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Report

Linking Social and Ecological Systems to Sustain Coral Reef Fisheries

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Summary

The ecosystem goods and services provided by coral reefs are critical to the social and economic welfare of hundreds of millions of people, overwhelmingly in developing countries [1]. Widespread reef degradation is severely eroding these goods and services, but the socioeconomic factors shaping the ways that societies use coral reefs are poorly understood [2]. We examine relationships between human population density, a multidimensional index of socioeconomic development, reef complexity, and the condition of coral reef fish populations in five countries across the Indian Ocean. In fished sites, fish biomass was negatively related to human population density, but it was best explained by reef complexity and a U-shaped relationship with socioeconomic development. The biomass of reef fishes was four times lower at locations with intermediate levels of economic development than at locations with both low and high development. In contrast, average biomass inside fishery closures was three times higher than in fished sites and was not associated with socioeconomic development. Sustaining coral reef fisheries requires an integrated approach that uses tools such as protected areas to quickly build reef resources while also building capacities and capital in societies over longer time frames to address the complex underlying causes of reef degradation.

Results and Discussion

Effectively confronting the coral reef crisis will require us to link social and ecological systems so that we can better understand and address the complex socioeconomic drivers that influence how societies use and ultimately govern their use of coral reefs [2, 3]. It is generally held that human use, driven primarily by population density, is a principal cause of coral reef degradation [4–7]. However, less is known about how other socioeconomic factors such as economic development shape societies' impacts on coral reefs [8, 9]. Sociological perspectives on human-environment interactions emphasize how socioeconomic development can affect a society's impact on the environment, often in nonlinear and sometimes positive ways [10, 11]. To explore these linkages in coral reef fisheries, we collected data on a composite index of village-level infrastructure (as a proxy for local-scale socioeconomic development), human population density, and structural complexity of reef habitat (rugosity) in 19 fished sites and 11 fishery closures across five countries in the western Indian Ocean. We evaluated these drivers' influence on the biomass of reef fishes, which is a variable sensitive to management and human impact [12].

First, we examined whether the biomass of reef fishes targeted in the multispecies fishery could be explained independently by human population density, structural complexity, and socioeconomic development. In fished sites, human population numbers had a significant but weak negative relationship to the biomass of target reef fishes ($n = 19$, $r^2 = 0.28$, $p = 0.02$; Figure 1A), and the benthic structural complexity had a moderate positive relationship ($n = 16$, $r^2 = 0.54$, $p = 0.001$; Figure 1B), consistent with previous studies on reef fishes [4, 7, 13, 14]. Our novel finding is that the strongest relationship to fish biomass was the quadratic function of the socioeconomic-development index, which displayed a U-shaped relationship ($n = 19$, $r^2 = 0.77$, $p < 0.001$; Figure 1C).

Second, we tested candidate models with all possible combinations of the three factors to determine the best combination of variables for explaining fish biomass in fished sites. We included country as a random effect to account for nonindependence of samples within countries [15]. A key and surprising finding from this study is that the best model included the quadratic socioeconomic-development index and reef structural complexity, but did not include human population density (likelihood-ratio test of nested models with and without this term; ratio = 0.166, $p = 0.684$) (Table 1). The quadratic term of the development index was highly significant in the selected model (likelihood ratio = 14.5, $p < 0.001$). Thus, fish biomass is highest where community development is very low or high, but low where development is intermediate (Figure 1C). Fish biomass (± the standard error of the mean) at the bottom of the curve (Takaungu, Kenya) was 77 ± 11.9 kg/ha, approximately 1/4 of the biomass of the sites with the highest and lowest levels of development (336 ± 52 kg/ha for Anse Volbert, Seychelles and 294 ± 57.3 kg/ha for Ambodilaitry, Madagascar, respectively) (Figure 1C).

These findings are consistent with the environmental Kuznets curve hypothesis, which predicts that increasing socioeconomic development results in ecological degradation until a point when environmental conditions improve as societies become increasingly affluent and begin to demand environmental quality (creating a U-shaped relationship between affluence and local environmental conditions) [10, 16, 17]. The causal mechanisms behind a Kuznets curve relationship are generally classed in three broad categories: (1) a technique effect, whereby societies may change the technologies used to produce goods and services, which may have differing levels of impact on the environment; (2) a composition effect, whereby the composition of the economy could change to

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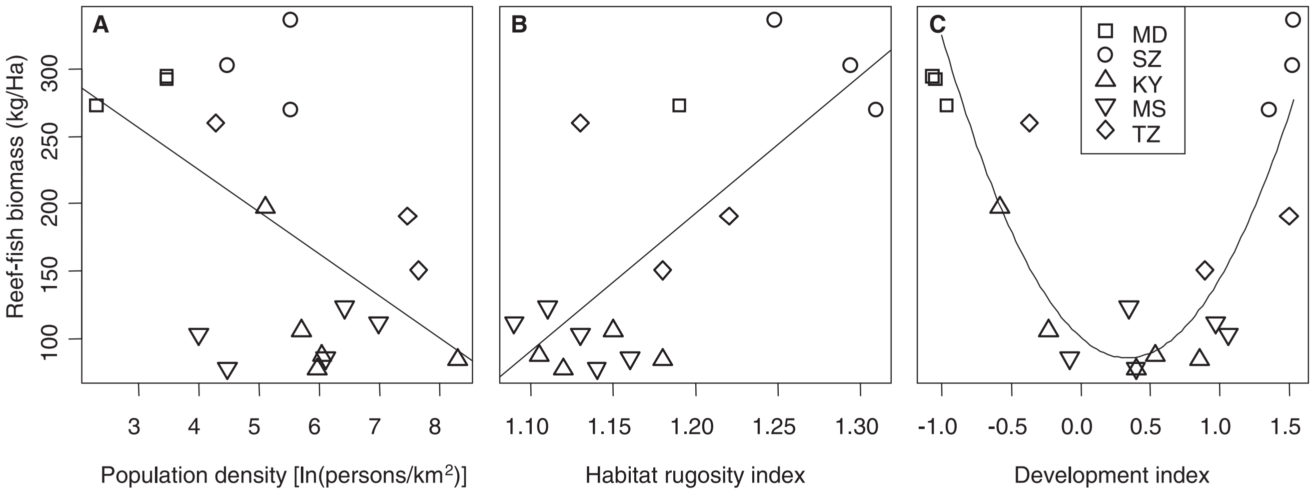

Figure 1. Fits of Reef-Fish Biomass

Fits of reef fish biomass as a function of (A) human population density ($r^2 = 0.28$), (B) habitat rugosity index ($r^2 = 0.54$), and (C) community-level socioeconomic-development index ($r^2 = 0.77$). Solid lines show curves fitted from linear (A and B) and quadratic (C) regressions. Data are distinguished by country as follows: MD, Madagascar; SZ, Seychelles; KY, Kenya; MS, Mauritius; TZ, Tanzania.

be less destructive to the local environment, for example, by switching from primary-resource extraction to a service industry; and (3) a scale effect, whereby wealthier societies displace local impacts, for example, by drawing resources from other areas, often those poorer or less regulated [16, 18]. The parallel sociological perspective of ecological modernization suggests that it is not economic development per se that leads changing environmental conditions, but rather the accompanying institutional changes, such as investments in scientific and natural-resource management organizations [19].

We used socioeconomic survey data from these communities to further examine how a combination of the technique, composition, and scale effects, and also aspects of local sociocultural institutions, may play a role in our observation of a Kuznets relationship for coral reef fishes in the western Indian Ocean (Table 2). Sites with low levels of development are characterized by high levels of dependence on fishing as a primary occupation, minimal engagement in salaried employment, and few boats with engines (Table 2 and Figure 2A). Although these low-development sites tend to have weak national governments [20], the presence of customary sociocultural institutions such as taboos may act to restrict fishing effort (although this later indicator was only suggestive at $p = 0.054$; Table 2). Together, these factors suggest that in low-development sites, technological constraints and social institutions may limit people's exploitation of marine resources. Reduced dependence on marine resources, variable access to boats but increasing access to engines and other technologies, high use of spear guns, and a lack of customary management institutions characterize communities with intermediate levels of development (Table 2 and Figure 2B). Factors such as reduced dependence on marine resources and increased technological efficiency can break down customary sociocultural institutions that may be critical in managing marine resources [21]. For example, in Kenya, which has some sites with the poorest fishery conditions, customary institutions were once widespread, but they have largely broken down in recent years [22], with destructive fishing techniques now practiced in some of these locations [6]. Sites with high socioeconomic development are generally characterized by effective national government [20], low dependence on fishing, reduced use of potentially damaging gear such as gill nets and higher use of more benign gear

Table 1. Comparison of Candidate Models

Model	Fixed Model Terms	df	n	AICc	BIC	ΔAICc	ΔBIC	AICc weight
1	no fixed terms	3	16	178.5	178.8	3.6	8.7	10%
2	quadratic development	5	16	177.9	175.7	3.1	5.6	13%
3	habitat rugosity	4	16	179.7	179.1	4.9	9.0	5%
4	log population density	4	16	179.5	179.0	4.7	8.9	6%
5	habitat rugosity + quadratic development	6	16	174.8	170.1	0.0	0.0	61%
6	log population density + quadratic development	6	16	182.8	178.1	8.0	8.0	1%
7	log population density + habitat rugosity	5	16	182.6	180.5	7.8	10.4	1%
8	log population density + habitat rugosity + quadratic development	7	16	181.3	172.7	6.5	2.6	2%

Comparison of candidate models with three fixed effects for reef-fish biomass: a quadratic function of our socioeconomic-development index, habitat rugosity index, and natural log of human population density. All models include a random effect of country. Model 5, including the development index and habitat complexity, has the lowest BIC and AICc scores, confirming it as the best fit. The following abbreviations were used: df, degrees of freedom; n, sample size; AICc, Akaike information criterion corrected for small sample sizes; BIC, Bayesian information criterion; ΔAICc and ΔBIC, difference from the criterion scores of the most favored model; AICc weight, likelihood weight based on the AICc values of all tested models [45].

Table 2. The Average Percentage of Low-, Medium-, and High-Development Communities Involved in Select Occupational and Fishing Activities

Factor	Level of Development: Low (n = 5)	Medium (n = 8–10)	High (n = 4)	F	Significance
Composition Effect Indicators					
Average % of households engaged in fishing	60 (48–88) %	23 (6–61) %	19 (11–33) %	10.2	0.002
Average % of households that listed fishing as their primary occupation	48 (28–75) %	17 (2–54) %	4 (0–10) %	10.4	0.002
Average % of households that engaged in regular salaried employment (manufacturing, teaching, etc.)	3 (1–4) %	34 (7–79) %	58 (52–64) %	149.3[a]	<0.0001
Technique Effect Indicators					
Average % of fishers using gill nets	20 (9–36)	11 (0–37)	1 (0–5)	7.1[a]	0.006
Average % of fishers using hand lines	21 (13–35)	20 (0–50)	47 (33–55)	7.1	0.006
Average % of fishers using spear guns	1 (0–3)	7.5 (0–25)	0 (0)	5.1[a]	0.03
Average % of fishers using seine nets	1 (0–3)	1 (0–8)	2 (0–8)	0.3	0.73
Average % of fishers using pelagic nets and lines	5.7 (0–19)	12 (0–28)	18 (8–27)	2.0	0.16
Scale Effect Indicators					
Average % of fishers with boats	90 (84–100) %	62 (0–98) %	89 (67–100) %	2.9[a]	0.082
Average % of boats with engines	5 (0–19) %	33 (0–88) %	78 (60–100) %	29.7[a]	<0.0001
Presence of Sociocultural Governance Institutions	3[b]	1[b]	0[b]	$\chi^2 = 6.4$[c]	0.054

Numbers in parentheses indicate the range.
[a] GLS model with varIdent function fitted for overcoming violation of homogeneity.
[b] Number of communities in group with customary sociocultural institutions that may help to govern marine resource use.
[c] Chi-square statistic (p value estimated by Monte Carlo simulation).

such as reef handlines, high levels of engagement in salaried employment, and high levels of access to boats with engines that allow for fishing further afield (Table 2 and Figure 2C).

The Role of Fishery Closures

Fishery closures can help to sustain reef fisheries by increasing fish biomass within their boundaries, protecting corals and other habitats for reef fishes from damage caused by uses such as destructive fishing practices, and providing "spillover" of adult fishes close to reserve boundaries (generally <500 m) [23]. Fishery closures exist along the full socioeconomic-development gradient of our study sites and, on average, have approximately three times the fish biomass of fished sites, with the difference between the lowest biomass in fished sites and the highest in a closure (~1200 kg/ha) being ~16-fold (both sites were in Kenya) (Figure 3). Variation in the biomass of fishes within closures can be partially attributed to differences in park compliance, buffer zones, closure size, and age [12, 24, 25]. Importantly, there is no clear relationship between biomass in closures and the gradient of development, suggesting that effective marine parks are not just a measure of community affluence [3]. This context suggests that although community development can result in modest variation of fish resources, improvements in fish biomass may be derived from local governance such as well-enforced fishery closures at most stages of socioeconomic development. The poor relationship between development and fish biomass in closures (Figure 3) suggests that other factors such as social capital, organization, and governance are important elements of successful closures [3, 6].

Although fish biomass was considerably higher inside most fishery closures, closures alone are unlikely to sustain coral reef fisheries throughout the region. This is in part because they cover too small an area to maintain system-wide resilience, with the current spatial extent of closures in the region ranging from 0.5%–15% of the total reef area per country [6]. After large-scale disturbances such as the 1998 coral bleaching event, the small and dispersed fishery closures in the western Indian Ocean were not able to prevent declines in key components of reef ecosystems (e.g., reef structural complexity and small-bodied herbivores) or promote faster recovery than that in fished areas [26]. Vastly expanding the

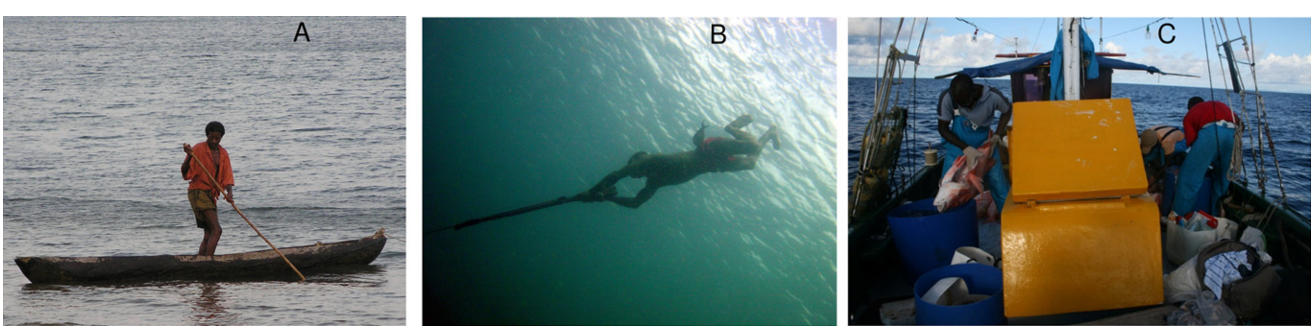

Figure 2. Fishing Practices Common in Different Stages of Socioeconomic Development
(A) A fisher from a low-development site in a small wooden canoe.
(B) A fisher from a moderate-development site using a spear gun.
(C) Fishers in a high-development site hand-line fishing from a motorized boat (source for photo: Seychelles Fishing Authority).

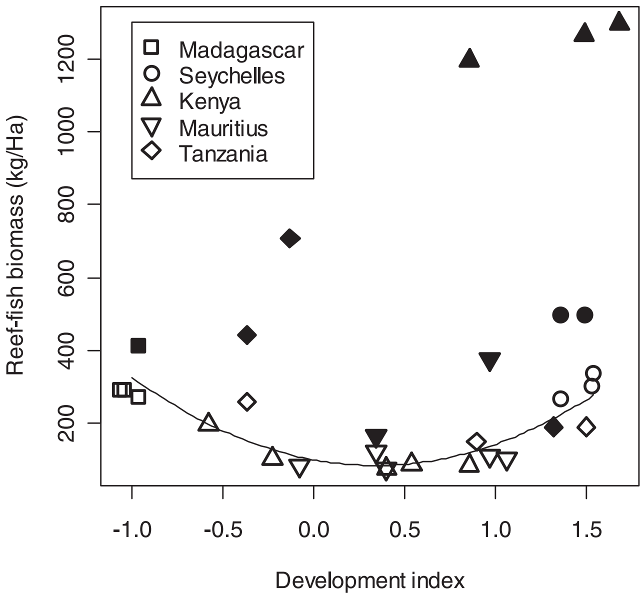

Figure 3. The Biomass of Reef Fish in Protected Sites and Fished Sites along a Gradient of Economic Development

Protected sites are indicated by filled symbols, and fished sites are indicated by open symbols. The solid line is the best-fit curve fitted with the quadratic regression of fished-site biomass and development. The fish biomass from protected sites was not included in the regression analysis.

area covered by fishery closures may promote system-wide resilience to some disturbances, for example, by improving ecosystem connectivity and enhancing the biomass of key herbivorous fish groups [27]. However, significant closed-area expansion is likely to be met with considerable resistance from stakeholders, and in many cases, it is socially and politically unrealistic. There is clearly a need to develop management strategies that foster resilience throughout the entire seascape, not just inside protected areas [2, 28].

An Integrated Approach Necessary to Sustain Coral Reef Fisheries

Sustaining coral reef fisheries will require moving toward an integrated social-ecological systems approach that better understands and incorporates the socioeconomic factors that shape the ways that societies interact with reefs [29]. By linking social science and ecology at a regional scale, this study provides a novel contribution to our understanding of how societies' socioeconomic conditions can influence reef fisheries. In regions such as East Africa, where persistent poverty is often coupled with resource degradation [3, 21, 30, 31], improving human welfare and institutional capacities will be an essential component of sustaining broader coral reef seascapes. Escaping these "poverty traps" [30, 31] will require governments and donors involved in the management of reefs to make meaningful investments in programs that improve governance, build social and physical infrastructure, address burgeoning population growth rates, and provide alternatives to heavy reliance on reef-based livelihoods [3, 32]. From the findings of this research, we suggest prioritization should be given to (1) assisting low-development sites to navigate the transition to improved welfare without dwelling in the intermediate-development stage, in which resources are likely to be most degraded, and (2) improving environmental conditions and welfare in intermediate-development sites in ways that do not use the extraction of reef resources as a major basis of development.

Efforts to improve human welfare in a reef-governance context will probably be ineffective and sometimes even counterproductive unless they are coupled with effective policies and governance, for two key reasons. First, relying on the assumption that resource conditions will improve with socioeconomic development does not account for potentially irreversible change in coral reef ecosystems [33]. Irreversible change may occur as a result of the heavy degradation at the bottom of the curve and prevent a rebound of fishery resources as development increases [16]. Policy tools such as closures will be critical in helping sustain fisheries and preventing these local ecological phase shifts, particularly for sites with transitioning economies. Along with closures, there is a need to identify successful aspects of fishery management from sites that sit along the low- or high-development sites and determine whether and how such measures might be applicable to other areas, particularly intermediate societies. Such policies may involve fostering or restoring traditional values and institutions [21], instituting property rights [34], switching to fishing practices that exploit different and more sustainable resources, or implementing restrictions on gear types that cause habitat damage [6].

Second, aspects of economic growth can contribute to larger-scale degradation of reef ecosystems. As societies become more affluent, they are able to extract resources from further afield [16, 35], and they contribute increasingly to larger-scale and more complex problems confronting reefs, such as coastal modification (e.g., dredging and land reclamation), land-based pollution (e.g., incorporating pesticides and fertilizers in agriculture), and high carbon emissions [10, 11]. To minimize the potential negative effects of economic growth on reef systems, socioeconomic development needs to be coupled with effective legislation, institutional strengthening, and regional agreements. For example, in Kenya, recent Beach Management Unit legislation provides a form of property rights to coastal fishers, which essentially restricts their ability to fish in distant fishing grounds and simultaneously provides incentives for stewardship of local resources. At a national level, this type of legislation may help to prevent more distant ecosystems from becoming degraded when there are improvements in local welfare. At a larger scale, multilateral agreements may be required that discourage wealthier countries from consuming the nearshore fishery resources of the poor. Furthermore, governments and donor agencies should make sustainability a cornerstone of development programs so that projects that aim to improve human welfare as part of reef management do not inadvertently result in increasing contributions to larger-scale threats to coral reefs [11].

These economic and policy approaches for sustaining coral reefs and associated fisheries operate on different, but complimentary, spatial and temporal scales. Policy approaches such as closures can operate on relatively fast temporal scales, with initial responses in fish populations detectable within 3–5 years [36], but their effects are highly localized. Protected areas may provide a lifeline to threatened fisheries regardless of societal trajectory, but there is also a need to govern the entire seascape, particularly with increased occurrence of global threats, such as coral bleaching, which can undermine reef systems both inside and outside protected areas [27, 28]. Conversely, socioeconomic development that reduces reliance on reef resources may take decades or generations, but it is likely to influence how resources are used throughout a society's entire fishing grounds, which are often much larger than protected areas in the region [37]. Sustaining coral reef fisheries will require using policy responses such as closures to build resources locally while simultaneously addressing key socioeconomic drivers of decline to confront both local and larger-scale drivers of reef degradation.

Experimental Procedures

Socioeconomic Field Studies

Study Sites

We studied 19 coastal communities and adjacent coral reef sites in the western Indian Ocean spanning five countries: Kenya, Tanzania, Seychelles, Mauritius, and Madagascar. We selected study sites to provide a gradient of economic development and human population density both within and between countries. At each site, we investigated the following socioeconomic indicators: community-level infrastructure (as a measure of economic development); human population density; the proportion of the community involved in fishing (and that ranked it as their primary livelihood strategy); the proportion engaged in salaried employment; the proportion of fishers that use gillnets, reef handlines, spearguns, small seine nets, and pelagic gear; the proportion of fishers that own boats and engines; and the presence of customary sociocultural institutions such as taboos that may restrict fishing.

Population Density

Population-density data were collected with the Socioeconomic Data and Applications Center (SEDAC) grided population of the world database (available online at http://sedac.ciesin.org/gpw/global.jsp). Geographic coordinates of field sites were overlaid on the grided population database. When a field site was near the border of two grids, we averaged those grids to give a mean population density. Grid cells were 4.66 km^2.

Community-Level Development

To measure community-level development, we recorded the presence of 16 community-scale infrastructure items [38] in each community by interviewing community leaders and triangulating results with direct observation. We ran a factor analysis on the presence or absence of infrastructure items to reduce these 16 items into a scale of socioeconomic development. This resulted in one factor that explained 51% of the variance [3]. The marginal variance explained by the subsequent factor was low (11%), so only the first factor was extracted. Factor loadings for the specific items were as follows: hard-top road = 0.893, phone service = 0.865, restaurant = 0.865, electric service = .0842, piped water = 0.831, public transportation = 0.802, fuel station = 0.758, food market = 0.735, doctor = 0.734, hotel = 0.695, septic tanks = 0.665, secondary school = 0.662, hospital = 0.506, primary school = 0.498, medical clinic = 0.457, and sewage treatment = 0.384. We used the subsequent factor scores for each community as a measure of community-level socioeconomic development. Because the Kuznets curve predicts a U-shaped relationship between affluence and environmental conditions, this economic-development index was included in regression models as a second-order polynomial.

Resource Use, Dependence, and Governance Indicators

To investigate potential causal mechanisms related to the observed environmental Kuznets curve, we conducted more detailed socioeconomic assessments in each site. We conducted 1412 household surveys in the 19 fished sites. Sampling of households within villages was based on a systematic design, in which a fraction of every i^{th} household (e.g., 2^{nd}, 3^{rd}, 4^{th}) was determined by dividing the total village population by the sample size [39]. There were 23–143 surveys conducted per site, depending on the population of the village. We examined dependence on fishing and salaried employment (e.g., teaching, government work, etc.) by asking respondents to list the jobs people in the household engaged in for food or money. We then asked respondents to rank these activities in order of importance. We asked fishers about the type of boat and gear they used to determine the following indicators: proportion of fishers with boats, proportion of fishers with boats that have engines, and type of gear used by fishers. In sites with few fishermen, additional systematic surveys were conducted from the population of fishers [3]. We also examined the presence of sociocultural institutions such as taboos that may help manage marine resources by using data from Cinner [40].

Ecological Field Studies

Study Sites

We collected ecological data from a total of 30 locations (19 fished sites and 11 fishery closures). We selected field sites that were as similar as possible in terms of reef structure, depth, and dominance of a hard-bottom substratum [27]. All sites were located on shallow reef lagoons and slopes on fringing reefs (<7 m depth). When sampling protected areas, we chose sites that were located in the center of the closures.

Reef-Fish Biomass

Biomass of fishes (kg/ha) was selected as an indicator of the condition of reef-fish assemblages and treated as the response variable in regressions. Fish biomass is a sensitive indicator of fishing pressure in these multispecies fisheries, and fishing pressure is the dominant local human impact on fish communities in the region [41]. Biomass was based on fishes >10 cm in length from diurnally active, noncryptic families that were extensively surveyed across all sites. Data on fish biomass were collected by underwater visual census by two experienced observers (T.R.M. and N.A.J.G.) whose detection ability is very similar [42]. All diurnally active, noncryptic, reef-associated fishes were identified to family or species level and counted, and their size was estimated to 5 or 10 cm intervals at each site. In Kenya, Tanzania, Mauritius, and Madagascar, three to five 100 m × 5 m belt transects were used for counting and estimating the numbers and sizes of fishes [43]. In Seychelles, 16 point counts of a 7 m radius were completed at each of three sites within each closure [14]. In both methods, observers avoided double counting by disregarding individuals that left the survey boundary and re-entered. Both methods covered a similar area of reef per site (~2000 m^2), and data were standardized to kg/ha. There may be small amounts of variation associated with different survey techniques and habitats; however, methods papers have found little difference between strip transects and point counts in estimating fish abundance [44], and all sites were in shallow fringing reef habitats. Wet weight (biomass) was estimated from the individual fish-length data with length-weight relationships for species or families [45].

Reef Complexity

We also examined habitat rugosity and a nominal term for country to account for two potentially confounding factors. Rugosity, or the topographic complexity of the reef substratum, has been associated with the biomass of reef-associated fish [46, 47]. At each site, we calculated 5–16 replicate measures of rugosity by measuring the linear distance covered by 10 m lengths of chain or weighted rope fitted to the contour of the reef surface [13]. Rugosity was, however, only available for 16 of the 19 field sites.

Analyses

We used multiple linear regression to compare the ability of human population density (natural log transformed), level of development (based on a quadratic function of the factor scores of community-level infrastructure), and rugosity of habitat at fish count sites to explain reef fish biomass. We fitted variables as fixed effects in a mixed model by using the nlme library in R. To account for nonindependence within countries, we added country as a random term, significantly improving the model (likelihood-ratio test on models fitted with restricted maximum likelihood adjusted for testing at the margin; ratio = 9.30, $p = 0.001$) [15]. The interclass correlation, indicating the relationship between points within the same country, was 0.998 [15].

All possible regression-model combinations of fixed variables were compared for their fit to the data with low-sample-corrected Akaike's information criterion (AICc) and Bayseian information criteria (BIC) values based on maximum-likelihood estimation [15, 48] (Table 1). The significances of individual terms were tested by likelihood-ratio tests [15]. Selected models were assessed for heteroscedacity and normality of residuals by visual assessment of plots and by addition of the varIdent variance structure to the random part, but this did not improve the model fit (likelihood ratio = 7.63, $p = 0.1057$).

To investigate whether there were differences in the assessed socioeconomic conditions in different parts of the U-shape curve, we used natural groupings of the data to divide communities into three groups. This resulted in groupings of the four sites with the highest development, the five sites with the lowest development, and ten sites with moderate development. We then used ANOVA to test for significant differences in socioeconomic conditions in these groups (Table 2). We used a generalized least-squares (GLS) model with the varIdent function in R to overcome violations of homogeneity in four indicators: percentage of households engaged in fishing, percentage of households that rank fishing as a primary occupation, percentage of households engaged in salaried employment, and percentage of fishers with boats that have engines.

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References

1. Moberg, F., and Folke, C. (1999). Ecological goods and services of coral reef ecosystems. Ecol. Econ. *29*, 215–233.
2. Hughes, T.P., Bellwood, D.R., Folke, C., Steneck, R.S., and Wilson, J. (2005). New paradigms for supporting the resilience of marine ecosystems. Trends Ecol. Evol. *20*, 380–386.
3. McClanahan, T.R., Cinner, J.E., Maina, J., Graham, N.A.J., Daw, T.M., Stead, S.M., Wamukota, A., Brown, K., Ateweberhan, M., Venus, V., et al. (2008). Conservation action in a changing climate. Conservation Letters *1*, 53–59.
4. Newton, K., Cote, I.M., Pilling, G.M., Jennings, S., and Dulvy, N.K. (2007). Current and future sustainability of island coral reef fisheries. Curr. Biol. *17*, 655–658.
5. Mora, C. (2008). A clear human footprint in the coral reefs of the Caribbean. Proc. Biol. Sci. *275*, 767–773.
6. McClanahan, T.R., Hicks, C.C., and Darling, E.S. (2008). Malthusian overfishing and efforts to overcome it on Kenyan coral reefs. Ecol. Appl. *18*, 1516–1529.
7. Sandin, S.A., Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander, A.M., Konotchick, T., Malay, M., Maragos, J.E., Obura, D., et al. (2008). Baselines and degradation of coral reefs in the Northern Line Islands. PLoS ONE *3*, e1548.
8. Sobhee, S.K. (2004). Economic development, income inequality and environmental degradation of fisheries resources in Mauritius. Environ. Manage. *34*, 150–157.
9. Cinner, J.E., and McClanahan, T.R. (2006). Socioeconomic factors that lead to overfishing in small-scale coral reef fisheries of Papua New Guinea. Environ. Conserv. *33*, 73–80.
10. York, R., Rosa, E.A., and Dietz, T. (2003). Footprints on the earth: The environmental consequences of modernity. Am. Sociol. Rev. *68*, 279–300.
11. Dietz, T., Rosa, E.A., and York, R. (2007). Driving the human ecological footprint. Frontiers in Ecology and the Environment *5*, 13–18.
12. Micheli, F., Halpern, B.S., Botsford, L.W., and Warner, R.R. (2004). Trajectories and correlates of community change in no-take marine reserves. Ecol. Appl. *14*, 1709–1723.
13. Risk, M.J. (1972). Fish diversity on a coral reef in the Virgin Islands. Atoll Res. Bull. *153*, 1–6.
14. Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P., and Robinson, J. (2006). Dynamic fragility of oceanic coral reef ecosystems. Proc. Natl. Acad. Sci. USA *103*, 8425–8429.
15. Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. (2009). Mixed Effects Models and Extensions in Ecology with R (New York: Springer), in press.
16. Arrow, K., Bolin, B., Costanza, R., Dasgupta, P., Folke, C., Holling, C.S., Jansson, B.O., Levin, S., Maler, K.G., Perrings, C., et al. (1995). Economic growth, carrying capacity, and the environment. Science *268*, 520–521.
17. Grossman, G.M., and Krueger, A.B. (1995). Economic growth and the environment. Q. J. Econ. *110*, 353–377.
18. Folke, C., Kautsky, N., Berg, H., Jansson, A., and Troell, M. (1998). The ecological footprint concept for sustainable seafood production: A review. Ecol. Appl. *8*, S63–S71.
19. Clausen, R., and York, R. (2008). Global biodiversity decline of marine and freshwater fish: A cross-national analysis of economic, demographic, and ecological influences. Soc. Sci. Res. *37*, 1310–1320.
20. Kaufmann, D., Kraay, A., and Mastruzzi, M. (2008). Governance Matters VII: Aggregate and Individual Governance Indicators 1996–2007. World Bank Working Paper 4654.
21. Cinner, J.E., and Aswani, S. (2007). Integrating customary management into marine conservation. Biol. Conserv. *140*, 201–216.
22. McClanahan, T.R., Glaesel, H., Rubens, J., and Kiambo, R. (1997). The effects of traditional fisheries management on fisheries yields and the coral-reef ecosystems of southern Kenya. Environ. Conserv. *24*, 105–120.
23. Russ, G.R. (2002). Marine reserves as reef fisheries management tools: Yet another review. In Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem, P.F. Sale, ed. (San Diego, CA: Academic Press), pp. 421–444.
24. Cote, I.M., Mosqueira, I., and Reynolds, J.D. (2001). Effects of marine reserve characteristics on the protection of fish populations: A meta-analysis. J. Fish Biol. *59*, 178–189.
25. Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenci, P., Garcia-Charton, J.-A., Perez-Ruzafa, A., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., et al. (2008). Marine reserves: Size and age do matter. Ecol. Lett. *11.* 10.1111/j.1461–0248.2008.01166.x.
26. Mumby, P.J., and Hastings, A. (2008). The impact of ecosystem connectivity on coral reef resilience. J. Appl. Ecol. *45*, 854–862.
27. Graham, N.A.J., McClanahan, T.R., MacNeil, M.A., Wilson, S.K., Polunin, N.V.C., Jennings, S., Chabanet, P., Clark, S., Spalding, M.D., Letourneur, Y., et al. (2008). Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. PLoS ONE *3*, e3039. 10.1371/journal.pone.0003039.
28. Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., et al. (2003). Climate change, human impacts, and the resilience of coral reefs. Science *301*, 929–933.
29. Bellwood, D.R., Hughes, T.P., Folke, C., and Nyström, M. (2004). Confronting the coral reef crisis. Nature *429*, 827–833.
30. Cinner, J.E., Daw, T.M., and McClanahan, T.R. (2008). Socioeconomic factors that affect artisanal fishers' readiness to exit a declining fishery. Conserv. Biol., in press. Published online September 4, 2008. 10.1111/j.1523-1739.2008.01041.x.
31. Enfors, E.I., and Gordon, L.J. (2008). Dealing with drought: The challenge of using water system technologies to break dryland poverty traps. Glob. Environ. Change *18*, 607–616.
32. Allison, E.H., and Ellis, F. (2001). The livelihoods approach and management of small-scale fisheries. Marine Policy *25*, 377–388.
33. McClanahan, T.R., Polunin, N.V.C., and Done, T. (2002). Ecological states and the resilience of coral reefs. Conservation Ecology *6*, 18.
34. Gelcich, S., Kaiser, M.J., Castilla, J.C., and Edwards-Jones, G. (2008). Engagement in co-management of marine benthic resources influences environmental perceptions of artisanal fishers. Environ. Conserv. *35*, 36–45.
35. Berkes, F., Hughes, T.P., Steneck, R.S., Wilson, J., Bellwood, D.R., Crona, B.I., Folke, C., Gunderson, L.H., Leslie, H.M., Norberg, J., et al. (2006). Globalization, roving bandits, and marine resources. Science *311*, 1557–1558.
36. Russ, G.R., Cheal, A.J., Dolman, A.M., Emslie, M.J., Evans, R.D., Miller, I., Sweatman, H., and Williamson, D.H. (2008). Rapid increase in fish numbers follows creation of world's largest marine reserve network. Curr. Biol. *18*, R514–R515.
37. Wells, S., Burgess, N., and Ngusaru, A. (2007). Towards the 2012 marine protected area targets in Eastern Africa. Ocean & Coastal Management *50*, 67–83.
38. Pollnac, R.B. (1998). Rapid Assessment of Management Parameters for Coral Reefs (Narragansett, RI: University of Rhode Island, Coastal Resources Center).
39. Henry, G. (1990). Practical Sampling (Newbury Park, CA: Sage Publications).
40. Cinner, J. (2007). The role of taboos in conserving coastal resources in Madagascar. SPC Traditional Marine Resource Management and Knowledge Information Bulletin. *22*, 15–23.
41. Jennings, S., Grandcourt, E.M., and Polunin, N.V.C. (1995). The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. Coral Reefs *14*, 225–235.
42. McClanahan, T.R., Graham, N.A.J., Maina, J., Chabanet, P., Bruggemann, J.H., and Polunin, N.V.C. (2007). Influence of instantaneous variation on estimates of coral reef fish populations and communities. Mar. Ecol. Prog. Ser. *340*, 221–234.

43. McClanahan, T.R. (1994). Kenyan coral reef lagoon fish: Effects of fishing, substrate complexity, and sea urchins. Coral Reefs *13*, 231–241.
44. Samoilys, M.A., and Carlos, G. (2000). Determining methods of underwater visual census for estimating the abundance of coral reef fishes. Environ. Biol. Fishes *57*, 289–304.
45. Froese, R., and Pauly, D. (2008). FishBase (http://www.fishbase.org).
46. Jennings, S., Boulle, D.P., and Polunin, N.V.C. (1996). Habitat correlates of the distribution and biomass of Seychelles reef fishes. Environ. Biol. Fishes *46*, 15–25.
47. Friedlander, A.M., and Parrish, J.D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J. Exp. Mar. Biol. Ecol. *224*, 1–30.
48. Burnham, K.P., and Anderson, D.R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (New York: Springer), 488 pp.