Differential and slow life-history responses of fishes to coral reef closures

T. R. McClanahan[1],*, A. T. Humphries[2,3]

[1]Marine Programs, Wildlife Conservation Society, Bronx, New York 10460, USA
[2]Coastal Research Group, Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa
[3]Coral Reef Conservation Project, Wildlife Conservation Society, PO Box 99470, Mombasa, Kenya

ABSTRACT: Life-history strategies are expected to underlie key ecological responses to disturbances and are becoming increasingly important in evaluations of the increasing frequency and magnitude of anthropogenic and climate stressors. Here, we evaluate changes in life histories of coral reef fishes after fishing disturbance, including feeding (mean trophic level), growth, reproduction, and mortality characteristics using a 42 yr fish biomass chronosequence created by Kenya's fisheries closures. As expected, the longer the closure, or time since fishing disturbance, the greater the mean age and body size metrics, and the lower the growth rate and mortality metrics. Unexpectedly, a linear decline in the mean trophic level of the fish community with the age of fisheries closure was found and was attributable to relatively slow recovery of the abundant herbivores. Trophic level and other life-history metrics were not significantly correlated with one another, and the life histories of herbivorous fishes (e.g. Acanthuridae, Scaridae) produced these weak relationships. None of the life-history metrics displayed clear leveling after 42 yr of closure, which corroborates other findings that indicate that the closures do not represent undisturbed or pristine ecosystems. Growth, reproduction, and mortality parameters are most influenced by the cessation of fishing, and these metrics indicate that herbivorous fishes can be slow to fully recover, necessitating appropriate restrictions to insure their populations and associated ecological functions are maintained.

KEY WORDS: Ecological indicators · Fisheries management · Life-history characteristics · Longevity · Marine protected areas · Succession · Reserves · Chronosequence

INTRODUCTION

Disturbance and recovery structure ecological communities, and these processes have implications for how natural resources are managed (Connell 1978, Tilman 1980, Russ & Alcala 2004). Fishing is a disturbance that preferentially removes individuals and species, which may have direct and indirect effects on fishes and their prey (Jennings & Kaiser 1998, Worm et al. 2006, O'Leary & McClanahan 2010). Recovery processes of fishes in coral reefs and other marine ecosystems are only crudely understood. Frequently, recovery dynamics and testing of

associated hypotheses are based on a limited number of site-specific closure studies (Russ & Alcala 2004) or meta-analyses that combine disparate sites and ecosystems (Halpern & Warner 2002, Micheli et al. 2004, Claudet et al. 2008, Guarderas et al. 2011). Responses have generally focused on the recovery of species targeted for fishing and those species influenced by the indirect effects of fishing (McClanahan & Graham 2005, Babcock et al. 2010), and only seldom have other metrics and proxies for ecological condition, such as life-history characteristics, been tested or compared (Claudet et al. 2010). As anthropogenic and climate-induced stressors are increas-

ingly changing the structure of many ecosystems, it is becoming useful to establish metrics that increase our understanding of how disturbances and recovery patterns influence complex ecological communities.

Fish communities are often organized around patterns of disturbance and associated life histories (Winemiller 1989, Winemiller & Rose 1992, Olden & Kennard 2010), which are frequently influenced by levels of and recovery from fishing (Winemiller 2005, Claudet et al. 2010, McClanahan & Hicks 2011). Recovery from fishing represents a less frequently disturbed environment, which is expected to result in changes in life-history characteristics of feeding, growth, reproduction, and mortality (Gleason 1917, Odum 1969, Huston & Smith 1987). Patterns of recovery operate to control ecological organization and processes by mediating competitive and predator-prey interactions (Tilman 1994). For example, species that have a high growth rate and low age at first maturity or short generation time are considered well-suited to ecological dominance immediately following a disturbance, and in ecosystems with frequent disturbances (Huston & Smith 1987). Additionally, species feeding high in the food web are expected to require recovery of lower trophic prey before their maximum abundance can be reached (Odum 1969, Sandin et al. 2008). However, life histories and superior competitive ability will vary with the complexity of ecological environments and not just disturbance frequency (Grime 1973, Olden & Kennard 2010). Life-history processes can change simultaneously and are not exclusive and, therefore, a more composite or portfolio view of life histories is needed to determine and predict the response of taxa to disturbance and other environmental factors.

Determining basic patterns of change after a disturbance is among the oldest activities in ecology, and many studies providing significant insights have used the space-for-time substitution or the chronosequence method (Cowles 1899, Cooper 1926, Olson 1958, Pickett et al. 1987). Chronosequences infer a time sequence of development or recovery from a series of sites differing in age since disturbance (i.e. time since the site became available for occupation or colonization after the cessation of a disturbance such as fishing). The analysis of a chronosequence can reveal broad, regional-scale trends in recovery patterns by averaging across site-to-site differences (Bakker et al. 1996). However, the chronosequence approach has a few well-recognized limitations that include the level of detail in which changes can be deduced (Pickett et al. 1987), or the assumption of dependency of a species on prior species (Connell &

Slatyer 1977). Here, we are not making this assumption of species replacement, but instead evaluating the fish community using more synthetic metrics of trophic level and life history as a function of time since fisheries closure, based on the more integrative family-level phylogeny (Stearns 1989, Branch et al. 2010). This approach reduces the chances of errors when interpreting sequential changes in species composition as being dependent on prior species rather than more complex interactions between phylogenies and the environment (Johnson & Miyanishi 2008). Consequently, we used the proportions of taxa at the family level, and trophic (diet), growth, age, and mortality variables as dependent on the time since fisheries closure.

In the present study, we used data on the recovery of fishes in Kenyan fisheries closures, which are among the oldest fully protected fisheries closures in the western Indian Ocean (McClanahan et al. 2009). A number of these closures were studied for >20 yr between 1988 and 2010, creating a 42 yr chronosequence (using a space-for-time substitution method) in which to evaluate the following hypotheses: that the mean trophic level, size, and age of the fish community should increase while growth, reproduction, and mortality metrics should decrease with the time since closure from fishing. We also looked for evidence for leveling or stability in these metrics at some time after closure by fitting a variety of common ecological population models and testing for improved fit to null and linear models.

MATERIALS AND METHODS

Study site

Data were collected in 4 no-take coral reef closures (marine parks) and 4 unmanaged sites along a 140 km stretch in Kenya (McClanahan & Graham 2005) between 1988 and 2010, where sampling was undertaken 22 times. Sampling at all sites took place annually, with the exception of 2002, when no sites were sampled. All sampling took place during the northeast monsoon season (between September and December) when meteorological parameters are characterized by low cloud cover, rainfall, river discharge, and wind energy, while solar insolation and temperatures are high (McClanahan 1988). Active management of no-take closures first commenced in Malindi in 1968, followed by Watamu in 1972, Mombasa in 1991, and Vipingo in 2005. These parks vary in size from 0.4 to 28 km^2 (Vipingo, 0.4 km^2; Mom-

basa, 6 km²; Malindi and Watamu, 10 km²). All sampled areas were from central areas inside the park in shallow (0.5 to 3 m depth at low tides where Kenya has a 4 m tidal range) and calm back-reef lagoons where the dominant coral cover is live and dead coral substratum with some seagrass and sand cover. The distances between all adjacent sites are >3 km, whereas the nearest distance between closure sites is 30 km and, therefore, each site represents a distinct reef. Habitat complexity and hard coral cover are similar between all parks (McClanahan & Graham 2005). Kenyan fisheries are highly unselective, and all fish of nearly all species >10 cm are captured for both sale and home consumption (McClanahan et al. 2008, Hicks & McClanahan 2012).

Field methods

A single investigator (T. McClanahan) collected all field data, including fish numbers and size at the family level, by underwater visual census (via snorkel) using 2 to 5 replicate 5 × 100 m belt transects (McClanahan 1994). Transects were conducted during neap tides when the water level was between ~1 and 4 m deep and in the same area annually (i.e. 'fixed' locations using GPS coordinates) (McClanahan & Kaunda-Arara 1996). Between 1988 and 2004, this method categorized all fish into 11 families (Acanthuridae, Balistidae, Chaetodontidae, Diodontidae, Labridae, Lutjanidae, Mullidae, Pomacanthidae, Pomacentridae, Scaridae, and Siganidae) and an 'others' category. After 2004, this method was extended to include 12 more uncommon families (Aulostomidae, Carangidae, Fistulariidae, Haemulidae, Holocentridae, Lethrinidae, Muraenidae, Pempheridae, Pinguipedidae, Scorpaenidae, Serranidae, and Sphyraenidae). Small and cryptic taxa such as blennies, tobies, and gobies were recorded but probably underestimated (Ackerman et al. 2004). Total lengths of all observed fish >3 cm were estimated and placed into 10 cm size categories (e.g. 3–10 cm, 11–20 cm, 21–30 cm), and any fishes >80 cm were placed in a 'greater than 80 cm' size class.

Data analyses

The midpoint of the size classes was used to estimate the wet mass of each size class based on established aggregate family-level length-weight relationships. Geographic-specific length-weight correlations were determined from measurements of the common species in each family taken at local fish-landing sites in Kenya (McClanahan & Kaunda-Arara 1996). The sum of all size classes was used to estimate the total wet mass for each transect, and the average of all transects was used to estimate the total wet mass for each site.

Chronosequences were established by assigning each sampling year to a year since fishing closure (McClanahan & Graham 2005); the areas closed to fishing (Mombasa, Malindi, Watamu, and Vipingo post-2005) were assigned to a year since fishing closure that was calculated by subtracting the sampling year from the year it was closed from fishing. For example, Vipingo in year 2007 is given a value of 2 for years since closure since it was closed to fishing in 2005. Similarly, Mombasa in year 1993 is given a value of 2 for years since closure since it was closed to fishing in 1991. The areas open to fishing (Kanamai, RasIwatine, Diani, and Vipingo pre-2005) were pooled and assigned Year 0 for the analyses.

We retrieved information about trophic level and 8 life-history characteristics for all fish species recorded in Kenya found in FishBase (www.fishbase.org) (n = 214). 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. The trophic level of a species represents its position in the food web. For example, a high trophic level value (i.e. 4.0) may represent a piscivorous species (e.g. apex predators such as sharks), and conversely, a low trophic level value (i.e. 2.0) may represent an herbivorous fish species (e.g. surgeon or parrotfishes). In FishBase, trophic level for each species is preferentially based on published studies reporting the percentage in weight or volume of different food items in the diet. Intrinsic growth rate is an estimate of the growth of individuals in size or length for a given time period as a fraction of the population at the beginning of a time period. Generation time represents the relative size of intervals of reproduction in a species. Length to achieve optimum yield uses growth and mortality data to calculate fish length as a proxy to a theoretical level of harvest that will allow the stock to replenish itself continuously. Family-level values for each life-history characteristic and trophic level were calculated by taking the mean for all Kenyan species found within each family (see Table 1). Individual life history and trophic level values for the 'others' category were calculated as the mean of all species summed across years. Weighted averages for life histories and trophic level (resulting in 'mean trophic level') were calculated for each year (k) as:

$$LH\_TL_k = \frac{\sum_i Y_{ik} LH\_TL}{\sum Y_{ik}} \qquad (1)$$

where Y_{ik} is the relative abundance/landings in the catch of Family i in Year k, and LH_TL is the life history characteristic or trophic level for Family i. Each life history was calculated independently.

The chronosequence method relies on the assumption that all sites used are similar enough to one another in their development that they have traced similar histories (Johnson & Miyanishi 2008). To address this assumption, we plotted and applied linear regressions to each weighted life-history characteristic and trophic level (as described above) of the fished sites (where 'year' was the independent variable) to test whether these fished reefs were changing in similar ways through the entire 22 yr data set (1988 to 2010). The plotted residuals from fitting linear models to the data showed a clear violation of the independence assumption; therefore, we extended the model to include a residual auto-correlation structure (Zuur et al. 2007). We fit an auto-regressive model of order 1 (AR-1) to all models that accounted for temporal auto-correlation by site (Zuur et al. 2009). The AR-1 residual structure accounts for time series data that is regularly spaced, i.e. 1 yr intervals (Zuur et al. 2009).

To model recovery trajectories and rates of change in life histories and trophic level, we selected 5 ecologically meaningful models: asymptotic, logistic, Ricker, linear, and exponential. The asymptotic model represents a population that reaches a new carrying capacity at a constant rate from an initial population size. The logistic model is similar to the asymptotic model; however, it reaches a new carrying capacity from an initial exponential phase. The Ricker model is a density-dependent fisheries recruitment model where a population reaches a resource peak at a given time by an initial rate of increase followed by a rate of decline (Ricker 1954). The linear model represents a population that increases or decreases from an original density at a constant rate without limit. The exponential model represents growth or decline from an initial population at an exponential rate without limit. For each model, we calculated the proportion of the variation explained by the model using a nonlinear approximation for R^2 and we also calculated a goodness-of-fit statistic (GOF) using a likelihood ratio test. Each of the models was run using maximum likelihood fits of the nonlinear regression (nls) routine in R software, version 2.13.0 (R Development Core Team 2011). Multiple data points at particular times in the chronosequence were averaged and mean values used in the model-fitting to avoid disproportionate pull of particular years (i.e. Year 0) in the models.

Akaike's information criterion (AIC) is a measure of goodness-of-fit that is penalized according to the number of parameters (Burnham & Anderson 2002). Model selection was performed using AIC, where the best-fit model, or the highest ranked (lowest AIC) model was considered to have the majority of support. If one or more of the models were within 2 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. We did not want to make model-based determinations of processes that generated the data and, therefore, we did not conduct formal multi-model inference (Burnham & Anderson 2002). To maximize the reliability of the hypothesis test, the assumptions of normality, homogeneity, and variances were evaluated by model residuals and quantile-quantile (Q-Q) plots.

To evaluate the uncertainty of model parameter estimates, we conducted a nonparametric nls bootstrap ($R = 1000$) for each life-history characteristic and trophic level given the selected best-fit model. We calculated a mean and 95% confidence interval, and plotted the corresponding nls and mean bootstrap parameter estimate curves throughout the chronosequence using the bootstrap predictions for each year since closure.

To compare trends between individual life-history characteristics and trophic level, we used a series of bubble charts and linear regression. We used the 15 most abundant fish families (which account for >98% of total biomass), and the radius was scaled to be directly proportional to the square root of the relative biomass summed across all years. Life span, natural mortality, and maximum length are the only life histories displayed because all others were highly correlated ($r > 0.80$) with one of these 3 and showed similar non-significant trends.

RESULTS

Herbivorous/detritivorous fish (Acanthuridae and Scaridae) represent the greatest proportion of biomass in our analysis and account for >37% of the total biomass (Table 1). Seven of the 23 families (including the 'others' group) account for >95% of the total biomass. Of the 9 life-history metrics, we found none of the models to be significant for the fished sites (at the 'site' and 'year' level) across the entire data set (F-values were always <3.21 and p-values >0.05).

Table 1. Mean ± SD of the relative biomass, trophic level, and life histories (n = 8) representing the 15 most abundant fish families in Kenya. Number of species used represents the number of species recorded in Kenya used to calculate family-level values

Family	No. of species	Relative biomass (%)	Trophic level	Maximum length (cm)	Growth rate (cm yr⁻¹)	Natural mortality (M)	Life span (yr)	Generation time (yr)	Age at first maturity (yr)	Length at first maturity (cm)	Length to achieve optimum yield (cm)
Acanthuridae	22	20.1	2.26 ± 0.48	46.35 ± 18.85	0.41 ± 0.21	0.85 ± 0.41	9.89 ± 5.61	3.01 ± 1.67	2.41 ± 1.25	22.63 ± 9.06	24.87 ± 11.47
Scaridae	18	17.51	2.02 ± 0.15	51.26 ± 24.13	0.47 ± 0.23	0.88 ± 0.41	8.14 ± 4.56	2.45 ± 1.45	1.92 ± 0.97	28.08 ± 10.27	31.91 ± 13.37
Pinguipedidae	11	10.64	3.62 ± 0.31	34.64 ± 24.78	0.51 ± 0.22	0.98 ± 0.5	7.17 ± 5.00	2.35 ± 1.54	1.78 ± 1	19.13 ± 12.78	20.93 ± 16.69
Labridae	44	9.66	3.48 ± 0.22	36.03 ± 26.13	0.39 ± 0.26	0.91 ± 0.6	11.48 ± 7.9	3.7 ± 2.35	2.81 ± 1.63	20.03 ± 12.05	22.07 ± 15.57
Haemulidae	5	9.34	4 ± 0.37	60 ± 20.91	0.18 ± 0.10	0.39 ± 0.19	15.9 ± 5.28	4.8 ± 1.65	3.6 ± 1.11	34.1 ± 10.11	39.4 ± 13.38
Holocentridae	5	6.85	3.63 ± 0.26	27.42 ± 11.14	0.76 ± 0.27	1.38 ± 0.46	4.26 ± 1.63	1.3 ± 0.42	1.1 ± 0.35	16.73 ± 6.02	17.44 ± 7.37
Others	41	5.97	2.95 ± 0.27	33.75 ± 18.41	0.51 ± 0.25	1.08 ± 0.47	8.62 ± 4.42	2.79 ± 1.36	2.16 ± 0.94	18.66 ± 8.70	20.26 ± 11.24
Serranidae	11	4.96	3.86 ± 0.37	56.78 ± 50.51	0.41 ± 0.36	0.72 ± 0.6	13.53 ± 11.72	4.31 ± 3.84	3.08 ± 2.27	29.04 ± 22.58	34.34 ± 31.12
Siganidae	5	3.0	2.0 ± 0.37	45 ± 8.58	0.87 ± 0.52	1.44 ± 0.81	3.3 ± 1.91	1 ± 0.6	0.8 ± 0.48	24.4 ± 4.25	27.6 ± 5.22
Balistidae	8	2.8	3.34 ± 0.27	42.25 ± 18.81	0.32 ± 0.11	0.67 ± 0.23	9.75 ± 4.4	2.86 ± 1.4	2.34 ± 0.9	24.65 ± 9.11	27.3 ± 11.92
Lethrinidae	12	2.53	3.6 ± 0.29	62.71 ± 19.25	0.22 ± 0.17	0.46 ± 0.29	17 ± 5.29	5.09 ± 1.6	3.93 ± 1.15	30.23 ± 8.57	34.47 ± 11.02
Pomacanthidae	7	2.41	2.69 ± 0.31	30 ± 13.52	0.4 ± 0.3	1.9 ± 0.65	10.59 ± 4.04	3.16 ± 1.03	2.66 ± 0.9	18.23 ± 7.42	19.43 ± 8.82
Pempheridae	3	1.52	3.4 ± 0.17	20 ± 5.87	0.47 ± 0.13	1.03 ± 0.35	6 ± 0.9	2.2 ± 0.3	1.6 ± 0.21	12.9 ± 1.83	12.8 ± 2.06
Chaetodontidae	16	1.48	3.26 ± 0.28	19.34 ± 4.42	0.96 ± 0.31	1.81 ± 0.55	4.12 ± 1.94	1.51 ± 0.74	1.13 ± 0.54	12.11 ± 2.62	11.94 ± 2.95
Mullidae	6	1.23	3.3 ± 0.19	43 ± 11.23	0.21 ± 0.26	0.55 ± 0.44	13.3 ± 2.85	3.7 ± 0.78	3.4 ± 0.69	18.6 ± 5.46	19.5 ± 6.65

The logistic and linear equations best quantified recovery parameters for all life-history characteristics and mean trophic level. The logistic model,

$$P(t) = \frac{K}{1 + \left(\dfrac{K - N_0}{N_0} \right) e^{-rt}} \qquad (2)$$

where the population metric (P) reaches a new carrying capacity (K) up to a maximum rate (r) through an initial exponential phase (time, $t < K/2$), and N_0 is the initial population size, best explained life histories related to body size: maximum length, length at first maturity, and length to achieve optimum yield (Table 2). On average, these logistic models explained 68 ± 3 % (mean ± SD) of the total variation, and each increased as a function of years since closure. The linear model,

$$P(t) = b + mt \qquad (3)$$

where the population metric (P) increases continuously from an original density (b) at a constant rate (m) through time (t) without limit, best explained trophic level, natural mortality, life span, growth rate, generation time, and age at first maturity (Table 3). These linear models explained on average 49 ± 9 % (mean ± SD) of the total variation. Trophic level, along with natural mortality and growth rate, declined as a function of years since closure, whereas life span, generation time, and age at first maturity all increased (Figs. 1 & 2). Several residual plots displayed some degree of heteroscedasticity with later years of protection (>15 yr), but this was to be expected given that more sites were used for the latter period than for the initial phase. Nevertheless, we did not weigh variances by site because the heteroscedasticity present did not confound our analyses. The relationships between trophic level and life span, natural mortality, and maximum body length were all weak and statistically non-significant (Fig. 3; p > 0.05).

DISCUSSION

The life-history metrics of Kenyan fish communities were predicted moderately well by time since fisheries closure. The directions of change after cessation of fishing were consistent with predictions for life-history characteristics, but not for trophic level. The longer the fisheries closure, or time after disturbance, the greater the weighted mean age and body size metrics, and the lower the growth rate and mortality metrics. In contrast, mean trophic level declined linearly for the full 42 yr chronosequence.

Table 2. Logistic curve parameter estimates (see Eq. 2 in 'Results') for the association between the age of fisheries closure and life-history characteristics. Estimators are random variables that are a function of the sample data used to estimate a parameter. CL: confidence limit, GOF: goodness of fit

Trait	GOF	R^2	K	K^a	95 % CL[a]	r	r^a	95 % CL[a]	N_0	N_0^a	95 % CL[a]
Maximum length	<0.001	0.716	48.727	48.797	(46.746, 58.594)	−33.753	−33.1294	(−50.497, −19.225)	21.954	22.277	(12.145, 60.471)
Length at first maturity	<0.001	0.675	25.0717	25.091	(24.627, 26.746)	−23.589	−23.5806	(−44.984, −14.281)	12.665	12.773	(7.760, 28.302)
Length to achieve optimum yield	<0.001	0.668	28.153	28.175	(27.571, 29.918)	−21.518	−21.4165	(−42.325, −13.003)	12.184	12.269	(7.314, 27.687)

[a]Estimates derived from a nonparametric bootstrap ($R = 1000$) for the logistic model

Table 3. Linear parameter estimates (see Eq. 3 in 'Results') for the association between the age of fisheries closure and life-history characteristics and trophic level. Estimators are random variables that are a function of the sample data used to estimate a parameter. CL: confidence limit, GOF: goodness of fit

Trait	GOF	R^2	b	b^a	95 % CL[a]	m	m^a	95 % CL[a]
Trophic level	<0.001	0.429	3.138	3.139	(3.074, 3.192)	−0.007	−0.007	(−0.010, −0.004)
Natural mortality	<0.001	0.615	0.989	0.990	(0.971, 1.008)	−0.004	−0.004	(−0.005, −0.003)
Life span	<0.001	0.380	9.043	9.040	(8.833, 9.242)	0.029	0.029	(0.021, 0.038)
Growth rate	<0.001	0.582	0.491	0.491	(0.481, 0.503)	−0.002	−0.002	(−0.002, −0.001)
Generation time	<0.001	0.450	2.745	2.744	(2.674, 2.812)	0.010	0.010	(0.007, 0.013)
Age at first maturity	<0.001	0.476	2.131	2.131	(2.079, 2.176)	0.008	0.008	(0.006, 0.010)

[a]Estimates derived from a nonparametric bootstrap ($R = 1000$) for the linear model
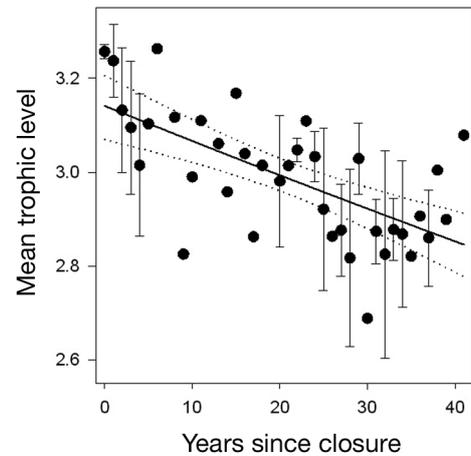

Fig. 1. Time since closure from fishing and weighted mean trophic level values for fish in Kenyan marine parks. Values are mean ± SE; solid line is the best-fit equation based on Akaike's information criteria (AIC), and dashed lines are 95 % confidence limits (see Table 3). Points with no error bars are those with only 1 site in the chronosequence, whereas points with error bars are represented by >1 site. Note that vertical axis does not start at zero

While this decline was minimal (3.24 in Year 0 vs. 3.08 in Year 42) and presumably ecologically unimportant, it does indicate a lack of evidence for a predicted increase (Sandin et al. 2008). Furthermore, our results show weak relationships between trophic level and other fish life-history characteristics, which may indicate weak or unexpected trophic responses in other ecosystems where there are weak relationships. Consequently, a life-history portfolio based on growth, reproduction, and mortality would appear to be more appropriate than trophic level for predicting the response of fishes to reduced fishing in Kenya.

An implicit assumption of many fisheries impacts is that fishing is focused on the higher trophic levels, and this produces the expectation that these levels will recover relatively fast and proportionate to the impact with the cessation of fishing (Pauly et al. 1998). This conceptual model has received considerable attention, but many fisheries have been shown to focus on larger parts of the food web (Branch et al. 2010), and there is limited predictability of the trophic level model predictions for a number of fish-
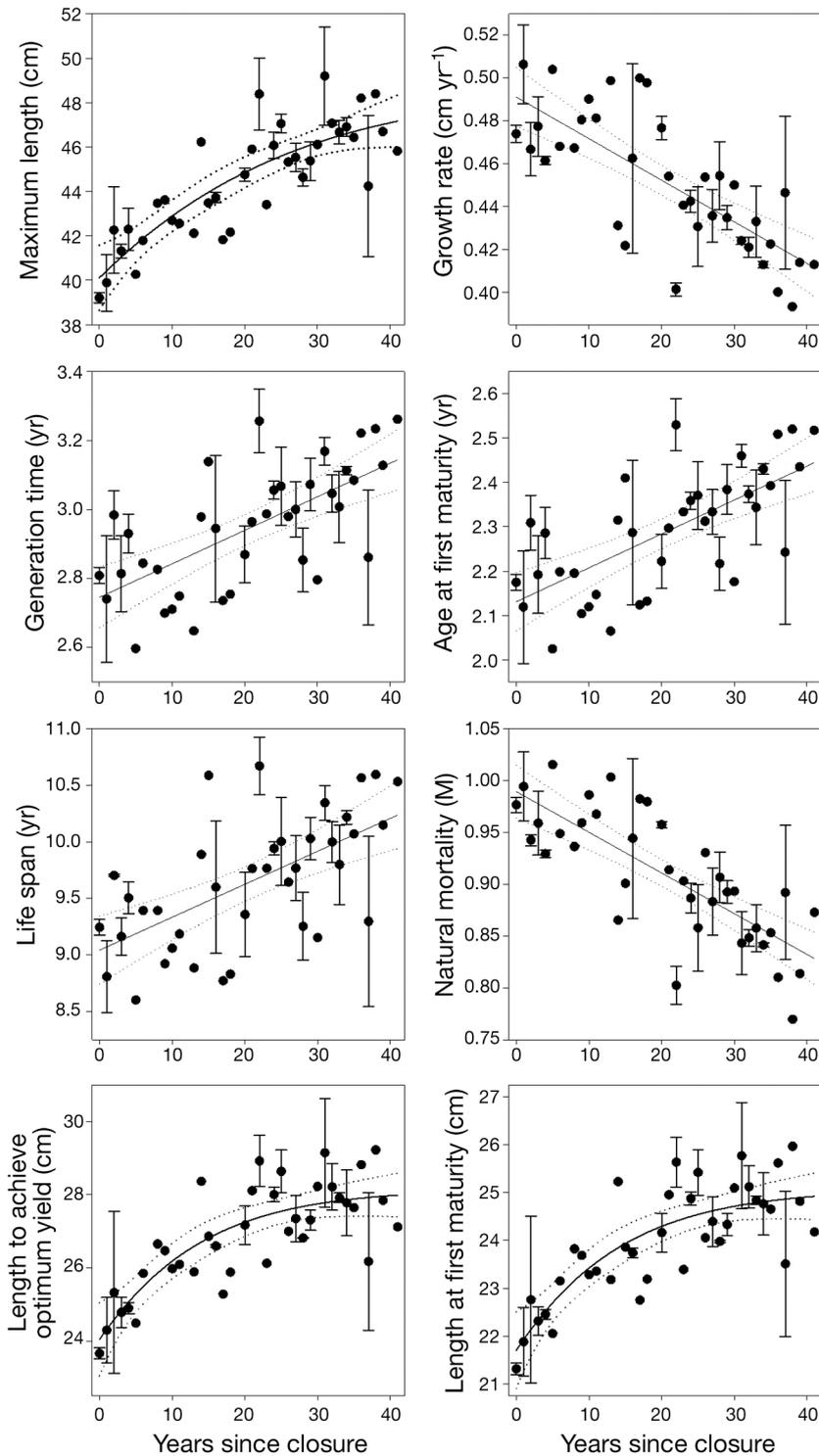
Fig. 2. Time since closure from fishing and 8 weighted life-history characteristics: maximum length, growth rate, generation time, age at first maturity, life span, natural mortality, length to achieve optimum yield, and length at first maturity. Values are mean ± SE; solid line is the best-fit equation based on Akaike's information criteria (AIC), and dashed lines are 95% confidence limits (see Tables 2 & 3). Points with no error bars are those with only 1 site in the chronosequence, whereas points with error bars are represented by >1 site. Note that vertical axes do not start at zero

eries (Essington et al. 2006). The trophic impact model might be a good proxy for life history if trophic level was strongly associated with the predicted growth and mortality life histories. As shown in the present study, however, there are many cases where trophic level is not associated with the expected life-history characteristics. For example, the 2 main herbivorous fish families, Scaridae and Acanthuridae, have very low rates of natural mortality while occupying a low trophic level. Also, the herbivorous fishes maintain large body sizes and moderate life spans. This is counterintuitive to predictions that organisms occupying lower trophic levels would be composed of smaller and short-lived species (Huston & Smith 1987). When all herbivorous fishes (Scaridae, Acanthuridae, Siganidae) are combined in the present analysis, they account for >40% of the total biomass and can, therefore, greatly influence weighted metrics. The links between trophic level and life-history characteristics shown here are weak at best, and this undermines the strength of the trophic impact model, even as a proxy for life-history changes.

The patterns of change discovered in the present study suggest that many ecological processes of recovery may be slow and incomplete even after 42 yr. The frequency of linear changes without deflection or saturation was unexpected given the length of the chronosequence. Trophic level, natural mortality, growth rate, life span, generation time, and age at first maturity all showed no evidence of saturation, and yet these models were predicting half of the total variance. Even the body length factors that fit well to the logistic model were clearly not leveling after 42 yr of fishing protection. This may be due to the inherently slow ecological processes in these coral reefs. Additionally, these closures may lack the space and habitat requirements of the large, migratory, or slow-growing species (Mumby et al. 2004).
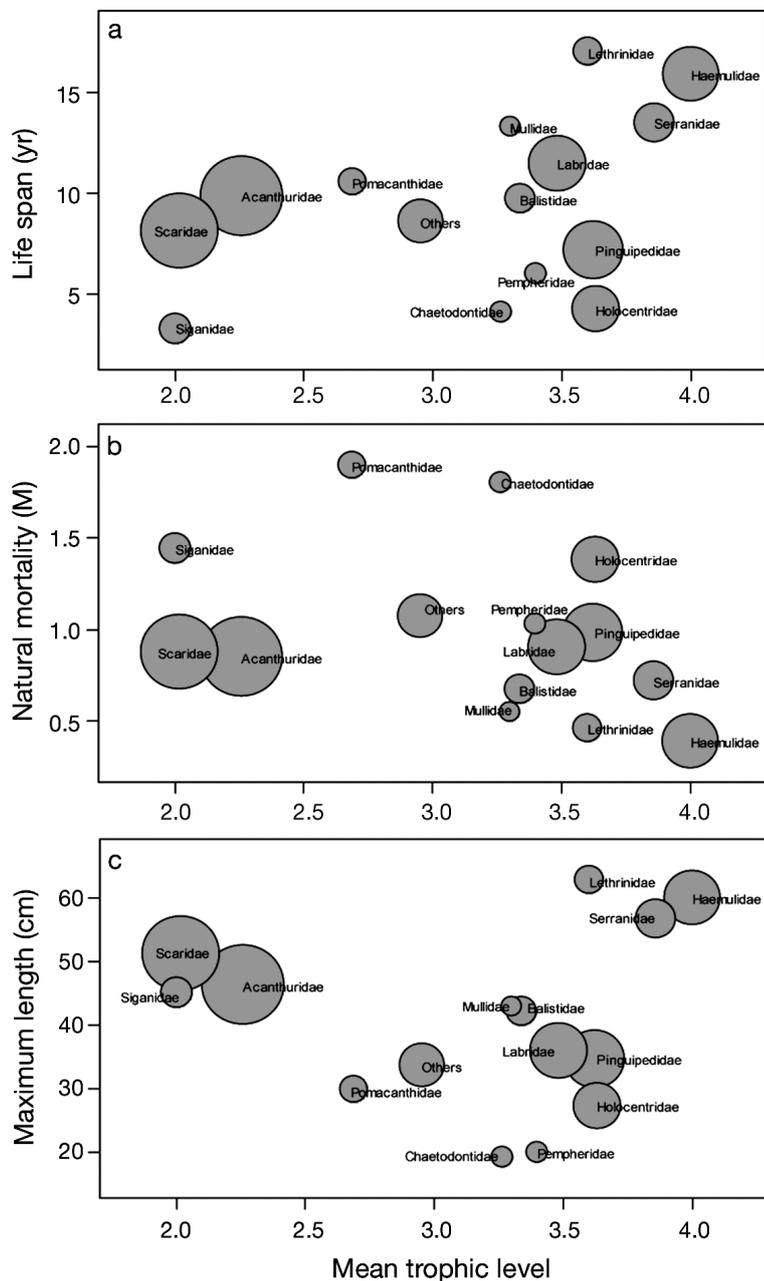
Fig. 3. Mean trophic level and 3 life-history characteristics for fish in Kenyan fisheries closures: (a) life span, (b) natural mortality, and (c) maximum length. Each data point represents one of the 15 most abundant fish families in Kenya, and the radius is directly proportional to the square root of the relative biomass summed across all years. Regression analyses found that all relationships were statistically non-significant (life span, $F = 2.75$; natural mortality, $F = 2.04$; maximum length, $F = 0.02$; df = 1,13; $p > 0.12$)

Fish species may have specific habitat requirements that preclude recruitment, which hinge upon substratum recovery or composition (Jones et al. 2004). This indirectly links fish recovery patterns to biotic and abiotic factors that alter the benthos or

structural complexity (Graham et al. 2006). Other site-specific studies of the recovery of coral reef fishes have argued that responses appeared coupled to the recovery of the benthos (Emslie et al. 2008). Nevertheless, a study of most western Indian Ocean reef closures found negligible effects of coral cover and benthic complexity on fish biomass or functional group composition for the existing range of these variables (McClanahan et al. 2009).

Life history and physiological traits are expected to constrain recovery patterns to a smaller subset of possible patterns and limit the potential for change (Huston & Smith 1987). Growth, reproduction, and mortality metrics constrain options for colonization depending on the window of the disturbance, but other factors, such as adult movements and larval dispersal, are also likely to be important (Cowen et al. 2000). In the present study, we are likely to be observing both the responses to dispersal and the development of the community after the fishing disturbance. For example, if the scale at which management strategies, such as fisheries closures, are not set by how far species travel or disperse, recruitment may become limiting and life histories may never fully recover (Mora & Sale 2002, Cowen et al. 2006). The growth and recruitment of many of these species can be slow, and the surrounding seascape may be depleted in terms of the most fishing-susceptible taxa (McClanahan et al. 2007a). Therefore, if areas adjacent to fisheries closures are 'deserts in the sea', recovery times in closures may be extended or never fully reached. This may be particularly relevant in Kenya, where the isolation and small area (~5% of the nearshore area) of the closures are surrounded by fished reefs that may contain as many as 30 fishers km^{-2} and as little as 23 kg of fish biomass per hectare (McClanahan et al. 2008).

The chronosequence method we used in the present study is useful for studying slow ecological processes, but is also open to a variety of criticisms, such as the taxonomic, spatial, and temporal heterogeneity that is common to ecosystems (Walker et al. 2010).

The appropriate use of a chronosequence relies on a few critical site-specific issues such as the similarity and history among sites (Johnson & Miyanishi 2008); inherent to using a space-for-time substitution method is the assumption that communities at younger sites are currently developing in a temporal pattern that resembles how the older sites developed. By having a large portion (>50%) of our chronosequence represented by >1 site, we were able to examine whether recovery trajectories were similar among sites. In the most critical parts of our chronosequence, which are the beginning years where the trajectory of recovery is set, and the final years where the curves end, recovery slopes at the site level were similar to one another. Furthermore, in fished sites over the entire 1988 to 2010 data set, weighted life-history metrics changed similarly with no site or year effect. These 2 results suggest that sites tracing dissimilar histories in the persistence and recovery of our metrics did not confound the chronosequence.

While sites may have significant differences in temporal development at a finer level of detail, the gross taxonomic and temporal resolution for which we analyzed the data may have aided in producing moderate predictive power. Species-level variability can be very high and change rapidly, which can challenge any efforts to evaluate a chronosequence at the species level (McClanahan et al. 2007b). The assumption here is that species-level metrics pooled at the family level can reflect the fish community. While this is not unreasonable to suggest, and life histories are often closely correlated with phylogenies (Stearn 1989, Darling et al. 2012), it needs further testing for coral reef fish. Previous studies of fish have often been constrained by the level at which fish are sampled in fisheries catches, which is often at the family level (Branch et al. 2010). However, in the present study, this was also a limitation to the data collection, because sampling diverse communities can be challenging and potentially troubled by species-level field identification issues.

The studied reefs were similar in being shallow (0.5 to 3 m) and part of a similar uniform nearshore fringing reef system, which may be an additional reason for the strong predictions. These reef systems have been shown to have generally lower between-site variability than, for example, patch reefs (Ault & Johnson 1998, McClanahan & Arthur 2001). This is likely to have reduced spatial variability common to coral reefs and contributed to the clear patterns. Results here can also be seen as further evidence that our sites were comparable and similar to one another,

and support our use of the chronosequence method (Johnson & Miyanishi 2008, Walker et al. 2010).

The findings have implications for management of closures and resource utilization in coral reef fisheries. First, it suggests that temporary closures will not recover the full diversity of life histories and probably not represent 'pristine' seascapes (Sandin et al. 2008, McClanahan & Omukoto 2011). It suggests that a combination of age, size of closures, and reduced resource use outside the closure may be needed to restore ecosystems to some crude facsimile of a historical baseline (McClanahan et al. 2009, Daw et al. 2011). Secondly, coral reef fisheries are largely composed of a few taxa that can be highly productive and sustain high fishing mortality (McClanahan et al. 2008). It is unlikely that moderate levels of fishing will be sustainable for a larger number of the coral reef taxa (McClanahan & Hicks 2011). A less obvious finding is that fish catches at high fishing mortality may often be composed of herbivorous species with rapid life histories that feed on seagrass (e.g. Siganidae), while herbivores with slow life histories associated with coral reefs (e.g. Acanthuridae, Scaridae) are likely to be quickly eliminated as fishing mortality increases. These herbivorous/detritivorous fishes associated with hard bottom reefs are considered important for the resilience of coral reefs to climatic and other disturbances (Bellwood et al. 2004, Mumby et al. 2006, Hughes et al. 2010). We view these specialized herbivores as vulnerable to fishing disturbances, and more restrictions on the capture of these species are needed when developing management systems for coral reefs.

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