# Fishing degrades size structure of coral reef fish communities

Running head: *Fishing alters reef fish size structure*

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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 of coral reef fish communities at 38 US-affiliated Pacific islands, spanning from near pristine to highly human populated. Reef fish community size spectra slopes ‘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. In contrast, total fish community biomass was substantially lower on inhabited islands than uninhabited ones, regardless of human population density. Comparing the relationship between size spectra and reef fish biomass, we found that on populated islands size spectra steepened linearly with declining biomass, whereas on uninhabited islands size spectra and biomass were unrelated. Size spectra slopes also 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 biophysical conditions, being influenced by oceanic productivity, sea surface temperature, island type, and habitat complexity. Our results suggest that community size structure is more robust than total 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

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abiotic variation across biogeographic regions, offer great potential for developing our understanding of fishing impacts in coral reef ecosystems.

## 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 alter the structure and function of marine ecosystems (Jackson et al., 2001; Travis et al., 2014). Selective fishing of large consumers can produce 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 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). 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 multi-species and multi-gear (Hicks & McClanahan, 2012), but catch and effort data are typically limited (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 systems, trophic interactions are size-based and 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 (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; Trebilco et al., 2013). 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), 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 metric of fishery health and of exploitation impacts at regional scales (Cinner et al., 2009; Cinner et al., 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., 2011), 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). Other direct comparisons between fished and protected areas have found that community size structure is highly variable and unrelated to exploitation, which may reflect unmeasured environmental influences (McClanahan & Graham, 2005; Graham et al., 2007). As a result, 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; MacNeil et al., 2015; McClanahan et al., 2015). Similar examination of reef fish community size structure across large spatial scales and gradients in fished biomass 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 slopes to assess shifts in community structure across a body size range from tiny planktivores (20g) to large piscivores (> 1kg), 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 2,124 sites located on 38 U.S.-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 2,235 people/km$^2$ forereef habitat (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), with each surveying one of two adjacent visually estimated 15 m diameter cylinders along a 30 m transect (survey area = 353 $m^2$). 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 analyse fishing impacts at the community level we aggregated all sites sampled in each year across each island (n = 70 island *x* 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 non-instantaneous 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).

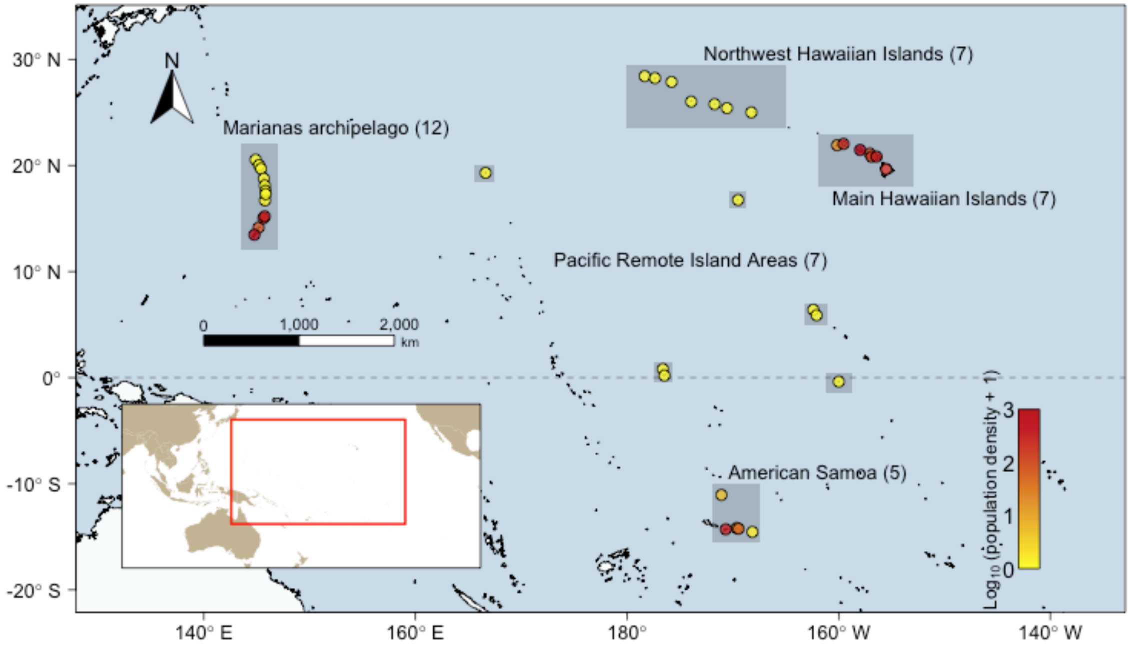

Fig. 1. Map of Pacific islands surveyed by CREP (n = 38) with each coloured by human population density. Human population density is population per forereef area ($km^2$) within a 20 km radius on a $\log_{10}$ scale.

*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 (Eq. 1) (Vidondo et al., 1997; Andersen & Beyer, 2006). Here, we used maximum likelihood estimation to estimate the size spectrum slope, $b$ (Vidondo et al.,

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1997; Edwards, 2008). We fitted body size data for individual fishes from each island, for each year, to a bounded power law distribution with probability density function:

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

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). Equation 1 is undefined for $b = -1$, but this value does not occur for our data. The log-likelihood of a bounded power law is:

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

(Edwards et al., in revision) and was numerically optimized to estimate $b$ (Edwards, 2008; Edwards et al., 2012). Unlike binning-based approaches to fitting frequency data, this method has the benefit of producing accurate estimates of $b$ (Edwards et al., in revision). In our maximum likelihood estimation, $x_{\min}$ and $x_{\max}$ are the minimum (i.e. 20 g) and maximum observed values at each island within a single survey year (Edwards et al., 2012). In most empirical analyses of the aquatic size spectrum, binning-based methods are used to estimate $b$, such that the regression slope is the parameter of interest and a 'steepening spectrum' is predicted following the selective exploitation of large body sizes (i.e. the regression slope, or $b$, becomes more negative as the abundance of the largest size classes is depleted relative to small size classes) (Daan et al., 2005; Blanchard et al., 2005; Graham et al., 2005; Petchey & Belgrano, 2010). For consistency with these studies, we refer to the power law exponent $b$ as the size spectrum slope (see also Edwards et al., in revision).

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We used a Monte Carlo resampling procedure to correct for differences in sampling effort (i.e. number of UVCs) at each island. Size spectrum slopes 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 slope estimate from 10,000 replicate random samples. Each island included in the analysis had at least 1000 individual fish observations (Table S2).

In addition to size spectra, we examined two biomass–based fisheries indicators. First, we quantified overall community fish biomass (kg ha$^{-1}$) 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 slopes 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 > 1kg 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 six 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; Cinner et al., 2012a; Williams et al., 2015), 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; 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 (°C) and oceanic productivity (mg C $m^{-2}$ $day^{-1}$) 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 75 km radius of each site (Appendix S1), classified each island as an atoll (e.g. Kure, Palmyra), island with lagoon or pseudo-lagoon ('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).

| | | | Size spectrum | Fish biomass | |
|---|---|---|---|---|---|
| Covariate | Definition | Source | -ve | +ve | -ve |
| Human population density | Total population within a 20 km radius per reef area (km$^2$) | 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 4x4 km resolution | CoRTAD | - | 12 | 13 |
| Mean productivity | Weekly mean of productivity (mg C m$^{-2}$ day$^{-1}$) values over 2002-2013 for at least 3 1x1 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 1x1 km resolution | MARSPEC | | | |
| Island type | Atoll, low (island with lagoon or pseudo-lagoon), high (island without lagoon) | D'Agata et al. (2014) | - | Highest at atolls (11) | |
| Land area | Land area within 75 km radius (km$^2$) | Millennium/Coral Reef Habitat Map | - | - | - |
| Reef area | Total reef area <30 m depth within 75 km radius (km$^2$) | 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)

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).

*Statistical modeling*

Prior to analyses, we applied $\log_{10}$ transformations to distance to market (km), population density per island ($\log_{10}$ (density + 1) per km$^2$), and reef area (km$^2$) to reduce skewness. We also centered and standardized all continuous covariates (Schielzeth, 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 modelled size spectra slopes and reef fish biomass estimates against the eight anthropogenic and environmental covariates at the island level. The distribution of size spectra 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 amongst them. To account for instances of islands 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 effects 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.

We used multimodel inference to examine models based on all possible subsets of our anthropogenic and environmental covariates using a dredge function (MuMIn package in R; Barton, 2015). We assessed model support with the Akaike Information Criterion adjusted for small sample sizes ($AIC_c$) (Burnham & Anderson, 2002) and found there was no single top model (i.e. $\Delta AIC_c > 2$). Instead, following Cade (2015) we examined weighted absolute t-statistic values across all subset models as a measure of covariate importance. The t-statistic can be used as a measure of effect size within models as it is the parameter estimate divided by the standard error. We weighted each t-statistic by the corresponding model probability (i.e. $AIC_c$ weight for each model $i$, $w_i$), and estimated the weighted sample variance ($\sigma^2$) for each t-value ($x_i$) for the weighted mean t-value ($\mu$):

$$\sigma^2_{weighted} = \sum_{i=1}^{N} w_i (x_i - \mu)^2 \qquad [3]$$

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.

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 if changes in size spectra corresponded with changes in reef fish biomass, and if those relationships differed between populated and uninhabited islands. We fitted linear mixed models to examine how size spectra changed across a gradient of reef fish biomass, treating populated and uninhabited islands separately and including 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 slopes using reef fish lengths and refitted our statistical models. Model averaged predictions and weighted mean t-statistic ratios for reef fish length spectra models were similar to results from mass spectra models (Figs. S2, S3, 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).

## Results

### *Size spectra analyses*

Reef fish community size structure varied considerably across the gradient of human impacts over 38 Pacific islands, with size spectra slopes (*b*) ranging from -1.13 down to -1.95 (Fig. 2a,b). The human disturbance and several environmental variables explained a large proportion of the variation in size spectra across islands. Across the top model set (all models < 7 ΔAICc), the range in $R^2$ was 0.56 – 0.59 and 0.61 – 0.65 for the proximity to market and human population density models, respectively (Table S3). Regardless of the metric used, human disturbance had the strongest effect on the size spectrum at a given island (Fig. 3a). Size spectra slopes decreased linearly with increasing proximity to market (model averaged t-statistic = 6.87) (Fig. 2a) and with increasing human population density (model averaged t-statistic = 7.85) (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 centres (Pearson correlation = 0.84) (Fig. 2a,b). Apart from human impact covariates, minimum SST (°C) had a strong positive effect on size spectra slopes in top model sets for both proximity to market (model averaged t-statistic = 6.23) and population density (4.93). The remaining environmental and biogeographic covariates had relatively weak effects on size spectra (all model averaged t-statistics < 2.4) (Fig. 3a).

*Biomass analyses*

Reef fish biomass varied across islands from an estimated 110 kg ha$^{-1}$ to over 2900 kg ha$^{-1}$, and was lowest at islands with high human presence. Across the top model set, $R^2$ ranged from 0.54 – 0.59 and 0.53 – 0.58 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 non-linearly with increasing proximity to market (Fig. 2c) and human population density (Fig. 2d), and only the remote, unpopulated islands supported biomass levels >1000 kg ha$^{-1}$. The lowest biomass levels (<200 kg ha$^{-1}$) were observed only at reefs with high human population density, which typically were also close to market centres (Fig. 2c,d). Several environmental covariates were also important drivers of reef fish biomass. Generally, islands with higher minimum SST (°C) and higher productivity supported greater biomass (Fig. 3b). However, the relative effects of SST and productivity on biomass differed slightly between model sets, with SST the stronger driver in the proximity to market model set (model averaged t-statistic = 4.33 for proximity to market; 3.40 for human population density) and productivity the stronger in the human population density model set (3.16 and 5.11). For both model sets, atolls supported greater biomass than high (t-statistics: 1.53 and 2.56 for proximity to market and human population density, respectively) and low islands (0.41 and 1.08), and more complex habitats were associated with higher biomass levels (2.32 and 1.23) (Fig. 3b).

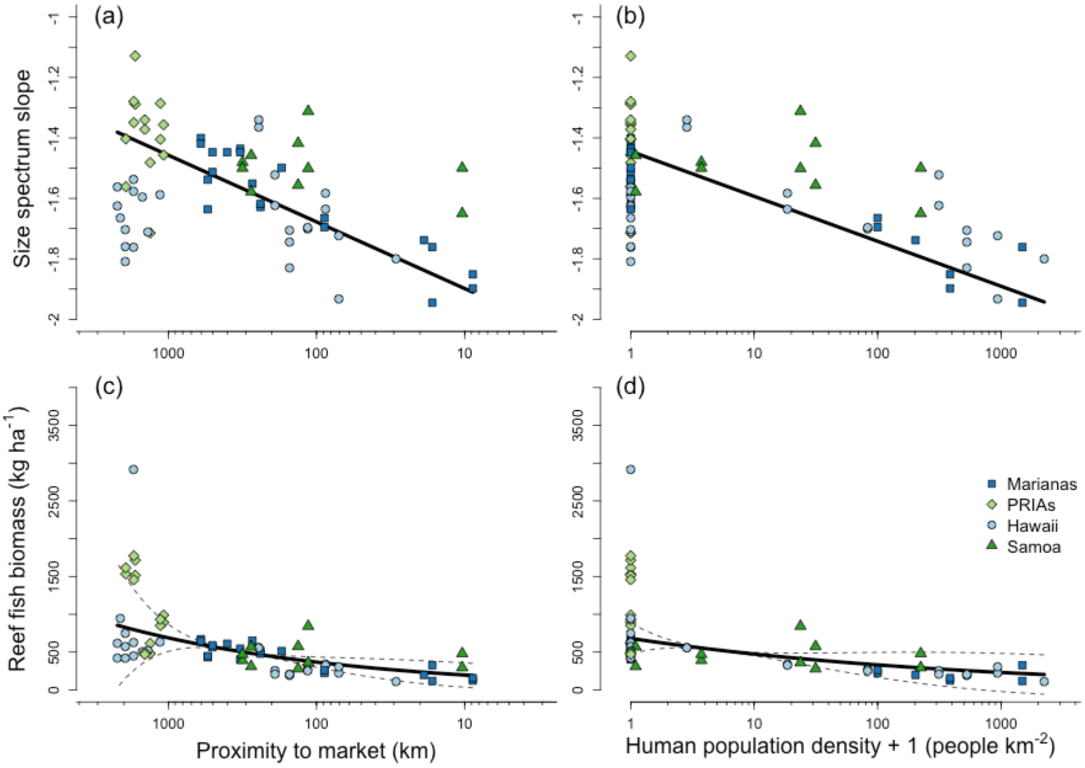

Fig. 2. Human drivers of coral reef fish community size structure and biomass (kg ha$^{-1}$). Size spectra (a) and reef fish biomass (b) relationships are model averaged predictions across the standardized range of observed log$_{10}$ proximity to provincial capital (km) and log$_{10}$ human population density per forereef area (km$^2$) (b, d respectively). Predictions were made across the top model set (ΔAICc < 7) and weighted using model probabilities (Tables S3, S4), while holding all other relevant covariates to their mean observed value. Dashed lines are the weighted sample variance at each value of human covariate (though 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 coloured by region (dark blue squares = Marianas archipelago; light blue circles = Hawaiian archipelago, light green diamonds = Pacific Remote Island Areas, dark green triangles = American Samoa).

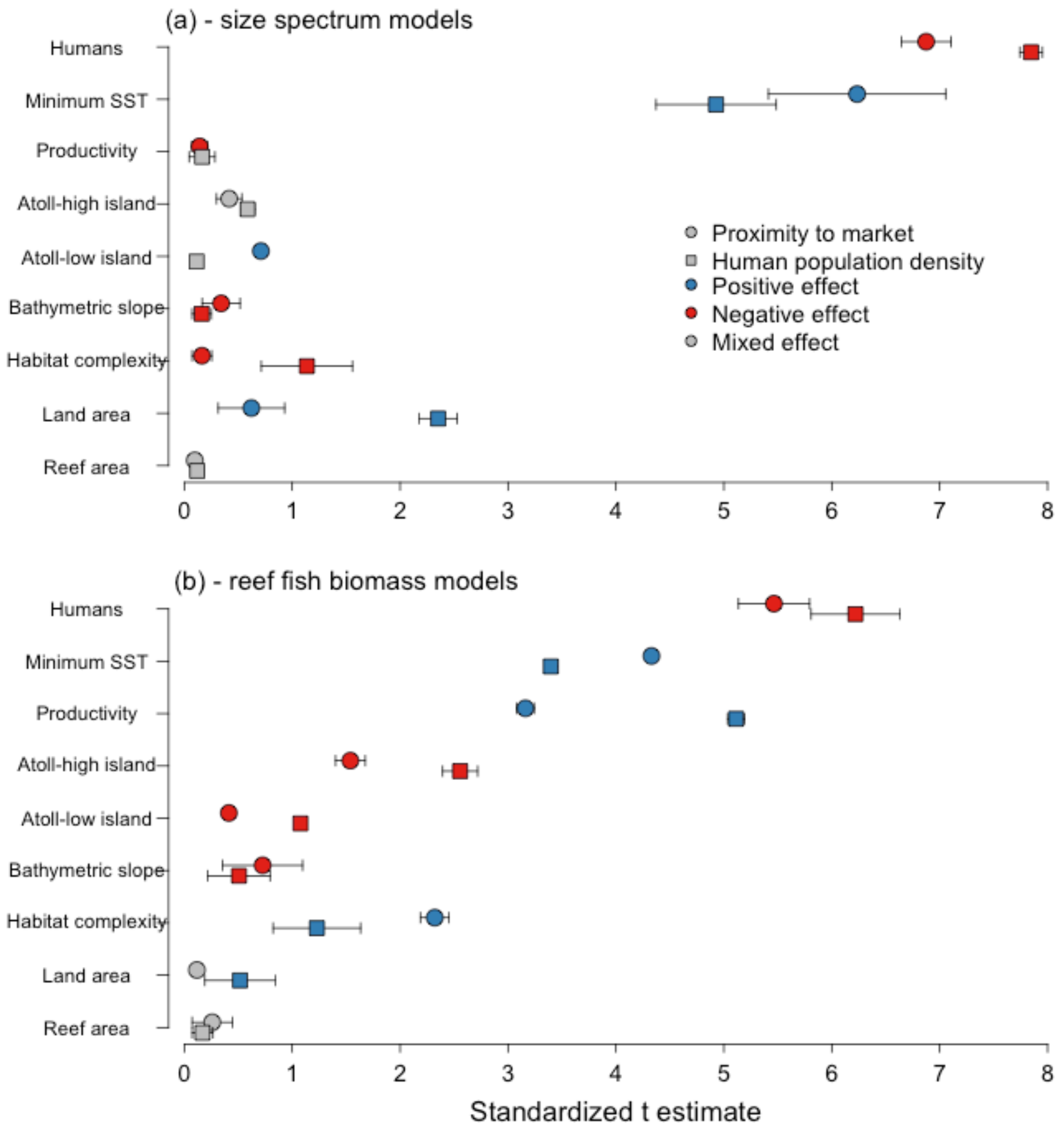

Fig. 3. Human and environmental drivers of reef fish size structure and biomass. Size spectra (a) and reef fish biomass (b) are presented for the distance to market (circles) and human population density (squares) full model sets. Points are the weighted absolute t-values for each explanatory covariate, 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; grey = mixed). See Tables S3 and S4 for further details.

*Populated vs. uninhabited reef fish community structure*

At the populated islands, there was a strong relationship between size spectra and reef fish biomass ($P < 0.001$, $R^2 = 0.70$) (Fig. 4). This relationship appeared to be explained by the disproportionate exploitation of large-bodied fishes, since the most negative (i.e. steepest) spectra slopes were associated with particularly low values for the large fish indicator (i.e. low relative biomass of large-bodied fish; $P < 0.001$, $R^2 = 0.30$) (Fig. S1). In contrast, despite substantial variation in size spectra slopes (-1.81 to -1.13) and reef fish biomass (402 to 2917 kg ha$^{-1}$), size spectra did not consistently covary with either fish biomass ($P = 0.172$, $R^2 = 0.05$) (Fig. 4) or the large fish indicator ($P = 0.316$, $R^2 = 0.03$) at the remote, uninhabited islands (Fig. S1).

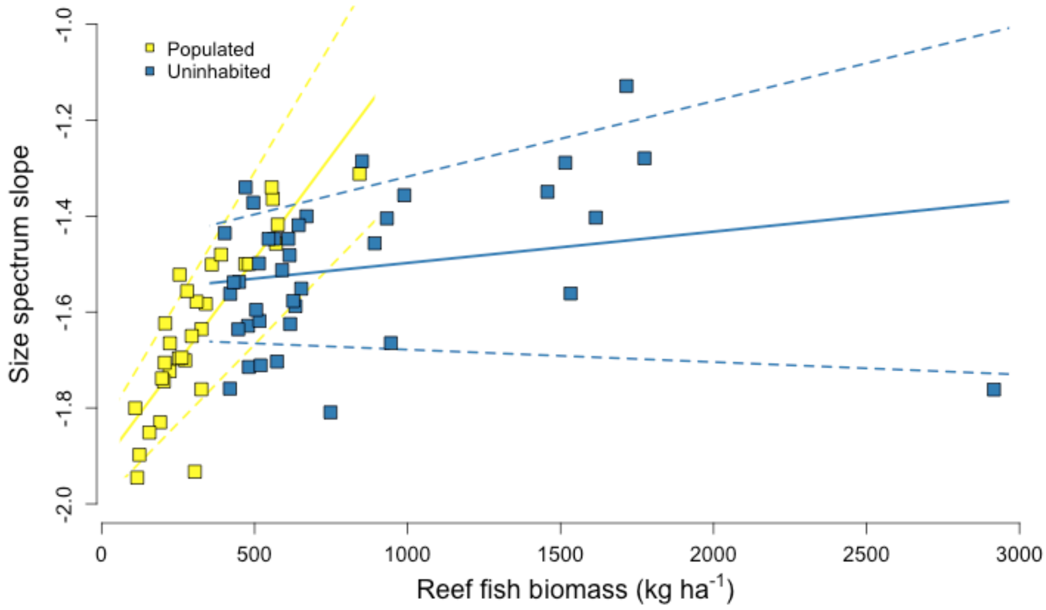

Fig. 4. Change in size spectra across the gradient of reef fish biomass. Size spectra ~ biomass relationships were fitted separately to uninhabited (blue) and populated (yellow) islands. Solid lines are linear regression slope estimates with 95% confidence intervals. Each point is a size spectrum slope and biomass estimate at one island in a single survey year.

## Discussion

Our analyses reveal that, along a disturbance gradient from reefs of near-pristine wilderness to degraded reefs at developed population centres, increasing human presence causes a gradual degradation of coral reef fish community size structure. At populated islands, steeper size spectrum slopes were associated with a reduction in total 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 to solely to human presence and sea surface temperature whereas total biomass was highly sensitive to low levels of human presence as well as influences of temperature, oceanic productivity, and island geomorphology.

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 slopes) to ones dominated by small fishes (steep slopes). Large-bodied fishes 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 encompass regions characterized by a high diversity of fishing gears (Dalzell et al., 1996; Fenner, 2012) and fish species (Kulbicki et al., 2013), and span a wider gradient in human population density (0 – 2,235 people per km$^2$ forereef area) than that of previous studies. As such, we show 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 apex predators feeding across large spatial scales and across trophic levels (McCauley et al., 2012; Frisch et al., 2014; Frisch et al., 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 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 slopes along either human covariate gradient contrasted with a rapid decrease in reef fish biomass from > 1500 kg ha$^{-1}$ at unpopulated islands to < 600 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 total community biomass. In contrast, the size spectra of lightly fished reefs were similar that of an undisturbed size spectrum despite supporting biomass values 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 total 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 kg ha$^{-1}$, despite total biomass falling far below that of neighbouring unexploited sites (McClanahan et al., 2015). Although recovery of reef fish biomass towards 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 for rebuilding 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 slopes, 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 small-scale 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. Since 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 strong influences of oceanic productivity and habitat complexity on reef fish biomass. These patterns are broadly consistent with previous observations that high oceanic production promotes planktivorous fish abundance (Barneche et al., 2014; Williams et al., 2015) and high structural complexity promotes survival of small-bodied fishes (Graham & Nash, 2012; Rogers et al., 2014). 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) though, 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 extra biomass afforded by high productivity and habitat complexity may be equitably 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.

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 programmes 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. Limitations of census methods can introduce error in the counts of small or large size classes (Bozec et al., 2011) that bias slope estimates or produce non-linear 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 even result in spectra slopes that differ by 1 (White et al., 2008). Difficulties in enumerating fishes accurately across the size spectrum suggest that it may be problematic to produce meaningful empirical estimates of baseline size spectra slopes, 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 slopes are a simple function of predator-prey mass ratio and trophic energy transfer efficiency (Brown & Gillooly, 2003; Jennings & Blanchard, 2004; Trebilco et al., 2013). Instead, 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.

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; Ruttenberg et al., 2011; McClanahan et al., 2015). However, despite the loss of biomass at lightly exploited islands, we detected weaker impacts on size spectra slopes 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**

Appendix S1. Explanatory covariate processing.

Figure S1. Relationship between size spectra slopes and the LFI at populated and uninhabited reef areas.

Figure S2. Length spectra slopes across proximity to market (a) and human population density (b).

Figure S3. Model parameter estimates for length spectra.

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 ($\Delta$AICc < 7).

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

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