Community biomass and life history benchmarks for coral reef fisheries

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Coral reef fisheries benchmarks

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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 histories characteristics were classified and described for total, fishable, target, and non-target groups. Benchmark biomass fell within a 95% confidence interval of ~1030 to 1250 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 1150 and 560 kg/ha are 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 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

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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 (Rochet & Trenkel 2003; Hall et al. 2006; Newman et al. 2006; Taylor et al. 2015; Nash et al. 2016). Establishing benchmarks for these variables is increasingly important for evaluating fish communities and fisheries status (McClanahan et al. 2015a; MacNeil et al. 2015). 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 sustainability (Worm et al. 2009). While the practical need is great, the high diversity and spatial heterogeneity of reef fishes may preclude the possibility of finding useful benchmarks. For example, 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 (Stevenson et al. 2007; McCauley et al. 2012; Bradley et al. 2017; Juhel et al. 2017). 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 status may, therefore, prove to be an ineffective unless benchmark variability can be reasonably bounded.

Unfished biomass, its inherent variability, and factors influencing it are critical to evaluating fisheries status. The B_0 benchmark is used to establish maximum sustained yield biomass (B_{msy}) when combined with recovery and density-dependent response parameters (Pella and 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 endogenous composition of multispecies fish communities, their consumption rates, habitat, and environmental variables that influence productivity (McClanahan 1992; Valdivia et al. 2017). Further, total biomass differs from catchable and target biomass because not all biomass can be fished and portions of the fishable biomass are not targeted for 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 and McClanahan 2017). Consequently, these species are often valued, recorded, studied, and understood differently (Pauly and Zeller 2016). Despite these potential complications, if this variability can be estimated and accounted for, then there is the potential to establish robust benchmarks to assist estimating sustainable catches.

A benchmark approach has the advantage that the cascading impacts of fishing on fish biomass often reflects the state of ecosystems (McClanahan et al. 2011; Karr et al. 2015). Therefore, fish biomass is one of the better metrics for evaluating fishing pressure, impacts, and ecosystem states (MacNeil et al. 2015; Cinner et al. 2016). Mean B_0 in fished landscapes appears to lie within a range of 1000 and 1200 kg/ha in the western Indian Ocean and perhaps globally (McClanahan et al. 2007; MacNeil et al. 2015; McClanahan & Graham 2015). 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 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 histories benchmarks as well as biomass need to be evaluated to determine fisheries status. Finally, benchmarks may be poorly bounded if these fish life history characteristics are contributing to biomass variability (Gilby et al. 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 (Wilson et al. 2008, 2009; Williams et al. 2015; Heenen et al. 2016; Cinner et al. 2016; Darling et al. 2017; Valdivia et al. 2017). There is also the suggestion that numbers of species influence biomass by increasing efficiency of resource use and production (Mora et al. 2014; Duffy et al. 2016). The influences and magnitude of this variability on biomass has, 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.

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

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 et al. 2009; McClanahan & Graham 2015). These studies determined that biomass does not level until >15 years after closure, in closures > 5km², 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 (Fig. 1). The data were from visual censuses of coral reefs fish based on a total of 133 transects. Biomass data were categorized and analyzed in 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, Rhinodontidae >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 and 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 (Nadon et al. 2012; Williams et al. 2015; Cinner et al. 2016; Valdivia & Bruno 2017). 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.

Fish census

Fish census and life history calculation methods have been described in previous publications (McClanahan et al. 2015a). The individual censuses were 500 m² 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 histories metrics of nine variables (trophic level, annual natural mortality, growth rate, age at maturity, generation time, life span, 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.

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 were recorded with a depth gauge while diving. Benthic cover was estimated using two methods. In shallow sites 6 to 9 10-

m standard line-intercept transects were completed in which coral and other functional groups under the line were recorded to the nearest centimeter. 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-m² 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.

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/>, Sept 24, 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) is defined as the temperature excess of

1°C or more above the climatologically long-term average warmest weekly periods of the year (Selig et al. 2010; Maina et al. 2011). 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 et al. 2015b). 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 et al. 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).

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 were undertaken for the raw and $\log_e$ transformed biomass and life history metrics. 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 if 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 (Kleypas et al. 1999; Maina et al. 2011; Bruno and Valdivia 2016) (Table 1).

229

230 Prior to testing the hypotheses that environment, habitat, fish life history, and species diversity
231 affect baseline biomass B_0 , correlation matrices were examined to evaluate the levels of
232 colinearity by the Variation Inflation Factor (VIF), an indicator of autocorrelation (Supporting
233 Information). Bivariate correlations with $r \geq 0.70$ were examined and redundant and less
234 ecologically meaningful or reliable variables removed. From these results, variables were
235 reduced to non-redundant metrics and these variables were used in a series of forward step-wise
236 regression analyses. For example, median sea surface temperature (SST) and Photosynthetic
237 Active Radiation (PAR) were used in favor of mean SST and maximum PAR because means
238 can be biased by right-tail distributions. Coral cover and topographic complexity are often
239 positively correlated (Darling et al. 2017) but there was no significant relationship in these data
240 (Spearman $\rho = -0.20$ $P = 0.27$). Further, a forward step-wise regression did not find a
241 relationship between topographic complexity and unfished biomass. Therefore, the more
242 commonly measured cover of coral was included in the final step-wise regression results. From
243 the autocorrelation and selection process 10 environmental, two habitat variables (depth and
244 ocean exposure), 3 benthic cover (hard and soft coral and erect algae), numbers of species, and
245 2 multivariate models resulted in a total of 18 independent variables chosen to test for their
246 potential influences on fish biomass.

247

248 Fish censuses were haphazardly done in time and space, transects were not fixed, and this led to
249 a total of 62 site and time replications. Various levels of data pooling were done to evaluate
250 possible influences of this decision but none were found. Additionally, to avoid potentially
251 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 runoff 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 was evaluated in an independent analysis. Regression analysis made selections based on inclusive or associative Aikake 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.

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):

$$1) \text{ MSY} = (rB_0 z)/(z+1)^{1/z+1}.$$

I used the lower, mean, and upper 95% CI of B_0 established in this study. The intrinsic rates of growth r has been estimated for multispecies reef fish biomass in this region as 0.23 ± 0.16 (95% CI) based on recovery rates in the studied high compliance closures in the western Indian Ocean region (McClanahan and 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 et al. 2012). The sensitivity of the B_0 (K), r, and z variables on yield estimates was evaluated by iteratively holding mean values for 2 of the 3 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 was also evaluated. Median CIs were based on a rank procedure and calculated in MiniTab version 17.1.0.

Results

Habitat and environmental variation

Study sites ranged in depth from shallow water to 11 meters 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

Table 1. Description of environmental traits (sample size, mean, median, standard deviation (SD), minimum (Min), maximum (Max)). SST = sea surface temperature, PAR = photosynthetically active radiation, ND = no data.

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 ^a	31.30 ^a
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 ^a	19.00 ^b 6.90 ^a
Depth (m)	38	2.55	2.00	2.23	1.50	11.00		
Environmental parameters								
							26.90 $\pm$ 1.30 _b	
SST median (°C)	38	27.14	27.38	0.77	24.23	27.67	27.60 $\pm$ 1.10 _c	
SST minimum (°C)	38	24.03	24.23	0.87	20.70	24.60	24.80 $\pm$ 1.80 _c	
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 _b	
Mean thermal stress anomaly (°C)	38	6.56	5.27	2.44	2.11	9.51	3.90 $\pm$ 1.40 ^b	
PAR median (E m ⁻² day ⁻¹)	38	49.46	49.23	2.95	41.67	53.27		
Suspended solids median (g m ⁻³)	38	0.63	0.70	0.16	0.41	0.85	0.80 $\pm$ 1.50 ^b	
Chlorophyll median (mg m ⁻³)	38	0.67	0.78	0.26	0.29	1.01	0.70 $\pm$ 1.20 ^b	
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 ^b	

^a Bruno and Valdivia (2016) ^b Maina *et al.* (2011) ^c Kleypas *et al.* (1999)

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.

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. 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 m² transects = 131.

		Total	Fishable	Target biomass	Non-target biomass
Biomass category (kg/ha)	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	0.04	NS	0.001	NS
Length at first maturity (cm)	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	0.07
Length to obtain optimum yield (cm)	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	0.001
Maximum length (cm)	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	0.001
Life span (yr)	Mean $\pm$ SD	9.49 $\pm$ 0.74	10.01 $\pm$ 0.72	10.71 $\pm$ 1.25	9.33 $\pm$ 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
	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	0.04	NS	0.001
Generation time (yr)	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	0.001	NS	0.01
Age at first maturity (yr)	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	0.001
Growth rate (cm yr ⁻¹)	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	0.045	0.01	0.02	NS
Annual natural mortality (yr ⁻¹)	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	0.04	NS	NS	NS
Trophic level	Mean $\pm$ SD	2.89 $\pm$ 0.18	2.90 $\pm$ 0.21	3.18 $\pm$ 0.30	2.60 $\pm$ 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	0.01

Distribution of unfished biomass

Mean total unfished biomass was not significantly larger (~100 kg) than fishable biomass at ~1100 kg/ha (Table 2a). 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; Fig. 3). Variation in biomass as measured by Coefficient of Variation (COVs) were moderately high with mean variance being ~40% to 60% of the means. There was 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 1030 and 1250 kg/ha. Mean target biomass ranged between 480 and 650 kg/ha. Biomass distributions 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. Target biomass was normalized by the log_e transformation but the other distributions were no longer normal after transformations (Table 2b).

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

Biomass category	Total biomass	Fishable biomass	Target biomass	Non-target biomass	F - value	P-value
Mean $\pm$ SD	1140.2 $\pm$ 436.0 ^a	1022.1 $\pm$ 411.0 ^a	563.9 $\pm$ 332.9 ^b	458.1 $\pm$ 234.1 ^b	58.80	0.0001
Length at first maturity (cm)	22.84 $\pm$ 2.20 ^a	24.45 $\pm$ 1.81 ^b	27.46 $\pm$ 2.29 ^c	20.92 $\pm$ 1.98 ^d	111.57	0.0001
Length to obtain optimum yield (cm)	25.53 $\pm$ 2.78 ^a	27.51 $\pm$ 2.34 ^b	31.41 $\pm$ 2.98 ^c	22.93 $\pm$ 2.43 ^d	117.38	0.0001
Maximum length (cm)	42.93 $\pm$ 4.49 ^a	46.33 $\pm$ 3.60 ^b	49.81 $\pm$ 4.01 ^c	42.68 $\pm$ 9.07 ^a	28.88	0.0001
Life span (yr)	9.49 $\pm$ 0.74 ^a	10.01 $\pm$ 0.72 ^b	10.71 $\pm$ 1.25 ^c	9.33 $\pm$ 0.91 ^c	27.44	0.0001
Generation time (yr)	2.96 $\pm$ 0.21 ^{a,c}	3.08 $\pm$ 0.22 ^a	3.28 $\pm$ 0.38 ^b	2.88 $\pm$ 0.27 ^c	24.00	0.0001
Age at first maturity (yr)	2.29 $\pm$ 0.16 ^a	2.39 $\pm$ 0.16 ^a	2.50 $\pm$ 0.28 ^b	2.29 $\pm$ 0.19 ^c	15.42	0.0001
Growth rate (cm yr ⁻¹)	0.45 $\pm$ 0.04 ^a	0.43 $\pm$ 0.04 ^{a,b}	0.42 $\pm$ 0.06 ^b	0.43 $\pm$ 0.04 ^b	5.06	0.0001
Annual natural mortality (M)	0.94 $\pm$ 0.08 ^a	0.88 $\pm$ 0.07 ^b	0.82 $\pm$ 0.10 ^c	0.95 $\pm$ 0.10 ^a	28.56	0.0001
Trophic level	2.89 $\pm$ 0.18 ^a	2.90 $\pm$ 0.21 ^a	3.18 $\pm$ 0.30 ^b	2.60 $\pm$ 0.24 ^c	64.07	0.0001

Figure 2. Frequency distributions of the four biomass categories for (top) raw and (bottom) $\log_e$ transformed data.

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_0 values.

339 Distribution of life history characteristics

340

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

Figure 4. Life history metrics (mean $\pm$ 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)

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 were generally small with COVs of ~10% of the mean values. Log_e 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_e 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_e and non-log_e 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 centimeters 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/yr but statistically lower for target and fishable than total and non-target biomass. Non-target biomass life histories of length, age, and trophic level metrics were lower than all other biomass categories.

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 (Fig. 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 positively, while life span and trophic level were negatively associated with non-target biomass and together explained 43% of the variance.

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.

(a) Total (Unfished) biomass (kg/ha)

AIC	Estimate (mean $\pm$ SE)	t-ratio	F-ratio	P > t	VIF	R ²	p > F
Intercept	142.42 $\pm$ 274.43	3.57	0	0.61		0.19	0.0007
Number of species	20.95 $\pm$ 5.87	0.52	12.75	0.0007	1.0		
Nine variables were not significant following AIC.							

(b) Fishable biomass (kg/ha)

AIC	Estimate (mean $\pm$ SE)	t-ratio	F-ratio	P > t	VIF	R ²	p > F
Intercept	228.89 $\pm$ 269.87	0.85	0	0.4		0.14	0.004
Number of species	17.37 $\pm$ 5.63	3.01	9.06	0.004	1.0		
Nine variables were not significant following AIC.							

(c) Target biomass (kg/ha)

AIC	Estimate (mean $\pm$ SE)	t-ratio	F-ratio	P > t	VIF	R ²	p > F
Intercept	-3178.39 $\pm$ 1033.17	-3.08		0.003		0.25	0.002
Length at first maturity (cm)	76.20 $\pm$ 22.32	3.41	11.6	0.001	2.31		
Number of species	11.11 $\pm$ 4.08	2.72	7.40	0.009	1.02		
Annual natural mortality (M)	1429.6 $\pm$ 556.31	2.57	6.60	0.01	2.34		
Seven variables were not significant following AIC.							

(d) Non-target biomass (kg/ha)

AIC	Estimate (mean $\pm$ SE)	t-ratio	F-ratio	P > t	VIF	R ²	p > F
Intercept	-748.25 $\pm$ 540.45	-1.38		0.17		0.43	0.0001
Generation time (yr)	5484.25 $\pm$ 1037.42	5.29	27.95	0.0001	62.76		
Life span (yr)	-1632.17 $\pm$ 318.41	-5.13	26.28	0.0001	92.89		
Length to obtain optimum yield (cm)	88.29 $\pm$ 26.50	3.33	11.10	0.002	8.07		
Trophic level	-656.33 $\pm$ 202.28	-3.24	10.53	0.002	1.88		
Number of species	7.24 $\pm$ 2.97	2.43	5.92	0.02	1.02		
Five variables were not significant following AIC.

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 B0. The 95% confidence intervals for mean and median estimates of unfished

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 (Table 5). The 17 variables evaluated had low levels of VIF, which reduced the chance of over-prediction. Nevertheless, only 3 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 1420 kg/ha to 1135 kg/ha along the full stress gradient of 0.50 to 0.98. Similarly, erect algae associations explained 2% of the variance and declined from 1240 to 1040 kg/ha along the full 0 to 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 ($r^2=0.56$). Ocean exposure had no effect but non-target biomass declined moderately with hard coral ($r^2=0.32$) and erect algal cover ($r^2=0.03$). Non-target biomass also increased somewhat ($r^2=0.07$) with the standard deviation of the SST.

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.

(a) Total (Unfished) biomass

AIC	Estimate (mean $\pm$ SE)	t-ratio	F-ratio	P > t	VIF	R ²	p > F
Intercept	2128.23 $\pm$ 413.18	5.15	0	0.0001		0.33	0.003
Ocean exposure	-300.67 $\pm$ 81.35	-3.7	13.66	0.0008	1.2		
Multivariate stress model	-1178.97 $\pm$ 478.32	-2.46	6.08	0.019	1.1		
Erect algae	-13.2 $\pm$ 6.33	-2.08	4.34	0.04	1.11		
14 variables were not significant after conducting the step-wise regression analysis.							

(b) Fishable biomass

AIC	Estimate (mean $\pm$ SE)	t-ratio	F-ratio	P > t	VIF	R ²	p > F
Intercept	1186.2 $\pm$ 144.01	8.24	0	0.0001		0.40	0.0005
Ocean exposure	-375.51 $\pm$ 81.04	-4.63	21.47	0.0001	1.44		
Chlorophyll median	-662.45 $\pm$ 225.17	-2.94	8.66	0.006	1.37		
Soft coral	46.91 $\pm$ 20.48	2.29	5.25	0.03	1.11		
14 variables were not significant after conducting the step-wise regression analysis.							

(c) Target biomass

AIC	Estimate (mean $\pm$ SE)	t-ratio	F-ratio	P > t	VIF	R ²	p > F
Intercept	365.43 $\pm$ 151.52	2.41	0	0.02		0.33	0.008
Ocean exposure	-315.27 $\pm$ 85.34	-3.69	13.65	0.0008	2.56		
Soft coral	45.71 $\pm$ 16.35	2.8	7.82	0.009	1.14		
Hard coral	6.14 $\pm$ 2.57	2.39	5.71	0.02	1.82		
14 variables were not significant after conducting the step-wise regression analysis.							

(d) Non-target biomass

AIC	Estimate (mean $\pm$ SE)	t-ratio	F-ratio	P > t	VIF	R ²	p > F
Intercept	383.18 $\pm$ 230.03	1.67	0.00	0.1		0.56	0.0001
Hard coral	-6.94 $\pm$ 1.27	-5.47	29.89	0.0001	1.24		
Erect algae	-12.75 $\pm$ 2.98	-4.18	18.31	0.0001	1.32		
SST SD	257.56 $\pm$ 123.19	2.09	4.37	0.04	1.25		
14 variables were not significant after conducting the step-wise regression analysis.							

Ranges of estimated yields

Modelled maximum sustained yield variability increased from B_0 , to z , to r for likely ranges of these values (Fig. 6). Using the 95% CI for the median and mean B_0 indicate 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/km²/y while the upper values produced 7.1 and 7.4 tons/km²/y, 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/km²/y 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 ± 2.8 ($\pm$ SD) and 30.1 ± 2.9 cm, for fishable and target fish, respectively.

Discussion

Unfished biomass (B_0) had moderate variability and possibly influenced by a limited number of variables. While habitat, number of 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 ~1030 to 1250 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 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.

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 m² 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 sub-tropical 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 (Graham et al. 2008; Pratchett et al. 2009; Friedlander et al. 2014, Lamy et al. 2015). 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 et al. (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 behavior and refuge, it also reduces the net organic production in favor of inorganic carbon production, which can reduce fish biomass (Sebastian and 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 and 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 et al. 2009). The shallow reefs studied here (<11m) 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 >11m may explain the lower biomass on ocean

519 exposed (often deeper reef edges) than sheltered reefs. The lack of association with depth may
520 also mean that these high compliance closures are not fully supporting the large predatory fishes
521 that can often be found in deep water (Kulbicki et al., 2015). Shallow water is more likely to
522 support smaller-bodied herbivores that migrate between moderate and shallow water in unfished
523 reefs (Russ 2003).

524
525 Some remote reefs of the Pacific have reported biomasses around half of those presented here
526 for the African coastline (Williams et al. 2015). Moreover, their reported chlorophyll-a
527 concentrations were low and ranged from 0.05 to 0.20 mg/m³ while chlorophyll values on the
528 African coastline were between 0.2 to 1.1 mg/m³. In the Pacific Island sample, when
529 chlorophyll-a was close to 0.2 the reported biomasses were closer to ~1000 kg/ha.

530 Consequently, seawater production levels in the Pacific island could be limiting biomass more
531 than the African continent. Moreover, chlorophyll-a in the water column may be a proxy for
532 benthic production limits due to shared nutrient limitations.

533
534 Number of species was weakly associated with unfished biomass but was still among the
535 strongest factor that might extend biomass variation beyond the normal CIs of the benchmark.
536 Cause and effect is, however, difficult to determine and the extent that species numbers control
537 versus simply responds to biomass is a persistent debate in ecology (Huston et al. 2000). These
538 two factors are not independent and the high variability here suggests a weak association.

539 Reducing biomass by fishing ultimately reduces numbers of fish species. Where fishing is not
540 present, the relationship appears weaker and the circularity of cause and effect challenges
541 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).

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 and Tomlinson 1969). In complex reef fisheries with many captured species, empirical yields have been preferred to multispecies yield models when estimating maximum yields (Samoilys et al. 2017). This assumption does, however, require confirmation from yield models but also yield time series studies to establish if the 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 (Fig. 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 systems boundary decision can have consequences for yield evaluations. For example, unfished biomass in exposed reefs was 854 ± 132 ($\pm$ SE) kg/ha compared to 1252 ± 65 kg/ha in sheltered reefs.

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

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-m² belt transects evaluated here. Between-transect variance is likely to decline with increasing spatial

scale, at least up to 500 m², but possibly for larger areas as animal sizes, spatial needs, and movements increase (McCauley et al. 2012; Bradley et al. 2017).

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 to 16 fishers use a square kilometer of reef and, given sufficient sampling their efforts results in stable per area yields over time and space (McClanahan and Abunge 2013). 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 ~1150 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 m². Conversely, management for protecting the resource and low risk using the upper confidence limit would have a similar scale and justification problem.

600

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

617

618 Median biomass values were not greatly different from mean values for total and fishable
619 biomass but they were lower for target and non-target groups. When they do differ, using
620 median values should reduce the chances of overestimating biomass and yields. Using median
621 estimates can reduce the right-tailed distributions affects observed in some animal and biomass
622 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.

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 modeled 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 and Graham 2015). The empirical values used here of 0.23 ± 0.16 (95%CI) were, however, close to mean values of 0.20 to 0.25 commonly used in fisheries modeling studies (Little and Grafton 2015; Rudd and Branch 2016). Nevertheless, empirical studies of recovery indicate high variation that is seldom well understood or modeled when estimating yields.

645 B_0 may prove most useful as a fisheries independent metric to evaluate the fisheries and
646 ecological and stock status of coral reefs independent of estimates based on empirical yields
647 (Newton et al. 2007). Changes in effort and per area yield over time are infrequently collected
648 and reported (Pauly and Zeller 2016). Therefore, biomass is valuable as an alternative fisheries-
649 independent metrics for in situ stock assessments (Branch et al. 2011; Hilborn and Branch
650 2013). Estimating and assessing stocks in coral reefs has generally been elusive due to the high
651 diversity of caught species and the poverty of management institutions (Worm et al. 2009;
652 Worm and Branch 2012). Underwater visual census methods have made estimating community
653 fish biomass in coral reefs a potential surrogate for standard catch-based stock assessments.
654 Moreover, biomass and associated feeding processes often drive ecological processes and
655 ecological services, such as reef calcification, and therefore provide ecosystem service criteria
656 for evaluating fisheries (McClanahan et al. 2011; McClanahan and Muthiga 2016).

657

658 Separating biomass into target categories was influential in estimating contributions to the
659 yields. Differences between total and fishable biomass yields were small but target and non-
660 target yields were around half the total yields. These estimates assume the same intrinsic rate of
661 increase for these two groups. While local recovery and yield data to distinguish these rates
662 were not available, differences in the weighted growth rates between these two groups were
663 small (Table 2). Target biomass, on the other hand, had larger body sizes, longer life spans,
664 lower natural mortality and higher trophic levels metrics. Therefore, target fish are expected to
665 mature slower than non-target groups before obtaining optimum yields. Consequently, high
666 fishing effort should lead to increasing dominance of non-target groups with faster life histories,
667 which may maintain production but at the cost of reducing valuable stocks. Target fish in

668 Kenya, for example, were purchased at landing sites for ~US \$1.67 versus \$1.06 per kilogram
669 for non-target groups during this study period (Wamukota and McClanahan 2017).
670

671 The fish biomass and weighted community life histories provide some simple metrics for
672 fisheries management decisions. For example, an overall proposed mean size to harvest reef fish
673 is provided by the community-weighted lengths to obtain optimum yield. These values may be
674 inappropriate for fish that differ greatly from average coral reef sizes (i.e. sharks and jacks) but
675 still provide guidance where species-specific recommendations and management are not
676 available. A common alternative to this weighted multispecies approach is to make decisions
677 based on the most resilient, common, or valuable target species. How these decisions affect
678 other species is, however, seldom evaluated. For example, in heavily fished Kenyan reefs
679 optimal mesh sizes have been estimated for 3 of the most commonly landed fish where their
680 lengths to obtain optimum yields ranged from 22 to 23 cm (Hicks and McClanahan 2012). Yet,
681 the larger community of fish has a weighted optimum capture length of ~27 cm for fishable and
682 ~31 cm for target taxa. Consequently, recommendations using the commonly landed species
683 would lead to overfishing of many unevaluated species. If this problem is pervasive, fisheries
684 recommendations may be underestimating the size of capture for most coral reef species. This
685 will promote capture and mesh-size recommendations only suitable for fast growing and early
686 maturing at the expense of many other common species. Certainly, the capture-size decision is
687 even more inappropriate for large-bodied species, such as sharks, groupers, and jacks.

688 Nevertheless, in coral reefs where the diversity of captured fish and fishing methods are high,
689 multispecies metrics provide a more species inclusive estimate and balances more of the many
690 tradeoffs required of management decisions in multispecies fisheries.

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Supporting Information

Correlation matrix showing correlations between biomass and the life history variables.