs. the inferred rate of recovery of commercially important predatory fish and found good correspondence with selected Philippine reserves. Their study within a single region suggests considerably slower recovery rates and stronger responses than have been detected in inferred studies using multiple and disparate

reserves (Halpern and Warner 2002b, Halpern 2003, Micheli et al. 2004). These longer-term recovery rates in the Philippines were supported by a subsequent space-for-time or chronosequence analysis of Kenyan coral reef marine parks that assessed recovery of total fish biomass and size spectra (McClanahan and Graham 2005). To further investigate recovery patterns there is a need to examine recovery data in greater detail, examining taxa-specific responses and alternate models of population recovery. This will enable more detailed, informative conclusions about recovery and production rates that can be used for the management of specific ecosystems.

This paper examines the recovery rates of the dominant fish families in coral reef reserves of Kenya with a focus on responses of density, size, biomass, and species richness. We test for time-dependent responses in each of these variables using a space-for-time substitution where four marine parks with different management starting dates were compared along with four unprotected control sites. We test the hypothesis that all of the above factors have time-dependent responses that are evident at the scale of 37 years. We examine the evidence that permanent fisheries closures can reach equilibrium or "pristine biomass" (B_0), which can be used to estimate stocks for fisheries yield models (Clark 1985).

METHODS

Study sites

Data were collected in four marine parks and four unmanaged sites in Kenya between 1987 and 2005, where sampling was undertaken 13 times, except in Kisite where only two samples were taken. Active management of the oldest marine park, Malindi, commenced in 1968, followed by Watamu in 1972, Kisite in 1978, and Mombasa in 1991. These parks vary in size from 6 km² to 28 km² (Mombasa, 6 km²; Watamu and Malindi, 10 km²; and Kisite, 28 km²), but the actual area occupied by coral reefs in each park is <10 km². All sampled areas were from central areas inside the park in shallow (0.5–3 m depth at low tide) and calm back reef lagoons where the dominant cover is live and dead coral substratum with some seagrass and sand cover. Hard coral cover and habitat complexity are similar between parks (McClanahan and Graham 2005).

Field methods

Fish were sampled by a single investigator (T. R. McClanahan) in replicate 5 × 100 m belt transects during neap tides when the water level was ~1–3 m deep. Two methods were employed to sample fish: one to obtain estimates of species richness (McClanahan 1994) and a second to estimate density and biomass to the family level (McClanahan and Kaunda-Arara 1996). The first method identified and counted all individuals in eight families (Acanthuridae, Balistidae, Chaetodontidae, Diodontidae, Labridae, Pomacanthidae, Pomacen-

tridae, and Scaridae) to the species level in belt transects, where families are sampled in discrete groups (DGS) during a single pass of the belt transect (McClanahan 1994). Four belt transects per site were consistently completed using this method, and data are presented as species/2000 m² based on the cumulative species in the four 500-m² transects. The DGS data were collected irregularly at the study sites; specifically, all sites were sampled in 1992 and 2003 while Kisite was additionally sampled in 2002 and 2004, and Mombasa in 1992, 1993, and 1998.

The second method identified all fish into the previous eight families, an additional three families (Lutjanidae, Mullidae, Siganidae), and an "others" category. The Lutjanidae is actually the sum of three closely related families, the Lutjanidae, Haemulidae, and Lethrinidae. Total lengths of individuals were estimated and placed into 10 cm size-class intervals, with a minimum size of 3–10 cm and a maximum size of >40 cm. Subsequent studies without an upper limit to the size classes bins indicate that this method reduces maximum biomass estimates by around 10% (T. McClanahan, *unpublished data*). The midpoint of the size classes was used to estimate the wet mass of each size class based on established length–mass relationships (McClanahan and Kaunda-Arara 1996), and the sum of all size classes was used to estimate the total wet mass. All sites were sampled annually from 1992 to 2004, with the exception of 2002, when no sites were sampled.

Recovery modeling

Chronosequences were established by assigning each sampling year to a year since fishing closure (McClanahan and Graham 2005). The areas open to fishing were pooled and assigned year 0 for the analyses. Where sufficient size class distribution was available, families were pooled into 10 cm size-class bins, and recovery trajectories across years of protection were assessed. Overall biomass was also analyzed for comparison to McClanahan and Graham (2005). Size class analyses are presented for density rather than biomass as the patterns were very similar, and as fish were counted in size class bins, the density counts are deemed more accurate. Furthermore, size-class densities have been useful in identifying effects of fishing and protection in various studies (Dulvy et al. 2004, Graham et al. 2005, McClanahan and Graham 2005). The DGS data were used to calculate Bray-Curtis similarity indices based on the eight families (Bray and Curtis 1957). We examined the similarity between parks in the chronosequence and Mombasa sampled in 1992: one year after it became a permanent closure. Linear regression was used to determine whether the community composition of the parks was becoming more or less similar to Mombasa's initial state through time of closure.

To model the recovery trajectories and rates of change in each fish subgroup, we selected five ecologically meaningful production models (asymptotic, Ricker,
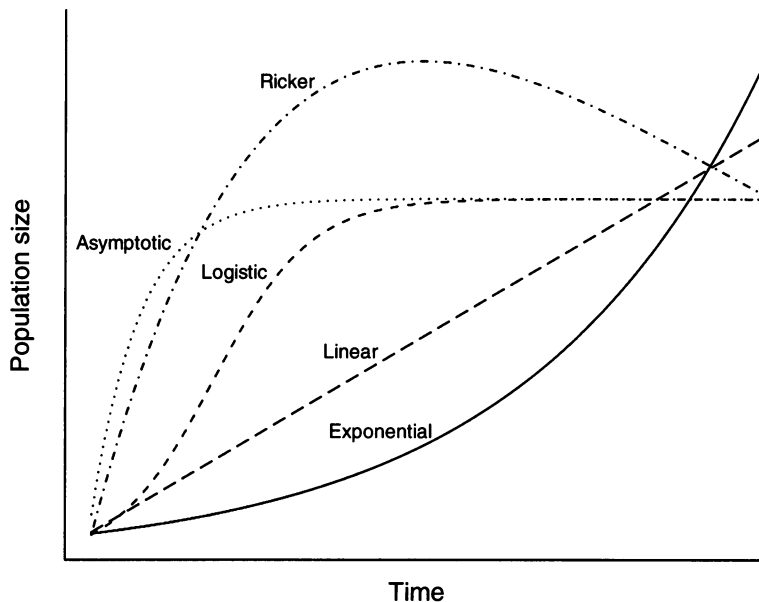
FIG. 1. The five candidate recovery curves used to quantify community turnover in Kenyan marine parks.

logistic, linear, and exponential; Fig. 1, Table 1) that encompassed potential community responses to fishing closure. Each of the models was run using maximum likelihood fits of the nonlinear regression (nls) routine in R 2.2.1 (R Development Core Team 2005). For each model we calculated the proportion of the variation explained by the model using a nonlinear approximation for R^2 where

$$R^2 = 1 - \frac{SS_{reg}}{SS_{tot}}. \tag{1}$$

Here, SS_{reg} is the residual sum of squares given the model, and SS_{tot} is the total sum of squares in the response. In addition we calculated a goodness of fit statistic (GOF) using a likelihood ratio test:

$$LRT = -2[\log_e(L_0) - \log_e(L_M)] \tag{2}$$

which is approximately χ^2 with $k - 1$ df, where k is the number of parameters in the given model, L_0 is the

likelihood of the grand mean (no model parameters), and L_M is the likelihood given the model used.

A best-fit model was selected using Akaike's Information Criterion (AIC), where the highest-ranked (lowest AIC) model was considered to have the majority of support, given the data, if it was >2 AIC values lower than the next lowest AIC model (Burnham and Anderson 2002). If one or more models were within two AIC values of the highest ranked model, we considered there to be equivalent support given the data, and we selected the model with the highest R^2 value for presentation. Groups with AIC-tied results were subsequently interpreted considering the model selection uncertainty present, however we did not conduct formal multi-model inference (Burnham and Anderson 2002), as our goal was to quantify community turnover rather than to make model-based determinations of processes that generated the data. Groups were considered to have no appropriately fitting model when

TABLE 1. Ecological equations used to model reef-fish recovery responses to fishing closure.

Model	Equation	Ecological interpretation
Asymptotic	$K + (N_0 - K)e^{-rt}$	Population reaches new carrying capacity (K) at constant rate (r); N_0 is initial population size.
Ricker	$N_0 + (\alpha t)e^{-\beta t}$	Population reaches a resource peak ($[\alpha/\beta]e^{-1}$) at a given time ($1/\beta$) by an initial rate of increase (α) and rate of decline (β).
Logistic	$\dfrac{K}{1 + \left(\dfrac{K - N_0}{N_0}\right)e^{-rt}}$	Population reaches a new carrying capacity (K) up to a maximum rate (r) through an initial exponential phase ($t < K/2$).
Linear	$b + mt$	Population increases continuously from an original density (b) at a constant rate (m) without limit.
Exponential	ae^{bt}	Population increases from an initial density (a) at an exponential rate (b) without limit.

TABLE 2. Ricker curve parameter estimates for reef-fish density and biomass groups.

Parameter, by fish group and size class (cm)	GOF†	R^2	$\hat{\alpha}$	$\hat{\alpha}$‡	95% CL‡	$\hat{\beta}$	$\hat{\beta}$‡	95% CL‡	$\hat{N}_0$	$\hat{N}_0$‡	95% CL‡
Total biomass	<0.001	0.55	138.0	158.1	(113.7, 205.1)	0.048	0.051	(0.039, 0.0622)	176.0	135.5	(36.67, 283.4)
Density											
Lab, all§	0.073	0.14	6.105	5.149	(2.245, 8.145)	0.087	0.059	(0.040, 0.074)	45.14	40.37	(29.94, 51.85)
Lab, 3–10	<0.001	0.40	8.596	8.276	(5.20, 11.38)	0.113	0.114	(0.094, 0.156)	22.09	23.53	(12.32, 32.21)
Lab, 10–20	0.004	0.27	2.760	1.557	(0.743, 2.798)	0.051	0.027	(0.001, 0.045)	3.64	6.27	(1.72, 9.61)
Lab, 20–30	0.020	0.22	0.482	0.291	(0.103, 0.592)	0.056	0.036	(0.006, 0.057)	0.51	0.89	(0.062, 1.72)
Lut, all	0.003	0.27	2.567	2.033	(0.898, 3.503)	0.049	0.038	(0.009, 0.061)	2.82	3.52	(0.713, 6.86)
Pac, all	<0.001	0.46	2.804	2.653	(1.898, 3.757)	0.145	0.148	(0.114, 0.215)	1.83	2.34	(0.909, 3.77)
Pom, all	0.090	0.13	15.13	11.14	(3.52, 25.03)	0.061	0.046	(0.012, 0.073)	96.55	102.66	(73.93, 124.92)
Sca, all	0.011	0.22	4.661	2.801	(0.751, 5.514)	0.055	0.035	(−0.008, 0.063)	15.47	18.41	(9.96, 27.51)
Sca, 10–20	0.079	0.15	2.999	2.557	(1.342, 3.856)	0.073	0.067	(0.043, 0.093)	0.54	1.58	(0, 5.76)
Biomass											
Lab, all	<0.001	0.39	9.545	5.817	(2.972, 9.051)	0.066	0.043	(0.019, 0.063)	18.28	23.63	(16.66, 32.33)
Lut, all	<0.001	0.32	14.26	19.70	(11.51, 30.68)	0.038	0.053	(0.033, 0.072)	19.36	10.56	(0, 35.44)
Pac, all	<0.001	0.31	6.655	7.047	(4.293, 11.18)	0.120	0.120	(0.092, 0.215)	5.53	4.95	(2.05, 10.67)
Richness, by family											
Aca	<0.001	0.72	1.975	2.019	(1.090, 3.092)	0.086	0.087	(0.058, 0.112)	2.62	2.56	(1.94, 3.34)
Cha	<0.001	0.72	0.347	0.355	(0.106, 0.614)	0.029	0.030	(−0.013, 0.050)	2.13	2.11	(1.75, 2.59)
Sca	<0.001	0.65	1.073	1.066	(0.744, 1.705)	0.054	0.053	(0.037, 0.084)	2.14	2.08	(1.38, 3.01)

Note: Hats on estimators indicate that they are random variables that are a function of the sample data used to estimate a parameter.

† GOF stands for goodness-of-fit.

‡ Estimates derived from a nonparametic bootstrap ($R = 9999$) of the Ricker model for reef-fish richness, density, and biomass groups.

§ "All" refers to all size classes pooled. Abbreviations in all tables are for groups Acanthuridae (Aca), Balistidae (Bal), Labridae (Lab), Lutjanidae (Lut), Pomacanthidae (Pom), Pomacentridae (Pac), Scaridae (Sca), and Siganidae (Sig).

the GOF statistic was >0.1 or the percentage variation explained was <10%. Normality of errors was evaluated from model residuals and quantile–quantile (Q–Q) plots.

To evaluate the uncertainty surrounding the parameter estimates, we conducted a nonparametric nls bootstrap ($R = 9999$) for each group given the selected best-fit model and calculated bootstrap parameter means and 0.95 quantile statistics. We plotted the corresponding nls and mean bootstrap parameter estimate curves for comparison and added 95% point confidence intervals

throughout the chronosequence using the 0.95 quantile bootstrap predictions for each management year.

RESULTS

Four model forms (Ricker, logistic, exponential, and linear) quantified recovery parameters among all fish groups, although there were wide variations in the precision of parameter estimates among families and size classes (Tables 2–4). On average, accepted models explained 36% ± 16% (mean ± SD) of the total variation in community recovery. Several residual plots

TABLE 3. Logistic curve parameter estimates for reef-fish density and biomass groups.

Parameter, by fish group and size class (cm)	GOF†	R^2	$\hat{K}$	$\hat{K}$‡	95% CL‡	$\hat{r}$	$\hat{r}$‡	95% CL‡	$\hat{N}_0$	$\hat{N}_0$‡	95% CL‡
Density											
Aca, all§	<0.001	0.70	80.9	94.3	(73.9, 199.9)	0.167	0.134	(0.083, 0.186)	11.5	13.4	(9.28, 17.7)
Aca, 10–20	<0.001	0.50	54.6	69.1	(57.3, 106.3)	0.182	0.132	(0.087, 0.179)	8.16	10.2	(6.06, 14.7)
Bal, all	<0.001	0.56	5.09	5.35	(3.99, 14.4)	0.143	0.158	(0.092, 0.316)	0.394	0.307	(0.034, 0.578)
Sca, 20–30	<0.001	0.33	14.3	16.7	(12.7, 28.1)	0.254	0.192	(0.111, 0.346)	1.61	1.97	(0.902, 3.31)
Sca, 30–40	0.002	0.29	6.27	6.52	(5.56, 7.845)	0.465	0.494	(0.249, 1.264)	0.480	0.438	(0.005, 1.84)
Biomass											
Sca, all	<0.001	0.53	239.1	247.0	(213.4, 295.9)	0.387	0.385	(0.228, 0.593)	15.7	16.3	(2.57, 41.1)

† GOF stands for goodness-of-fit.

‡ Estimates derived from a nonparametic bootstrap ($R = 9999$) of the logistic model for reef-fish density and biomass groups.

§ Table 2 gives a listing of family name abbreviations. "All" refers to all size classes pooled.

TABLE 4. Exponential curve parameter estimates for reef-fish density and biomass groups.

Parameter, by fish group and size class (cm)	GOF†	R^2	$\hat{\alpha}$	$\hat{\alpha}$‡	95% CL‡	$\hat{b}$	$\hat{b}$‡	95% CL‡
Density								
Sig, all§	<0.001	0.31	0.930	0.431	(0.028, 1.146)	0.078	0.108	(0.072, 0.202)
Aca, 20–30	<0.001	0.43	1.328	3.006	(0.437, 4.920)	0.091	0.058	(0.034, 0.131)
Bal, 20–30	<0.001	0.63	0.259	0.393	(0.241, 0.569)	0.076	0.058	(0.044, 0.080)
Bal, 30–40	0.007	0.21	0.244	0.208	(0.058, 0.371)	0.046	0.055	(0.031, 0.102)
Sig, 10–20	0.009	0.25	0.651	0.639	(0.151, 1.290)	0.071	0.071	(0.042, 0.122)
Biomass								
Aca, all	<0.001	0.58	62.9	63.0	(47.9, 79.0)	0.050	0.049	(0.037, 0.062)
Bal, all	<0.001	0.47	9.335	6.889	(4.028, 9.828)	0.053	0.070	(0.054, 0.091)
Sig, all	0.007	0.20	4.188	3.944	(1.700, 6.392)	0.051	0.056	(0.032, 0.090)

† GOF stands for goodness-of-fit.
‡ Estimates derived from a nonparametic bootstrap ($R = 9999$) of the exponential model for reef-fish density and biomass groups.
§ Table 2 gives a listing of family name abbreviations. "All" refers to all size classes pooled.

showed some degree of heteroscedasticity with later years of protection, but this was to be expected given that more sites were used for the latter period (15+ yr) of the chronosequence than for the initial phase. The heteroscedasticity present did not appear to greatly confound our analysis, however, and we did not weight model variances by sites.

The relationship between time since closure and total species richness in sample areas of 2000 m² demonstrated an asymptotic trend whereby a rapid rise in the years following closure stabilized at 10 yr of protection independent of sampling scale (Fig. 2). Trends at the family level varied, with acanthurids, scarids, and chaetodontids showing a Ricker response (Table 2), whereas balistids, labrids, and pomacentrids responded linearly (Table 5, Fig. 2). Our Bray-Curtis analysis indicated low species similarity between sites but a significant decline in similarity between protected sites relative to the earliest time after closure in Mombasa 1992 (Fig. 3).

Sufficient size-class densities were present to analyze density recovery by size for six families: the Acanthuridae, Scaridae, Balistidae, Labridae, Mullidae, and Siganidae (Fig. 4). The dominant herbivores, Acanthuridae and Scaridae, demonstrated different responses with years of closure (Fig. 4). The Acanthuridae had a logistic response in total density over the 37-yr interval, whereas the Scaridae reached a peak total density at between 18 and 28 yr. These patterns were reflected in the responses of some individual size classes. The smallest Acanthuridae and Scaridae did not appreciably change with years of closure. Acanthuridae sized 10–20 cm dominated the overall response, reaching an apparent resource maximum at ~25 yr, while the 20–30 cm category increased exponentially up to 36 yr of closure. All of the larger (>10cm) Scaridae size classes peaked or declined by ~20 yr of closure, with a substantial decline in the 10–20 cm categories after ~10 yr of closure.

The two invertivorous families, Labridae and Balistidae, showed similar patterns to the herbivorous groups,

with the total Balistidae density increasing several-fold over 37 closure years while the Labridae appeared to decline after ~15–23 yr of closure (Fig. 4). There were, however, few Balistidae observed throughout the experiment relative to the other family groups, and no 3–10 cm fish were seen. The two largest size classes of the Balistidae showed steady increases through closure time, while the 10–20 cm class produced no trend. The Labridae rose and declined in all but the largest size class between 7 and 20 yr of closure and there was no obvious pattern present in the largest size class.

The Mullidae showed no demonstrable trends through closure time, while an exponential rise in the Siganidae was largely attributable to an increase in the 10–20 cm size class (Fig. 4). Both the Lutjanidae and Pomacanthidae were similar in recovery response among all size classes; the Lutjanidae reached a resource peak near 20–26 yr before declining, while the Pomacanthidae peaked at seven years before subsequently declining (Fig. 4). The Chaetodontidae and Pomacentridae did not significantly change through time given our candidate model set (GOF > 0.2; Fig. 4).

Scatter plots of wet masses of 10 of the families with time-dependent patterns further clarify the patterns with size and density (Fig. 5). The Acanthuridae rose steadily from <50 kg/ha to around 400 kg/ha after 37 yr of closure while the Scaridae reached an asymptote at ~250 kg/ha after 20–25 yr of closure. Balistid biomass rose exponentially to reach between 60–80 kg/ha and the Labridae peaked at ~80 kg/ha after 15–23 yr of closure before declining to ~30 kg/ha at the end of the chronosequence. Mullidae biomass did not appreciably change with closure, while Siganidae biomass increased exponentially. The Lutjanidae had the third highest biomass in the closed areas where wet masses in the older parks were ~200 kg/ha but with high scatter among areas. Pomacentridae and Chaetodontidae biomasses showed no appreciable changes with protection duration, despite Pomacentridae being an abundant family with mean maximum wet masses just less than
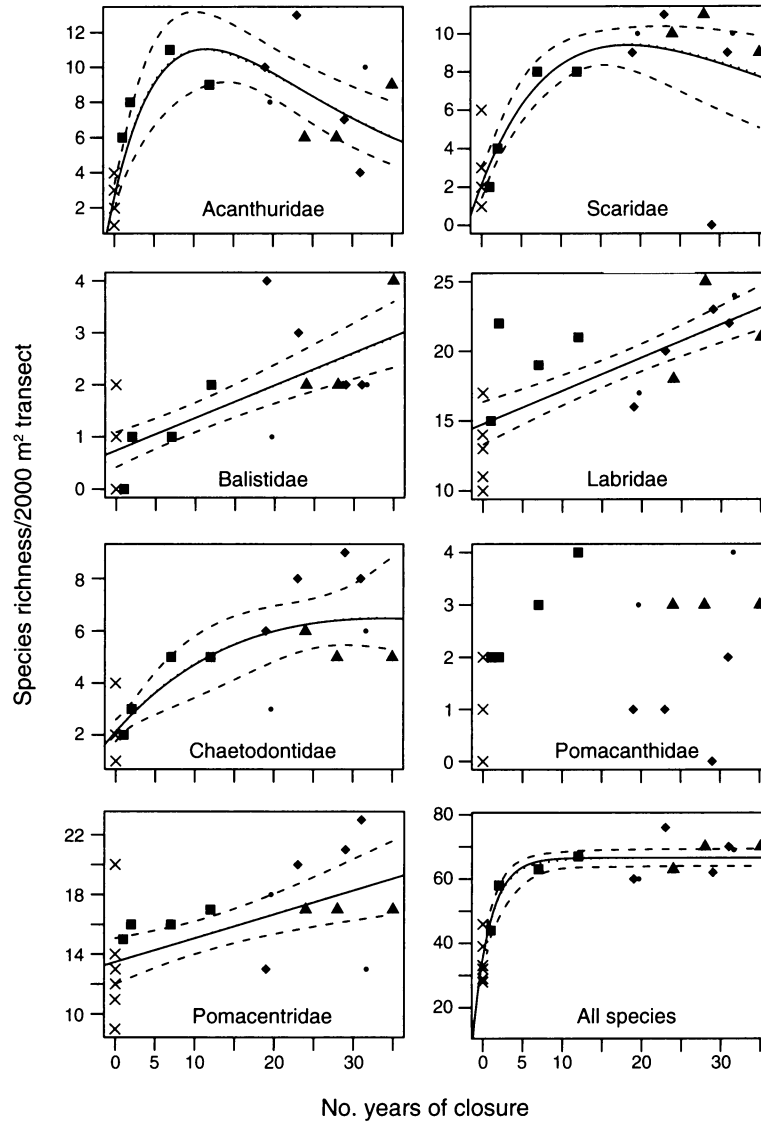
Fig. 2. Recovery curves for family-level and total fish-species richness in Kenyan marine parks in relation to the number of years of marine protection (closure) for pooled 2000-m² transects. Symbols represent parks: unprotected parks (×), Mombasa (square), Kisite (diamond), Watamu (circle), and Malindi (triangle).

TABLE 5. Linear parameter estimates for reef-fish species richness

Group size by family	GOF†	R^2	$\hat{b}$	$\hat{b}$‡	95% CL‡	$\hat{m}$	$\hat{m}$‡	95% CL‡
Richness, by family								
Bal§	<0.001	0.52	0.74	0.74	(0.42, 1.09)	0.062	0.62	(0.042, 0.085)
Lab	<0.001	0.43	14.77	14.76	(13.30, 16.36)	0.239	0.239	(0.166, 0.306)
Pom	0.016	0.33	13.47	13.46	(12.01, 15.07)	0.160	0.160	(0.067, 0.160)

† GOF stands for goodness-of-fit.
‡ Estimates derived from a nonparametic bootstrap ($R = 9999$) for the linear model for reef-fish richness groups.
§ Table 2 gives a listing of family name abbreviations.

100 kg/ha. Pomacanthidae biomass peaked at eight years of closure to between 20 and 30 kg/ha before subsequently declining to ~10 kg/ha.

Total community biomass among all sites showed a Ricker response to years of closure, and although initial biomass (N_0) was often not well estimated (Table 1), α and β parameters were reasonably precise. Total biomass reached a peak at 20 yr and ~1100 kg/ha.

DISCUSSION

Results from this closure chronosequence indicate strong time-dependent patterns in numbers of species, size classes, overall densities, and biomasses for many of the studied families. The chronosequence methodology (the process of sequentially organizing different sites into a time series) has the potential to produce results that are not attributable to time because site specificity and high spatial and environmental variability can confound estimates of temporal variability (Stewart-Oaten et al. 1995). For example, only one site was studied from the initiation of closure, which led to weaker power but also lower variance in the early years of closure. Additionally, there were some examples of temporal synchrony in our study, such as in the simultaneous reduction of the 3–10 cm size class in the Acanthuridae in all closed sites. This is most likely representative of a large-scale recruitment and mortality response that affected all the parks and not a response to the time since closure. Despite these weaknesses, the study has the strength of using replicate sites from a similar management, fishing, habitat, and ecological region and provides a useful evaluation of reef recovery under these specific conditions.

Our analysis relies on the assumption that the effects of fishing protection are sufficiently strong to reliably estimate post-closure recovery rates using sites that co-existed in time. Despite the potential for spatial variability and low population densities in some groups, the use of aggregate measures such as family level density, wet masses, and numbers of species produce strong trends that directly correlate with time of closure. This is not surprising given the high intensity of fishing (~10–20 fishermen/km^2) and the large differences in fish communities between closed and open reefs (McClanahan and Mangi 2000, 2001). Côté et al. (2001) found few significant relationships between reserve characteristics such as size and duration, arguing that fishing intensity around reserves may be the strongest factor influencing meta-analyses. For total richness, numbers, and biomasses in our study, closures exceeded non-closures by factors of 2, 2, and 10, respectively (McClanahan and Arthur 2001, McClanahan and Graham 2005), suggesting considerable responses to moderately sized closures in the presence of high fishing pressure, although these effects could potentially be much higher in unfished areas of larger spatial scale (Newman et al. 2006, Stevenson et al. 2007).
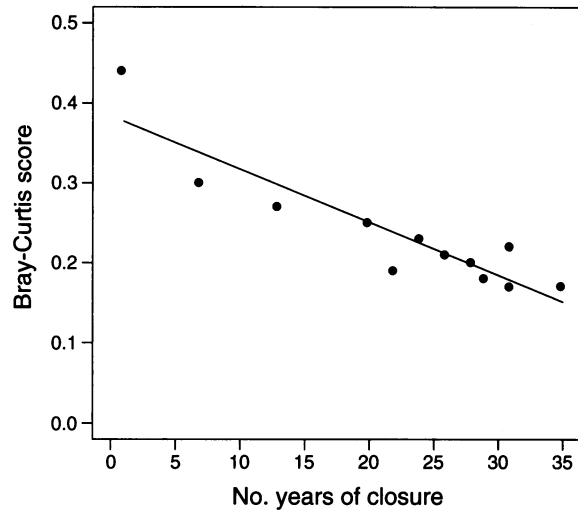

FIG. 3. Trend in Bray-Curtis similarity by duration of protection (closure) relative to the Mombasa 1992 reference point.

Fishing is eliminating many species at the scale of our sampling, and there is moderately fast recovery in species richness after closures of ~10 yr, after which there appears to be an asymptote in species richness. It is also reasonable however, to assume that species composition may change with time and some species will be extirpated as the succession matures and competition and predation increase (Tilman 1982, Hixon 1991, Graham et al. 2003, Graham et al. 2007). This, along with other sources of environmental variation, would explain the fairly low community similarity estimates between fished and closed sites (McClanahan 1994) and between parks of varying age, despite clear trends in recovery at aggregated family levels.

Trajectories in population density and biomass differed between families and among size classes within families. Recovery was generally slow, with peak densities or biomass varying from ~7–10 yr up to the full 37-yr duration of the study. Many coral reef fish species reach growth asymptotes and maximum life spans at times >10 yr (Choat and Robertson 2002), supporting the patterns we observed. Although ours are gross descriptions of taxa, there are some relationships between families that are consistent with field observations of resource competition. Two different patterns of recovery of the dominant herbivore and detritivore groups suggest that acanthurids may be better competitors than scarids in older closures. Total density of acanthurids has a logistic response with years of closure, whereas scarids have a Ricker response. For biomass, these curves are exponential and logistic respectively, suggesting that the decline in scarid density in older parks is related to declines in smaller individuals; the size class plots for this family support this. Furthermore, the largely detritivorous *Ctenochaetus striatus* (Choat et al.
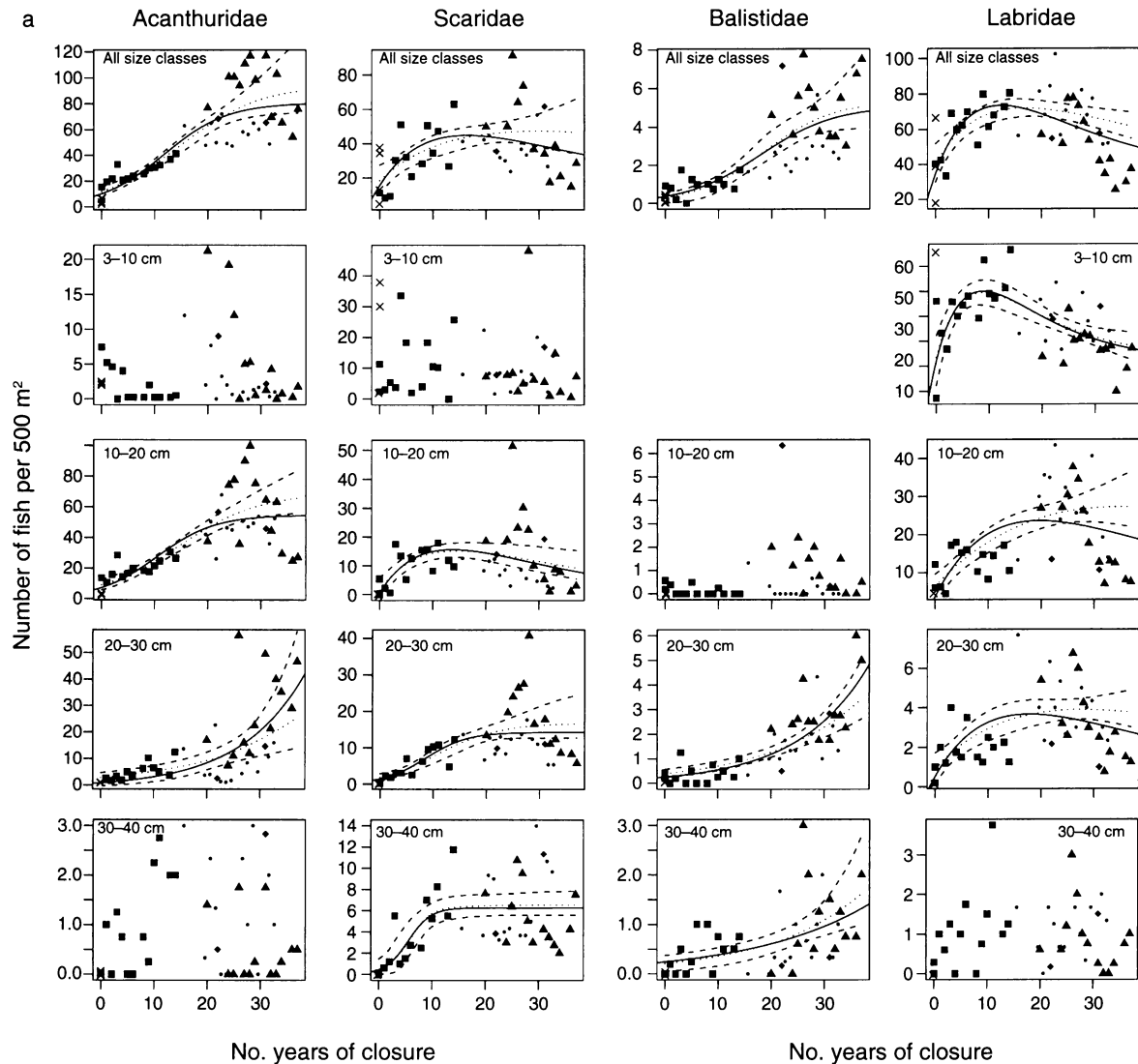
FIG. 4. Recovery curves for fish-family densities (total and by available size class) in Kenyan marine parks in reference to years of marine protection. Note the differing scales on the y-axis of the different size classes within each family. Chaetodontidae, Lutjanidae, Pomacanthidae, and Pomacentridae are not broken down by size class due to insufficient data. Symbols represent parks: unprotected parks (×), Mombasa (square), Kisite (diamond), Watamu (circle), and Malindi (triangle).

2002, 2004) is the dominant acanthurid in the older parks (McClanahan 1994). This species is not territorial and is tolerated by other territorial acanthurids (Robertson et al. 1979), likely due to their different feeding morphology and diet preferences (Purcell and Bellwood 1993). It is possible that the flexible jaws of acanthurids are more efficient and tolerant of lower resources than the fused-tooth scarids (Choat et al. 2002, 2004). Additionally, acanthurids are reported to have greater longevity (30–45 yr; Choat and Axe 1996) than scarids (5–20 years; Choat et al. 1996) and may therefore have a lower resource tolerance that gives them a competitive advantage in the oldest closures. An alternative mechanism may be that scarids are less tolerant of piscivory, which may be expected to increase with time since

closure (Micheli et al. 2004), and their high growth and mortality rates cannot compensate for what may be poorer defenses. Scarids have been shown to be susceptible to predatory control in previous studies (Graham et al. 2003, Mumby et al. 2006), and our data suggest that the declines are occurring in smaller size classes.

The two key invertebrate-feeding families, Balistidae and Labridae, also appear to be responding in different ways, suggesting competitive interactions with time. Total density of balistids shows a logistic response, whereas biomass has an exponential recovery driven by the larger size classes. In both cases, recovery accelerates after 10–20 yr of closure. Conversely, labrid total density, density within size classes, and biomass all
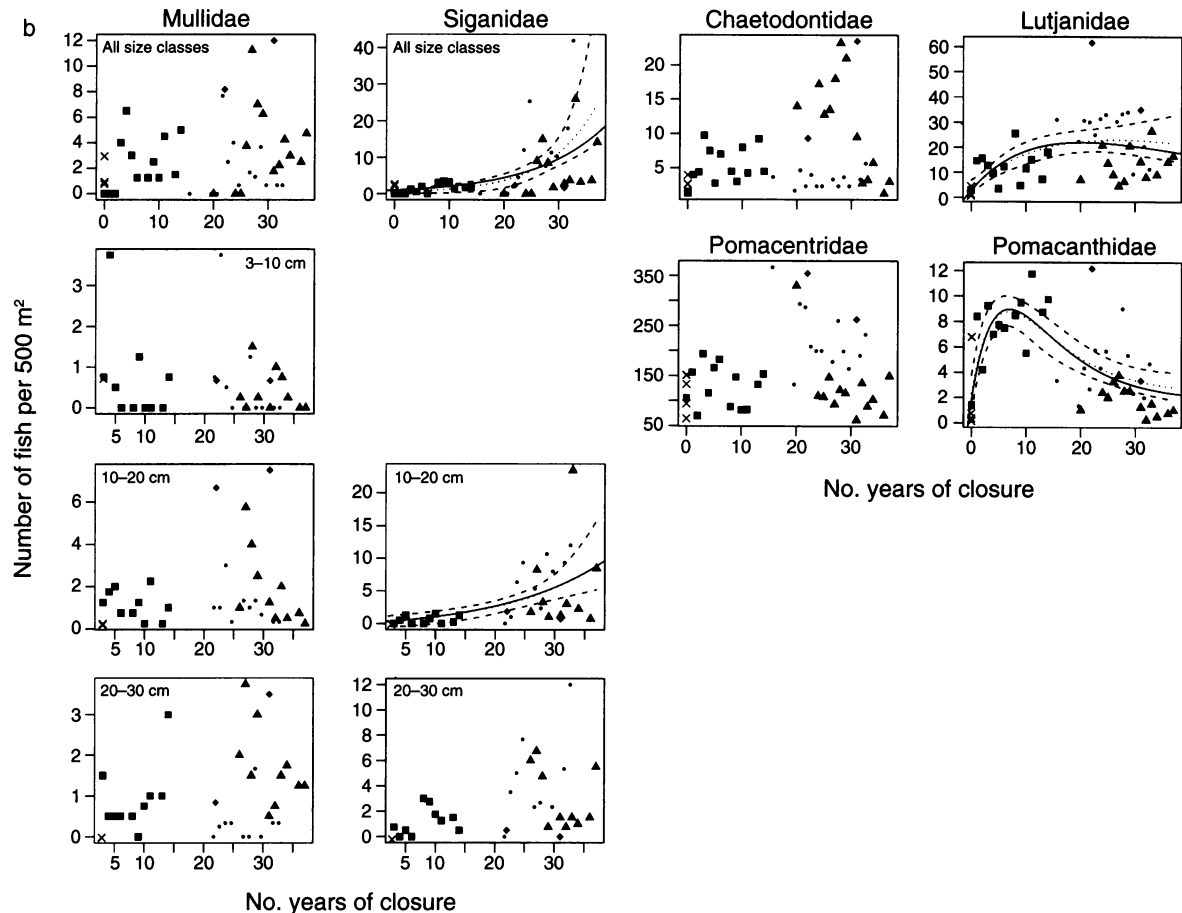
FIG. 4. Continued.

display Ricker functions with peaks after ~10 years of closure. Approximately 50% of the balistid counts were attributable to a single species, *Balistapus undulatus* (McClanahan 1994), which exhibits aggressive behavior toward labrids and other invertebrate-eating taxa and has been shown to competitively exclude subordinate species from resources through interference competition (McClanahan 2000). Consequently, the shape of the density and biomass recovery curves may reflect competitive dominance of *B. undulatus* in the oldest closures, resulting in reduced density and biomass of the more diverse and subordinate labrids. Pomacanthid density and biomass also declines after a fairly rapid initial recovery, and it is possible that they are excluded by a similar interaction.

Mullids and diodontids were highly variable and thus few clear trends were found. Siganids show an exponential recovery for total density and biomass; however, they have an aggregating behavior that probably leads to high variation, and they have a cryptic behavior such that the smallest size class was not effectively sampled. Other than the chaetodontids, which show little recovery, the remaining families display Ricker functions that peak at 5–15 yr depending on the family.

Various interactions with habitat may influence these trajectories, particularly for the smaller and coral-dependent chaetodontids and pomacentrids (Munday and Jones 1998, Wilson et al. 2006). However, fairly consistent throughout all families surveyed is a decline in smaller size classes, or families with small body size, with time since closure, which may indicate some size- and species-specific predatory control (Graham et al. 2003, Dulvy et al. 2004).

Ecosystem effects of fishes have been found in previous studies, the most common being a decline in sea urchins and an increase in calcifying algae (McClanahan and Arthur 2001, McClanahan and Graham 2005). Sea urchin decline has been shown to occur with the rise in invertivores, such as *B. undulatus*, where urchin levels plateau to long-term closure levels after ~15 years (McClanahan 2000). Calcifying algae rises slowly and shows no signs of stabilizing, even in the oldest closures (McClanahan and Graham 2005). In combination, these studies suggest that after closure there is a rapid rise in labrids and scarids, followed by a slower rise in balistids and acanthurids, with sea urchins declining to very low levels at some intermediate time; this is often followed by dominance of calcifying algae.
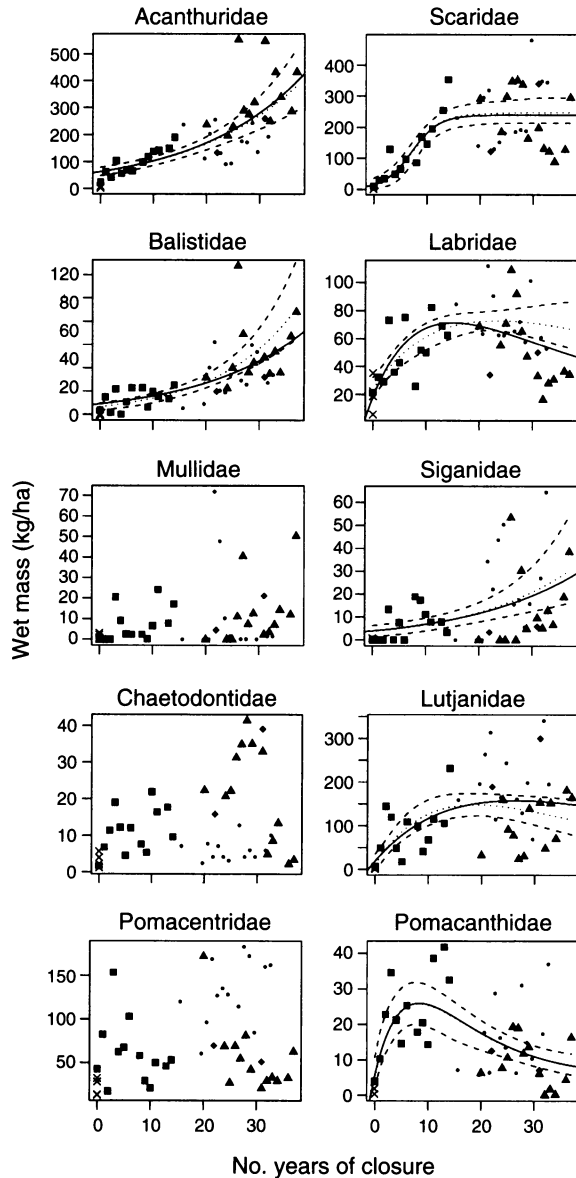
FIG. 5. Recovery curves for total fish-family biomass in Kenyan marine parks with years of marine protection. Symbols represent parks: unprotected parks (×), Mombasa (square), Kisite (diamond), Watamu (circle), and Malindi (triangle).

Consequently, it is also likely that the benthic community changes form a system where net benthic production is high and calcification and detrital production low, to one where, as the system ages, there is lower net production with higher levels of calcification and detrital production (Steneck and Dethier 1994). Current understanding of coral reef ecology indicates a system of causation for these hypothesized interactions, and the time scales of change we observed are consistent with this proposed causation. However, these interactions and processes need to be fully tested through long-term manipulative or natural experiments.

Our findings contribute to the understanding of the equilibrium concept of theoretical ecology as applied to coral reefs. Equilibrium, or a steady state, may be observed in the oldest closures, but even here, the combined studies suggest that there are increases in acanthurids, balistids, siganids, and calcifying algae that may exceed the 37-yr time scale of this study. Overall there is a modest decline in total fish density and a smaller decline in total fish biomass. This is likely to indicate a process of selection for larger, but fewer, individuals of fish and possibly reduced net production of the benthos. What the final equilibrium will be is possibly similar to that described for remote and lightly fished reefs, such as those found on the outer Great Barrier Reef (Dudgeon et al. 2000, Fabricius and De'ath 2001, Choat et al. 2004) or Maldives (Sluka and Miller 2001), where encrusting corallines are common, grazer/detritivores exhibit stunting, and detritivory is common. The alternative explanation is that these older parks have experienced environmental degradation, including coral bleaching, degraded water quality, and heavy fishing around the park boundaries (McClanahan and Obura 1997, McClanahan and Mangi 2000, McClanahan et al. 2001). These factors have certainly affected these reefs, however the responses would more often be toward an earlier state of succession and not toward the aging we described here. It is possible that these anthropogenic factors have played a role in slowing the process of succession such that, in less disturbed systems, the aging process would occur on a faster time scale. It should also be appreciated that the "equilibrium" or "pristine" biomass we report here is specific to modern conditions in Kenyan reefs and useful for modern fisheries management, but not to be taken as a resemblance of a pristine ecosystem uninfluenced by human activities, of which the reconstruction is largely reliant on the fossil record and speculation (Jackson et al. 2001, Pandolfi et al. 2003).

Our results from the Bray-Curtis similarity analysis are consistent with those of Micheli et al. (2004) who also found a significant negative relationship between species similarity and duration of protection for tropical fish assemblages. Although reefs are effectively changing over time in response to protection, the low similarity between the parks also suggests that there are other strong site-specific factors that are involved in determining the structure of fish assemblages (Micheli et al. 2004). Regardless of a lack of community similarity among parks, aggregate measures, such as the taxonomic family used here, appear to produce moderate to strong time-since-closure trends across parks.

There is considerable variation in reported recovery times of fish from other published studies, with some meta-analyses of recovery (pooled studies from different regions and ecosystems) finding that time since closure is a weak predictor of recovery of population densities (Halpern and Warner 2002b, Halpern 2003, Micheli et al. 2004). Using aggregate measures, Halpern and

Warner (2002b) argue that change in closures are rapid (less then three years) although time was not a significant factor in their study, and high variation associated with pooling many studies over many regions, ecosystems, and management systems may have overridden potential effects of closure time. Similarly, the authors of a study of density and community structure measures from underwater nuclear blast tests in Mururoa Atoll suggested that recovery was rapid (estimated at 1–5 yr), although some of their sites showed considerably slower recovery by their measure (Planes et al. 2005). However, spatial variation was high, and medium scale (12.5 km^2) blast pulses may be a poor analogue for fishing, which is a continuous press effect and occurs on the scale of hundreds of kilometers. In cases where the fish community is intact around the edges of a disturbance, migration is likely to be the most important driver of recovery, and thus rates of recovery are faster than in isolated closures in a seascape of heavy fishing. Conversely, Micheli et al. (2004) suggest that piscivores and community structure changes can be slow, on the scale of decades, however both factors exhibited considerable variation and low predictive power. Generally the strongest responses are often found for large-bodied target families, such as Serranidae, Lethrinidae, and Scaridae (Mosquera et al. 2000).

Our findings agree well with another long-term study of coral reef closed areas in the Philippines where fishing pressure is also high; recovery of target species inside enclosures was estimated at 15–40 yr given a best-fit logistic growth curve (Russ and Alcala 2004, Abesamis and Russ 2005). This time frame and the rates of recovery were similar for both space-for-time substitutions and following individual closure areas over time (Russ et al. 2005). Studies lacked data past 20 years of closure, and therefore, the extrapolation based on the logistic function would seem reasonable. We did not, however, find a logistic relationship for all groups, as there was a rapid rise in the first few years in some cases and a decline in both density and biomass after 20 years. The balistids and acanthurids may be exceptions, as there is a delay in their responses after closure, but at 37 years they had yet to reach a stable state. For some groups and habitats, recovery trajectories may be better described by other equation forms (Jennings and Polunin 1996a). Our study includes more taxa than previous work, and although it supports the general conclusion about the time scale of recovery reported by Russ and colleagues (2005), it suggests different response curves for different taxa.

This study provides an opportunity to estimate what fisheries modelers refer to as pristine biomass (B_0) for Kenyan coral reefs, either as the maximum or as the final biomass reported from the curves. These two critical points create a possible dilemma for fisheries managers who need to estimate the biomass at which maximum sustained or surplus yields (MSY) will be achieved (Clark 1985). For families with consistent increases over time, the B_0 is expected to be at or near what was observed toward the end of our study but, for some families and for total fish biomass, recovery responses peak in mid-chronosequence. Given that MSY calculations are based on estimating the position on the production–biomass curve where maximum net production is estimated, it is reasonable to assume that 1100–1200 kg/ha is an informative estimate of B_0 for the current shallow Kenyan reefs. Using the MSY level of 40% used for some multi-species fisheries (Hilborn et al. 2004), Kenyan reef MSYs would be achieved at ~500–600 kg/ha. These values are for the current species composition equilibrium and not what might have been for past, undisturbed reefs.

From this study, there are at least two major problems with implementing a standard yield model. First, each species or functional group has its own response curve that depends on the state of the ecosystem and its production. This study indicates that some groups, including species of balistids and acanthurids, have low production and recovery rates and that MSY cannot easily be calculated from the exhibited recovery responses. Secondly, our study suggests that the logistic curve is not always a good description of recovery, which in many cases follows a steadily rising or, more critically, a steadily declining rate of change or net production. The lack of inflection point even when biomass was reduced to one-tenth of the maximum biomass makes it unlikely that the recovery responses are all logistic. Practically, coral reef fisheries studies have shown that fishing produces a rapid decline in biomass at low levels of effort, but biomass and yields remain steady as effort increases (Jennings et al. 1995, Jennings and Polunin 1995, 1996b). Studies in Fiji, Seychelles, and Kenya suggest similar biomass values in fished reefs of between 100 and 200 kg/ha, or nearly one order of magnitude below our estimate of B_0. This indicates high levels of overfishing given our estimate of MSY, which suggests compensation in production of fish at moderate to high levels of effort and a potential difficulty in detecting a declining inflection in the yield curve at low biomass or high levels of effort.

These findings are not consistent with the predictions of the logistic theory of surplus production, but are consistent with our recovery responses where net production of fish steadily declines with the age of closure. Specifically, the rate of change in biomass is given by the derivative of the Ricker function for total biomass recovery of all fish >3 cm:

$$\frac{d\alpha t e^{-\beta t}}{dt} = \alpha(1 - \beta t)e^{-\beta t} \qquad (3)$$

and has a maximum in year 0 equal to α (138—158 kg/ha = 14–16 tons/km^2 [1 metric ton = 1 Mg]). See Table 1 for an explanation of these symbols and variables.

The net fish production values from this equation are somewhat higher but within the ranges of estimated

rates of fisheries production in shallow reefs in the Indo Pacific, which display considerable variation, with reports ranging from 0.1 to 44 ton/km^2 (McClanahan 2006). The estimated near-shore production for East Africa coral reefs is 6.9 ± 4.1 ton·km^{-2}·yr^{-1} (mean ± SD), which is close to the world average of 6.6 ± 9.0 ton·km^{-2}·yr^{-1}; McClanahan 2006). Yields will be reduced as biomass increases and net production decreases until net production is 0 at ~22 yr after closure. Given that coral reef fisheries are likely to exist in conditions similar to our models of the first few years of closure, there is reasonable correspondence between estimated fisheries production and recovery rates from our study. There is, however, high variation in the reported catches, and net production is expected to change due to many factors, including region, habitat, catch selectivity, and migration.

One reason the Kenyan study may have high production and fast recovery in the early stages after fishing may be migration into these lagoons from the outer reef edge (McClanahan and Mangi 2000). This would be expected to create a recovery curve that lacks a delayed increase and that can maintain high production at low biomass. It may also explain the different responses found between this study and those in the Philippines, which are largely isolated reef edges that may not have the same level of migration as in Kenyan lagoons (Russ et al. 2005). These findings suggest that coral reef fisheries can maintain high production at high levels of effort and low biomass but that it occurs at the expense of losses of species and taxa with low production and may also depend on migration into the fishery from less fished environments.

Fished coral reef ecosystems take a considerable time to recover the full diversity, biomass, and ecological states and processes after the cessation of heavy fishing, particularly where heavy fishing continues around the borders of closures. This finding suggests that permanent closures (>37 yr) are required to maintain ecological states that are representative of unfished ecosystems and for management programs that wish to maintain representative reefs. Periodic and small closures, which are likely to gain more support from local-level management (McClanahan et al. 2006a), have limits to preserving fishery-sensitive species and ecological processes (McClanahan et al. 2006b).

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