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# Multivariate environment-fish biomass model informs sustainability and lost income in Indian Ocean coral reefs

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## Abstract :

Many tropical reef fisheries are underperforming relative to maximum sustained yields despite their importance for the economies and food security of natural resource dependent people. Assessments of fisheries in tropical reefs have been hampered by the logistic difficulty and costs of making empirical estimates of sustainable yields in multi-species fisheries. To overcome this limitation, we used empirical fish biomass recovery data in high-compliance closures to create a production curve estimate that established biomass and yields at maximum sustained yield (Bmsy). A multivariate machine learning model using environmental and human influence proxies made biomass and yield estimates in 10,815 ~6.25 km2 Indian Ocean cells. Subsequent analyses determined the national over- and under-fishing status. Identified proxies of travel time from markets, depth, and fisheries management were the main drivers of biomass and subsequent status. The East African countries of Kenya, Tanzania, and Mozambique had 18,500 km2 of reef and the lowest regional estimated biomass - losing 17,600 tons of commercial target fish per year. Therefore, the estimated loss is between US$ 50–150 million per year depending on the worth in the fisheries trade's value chain The more populated islands of Reunion, Mauritius, Mayotte, and Comoros have smaller areas (5000 km2) and losing 3000 tons/year, and >US$ 9 million per year. Madagascar has many reefs (13,700 km2) and larger variation in yields with an estimated loss of ~6000 tons/y. Increased restrictions could greatly increase the value of Indian Ocean fisheries by promoting the recovery of target biomass and recovering lost income.

## Highlights

► A stock biomass and yield model created for 10,815 ~6.25 km$^2$ reef cells of the Indian Ocean. ► Seven environmental variables were highly predictive of fish stock biomass. ► Depth, travel time, fisheries restrictions, and governance were key manageable variables. ► 55% of the 70,000 km$^2$ of reef were losing 27,000 tons/year due to overfishing. ► Estimated lost annual income was > 80–270 million US$ depending on value chain position.

**Keywords** : Africa, Fisheries yield, MSY, Stock assessment, Productivity, Poverty, Trade

## 1. Introduction

Sustaining fisheries yields is among humanity's most pressing problems, as outlined in United Nations Sustainable Development Goals. Moreover, eating nutritious fish is among key recommendations for improving nutrition and food security, in both poor and wealthy countries (Willet et al., 2019; Hicks et al., 2019). The Indian Ocean and African regions are among the least nutrition and food secure, with evidence of excess effort and low fish biomass (McClanahan et al., 2016; Zeller et al., 2021). For example, fisheries yields have been estimated to be declining at around 1 million tons per year across the African continent, transforming African countries from a net exporter to net importers of fish food (Srinivasan et al., 2010). Much of this decline may be caused by excess effort. For example, a ~90% decline in catch-per-unit-effort (CPUE) has been reported in the Mozambique Channel between 1950 and 2016 (Zeller et al., 2021). Recovering fish biomass and yields is expected to reverse this decline where underperforming fisheries are identified (McClanahan et al., 2016). Achieving sustainability will require assessing the large-scale state of the fishable biomass, key drivers, and evaluating the feasibility of restrictions. Proposed assessments need to be relevant on a large enough scale to assist national fisheries planning and transboundary governance in a manner that considers socio-economic contexts.

Estimating fish biomass and yields is challenging because biomass values vary with human, environmental, geographic, and ecological influences (McClanahan et al., 2019, 2021, 2022). Fisheries biomass and yield estimates are increasingly being evaluated, better understood, recognized as potentially predictable and therefore relevant to fisheries planning (MacNeil et al., 2015; Cinner et al., 2016, 2018; Maire et al., 2016; Harborne et al., 2018; Gorospe et al., 2018; McClanahan et al., 2019, 2021, 2022; Griffiths et al., 2022). Important human influences on fish biomass include fisheries closures, human population density, markets, travel times to markets, and subsequent fishing effort and management of gear (McClanahan et al., 2015, 2020; Cinner et al., 2016, 2018). Environmental factors are also important and potentially include depth, wave and current energies, temperature, and ocean and benthic productivity metrics among others (Williams et al., 2015; Harborne et al., 2018; McClanahan 2019). These variables can be derived from models and satellite data and therefore used to evaluate potential drivers at global scales (Maire et al. 2016; Pilowsky et al. 2022). As drivers of fish production and biomass are being better understood, so is the potential for scaling and making coarse-scale predictions. Thereby evaluating fisheries status of biomass, yields, and incomes at national scales. Furthermore, it is increasingly possible to explore scenarios, problems, and to compare proposed solutions.

Data-intensive machine learning methods have the potential to identify key drivers and estimate fishable biomass on large scales. These algorithms can improve predictions and evidence-based decision-making. Yet, extensive empirical data are a prerequisite for building and using these algorithms. The efforts of several fish biologists to estimate and share coral reef biomass over large areas in the Indian Ocean and elsewhere makes these data-intensive approaches a possibility in data-poor countries (McClanahan et al., 2021, 2022). Additionally, coral reef maps and environmental data are available at 4 to 10 km$^2$ spatial resolutions (Burke et al., 2011; Yeager et al., 2017). Thus, it is possible to use environmental data and machine learning methods to evaluate drivers or associations with fish biomass and map it at moderate scales. These tools were used by us to make first estimates of fishable and target biomass and production for to faunal province.

The following describes our use of empirical visual census-based biomass to estimate metrics of concern for coral reef fisheries. This included recovery and production of fish in high compliance fisheries closures, evaluations and mapping biomass using multiple environmental variable map layers, and machine learning solutions to make biomass predictions. Combining these data and tools, we made coarse-scale (6.25 km$^2$) approximations of the estimated fishable and target biomass in all the mapped reef cells of the Central and Western Indian Ocean provinces (~10,000 cells). Biomass and production estimates from multiple fisheries closures allowed estimates of biomass and yield benchmarks to determine fisheries status relative to sustainable yields ($B_{msy}$

and $Y_{msy}$). Thereby, allowing estimates of potential yields and subsequently their lost potential yields and income. Reasonable yield estimates are feasible as both fisheries dependent and independent production estimates indicate similar recovery and catch production responses (McClanahan and Graham 2015; McClanahan 2022). Therefore, coarse-scale estimates at this cellular scale were made for fishable and target biomasses relative to MSY thresholds (McClanahan et al 2018). The current losses of yields and income due to over- and under-fishing was therefore made at spatial scales relevant to national and regional planning.

## 2. Methods

### 2.1 Region and study sites

Our study focused on the species diverse Western Indian Ocean tropical reefs where there is a high dependency on fisheries (Hicks 2011). For example, Obeiro et al., (2019) estimated that East African people will have increased fish consumption from 4.8 kg per year in 2013 to 5.5. kg in 2022. There are 12 national jurisdictions and 11 ecoregions within two faunal provinces studied here, namely the Central and Western Indian Ocean faunal provinces ($32^0$E, $27^0$S; $73^0$E -$7^0$N). Coral reef fish communities are notably diverse and productive and a habitat where fishing is focused in all locations except for the pelagic tuna target focus in the Maldives. Many coral reef fisheries have reported leveling to declining total yields associated with increasing fishing power and reduced catch per unit effort (Zeller et al., 2021).

Unsustainable use of fisheries associated with excess fishing effort in near shore areas is frequently reported (McClanahan et al., 2016; Samoilys et al., 2017; McClanahan 2022). Many African coastal reefs and ecoregions lack coral reefs distant from shore. Therefore, nearshore reefs are potentially vulnerable to both growth and recruitment overfishing (McClanahan 2020). Some of the patterns in biomass production and limits appear to be region-wide and moderately predictable based on evaluations of several environmental and human influences (McClanahan 2019).

Provincial-wide studies of biomass found the strongest factors were the differences between fished and unfished seascapes with weaker environmental effects (McClanahan et al., 2021). Similarly, multispecies production or recovery rates of total or fishable biomass in various regional compilations generally indicate mean r values of ~0.23+0.08 (SEM) with moderate variability between classifications, such as total, fishable, and target groupings (McClanahan 2022). Therefore, coarse, and large-scale evaluations of unfished biomass and recovery data in fished seascapes should fall within modest intervals and allow for making first approximations of fisheries status and yields (McClanahan 2022). Unfished seascapes or wilderness display different patterns of biomass and possibly recovery rates than fished seascapes (McClanahan et al., 2019, 2022). Here, we focus and use the variables appropriate for the biomasses and production values for fished seascapes.

## 2.2 Model overview

Below we describe the process of estimating biomass and production using four statistical options including a Random Forest machine learning algorithm. We chose the strongest option to estimate fishable and target biomasses and subsequent production models. Models used field-based compilation of fishable and target biomass records from underwater surveys in several countries and ecoregions of the two faunal provinces. We compiled environmental variables to build and compare statistical models. This process allowed us to make predictions of biomass in reef-dominated cells or planning units where biomass assessments were not available. To evaluate the status of these biomass estimates, we developed a biomass-production model based on the same census-based empirical data collected in high compliance closures of different ages or time since closure to fishing. This allowed estimates of biomass and yield benchmarks that could contextualize the larger scale biomass estimates. The larger scale spatial database or map (10,815 reef cells at the ~6.25 km$^2$) was based on a large but still limited empirical fishable biomass data set (591 sites) relative to the estimated 67,600 km$^2$ of reef areas in the two provinces. Therefore, this sets limits to evaluating large and finer scale variability. Yet, studies in this region suggest modest confidence intervals around biomass, recovery, and production estimates (McClanahan et al. 2021). We present our model results to demonstrate the capacity of current knowledge and tools to make large-scale predictions. Future efforts may be able to make more spatially resolved models.

### 2.3 Biomass estimates

Experienced field investigators used similar belt-transect methods to contribute 591 sites to the coral reef fish census data (R. Bemahafaly, H. Bruggemann, P. Chabanet, S. D'Agata, N. Graham, and T. McClanahan). The study sites were located on the windward and leeward sides of coral reefs in depths from 1 up to 20 meters at low tide (the region's tidal range is ~1 to 4 meters). Visual censuses were undertaken between the years 2005 and 2019. Sites included a variety of management systems and reef habitats, including reef slopes, crests, and lagoons in depths between 1 and 20 m. Sites were all located on calcium carbonate dead coral bottoms colonized by hard and soft corals and various algae, with sand and seagrass being a smaller portion of the cover. Average fish biomass estimates from repeated field transects were pooled at the site and cell level. We pooled the three most recent sampled years and samples taken under the same management and habitat classifications. Data across this 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 maximum biomass levels and life histories (McClanahan et al., 2021, 2022).

Biomass estimates were based on instantaneous visual counts. Reef-associated fishes were identified to family or species level, numbers counted, total lengths (TL) estimated, and converted to weights with length-weight relationships (McClanahan & Kaunda-Arara 1996; Kulbicki et al., 2005). We pooled biomass and evaluated in the two groups of fishable and target biomass. These groups have different maximum biomasses as target is a portion of fishable biomass. Moreover, evaluations of recovery in closures indicate they have somewhat different recovery or production rates (McClanahan 2022). Fishable biomass summed the weights of all observed individuals >10-cm in 23 families (McClanahan et al., 2019). These included the key caught families and included the Acanthuridae, Aulostomidae, Balistidae, Carangidae, Chaetodontidae, Diodontidae, Fistularidae, Haemulidae, Holocentridae, Labridae, Lethrinidae, Lutjanidae/Nemiperitidae, Muraenidae, Monacanthidae, Mullidae, Pinguipedidae, Pomacanthidae, Scaridae, Serranidae, Scorpaenidae, Siganidae, and Sphyraenidae. Sharks, damselfish, and some plankton feeding groups (i.e., Caesionidae) high in the water column were excluded due to the difficulty of detection and variable but often low influences on fish biomass between regions, remoteness, and fishing impacts (D'Agata et al., 2016; Juhel et al., 2018). Target biomass was the sum of all commercially exploited reef taxa >10-cm, which included Carangidae, Haemulidae, Holocentridae, Lethrinidae, Lutjanidae/Nemipteridae, Mullidae, Scaridae, Serranidae, Siganidae, Sphyraenidae, and Labridae >20cm (McClanahan 2022). Fishable and target biomass values were strongly positive correlation (r=0.96) (Supplementary Figure 1). Target being around 48% of fishable biomass with some deviance from the best-fit line in some of the high biomass sites. Target biomass are the most economically valuable and their yield is a proxy of commercial value whereas fishable includes taxa that are locally consumed and important for food security.

## 2.4 Fisheries independent and dependent yield estimates

Fisheries yield estimates are published estimates of fisheries-independent production based on measured biomass recovery rates in fisheries closures (McClanahan 2022). We evaluated biomass recovery in fished seascapes in 13 high compliance fisheries closures in 5 Indian Ocean countries (McClanahan 2022). Biomass estimates from transects were pooled into fishable and target groups as above, plotted against time since closure to fishing, and r and K values determined from best-fit logistic models. The fits were therefore based on 99 replicates in total for a range of cessation of fishing between 0 and 45 years. The best-fit K for fishable biomass was 113 tons/km$^2$ and r was 0.27. For target biomass, the K was 54 tons/km$^2$ and r was 0.29. Using the Schaefer model this would suggest a sustainable fishable yield or $Y_{msy}$ of 7.6 tons/km$^2$/y at a $B_{msy}$ of 57 tons/km$^2$ and a target $Y_{msy}$ of ~4.0 at $B_{msy}$ of 27 tons/km$^2$. These values therefore provided sustainable biomass ($B_{msy}$) and yield ($Y_{msy}$) benchmarks for the status of fisheries in the evaluated cells.

Fisheries dependent field-based measurements of yields from 2 reef fisheries catch compilations reported 3.0 (SD=2.7) and 5.6 (SD=3.8) tons/km$^2$/y for 7 countries in the Indian Ocean (Samoilys et al., 2017; McClanahan 2018 supplement). There was high variation, that might be explained by variable biomass and effort relative to MSY. Furthermore, landed catch values are expected to be lower than fisheries independent models for several reasons but primarily because not all landed catch are weighted. Moreover, the above fisheries independent biomass recovery data has been tested for the ability of various fisheries production models to predict long term (18-23 years) yields in Kenyan fringing reefs (McClanahan and Azali 2020). Equilibrium and non-equilibrium variations of the Fox, Schaefer, and Pella-Tomlinson models have been evaluated. The best-fit models were the non-equilibrium Schaefer or logistic and Pella-Tomlinson when the above independent recovery r and unfished K biomass values were used. These models differed based on the various aspects of the data, such weather or not the data were pooled by landing sites, the catch was rising or declining, and r and K were fixed. The Pella-Tomlinson model using pooled data predicted a MSY between 4.9 - 6.7 tons/km$^2$/y and Schaefer between 5.5 - 5.7 tons/km$^2$/y. The higher variability in the Pella-Tomlinson was due to a need to consider reasonable recruitment rate parameters or z value. Therefore, to reduce assumptions and variability we used the Schaefer or logistic growth model with the above r and K values (Equation 1).

**Equation 1.** Logistic growth equation, $B_t$ is the biomass in year $_t$, Bo is the initial biomass, K is the carrying capacity, r is the recovery rate:

$$B_t = \frac{K}{1 + \left(\frac{K - Bo}{Bo}\right) e^{-rt}}$$

Fisheries yields were estimated using the predictions of the differential equation from the logistic growth model or the Verhulst equation (Verhulst 1838; Bacaër 2011), which predicts yields for biomasses obtained from the environmental biomass model described below (Equation 2).

**Equation 2.** Verhulst differential equation of logistic growth, where B > K estimates the yield at the given B:

$$\frac{dB_t}{dt} = rB\left(1 - \frac{B}{K}\right)$$

**Equation 3.** The MSY can also be calculated for the cells K with this equation:

$$Ymsy = \frac{rK}{4}$$

The state of the fisheries is often presented as relative to $B_{msy}$ or $Y_{msy}$ as either “over or under fished” or > <MSY. In some cases, in remote reefs where predicted biomass (B) of a cell exceeded the carrying capacity (K) of the estimated logistic growth equation, yields were set to zero. Empirical evaluations of fish biomass suggest that MSY also align with some other important metrics of fisheries ecosystems including species diversity and ecological processes (Graham et al., 2017; McClanahan 2018; 2022).

## 2.5 Building the spatial model

We examined the empirical relationships between the fishable and target biomass and several key environmental and human pressure variables expected to influence the fish communities and biomass (Supplementary Table 2). The best models were then used to predict biomass and yields and compare them to the benchmarks in all examined reef cells.

### 2.5.1 Environmental and geographic variables

Several environmental and human pressure covariates were evaluated for potential proxies of biomass. Environmental variables included sea surface temperatures, net primary productivity, wave energy, reef area, sediments, and a climate stress index developed for coral reef habitats (Maina et al. 2011). Daily sea surface temperatures (SST,°C) from 1985 to 2017, were obtained from the National Oceanic and Atmospheric Administration (NOAA), Coraltemp v1.0 dataset provided at a ~5km spatial resolution. We computed the mean, median, maximum, and minimum SSTs for each site and reef cell spanning the entire 1985 – 2017 period. We retained SST median for further analysis due to its higher predictive power and low correlations with other variables. The climate stress index includes exposure of corals to radiation stress factors (i.e., temperature, ultra-violet light, and doldrums) and stress-reducing factors (i.e., tidal range and temperature variability). We derived the sedimentation index from merged satellite sensor case 1 and case 2 mean chlorophyll-*a* (mg $m^{-3}$) estimates obtained from ocean color observations (http://hermes.acri.fr/GlobColour).

We obtained net primary productivity (NPP, mg C $m^{-2}$ $day^{-1}$), wave energy (KW/m), and the total reef area ($km^2$) in a 100-km buffer radius from the Marine Socio-Environmental Covariates (MSEC) dataset (Yeager et al. 2017) provided at a resolution of ~2.5 arc minutes (~4.6-km at the equator), by the National Social Environmental Synthesis Center (SESYNC). MSEC mean net primary productivity estimates were derived from modelled NOAA Coast Watch 8-day composite layers for the 2003 – 2013 period (http://coastwatch.pfeg.noaa.gov/). Wave energy flux mean estimates were derived from the NOAA Wavewatch III hindcast cast dataset based on gridded wind data from climate reanalysis and spans a 31-year period from 1979 – 2009 (http://polar.ncep.noaa.gov/waves/CFSR_hindcast.shtml). We derived reef area estimates from the 500-m resolution global coral reef habitat maps provided by Reefs at Risk Revisited (Burke et al., 2011). To estimate the total reef area at 100-km radius, we created a corresponding buffer based on user supplied geographic coordinates and the number of reef cells falling within the buffer, which were then multiplied by 0.25 $km^2$ (area of the 500-m reef cell). These metrics should be seen as proxies for potential causative effects that cannot be explicitly evaluated due to mismatches in the spatial and temporal resolution of the various data sets.

### 2.5.2 Human pressure variables

We used travel time to the closest market (i.e., country, and regional capitals) or nearest human settlement with population of >25,000 as a proxy of fishing pressure (D'Agata et al., 2016; Maire et al., 2016). We derived population estimates from the CIESIN Gridded Population of the World (GPW 2015 v4) dataset produced by the Socioeconomic Data and Applications Center (SEDAC) at 250-m spatial resolution (Ciesin 2016). We estimated the travel time using the friction layer after Weiss et al., (2018) and the modified average boat speed of 7 km $h^{-1}$ in seven countries (Maldives, Comoros, Mauritius, Madagascar, Mozambique, Kenya and Tanzania) and 15 km $h^{-1}$ in five wealthier territories (Reunion island, Seychelles, Mayotte, Chagos). We used the nation as a covariate in the model since it was likely that national laws or cultures would affect fishing. Several countries have national fishing laws, but compliance and enforcement vary. Governance and cultural factors should influence national fishing behaviors.

We derived our spatial map of human use or management from The United Nations Environmental Program – World Conservation Monitoring Center (UNEP-WCMC) coral reef distribution data, which we modified further based on our experiences and observations of management (McClanahan et al., 2016). We classified the management at each cell into four categories, namely low and high compliance no-take closures, and restricted and unrestricted fishing. The management categories for each cell were based on maps, legal records, published literature, and expert knowledge. We included all these categories as covariates in the model for each grid-level biomass record. Following an evaluation of the biomass data, we pooled the restricted fishing and low compliance closures as their biomasses were statistically similar. This pooled group did, however, differ statistically from unrestricted fishing and high compliance closures. For the few cell locations where the reef area was under more than one management system, we used the dominant management coverage. The resulting data allowed us to evaluate 10,815 cells according to their fisheries status, as open-access fisheries, restricted fishing gears, and high compliance closures by ecoregion and nation.

### 2.6 Statistical models

We compiled a total of 15 geography, environmental and human pressure variables. Variables matched the locations of the fish biomass field data including country, depth, habitat types, reef area in the surrounding 100-km, net primary productivity, sediment index, median sea surface temperatures, climate stress index, wave energy, fisheries management, closure age, nearest market and settlements travel times and gravity (Supplementary table 2).  We investigated collinearity between predictor variables through Spearman rank correlations and variance inflation factors and retained variables with correlation coefficients <0.7 and VIF < 5 (Dormann et al. 2013). Further selection of variables followed Akaike information criterion (AIC) in the generalized linear and additive mixed models, and we included two randomly generated variables in the random forest and boosted regression models to assess importance of retained variables. We retained seven out of the initial fifteen variables for further evaluation based on fits to biomass data.

We tested four statistical models for their ability to predict the fish biomass field data using the above environmental and human pressure variables. These were: Generalized Linear Mixed Model (GLMM), Generalized Additive Mixed Model (GAMM), Random Forest Model (RFM) and Boosted Regression Tree (BRT). Prior to testing, we partitioned the observed biomass into two nested datasets: 1) a calibration dataset made up of 70% of the total dataset (n=430) used to estimate the model parameters; and 2) a validation dataset (n=164) used to assess model predictive ability. We chose the 70/30% ratio as a tradeoff between precise estimates of model parameters and accurate validation of the model (Authier et al., 2017). We then fitted the four models using the above variable to predict the fishable and target biomass response variables using the test dataset. Thereafter, we compared the predicted biomass with the actual observed biomass of the validation data. This procedure provided an independent parameter estimation to assess and compare the predictive abilities of the models. Thereby, we used the Theil's inequality coefficient (U) and the adjusted $R^2$ between the observed and predicted values to estimate each model's forecasting capabilities (Theil 1966). The closer U was to 0, the better the forecast method, while a value closer to 1 was no better than a naive forecast.

### 2.6 Spatial mapping

Finally, we used the spatial grid map, environmental and human pressure database, and best-fit model described above to predict biomass and yield in each spatial cell. RFM algorithms cannot predict values outside the range of training set. As a precaution to avoid predictive extrapolation, we filtered the spatial dataset so that the range of each predictive variable was comprised in the range of the explanatory variables used in the dataset used for model building. Overall, we used 94% of the database to predict fishable biomass at 5 meters. We determined the lost yield potential due to overfishing or underfishing as the absolute difference between the estimated yields at each reef cell and the maximum sustainable yield ($Y_{msy}$; Equation 3) (Schaefer 1954). Thereafter, we multiplied the lost potential yields by the reef area in each cell (ranging from 4.5 to 6.1 $km^2$ depending on latitude) and summarized values at the country or ecoregion levels (Spalding et al., 2007). For visualization and mapping purposes, we divided the cells in 3 categories, namely overfished ($B/Bmsy < 0.9$), sustainable ($B/Bmsy$ 0.9 - 1.1, i.e., within 10% of MSY), and underfished ($B/Bmsy > 1.1$).

## 3. **Results**

### 3.1 Biomass predictive models

Biomass models fitted to the four modelling options indicated that the Random Forest Model (RFM) had the best-fit between environmental variables and biomass (Supplementary Figure 2).

RFM had a high best-fit (cross-validation $r_{cv}^2$=0.85) and the highest predictive accuracy measured by the TheilU index (TheilU = 0.06). The fits to the other models were modest to good but fits declined relative to RFM for the Boosted Regression Tree (BRT; $r_{CV}^2$=0.71, TheilU=0.08), Generalized Additive Mixed Model (GAMM; $r_{CV}^2$=0.60, TheilU=0.09), and Generalized Linear Mixed Model (GLMM; $r_{CV}^2$=0.53, TheilU=0.10). Therefore, the following evaluation of biomass and yields are based on the RFM model at 5 meters.

## 3.2 Environmental associations

Partial plots of the covariate associations with the target biomass indicate, in order of declining importance, depth, travel time, management, country, sea-surface temperature (SST), reef area, and mean net primary productivity (Fig. 1a). Target biomass increased with depth, travel time, and with increasing fisheries management restrictions (Figs. 1b, c, d). Maximum target biomass for the temperature metric was unimodal and predicted to peak at a mean value of between 28-29$^{o}$C (Fig. 1f). Similarly, the biomass productivity relationship was unimodal hump-shaped with a maximum at around 1500-1600 gC $m^{-2}$ $day^{-1}$ (Fig. 1h). Reef area was also unimodal but u-shaped with a minimum partial biomass at low to intermediate reef densities (Fig. 1g). Higher partial biomasses at the national level were found on remote northern island nations, such as the Chagos, Maldives, and Seychelles, and lower biomass on the landmass of the East African coastline and large island of Madagascar (Fig. 1e). Additionally, the islands of Mauritius, Comoros, and Reunion had low partial biomass. There were similar strong fits and patterns with environmental variables for the fishable biomass, except that country was a less important variable than found for target biomass (Supplementary Figure 3). Moreover, the environmental associations with fishable biomass were largely comparable with target responses. However, NPP was not unimodal, and biomass declined at high levels of NPP production, and there was less variability with SST and reef area variables.

## 3.3 Spatial model of fish biomass

Using the RFM-calibrated model, we mapped and pooled predicted biomasses at the grid level and jurisdictional levels in 11 ecoregions across the 12 nations (Fig. 2). The distribution among fisheries restriction categories indicated that fished reefs had variable biomass, but median values were often below a $B_{msy}$ that would achieve the target $Y_{msy}$ of ~4.0 tons/km$^2$/year (Fig. 3). Median restricted fishing areas were often close to the MSY, while unfished reefs occupied the high biomass and lower yield levels.

Presenting target biomass levels in 5 categories, two below (0 to 13.5 and 13.5 to 27 tons/km$^2$) and three above (27 to 40, 40 to 53 and > 53 tons/km$^2$) the MSY threshold, indicated large heterogeneity among jurisdictions (Table 1). Thus, among the 10,815 grid cell reef locations, 19.6% were estimated to have severely depleted biomass of <13.5 tons/km$^2$ and 54.8% to have unsustainable biomasses. The most depleted and unsustainable locations were along the African coastline from Kenya to Mozambique but also Comoros and Mauritius (Fig. 2). The model estimated that Mauritius had high biomass among reef territories far from the main island in remote areas, similar to the Chagos Archipelago (British Indian Ocean Territory).

Evaluating fishable biomass at the ecoregional scale indicated distinct ecoregions. The most numbers of reef cells (the Maldives, Western and Northern Madagascar and East African Coral Coast) showed considerable variation in their biomass status (Supplementary Table 1). For example, 88% of Maldives cells had biomass above $B_{msy}$, whereas only 9% of East African Coral Coast was above $B_{msy}$. Western and Northern Madagascar biomass were more evenly distributed, with half the biomass both above and below $B_{msy}$ (Table 1a).

### 3.4 Biomass and yield patterns in nations and ecoregions

Target biomass was highly variable among the 12 national jurisdictions (Fig. 2; Table 2). For the whole region, the model predicted that overfishing resulted in an estimated loss of 26,400 tons/year largely located along the African coastline. The few areas with sustainable or underfishing were associated with unfished fisheries closures. For example, these locations were cells in Kenya, Tanzania, and Mozambique designated marine reserves. Madagascar, Mozambique, and Tanzania had large numbers of reefs and therefore estimated to be missing a yield potential of 6000 and 8800 tons per country per year due to overfishing. Countries, such as

Comoros, Mayotte, Kenya, and Reunion also had biomass below $B_{msy}$, but sourced from smaller reef areas and therefore more modest estimated losses in target yields due to overfishing.

Total potential yields lost due to underfishing was 46,900 tons/year of which most was in the marine protected area of the Chagos or British Indian Ocean Territory with contributions from the Maldives and remote areas of Mauritius and Madagascar. In Chagos Islands, 100% of the reefs had estimated target biomass >54 tons/km$^2$. Nearly all the lost estimated yield was due to underfishing at long distances from the shoreline and cities. Using the 3 category status outputs (overfished, sustainable, underfished) (Fig. 2), the model predicts, 14% of the reef cells in this region were fished sustainably ($B/B_{msy} = 0.9 – 1.1$), 37% were unsustainably fished ($B/B_{msy} < 0.9$), while 49% were underfished, ($B/B_{msy} > 1.1$).

## 4. **Discussion**

Our comparative modelling procedure indicated the potential to make reliable coarse-scale estimates of fishable biomass and yields. Specifically, we identified 3 common human variables (travel time, fisheries management, and country), 2 geographic (depth and reef area), and 2 environmental variables (SST and NPP). Therefore, with 7 variables, the Random Forest Model (RFM) algorithm was able to predict fish census biomass data with 85% accuracy as determined by cross validation. Even the weakest method, GLMM, had a moderate fit that predicted 53% of the variation. This improves a previous model used to predict biomass and recovery rates based on 7 variables and GAMM statistical method (Adjusted $r^2$=66%) (McClanahan et al., 2016). The previous model was based on less field biomass estimates, more management categories, maximum rather than mean temperatures, and human population, but contained no ocean productivity or national variables. The response patterns between models were similar but some combination of more data, the RFM structure (e.g., non-linearity and complex interactions among explanatory variables), and additions, such as the inclusion of nation, improved the model fit to this high predictive level. Including nation was important and may reflect some aspects of either the national fishing cultures or governance, diets, and management effectiveness not easily obtainable and quantified (Mora et al., 2009).

Biomass is a key variable for evaluating highly diverse and spatially variable reef communities (McClanahan et al. 2011). It has been hard to estimate from fisheries dependent methods and requires visual census expertise that is restricted to small-scale sampling. Therefore, it has been missing for most tropical countries with coral reef fisheries and undermined efforts to evaluate fisheries status on a global basis (Worm et al., 2009; Hilborn et al., 2020). The approach we used suggests a way forward, potentially connecting smaller-scale field sampling with high coverage proxies to increase the scale of evaluations (Harborne et al., 2018; Griffiths et al., 2022). Given the paucity of reef fish biomass assessments in the tropics, this approach is needed to evaluate status and a focus on sustainable management to reduce lost food and income. It also identified potentially manageable drivers of their status, such as markets, travel times, national governance, depth, and fisheries restrictions and closures.

While there was considerable spatial variability in fish biomass at multiple scales, the single most important finding was the broad extent of overfishing in reefs accessible to fishing. Our methods allowed identification of areas with lost yields and income potential, sustainable yields, and the remote or wilderness locations that may require special conservation status (McClanahan 2020). Much of the variability reflects accessibility, dependence, market distances, and management of these fisheries but with some unimodal influences of temperature, reef area, and productivity. Sustainable fishing was uncommon unless cells were far from shore and people or there were active fisheries restrictions, which was a small part of the total reef area. Underfishing was largely a reflection of travel and capital costs to access remote biomass. There are likely no net profits when fishing far from shore and markets depending on the methods and costs used to capture fish (Kamakuru 1992). Further, a large-scale evaluation of the expenditures of energy used to capture fish in this region suggest little net energy gains in recent times (Zeller et al., 2021). Thus, fisheries subsidies may make capture cost effective for fishers but at the long-term cost of further declines in biomass and increased long-term poverty (Sala et al., 2018; McClanahan and Kosgei 2019).

### 4.1 Evaluations of national status

Most of the East African Coral Coast ecoregion (Kenya, Tanzania, and Mozambique) has been fished unsustainably. Here, fishers have largely been reliant on human and natural power to access reefs and their diets are highly dependent on local natural resources (Hicks 2011; Zeller et al., 2021). These three countries having uniquely severe overfished reefs with estimated target biomass often <13.5 tons/km$^2$. Kenya has the most extreme overfishing with estimates of 57% of the reefs severely overfished, 78% overfished, and most of the remainder being either near the national parks and reserves or the remote reefs of northern Kenya. Kenyan reefs are close to shore (<2 km) and this easy accessibility has likely resulted in an estimated national level loss of 2,400 tons/year of target yields due to overfishing. This is a conservative estimate of lost potential as it would double if fishable biomass was included.

An independent evaluation of Kenyan catch at landing sites suggested that about 40 to 50% of the total reef catch is used for local and home consumption and not entering the commercial trade (Wamukota and McClanahan 2017). Target yields are a good estimate of lost income, as these yields are valued commercially whereas non-target taxa are used for home consumption. Target yields more easily enter local and national markets, and prices vary from landing site to final sales ranging between US$ 3 – 10 per kg (McClanahan, T. unpublished data). Therefore, depending on the position in value chain, the model suggests that no less than US$ 7.2 – 24.0 million dollars are being lost annually. The loss of non-target or local food fish has a lower value of ~ $1.5 - 2.0 per kg but would add considerably to the total potential loss in economic value.

Mozambique and Tanzanian reefs are generally further offshore than Kenya, have lower human population densities, and greater distances to markets. Nevertheless, biomass and yield estimates in both countries indicated pervasive unsustainable fishing of target biomass, or 91% and 96% for Mozambique and Tanzania respectively (Table 2). Two exceptions were the reefs around the Mafia Island Marine Park in Tanzania and the Delagoa area (89 reef cells) of southern Mozambique. These two areas are large enough that they might be the most extensive reef areas with modest fishing impacts. These two countries have large reef areas and therefore the total estimated losses of 6450 tons year$^{-1}$ and 8800 tons year$^{-1}$ indicates total losses of income 3 to 4 times those of Kenya. Therefore, the estimated loss of export market value for reef production due to overfishing in these 3 countries would be ~$53 to 175 million per year depending on the estimated value along the market chain. Again, this did not include the value of the catch primarily used for local food or other non-reef habitats that may be similarly overfished in these subsistence economies.

If as suggested by Obiero et al., (2019), East Africans eat 5 kg per person per year, this loss could provide the annual fish consumption needs for 1.3 and 1.8 million people in these two countries or 5.6 million in the region if the same consumption rates applied. And yet, the lack of wilderness in the East African Ecoregion leaves these fisheries susceptible to recruitment overfishing and the loss of species, as has already been identified for Kenyan reefs (Buckley et al 2017; McClanahan 2021). Given the lack of wilderness and the considerable losses of income and food security, there are clear incentives for improved fisheries restrictions to avoid further losses and possible fisheries collapses.

Madagascar has a large total reef area and appeared to have more variability in terms of sustainability. The southern part of the country near Toliara city was overfished but sustainable estimates more patchily distributed in the west and north. The aridity of southern Madagascar and the Toliara market creates a high dependence on marine resources and incentives to overfish. Here, the fisheries are highly dependent on small and productive fish and invertebrate species, such as octopus (Bruggemann et al., 2012; LeManach et al., 2012). Overfishing has led to large changes in the ecology of southwestern reefs that, when combined with rare deadly temperature fluctuations, has led to major losses of coral cover and replacement by large fleshy algae stands (McClanahan et al., 2009; Bruggemann et al., 2012). Small community octopus' closures are currently being adopted to maintain fisheries production to provide for export incomes (Oliver et al., 2015; Rocliffe and Harris 2016). The northern and eastern regions of Madagascar are more variable in markets, access, and dependence on fisheries and thus have more moderate biomass and levels of sustainability (McClanahan and Jadot 2017). It is likely that the higher rainfall in the north and eastern regions creates less dependency on marine resources. Therefore, the status of sustainability in Madagascar is variable and nationally not an overfished "dark-spot", as has been suggested when relying on more spatially limited biomass and yield estimates near Toliara and other population centers (Cinner et al., 2016; Golden et al., 2021).

Estimates in smaller islands of the Indian Ocean also indicated a variable status that reflected several of the studied variables and the overriding importance of the nation. Some of this variability was likely due to human population densities but with notable deviations. The islands of Reunion, Mayotte, Comoros, and Mauritius (including Rodrigues) have high population densities that differ in their wealth and reliance on tourism. Mauritius was predicted to have high biomass in remote islands, such as Agaléga and Saint Brandon (Cargados Carajos) that bring up the national average, but the main densely populated island had few underfished locations. Cargados/Carajos and Tromelin Island are unique, remote, and understudied ecoregions with 118 reef cells.

The reef area in Reunion is very small and near to shore. Thus, these factors combined with the high human population density was the likely cause of overfishing. Poaching has been reported in the reserves and therefore these were classified as low compliance (P. Chabanet, personal communication). Comoros has more limited area-based conservation and higher poverty and dependence on agriculture and pelagic tuna fisheries (Chassot et al., 2019; Ibouroi et al., 2021). The model predicts the highest target biomass occur on the island of Moheli, which has a large marine national park on smaller satellite islands (Granek and Brown 2005). These 4 countries have a more modest loss of ~3000 tons/year due to more limited reef area. However, this still comprises a lost commercial value of >US$ 9 million.

The Maldivian ecoregion is unique in that the population is dependent on offshore pelagic fisheries and high-end tourism and, thus 89% of the reef cells were estimated to be sustainably fished. Reef fish caught in the Maldives are often used as bait in the tuna fishery. Seychelles reefs represent a mixture of inhabited and uninhabited islands with an estimated 69% of their biomass above sustainable levels and a smaller estimated loss of ~100 tons/km$^2$/y due to overfishing. The underfished islands of the region were largely (67%) located in remote areas that were not legally, easily, or profitably accessed by fisheries. For example, the Chagos Archipelago, which has 1211 reef cells or 8740 $km^2$ of reef contained in a large, protected area still exhibits some losses of top predators and biomass (Graham and McClanahan 2013).

## 4.2 Caveats

Despite the good fit of the RFM, there are several potential weaknesses and caveats that require consideration. These are primarily the coarse scale, uneven distribution of data collection in the region with a bias towards accessible reefs, the use of a single yield model and coefficients for all cells, no temporal variability in environmental conditions, and the potential failure to not evaluate important variables that could create variable-omission "blind spots". The coarse mapping at the cell scale will contain a considerable amount of diversity of habitats, depths, and other local factors that will limit precise spatial predictive capacity. The spatial scale of the biomass estimates at ~6.25 $km^2$ is, however, probably appropriated the scale of fisher movements and gross level biomass estimates in much of the region. While movement capacity has increased greatly during the past 70 years, much of powerboat fishing has not been focused on nearshore and shallow coral reefs that we evaluated (McClanahan and Abunge 2018; Zeller et al., 2021).

Our purpose was to make gross estimates that can identify areas and approximate amount of the losses of yields, food, and income. Thereby creating an incentive to invest in actions to improve management and recover the losses. So, while future efforts will require more refined or precise mapping and biomass estimates, these are not likely to change the overall picture of the need for protecting resources to avoid poverty. Future efforts should consider environmental and habitat variability and especially where lower productive potential exists in this region. Overestimates of production potential can lead to unrealistic policies to attempt to access resources that are not available or have not net profits (Pauly and Zeller 2016). Our methods do not account well for the costs and changes in actual local fishing effort and restrictions, which may all influence yields and profits in both negative and positive ways (McClanahan and Azali 2020; McClanahan 2020). For example, there can be fairly large differences in the success of restrictive management based on the temporal and spatial extents of the restrictions (McClanahan and Graham 2015; McClanahan et al., 2022). Travel distance used here was expected to account for some of this variability in effort but other local factors such as boats sizes, power, and gear use may add to the unexplained variability.

Our model settings used 5-m depth to estimate biomass on this scale of the cell, whereas the cells are expected to have more variable depths. This decision was made to simplify the presentation and because the artisanal fishing in this region is largely focused on the accessible shallow water reefs and seagrass ecosystems. Our choice was intentional to help identify areas of overfishing and to balance the various aspects of fishing effort, benthic and fisheries productivity, in the absence of high-resolution bottom mapping. Using a greater mean depth in the model would decrease the estimates of unsustainable fishing. Depth is a refuge from fishing in this region (Tyler et al., 2009; Osuka et al., 2022), but it is expected that the larger the shallow area of a reef cell, the higher the fishing impacts, productivity, and yields (McClanahan 2019).

Our yield model was created from the recovery of fish biomass in 13 fisheries closures spread throughout the region. Subsequent broad-scale studies of biomass throughout the two faunal provinces evaluated here suggest modest variability in the final biomass or K within fished seascapes (McClanahan et al., 2021). Spatial variability in the growth or the r coefficient are more difficult to evaluate as they require studying recovery of fish biomass over time in specific environments. To do this, it is often necessary to pool data from different habitats and environments to sufficiently replicate across what is often >40-years to measure full biomass recovery. While our sample of diverse closures throughout the region found a good logistic fit to the recovery of target biomass with time ($R^2$ = 72%; McClanahan 2022), there are recovery compilations with lower r values (MacNeil et al., 2015). The degree to which this is due to variability in the types of biomasses, ocean basins, or environments is not known but remains an important area for future research. Biomass and recovery compilations suggest that r and K values are steeply inversely related and likely driven by differences in body sizes, growth rates, and population connectedness in the seascape (McClanahan and Azali 2021; McClanahan et al., 2022). Thus, in wilderness coral reefs, large-bodied sharks, groupers, and jacks may increase equilibrium biomasses but reduce the long-term production. Our model was therefore calibrated for the common fished seascapes. This region is likely to have higher environmental productivity but also smaller and more productive species than some other reef environments.

Finally, our model was developed on biomass data collected in the past. However, climate change is expected to lead to a change in marine animal biomass in many regions, potentially negatively affecting fisheries (Cheung et al., 2013; Tittensor et al., 2021). Our and a similar previous model suggested an optimal mean and maximum temperature as well as productivity range for reef fish biomass (McClanahan et al., 2016; Harborne et al., 2018). Recent studies have shown that among the correlates of fish biomass are biodiversity, global temperature gradients, and human impacts (Duffy et al., 2016; Mellin et al., 2016; McClanahan 2022). It is expected that the temperatures and productivity in this region will move further away from these optimal levels with consequences for biomass and yields. Further, climate driven benthic changes to coral reefs may alter dominance among targeted fish, thereby influencing yields (Robinson et al., 2019), and reef management responses (Graham et al., 2020). Future work will need to evaluate the consequences of these various simplifying assumptions. Our results do, however, identify the gross scale of the problem and where management responses are most needed.

### 4.3 Conclusions

The WIO region is faced with challenges for food insecurity and biodiversity losses. These are associated with losses of fisheries yields and income. Nevertheless, MSY models for the better studied fisheries in Kenya indicate that employment could be more than doubled by increasing biomass closer to $B_{msy}$ (McClanahan and Azali 2020). Thus, in much of this region, there is not yet a hard trade-off between production, employment, and biodiversity (Brander 2010; Hilborn et al., 2021). Increasing biomass will increase all the above measures of fisheries success. By increasing biomass to more sustainable level, estimated at 27 tons/km$^2$ for target and 50 tons/km$^2$ for fishable biomass, employment rates could double, and biodiversity increase by 15 to 40% (McClanahan and Azali 2020; McClanahan 2022).

Biomass restoration activities on a very large scale are needed. This would include a mixture of changing boat power and gears, temporary reductions in fishing effort to allow for biomass recovery, and marine reserves. Some limited evidence suggests that the existence of no-take closures can increase fisheries productivity in adjacent fisheries, especially where there are recruitment limitations (McClanahan and Kosgei 2019; McClanahan 2021). The generality of these findings needs further testing and therefore not included here. Yet, many of the current management policies are towards subsidizing resource extraction rather than resource protection (Sumaila et al., 2016). The political expediency of financially assisting poor fishers by reducing their costs of fishing is the likely cause of these policies. While poverty has often been used to support resource-extraction subsidy policies, these subsidies have often further increased poverty (McClanahan and Kosgei 2019). Nevertheless, there are cases in our study region and impoverished contexts where resource-protection subsidies and actions have increased biomass and yields (McClanahan 2010, 2021; McClanahan et al., 2015). A need to reverse the current policies and instigate restoration of resources, their profitability, and employment capacity is evident (Zeller et al., 2021). This will require a change in priorities towards subsidizing protection rather than the capture of the resources.

Tools for the management of fisheries are needed for recovery and will include a variety of restrictions. At present, the main restrictions outside of the parks and reserves is the high costs associated with distance from shore and depth of fishing. The impacts of this passive management can be approximated by the distance from people or markets (Cinner et al., 2016, 2020). Some compilations have shown the distance to people and market factors can influence and degrade the ecology of marine reserves (Cinner et al., 2019). Here, however, we show fewer negative impacts in nearshore no-take high compliance closures. Two studies in Africa found greater fisheries production resulting from these nearshore no-take closures (Kerwath et al., 2013; McClanahan 2021). Restrictions to access in space should benefit from a mixture of nearshore closures but modifying the incentives or increasing the costs to overfish in nearshore areas. This might include negative subsidies including taxing policies that further restrict travel, fuel use, boat size, and gear to restrict access away from shore and markets (Cramer and Kittinger 2021). Cost and benefit planning scenarios can be done at various scales to promote the needed biomass recovery and will require broad-scale engagement in the management needs.

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## Figures:

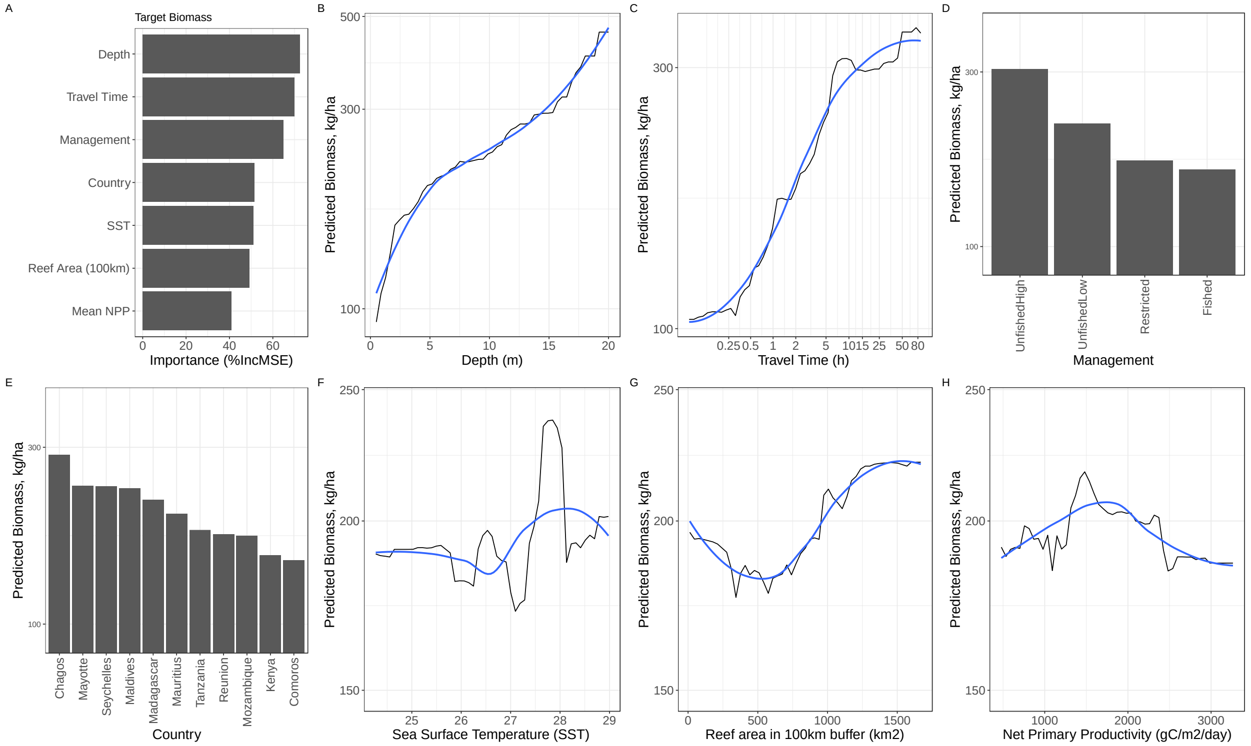


**Figure 1.** Partial dependence plots of the significant variables associated with target biomass for the Random Forest Tree model ($R^2$=0.85). Blue lines are loess smoothing or locally weighted smoothing. See supplementary Figure 3 for fishable biomass results.

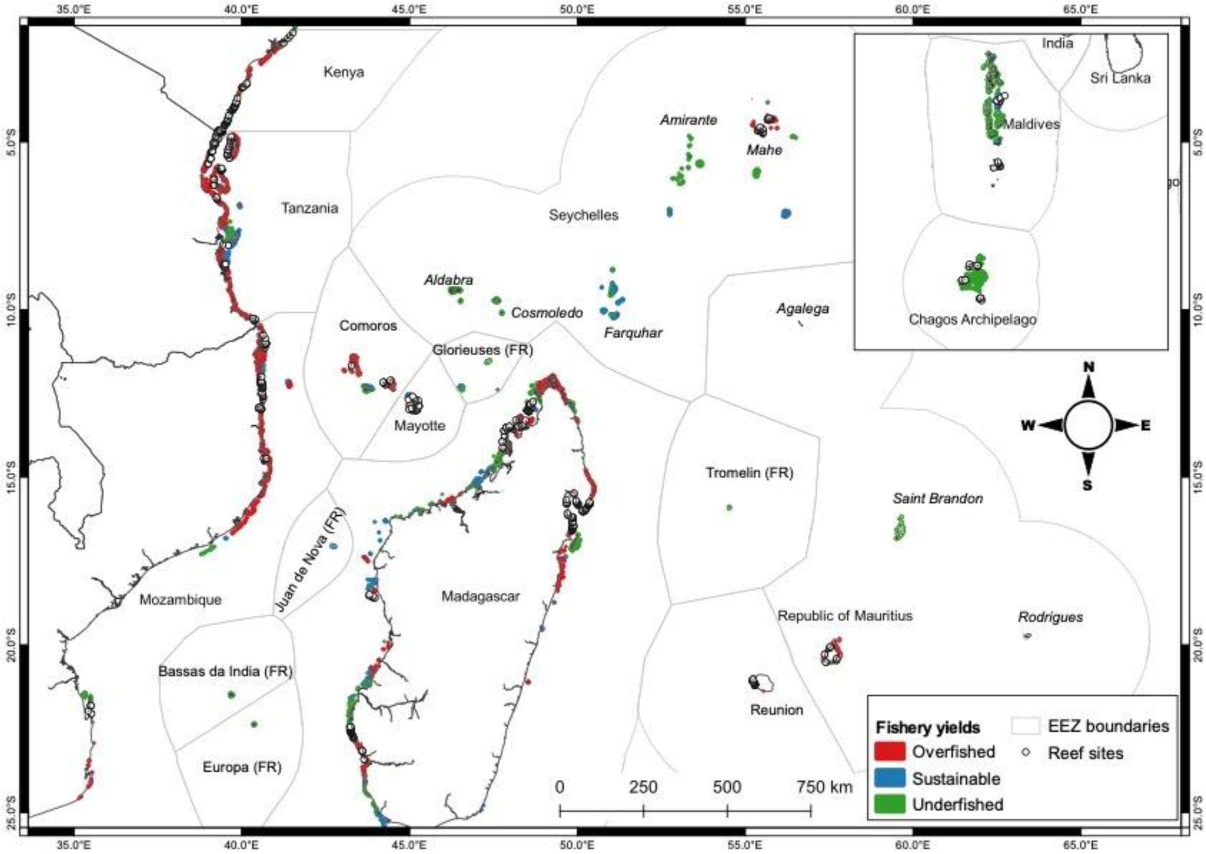


**Figure 2.** Map of the distribution of coral reef cells relative to their sustainable yields. Three categories are presented that include cells estimated to have lost potential yields due to overfishing ($B/B_{msy} < 0.9$), underfishing ($B/B_{msy} > 1.1$), and within maximum sustainable yield ($B/B_{msy} = 0.9 – 1.1$). FR = French Southern Territories.

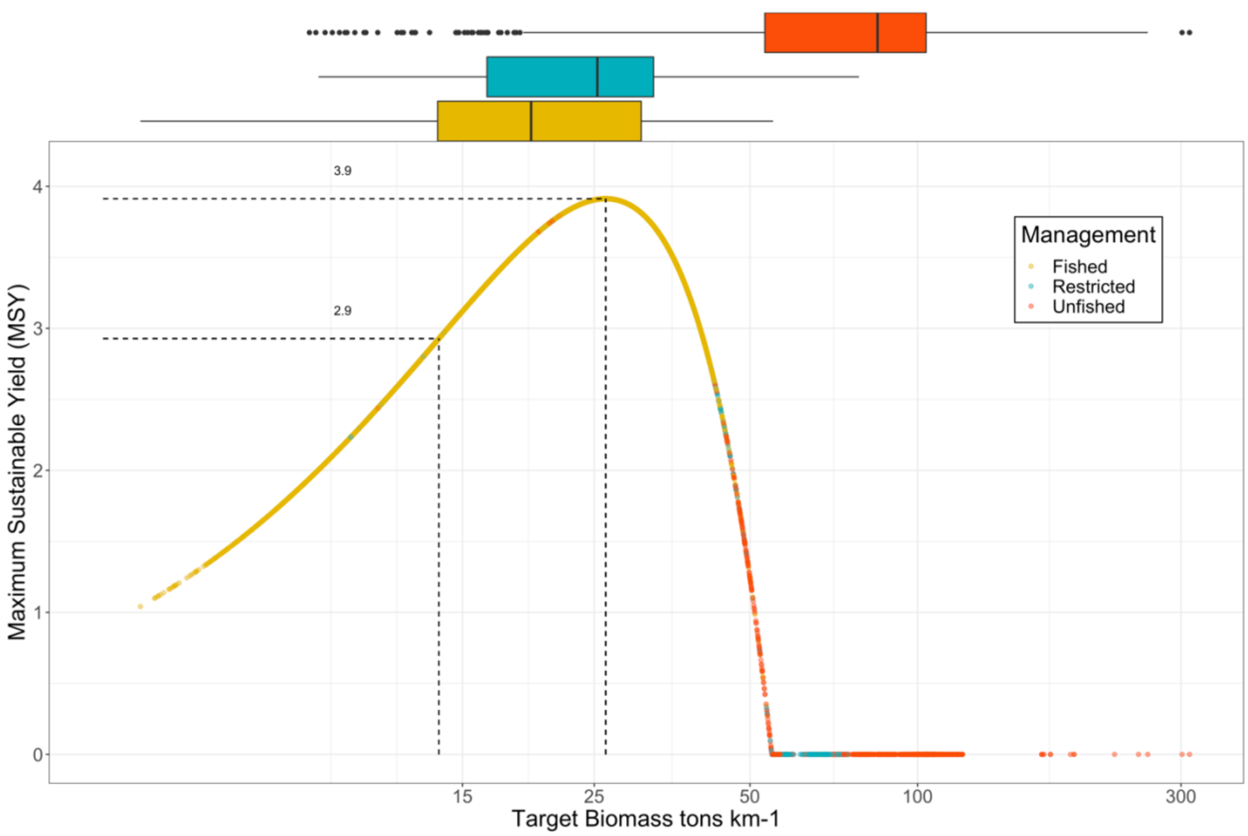


**Figure 3**. Relationship between target coral reef stock biomass and the estimated yields (at 5 m depth) for the studied 10,815 Indian Ocean coral reef cells. Yield was estimated as described in the methods section from the derivative of the biomass recovery data in fully protected areas in the region. See supplementary figure 4 for fishable biomass.

**Tables**

**Table 1:** Distribution of target biomass at 5-m depth as a percentage of reef cells according to the biomass category quintiles for the 12 national jurisdictions.

| Country | Human population[1] | Human density[2] | Number of cells | Coral reef area, km$^2$ | 0-13.5 | 13.5-27 | 27-40.5 | 40.5-54 | 54-309 |
|---|---|---|---|---|---|---|---|---|---|
| French Southern Territories | 0 | 0 | 132 | 794 | 0 | 0 | 34.8 | 44.7 | 20.5 |
| British Indian Ocean Territory (Chagos) | 3.5 | 75 | 1211 | 8742 | 0 | 0 | 0 | 0 | 100 |
| Seychelles | 95 | 214 | 682 | 4206 | 0 | 31.2 | 67 | 1.8 | 0 |
| Mayotte | 240 | 728 | 262 | 1614 | 20.6 | 69.5 | 8 | 1.9 | 0 |
| Maldives | 455 | 1802 | 2817 | 19092 | 0 | 10.9 | 82.9 | 4.1 | 2.2 |
| Comoros | 777 | 467 | 223 | 1428 | 58.7 | 24.2 | 17 | 0 | 0 |
| Reunion | 863 | 340 | 15 | 150 | 26.7 | 66.7 | 6.7 | 0 | 0 |
| Mauritius | 1259 | 628 | 267 | 1824 | 5.2 | 50.6 | 3 | 0 | 41.2 |
| Madagascar | 24234 | 48 | 2179 | 13692 | 19.4 | 46.6 | 27.4 | 6.2 | 0.3 |
| Mozambique | 27042 | 40 | 1154 | 7116 | 42.8 | 49.0 | 3.3 | 4.2 | 0.8 |
| Kenya | 47878 | 94 | 368 | 2232 | 57.3 | 21.5 | 13.9 | 6.5 | 0.8 |
| Tanzania | 51483 | 67 | 1505 | 9144 | 50.1 | 46.4 | 3.5 | 0 | 0 |
| WIO | 154330 | 375.2 | 10815 | 70068 | 19.6 | 35.2 | 27.8 | 4.7 | 12.7 |

**Table 2.** The mean (+SD) stock target biomass (at 5-m depth) and yields for the 12 nations. Biomass and yields are also presented as mean (± SD) on a per reef cell area basis, or multiplied by the area of the spatial cells, which is ~6km$^2$ but varies with geography. Predicted and lost potential yields for target fish biomass due to overfishing and underfishing. Data expressed as country level basis (summed across all cells of a country). The target biomass threshold for under- and overfishing was 27 tons/km$^2$.

| Country | Biomass, tons/km$^2$ | Cell Biomass, tons/~6km$^2$ | Yield, tons/km$^2$ | Cell Yield, tons/6km$^2$ | Underfished | Overfished | Total |
|---|---|---|---|---|---|---|---|
| British Indian Ocean Territory (Chagos) | 198.7 (52.2) | 1228.4 (322.9) | 0 (0) | 0 (0) | 29294 | 0 | 29294 |
| French Southern Territories | 45.4 (8.8) | 259.5 (43.8) | 1.9 (1.4) | 11.1 (8.6) | 1509 | 0 | 1509 |
| Mauritius | 35.8 (22.3) | 203.5 (130.2) | 2.0 (1.7) | 10.8 (9.2) | 2473 | 498 | 2972 |
| Maldives | 34.5 (6.4) | 214.6 (39.8) | 3.4 (0.8) | 21.1 (4.7) | 9027 | 95 | 9123 |
| Seychelles | 29.4 (5.2) | 180.4 (32.7) | 3.7 (0.3) | 22.9 (1.5) | 632 | 99 | 732 |
| Madagascar | 23.1 (10.5) | 132 (61.2) | 3.2 (0.7) | 18.5 (3.9) | 2388 | 5966 | 8354 |
| Mayotte | 19.5 (7.2) | 115.7 (42.5) | 3.3 (0.5) | 19.8 (2.9) | 77 | 824 | 901 |
| Kenya | 17.4 (12.1) | 108.6 (75.3) | 2.6 (0.7) | 16.5 (4.6) | 499 | 2395 | 2894 |
| Reunion | 16.7 (4.7) | 91 (25.7) | 3.2 (0.5) | 17.6 (2.6) | 0 | 55 | 55 |
| Comoros | 16.3 (7.5) | 97.2 (44.4) | 3.0 (0.5) | 17.9 (2.9) | 26 | 1195 | 1221 |
| Mozambique | 16.0 (9.2) | 93.1 (49.2) | 2.8 (0.7) | 16.6 (4.3) | 954 | 6453 | 7408 |
| Tanzania | 15.0 (5.7) | 91.9 (34.8) | 3.0 (0.6) | 18.2 (3.9) | 14 | 8796 | 8809 |
| WIO | 31.7 (25.6) | 192.4 (159.0) | 2.8 (1.2) | 16.9 (7.5) | 46893 | 26376 | 73272 |

## Supplementary Information

**Supplementary Table 1:** Predicted fishable biomass for as the proportion of reef cell planning units for the five categories of biomass evaluated on the 11 ecoregions and mean stock biomass and estimated yields (x±SD).

| Ecoregion | Biomass, tons/km$^2$ | Yield, tons/km$^2$ | Number of cells | Coral reef area, km$^2$ | 0-25 | 25-50 | 50-75 | 75-100 | 100-386 |
|---|---|---|---|---|---|---|---|---|---|
| Chagos | 188.7 (49.4) | 0.2 (0.8) | 1211 | 8742 | 0.0 | 0.0 | 0.3 | 4.5 | 95.2 |
| Cargados Carajos/Tromelin Island | 107.9 (11.1) | 0.4 (1.5) | 118 | 846 | 0.0 | 0.0 | 6.8 | 0.0 | 93.2 |
| Maldives | 79.7 (22.5) | 3.6 (2.5) | 2817 | 19092 | 0.0 | 11.8 | 30.6 | 45.9 | 11.8 |
| Delagoa | 67.8 (32.7) | 3.4 (2.7) | 94 | 576 | 0.0 | 45.7 | 2.1 | 28.7 | 23.4 |
| Seychelles | 54.2 (7.5) | 6.5 (0.3) | 682 | 4206 | 0.0 | 23.0 | 77.0 | 0.0 | 0.0 |
| Western and Northern Madagascar | 48.8 (19.1) | 5.8 (1.1) | 2761 | 17124 | 8.4 | 42.4 | 41.2 | 7.0 | 1.0 |
| Northern Monsoon Current Coast | 47.7 (18.3) | 5.8 (0.5) | 126 | 780 | 6.3 | 47.6 | 46.0 | 0.0 | 0.0 |
| Bight of Sofala/Swamp Coast | 44.6 (19.5) | 5.6 (1.4) | 118 | 678 | 0.8 | 66.1 | 26.3 | 5.1 | 1.7 |
| Mascarene Islands | 42.4 (8.4) | 6.4 (0.2) | 172 | 1176 | 0.0 | 83.7 | 16.3 | 0.0 | 0.0 |
| Southeast Madagascar | 39.8 (7.3) | 6.3 (0.4) | 27 | 390 | 0.0 | 92.6 | 7.4 | 0.0 | 0.0 |
| East African Coral Coast | 34.3 (10.0) | 5.8 (0.7) | 2689 | 16458 | 14.8 | 76.1 | 9.1 | 0.1 | 0.0 |

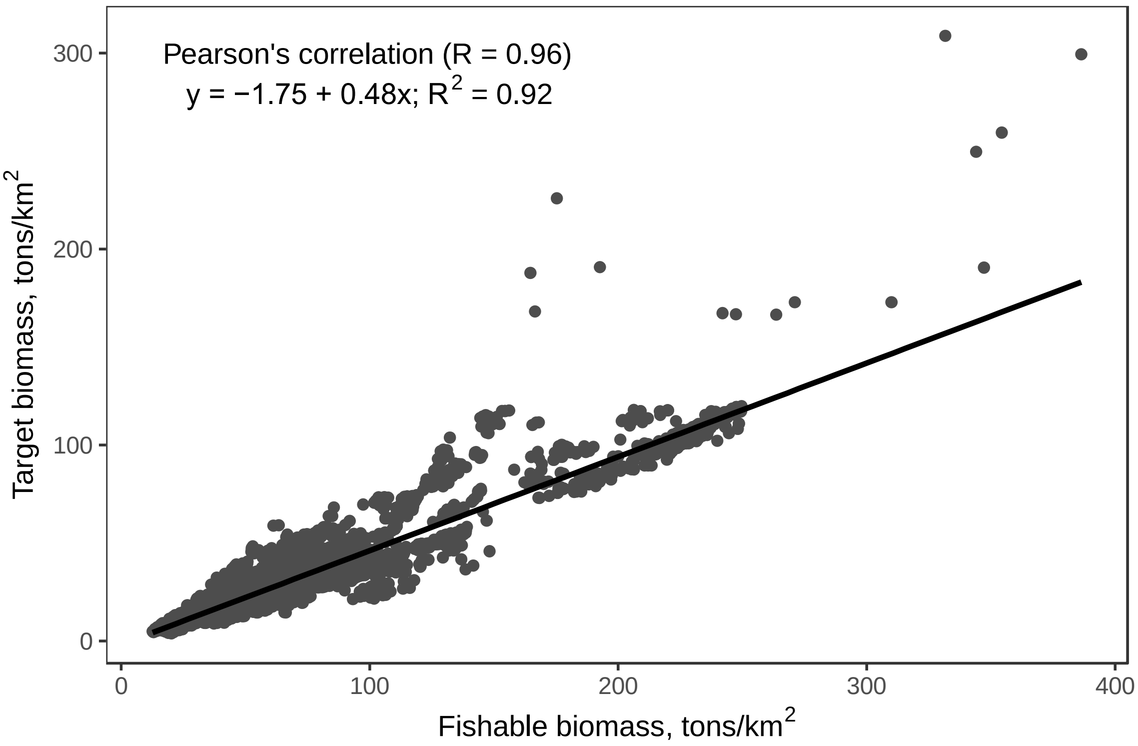
**Supplementary Table 2.** Explanatory variables evaluated in building predictive models of fish biomass.

| Parameter | Variable | Units or categories | Spatial scale | Description | Source |
|---|---|---|---|---|---|
| Geography | Country | unitless | | Maritime Boundaries and Exclusive Economic Zones (200NM) | Flanders Marine Institute (2018). Maritime Boundaries Geodatabase: Maritime Boundaries and Exclusive Economic Zones (200NM), version 10. Available online at https://www.marineregions.org/ [https://doi.org/10.14284/312](https://doi.org/10.14284/312) |
| Habitat | Depth | meters | | Depths of reef surveys in meters to account for broad differences in reef fish community structure attributable to several inter-linked depth-related factors. | Data observers |
| | Habitat (Reef zone) | slope/crest/ flat/lagoon or backreef | | (i) Slope - typically on the ocean side of a reef, where the reef slopes down into deeper water.<br>(ii) Crest - the section that joins a reef slope to the reef flat. The zone is typified by high wave energy (that is, where the waves break). It is also typified by a change in the angle of the reef from an inclined slope to a horizontal reef flat.<br>(iii) Flat - typically horizontal and extends back from the reef crest for 10's to 100's of meters.<br>(iv) Lagoon/back reef - where the continuous reef flat breaks up into more patchy reef environments sheltered from wave energy. These habitats can be behind | Data collectors |

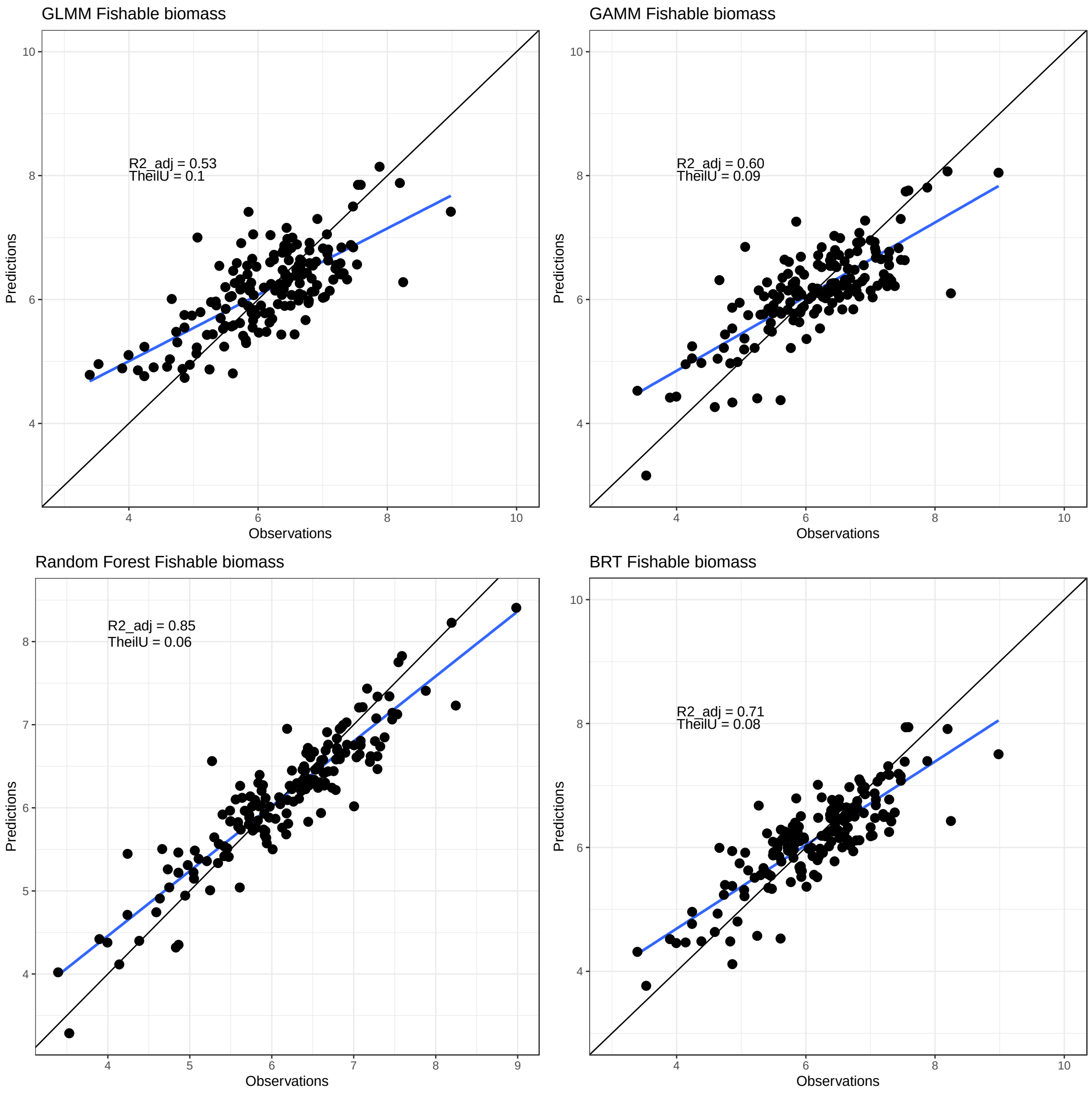
| | | | | | |
|---|---|---|---|---|---|
| | | | | barrier/fringing reefs or within atolls. Back reef habitats are similar broken habitats where the wave energy does not typically reach the reefs and thus forms a less continuous ‘lagoon style’ reef habitat. | |
| Connectivity | Reef area (100km) | km$^2$ | ~4.6km | A 100km radius buffer is created from supplied reef geographic coordinates. All 500m reef cells falling within the buffer are counted and multiplied by 0.25km$^2$ (area of a single cell) | Yeager, L. A., Marchand, P., Gill, D. A., Baum, J. K., & McPherson, J. M. (2017). Marine socio-environmental covariates: Queryable global layers of environmental and anthropogenic variables for marine ecosystem studies. Ecology, 98(7), 1976-1976. https://doi.org/10.1002/ecy.1884 |
| Environmental | Net primary productivity | mg C/m$^2$/day | ~4.6km | Aggregate means from NOAA Coast Watch 8-day interval marine net primary productivity rasters from July 2002 to October 2013 | Yeager, L. A., Marchand, P., Gill, D. A., Baum, J. K., & McPherson, J. M. (2017). Marine socio-environmental covariates: Queryable global layers of environmental and anthropogenic variables for marine ecosystem studies. Ecology, 98(7), 1976-1976. https://doi.org/10.1002/ecy.1884 |
| | Sediment index | unitless | 5km | Satellite derived ocean color observations for total suspended matter and chlorophyll-a | Maina, J., McClanahan, T. R., Venus, V., Ateweberhan, M., & Madin, J. (2011). Global gradients of coral exposure to environmental stresses and implications for local management. PLoS One, 6(8), e23064. https://doi.org/10.1271/journal.pone.0023064 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| Environmental exposure | Median SST | ºC | 5km | Calculated over the entire 1985 – 2020 period from daily SST values per reef pixel | NOAA Coral Reef Watch. 2018, updated daily. *NOAA Coral Reef Watch Version 3.1 Daily Global 5km Satellite Sea Surface Temperature Product*, College Park, Maryland, USA: NOAA Coral Reef Watch. ftp://ftp.star.nesdis.noaa.gov/pub/sod/mecb/crw/data/5km/v3.1/nc/v1.0/daily/sst/ |
|  | Climate stress model | unitless | 5km | Multivariate model including radiation stress factors (temperature, UV light, doldrums, and stress reducing factors (temperature variability and tidal amplitude) | Maina, J., McClanahan, T. R., Venus, V., Ateweberhan, M., & Madin, J. (2011). Global gradients of coral exposure to environmental stresses and implications for local management. PLoS One, 6(8), e23064. https://doi.org/10.1271/journal.pone.0023064 |
|  | Wave energy | kW.m$^{-1}$ | ~4.6km | Intra-annual variation in wave energy from WAVEWATCH III hindcasts from 1979-2009 | Yeager, L. A., Marchand, P., Gill, D. A., Baum, J. K., & McPherson, J. M. (2017). Marine socio-environmental covariates: Queryable global layers of environmental and anthropogenic variables for marine ecosystem studies. Ecology, 98(7), 1976-1976. https://doi.org/10.1002/ecy.1884 |
| Human influences | Travel time | Hours | 5km | The least ‘cost’ (in hours) of travelling between a reef site to nearest market or settlement on a regular raster grid computed using a cost-distance algorithm. | Maire, E., Cinner, J., Velez, L., Huchery, C., Mora, C., Dagata, S., Vigliola, L., Wantiez, L., Kulbicki, M., & Mouillot, D. (2016). How accessible are coral reefs to people? A global assessment based on travel time. Ecology Letters, 19(4), 351-360. |

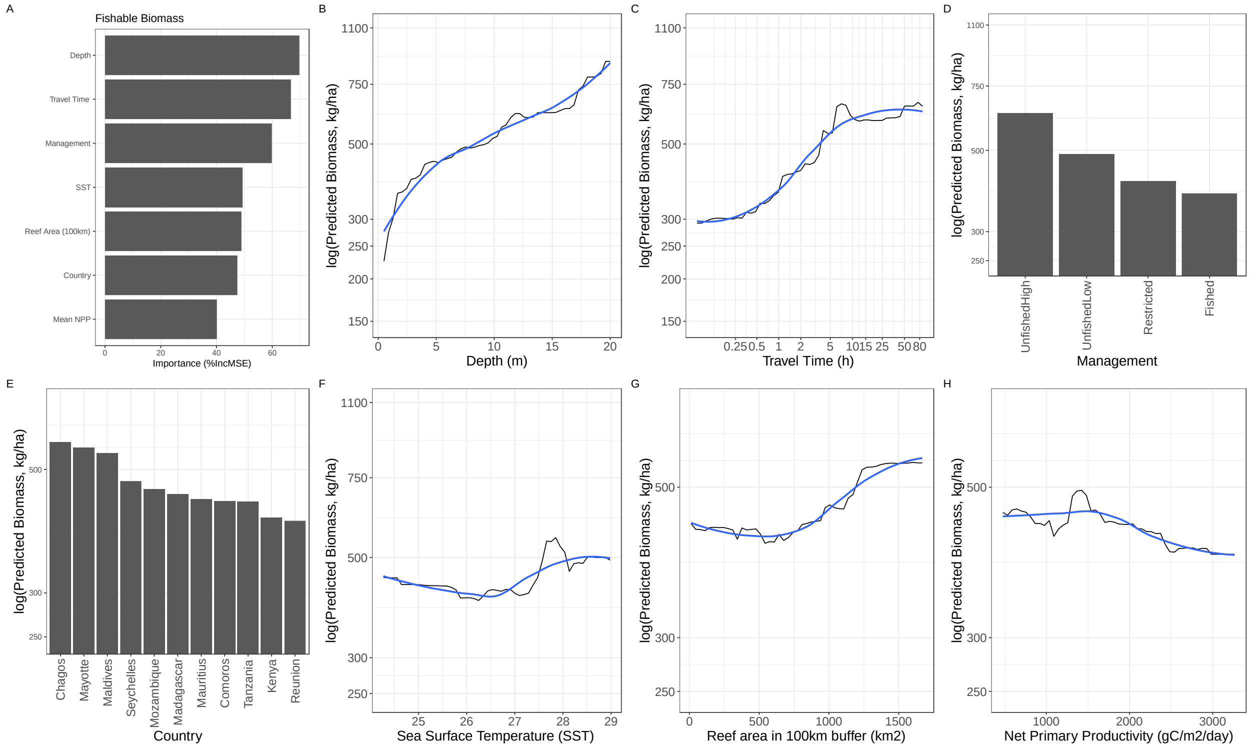
| | | | | | |
|---|---|---|---|---|---|
| | Gravity | population/ travel time (hrs)$^2$ | 5km | Population of the nearest major market or settlement, divided by the squared travel time between the market and the site. | Cinner, J. E., Maire, E., Huchery, C., MacNeil, M. A., Graham, N. A., Mora, C., McClanahan, T. R., Barnes, M. L., Kittinger, J. N., Hicks, C. C., D'Agata, S., Hoey, A., S. , Gurney, G., G. , Feary, D., A. , Williams, I., D. , Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G. J., . . . Mouillot, D. (2018). Gravity of human impacts mediates coral reef conservation gains. Proceedings of the National Academy of Sciences, 115(27), E6116 - E6125. https://doi.org/10.1073/pnas.1708001115 |
| | Empirical fisheries management effectiveness | 4 categories- fished, restricted, low compliance closures, and high compliance closures | | Classification based on national and local laws, as well as communication with stakeholders and expert opinions | 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. https://doi.org/10.1111/cobi.12430 |
| | Closure age | Years | | Time in years, since implementation of fisheries closures | McClanahan, T. R., and N. A. J. Graham. 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: e20151938. |



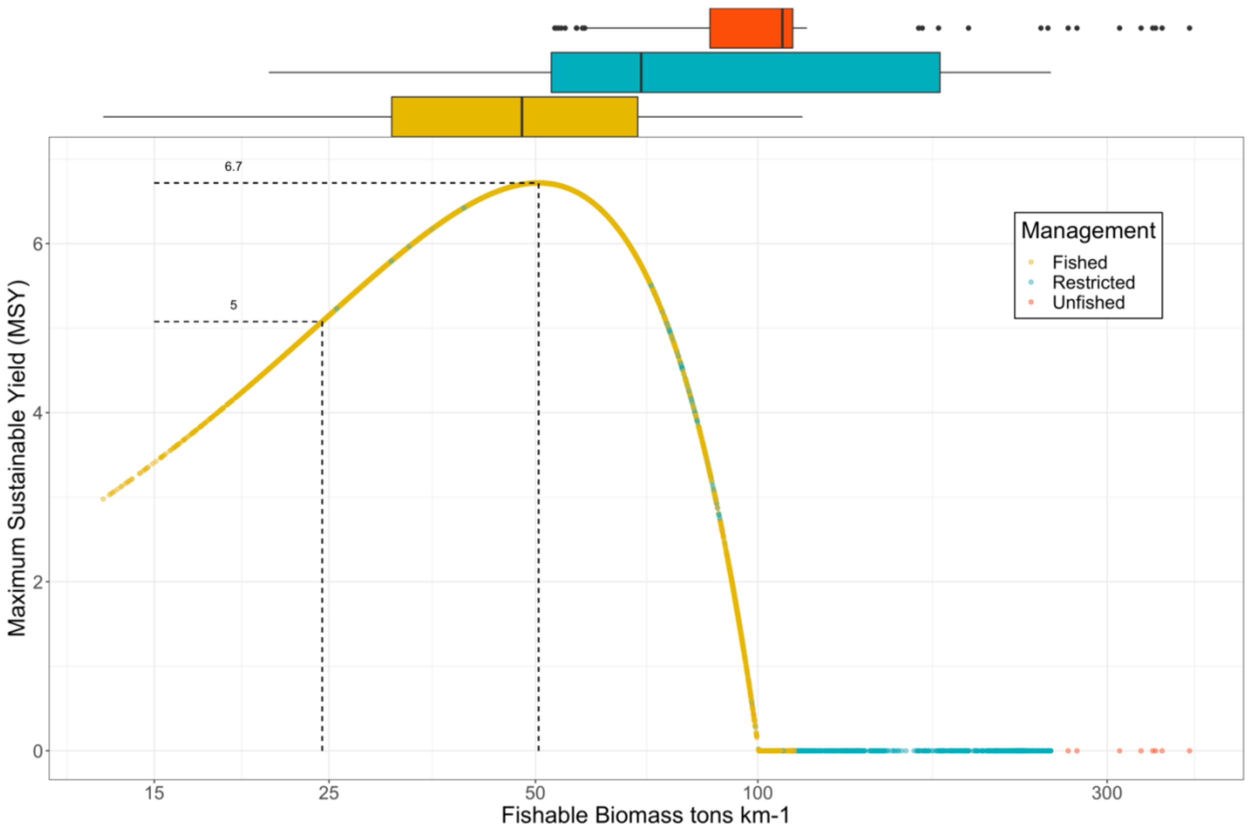
**Supplementary Figure 1**. Correlation and linear relationships between predicted target and fishable biomass for the studied 10,815 Indian Ocean coral reef cells.



**Supplementary Figure 2.** Comparisons of the four statistical models used to predict fishable. Black line is the 1:1 line.



**Supplementary Figure 3**. Partial plots of the significant variables associated with fishable biomass for the best statistical or Random Forest Tree model ($R^2$=0.85).



**Supplementary Figure 4**. Relationship between fishable coral reef stock biomass and the estimated yields (at 5 m depth) for the studied 10,815 Indian Ocean coral reef cells. Yield was estimated as described in the methods section from the derivative of the biomass recovery data in fully protected areas in the region.