

## Environmental variability indicates a climate-adaptive center under threat in northern Mozambique coral reefs

TIMOTHY R. McCLANAHAN<sup>1,2,†</sup> AND NYAWIRA A. MUTHIGA<sup>1,2</sup>

<sup>1</sup>The Wildlife Conservation Society, Marine Programs, Bronx, New York 10460 USA

<sup>2</sup>The Wildlife Conservation Society, Marine Programs, P.O. Box 99470, Mombasa, Kenya

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**Abstract.** A priority for modern conservation is finding and managing regions with environmental and biodiversity portfolio characteristics that will promote adaptation and the persistence of species during times of rapid climate change. The latitudinal edges of high-diversity biomes are likely to provide a mixture of environmental gradients and biological diversity that meet the portfolio criteria needed for adaptive systems. Northern Mozambique and the Quirimbas Islands represent the edge of a coral reef diversity center with limited potential to expand because of geologic and oceanographic limits on the southern edges. This region does, however, have the potential to be its own discrete adaptive center if it contains climate refugia and there are environmental gradients that promote acclimatization, ecological reorganization, and natural selection. Consequently, to evaluate this potential we tested for strong regional environmental spatial heterogeneity that might indicate a climate-adaptive center. Additionally, we evaluated human influences and environmental and demographic data on finfish, coral, and sea urchins in 66 reefs across  $\sim 4^\circ$  of latitude to evaluate ecological changes and human threats. A number of clear gradients in environmental and human influences were observed. For example, temperature increased and became more centralized and right-skewed, while water quality decreased to the south. Coral communities susceptible to thermal stress were found in the north where dispersed temperatures indicated a location with either tolerance to or refugium from recent thermal disturbances. Nevertheless, high coral diversity was found in southern deep-water channels. Further, spatial patterns for corals and fish differed indicating complex geographic-fishing-biodiversity gradients. Consequently, environmental conditions for an adaptive portfolio exist and include refugia for preserving climate-sensitive and for numbers of coral taxa. Fishing and urban threats were observable as reduced fish biomass, diversity, and body sizes but higher biomass of sea urchins. We observed that many remote and protected areas had fish biomass values lower than expected or near maximum sustainable yields. This indicates low compliance and widespread migratory fishing, which is reducing fish diversity below maximum levels. Recommendations to sustain this adaptive center are to maintain fish biomass  $>500$  kg/ha by increasing fisheries restrictions and compliance.

**Key words:** Africa; climate refugia; environmental gradients; fishing impacts; latitudinal limits.

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† **E-mail:** tmccclanahan@wcs.org

### INTRODUCTION

Climate disturbances and human use are major ecological forces that are potentially threatening coral reef diversity and ecological

services (Hughes et al. 2003, Hoegh-Guldberg et al. 2007, McClanahan and Muthiga 2016a). Rapid climate change is diminishing viable reef-building coral communities and prompting the necessity to identify and increase management

effectiveness (Pandolfi 2015). Priority locations include regions with low historical and projected environmental extremes (Maina et al. 2008, 2011, Cacciapaglia and van Woesik 2015, Heron et al. 2016) but also areas with moderate environmental variation that create conditions for adaptation to these extremes (McClanahan et al. 2007a, 2012, 2015a, Oliver and Palumbi 2011). Consequently, persistence into the future requires planning for uncertainty and ecological–evolutionary processes of acclimatization, community change, and genetic adaptation (Hughes et al. 2003, Pandolfi 2015). Recognition of uncertainty and adaptation has prompted an adaptive portfolio approach where priorities for conservation are locations with environmental heterogeneity that promote local adaptation (Heller and Zavaleta 2009, Dawson et al. 2011, Webster et al. 2017). Conservation science priorities for climate adaptation strategies are to identify these locations, their environmental conditions, and managing threats.

The western Indian Ocean (WIO) is a peak-diversity biogeographic region within the Indian Ocean and the larger Indo-Pacific province (Connolly et al. 2003, Obura 2012, Hoareau et al. 2013, Parravicini et al. 2013, Borsa et al. 2016). Within the WIO, the northern Mozambique Channel has a number of smaller diversity peaks including the southern Tanzania–northern Mozambique region (McClanahan 2015, Ateweberhan and McClanahan 2016). Coral reefs in this region are located on the southern edge of carbonate-forming reefs that extend along the eastern tropical coastline of Africa. While there are some smaller carbonate-forming reefs south in Bazaruto, the Premerio and Segundo Islands, and Inhaca, they are small, offshore, not continuous, and low-diversity (Perry 2003, McClanahan 2015). This limit to reef building and associated diversity appears to be set by geologic and oceanographic conditions south of the Quirimbas Islands. Consequently, being at the terminal end of the African reef-building biome, there is limited potential for the reefs to expand in a warming climate. Nevertheless, terminal reefs may have the environmental heterogeneity and portfolio attributes required for a climate-adaptive center (Pandolfi and Keesling 2014). If so, and if human threats can be managed, these reefs are a global priority for area-based protective management.

Here, we evaluate the environmental conditions and gradients at the end of this reef-building terminus and the human influences that are likely to threaten their potential to adapt to climate change. Our hypothesis was that this region has strong environmental gradients that reflect a mixture of stable refugia and high environmental variability. The coral reef community attributes should reflect this variability by a gradient or complexities in communities over a relatively short geographic distance (i.e., ~400 km). Specifically, corals in stable thermal conditions would be composed of temperature-sensitive and diverse coral taxa and communities. Fishing impacts would be reflected in lower fish biomass, diversity, and fast life history attributes of the fish communities as well as greater abundance of key prey, such as sea urchins (McClanahan 2015). The region was evaluated within the larger context of a geographic urban-to-rural human and environmental gradients expected to influence reef diversity and ecology. The goals were to determine (1) the major ecological structuring forces along the human and environmental gradients that would indicate status and (2) whether this region fits criteria of a climate-adaptive location.

## METHODS

### Study sites

Ecological surveys were undertaken in 66 reefs between 2008 and 2015 ranging from reefs near urban areas including Nacala and Pemba cities in the south to the remote Tekomaji Island in the north (Fig. 1). Some sites were sampled more than once, giving a total of 96 site × time replications. The sampled reefs ranged in depth from 1 to 20 m and were typical carbonate reef locations. Each site was described in terms of its management, depth, habitat, distance from shore and nearest large markets, surrounding population density, and the environmental exposure variables derived from satellite readings. To evaluate discrete social–ecological locations, reefs were pooled into three large geographic categories; these were the urban reefs near the cities of Nacala and Pemba, reefs within the Quirimbas National Park boundaries (QNP), and northern Quirimbas Island reefs around Vamizi Island, referred to as non-QNP reefs. The urban areas represent areas with high fishing effort and no regulated gear or

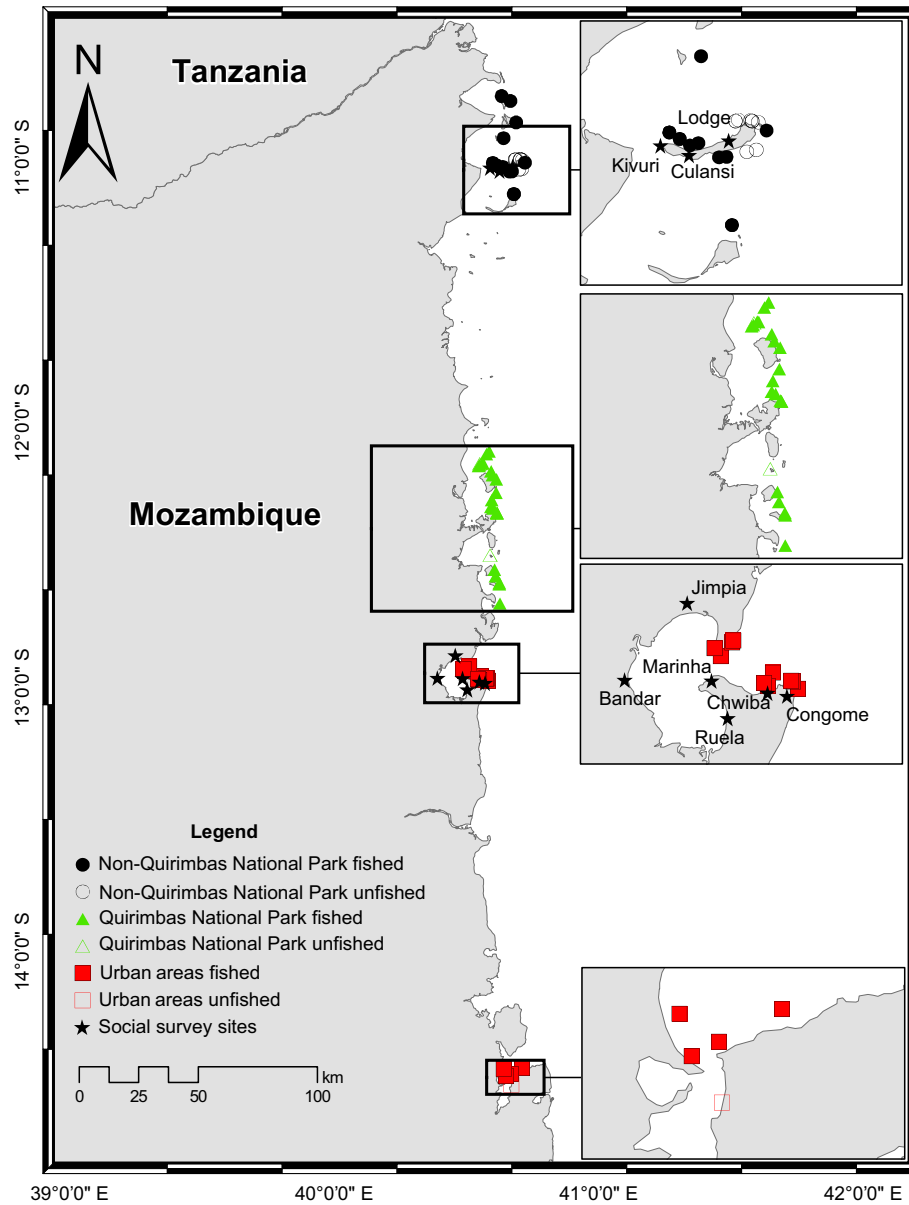


Fig. 1. Map of the study area showing the location of ecological field sampling sites and the three social-ecological locations, including the Quirimbas National Park (QNP), remote non-QNP in the north, and urban areas in the south.

closures. The QNP is a national park but is populated by people living on the islands that have trade connections to the mainland and cities. World Wildlife Fund for Nature managed QNP in partnership with the Mozambique government from 2002 to 2010. The government conservation agency subsequently took over QNP's management with efforts to manage at the community

level and zoning but lacked strong participation or enforcement during this study period (Gill et al. 2017). Non-QNP reefs are remote and include a private interest-community (Friends of Vamizi Trust and the Vamizi Island community) closure arrangement on the northeastern end of Vamizi Island and restrictive gear management around the closure. Reefs fringing the islands near

Vamizi are remote, mostly accessed by migratory fishers, and not regulated in terms of gear management or closures.

**Research design**

Sampling and statistical analyses evaluated spatial gradients of environmental data at 4 km<sup>2</sup> resolution, human influences based on distance to population or market centers, three discrete environmental-management locations, and four levels of fisheries management restrictions. Analysis of these gradients and discrete locations and management groupings was expected to uncover the ecological conditions, adaptive potential, and threats in this region. The management designations were not evenly distributed among the three environmental-management locations, which precluded the use of a two-way interaction statistical design.

*Environmental influences.*—Environmental gradients were obtained from satellite-derived temperature, light, and water quality data available from the U.S. National Oceanographic Atmospheric Administration and the European Space Agency. U.S. National Oceanographic Atmospheric Administration data are from the CoRTAD environmental satellite database (<http://www.nodc.noaa.gov/sog/cortad/>), which contains sea-surface temperature collected weekly at 4 km resolution from 1982. Light and water quality variables (chlorophyll-*a* and total suspended solids concentration) were obtained from the European Space Agency’s COASTCOLOUR project (<http://www.coastcolour.org/>). Temperature-derived variables were aggregated for the period 1982–2012 into thermal stress anomaly (TSA), weekly thermal stress anomaly (WSSTA), frequency of TSA and WSSTA, and median, standard deviation, kurtosis, and skewness of the temperature time series. Maina et al. (2011) developed a climate exposure and composite stress model to estimate the combined impacts of these environmental variables on hard corals. Models are based on weighted effects of each environmental variable on reports of coral bleaching and have been successfully used to evaluate coral communities’ responses to environmental stress in the WIO (McClanahan et al. 2015a). The exposure model includes environmental variables that contribute to thermal stress (i.e., water temperature and light), while the composite stress model

includes attenuating factors, such as water movement and quality. A full description of each of these variables, how they were calculated, and those included in the model is given in Maina et al. (2011).

*Demographic influences.*—A Human Influence metric was developed based on human population density and distance to nearest markets (Brewer et al. 2013). Population data were derived from the Euclidean distance of sites to the nearest town, and the populations of the town were added for each record. We used population data from the Gridded Population of the World database (<http://sedac.ciesin.columbia.edu/plue/cenguide.html>). Human Influence was calculated using Brewer et al.’s (2013) modified formula:

$$\text{Human Influence} = \log \left( \frac{1 + \text{human population count at market}}{(1 + \text{distance from market to the reef})^2} \right).$$

*Social–ecological locations and management restrictions.*—Comparisons of the southerly located urban reefs, centrally located QNP reefs, and northerly located non-QNP reefs were undertaken to evaluate three distinct social–ecological systems. This evaluation was expected to uncover some of the impacts or subregional heterogeneity in resource use, impacts, and threats in this region.

Fisheries closure and gear restriction management were evaluated to further determine the influence of reefs along the environmental and human influence gradients and evaluate the extent of the threats. Management classification included two basic gear use restrictions, none and some gear restrictions; and two levels of fisheries closure compliance, low and high (McClanahan et al. 2015b). The low and high compliance classifications were based on observations at the sites and discussions with knowledgeable stakeholders. For example, if abandoned line and trap gear were seen on the bottom or if fishers were seen fishing in the closure, the reef was classified as low compliance. This classification applied to each study site regardless of the stated or legal status of the sites. For example, observations in the private-community closure at Vamizi indicated the northern side was a high and the southern side a low-compliance closure because fishing

was occasionally observed in the south but never in the north. The combination of the spatial gradients, social–ecological units, and management classifications formed the basis for statistical analyses.

**Ecological field methods**

We estimated numbers of fish and sea urchin species and biomass, benthic cover, and coral taxa abundance and susceptibility to thermal stress.

*Fish biomass and life histories.*—The biomasses of fish functional groups were estimated using underwater visual census of the numbers and sizes of fish in 23 fish families observed within replicate 5 × 100 m belt transects (McClanahan et al. 2007c). Individual fish were identified to the family and their total lengths estimated and placed into 10-cm size interval classes. Fish families included the Acanthuridae, Aulostomidae, Balistidae, Carangidae, Chaetodontidae, Diodontidae, Fistularidae, Haemulidae, Holocentridae, Labridae, Lethrinidae, Lutjanidae, Muraenidae, Mullidae, Pempheridae, Pinguipedidae, Pomacanthidae, Pomacentridae, Scaridae, Serranidae, Scorpaenidae, Siganidae, and Sphyrnaeidae and an “others” category for individuals not in these families. The midpoint of the fish size classes was used to estimate the wet mass of each size class based on established length–weight relationships for each family and summed across all size classes to get a family wet weight estimate (McClanahan and Kaunda-Arara 1996). Length–weight relationships were obtained from common species pooled and averaged at the family level. The sum of all size classes and families was used to estimate the total wet mass, and values were converted to a per-hectare unit for comparison with other field studies. The fishable biomass is a useful measure of the state of the reef fisheries and is estimated by removing damselfish and all fish <10 cm in body size.

Life history metrics have proved to be useful way to evaluate the status of reef fishes (McClanahan and Humphries 2012, Taylor et al. 2014, McClanahan et al. 2015b) and may be more sensitive to fishing than fish biomass (McClanahan and Graham 2015). Fish community-level life history characteristics of the families were compiled using life history data available in FishBase (www.fishbase.org). The life history parameters

included were maximum length (cm), growth rate (cm/yr), 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), and trophic level. We extracted the values from the dominant species we counted in transects and used the averages of these in our family-level evaluations (McClanahan and Humphries 2012). Values of community life histories are weighted such that the mean value for a site was calculated as the biomass of each family group times the mean life history metric for the specific metric, summed for all families, and divided by the total biomass.

*Coral community.*—The coral reef communities were evaluated by an observer who counted corals in ~15–20 haphazardly chosen 2-m<sup>2</sup> quadrats at each site (McClanahan et al. 2007a). Benthic cover was based on visual estimates of hard and soft coral, and erect fleshy algae estimated to the nearest 5%. Hard corals in the quadrats were further identified to the genus with the exceptions that *Porites* were separated into branching and massive forms and *Synarea*, and *Galaxea* were separated into *Galaxea fascicularis* and *Galaxea astreata*. These distinctions were made because these species or forms are associated with different life histories that are not distinguished by genus-level classification (Darling et al. 2012). The site-level percentage of hard and soft coral and erect algae cover, number of coral taxa per site, coral dominance/diversity (modified Simpson’s Index), and the coral community bleaching susceptibility index were metrics calculated from the replicate quadrats.

The community bleaching susceptibility index is based on a large database of observations of corals during the warm season and the degree to which they pale, bleach, and die (McClanahan et al. 2007a). The relative abundance of each taxon is multiplied by this metric of bleaching and averaged to obtain the community susceptibility index where higher numbers represent communities composed of taxa that bleach more during warm-water periods. This metric should represent a site’s history of thermal stress, the time since a stress, or resistance to stress.

*Sea urchin community.*—Sea urchin numbers and biomass were estimated in each site by haphazardly tossing a weighted marked rope, using the rope as the radius of a 10-m<sup>2</sup> plot, and



identifying sea urchins to the species and counting their numbers within this circular plot. The species-specific density was multiplied by a mean body weight estimated from field measurements and summed across all taxa to calculate total sea urchin biomass (McClanahan 1998).

**Statistical analyses**

Relationships between environmental variables were explored first with correlation matrices and then related to ecological variables using either stepwise least squares regression analyses or model fitting. The correlation analyses allowed us to examine and select the strongest environmental associations and identify potentially autocorrelated and redundant variables for further analysis. The strongly associated variables theorized to have causative relationships were plotted and examined in the model fit analyses. Comparisons of ecological data between the three social-ecological location and four management classifications were tested separately for difference using standard one-way treatment comparison statistics followed by post hoc comparisons of individual categories or treatments. ANOVA, Tukey, or Kruskal-Wallis tests were used based on whether or not the data fit parametric data assumptions. All statistics were performed using JMP statistical software (Sall et al. 2001) and SigmaPlot (Systat Software Inc., San Jose, California, USA).

**RESULTS**

**Geographic gradients**

*Environmental gradients.*—Despite the reefs being located along a fairly small latitudinal gradient between 10.5 and 14.5° S, there were clear gradients in the environmental variables (Fig. 2). Light intensity or radiation, maximum temperatures, and temperature anomalies increased to the south (Fig. 2a–c). Temperature increased consistently from 11.0 to 14.5° S of the equator, but radiation stabilized at ~13.0° S. There was also an increase in right skew and centralized temperature distributions (positive skewness and kurtosis) toward the south. Similarly, water quality metrics of chlorophyll-*a* and suspended solids concentrations increased to the south (Fig. 2d–g). Finally, the composite stress model that combines a number of these and other variables indicated increased stress for corals from 11.0 to 13.0° S

(Fig. 2h). Radiation, chlorophyll, suspended solids, and the stress model index increased but stabilized at ~13.0° S.

Evaluating relationships between environmental variables, coral cover, number of taxa, and community susceptibility using stepwise regression analyses found significant weak-to-modest associations for hard coral cover ( $R^2 = 0.16$ ) and susceptibility ( $R^2 = 0.29$ ) but not numbers of taxa (Table 1). While most single environmental variables were not significantly associated with the coral metrics, photosynthetic active radiation (PAR) was positively and median chlorophyll-*a* negatively associated with cover. The climate exposure model index was the single variable negatively associated with the coral community's susceptibility. Scatterplots of the relationships between the stress metric and the coral cover, number of taxa, and community susceptibility to bleaching indicate no relationship with cover, a weak positive correlation with number of genera, and a moderate negative relationship with susceptibility (Fig. 3).

*Demographic gradients.*—There were a number of weak statistically significant relationships between the Human Influence metric and key fish and coral variables (Fig. 4, Table 2). The total biomass of fish declined with human influence but showed notably high scatter at the low end of human influence with values ranging from ~250 to 1800 kg/ha. This produced a triangular shape response and a low fit to a linear model ( $r^2 = 0.14$ ). Biomasses rarely exceeded 500 kg/ha at moderate-to-high human influence. Numbers of fish species also declined linearly from ~50 to 40 species per 500 m<sup>2</sup> along this gradient with somewhat more consistency ( $r^2 = 0.24$ ). Coral cover and number of taxa both increased with the Human Influence metric, but there was also high variance around these best-fit models, explaining only 7% and 18% of the variance, respectively.

**Reef ecology and threats**

*Consumers.*—Comparisons in the reef consumers between the three regions (QNP, remote non-QNP, and urban) indicate statistically significant differences in fish biomass, numbers of fish species, and sea urchin biomass and diversity (Table 3). The highest total fish biomass was found in the non-QNP and QNP reefs at ~664 and

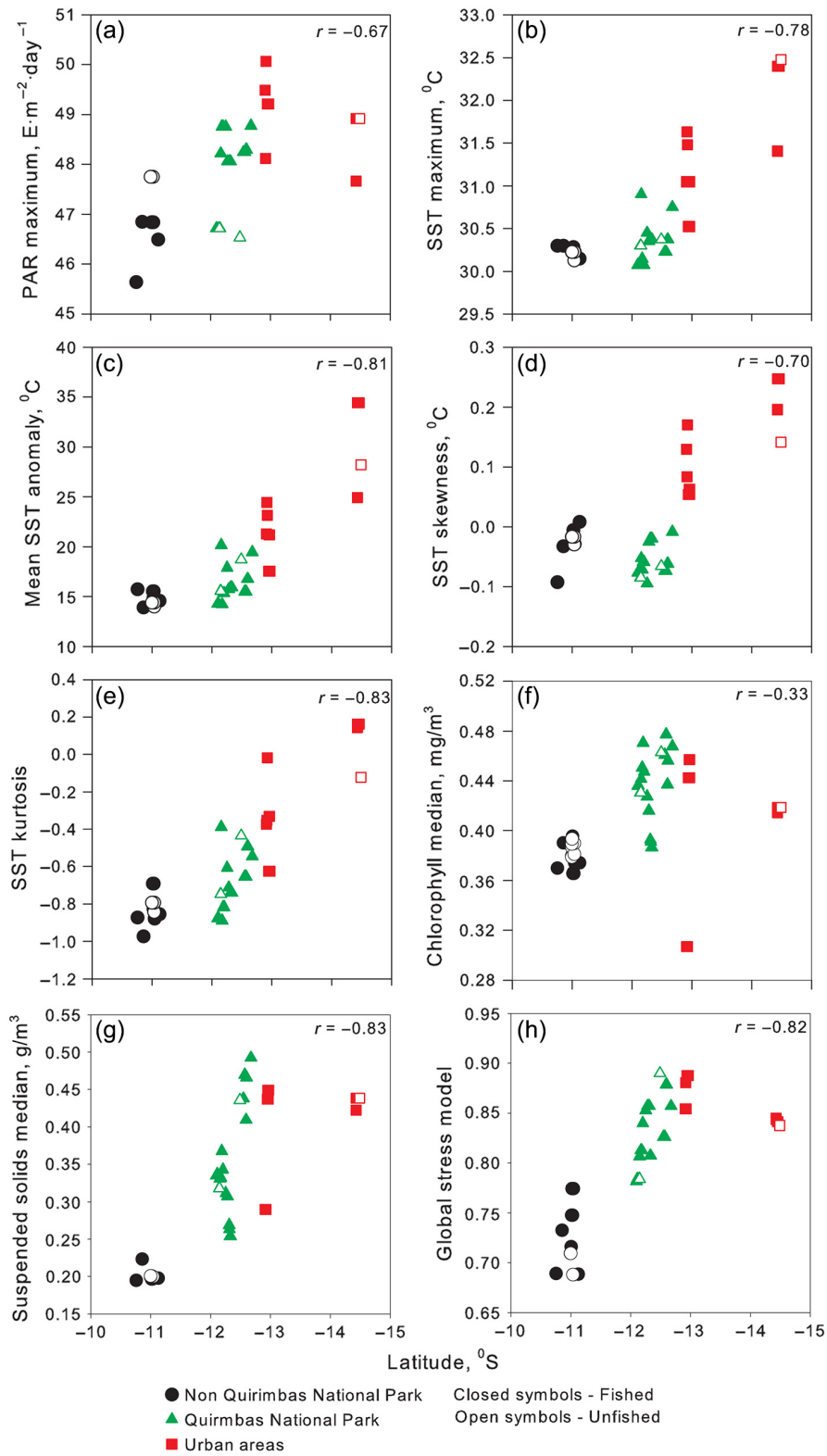


Fig. 2. Relationships between selected environmental variables and latitude.

Table 1. Relationships between environmental variables and (a) coral cover and (b) bleaching susceptibility from a forward stepwise linear regression analysis.

Parameter	Estimate	t Ratio	F ratio	Prob > F	R <sup>2</sup>	Whole model P
(a) Coral cover						
Intercept	-134.2 ± 68.4	-1.96	0	0.0542	0.16	0.0044
PAR maximum, E·m <sup>-2</sup> ·d <sup>-1</sup>	4.3 ± 1.4	3.00	9.00	0.004		
Chlorophyll median, mg/m <sup>3</sup>	-77.1 ± 35.5	-2.17	4.71	0.034		
SST kurtosis			1.09	NS		
SST minimum, °C			0.38	NS		
Composite stress model			0.35	NS		
Mean SST anomaly, °C			0.28	NS		
Climate exposure			0.14	NS		
Suspended solids median, g/m <sup>3</sup>			0.11	NS		
SST standard deviation, °C			0.07	NS		
SST skewness, °C			0.02	NS		
(b) Bleaching susceptibility						
Intercept	28.4 ± 2.2	12.76	0	<0.0001	0.29	<0.0001
Climate exposure	-16.7 ± 3.3	-5.02	25.21	<0.0001		
SST skewness, °C			1.76	NS		
Composite stress model			1.43	NS		
SST minimum, °C			1.05	NS		
PAR maximum, E m <sup>-2</sup> ·d <sup>-1</sup>			1.01	NS		
Suspended solids median, g/m <sup>3</sup>			0.87	NS		
Chlorophyll median, mg/m <sup>3</sup>			0.55	NS		
SST standard deviation, °C			0.28	NS		
SST kurtosis			0.01	NS		
Mean SST anomaly, °C			0	NS		

Notes: Variables not included were found to be strongly correlated ( $r > 0.85$ ) with those used here. No variable was found to be significant for the stepwise linear regression with number of coral taxa as the response variable. SST = sea surface temperature; PAR = photosynthetic active radiation.

613 kg/ha, respectively, while urban reefs had lower total and fishable biomass at ~360 kg/ha. Number of fish species was higher in Quirimbas than in the urban reefs by ~10 species per 500 m<sup>2</sup>. Sea urchin biomass was highest in urban areas but not statistically different from QNP reefs, due to high variation. Sea urchin diversity was lowest in non-QNP and QNP reefs compared to urban reefs.

Evaluating consumers by the reef’s fisheries management systems found statistical differences in the total and fishable biomass, numbers of fish and species, and sea urchin biomass (Table 4). With the exception of fishable biomass, which was highest in the high compliance closures at ~1000 kg/ha, there were no other differences in fish community metrics between the low and high compliance closure systems. Low compliance closures were also not different from fished reefs except the lowest numbers of individuals were found in reefs where gears were restricted. Reefs without gear restrictions had the

lowest numbers of fish species. Reefs with gear restrictions had more biomass and numbers of species, but fewer individuals than reefs with no gear restrictions. Sea urchin biomass was different between the management categories and showed lower values in the low and high compliance closures but, due to high variation, high compliance closures were not different from gear-restricted reefs. There were no differences in number of sea urchin individuals and diversity of sea urchins in the management categories.

*Fish community life histories.*—Community life history metrics were evaluated by social-ecological location and all metrics except generation time differed between locations. Many of these differences were due to differences between urban and Quirimbas reefs (Table 5). For example, the urban reefs had smaller community-level maximum body lengths, lengths at maturity, and length at optimal yield and higher natural mortality than both Quirimbas locations. Lifespan and generation time were marginally different



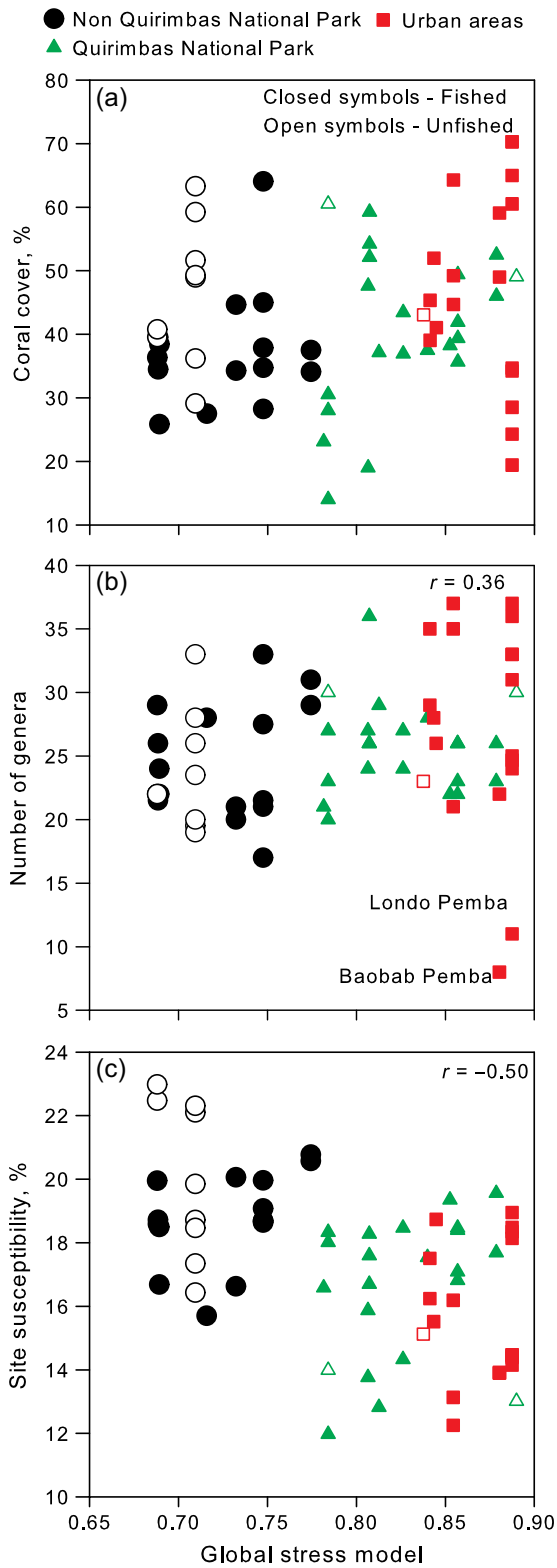


Fig. 3. Relationships between the composite stress

(Fig. 3. Continued)

model and hard coral (a) cover, (b) number of taxa, and (c) susceptibility to bleaching.

when comparing all locations, but there were no differences for pairwise comparisons. Trophic levels were higher in the QNP than in the non-QNP and urban reefs. Community growth rates were higher in urban than in QNP and non-QNP reefs.

Comparing community life histories by management categories found differences in the length and natural mortality metrics but not the other factors (Table 6). Body lengths were smallest in the reefs with no-gear restrictions, and maximum lengths were highest in the high compliance closures. Natural mortality was highest in the no-gear restricted management but not statistically different with low compliance closures or reefs where gears were restricted. The high compliance closure had the lowest natural mortality, but it was not statistically different from reefs with low closure compliance and destructive gears restricted.

Scatterplots between the fishable biomass and selected fish community diversity and life history metrics indicated a number of significant patterns (Fig. 5, Table 7). Number of species increased rapidly with biomass, saturating at ~55 species and 500 kg/ha. The best-fit curve was an asymptotic curve that suggested that biomass predicted 50% of the variation in the number of species. The length of capture for optimum yield also fit well to an asymptotic curve, and biomass predicted 52% of the variation. Optimum length increased rapidly from a low of ~22 cm and saturated at a high of 28.6 cm. Conversely, natural mortality declined from ~1.1 and saturated at ~0.85, but the best-fit equations predicted only 36% of the variation. Age at maturity indicated a highly variable ( $r^2 = 0.13$ ) linear and non-saturating increase along the full biomass sequence.

*Benthic cover.*—Coral cover (~45%) and numbers of taxa (~26 per sample) were high, and there were no statistically significant differences between locations (Table 3). Number of coral taxa was weakly positively correlated with coral cover, but there was no relationship between cover and coral community bleaching susceptibility (Fig. 6). Erect algae were also moderately high (~15%) and not different between locations,

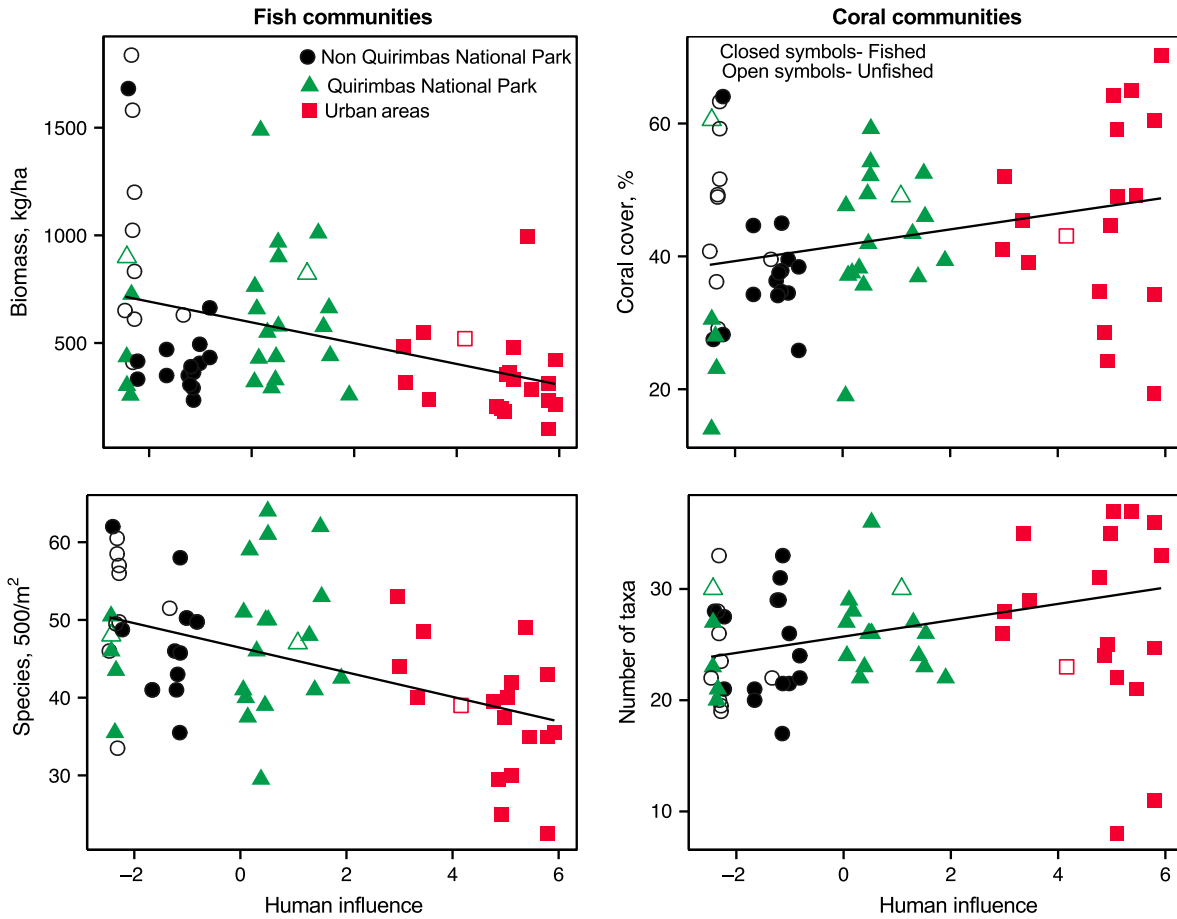


Fig. 4. Relationships between the Human Influence metric ( $=\log(1 + \text{human population count})/(1 + \text{distance from market to the reef})^2$ ) and key fish and coral variables. Best-fit equations are given in Table 2.

Table 2. Best-fit linear relationships between the Human Influence metric (population and distance to reef) and (a) total fish biomass, (b) number of fish species, (c) hard coral cover, and (d) number of coral taxa.

Term	Estimate	t Ratio	Prob >  t	R <sup>2</sup>	Prob > F
(a) Total fish biomass, kg/ha					
Intercept	595.8 ± 43.8	13.61	<0.0001	0.14	0.0017
Human influence	-48.3 ± 14.7	-3.28	0.0017		
(b) Fish species/500 m <sup>2</sup>					
Intercept	46.4 ± 1	44.5	<0.0001	0.24	<0.0001
Human influence	-1.6 ± 0.3	-4.51	<0.0001		
(c) Coral cover					
Intercept	41.7 ± 1.6	26.07	<0.0001	0.07	0.029
Human influence	1.2 ± 0.5	2.23	0.029		
(d) Number of taxa					
Intercept	25.7 ± 0.6	44.03	<0.0001	0.18	0.0006
Human influence	0.7 ± 0.2	3.62	0.0006		

Note: Data scatterplots of the relationships are shown in Fig. 4.

Table 3. One-way ANOVA tests of significance and post hoc pairwise tests for comparisons of measured parameters between the three social-ecological locations of the Quirimbas National Park (QNP), remote non-QNP, and urban areas.

Parameters	QNP, <i>n</i> = 23	Non-QNP, <i>n</i> = 24	Urban areas, <i>n</i> = 19	<i>F</i> ratio	Prob > <i>F</i>
<b>Consumers</b>					
Total fish biomass, kg/ha	AB 613.1 ± 63.6	A 664.9 ± 94.6	B 357.1 ± 45.5	4.54	0.01
Fishable biomass, kg/ha	A 546.5 ± 60.0	A 603.7 ± 92.6	B 252.7 ± 43.7	6.34	0.003
Fish species/500 m <sup>2</sup>	A 47.2 ± 1.8	A 48.9 ± 1.6	B 38.08 ± 1.8	10.36	0.0001
Fish individuals/500 m <sup>2</sup>	A 449.2 ± 64.0	A 496.0 ± 44.5	A 623.7 ± 89.5	1.77	NS
Sea urchin biomass, kg/ha	B 208.3 ± 101.6	AB 532.2 ± 245.2	A 1347.8 ± 444.4	4.21	0.02
Sea urchin numbers/10 m <sup>2</sup>	A 21.4 ± 6.0	A 15.9 ± 4.7	A 12.9 ± 3.6	0.76	NS
Urchin diversity, <i>D</i>	B 0.04 ± 0.03	AB 0.18 ± 0.05	A 0.23 ± 0.05	5.20	0.009
<b>Benthic cover</b>					
Hard coral, %	A 40.7 ± 2.7	A 40.9 ± 2.2	A 47.1 ± 3.5	1.64	NS
Number of coral genera	A 25.7 ± 0.8	A 24.4 ± 0.9	A 27.3 ± 1.9	1.45	NS
Bleaching index, %	A 0.13 ± 0.05	A 0.25 ± 0.09	A 0.47 ± 0.16	2.60	0.08
Site susceptibility, %	B 16.6 ± 0.5	A 19.2 ± 0.4	B 15.7 ± 0.5	17.07	0.0001
Coral species diversity, <i>D</i>	A 0.88 ± 0.01	B 0.75 ± 0.02	A 0.85 ± 0.02	15.34	0.0001
Macroalgae cover, %	A 14.3 ± 1.2	A 16.1 ± 2.6	A 15.2 ± 1.4	0.24	NS

Notes: There was no significant difference where values are preceded by the same letters. When metrics fit the assumptions of ANOVA, then the post hoc Tukey test was used; otherwise, Kruskal-Wallis and the post hoc pairwise Wilcoxon tests were used.

and there was a weak significant negative correlation between hard coral and erect algae cover ( $r = -0.12$ ,  $P < 0.05$ ). The percentage of corals that were bleached was low, and while there appeared to be a gradient of increase from Quirimbas Park to urban reefs, these differences were short of statistical significance ( $P < 0.08$ ). There were, however, differences in the community

bleaching susceptibility and diversity metrics with the non-QNP location having the highest susceptibility and no differences between the QNP and urban locations. Hard coral diversity or low dominance was highest in the park and urban locations compared to non-QNP reefs.

The cover, numbers of taxa, and bleaching indices of hard corals as well as macroalgae

Table 4. One-way ANOVA tests of significance and post hoc pairwise tests for comparisons of consumers and benthic cover between four fisheries management regimes of northern Mozambique.

Parameters	High compliance closure, <i>n</i> = 7	Low compliance and young closure, <i>n</i> = 5	Gear restricted, <i>n</i> = 40	No gears restricted, <i>n</i> = 14	<i>F</i> ratio	Prob > <i>F</i>
<b>Consumers</b>						
Total fish biomass, kg/ha	A 1070.8 ± 193.5	AB 704.4 ± 68.5	B 538.8 ± 51.1	C 305.3 ± 34.4	22.79	<0.0001
Fishable biomass, kg/ha	A 990.7 ± 186.5	AB 590.2 ± 52.7	B 480.9 ± 50.2	C 195.6 ± 31.8	30.47	<0.0001
Fish species/500 m <sup>2</sup>	A 52.1 ± 3.5	AB 46.3 ± 2.1	A 46.5 ± 1.3	B 37.5 ± 2.3	5.99	0.001
Fish individuals/500 m <sup>2</sup>	AB 607.7 ± 110.8	A 839.9 ± 173.3	B 417.4 ± 32.0	AB 632.6 ± 113.9	4.69	0.005
Sea urchin biomass, kg/ha	AB 76.0 ± 42.0	A 36.0 ± 36.0	B 428.5 ± 153.1	C 1609.0 ± 514.7	18.27	0.0004
Sea urchin numbers/10 m <sup>2</sup>	A 29.1 ± 16.6	A 3.0 ± 3.0	A 17.4 ± 3.8	A 15.5 ± 4.0	1.13	NS
Urchin species diversity	A 0.08 ± 0.07	A 0.09 ± 0.09	0.11 ± 0.03	A 0.25 ± 0.05	1.88	NS
<b>Benthic cover</b>						
Hard coral, %	A 48.2 ± 4.6	A 46.6 ± 3.9	41.5 ± 2.17	A 41.5 ± 3.3	0.73	NS
Number of coral genera	A 24.1 ± 2.0	A 25.4 ± 1.9	26.1 ± 0.8	A 25.4 ± 2.2	0.25	NS
Bleaching index, %	A 0.26 ± 0.13	A 0.08 ± 0.05	0.21 ± 0.06	A 0.54 ± 0.21	1.85	NS
Site susceptibility, %	A 19.32 ± 0.9	AB 17.51 ± 2.2	AB 17.5 ± 0.3	B 15.7 ± 0.6	3.79	0.015
Coral species diversity, <i>D</i>	B 0.72 ± 0.1	AB 0.77 ± 0.1	A 0.84 ± 0.01	A 0.84 ± 0.02	5.06	0.003
Macroalgae cover, %	A 8.6 ± 3.0	A 19.9 ± 5.1	15.2 ± 1.3	A 15.8 ± 2.1	1.74	NS

Note: There was no significant difference where values are preceded by the same letters.

Table 5. One-way ANOVA tests of significance and post hoc pairwise tests for comparisons of fishable biomass life histories between the three social-ecological locations Quirimbas National Park (QNP), remote non-QNP, and urban areas.

Parameter	QNP	Non-QNP	Urban areas	F ratio	Prob > F
Trophic level	A 3.09 ± 0.05	B 2.82 ± 0.05	AB 2.97 ± 0.04	8.95	0.0004
Maximum length, cm	A 43.1 ± 0.8	A 43.7 ± 0.5	B 39.4 ± 0.7	11.16	<0.0001
Length at maturity, cm	A 23.1 ± 0.4	A 23.1 ± 0.2	B 21.1 ± 0.3	11.65	<0.0001
Length at optimum yield, cm	A 25.6 ± 0.5	A 25.7 ± 0.3	B 23.2 ± 0.4	11.38	<0.0001
Growth rate, cm/yr	B 0.43 ± 0.01	AB 0.46 ± 0.01	A 0.47 ± 0.01	4.50	0.01
Natural mortality, M	B 0.91 ± 0.02	B 0.95 ± 0.01	A 1.02 ± 0.02	8.17	0.0007
Lifespan, yr	A 10.18 ± 0.15	A 9.73 ± 0.12	A 9.78 ± 0.15	3.21	0.05
Generation time, yr	A 3.14 ± 0.04	A 3.01 ± 0.03	A 3.06 ± 0.04	2.74	0.07
Age at maturity, yr	A 2.45 ± 0.03	B 2.35 ± 0.02	AB 2.39 ± 0.03	3.29	0.04

Note: There was no significant difference where values are preceded by the same letters in the post hoc Tukey test.

cover were not different for comparisons of fisheries management categories (Table 4). The coral site susceptibility to bleaching was, however, different and highest in the high compliance closures and lowest in the no-gear-restricted reefs. Coral diversity was, however, lowest in the high compliance closures.

DISCUSSION

*A portfolio for climate change adaptation?*

The northern Mozambique region contains reefs on the latitudinal edge of high diversity and exhibits strong gradients in environmental and demographic forces. As reported in other regions, these gradients can interact creating a complex mosaic of reef communities (Newman et al. 2006, Williams et al. 2008, 2015, Hughes et al. 2012, Houk et al. 2014). Some of the complex patterns resulted in weak univariate relationships and,

when comparing fish and corals, different geographic responses. For example, coral stress increased to the south, which was reflected in coral communities' susceptibility to bleaching (Fig. 3). Nevertheless, higher numbers of coral taxa were found in the deep-water shipping channels of the south. It is expected that these differences in depth provide thermal and light gradients and deep-water thermal stability that promote zonation and high numbers of coral taxa (Sheppard 1990). Variability in coral cover and taxa was high in reefs near urban areas indicating many influential factors. In the south, for example, higher solar radiation might explain higher coral cover, but chlorophyll-*a* concentrations were also higher and negatively associated with cover. Overall, there was no decline in coral cover or numbers of taxa with human-influenced environmental factors hypothesized to influence coral abundance and diversity (Smith et al. 2016).

Table 6. One-way ANOVA tests of significance and post hoc pairwise tests for comparisons of fishable biomass life histories between four fisheries management regimes.

Life histories	High compliance closure	Low compliance and young closure	Gear restricted	No gears restricted	F ratio	Prob > F
Trophic level	A 2.92 ± 0.12	A 3.05 ± 0.17	A 2.96 ± 0.04	A 2.93 ± 0.05	0.38	NS
Maximum length, cm	A 46.0 ± 0.8	AB 44.2 ± 0.8	B 42.5 ± 0.6	C 39.2 ± 0.6	8.73	<0.0001
Length at maturity, cm	A 24.2 ± 0.5	A 23.5 ± 0.7	A 22.6 ± 0.2	B 20.8 ± 0.4	9.72	<0.0001
Length at optimum yield, cm	A 27.1 ± 1.6	AB 26.3 ± 1.2	B 25.1 ± 2.1	C 22.9 ± 1.0	9.92	<0.0001
Growth rate, cm/yr	A 0.43 ± 0.01	A 0.43 ± 0.01	A 0.45 ± 0.01	A 0.47 ± 0.01	1.34	NS
Natural mortality, M	B 0.90 ± 0.02	AB 0.92 ± 0.03	AB 0.95 ± 0.02	A 1.03 ± 0.02	3.97	0.01
Lifespan, yr	A 10.16 ± 0.20	A 10.18 ± 0.26	A 9.89 ± 0.12	A 9.70 ± 0.15	1.04	NS
Generation time, yr	A 3.12 ± 0.06	A 3.15 ± 0.08	A 3.06 ± 0.03	A 3.04 ± 0.05	0.61	NS
Age at maturity, yr	A 2.43 ± 0.04	A 2.44 ± 0.06	A 2.39 ± 0.02	A 2.38 ± 0.04	0.41	NS

Note: There was no significant difference where values are preceded by the same letters in the post hoc Tukey test.

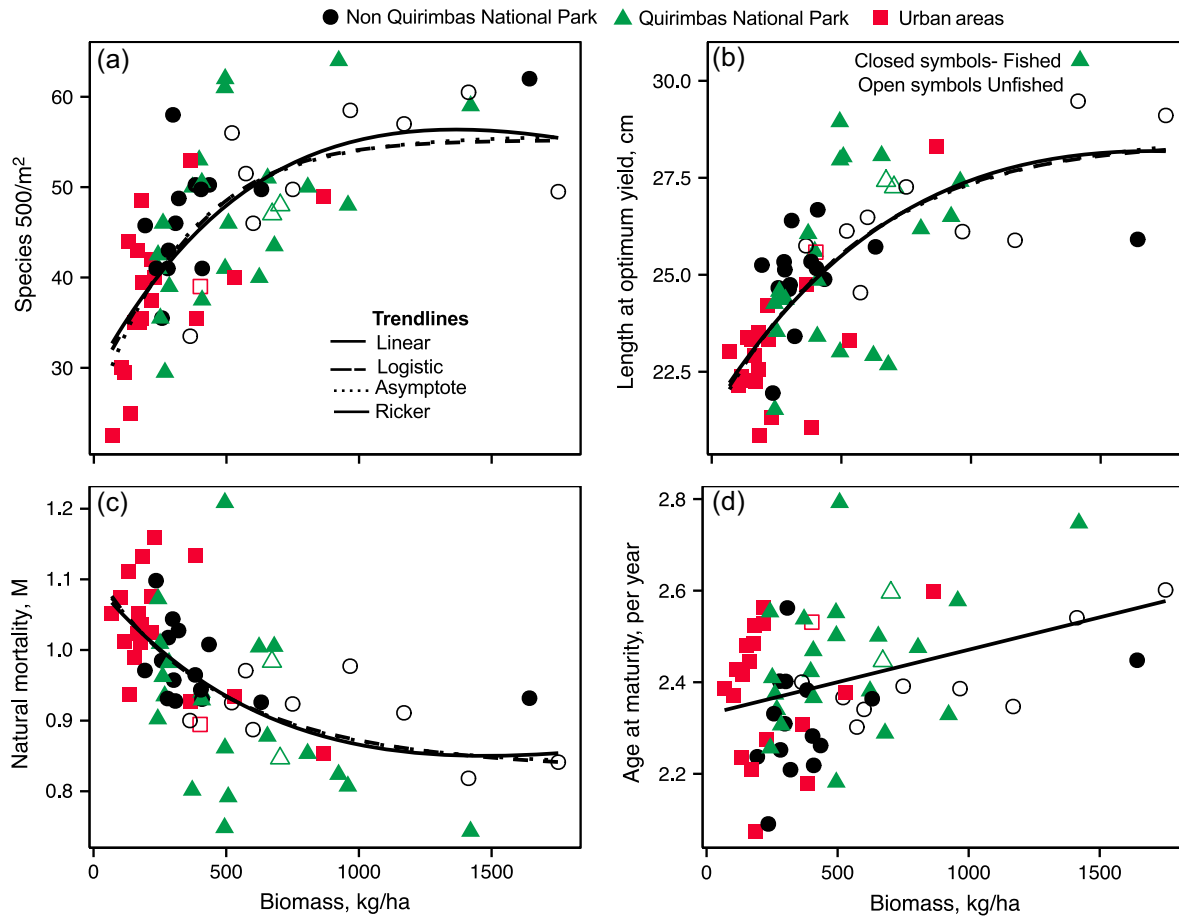


Fig. 5. Relationships between fishable biomass and community life-history characteristics of (a) number of species, (b) length at optimum yield, (c) natural mortality, and (d) age at maturity.

Consequently, coral communities were responding to a variety of environmental forces and refuge from stress as found in other regional surveys (Hughes et al. 2012).

Water depth associated with shipping channels increased the numbers of coral taxa in the south, while sea-surface thermal stability or lack of extreme temperatures appeared important for the persistence of sensitive taxa in the north. These two distinct environmental characteristics indicate two types of coral refugium in the same region. We suggest refugium for susceptible corals and diversity and the overall environmental heterogeneity combine to create an environmental portfolio that will promote adaptation and the persistence of species (McClanahan et al. 2015c, Webster et al. 2017).

The high-susceptibility corals located in the north indicate that sensitive taxa have persisted despite a larger number of thermal disturbances in the WIO region (McClanahan et al. 2014). The high coral diversity in these southern sites is among the highest reported in the WIO region (Obura 2012, Ateweberhan and McClanahan 2016). On the large WIO scale, thermal stress declines toward the south and the cover of sensitive taxa is also declining slower (McClanahan et al. 2011a, 2014). Consequently, we suggest that the convergence of these large-scale WIO and the smaller-scale Quirimbas patterns discovered here create the desired coral adaptation portfolio. The outcome will, however, depend on the second major source of impacts, namely fishing and the ability to successfully manage it (Gill et al. 2017).



Table 7. Statistical results of modeled relationships between biomass and (a) number of fish species, as well as fish life history characteristics, (b) length at optimum yield, (c) natural mortality, and (d) age at first maturity.

Model	Term	Estimate	t Value	Pr(> t )	AIC	P	R <sup>2</sup>
(a) Fish species, 500 m <sup>-2</sup>							
Asymptote	K	55.7 ± 2.88	19.32	<0.0001	435.08	<0.0001	0.50
	Bo	24.51 ± 5.13	4.78	<0.0001			
	R	0.003 ± 0.001	2.99	0.004			
Ricker	Bo	29.16 ± 3.05	9.57	<0.0001	436.38	<0.0001	0.49
	A	0.05 ± 0.01	3.83	<0.0001			
	B	0.001 ± 0.0002	4.69	<0.0001			
Logistic	K	55.21 ± 2.63	20.99	<0.0001	436.46	<0.0001	0.49
	Bo	28.4 ± 3.44	8.25	<0.0001			
	R	0.004 ± 0.001	3.29	0.002			
Linear	Intercept	37.44 ± 1.49	25.07	<0.0001	445.50	<0.0001	0.40
	Fishable biomass, kg/ha	0.02 ± 0.002	6.43	<0.0001			
(b) Length at optimum yield, cm							
Asymptote	K	28.64 ± 1.18	24.31	<0.0001	249.23	<0.0001	0.52
	Bo	21.21 ± 0.86	24.59	<0.0001			
	R	0.002 ± 0.001	2.47	0.02			
Logistic	K	28.45 ± 1.02	27.88	<0.0001	249.36	<0.0001	0.52
	Bo	21.38 ± 0.77	27.89	<0.0001			
	R	0.002 ± 0.001	2.85	0.006			
Ricker	Bo	21.51 ± 0.67	32.20	<0.0001	249.51	<0.0001	0.52
	A	0.01 ± 0.003	3.64	<0.0001			
	B	0.001 ± 0.0002	3.57	<0.0001			
Linear	Intercept	22.99 ± 0.33	69.06	<0.0001	255.19	<0.0001	0.46
	Fishable biomass, kg/ha	0.004 ± 0.001	7.32	<0.0001			
(c) Natural mortality, M							
Ricker	Bo	1.1 ± 0.04	31.27	<0.0001	-143.69	<0.0001	0.36
	A	-0.0005 ± 0.0002	-2.85	0.006			
	B	0.001 ± 0.0002	3.23	0.002			
Asymptote	K	0.84 ± 0.05	17.10	<0.0001	-143.68	<0.0001	0.36
	Bo	1.11 ± 0.05	23.08	<0.0001			
	R	0.002 ± 0.001	1.97	0.05			
Logistic	K	0.83 ± 0.06	14.58	<0.0001	-143.66	<0.0001	0.36
	Bo	1.12 ± 0.05	20.68	<0.0001			
	R	0.002 ± 0.001	1.65	NS			
Linear	Intercept	1.03 ± 0.02	61.53	<0.0001	-139.59	<0.0001	0.30
	Fishable biomass, kg/ha	-0.0001 ± 0.00003	-5.27	<0.0001			
(d) Age at maturity, yr <sup>-1</sup>							
Linear	Intercept	2.33 ± 0.03	86.08	<0.0001		0.002	0.13
	Fishable biomass, kg/ha	0.0001 ± 0.00004	3.16	0.002			

Notes: K is the carrying capacity or the maximum biomass, R is the rate at which the population approaches the carrying capacity, Bo is the initial population, A is the rate of increase, and B the rate of decline.

**Ecological influences, human impacts, and threats**

Some impacts and threats followed those expected by environmental stress, fishing, and fishing closures, while some responses were less easily attributed to these two gradients. A gradient in fish biomass was evident along the urban-to-rural demographic gradient (Table 3). Nevertheless, there was high variability, particularly at the lowest levels of our Human Influence metric. This variability can largely be attributed to the Vamizi

closure where the combination of remoteness and a fisheries closure produced high fish biomass. However, remote reefs without high compliance closures did not always have high biomass. For example, all non-closure areas throughout the region, many being remote and offshore, had biomass levels within a proposed sustainable fisheries window of 300–600 kg/ha (McClanahan et al. 2011b). Consequently, it is likely that some combination of local consumption, the vagility of

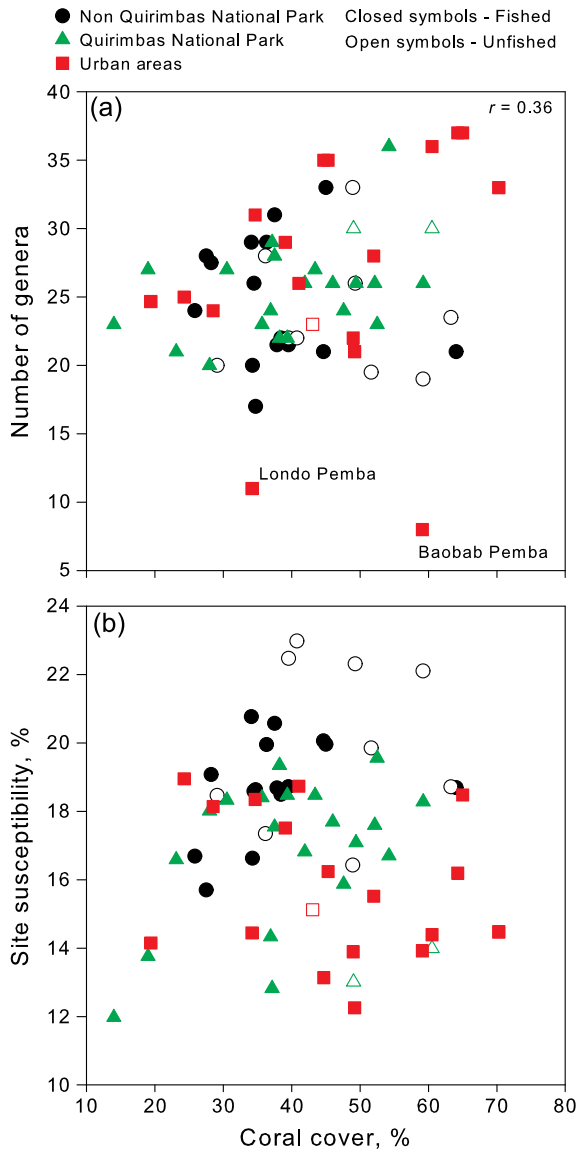


Fig. 6. Scatterplots showing the relationships between coral cover and (a) the number of coral taxa and (b) the site susceptibility.

migrant fishers, and market accessibility are reducing fish biomass over a large scale throughout the Quirimbas. Within the QNP, for example, 13 of the 23 studied reefs had fishable biomass levels within or below 600 kg/ha. We found that below a biomass of 500 kg/ha, the numbers of fish species declined. Consequently, many reefs in this park were probably exploited to maximum fisheries production levels, leading to losses of

species, change in fish life histories, and associated ecological functions.

Reduced biomass levels were associated with losses or replacement of large-bodied, slow-growing, and late-maturing with small-bodied, fast-growing, and early-maturing taxa. Here, we also found a better fit to biomass than the Human Influence metric for some life histories and numbers of species. This study further supports findings that reducing biomass changes life history composition and possibly reduces ecological functions (Hill et al. 2009, Brewer et al. 2013, D'agata et al. 2014, Advani et al. 2015, MacNeil et al. 2015, McClanahan et al. 2015b).

Biomass and human influences were strong predictors of numbers of fish species, which indicates a weaker role of other environmental factors. Global and regional studies report that geography and associated environmental factors play an important role in diversity (Connolly et al. 2003, Mora and Robertson 2005, Pellissier et al. 2014). And, in the Quirimbas region, the highest numbers of fish species were found in the north. Nevertheless, in the WIO and northern Mozambique, geography predicts a smaller percentage of the variance in species numbers than biomass (McClanahan 2015). The combination of geographic factors and remoteness suggests the Quirimbas has high numbers of fish species. Yet, many sites were likely to be losing this diversity, probably associated with reduced biomass via fishing impacts (Hill et al. 2009). Maintaining fish biomass above the 500- to 600-kg/ha recommendations is a primary way to maintain high fish diversity and associated ecological functions (McClanahan et al. 2015b).

The effects of management on fish biomass were present in the studied reefs. Total and fishable biomass were higher in the full and low compliance closures than in the reef where no gears were restricted (Table 4). However, the total area under full protective management was small. Only the Vamizi Community Reserve in the north met the criteria of a high compliance closure. Fishing or fishing gear was seen or reported in other closures or portions of them. Consequently, it is not surprising that total and fishable biomass were not significantly different between low compliance closure and reefs where destructive gears were restricted. Restrictions on gears resulted in twice the fish biomass compared to reefs with no gear

restrictions. Regardless, biomass was also close to the 500-kg/ha-biomass-diversity threshold. Given the very small total areas in closures, regardless of compliance level, and the lack of large areas with enforced gear restrictions, management effects were restricted to very few reefs. The influence of management is therefore limited on the larger scale. At the time of this study, most reefs were fished at or below sustainable biomass levels.

Evidence for trophic cascade effects caused by overfishing was present but not strong. Sea urchin biomass increased as restrictions declined, but the mean maximum values of ~1600 kg/ha were generally low compared to the larger region where values >2300 kg/ha were found in >65% of WIO reefs (McClanahan and Muthiga 2016b). Erect algae cover is usually found to be ~5% in the region, and therefore, the 15% cover found here suggests high algae and some evidence for weak competition with hard corals. Consequently, the ecological state of Quirimbas reefs reflects moderate levels of fishing and ecological impacts.

## CONCLUSIONS

Northern Mozambique Quirimbas reefs have a variety of refugia, environmental variability, and high diversity that give these reefs a high potential to adapt to rapid climate change. Our findings were, however, generally supportive of the lack of a strong negative impact of local human influences and management on coral communities—indicating climate disturbances were more important (Bruno and Selig 2007, Ateweberhan et al. 2011, McClanahan et al. 2015a, Ateweberhan and McClanahan 2016). Nevertheless, moderate fish biomass and low compliance with management indicate widespread fishing. Impacts were not just restricted to reefs close to human markets but influenced by the large number of migratory fishers that travel throughout the region and who supply fish to urban markets. Yields at the time of the study were likely to be close to maximum sustained yields with limited ability to increase without further ecological degradation and losses of fisheries value. A significant percent of the reefs were also below estimated maximum sustained yield levels. Effects of reduced fish diversity, their life histories, and increased sea urchin biomass were evident. At

the time of the study, fishing impacts were less than reported elsewhere in the WIO (McClanahan and Muthiga 2016a, b). Nevertheless, if this region is to provide adaptive potential to climate change, fishing at sustainable levels and maintaining reef fish biomass, life histories, and functions is a high priority.

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## LITERATURE CITED

- Advani, S., L. N. Rix, D. M. Aherne, M. A. Alwany, and D. M. Bailey. 2015. Distance from a fishing community explains fish abundance in a no-take zone with weak compliance. *PLoS ONE* 10:e0126098.
- Ateweberhan, M., and T. R. McClanahan. 2016. Partitioning scleractinian coral diversity across reef sites and regions in the western Indian Ocean. *Ecosphere* 7:e01243.
- Ateweberhan, M., T. R. McClanahan, N. A. J. Graham, and C. Sheppard. 2011. Episodic heterogeneous decline and recovery of coral cover in the western Indian Ocean. *Coral Reefs* 30:739–752.
- Borsa, P., J. D. Durand, W. J. Chen, N. Hubert, D. Muths, G. Mou-Tham, and M. Kulbicki. 2016. Comparative phylogeography of the western Indian Ocean reef fauna. *Acta Oecologica* 72:72–86.
- Brewer, T. D., J. E. Cinner, A. Green, and R. L. Pressey. 2013. Effects of human population density and proximity to markets on coral reef fishes vulnerable to extinction by fishing. *Conservation Biology* 27:443–452.
- Bruno, J. F., and E. R. Selig. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* 2:e711.
- Cacciapaglia, C., and R. van Woesik. 2015. Reef-coral refugia in a rapidly changing ocean. *Global Change Biology* 21:2272–2282.

- Connolly, S. R., D. R. Bellwood, and T. P. Hughes. 2003. Indo-Pacific biodiversity of coral reefs: deviations from a mid-domain model. *Ecology* 84: 2178–2190.
- D’agata, S., D. Mouillot, M. Kulbicki, S. Andrefouet, D. R. Bellwood, J. E. Cinner, P. F. Cowman, M. Kronen, S. Pinca, and L. Vigliola. 2014. Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. *Current Biology* 24:555–560.
- Darling, E. S., L. Alvarez-Filip, T. A. Oliver, T. R. McClanahan, and I. M. Cote. 2012. Evaluating life history strategies of reef corals from species traits. *Ecology Letters* 15:1378–1386.
- Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* 332:53–58.
- Gill, D. A., et al. 2017. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* 543:665–669.
- Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation* 142:14–32.
- Heron, S. F., J. A. Maynard, R. van Hooidonk, and M. C. Eakin. 2016. Stress of the world’s coral reefs 1985–2012. *Scientific Reports* 6:38402.
- Hill, N. A. O., J. Davidson, I. Silva, S. Mucave, L. Muaves, A. Guissamulo, A. Debney, and J. Garnier. 2009. Coral and reef fish in the northern Quirimbas Archipelago, Mozambique – A first assessment. *Western Indian Ocean Journal of Marine Science* 8:113–125.
- Hoareau, T. B., E. Boissin, G. Paulay, and J. H. Bruggemann. 2013. The southwestern Indian Ocean as a potential marine evolutionary hotspot: perspectives from comparative phylogeography of reef brittle-stars. *Journal of Biogeography* 40:2167–2179.
- Hoegh-Guldberg, O., et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.
- Houk, P., D. Benavente, J. Iguel, S. Johnson, and R. Okano. 2014. Coral reef disturbance and recovery dynamics differ across gradients of localized stressors in the Mariana Islands. *PLoS ONE* 9:e110068.
- Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschanowskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 2012. Assembly rules of reef corals are flexible along a steep climatic gradient. *Current Biology* 22:736–741.
- Hughes, T. P., et al. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933.
- MacNeil, M. A., N. A. J. Graham, J. E. Cinner, S. K. Wilson, I. D. Williams, J. Maina, S. Newman, A. M. Friedlander, S. D. Jupiter, and N. V. C. Polunin. 2015. Recovery potential of the world’s coral reef fishes. *Nature* 520:341–344.
- Maina, J., T. R. McClanahan, V. Venus, M. Ateweberhan, and J. Madin. 2011. Global gradients of coral exposure to environmental stresses and implications for local management. *PLoS ONE* 6:e23064.
- Maina, J., V. Venus, T. R. McClanahan, and M. Ateweberhan. 2008. Modelling susceptibility of coral reefs to environmental stress using remote sensing data and GIS models in the western Indian Ocean. *Ecological Modelling* 212:180–199.
- McClanahan, T. R. 1998. Predation and the distribution and abundance of tropical sea urchin populations. *Journal of Experimental Marine Biology and Ecology* 221:231–255.
- McClanahan, T. R. 2015. Biogeography versus resource management: How do they compare when prioritizing the management of coral reef fishes in the southwestern Indian Ocean? *Journal of Biogeography* 42:2414–2426.
- McClanahan, T. R., M. Ateweberhan, E. S. Darling, N. A. J. Graham, and N. A. Muthiga. 2014. Biogeography and change among regional coral communities across the western Indian Ocean. *PLoS ONE* 9:e93385.
- McClanahan, T. R., M. Ateweberhan, C. A. Muhando, J. Maina, and M. S. Mohammed. 2007a. Effects of climate and seawater temperature variation on coral bleaching and mortality. *Ecological Monographs* 77:503–525.
- McClanahan, T. R., M. Ateweberhan, C. R. Sebastian, N. A. J. Graham, S. K. Wilson, M. M. M. Guillaume, and J. H. Bruggemann. 2007b. Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Marine Ecology Progress Series* 337:1–13.
- McClanahan, T. R., and N. A. Graham. 2015. Marine reserve recovery rates towards a baseline are slower for reef fish community life histories than biomass. *Proceedings of the Royal Society of London B: Biological Sciences* 282:20151938.
- McClanahan, T. R., N. A. J. Graham, J. M. Calnan, and M. A. MacNeil. 2007c. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Applications* 17: 1055–1067.
- McClanahan, T. R., N. A. Graham, M. A. MacNeil, and J. E. Cinner. 2015b. Biomass-based targets and the management of multispecies coral reef fisheries. *Conservation Biology* 29:409–417.
- McClanahan, T. R., N. A. J. Graham, M. A. MacNeil, N. A. Muthiga, J. E. Cinner, J. H. Bruggemann, and S. K. Wilson. 2011b. Critical thresholds and tangible targets for ecosystem-based management of



- coral reef fisheries. *Proceedings of the National Academy of Sciences USA* 108:17230–17233.
- McClanahan, T. R., and A. Humphries. 2012. Differential and slow life-histories responses of fishes to coral reef closures. *Marine Ecology Progress Series* 469:121–131.
- McClanahan, T. R., and B. Kaunda-Arara. 1996. Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conservation Biology* 10:1187–1199.
- McClanahan, T. R., J. Maina, and M. Ateweberhan. 2015a. Regional coral responses to climate disturbances and warming is predicted by multivariate stress model and not temperature threshold metrics. *Climatic Change* 131:607–620.
- McClanahan, T. R., J. M. Maina, and N. A. Muthiga. 2011a. Associations between climate stress and coral reef diversity in the western Indian Ocean. *Global Change Biology* 17:2023–2032.
- McClanahan, T. R., and N. A. Muthiga. 2016a. Geographic extent and variation of a coral reef trophic cascade. *Ecology* 97:1862–1872.
- McClanahan, T. R., and N. A. Muthiga. 2016b. Similar impacts of fishing and environmental stress on calcifying organisms in Indian Ocean coral reefs. *Marine Ecology Progress Series* 560:87–103.
- McClanahan, T. R., C. J. Starger, and A. C. Baker. 2015c. Decadal changes in common reef coral populations and their associations with algal symbionts (*Symbiodinium* spp.). *Marine Ecology* 36:1215–1229.
- McClanahan, T. R., et al. 2012. Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLoS ONE* 7:e42884.
- Mora, C., and D. R. Robertson. 2005. Causes of latitudinal gradients in species richness: a test with fishes of the Tropical Eastern Pacific. *Ecology* 86:1771–1782.
- Newman, M. J. H., G. A. Paredes, E. Sala, and J. B. C. Jackson. 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecology Letters* 9:1216–1227.
- Obura, D. 2012. The diversity and biogeography of western Indian Ocean reef-building corals. *PLoS ONE* 7:e45013.
- Oliver, T. A., and S. R. Palumbi. 2011. Do fluctuating temperature environments elevate coral thermal tolerance? *Coral Reefs* 30:429–440.
- Pandolfi, J. M. 2015. Incorporating uncertainty in predicting the future response of coral reefs to climate change. *Annual Review of Ecology, Evolution, and Systematics* 48:281–303.
- Pandolfi, J. M., and W. Kiessling. 2014. Gaining insights from past reefs to inform understanding of coral reef response to global climate change. *Current Opinion in Environmental Sustainability* 7:52–58.
- Parravicini, V., M. Kulbicki, D. R. Bellwood, A. M. Friedlander, J. E. Arias-Gonzalez, P. Chabanet, S. R. Floeter, R. Myers, L. Vigliola, and S. D’Agata. 2013. Global patterns and predictors of tropical reef fish species richness. *Ecography* 36:1254–1262.
- Pellissier, L., F. Leprieur, V. Parravicini, P. F. Cowman, M. Kulbicki, G. Litsios, S. M. Olsen, M. S. Wisz, D. R. Bellwood, and D. Mouillot. 2014. Quaternary coral reef refugia preserved fish diversity. *Science* 344:1016–1019.
- Perry, C. T. 2003. Coral reefs in a high-latitude, siliciclastic barrier island setting: reef framework and sediment production at Inhaca Island, southern Mozambique. *Coral Reefs* 22:485–497.
- Sall, J., A. Lehmaan, and L. Creighton. 2001. JMP start statistics. Thomson Learning, Duxbury, Massachusetts, USA.
- Sheppard, C. R. C. 1990. Coral cover, zonation and diversity on reef slopes of Chagos atolls, and population structures of the major species. *Marine Ecology Progress Series* 2:193–205.
- Smith, J. E., et al. 2016. Re-evaluating the health of coral reef communities: baselines and evidence for human impacts across the central Pacific. *Proceedings of the Royal Society of London B: Biological Sciences* 283:e20151985.
- Taylor, B. M., P. Houk, G. R. Russ, and J. H. Choat. 2014. Life histories predict vulnerability to over-exploitation in parrotfishes. *Coral Reefs* 33: 869–878.
- Webster, M. S., M. A. Colton, E. S. Darling, J. Armstrong, M. L. Pinsky, N. Knowlton, and D. E. Schindler. 2017. Who should pick the winners of climate change? *Trends in Ecology and Evolution*. <https://doi.org/10.1016/j.tree.2016.1012.1007>
- Williams, I. D., J. K. Baum, A. Heenan, K. M. Hanson, M. O. Nadon, and R. E. Brainard. 2015. Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS ONE* 10:e0120516.
- Williams, I. D., W. J. Walsh, R. E. Schroeder, A. M. Friedlander, B. L. Richards, and K. A. Stamoulis. 2008. Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. *Environmental Conservation* 35:261–272.