ARTICLE

Trophic roles determine coral reef fish community size structure[1]

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Abstract: 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 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 (*i*) are size structured and (*ii*) follow metabolic scaling rules. After examining individuals from over 160 species 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 (carnivorous fishes) scaled more steeply than those individuals sharing a common energy source (herbivorous fishes). Estimated size spectra were, however, shallower than 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 tropical food web. Size-based approaches hold great promise for integrating the complexities of food webs into simple quantitative measures, thus providing new insights into the structure and function of aquatic ecosystems.

Résumé : Les relations entre abondance et taille du corps et entre position trophique et taille du corps peuvent révéler une structuration des tailles dans les réseaux trophiques et permettre de valider des théories écologiques. Si la preuve à l'appui d'une structuration des tailles dans les réseaux trophiques aquatiques tempérés est considérable, les connaissances sur la structure des réseaux trophiques de récifs de corail tropicaux sont très limitées. Nous utilisons des données de recensement visuel sous l'eau et d'analyse des isotopes stables d'azote pour vérifier si les communautés de poissons de récifs coralliens (*i*) sont structurées selon la taille et (*ii*) suivent des règles d'échelle métaboliques. L'examen d'individus de plus de 160 espèces couvrant quatre ordres de grandeur de taille du corps démontre que l'abondance varie selon une relation d'échelle négative par rapport à la taille du corps et, comme prévu, les individus qui s'échangent de l'énergie par l'entremise de la prédation (les poissons carnivores) changent d'échelle plus abruptement que ceux qui partagent une même source d'énergie (les poissons herbivores). Les spectres de tailles estimés sont toutefois moins abrupts que le prédit la théorie métabolique. L'échelle de position trophique est positivement reliée à la taille du corps pour toutes les espèces et tous les individus, ce qui fournit de nouvelles preuves d'une structuration des tailles dans un réseau trophique tropical diversifié. Les approches basées sur la taille sont très prometteuses pour ce qui est d'intégrer les complexités des réseaux trophiques en des mesures quantitatives simples, jetant ainsi un nouvel éclairage sur la structure et la fonction des écosystèmes aquatiques. [Traduit par la Rédaction]

Introduction

Elucidating the structure of natural food webs can provide fundamental insight 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 and McCann 2012). General patterns relating to body size may be of particular importance as individual 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 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 and Gillooly 2003). 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 and 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 10^4 and transfer efficiency is 10% (Jennings and Mackinson 2003; Trebilco et al. 2013).

Size structuring in aquatic food webs is driven by two mechanisms that reflect size-based feeding among 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 and Persson 1998). As a result, trophic position is often positively related to body size in aquatic food webs both at the species level (Brose et al. 2006) and at the individual level (Jennings et al. 2001). Size structuring of abundance and individual trophic position has been clearly demonstrated in both temperate freshwater (Mittelbach and Persson 1998; Cohen et al. 2003) and marine (Jennings et al. 2001; Jennings and Mackinson 2003) food webs. Similarly, metabolic scaling predictions (Brown and Gillooly 2003) have been broadly validated in freshwater (Reuman et al. 2008) and marine (Jennings and Mackinson 2003) food webs. However, equivalent tests of size

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structuring in tropical systems are few, and tests of metabolic predictions are lacking entirely. One study of a tropical 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 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, community-wide analyses of tropical size structure remain relatively unexplored.

On tropical coral reefs, the application of sized-based approaches has been restricted to observations of body size distributions in degraded regions or to diet analyses of individual species. For example, size spectra — a widely used form of 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. 2010) and habitat complexity (Alvarez-Filip et al. 2011). Though consistent with size-structured abundances, size spectra have typically been fitted to narrow body size ranges (~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 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 utilized within a community (Brown and Gillooly 2003). For example, in the North 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 and Jennings 2006; Blanchard et al. 2009). Distinct trophic pathways also are 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 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 herbivores and carnivores, we can examine food web structure in the context of metabolic predictions.

Here, we capitalize on the opportunity to sample a minimally impacted coral reef to empirically test the hypotheses that coral reef food webs are size structured 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 Ocean, to 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 in a predation-based community (carnivores) relative to an energy-sharing community (herbivores).

Materials and methods

Study site and data collection

We examined a minimally disturbed coral reef fish community on Kiritimati (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 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 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 off the north, east, and south coasts are relatively undisturbed (Walsh 2011; Watson et al. 2016). The northwest coast of Kiritimati is also subject to oceanic upwelling of nutrients, but industrial and agricultural nutrient runoff is virtually nonexistent around the atoll (Walsh 2011). We enumerated and sampled coral reef fishes at 14 minimally disturbed sites on Kiritimati's north and east coasts (Fig. 1) to reduce potentially confounding effects of fishing and nutrient inputs on trophic 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. 1). During each census, two experienced scientific divers identified, counted, and sized (total length, to the nearest centimetre) reef fishes by swimming in tandem along 25 m long belt transects; transect 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 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 m² (i.e., 3 × 25 × 8 m) for large fishes and 300 m² for small fishes. Before analyzing 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 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 Kiritimati immediately before beginning visual censuses, divers re-familiarized 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., ±3%). Fish length estimates were converted to body mass (grams) using published species-specific length–weight relationships (Kulbicki et al. 2005; Froese and Pauly 2014).

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 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' 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 ~4–8 h between collection and dissection). Prior to dissection, each individual was photographed, weighed, and measured to the nearest millimetre with vernier calipers (for standard, fork, and total length). We then excised a small sample (~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 Victoria and then stored at –20 °C until processing.

Each white muscle tissue sample was rinsed with de-ionized water, dried at 60 °C for 48 h, 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 concentrations at the Mazumder laboratory (Department of Biology, University of Victoria, British Columbia, Canada). Relative nitrogen content was estimated by continuous flow isotope ratio

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 coasts of the atoll, which is outside the upwelling zone on the leeward (lagoon facing) side. Fish specimens were collected at 10 sites in July–August of 2011 and 2012 (triangles). Underwater visual 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 population sizes.
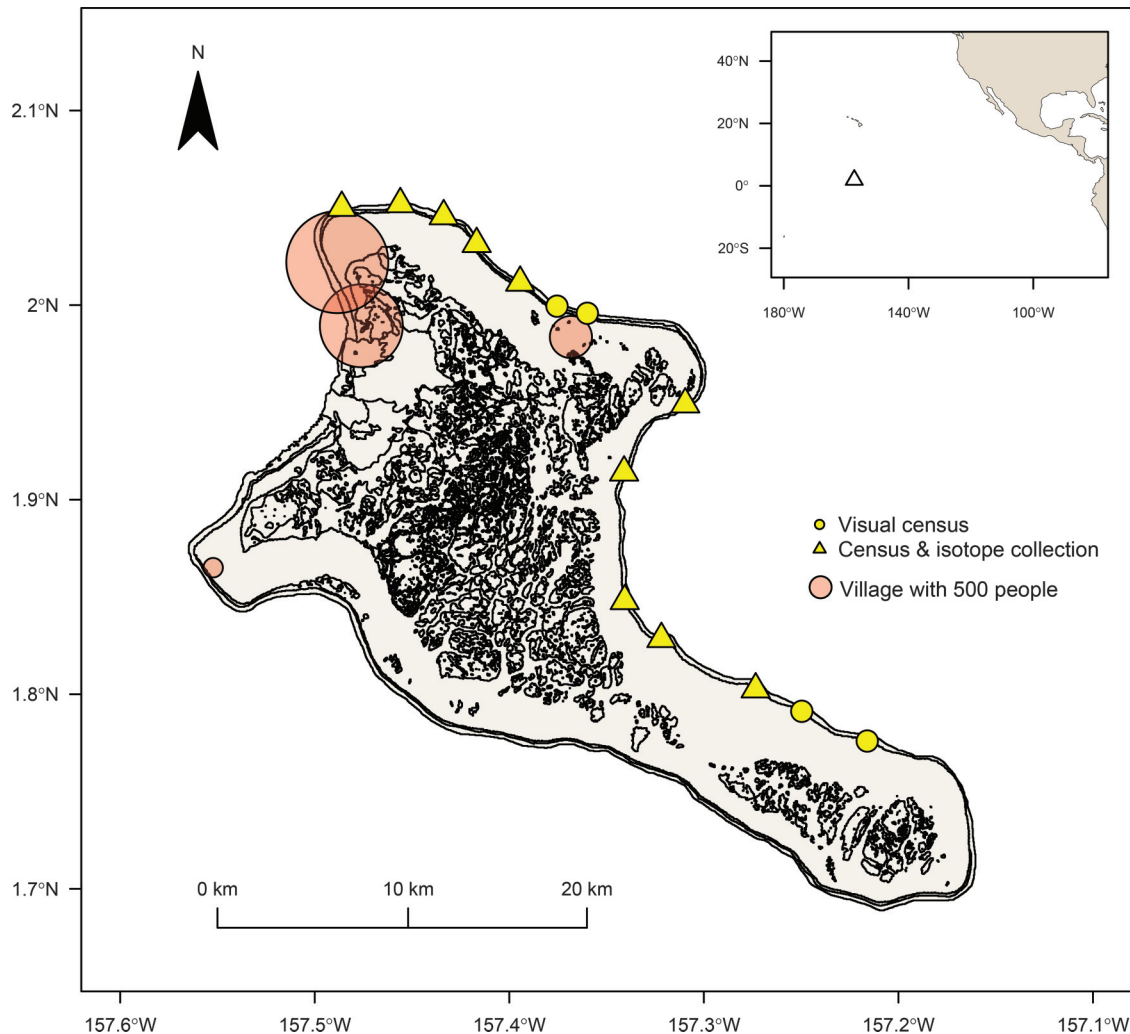
mass spectrometer and reported in parts per million relative to atmospheric N² (δ^{15}N).

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 plant material and detritus. Gut content analyses of our specimens were used to confirm the functional group of each species.

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 (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 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 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 carnivores did not qualitatively change our results (see Supplementary material[2]).

Abundance – body size analyses

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 linear regression fit to abundance data binned into body size classes (e.g., Jennings et al. 2001; Jennings and 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 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 power law distribution:

Table 1. Body sizes, $\delta^{15}N$ values, and sample sizes (N) for the 23 fish species sampled on Kiritimati for the stable isotope analyses, with each species assigned a trophic pathway (carnivore or herbivore) based on their functional group (FG: BI, 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
Carnivore								
BI	Chaetodontidae	*Chaetodon auriga*	Threadfin butterflyfish	87.36	58–98	14.44	13.68–15.60	9
		Chaetodon ornatissimus	Ornate butterflyfish	115.84	39–173	13.38	11.98–15.03	21
	Lethrinidae	*Monotaxis grandoculis*	Humpnose large-eyed bream	413.38	200–1091	14.96	12.90–15.83	20
	Cirrhitidae	*Paracirrhites arcatus*	Arc-eye hawkfish	13.28	2–31	13.15	12.28–13.99	10
	Mullidae	*Parupeneus insularis*	Two-saddle goatfish	221.78	45–520	12.46	11.22–14.40	30
Pi	Carangidae	*Caranx ignobilis*	Giant trevally	6350.29	—	12.23	12.23–12.23	1
		Caranx melampygus	Bluefin trevally	1851.62	127–3719	12.01	11.21–13.28	8
		Carangoides orthogrammus	Island trevally	1732.50	—	13.74	13.74–13.74	1
	Lutjanidae	*Aphareus furca*	Grey jobfish	274.47	200–420	11.40	10.86–11.98	17
		Lutjanus bohar	Two-spot red snapper	1092.67	133–4540	12.23	10.91–13.68	23
	Serranidae	*Cephalopholis argus*	Peacock hind	382.74	201–1100	13.74	11.71–15.67	18
		Cephalopholis urodeta	Darkfin hind	81.67	27–151	11.71	9.11–13.59	22
		Variola louti	Yellow-edged lyretail	1713.30	128–3405	12.90	11.73–14.40	6
ZP	Caesionidae	*Caesio teres*	Yellow and blueback fusilier	213.29	7–471	9.59	9.02–10.23	19
		Pterocaesio tile	Dark-banded fusilier	57.60	4–167	9.08	8.50–9.70	11
	Pomacentridae	*Chromis vanderbilti*	Vanderbilt's chromis	0.79	0–2	9.68	8.91–10.26	7
	Serranidae	*Pseudanthias bartlettorum*	Bartlett's anthias	2.88	1–4	9.11	7.94–9.84	5
		Pseudanthias olivaceus	Olive anthias	5.93	1–15	9.31	8.07–10.32	30
Herbivore								
He	Acanthuridae	*Acanthurus nigricans*	Whitecheek surgeonfish	112.53	44–207	12.43	11.04–13.22	6
	Pomacanthidae	*Centropyge flavissima*	Lemonpeel angelfish	14.32	6–22	12.58	11.14–13.21	10
	Scaridae	*Chlorurus sordidus*	Daisy parrotfish	309.83	43–807	12.93	11.99–14.66	20
		Scarus frenatus	Bridled parrotfish	794.22	388–1954	13.86	12.72–15.17	24
De	Acanthuridae	*Ctenochaetus marginatus*	Striped-fin surgeonfish	138.28	42–259	13.36	12.23–14.37	26

$$(1) \qquad (b+1)\left(x_{max}^{b+1} - x_{min}^{b+1}\right)^{-1} x^{b}$$

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 (White et al. 2008). We used maximum likelihood methods to estimate b with a 95% confidence interval (CI) (Edwards et al. 2012).

Interpretations of how empirical size spectra relate to theoretical metabolic predictions can be confounded by the method used to estimate the slope. Here, we explain how our estimates of b relate to Brown and Gillooly's (2003) theoretical predictions and to the empirical estimates of others. First, our maximum likelihood 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 and Gillooly's (2003) predicted slopes will be one unit shallower than the scaling exponent of a power law distribution (Andersen and 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 and Mackinson 2003; Blanchard et al. 2009) can also 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 fit the size spectrum of (*i*) the full reef fish community and (*ii*) each putative trophic pathway (carnivores and herbivores). We tested the robustness of our results in several 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 our survey sites were selected to minimize fishing effects on reef trophic structure, we recognize that sites on Kiritimati's north coast may experience light fishing pressure. To test for potential fishing effects, we removed sites from the north coast that are nearest to Kiritimati's population centres and refitted spectra and also compared size spectra for north vs. east coast sites (Supplementary material[2]). Third, we tested the effect of fitting different body size ranges on exponent estimates, thus excluding either the smallest fishes (because our UVCs may have undersampled them) or the largest fishes (because these may be targeted by fishers) (Supplementary material[2]).

Trophic position estimation

We assigned all fish specimens to $\log_2$ mass bins (grams) and converted the $\delta^{15}N$ values of each individual to trophic position. $\delta^{15}N$ of an organism's tissue reflects its diet, and given that $\delta^{15}N$ increases by a known discrimination factor ($\Delta^{15}N$) 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‰, although recent work has revealed that $\Delta^{15}N$ decreases with the $\delta^{15}N$ of an organism's diet such that upper trophic positions may previously have been underestimated (Caut et al. 2009; Hussey et al. 2014).

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

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

This method was developed in a meta-analysis of experimental isotope studies of marine and freshwater fishes in which $\delta^{15}N_{lim}$ (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 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 that we sampled on Kiritimati (*Chromis vanderbilti*, $\delta^{15}N_{base} = 10.26$, mass = 0.1 g).

Herbivores are known to fractionate differently than carnivores, with recorded $\Delta^{15}N$ values ranging from –0.7‰ to 9.2‰ (Zanden and Rasmussen 2001). In herbivorous reef fish, substantially higher feeding and excretion rates are required to subsist on low-energy algal food sources, driving higher $\Delta^{15}N$ rates ranging from 2.79‰ to 7.22‰ (Mill et al. 2007). We found no evidence of herbivore $\Delta^{15}N$ varying with dietary $\delta^{15}N$. Instead, we used published $\Delta^{15}N$ estimates (Mill et al. 2007) to calculate a mean $\Delta^{15}N$ of herbivorous reef fish (4.778‰) before calculating individual trophic position with an additive approach (eq. 3) following Post (2002) and Hussey et al. (2014):

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

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).

Trophic position – body size analyses

Although species-level predator–prey mass ratios are generally positive (Brose et al. 2006), others have suggested that when ontogenetic niche shifts are prevalent, size structuring 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., "cross-species approach" sensu Jennings et al. 2001) and at the individual level to test the hypothesis that coral reef food webs are size structured and, if so, at what level of organization is size structuring evident.

Phylogenetic patterns in trophic position – body size relationships can result in non-independence of data points that can bias analyses of community structure (Jennings 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 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 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 within families. Specifically, we fitted family as a random effect to account for non-independence of trophic position – body mass relationships within families and then 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. 2009). Second, in the individual-based analyses, we examined the relationship between the trophic position of individual fishes and their log_2 body mass class. To account for the 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- and individual-based analyses, we tested for differences in slopes of trophic position – body mass relationships between our two putative trophic pathways, carnivores and herbivores, by assessing the significance of trophic pathway as an interaction term with AIC_c (Burnham and Anderson 2002). We measured the goodness-of-fit of the fixed covariates in each analysis by estimating the marginal R^2 of each model (Nakagawa and Schielzeth 2012). Finally, we

conducted sensitivity analyses to test the robustness of our results to different herbivore fractionation values ($\Delta^{15}N$) and different sampling locations (Supplementary material[2]). We note that there are multiple families included in each trophic pathway (Table 1). Thus, although no family contains individuals from both 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 phylogeny).

All abundance – body size and trophic position – body size analyses were performed in R (version 3.0.2; R Core Team 2013) using the packages MuMIn (Barton 2013) and nlme (Pinheiro et al. 2015). The R code used in our analyses is available on Github (https://github.com/baumlab/Robinson-Baum_2016_CJFAS).

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 size of the herbivore group (mean mass = 230.63 g, SE = 14.72) was greater than that of the carnivore group (mean mass = 188.83 g, SE = 16.78). These average sizes reflect the high proportion of small planktivores in the carnivore group rather than a disproportionate abundance of large herbivores. For example, for fishes > 20 g, mean carnivore mass 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 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 ($b = -1.270$, 95% CI = (–1.281, –1.260)) being significantly shallower than that of the carnivore group ($b = -1.644$, 95% CI = (–1.649, –1.638)). In the context of metabolic predictions, the 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 and Gillooly 2003; Reuman et al. 2008). We also examined the effect of sampling bias on b by fitting spectra across different body 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, whereas removing the smallest individuals steepened the slope of both carnivores and herbivores considerably (Supplementary material[2]). 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[2]). Overall, across all body size ranges 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 carnivore spectrum and the slopes for herbivores and carnivores were always shallower than predicted by metabolic theory (Supplementary material[2]).

Trophic position – body size relationships

From 23 species within five functional groups, we sampled a total of 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

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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, $n = 25\,344$ 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% CI for carnivores (blue) and herbivores (green).
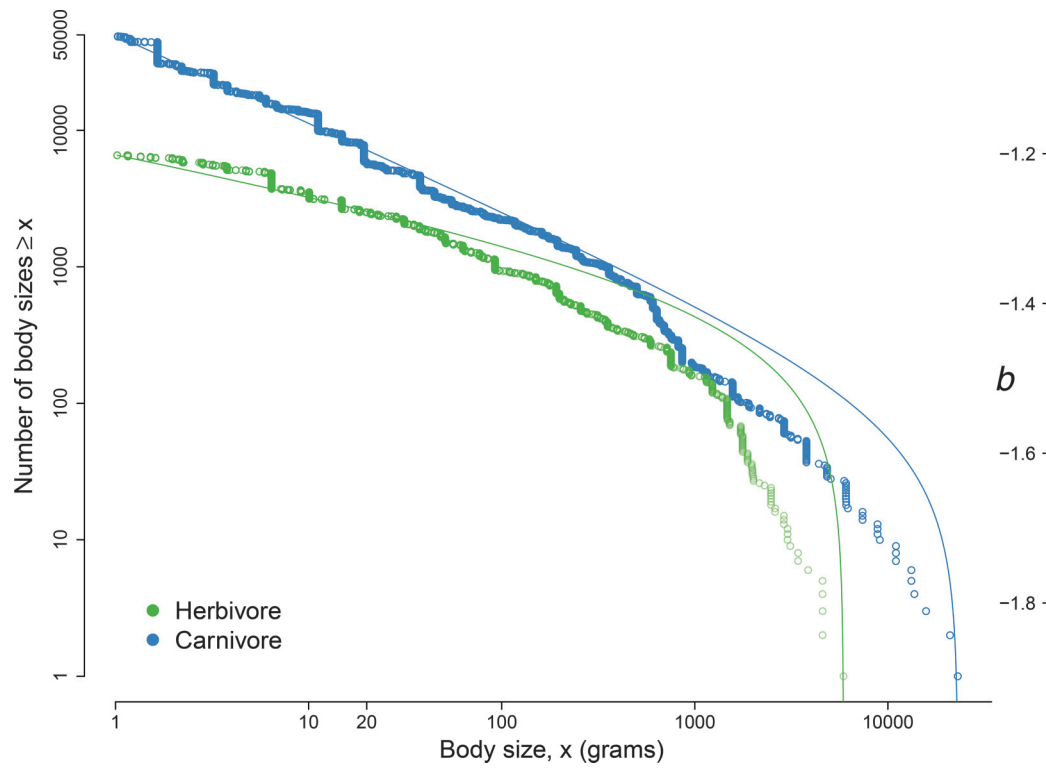
AIC$_c$) was the random intercept model with family as a random effect (so accounting for similar trophic position – body mass relationships within families) and with trophic pathway (carnivore, herbivore) included as an interaction term (Fig. 3b; Table 2). The relationship was positive and significant between trophic position and maximum log$_2$ body mass (estimate = 0.114, $P = 0.002$) but was not significantly 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 (Fig. 3b) than the model in which all species were aggregated (Fig. 3a). In the individual-based analysis, the trophic position of individual fishes also increased significantly with 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 explained (Fig. 3c). Once trophic pathways were included, as with the species-based analysis, the optimum individual-based model included the log$_2$ body mass class – trophic pathway interaction term and much more of the variability was explained: the slope of the relationship between trophic position and body size was positive and significant (estimate = 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 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[2]). For both the species- and individual-based models, 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). We note that in the individual-based models, had we not taken into account non-independence 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 (sites off the north or south coasts) or our assumed herbivore fractionation value (Supplementary material[2]).

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 accordance with size-based theory (Trebilco et al. 2013). Trophic position – body mass relationships were significantly positive across species and across individuals, revealing 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 Brown and Gillooly's (2003) prediction that body size scaling relationships reflect differences in energy acquisition between individuals sharing energy and individuals competing across trophic levels.

Abundance – body size relationships

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 size. Our results align with ecological theory that energetic constraints cause abundance to scale negatively with body size (Brown and Gillooly 2003; Jennings and Mackinson 2003; 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 species sharing energy within a trophic level (herbivores) (Brown and Gillooly 2003). Previous analyses of size spectra on coral reefs, which were focused on examining how size

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) and (*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% CI 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 jitter, shaded colour), and overlaid with mean trophic position (solid colour) of each body mass class.
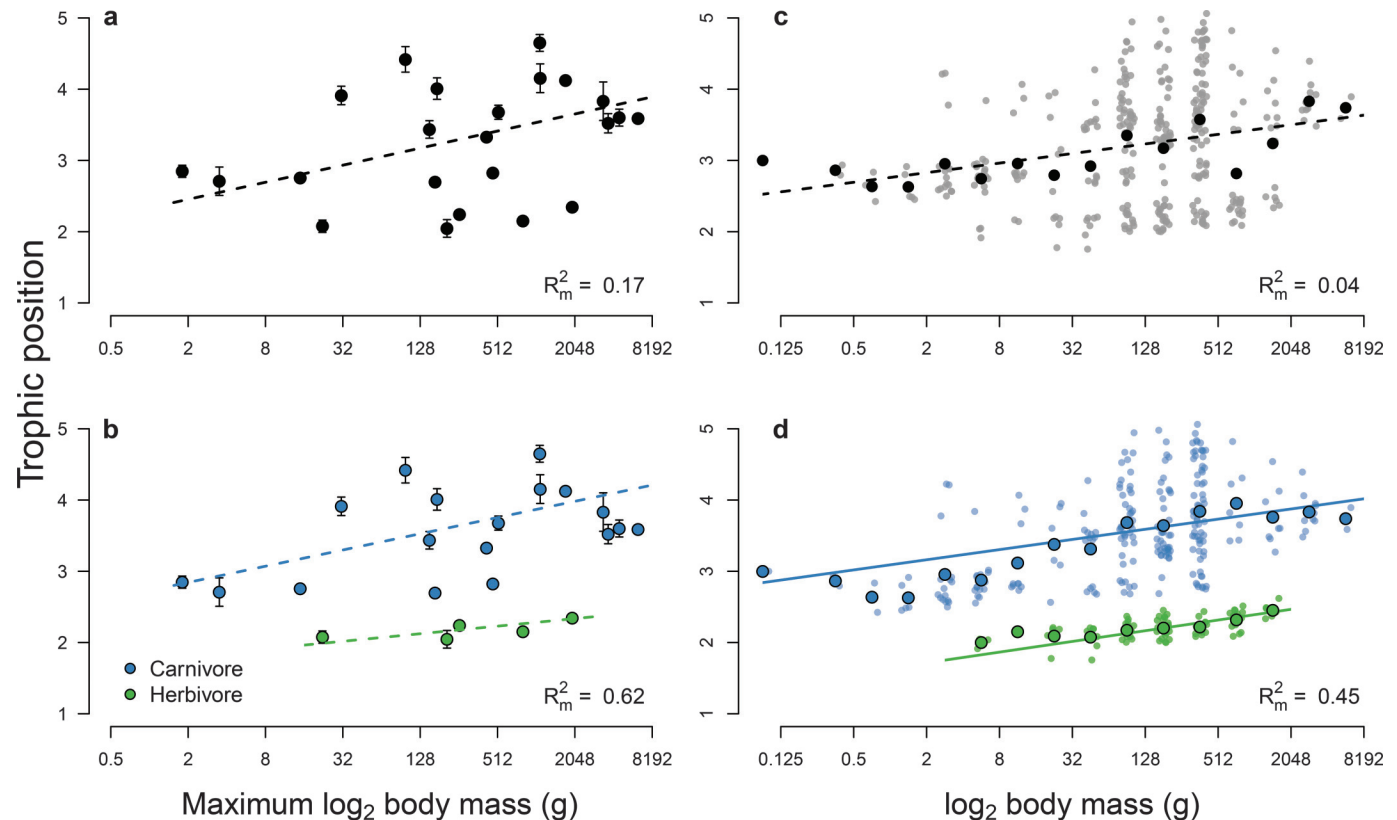

Table 2. Parameter estimates of the best model (as evaluated by AIC_c) for trophic position–$\log_2$ body mass relationships in the species-based (linear mixed effects model with family as a random effect) and individual-based (linear mixed effects model with species nested within family as a random effect) analyses.

	Coefficient	Estimate	Standard error	P value	Marginal R^2	ΔAIC_c
Species-based	Intercept	2.334	0.328	<0.001	0.17	5.45
	$\log_2$ mass	0.120	0.029	0.002		
Species-based with trophic pathway	Intercept	2.730	0.282	<0.001	0.62	0
	Intercept (herbivore)	−0.978	1.018	0.359		
	$\log_2$ mass	0.114	0.028	0.003		
	$\log_2$ mass·herbivore	−0.061	0.124	0.636		
Individual-based	Intercept	2.761	0.242	<0.001	0.04	8.84
	$\log_2$ mass	0.067	0.020	<0.001		
Individual-based with trophic pathway	Intercept	3.090	0.186	<0.001	0.45	0
	Intercept (herbivore)	−1.450	0.398	0.004		
	$\log_2$ mass	0.071	0.024	0.005		
	$\log_2$ mass·herbivore	0.004	0.052	0.943		

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 with body lengths rather than masses, making direct comparisons with our results difficult. Our results are more directly comparable with Ackerman et al.'s (2004) census of reef

fish > 1 g that, once corrected for their binning-based slope estimate, yields a size spectrum slope of *b* = −1.75 ± 0.34 95% CI, which is steeper than our 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 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 governed by ener-

getic constraints on size spectra that are similar to predictions for pelagic marine ecosystems (Brown and Gillooly 2003; Blanchard et al. 2009).

Our size spectra estimates were, however, shallower than predictions from metabolic theory and size-based theory for body size scaling relationships (i.e., the energetic equivalence hypothesis and the trophic transfer correction) (Brown and Gillooly 2003; Trebilco et al. 2013). Empirical tests of abundance – body size relationships may deviate from theory when abundance estimates fail to account for every species that shares energy within the community (Maxwell and Jennings 2006; Jennings et al. 2007). 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 (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 smallest size classes from the data set, suggesting that our UVCs had not quantified all of the smallest fishes in the community. Non-instantaneous UVC methods also can over- or under-estimate the abundance of large mobile fishes depending on fish behaviour (Ward-Paige et al. 2010; Bozec et al. 2011) and thus bias spectra estimates upwards or downwards. However, given that large individuals are considerably lower in abundance than small individuals and that each individual counted is treated equally in probabilistic spectra fitting methods, we expect that this bias would be quite small.

In addition to the potential bias introduced by UVC 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 potential influence 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 sites nearest to Kiritimati's villages, consistent with predicted fishing effects on the size spectrum (Supplementary material[2]). Nevertheless, our observed pattern that herbivore size spectra were significantly shallower than carnivore size spectra was consistent across all sites and body size ranges (Supplementary material[2]), indicating that the influence of fishing on our results is minimal.

Trophic position – body size relationships

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 results suggest that coral reef food webs are structured by size-based feeding relationships at both the species and individual levels. For example, previous tests of feeding relationships have reported positive, negative, and nonsignificant relationships between $\delta^{15}N$ and body size within individual reef fish species (Greenwood et al. 2010). However, a lack of statistical power can prevent detection of intraspecific shifts in $\delta^{15}N$ (Galván et al. 2010). In the only previous comparison of feeding relationships across multiple coral reef species of which we are aware, $\delta^{15}N$ – body length relationships were positive across five carnivorous species, consistent with the carnivore size structuring in our results, but nonsignificant across four herbivorous species (de la Morinière et al. 2003). Our finding that the trophic position of herbivorous fish increased with body size (from 1.76 to 2.62) was therefore unexpected. Enriched individual $\delta^{15}N$ may result from increased consumption of detritus and small benthic invertebrates by herbivorous surgeonfish species (Acanthuridae) (Carassou et al. 2008; Dromard et al. 2015). We note that, in general, understanding of trophic fractionation in herbivorous fishes remains 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 relationships are robust to varying ΔN (Supplementary material[2]), indicating that the consumption of $\delta^{15}N$ enriched detritus and invertebrates may increase with herbivore body size.

Despite evidence from gut content analyses that fish predators are generally larger 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, Jennings et al.'s (2001) study found a positive trophic position – body size relationship for fishes in the Celtic Sea but a nonsignificant relationship for fishes in the North Sea. In a tropical stream food web, despite gut content analysis revealing size-structured feeding relationships, isotope analysis of the full food web found no relationship between 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 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 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 individual and the species levels.

Two additional factors that may have limited the ability of previous studies to detect positive trophic position – body size relationships are variability in trophic fractionation values between trophic positions (Hussey et al. 2014) and confounding effects of phylogeny (Romanuk et al. 2011). Romanuk et al. (2011), for example, highlighted the importance of considering evolutionary history in analyses of diverse 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 – 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 difference between the trophic position – body mass relationships of carnivore and herbivores. Without appropriate consideration of potential errors in the conversion of $\delta^{15}N$ to trophic positions and in the statistical treatment of phylogenetic relationships, examination of trophic structure from stable isotope analyses can be misleading.

Trophic pathways on coral reefs

We found that carnivores and herbivores were characterized by distinct abundance – body size relationships, although 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 with observations that the North Sea benthic community has a shallower spectrum than the pelagic community (Maxwell and Jennings 2006; Blanchard et al. 2009). In the North 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) examined how the energy-sharing community could be coupled to a steep predation-based community by large mobile predators to confer food web stability. Their model has 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). Although Rogers et al. (2014) did not compare size spectrum slope estimates between groups, our analyses provide empirical support for distinct structuring of herbivore and carnivore groups.

Beyond body size relationships, analysis of trophic pathways in other systems have used carbon isotope signatures to identify distinct energy sources and thus track energy flux through food web compartments or "channels" (Rooney et al. 2006). Although we did not have sufficient carbon samples for the reef fish that we sampled on Kiritimati, 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 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 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. 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 we develop a greater understanding of how differences in energy utilization between trophic pathways may define the structure of coral reef food webs.

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. 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 spectra of carnivores and herbivores reflected energetic constraints on abundance – body size relationships between individuals sharing energy and those competing across trophic 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 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 food webs into simple, quantitative measures and elucidating fundamental properties of aquatic ecosystems.

Acknowledgements

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