Fishing and habitat condition differentially affect size spectra slopes of coral reef fishes

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Abstract. Marine food webs are structured through a combination of top-down and bottom-up processes. In coral reef ecosystems, fish size is related to life-history characteristics and size-based indicators can represent the distribution and flow of energy through the food web. Thus, size spectra can be a useful tool for investigating the impacts of both fishing and habitat condition on the health and productivity of coral reef fisheries. In addition, coral reef fisheries are often data-limited and size spectra analysis can be a relatively cost-effective and simple method for assessing fish populations. Abundance size spectra are widely used and quantify the relationship between organism size and relative abundance. Previous studies that have investigated the impacts of fishing and habitat condition together on the size distribution of coral reef fishes, however, have aggregated all fishes regardless of taxonomic identity. This leads to a poor understanding of how fishes with different feeding strategies, body size-abundance relationships, or catchability might be influenced by top-down and bottom-up drivers. To address this gap, we quantified size spectra slopes of carnivorous and herbivorous coral reef fishes across three regions of Indonesia representing a gradient in fishing pressure and habitat conditions. We show that fishing pressure was the dominant driver of size spectra slopes such that they became steeper as fishing pressure increased, which was due to the removal of large-bodied fishes. When considering fish functional groups separately, however, carnivore size spectra slopes were more heavily impacted by fishing than herbivores. Also, structural complexity, which can mediate predator-prey interactions and provisioning of resources, was a relatively important driver of herbivore size spectra slopes such that slopes were shallower in more complex habitats. Our results show that size spectra slopes can be used as indicators of fishing pressure on coral reef fishes, but aggregating fish regardless of trophic identity or functional role overlooks differential impacts of fishing pressure and habitat condition on carnivore and herbivore size distributions.

Key words: community ecology; coral reef fisheries; ecosystem indicators; ecosystem-based management; fisheries ecology; fisheries management; Indonesia; size spectra.

Introduction

Coral reefs provide vital sources of nutrition and income for hundreds of millions of people worldwide (Wilkinson 2008). Most coral reefs are located in developing countries with limited resources for monitoring and enforcement (Johnson et al. 2013). Consequently, a majority of coral reef fisheries remain unassessed or are fished unsustainably (Newton et al. 2007, Costello et al. 2012). Traditional stock assessment methods require extensive biological data and technical expertise (Walters and Martell 2004), which are often unavailable for small-scale, dispersed, multi-gear and multi-species coral reef fisheries (Sadovy and Domeier 2005, Erisman et al. 2014). However, fisheries-independent indicators can be cost-effective tools to monitor ecosystem health and assess the impacts of fishing and habitat condition on fisheries productivity (Mangi et al. 2007, Nash and Graham 2016).

Size-based indicators can be particularly useful for coral reef fisheries because many life-history characteristics of fishes, such as age at maturity, fecundity, and natural mortality are size dependent (Kerr and Dickie 2001). In addition, trophic positions of coral reef fishes have been shown to be positively correlated with body size due to ontogenetic diet shifts (Cocheret de la Morinière et al. 2003). Thus, size-based indicators can represent the distribution and flow of energy within a food web (Shin et al. 2005). The abundance size spectrum slope is a commonly used size-based indicator that quantifies the relative abundance of organisms based on body size (length or mass) regardless of taxonomic identity (Boudreau and Dickie 1992, Jennings and Mackinson 2003). Abundance typically has a negative linear relationship with body size on logarithmic axes—as body size increases the abundance of organisms decreases geometrically (Rice and Gislason 1996). Size spectra slopes have been used in temperate and tropical marine systems to examine the impacts of fishing and habitat condition on size distributions of fish assemblages (Blanchard et al. 2005, Wilson et al. 2010).

Coral reef food webs experience top-down control via predation, which controls prey populations (Roff et al. 2016), and herbivory, affecting algal growth and regulating shifts from coral- to macroalgal-dominated reefs (Rasher et al. 2013). However, the effects of fishing pressure can overshadow the impacts of natural top-down processes and act as the primary mechanism structuring marine food webs (Smith et al. 2010). Top-down pressure from fishing can directly affect the size spectra slopes of coral reef fishes by selectively removing large-bodied species (Graham et al. 2005; Wilson et al. 2010; Robinson et al. 2017). Also, the removal of large-bodied, carnivorous fishes can have indirect effects on size spectra slopes through prey-release, whereby smaller prey organisms proliferate in the absence of top-down control from predators (Dulvy et al. 2004, Robinson et al. 2017). The effects of fishing, both direct and indirect, can be observed through comparing size spectra slopes of fish communities that endure various levels of fishing pressure.

Habitat condition and bottom-up processes also affect coral reef food webs and ecosystems. For example, structural complexity of reef building corals provide prey refugia for small-bodied fishes to avoid predation (Hixon and Beets 1993, Rogers et al. 2014). Structural complexity and low macroalgal cover have also been shown to mediate herbivorous fish populations that crop algae from reefs, such as acanthurids and siganids (Robinson et al. 2020). Therefore, degraded reefs with low structural complexity can limit prey refugia or food sources and reduce the abundance of small-bodied reef fishes, which results in shallower size spectra (Wilson et al. 2010, Alvarez-Filip et al. 2011, Rogers et al. 2014). Thus, top-down fishing impacts and bottom-up habitat change can impact fishes along the entire size spectrum and severely compromise biological processes and functions carried out by fishes on coral reefs (e.g., predation and herbivory).

Previous studies that have examined fish size spectra slopes in response to fishing and habitat condition aggregated individuals from the entire assemblage (Wilson et al. 2010, Robinson et al. 2017), thus overlooking potentially important changes for organisms that respond differently to these drivers, such as carnivores and herbivores (Blanchard et al. 2009). For example, fishes that feed at the same trophic level (e.g., herbivores) are expected to exhibit abundance–body size relationships in accordance with the energetic equivalence hypothesis such that abundance scales with body mass (M) as $M^{-0.75}$ (Trebilco et al. 2013). In contrast, the abundance–body size relationship for fishes that feed across trophic levels (e.g., carnivores) is expected to be constrained by inefficient energy transfer such that abundance scales with body mass as M^{-1} (Trebilco et al. 2013). Robinson and Baum (2016) investigated the size spectra slopes of carnivores and herbivores on relatively undisturbed coral reefs around Kiritimati Island and found that the carnivore size spectrum slope was indeed steeper than that of herbivores. Here, we build on these findings by investigating the size spectra slopes of carnivorous and herbivorous reef fishes across a gradient of fishing pressure and various habitat conditions in Indonesia (Fig. 1). Our study sites span three regions of Indonesia (i.e., Raja Ampat, Wakatobi, and Lombok) with varying human population densities and exploitation levels (Cinner et al. 2018). Our goal was to determine how the influence of fishing and habitat condition change when fish assemblages are divided into groups that have different feeding strategies, abundance–body size relationships, and are targeted differently in the fishery. We hypothesize that fishing will be the dominant driver of size spectra slopes when all species are aggregated because fishers typically target large-bodied individuals as was the case for reef fishes in Fiji and US-affiliated Pacific islands (Wilson et al. 2010, Robinson et al. 2017). Also, we predict that fishing will have a greater impact on size spectra slopes of carnivores than herbivores due to the high value and desirability of large-bodied piscivores in Indonesian export markets (Efendi et al. 2020). Although previous studies found that empirically estimated size spectra slopes (all species aggregated) were insensitive to habitat conditions (Nash et al. 2016, Robinson et al. 2017), food web models suggest that structural complexity and benthic resources can affect the size distribution of carnivores and herbivores (Rogers et al. 2014, Rogers et al. 2017). Thus, we expect habitat condition to differentially affect carnivores and herbivores, but to a lesser extent than fishing pressure.

METHODS

Study sites

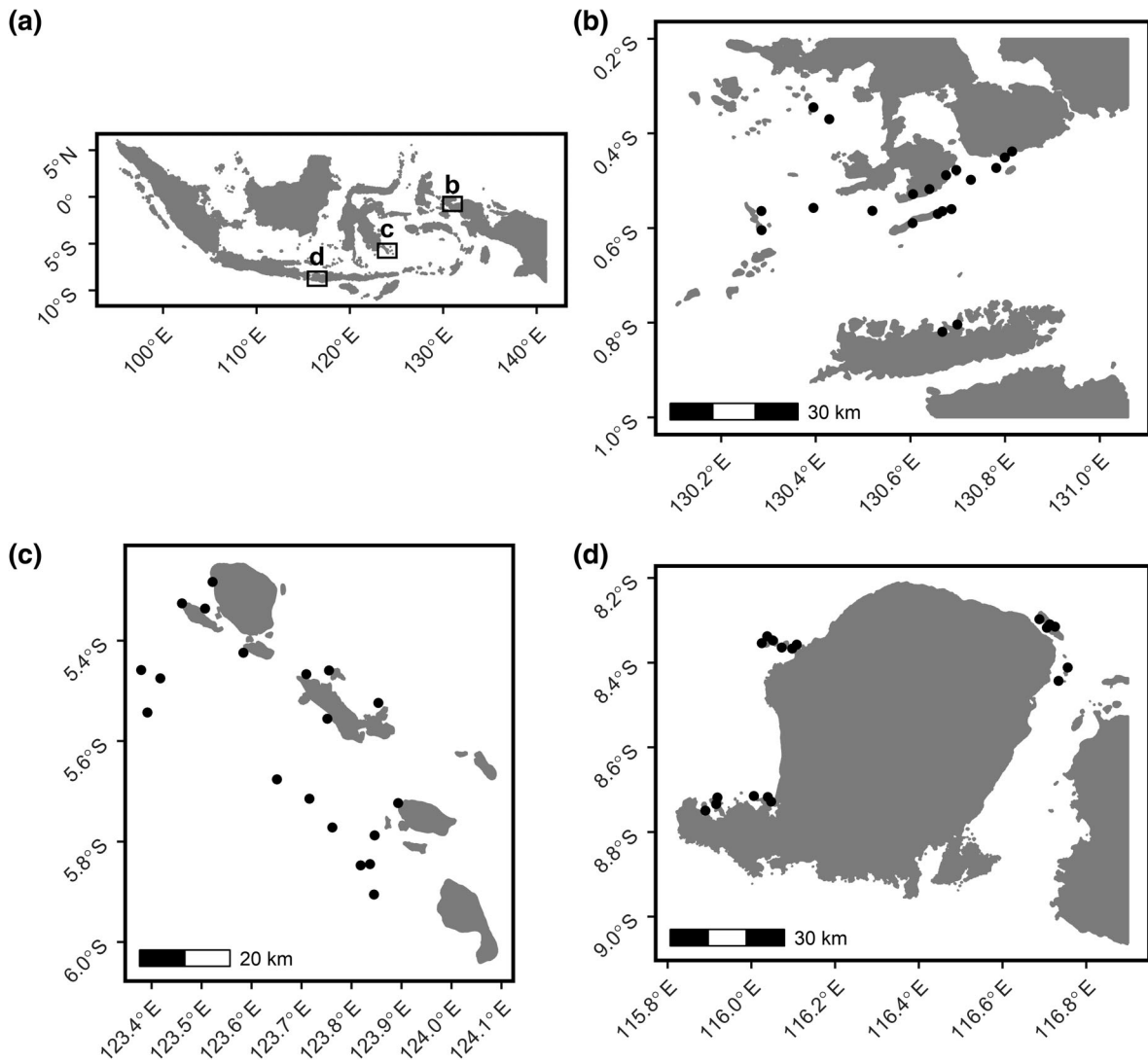We conducted fish and benthic surveys at 57 sites across Indonesia: 20 sites in Raja Ampat, 19 sites in

FIG. 1. Map of Indonesia (a) and underwater visual census sites in Raja Ampat ($n = 20$; b), Wakatobi ($n = 19$; c) and Lombok ($n = 18$; d).

Wakatobi Marine National Park, and 18 sites in Lombok (Fig. 1). In general, Indonesia is underrepresented in the scientific literature (MacNeil et al. 2015). Thus, analysis of size spectra slopes can provide a cost-effective and relatively easy assessment of fish populations targeted by small-scale fishers on Indonesian coral reefs.

Raja Ampat is located in West Papua in Eastern Indonesia, the center of the Coral Triangle (Fig. 1b), and contains coral reefs with exceptional biodiversity that support both fishing and tourism industries (Allen and Erdmann 2009, Veron et al. 2009). Many coral reefs in Raja Ampat are remote and away from major human development. However, transmigration of people from more densely populated areas to Raja Ampat has increased fishing pressure and some stocks are declining (Ainsworth et al. 2008). Thus, the Raja Ampat regency

has established six locally managed Marine Protected Areas (MPAs), with assistance from Conservation International and The Nature Conservancy, to promote conservation and tourism (Atmodjo et al. 2017; Fig. 1c).

Wakatobi Marine National Park (hereafter referred to as Wakatobi) is located south-west of Raja Ampat in Southeast Sulawesi. Wakatobi is the third largest Marine Protected Area (MPA) in Indonesia and covers 13,900 km² (Clifton 2013). Wakatobi is composed of four main islands: Wangi-wangi, Kaledupa, Tomia, and Binongko. In addition, there are two large atolls to the west of the main islands that are frequented by fishers (von Heland and Clifton 2015). Wakatobi is designated as a mutli-use MPA and, thus, fishing occurs in most areas of the MPA. Wakatobi has a human population of about 100,000 that is dependent on fisheries and

agricultural industries (Clifton 2013). Unlike the locally managed MPAs of Raja Ampat, Wakatobi management remains centralized by the Indonesia government and is regulated by the Ministry of Forestry (Clifton 2013).

Lombok is located to the east of Bali in the Lesser Sunda Seascape (Fig. 1d) and has a population of ~3 million people. Fishing is one of the primary forms of livelihood in Lombok. We excluded management status of each site from our analyses because enforcement of fishing closures was very weak; fishers were present at >90% of sites designated as no-take MPAs across all three regions (direct observation from authors). Lombok has a high level of reef fish endemism, even when compared with other locations within the Coral Triangle, but few studies have examined the impacts of fishing on reef fish populations in this region (but see Humphries et al. 2019).

Data collection

Fish and benthic communities were surveyed using underwater visual census (UVC) along shallow reef slopes (3–10 m deep). Raja Ampat was surveyed in January 2018, Wakatobi in May 2018, and Lombok in July 2018. Three to six 5×50 m belt transects were conducted at each site. Diurnal, noncryptic fishes were identified to the lowest taxonomic level possible and sizes were estimated to the nearest cm. Throughout survey periods, divers routinely calibrated size estimation by estimating PVC pipes of known length. Large, flighty fishes (e.g., lutjanids) were surveyed before small, territorial fishes (e.g., pomacentrids) to minimize bias against fishes that tend to flee in the presence of divers. The point-intercept method was used to survey benthic communities at 0.5 m intervals along the same transects as fish surveys. Structural complexity was represented by a five-point visual scale (one being a flat area with no vertical relief to five being the most complex vertical structure with caves and overhangs) and recorded at 10 m intervals along each belt transect (Polunin and Roberts 1993).

The mass of individual fishes were calculated using the standard conversion equation (from cm to g), $W = \alpha L^{\beta}$, where W is mass in g, L is length in cm, and the α and β parameters were obtained from FishBase (Froese and Pauly 2020). In addition, fish functional groups were identified from diet information and published literature (MacNeil et al. 2015, Froese and Pauly 2020). Fishes were designated as carnivores, herbivores, or placed into an "other" category and excluded from the carnivore versus herbivore analyses.

Fishing intensity

Fish biomass density (kg/ha) was used as a proxy for fishing intensity at each site, such that high fish biomass indicates low fishing pressure and low fish biomass indicates high fishing pressure. Fish biomass is widely used

as a proxy for fishing pressure (McClanahan et al. 2011, 2015, Nash et al. 2016) as studies have found negative relationships between fish biomass and human population density and other metrics for fishing pressure in coral reef fisheries (Cinner et al. 2009, Cinner et al. 2013, Gorospe et al. 2018, Campbell et al. 2020). To validate the relationship between fish biomass and fishing intensity in this study, we performed an analysis of fish biomass density in relation to human population gravity, a metric of fishing intensity that considers human population density and distance to reef (Cinner et al. 2018).

Estimating size spectra slopes

Previous studies that have investigated the influence of fishing pressure on size spectra slopes of coral reef fish communities used linear regression for binned abundance data (using arbitrary bin sizes) on a logarithmic scale (Graham et al. 2005, Wilson et al. 2010). However, Edwards et al. (2017) used simulated data to show that linear regression of log-transformed and binned abundance data yield biased slope estimates with wide confidence intervals. Edwards et al. (2017) found that treating abundance and body-size data as a probability distribution (i.e., power-law distribution; $f(x) = Cx^b$) and solving for the exponent b (using likelihood methods) was analogous to calculating the slope through linear regression on logarithmic axes. Thus, the bounded power-law distribution, more specifically the abundance density function (Edwards et al. 2017), was used here to estimate size spectra exponent, b (hereafter referred to as size spectra slope to remain consistent with existing literature):

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

where n is the number of individuals, x is fish mass (kg), $x_{\max}$ is the maximum mass of fish at 65 cm, and $x_{\min}$ is the minimum mass of fish at 10 cm. The maximum and minimum lengths indicate fish sizes that can be surveyed effectively using our UVC method (Kulbicki 1998, Ackerman and Bellwood 2000). Size spectrum slope (b) describes the relative abundance in relation to body sizes and b is negative for size structure communities (i.e., as the size of fishes increase the relative abundance decreases). A steeper size spectrum slope (i.e., more negative b) indicates fewer large-bodied and/or more small-bodied fishes. Estimated size spectra slopes for each diver were compared across regions, and one diver in Lombok had significantly shallower slopes than other divers (Appendix S1: Fig. S1). Thus, data from this diver were removed from the analyses.

Size spectra slopes were estimated for each region (Raja Ampat, Wakatobi and Lombok) and each survey site within regions (57 total sites). Generalized additive

models (GAMs) were used to determine the impact of fishing pressure (fish biomass density as a proxy) and habitat condition (hard coral cover, algal cover, and structural complexity) on size spectra slopes at each site, and region was treated as a fixed effect in our models to account for site similarities within regions (mgcv R package, Wood 2011). GAMs were also used to allow for non-linear relationships between size spectra slopes and predictor variables, and the number of basis functions was set to $k = 3$ to prevent overfitting (Zuur et al. 2009). In addition, we used a gamma log-link because size spectrum slope was a continuous variable with a skewed distribution, and the absolute values of size spectra slopes were assumed to be $|b| > 0$ for size structured communities. To account for uncertainty in estimates of size spectra slopes, inverse-variance weights were used for the GAMs. Correlations between predictor variables were examined using the concurvity function in the mgcv R package, which is a generalization of co-linearity (Wood 2011). Concurvity values range from 0 to 1, with 0 indicating no correlation and 1 indicating absence of identifiability between predictor variables. A concurvity threshold of 0.3 was used such that predictor variables with concurvity ≥0.3 were run in separate models. We acknowledge this threshold to be somewhat arbitrary, but we expect this level to be a conservative threshold for detecting predictor variables with moderate to high correlations (Johnston et al. 2019). Concurvity between structural complexity and hard coral cover was >0.3 (Appendix S1: Table S1) and, thus, separate models were fitted for these variables. Residual plots were used to check model assumptions (Appendix S1: Figs. S2, S3). All combinations within the global model structures ($|b|$ ~ region + s(biomass, $k = 3$) + s(algal cover, $k = 3$) + s(hard coral cover, $k = 3$) and $|b|$ ~ region + s(biomass, $k = 3$) + s(algal cover, $k = 3$) + s(structural complexity, $k = 3$)) were tested using the MuMIn R package (Barton 2013). The difference in Akaike's information criteria corrected for small sample sizes (AIC_c) between the GAMs was <2 and, thus, we present results from both models (one with hard coral cover and one with structural complexity). The relative impacts of each predictor variable on size spectra slopes were assessed by summing the AIC_c weights across all models including each variable (Appendix S1: Tables S2, S3). Relationships between predictor variables and size spectra slopes were visualized using partial effects plots.

Separate size spectra slopes were estimated for carnivores and herbivores for all regions combined and at the site level. GAMs were used to test the effects of fishing pressure and habitat condition on carnivore and herbivore size spectra slopes. The global model structures for carnivores and herbivores were consistent with the GAM models above; however, biomass represented separate carnivore and herbivore biomass values rather than total site biomass. Models with total site biomass as a predictor variable were examined, but separate biomass values for carnivores and herbivores provided

better model fits. We repeated all of the above analyses using binned likelihood estimation methods for size spectra slopes that account for uncertainty in estimated fish mass after converting from length (Edwards et al. 2020) and our results were robust to this uncertainty.

RESULTS

Our study regions represented a gradient in fishing pressure where Raja Ampat had the lowest pressure (i.e., highest mean biomass density) and Lombok had the highest (Appendix S1: Fig. S4). Fish biomass was negatively, and significantly ($P < 0.001$), related to human population gravity (Appendix S1: Fig. S4), and this relationship has been attributed primarily to fishing intensity (Cinner et al. 2018). The estimated size spectra slopes reflected this gradient in fishing pressure and were significantly different between regions (Fig. 2). Raja Ampat had the shallowest size spectrum slope ($b = -1.58$, 95% CI = [−1.60, −1.56]), followed by Wakatobi ($b = -1.71$, 95% CI = [−1.74, −1.68]), and then Lombok ($b = -2.06$, 95% CI = [−2.08, −2.02]). Shallower size spectra slopes indicate the presence of more large-bodied fishes and/or less small-bodied fishes. Raja Ampat had higher relative biomass of large- ($x \geq 1$ kg) and medium-bodied fishes (0.2 kg $\leq x < 1$ kg) than Wakatobi and Lombok, and Lombok had the highest relative biomass of small-bodied fishes ($x < 0.2$ kg; Appendix S1: Fig. S5).

Fish biomass (proxy for fishing pressure) and region were significant drivers of size spectra slopes across all study sites. Also, fish biomass had the highest summed AIC_c weights with a positive and non-linear relationship with slope, such that slopes became shallower as fish biomass increased (Fig. 3). At sites with low fish biomass, size spectra slopes were steep (e.g., $b = -1.81$, 95% CI = [−2.02, −1.62], at 36 kg/ha), and slopes were shallower for sites with high fish biomass (e.g., $b = -1.20$, 95% CI = [−1.37, −1.05], at 2,371 kg/ha; Fig. 3). Habitat condition variables (hard coral cover, algae cover, and structural complexity) were not significant predictors of size spectra slopes for the entire fish assemblage and had low summed AIC_c weights (Fig. 3; Appendix S1: Figs. S6, S7).

We found that the estimated size spectrum slope for carnivores aggregated across all study sites was significantly steeper ($b = -1.97$, 95% CI = [−2.00, −1.94]) than herbivores ($b = -1.54$, 95% CI = [−1.56, −1.52]; Fig. 4). Fishing pressure was a significant driver for size spectra slopes of carnivores and herbivores at each site, but we also found that habitat drivers (i.e., hard coral cover and structural complexity) were relatively important for herbivores (Fig. 5; Appendix S1: Tables S4–S7). For carnivores, we found that the size spectrum slope at high fishing pressure (17.47 kg/ha of carnivores) was $b = -2.08$ (95% CI = [−2.32, −1.86]; GAM with hard coral cover) and −1.94 (95% CI = [−2.20, −1.72]; GAM with hard coral cover) and became shallower as fishing pressure decreased (Fig. 6a, b). Size spectra slopes of
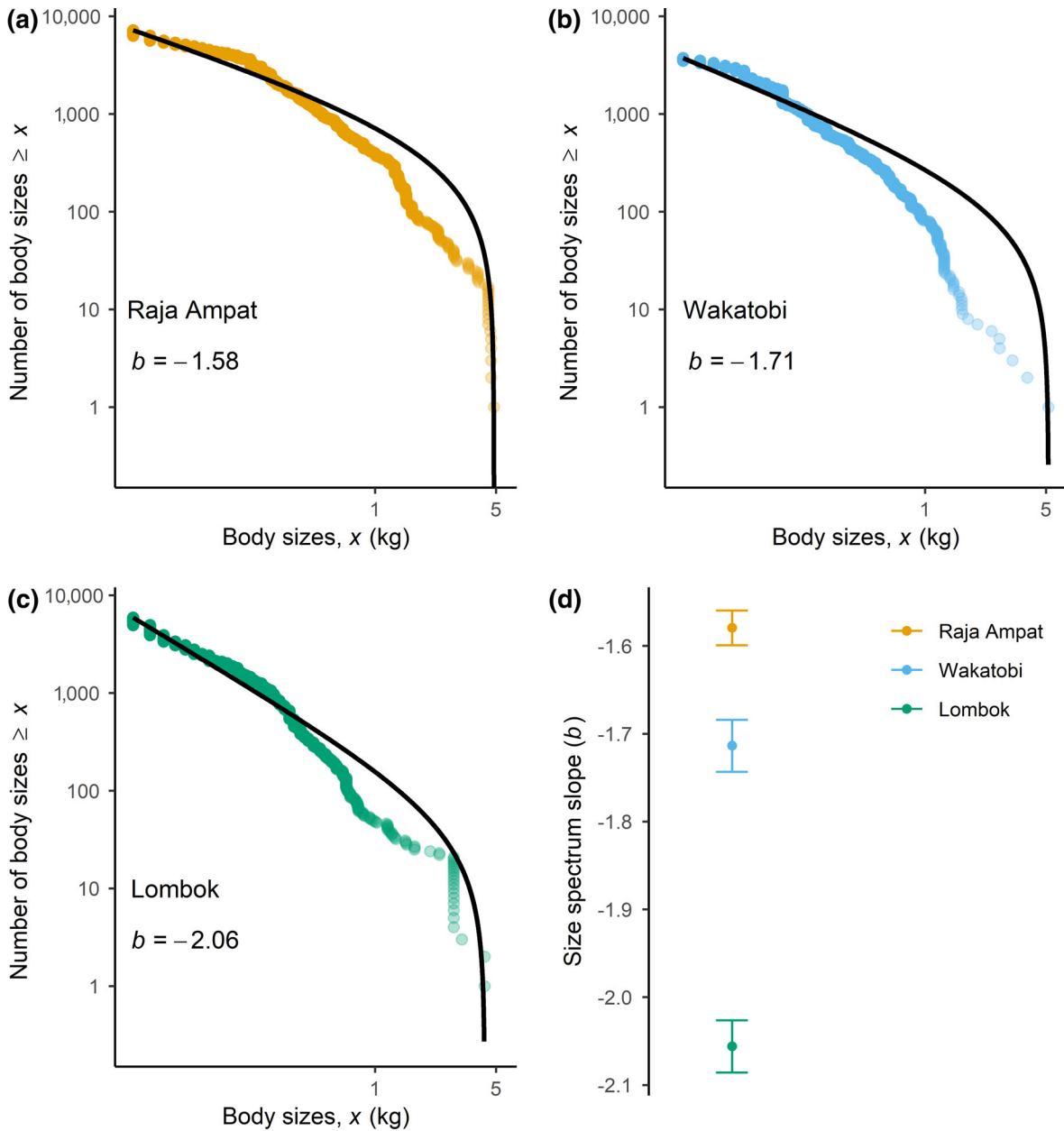
FIG. 2. The rank, or number of individuals $\geq$ body size x, in relation to body size (x) on logarithmic scales (a, b, and c), and size spectrum slope point estimates with 95% confidence intervals (d). The rank frequency plots visualize the fit of size spectra slopes using maximum likelihood estimation of a bounded power-law distribution (Equation 1) for Raja Ampat ($b = -1.58 \pm 0.02$ 95% CI), Wakatobi ($b = -1.71 \pm 0.03$ 95% CI) and Lombok ($b = -2 \pm 0.02$ 95% CI).

carnivores at low fishing pressure (803.52 kg/ha) were $b = -1.24$ (95% CI = [$-1.46, -1.05$]; GAM with hard coral cover) and -1.12 (95% CI = [$-1.34, -0.93$]; GAM with structural complexity; Fig. 6a, b). Habitat condition variables (hard coral cover, algal cover, and structural complexity) were not significant drivers of carnivore size spectra slopes (Appendix S1: Figs. S8, S9). However, we found that region had a significant effect on carnivore size spectra slopes. For each GAM (one with hard coral cover and the other with structural complexity as characteristics), mean of size spectra slopes for carnivores were significantly lower in Lombok than in Wakatobi and Raja Ampat (Appendix S1: Figs. S8, S9). However, Wakatobi had a significantly shallower mean carnivore slope than Raja Ampat in the GAM with hard coral cover (Appendix S1: Fig. S8) and
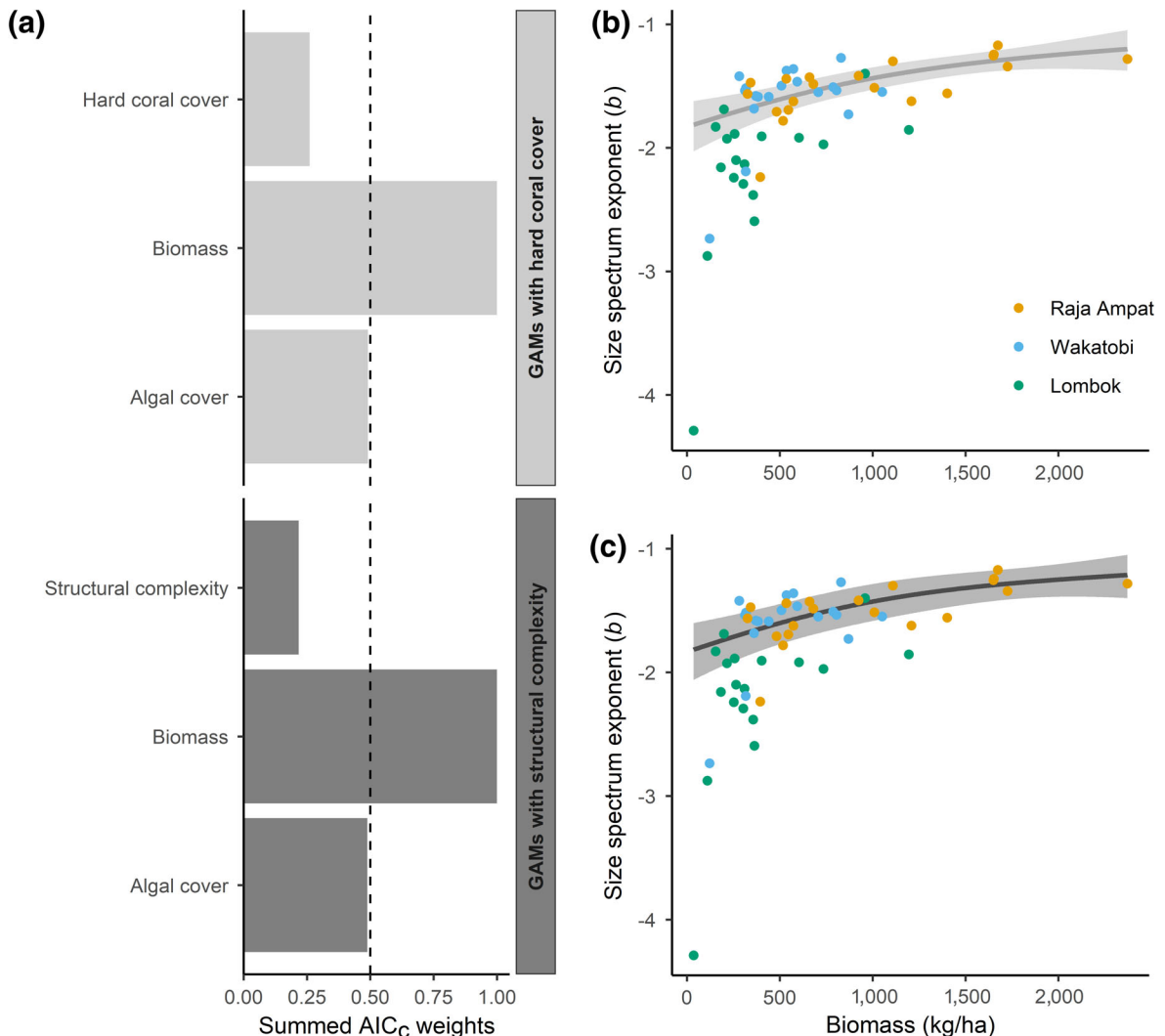
FIG. 3. Summed AIC_c weights for all models including each driver (a) and partial effects of fish biomass (proxy for fishing pressure) on size spectra slopes (b, c). The light gray bars (a) and lines with shaded boundaries (b, c) represent generalized additive models with hard coral cover as a driver, and dark gray represents models with structure complexity. In the partial effects plots (b, c), shaded areas indicate 95% confidence intervals and dots represent raw data. Colors indicate study region.

no significant difference between the regions for the GAM with structural complexity (Appendix S1: Fig. S9).

Fishing pressure was the only significant predictor for herbivore size spectra slopes, but summed AIC_c weights across models revealed that hard coral cover and structural complexity were also relatively important (summed AIC_c weights > 0.5; Figs. 5, 6). At high fishing pressure for herbivores (16.67 kg/ha) size spectra slopes were $b = -1.26$ (95% CI = [−1.45, −1.10]; GAM with hard coral cover) and −1.34 (95% CI = [−1.61, −1.12]; GAM with structural complexity; Fig. 6c, d). The slopes for herbivores at low fishing pressure (1,431.30 kg/ha) were $b = -0.89$ (95% CI = [−1.09, −0.73]; GAM with hard coral cover) and −0.99 (95% CI = [−1.23, −0.80]; GAM with structural complexity; Fig. 6c, d). Overall, the difference in size spectra slopes from high to low fishing pressure was smaller for herbivores (~0.36 difference in b) than carnivores (~0.83 difference in b). For the GAM with hard coral cover as a driver, herbivore size spectra slopes were significantly different across regions such that slopes were shallowest in Raja Ampat and steepest in Lombok (Appendix S1: Fig. S10). However, the GAM with structural complexity as a driver only detected a significant difference for Raja Ampat, which was shallower than Wakatobi and Lombok (Appendix S1: Fig. S11). Herbivore size spectra slopes were slightly steeper at intermediate hard coral cover, but structural complexity had higher summed AIC_c weights and a positive liner relationship with herbivore slopes (Fig. 6e, f). Herbivore size spectra slopes were $b = -1.48$ (95% CI = [−2.00, −1.10]) at low structural complexity and
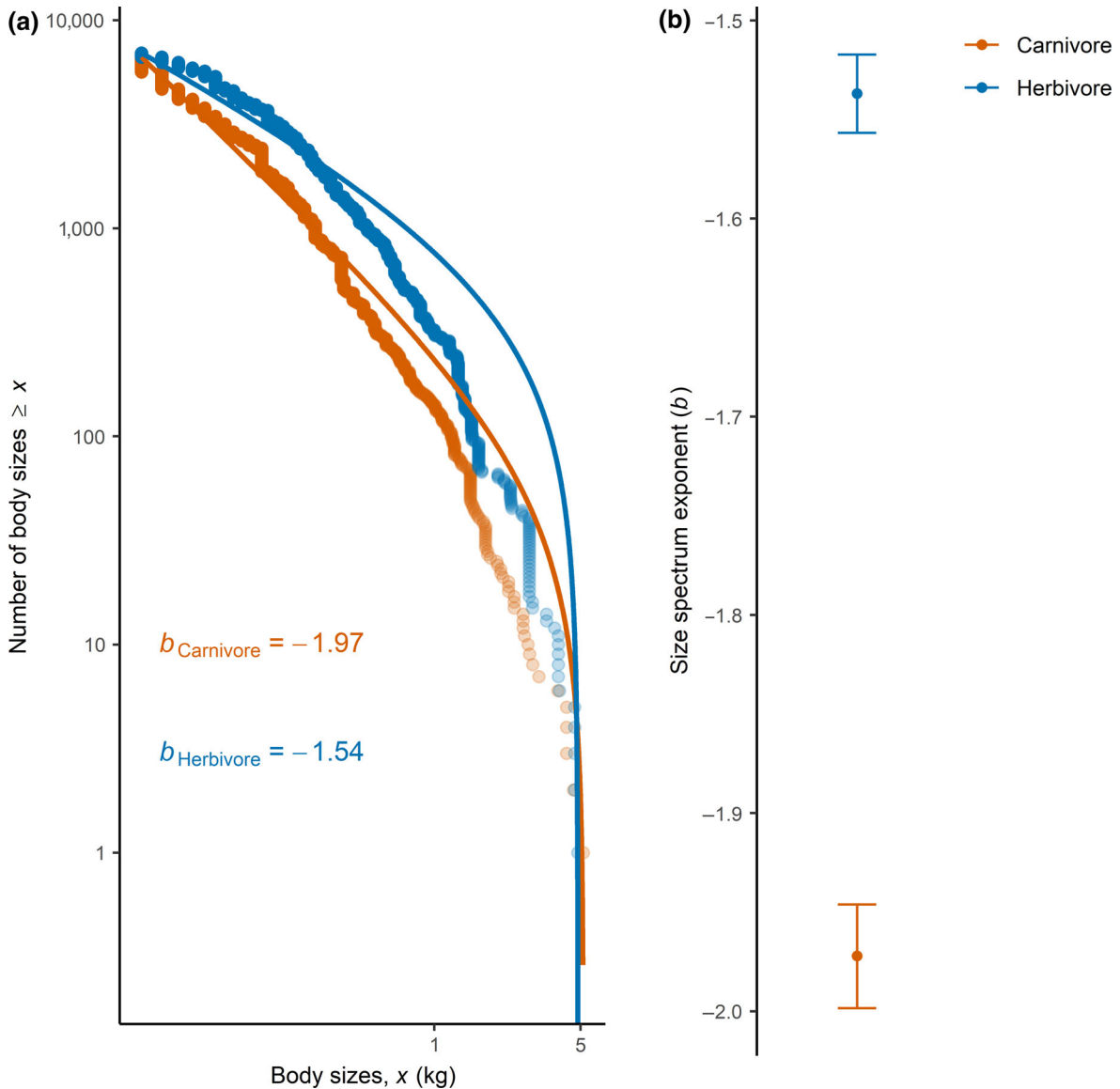
(a)

(b)

FIG. 4. The rank, or number of individuals ≥ body size x, in relation to body size (x) on logarithmic scales (a) and size spectrum point estimates with 95% confidence intervals (b). The rank frequency plot visualizes the fit of size spectra slopes using maximum likelihood estimation of a bounded power-law distribution (Equation 1) for carnivores ($b = -1.98 \pm 0.03$ 95% CI) and herbivores ($b = -1.55 \pm 0.02$ 95% CI). Data are aggregated across all study sites ($n = 57$) and regions (Raja Ampat, Wakatobi and Lombok), and colors indicate carnivores and herbivores.

$b = -1.04$ (95% CI = [−1.18, −0.92]) at high structural complexity (Fig. 6f).

DISCUSSION

Our results highlight important differences in the relative impacts of fishing and habitat condition on carnivore and herbivore size spectra slopes that are overlooked when fish are aggregated regardless of trophic identities. We found that fishing was a primary driver of both carnivore and herbivore size spectra

slopes, but the relative impact differed between groups such that carnivores had a higher difference in slope from low to high fishing pressure than herbivores. Although catch compositions in coral reef fisheries are often diverse and include fishes from most trophic and functional roles (Humphries et al. 2019), fishers in Indonesia typically target large carnivorous fishes as they are highly valued in export markets (Khasanah et al. 2020). For example, the export of snappers (Lutjanidae) and groupers (Serranidae) is a lucrative industry in Indonesia that yields approximately 56 million dollars
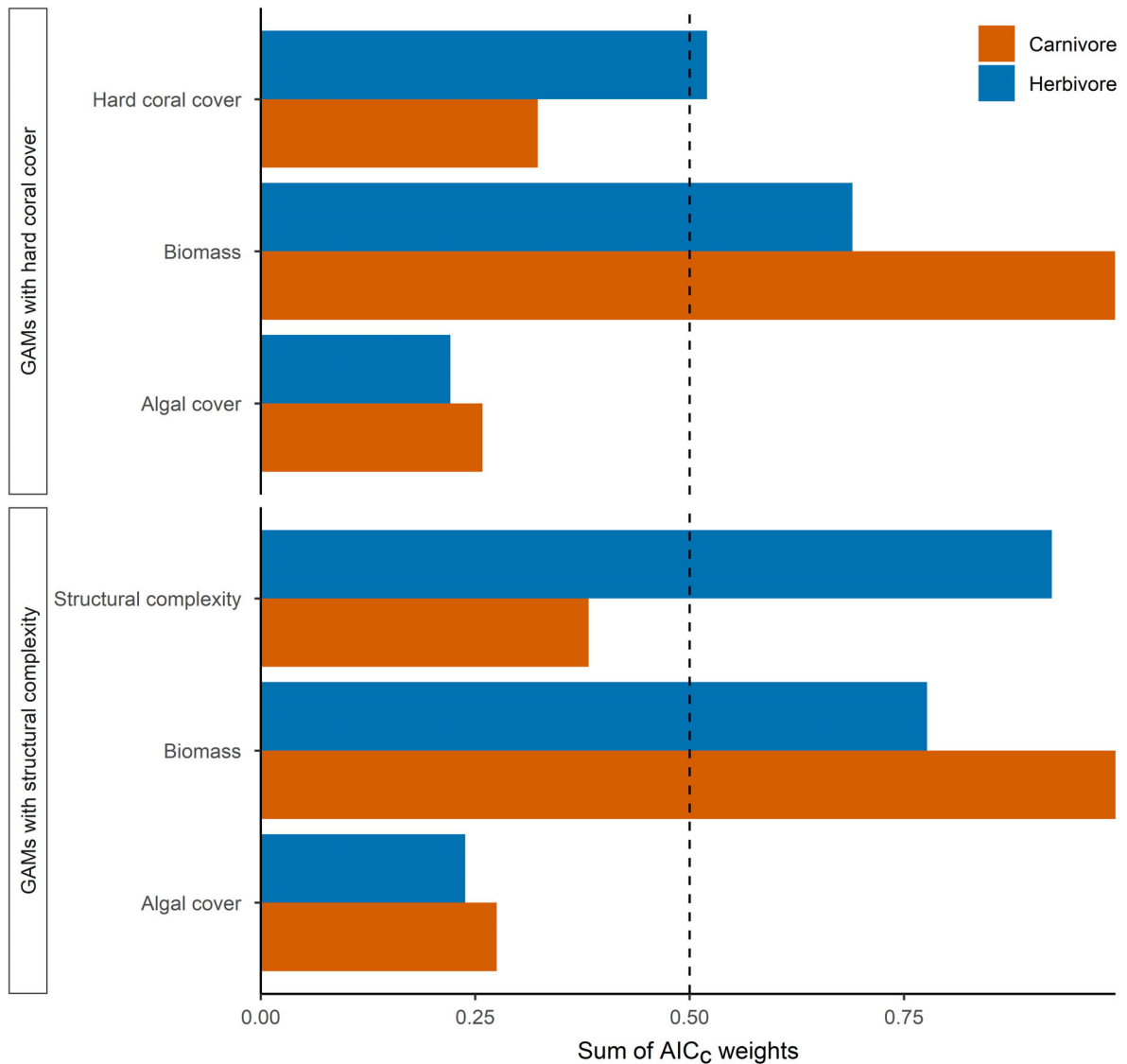
FIG. 5. Summed AIC_c weights for all models including each driver for carnivores and herbivores. Fish biomass was used as a proxy for fishing pressure. The top set of bars represents AIC_c weights for generalized additive models with hard coral cover as a driver, and the bottom set represents models with structural complexity. Colors indicate carnivores and herbivores.

annually and has resulted in overexploitation for many of these species (Efendi et al. 2020). Thus, export markets incentivize exploitation of carnivores and can lead to more dramatic impacts on carnivores than herbivores. Consequently, lower abundance and degraded size structure of carnivores in marine systems can lead to less stable ecological communities that are more susceptible to environmental disturbances (Britten et al. 2014).

Fishing may have had a lower impact on herbivore than carnivore size spectra slopes but it was still a significant driver. Similar to carnivores, large herbivores such as bumphead parrotfish (*Bolbometopon muricatum*) are highly valued in small-scale coral reef fisheries and their numbers have been reduced globally (Edwards et al.

2013). The removal of large herbivores can have severe consequences for reef health and resilience because herbivore forage capacities and functional roles are size-dependent (Bonaldo and Bellwood 2008, Humphries et al. 2014). Thus, future studies that investigate grazing capacities and herbivore functional roles in relation to gradients of size spectra slopes could help assess data-poor coral reef fisheries and ecosystems.

Overall, carnivores had steeper size spectra slopes than herbivores when data were aggregated across all study regions. This finding supports ecological theory, which predicts that carnivores will have steeper size spectra slopes than herbivores because herbivores acquire energy at the same trophic level (i.e., energetic
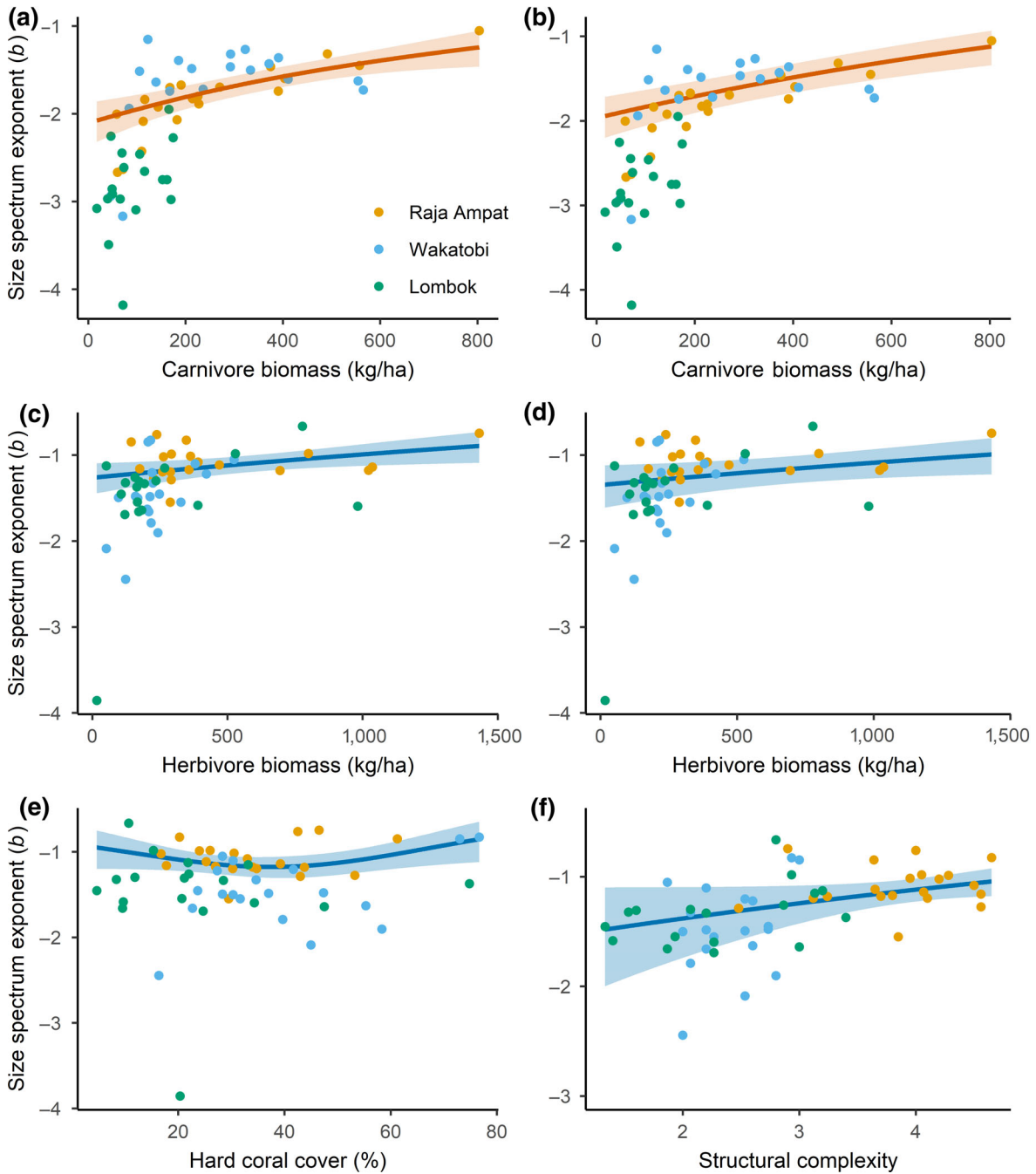
Fig. 6. Partial effects of carnivore biomass (proxy for fishing pressure) on carnivore size spectra slopes (a, b), and partial effects of herbivore biomass (proxy for fishing pressure; c and d), hard coral cover (e), and structural complexity (f) on herbivore slopes. Lines represent partial effects and shaded areas show 95% confidence intervals. Line colors indicate carnivore and herbivore generalized additive models. Dots represent raw data and colors indicate study region.

equivalence hypothesis), while carnivores consume prey across trophic levels and abundance-body size relationships are constrained by inefficient energy transfer (Brown and Gillooly 2003, Trebilco et al. 2013). Our results also align with findings from relatively undisturbed coral reefs in Kiritimati Island, an atoll in the

Line Islands, where carnivores had steeper slopes than herbivores and trophic position scaled positively with body size (Robinson and Baum 2016). The overall smaller body sizes of herbivores, which is associated with higher production rates and lower vulnerabilities to fishing (Abesamis et al. 2014, compared with carnivores is

likely contributing to the lower impact of fishing on herbivore size spectra slopes in our study.

Structural complexity, which was correlated with hard coral cover, was also a relatively important driver of herbivore size spectra slopes across our study sites. We found that herbivore size spectra slopes were shallower at sites with high structural complexity and steeper at sites with low complexity. Structural complexity has been shown to mediate predator-prey interactions and competition through provisioning of prey refugia (Rogers et al. 2014). For example, higher structural complexity, or diversity in available prey refugia, can result in a wider range of fish body sizes that are unavailable as prey and lower average herbivore size on reefs lacking structural complexity (Rogers et al. 2017). However, size distributions of reef fishes may be robust to initial losses in structural complexity due to increased abundance of benthic resources, such as turf algae (Rogers et al. 2017). Although carnivore size spectra slopes can be affected by structural complexity through benthic resource and refuge availability (Rogers et al. 2014, 2017), we suspect that this was overshadowed by the dominant impact of fishing pressure on carnivore slopes.

We also provide evidence that fishing has a substantial impact on the size spectra slopes of coral reef fishes when aggregated regardless of trophic group, such that slopes became steeper as average fish biomass decreased (i.e., fishing pressure increased). This result corroborates findings from studies in Fiji and US-affiliated Pacific islands that investigated the relationship between spatial and temporal differences in fishing pressure and size spectra slopes of coral reef fishes (Graham et al. 2005, Wilson et al. 2010, Robinson et al. 2017). As indicated above for carnivores and herbivores, our findings suggest that steeper size spectra slopes were a consequence of coral reef fishers selectively removing large-bodied fishes. Indeed, Raja Ampat had the least fishing pressure, shallowest size spectrum slope, and higher biomass of large- ($x \geq 1$ kg) and medium-bodied fishes (0.2 kg $\leq$ $x < 1$ kg) than Wakatobi and Lombok. Similarly, Robinson et al. (2017) found steeper size spectra slopes at sites with low fish biomass, which was attributed to the disproportionate removal of large fishes. In addition, our results show a slight decoupling between size spectra slopes at low fishing pressure (as in Robinson et al. 2017), which suggests that unmeasured processes such as temperature and primary productivity are driving increases in biomass while size spectra slopes level off.

In addition to the removal of large-bodied fish, prey-release can indirectly effect size spectra slopes. Prey-release occurs when prey species proliferate in the absence of, or reduced, top-down control from predators (Dulvy et al. 2004). We found that the relative biomass of small-bodied fishes ($x < 0.2$ kg) was highest in Lombok (region with highest fishing pressure) and lowest in Raja Ampat. However, the actual biomass densities of small fishes were similar across regions. Without fisheries-dependent information on the relative catch of each size

class, we were unable to determine the combined effects of fishing and prey-release on size spectra slopes.

Size spectra slopes are typically estimated through linear regression of log-transformed abundance and binned size-classes (Dulvy et al. 2004, Graham et al. 2005, Wilson et al. 2010). Edwards et al. (2017) reviewed methods for estimating size spectra and found that maximum likelihood estimation (MLE) of a bounded power-law distribution estimated slopes closer to theoretical values and with narrower confidence intervals than linear regression on log-transformed data. In this study, we used the MLE method on fish mass, and thus, direct comparisons of our estimated size spectra slopes with the estimated slopes from other studies that use linear regression on log-transformed data would be problematic as estimates from each method can differ by 1 to 2 (Edwards et al. 2017). Nevertheless, qualitative results which lead to the conclusion that fishing pressure affects size spectra of coral reef fishes holds across studies that use both methods (Wilson et al. 2010, Robinson et al. 2017).

Our estimated size spectra for carnivores, when data were aggregated across regions ($b = -1.98$, 95% CI = [-2.01, -1.95]), agreed with ecological theory, which predicts $b \sim -2$ (Brown and Gillooly 2003, Reuman et al. 2008, Robinson and Baum 2016). However, our estimated size spectra for herbivores ($b = -1.55$, 95% CI = [-1.57, -1.53]) were shallower than predicted, $b \sim -1.75$ (Brown and Gillooly 2003, Reuman et al. 2008, Robinson and Baum 2016). We expected size spectra slopes for carnivores and herbivores to be steeper than values predicted by theory due to the effects of fishing pressure and removal of large fishes. Theoretical predictions, however, are for closed systems where energy is transferred from primary producers to top-level consumers (Trebilco et al. 2013), and our observations only capture a subset of reef fishes (non-cryptic and diurnally active) within a size range appropriately surveyed by underwater visual census (Kulbicki 1998, Ackerman and Bellwood 2000). Thus, we exclude taxa that interact with coral reef fishes such as invertebrates and pelagic species that would need to be surveyed for comparison with theoretical predictions of size spectra slopes.

To the best of our knowledge, we provide the first analysis of carnivore and herbivore size spectra in response to fishing pressure and habitat condition on coral reefs. We found that fishing was a significant driver of carnivore and herbivore size spectra slopes, but carnivores were more heavily impacted. In addition, we found that structural complexity was a relatively important driver of herbivore size spectra slopes. These findings can be overlooked when size spectra slopes are estimated for all species aggregated regardless of trophic identity or functional role. Overall, we provide evidence that size spectra analysis can be a powerful fisheries-independent indicator for assessing data-poor coral reef fisheries and ecosystems.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2345/full

Data Availability

Data and code (Carvalho et al. 2021) are provided in the Dryad Digital Repository: https://doi.org/10.7291/D1DM42