Fisheries yields and species declines in coral reefs

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Abstract

Negative trade-offs between food production and biodiversity and the positive functional diversity–productivity relationships are potentially conflicting paradigms that are frequently evoked in conservation and sustainability science and management. While the complementary niches of species could potentially increase fisheries yields, stark food-diversity trade-offs have been proposed for wild-caught fisheries. Nevertheless, this first evaluation of stock biomass, yields, and species relationships in 115 coral reef locations in the Western Indian Ocean found that management for multispecies-maximum sustained yield (MMSY) will increase both food production and numbers of species relative to open access fisheries. A precipitous loss of >50% of species did not occur until >70% of the fishable and target biomasses was depleted. At MMSY, 6%–15% of total predicted number of fish species were lost indicating a need for other conservation mechanisms. These patterns occurred because the best-fit to the yield-numbers of species relationship was either a saturation or convex parabolic relationship. Fishing at MMSY in coral reefs should provide considerable diversity required to support many ecosystem services. Low biomass and overfishing were common and around 80% of studied locations were losing ~2.0–2.5 tons km$^{-2}$ yr$^{-1}$ and 15%–40% of their species relative to MMSY.

1. Introduction

The aim of this study was to evaluate the potential to increase food production while maintaining high biodiversity in African coral reef fisheries. This project of protecting species while feeding a growing human population is, in principle, one of the central trade-offs facing humans in the Anthropocene (Green et al 2005). Declining biodiversity with food production is predicted from studies of the impacts of grazing, farming, and fishing (Mastrangelo and Gavin 2012, Gabriel et al 2013, Hilborn et al 2020). This pattern seems self-evident in terrestrial systems where there is widespread conversion of wildlands to agriculture (Rodriguez et al 2006). There are, however, several alternative diversity-human food responses in private-, common-property, and wild ecosystems (figure 1). For example, a number of food production–diversity studies suggest a parabolic relationship; some diversity contributes to the production of extracted resources but, as commercial species production and extraction intensifies, diversity declines (model a in figure 1) (Brander 2010). This convex yield-diversity response with increasing resource-extraction or domestic intensification is most likely to occur in terrestrial and privately owned commercial production systems.

The saturating diversity–productivity relationship found in many ecological studies suggest an alternative view where diversity is critical to resource production (Hooper et al 2005, Cardinale et al 2013). Many correlational and experimental studies have found that functional diversity has a positive but declining impact on productivity as numbers of functional groups increase (model (b) in figure 1). In contrast, some studies suggest marginal contribution of captured species to food and fisheries production. For example, when many fish species are a minor contributor to production, the impacts of bycatch, habitat degradation, and food web changes can produce a convex food-diversity tradeoff (model (c) in figure 1) (Levin et al 2009, Hilborn et al 2020). For example, there are large-scale fisheries that have eliminated all but the most productive species and
Figure 1. Theorized and observed diversity-yield/productivity relationships. (a) Mixed diversity contribution and tradeoff: yields and productivity follow a parabolic relationship with increases in biodiversity causing some increase in production as species contribute production but declines as space is used for the intense production of commercial species and eliminates species sensitive to losses of habitat or other sources of high mortality decline (Levin et al 2009, Brander 2010). (b) Functional contribution: production of ecosystems increases as functional niches increase but additions of species to production are marginal as contributions to production decline with finer niche partitioning (Hooper et al 2005, Cardinale et al 2013). (c) Stark tradeoff: yields are high and driven by a few highly productive species at low biodiversity levels and eventually declines as the productive species succumb to lower yielding predators and competitors (Levin et al 2009, Szuwalski et al 2017, Hilborn et al 2020). (d) Diversity driven a convex relationship where production and yields increase exponentially as finely divided ecological niches greatly increase production (Mora et al 2011, 2014, Duffy et al 2016). Note that the x and y axes can often be interchanged in these studies depending on the investigator’s perception of causation. That is whether diversity (x) is the cause of the production or yields (y) or if resource extraction or yields (x) negatively impacts diversity (y). The two factors are expected to be interactive but, in this study, yields are hypothesized to impact diversity through a reduction in stock biomass and therefore yields are presented as x and numbers of species as y.

still maintained high yields, often composed of fast-growing species feeding on abundant resources low in the food web. These populations have presumably flourished in the absence of their usual predators and competitors (Szuwalski et al 2017). However, specific responses and the extent of biodiversity losses depend on how species and functional diversity are estimated or modeled. For example, prior studies have used fished area, biomass, and species richness-biomass relationships as proxies of diversity. Results have produced both convex and parabolic yield-diversity relationships, dependent on selectivity of the gear and associated mortality rates (Levin et al 2009).

Many wild species contribute significantly to fisheries. Therefore, production should benefit from protecting species and natural habitats rather than replacing wild with domesticated or highly altered ecosystems (Hilborn et al 2018, Sala et al 2021). Managed fisheries can often be less destructive to habitat by focusing on target species and not all capturable species (Hilborn and Sinclair 2021). Thus, selective gear, such as handlines, spears, and some nets should allow species to be targeted when not challenged by economic dependency and competition for fish resources (Hastings et al 2017, Mbaru et al 2020). While the stock status of selected or targeted wild species can directly affect production, there is also evidence that ‘by-catch’ species are sensitive to fishing and can have indirect ecological effects on, for example, reef habitats and long-term sustainability (McClanahan and Muthiga 2016). In some highly diverse systems, such as coral reefs, investigators have also argued that diversity–production relationships can be concave or exponential due to an amplifying effects of niche partitioning on biomass and production (model d in figure 1) (Mora et al 2011, 2014, Duffy et al 2016).

Several yield-diversity responses have therefore been theorized and observed in wild-caught fisheries. Confidently embracing and managing fisheries based on any of the above yield-diversity concepts is therefore risky. The few focused studies on marine fisheries yield-diversity studies suggest the common strong convex tradeoff between yields and diversity (Levin et al 2009, Hilborn et al 2020). Nevertheless, given the variable concepts, methods and emerging patterns provokes the need to evaluate outcomes in specific fisheries ecosystems. Knowing yield-diversity relationships should be particularly useful in tropical nations where biodiversity is high and food
security low—creating a potentially difficult trade-off for resource stakeholders to navigate (McClanahan et al. 2015a, Selig et al. 2019).

Here, stocks and the inter-relationships between yields and species richness in coral reefs of the Western Indian Ocean (WIO) were evaluated. Biomass of fishable and target stocks and a proxy for the total numbers of fish species were derived from field studies in eight WIO countries. Biomass recovery rates in no-take marine reserves were used to calibrate the Schaefer’s fisheries yield model to estimate multi-species maximum sustained yields (MMSYs) for 115 locations among four management systems. These metrics combined allowed an estimate of the impacts of fishing on the status of WIO coral reefs—a region with declining fisheries yields and food security (Srinivasan et al. 2010, McClanahan et al. 2016, Zeller et al. 2021). The question remains how much of the potential yields and diversity are being lost and if managing for MMSY could attenuate current losses?

2. Methods

2.1. Field studies

2.1.1 Study sites

Ecological field studies were in four ecoregions and eight countries that ranged in latitude from 2.04° S (Kenya) to 26.08° S (Mozambique) and longitudes of 32.96° E (Mozambique) to 57.71° E (Mauritius) (figure 2). Ecological sites were located on the windward and leeward sides of coral reefs in depths from 1.5 to 20 m depth at low tide (the region's tidal range is ~1–4 m). Sites were located in reef lagoons, crests, and edges on calcium carbonate coral bottoms colonized by hard and soft corals and various algae, with sand and seagrass being a smaller portion of the cover (McClanahan and Mutiga 2016).

2.1.2 Field studies

Fish families were sampled using two separate transect methods, one for numbers of species and the other for stock biomass. Sampling for diversity, focused on counting individuals in nine selected families that were chosen for their high numbers of species and as a proxy of the total number of species in a location (Allen and Werner 2002, Kulbicki and Boze 2005). These nine families contained a mix of life histories and fished and unfished species. Biomass was estimated by counting and sizing individuals in 24 families and an ‘others’ category. These 25 groups contributed to most of the total biomass and catch from coral reefs (i.e. >95%). In the biomass method, individual fish sizes were estimated in 10 cm size interval classes with a minimum size for counting cut-off of 3 cm.

During subsequent passes of the transect individuals from the different families were counted. During species richness surveys, all individuals in the families marked with an asterisk were identified to the species level while during biomass surveys all individuals in all families were sized. The counted fish families included the Acanthuridae*, Aulostomidae, Balistidae*, Caesionidae, Carangidae, Chaetodontidae*, Diodontidae*, Fistularidae, Haemulidae, Holocentridae, Labridae*, Lethrinidae, Lutjanidae, Muraenidae, Monacanthidae*, Mullidae, Pempheridae, Pinguipedidae, Pomacanthidae*, Pomacentridae*, Scaridae*, Serranidae, Scaridae, Siganidae, Sphyraenidae. All individuals not in these families were placed in an ‘others’ category for biomass. At each site, one to nine 500 m² belt transect replicates were completed between 2005 and 2019. This dual sampling method limits the number of variables being recorded and improves the accuracy of each variable.

2.2. Fisheries evaluations

2.2.1. Fished locations

Sampled areas in each site for fish biomass were small, often <1000 m², and relevant for ecological studies. Therefore, for fisheries evaluations, sites were pooled into larger units or locations based on shared habitats for evaluation at the fisheries scale and yield contexts. Ecological sites under the same management and habitat classifications were pooled into clusters termed locations within a 4 km² buffer area using the ‘hclust()’ function in R version 4.0.2. The shared-area habitat pooling process produced 115 locations arising from 227 site × time replicates (table 1). Out of the 115 locations, 9 were high compliance closures used as benchmarks for species richness, 106 were fished in either low compliance reserves, restricted, and unrestricted fishing areas. All locations were evaluated for yields relative to MMSY predictions derived from an empirically derived fisheries production model described below. Locations were pooled into four management classifications for some presentations.

2.2.2. Fisheries management categories

Locations were distributed among four management categories, namely, high compliance no-take reserves, low compliance reserves, restricted and unrestricted fishing, as previously described and classified (McClanahan et al. 2015b). High compliance closures have well enforced management areas >5 km² that have been closed to fishing for over 15 years. Low compliance closures were areas legally gazetted as marine reserves but where fishing was evident by the author’s personal observations or reported in the literature. Restricted fishing in some locations had restrictions in the usage of small-meshed nets or spearguns. Locations were not randomly selected but biased towards sampling most of the marine protected areas in this region with additional sampling in comparable location without area-based management. Thus, the results do not represent outcomes of
random sampling that would be needed to evaluate the status of the fisheries, as done previously for this region (McClanahan et al 2016).

2.2.3. Fisheries stock biomass
The stock biomass was calculated as either fishable or target stocks. Fishable biomass is the sum of all individual weights >10 cm excluding pomacentrids. Target biomass eliminates some low value and by-catch taxa, including Aulostomidae, Balistidae, Chaetodontidae, Diodontidae, Fistularidae, Muraenidae, Pempheridae, Penguipedidae, Pomacanthidae, Pomacentridae, Scorpaenidae, Caesionidae, and the others category, including wrasses <20 cm. These categorizations align with fishers’ preferences for sale (target) versus home usage (nontarget) of fish in the region. Biomass and yield values are presented as a tons per square kilometer units to be consistent with common usage in the fisheries yield literature. Fishable and target biomasses were used to estimate the yield for each location to compare yield-species richness relationships for these two management options. Differences between specific locations and the expected fully recovered biomasses ($K$) for fishable and target biomasses from the old and high compliance closures were used to estimate the depletion of biomass at each site.

2.2.4. Fisheries yield estimates
Biomass recovered stock biomass and recovery rates among reef fish communities in 13 high compliance closures were used to calibrate the fisheries model.

Figure 2. Location of studied coral reef locations in the Western Indian Ocean.
Table 1. (a) Summary statistics of biomass (tons km\(^{-2}\)) and yield relative to multi-species maximum sustainable yield (MMSY). SD = standard deviation.

| Metric                          | Statistic | Fishable stocks | Target stocks |
|---------------------------------|-----------|-----------------|---------------|
|                                 |           | High compliance reserves | Low compliance reserves | Restricted fishing | Unrestricted fishing | High compliance reserves | Low compliance reserves | Restricted fishing | Unrestricted fishing |
| Biomass (tons km\(^{-2}\))      | N         | 9               | 33            | 34            | 39            | 9               | 33            | 34            | 38            |
|                                 | Mean      | 89.9            | 45.2          | 33.0          | 30.4          | 44.9            | 15.4          | 12.0          | 10.3          |
|                                 | SD        | 19.1            | 27.0          | 22.1          | 21.7          | 17.3            | 14.2          | 12.3          | 11.5          |
|                                 | Upper 95% mean | 104.5        | 54.7          | 40.7          | 37.4          | 58.2            | 20.4          | 16.3          | 14.1          |
|                                 | Lower 95% mean | 75.2           | 35.6          | 25.3          | 23.3          | 31.6            | 10.4          | 7.7           | 6.5           |
|                                 | Median    | 97.9            | 38.0          | 28.7          | 26.8          | 50.6            | 11.3          | 8.6           | 6.1           |
|                                 | Mean      | −4.6            | −1.9          | −2.0          | −2.3          | −2.4            | −1.8          | −2.0          | −2.2          |
| Yield relative to MMSY (tons\(^{-1}\) km\(^{-2}\) yr\(^{-1}\)) | SD        | 2.8             | 2.0           | 1.8           | 1.9           | 1.6             | 1.2           | 1.3           | 1.3           |
|                                 | Upper 95% mean | −2.4           | −1.2          | −1.3          | −1.7          | −1.1            | −1.3          | −1.5          | −1.8          |
|                                 | Lower 95% mean | −6.8           | −2.6          | −2.6          | −2.9          | −3.7            | −2.2          | −2.4          | −2.6          |
|                                 | Median    | −6.3            | −1.0          | −1.3          | −1.6          | −3.0            | −1.6          | −1.8          | −2.3          |

(b) Summary statistics of species counts 500 m\(^{-2}\). SD = standard deviation

| Statistic | Fishable stocks | Target stocks |
|-----------|-----------------|---------------|
|           | High compliance reserves | Low compliance reserves | Restricted fishing | Unrestricted fishing |
| N         | 9               | 33            | 34            | 39            |
| Mean      | 56.2            | 43.9          | 43.6          | 41.8          |
| SD        | 4.6             | 11.0          | 10.8          | 11.2          |
| Upper 95% mean | 59.8        | 47.9          | 47.3          | 45.4          |
| Lower 95% mean | 52.7           | 40.0          | 39.8          | 38.2          |
| Median    | 56.5            | 46            | 43.3          | 43            |
Figure 3. Scatter plots of the recovery of biomass in fisheries closures. Recovery as a function of the age of high compliance no-take marine reserve in the Western Indian Ocean for four categories of fish including (a) total ($K$, $B_i$, $r$, mean ± 95% CI), (b) fishable, (c) target, and (d) non-target stock biomasses. Data are based on a compilation of 13 high compliance closures in five countries (Kenya, Tanzania, Seychelles, Mayotte, and Mozambique) with data fitted to logistic models. Best-fit equations and 95% CIs are based on 99 marine reserves × time replicates. These recovery rates of fishable and target final biomasses ($B_i$) were used to evaluate the yields in this study. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Values were derived from 99 time-since-closure replicates in five WIO countries (McClanahan and Graham 2015). Biomass data for specific times-since-closure were pooled into four fisheries stock categories and fit to the logistic or Schaefer model for total, fishable, target, and non-target taxa. The logistic model requires fewer assumptions about parameters that are poorly known for specific tropical fisheries model options. For example, the $z$ values of the best-fit model of the Pella–Tomlinson model were similar for fits of the logistic or Schaefer model for comparisons with long-term empirical yield data from Kenya (McClanahan and Azali 2020).
stock categories. This includes $r$ or the recruitment parameter, for either target versus non-target stocks.

Fitting stock recovery data to the logistic equation allowed easy differentiation of important fisheries categories, such as the fishable and target taxa biomass. For example, based on the empirical recovery rates in high compliance closures, key parameters in the model for fishable stocks were $K = 99.5$ tons km$^{-2}$, $r = 0.27$, and an initial biomass ($B_i$) = 8 tons km$^{-2}$. For target stocks, a $K = 54$ tons km$^{-2}$, $r = 0.29$, and $B_i = 0.4$ tons km$^{-2}$ was used. $B_i$ values used here were chosen to be less than the empirical fits to mean biomass at zero years of no fishing. Rather, I used the lower 95% confidence interval of the fished locations to establish the initial stock biomass ($B_i$). Some values, such as $K$ for no-take marine reserves, appear to be consistent across large reef areas of the Indian Ocean under similar conditions of human influence of the seascape (McClanahan et al 2021a). Remote marine wilderness has higher $K$ values than high compliance closures within fished seascapes (McClanahan et al 2019). Consequently, the evaluation here should be seen as relevant for fished and not wilderness seascapes, which would require higher $K$ and lower $r$ values (McClanahan et al 2021b).

2.2.5. Fisheries yield equations

Fisheries yields can be estimated from biomass by solving the logistic equation for time and substituting the derivative of the logistic biomass equation, which is an estimate of production or yield, as described below:

(a) Logistic growth for biomass at recovery time:

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

where $B_i$ is the initial biomass, $K$ is the carrying capacity, $r$ is the intrinsic rate of population growth and $t$ is time, usually one year.

(b) Logistic growth solved for time:

$$t = \frac{\ln \left( \frac{K-B_i}{B_i(K-K_{B_i})} \right)}{r}.$$

(c) Derivative of logistic growth as our metric of fisheries yield:

$$\frac{dB_t}{dt} = \frac{B_t K (K - B_t) r e^{rt}}{(B_t e^{rt} + K - B_t)^2}.$$

(d) Yield estimate where biomass substitutes for time $t$:

$$\frac{dB_t}{dt} = \left[ \frac{B_t K (K - B_t) r e^{rt}}{(B_t e^{rt} + K - B_t)^2} \right] \left[ \frac{B_t e^{rt} + K - B_t}{B_t e^{rt} + K - B_t} \right].$$

The above equation is solved for the biomass at each location to give mean yield estimates as tons km$^{-2}$ year.

2.2.6. Yield and number of species calculations

Estimated yields were categorized as either over-fished or under-fished relative to the Schaefer’s MMSY estimate (MMSY = 0.5 K) as a first heuristic step to evaluate relationships and lost yields and species. This logistic MMSY estimate has been shown to be accurate for both productive and reef fisheries compared to other options where the parameters for reef fishes are unknown (Zhang 2013, McClanahan and Azali 2020). A scale of yields was calculated relative to MMSY with over- and under-fished yields relative to the fishable and target MMSYs. Summaries of mean yields lost from both over- and under-fishing were calculated for all locations resulting in negative values in comparison to the zero loss for MMSY. Negative values arise from being either above or below the MMSY estimate.

Changes in numbers of species were calculated relative to the values from the nine unfished high compliance marine reserves benchmark. The differences between the number of species at each location versus the numbers in high compliance closures were calculated for the three fished management systems. Yield-number of species relationships for each location were evaluated for fits to linear and 2nd order polynomial relationship using the R package ‘stats’ version 3.6.2 and visualized using ‘ggplot 2’ version 3.3.2 in R version 4.0.2.

3. Results

3.1. Benchmark values

Based on the recovery rate information of fish stocks in marine reserves (figure 3), the estimated fishable Schaefer MMSY estimate was 6.7 (1.9 ± SD) tons km$^{-2}$ yr$^{-1}$ achieved at a fishable stock biomass of 49.7 tons km$^{-2}$ ($B_{mmsy}$). Evaluating yields for just the target stocks, produced a MMSY estimate of 3.9 tons km$^{-2}$ yr$^{-1}$ achieved at a target biomass of 27.0 tons km$^{-2}$. The benchmark number of species based on the nine high compliance closures was 56.2 (4.6 ± SD) species per 500 m$^2$. Compared to the two benchmark recovered biomass or $K$ of 99.5 tons km$^{-2}$ and 54.0 tons km$^{-2}$; biomass depletion indicate abrupt declines to <20 species per 500 m$^2$ when fishable stocks declined by ~70 tons km$^2$ and target stocks declined by ~40 tons km$^2$, respectively (figure 4(a)). Consequently, abrupt declines in numbers of species occurred when total stock biomass was depleted by ~70% or 0.30 K of the benchmark.

3.2. Stock biomass and yield status

Evaluation of fishable stocks indicated that all management systems were losing biomass and
yields relative to MMSY but most due to over- and fewer to under-fishing. For example, when area is removed from the fishery to create the high compliance closures, the lost yield is 4.6 (±2.8) tons km$^{-2}$ year$^{-1}$. The lack of a total projected loss of 6.7 tons km$^{-2}$ yr$^{-1}$ was due to the maximum biomass in these locations being lower at 89.9 tons km$^{-2}$ than the fully recovered biomass of model or a $K$ of 99.5 tons km$^{-2}$.

Low compliance closure and restricted fishing locations were losing approximately the same fishable stocks $\sim 2.0 \pm 2.0$ tons km$^{-2}$ year$^{-1}$ through a mixture of
biodiversity above and below the expected $B_{\text{mmsy}}$. Unrestricted fishing locations were losing the most yield, or 2.4 ± 1.9 tons km$^{-2}$ yr$^{-1}$, due to $B_{\text{mmsy}}$ being lower for nearly all locations (figures 4(b) and (c)).

Losses in yields were smaller when fishing targeted compared to total fishable stocks. For example, yields lost in the three fished categories ranged from 1.8 to 2.2 tons km$^{-2}$ yr$^{-1}$ across the low compliance to unrestricted fishing restriction gradient. In high compliance reserves, target yield losses were 2.3 tons km$^{-2}$ yr$^{-1}$ or half the biomass lost for fishable stock yields (4.6 tons km$^{-2}$ yr$^{-1}$). Thus, the policy of fishing target stocks left more low-value biomass in the fisheries ecosystem, which reduced the losses of yields.

Evaluating the frequency of locations as either under- or over-fished relative to MMSY, indicated 78% were over- and 26% were under-fished by the MMSY fishable stock criteria. For target stocks, the frequencies were 82% over- and 18% under-fished (table 2). There was also a clear gradient in over-fishing along the low compliance reserves, restricted, and unrestricted fishing management systems as 61%, 76%, and 82% of the locations were classified as over-fished, respectively (supplementary table 1(a) available online at stacks.iop.org/ERL/17/044023/mmedia). Evaluation of the targeted stock biomass category, indicated the frequency of over-fished locations was similar among the three fished management categories at ~80% (supplementary table 1(b)).

### 3.3. Yield-number of species relationships

Fisheries yield and numbers of species relationships indicate positive and saturating relationships with fishable and target stock biomasses (figures 4(b) and (c)). There was high scatter but better fits to the 2nd order polynomial than the linear equations for both fishable and target stocks (supplementary table 2). The expected number of species at MMSY for the best-fit equations was 48 for fishable and 53 for target stocks or 15% and 6% below the benchmark number of species, respectively. Number of species for the target stock species prediction lies within one SD and the fishable stock within two SDs from the high compliance closure benchmark (56.2 ± 4.6 species per 500 m$^3$).

Losses of species were common in all studied locations and countries for both fishable and target stock evaluations (table 2). Compared to the benchmark, an average of 14–15 species were lost (25%–26% fewer species) for fishable and target stocks for all over-fished locations. Under-fished locations still lose species relative to the benchmark and therefore lost an average of eight species or 14%–15% fewer species. Losses of species among the three fished management categories were between 13 and 17 or 22%–33% of species for fishable and target stocks, respectively (supplementary table 2). There were fewer under-fished locations making accurate estimates more difficult. Among these under-fished locations, fewer species were lost, or between 3 and 12, or 6%–21% of the benchmark, depending on the management category.

### 4. Discussion

Fish stock biomass and number of species provide two useful ways to evaluate fishing impacts on coral reefs (Mora et al. 2011, Duffy et al. 2016). Other environmental, location, and habitat factors, while important for fish community structure, have generally been shown to be weak compared to biomass in predicting numbers of species (McClanahan 2015, 2019). The compilation of the stock recovery rates in high compliance closures allowed the calibration of a fisheries-independent production models on a regional basis. Most importantly the key parameters of $r$ and $K$ for both total and target fish stock biomass. This provided a basis for evaluating changes in species as a function of yields in the context of over- and under-fishing and the conclusion that both are associated with quantifiable losses of species relative to the no-fishing benchmark.

Production estimates have been reported for the logistic and the Pella–Tomlinson models, with modest differences. For example, one of the best models
for predicting reef fish yields in Kenya’s fisheries was a Pella–Tomlinson model where $z = 1.2$ and the estimated MMSY was $5.4 \pm 0.6$ tons km$^{-2}$ yr$^{-1}$, somewhat lower but close to the confidence intervals of both models (McClanahan and Azali 2020). The logistic model used here may overestimate fisheries production but will subsequently underestimate the extent of overfishing. Models with more conservative yields and recruitment rates may, however, better estimate yield potentials that avoid overfishing. Yet, an advantage of using the empirical recovery data and logistic fit is the independence of the model with catch data and less need to make assumptions about unknown variables. Moreover, distinguishing fishable and target catch groups was possible by using their respective $K$ and $r$ values, which produced different recommended MSY outcomes. The two MSY estimates, and associated policies will have consequences for biodiversity as well as usage, such home consumption versus sales to various markets (Wamukota and McClanahan 2017). The current trend is towards urbanization and commercialization of reef fisheries, which may favor the use of the targeted fish model (McClanahan et al 2021c).

Any biomass reduction due to fishing or other factors is shown to be associated with reduced numbers of species. However, the effect varied with declining stocks and was small until biomasses dropped below 0.3 K. Therefore, rather than the continuous convex yield-species declining trade-off relationship, there was an initial drop in species when seascapes were disturbed by fishing, followed by smaller losses in numbers of species until biomass was severely depleted. In this region, the yield-number of species relationships were positive and saturating. This is notably different from methods that used fished area and stock biomass as proxies for numbers of species (Levin et al 2018, Hilborn et al 2020). The biomass proxy method has predicted a continuous and predictable decline in numbers of species with any level of fishing intensity and rising yields in California and Alaskan fisheries. Beyond differences in methods, these North Pacific fisheries have been mostly reported as underfished (Hilborn et al 2012). Therefore, Indian Ocean and North Pacific studies are reporting outcomes on different scales or windows of biomass and the predicted bell-shaped yield-diversity relationships (Branden 2010; figure 1(a)). In the WIO region, at least $\sim 80\%$ of the studied locations were overfished. Numbers of species increases with biomass in both regions but the relationship with yields depends on whether the biomass levels are associated with high or low yields relative to MSY.

Studied species were chosen for their visibility and value as a proxy for total reef fish diversity. Consequently, some sparsely distributed species of conservation concern were unlikely to be counted and evaluated. These species may, however, be important for their fisheries and ecological roles. Nevertheless, it is possible to have moderate levels of fishing and moderate to high numbers of species. Yet, below $B_{\text{MMSY}}$, variability declined and there were 2.2–3.0 proxy species lost for every metric ton of overfishing of fishable biomass. For target species and lower potential yields, losses increased to 3.6–4.8 species per ton lost to overfishing. This was in the range of 4%–15% losses of all species per ton when compared to the benchmark or no-fishing closures mean number of species. Consequently, conserving the largest fraction of biodiversity in these reef systems can be quite sensitive to maintaining yields at $\sim 0.5$ K and especially not $< 0.3$ K. Recommendations here align with those of the California Current fisheries, where area- or species-capture restrictions were recommended to sustain species not protected by MMSY policies. Remote wilderness may be required to conserve species with large space requirements, which is limited in the WIO (McClanahan 2020, McClanahan et al 2021b). Nevertheless, several of the more numerous and resilient species should be maintained if fishing maximizes sustainable yields.

The consequences of any fishing, even when forgoing maximum yields, was to lose species relative to the mean species found in the old and large no-fishing benchmark closures. Underfishing losses were, however, smaller, and more variable than overfishing. The cause of this high variation is unknown, but differences in fishing effort among locations and categories is the most likely explanation. For example, factors like distance to fish markets can influence biomass among additional social-ecological characteristic (Cinner et al 2018, 2020). Locations falling within the unrestricted fishing category have variable biomasses because reefs at variable distances from shore, without legally stated or enforced restrictions, were included. Therefore, fishing effort was more variable than either restricted fishing or fisheries closure management categories, as indicated in the large spread of these locations along the yield gradients. Accurately estimating fishing effort during short field visits is difficult and a limitation to accurate evaluations of fishing impacts. Consequently, biomass relative to some unfished value is often used as a proxy for fishing impacts. Here, I was able to use previously unknown recovery rates and saturation of biomass in closures to connect recovery and yield relationships.

From initial unfished biomass in reserves, a considerable loss of biomass can occur before a decline in the numbers of species. This reflects an initially flat to shallow biomass-species convex relationship that plummets when biomass drops below 70% of the benchmark unfished biomass. This pattern is different from previous estimates of species losses that assumed species were the cause rather than the consequence of high biomass (Mora et al 2011, Duffy et al 2016). I attributed the positive
exponential species ($x$-axis)-biomass ($y$ = axis) relationship reported in some studies to the high variability in biomass at the local maximum numbers of species, rather than niche partitioning enhanced production (McClanahan 2015). Due to lower functional redundancy at low biomass, the functional effects of diversity on biomass and yields should occur at low rather than high biomass (Hooper et al 2005, Duffy et al 2016). Therefore, in wild-caught fisheries, declines in productivity with reduced niche-occupation are expected to be most evident at low biomass. This proposed niche-productivity dependence may explain the better fit of the parabolic than the linear or convex trade-off models. Experimental manipulations with fished species will be needed to definitively distinguish the mechanisms influencing productivity and yields, especially where fisheries production is maintained primarily by a few high production species with a widespread resource base (Szuwalski et al 2017). Coral reefs may lack these conditions based on the evenness and diversity of fish life histories and variability in resources that can be sparsely located in space (McClanahan and Humphries 2012, Prince et al 2015, McClanahan et al 2021b). However, the adjacent seagrass ecosystems that can provide considerable yield in nearshore tropical fisheries are more likely to be driven by a few highly productive species (Hicks and McClanahan 2012).

Proxies of fishing effects, such as biomass, management categorization of fished area, are often required to estimate fishing impacts. Fishing effort and yields are difficult to estimate, and it can also take many years for fish to recover and gear use-effort-yield relationships to equilibrate (MacNeil et al 2015, McClanahan 2021). Here, gross categories of restricted fishing were evaluated spatially rather than through the control of fishing gear and effort, which may have produced high variability in biomass within management categories. Fishing experiments combined with fisheries model predictions have helped to estimate production and equilibrium yields (McClanahan 2021). In coral reefs, biomass is generally a better predictor of numbers of fish species than location, area, and environmental factors (McClanahan 2019, McClanahan et al 2021a).

Thus, I have argued that protecting fish biomass is a more important conservation measure for fish than the placement of marine reserves in potentially high diversity locations (McClanahan 2015). In some cases where fishing effort is difficult to regulate, biomass is best protected in closures and shown to increase potential population growth rates in adjacent fishing grounds (McClanahan 2021).

The variability in numbers of species in the high compliance closures was small. Therefore, these benchmarks were useful for estimating potential losses of species in other management systems. What is less well understood, is the potential losses that occur between the isolated benchmark marine reserves studied here and the remote and ecologically connected baseline reefs without human habitation (McClanahan et al 2021a, 2021b). Studies comparing biomass in reserve benchmark and remote baselines have shown that biomass declines as reserves become isolated in human-dominated and disturbed seascapes (Cinner et al 2018, McClanahan et al 2019). It may be that this large loss in biomass is caused by a few species with large body sizes, such as sharks, groupers, and jacks, that contribute greatly to biomass but less to total species richness (MacNeil et al 2020, McClanahan et al 2021b). The consequences of these losses for ecological function and yield may be important but are not well understood (Roff et al 2016).

Many countries were sampled insufficiently to determine the national-level status of fishing. Yet, there appears to be a propensity to reduce fish populations in nearshore coral reefs in this region to about one half the stock values where MMSY is achieved (McClanahan et al 2016, Zeller et al 2021). The patterns observed here and from models indicate that over-fishing is pervasive even in the region’s many low compliance marine reserves (McClanahan et al 2015, 2016). As found in previous evaluations, the losses in biomass and species were more pronounced in Kenya, Tanzania, and Mauritius than in Madagascar, Mayotte, and Mozambique (McClanahan and Jadot 2017, McClanahan 2019). The status of fish has consequences for the ecology of these reefs, such as the abundance of sea urchins and calcifying benthic organisms, that may influence reef fisheries productivity (McClanahan and Muthiga 2016).

Locations selected here were used to evaluate management and not a random selection needed to evaluate status on the broader national and regional scales. Randomized or full-coverage selection suggests that the status is poorer than estimates arising from non-random evaluations (McClanahan et al 2016). Furthermore, the WIO lacks extensive remote reefs or wilderness that might buffer or provide refuge needed to promote the recovery of the currently over-exploited populations (McClanahan 2020). Additionally, maintaining optimal stocks is challenged by poverty and few employment alternatives and policies that subsize or lower costs of fishing (Daw et al 2012, McClanahan and Kosgei 2019). Consequently, active resource protection subsidies rather than passive and extractive subsidy management will be needed to increase food production and protect vulnerable species. Fortunately for biodiversity conservation, the weak yield-diversity trade off at moderate fishing indicates that high diversity can coexist with optimal yields. Nevertheless, the most vulnerable species will need species-specific restrictions and large unfished space to maintain their populations.
Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: 10.5063/F1NG4P2Y.

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