Original Articles

Coral reef fish community life history traits as potential global indicators of ecological and fisheries status

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ABSTRACT

The productivity and diversity of coral reefs is being threatened by a number of human disturbances that could be better understood and managed with appropriate indicators. Here, I evaluated 9 biomass-weighted fish life history trait metrics and 4 categories of biomass (total, fishable, target, and non-target) using a large single-observer census of fish communities in 449 Indian Ocean reef sites. Comparisons and changes across a full gradient of fishing effort were made and fish traits compared between long unfished benchmark reefs (n = 62 sites) and reefs with variable fishing effort (n = 387 sites). I hypothesized that traits would differ between fished and the unfished benchmark sites and, as biomass increased, asymptotically approach benchmark values. Most weighted traits responded as predicted but variation among biomass categories, traits, and their responses to fishing and biomass was variable. For most traits, predictions for the total and fishable biomass fit better than target and non-target categories. Further, length-based traits were among the best indicator of status where as some commonly used traits like age-at-first maturity and trophic level were poor or responded contrary to predictions. Using multivariate analyses of all 9 traits did not strongly increase the predictive ability. Consequently, I suggest that geography, a large range in fishing pressure, and the inherent complexity of reef fish communities explains the variability better than the trait-specificity. Nevertheless, convergence between biomass and length-based traits occurred and suggest trait stability at an unfished biomass ~1000–1200 kg/ha. Biomass and length-based traits may have the broadest use in estimating sustainable fishing while other traits are unlikely to have global benchmarks. Thus, future research will need to account for spatial variation in environmental forces and fishing disturbances when using life-history traits. The practice of focusing on temporal responses to disturbances in comparable environments is recommended for impact studies.

1. Introduction

Coral reefs are being exposed to a number of environmental and human stresses and disturbances that are potentially undermining their ecological health and fisheries production (Cinner et al., 2016). One of the main solutions to many of these problems is to promote sustainable fishing that use indicators that respond well to changes in fishing pressure and reef ecology (McClanahan et al., 2015). Metrics, such as fish biomass and coral cover, are common means to evaluate reef condition but communities are expected to change in ways that are not fully reflected by these simple metrics (McClanahan and Graham, 2015; Bruno and Valdivia, 2016; Nash et al., 2016). Consequently, it behooves reef investigators and managers to examine other potentially useful indicators, particularly metrics that relate most directly to fisheries, their yields, and sustainability – key concerns of coral reef stakeholders in poor tropical countries (Hicks et al., 2013).

Coral reef fish and fisheries are complex multispecies communities

influenced by a number of environmental, habitat, and food web dynamics (Nash et al., 2015; Graham et al., 2017). Communities are expected to change as biomass is reduced by fishing but the predictability of these changes and how to effectively measure change can be better understood (McClanahan, 2018a). Fish life history metrics, such as growth, size, life span, and mortality, are common ways to evaluate species level status for recovery from fishing and harvesting criteria (Worm et al., 2009; Coleman et al., 2015). Yet, species-level data are often missing in fish and fisheries studies and more holistic community metrics are often regarded as among the best indicators of fishing pressure (Nicholson and Jennings, 2004; Fulton et al., 2005; McClanahan and Hicks, 2011). Consequently, given the largely non-specific capture of coral reef fishes, an alternative approach is to weight life histories proportional to the community biomass of each taxonomic group (McClanahan and Humphries, 2012).

Life history traits weighted by the biomass of taxa or functional groups have been used to evaluate the trophic levels of fisheries (Pauly
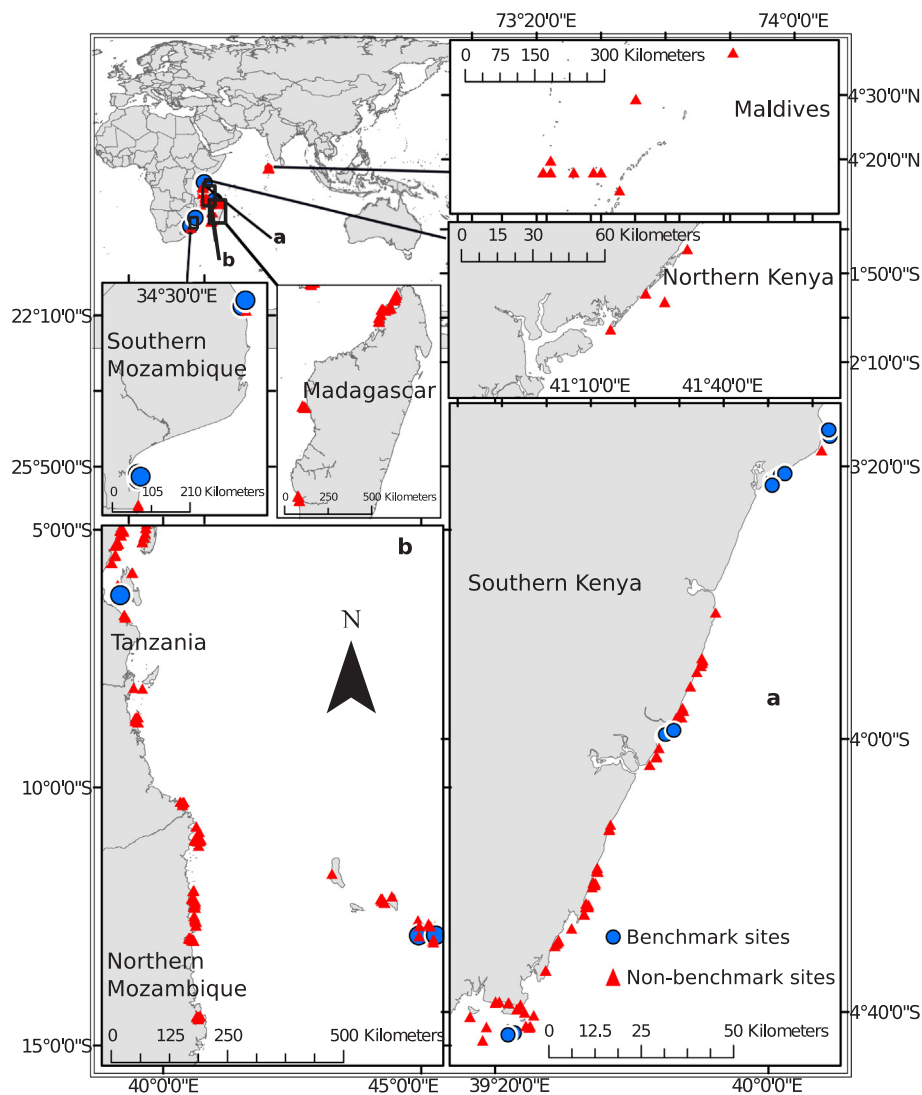

Fig. 1. Map of the western Indian Ocean study region and the location of fished and unfished or benchmarks reef sites.

et al., 2000). Similar principles and methods have been applied to evaluate changing coral reef fish life histories (McClanahan and Humphries, 2012; McClanahan and Graham, 2015). Yet, the usefulness of community life history or traits and how they compare to benchmark or unfished conditions is still poorly studied for marine and coral reef fisheries. It is generally expected that weighted community traits will approach benchmarks asymptotically over time or as a community reaches its maximum biomass and energy consumption (Odum, 1969, 1988). Predictions would be that community length, age, and trophic level should decrease while growth and mortality traits would increase as fishing effort increases and biomass declines (McClanahan and Graham, 2015). However, traits will vary in their sensitivity to changes of fishing effort, biomass, successional time, resource limitations, and other ecological conditions (Tilman, 1990). Consequently, knowing how traits respond and comparing their variation will better assist making evaluations and robust predictions of status (Jennings, 2005). To test these hypotheses, I used 9 common traits as potential indicators of fish community responses along a fishing effort-biomass gradient. The expectation was that as the biomass of the sites increased, single and multivariate community traits should asymptotically approach metrics calculated for unfished benchmark reefs. Thus, comparing single and multivariate responses provides a basis for evaluating the generality and variability in responses and determining the possibility of having global trait metrics for evaluating reef fish status.

2. Materials and methods

The evaluation used biomass data derived from Underwater Visual Census (UVC) of coral reef fish communities in the western Indian Ocean collected by a single observer (McClanahan, 2018a). Data were collected in 449 sites between 2005 and 2016 in reefs over 20° of latitude and longitude and 11 m of depth (Fig. 1). Studied sites included a full range of fishing effort and biomass but also included the oldest and largest fisheries closures in the western Indian Ocean (McClanahan et al., 2015, 2018a). More than 95% of the sites were sampled only once and mostly for two replicate transects or an area of $1000\,m^2$. A small number of sites had more samples either in time or space and transects were pooled into annual increments and the site/time averages used in the evaluations. The individual censuses were $500\,m^2$ areas in which individual fish were identified to 23 families and sized into 10 cm intervals. These count and size data were converted into wet weights using family-specific length-weight relationships. Biomass data were further categorized and analyzed in four partially overlapping 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 > 10 cm

Table 1

Summary statistics of biomass and community-weighted life history traits (mean ± SE) comparing indicators when all studied families and a restricted group were calculated. The restricted family benchmark eliminates the larger and more wide-ranging taxa that are included in the all family evaluation. Kruskal-Wallis tests of significance between all and restricted family benchmarks (n = 62).

	Category	Total	Fishable	Target	Non-target
Biomass, kg/ha	All families benchmark	1140.21 ± 55.37	1022.08 ± 52.20	563.94 ± 42.28	458.14 ± 25.45
	Restricted family benchmark	1132.10 ± 54.78	1013.98 ± 51.58	555.84 ± 41.72	458.14 ± 25.45
	Chi-square	0.02	0.03	0.03	0
	P-value	NS	NS	NS	NS
Maximum length	All families benchmark	42.86 ± 0.57	46.26 ± 0.45	51.26 ± 0.65	39.98 ± 0.38
	Restricted family benchmark	42.23 ± 0.47	45.60 ± 0.34	50.19 ± 0.49	39.98 ± 0.38
	Chi-square	0.71	0.58	1.14	0
	P-value	NS	NS	NS	NS
Length at first maturity	All families benchmark	22.81 ± 0.28	24.42 ± 0.23	27.46 ± 0.29	20.69 ± 0.17
	Restricted family benchmark	22.55 ± 0.24	24.15 ± 0.19	27.03 ± 0.23	20.69 ± 0.17
	Chi-square	0.51	0.51	0.96	0
	P-value	NS	NS	NS	NS
Optimum length	All families benchmark	25.50 ± 0.35	27.47 ± 0.30	31.41 ± 0.38	22.63 ± 0.20
	Restricted family benchmark	25.14 ± 0.30	27.09 ± 0.23	30.81 ± 0.29	22.63 ± 0.20
	Chi-square	0.51	0.6	0.97	0
	P-value	NS	NS	NS	NS
Natural mortality	All families benchmark	0.95 ± 0.01	0.88 ± 0.01	0.82 ± 0.01	0.96 ± 0.01
	Restricted family benchmark	0.95 ± 0.01	0.89 ± 0.01	0.83 ± 0.01	0.96 ± 0.01
	Chi-square	0.43	0.07	0.06	0
	P-value	NS	NS	NS	NS
Generation time	All families benchmark	2.96 ± 0.03	3.08 ± 0.03	3.29 ± 0.05	2.84 ± 0.02
	Restricted family benchmark	2.95 ± 0.03	3.07 ± 0.03	3.27 ± 0.05	2.84 ± 0.02
	Chi-square	0.11	0.09	0.09	0
	P-value	NS	NS	NS	NS
Life span	All families benchmark	9.50 ± 0.09	10.02 ± 0.09	10.72 ± 0.16	9.20 ± 0.07
	Restricted family benchmark	9.47 ± 0.09	9.98 ± 0.09	10.67 ± 0.16	9.20 ± 0.07
	Chi-square	0.08	0.07	0.07	0
	P-value	NS	NS	NS	NS
Trophic	All families benchmark	2.89 ± 0.02	2.90 ± 0.03	3.43 ± 0.05	2.33 ± 0.02
	Restricted family benchmark	2.88 ± 0.02	2.89 ± 0.03	3.42 ± 0.05	2.33 ± 0.02
	Chi-square	0.06	0.07	0.03	0
	P-value	NS	NS	NS	NS
Age at first maturity	All families benchmark	2.29 ± 0.02	2.39 ± 0.02	2.51 ± 0.04	2.26 ± 0.02
	Restricted family benchmark	2.29 ± 0.02	2.39 ± 0.02	2.50 ± 0.04	2.26 ± 0.02
	Chi-square	0.05	0.02	0.02	0
	P-value	NS	NS	NS	NS
Growth rate	All families benchmark	0.45 ± 0.005	0.43 ± 0.005	0.45 ± 0.01	0.40 ± 0.01
	Restricted family benchmark	0.45 ± 0.005	0.43 ± 0.04	0.45 ± 0.01	0.40 ± 0.01
	Chi-square	0.03	0.02	0.05	0
	P-value	NS	NS	NS	NS

and Labridae > 20 cm in length. Non-target biomass was the difference between fishable and target biomass. These classifications were based on observations and collections 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. While planktivores can have high reported biomass and a positive role of water column plankton production (Nadon et al., 2012; Williams et al., 2015; Valdivia et al., 2017), these groups were not included because of the high variability and difficulties of accurately sampling them in deeper water sites.

Life history calculation methods have been described in previous publications (McClanahan and Humphries, 2012; McClanahan, 2018a). Briefly, published life histories metrics of 9 traits (feeding (trophic) level, annual natural mortality, growth rate, age at maturity, generation time, life span, maximum length, length to obtain optimum yields (suggested minimum size to capture a species), and length at maturity (first reproduction)) were compiled for the dominant species in the African coastline region (McClanahan, 2018a, unpublished data, Fishbase.org, February 1, 2013). To weight values for the community-level traits, the biomass of the family was multiplied by the family's mean life history, summed across all families, and divided by the total biomass of

all (LH_k).

$$\bar{LH}_k = \frac{\sum_i^n (B_{ik} * LH_{ik})}{\sum_i^n B_{ik}}$$

where k is the year, *i* is the first family, n is the nth family.

There was concern that the weighted traits would be sensitive to the families included, particularly the inclusion or exclusion of the large-bodied and transient members of the reef, which include the Cacharinade, Carangidae, Ginglymostomatidae, and Sphyraenidae. In terms of their life histories, these groups can differ considerably compared to more site-attached coral reef species (McClanahan, 2018a). These families were, however, not frequently observed in UVC transects and may not play a large role in the weighting procedure. Prior to deciding on the appropriate family composition benchmark, the biomass and weighted life histories were tested for differences between traits for all 23 families versus the 19 resident taxa families. There were no significant differences between these two classifications and therefore all families were used in the presented community-level traits (Table 1).

Benchmark community-level traits were calculated from fish communities censused in reefs closed to fishing. Previous regional studies

Table 2
Summary comparisons of weighted coral reef fish community traits (mean $\pm$ SEM) between unfished high compliance closure benchmarks (n = 62) and fished communities (n = 387) based on all censused families. Kruskal-Wallis tests of significance between benchmark (n = 62) non-benchmark sites (n = 387).

Indicators	Category	Total	Fishable	Target	Non-target
Biomass category, kg/ha	Benchmark	1140.21 ± 55.37	1022.08 ± 52.20	563.94 ± 42.28	458.14 ± 25.45
	Non-benchmark	532.14 ± 24.70	460.24 ± 23.52	203.61 ± 14.20	256.64 ± 12.55
	Chi-square	83.23	83.14	86.95	60.78
	P-value	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Length to obtain optimum yield, cm	Benchmark	25.50 ± 0.35	27.47 ± 0.30	31.41 ± 0.38	22.63 ± 0.20
	Non-benchmark	22.26 ± 0.20	25.00 ± 0.17	29.99 ± 0.27	21.79 ± 0.11
	Chi-square	48.87	47.61	9.54	9.12
	P-value	< 0.0001	< 0.0001	0.002	0.003
Length at first maturity, cm	Benchmark	22.81 ± 0.28	24.42 ± 0.23	27.46 ± 0.29	20.69 ± 0.17
	Non-benchmark	20.24 ± 0.16	22.07 ± 0.11	26.36 ± 0.21	19.07 ± 0.24
	Chi-square	47.74	64.43	8.79	19.9
	P-value	< 0.0001	< 0.0001	0.003	< 0.0001
Maximum length, cm	Benchmark	42.86 ± 0.57	46.26 ± 0.45	51.26 ± 0.65	39.98 ± 0.38
	Non-benchmark	37.75 ± 0.35	42.57 ± 0.28	49.58 ± 0.44	38.08 ± 0.23
	Chi-square	43.58	42.34	5.9	9.99
	P-value	< 0.0001	< 0.0001	0.02	0.002
Annual natural mortality, M	Benchmark	0.95 ± 0.01	0.88 ± 0.01	0.82 ± 0.01	0.96 ± 0.01
	Non-benchmark	1.02 ± 0.01	0.93 ± 0.005	0.83 ± 0.01	0.98 ± 0.01
	Chi-square	24.77	16.81	0.56	3.31
	P-value	< 0.0001	< 0.0001	NS	NS
Life span, yr	Benchmark	9.50 ± 0.09	10.01 ± 0.09	10.72 ± 0.16	9.20 ± 0.07
	Non-benchmark	8.96 ± 0.05	9.74 ± 0.05	10.44 ± 0.10	9.28 ± 0.04
	Chi-square	16.73	4.73	1.33	4.26
	P-value	< 0.0001	0.03	NS	0.04
Growth rate, cm/yr	Benchmark	0.45 ± 0.005	0.43 ± 0.005	0.45 ± 0.01	0.40 ± 0.01
	Non-benchmark	0.47 ± 0.003	0.44 ± 0.003	0.42 ± 0.004	0.45 ± 0.003
	Chi-square	13.14	6.44	9.28	56.69
	P-value	0.0003	0.01	0.002	< .0001
Generation time, yr	Benchmark	2.96 ± 0.03	3.08 ± 0.03	3.29 ± 0.05	2.84 ± 0.02
	Non-benchmark	2.85 ± 0.01	3.02 ± 0.01	3.19 ± 0.03	2.91 ± 0.01
	Chi-square	10.52	2.0	1.61	11.81
	P-value	0.001	NS	NS	0.001
Age at first maturity, yr	Benchmark	2.29 ± 0.02	2.39 ± 0.02	2.51 ± 0.04	2.26 ± 0.02
	Non-benchmark	2.20 ± 0.01	2.33 ± 0.01	2.41 ± 0.02	2.29 ± 0.01
	Chi-square	9.74	3.61	2.51	5.19
	P-value	0.002	NS	NS	0.02
Trophic level	Benchmark	2.89 ± 0.02	2.90 ± 0.03	3.43 ± 0.05	2.33 ± 0.02
	Non-benchmark	2.86 ± 0.01	2.88 ± 0.01	3.09 ± 0.03	2.73 ± 0.01
	Chi-square	0.75	0.47	24.84	101.83
	P-value	NS	NS	< 0.0001	< .0001

evaluated the effects of compliance, size, and ages of closures and found that fish biomass does not level until > 15 years after closure, in closures > 5 km², and only where compliance with the no-fishing regulation is high (McClanahan et al., 2009; McClanahan and Graham, 2015). Previous studies in this region have also examined the effects of environment and benthic variables on fish communities in fished and unfished reefs and found only minor influences (McClanahan and Jadot, 2017; McClanahan, 2018a). The 62 benchmark sites chosen had these same characteristics and were broadly distributed in the region (Fig. 1). They were previously fully evaluated for variation in terms of multiple factors of environment, habitat, and some fish community metrics (McClanahan, 2018a). Similarly, a broad-scale study of fished reefs in Madagascar found very little variation (~10%) was explained by common habitat and environmental factors. Consequently, in this study the focus of variation was on fishing via biomass and high compliance closure and life histories rather than environmental and habitat variation.

2.1. Data analyses

The biomass and weighted traits of benchmarks and non-benchmark sites were tested for differences between the four biomass

classifications – total, fishable, target, and non-target. Tests of normality found that these data did not fit the assumptions of parametric statistics and, therefore, Kruskal-Wallis tests were undertaken to test for differences between the 62 benchmark and 387 non-benchmark populations. The differences between benchmark and non-benchmark populations were used to scale the strength of each community trait. Kruskal-Wallis statistical analyses were undertaken with JMP Software (version 12.0) (Sall et al., 2001). A multivariate trait metric was developed from a Principal Component Analyses (PCA) based on all 9 community traits (R package version 1.0.5; https://CRAN.R-project.org/package=factoextra). PCA axes 1 and 2 were calculated for all sites to test for differences between benchmark and non-benchmark sites and for the predicted asymptotic response with biomass.

Each of the single and multivariate trait metrics were plotted against the four biomass category distributions and examined for their fit to three possible responses. The asymptotic and saturation equations were used to test two possible predicted saturation-type responses, whereas the linear equation acted as a control for the predicted responses. Indicators and biomass were plotted using the R package ggplot2 v 2.2.1 to establish starting values for modelling and regression analyses to compare fits to linear, asymptotic, and saturation (Ricker equations) curves (R package version 1.2.1; https://CRAN.R-project.
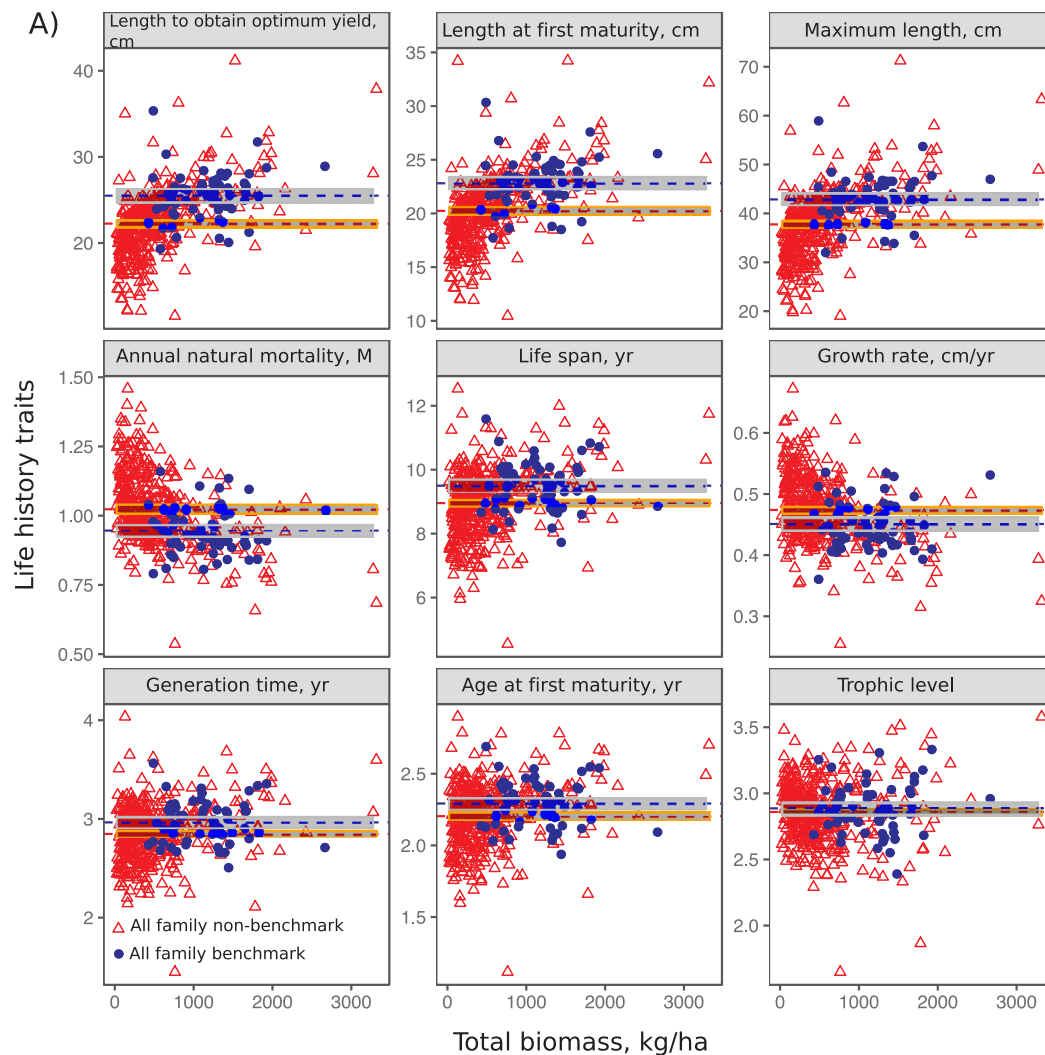
Fig. 2. Scatterplots of the relationship between the ecological traits and biomass in relationship to benchmarks derived from all studied fish families for (a) total, (b) fishable, (c) target, and (d) non-target taxa of the fish communities. Dashed and shaded lines represent the mean and 95% confidence intervals for the benchmark and non-benchmark sites.

org/package = minpack.lm). Thereafter, best-fit equations were used to determine where indicators meet or crossed the average benchmark values using inverse predictions in R package Investr v 1.4.0.

3. Results

3.1. Comparisons between benchmarks and non-benchmark sites

The benchmark sites had about twice the biomass as non-benchmark sites for all four biomass categories (Table 2). The largest difference between benchmarks and non-benchmarks weighted life histories were for the three length-based traits (Fig. 2). Differences between length indicators for all fish biomass categories were, however, small to modest, ranging from ~1 to 5 cm. The largest length difference was ~5 cm for the maximum lengths of the total biomass. Total and fishable biomass were similar for comparisons of length traits but fishable lengths were 2–4 cm larger than total biomass depending on the trait. Target lengths were larger still and all categories were larger than non-target biomass. For example, the length to obtain optimum yield was 22.6 cm for non-target but 31.4 cm for target biomass. Consequently, estimates of lengths for capture will depend on the biomass categories used to evaluate them.

As predicted, natural mortality rates were lower in benchmark than

non-benchmarks for total and fishable but not target and non-target biomass. Subsequently, life spans were longer for total and fishable biomass groups. However, there were no life span differences for target biomass and a very minor increase in non-target biomass when comparing benchmark and non-benchmark sites. Moreover, natural mortalities were not different for benchmark-non-benchmark comparison of target and non-target biomass. Generation time was a weak age indicator but longer in benchmarks for total biomass and shorter for non-target biomass. These same patterns were significant but weak for age-at-first maturity. Benchmark-non-benchmarks differences in growth rates were modest and higher in non-benchmark sites for all biomass categories except target biomass. Mean trophic level was the least differentiated trait for benchmark-non-benchmark comparison and not different for total and fishable biomass. Trophic level responses were different for target and non-target biomass, being higher in benchmarks for target but lower for non-target biomasses.

The multivariate PCA analyses of the first two dimensions for the 9 traits indicate individual sites were strongly differentiated by the first axes; however, benchmark and non-benchmark sites were weakly differentiated (Fig. 3). The first dimension of the total biomass category explained 73% and the second 15% of the variance. Similar percentage variation patterns were observed for fishable and target biomasses. The traits driving the first axes were length and to a lesser extent age,
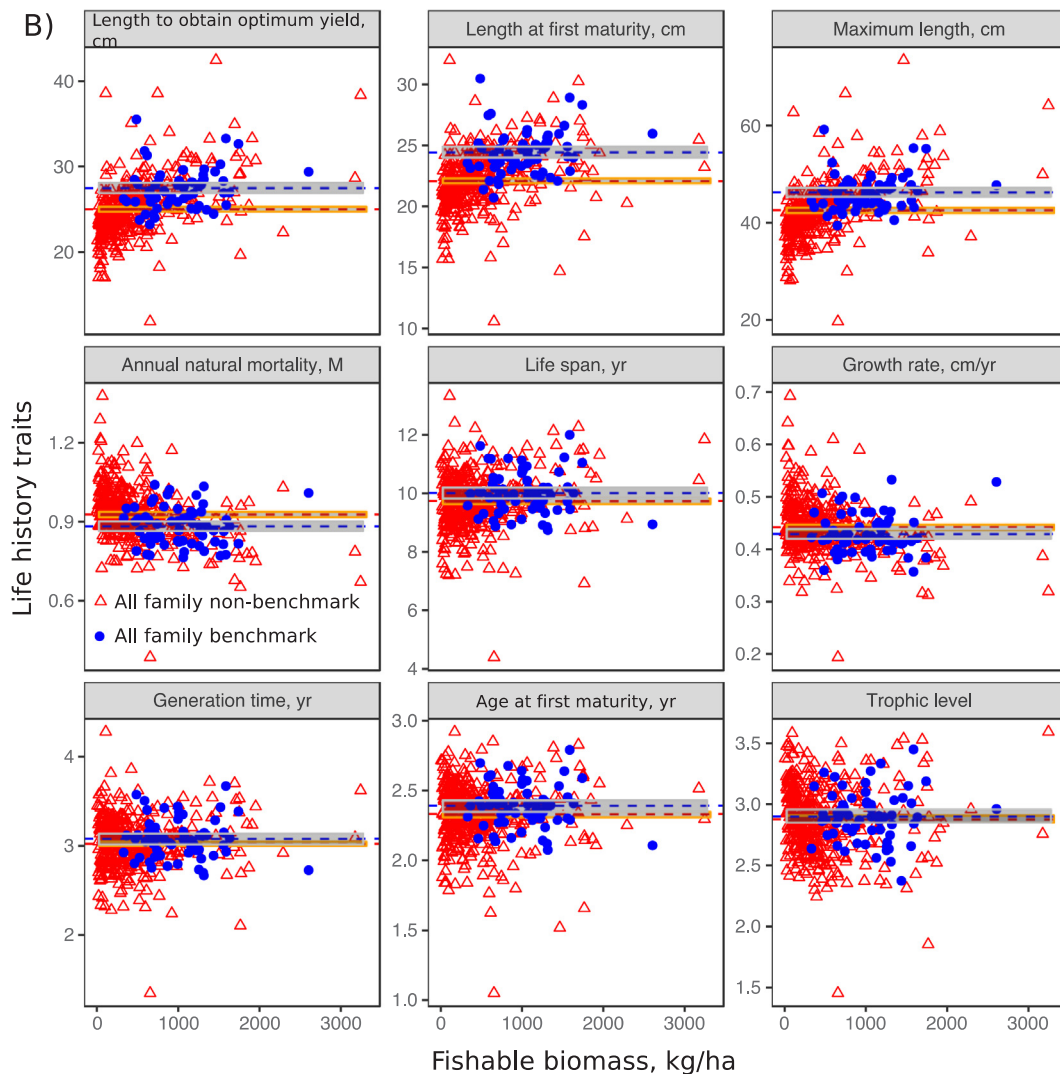
Fig. 2. (*continued*)

mortality, and growth traits, which, as predicted, differentiated sites in the opposite directions. The first axes were also strong for target biomass (65%) but declined with fishable (56%) and weakest for non-target community biomass (48%). The second axes were driven by the weaker influence of trophic level for these 3 biomass groups. However, non-target biomass had the most variation explained by the second axis (28%) associated with increasing trophic level, natural mortality, and growth rates.

3.2. Biomass-community trait relationships

Plots and analyses of biomass – trait relationships found high variability and a mixture of responses that differed for the four biomass categories (Fig. 2; Table 3). Fits to the 3 equations were low to moderate – the best fits for total and fishable biomass explained only 30% of the variance. Target and non-target trait fits to equations were often statistically significant but the best-fits explained < 10–20% of the variation. Community body length and life span traits increased and annual natural mortality and growth rates decreased with biomass. The predicted saturation-type responses were more commonly picked for the highest predicted variation over the linear model with some exceptions. For example, the optimal, length-at-first maturity, and maximum lengths had the strongest positive fits to asymptotic and saturation equations (based on AIC criteria). In contrast, annual natural mortality had the next strongest relationships, declined linearly with

biomass, but relationships were weak for target and non-target biomass.

Community life spans were weakly linear for total, asymptotic for fishable, and not significant for target and non-target biomass. Growth rates declined with biomass and were not easily distinguished by the models for total and fishable, not statistically significant for target, and declined asymptotically for non-target biomass. Generation time and age-at-first maturity relationships were occasionally statistically significant but fits were often weak ($R^2 < 0.07$) for all biomass groups. Trophic level was not significant for total and fishable and very weak for target biomass. However, trophic level was the strongest community trait ($R^2 = 0.3$) for non-target biomass and against prediction declined asymptotically with biomass.

Biomass and PCA axes relationships indicate similar levels of fit and responses as those found for individual traits (Table 4). The strongest fits were for the first PCA axis and the total biomass ($R^2 = 0.23$). By AIC criteria, the best fits were for the asymptotic and saturation curves. The second PCA axis had modest fits ($R^2 = 0.23$) to the saturation curves for the fishable and non-target biomass. Otherwise, relationships were statistically significant but weak. The first dimension of the non-target biomass was not significantly associated with biomass.

3.3. The intercepts between biomass and traits

Best-fit community trait- biomass equations intercepted with mean benchmark biomass within modest ranges and variation followed the
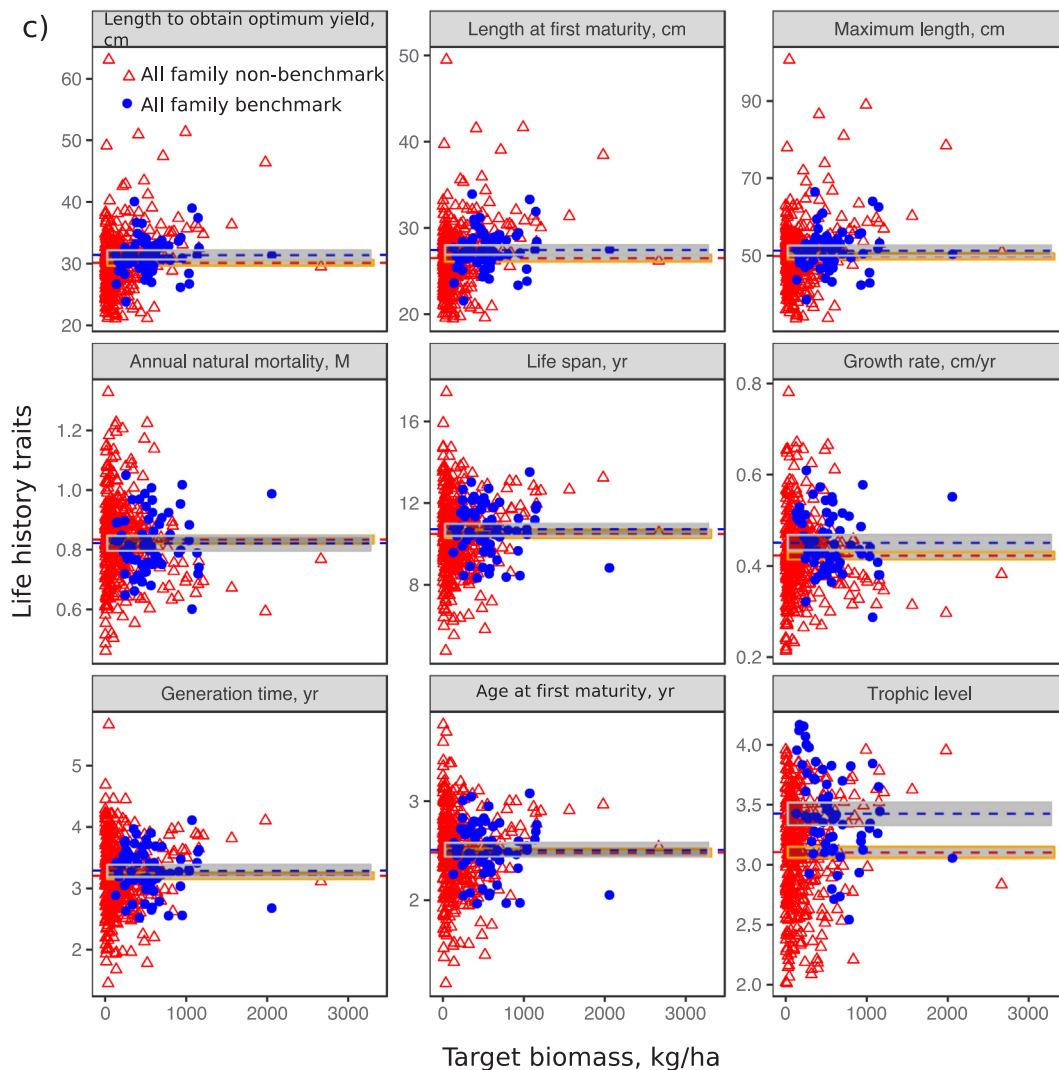
Fig. 2. (*continued*)

goodness-of-fit patterns for the biomass categories. For example, the least variable intercepts were found for total biomass, where all significant community traits fit intercepted benchmark biomass between ~ 975 and 1380 kg/ha. The least variable intercepts were found for length-based traits that intercepted benchmark biomass within a narrow range of ~ 1035 and 1250 kg/ha. The growth rate had the lowest intercept at 975 kg/ha of the total biomass. Fishable biomass intercepts were more variable ranging from ~ 890 to 2100, followed by target at ~ 200–645, and non-target at 315–1100 kg/ha.

4. Discussion

Community traits showed some of the predicted difference between fished and unfished benchmarks and saturation-type responses along the biomass gradient. There was, however, notable variation among biomass categories, life history traits, and their associations. First, there was high variability indicating the complexity of reef fish communities within this region. Second, total and fishable biomass categories were better than target and non-target groupings for most community indicators of status. Thirdly, length-based traits were among the best indicator of status as reflected in larger differences between fished and unfished reefs and also more predictable patterns along the biomass gradient. Fourthly, best-fit equation intercepts with benchmarks indicate there is some convergence between benchmark biomass and length traits, particularly for the total biomass. Fifth, some common

traits including age-at-first reproduction and mean trophic level were not good indicators of fish community status by either evaluation. Finally, multivariate analyses did not clearly improve biomass-community predictions – confirming variability is inherent to the community's taxonomic composition and not just a result of examining isolated single traits. Consequently, single and multiple community traits and biomass categorization are variable. Therefore, metrics of status are unequal and modest to weak in their ability to evaluate reef fish communities at large spatial scales.

Coral reefs are legendary for their high species diversity and spatial and temporal variation (Parravicini et al., 2013). Reef fish can exhibit variability on many scales of time and space of which ~ 20% is attributable to daily or rapid movements rather than substantial changes in populations (McClanahan et al., 2007; Kruse et al., 2015). Consequently, when sampling over different habitats, depths, and other environmental conditions, variability is likely to increase. Pooling transects and using integrative metrics should reduce some of this variability. For example, the family level groupings used here produced a limited number of categorizations that suggest lower variation than expected at finer scales of taxonomic resolution (McClanahan and Jadot, 2017). Moreover, pooling transects has a similar effect of reducing variation but here < 5% of the sites pooled transects when sampling was spread over < 1 year (Anderson and Millar, 2004). Overall, there was still considerable variation even when using integrative metrics such as weighted traits and multivariate analyses. Despite this
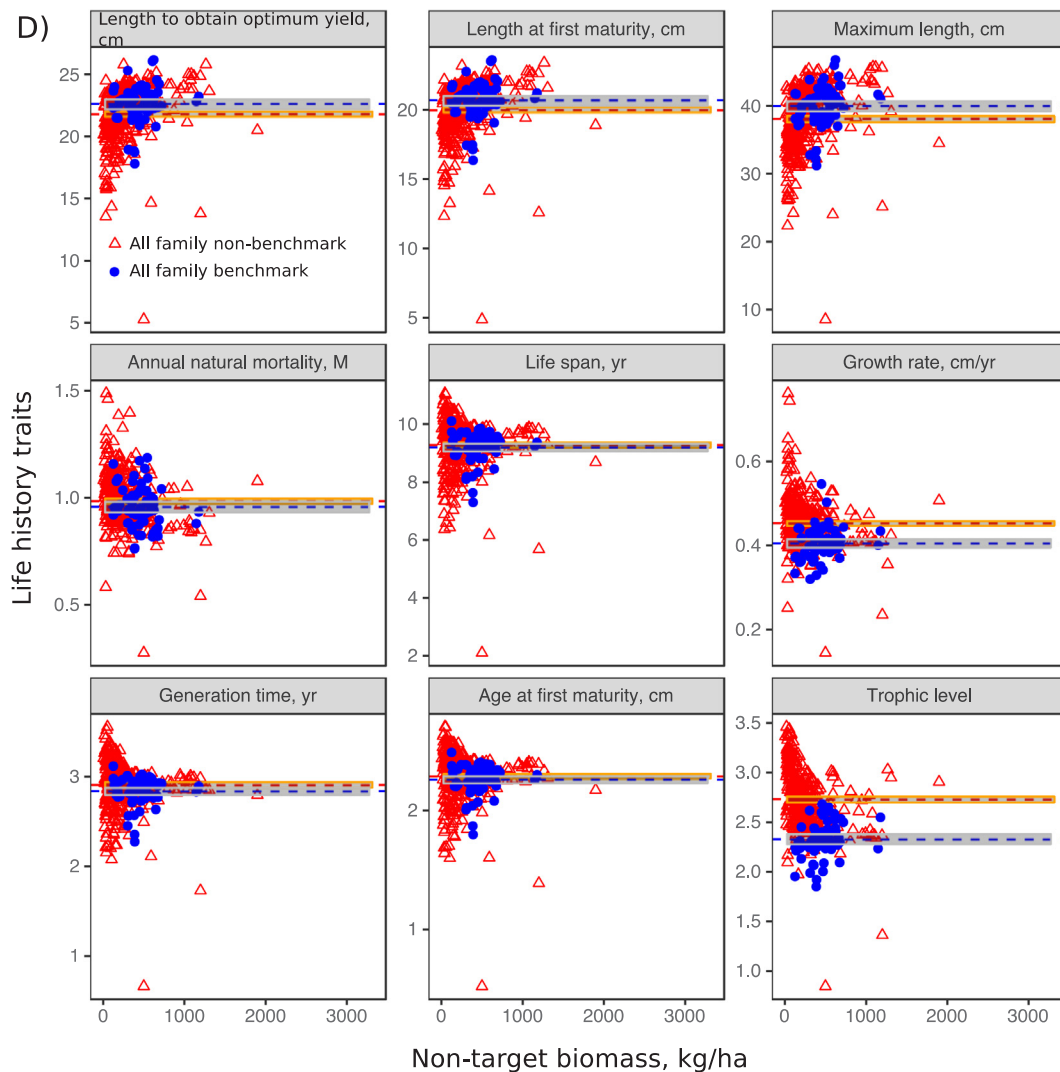
Fig. 2. (*continued*)

variation, expected patterns were supported but outcomes and predictive powers depended on the biomass categories and life history traits.

Biomass itself is a metric that integrates taxa, sizes, and abundance and proved to be one of the most differentiating metrics when comparing fished with unfished benchmarks. Biomass increases somewhat predictively when fishing effort is reduced or eliminated (Russ and Alcala, 1996; Lester et al., 2009; MacNeil et al., 2015). Further, biomass categorization is critical for distinguishing general ecological and fisheries status (McClanahan et al., 2011; Karr et al., 2015). It is also among the critical values used in estimating multispecies fisheries yields (Rankin and Lemos, 2015; McClanahan, 2018a). Further, evidence for a stable unfished biomass level of ~1000–1400 kg/ha for coral reefs is accumulating (MacNeil et al., 2015; McClanahan, 2018a,b). Consequently, unfished biomass was the core benchmark for evaluating traits. Nevertheless, fisheries evaluations use these traits to evaluate status as they reflect important features of fish communities and fisheries that are not always replaced by biomass. For example, fisheries management models use growth, mortality, and body lengths to estimate species status and yields (Pauly and Morgan, 1987).

Evaluating the 9 traits separately found community length-based indicators were the most powerful for distinguishing sites by management status and relationships with biomass. Length traits were strong indicators because fishing captures larger fish and changes body size spectrums in fished ecosystems (Rochet and Trenkel, 2003; Robinson et al., 2016). Additionally, these traits are potentially useful for predicting environmental and climate effects (Mangano et al., 2018; Martinez et al., 2018). Length has an approximately cubic relationship with biomass, making both metrics sensitive to changes in either. Length traits, therefore, tie directly to fisheries management and many taxa-specific recommendations for management are based on minimum and optimal length estimates. Length-based management is less frequently used in complex multispecies fisheries such as coral reefs. Nevertheless, community length information provides guidelines for managers lacking the ability to enforce taxa-specific length guidelines (McClanahan, 2018a). For example, my results indicate that community lengths at optimum yield will differ depending on the biomass categories being used – target biomass lengths being longer than non-target and fishable biomass lengths. Consequently, length indicators have considerable potential for evaluating fisheries status and making simple recommendations while acknowledging site and fisheries variability (Houk et al., 2018a).

Combined traits of natural mortality, life span, and age behaved as predicted but relationships and their power to differentiate sites was weak to moderate. Predicted changes in age traits would be strong for target biomass but also for all biomass categories because of indiscriminate fishing. Multivariate analyses suggest patterns were predictable at the site but benchmark and non-benchmark sites had considerable overlap. Multivariate traits were clearly different when biomass was very low but patterns were only modest when biomass
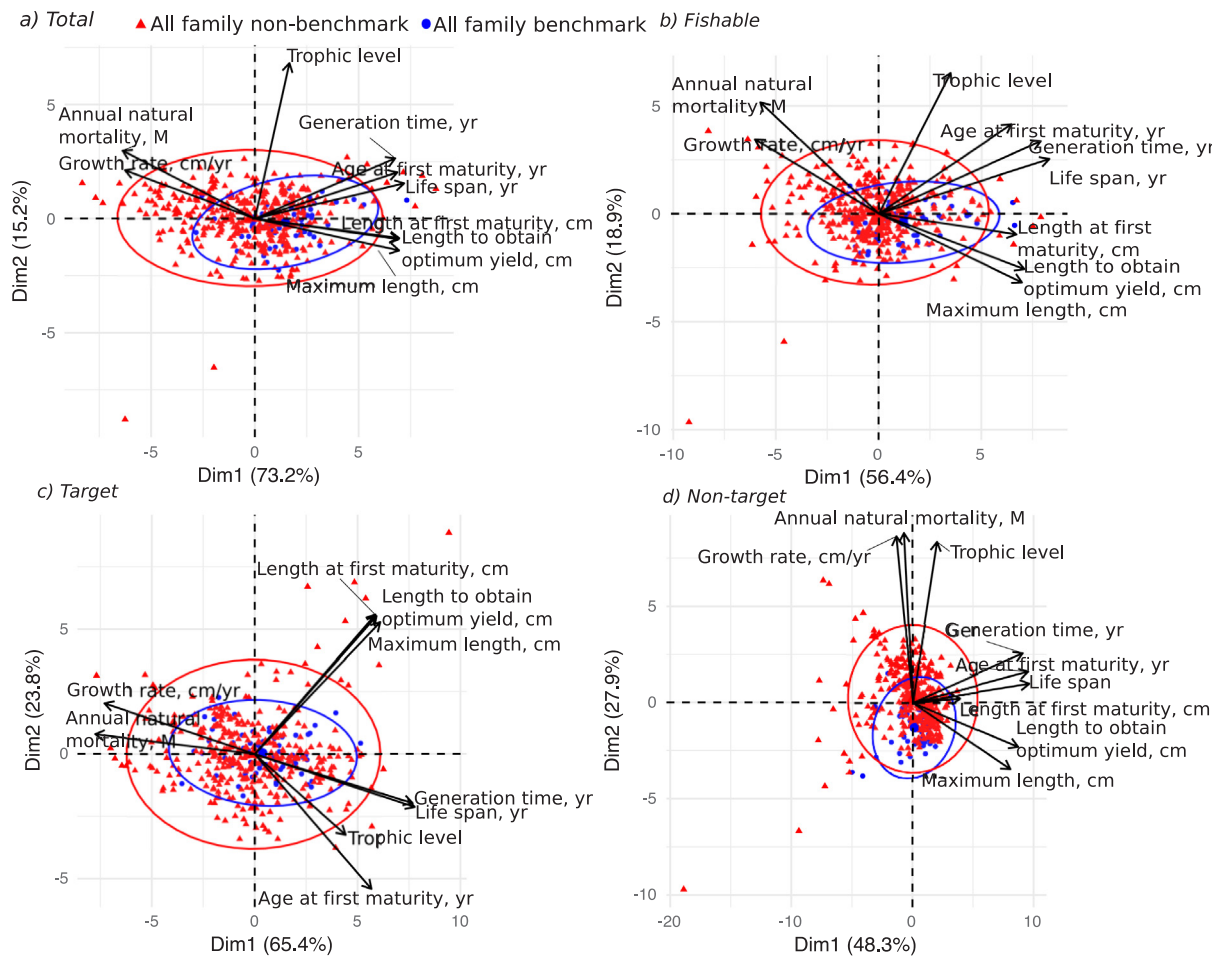
Fig. 3. Principal component analyses (PCA) of the first two dimensions of the relationships between sites and the 9 life history traits for benchmark and non-benchmark sites for (a) total, (b) fishable, (c) target, and (d) non-target taxa of the fish communities. Ellipses represent 95% confidence intervals for the benchmarks (blue) and non-benchmark sites (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increased. Relationships between closure time and trait have found reasonable fits but also appear to depend on the spatial extent of the study. For example, a study evaluating just four closures in Kenya found strong patterns ($R^2 = 0.66$–0.71) with time and trait changes. The time scale was long at 42 years of closure time but the sites were not distributed across large areas (~140 km of coastline, McClanahan and Humphries, 2012). In contrast, a broader scale survey of 135 sites in most of the Western Indian Ocean reefs closed to fishing for up to 45 years found lower fits ($R^2 = 0.12$–0.26); fits more in line with the findings presented here (McClanahan and Graham, 2015). This suggests that restricting the spatial extent of sites is more likely to reduce variation and produce predicted changes that might be diluted when the spatial extent of the studies is increased. A key need for applying indicators to management impacts is to find the balance between the replication needed to detect significant change while reducing the noise-to-signal ratio created by spatial heterogeneity (Stewart-Oaten et al., 1986).

A state-pressure-response indicators has been used to overcome the common problem of using fisheries indicators with weak predictive power (Jennings, 2005). Combining indicators is expected to be more predictive than simple single-state indicators with high noise-to-signal ratios. Findings here suggest this high variability will also be a common problem for coral reef fish communities. Consequently, knowing fishing pressure along the biomass-life history gradient should help to constrain fishing and differentiate fishing from other sources of variability. Improving state indicators will require better understanding how geography and other environmental and habitat forces influence variability

(McClanahan, 2018a). Future studies will need to evaluate the many scales and forces creating the heterogeneity inherent in complex reef fish communities. Additionally, it is at low levels of biomass that most detectable responses are observed, which limits the value of indicators in reefs less disturbed by fishing.

Trophic level is frequently used as an indicator of the status of fisheries despite weak empirical support (Branch et al., 2010). Use of the trophic level indicator has been criticized as oversimplifying fishing as a top-down activity versus a more evenly distributed impact occurring through food webs (Essington et al., 2006). For example, energetic models indicate that small herbivorous fish can be a large part of many coral reef fisheries because they feed low in the food web and are abundant and productive (McClanahan, 1995; Rogers et al., 2017; Houk et al., 2018b). Some target taxa, such as large parrotfish, have slow life history traits that make them susceptible to overexploitation and poor recovery when fishing effort is reduced (McClanahan et al., 2011; Abesamis et al., 2014; Taylor et al., 2014; Houk et al., 2018a). Therefore, unexpected outcomes, such as the reduction in the mean trophic level of fish communities over closure times or after species-level restrictions on catch, have been reported for coral reefs (McClanahan and Humphries, 2012; Babcock et al., 2013). Conversely, stable or increasing trophic levels can hide intensifying fishing and even collapses (Branch et al., 2010). This is expected when trophic level is poorly correlated with other abundance, size, age, and mortality life histories. Evaluating a large data set on reef fish trophic structure indicated that the mean or a declining trophic level of reef fish was a poor indicator of fishing impacts (Graham et al., 2017). This occurred because of the

Table 3

Comparison of best-fit equations of the community-weighted life history characteristics and (a) total, (b) fishable, (c) target, and (d) non-target biomasses. Fitted equations include fits to linear [lm(y–x)], asymptotic [y–k + (Bo − k) * exp(−r * X)], and saturation (Ricker [y–Bo + (a * X) * exp(−r * X)] equation models. Also presented is biomass level where the best-fit equation meets or crosses the life history benchmark (n = 66 high compliance closures > 15 years old). Best-model based on AIC criteria marked in bold.

a) Total biomass

Indicator	Equation type	Best-fit equation	R^2	AIC	P-value	Benchmark intercept, mean ± 95% CI (Lower; Upper)
Length to obtain optimum yield, cm	Linear	Y = 0.005X + 19.82	0.32	2015.20	0.0001	1246.90 (1133.88; 1391.15)
	Asymptotic	**Y = 30.46 + (18.71–30.46) * exp(−0.001 * X)**	**0.34**	**2004.10**	**0.0001**	**1110.28 (976.69; 1285.34)**
	Saturation	Y = 18.86 + (0.01 * X) * exp(−0.0002 * X)	0.34	2004.95	0.0001	1107.67 (976.65; 1273.56)
Length at first maturity, cm	Linear	Y = 0.004X + 18.31	0.30	1869.50	0.0001	1250.84 (1132.55; 1403.70)
	Asymptotic	**Y = 26.44 + (17.37 − 26.44) * exp(−0.001 * X)**	**0.25**	**1858.42**	**0.0001**	**1109.02 (968.59; 1299.94)**
	Saturation	Y = 17.51 + (0.01 * X)*exp(−0.0003*X)	0.25	1859.32	0.0001	1105.39 (968.24;1282.79)
Maximum length, cm	Linear	Y = 0.001X + 33.57	0.31	2453.13	0.0001	1190.69 (1080.80; 1330.92)
	Asymptotic	**Y = 50.72 + (31.43 − 50.72) * exp(−0.001 * X)**	**0.33**	**2440.64**	**0.0001**	**1033.22 (905.39; 1197.67)**
	Saturation	Y = 31.78 + (0.01 * X) * exp(−0.0003 * X)	0.26	2441.77	0.0001	1034.53 (909.73; 1191.57)
Annual natural mortality, M	**Linear**	**Y = −0.0001X + 1.09**	**0.21**	**−572.71**	**0.0001**	**1222.14 (1078.66; 1420.93)**
	Asymptotic	Y = 0.81 + (1.12 − 0.81) * exp(−0.001 * X)	0.22	1577.84	0.0001	1080.77 (910.77; 1327.26)
	Saturation	Y = 1.11 + (−0.0002 * X) * exp(−0.0003 * X)	0.22	−577.33	0.0001	
Life span, yr	**Linear**	**Y = 0.001X + 8.58**	**0.11**	**1106.30**	**0.0001**	**1284.63 (1072.85; 1636.14)**
	Asymptotic	Y = 16.78 + (8.57 − 16.78) * exp(−0.0001 * X)	0.11	1108.22	0.0001	1264.11 (1007.95; 1630.96)
	Saturation	Y = 8.55 + (0.001 * X) * exp(−0.0004 * X)	0.11	1108.22	0.0001	1264.40 (1008.55; 1631.17)
Growth rate, cm/yr	**Linear**	**Y = −0.0004X + 0.5**	**0.15**	**−1221.03**	**0.0001**	**1084.25 (935.20; 1298.60)**
	Asymptotic	Y = 0.37 + (0.50 − 0.37) * exp(−0.001 * X)	0.16	−1221.30	0.0001	976.25 (798.25; 1214.01)
	Saturation	Y = 0.50 + (−0.0001 * X) * exp(−0.0002 * X)	0.16	−1221.13	0.0001	983.74 (808.76 l; 1222.44)
Generation time, yr	**Linear**	**Y = 0.0001X + 2.77**	**0.06**	**109.06**	**0.0001**	**1314.75 (1036.98; 1884.74)**
	Asymptotic	Y = 127.1 + (2.77 − 127.1) * exp(−0.000001 * X)	0.06	111.07	0.0001	
	Saturation	Y = 2.78 + (0.0001 * X) * exp(0.0002 * X)	0.06	110.50	0.0001	1378.46 (1043.23; 1870.45)
Age at first maturity, yr	Linear	Y = 0.0001X + 2.14	0.07	−88.36	0.0001	1262.61 (1007.60;1757.16)
	Asymptotic	**Y = 49.53 + (2.14 − 49.53) * exp(−0.000002 * X)**	**0.07**	**−86.35**	**0.0001**	
	Saturation	Y = 2.15 + (0.0001 * X) * exp(0.0001 * X)	0.07	−86.47	0.0001	1293.63 (980.56; 1763.31)
Trophic level	Linear	NS				
	Asymptotic	NS				
	Saturation	NS				

b) Fishable biomass

Indicator	Equation type	Best-fit equation	R^2	AIC	P-value	Benchmark intercept, mean ± 95% CI
Length to obtain optimum yield, cm	Linear	Y = 0.004X + 23.37	0.25	1902.90	0.0001	1166.97 (1039.85; 1336.94)
	Asymptotic	**Y = 30.62 + (22.56 − 30.62) * exp(−0.001 * X)**	**0.28**	**1893.64**	**0.0001**	**1014.28 (863.02; 1234.34)**
	Saturation	Y = 22.70 + (0.001 * X) * exp(−0.0003 * X)	0.27	1894.72	0.0001	
Length at first maturity, cm	Linear	Y = 0.001X + 21.37	0.10	1677.50	0.0001	2010.76 (1636.04; 2684.62)
	Asymptotic	**Y = 23.40 + (20.38 − 23.40) * exp(−0.003 * X)**	**0.14**	**1663.62**	**0.0001**	
	Saturation	Y = 20.71 + (0.004 * X) * exp(−0.001 * X)	0.13	1665.60	0.0001	
Maximum length, cm	Linear	Y = 0.01X + 39.79	0.26	2303.25	0.0001	1080.68 (965.29; 1232.37)
	Asymptotic	**Y = 51.30 + (38.21 − 51.30) * exp(−0.001 * X)**	**0.29**	**2291.57**	**0.0001**	**899.18 (766.84; 1077.02)**
	Saturation	Y = 38.54 + (0.01 * X) * exp(−0.0004 * X)	0.28	2293.18	0.0001	908.39 (780.55; 1074.87)
Annual natural mortality, M	**Linear**	**Y = −0.0001X + 0.97**	**0.15**	**−764.98**	**0.0001**	**1051.03 (899.28; 1273.78)**
	Asymptotic	Y = 0.79 + (0.98 − 0.79) * exp(−0.001 * X)	0.16	−767.56	0.0001	893.81 (716.60; 1150.93)
	Saturation	Y = 0.98 + (−0.0001 * X) * exp(−0.0003 * X)	0.16	−767.01	0.0001	
Life span, yr	Linear	NS				
	Asymptotic	**Y = 609.9 + (9.60 − 609.9) * exp(−0.0001 * X)**	**0.02**	**1055.27**	**0.01**	
	Saturation	NS				
Growth rate, cm/yr	Linear	Y = −0.00003X + 0.46	0.09	−1258.50	0.0001	843.15 (677.63; 1098.61)
	Asymptotic	Y = 0.37 + (0.46 − 0.37) * exp(−0.001 * X)	0.09	−1257.59	0.0001	735.74 (549.75; 1019.10)
	Saturation	**Y = 0.46 + (−0.00004 * X) * exp(−0.0002 * X)**	**0.09**	**−1257.44**	**0.0001**	
Generation time, yr	Linear	NS				
	Asymptotic	NS				
	Saturation	NS				
Age at first maturity, yr	Linear	NS				
	Asymptotic	NS				
	Saturation	NS				
Trophic level	Linear	NS				
	Asymptotic	NS				
	Saturation	NS				

c) Target biomass

Indicator	Equation type	Best-fit equation	R^2	AIC	P-value	Benchmark intercept, mean ± 95% CI
Length to obtain optimum yield, cm	Linear	Y = 0.01X + 29.10	0.09	2281.61	0.0001	450.64 (348.32; 611.35)
	Asymptotic	Y = 42.13 + (28.84 − 42.13) * exp(−0.001 * X)	0.09	2281.12	0.0001	
	Saturation	**Y = 28.82 + (0.01 * X) * exp(−0.0003 * X)**	**0.09**	**2280.82**	**0.0001**	
Length at first maturity, cm	Linear	Y = 0.004X + 25.71	0.09	2058.40	0.0001	452.71 (350.79; 612.50)
	Asymptotic	Y = 35.71 + (25.52 − 35.71) * exp(−0.001 * X)	0.09	2057.97	0.0001	
	Saturation	**Y = 25.50 + (0.01 * X) * exp(−0.0003 * X)**	**0.09**	**2057.67**	**0.0001**	
Maximum length, cm	**Linear**	**Y = 0.01X + 48.16**	**0.08**	**2666.53**	**0.0001**	**201.18 (100.76; 300.70)**
	Asymptotic	Y = 80.78 + (47.94 − 80.78) * exp(−0.003 * X)	0.08	2667.67	0.0001	
	Saturation	Y = 47.92 + (0.01 * X) * exp(−0.0002 * X)	0.08	2667.56	0.0001	
Annual natural mortality, M	Linear	Y = −0.00001X + 0.85	0.02	−463.22	0.01	435.99 (227.03; 1223.89)
	Asymptotic	**Y = −0.001 + (0.85 + 0.001) * exp(−0.000001 * X)**	**0.02**	**−461.22**	**0.03**	
	Saturation	Y = 0.85 + (−0.00004 * X) * exp(0.0002 * X)	0.02	−461.62	0.03	
Life span, yr	Linear	NS				
	Asymptotic	NS				
	Saturation	NS				
Growth rate, cm/yr	Linear	NS				
	Asymptotic	NS				
	Saturation	NS				
Generation time, yr	Linear	NS				
	Asymptotic	NS				
	Saturation	NS				
Age at first maturity, yr	Linear	NS				
	Asymptotic	NS				
	Saturation	NS				
Trophic level	**Linear**	**Y = 0.0002X + 3.07**	**0.01**	**469.57**	**0.03**	**646.60 (354.73; 5830.78)**
	Asymptotic	NS				
	Saturation	NS				

d) Non-target biomass

Indicator	Equation type	Best-fit equation	R^2	AIC	P-value	Benchmark intercept, mean ± 95% CI
Length to obtain optimum yield, cm	Linear	Y = 0.002X + 21.21	0.07	1665.15	0.0001	766.10 (606.10; 1092.24)
	Asymptotic	**Y = 22.69 + (19.64 − 22.69) * exp(−0.01 * X)**	**0.12**	**1644.04**	**0.0001**	
	Saturation	Y = 20.28 + (0.01 * X) * exp(−0.001 * X)	0.11	1647.27	0.0001	
Length at first maturity, cm	Linear	Y = 0.002X + 19.47	0.07	1558.86	0.0001	751.24 (593.30; 1074.61)
	Asymptotic	Y = −0.003 + (19.47 + 0.003) * exp(0.000001 * X)	0.07	1560.87	0.0001	
	Saturation	**Y = 18.64 + (0.01 * X) * exp(−0.001 * X)**	**0.11**	**1540.26**	**0.0001**	
Maximum length, cm	Linear	Y = 0.01X + 36.68	0.09	2226.11	0.0001	1099.84 (885.49; 1503.04)
	Asymptotic	**Y = 40.35 + (32.48 − 40.35) * exp(−0.01 * X)**	**0.18**	**2187.05**	**0.0001**	
	Saturation	Y = 34.03 + (0.03 * X) * exp(−0.002 * X)	0.17	2191.04	0.0001	
Annual natural mortality, M	**Linear**	**Y = −0.0001X + 1.01**	**0.07**	**−572.73**	**0.0001**	**522.01 (416.24; 706.90)**
	Asymptotic	Y = 0.86 + (1.04 − 0.86) * exp(−0.002 * X)	0.08	−575.11	0.0001	
	Saturation	Y = 1.04 + (−0.0003 * X) * exp(−0.001 * X)	0.08	−575.47	0.0001	
Life span, yr	Linear	NS				
	Asymptotic	NS				
	Saturation	NS				
Growth rate, cm/yr	**Linear**	**Y = −0.0001X + 0.47**	**0.06**	**−1152.43**	**0.0001**	**679.78 (529.26; 1000.81)**
	Asymptotic	Y = 70.31 + (0.47 − 70.31) * exp(0.000001 * X)	0.06	−1150.42	0.0001	
	Saturation	Y = 0.48 + (−0.0001 * X) * exp(−0.001 * X)	0.07	−1157.06	0.0001	
Generation time, yr	Linear	Y = −0.0002X + 2.95	0.02	52.22	0.002	436.19 (276.89; 850.00)
	Asymptotic	Y = 2.8 + (3.0 − 2.8) * exp(−0.003 * X)	0.03	50.87	0.002	
	Saturation	**Y = 3.0 + (−0.001 * X) * exp(−0.001 * X)**	**0.03**	**50.66**	**0.002**	
Age at first maturity, yr	Linear	NS				
	Asymptotic	NS				
	Saturation	NS				
Trophic level	Linear	Y = −0.0004X + 2.85	0.16	76.04	0.0001	535.60 (462.28; 639.91)
	Asymptotic	**Y = 2.51 + (3.14 − 2.51) * exp(−0.01 * X)**	**0.30**	**8.40**	**0.0001**	**314.28 (265.27; 397.58)**
	Saturation	Y = 3.07 + (−0.002 * X) * exp(−0.001 * X)	0.30	10.37	0.0001	

replacement of fish by other non-fish organisms (i.e. sea urchins) but also the existence of a concave rather than pyramid shaped food web structure in the absence of fishing.

Convergence of benchmark biomass and traits was evaluated to test for points of stability in the fish community. In principle, once reef energy sources are fully utilized, biomass should stabilize but be followed by a slow declining rate of change in the life history traits (McClanahan and Graham, 2015). My findings support this theory

Table 4
Comparison of best-fit equations of the first two dimensions of the Principal Component Analyses with (a) total, (b) fishable, (c) target, and (d) non-target biomasses. Fitted equations include fits to linear [lm(y–x)], asymptotic [y–k + (Bo − k) * exp(−r * X)], and saturation (Ricker [y–Bo + (a * X) * exp(−r * X)] equation models. Best-model based on AIC criteria marked in bold.

Biomass	PCA Axis	Equation type	Best-fit equation	R^2	AIC	P-value
Total	Dim.1	Linear	Y = 0.002 − 1.42X	0.22	2016.09	0.0001
		Asymptotic	Y = 4.14 + (−1.94 − 4.14) * exp(−0.001 * X)	0.23	2011.99	0.0001
		Ricker	Y = −1.85 + (0.004 * X) * exp(−0.0003 * X)	0.23	2012.56	0.0001
	Dim.2	Linear	Y = 0.28X − 0.0005	0.04	1400.50	0.0001
		Asymptotic	NS			
		Ricker	**Y = 0.98 + (−0.04 * X) * exp(−0.001 * X)**	**0.10**	**1372.97**	**0.0001**
Fishable	Dim.1	**Linear**	**Y = 0.002 − 0.86X**	**0.12**	**1949.77**	**0.0001**
		Asymptotic	Y = 3.83 + (−1.07 − 3.83) * exp(−0.001 * X)	0.13	1949.78	0.0001
		Ricker	Y = −1.05 + (0.002 * X) * exp(−0.0002 * X)	0.13	1949.86	0.0001
	Dim.2	Linear	Y = 0.55X − 0.001	0.15	1444.31	0.0001
		Asymptotic	Y = 1756.0 + (0.55 − 1756.0) * exp(0.000001 * X)	0.15	1446.33	0.0001
		Ricker	**Y = 1.27 + (−0.004 * X) * exp(−0.001 * X)**	**0.23**	**1404.71**	**0.0001**
Target	Dim.1	**Linear**	**Y = 0.001 − 0.32X**	**0.03**	**2055.51**	**0.001**
		Asymptotic	Y = 20.12 + (−0.32 − 20.12) * exp(−0.0001 * X)	0.03	2057.49	0.003
		Ricker	Y = −0.32 + (0.001 * X) * exp(−0.00004 * X)	0.03	2057.49	0.003
	Dim.2	Linear	Y = 0.001 − 0.26X	0.05	1593.26	0.0001
		Asymptotic	Y = 1.04 + (−0.42 − 1.04) * exp(−0.002 * X)	0.06	1590.22	0.0001
		Ricker	**Y = −0.41 + (0.002 * X) * exp(−0.001 * X)**	**0.06**	**1590.14**	**0.0001**
Non-target	Dim.1	Linear	NS			
		Asymptotic	NS			
		Ricker	NS			
	Dim.2	Linear	Y = 0.76X − 0.003	0.18	1606.60	0.0001
		Asymptotic	**Y = −1.22 + (2.00 + 1.22) * exp(−0.005 * X)**	**0.27**	**1556.55**	**0.0001**
		Ricker	Y = 1.68 + (−0.01 * 1.68) * exp(−0.001 * X)	0.26	1558.40	0.0001

particularly for total biomass but with less clear relationships among the other 3 biomass categories. As would be predicted, growth rates intercepted at the lowest (< 1000 kg/ha) while size and age traits intercepted at higher biomass levels (1100–1400 kg/ha). This suggests that growth rates decline earlier than size and age traits along the biomass continuum. The general range of biomass, age, and size traits intercepts between 1000 and 1400 kg/ha is significant as this range represents an undisturbed pristine biomass (MacNeil et al., 2015). Consequently, this convergence is another line of evidence that there is some stable level of biomass and some life histories, even if there is modest variability around these stability benchmark.

Predictions of biomass-trait relationships were largely upheld with the exception of trophic level – a metric reported to be problematic in many fisheries-ecosystem studies (Essington et al., 2006; Branch et al., 2010). Nevertheless, the observed variability suggests a number of recommendations for using fish traits. First, life histories are most useful when biomass is low and fishing pressure high and mostly for total fish rather than the other biomass categories. Moreover, length-based traits are good but biomass is probably the single best integrative metric of status. Finally, a good deal of variation is spatial and therefore the weak patterns found here are associated with a large scale and the potential influences of other habitat and environmental variables (McClanahan, 2018a). Theses influences have, however, not been shown to be large and therefore support the conclusion that much variability is endogenous to the fish community (McClanahan and Jadot, 2017). Overall, length traits are likely to have the broadest usage but a number of trait metrics are unlikely to have global benchmarks. This suggests the need to restrict the spatial scale and variability when evaluating traits and to account for this variation by picking control, references, or benchmarks sites that are comparable. As in most impact studies, changes or variation in time are better indicators than changes in space (Stewart-Oaten et al., 1986). Fish life history traits add to the tool box of coral reef indicators but must be applied judiciously.

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