Harnessing fishery-independent indicators to aid management of data-poor fisheries: weighing habitat and fishing effects

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Abstract.   State indicators, e.g., mean size and trophic level of the fish assemblage, can provide important insights into the effects of fishing on ecosystems and the resource potential of the fishery. On coral reefs, few studies have examined the relative effects of fishing and other drivers, such as habitat, on these indicators. In light of habitat heterogeneity and increasing habitat degradation, this lack of understanding limits the usefulness of indicators for monitoring the effect of fishery management actions. Identifying thresholds or nonlinearities in relationships between fishing pressure and state indicators has been suggested as a basis for biomass-based targets to support management efforts in low research capacity contexts. Using data collected in Seychelles, we examined the relative influences of fishable biomass (proxy for fishing pressure) and the benthic habitat on fisheries-independent indicators characterizing attributes of the fish community important for fisheries production. We characterized the driver–indicator relationships, and compared local-scale relationships for Seychelles with large-scale relationships published for the Indian Ocean. We found that both habitat and fishing pressure influenced indicators, but habitat effects were particularly strong. This knowledge provides managers with the capacity to implement a diverse array of complementary management actions targeting these drivers. A number of the Seychelles scale driver–indicator relationships were linear, suggesting gradual changes in indicators in response to changes to drivers. This contrasted with relationships published for the Indian Ocean, which were characterized by thresholds below which exploitation is likely to have significant detrimental effects on the functioning of important ecosystem processes. These scale-specific differences are likely driven by the narrower range of fishing pressures found in Seychelles. Importantly, it indicates that, although biomass-based targets derived from large-scale relationships may provide a useful starting point for setting management targets, the local context must be considered.

Key words: biomass-based target; coral reef; ecological thresholds; ecosystem-based management; functional relationship; indicator; scale; specificity.

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INTRODUCTION

Fisheries management has traditionally relied on information derived from stock assessments (Travis et al. 2014). However, many fisheries are data-poor, particularly in developing and tropical nations, with insufficient information for such quantitative approaches (Erisman et al. 2014).

This deficiency of data and absence of stock assessments has been linked to a lack of sustainability for small-scale fisheries (Costello et al. 2012). A variety of indicators have been developed, primarily in temperate regions, to replace formal stock analysis when data are limited, or for managing multispecies fisheries (Rochet and Trenkel 2003). These indicators inform management by characterizing the pressures acting on the system, the state of the system, and system responses to management (Rogers and Greenaway 2005, Mangi et al. 2007). Coral reef fisheries are a classic example of the need for such approaches, often being multispecies, small-scale, and artisanal in nature. Reef fisheries commonly exist in data-poor contexts, and as a consequence suffer from limited or ineffective management (Johnson et al. 2013); over 50% of coral reefs found around islands are estimated to be fished unsustainably (Newton et al. 2007). This is of significant concern as these fisheries are essential sources of food and income in many tropical countries, supporting in excess of 1 billion people (UNEP 2004).

State indicators address attributes of the fish community, such as mean size and the broader ecosystem effects of fishing (Jennings and Dulvy 2005, Travis et al. 2014). Importantly, many of these indicators can be estimated from fisheries-independent data and thus do not rely on extensive catch surveys (Starr et al. 2010, Smith et al. 2011). Capturing changes in indicators that characterize the fish community, e.g., total biomass or slope of the size spectrum, is significant in terms of evaluating how exploitation is impacting fishes and the influence of targeted management actions (Rochet and Trenkel 2003, Shin et al. 2005). State indicator trends also have implications for fisheries production; patterns in indicators may support an understanding of the relative resource potential of the fishery at different locations. However, many proposed indicators are affected by factors other than fishing, such as season, pollution, and habitat (Grigg 1994, Pinca et al. 2012, Wilson et al. 2012*a*). The relative influence of fishing compared to these other variables is termed the 'specificity' of the indicator to fishing (Rice and Rochet 2005). A low specificity implies that an indicator is poorly suited to supporting fisheries management decisions (Houle et al. 2012). However, where factors related to habitat systematically affect fishery indicators, this knowledge can inform habitat management to support characteristics of the fish community that are important to fishers. For example, Rogers et al. (2014) demonstrated how loss of reef structural complexity can drive significant declines in the productivity of coral reef fisheries, highlighting that management actions which support reef accretion would in turn promote fishery productivity. Thus, habitat management may complement more traditional fishery management strategies aimed at controlling fishing inputs (e.g. effort restrictions) or outputs (e.g. quotas; Pope 2009), as advocated by ecosystem-based approaches to fisheries management (Pikitch et al. 2004, Thrush and Dayton 2010).

A wide range of fishery-independent state indicators have been used in coral reef contexts. But a number of studies have shown the potential for habitat variability to mask or overpower fishing effects on different aspects of the fish community (e.g., Friedlander et al. 2007, Wilson et al. 2008, Guillemot et al. 2014). Nonetheless, nearly 50% of studies examining fisheries indicators reviewed by Nash and Graham (2016) did not evaluate the influence of habitat, and the number of studies accounting for habitat is not increasing over time (Miller and Russ 2014). As a result, a comprehensive understanding of habitat effects across multiple indicators is lacking for coral reefs. In light of the often significant gradients in habitat condition (e.g., Fabricius et al. 2005) and the increasing anthropogenic impacts driving broad-scale benthic changes on coral reefs (e.g., Fabricius et al. 2005, Alvarez-Filip et al. 2009, De'ath et al. 2012), this poor understanding of how habitat may influence indicators is a serious oversight.

Estimating ecosystem indicators and understanding their specificity to fishing may provide some perspective on the state of the fishery and resource potential, but there is a disconnect between this understanding and developing management control rules (Jennings and Dulvy 2005, Samhouri et al. 2012). An important step in setting decision criteria is explicitly characterizing the functional relationships between indicators and different drivers (Appendix S1: Fig. S1a; Samhouri et al. 2010, McClanahan et al. 2011). Nonlinearities or inflexion points in these relationships suggest thresholds to be avoided, by identifying the levels of fishery exploitation or
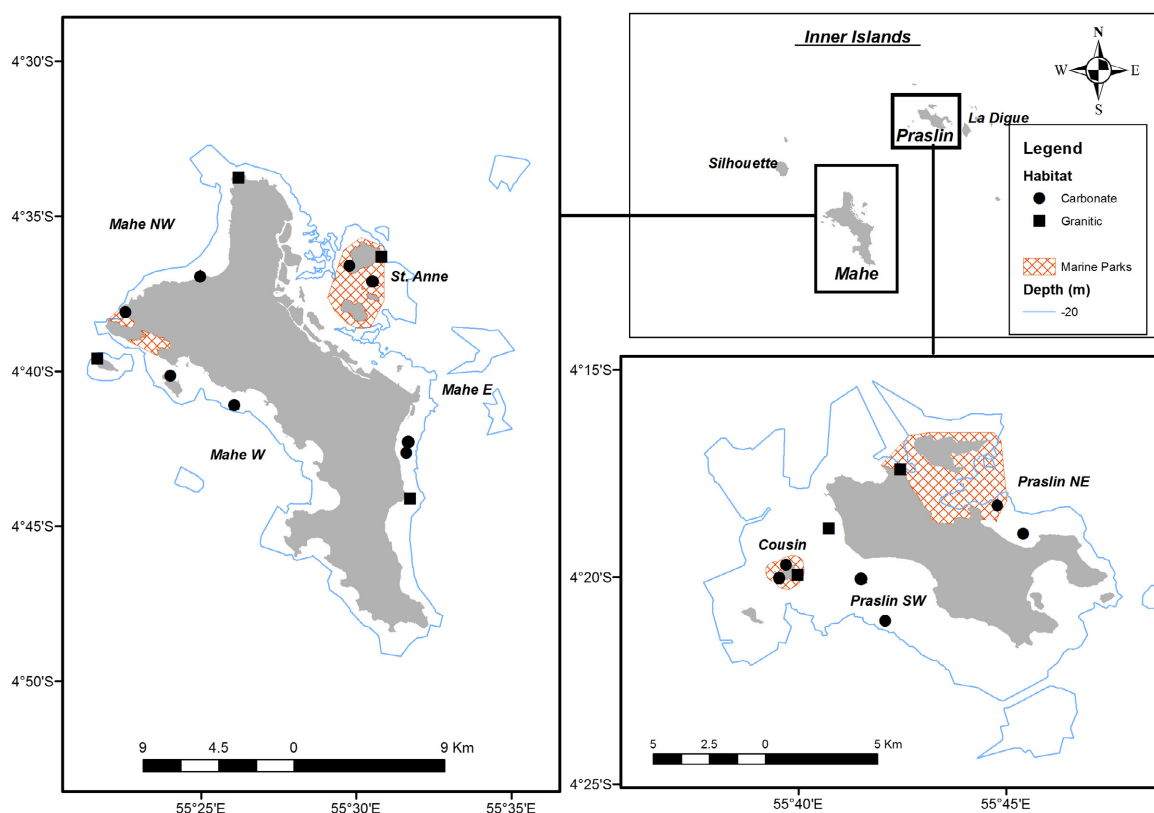
Fig. 1.   Map of study sites. No-take areas are highlighted in red.

habitat variability beyond which there are likely to be significant detrimental effects on the functioning of important ecosystem processes or on the fish community itself (Martin et al. 2009). Management intervention may be required before these threshold values are reached (Samhouri et al. 2010). In contrast, optima in functional relationships may suggest useful targets around which management actions can focus (Martin et al. 2009). Research into the functional relationships between fishable biomass and an array of indicators has provided a range of biomass-based targets for coral reef fisheries in the Caribbean and Indian Ocean. This knowledge may support management where limited research capacity might otherwise reduce management effectiveness (McClanahan et al. 2011, 2015, Karr et al. 2015). Research in the Caribbean suggests that these relationships are qualitatively similar across spatial scales (Karr et al. 2015). Similar multiscale analysis of these relationships is currently lacking for the Indian Ocean; due to important structural and functional differences

between the Caribbean and Indian Ocean (Roff and Mumby 2012), the relevance of large-scale relationships to small-scale management focused on local fishing effects needs to be assessed independently for each region.

In Seychelles, the fisheries sector is critically important for food and revenue. A considerable proportion of the artisanal multispecies, multigear inshore fishery is supported by coral reef habitats of the inner granitic islands (SFA 2014). Fishers on small outboard-powered coastal vessels deploy gears such as handlines, traps, and gillnets, targeting a broad range of reef-associated species (SFA 2009). The fringing reefs were extensively disturbed in 1998 when elevated water temperatures resulted in coral bleaching and a loss of >90% live coral cover (Wilkinson 2000). Subsequently, some reefs have shown signs of recovery, whereas other areas are shifting to an algal-dominated state resulting in large habitat differences among sites (Chong-Seng et al. 2012, Graham et al. 2015). Fisheries-dependent data are collected but their usefulness in supporting

management is limited by their low resolution and poor representation of the spatial distribution in fishing pressure (SFA 2009, Daw et al. 2011). This paucity of data seriously undermines fisheries management for reef-associated fish species. Fisheries-independent data are available for Seychelles, characterizing both fish and benthic communities (Graham et al. 2015). Thus, in the absence of fisheries-dependent data, we were interested in examining how state indicators important to the resource potential of the fishery respond to fishing pressure and differences in habitat condition. This knowledge will aid in the understanding of functional relationships between the indicators and habitat or fishing pressure, and highlight potential reference points for management action.

Specific objectives of the study were to (1) examine the specificity of indicators that characterize fish community attributes; (2) determine functional relationships between these indicators and the benthic environment or fishing pressure; and (3) evaluate how local-scale Seychelles specific relationships between fishing pressure and the indicators correspond to large-scale published relationships for the Indian Ocean region.

Materials and Methods

Study sites

The study encompassed 21 sites on the fringing reef of the inner Seychelles (Fig. 1). Nine of the sites were located in no-take areas, although levels of compliance for these marine reserves varied among sites (Appendix S1: Table S1). Seven of the sites were located on granitic reefs, whereas the remaining 14 sites were on carbonate-based reefs.

Field methods

Fish and benthic communities were surveyed on the reef slope at each site in 2014. Fish abundance and individual body length (to the nearest cm) of diurnally active noncryptic species of 10 cm in length or larger were estimated in eight replicate survey areas (7 m radius; 154 m^2 per count) located in 4.5–9.5 m depth at each site, using instantaneous underwater visual census (UVC). Larger, mobile species were recorded before smaller, more site-attached

species to minimize bias caused by diver effects. The accuracy of fish body length estimations were assessed daily using sections of PVC pipe prior to the start of data collection, and length estimates were consistently within 9% of actual lengths. On completion of each UVC replicate, the percent cover of different benthic components (e.g., macroalgae and hard coral) were estimated using a 10-m line intercept transect. The structural complexity of the reef (six-point visual scale) was also recorded (Wilson et al. 2007). Individual body mass was estimated from body length using published length–mass relationships (Froese and Pauly 2012).

Indicator estimation

To assess spatial variation in the potential impacts of fishing and habitat on these communities, we selected a short list of ecological indicators from a review of the literature (Nash and Graham 2016). Indicators were selected if they characterized an aspect of the fish community important to the resource potential of the fishery, such as life history traits linked to productivity, or if they were linked to the integrity of ecosystem functioning such as fish functional richness. The chosen indicators needed to be measurable based on the available UVC data. The indicators were assigned to one of three groups: (1) size, (2) functional, and (3) life history-based indicators (Table 1). The UVC data were used to estimate these indicators and that of fish biomass at the site level by averaging values across point counts at each site (indicator equations provided in Table 1). It should be noted that the UVC method undersamples cryptic species, and therefore the indicator estimates did not account for changes in these species in space.

Data analysis

To assess the relative effects of fishing and the habitat on spatial trends in the indicators, we modeled indicator values as a function of fish biomass and benthic composition. We used fishable biomass (all fish ≥10 cm in length) as a proxy of fishing pressure, where low fish biomass represents high fishing pressure and vice versa. This provides a conservative estimate of the weight of fish available to fishers, is a level that has been widely applied to multigear

Table 1. Equations for estimating indicators and the fishing pressure proxy: (A) size, (B) functional and (C) life history-based indicators, and (D) fishable biomass.

Indicator	Estimation	Example references
(A) Size-based indicators		
Mean size	$(\sum L)/N$	Dulvy et al. (2004)
Mean maximum size (Lmax)	$\sum_i^S (\text{Lmax}_i \times N_i)/\sum_i^S N_i$	McClanahan et al. (2015)
Proportion large fish	$(N > 30\ \text{cm})/N$	Guillemot et al. (2014)
Ratio of mean size to max size	$\sum_i^S N_i \times (\bar{L}_i/\text{Lmax}_i)/\sum_i^S N_i$	Dulvy et al. (2004)
Ratio of mean size to size at maturity	$\sum_i^S N_i \times (\bar{L}_i/\text{Lmat}_i)/\sum_i^S N_i$	Babcock et al. (2013)
Size spectra slope†	$\text{Log}(N) \sim \text{Log}(L)$	Graham et al. (2005)
(B) Function-based indicators		
Functional richness	No. FG	Micheli et al. (2014)
Functional diversity	$-\sum_i^{\text{FG}} p_i \ln p_i$	Micheli et al. (2014)
Piscivores as proportion of community	B_{Pisc}/B	McClanahan et al. (2015)
Herbivores as proportion of community	B_{Herb}/B	McClanahan et al. (2011)
Ratio of piscivore to herbivore biomass	$B_{\text{Pisc}}/B_{\text{Herb}}$	Arias-Gonzalez (1998)
(C) Life history-based indicators		
Mean growth rate (k)	$\sum_i^S (k_i \times N_i)/\sum_i^S N_i$	McClanahan and Humphries (2012)
Mean natural mortality (M)	$\sum_i^S (M_i \times N_i)/\sum_i^S N_i$	McClanahan et al. (2015)
Mean lifespan (tmax)	$\sum_i^S (\text{tmax}_i \times N_i)/\sum_i^S N_i$	Taylor et al. (2014)
Mean generation time (G)	$\sum_i^S (G_i \times N_i)/\sum_i^S N_i$	McClanahan and Humphries (2012)
Mean age at maturity (tmat)	$\sum_i^S (\text{tmat}_i \times N_i)/\sum_i^S N_i$	Taylor et al. (2014)
Mean length to achieve optimum yield (Lopt)	$\sum_i^S (\text{Lopt}_i \times N_i)/\sum_i^S N_i$	McClanahan and Humphries (2012)
Mean trophic level (TL)	$\sum_i^S (TL_i \times N_i)/\sum_i^S N_i$	McClanahan and Humphries (2012)
(D) Fishable biomass (proxy of fishing pressure)		
Biomass per unit area	$(\sum_i^S B_i)/A$	Jennings et al. (1995)

Notes: L is fish body length in cm; N is total fish abundance; i is species i; S is number of species; Lmax is maximum length from literature; Lmat is length at maturity from literature; B is biomass; FG is functional group; p is proportion of total individuals in functional group i; k is von Bertalanffy growth parameter; A is area. Values were estimated for each point count and then the mean taken across counts.

† Normalize data by dividing density in size class by width of size class.

reef fisheries (following McClanahan et al. 2011, 2015), and has been shown to be a sensitive indicator to a range of metrics of fishing pressure (Cinner et al. 2009, 2013). Principle component analysis (PCA) was used to condense the benthic variables (different types of coral cover, algae cover, and structural complexity) into two PCA axis variables for use in later analyses. PC1, which explained 44% of the variation among sites, represented a gradient from high macroalgal cover (negative values) to high structural complexity (positive values; Appendix S1: Fig. S2). PC2, which explained 31% of the variation among sites, represented a gradient from high massive and branching coral cover (negative values) to high encrusting and tabular coral cover (positive values). Sites were located in two habitat types: granitic reefs and carbonate reefs. These habitat differences were captured by the PCA of the benthic variables, particularly PC2 where granitic sites are characterized by encrusting and tabulate corals (Wilson et al.

2012*b*, Harris et al. 2014). Hence, we did not include habitat type as a separate variable in the analyses. Furthermore, since the 1998 bleaching event, some sites have degraded over time, becoming dominated by macroalgae (regime-shifted), whereas other sites have recovered to being coral-dominated (recovering) (Graham et al. 2015). The state of the reef (regime-shifted vs. recovering) was collinear with PC1, and therefore reef state was not included in the models as an additional explanatory variable.

Generalized additive models (GAM) were fitted to evaluate the relative effects of fishing (fish biomass—Bm) and the benthos (PC1 and PC2) on the indicators (mgcv package in R; Wood 2011). All possible models within the global model ($\sim s$(Biomass, $k = 3$) + s(PC1, $k = 3$) + s(PC2, $k = 3$)) were compared using Akaike information criteria adjusted for small sample sizes (AICc), for each indicator (MuMIn package in R; Barton 2013). The number of knots for each smoother were set at 3 ($k = 3$) to allow for nonlinear relationships but prevent overfitting (Zuur et al. 2009). Model averaging was used to estimate coefficients for each explanatory variable, and to explore their relative importance, AICc weights were summed across all models incorporating each explanatory variable. All models with substantial support (< 2 AICc units of the best model; Burnham and Anderson 2002), and those variables contributing to over 0.5 of AICc weights are highlighted. The assumptions of the models were assessed by examining residual plots, and transformations made where appropriate (Table 2). Where examination of the data suggested potentially influential outliers in a model, the analysis was repeated including and excluding the outlier.

We visually compared local-scale relationships (Seychelles) between fish biomass and the indicators with the corresponding, preidentified relationships estimated for the Western Indian Ocean region (McClanahan et al. 2011, 2015). Next, we overlaid independently collected Seychelles values for the indicators on the relevant fitted relationships provided by McClanahan et al. (2011, 2015). We compared the distribution of these values in relation to thresholds in the different relationships identified by McClanahan et al. (2011, 2015) and McClanahan et al.'s (2011) proposed biomass-based maximum sustainable yield (B_{MMSY}) for coral reefs.

RESULTS

Indicator specificity

Specificity among indicators varied considerably such that some highlight differences in habitat and others respond more strongly to fishing impacts (Fig. 2; Appendix S1). Some size (maximum size, the ratios between mean size and maximum size, and mean size and size at maturity), function (functional diversity, the proportion of herbivores, and piscivore to herbivore ratio), and life history (length to achieve optimal yield and trophic level)-based indicators were predominantly influenced by benthic differences among reefs (Table 2; Fig. 3; Appendix S1: Figs. S3–S5). This effect was largely driven by the gradient from high macroalgae and low structural complexity to low macroalgae and high complexity, rather than differences in coral life form composition among sites (as evidenced by greater summed AICc weights for PC1 in Fig. 3). In contrast, the proportion of large fish, slope of the size spectrum, and growth rate were more influenced by fishing pressure (Table 2; Fig. 3; Appendix S1: Figs. S3 and S5). Mean size of fish in the community and functional richness were affected by both fishing pressure and the benthic condition (Table 2; Fig. 3; Appendix S1: Figs. S3 and S4).

Functional relationships

When considering the influence of the explanatory variables on the different indicators (only those variables where the summed AICc weight across models was >0.5), the majority of the relationships between the indicators and PC1 were nonlinear, with a decline in the rate of change in indicator values at moderate to high values of structural complexity (Fig. 4). In contrast, three of the four relationships between the indicators and PC2 were positive and linear (Fig. 5). The relationships between fish biomass and the indicators exhibited a range of forms, including linear and unimodal (Fig. 6).

Scale-specific relationships

The relationships between biomass and the different indicators for Seychelles contrasted with those found at the broader spatial scale of the Western Indian Ocean. The large-scale relationships were all nonlinear, with inflexions commonly found at biomass values below those
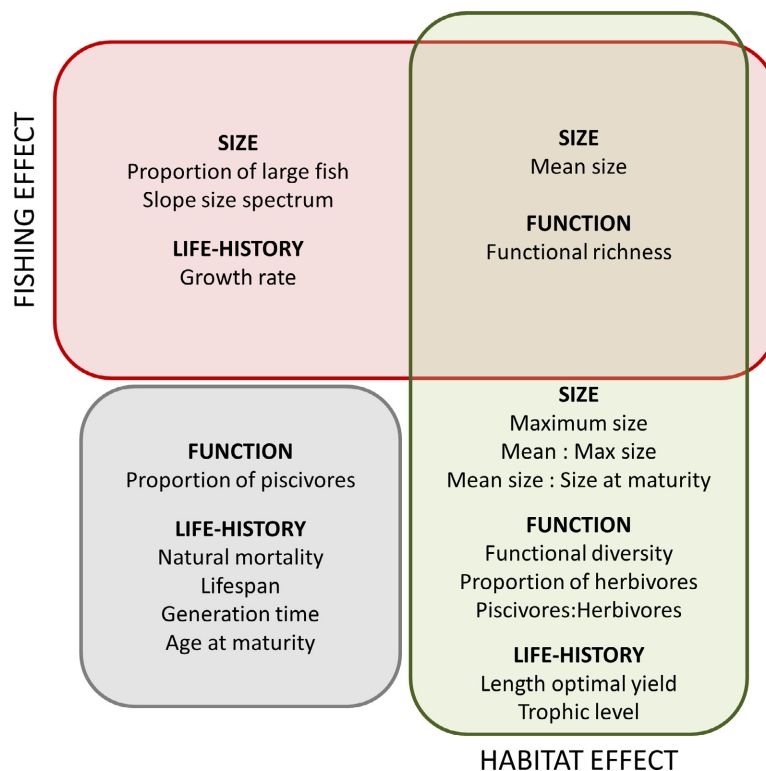
Fig. 2. Specificity of different indicators to fishing pressure or benthic effects (summed AICc weights >0.5). Indicators in gray-shaded box were not strongly related to either fishing or benthic drivers (summed AICc weights <0.5).

observed in the Seychelles (fitted lines Fig. 7). Many of the relationships found between indicators and fish biomass at the Indian Ocean scale were not well supported in the Seychelles modeling framework with the null model (natural mortality, lifespan, generation time, and age at maturity) performing better or the benthic variables (maximum length and proportion of herbivores) showing a stronger influence on indicator values (Table 2, Fig. 7). Where relationships between indicators and fish biomass were supported by model selection at both scales (growth rate), these relationships took different forms (unimodal at Seychelles scale vs. nonlinear decline at Indian Ocean scale; Figs. 6 and 7).

Overlaying the data from Seychelles on the Indian Ocean relationships showed that the fish biomass at Seychelles sites stretches from low to moderate levels compared to Indian Ocean data (Fig. 7). These Seychelles values are well below the unexploited biomass for coral reefs estimated by McClanahan et al. (2011) based on unfished

and long-protected areas from the Indo-Pacific region: $B_0 = 1200$ kg/ha ± 110 95%CI. Nonetheless, most sites have a fish biomass within or greater than the multispecies maximum sustainable yield ($B_{MMSY} = 300 \pm 28$–600 ± 54 kg/ha) proposed by McClanahan et al. (2011). For the life history traits, most of the Seychelles sites sit either below (maximum length, lifespan, generation time, and age at maturity) or above (growth rate and natural mortality) the fitted lines identified by McClanahan et al. (2015) (Fig. 7). Thus, although the Seychelles biomass values generally sit above the inflexion points (to the right on x axis— greater fish biomass) for the large-scale, Indian Ocean fitted relationships, the Seychelles data correspond to values of the indicators commonly found at much lower fish biomass (greater fishing pressure) across the Indian Ocean. In other words, the levels of fish biomass in Seychelles are usually associated with communities comprising larger, slower growing species than the smaller, faster growing species observed in Seychelles.

Table 2. Model selection comparing the relative influence of the benthos (PC1 and PC2, see Appendix S1: Fig. S2) and fishing pressure (fish biomass (Bm) as proxy) on different indicators.

Variable	Bm	R^2	df	AICc	ΔAICc	AICcWt
Mean size	Bm + PC2	0.65	4.00	72.90	0.00	0.72
Maximum size	PC1	0.28	3.53	136.99	0.00	0.41
	Bm + PC1	0.40	5.14	138.95	1.95	0.16
Prop. large fish	Bm	0.25	3.60	−11.67	0.00	0.35
	Bm + PC2	0.32	4.61	−10.11	1.57	0.16
	Null	0.00	2.00	−10.06	1.61	0.16
	PC2	0.11	3.00	−9.74	1.94	0.13
Mean: max size†	PC1	0.34	3.00	−83.31	0.00	0.47
	PC1 + PC2	0.44	4.43	−82.46	0.85	0.31
Mean size: size at maturity†	PC1 + PC2	0.56	4.99	12.44	0.00	0.56
	PC1	0.34	3.00	14.22	1.78	0.23
Slope size spectrum‡	Bm	0.49	3.75	−57.99	0.00	0.46
	Bm + PC2	0.55	4.77	−57.46	0.53	0.35
Functional richness	Bm + PC1	0.69	4.00	41.15	0.00	0.70
Functional diversity	PC1	0.65	3.00	−25.79	0.00	0.41
	Bm + PC1	0.73	4.57	−25.67	0.13	0.39
Proportion of biomass-piscivores‡	Null	0.00	2.00	12.47	0.00	0.24
	PC1 + PC2	0.41	5.47	12.60	0.13	0.23
	Bm	0.19	3.73	12.97	0.49	0.19
	PC1	0.17	3.74	13.62	1.15	0.14
Prop. of biomass-herbivores	Bm	0.44	3.86	−22.06	0.00	0.56
Prop. of biomass-herbivores no outlier	PC2	0.28	3.00	−36.19	0.00	0.59
Piscivore:herbivore‡	PC1 + PC2	0.47	5.54	31.12	0.00	0.33
	Bm	0.26	3.75	31.67	0.55	0.25
	Null	0.00	2.00	33.01	1.89	0.13
Growth rate	Bm	0.27	3.86	−45.70	0.00	0.36
	Null	0.00	2.00	−44.41	1.29	0.19
	Bm + PC2	0.32	4.86	−43.78	1.91	0.14
Natural mortality	Bm	0.25	3.84	−18.43	0.00	0.24
	PC1	0.21	3.73	−17.85	0.59	0.18
	Null	0.00	2.00	−17.75	0.69	0.17
	Bm + PC2	0.33	4.85	−17.43	1.00	0.14
	Bm + PC1	0.38	5.45	−16.73	1.71	0.10
	PC2	0.08	3.00	−16.71	1.72	0.10
Natural mortality no outlier	Null	0.00	2.00	−20.07	0.00	0.28
	PC2	0.12	3.00	−19.54	0.53	0.21
	Bm	0.09	3.00	−19.10	0.97	0.17
	PC1	0.20	3.77	−19.07	0.99	0.17
Lifespan	Null	0.00	2.00	60.01	0.00	0.35
	Bm	0.19	3.76	60.67	0.66	0.25
Generation time	Null	0.00	2.00	6.90	0.00	0.35
	Bm	0.18	3.76	7.69	0.79	0.23
Age at maturity§	Null	0.00	2.00	−47.03	0.00	0.36
	Bm	0.16	3.69	−45.76	1.26	0.19
	PC1	0.12	3.61	−45.17	1.86	0.14
Length optimal yield	PC1	0.31	3.63	112.51	0.00	0.36
	Bm + PC1	0.44	5.24	113.71	1.20	0.20
	PC1 + PC2	0.31	4.00	113.91	1.40	0.18
Trophic level	Bm	0.38	3.90	−13.22	0.00	0.33
	Bm + PC2	0.54	5.72	−13.11	0.11	0.31
	Bm + PC1	0.43	4.91	−11.71	1.51	0.16

Table 2. Continued.

Variable	Bm	R^2	df	AICc	ΔAICc	AICcWt
Trophic level no outlier	PC1 + PC2	0.48	4.43	−19.09	0.00	0.31
	PC2	0.38	3.64	−18.69	0.40	0.25
	Bm + PC2	0.44	4.48	−17.45	1.64	0.14
	PC1	0.25	3.00	−17.40	1.69	0.13

Notes: Generalized additive models were used (mgcv package in R). The number of knots was set to 3 to allow for nonlinear relationships but avoid overfitting. † Fourth power transformation; ‡ log10 transformation; § square root transformation. Only those models within 2 AICc units of the best model are shown (see Appendix S1: Table S2 for all models).
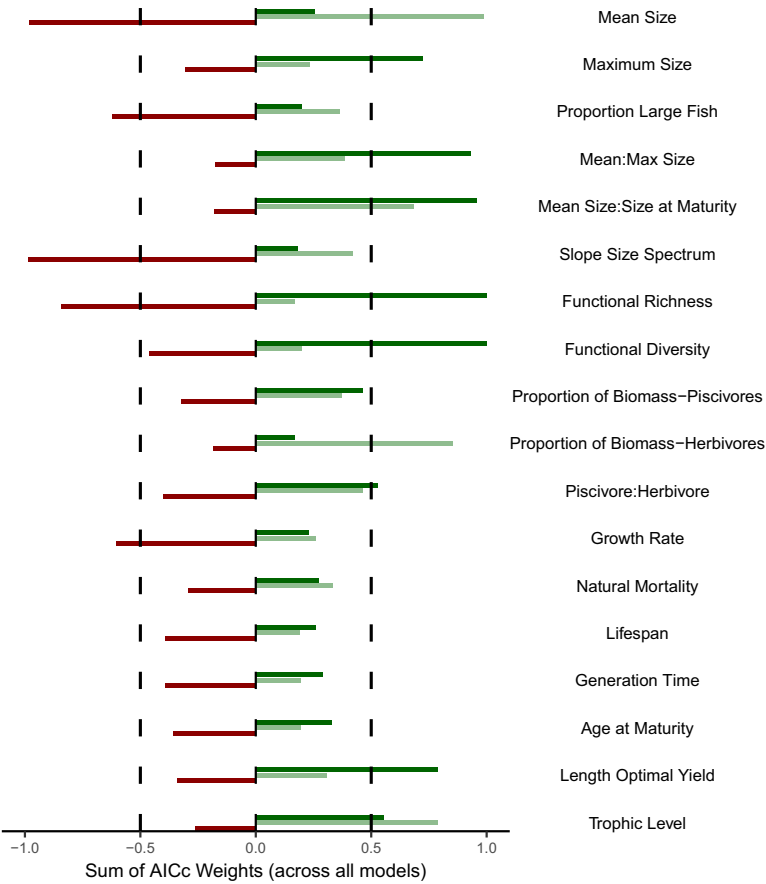
Fig. 3. Relative importance of fishing and habitat effects on the different indicators based on the sum of AICc weights across all models incorporating each explanatory variable. Color of bars represents different variables: dark green—macroalgae to structural complexity gradient (PC1), light green—coral life form (PC2), red—fishable biomass. Dashed lines represent summed AICc weights of 0.5.

Discussion

Management efforts need to be strengthened to address issues of sustainability in coral reef fisheries (Newton et al. 2007, Johnson et al. 2013, MacNeil et al. 2015). Ecological indicators that are incorporated into pressure-state-response frameworks can help support fisheries management. The usefulness of indicators in this context is dependent on our understanding of how they respond to fishing and other drivers, and on characterizing the functional relationship
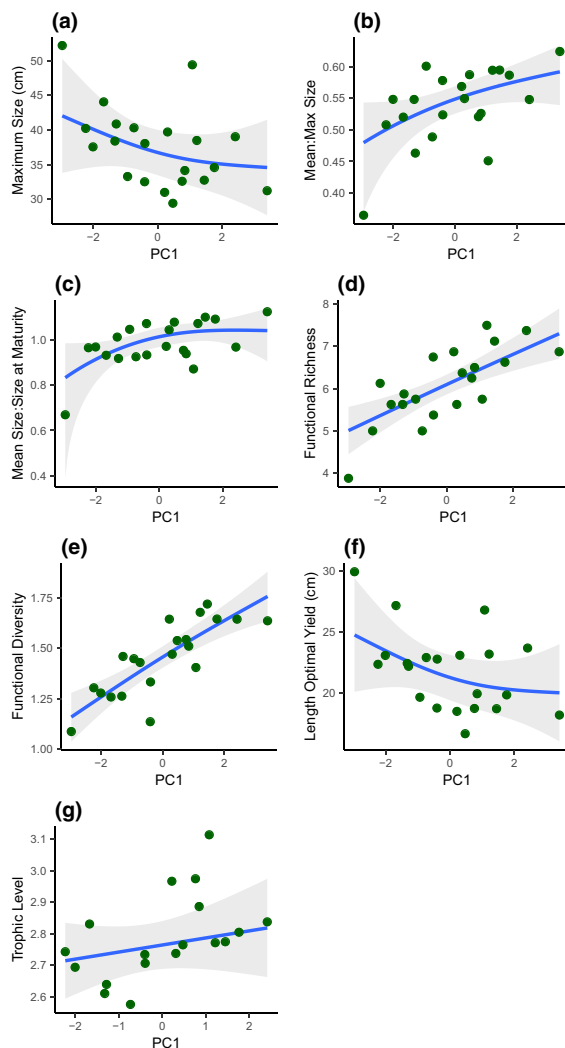
Fig. 4. Influence of benthic condition (PC1) on different fisheries indicators: (a) Maximum size; (b) Ratio of mean to maximum size; (c) Ratio of mean size to size at maturity; (d) Functional richness; (e) Functional diversity; (f) Length to achieve optimal yield; (g) Trophic level. Fitted lines are partial effects estimated using model averaging, shaded areas are 95% confidence intervals for fitted lines, and circles represent raw data. High levels of macroalgal cover and low structural complexity are found at negative values of PC1, whereas low macroalgal cover and high complexity characterize sites at positive values of PC1. Only those relationships where PC1 had a summed AICc weight of >0.5 are shown.
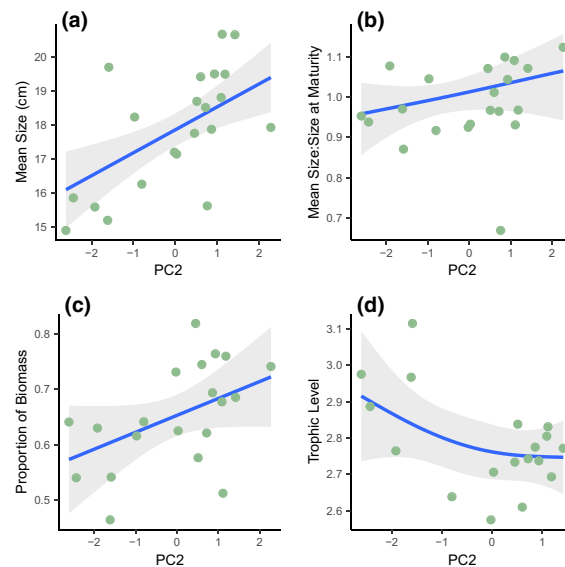

Fig. 5. Influence of benthic condition (PC2) on different fisheries indicators: (a) Mean size; (b) Ratio of mean size to size at maturity; (c) Herbivores as proportion of total fish biomass; (d) Trophic level. Fitted lines are partial effects estimated using model averaging, shaded areas are 95% confidence intervals for fitted lines, and circles represent raw data. High cover of branching and massive corals is found at negative values of PC2, whereas high encrusting and tabular coral cover characterize sites at positive values of PC2. Only those relationships where PC2 had a summed AICc weight of >0.5 are shown.

between state and driver, including the identification of thresholds or nonlinearities. Our study highlights the specific and important impacts of benthic condition on a range of fisheries indicators, and builds knowledge on scale-specific differences in these state–driver relationships.

Indicator specificity

Fishing is expected to drive changes in size, function and life history-based community indicators. Fishers may preferentially target larger individuals and large species are often more vulnerable to a given level of fishing pressure due to low rates of population increase (Jennings et al. 1998, Pauly et al. 1998). This has clear implications for life history indicators due to the correlation between many life history traits and size (Abesamis et al. 2014). There is also evidence for fishing driving a decline in the trophic level of fish communities (Pauly et al. 1998). We found strong effects of both habitat and fishing pressure on the community
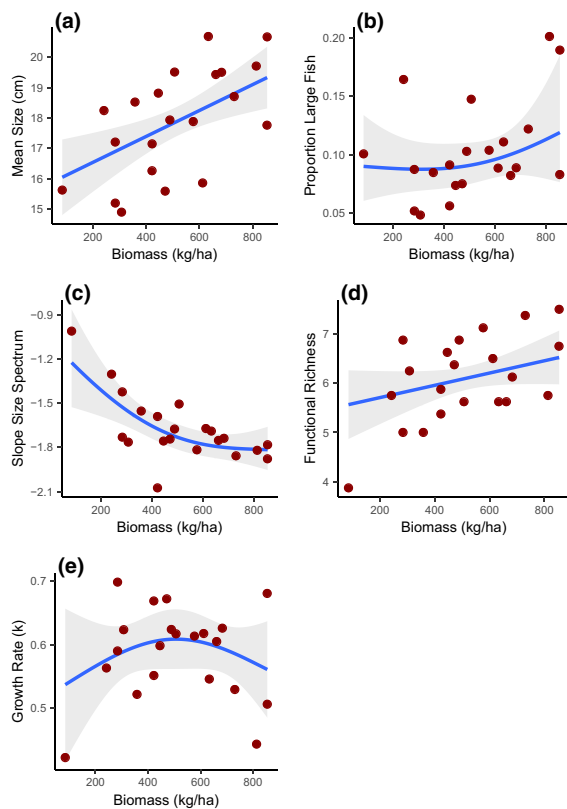
Fig. 6. Influence of fishing pressure (fish biomass as proxy) on different fisheries indicators: (a) Mean size; (b) Proportion of large fish; (c) Slope of size spectrum; (d) Functional richness; (e) Growth rate. Fitted lines are partial effects estimated using model averaging, shaded areas are 95% confidence intervals for fitted lines, and circles represent raw data. Only those relationships where fish biomass had a summed AICc weight of >0.5 are shown.
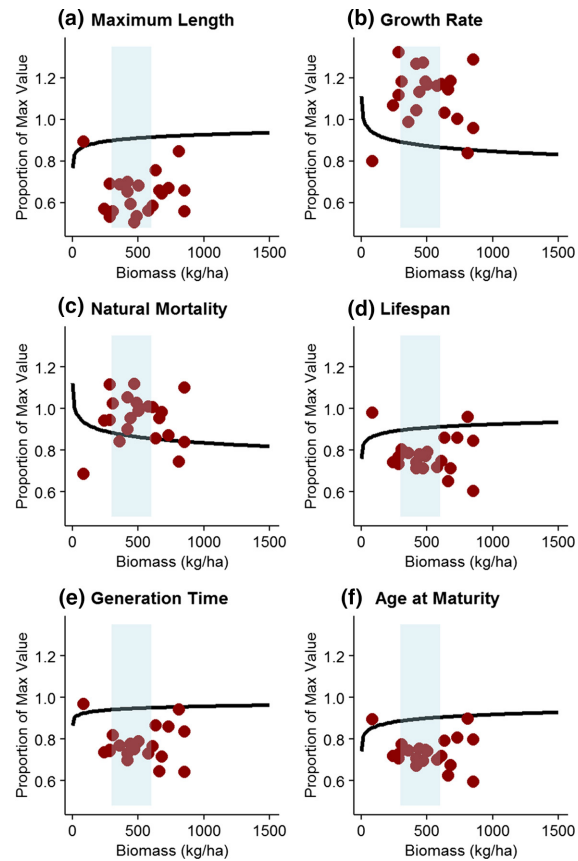

Fig. 7. Large-scale relationship between fishing pressure and the different fisheries indicators. Fitted lines represent relationships for data sourced from nine countries across the western Indian Ocean (McClanahan et al. 2011, 2015). Symbols represent data for the 21 sites in Seychelles in 2014. Shaded areas represent biomass-based multispecies maximum sustainable yield (B_{MMSY}; McClanahan et al. 2011).

indicators. However, many of the indicators were related to habitat effects rather than fishing, e.g., ratio of mean to maximum size and trophic level. These results may stem from the high diversity and heterogeneity of coral reef ecosystems, and the multigear, multispecies nature of reef fisheries, which give rise to complex, indirect relationships (Hixon 1991, Yodzis 2000, Worm and Branch 2012), and the tight coupling between habitat and fish communities found in coral reef systems (Graham and Nash 2013). Furthermore, Seychelles reefs are characterized by both a comparatively narrow gradient in fishing pressure, and large habitat differences due to site-specific variation

in recovery postdisturbance (PC1 and PC2) and differences in the underlying substrate, i.e., granitic vs. carbonate reefs (PC2). Thus, the effect of fishing on the indicators may be relatively more difficult to identify compared to other locations. A component of the habitat differences we observed among sites in Seychelles may be linked to the relative depth of the reef slopes at the different locations (Graham et al. 2015). Monitoring programs typically try to remove such differences by standardizing environmental conditions where they survey, e.g., zone and wave exposure (Sweatman et al. 2008). But, with increasing

coral reef degradation (Hoegh-Guldberg et al. 2007, Alvarez-Filip et al. 2009), it is inevitable that long-term monitoring programs will encounter fundamental changes in the benthos that are likely to have profound effects on fish. These changes will also influence many of the indicators that have been used to assess the effects of fishing and it is therefore imperative that habitat be incorporated into surveys and analyses of indicators (Miller and Russ 2014, Nash and Graham 2016).

An understanding of how different drivers affect fish communities provides managers with the capacity to implement a diverse array of complementary management actions targeting these drivers. Two examples of this potential for complementarity were highlighted in our size and life history-based indicators. In terms of size-based indicators, we found that benthic habitat, particularly macroalgal cover and structural complexity had a significant effect on the ratio of mean size to size at maturity of reef fish; mean size was greater than size at maturity for reefs with high structural complexity, but smaller than size at maturity for reefs with high macroalgal cover. Thus, by supporting reef accretion and a diversity of herbivores, managers may help ensure that fish have greater probability of reproducing prior to being caught (Froese 2004, Babcock et al. 2013). In contrast, fishing pressure was a key driver of the proportion of large fish, with a greater proportion at sites with low fishing pressure (high biomass) compared with high fishing pressure (low biomass). Thus, if management objectives are focused on the capacity to catch large individuals, fishing controls such as effort limitation or size limits may be appropriate (Pope 2009).

In terms of life history-based indicators, similar targeted management actions can be used to drive changes in different traits contributing to fish community productivity. We found that reefs with high structural complexity have fish communities with a lower mean length to achieve optimal yield. Thus, restrictions on destructive fishing gears that reduce structural complexity could support fishery yields (Rogers et al. 2014), although the benefits of this will depend on the relationship between the length to achieve optimal yield and mean length at maturity, and the prevalence of destructive gears, which are not

common in Seychelles fisheries. Moreover, the appropriateness of supporting a low length to achieve optimal yield will depend on the relative desirability of high productivity vs. the potentially lower value of smaller, fast growing fish. A further consideration is that some valuable fishery species may recruit to macroalgal areas (Wilson et al. 2010, Evans et al. 2014) and a combination of habitat types may be best. In contrast, the unimodal relationship between fish biomass and growth rate implies that a greater fish community mean growth rate will be supported by strategies aimed at fishing biomass down to moderate levels.

The selection of a specific management action and criteria to determine when to implement the action will rely on a priori defined management objectives and knowledge of how the action impacts fishing pressure or the habitat (Jennings 2005). Nonetheless, knowledge of indicator specificity, in this case the relative effects of habitat and fishing pressure, has the potential to give managers considerable power to develop more nuanced management plans. Such an approach complements the increasing desire to focus on ecosystem-based management, where functioning of the broader ecosystem and ecological resilience are considered critical (Francis et al. 2007).

Functional relationships

The shape of the relationships between indicators and both the fishing pressure and benthic habitat were variable for the Seychelles data, i.e., both linear and nonlinear relationships were found. Where nonlinearities were detected, the location of these inflexions may inform biomass-based (e.g., growth rate) targets for managers (Samhouri et al. 2010, McClanahan et al. 2015). Nonetheless, this variability suggests that, at the Seychelles scale, there is a need for an in-depth exploration of the different ecological trade-offs associated with setting specific biomass target or limit reference points to guide management (Samhouri et al. 2012).

The findings address gaps in our understanding of the range of values over which an indicator is most useful in the monitoring context (Jennings and Kaiser 1998, Tallis et al. 2010). An evaluation of a particular management action may show limited effectiveness if these actions are implemented

across a range of fishing pressures that prompt little change in indicator values (Appendix S1: Fig. S1b; Jennings and Kaiser 1998). For example, our results suggest that, at the Seychelles scale, the slope of the size spectrum does not vary from moderate to high levels of fish biomass, but becomes more negative from low to moderate levels of fish biomass. Thus, the slope of the size spectrum is likely to be a more effective indicator of fishing pressure at high levels of exploitation (low biomass). In contrast, a number of the other Seychelles relationships were linear, suggesting that these indicators may be useful across the full range of fishing pressures found around the islands.

Scale-specific relationships

There were large differences in the fitted relationships between the indicators and fishable biomass at local (Seychelles) and broad (ocean) scales. This contrasts with findings from the Caribbean where qualitatively similar relationships were found at local and regional scales (Karr et al. 2015). Comparison of fish biomass at Seychelles sites with those from the broader Indian Ocean suggests that Seychelles reefs are subject to a relatively narrow range of fishing intensities. The apparent functional relationship between drivers and state indicators may vary with the breadth of the fishing gradient (Appendix S1: Fig. S1c), thus, the small localized fishing gradient may explain these scale-specific differences. Similarly, Seychelles sites are characterized by extensive benthic variability in space and time (Chong-Seng et al. 2012). Locations characterized by less heterogeneous habitats may show a more limited influence of the benthos on indicator values. These results underline the importance of quantifying fishing and habitat gradients and explicitly accounting for scale to ensure indicator trends are interpreted appropriately (Jennings et al. 1995, Appeldoorn 2008).

The overlay of Seychelles data on the Indian Ocean relationships suggests fishing is sustainable at most sites because biomass values are generally within or above the range of B_{MMSY} proposed by McClanahan et al. (2011). The sustainability of Seychelles fisheries may be due to the targeting of high productivity species such as rabbitfishes (Grandcourt 1999, SFA 2009), and the presence of less fished offshore reefs outside

our survey area, which may act as larval sources to more heavily fished inshore reefs (Daw et al. 2011). Furthermore, Seychelles fish biomass values were generally above inflexion points, where small increases in fishing pressure are likely to have significant detrimental effects on aspects of the fish community important for productivity or ecosystem function (McClanahan et al. 2011, 2015). However, values of certain life history indicators may be cause for concern as Seychelles values were similar to those found at sites exposed to much higher levels of fishing pressure (lower fish biomass) in the analyses by McClanahan et al. (2011, 2015). This may be driven by the relatively larger proportion of herbivorous fish found at Seychelles sites compared with the broader Indian Ocean. These herbivorous species often exhibit life history traits associated with high productivity (Abesamis et al. 2014), and potentially explains the lower length to achieve optimal yield found at high complexity sites. Thus, although B_{MMSY} and broad-scale thresholds can provide a useful starting point for setting biomass-based targets, they may mask important changes occurring at smaller scales or at finer resolution within the fish community.

Selection of fishing pressure proxies and ecological indicators

We used fish biomass as a proxy of fishing pressure because it has been shown to reflect a range of metrics of fishing pressure (Cinner et al. 2009, 2013), and although catch and effort data are collected for the small boat fishery in Seychelles, they are not readily disaggregated to represent the spatial distribution of fishing pressure (SFA 2009, Daw et al. 2011). However, due to the calculation of fish biomass from UVC abundance and size data, caution is needed when interpreting the relationships between the size indicators and fish biomass. For example, fish biomass is disproportionately driven by large individuals, thus we would expect the strong relationship found between fish biomass and the proportion of large fish, and the apparent influence of fishing pressure on the presence of large fish needs to be viewed conservatively. Interestingly, despite the overlap in the data used to estimate fish biomass and the size-based indicators, there were stronger

relationships between these indicators and the habitat variables. Nonetheless, quantification of fishing pressure using effort, catch data or access to markets is desirable where such information is available (Cinner et al. 2013). Further research is now needed to assess specificity patterns for state indicators using a broader range of these fishing pressure metrics.

We examined a wide range of indicators in this study to provide a detailed exploration of specificity, functional relationships, and scale-specific patterns in state indicators. Many of these indicators are closely linked, e.g., due to collinearity between size and other life history traits (Abesamis et al. 2014), or due to their estimation from overlapping information, such as those characterizing functional aspects of the fish community (Table 1). Thus, it is not surprising that there were similar outcomes among certain sets of indicators, for example, a strong positive relationship between PC1 and both functional richness and functional diversity. Consequently, we are not advocating estimating such a wide range of indicators within a particular fisheries monitoring program, rather distinct suites of indicators might be selected for specific contexts (Rice and Rochet 2005). But, knowledge of indicator specificity and scale-dependent responses for a broad range of indicators will underpin the informed selection of indicators with respect to specific management objectives and logistical constraints (e.g., limited data or manpower; Newson et al. 2009).

Conclusions

Human-mediated disturbances are causing significant changes to reef communities through impacts such as elevated water temperatures and overfishing (Hughes 1994, Gardner et al. 2003). Teasing apart fishing effects from the influence of other drivers is likely to become progressively more complex as impacts increase (Jennings and Kaiser 1998), and driver–state relationships are likely to evolve as ecosystems take on different configurations (Samhouri et al. 2010). For example, the reefs of Seychelles currently exhibit a wide range of habitat types, stretching from structurally complex coral-dominated environments to flatter, macroalgal-dominated reefs (Graham et al. 2015). This diversity may decline if reefs continue to degrade

to low complexity environments (Alvarez-Filip et al. 2009). In contrast, in other areas, habitat heterogeneity may increase as reefs exhibit differential responses to disturbance (Obura 2005). Similarly, the effect of fishing on state indicators is likely to evolve in response to increased human demands and changes in what and how we extract fishery resources from the ocean (Watson et al. 2013, 2015, Zhou et al. 2015). This heterogeneity in driver–state relationships in space and time will require the development of dynamic management strategies that use different relationships in different environmental or exploitation contexts (Samhouri et al. 2010).

We describe the functional relationships between drivers and state indicators, highlighting thresholds and the importance of scale. This information is only the first step in developing decision-making criteria to manage a fishery because thresholds and targets identified and defined in this manner do not equate to management targets (Samhouri et al. 2012). Rather an understanding of the how the state–driver relationships vary across scales must be combined with (1) context specific management objectives to set management targets or limits; (2) knowledge of the likely impact of specific management actions to set control rules; and (3) monitoring of how habitat, fish, and management actions change relative to each other to support effective adaptive management (Clua et al. 2005, Jennings 2005, Mangi et al. 2007, Lindenmayer et al. 2013). In this way, management targets can integrate knowledge of ecological thresholds with stakeholder values and levels of acceptable risk (Francis and Shotton 1997, Samhouri et al. 2012).

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1362/supinfo