

Evaluating the role of 3D complexity in shaping animal distributions and nutrient hotspots in coral reef environments

by

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## Abstract

Three-dimensional (3D) habitat complexity is a primary driver of species distributions and biodiversity across ecosystems. Animal communities, in turn, provide key ecological services that reciprocally modify habitat structure and heterogeneity, such as creating 'hotspots' of biogeochemical activity via nutrient recycling. To better define hotspots of ecological services from animal communities and identify conditions under which they form in habitats characterized by continuous measures of complexity, we studied relationships between 3D complexity, animal distribution, and nutrients on coral reefs— one of the most structurally complex and biologically diverse ecosystems on the planet. From May to July 2019, we measured large- and small-scale intra-habitat structural complexity (25 m<sup>2</sup>), surveyed the abundances of fish functional groups, and quantified nutrient composition of macroalgae across eight reefscapes (~2500 m<sup>2</sup>) within the Florida Keys, FL, USA. We first used these data in a hierarchical clustering analysis to group 80 species by five traits (diet, social level, body size, cryptic, activity period) related to species habitat use and feeding guild rather than taxonomic structure to generate mechanistic insights into consumer-habitat complexity relationships (Chapter 2). We evaluated relationships between the resulting trait-based functional groups (k=9) and four metrics of habitat complexity (large-scale: vertical relief, linked to prey refuge space; small-scale: vector ruggedness [VRM at 1cm], VRM deviation, and profile curvature, linked to availability of fish recruitment habitat and attachment sites for foraging resources). We found that functional groups respond variably to complexity. For example, schooling herbivores (Cluster 7) respond strongly to increases in small-scale complexity across reefscapes, but this effect is seen only in shoaling herbivores (Cluster 5) when small-scale complexity occurs in low-relief habitat. The general relationships we identified using species traits could provide a

predictive framework for understanding fish community responses as reefs lose or gain structural complexity globally, particularly to predict functional responses to small-scale habitat augmentation such as through coral restoration. Next, we explored the shape and magnitude of relationships between habitat complexity, fish-derived nutrient supply (nitrogen [N] and phosphorous [P]), and producer nutrient uptake (macroalgal %N and %P) across six of the reefs in the Florida Keys (Chapter 3). We found that intra-reef complexity influenced N and P supply across reefs but identified a threshold (~2.8 m of relief) above which this effect dampens. Macroalgal nutrient content was also non-linearly related to nutrient supply from fishes, with supplies exceeding  $\sim 250 \text{ mg N m}^{-2} \text{ day}^{-1}$  and  $\sim 35 \text{ mg P m}^{-2} \text{ day}^{-1}$  having no measurable effect on macroalgal content. Taken together, our findings demonstrate the importance of habitat structural complexity in shaping abundances of fish functional groups and as a driver of nutrient heterogeneity within reefs. Preserving 3D habitat complexity by protecting or augmenting (through restoration) foundational organisms that provide physical structure is critical to supporting diverse animal communities and the important functions they provide.

## **Preface**

This thesis is an original work by Noelle Helder. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Name “Effect of coral reef restoration on the spatial and temporal dynamics of reef fish community assemblages”, Study ID AUP00003176, April 26, 2019.

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# Chapter 1: Introduction

## 1.1 Background

Animal consumers play a crucial role in regulating community structure and function across ecosystems. In particular, herbivory and nutrient recycling by mobile consumers can mediate interactions between competing habitat-forming species and alter rates of primary production (van der Heide et al. 2012, Bozec et al. 2013). Studies ranging from arctic tundra to savannas demonstrate that plant-herbivore interactions can create intensively grazed ‘lawns’ irregularly dispersed amongst ungrazed regions, generating patches with unique communities and distributions (McNaughton 1984). Intensive grazing within these patches combined with excretion facilitates growth rates of nutrient-enriched vegetation, enforcing spatial heterogeneity across the landscape through positive feedbacks (Adler et al. 2001).

Yet animals both create spatial heterogeneity as well as respond to existing habitat characteristics, with distributions of animals tightly linked with resource availability including the quality and quantity of suitable habitat. The three-dimensional (3D) shape and structure of ecosystems created by both biotic habitat-forming foundation species (Dayton 1972), such as trees in forests, kelp fronds in kelp forests, or grasses in prairies, and by abiotic structures like mineral components and topography increases the available niche space for resident species, thereby supporting greater species abundances and diversity (Levins 1979, Huston and DeAngelis 1994). Habitat complexity is widely known influence key ecosystem dynamics (Calders et al. 2020) including predator-prey interactions (Hixon and Beets 1993) and population oscillations (Scheffer and De Boer 1995). The fundamental role of habitat complexity in structuring patterns of biodiversity and ecological functioning has been demonstrated in

terrestrial (Tews et al. 2004), freshwater (Taniguchi et al. 2003), and marine ecosystems (Pygas et al. 2020). Understanding potential feedbacks between animals and habitat complexity is of particular importance, as loss of complexity with increasing fragmentation and habitat degradation poses an extreme threat to dependent animal communities (Pratchett et al. 2008).

As one of the most biodiverse and productive habitats across the globe, coral reefs offer a unique opportunity to evaluate dynamics between structural complexity and animals (Reaka-Kudla 1997). Living scleractinian (stony) corals produce calcium carbonate layers that, over time, slowly build up into a complex structure that is reinforced by calcareous algae. Habitat complexity provided by this underlying geologic structure is augmented by living cover of hard and soft corals, sponges, and algae, which together support over 900 species of corals, 5000 species of fish, and even more invertebrates (Fisher et al. 2015). As foundational species, corals in shallow tropical seas provide microhabitat for a number of species and create large habitat structures known as reefs that mediate biophysical properties, including nutrient flows and wave activity (Hatcher 1997). The 3D structure of coral reefs also provide numerous ecosystem goods and services to people across the globe, both directly through coastline protection from erosion and indirectly through tourism and food provisioning (Cruz-Trinidad et al. 2014, Harris et al. 2018).

The effects of habitat complexity on fish assemblages may play a particularly important role in ecosystem dynamics on coral reefs, as fish comprise a significant proportion of the consumer biomass (Newman et al. 2006) and are a key link in the biogeochemical cycle (Meyer and Schultz 1985). Reef fish distribution is tightly linked with reef structure (Graham and Nash 2013), and in general increasing structural complexity supports greater fish abundances and diversity (e.g., Luckhurst and Luckhurst 1978). However, these relationships vary with numerous

factors, including the spatial scale considered, species life history, and the variable ways ‘complexity’ is measured (reviewed in Kovalenko et al. 2012, Pygas et al. 2020). The focus on taxon-specific relationships limits their applicability to regions without shared taxonomic structure, preventing a general understanding of critical scales and metrics driving fish community habitat associations. Further, losses of structural complexity through declines in living coral cover, coral bleaching events, and reef bioerosion can change species abundances, distributions, and alter the size-spectra of resident fish communities (Pratchett et al. 2008, Graham 2014, Alvarez-Filip et al. 2015). Because of the critical role of habitat structure in maintaining reef fish communities, a mechanistic understanding of generalized fish-habitat relationships at relevant spatial scales is sorely needed.

Reef fish communities provide key ecological services to maintain reef function, including through predator-prey dynamics, bioerosion, and herbivory (Brandl et al. 2019). Reef fish are also increasingly recognized as a key source of limiting nutrients in low-nutrient reef systems through excretion (Allgeier et al. 2017). In the Florida Keys, for example, reef fish contribute more than 25 times the amount of nitrogen at reef-wide scales than any other sources combined, including from anthropogenic eutrophication (Burkepile et al. 2013). Many species also translocate nutrients from other habitats through feeding migrations, thereby acting as a key source of nutrients to boost reef productivity (Meyer and Schultz 1985, Francis and Côté 2018). Further, fish aggregations within reefs can drive ecological productivity by generating a consistent supply of nutrients that is rapidly taken up by primary producers, generating ‘hotspots’ of productivity (Shantz et al. 2015). Because fish distributions are linked with habitat complexity, the spatial patterns of services like nutrient recycling from fishes will likely also vary with complexity. The few studies that have implicitly linked structure to fish-derived

nutrients have largely been limited to discrete units or isolated habitat patches (Layman et al. 2013, Shantz et al. 2015, Francis and Côté 2018), but the role of gradients of complexity in generating nutrient hot spots has not been evaluated. Because fish could facilitate coral growth and generate spatial heterogeneity in resource availability, changes in habitat use by fishes as reefs lose or gain structural complexity could be a critically underexamined feedback loop influencing coral reef resilience.

This thesis aims to provide insight on the extent to which habitat structural complexity influences interactions between consumers and their resources on coral reefs. Specifically, in Chapter 2 we evaluate the relationship between multiple habitat structural complexity metrics that capture both large and small-scale complexity derived from SfM photogrammetry and the distribution of trait-specific functional group abundances within continuous reefs. In Chapter 3, we explore relationships between habitat complexity and spatial variability in estimated nutrient supply from fishes, and the consequences for benthic communities. To do this, we use data collected from the Florida Reef Tract within the Florida Keys National Marine Sanctuary (FL, USA), that has experienced extensive declines in living hard coral cover as a result of numerous long-term stressors (Ruzicka et al. 2013) compounded by a recent multi-year disease event (Muller et al. 2020, Neely and Lewis 2020).

In Chapter 2, we pair fine-scale surveys of fish community distributions with multiple habitat structural complexity metrics derived from large-scale photogrammetry at 780 2-m<sup>2</sup> plots at eight reefscape locations. As an alternative to traditional fish functional groupings based solely on dietary niche widely used in the literature, we explore the effectiveness of multivariate clustering techniques on the fish community trait matrix in identifying clusters of species that may exhibit similar responses to habitat based on traits. We then model the abundance of each derived



functional group as a function of several metrics known to influence fish communities at multiple spatial scales: vertical relief, vector ruggedness, and profile curvature. This approach advances current knowledge by providing a fine-scale analysis of relationships across the seascape, and explicitly connects ecological mechanisms with trait-specific identities. We show that functional groups of fishes respond independently to measures of large (vertical relief) and small-scale (VRM, curvature) complexity independently, shedding light on the ecological mechanisms driving species associations with habitat.

To provide insight on the patterns of fish-derived nutrients within reefs as a function of habitat structure, in Chapter 3 we use bioenergetics models to estimate nitrogen and phosphorous supplies ( $\text{mg nutrient m}^{-2} \text{ day}^{-1}$ ) from fishes and pair these data with habitat structural complexity measures at six reefscales. We explore if patterns in nutrient excretion are explained by habitat complexity, and the extent to which nutrient supply can enrich the primary producer community. Importantly, we show that nutrient supply from fishes increases non-linearly with habitat complexity, with a threshold in supply occurring around  $\sim 2.8$  m of vertical relief. Similarly, we identified a potential threshold in the effect of supply on nutrient enrichment, with nitrogen supply above  $\sim 250 \text{ mg m}^{-2} \text{ day}^{-1}$  and phosphorous supply above  $\sim 35 \text{ mg m}^{-2} \text{ day}^{-1}$  having little to no effect on macroalgal nutrient content. Together, these insights provide important insights into the patterns and processes that create nutrient heterogeneity within complex reefscales and provide general relationships that could inform ecosystem management and restoration objectives.

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## **Chapter 2: Intra-habitat structural complexity drives the distribution of fish trait groups on coral reefs**

### **2.1 Introduction**

Habitat structural complexity, defined as the three-dimensional (3D) physical structure of an ecosystem, plays a critical role in mediating the dynamics of biological communities (e.g., Bell et al. 1991). Increasingly complex 3D structure provides more heterogenous habitat space, and thus a diverse array of refuge types, foraging opportunities, and additional resources which are linked to high species diversity and abundance (MacArthur and MacArthur 1961, Tews et al. 2004). Complexity also may mediate the location and intensity of important ecosystem processes, including predation and foraging efficiency (Hixon and Beets 1993, Pickett and Cadenasso 1995, Grabowski 2004).

Yet, despite being a major theme in ecological research, measuring and understanding the role of 3D complexity in driving major biotic processes has been challenging (Kovalenko et al. 2012). Lack of consistent terminology and the scale-dependent nature of observing complexity make it difficult to generalize findings across studies and systems. For example, often ‘habitat complexity’ is used interchangeably with terms like ‘habitat heterogeneity’ (e.g., Taniguchi et al. 2003) or ‘architectural complexity’ (Bozec et al. 2014), blurring the specific components under investigation. As an inherently scale-dependent process, both the elements and processes generating complexity depend on the spatial scale considered (Fulton et al. 2016). For example, a seagrass bed may be highly complex at the centimeter scale, but relatively homogenous at the scale of ~100 meters (Williams and Hill 2001). Habitat complexity is itself a multifaceted term including the diversity of structural elements as well as their size, abundance, and spatial arrangement (Tokeshi and Arakaki 2012). There remains a need to explicitly identify the most

important aspects of complexity structuring biotic assemblages and affecting ecological processes at appropriate spatial scales across ecosystems (McCormick 1994, Kovalenko et al. 2012).

Numerous studies have explored the effects of various measures of habitat complexity on the taxonomic diversity and structure of communities (e.g., MacArthur and MacArthur 1961, Roberts and Ormond 1987, Rosenzweig 1995). However, there is growing interest in evaluating relationships between structure and general ecological characteristics of organisms to facilitate prediction across systems. Species traits—defined as any biological attribute measurable for an individual and that can be used to assess how communities interact with their environment, as well as how functional diversity relates to ecosystem services (Villéger et al. 2017) - are increasingly used to understand the ecological roles of organisms across systems and offers a link between individual species and multiple ecosystem-level functions (Mouillot et al. 2013). For example, trait composition can mediate species interactions (Fortunel et al. 2016), shape ecological niches (Kraft et al. 2008), and influence responses to changes in the environment (McLean et al. 2019). Most frequently, species are classified by functional feeding groups, which has provided critical insights into complexity's role in mediating animal distributions and services (e.g., Osuka et al. 2018). Such analyses typically involve assigning individuals to groups based on only a single trait, such as trophic level. However, focusing on a single ecological characteristic may mask underlying mechanisms driving habitat selection, which may also be influenced by traits including body size (Harborne et al. 2011, Nash et al. 2013), mobility (Welsh et al. 2013), and other resource needs (Bozec et al. 2013). Trait-based approaches offer an advantage over species- or taxon-specific studies by uncovering generalities that are applicable

across regional boundaries and could facilitate forecasting community responses under new conditions (Mcgill et al. 2006, Stuart-Smith et al. 2013).

As one of the most biodiverse ecosystems on the planet, coral reefs are an excellent model system in which to test the utility of trait-based approaches for evaluating general animal-habitat relationships across scales. 3D complexity on reefs is provided by living corals at the scale of microhabitats (sub-meter; Jones et al. 1994, Agudo-Adriani et al. 2016) and augmented by the underlying geologic features and carbonate structural matrix built up over time at reef-wide to regional scales (~100s – >1000s of meters; Pittman et al. 2009). Reefs with increasing complexity at both scales support greater abundances, biomass, and species diversity of reef-associated organisms, and in particular fishes (e.g., Luckhurst and Luckhurst 1978, Bell et al. 1991, Graham and Nash 2013). Coral growth creates small crevices that may provide sites for fish spawning and recruitment at microhabitat scales (i.e. a few meters; Sale 1985), while carbonate ridges with high vertical relief can alter hydrodynamics, increase turbulence, and alter predator-prey dynamics at reef-wide scales (i.e. 100s – >1000s of meters; Alvarez-Filip et al. 2009, Hughes et al. 2010). At the scale of tens of meters (termed ‘meso-scale’; Harborne et al. 2011, 2012), abiotic and biotic conditions interact to drive spatially variable distributions and densities of coral colonies and underlying substrate compositions, yet this intra-reef variability is infrequently quantified in reef studies. Intra-reef complexity may mediate local dynamics by altering predation efficiency (Hixon and Beets 1993) and spatial patterns of herbivory (Ferrari et al. 2012) and fish-derived nutrients (Shantz et al. 2015). While intra-reef complexity is an important driver of reef fish distributions (Harborne et al. 2012), a comprehensive understanding of the aspects of complexity (i.e. measures and metrics) driving reef fish distributions and, by extension, the spatial array of services they provide, is lacking. Moreover, global declines in

living coral cover as a result of climate change and local disturbance events coupled with altered carbonate budgets resulting in annual net loss of carbonate structures has dramatically altered the complexity landscape of reef environments, with important consequences for biodiversity and ecosystem services derived from coral reef ecosystems (Hughes 1994, Alvarez-Filip et al. 2009, 2015). Uncovering specific metrics and scales at which complexity is functionally important for reef fishes is therefore a critical component in forecasting the productivity of reef ecosystems into the future.

To date, analyses of fish-habitat complexity relationships have primarily focused on differences among taxonomic and trophic groups (Rees et al. 2014, Ferrari et al. 2018, Fukunaga et al. 2020, González-Rivero et al. 2017, Ferrari et al. 2018). For example, carnivores may be attracted to high-relief habitat patches within the reef landscape for food and shelter (Ferrari et al. 2018). In contrast, herbivores may prefer less complex habitat space for feeding opportunities that offer an increased view of predators (Rilov et al. 2007, Oakley-Cogan et al. 2020). However, fish functions are increasingly studied from the perspective of an increasingly broad set of traits (e.g., Bellwood et al. 2003, 2004), such as body size, mobility, or morphology, as the abundance and distribution of traits can provide further insight into community assembly and function on coral reefs and uncover generalizable habitat selection patterns to improve cross-system predictive capacity (Mouillot et al. 2013, Graham et al. 2015). Differential types of habitat structure provided by a range of coral species and growth forms mediates the functional richness (including body size, diet, mobility, position, activity, and social) of fish communities at broad scales (i.e. between habitat types; Richardson et al. 2017b); however, a fine-scale understanding of how habitat complexity affects the distribution and abundance of fish functional groups on reefs is lacking.



Here we investigate the role of structural complexity in driving fish habitat use within continuous reef systems using a functional trait-based approach that can be generalized across communities with different taxonomic compositions. We focus specifically on intra-habitat variability in reef fish distribution (i.e. mesoscale, here 25 m<sup>2</sup> plots within ~2500 m<sup>2</sup> study areas, or ‘reefscapes’), as this is an important but overlooked scale influencing reef ecosystem function (Harborne et al. 2012). To explore trait-specific differences in habitat use, we used a hierarchical clustering analysis to identify groups of species with shared general morphological and behavioral traits that recur across species and are hypothesized to influence patterns of within-reef habitat use (**Table 1**). In particular, traits beyond feeding mode may influence an individual’s resource requirements and habitat preferences, ultimately mediating relationships with complexity (Gardiner and Jones 2010, Huijbers et al. 2011, Nash et al. 2013). For example, species that frequently school may be less dependent on habitat structure as a source of refuge from predators compared with solitary species. Additionally, groups with shared traits (such as size class, home range, body shape) may reflect important functions provided by resident fish communities (Guillemot et al. 2011). We modelled total abundance, richness, and the abundances of each resulting cluster based on these traits as a function of metrics of small- and large-scale habitat complexity representing different ecological features and resources for fishes (**Table 2**). As the structural integrity of coral reef habitats globally is expected to continue to decline over time, understanding how habitat influences species trait distributions is critical for our efforts to predicting and sustaining fish-derived services under future reef conditions. Assessing relationships through species traits may provide functional insights into the scales and drivers of reef fish distributions that can be applied across regions.

## 2.2. Methods

### 2.2.1. Study area and sampling design

To evaluate the role of intra-habitat variability in topographic complexity on the distribution and abundance of fish functional groups (defined by shared morphological and behavioural traits), we conducted a field study of habitat complexity and fish community structure at 784 plots located within eight reefscales (96 or 100 plots per reefscape) within the Florida Keys National Marine Sanctuary between June and July 2019 (FKNMS; **Figure 1**). FKNMS is located within the Florida Keys Reef Tract, which runs parallel to shore for 250 km from Miami to Key West along the southeastern Florida coast (**Figure 1**). The reef system extends 8 km seaward from the islands of the Florida Keys and includes a mosaic of reef/hard-bottom habitats, sand, seagrass, and mangroves (Keller and Causey 2005). Because we were interested in evaluating relationships on continuous reefs (as opposed to patch reefs, which represent small, isolated pockets of high complexity habitat interspersed within relatively flat sand and seagrass beds), we sited the eight focal areas within high-relief spur and groove habitat that occurs at a depth range of ~2-10 m within the larger reef system. At a seascape scale (i.e.  $>1 \text{ km}^2$ ), these habitats are classified broadly as ‘high-relief habitat’ but are composed of a mixture of high-relief spurs, low-relief reef, sand channels, and boulder-rubble fields that are likely to vary greatly in topographic complexity, and thus fish habitat use.

The locations of sites varied widely to capture natural gradients of complexity present within this system, with half the sites in areas of past coral restoration (i.e. replanting of live coral) and half that had not received restored corals (a design aspect for another study by the authors that had no influence on the research questions or analyses of intra-reef relationships examined here; see Data Analysis section). At each reefscape, we established permanent areas for fish

community surveys and habitat measurements with given dimensions depending on the reef structure: a 30x80 m survey area (2400 m<sup>2</sup>) consisting of 96 continuous 5x5 m plots (25 m<sup>2</sup> each), or a 50x50 m area (2500 m<sup>2</sup>) consisting of 100 continuous 5x5 m plots. The corners of each plot were marked and clearly labelled to ensure they were consistently located. All fish and habitat measurements were collected at the plot scale (25 m<sup>2</sup>; **Figure 2**).

## ***2.2.2. Assessing benthic habitat complexity***

### *2.1.1.1. Image acquisition and model building*

We conducted benthic habitat mapping once during the study period for each of the eight reefs, using in-water photogrammetry to build Digital Elevation Models (DEMs) for all 25 m<sup>2</sup> plots per reef (**Figure 1; Figure 2**), from which we extracted habitat complexity metrics that capture multiple scales of complexity (Lazarus and Belmaker 2021; details below). As overall average structural complexity was unlikely to change significantly during the two-month study period, we conducted habitat mapping only once for each site. Following the procedures of Burns *et al.* (2015) and Bayley and Mogg (2020), each reefscape was imaged across its full area (2400-2500 m<sup>2</sup>) by a diver swimming slowly ~2 m above the substrate (depending on visibility) in a lawn-mower pattern with a Canon EOS 80D camera with a fixed 50 mm lens and 8” hemispheric dome fitted in Ikelite underwater housing to capture high detail overlapping images of the benthic environment (aiming for 70-80% overlap). The focal length was set to 28 mm, and shutter speed and aperture were set to 1/250 and f/10, respectively. Cameras were programmed to take 1 photo per second, and images were stored in RAW file format. Reference points were deployed throughout the site for accurate georeferencing and scaling (x, y, z), and their depths recorded.

Following image color correction, we used Agisoft Metashape Professional v.1.4 (Agisoft LLC., St. Petersburg, Russia) to process the overlapping images and create spatially accurate three-dimensional (3D) models of each reefscape. Due to the large size of the imaged areas, each total reef area ( $\sim 2500 \text{ m}^2$ ) was subdivided into 3 or 5 sections for model building to improve computational and storage efficiency. Metashape software uses Brown's distortion model to calibrate and optimize the cameras and resolves the lens optical characteristics from the image metadata. Model processing for large scale reef imagery followed the protocols and guidelines of Fukunaga et al. (2020) and Bayley and Mogg (2020). We used this 3D workflow and photogrammetric techniques to produce two data products from each model: a digital elevation model (DEM; a raster representing the 3D elevation of the reef substrate as a grid of squares) and an orthophotomosaic (an orthorectified, high-resolution image created from the source photos).

To quantify topographical complexity for each of the  $25 \text{ m}^2$  plots per reefscape, we first exported whole DEMs and orthomosaics of each area at a raster cell resolution of 1 cm from Metashape and imported them as layers in ArcMap. We then clipped each individual  $25\text{-m}^2$  plot from the DEM using the location of plot corner tags (located in the orthomosaic) as markers (96 or 100 plots per reefscape  $\times$  8 reefscape = 784 plots total). If a corner tag could not be identified, the corner position was estimated at 5 m from the previous marker.

#### *2.1.1.2. Quantifying habitat complexity*

We quantified nine structural complexity metrics from each plot DEM that are likely to capture variability in small- and large-scale topographic features that are ecologically relevant for the biodiversity, distribution, and abundance of reef fish (González-Rivero et al. 2017, Ferrari et al. 2018, Fukunaga et al. 2020, Lazarus and Belmaker 2021) (**Table 1**). Small-scale metrics quantify distinct crevices and bulges within the landscape largely driven by variation in benthic

growth forms, and reflect the amount of available local shelter from predators (i.e. predator-free space; Friedlander and Parrish 1998, Gratwicke and Speight 2005, Lazarus and Belmaker 2021). Metrics included curvature (profile and planar), vector ruggedness (VRM), fractal dimensions, and slope (**Table 1**). Large-scale complexity metrics reflect depth variability across the landscape generated by large elements such as ridges and ledges. Such measures have been associated with high fish abundance, biomass, and richness (Ault and Johnson 1998, Rilov et al. 2007) and may promote ecological processes including recruitment and the growth of substrate attached organisms (Guichard and Bourget 1998). We calculated both vertical relief and surface complexity as large-scale complexity measures (**Table 1**). All metrics were calculated using a published script for R software (Fukunaga et al. 2019). Such metrics derived from DEMs of coral reef environments are suitable for classifying topographic variation of reef plots imaged from planar angles (Burns et al. 2015, Fukunaga and Burns 2020).

Many of the nine metrics were highly correlated with one another (**Figure 3**). We thus retained only 4 metrics that were not highly correlated ( $r < 0.6$ ) and captured complexity provided at both small and large scales (as described above) as predictors in subsequent modeling with fish community data: profile curvature, vertical relief, vector ruggedness (VRM) at 1cm, and VRM at 4 cm resolution (**Table 1**). Profile curvature quantifies the rate of change in slope parallel to the slope. Values of 0 represent a flat surface, while positive and negative values indicate a surface that is upwardly convex or concave, respectively. Profile curvature captures the variability in the surface topography created by small changes in structure provided by crevices and holes. As large values in both the positive and negative directions represent a more complex environment generally, we used the absolute value of profile curvature in our models. Vector ruggedness (VRM) describes the 3D dispersion orthogonal to the surface of the DEM. At

1 cm resolution, VRM accurately captures the microscale complexity of interstitial spaces within complex growth forms such as branching corals, while the complexity of mounding and tabulate growth forms is captured by VRM at 4 cm (Fukunaga et al. 2020). Because VRM at 1 and 4 cm was highly correlated, we used VRM at 1cm as well as the deviation between resolutions (VRM at 4cm – VRM at 1cm; Fukunaga et al. 2020). Lastly, we included vertical relief to capture the topographic variation provided by spurs and large coral heads common in this continuous reef habitat (Lazarus and Belmaker 2021).

### ***2.2.3. Assessing fish community structure***

#### *2.2.3.1. Fish observational surveys*

To quantify reef fish community structure in each of the 25-m<sup>2</sup> plots per reefscape (**Figure 2**; n=8 reefscapes), we conducted underwater visual surveys on which we recorded the species, abundance, and total length to the nearest centimeter of all individuals  $\geq 15$  cm. Smaller size classes of fish were excluded from our surveys, as well as large-bodied pelagic and semi-pelagic species not typically associated with the reef environment (e.g. tarpon, sharks, rays) as we were primarily interested in exploring relationships with species that contributed significantly to community abundance and biomass at the spatial scale of our observations. To survey the study plots, three divers trained in Caribbean fish species identification and sizing first simultaneously deployed parallel transect lines that divided the gridded study area into thirds. The transect lines served as guides for organizing the order of plots for which data were collected by the three observers, which reduced the time it took to collect data for the entire reefscape while minimizing the disturbance of fishes in adjacent plots due to the presence of multiple divers on the site. Transects were left undisturbed for five minutes to allow the fish community to adapt to the disturbance. The divers then slowly and methodically surveyed each 5x5 m plot

on either side of their transect line, counting and sizing all fish within a single plot before continuing (20 or 32 plots per diver per survey). Large, conspicuous individuals in each plot were first identified, sized, and counted, followed by a thorough search of the habitat for inconspicuous individuals that may be camouflaged by the substrate or sheltering within the habitat. All fish  $\geq 15$  cm total length that entered the quadrat during the survey period were counted and sized to the nearest centimeter. Large groups of roving fishes that swam through the study area but did not associate with the habitat for longer than 30 seconds and were clearly migrating to a different part of the reef, such as large schools of parrotfishes and tangs, were recorded as ‘transient’ and excluded from further analysis because we were explicitly interested in resident fish relationships with reef habitat. Large schools of resting fishes (i.e. stationary when observed) such as grunts (Haemulidae) and snappers (Lutjanidae) were common in our surveys. To ensure accurate estimates of abundance, schools were filmed with GoPro cameras and their counts verified. Care was taken to ensure that individuals that moved between plots during surveys were only recorded once. During surveys, the divers moved slowly to reduce the likelihood of “herding” or frightening fish into or out of each plot and little diver-induced migration was observed. We conducted this survey procedure approximately every 5 days over the study period (n = 4-6 surveys per plot per reefscape; 4308 total plot-level observations).

#### 2.2.3.2. *Fish traits cluster analysis*

To explore trait-specific fish relationships with habitat complexity, we classified each species observed in terms of five behavioural and morphological traits hypothesized to influence adult fish habitat use at the spatial scale considered: diet, activity period, gregariousness (aggregation behaviour), size class, and cryptic behavior (**Table 2**). We initially included water

column position (benthic, demersal, and pelagic), but the trait was excluded from further analysis as ~97% of the species we observed were classified as ‘demersal’. We expected that species with shared traits may share similar habitat and resource needs and thus respond to measures of habitat complexity similarly. All trait data were extracted from FishBase (2019). We conducted all data visualization and statistical analyses in R Version 4.0.2 (RStudio Team 2020). To identify discrete groups of species that might respond to within-reef topographic complexity similarly based on combinations of shared traits, we used a clustering technique to generate functional habitat use groups from our completed species by trait matrix. We first calculated a species-by-species functional distance matrix using Gower’s distance to determine similarities/dissimilarities among species (Pavoine et al. 2009) using the *cluster* package (Maechler et al. 2019). We then used a hierarchical agglomerative clustering analysis with complete linkages to categorize the 80 fish species into groups (clusters) based on the distance matrix using function *hclust* (‘stats’ package; R Core Team 2020; Alboukadel Kassambara 2017). The ideal number of clusters was identified with respect to dendrogram balance and evaluated by comparing cluster numbers using the Silhouette Index (Rousseeuw 1987) as a measure of internal evaluation. The ideal cluster number in our analysis separated our fish trait data into nine discrete trait groups (hereafter referred to as functional groups for simplicity) based on five traits for the 80 observed species (**Figure 4; Appendix A2.2**).

#### ***2.2.4. Modeling fish-habitat relationships***

We evaluated relationships between fish community structure (measured as total abundance, species richness, and the abundance or presence/absence of functional groups [response variables]) and four measures of intra-reef habitat complexity (explanatory variables) capturing both small (VRM at 1cm, VRM deviation at 4cm, absolute profile curvature) and large-scale



processes (vertical relief; ) using generalized linear mixed effects models (GLMMs). We chose GLMMs to account for the hierarchical sampling design of location (plots nested within reef sites), repeated surveys of each plot, potential zero inflation and overdispersion, and potential spatial autocorrelation.

We modelled total fish abundance (i.e. all species pooled) and the abundances of six functional groups identified from the cluster analysis using a negative binomial distribution, which is appropriate for overdispersed count data (Zuur et al. 2009). We modelled fish species richness using a Poisson distribution, which is appropriate for non overdispersed counts (Nelder and Wedderburn 1972). We modelled the presence (binary; 1/0) of large, solitary, nocturnal carnivores (Cluster 7) with logistic regression due to limited observations. Clusters 8 and 9 were excluded from analysis as they were not observed in great enough abundances to model appropriately, resulting in a total of 8 models. All models were fit using the packages lme4 (Bates et al. 2013) and glmmTMB (Brooks et al. 2017).

In each model, we included the four habitat complexity metrics (vertical relief, VRM, VRM deviation, absolute profile curvature) as continuous fixed effects. Additionally, we hypothesized that the effects of small-scale complexity on species distributions might vary depending on large-scale complexity (vertical relief). For example, herbivores may be positively associated with small-scale complexity provided by corals and other benthic growth forms in low-relief reef flats due to additional foraging opportunities paired with an open field of view, but may be uninfluenced or negatively influenced by small-scale complexity in high-relief habitats due to the added risk of predation at high relief (Ferrari et al. 2018). To test these hypotheses, we included three interaction terms in each model in addition to the four main effects: the interaction between relief and VRM at 1cm, relief and VRM deviation at 4 cm, and relief and absolute profile

curvature. Prior to analysis, all continuous explanatory variables were centered and scaled using the ‘scale’ function in base R (R Core Team 2020).

To account for potential correlation among fish abundances from plots within the same study area (i.e. reefscape) and for repeated surveys at each plot, we first included reefscape (n=8) and visit (repeated surveys; n=4-6) as crossed random effects in each full model. If no significant improvement in model fit was observed, the random effects were dropped from the model. Site always improved model fit and was maintained in each subsequent model, while visit was removed from a subset of the final models. Models were simplified using backwards selection following the principle of parsimony, and tested using Akaike’s Information Criterion to determine the best model (Zuur et al. 2009, Bolker et al. 2009). Model assumptions were checked using residual plots with the DHARMA package (Hartig 2020). Assumptions of independence (spatial autocorrelation) were assessed visually with spline correlograms (**Appendix A2.1**).

## **2.3. Results**

### ***2.3.1. Clustering fish habitat use traits***

We observed a total of 32,754 fish from 80 species and 21 families across 784 plots at the eight focal reefs during the two-month study period. The most abundant species were *Haemulon flavolineatum*, *H. aurolineatum*, *Sparisoma aurofrenatum*, *H. sciurus*, *Acanthurus coeruleus*, and *Sparisoma viride* (> 2000 individuals each). Haemulidae was by far the most abundant family (12,254 individuals), followed by Scaridae (6,237) and Acanthuridae (4,575).

The 80 fish species grouped into nine clusters based on the five behavioural and morphological traits we hypothesized affected habitat use (**Figure 2.4**), with the smallest cluster

including only two species classified as carnivores active both diurnally and nocturnally (**Figure 2.4; Appendix A2.2**). The remaining eight clusters ranged in size from five to 15 species (**Figure 2.4**). Clusters 1 (non-cryptic, diurnal invertivores) and 5 (shoaling herbivores) were the most abundant groups with > 7,000 individuals observed. The smallest groups (Clusters 8 and Cluster 9) included < 100 observations across all surveys and was subsequently excluded from analysis, resulting in a total of seven functional groups used as response variables in models relating fish community structure and habitat complexity.

### ***2.3.2. Modeling fish habitat relationships***

Vertical relief, which characterizes the large-scale depth variation within a plot, positively influenced total fish abundance, species richness, and the abundance of five of the seven functional clusters (**Table 2.3; Figure 2.5, 2.6**). The effect of relief was largest for large-bodied carnivores, both nocturnal (Cluster 7) and diurnal (Cluster 5), followed by the abundance of small, cryptic invertivores (Cluster 2). Relief was not a significant predictor for either cluster of herbivores (Clusters 3 and 5), and was only weakly significant ( $p < 0.05$ ) in explaining abundances of social (i.e. schooling or shoaling) diurnal invertivores (**Table 2.4**).

Absolute profile curvature (here, ‘curvature’), which characterizes small-scale topographical variation due to crevices and holes within the reef structure (**Table 2.2**), was an important explanatory variable for both fish community-level responses (total abundance and species richness), but for only three functional groups (**Table 2.4**). Curvature was negatively related to total abundance and species richness (**Table 2.4**). Curvature had a strong but highly variable positive effect on the abundances of social, diurnal invertivores (Cluster 1) and large, diurnal carnivores (Cluster 4; **Figure 2.6**), but was negatively related to the abundance of cryptic

invertivores (Cluster 2; **Figure 2.6**). Small-scale complexity as measured by curvature was not an important driver of the abundances of schooling, non-cryptic species (Cluster 3), shoaling herbivores (Cluster 5), or schooling, nocturnal invertivores (Cluster 6), nor the presence of nocturnal carnivores (Cluster 7; **Table 2.4**).

We identified a significant interaction between relief and absolute profile curvature for three of the nine fish trait groups, with the effect differing greatly between functional groups (**Table 2.4; Figure 2.6**). The abundance of cryptic invertivores (Cluster 2) increased with greater curvature in high relief plots, but the effect of curvature on abundance was diminished in low relief plots (**Appendix A2.6C**). In contrast, the abundances of social, diurnal invertivores (Cluster 1; **Appendix A2.5C**) and diurnal carnivores (Cluster 4) increased with large curvature values in low relief plots but had no effect on abundances as relief increases (**Appendix A2.7**).

Microscale complexity measured by VRM at 1cm was positively associated with total abundance and species richness, and the abundances of all but two functional groups: both diurnal (Cluster 4) and nocturnal, cryptic carnivores (Cluster 7; **Table 4**). VRM at 1cm had the greatest positive effect on the abundance of solitary, cryptic invertivores and smallest for richness (**Table 2.4**). We also found significant evidence for an interaction between relief and VRM at 1cm for total fish abundance and four of the fish functional groups (abundances of social invertivores [Cluster 1]; solitary, cryptic invertivores [Cluster 2]; shoaling herbivores [Cluster 5]; and schooling, nocturnal invertivores [Cluster 6]; **Table 2.4**), with VRM at 1cm positively influencing abundances at low relief plots, but the effect diminishing or becoming negative as relief increased (e.g., **Appendix A2.5A**).

Lastly, VRM deviation, which characterizes mesoscale complexity of boulder-type benthic growth, was a significant predictor of eight fish metrics (**Table 2.4**). As VRM at 4 cm increased, total fish abundance, species richness, and the abundances of all but the nocturnal carnivores (Cluster 7) increased (**Table 2.4**). VRM deviation had the strongest influence on the abundances of cryptic carnivores (Cluster 2) and large-bodied, diurnal carnivores (Cluster 4), and the weakest influence (as measured by the magnitude of the coefficients) on species richness and abundances of shoaling herbivores (Cluster 5; **Figure 6**). The interaction between relief and VRM deviation was also significant for total fish abundance, species richness, and the abundances of Clusters 1, 2, 5, and 6 (**Table 4**). The positive effect of VRM deviation increased as relief decreased (e.g, **Appendix A2.6B**), but for species richness and abundances of Clusters 1, 5, and 6, the VRM effect was diminished or became slightly negative in high relief plots (**Appendix A2.4B, C; A2.8B, A2.9B**).

## 2.4. Discussion

Understanding functionally important relationships between habitat complexity and fish assemblages is a key issue in coral reef ecology, particularly in light of rapid changes in reef structural complexity over the last few decades (Alvarez-Filip et al. 2009). By investigating links between quantitative metrics that capture unique aspects of 3D structural habitat complexity and the abundance of species possessing unique combinations of traits (diet, diel activity, gregariousness, body size, and cryptic behavior), we demonstrate that multiple metrics of structural complexity are important predictors of variation in fish community composition and abundance at meso-scales (i.e. 25m<sup>2</sup>) within reef habitats. Importantly, we found that the attributes of structural complexity driving fish abundances vary substantially between trait-based functional groups (**Table 2.4; Figure 2.6**). Numerous studies describe the importance of scale in understanding how

biotic communities use space in complex environments (Tokeshi and Arakaki 2012, Rees et al. 2014, Ferrari et al. 2018). In a recent review, Lazarus et al. (2021) found that more than half of published studies in coral reef systems incorporated only a single measure of habitat complexity and instead, encouraged the use of complementary indices that capture cross-scale heterogeneity. In the present study, we found that sub-groups of species (i.e. trait clusters) responded to both large (vertical relief) and small-scale (VRM and curvature) intra-reef complexity indexes independently (**Figure 2.6**). It appears that reef fishes respond to habitat at a range of spatial extents and are therefore influenced by multiple aspects of habitat structure, highlighting the need to consider multiple metrics to improve ecological predictions (González-Rivero et al. 2017).

A growing body of work identifies variable responses to habitat complexity across trophic sub-groups of reef fishes (e.g., Rees et al. 2014, Ferrari et al. 2018, Fukunaga and Burns 2020). Broadly, our results align with assumptions that increasing complexity positively influences fish abundance, but we also demonstrate the utility of incorporating a range of behavioral and morphological traits beyond trophic group to uncover unique environmental relationships. For example, vertical relief is an indicator of gross reef morphology (Luckhurst and Luckhurst 1978) and, in spur-and-groove type habitat like that sampled in this study, reflects topography such as that provided by ridges and large coral colonies (Lazarus and Belmaker 2021). The effect of relief was comparatively large for both nocturnal-cryptic (Cluster 7) and diurnal (Cluster 4) carnivores, highlighting a shared preference for high relief features within the broader forereef habitat (Connell 1997; **Appendix A2.3A**). This aligns with previous studies where large-bodied carnivores may benefit from high-relief habitat space, likely because it increases their prey availability (Sale 1985). Nocturnal species (Cluster 7) also likely take advantage of available shelter options within high-relief ridges for refuge during the day (Kerry and Bellwood 2015).

In contrast, clusters dominated by schooling or shoaling herbivores (Cluster 3 and Cluster 5) were positively influenced only by increasing small-scale complexity (**Table 2.4**). Both clusters were positively associated with complexity provided by benthic growth forms (VRM 1cm and VRM deviation at 4cm), but, importantly, differed in their responses across levels of vertical relief (**Appendix A2.3CB**). While schooling herbivores (Cluster 3) were positively associated with both measures of VRM across all plots, shoaling herbivores (Cluster 5) were positively influenced by VRM only in low-relief plots. This result complements previous literature that indicates a potential trade-off between the quality of food and predation (Catano et al. 2016), as shoaling herbivores may preferentially feed in low relief habitat ('reef flats') that has a greater field of view of predators as opposed to feeding on or near high-relief features with higher quality food (Ferrari et al. 2018, Oakley-Cogan et al. 2020). The main differentiating factor between these clusters was gregariousness: all species schooled in Cluster 3, while all species in Cluster 5 were classified as 'shoaling' (sometimes in groups, but often solitary). Increasing relief may result in increased exposure to predators, and previous literature has shown that parrotfishes may avoid the highest relief habitat spaces to avoid predation (Rilov et al. 2007). In one of the few other studies to explicitly explore meso-scale complexity, Harborne et al. (2012) also identified a non-linear relationship between total parrotfish biomass and mean coral height within a plot, suggesting that while parrotfishes prefer the algal food sources on tall colonies, they may risk exposure from moving too high into the water column. Schooling may offer additional protection from predators, allowing these species (Cluster 3) to take advantage of their preferred complexity provided by benthic cover regardless of exposure levels (i.e., increasing vertical relief). Disentangling drivers of herbivore distributions within reefs is a priority to maintain ecosystem function due to the benefits of herbivory to corals by removing algal

biomass (Adam et al. 2015). Our approach identifies unique relationship within the broader herbivore functional class, highlighting trait-specific differences.

Distributions of reef fishes have strong links with benthic composition, usually measured by coral cover or diversity, which is often attributed to shelter provision for small fishes and to food resources for specialized species that feed on living coral (Chabanet et al. 1997, Pratchett et al. 2008, Coker et al. 2017, Darling et al. 2017). At different resolutions, vector ruggedness quantifies the micro-complexities provided by branching corals (VRM at 1cm) and the small-scale complexity provided by encrusting or table (VRM at 4 cm) coral growth forms in the Northwestern Hawaiian Islands (Fukunaga and Burns 2020a, b). The relationships we observed are comparable to those from Hawaii; however, it is less clear what specific benthic components may be driving the differences in complexity in this system because in the Florida Keys, stony corals are no longer the dominant benthic group on many reefs. In fact, shallow forereef habitats in the northern Keys where our study took place generally have <2-5% living coral cover (Ruzicka et al. 2013). Instead, the complexity provided by biotic organisms is largely derived from macroalgae, soft corals, encrusting zoanthids, and sponges. Whereas many studies explore relationships with coral and/or algal cover, there is limited data evaluating the complexity provided by other benthic groups as related to associations with fish assemblages, particularly with soft corals such as gorgonians, despite their increase in densities in hard-bottom reef habitats (Norström et al. 2009, Ruzicka et al. 2013). While typically assumed to be poor habitat for reef fish, recent evidence suggests that this assumption may be undue: Epstein and Kingsford (2019) examined relationships identified positive relationships between soft corals and fish species richness, and that fish communities regularly utilized soft coral habitat as a source of both food and shelter. Taken together, their work and our results suggest that benthic habitats



dominated by other benthic organisms in addition to living stony corals can similarly increase benthic complexity and can influence reef fish community distributions.

Species traits are increasingly recognized for their role in governing ecosystem function (de Bello et al. 2010, Rosenfield and Müller 2020). On shallow coral reefs, fish functions (i.e. predation, nutrient cycling, and bioerosion) are ensured through a surprisingly low number of core trait combinations across the globe (Graham et al. 2015, McLean et al. 2021), which indicates the critical need for and value of considering traits-based approaches within management across regions. The relationships identified here could provide a useful predictive tool to understand group-specific responses by fishes that are functionally similar but distantly related as reefs lose or gain structural complexity globally. In the context of coral restoration efforts, group-specific changes in fish communities is an important aspect of restoration success (Seraphim et al. 2020, Ladd and Shantz 2020). For example, our results show that functional groups, such as schooling herbivores (Cluster 7), could respond to small increases in complexity, such as that provided by coral outplants, while others, such as schooling and solitary invertivores (Clusters 6; Cluster 2) and shoaling herbivores (Cluster 5) may respond positively only to outplants added to low-relief habitat. Restoration impacts on fish communities has so far been limited (Ladd et al. 2019) and less than 6% of projects monitor fish communities post restoration (Boström-Einarsson et al. 2020). A predictive framework that incorporates globally shared (McLean et al. 2021) and easily accessible species traits information (e.g., FishBase.com) could be a key tool to better understand the scope of influence that moderate increases in habitat complexity through outplanting could have on reef fish communities.

Identifying key habitat features that influence abundances is imperative to defining conservation targets, particularly when relationships are transferable across locations (Ferrier

2002). Beyond herbivory, the functional groups identified here provide a range of other key ecological services within reefs, including predation (Cluster 4, 7; Boaden and Kingsford 2015), bioerosion (Cluster 5; Adam et al. 2015), and nutrient recycling (all clusters; Shantz et al. 2015, Allgeier et al. 2017), the locations and intensities of which shape intra-reef heterogeneity. Based on our results, we expect the distributions and therefore the resulting spatial patterns of fish functions to vary with different aspects of structural complexity across reefscapes. For example, schooling invertivores (Cluster 6) that concentrate nutrient supply locally, creating ‘hot spots’ of limiting nitrogen and phosphorous (Shantz et al. 2015, Francis and Côté 2018), were positively associated with high-relief habitat, but also with small-scale complexity in low-relief habitat, indicating that both small and large-scale complexity could serve as aggregation points for schooling invertivores and thus shape patterns of local nutrient supply. Local management decisions to preserve (through protection e.g. marine protected areas) and/or augment both small (e.g. coral outplanting) and large-scale complexity (e.g. artificial structures) could take advantage of fine-scale habitat associations to target the specific processes and functions that most need protection/restoration.

Trait-based approaches are a rapidly developing research area in ecology (Webb et al. 2010). Such approaches to organism-environment relationships may be advantageous to taxonomy because they offer improved mechanistic understanding (Keddy 1992, Townsend and Hildrew 1994) and greater generality because they could be applied across regions (Verberk et al. 2013). Our results show potential usefulness of incorporating multiple species traits for evaluating fine-scale responses to habitat structure. The traits included and potential processes driving our observations, such as predatory-prey dynamics and grazing resource availability, are also widely important in shaping animal distributions across systems. Because this approach is

based on commonality in traits rather than species identities, our results could facilitate regional and potentially cross-system comparisons to isolate the mechanisms driving species-environment relationships (Verberk et al. 2013). As habitat loss, fragmentation, and homogenization will continue to threaten biodiversity and productivity across habitats, establishing generalizable relationships with habitat could support more effective management, conservation, and prediction to preserve ecosystem function.

**Table 2.1** Description of traits used in clustering analysis. *Category* describes the ecological relevance of the trait considered. *Levels* indicates the possible trait levels assigned to a species for that trait. *Description* defines each level.

<b>Trait</b>	<b>Category</b>	<b>Levels</b>	<b>Description</b>
diet	Trophic niche/ food acquisition	Herbivore, browser	Feeds on macroalgae
		Herbivore, excavator	Feeds on epilithic algal turf and removes carbonate structure
		Herbivore, scraper	Feeds on epilithic algal turf by closely cropping
		Herbivore, grazer/detritivore	Feeds on algal turf and detritus
		Planktivore	Feeds on plankton
		Omnivore	Feeds on multiple food items (animal and plants)
		Invertivore	Feeds on invertebrates
		Carnivore (Mixed) Piscivore	Feeds on fish and invertebrates Feeds on fish and invertebrates
activity	Habitat use	Diurnal	Active mostly during the day
		Nocturnal	Active mostly at night
		Both	Active during both
social	Predator-prey avoidance	Solitary	Generally found alone
		Shoaling	Often seen in groups, sometimes alone
		Schooling	Typically seen in groups
position	Habitat use	Benthic	Species spend most of their time near the benthos
		Demersal	Species generally swimming just above the benthos
		Pelagic	Species generally swimming high above benthos
cryptic	Habitat use; predator-prey avoidance	1	Documented to exhibit cryptic behaviour (i.e. hiding within the reef structure)
		0	Does not exhibit cryptic behaviour

**Table 2.2** Summary of habitat complexity metrics calculated in this study. Metric lists the name used for each metric, as well as abbreviations used in this paper. Explanation describes what each metric quantifies. Calculation is how the metrics are calculated from a DEM raster. Ecological implications describe the possible ecological inferences from each metric. Reference cites the initial study that formulated the metric and/or derived applications.

<b>Scale</b>	<b>Metric</b>	<b>Explanation</b>	<b>Calculation</b>	<b>Ecological Implication</b>	<b>Reference</b>
<i>Large scale:</i>	Vertical Relief	Range of depth variation within a DEM; vertical relief	Maximum z value within the DEM window - minimum z value	Large values reflect variation provided by large-scale topographic variation, such as ridge or 'patch' type reefs within the landscape	Luckhurt and Luckhurst 1978
	Surface complexity	Ratio of convoluted area to planar of DEM surface; otherwise called surface or 3-D rugosity; resolution = grain size of DEM; extent = area; this is analogous to the traditional 'chain-and-tape' rugosity measure	3D area/2D area	High values indicate a heterogenous profile. Similar values can be achieved with different elements of complexity (i.e. depth variation, ruggedness).	Risk 1972
<i>Small scale:</i>	Vector Ruggedness Measure (VRM)	Combination of variation in slope and orientation	3D vector dispersion of a DEM cell calculated from a 3x3 neighbouring cell window, then averaged for all cells within the plot	Changes with resolution considered. At high resolution (1-2 cm), VRM captures microscale complexity provided by branching growth forms. At 4 cm resolution, VRM quantifies moderate complexity provided by less complex growth forms including boulder and tabulate corals. At >4cm resolutions, VRM may capture overall topographical variation of a coral reef.	Sappington, Longshore, and Thompson 2007; Fukunaga et al. 2020a
	VRM deviation (4cm)	Difference in VRM measured at different resolutions	VRM at 4cm resolution - VRM at 1cm resolution	Smaller values of deviation reflect a plot with more complex branching growth generating more micro-complexity, larger values reflect a plot with more complexity provide by less complex growth forms, such as boulder corals. .	Fukunaga et al. 2020b

Slope	Rate of change between a DEM cell and its neighbours, identifies the steepest direction downhill	Maximum rate of change in slope between a DEM cell and its neighbours in a 3x3 window	Larger values reflect steeper terrain, smaller values reflect less-steep terrain.	Walbridge et al. 2018
Curvature	Rate of change in slope in various directions	calculated from a 3x3 neighbouring cell window, then averaged for all cells within the plot DEM	Captures structural complexity of fine-scale holes, ridges, and crevices in reef topography. Positive values reflect complexity from upward convexities, negative values reflect concavities, and 0 is a flat surface.	Zevenbergen and Thorne 1987
<i>Profile</i>	Degree of concavity/convexity parallel to the direction of minimum slope	calculated from a 3x3 neighbouring cell window, then averaged for all cells within the plot DEM	See above.	Zevenbergen and Thorne 1987
<i>Planar</i>	Degree of concavity/convexity perpendicular to the direction of max slope	calculated from a 3x3 neighbouring cell window, then averaged for all cells within the plot DEM	See above.	Zevenbergen and Thorne 1987
Fractal dimensions (D)	A (unitless) measure of surface roughness with values between 2-3. Captures the rate of change of surface complexity across resolutions	$D = \log(N) / \log(r)$	Higher fractal dimension reflects a habitat with more microhabitats that is independent of resolution	Sugihara and May 1990

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**Table 2.3** List of species included in each of k=9 clusters resulting from hierarchical clustering analysis. *Cluster* includes the number and dominant traits for each cluster used to simplify naming in the text.

<b>Cluster</b>	<b>Family</b>	<b>Species</b>
1: non-cryptic, social invertivores	Balistidae	<i>Canthidermis sufflamen</i>
	Chaetodontidae	<i>Chaetodon ocellatus</i>
	Diodontidae	<i>Diodon holocanthus</i>
	Haemulidae	<i>Haemulon aurolineatum</i>
		<i>Haemulon plumierii</i>
		<i>Haemulon sciurus</i>
	Labridae	<i>Bodianus rufus</i>
		<i>Halichoeres radiatus</i>
		<i>Lachnolaimus maximus</i>
	Mullidae	<i>Mulloidichthys martinicus</i>
		<i>Pseudupeneus maculatus</i>
	Ostraciidae	<i>Acanthostracion polygonius</i>
		<i>Lactophrys triqueter</i>
	Pomacanthidae	<i>Holacanthus ciliaris</i>
Serranidae	<i>Serranus tigrinus</i>	
2: cryptic invertivores	Chaetodontidae	<i>Chaetodon capistratus</i>
		<i>Chaetodon sedentarius</i>
		<i>Chaetodon striatus</i>
	Diodontidae	<i>Diodon hystrix</i>
		<i>Anisotremus surinamensis</i>
		<i>Haemulon flavolineatum</i>
	Holocentridae	<i>Holocentrus adscensionis</i>
		<i>Sargocentron vexillarium</i>
	Pomacanthidae	<i>Holacanthus tricolor</i>
	Sciaenidae	<i>Equetus punctatus</i>
		<i>Odontoscion dentex</i>
		<i>Pareques acuminatus</i>
	3: schooling non-cryptic herbivores	Acanthuridae
<i>Acanthurus coeruleus</i>		
<i>Acanthurus tractus</i>		
Carangidae		<i>Carangoides ruber</i>
Haemulidae		<i>Haemulon macrostomum</i>
		<i>Haemulon striatum</i>
Kyphosidae		<i>Kyphosus cinerascens</i>
		<i>Kyphosus sectatrix</i>
		<i>Kyphosus vaigiensis</i>
Labridae		<i>Clepticus parrae</i>
4: diurnal carnivores	Lutjanidae	<i>Lutjanus analis</i>
		<i>Lutjanus griseus</i>
		<i>Lutjanus jocu</i>

	Serranidae	<i>Epinephelus morio</i> <i>Epinephelus striatus</i> <i>Mycteroperca bonaci</i>
	Sparidae	<i>Calamus calamus</i>
	Sphyraenidae	<i>Sphyraena barracuda</i>
	Synodontidae	<i>Synodus intermedius</i>
5: shoaling herbivores	Labridae	<i>Halichoeres bivittatus</i>
	Lutjanidae	<i>Lutjanus mahogoni</i>
	Pomacanthidae	<i>Pomacanthus arcuatus</i> <i>Pomacanthus paru</i>
	Scaridae	<i>Scarus coelestinus</i> <i>Scarus coeruleus</i> <i>Scarus guacamaia</i> <i>Scarus iserti</i> <i>Scarus taeniopterus</i> <i>Scarus vetula</i> <i>Sparisoma aurofrenatum</i> <i>Sparisoma chrysopterus</i> <i>Sparisoma rubripinne</i> <i>Sparisoma viride</i>
6: schooling, nocturnal invertivores	Haemulidae	<i>Anisotremus virginicus</i> <i>Haemulon album</i> <i>Haemulon carbonarium</i> <i>Haemulon chrysargyreum</i> <i>Haemulon parra</i>
	Lutjanidae	<i>Lutjanus synagris</i> <i>Ocyurus chrysurus</i>
7: cryptic, nocturnal carnivores	Muraenidae	<i>Gymnothorax funebris</i> <i>Gymnothorax miliaris</i> <i>Gymnothorax moringa</i>
	Serranidae	<i>Cephalopholis cruentata</i> <i>Rypticus saponaceus</i>
8: solitary omnivores	Monacanthidae	<i>Aluterus scriptus</i> <i>Cantherhines macrocerus</i> <i>Cantherhines pullus</i> <i>Acanthostracion</i>
	Ostraciidae	<i>quadricornis</i> <i>Lactophrys bicaudalis</i> <i>Lactophrys trigonus</i>
9: diurnal/nocturnal cryptic carnivores	Aulostomidae	<i>Aulostomus maculatus</i>
	Lutjanidae	<i>Lutjanus apodus</i>

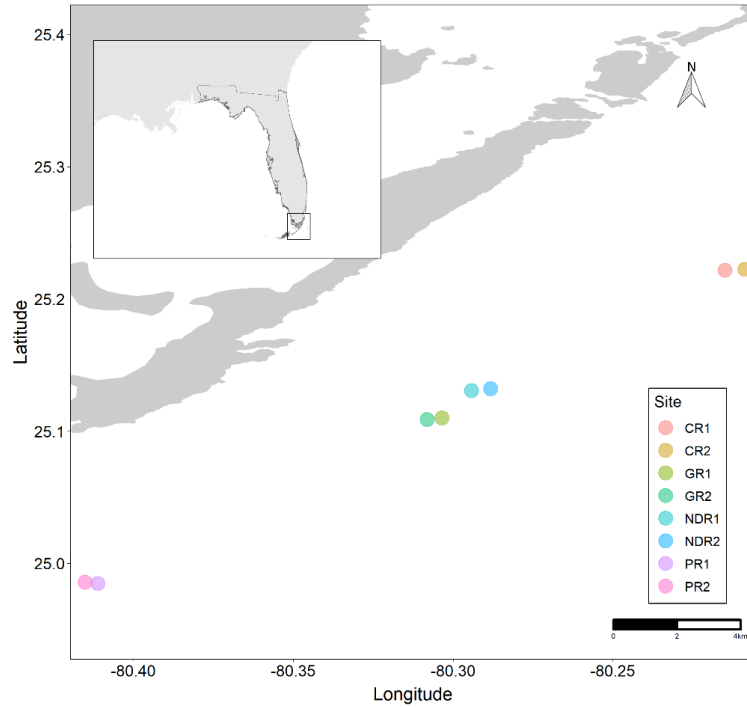
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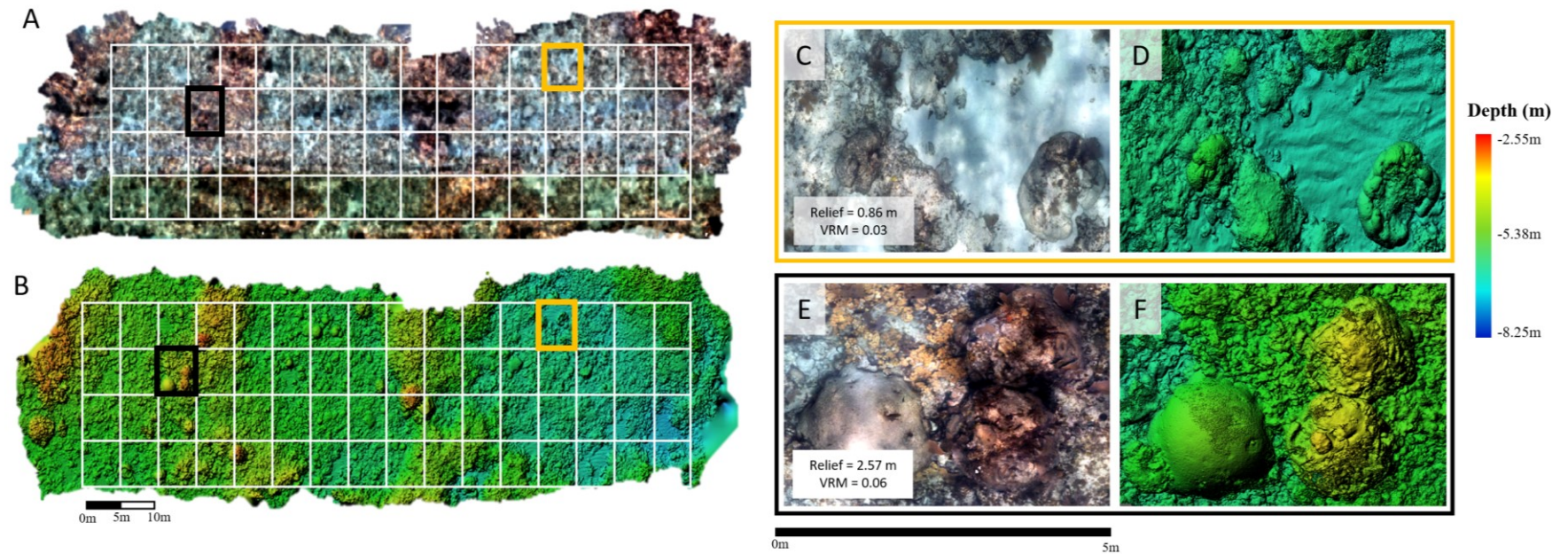
**Table 2.4** Beta coefficients for generalized linear mixed effects models of fish-habitat relationships. Standardized coefficient estimates for fixed effects (rows) in the top model for each response (columns; bold text) are shown along with their 95% confidence intervals in parenthesis. Asterisks indicate significance, with \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ . Dashes indicate fixed terms that were not included in the final models for that response metric. Cluster models 1-6 and total abundance models were fit with a negative binomial error distribution with log link function, while richness was fit with a Poisson with log link function. Cluster 7 model was logistic regression (presence/absence).

	<i>Community:</i>		<i>Functional Groups:</i>						
	<b>Abundance</b>	<b>Richness</b>	<b>Cluster 1</b>	<b>Cluster 2</b>	<b>Cluster 3</b>	<b>Cluster 4</b>	<b>Cluster 5</b>	<b>Cluster 6</b>	<b>Cluster 7</b>
Relief	0.20*** (0.15 - 0.26)	0.09*** (0.07 - 0.11)	0.26*** (0.14 - 0.38)	0.50*** (0.39 - 0.61)	0.10*** (0.05 - 0.15)	-	0.13*** (0.07 - 0.19)	0.17* (0.03 - 0.30)	-
Curvature	0.13*** (0.09 - 0.18)	0.05*** (0.03 - 0.07)	0.13* (0.02 - 0.23)	0.30*** (0.22 - 0.37)	-	0.43*** (0.26 - 0.60)	0.01 (-0.04 - 0.06)	0.20*** (0.09 - 0.31)	0.30*** (0.16 - 0.44)
VRM (1cm)	0.24*** (0.20 - 0.28)	0.08*** (0.07 - 0.10)	0.29*** (0.20 - 0.37)	0.47*** (0.40 - 0.54)	0.11*** (0.07 - 0.15)	0.45*** (0.30 - 0.60)	0.08*** (0.03 - 0.12)	0.35*** (0.26 - 0.45)	-
VRM dev	-0.05** (-0.09 - -0.01)	-0.02** (-0.04 - -0.01)	0.60*** (0.44 - 0.76)	-0.46*** (-0.60 - -0.32)	-	0.49*** (0.24 - 0.74)	-	-	-
Relief*Curvature	-	-	-0.18*** (-0.25 - -0.11)	0.14*** (0.08 - 0.21)	-	-0.19*** (-0.29 - -0.08)	-	-	-
Relief*VRM	-0.05*** (-0.09 - -0.02)	-	-0.16*** (-0.23 - -0.09)	-0.16*** (-0.22 - -0.10)	-	-	-0.05** (-0.09 - -0.02)	-0.09* (-0.17 - -0.02)	-

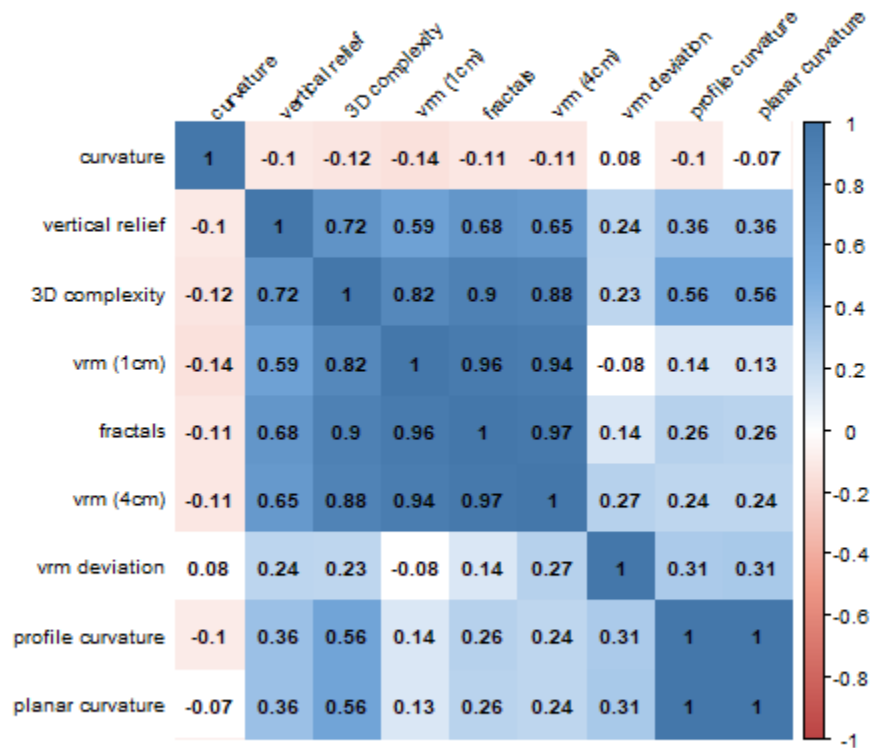
Relief*VRM deviation	-0.04*	-0.02***	-0.10**	-0.09***	-	-	-0.04*	-0.10*	-
	(-0.07 - -0.01)	(-0.04 - -0.01)	(-0.18 - -0.03)	(-0.15 - -0.04)			(-0.08 - -0.01)	(-0.19 - -0.01)	
Intercept	1.85***	1.83***	-0.03	-0.33	0.23**	-2.73***	0.49***	-0.49	-3.03***
	(1.62 - 2.08)	(1.77 - 1.89)	(-0.69 - 0.63)	(-0.85 - 0.19)	(0.08 - 0.37)	(-3.66 - -1.81)	(0.35 - 0.63)	(-0.99 - 0.02)	(-3.26 - -2.79)



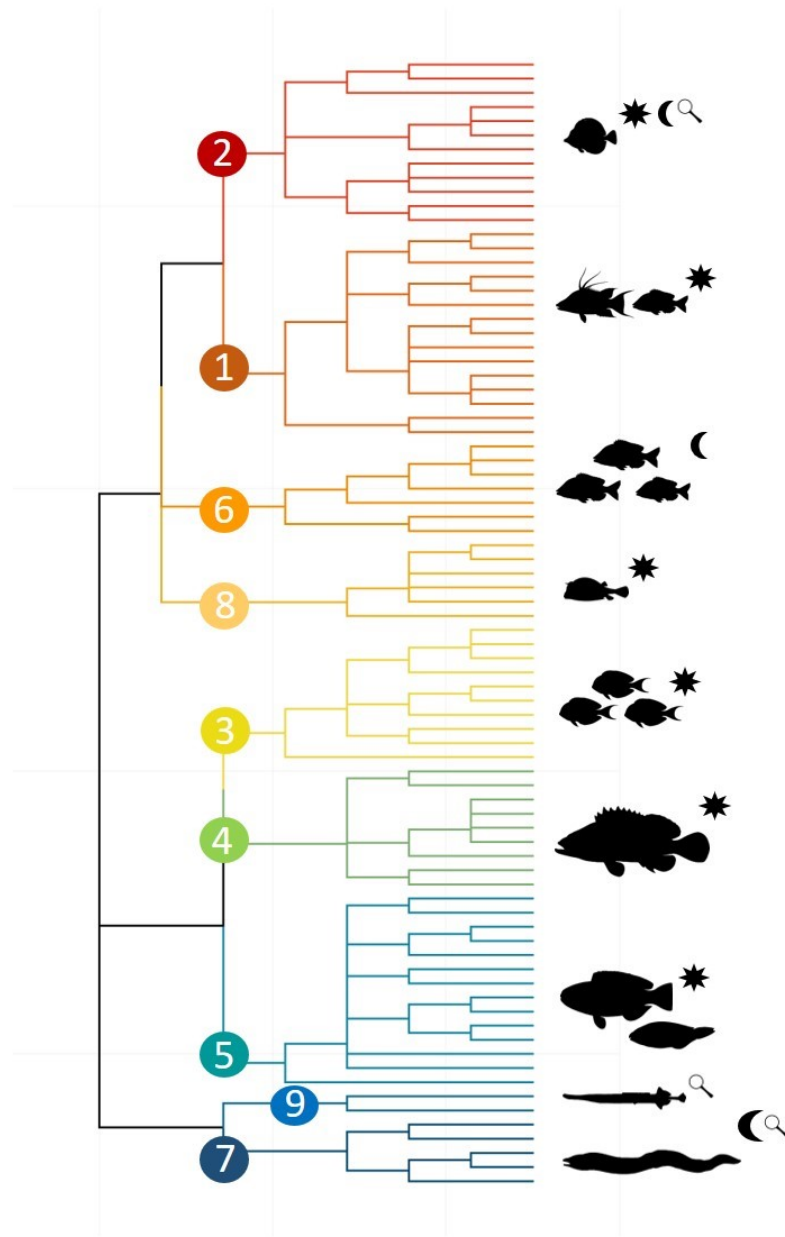
**Figure 2.1** Map of the eight reefscales at which we examined intra-reef habitat variation and the distribution of reef fish functional groups in the Florida Keys, FL, USA within the Florida Keys National Marine Sanctuary. CR = Carysfort Reef; NDR = North Dry Rocks; GR = Grecian Rocks; PR = Pickles Reef.



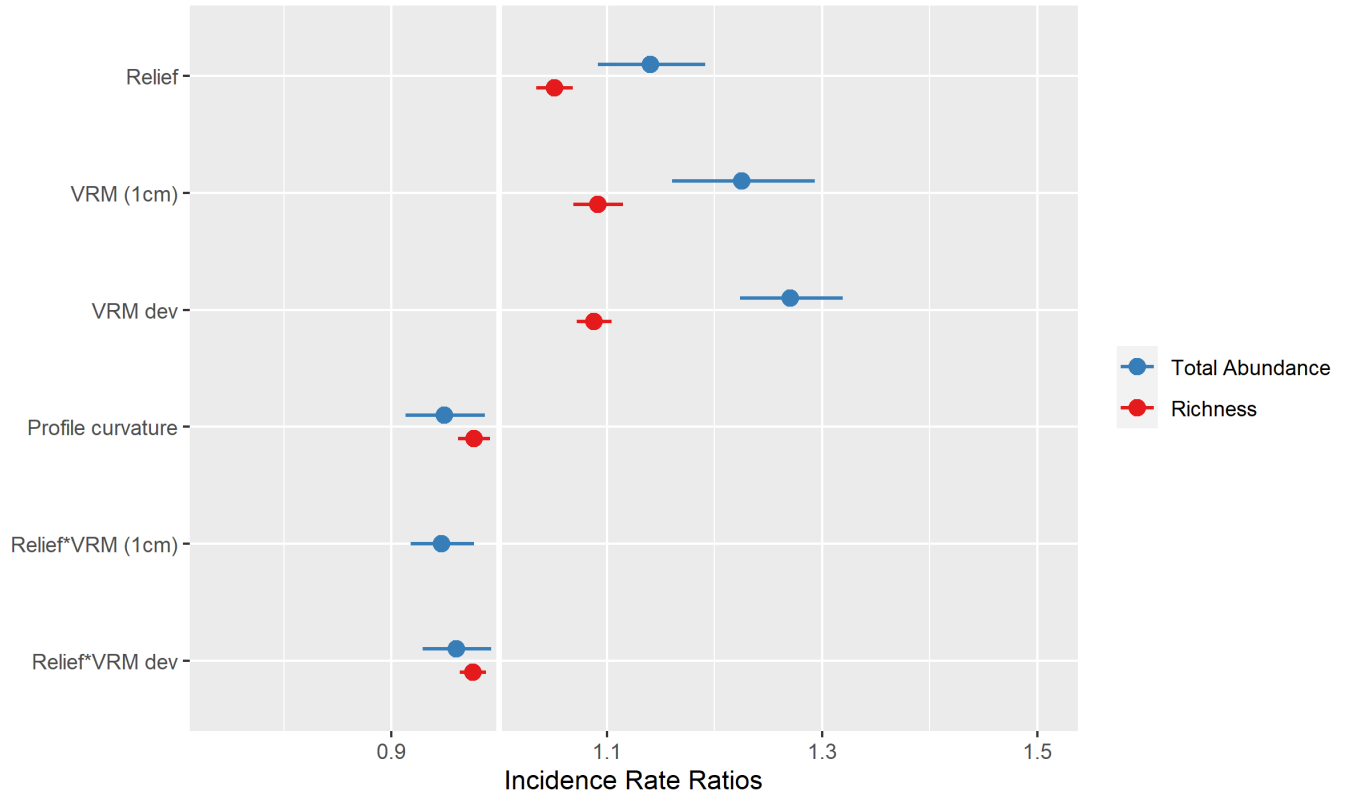
**Figure 2.2** (A) Illustrating our within-reefscape gridded sampling design from an image orthomosaic at Grecian Rocks (GR2; total area sampled = 2400 m<sup>2</sup>; total area shown = 1600 m<sup>2</sup>). White lines denote the boundaries of 25m<sup>2</sup> sampling plots in which fish community and habitat complexity data were collected across the reefscape. (B) High resolution Digital Elevation Model (DEM; 1cm x 1cm) showing depth variation across the reefscape derived from photogrammetry for the same area imaged in (A). Plot with dark orange outline in A&B illustrates low habitat complexity (i.e. low relief and low VRM), as visualized from the orthomosaic (C) and corresponding DEM (D). Plot with black outline in A&B illustrates high complexity habitat (i.e. with high relief and high VRM) as visualized from the orthomosaic (E) and corresponding DEM (F). Color intensity for B, D, and F only and shows depth (m).



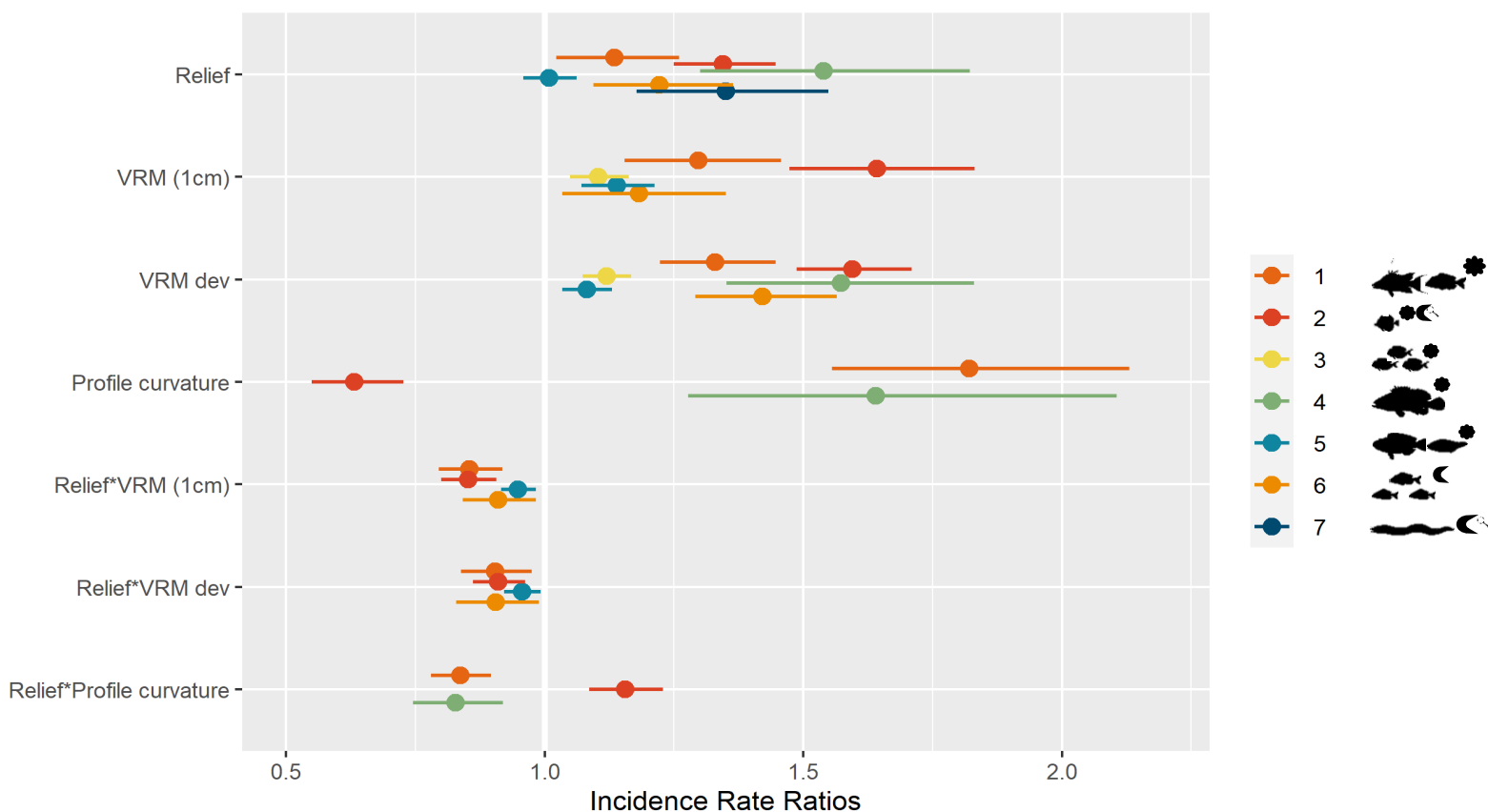
**Figure 2.3** Correlation matrix for all habitat complexity metrics quantified from DEMs for 752 plots at eight reefscales. Final metrics included in models were absolute profile curvature, VRM (1cm), VRM deviation, and vertical relief. Values are Pearson correlation coefficients. See **Table 2** for detailed descriptions of each metric.



**Figure 2.4** Dendrogram visualizing hierarchical clusters of reef fishes based on behavioural and morphological traits ( $k=9$  clusters) created using Gower's distance on the species-trait matrix. Shapes to the right of the dendrogram reflect dominant traits contained within each cluster: fish shape indicates a representative species and diet type; image size reflects maximum body size; number of individuals indicates social behaviour, with one indicating solitary, two indicating shoaling, and three indicating schooling taxa; \* indicates diurnal activity for that cluster; ☾ indicates nocturnal activity; 🔍 indicates species with cryptic behaviours.



**Figure 2.5** Incidence rate ratios and 95% confidence intervals (CI) for fixed effects from the top GLMM for each community-level response metric (total abundance and species richness). Values above one indicate a positive effect on the response metric, while values below one indicate a negative effect. CIs that cross the center line at one indicate no effect of the variable on fish response. Vertical relief measures large-scale topographic variation; VRM (1cm) measures micro complexity of branching benthic growth; VRM deviation (VRM 4cm -VRM 1cm) measures small-scale complexity of non-branching benthic growth; Profile curvature measures small-scale holes and crevices in the reef.



**Figure 2.6** Incidence rate ratios and 95% confidence intervals (CI) for fixed effects from the top GLMM for each cluster ( $k=9$ ; only clusters 1-7 modelled). Values above one indicate a positive effect on the response metric, while values below one indicate a negative effect. CIs that cross the center line at one indicate no effect of the variable on fish response. Vertical relief measures large-scale topographic variation; VRM (1cm) measures micro complexity of branching benthic growth; VRM deviation (VRM 4cm -VRM 1cm) measures small-scale complexity of non-branching benthic growth; Profile curvature measures small-scale holes and crevices in the reef.



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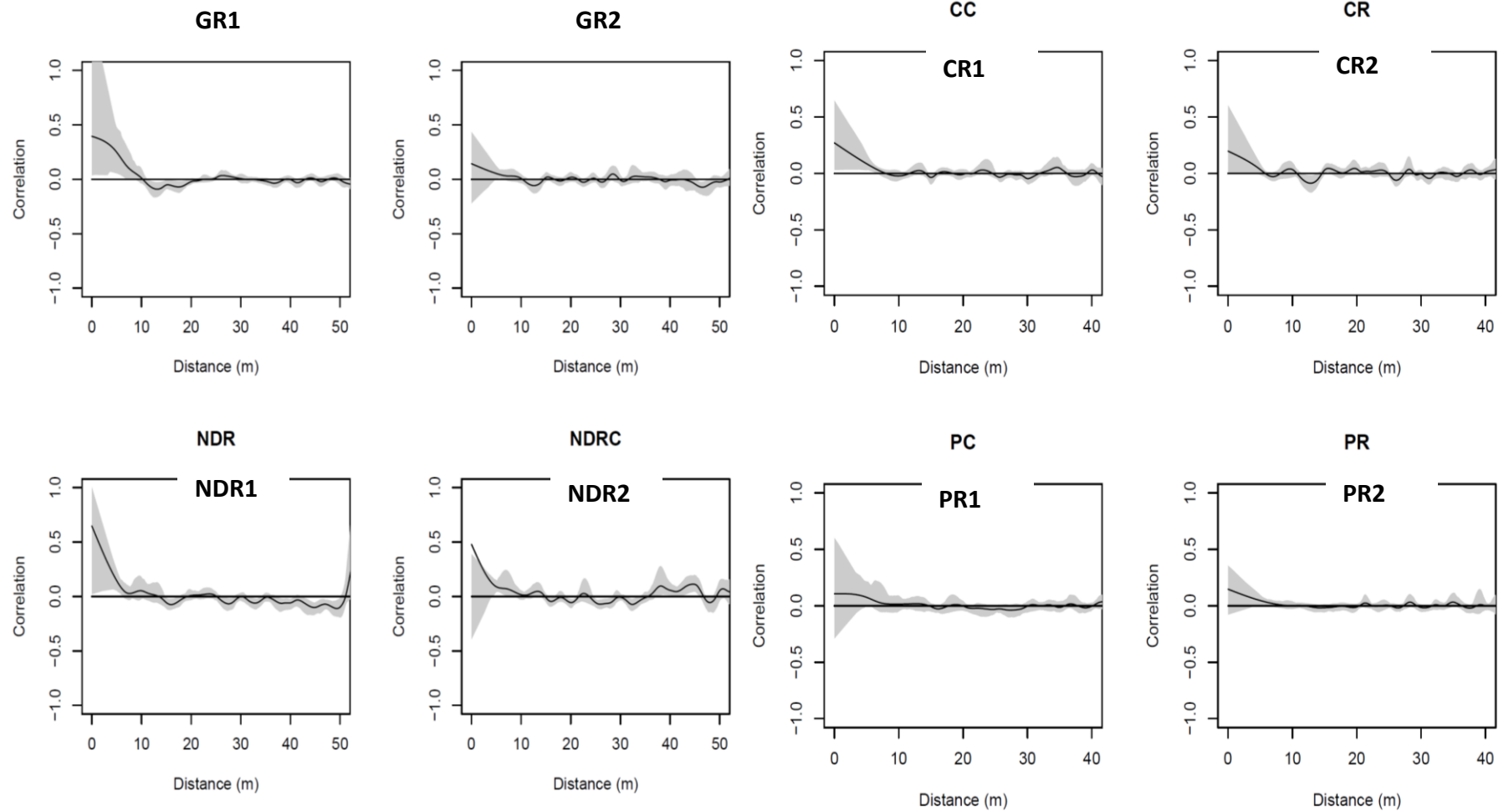
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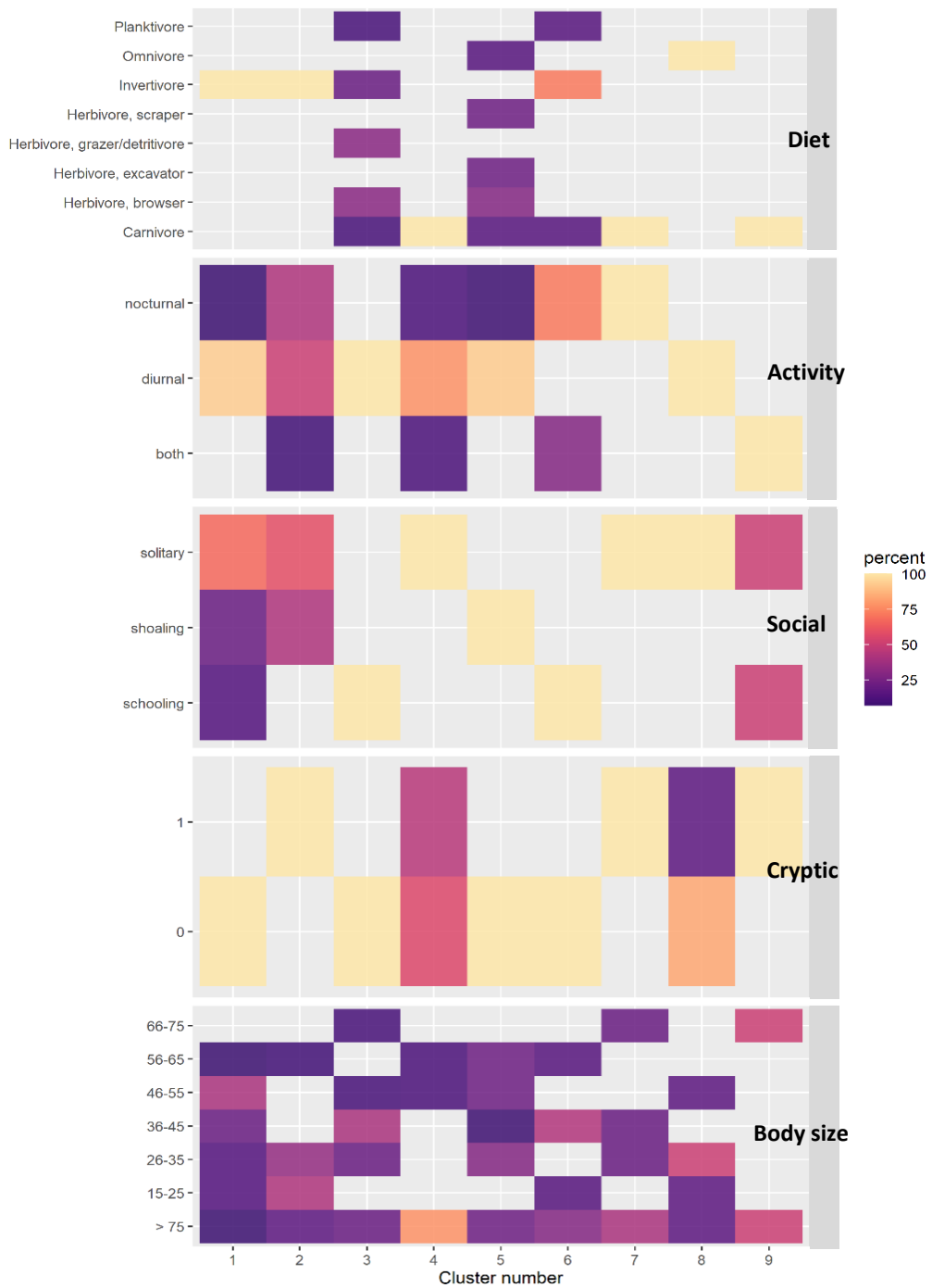


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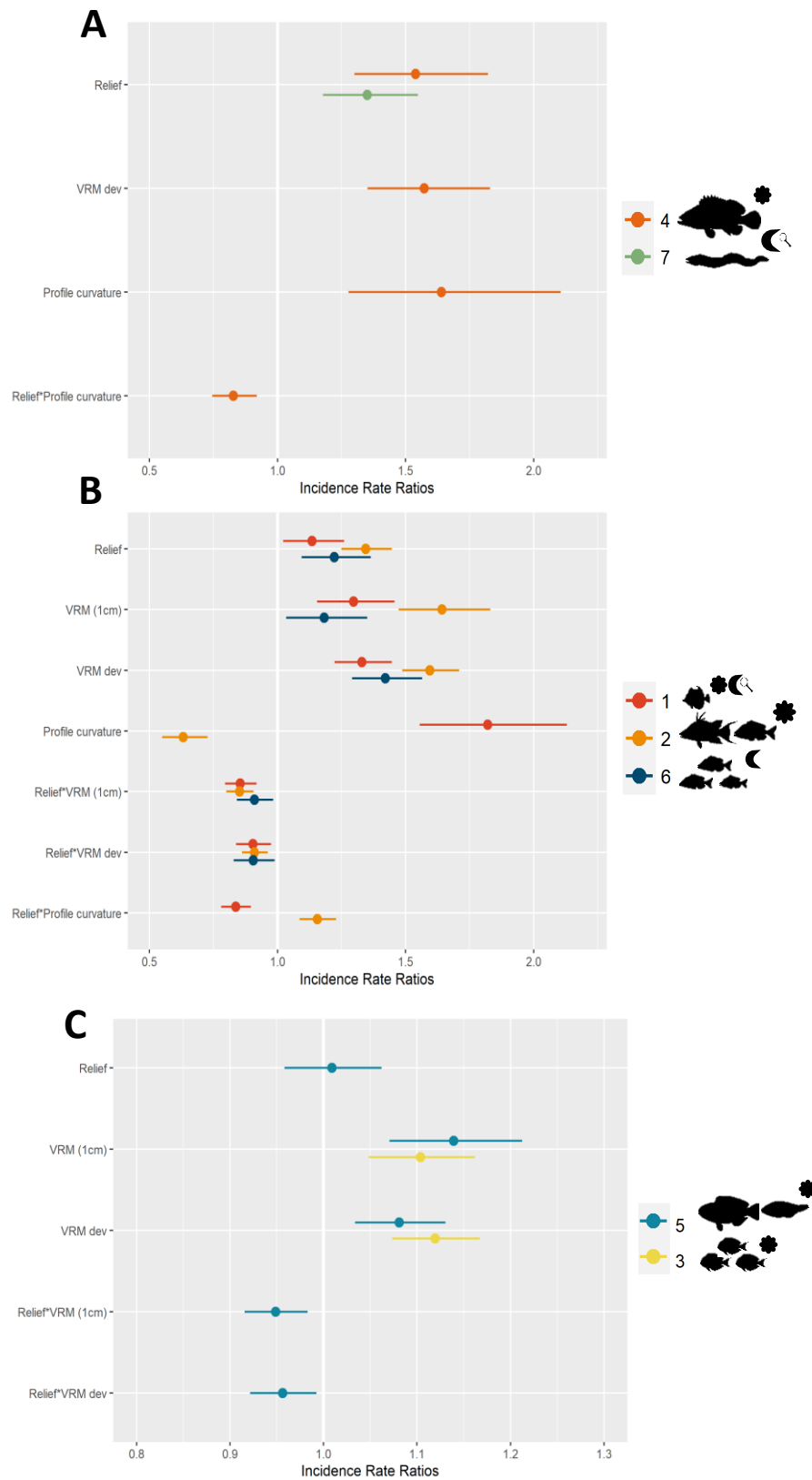
## 2.6. Appendix



**Figure A2.1** Spline correlograms exploring spatial autocorrelation with 95% pointwise bootstrap confidence intervals in raw fish abundance data for each of the eight reef sites.

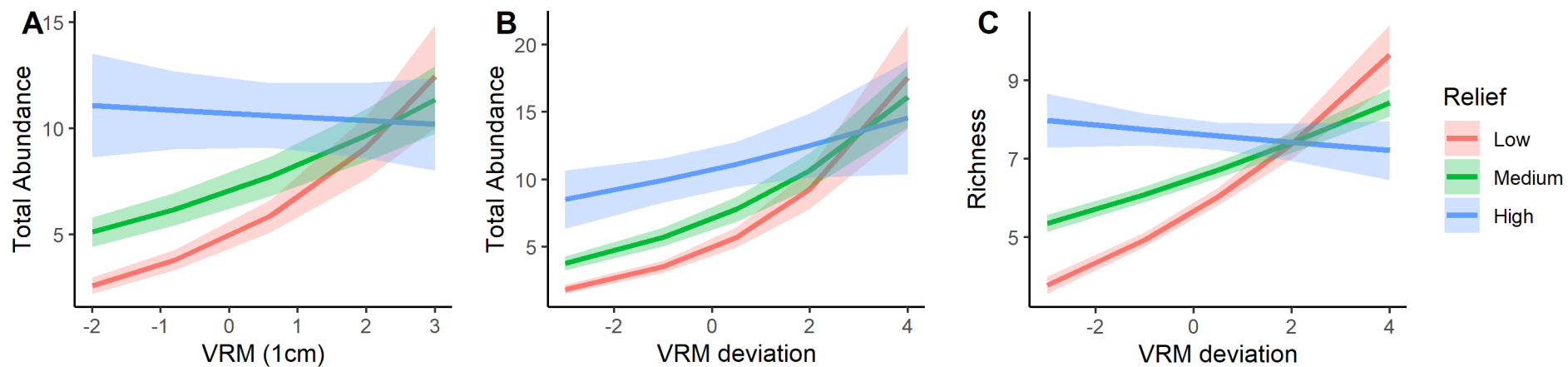


**Figure A2.2** Trait composition of each cluster ( $k=9$ ) resulting from hierarchical clustering analysis. Traits include diet, activity, social behaviour (i.e. gregariousness), cryptic behaviour, and maximum body size (**Table 2**). Lighter colors indicate that a higher percentage of species in that cluster were characterized by the corresponding trait level, while darker colors indicate the opposite.

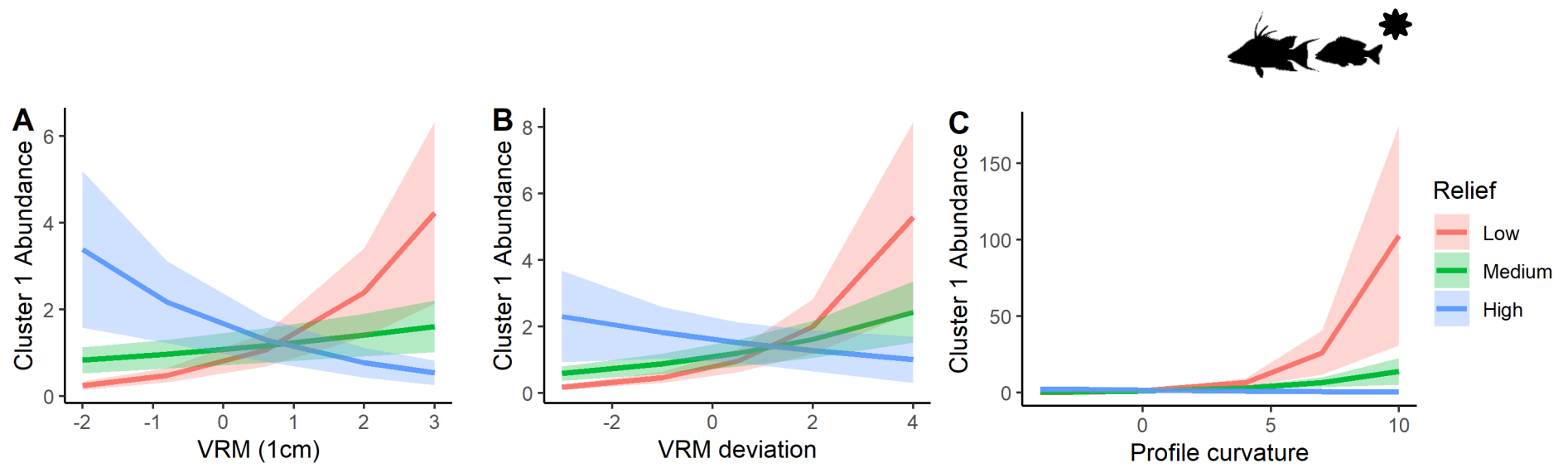


**Figure A2.3** Comparing incidence rate ratios and 95% confidence intervals (CI) for fixed effects from the top GLMM for each cluster within the three major trophic groups observed: (A) carnivores, (B) invertivores, and (C) herbivores. Numbers indicate cluster numbers (see **Figure 2.4**). Values above one indicate a positive effect on the response metric, while values below one indicate a negative effect. CIs that cross the center line at one indicate no effect of the variable

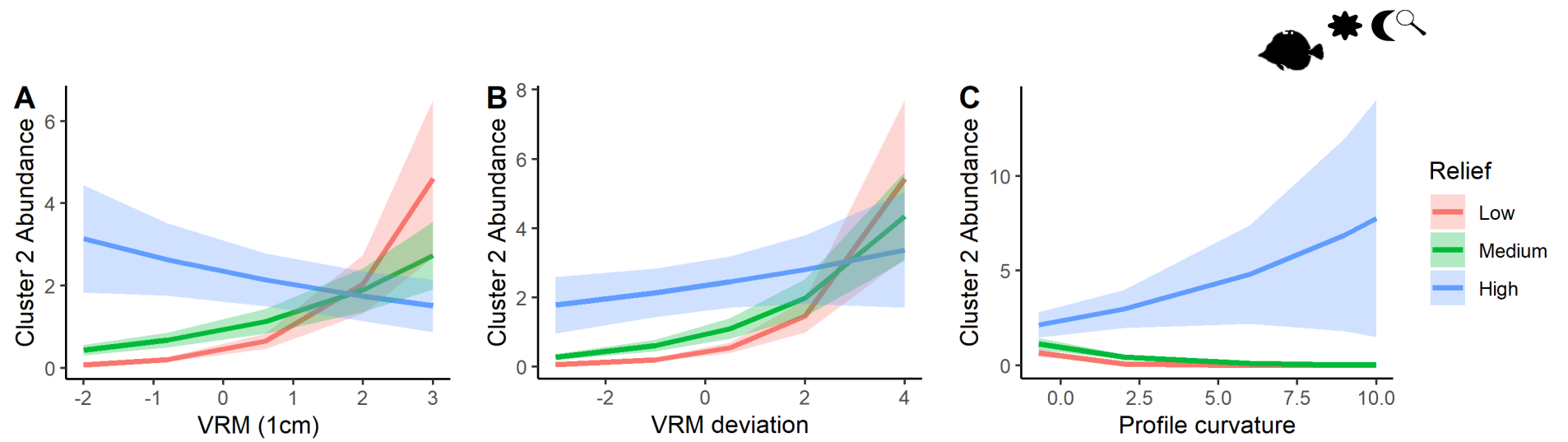
on fish response. Vertical relief measures large-scale topographic variation; VRM (1cm) measures micro complexity of branching benthic growth; VRM deviation (VRM 4cm -VRM 1cm) measures small-scale complexity of non-branching benthic growth; Profile curvature measures small-scale holes and crevices in the reef.



**Figure A2.4** Estimated effects of (A) VRM and (B) VRM deviation across levels of vertical relief on estimated community abundance, and (C) VRM derivation across levels of vertical relief on species richness.

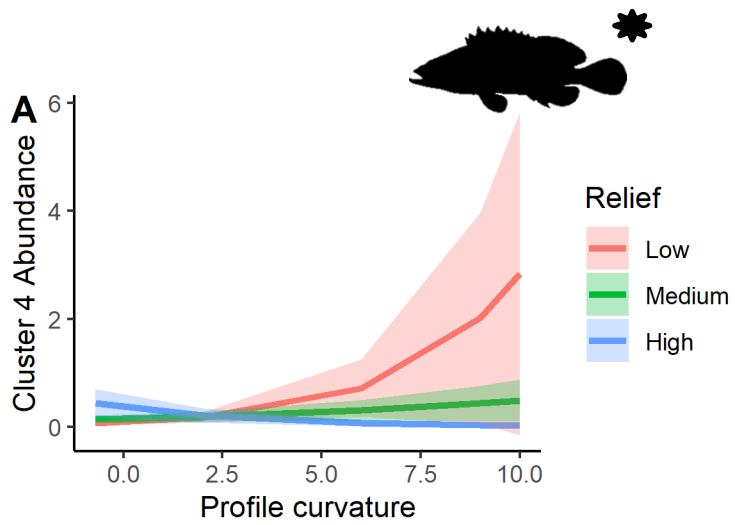


**Figure A2.5** Estimated effects of (A) VRM (B) VRM deviation and (C) profile curvature across levels of vertical relief on the estimated abundance of Cluster 1.

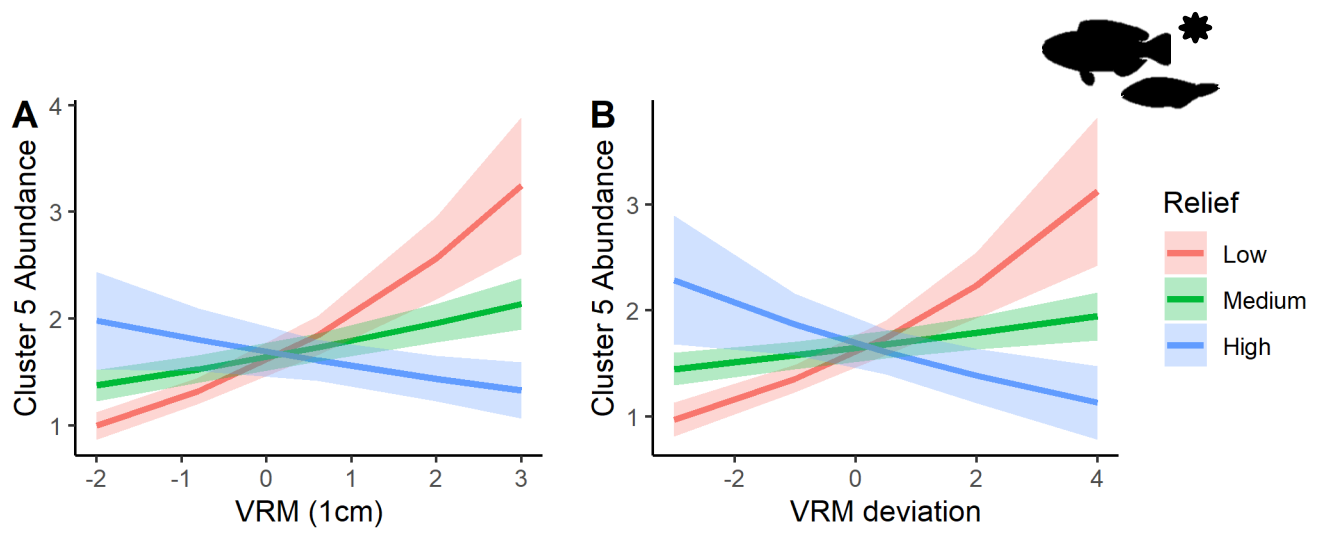


**Figure A2.6** Estimated effects of (A) VRM (B) VRM deviation and (C) profile curvature across levels of vertical relief on the abundance of Cluster 2.

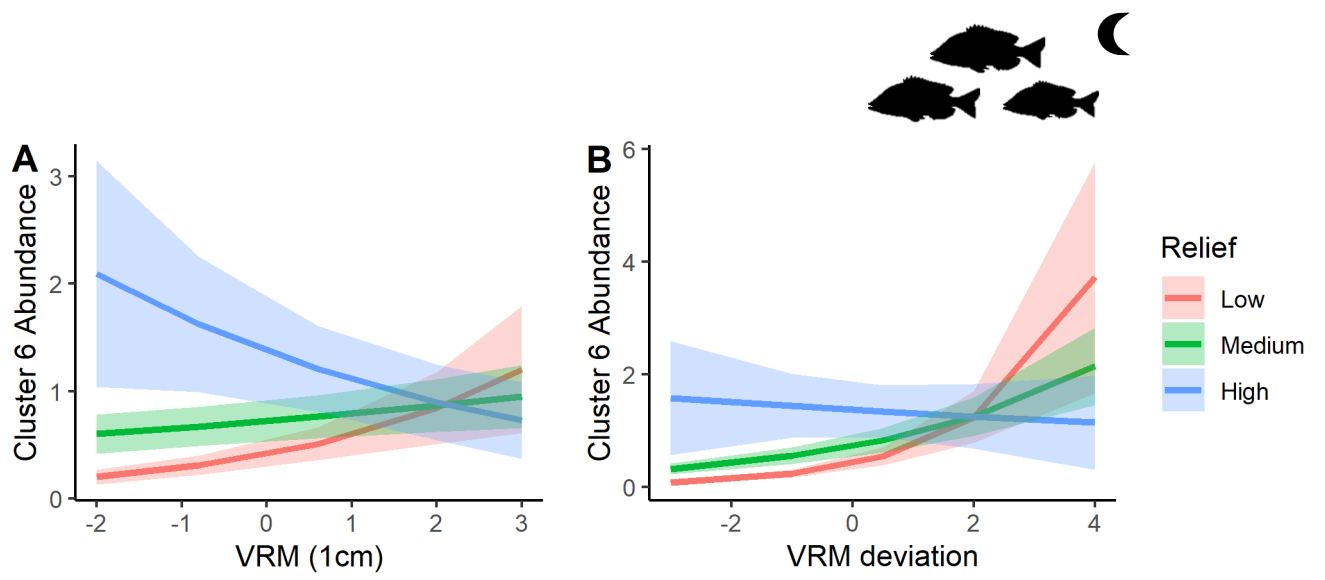




**Figure A2.7** Estimated effects of profile curvature across levels of vertical relief on the estimated abundance of Cluster 4.



**Figure A2.8** Estimated effects of (A) VRM and (B) VRM deviation across levels of vertical relief on the estimated abundance of Cluster 5.



**Figure A2.9** Estimated effects of (A) VRM and (B) VRM deviation across levels of vertical relief on the estimated abundance of Cluster 6.

## **Chapter 3: Quantifying fish-derived nutrient hotspots across the reefscape**

### **3.1. Introduction**

Animal consumers are increasingly recognized for their vital role in structuring primary production across ecosystems (Vanni 2002, Allgeier et al. 2017, Schmitz and Leroux 2020). Animals can mediate nutrient availability within and across ecosystems by storing and retaining nutrients within body tissues (Sterner and Elser 2002) and by supplying nutrients through egestion and excretion (Elser and Urabe 1999). Importantly, animals produce readily bioavailable forms of nitrogen (N) and phosphorous (P) which often limit primary production (Vanni et al. 2002). Animal-mediated nutrient supplies have been historically well studied in terrestrial (McNaughton 1984, Frank et al. 1994) and aquatic systems (Kitchell et al. 1979), and recently acknowledged as critical components of marine ecosystem function (Turner 2015, Allgeier et al. 2017).

The significance of consumer-derived nutrients within an ecosystem depends on interactions between abiotic and biotic characteristics along with animal densities and behaviours across space and over time (Vanni 2002, McClain et al. 2003). In particular, aggregations of animals can create biogeochemical ‘hotspots’ within a landscape, characterized as a patch of intensified biogeochemical reaction rates relative to the surrounding habitat matrix (McClain et al. 2003). Hotspots influence nearby primary producer performance and competitive interactions (Shantz et al. 2015), ultimately shaping the abundances and distributions of the surrounding producer community (Bokhorst et al. 2019). Studies from arctic tundra to savannas demonstrate that plant-herbivore interactions can create irregularly dispersed grazing ‘lawns’ within a landscape characterized by increased grass productivity through concentrated animal consumption and

excretion (e.g., McNaughton 1984). Similarly, variable invertebrate densities across marine tidepools can drive differential rates of nutrient uptake through mediated nutrient supplies (Bracken and Nielsen 2004), while patches of plants (Tall et al. 2011) and mussels (Bruesewitz et al. 2009) in aquatic systems create spatial variation in denitrification by altering water movement and light attenuation.

Current understanding of the ecological role of consumer-derived nutrients is generally limited to isolated habitat patches with clearly defined boundaries between ‘enriched’ (i.e. hotspots) and ‘unenriched’ areas. Such boundaries are less clear in structurally complex, heterogenous ecosystems, requiring a more nuanced understanding of the drivers and spatial scales of animal-derived nutrient supplies. Variable animal densities are driven by environmental characteristics, which influences patterns of nutrient deposition (Layman et al. 2013); yet few studies have explored the capacity of habitat features across a land- or seascape for predicting where or how hotspots form. In one of the few exceptions, McIntyre et al. (2008) found that distinct geomorphic features within rivers (riffles and runs) supported different fish communities which could be used to predict differences in the nutrient landscape, highlighting the importance of habitat features in creating nutrient heterogeneity. The links between environments, nutrient supply, and productivity are key to defining a hot spot, but the shape (i.e. linear or non-linear) of these relationships in continuous environments is not well understood.

Coral reefs are an excellent model system in which to refine the definition of consumer-derived nutrient hotspots and examine the environmental conditions influencing where and when they might form. Because coral reefs thrive in nutrient poor (i.e. oligotrophic) waters, they develop primarily in regions that lack major abiotic nutrient pulses, like upwelling events or riverine inputs (Goeij et al. 2013), making consumer-driven nutrient storage and supply an

important process regulating reef nutrient capacity (Crandall and Teece 2012, Burkepile et al. 2013, Allgeier et al. 2014, 2017). Coral reefs are also facing mounting threats on both local and global scales, with increasing risk of altering or losing critical reef ecosystem goods and services due to precipitous declines in coral cover (Gardner 2003). Coral restoration efforts are increasingly used to reverse local coral loss, but success has been variable (Ladd et al. 2019, Hein et al. 2020). Theory suggests that incorporating ecological processes, such as consumer-derived nutrient supply, into restoration planning could increase restoration success (Shaver and Silliman 2017, Opel et al. 2017, Seraphim et al. 2020, Ladd and Shantz 2020). A spatially explicit understanding of how consumer-derived nutrient deposition varies across structurally heterogeneous coral reef environments is critical to inform where and when restoration efforts should occur to maximize restoration outcomes.

At the scale of individual producers, fish nutrient supplies can increase coral growth (Meyer et al. 1983, Meyer and Schultz 1985a, Holbrook et al. 2008, Shantz et al. 2015) and may reduce susceptibility to coral bleaching (Chase et al. 2018). Nutrients from fishes are also taken up by other producers including macroalgae, which compete with corals for space on reefs (Connell et al. 2004). At the habitat patch scale (i.e.  $\sim <1\text{m}^2$ ), herbivores target nutrient-enriched algae growing near fish aggregations, which further shifts competitive dynamics between corals and macroalgae (Shantz et al. 2015). However, at the seascape scale (i.e. between sites;  $>100\text{ m}$ ), fish-derived nutrient loads are positively associated with macroalgal cover and negatively with coral recruitment when initial coral cover is low, suggesting that the effects of animal-driven nutrients may be both context and scale dependent (Burkepile et al. 2013). Within a reefscape (i.e.  $<100\text{m}$ ), distributions of fishes are linked with habitat structural complexity, which enhances important resources including food and shelter (Ault and Johnson 1998; Helder et al. *in prep*).

The distribution of key consumers likely influences the distribution of nutrients at this same scale, but these relationships have not yet been evaluated.

Here, we explore patterns of fish-derived nutrient excretion within continuous coral reef environments to examine the definition of consumer-derived nutrient hotspots and explore the environmental conditions influencing where and when they might form. Specifically, we tested 1) the role of structural complexity in generating nutrient provisioning services within reefs, including the shape of the relationship between complexity and supply (i.e. linear or non-linear) in order to evaluate whether thresholds of structure can be used to define ‘hotspots’ of supply, and 2) the extent to which consumer-derived nutrient supply translates into altered benthic communities across gradients of habitat structure. To accomplish these objectives, we estimated rates of nutrient provisioning of nitrogen (N) and phosphorous (P) by fishes across heterogeneous reefscapes (2400-2500 m<sup>2</sup>) in the Florida Keys using bioenergetics models and modelled these estimates as a function of fine-scale (25 m<sup>2</sup>) habitat complexity (vertical relief and vector ruggedness) within the reefscape. We then linked spatial patterns of macroalgal nutrient content to nutrient supply to test the shape of the relationships between habitat structure, nutrient supply, and primary productivity. We hypothesized that aggregations of fishes would be driven by habitat structure, which could create hotspots of N and P delivery, and that the effect of these concentrated nutrients would directly translate (i.e. linearly) into enrichment within surrounding benthic communities (Shantz et al. 2015). We also predicted that the effects of concentrated nutrients would decrease with increasing distances from hotspots (Layman et al. 2013), but that this pattern would be influenced by gradients in habitat structure driving differential fish nutrient supply rates in heterogeneous systems.

## **3.2. Methods**

### ***3.2.1. Study area and sampling design***

To explore the role of fishes as generators of nutrient hotspots within coral reefs, we conducted field observations of fish communities, habitat complexity, and benthic algal nutrient content across six reefscales within the Florida Keys National Marine Sanctuary (FKNMS) between June and July 2019. FKNMS is located within the Florida Keys Reef Tract, which runs parallel to shore for 250 km from Miami to Key West along the southeastern Florida coast (**Figure 1**). The reef system extends >8 km seaward from the islands of the Florida Keys and includes a mosaic of reef/hard-bottom habitats, sand, seagrass, and mangroves (Keller and Causey 2005). Because we were interested in evaluating relationships on continuous reefs (as opposed to patch reefs, which represent small, isolated pockets of high complexity habitat interspersed within relatively flat sand and seagrass beds), we sited the eight focal areas within high-relief spur and groove habitat that occurs at a depth range of ~2-10 m within the larger reef system. At a seascape scale (i.e. >1 km<sup>2</sup>), these habitats are classified broadly as ‘high-relief habitat’ but are composed of a mixture of high-relief spurs, low-relief reef, sand channels, and boulder-rubble fields that are likely to vary greatly in topographic complexity. Within each reefscape, we established a permanent area for fish community surveys, habitat measurements, and algal sample collections with dimensions of either 30x80 m (2400 m<sup>2</sup>) or 50x50 m (2500 m<sup>2</sup>). Each reefscape was further subdivided into a grid of 5x5 m plots (25 m<sup>2</sup>), with each site including a total of 96 (2400 m<sup>2</sup> sites) or 100 (2500 m<sup>2</sup> sites) 25 m<sup>2</sup> plots. The corners of each plot were clearly marked and labelled to ensure they were consistently located. All fish and habitat measurements were collected at the plot scale (25 m<sup>2</sup>).

### ***3.2.2. Assessing benthic habitat complexity***



To quantify the role of reef structural complexity in predicting nutrient hotspots, we used in-water structure-from-motion (SfM) photogrammetry to quantify high-resolution habitat complexity measures for each 25 m<sup>2</sup> plot (n=584) within a reefscape. As overall average topography was unlikely to change significantly during the two-month study period, we conducted habitat mapping only once for each site. The in-water image collection process has been described previously in detail (see Chapter 1 ‘Methods’; Burns et al. 2015, Bailey and Mogg 2020). Each reef site was imaged across its full area (2500- 2500 m<sup>2</sup>) by a diver swimming ~2 m above the substrate in a lawn-mower pattern to capture overlapping (70-80% targeted overlap) images of the benthic habitat structure. We used Agisoft Metashape Professional v.1.4 (Agisoft LLC., St. Petersburg, Russia) to build three-dimensional (3D) models of each reef. Due to the large size of the imaged areas, each total reef area (~2500 m<sup>2</sup>) was subdivided into 3 or 5 sections for model building to improve computational and storage efficiency. From each 3D reef model, we exported a digital elevation model at 1 cm resolution (DEM) and orthophotomosaic for subsequent analysis.

To quantify complexity for each 25 m<sup>2</sup> plot per reef site, we used ArcMap to identify and clip the full site DEM to each corresponding 25 m<sup>2</sup> plot. Of the 584 original plots surveyed, 558 were successfully imaged and used for analyses. For each plot, we quantified 3 measures of habitat complexity that captured small and large-scale components and were not severely autocorrelated (see Chapter 1 ‘Methods’ for detailed protocol). Final metrics included vertical relief, vector ruggedness at 1cm (VRM 1cm), and the VRM deviation between 1 and 4cm (VRM 4cm – VRM 1cm). Vertical relief is a widely used metric to quantify large-scale variation in reef topography (Luckhurst and Luckhurst 1978). In the spur-and-groove habitat, relief captures the overall habitat structure provided by ridgelines and large coral heads, and is positively correlated

with fish abundances and biomass (Lazarus and Belmaker 2021; Helder et al. *in prep*). Vector ruggedness measure (VRM) quantifies the various face directions of each DEM cell (at 1 cm resolution, each cell is 1x1 cm), and is then averaged across all cells within the plot. VRM at 1-cm resolution captures fine-scale complexity provided by benthic growth, such as branching coral colonies, which may provide habitat and resources for reef fish, whereas VRM at 4cm captures less complex growth forms which differentially influence fish communities (Fukunaga and Burns 2020, Fukunaga et al. 2020). VRM at 1cm and VRM at 4cm are highly correlated, so we followed Fukunaga et al. (2020) and calculated VRM deviation between resolutions. Larger values of VRM deviation reflect plots with increased complexity from non-branching growth forms, while smaller values indicate plots with more fine-scale complexity. See **Table 2.1** for detailed descriptions of each metric.

### ***3.2.3. Estimating fish-derived nutrient supply***

#### *3.2.3.1. Fish surveys*

To quantify reef fish community structure in each of the 25 m<sup>2</sup> plots, we conducted underwater visual surveys to record species abundances and total length to the nearest centimeter for all individuals  $\geq 15$  cm (see Chapter 1 ‘Methods’ for detailed protocol). We focused on larger size classes because of our interest in individuals **contributing most to community biomass and thus excretion** (Burkpile et al. 2013). We completed surveys approximately every 5 days over the study period for a total of 5-6 surveys per reef plot (n=4108 total plot-level observations) to understand fish biomass distributions over time and to identify plots with consistently elevated biomass relative to others as a function of habitat.

#### *3.2.3.2. Estimating nutrient delivery*

We used bioenergetics modeling from Burkepile et al. (2013) to estimate fish-derived nutrient supply at each plot. Bioenergetics models are frequently used as a tool to estimate nutrient excretion, growth, and feeding for marine fishes (Layman et al. 2013, Burkepile et al. 2013). Given *a priori* information on a species' diet and physiology, bioenergetics models use a **mass-balance approach** to estimate fish excretion using linear models. We used published models from Burkepile et al. (2013) to estimate nitrogen and phosphorous delivery from reef fish communities at each 25 m<sup>2</sup> plot (mg N or P m<sup>-2</sup> day<sup>-1</sup>). Fish total length was first converted to biomass via length-weight regressions for 80 species observed using data obtained from FishBase ([www.FishBase.com](http://www.FishBase.com)). Individual biomass was then used to estimate excretion (N and P) for each individual using linear regressions of wet mass and excretion (Burkepile et al. 2013). N and P supply estimates for individuals were pooled for each plot (25 m<sup>2</sup> sampling unit) at a given survey date, then averaged across all surveys (n=5-6 surveys) for subsequent analyses.

#### **3.2.4. Sampling macroalgae nutrient content**

To explore the extent to which predicted nutrient supply from aggregations of fishes distributed across high-complexity spur-and-groove reef systems influenced benthic community productivity, we measured macroalgal tissue nutrient content (%N and %P) from samples collected across two of the reefscape (**Figure 1**). Macroalgal nutrient analysis is commonly used in marine studies to validate nutrient supplementation, as it reflects ambient conditions over relatively long timeframes (Atkinson and Smith 1983). Therefore, we would expect algae growing near locations with increased rates of nutrient deposition to typically have higher nutrient content (Vega Thurber et al. 2014, Shantz et al. 2015).

Based on our prior observations of the fish community at the reefs, we identified one plot within each reefscape that consistently hosted a high biomass of schooling, resting (i.e.

stationary) fishes relative to the surrounding habitat (i.e. hypothesized ‘hotspots’) for macroalgal sampling, and one plot within each reefscape that hosted a lower biomass of fish (n=4 total macroalgal focal plots; Figure 2). We collected samples of the common brown algae *Dictyota* spp. in a spatially explicit fashion on three 12 m transects radiating away from each focal plot. Each transect originated at the centre of the focal plot (0 m distance) and extended through three consecutive neighbouring plots at 5, 10, and 15 m intervals, ensuring we could compare N and P delivery estimates from our fish surveys and habitat complexity metrics for each plot with observed macroalgal nutrient content. Because sampling was conducted within complex continuous reef habitat that includes a mixture of high-relief ridges, hard pan reef flats, sand channels, and rubble fields, transects crossed through a variety of habitat types to explore natural patterns of fish-derived nutrients in a complex natural environment.

We collected multiple *Dictyota* spp. samples per plot along each transect (n=21 samples per transect; 3-6 samples per plot). Samples were immediately frozen after collection and transported to the University of Alberta for processing. Each sample was rinsed with deionized water and scraped of epiphytes before drying at 45° C for 72 hours, then homogenized with a ball mill grinder (Retsch MM400; frequency= 20 Hz; time = 45s). Ground samples were analysed for nitrogen and phosphorous content using a CHN elemental analyzer (CE440 Elemental Analyzer) and for phosphorous by flow injection analysis (Lachat QuikChem 8500 FIA automated ion analyzer). All analyses were completed at the Biogeochemical Analytical Services Laboratory at the University of Alberta (Edmonton, AB, CA). We analysed a total of 206 samples from 40 plots across the four focal areas (two high fish biomass and two low fish biomass) for %N content, and a total of 66 samples from 20 plots from the two focal areas surrounding high fish biomass plots only for %P (Figure 2).

### 3.2.5 Statistical analyses

#### 3.2.5.1 Does structural complexity predict fish-derived nutrient supply?

We evaluated the relationships between estimated nutrient delivery (N and P) and measures of habitat structural complexity (VRM at 1cm, VRM deviation, vertical relief) for all plots (n=558 25 m<sup>2</sup> plots) using linear mixed effects models (LMMs). We also included quadratic terms for each complexity metric to investigate the potential for non-linear relationships. Additionally, we hypothesized that the effects of small-scale complexity on species distributions might vary depending on large-scale complexity (vertical relief; Helder et al. *in prep*). For example, herbivores may be positively associated with small-scale complexity provided by corals and other benthic growth forms in low-relief reef flats due to additional foraging opportunities paired with an open field of view, but may be uninfluenced or negatively influenced by small-scale complexity in high-relief habitats due to the added risk of predation at high relief (Ferrari et al. 2018). To test these hypotheses, we included two interaction terms in each model in addition to the three main effects: the interaction between relief and VRM at 1 cm, and between relief and VRM deviation at 4 cm. Prior to analysis, VRM deviation and VRM (1cm) were centered and scaled using the ‘scale’ function in base R (R Core Team 2020).

We included reefscape (n=6) as a random effect in the models to account for potential correlation among estimates from plots within the same reef. We modelled N and P estimates (our two response variables, which were highly correlated;  $r=0.95$ ) separately. Prior to model construction, we log transformed both N and P estimates to meet assumptions of normality and homoscedasticity. We also assessed assumptions of independence (spatial autocorrelation) visually with spline correlograms (**Appendix A3.2**). Models were simplified using backwards selection following the principle of parsimony, and tested using Akaike’s Information Criterion

to determine the best model (Zuur et al. 2009, Bolker et al. 2009). All analyses were completed in the R software version 4.0.2 (R Core Team 2020) using the package lme4 (Bates et al. 2015).

### *3.2.5.2 Does nutrient supply predict macroalgal nutrient content?*

We evaluated whether predicted fish-derived nutrient supply rates per plot (mean estimated mg of nutrient m<sup>-2</sup> day<sup>-1</sup>) explained observed patterns of macroalgal nutrient content (%N and %P) using a linear mixed effects model, including a quadratic term to investigate any non-linear relationships. We modelled nitrogen estimates from 205 macroalgal samples taken at 40 plots as described above (see Section 2.3.3; **Figure 2**). We included plot nested within site (i.e. reefscape; n=2) as a random effect term to account for correlation between samples from the same plots within the reefscape. We also modelled phosphorous from 66 total macroalgae samples from 24 plots, with plot nested in site (i.e. reefscape) as a random effect. All analyses were completed in the R software version 4.0.2 (R Core Team 2020) using the package lme4 (Bates et al. 2015).

Lastly, we visualized patterns across transects radiating away from the four focal plots to illustrate how fine-scale (i.e. plot-level) complexity mediates the designation of consumer-derived nutrient hotspots, and the spatial extent of their influence on benthic nutrient enrichment. We hypothesized that, because habitat structure influences fish distributions, the shape and extent of a hotspot's effects on benthic communities would vary with the gradient of habitat structure driving variable nutrient supply via fishes (the ecological driver).

### 3.3 Results

#### 3.3.1 *Does structural complexity predict fish-derived nutrient supply?*

Multiple aspects of habitat complexity significantly predicted rates of fish-derived nitrogen and phosphorous supply across continuous reefscapes (**Table 1, Figure 3**). We identified a non-linear relationship between fish nutrient excretion and habitat vertical relief, with nitrogen excretion increasing steadily up to a threshold around  $\sim 2.8$  m of relief before beginning to level off on reefs with increasing vertical relief (**Table 1, Figure 3A, D**). N and P supply were also linearly related to both VRM at 1cm and VRM deviation (**Table 1; Figure 3B, E; C, F**). We also identified an interaction between vertical relief and VRM deviation for both N and P models (**Figure 4**), indicating that the relationship between VRM deviation and estimates of both nitrogen and phosphorous delivery was strongest at plots (i.e. at the scale of  $25 \text{ m}^2$ ) with low and medium levels of relief within each reefscape (**Figure 4A, B**). Nutrient supply explained 27% and 29% of the variation in nitrogen and phosphorous estimates in our models, respectively.

#### 3.3.2 *Does nutrient supply predict benthic nutrient content?*

Rates of nutrient supply from fishes significantly predicted observed macroalgal nutrient content (%N and %P). Macroalgal nitrogen and phosphorous were non-linearly related to estimated supply, peaking in plots with fish excretion rates of  $\sim 250 \text{ mg N m}^{-2} \text{ day}^{-1}$  and  $\sim 35 \text{ mg P m}^{-2} \text{ day}^{-1}$ , respectively, before decreasing again up to  $403.8 \text{ mg N m}^{-2} \text{ day}^{-1}$  and  $53.9 \text{ mg P m}^{-2} \text{ day}^{-1}$  (**Figure 5A; 5B**). Final models of estimated nitrogen supply explained 33% of the variation in macroalgal %N. The non-linear relationships were largely driven by the NDR hotspot, where the range of predicted N supply was seven times greater than at CR and predicted P supply was four times greater than CR (**Appendix A3.1**). The final model for relationships between %P and estimated P supply explained 23% of the observed variation.

Qualitatively, the shape of the relationship between macroalgal nutrient content and distance varied across transects with different levels of change in vertical relief (**Figure 7**). Transects with minimal change in overall relief from the high fish biomass focal plot (i.e., ‘hotspot’) at NDR (**Figure 7A-C**) and, to a lesser extent, CR (**Figure 7G-I**), showed minimal variation in enrichment (%N) compared with transects with ~1.5m of relief change (**Figure 7D-F; J-L**). These transects showed decreasing %N with increasing distance from hotspots.

### 3.4 Discussion

Using coral reefs as a model ecosystem, we explored the relationships between gradients of habitat structural complexity, animal-driven nutrient supply, and benthic community enrichment to refine the definition of nutrient hotspots and examine conditions influencing where and when they might form in ecosystems characterized by continuous habitat features. We found that aspects of reef structural complexity non-linearly influenced spatial patterns of nutrient supply by mediating reef fish biomass distributions. Estimated N and P supply increased with increasing vertical relief up to ~2.8 m, with no effect at higher values, suggesting that supply saturates and ‘hotspots’ can form within the reefscape once relief reaches this level. Interestingly, benthic enrichment (measured as macroalgal %N and % P) by biotic nutrients reached a saturation threshold once fish-derived supply reached ~275 mg N m<sup>-2</sup> day<sup>-1</sup> and ~35 mg P m<sup>-2</sup> day<sup>-1</sup>, suggesting there may be limits to the influence of nutrient-supply hotspots on macroalgal enrichment in continuous reef habitats. Overall, our results suggest that hotspots of fish-derived nutrient supply, defined as levels of supply above a threshold in vertical relief on continuous habitat, are critical nodes of ecosystem function and suggest that environmental context may influence the resulting effects of hotspots on surrounding community productivity.



Predicting where consistent aggregations of consumers occur is necessary to understand nutrient provisioning across seascapes. Fish distributions are tightly linked with habitat structural complexity, and numerous studies have explored variation in the strength of species-habitat relationships across spatial scales (e.g., Risk 1972, Harborne et al. 2012, Ferrari et al. 2018; Helder et al. *in prep*). However, to our knowledge, our study is the first to investigate the interconnection between consumer-habitat relationships and nutrient supply along gradients of habitat complexity in coral reef ecosystems. Specifically, we found that nutrient supply from fishes (the dominant consumer in reef ecosystems) increases with measures of habitat structural complexity and identified a threshold in supply with increasing relief. This suggests that thresholds in supply with habitat features could be used as indicators of hotspots within continuous environments. These relationships reflect fish community biomass associations with habitat structure, which have been shown to increase non-linearly with coral height at this spatial extent (Harborne et al. 2012). The spatial distribution of nutrients within a system may be as important as the total nutrient supply across the system, as heterogeneity in resource supply can generate gradients in species performances (Allgeier et al. 2013, Layman et al. 2013, Burkepile et al. 2013, Shantz et al. 2015) and alter consumer distributions (Shantz et al. 2015). Our results highlight the importance of continuous habitat measures as drivers of nutrient heterogeneity across the reefscape. This information is a critically overlooked component of nutrient cycling in marine ecosystems and provides important information for predicting reefscape productivity.

While habitat relief was a major non-linear driver of nitrogen supply within reefscales, the significant interaction between relief and small-scale complexity (measured as VRM deviation) suggests that small increases in complexity generated by benthic communities may promote fish-derived nutrient supplies most in low relief habitat plots. Augmenting structural

complexity in low relief habitat (and typically “lower quality” habitat) may provide aggregation points for reef fish communities within otherwise resource-poor landscape. These findings align with habitat selection studies in coral and oyster reef environments, where additions of habitat complexity in already heterogenous environments (i.e. high relief plots) had smaller effects on resident community dynamics (Grabowski et al. 2005; Garg et al. *in prep*). From these results, adding small-scale complexity through coral outplanting would therefore have the greatest impact on fish nutrient supply in low-relief habitats as compared with high-relief habitats.

High rates of nutrient delivery can mediate limiting nutrient availability, shift primary producer community abundances, and ultimately drive ecosystem productivity (Chapin et al. 1997, McClain et al. 2003, Shantz et al. 2015). In the Florida Keys, reef fish contribute 25 times more nitrogen to the reefscape than any other source (Burkepile et al. 2013). Here, we document one of the largest ranges of biotic nutrient supply in reef ecosystems found in the literature (0 – 403.80 mg N m<sup>-2</sup> day<sup>-1</sup>) and, importantly, identified a threshold in benthic enrichment as a function of supply: evidence that consistent aggregations of fishes driven by habitat structure can generate hotspots of nutrients that influenced benthic community productivity. Macroalgae in the Florida Keys is generally assumed to be nitrogen limited, although there is some evidence that anthropogenic eutrophication may promote phosphorous limitation (Lapointe et al. 2019). Our results suggest that concentrated fish aggregations may supply limiting nutrients at high enough rates to potentially saturate primary producer biotic nitrogen supplies and identified potential limits of enrichment from fish hotspots.

Other potential sources of nutrients in the Florida Keys include anthropogenic runoff and internal waves, which are episodic tidal pulses that move subsurface, nutrient rich water towards the reef tract (Boyer and Jones 2002). However, internal waves are unlikely to reach the shallow

forereef depths in which this study occurred, making this an unlikely explanation for the observed spatial patterns in fish or macroalgal nutrients (Leichter et al. 2003). Anthropogenic runoff does have potential to influence overall nutrient availability within the Florida Keys Reef Tract (Lapointe et al. 2019). However, it is unlikely that nutrient supply resulting from regional anthropogenic runoff would influence the small-scale patterns of nitrogen variation (~5 m) observed at our sites that are more than 10 km offshore.

Defining the spatial extent of hotspots of consumer-derived nutrient provision to benthic communities is an important step in determining how to incorporate nutrient dynamics in ecosystem restoration or management planning. Previous experiments in seagrass ecosystems identified distinct thresholds in productivity responses with increasing distances from artificial habitat patches within homogenous seagrass flats that served as aggregation points for fish biomass (Layman et al. 2013). Indeed, understanding the spatial scale of nutrient provision is more complicated in complex continuous habitats. Because habitat features generate gradients of animal distributions and thus nutrients, the shape of relationships between habitat and enrichment may vary when considering different degrees of habitat structure (**Figure 7**). In our case, sampling along a high-relief ridgeline indicated no clear pattern in nutrient enrichment over distance (i.e. no ‘hotspot’, as traditionally defined by areas of enrichment vs non-enrichment), as the habitat provides additional resources to support higher fish biomass, and thus nutrient supply, across this area (**Figure 7A-C**). In contrast, when we sampled a transect that traversed from the high-relief hot spot into adjacent homogenous reef flats (i.e. low relief), we saw distinct thresholds in enrichment at 5 m (**Figure 7D-F**). Further, visual assessments suggest that the trends of enrichment (%N) across distances do not necessarily show the same shape as nutrient supply. We hypothesize that there could be a degree of ‘spillover’ in nutrient supply between

plots, making the potential area of influence larger than that considered here. This variation could have important implications for identifying and defining the spatial extent of nutrient hotspots; however further study is needed to determine the extent to which these observations hold across systems and ranges of nutrient supply.

While we found evidence that fish-derived nutrients can influence benthic productivity, future studies should also explore how the thresholds identified here apply to patterns of coral growth and health. Previous experiments suggest that concentrated nutrients from fishes can drive positive feedback loops by attracting herbivores to nutrient-rich algal food resources, resulting in a reduction in the biomass of these coral competitors (Shantz et al. 2015). Further, there is evidence that fish excrete nutrients at the prime N:P ratio for corals (Allgeier et al. 2014), which can result in increased coral growth under conditions of high nutrient supply for corals that shelter fishes within the branches or at sub-meter distances from fish schools (Meyer and Schultz 1985, Shantz et al. 2015). Given the link we identified between fish-derived supply and algal nutrient enrichment at the larger spatial scale of our study (25 m<sup>2</sup> plots within 2,500 m<sup>2</sup> reefscapes compared with ~1 m<sup>2</sup> colony experiments), it is likely that nutrient supply could also affect coral growth rates at this scale too. Identifying the extent to which habitat complexity-nutrient supply relationships extend to promoting coral growth and productivity is key to understanding how and when local strategies such as coral restoration efforts could harness fish-derived positive feedback loops to promote reef recovery.

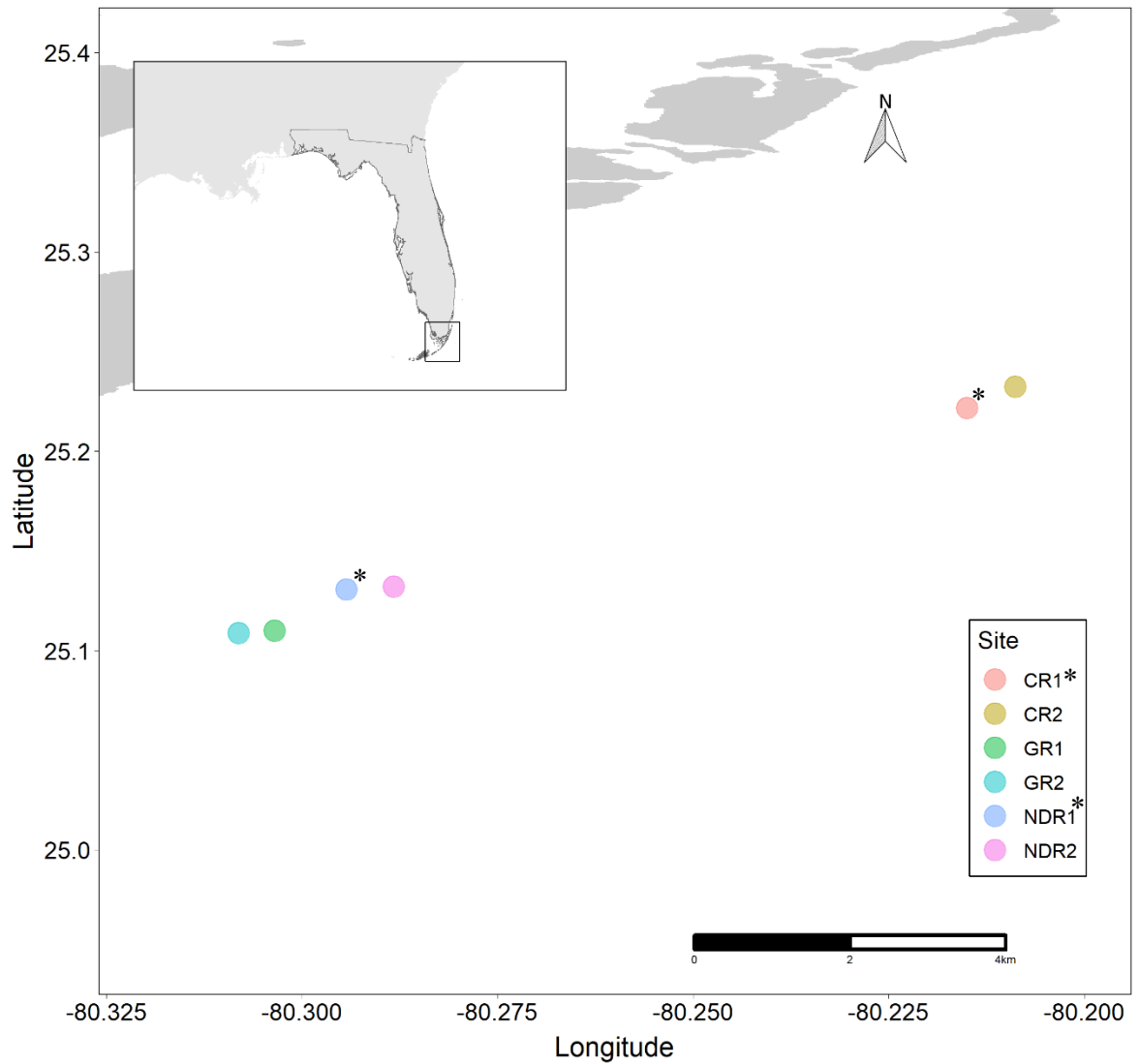
An important point to consider contextualizing these findings may be the temporal patterns of fish movement within and across the seascape. Nutrient supply is linked with spatial variation in fish communities over time as fish move on and off of reefs, and may vary considerably over longer time scales than that considered here (e.g. years; Francis and Côté

2018). Also, our surveys were only conducted during daytime hours and could therefore over estimate supply rates, as supply is likely to be lower on reefs at night as fish rest and/or leave the reef to feed in nearby habitats (Francis and Côté 2018). Future studies over longer timeframes will help to clarify the persistence of fish-derived nutrient hotspots and resulting applicability to reef management efforts.

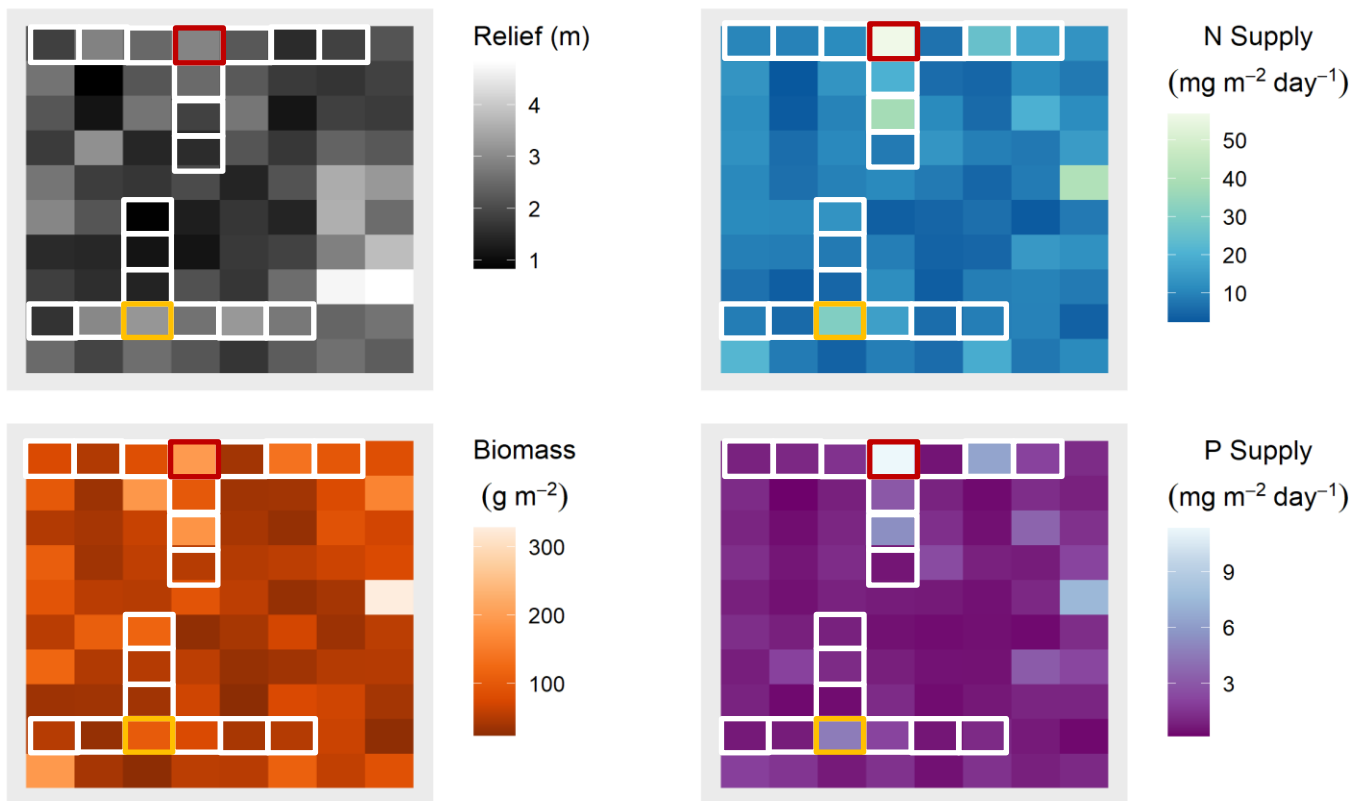
Identifying ecological thresholds, where key ecological components and processes are non-linearly related, can help to explain complex phenomena in real ecosystems. Understanding environmental drivers of local variation in animal-driven nutrient supply is critical to maintaining the processes that promote reef function and heterogeneity. In coral reefs, local and global pressures will continue to threaten reef structural integrity and disrupt consumer-habitat relationships. We demonstrate here that linking fish nutrient provisioning with habitat complexity can help predict primary productivity across and within the seascape and highlights the importance of considering habitat structure in conservation efforts to preserve reef function. Future studies that investigate how nutrient connectivity across landscapes, and the indirect role of habitat fragmentation in disrupting animal driven nutrient-exchange mechanisms, are urgently needed to preserve critical nutrient flows within and across landscapes.

**Table 3.1** Summary of linear mixed models exploring the effect of habitat structural complexity on estimates of fish-derived log-transformed nitrogen and phosphorous ( $\ln \text{ mg m}^{-2} \text{ day}^{-1}$ ). Mean coefficient estimates for the fixed effects (relief, relief<sup>2</sup>, VRM deviation, VRM [1cm], the relief x VRM deviation interaction, and relief<sup>2</sup> x VRM deviation interaction) are shown along with their 95% confidence intervals. Asterisks indicate significance, with \*p<0.05, \*\*p<0.01, \*\*\*p<0.001

	<b>N</b> <b>mg m<sup>-2</sup> day<sup>-1</sup></b>	<b>P</b> <b>mg m<sup>-2</sup> day<sup>-1</sup></b>
Relief	5.01*** (3.10 - 6.91)	6.52*** (4.35 - 8.69)
Relief <sup>2</sup>	-2.14* (-3.80 - -0.49)	-1.69* (-3.58 - -0.20)
VRM Dev	0.27*** (0.19 - 0.35)	0.29*** (0.20 - 0.39)
VRM (1cm)	0.17*** (0.08 - 0.26)	0.18*** (0.07 - 0.28)
Relief*VRM Dev	-2.50** (-4.15 - -0.84)	-2.41* (-4.30 - -0.53)
Relief <sup>2</sup> *VRM Dev	0.43 (-1.10 - 1.96)	0.44 (-1.31 - 2.19)
Intercept	2.32*** (2.11 - 2.53)	0.15 (-0.12 - 0.43)

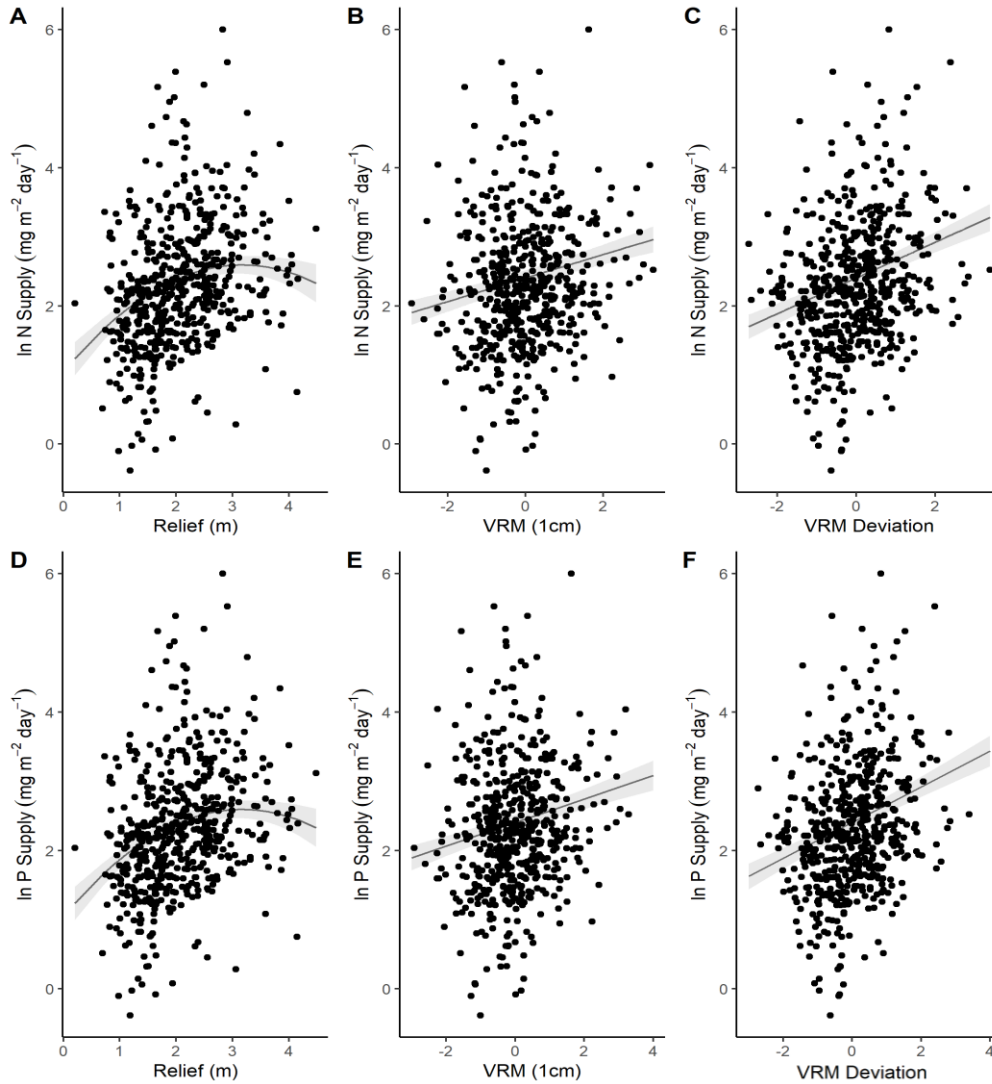


**Figure 3.1** Map of the six reefscape on which we surveyed fish communities and mapped habitat complexity in the Florida Keys, FL, USA. CR= Carysfort; CC = Carysfort Control; GR = Grecian; GC= Grecian Control; NDR = North Dry Rocks. Asterisks indicate reefscape where macroalgal sampling was conducted (NDR1 and CR1).

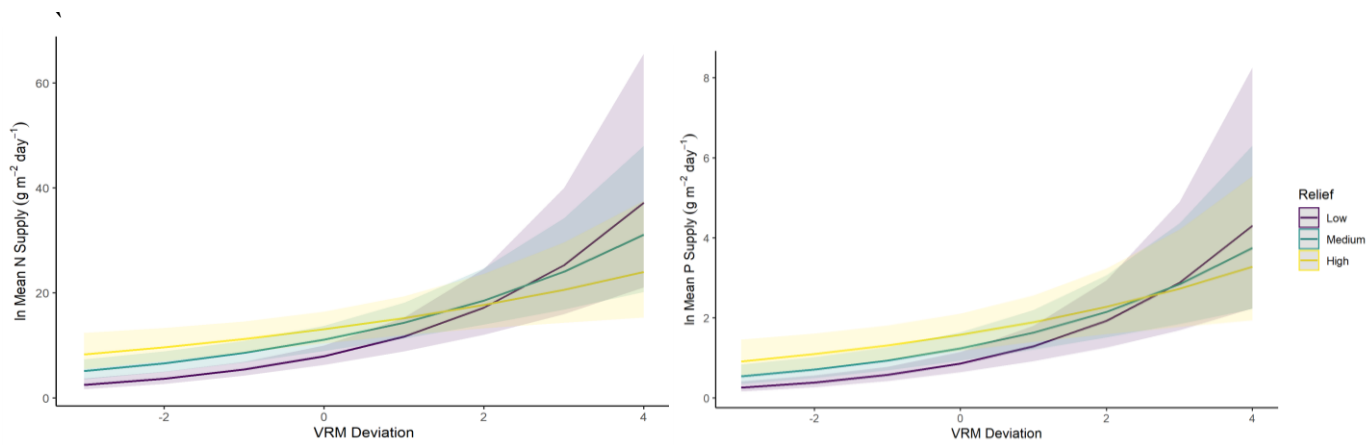


**Figure 3.2** Example of the study design at a subset of the Carysfort reefscape (CR1) showing a 2000 m<sup>2</sup> area divided into 5x5 m sampling plots (individual cells) for habitat complexity measurements, fish surveys, and macroalgal sampling. Red outlined plots in (A-D) indicate the location of sampled high fish biomass (i.e. hypothesized ‘hotspots’) with corresponding transects (n=3) passing through three neighboring plots at increasing distances (0, 5, 10, and 15 m distances) outlined in white, which include corresponding macroalgae samples. Yellow outlined plots in (A-D) indicate the locations of the low fish biomass sampling plots and corresponding transects with plots outlined in white. Spatial distribution within Carysfort reef of (B) vertical relief (m), (C) mean fish biomass (g m<sup>-2</sup>), (D) estimated nitrogen supply (mg m<sup>-2</sup> day<sup>-1</sup>) and (E) estimated phosphorous supply (mg m<sup>-2</sup> day<sup>-1</sup>).

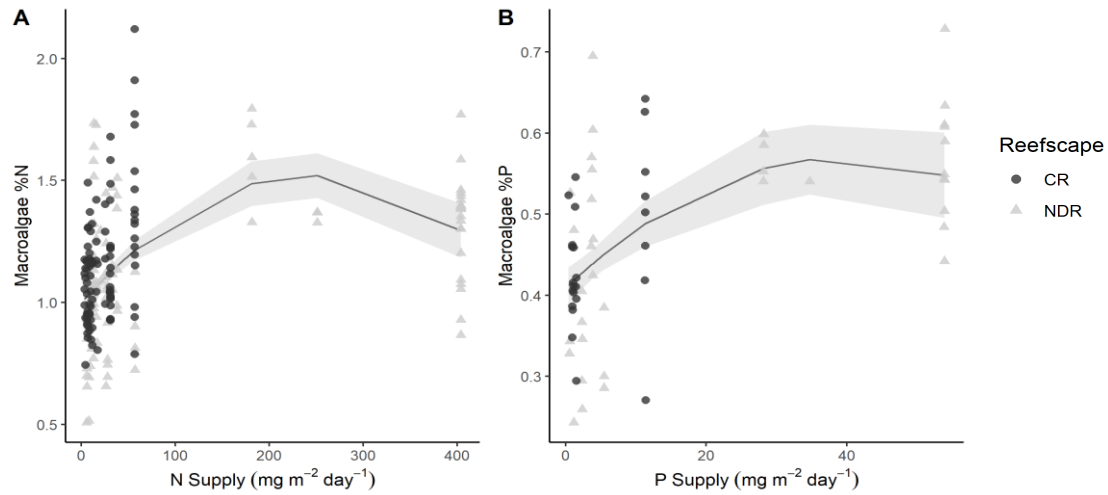




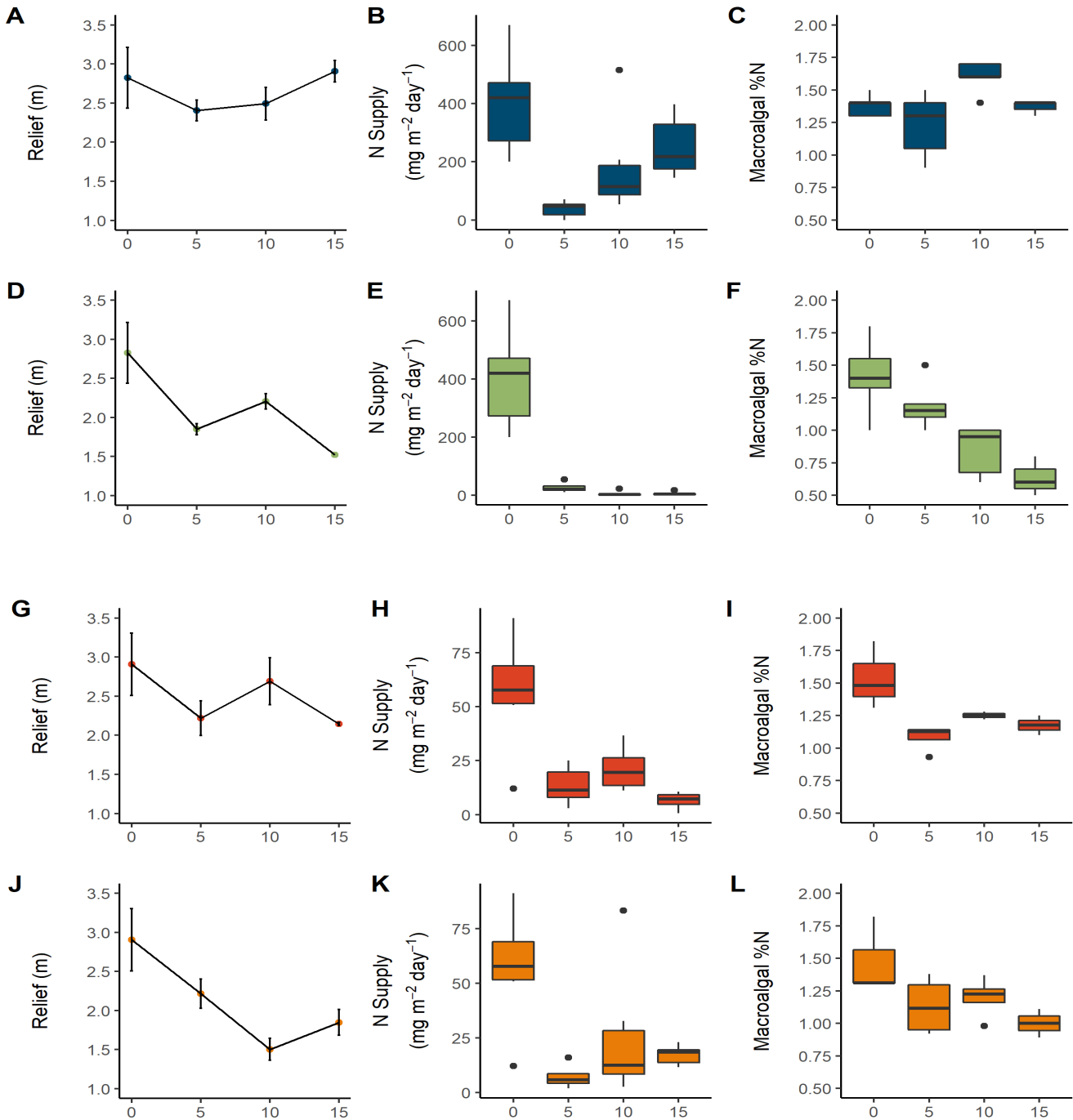
**Figure 3.3** Relationships between log transformed rates of fish-derived nitrogen (A-C) and phosphorous (D-F) supply from bioenergetics models and vertical relief (A, D), VRM (1 cm resolution; B, E), and VRM deviation (C,F). Black lines show predictions from linear mixed models including a polynomial term for vertical relief with standard errors (grey shading) for 558 plots across 6 reefscapes.



**Figure 3.4** Estimated effects of VRM deviation across different levels of vertical relief on (A) nitrogen and (B) phosphorous supply ( $\text{mg m}^{-2} \text{day}^{-1}$ ).



**Figure 3.5** Relationship between estimated fish nutrient supply from fishes ( $\text{mg m}^{-2} \text{day}^{-1}$ ) and macroalgal tissue nutrient content (%) for (A) nitrogen ( $n=206$ ) and (B) phosphorous ( $n=66$ ). Black lines show model predictions from mixed effects models including a polynomial term, with standard errors (grey shading). Shapes represent reefscape (circle = Carysfort; triangles = NDR).



**Figure 3.6** Relationships between mean vertical relief (m) and CI, estimated nitrogen supply from fishes ( $\text{mg N m}^{-2} \text{ day}^{-1}$ ), and macroalgae enrichment (%N) per  $25 \text{ m}^2$  plot at increasing distances along transects (one per row) radiating from high fish biomass focal plots at two reefscales: NDR (A-F) and CR1 (G-L). Transects with smaller changes in relief (A-C) and (G-I) show correspondingly smaller difference in consumer-mediated N supply and macroalgal %N enrichment, whereas transects with greater changes in relief (D-F) and (J-L) show steep declines in both N supply and benthic enrichment. Note the different scales of estimated nitrogen supply for transects from CR (E, K, and N) and NDR (B, H, Q), due to differences in observed fish biomass.

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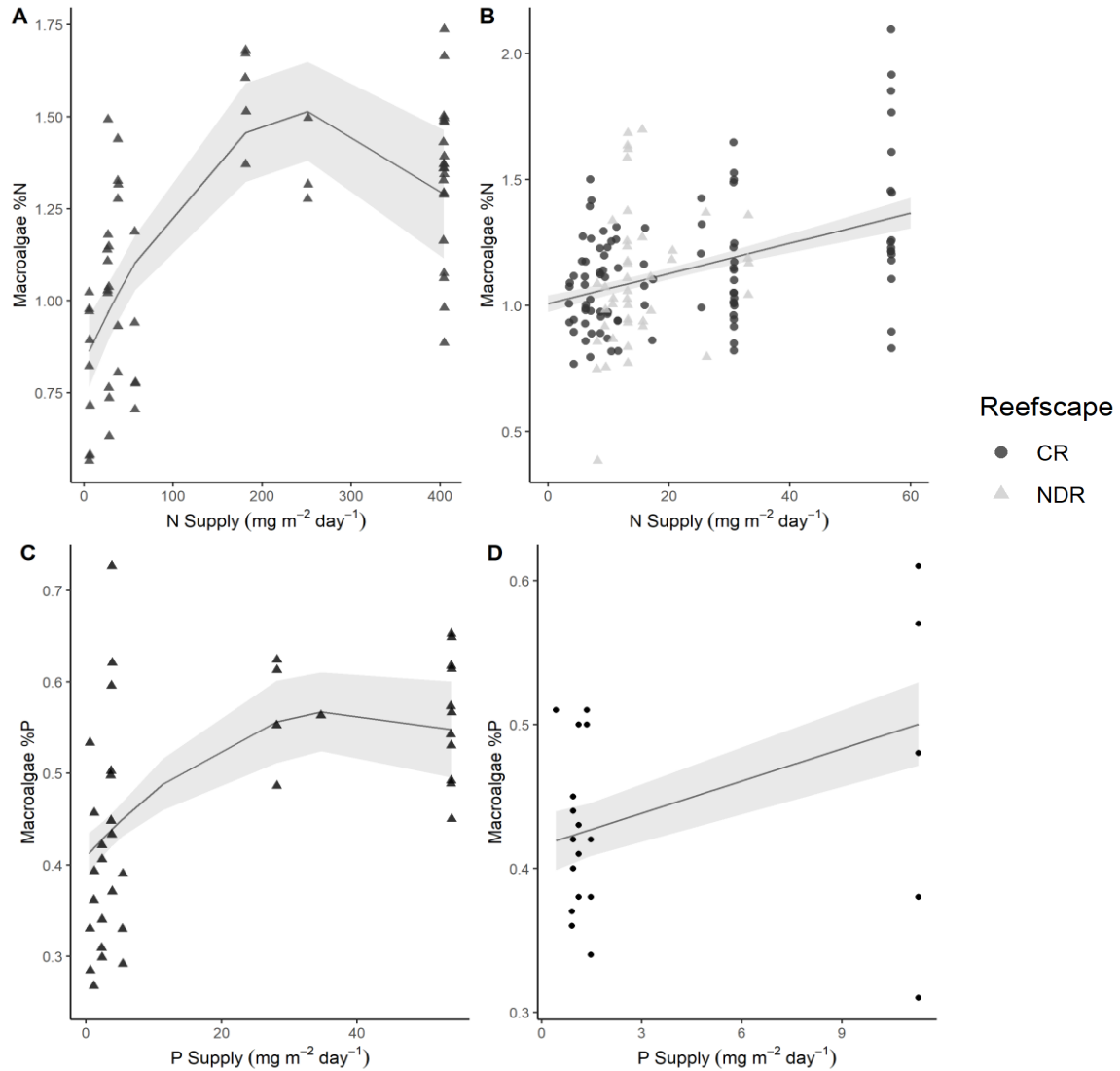
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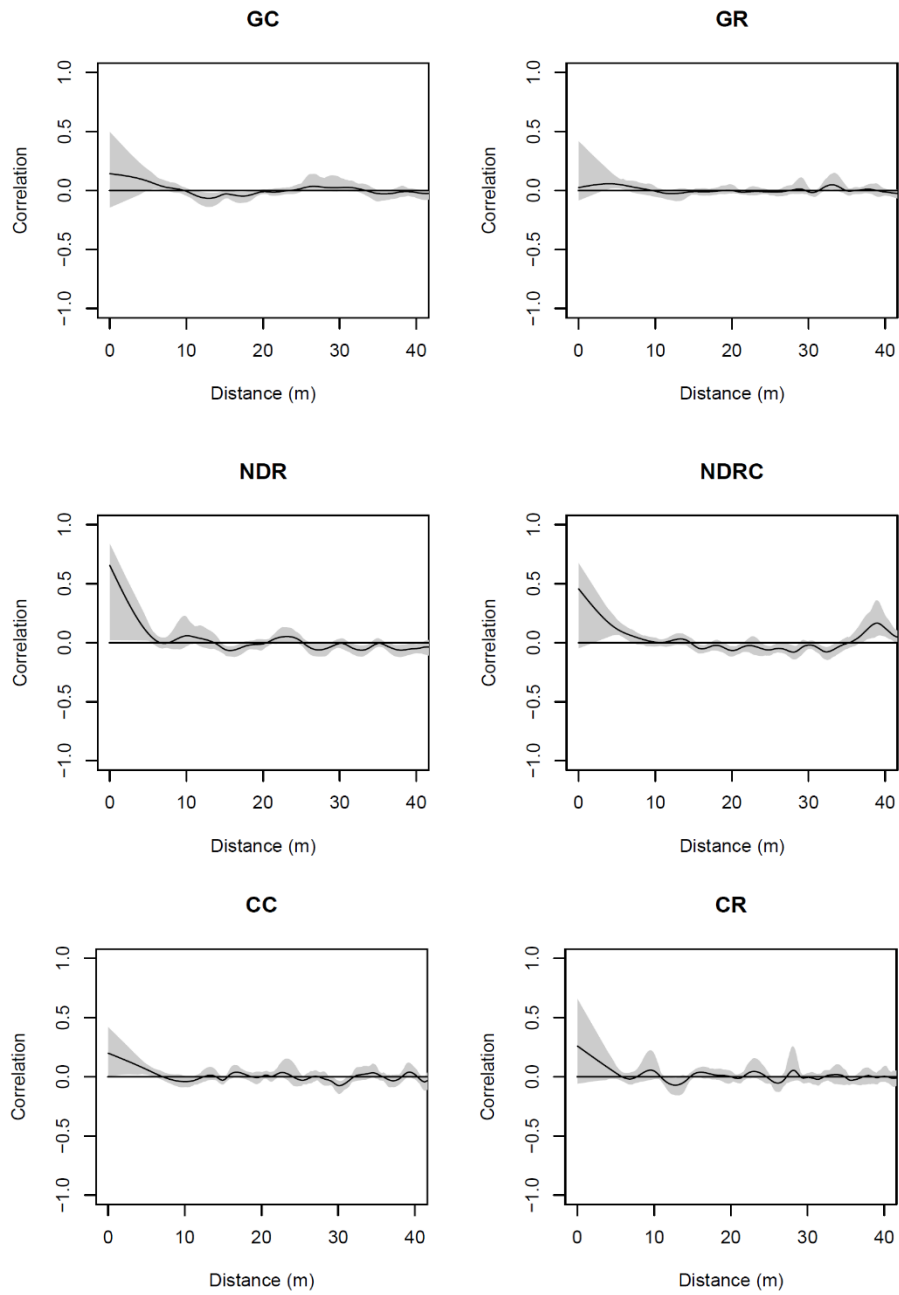
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### 3.6.Appendix



**Figure 3A.1** Relationships between estimated fish nutrient supply from fishes ( $\text{mg m}^{-2} \text{ day}^{-1}$ ) and macroalgal tissue nutrient content for nitrogen (A,B) and phosphorous (C,D). (A) Relationship for NDR nitrogen at the high biomass focal plot only driving non-linear relationship ( $n=60$ ) and (B) for combined focal points from CR and NDR ( $n=139$ ). (C) Relationship for NDR phosphorous at the high biomass focal plot only driving non-linear relationship ( $n=33$ ) and (D) CR phosphorous ( $n=33$ ). Black lines show model predictions from mixed effects models including a polynomial term, with standard errors (grey shading). Shapes represent reefscape (circle = CR; triangles = NDR).



**Figure 3A.2** Spline correlograms exploring spatial autocorrelation with 95% pointwise bootstrap confidence intervals in estimated fish nitrogen supply for each of the six reefscapes.

## Chapter 4: Conclusion

Habitat structural complexity underpins ecosystem functioning and drives animal community abundances, distributions, and diversity (Graham and Nash 2015). In complex and highly threatened coral reef ecosystems, uncovering specific metrics and scales at which complexity is functionally important for reef fishes is key to forecasting the productivity of reef ecosystems into the future. We conducted an observational study within the Florida Keys Reef Tract – a highly threatened coral reef ecosystem – in which we paired reef fish community surveys with intra-habitat complexity measures at eight reefscapes (each ~2500 m<sup>2</sup>). Through this research, we show that functional groups of fishes defined by shared traits (beyond only trophic level) respond uniquely to the scales and measures of complexity we considered. Our results have potential applications to coral reef ecosystems globally, as the trait-based relationships uncovered could be extended to regions with diverse taxonomic community structures but shared ecological functions. For example, relationships with habitat complexity could be used to predict community responses and the corresponding impacts on fish functions as reefs lose (i.e. through degradation, storm events, coral bleaching) or gain structural complexity (i.e. coral outplanting). As reef fish provide critical ecosystem services to coral reefs that promote coral health including removing macroalgal competitors and providing limiting nutrients (Brandl et al. 2018), our results suggest that habitat drivers of fish functional group abundance within reefs also likely mediates the distribution of these services.

Animal distributions shape nutrient availability within habitats, and habitat features that concentrate animal biomass could create ‘hotspots’ of nutrient supply (McIntyre et al. 2008). Yet, the links between habitat, animal distributions, and nutrient enrichment are sorely

overlooked – particularly in habitats with continuous habitat structural complexity - despite being a critical source of limiting nutrients in low-nutrient ecosystems across the globe (Allgeier et al. 2017). Using bioenergetics models to estimate nutrient supply (N and P) from fishes at six reefscales in the Florida Keys, our analysis uncovered a strong relationship between habitat structure and nutrient supply within coral reefs, highlighting environmental features as a driver of nutrient heterogeneity within landscapes. In contrast with classic studies that compare discrete hotspots with clear ‘non-hotspots’ (e.g. Shantz et al. 2015), gradients of structure in continuous environments mediate differential nutrient supplies from consumers, making the effects on nutrient enrichment complex and highly dependent on habitat context. Our results suggest that thresholds in nutrient supply with increasing habitat structural complexity could serve as helpful indicators of hotspots across reefscales, which we identified at ~2.8m of vertical relief in spur-and-groove habitat types featuring high-relief ridges. In contrast to our predictions, nutrient supply did not linearly relate to the degree of nutrient enrichment within benthic primary producers. Instead, we observed a saturation threshold in nitrogen (~275 mg m<sup>-2</sup> day<sup>-1</sup>) and phosphorous supply (~35 mg P m<sup>-2</sup> day<sup>-1</sup>), above which supply had little to no effect on surrounding macroalgal nutrient content.

The findings from this thesis have direct applications to coral reef ecosystem management broadly, and to the placement of coral restoration projects specifically. As reefs face mounting global and local stressors that compromise structural integrity and ecosystem resilience (Gardner et al. 2003), predicting how resident communities will respond and what these means for the important services they provide is key to successfully preserving these mechanisms (Shaver and Silliman 2017). It is clear from our results that preserving both small- and large-scale complexity is critical for reef fish communities. Coral restoration efforts are

hypothesized to benefit from outplanting in areas near fish aggregations to harness positive feedback loops from fishes (Shantz et al. 2015; Ladd and Shantz 2020). Our results could be used to guide the placement of restoration which augments small-scale complexity in the context of large-scale reefscapes. Small additions to complexity through outplanting could positively influence fish community abundances and estimated nutrient supply, particularly when added to low-complexity (low relief) habitat.

Structurally complex habitats and foundation species are increasingly threatened through a range of global and local stressors, particularly through habitat degradation from climate change, exploitation, and fragmentation, placing the species they support and services they provide at risk. Understanding the way that species respond to changes in 3D complexity and the resulting implications for ecosystem function are imperative for improved management and preservation of these invaluable systems into the future.

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