Variability in coral reef fish baseline and benchmark biomass in the central and western Indian Ocean provinces

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Abstract :

1. Reef fish biomass is increasingly recognized as a key indicator of fishery and biodiversity status linked to ecosystem integrity on coral reefs, and yet the evaluation of appropriate baselines for biomass, and what drives variation in potential baselines, is sparse.

2. Variability in reef fishable biomass was assessed to test for the existence of baselines or benchmarks (B&Bs), based on field studies of 223 reef sites in remote uninhabited reefs, in high-compliance closures of >5 km2, and among the increasing number of small and recent closures.

3. The purpose of the study was to examine the effects of human habitation, travel time and distance to cities, habitat, depth, benthic cover, and environmental variables on fish B&Bs.

4. There were large differences in the three categories of 'no fishing', with human habitation being the single best predictor of biomass. In remote areas without people (>9 hours of travel time), fish biomass had a mean of 2,450 kg ha–1 (95% confidence interval, 95% CI, 2,130–2,770 kg ha–1; median = 1,885 kg ha–1).

5. In these remote areas, biomass was weakly associated with human travel time to the site and, to a lesser extent, wave energy. In high-compliance closures, fish biomass peaked at 20 years and 5–10 km2, and levelled at 910 kg ha–1 (95% CI 823–989 kg ha–1) for both closure age and size. There was little evidence that human travel time and environmental factors influenced biomass greatly in these established closures. In small and recent closures (<15 years), habitat, depth and closure age were the best predictors of fish biomass.

6. Based on the weakness of environmental factors, country or site-specific B&Bs are not required in these two provinces. However, human habitation in the seascape as well as the size and age of closures set limits to the maximum achievable biomass. The importance of environmental factors increases as the no-fishing areas and closure times decline. Reef wilderness is not widespread in these provinces, but

provides key services and therefore needs to be included in conservation and fisheries policy and management goals.

1.0 Introduction

The global status of fisheries and their sustainable yields are critical for feeding the projected 9.7 billion people on the planet by 2050 (Willet *et al.*, 2019). This is particularly true for the Indian Ocean and African regions where high human population numbers and growth, along with a high prevalence of malnutrition, will challenge projected food requirements (Levin *et al.*, 2018). Large numbers of coral reefs in Africa, Asia, the Caribbean, and elsewhere lack refuge from human fishing pressure and will therefore fail to provide the full potential for food and other important ecological services (McClanahan, 2020). Assessing the status of fish stocks critically relies on knowing baseline or benchmark (B&B) values needed to examine current stock status (Worm *et al.*, 2009). One of the few practical options for evaluating multispecies tropical fish stocks is to pool species and sizes into biomass categories. Pooled multispecies (MS) biomass and growth rates can then be used to estimate fisheries status, fishing effort, and yield potentials (McClanahan, 2018). Thus, the accuracy of fisheries yield estimates could be improved by knowing the local carrying capacity or unfished biomass (K) within a region McClanahan and Azali, 2020).

Estimating multispecies B&B is challenging because values may vary depending on a variety of definitions of what constitutes unfished stocks and their various ecological influences. Historical biomass is often a proxy for unfished stocks, but these estimates can poorly reflect

the long history of fishing, especially in nearshore inhabited ecosystems where impact of fishing predates most biomass assessments (Jackson *et al.*, 2001; McClenachan and Kittinger, 2013). Furthermore, diverse stocks will have a variety of life histories that reflect a wide range of movement patterns and subsequent area requirements for individual species (Cowman and Bellwood, 2013; Green *et al.*, 2015). Consequently, the interaction between species life histories and histories of fishing will influence estimates of unfished biomass. For example, a large scale study of older high compliance marine reserves in inhabited coastal reefs found stock biomasses were ~40% of those in remote offshore un- or sparsely inhabited reef seascapes (McClanahan *et al.*, 2019). Thus, fractured seascapes may have a different maximum potential biomass compared to remote intact regions, which is largely influenced by the distance and travel times to human populations (Cinner *et al.*, 2018, 2020). This indicates the increasing vulnerability of larger mobile fish to the effects of the increasing efforts to create smaller marine reserves (Graham and McClanahan, 2013; Rocliffe *et al.*, 2014). Responses of multispecies B&B have been shown to vary with the size of no-fishing areas, level of protection, and time since implementation (McClanahan *et al.*, 2009; Krueck *et al.*, 2018). For example, older, high compliance fisheries closures having higher biomass than younger closures with low compliance (McClanahan and Graham, 2015). Thus, an important question for effective resource management is how might the history and scale of fishing disturbance and subsequent conservation efforts influence estimates of B&B?

In addition to historical and island biogeographic considerations (Cowman & Bellwood 2013; Paravicini *et al.*, 2013), there are a number of local environmental and food-web factors that could potentially influence B&B estimates (Bellmaker and Jetz, 2011). Stock biomass is a product of local oceanography, habitat, and human influences (Pauly *et al.*, 2002). For example, biomass from subtropical and tropical regions in the Pacific and Indian Oceans have been shown to differ due to differences in solar energy, SST, and primary productivity

(McClanahan *et al*., 2019). These types of gradients may also exist within ocean basins and require consideration before establishing specific B&Bs (Cowman and Bellwood, 2013; Paravicini *et al*., 2013). Thus, investigating variability in B&Bs is advisable prior to their common usage in evaluating status and fisheries models (McClanahan and Azali, 2020). Consequently, to make more confident estimates of coral reef fish B&B, the potential influences of human habitation, protection measures, marine protected area (MPA) characteristics, and environmental factors needs to be considered. A finer-scale evaluation of coral reef fish B&B is now possible due to the increasing number of field studies of reef fish combined with advances in fine scale mapping of coral reefs, human distributions, and satellite proxies for environmental conditions (Burke *et al*., 2011; Marie *et al*., 2016; Yeager *et al*., 2017; McClanahan, 2020). Here, these advances are combined to test how inclusion of finer-scale spatial data, management systems, and no-fishing influences B&B estimates. Three common and replicated no-fishing conditions were therefore evaluated and tested for the potential influences of environmental and human variables. The hypotheses being tested were that unfished biomass would decline with increasing human influence and a reduction in the no-fishing area.

2.0 Methods

2.1 Study sites

Sampling locations ranged in latitude from 3.26^{o}S (Malindi, Kenya) to 26.08^{o}S (Ponto Torres Inhaca, Mozambique) and longitudes of 32.90^{o}E (Berreira Vermelha, Mozambique) to 72.5^{o}W (Diego Garcia, Chagos), including Iles Eparses (Juan de Nova, Glorieuses), Seychelles islands and Mascarene Islands (Reunion, Mauritius). Sites included only areas where there was no fishing on reef slopes, crests, and lagoons in depths between 1 and 20 m (Table 1). The legal designation of no-fishing for classifying sites was not relied on, as many

of sites in this region were legally designated as no-fishing but practically allowed fishing or did not enforce restrictions (McClanahan *et al*., 2015). Rather, the lack of fishing is based on the observer's long-term study of most of the studied sites or, when visiting, by interviewing knowledgeable people or consulting the published literature.

Study sites were classified into 3 categories for evaluations, these were 1) remote, 2) large-old closures, and 3) small-young closures. Remote sites were those >9 hours travel times to nearest regional cities or major markets using common local fishing transportation methods (Maire *et al*., 2016). A number of evaluations suggest that a 9-hour threshold is good trade-off between inclusion and maximum biomass. This is because mean biomass at 9 hours lies within the 95% confidence intervals (CI) of the equilibrium biomass for the travel time-biomass relationship based on large samples (D'agata *et al*., 2016; McClanahan, 2020). This threshold resulted 134 of the 223 sampled sites classified as remote. The two other categories of national or community closures were all <9-hour travel time. These sites also fell naturally within the two groups. The first being young since closure (<15 years) and small (<5km^2). All other sites fit within the second category of closures, or old (>15 years) and large (>5 km^2). These classifications fit because the historical trend in this region has been to create larger closures prior to 2000 and small community or national closures after that date (Wells *et al*., 2007; Rocliffe et al., 2014). Nevertheless, the 5 km^2 threshold is supported by studies that have evaluated biomass-closures size relationships in nearshore coral reefs (McClanahan *et al*., 2009; Krueck *et al*., 2018). Moreover, a number of studies using data from this region have found levelling of biomass in high compliance closures between 15 and 25 years (McClanahan *et al*., 2009; McClanahan and Graham, 2015). Locations with slower recovery times have used Pacific coral reefs in their data set (MacNeil *et al*., 2015). All closure sites fell within these two groups, and produced 70 old-large and 19 young-small closure replicates.

2.2 Field studies

Five experienced investigators contributed the coral reef fish census data (H. Bruggemann, P. Chabanet, A. Friedlander, N. Graham, T. McClanahan) collected in central and western Indian Ocean reefs (Fig. 1; Table 1). All estimates were based on instantaneous visual counts where reef-associated fishes were identified to family or species level, numbers counted, total lengths (TL) estimated, and converted to weights (McClanahan & Kaunda-Arara, 1996; Kulbicki *et al*., 2005). Biomass estimates and the presented fishable biomass were based on fish families that were consistently censused between observers while removing some transient or strictly plankton-feeding groups, such as Caesionidae and Pomacentridae (see McClanahan *et al*., 2019 for a list of taxa). Caesionidae, for example, are not dependent on the reef benthos for food or shelter and are often present in deeper water high above the observer and therefore not observed and counted accurately. Fishable biomass is based on individuals >10 cm in 22 families. Fish <10 cm are seldom captured by artisanal fishers using the common gear of lines, spears, traps, and nets. Damselfish were excluded because, when abundant, they are often planktivores, not fished, and estimates of weights of their small body sizes are not accurate and yet create high variability in total biomass estimates. Sharks were removed as well, as their presence in censuses is very patchy, their body weights are large, and their inclusion increases the variability without accurately estimating the more permanent biomass at a site (D'Agata *et al*., 2016; Juhel *et al*., 2017). Consequently, on the whole, median fish biomass determined using this criteria of fish families contributes to ~88.9% (lower CI = 87.7% and upper CI= 90.1) of the median biomass of all families censused by observers. The focus here was to establish B&Bs, which required constraining episodic variability or the right-tail of the fish biomass distributions (McClanahan *et al*., 2019). Data evaluated in this way and across the sampled region have successfully been combined in the past to address questions such as ecosystem tipping points (McClanahan *et al*., 2011), reef

fish trophic structure (Graham *et al*., 2017), and sustainable yields (McClanahan and Azali, 2020).

Fish were sized and identified to the lowest possible taxonomic level, and then aggregated to calculate biomass at the family level. Transects were pooled within sites, where a site was defined as censuses conducted within a 4-km^2 buffer area under the same management and habitat classifications. Censuses were undertaken between the years 2005 and 2019. When censuses were repeated over time at the same site, data were pooled before analyses. Estimates of fish biomass using instantaneous point counts and belt transects are comparable (Samoilys and Carlos 2000), and combining these survey methods have been used to infer large-scale correlative patterns for coral reefs in multiple studies (e.g. MacNeil *et al*., 2015; Cinner *et al*., 2016; Graham *et al*., 2017). All surveys were designed to minimise diver avoidance or attracting fish. In point counts, large mobile species were counted before smaller territorial species. Similarly, in belt transects larger mobile fish were surveyed in a first pass of the transect, or by observing individuals ahead of the observer along the transect tape, before smaller site-attached species were recorded. For both survey types, all diurnal, non-cryptic reef-associated fish were counted and their total length estimated. Observer and methods effects were tested by analysis of variance (ANOVA) and least square means Tukey's honestly significant difference (HSD), to detect potential observer and methods differences. No significant differences were found in log_e biomass estimates among observers/methods for comparisons of similar no-fishing categories ($p > 0.05$) (JMP 13.0 software).

2.3 Habitat variables

Reefs were classified geographically as continental shelf, continental island (i.e. Zanzibar), inhabited oceanic island (i.e. Reunion), or uninhabited oceanic island (i.e. most of Chagos).

Continental islands were defined as islands <9-hrs from the nearest cities on the continental shelf, whereas oceanic islands were considered as >9-hrs in travel time from the continental shelf. Reef area (km^2) was calculated from the Marine Social Environmental Covariates (MSEC) online platform as the total amount of coral reef area within the surrounding landscape of a site at a buffer distance of 20-km (Yeager, 2017). Habitats were classified from observations of reef profile and depth with a depth gauge. The habitat categories used were reef lagoon/back reef, flat, crest, and slope. Data were pooled into three depth categories: 0-4m, 4-10m, and >10m. Coral cover was estimated at each site using line-intercept and point-intercept methods according to the observer's protocols. In some of the deeper sites (>10 m) visual estimates of hard coral cover were made in 15 to 20 2-m^2 quadrats per site.

2.4 Environmental variables

The environmental variables evaluated were net primary productivity (NPP), wave energy, chlorophyll-*a*, photosynthetic active radiation (PAR), reef area, and percentage coral cover. NPP (mg C m^{-2} day^{-1}) and wave energy (kW m^{-1}). Chlorophyll-*a* (mg m^{-3}) and PAR (Einstein's m^{-2} day^{-1}) data were obtained from GlobColour (www.globcolour.info/). Net primary productivity (NPP) and wave energy were accessed from SESYNC-Marine Social-Environmental Covariates database (www.shiny.sesync.org/apps/msec/) (Yeager, 2017). The NPP data extracted was the 8-day composite layers for the 2003-2013 period produced by NOAA Coast Watch. The extracted wave energy was from the WAVEWATCH III hind cast dataset (http://polar.ncep.noaa.gov/waves/CFSR_hindcast.shtml), which spans over 31 years (1979-2009). Means were determined for these two variables from the beginning of the time series (1998 for Chl-*a* and 2002 for PAR) to the end of the available time series in 2018.

2.5 Human variables

Sites were categorized based on human habitation, closure type, and distance or travel times to human populations (Table 1). First, sites were categorized as either inhabited or uninhabited, where uninhabited meant that there were no permanent settlements. Secondly, site data were pooled into the above three distance from cities and size-age categories. Finally, human influence and gravity for each site were calculated based on human population density derived from the MSEC database and distance or travel time as described by Maire *et al*., (2016). The human influence variable was calculated using the human population within a 100-km radius of each site for the year 2015. Human influence was calculated using the following formula:

$$Human\ Influence = log_e \left(\frac{1+human\ count\ \text{within 100−km radius}}{(1+distance\ \text{of population}\ to\ the\ reef)^2} \right) (1)$$

The two metrics of gravity were calculated using the same formula except that distance in kilometres was replaced with travel time in hours to the two human population metrics. The first gravity metric uses the human population within 500-km radius while the second uses the population of the nearest geographically defined city (Cinner *et al*., 2018).

2.5 Data analysis

Sites were mapped using open source GIS software QGIS version 3.6.2-Noosa. Prior to statistical tests, Mahanalobis multivariate outlier analysis were conducted for biomass values versus habitation, the no-fishing classifications, and geographic location (JMP 13.0 software; Sall *et al*., 2001). From the 253 site x time replicates, 30 sites identified as outliers by the multivariate Mahalanobis outlier analysis were removed, which reduced the total of number of replicates to 223 sites. These outliers were not retained as the study focus was on establishing B&Bs for biomass that might be skewed by the inclusion of outliers. Thereafter, biomass means, medians, standard deviations, and 95% CIs for all sites and classifications

were calculated. Kolmogorov-Smirnov tests of normality on $\log_e$ transformed data indicated better fits to normality due to the positive skewness of the data. Therefore, data were log transformed in all statistical testing.

As a first step, the differences between the three no-fishing categories were tested using Analysis of Variance (ANOVA) and post-hoc Tukey HSD tests using $\log_e$ biomass. Thereafter, were summarized the statistical distributions of these 3 no-fishing categories and all sites combined. Next, habitation, no-fishing, and geography categories were evaluated for differences in biomass by bivariate analysis of variance (ANOVA). Thereafter, $\log_e$ biomass were modelled using Generalized Linear Mixed Effects Modelling (GLMM) versus normalized covariates for no-fishing categories with different transect sizes, namely, remote areas and small and young closures using the 'lme4' package and 'lmer' function in R (version 3.6.0). Transect size was set as a random effect in the GLMM model in order to test for observer effects in the estimation of fish biomass. In the case of large and old closures where all sites were of the same transect size, generalized linear modelling (GLM) with a Gaussian distribution error and 'identity' link function was used. Best models were determined using the 'dredge ()' function in the package 'MuMIn' version 1.43.6. Next, biomass was examined as a function of closure age and size using non-linear least squares logistic and asymptotic regressions with the R package 'nlstools' version 1.0-2. To reduce the effect of data distribution skewness, medians were used rather than means in these analyses. To compare results with other studies, available biomass were summarized by no-fishing categories obtained from other biogeographic provinces using a database compiled by McClanahan *et al*., (2019).

3.0 Results

Overall mean biomass for all sites was 1770 (95% CI= 1552-1994) kg/ha but had a high coefficient of variation (Fig. 2, Table 3). Remote sites had the highest mean biomass of 2450 (95% CI= 2132-2767) and also had high mean variance, with centralized and right-skewed distributions. Consequently, the median biomass was considerably lower, with overall biomass at 1130 (95% CI=987-1259) kg/ha and, in remote sites, 1885 (95% CI=1590-2202) kg/ha. The no-fishing closures had considerably lower biomass and variance with more neutral centralization and less skewness. Old and large closures had 2.6 times the mean biomass (870 (95% CI=804-931) as young and small closures (335 (95% CI=256-413) kg/ha).

All the factors of human habitation, no-fishing categories (remote, old and large closure, young and small closure), reef location, and depth were all statistically significant (Fig. 2; Table 4). Habitation was the most influential factor, followed by the no-fishing category, reef location, and depth. Closure age and size were statistically significant variables for old and large closures based on fits to the logistic model (Fig. 3a; Table 5a). When fitting old and large closures data with the asymptotic model, variables were statistically significant except for the starting points (B_0). Biomass levelled off at 910 (95% CI=823-989) kg/ha for both the logistic and asymptotic models. Closure age and size relationships for young and small closures were only significant for the levelling points of biomass versus closure age at 370 kg/ha (95% CI=287-440) and not statistically significant for the other parameters (Fig. 3b; Table 5c). Closure age and size relationships for young and small closures were not statistically significant for biomass (Table 5d).

Results of GLMM and GLM models for the environmental traits suggest that there were not strong environment-biomass relationships (Table 6). For example, remote sites had an overall

explained variance of around 11% with the selected variables, which were human travel time and to a lesser extent wave energy. The large and old closures had around 4% of the variance explained and the selected human influence metric was not significant. The exception to these patterns was seen in the young and small closures where 82% of the variance was explained by habitat and $\log_e$ transformed closure age. Slopes had the highest biomass, followed by the crest, lagoon/back reef and flat habitats (Table 3). Intra-class correlation coefficients (ICC) for transect size were low for remote areas and small and young closures (<0.15). Transect size explained ~0.05% of the variance in remote areas while in young and small closures this factor did not explain any variance.

4.0 Discussion

Maximum obtainable reef fish biomass in the region is greatly influenced by the social-ecological seascape in terms of human habitation and the size and time attributes of the area of no-fishing. In contrast, the evidence for and influence of strong gradients in environmental variables was weak and of marginal importance in estimating maximum biomass values. This, in principle, greatly simplifies using estimates of K needed for accurately calibrating fisheries yield potentials within this region (Kirkwood and Constable, 2001; McClanahan and Azali, 2020). Consequently, it is likely that fisheries models created from data in specific locations or pooled data may have relevance to reefs throughout the Indian Ocean and more broadly (McClanahan and Graham, 2015). This simplifies the project to estimate sustainable yields along the African coastline and associated islands (McClanahan *et al*., 2016).

Human habitation and the space and time of no-fishing areas were the key drivers of saturated biomass in the region. Habitation was the strongest single variable, which suggests that human impacts were influential – possibly just by being present in the seascape as military, patrolling, migrating fishers, or other economic influences. Concerns over the

conservation of sharks uncovered that the presence of humans, even if they are not fishing, can negatively influence these large predators (Juhel *et al*., 2018). The findings here show that biomass declining with remoteness and closure area is not just a factor for sharks but also other taxa of bony fishes, possibly those with large spatial requirements (Graham and McClanahan, 2013; Cinner *et al*., 2018, 2020). Space-requiring life histories vary considerably for reef fishes, many of which use the reef to aggregate and feed over much larger areas for daily and seasonal migration (Green *et al*., 2015; Khan *et al*., 2017). Thus, the biomass of migrating groupers, grunts, and other fishes that require large foraging or mating grounds are expected to decline as the seascape becomes increasingly fractured by human presence or usage. These movement will not be contained by either the both small and large closures studied here for many species. There may be other life history attributes that influence these patterns of loss that will require further study.

By restricting the study to no-fishing areas and unfished biomass, some habitat-environment-fish interactions that fishing impacts can provoke were eliminated, such as damaging corals or promoting unfished organisms (Graham *et al*., 2017). Nevertheless, the study cannot control for the larger scale influences of climate extremes, rat invasion, bird rookeries, and nutrification (Graham *et al*., 2018; MacNeil *et al*., 2019; Robinson *et al*., 2019). A number of these unfished sites have been impacted by water quality and climate change impacts and therefore do not represent ecosystems completely lacking human influences (McClanahan and Obura, 1997; Darling *et al*., 2013; Graham *et al*., 2015; Chabanet *et al*., 2016). Generally, while environmental drivers of fish biomass can be statistically significant in the tropics, their effect size is often not strong. Remote reefs have been shown to have high biomass even though they can have lower coral cover than nearshore reefs (Friedlander *et al*., 2014; McClanahan *et al*., 2019). Perhaps attributable to lower thermal stress and coral mortality due to reduced light penetration in coastal than oceanic waters (Bruno and Valdivia 2016).

Nevertheless, a study in the Seychelles suggested that catch rates of some groupers in Aldabra Atoll declined across a period of climate stress (Pistorius and Taylor, 2009). However, the biomass and productivity of herbivorous fish has been known to increase with declines in corals (McClanahan *et al*., 2002; Morais *et al*., 2020). In general, losses of coral appears to have the largest impacts on small-bodied species that are not greatly influencing the fishable biomass metric (Graham *et al*., 2008, 2011). Fish biomass on remote Pacific Islands may, however, be more influenced by environmental factors than found in the provinces studied here (Williams *et al*., 2015a). For example, planktivores, which were not included in this study, responded positively to increased primary productivity in remote Pacific Islands. It may well be that the larger benthic-associated fish species studied here responded less in term of biomass to oceanographic drivers than planktivores.

Findings support other observations that environmental drivers are often significant but interact with human impacts (Cinner *et al*., 2018, 2020; Goropse *et al*., 2018). In some cases, human impacts override the environmental drivers by influencing reef fish habitat (Williams *et al*., 2015b). For instance, fishing is associated with changes in the benthic cover that could potentially influence refuge and fisheries production (Robinson *et al*., 2017; Morais *et al*., 2020). Thus, there are likely to be various feedbacks between human impacts on habitat and fish populations, making it challenging to understand cause and effect and outcomes on ecosystem functions, such as fisheries production (Williams and Graham, 2019). The findings here show, however, that the scale of human disturbance in terms of the area of no-fishing is the primary driver of fish biomass, when comparing no-fishing categories. Consequently, differences in reef functions are expected to depend on the scale of seascape fracturing, often determined by habitation and distance from cities and markets (Cinner *et al*, 2020).

In the absence of people in remote areas (>9 hours travel time), fish biomass had a mean of 2450 kg/ha (2130-2770 kg/ha, 95% CIs), or nearly 3 and up to 7 times higher than large and old closures or small and young closures, respectively. These differences are not unusual when comparing study locations here with those in other biogeographical provinces (Table 7). For examples, the well-sampled Tropical Southwestern Pacific Province's remote reefs have 2.5 times higher mean biomass than found in their large and old closures. These patterns and differences may be more pronounced in the tropics than studied temperate reefs where biomass is lower overall (McClanahan *et al*., 2019). Yet, when comparing tropical reefs, the environmental influences were generally small and difficult to detect given the high site variance. When data were further constrained to just one region and do not include planktivores and sharks, a number of these potential drivers were further reduced. At the Pacific and Indian Ocean scales, weak drivers of ocean productivity and coral cover were found (McClanahan *et al*., 2019). Yet, here in this study of two adjacent biogeographic provinces, evidence for their influence on fishable biomass was not evident. These findings suggests that human habitation and resource extraction influences are the major drivers of coral reef fish biomass on a very broad global scale.

In contrast to Cinner *et al*., (2018), biomass inside large and older marine reserves was not influenced by human travel time or distance. This study was restricted to those reserves that we deemed to be high compliance. Previous studies in this region and elsewhere have shown that low compliance reserves have lower biomass and the differences in the food web are similar to those observed in gear-restricted fisheries (McClanahan *et al*., 2015; Gill *et al*., 2017; Campbell *et al*., 2020). Nearly half of the legally gazetted marine reserves in this region are low compliance and their inclusion in the analysis would likely find a greater influence of human travel time and distance (McClanahan *et al*., 2015). Consequently, this study suggests that well-enforced reserves near urban areas can attain high levels of fish

biomass but that a fractured seascape appears to limit biomass more than other direct effects of humans, such as fishing (Pollnac *et al*., 2010).

Fish biomass within the smallest and youngest reserves were found to be highly influenced by size, time, and depth within these reserves. Numbers of small marine reserves are increasing in this region but the consequences for fish biomass and recovery are not well understood (Rocliffe *et al.*, 2014; Oliver *et al*., 2015; McClanahan *et al.*, 2016; Kawaka *et al.*, 2017). Here, limitations to the potential maximum biomass were shown within these small reserves and efforts to increase their size, permanence, and inclusion of deep water are expected to increase biomass further. While the recent proliferation of small reserves may have some social, resource, and conservation benefits, the impacts should not be conflated with biomass numbers observed in the larger seascape. Small closures may be appropriate in specific social-ecological contexts and should be encouraged to increase local biomass and recruitment where it is limiting fisheries production (McClanahan and Kosgei, 2019). Yet, the limitations of small reserves should be acknowledged and benefits not assumed for many space-requiring species and their ecological services. The findings here show that protecting wilderness or remote reefs is critical to maintaining high stock biomass that provide ecological services to many people reliant on reef fisheries (O'Leary *et al.*, 2016). This stock total biomass and of many individual species maintained in remote reefs are seldom compensated for by the past and current proliferation of national and community closures of modest sizes. Therefore, acknowledging, delineating, and managing remote or wilderness reefs should be seen as priority action for the various conservation and sustainable fisheries goals being promoted by a number of global agendas (McClanahan, 2020).

Acknowledgements

References

Belmaker, J., & Jetz, W. (2011). Cross-scale variation in species richness–environment associations. *Global Ecology and Biogeography, 20*(3), 464-474. doi:10.1111/j.1466-8238.2010.00615.x

Bruno, J. F., & Valdivia, A. (2016). Coral reef degradation is not correlated with local human population density. *Scientific Reports, 6*, 29778. doi:10.1038/srep29778

Burke, L., Reytar, K., Spalding, M., & Perry, A. (2011). *Reefs at risk revisited* (E. Cooper, B. Kushner, E. Selig, B. Starkhouse, K. Teleki, R. Waite, C. Wilkinson, & T. Young Eds.). Washington, D.C.: World Resources Institute.

Campbell, S. J., Darling, E. S., Pardede, S., Ahmadia, G., Mangubhai, S., & Maire, E. (2020). Fishing restrictions and remoteness deliver conservation outcomes for Indonesia's coral reef fisheries. *Conservation letters, 13*(2), e12698. doi:10.1111/conl.12698

Chabanet, P., Bigot, L., Nicet, J. B., Durville, P., Massé, L., Mulochau, T., . . . Obura, D. (2016). Coral reef monitoring in the Iles Eparses, Mozambique Channel (2011–2013). *Acta Oecologica, 72*, 62-71. doi:10.1016/j.actao.2015.10.010

Cinner, J. E., Maire, E., Huchery, C., MacNeil, M. A., Graham, N. A., Mora, C., . . . Mouillot, D. (2018). Gravity of human impacts mediates coral reef conservation gains. *Proceedings of the National Academy of Sciences 115*(27), E6116 - E6125. doi:10.1073/pnas.1708001115

Cinner, J. E., Zamborain-Mason, J., Gurney, G. G., Graham, N. A. J., MacNeil, M. A., Hoey, A. S., . . . David Mouillot, D. (2020). Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science, 368*(6488), 307-311. doi:10.1126/science.aax9412

Cowman, P. F., & Bellwood, D. R. (2013). The historical biogeography of coral reef fishes: Global patterns of origination and dispersal. *Journal of Biogeography, 40*(2), 209-224. doi:10.1111/jbi.12003

D'agata, S., Mouillot, D., Wantiez, L., Friedlander, A. M., Kulbicki, M., & Vigilola, M. (2016). Marine reserves lag behind wilderness in the conservation of key functional roles. *Nature Communications, 7*, 72000. doi:10.1038/ncomms12000

Darling, E. S., McClanahan, T. R., & Côté, I. M. (2013). Life histories predict coral

    community disassembly under multiple stressors. *Global Change Biology, 19*(6),

    1930-1940. doi:10.1111/gcb.12191

Friedlander, A. M., Obura, D., Aumeeruddy, R., Ballesteros, E., Church, J., Cebrian, E., &

    Sala, E. (2014). Coexistence of low coral cover and high fish biomass at Farquhar

    Atoll, Seychelles. *PLoS One, 9*(1), e87359. doi:10.1371/journal.pone.0087359

Gill, D. A., Mascia, M. B., Ahmadia, G. N., Glew, L., Lester, S. E., Barnes, M., . . . Holst, S.

    (2017). Capacity shortfalls hinder the performance of marine protected areas globally.

    Nature, 543(7647), 665-669. doi:10.1038/nature21708

Gorospe, K. D., Donahue, M. J., Heenan, A., Gove, J. M., Williams, I. D., & Brainard, R. E.

    (2018). Local biomass baselines and the recovery potential for Hawaiian coral reef

    fish communities. . *Frontiers in Marine Science, 5*, 162.

    doi:10.3389/fmars.2018.00162

Graham, N. A., Chabanet, P., Evans, R. D., Jennings, S., Letourneur, Y., Aaron MacNeil, M.,

    . . . Wilson, S. K. (2011). Extinction vulnerability of coral reef fishes. *Ecology*

    Letters, 14(4), 341-348. doi:10.1111/j.1461-0248.2011.01592.x

Graham, N. A., Jennings, S., MacNeil, M. A., Mouillot, D., & Wilson, S. K. (2015).

    Predicting climate-driven regime shifts versus rebound potential in coral reefs.

    Nature, 518(7537), 94-97. doi:10.1038/nature14140

Graham, N. A., McClanahan, T. R., MacNeil, M. A., Wilson, S. K., Polunin, N. V., Jennings,

    S., . . . Bigot, L. (2008). Climate warming, marine protected areas and the ocean-scale

    integrity of coral reef ecosystems. *PLoS One, 3*(8), 10.1371/journal.pone.0003039.

    doi:10.1371/journal.pone.0003039

Graham, N. A., Wilson, S. K., Carr, P., Hoey, A. S., Jennings, S., & MacNeil, M. A. (2018). Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature, 559*(7713), 250. doi:10.1038/s41586-018-0202-3

Graham, N. A. J., Cinner, J. E., Holmes, T. H., Huchery, C., MacNeil, M. A., McClanahan, T. R., & Wilson, S. K. (2017). Human disruption of coral reef trophic structure. *Current Biology, 27*(2), 231-236. doi:10.1016/j.cub.2016.10.062

Graham, N. A. J., & McClanahan, T. R. (2013). The last call for marine wilderness? *BioScience, 63*(5), 397-402. doi:10.1525/bio.2013.63.5.13

Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., . . . White, A. T. (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews, 90*(4), 1215-1247. doi:10.1111/brv.12155

Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., & Hughes, T. P. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science, 293*(5530), 629-637. doi:10.1126/science.1059199

Juhel, J. B., Vigliola, L., Mouillot, D., Kulbicki, M., Letessier, T. B., Meeuwig, J. J., & Wantiez, L. (2018). Reef accessibility impairs the protection of sharks. *Journal of Applied Ecology, 55*(2), 673-683. doi:10.1111/1365-2664.13007

Kawaka, J. A., Samoilys, M. A., Murunga, M., Church, J., Abunge, C., & Maina, G. W. (2017). Developing locally managed marine areas: Lessons learnt from Kenya. *Ocean & Coastal Management, 135*, 1-10. doi:10.1016/j.ocecoaman.2016.10.013

Khan, J. A., Goatley, C. H., Brandl, S. J., Tebbett, S. B., & Bellwood, D. R. (2017). Shelter use by large reef fishes: long-term occupancy and the impacts of disturbance. *Coral Reefs, 36*(4), 1123-1132. doi:10.1007/s00338-017-1604-7

Kirkwood, G. P., & Constable, A. J. (2001). Integration of CPUE data into assessments using the generalised yield model. *CCAMLR Science, 8*, 65-74.

Krueck, N. C., Legrand, C., Ahmadia, G. N., Green, A., Jones, G. P., Riginos, C., . . . Mumby, P. J. (2018). Reserve sizes needed to protect coral reef fishes. *Conservation letters, 11*(3), e12415.

Kulbicki, M., Guillemot, N., & Amand, M. (2005). A general approach to length-weight relationships for New Caledonian lagoon fishes. *Cybium, 29*(3), 235-252.

Levin, N., Beger, M., Maina, J., McClanahan, T., & Kark, S. (2018). Evaluating the potential for transboundary management of marine biodiversity in the Western Indian Ocean. *Australasian Journal of Environmental Management, 25*(1), 62-85. doi:10.1080/14486563.2017.1417167

MacNeil, M. A., Graham, N. A., Cinner, J. E., Wilson, S. K., Williams, I. D., Maina, J., . . . McClanahan, T. R. (2015). Recovery potential of the world's coral reef fishes. *Nature, 520*(7547), 341-344. doi:10.1038/nature14358

MacNeil, M. A., Mellin, C., Matthews, S., Wolff, N. H., McClanahan, T. R., Devlin, M., . . . Graham, N. A. J. (2019). Water quality mediates resilience on the Great Barrier Reef. *Nature Ecology & Evolution, 3*(4), 620. doi:10.1038/s41559-019-0832-3

Maire, E., Cinner, J., Velez, L., Huchery, C., Mora, C., Dagata, S., . . . Mouillot, D. (2016). How accessible are coral reefs to people? A global assessment based on travel time. *Ecology Letters, 19*(4), 351-360. doi:10.1111/ele.12577

McClanahan, T., Maina, J., & Pet-Soede, L. (2002). Effects of the 1998 coral morality event on Kenyan coral reefs and fisheries. *AMBIO: A Journal of the Human Environment, 31*(7), 543-550.

McClanahan, T., Muthiga, N. A., & Abunge, C. A. (2016). Establishment of community

    managed fisheries' closures in Kenya: Early evolution of the tengefu movement.

    Coastal Management, 44(1), 1-20. doi:10.1080/08920753.2016.1116667

McClanahan, T. R. (2018). Multicriteria estimate of coral reef fishery sustainability. *Fish and*

    Fisheries, 19(5), 807 - 820. doi:10.1111/faf.12293

McClanahan, T. R. (2020). Wilderness and conservation policies needed to avoid a coral reef

    fisheries crisis. *Marine Policy, 119*, 104022. doi:10.1016/j.marpol.2020.104022

McClanahan, T. R., & Azali, M. K. (2020). Improving sustainable yield estimates for tropical

    reef fisheries. *Fish and Fisheries*, Doi:10.1111/faf.12454. doi:10.1111/faf.12454

McClanahan, T. R., & Graham, N. A. J. (2015). Marine reserve recovery rates towards a

    baseline are slower for reef fish community life histories than biomass. *Proceedings*

    of the Royal Society B: Biological Sciences, 282(1821), e20151938.

    doi:10.1098/rspb.2015.1938

McClanahan, T. R., Graham, N. A. J., MacNeil, M. A., & Cinner, J. E. (2015). Biomass-

    based targets and the management of multispecies coral reef fisheries. *Conservation*

    Biology, 29(2), 409-417. doi:10.1111/cobi.12430

McClanahan, T. R., Graham, N. A. J., MacNeil, M. A., Muthiga, N. A., Cinner, J. E.,

    Bruggemann, J. H., & Wilson, S. K. (2011). Critical thresholds and tangible targets

    for ecosystem-based management of coral reef fisheries. *Proceedings of the National*

    Academy of Sciences, 108(41), 17230-17233. doi:10.1073/pnas.1106861108

McClanahan, T. R., & Kaunda-Arara, B. (1996). Fishery recovery in a coral-reef marine park

    and its effect on the adjacent fishery. *Conservation Biology, 10*(4), 1187-1199.

    doi:10.1046/j.1523-1739.1996.10041187.x

McClanahan, T. R., & Kosgei, J. (2019). Outcomes of gear and closure subsidies in artisanal coral reef fisheries. *Conservation Science and Practice, 1*(10), e114. doi:DOI: 10.1111/csp2.114

McClanahan, T. R., Maina, J. M., Graham, N. A. J., & Jones, K. R. (2016). Modeling reef fish biomass, recovery potential, and management priorities in the Western Indian Ocean. *PLoS One, 11*(5), e0154585. doi:10.1371/journal.pone.0154585

McClanahan, T. R., & Obura, D. (1997). Sedimentation effects on shallow coral communities in Kenya. *Journal of Experimental Marine Biology and Ecology, 209*(1), 103-122. doi:10.1016/S0022-0981(96)02663-9

McClanahan, T. R., Schroeder, R. E., Friedlander, A. M., Vigliola, L., Wantiez, L., Caselle, J. E., . . . Cinner, J. C. (2019). Global baselines and benchmarks for fish biomass: Comparing remote and fisheries closures. *Marine Ecology Progress Series, 612*, 167–192. doi:doi:https://doi.org/10.3354/meps12874.

McClenachan, L., & Kittinger, J. N. (2013). Multicentury trends and the sustainability of coral reef fisheries in Hawai 'i and Florida. *Fish and Fisheries, 14*(3), 239-255.

Morais, R. A., Depczynski, M., Fulton, C., Marnane, M., Narvaez, P., Huertas, V., . . . Bellwood, D. R. (2020). Severe coral loss shifts energetic dynamics on a coral reef. *Functional Ecology*.

O'Leary, B. C., Winther-Janson, M., Bainbridge, J. M., Aitken, J., Hawkins, J. P., & Roberts, C. M. (2016). Effective coverage targets for ocean protection. *Conservation letters, 9*(6), 398-404. doi:10.1111/conl.12247

Oliver, T. A., Oleson, K. L., Ratsimbazafy, H., Raberinary, D., Benbow, S., & Harris, A. (2015). Positive catch and economic benefits of periodic octopus fishery closures: Do effective, narrowly targeted actions 'catalyze' broader management? *PLoS One, 10*(6), e0129075. doi:10.1371/journal.pone.0129075

Parravicini, V., Kulbicki, M., Bellwood, D. R., Friedlander, A. M., Arias-Gonzalez, J. E., Chabanet, P., . . . Mouillot, D. (2013). Global patterns and predictors of tropical reef fish species richness. *Ecography, 36*(12), 1254-1262. doi:10.1111/j.1600-0587.2013.00291.x

Pauly, D., Christensen, V., Guenette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., . . . Zeller, D. (2002). Towards sustainability in world fisheries. *Nature, 418*(6898), 689-695. doi:10.1038/nature01017

Pistorius, P. A., & Taylor, F. E. (2009). Declining catch rates of reef fish in Aldabra's marine protected area. *Aquatic Conservation: Marine and Freshwater Ecosystems, 19*(S1), S2-S9. doi:10.1002/aqc.1035

Pollnac, R., Christie, P., Cinner, J. E., Dalton, T., Daw, T. M., Forrester, G. E., . . . McClanahan, T. R. (2010). Marine reserves as linked social-ecological systems. *Proceedings of the National Academy of Sciences, 107*(43), 18262-18265. doi:10.1073/pnas.0908266107

Robinson, J. P., Wilson, S. K., Robinson, J., Gerry, C., Lucas, J., Assan, C., . . . Graham, N. A. (2019). Productive instability of coral reef fisheries after climate-driven regime shifts. *Nature Ecology & Evolution, 3*(2), 183-190. doi:10.1038/s41559-018-0715-z

Robinson, J. P. W., Williams, I. D., Edwards, A. M., McPherson, J., Yeager, L., Vigliola, L., . . . Baum, J. K. (2017). Fishing degrades size structure of coral reef fish communities. *Global Change Biology 23*(3), 1009–1022 doi:10.1111/gcb.13482

Rocliffe, S., Peabody, S., Samoilys, M., & Hawkins, J. P. (2014). Towards a network of locally managed marine areas (LMMAs) in the Western Indian Ocean. *PLoS One, 9*(7), e103000. doi:10.1371/journal.pone.0103000

Sall, J., Lehman, A., & Creighton, L. (2001). *JMP start statistics A guide to statistics and data analysis using JMP and JMP IN software* (Second ed.). *Carey, Notth Carolina, USA*: *SAS Institute Inc*.

Wells, S., Burgess, N., & Ngusaru, A. (2007). Towards the 2012 marine protected area targets in Eastern Africa. *Ocean & Coastal Management, 50*(1), 67-83. doi:10.1016/j.ocecoaman.2006.08.012

Willett, W., Rockström, J., Loken, B., Springmann, M., Lang, T., Vermeulen, S., . . . Jonell, M. (2019). Food in the Anthropocene: The EAT–Lancet Commission on healthy diets from sustainable food systems. *The Lancet, 393*(10170), 447-492. doi:10.1016/S0140-6736(18)31788-4

Williams, G. J., Gove, J. M., Eynaud, Y., Zgliczynski, B. J., & Sandin, S. A. (2015bb). Local human impacts decouple natural biophysical relationships on Pacific coral reefs. *Ecography, 38*(8), 751-761. doi:10.1111/ecog.01353

Williams, G. J., & Graham, N. A. J. (2019). Rethinking coral reef functional futures. *Functional Ecology, 33*(6). doi:10.1111/1365-2435.13374

Williams, I. D., Baum, J. K., Heenan, A., Hanson, K. M., Nadon, M. O., & Brainard, R. E. (2015a). Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS One, 10*(4), e0120516. doi:10.1371/journal.pone.0120516

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., . . . Jensen, O. P. (2009). Rebuilding global fisheries. *Science, 325*(5940), 578 - 585. doi:10:1126/science.1173146

Yeager, L. A., Deith, M. C., McPherson, J. M., Williams, I. D., & Baum, J. K. (2017). Scale dependence of environmental controls on the functional diversity of coral reef fish

communities. *Global Ecology and Biogeography, 26*(10), 1177-1189.

doi:10.1111/geb.12628

Table legend

Table 1. Site categorical classifications, criteria and replicates used in the central and western Indian Ocean coral reef fish baseline and benchmark study.

Table 2. Summary statistics of continuous variables tested for influences on coral reef fish biomass in the central and western Indian Ocean region.

Table 3. Summary statistics of fishable biomass (kg ha^{-1}) for baseline and benchmark sites in the central and western Indian Ocean region. Includes mean, median, standard deviation (SD), 95% confidence intervals, and sample sizes. Tests of normality based on $\log_e$ (ln) transformed data. SD = standard deviation. COV = coefficient of variation. CI (L:U) = confidence interval (lower, upper). KS = Kolmogorov Smirnov values as test of normality. Fishable biomass (kg ha^{-1}) statistics for sites in remote areas, old and large closures, and young and small closures.

Table 4. Summary statistics of categorical variables and tests if significance for biomass comparisons in the central and western $^{-}$Indian Ocean. Categories with the same letter superscripts are not significantly different from each other (P>0.05) based on least square means Tukey Honestly Significant Difference (HSD) tests. ANOVA F Ratios and Tukey HSD tests are determined using $\log_e$ biomass.

Table 5. Parameter estimates for non-linear least square regressions of fishable biomass (kg/ ha) versus closure age (years) and closure size (km^2) in old-large closures and young-small closures. SEM = standard error of the mean.

Table 6. Top models computed using generalized linear mixed effect (GLMM) and generalized linear modelling (GLM) and the dredge function in the central and western Indian Ocean for: a) remote areas, b) old and large closures, and c) small and young closures. Models presented for all categories with Delta AIC = 0. SEM = standard error of the mean and ICC = Intra-class correlation coefficient.

Table 7. Summary statistics of coral reef fish fishable biomass at the province biogeographical scale in remote reefs and closures of the Indo-Pacific.

Figure legend

Figure 1. Location of study sites in Central and Western Indian Ocean and studied ecoregion. The colour intensity of site symbols indicates the sample size

Figure 2. Fishable biomass (kg ha^{-1}) distributions in the Central and Western Indian Ocean

Figure 3. Fishable biomass as a function of closure age and size in Central and Western Indian Ocean coral reefs for old and large closures and for young and small closures:(a) biomass versus closure age; (b) biomass versus closure area. Model lines in green represent old and large closures, whereas lines in black represent small and young closures.

Tables

Table 1. Site categorical classifications, criteria and replicates used in the central and western Indian Ocean coral reef fish baseline and benchmark study.

Classification	Criteria	Country (site replicates)
Habitation		
Uninhabited	Remote site absent of humans	Chagos (29); Seychelles (98), Iles Esparses (7)
Inhabited	Site with human inhabitants	Kenya (78); Mayotte (4); Mozambique (2); Reunion (3); Tanzania (2).
Closure type		
Remote area	Sites with >9hrs travel time to nearest market	Chagos [a] (29); Iles Esparses[b] (7); Seychelles[c] (98).
Old large closure	Sites in a high compliance closure >5km^2 and >15yrs of age	Kenya[d] (62); Mayotte[e] (4); Mozambique[f] (2); Tanzania[g] (2).
Young small closure	Sites in a high compliance closure <5km^2 and <15yrs of age	Kenya[h] (16); Reunion[i] (3).
Reef location		
Uninhabited oceanic island	Site on island >9hrs travel time from nearest market	Chagos (29); Iles Esparses (7); Seychelles (98).
Inhabited oceanic island	Site on island <9hrs travel time from nearest market	Mayotte (4); Reunion (3).
Continental island	Site on island <9hrs travel time from market on continental shelf	Kenya (7); Tanzania (2).
Continental shelf	Site located on the continental shelf	Kenya (71); Mozambique (2).

Closure name (year of establishment; size in km^2): a. Chagos Archipelago MPA (2010; 640,000 km^2) b. Iles Glorieuses Nature Reserve (1975; 5 km^2); Ilot de Bassas de India Nature Reserve (1975; 4.8 km^2) c. Aldabra Special Nature Reserve (1981; 142km^2) d. Malindi Marine Park (1968; 6.3 km^2); Watamu Marine Park (1968; 32 km^2); Mombasa (1986;10 km^2); Kisite Marine Park (1978; 28 km^2) e. Passe de Longongori Strict Fishing Reserve (1991; 13.8 km^2) f. Ilhas da Inhaca e dos Portugueses Faunal Reserve (1965; 20km^2) g. Misali Locally Managed Marine Area (LMMA) (1998; 1.4km^2) h. Vipingo LMMA (2005; 0.29km^2); Wasini LMMA (2009; 0.5 km^2); Kibuyuni LMMA (2010; 0.28 km^2); i. Saline l'Hermitage (lagoon) Fishing Reserve (1992; 0.19km^2).

Table 2. Summary statistics of continuous variables tested for influences on coral reef fish biomass in the central and western Indian Ocean region.

Variable	Young & small		Old & large		Remote	
	Mean ± SD	Range (min - max)	Mean ± SD	Range (min - max)	Mean ± SD	Range (min - max)
Closure age (years)	6.2 ± 3.0	1.0 - 11.0	28.6 ± 9.0	15.0 - 45.0	NA	NA
Closure area (km^2)	0.3 ± 0.1	0.2 - 0.5	10.4 ± 6.6	6.0 - 28.0	NA	NA
Chlorophyll–a (mg m^{-3})	0.8 ± 0.7	0.1 - 2.4	0.9 ± 0.3	0.3 - 2.1	0.5 ± 0.3	0.2 - 1.5
Photosynthetically active radiation (E m^{-2} day^{-1})	47.1 ± 3.4	39.5 - 48.5	47.6 ± 1.2	41.6 - 48.2	45.7 ± 1.3	42.7 - 47.9
Net primary productivity (C (m^2 day)$^{-1}$)	895.7 ± 184.1	478.9 - 971.0	1400.9 ± 456.7	729 .0- 2114.0	887.0 ± 319.1	645.0 – 2199.0
Wave energy (kW m^{-1})	9.6 ± 8.9	0 - 40.4	9.3 ± 2.6	0.8 - 11.0	16.1 ± 7.9	0 – 37.0
Hard coral (%)	25.7 ± 8.8	16.0 - 14.0	27.4 ± 13.2	10.4 - 50.5	32.6 ± 19.7	1.9 - 85.6
Reef area within a radius of 20 km^2	55.8 ± 31.7	20.5 - 116.8	79.1 ± 34.6	4.3 - 186.0	94.7 ± 52.0	6.5 - 222.5
Distance to market (km)	38.5 ± 8.4	33.4 - 54.5	63.9 ± 36.2	9.7 - 103.0	614.2 ± 529.6	224.7 - 1713.0
Human influence	7.4 ± 0.5	6.3 - 7.8	6.8 ± 1.7	5.1 - 9.6	-8.7 ± 3.5	-14.9 - 5.3
Travel time to the nearest human population (hours)	0.3 ± 0.1	0.01 – 0.3	0.1 ± 0.1	0.02 – 0.5	8.0 ± 14.0	0.01 – 42.6
Travel time to the nearest market (hours)	1.1 ± 0.3	0.9 – 1.8	1.6 ± 0.7	0.4 – 2.2	27.9 ± 19.8	10.8 – 73.6
Gravity to the nearest human population	30.3 ± 130.5	0.02 - 569.0	34.2 ± 57.8	0.003 - 123.0	0.04 ± 0.1	0.000006 - 1.0
Gravity to the nearest market	145.8 ± 68.3	43.6 - 196.2	301.0 ± 479.0	2.9 - 1224.4	0.06 ± 0.05	0.005 - 0.2

Table 3. Summary statistics of fishable biomass (kg ha^{-1}) for baseline and benchmark sites in the central and western Indian Ocean region. Includes mean, median, standard deviation (SD), 95% confidence intervals, and sample sizes. Tests of normality based on log$_e$ (ln) transformed data. SD = standard deviation. COV = coefficient of variation. CI (L:U) = confidence interval (lower, upper). KS = Kolmogorov Smirnov values as test of normality. Fishable biomass (kg ha^{-1}) statistics for sites in remote areas, old and large closures, and young and small closures.

	All sites	Remote areas	Old and large closures	Young and small closures
N=	223	134	70	19
Mean ± SD	1773.1 ± 1674.5	2449.9 ± 1857.9	867.7 ± 264.3	335.2 ± 163.0
COV	94.4	75.8	30.5	48.6
95 % CI (L:U)	(1552.1;1994.0)	(2132.4;2767.4)	(804.6;930.7)	(256.6;413.8)
Median	1134.6	1885.3	853.2	300.5
95 % CI (L:U)	(987.1;1258.9)	(1590.2;2202.0)	(794.2;896.9)	(251.8;433.4)
Kurtosis	3.1	0.9	-0.4	-0.1
Skewness	1.8	1.3	0.3	0.7
KS (D)	1	1	1	1
P-value	0.0001	0.0001	0.0001	0.0001

Table 4. Summary statistics of categorical variables and tests if significance for biomass comparisons in the central and western ⁻Indian Ocean. Categories with the same letter superscripts are not significantly different from each other (P>0.05) based on least square means Tukey Honestly Significant Difference (HSD) tests. ANOVA F Ratios and Tukey HSD tests are determined using $\log_e$ biomass.

Variable	n	Median biomass (kg ha^{-1})	Mean biomass (kg ha^{-1}) ± SD	F Ratio	P > F
Habitation				115.7	0.0001
Inhabited[A]	89	738.7	754.0 ± 329.2		
Uninhabited[B]	134	1885.3	2449.9 ± 1857.9		
Closure type				86.6	0.0001
Young and small[C]	19	300.5	335.2 ± 163.0		
Old and large[D]	70	853.2	867.7 ± 264.3		
Remote[E]	134	1885.3	2449.9 ± 1857.9		
Depth				42.1	0.0001
0-4m[F]	84	809.3	845.6 ± 632.5		
4-10m[G]	83	1510.9	2217.0 ± 1875.2		
>10m[G]	56	1859.6	2506.3 ± 1820.1		
Reef location				38.9	0.0001
Continental shelf[H]	73	714.2	749.9 ± 333.2		
Continental island[H]	9	798.0	851.3 ± 284.3		
Inhabited oceanic island[H]	7	803.8	671.7 ± 356.2		
Uninhabited oceanic island[I]	134	1885.3	2449.9 ± 1857.9		
Habitat				20.6	0.0001
Lagoon/Back reef[I]	69	798.0	945.5 ± 829.8		
Flat[IJ]	1	175.2	175.2		
Crest[J]	12	908.5	1395.3 ± 1363.3		
Slope[J]	141	1510.9	2221.6 ± 1842.6		

Table 5. Parameter estimates for non-linear least square regressions of fishable biomass (kg/ha) versus closure age (years) and closure size (km^2) in old-large closures and young-small closures. SEM = standard error of the mean.

a. Old and large closures fishable biomass (kg/ha) versus closure age (years)

Parameter	Estimate	Lower 95% CI	Upper 95% CI	SEM	t value	Pr(>|t|)
Logistic						
K	906.9	823.0	988.8	41.1	22.1	<0.001
B_0	245.5	33.2	457.8	106.6	2.3	0.02
r	0.2	0.03	0.4	0.1	2.4	0.02
Asymptotic						
K	917.7	814.7	1020.8	51.7	17.7	<0.001
B_0	193.1	-114.8	500.9	154.6	1.2	0.2
r	0.1	0.01	0.2	0.05	2.3	0.02

b. Old and large closures fishable biomass (kg/ha) versus closure area (km^2)

Parameter	Estimate	Lower 95% CI	Upper 95% CI	SEM	t value	Pr(>|t|)
Logistic						
K	908.5	690.0	1127.1	109.7	8.3	<0.001
B0	619.2	61.9	1176.6	279.8	2.2	0.03
r	0.2	-0.4	0.8	0.3	0.7	0.5
Asymptotic						
K	911.0	674.4	1147.6	118.8	7.7	<0.001
B_0	613.2	-34.6	1261.0	325.2	1.9	0.06
r	0.2	-0.3	0.7	0.2	0.7	0.5

c. Young and small closures fishable biomass (kg/ha) versus closure age (years)

Parameter	Estimate	Lower 95% CI	Upper 95% CI	SEM	t value	Pr(>|t|)
Logistic						
K	363.4	286.6	440.1	36.2	10.0	<0.001
B_0	9.2	-64.1	82.6	34.6	0.3	0.8
r	1.8	-2.1	5.7	1.8	1.0	0.3
Asymptotic						
K	369.8	264.8	474.9	49.6	7.5	<0.001
B_0	11.3	-255.0	277.5	125.6	0.09	0.9
r	0.5	-0.3	1.4	0.4	1.4	0.2

d. Young and small closures fishable biomass (kg/ha) versus closure area (km^2)

Parameter	Estimate	Lower 95% CI	Upper 95% CI	SEM	t value	Pr(>|t|)
Logistic						
K	-1.6 E+8	-1.7 E+15	1.7 E+15	8.0 E+14	0	1.0
B_0	174.8	-643.7	993.3	387.9	0.5	0.7
r	2.0	-43.3	47.3	21.5	0.09	0.9
Asymptotic						
K	511.4	-536.3	1559.1	496.6	1.0	0.3
B_0	-358.5	-4471.9	3754.7	1949.6	-0.2	0.9
r	5.1	-24.6	34.9	14.1	0.4	0.7

Table 6. Top models computed using generalized linear mixed effect (GLMM) and generalized linear modelling (GLM) and the dredge function in the central and western Indian Ocean for: a) remote areas, b) old and large closures, and c) small and young closures. Models presented for all categories with Delta AIC = 0. SEM = standard error of the mean and ICC = Intra-class correlation coefficient.

a. Remote areas best model using generalized linear mixed effect modelling

Predictors	Estimates	SEM	p
(Intercept)	7.88	0.22	**<0.001**
Travel time to nearest human population (hrs)	-0.64	0.37	0.081
Wave energy	-0.65	0.3	**0.028**
Observations		134	
Marginal R^2		0.11	
Conditional R^2		0.16	
ICC		0.14	
AIC		309.727	

b. Old and large closures using generalized linear modelling

Predictors	Estimates	SEM	p
(Intercept)	6.97	0.15	**<0.001**
Human influence	-0.04	0.02	0.093
Observations		70	
R^2 Nagelkerke		0.04	
AIC		40.62	

c. Young and small closures using generalized linear mixed effect modelling

Predictors	Estimates	SEM	p
(Intercept)	4.17	0.31	**<0.001**
Lagoon/Back reef	0.29	0.3	0.338
Slope	1.31	0.41	**0.002**
Log closure age	2.11	0.25	**<0.001**
Observations		16	
Marginal R^2		0.82	
Conditional R^2		NA	
ICC		NA	
AIC		20.79	

Table 7. Summary statistics of coral reef fish fishable biomass at the province biogeographical scale in remote reefs and closures of the Indo-Pacific.

Biogeographic Province	No-fishing Category	n	Median biomass (kg ha^{-1})	95% CI (Upper; lower)	Mean biomass (kg ha^{-1})	95% CI (Upper; lower)
Western Indian Ocean	Remote sites	105	2053.9	1753.4; 2501.8	2053	3002.9; 2267.7
	Large and old closures	70	853.2	896.9; 794.2	867.7	930.7; 804.6
	Small and young closures	19	300.5	433.4; 251.8	335.2	413.7; 256.6
	Pooled	194	1130.1	1253.4;987.1	1772.2	2012.4; 1532.1
Western Indian Ocean*	Remote sites	97	2007.1	2501.9; 1725.9	2546.9	2893.6; 2200.1
	Large and old closures	65	821.9	951.0; 713.2	872.3	960.6; 784.0
	Pooled	162	1278.4	1129.7; 1457.1	1875	2120.0; 1630.0
Central Indian Ocean Islands	Remote sites	29	1258.9	1605.7; 857.5	1778.7	2368.3; 1189.1
Central Indian Ocean Islands*	Remote sites	33	959.5	1510.9; 767.1	1576.7	2126.9; 1026.5
Western Coral Triangle*	Large and old closures	28	196.4	344.7; 127.0	348.4	521.7; 175.1
Northwest Australian Shelf*	Remote sites	4	1022.8	1790.5; 498.4	1083	1984.5; 182.8
Tropical Northwestern Pacific*	Remote sites	45	504.5	639.4; 415.5	666.8	850.3; 483.3
Northeast Australian Shelf*	Large and old closures	15	609.9	921.9; 366.6	710.5	897.2; 523.8
Tropical Southwestern Pacific*	Remote sites	181	1238.6	1423.3; 1082.5	1733.5	1950.2; 1477.6
	Large and old closures	52	551.9	860.8'438.7	699.1	835.9; 562.3
	Pooled	233	1044.3	1228.1; 917.2	1502.7	1682.1; 1323.2
Central Polynesia*	Remote sites	107	834.7	1200.0; 644.1	1044.2	1182.5; 905.9
Southeast Polynesia*	Remote sites	127	740.2	878.4; 610.8	991.2	1152.3; 830.2
Hawaii*	Remote sites	192	752.9	859.8; 652.5	926.4	1028.5; 824.2
Tropical East Pacific*	Remote sites	65	2121.7	2522.9; 1569.6	2310.3	2651.8; 1967.7
Easter Island*	Remote sites	20	508.2	788.5; 258.1	792.4	1229.5; 355.3

* Estimates obtained from remote reefs and high compliance closure data presented in McClanahan et. al. (2019)
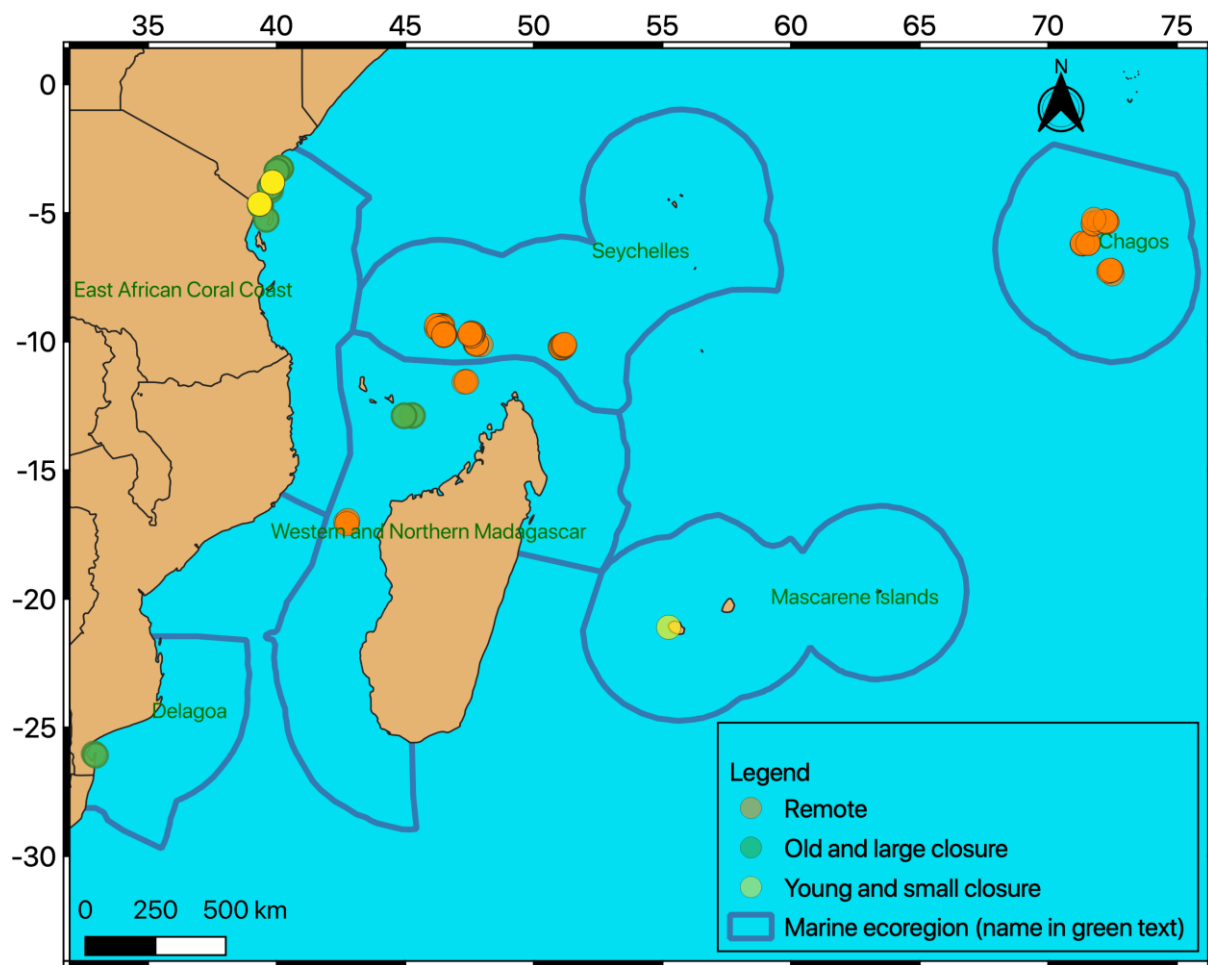
Figures

Figure 1. Location of study sites in Central and Western Indian Ocean and studied ecoregion. The colour intensity of site symbols indicates the sample size
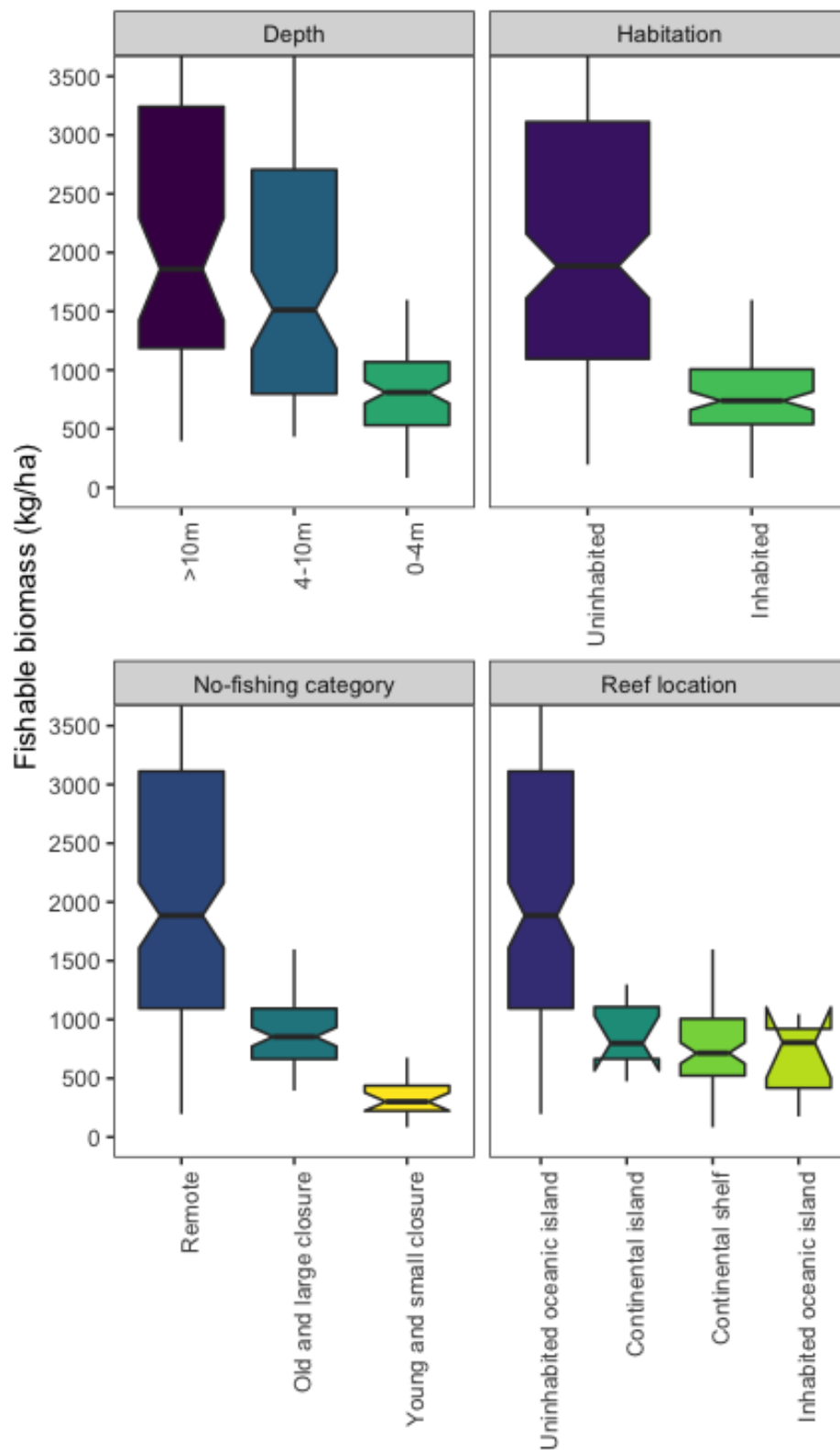
Figure 2. Fishable biomass (kg ha^{-1}) distributions in the Central and Western Indian Ocean
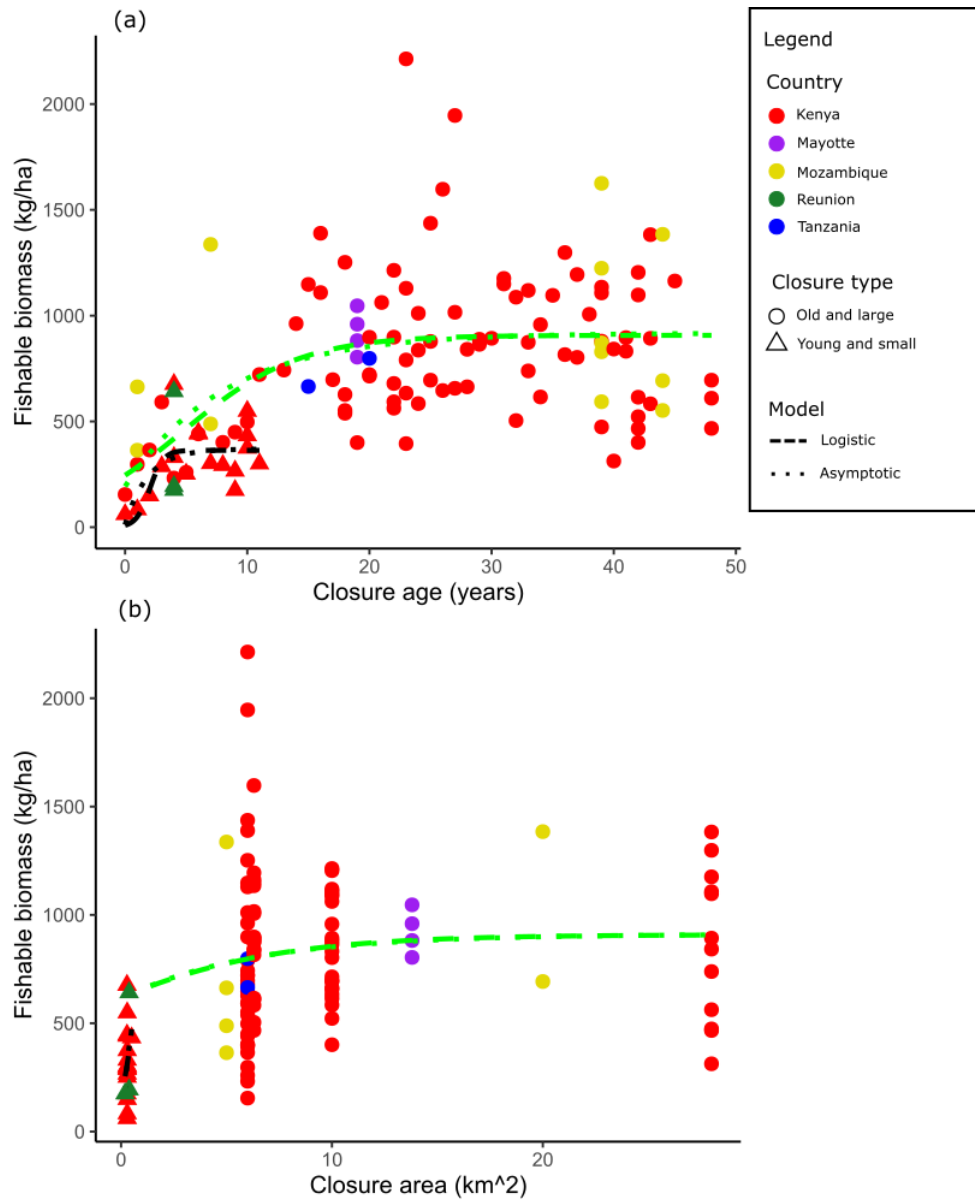
Figure 3. Fishable biomass as a function of closure age and size in Central and Western Indian Ocean coral reefs for old and large closures and for young and small closures:(a) biomass versus closure age; (b) biomass versus closure area. Model lines in green represent old and large closures, whereas lines in black represent small and young closures.