

Size structuring and allometric scaling relationships in coral reef fishes

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Summary

1. Temperate marine fish communities are often size-structured, with predators consuming increasingly larger prey and feeding at higher trophic levels as they grow. Gape limitation and ontogenetic diet shifts are key mechanisms by which size structuring arises in these communities. Little is known, however, about size structuring in coral reef fishes.

2. Here, we aimed to advance understanding of size structuring in coral reef food webs by examining the evidence for these mechanisms in two groups of reef predators. Given the diversity of feeding modes amongst coral reef fishes, we also compared gape size–body size allometric relationships across functional groups to determine whether they are reliable indicators of size structuring.

3. We used gut content analysis and quantile regressions of predator size–prey size relationships to test for evidence of gape limitation and ontogenetic niche shifts in reef piscivores ($n = 13$ species) and benthic invertivores ($n = 3$ species). We then estimated gape size–body size allometric scaling coefficients for 21 different species from four functional groups, including herbivores/detritivores, which are not expected to be gape-limited.

4. We found evidence of both mechanisms for size structuring in coral reef piscivores, with maximum prey size scaling positively with predator body size, and ontogenetic diet shifts including prey type and expansion of prey size. There was, however, little evidence of size structuring in benthic invertivores. Across species and functional groups, absolute and relative gape sizes were largest in piscivores as expected, but gape size–body size scaling relationships were not indicative of size structuring. Instead, relative gape sizes and mouth morphologies may be better indicators.

5. Our results provide evidence that coral reef piscivores are size-structured and that gape limitation and ontogenetic niche shifts are the mechanisms from which this structure arises. Although gape allometry was not indicative of size structuring, it may have implications for ecosystem function: positively allometric gape size–body size scaling relationships in herbivores/detritivores suggests that loss of large-bodied individuals of these species will have a disproportionately negative impact on reef grazing pressure.

Key-words: allometry, body size, coral reef, functional groups, gape limitation, herbivory, ontogenetic diet shift, predation, size-based approach, size structuring

Introduction

Body size is a fundamentally important biological trait, influencing metabolic rates, energy flows and population abundances in organisms across taxa (Peters 1983; Werner & Gilliam 1984; Brown *et al.* 2004; Brose *et al.* 2006). Size-structured food webs reflect size-based feeding by

individuals (Cohen *et al.* 1993). In these systems, an individual's size may serve as a better indicator of its role in the ecosystem than its taxonomic identity (Jennings *et al.* 2001; Barnes *et al.* 2010). Size structuring has been demonstrated consistently for temperate marine and freshwater food webs (Cohen *et al.* 1993; Mittelbach & Persson 1998; Jennings *et al.* 2001; Jennings & Mackinson 2003). Despite its importance, prevalence in temperate aquatic systems and the growing interest in using size-based approaches for ecosystem modelling and as ecosystem indicators (Jennings *et al.* 2002; Petchey & Belgrano

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2010; Andersen & Beyer 2015), little is known about the presence or nature of size structuring in tropical marine food webs (Layman *et al.* 2005).

Gape limitation is the most commonly invoked mechanism for overall size structuring of aquatic food webs (Pimm 1982; Hairston & Hairston 1993; Hambright 1994; Arim, Bozinovic & Marquet 2007). Gape size is hypothesized to constrain the range of prey available to predatory fishes (Hairston & Hairston 1993) because fish lack jointed appendages, which limits prey handling ability, and in piscivores, gape size typically sets the upper limit of potential prey size (e.g. Persson *et al.* 1996; Nilsson & Brönmark 2000). Scharf, Juanes & Roundtree (2000), for example, found that increases in maximum prey size corresponded with increases in gape size in five of eight predatory fishes studied off the northeast coast of the United States. More recently, Johnson *et al.* (2012) found the same relationship in six of nine Mediterranean demersal fish species and Bachiller & Irigoien (2013) found that in small pelagic fish, such as the European anchovy and Atlantic mackerel, mean and maximum prey size increased with predator gape size.

Size structuring also can arise from ontogenetic niche shifts. As individual fish grow, they often shift their diet composition, from zooplankton to small invertebrates to fish (Wainwright & Richard 1995; Scharf *et al.* 1997), and expand their niche breadth, in terms of diet composition or the range of prey sizes consumed. These changes usually lead to increases in trophic position as individuals grow (Mittelbach & Persson 1998), such that trophic position is generally positively related to body size in aquatic food webs (Jennings *et al.* 2001; Romanuk, Hayward & Hutchings 2011; Hussey *et al.* 2014). Ontogenetic niche shifts are often associated with increases in gape size (Scharf, Juanes & Roundtree 2000), but they can also occur due to changes in predator foraging behaviour (Scharf, Buckel, & Juanes 2009) and so can indicate size structuring that is not driven through gape limitation.

Additionally, allometric scaling relationships between gape size and body size could also be indicative of size structuring, if gape allometry is linked to gape limitation. In predatory groups, gape limitation is commonly observed in juvenile fishes or those that are still significantly smaller than the maximum adult size (e.g. Wanzböck 1995; St John 1999), as at small body sizes, predators have the most limited range of accessible prey items. If large relative gape sizes are most advantageous at these small body sizes in order to access larger, higher quality prey (Kerr 1971; Pazzia *et al.* 2002; Sherwood *et al.* 2002), then as predators grow, there are likely to be diminishing returns on large relative gape size (Juanes 2016). This would give rise to a negatively allometric relationship between gape size and body size. Negative allometry has been observed in banded water snakes, a group of predators subject to gape limitation given their limited ability to handle prey (Vincent *et al.* 2005). Piscivorous fishes also might be expected to exhibit negative

allometry, but the evidence to date is mixed: Richard & Wainwright (1995) found that gape height scaled isometrically in large-mouth bass (*Micropterus salmoides*), Hernández (2000) found that gape height in zebrafish (*Danio rerio*) scaled with positive allometry and Karachle & Stergiou (2011) found mixed results for 61 Mediterranean fish species.

Few studies have examined gape limitation, ontogenetic niche shifts or overall size structuring in coral reefs. Recently, one study provided evidence that, as in temperate communities, the trophic level of coral reef predators also increases with body size (Robinson & Baum 2015). Coral reef fish communities are, however, composed of much more than just their predators, and in particular, herbivorous fishes are a ubiquitous feature of these diverse systems (Kotrschal 1988; Harmelin-Vivien 2002; Wainwright & Bellwood 2002). Differences in energy sources between coral reef predators and herbivores are expected to give rise to differences in size structuring. Indeed, building upon Blanchard *et al.*'s (2009) work in the North Sea, Robinson & Baum (2015) found that abundance–body mass relationships scaled more steeply for coral reef predators than for herbivores and detritivores, which share a common energy source regardless of body size. The mechanisms underlying this apparent size structuring, however, remain unclear.

Here, with the objective of elucidating the mechanisms of size structuring in coral reef fish communities, we examine predator–prey relationships in piscivores and benthic invertivores to determine whether these species and functional groups are gape-limited and whether they undergo ontogenetic niche shifts. We then compare absolute and relative gape sizes, as well as gape size–body size allometric scaling coefficients across a suite of coral reef fish species, including herbivore/detritivore species, which are not expected to be gape-limited. We expected piscivores and benthic invertivores to show evidence of both mechanisms of size structuring, for these predators to exhibit negative allometry, and for gape allometry in other coral reef functional groups to be isometric (i.e. proportional increases in gape size with increasing body size). By comparing gape size–body size scaling relationships across predatory and non-predatory functional groups, we aimed to evaluate whether gape allometry is indicative of size structuring.

Materials and methods

STUDY SITE AND DESIGN

Situated within the central Pacific Ocean's Northern Line Islands (01°52' N, 157°24' W), Kiritimati (Christmas) has the greatest land area of any atoll in the world (Fig. S1, Supporting Information; Watson, Claar & Baum 2016). As part of a larger food web study (detailed in Robinson & Baum 2015), fish were captured between depths of 8 and 12 m around Kiritimati's fore

reef by scientific divers spearfishing using custom-built microspears, pole spears or spear guns. For this study, we sampled fishes across four functional groups, distinguished by broad diet composition: piscivores, benthic invertivores, zooplanktivores and herbivores/detritivores (Table 1; Robinson & Baum 2015). We note that species within the herbivore/detritivore group feed on both plant matter and detritus and that this group encompasses species with three distinct feeding modes (Table 1; Green & Bellwood 2009). Within each functional group, we targeted the most abundant species as determined by underwater visual censuses of Kiritimati's fish communities in 2007 (Walsh 2011)

and 2009 for collection. Within each species, we targeted collections to span the full size range of the species to the extent possible. A total of 28 fish species were sampled from across 19 genera and 12 families (Tables 1 and 2). Of these, we conducted a predator size–prey size analysis on the 13 piscivores and three benthic invertivore species for which these data were available. Gape measurements were made for 21 of the fish species across the four functional groups. Fish diets were determined from the literature (Randall 2005; Wilson *et al.* 2008; Green & Bellwood 2009) and verified using gut contents of our dissected specimens.

Table 1. Sampled piscivore (PI) and benthic invertivore (BI) fish species, ordered by functional group (PI, BI) and family, including mean standard length (SL, mm), the range of the measured fish (mm), maximum recorded total length (TL, mm, from FishBase) and sample sizes for the nine species included in the gape size–body size analysis and the sixteen species included in the predator size–prey size analysis

FG	Family	Scientific name	Common name	Mean SL	Range	Max TL	Gape analysis, <i>n</i>	Prey size analysis, <i>n</i>
PI	Carangidae (Jacks)	<i>Caranx melampygus</i>	Bluefin trevally	425.3	179–595	1170*	12	6
		<i>Carangoides orthogrammus</i>	Island trevally	392.5	390–395	750	–	2
	Lutjanidae (Snappers)	<i>Aphareus furca</i>	Grey jobfish	241.3	193–320	700	36	13
		<i>Aprion virescens</i>	Green jobfish	480	480	1120	–	1
		<i>Lutjanus bohar</i>	Two-spot red snapper	241.9	101–538	900	45	15
	Serranidae (Groupers)	<i>Lutjanus kasmira</i>	Bluestripe snapper	160.0	160	400	–	1
		<i>Cephalopholis argus</i>	Peacock hind	232.6	134–335	600	23	11
		<i>Cephalopholis urodeta</i>	Darkfin hind	138.2	60–178	280	39	27
		<i>Epinephelus hexagonatus</i>	Starspotted grouper	204.7	162–229	275	–	3
		<i>Epinephelus maculatus</i>	Highfin grouper	227	227	605	–	1
		<i>Epinephelus spilotoceps</i>	Foursaddle grouper	190.5	181–200	350	–	2
		<i>Epinephelus tauvina</i>	Greasy grouper	258.5	242–275	1000	–	2
		<i>Variola louti</i>	Yellow-edged lyretail	373.4	172–606	830	12	8
BI	Cirrhitidae (Hawkfish)	<i>Paracirrhites arcatus</i>	Arc-eye hawkfish	68.6	41–97	200	24	5
	Lethrinidae (Emperors)	<i>Monotaxis grandoculis</i>	Humpnose large-eyed bream	199.2	121–311	600	66	4
	Mullidae (Goatfish)	<i>Parupeneus insularis</i>	Two-saddle goatfish	182.6	60–298	300	86	99
Total							343	200

*Max length is fork length.

Table 2. Sampled zooplanktivore (ZP) and herbivore (HE/DE) fish species, ordered by functional group (ZP, HE/DE) and family, including mean standard length (SL, mm), the range of the measured fish (mm), maximum recorded total length (TL, mm, from FishBase) and sample sizes for the twelve species included in the gape size–body size analysis. The HE/DE group includes three distinct feeding modes: excavators (E), grazers (G) and scrapers (S)

FG	Family	Scientific name	Common name and feeding mode (E, G, S)	Mean SL	Range	Max TL	Gape analysis, <i>n</i>
ZP	Caesionidae	<i>Caesio teres</i>	Yellow and blueback fusilier	206.7	136–270	400	23
		<i>Pterocaesio tile</i>	Dark-banded fusilier	115.2	66–202	300	34
	Pomacentridae	<i>Chromis vanderbilti</i>	Vanderbilt's chromis	32.2	21–42	60	63
	Serranidae	<i>Pseudanthias bartlettorum</i>	Bartlett's anthias	45.0	24–57	90	8
		<i>Pseudanthias dispar</i>	Peach fairy basslet	50.4	39–57	95	10
		<i>Pseudanthias olivaceus</i>	Olive anthias	51.7	26–79	120	85
HE/DE	Acanthuridae	<i>Acanthurus nigricans</i>	Whitecheek surgeonfish (G)	130.3	79–172	213	25
		<i>Acanthurus olivaceus</i>	Orangespot surgeonfish (G)	182.7	151–222	350	7
	Pomacanthidae	<i>Centropyge flavissima</i>	Lemonpeel angelfish (G)	60.9	40–81	140	34
	Labridae	<i>Chlorurus sordidus</i>	Daisy parrotfish (E)	203.3	68–290	470	71
		<i>Scarus frenatus</i>	Bridled parrotfish (S)	261.1	108–370	700	50
		<i>Scarus rubroviolaceus</i>	Ember parrotfish (S)	316.2	80–420	200	10
Total							420

FISH MEASUREMENTS

Prior to dissection, each fish was identified to species, photographed, weighed and measured to the nearest millimetre using vernier calipers. Standard length was measured from the tip of the snout to the end of the hypural plate. Following Scharf, Juanes & Roundtree (2000), gape height and gape width were measured as the maximum linear distances between the upper and lower jaws with the mouth stretched open and between the left and right corners of the mouth, respectively. In addition to morphological measurements, gut contents were described and wherever possible, prey items were measured using vernier calipers and photographed. Measured prey length was made on intact and partially digested prey items, and hence taken to be the minimum prey size. Total length, carapace width and shell width were measured for fish, crab and gastropod prey items, respectively. We used prey length as a proxy for prey depth because only length data were available for most prey items.

STATISTICAL ANALYSES

We analysed predator length–prey length relationships using quantile regressions in the R package ‘quantreg’ (Koenker 2013). In general, quantile regression can reveal relationships between variables that might be obscured by only looking at the mean regression value, particularly when scatter plots of data are polygonal (Scharf, Juanes & Sutherland 1998). Here, we used quantile regression to examine the relationships between predator standard length and the minimum, median and maximum prey standard length. The 10th and 90th quantiles were selected for the minimum and maximum based on sample size using the formulae $n > \frac{10}{1-q}$ and $n > \frac{10}{q}$, as suggested by Scharf, Juanes & Sutherland (1998). When more than one prey item was found in a predator stomach, it was treated as an independent feeding event. We conducted these regressions for: (i) all piscivores together, (ii) the two most commonly sampled piscivore families individually (Lutjanidae and Serranidae), (iii) all benthic invertivores and (iv) the most commonly sampled benthic invertivore family (Mullidae), which contained only the single species *Parupeneus insularis*. We then assessed the trophic niche breadth of these predator groups by determining changes in the range of prey sizes with increasing predator size: following the general approach of Scharf, Juanes & Roundtree (2000), we compared the upper (90th quantile) and lower (10th quantile) prey size bounds, with significant differences in slopes indicating a change in trophic niche breadth with predator size. Convergent slopes indicated a decrease; divergent slopes indicated an increase (Scharf, Juanes & Roundtree 2000).

For gape sizes, we calculated the absolute and relative gape sizes for each species, estimated the allometric relationships for each predator species and functional group (piscivore, benthic invertivore), and then compared these allometric relationships to two groups of coral reef fishes with contrasting feeding habits, zooplanktivores and herbivores/detritivores. Allometric relationships can be modelled using a power function, $y = ax^b$, where b is the scaling exponent and represents the rate of change in y with respect to x (Peters 1983; Schmidt-Nielsen 1984; Brown *et al.* 2002). Here, we used power functions to describe the scaling relationships between gape size (i.e. gape height or gape width) and body size (i.e. mass or standard length). For each species, we performed standardized major axis (SMA) regression on

\log_{10} -transformed data in the R statistical package ‘smatr 3’ (Warton *et al.* 2012). To assess whether species-specific gape size (i.e. gape height and gape width) and body size relationships were isometric (i.e. slope = 1 for gape size–standard length relationships, slope = 0.33 for gape size–body mass relationships), we used the `slopetest` function in the R statistical package ‘smatr 3’ (Warton *et al.* 2012). In all SMA analyses, we used the robust option, which uses Huber’s M-estimator to handle outliers (Taskinen & Warton 2013). We verified SMA assumptions using residual plots. To assess potential measurement errors by observers, we visually examined the data grouped by observer and removed data for one observer whose measurements were obvious outliers. After calculating allometric coefficients for each species using SMA regression, we compared allometric coefficients across functional groups using a linear model. We present the results from the gape size–standard length relationship because the gape size–body mass relationships yielded the same results. Further, we focus herein on results for the gape height–body size analyses; results for the gape width–body size analyses were similar and are presented only when they differ from the former.

All analyses were performed in R 3.2.3 (R Core Team 2015).

Results

PREDATOR SIZE–PREY SIZE ANALYSIS

Overall, the piscivores, a group comprised of snappers, jacks and groupers, showed significant increases in the maximum, median and minimum prey size consumed with increasing body size (Fig. 1a). Additionally, the increase in maximum prey size was significantly greater than the increase in minimum prey size ($P = 0.024$), indicative of an expansion in piscivore trophic niche breadth with increasing body size. Larger piscivores also were more likely to consume fish than invertebrates, and no piscivore greater than 300 mm standard length had an invertebrate prey item in its stomach (Fig. 1a). Although there were too few data points to estimate the error associated with the minimum and maximum quantile regression slope estimates for the snapper (Family Lutjanidae; Fig. 1b) and grouper (Family Serranidae; Fig. 1c) families, visually, the steeper maximum prey size regression relationships suggest that trophic niche breadth expansion occurs in both of these families. When either predator gape height or gape width was analysed in place of predator standard length, these results held (Fig. S2).

In contrast, benthic invertivores, a group that primarily consumes benthic crustaceans and gastropods and included three species from three different families (the hawkfish, the emperors and the goatfish), showed no significant change in maximum or median prey size as predator body size (or gape size) increased (Fig. 1d). Although there was a statistically significant increase in minimum prey size with predator body size, the estimated increase was close to zero (Slope = 0.02, $P < 0.001$). These results suggest that benthic invertivores do not expand their trophic niche breadth as they grow. As with the piscivores, these results held true when prey size was

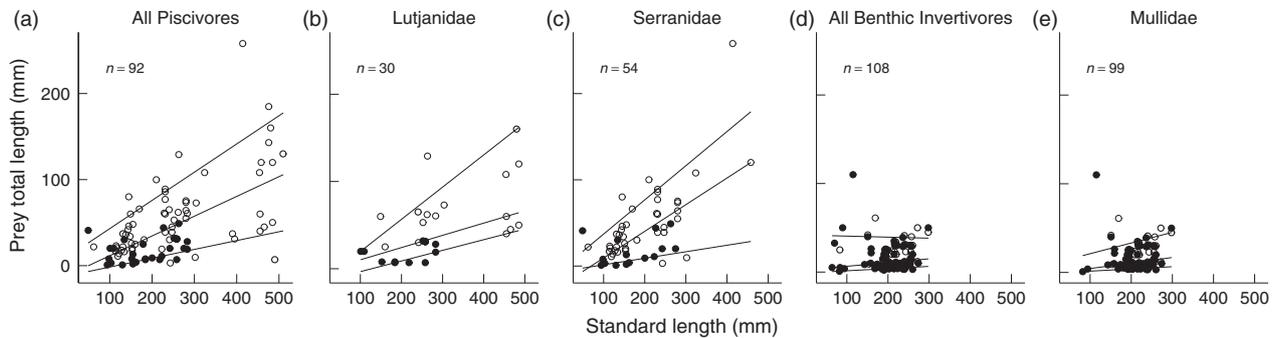


Fig. 1. Quantile regressions (10th, 50th and 90th quantiles) of the relationships between prey total length (mm) and predator standard length (mm) for (a) all piscivores (68 predator individuals), the two most sampled piscivore families (b) Lutjanidae and (c) Serranidae, (d) all benthic invertivores (77 predator individuals) and the most sampled benthic invertivore (e) *Parupeneus insularis* (68 predator individuals). Each point represents a single fish (open circles) or invertebrate (solid circles) prey item found in a predator stomach. The sample size of prey items plotted is labelled on the plot as n = number of prey items. Prey size is the measured length (mm) of the intact or partially digested prey items, and hence taken to be the minimum prey size.

compared to predator gape height and width (Fig. S2). Almost all of the data included in the quantile regression for benthic invertivores was from a single species, the goatfish (*P. insularis*; $n = 99$ of 108 prey items). When *P. insularis* was considered alone (Fig. 1e), there was no significant change in minimum or median prey size but maximum prey size did increase with body size (Slope = 0.12, $P = 0.045$). However, in the gape size–prey size analysis, there was no relationship between *P. insularis* gape width or height and its minimum, median or maximum prey size (Fig. S2), providing weak evidence of gape limitation.

GAPE SIZE–BODY SIZE

Gape sizes were highly variable: absolute gape heights varied by over an order of magnitude and relative gape size ranged from 0.08 to 0.27 amongst the sampled species (Fig. 2 and Fig. S3). Piscivores had the largest absolute gape heights (mean = 51 mm compared to mean of all other species = 19 mm; Fig. 2a) and relative gape heights (mean = 0.23 compared to mean of all other species = 0.13; Fig. 2b). Within the piscivores, *Caranx melampygus* had a similar absolute gape size as the other species but an exceptionally small relative gape size (mean = 0.12; Fig. 2b) because of its much large body size. Benthic invertivores had smaller absolute gape sizes than piscivores (mean = 28 mm). Within this group, the hawkfish had the smallest absolute gape (mean = 15 mm) size but the largest relative gape size (mean = 0.23). Of the four functional groups, the zooplanktivores had the smallest absolute gape sizes (mean = 8.6 mm) and their relative gape sizes (mean = 0.13) were more similar to those of the herbivore/detritivore group (mean = 0.12) than other predators. Within the herbivore/detritivore group, the parrotfishes (*Scarus rubroviolaceus*, *Scarus frenatus* and *Chlorurus sordidus*), which are scraping and excavating species, had large absolute (mean = 31 mm) and relative gape sizes (mean = 0.13) compared to the

grazers (*Acanthurus nigricans*, *Acanthurus olivaceus*, *Centropyge flavissima*; mean absolute gape = 8.7 mm; mean relative gape height = 0.09).

For both the piscivore and benthic invertivore functional groups, gape sizes increased with body sizes isometrically (Fig. 3 and Fig. S4). At the species level, piscivore gape allometries also were consistently isometric with the exception of the snapper *Lutjanus bohar*'s gape height–body size relationship, which was negatively allometric (Slope = 0.81, $P < 0.001$, 95% CI: 0.74–0.89; Fig. 4a). Piscivore gape width–body size analyses similarly showed isometric gape allometries, except for *L. bohar* and *Apharus furca*, which had negative allometries (Fig. S5a). Similar to the piscivores, the benthic invertivore species also had isometric gape size–body size relationships, with the exception of *Monotaxis grandoculis*, which exhibited positive allometry in both its gape height–body size and gape width–body size relationships (Slope = 1.6, 95% CI: 1.3–1.9) (Fig. 4b and Fig. S5b).

As with the other two predator groups, the overall zooplanktivore gape height–body size relationship was isometric (Fig. 3a); this group's overall gape width–body size relationship was, however, positively allometric (Fig. 3b). Within this group, most species had isometric gape height–body size relationships (Fig. 5a), except *Chromis vanderbilti*, which had a positively allometric gape height–body size relationship (Slope = 1.3, 95% CI: 1.0–1.54). Similarly, in the gape width–body size relationships, only *C. vanderbilti* and *Pterocaesio tile* had positively allometric gape widths (Fig. S6a).

Unlike the predator functional groups, the energy-sharing herbivore/detritivore group had positively allometric gape size–body size relationships in both gape dimensions (Fig. 3a and b). Within this group, all three parrotfish species had positively allometric gape height–body size relationships (Fig. 5b). The two surgeonfishes, *A. nigricans* and *A. olivaceus*, also had steep gape height–body size slopes, although only the former was significantly positively allometric (Fig. 5b). The sole angelfish,

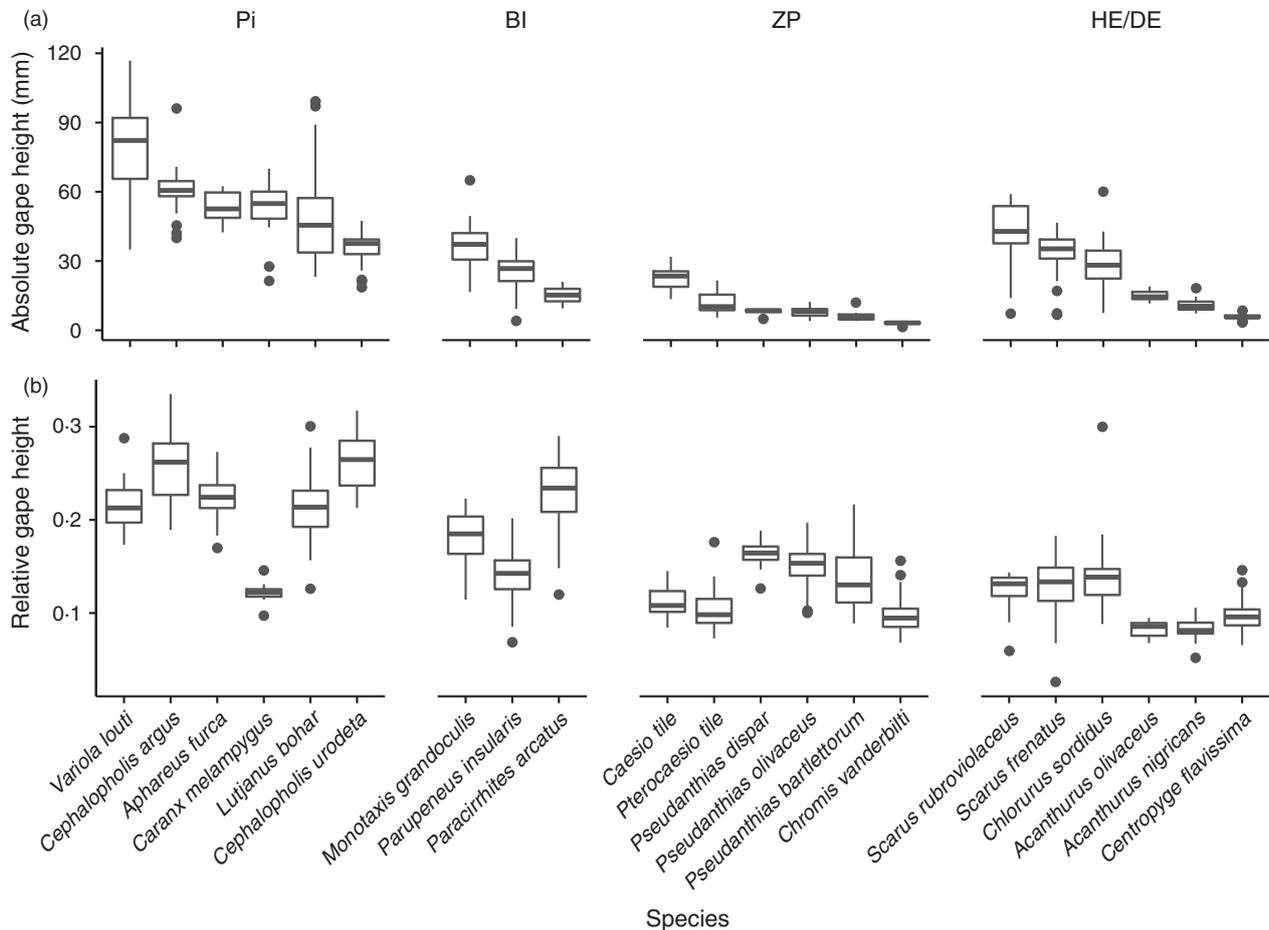


Fig. 2. (a) Absolute gape height (mm) and (b) relative gape height, calculated as gape height (mm)/standard length (mm) for all species ordered within each functional group by decreasing absolute gape height. A single outlier (64 mm) for *Cephalopholis argus* is not shown.

C. flavissima, exhibited isometry in its gape height–body size relationship (Fig. 5b). Gape width–body size relationships in this functional group were, however, only positively allometric for *C. flavissima* and *C. sordidus*, with relationships for the remaining four species isometric (Fig. S6b).

Discussion

SIZE STRUCTURING IN CORALS REEFS

Our study provides two lines of evidence for size structuring amongst piscivorous fishes in coral reef food webs. First, coral reef piscivores showed significant positive correlations in both their maximum and median prey size with body size and also with gape size, suggesting that gape limitation restricts the size of their prey. Gape limitation is hypothesized to be the primary determinant of maximum prey size in fishes (Hoyle & Keast 1987; Persson *et al.* 1996; Mittelbach & Persson 1998) and although there is considerable empirical evidence to support this hypothesis from temperate marine and freshwater ecosystems (Scharf, Juanes & Roundtree 2000; Magnhagen & Heibo 2001; Bachiller & Irigoien 2013), evidence from coral reef ecosystems has

been limited. For example, gut content analysis of the grouper *Plectropomus leopardus* on the Great Barrier Reef provided evidence of gape-limited predation only in the smallest size classes; across the largest size classes, prey size and diet composition were stable (St John 1999). More recently, Holmes & McCormick's (2010) aquarium-based feeding experiment with four coral reef predators found no clear pattern of prey size–selectivity across predator sizes and only minimal evidence for gape limitation, although their results may be attributed to the small size of prey (post-settlement damselfish) tested. In contrast, we found evidence of gape limitation for coral reef piscivores (as a group) and the piscivore families Lutjanidae and Serranidae. Second, we found evidence of ontogenetic diet shifts, with piscivores expanding their trophic niche breadth (in terms of prey size) and shifting from a mixed invertebrate fish diet to fish prey only with increasing body size. Along with gape limitation, such ontogenetic diet changes often lead to increases in trophic position with body size (Mittelbach & Persson 1998) and hence the positive body size–trophic level relationships that are often observed in aquatic ecosystems (Jennings *et al.* 2001; Romanuk, Hayward & Hutchings 2011). Although we did not examine trophic levels in this study, recent stable isotope analyses of

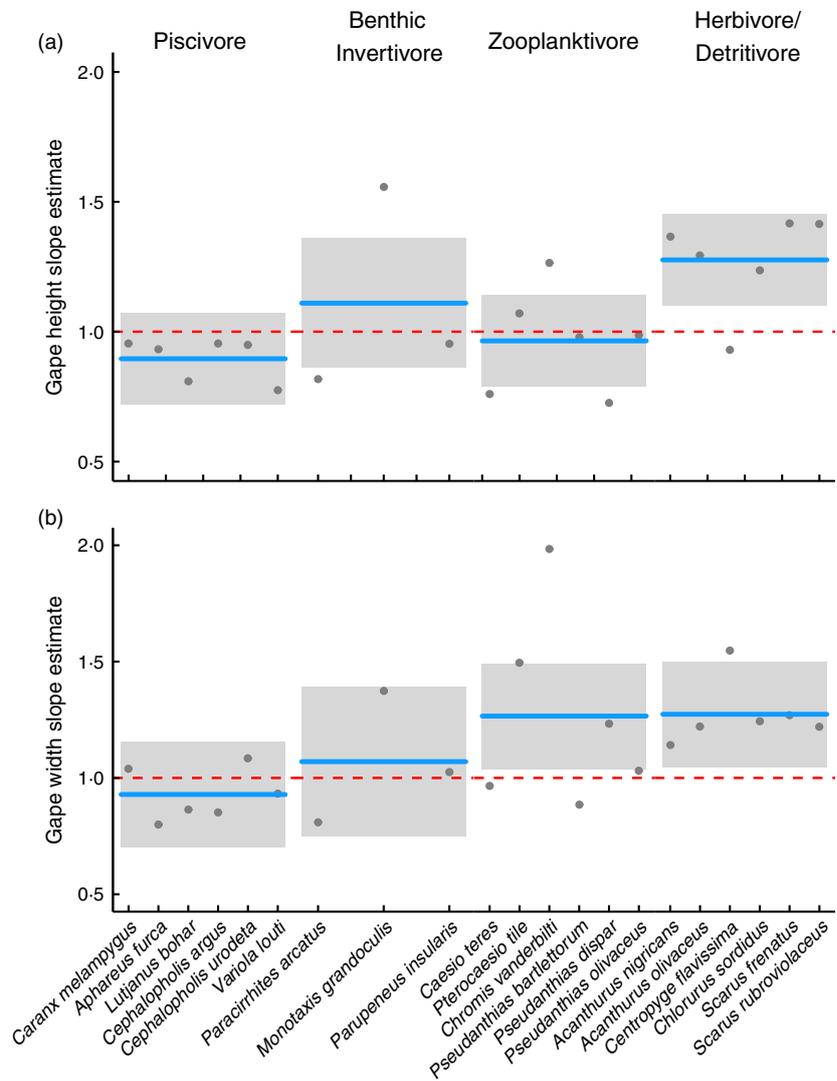


Fig. 3. Comparison of allometric coefficients across functional groups, calculated using a linear model for (a) gape height–standard length and (b) gape width–standard length relationships. Estimates of functional group mean slopes are shown by the solid blue line, species mean slopes are plotted as grey points and confidence limits are bounded by the grey box. For reference, isometry (slope = 1) is plotted as the red dashed line. [Colour figure can be viewed at wileyonlinelibrary.com]

coral reef predators in the Solomon Islands and on Kiritimati provide evidence that trophic level scales positively with predator body size in these ecosystems as well (Greenwood, Sweeting & Polunin 2010; Robinson & Baum 2015).

Unlike the piscivores, evidence for size structuring in the benthic invertivores was weak. *Parupeneus insularis*' maximum prey size did increase with its body size, but there was no significant relationship between its maximum prey size and its gape size, suggesting that it is not gape-limited. Similarly, Lukoschek & McCormick (2001) found that the congener *Parupeneus barberinus* was not gape-limited: although its maximum prey size was positively correlated with its body size, it was unrelated to its gape size. Despite little evidence for gape-limited predation or ontogenetic diet shifts amongst the benthic invertivores in our study, positive relationships between body size and trophic level–body size relationships have been documented for groups of coral reef predators that included benthic invertivores (Mill 2007; Robinson & Baum 2015). It is possible that evidence of size structuring in *P. insularis* was limited by our inability to detect small prey such

as ostracods and nematodes, which have been more commonly found in small (less than 110 mm) *P. barberinus* individuals than large *P. barberinus* individuals (Lukoschek & McCormick 2001). However, given our data, size structuring in coral reef benthic invertivores may be driven by changes in foraging behaviour or by morphological characteristics such as snout depth rather than gape limitation.

GAPE SIZES AND ALLOMETRY ACROSS FUNCTIONAL GROUPS

As expected, piscivores tended to have the largest absolute and relative gape sizes. Large gape sizes improve foraging opportunities by providing piscivores with a larger size range of accessible prey (Brooks & Dodson 1965; Nielsen 1980; Scharf, Juanes & Roundtree 2000; Magnhagen & Heibo 2001); we found evidence of this with many piscivore prey items substantially larger than those of the smaller-gaped benthic invertivores. However, contrary to our expectation of negative gape size–body size allometry

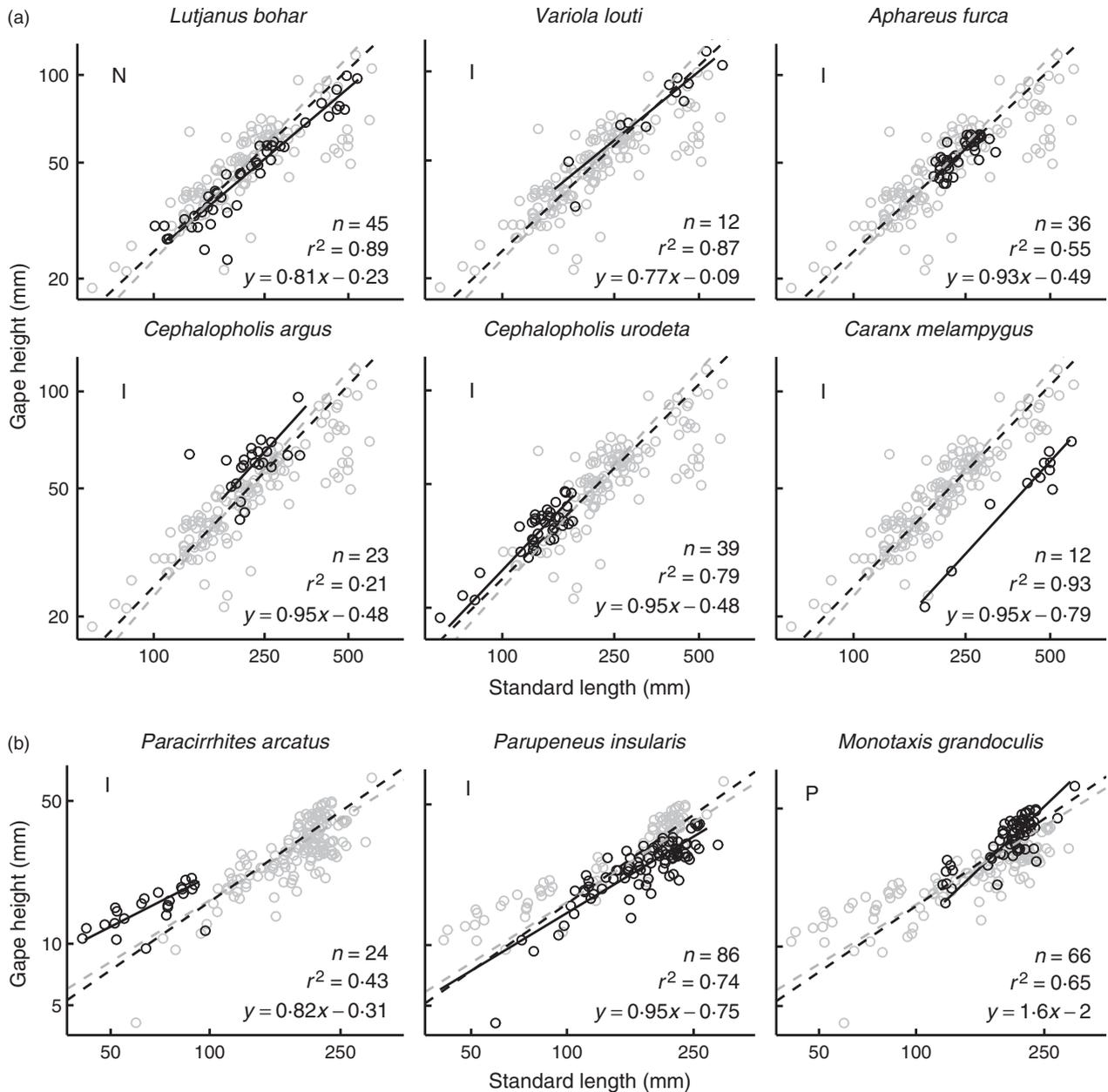


Fig. 4. Gape height–standard length relationships for the nine species sampled from two predatory functional groups: (a) piscivores and (b) benthic invertivores. Within each functional group, species are in order of increasing slope of the allometric relationship. Individual fish from each species are shown in open black circles, along with the fitted standardized major axis (SMA) regression for each respective species (black line). The associated sample size, regression equation and r^2 value are inset in each plot. The gape allometry for each species is indicated by the N (negative allometry), I (isometry) or P (positive allometry). For comparison, individual fish belonging to other species within the functional group is plotted in open grey circles; also shown is the line of isometry (slope = 1; dashed grey line) and the functional groups fitted SMA regression (dashed black line), both plotted through the midpoint of the functional group-level relationship.

in piscivores, only one species *L. bohar* exhibited this relationship in both gape dimensions. All other piscivore species – including *Variola louti*, which had the largest absolute gape size and hence would be the best candidate species for negative gape size allometry – exhibited isometric gape size growth, suggesting that they remain gape-limited throughout their lifespan.

Differences in gape sizes and allometries amongst the three benthic invertivores likely reflect the distinct

feeding modes of these species. *Monotaxis grandoculis*, which feeds by crushing hard-shelled invertebrates (Randall 2005), had the largest absolute gape size of the benthic invertivores and was the only one with a positively allometric gape size–body size relationship. Crushing strength has been shown to scale positively allometrically with body size in other shell-crushing invertivores including wrasses in the *Halichoeres* genus (Wainwright 1988) and the sheephead *Archosargus probatocephalus*

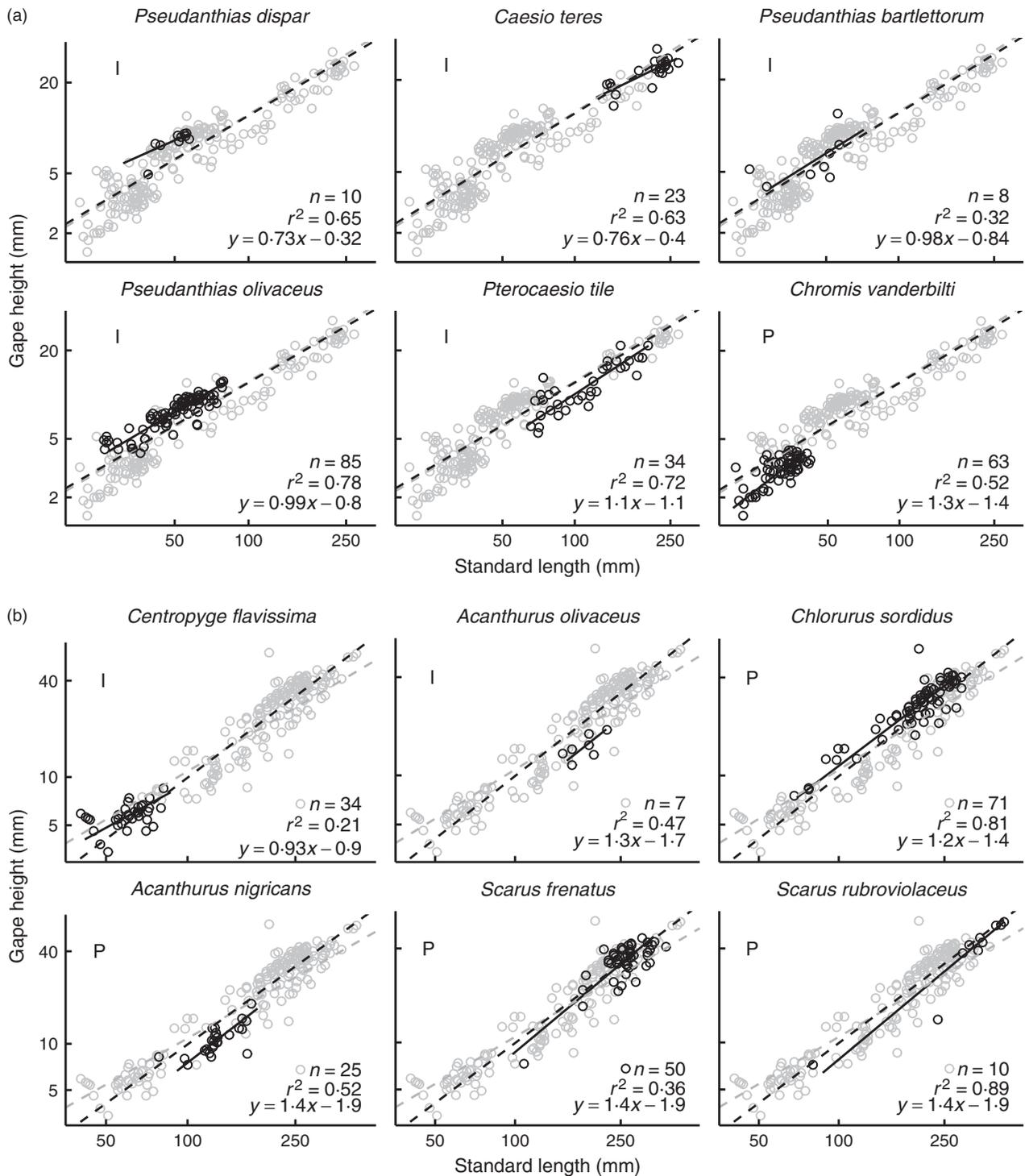


Fig. 5. Gape height–standard length relationships for the (a) six zooplanktivores and (b) six energy-sharing herbivorous and detritivorous species, in order of increasing slope. Plot details are the same as in Fig. 4.

(Hernandez & Motta 1997). Positive allometry may therefore enable shell-crushing predators to successfully prey upon larger mollusks. As such, we expect that predator size–prey size relationships in these species should be positive. In contrast, *P. insularis*, a benthic invertivore that primarily consumes crustaceans (Randall & Myers 2002) and does not crush hard-shelled

invertebrates, had a small absolute gape size, an isometric scaling relationship, and its prey size did not increase significantly with gape size. Finally, the hawkfish, *Paracirrhites arcatus*, had a large relative gape size, which we attribute to this small-bodied predator being the only sampled benthic invertivore to regularly consume fish.

Zooplanktivores had small absolute and relative gape sizes compared to the other predators, and positively allometric gape width–body size relationships. The mechanisms underpinning these results are, however, unclear given that other studies have found gape limitation to be most important at small body sizes (Zaret 1980; Wanzenböck 1995; St John 1999). For example, Schmitt & Holbrook (1984) suggested that small, early-stage black surfperch (a zooplanktivore from shallow reefs of Southern California) were likely gape-limited because their gapes were smaller than the maximum size of potential prey in their environment, whereas gut content analyses of the adults showed that they were not gape-limited, having large gape sizes but still consuming small prey. For zooplanktivores, which are typically jaw-ram suction feeders, gape morphologies that affect feeding mechanics such as suction power, or protrusion speed, may be more important than gape limitation (Holzman & Wainwright 2009). Wanzenböck (1995), for example, estimated that the optimal prey size for zooplanktivores, as determined using the ratio of prey dry weight to prey handling time, was near maximum gape size when zooplanktivores were small (10–15 mm standard length) but only 50% of maximum gape size when zooplanktivores exceeded 40 mm standard length.

In comparison with the other herbivore/detrivore species, parrotfishes had substantially larger absolute and relative gape sizes; these species also exhibited positively allometric gape size–body size relationships. Parrotfishes (scarines) are bioeroders that scrape (*S. frenatus*, *S. rubroviolaceus*) and excavate (*C. sordidus*) hard substrates such as coral skeletons covered in algal turf (Bellwood & Choat 1990; Wainwright & Bellwood 2002; Green & Bellwood 2009). Because algae and detritus are nutrient-poor (relative to fish prey; Wilson *et al.* 2003), coral reef herbivores and detritivores have developed strategies to extract adequate nutrition from these resources including having long digestive tracts (Elliott & Bellwood 2003) and high ingestion rates (Wilson & Bellwood 1997). Parrotfishes' large gape sizes – which were similar in size to many of the piscivore and benthic invertivore species – and their positive allometry may be additional means of maximizing feeding efficiency, by providing them with more leverage to bite off hard coral substrate and enabling them to take larger bites. Indeed, Lokrantz *et al.* (2008) found positively allometric scaling of algae removal and body size in three coral reef parrotfish species including one we studied, *C. sordidus*. The two algal turf and filamentous algae grazers, *A. nigricans* and *C. flavissima* (Choat, Clements & Robbins 2002; Green & Bellwood 2009), also had positively allometric gape size–body size relationships, which may also allow these species to graze more effectively. Further, unlike predatory functional groups, macroalgae and detritus are size invariant and so positive allometry, which increases relative gape size at a disproportionately fast rate, may be another strategy by which herbivores and detritivores compensate for the nonlinear increase in energy

demand with increasing body size (Peters 1983; Brown *et al.* 2004).

Herbivores are important contributors to coral reef resilience (Mumby *et al.* 2006). Our study adds to the growing literature demonstrating that body size is an important indicator of the functional impact of these species on coral reefs (Bruggemann *et al.* 1996; Bonaldo & Bellwood 2008; Streit, Hoey & Bellwood 2015). If positive allometry of gape size in the herbivore/detrivore community leads to larger individuals consuming increasingly higher volumes of macroalgae and detritus (Lokrantz *et al.* 2008), then the removal of large-bodied herbivores and detritivores through fishing may have a disproportionately large effect on the functions these species provide. This effect could be compounded given that foraging home range and body size also scale positively (Nash, Graham & Bellwood 2013; Welsh, Goatley & Bellwood 2013; Tamburello, Côté & Dulvy 2015).

CAVEATS AND FUTURE DIRECTIONS

Coral reefs are highly diverse ecosystems, making it intractable to sample all fish species. Although we collected data for 28 species from four different functional groups, some functional groups still had few species sampled and/or unbalanced sampling across species. In particular, the predator–prey data for benthic invertivores were dominated by a single species, and it would be interesting for future studies to examine the predator size–prey size relationship in *Monotaxis grandoculus* and other shell-crushing invertivores to see whether these species are gape-limited. It also would be useful to investigate predator size–prey size relationships and ontogenetic diet shifts in a broader range of coral reef predator species to determine how general size structuring is in coral reef food webs. Sharks, for example, are important coral reef predators that were not included in this analysis, but which may play a key role in ecosystem function (Osgood & Baum 2015; Roff *et al.* 2016). Little is known, however, about the strength of trophic level–body size scaling relationships in this predatory group, and evidence of gape limitation is weak (Romanuk, Hayward & Hutchings 2011). Inclusion of shark species in predator size–prey size and gape limitation analyses would therefore provide complementary information about the nature of size structuring in coral reefs. Finally, future analyses making comparisons across many species should use a phylogenetic approach (e.g. using a phylogenetic generalized least-squares regression (ppls) analysis) to account for the non-independence of related species (Westoby, Leishman & Lord 1995). We aimed to do so herein, but were limited by the lack of a published coral reef fish phylogeny. Instead, we tested for differences in gape allometry across functional groups using a random effects model with family as a random effect but our results were unchanged.

Conclusions

Taken together, our results provide new insights about predator–prey relationships and gape morphologies of fishes in coral reef ecosystems. We provide evidence of gape limitation and ontogenetic niche shifts in coral reef piscivores, which adds to the nascent literature indicating that these species are size-structured. Our findings do suggest, however, that size structuring is weak in coral reef benthic invertivores. We believe that these patterns in size structuring likely generalize across site and regions because predator–prey mass ratios (a related size-based metric) have not been shown to vary significantly with temperature, latitude, depth or primary production (Barnes *et al.* 2010). Unexpectedly, differences in gape allometry did not seem related to the strength of size structuring across coral reef functional groups. Instead, gape allometries seemed to vary based on feeding mode and these differences may have implications for the functional role of different groups in a coral reef community, particularly for the herbivore/detritivores species that exhibited positively allometric gape size–body size relationships. With size structure being increasingly used in ecosystem models (Andersen & Beyer 2015) and in management contexts, it is important to understand the mechanisms that are hypothesized to generate such relationships. Our work suggests that understanding the relationships between prey size, gape size and body size may be important to understanding how coral reef communities may be impacted by size-selective anthropogenic stressors such as fishing.

Authors' contributions

J.K.B. conceived the ideas and collected the data; J.C.D. analysed the data; J.C.D. and J.K.B. led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data used in this paper are deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.5th45> (Dunic & Baum 2017). Associated R scripts can be accessed at https://github.com/baumlab/Dunic-Baum_2017-JAE, <http://dx.doi.org/10.5281/zenodo.290697> (Dunic 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Study site, Kiritimati (Christmas) Island, showing the 23 sampling locations around the atoll.

Fig. S2. Quantile regressions (10th, 50th, and 90th quantiles) of the relationships between prey total length (mm) and (a) predator gape height (mm) and (b) for predator gape width for all piscivores, the two most sampled piscivore families Lutjanidae and Serranidae, all benthic invertivores, and the most sampled benthic invertivore *Parupeneus insularis*.

Fig. S3. (a) Absolute gape width (mm) and (b) relative gape width, calculated as gape width (mm)/standard length (mm) for all species ordered within each functional group by decreasing absolute gape height.

Fig. S4. Comparison of allometric coefficients across functional groups, calculated using a linear model for (a) gape height ~ body mass and (b) gape width ~ body mass relationships.

Fig. S5. Gape width ~ standard length relationships for the nine species sampled from two predatory functional groups: (a) piscivores and (b) benthic invertivores.

Fig. S6. Gape width ~ standard length relationships for the (a) six zooplanktivore and (b) six energy-sharing herbivorous and detritivorous species, in order of increasing slope.