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### **Size-spectra of reef fish assemblages within distinct coral habitats, before and after a mass coral bleaching event**

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# Size-spectra of reef fish assemblages within distinct coral habitats, before and after a mass coral bleaching event

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PRIFYSGOL  
**BANGOR**  
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School of Ocean Sciences  
College of Environmental Science

Submitted in partial fulfillment of the requirements for the  
Degree of Master of Science by Research  
in Ocean Sciences

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January 2023

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

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Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

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# 1 | Acknowledgements

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## 2 | Abstract

Habitat-forming species perform a crucial function in size-structuring associated communities. The variable morphology of different species creates structurally distinct habitats that differ in resource availability. However, climate-driven disturbances have altered the composition of coral species and affected reef fish assemblages. Reef fish select habitat refuge in relation to body-size, yet despite the known variation in resource provisions within distinct coral habitats, how reef fish body-size distributions among these habitats covary with habitat structural complexity remains unknown. Considering the disparity of coral structural morphologies in provisions of refugia availability for reef fish communities, this data analysis study was conducted to assess body size-spectra of carnivore and herbivore reef fish within six distinct coral habitats (i.e., reefs characterised by predominance of specific coral taxa, mixed coral taxa, or low coral cover). Specifically, pre-existing data from Lizard Island (Richardson et al. 2017 & 2018) was used to understand the (a) correlation with structural complexity at five spatial scales of measurement (4-64 cm) and (b) the impact of a mass coral bleaching event. Here, carnivore and herbivore size-spectra differed within the distinct coral habitats. Pre-bleaching disturbance, the size-spectra of both trophic guilds correlated with the largest structural complexity scales (32 and 64 cm scale). After the bleaching event, the size-spectra of both trophic guilds steepened due to a relative reduction in smaller-bodied fishes (or an increase in larger). The steepening in carnivore size-spectra slopes was significant as the composition of carnivore species homogenised among the habitats. This study supports evidence that trophic guild size-spectra can be a responsive ecological indicator of habitat and disturbance effects, and as novel habitat configurations emerge, monitoring changes in guild size-spectra will provide important insight into altered ecosystem functions.

### 3 | Introduction

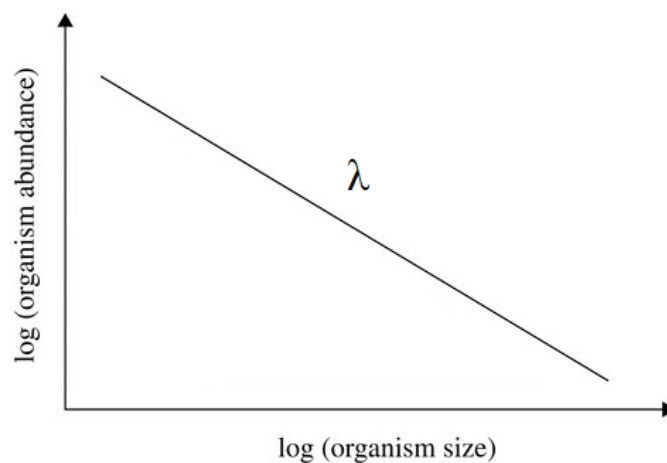
Body-size of an organism is a ‘super trait’ that governs biological processes and ecological interactions (Brown et al. 2004; Thygesen et al. 2005; Woodward et al. 2005; White et al. 2007). The size structuring of aquatic communities (i.e., defined as a group of interacting species occupying the same geographical area; Stroud et al. 2015). occurs from ontogenetic diet shifts. Individual fish often shift diet composition during development, expanding the range of prey size consumed (Werner & Gilliam 1984). This change leads to increased trophic position with individual growth as large-bodied organisms consume smaller ones (Sánchez-Hernández et al. 2019), forming a greater abundance of small-bodied organisms than larger ones within ecological communities (White et al. 2007; Blanchard et al. 2009). The negative relationship between abundance and body-size is also linked to trophic transfer efficiency in food webs, predators are generally larger-bodied than prey and energetic constraints by inefficient energy transfer cause abundance to scale with body-size (Trebilco et al. 2013; Sprules & Barth 2016). Size-based indicators quantify biomass distributions, determining community characteristics such as predator and prey body-sizes and energetic pathways (Woodward et al. 2005; Norkko et al. 2013; Trebilco et al. 2013), as outlined by metabolic theory (Brown et al. 2004). Thus, revealing the constraints on community structure that provide a baseline for ecosystems dynamics and response to disturbances (Gardner et al. 2011; Yvon-Durocher et al. 2011; Dossena et al. 2012; O’Gorman et al. 2012; Yvon-Durocher & Allen 2012).

The size spectrum, a well-established size-based indicator by Sheldon et al. (1972), describes the relationship between organism body-size distributions and community abundance or biomass in aquatic systems. Specifically, the theory indicates total biomass remains approximately constant across all size classes (Sheldon et al. 1972). When plotted in logarithmic space, extracting coefficients, such as the slope or intercept, provide a simple approach to summarise community structure (Figure 1; Trebilco et al. 2013; Sprules & Barth 2016; Guet et al. 2016; Blanchard et al. 2017). For instance, the size-spectra slope outlines the rate of decrease in abundance or biomass with increased body-size within a given community (Figure 1; Sheldon et al. 1972; Rice & Gislason 1996; Petchey & Belgrano 2010). At a community level, the slope estimates clearly demonstrate the decreased energy availability with increased body-size and in the efficiency of energy transfer (~10%) across trophic levels, capturing complex predator-prey dynamics (Sprules & Barth 2016; Trebilco et al. 2013; Guet et al. 2016). This relationship is predicted to be shallower within trophic guilds, where a group of species exploit the same resources in similar ways (Stroud et al. 2015). Within trophic guilds sharing an energy base, such as herbivores, energy is not lost between trophic levels, meaning that the abundance is constrained simply by energetic demands and metabolic rates (Trebilco et al. 2013), leading to theoretical predictions that size spectrum slopes  $\approx 0.75$  (Brown & Gillooly 2003). For trophic guilds that are size-structured (large-bodied individuals prey upon small-bodied), such as



carnivorous fishes, the size spectrum includes multiple trophic levels and thus trophic transfer inefficiency (Trebilco et al. 2013), leading to slopes  $\sim -1$  (Brown & Gillooly 2003). Size-spectra relationships (i.e., a strong negative linear slope) have been consistently observed in various aquatic ecosystems (Jennings & Blanchard 2004; Trebilco et al. 2013; Blanchard et al. 2017; Mazurkiewicz et al. 2019; Mazurkiewicz et al. 2020; Fraser et al. 2021; Hatton et al. 2021; Heather et al. 2021) have established ecological baselines and led to recommendations to use size-spectra coefficients as indicators of ecological health (Petchey & Belgrano 2010; Sprules & Barth 2016).

While size-spectra slopes for marine communities are consistent (i.e., often near -1.0; Sprules & Barth 2016), they can deviate in response to anthropogenic and natural disturbances (i.e., Górska & Włodarska-Kowalczyk 2017; Petchey & Belgrano 2010; Guiet et al. 2016). A steeper slope (i.e., the relation between body-size and abundance becomes more negative) indicates more small-bodied organisms and fewer large-bodied than expected, while the opposite for shallow slopes (i.e., becomes more positive). For instance, deviations from this anticipated slope have occurred in marine systems due to anthropogenic and climate drivers, including overfishing (Blanchard et al. 2005; Daan et al. 2005; Graham et al. 2005; Robinson et al. 2017; Carvalho et al. 2021; Zgliczynski & Sandin 2017), habitat degradation (Graham et al. 2007, Wilson et al. 2010; Rogers et al. 2014; Rogers et al. 2018), pollution (Pomeranz et al. 2019; Arranz et al. 2021) and non-native species invasion (Kopf et al. 2019; Barth et al. 2019). Alternatively, natural drivers of variation in size-spectra slopes include habitat structural complexity (Alvarez-Filip et al. 2011b; Nash et al. 2013a), energetic resource subsidies (Perkins et al. 2018), and seasonal variations (McGarvey & Kirk 2018; Evans et al. 2022). Due to the size-selective responses of organisms to natural environmental variation and anthropogenic impacts (Petchey & Belgrano 2010; Guiet et al. 2016; Pomeranz et al. 2019), we can assess deviations from theoretical expectations to quantify community responses to perturbation.



**Figure 1.** Size-spectra describes the relationship between organism body-size (length, weight, or volume) and abundance or biomass, illustrated by the spectra slope ( $b$ ). Modified from Petchey & Belgrano (2010) & Guiet et al. (2016).

In tropical regions, coral reefs are among the most biodiverse marine ecosystems, yet reef communities are threatened by cumulative disturbances (Bellwood et al. 2004; Hughes et al. 2017; Hughes et al. 2018a; Hughes et al. 2018b). These ecosystems are primarily formed by scleractinian coral species that create physical structures that are essential for providing habitat to reef-associated organisms (Nash et al. 2013a; Graham & Nash 2013). The variable morphology of different coral species creates structurally distinct habitats, supporting a diverse assemblage (i.e., defined as a taxonomically related group of species populations that occur in the same geographical area; Stroud et al. 2015) of reef fishes (Komyakova et al. 2018; Richardson et al. 2018; Richardson et al. 2020). For instance, coral morphology ranges from simple more planar forms (e.g., encrusting and massive) to structurally complex (e.g., branching and foliose), and different configurations of these morphologies contribute to broader scale reef habitat structure (Alvarez-Filip et al. 2011a; Graham & Nash 2013; Gonzalez-Rivero et al. 2017). The structural complexity of habitats is often discussed as the measure of rugosity or the abundance of crevices or spaces within and between colony structure of dimensions relating to organism body-sizes (Hixon & Beets 1993, Willis & Anderson 2003). For instance, reefs dominated by complex species, such as branching *Acropora*, support broad reef fish and invertebrate body-size distributions (Graham et al. 2007; Wilson et al. 2010; Alvarez-Filip et al. 2011b; Graham & Nash 2013; Nash et al. 2013a; Rogers et al. 2014; Darling et al. 2017; Ware et al. 2019; Fontoura et al. 2020). Structurally complex coral reefs are especially important for small-bodied mobile organisms, including new recruits, juveniles, and small adults, that require refuge from predation and environmental stressors (Friedlander & Parrish 1998, Graham & Nash 2013). Thus, the availability of coral reef habitat refugia at a range of suitable dimensions can support a wider spectrum of body-sizes of mobile organisms (Hixon & Beets 1993; Gonzalez-Rivero et al. 2017).

However, coral reef structural complexity can vary depending on the composition of benthic species (Curtis & Vincent 2005; Alvarez-Filip et al. 2011a; Jinks et al. 2019; Seitz et al. 2020; Fontoura et al. 2020) and are differentially altered by climate-driven disturbances (e.g., thermal heatwaves, severe storms, and ocean acidification; Hoegh-Guldberg & Bruno 2010; Hughes et al. 2018b; Sully et al. 2019; Marzonie et al. 2022). Since coral taxa vary in susceptibility to stressors like coral bleaching and ocean warming (Fabricius et al. 2011; Grottoli et al. 2014; Edmunds et al. 2021; Marzonie et al. 2022), these disturbances have caused unprecedented loss of coral cover and distinct shifts towards reefs dominated by stress-tolerant and fast-growing weedy species (e.g., *Acropora*; Madin et al. 2018; Darling et al. 2012; Darling et al. 2013; Fabricius et al. 2011; van Woesik et al. 2011; Alvarez-Filip et al. 2011a). Consequently, a shift in coral species or severe coral loss can alter habitat structural complexity, changing the composition of associated fish assemblages and shifting energetic dynamics (Wilson et al. 2010; Graham & Nash 2013; Dornelas et al. 2014; Rogers et al. 2014; Morais et al. 2020). For instance, a shift to more planar species would reduce the availability of fine-scale refugia (Rogers et al. 2014; Rogers et al. 2018), disproportionately impacting small-bodied

reef fish and shallowing spectra slopes due to the loss of these smaller-size classes (Graham et al. 2007; Coker et al. 2009; Wilson et al. 2010; Alvarez-Filip et al. 2011b; Nash et al. 2013a; Madin et al. 2018; Fontoura et al. 2020). Given the relationship between coral habitat configurations and reef fish assemblages (Alvarez-Filip et al. 2011b; Nash et al. 2013a; Rogers et al. 2014), we might expect body-size distributions to vary among distinct habitat types, yet this remains unknown.

Size-spectra studies that assess reef fish response to disturbance have typically aggregated all species biomass (i.e., Wilson et al. 2010; Alvarez-Filip et al. 2011b; Fontoura et al. 2020), limiting our understanding of how trophic guilds may respond. Distinct trophic guilds of reef fish perform vital feeding roles, contributing to ecosystem function. For instance, carnivores maintain ecosystem balance through predation of lower trophic levels (Roff et al. 2016), while herbivores mediate coral-algal competitive dynamics (Fox & Bellwood 2014; Bellwood et al. 2019). Carnivores generally exhibit steeper size-spectra slopes (estimate = -1.64; Robinson & Baum 2016) due to the inefficiency of energy transfer between trophic levels (Trebilco et al. 2013), while herbivores exhibit shallower slopes (estimates = -1.2) due to sharing energy within a trophic level (Robinson & Baum 2016; Trebilco et al. 2013). Both guilds similarly respond to anthropogenic and climate disturbances (Graham et al. 2007). For example, fishing pressures steepen carnivore and herbivore spectra slopes due to the targeted extraction of large-bodied fish, whereas reduced habitat structural complexity shallows slopes due to a reduction in the abundance of small-bodied fish (Rogers et al. 2014; Rogers et al. 2018). However, herbivore foraging in low-complexity reefs (i.e., slightly raised above a flattened substrate) may outweigh the loss of refugia (Nash et al. 2013a; Richardson et al. 2020), opposing the refuge-availability hypothesis. At present, the greatest climate threat to coral-dominated habitats is mass coral bleaching driven by severe thermal stress (Hoegh-Guldberg et al. 2007; Spalding & Brown 2015; Eakin et al. 2016; Hughes et al. 2017; Hughes et al. 2018a; Hughes et al. 2018b). Bleaching can cause extensive coral mortality, altering coral species configurations (Hughes et al. 2018b) and the structure of reef fish assemblages (Graham et al. 2007; Pratchett et al. 2011). While habitat degradation has altered the size-spectra of functional reef fish guilds (Rogers et al. 2018; Carvalho et al. 2020), the response to an acute thermal disturbance event will depend on thermal tolerance and degree of habitat dependence associated with each distinct coral habitat (Graham et al. 2011; Richardson et al. 2017; Richardson et al. 2018).

Despite the importance of coral habitat structures on size structuring associated fish assemblages (Nash et al. 2013a; Graham & Nash 2013), the variation in size-spectra of reef fish trophic guilds among distinct coral habitats and how a heatwave may impact spectra slopes within those habitats is not yet known. This limits our understanding of how size-spectra of different trophic guilds are spatially shaped by cross-scale structural complexity and temporally changed by an acute thermal disturbance event. Here, pre-existing datasets collected by Richardson et al. (2017 & 2018) from Lizard Island, Australia (Figure 2) were used to assess the variation in body-size distributions of

functionally important reef fish among six taxonomically distinct coral reef habitats, characterized by a disproportionate cover of individual coral taxa, mixed coral species, or low coral cover). Specifically, this study (i) assessed whether carnivore and herbivore size-spectra slopes correlated with varying habitat structural complexity across five specific spatial scales (from 4-64 cm) among these habitats 6 months (September 2015) before the bleaching event; and (ii) quantified temporal variation in habitat-specific size-spectra before versus 6 months (October 2016) after a severe coral bleaching event that caused 43-67% of corals to become bleached (Richardson et al. 2017).

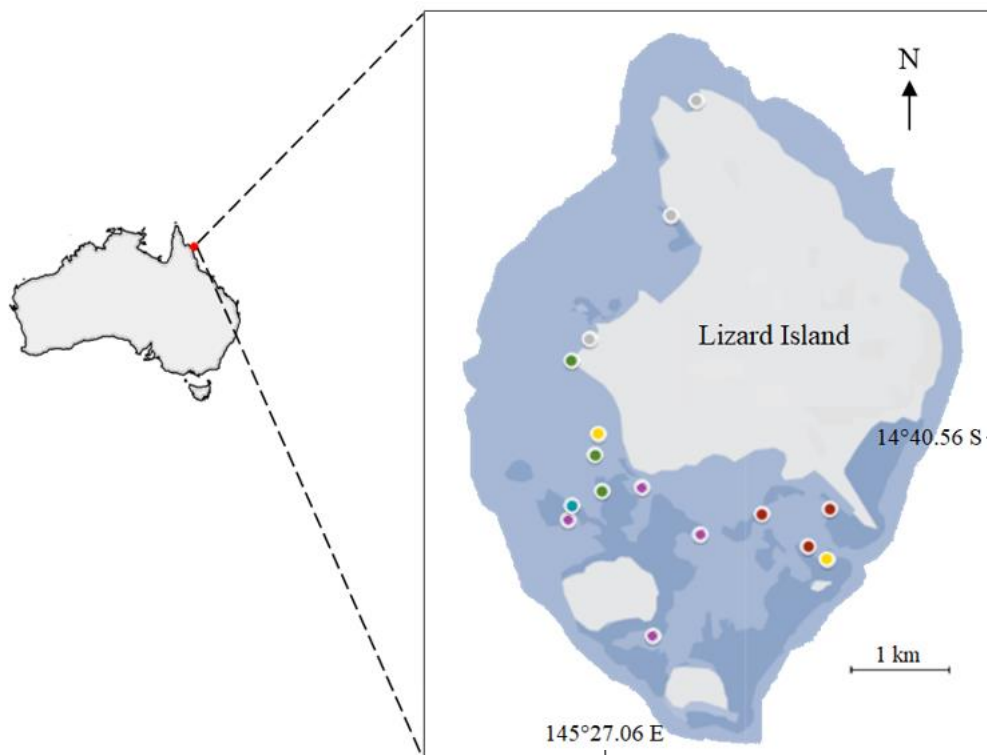
This study hypothesised that variation in size-spectra of carnivore and herbivore guilds would correlate with cross-scale habitat structural complexity measures, particularly at the smaller scale. Structurally complex habitats at the smaller scale supported more small-bodied fishes, while less structurally complex habitats would support less small-bodied fishes (Nash et al. 2013a; Rogers et al. 2014; Rogers et al. 2018). This study also hypothesised that the size-spectra of both guilds steepened (i.e., due to a reduction of small-bodied fishes) after the mass coral bleaching event. Carnivores (i.e., planktivores, invertivores, and piscivores) typically have a greater relative abundance of small-bodied fish than herbivores (Robinson & Baum 2016) due to an inefficient energy transfer from predation whereas herbivores share a common energy source (Trebilco et al. 2013). Thus, alterations in the composition of coral species and habitat degradation, resulting in a reduction in small-bodied fishes, would have a greater impact on carnivore slopes than herbivores (Rogers et al. 2018). In addition, this study (iii) quantified the taxonomic structure of carnivore and herbivore guilds within those habitats, before and after bleaching, to assess how they changed to elucidate further the resulting change in body-size distributions of both guilds within the distinct coral habitats.

## 4| Method

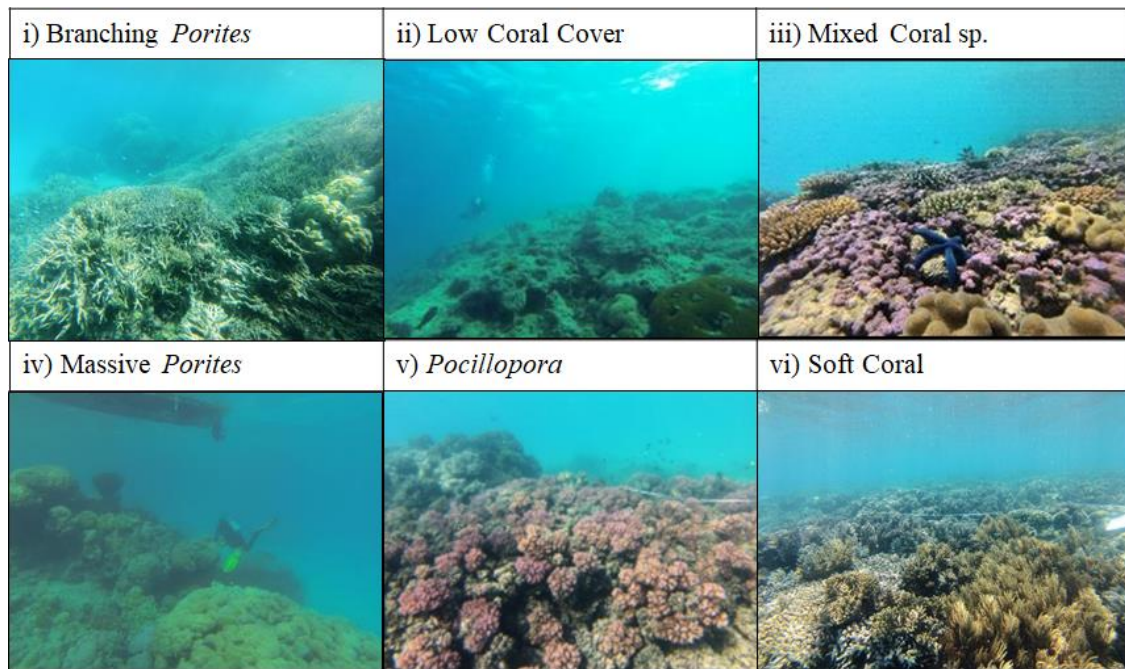
### 4.1 | Study sites

Underwater visual censuses surveys were conducted by Richardson et al. (2017 & 2018) on reefs around Lizard Island (14°410S, 145°270E; Figure 2 & 3), known as Dyii gurra to the Dinggaal Aboriginal people and situated in the northern section of the Great Barrier Reef (GBR), Australia. In April 2016, these reefs experienced a system-wide mass coral bleaching event prompted by the accumulation of sea surface heat stress from >8-degree heating weeks (i.e., the duration and intensity of exceeding the bleaching threshold; Hughes et al. 2018a) as maximum daily sea surface temperatures reached ~32.8 °C (Hughes et al. 2018a).

Data on fish assemblage and cross-scale habitat structural complexity were collected (by Richardson et al. 2017 & 2018) simultaneously at 16 sites on the leeward side of the granitic island before (September 2015) and after (October 2016) the mass coral bleaching event (Figure 2). All sites were haphazardly selected in September 2015, were characterised by shallow (<6 m depth) reef edges, and protected from fishing (i.e., located within a Marine National Park Zone managed by the GBR Marine Park Authority) and the southeast prevailing swell. Adjacent sites were separated by >500 m. Based on pre-published studies (Richardson et al. 2017 & 2018), the experimental design was centred around pre-identified habitat types (Figure 3) characterised by a disproportionate cover (25-58% of the total benthos; see Appendix 1) of (i) branching *Porites* (mostly *P. cylindrica*), (ii) massive *Porites*, (iii) mixed coral species, (iv) *Pocillopora*, (v) soft coral, and (vi) low coral cover (i.e., <10% live coral cover).



**Figure 2.** A map of Lizard Island (14°410S, 145°270E) located 30 km offshore from mainland Australia in the northern section of the Great Barrier. The coloured points represent the locations of the study sites (n=16): branching *Porites* (red, n=3), low coral cover (grey, n=3), massive *Porites* (yellow, n=2), mixed coral spp (purple, n=4), *Pocillopora* (blue, n=1), and soft coral (green, n=3). See Appendix 2 for site coordinates.



**Figure 3.** Illustrative images of the six distinct coral habitat types at Lizard Island taken in September 2015 (by Laura Richardson). Scales of photos are not equivalent, and images were not used for data collection.

#### 4.2 | Assessment of fish assemblages

At each site, six 30 m belt transects were conducted, equating to a total of 192 transects during the two survey years. Transects were placed along the reef-sand interface with a minimum of 5 m between adjacent transects. Transect placement was initially haphazard in September 2015 and repeated approximately (within 1-2 m) in October 2016 through visual identification by Richardson et al. (2017 & 2018).

A single diver (i.e., Richardson et al. 2017 & 2018) recorded the abundance and estimated body-size (total length; TL) to the nearest cm of diurnally active, non-cryptic fish identified to species level where possible. Large-bodied mobile fishes (>10 cm TL) were recorded within a 5 m wide belt during transect placement to avoid scaring them away before counting, thus reducing observer disturbance. Smaller-site-attached fishes ( $\leq 10$  cm total length) were recorded on the return swim along the transect within a 1 m wide belt. Fish counts were standardised to 150 m<sup>2</sup>. Body-size estimates were visually calibrated to reduce visual error by comparing the TL of PVC pipes underwater with known lengths (Nash et al. 2013a). Fish individuals were categorized into trophic guilds, (i.e., carnivores and herbivores) based on feeding preferences described in the literature (Appendix 3). Despite there being an expected bias with small-size class estimates using UVC survey methods (Ackerman & Bellwood 2000), the removal of fishes <10 cm would exclude a large majority of small-bodied fishes (Heather et al. 2021). Thus, all carnivore and herbivore size classes were

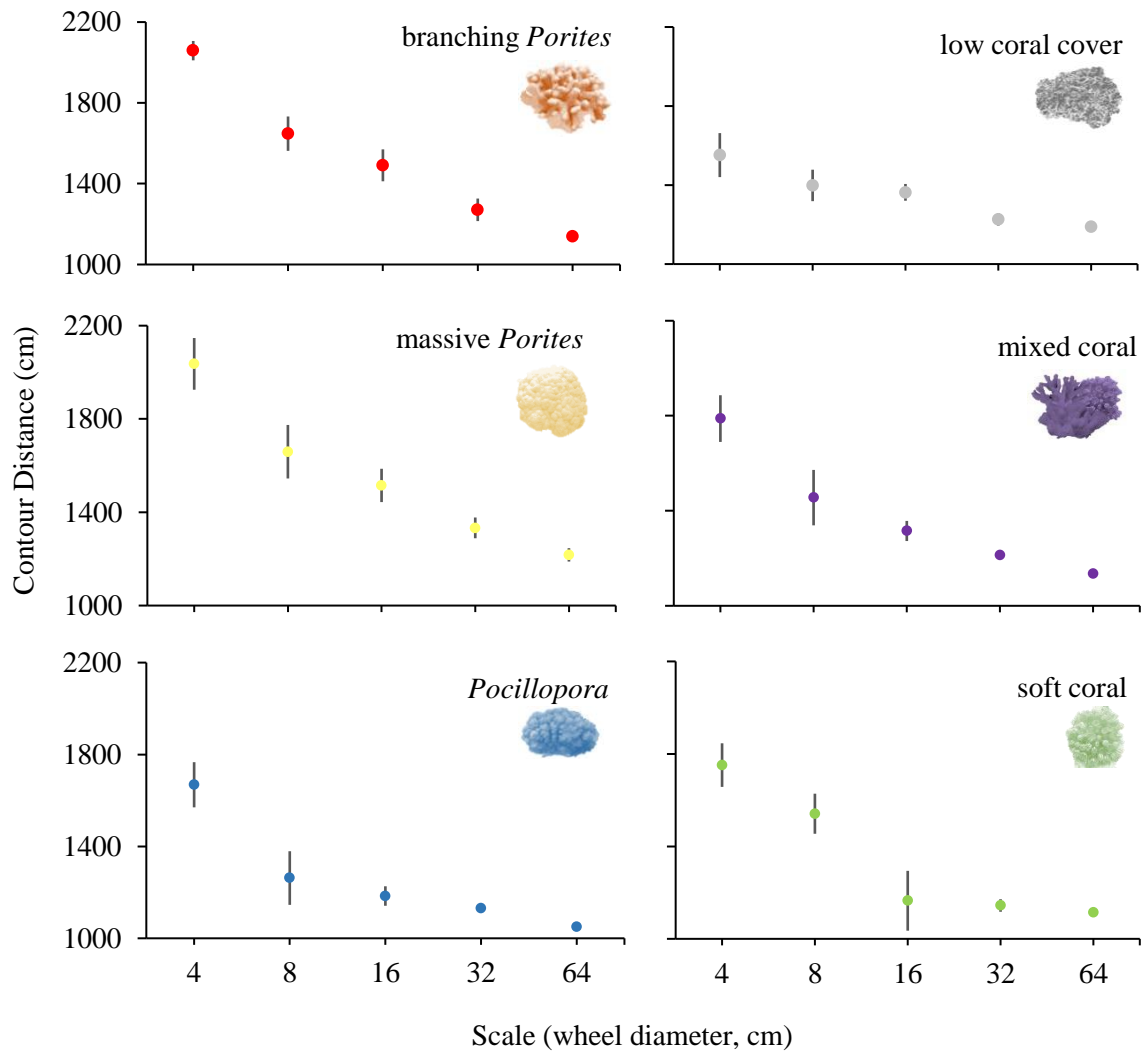
included in the analysis to maintain an approximate representation of carnivore and herbivore body-size distributions (i.e., Heather et al. 2021; Coghlan et al. 2022). Obligate corallivores were excluded from the study due to feeding on a different energetic pathway (i.e., predate on coral species), and therefore, such assemblages are directly altered by bleaching through the loss of prey species (Graham et al. 2009). Additionally, this study followed previous body size-spectra studies that focused on carnivore and herbivore reef fish (i.e., Rogers et al. 2014; Rogers et al. 2017; Robinson & Baum 2016; Carvalho et al. 2020).

Individual fish lengths were converted to weight using the standard equation,  $W=\alpha L^\beta$  (where  $W$  is mass in g and  $L$  is the total length in cm). Species  $\alpha$  and  $\beta$  parameters were sourced from FishBase Bayesian estimates (Froese et al. 2014; Froese & Pauly 2022). A total of 185 fish species (127 carnivore species and 58 herbivores) were identified between 2015 and 2016 (a list of fish species with functional guild classification is available in Appendix 3). Carnivore individuals ranged in body mass from 0.01 to 6330 g, and herbivores from 0.01 to 3366 g.

### **4.3 | Assessment of benthic habitat and structural complexity**

To estimate benthic habitat composition, six 30 m point-intercept transects were simultaneously conducted on the same fish transects. For each transect, the total percentage cover of benthic substrate types was recorded by Richardson et al. (2017 & 2018) directly under the transect tape at regular 25 cm intervals (total = 120 points per transect). Scleractinian corals were identified to genus level, and the remaining substrate as soft (alcyonarian) coral, other sessile invertebrates (i.e., ascidians, giant clams, and sponges), crustose coralline algae, macroalgae (calcifying or fleshy), dead coral (with turf algae, filamentous algae, or CCA), rubble (with turf or filamentous algae), and sand.

To estimate reef structural complexity across spatial scales, 10 m transects positioned in the mid-section (~10 to 20 m) of the first four transect lines were conducted at each site before the bleaching event by Richardson et al. (2017). Reef contour distances were measured by rolling five wheels ranging from 4–64 cm in diameter along each linear transect length (Figure 4). These diameters were selected to correspond with non-cryptic fish body depths (Nash et al. 2013a; Richardson et al. 2017). Contour distance was used as a proxy for the reef habitat structural complexity to compare the cross-scale physical structure among the study habitats (Nash et al. 2013a; Richardson et al. 2017). The contour distances at each spatial were determined by the number of wheel rotations along each 10 m transect (full and partial) multiplied by the wheel circumference. The structural complexity measurements were conducted in September 2015 only.



**Figure 4.** Mean contour distance ( $\pm$  standard error) measured using wheels ranging in scales of 4-64 cm (wheel diameters) within each habitat. Modified from figure S1 Richardson et al. (2017).

#### 4.4 | Estimating size-spectra slopes

Traditionally, size-spectra studies have analysed coral reef fish assemblages using linear regression models, where the regression slope is comparable to the spectra slope for binned abundance data on a logarithmic scale (i.e., Graham et al. 2005; Wilson et al. 2010; Alvarez-Filip et al. 2011b; Fontoura et al. 2020). However, this method does not account for bin structure bias and can produce inaccurate spectra slope estimates and confidence intervals (Edwards et al. 2017). Since slope estimates are not standardised, there is also limited comparability among studies that have used a regression-based method (Edwards et al. 2017). The extended likelihood method quantifies the probability distribution of body-sizes and is the least-biased method of estimating spectra slopes and confidence intervals. This function accounts for the bin structure of species-specific length data during the length-mass



conversion (Edwards et al. 2017). Here, the sizeSpectra R package (Edwards et al. 2020) was used to examine the size structure of reef fish abundance by fitting the body mass data to a bounded power-law distribution:

$$f(x) = Cxb^b, \quad x_{\min} \leq x \leq x_{\max}$$

where  $x_{\min}$  and  $x_{\max}$  are the minimum and maximum body mass (g), and the slope ( $b$ ) describes the abundance of body size classes (White et al. 2007). The extended likelihood method was used to estimate  $b$  with a 95% confidence interval (Edwards et al. 2017). Body-size data points were visualised on the spectra slope using log-log mass and abundance plots, as recommended by Edwards et al. (2017). Separate spectra-slopes were estimated for carnivores and herbivores at the transect level (combined total = 378 slope estimates).

## 4.5 | Statistical analysis

Models were checked for multicollinearity among predictor variables using the variance inflation factor (VIF) function in the car package (Dormann et al. 2012; Naimi et al. 2014). Coral cover was collinear with structural complexity metrics, identified by values  $>3$  (Zuur et al. 2010) and was not included in the model. Similarly, the 8 cm structural complexity scale was collinear with the other structural complexity metrics and was not included in the herbivore model. The assumptions of the linear mixed models were separately checked by plotting model residuals, ensuring primarily homogeneity of variance since mixed models are generally considered robust to mild skews from assumptions of normality (Schielzeth et al. 2020). Confidence intervals determined the strength and direction of the effect of predictors on size-spectra (Halsey 2019; Stahel 2021). All analyses were performed in R (R Core Team, 2022).

### 4.5.1 | Fish size-spectra correlation with habitat structural complexity scales

Linear mixed models were used with Gaussian distributions, using the lmer function in the lme4 R package (Schielzeth & Nakagawa 2013; Bates et al. 2015; Harrison et al. 2018) and included site as a random effect to account for size-spectra variation within each habitat. Separate linear mixed models were applied for each guild (i.e., carnivore and herbivore) using size-spectra slopes as a response variable and habitat type (six levels) and each contour measure (4, 8, 16, 32, 64 cm) as predictors. The models here only used transects from the 2015 survey period (i.e., before bleaching) and included four transects for each site that had corresponding habitat structural complexity and fish assemblage data, and contour distances were centred and standardised to allow for comparison. Post-hoc Tukey tests

were used on the linear mixed models to conduct pairwise comparisons of fish size-spectra between distinct habitats and structural complexity scales.

#### **4.5.2 | Fish size-spectra within distinct habitats**

Separate linear mixed models were used for carnivore and herbivore guilds using size-spectra as a response variable, with habitat type (6 levels) and survey period (2 levels) as predictors, and site as a random intercept. Planned comparisons were conducted on how size-spectra temporally changed within habitats following bleaching-induced coral mortality, using estimated marginal means fitted with the *emmeans* function in the *emmeans* package (Searle et al. 1980).

#### **4.5.3 | Fish species composition within distinct habitats**

A permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; Anderson 2017; McArdle & Anderson 2001; Anderson & Walsh 2013) was used to determine whether carnivore and herbivore species composition varied within the distinct coral habitats after the bleaching event. PERMANOVA models were built using a Bray-Curtis matrix, with 12 sum-of-squares for carnivore guilds and 8 sum-of-squares for herbivores, and 9999 random permutations of the raw data by applying the *adonis2* function in the *vegan* package (Oksanen et al. 2020). PERMANOVA, a robust alternative to the parametric multivariate analysis of variance (MANOVA; Anderson 2017), was used due to non-equal variances reported in the Levene's test. Separate PERMANOVA tests were run for each guild using multivariate species abundance as the response and habitat type and survey period as predictors. The Bray-Curtis dissimilarity distance was used derived from a matrix of pairwise differences between species abundance using the *vegdist* function in the *vegan* package (Anderson 2017; Oksanen et al. 2020). Multivariate homogeneity of dispersion in each habitat type was tested using the *betadisper* function in the *vegan* package (Oksanen et al. 2020) and fitted with a bias adjustment:

$$\sqrt{n/(n-1)}$$

where  $n$  is species abundance, to avoid a downward bias caused by partial observability when comparing species composition (Anderson 2006; Stier et al. 2013). A multidimensional scaling method, known as principal coordinates analysis (PCoA), was used to visually explore the dissimilarities of carnivore and herbivore species composition among habitat types and across the survey periods. The PCoA1 and 2 components were plotted (see Figure 9). A permutation test was built using 999 permutations using the *permutest* function in the *vegan* package (Anderson 2006; Anderson et al. 2006; Oksanen et al. 2020) to determine the homogeneity of dispersion among the

habitat types. Also, the TukeyHSD function in the vegan package (Oksanen et al. 2020) was used to conduct pairwise comparisons. Confidence intervals were used to determine the strength and direction around the impact of the predictors on multivariate comparisons (Halsey 2019; Stahel 2021).

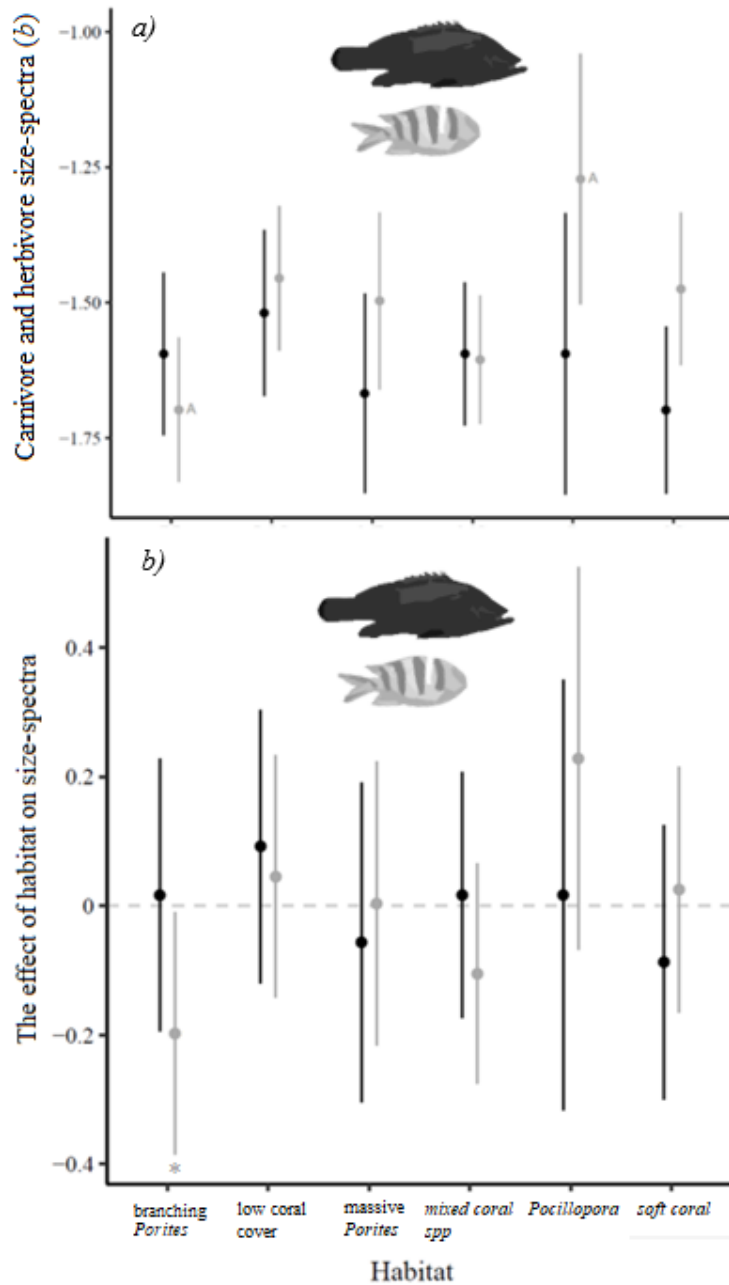
## 5 | Results

Across the survey period, carnivore and herbivore mean size-spectra slopes differed among the distinct coral habitats. Although carnivore mean size-spectra slopes were typically steeper (ranging from -1.52 to -1.70) than herbivores (ranging from -1.26 to -1.69; Figure 5a), the confidence intervals at each habitat type overlapped between both guilds. While the confidence intervals of carnivore size-spectra across the survey period overlapped among all habitat types, herbivore body size-spectra on average were significantly steeper in habitats dominated by branching *Porites* than *Pocillopora* by -0.43 (confidence interval (CI): -0.84 | -0.01; Figure 5a) in 2015, with no variation in slopes accounted for by sites. Additionally, the effect of each distinct habitat across the survey period was not significant on carnivore spectra slopes (Figure 5b), with a 15% variance in slope estimates was accounted for by sites. Simultaneously, branching *Porites*-dominated habitats were the only distinct habitat type that had a significant effect on herbivore size-spectra. The mean herbivore slope estimate in branching *Porites* habitats was typically steeper than the other coral habitats on average by -0.20 (CI: -0.39 | -0.01; Figure 5b).

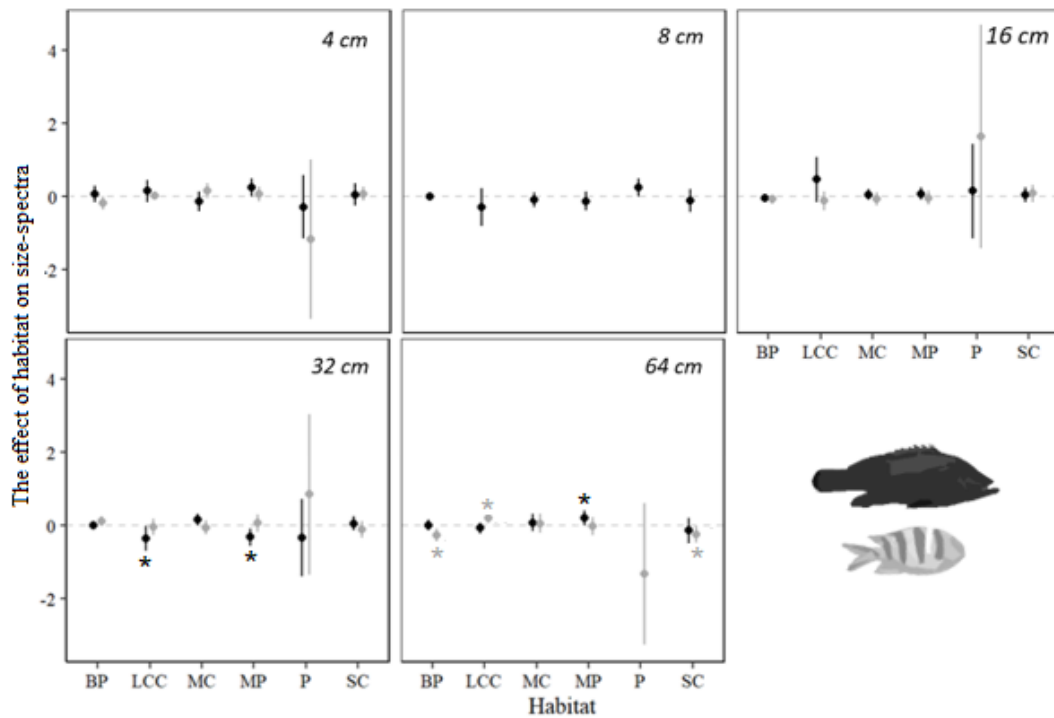
### 5.1 | Fish size-spectra correlation with habitat structural complexity scales

Carnivore size-spectra, consisting of a greater relative abundance of smaller-bodied fishes (or lower relative of larger), significantly correlated with the habitat structural complexity scale of 32 cm ( $p < 0.05$ ). At this scale, carnivore spectra slopes showed a significant negative correlation with massive *Porites*-dominated (slope = -0.32, CI: -5.58 | -0.08) and low coral cover habitats (-0.36, CI: -7.04 | -0.02; Figure 6). Carnivore slopes also showed but significantly positive correlation with the largest scale of 64 cm in massive *Porites*-dominated habitats (0.20, CI: 4.68 | 0.40; Figure 6). There was no significant association of carnivore size-spectra with the smaller spatial scales within habitats or scales in habitats dominated by branching *Porites*-, low coral cover-, *Pocillopora*-, and soft coral-dominated habitats (Figure 6). Herbivore size-spectra, consisting of a greater relative abundance of larger-bodied fishes (or lower abundance of smaller), were significantly correlated with the largest structural complexity scale of 64 cm ( $p < 0.01$ ). At this scale, herbivore spectra slopes were steeper in branching *Porites*- (-0.27, CI: -0.45 | -0.10) and soft coral-dominated habitats (-0.24, CI: -0.46 | -0.02; Figure 6) and shallower in low coral cover habitats (0.20, CI: 0.06 | 0.34). There was no association in

herbivore spectra slopes with the smaller structural complexity scales or across all scales massive *Porites*- and *Pocillopora*-dominated, and mixed coral species habitats (Figure 6).



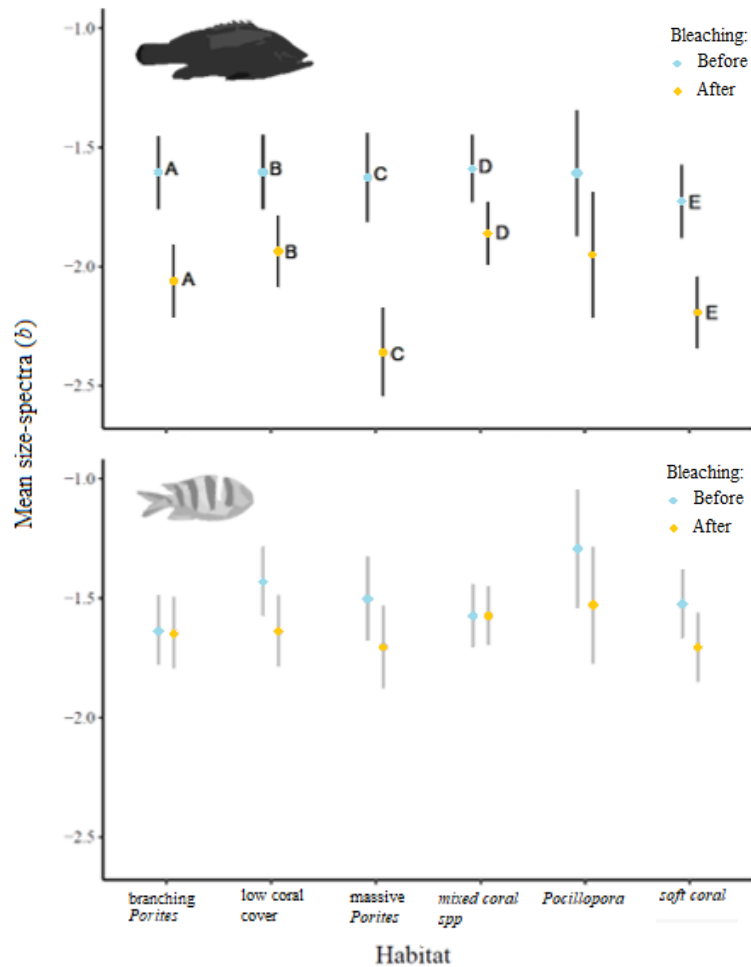
**Figure 5.** a) Carnivore (black) and herbivore (grey) average size-spectra ( $\pm$  95% confidence intervals) within distinct coral habitats across the survey period. Planned comparisons between the average size-spectra were quantified using estimated marginal means. A significant difference in size-spectra between habitat types are represented by letter pairings (A). b) The effect ( $\pm$  95% confidence intervals) of habitat type on size-spectra were quantified using planned comparisons and a significant effect is represented by an \*.



**Figure 6.** The effect ( $\pm$  95% confidence intervals) of habitat type, at each structural complexity scale (4-64 cm), on carnivore (black) and herbivore (grey) body size-spectra. A significant effect of habitat type on guild size-spectra is represented by an \*. Habitat types are BP – branching *Porites*, LCC – low coral cover, MP – massive *Porites*, MC – mixed coral species, P – *Pocillopora*, SC – soft coral.

## 5.2 | Temporal changes in fish size-spectra within distinct habitats

The size-spectra of carnivore and herbivore guilds differentially responded following a bleaching event. Carnivore size-spectra significantly steepened following bleaching among all habitats apart from *Pocillopora*-dominated ones (Figure 7). The greatest temporal change occurred in habitats which exhibited the highest structural complexity at the 4 cm scale (Figure 4). For example, slope estimates steepened by -0.73 in massive *Porites*-dominated habitats. On average, carnivore size-spectra slopes steepened significantly more in massive *Porites*-dominated habitats than in low coral cover (-0.42) and mixed coral species (-0.5) habitats. Alternatively, herbivore spectra slopes, unlike carnivores, had no detectable change following bleaching (Figure 7) and had no significant difference among habitats. In comparison, carnivore size-spectra were steeper on average by -0.66 than herbivores in structurally complex habitats at the 4 cm scale (branching *Porites*- and massive *Porites*-dominated habitats; Figure 7).



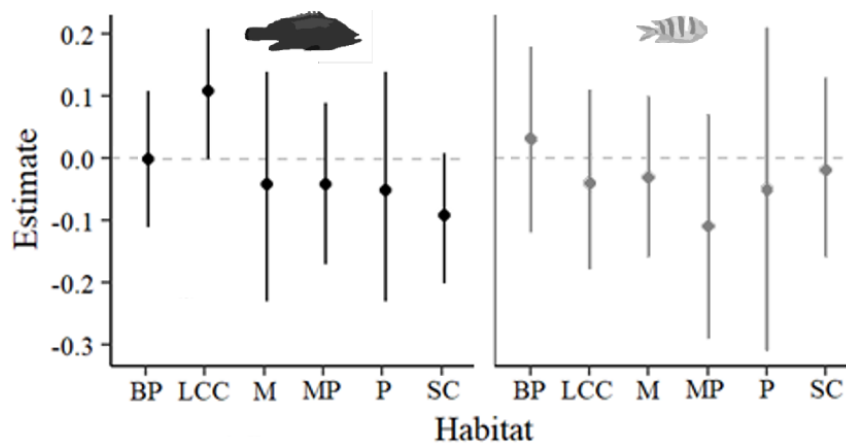
**Figure 7.** Estimated marginal mean size-spectra ( $\pm$  95% confidence intervals) of carnivores (black) and herbivores (grey) before (blue) and after (orange) the bleaching event, within each coral habitat type. Significant differences between mean size-spectra within each habitat were quantified using planned comparisons and are represented by letter pairings (i.e., A, B, C, D, E).

### 5.3 | Temporal changes in fish species composition within distinct habitats

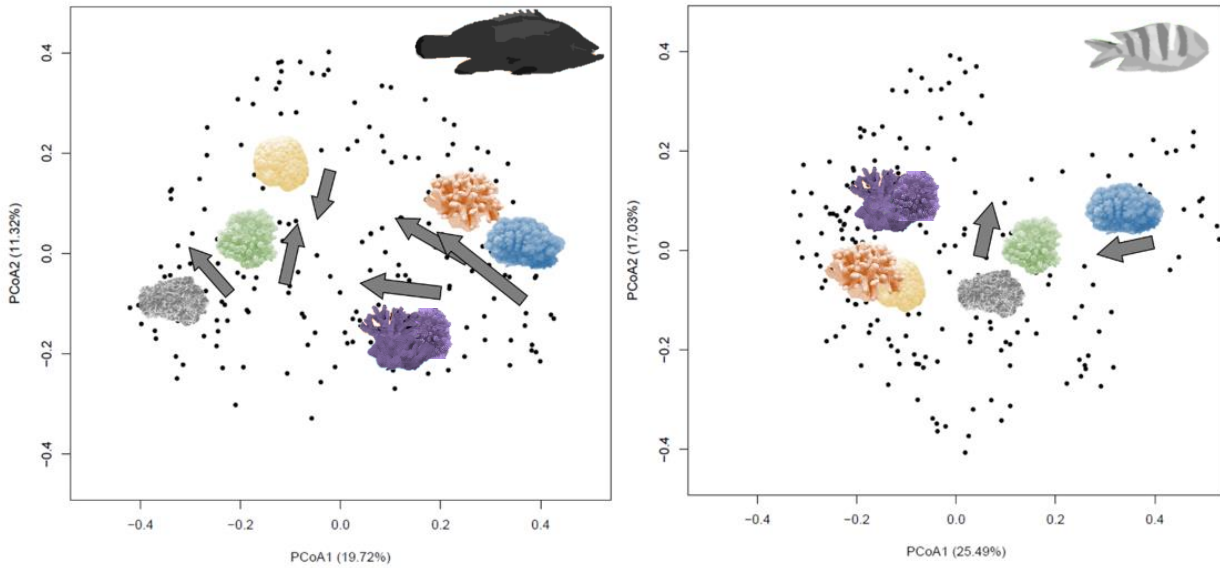
Differential taxonomical changes occurred between carnivore and herbivore guilds within the distinct coral habitats from before to after the bleaching event. The composition of carnivore species significantly differed among the habitats across both survey periods (PERMANOVA:  $R^2 = 0.26$ ,  $F_{11} = 5.53$ ,  $p < 0.05$ ), with 26% of the variation explained by the survey period. A significant shift in carnivore species composition occurred in low coral cover habitats (Figure 8). The two PCoA axes explained 22.04% of carnivore species composition among the distinct coral habitat types, before and after the bleaching event (Figure 9). Carnivore guilds in habitats dominated by branching *Porites*, mixed coral species or *Pocillopora* clustered to the right of PCoA1, while those in low coral cover or soft coral-dominated habitats clustered to the left of PCoA1. PCoA2 separated carnivore guilds in massive *Porites*-dominated habitats from the other habitats. Following the bleaching event, the

composition of carnivore species shifted with the increased variance within the habitats (permutest:  $F_{11} = 3.78$ , permutations = 999,  $p < 0.05$ ), and became homogenised among most of the habitat types. For instance, carnivore guilds in coral-dominated habitats shifted to the centre of PCoA1 and 2 and clustered more closely together. However, carnivore guilds in low coral cover habitats shifted left along PCoA1 and remained separated.

Additionally, the composition of herbivore species significantly differed among the habitats (PERMANOVA:  $R^2 = 0.22$ ,  $F = 4.46$ ,  $p < 0.05$ ), with 22% of the variation explained by the survey period. The two PCoA axes explained 42.52% of herbivore species composition across the distinct coral habitat types, before and after the bleaching event (Figure 9). Before the bleaching event, the composition of herbivore species was similar among the coral habitats. For instance, herbivore guilds in habitats dominated by branching *Porites*, low coral cover, massive *Porites*, mixed coral species, and soft coral clustered in the middle of PCoA1 and 2. Herbivore guilds in the structurally complex habitats are clustered more closely on PCoA1 and 2, while those in the least structurally complex habitats occupied the right of PCoA1. Following the bleaching event, although the composition of herbivore species remained relatively unchanged (Figure 9), a shift with increased variance in herbivore composition occurred within the habitats (permutest:  $F = 2.93$ , permutations = 999,  $p < 0.05$ ). For instance, herbivore guilds in the *Pocillopora* habitat shifted left, positioning closer to the centre of PCoA1 and clustered with low coral cover, while soft coral-dominated habitats shifted up from the centre of PCoA2.



**Figure 8.** Pairwise comparison estimates of guild size-spectra from before and after the bleaching event ( $\pm$  95% confidence intervals) within each coral habitat type (BP – branching *Porites*, LCC – low coral cover, MP – massive *Porites*, MC – mixed coral species, P – *Pocillopora*, SC – soft coral). Separate analysis was conducted for carnivores (black) and herbivores (grey).



**Figure 9.** Principal coordinate analysis (PCoA) plots in two dimensions show the change in carnivore and herbivore species composition from before to after the bleaching event, within the distinct coral habitats (branching *Porites* – red, low coral cover – grey, massive *Porites* – yellow, mixed coral species – purple, *Pocillopora* – blue, soft coral – green) in a functional space. The direction of change in assemblages (i.e., from before to after bleaching) in each habitat is illustrated by a grey arrow and habitats with minimal or no change in species composition are absent of an arrow. The black points represent species composition and the coloured habitat type icons show the average position of species composition in a functional space.

## 6 | Discussion

Reef fish abundance scaled negatively with body-size (i.e., more abundant small-bodied individuals and fewer larger ones), which is consistent with ecological theory and represents the energetic constraints on fish assemblage size-structure (Trebilco et al. 2013). When comparing feeding guilds, carnivores compete for energy through predation had steeper spectra slopes than herbivores who share an energy resource. This aligns with in-situ studies (Robinson & Baum 2016; Carvalho et al. 2021) as the abundance of herbivores scales with body mass as outlined in the energetic equivalence theory while carnivores are constraint by inefficient energy transfer across trophic levels (Trebilco et al. 2013). In both survey periods, estimated size-spectra slopes among the distinct coral habitats for herbivores ( $b \sim -1.75$ ) were in line with theoretical expectations (Reuman et al. 2008; Robinson & Baum 2016), while carnivores ( $\sim -2$ ) on average varied from theoretical predictions. However, carnivore estimates before bleaching (September 2015) were shallower than estimates following bleaching (October 2016) and aligned with theory (Reuman et al. 2008; Robinson & Baum 2016). The derived theoretical predictions are designed for closed systems that directly transfer energy from primary producers to high-level consumers (Trebilco et al. 2013). The underwater visual census



surveys in this study only documented a subset of reef fish assemblages (i.e., non-cryptic, and diurnally active; Ackerman & Bellwood 2003). Thus, a comprehensive survey method (Brock 1982; Caldwell et al. 2016) that includes small-bodied and cryptic fish, large-bodied fish that are hard to capture in belt transects, and nocturnally active fish may reveal alternative size-spectra relative to theoretical predictions.

Configurations of coral species form distinct habitats of variable structural complexity that structure associated reef fish assemblages (Alvarez-Filip et al. 2011b; Nash et al. 2014), yet disturbances can shift the composition of coral species and impact fish communities (Wilson et al. 2010; Graham & Nash 2013; Rogers et al. 2014; Morais et al. 2020). Here, analysing underwater visual census data of carnivore and herbivore guilds are differentially size structured among taxonomically distinct coral reef habitats. Before the bleaching, carnivore size-spectra slopes had minimal difference among the distinct habitats, though the steepest slope was supported by structurally complex habitats at the 8 cm scale (soft coral-dominated). Following bleaching, carnivore slopes differed among the distinct habitats with the steepest supported by structurally complex habitats at the 4 cm scale (massive *Porites*-dominated), while the shallowest were supported by intermediate structurally complex habitats at the 4 cm scale (mixed coral species). Emerging novel coral configurations under a changing climate could reduce the abundance of smaller-bodied fish to predate on, impacting the abundance of larger-bodied carnivores (Robinson et al. 2019). Thus, a reduction in large-bodied carnivorous fish species may create unstable fish assemblages (Williams et al. 2010; Britten et al. 2014).

In comparison, before the bleaching event herbivore size-spectra differed among the distinct habitats, the steepest spectra slopes were supported by structurally complex habitats at the 4 cm scale (branching *Porites*-dominated), and the shallowest were supported by the least structurally complex at the 8 cm scale (*Pocillopora*-dominated). The implication for novel emerging coral reef configurations on herbivore guilds can differ depending on the complexity of benthic species configurations. For instance, a shift in habitat composition to more complex coral species might increase the relative abundance of small-bodied herbivores, as increased refugia availability may reduce predation pressure on them (Graham et al. 2007; Nash et al. 2013a; Rogers et al. 2014; Rogers et al. 2018), while potentially impeding predator detection and escape for large-bodied fishes (Catano et al. 2015). Alternatively, a shift to more planar coral or algae species that form low relief habitats could increase the relative abundance of large-bodied roving herbivores. The reduced refugia availability may increase predation on smaller-bodied fishes (Rogers et al. 2014; Rogers et al. 2018) while increasing energy resources and reducing the reefscape of fear (by reducing visual occlusion of predators) for large-bodied fishes (Nash et al. 2013a; Catano et al. 2015). Among the habitats studied, the most likely habitat configurations for the future of reef fish assemblages include the least structurally complex habitats at the 4 cm scale, such as low coral cover and *Pocillopora*-dominated. In addition,

future reefs may also be dominated by massive *Porites* forming structurally complex habitats at the 4 scale that are robust to thermal-induced disturbances (Darling et al. 2013), having experienced minimal change in coral cover following a thermal-induced bleaching event (Robinson et al. 2018). Thus, the forecast for sustained ecosystem structure would support steepened carnivore and herbivore size-spectra slopes.

### **6.1 | Fish size-spectra structured by habitat structural complexity**

The variable morphology of different coral species creates structurally distinct habitats with varied cross-scale structurally complex that structure reef fish body-size distributions (Alvarez-Filip et al. 2011b; Nash et al. 2013a; Darling et al. 2017; Rogers et al. 2018). Here, both trophic guilds are size-structured by the largest structural complexity scales (carnivore: 32 cm, herbivore: 64 cm) of distinct coral habitats, supporting differences in size-spectra. Theory predicts that structural complexity at the smaller spatial scales should favour small-bodied individuals (Alvarez-Filip et al. 2011b; Nash et al. 2013a; Rogers et al. 2018) and is supported by empirical observations across a range of marine habitats, such as macroalgae (Trebilco et al. 2015; Seitz et al. 2020), seagrass (Jinks et al. 2019), and scleractinian corals (Alvarez-Filip et al. 2011a). In contrast, the steep carnivore size-spectra slopes that demonstrate a greater relative abundance of small-bodied fish would typically correlate with the smallest scales of structural complexity measurements (4-8 cm) (Friedlander & Parrish 1998; Wilson et al. 2010; Graham & Nash 2013). However, carnivore spectra slopes may have correlated with the 32 cm scale due to feeding behaviour. Since carnivorous reef fish forage by predation on smaller-size fish relative to gape size (Dunic & Baum 2017), prey capture in structurally complex reefs may be limited to species feeding technique and gape size relative to crevice opening size. In addition, herbivore size-spectra slopes were generally shallow, especially in less structurally complex habitats across all scales (i.e., low coral cover). Herbivore spectra slopes may have correlated with the 64 cm scale due to the low coral cover habitats that provide flatter reefscapes, supporting the foraging activity of roving large-bodied herbivores (Catano et al. 2015). Moreover, herbivore size-spectra slightly steepened in complex habitats (i.e., branching *Porites*-dominated) due to fear of predation and increased predator refugia for small-bodied herbivores (Alvarez-Filip et al. 2011b; Graham & Nash 2013; Rogers et al. 2014; Catano et al. 2015). Although these herbivore findings oppose in-situ studies in Indonesia (Carvalho et al. 2021), structurally complex habitats supported shallower size-spectra and low complex habitats supported steeper slopes, they align with theoretical models (Rogers et al. 2014; Rogers et al. 2018). The disparity in Carvalho et al. (2021) size-spectra may have been confounded by fishing pressures.

## 6.2 | Variation in fish size-spectra within distinct habitats

Here, the temporal difference between carnivore and herbivore reef fish guilds in response to an acute thermal disturbance event is shown. The carnivore size-spectra averages steepened after the bleaching event among all the distinct coral habitats, except in *Pocillopora*-dominated habitats. The largest temporal steepening occurred in one of the most structurally complex habitats across all scales (Richardson et al. 2017), massive *Porites* habitats, a slow-growing species that are tolerant to disturbances such as thermal stress (Darling et al. 2013). A reduced relative abundance in large-bodied carnivores after bleaching contributed to the steepened slopes, despite massive *Porites*-dominated habitats maintaining pre-bleaching coral cover after the disturbance indicates thermal stress may reduce predator interactions (i.e., Robinson et al. 2019). This is further evident in another structurally complex habitat across scales (Richardson et al. 2017), branching *Porites*, a relatively fast-growing species with varied thermal tolerance (Darling et al. 2013; McClanahan 2017). Though carnivore slopes steepened here, the direction was less than in massive *Porites* habitats, indicating the persistence of refugia availability to support broad carnivore body-size distributions (Alvarez-Filip et al. 2011b). Although carnivore size-spectra remained unchanged in *Pocillopora*-dominated habitats, the least structurally complex across scales (Richardson et al. 2017), this may be owed to the variation in slope estimates within the one surveyed site. However, *Pocillopora* at a fine scale (< 4 cm) is a structurally intricate species (Richardson et al. 2017) that may provide refugia for associated reef fishes (Coker et al. 2009), for which cryptic or very small-bodied fishes may not have been detected (Ackerman & Bellwood 2003).

In addition, herbivore size-spectra experienced minimal change among all the distinct coral habitats following bleaching. The body-size distributions of herbivorous reef fishes may have been robust to initial reduction or alterations in structural complexity due to a combination of increased algal productivity (Rogers et al. 2018; Robinson et al. 2019) and feeding by roving herbivores (i.e., browsers) tends to be greater in low relief habitats (Nash et al. 2013a; Catano et al. 2015). Since herbivore size-spectra remained unchanged here and these species are associated with recovering reefs (Richardson et al. 2018), herbivore guilds may be robust to certain disturbances. Additionally, the stable herbivore guilds after bleaching may help to sustain future herbivore populations (Graham et al. 2007; Robinson et al. 2019). However, a lagged decline in juveniles of large-bodied species that rely on small-scale habitat structural complexity (Graham et al. 2007) could impact populations. A marine heatwave may have directly led to habitat-induced shifts of trophic reef fish size-spectra in Lizard Island coral reefs, in alignment with Robinson et al. (2019). The decline in carnivore biomass following bleaching while herbivore biomass increased (Appendix 4 & 5) was similarly observed in the Seychelles on fished and protected reefs (Graham et al. 2007; Robinson et al. 2019). This suggests the loss of larger-bodied carnivores may have contributed to the biomass decline, while an increase in large-bodied herbivores contributed to an increase. The contrasting responses between carnivore and

herbivore size-spectra in response to habitat and disturbance effects support evidence that trophic guild size-spectra can be a responsive ecological indicator (Brown & Gillooly 2003; Trebilco et al. 2013).

### **6.3 | Variation in fish species composition within distinct habitats**

Although trophic guilds determine the size structure of coral reef fish (Robinson & Baum 2016), the composition of species may change due to disturbance vulnerability (Graham et al. 2011; McClanahan et al. 2014). Here, the contrasting effect of bleaching on carnivore and herbivore species composition within habitats of varying scales of structural complexity is shown. Although different configurations of coral species are important for shaping trophic guild body-size distributions (Alvarez-Filip et al. 2011b; Graham & Nash 2013), the distinct foraging behaviours of guilds may cause a different response to disturbance. For example, the highest species count for both trophic guilds was supported by stress-tolerant and structurally complex coral habitats. However, the composition of herbivore species remained the same, while the composition of carnivores reduced in massive *Porites*-dominated habitats following bleaching. These findings are consistent with empirical studies in the Seychelles (Robinson et al. 2019). Structurally complex habitats supported the highest species diversity, yet massive *Porites*-dominated habitats following bleaching negated reduced diversity following a shift from branching coral formations. The robust coral habitats here in Lizard Island may have possibly lost other corals or benthic species that contributed to the structural complexity (González-Rivero et al. 2017).

The composition of carnivore and herbivore species differentially responded following the bleaching event. The composition of carnivore species shifted, becoming more homogenised among the distinct coral habitats and experienced a significant temporal shift in low coral cover habitats. Homogenised fish assemblages were similarly observed by Richardson et al. (2018) after bleaching and are considered a vital component of the biodiversity crisis (McGill et al. 2015). In contrast, the composition of herbivore species after bleaching remained relatively the same within the habitats. Long-term studies (7 years post-bleaching) in the Seychelles on regime-shifted reefs reported a reduction in carnivore species and an increase in herbivore species to pre-bleaching levels (Robinson et al. 2019). Although the surveys here at Lizard Island were taken within a short time frame following bleaching (6 months), there was no evidence of a distinct regime shift. However, short- and long-term responses of trophic guilds (Graham et al. 2007) following bleaching were similar, indicating the immediate vulnerability of carnivorous species to disturbance (i.e., Graham et al. 2011). Moreover, the dissimilarity of carnivore and herbivore guilds within habitats after bleaching, indicates other environmental parameters or biological traits may have contributed to the composition of these guilds (Richards et al. 2012).

## 6.4 | Limitations

Direct comparisons with size-spectra studies on habitat structural complexity and degradation (i.e., Wilson et al. 2010; Alvarez-Filip et al. 2011; Fontoura et al. 2020) are difficult as these studies used various binning-based methods to estimate size-spectra slopes and aggregated reef fish species (Graham et al. 2005; Blanchard et al. 2017; Edwards et al. 2017). However, these results are consistent with size-spectra estimates from studies that used the likelihood-based method (i.e., Edwards et al. 2017; Edwards et al. 2020) investigating trophic guilds in reefs (Robinson & Baum 2016), biophysical gradients (Fidler et al. 2021), and fishing pressures (Carvalho et al. 2021). In addition, empirical size-spectra can deviate from expected slope estimates when not all species within an energetic community are accounted for (Jennings et al. 2007). Accounting for cryptic, nocturnal, and invertebrate species (Ackerman et al. 2004) is difficult when using underwater visual census methods. Not including such species that contribute to associated reef communities could bias size-spectra estimates (i.e., become shallower). Although the proportion of nocturnal and cryptic carnivore and herbivore fishes remains unknown, when the smallest body-size classes were removed from the dataset (<10 g), the spectra slopes shallowed indicating the surveys included a large proportion of the smallest fish in the community. Furthermore, biased slope estimates (i.e., either steeper or shallower) can also be caused by over or underestimating the abundance of large-bodied, more mobile fish due to behaviour, such as diver avoidance, roving, and attracted to diver presence (Ward-Paige et al. 2010; Dickens et al. 2011; Usseglio 2015). Since large-bodied fish are lower in abundance compared to small-bodied fish (Sheldon et al. 1972; Rice & Gislason 1996), the bias would be relatively small. Since these results are from a short-term observation of a complex system, caution should be applied when incorporating the findings into long-term observations. Thus, it remains unclear if the observed change in size-spectra among distinct habitats is a temporary alteration shortly after a mass coral bleaching event or if there is a lag or persistent response (i.e., Graham et al. 2007; Robinson et al. 2019).

## 6.5 | Implications

These findings provide insight into how the body-size distributions of specific trophic guilds can vary among reef habitats. This research builds on previous studies on carnivore and herbivore reef fish body-size distributions in response to anthropogenic impacts (e.g., Rogers et al. 2014; Robinson & Baum 2016; Rogers et al. 2018; Carvalho et al. 2021) by focusing on an acute thermal disturbance event (i.e., coral bleaching), whilst applying an analytical method (Edwards et al. 2020) that has never been used to assess the implications fish body-size distributions among distinct coral configurations. These findings indicate how carnivore guilds of reef fish vary in response to distinct coral habitats and an extreme marine heatwave event. Since large-bodied carnivores are important for maintaining

healthy ecosystems through predation on multiple trophic levels (Blanchard et al. 2009; Britten et al. 2014), the loss of large-bodied carnivorous reef fishes by climate-driven disturbance as seen here, can lead to shortened food chains and unstable fish assemblages that are vulnerable to future disturbances (Williams et al. 2010; Britten et al. 2014). In contrast, herbivorous reef fishes are typically considered ‘winners’, seemingly benefiting from habitat degradation (Catano et al. 2015). However, by ~2050 over 60% of reefs are estimated to experience acute thermal stress annually (van Hooidonk et al. 2016). Since the temporal recovery of ~6 years (Hughes et al. 2018b), it is vital to understand how habitat configurations shape differences in trophic guild size-spectra under a changing climate (Graham et al. 2014; Williams & Graham 2019; Woodhead et al. 2019). Since marine heatwaves are projected to increase in intensity and frequency (Hughes et al. 2017; Hughes et al. 2018a), the change in large-bodied reef fish could have cascading effects on entire reef ecosystems. A reduction in large-bodied carnivores may cause an abundance of small-bodied prey from the absence of top down-control (Dulvy et al. 2004; Robinson et al. 2017), while an increase in large-bodied herbivores may directly increase grazing pressures on competitive algae and benefit recruiting corals (Williams et al. 2019).

This study was based on data collected at Lizard Island, a no-take area situated mid-shelf from mainland-based anthropogenic impacts. The findings of this coral reef study system, therefore, demonstrate the interactive effect of heat stress and habitat composition dependencies on trophic guild size-spectra at Lizard Island which could provide an opportunity for a broader understanding of climate disturbance on trophic guild size-spectra in other marine ecosystems. For instance, fish body-size distributions in coral reefs, kelp forests and sea grass beds are shaped by habitat structural complexity, likely due to refugia availability (i.e., Alvarez-Filip et al. 2011b; Nash et al. 2014; Jinks et al. 2019; Ware et al. 2019). These marine habitats are facing climate change disturbances (Hoegh-Guldberg & Bruno 2010; Malhi et al. 2020), altering habitat configurations and body-size distributions of associated fish assemblages (Graham et al. 2007; Rogers et al. 2014; Rogers et al. 2018). Such changes in trophic guild size-spectra could have implications on marine conservation and management strategies, implementing the protection of large-bodied piscivores for fisheries productivity (i.e., Pikitch et al. 2004), and large-bodied piscivores and herbivores for ecosystem function (i.e., Nash et al. 2013b; Richards et al. 2012). Moreover, size-spectra analyses have been proposed as beneficial for evaluating changes in communities in response to disturbance (Petchey & Belgrano 2010; Guet et al. 2016). In this context, the result of this study supports evidence that specific trophic guild size-spectra can also be a responsive ecological indicator of the effects of habitat composition and disturbance (i.e., Jinks et al. 2019; Seitz et al. 2020; Carvalho et al. 2021; Britten et al. 2014). As novel habitat configurations emerge (i.e., Rogers et al. 2018; McPherson et al. 2021), monitoring changes in trophic guild size-spectra will provide insight into how guilds may change and the subsequent alterations in functions provided.

## 7 | Conclusion

These findings demonstrate the different response of trophic guild size-spectra among distinct coral configurations, indicating cross-scale habitat structural complexity and an acute thermal disturbance event have direct effects on associated coral reef fish assemblages. The correlation with the largest structural complexity spatial scale and steepening in body size-spectra after disturbance suggest that large reef fish may drive changes in fish assemblages. This provides further insight into the distribution of coral reef fishes that can commonly be overlooked when aggregating reef species regardless of functional or trophic positioning. Additional empirical observations should strive to incorporate invertebrate species (i.e., Brandl et al. 2019) and be conducted over longer time periods after acute disturbance events to further delineate are understanding of how aquatic communities are size structured by distinct habitats configurations. Overall, this study highlights the habitat dependencies of fish assemblages, which under a changing climate may have implications for management and conservation strategies of marine ecosystems (i.e., (Woodhead et al. 2019; do Amaral Camara Lima et al. 2023; Eger et al. 2023).

## 8 | References

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## 9 | Appendices

**Appendix 1:** Mean  $\pm$  benthic cover (%) of coral reef habitats, before (September 2015) and after (October 2016) the bleaching event. Modified from S3 Richardson et al. (2018).

<b>Habitat</b>	<b>Survey period</b>	<b>Total coral cover (%)</b>	<b>Dominant coral taxa or substrate</b>	<b>Proportion of total coral cover (%)</b>
<i>Branching Porites</i>	Sept 2015	57.13 $\pm$ 2.79	<i>Branching Porites</i>	78.03 $\pm$ 4.83
	Oct 2016	42.08 $\pm$ 2.30		73.07 $\pm$ 5.30
Low coral cover	Sept 2015	10.46 $\pm$ 1.80	Dead substrate and macroalgae	66.29 $\pm$ 2.74
	Oct 2016	14.63 $\pm$ 1.87		57.78 $\pm$ 2.25
<i>Massive Porites</i>	Sept 2015	49.37 $\pm$ 2.81	<i>Massive Porites</i>	51.47 $\pm$ 4.55
	Oct 2016	46.60 $\pm$ 3.19		63.01 $\pm$ 5.55
Mixed	Sept 2015	46.63 $\pm$ 3.07	n/a	-
	Oct 2016	29.03 $\pm$ 2.43		-
<i>Pocillopora</i>	Sept 2015	39.31 $\pm$ 6.01	<i>Pocillopora</i>	62.89 $\pm$ 4.15
	Oct 2016	35.83 $\pm$ 3.41		75.25 $\pm$ 6.27
Soft coral	Sept 2015	59.49 $\pm$ 1.93	Soft coral	90.05 $\pm$ 2.02
	Oct 2016	28.56 $\pm$ 2.65		71.64 $\pm$ 5.54

**Appendix 2.** The latitude and longitude coordinates for each site.

<b>Habitat</b>	<b>Site</b>	<b>Latitude</b>	<b>Longitude</b>
Branching <i>Porites</i>	BP1	14°41'5.92"S	145°28'0.24"E
Branching <i>Porites</i>	BP2	14°41'18.18"S	145°27'52.81"E
Branching <i>Porites</i>	BP3	14°41'7.59"S	145°27'36.98"E
Low coral cover	DGD1	14°38'50.84"S	145°27'14.88"E
Low coral cover	DGD2	14°39'29.04"S	145°27'6.34"E
Low coral cover	DGD3	14°40'9.66"S	145°26'38.88"E
Massive <i>Porites</i>	MP1	14°41'22.42"S	145°27'59.82"E
Massive <i>Porites</i>	MP2	14°40'41.33"S	145°26'41.55"E
Mixed coral spp	Mix1	14°41'9.52"S	145°26'31.15"E
Mixed coral spp	Mix2	14°41'47.47"S	145°26'59.93"E
Mixed coral spp	Mix3	14°41'13.74"S	145°27'16.47"E
Mixed coral spp	Mix4	14°40'58.39"S	145°26'56.55"E
<i>Pocillopora</i>	PO1	14°41'4.42"S	145°26'32.35"E
Soft coral	SC1	14°40'59.70"S	145°26'43.02"E
Soft coral	SC2	14°40'47.95"S	145°26'40.49"E
Soft coral	SC3	14°40'16.46"S	145°26'32.43"E

**Appendix 3.** Coral reef fish species list and trophic guild classification (carnivore or herbivore) using Parravicini et al. (2020) as the main source of literature. Species missing in the Parravicini et al. (2020) dataset were then sourced from MacNeil et al. 2015, Green & Bellwood (2009) and Richardson et al. (2018).

Species	Functional Group	Parravicini et al (2020)	MacNeil et al (2015)	Green & Bellwood (2009)	Richardson et al (2018)
<i>Abudefduf bengalensis</i>	Carnivore	Planktivore			Planktivore
<i>Abudefduf sexfasciatus</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Abudefduf vaigiensis</i>	Carnivore	Planktivore	Planktivore		Mixed Diet
<i>Abudefduf whitleyi</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Acanthochromis polyacanthus</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Acanthurus blochii</i>	Herbivore	Herbivore/microvores/detritivores	Grazer	Grazer/detritivore	Grazer/detritivore
<i>Acanthurus dussumieri</i>	Herbivore	Herbivore/microvores/detritivores	Grazer	Grazer/detritivore	Grazer/detritivore
<i>Acanthurus grammoptilus</i>	Herbivore	Herbivore/microvores/detritivores	Grazer		Grazer/detritivore
<i>Acanthurus lineatus</i>	Herbivore	Herbivore/microvores/detritivores	Grazer	Grazer/detritivore	Mixed Diet
<i>Acanthurus nigricauda</i>	Herbivore	Herbivore/microvores/detritivores	Grazer	Grazer/detritivore	Grazer/detritivore
<i>Acanthurus nigrofuscus</i>	Herbivore	Herbivore/microvores/detritivores	Grazer	Grazer/detritivore	Grazer/detritivore
<i>Acanthurus olivaceus</i>	Herbivore	Herbivore/microvores/detritivores	Detritivore	Grazer/detritivore	Grazer/detritivore
<i>Acanthurus xanthopterus</i>	Herbivore	Herbivore/microvores/detritivores	Grazer	Grazer/detritivore	Grazer/detritivore
<i>Amblyglyphidodon curacao</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Amblyglyphidodon leucogaster</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Amphiprion clarkii</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Amphiprion melanopus</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Anampses geographicus</i>	Carnivore	Microinvertivore			Invertivore
<i>Apogon compressus</i>	Carnivore				Planktivore
<i>Apogon cyanosoma</i>	Carnivore		Planktivore		Planktivore
<i>Aprion virescens</i>	Carnivore	Piscivore	Piscivore		Piscivore
<i>Arothron hispidus</i>	Carnivore	Macroinvertivore	Invertivore		Mixed Diet
<i>Arothron nigropunctatus</i>	NA	Corallivore	Corallivore		Corallivore
<i>Arothron stellatus</i>	Carnivore	Macroinvertivore	Invertivore		Mixed Diet
<i>Balistapus undulatus</i>	Carnivore	Macroinvertivore	Invertivore		Invertivore
<i>Balistoides viridescens</i>	Carnivore	Macroinvertivore	Macroinvertivore		Corallivore
<i>Bodianus</i>	Carnivore	Macroinvertivore	Micro-		Invertivore

<i>mesothorax</i>			invertivore		
<i>Caesio cuning</i>	Carnivore		Planktivore		Planktivore
<i>Canthigaster amboinensis</i>	Carnivore	Sessile invertivores	Micro-invertivore		Mixed Diet
<i>Canthigaster solandri</i>	Carnivore	Herbivores/microvores/detritivores	Micro-invertivore		Mixed Diet
<i>Canthigaster valentini</i>	Carnivore	Sessile invertivores	Micro-invertivore		Mixed Diet
<i>Caranx ignobilis</i>	Carnivore	Piscivore	Piscivore		Piscivore
<i>Caranx melampygus</i>	Carnivore	Piscivore	Piscivore		Piscivore
<i>Centropyge bicolor</i>	Carnivore	Sessile invertivores	Micro-invertivore		Grazer/detritivore
<i>Centropyge vrolikii</i>	Carnivore	Sessile invertivores	Micro-invertivore		Grazer/detritivore
<i>Cephalopholis cyanostigma</i>	Carnivore	Piscivore	Pisci-invertivore		Mixed Diet
<i>Cephalopholis microprion</i>	Carnivore	Crustacivore	Pisci-invertivore		Mixed Diet
<i>Cetoscarus ocellatus</i>	Herbivore	Herbivores/microvores/detritivores	Excavator/Scraper		Excavator
<i>Chaetodon aureofasciatus</i>	NA	Corallivore	Corallivore		Corallivore
<i>Chaetodon auriga</i>	NA	Corallivore	Micro-invertivore		Invertivore
<i>Chaetodon baronessa</i>	NA	Corallivore	Corallivore		Corallivore
<i>Chaetodon citrinellus</i>	NA	Corallivore	Micro-invertivore		Corallivore
<i>Chaetodon ephippium</i>	NA	Corallivore	Micro-invertivore		Invertivore
<i>Chaetodon kleinii</i>	Carnivore	Planktivore	Micro-invertivore		Corallivore
<i>Chaetodon lineolatus</i>	NA	Corallivore	Micro-invertivore		Invertivore
<i>Chaetodon lunulatus</i>	NA	Corallivore	Corallivore		Corallivore
<i>Chaetodon melannotus</i>	NA	Corallivore	Corallivore		Corallivore
<i>Chaetodon plebeius</i>	NA	Corallivore	Corallivore		Corallivore
<i>Chaetodon rafflesi</i>	NA	Corallivore	Micro-invertivore		Invertivore
<i>Chaetodon rainfordi</i>	NA	Corallivore	Corallivore		Corallivore
<i>Chaetodon trifascialis</i>	NA	Corallivore	Corallivore		Corallivore
<i>Chaetodon vagabundus</i>	NA	Corallivore	Micro-invertivore		Invertivore
<i>Cheilinus chlorourus</i>	Carnivore	Crustacivore	Macro-invertivore		Invertivore
<i>Cheilinus fasciatus</i>	Carnivore	Crustacivore	Macro-invertivore		Invertivore
<i>Cheilinus trilobatus</i>	Carnivore	Macroinvertivore	Macro-invertivore		Invertivore
<i>Cheilinus undulatus</i>	Carnivore	Macroinvertivore	Macro-invertivore		Mixed Diet



<i>Cheilodipterus artus</i>	Carnivore	Crustacivore	Planktivore		Piscivore
<i>Cheilodipterus macrodon</i>	Carnivore	Crustacivore	Planktivore		Mixed Diet
<i>Cheilodipterus quinquelineatus</i>	Carnivore	Crustacivore	Planktivore		Mixed Diet
<i>Cheiloprion labiatus</i>	NA	Corallivore			Corallivore
<i>Chelmon rostratus</i>	Carnivore	Microinvertivore	Mico-invertivore		Invertivore
<i>Chlorurus bleekeri</i>	Herbivore	Herbivores/microvores/detritivores	Excavator/Scrapers	Scrapers/Excavators	Excavator
<i>Chlorurus microrhinos</i>	Herbivore	Herbivores/microvores/detritivores	Excavator/Scrapers	Scrapers/Excavators/Bioeroders	Excavator
<i>Chlorurus sordidus</i>	Herbivore	Herbivores/microvores/detritivores	Excavator/Scrapers	Scrapers/Excavators	Excavator
<i>Choerodon anchorago</i>	Carnivore	Macroinvertivore	Micro-invertivore		Invertivore
<i>Choerodon schoenleinii</i>	Carnivore	Macroinvertivore			Invertivore
<i>Chromis atripectoralis</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Chromis sp</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Chromis ternatensis</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Chromis viridis</i>	Carnivore	Microinvertivore	Planktivore		Planktivore
<i>Chrysiptera cyanea</i>	Carnivore	Planktivore	Grazer		Planktivore
<i>Chrysiptera flavipinnis</i>	Carnivore	Planktivore			Planktivore
<i>Chrysiptera rollandi</i>	Carnivore	Planktivore	Micro-invertivore		Planktivore
<i>Coris aygula</i>	Carnivore	Macroinvertivore	Macro-invertivore		Invertivore
<i>Coris batuensis</i>	Carnivore	Microinvertivore	Micro-invertivore		Invertivore
<i>Corythoichthys sp</i>	Carnivore				Invertivore
<i>Cromileptes altivelis</i>	Carnivore	Crustacivore	Piscivore		Piscivore
<i>Ctenochaetus binotatus</i>	Herbivore	Herbivore/microvores/detritivores	Detritivore		Grazer/detritivore
<i>Ctenochaetus cyanocheilus</i>	Herbivore	Herbivore/microvores/detritivores	Detritivore		Grazer/detritivore
<i>Ctenochaetus striatus</i>	Herbivore	Herbivore/microvores/detritivores	Detritivore		Grazer/detritivore
<i>Dascyllus aruanus</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Dascyllus reticulatus</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Dascyllus trimaculatus</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Diagramma pictum</i>	Carnivore	Macroinvertivore	Micro-invertivore		Invertivore
<i>Dischistodus melanotus</i>	Carnivore	Planktivore	Detritivore		Farmer
<i>Dischistodus perspicillatus</i>	Carnivore	Planktivore	Detritivore		Farmer
<i>Dischistodus prosopotaenia</i>	Carnivore	Planktivore	Detritivore		Farmer

<i>Dischistodus pseudochrysopoecilus</i>	Carnivore	Planktivore	Detritivore		Farmer
<i>Epibulus insidiator</i>	Carnivore	Crustacivore	Pisci-invertivore		Piscivore
<i>Epinephelus hexagonatus</i>	Carnivore	Piscivore	Piscivore		Mixed Diet
<i>Epinephelus maculatus</i>	Carnivore	Crustacivore	Piscivore		Mixed Diet
<i>Epinephelus merra</i>	Carnivore	Crustacivore	Piscivore		Mixed Diet
<i>Fistularia commersonii</i>	Carnivore	Piscivore	Piscivore		Piscivore
<i>Gomphosus varius</i>	Carnivore	Crustacivore	Micro-invertivore		Invertivore
<i>Halichoeres chloropterus</i>	Carnivore	Microinvertivore			Invertivore
<i>Halichoeres hortulanus</i>	Carnivore	Macroinvertivore	Micro-invertivore		Invertivore
<i>Halichoeres melanurus</i>	Carnivore	Microinvertivore	Micro-invertivore		Invertivore
<i>Halichoeres nebulosus</i>	Carnivore	Macroinvertivore	Micro-invertivore		Invertivore
<i>Hemigymnus fasciatus</i>	Carnivore	Planktivore	Macro-invertivore		Invertivore
<i>Hemigymnus melapterus</i>	Carnivore	Microinvertivore	Macro-invertivore		Invertivore
<i>Heniochus chrysostomus</i>	NA	Corallivore	Micro-invertivore		Corallivore
<i>Heniochus varius</i>	NA	Corallivore	Micro-invertivore		Invertivore
<i>Hipposcarus longiceps</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scraper	Scrapers/Excavators	Scraper
<i>Holocentridae sp</i>	Carnivore				Mixed Diet
<i>Kyphosus cinerascens</i>	Herbivore	Herbivore/microvores/detritivores	Browser	Browsers	Browser
<i>Kyphosus vaigiensis</i>	Herbivore	Herbivore/microvores/detritivores	Browser	Browsers	Browser
<i>Labrichthys unilineatus</i>	NA	Corallivore	Corallivore		Corallivore
<i>Labroides dimidiatus</i>	Carnivore	Planktivore	Micro-invertivore		Invertivore
<i>Lates calcarifer</i>	Carnivore				Mixed Diet
<i>Lethrinus nebulosus</i>	Carnivore	Piscivore	Pisci-invertivore		Mixed Diet
<i>Lethrinus obsoletus</i>	Carnivore	Microinvertivore	Pisci-invertivore		Mixed Diet
<i>Lutjanus bohar</i>	Carnivore	Crustacivore	Piscivore		Piscivore
<i>Lutjanus carponotatus</i>	Carnivore	Crustacivore	Pisci-invertivore		Mixed Diet
<i>Lutjanus ehrenbergii</i>	Carnivore	Crustacivore	Pisci-invertivore		Mixed Diet
<i>Lutjanus fulvus</i>	Carnivore	Crustacivore	Pisci-invertivore		Piscivore
<i>Lutjanus gibbus</i>	Carnivore	Crustacivore	Pisci-invertivore		Piscivore
<i>Lutjanus kasmira</i>	Carnivore	Crustacivore	Pisci-invertivore		Mixed Diet

<i>Lutjanus quinquelineatus</i>	Carnivore	Crustacivore	Pisci-invertivore		Mixed Diet
<i>Lutjanus russelli</i>	Carnivore	Crustacivore	Pisci-invertivore		Piscivore
<i>Macropharyngodon meleagris</i>	Herbivore	Herbivore/microvores/detritivores	Micro-invertivore		Invertivore
<i>Monotaxis grandoculis</i>	Carnivore	Macroinvertivore	Macro-invertivore		Invertivore
<i>Mulloidichthys flavolineatus</i>	Carnivore	Macroinvertivore	Macro-invertivore		Invertivore
<i>Myripristis sp</i>	Carnivore	Crustacivore/planktivore?	Planktivore		Planktivore
<i>Naso brevirostris</i>	Herbivore	Herbivore/Microvores/Detritivore	Planktivore	Browser	Grazer/detritivore
<i>Naso lituratus</i>	Herbivore	Herbivore/microvores/detritivores	Browser	Browser	Browser
<i>Naso unicornis</i>	Herbivore	Herbivore/microvores/detritivores	Browser	Browser	Browser
<i>Naso vlamingii</i>	Herbivore	Herbivore/microvores/detritivores	Planktivore	Browser	Planktivore
<i>Neoglyphidodon melas</i>	Carnivore	Planktivore	Micro-invertivore		Corallivore
<i>Neoglyphidodon nigroris</i>	Carnivore	Planktivore	Planktivore		Mixed Diet
<i>Neopomacentrus azyron</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Neopomacentrus bankieri</i>	Carnivore	Planktivore			Planktivore
<i>Oxycheilinus digramma</i>	Carnivore	Crustacivore	Pisci-invertivore		Piscivore
<i>Parupeneus barberinus</i>	Carnivore	Crustacivore	Macro-invertivore		Invertivore
<i>Parupeneus ciliatus</i>	Carnivore	Crustacivore	Micro-invertivore		Invertivore
<i>Parupeneus cyclostomus</i>	Carnivore	Crustacivore	Pisci-invertivore		Piscivore
<i>Parupeneus multifasciatus</i>	Carnivore	Crustacivore	Macro-invertivore		Invertivore
<i>Plagiotremus tapeinosoma</i>	Herbivore	Herbivore/microvores/detritivores	Micro-invertivore		Mixed Diet
<i>Platax pinnatus</i>	Herbivore			Browser	Mixed Diet
<i>Plectorhinchus albovittatus</i>	Carnivore	Macroinvertivore	Pisci-invertivore		Mixed Diet
<i>Plectorhinchus chaetodonoides</i>	Carnivore	Macroinvertivore	Micro-invertivore		Invertivore
<i>Plectorhinchus chrysotaenia</i>	Carnivore	Macroinvertivore			Invertivore
<i>Plectorhinchus gibbosus</i>	Carnivore	Macroinvertivore	Micro-invertivore		Invertivore
<i>Plectorhinchus lineatus</i>	Carnivore	Macroinvertivore			Invertivore
<i>Plectroglyphidodon dickii</i>	Herbivore	Herbivore/microvores/detritivores	Micro-invertivore		Mixed Diet
<i>Plectroglyphidodon lacrymatus</i>	Herbivore	Herbivore/microvores/detritivores	Grazer		Farmer
<i>Plectropomus laevis</i>	Carnivore	Piscivore	Piscivore		Piscivore
<i>Plectropomus</i>	Carnivore	Piscivore	Piscivore		Piscivore

<i>leopardus</i>					
<i>Pomacanthus sexstriatus</i>	Carnivore	Sessile invertivores	Spongivore		Mixed Diet
<i>Pomacentrus adelus</i>	Herbivore	Herbivore/microvores/detritivores	Planktivore		Farmer
<i>Pomacentrus amboinensis</i>	Carnivore	Planktivore	Spongivore		Planktivore
<i>Pomacentrus bankanensis</i>	Herbivore	Herbivore/microvores/detritivores	Spongivore		Farmer
<i>Pomacentrus brachialis</i>	Carnivore		Planktivore		Farmer
<i>Pomacentrus chrysurus</i>	Herbivore	Herbivore/microvores/detritivores			Farmer
<i>Pomacentrus grammorhynchus</i>	Carnivore	Planktivore			Farmer
<i>Pomacentrus lepidogenys</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Pomacentrus moluccensis</i>	Carnivore	Planktivore	Spongivore		Planktivore
<i>Pomacentrus nagasakiensis</i>	Herbivore	Herbivore/microvores/detritivores	Planktivore		Planktivore
<i>Pomacentrus reidi</i>	Herbivore	Herbivore/microvores/detritivores			Mixed Diet
<i>Pomacentrus tripunctatus</i>	Herbivore	Herbivore/microvores/detritivores			Mixed Diet
<i>Pomacentrus wardi</i>	Carnivore	Planktivore	Grazer		Farmer
<i>Priacanthus hamrur</i>	Carnivore	Crustacivore	Pisci-invertivore		Mixed Diet
<i>Pseudocheilinus evanidus</i>	Carnivore	Planktivore			Invertivore
<i>Ptereleotris evides</i>	Carnivore	Planktivore	Planktivore		Planktivore
<i>Pterocaesio marri</i>	Carnivore		Planktivore		Planktivore
<i>Sargocentron spiniferum</i>	Carnivore	Crustacivore	Pisci-invertivore		Mixed Diet
<i>Scarus altipinnis</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scrapper	Scrapers/Excavators	Scraper
<i>Scarus chameleon</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scrapper	Scrapers/Excavators	Scraper
<i>Scarus dimidiatus</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scrapper	Scrapers/Excavators	Scraper
<i>Scarus flavipectoralis</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scrapper	Scrapers/Excavators	Scraper
<i>Scarus frenatus</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scrapper	Scrapers/Excavators	Scraper
<i>Scarus ghobban</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scrapper	Scrapers/Excavators	Scraper
<i>Scarus globiceps</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scrapper	Scrapers/Excavators	Scraper
<i>Scarus niger</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scrapper	Scrapers/Excavators	Scraper
<i>Scarus oviceps</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scrapper	Scrapers/Excavators	Scraper
<i>Scarus psittacus</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scrapper	Scrapers/Excavators	Scraper
<i>Scarus rivulatus</i>	Herbivore	Herbivore/microvores/detritivores	Excavator/Scrapper	Scrapers/Excavators	Scraper
<i>Scarus schlegeli</i>	Herbivore	Herbivore/microvor	Excavator/S	Scrapers/Excavato	Scraper

		es/detritivores	craper	rs	
<i>Scarus sp</i>	Herbivore	Herbivore/microvor es/detritivores	Excavator/S craper	Scrapers/Excavato rs	Scraper
<i>Scarus spinus</i>	Herbivore	Herbivore/microvor es/detritivores	Excavator/S craper	Scrapers/Excavato rs	Scraper
<i>Scolopsis bilineata</i>	Carnivore	Microinvertivore	Micro- invertivore		Invertivore
<i>Scolopsis lineata</i>	Carnivore	Microinvertivore	Micro- invertivore		Invertivore
<i>Scolopsis margaritifer</i>	Carnivore	Microinvertivore	Micro- invertivore		Invertivore
<i>Scolopsis monogramma</i>	Carnivore	Microinvertivore			Invertivore
<i>Scorpaenopsis sp</i>	Carnivore		Pisci- invertivore		Mixed Diet
<i>Siganus corallinus</i>	Herbivore	Herbivore/microvor es/detritivores	grazer	Grazer/Detritivore	Grazer/detritiv ore
<i>Siganus doliatus</i>	Herbivore	Herbivore/microvor es/detritivores	Grazer	Grazer/Detritivore	Grazer/detritiv ore
<i>Siganus lineatus</i>	Herbivore	Herbivore/microvor es/detritivores	Grazer	Grazer/Detritivore	Grazer/detritiv ore
<i>Siganus puellus</i>	Herbivore	Herbivore/microvor es/detritivores	Grazer	Grazer/Detritivore	Grazer/detritiv ore
<i>Siganus punctatus</i>	Herbivore	Herbivore/microvor es/detritivores	Grazer	Grazer/Detritivore	Grazer/detritiv ore
<i>Siganus sp</i>	Herbivore	Herbivore/microvor es/detritivores	Grazer	Grazer/Detritivore	Grazer/detritiv ore
<i>Siganus vulpinus</i>	Herbivore	Herbivore/microvor es/detritivores	Grazer	Grazer/Detritivore	Grazer/detritiv ore
<i>Sphaeramia nematoptera</i>	Carnivore	Microinvertivore			Invertivore
<i>Stegastes apicalis</i>	Herbivore	Herbivore/microvor es/detritivores	Grazer		Farmer
<i>Stegastes nigricans</i>	Herbivore	Herbivore/microvor es/detritivores	Grazer		Farmer
<i>Stethojulis bandanensis</i>	Carnivore	Microinvertivore	Micro- invertivore		Invertivore
<i>Stethojulis interrupta</i>	Carnivore	Microinvertivore			Invertivore
<i>Sufflamen chrysopterum</i>	Carnivore	Microinvertivore	Micro- invertivore		Invertivore
<i>Taeniamia zosterophora</i>	Carnivore				Planktivore
<i>Thalassoma hardwicke</i>	Carnivore	Microinvertivore	Micro- invertivore		Invertivore
<i>Thalassoma janseni</i>	Carnivore	Microinvertivore	Micro- invertivore		Invertivore
<i>Thalassoma lunare</i>	Carnivore	Planktivore	Micro- invertivore		Invertivore
<i>Zanclus cornutus</i>	Carnivore	Sessile invertivores	Micro- invertivore		Mixed Diet
<i>Zebrasoma scopas</i>	Herbivore	Herbivore/microvor es/detritivores	Grazer	Grazer/Detritivore	Grazer/detritiv ore
<i>Zebrasoma velifer</i>	Herbivore	Herbivore/microvor es/detritivores	Grazer	Grazer/Detritivore	Grazer/detritiv ore

**Appendix 4.** Summary of trophic guilds mass, sample size, and species count at each habitat type.

a) Carnivore reef fish

<b>Bleaching</b>	<b>Habitat Type</b>	<b>Min (g)</b>	<b>Max (g)</b>	<b>Mean (g)</b>	<b>SE</b>	<b>Sample</b>	<b>Species</b>
Before	Branching <i>Porites</i>	0.01	2719.44	8.34	0.49	16758	65
Before	Low coral cover	0.01	720.28	8.41	0.56	4253	56
Before	Massive <i>Porites</i>	0.01	1230.74	12.75	1.00	3850	54
Before	Mixed coral spp.	0.01	6330.10	17.23	1.19	11282	83
Before	Pocillopora	0.02	1081.71	8.34	0.56	4645	52
Before	Soft coral	0.01	1287.60	12.18	0.98	4354	55
After	Branching <i>Porites</i>	0.01	3396.57	5.33	0.44	12065	61
After	Low coral cover	0.01	1628.98	8.24	0.66	4937	64
After	Massive <i>Porites</i>	0.01	1976.39	6.46	0.69	4675	58
After	Mixed coral spp.	0.01	4571.59	15.31	0.99	10510	76
After	Pocillopora	0.01	336.27	4.87	0.21	3322	43
After	Soft coral	0.01	3368.42	7.52	0.78	7781	67
Both	Branching <i>Porites</i>	0.01	3396.57	7.08	0.34	28823	81
Both	Low coral cover	0.01	1629.98	8.32	0.44	9190	75
Both	Massive <i>Porites</i>	0.01	1976.39	9.30	0.59	8525	75
Both	Mixed coral spp.	0.01	6330.10	16.30	0.78	8525	97
Both	Pocillopora	0.01	1081.71	6.90	0.34	7967	65
Both	Soft coral	0.01	3668.42	9.20	0.61	12135	78

b) Herbivore reef fish

<b>Bleaching</b>	<b>Habitat Type</b>	<b>Min (g)</b>	<b>Max (g)</b>	<b>Mean (g)</b>	<b>SE</b>	<b>Sample</b>	<b>Species</b>
Before	Branching <i>Porites</i>	0.02	2409.46	31.52	3.50	1451	25
Before	Low coral cover	0.03	3060.79	49.93	4.67	1015	28
Before	Massive <i>Porites</i>	0.34	1267.34	39.61	3.58	900	30
Before	Mixed coral spp.	0.18	1359.75	25.45	1.40	3072	34
Before	Pocillopora	0.60	2046.52	53.24	6.55	467	30
Before	Soft coral	0.02	3365.99	36.01	3.26	1630	40
After	Branching <i>Porites</i>	0.01	631.32	29.21	2.31	1348	30
After	Low coral cover	0.02	1283.44	30.44	2.81	1056	29
After	Massive <i>Porites</i>	0.02	627.04	26.99	2.91	736	27
After	Mixed coral spp.	0.02	1168.42	21.48	1.31	3189	41
After	Pocillopora	0.01	1043.15	26.76	4.82	329	21
After	Soft coral	0.01	1140.26	16.12	1.39	2283	34
Both	Branching <i>Porites</i>	0.01	2409.46	30.41	2.13	2799	35
Both	Low coral cover	0.02	3060.79	39.99	2.71	2071	35

Both	Massive <i>Porites</i>	0.02	1267.34	33.93	2.37	1636	39
Both	Mixed coral spp.	0.02	1359.75	23.42	0.96	6261	46
Both	Pocillopora	0.01	2046.52	42.29	4.35	796	32
Both	Soft coral	0.01	3365.99	24.41	1.59	3913	40

**Appendix 5.** Box-plot distribution of carnivore and herbivore reef fish individual mean mass and total biomass in grams per transect (150 m<sup>2</sup>), and size-spectra slopes (b) ‘before’ (September 2015) and ‘after’ (October 2016) the bleaching event. The dashed grey line between spectra slopes visualises the change in body size distributions after bleaching.

