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Trophic roles determine coral reef fish community size structure

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	Trophic roles determine coral reef fish community size structure
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Abstract

- 32 Relationships between abundance ~ body size and trophic position ~ body size can reveal size structuring in food webs, and test ecological theory. Although there is considerable
- 34 evidence of size structuring in temperate aquatic food webs, little is known about the structure of tropical coral reef food webs. Here, we use underwater visual census data and
- nitrogen stable isotope analysis to test if coral reef fish communities are 1) size structuredand 2) follow metabolic scaling rules. Examining individuals from over 160 species
- 38 spanning four orders of magnitude in body size, we show that abundance scaled negatively with body size and, as predicted, individuals sharing energy through predation
- 40 (carnivorous fishes) scaled more steeply than those individuals sharing a common energy source (herbivorous fishes). Estimated size spectra were, however, shallower than
- 42 predicted by metabolic theory. Trophic position scaled positively with body size across species and across individuals, providing novel evidence of size structuring in a diverse
- 44 tropical food web. Size-based approaches hold great promise for integrating the complexities of food webs into simple quantitative measures, thus providing new insights

46 into the structure and function of aquatic ecosystems.

48 Keywords: Body size; size spectrum; metabolic theory; herbivory; stable isotopes

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54 Introduction

Elucidating the structure of natural food webs can provide fundamental insight 56 into ecosystem dynamics, including energy fluxes (Lindeman 1942; Rooney et al. 2008), trophic cascades (Bascompte et al. 2005; Tunney et al. 2012), and potentially the

mechanisms underlying ecosystem stability (May 1973; Rooney & McCann 2012).General patterns relating to body size may be of particular importance since individual

- 60 metabolic rates, and thus many important biological processes, vary consistently with body size (Peters 1983; Brown et al. 2004). In size-structured food webs, predators are
- 62 typically larger than their prey (Elton 1927; Brose et al. 2006) and abundance is predicted to scale with body size due to energetic constraints (Brown & Gillooly 2003).
- 64 Specifically, when individuals share a common energy source abundance is predicted to scale with body mass (M) as $\sim M^{-3/4}$ (the energetic equivalence hypothesis) (Brown &
- 66 Gillooly 2003), whereas when individuals compete for energy through predation at multiple trophic levels, abundance is further constrained by inefficient energy transfer
- across trophic levels and predicted to scale as $\sim M^{-1}$ (trophic transfer correction) when the predator-prey mass ratio is 10⁴ and transfer efficiency is 10% (Jennings & Mackinson
- 70 2003; Trebilco et al. 2013).

Size structuring in aquatic food webs is driven by two mechanisms that reflect

72 size-based feeding amongst individuals: first, gape limitation restricts the size of prey that many aquatic species can consume (Brose et al. 2006; Barnes et al. 2010), and second,

- ontogenetic diet shifts often lead to increases in trophic position as individuals grow(Mittelbach & Persson 1998). As a result, trophic position is often positively related to
- body size in aquatic food webs both at the species (Brose et al. 2006) and individual level

(Jennings et al. 2001). Size structuring of abundance and individual trophic position has

- been clearly demonstrated in both temperate freshwater (Mittelbach & Persson 1998,Cohen et al. 2003) and marine food webs (Jennings et al. 2001; Jennings & Mackinson
- 2003). Similarly, metabolic scaling predictions (Brown & Gillooly 2003) have beenbroadly validated in freshwater (Reuman et al. 2008) and marine food webs (Jennings &
- 82 Mackinson 2003). However, equivalent tests of size structuring in tropical systems are few, and tests of metabolic predictions are lacking entirely. One study of a tropical
- 84 riverine food web, which found that trophic position was unrelated to body size despite a significant positive correlation between mean predator body size and prey size (Layman
- 86 et al. 2005), concluded that the broad range of primary consumer body sizes in their system accounted for this difference from the structure of temperate food webs. However,
- 88 community-wide analyses of tropical size structure remain relatively unexplored. On tropical coral reefs, the application of sized-based approaches has been
- 90 restricted to observations of body size distributions in degraded regions or to diet
- 92 individual abundance body size relationship have been used to describe reef fish community structure along gradients of fishing effort (Dulvy et al. 2004; Wilson et al.

analyses of individual species. For example, size spectra – a widely used form of

- 94 2010) and habitat complexity (Alvarez-Filip et al. 2011). Though consistent with sizestructured abundances, size spectra have typically been fitted to narrow body size ranges
- 96 (~ 10-60 cm) and used to detect community change rather than to delineate trophic
 structure. Similarly, tests of ontogenetic diet shifts often focus on intraspecific
- relationships for single or few species (Greenwood et al. 2010; Plass-Johnson et al. 2012;

Hilting et al. 2013) and thus fail to examine size-based relationships at the community 100 level.

Attempts to infer food web structure through body size relationships should also

- account for distinct feeding strategies within the same community size spectrum.Metabolic theory predicts that abundance body size relationships are dependent on how
- energy is utilised within a community (Brown & Gillooly 2003). For example, in theNorth Sea food web, the size spectrum of the benthic community that feeds on a shared
- energy source is shallower than the predation-based pelagic community size spectrum(Maxwell & Jennings 2006; Blanchard et al. 2009). Distinct trophic pathways also are
- 108 expected in coral reef ecosystems where, specifically, herbivorous and detritivorous fishes share benthic material (Dromard et al. 2015) while planktivorous fishes derive
- energy from pelagic sources (Wyatt et al. 2012). Small to medium-sized mesopredator fishes feed on reef fish and invertebrate species, thus accessing benthic and pelagic
- 112 energy sources within the reef habitat and competing across trophic levels (Rogers et al 2014), while large predatory reef fish may forage more widely than mesopredators and
- couple pelagic open-ocean and benthic reef habitats (McCauley et al. 2012; Frisch et al.2014). By considering size-based patterns within the distinct trophic pathways of
- 116 herbivores and carnivores we can examine food web structure in the context of metabolic predictions.
- 118 Here, we capitalize on the opportunity to sample a minimally impacted coral reef in order to empirically test the hypotheses that coral reef food webs are size structured
- 120 and fit predictions from metabolic theory. We combine visual census data with stable isotope samples from Kiritimati, a remote atoll in the central equatorial Pacific, to

- 122 examine the food web structure of a diverse tropical fish community spanning four orders of magnitude in body mass. We expected negative abundance - body size relationships
- and positive trophic position body size relationships, consistent with size structuring.We also expected steeper body size relationships for both trophic position and abundance
- 126 in a predation-based community (carnivores) relative to an energy-sharing community (herbivores).

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Materials and methods

130 Study site and data collection

We examined a minimally disturbed coral reef fish community on Kiritimati

- 132 (Christmas Island) in the equatorial Pacific Ocean (Fig. 1). Kiritimati supports a population of at least 5500 people that is concentrated around several villages on the
- 134 northwest coast (Kiribati National Statistics Office 2012). Subsistence fishing is the primary human impact on the atoll, and has been associated with decreases in reef fish
- 136 biomass and top predator abundance (Sandin et al. 2008). Fishing activities are, however, mostly concentrated around the villages on the northwest coast, whereas the reefs on the
- north, east, and south coasts are relatively undisturbed (Walsh 2011; M. Watson, D.Claar, J. Baum, unpublished data). The northwest coast of Kiritimati is also subject to
- 140 oceanic upwelling of nutrients, but industrial and agricultural nutrient run-off is virtually non-existent around the atoll (Walsh 2011). We enumerated and sampled coral reef fishes
- 142 at fourteen minimally disturbed sites on Kiritimati's north and east coasts (Fig. 1), in order to reduce potentially confounding effects of fishing and nutrient inputs on trophic
- 144 structure (Post 2002).

To quantify coral reef fish community structure, fish abundance and size data were recorded during SCUBA underwater visual censuses (UVC) at shallow forereef sites (n = 14, 10-12 m depth) around Kiritimati in July and August of 2011 and 2013 (Fig.

- 148 1). During each census, two experienced scientific divers identified, counted and sized (total length, to the nearest cm) reef fishes by swimming in tandem along 25 m long belt
- transects whose bearings were determined haphazardly such that they remained within the 10-12 m depth isobath. On each transect, fishes ≥ 20 cm total length were counted
- 152 along the transect in an 8 m wide strip, before counting fishes < 20 cm total length along the reverse direction in a 4 m wide strip. Three transects, each separated by 10 m, were
- surveyed at each site during each UVC such that the total area surveyed per UVC was 600 m^2 (i.e. 3 X 25 X 8 m) for large fishes and 300 m² for small fishes. Before analyzing
- 156 the UVC data, we standardized the sampling area by doubling all counts of the small fishes (< 20 cm) for each transect. Each site was surveyed once in 2011 and twice in
- 158 2013, all during daylight hours. All surveys were conducted by only four divers, with a single diver participating in every survey. To reduce observation error, for two days on
- 160 Kiritimati immediately before beginning visual censuses, each diver refamiliarized themselves with fish species identification as well as with underwater size estimation,
- using PVC objects of fixed sizes (Bell et al. 1985); divers typically could estimate fish lengths with minimal error (e.g. $\pm 3\%$). Fish length estimates were converted to body
- 164 mass (grams) using published species-specific length-weight relationships (Kulbicki et al.
 2005; Froese and Pauly 2012).
- 166 To quantify coral reef trophic structure, we collected specimens of the most abundant fish species on Kiritimati (as determined by UVCs conducted in 2007 (Walsh

- 168 2011) and 2009) for each of the five major putative functional groups (described below;Table 1). For each species, we aimed to collect individuals spanning the entire species'
- 170 body size range, with a minimum of three individuals in each \log_2 mass bin. In July-August of 2011 and 2012, divers captured fish using a combination of custom built
- microspears, pole spears, and spear guns at shallow forereef sites (n = 10, 8-12 m depth).Fish were captured opportunistically, and the number of specimens per site varied from 6
- to 79 (mean = 34). Specimens were immediately put on ice until dissection later that evening (typically \sim 4-8 hours between collection and dissection). Prior to dissection,
- 176 each individual was photographed, weighed, and measured to the nearest millimeter with vernier calipers (for standard, fork, and total length). We then excised a small sample
- 178 (~10 g) of dorso-lateral white muscle tissue from each fish before freezing at -20 °C.Samples were kept frozen with dry ice for transport from Kiritimati to the University of

180 Victoria and then stored at -20 °C until processing. Each white muscle tissue sample was rinsed with de-ionized water, dried at 60 °C

- 182 for 48 hours, and ground to a powder with a mortar and pestle. Tissue samples were weighed to 10 mg and placed into a tin capsule before analysis of nitrogen stable isotope
- 184 concentrations at the Mazumder laboratory (Department of Biology, University of Victoria, BC, Canada). Relative nitrogen content was estimated by continuous flow
- 186 isotope ratio mass spectrometer and reported in parts per million relative to atmospheric $N^2 (\delta^{15}N)$.

188 Coral reef fish functional groups and trophic pathways

We assigned each fish species recorded in our underwater visual censuses to one of five functional groups distinguished by their diet preferences following Deith (2014) (Table 1). We note that species within the 'herbivore' functional group can feed on both

- 192 plant material and detritus. Gut content analyses of our specimens were used to confirm the functional group of each species.
- 194 To account for differences in energy acquisition within the fish community, we aggregated our visual census and isotope data into two groups, carnivores and herbivores
- 196 (Table 1). We hypothesized that planktivores, benthic invertivores, corallivores and piscivores compete for energy in a group that is structured by predation (as in Rogers et
- 198 al. 2014), whereas herbivorous and detritivorous species compete for a shared energy source of plant material and detritus in a separate herbivore group (Choat 1991). In our
- 200 UVC data, nine species were classed as omnivores (Deith 2014). Because omnivores feed on both plant and animal material, these species did not fit into either trophic pathway
- and so were omitted from all analyses. Omnivores comprised only 8.4% of the numerical abundance of fishes in our UVC surveys, and their inclusion as either herbivores or
- 204 carnivores did not qualitatively change our results (see Supplementary Material).

Abundance – body size analyses

- 206 In aquatic systems, the relationship between individual abundance and body size (or size spectrum) has typically been estimated on a logarithmic scale as the slope of the
- 208 linear regression fit to abundance data binned into body size classes (e.g. Jennings et al.
 2001; Jennings & Mackinson 2003). However, recent studies have recognized that, rather
- than forming a bivariate relationship, these types of data follow a frequency distribution(i.e. of the number of individuals at each size), and that binning-based methods yield
- 212 biased slope estimates (Edwards 2008; White et al. 2008). As such, we examined the size structure of fish abundances by fitting the visual census body mass data to a bounded

214 power law distribution (Equation 1):

(1)
$$(b+1)(x_{max}^{b+1}-x_{min}^{b+1})^{-1}x^{b}$$

- 216 where x_{min} and x_{max} are the minimum and maximum observed body masses, respectively, and the exponent *b* describes the relative abundance of different body sizes (Edwards et
- al. 2012). We used maximum likelihood methods to estimate *b* with 95% confidence limits (White et al. 2008).
- 220 Interpretations of how empirical size spectra relate to theoretical metabolic predictions can be confounded by the method used to estimate the slope. Here, we
- 222 explain how our estimates of *b* relate to Brown & Gillooly's (2003) theoretical predictions and to the empirical estimates of others. First, our maximum likelihood
- 224 approach treats untransformed body size data as a continuous variable, whereas metabolic theory describes abundance body mass relationships across logarithmic size bins
- (Brown et al. 2004). As outlined by Reuman et al. (2008), this implies that Brown &Gillooly's (2003) predicted slopes will be one unit shallower than the scaling exponent of
- 228 a power law distribution (Andersen & Beyer 2006). That is, the predicted abundance body mass scaling exponents are b = -1.75 under the energetic equivalence hypothesis
- and b = -2 with the trophic transfer correction (Trebilco et al. 2013), rather than -0.75 and -1 respectively. Second, size spectra slopes are typically estimated empirically using a
- simple logarithmic binning method that also estimates a shallower slope. Here, b + 1 is analogous to a size spectrum slope estimated with a regression of numerical abundance
- against the midpoints of size bins on a log-log scale (Reuman et al. 2008; White et al.2008), but is an unbiased estimate of the relationship. Thus, previous empirical tests of
- theoretical predictions (e.g. Jennings & Mackinson 2003; Blanchard et al. 2009) can also

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simply be corrected (true b = slope - 1) to serve as a useful guideline for interpreting the slopes of our community size spectra.

Here, all observed body masses > 1 g were summed across visual census sites to

- 240 fit the size spectrum of 1) the full reef fish community and 2) each putative trophic pathway (carnivores and herbivores). We tested the robustness of our results several
- 242 ways. First, we examined the potential influences of year and observer by fitting separate size spectra for each year (2011, 2013) and for each dive team (n = 3). Second, although
- 244 our survey sites were selected in order to minimize fishing effects on reef trophic structure, we recognize that sites on Kiritimati's north coast may experience light fishing
- 246 pressure. To test for potential fishing effects we removed north coast sites that are nearest to Kiritimati's population centres and refitted spectra, and also compared size spectra for
- 248 north vs. east coast sites (Supplementary Material). Third, we tested the effect of fitting different body size ranges on exponent estimates, thus excluding either the smallest fishes
- 250 (because our UVCs may have undersampled them) or the largest fishes (because these may be targeted by fishers) (Supplementary Material).

252 **Trophic position estimation**

We assigned all fish specimens to log₂ mass bins (grams) and converted the δ¹⁵N
 values of each individual to trophic position. δ¹⁵N of an organism's tissue reflects its diet and, given that δ¹⁵N increases by a known discrimination factor (Δ¹⁵N) between predator

- and prey, $\delta^{15}N$ can be used as a proxy for trophic position (Post 2002). $\Delta^{15}N$ is commonly set at 3.4‰, though recent work has revealed that $\Delta^{15}N$ decreases with the $\delta^{15}N$ of an
- 258 organism's diet such that upper trophic positions may previously have been underestimated (Caut et al. 2009; Hussey et al. 2014).

260 We estimated carnivore trophic position using Hussey et al.'s (2014) scaled method, which accounts for variation in $\Delta^{15}N$ due to dietary $\delta^{15}N$ (Equation 2):

262 (2)
$$TP_{scaled} = TP_{base} + \frac{\log(\delta^{15}N_{lim} - \delta^{15}N_{base}) - \log(\delta^{15}N_{lim} - \delta^{15}N_{fish})}{k}$$

This method was developed in a meta-analysis of experimental isotope studies of marine

- and freshwater fishes, where $\delta^{15}N_{lim}$ (21.926) and *k* (0.315) are derived from the intercept and slope of the relationship between ΔN and dietary $\delta^{15}N$ (Hussey et al. 2014). Trophic
- 266 position (TP) was estimated relative to the $\delta^{15}N$ of a baseline organism, where TP_{base} was set to 3 and $\delta^{15}N_{base}$ was the mean $\delta^{15}N$ of the smallest planktivore species we sampled on
- 268 Kiritimati (*Chromis vanderbilti*, $\delta^{15}N_{\text{base}} = 10.26$, mass = 0.1 g).

Herbivores are known to fractionate differently than carnivores, with recorded

- 270 Δ^{15} N values ranging from -0.7‰ to 9.2‰ (Vander Zanden & Rasmussen 2001). In herbivorous reef fish, substantially higher feeding and excretion rates are required to
- subsist on low energy algal food sources, driving higher Δ^{15} N rates that range from 2.79 7.22‰ (Mill et al. 2007). We found no evidence of herbivore Δ^{15} N varying with dietary
- 274 δ^{15} N. Instead, we used published Δ^{15} N estimates (Mill et al. 2007) to calculate a mean Δ^{15} N of herbivorous reef fish (4.778‰), before calculating individual trophic position
- with an additive approach (Equation 3) following Post (2002) and Hussey et al. (2014).

(3)
$$TP_{additive} = TP_{base} + \frac{\delta^{15}N_{fish} - \delta^{15}N_{base}}{4.778}$$

- 278 TP_{base} was set to 2 and $\delta^{15}N_{base}$ was the mean $\delta^{15}N$ of the smallest herbivore species (*Centropyge flavissima*, $\delta^{15}N_{base} = 12.21$, mass = 6.5 g).
- **280** Trophic position body size analyses

Though species level predator-prev mass ratios are generally positive (Brose et al.

- 2006), others have suggested that when ontogenetic niche shifts are prevalent, sizestructuring should operate most strongly at the individual level (Jennings et al. 2001). As
- such, we conducted trophic position body size analyses at the species level (i.e. 'crossspecies approach' *sensu* Jennings et al. 2001) and at the individual level to test the
- 286 hypothesis that coral reef food webs are size-structured, and if so, at what level of organization size structuring is evident.
- 288 Phylogenetic patterns in trophic position body size relationships can result in non-independence of data points that can bias analyses of community structure (Jennings
- 290 et al. 2001; Romanuk et al. 2011). To account for this non-independence we used mixed models to fit random structures that accounted for variation shared between individuals of
- 292 the same species and/or family (detailed below). First, in the species-based analyses, we used linear mixed effects models to examine the relationship between the mean trophic
- 294 position of each species and the maximum observed \log_2 body mass of each species across the entire community, while accounting for phylogenetic relatedness of species
- 296 within families. Specifically, we fitted family as a random effect in order to account for non-independence of trophic position - body mass relationships within families, and then
- 298 used the Akaike Information Criterion for small sample sizes (AIC_c) to select the optimum random effects structure (random slope or random intercept model) (Zuur et al.
- 300 2009). Second, in the individual-based analyses, we examined the relationship betweenthe trophic position of individual fishes and their log₂ body mass class. To account for the
- 302 non-independence of individual fishes within species, and species within families, we included both species and family as random effects in a linear mixed effects model and

- again used AIC_c to select the optimum random effects structure. In both the species-based and the individual-based analysis, we tested for differences in slopes of trophic position \sim
- 306 body mass relationships between our two putative trophic pathways, carnivores and herbivores, by assessing the significance of trophic pathway as an interaction term with
- 308 AICc (Burnham & Anderson 2002). We measured the goodness-of-fit of the fixed covariates in each analysis by estimating the marginal R² of each model (Nakagawa &
- 310 Schielzeth 2012). Finally, we conducted sensitivity analyses to test the robustness of our results to different herbivore fractionation values (Δ^{15} N) and different sampling locations
- 312 (Supplementary Material). We note that there are multiple families included in each trophic pathway (Table 1). Thus, although no family contains individuals from both
- 314 trophic pathways, it seems likely that any observed differences in slopes can be attributed to true differences between herbivores and carnivores (as opposed to being conflated with

316 phylogeny).

All abundance ~ body size and trophic position ~ body size analyses were

- performed in R (version 3.0.2; R Development Core Team 2013) using the packagesMuMIn (Barton 2013) and nlme (Pinheiro et al. 2015). The R code used in our analyses
- 320 is available on Github (https://github.com/baumlab/Robinson-Baum_2016_CJFAS).

322 **Results**

Abundance – body size relationships

- In total, 28 831 individual fish from 163 species, ranging in body mass from 1.02 g to 23.04 kg were enumerated in our underwater visual censuses. Of these, 3602 were
- herbivores from 44 species that ranged in size from 1.02 g to 5.87 kg, and 25 229 were

carnivores from 119 species that ranged in size from 1.03 g to 23.04 kg. Mean individual

- 328 size of the herbivore group (mean mass = 230.63 g, SE = 14.72) was greater than the carnivore group (mean mass = 188.83 g, SE = 16.78). These average sizes reflect the high
- 330 proportion of small planktivores in the carnivore group, rather than a disproportionate abundance of large herbivores. For example, for fishes above 20 g, mean carnivore mass
- 332 was 488.74 g and mean herbivore mass was 401.89 g.

When all individual fishes from the full reef fish community were considered

- together, the size spectrum had a negative slope (b = -1.580, 95% CI = -1.585, -1.576), indicating a strong decrease in abundance with increasing body size, consistent with size
- 336 structuring of community abundances. Size spectrum slopes were, however, distinct for herbivore and carnivore trophic pathways (Fig. 2), with the slope of the herbivore group
- 338 (b = -1.270, 95% CI = -1.281, -1.260) significantly shallower than that of the carnivore group (b = -1.644, 95% CI = -1.649, -1.638). In the context of metabolic predictions, the
- 340 herbivore slope (b = -1.270) is shallower than predicted for species within one trophic level (~ -1.75) and the carnivore slope (b = -1.644) is shallower than predicted for species
- across trophic levels (~ -2) (modified from Brown & Gillooly 2003; Reuman et al. 2008).We also examined the effect of sampling bias on *b* by fitting spectra across different body
- 344 size ranges. We found that removing the largest individuals had a minimal effect on the *b* estimate for carnivores but made the herbivore estimate shallower, while removing the
- 346 smallest individuals steepened the slope of both carnivores and herbivores considerably(Supplementary Material). For example, by only including fishes > 8 g in our analyses
- our estimated size spectrum slopes for herbivores and carnivores were b = -1.494 and b = -1.775, respectively (Supplementary Material). Overall, across all body size ranges

- 350 sampled as well as all other sensitivity analyses (i.e. across different years, divers, and sampling locations), the herbivore spectrum was always significantly shallower than the
- 352 carnivore spectrum and the slopes for herbivores and carnivores were always shallower than predicted by metabolic theory (Supplementary Material).

354 **Trophic position – body size relationships**

From twenty-three species within five functional groups, we sampled a total of 356 344 fish ranging in body size from 0.1 g to 6.35 kg (Table 1). Of these, the trophic position of herbivores ranged from 1.76 to 2.62, and that of carnivores ranged from 2.42

- to 5.06. In the species-based analysis, trophic position increased significantly with maximum \log_2 body mass across all species (estimate = 0.12, P = 0.002) (Fig. 3a; Table
- 2). After aggregating individuals according to their trophic pathway, we found that the best model (as assessed by AIC_c) was the random intercept model with family as a
- 362 random effect (so accounting for similar trophic position body mass relationships within families) and with trophic pathway (carnivore, herbivore) included as an interaction term
- 364 (Fig. 3b; Table 2). The relationship between trophic position and maximum \log_2 body mass was positive and significant (estimate = 0.114, P = 0.002), but was not significantly
- 366 different between carnivores and herbivores (estimate = -0.061, P = 0.636; Table 2). This form of the model did, however, account for a much greater proportion of the variability
- 368 (Fig. 3b) than the model in which all species were aggregated (Fig. 3a). In the individualbased analysis, the trophic position of individual fishes also increased significantly with
- 370 their \log_2 body mass across the community, but with a shallower slope than in the species-based analysis (estimate = 0.067, P < 0.001) and with very little of the variability
- 372 explained (Fig. 3c). Once trophic pathways were included, as with the species-based

analysis, the optimum individual-based model included the log₂ body mass class*trophic

- 374 pathway interaction term and much more of the variability was explained: the slope of the relationship between trophic position body size was positive and significant (estimate =
- 376 0.071, P = 0.004), but again was not significantly different between carnivores and herbivores (estimate = 0.004, P = 0.943) (Fig. 3d, Table 2). In both individual-based
- 378 models (i.e. with and without trophic pathways considered), AIC_c supported a random slope and intercept structure with species nested within family as the random effect, thus
- allowing trophic position body mass relationships to vary between species and families(Supplementary Material). For both the species-based and individual-based models,
- 382 slopes were not distinct between herbivores and carnivores for any of the random effects structures that we fitted (random slopes or random intercepts, families and/or species).
- 384 We note that, in the individual-based models, had we not taken into account nonindependence between species and families we would have found significantly different
- slopes between carnivores and herbivores (estimate = -0.066, P = 0.022). We found no evidence that relationships were influenced by sampling location (north or south coast
- 388 sites) or our assumed herbivore fractionation value (Supplementary Material).

390 **Discussion**

Our analyses of visual census and stable isotope data provide solid quantitative evidence that coral reef food webs are size structured. Abundance - body mass relationships were negative, indicating energetic constraints on community structure in

394 accordance with size-based theory (Trebilco et al. 2013). Trophic position - body mass relationships were significantly positive across species and across individuals, revealing

- 396 strong size-based feeding in a diverse tropical food web. We also found differences in size spectra between carnivorous and herbivorous fish species that are consistent with
- 398 Brown & Gillooly's (2003) prediction that body size scaling relationships reflect differences in energy acquisition between individuals sharing energy and individuals
- 400 competing across trophic levels.

Abundance - body size relationships

- 402 We found strong evidence that abundance scales negatively with body size in coral reef communities, for individuals spanning across four orders of magnitude in body
- 404 size. Our results align with ecological theory that energetic constraints cause abundance to scale negatively with body size (Brown & Gillooly 2003; Jennings & Mackinson 2003;
- 406 Trebilco et al. 2013) and, specifically, provide the first evidence that reef fish species competing across trophic levels (carnivores) have a steeper size spectrum than reef fish
- 408 species sharing energy within a trophic level (herbivores) (Brown & Gillooly 2003). Previous analyses of size spectra on coral reefs, which were focused on examining how
- 410 size spectra change with fishing pressure rather than testing macroecological theory, examined data from moderately to highly degraded systems and sampled individuals
- from a narrower range of body sizes (~10-60 cm) (Dulvy et al. 2004; Graham et al. 2005;Wilson et al. 2010). These studies used binning-based methods and fitted size spectra
- 414 with body lengths rather than masses making direct comparisons to our results difficult. Our results are more directly comparable with Ackerman et al.'s (2004) census of reef
- 416 fish > 1 g that, once corrected for their binning-based slope estimate, yields a size spectrum slope of $b = -1.75 \pm 0.34$ 95% confidence interval, which is steeper than our
- 418 estimate for the full community size spectrum slope (b = -1.580) but still overlaps our

95% CI. Herein, we have also extended the size spectrum approach to show that the size

- 420 structuring of reef fish abundances is dependent on how energy is shared within the reef community, suggesting that the food web structure of a diverse tropical community is
- 422 governed by energetic constraints on size spectra that are similar to predictions for pelagic marine ecosystems (Brown & Gillooly 2003; Blanchard et al. 2009).
- 424 Our size spectra estimates were, however, shallower than predictions from metabolic theory and size-based theory for body size scaling relationships (i.e. the
- 426 energetic equivalence hypothesis, and the trophic transfer correction) (Brown & Gillooly 2003; Trebilco et al. 2013). Empirical tests of abundance body size relationships may
- 428 deviate from theory when abundance estimates fail to account for every species that shares energy within the community (Maxwell & Jennings 2006; Jennings et al. 2007).
- 430 Accurately quantifying the abundance of small cryptic fish species (Bozec et al. 2011), nocturnal fish species, and the invertebrate species that compete with small fishes
- 432 (Ackerman et al. 2004) is a challenge inherent to all UVC methods, including ours on Kiritimati. By underestimating the smallest individuals that contribute to energy flux in
- the coral reef food web, size spectra slope estimates will be biased upwards. Indeed, we found that our estimated size spectra slopes steepened when we sequentially removed the
- 436 smallest size classes from the data set, suggesting that our underwater visual censuses had not quantified all of the smallest fishes in the community. Non-instantaneous UVC
- 438 methods also can overestimate or underestimate the abundance of large mobile fishes depending on fish behaviour (Ward-Paige et al. 2010; Bozec et al. 2011), and thus bias
- 440 spectra estimates upwards or downwards. However, given that large individuals are considerably lower in abundance than small individuals, and that in probabilistic spectra

- 442 fitting methods each individual counted is treated equally, we expect that this bias would be quite small.
- 444 In addition to the potential bias introduced by underwater visual census methods, exploitation pressure can steepen the size spectrum by reducing the abundance of the
- largest size classes (Blanchard et al. 2009). We attempted to reduce any potentialinfluence of fishing pressure on trophic structure by sampling at minimally disturbed sites
- on Kiritimati. However, slopes did become slightly shallower (from -1.644 and -1.270 to
 -1.553 and -1.223 for carnivores and herbivores, respectively) after excluding the four
- 450 sites nearest to Kiritimati's villages, consistent with predicted fishing effects on the size spectrum (Supplementary Material). Nevertheless, the pattern we observed that herbivore
- 452 size spectra were significantly shallower than carnivore size spectra was consistent across all sites and body size ranges (Supplementary Material), indicating that the influence of
- 454 fishing on our results is minimal.

Trophic position - body size relationships

- 456 We also found strong evidence that trophic position increases with body size in coral reef food webs. In contrast to previous stable isotope analyses in reef systems, our
- 458 results suggest that coral reef food webs are structured by size-based feeding relationships at both the species and individual level. For example, previous tests of
- 460 feeding relationships have reported positive, negative and non-significant relationships between δ^{15} N and body size within individual reef fish species (Greenwood et al. 2010).
- 462 However, a lack of statistical power can prevent detection of intra-specific shifts in δ^{15} N (Galvan et al. 2010). In the only previous comparison of feeding relationships across
- 464 multiple coral reef species that we are aware of, δ^{15} N body length relationships were

positive across five carnivorous species, consistent with the carnivore size structuring in

- 466 our results, but non-significant across four herbivorous species (de la Morinière et al.2003). Our finding that the trophic position of herbivorous fish increased with body size
- 468 (from 1.76 to 2.62) was therefore unexpected. Enriched individual δ^{15} N may result from increased consumption of detritus and small benthic invertebrates by herbivorous
- 470 surgeonfish species (Acanthuridae) (Carassou et al. 2008; Dromard et al. 2015). We note that, in general, understanding of trophic fractionation in herbivorous fishes remains
- 472 limited (Mill et al. 2007) and assigning trophic positions to herbivorous reef fish is an area requiring further study. Nevertheless, our herbivore trophic position body size
- 474 relationships are robust to varying ΔN (Supplementary Material), indicating that the consumption of $\delta^{15}N$ enriched detritus and invertebrates may increase with herbivore
- 476 body size.

Despite evidence from gut content analyses that fish predators are generally larger

- 478 than their prey in temperate marine systems (Barnes et al. 2010), species-based tests of size structure using stable isotopes have produced equivocal results. For example,
- 480 Jennings et al.'s (2001) study found a positive trophic position body size relationship for fishes in the Celtic Sea but a non-significant relationship for fishes in the North Sea. In a
- 482 tropical stream food web, despite gut content analysis revealing size-structured feeding relationships, isotope analysis of the full food web found no relationship between
- 484 predator size and trophic position (Layman et al. 2005). We caution that in size-structured communities, where an individual's ecological role is best defined by its size rather than
- 486 its species, species-based tests may obscure positive relationships between trophic position and body size that are evident at the individual level, if size is not controlled for

- 488 in the study design. Here, because we sampled across the size range of each species we were able to detect positive trophic position body size relationships at both the
- 490 individual and the species level.

Two additional factors that may have limited the ability of previous studies to

- 492 detect positive trophic position body size relationships are variability in trophic fractionation values between trophic positions (Hussey et al. 2014) and confounding
- 494 effects of phylogeny (Romanuk et al. 2011). Romanuk et al. (2011), for example,highlighted the importance of considering evolutionary history in analyses of diverse
- 496 communities where, by accounting for the non-independence of species within orders, their analysis of a global dataset of fish species found that species-based trophic position
- 498 body size relationships are positive. In contrast, if we had failed to include a random effects structure in our individual-based model, we would have identified a significant
- 500 difference between the trophic position body mass relationships of carnivore and herbivores. Without appropriate consideration of potential errors in the conversion of
- 502 δ^{15} N to trophic positions and in the statistical treatment of phylogenetic relationships, examination of trophic structure from stable isotope analyses can be misleading.

504

Trophic pathways on coral reefs

- We found that carnivores and herbivores were characterized by distinct
 abundance body size relationships, though they had similar trophic position body size
 relationships. Only a few previous studies have examined the effect of metabolic
 constraints on abundance body size relationships as we did here. Our results align well
- 510 with observations that the North Sea benthic community has a shallower spectrum than

the belagic community (Maxwell & Jennings 2006, Blanchard et al. 2009). In the No	the 1	pelagic	community	(Maxwell)	& Jenn	ings 2006	Blanchard	et al	2009)	In the	Nor
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- 512 Sea, the detection of size spectra based on different modes of energy acquisition provided further insights into energy flux through the food web, where Blanchard et al. (2009)
- 514 examined how the energy-sharing community could be coupled to a steep predationbased community by large mobile predators to confer food web stability. Their model has
- 516 since been adapted to examine the coupling of size spectra between carnivore and herbivore groups in a Caribbean reef food web (Rogers et al. 2014). Though Rogers et al.
- 518 (2014) did not compare size spectrum slope estimates between groups, our analyses provide empirical support for distinct structuring of herbivore and carnivore groups.
- 520 Beyond body size relationships, analysis of trophic pathways in other systems have used carbon isotope signatures to identify distinct energy sources and thus track
- 522 energy flux through food web compartments or 'channels' (Rooney et al. 2006). Though we did not have sufficient carbon samples for the reef fish we sampled on Kiritimati,
- 524 others have identified discrete benthic (Dromard et al. 2015) and pelagic (Wyatt et al. 2012) energy sources on coral reefs, and mixed benthic-pelagic diets of large predatory
- 526 fish species in these ecosystems (McCauley et al. 2012; Frisch et al. 2014). We suggest that our results provide a useful foundation for future examination of coupled food web
- 528 structure in coral reef systems. Notably, theoretical models and empirical analyses suggest that coupling by mobile consumers can foster food web stability (Rooney et al.
- 530 2006; Blanchard et al. 2009; Britten et al. 2014) and, given the widespread decline in top predator abundance on reefs (Williams et al. 2010; Nadon et al. 2012), it is critical that
- 532 we develop a greater understanding of how differences in energy utilization between trophic pathways may define the structure of coral reef food webs.

- 534 We present novel evidence of size structuring in a minimally impacted diverse tropical food web, spanning 163 species across four orders of magnitude in body mass.
- 536 By combining visual census data with stable isotope analysis we were able to examine the scaling of body size with both abundance and trophic position. Differences in the size
- 538 spectra of carnivores and herbivores reflected energetic constraints on abundance body size relationships between individuals sharing energy and those competing across trophic
- 540 levels, but did not tightly match theoretical predictions. Our analyses offer new perspectives on the structure of coral reef food webs, and we suggest that future studies
- 542 strive to further delineate community structure through the lens of body size distributions.Overall, size-based approaches hold great promise for integrating the complexities of
- 544 food webs into simple quantitative measures and elucidating fundamental properties of aquatic ecosystems.

546

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Table 1. Body sizes, δ^{15} N values, and sample sizes (*N*) for the twenty-three fish species

- 766 sampled on Kiritimati for the stable isotope analyses, with each species assigned an trophic pathway (carnivore or herbivore) based on their functional group (FG: BI =
- 768 benthic invertivore, Pi = piscivore, ZP = zooplanktivore, De = detritivore, He = herbivore).

			Species		Body	mass (g)		$\delta^{15}N$	
	FG	Family	Scientific name	Common name	Mean	Range	Mean	Range	N
	BI (Chaetodontidae	Chaetodon auriga	Threadfin butterflyfish	87.36	58 - 98.3	14.44	13.68 - 15.6	9
Carnivore			Chaetodon ornatissimus	Ornate butterflyfish	115.84	39 - 173.1	13.38	11.98 - 15.03	21
	Ι	Lethrinidae	Monotaxis grandoculis	Humpnose large-eyed bream	413.38	200 - 1090.8	14.96	12.9 - 15.83	20
	(Cirrhitidae	Paracirrhites arcatus	Arc-eye hawkfish	13.28	2.35 - 31.13	13.15	12.28 - 13.99	10
	N	Mullidae	Parupeneus insularis	Two-saddle goatfish	221.78	45 - 520	12.46	11.22 - 14.4	30
	Pi (Carangidae	Caranx ignobilis	Giant trevally	6350.29	-	12.23	12.23 - 12.23	1
			Caranx melampygus	Bluefin trevally	1851.62	126.6 - 3719.45	12.01	11.21 - 13.28	8
			Carangoides orthogrammus	Island trevally	1732.5	-	13.74	13.74 - 13.74	1
	I	Lutjanidae	Aphareus furca Lutianus bohar	Grey jobfish	274.47	200 - 420	11.4	10.86 - 11.98	17
	ç	Serranidae	Cenhalonholis	red snapper	1092.67	132.7 - 4540	12.23	10.91 - 13.68	23
	L	Serraindae	argus	hind	382.74	200.6 - 1100	13.74	11.71 - 15.67	18
			Cephalopholis urodeta	Darkfin hind	81.67	27.1 - 151.1	11.71	9.11 - 13.59	22
-			Variola louti	Yellow- edged lyretail	1713.3	127.7 - 3405	12.9	11.73 - 14.4	6
	ZP (Caesionidae	Caesio teres	Yellow and blueback fusilier	213.29	6.8 - 470.5	9.59	9.02 - 10.23	19
			Pterocaesio tile	Dark- banded fusilier	57.6	3.7 - 167.2	9.08	8.5 - 9.7	11
	Ι	Pomacentridae	Chromis vanderbilti	Vanderbilt's chromis	0.79	0.1 - 1.8	9.68	8.91 - 10.26	7
	S	Serranidae	Pseudanthias bartlettorum	Bartlett's anthias	2.88	0.8 - 3.5	9.11	7.94 - 9.84	5
			Pseudanthias olivaceus	Olive anthias	5.93	1.2 - 14.9	9.31	8.07 - 10.32	30
	He	Acanthuridae	Acanthurus nigricans	Whitecheek surgeonfish	112.53	44 - 207.06	12.43	11.04 - 13.22	6
Herbivore	F	Pomacanthidae	Centropyge flavissima	Lemonpeel angelfish	14.32	5.53 - 22.2	12.58	11.14 - 13.21	10
	S	Scaridae	Chlorurus sordidus	Daisy parrotfish	309.83	43.1 - 807.3	12.93	11.99 - 14.66	20
			Scarus frenatus	Bridled parrotfish	794.22	388.2 - 1954	13.86	12.72 - 15.17	24
	De	Acanthuridae	Ctenochaetus marginatus	Striped-fin surgeonfish	138.28	41.9 - 258.9	13.36	12.23 - 14.37	26

- Table 2. Parameter estimates of the best model (as evaluated by AIC_c) for trophicposition log₂ body mass relationships in the species-based (linear mixed effects model
- with family as a random effect) and individual-based (linear mixed effects model with species nested within family as a random effect) analyses.

	Coefficient	Estimate	Standard error	P value	Marginal R ²	ΔAIC _c
Spagios basad	Intercept	2.33	0.328	< 0.001	0.17	5 15
Species-based	log_2 mass	^{SS} 0.12 0.029 0.002		0.17	5.45	
	Intercept	2.73	0.282	< 0.001		0
Species-based with trophic	Intercept (herbivore)	-0.978	1.018	0.359	0.62	
pathway	log ₂ mass	0.114	0.028	0.003	0.02	
	log ₂ mass*herbivore	-0.061	0.124	0.636		
Individual-based	Intercept	2.76	0.242	< 0.001	0.04	8.8
	log ₂ mass	0.067	0.02	< 0.001	0.04	
	Intercept	3.09	0.186	< 0.001		
Individual-based with	Intercept (herbivore)	-1.45	0.398	0.004		
trophic pathway	log ₂ mass	0.071	0.024	0.005	0.45	0
	log ₂ mass*herbivore	0.004	0.052	0.943		

- **Fig. 1**. Study sites on Kiritimati, Line Islands, Republic of Kiribati. All sites have minimal fishing pressure and are located on the north and east coast of the atoll, which is
- 778 outside of the upwelling zone on the leeward (lagoon facing) side. Fish specimens were collected at 10 sites in July-Aug of 2011 and 2012 (triangles). Underwater visual
- 780 censuses were carried out at 14 sites in the summers of 2011 and/or 2013 (denoted by circles and triangles). Villages are marked with red circles that are scaled to their
- 782 population sizes.

Fig. 2. Size spectra (i.e. abundance - body size relationships) of the coral reef fish

- community. Left: Rank-frequency plot of reef fish body masses for carnivores (blue, n = 25344 fish) and herbivores (green, n = 3628 fish). Individual body masses are plotted as
- points and overlaid with the fitted size spectrum (i.e. bounded power law distribution).Right: size spectra slopes (*b*) with 95% confidence intervals for carnivores (blue) and

788 herbivores (green).

Fig. 3. Trophic level - body size relationships a, b: Species-based analyses. Linear mixed

- effects models of trophic position and log_2 body mass (g) in the coral reef fish community (a) across all species (n = 23), (b) for the two trophic pathways, carnivores (blue, n = 18
- species) and herbivores (green, n = 5 species). For each species, the mean trophic position and 95% confidence intervals are plotted against its maximum mass. **c**, **d**: Individual-
- based analyses. Linear mixed effects models individual trophic position and of individual \log_2 body mass (g) in the coral reef fish community (c) across all individuals (n = 344)
- and (d) for the two trophic pathways, carnivores (blue, n = 258) and herbivores (green, n = 86). Individual trophic position estimates are plotted against body mass class (with

798 jitter, transparent colour), and overlaid with mean trophic position (solid colour) of each body mass class.



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