Habitat complexity influences the structure of food webs in Great Barrier Reef seagrass meadows

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Abstract. Structural habitat complexity is a fundamental attribute influencing ecological food webs. Simplification of complex habitats occurs due to both natural and anthropogenic pressures that can alter productivity of food webs. Relationships between food web structure and habitat complexity may be influenced by multiple mechanisms, and untangling these can be challenging. We investigated whether (1) size spectra vary across a gradient of habitat complexity in seagrass meadows and (2) structural complexity changes the importance of different primary producers supporting the food web (determined using stable isotope analysis) in the Great Barrier Reef World Heritage Area. We found that moderately complex meadows had much steeper size spectra slopes, caused by a higher abundance of smaller animals and fewer larger animals, while meadows on either end of the complexity scale (low and a single meadow with very high complexity) had shallower slopes, indicative of a more balanced distribution of animal sizes across the spectrum. We also found that the importance of epiphytic algae as a food source was high in most meadows, despite the increase in seagrass surface area on which epiphytes could grow. The consistent importance of epiphytic algae suggests that the changes in the availability of different potential food sources did not affect food web structure. Our findings indicate that food web structure may change with variations in structural complexity because of changes in the abundance of smaller and/or larger animals. Food web structure and food sources are important determinants of the dynamic stability of food webs. Size spectra analysis is already used as a monitoring tool for assessing populations of key fisheries species in commercial fishing operations, and thus, we recommend using size spectra as a proxy for assessing the structure of the food webs in different types of seagrass meadows. Size spectra may be a useful indicator of how different meadows provide for ecosystem services such as fisheries.

Key words: abundance–biomass size spectra; Great Barrier Reef; habitat complexity; predator–prey interactions; seagrass; size spectra; stable isotope analysis; structural complexity.

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INTRODUCTION

The structural complexity of habitats is a fundamental attribute shaping the dynamics of food webs (Alvarez-Filip et al. 2011). Human pressures often simplify habitat structure with far-reaching consequences for ecosystem productivity (Gamez-Virues et al. 2015, Nagelkerken

et al. 2015). Multiple mechanisms may manifest simultaneously to affect food web productivity in structurally complex habitats, because structure determines the diversity of niches, increases refuge availability, and can provide protection from environmental variables (Langellotto and Denno 2006, Graham and Nash 2012). For example, there could be an over-abundance of smaller animals compared with larger animals (altering the predator–prey ratio) due to refuge availability, or there could be an uneven distribution of different size classes as a result of selective fishing pressure (Wilson et al. 2010, Graham and Nash 2012, Trebilco et al. 2013). It is therefore important to identify the key mechanisms involved because if the structure of a habitat directly affects productivity of a food web, then a change or loss of structure results in a change or loss of production (Rogers et al. 2014).

In aquatic habitats, greater structural complexity increases the surface area available for primary production (Bologna and Heck 1999), traps more organic material (e.g., detritus; Kennedy et al. 2010), and provides greater subsidies from animals (e.g., temporary aggregations of predators seeking refuge; Horinouchi 2007). The effects of structural complexity highlight the importance of determining the mechanisms driving productivity, because each implies a different pattern of change in food web productivity if habitat structure is simplified.

Theories of energy and matter transfer in food webs can help to distinguish among mechanisms that cause relationships between structural complexity and productivity. Mechanisms that might influence productivity include which sources of primary productivity support the food web, how effectively the food web is transferring energy to higher trophic levels, the distribution of predators and prey within a food web, and the presence of energetic subsidies (Jennings and Mackinson 2003, Trebilco et al. 2013). Animal size spectra and isotopic diet studies can help to understand which of these mechanisms are operating. Size spectra are expressed as a slope exponent (b) for body mass (M) and b scales with either abundance, biomass, or energy use in a predictable way (Trebilco et al. 2013). When analyzing the body mass–abundance relationship in size-structured communities, slopes are typically expected to be more negative (steeper) than the predicted threshold of $b = -0.75$ (Trebilco et al. 2013). Slopes that have values for b less negative than -0.75 (or even positive values for b) can indicate the presence of energetic subsidies (Trebilco et al. 2013), and slopes with values more negative for b (b of approximately -1.2) indicate stable environments with smaller predator–prey ratios (Jennings and Mackinson 2003, Jennings and Warr 2003). Analyzing dietary information can assist in determining the extent to which different primary sources of production support food webs, and analyzing this with structural complexity can indicate whether key sources of primary production change with availability of plant biomass.

The theory of size spectra has been well studied in aquatic environments such as lakes (Arranz et al. 2019) and marine habitats (Jennings et al. 2002), and changes in the spectrum of animal size in coral reefs have been used to specifically understand the role of habitat complexity (Wilson et al. 2010, Rogers et al. 2014). Seagrass is an important habitat (Cullen-Unsworth and Unsworth 2018) that provides widely varying structural complexity (York et al. 2017), yet to our knowledge, there are no studies that have analyzed how the size spectra of animals in seagrass might vary with habitat complexity. Globally, seagrass loss has been documented at greater than 100 km^2 per year since 1980 (Waycott et al. 2009) and further losses are predicted in critical places as a result of multiple impacts (Unsworth et al. 2018). Seagrass loss means a loss of a wide range of important ecosystem services, including food web support for endangered fauna (Scott et al. 2018, Sievers et al. 2019), and a greater understanding of how seagrasses provide these services is required to manage impacts on seagrass (Unsworth et al. 2019). In the Great Barrier Reef World Heritage Area (GBRWHA), seagrass is a key habitat supporting the outstanding universal values that led to its World Heritage status and is a critical habitat supporting fisheries production (Coles et al. 2015). As with many places around the globe, seagrasses in the GBRWHA are subject to increasing human pressures that can result in their degradation and thus habitat simplification. Therefore, we asked whether the animal size spectra in seagrass meadows in the GBRWHA varies across a gradient of structural complexity,

and whether habitat complexity affects the relative contributions of different primary producers to food webs.

We tested several mechanisms to determine how structural habitat complexity might influence food webs and proposed three hypotheses. Hypothesis 1: Total animal biomass will be positively related to structural habitat complexity because greater complexity increases the availability of habitat. Hypothesis 2: The steepness of animal size spectra slopes will increase with increasing structural complexity, indicating more balanced food webs in complex meadows. Hypothesis 3: Epiphyte and seagrass contribution to food webs will increase with structural complexity because structurally simple meadows will show a higher reliance on benthic microalgae due to availability of space for algae to colonize. We tested these hypotheses using nine seagrass meadows from the GBRWHA that ranged widely in structural complexity determined using a combination of different habitat variables.

Methods

We collected primary producers and animals from nine individual seagrass meadows in the GBRWHA. Each meadow was dominated by one of five seagrass species with different morphological characteristics (*Cymodocea serrulata*, *Halophila ovalis*, *Halophila spinulosa*, *Halodule uninervis*, or *Zostera muelleri*; see Appendix S1: Table S1 for details on each meadow). Although each of the species has clear morphological differences, we used other common metrics to determine the complexity of the meadow because intraspecific variability in morphology can occur in seagrasses depending on growth conditions or disturbances (Abal et al. 1994, Maxwell et al. 2014). The seagrass metrics used to describe habitat complexity were aboveground biomass ($g \cdot DW^{-1} \cdot m^{-2}$), canopy height (mm), leaf area index (m^{-2}), and shoot density (m^{-2}; Appendix S1: Table S1). Leaf area index was calculated as the number of leaves multiplied by the average leaf height and leaf width, then divided by ground area of the core sample. We synthesized the four metrics using a principal component analysis (PCA) to extract the dominant axes of variation. We ran the PCA using the prcomp function in the stats package in R (R Development Core Team 2017).

Principal component 1 (PC1) explained 88% of the variation of the four habitat complexity metrics, with higher values of PC1 representative of meadows having overall more seagrass of greater complexity (taller canopy, greater biomass, greater shoot density, and larger leaves; see Appendix S1: Table S2 for loadings from PCA). Because of the presence of a single meadow with a very high value for PC1 (meadow 9; Appendix S1: Table S3), we tested the sensitivity of PC1 by running the PCA without this meadow. We found that the resulting PC1 values for the re-tested eight meadows were highly correlated with the original PC1 values for these same meadows (see Appendix S1: Note S1, Fig. S1 for details). Therefore, we retained the original PC1 values to represent complexity for all nine seagrass meadows.

Seagrass animals were sampled using multiple tows of a beam trawl (2-mm mesh) in each meadow (see Appendix S1: Table S4 for details). This method reliably collects resident species we were targeting (e.g., animals small enough to spend most of their time in the meadow). By sampling at night, and at a slow speed (drifting speed up to 2 knots maximum), we maximized trawl catches (Warburton 1989, Guest et al. 2003). All animals were identified, counted, and measured for size spectra analysis, and a mix of species across a range of size classes was retained for isotopic analysis (Appendix S1: Table S5). Biomass was calculated for fish species using the length–weight relationship information from fishbase.org. For crustaceans and invertebrates, wet weights of representative size classes of different species were recorded, and samples were then dried to a constant weight at 60°C and weighed again to obtain percent change from wet to dry weight. The percent change in weight was then applied to all wet weights obtained in the field for an estimation of biomass for all individuals of different size classes and classifications.

C, N, and S isotope values of animals (using white muscle tissue) and plants were obtained on an elemental analyzer–isotope-ratio mass spectrometer (EA-IRMS). Three primary producer types identified as potentially contributing to food webs were collected at each meadow: (1) seagrass leaves; (2) epiphytic algae on seagrass leaves; and (3) benthic microalgae. Epiphytes were scraped from seagrass leaves and analyzed

separately. Benthic microalgal samples were collected from the surficial layer of sediment within and around the seagrass meadows, and clean algal cell samples were obtained by centrifuging in a seawater/silica solution as per Hamilton et al. (2005). We acknowledge that it is important to obtain baseline data from individual meadows for isotopic analysis; however, for epiphytes at five meadows, and benthic microalgae at two meadows, we were unable to obtain a clean (uncontaminated) sample from the collections, or the content of C, N, and/or S within the sample was too small for a reliable signature to be detected by the EA-IRMS. To account for these missing values and to ensure we fairly represented the sources available in the food webs, we used the mean and standard deviation (SD) from all other meadows to represent the values for missing epiphytic and benthic microalgal sources. At an additional three meadows, only one sample of benthic microalgae, and at an additional meadow, only one sample of epiphytic algae were large enough to be analyzed for C/N/S by the EA-IRMS, and in those cases, we used the average SD across all meadows.

We analyzed abundance and body mass of individual animals using a maximum likelihood estimation (MLE) for the slope exponent, b, of the size spectra (M^b) and its associated standard error (SE; Edwards et al. 2017, Appendix S1: Table S3). Analyzing individual size distribution is preferred to categorizing species into trophic groups because it is a better representation of energy transfer (Trebilco et al. 2013) and MLE is the most accurate and thus comparable method (Edwards et al. 2017). Some individuals were identified as outliers (smaller or larger than expected for this sampling method) and were excluded from analysis. The size range for analysis of size spectra was therefore limited to 0.08–32 g dry weight, to avoid sampling artefacts and to limit the upper and lower bounds, which is appropriate for MLE analysis (White et al. 2008). Animals measured within this size range are likely not to be directly affected by fishing pressure (Jennings and Mackinson 2003).

We analyzed the relationship between structural habitat complexity with total animal biomass, and with the exponent for the slope of the size spectra, b. We used meta-analytic regressions to regress total animal biomass against the PCA and to regress b against the PCA (from the R package metafor; Wood 2011). Meta-analytic regression was used so that the influence on site-specific estimates on the regression was weighted by their SEs. Inspection of residuals from the linear regression of b and the PCA indicated non-linearity, so we refitted this model with a spline with two knots and compared the parsimony of the linear and non-linear models using the Akaike's information criterion (Burnham and Anderson 2002).

The stable isotope mixing model MixSIAR (Stock and Semmens 2013) using the residual error term only (Parnell et al. 2010) was used to estimate the proportional contributions of each of the three primary producers to the diet of representative species from a range of size classes (based on biomass) using C, N, and S isotopes (Appendix S1: Tables S5, S6). Trophic levels were determined using FishBase.org and published values. Trophic enrichment factors per level were 1‰ for C, ranged from 2‰ to 3‰ for N, and 0‰ for S based on McCutchan et al. (2003). We used individual animal biomass ($\log_{10}$) as a covariate in the mixing model to determine whether contribution of the different plant sources varied with size of the animals. We then investigated the relationship between source contribution and aboveground plant biomass using a meta-analytic regression to regress mean source contribution against the PCA, accounting for the SEs of the mean contributions (from the R package metafor; Wood 2011). Aboveground biomass was chosen as the most important habitat metric to compare with source contribution because we wanted to test the hypothesis that greater seagrass biomass results in a greater contribution of seagrass and epiphytes to the food web.

Results

Total animal biomass and biomass–abundance size spectra slopes varied among meadows, but in different ways. Total animal biomass varied between meadows, but no significant relationship was found with the PC of complexity ($P = 0.711$; Appendix S1: Fig. S2). The animal size spectra were more negative than the expected theoretical threshold of $M^{-0.75}$ in all
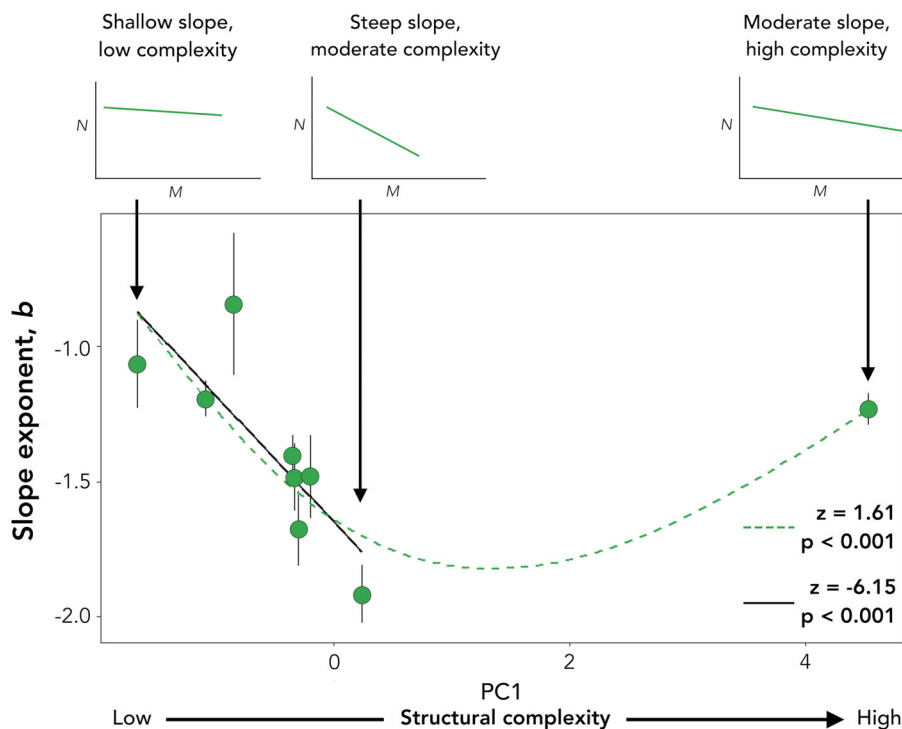
Fig. 1. Relationship between the animal abundance (N)–biomass (M) size spectra and structural habitat complexity in nine seagrass meadows. Size spectra are represented by the slope exponent, b (se—black bars), measured using maximum likelihood estimation (Edwards et al. 2017), and complexity of the meadows is represented by principal component 1 (PC1) from a principal component analysis. Green dashed line and black line indicate non-linear (for all nine meadows) and linear (for the first eight meadows only) meta-analytic regressions, respectively, with z- and P-values displayed for each test. Example slopes are shown above to depict a shallow, steep, and moderate slope with the corresponding b value (slopes using real values can be found in Appendix S1: Fig. S3).

cases and ranged from $M^{-0.84}$ (shallowest slope) to $M^{-1.92}$ (steepest slope) for the nine meadows (Appendix S1: Fig. S3). The slopes of the size spectra generally fitted the distribution of body sizes closely, and there were relatively few large individuals that fell below the slope in some meadows (Appendix S1: Fig S3).

For eight of the nine meadows, there was a trend of more negative slopes with increasing complexity (Fig. 1). The slope exponent, b, declined from -1.07 to -1.92 from low to moderate complexity, an effect that exceeded errors in measurement of b at individual meadows. A single outlier with very high complexity had high leverage on the model (30% weighting), and the linear trend was nonsignificant ($z = -0.13$, SE = 0.061, $n = 9$, $P = 0.896$). Because of the high

weighting on the outlier, we excluded this meadow and re-ran the linear model on the first eight meadows alone, to demonstrate the significant negative trend ($z = -6.15$, SE = 0.073, $n = 8$, $P < 0.001$; Fig. 1). To further test the relationship of all levels of complexity, we fitted a non-linear model to all nine meadows, which was also significant ($z = -5.61$, SE = 0.294, $n = 9$, $P < 0.001$; Fig. 1).

We found no relationship with aboveground plant biomass and mean contribution of any of the three sources to the seagrass food webs. Epiphytes were the main source contributing to the food webs for eight of the nine meadows (Fig. 2). The combined mean contribution from seagrass and epiphytes was greater than 75% for all except one meadow that had a higher
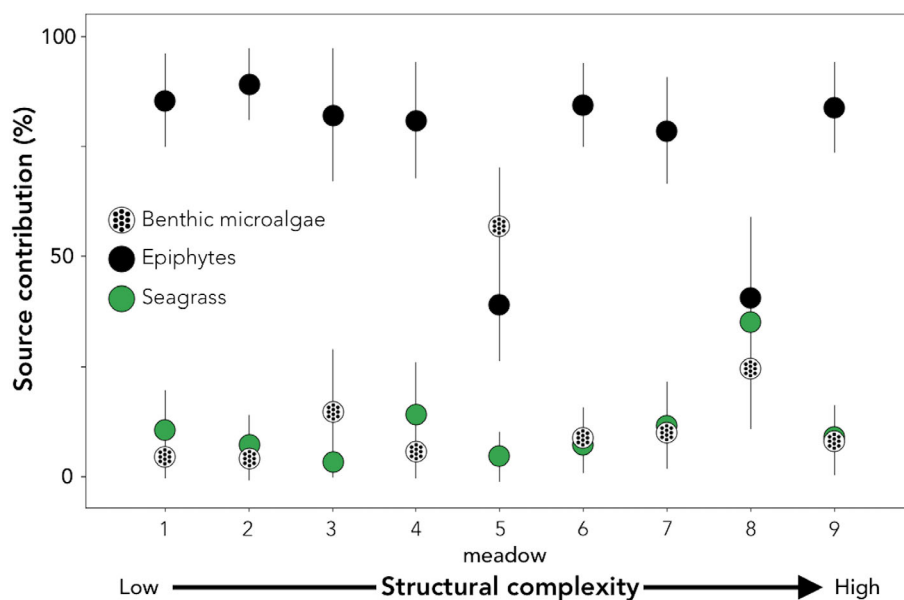
Fig. 2. Contribution (mean, standard deviation) of three major plant sources (benthic microalgae, epiphytes, and seagrass) to the food webs of nine seagrass meadows in the Great Barrier Reef World Heritage Area. Meadows are in order of the least complex to most complex based on the results of a principal component analysis.

contribution of benthic microalgae (meadow 5, Fig. 2). Outputs from mixing models showed that, in most cases, the contribution of plant sources did not change with biomass of representative species; that is, contribution estimates remained the same despite the change in animal biomass (see examples in Appendix S1: Fig. S4, panel a–b). Two exceptions, meadow 6 (Appendix S1: Fig. S4, panel c) and meadow 8 (Appendix S1: Fig. S4, panel d), showed a clear change in contribution from epiphytes to seagrass in larger-bodied animals; however, the contribution from benthic microalgae was not greatly affected by biomass.

DISCUSSION

Different mechanisms, such as an abundance of smaller animals, a lack of larger animals, or both, could be responsible for the relationship between structural complexity of seagrass meadows and food web structure that we observed. Our findings did not support hypothesis 1—that total animal biomass will be positively related to structural habitat complexity. Instead, we found that multiple mechanisms explain the relationship between

size spectra and habitat complexity as postulated in hypothesis 2. We found that as habitat complexity increased from low to moderate, animal size spectra slopes became much steeper than expected ($b = -1.92$ at the steepest), indicating a change in the distribution of animal sizes with complexity, with a greater abundance of smaller animals found in moderately complex meadows. However, the most complex habitat had a slope that was shallower ($b = -1.23$) than moderately complex meadows, the highest total animal biomass, and a much more even distribution of body sizes (Fig. 1; Appendix S1: Fig. S2), indicating a further change in animal size distributions toward a more balanced food web. It is important to note that the relationship with the most complex meadow and size spectra is based on only one example and further investigation into seagrass meadows with greater structural complexity is necessary to confirm these findings. For hypothesis 3, we did not see an increase in seagrass and epiphyte contribution with habitat complexity and instead found that the importance of epiphytes as a source of primary production was high, regardless of structural complexity (Fig. 2). However, there were indications that the importance of seagrass as a food
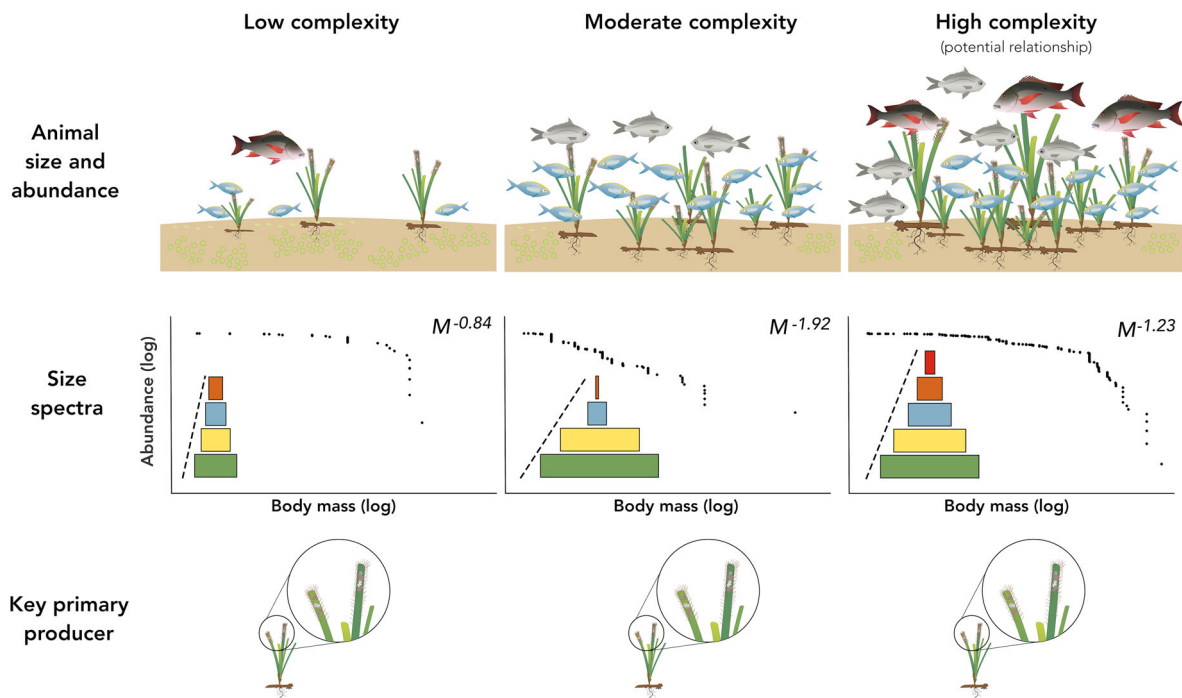
Fig. 3. Conceptual summary of findings for food web variables with habitat complexity in nine seagrass meadows. Meadows with low complexity had shallower animal size spectra slopes ($M^{-0.84}$), meadows with moderate complexity had the steepest slopes ($M^{-1.92}$) due to fewer larger-bodied animals and many smaller-bodied animals (indicating a smaller predator–prey ratio), and a single meadow with highest complexity (therefore, a "potential" relationship) had a less steep slope with high animal biomass ($M^{-1.23}$). Epiphytic algae were the key primary producers contributing to the food webs across all meadows, regardless of structural complexity. Size spectra are calculated using the log of the body mass of individuals and the cumulative abundance of individuals of that biomass (see Appendix S1: Fig. S3 for all slopes and axis values). Biomass pyramids are included for a visual representation of how the slope relates to a pyramid structure. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

source increased for larger fish in at least some of the meadows (Appendix S1: Fig. S4, panels c–d). We have summarized the size spectra complexity results and isotope food web findings to conceptualize the potential mechanisms at play with an example for simple, moderate, and the single, highly complex meadow (Fig. 3).

We found that animal size spectra slopes in seagrass meadows steepened (the slope value became more negative) as habitat complexity increased from simple to moderately complex meadows (partial support for hypothesis 2), indicating that the distribution of animal size and abundance changed with structural complexity. Steeper size spectra can be caused by either a reduction in larger-bodied animals or an increase in the number of smaller-bodied animals, or both mechanisms can work together (Graham et al. 2005). Habitat complexity has previously been linked to a change in size spectra slopes in other ecosystems. In Seychelles coral reefs, shallower slopes were found on more structurally simple reefs that were damaged by coral bleaching (Graham et al. 2007). In the Lau Islands of Fiji, size spectra slopes also became shallower with a reduction in habitat complexity, yet in the same habitat, fishing pressure was associated with a steepening of slopes (Wilson et al. 2010). The impact of fishing has been linked to steeper size spectra slopes for fish communities (Graham et al. 2005); however, this is not always the cause for a steeper slope. For example, in the

Caribbean, steeper slopes occurred in coral reefs with high habitat complexity, and this was attributed to a greater number of smaller-bodied fish utilizing the complex habitat rather than fishing pressure, because larger predators were protected from fishing (Alvarez-Filip et al. 2011). Our results were consistent with these studies in that size spectra slopes were steeper for moderate complexity meadows when compared to low complexity meadows. This result is consistent with smaller animals being more prevalent in structurally complex habitats where they are less vulnerable to predation than in structurally simple habitats (Horinouchi 2007).

Despite our general finding of steeper slopes with greater complexity, a single meadow with the highest value for complexity had a shallower slope ($b = -1.23$) compared to moderately complex meadows. This meadow also had the highest total animal biomass (Appendix S1: Fig. S2) and one of the largest size ranges of animals (Fig. 3; Appendix S1: Fig. S3). Size spectra slopes of fish communities with values of approximately -1.2 for b occur where there are smaller predator–prey mass ratios, and these food webs have been linked to more stable environments (Jennings and Mackinson 2003, Jennings and Warr 2003, Alvarez-Filip et al. 2011). This finding somewhat contradicts our prediction for hypothesis 2; however due to the lack of available data, we can only speculate about the importance of very highly complex seagrass meadows and their link with stable environments. We encourage further investigation, particularly to expand sampling of meadows with very high structural complexity, with which these findings can be compared.

Some non-linear patterns were evident in the size spectra slopes, with obvious deviations from the slope where larger individuals were rare and where there appeared to be a disproportionate abundance of some size classes (Appendix S1: Fig. S3). Size spectra slopes are known to exhibit non-linearity and deviations from the slope where low abundance and/or smaller size classes of predatory species occur (Arranz et al. 2019). With fewer larger animals, there is opportunity for an increase in the abundance of certain size classes, which in turn reduces predation pressure on other size classes. This could be due to the specialization of predatory species preferring

certain prey size classes (Law et al. 2009) or a result of fishing pressure (Benoît and Rochet 2004). These non-linear patterns have previously been used to predict the level of exploitation of fisheries resources in a habitat (Shin and Cury 2004). Because of the size range of the animals we analyzed (resident seagrass animals are typically not of a harvestable size), fishing pressure is an unlikely explanation for our findings; however, there could be an indirect top-down effect of fishing altering higher trophic levels not sampled by our methods. To test this explanation, size spectra would need to be analyzed beyond resident seagrass animals.

There was no change in the contribution of the primary producers to the food webs with increasing plant biomass (hypothesis 3); instead, we found that epiphytes were important contributors for most food webs regardless of the amount of plant biomass. This finding hints at the importance of epiphytes in seagrass food webs, regardless of habitat complexity. Although the proportion of epiphytes contributing to food webs did not change, these findings allude to the notion that greater surface area in seagrass meadows leads to higher availability of epiphytes, which in turn could support a larger community of animals. The importance of epiphytes has been demonstrated in seagrass food webs previously (Bologna and Heck 1999, Moncrieff and Sullivan 2001, Connolly and Waltham 2015), and herbivorous species are known to prefer leaves covered in epiphytes (Marco-Méndez et al. 2015). The results from our findings of high epiphyte contribution might be interpreted with caution due to the lack of available baseline data at some of our meadows; however, this finding is strongly supported by previous work (Orth and van Montfrans 1984, Vizzini 2009) so it is likely to be accurate regardless of the lack of baseline data. In order to provide greater resolution in future, isotopic enrichment experiments could be particularly powerful, given our focus on resident fauna (Winning et al. 1999, Oakes et al. 2010).

Animal size spectra have been well studied in many aquatic habitats (Brown and Gillooly 2003, Jennings and Mackinson 2003, Wilson et al. 2010), but only a few studies exist for seagrass meadows. Size spectra have been analyzed on nematodes in *Thalassia testudinum* meadows in

the Caribbean (Armenteros and Ruiz-Abierno 2015), and across entire food webs in *Posidonia oceanica* meadows in the Mediterranean (Macpherson et al. 2002), coastal seagrass meadows in Boston Harbor, USA (France et al. 1998), and *Zostera marina* meadows in Denmark (Thormar et al. 2016). Our shallowest slope value ($b = -0.84$) was similar to size spectra slopes in unprotected *P. oceanica* meadows; however in protected *P. oceanica* meadows, slopes were much shallower due to a larger proportion of biomass predominantly from a few species including *Sarpa salpa* (Macpherson et al. 2002). These findings are similar to ours, in that steeper slopes were a result of a lack of larger animals in the food web. Our slope values were different from *Z. marina* meadows in Denmark, potentially due to the methods used for size-based analyses; however, the authors found that the meadow with the steeper slope was representative of a more stable food web (Thormar et al. 2016). Only ambiguous comparisons can be made here due to the varying size ranges of animals analyzed and the type of size-based analyses applied. Furthermore, there are substantial differences in seagrass morphology (many of these studies focused on larger growing temperate species), and the focus has surrounded temperate, rather than tropical systems, where strong differences in biodiversity–ecosystem function are expected (Clarke et al. 2017). We recommend further studies in seagrass meadows and adopting a common size-based approach in order to generalize size spectra interpretations so that global seagrass research is enhanced and replicable across all locations (Duffy et al. 2019).

We have demonstrated that seagrass food webs, measured using the distribution of animal sizes, differ with structural habitat complexity. Analysis of size spectra has been proposed as a useful tool to evaluate changes in ecosystems in response to disturbance (Petchey and Belgrano 2010). Given the threats facing seagrass meadows (Grech et al. 2012) and the valuable ecosystem services they provide (Nordlund et al. 2016), we encourage further investigation into developing baseline size spectra for seagrass meadows. Baseline size spectra can be used to assess the health and value of different types of meadows, providing a tool for management to understand how different meadows might provide for

ecosystem services such as fisheries (Scott et al. 2018). Size spectra may also be indicative of the dynamic stability of food webs (Law et al. 2009), and so may help to evaluate how structural complexity can support ecosystem services. Our findings have highlighted the importance of understanding how structural complexity in seagrass meadows affects food webs and thus highlights the importance of human impacts that might simplify meadows.

Acknowledgments

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