

# Fishing degrades size structure of coral reef fish communities

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## Abstract

Fishing pressure on coral reef ecosystems has been frequently linked to reductions of large fishes and reef fish biomass. Associated impacts on overall community structure are, however, less clear. In size-structured aquatic ecosystems, fishing impacts are commonly quantified using size spectra, which describe the distribution of individual body sizes within a community. We examined the size spectra and biomass of coral reef fish communities at 38 US-affiliated Pacific islands that ranged in human presence from near pristine to human population centers. Size spectra 'steepened' steadily with increasing human population and proximity to market due to a reduction in the relative biomass of large fishes and an increase in the dominance of small fishes. Reef fish biomass was substantially lower on inhabited islands than uninhabited ones, even at inhabited islands with the lowest levels of human presence. We found that on populated islands size spectra exponents decreased (analogous to size spectra steepening) linearly with declining biomass, whereas on uninhabited islands there was no relationship. Size spectra were steeper in regions of low sea surface temperature but were insensitive to variation in other environmental and geomorphic covariates. In contrast, reef fish biomass was highly sensitive to oceanographic conditions, being influenced by both oceanic productivity and sea surface temperature. Our results suggest that community size structure may be a more robust indicator than fish biomass to increasing human presence and that size spectra are reliable indicators of exploitation impacts across regions of different fish community compositions, environmental drivers, and fisheries types. Size-based approaches that link directly to functional properties of fish communities, and are relatively insensitive to abiotic variation across biogeographic regions, offer great potential for developing our understanding of fishing impacts in coral reef ecosystems.

**Keywords:** body size, community structure, coral reef fish, exploitation, fisheries, macroecology, overfishing, size spectra, size-based approaches

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## Introduction

Overexploitation of marine species can cause system-wide shifts in species abundances and interactions (Bascompte *et al.*, 2005; Britten *et al.*, 2014), which in turn may alter the structure and function of marine ecosystems (Jackson *et al.*, 2001; Travis *et al.*, 2014). Selective fishing of large consumers can result in trophic cascades (Bascompte *et al.*, 2005; Baum & Worm, 2009) and destabilize predator–prey dynamics

(Britten *et al.*, 2014), while sustained exploitation at lower trophic levels can collapse prey populations (Essington *et al.*, 2015). In temperate systems, broad fishing impacts are often evaluated using complex ecosystem-based models that require high-resolution species-specific ecological and exploitation data (Thorpe *et al.*, 2015). However, when ecosystems are characterized by high ecological diversity or limited catch data, these approaches are infeasible. Instead, community-level indicators that are simple to estimate, grounded in ecological theory, and generalizable across ecosystems can provide informative assessments of fishing impacts (Rochet & Trenkel, 2003; Thrush & Dayton, 2010).

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Gaining such insights is of paramount importance for subsistence coral reef fisheries, which provide important sources of protein and livelihoods to millions of people across the world's tropical island nations (Sadovy, 2005; Newton *et al.*, 2007). Coral reef fish assemblages are highly diverse (Kulbicki *et al.*, 2013) and their fisheries are multispecies and multigear (Hicks & McClanahan, 2012), but catch and effort data are typically limited or nonexistent (Sadovy, 2005; Zeller *et al.*, 2015). As a result, exploitation impacts can be particularly difficult to quantify (McClanahan *et al.*, 2015; Nash & Graham, 2016), underscoring the need for simple, community-level indicators of exploitation impacts.

In aquatic ecosystems, because body size and individual trophic level are tightly linked (Jennings *et al.*, 2001; Barnes *et al.*, 2010), size-based approaches that generalize across species but preserve links to community-level traits may provide significant insights into the impacts of exploitation in complex systems such as coral reefs (Jennings, 2005; Nash & Graham, 2016). Body size also scales predictably with a number of important ecological processes, from metabolic rate at the individual scale (West *et al.*, 2001) to biomass turnover at the population scale (Brown *et al.*, 2004). Therefore, size-based approaches offer powerful methods of assessing ecological structure across distinct communities and link directly to functional traits that are otherwise difficult to estimate in data-poor systems (Taylor *et al.*, 2014). One metric, the size spectrum, describes the distribution of individuals across body sizes irrespective of species (White *et al.*, 2007; Sprules & Barth, 2016). The size spectrum has been used to assess fishing impacts across a range of temperate marine (Blanchard *et al.*, 2005; Daan *et al.*, 2005; Sweeting *et al.*, 2009) and freshwater fish communities (Sprules, 2008; Kolding *et al.*, 2016), where community size structure is represented by the slope of the relationship between abundance and body size on logarithmic scales (White *et al.*, 2007). Size-selective fishing causes the spectrum slope to decrease or 'steepen' as large fishes are depleted and prey species are released from predation (Daan *et al.*, 2005; Shin *et al.*, 2005; Fung *et al.*, 2013). Metabolic and size-based theory predicts that a reduction in large fishes will produce shifts in size-linked life-history traits such that overexploited communities are characterized by a greater dominance of small individuals, and concomitant higher productivity and faster biomass turnover times (Jennings & Blanchard, 2004; McCann *et al.*, 2016).

In small-scale, artisanal coral reef fisheries, overexploitation is a pervasive issue that threatens the

sustainability of a vital food resource for developing coastal countries (Newton *et al.*, 2007; Cinner *et al.*, 2009; Johnson *et al.*, 2013). Standing stock biomass is widely used as a metric of fishery health and of exploitation impacts at regional scales (Cinner *et al.*, 2009, 2012a; MacNeil *et al.*, 2015) and, although declines in the abundance of large fishes on coral reefs are well documented (Sandin *et al.*, 2008; Williams *et al.*, 2015), analyses of associated impacts on coral reef fish community size structure have been infrequent (Nash & Graham, 2016). Steepening of size spectra slopes due to overfishing of large fishes has thus far been detected only in Fijian small-scale reef fisheries, and across only moderate gradients in exploitation pressure (Dulvy *et al.*, 2004; Graham *et al.*, 2005; Wilson *et al.*, 2010; though see Edwards *et al.*, 2016). Other direct comparisons between fished and protected areas have found that community size structure is highly variable and unrelated to exploitation (McClanahan & Graham, 2005; Graham *et al.*, 2007), which may reflect unmeasured environmental influences. Consequently, it remains unclear whether degradation in overall community size structure occurs across extreme gradients in exploitation pressure, such as from pristine to overexploited reef communities, and if these patterns are dependent on the fisheries' species composition. At regional and global scales, recent macroecological analyses of coral reef fish trophic structure and life-history traits indicate that biomass and ecological functions may be broadly preserved in lightly exploited communities (McClanahan *et al.*, 2011, 2015; MacNeil *et al.*, 2015). Similar examination of reef fish community size structure across large spatial scales and large gradients in fishing pressure would provide additional insights into the state of coral reef fisheries relative to unexploited ecosystems.

Here, we use a large-scale dataset of Pacific reef fish abundances spanning from remote, near-pristine islands and atolls to highly populated ones, to examine how human impacts alter the size structure of reef fish communities. The reefs included in our analyses also span strong gradients in environmental covariates (Williams *et al.*, 2015) and differ substantially in their species compositions (Kulbicki *et al.*, 2013) and exploitation history (Dalzell *et al.*, 1996; Houk *et al.*, 2012). We estimated size spectrum exponents to assess shifts in community structure across a body size range from tiny planktivores (20 g) to large piscivores (>1 kg) and quantified the biomass of large fishes relative to the total fish community to determine whether exploitation was size selective. To examine how changes in size structure corresponded with more

conventional biomass-based indicators, we also compared trends in size spectra with trends in total community biomass.

## Materials and methods

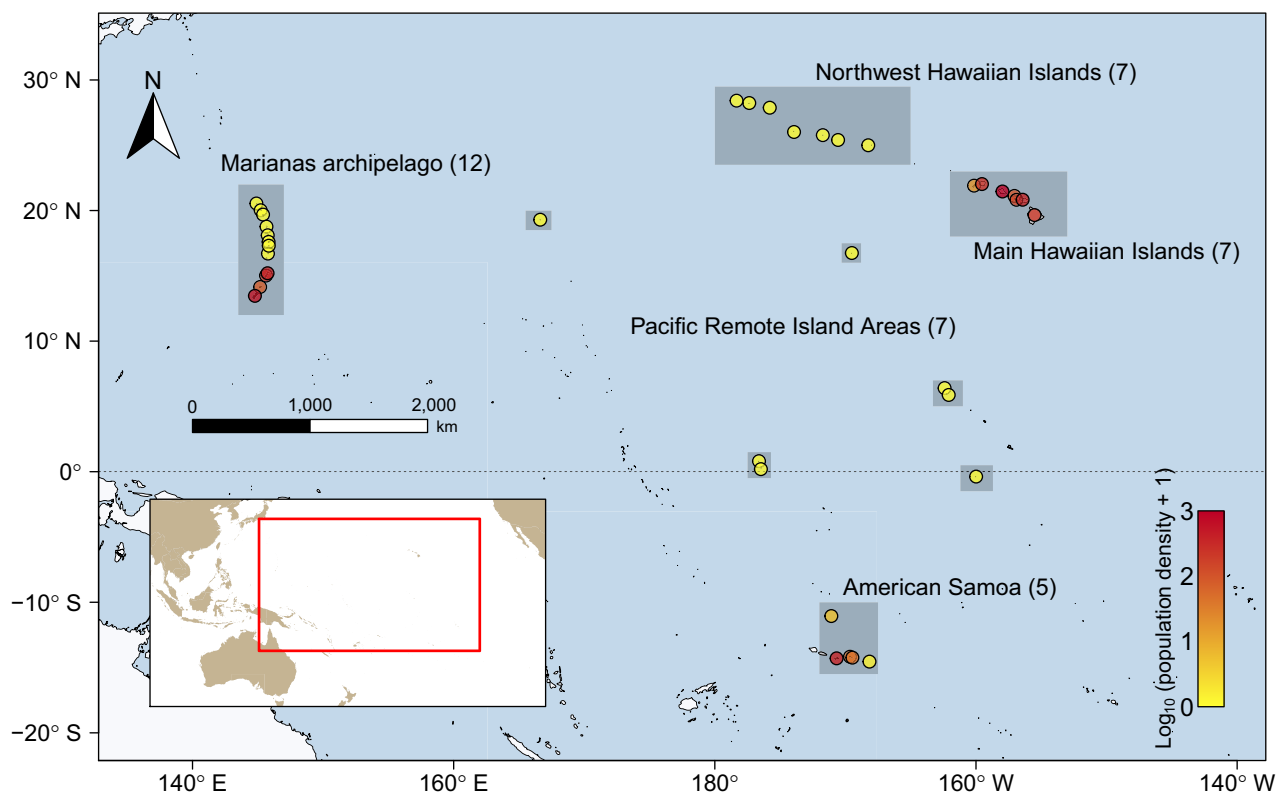
### Study location and survey data

We examined reef fish communities at 2124 sites located on 38 US-affiliated Pacific islands, atolls, and banks (hereafter islands) (Fig. 1) that were surveyed between 2010 and 2014 by the Pacific Reef Assessment and Monitoring Program (Pacific RAMP) of NOAA's Coral Reef Ecosystem Program (CREP). Surveyed islands encompass substantial gradients in biodiversity, productivity, and temperature, and span human population densities from uninhabited atolls to densely populated islands supporting up to 2235 people per km<sup>2</sup> of forereef area (forereef is also referred to as the reef slope, or outer reef) (Table S1) (Williams *et al.*, 2015).

The survey data (Coral Reef Ecosystem Program; Pacific Islands Fisheries Science Center 2015) consist of observations of individual fish made during underwater visual censuses (UVCs) by CREP's highly trained scientific divers. Two divers conducted stationary point counts (SPC), each diver surveying one of two visually estimated adjacent 15 m diameter cylinders along a 30 m transect (survey area = 353 m<sup>2</sup>). Each diver identified every fish species present in or transient through

their cylinder, before enumerating and sizing (total length to the nearest cm) all observed fishes (Ayotte *et al.*, 2011). CREP surveys were stratified by depth bin, into shallow (0–6 m), mid- (6–18 m) and deep (18–30 m) zones, and we only examined surveys conducted on forereef habitat. The number of surveys at each island was proportional to the total forereef area.

We considered each individual UVC survey recorded by a pair of divers (two CREP cylinders) as a unique site. To analyze fishing impacts at the community level, we aggregated all sites sampled in each year across each island ( $n = 70$  island  $\times$  year combinations). We converted the length estimate from each individual fish to body mass (to the nearest gram) using published length–weight relationships for species or families (Kulbicki *et al.*, 2005; Froese & Pauly, 2016). Because UVC methods of coral reef fish communities can be subject to several potential biases (Bozec *et al.*, 2011), we excluded all fish < 20 g body mass to avoid underestimating the abundance of small cryptic fishes (Ackerman & Bellwood, 2000; Wilson *et al.*, 2010). In addition, large mobile piscivores (i.e., sharks and jacks) are often overestimated in small-scale noninstantaneous underwater visual surveys (Ward-Paige *et al.*, 2010) and may also be attracted to divers at remote islands (Parrish *et al.*, 2000; Richards *et al.*, 2011). Both biases can substantially inflate biomass estimates, and we therefore followed other recent large-scale studies of reef fish communities by excluding sharks and jacks from our analyses (MacNeil *et al.*, 2015; Williams *et al.*, 2015).



**Fig. 1** Map of Pacific islands surveyed by CREP ( $n = 38$ ) with each island color coded by human population density [population within a 20 km radius divided by forereef area (km<sup>2</sup>)].

### Reef fish community analyses

We used size spectra to quantify reef fish community structure. The size spectrum is usually fitted to frequencies of body sizes and predicted to approximate a power law distribution (Vidondo *et al.*, 1997; Andersen & Beyer, 2006). Here, we used maximum likelihood estimation to estimate the size spectrum exponent,  $b$  (Vidondo *et al.*, 1997; Edwards, 2008; White *et al.*, 2008; Edwards *et al.*, 2016). We fitted body size data for individual fishes from each island, for each year, to a bounded power law distribution with probability density function

$$f(x) = \frac{(b+1)x^b}{x_{\max}^{b+1} - x_{\min}^{b+1}} \quad (1)$$

where  $x$  is body mass,  $b$  is the scaling exponent, and the distribution is bounded by the minimum and maximum possible body sizes ( $x_{\min}$ ,  $x_{\max}$ ) (White *et al.*, 2008; Edwards *et al.*, 2016). An alternative formulation is required for  $b = -1$ , but this value does not occur for our data. The log-likelihood of a bounded power law is

$$\log[L(b|\text{data})] = n \log \left( \frac{b+1}{x_{\max}^{b+1} - x_{\min}^{b+1}} \right) + b \sum_{j=1}^n \log x_j \quad (2)$$

(Edwards *et al.*, 2016) and was numerically optimized to estimate  $b$ , adapting code from Edwards *et al.* (2012). Unlike binning-based approaches to fitting frequency data, this method has the benefit of consistently producing accurate estimates of  $b$  (Edwards *et al.*, 2016). In our maximum likelihood estimation,  $x_{\min}$  and  $x_{\max}$  are the minimum (i.e.,  $\geq 20$  g) and maximum observed values at each island for each survey year (Edwards *et al.*, 2016).

In most empirical analyses of the aquatic size spectrum, binning-based regression methods are used to estimate a size spectrum slope, and a 'steepening spectrum' is predicted following the selective exploitation of large body sizes (i.e., the slope becomes more negative as the abundance of the largest size classes is depleted relative to small size classes) (e.g., Blanchard *et al.*, 2005; Daan *et al.*, 2005; Graham *et al.*, 2005; Petchey & Belgrano, 2010). Similarly, a 'steepening spectrum' here corresponds to the size spectrum exponent  $b$  becoming more negative. The methods previously used to calculate slopes are inaccurate, and the resulting slopes can be equivalent to either  $b$ ,  $b+1$ , or  $b+2$  depending upon the method (Edwards *et al.*, 2016).

We used a Monte Carlo resampling procedure to correct for differences in sampling effort (i.e., number of UVCs) at each island. Size spectrum exponents were estimated for a random sample (without replacement) of 1000 individual fish at each island in each survey year, and the size spectrum slope was the mean exponent estimate from 10 000 replicate random samples. We used 1000 fish as the number for the random samples to minimize bias in size spectra at low sample sizes while maximizing the number of island-survey year combinations included in our analysis (Fig. S1). Each island-year observation included in the analysis had at least 1000 individual fish observations (Table S2), and we provide example model fits in Fig. S2.

In addition to size spectra, we examined two biomass-based fisheries indicators. First, we quantified overall community

fish biomass ( $\text{kg ha}^{-1}$ , where  $1 \text{ kg ha}^{-1} = 100 \text{ kg km}^{-2}$ ) by averaging biomass across all UVCs at each island for each year. Second, to investigate the extent to which size-selective fishing was responsible for the observed patterns in size spectra exponents and overall community biomass, we estimated the proportion of large fish at each island using a large fish indicator (LFI) (Greenstreet *et al.*, 2011). We defined the LFI as the biomass of fish  $>1$  kg divided by the total biomass of the fish community, averaged across all UVCs at each island for each year.

### Explanatory covariates

We examined variation in community size spectra and fish biomass in relation to two anthropogenic and seven environmental covariates (Tables 1, S1). No standard measure of fishing effort was available across all islands sampled. Instead, we estimated both human population density, expressed as number of people within a 20 km radius divided by the forereef area (Williams *et al.*, 2015), and distance to market (defined as the distance to provincial capital) (Cinner *et al.*, 2012a) as distal metrics of exploitation pressure on coral reef fish communities (Appendix S1). Although human population density is often strongly correlated with a loss of reef fish biomass (Mora, 2008; Williams *et al.*, 2011, 2015; Cinner *et al.*, 2012a), distance to market, which is less commonly employed, may be a more sensitive indicator of fishing intensity on sparsely populated coral reefs (Brewer *et al.*, 2012; Cinner *et al.*, 2012a; D'Agata *et al.*, 2016; Maire *et al.*, 2016). Sea surface temperature (SST) and oceanic productivity also can both positively influence reef fish biomass (Williams *et al.*, 2015), but their influence on community size structure remains unclear. We used remote sensing data to calculate time-averaged estimates of SST ( $^{\circ}\text{C}$ ) and oceanic productivity ( $\text{mg C m}^{-2} \text{ day}^{-1}$ ) at each site (Appendix S1). In addition to oceanographic factors, coral reef fish communities may be influenced by a suite of other biophysical characteristics (Table 1). For example, reef area and island type have been shown to influence reef fish biomass (Cinner *et al.*, 2012a) while at the site-level reefs of high complexity are thought to offer extensive prey refugia that support greater densities of small-bodied fish and steeper size spectra (Wilson *et al.*, 2010; Alvarez-Filip *et al.*, 2011; Rogers *et al.*, 2014). We estimated land area and reef area within a 75 km radius of each site (Appendix S1), classified each island as an atoll (e.g., Kure, Palmyra), island with lagoon or pseudolagoon ('low' island, e.g., Saipan), or island without a lagoon ('high' island, e.g., Oahu) following D'Agata *et al.* (2014), and quantified habitat complexity with both *in situ* (habitat complexity) and remotely sensed (bathymetric slope) estimates at each site (Appendix S1). All site-level explanatory covariates were averaged to give estimates for each island (Table S1).

### Statistical modeling

Prior to analyses, we applied  $\log_{10}$  transformations to distance to market (km), population density per island ( $\log_{10}$  (population + 1) per  $\text{km}^2$ ), and reef area ( $\text{km}^2$ ) to reduce skewness. We



**Table 1** Anthropogenic and environmental covariates included in size spectra and biomass models. Previous studies that examined the influence of each covariate on size spectra and biomass are numbered and categorized by the direction of the relationship they observed (positive, +ve; negative, -ve)

Covariate	Definition	Source	Size spectrum	Fish biomass	
			-ve	+ve	-ve
Human population density	Total population within a 20 km radius divided by forereef area (km <sup>2</sup> ) (2010 estimates)	SEDAC	1, 2, 3	–	6, 7, 8, 9, 10, 11, 12
Proximity to market	Distance to nearest provincial capital (km)	ARC GIS	–	–	10, 11
Minimum SST	Mean of weekly minimum SST (°C) values over 1982–2009 at 4 × 4 km resolution	CoRTAD	–	12	13
Mean productivity	Weekly mean of productivity (mg C m <sup>-2</sup> day <sup>-1</sup> ) values over 2002–2013 for at least 3 1 × 1 km cells	NOAA CoastWatch	–	12, 13	–
Habitat complexity	Mean substrate height within point count cylinder	CREP	3, 4, 5	12, 14, 15	–
Bathymetric slope	Bathymetric slope extent (0–90°) at 1 × 1 km resolution	MARSPEC			
Island type	Atoll, low (island with lagoon or pseudolagoon), high (island without lagoon)	D'Agata <i>et al.</i> (2014)	–		Highest at atolls (11)
Land area	Land area within 75 km radius (km <sup>2</sup> )	Millennium/Coral Reef Habitat Map	–	–	–
Reef area	Total reef area <30 m depth within 75 km radius (km <sup>2</sup> )	Millennium/Coral Reef Habitat Map	–		No effect (11)

Source references and methodological details in Appendix S1. Example references: 1. Dulvy *et al.* (2004); 2. Graham *et al.* (2005); 3. Wilson *et al.* (2010); 4. Alvarez-Filip *et al.* (2011); 5. Rogers *et al.* (2014); 6. Jennings *et al.* (1995); 7. Jennings & Polunin (1997); 8. Mora *et al.* (2011); 9. Williams *et al.* (2011); 10. Brewer *et al.* (2012); 11. Cinner *et al.* (2012a); 12. Williams *et al.* (2015); 13. Barneche *et al.* (2014); 14. Friedlander *et al.* (2003); 15. Graham & Nash (2012).

also centered and standardized all continuous covariates by setting the mean of each covariate to zero and dividing by its standard deviation (Schielezth, 2010). Island type (atoll, low island, high island) was coded as two dummy variables before centering to a mean of zero. Distance to market and population density were strongly negatively correlated ( $r = -0.84$ ), so to avoid collinearity issues, we fitted separate models for each human covariate.

We modeled size spectra exponents and reef fish biomass estimates at the island level. Models were built separately for distance to market and human population density, and the eight environmental covariates were included in every model, producing four saturated models (Appendix S1). The distribution of size spectra exponent estimates  $b$  was normal (Shapiro–Wilk normality test:  $W = 0.992$ ;  $P = 0.934$ ) so we used linear mixed effects models (LME4 package in R; Bates *et al.*, 2015) to examine variation among them. To account for nonindependence of islands that were sampled in multiple years, survey year ( $j$ ) was included as a random effect ( $\rho_j$ ). We modeled reef fish biomass with a gamma distribution and a log link (Zuur *et al.*, 2009), and the same fixed and random effect structure as the size spectra models. Prior to model selection procedures, we assessed evidence of collinearity with variance inflation factors (VIF), where variables with VIF >10 were considered evidence of strong multicollinearity (Zuur *et al.*, 2009). In the saturated size spectrum and reef fish

biomass models every explanatory variable had a VIF <6 so we retained all variables.

We used multimodel inference to examine the fit and parameter importance across different models, which were compiled for all possible subsets of our four saturated models using a dredge function (MUMIN package in R; Barton, 2015). We assessed model support with the Akaike information criterion adjusted for small sample sizes (AIC<sub>c</sub>) (Burnham & Anderson, 2002) and found there was no single top model (i.e., in addition to the best model, there were models with  $\Delta AIC_c < 2$ ). Marginal  $R$ -squared values were estimated for each model using the  $r.squaredGLMM$  function in the MUMIN package. Additionally, following Cade (2015) we examined weighted absolute  $t$ -statistic values across all subset models as a measure of covariate importance. The  $t$ -statistic, which is the parameter estimate divided by the standard error, can be used as a measure of effect size within models. We weighted each absolute  $t$ -statistic by the corresponding model probability (i.e., AIC<sub>c</sub> weight for each model  $i$ ,  $w_i$ ), and to generate confidence intervals, we estimated the weighted sample variance ( $\sigma^2_{\text{weighted}}$ ) for each absolute  $t$ -value ( $t_i$ ) for the weighted mean  $t$ -value ( $\mu$ ):

$$\sigma^2_{\text{weighted}} = \sum_{i=1}^N w_i (t_i - \mu)^2 \quad (3)$$

In this way, the variables that were most important in predicting the given response (i.e., had the strongest effects in the

more probable models) had the largest weighted absolute  $t$ -statistic (Cade, 2015).

To visualize how the most important explanatory covariates influenced size spectra and reef fish biomass, we examined model predictions for each explanatory covariate across the range of observed values while holding all other predictor covariates at their means. We plotted the model-averaged prediction across the top model set ( $\Delta AIC_c < 7$ ) weighted by the corresponding model probabilities (Burnham & Anderson, 2002), and estimated the weighted sample variance as a measure of variability in predictions across the top model set. We visualized the predictions concerning distance-to-market models in the same direction as human population density by plotting predictions against the inverse of distance to market (hereafter 'proximity to market', i.e., for the scaled covariates, islands with high population estimates also had high proximity to market estimates).

We also examined whether changes in size spectra corresponded with changes in reef fish biomass, and whether those relationships differed between populated and uninhabited islands. We fitted linear mixed effects models to examine how size spectra changed across a gradient of reef fish biomass, with habitation (populated or uninhabited islands) as an interaction effect and survey year as a random effect. To explicitly test for size-selective fishing of large body sizes, we used the same approach to examine the relationship between size spectra and the LFI at populated and uninhabited islands (Fig. S1).

Finally, we conducted sensitivity analyses to test the robustness of our results to different treatments of the datasets. UVC methods provide estimates of length rather than mass, and previous studies of reef fish communities have generally fitted length spectra (Dulvy *et al.*, 2004; Graham *et al.*, 2005; Wilson *et al.*, 2010). As such, we also estimated size spectra exponents using reef fish lengths and refitted our statistical models. Model-averaged predictions and weighted mean  $t$ -statistic ratios for reef fish length spectra models identified the same major drivers of spectra exponents as the mass spectra models (Figs S4, S5, Table S5). Estimates of mass spectra facilitate comparisons with our analyses of reef fish biomass, and as a result, we decided to present mass spectra rather than length spectra as our main results.

All analyses were conducted using R version 3.2.0 (R Core Team, 2015), and we provide our code at an open source repository ([github.com/baumlab/robinson-reefs-spectra](https://github.com/baumlab/robinson-reefs-spectra)).

## Results

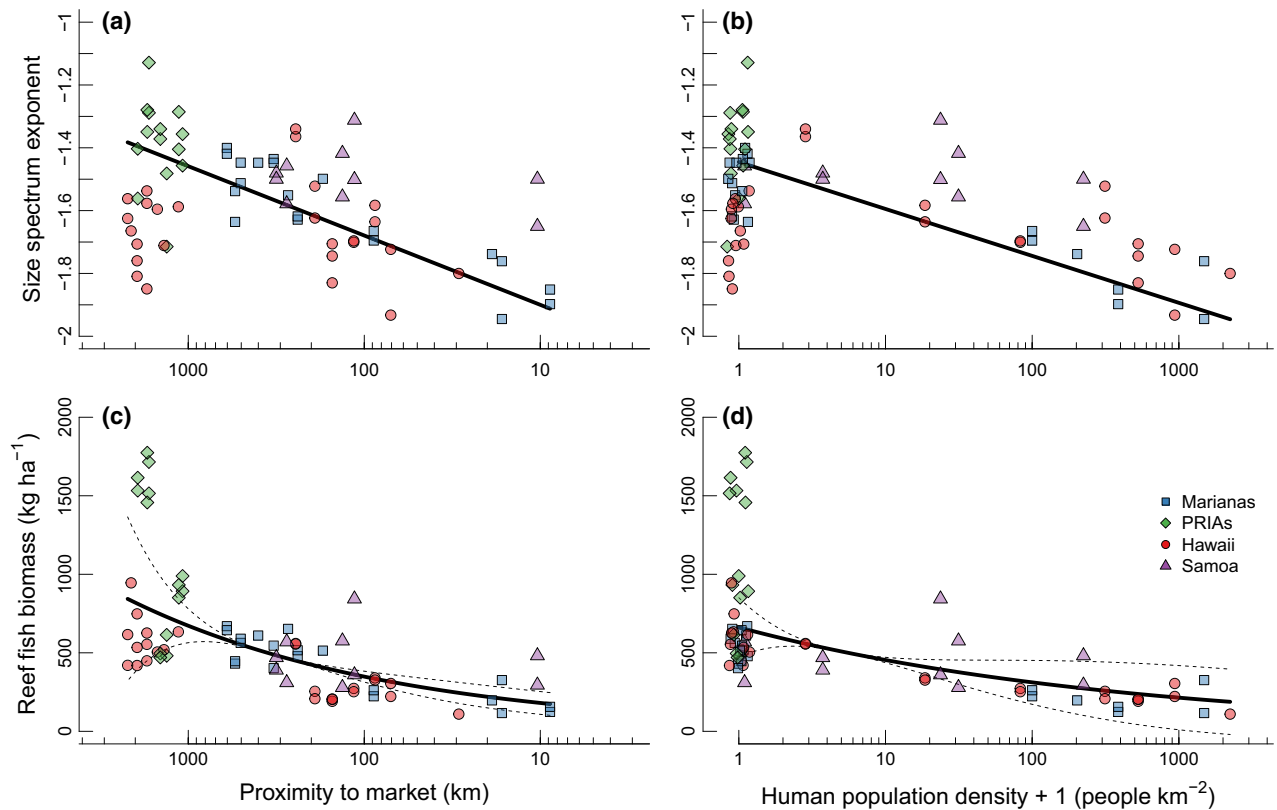
### Size spectra analyses

Reef fish community size structure varied considerably across the gradient of human impacts over the 38 Pacific islands, with size spectra exponents ( $b$ ) ranging from  $-1.95$  to  $-1.13$  (Fig. 2a, b). Modeled anthropogenic and environmental variables explained a large proportion of the variation in size spectra across islands: Across the top model set (all models  $\Delta AIC_c < 7$ ), the range in

$R^2$  was  $0.55$ – $0.58$  and  $0.58$ – $0.60$  for the proximity to market and the human population density models, respectively (Table S3). Size spectra exponents decreased linearly with increasing proximity to market (model-averaged  $t$ -statistic =  $6.77$ ) (Fig. 2a) and with increasing human population density (model-averaged  $t$ -statistic =  $7.83$ ) (Fig. 2b). The steepest size spectra ( $b < -1.8$ ) were generally observed only at reefs with high human population density, which typically also were close to market centers (Pearson correlation =  $0.84$ ), such as Guam, Hawaii, and Oahu (Fig. 2a, b). Regardless of the metric used, human disturbance had the strongest effect on the island-specific size spectra (Fig. 3a). Minimum SST ( $^{\circ}\text{C}$ ) had a strong positive effect on size spectra exponents in top model sets for both proximity to market (model-averaged  $t$ -statistic =  $6.18$ ) and population density ( $4.84$ ) (Fig. 3a), meaning that the size spectra were steeper on cooler islands. The remaining environmental and biogeographic covariates had relatively weak effects on size spectra (all model-averaged  $t$ -statistics  $< 2.2$ ) (Fig. 3a).

### Biomass analyses

Reef fish biomass varied across islands from an estimated  $110 \text{ kg ha}^{-1}$  to over  $1770 \text{ kg ha}^{-1}$  and was lowest at islands with high human presence (Fig. 2c, d). Across the top model set,  $R^2$  ranged from  $0.69$  to  $0.76$  and  $0.67$  to  $0.75$  for the proximity to market and human population density models, respectively (Table S4). As with the size spectra models, human disturbance covariates were the strongest drivers of reef fish biomass (Fig. 3b): reef fish biomass decreased nonlinearly with increasing proximity to market (Fig. 2c) and human population density (Fig. 2d), and only the remote, unpopulated islands supported biomass levels  $> 1000 \text{ kg ha}^{-1}$ . The lowest biomass levels ( $< 200 \text{ kg ha}^{-1}$ ) were observed only at reefs with high human population density, which typically were also close to market centers (Fig. 2c, d). Several environmental covariates were also important drivers of reef fish biomass. Generally, islands with higher minimum SST ( $^{\circ}\text{C}$ ) and higher productivity supported greater biomass (Fig. 3b). However, the relative effects of SST and productivity on biomass differed slightly between model sets (Fig. 3b), with SST the stronger driver in the proximity to market model set (model-averaged  $t$ -statistic =  $4.88$  for proximity to market;  $3.77$  for human population density) and productivity the stronger in the human population density model set ( $2.69$  and  $5.60$ ). Remaining environmental and biogeographic covariates had relatively weak effects on reef fish biomass (all model-averaged  $t$ -statistics  $< 2$ ) (Fig. 3b).



**Fig. 2** Human drivers of coral reef fish size structure and biomass ( $\text{kg ha}^{-1}$ ). Size spectra (a, b) and reef fish biomass (c, d) relationships are model-averaged predictions across the standardized range of (a, c) observed  $\log_{10}$  proximity to provincial capital (km) and (b, d)  $\log_{10}$  (human population density per forereef area + 1) ( $\text{km}^2$ ). Dashed lines are the weighted sample variance at each value of the human covariate (although these are indistinguishable from the model predictions in the size spectra analyses). For visualization purposes, we included the observed data as points plotted against the untransformed human covariates and colored by region (blue squares = Marianas archipelago; red circles = Hawaiian archipelago; green diamonds = Pacific Remote Island Areas; purple triangles = American Samoa). Unpopulated islands have been jittered to distinguish between points with human population density = 0 (b, d).

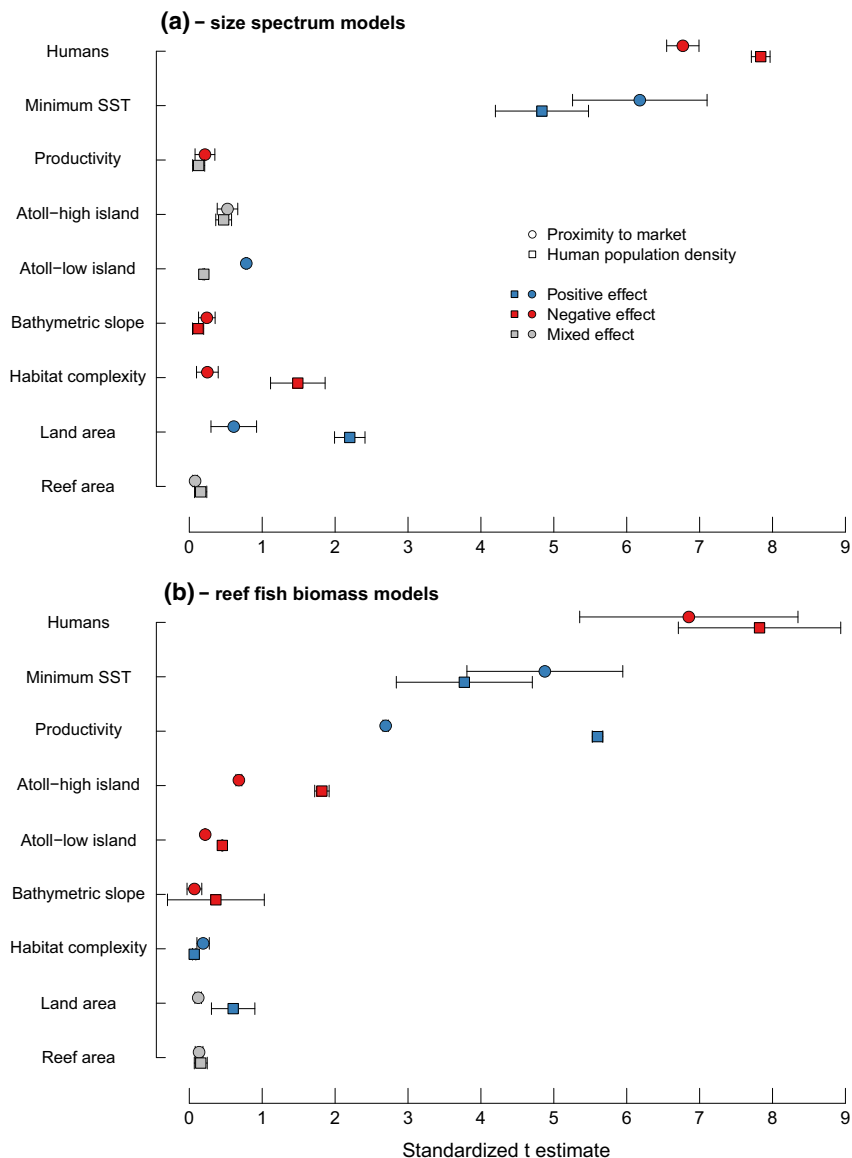
#### *Populated vs. uninhabited reef fish community structure*

At the populated islands, there was a strong relationship between size spectra and reef fish biomass (slope = 0.0008,  $P < 0.001$ ), in which reefs with the steepest size spectra and lowest reef fish biomass were those closest to market centers (Fig. 4). This relationship appeared to be explained by the disproportionate exploitation of large-bodied fishes, as the most negative (i.e., steepest) spectra exponents were associated with particularly low values for the large fish indicator (i.e., low relative biomass of large-bodied fish; slope = 0.9923,  $P < 0.001$ ) (Fig. S3). In contrast, despite substantial variation in size spectra exponents (−1.85 to −1.13) and reef fish biomass (402–1774  $\text{kg ha}^{-1}$ ), both size spectra ~ biomass (Fig. 4; slope = 0.0002) and size spectra ~ LFI relationships (Fig. S3; slope = −0.204) were significantly weaker at the remote, uninhabited islands ( $P < 0.001$ ).

#### **Discussion**

Our analyses reveal that, along a disturbance gradient from reefs of near-pristine wilderness to ones near large population centers, increasing human presence causes a degradation of coral reef fish community size structure. At populated islands, steeper size spectra were associated with a reduction in reef fish biomass and the relative biomass of large-bodied fishes. The specificity of each ecological indicator to human impacts was markedly different, such that size spectra responded solely to human presence and sea surface temperature whereas fish biomass was highly sensitive to even low levels of human presence as well as the influences of temperature and oceanic productivity.

At populated islands, steepening size spectra represent a gradual shift in body size distributions from fish communities with a high relative proportion of large fish (shallow spectra) to ones dominated by small fishes

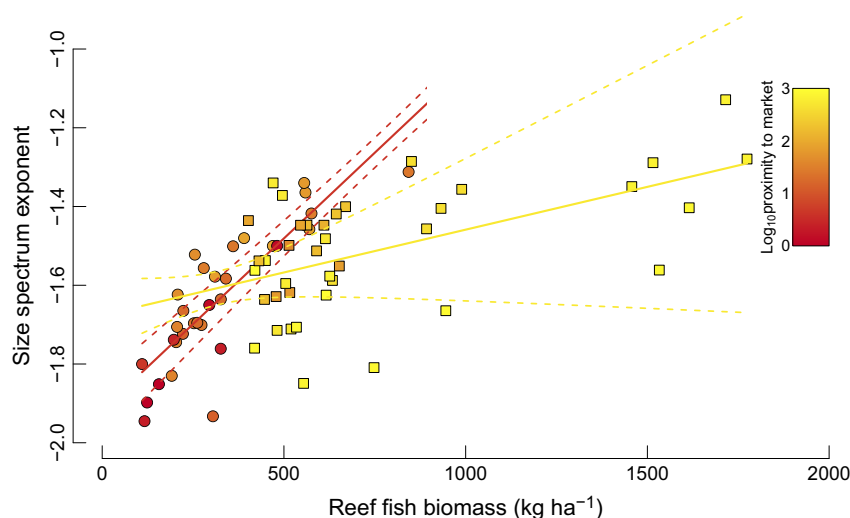


**Fig. 3** Human and environmental drivers of reef fish size structure and biomass. Size spectra (a) and reef fish biomass (b) are presented for the proximity to market (circles) and human population density (squares) full model sets. Points are the weighted absolute  $t$ -values for each explanatory covariate, with weighted sample variance as error bars.  $t$ -values indicate the magnitude of each covariate effect, and colors indicate the direction of each covariate effect (blue = positive; red = negative; gray = mixed). See Tables S3 and S4 for further details.

(steep spectra). Large-bodied fishes can play important roles in maintaining reef functions, suggesting that the loss of these individuals due to size-selective exploitation may have disproportionate functional impacts on coral reefs. For example, many large herbivorous fishes are important bioeroders and control algal growth (Bellwood *et al.*, 2011; Edwards *et al.*, 2013). More generally, large predators can control the stability of prey populations across habitats (Rooney *et al.*, 2006; Britten *et al.*, 2014). Size-selective exploitation of these fishes may therefore impair the ability of reefs to recover from

additional disturbances such as coral bleaching and hurricane damage (Cheal *et al.*, 2013). Size spectra analyses of moderately exploited reef fisheries in Fiji (Dulvy *et al.*, 2004: 1–100 people per km reef front; Graham *et al.*, 2005: 3–300 people per km reef front) previously suggested that harvesting of large-bodied fishes steepens size spectra at small spatial scales. Fishing practices across the Pacific are, however, highly variable, with the gear and associated target species varying across islands and regions (Friedlander & Parrish, 1997; Craig *et al.*, 2008; Houk *et al.*, 2012). Our analyses





**Fig. 4** Change in size spectra across the gradient of reef fish biomass. Each point is a size spectrum exponent and biomass estimate at one island in a single survey year, colored according to  $\log_{10}$  proximity to market estimates. Solid lines are parameter estimates with dashed 95% confidence intervals from a mixed effects model with habitation as an interaction effect. Size spectra  $\sim$  biomass relationships were significantly different between uninhabited (yellow line) and populated (red line) islands.

encompassed regions characterized by a high diversity of fishing gears (Dalzell *et al.*, 1996; Fenner, 2012) and fish species (Kulbicki *et al.*, 2013) and spanned a wider gradient in human population density (0–2235 people per  $\text{km}^2$  forereef area) than previous reef size spectrum studies. Moreover, our two proxies for fishing pressure performed equally well in accounting for these differences in fisheries types (although we note that for future analyses market-based metrics could provide additional information on fishing pressure (Maire *et al.*, 2016), particularly for uninhabited reefs). Overall, our analyses suggest that size-selective exploitation is a pervasive issue on coral reefs at ocean-basin scales, which consistently alters reef community size structure.

Altered community size structure also may have important functional consequences that extend beyond a loss of large-bodied individuals. Size structuring of trophic interactions on coral reefs (Robinson & Baum, 2016) means that communities with steeper size spectra will have a lower mean trophic level (Jennings *et al.*, 2002), consistent with evidence that the mean trophic level of reef fisheries catch is negatively correlated with human population density (Houk *et al.*, 2012). Moreover, communities dominated by smaller individuals have faster rates of population growth (Brown *et al.*, 2004; Blanchard *et al.*, 2012) and biomass turnover (Jennings & Blanchard, 2004), and communities with lower mean trophic level may be less stable (Blanchard *et al.*, 2012; Rochet & Benoit, 2012; Britten *et al.*, 2014) and more sensitive to environmental change (Jennings & Blanchard, 2004). Exploitation of large size classes also may release prey populations from predation pressure

and thus further steepen size spectra (Daan *et al.*, 2005). However, such cascading effects may be difficult to detect in reef systems in which predator–prey interaction strengths are dampened due to large-bodied predators feeding across large spatial scales and across trophic levels (McCauley *et al.*, 2012; Frisch *et al.*, 2014, 2016; Roff *et al.*, 2016). In addition, exploited reef fisheries likely also target medium- and small-bodied fishes, thus depressing any compensatory growth by prey populations. Disentangling the combined effects of trophic release of prey populations and exploitation of smaller size classes therefore remains problematic, but shifts in community size structure along human disturbance gradients may provide an early warning of impacts on functional properties at the community level.

Human-associated declines in total community biomass and large fish biomass have been documented globally across distinct coral reef regions (Roberts, 1995; Mora, 2008; Cinner *et al.*, 2012a; MacNeil *et al.*, 2015; Williams *et al.*, 2015; Nash & Graham, 2016), but the link between community size structure and biomass has not previously been examined. We found that gradual declines in size spectra exponents along either human covariate gradient contrasted with a rapid decrease in reef fish biomass from  $>1500 \text{ kg ha}^{-1}$  at unpopulated islands to  $<600 \text{ kg ha}^{-1}$  at islands with the lowest human presence. These different patterns likely arose because biomass estimates are most strongly influenced by the number of large-bodied fish that are present (Nash & Graham, 2016), whereas size spectra respond to shifts across the entire distribution

of body sizes from the smallest to largest fish, and treat each individual fish equally. At the most degraded reefs where large fishes are absent, fishing of medium- and small-sized fish would further deteriorate community structure but cause less dramatic reductions in fish biomass. In contrast, the size spectra of lightly fished reefs were similar to an undisturbed size spectrum despite biomass values being typical of more heavily disturbed communities. The differential response of community size spectra and community biomass suggests that community size structure may be more resilient than fish biomass to light exploitation. These findings are consistent with patterns at coral reefs in the Indian Ocean where the functional composition of fished reefs remains partially intact at biomass levels  $>600 \text{ kg ha}^{-1}$ , despite biomass falling far below that of neighboring unexploited sites (McClanahan *et al.*, 2015). Although recovery of reef fish biomass toward natural baseline levels is an important conservation target that aims to restore ecosystem properties by preserving functionally important species (Knowlton & Jackson, 2008; Bellwood *et al.*, 2011; MacNeil *et al.*, 2015), the maintenance of productive fisheries in populated regions is also a priority (Cinner *et al.*, 2012b; Zeller *et al.*, 2015). Rebuilding community size structure in exploited regions is a realistic management target that may be achieved without implementing the fisheries closures necessary to rebuild pristine biomass (MacNeil *et al.*, 2015). Management for the recovery of community size structure would also benefit from assessments of the influence of shark and jack populations on spectra exponents, as these top predators likely play important roles in structuring reef food webs (Bascompte *et al.*, 2005; Rooney *et al.*, 2006) but are largely absent in heavily exploited regions (Roff *et al.*, 2016).

Although human covariates were the strongest predictors of size spectra, additional variation was attributed to differences in sea surface temperature. Metabolic principles predict that, in warmer environments, increases in individual energy demands drive greater per-capita consumption rates and strengthen top-down control of prey populations (Bruno *et al.*, 2015; DeLong *et al.*, 2015). Therefore, in agreement with our results, warmer islands should be characterized by shallower size spectra (lower abundance of small-bodied fish relative to large-bodied fish). However, difficulties with UVC methods in accurately enumerating large predator populations (Ward-Paige *et al.*, 2010) prevented the inclusion of some groups of large predators in our size spectra analyses; our results, therefore, can provide only incomplete evidence in support of stronger top-down control. Although metabolic approaches have provided valuable insights into environmental constraints on reef fish community biomass and trophic

structure (Barneche *et al.*, 2014, 2016), theoretical predictions of the effect of temperature on reef fish size distributions are lacking. As size spectra were robust across gradients in other environmental covariates, improved understanding of temperature control of size spectra would help the development of predictions of natural baselines for reef fish community size structure. Such understanding also is increasingly important as climate change warms reef systems and degrades fish habitat, further stressing reef fish populations (Hoegh-Guldberg *et al.*, 2007).

We also detected a strong influence of oceanic productivity on reef fish biomass, which is consistent with previous observations that high oceanic production promotes planktivorous fish abundance (Barneche *et al.*, 2014; Williams *et al.*, 2015). Subsequent increases in energy availability to upper trophic levels promote greater total community biomass (Friedlander *et al.*, 2003; Cinner *et al.*, 2009; Williams *et al.*, 2015) although, interestingly, these apparent differences in energy availability did not affect size spectra. The lack of a strong response by size spectra at the island scale suggests that the extrabiomass afforded by high productivity may be evenly redistributed among all body sizes. Temperature was also a positive influence on biomass. A previous analysis of the CREP dataset detected this effect only in planktivorous fishes (Williams *et al.*, 2015), and other studies have variously noted positive (Richards *et al.*, 2012) and negative (Barneche *et al.*, 2014) effects of temperature on reef fishes, indicating that further study of the influence of temperature on biomass is warranted. We did not detect a strong influence of habitat complexity on either reef fish size spectra or biomass, despite evidence that habitat complexity enhances reef fish biomass and steepens size spectra by increasing survival rates of small-bodied fishes (Graham & Nash, 2012; Rogers *et al.*, 2014). The influence of habitat complexity on reef fish assemblages may only be detectable at smaller spatial scales than our island-scale approach (which required averaging of structural complexity estimates across survey sites), and this variable should not be overlooked in future analyses of reef fish size spectra.

The apparent lack of environmental influences on size spectra – with the exception of temperature – across islands that varied greatly in environmental setting and biogeographic context supports the utility of size spectra as a robust ecological indicator of fishing. In temperate systems, size-based indicators have proven to be powerful methods of assessing exploitation effects across communities of different compositions (Bianchi *et al.*, 2000; Shin *et al.*, 2005). In reef fisheries, which typically lack adequate catch and survey data (Sadovy, 2005), UVC monitoring programs can provide

the body length information required for size spectra analyses (Graham *et al.*, 2005; Nash & Graham, 2016). Size-based indicators also can effectively link patterns in community structure with less tangible community-level properties such as production and biomass turnover rates. Given their sensitivity to environmental influences and strong response at low levels of exploitation, biomass estimates may be less reliable as ecological indicators at large spatial scales.

Although we accounted for several potential sampling issues in our analyses, size spectra estimates derived from different UVC methods might vary substantially and we therefore caution against comparisons of size spectra derived from different UVC sampling methods or and from different analytical techniques (Edwards *et al.*, 2016). Limitations of census methods can introduce error in the counts of small or large size classes (Bozec *et al.*, 2011) that bias exponent estimates or produce nonlinear size spectra (Ackerman *et al.*, 2004). Spectra estimated with biased binning-based methods (e.g., earlier reef spectra studies (Dulvy *et al.*, 2004; Graham *et al.*, 2005)) can also introduce error in size spectra analyses, while subtle differences between these methods can result in spectra exponents that differ by 1 or 2 (White *et al.*, 2008; Edwards *et al.*, 2016). Difficulties in enumerating fishes accurately across the size spectrum suggest that it may be problematic to produce meaningful empirical estimates of baseline size spectra exponents for coral reefs, as has been done for temperate marine ecosystems (Jennings & Blanchard, 2004). Importantly, by removing some of the largest fish species (the sharks and jacks) that are heavily targeted by fishers, our results are almost certainly a conservative estimate of fishing impacts on reefs and are unlikely to match metabolic predictions for size spectra in which exponents are a simple function of predator–prey mass ratio and trophic energy transfer efficiency (Brown & Gillooly, 2003; Jennings & Blanchard, 2004; Trebilco *et al.*, 2013). For example, excluding sharks and jacks caused size spectra exponents to steepen slightly at most islands in the dataset, and this effect was most pronounced at islands where those species comprised a high proportion of the community abundance (Fig. S6). Without accurate estimates of the true relative abundances of small, medium, and large-bodied fishes, size spectra may be most informative if used to assess relative differences among communities in a space-for-time approach (as we did here) or to assess temporal changes in community size structure (Jennings & Dulvy, 2005).

Across tropical Pacific coral reef ecosystems, islands with a strong human presence were characterized by degraded coral reef fish community size structure. Steepening size spectra suggest a shift in size-linked

life-history traits, implying that fished communities may have reduced resilience to further exploitation and future environmental change. Given comparative insensitivity to variation in environmental conditions, size spectra may prove to be effective ecological indicators of exploitation impacts on reef fisheries (Graham *et al.*, 2005; Shin *et al.*, 2005; Nash & Graham, 2016). Extreme reductions in reef fish biomass can have potentially wide-ranging and pervasive consequences for reef ecosystems, particularly when species or trophic groups that provide key ecosystem functions are depleted (Bellwood *et al.*, 2011; McClanahan *et al.*, 2011, 2015; Ruttenberg *et al.*, 2011). However, despite the loss of biomass at lightly exploited islands, we detected weaker impacts on size spectra exponents that suggest that maintenance of ecological size structure is a tangible management target that could enhance the ecological resilience of coral reef ecosystems.

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## Supporting Information

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

**Appendix S1.** Explanatory covariate processing.

**Figure S1.** Sensitivity of size spectrum exponent to bootstrap sample size.

**Figure S2.** Fit of size spectrum model to reef fish data.

**Figure S3.** Relationship between size spectra exponents and the LFI.

**Figure S4.** Length spectra exponents across proximity to market (a) and human population density (b).

**Figure S5.** Model parameter estimates for length spectra.

**Figure S6.** Influence of shark and jack species on size spectrum exponent.

**Table S1.** Covariate estimates for CREP reef areas.

**Table S2.** Reef areas surveyed in the CREP dataset.

**Table S3.** Parameter estimates and model fit for top size spectra model set ( $\Delta\text{AICc} < 7$ ).

**Table S4.** Parameter estimates and model fit for top biomass model set ( $\Delta\text{AICc} < 7$ ).

**Table S5.** Parameter estimates and model fit for top length spectra model set ( $\Delta\text{AICc} < 7$ ).