**Community size structure varies with predator-prey size relationships and temperature across Australian reefs**

**ABSTRACT**

Climate change and fisheries exploitation are dramatically changing the species composition, abundances, and size spectra of fish communities. We explore whether variation in abundance-size spectra, a widely studied ecosystem feature, is influenced by a critical parameter thought to govern the shape of size-structured ecosystems—the relationship between the sizes of predators and their prey (predator-prey mass ratios, or PPMRs). PPMR estimates are lacking for vast numbers of fish species, including at the broader trophic guild scale. Using measurements of 8,128 prey items in gut contents of 97 reef fish species, we established predator-prey mass ratios (PPMRs) for four major trophic guilds (piscivores, invertivores, planktivores and herbivores) using linear mixed effects models. To assess theoretical predictions that higher mean community-level PPMR leads to shallower size spectrum slopes, we compared observations of mean community-level PPMR with size spectrum slopes for coastal reef sites distributed around Australia. PPMRs of individual fishes were remarkably high (median ~71,000), with significant variation between different trophic guilds (~890 for piscivores; ~83,000 for planktivores), and ~8,700 for whole communities. Community-level PPMRs were positively related to size spectrum slopes, broadly consistent with theory, however, this pattern was also influenced by the latitudinal temperature gradient. Tropical reefs showed a stronger relationship between community-level PPMRs and community size spectrum slopes than temperate reefs. The extent that these patterns apply outside Australia, and consequences for community structure and dynamics, are key areas for future investigation.

**KEY WORDS**

Size Spectrum, Predator Prey Mass Ratio, Predation, Habitat Complexity, Coastal Ecosystems, Community Composition

**INTRODUCTION**

Despite accounting for only ~6% of the global surface, coastal seas contribute ~40% of estimated global ecosystem services (Costanza *et al.*, 1998) and support commercial, recreational, and artisanal fisheries worldwide. Currently, fisheries and climate change are causing dramatic changes in both the species composition and body size structure of coastal fish communities (Audzijonyte *et al.*, 2016, 2020; Waples & Audzijonyte, 2016). This has important implications for food webs because body size is the single-most important biological trait determining an organism’s vital rates (metabolism, respiration, and development) and ecological interactions (movement capacity, predation risk, and trophic position) (Peters, 1983). As many marine animals increase in body size by several orders of magnitude from larva to adult (Sibly *et al.*, 2015), the ecological interactions and dietary niches of these individuals are particularly subject to changes in size-structure (Sánchez‐Hernández *et al.*, 2019, and references therein).

Ecological community size-structure is often described through ‘size spectra’, where the number of individuals (or their summed biomass) are shown in relation to body size classes (Sheldon et al. 1972, Sprules and Barth 2016). In the absence of fishing, both empirical and theoretical studies have shown that abundance declines with body size with a slope close to -1, corresponding to roughly equal biomass in size class bins, on a logarithmic scale (Sprules & Barth, 2016; Blanchard *et al.*, 2017a). However, despite its conservative nature, several factors can affect size spectra, most notably the selective removal of larger-bodied individuals (*e.g.,* via fishing), which results in fewer larger-bodied individuals relative to smaller-bodied individuals, thus steeper size spectrum slopes (Dulvy *et al.*, 2004; Graham *et al.*, 2005; Robinson *et al.*, 2017); along with increasing temperature (Blanchard *et al.*, 2005; Pomeranz *et al.*, 2022), and pollution (Arranz *et al.*, 2021). Consequently, the slope of size spectra provides a useful indicator of reef ecosystem health, and improved understanding of ecological baselines and responses to different pressures is needed (Nash & Graham, 2016).

A critical parameter governing theoretical community size spectra is the ratio between a predator’s body size or mass and that of its prey (‘Predator Prey Mass Ratio’, PPMR) (Jennings *et al.*, 2002; Andersen *et al.*, 2016b,a; Andersen, 2019). Higher PPMR values (> 1) indicate that a predator is consuming prey relatively smaller than itself, whereas lower PPMRs (closer to 1) indicate that a predator consumes prey closer to its own body size (and often, trophic level) (Jennings & Mackinson, 2003; Jennings & Warr, 2003; Jennings *et al.*, 2007). Meanwhile, PPMRs <1 suggest a predator is consuming prey larger than itself, a predation strategy (including work-arounds such as ‘pack hunting’ to take down larger prey) which is remarkably uncommon in marine systems in comparison to size-constrained predation (Trebilco *et al.*, 2013; Woodson *et al.*, 2018). A common constraint on the upper limit of prey size in many marine predators is ‘gape-limitation’, where predators are restricted to only consuming whole prey that can fit through their jaws’ (Mihalitsis & Bellwood, 2017). Below this upper size limit, many gape-limited predators feed on a wide range of prey sizes, depending on predator traits such as morphology, behaviour, and body size (Scharf *et al.*, 2000; Barnes *et al.*, 2010), leading to considerable individual-level variation in PPMRs. Subsequently, by averaging PPMR values across the range of individuals (and traits) that compose a community (deriving community-level or cPPMR), insights can be gained into the energetics and functioning of the broader system (Dornburg *et al.*, 2017; Troudet *et al.*, 2017; Bellwood *et al.*, 2020), including the number of trophic levels possible in the food web, and the steepness of size spectrum slopes.

According to the ‘Energetic Equivalence Hypothesis with Trophic Transfer Correction’, the unexploited biomass size spectrum slope (*b*) and abundance size spectrum slope (*b-1*), can be estimated with just two key community parameters - the cPPMR and trophic efficiency (*TE)* (Jennings & Mackinson, 2003; Reuman *et al.*, 2009):

**(1)**

Here ‘0.25’ accounts for the average scaling of an animal’s metabolic rate as body mass increases (Von Bertalanffy, 1957; Brown *et al.*, 2004; Sibly *et al.*, 2015a). *TE* describes the average proportion of biomass transferred between trophic levels, and *cPPMR* is the community averaged individual PPMR values (equation 1). In this equation TE and cPPMR are considered independent, i.e. energy transfer efficiency is not influenced by cPPMR values (Reuman *et al.*, 2009). Several constraints apply to the magnitude of the values in equation (1) and consequently restrict the possible range of ‘*b*’ (Trebilco *et al.*, 2013; Woodson *et al.*, 2018). TE, for instance, cannot exceed 1 (*i.e.,* due to the laws of thermodynamics, a predator cannot gain more energy than is present within the prey) and is often considered to be ~0.1, due to energy losses in the capture, handling and digestion of prey, along with the metabolic costs of the predator (Lindeman, 1942; Andersen *et al.*, 2009; although see Eddy *et al*., 2021).

While cPPMR is generally > 1 for marine fishes, empirical estimates of cPPMR rely on dietary or stable isotope data which are inherently difficult to attain for whole communities, and consequently such information is widely unavailable. The few empirical cPPMR compilations that do exist for marine environments range from 390 for the North Sea shelf (Jennings & Blanchard, 2004), 1,047 for a Bahamian tropical reef (Zhu *et al.*, 2019), 1,650 for a kelp forest reef (Trebilco *et al.*, 2016), and 7,792 for a tropical reef in the Western Arabian Sea (Al-Habsi *et al.*, 2008). Importantly, across a cPPMR range of 100-10000, when TE is 0.1, equation (1) predicts biomass size spectrum slopes ‘*b*’ that span both negative and positive values (Trebilco et al., 2016), the latter resulting in ‘top-heavy’ ecosystems and relatively higher abundance of larger to smaller sized individuals (Trebilco *et al.*, 2013; Woodson *et al.*, 2018, Jennings & Mackinson 2003), often cited for ‘pristine’ marine ecosystems (Trebilco *et al.*, 2013, 2016; McCauley *et al.*, 2018; Woodson *et al.*, 2018). Many reefs are dominated by herbivores, invertivores, planktivores, and detritivores that may consume small-bodied prey throughout their lifetime (resulting in higher PPMRs when they become larger). The consumption of relatively small prey may energetically permit these trophic guilds to become more abundant at large sizes (Woodson et al. 2018), leading to shallower size spectrum slopes (Fig. 1).

The contribution of differences in cPPMR to variation in abundance size-spectrum slopes has not been empirically assessed across large scales. Globally, empirical abundance size spectra have generally been found to approach the expected slopes (*b-1*) of approximately -1 (Heather *et al.*, 2021a). This applies to lightly exploited reef communities when including both fishes and invertebrates. Yet, there was also reasonable variation in slope estimates across reef sites and locations (min: -2.5; max: 2.1 Heather *et al.*, 2021a). Such variation may result from large differences in the community composition at sites, such that the relative contribution of fish groups with low (*e.g.,* herbivore, invertivore) or high (*e.g.,* piscivore) PPMRs leads to higher or lower cPPMRs, respectively. Here, we test whether higher cPPMRs lead to shallower size spectrum slopes for reef communities (as predicted by equation (1)). We consider reefs from warm tropical seas (coral reefs, including in the Great Barrier Reef) to cool temperate rocky reefs around the entire Australian continent, so we also consider variation associated with the large temperature gradient observed across sites. First, we establish a trait-based model of individual-level PPMR using 8,128 individual prey size measurements from 97 common fish species, representing four broad trophic guilds (herbivores, invertivores, planktivores and piscivores) that dominate reefs. Second, we apply the model to estimate cPPMR using empirical data on trophic guild and size structure of reef fish communities from ~15,000 underwater visual surveys around Australia. Finally, we test whether abundance size spectrum slopes, from these same survey data, are positively related with cPPMR, such that shallower slopes are generally associated with higher cPPMR, as predicted by theory (Fig. 1).

Chart

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**Figure 1.** Conceptual diagram illustrating relationship between community size spectrum slope and cPPMR (assuming the same transfer efficiency (TE) across trophic levels, and similar abundances at the smallest size class). The abundance of large-bodied fish is greater when **cPPMR** is high (represented by the relatively small size of prey in the outlined fish), with large fish abundance decreasing with lower cPPMR, resulting in steep, or shallow abundance **size spectrum slopes (*b-1*)**). High cPPMR is further associated with fewer steps in the food chain as large-bodied fish consume relatively smaller prey, leaving fewer trophic steps in between, and fewer **trophic levels** overall.

**METHODS**

**Sample collections and trophic guild identification**

To assess coastal reef community cPPMR, we first characterised individual-level predator-prey size relationships for major trophic guilds. We collected 8,128 individual predator-prey measurements from the stomach contents of 325 individual fishes spanning 97 species and 1.97 g – 7,878 g in body mass, from coastal reef sites (<15 m depth) over ~30 degrees latitude along Australia’s eastern seaboard (Fig. S1). Fish were collected by spearfishing and placed on ice or frozen until dissection. Prior to dissection, fishes were identified to species and weighed (grams) to provide predator mass. The predominant habitat substrata at sites transitioned from rocky algal dominated reefs in the south to coral dominated reefs in the North. Whilst the sampling scheme did not permit to sample full ontogenetic range of body sizes in each species, considerable fish size variation was sampled within each trophic guild (Table S1), which was the focus of our analyses (see below).

In general, species assemblages across ecosystems (including complex coral reefs) are characterised by a few, abundant (‘dominant’) species and a large number of comparatively rare species (Avolio *et al.*, 2019). As the focus of this study was to explore general, trophic guild level PPMR values in coastal fish communities, our sampling effort concentrated on collecting individuals of locally abundant species from broad trophic guilds present at each site (Table S1). Although considerable variation in diet is known from within trophic guilds (Parravicini *et al.*, 2020a), generalist diets are common within reef fish guilds (Van Denderen *et al.*, 2018). Furthermore, a recent study of over 13,000 individuals from 615 fish species revealed trophic guilds were highly conserved within families, and that body size and phylogeny alone (both included as fixed and random effects in the present study) were sufficient for predicting the trophic guild for 97% of fish in the dataset (Parravicini *et al.*, 2020a). Therefore research suggests that, despite the extraordinary morphological specialisation of reef fish, specialised morphologies may be more indicative of ‘how’ a species eats, rather than ‘what’ they eat (Bellwood *et al.*, 2006; Brandl *et al.*, 2015; deVries, Maya *et al.*, 2016). This means that the use of broad trophic guilds likely captures general feeding patterns across a range of morphologies and taxonomic levels.

Accordingly, fish species in the present study were first classified into nine trophic guilds as per Stuart-Smith *et al.* (2013), then, to maximise sample sizes within each trophic guild and reduce possible misclassification error (Parravicini *et al.*, 2020b), these classifications were further consolidated into four main trophic guilds — Herbivores: consisting of nominal and obligative herbivores; Planktivores: diets mainly consisting of zooplankton; Invertivores: omnivores, and diets mainly consisting of benthic invertebrates; and Piscivores: diets mainly consisting of large or highly mobile prey such as fish or cephalopods (Table S1). Fishes classified in (Stuart-Smith *et al.*, 2013) as ‘Algal Farmers’ or ‘Browsing Herbivores’, ‘Scraping Herbivores’ or ‘Excavators’ were all grouped into ‘Herbivores’; ‘Benthic Invertivores’, ‘Omnivores’ or ‘Corallivores’ were grouped into ‘Invertivores’; ‘Higher Carnivores’ (including generalist higher predators, such as fish which feed on cephalopods) were named ‘Piscivores’. Herbivores are generally assumed to derive most of their nutrition from plant and algal material, which cannot be sized in the gut contents. However, as there were also considerable numbers of small invertebrates in the gut contents of herbivores (perhaps consumed incidentally) these were identified and measured, and the PPMR of this guild included to provide a comparison to guilds that actively target animal prey.

**Gut content analysis and prey length-weight conversions**

To assess prey sizes of the sampled fishes, we preserved and analysed guts of fish collected. As soon as possible after field collection (or immediately upon thawing), gut contents were preserved in > 70% ethanol after removal from either the stomach or the anterior alimentary canal where defined stomachs were not present (very small specimens often precluded the separation of fore and hind guts). Prey items that were sufficiently undigested to enable identification (to phylum, order, or family level for the application of length-weight conversion factors) and differentiation of the major body axis, were further separated out for measurement.

For planktivores, all prey > 0.5 mm were separated from the sample, identified and measured (majority of prey were < 2 mm); for other trophic guilds only prey > 1mm were measured due to the time-consuming nature of the work. The difference in the minimum prey size measured applies to all planktivores evenly, however, applying the 1mm cut-off to this guild would likely reduce planktivore PPMR estimates. The smallest prey sizes are likely to be underestimated in all trophic guilds, as small prey are digested faster. However, we also note that our PPMR estimates are biomass-weighted, meaning that small prey sizes are contributing considerably less to the cPPMR values. In cases where more than ~ 200 prey items per gut were present, a subsample of gut contents was measured. Where traditional standard-length measurements could not be applied (e.g. barnacles, hermit-crabs in shell), the longest body axis was measured (e.g. widest part of shell for barnacles). Prey items were photographed with a scale and measured using the program CPCe (Kohler & Gill, 2006) (see example Fig. S3). To convert prey length measurements into body mass, prey were classified to the lowest taxonomic resolution possible and length-weight conversions from different literature sources applied (Table S2). Where conversions are length to dry weight, a dry the wet weight conversion factor described by (Ricciardi & Bourget, 1998) was applied.

Stable isotope data was available for a subset of the fish in this study (280 individuals) and we therefore cross-validated the two types of data. We expected a positive relationship between prey sizes and trophic position, and such relationship was indeed found (Fig S4), suggesting that the ‘snapshot’ of species diets assessed in our study was indeed reflective of the fish’s trophic position over longer time periods (see Supporting information).

**Trophic guild level predator prey mass (PPMR) relationships**

To quantify the relationship between predator and prey sizes and determine differences between guilds, we used weighted linear mixed effects models. All data analysis was performed using the R statistical language (R Development Core Team, 2021). We then used the package ‘lme4’ (Bates *et al.*, 2012) to model prey mass as a function of predator mass and trophic guild identity, treating genus as a random intercept effect (after investigating alternative taxonomic random effects structures including species, family and nested alternatives; S5). Furthermore, we biomass-weighted the model to account for the varying contributions of small versus large prey items to a predator’s energetic intake (see Reum *et al.*, 2019).

Predator mass was considered an independent variable as directly measured, whereas each unique fish number (predator ID) was treated as a random effect to account for the repeated measures of prey items for one predator. To account for any phylogenetic influences on prey size arising from unmeasured aspects of foraging behaviour, we included a nested random effects term ‘Genus’ in our model, within which an individual fish (ID) was nested (‘Genus/ID’). Different fixed and random effects structures were compared (Tables S4 and S5), and although all differences in the Akaike information criterion (AIC) values were below 4 (Table S4), the model with the lowest (AIC) value contained the fixed effects of predator mass (log10 transformed; continuous), trophic guild (categorical) and their interaction, and the nested, random effects term ‘Genus/ID’:

, (2)

where is the log10 transformed individual prey mass, is the log10 transformed individual predator mass, is the categorical value defining predator’s trophic guild, is the random intercept effect and *β*0, *β*1, *β*2,T and *β*3,T are body mass, trophic-guild and interaction coefficients to be estimated. Restricted Maximum Likelihood (REML) was applied to all models, and residual and Q-Q plots were checked to ensure sufficient concordance with model assumptions. In order to weight the individual prey items via total prey biomass, a weighting term, was added to the model (in lme4, syntax: weights = wt). We calculated PPMR by dividing the model prey size predictions (with and without the random effects) by the predator mass, and visualised the outcomes (as per Barnes *et al.*, 2010; see Fig. 3 below).

**Community level PPMR estimates**

Community-level PPMR (cPPMR) was obtained by averaging the individual PPMR of all predators within a given study area (Nakazawa, 2017; Reum *et al.*, 2019b). Calculating a cPPMR requires information on the sizes of the individual predators and their prey in size class bins (Blanchard *et al.*, 2017b; Nakazawa, 2017; Reum *et al.*, 2019b). Data on the size ranges and abundances of the four trophic groups in coastal communities came from underwater visual censuses on shallow reefs by the Reef Life Survey (RLS) and Australian Temperate Reef Collaboration (ATRC) programs (Edgar & Barrett, 2012; Edgar & Stuart-Smith, 2014; Edgar *et al.*, 2020). The RLS and ATRC data, accessed through the Integrated Marine Observing System’s National Reef Monitoring Network facility ([https://portal.aodn.org.au/ search](https://portal.aodn.org.au/%20search), Accessed 21/08/2020), include the abundance and size classes of all fish species observed within 500 m2 belt transects on shallow rocky and coral reefs (for details on underwater transect methods see Edgar & Barrett 2012, Edgar & Stuart-Smith 2014, Edgar et al. 2020). Only transects from Australia surveyed from 2007 onwards, with biomass estimates available for all species, were included; resulting in a total of 14,941 transects.

All fish in the visual survey dataset were classified into the four trophic guilds, as described above. Next, using the linear mixed effects model, prey mass was estimated for each individual observed fish in the survey, using the fish’s wet mass (g), estimated from the observed length, and its trophic guild identity. Nearly all fish surveyed could be categorised into one of the four broad trophic guilds, however species classified as ‘cleaners’ (e.g., cleaner wrasse), along with some non-fish predators (marine mammals, reptiles and birds) were excluded from the dataset. With this data, we then calculated transect level PPMR (cPPMR) by summing the PPMRs of fish in each trophic guild and size class combination, and dividing by the total number of individuals observed:

(3)

where *PPMRi,M*is the estimated PPMR value of trophic guild *i* at size group *M*, and N*i,M*is the number of individuals observed. To determine the sensitivity of the cPPMR metric to the exclusion of trophic guilds, we tested the resulting values by excluding one trophic guild at a time, and re-running the calculation (Table S6, Fig. S6). Only the exclusion of invertivores had a large impact on the resulting cPPMR, however as we are interested in the whole community, all trophic guilds were included in subsequent analyses.

**Size spectrum models**

The term ‘abundance size spectrum’ refers to the relationship between body size (e.g. mass) and abundance, and is often represented on the log-log scale, *i.e.*, the logarithmic abundance of individuals within logarithmic body size classes (Fig. 1). Here, we used Australian rocky and coral reef community abundance size spectrum slopes (equivalent to b-1 in terms biomass size spectrum slopes), from Heather *et al.* (2021a), where slopes were estimated by fitting a linear mixed effects model with log abundance as the response variable, log body size class as a fixed predictor variable, and with site nested within ecoregion as random predictor variables. The community size spectra data derived from RLS transects used in the present study included both fish and invertebrate size and abundance data. As assessed in Heather *et al.*, (2021a) excluding invertebrates from community size spectrum data can lead to a spurious interpretations. As discussed in Heather *et al.*, (2021b), the inclusion of the smallest body size classes of fish and invertebrates (< 32 g) in diver surveys has been questioned due to possible methodological issues influencing survey observations. However, the authors recommended the inclusion of both invertebrates and the smallest body size classes as the reduced abundance of the smallest individuals observed in these size spectra may be a true component of the underlying body size distribution (as discussed in Heather *et al,* 2021b). We use the complete fish and invertebrate dataset for our analysis as the predators sampled consumed both small-sized and invertebrate prey and truncating the dataset at fish > 32g (removing all fish smaller than 13-16 cm) would exclude a vast majority of planktivores, resulting in a biased representation of the community.

**Relationship between cPPMR and size spectrum slope**

Size based theory predicts that animal communities with higher cPPMRs will have shallower size spectrum slopes, which means they will have a relatively greater number of large-bodied individuals than communities with low cPPMRs. To test this hypothesis we linearly regressed our estimated cPPMR from each transect to fish and invertebrate community slope values estimated for the same transects by Heather *et al.* (2021b). We applied a Linear Mixed Effects models in the R language package ‘lme4’ (Bates *et al.*, 2012). The RLS-ATRC sites in our dataset were surveyed over a range of years and span a large spatial temperature gradient from annual mean sea surface temperatures (SST) of ~14oC up to ~28oC, so we included annual mean SST as either a fixed or random intercept effect (Table 1, Table S7). Mean SST data were derived from Bio-ORACLE (Tyberghein *et al.*, 2012) and matched to RLS-ATRC sites. We further included site nested in year as random intercept effects, given that some sites were repeat sampled over multiple years. We also ran the model excluding the 1st and 99th percentiles of cPPMR to determine if our results were sensitive to extreme values of cPPMR caused by unusual fish composition at a site (Table S9).

**Data and code availability**

Underwater visual survey abundance datasets are available through the Integrated Marine Observing System’s National Reef Monitoring Network facility (https://portal.aodn.org.au/search). The slope calculation datasets are available from Heather *et al.*, 2021a and 2021b. The gut content analysis datasets used in this analysis and all R code is available through the code repository at *https://github.com/amroco/Reef\_fish\_cPPMR.*

**RESULTS**

**Establishing predator prey mass ratios from individual scale measurements**

Out of the 992 fish individuals collected by the study (148 species), 325 fish had non-empty stomachs with sizeable prey items (97 species). For these fish, prey sizes ranged from 0.12 mm – 189.59 mm (Table S1). The mixed effect model analysis showed that for all fishes sampled, ~33% of the variation in the measured prey mass (marginal R2) could be explained by the two predictor variables (body size and trophic guild) and their interaction (Fig. S5, Table S3). The models showed that prey mass increased with the predator mass (significantly positive slopes, Fig. 2, Table S3) in three of the four trophic guilds. These slopes were steepest in piscivores (Fig. 2, Table S3; slope: 2.22; *p* <0.001), shallower but still significantly positive in invertivores (slope: 0.68, *p* = 0.025), positive although not significant in planktivores (slope: 0.47, *p* = 0.14) and not significant in herbivores (slope: 0.11; *p* = 0.664; Table S3).

Diagram

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**Figure 2. Predator prey mass relationships.**

Predictions and 95% confidence intervals generated by linear mixed effects model for prey mass as a function of predator mass (log10, g) and trophic guild. The regression lines of the model reflect the biomass-weighting of individual prey within a predator, whilst data points represent prey items from the gut contents of individual fishes (see Table S1 for species assigned to each trophic guild). Marginal and conditional R2 for the model were 0.33 and 0.995 (note: individual was included as a random effect).

To explore the implications of the nested random effects structure and visualise the general relationship between predator size and its PPMR in each of the four trophic guilds (as per Barnes *et al.*, 2010), we show a range of model predictions using a full and simplified random effect structure (Fig. 3). By deriving the predicted PPMR using the model predictions of prey mass (log10 (g)) and the individual weight of predators (log10 (g)) we show the extent to which random and fixed effects contribute to the model’s predictions. Here predictions are converted to PPMR (rather than prey mass) versus predator mass, to make them more comparable to Barnes *et al.* (2010) analyses. These visualisations show, as was also the case in Barnes *et al.* (2010), that a large proportion of variation is accounted by individual level variation across predators (Fig. 3a). Nevertheless, both removing random individual effects but maintaining the taxonomic groupings (genus level random effects; Fig. 3b) and reducing the model predictions to the four trophic guilds (no random effects; Fig. 3c) provide a similar trend between PPMR and predator’s body size. Importantly, this relationship reveals that PPMR values are not fixed across predators’ body sizes. For instance, steep increases in PPMR with body size are apparent for herbivores (*i.e*., larger fish feed on relatively smaller prey), in contrast, steep decreases in PPMR with body size are apparent for piscivores (*i.e.,* large predators feed on relatively larger prey). As we were interested in broadscale estimates at the trophic guild level, we did not propagate error from individuals or other random effects up to the cPPMR level, but note that the random effects introduced through genus, as included in the model, still produced the same visual pattern as the fixed effects alone.

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**Figure 3** Predictions of the linear mixed effects model with the fixed effects Trophic Guild and Log10 Predator Mass (g), with the random effects structure individual fish nested in Genus. Predictions are shown based upon: **(A)** including random effects of genus and individual; **(B)** including only random effect of genus and excluding the effects of individual; **(C)** fixed effects only (trophic guild).

**Relationship between community-level PPMR and size spectrum slopes**

Scaling the measured relationships between fish and prey sizes up to the community data from reef fish surveys revealed an overall mean community PPMR (cPPMR) of ~8,700 (across site variation: minimum 21; 1st quartile 5,751; median 8,305; 3rd quartile 12,507; maximum 15,776,588). This overall mean takes into account the trophic guild composition and size structure observed in Australian coral and rocky reef fish communities.

As predicted by equation (1), communities with higher cPPMRs possessed shallower size spectrum slopes (thus including a greater proportion of large-bodied individuals, than communities with low cPPMRs), when using the full fish and invertebrate size spectrum slope dataset. We found a significant, positive, relationship between log10 cPPMR and abundance size spectra slope both when including (P < 0.001; Marginal R2/Conditional R2 0.20/0.51; Table S1) and excluding (P < 0.001; Marginal R2/Conditional R2 0.03/0.54; Table S7) mean sea surface temperature (mean SST) as an explanatory variable, interacting with cPPMR. When cPPMR was removed from models aiming to predict size spectrum slope from SST alone, the model predictive power was considerably weaker (delta AIC > 150). The model with cPPMR interacting with mean SST had the greatest explanatory power of all possible predictor combinations (Table S8, delta AIC ~ 35) and showed that the relationship between cPPMR and community size spectrum slope *b-1* was strongest in the tropics, weakening towards cooler temperatures (Interaction term *p* < 0.001, Table 1, Fig. 4) and close to no relationship in the coolest, temperate Tasmanian sites (Fig. 2).

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**Figure 4** **Relationship between fish and invertebrate abundance size spectrum slope (b-1) and log10 cPPMR values for fish communities.**

Predictions and confidence intervals of linear mixed effects model for abundance size spectrum slope as a function of log10 cPPMR (g) and temperature (mean annual SST, oC), with site and year as random effects (see Fig. S7 for the data excluding the 0.01 and 0.99 quantiles, direction and significance of predictions are the same). Marginal and conditional R2 for the model were 0.20 and 0.51. Data points represent fish communities per individual RLS transect. To visualise the interaction effect, trendlines are provided for the three temperature values corresponding to averages in Tasmania, New South Wales and Queensland (15, 21, and 29 oC). Confidence intervals (ribbons either side of lines) for the interaction prediction lines likely underestimate the compound error as they represent one discrete value of a continuous variable (temperature).

**Table 1: Linear mixed effects statistics for the model used to predict fish community size spectrum slope** (*b-1*), according to log10 cPPMR and mean Sea Surface Temperature (Mean SST; o C). Fixed effects: **log10** **cPPMR** (continuous) and **Mean SST** (continuous, o C). Random effects: **site** (as multiple transects were sometimes conducted at the same site within the same year) and **year** (some sites were repeatedly sampled over years). Model syntax in package: lmer(*b* ~ cPPMR \* Mean SST + (1|Year/Site), REML = T). “Drop1” analysis of the model’s structure revealed the interaction term of the model could not be dropped without significant effects on the model output (P < 0.001).

|  |  |  |  |
| --- | --- | --- | --- |
|  | ***Size spectrum slope*** | | |
| **Predictors** | **Estimates** | **CI** | **p** |
| (Intercept) | 1.67 | 1.03 – 2.31 | **<0.001** |
| Log10 cPPMR | -0.40 | -0.56 – -0.23 | **<0.001** |
| Mean SST | -0.13 | -0.16 – -0.10 | **<0.001** |
| Log10 cPPMR \* Mean SST | 0.03 | 0.02 – 0.04 | **<0.001** |
| **Random Effects** | | | |
| σ2 | 0.03 | | |
| τ00 Site:Year | 0.02 | | |
| τ00 Year | 0.00 | | |
| ICC | 0.39 | | |
| N site | 1,220 | | |
| N mean SST | 11 | | |
| Observations (transects) | 5,401 | | |
| Marginal R2 / Conditional R2 | 0.197 / 0.508 | | |

Results were similar in direction, significance and resulting marginal and conditional R2 values when the same analysis was run with the 1st and 99th percentile cPPMRs excluded (removing 109 transects from the dataset; Table S9), suggesting the results are rigorous to the removal of cPPMR outliers (*i.e.,* transects dominated by small or large fish aggregations, Fig. S7).

**DISCUSSION**

Our study presents evidence for the key role of cPPMRs in size structuring reef fish communities. In doing so, we provide four main findings: (1) PPMR of reef fishes varies differently with body size both between and within trophic guilds; (2) cPPMR of Australian rocky and coral reef fishes appear considerably higher than has been assumed by most modelling studies; (3) a significant positive relationship exists between reef abundance size spectra slopes and cPPMR, suggesting that cPPMR partly explains variation in natural size structure of reef communities; and (4) the relationship between cPPMR and size spectrum slopes strongly depends on temperature.

***High community PPMR values in coastal Australian reefs***

We found that PPMR increased with increasing body size across three trophic groups (piscivores, invertivores and planktivores), but decreased with body size in herbivores (the only trophic guild assumed to not actively target animal prey; Fig. 3). Increasing PPMR with body size is consistent with previous studies (Edgar & Shaw, 1995; Scharf *et al.*, 2000; Reum & Hunsicker, 2012; Niiranen *et al.*, 2019; Griffiths, 2020; Wilson & Kimmel, 2022), including the general positive trend across an extensive dataset of fish and squid (regardless of trophic guild) found using gut content analysis by Barnes *et al.*, (2010). Whilst specific PPMR values may be applied to different predators (both at the species, Andersen, 2019; and trophic guild levels, Reum *et al.*, 2019a), treating these PPMR values as constant regardless of body size is common-practice in size-based ecosystem models (likely due to the paucity of data). A positive relationship between PPMR with body size may have considerable implications for energy transfer in ecosystems, as it suggests large-bodied predators continue to receive energy from small-bodied (Scharf *et al.*, 2000; Tsai *et al.*, 2016; Griffiths, 2020), lower trophic level prey, thus losing less energy through transfer inefficiencies (Barnes *et al.*, 2010) and facilitating higher abundances of these predators at large body sizes. Our results suggest that holding PPMR estimates constant regardless of predator body size may mislead predictions from size-based ecosystem models, including when scaling up to the community level.

Community-level PPMR integrates taxonomic composition, size distributions and feeding preference into one ecologically important summary statistic (Brose *et al.*, 2019). Yet, despite being a valuable metric, estimation of cPPMR values remains rare and varies greatly across species and ecosystems (Brose *et al.*, 2006, 2019). This study provides the first approximate estimate of community predator prey mass ratios (cPPMRs) for shallow eastern Australian rocky and coral reefs and shows that mean values observed (~8,700) are similar to those found by Stable Isotope Analysis (SIA) for a tropical reef system (Al-Habsi *et al.*, 2008), but up to ~20 times higher than previous SIA-based studies for open shelf and other temperate and tropical reef systems (Jennings & Blanchard, 2004; Trebilco *et al.*, 2016; Zhu *et al.*, 2019).

Several methodological reasons may explain the variable cPPMR values observed across studies (beyond ecosystem type; Tsai *et al.*, 2016; Nakazawa, 2017; Reum *et al.*, 2019b). First, some of the differences between our results and other studies may be because all other marine cPPMR estimates were based on SIA, whereas we used direct prey size analyses from stomach contents. The advantage of SIA is that it integrates information on species diets over longer timeframes (days to years depending on the tissue type; Vanderklift & Ponsard, 2003; Jennings *et al.*, 2008; Boecklen *et al.*, 2011; Nielsen *et al.*, 2018) and is less prone to random spatial and temporal variation. However, a major challenge is that currently most SIA-derived cPPMR estimates are based on ‘raw’, non-baseline-corrected δ15N values, and therefore do not account for differences in isotopic baselines between locations. We also collected δ15N data and observed large differences in isotopic baselines across our sampled locations, which suggests that deriving PPMR estimates using the common SIA approach would be misleading. Nevertheless, the δ15N data available for a subset of the fish analysed here (280 individuals), generally confirmed the robustness of our dietary analyses. The expected positive relationship between prey sizes and trophic position (Jennings *et al.*, 2002) was indeed evident in our samples (Fig. S4), suggesting that the ‘snapshot’ of species diets assessed in our study using gut contents was reflective of the fish’s trophic position over longer time periods. Additionally, we note that our results are in the same magnitude as a study using SIA on reef fish communities (Al-Habsi *et al.*, 2008).

Another possible reason for differences in our cPPMR estimates to those from other reef studies (namely Trebilco *et al.*, 2016; Zhu *et al.*, 2019) is that our limited sample sizes prohibited accurate evaluation of ontogenetic and spatial trends in PPMR within species, although these likely occur. Gut content analysis typically exhibit a high degree of noise due to samples providing a brief snapshot of a fish’s diet (Nielsen *et al.*, 2018). Yet, the focus of this study was not on the type of prey, but the size of prey, within broad trophic guilds, and the statistical models used here aimed to account for random variation associated with individual, its genus and sampling sites. Earlier studies have shown that predator size alone is an important predictor of prey sizes (Soler *et al.*, 2016) and here we refine this prediction with addition of four trophic guilds. Thus, despite the possible methodological issues, we believe that our results show genuinely high cPPMR values for coastal reef communities.

The high cPPMR values observed for reef versus pelagic or shelf habitats (such as Jennings & Blanchard, 2004) could be explained by the high degree of structural complexity in these habitats, which provide abundant refuges for a range of predator and prey sizes (Wang *et al.*, 2009; Brose *et al.*, 2019). Whilst refuges ‘lock’ some prey away from predation, both prey and their predators are more abundant when refuges are present (Hixon & Beets, 1993); and habitat complexity only provides refuges for prey up until either the point of refuge saturation, or when prey themselves must exit the refuge to forage (Donelan *et al.*, 2016). More complex habitats could therefore provide a stable trickle of prey (Rogers *et al.*, 2014, 2018), allowing reef fishes to feed on relatively small, and sub-optimal, prey sizes (Portalier *et al.*, 2019; Griffiths, 2020). Empirical studies have shown that even whilst maximum and mean prey size usually increase with predator size, small prey often continue to be consumed (Juanes & Conover, 1994; Floeter & Temming, 2003, 2005; Ménard *et al.*, 2006; Gaeta *et al.*, 2018). This hypothesis could be addressed in future studies by adding habitat complexity metrics as additional predictors of variation in cPPMR.

Further, in coastal ecosystems multiple, largely independent, sources of primary production may provide alternative food supply sources (i.e. benthic and pelagic, unicellular and macrophytic) (Trebilco et al. 2016). Along with the nutritional and structural components of benthic primary productivity on reefs, planktonic primary productivity is well recognised as a substantive contributor to reef fish trophodynamics (Odum & Odum, 1955; Bray *et al.*, 1981; Hamner *et al.*, 1988; Polunin, 1996; Wyatt *et al.*, 2012; Truong *et al.*, 2017; Morais & Bellwood, 2019; Holland *et al.*, 2020). The turnover of benthic and planktonic primary producers generally operates over different timescales, and can therefore fuel reefs through contrasting perturbations, stabilising the supply of energy higher up the food chain (Rooney *et al.*, 2006). In a global study of marine teleosts, generalist diets were found to be favoured over specialist where benthic and pelagic sources both contribute to primary productivity, opposed to pelagic only pathways (Van Denderen *et al.*, 2018). In summary, by providing alternative, persistent, and predictable prey sources alternative sources of primary production, rocky and coral reef ecosystems may enable consumption of smaller, less energetically rich prey, facilitating the establishment of high PPMRs.

***Community PPMR and temperature are important predictors of size spectrum slopes***

Our study shows that both cPPMR and site temperature (here measured as mean annual sea surface temperature) explain some variation in community size spectrum slopes (*b-1*) and that there is significant interaction between these factors. A recent study (Heather *et al.*, 2021a) showed that abundance-based size spectrum slopes around Australia varied considerably around the theoretical expected mean of -1 (although our slopes are shallower, as unlike Heather *et al.,* 2021a, we included the full range of sizes observed). A large body of literature has demonstrated that temperature is an important predictor of community size spectrum slope and that these slopes are usually steeper in higher temperatures (Heneghan *et al.*, 2019; Pomeranz *et al.*, 2022). Here we show that that cPPMR also explains a significant amount of variation in size spectrum slopes, but not in cool temperate areas. In tropical areas, the relationship between size spectrum slope and cPPMR was quite steep, whereas in cool temperate reefs, it was close to zero (Fig. 4). There are several possible reasons for this interaction.

The relationship between size spectrum slopes (*b-1*) and the cPPMR-mean SST interaction may be a consequence of our cPPMR data not including invertebrate PPMRs. As described in Heather *et al.* (2021a) excluding either the invertebrate or fish components of a community may result to misleading patterns, as the relative contribution of invertebrates to overall community composition and trophic ecology is greater in marine systems at higher latitudes with lower mean SSTs. Furthermore, our study may not have fully captured temperature-related differences in trophic guild PPMR, as the limited sample size precluded detailed comparisons across temperatures. If individual fish PPMRs change with temperature, our cPPMRs would also change, possibly explaining more of the size spectra slopes in temperate ecosystems. Yet, it is also possible that at colder temperatures, the other term in equation (1) – trophic transfer efficiency (TE) – is more variable and provides a compensatory role. A tight relationship between cPPMR and size spectrum slope would assume that TE is similar across sites, while highly variable TE would randomise the relationship between *b-1* and cPPMR. A recent review revealed considerable variation in estimates of the mean value of trophic transfer efficiency (TE) globally, with a general trend of higher estimated TE in colder ecosystems (Eddy *et al.*, 2021).

Finally, systematic variation in size spectrum slopes could be explained by human impacts (*e.g.,* fishing, pollution) or environmental differences that were not accounted for in the slopes used here (Dulvy *et al.*, 2004; Graham *et al.*, 2005; Nash & Graham, 2016; Robinson *et al.*, 2017); although we note that many of our sites and species are lightly exploited by global standards (see Audzijonyte *et al.*, 2020). Understanding and disentangling the nature of these influences requires improved site level covariate data to investigate factors contributing to interactions in greater detail.

In conclusion, our study—the first general estimate of cPPMRs across Australian coastal reef communities—revealed mean cPPMR values up to threefold higher than many previous estimates, but consistent with values observed for a tropical reef (Al-Habsi *et al.*, 2008). This finding has considerable implications for size-based models, which are currently based upon limited and variable estimates for cPPMR in marine systems. By providing empirical estimates of cPPMR for this system, this study may improve our capacity to predict changes in reef fish community structure, and its responses to human and environmental pressures.

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