

# Thresholds in Caribbean coral reefs: implications for ecosystem-based fishery management

Kendra A. Karr<sup>1,2\*</sup>, Rod Fujita<sup>1,3</sup>, Benjamin S. Halpern<sup>4,5,6</sup>, Carrie V. Kappel<sup>4</sup>, Larry Crowder<sup>3</sup>, Kimberly A. Selkoe<sup>4,7</sup>, Pedro M. Alcolado<sup>8</sup> and Doug Rader<sup>9</sup>

<sup>1</sup>Oceans Program, Environmental Defense Fund, 123 Mission Street, 28th Floor, San Francisco, CA 94105, USA;

<sup>2</sup>Ecology and Evolutionary Biology, 100 Shaffer Road, University of California Santa Cruz, Santa Cruz, CA 95064,

USA; <sup>3</sup>Center for Ocean Solutions, Woods Institute for the Environment, Stanford University, 99 Pacific St., Suite

555E, Monterey, CA 93940, USA; <sup>4</sup>National Center for Ecological Analysis and Synthesis, 735 State St. Suite 300,

Santa Barbara, CA 93101, USA; <sup>5</sup>Bren School of Environmental Science and Management, University of California,

Santa Barbara, CA 93016, USA; <sup>6</sup>Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY,

UK; <sup>7</sup>Hawaii Institute of Marine Biology, University of Hawai'i, Kane'ohe, HI 97644, USA; <sup>8</sup>Instituto de Oceanología,

Calle 1ra. E No. 18406, Playa, Ciudad Habana, Cuba; and <sup>9</sup>Oceans Program, Environmental Defense Fund, 4000

Westchase Blvd., Suite 510, Raleigh, NC 27607, USA

## Summary

1. Ecosystem-based management of coral reef fisheries aims to sustainably deliver a diverse portfolio of ecosystem services. This goal can be undermined if the ecosystem shifts into a different state, with altered ecosystem functions and benefits to people. If levels of drivers that cause transitions between states are identified, management measures could be aimed at maintaining drivers below these levels to avoid ecosystem shifts.

2. Analysing data from a large number of Caribbean coral reefs ( $N = 2001$ ), suites of non-linear thresholds were identified between metrics of coral reef processes and structure along a gradient of total fish biomass (a proxy for fishing pressure). Several metrics (macroalgal cover, invertivorous fishes and fish species richness) associated with coral-dominated reefs exhibited thresholds at relatively high fish biomass levels (50–88% of unfished biomass). Other metrics (urchin biomass, ratio of macroalgal to coral cover, herbivorous fishes and coral cover) showed thresholds at lower fish biomass levels (28–37% of unfished biomass).

3. Ratios of total fish biomass in fishing areas to closed areas (unfished biomass) in the Caribbean indicate that reefs may generally be at risk for change at ratios between 0.5 (coral dominated) and 0.3 (macroalgal dominated). Similar relationships were found for coral reefs in the Indian Ocean. While these results illustrate thresholds at the scale of the entire Caribbean, assessing local reefs is advisable because biomass levels vary within the region, and reef trajectories depend on past, present and future local conditions.

4. *Synthesis and applications.* If the thresholds in this study are generalizable to scales relevant to management, it may be possible to produce sustainable yield while simultaneously maintaining coral-dominated reefs by restricting fishing mortality to levels that result in biomass ratios near 0.5. Fishing down to biomass ratios near 0.3 may increase the risk of overfishing (resulting in lower long-term yields) and transition to macroalgal-dominated reefs. Thresholds offer a simple and powerful way for managers to operationalize precautionary ecosystem-based fishery management by adaptively limiting fishing pressure in order to (i) maintain desirable coral reef conditions, (ii) establish a system-specific target for generating pretty good yield and (iii) maintain sustainable multi-species fishery yields.

**Key-words:** adaptive management, Caribbean, coral reefs, fisheries, nonlinear, overfishing, resilience, sustainability, thresholds tipping points

\*Correspondence author. E-mail: [kkarr@edf.org](mailto:kkarr@edf.org)

## Introduction

Coral reefs provide many valuable ecosystem services, including seafood, livelihoods, tourism, recreation and biodiversity. Coral-dominated reefs have higher perceived value and produce higher levels of more ecosystem services than states dominated by macroalgae, urchin barrens, soft corals or sponges (Moberg & Folke 1999). Reducing local chronic drivers that degrade reefs and decrease resilience (e.g. Mumby & Steneck 2008; Bellwood, Hoey & Hughes 2012; Graham *et al.* 2013) should help maintain healthy coral reefs, sustaining local ecosystem goods and services.

Coral reefs can exhibit nonlinear changes in ecosystem state (e.g. Bellwood *et al.* 2004; Roff & Mumby 2012; Hughes *et al.* 2013). As such, management ideally should explicitly aim to avoid crossing thresholds that lead to state change (Kelly *et al.* 2015) and control the most important drivers of change on coral reefs. In the case of fisheries, setting reference points for harvest control rules based on empirical thresholds associated with changes in reef structure may help to avoid undesirable ecosystem shifts. The challenge then is to quantify driver levels that correspond to these thresholds (McClanahan *et al.* 2011; Fujita *et al.* 2012; Travis *et al.* 2014).

Fishing is a key driver of ecosystem change because fish regulate key processes that maintain coral reefs in a state of coral dominance. For instance, herbivorous fish exert top-down control of algae and regulate coral–algae competition (Mumby *et al.* 2006; Hughes *et al.* 2007). In other cases, reductions in predatory fish abundance can release other species, which in turn induce state changes in coral reef ecosystems (Ruttenberg *et al.* 2011). While many other factors such as pollution, climate change, disease and habitat degradation also affect coral reef state (Hughes *et al.* 2003, 2013; Bellwood *et al.* 2004), the importance of fish in regulating coral reef ecosystem structure and function is clear (e.g. Mumby *et al.* 2006; Hughes *et al.* 2007; Ruppert *et al.* 2013; Edwards *et al.* 2014).

A recent study by McClanahan *et al.* (2011) in the Indian Ocean found nonlinear relationships between fishable biomass and a suite of reef health metrics (e.g. macroalgae cover, coral cover, ratio of macroalgae to hard coral cover, fish species richness, herbivorous fish, urchin predation and sea urchin biomass) that represent key processes and structure of coral reef ecosystems. Here, we test whether these findings hold for Caribbean coral reefs, which differ dramatically from Indian Ocean coral reefs in their diversity and distribution. If similar quantitative thresholds exist, they could provide guidance for management aimed at lowering the risk of altering important processes and the structure of coral reefs.

## Materials and methods

### GENERAL FRAMEWORK

Rather than using a deterministic model to explore the relationships between ecosystem state and fish biomass, here, we examine

the statistical relationships between fish biomass and several metrics of coral reef status to identify potential thresholds. We define metrics of coral reef ecosystem status in terms of both structure (e.g. community composition) and process (e.g. herbivorous fish and urchin biomass as proxies for grazing pressure). We assessed coral cover, ratio of macroalgae to coral cover, and macroalgae cover as metrics of coral reef structure. We quantified herbivorous fish biomass, urchin biomass, fish species richness and invertivorous fish biomass as metrics of coral reef processes. All metrics were evaluated using methods similar (neither urchin predation or calcifying algae were included in the analyses) to those of McClanahan *et al.* (2011). Collectively, these metrics capture important changes in ecological structure and processes of coral reefs (Hughes *et al.* 2007; Mumby, Hastings & Edwards 2007).

We identified thresholds for coral reef status by determining points of nonlinear change in the value of each ecosystem metric along a gradient of total fish biomass, which serves as a proxy for the driver, fishing pressure. We define a threshold as a nonlinear and statistically significant change in the variance or relationship between fish biomass and each of the state variables, the metrics of coral reef structure and processes. We use a space for time substitution approach and therefore cannot delineate the trajectory of individual reefs, but nonetheless can provide important information about reef status and the relationship between individual reef metrics and fish biomass.

To evaluate the potential effects of fisheries yield on management aimed at avoiding thresholds of reef change, we calculated the ratio of biomass in areas open to fishing to biomass in closed areas (a proxy for unfished biomass) and compared it to biomass ratios calculated to achieve maximum sustainable yield or pretty good yield in other systems (Hilborn 2010). We estimated unfished biomass from fish survey data from no-take marine protected areas.

### DATA COLLECTION

We compiled ecosystem metric data from peer-reviewed literature and standardized monitoring programs (Appendix S1 and Table S1 in Supporting Information) for a total of 2001 individual sites from 26 countries across the Caribbean spanning the years 1993 to 2011 (Fig. 1). We summarized data on coral reef benthic habitat and fauna (Table S1), urchin predators (Table S2), urchin biomass (Table S3) and presence of no-take reserves (Table S4).

The standardized monitoring programs include data from volunteer (Reef Check) and professional programs (e.g. AGRRA and Healthy Reefs). To examine the sensitivity of results to these different data sources, we conducted separate analyses for each data source and compared the results (Appendix S1; Table S5; Figures S1 and S2).

### STANDARDIZATION

We standardized data on metrics of coral reef structure and function from each site and year to area (i.e. kg ha<sup>-1</sup>). We normalized the coral reef metrics by transforming each observation into standard deviation units; using standard deviation units enables comparison of data and analyses across the spatial scale of the Caribbean and between ecosystem metrics. Fish length data (TL) were converted to biomass per unit area of reef (kg ha<sup>-1</sup>) using the allometric length–weight conversion  $W = aTL^b$ , with parameter values obtained from FishBase (Froese & Pauly 2013) estimates

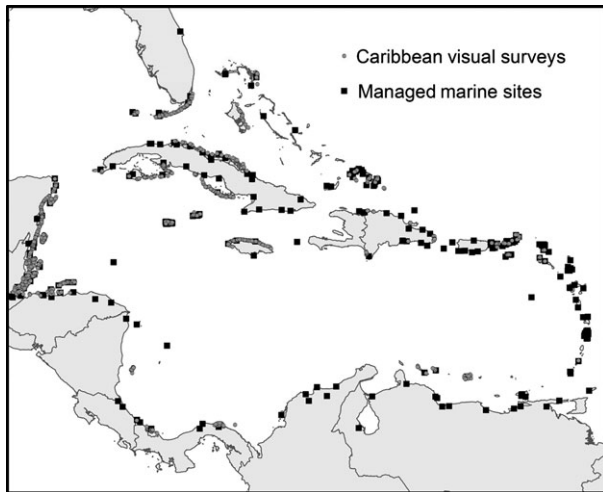


Fig. 1. Distribution and abundance of survey sites (grey, circles) and managed marine sites (black, squares) in the wider Caribbean.

for each country. Fish were categorized by functional groups, and mean proportions of total fish biomass of each functional group within each survey site were calculated. Sea urchin abundance data were transformed to biomass, the mean test size (mm) of *Diadema* spp. in each country (Table S3) was multiplied by the abundance in each site, using Levitan (1988) equation to estimate average body weight from test size ( $2.99 \times \log \text{test size (mm)} - 3.20$ ). All data manipulation and statistical analyses were performed in R (Cury *et al.* 2011; R Development Core Team 2012).

#### DATA ANALYSIS

##### *Ecosystem thresholds across the Caribbean*

We used simple statistics to determine whether ecosystem metrics exhibit nonlinear changes at certain levels of fish biomass. First, we used generalized additive models (GAMs) to fit the relationship between fish biomass and normalized Caribbean ecosystem metrics. Sequential *t*-tests were used to find the point at which a small change in fish biomass corresponds to the greatest change in slope in the coral reef metric. This change-point analysis (Killick & Eckley 2011) identifies and quantifies thresholds in metrics, which are thought to be related to nonlinear changes (Chen & Gupta 2000) in coral reefs. The data set was sampled 1000 times with replacement, the 2.5% and 97.5% quantiles of the 1000 estimates were considered as the 95% confidence intervals (CI) for the threshold. The significance and magnitude of change in variance around each threshold was calculated with a Bartlett *F*-test. Detecting variance in a spatial data set allows analysis of data with noise and low resolution (Fernandez & Fort 2009) and provides an early warning of impending change using coarse resolution data (Donangelo *et al.* 2010). The Shapiro test for normality was applied to each set of observations prior to analysis (Zuur, Ieno & Elphick 2010; additional methods in Appendix S2).

##### *Ecosystem thresholds at smaller scales*

To determine whether the thresholds estimated for the entire Caribbean differ at the scale of single countries or regions or

across levels of data richness (availability), we used the same methods as above on both subsets of data by country and data richness. Three levels of data richness (e.g. high, moderate and low) were defined by the extent of data availability. The data-rich level describes countries with >300 observations; moderate represents 50–300 observations; and data limited is defined by countries with <50 observations. In two separate analyses, we randomly subsampled the larger data base for each country and level of data richness in order to determine whether thresholds estimated for the entire Caribbean occur at the smaller scales. GAMs for each ecosystem metric were also compared to the best-fit models from the Caribbean-wide assessment using the *nls* and *AIC* function (Appendix S2).

## Results

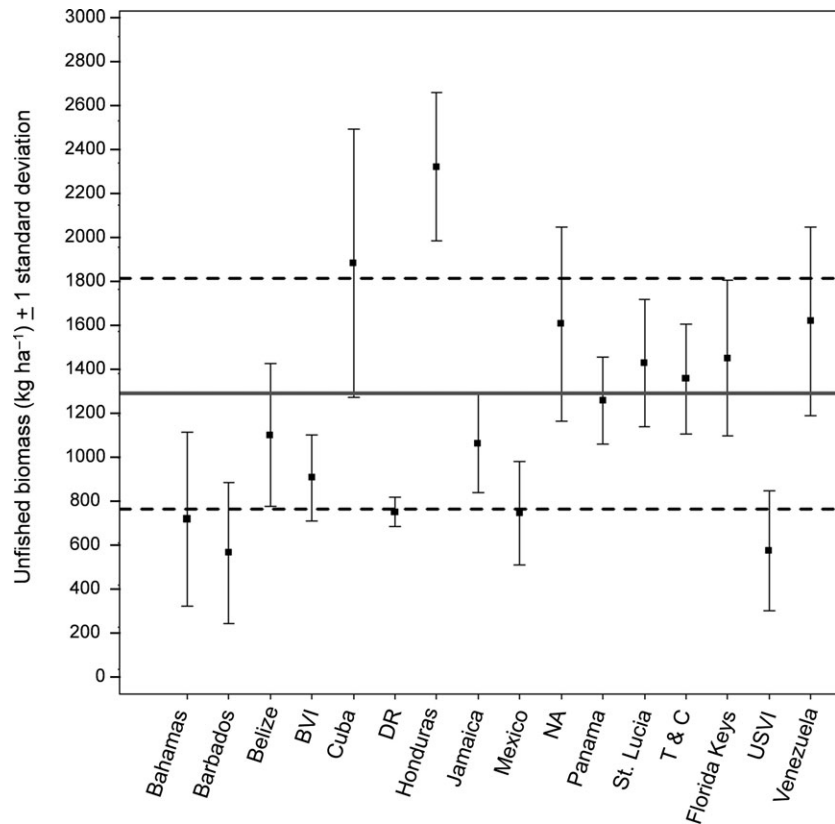
### ECOSYSTEM THRESHOLDS ACROSS THE CARIBBEAN

Of the 2001 individual sites, 132 managed marine sites were on coral reefs within no-take fisheries closures (i.e. no-take marine protected areas or reserves). Mean unfished biomass across the Caribbean was estimated from surveys in no-take reserves with observations in at least two consecutive years ( $N = 126$ ). Fish biomass levels ( $B_{\text{unfished}}$ ) varied markedly across these sites (range 551–1925  $\text{kg ha}^{-1}$ ; Fig. 2; Table S4). Fish biomass close to the mean unfished biomass (mean  $\pm$  SD =  $1306 \pm 547 \text{ kg ha}^{-1}$ ) level was associated with low macroalgal cover, high proportions of invertivorous fishes, high levels of fish species richness, low urchin biomass, low ratios of macroalgal to coral cover, high proportions of herbivorous fishes and high levels of coral cover (as much as 57% cover; Fig. S3).

All ecosystem status metrics showed nonlinear relationships (segmented, logistic, or asymptotic – Table S6) with fish biomass (Table 1). At high fish biomass levels (above 1100  $\text{kg ha}^{-1}$ ), all metrics were at levels associated with the coral-dominated state: coral cover was high, macroalgal cover was low, fish diversity was high, and urchin biomass was high.

The proportion of invertivorous fishes and species richness both decreased at fish biomass levels of 600–800  $\text{kg ha}^{-1}$ . At fish biomass levels below 500  $\text{kg ha}^{-1}$ , several metrics changed sequentially: variance in urchin biomass increased, followed by an increase in the ratio of macroalgal to coral cover and a reduced proportion of herbivorous fishes. In over 60% of the sites with biomass <360  $\text{kg ha}^{-1}$ , coral cover was reduced to an average of 15% ( $\pm 13\%$ ).

Variance associated with several metrics increased substantially at fish biomass just above observed threshold levels. At fish biomass slightly less than  $B_{\text{unfished}}$  but slightly above the threshold for increased macroalgal cover ( $1146 \pm 236 \text{ kg ha}^{-1}$ ;  $c. 0.9 B_{\text{unfished}}$ ), variance in macroalgal cover increased 1.31 times ( $F_{579,1241} = 1.3142$ ;  $P < 0.0001$ ). Variance in invertivorous fish biomass, fish species richness and urchin biomass also showed marked increases just above the thresholds associated with these



**Fig. 2.** Mean unfished fish biomass ( $\text{kg ha}^{-1}$ ) by country (black points,  $\pm 1$  SD indicated by vertical black lines) compared to mean unfished biomass ( $\text{kg ha}^{-1}$ ) across all no-take reserves in the Caribbean (dark grey horizontal line and  $\pm 1$  SD indicated by dashed lines). Caribbean countries on the  $x$ -axis: Bahamas, Barbados, Belize, (BVI) British Virgin Islands, Cuba, (DR) Dominican Republic, Honduras, Jamaica, Mexico, (NA) Netherland Antilles, Panama, St. Lucia, (T & C) Turks & Caicos, Florida Keys, (USVI) US Virgin Islands, Venezuela. Estimates based on countries with greater than two consecutive years of observation in no-take reserves.

**Table 1.** Metrics of coral reef health, estimated threshold levels in fish biomass, biomass ratio ( $B_{\text{threshold}}/B_{\text{unfished}}$ ), magnitude of variance of the threshold, best-fit functions (Table S6) and percentage of observations across the Caribbean that are under the threshold in fish biomass

Metrics of coral reef health	Threshold fish biomass level ( $\text{kg ha}^{-1}$ )	Biomass ratio	Variance	Best-fit function	Percentage of sites that fall below the threshold in fish biomass
Percent macroalgal cover	1146	0.88	1.31	Logistic	84.3
Proportion of invertivorous fishes	824	0.63	1.70	Logistic	78.5
Fish species richness	611	0.47	1.29	Asymptotic	72.2
Urchin biomass ( $\text{kg ha}^{-1}$ )	480	0.37	2.14	Logistic	67.7
Ratio of macroalgae to coral cover	470	0.36	6.80	Segmented	67.1
Proportion of herbivorous fishes	410	0.31	0.99	Logistic	63.9
Percent coral cover	360	0.28	0.98	Segmented	61.4

metrics ( $F_{655,317} = 1.2928$ ,  $P < 0.011.29$ ;  $F_{395,532} = 0.743$ ,  $P < 0.01$  and  $F_{915,815} = 6.6881$ ,  $P < 0.0001$ , respectively) (Table 1).

Three ecosystem metrics show thresholds at fish biomass levels less than or close to  $0.3 B_{\text{unfished}}$ , including the ratio of macroalgal to coral cover at  $470 \pm 103$  ( $\text{kg ha}^{-1}$ ), herbivorous fishes at  $410 \pm 40$  ( $\text{kg ha}^{-1}$ ) and coral cover at  $360 \pm 100$  ( $\text{kg ha}^{-1}$ ) (Table 1). The ratio of macroalgal to coral cover showed a large increase in variance above the threshold (6.8 times higher above the threshold;  $F_{520,1811} = 4.2001$ ;  $P < 0.0001$ ), while coral cover ( $F_{662,1195} = 0.9819$ ;  $P < 0.1$ ) and the proportion of herbivorous fishes ( $F_{625,1371} = 0.9931$ ;  $P < 0.01$ ) showed no significant changes in variance around their thresholds, at 0.98 and 0.99 times, respectively.

#### ECOSYSTEM THRESHOLDS AT SMALLER SCALES

Country or regional thresholds adhered strongly to the pan-Caribbean estimates for all metrics of coral reef health except macroalgal cover ( $t_{18} = -6.177$ ;  $P < 0.001$ , Table S7). Local thresholds for macroalgal cover fell outside the confidence intervals of the Caribbean-wide biomass ratio. Similarly, estimated thresholds did not vary significantly across the three levels of data richness (Fig. 5), except in the case of macroalgal cover, which exhibited significant variability across the three levels of data richness.  $B_{\text{unfished}}$  estimates for all of the countries surveyed (observations were available for 80% of the countries) were unavailable; instead, the Caribbean-wide mean  $B_{\text{unfished}}$  was used to estimate local biomass ratios for each

country (Table S7). A few countries (Dominican Republic, Jamaica, Nicaragua and Turks and Caicos) showed consistently low biomass ratios ( $<0.25 B_{\text{unfished}}$ ; Fig. 4) across each ecosystem metric.

## Discussion

Coral reefs provide a suite of valuable ecosystem services, but many Caribbean coral reefs are degraded (Gardner *et al.* 2003; Pandolfi *et al.* 2005; Jackson *et al.* 2014). While sites in our data set with high fish biomass exhibited characteristics associated with healthy, coral-dominated reef states, the majority of reefs in our data set (60%) had fish biomass levels below the coral cover threshold for state change (Table 1). In between these two endpoints, reefs exhibited distinct intermediate stages defined by nonlinear shifts in seven ecosystem metrics of process and community structure, each associated with particular levels of fish biomass at both local and Caribbean-wide scales. The data compiled here spanned an 18-year time period, a very large spatial scale and a variety of survey methods. Despite that heterogeneity, thresholds with fish biomass emerged in all seven ecosystem metrics, suggesting that the thresholds may be relatively robust and general. Variability around the nonlinear relationships that emerged from the data may be partly due to the timing of reef sampling relative to recent disturbance as well as the number and severity of non-fishing-related impacts that contribute to reef state change. Even with numerous factors left unaccounted, the compilation of spatial data revealed correlations that fit with current understanding of system dynamics and phase transitions on coral reefs derived from observations, experiments and time series data.

Other studies have identified nonlinear state changes in coral reefs (e.g. Mumby *et al.* 2006; Mumby, Hastings & Edwards 2007 among others). Our analysis adds to these results by showing that fish biomass, which is relatively easy to measure, may be a useful indicator of overall risk of shifts in coral reefs. Our results also provide empirical support, from a large and diverse set of coral reefs, for the role of fish as important regulators of coral and macroalgal cover (Mumby *et al.* 2006; Hughes *et al.* 2007), and the importance of changes in fish assemblage dynamics as an indicator of ecosystem instability preceding changes in coral reefs (Newman *et al.* 2006; Paddack *et al.* 2009; Scheffer *et al.* 2009; McClanahan *et al.* 2011).

The nonlinear relationships we quantified here were similar to those McClanahan *et al.* (2011) found between coral reef metrics and fish biomass in the Indian Ocean, despite many differences between Indian Ocean and Caribbean coral reefs. The two ocean basins also exhibited similar shifts in reef metrics at three distinct biomass ratios:  $\sim 1.0$ ,  $0.5$  and  $0.25$  for the Indian Ocean and  $0.9$ ,  $0.5$ , and  $0.3$  in the Caribbean (Table 1; Fig. 4). The existence of several distinct sets of thresholds may reflect a series of changes in ecosystem structure and function as

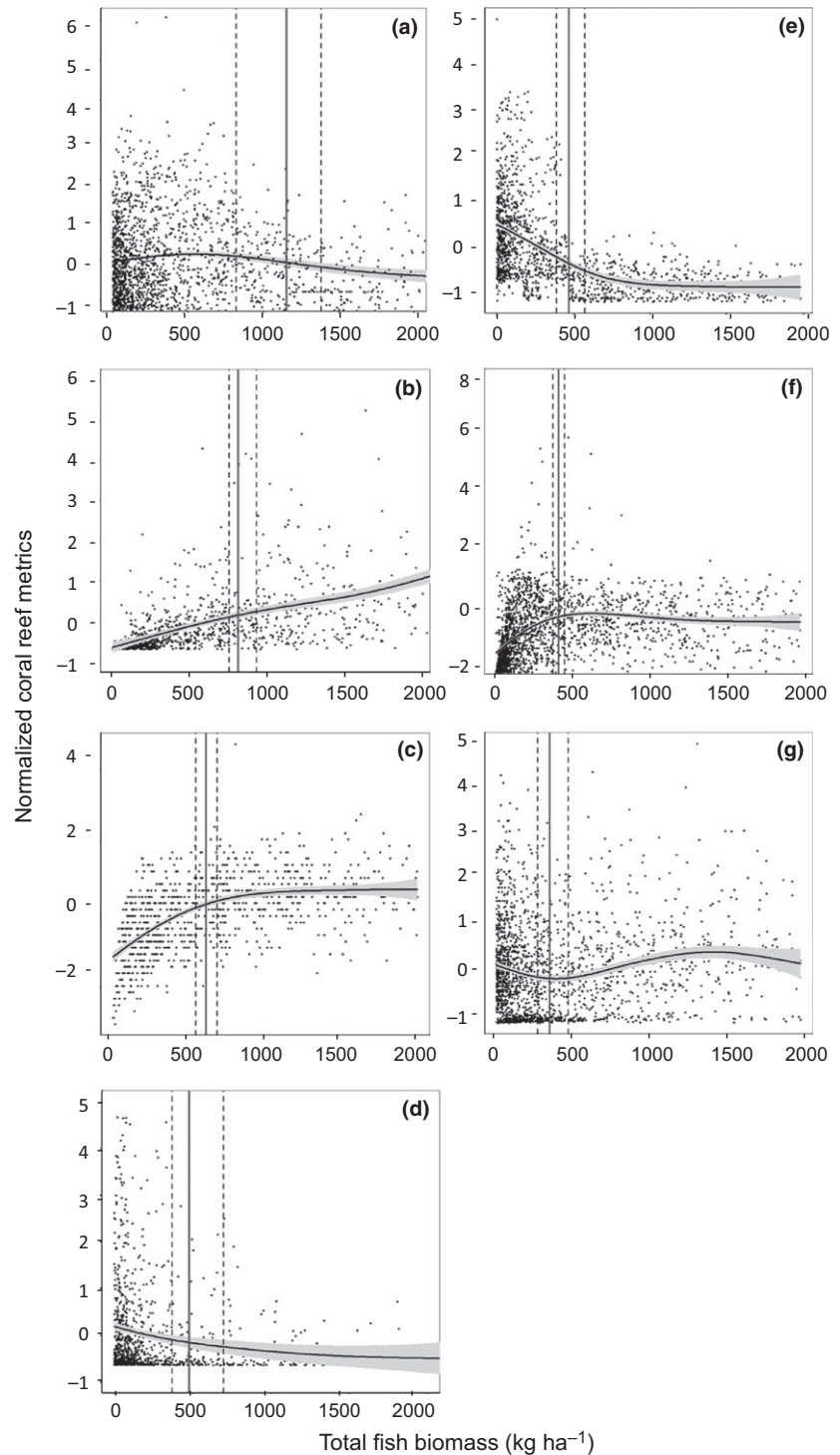
reefs transition from a coral-dominated state at fish biomass ratio above  $0.5 B_{\text{unfished}}$  to macroalgal dominance below  $0.3 B_{\text{unfished}}$ . Clustering of nonlinear changes in several metrics suggests that these biomass ratios are generally associated with state transitions of Caribbean reefs and perhaps stepwise loss of reef resilience (Table 1). Differences in environmental context from site to site (e.g. variation in primary productivity) will lead to variation in the precise location of the thresholds for any given reef. It is also important to note that a snapshot measure of fish biomass cannot tell us whether a given reef is headed towards an ecosystem transition: understanding the trajectory that reef is on depends on monitoring data and knowledge of past disturbances, management interventions and likely future impacts. Nonetheless, these biomass ratios may have value as a 'rule of thumb' for managers in data-poor regions seeking tools for reef conservation and ecosystem-based fisheries management.

### CAVEATS FOR THE USE OF UNFISHED BIOMASS ESTIMATES FROM NO-TAKE RESERVES

We used an estimate of unfished biomass as a basic reference point to facilitate comparison of threshold results across countries and/or regions and different spatial scales of analysis. Considering the well-documented trajectory of general reef degradation in the Caribbean, the estimated unfished biomass was high at *c.*  $1300 \text{ kg ha}^{-1}$  (Figs 2, S1 and S2) compared to estimates resulting from a similar study of Indian Ocean reefs (*c.*  $1200 \pm 110 \text{ kg ha}^{-1}$ ; McClanahan *et al.* 2011). Reserve biomass might be higher than expected if reserves are sited in areas of unusually high habitat quality, contributing to a positive correlation between coral cover and fish biomass unrelated to the regulatory effects of fish populations. A correlation of this nature could confound our results. Additionally, unfished biomass estimates were derived from measurements in no-take reserves that have been in place for varying lengths of time, one as early as 1954. Given that the benefits of reserves for commercial species appear to increase with size of the reserve and years since establishment (Claudet *et al.* 2008), older, larger, well-enforced no-take reserves, in which fish populations have had sufficient time to equilibrate, should serve as better proxies for unfished biomass (McClanahan *et al.* 2007, 2011).

### Leading and lagging indicators of reef shifts across the Caribbean

As noted above, we observed clusters of nonlinear shifts in reef metrics associated with three distinct biomass ratio thresholds. Macroalgal cover responded earliest to small changes in fish biomass. Across the Caribbean, macroalgal cover averaged  $25.7\%$  ( $\pm 22.8\%$ ), but was higher (up to  $67\%$ ) where fish biomass was less than half of unfished biomass ( $639 \text{ kg ha}^{-1}$ ;  $72\%$  of the sites). This increase in



**Fig. 3.** Comparisons of the nonlinear relationship between normalized (standard deviation units) coral reef metrics and total fish biomass ( $\text{kg ha}^{-1}$ ) for (a) proportion of macroalgae cover, (b) proportion of invertivorous fishes, (c) fish species richness, (d) urchin biomass, (e) ratio of macroalgae to coral cover, (f) proportion of herbivorous fishes and (g) proportion of coral cover across the Caribbean. Each observation is plotted with the predictions of a generalized additive model (GAM) (black line), the grey region represents the confidence interval ( $\pm 95\%$ ) of the fitted GAM, black vertical lines indicate the estimated threshold fish biomass levels with bootstrapped confidence interval as dashed vertical black lines, as detected from a change-point analysis. Note the variation in the scale of the y-axis.

macroalgal cover was correlated with declines in grazers (urchins and herbivorous fishes) (Figs 3 and S3; Table S7).

Initial differences in fish assemblages (change in proportion of invertivorous fishes, followed by decreases in fish species richness) were observed at 0.5–0.6  $B_{\text{unfished}}$  (Table 1; Fig. 3b–c). This might be a result of different life history strategies among species in these functional groups (e.g. growth rates, changing sex ratios) making some more vulnerable to fishing pressure than others, increased turnover rate from fishing pressure and selection

(McClanahan & Humphries 2012), and/or decreased resilience in the absence of predators (Bellwood *et al.* 2004), among other factors. Long-term fishing patterns across the Caribbean may also result in fish assemblage changes (Mora 2008).

Herbivorous fish biomass exhibited a threshold at relatively low fish biomass levels (Fig. 3f), despite a strong correlation with total fish biomass ( $r = 0.68$ ). This suggests it may be less useful as an indicator for management as it lags changes in other metrics. It is possible that

herbivorous fish abundance changes dramatically only at relatively low levels of total fish biomass because this is often one of the last groups of fishes targeted, after other groups are fished down (e.g. Newman *et al.* 2006; Mora 2008; Paddock *et al.* 2009); however, the critical level of herbivory needed to convey reef resilience could have been passed well before the threshold change in herbivorous fish biomass was observed.

Changes in coral cover were associated with some of the lowest levels of fish biomass (360 kg ha<sup>-1</sup>; Figs 3g and S3g), well below thresholds where other important regulatory processes and actors (e.g. urchins, herbivorous fish) had been severely altered. As pointed out by other authors, coral cover may remain high until a shock to the system (e.g. a bleaching event or hurricane) kills corals. But once the coral cover threshold is crossed, potential for recovery may be limited, at least at the temporal scales relevant for management, because processes such as grazing that support coral recruitment and recovery have been undermined (reviewed in Hughes *et al.* 2010). Therefore, coral cover *per se* does not appear to be a good indicator of reef status if the intent is to prevent state change, as it appears to be relatively insensitive to changes in fish biomass. Coral cover also appears to be a lagging indicator for Indian Ocean coral reefs (McClanahan *et al.* 2011).

Theory predicts that both spatial and temporal variance in various state metrics will increase as a complex system approaches a change (Scheffer *et al.* 2009; Donangelo *et al.* 2010; Carpenter *et al.* 2011). However, the increased variation at biomass ratios just above thresholds for many of the metrics evaluated in this study are difficult to interpret without understanding the underlying dynamics of each reef in the data set. One might expect higher variation in state metrics across both space and time as regulatory controls (e.g. a reduction in predation or grazing pressure) are reduced prior to state change (Donangelo *et al.* 2010), since individual reefs vary considerably in resilience. Drivers affecting a set of reefs with varying resilience could cause variance in state metrics to increase across the entire set, as some reefs cross thresholds while others continue to resist change.

#### *Ecosystem thresholds at smaller scales*

Thresholds in coral reef ecosystem metrics identified using data from individual countries and across different levels of data availability adhered well to the thresholds derived at the Caribbean-wide scale (Fig. 4), suggesting that large scale patterns may be useful to guide management at smaller scales. However, reef-specific analyses and monitoring over time will be necessary to determine whether changes in fishery management are likely to result in improved yields and/or recovery of desirable ecosystem states. Both unfished biomass (Fig. 1) and ecological thresholds varied among countries (Tables S4–S7, Figs S1 and S2), but fell within the confidence intervals delineated for the Caribbean, except for a few countries with low fish

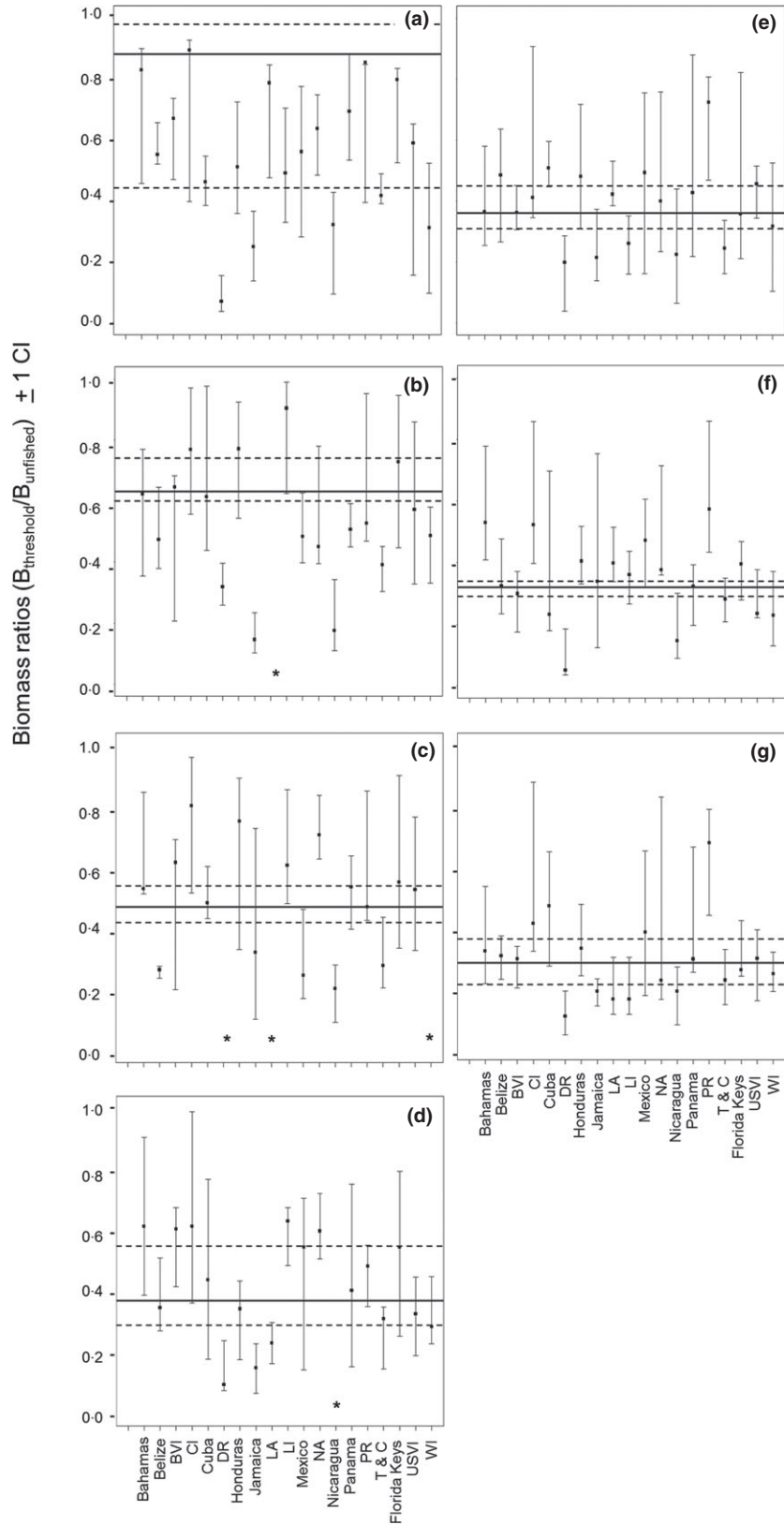
biomass levels and sample size. Several factors could contribute to these differences, including lack of high quality habitat, inadequately enforced no-take reserves or non-fishing sources of fish mortality. Spatial variability in coral reef state is typically large (Figs 4 and 5; Table S7), and often compounded by local (e.g. fishing pressure, land use) and global (e.g. hurricanes, changes in sea surface temperatures) scale impacts (reviewed in Hughes *et al.* 2010; Hughes *et al.* 2013).

#### *Application to coral reef management*

While the existence of coral reef ecosystem alternative states has been documented for some time, quantitative thresholds that can be used in management aimed at maintaining reef resilience have seldom been documented (see Mumby *et al.* 2014). In addition to sound recommendations to reduce fishing mortality on parrotfish and reduce other local stressors (e.g. Bellwood, Hoey & Hughes 2012; Jackson *et al.* 2014), and avoid crossing ecosystem thresholds (Biggs, Carpenter & Brock 2009; McClanahan *et al.* 2011; Fujita *et al.* 2013), managers could benefit from practical, quantitative targets for how much drivers of change should be reduced. Such numerical targets are important because altering driver levels generally has accompanying social and economic trade-offs that managers will be expected to minimize (e.g. loss of fisheries revenue). They are also elusive in the data-poor, multi-species fisheries that characterize coral reef management settings.

In theory, there is an intermediate range of biomass ratios ( $B_{\text{fished}} : B_{\text{unfished}}$ ) that produce high sustainable yields, because low biomass ratios associated with an overfished state should produce lower yields, as should very high biomass ratios associated with a lightly fished stock. For single fish stocks in temperate systems (typically with relatively low diversity and high productivity), biomass ratios near 0.5 are thought to be associated with maximum sustainable yield, ratios near 0.2 are thought to be associated with overfished status, and ratios between 0.2 and 0.5 are associated with pretty good yield (*c.* 80% of maximum sustainable yield, MSY) (Hilborn 2010). Exact values depend on several biological parameters, including the steepness of the stock–recruitment relationship, which is related to the resilience of the species to fishing pressure. Coral reef stocks are highly diverse, and coral reef ecosystems are thought to be less productive than many temperate marine ecosystems; therefore, biomass ratios in coral reefs associated with overfished state may be somewhat higher than 0.2, the lower end of the pretty good yield range for temperate stocks (Hilborn 2010).

Our results suggest that in data-limited coral reef fisheries, the ratio of fish biomass to unfished fish biomass can be used as a quantitative measure of the risk of ecosystem state change to guide precautionary management. For example, Caribbean reefs with fish biomass

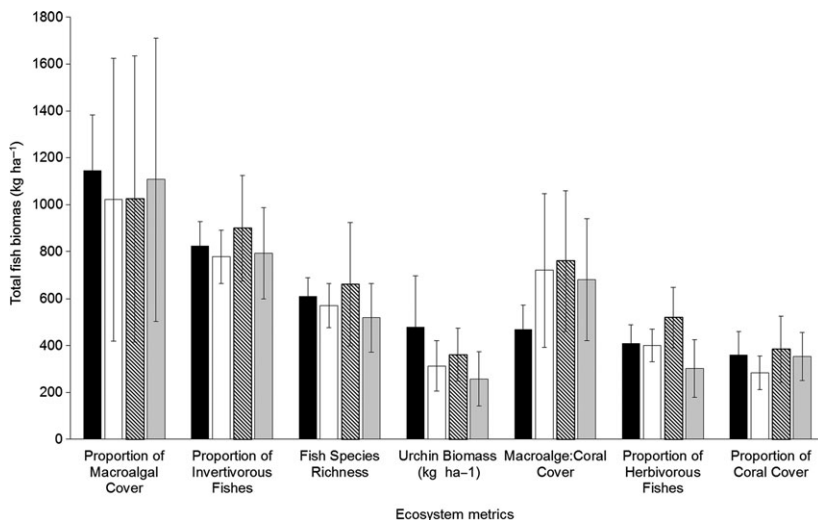


**Fig. 4.** Comparison of mean biomass ratios among countries and/or regions of the Caribbean (means are black points with 95% confidence intervals as vertical black lines) to the estimated biomass ratio for the Caribbean (mean is horizontal grey line, confidence intervals are dashed lines) for (a) proportion of macroalgal cover, (b) proportion of invertivorous fishes, (c) fish species richness, (d) urchin biomass, (e) ratio of macroalgal to coral cover, (f) proportion of herbivorous fishes and (g) proportion of coral cover across the Caribbean and Caribbean countries: Bahamas, Belize, (BVI) British Virgin Islands, (CI) Cayman Islands, Cuba, (DR) Dominican Republic, Honduras, Jamaica, (LA) Leeward Antilles, (LI) Leeward Islands, Mexico, (NA) Netherland Antilles, Nicaragua, Panama, (PR) Puerto Rico, (T & C) Turks & Caicos, Florida Keys, (USVI) US Virgin Islands, (WI) Windward Islands. \* – indicates no data present.

levels > 80–90% of local unfished levels appear to be at low risk of either being overfished or shift in structure and processes, but should be monitored for further reductions in fish biomass. The probability of reversing a

given shift is likely to be much greater in the initial part of the transition, rather than after the system has stabilized (Graham *et al.* 2013). High levels of fish biomass may be appropriate for the provisioning of multiple eco-





**Fig. 5.** Comparison of threshold estimates at different levels of data richness for proportion of macroalgal cover, proportion of invertivorous fishes, fish species richness, urchin biomass, ratio of macroalgal to coral cover, proportion of herbivorous fishes and proportion of coral cover across the Caribbean (black) data rich (white), data moderate (black and white diagonal hatches) and data limited (grey) with  $\pm 95\%$  confidence intervals as vertical black lines.

system services, beyond maximizing fishery yield. But if maximizing fishery yield is a central concern, our results suggest that maintaining fished to unfished biomass ratios near 0.5 can maintain a coral-dominated state and also produce pretty good yield (*c.* 80% of MSY depending on the strength of recruitment compensation; Hilborn 2010), with relatively low risk of ecosystem change. Biomass ratios  $<0.3$  indicate a higher risk of a transition to a macroalgal-dominated ecosystem. In general, coral reef fish stocks may be less resilient than the temperate stocks for which biomass ratio reference values have been quantified (e.g. Hilborn 2010); therefore, fishing stocks down to the lower end of the range of biomass ratios that are associated with pretty good yield also carries with it a risk of overfishing. Management strategy evaluations (simulation studies of the response of stock status and yield to management measures) indicate that control rules based on this ratio can generate high proportions of potential yield in fisheries that lack catch, effort and other more conventional fishery data sources (Babcock & MacCall 2011; McGilliard *et al.* 2011), as is common in coral reef fisheries.

The Caribbean has experienced a slow and patchy transition from a coral-dominated system to a macroalgae-dominated system over the last 30 years (Gardner *et al.* 2003; Hughes *et al.* 2010, 2013). The paucity of historical data means that our Caribbean-wide analysis is necessarily based on data collected during a recent period of this long transition, during which a variety of factors – including nutrient enrichment, climate change, mass coral bleaching, urchin die-offs and probably overfishing – have been in play on these reefs. The effects of these drivers of change vary across the Caribbean, in part due to differences in reef resilience (e.g. Bellwood *et al.* 2006), sea urchin biomass (reviewed in Hughes *et al.* 2010; Appendix S2) and management regimes (Salas *et al.* 2007). This is an important context for setting management expectations: efforts to recover fish populations and desirable ecosystem states may be unsuccessful where coral reefs have already transitioned to

less desirable alternative stable states, and recovery is impeded by feedback loops and/or poor management. Nevertheless, the high fish biomass levels in no-take reserves established relatively recently (*c.* 10 years ago) suggest that managing fishing pressure in order to rebuild fish biomass could result in recovery of many Caribbean coral reefs.

## Conclusions

Effective coral reef management is often hindered by the lack of capacity to collect and analyse data that can be used to generate scientific guidance for management. Many coral reef fisheries in the Caribbean are data limited, multi-species fisheries, with limited scientific and management capacity, weak enforcement and minimal compliance with regulations (Salas *et al.* 2007). Our results could help overcome capacity limitations by providing an easily measured parameter – total fish biomass – that could be used to monitor reef community structure and the processes that support coral-dominated reefs and inform a risk-based approach to fisheries management. We only examined one driver, but hope that this work will lead to future collaborations and alternative analyses to quantify threshold relationships at multiple scales and for multiple drivers, and more directly address how these drivers impact reef resilience. For coral reef fisheries, a system-specific total fish biomass target for generating pretty good yield and maintaining desirable coral reef states can guide precautionary management. Such a target should be integrated with other data-limited methods that combine assessments of stock vulnerability with measures of depletion or fishing pressure and applied cautiously in an adaptive management framework designed to address high levels of uncertainty and evaluate alternative explanations for observed relationships (Fujita *et al.* 2013).

Quantitative thresholds in fish biomass can provide useful guidance for management aimed at both producing sustainable yields and maintaining desirable ecosystem

states capable of producing a diverse portfolio of ecosystem services. However, improved institutional capacity, including policies and management measures that create incentives for compliance with harvest control rules, such as territorial use rights for fishing (Gutiérrez, Hilborn & Defeo 2011; Ovando *et al.* 2012) and that provide easy ways for fishermen to achieve harvest control goals (Hicks & McClanahan 2012) are also essential. Otherwise, compliance will be low unless enforcement capacity is high – which is rare in many coral reef countries (Haughton 2003). Moreover, specific target levels for manageable drivers of coral reef change such as fishing pressure are necessary so that managers and stakeholders know the extent to which drivers must be reduced to obtain the desired outcomes and to elucidate the trade-offs that are often involved in resource management. All of these ingredients will be necessary for translating thresholds of coral reef state change into actions that result in better outcomes for coral reefs and the people who depend on them.

## Acknowledgements

The authors would like to acknowledge the contributions of T. McClanahan and A. MacNeil and two anonymous reviewers for suggestions that improved the manuscript, M. McField, K. Marks and J. Bruno for data, and P. Raimondi and R. Killick for statistical advice.

## Data accessibility

Data on coral reef metrics (e.g. fish abundance by species, urchin abundance, coral and macroalgae cover) used in the analyses are available for direct download from the Atlantic and Gulf Rapid Reef Assessment ([www.agrra.org](http://www.agrra.org)), CARICOMP - Caribbean Coastal Marine Productivity Program ([clmeims.gcfi.org/monitoring-programs/caribbean-coastal-marine-productivity-program-caricomp-data-archives](http://clmeims.gcfi.org/monitoring-programs/caribbean-coastal-marine-productivity-program-caricomp-data-archives)), NOAA - Center for Coastal Monitoring and Assessment ([www8.nos.noaa.gov/bioge\\_public/query\\_main.aspx](http://www8.nos.noaa.gov/bioge_public/query_main.aspx)) and by inquiry from Healthy Reefs Initiative ([www.healthy-reefs.org](http://www.healthy-reefs.org)), Reef Check ([www.reefcheck.org](http://www.reefcheck.org)) and peer-reviewed literature, all of these resources are summarized in Table S1.

Urchin biomass estimates of mean test size are based on peer-reviewed literature, mean test estimates and sources are available in Table S3.

Access to background information on the location, date and age of the no-takes reserves is from CaMPAM: Caribbean Marine Protected Area Management (<http://campam.gcfi.org/CaribbeanMPA/CaribbeanMPA.php>) and the MPA Global data base ([www.mpaglobal.org](http://www.mpaglobal.org)), summarized in Table S4.

## References

Babcock, E.A. & MacCall, A.D. (2011) How useful is the ratio of fish density outside versus inside no-take marine reserves as a metric for fishery management control rules? *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 343–359.

Bellwood, D.R., Hoey, A.S. & Hughes, T.P. (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society. B, Biological Sciences*, **279**, 1621–1629.

Bellwood, D.R., Hughes, T.P., Folke, C. & Nyström, M. (2004) Confronting the coral reef crisis. *Nature*, **429**, 827–833.

Bellwood, D.R., Hoey, A.S., Ackerman, J.L. & Depczynski, M. (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology*, **12**, 1587–1594.

Biggs, R., Carpenter, S.R. & Brock, W.A. (2009) Turning back from the brink: detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences*, **106**, 826–831.

Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R., Brock, W.A., Cline, T. *et al.* (2011) Early warnings of regime shifts: a whole-ecosystem experiment. *Science*, **332**, 1079–1082.

Chen, S.J. & Gupta, A.K. (2000) *Parametric Statistical Change Point Analysis*. Birkhäuser, Boston, MA.

Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.-A., Pérez-Ruzafa, A. *et al.* (2008) Marine reserves: size and age do matter. *Ecology Letters*, **11**, 481–489.

Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W. *et al.* (2011) Global seabird response to forage fish depletion—one-third for the birds. *Science*, **334**, 1703–1706.

Donangelo, R., Fort, H., Dakos, V., Scheffer, M., Egbert, H. & Nes, V. (2010) Early warnings for catastrophic shifts in ecosystems: comparison between spatial and temporal indicators. *International Journal of Bifurcation and Chaos*, **20**, 315–321.

Edwards, C.B., Friedlander, A.M., Green, A.G., Hardt, M.J., Sala, E., Sweatman, H.P. *et al.* (2014) Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proceedings of the Royal Society. B, Biological Sciences*, **281**, 20131835.

Fernandez, A. & Fort, H. (2009) Catastrophic phase transitions and early warnings in a spatial ecological model. *Journal of Statistical Mechanics: Theory and Experiment*, **2009**, P09014.

Froese, R. & Pauly, D. (eds) (2013) FishBase. Available from <http://www.fishbase.org> (accessed 30 October 2013).

Fujita, R., Moxley, J.H., DeBey, H., Van Leuvan, T., Leumer, A., Honey, K. *et al.* (2012) Managing for a resilient ocean. *Marine Policy*, **38**, 538–544.

Fujita, R., Thornhill, D.J., Karr, K., Cooper, C.H. & Dee, L.E. (2013) Assessing and managing data-limited ornamental fisheries in coral reefs. *Fish and Fisheries*, **15**, 661–675.

Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2003) Long-term region-wide declines in Caribbean corals. *Science*, **301**, 958–960.

Graham, N.A., Bellwood, D.R., Cinner, J.E., Hughes, T.P., Norström, A.V. & Nyström, M. (2013) Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment*, **11**, 541–548.

Gutiérrez, N.L., Hilborn, R. & Defeo, O. (2011) Leadership, social capital and incentives promote successful fisheries. *Nature*, **470**, 386–389.

Haughton, M.O. (2003) Compliance and enforcement of fisheries regulations in the Caribbean. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **54**, 188–201.

Hicks, C.C. & McClanahan, T.R. (2012) Assessing gear modifications needed to optimize yields in a heavily exploited, multi-species, seagrass and coral reef fishery. *PLoS One*, **7**, e36022.

Hilborn, R. (2010) Pretty good yield and exploited fishes. *Marine Policy*, **34**, 193–196.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C. *et al.* (2003) Climate change, human impacts, and the resilience of coral reefs. *Science*, **301**, 929–933.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L. *et al.* (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, **17**, 360–365.

Hughes, T.P., Graham, N.A.J., Jackson, J.B.C., Mumby, P.J., & Steneck, R.S. (2010) Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution*, **25**, 633–642.

Hughes, T.P., Linares, C., Dakos, V., van de Leemput, I.A. & van Nes, E.H. (2013) Living dangerously on borrowed time during slow, unrecognition regime shifts. *Trends in Ecology & Evolution*, **28**, 149–155.

Jackson, J.B.C., Donovan, M.K., Cramer, K.L., & Lam, V.V. (eds.) (2014) *Status and Trends of Caribbean Coral Reefs; 1970–2012*. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.

Kelly, R.P., Erickson, A., Mease, L., Battista, W., Kittinger, J. & Fujita, R. (2015) Embracing thresholds for better environmental management. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **370**, 20130276.

Killick, R. & Eckley, I. (2011) ChangePoint: contains functions that run various single and multiple changepoint methods (version 0.3).

- <http://cran.r-project.org/web/packages/changepoint/index.html>. (accessed 4 January 2012).
- Levitan, D.R. (1988) Density-dependent size regulation and negative growth in the sea urchin *Diadema antillarum* (Philippi). *Oecologia*, **76**, 627–629.
- McClanahan, T. & Humphries, A. (2012) Differential and slow life-history responses of fishes to coral reef closures. *Marine Ecology Progress Series*, **469**, 121–131.
- McClanahan, T.R., Graham, N.A.J., Calnan, J.M. & MacNeil, M.A. (2007) Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Applications*, **17**, 1055–1067.
- McClanahan, T.R., Graham, N.A.J., MacNeil, M.A., Muthiga, N.A., Cinner, J.E., Bruggemann, J.H. *et al.* (2011) Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proceedings of the National Academy of Sciences*, **108**, 17230–17233.
- McGilliard, C.R., Hilborn, R., MacCall, A., Punt, A.E. & Field, J.C. (2011) Can information from marine protected areas be used to inform control-rule-based management of small-scale, data-poor stocks? *ICES Journal of Marine Science*, **68**, 201–211.
- Moberg, F. & Folke, C. (1999) Ecological goods and services of coral reef ecosystems. *Ecological Economics*, **29**, 215–233.
- Mora, C. (2008) A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society. B, Biological Sciences*, **275**, 767–773.
- Mumby, P.J., Hastings, A. & Edwards, H.J. (2007) Thresholds and the resilience of Caribbean coral reefs. *Nature*, **450**, 98–101.
- Mumby, P.J. & Steneck, R.S. (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends in Ecology & Evolution*, **23**, 555–563.
- Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R. *et al.* (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, **311**, 98–101.
- Mumby, P.J., Wolff, N.H., Bozec, Y.-M., Chollett, I. & Halloran, P. (2014) Operationalizing the resilience of coral reefs in an era of climate change. *Conservation Letters*, **7**, 176–187.
- Newman, M.J.H., Paredes, G.A., Sala, E. & Jackson, J.B.C. (2006) Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecology Letters*, **9**, 1216–1227.
- Ovando, D.A., Deacon, R.T., Lester, S.E., Costello, C., Van Leuvan, T., McIlwain, K. *et al.* (2012) Conservation incentives and collective choices in cooperative fisheries. *Marine Policy*, **37**, 132–140.
- Paddack, M.J., Reynolds, J.D., Aguilar, C., Appeldoorn, R.S., Beets, J., Burkett, E.W. *et al.* (2009) Recent region-wide declines in Caribbean reef fish abundance. *Current Biology*, **19**, 590–595.
- Pandolfi, J.M., Jackson, J.B.C., Baron, N., Bradbury, R.H., Guzman, H.M., Hughes, T.P. *et al.* (2005) Ecology. Are U.S. coral reefs on the slippery slope to slime? *Science*, **307**, 1725–1726.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>. (accessed 5 January 2014).
- Roff, G. & Mumby, P.J. (2012) Global disparity in the resilience of coral reefs. *Trends in Ecology & Evolution*, **27**, 404–413.
- Ruppert, J.L.W., Travers, M.J., Smith, L.L., Fortin, M.-J. & Meekan, M.G. (2013) Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. *PLoS One*, **8**, e74648.
- Ruttenberg, B.I., Hamilton, S.L., Walsh, S.M., Donovan, M.K., Friedlander, A., DeMartini, E. *et al.* (2011) Predator-induced demographic shifts in coral reef fish assemblages. *PLoS One*, **6**, e21062.
- Salas, S., Chuenpagdee, R., Seijo, J.C. & Charles, A. (2007) Challenges in the assessment and management of small-scale fisheries in Latin America and the Caribbean. *Fisheries Research*, **87**, 5–16.
- Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V. *et al.* (2009) Early-warning signals for critical transitions. *Nature*, **461**, 53–59.
- Travis, J., Coleman, F.C., Auster, P.J., Cury, P.M., Estes, J.A., Orensanz, J. *et al.* (2014) Integrating the invisible fabric of nature into fisheries management. *Proceedings of the National Academy of Sciences*, **111**, 581–584.
- Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.

Received 20 June 2014; accepted 22 December 2014

Handling Editor: C. Frid

## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Description and comparison of data sources.

**Appendix S2.** Methods to assess linear and non-linear relationships across the Caribbean.

**Table S1.** Description of data sources and references.

**Table S2.** Identity of invertivorous fishes.

**Table S3.** Estimates of *Diadema* test size and biomass across the Caribbean.

**Table S4.** Estimates of local unfished biomass in no-take areas.

**Table S5.** Estimated thresholds, without Reef Check data.

**Table S6.** Model selection and AIC scores.

**Table S7.** Estimated fish biomass thresholds by country.

**Fig. S1.** Comparison of unfished biomass between data sources.

**Fig. S2.** Comparison of unfished biomass between data sources and countries.

**Fig. S3.** Comparisons of the non-linear relationship between coral reef metrics and total fish biomass ( $\text{kg ha}^{-1}$ ).