Impact of climate change and adaptation strategy for the coral reefs of Quirimbas National Park

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Lionfish at Quilalea reef Photo © T. R. McClanahan/WCS

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Status and adaptation strategy for the coral reefs of Northern Mozambique and Quirimbas National Park

Report to WWF - Mozambique

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Executive Summary

Introduction

This report presents the findings of a study of the reefs of the Quirimbas national park (QNP) aimed at evaluating the ecological status of the reefs, anthropogenic and climate impacts and recommendations for management.

Methods

The status of the Quirimbas National Park coral reef habits was evaluated from the 27th June to 7th July based on assessments of the benthic substrate, coral community assemblage, the finfish and sea urchin community and the environmental characteristics of the reefs. The benthic substrate and coral taxa surveys consisted of recording benthic cover in quadrates and the coral genera and bleaching level of each colony of hard coral within the quadrate. Fish surveys consisted of visual counts of fish along belt transects within the major fish families. Surveys were undertaken using SCUBA or snorkel depending on the depth and at each site, physical data including depth, exposure and the GPS position were recorded. The sites were also classified into management categories that included two basic gear use restrictions, none and some gear restrictions, and two levels of closure compliance, low and high. The results were compared with data from previous surveys that were carried out from Nacala south to Pemba north from 2008 to 2014 in order to get a more comprehensive understanding of the climate impacts and human pressures of the larger Quirimbas area.

Summary of key findings

Finfish and fishable biomass: The average biomass of reef fish in the QNP was ~ 700 kg/ha (range 260 kg/ha to 1490 kg/ha). The biomass was highest at Matemo, Dogtooth and Lighthouse (1488 kg/ha, 1011 kg/ha, 968 kg/ha respectively). The fishable biomass averaged 633 kg/ha (range 270 kg/ha – 1420kg/ha) the same sites also had the highest fishable biomass of reef fish (1420 kg/ha, 958 kg/ha, 920 kg/ha respectively). Studies in the WIO have shown that fishable biomass of reef fish below 300kg/ha show rapid changes leading to phase shifts to highly degraded states, between 300 – 600kg/ha confer some resilience and reduce the chances of deleterious phase shifts while fishable biomass above 600kg/ha maintain ecological integrity and potential resilience to climate change. Reefs at Rolas E, Luju and Pachamba had fishable biomass below 300kg/ha; sites at Buntings and Coliseum had ~400 – 500 kg/ha while Rolas W, Quilelea, Lighthouse (1 and 2), Dogtooth and Matemo had fishable biomass of 600 – 1400kg/ha. The Matemo site had fishable biomass that was above 1200kg/ha the pristine biomass level for the WIO. More than two thirds of the reefs are being exploited at a level showing loss of species especially of the large bodied fish species.

Comparison between QNP, non-QNP and urban reefs showed no significant differences between the QNP and non-QNP reefs but total and fishable biomass were significantly higher on the Qurimbas reefs (30%) than on urban reefs. Fish diversity was also higher in these sites than urban reefs. In addition, fish in the urban reefs differed from the QNP and non-QNP reefs in their life histories with urban reefs having smaller fish, smaller lengths at sexual maturity and higher mortality than the Quirimbas reefs. There was not only no significant differences in fish biomass and fishable biomass between the QNP and non-QNP reefs, but life histories of fish also did not differ. Of the non-QNP sites, the Vamizi closure had the highest total fish biomass and fishable biomass ~1500kg/ha.

Sea urchin biomass: The biomass of sea urchins in the QNP averaged 150kg/ha and ranged from < 10 to ~730 kg/ha with most sites below the problem level threshold for urchin biomass. When sites within the larger Quirimbas archipelago were compared, the sea urchin biomass showed high variability and a general but statistically insignificant increase from QNP to non-QNP to urban reefs and low values in the low to high compliance closures and high values in the reefs were no gears were restricted.

Coral cover and diversity: The reefs within the QNP had hard coral cover and coral diversity that ranged between 30% and 59% generally higher on average than the WIO regional averages for these metrics, underscoring the importance of these reefs for the WIO. Hard coral cover was particularly high in the Lighthouse, Bunting and Quilelea reefs (59%, 52%, 49% respectively) and lowest at Rolas East, Pachamba and Coliseum (30%, 36% and 37% respectively). In general coral taxa diversity were relatively similar across all sites and was highest at Lighthouse (36 genera) and lowest at Rolas west. Comparison with previously sampled sites within the broader Quirimbas archipelago and urban areas showed no significant differences in coral cover but the coral community bleaching susceptibility was highest in the non-QNP sites and lower but insignificant differences were found between the QNP and urban sites. When comparing sites by management category, coral site susceptibility was highest and coral diversity lowest in the high compliance closures.

Environmental gradient and bleaching susceptibility:
There was no significant difference between the sites within the QNP and reefs in the Quirimbas archipelago and the urban areas.

Recommendations

1. *Adaptive management:* Build the capacity for adaptive management of the QNP including the related training in monitoring and enforcement. Setting management targets based on a fishable biomass above 500kg/ha will ensure that the habitat and species are protected while sustaining fisheries.

2. *Improved regulation of fishing:* One third of reefs within the QNP had fishable biomass levels that were below the recommended levels for maintaining fishing will retaining ecological integrity (500kg/ha). Better regulation of fishing is recommended, especially the restriction of highly destructive gears, better enforcement of fishing activities to ensure only licensed fishers are allowed into the QNP. Restriction of migrant fishers who typically have no incentive to comply with the rules. In addition, gear management measures such as the use of modified basket traps that allow reduce bycatch and enhance catch quality can be trailed and if successful under the conditions in the QNP can be an effective fisheries management intervention.

3. *Zoning:* Currently only one site Quilelea is a high compliance closure within the QNP, the other high compliance closure area in the Quirimbas is Vamizi outside the QNP. This is not sufficient to protect the QNP from the potential increase in fishing effort as the population within and outside the QNP increases as well as the impacts of climate change. Additional closures sites can be selected based either their high site susceptibility and high fishable biomass; Lighthouse and Matemo to increase protection of biodiversity in the QNP or their low fishable biomass; Luju, Pachamba and Rolas to enhance sustainable fisheries and recovery of the coral reefs in these areas.

4. *Community closures:* Consider the establishment of community-managed closures. These have the potential to raise awareness about the conservation of habitats and recovery of fisheries stocks but also can benefit communities through enhanced for food security and contribution to livelihoods.

5. *Learning forum:* Create a learning and exchange network for local communities similar to the Annual Fishers Forum in Kenya that is organized by WCS and the Department of Fisheries. The Forum brings together fishers, scientists and management institutions where findings from research are reviewed and management interventions are discussed and trialed. Learning exchanges should serve to educate and raise awareness on marine conservation, enhance social organization and more effective participation of coastal communities in the management of marine resources.

6. *Livelihood diversification:* Increasing livelihood options to reduce nearshore fishing effort and pressure has the potential to enhance recovery and biodiversity protection of the QNP. This could be done through testing and piloting alternative livelihood projects such as mariculture, microcredit and ecotourism ventures.

7. *Research:* In order to better manage the QNP, he social and institutional factors that impede management effectiveness. Since there is such variability across communities, it is important to understand the local context in order to inform and strengthen community management most effectively;

INTRODUCTION

Northern Mozambique and the Quirimbas National Park lie within the coral reef biodiversity center of the western Indian Ocean (McClanahan et al. 2011a; Obura 2012; Horeau et al. 2013; McClanahan 2015). The environmental conditions in this location appear to have enough variability to create acclimation but also to be more stable across strong oceanographic oscillations, such that harsh regional oscillations do not threaten the high biodiversity (McClanahan et al. 2007, 2014). Thus, the region is a high priority for conservation actions to increase the chances that coral reef diversity survive across the coming period of climate change (Sheppard 2003; McClanahan et al. 2011a). Nevertheless, fishing impacts have been shown to reduce fish stocks and diversity and intense and destructive forms of fishing can also reduce coral cover, the reef calcification processes, and the associated structure and habitat that maintains the high diversity (McClanahan et al. 2011b; Graham and Nash 2013; Karr et al. 2014; McClanahan 2015). Therefore, the dual impacts of climate disturbances and fishing have the potential to undermine the habitat that promotes this diversity.

Research in this region has shown that reef degradation is often greatly influenced by the biomass of fish and often through other animals and their grazing impacts, such as sea urchins (O'Leary and McClanahan 2010; McClanahan 2015). Reefs appear to degrade in a step-wise manner as fish biomass declines and with most of the degradation occurring below biomass levels of 300 to 500 kg/ha (McClanahan et al. 2011b; MacNeil et al. 2015). This knowledge provides a useful way to evaluate the condition of reefs and to estimate their long-term prospects for resilience to climate change. It has also be shown that the coral community itself reflects the past history of temperature stresses in terms of the proportion of taxa and their known resilience to heat stress (McClanahan et al. 2007; 2015). Knowing this exposure to thermal stress and the response of the coral community to it, should improve the ability to develop an appropriate adaptation strategy. Environmental exposure information provides a basis for evaluating reefs and in combination with ecological status metrics, such as fish biomass, provides insight into the factors most likely to undermine ecological structures and diversity.

In areas with some natural resistance to climate impacts, such as northern Mozambique, controlling fishing intensity and its destructive effects are a high priority for promoting the future persistence of this diversity center. This requires understanding the current state of the ecosystem, the human drivers that are extracting and managing the resource, and making management recommendations that are likely to support a social-ecological system resilient to large or catastrophic change (McClanahan et al. 2012; Anthony et al. 2015; Selkoe et al. 2015). The success of any management interventions will, however, depend greatly on the social acceptance and likelihood of compliance of the proposed management (McClanahan et al. 2008; Cinner et al. 2012). Management preferences have been shown to vary by community and regionally and perceived social disparity or poor fits between management policies and local perceptions and needs, are expected to undermine local support and adoption of management recommendations (Bunce et al. 2010; McClanahan and Abunge 2015).

This study was undertaken to evaluate the environmental conditions and ecological and management preferences status of this northern Mozambique region with a focus on the Quirimbas National Park (QNP). The park is evaluated within the larger context of an urban to rural human and geographic gradients expected to influence reef status. The goals were to determine the status of the Park relative to other reefs environments to the north around Vamizi and the urban reefs themselves compared to QNP. Quirimbas fishing communities and reefs are better connected commercially to the southern urban cities of Pemba and Nacala than Vamizi reefs to the north (Fig. 1). This results in two types of controls for QNP, one a more urbanized and another more rural environment. This comparison along with an evaluation of the environmental conditions and potential stress experienced by corals provide a basis to develop a climate impact and adaptation strategy that is realistic about the stress conditions and acceptable forms of management. The ultimate goal is to provide information to promote management needed for the persistence of these unusually high levels of coral reef diversity.

The ecological state model

Ecological studies in the region have led to a conceptual model or working hypothesis of reef state, health and degradation that provides a framework to interpret and understand the ecological data (O'Leary and McClanahan 2010; McClanahan et al. 2011). The working model proposes that fish biomass is one of the key drivers of the state of the ecosystem and, as biomass declines due to fishing impacts, the rates of predation and herbivory decline leading to increases in either sea urchin biomass or erect algae. When sea urchins become abundant, coral cover and calcifying algae is reduced, which can further reduce hard coral recruitment (O'Leary et al. 2012, 2013). When sea urchins do not become abundant, erect algae can dominant and this can lead to competition and reduce hard coral cover. Fishing effort, which is in turn influenced by the management restrictions, distance from markets, and human population density near reefs and markets, determine fishing impacts and reduction of fish biomass (Brewer et al. 2013; McClanahan et al. 2011, in review).

Interacting with the above ecological processes are climatic disturbances that can be patchy and variable in the region but seem to be strongly influenced by background and episodic thermal exposure (McClanahan et al. 2007a,b; Maina et al. 2008, 2010). Thermal exposure of temperature and light can further be attenuated by water motion or ameliorated by water quality metrics (chlorophyll and suspended solids). These exposure factors are influenced by the latitude, reef's windward-leeward position, currents and waves, and land-based influences (McClanahan and Maina 2003; McClanahan et al. 2005, 2007, 2009; 2014; Maina et al. 2014). The interactions between the fishing and exposure effects are predicted to determine the state of the reef, which is the guiding hypothesis of this study.

Methods

Study sites

Ecological surveys were undertaken in 66 reefs between 2008 (previous surveys) and 2015 (recent surveys) ranging from reefs near urban areas including Nacala and Pemba in the south to Tekomaji Island in the north (Fig. 1; Table 1). Some sites were sampled more than once, giving a total of 96 site x time replications. Each site was described in terms of their management type, depth, habitat type, distance from shore and nearest large markets, surrounding population density, and the environmental exposure variables derived from satellites. For some of the analyses, 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. Non-QNP reefs included a private interest-community closure arrangement on the northeastern end of Vamizi Island. Reefs around this closure and in nearby islands had various forms of gear management while reefs around Vamizi were not regulated in terms of gear management or closures. The sampled reefs ranged in depth from 1 to 20 m and were typical carbonate reef locations.

Research design

The above sampling allowed for a comparison of the urban reefs, with QNP and non-QNP reefs. Management classification included two basic gear use restrictions, none and some gear restrictions, and two levels of closure compliance, low and high (McClanahan et al. 2015). 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. Observations in the Vamizi closure were that the northern side was a high and the southern side a low compliance closure and sites and analyses were classified accordingly. These classifications and variables formed the basis for comparisons and statistical analyses.

Environmental and demographic data

The environmental exposures data is from the CoRTAD environmental satellite database (http://www.nodc.noaa.gov/sog/cortad/), which contains sea surface temperature collected weekly at 4-km resolution from1982. 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. Full description of the variables and how they were calculated are given in Maina et al. (2011).

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 (CIESIN, 1996; http://sedac.ciesin.columbia.edu/plue/cenguide.html, retrieved Dec 15, 2013). Human influence was calculated with the following formula:

Human Influence = log(1+ human population count at market)/(1+distance from market to the reef)^2)

Ecological Field methods

The study used a number of field methods for estimating fish numbers and biomass, sea urchin species abundance and biomass, and benthic cover and coral taxa abundance.

Fish biomass. The biomass of fish functional groups were estimated using underwater visual census of the numbers and sizes of fish in 23 fish families in replicate 5 x 100 m belt transects (McClanahan et al. 2007). 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, Penguipedidae, Pomacanthidae, Pomacentridae, Scaridae, Serranidae, Scorpaenidae, Siganidae, and Sphyraenidae and an “others” category for individuals not in these families. The midpoint of the fish size classes were 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). The sum of all size classes and families were 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 and is estimated by removing damselfish and all fish <10 cm in body size.

The biomass of fish was estimated from individual fish-length data using length–weight relationships for species but combined at the family level. Fish community-level life histories characteristics of the families were compiled using life history data available in FishBase. The life history parameters included were; maximum length (cm), growth rate (cm yr^{-1}), natural mortality (M), life span (yr), generation time (yr), age at first maturity (yr), length at first maturity (cm), length to achieve optimum yield (cm), 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 2011). Calculations of community life histories are weighted values 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 estimated using roving observer surveys where twenty 2-m^2 quadrats were completed at each site (McClanahan et al. 2007). Benthic cover estimates were 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 *G. astreata*. These distinctions are 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 coverage of each genus and all hard coral combined were calculated. The metrics that were included in this study were total 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. The 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, or die (McClanahan et al., 2007). The relative abundance of each taxon is multiplied by this metric of bleaching and averaged to obtain the index where higher numbers represent communities that bleach more during warm water periods.

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^2 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).

Management preferences field methods

Surveys of fishers in fishing villages used the original field methodology described in McClanahan, et al. 2012 and 2013. A standard questionnaire was used in all eight studied fish landing sites from 3 dictricts of Mozambique namely Matuge, Pemba and Palma. Within Matuge, only 2 sites were studied, Bandar and Jimpia. Sites in Pemba included Chwiba, Congome, Marinha and Ruela. One of the largest landing sites, Ruela, was sampled twice once in 2008 and again in 2011 but with no effort to sample the same fishers. In Palma, the study was undertaken within Vamizi in different locations that included Culansi, Kivuri and Vamizi lodge.

To assess the perception of the value of restrictions and the beneficiaries, we asked respondents to scale their perception of ways that fisheries could be improved or become more sustainable and the benefits to stakeholders based on six management restrictions. The respondent was asked if they believed the specific restriction would improve the fishery where each specific restriction was addressed separately and included minimum fish size, gear restrictions, closed seasons, species selection, protected areas, and closed areas. Respondents were requested to rate their level of support on a six-choice Likert scale that included agree completely, agree somewhat, neutral, disagree somewhat, disagree completely and don't know. The Likert scales for restrictions were coded into -2 to +2 values, the lowest value for disagree completely and highest value for agree completely. “Don't know” responses was not included in the analyses.

To assess who benefited from the restrictions, we asked respondents to scale how much the individual resource user, their community, and the national government benefited from each of the restriction options by marking a location on a 10-point continuous Likert scale that represented low to high benefits. This scale was measured with a ruler and used as the mean perceived benefit. Perceived social disparity was then measured as the difference in the perceived scaled benefits to accrue to each social scale. We found that scaling of benefits for the individual and community were strongly correlated but both differed when compared to government or national levels benefits (McClanahan et al. 2012). Consequently, our measure of social disparity was the average difference between national government and community and self-benefits using the following formula:

Disparity = (Benefit Government-Benefit Community) + (Benefit Government-Benefit Self)/2

The fisheries benefits and social disparity questions were followed with standard questions intended to evaluate the potential influence of the underlying socio-economic demographic and structural factors. These included the number of years in occupation, household size, fortnight expenditure, years living in the current place, age, level of education, material style of life (MSL= physical capital), and social capital measured as the involvement in community organizations and fishing conservation groups. Material style of life questions (MSL) on house type and house possessions is based on the presence or absence of household items (radio, construction materials used, etc). The Material Style of Life (MSL) indicator of relative wealth or social status metric was calculated using Principle Component Analysis (Cinner and Pollnac 2004). If key items were missing or not answered then the respondent was dropped from the analyses. The analyses pooled individuals into villages and were therefore based on community level averages.

Statistical analyses

Ecological data were tested for difference between the three location and four management classifications using standard populations comparison statistics followed by post-hoc comparisons of individual treatments. Tukey or Kruskall Wallis tests were used based on whether or not the data fit the ANOVA assumptions. Relationships between ecological and environmental variables were explored first with correlation matrices and then either model fitting or step-wise least squares regression analyses. The correlation analyses allowed us to examine and chose the strong associations. The strongly associated variables with likely causative relationships were plotted and examined in the model fit analyses.

Village level preference response data for five management options namely minimum fish of captured size, gear restrictions, species selection and closed seasons and areas were compared using cluster analysis, using ANOVA similarity and Ward clustering methods. Marine Protected Area was dropped from the analysis due to limited responses from some sites. Cluster analysis distinguished two distinct village groups that were further analyzed for comparison of means and associations with socio economic variables. Data on perceived restriction benefits and social disparity were tested for the effects of restriction type, profession, country and their various interactions. A step-wise forward logistic regression procedure and pair wise correlation matrix analysis of various socio-economic characteristics was used to test for associations between socioeconomic, management preferences benefits, and perceived social disparity variables. Perceived disparity data was log transformed prior to the multivariate analysis. All statistics were performed using JMP statistical software (Sall et al. 2001) and Sigma plot.

Results

Ecological status

Consumers (finfish and sea urchins)

Comparisons in the reef consumers between the three regions (QNP, non-QNP and urban) indicate statistically significant differences in fish biomass, numbers of fish species, sea urchin biomass and diversity (Table 1a). The highest total fish biomass was found in the non-QNP and QNP reefs at ~664 kg/ha and 613 kg/ha, respectively. The urban areas had lower total and fishable biomass at ~360 kg/ha. Statistical comparisons of fishable biomass were similar but had biomass levels of about 10% lower for the Quirimbas sites but 30% lower for urban areas. Number of fish species was higher in Quirimbas than the urban reefs by ~10 species per 500 m^2. Mean sea urchin biomass was lowest in the QNP reefs, followed by the non-QNP and highest in the urban reefs but the variation was high and therefore not statistically different between QNP and non-QNP reefs and non-QNP and urban areas. There were low numbers of sea urchin species and their numbers increased from park to non-park in the Quirimbas to the 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 1b). With the exception of fishable biomass, which was highest in the high compliance closures at ~1000 kg/ha, there were no differences in the low and high compliance closure systems. However, the low compliance closures were also not different from fished reefs except for having a higher number of individuals than the reefs in the most destructive gear restricted category. Reefs without gear restrictions had the lowest numbers of fish species but those reefs with no and most destructive gear restricted were not different for numbers of individuals and fish biomass. Sea urchin biomass was different between the management categories and showed low values in the low and high compliance closures but moderate and high values in the reefs with most and no gears restricted. There were no differences in number of sea urchin individuals and diversity in the management categories.

Fish community life histories

Fishable biomass community level life history metrics were evaluated by location and management categories (Table 2). All life history metrics except generation time differed between the three locations and many of these differences were due to differences between urban and Quirimbas reefs. For example, the urban reefs had smaller community-level maximum body lengths, lengths at maturity, length at option yield, and higher natural mortality than both Quirimbas locations. Life span and generation time were marginally different when comparing all locations but there were no differences for pair-wise comparisons. Trophic levels were higher in the QNP than the non-QNP and urban reefs. Growth rates were higher in urban than 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 2b). Body lengths were smallest in the no-gear restricted reefs and maximum lengths were highest in the high compliance closures. Natural mortality was also highest in the no-gear restricted and low compliance closure reefs and highest in the high compliance closure and most-destructive gear restricted reefs.

Scatterplots between the fishable biomass and selected fish community diversity and life history metrics indicates a number of significant patterns (Fig. 2; Table 3). 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 number of species variation. The length at 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 saturates at a high of 28.6 cm. Conversely, natural mortality declines from ~1.1 and saturates at ~0.85 but the best-fit equations predicted only 36% of the variation. Age at maturity indicates a highly variable ($r^2 = 0.13$) linear and non-saturating increase along the full biomass sequence.

Benthic cover

Coral cover was high (~45%) as well as numbers of genera (~26 per sample) and there were no statistically significant differences between locations (Table 1a). Number of coral taxa was weakly positively correlated to coral cover but there was no relationship between cover and coral community bleaching susceptibility (Fig. 3). Erect algae were also moderately high (~15%) and not different between locations and there was a weak significant negative correlation between hard coral and erect algae cover ($r = -0.12$, $p<0.05$). The percentage of bleaching corals was low and while there appeared to be a gradient of increase from Quirimbas Park to urban reefs, these differences were short of statistically significant ($P<0.08$). 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 park 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 cover were not different for comparisons of fisheries management categories (Table 1b). The coral site susceptibility 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.

Environmental and demographic relationships

Despite the reefs being located along a fairly small latitudinal gradient of <5°, there were clear patterns in the environmental variables (Fig. 4). Light intensity or radiation, maximum temperatures and temperature anomalies increased to the south (Fig. 4a,b,c). Temperature variables increased consistently from 11.0 to 14.5° south of the equator but radiation stabilized at ~13.0° south. There was also an increase in right skew and peaky temperature distributions (positive skewness and kurtosis) towards the south. Similarly, water quality metrics of chlorophyll-a and suspended solids concentrations increased to the south (Fig. 4d,e,f,g). Finally, the global stress model that combines some of these and other variables indicated increased stress for corals from 11.0 to 13.0° south (Fig. 4h). Radiation, chlorophyll, suspended solids, and the stress model all stabilized at 13.0° south.

Step-wise regression analyses of these environmental variables against the hard coral variables of cover, number of taxa, and community susceptibility found significant associations for hard coral cover and susceptibility but not numbers of taxa (Table 4). Most environmental variables were not significantly associated with the coral metrics but radiation (PAR) was positively and median chlorophyll-a negatively associated with cover. The composite climate exposure model was the single variable negatively associated with community susceptibility. Scatterplots of the relationships between the Global Stress Model and the coral cover, number of taxa, and community susceptibility to bleaching indicates no relationship with cover, a weak positive correlation with number of genera, and a moderate negative relationship with susceptibility (Fig. 5).

Scatterplots and regression analyses of the Human Influence metric with key fish and coral variables indicate a number of statistically significant but weak relationships and different responses for fish and corals (Fig. 6; Table 5). Total biomass of fish declined with human influence but showed notably high scatter at the low ends 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). Very few reef sites exceeded 500 kg/ha at moderate to high Human Influence. Numbers of fish species also declines linearly from ~50 to 40 species per 500 m^2 but also generally more consistent variation along this gradient ($r^2 = 0.24$). Coral cover and number of taxa both increased with the Human Influence metric but there is also high variance around these best-fit lines, model-fits explaining only 7 and 18% of the variance, respectively.

The Quirimbas Park reefs biomass and stress gradients

A more detailed map of the Quirimbas Park shows that sampling was well spread within the park boundaries (Fig. 7). Sorting these reef sites along a biomass gradient indicated that biomass is distributed unevenly throughout the park with no clear latitudinal or park border gradients (Fig. 8). Low biomass sites occur in the north at Zala, in the south at Luju, and in the middle between Ibo and Matemo Islands at Pachamba. Similarly, high biomass sites are located at Rolas East and Dos Piedras in the north, Lighthouse and Matemo East in the middle, and Quilelas and Dogtooth in the south. Numbers of fish species generally increased along this biomass gradient and some notably high diversity sites were observed at Lighthouse and Buntings.

Coral cover was quite variable ranging from ~15 to 60% with some low cover areas in the north at Rojas and Zala Vineyard and high values at Dos Piedras and Lighthouse. Number of coral taxa was more constant among the park sites, ranging from 20 to 35 genera and the one unusually high value was found at one of the Lighthouse reef site sampled in 2013 (36 genera). Coral community susceptibility was generally high but with a few low values in the Rolas reefs and higher values in Matemo, some Lighthouse, and Buntings sites.

Sorting Quirimbas reefs along a Global Stress Gradient suggested a number of the northern reefs had lower stress than southern reefs and the middle areas around Ibo had intermediate stress (Fig. 9). Fish biomass distribution along this gradient generally found high biomass in these intermediate stressed reefs but with high variation. Number of fish species and coral taxa was also variable along this stress gradient where as coral cover generally increased along the stress gradient. Dos Piedras stood out as a low stress reef with high coral cover and numbers of taxa and some Lighthouse reefs had high coral cover and number of taxa and intermediate stress.

Fishing village studies

Socio-economic characteristics of sites within clusters

The villages differed in all of the socioeconomic metrics that we studied (Table 6). Biweekly expenditures ranged from ~1400 to 3600 MZN (~25 MZN/$ rate during the sampling periods) with the highest values in the Pemba City fishing village of Ruela in 2011. Most of the respondents were long time residents of the villages, generally there was a group of villages where respondents had lived more then 27 years in the southern villages of Matuge and Pemba districts and those that had lived less than that in the northern villages of Palma district. Respondents were middle aged, ranging in mean age from 37 to 52 years. Education levels were low ranging from none to 7 years but with no clear patterns by district. There was a halving in years of education between the fishers sampled in Ruela in 2008 and 2011. Very few fishers were part of community organizations with the exception of Chwiba village and most were part of large households ranging from 5 to 12 members. The size of fisher households in Ruela also doubled from 5.9 to 11.5 between 2008 and 2011. The numbers of jobs per household was high from 1.3 to 3.2 with no clear patterns by district.

Management preferences, benefits, and perceived social disparity among groups of clusters

Cluster analysis of the management preferences responses among the 10 studied fishing villages indicates two main and significantly different preference groups (Table 7; *$F = 12.7$, $p < 0.0005$).* All villages scaled preferences positively but Cluster 1 contained 7 landing sites that rated restrictions more positively (mean of all restrictions combined = 1.58 ± 0.6; Chwiba, Ruela 2008 and 2011, Jimpia, Cungome, Bandar, and Vamizi-Culansi) compared to the 3 villages in cluster 2 (mean = 1.23 ± 0.7; Marinha, Vamizi-Kivuri, Vamizi-Lodge) (Fig. 11). Vamizi-Culansi is the one northern village in cluster 1 whereas Marinha is the single southern village in cluster 2. The main differences between these two groups were that the most positive group scaled the minimum fish size, closed seasons, and closed areas higher than the weakly positive group (Fig. 12). Gear restriction and species selection were scaled the same.

The two clusters differed in terms of socio-economic characteristics except in the age of respondents, fortnight expenditure and occupational multiplicity (Table 7). The most positive cluster had fishers who had stayed in the place of origin the longest, were more educated, had larger households, and more social capital in terms of being involved in community organizations. A number of these socio-economic characteristics, including education, number of years one has lived in a place, and total jobs, were correlated with perceived benefits of restrictions (Table 8). Number of years in a place was positively associated with perceived benefits of gear and species selection restrictions and level of education was negatively associated with gear restriction benefits. There were no socio-economic characteristics associated with fisher's perception on closed areas and seasons.

Perceived social disparity and perceived benefits associations were weak and not significant in both clusters (Table 9). Respondents in the most positive cluster perceived highest disparity in species restrictions and closed seasons, low disparity in gear restrictions and closed areas, and no disparity in minimum size of fish restrictions (Fig. 12). The positive cluster perceived modest social disparity in benefit in minimum fish size, gear restrictions and species selection and lower disparity in closed seasons and slightly higher benefits to them and their community than the government with closed area restrictions.

Correlations between the various socio-economic and social disparity variables were weak but indicated a number of statistically significant relationships for the most positive cluster (Table 9). Mean perceived benefits declined with years in school in the most positive cluster. Perceptions of disparity increased with years in occupation in both clusters. It also increased with age, total number of jobs, and levels of education but declined with years living in a place in the most positive cluster (Table 9). Household size increased with years living in a place, years in occupation, and fortnight expenditure and declined with years of education. Education was also positively correlated with total number of jobs in a household.

Discussion

The northern Mozambique region provides a high diversity tropical location where a number of geographic, environmental, and demographic gradients occur and interact with human influences. Some of the observed patterns are expected based on the factors of environmental stress and human influences on fish resources and the role of protected area management while others are less easily explained by these patterns. For example, the urban-to-rural demographic gradient in this region was associated with a gradient in fish biomass but the fit was poor and even at the lowest Human Influence levels, there was high variability in fish biomass. This variability can largely be attributed to the Vamizi closure where the combination of remoteness and closure produced the highest biomass levels in this region. Nevertheless, remoteness, by itself does not appear to lead to high biomass because nearly all non-closure areas had biomass levels that we consider to be within the sustainable fisheries window of 300 to 600 kg/ha. Consequently, it is likely that some combination of local consumption, migrant, and market influences are reducing fish biomass to these levels throughout the Quirimbas reefs. For example, in QNP 13 of the 23 studied reefs had fishable biomass levels within or below this 600 kg/ha upper estimate. We found that below 500 kg/ha the numbers of fish species also declined. Consequently, a good proportion of the reefs are being exploited to maximum production levels where local losses of species are occurring. Typically, these were due to the loss or replacement of large bodied, slow growing, and late maturing species by small and fast growing and maturing species, as indicated in our community life history metrics.

The latitudinal and environmental gradient also indicated a number of complex interactions where responses were not always consistent between fish and corals and depended on the metrics. For example, the stress to corals increased to the south and this was reflected by the lower coral susceptibility measured in the south but was also associated with higher coral cover and number of taxa. Reefs with some of the lowest but also some of the highest number of taxa were found in the southern urban areas. The higher solar radiation in the south may explain this higher coral cover but chlorophyll-a concentrations also increased in this direction and were negatively associated with coral cover. There was no decline in coral cover or numbers of taxa with human influence or with a number of other environmental factors that might be expected to influence coral abundance and diversity. It is further interesting to note that northern Mozambique the area largely represents the southern end of large carbonate-forming reefs along this coastline. While there are some smaller carbonate-forming reefs in Bazaruto, the Premerio and Segundo Islands, and Inhaca to the south, they are small, offshore, and not continuous (Perry 2003). This indicates a complex response between corals and their environment that requires further investigation.

The fish community contrasted with this coral associations where both biomass and number of species declined with human influence. This decline is expected from studies in the western Indian Ocean (WIO) and other regions (Hill et al. 2009; Brewer et al. 2013, Advani et al. 2015). Because biomass and human influences were such strong predictors of numbers of species it is difficult to know what other factors influenced numbers of species. Regional studies have found that latitude plays a role with the highest numbers of fish species found in the northern part of this range but that geography predicts a small percentage of the variance and plays a small role relative to biomass (McClanahan 2015). Nevertheless, the combination of geographic factors and remoteness suggest the Quirimbas has very high diversity and direct comparisons of the QNP and non-QNP locations indicated no differences. Two of the highest fish diversity reefs in this study were found at Lighthouse in QNP and Vamizi forereefs in non-QNP reefs. Clearly, maintaining fish biomass above 500 to 600 kg/ha as suggested here and as shown in regional studies of fish diversity in this region is the primary way to maintain high fish diversity (McClanahan 2015).

Management effects are present in the studied reefs with higher total and fishable biomass in the full and low compliance closures than the reef where no gears were restricted. However, the area under full protective management is small. Only the northern reefs within the Vamizi Community Reserve met the criteria of a high compliance closure. This is because either fishing or fishing gear were seen or reported in other closures or portions of it. Consequently, it is not surprising that total and fishable biomass where not significantly different in the low compliance closure reefs where most-destructive gears were restricted. Reefs where most destructive gear were restricted had more than twice the biomass of reefs with no gear restrictions but biomass was also close to the 500 kg/ha threshold suggested to maintain fish diversity. Given the very small total areas in closures, regardless of compliance level, and the lack of large areas with any enforced gear restrictions, the management effects are restricted to few reefs. Management is therefore not having an impact on the larger scale of the whole reef system.

The evidence for major changes or trophic cascade effects on the rest of the ecosystem that might be caused by overfishing was present but not strong. There was a gradient of increasing sea urchin biomass as restrictions declined but the mean maximum values of ~1600 kg/ha were generally low compared to the larger region where values >2000 kg/ha were found in >65% of WIO reefs (McClanahan and Muthiga in press). Erect algae cover is usually found to be ~5% in the region and therefore the 15% cover found here suggest a generally high algal cover level and with some evidence for weak competition with hard corals. Consequently, the ecological state of Quirimbas reefs reflects moderate levels of fishing and ecological impacts. The moderate biomass throughout the Quirimbas indicates that fishing is widespread and not just restricted to reefs close to human markets. This may indicate widespread impacts by migrant fishers that are able to travel throughout the region and get the resource to the markets. Yields are therefore likely to be close to maximum sustained yields. Of concern is that a significant percent of the reefs were below these MSY levels. Some of the effects of reduced fish diversity and increased sea urchin biomass were evident but without strong impacts on the coral communities, which appear more influenced by the environmental conditions. Consequently, it would seem that any further unrestricted fishing pressure is likely to lead to further losses in fish diversity and other deleterious ecological changes.

Fisher's perceptions

Interviewed fishers in the region were generally positive about the benefits of access restrictions. The differences between villages largely reflected differences between Pemba City and surrounding villages and Vamizi with overall more positive views in the villages around Pemba than those around Vamizi. Closures were rated highly in these Pemba villages but they also had no practical experience compared to Vamizi, which had the most successful closure of the studied reefs. In some cases, the creation of closures creates more opinions, some negative, which may reflect more exposure to the costs or possibly the perceived social disparity created by closures (McClanahan and Abunge 2015). Given the generally positive view of restrictions, it would seem appropriate to increase their implementation beginning with the least contentious restrictions, such as gear restrictions.

Socioeconomic relationships with perceptions of benefits and social disparity were present but generally weak, suggesting opinions were influenced by other unmeasured factors. These might include the village history and cultural traditions but can also reflect strong uniformity in socioeconomic conditions that makes it difficult to find social-structure patterns. The main migrant or mobile fishing village in Pemba City, Marinha, was lower in terms of benefit scaling. These mobile fishers have large boats, travel north to the Quirimbas and use ring nets to capture fish. This fishing life style is not likely to appreciate the benefits of some types of restrictions and maybe why the minimum size of fish restriction was not scaled highly in this cluster. The lack of participation in community organization in Marinha may be an important factor that could increase information sharing and agreement on the potential benefits of management restrictions.

Many of the differences and associations between the two cluster may be attributable to the different gross socioeconomic conditions in and around these two locations. Pemba city and adjacent villages had longer residence, years of education, and expenditures than Vamizi villages. Long residency appeared to be positively associated with positive perceptions of minimum size of fish, species and gear restrictions and suggests a potential role of local and elder fishers in promoting these basic fisheries management options. Despite the long residence, there may also be changes in people who fish in the same village. For example, in the one repeated village, Ruela, there were large differences in the people that were interviewed, which is likely to reflect changes among those people who chose to fish across these two time periods. In this case, fishers were less educated living in larger households with larger household expenditures between the 2008 and 2011 samples. Education appears to heighten fishers awareness of social disparity of some restrictions. Overall, the socioeconomic correlations were weak, which suggests little social structure, greater importance of local cultures and history, or a diversity of opinions that could lead to productive discussion forums.

Recommendations

Table legends

Table 1. Consumers and benthic cover variables by location and management

Table 2. Fish life history characteristics

Table 3. Statistical results of relationships between biomass and life history

Table 4. Step-wise results for environmental and coral cover variables.

Table 5. Statistical results of relationships between Human Influence and key fish and coral variables

Table 6. Fishing landing site characteristics

Table 7. Comparisons of the socioeconomic characteristics

Table 8. Factors influencing fisher's level of agreement

Table 9. Pairwise socioeconomic correlations

Table 1. One-way ANOVAs tests of significance and post-hoc pair-wise tests for comparisons of biophysical parameters between (a) Quirimbas Marine Park (QNP), Non-QNP and Urban areas; (b) four fisheries management regimes of Northern Mozambique. 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 Kruskall-Wallis and the post-hoc Wilcoxon each pair tests were used.

a)

	Quirimbas Park (QNP), n=23	Quirimbas Non-Park (Non-QNP), n=24	Urban Areas, n=19	F Ratio	Prob > F
Consumers					
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/500m^2	A 47.2 ± 1.8	A 48.9 ± 1.6	B 38.08 ± 1.8	10.36	0.0001
Fish Individuals/500m^2	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/10m^2	A 21.4 ± 6.0	A 15.9 ± 4.7	A 12.9 ± 3.6	0.76	NS
Urchin diversity, D	B 0.04 ± 0.03	AB 0.18 ± 0.05	A 0.23 ± 0.05	5.20	0.009
Benthic cover					
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, D	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

b)

	High compliance closure, n=7	Low compliance and young closure, n=5	Most destructive gear restricted, n=40	No gears restricted, n=14	F Ratio	Prob > F
Consumers						
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	<.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	<.0001
Fish species/500m^2	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^2	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/10m^2	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
Benthic cover						
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, D	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

Table 2. One-way ANOVAs tests of significance and post-hoc pair-wise for comparisons of fishable biomass life histories between (a) Quirimbas Park (QNP), Non-QNP and Urban areas; (b) four fisheries management regimes of Northern Mozambique. There was no significant difference where values are preceded by the same letters in the post-hoc Tukey test.

a)

	Quirimbas Park (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	<.0001
Length at maturity, cm	A 23.1 ± 0.4	A 23.1 ± 0.2	B 21.1 ± 0.3	11.65	<.0001
Length at optimum yield, cm	A 25.6 ± 0.5	A 25.7 ± 0.3	B 23.2 ± 0.4	11.38	<.0001
Growth rate, cm y^{-1}	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, y	A 10.18 ± 0.15	A 9.73 ± 0.12	A 9.78 ± 0.15	3.21	0.05
Generation time, y	A 3.14 ± 0.04	A 3.01 ± 0.03	A 3.06 ± 0.04	2.74	0.07
Age at maturity, y	A 2.45 ± 0.03	B 2.35 ± 0.02	AB 2.39 ± 0.03	3.29	0.04

b)

	High compliance closure	Low compliance and young closure	Most destructive 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	<.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	<.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	<.0001
Growth rate, cm y^{-1}	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 ± 0.0.02	3.97	0.01
Lifespan, y	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, y	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, y	A 2.43 ± 0.04	A 2.44 ± 0.06	A 2.39 ± 0.02	A 2.38 ± 0.04	0.41	NS

Table 3. Statistical results of relationships between biomass and a) number of fish species, as well as fish life history characteristics b) length at optimum yield, c) natural mortality, d) age at first maturity.

a) Fish species, $500m^{-2}$

Model	Term	Estimate	t value	Pr(>|t|)	AIC	P	R^2
Asymptote	k	55.7 ± 2.88	19.32	<.0001	435.08	<.0001	0.50
	Bo	24.51 ± 5.13	4.78	<.0001			
	r	0.003 ± 0.001	2.99	0.004			
Ricker	Bo	29.16 ± 3.05	9.57	<.0001	436.38	<.0001	0.49
	a	0.05 ± 0.01	3.83	<.0001			
	b	0.001 ± 0.0002	4.69	<.0001			
Logistic	k	55.21 ± 2.63	20.99	<.0001	436.46	<.0001	0.49
	Bo	28.4 ± 3.44	8.25	<.0001			
	r	0.004 ± 0.001	3.29	0.002			
Linear	Intercept	37.44 ± 1.49	25.07	<.0001	445.50	<.0001	0.40
	Fishable biomass, kg/ha	0.02 ± 0.002	6.43	<.0001			

b) Length at optimum yield, cm

Model	Term	Estimate	t value	Pr(>|t|)	AIC	P	R^2
Asymptote	k	28.64 ± 1.18	24.31	<.0001	249.23	<.0001	0.52
	Bo	21.21 ± 0.86	24.59	<.0001			
	r	0.002 ± 0.001	2.47	0.02			
Logistic	k	28.45 ± 1.02	27.88	<.0001	249.36	<.0001	0.52
	Bo	21.38 ± 0.77	27.89	<.0001			
	r	0.002 ± 0.001	2.85	0.006			
Ricker	Bo	21.51 ± 0.67	32.20	<.0001	249.51	<.0001	0.52
	a	0.01 ± 0.003	3.64	<.0001			
	b	0.001 ± 0.0002	3.57	<.0001			
Linear	Intercept	22.99 ± 0.33	69.06	<.0001	255.19	<.0001	0.46
	Fishable biomass, kg/ha	0.004 ± 0.001	7.32	<.0001			

c) Natural mortality, M

Model	Term	Estimate	t value	Pr(>|t|)	AIC	P	R^2
Ricker	Bo	1.1 ± 0.04	31.27	<.0001	-143.69	<.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	<.0001	-143.68	<.0001	0.36
	Bo	1.11 ± 0.05	23.08	<.0001			
	r	0.002 ± 0.001	1.97	0.05			
Logistic	k	0.83 ± 0.06	14.58	<.0001	-143.66	<.0001	0.36
	Bo	1.12 ± 0.05	20.68	<.0001			
	r	0.002 ± 0.001	1.65	NS			
Linear	Intercept	1.03 ± 0.02	61.53	<.0001	-139.59	<.0001	0.30

	Fishable biomass, kg/ha	-0.0001 ± 0.00003	-5.27	<.0001			
d) Age at maturity, y^{-1}							
Model	Term	Estimate	t value	Pr(>|t|)	AIC	P	R^2
Linear	Intercept	2.33 ± 0.03	86.08	<.0001		0.002	0.13
	Fishable biomass, kg/ha	0.0001 ± 0.00004	3.16	0.002			

Table 4. Relationships between environmental variables and (a) coral cover and (b) bleaching susceptibility from a forward stepwise linear regression analyses. Variables not included were found to be strongly correlated (r>0.85) with those used here. No variable were found to be significant for the stepwise linear regression with number of coral taxa as the response variable.

a)

Parameter	Estimate	t ratio	F ratio	Prob>F	R^2	Whole model P
Intercept	-134.2 ± 68.4	-1.96	0	0.0542	0.16	0.0044
PAR Maximum, E m^{-2} day^{-1}	4.3 ± 1.4	3.00	9.00	0.004		
Chlorophyll median, mg m^{-3}	-77.1 ± 35.5	-2.17	4.71	0.034		
SST kurtosis			1.09	NS		
SST minimum, ^0C			0.38	NS		
Global stress model			0.35	NS		
Mean SST anomaly, ^0C			0.28	NS		
Climate exposure			0.14	NS		
Suspended solids median, g m^{-3}			0.11	NS		
SST standard deviation, ^0C			0.07	NS		
SST skewness, ^0C			0.02	NS		

b)

Parameter	Estimate	t ratio	F ratio	Prob>F	R^2	Whole model P
Intercept	28.4 ± 2.2	12.76	0	<.0001	0.29	<.0001
Climate exposure	-16.7 ±3.3	-5.02	25.21	<.0001		
SST skewness, ^0C			1.76	NS		
Global stress model			1.43	NS		
SST minimum, ^0C			1.05	NS		
PAR Maximum, E m^{-2} day^{-1}			1.01	NS		
Suspended solids median, g m^{-3}			0.87	NS		
Chlorophyll median, mg m^{-3}			0.55	NS		
SST standard deviation, ^0C			0.28	NS		
SST kurtosis			0.01	NS		
Mean SST anomaly, ^0C			0	NS		

Table 5. 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.

a) Total fish biomass, kg/ha					
Term	Estimate	t Ratio	Prob>|t|	R^2	Prob > F
Intercept	595.8 ± 43.8	13.61	<.0001	0.14	0.0017
Human influence	-48.3 ± 14.7	-3.28	0.0017		
b) Fish species, $500m^{-2}$					
Term	Estimate	t Ratio	Prob>|t|	R^2	Prob > F
Intercept	46.4 ± 1	44.5	<.0001	0.24	<.0001
Human influence	-1.6 ± 0.3	-4.51	<.0001		
c) Coral cover					
Term	Estimate	t Ratio	Prob>|t|	R^2	Prob > F
Intercept	41.7 ± 1.6	26.07	<.0001	0.07	0.029
Human influence	1.2 ± 0.5	2.23	0.029		
d) Number of taxa					
Term	Estimate	t Ratio	Prob>|t|	R^2	Prob > F
Intercept	25.7 ± 0.6	44.03	<.0001	0.18	0.0006
Human influence	0.7 ± 0.2	3.62	0.0006		

Table 6. Fishing landing site characteristics showing sites by districts, sample size, means and Standard deviation of, biweekly expenditure, number of years living in place, age of respondent, level of education, number of community organizations, household size and total jobs per household.

Districts	**Landing sites**	**n**	**Biweekly expenditure, MZN**	**Number of years living in place**	**Age of respondent, years**	**Level of education, years**	**Community organizations, n**	**People per household**	**Total jobs per household**
Matuge	Bandar	10	1405 ± 376 *C*	39.2 ± 24.6 *A*	44.0 ± 19.5 *AB*	3.3 ± 1.3 *BCD*	0.10 ± 0.32 *AB*	11.7 ± 1.7 *AB*	3.1 ± 4.5 *A*
	Jimpia	10	1793 ± 1073 *BC*	29.7 ± 13.7 *A*	29.5 ± 9.9 *B*	4.3 ± 2.0 *BCD*	0.4 ± 0.52 *AB*	7.8 ± 1.7 *ABC*	2.1 ± 0.9 *AB*
Pemba	Chwiba	19	1832 ± 914 *C*	35.8 ± 16.7 *A*	51.8 ± 10.8 *A*	5.4 ± 2.7 *BC*	0.95 ± 0.84 *A*	7.6 ± 1.2 *ABC*	1.3 ± 0.4 *B*
	Congome	11	2164 ± 757 *ABC*	28.6 ± 11.0 *A*	37.5 ± 8.2 *AB*	1.3 ± 2.9 *D*	0.66 ± 0.87 *AB*	6.2 ± 1.8 *ABC*	3.2 ± 1.1 *A*
	Marinha	9	2164 ± 1562 *ABC*	27.3 ± 20.6 *AB*	37.8 ± 11.1 *AB*	3.6 ± 0.8 *BCD*	0.0 ± 0.0 *AB*	9.2 ± 1.8 *ABC*	1.7 ± 0.8 *AB*
	Ruela, 2008	36	1544 ± 641 *C*	25.9 ± 16.2 *A*	43.4 ± 9.2 *AB*	6.8 ± 3.1 *B*	0.65 ± 0.73 *AB*	5.9 ± 0.9 *A*	1.5 ± 0.6 *B*
	Ruela, 2011	27	3621 ± 2116 *AB*	34.0 ± 19.5 *A*	37.2 ± 12.1 *B*	2.7 ± 2.3 *CD*	0.63 ± 1.11 *AB*	11.5 ± 1.0 *BC*	1.9 ± 0.8 *AB*
Palma	Vamizi Culansi	7	1586 ± 689 *BC*	22.3 ± 21.7 *AB*	46.9 ± 14.3 *AB*	0 ± 0 *D*	0.29 ± 0.4 *AB*	6.1 ± 1.9 *ABC*	2.4 ± 1.0 *AB*
	Vamizi Kivuri	31	1561 ± 912 *C*	7.7 ± 11.2 *B*	38.5 ± 11.0 *B*	1.7 ± 2.4 *D*	0.20 ± 0.42 *AB*	5.1 ± 0.9 *C*	1.7 ± 0.8 *AB*
	Vamizi Lodge	7	2600 ± 2190 *ABC*	18.0 ± 12.2 *AB*	42.5 ± 9.5 *AB*	4.8 ± 6.3 *BCD*	0.33 ± 0.58 *AB*	6.0 ± 2.6 ABC	1.3 ± 0.5 *AB*
	ANOVA								
	R^2		0.27	0.26	0.21	0.48	0.13	0.18	0.15
	F ratio		5.29	6.36	4.00	12.67	2.28	3.30	2.60
	P <		<..0001	<..0001	<. 0001	<. 0001	0.006	0.007	0.006

Table 7. Comparisons of the socioeconomic characteristics for the two cluster groups. The cluster was produced from the hierarchical clustering analysis of similarities in the respondents' level of agreement with the various management options and nested analysis of the clusters and landing sites within the clusters.

Variables	*Cluster 1*	*Cluster 2*	*R^2*	*F ratio*	*P value*
Number of landing sites	7.0	3.0			
Mean perceived benefits	1.58 ± 0.6	1.23 ± 0.7	0.17	12.47	**0.0005**
Years living in a place	30.82 ± 17.9	12.6 ± 16.2	0.17	30.8	**0.0001**
Age of respondent	48.30 ± 12.9	38.19 ± 10.3	0.02	2.80	0.096
Level of education	4.04 ± 3.22	2.07 ± 2.3	0.07	12.61	**0.0005**
Bi-weekly expenditure	2140 ± 15.6	1827 ± 1302	0.01	1.30	0.255
Number of people per household	8.23 ± 6.2	6.04 ± 3.1	0.03	4.87	**0.029**
Number of organizations	0.62 ± 0.9	0.16 ± 0.4	0.07	11.14	**0.001**
Total jobs	1.96 ± 1.6	1.67 ± 0.2	0.01	1.24	0.268
Years in occupation	18.67 ± 12.7	11.89 ± 10.8	0.06	7.08	**0.009**

Table 8. Factors influencing fisher's level of agreement of various management options based on step-wise multiple regression analysis. Variables included are those that remained after the stepwise screening procedure.)

Management options	*Variables*	*F ratio*	*P value*	*Direction of association*
Minimum fish size				
	Number of years in place	1.63	0.20	Positive
Gear restriction				
	Number of years in place	4.69	**0.033**	Positive
	Level of education	15.36	**0.0002**	Negative
	Years in occupation	0.21	**0.054**	Negative
Closed seasons	NA			
Species selection	Number of years in place	3.77	**0.056**	Positive
	Age of respondents	0.75	0.39	Negative
	Fortnight expenditure	2.42	0.12	Negative
Closed areas	N/A			

Table 9. Pair-wise matrix of socio-economic factors associated with perceived benefits of the combined fishing access restrictions for resource users, their correlations, and levels of significance. Non-significant relationships are not shown: * = P<0.05, **P<0.01, ***P<0.001.

Cluster 1							
Variables	Mean perceived benefit	Perceived social disparity	Years in occupation	Years living in a place	Level of education	Household size	Fortnight expenditure
Mean perceived benefit		-0.36					
Perceived disparity							
Years in occupation		0.34**					
Years living in a place		-0.24*	0.39***				
Age of respondents		0.29*	0.53***	0.38***			
Level of education	-0.29*	0.23*					
Household size			0.30*	0.19*	-0.21*		0.43***
Fortnight expenditure			0.22*				
Total jobs		0.34**	-0.27*		0.47***		
Cluster 2							
Age of respondents				0.42***			
Level of education		0.27*		0.24*			
Household size				0.21*			
Fortnight expenditure					0.54**		

Total jobs	0.48***

Figure legends

Figure 1. Map of the study area showing the location of field sampling for ecological and landings sites where interviews were done and the location of Quirimbas National Park.

Fig. 2. Relationships between fishable biomass and community characteristics of (a) numbers of species, (b) length at optimum yield, (c) natural mortality, and (d) age at maturity life histories.

Fig. 3. Scatterplots showing the relationships between coral cover and (a) number of coral taxa and (b) site susceptibility.

Fig. 4. Relationships between selected environmental variables with latitude.

Fig. 5. Relationships between the Global Stress Model and hard coral (a) cover, (b) number of taxa, and (c) susceptibility to bleaching.

Fig. 6. Relationships between the Human Influence (= log(1+ human population count)/(1+distance from market to the reef)^2) and key fish and coral variables.

Fig. 7. Map of the Quirimbas National Park showing the sampling locations and names of the studied reefs.

Fig. 8. Distribution of studied the Quirimbas National Park reefs along a fish biomass gradient. Colors indicate reefs that are considered to be below sustainable yields (red), within sustainable yields (yellow), and above sustainable yields (green).

Fig. 9. Distribution of studied Quirimbas National Park reefs along a multivariate environmental stress gradient. This stress gradient is composed of a number of variables associated with coral bleaching and shown to a good predictor of coral mortality after warm temperature anomalies (McClanahan et al. 2015).

Fig. 10. Hierarchical clustering analysis of similarities in the respondents' level of agreement with the various management options and nested analysis of the clusters and landing sites within the clusters

Fig 11. Scaled perception of the benefits of fisheries management restriction (ability to improve fisheries production and sustainability) for the two associated groups. Perceptions were scaled from -2 to +2 where -2 means disagree completely and + 2 agree completely.

Fig 12. Mean difference of perception of who benefits from each restriction. Differences are those between the self and community and the government or nation.