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Multicriteria estimate of coral reef fishery sustainability

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Abstract

A holistic basis for achieving ecosystem-based management is needed to counter the continuing degradation of coral reefs. The high variation in recovery rates of fish, corresponding to fisheries yields, and the ecological complexity of coral reefs have challenged efforts to estimate fisheries sustainability. Yet, estimating stable yields can be determined when biomass, recovery, changes in per area yields and ecological change are evaluated together. Long-term rates of change in yields and fishable biomass-yield ratios have been the key missing variables for most coral reef assessments. Calibrating a fishery yield model using independently collected fishable biomass and recovery data produced large confidence intervals driven by high variability in biomass recovery rates that precluded accurate or universal yields for coral reefs. To test the model's predictions, I present changes in Kenyan reef fisheries for >20 years. Here, exceeding yields above 6 tonnes km^{-2} year^{-1} when fishable biomass was ~20 tonnes/km^2 (~20% of unfished biomass) resulted in a >2.4% annual decline. Therefore, rates of decline fit the mean settings well and model predictions may therefore be used as a benchmark in reefs with mean recovery rates (i.e. r = 0.20–0.25). The mean model settings indicate a maximum sustained yield (MSY) of ~6 tonnes km^{-2} year^{-1} when fishable biomass was ~50 tonnes/km^2. Variable reported recovery rates indicate that high sustainable yields will depend greatly on maintaining these rates, which can be reduced if productivity declines and management of stocks and functional diversity are ineffective. A number of ecological state-yield trade-off occurs as abrupt ecological changes prior to biomass levels that produce MSY.

KEYWORDS

ecosystem-based management, fisheries restoration, socio-ecological trade-offs, stock–yield relationships, sustainable marine fisheries

1 | INTRODUCTION

Holistic sustainability of marine fisheries ecosystems—maintaining social needs and ecological conditions in a way that meets both conservation and harvest objectives—is an increasingly important management approach, but poorly quantified and applied (Hilborn et al., 2015; Salomon et al., 2011). In part, this is due to high variability in social, ecological and environmental conditions among the world's many marine fisheries (Cinner et al., 2016). However, many of the most important concepts in defining holistic sustainability are general, including how much fish can be removed without reducing the recovery of fishable biomass, yields, changing species composition and other ecosystem services (Table 1; Levin & Lubchenco, 2008). For most fisheries, this includes questions of how much fish biomass is needed to have stable, high and profitable yields contextualized within the social, ecological and economic trade-offs inherent in fisheries harvest systems (Daw et al., 2015). Furthermore, the long-standing controversies of using one or a few metrics suggest a need to integrate, and include more criteria to evaluate and potentially supplement classical biomass harvesting models (Selkoe et al., 2015). For diverse ecosystems, such as coral reefs, this integration of fisheries production, ecological functions, species composition and ecosystem state stability remains a scientific and management challenge.

Classical fisheries management is principally focused on managing fishing pressure, with the goal of keeping individual stocks abundant enough to produce large and persistent yields. A debate as to whether fish stocks (fishable biomass) or yields are the best metric to estimate fisheries status has ensued (Pauly, Hilborn, & Branch, 2013). Each metric has theoretical and practical strengths and weaknesses that can be better understood when combined and compared with other metrics and proxies of ecological and fisheries status (Worm et al., 2006, 2009). Proxies of maximum sustained yields (MSY) frequently use either inflexion points from effort–yield relationships (Schaefer and Fox estimates) or maximum yields from empirical time series (Halpern et al., 2012; Newton, Cote, Pilling, Jennings, & Dulvy, 2007). These expedient targets have, however, not been evaluated for their variability, relationships with stocks and poorly integrated with ecological change.

Empirical evidence to show that the above MSY methods are accurate for coral reefs is lacking. While simple rules and proxies can help in the absence of appropriate data, yield compilations indicate high variability and some unusually large yields within and among ocean basins (Table S1). Consequently, using

TABLE 1 Ecosystem-based management fisheries goals, metrics, indicators of unsustainability and proposed management decisions and actions. Recommendations based on studies of coral reef fisheries in the western Indian Ocean (McClanahan, 2018; McClanahan et al., 2011)

Fisheries goals	Common metrics	Indicators of (un) sustainability	Management decisions and actions
Persistent high yields with high net economic returns	Yield rates per unit area over time	Declining total yields and net incomes over time	Reduce fishing capital, effort and gear efficiency
Intermediate fishable biomass	Comparison to unfished benchmark	Biomass below 50% of ~100 tonnes/km^2 benchmark	Promote recovery via closures, reduced fishing capital, effort and gear efficiency
Maintain ecological functions and services	Rapid ecological change and degraded ecological processes and services	Increases in unfished taxa and declines in fished taxa beyond those expected from fishing effort alone. Lost production channelled into fished taxa	Promote recovery via closures, reduced fishing capital, effort and gear efficiency. Fishing bans on fished species preying on unfished taxa exhibiting large numbers and increases (i.e. sea urchin biomass >200 tonnes/km^2)
Maximize numbers of species	Comparison of numbers of species to unfished benchmark	Declining numbers of species in catch and ecosystems over time	Promote recovery via closures, reduced fishing capital, effort and gear efficiency, and restrictions on captured sizes and species experiencing declines
Employment and income equity	Employment numbers and income rates and distributions	Low incomes (i.e. <$2 per person per day) and inequality (i.e. >50% income going to owners of fishing capial) created by low yields and unequal wealth distribution	Promote alternative employment, better money management and negotiating or regulating fairer income distributions

high values from data with right-skewed distributions should frequently overestimate sustainable yields. Sustainability, as defined as no permanent change, requires evaluating status, changes and interrelationships between fishable biomass and yields over time. The second downward deflection point method also lacks many supporting empirical cases from tropical fisheries (McClanahan, Hicks, & Darling, 2008). Where profits, rather than food security or employment, drive fishing effort lost net profits often produces an inflexion point and a close relationship between MSY and maximum profits (Froese, Zeller, Kleisner, & Pauly, 2012). Yet, in poor and diverse multispecies tropical fisheries, there is less concern for market preferences, profits and species can therefore be serially depleted with increasing fishing effort (McClanahan & Abunge, 2017; McClanahan et al., 2008). Behavioural forces of culture, costs and time discounting can maintain high fishing effort and produce persistently low profits and potentially unsustainable yields (Teh, Teh, & Sumaila, 2013). Again, without supporting evidence, this inflexion-net profit approach may be a poor proxy for MSY in coral reefs.

The problem of choosing and measuring appropriate metrics to evaluate sustainability has troubled coral reef fisheries and ecosystem-based fisheries management. To begin filling this knowledge gap, I summarize and combine a variety of concepts, fisheries ecosystem metrics and long-term Kenyan fisheries data to evaluate their contribution to understanding sustainable fishing of coral reefs. Metrics evaluated include fisheries yields, stability of these yields, pristine and fished biomass, biomass recovery rates and rapid ecological change or switch points. Specifically, I evaluate the decay rates of yields in a well-studied Kenyan reef fishery where biomass yields have declined over time. Decay rates and fishable biomass combined can be used to estimate zero net fisheries production or MSY. MSY estimates are then compared with ecological change metrics to evaluate correspondences between biomass, yield and ecological states; thus, providing a multiple criteria window of sustainability.

2 | METHODS

2.1 | Global yield literature search

The tropical fisheries literature was searched for reports of yield estimates. Coral reef fish yields are typically unselective and catch is composed of a large variety of species that support trade but also subsistence livelihoods. Fishable biomass and yields reported are the sum of all species captured within a specific reef or nearshore area. The presented finding only included studies where the reef area for the catch was carefully estimated. Here, the median and median absolute deviation (MAD) were used to evaluate yields for comparisons between ocean basins. The median and MAD were used rather means and standard deviations (*SD*) because the data have a right-skewed distribution, driven by high but uncommon catches, which will overestimate catches and long-term sustainable yield estimates. As the models will lack right-skewed stochastic behaviours, comparing median empirical with mean model outputs is more appropriate.

2.2 | Maximum sustained fisheries yield model

A common equation for estimating maximum sustained fisheries yields is the stock-yield equation of Pella and Tomlinson (1969):

$$\mathrm{MSY} = (rB_0z)/(z+1)^{1/z+1}. \tag{1}$$

Using this equation to estimate MSYs requires knowing the pristine biomass (B_0), the intrinsic rates of growth *r*, and *z* or the density-dependent shape parameters. For coral reefs, the first two values are known from a study of the large and well-enforced Indian Ocean closures where biomass recovered to 115.0 ± 11 (95% CI) tonnes/km^2 (McClanahan & Graham, 2015). From the same data source, reported recovery rates were $r = 0.23 \pm 0.16$ (95% CI), which produces mean recovery times between ~18 and 23 years. *z* values are unknown for coral reef fishes but well-studied temperate fisheries stocks indicate lower and upper values of 0.8 and 1.2 (Thorson, Cope, Branch, & Jensen, 2012), which has minor effects on reef fish yields (McClanahan, 2018). Additionally, I also present a fisheries management working rule that multispecies MSY (MMSY) can be achieved when biomass is between 0.25 and 0.5 B_0 (Hilborn & Stokes, 2010). This range creates a MMSY window rather than a specific target.

2.3 | Kenyan fisheries yield time series

Fisheries catches were measured in 10 southern Kenyan landing sites across a ~60 km coastline between 1996 and 2016. These were small-scale artisanal fisheries that use small boats that lack engines and use a mix of hand and wind power for transportation. Fishing gear included hook and line, traditional basket traps, various gill nets, beach seine nets and various types of spears. In order to control for fishing area and the occasional fishing offshore in the calm season, seasonally large catches of pelagic fishes, such as anchovies, were removed from the analyses. The sites evaluated were locations with clearly defined nearshore boundaries not used by offshore or migrant fishers to land their catch. Control of fishing area was possible because we selected fish landing sites behind a continuous fringing reef that lay around 1 km from shore. The mean nearest neighbour distance between landing sites is 2.4 ± 1.4 (*SD*) km.

At each landing site, fish were weighed by the natural grouping used by the fishermen, which is based on their markets and prices. These groups include scavengers, rabbitfish, parrotfish, goatfish, octopus and a “mixed group” of diverse coral reef fishes of low market values. Fish landing sites were visited two to three times per month at haphazardly selected days and the weights of the above groups taken to the nearest 0.5 kg and the numbers of boats, fishers and their gear use associated with the catch recorded. The annual catch was estimated as the mean daily catch multiplied by 220 fishing days per year (McClanahan et al., 2008). Catches at each landing site were classified hierarchically using the Bray–Curtis distance and Ward's minimum distance methods. Groupings were then evaluated by principal component analysis to determine their associations with catch groups and initial yields, effort and rates of decline where these variables and sites/times were included as supplementary variables.

2.4 | Rates of change and sustainability estimates

Sustainable yields were estimated by evaluated by plotting the initial yields and efforts vs. the rate of decline for each landing site and solving the linear regressions for zero net change in yield. To estimate the rates of decline, the first year of sampling was set to time 0 and catch data pooled and means presented for 1-year intervals from 1996 to 2016. Eight sites exhibited a decline over the full sampling period while two sites had short intervals of reversed declines often associated with temporarily improved management or spillover from the Mombasa Park closure (McClanahan & Mangi, 2000). These periods of reversal were removed from the time series prior to analysing decay rates. Landing sites were tested for autocorrelation with time by plotting the residuals and Durbin Watson tests from the fitted linear models. Results indicated violation of the independence for two of the 10 landing sites, namely Kenyatta and Marina (DW < 2.0). For these two sites, the zero change error estimates were adjusted to account for non-independence (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Initial yields, slopes and standard errors, and the inverse prediction or calibration method were used to estimate rates of decline and 95% confidence (mean estimates) and predicted intervals (sampling estimate) for the sustainable yields.

2.5 | Fishable biomass estimates

Fish biomass has been estimated in Kenyan reefs from visual underwater census undertaken between 1991 and 2015 in a number of reef sites with different management systems (McClanahan, Graham, MacNeil, & Cinner, 2015). These data were summarized at the site level (means); the sites (n = 70) were then classified into four major management categories based on expert knowledge of existing protection, gear restrictions and age of closures. The means for the various management categories were computed and were weighted by the area coverage (mean and 95% CI) of the management categories of the nearshore to give the mean biomass for fished and all reefs in Kenya. Low compliance, most destructive gear-restricted and no gear-restricted sites were further classified as fished sites while high compliance closures were classified as unfished. Fishable biomass weight and confidence intervals (CI) were plotted against estimated Kenyan fisheries yields.

2.6 | Fish community growth rates

A concern for accurate yield estimates is that a logistic model fitted with simple or mean "constants" will underestimate yields if significant positive growth compensation occurs at low biomass. This compensatory process among other factors, such as immigration of fish from offshore or closures, or harvesting productive non-fish species such as octopus, can produce shallow declining total fisheries yields at low fishable biomass (McClanahan et al., 2008). Testing for a compensatory increase in growth rates and yield at the community level is possible by evaluating changing taxonomic composition and associated growth rates across biomass gradients. Community growth rates were estimated for the best-sampled sites using the fish biomass monitoring and published growth rate of the common coral reef families. Growth rates of each family were estimated from summarized growth rates using FishBase summaries compiled for common species within each sampled family, multiplied by the wet weight of each family, and summed for all fishable individuals >10 cm and families caught by fishers (McClanahan, 2015a). This community growth rate was plotted against the mean biomass of the sites to test the hypothesis that growth rates increased as biomass declined.

2.7 | Ecosystem thresholds

A final criterion of sustainability is the state of reef ecosystems and how it changes as fish biomass is reduced. The removal of fish affects basic ecological processes that, in turn, influence ecosystem states and functions (Worm et al., 2006). In coral reefs, many ecological changes have been reported along fishing gradients (Houk et al., 2014; Karr et al., 2015; McClanahan et al., 2011). These changes potentially reduce key ecological services, such as reef calcification and fisheries production (Heenan & Williams, 2013; Houk & Musburger, 2013). Furthermore, fishing impacts appear to display ecological threshold behaviour—rapid ecological change in specific ecological factors associated with smaller changes in key drivers (Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015; Robinson et al., 2017). These successive and rapid switches or tipping points are a non-resource part of sustainability that can easily be ignored by resource assessment methods but potentially have long-term consequences for production and ecosystem services (Daw et al., 2016). Here, I present these switch-point indicators and their variance along the fishable biomass using an extensive field-based compilation of Indian Ocean reefs (McClanahan et al., 2011).

3 | RESULTS

3.1 | Empirical and modelled fisheries yields

Literature summaries of coral reef fisheries yields indicate high median yields and variation of 3.3 ± 2.75 tonnes km^{-2} year^{-1} (±95% CI) based on MAD from 44 coral reef fisheries studies (Figure 1; Table S1). Much of this reported global variation can be attributed to variable production estimates in different ocean basins, including the lowest values in the Caribbean

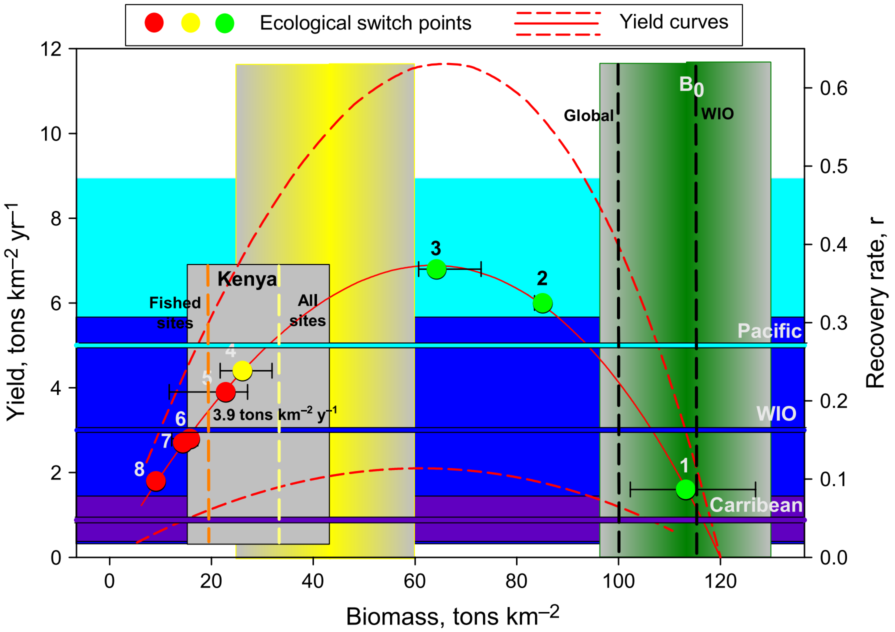

FIGURE 1 Multicriteria framework for estimating coral reef fisheries sustainability plotted along a realistic fishable biomass on the *x*-axis (MacNeil et al., 2015; McClanahan & Graham, 2015). Plot of the ranges of biomass, median yields, recovery rates, ecosystems thresholds and ranges of yields. Reported yields (mean ± 95% CI) are summarized for the three ocean basins for data in Table S1 (horizontal bars are the ranges for each region where purple = Caribbean, blue = Western Indian Ocean, light blue = Pacific Ocean). Vertical bars are pristine fishable biomass (B_0 = green box) and multispecies maximum sustained yield (MSY) biomass windows (multispecies MSY = 0.25–0.5; B_0 = yellow box). Hump-shaped red curves are yield estimate ranges from logistic growth equation calibrated for mean and upper and lower 95% CI (dashed red lines) based on *r* values recorded for the fishable biomass in the western Indian Ocean high compliance closures (McClanahan & Graham, 2015). Green, yellow and red points represent ecological change thresholds (mean ± 95% CI) based on compilations of ecological field studies in western Indian Ocean coral reefs (McClanahan et al., 2011). These are: (1) macroalgae variance, (2) macroalgae-hard coral ratio, (3) predation rates on sea urchins, (4) numbers of fish species, (5) percentage of herbivorous fish, (6) sea urchin biomass, (7) percentage calcifying algae and (8) percentage of hard coral cover. The grey box indicates the window for fishable biomass and sustainable yields in Kenyan reefs where the red line is the mean biomass in fished reefs and the yellow line is the biomass if fisheries closures were included in a weighted mean. The 3.9 tonnes km^{-2} year^{-1} value represents the model's mean predicted yield for Kenya based on the Kenyan fishing area fishable biomass and recovery rates

(0.9 ± 0.5 tonnes km^{-2} year^{-1}), followed by the Indian Ocean (3.0 ± 2.7 tonnes km^{-2} year^{-1}) and the Pacific Ocean having the highest yields (5.0 ± 4.0 tonnes km^{-2} year^{-1}) (Table S1).

Calibrating the yield model with the reported western Indian Ocean *r* and B_0 variables and their 95% CIs and a *z* of 1 produces a large MSY range between 1.9 and 12.7 with a mean of 6.9 tonnes km^{-2} year^{-1} (Figure 1). High variation in recovery rates is the primary driver of the variability.

3.2 | Kenyan fisheries yield time series

There were two major groupings of fishing landing sites based on catch, which reflected the gears used (Figure 2a). Both groupings showed generally declining annual yields over time with site variation that often declined proportional to initial yields (Figure 2b,c). Seven landing sites were composed of moderate effort and diverse fishing gear that caught a variety of fish including coral reef–dependent taxa (Figure 3a). These landing had a mixture of initial yields and rates of decline with Mtwapa and Tradewinds having the lowest negative rates of decline and initial yields compared to the five other gear-diverse sites with high initial yields and negative declines (Figure 3b). Three sites had high fishing effort dominated by beach seines and catch of the seagrass-associated species marbled parrotfish (*Leptoscarus vaigiensis*, Labridae) and shoemaker spinefoot rabbitfish (*Siganus sutor*, Siganidae) and some mixed fish. Seine net sites exhibited higher variability than the mixed-gear landing sites; but, with only three sites, high effort is the main distinguishing factor among these sites.

The mean yield of Kenyan landing sites over this study period was 6.56 ± 2.58 (±*SD*) tonnes km^{-2} year^{-1}. Most of the landing sites displayed an overall slow but a consistent annual rate of decline in total per area yields as a function of initial yield and effort (Figure 4a,b). Plots of the rate of change in yields as a function of the initial yields and efforts indicates a moderate fit (Figure 4a; r^2 = .47 and .46). Annual catch rates declined consistently at a rate of −0.05 ± 0.02 (±*SEM*) tonnes km^{-2} year^{-1} but the *y* intercept had high variation (0.19 ± 0.15) indicating variable decay responses depending on initial yields. Decay rates also declined with fishing effort at a rate of 0.02 ± 0.007 tonnes km^{-2} year^{-1} per fisher. The zero intercept of the initial yield decay relationships used as a proxy for MMSY was ~3.9 tonnes km^{-2} year^{-1} at 4.4 fisher/km^2. The total variation around

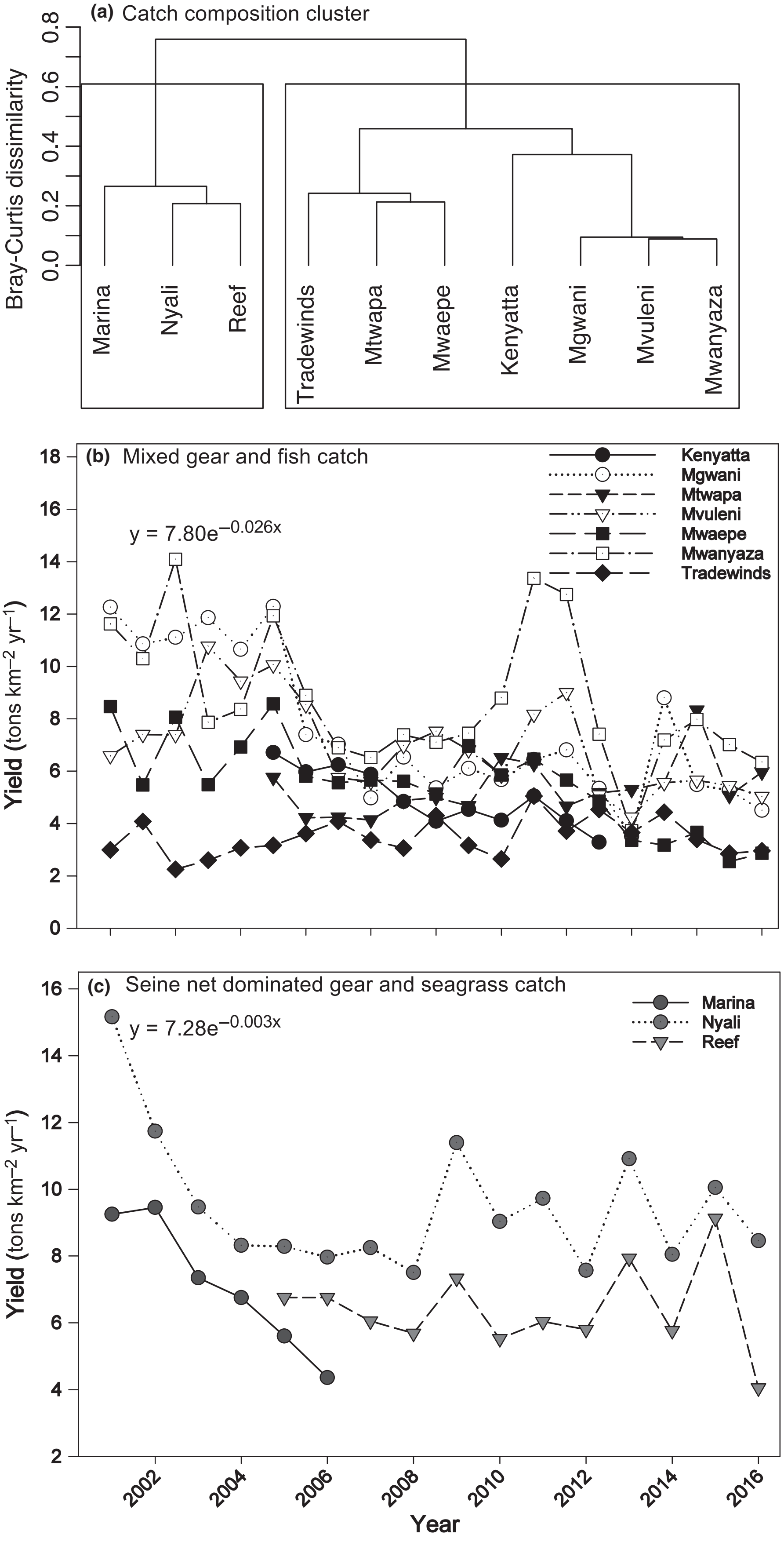

FIGURE 2 Kenyan coral reef fisheries showing (a) cluster analysis of landing sites based on catch composition and long-term annual trends in yields for (b) the common mixed-gear and (c) seine net dominated landing site groups

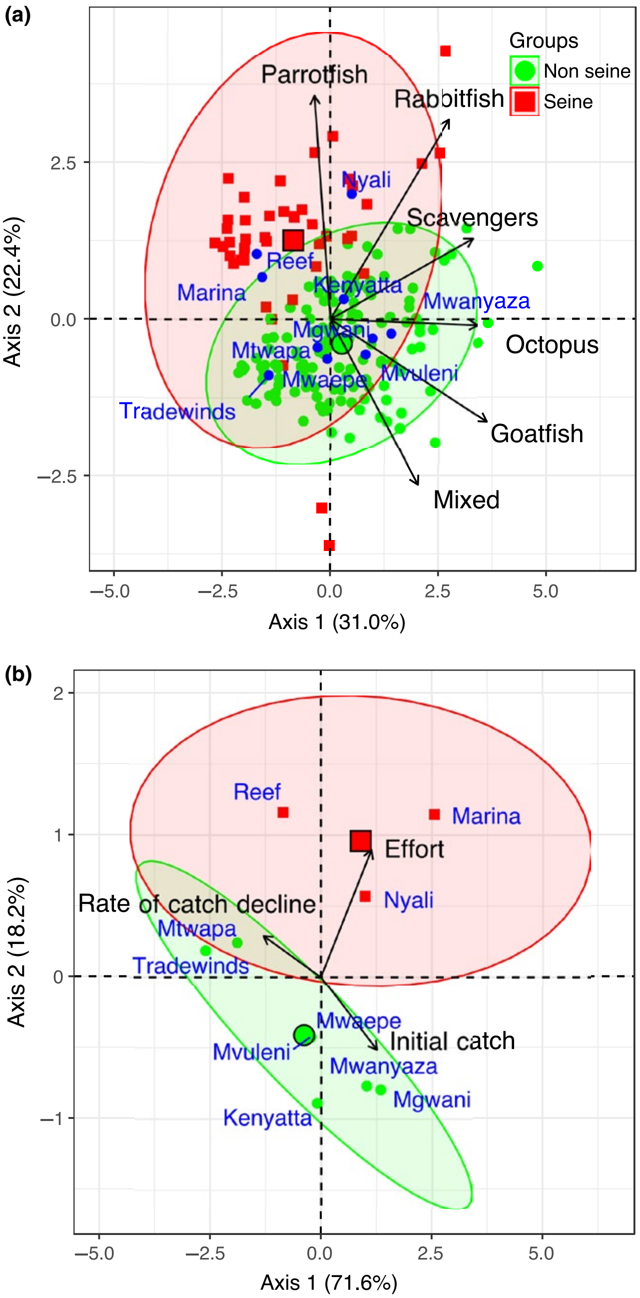

FIGURE 3 Multivariate analyses (principal component analyses) showing landing site group associations with (a) catch composition and (b) initial catch, effort and rate of catch decline as supplementary variables

this mean yield is, however, large with the upper 95% CI yields of 6.4 tonnes km^{-2} year^{-1} and 10.9 fishers/km^2—the highest prediction interval was 12 tonnes km^{-2} year^{-1}. The lowest sustainable yield confidence and prediction intervals were below zero, conservatively indicating that none of these fisheries may be sustainable. The fit between the initial and the decline in effort was a strong (Figure 4c; $r^2 = .94$) with no change in effort at 5.1 and a lower and upper 95% CI of 2.3 and 7.1 fishers/km^2. The estimated MMSY for a biomass of 50 tonnes/km^2 is 10.8 fishers/km^2.

3.3 | Fishable biomass

To test the reliability of the sustainable yield model estimate, production estimates need to be contextualized with local fishable biomass. Fishable biomass summarized for 70 independent sites in various management systems indicates that fished reefs have mean biomass of 19.2 tonnes/km^2 but 33.4 tonnes/km^2 if the closures are included and biomass weighed by the reef area in each management system (Table 2). When the fishable biomass from fished reefs and locally reported biomass recovery rates were used in the yield equation (B_0 = 10.5 tonnes/km^2, r = 0.25) a yield of 3.6 tonnes km^{-2} year^{-1} is predicted, which corresponds well with the empirically predicted MSY of 3.9 tonnes km^{-2} year^{-1}. However, including the fishable biomass of fish in the closure increases the yield estimate to less accurate value of 5.4 tonnes km^{-2} year^{-1}. The fishable biomass in fished reefs falls below the lower edge of the 0.25 B_0 or ~25 tonnes/km^2 heuristic MMSY window (grey box, Figure 1). If biomass in fisheries closures is weighted in the biomass calculation, fishable biomass is just above the lower edge of the MMSY window.

3.4 | Growth rate compensation

Testing for compensatory growth as a function of fishable biomass found some community level increase in predicted growth and also high site variability (Figure 5). The average growth compensation increase is about 10% above the baseline and would, therefore, explain a small and variable proportion of yields at low biomass.

3.5 | Ecosystem thresholds

Non-linear switch-point thresholds occur as fish biomass declines. A number of thresholds were passed before reaching 0.50 B_0, one on the lower end and four below the 0.25 B_0 MMSY window (Figure 1). Rapid changes above the mean MMSY (z = 1, r = 0.23) include the macroalgae variance and the ratio of hard coral to macroalgal cover. Predation rates on sea urchins lie on the MSY inflexion point. Switches in number of fish species, percentage of herbivorous fish, sea urchin biomass, percentage calcifying algae and percentage of hard coral cover were below this MMSY.

4 | DISCUSSION

The model and various sources of fisheries yield data correspond in the sense of having similar median and mean yields that lies within the expected but high variability in the model's predictions. This variability is not clearly constrained but largely supported by multiple sources of information. In terms of the reported global yield data, most published data are from snapshots in time and not based on time series sufficiently long enough to allow estimates of per area yield stability. Consequently, sustainable yield levels are difficult to estimate from reported catch and, based on this literature compilation, appear to vary strongly with geography. The Kenyan yield

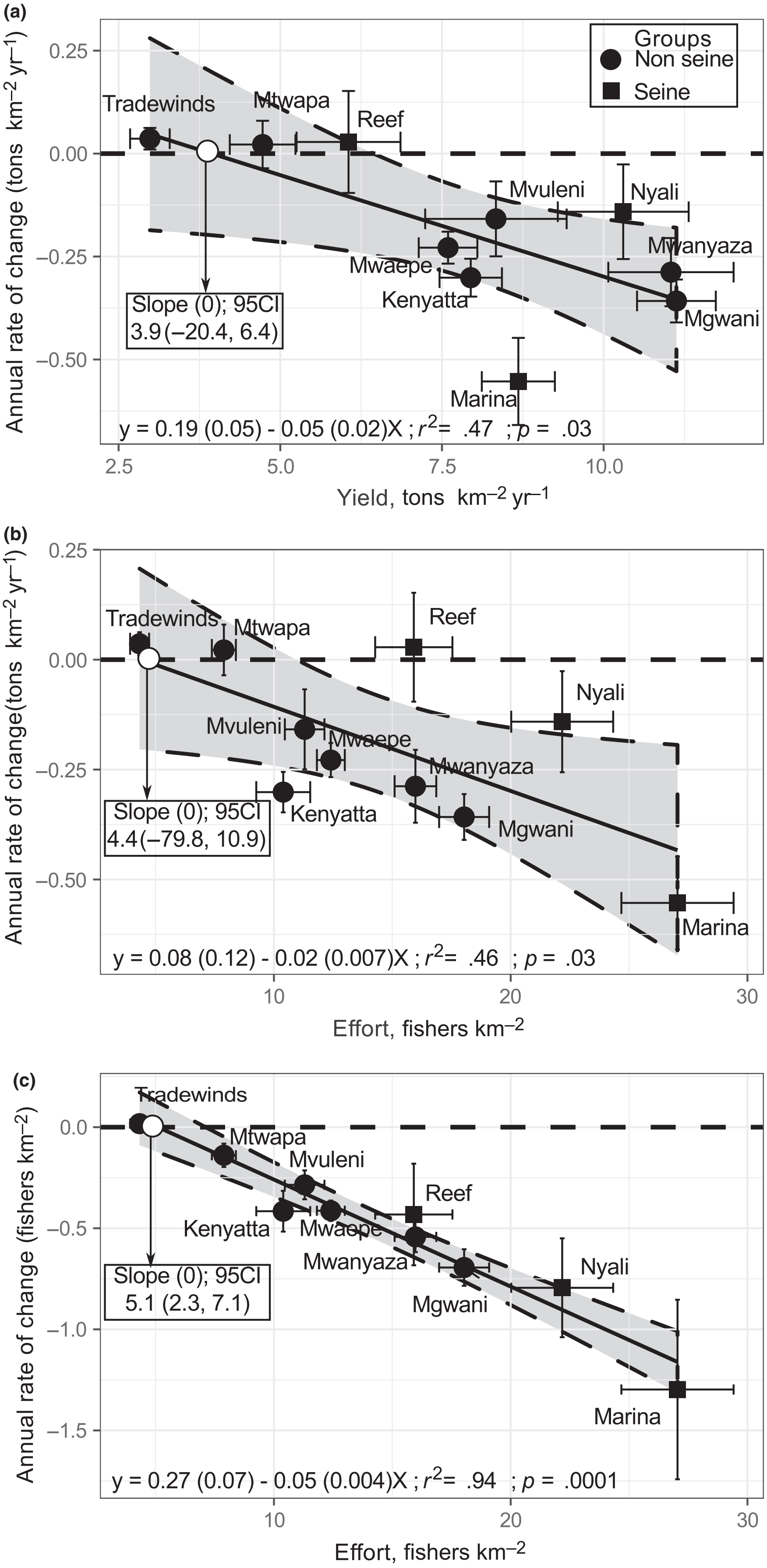
(a)
Annual rate of change (tons km^{-2} yr^{-1})
0.25
0.00
−0.25
−0.50
Groups
Non seine
Seine
Tradewinds
Mtwapa
Reef
Mvuleni
Nyali
Mwanyaza
Mwaepe
Kenyatta
Mgwani
Marina
Slope (0); 95CI
3.9 (−20.4, 6.4)
y = 0.19 (0.05) - 0.05 (0.02)X ; r^2= .47 ; p = .03
2.5
5.0
7.5
10.0
Yield, tons km^{-2} yr^{-1}
(b)
Annual rate of change(tons km^{-2} yr^{-1})
0.25
0.00
−0.25
−0.50
Tradewinds
Mtwapa
Reef
Nyali
Mvuleni
Mwaepe
Mwanyaza
Kenyatta
Mgwani
Marina
Slope (0); 95CI
4.4 (−79.8, 10.9)
y = 0.08 (0.12) - 0.02 (0.007)X ; r^2= .46 ; p = .03
10
20
30
Effort, fishers km^{-2}
(c)
Annual rate of change (fishers km^{-2})
0.0
−0.5
−1.0
−1.5
Tradewinds
Mtwapa
Mvuleni
Reef
Kenyatta
Mwaepe
Mwanyaza
Nyali
Mgwani
Marina
Slope (0); 95CI
5.1 (2.3, 7.1)
y = 0.27 (0.07) - 0.05 (0.004)X ; r^2= .94 ; p = .0001
10
20
30
Effort, fishers km^{-2}

FIGURE 4 Plots of (a) fisheries yields and (b) fishing effort vs. their annual rates of change in yields. (c) relationship between initial fishing effort and the rate of change in fishing effort in 10 Kenyan coral reef fisheries studied from 2001 to 2016. The best-fit equation accounts for temporal autocorrelation found in two of the 10 sites

time-series data and decay rates were a helpful source of additional information but still indicate considerable yield variability driven largely by initial effort and yields. Finally, knowing B_0 and r provided key empirical information for calibrating the MSY model but high variability in r indicates that the recovery rate is the key source of the yield uncertainty (McClanahan, 2018).

Variation in yield estimates are typically attributable to variation in production, multiple sources of primary production (including corals, reef algae, seagrass and plankton), complexity of species life histories, temporary large biomass removals that produce short-term high yields and the vagile, flexible and efficient behaviours of both fish and fishers (Albert, Aswani, Fisher, & Albert, 2015; McClanahan et al., 2008; Zeller, Stoute, & Russ, 2003). Yet, environmental and ecological variation in Kenya is likely to be small because this single fringing reef system has clear geophysical boundaries containing similar habitats, species and environmental conditions (Carreiro-Silva & McClanahan, 2012; Maina et al., 2015). Consequently, environmental and ecological complexity is unlikely to explain much of the observed variation. More likely, effort and initial yields drove declines because reefs with high initial yields had faster losses of yields and effort. There were, however, large confidence intervals on yields. Three landing site (Tradewinds, Mtwapa and Reef) displayed relatively stable yields and their yields varied between ~3.0 and 6.0 tonnes km^{-2} year^{-1}. High variation on the zero-intercept decay rate indicates that mean sustainable yields could be not only as high as 6.4 tonnes km^{-2} year^{-1} but also zero. Given the closeness of landing sites and interconnected nature of the fish populations, it is arguable that sustainable yield predictions will also depend on the yields, effort and management of neighbouring landing sites.

Sustainability, in the sense of persisting into the future without losses of production, diversity and ecosystem services, has been estimated by proxies, such as maximum reported catches over a time series (Halpern et al., 2012). This method would recommend a MSY of ~12 tonnes km^{-2} year^{-1} based on the global literature, Kenyan yield time series, maximum decay rate interval predictions and the highest fishable biomass recovery rates. Using maximum rates of recovery observed in some small and poorly enforced closures would also overestimate sustainable yields (McClanahan & Graham, 2015). Yet, all Kenyan fisheries time series yields >6.0 tonnes km^{-2} year^{-1} declined over the 20-year study period. Consequently, the time-series decay rate indicates a MSY half that suggested by the maximum yield reports and when calibrating the model using the upper recovery rate confidence intervals. Additionally, Kenya's fishing effort was not strongly sensitive to declining profits and yields, resulting in less self-regulation around MSY or maximum profits (Daw et al., 2012; Teh et al., 2013). Therefore, some commonly used MSY proxies should grossly overestimate MSY and their recommendations would hasten declines.

The problem of evaluating yield equilibriums based on stocks, effort or yield time series stimulates much disagreement on the status of fisheries (Branch, Jensen, Ricard, Ye, & Hilborn, 2011; Froese et al., 2012; Pauly et al., 2013). The problems of data scarcity, methodologies, environmental change, decoupling stock–yield relationships and time lags are particularly acute problems for both single or dual criteria evaluations. The Kenyan fishery indicates that evaluating per area yields and effort, combining sites and estimating decay rates over a number of years was helpful but failed to produce small MMSY confidence intervals. There was good correspondence between the model's prediction for the fishable biomass of 3.6 tonnes km^{-2} year^{-1} and the time-series decay method of ~3.9 tonnes km^{-2} year^{-1} when the model was calibrated with mean recovery values. Consequently, mean model settings may be appropriate for the conditions in Kenya in the recent past. Therefore, a MMSY of 6.3 tonnes km^{-2} year^{-1} could be achieved by 10.8 fishers/km^2 if fishable biomass was raised to ~50 tonnes/km^2. The model was, however, less accurate but still

TABLE 2 Mean fishable biomass (tonnes/km^2) of southern Kenya reefs where fisheries catch estimates were measured. The types of management and the area under each management system are presented and biomass is weighted by the coverage (km^2) of the different management categories

Management	Mean (tonnes/km^2)	Coverage (km^2)	Study sites, *N*	Standard deviation	Standard error	95% CI
High compliance closure	93.7	133	17	50.5	12.2	24.0
Low compliance and young closure	19.9	4.3	8	10.0	3.6	7.0
Most destructive gear restricted	19.7	251	29	13.9	2.6	5.1
No gears restricted	18.2	298	16	15.8	3.9	7.7
Fished sites	19.2		45	14.4	2.2	4.2
Unfished sites	70.1		25	54.4	10.9	21.3
All sites (weighted)	33.4		70	21.8	5.1	9.9

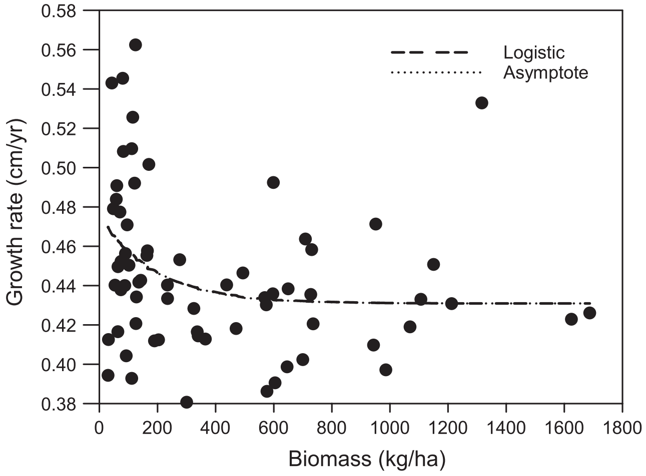

FIGURE 5 Estimated community growth rates of the fishable biomass community as a function of fish biomass based on biomass-weighted growth estimates at the family level (see Methods)

within the confidence intervals when fishable biomass in closures was included, predicting 5.4 tonnes km^{-2} year^{-1}. Therefore, if the model settings reflect real and repeatable processes, increasing biomass in closures would be less effective for increasing yields than raising biomass in fished reefs.

Evaluating stocks or fishable biomass and establishing a target window is a common approach to estimate multispecies MSY (Hilborn & Stokes, 2010). In principle, if fishable biomass values fall between the 0.25 and 0.50 pristine biomass (B_0), high and persistent yields are predicted (Thorson et al., 2012). Using field census from >800 reefs, (MacNeil et al., 2015) estimated a global average B_0 of ~100 tonnes/km^2. The estimate is close but somewhat lower than previous Indian Ocean estimates of 104–120 tonnes/km^2 (McClanahan & Graham, 2015; McClanahan, Graham, Calnan, & MacNeil, 2007; green box, 1). While this B_0 metric helps set a window to evaluate status, the potential range of yields still ranges over ~12 tonnes km^{-2} year^{-1} due to variation in *r* estimates (yellow box, Figure 1). Clearly, recovery rates are the key variable for evaluating actual rather than relative yields (McClanahan, 2018).

Assuming logistic growth during recovery, the intrinsic rate of increase *r* and fishable biomass, the MMSY is equal to B_0 *r*/4 (Caughley & Sinclair, 1994). The accumulation of fish biomass in fisheries closures is used to approximate the intrinsic rate of increase (MacNeil et al., 2015; McClanahan & Graham, 2015). Reported variability in rates is high and some of this variation is due to compliance with the closures, size and configurational aspects of the closures, variable fish production, habitats, ecosystem coverage, fish movements and appropriate control sites (Halpern & Warner, 2002; McClanahan, Graham, Wilson, Letourneur, & Fisher, 2009; Molloy, McLean, & Cote, 2009). For example, net fish immigration into closures will overestimate and emigration underestimate intrinsic fish production. Indian Ocean studies of recovery in closures have been consistently collected by a few investigators and have produced less variable results indicating a ~20-year recovery period for fishable biomass (McClanahan et al., 2007, 2009). A global compilation study combining many regions and ecosystems supports this finding (Molloy et al., 2009). Moreover, the most comprehensive Indian Ocean study found recovery rates depended on the management compliance levels and sizes of the closures (McClanahan & Graham, 2015), consistent with global evaluations (Pollnac et al., 2010). Consequently, closure size and compliance must be considered when selecting sites for estimating endogenous biomass production.

A global compilation of Caribbean and Pacific closures produced a mean *r* of ~0.07 (MacNeil et al., 2015), which is at the low end for high compliance closure in the Indian Ocean (McClanahan & Graham, 2015). This *r* produces a MMSY estimate of 1.7 tonnes km^{-2} year^{-1}, which is not far from the Caribbean median yields (0.9 ± 0.5 tonnes km^{-2} year^{-1}) but low for reported estimated yields for the Pacific (5.0 ± 4.0) (Table S1). Comparing the mean rather than medians yields would further exasperate the differences between field studies and model results. The right-skewed distribution of yields, created by reporting temporarily high and probably unsustainable yields should be responsible for some reported yield disparities. This suggests that yields are ocean-basin dependent and average *r* values need to be used for specific regions to account for this variable recovery (Pollnac et al., 2010; Wood, Fish, Laughren, & Pauly, 2008).

Accurately estimating yields is challenged by variability associated with changing effort, efficiency, consistent and complete measurements, poor or changing estimates of fishing area and environmental change (Albert et al., 2015; Pauly & Zeller, 2016). Some of these issues have been overcome in the Kenyan case where yields were constrained by the simple fringing reef system and the use of natural power (wind, tides and human effort) to capture fish. Official Kenyan reef fisheries statistics have reported high yields of ~10 tonnes km^{-2} year^{-1} for the whole nearshore fisheries (Tuda & Wolff, 2015). While similarly high yields are reported here, they and fishing effort were steadily declining. Government-independent fisheries studies indicate variable yields along effort gradients, ranging from 3 to 16 tonnes km^{-2} year^{-1}, and small- and fast-growing seagrass-associated fish and octopus were the dominant catch at high fishing effort (Hicks & McClanahan, 2012; McClanahan et al., 2008; Samoilys, Osuka, Maina, & Obura, 2017). A time series of catch collected by the Kenyan fisheries department found that more resilient stocks, such as rabbitfish, were replacing larger and long-lived species, such as groupers (Kaunda-Arara, Rose, Muchiri, & Kaka, 2004). Because of species replacement along fishing effort gradients, plots of effort and yield relationships have not displayed strong yield-deflections or declines at high effort. Rather, there is levelling and high variability in yields at high effort (McClanahan et al., 2008). Consequently, both government and independent data sources confirm the yield declines and lack of temporal stability. However, the classical fisheries indicator of a MSY inflexion point at high effort was not found in these analyses despite effort strongly declining in proportion to initial yields in this study. Decay rates of yields and effort derived from moderate time series may therefore be critical to evaluating sustainable yields in tropical reef fisheries.

Replacement of slow with faster growing taxa should help to maintain yields at high effort. The community growth rate analysis presented here suggests that it does occur but the overall effect was small and largely present only at the lowest biomass levels. Consequently, an underestimation of the logistic equations production or *r*-value at low biomass is likely to be a small portion of the overall variation. The analysis does not, however, account for both compensatory increases in growth within taxa or for non-bony fish taxa. There is evidence that common fisheries species, such as the marbled parrotfish (*L. vaigiensis*), adjust their life histories in response to increasing fishing pressure (Locham, Kaunda-Arara, Wakibia, & Muya, 2014). Additionally, octopus is a taxa known to have fast life histories that becomes common in the fisheries at high yields and low fish biomass (McClanahan et al., 2008). Consequently, a combination of compensatory growth, taxa switching, immigration of fish inshore from offshore sites and increased per fisher effort and efficiency are likely to contribute to the high yields at high effort. Regardless of the mechanisms, most Kenyan reef fisheries do not pass either temporal or taxonomic stability tests of sustainability. If sustainability guidelines included persistence of slow-growing species, then Kenya fisheries might be sustainable if these species were present and viable in the existing closures. Taxa with large body size and slow growth life histories have been shown to recover slower than overall fish biomass in Indian Ocean closures (McClanahan & Graham, 2015). This finding indicates the importance of old and large closures (>40 years) as part of national fisheries sustainability practices.

Ecological switch points have been studied on Indian Ocean reefs and are considered robust indicators of ecosystem change (McClanahan et al., 2011). These changes reflect changes in key ecosystem processes and increased spatial variability as fish consumers and their impacts are diminished (Biggs, Carpenter, & Brock, 2009). Here, ecological switches are first observed as changes in macroalgae variation but eventually associated with losses in coral and calcium carbonate cover, metrics of reef growth (McClanahan & Muthiga, 2016; Perry et al., 2015). In short, these tipping points are steps down a ladder of ecological degradation; a phenomenon being uncovered in other fisheries ecosystems (Karr et al., 2015; Selkoe et al., 2015). When these switch points are plotted along with other criteria, the constraints and trade-offs between maintaining habitat and ecosystem function and sustainable yields are further illuminated. Interestingly, intermediate or MMSY biomass corresponds with estimates of the maximum number of local fish species (McClanahan, 2015b). Consequently, along the East African coastline, sustainable yields and local fish diversity are maximized at nearly the same biomass location.

Ecological tipping points may be widespread and provide another simple rule-of-thumb metric that can increase the criteria used to evaluate fisheries status (Karr et al., 2015). A tipping point approach has the benefit of being inclusive of ecosystem states, processes and biodiversity, and aligned more with slower scales of habitat change that should be seen as appropriate for judging long-term sustainability. Ecosystem tipping points do, however, have similar problems because measurement at one site and time cannot assume equilibrium. Tipping points are statistical properties that arise from evaluating many sites. Nevertheless, using ecological thresholds reference points among other criteria can help identify probable ecological transitions that are increasingly considered important for evaluating status, yields and ecosystem service trade-offs (Levin & Lubchenco, 2008). Most importantly, from a fisheries management point of view, is that change points indicate that production is being channelled into unfished species, which will reduce the production of edible fish.

4.1 | Advice for managers

This review provides managers with a variety of metrics to evaluate coral reef fisheries ecosystems. There is not only clear alignment between biomass, recovery rates, yields, models and ecological changes but also high variability that challenges efforts to make simple and universal guidelines for managing specific reef fisheries. In fact, results strongly suggest that sustainable yields for coral reefs have wide confidence intervals and will be uncertain unless key information is known. The decline in fishing effort with declining yields was, however, highly predictable and therefore a good indicator of fishing beyond sustainable levels. Reduced fishing effort associated with biomass below the MMSY window is therefore a good indicator of overfishing that provides another approach to evaluating sustainability. The Kenyan case study suggests that this decline of yields and fishing effort will stop at 4 and 5 fishers/km^2 for the fishable biomass in these reefs. If so, fishing effort can be increased to ~10 fishers/km^2 when biomass exceeds the MMSY of ~50 tonnes/km^2.

Yields appear to be regionally specific and this is likely to reflect different production and recovery rates of fishable biomass—the Caribbean having the lowest yields, followed by the Indian Ocean and Pacific. Consequently, expectations need to be regionally specific unless local recovery rates are well known. Another emerging finding is that pristine biomass, while variable for specific reefs, appears to fall within a narrow range close to 100 tonnes/km^2, when well sampled (MacNeil et al., 2015; McClanahan & Graham, 2015). Consequently, models indicate that the MMSY yields should occur where biomass is around half of this pristine biomass level. However, biomass alone does not predict yields, which are highly sensitive to biomass recovery rates (McClanahan, 2018). Consequently, knowing and maintaining high recovery rates will be critical to any fisheries policies aimed at promoting sustainable yields and maintaining high fisheries production. Maintaining recovery rates includes common fisheries management actions of closures, maintenance of functional diversity and balancing fishing capital, gear and effort capture with fish production (Table 1). In the absence of criteria evaluated here, the status of reef fisheries can be simplified by knowing the fishable biomass and applying management changes as appropriate.

In Kenya and possibly the western Indian Ocean, the evidence here suggests that yields above ~6 tonnes km^{-2} year^{-1} are unsustainable, especially when biomass is below 50 tonnes/km^2. Higher biomass and lower yields may be sustainable but other information, such as interannual rates of change in per area yield are needed to verify sustainability in specific fisheries. A common universal sustainable yield rule-of-thumb of 5 tonnes km^{-2} $year^{-1}$ is not reliable. The estimate depends greatly on ecological production and fish biomass and recovery, which varies by region. Furthermore, one of the largest problems with current efforts to know and maintain sustainable stocks is good estimates of the area of fishing grounds. Yields are commonly reported without this information and, yet, knowing this would greatly enhance the ability to evaluate yield stability and sustainability. Given that fishing grounds change with fishing capital, effort and stock status, there is a need to record the actual changes in fishing areas over time. The practice of using Exclusive Economic Zones or generic travel distances is less convincing than using clear geophysical limitations and empirical evaluations.

The key finding of the eclectic measurements used here is that high variance in yields is confirmed by the confluence of multiple criteria but the sources of this variation are also uncovered. Consequently, key variables that are most critical to measure for specific fisheries include fishing area, fishable biomass and recovery rates. Given that many reef yield studies report widespread and unsustainable fishing (Newton et al., 2007; Teh et al., 2013), it is critical that resource-limited managers focus on collecting the most useful metrics to determine status and management actions. The suggested metrics of biomass, declining effort and production should improve evaluations of status to provide targets that stimulate appropriate management actions.

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SUPPORTING INFORMATION

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