

# Community biomass and life history benchmarks for coral reef fisheries

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## Abstract

The status of fisheries requires establishing and evaluating benchmarks derived from unfished ecosystems. Habitats, environmental conditions, properties of the fish communities and management systems could potentially influence the variability surrounding benchmarks. Consequently, eighteen variables including habitat, number of species, life histories, thermal and productivity environments were tested for influences on reef fish biomass in 62 reefs within old high compliance closures along the east African coastline. Biomass and weighted life history characteristics were classified and described for total, fishable, target and non-target groups. Benchmark biomass fell within a 95% confidence interval of ~1,030–1,250 kg/ha and equally distributed among target and non-target groups. While some relationships were statistically significant, most were weak, poorly sampled (ocean exposed reefs), had uncertain relationships with biomass (number of species), or the explained variation was bounded within the above confidence intervals (habitat and environment). Therefore, a regional unfished biomass benchmark ( $B_0$ ) of 1,150 and 560 kg/ha is recommended for total and target biomasses, respectively. Weighted life history metrics indicate that the target had slower life histories than the non-target fish communities. Consequently, they will be fished unsustainably if yield recommendations are derived from the total, resilient or non-target fish life history metrics. The intrinsic rates of increase ( $r$ ) and target categorization of biomass were the most influential metrics in estimating yields.

## KEYWORDS

coral reef, fisheries indicators, maximum sustained yields, pristine, sustainability, virgin biomass

## 1 | INTRODUCTION

Biomass, numbers of species, body length and growth metrics are among key variables used to evaluate fish communities, ecological impacts and potential fisheries yields (Hall et al., 2006; Nash, Bijoux, Robinson, Wilson, & Graham, 2016; Newman, Paredes, Sala, & Jackson, 2006; Rochet & Trenkel, 2003; Taylor, Lindfield, & Choat, 2015). Establishing benchmarks for these variables is increasingly important for evaluating fish communities and fisheries status (MacNeil et al., 2015; McClanahan, Maina, Graham, & Jones, 2016). Evaluating coral reef fisheries is particularly challenging because of the high diversity

of target taxa and the lack of taxa or stock-specific evaluations of their status (Worm et al., 2009). While the practical need is great, the high diversity and spatial heterogeneity of reef fishes may preclude finding useful sustainability benchmarks. For example, the maximum biomass of fish has been reported over large ranges and often associated with isolation from human influences and the existence of large roaming predators, such as sharks (Bradley et al., 2017; Juhel et al., 2017; McCauley et al., 2012; Stevenson et al., 2007). Further, large differences in biomass exist between remote wilderness and unfished national parks, indicating that human disturbance is widespread and not just limited to local fishing impacts (Graham & McClanahan, 2013).

Evaluations of fish and fisheries status may therefore prove to be inadequate unless benchmark variability can be reasonably bounded.

Unfished biomass, its inherent variability and factors influencing it are critical to evaluating fisheries. The  $B_0$  benchmark is used to establish maximum sustained yield biomass ( $B_{msy}$ ) when combined with recovery and density-dependent parameters (Pella & Tomlinson, 1969). Further, the yield status of a fishery can be known in terms of the  $B/B_{msy}$  where  $B_{MSY}$  is determined from  $B_0$  (Worm et al., 2009). Yet,  $B_0$  is seldom critically evaluated in terms of the factors that influence its variability. These include the influences of the endogenous composition of multispecies fish communities, their consumption rates, habitat and environmental variables that influence productivity (McClanahan, 1992; Valdivia, Cox, & Bruno, 2017). Further, total differs from catchable and target biomass because not all biomass can be fished and portions of the fishable biomass are not targeted for the catch. Target catches are composed of preferred taxa or sizes of fish that have markets, good prices and stimulate research, while non-target catches can be critical for local consumption and food security (Wamukota & McClanahan, 2017). Consequently, these taxa are often valued, recorded, studied and understood differently (Pauly & Zeller, 2016). Despite these potential complications, if this variability can be estimated and accounted for, then there is the potential to establish robust benchmarks for estimating sustainable catches.

A benchmark approach has the advantage that the cascading impacts of fishing often reflect the state of ecosystems (Karr et al., 2015; McClanahan et al., 2011). Therefore, fish biomass is one of the better metrics for evaluating fishing pressure, impacts and ecosystem states (Cinner et al., 2016; MacNeil et al., 2015). Mean  $B_0$  in fished landscapes appears to lie within a range of 1,000 and 1,200 kg/ha in the western Indian Ocean and perhaps globally (MacNeil et al., 2015; McClanahan & Graham, 2015; McClanahan, Graham, Calnan, & MacNeil, 2007). Nevertheless, reef fish communities are complex and composed of species with many life histories, and therefore, simple biomass proxies may poorly represent their status. For example, changes in fish life history characteristics along a time since the cessation of the fishing sequence provided evidence that biomass may be a poor proxy for fish status (McClanahan & Graham, 2015). Key community maturity variables, such as body size, natural mortality, growth rates and trophic levels, changed long after biomass stabilized. Therefore, life history benchmarks and biomass need to be evaluated to determine fisheries status. Finally, benchmarks may be poorly bounded if these fish life history characteristics are contributing to the variability in biomass (Gilby, Tibbetts, Olds, Maxwell, & Stevens, 2016; Graham et al., 2017).

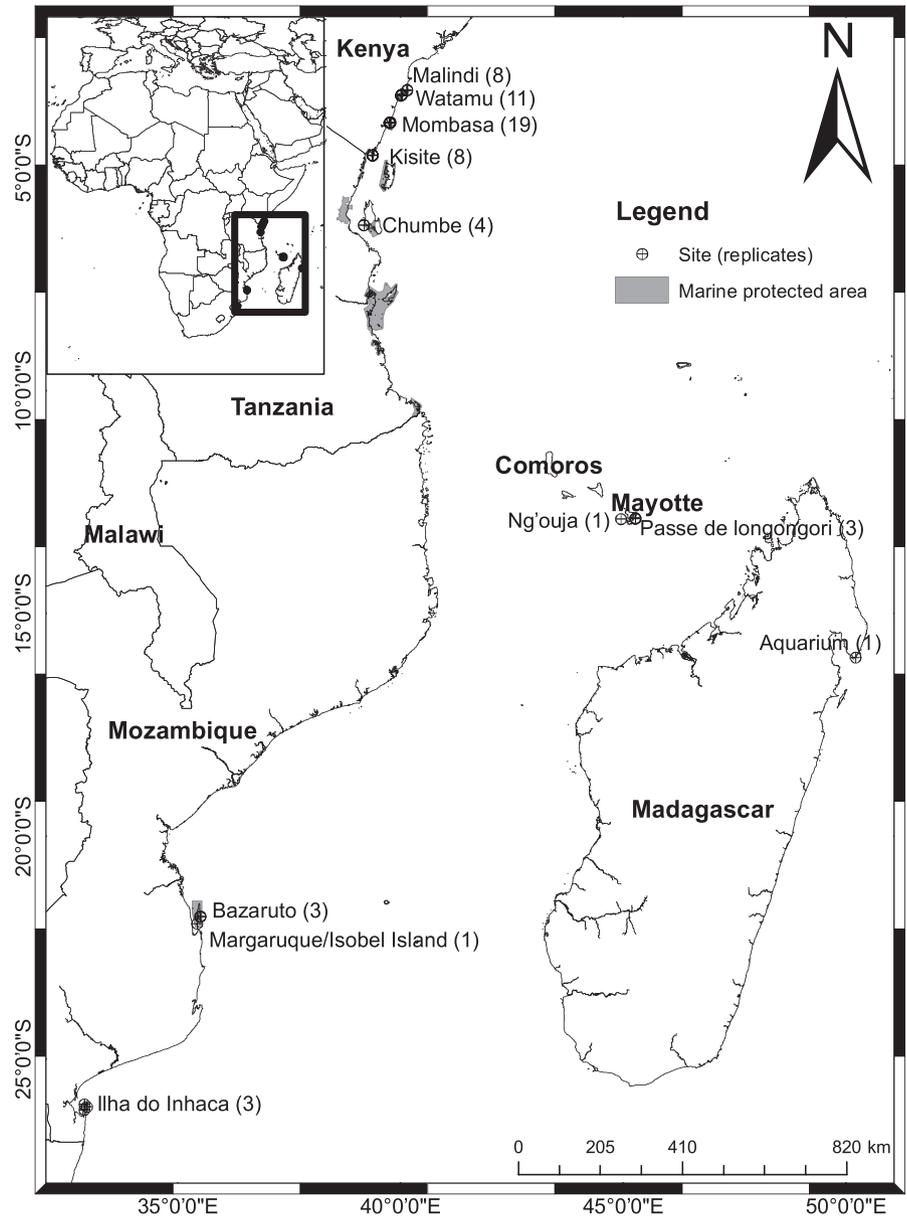
Establishing meaningful benchmarks may be further precluded by the diversity of species, habitat, environmental forces, and their magnitude and variability. Common medium-scale ecological field studies have found the cover of hard coral, reef complexity, habitat and productivity of interacting ecosystems can significantly influence coral reef fish community metrics (Cinner et al., 2016; Darling et al., 2017; Heenan, Hoey, Williams, & Williams, 2016; Williams et al., 2015; Valdivia et al., 2017; Wilson et al., 2008, 2009). There is also the suggestion that numbers of species influence biomass

by increasing efficiency of resource use and production (Duffy, Lefcheck, Stuart-Smith, Navarrete, & Edgar, 2016; Mora, Danovaro, & Loreau, 2014). The influences and magnitude of this variability on biomass have, however, not been well evaluated or bounded where there is no fishing. Consequently, the null hypotheses for this study were that  $B_0$  is not influenced by habitat, environmental variables of productivity, exposure to the ocean, community life histories and numbers of species metrics.

## 2 | METHODS

Estimating unfished biomass was the primary focus and estimates were based on censuses undertaken in western Indian Ocean reefs within high compliance closures, closed to fishing for >15 years. Compliance, size and ages of closures strongly influence unfished biomass estimates and were fully evaluated in two companion papers (McClanahan & Graham, 2015; McClanahan, Graham, Wilson, Letourneur, & Fisher, 2009). These studies determined that biomass does not level until >15 years after closure, in closures >5 km<sup>2</sup>, and only where no-fishing compliance is high. Consequently, this study restricted fish biomass data to reef locations that fit these criteria. Data were collected between 2005 and 2016 in reefs over 20° of latitude and longitude and 11 m of depth in the oldest and largest fisheries closures in the western Indian Ocean (Figure 1). The data were from visual censuses of coral reefs fish based on a total of 133 transects. Biomass data were categorized and analysed into four categories: total unfished biomass, fishable biomass, targeted biomass and non-targeted biomass. Here, I defined fishable biomass as the biomass of all fish >10 cm excluding all damselfishes. Targeted biomass was the sum of the following families: Carangidae, Haemulidae, Holocentridae, Lethrinidae, Lutjanidae, Mullidae, Scaridae, Serranidae, Siganidae, Sphyraenidae, Carcharhinidae, Ginglymostomatidae, Rhincodontidae >10 cm and Labridae >20 cm in length. Non-target biomass was the difference between fishable and target biomass. These classifications were based on many years of observation and collection of fish landing data in East Africa (McClanahan & Abunge, 2014).

The primary focus here was on benchmarks for benthic-attached species, and therefore, planktivorous species were not included in the analyses. Some studies have reported high biomass and a positive role of water-column plankton production on planktivores (Cinner et al., 2016; Nadon et al., 2012; Valdivia et al., 2017; Williams et al., 2015). These groups were not included in the African coastline analysis because of the high variability and difficulties of accurately sampling planktivores. The inclusion of planktivores should increase variance and potentially obscure relationships with the benthos because of variable water-column production. Planktivores can reach high biomass in some reefs where they aggregate and swim quickly across depths, which can make them difficult to accurately census in deep water because they are frequently above the visual field of the observer.



**FIGURE 1** Map of the African coastline region, the location of old fisheries closures and number of sampled study sites

### 2.1 | Fish census

Fish census and life history calculation methods have been described in previous publications (McClanahan, Graham, MacNeil, & Cinner, 2015). The individual censuses were 500 m<sup>2</sup> areas in which individual fish were identified to the family level and sized into 10-cm intervals. These count and size data were converted into wet weights using family-specific length–weight relationships. Published life history metrics of nine variables (trophic level, annual natural mortality, growth rate, age at maturity, generation time, lifespan, maximum length, length to obtain optimum yield (suggested minimum size to capture a species) and length at maturity (first reproduction)) were compiled for the dominant species in the African coastline region (Fishbase.org, February 1, 2013). The biomass of the family was multiplied by the mean life history and summed across all families to obtain the total weighted community life history metric. This metric was

calculated for the total, fishable, target and non-target categories of the biomass.

### 2.2 | Habitat and benthic cover

Sites were classified as two levels of exposure to the open ocean: exposed (i.e., reef crests and slopes) and sheltered (i.e., back reefs and lagoons). Water depth was recorded with a depth gauge while diving. Benthic cover was estimated using two methods. In shallow sites, six to nine 10-m standard line-intercept transects were completed in which coral and other functional groups under the line were recorded to the nearest centimetre. In 38 sites, topographic complexity of the bottom was measured by pressing a 10-m weighted line across the bottom contour, measuring the straight-line distance that it travelled and dividing this number into the transect line distance. In deeper sites, visual estimates of hard coral, soft coral and erect algae were

made in ~15 2-m<sup>2</sup> quadrats, but no topographic complexity measurements were made. Comparisons of visual and line transects comparison found similar results, largely with <5% cover differences between methods.

### 2.3 | Environmental variables

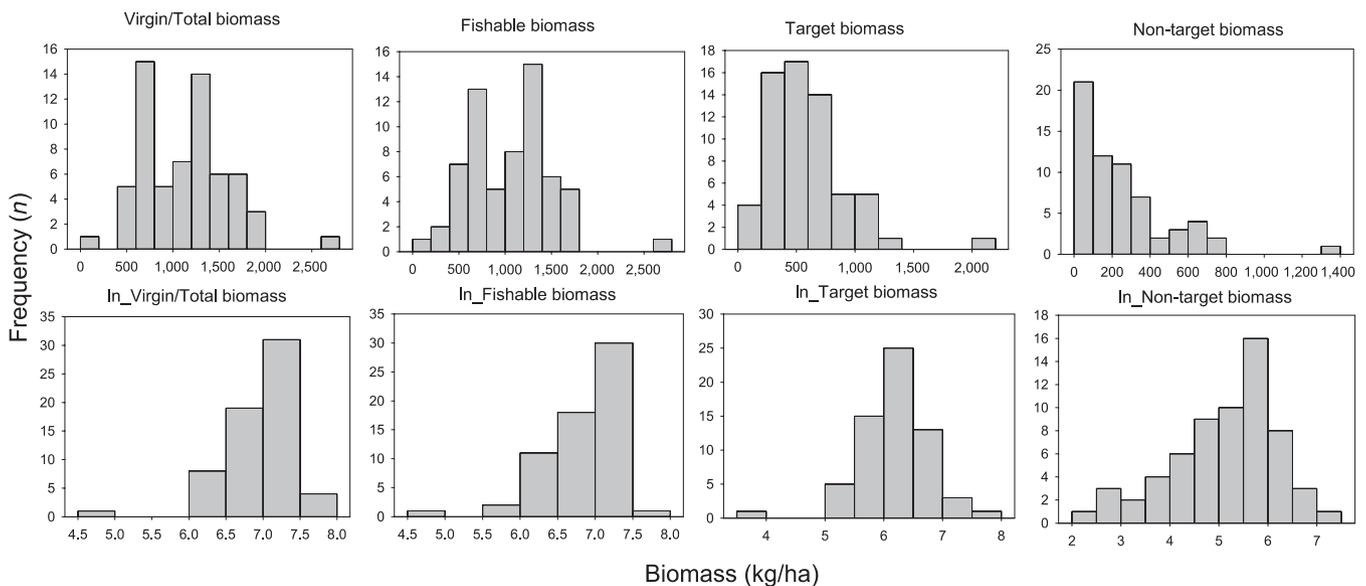
Satellite-based environmental parameters of temperature, light and water quality were accessed from open access data sources provided by the United States National Oceanographic Atmospheric Administration (NOAA) and European Space Agency. NOAA provides data via CoRTAD (<http://www.nodc.noaa.gov/sog/cortad/>, July 14, 2015), which contains sea surface temperature collected weekly at 4-km resolution from 1982. Light and water quality variables (chlorophyll-a and total suspended solids concentration) were obtained from the European Space Agency's COASTCOLOUR project (<http://www.coastcolour.org/>, 24 September 2016). Temperature-derived variables for each study site were pooled for the period 1982 – 2012, and standard statistics of mean, median, standard deviation, kurtosis and skewness were calculated along with a metric of thermal stress anomaly (TSA). CORTAD defines SST anomaly (SSTA) as the averaged temperature over a week in excess of 1°C or more above that period's long-term average value, whereas thermal stress anomalies (TSAs) are defined as the temperature excess of 1°C or more above the climatologically long-term average warmest weekly periods of the year (Maina, McClanahan, Venus, Ateweberhan, & Madin, 2011; Selig, Casey, & Bruno, 2010). Lastly, a multivariate exposure and global stress model were used in evaluations as they have been shown to be effective in predicting reef stress (McClanahan, Maina, & Ateweberhan, 2015). These estimates of exposure combined and weighted impacts of light and water temperature thermal variables on the exposure of hard corals to thermal stress (Maina, Venus, McClanahan, & Ateweberhan, 2008). The second version of the multivariate global stress model

combines the thermal stress with attenuating factors, such as water movement and quality (see Maina et al., 2011 for a full explanation).

### 2.4 | Data analyses

The establishment of benchmarks requires a full evaluation of the data distributions, and therefore, descriptive statistics of biomass and life history characteristics are presented. Additionally, to further evaluate the data distributions, Kolmogorov-Smirnov test of normality was undertaken for the raw and log<sub>e</sub> transformed biomass and life history metrics (Figure 2). Mean life history characteristics based on compilations of common species at the family level were plotted and tested for differences with one-way ANOVA and post hoc pair-wise comparisons with the Tukey test. Plots of the ratio of the biomass categories relative to unfished  $B_0$  and life history characteristics are presented for the total and family-level biomass. It is also important to determine whether the habitat and environmental variables reported here are typical of coral reefs for the findings to be applicable more broadly. Therefore, descriptive statistics from global compilation of environmental variables are presented (Bruno & Valdivia, 2016; Kleypas, McManus, & Menez, 1999; Maina et al., 2011) (Table 1).

Prior to testing the hypotheses that environment, habitat, fish life history and species diversity affect baseline biomass  $B_0$ , correlation matrices were examined to evaluate the levels of collinearity by the Variation Inflation Factor (VIF), an indicator of autocorrelation (Figure S1). Bivariate correlations with  $r \geq .70$  were examined and redundant and less ecologically meaningful or reliable variables removed. From these results, variables were reduced to non-redundant metrics and these variables were used in a series of forward stepwise regression analyses. For example, median sea surface temperature (SST) and Photosynthetic Active Radiation (PAR) were used in favour of mean SST and maximum PAR because means can be biased by right-tail distributions. Coral



**FIGURE 2** Frequency distributions of the four biomass categories for (top) raw and (bottom) log<sub>e</sub> transformed data

cover and topographic complexity are often positively correlated (Darling et al., 2017), but there was no significant relationship in these data (Spearman  $\rho = -0.20$   $p = .27$ ). Further, a forward stepwise regression did not find a relationship between topographic complexity and unfished biomass. Therefore, the more commonly measured cover of coral was included in the final stepwise regression results. From the autocorrelation and selection process, 10 environmental, two habitat variables (depth and ocean exposure), three benthic cover (hard and soft coral and erect algae), numbers of species and two multivariate models resulted in a total of 18 independent variables chosen to test for their potential influences on fish biomass.

Fish censuses were haphazardly done in time and space, transects were not fixed, and this led to a total of 62 site and time replications. Various levels of data pooling were done to evaluate possible influences of this decision, but none were found. Additionally, to avoid potentially spurious results that might arise from small single variable effects, I identified a few reefs with low water quality and high soft coral cover that were removed from the regression analyses. One reef edge, in particular, was exposed to heavy river run-off and its visibility was reduced most of the year. Consequently, the fish census was undertaken during a short window of high visibility and the biomass was low. Coral bleaching may have damaged the second unusual site where soft coral was very high and may have replaced hard corals (T.R. McClanahan, personal observation). Some habitat and bottom complexity data were missing, which reduced the number of replicates to 38 for evaluations of relationships between biomass and habitat. The nine life history traits and number of species were evaluated in an independent analysis. Regression analysis made selections based on inclusive or associative Akaike information criteria (AIC) and exclusive or predictive Bayesian information criteria (BIC). When selections by these two methods were the same, the AIC results were presented.

## 2.5 | Fisheries yields

Maximum sustained fisheries yields have been estimated based on expected ranges of the three parameters of the stock-yield equation of Pella and Tomlinson (1969):

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

I used the lower, mean and upper 95% CI of  $B_0$  established in this study. The intrinsic rates of growth  $r$  have been estimated for multispecies reef fish biomass in this region as  $0.23 \pm 0.16$  (95% CI) based on recovery rates in the studied high compliance closures in the western Indian Ocean region (McClanahan & Graham, 2015). The density-dependent shape  $z$  parameters are unknown for coral reef fishes and as a group, but lower and upper values of 0.8 and 1.2 were used and correspond to the full ranges of well-studied temperate fisheries stocks (Thorson, Cope, Branch, Jensen, & Walters, 2012). The sensitivity of the  $B_0$  ( $K$ ),  $r$  and  $z$  variables on

yield estimates was evaluated by iteratively holding mean values for two of the three variables constant and solving for the lower, mean and upper values of the 3rd variable. The maximum ranges were also evaluated by solving for all minimum, mean and maximum  $B_0$ ,  $r$  and  $z$  values combined. Additionally, the influences of using either the mean or median values of  $B_0$  were also evaluated. Median CIs were based on a rank procedure and calculated in MiniTab version 17.1.0.

## 3 | RESULTS

### 3.1 | Habitat and environmental variation

Study sites ranged in depth from shallow water to 11 metres and were dominated by turf and coralline algae matrix that covered ~50% of the bottom cover. Coral cover was that next largest functional group at ~35% cover with a large variation ranging from 10 to 90% cover (Table 1). Erect algae were 10% of the cover and also had high variation from 0 to 35% cover with standard variance equal to the mean. Soft coral cover was ~5% with a maximum of 10% cover.

Median water temperatures were ~27°C with small variation, having a minimum temperature of ~24°C and negative kurtosis (flattish distributions) and positive skewness (occasional high temperatures) (Table 2). The weekly thermal stress metric indicates that these reefs had experienced anomalous temperatures. PAR was high at ~49  $E\ m^{-2}\ day^{-1}$  and had modest variation ranging from 42 to 53  $E\ m^{-2}\ day^{-1}$ . Mean chlorophyll-a values were similar, while suspended solids were lower than the global means. Suspended solid variation was low, while chlorophyll-a variation was modest. The mean multivariate climate exposure and stress models metrics for this region were above the global mean but had high variation.

### 3.2 | Distribution of unfished biomass

Mean total unfished biomass was not significantly larger (~100 kg) than fishable biomass at ~1,100 kg/ha (Table 2). Additionally, fisheries target and non-target biomass were not statistically different from each other, sharing an equal proportion of the total biomass, but different from total and fishable biomass (Table 3; Figure 3). Variation in biomass as measured by coefficient of variation (COV) was moderately high with mean variance being ~40%–60% of the means. There was a higher variation for the target and non-target than the total and fishable biomass. The 95% CIs estimates of the means were more constrained and suggest that mean unfished biomasses fell between 1,030 and 1,250 kg/ha. Mean target biomass ranged between 480 and 650 kg/ha. Biomass distribution categories except for target biomass were not significantly different from normal. Target biomass had high kurtosis and skewness, which indicated a centralized and right-tailed distribution (Figure 2). Target biomass was normalized by the  $\log_e$  transformation, but the other distributions were no longer normal after transformations.

**TABLE 1** Description of environmental traits (sample size, mean, median, standard deviation (SD), minimum (Min), maximum (Max))

Trait	N	Mean	Median	SD	Min	Max	Global estimates	
							Mean $\pm$ SD	Median
Habitat								
Hard coral (%)	38	35.88	29.75	20.70	10.36	91.54	32.50 $\pm$ ND <sup>a</sup>	31.30 <sup>a</sup>
Soft coral (%)	38	2.51	2.00	2.57	0.00	10.50		
Erect algae (%)	38	9.40	7.46	9.11	0.00	35.40	10.20 $\pm$ ND <sup>a</sup>	19.00 <sup>b</sup> 6.90 <sup>a</sup>
Depth (m)	38	2.55	2.00	2.23	1.50	11.00		
Environmental parameters								
SST median (°C)	38	27.14	27.38	0.77	24.23	27.67	26.90 $\pm$ 1.30 <sup>b</sup> 27.60 $\pm$ 1.10 <sup>c</sup>	
SST minimum (°C)	38	24.03	24.23	0.87	20.70	24.60	24.80 $\pm$ 1.80 <sup>c</sup>	
SST SD (°C)	38	1.79	1.90	0.21	1.56	2.28		
SST kurtosis	38	-0.39	-0.25	0.37	-1.23	-0.05		
SST skewness	38	0.21	0.12	0.19	-0.06	0.46		
Mean SST anomaly (°C)	38	18.88	16.59	3.63	12.78	24.11	16.00 $\pm$ 1.20 <sup>b</sup>	
Mean thermal stress anomaly (°C)	38	6.56	5.27	2.44	2.11	9.51	3.90 $\pm$ 1.40 <sup>b</sup>	
PAR median (E m <sup>-2</sup> day <sup>-1</sup> )	38	49.46	49.23	2.95	41.67	53.27		
Suspended solids median (g/m <sup>3</sup> )	38	0.63	0.70	0.16	0.41	0.85	0.80 $\pm$ 1.50 <sup>b</sup>	
Chlorophyll median (mg/m <sup>3</sup> )	38	0.67	0.78	0.26	0.29	1.01	0.70 $\pm$ 1.20 <sup>b</sup>	
Multiple variable models								
Climate exposure	38	0.62	0.64	0.16	0.21	0.78		
Multivariate stress model	38	0.87	0.91	0.12	0.52	0.98	0.70 $\pm$ ND <sup>b</sup>	

<sup>a</sup>Bruno and Valdivia (2016), <sup>b</sup>Maina et al. (2011), <sup>c</sup>Kleypas et al. (1999).

SST, sea surface temperature; PAR, photosynthetically active radiation; ND, no data.

### 3.3 | Distribution of life history characteristics

Mean body sizes of fish families showed high variation but were predictable based on the families for most life history characteristics apart from the trophic levels of their diet (Figure 4). Length measurements corresponded well to the families with length at maturity being the smallest length metric, followed by length to obtain optimum yield, and maximum lengths. For example, among the 23 families, values for the length to obtain optimum yield ranged from 7.1 cm for Pomacentridae to nearly 219.3 cm for Ginglymostomatidae. Age of fish was more variable by family but clearly declined along the mean family size gradient. Average lifespans ranged from 4.6 years for Pomacentridae to 15.3 years for Ginglymostomatidae. Growth and mortality metrics were the opposite of length and lifespan metrics with sharks and jacks having the slowest and damselfish and butterflyfish having among the highest growth and annual natural mortality rates. Trophic level was less predictable along this body size gradient with some intermediate sized fish being herbivores and many small-body sized families having mid to high trophic levels diets.

Total, fishable and target biomass weighted life history distributions were not different from normal with the exception of growth rate estimates, which had negative kurtosis and positive skewness (Table 2). Site variation in life history characteristics was generally small with COVs of ~10% of the mean values. Log<sub>e</sub> transformations of these data produced distributions that were more frequently non-normal compared to the non-transformed data but still often normally distributed. Non-target biomass distributions were mixed in their distributions. Log<sub>e</sub> transformation of non-target biomass further reduced the number of life history characteristics that were normally distributed.

Differences between the four biomass categories for weighted community life histories were evaluated. Similar patterns were observed for evaluations using log<sub>e</sub> and non-log<sub>e</sub> transformations of the data. Tests of differences based on non-transformed data found differences among biomass categories for all community metrics (Table 3). However, weighted life history characteristics between total and fishable biomass were only significantly different for length at maturity and maximum lengths, being a few centimetres

**TABLE 2** Summary statistics for biomass and nine community-weighted life history variables calculated for the four biomass categories of the unfished biomass data. Tests of normality based on raw data

	Total	Fishable	Target biomass	Non-target biomass
<b>Biomass category (kg/ha)</b>				
Mean ± SD	1140.2 ± 436	1022.1 ± 411.0	563.9 ± 332.9	458.1 ± 234.1
COV	38.23	40.21	59.04	51.10
95% CI (L;U)	1029.5; 1250.9	917.7; 1126.4	479.4; 648.5	398.7; 517.6
Median	1148.2	1009.4	511.48	457.05
95% CI (L;U)	913.9; 1307.4	828.8; 1159.6	479.39; 648.49	387.71; 515.82
Kurtosis	0.94	0.23	5.37	3.48
Skewness	0.65	0.21	1.75	0.22
KS	0.116	0.08	0.15	0.11
p-value	.04	NS	.001	NS
<b>Length at first maturity (cm)</b>				
Mean ± SD	22.84 ± 2.2	24.45 ± 1.81	27.46 ± 2.29	20.92 ± 1.98
COV	9.64	7.38	8.33	9.45
95% CI (L;U)	22.28 ± 23.39	23.99; 24.91	26.88; 28.04	20.42; 21.43
Median	23	24.29	27.31	20.88
95% CI (L;U)	22.43; 22.5	23.82; 24.86	26.88; 28.37	20.44; 21.21
Kurtosis	1.67	1.45	0.92	9.89
Skewness	0.29	0.80	0.29	1.91
KS	0.08	0.09	0.08	0.11
p-value	NS	NS	NS	.07
<b>Length to obtain optimum yield (cm)</b>				
Mean ± SD	25.53 ± 2.78	27.51 ± 2.34	31.41 ± 2.98	22.93 ± 2.43
COV	10.88	8.51	9.49	10.58
95% CI (L;U)	24.82; 26.23	26.91; 28.10	30.65; 32.17	22.31; 23.55
Median	25.66	27.39	31.33	22.86
95% CI (L;U)	24.89; 26.4	26.60; 27.92	30.64; 32.31	22.30; 23.17
Kurtosis	1.89	1.60	1.07	11.49
Skewness	0.43	0.92	0.40	2.30
KS	0.08	0.10	0.07	0.18
p-value	NS	NS	NS	.001
<b>Maximum length (cm)</b>				
Mean ± SD	42.93 ± 4.49	46.33 ± 3.60	49.81 ± 4.01	42.68 ± 9.07
COV	10.45	7.77	8.05	21.24
95% CI (L;U)	41.79; 44.07	45.42; 47.25	48.79; 50.82	40.38; 44.99
Median	42.98	46.12	50.27	41.07
95% CI (L;U)	42.53; 44.3	44.82; 47.28	48.47; 51.63	40.38; 44.99
Kurtosis	2.26	2.17	0.31	22.63
Skewness	0.32	1.05	-0.26	4.11
KS	0.11	0.08	0.06	0.23
p-value	NS	NS	NS	.001
<b>Lifespan (years)</b>				
Mean ± SD	9.49 ± 0.74	10.01 ± 0.72	10.71 ± 1.25	9.33 ± 0.91
COV	7.82	7.24	11.67	9.77
95% CI (L;U)	9.31; 9.68	9.83; 10.19	10.39; 11.02	9.10; 9.56

(Continues)

TABLE 2 (Continued)

	Total	Fishable	Target biomass	Non-target biomass
Median	9.52	9.97	10.71	9.36
95% CI (L;U)	9.19; 9.71	9.84; 10.13	10.41; 11.19	9.19; 9.45
Kurtosis	0.14	-0.02	-0.52	24.12
Skewness	0.18	0.47	-0.15	3.67
KS	0.07	0.12	0.07	0.25
p-value	NS	.04	NS	.001
Generation time (years)				
Mean $\pm$ SD	2.96 $\pm$ 0.21	3.08 $\pm$ 0.22	3.28 $\pm$ 0.38	2.88 $\pm$ 0.27
COV	7.11	7.22	11.63	9.43
95% CI (L;U)	2.91; 3.02	3.02; 3.13	3.19; 3.38	2.81; 2.95
Median	2.95	3.08	3.29	2.90
95% CI (L;U)	2.88; 3.03	3.02; 3.12	3.18; 3.42	2.83; 2.92
Kurtosis	0.006	-0.06	-0.55	25.25
Skewness	0.36	0.41	-0.22	3.80
KS	0.06	0.13	0.07	0.25
p-value	NS	.001	NS	.01
Age at first maturity (years)				
Mean $\pm$ SD	2.29 $\pm$ 0.16	2.39 $\pm$ 0.16	2.50 $\pm$ 0.28	2.29 $\pm$ 0.19
COV	6.79	6.53	10.98	8.24
95% CI (L;U)	2.25; 2.33	2.35; 2.43	2.43; 2.57	2.24; 2.34
Median	2.3	2.40	2.51	2.30
95% CI (L;U)	2.25; 2.33	2.34; 2.41	2.45; 2.60	2.26; 2.32
Kurtosis	-0.34	-0.13	-0.39	17.66
Skewness	0.05	0.16	-0.21	2.61
KS	0.07	0.08	0.07	0.21
p-value	NS	NS	NS	.001
Growth rate (cm/years)				
Mean $\pm$ SD	0.45 $\pm$ 0.04	0.43 $\pm$ 0.04	0.42 $\pm$ 0.06	0.43 $\pm$ 0.04
COV	8.44	8.75	14.75	8.31
95% CI (L;U)	0.44; 0.46	0.42; 0.44	0.41; 0.44	0.42; 0.44
Median	0.44	0.42	0.41	0.43
95% CI (L;U)	0.43; 0.46	0.42; 0.43	0.40; 0.43	0.42; 0.44
Kurtosis	-0.2	0.49	-0.19	2.28
Skewness	0.41	0.56	0.40	0.54
KS	0.12	0.14	0.13	0.12
p-value	.045	.01	.02	NS
Annual natural mortality(M)				
Mean $\pm$ SD	0.94 $\pm$ 0.08	0.88 $\pm$ 0.07	0.82 $\pm$ 0.10	0.95 $\pm$ 0.10
COV	8.44	8.06	12.11	11.02
95% CI (L;U)	0.92; 0.97	0.86; 0.90	0.8; 0.85	0.92; 0.97
Median	0.92	0.88	0.80	0.94
95% CI (L;U)	0.91; 0.97	0.85; 0.90	0.78; 0.84	0.92; 0.97
Kurtosis	-0.06	-0.74	-0.42	-0.23
Skewness	0.45	0.23	0.30	0.28
KS	0.12	0.08	0.09	0.07
p-value	.04	NS	NS	NS

(Continues)

**TABLE 2** (Continued)

	Total	Fishable	Target biomass	Non-target biomass
Trophic level				
Mean ± SD	2.89 ± 0.18	2.90 ± 0.21	3.18 ± 0.30	2.60 ± 0.24
COV	6.4	7.19	9.43	9.26
95% CI (L;U)	2.84; 2.93	2.84; 2.95	3.11; 3.26	2.54; 2.66
Median	2.89	2.90	3.20	2.60
95% CI (L;U)	2.84; 2.93	2.84; 2.92	3.1; 3.32	2.55; 2.63
Kurtosis	0.34	0.23	-0.50	12.00
Skewness	0.09	0.21	-0.16	2.14
KS	0.06	0.07	0.07	0.14
p-value	NS	NS	NS	.01

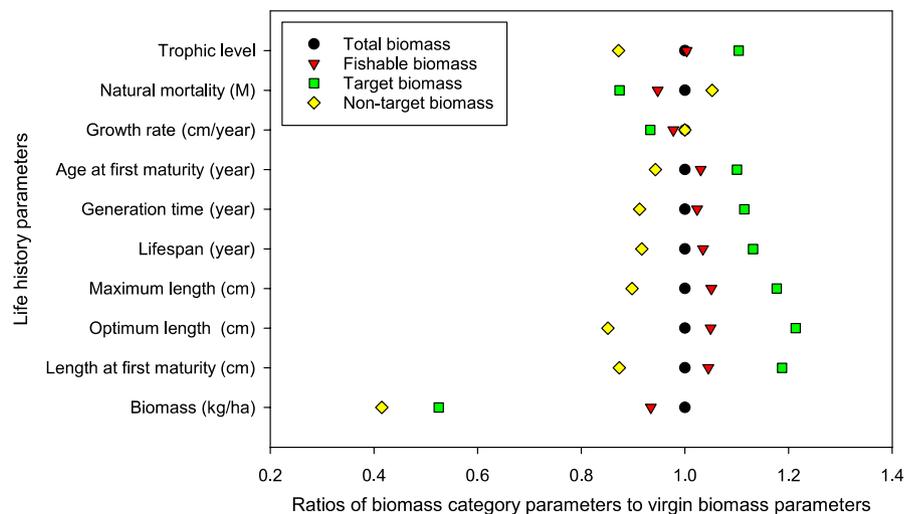
SD, standard deviation; COV, coefficient of variation. CI (L;U), confidence interval (lower, upper); KS, Kolmogorov-Smirnov values as test of normality. n = 62, 500 m<sup>2</sup> transects = 131.

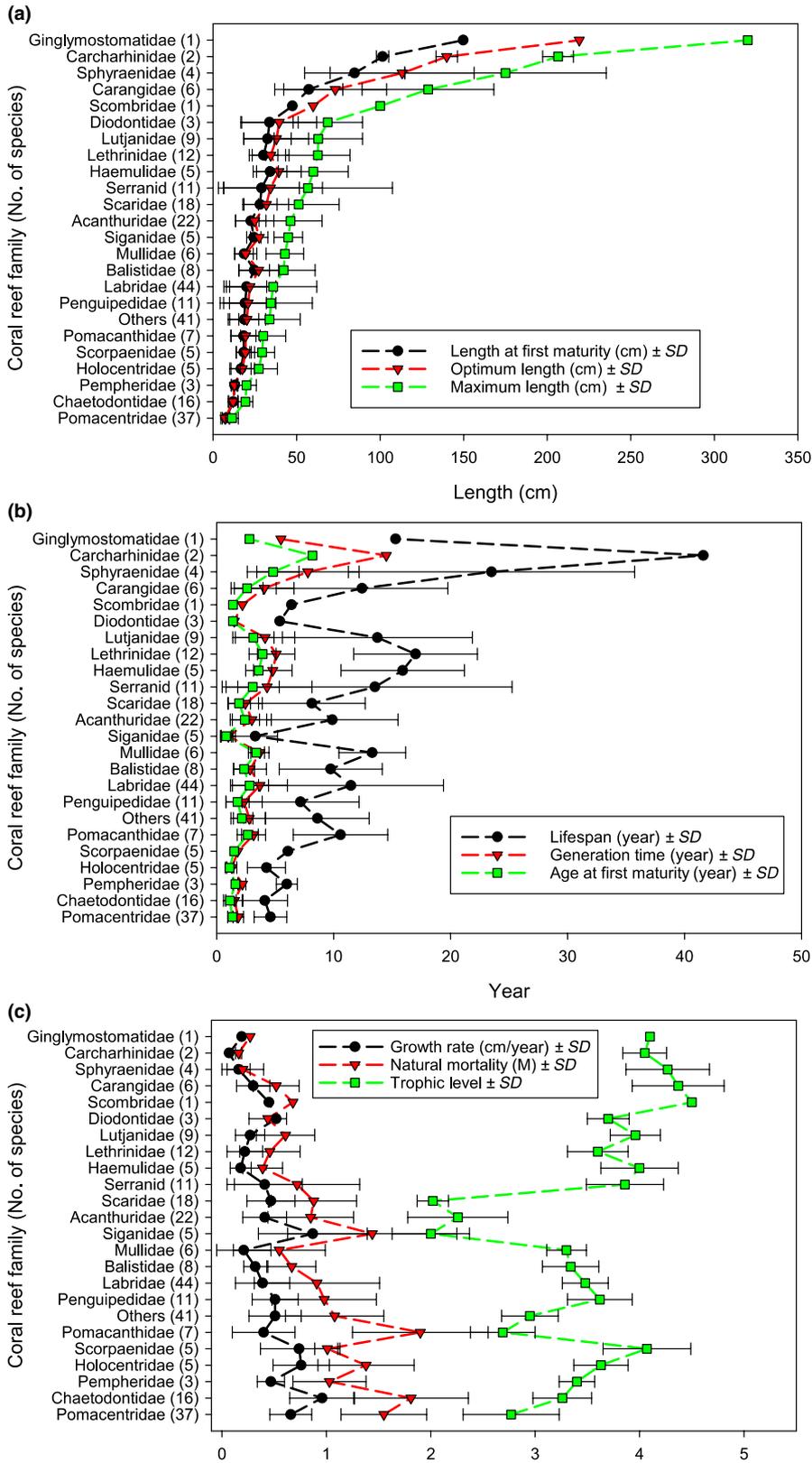
**TABLE 3** Comparisons of life history characteristics for five fish biomass categories based on one-way ANOVA

Biomass category	Total biomass	Fishable biomass	Target biomass	Non-target biomass	F-value	p-value
Mean ± SD	1140.2 ± 436.0 <sup>a</sup>	1022.1 ± 411.0 <sup>a</sup>	563.9 ± 332.9 <sup>b</sup>	458.1 ± 234.1 <sup>b</sup>	58.80	.0001
Length at first maturity (cm)	22.84 ± 2.20 <sup>a</sup>	24.45 ± 1.81 <sup>b</sup>	27.46 ± 2.29 <sup>c</sup>	20.92 ± 1.98 <sup>d</sup>	111.57	.0001
Length to obtain optimum yield (cm)	25.53 ± 2.78 <sup>a</sup>	27.51 ± 2.34 <sup>b</sup>	31.41 ± 2.98 <sup>c</sup>	22.93 ± 2.43 <sup>d</sup>	117.38	.0001
Maximum length (cm)	42.93 ± 4.49 <sup>a</sup>	46.33 ± 3.60 <sup>b</sup>	49.81 ± 4.01 <sup>c</sup>	42.68 ± 9.07 <sup>a</sup>	28.88	.0001
Lifespan (year)	9.49 ± 0.74 <sup>a</sup>	10.01 ± 0.72 <sup>b</sup>	10.71 ± 1.25 <sup>c</sup>	9.33 ± 0.91 <sup>c</sup>	27.44	.0001
Generation time (year)	2.96 ± 0.21 <sup>a,c</sup>	3.08 ± 0.22 <sup>a</sup>	3.28 ± 0.38 <sup>b</sup>	2.88 ± 0.27 <sup>c</sup>	24.00	.0001
Age at first maturity (year)	2.29 ± 0.16 <sup>a</sup>	2.39 ± 0.16 <sup>a</sup>	2.50 ± 0.28 <sup>b</sup>	2.29 ± 0.19 <sup>c</sup>	15.42	.0001
Growth rate (cm/ year)	0.45 ± 0.04 <sup>a</sup>	0.43 ± 0.04 <sup>a,b</sup>	0.42 ± 0.06 <sup>b</sup>	0.43 ± 0.04 <sup>b</sup>	5.06	.0001
Annual natural mortality (M)	0.94 ± 0.08 <sup>a</sup>	0.88 ± 0.07 <sup>b</sup>	0.82 ± 0.10 <sup>c</sup>	0.95 ± 0.10 <sup>a</sup>	28.56	.0001
Trophic level	2.89 ± 0.18 <sup>a</sup>	2.90 ± 0.21 <sup>a</sup>	3.18 ± 0.30 <sup>b</sup>	2.60 ± 0.24 <sup>c</sup>	64.07	.0001

Means are presented as raw data values but tested for differences based on loge transformed data. Categories connected by the same letter are not statistically different for post hoc Tukey tests. Site x time n = 62, transects = 131.

**FIGURE 3** Plots of the ratio of biomass and life history variables of the three fish type categories (fishable, target and non-target) relative to the community-wide unfished biomass or B<sub>0</sub> values





**FIGURE 4** Life history metrics (mean ± SD) of coral reef fish families organized on the y-axis from smallest to largest mean family body sizes versus (a) mean size-based characteristics (length at maturity, length to obtain optimum yield and maximum length), (b) age-based characteristics (lifespan, generation time and age at first maturity) and (c) growth rate and annual natural mortality. Number of species used in the estimates given in parentheses

larger in the fishable than the total biomass. As expected, there were more differences between target and non-target biomass, with target biomass having larger length, age and higher trophic level but lower natural mortality. For example, the lengths at maturity and to obtain optimum yield were ~27 and 31 cm for target community

biomass compared to ~23 and 26 cm for total, 24 and 28 for fishable biomass and 21 and 23 for non-target biomass. Weighted growth rates were not largely different among the biomass categories at 0.42–0.45 cm/years but statistically lower for target and fishable than total and non-target biomass. Non-target biomass life histories

**TABLE 4** Forward stepwise regression results for four biomass categories (site  $n = 57$ , transects = 125) evaluating the influences of life history traits. The same variables were picked in the models following BIC

AIC	Estimate (mean $\pm$ SE)	t-ratio	F-ratio	$p >  t $	VIF	$R^2$	$p > F$
<b>(a) Total (Unfished) biomass (kg/ha)<sup>a</sup></b>							
Intercept	142.42 $\pm$ 274.43	3.57	0	.61		.19	.0007
Number of species	20.95 $\pm$ 5.87	0.52	12.75	.0007	1.0		
<b>(b) Fishable biomass (kg/ha)<sup>a</sup></b>							
Intercept	228.89 $\pm$ 269.87	0.85	0	.4		.14	.004
Number of species	17.37 $\pm$ 5.63	3.01	9.06	.004	1.0		
<b>(c) Target biomass (kg/ha) (mean <math>\pm</math> SE)<sup>b</sup></b>							
Intercept	-3178.39 $\pm$ 1033.17	-3.08		.003		.25	.002
Length at first maturity (cm)	76.20 $\pm$ 22.32	3.41	11.66	.001	2.31		
Number of species	11.11 $\pm$ 4.08	2.72	7.40	.009	1.02		
Annual natural mortality (M)	1429.6 $\pm$ 556.31	2.57	6.60	.01	2.34		
<b>(d) Non-target biomass (kg/ha)<sup>c</sup></b>							
Intercept	-748.25 $\pm$ 540.45	-1.38		.17		.43	.0001
Generation time (year)	5484.25 $\pm$ 1037.42	5.29	27.95	.0001	62.76		
Lifespan (year)	-1632.17 $\pm$ 318.41	-5.13	26.28	.0001	92.89		
Length to obtain optimum yield (cm)	88.29 $\pm$ 26.50	3.33	11.10	.002	8.07		
Trophic level	-656.33 $\pm$ 202.28	-3.24	10.53	.002	1.88		
Number of species	7.24 $\pm$ 2.97	2.43	5.92	.02	1.02		

<sup>a</sup>Nine variables were not significant following AIC.

<sup>b</sup>Seven variables were not significant following AIC.

<sup>c</sup>Five variables were not significant following AIC.

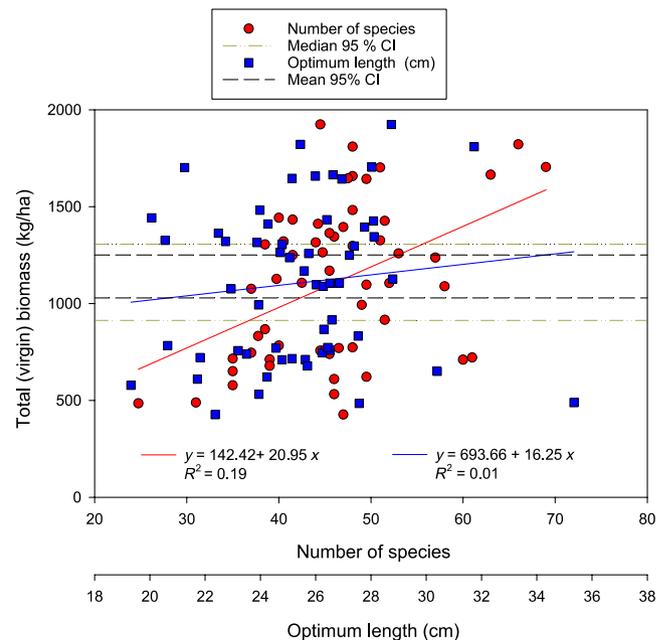
of length, age and trophic level metrics were lower than all other biomass categories.

### 3.4 | Relationships with life histories and number of species

Life history metrics were poor predictors of total unfished biomass with no variable picked as significant by the stepwise regression using BIC criteria (Table 4). Number of species was, however, significant and positive for all biomass categories and explained 19% and 14% of the variance in unfished and fishable biomass, respectively (Figure 5). Target biomass was also positively associated with length at maturity and natural mortality and, in combination with number of species, explained 25% of the variance. Non-target biomass had the largest number of significant associations even after retaining only one length-based metric. Generation time, length to obtain optimum yield and numbers of species were positive, while lifespan and trophic level were negatively associated with non-target biomass and together explained 43% of the variance.

### 3.5 | Relationships with habitat and environment

Habitat and environmental associations predicted 33% of the variance in the unfished biomass but indicated only a few significant variables



**FIGURE 5** Scatterplots and best-fit lines and equations for statistically significant relationships between number of species and length to obtain optimum yield and total unfished biomass  $B_0$ . The 95% confidence intervals for mean and median estimates of unfished biomass are shown as the horizontal lines

**TABLE 5** Forward stepwise regression results for the biomass categories (kg/ha) tested for relationships with 17 habitat and environmental variables. Site  $n = 38$ , transects = 95. NB: the same parameters were selected using BIC for all biomass categories. Location exposures were all negative indicating lower biomass on exposed than sheltered reef sites

AIC	Estimate (mean $\pm$ SE)	t-ratio	F-ratio	$p >  t $	VIF	c	$p > F$
(a) Total (Unfished) biomass <sup>a</sup>							
Intercept	2128.23 $\pm$ 413.18	5.15	0	.0001		0.33	.003
Ocean exposure	-300.67 $\pm$ 81.35	-3.7	13.66	.0008	1.2		
Multivariate stress model	-1178.97 $\pm$ 478.32	-2.46	6.08	.019	1.1		
Erect algae	-13.2 $\pm$ 6.33	-2.08	4.34	.04	1.11		
(b) Fishable biomass <sup>a</sup>							
Intercept	1186.2 $\pm$ 144.01	8.24	0	.0001		0.40	.0005
Ocean exposure	-375.51 $\pm$ 81.04	-4.63	21.47	.0001	1.44		
Chlorophyll median	-662.45 $\pm$ 225.17	-2.94	8.66	.006	1.37		
Soft coral	46.91 $\pm$ 20.48	2.29	5.25	.03	1.11		
(c) Target biomass <sup>a</sup>							
Intercept	365.43 $\pm$ 151.52	2.41	0	.02		0.33	.008
Ocean exposure	-315.27 $\pm$ 85.34	-3.69	13.65	.0008	2.56		
Soft coral	45.71 $\pm$ 16.35	2.8	7.82	.009	1.14		
Hard coral	6.14 $\pm$ 2.57	2.39	5.71	.02	1.82		
(d) Non-target biomass <sup>a</sup>							
Intercept	383.18 $\pm$ 230.03	1.67	0.00	.1		0.56	.0001
Hard coral	-6.94 $\pm$ 1.27	-5.47	29.89	.0001	1.24		
Erect algae	-12.75 $\pm$ 2.98	-4.18	18.31	.0001	1.32		
SST SD	257.56 $\pm$ 123.19	2.09	4.37	.04	1.25		

<sup>a</sup>Fourteen variables were not significant after conducting the stepwise regression analysis.

(Table 5). The 17 variables evaluated had low levels of VIF, which reduced the chance of over-prediction. Nevertheless, only three variables were statistically significant; these were ocean exposure, the multivariate thermal stress metric and erect algae. Ocean exposure was the strongest variable, and exposed reefs had ~300 kg/ha less biomass than sheltered sites. Biomass also declined with the stress metric and erect algae, but relationships were weak. For example, thermal stress explained only 4% of the variance and biomass declined from 1,420 kg/ha to 1,135 kg/ha along the full stress gradient of 0.50–0.98. Similarly, erect algae associations explained 2% of the variance and declined from 1,240 to 1,040 kg/ha along the full 0–35.4% algal cover gradient. Again, possible habitat and environmental variables lay within or slightly above the 95% CI intervals of unfished biomass estimates.

Fishable biomass was reduced by exposure and seawater chlorophyll-a concentrations but was positively associated with soft coral cover (Table 5). Most of the 40% variation explained was the exposure variable as chlorophyll-a and soft coral combined explained <2% of this variance. Target biomass showed no influence of chlorophyll-a but biomass increased with both soft and hard coral. However, both variables combined contributed <7% of the 33% total variance explained. Again, non-target biomass was the category most associated with habitat and environmental variables ( $r^2 = .56$ ). Ocean exposure had no effect, but non-target biomass declined moderately with hard

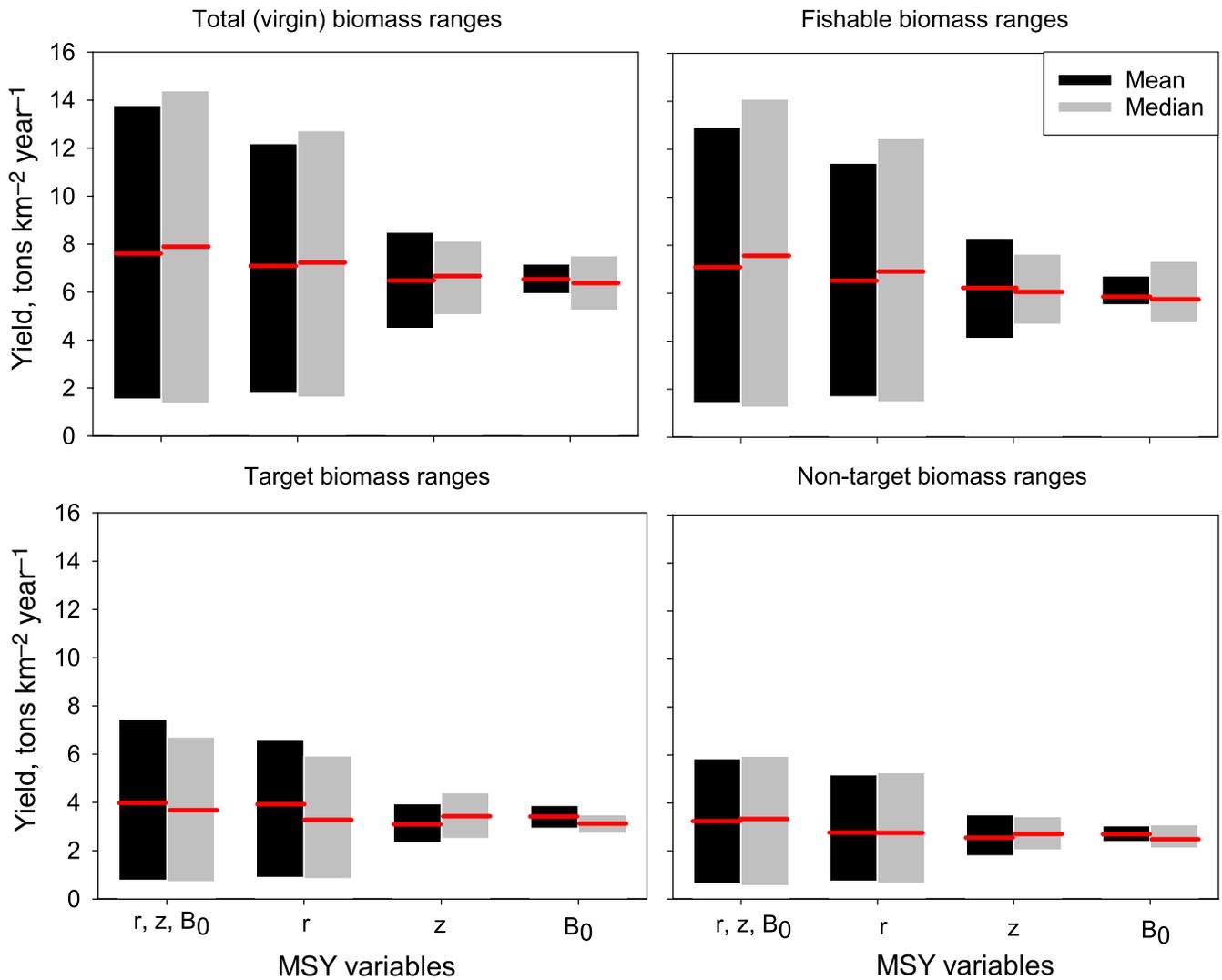
coral ( $r^2 = .32$ ) and erect algal cover ( $r^2 = .03$ ). Non-target biomass also increased somewhat ( $r^2 = .07$ ) with the standard deviation of the SST.

### 3.6 | Ranges of estimated yields

Modelled maximum sustained yield variability increased from  $B_0$ , to  $z$ , to  $r$  for likely ranges of these values (Figure 6). Using the 95% CI for the median and mean  $B_0$  indicates that medians generally predicted higher variation in the yields for all biomass categories except the target catch. For example, the lower CI of  $B_0$  mean and median estimates produced yields of 5.2 and 5.8 tons/km<sup>2</sup>/years, while the upper values produced 7.1 and 7.4 tons/km<sup>2</sup>/years, respectively. Ranges for the poorly known  $z$  values were slightly larger than  $B_0$ , but the CIs of the known intrinsic rate of growth  $r$  produced high variation in the yield estimates that ranged from 1.3 to 14.4 tons/km<sup>2</sup>/years for total yields depending on upper and lower bounds of  $B_0$  and  $z$ . The mean community-level fish lengths at this optimal yield were estimated at 26.7  $\pm$  2.8 ( $\pm$ SD) and 30.1  $\pm$  2.9 cm, for fishable and target fish, respectively.

## 4 | DISCUSSION

Unfished biomass ( $B_0$ ) had moderate variability and possibly influenced by a limited number of variables. While habitat, number of



**FIGURE 6** Estimated maximum sustained yields (MSY) of coral reef fisheries for estimated ranges of pristine biomass ( $B_0$ ), intrinsic of increase ( $r$ ), density-dependent shape parameter ( $z$ ) for the four fisheries biomass categories. Values are based on permutations of the upper and lower 95% confidence intervals of  $B_0$  and  $r$  established for the region (see methods)

species, some environmental variables and community life histories were significantly associated with and possibly driving  $B_0$  variability, these variables mostly explained variation contained within the 95% CI range of ~1,030–1,250 kg/ha. It was less commonly observed that these variables either drove or were associated with  $B_0$  beyond the estimated CI range. Further, distinguishing causation from the association is challenging because of high variation and possible co-dependencies among some variables, such as biomass and number of species. Consequently, while some of the 18 studied variables contribute to the total variation, the variation is maintained within limits that allow for reasonable benchmarks.

#### 4.1 | Factors influencing the benchmark

Previous ecological studies of fish communities have reported a variety of ecological, habitat and environmental associations with fish communities that were generally stronger than found here. These

studies were typically evaluating larger gradients in biomass, fishing, habitats and environments. Here, I focused on shallow reefs in high compliance closures >15 years old at the 500 m<sup>2</sup> scale along the African coastline. Consequently, narrowing the site selection to evaluate a subset of unfished reefs may explain the lower variation and the fewer significant associations. Nevertheless, the reef habitat and environmental gradients reported here appeared to be typical or lie within the normal ranges of coral reef benthic and environmental gradients (Table 1). Cover of coral in these reefs had a high range of variability, but the mean values were similar to global compilations. Stress was high but possibly not unusual for tropical as opposed to subtropical environments.

Despite the regional similarities with global values, there were poor relationships between coral cover and bottom complexity and neither variable was strongly associated with unfished biomass. Non-target biomass was also unexpectedly negatively associated with hard coral cover. Ecological studies reporting more significant associations

may be reporting responses on smaller spatial scales or from reefs where target biomass was reduced by fishing. Studies of the responses of fish to losses of hard coral cover often report reductions in small-bodied and coral-dependent species, which do not contribute greatly to total biomass (Friedlander et al., 2014; Graham et al., 2008; Lamy, Legendre, Chancerelle, Siu, & Claudet, 2015; Pratchett et al., 2009). Some studies indicate that diversity of benthic-attached reef fish is maximized at modest levels of coral cover of ~25% (Wilson et al., 2009). Yet, how coral cover impacts the numbers and biomass of target fisheries taxa and in unfished reefs is unclear (Graham et al., 2008). Lamy, Galzin, Kulbicki, Lison de Loma, and Claudet (2016) reported that above 10% coral cover fish numbers were resilient to losses of coral, which is lower cover than reported here. An additional consideration is that while coral cover creates complexity and possible aggregation behaviour and refuge, it also reduces the net organic production in favour of inorganic carbon production, which can reduce fish biomass (Sebastian & McClanahan, 2013). The coral cover reported in these African closures may have been sufficient to avoid negative influences on fish biomass. A study of fishing and climate disturbance in Kenyan reefs found that target catches were not clearly affected by the loss of coral over the 1998 thermal anomaly but more by fisheries restrictions (McClanahan & Abunge, 2014). The patterns found here indicate that non-target taxa may be observed to respond differently depending on the spatial scale of the study and the history of fishing. Coral bleaching and associated disturbances were generally observed to be more prevalent on the ocean exposed reefs, and the negative relationship between biomass and the multivariate thermal exposure metric may also contribute to lower biomass.

Depth is often a refuge from fishing in this region and therefore a better predictor of biomass in fished reefs (Tyler, Speight, Henderson, & Manica, 2009). The shallow reefs studied here (<11 m) will influence fishes responding to light, surface water motion and high benthic production. Some fish aggregate at greater depths and the lack of sampling in reefs >11 m may explain the lower biomass on ocean exposed (often deeper reef edges) than sheltered reefs. The lack of association with depth may also mean that these high compliance closures are not fully supporting the large predatory fishes that can often be found in deep water (Kulbicki, Parravicini, & Mouillot, 2015). Shallow water is more likely to support smaller-bodied herbivores that migrate between moderate and shallow water in unfished reefs (Russ, 2003).

Some remote reefs of the Pacific have reported biomasses around half of those presented here for the African coastline (Williams et al., 2015). Moreover, their reported chlorophyll-a concentrations were low and ranged from 0.05 to 0.20 mg/m<sup>3</sup>, while chlorophyll values on the African coastline were between 0.2 and 1.1 mg/m<sup>3</sup>. In the Pacific Island sample, when chlorophyll-a was close to 0.2, the reported biomasses were closer to ~1,000 kg/ha. Consequently, seawater production levels in the Pacific island could be limiting biomass more than the African continent. Moreover, chlorophyll-a in the water column may be a proxy for benthic production limits due to shared nutrient limitations.

Number of species was weakly associated with unfished biomass but was still among the strongest factor that might extend biomass

variation beyond the normal CIs of the benchmark. Cause and effect are, however, difficult to determine and the extent that species numbers control versus simply responds to biomass is a persistent debate in ecology (Huston et al., 2000). These two factors are not independent, and the high variability here suggests a weak association. Reducing biomass by fishing ultimately reduces numbers of fish species. Where fishing is not present, the relationship appears weaker and the circularity of cause and effect challenges separating the two influences (McClanahan, 2015). It remains to be seen if larger scale biogeographic differences in numbers of species will have consequences for biomass. Duffy et al. (2016) suggest it does but their relationship was highly dependent on including high latitude ecosystems—reporting no clear and positive species–biomass relationship for the tropics. In the western Indian Ocean, number of species–biomass patterns were weaker (McClanahan, 2015).

## 4.2 | What are the benchmarks and yields?

Fisheries yield estimates based on population models are dependent on knowing the ranges of the common metrics of  $B_0$ ,  $r$  and  $z$  as described in equation 1 above (Pella & Tomlinson, 1969). In complex reef fisheries with many captured species, empirical yields have been preferred to multispecies yield models when estimating maximum yields (Samoilys, Osuka, Maina, & Obura, 2017). This preference does, however, require confirmation from yield models and yield time series studies to establish whether empirically reported maximum yields are stable. Otherwise, empirical yield results could reflect temporary mining of stocks, overharvesting or unusual aggregations or productive times. The values presented here for  $B_0$  and  $r$  provide an independent empirical basis for estimating parameters and yields from models (Figure 6). This synthesis shows that yields can be quite variable because of the high CIs, particularly in biomass recovery rates or  $r$ . Therefore, the first question is whether the low, mean or upper CI should be used to estimate yields. Second, whether model values should be specific to the context of significant factors, such as ocean exposure. Given that the range of  $B_0$  is ~300 kg, or a significant proportion of the total range of biomass values, this system boundary decision can have consequences for yield evaluations. For example, unfished biomass in exposed reefs was  $854 \pm 132$  ( $\pm$ SE) kg/ha compared to  $1,252 \pm 65$  kg/ha in sheltered reefs.

Fisheries scales and management needs will differ from ecological status studies. Fisheries predictions, for example, will be less concerned with the influences and variance of local habitat and benthic characteristics but rather with larger scale production influences, like light, water motion and the diversity of habitats. This ecological and scale effect was observed, for example, in the different response of target and non-target fish to benthic factors. Moreover, the spatial scale used for estimating fisheries stock and yield variance is larger than the 500-m<sup>2</sup> belt transects evaluated here. Between-transect variance is likely to decline with increasing spatial scale, at least up to 500 m<sup>2</sup>, but possibly for larger areas as animal sizes, spatial needs and movements increase (Bradley et al., 2017; McCauley et al., 2012).

Variance and local factors that influence it diminish and stabilize when approaching the larger spatial scale relevant to fisheries capture. For coral reefs, this is likely to be above a hectare or 20 times the areas sampled in these transects. For example, in southern Kenya, 3–16 fishers use a square kilometre of reef and, given sufficient sampling, their efforts result in stable per area yields over time and space (McClanahan, Hicks, & Darling, 2008). At this scale of fisheries capture, variance is reduced and the biomass variability needed to evaluate status will be smaller than the ~40% COV reported for transects used here. Certainly, yields can be variable on a day-to-day basis but, over the course of time, the mean yields are more stable and change little in tropical fisheries unless fishing effort and gear use change (McClanahan, 2010).

The discussion above argues for using the mean or median values for estimating fisheries status rather than lower or upper CIs. At scales above a hectare, CIs will be smaller than at the transect level. And, this is the scale where fisheries production estimates and management decisions are made. Consequently, I consider the mean and median values of ~1,150 kg/ha as a recommended benchmark for evaluating biomass status in this region. Fisheries management decisions that are pro-effort and high risk might consider using the lower bounds of 915 kg/ha. Fewer reefs would be classified as being overexploited, but there is no reason to believe these lower ranges will be more accurate in predicting status or yields for scales above 500 m<sup>2</sup>. Conversely, management for protecting the resource and low risk using the upper confidence limit would have a similar scale and justification problem.

Evaluations of fisheries should consider that the benchmark reported here is already biased towards yields and risk because it was established from closures often in heavily fished seascapes. Reported biomass in closures is lower, possibly 2 times lower, than reports in the very few remaining wilderness seascapes of the Indian Ocean (Friedlander et al., 2014; Graham & McClanahan, 2013). These differences are caused by greater numbers of large-bodied and roaming species, including groupers, jacks, snappers, sweetlips and shark populations, in wilderness than closures (Bradley et al., 2017; Juhel et al., 2017; McCauley et al., 2012; Nadon et al., 2012). Populations of these taxa decline with very low levels of fishing effort, and most closures in fished landscapes do not sustain large-bodied and space requiring species (Graham et al., 2017; McClanahan, Graham, et al., 2015). Therefore, the benchmark biomass derived from closures is underestimated relative to pristine ecosystems. Consequently, the community biomass approach developed here should not be seen as a replacement for stock-level management of these larger and mobile species. Rather, the suggested benchmark is for the many benthic and site-attached coral reef fish with more modest space requirements. These two groups of species will need different types of management and levels of fishing to sustain their populations.

Median biomass values were not greatly different from mean values for total and fishable biomass, but they were lower for target and non-target groups. When they do differ, using median values should reduce the chances of overestimating biomass and yields. Using median estimates can reduce the right-tailed distribution affects observed in some animal and biomass abundances distributions that occur when

fish aggregate in preferred resting habitats, like coral reefs. Target fish biomass could be overestimated because of its right-tailed distribution. As a result, the upper 95% CI of the median is below the lower 95% CI of the mean value. The choice between mean and medians will therefore have consequences for evaluating target biomass status and sustainable yields. Using medians is recommended as it will be more representative of values on larger scales where local aggregation effects are not important for estimating biomass.

### 4.3 | Implications for fisheries

The yield model indicates that among the three key fisheries model parameters,  $B_0$  had the weakest effect on estimating the variability or range of potential yields. In fact, both  $B_0$  and  $z$  influences were small relative to large CIs and variation created by the intrinsic rates of increase. Yet, as described above, the effect of  $B_0$  on variability may be even smaller than modelled here because of reduced variation with increasing spatial scale at which fishing operates. Consequently, to improve estimates of yields, better estimates of  $B_0$  are a lower priority than understanding and estimating  $r$ . Rates of recovery have been shown to vary with a number of factors but most importantly the effectiveness and size of fishing closures (McClanahan & Graham, 2015). The empirical values used here of  $0.23 \pm 0.16$  (95% CI) were, however, close to mean values of 0.20–0.25 commonly used in fisheries modelling studies (Little & Grafton, 2015; Rudd & Branch, 2016). Nevertheless, empirical studies of recovery indicate high variation that is seldom well understood or modelled when estimating yields.

$B_0$  may prove most useful as a fisheries-independent metric to evaluate the fisheries and ecological and stock status of coral reefs independent of estimates based on empirical yields (Newton, Cote, Pilling, Jennings, & Dulvy, 2007). Changes in effort and per area yield over time are infrequently collected and reported (Pauly & Zeller, 2016). Therefore, biomass is valuable as an alternative fisheries-independent metrics for in situ stock assessments (Branch, Jensen, Ricard, Ye, & Hilborn, 2011; Hilborn & Branch, 2013). Estimating and assessing stocks in coral reefs has generally been elusive due to the high diversity of caught species and the poverty of management institutions (Worm & Branch, 2012; Worm et al., 2009). Underwater visual census methods have made estimating community fish biomass in coral reefs a potential surrogate for standard catch-based stock assessments. Moreover, biomass and associated feeding processes often drive ecological processes and ecological services, such as reef calcification, and therefore provide ecosystem service criteria for evaluating fisheries (McClanahan & Muthiga, 2016; McClanahan et al., 2011).

Separating biomass into target categories was influential in estimating contributions to the yields. Differences between total and fishable biomass yields were small, but target and non-target yields were around half the total yields. These estimates assume the same intrinsic rate of increase for these two groups. While local recovery and yield data to distinguish these rates were not available, differences in the weighted growth rates between these two groups were small (Table 2). Target biomass, on the other hand, had larger body

sizes, longer lifespans, lower natural mortality and higher trophic levels metrics. Therefore, target fish are expected to mature slower than non-target groups before obtaining optimum yields. Consequently, high fishing effort should lead to increasing dominance of non-target groups with faster life histories, which may maintain production but at the cost of reducing valuable stocks. Target fish in Kenya, for example, was purchased at landing sites for ~US \$1.67 versus \$1.06 per kilogram for non-target groups during this study period (Wamukota & McClanahan, 2017).

The fish biomass and weighted community life histories provide some simple metrics for fisheries management decisions. For example, an overall proposed mean size to harvest reef fish is provided by the community-weighted lengths to obtain optimum yield. These values may be inappropriate for fish that differ greatly from average coral reef sizes (i.e., sharks and jacks) but still provide guidance where species-specific recommendations and management are not available. A common alternative to this weighted multispecies approach is to make decisions based on the most resilient, common or valuable target species. How these decisions affect other species is, however, seldom evaluated. For example, in heavily fished Kenyan reefs, optimal mesh sizes have been estimated for three of the most commonly landed fish where their lengths to obtain optimum yields ranged from 22 to 23 cm (Hicks and McClanahan 2012). Yet, the larger community of fish has a weighted optimum capture length of ~27 cm for fishable and ~31 cm for target taxa. Consequently, recommendations using the commonly landed species would lead to overfishing of many unevaluated species. If this problem is pervasive, fisheries recommendations may be underestimating the size of capture for most coral reef species. This will promote capture and mesh-size recommendations only suitable for fast growing and early maturing at the expense of many other common species. Certainly, the capture-size decision is even more inappropriate for large-bodied species, such as sharks, groupers and jacks. Nevertheless, in coral reefs where the diversity of captured fish and fishing methods is high, multispecies metrics provide a more species inclusive estimate and balances more of the many trade-offs required of management decisions in multispecies fisheries.

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