Habitat Structural Complexity of Caribbean Coral Reefs and its Relationships with Fish Community Structure

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Abstract

Habitat structural complexity (HSC) is a key component of natural ecosystems. It helps to describe the morphological characteristics of the three-dimensional space that floral and faunal communities exist within. The physical structure can have a profound influence on the associated diversity and functioning of the ecosystem. This thesis is a macroecological study of Caribbean coral reef HSC and how changes in it might influence associated fish communities. An assessment of contemporary reef HSC in 15 countries and its relationship with spatial, environmental and anthropogenic variables, identified the degree and frequency of physical disturbance as significant drivers. There was also a strong link between live coral and HSC indicating that, despite region-wide declines in coral cover, there has not been a decoupling of complexity and coral, and that healthy coral populations facilitate the persistence of structurally complex coral habitats. To examine the relationships between different measures of HSC and their relevance to the fish community, a multidimensional model of HSC was developed. Through this approach it was possible to combine a number of variables which individually indicate different components of reef HSC, and derive compound 'refuge' and 'complexity' variables which are expected to be of greater relevance to the fish community, and potentially of greater use to understanding macroecological relationships on coral reefs. This approach was used to identify relationships between the Caribbean reef fish functional community structure and the derived refuge variable. Sites with low refuge levels were dominated by generalist fish species and had low levels of functional diversity. Additionally, the biomass of a number of fish functional groups and the size structure of groups was found to be related to the refuge characteristics of coral reefs. The examination of fish communities at night revealed a continued relationship with HSC over the entire diel cycle for some functional groups while others varied in their association with reef structure. Nocturnally active groups decoupled from HSC as they moved over flatter areas of reef to feed, while diurnally active groups moved into the reef to shelter. Observations of behaviour and feature preferences identified potential drivers behind the numerical relationships between the fish community and HSC. Some species have strong behavioural associations with HSC or features of reef structure and may suffer as result of habitat complexity declines. However, small non-fisheries target species such as wrasse and damsels, with less direct physical ties to the habitat structure are those most likely to persist after habitat degradation. The thesis highlights the state of and threats to Caribbean HSC and the pivotal role it plays in determining fish community structure.

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Glossary

Habitat – the physical environment in which organisms live. In this thesis this is considered to refer to a reef-scale environment.

Habitat complexity – A broad term used to describe the structure, heterogeneity and diversity of a habitat in which animals live.

Habitat heterogeneity – The spatial diversity or arrangement of habitat features across an area. More heterogeneous habitats will have a high diversity of features and low evenness.

Habitat structural complexity – A description of the morphological characteristics and structural components of the habitat. Diverse and heterogeneous areas of varying relief and density, with high refuge availability are considered more complex.

Habitat Feature – A distinct structure on a reef which can be utilised by an animal for specific behaviours e.g. a tower as a point of convergence for schooling fish.

Microhabitat – a sub-section of the habitat. Here this is on an organism-scale and can refer to components of the reef environment including a coral colony or refuge hole.

Refuge – The space created by habitat structure in which fish can shelter from predators. On coral reefs this is commonly provided by holes or fissure in the reef matrix.

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1. Introduction

"The complexity of nature is a fact of nature, and has to be studied as such" – Elton and Miller, 1954

1.1. Habitat complexity

Habitat complexity is a prominent theme running through recent ecological study. It has been used as a broad term which can include the structure, heterogeneity and diversity of a habitat. The overarching idea is one of a number of elements which combine to create a range of different types of habitats which fall along a complexity gradient. These elements can include vegetation such as trees, grasses or kelp; sessile animals such as corals, tubeworms or oysters; or inorganic structures such as cliffs, rocks or pebbles. These easily identified elements enable us to make simple qualitative assessments of a habitat complexity. However, quantitatively measuring habitat complexity can be quite challenging and often overlooks this qualitative aspect of complexity in favour of one-dimensional numeric measurements.

In order to simplify this process, it is helpful to examine aspects of habitat complexity separately. Habitat complexity has been discussed in a number of different ways. One of the earliest definitions by McCoy and Bell (1991) suggests habitat complexity is "the arrangement of objects in space". However, as this topic is explored in greater detail this definition becomes somewhat simplistic. A more recent review by Tokeshi and Arakaki (2012) suggests that at least five traits should be recognised when discussing habitat complexity:

1. Scale of habitat structure
2. Diversity of complexity generating elements
3. Spatial arrangement of elements
4. Size of elements
5. Abundance/density of elements

This more directed approach to complexity enables a more holistic examination of the habitat being discussed. It encourages one to move beyond a one-dimensional approach and is likely to generate studies which are of greater relevance to the habitat and the organisms which it supports. At this point it becomes necessary to make a distinction between habitat structural complexity, which is the focus of this thesis, and habitat heterogeneity. Structural complexity is then the morphological characteristics of the structure while habitat heterogeneity is the arrangement of these structures in space (Jana and Bairagi 2014).

1.1.1. *Quantifying habitat structure*

Defining and measuring habitat structure is a challenging task which is invariably subject to some form of measurement bias. Observers or quantifiers of this structure must aim to create a measurement which is ecologically relevant to the habitat and organisms which are being examined. In some of the earliest work examining the influence of habitat structure on species diversity, MacArthur & MacArthur (1961) used foliage density at three vertical heights in the canopy as a measure of structure. The density of the foliage in these three layers was found to be related to bird diversity at these heights. However, this finding does not necessarily qualify the measure as the only or the best way to explore this relationship. The three layers are arbitrary, albeit with some theoretical reasoning, and may not be related to the way the birds actually perceive and utilise that habitat.

Since MacArthur & MacArthur's (1961) work a number of alternative methods have been used in an effort to obtain quantifiable information about the habitat in question to explain relationships with the associated communities. The density, diversity and biomass of plants are the most commonly used variables when measuring vegetation structural complexity (Heck Jr and Wetstone 1977, August 1983, Wiens et al. 1986, Halaj et al. 2000, Warfe and Barmuta 2004). Fallen plant matter can also provide complexity in other habitats such as woody debris in streams (Everett and Ruiz 1993) or leaf litter on forest floors (Hansen 2000).

Surface topography was the first habitat structure variable to be measured on coral reefs (Risk 1971) followed by the vertical relief of the structure (Luckhurst and Luckhurst 1978a) and refuge or shelter availability (Shulman 1984). A number of measures have been added to this list, including: fractal measurements (Nash et al. 2013), density of refuge (Buchheim and Hixon 1992) and growth forms (Friedlander et al. 2003). These variables are designed to examine relationships between organisms and specific components of the habitat, though they are frequently used as proxy variables for habitat structural complexity, and as explanatory variables for community wide relationships. However, it is highly unlikely that one species, let alone a whole community, will be reliant on a single aspect of the environment. It is more likely that a particular variable, such as refuge, is of importance during part of a species' activities, while a separate component of structural complexity such as vertical relief, is important for other activities.

Given the specificity of the habitat structure variables discussed there is a need to produce methods for quantifying complexity which more fully describe the habitat and could be applicable for multiple environments. Bartholomew et al. (2000) created two "dimensionless" indices of habitat complexity (Equations 1.1 and 1.2).

$$Area\ of\ refuge\ = \frac{Total\ area\ of\ cover\ with\quad a\ habitat}{Total\ area\ of\ the\ habitat} \qquad \text{Equation 1.1}$$

and

$$Predator\ free\ space\ = \frac{Average\ inter{-}structural\ space}{Size\ of\ the\ predator} \qquad \text{Equation 1.2}$$

However, both measures are concerned with the relationship between the habitat and predator mediation which is not relevant to all species or habitats, and notably the second index is specific to only one predator of one size at a time, a relationship that will also change ontogenetically. A more generic cross-habitat metric was designed by Gratwicke & Speight (2005) who combined five measures of complexity on a qualitative scale of 1-5 and used the combined data to produce a “Habitat Assessment Score”. This approach has the benefit of utilising multiple traits of habitat complexity as suggested by Tokeshi & Arakaki (2012) and providing simple, analysable output. However, the methods used and the final score remain a subjective simplification of the habitat. A data driven approach to combining multiple variables has involved the use of principal components analysis (PCA) (August 1983, Chong-Seng et al. 2012). This approach relies on correlation-based ordinations which lose much of the original information and prevent the role of each measure of complexity being examined. PCA derived indices also lack consideration of the interaction between complexity variables, overlooking combined and indirect effects. Pertinent data are needed on a range of habitat complexity components and a method of combining these in an ecologically meaningful manner, accounting for any emergent or indirect effects of these components.

1.1.2. *Animals and habitat structure*

Darwin (1859) first suggested that a relationship is likely to exist between animals and their physical environment, and that changes in these conditions are likely to lead to changes in the animal community. Elton (1946) proposed that the structure of communities in complex habitats may differ from those of simpler habitats. The first quantitative study of the effects of habitat structural complexity was by MacArthur & MacArthur (1961) which found the diversity of bird species in a woodland area increased with number of vegetation strata. These findings have been echoed in the significant body of work which has followed. Many of these studies have found increases in both abundance and diversity with complexity across a range of habitats including grasslands (Wiens et al. 1986), streams (O’Connor 1991), seagrass (Heck Jr & Wetstone 1977), mangroves (Nagelkerken et al. 2010) and coral reefs (Hixon & Beets 1993; Gratwicke & Speight 2005).

The mechanisms behind this relationship are likely to be diverse, and a number of theories regarding the relationships still exist. Initially it was believed that this relationship was associated with increases in surface area found in more structurally complex habitats (Risk 1972; Dean & Connell 1987). However, studies since have demonstrated that more complex areas do not necessarily have greater surface areas (Sher-Kaul et al. 1995; Warfe et al. 2008) indicating this relationship is more complex. Another hypothesis is that more complex habitats contain a greater number of niches due to the diversity of microhabitats available (Kovalenko et al. 2011). In a complex habitat, the physical structure available will influence niche availability and this will play a role in the distribution of organisms (Menge & Sutherland 1976). This idea has been examined using specific habitat structures to explore relationships independent of surface area (O'Connor 1991; Forrester et al. 2004; Beck 2006). Examples of these structures include holes for refuge (Hixon & Beets 1993) or nest sites (Newton 1994), trees for foraging (Robinson & Holmes 1982) and vegetation for ambush predators (Heck & Crowder 1991). A number of these structures have been found to have important roles for the associated communities. However, any positive effect these structures have on diversity or abundance will likely decline with increasing density of physically uniform structures (Kovalenko et al. 2011). This means that one dimensional measures of habitat complexity are unlikely to be representative and will be less relevant to community dynamics. It is therefore necessary to record multiple measures of habitat complexity such as the five traits noted by Tokeshi & Arakaki (2012).

1.1.3. *Coral reef fish and habitat structural complexity*

Coral reefs are environments with a high degree of spatial heterogeneity and this spatial diversity has likely led to much of the diversity present on coral reefs (Goreau 1959, Glynn 1976, McCoy and Bell 1991, Tews et al. 2004). This can be seen explicitly in some of the species which undergo ontogenic shifts in their habitat selection, immigrating from nearby habitats or moving to different reef zones or areas as they outgrow nursery habitats or undergo dietary shifts (Lirman 1994, Dahlgren and Eggleston 2000, reviewed in Adams et al. 2006). In Nassau grouper (*Epinephelus striatus*), macroalgal-dominated areas are key settlement habitats for larval recruits (Eggleston 1995). Growth precedes movement to new habitats as individuals transition between juvenile stages; these ontogenic habitat shifts were linked to size-dependent trade-offs between refuge from predation and foraging (Dahlgren and Eggleston 2000), indicating a close link between the structure of reefs and habitat preferences. Even species that remain relatively small throughout their life-time undergo cross-patch migrations on reefs. Threespot damselfish (*Stegastes planifrons*) juveniles are primarily found in lagoon or back-reef areas before migrating to the fore-reef as adults (Lirman 1994). This may be a result of the highly territorial nature of threespot damselfish, where adults outcompete juveniles for favourable habitat on the main reef displacing them to less desirable areas.

Reef condition can influence which species are present in a given area. There are a number of species on coral reefs that are highly specialised to certain habitats (Wilson et al. 2008a). This is unsurprising given the high number of niche environments the coral reef ecosystem possesses (Sale 1977). The extent of a species' specialisation to certain habitat features has been found to be one of the characteristics which determine how that species responds to changes in its environment (Feary et al. 2007b, Wilson et al. 2008a). The degree of specialisation or generalisation exhibited by a species falls somewhere along a gradient which can be measured by the number of different habitats within the system a species can be recorded as using (Devictor et al. 2008). In the Indo-Pacific region there are a number of species that rely almost exclusively on live coral for food or shelter, unsurprisingly these species have suffered more severe declines in response to disturbance events which reduce live coral cover (Feary 2007, Graham et al. 2007, Pratchett et al. 2008, Wilson et al. 2008a). Unlike their Indo-Pacific counterparts, Caribbean reef fish are less dependent on living corals for food or refuge (Paddack et al. 2009). This is not to say that Caribbean reef fishes are not coral-habitat specialists' only that their level of specialisation is likely to be based more on the habitat features with which they associate rather than with live coral cover as in the Indo-

Pacific (Freeman and Alevizon 1983, Ménard et al. 2007, Precht et al. 2010). Alvarez-Filip et al. (2015) identified a decline in specialists on Caribbean reefs through a broad-scale trend-based approach. This has highlighted the species which are more susceptible to the loss of reef structure. Understanding habitat use gives insights into the manner in which changes to the environment will affect the associated communities. The ongoing changes to Caribbean reefs make it increasingly important to understand these complicated species-habitat relationships and how further degradation will alter these relationships and ultimately the survivorship of more specialist species.

Observations of fish utilising specific structures have identified strong links between the two. Habitat features, such as coral patches and bowls are used as schooling areas which fish return to daily (McFarland and Hillis 1982), sometimes over many generations (Ogden and Ehrlich 1977). Increasing the number of tabular structures on a fringing reef in Australia was found to alter the abundances of fishes in several families (Kerry and Bellwood 2015a). This appears to be because they provide necessary shade in shallow tropical water where the sun's UV rays can penetrate, rather than acting as shelter from predation (Kerry and Bellwood 2015b). The negative effects of UV rays have only recently been identified as a danger to fish (Sweet et al. 2012) but this effect could potentially play a key role in controlling how fish utilise structures. Further examination of the pathways between fish and structure will undoubtedly shed greater light on the number of services habitat structural complexity will provide. This puts increased importance on shade-providing structures such as large towers or overhangs, especially in the Caribbean where tabular corals are not present. Female bluehead wrasse (*Thalassoma bifasciatum*) select spawning sites based on habitat structure rather than the quality of the male (Warner 1987). Preferred sites are those on the edge of the reef with vertical projections which lessen the distance to the open water.

In addition to the structural features on a reef there is also the space created in-between these features. Where this space is small enough so as to exclude larger predators it can provide an area of permanent refuge for smaller individuals where they can remain safe until they need to venture out (Buchheim and Hixon 1992). Alternative areas of refuge may be important for temporarily escaping the visual field of predators (Samhouri et al. 2009). It is therefore important to understand the relationships between communities and refuge in order to understand and identify specific patterns such as whether body-size is closely linked to refuge utility or whether a larger shelter will provide refuge for a greater number of individuals.

1.1.4. Role of the diel cycle on habitat structural complexity relationships

Circadian rhythms have been detected in a range of phyla (Edgar et al. 2012) and changes in behaviour widely are observed in animal taxa which experience changes in light levels over the diel cycle (Wager-Smith and Kay 2000, Reebs 2002, Reppert and Weaver 2002). However, given that species likely utilise structure differently based on these activity patterns it is surprising that thus far relatively little attention has been paid to structural associations over the diel cycle. Where this relationship has been examined there appears to be a bimodal relationship with structure at night. Those groups which are nocturnally active move into more open areas to feed, examples of these species include: rabbits (Moreno et al. 1996), salmonids (Jakober et al. 2000), plovers (Thibault and McNeil 1994) and freshwater shrimps (Elliott 2005). In contrast, many organisms, including: baboons (Cowlishaw 1997), parrotfish (Helfman 1986) and many bird species (Buttemer 1985, Martin 2010) which forage during the day retreat into shelter created by a range of structures. Closer understanding of these relationships is important when examining the interaction between communities and habitat structural complexity and the relationship between the two will be better understood when the nocturnal relationships are investigated.

Refuge is a key feature of the habitat which is used by nocturnally active species during the day (Ménard et al. 2007) and by diurnally active species during the night (Helfman 1986). Utilisation of space on the reef also changes with the diel cycle, nocturnally active families such as grunts (Haemulidae) and snappers (Lutjanidae) aggregate on reefs during the day, and migrate to flatter, less complex areas to forage at night (Burke 1995, Hitt et al. 2011). Understanding how these groups relate to reef structure nocturnally as well as diurnally is key in filling in knowledge gaps as to how the reef community relates to habitat structural complexity.

1.2. Functional Diversity

Species diversity is commonly measured as a function of the abundance and variety of taxonomically distinct species present. This diversity is an important factor in the health of a system, and plays an important role in the structure of animal assemblages (Feary et al. 2007a). The degree of susceptibility of animals to changes in habitat quality is seemingly species-specific and highly dependent on the resource requirements of the particular species. Though this level of information about the community provides detail about the relationships between the habitat and organisms, species diversity reveals little of the functional ecology of an environment and the mechanistic details of how community change can impact an ecosystem.

Species within an ecosystem can be described as having functional roles. One method of determining this role is through the examination of a species' functional traits. A trait is defined as a morphological, physiological, behavioural or phenological feature measurable at the individual level (Violle et al. 2007). A functional trait is a descriptor of how organisms interact with the environment and each other (Lefcheck et al. 2015). Functional diversity is then the community-wide variation in functional traits among organisms (Lefcheck et al. 2014). Understanding the functional diversity of a habitat reveals the range of strategies used in a system and the number of species using those strategies (Villéger et al. 2010). A complex environment such as a healthy coral reef or kelp forest would therefore be expected to have a high functional diversity in order to fill the many niches created when compared to degraded reefs or urchin barrens respectively (Steneck et al. 2002, Mouillot et al. 2014). Importantly, the functional diversity held within a system can enhance positive feedbacks, further enhancing habitat quality through defined functional roles. Consequently, the higher the number of species that are capable of playing key functional roles, the higher the system's functional redundancy and the more resilient a system will be to perturbations.

Functional redundancy is the ability of multiple species to contribute to the functioning of an ecosystem in equivalent ways, such that one may be substituted for another (Lawton and Brown 1993, Fonseca and Ganade 2001). All roles in maintaining the vital equilibrium of a system must be fulfilled, whether it is by one or one thousand species (Fonseca and Ganade 2001), meaning that many species may have the same role. If the population size of those species is directly controlled by the abundance of other species within the same functional role, it could be suggested that the more species there are to fulfil that role, the higher the functional redundancy.

1.2.1. *Measuring Functional diversity*

Functional diversity is a multifaceted measure and should be examined as such. Measures of functional diversity have received much recent attention and have been the subject of two detailed reviews (Mouchet et al. 2010, Schleuter et al. 2010). There are considered to be three components of functional diversity: functional richness, functional evenness and functional divergence (Mason et al. 2005) and a range of indices have been created in order to capture these. However, these indices are not always independent of one another and their ability to describe the two key issues concerning functional ecology, the influence of diversity on ecosystem functioning and the ability of indices to reveal assembly rules, is mixed (Mouchet et al. 2010). Mason et al. (2003) proposed ten criteria which an index of functional diversity should capture.

Three complementary indices, FRic, FEve and FDiv, proposed by Villéger et al. (2008), can be used in combination to more fully describe the functional community, and which when combined meet the ten functional diversity criteria (Mason et al. 2003). FRic provides a measure of functional richness which is the range of trait values present in the community when all traits are considered together, and is calculated as the minimum convex hull volume that includes all species in the community (Villéger et al. 2008). FEve captures functional evenness through the distribution of abundance in functional trait space (Mason et al. 2005). The index decreases when abundance is less evenly distributed among traits and species (Villéger et al. 2008). FDiv measures functional divergence which identifies how abundances are distributed across the functional trait axis, within the range of the observed community (Mason et al. 2005), informing whether the most abundant species in a community have common or rarer traits. Utilising this approach provides a clear structure for more directly addressing questions about how changes in the environment will influence the functional diversity of a community. Through these three components it is possible to understand how their interactions with environmental processes will affect ecosystem productivity, resilience and resistance to invasion (Mouchet et al. 2010).

1.2.2. *Functional groups*

A functional group can be defined as a collection of species that perform a similar function, irrespective of their taxonomic resemblance, and identified by their roles in ecosystem processes (Hooper et al. 2002, Cadotte et al. 2011). It is the diversity and abundance of these groups which influence ecosystem functioning. Coral reefs are an ecosystem which sustains a diverse assembly of functional groups (Elmqvist et al. 2003), from the framework builders themselves (the scleractinian corals), and primary producers, to the herbivores and higher predators (Done et al. 1996). The functional groups fulfilled within a coral reef community will not necessarily vary between sites, but the species richness and taxonomic composition within those functional groups may be markedly different (Bellwood et al. 2004). Species are collated into functional groups based on their functional traits. A healthy and resilient system would be expected to retain all the functional groups necessary for ecosystem functioning, and for those groups to contain a number of species capable of performing that specific role, making it functionally diverse with high inbuilt levels of redundancy.

The most commonly employed groupings are based on diet, as this information is relatively easy to access and gives a level of detail as to how groups interact within the system. This can be useful as a broad measure given that herbivore populations are important to ecosystem resilience (Scheffer et al. 2001) and predators can influence important trophic cascades and can protect against invasive species (Ritchie et al. 2012). The use of multiple traits will further separate groups and can provide a more accurate representation of the position and function of a group within the system. For example, not all predators are identical in their role, and including size alongside diet will separate this into multiple groups revealing much more about the potential influence a group will have on ecosystem processes. Functional groups have already provided a basis for considering the roles played by coral reef fish within the system, and their relative importance in maintaining the resilience of the reef and avoiding ecological phase shifts (Hughes et al. 2003). However, the impact that changes in the coral reef environment will have on the functional groups has received less attention (but see Mouillot et al. 2013) and the potential impacts of habitat degradation must be more fully understood.

1.3. Coastal waters of the Caribbean

The greater Caribbean region lies between 8 and 23°N and -59 and -89°E (Figure 1.1) and includes the area as far north as the Turks and Caicos Islands, south to Leeward Antilles, east

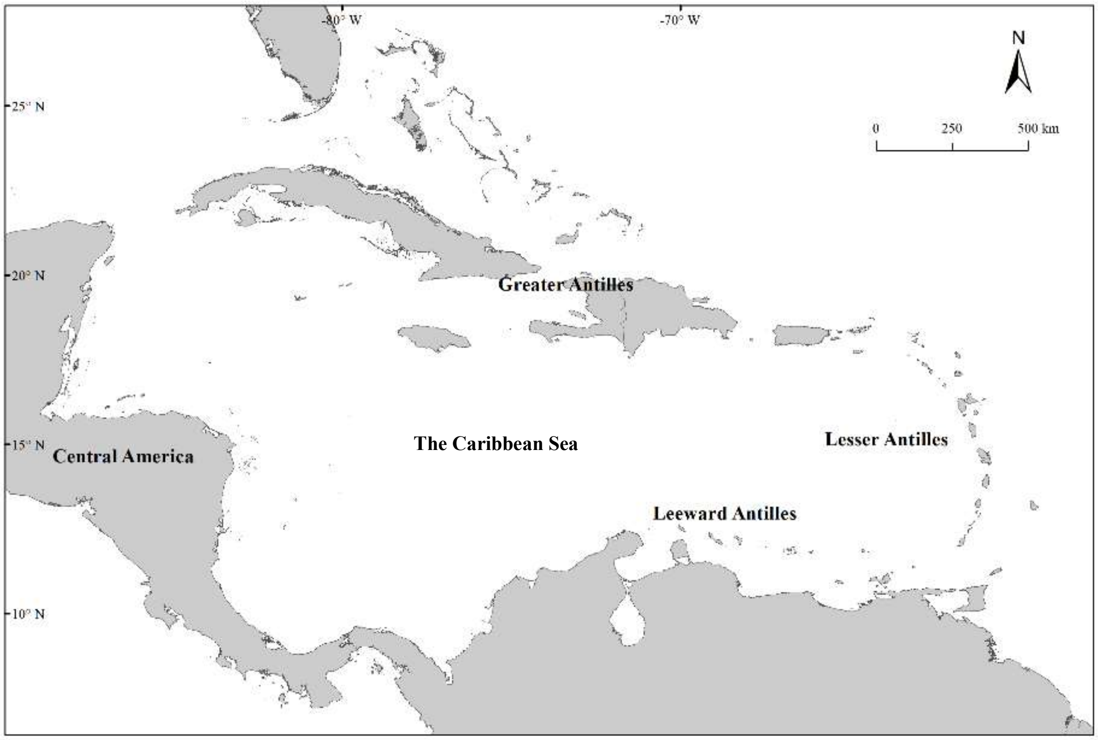

Figure 1.1 The greater Caribbean region which is divided into four sub-regions as indicated. Countries within Central America include Mexico, Belize, Honduras, Costa Rica, Panama and Nicaragua. The Greater Antilles are in the north of the Caribbean and run from Cuba in the west to Puerto Rico in the east. The Lesser Antilles island chain in the east lie between the Virgin Islands in the north and Trinidad & Tobago in the south. The three countries of the Lesser Antilles are Aruba, Curaçao and Bonaire.

to Barbados and west to the coast of Central America. The Caribbean region has traditionally been divided into four sub-regions (Table 1.1). The largest of the island sub-regions is the Greater Antilles which makes up 88% of the Caribbean’s island land area. The Lesser Antilles extend from the Virgin Islands south to Trinidad & Tobago. The Leeward Antilles are made up of Aruba, Bonaire and Curacao in the far south of the Caribbean Sea, off the coast of Venezuela. The other two sub-regions are the Lucayan Archipelago to the north of Cuba, which includes the Bahamas and the Turks & Caicos Islands and the Caribbean coast of Central America. The Caribbean has a diversity of landforms; some islands are mountainous while others are virtually flat. There are also a range of land sizes from small islets to the continental landmass of Central America. The region has at least 17 active volcanoes, and it is the contact point for six tectonic plates with the majority of islands found on the edge of the Caribbean Plate. At its eastern edge the denser Atlantic Plate is subducting beneath the Caribbean Plate which created the mountainous Lesser Antilles. To the north the Caribbean and North American Plates are sliding past each other, resulting earthquakes can impact the northern Caribbean islands from Cuba to Antigua. Several of the low-lying islands are products of coral reef growths on submerged banks.

With the exception of the northern two thirds of the Bahamas, all of the Caribbean lies within the tropics, resulting in a narrow temperature range, between 24 and 32^{o}C. The differences in size, shape, topography and orientation greatly influence the amount of rainfall received by the various landmasses. The windward sides of the larger more mountainous areas can receive much rain, whereas leeward sides can have very dry conditions. Flat islands will receive less but more consistent rain across the island. Hurricanes are a key feature the region's climatology, with the season lasing from June to November. They develop in the North Atlantic when the sea surface temperature is high, and tend to travel in a north westerly direction across the Caribbean, following a range of pathways. Islands in the southern region are rarely subject to hurricanes, while those in the north and east are frequently hit. Hurricanes can cause severe ecological and economical damage.

The prevailing currents through the Caribbean run in a westerly direction. Water flows in from the Western Atlantic, through the leeward Antilles towards Central America (Murphy et al. 1999). This flow regime can have a profound influence on connectivity between islands and reef areas. The Caribbean has four regions of connectivity, the eastern Caribbean, the western Caribbean, the Bahamas and the Turks and Caicos Islands, and the area along the coasts of Columbia and Panama in the south west (Cowen et al. 2006). The area around Jamaica and Hispaniola are in a zone of mixing between regions, meaning it has multiple sources of larval input (Roberts 1997, Cowen et al. 2006). Despite the apparent connectivity within regions across the Caribbean there are also individual islands which are more isolated. Both Barbados and Trinidad & Tobago are outside of the prevailing flow meaning they have little influx of larval recruits, therefore the reefs must be primarily self-seeded (Roberts 1997, Cowen et al. 2006). These patterns of connectivity can have important consequences for the coral and fish species of the region (Baums et al. 2005, Jones et al. 2009). This is also true for more sinister influences on the Caribbean reef community. Water-borne diseases are able to travel throughout the region relatively rapidly which can cause severe damage to the reefs (Lessios et al. 1984, Aronson and Precht 2001). Invasive species are also a potential threat to the ecosystem of the region; species of coral (Riul et al. 2013) and fish (Schofield 2009) have been transported throughout the region by the currents.

Attempts have been made to categorise the marine regions of the Caribbean, both as part of a global ecosystem mapping process (Spalding et al. 2007, Sherman and Hempel 2009, Longhurst 2010) and as a targeted Caribbean study (Chollett et al. 2012). These regional mapping projects have taken different approaches. Spalding et al. (2007) used an expert-driven approach, utilising existing literature to classify the Caribbean into nine ecoregions within the larger Tropical Northwestern Atlantic province. Utilising a large marine ecosystem (LME) approach the Caribbean has also been viewed as two regional units (Sherman and Hempel 2009, Longhurst 2010). A potentially more ecologically relevant approach has divided the region into 16 physiochemical environments based on environmental data (Chollett et al. 2012). Attempts have also been made to produce biogeographical maps of the Caribbean (Miloslavich et al. 2010), however there appears to be no biogeographic regionalisation of the Caribbean, though detailed regional studies are lacking (Miloslavich et al. 2010).

Table 1.1 Total population, land area and population density of countries within the Caribbean region. Source www.dataworldbank.org unless otherwise stated. *source www.insee.fr/en/,+source www.caricomstats.org,†source www.statline.cbs.nl

Sub-region	Country Name	Total population	Total land area (km^2)	Population density (km^2)
Central America	Belize	331,900	22810	15
	Nicaragua	6,080,478	120340	51
	Honduras	8,097,688	111890	72
	Panama	3,864,170	74340	52
	Costa Rica	4,872,166	51060	95
Greater Antilles	Cuba	11,265,629	106440	106
	Cayman Islands	58,435	240	243
	Dominican Republic	10,403,761	48320	215
	Haiti	10,317,461	27560	374
	Jamaica	2,715,000	10830	251
	Puerto Rico	3,615,086	8870	408
Lesser Antilles	Anguilla			
	Antigua & Barbuda	89,985	440	205
	Barbados	284,644	430	662
	Dominica	72,003	750	96
	Grenada	105,897	340	311
	Guadeloupe*	405,739	1628	249
	Martinique*	386,486	1128	343
	Montserrat+	4,922	104	47
	Saba”	1,991	13	153
	St. Barthélemy*	9,035	25	361
	St. Eustatius”	3,897	21	186
	St. Kitts & Nevis	54,191	260	208
	St. Lucia	182,273	610	299
	St. Martin (French)	31,264	54.4	575
	St. Maarten (Dutch)	39,689	34	1167
	St. Vincent & the Grenadines	109,373	390	280
	Trinidad & Tobago	1,341,151	5130	261
	Virgin Islands (U.K.) +	2,700	153	18
	Virgin Islands (U.S.)	104,737	350	299
Leeward Antilles	Aruba	102,911	180	572
	Bonaire†	15,666	294	53
	Curaçao	153,500	444	346
Lucayan Archipelago	Turks & Caicos Islands	33,098	950	35
	Bahamas	319,031	13,878	23

1.4. Coral reefs of the Caribbean

The coral reefs of the Caribbean are extensive, covering approximately 26,000km^2 (Burke and Maidens 2004). They are frequently associated with seagrass beds (66,000km^2 (Jackson 1997)) and mangrove habitats (11,560km^2 (FAOSTAT 2014)), creating a biodiverse and expansive environment crucial to the ecological health of the Caribbean region. The Caribbean is home to the second largest barrier reef in the world, the Mesoamerican Reef, which is ca.1000km long, stretching between the tip of the Yucatán Peninsula, down the coasts of Mexico, Belize, Guatemala and the Bay Islands of Honduras. The dominant reef types around the Caribbean islands are fringing reefs which have built up along the edges of islands over geological time scales.

1.4.1. *Corals*

The Caribbean has only ca. one seventh the number of coral species of the Indo-pacific (Bellwood et al. 2004) in all there are ca. 70 species of scleractinian reef building corals. The corals are often divided into groups by their morphology (Table 1.2) which allows for a better understanding of their ecological role. These hard corals are the building blocks of the reef environment creating the framework upon which the coral reef ecosystem rests. The structure they create provides a range of ecosystem services and provides the platform for all other life on the reef to settle, grow and live.

1.4.2. *Non-Coral Benthos*

Key non-hard coral groups include octocorals, sponges, turf algae and macroalgae. Non-coral benthic species are likely to be more temporally dynamic due to rapid growth rates and susceptibility to disturbances (Syms and Jones 2001). These groups also provide an additional suite of growth forms on the reef which, for soft coral and sponges, can add significantly to the structure of the reef and may also provide habitats and food for reef fauna. The role of sponges on reefs varies by species; burrowing sponges may decrease reef structure and stability while accreting species provide unique structures and many have epizoic relationships with fish and invertebrates (Diaz & Rützler 2001). Turf algae are a key food source for the herbivorous fish populations on reefs, however they can inhibit the settlement of coral larvae (Arnold et al. 2010). If unchecked algal turfs can become dense fleshy macroalgae patches, which are unattractive (Hoey and Bellwood 2011) and inedible to most herbivorous fish species (Bellwood et al. 2006) and it can take disturbance events to remove them (Mumby et al. 2005). However, following these events algae, if not grazed, appear to be better at occupying free space on the reef (Williams et al. 2001), preventing settlement of juvenile corals and regrowth of mature corals (Box and Mumby 2007). These algal growths provide little food or refuge to for reef fauna and can grow over holes and crevices, further reducing habitable space on the reef. Non-living substrate including: boulders, sand, rubble and caves is also a key component of coral reefs, providing important habitat for reef fauna (McCormick and Makey 1997, Nagelkerken et al. 2000, Depczynski and Bellwood 2004).

Table 1.2 Common morphological groupings of Caribbean corals

Morphology	Description	Example species	Diagram
Branching	Coral grows in a dendritic shape with long tapered branches and regular splitting	*Acropora palmata* *Acropora cervicornis*	
Boulder	Dense spherical or hemispherical corals	*Siderastrea siderea* *Diploria strigosa*	
Massive	Have knobs, columns or wedges protruding form an encrusting base	*Orbicella annularis*	
Encrusting	Grow as a thin layer over the substrate	*Porites astreoides* *Siderastrea radians*	
Foliose	Have thin plate-like portions rising above the substrate	*Agaricia agaricites* *Agaricia tenuifolia*	
Digitate	Finger-like growths which do not have splitting	*Porites furcata* *Madracis auretenra*	

1.4.3. *Fish community*

There are approximately 1500 marine fish species in the Caribbean (Froese and Pauly 2014), of which ca. 600 species are reef associated, with many more utilising the reef for parts of their life histories. The diversity of the fish community is seen as a key facet in the functioning of the reef itself. Coral reefs in the Caribbean have a lower number of fish species than their Indo-Pacific counterparts (Spalding et al. 2007). This means that the loss of a species will potentially be more keenly felt in the Caribbean as there are fewer alternative species to fill vacant ecological niches, and as such the fish community on coral reefs in the Caribbean has lower levels of functional redundancy than in the Indo-Pacific region (Mouillot et al. 2014).

1.4.4. *Importance of reefs to humans*

This fish community is also an important resource for human well-being across the Caribbean region. The reef fisheries provide a source of income for an estimated 120,000 full-time fishers (Burke and Maidens 2004), plus many additional part-time workers. The fish are popular with tourists and can be sold to restaurants and hotels, providing a steady source of income. Fish are also an important source of food for many coastal people (Chakalall et al. 2007). The reefs have traditionally been an easy, cheap and open access resource. However, changes in reef health and fish populations have changed the relationship between the reefs and the people of the Caribbean. Coral reefs are also a key part of the Caribbean's tourism industry which is ranked first in terms of the sector's contribution to national economies (WTTC 2016). Therefore, maintaining healthy and visually appealing reefs should be a significant priority for the region.

1.5. Caribbean Coral reef degradation

Threats to the coral reef environment come from a range of both chronic and acute, and local and global scale processes. These threats have intensified over recent decades as a result of increases in population sizes, fishing pressure, coastal development, global temperatures, CO_2 levels and incidences of disease (Gardner et al. 2003). The coral reef ecosystems in the Caribbean appear to have been in decline since the first comparative studies in the 1970s (Hughes 1994). Evidence for reef degradation comes from decreased hard coral cover, increased algae cover, decline in habitat structural complexity and declines in fish numbers, notably herbivores and higher order carnivores (Hughes 1994, Gardner et al. 2003, Pandolfi and Jackson 2006, Alvarez-Filip et al. 2009).

1.5.1. *Overfishing*

There has been human pressure on the fish community since the Caribbean was first colonised, and by the 1960s there was believed to have already been up to an 80% decline in fish biomass in some areas of the Caribbean (Hughes 1994). The reef fishery has traditionally been intensely over-fishing species form all trophic levels on the reef (Jackson et al. 2001; Newman et al. 2006). This has changed the taxonomic composition of the fish community markedly as a result of the vulnerability of large bodied predators to fishing impacts (Stallings 2009). Large predatory species such as sharks, snappers, groupers and jacks have virtually disappeared from some locations (Hughes 1994) and those species remaining within these at risk families tend to be smaller bodied (Hawkins & Roberts 2004).

The use of traps to catch herbivorous fish species, notably surgeonfish and parrotfish has greatly reduced the amount of fishes grazing on algae, leaving the reefs heavily reliant on invertebrate herbivores to mitigate the impacts of fish herbivore removal (Hughes 1994). The most important of these invertebrate herbivores, the long-spined sea urchin (*Diadema antillarium*), suffered a mass-mortality event in 1983-84 which affected its entire Caribbean range (Lessios et al. 1984). Model projections suggest that coral cover may still have increased in the face of both hurricanes and significant nutrient impacts provided healthy urchin populations were maintained (Mumby et al. 2006b). However, in the absence of the urchins and with the continued over-exploitation of herbivorous fishes there remained little to prevent algal overgrowth of free space on the reefs. In many places this has led to a shift from coral to algal dominated reefs (Gardner et al. 2003, Mumby et al. 2007).

1.5.2. *Hurricanes*

Hurricanes are one of the most visually distinct disturbances affecting coral reefs, but may help maintain their biological diversity, preventing the dominance of certain strong competitors and freeing space for other species to settle (Connell et al. 2004). However, against the background of declining reef health and the low herbivore numbers in the Caribbean it is unlikely that these disturbances have this positive effect. Gardner et al. (2005) suggested four trajectories for these declining reefs in the aftermath of a hurricane (Figure 1.2): recovery, stasis, resumption or synergy.

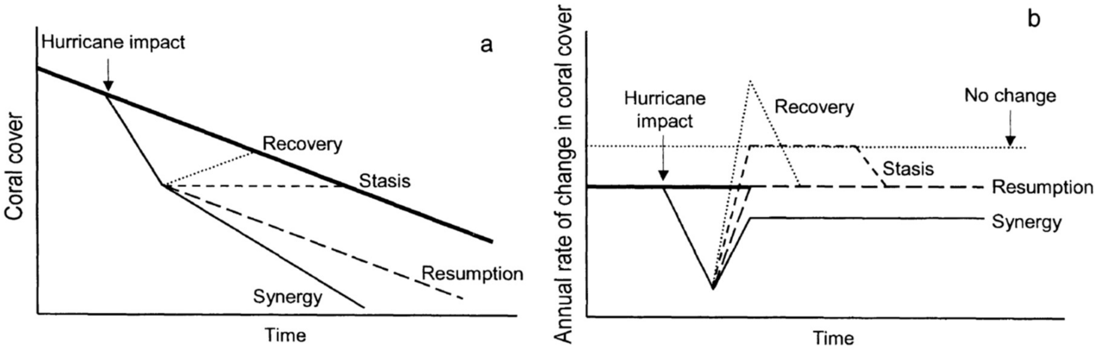

Figure 1.2 Four potential trajectories of coral cover following a hurricane on an already declining coral reef, shown as a. absolute coral cover and b. annual rate of change in coral cover. Bold lines represent change in coral cover at non-impacted sites (taken from Gardner et al. 2005).

Branching corals such as *Acropora* spp. are the most susceptible to hurricane damage, however they may benefit from hurricane disturbance due the dispersal of fragments which can settle and re-grow (Fong & Lirman 1995). More robust morphologies, such as massive or encrusting corals, are better able to withstand hurricane damage, are less likely to be broken like branching corals, and are more resilient to the direct impacts of hurricanes (Foster et al. 2013). This means hurricanes will have an immediate impact on the structural complexity of coral reefs, clearing areas of highly complex but structurally fragile corals, leaving less complex growth forms. On a healthy, resilient reef, the fragments of the fast-growing branching species should help regenerate the habitat structure, however with the multitude of threats to Caribbean reefs, the damage caused by hurricanes can be long term (Hughes 1994).

The range and severity of hurricane damage are dependent on its intensity which, even for the most severe, is unlikely to damage reefs outside of a 100km diameter (Gardner et al. 2005). They are therefore important at some localities but they do not explain regional patterns of decline across the Caribbean, especially as the southern Caribbean is rarely in the path of hurricanes.

1.5.3. *Disease*

The acute degradation of Caribbean reefs is believed to have started with an outbreak of white-band disease (WBD) which led to wide-spread declines in the cover of *Acropora* spp. coral (Aronson and Precht 2001, Schutte et al. 2010). This disease is now prevalent across the whole Caribbean region and has resulted in the death of a large proportion of the acroporid colonies (Goreau et al. 1998). A number of other Caribbean coral diseases including black band, dark spots, white pox, yellow band and white plague (Sutherland et al. 2004) cause varying degrees of coral mortality, with some having been present for many years, while others have apparently emerged more recently. Different diseases appear to be more common on some coral species than others, however the ultimate causes of these diseases is unknown. Only black band disease is correlated with pollution levels (Jones et al. 2012), however it can now be found in most places, even those lacking any significant levels of water pollution (Sato et al. 2016). Most coral diseases in the Caribbean have now spread throughout the region and are prevalent on coral reefs in even the most remote areas (Weil and Rogers 2011).

Environmental stresses such as abnormal shifts in temperature, salinity, water clarity, oxygen, nutrients or sedimentation can cause stress in coral colonies leaving them more susceptible to diseases (Weil and Rogers 2011). Coral diseases are now commonplace across the Caribbean, and as a result of the highly connected nature of the marine environment it is unlikely that this situation will change; in fact, it is believed that the effects of climate change and ocean acidification are likely to lead to increases in the prevalence and severity of diseases (Hoegh-Guldberg et al. 2007).

1.5.4. *Global threats*

Caribbean reefs are subject to an array of pressures acting on a global scale. These are primarily linked to unprecedented rates of change in global temperatures and atmospheric concentrations of CO_2 (IPCC 2014). The impact of these on coral reefs can be seen in a number of different ways. Increased sea temperatures can lead to coral bleaching, with significant events happening in the Caribbean in 1998, 2005, 2010 and 2016 (Hoegh-Guldberg 1999a, Donner et al. 2007, Alemu and Clement 2014, Eakin et al. 2016). The most severe of these caused up to 80 per cent of corals to bleach in some areas resulting in a mean mortality of over 60 per cent (Eakin et al. 2010). Additional effects of temperatures include stress to the coral, which can leave them more susceptible to disease or being out competed (Hoegh-Guldberg 1999a, Hughes et al. 2003). In addition to increasing temperatures greater levels of CO_2 in the atmosphere is driving ocean acidification (Hoegh-Guldberg et al. 2007). Though this has not yet reached levels which measurably affects corals, it has the potential to severely impact on coral calcification rates (Evenhuis et al. 2015) and add significantly to the stressors which will drive coral reef futures (Pandolfi et al. 2011).

1.6. Justification

Understanding these threats requires an improved comprehension of the ecosystem processes which underlie the functioning of coral reefs. Key amongst these is the role of the physical structure of the reef itself. The range of complexities created by different reef formations and coral species have made for an environment which is conducive to examining these relationships, yet little is known about how mobile species interact with the reef framework. The utilisation of space on reefs by animals such as fish is key to predicting how degradation will affect the ecosystem and the humans that rely on them. Such understanding will offer insight into how species, functional groups and size classes react to loss of habitat structure.

The Caribbean has been undergoing the continued loss of structurally complex corals since the 1970s. Over this time alternative species and growth forms have provided the framework (McClanahan & Muthiga 1998). Artificial reef structures have been constructed at small scales, in an effort to maintain the reef structure in the face on continued coral loss (Clark and Edwards 1999, Edwards and Gomez 2007). A primary justification for this work is that the examination of reef architecture will serve to expand our understanding of the form and function of the reef as a habitat, identifying the details of the reef matrix which may have thus far gone unnoticed or evaluated.

The coral cover of Caribbean reefs has been declining for 40 years, changes in associated fish community structure were negligible until 10 years ago (Paddack et al. 2009); the lag response of reef fish to coral loss events in the Indo-Pacific of 5-10 years (Graham et al. 2007) looks to be significantly shorter than that experienced across the Caribbean. These changes in the Caribbean fish communities are thus unlikely to be exclusively linked to live coral-cover loss. Unlike their Indo-Pacific counterparts, no Caribbean reef fish are obligately dependent on living corals for food, therefore decline in reef fish communities appears to more closely relate to generic effects of the loss of reef structure. Directly examining the relationship between the fish community and the services the reef matrix provides is clearly needed.

While temporal trends in Caribbean reef complexity and community structure have been explored through sparse existing data (Risk 1972; Gratwicke & Speight 2005; Alvarez-Filip et al. 2009; Alvarez-Filip et al. 2011) there is at present no methodologically-constrained information on spatial trends in Caribbean regional complexity and biodiversity, yet this is crucial for understanding the current status of reefs, the extent of ongoing changes, and the implications for environmental managers. The present work will provide a contemporary, Caribbean-wide understanding of the structural condition of reefs in the region and identify the environmental drivers for this and the implications for fish communities.

1.7. Thesis outline

This thesis is a macroecological study of Caribbean coral reef habitat structural complexity and how changes in reef structure might influence associated fish communities. First, using an extensive spatial and environmental data set it aims to examine the dynamics driving structural complexity across the Caribbean. An assessment of contemporary reef habitat structural complexity in 15 countries was performed and relationships with spatial, environmental and anthropogenic variables were used to examine their influence on reef structure. In the second data chapter the method in which habitat structural complexity is measured is examined. Given the idea that habitat structural complexity is a human construct derived from observing the shape and three-dimensional structure of a habitat, it follows that measurements have traditionally be based on human perception. Here the aim was to develop a multivariate model which better captures habitat structural complexity as a multidimensional feature using a pathway modelling approach which allows multiple variables to be combined and the direct and indirect relationships examined. This approach is then tested in the following data chapter using a refuge variable derived from this pathway methodology. The relationship between refuge and the functional community of Caribbean coral reef fish was examined. Using refuge as a predictor, the effects of changes in habitat structural complexity on the functional diversity, functional groups and size ranges of groups of was determined. The final data chapter investigates both the relationship between the fish community and habitat structural complexity at night and diurnal behavioural relationships with reef structure. A paucity of data in these two areas have left significant gaps in the knowledge about fish community – habitat structural complexity relationships. Through this analysis changes in community relationships across the diel cycle with the reef structure are revealed and by observing behavioural interactions with the structure a range of mechanistic pathways for community level changes in response to modifications in habitat structural complexity are elucidated. In the final chapter the findings of the thesis are reviewed and the outputs placed within the wider field of ecology and how it might add insight into how changes in coral reef habitat structural complexity have occurred and affected the associated fish communities. A potential future for reefs in light of this research and the current knowledge on the impacts of climate change is postulated. Finally, the management implications of the findings presented are discussed and future directions for research in habitat structural complexity and its relationship with associated communities are suggested.

2. Spatial dynamics of Caribbean structural complexity

2.1. Introduction

Coral reefs are dynamic, biogenic ecosystems which experience a broad range of natural and anthropogenic forcings that interact to shape the reef environment. The calcium carbonate skeleton hard corals produce provides the building blocks for one of the most diverse ecosystems on the planet (Connell 1978). This physical structure has a profound influence on the associated diversity and functioning of the reef ecosystem (Pratchett et al. 2011). However corals are currently facing an increasing number disturbances (Glassom 2014) which are shifting the dynamics of the reef environment from one which rebounds and diversifies following a disturbance (Pearson 1981, Aronson and Precht 1995, Syms and Jones 2000) to one which continues to lose living coral and can ultimately shift to an alternative state (Hughes 1994, Bellwood et al. 2004, Mumby et al. 2007, Norström et al. 2009). This has led to significant declines in hard coral cover on reefs throughout the world's coral reefs (Gardner et al. 2003, Bruno and Selig 2007, De'ath et al. 2012). The impacts of coral loss on the wider reef ecosystem may have been mitigated somewhat by the persistence of the coral skeleton after death (Wilson et al. 2006, Graham et al. 2007, Pratchett et al. 2008). However the contemporary decline of physical structure of reefs in the Caribbean (Alvarez-Filip et al. 2009) and elsewhere (Wilson et al. 2006, De'ath et al. 2012) will have impacts on communities and ecosystem goods and services (Burke et al. 2008, Pratchett et al. 2008, Wilson et al. 2008a, Alvarez-Filip et al. 2011c, 2015, Ferrario et al. 2014).

Coral reef structural complexity is important both ecologically and socio-economically (Alvarez-Filip et al. 2011a, Graham and Nash 2012, Ferrario et al. 2014). Reef structure provides a 3-dimensional habitat which is home to a diverse range of species and communities. This structure provides shelter from predation (Hixon and Beets 1993), mating sites (Warner 1987) and increased foraging opportunities (Almany 2004b). As a result the abundance, diversity and biomass of both coral reef fishes and invertebrates are all influenced by reef habitat structural complexity (Dean and Connell 1987, Wilson et al. 2008a, Alvarez-Filip et al. 2015). Therefore, the loss of structural complexity is likely to drive declines in a number of aspects of the reef community (Newman et al. 2015) and subsequently affect fishery productivity (Micheli et al. 2014). The structure of nearshore coral reefs also plays an important role in the provision of services to coastal communities, including healthier fish populations for artisanal fisheries, increased desirability to tourists and enhanced coastal protection through wave energy attenuation (van Zanten et al. 2014).

A recent regional-scale analysis identified a significant decline in the structural complexity of Caribbean coral reefs (Alvarez-Filip et al. 2009). This study used the rugosity index (RI) measure of structural complexity (Risk 1971) to place reefs into five RI categories (1.0–1.49, 1.5–1.99, 2.0–2.49, 2.5–2.99 and >3.0), the proportion of complex reefs (defined as an RI >2) had declined from ca. 45% to ca. 2% over the past 40 years. Spatial patterns of structural complexity across the region have not been examined in detail, leaving a gap in our knowledge about the structural complexity of reefs across the region. A range of factors influence reef complexity at a given location and understanding how these interact will allow predictions of future changes in complexity and concomitant functioning of coral reefs. Degradation of coral structure appears to have begun at a similar time to the early coral die-off and continued in three distinct phases over the last 50 years (Alvarez-Filip et al. 2009). Despite this concurrent loss in both corals and structure, total coral cover has not been found to explain changes in complexity (Alvarez-Filip et al. 2011b). Therefore, it is necessary to understand the impacts of other potential drivers of complexity in the region.

A range of different environmental and anthropogenic drivers are likely to have had an influence on Caribbean coral reef structural complexity over this time frame. Hurricanes, wave exposure and sea surface temperature (SST) all have the potential to degrade reef structure. Hurricanes can cause severe structural damage (Hughes 1994, Goldenberg et al. 2001). However the scale of their impact can be highly variable and reefs in close proximity to one another can experience different levels of damage (Bythell et al. 1993). This has been ascribed to variation in reef structure, presence of alternative stressors or the scale of observation (Gardner et al. 2005). Wave exposure has been shown to affect colony growth and reef formation (Yamano et al. 2003, Kench and Brander 2006). Furthermore high wave exposure can mobilise sediment which has a scouring effect on the reef area, preventing settlement and survival of new recruits (Dahlgren 1989, Torres et al. 2001) and reducing further structural growth. The distribution of *Orbicella annularis*, a key structure building coral, is strongly influenced by wave exposure in the Caribbean (Chollett and Mumby 2012). SST will have indirect effects on coral structure as high temperatures can lead to coral bleaching, which if prolonged can lead to colony death (Jackson et al. 2014). This prevents coral growth and leaves the remaining coral structure at a greater risk of erosion (Graham et al. 2006).

Proximity to human populations can also put reefs at risk of degradation through a number of direct and indirect pathways. Anchor damage, ship groundings, diver damage and destructive fishing practices can all cause breakage to coral colonies (Chabanet et al. 2005). Overfishing, nutrient runoff or sediment from developments can increase stress on corals leading to death over time (Nyström et al. 2000). However, capturing these independent effects is logistically challenging. As the value of healthy coral reefs for tourism increases, many areas close to tourist developments have become part of marine protected areas (MPAs), which may increase coral survivorship and help maintain structure at higher levels than surrounding, unprotected areas (Hughes et al. 2003), making them more attractive tourist destinations.

When systems are stacked in space, and the entity is itself fixed in space, then it is inevitable that many of the system drivers (e.g. weather, temperature) are bound to be co-related. They are also therefore almost guaranteed to interact both directly and indirectly in their effects on system function. This is particularly true for coral reef systems where the position of a coral at settlement dictates the range and magnitude of environmental drivers such as hurricanes and SST and the proximity to human populations, which can all affect future reef growth and development.

Due to the functional importance of coral reef structural complexity to the Caribbean coral reef community (Newman et al. 2015) understanding the drivers of structural complexity and the subsequent spatial patterns of reef structure across the region is essential. Here an extensive dataset covering 15 countries and a range of reef types has been examined for spatial patterns and environmental and anthropogenic drivers of reef structural complexity. The specific objectives of the study were to 1) examine the contemporary state of coral reef structural complexity in the Caribbean basin and through examination of the correlation structure of the data, identify spatial relationships in it and 2) analyse environmental and anthropogenic drivers of structural complexity across the Caribbean region and identify geographic patterns in these.

2.2. **Methods**

Sites were selected based on the availability of complexity and coral cover data. All rugosity and coral cover data were provided directly by the principal investigator of a given study collecting relevant data within the five-year time period from 2007 to 2012. In total data from 265 sites across 15 different Caribbean countries[1]: Anguilla[†], Antigua[*], Barbados[*], Belize[*], Bonaire[*], the British Virgin Islands[†], Curaçao[*], Dominican Republic[*], Honduras[*], Jamaica[*], Mexico, Puerto Rico, St. Lucia[*], St. Vincent & the Grenadines[*] and the Turks & Caicos

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[1] Data used in this chapter includes the full FORCE dataset (10 countries indicated by[*]), the UKOT dataset (3 countries indicated by†), plus additional data provided by E. Arias-Gonzales (Mexico – Yucatan), L. Alvarez-Filip (Mexico – Cozumel) and S. Williams (Puerto Rico). Wave exposure, SST, hurricane and hum population data were provided by I. Chollet.

Islands† (Figure 2.1) were included in the study. Reef surveys were performed on the reef slope at depths of 10 – 17 m. At each site transects were placed haphazardly on the reef slope and parallel to the shore. Where multiple transects were performed at a site, they were laid in line with the start of the next transect was no closer than 5 m to the end of the previous.

2.2.1. Reef structural complexity

A range of methods have been used to quantify structural complexity on coral reefs which differ in the aspect of complexity they measure, the scale of the measurement and the degree of subjectivity applied by the observer. The most frequently used method is the rugosity index (RI) (Alvarez-Filip et al. 2009), which provides an objective measure of the reef topography, allowing for the inclusion of data from multiple datasets and was therefore selected for use here. A fine link chain (link size 10 mm – 12 mm) was draped over the reef, ensuring it closely followed the contours of the reef structure. The ratio of the straight line distance to the total length of the chain was then calculated giving a value for surface rugosity. The length of chain used, amount of replications and surveyor varied by location (Table 1). The RI measures were then categorise by RI interval (1.0–1.24, 1.25–1.49, 1.5–1.99 and > 2.0) to examine the difference in spatial variation in the different complexity categories (Alvarez-Filip et al. 2009).

2.2.2. Environmental drivers

Coral cover data were collected using the point intercept method which gave an estimate of live hard coral cover on transects at each site. A detailed breakdown of biological survey methods used at each survey location is provided in Table 2.1. Remaining environmental data was provided by I. Chollet and additional detail can be found in Chollett and Mumby (2012 & 2013) and Chollett et al. (2012). **Wave exposure** in this analysis is a measure of the degree of wave action on the shore, governed by the fetch, the strength and the direction of the winds. Fetch was measured using the global, self-consistent, hierarchical, high-resolution shoreline database GSHHS version 1.5 (Wessel and Smith 1996). Wind speed and direction were gathered from the QuikSCAT (NASA) satellite scatterometer from 1999 – 2010. The wave exposure of a given location was then the function of the shape of the basin, wind speed and direction (Ekebom et al. 2003). However in order to describe wave exposure in a large basin such as the Caribbean it was also necessary to account for the difference between "fetch-limited" and "fully developed" seas given there is a limited height to which waves can grow (Chollett and Mumby 2012). Therefore, the shift between equations governing the two had to be specified. Daily wave exposure was calculated, and then averaged (mean) for the time period which allowed for the inclusion of strong sporadic winds.

Sea Surface Temperature was obtained from infrared observations collected by the Advanced Very High Resolution Radiometer (AVHRR) sensors on NOAA's Polar Orbiting Satellite Series (satellites 11 – 18). Data from 1993 to 2010 at a 1km^2 resolution were processed and archived by the Institute for Marine Remote Sensing (IMaRS). Weekly average SST maps for the study area were created by overlaying data from successive night satellite observations. The overall effect of the compositing procedure was to increase the accuracy of the result (by reducing the effect of both cloud contamination and 'warm skin' effect associated with periods of minimal wind-mixing) and to reduce the areas of the map for which no data were available because of cloud contamination. Further gap-filling was done by averaging adjacent weeks.These data were then used to calculate the average number of days a year SST was greater than 31^{o}C, a temperature above which corals are likely to undergo thermal stress, potentially leading to bleaching in the Caribbean (Toscano et al. 2002).

Hurricane return period is the frequency at which a hurricane (Saffir-Simpson intensity ≥ 1) can be expected at a given location. Data were extracted from the Atlantic Hurricane data set (Jarvinen et al. 1984) and return period were calculated using equation 2.1 where *n* is the number of years in the record (157), and *m* is the number of recorded occurrences of hurricanes at the site. **Time since last hurricane** and **strength of last hurricane** were also used because of the large range in wind strength (>200 kph) between category 1 and category 5 hurricanes, and given that the impacts of more recent hurricanes are more likely to have been detected by the rugosity surveys; time since last hurricane (in days) and the strength of the most recent hurricane (Saffir-Simpson intensity ≥1) were also extracted from the Atlantic Hurricane data set (Jarvinen et al. 1984).

$$return\ period = \frac{n+1}{m} \qquad \text{Equation 2.1}$$

2.2.3. Human population and management

Human population data were extracted from the Global Rural-Urban Mapping Project (GRUMPv1), which provides population density in persons per km^2 from the year 2000, adjusted to match UN country totals. For the development of the GRUMP population grids, points representing settlements smaller than 1,000 persons were also used, where available and appropriate. The data are stored in geographic coordinates of decimal degrees based on the World Geodetic System spheroid of 1984 (WGS84). In order to calculate the number of people within 2 km of each survey site, radial buffers of 2 km diameter were created around each reef survey site and the number of people within each of the radial areas was calculated. **Management** of a reef area was defined as the length of time a reef had been protected (e.g. marine reserve status) up to the date of the rugosity and coral surveys. There is no single comprehensive database for Caribbean marine protected areas (MPAs), therefore data were extracted from the MPA databases maintained by CaribbeanMPA (CaMPAM) (Gulf and Caribbean Fisheries Insitute 2010), MPA Global (Wood 2007), and Protected Planet (IUCN and UNEP-WCMC 2014)

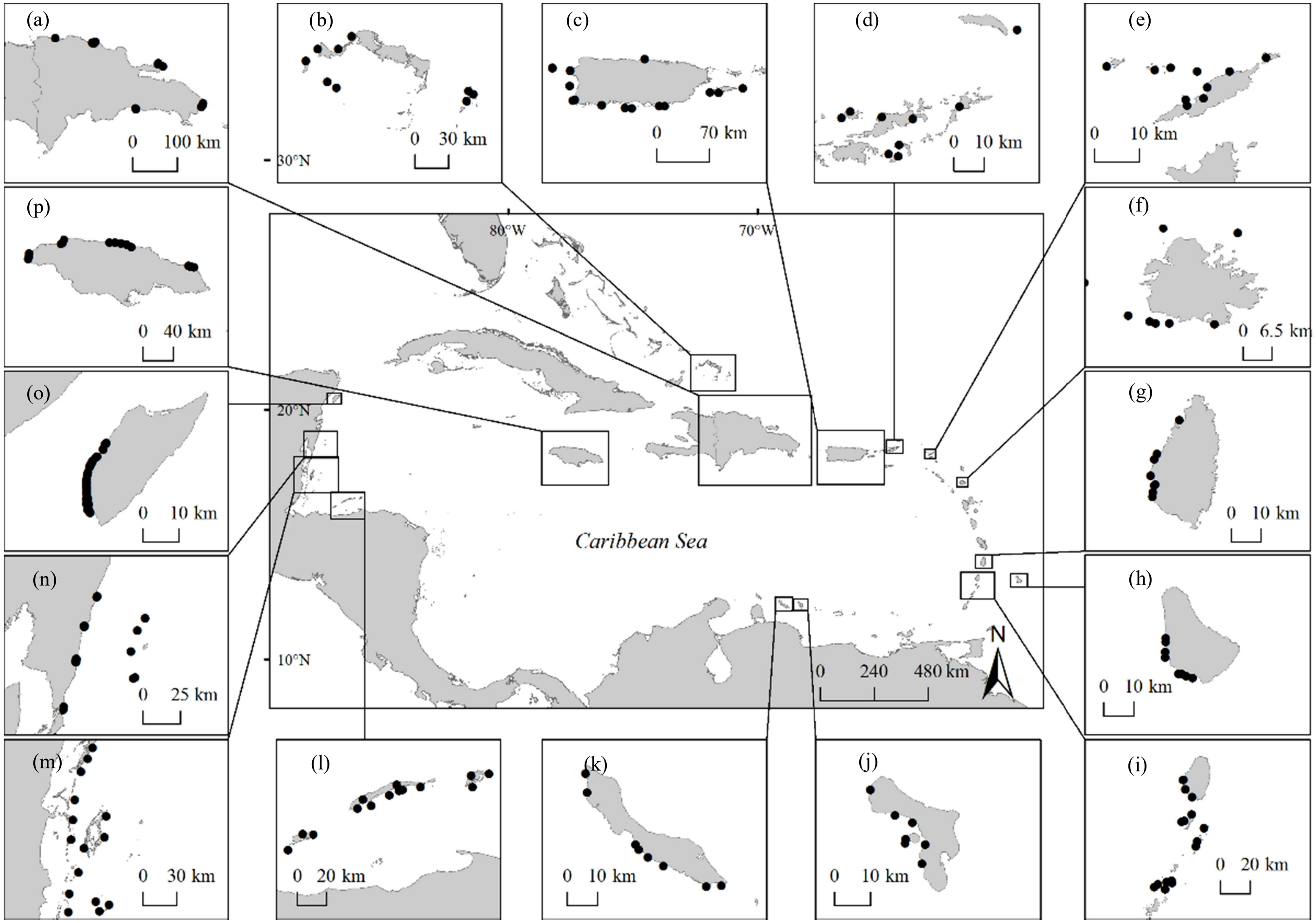

Figure 2.1 Distribution of study sites throughout the Caribbean. Study sites are shown in black circles on each individual survey inset. Areas surveyed were: (a) Dominican Republic, (b) the Turks & Caicos Islands, (c) Puerto Rico, (d) the British Virgin Islands, (e) Anguilla, (f) Antigua, (g) St. Lucia, (h) Barbados, (i) St. Vincent & the Grenadines, (j) Bonaire, (k) Curacao, (l) the bay islands, Honduras, (m) Belize, (o) Quintana Roo, Mexico, (o) Cozumel, Mexico and (p) Jamaica

Table 2.1 Summary of sites with details of RI measurement approach (chain length, replicates per site) and coral cover transects (length, replicates per site)

Surveyor[†]	Country/Island	Year	No. of Sites	Chain Length (m)	Chain replicates	Length of coral transects (m)	Coral transect replicates
CS	Anguilla	2012	8	10	4	10	6
CD	Antigua	2011	8	10	4	10	6
CD	Barbados	2011	8	10	4	10	6
CD	Belize	2010	15	10	4	10	6
CD	Bonaire	2011	7	10	4	10	6
CD	British Virgin Islands	2012	8	10	4	10	4
CD	Curaçao	2011	8	10	4	10	6
CD	Honduras	2010	14	10	4	10	6
CD	Jamaica	2011	15	10	4	10	6
LA-F	Mexico (Cozumel)	2007/08	81	3	5	30	1
EA-G	Mexico (Yucatan)	2007	31	10	4	10	4
SW	Puerto Rico	2012	20	*	5	10	5
CD	St. Lucia	2011	8	10	4	10	4
CD	St. Vincent & the Grenadines	2011	15	10	4	10	4
CD	Turks & Caicos Islands	2012	9	10	4	10	4

*The chain in Puerto Rico was laid between two points marking the start and end of permanent transects, points were 10 m apart and the length required to connect the two was used to calculate the RI at these sites. [†] CS: Christina Skinner, CD: Charlie Dryden, LA-F: Lorenzo Alvarez-Filip, EA-G: Ernesto Arias-Gonzalez and SW: Stacey Williams

2.2.4. Data Analysis

Spatial patterns of structural complexity were explored through a generalised least squares (GLS) model using the environmental variables. The spatial distribution was added to the model as a correlation structure (Pinheiro and Bates 2000). Correlation structures can be used to model the dependence among observations which allows the data to be analysed for autocorrelation across space. Using this approach, it was possible to determine whether sites closer together were more similar. This was then used to plot a semi-variogram for the data to visually represent this spatial pattern. In order to check whether Caribbean-wide processes might mask regional patterns, data were separated into three sub-regions: Central America, Greater Antilles and Lesser Antilles (including Curaçao and Bonaire).

Pathway analysis using a structural equation modelling (SEM) approach was used to examine relationships between reef rugosity and a range of environmental and human drivers. The use of a covariance matrix to calculate the regression and covariance relationships permitted examination of the interactions between predictor variables, giving a greater understanding of each of the variables' influence on reef rugosity. Prior to analysis, a hypothetical model was developed containing theoretical pathways of influence (Figure 2.2). This model was tested with empirical data and the paths between variables defined in equation form. Four models were developed, one for the whole Caribbean and one for each of the three sub-regions used in the spatial autocorrelation analysis as these had sufficient data available. The hypothetical model structure was the same for each dataset. There is some disagreement over a minimum sample size required for SEM, however it is generally agreed that $n \geq 200$ is appropriate to develop a SEM model (Ding et al. 1995), however the sub-regional data had $n < 200$, and therefore a bootstrapping approach was utilised (Khan et al. 2013). The model was run 100 times with 100 separate sets of data comprising random samples of 75% of the total dataset. This allowed estimation of means and standard errors for SEM parameter estimates.

The hypothetical models were first fitted with all predicted pathways. In order to build the simplest significant working model, pathways where the 95% confidence intervals for the bootstrapped estimates of coefficient included zero (indicating no effect) were removed. The significance of the model was tested using the χ^2 statistic, non-significance indicating no difference between the predicted and observed covariance structure. The model goodness of fit was assessed using the comparative fit index (CFI) and the root mean square error of approximation (RMSEA). For the regional models, the bootstrapped CFI and RMSEA values were used. A CFI >0.95 (Hu and Bentler 1998) and RMSEA <0.8 (Browne and Cudeck 1992) were considered to represent a reasonable fit for SEMs. All models were fitted using the lavaan package (Rosseel 2012) in R 3.0.1 (R Core Team 2014). Predictor variables were tested for collinearity and variance inflation factors (VIF) using the AED R package (Zuur 2010) with a VIF <3 considered acceptable. All variables were log10(x+1) transformed to reduce standard deviation, allowing the model to run correctly.

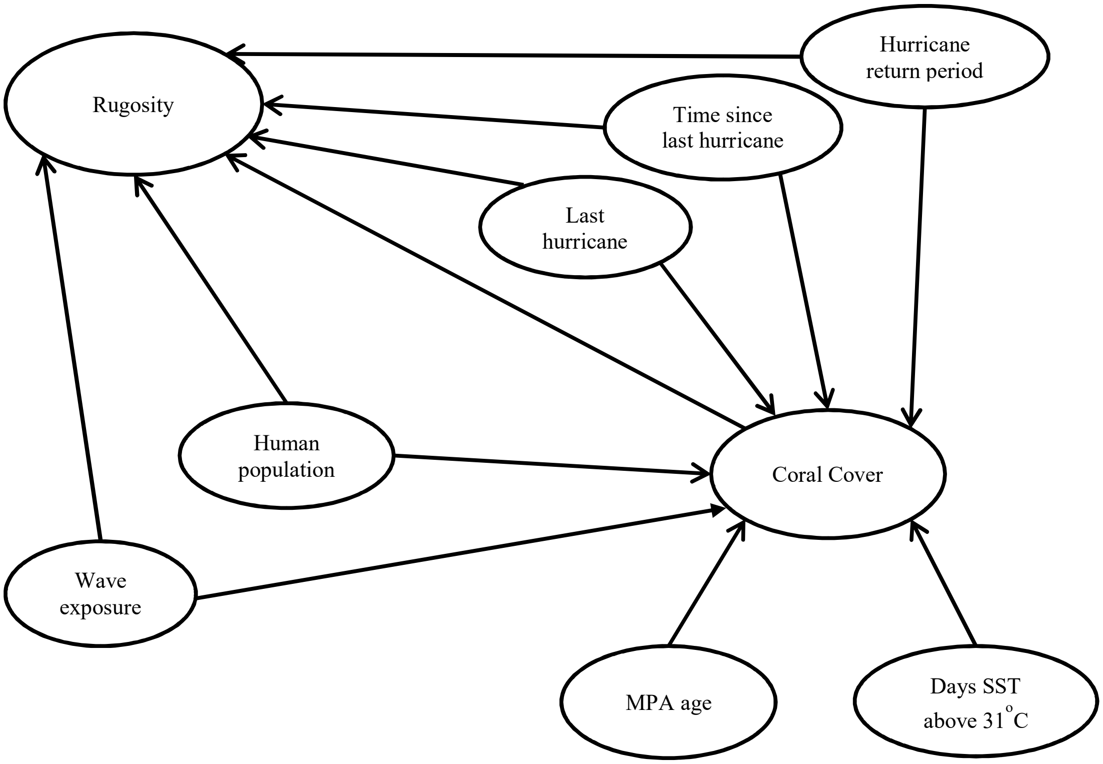

Figure 2.2 Full model of the hypothetical pathways of influence on rugosity on Caribbean coral reefs. Directions of arrows indicates the proposed direction of influence

2.3. **Results**

2.3.1. Caribbean coral reef structural complexity

The rugosity index (RI) of sites surveyed ranged between 1.02 and 2.05 with a mean of 1.38 (±0.013 s.e. n = 265). The proportion of complex reefs (RI >2) across all the Caribbean sites was less than 2%, and these reefs were absent from the Greater Antilles (Figure 2.3). The mean RI across the region was low, however it was significantly greater in the Lesser Antilles (Figure 2.3). GLS models which included the spatial correlation structure did not lead to a significant increase in the variation explained by the model (ANOVA, p >0.05). This indicates that there was no pattern of autocorrelation in the data and therefore reefs close to each other in space were no more likely to be of similar structural complexity than to those further away. The remainder of the results are therefore based on analyses which did not include spatial autocorrelation.

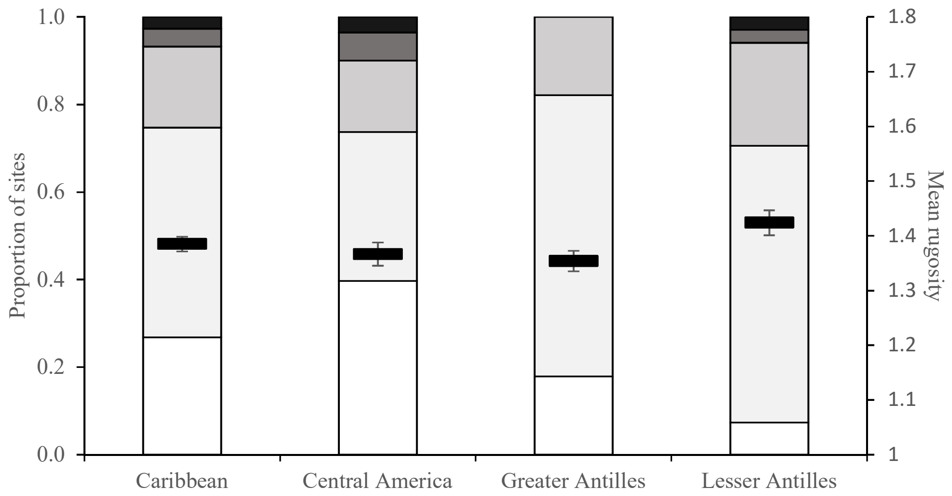

Figure 2.3 Proportion of reefs in five rugosity index categories across all Caribbean sites and by the geographic regions. Black = >2; dark grey = 1.75-2; mid grey = 1.5-1.75; light grey = 1.25-1.5; white = 1-1.25. Mean rugosity for each geographic region is shown by the bold "-" on the secondary y-axis. Error bars represent standard error of the mean rugosity.

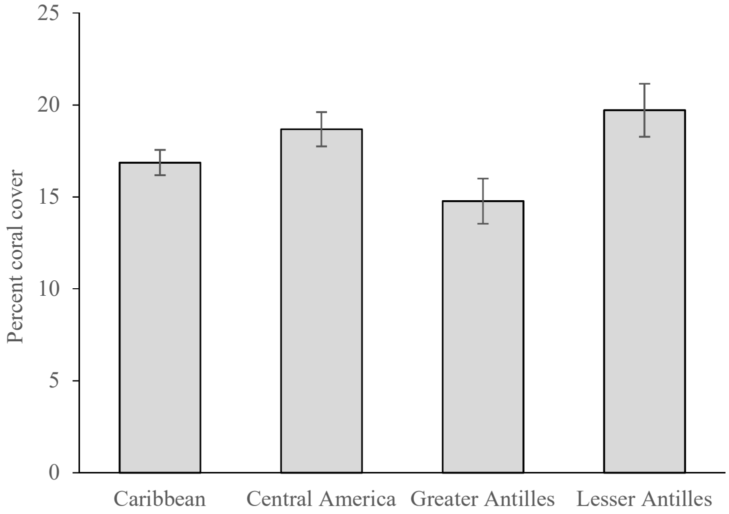

Figure 2.4 Mean percent coral cover across the all Caribbean sites and by the geographic regions. Error bars represent standard error of the mean.

2.3.2. *Drivers of structural complexity*

The full SEMs, including all hypothesised pathways had significant p-values but high RMSEA values which indicated poorly fitting models that differed from the observed structure. Many variables were non-significant contributors to the observed correlation structure in the data (Table 2.2) and thus were removed for the final model (Table 2.3). The final model structure varied by region; the path diagrams for the final models with all significant pathway coefficients show the different model structures (Figure 2.5).

Hurricanes were the only driver significantly related to RI across the Caribbean region and in all sub-regions. Hurricane return period (durations between hurricanes) was either directly or indirectly positively related to the RI in all models. In the Lesser Antilles this was found to be an indirect relationship through a positive relationship with coral cover. The Saffir-Simpson category of the most recent hurricane was negatively related to RI in the Greater and the Lesser Antilles. The length of time since a reef was last impacted by a hurricane had no relationship with RI. The hypothesised model predicted indirect effects on RI through a relationship with coral cover, however this pathway was only significant in the Lesser Antilles.

Wave exposure was found to have a direct negative relationship with RI at the basin scale and across two of the sub-regions, the Greater Antilles and Central America, but not in the Lesser Antilles. The hypothesised pathway between wave exposure and coral cover was not significant in any models. There was a positive relationship between coral cover and RI in the Caribbean region, Central America and the Lesser Antilles sub-region models. However, there was no significant relationship in the Greater Antilles. Therefore, there were no indirect relationships between any of the drivers and RI in this model because a relationship with coral cover would not have affected RI. Mean coral cover for the region was ca. 17% (Figure 2.4), however, it was significantly lower in the Greater Antilles than in the other two regions (ANOVA, $p < 0.05$).

The number of people in close proximity to reefs had a mixed relationship with RI. In Central America the human population was a positively related to coral cover, and therefore had an indirect positive relationship with RI. However, in the Lesser Antilles human population had a direct negative relationship with RI, and no significant relationship with coral cover. This mixed relationship is reflected in the Caribbean region model, where human population had a direct negative relationship with RI and an indirect positive relationship through coral cover. There was no relationship between human population and RI in the Greater Antilles. The predicted indirect pathways between the length of coral reef protection and the number of days SST was above the bleaching threshold were not significant in any of the models and were therefore removed from all final models.

Table 2.2 Correlation matrix for the significant pathways of influence for RI and coral cover SEM analyses for reefs in the Caribbean region and Central America, Greater Antilles and Lesser Antilles sub-regions. ‘-‘represents a pathway that was non-significant and therefore removed from that particular model.

		Whole Caribbean			Central America			Greater Antilles			Lesser Antilles		
From	To	Coefficient	Lower 95% CI	Upper 95% CI	Coefficient	Lower 95% CI	Upper 95% CI	Coefficient	Lower 95% CI	Upper 95% CI	Coefficient	Lower 95% CI	Upper 95% CI
Coral cover	Rugosity	0.052	0.04	0.0623	0.069	0.056	0.083				0.029	0.006	0.049
Human population	Rugosity	-0.080	-0.110	-0.047	-	-	-				-0.081	-0.142	-0.031
Wave exposure	Rugosity	-0.015	-0.020	-0.010	-0.017	-0.024	-0.011	-0.007	-0.016	0.001	-	-	-
Hurricane return period	Rugosity	-	-	-	-	-	-	0.154	0.108	0.218	-	-	-
Time since last hurricane	Rugosity	-	-	-	-	-	-	-	-	-	-	-	-
Last hurricane category	Rugosity	-	-	-	-	-	-	-0.082	-0.122	-0.046	-0.087	-0.129	-0.036
Human population	Coral cover	0.042	0.009	0.08	0.145	0.054	0.273				0.019	0.028	0.062
Hurricane return period	Coral cover	0.439	0.339	0.525	2.490	1.573	3.826				0.447	0.298	0.582
Time since last hurricane	Coral cover	-	-	-	-	-	-				-	-	-
Last hurricane category	Coral cover	-	-	-	-	-	-				-	-	-
Days SST over 31°C	Coral cover	-	-	-	-	-	-				-	-	-
MPA age	Coral cover	-	-	-	-	-	-				-	-	-
Rugosity	Rugosity	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.001	0.000	0.001
Coral cover	Coral cover	0.105	0.085	0.124	0.124	0.102	0.151	0.057	0.024	0.106	0.034	0.022	0.048

* No values for pathways between parameters and coral cover in the Greater Antilles model are included as coral cover was found to have no relationship with rugosity

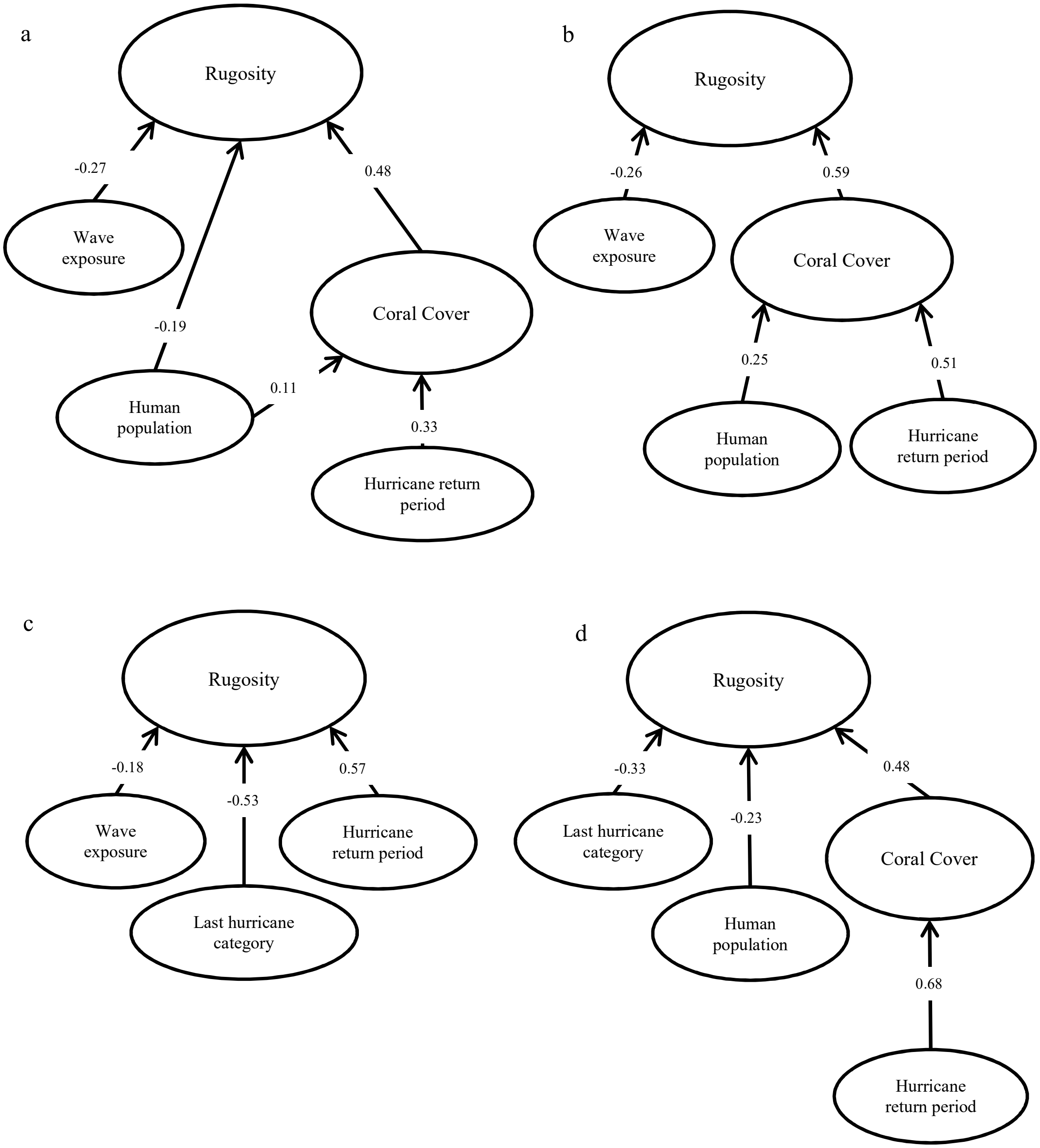

Figure 2.5 All significant pathways with standardised coefficients for (a) Caribbean region, (b) Central America, (c) Greater Antilles and (d) Lesser Antilles SEMs. The standardised coefficient represents the impact of a one standard deviation (SD) change in the independent variable on the variable of interest. Thus, unit change in SD of coral cover in the Caribbean region (a) gave rise to 0.48 units change in the Rugosity.

Table 2.3 Precision and measures of fit for SEMs relating environmental and anthropogenic drivers of RI in the Caribbean basin and sub-regions.

Area	R-squared	RMSEA	CFI	p-value
Whole Caribbean	0.30	0.037	0.98	0.236
Central America	0.43	0.018	0.99	0.352
Greater Antilles	0.40	0.062	0.96	0.294
Lesser Antilles	0.31	0.058	0.96	0.451

2.4. **Discussion**

The level of structural complexity of Caribbean coral reefs was low across the surveyed region. A very small proportion of the reefs surveyed had RI values greater than 1.75, which suggests a severely depressed level of structural complexity compared to historical reefs (Alvarez-Filip et al. 2009). The degree of structural complexity on contemporary Caribbean coral reefs was driven primarily by physical disturbance through hurricanes and wave exposure. However, the positive relationship between live coral cover and structural complexity found here suggests that on those reefs where coral cover is high, reefs may be more resilient to these physical disturbances. The lack of spatial autocorrelation in the results, combined with the observation that all regions retain a range of structural complexities, indicates that despite ongoing degradation, reefs in the Caribbean region have not become homogeneously flat.

The hypothesis that there has been a flattening of coral reefs across the Caribbean (Alvarez-Filip et al. 2009) is supported by the findings of this study, which suggest the region surveyed retains few reefs with high structural complexity. Caribbean coral reefs were once a diverse mix of corals providing a range of growth forms (Porter 1976). Contemporary Caribbean reefs have undergone significant loss of two of these key species, *Acropora palmata* and *A. cervicornis* (Aronson and Precht 2001). The loss of these branching corals means many reefs have become comparatively flattened or comprise less complex corals (Perry et al. 2014b). Those reefs which are still highly complex are now constructed of more massive corals such as orbicellids (Alvarez-Filip et al. 2011b). A number of structurally complex reefs are now reliant on dead coral skeletons (personal observation), leaving these reefs at significant risk of 'rapid' structural collapse.

Acroporid corals have an important ecological role in coral reefs globally because of their relatively fast growth rates (Gladfelter et al. 1978) and ability to regrow from fragments following acute disturbances (Highsmith et al. 1980). This means that in areas under significant threat from storms these species are likely to be the main source of structure. The slow growth rates of other coral species, may leave them susceptible to storm events which have short return periods. The loss of acroporids due to disease outbreaks (Aronson and Precht 2001) means that, despite the opportunity to recolonise following storms, populations are too small to provide this essential service (Hughes and Connell 1999). Areas with shorter durations between storms are therefore not able to recover in the manner Caribbean reefs were able to historically; complexity remains low and reefs may be dominated by macroalgae, or less complex boulder or encrusting corals (Jackson et al. 2014).

Areas with high levels of wave exposure are unlikely to have ever developed structurally complex habitats because the chronic disturbance from wave affects coral growth and zonation (Dollar 1982, Done 1983). This is supported by the strong negative relationships found between wave exposure and RI in this study. This finding comes despite a low number of highly exposed sites included in the study, given the logistical difficulties of surveying these locations. This relationship might be expected to be even stronger had more exposed areas been surveyed, notably those on the windward shores of the Lesser Antilles. High wave exposure can lead to changes in skeletogenesis (Scoffin et al. 1992), reduced accretion rates (Grigg 1998, Yamano et al. 2003) and reduced settlement or growth (Chollett and Mumby 2012). This results in reef frameworks on exposed shores which are less complex, but more robust when compared to those in sheltered areas (Yamano et al. 2003, Hongo and Kayanne 2009). In areas of lower wave exposure corals are able to develop more complex forms. There is a close relationship between wave exposure and *Orbicella annularis* reefs (Chollett and Mumby 2012). In areas where hurricanes are infrequent and wave exposure is low, *O. annularis* can provide resilient and complex reef developments, such as in Belize (Chollett and Mumby 2012) and Bonaire (Meyer et al. 2003). Though there was no direct pathway between wave exposure and coral cover in this study, the negative relationship between waves and RI indicates that degree of exposure would have affected the diversity of species present by restricting the presence of corals with certain growth forms. This would lead to less structurally complex corals being more prevalent in wave exposed areas.

The positive relationship between live coral cover and RI found here is could be a positive sign for Caribbean coral reefs. This potentially suggests that structurally complex corals still drive complexity on these reefs, as opposed to dead skeleton, rock or alternative biogenic structures (Hobbs et al. 2009). Where studies have failed to find a relationship between coral cover and complexity in the Caribbean (see Graham and Nash 2012), low levels of coral cover have been suggested as the cause. However, the scale of this study has enabled inclusion of a range of coral cover data from across the Caribbean, allowing an interpretation of the relationship at the basin scale. Coral cover and structural complexity have been declining across the Caribbean (Gardner et al. 2003, Alvarez-Filip et al. 2009), however their rates of loss do not co-vary (Alvarez-Filip et al. 2011a) suggesting that although coral cover is important to complexity, the identity of the species of coral present is significant. Where this has been examined, the most complex reefs were those with a low taxonomic evenness and dominated by *Orbicella* spp (Alvarez-Filip et al. 2011b).

The only sub-region where no relationship existed between coral cover and RI was the Greater Antilles. A possible explanation for this is the strong negative relationship hurricanes had with coral cover in the rest of the Caribbean. This sub-region has suffered significant hurricane damage (Hughes 1994, Gardner et al. 2005) and has highly wave exposed shorelines (Chollett et al. 2012), which have evidently been conducive to the low levels of RI found here, and may have decoupled the relationship between coral cover and structural complexity. Coral cover can also be significantly reduced as a result of hurricanes, and coral cover at impacted sites declines at a faster rate than at less impacted sites (Gardner et al. 2005). Therefore, the greater the time between subsequent hurricanes, the higher the potential for coral growth. Climate change is predicted to increase the frequency and severity of hurricanes (Bender et al. 2010). This is likely to have strong negative impacts on structural complexity and the health of Caribbean reefs. A decline in return periods will give structure-creating corals much shorter growth periods between disturbances, which likely will severely reduce *Acropora* growth and recruitment (Lirman 2003) and in the absence of these fast growing species this will likely result in further reef flattening.

The absence of any relationship with SST may mean that the effects of temperature anomalies are yet to manifest as declines in structural complexity. However, given the strong relationships with coral cover, it is likely that the effects of bleaching-related coral death will eventually have strong indirect consequences for reef structural complexity (Graham et al. 2006). Death of the coral leaves the skeleton exposed to the risk of erosion through physical and biological pathways (Hoegh-Guldberg 1999a). Additionally hurricanes can drive asexual recruitment of corals (Fong and Lirman 1995, Foster et al. 2013) which can lead to lower genetic diversity within a community. This may put these communities at greater risk from perturbations such as disease or warming events where diversity may confer a level of resilience (Cróquer and Weil 2009).

It is hoped that formally protecting areas of coral reef may confer some resilience against negative pressures, however the findings of this study suggest that existing management may do little to help maintain structure. This might be because there is little that protection of reef areas can achieve in the face of the physical disturbances which appear to drive regional complexity. Alternatively, it may be that despite the present data on effects of MPA age, the time period required for management to positively influence structure is greater than that which areas of the Caribbean have thus far been protected for. The benefits of management to structure are hypothesised to result from the positive feedback loops associated with herbivores (Bozec et al. 2013), however increased levels of bioerosion by herbivores within MPAs may reduce complexity (Alvarez-Filip et al. 2011d). Though the benefits of herbivores are likely to outweigh the costs (Bozec et al. 2014), where structure is maintained by remnant dead coral skeleton, any increase in erosive processes is likely to perpetuate rapid decline in structural complexity.

Although there was no relationship with management, proximity to human population did influence RI through both direct and indirect pathways. However, the conflicting relationship the human population measure had with RI suggests that the metric used here did not provide enough detail to draw definitive conclusions about the impact of human populations on complexity. It might instead be more important to understand reef use and economies in the areas involved. The negative direct relationship with RI was primarily driven by the Lesser Antilles. On these small islands population centres are hubs for fishing, cruise terminals or capital cities, which are expected to directly impact reef health (Chabanet et al. 2005). The positive relationship with RI was largely driven by the Central American model. The sites in this sub-region had consistently lower human population densities and tended to be situated further away from high population densities on atolls (e.g. Turneffe and Glovers), sparsely populated coastlines (e.g. Quintana Roo) or islands away from the mainland (e.g. Cozumel, Belize cays). The most densely populated area was Cozumel in Mexico. The reefs surrounding Cozumel all lie within an MPA and are in the upper range of Caribbean reef health (Bozec et al. 2014). This island is an important tourism area and maintenance of attractive and complex reefs is likely to be a priority.

The lack of spatial autocorrelation in the data reveals reefs in the Caribbean are not continuous stretches of homogeneous structure, but a mosaic of different structures and complexities. This study examined reefs at multiple scales, from < 0.1 to > 100 km apart and the findings suggest that reefs closer to one another are no more likely to be similar in complexity than those many kilometres apart. Spatial patterns in physical structure have been identified in previous spatial habitat surveys (Bell et al. 1993, García-Charton and Pérez-Ruzafa 2001). However the dynamic nature of coral reefs and the varied responses of different species and morphologies to disturbances, even on a local scale (Bythell et al. 1993), suggest the distribution of coral reef complexity may not be consistent along a shoreline. Studies on multiple scales have found reefs at similar locations may have very different levels of health (Idjadi et al. 2006, Edmunds 2015). This suggests that simply being in close proximity may not cause two reefs to be similar and there are in fact likely to be a number of local-scale process occurring which may lead to differences between the reefs which is likely to be true of complexity also. Bythell et al. (1993) found the response of reefs to a category 4 hurricane was highly localised, with some reefs virtually flattened whilst others showed no measurable change in structure. There is also documented recovery or persistence of structurally complex acroporid corals in a number of locations across the region including Honduras (Keck et al. 2005), Jamaica (Idjadi et al. 2006), the Turks and Caicos Islands (K. Hart, pers. comm.), Anguilla, Antigua, Bonaire and the British Virgin Islands (pers. obs.). The presence of isolated patches indicates that surrounding reefs need not be complex provided there is opportunity for larvae to arrive and settle.

This analysis has examined Caribbean structural complexity with a level of detail and at spatial scales not previously available. Through the identification of a number of important relationships with complexity it has been possible to suggest pathways of change in reef structure enabling a better picture of how reefs in the region may progress in the future. However, as with much ecological modelling, additional data would have enabled new avenues for analytical approach. For example Chollett et al. (2012) identified seven different physical environments in the area surveyed in this study. Analysis of these environments might have found a variation in the physio-chemical drivers of reef structural complexity among them. Unfortunately, there were not enough survey sites in the study to examine the data in this level of spatial detail. Given the potential for feedback loops between the herbivorous community and structural complexity (Alvarez-Filip et al. 2011d, Bozec et al. 2013), it may also have been useful to include biomass of grazing herbivores such as parrotfish or the urchin *Diadema antillarum* as indirect predictors of RI. These processes significantly influence the carbonate budget on Caribbean reefs (Perry et al. 2012) and are likely to play a role in the dynamics of structural complexity of the region’s coral reefs. However, herbivore data were not available from all sites included in this study and therefore could not be included in the final models.

Although the measure of RI provides a useful insight into the structural condition of a given reef, it may limit the broader inferences about the influence of regional structural complexity on the associated fish communities (Chapter 3). Other variables capturing aspects of reef habitat structural complexity include: vertical relief, number of shelter holes, visual estimates and fractals measurements (Wilson et al. 2007, Graham and Nash 2012). These measures are all inter-related (Wilson et al. 2007, Kovalenko et al. 2011), but the different approaches presumably capture different aspects of reef structural complexity and may therefore produce different results regarding structural complexity across the Caribbean and the impacts of changes in it. This may be of importance when relating the reef community to habitat structural complexity. This highlights the importance of including structural complexity measurements in reef monitoring protocols in order to build a more complete spatial picture of Caribbean region-wide structural complexity and it drivers.

3. A multidimensional approach to habitat structural complexity

3.1. Introduction

The requirement to quantify habitat characteristics is a core tenet of ecological study (Southwood 1977). One such characteristic is habitat complexity, which is defined as the physical structure in space formed of any biotic or abiotic substance (McCoy and Bell 1991). This is made up of two components: 1) physical structural complexity, which is the morphological characteristics of the structure and 2) habitat heterogeneity, which is the arrangement of these structures in space (Jana and Bairagi 2014).

This study focuses on the structural complexity component, given its importance in structuring animal communities in a range of ecosystems (Stoner and Lewis III 1985, Heck Jr and Crowder 1991, Beck 2000, McElhinny et al. 2005, Graham and Nash 2012). Structural complexity is essentially a human construct derived from observing the shape and three-dimensional construction of a habitat in which organisms are found. Meaningfully and comprehensively measuring it has proven challenging. Typically, measurements are taken of specific structural components which capture information limited to a specific habitat component, restricting their use and interpretation (Beck 2000). These proxy measurements have been used in order to indicate the presence and degree of complexity, and have been employed to reveal relevant relationships between organisms and their physical surroundings (MacArthur and MacArthur 1961, Risk 1971, August 1983, Sullivan et al. 2001, Gratwicke and Speight 2005a). Understanding what species actually perceive as opposed to the human perception of the habitat is crucial to understanding the role of complexity in the natural environment. This is especially important, as examining the relationship between organisms and complexity is likely to be context specific. There is no guarantee that what researchers perceive and measure is what the individual organism perceives; complexity for a bacterium is different to that for a coral which is different again for a fish.

Indicators are important because they relay a complex message in a simplified manner (Jackson et al. 2000) which can be used to reveal pertinent information about the environment. Yet rarely are formal criteria applied to the selection of an indicator measurement's utility, and as a result the variables selected as indicators are often based on arbitrary decisions or previous studies dealing with similar subject matter (Niemeijer and de Groot 2008). It is therefore important to understand what a particular variable (indicator) reveals about the environment and how that variable relates to and can interact with other variables to provide a greater level of detail.

The key issue is the oversimplification of the measurement approach. Studies on relationships between structural complexity and community structure have relied upon single complexity variables (Risk 1971, Heck Jr and Crowder 1991) or compared multiple variables (Humphrey et al. 1999, Loeb and O'keefe 2006, Harborne et al. 2012, Newman et al. 2015) to develop measures of the abstract concept through simple complexity variables that might reflect it. Individual variables provide a rapid way of characterising a habitat and can aid in understanding relationships between specific components of the habitat and associated communities. However, many additional facets of structural complexity are likely to come into play when examining the relationships across whole communities, and the effects of these facets or interactions between them will be overlooked. For example the measure of foliage density which influences bird species diversity in vegetated areas (MacArthur and MacArthur 1961) excludes other potentially important information such as plant height or interstitial spaces that may influence suitability for some bird species. The single measures of structural complexity are point samples attempting to indicate the complexity of an area. It is hoped that when using a measure of complexity, it is sufficiently influential on the multiple processes that actually dictate species abundances or diversity that it serves as a useful proxy. Comparisons of multiple measures of complexity, while increasing the likelihood of capturing explanatory habitat components, overlook any additive or indirect effects of multiple facets of complexity that may be present in the habitat.

Dimensionality reduction techniques, such as principal components analysis (PCA) or multidimensional scaling (MDS) can be used here to find major trends through multifactorial and multivariate descriptions of habitat quality (Vaughan and Ormerod 2003). These have been used to provide relative measures of habitat complexity (August 1983, Chong-Seng et al. 2012) and the results of such analyses are relative, in that they quantify differences between entities (habitats) in a data set by simplifying to one or two variables, represented by orthogonal axes. Of course these are variables that are derived mathematically and can be somewhat detached from the original variables used. This could result in a numerical relationship with the community, however it may be more difficult to discuss causality when no longer discussing the actual habitat components. In addition to this, many data sets contain non-linear relationships which are undetected by common dimensionality reduction techniques (Tenenbaum et al. 2000). PCA and MDS see only the Euclidean structure of the data, missing much of the intrinsic multidimensionality (Tenenbaum et al. 2000). Most important from a theoretical viewpoint is that this approach is data driven which can lack a mechanistic approach. Focusing on data alone can overlook the mechanisms underlying the ecological role of complexity in favour of a post-hoc data driven approach which may be less ecologically relevant.

Studies to date have not incorporated relationships between components of structural complexity which may be important. For example refuge size will affect the density of refuges available in a given area, plant height can affect the number of leaves or branches produced (Westoby et al. 2002) and complex areas in streams may be self-perpetuating, with a greater ability to snag more debris (O'Connor 1991). Traditional methods used in isolation can also over-simplify the spatial arrangement of structures in the habitat. For example, a mound or a recess on a rocky reef may have the same fractal or rugosity measurements, however they offer different types of structure. Additionally, the scalar quantity measured by these approaches may not actually capture enough information to (i) quantify process or (ii) capture anything other than correlation, which may not be causal.

The coral reef is paradigmatic for investigating the roles of different aspects of structural complexity in determining community structure. Coral reefs exhibit relationships between structural complexity and fish assemblage structure (Risk 1971, Caley and St John 1996, Almany 2004b, Gratwicke and Speight 2005a, Graham et al. 2007, Harborne et al. 2012, Nash et al. 2013). A suite of different variables have been used to quantify complexity on reefs, including: chain (Risk 1971), relief height (Harborne et al. 2012), hole counts (Graham et al. 2003), fractal dimensions (Nash et al. 2013) and digitally using pressure changes (Dustan et al. 2013). These variables used in isolation are point samples indicating facets of reef structural complexity. An estimate of structural complexity using a visual grading system (Gratwicke and Speight 2005a, Wilson et al. 2007) has been widely used to combine these variables into an overall assessment of complexity where reefs are awarded a complexity grade. This approach provides a quick method of assessing the multiple components of reef structure. However, it is also a subjective human perception of the reef and it can be difficult to know how much weight to give each different aspect of complexity.

A second approach to quantifying reef complexity is by examining the refuge space available (Hixon and Beets 1993, Forrester and Steele 2004, Wilson et al. 2007). Refuge is the space created by the structure of the reef, it is therefore both a separate entity and entirely reliant on the reef structure at the same time. Refuge in reef systems can also be multifactorial, and therefore requires similar considerations to whole reef complexity and must also be measured in multiple ways. However, in addition it reflects an interaction between physical structure and species shape, size, and behaviour (Hixon and Beets 1993). The refuge provided by holes on a coral reef offer spaces where prey are potentially invulnerable to predation through exclusion of predators (Hixon and Menge 1991a).

The aim of this study was to develop a multivariate model to examine fish diversity on coral reefs, based on habitat variables describing facets of reef structure. Fishes are able to make use of the three dimensional nature of their environment, utilising a greater number of microhabitats as a habitat becomes increasingly complex (Hixon and Menge 1991a). Better understanding of relationships between fish communities and reef habitat physical structure is likely to require the measurement and combination of many facets of complexity. Multiple measures of habitat complexity will be combined through pathway analysis to elucidate the processes which make up structural complexity on coral reefs. This will allow the study of a hypothetical construct the measurement of which has proven a significant challenge (MacCallum and Austin 2000). Here complexity is a concept which is revealed through the use of a number of variables. This latent variable model based approach is then compared with a PCA to determine whether this approach represents an improvement.

3.2. **Methods**

3.2.1. Study site

In total 336 transects across 84 sites from eight different countries[2] in the Caribbean region were surveyed between January and August 2011. On average four transects were performed per site except for three at one site (Vigie Beach in St. Lucia) and one site (Playa Grande in Curacao) where five transects were completed. Measurements were performed on 10m x 1m transects. Transects were haphazardly placed between 10 and 15 m depth, parallel to shore. Transect site was selected using a stratified random sampling procedure.

3.2.2. Data collection

Reef structural complexity was quantified through four commonly used methods that likely capture different aspects of complexity: chain length (rugosity), hole counts, relief height and slope angle (detailed in Table 3.1). The mid-range for each hole class (Table 1) was used for the calculation of mean hole size for the model. Refuge diversity was calculated using the Shannon-Weiner index which is more sensitive to rare categories (Krebs 1999), and the occurrence of larger refuges was suitably accounted for. Fish community data were collected on the same reef transects as complexity measures using 10 x 4m belt transects. All fish observed were counted and identified to species level. Fish species diversity was then calculated using Fisher’s alpha as the communities varied greatly in the number of individuals and Fisher’s alpha is independent of sample size (Magurran 2004).

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[2] Data used in this chapter includes a subset of eight countries from the FORCE dataset. All structural complexity data were collected by C. Dryden and all fish data were collected by S. Newman. Due to different methodologies used in collecting fish community data from Honduras and Belize these countries were excluded from the analysis of this chapter.

Table 3.1 Complexity variables collected, the method used ere, the aspect of complexity measured, limitation of each measure and previous studies which have used each measurement. Range and standard deviation calculated for data collected in this study.

Variable	**Measurement**	**Interpretation**	**Examples of previous use in the literature**	**Range sampled**	**Mean, ± Standard deviation**
Rugosity	Chain (link size 11 mm) was draped over the bottom. The ratio of direct line length to actual chain length is used.	Measure of the surface area of the topography. Closely follows the contours of the reef. Misses key features such as overhangs and holes and only samples a very narrow line along the transect. Is quick, objective and highly replicable	Risk 1972, Luckhurst and Luckhurst 1978, Wilson et al. 2006, Alvarez-Filip et al. 2009	1.01 - 1.80	1.4 ±0.15
Hole counts	All holes in 5 cm size classes (0-5, 5-10 etc.) were counted along 10 x 1 m belt transects. Density was then calculated as hole number/10 m to provide a uniform scale	Measure of absolute refuge available for species of different sizes on the reef. No information on topography or temporary refuge/shelter created by features such as towers. Used to calculate hole density, mean hole size and hole diversity	Friedlander and Parrish 1998, Almany 2004, Wilson et al. 2006	7 - 1987	165.64 ±153.30
Relief height	Relief height was quantified within a 1 m radius at four locations (2.5 m, 5 m, 7.5 m and 10 m) along the transect by measuring the highest point above the substrate	Measure of the maximum vertical height of structure above the substrate floor in an area. Taken over a wider area than the rugosity, therefore taking into account more of the habitat. Misses similar aspects as rugosity and only measures isolated growths. Targeting the tallest growths may also lead to bias in the data	Luckhurst and Luckhurst 1978, Almany 2004, Wilson et al. 2006 Harborne et al. 2012b	8.00 - 174.75	63.70 ±28.58
Slope angle	Visual estimate of the angle of the reef slope at the start and end of each transect. This was averaged to give a mean slope angle for the transect	Measure of the steepness of the reef slope. This gives no further details on substrate development or refuge availability. But steeper slopes typically have greater coral development, and coral development is related to complexity.	Jones and Chase 1975	0 - 80	20.90 ±21.74

3.2.3. Structural equation modelling

Physical components that create structural complexity are subject to interacting processes; they co-occur and occupy the same space. Therefore, the suitability of one measure to confer structural complexity of a habitat depends on others. Changes to the structure of these environments (e.g. the erosion of a tall pillar of reef) will have direct and indirect effects on other complexity components and the overall complexity. Since simple linear regressions do not account for the complex interactions inherent in our hypotheses, structural equation modelling (SEM) and pathway analysis (Fox 2006) was used to investigate the relative effects of different complexity components on overall reef complexity.

SEM allows the use of both observed and latent variables. Latent variables in SEM are typically represented by multiple observed variables which act as indicators of the construct (MacCallum and Austin 2000). Hypothetical pathways between variables developed *a priori* can then be tested using empirical data and the paths between variables defined in equation form. SEM has had limited use in natural sciences (Palomares et al. 1998, Wootton 2002, Elmhagen and Rushton 2007), though its predecessor path analysis has been widely used (Wootton 1994, Shipley 2002). SEM will be useful here for a number of reasons put forward by Grace et al., (2010) as it: (1) is theory rather than hypothesis orientated, (2) incorporates causal networks of a system, (3) can test between competing models, and (4) can organise and interpret models involving high numbers of observed and unobserved variables with complex pathways.

3.2.4. Hypothetical models

Two models were developed to examine the relative contribution of interacting covariates in determining reef complexity and the diversity of an associated fish community (Figure 3.1). This work compares the two models examining the influence of structural complexity on coral reef fish diversity. The first model (model A) uses only observed, measurable structural complexity variables. The second (model B) involves the use of both observed and latent variables. Hypothetical pathway models of both model A and B were developed *a priori* (Figure 3.1), and tested using real data through SEM to examine both the relative contribution of interacting covariates in determining coral reef structural complexity and their influence on coral reef fish diversity.

The concept governing the hypothetical development of model B, was that complexity on coral reefs is a multifactorial characteristic driven by two distinct but related pathways. The first is the physical structure of the reef habitat, created by towers, topography, slope etc. The second pathway is the refuge available which can be said to be the space created by the physical structure. This is the interstitial space in which the fish community shelters and manoeuvers. The first pathway included the rugosity, relief height and slope measures. Relief height and rugosity are intrinsically related with greater relief leading to a greater rugosity. Slope angle affects coral growth and development through changing current flows which will carry nutrients or deposit sediments (Jones and Chase 1975). Therefore, changes in the slope of the reef were expected to influence coral development, and thus structural complexity on coral reefs. The second pathway included hole density, mean hole size and hole diversity which were combined to create a single “refuge” latent variable. This allowed for the examination of the contribution of refuge to overall structural complexity but also as a separate entity. Refuge availability was measured by unit area, therefore the values for each variable will likely co-vary, for example smaller mean hole size for an area will predictably result in higher densities and lower diversity of holes. The latent refuge variable was then combined with the other structural complexity variables to create a latent complexity variable which accounts for the multiple measures.

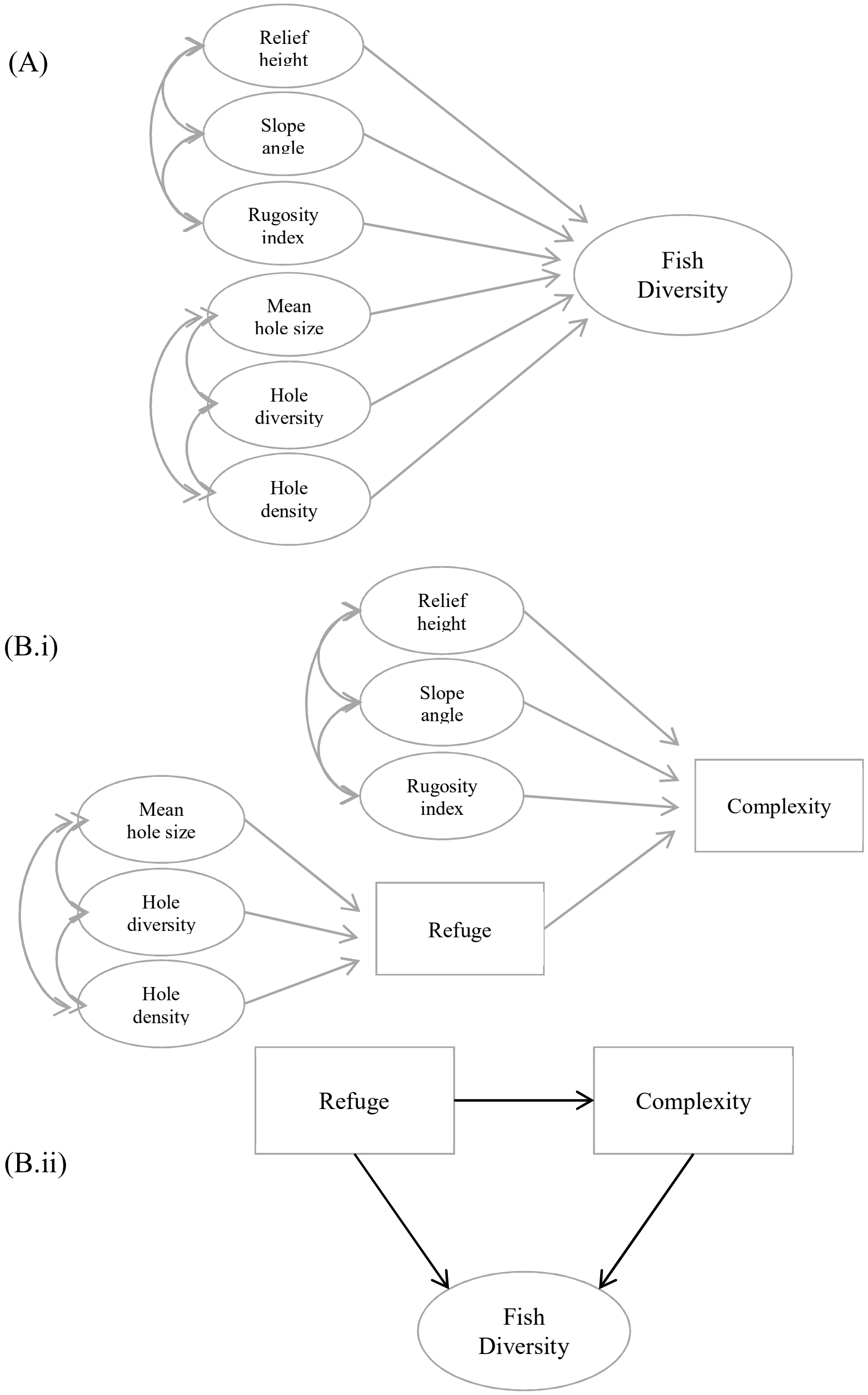

Figure 3.1 The substantive hypothetical pathway models of (A) the non-latent variable model, (B.i) the multiple measures of structural complexity and latent reef structure measures and (B.ii) latent refuge, latent structural complexity and coral reef fish diversity.

3.2.5. SEM fitting

The analysis of a SEM is normally based on a covariance matrix which shows how each of the components and measurements co-vary in a particular system. However, as data did not meet the assumption of normality, polychoric correlations (Fox 2009) were used to create a correlation matrix for analysis in the SEM. Since these correlations are rarely bivariate normal themselves, and are therefore likely to be biased, a bootstrapping approach was used to estimate means and standard errors for the SEM parameter estimates (Fox 2006). Bootstrapping was performed by running the model 100 times with 100 separate sets of data comprising random samples of 75% of the total data set to minimise bias in SEM parameter estimates.

The model procedure was first to fit the hypothetical models, with all predicted pathways. In order to build the simplest significant working model, all non-significant pathways were removed and modification indices (Fox et al. 2009) used to identify overlooked significant pathways which were theoretically justifiable. Model significance was tested using the χ^2 statistic, non-significance indicating no difference between the predicted and observed covariance-structure. Model goodness of fit was determined by assessing the root mean square error of approximation (RMSEA) value of association statistics, comparative fit index (CFI) and the standard errors of the parameter estimates from the bootstrapped 95% confidence limits for each coefficient. An RMSEA of <0.08 (Browne and Cudeck 1993) and a CFI > 0.95 (Hu and Bentler 1998) are considered to represent a reasonable fit for SEM models. All models were fit using the 'sem' package (Fox et al. 2009) in R 2.14.2 (R Core Team 2011). For standardised coefficients, predicted change was measured by standard deviation units which made it possible to examine the relative influences of the measured variables on the latent variables. If an observed variable is changed by 1.0 standard deviation, while holding all other measures constant, refuge would be expected to vary by the standardised pathway coefficient value. For the final models, the hypothetical models were simplified by removing the non-significant covariance pathways.

3.2.6. Principal components analysis

A PCA was performed using the six habitat complexity variables to create an ordination of transects surveyed. The orthogonal PCA axes were then used as explanatory variables. A linear regression was then used to test the relationship between the PC axes and fish diversity. Hole density was log transformed to meet the assumption of normality The same alpha measure of diversity as that used in the SEM analysis was used here. This analysis was performed in R 2.14.2 using the base R base package (R Core Team 2011).

3.3. **Results**

3.3.1. SEM models

3.3.1.1. Model A

Covariance pathways between hole density and both relief height and rugosity index were added to the model as significant pathways which improved model fit. The mean RMSEA score from 100 runs of the final model was 0.124 ±0.006 S.D. and the mean CFI score was 0.91 ±0.004 S.D. which both indicate a poor model fit. The chi square is significant (χ^2 = 87.47, df = 6, p <0.05) which suggests that the predictive model differs from the observed data.

3.3.1.2. Model B

Pathways between mean hole size and diversity and between slope angle and both rugosity and relief were non-significant and removal improved model fit. To allow the model to converge, a covariance pathway between relief height and hole diversity was added. The mean RMSEA score from the 100 runs of the final model was 0.062 ±0.002 S.D. The mean

CFI score was 0.98 ±0.004 S.D. which suggested the model was a good fit for the data. The chi square was significant ($\chi2 = 16.33$, df = 7, $p < 0.05$). Both the CFI and RMSEA exceeded cut-off values and it can be concluded the model fitted despite the significant chi-square.

3.3.2. Pathways

3.3.2.1. Model A

All pathways retained in the final model (Figure 3.2) were significant (Table 3.2) for the relevant unstandardised parameters. All measured reef structure variables had a direct effect on fish diversity. In addition to the hypothesised covariance structure covariance pathways between hole density and both rugosity index and relief height were added to the final model to improve model fit.

3.3.2.2. Model B

All pathways retained in the final model (Figure 3.3 (A) and (B)) were significant (Table 3.3) for the relevant unstandardised parameters, except for paths from mean hole size to refuge and relief height to latent complexity which were set to fixed values to establish the scales for the latent variables. The latent refuge and structural complexity variables had both direct and indirect influences on fish diversity (Figure 3.3(B)). The refuge of a reef was influenced to a greater degree by mean hole size and hole density than hole diversity (Table 3.3). All variables used to quantify refuge on reefs were correlated, indicating that along with their pathway each variable had strong indirect effects on overall refuge quantification.

Relief height had the greatest effect on latent complexity, while rugosity and refuge had similar effects. Slope angle of the reef had the smallest effect. Relief height and rugosity had a weak negative correlation with each other, while neither correlated with slope angle. Relief height had a weak negative correlation with hole diversity.

Table 3.2 Parameter estimates and 95% CIs (in parentheses) for final model A, the structural equation model relating observed complexity variables to fish diversity. “From” and “to” represent the interaction between various correlates fish diversity.

From	to	Pathway Coefficients	Standardised Coefficient	z value	Pr(>|z|)
Pathways					
Hole diversity	Fish Diversity	0.131 (0.127,0.135)	0.129	2.376	<0.01
Mean hole size	Fish Diversity	0.157 (0.154, 0.161)	1.124	2.872	<0.01
Hole density	Fish Diversity	0.263 (0.260, 0.267)	1.239	5.001	<0.01
Relief height	Fish Diversity	0.289 (0.286, 0.293)	0.908	5.559	<0.01
Rugosity index	Fish Diversity	0.247 (0.244, 0.251)	0.652	4.661	<0.01
Slope angle	Fish Diversity	0.209 (0.206, 0.213)	0.442	3.902	<0.01
Covariates					
Mean hole size	Hole density	-0.347 (-0.351, -0.342)	-1.683	-2.027	<0.01
Hole diversity	Hole density	-0.398 (-0.403, -0.394)	-1.184	-4.259	<0.01
Mean hole size	Hole diversity	0.872 (0.871, 0.873)		12.176	<0.01
Relief height	Rugosity	0.474 (0.471, 0.476)	-0.017	8.907	<0.01
Rugosity	Slope	0.038 (0.034, 0.042)	-0.120	3.686	<0.01
Relief height	Slope	0.227 (0.223, 0.231)	0.059	6.628	<0.01
Rugosity	Hole density	0.468 (0.464, 0.473)	0.441	8.340	<0.01
Relief height	Hole density	0.407 (0.402, 0.411)	0.393	7.901	<0.01
Residual variances					
Hole diversity	Hole diversity	0.468 (0.464, 0.473)	0.454	12.942	<0.01
Mean hole size	Mean hole size	0.407 (0.402, 0.411)	-0.459	13.520	<0.01
Hole density	Hole density	0.983 (0.981, 0.984)	-0.794	13.123	<0.01
Relief height	Relief height	0.975 (0.974, 0.976)	0.129	12.948	<0.01
Rugosity	Rugosity	1.066 (1.062, 1.070)	0.575	12.942	<0.01
Slope angle	Slope angle	0.851 (0.849, 0.853)	0.805	12.942	<0.01
Fish diversity	Fish diversity	0.926 (0.924, 0.928)	1.000	12.942	<0.01

*Outputs were derived from 100 bootstrapped models run with 90% random samples of the complexity dataset for each model run.

Table 3.3 Parameter estimates and 95% CIs (in parentheses) for final model B, the structural equation model relating observed complexity variables to latent variables and fish diversity. "From" and "to" represent the interaction between various correlates in influencing complexity and fish diversity.

From	**to**	**Pathway Coefficients**	**Standardised Coefficient**	**z value**	**Pr(>|z|)**
Pathways					
Hole diversity	Refuge	0.611 (0.610,0.613)	0.739	9.624	<0.01
Mean hole size[†]	Refuge		1.124		
Hole density	Refuge	1.110 (1.106,1.113)	1.239	6.312	<0.01
Relief height [†]	Complexity		0.908		
Rugosity index	Complexity	0.699 (0.697,0.701)	0.652	7.897	<0.01
Slope angle	Complexity	0.474 (0.473,0.475)	0.442	5.948	<0.01
Refuge	Complexity	0.669 (0.667,0.671)	0.562	7.120	<0.01
Complexity	Fish diversity	0.300 (0.299,0.301)	0.344	5.784	<0.01
Refuge	Fish diversity	-0.023 (-0.023,-0.022)	-0.019	-0.684	<0.01
Covariates					<0.01
Mean hole size	Hole density	-1.684 (-1.692,-1.676)	-1.683	-4.875	<0.01
Hole diversity	Hole density	-1.183 (-1.187,-1.179)	-1.184	-7.153	<0.01
Relief height	Rugosity	-0.016 (-0.018,-0.015)	-0.017	-0.262	<0.01
Relief height	Hole diversity	0.059 (0.059,0.059)	0.059	2.853	<0.01
Residual variances					<0.01
Hole diversity	Hole diversity	0.452 (0.451,0.453)	0.454	7.515	<0.01
Mean hole size	Mean hole size	-0.459 (-0.462,-0.456)	-0.459	-3.332	<0.01
Hole density	Hole density	-0.797 (-0.810,-0.784)	-0.794	-1.343	<0.01
Relief height	Relief height	0.130 (0.127,0.133)	0.129	0.940	<0.01
Rugosity	Rugosity	0.575 (0.574,0.576)	0.575	8.468	<0.01
Slope angle	Slope angle	0.805 (0.804,0.805)	0.805	12.386	<0.01
Refuge	Refuge	0.780 (0.776,0.783)	0.897	5.145	<0.01
Complexity	Complexity	1.078 (1.074,1.083)	0.739	5.943	<0.01
Fish diversity	Fish diversity	1.000 (1.000,1.000)	1.000	12.942	<0.01

*Outputs were derived from 100 bootstrapped models run with 90% random samples of the complexity dataset for each model run. [†]Represents fixed parameters

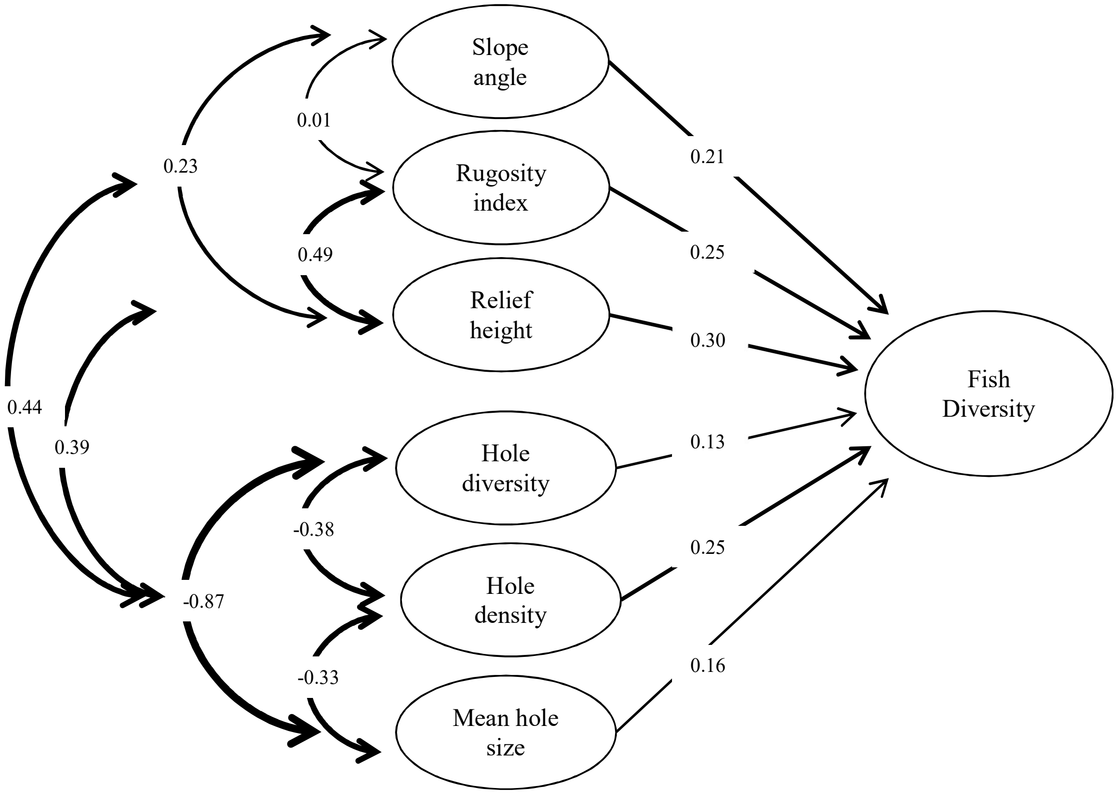

Figure 3.2 Significant pathways of Model A, between observed complexity variables and fish diversity. Values within the single-headed arrows represent effects of a unit change in standard deviation (SD) of the variable at the base of the arrow on the outcome at the head of the arrow. Values within the double headed arrows represent covariance of the observed variables. The boldness of the arrow represents the strength of the pathway Model estimates are derived from 100 bootstraps of 90% random samples from the full data set.

3.3.3. Reef structure and fish diversity

In model A all observed reef structure variables had significant positive effects on fish diversity with relief height having the greatest (unstandardised coefficient = 0.289 ±0.004) and hole diversity having the least (unstandardised coefficient = 0.131 ±0.004). Complexity had a positive effect on fish diversity, while refuge had a negligible direct influence (Table 3.3). The combination of direct and indirect effects of refuge on fish diversity is its pathway to diversity plus the pathway to complexity multiplied by the pathway from complexity to diversity (-0.019+0.562 x 0.344 = 0.174). Refuge therefore had an overall positive effect on fish diversity.

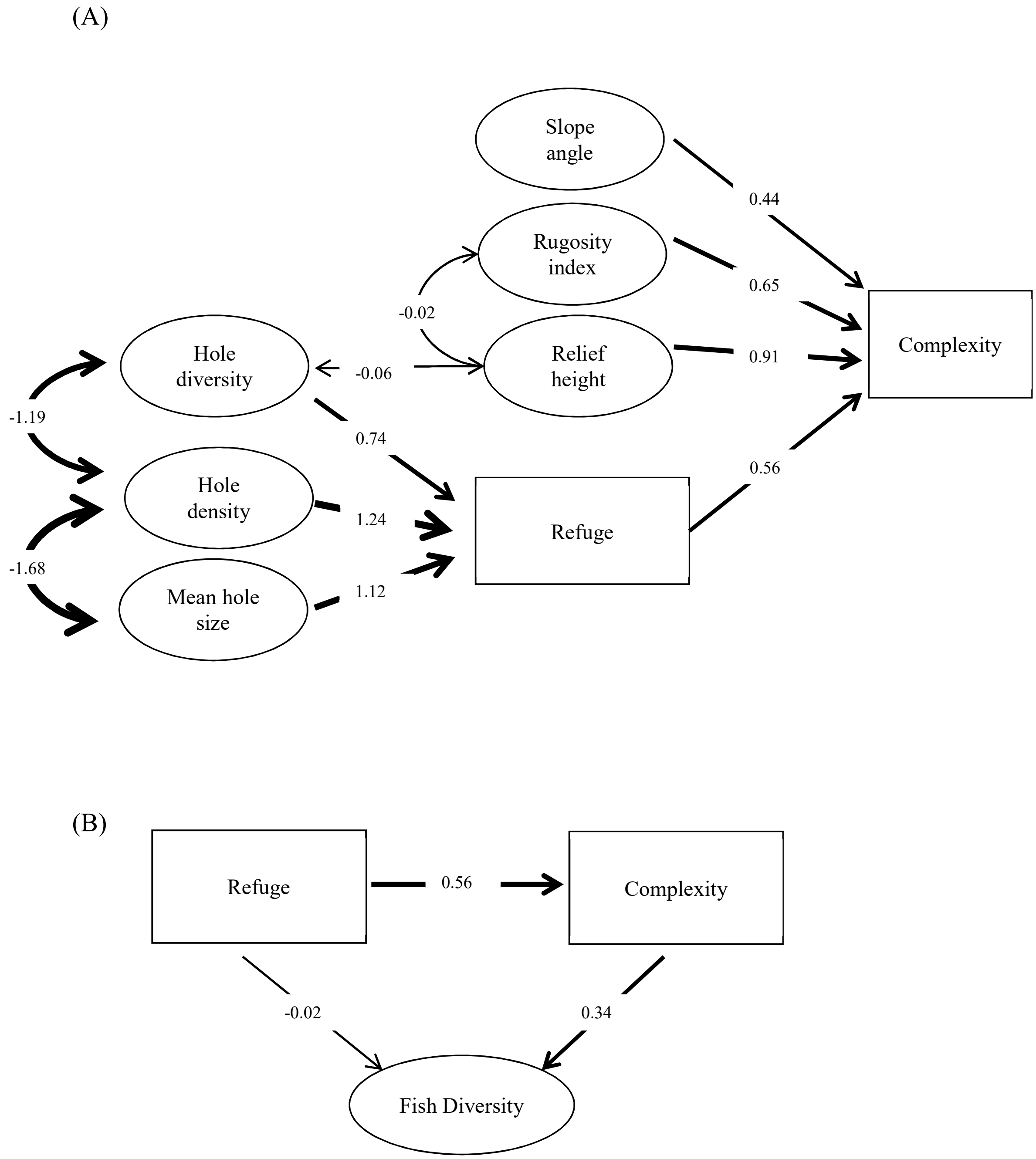

Figure 3.3 Simplified model of the standardised coefficients of (A) significant SEM pathways of influence to the refuge of a coral reef and overall coral reef complexity and (B) latent complexity variables and coral reef fish diversity. Values within single-headed arrows represent the effects of a unit change in standard deviation (SD) of the variable at the base of the arrow on the outcome at the head of the arrow. Values within the double headed arrows represent covariance of the observed variables. The boldness of the arrow represents the strength of the pathway. Model estimates are derived from 100 bootstraps of 90% random samples from the full data set.

3.3.4. PCA

The first principal component axis (PC1) delineated transects along a gradient primarily from high to low structural complexity with high rugosity (up to 1.84) and high relief (1.74 cm) having negative PC1 scores (Figure 3.4). This axis explained 53% of the variation between transects. The separation between transects based on refuge characteristics was shown by PC2 which explained 28% of the variance between transects. Transects with greater hole density (up to 150 holes/m^2) had positive PC2 scores and sites with greater hole diversity (Shannon-Weiner index of 0.75) and average hole size (up to 12 cm) had negative scores. Multiple linear regression revealed a significant relationship between the first two PC axes and fish diversity ($R^2 = 0.11$, F-statistic = 22.3, $p < 0.001$). There was a significant positive relationship between PC axes 1 (coeff = 1.174, t value = 6.292, $p < 0.001$) and 2 (coeff = 0.582, t value = 2.253, $p < 0.05$) and fish diversity. No other PC axes had a significant relationship ($p < 0.05$).

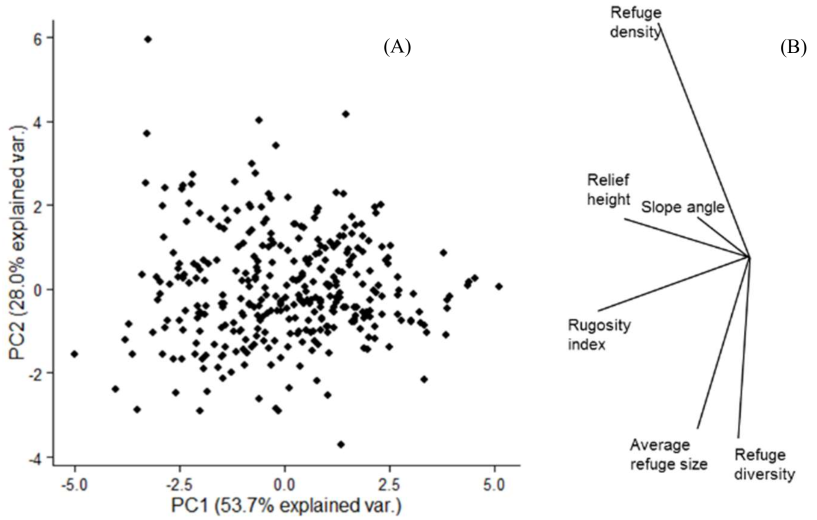

Figure 3.4 Principal components analysis of complexity variables. (A) Variation in PC space of complexity on reefs, shown for the first two principal components. (B) The relative contribution of the six complexity variables to the variation in reef complexity

3.4. **Discussion**

The latent variable model (model B) was a better fit for the data; it had a lower RMSEA and a higher CFI value. The model evaluation fit indices suggest that model A is a poor fit for the data despite its significant pathways and the model should be rejected (Browne and Cudeck 1993). This result suggests the use of latent variable models in the analysis of structural complexity effects on fish diversity is an improvement on previous techniques. Both models show that individual variables influence fish diversity. However, it is only through the use of unobserved structural concepts that it is possible to identify the interactions between variables and understand how they combine to have this influence. The poor fit of model A suggests that despite the significance of the individual variables they do not act independently and the relationship with fish diversity is better represented by the latent variables. In comparison with the PC axes, model B better explained the variation in fish diversity whilst also retaining information about the individual complexity variables and their specific relationships with diversity.

The latent complexity variable was significantly related to all of the measures used (Figure 3 (A)), supporting the hypothetical model that structural complexity is made up of multiple components which will help understand its influence on community structure. The pathway analysis from both models also showed how interrelated complexity variables are in these systems, indicating the measurement of one variable allows the prediction of other variables. This also suggests that the measures used for single variable studies may still give us information about different aspects of a reef's structural complexity if the measured variable co-varies with other, unmeasured variables.

Refuge is expected to influence inter-species interactions particularly by providing safety from predation (Hixon and Beets 1993) or altering competition (Holbrook and Schmitt 2002).

Refuge in this study was contributed to approximately equally by mean hole size and hole density, with a lesser contribution of hole diversity (Fig. 3(A)). This suggests the number and size of holes in a Caribbean reef will better predict refuge than the diversity of hole sizes available. This is not to state that hole diversity is not important; given the pathway's significance, relatively high coefficient and high level of covariance between refuge measurements, its measurement remains important in the characterisation of refuge availability and overall reef structural complexity. The role of refuge size diversity has been overlooked in many studies which instead simplify this to small and large holes and focused more on their abundance (Roberts and Ormond 1987, Hixon and Beets 1993, Caley and St John 1996).

The low level of correlation between observed complexity variables suggests that these measures are not good indicators of each other, or unrelated. Removal of the pathways between slope angle and both relief height and rugosity index, contrasts with Jones and Chase (1975) who found more coral development on sloped than on flat reefs. The negligible covariance between relief height and rugosity index was unexpected, because both are measures of surface topography. The negligible relationship may however be a function of the different types of topography that they are likely to detect. While relief height measurement involves searching for and measuring the highest point in an area, the rugosity index covers only a narrow transect and is more likely to reflect effects of channels or grooves running perpendicular to the transect. One is a measure of fine surface rugosity while the other is of sparse columns, and these need not co-vary.

The PCA separated the habitat complexity variables along two clearly defined orthogonal PC axes. PC1 positioned sites along a structural gradient, highlighting variation in rugosity and relief heights. PC2 separated sites along a refuge gradient where reefs with a high density of small holes were opposite to those with a more diverse refuge regime. This provides an insight into how reefs with different structural complexity characteristics are positioned in orthogonal space and also supports the theory underlying the SEM model used here regarding the two separate pathways of complexity. However, this approach has only revealed the linear relationships between the variables and simplifies their interactions inhibiting a greater understanding of the role of each individual variable. The significance of the relationship between both PC axes and fish diversity supports the use of this dimensionality reduction approach on reef complexity variables. However, the explanatory power of the PCA used here is shown to be inferior to the SEM approach both in elucidating the overall relationship with fish diversity, and in improving understanding the relative role of each individual variable. Though PCA and alternative dimensionality reduction techniques such as MDS are powerful approaches to objectively characterising multivariate data, their constraint in detecting only linear structure limits the conclusions that can be drawn (Monahan 2001).

Using key indicators of structural complexity, previous studies have identified positive, non-random relationships with community composition measures (MacArthur and MacArthur 1961, Risk 1971, August 1983, Nash et al. 2013). These findings have paved the way for a more holistic approach to complexity analysis, whereby the multiple facets are examined for both their individual contribution and combined as a more complete measure of structural complexity. The integrated complexity measure developed here increased confidence in the hypothesis that complexity has a positive effect on the diversity of the associated organisms (MacArthur and MacArthur 1961, Heck and Wetstone 1977, O'Connor 1991, Hurlbert 2004, Gratwicke and Speight 2005a). Through the combination of multiple complexity indicators, it has been possible to examine more fully the role and relative importance of structural complexity components to habitat structural complexity and subsequently the associated community. This suggests that a more ecologically relevant measure of structural complexity was captured than those based on a single indicator, comparative studies or a simple index, thus the association with community diversity is likely to be of greater significance.

In this study refuge had a negligible direct influence on reef fish diversity. Experimental work using artificial reefs has found either no direct relationship between refuge availability and fish diversity (Caley and St John 1996) or an asymptotic relationship with a threshold beyond which increased refuge habitat does not influence fish communities (Hixon and Beets 1993). The results here may support either of these findings and a closer analysis of the refuge relationship with different fish community variables is therefore necessary. The SEM model structure made it possible to examine direct and indirect effects of refuge on fish diversity. The direct and indirect effects together had a positive effect on fish diversity. Field experiments have shown that species richness may not be directly related to refuge, however the availability of refuge can have indirect positive effects on species richness through a positive relationship with fish abundance (Caley and St John 1996).

The specification and development of a SEM requires careful consideration of the theory of the system being evaluated and of the mechanisms being measured. Here the focus was on a discrete set of variables which contribute towards structural complexity, benefitting from the substantial literature which has utilised a broad range of indicators designed to focus on different attributes of reef structural complexity. There are a number of additional measures that could have been included such as hole depth and volume, coral species or growth forms and more relief variables (mean height, variance of height, number of tall growths/rocks over certain height), which may have further improved the latent complexity variable’s ecological relevance. However, this study should provide a starting point for a more holistic approach to answering the numerous and complicated questions about the measurement and role of structural complexity. The present study has shown that both refuge and structural complexity are quantifiable giving a means of examining interactions between these and different habitat states.

Once the relationships between structural complexity variables and between components of the physical environment and the biota are more fully understood it may be possible to address challenges in management using these easily collected data (McArthur et al. 2010). The range of concepts and variables available make selecting appropriate data challenging, however a thorough knowledge of the underlying theory and the mathematical properties of that variable should inform its use and the subsequent analysis based on it (McArthur et al. 2010). The law of diminishing returns suggests adding new ways to indicate reef structural complexity will offer less value than focusing on methods which allow for the instrumental application of these measures (Rapport and Hildén 2013). Through the creation of this multidimensional model it has been possible to combine a number of variables which, individually indicate a single component of reef structural complexity and derive a compound variable which is likely to be of greater relevance to the fish community and potentially of greater use to the understanding of relationships on coral reefs and other structurally complex ecosystems. However the author acknowledges this is a rather data hungry approach!

4. The importance of refuge to the reef fish functional community

4.1. Introduction

Understanding the influence of the various components which make up the physical habitat in which organisms reside is a significant challenge in science (Wilson et al. 2010). Refuge created by the habitat structure is one such component which can influence faunal communities across a range of habitats including lakes (Persson 1993), alpine ranges (Martín and López 1999), deserts (Cowlishaw 1997), kelp forests (Anderson 2001), rocky shores (Garrity 1984) and coral reefs (Beukers and Jones 1998). Refuge can affect communities through the regulation of predator – prey interactions (Crowder and Cooper 1982, Beukers and Jones 1998) or competition (Shulman 1985b, Persson 1993) and the provision of shelter from abiotic stresses (Garrity 1984, Menge and Sutherland 1987). Refuge can be considered the antithesis of the physical structure in that it is the habitable space between the hard structures which makes up the reef framework.

The availability of refuge creates the environment necessary for density dependent controls on population processes (Hixon et al. 2012). Here populations are regulated by the proportion of prey in refuges, which are therefore unavailable to predation. The function of refuge in the presence of predators is to allow prey to remain unseen, or when fleeing to elude capture, as a result individuals will likely spend a greater amount of time in proximity to refuge where possible (Lima and Dill 1990). The distance to refuge may also influence other behaviours such as choice of food, vigilance and habitat choice (Lazarus and Symonds 1992, Brown 1999, Almany 2004b). The presence of refuge in a habitat has a stabilising effect between predators and prey. In order for this stabilising effect to be maintained the proportion of prey in refuge must either increase with increasing predation pressure or decrease with increasing prey density (Sih 1987). In the absence of refuge, alternative predator-avoidance strategies such as camouflage or group formation, are required so as to avoid complete removal of prey from the habitat (Ydenberg and Dill 1986). Aggregative group formation may be a behavioural response of certain species when the number of prey is proportionally greater than refuge (Anderson 2001). This can help stabilise the predator-prey relationship in the absence of refuge. Theoretical studies have also suggested that through this stabilising effect refuges play an important part in managing population structures (Ma et al. 2009). Variations in refuge can also affect the breadth of predator diets (Eklöv 1997). At higher or lower levels of refuge, predator diets are narrower than at intermediate refuge levels (Crowder and Cooper 1982). When there is little refuge there are reduced prey numbers present, where refuge is high there is reduced prey availability.

The coral growth on tropical reefs creates a range of refuge shapes and sizes, making them a good environment for species adapted to their use. The refuge available has a range of characteristics which can be important for the species present (Hixon et al. 1989, Ménard et al. 2007). The abundance and richness of fish species on coral reefs has been found to increase with the diversity and number of refuges available (Hixon and Menge 1991a, Caley and St John 1996). Competition for limited refuge space between conspecifics may result in density dependent mortality for inferior competitors (Holbrook and Schmitt 2002, Geange 2010). Several studies have suggested a close match between fish size and shelter size (Robertson and Sheldon 1979, Hixon et al. 1989, Friedlander and Parrish 1998, Nash et al. 2013). This provides further support for the role of predators in structuring the fish community, where prey compete for a limited number of suitable refuges (Hixon 1991). The "musical-chairs" mortality functions proposed by Samhouri et al. (2009) suggest that prey will spend the majority of their time in the open, and only retreat to cover in the presence of a predator. This behaviour is common in diurnally active coral reef fish species, the majority of which do not actively defend refuge spaces, supporting the hypothesis that on coral reefs there is likely to be a link between fish and the refuge available. This may explain why Ménard et al. (2012) found larger shelters on coral reefs in Barbados to be relatively more important to the fish community. Larger holes were occupied more frequently and, if occupied were more likely to contain multiple fishes. In the "musical-chairs" scenario, fish may flee into the first available refuge. Here it is more important to rapidly flee the predator's field of view than spend time searching for the perfect sized refuge. Differences in results between the studies may be explained by the species studied or the refuge characteristics of the reef, however both provide support for the important role refuge availability plays on coral reefs. It is therefore necessary to understand how changes in the refuge characteristics on reefs will affect the fish community.

Degradation of coral reefs is occurring globally due to a range of environmental and human factors (Hughes et al. 2003, Pandolfi et al. 2011). This decline in reef health has led to a loss of structural complexity in a number of reef areas, particularly across the Caribbean region (Alvarez-Filip et al. 2009), which is linked to subsequent overall decline in the abundance of reef fish in the Caribbean (Paddack et al. 2009). The decline is markedly more significant in populations of habitat specialists (Alvarez-Filip et al. 2015). The loss of specialised reef fish species could have deleterious effects on the ecological function of the Caribbean coral reef ecosystem. The loss of refuge space can result in significant declines in productivity (Rogers et al. 2014), species losses (Graham et al. 2006) and potentially to localised extinctions (Pratchett et al. 2008). It is therefore important to understand what the key drivers behind this decline are. The refuge space available on reefs is one such component of the reef habitat which has the potential for specialist utilisation. Refuge is positively correlated with habitat structural complexity on reefs (Wilson et al. 2007, Chapter 3), therefore the degradation of reef structure in the Caribbean will lead to a reduction in the refuge available. This shift could potentially result in changes to the fish community which utilise the refuge created by the reef framework.

Diversity of the fish community is commonly measured as the function of the abundance and variety of taxonomically distinct species present. However, changes in the environment, such as those perpetuated by coral reef degradation, are likely to have a “filtering” effect on the local community (Lebrija-Trejos et al. 2010, Weiher et al. 2011). Habitat filtering is the reduction in the number of successful strategies available to species in a given habitat (Cornwell et al. 2006). The strategies utilised by fish are elucidated by their functional traits, which indicate specific adaptations to an environment. This filtering suggests that a species is likely to be present in the community only if it has the functional traits to overcome site-specific environmental challenges. Understanding the functional diversity of a habitat reveals the range of strategies used in a system and the number of species using those strategies (Villéger et al. 2010). A complex and nuanced environment such as a healthy coral reef would therefore be expected to have a high functional diversity in order to fill the many niches created (Mouillot et al. 2014). In areas impacted by human activities there may be changes in the functional faunal communities (Flynn et al. 2009, Villéger et al. 2010). In a topical fish community, Villéger et al. (2010) found that changes to the habitat may have led to a loss of functional diversity, even while species richness increases. Here changes in the habitat resulted in a loss of specialist species, while a number of generalists may be able to take advantage of a new, simplified habitat. Therefore, an improved understanding of the functional traits associated with a specific suite of environmental conditions will reveal how changes to the reef environment will affect the fish community. It has been shown that functional diversity and functional group composition is important for ecosystem functioning and to maintaining ecosystem resilience (Bellwood et al. 2003, Pratchett et al. 2011, Cadotte et al. 2012).

Advancements beyond simple species diversity measures are important for understanding the current state of and predicting future pathways for coral reefs. Species diversity reveals limited information about the functional ecology of an environment. Grouping species by one-dimensional traits, such as diet or size, can reveal information about the abilities of these groups. The inclusion of additional traits (e.g. behavioural) can be used to give greater insight into organismal performance and how these groups interact with and affect their environment (Violle et al. 2007)

Refuge, as a key component of the reef habitat, is likely to have a filtering effect on fish functional traits either through its influence on predator-prey relationships and competition (Hixon 1991, Anderson 2001, Samhouri et al. 2009, Geange 2010, Rogers et al. 2014) and/or through the provision of shelter from environmental factors such as physical disturbances, UV light or strong currents (Krause et al. 2002, Sweet et al. 2012). If changes occur in the environment, a different suite of functional traits is required for an organism to survive and reproduce. This is a considerable issue for the fish communities of the Caribbean where a less diverse community relies on fewer species to fill the functional space than on reefs in the Indo-Pacific region, and functional redundancy for the region is low (Mouillot et al. 2014). It is therefore important that a broad understanding of the functional structure of a community is gained in order to fully understand the changes. To that end functional diversity is a multifaceted measure and should be examined as such. Reviews of functional measures (Mouchet et al. 2010, Schleuter et al. 2010) have identified three complementary functional diversity indices – functional richness, functional evenness and functional divergence – which when examined together account for the independent facets of functional diversity (Mouchet et al. 2010). Understanding drivers of fish functional composition on coral reefs will improve understanding as to how changes in the reef environment will affect the fish community and thus resilience of the system (Bellwood et al. 2003). It is therefore also important to identify the functional groups present in the region, the species distribution amongst these groups and how both these groups and the measures of functional diversity are related to habitat quality and the implications of any changes.

Relationships between fish size and refuge will provide insight into the spatial scale over which refuge is likely to affect community functioning. Body size has been identified as being a meaningful proxy for a species' scale of influence (Holling 1992, Nash et al. 2013). Therefore, identifying the size ranges influenced by refuge availability is likely to reveal information about the scale of influence of refuge both ontogenetically and spatially across the reef. The spatial scale over which a functional group operates is important to understanding the effect it may have on the environment. Species that are less mobile will have only a small sphere of influence but more concentrated effects on their surrounding habitat. Those that are more mobile will affect a larger area but in a more diffuse manner. Therefore, understanding the presence of these traits at different spatial scales will be key to understanding how communities will respond to environmental changes such as disturbance events (Peterson et al. 1998). If all the species within a functional group are all equally impacted by a disturbance, then the redundancy of that function or functional group may in fact be low regardless of the number of species present. If there is a large size range within a trait or functional group, there is likely to be inbuilt redundancy. It is therefore important when examining the drivers of functional diversity of the coral reef environment to include an analysis of size in order to better understand ecosystem functioning and functional redundancy. The utility of refuge is dependent on the size of the refuge in comparison to the fish. In the absence of size appropriate refuge, fish are at a greater risk of predation. Therefore, understanding size dependent relationships between refuge and fish will reveal how changes in refuge size will affect the scale of influence of a functional trait or group.

Functional diversity of Caribbean coral fish communities was determined using a number of pertinent traits and divided into functional groups using a hierarchical approach. Refuge was quantified through two approaches. Through the compound measure developed using the SEM approach described in chapter 3, henceforth known as site refuge, and through counts of actual shelter (hole) size. This information was then used to: 1) determine how changes on reefs might affect functional diversity, 2) identify relationships between functional groups and site refuge and hole size and 3) understand the size-specific relationships within functional groups with site refuge and hole size.

4.2. **Methods**

4.2.1. Study site and data collection

Eight countries[3] were surveyed within the Caribbean (Figure 4.1) which represented a range of reef and fish community conditions. Between 7 and 15 sites were surveyed within each country, dependent on country size. Site locations represented a range of geographical and ecological conditions. Areas of reef were identified through satellite images and the Reef Base database. These were entered into ArcGIS 9.2 (ESRI, 2009) as polygons and using Hawth's tools (Beyer, 2004) random sites were selected for surveys within a reef area. The fish community and refuge was characterised at 84 sites on transects 10-15 m deep and parallel to the shore between January and August 2011.

Fish less than 20 cm total length (TL) were surveyed on four 10 x 4 m transects per site. Fish greater than 20 cm TL were surveyed using eight 30 x 4 m transects. All fish observed were counted and identified to species level and their TL was estimated to the nearest centimetre.

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[3] Data used in this chapter includes the same subset of eight countries from the FORCE dataset used in chapter 3. All structural complexity data were collected by C. Dryden and all fish data were collected by S. Newman. Due to different methodologies used in collecting fish community data from Honduras and Belize these countries were excluded from this chapter.

Mean abundances were calculated across transects and then standardised to biomass (g per 10 m^2) at the site. Biomass was calculated using length-weight formulae available on FishBase (Froese and Pauly 2014). Counts of holes were performed on four 10 x 1 m transects at each site. Holes were counted in 5 cm size classes up to 50 cm in diameter. Holes with a diameter greater than 50 cm were grouped as one hole class noted as >50 cm. Mean number of holes was calculated across transects to give holes density per 10 m^2 at each site.

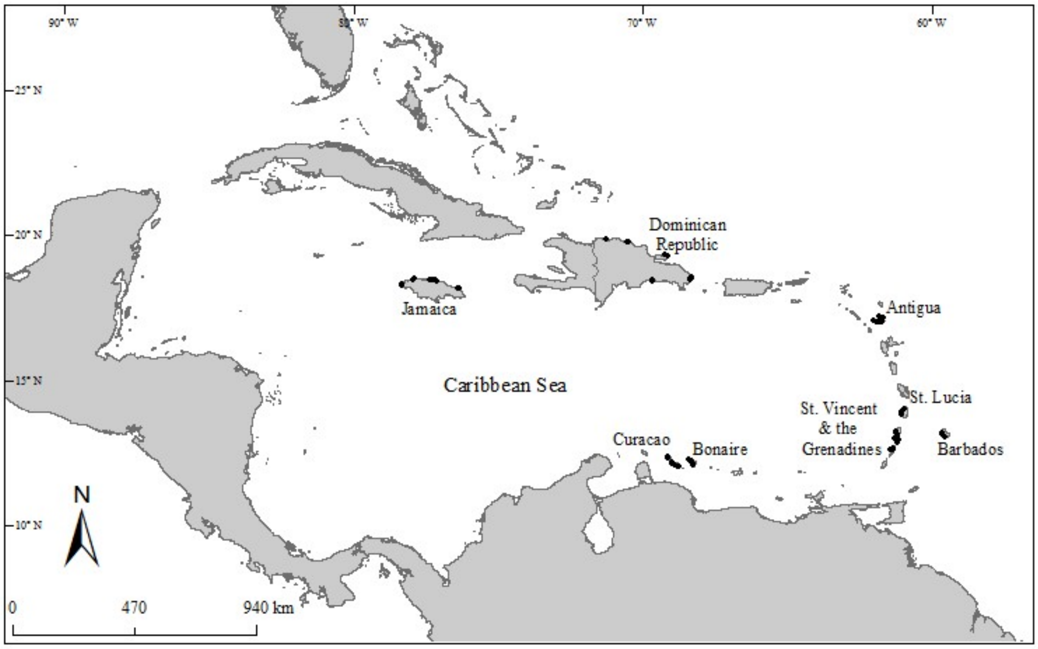

Figure 4.1 Location of survey sites across eight Caribbean countries. Points indicate site locations.

4.2.2. Creating functional indices and functional groups

Fish species present at a minimum of five survey sites (n=159 species) were used to characterise the "regional community" of the Caribbean in this study. All species were assigned a value or category in each of the six fish functional traits used (Table 4.1). This set of six complementary traits are considered suitable for describing the facets of the reef fish community (Guillemot et al. 2011, D'agata et al. 2014, Mouillot et al. 2014). The trait information for each species was retrieved from FishBase (Froese and Pauly 2014). Body depth was used for size as this will better relate to refuge use (Nash et al. 2013). Where information for a species was unavailable, personal observations or a similar species from the same family were used to assign trait values. Functional richness, functional evenness and functional divergence (reviewed in Mouchet et al. 2010, Schleuter et al. 2010) were calculated using the FD package (Laliberté et al. 2014) in R version 3.0.1. (R Core Team 2014).

Functional richness is a measure of the range of trait values present in the community when all traits are considered together, and is calculated as the minimum convex hull volume that includes all species in the community (Villéger et al. 2008). Functional evenness is a measure of the distribution of abundance in functional trait space (Mason et al. 2005). The index decreases when abundance is less evenly distributed among traits and species (Villéger et al. 2008). Functional divergence identifies how far high species abundances are from the centre of the functional space (Mouchet et al. 2010), informing whether the most abundant species in a community have common or rarer traits. FRic, FEve and FDiv (Villéger et al. 2008) were used as the metrics for functional richness, evenness and diversity respectively. All functional indices are presented as a value between 0 and 1. Functional groups were created following a dendrogram approach (Petchey and Gaston 2006) using the FD package (Laliberté et al. 2014) in R (R Core Team 2014). A hierarchical cluster analysis using Ward’s distance method (Murtagh and Legendre 2014) was used to create the functional dendrogram. The number of groups selected was based on the sum of squares merging costs and logical grouping of the species (Mouchet et al. 2008). The biomass of the species within each functional group were then summed to give biomass by functional group at each site.

Table 4.1 Functional traits used for classifying fish into functional groups. These traits have been in previous studies (Guillemot et al. 2011, Mouillot et al. 2014) and were retrieved from FishBase (Froese and Pauly 2014).

Trait	Variable type	Categories used	Trait description	Justification
Max Body Depth	Continuous	N/A	Maximum body depth of species	The refuge available will determine which sized fishes are able to shelter from predators
Diet	Categorical	A: Piscivore; B: Invertivore; C: Herbivore; D: Planktivore; E: Detritivore	Primary diet	Feeding groups use refuge in different ways, therefore group response to available refuge is likely to vary
Mobility	Categorical	S: Sedentary; M: Mobile; R: Roaming	The home range and common movement of species	Mobility will influence a group's response to changes in refuge across spatial scales
Gregariousness	Categorical	I: Individual; P: Paired; SS: Small schools of 3- 20; MS: Medium schools of 21-50; LS: Large schools of >50	The common school size of species	Gregariousness is linked to anti-predator behaviour and therefore refuge use.
Reef Zone	Categorical	B: Benthic; B-P; Reef matrix; P: Pelagic/Water column	Area of the reef habitat a species is primarily associated with during diurnal activities	Will indicate how much time is spent in proximity to refuge
Diel activity period	Categorical	D: Diurnal; N: Nocturnal	Binary categorical measure of the period over the diel cycle when a species is most active	The interaction between a species and refuge may change over the diel cycle

4.2.3. Data analysis

Hole counts were grouped into tiny (0-5 cm), small (5-15 cm), medium (15-30 cm) and large (>30 cm) hole classes in order to reduce collinearity between the hole variables. The compound site refuge measure described in chapter 3 was extracted from the SEM model using the fscores function in the 'sem' package (Fox et al. 2009) in R 3.0.1. (R Core Team 2014). This produced a holistic measure of refuge which gave a novel overarching measure of the reef refuge. The hole size counts provided a measure that was comparable with previous studies and will provide a different insight to utility of different refuge sizes. Utilising both allowed the investigation of relationships with hole size which is comparable to other studies and also allowed identification of specific hole size relationships, while the use of site refuge provided a unique perspective on relationships with the refuge structure on reefs.

In order to explore relationships between functional indices and biomass of functional groups with habitat refuge, generalised linear regression models (GLMs) were used. One set of models was developed using site refuge as the predictor and a second set using the four hole size categories as predictor variables. In all models both linear and asymptotic terms (to detect possible asymptotic relationships) were considered. Akaike's information criterion (AIC) and Bayesian information criterion (BIC) were used for model comparisons. Predictor variables were transformed where necessary; tiny holes were square root transformed and medium and large holes were $\log_{10}+1$ transformed to reduce deviations from normality and variance homogeneity. Predictor variables were examined for collinearity and variance inflation factors (VIF) using the R package AED (Zuur 2010) with a cut-off of 3 (Zuur et al. 2010). GLMs generate measures of null and residual deviance that can be used to calculate a 'pseudo R^2 for the model using Equation 4.1 (Zuur et al. 2009) which can be used to discuss the deviance explained by the model.

$$R^2 = \frac{\text{Null deviance} - \text{Residual deviance}}{\text{Null deviance}} \qquad \text{Equation 4.1}$$

GLMs were run in R 3.0.1. (R Core Team 2014). Normality of residuals and variance homogeneity were evaluated with QQ plots of standardised residuals and plots of residuals against fitted values. Optimum models for the hole class analysis were created by following a stepwise deletion process and simplified by dropping non-significant predictors.

In order to examine the relationship between fish size and site refuge and hole size five functional groups which had a size range greater than 20 cm were subdivided into 5 cm size classes. The relationship between these size classes and the site refuge and hole sizes was then examined using the same GLM process described above.

4.3. **Results**

In total 158,271 individuals from 159 species were recorded from 1,005 transects at 84 sites. These species were classified into 81 genera in 43 families. Species were spread across all categories within traits with a minimum of 2 species in a categorical trait and body depth range of 0.37 – 44.10 cm.

4.3.1. Functional analysis

Fourteen functional groups were identified based on the trait characterisation approach utilised (Table 4.2). This approach clustered species as shown in the trait-based dendrogram (Figure 4.3) which was cut at a height of 0.55. The number of species in these groups ranged from 4 – 26. The mean number of functional groups present at survey sites was 12.2 (±1.4 SD). Five functional groups (1, 3, 4, 6 and 12 (Table 4.2)) were present at all sites and functional groups 2, 9 and 14 were absent from at least 25% of the sites. The distribution in functional space of all fish species observed in this study (Figure 4.2) shows how species are positioned, and how the position and abundances of traits in functional space affects the functional diversity indices.

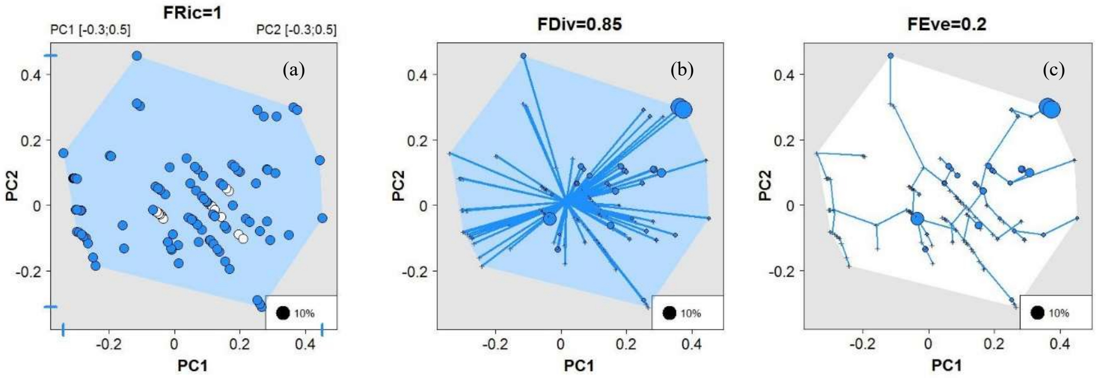

Figure 4.2 Illustration of the multidimensional functional diversity indices of the Caribbean reef fish community observed in this study. Species are plotted in two-dimensional functional space according to their respective trait values. Axes are the first two principal coordinates traits extracted from a principal coordinates analysis of all traits. Circle sizes are proportion of species represented by the circle. (a) Shows the proportion of functional space filled by the community and the relative position of species within functional space. Here functional richness is equal to 1 as all species observed are included. (b) Indicates the proportion of the total abundances of traits and their distance from the centre of functional space. Functional traits found in fewer species are those which are furthest from the centre of functional space. (c) Shows the regularity of abundance distributions in functional space (along the shortest minimum spanning tree linking all species).

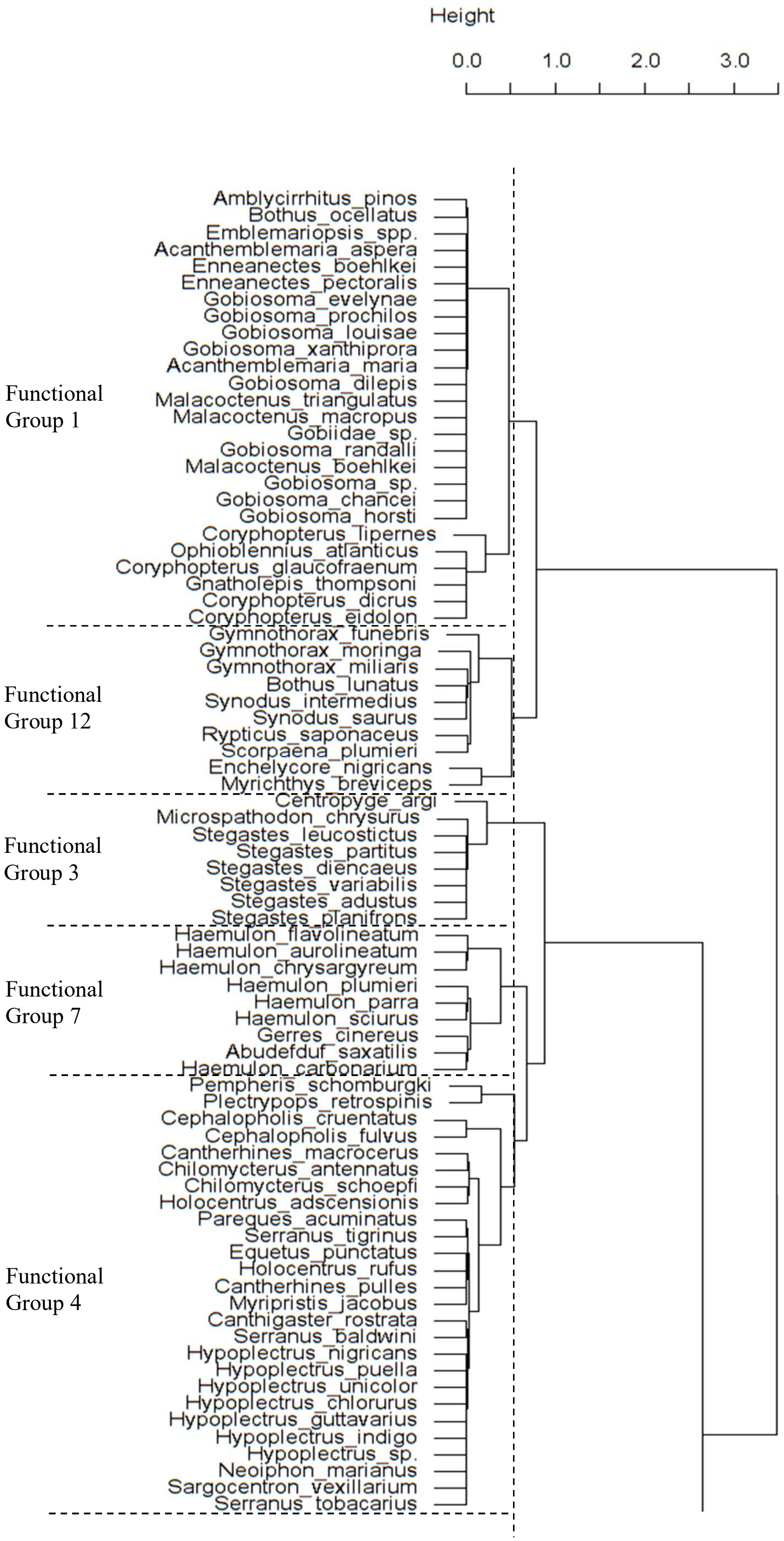

Figure 4.3 (continued on next page) Functional dendrogram created using hierarchical clustering approach and Ward's cluster algorithm in FD package (Laliberté et al. 2014) Continued on the next page. The vertical dashed line represents the height at which the dendrogram was cut. The horizontal dashed lines represent the breaks between functional groups (labelled) described in Table 4.2. The dendrogram is not ordered by functional group. (Continued on next page)

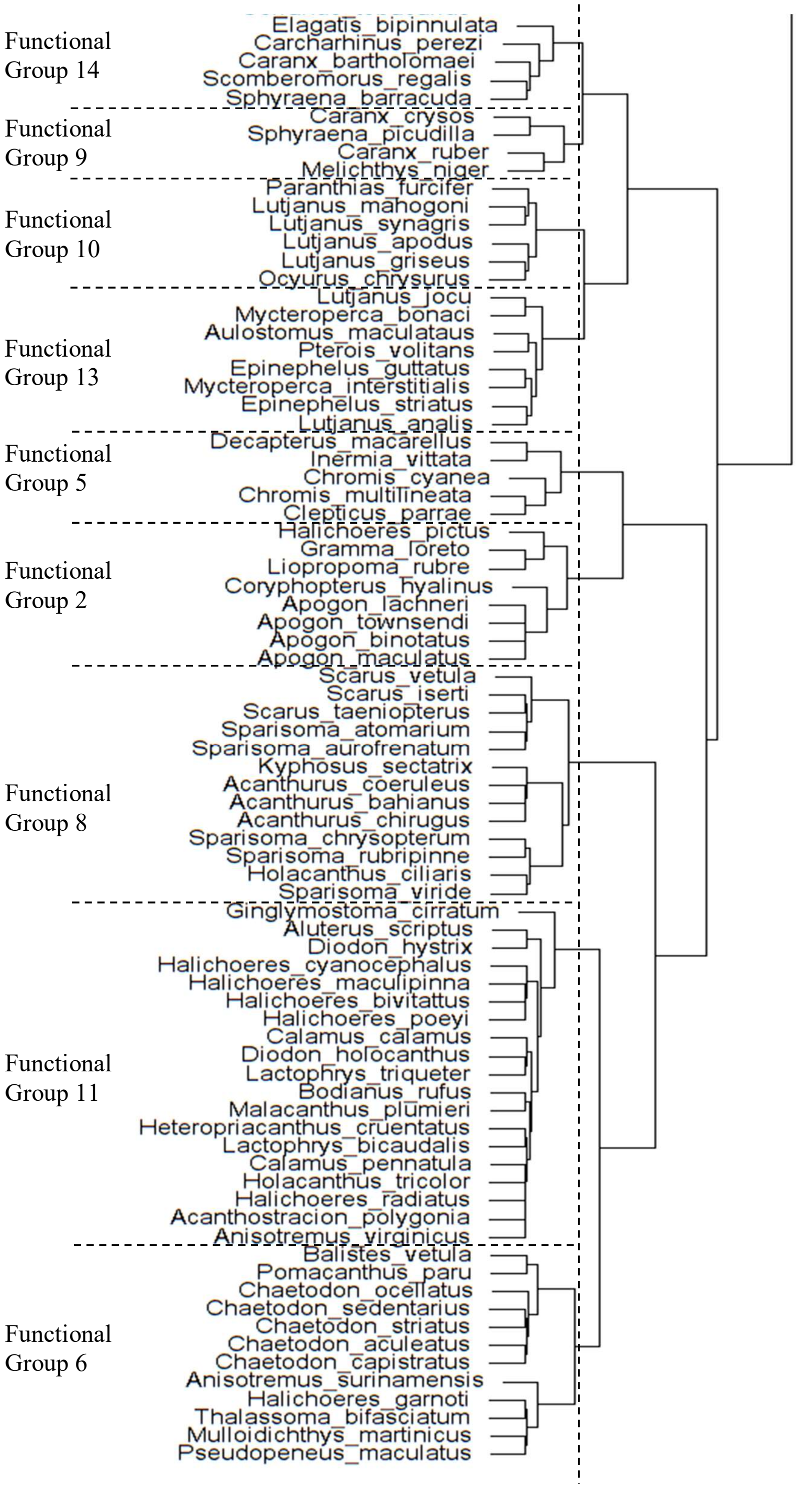
Functional Group 14
Elagatis_bipinnulata
Carcharhinus_perezi
Caranx_bartholomaei
Scomberomorus_regalis
Sphyraena_barracuda
Functional Group 9
Caranx_crysos
Sphyraena_picudilla
Caranx_ruber
Melichthys_niger
Functional Group 10
Paranthias_furcifer
Lutjanus_mahogoni
Lutjanus_synagris
Lutjanus_apodus
Lutjanus_griseus
Ocyurus_chrysurus
Functional Group 13
Lutjanus_jocu
Mycteroperca_bonaci
Aulostomus_maculataus
Pterois_volitans
Epinephelus_guttatus
Mycteroperca_interstitialis
Epinephelus_striatus
Lutjanus_analis
Functional Group 5
Decapterus_macarellus
Inermia_vittata
Chromis_cyanea
Chromis_multilineata
Clepticus_parrae
Functional Group 2
Halichoeres_pictus
Gramma_loreto
Liopropoma_rubre
Coryphopterus_hyalinus
Apogon_lachneri
Apogon_townsendi
Apogon_binotatus
Apogon_maculatus
Functional Group 8
Scarus_vetula
Scarus_iserti
Scarus_taeniopterus
Sparisoma_atomarium
Sparisoma_aurofrenatum
Kyphosus_sectatrix
Acanthurus_coeruleus
Acanthurus_bahianus
Acanthurus_chirugus
Sparisoma_chrysopterum
Sparisoma_rubripinne
Holacanthus_ciliaris
Sparisoma_viride
Functional Group 11
Ginglymostoma_cirratum
Aluterus_scriptus
Diodon_hystrix
Halichoeres_cyanocephalus
Halichoeres_maculipinna
Halichoeres_bivitattus
Halichoeres_poeyi
Calamus_calamus
Diodon_holocanthus
Lactophrys_triqueter
Bodianus_rufus
Malacanthus_plumieri
Heteropriacanthus_cruentatus
Lactophrys_bicaudalis
Calamus_pennatula
Holacanthus_tricolor
Halichoeres_radiatus
Acanthostracion_polygonia
Anisotremus_virginicus
Functional Group 6
Balistes_vetula
Pomacanthus_paru
Chaetodon_ocellatus
Chaetodon_sedentarius
Chaetodon_striatus
Chaetodon_aculeatus
Chaetodon_capistratus
Anisotremus_surinamensis
Halichoeres_garnoti
Thalassoma_bifasciatum
Mulloidichthys_martinicus
Pseudopeneus_maculatus

Table 4.2 The 14 Caribbean coral reef fish functional groups created through the functional diversity analysis. Functional groups are not ordered or ranked by any measure

Functional Group	**Mean body depth (cm) (± SD)**	**Diet class**	**Mobility**	**Vertical position**	**Gregariousness**	**No. species**	**Characterisation**	**Example groups**
Group 1	1.09 (0.68)	Invertivores and herbivores	Sedentary	Benthic	Individual	26	Very small species feeding on sessile inverts and algae, benthic and individual	Blenniidae; Gobiidae
Group 2	2.21 (0.96)	Planktivores	Sedentary	Reef matrix	Mixed	7	Small relatively immobile invertivores	Apogonidae; Grammatidae
Group 3	5.16 (1.68)	Herbivores	Mobile	Reef matrix	Individual	8	Small territorial herbivores which interact with the reef structure	Pomacentridae
Group 4	8.20 (4.01)	Invertivores	Mobile	Benthic	Individual	24	Small-medium mobile (hunting) reef matrix using invertivores and piscivores	Serranidae: *Hypoplectrus*; Holocentridae
Group 5	6.38 (1.28)	Planktivores	Mobile	Water column	Large schools	5	Small-medium planktivores forming large schools which dwell in the water column	*Chromis* spp.; *Clepticus parrae*
Group 6	12.00 (8.78)	Invertivores	Roaming	Reef matrix	Pairs and small schools	12	Small-medium roaming invertivores which form pairs or small schools	Chaetodontidae; *Halichoeres Garnoti*; Mullidae
Group 7	12.81 (4.11)	Invertivores	Mobile	Reef matrix	Mixed schools	9	Medium, mobile, schooling invertivores utilising the reef matrix	Haemulidae
Group 8	15.43 (4.90)	Herbivores	Roaming	Reef matrix	Mixed schools	13	Medium-large roaming herbivores which utilise reef matrix and form mixed sized schools	Acanthuridae; Scaridae
Group 9	16.16 (6.18)	Piscivores	Roaming	Water column	Mixed schools	4	Medium large roaming pelagics forming mixed sized schools in water column	Carangidae; *Sphyraena borealis*
Group 10	18.17 (7.55)	Piscivores	Roaming	Reef matrix	Small schools	6	Large piscivores which form small schools on reef matrix	Small Lutjanidae
Group 11	16.34 (8.40)	Invertivores	Roaming	Reef matrix	Individual	20	Medium invertivores mobile and solitary	Labridae: *Halichoeres*; Ostraciidae; Tetraodontidae
Group 12	7.82 (4.01)	Piscivores	Mixed	Benthic	Individual	10	Large thin benthic piscivores	Muraenidae; Scorpaenidae; Synodontidae
Group 13	24.90 (12.45)	Piscivores	Roaming	Reef matrix	Individual	10	Large roaming piscivores which utilise the reef matrix	Serranidae; Large Lutjanidae; *Pterois*
Group 14	32.36 (7.07)	Piscivores	Roaming	Water column	Individual	5	Large roaming pelagic piscivores	Sphyraenidae; *Scomberomorus regalis*

4.3.2. Functional diversity and refuge

Both functional richness and functional divergence had significant positive relationships with site refuge, though it was unrelated to functional evenness (Figure 4.4). However, site refuge explained relatively low deviance for functional richness ($R^2 = 0.15$) (Table 4.3). Site refuge explained a greater amount of deviance in functional divergence ($R^2 = 0.31$). The frequency of medium and large holes had a significant positive relationship with functional evenness. The frequency of small and medium holes was positively related to functional divergence. There was no significant relationship between functional richness and any of the hole size classes. The deviance explained was low ($R^2 = 0.14$) for functional evenness, but higher ($R^2 = 0.37$) for functional divergence. This means that as site refuge increased a greater number of traits were present in the system (functional richness), however hole size had no effect on this. Hole size did affect how evenly the community biomass was spread across the traits present. The presence of rare traits (functional divergence) was related to both site refuge and hole size.

Table 4.3 Relationships between site refuge and hole size frequencies and functional diversity indices of the Caribbean fish community determined by GLMs. *** = p <0.001, ** = p <0.01, * = p <0.05, NS = no variables in the model were significant (p <0.05).

Variable		**Coefficient**	**SE**	***t* value**	**Significance**	**Pseudo R^2**
Functional Richness						
Site refuge		0.200	0.000	3.746	***	0.15
Hole count	NS					
Functional Evenness						
Site refuge	NS					
Hole count	Medium	-0.002	0.001	-3.019	**	0.14
	Large	0.068	0.033	2.028	*	
Functional Divergence						
Site refuge		1.906	0.334	5.699	***	0.31
Hole count	Small	0.001	0.005	3.320	**	0.37
	Medium	0.164	0.070	2.607	*	

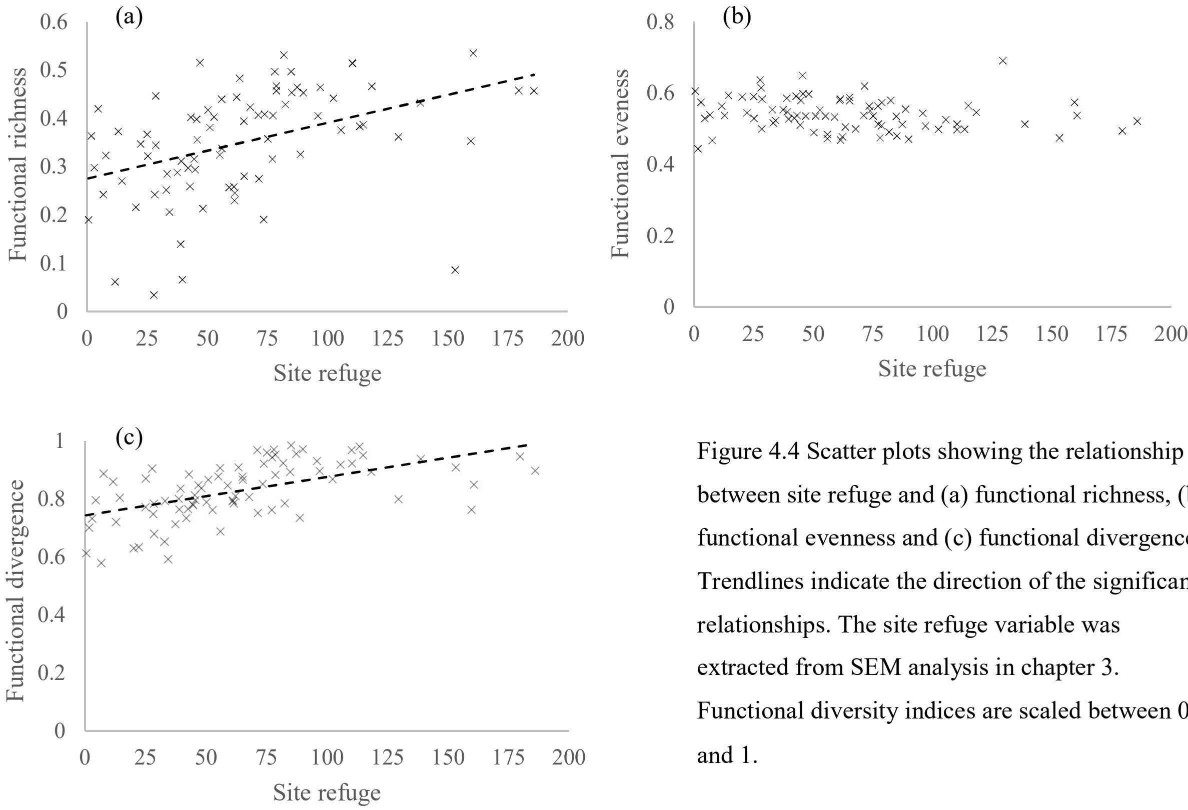

Figure 4.4 Scatter plots showing the relationship between site refuge and (a) functional richness, (b) functional evenness and (c) functional divergence. Trendlines indicate the direction of the significant relationships. The site refuge variable was extracted from SEM analysis in chapter 3. Functional diversity indices are scaled between 0 and 1.

4.3.3. The importance of refuge to functional groups

Higher levels of site refuge were significantly related to higher biomass of functional groups 2, 3, 4, 5, 13 (Table 4.4). The deviance explained for these models ranged from group 13 (reef piscivores) ($R^2 = 0.11$) to group 2 (small invertivores) ($R^2 = 0.33$). Group 11 (large, mobile invertivores) had a negative relationship with site refuge. The analysis of functional groups with hole size frequencies found significant relationships (GLM, $p < 0.05$) between the biomass of all functional groups except 6 (small roaming invertivores) and 14 (solitary, pelagic piscivores). The deviance explained for these models ranged between group 12 (benthic piscivores) ($R^2 = 0.08$) and groups 2 ($R^2 = 0.38$). However, the biomass of groups 8, 9 and 10 had mixed relationships with hole classes and groups 7 and 11 were negatively related to hole sizes. Functional groups 6 and 14 were unrelated to any of the hole size variables.

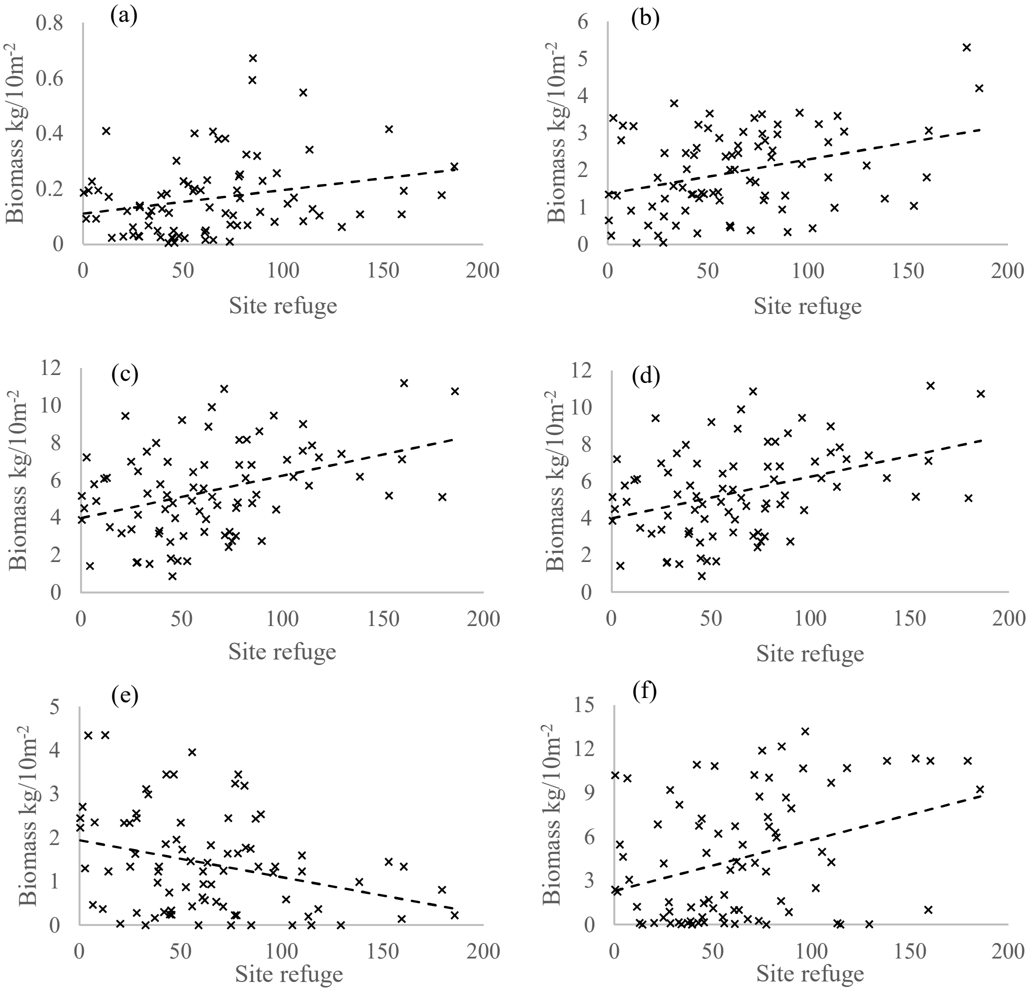

Figure 4.5 Scatter plots showing the significant relationships between site refuge and the biomass of functional groups (a) two, (b) three, (c) four, (d) five, (e) eleven and (f) thirteen. The site refuge variable was extracted from SEM analysis in chapter 3. The trendlines indicate the direction of the significant relationships.

Table 4.4 Significant relationships between site refuge and fish functional groups across the Caribbean determined by GLMs. Fish functional groups are described in Table 1. ** = p <0.01, * = p <0.05. † Indicates that the asymptotic model was a better fit to the data and the results of this model are shown.

Functional group	**Coefficient**	**SE**	***t* value**	**Significance**	**Pseudo R^2**
2	0.021	0.004	5.356	**	0.33
3	1.881	0.826	2.277	*	0.15
4	1.313	0.446	2.941	**	0.19
5	0.014	0.003	4.626	**	0.23
11	-0.009	0.003	-2.767	**	0.11
13	0.012	0.005	2.368	*	0.11

Table 4.5 Significant results between hole size frequencies and fish functional groups across the Caribbean determined by GLMs. Fish functional groups are described in Table 1. ** = p <0.01, * = p <0.05. † Indicates that the asymptotic model was a better fit to the data and the results of this model are shown**.**

Functional Group	**Variable**	**Coefficient**	**SE**	***t* value**	**Significance**	**Pseudo R^2**
1	Medium	0.021	0.011	3.152	**	0.11
2	Small	0.122	0.013	2.383	*	0.38
	Large	2.261	0.786	2.923	**	
3	Large	0.613	0.233	2.644	*	0.28
4	Medium	0.251	0.363	2.635	*	0.12
	Large	0.082	0.011	2.402	*	
5	Medium	0.031	0.016	1.998	*	0.18
7	Medium	-0.024	0.018	-2.036	*	0.11
	Large	-1.933	0.535	-3.664	**	
8	Medium	0.035	0.003	6.762	**	0.31
	Large	-0.566	0.228	-2.584	*	
9	Small	-0.022	0.014	-1.983	*	0.18
	Medium	0.056	0.023	2.996	**	
10	Tiny	0.088	0.022	3.392	**	0.14
	Small	-0.016	0.015	-2.146	*	
11	Medium	-0.903	0.393	-2.333	*	0.12
12	Medium	0.028	0.014	2.246	*	0.08
13	Large	0.459	0.182	2.445	*	0.08

The body depth distribution of the fish community (Figure 4.6) shows the range and abundance of size classes present in the Caribbean coral reef fish community. Those functional groups with a range of size classes were divided into 5 cm size classes and the GLM process was again used to determine the relationships with shelter characteristics across sites (Table 4.6 and Table 4.7). There was no clear pattern in the relationships exhibited between size classes and either site refuge or hole classes. Small size classes did not have stronger relationships with refuge on reefs than medium or larger individuals.

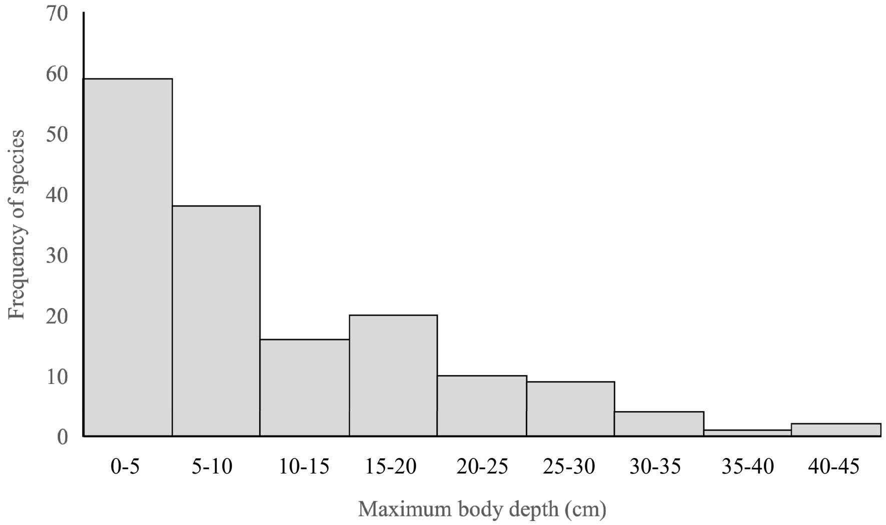

Figure 4.6 Body depth frequency histogram of the fish community from all surveys at all sites

Separate functional groups had different relationships. Only the 5-9 cm size class in functional group 3 (small territorial herbivores) had a significant relationship with site refuge (GLM, $p < 0.05$). 5-9 cm fish had a relationship with large shelter holes and 10-14 cm sizes had an asymptotic relationship with small shelter holes. Functional group 7 (mobile schooling invertivores) exhibited a significant relationship with site refuge in less than 10 cm (GLM, $p < 0.05$) and 16-20 cm (GLM $p < 0.01$) size classes. Less than 10 cm fish also had a relationship with small holes and 11-15 cm and 16-20 cm individuals were related to medium and large holes. All size classes greater than 20 cm in functional group 8 (large roaming herbivores) were significantly related to site refuge (GLM, $p < 0.01$). Less than 9 cm fish in functional group 8 were significantly related to medium and large shelter holes. Fish 15-19 cm and 30-34 cm in length were significantly related to medium and large holes respectively. Fish less than 10 cm in functional group 11 (large, mobile invertivores) were significantly related to site refuge (GLM, $p < 0.05$). Fish 5-9 cm were significantly related to small size holes, and fish greater than 24 cm were significantly related to small and medium holes. Size classes 10-14 cm and 25-29 cm of functional group 13 exhibited a significant (GLM, $p < 0.05$) relationship with site refuge. Only individuals between 15-19 cm were related to the small hole model.

Table 4.6 Significant results between site refuge and fish size from the functional groups 3, 7, 8, 11 and 13 as determined by GLMs. Fish functional groups are described in . ** = p <0.01, * = p <0.05.

Size class	**Coefficient**	**SE**	**t value**	**Significance**	**Pseudo R^2**
Functional group 3					
5-9 cm	0.005	0.002	2.151	*	0.05
Functional group 7					
≤9 cm	0.015	0.005	2.884	**	0.14
15-19 cm	-0.037	0.016	-2.367	*	0.23
Functional group 8					
20-24 cm	0.006	0.002	3.400	**	0.12
25-29 cm	0.007	0.002	3.447	**	0.12
30-34 cm	0.013	0.004	3.694	**	0.18
35-49 cm	0.014	0.004	3.624	**	0.18
≥40 cm	0.012	0.004	2.672	**	0.11
Functional group 11					
5-9	0.011	70.005	2.445	*	0.10
10-14 cm	0.009	0.004	2.311	*	0.08
Functional group 13					
10-14 cm	0.005	0.002	2.310	*	0.06
25-29 cm	2.002	0.972	2.058	*	0.04

[†] Indicates that the asymptotic model was a better fit to the data and the results of this model are shown.

Table 4.7 Significant results between hole size frequencies and the fish functional groups size classes 3, 7, 8, 11 and 13 as determined by GLMs. Fish functional groups are described in Table 1. *** = p <0.001, ** = p <0.01, * = p <0.05. † Indicates that the asymptotic model was a better fit to the data and the results of this model are shown.

Fish size class	Shelter hole class	Coefficient	SE	*t* value	Significance	Pseudo R^2
Functional group 3						
5-9 cm	Large	-0.305	0.121	-2.556	*	0.08
10-14 cm	Small†	11.646	5.022	2.323	*	0.26
Functional group 7						
≤9 cm	Small	0.034	0.023	2.285	*	0.34
10-14 cm	Medium	0.025	0.012	2.051	*	0.35
	Large	1.582	0.434	3.644	**	
15-19 cm	Medium	0.045	0.020	2.283	*	0.56
	Large	2.160	0.740	2.919	**	
Functional group 8						
≤9 cm	Medium	0.039	0.005	7.359	***	0.43
	Large	-0.343	0.122	-2.805	**	
10-14 cm	Medium	0.020	0.006	3.180	**	0.22
	Large	-0.306	0.128	-2.381	*	
15-19 cm	Medium	0.015	0.006	2.300	*	0.07
30-34 cm	Large	1.065	0.310	3.436	*	0.32
Functional group 11						
5-9 cm	Small†	8.736	3.286	2.658	*	0.16
Functional group 13						
15-19	Small†	-1.710	5.331	-2.197	*	0.12

†Indicates that the asymptotic model was a better fit to the data and the results of this model are shown.

4.4. **Discussion**

Through the use of a refuge variable derived from structural equation modelling this study has been able to examine the combined effects of the refuge characteristics of Caribbean reefs. The site refuge variable encompasses frequency, diversity and size of refuge which reveals broader patterns in the relationship with the fish community than using the refuge variables individually. Examining this alongside individual hole size classes enabled an exploration of the relationships with this more holistic measure of the refuge on a coral reef and of distinct relationships with specific refuge sizes. Using a dataset which encompassed a large spatial scale and a range of reef conditions allowed for a representation of the importance of refuge across the whole Caribbean region and how these relationships may affect the fish community.

Changes in site refuge and hole frequency resulted in significant changes in the functional diversity of the Caribbean coral reef fish community. There were also relationships across a range of functional groups indicating the importance of the refuge and hole characteristics to specific components of the fish community. Reefs with greater site refuge supported species with a broader range of functional traits as shown by the functional richness data. This did not appear to be associated with any one hole size category, but instead with the overall refuge characteristics of the reef as indicated by site refuge. However, the spread of traits within the functional space, represented by functional evenness, was related to the presence of medium (15-30 cm) and large (greater than 30 cm) sized holes and not to the site refuge of the reef. These hole sizes represent the size of most Caribbean reef fish species' adult phases. This suggests that these hole sizes are of importance to ensuring an even spread of traits across the community, possibly through the facilitation of species coexistence (Caley and St John 1996). It may also be that the presence of these hole sizes indicates a more structurally complex reef, however disentangling the role of the two factors is not possible here and would require a behavioural examination of the use of reef structure. Refuge on coral reefs is known to be important for individual or localised species survivorship through predator avoidance (Buchheim and Hixon 1992, Hixon and Beets 1993), however these findings suggest that refuge plays an important role across the fish community and that a detailed exploration of this relationship reveals close functional relationships.

Functional divergence had a strong positive relationship with both site refuge and the frequencies of small and medium holes. High functional divergence indicates greater niche differentiation and therefore low resource competition (Mason et al. 2005). This indicates that increasing refuge on coral reefs is likely to increase the abundance of species with rarer traits and potentially lead to improved ecosystem functioning through more efficient resource use (Mason et al. 2005). Rare traits as identified by this study included the diet classes detritivores (2 species) and planktivores (10 species), and a gregariousness of either paired (eight species) or large schooling (7 species). The lower coefficients and deviance explained values for both functional evenness and richness suggest that the refuge characteristics of reefs had a smaller influence on the range and the spread of traits present on Caribbean reefs. However the identification of significant relationships shows shelter was important to ensure all the resources available and niches created by the habitat were more fully utilised, which can lead to increased productivity and greater resilience (Petchey 2003). Sites with low levels of refuge are therefore more likely to be dominated by generalist species with overlapping traits.

Examining the relationship between specific functional groups and refuge on coral reefs allows for a greater understanding of how the functional reef community may be affected by changes to the reef structure. Through the identification of the groups which rely on shelter on reefs it is possible to make predictions as to the services which will be altered by changing shelter availability. For example, the strong relationships exhibited by functional groups 2 (small invertivores), 4 (medium solitary invertivores) and 5 (small, schooling, pelagic planktivores) with both site refuge and hole size frequencies indicates that the ability of these groups to fulfil their functional roles for these groups will be altered by changing refuge. Groups 2 and 5 contain important prey species for medium bodied piscivores, providing a link between plankton in the water column and piscivorous fish (Hobson 1991, Webster and Almany 2002). Group 4 is an important component of the nocturnal fish community, leaving diurnal shelters to actively forage on reef invertebrates (Wyatt 1983). These medium sized invertivores are an important link in the food web of coral reefs as they feed on smaller invertebrates while themselves featuring in the diet of larger predatory fish (Randall 1967).

Functional groups 3 (small, territorial herbivores) and 8 (large, mobile herbivores) had strong relationships with holes of specific sizes. Highly territorial pomacentrids in functional group 3 have an impact on the both fish communities (Williams 1980) and the benthic habitat (Ceccarelli 2007). The relationship with holes identified here suggests that they may be an important component of Pomacentrid territories. Therefore, the presence or absence of refuge may be important in understanding the likelihood of pomacentrid territoriality and all the combined impacts on reef functioning that may have (Williams 1980). The herbivores in group 8 have been identified as key to maintaining the coral reef habitat through the removal of algae (Mumby et al. 2006a). Refuge is useful for predator avoidance, especially during nocturnal periods when scarids retreat into the reef matrix (Tzadik and Appeldoorn 2013). Herbivores may also have an important role in the maintenance of refuge on reefs, where overgrowth of algae may lead to a loss of refuge which can impact future ecological functioning.

The relationships between functional group size classes and site refuge and hole sizes suggest changes in the way fish utilise shelter over their life history. It may also give some insight into the scale over which refuge is likely to affect community functioning. Body size has been identified as being a meaningful proxy for this (Holling 1992, Nash et al. 2013) and therefore identifying the size ranges influenced by refuge availability is likely to reveal information about the scale of influence of refuge. Many of the small size classes had negative relationships with larger holes. Large holes are likely to be used by larger species and may be avoided by small fish as they might be predation spots. In the five groups analysed it was possible to identify specific patterns - or a lack thereof - which are like to be specifically related to the traits of these groups.

Haemulid species which primarily make up group 7, are known to form large schools on the reef slope during the day and disperse to feed individually during the night (Helfman et al. 1982). Given the use of schooling as a primary method of predator avoidance (Huijbers et al. 2011) it is unlikely that this group utilises refuge for protection beyond their juvenile phase. However, they are generally found near coral formations on the reef, and formations such as medium and large holes may act as focal points for schooling. Group 8 (large, roaming herbivores) larger than 20 cm had a significant relationship with the site refuge. This is supported by relationships with the shelter hole sizes where those greater than 15 cm show associations with holes of a similar size to their body. The exception here is the negative relationship between the smallest fish and large holes. The shade created by larger holes and overhangs creates suitable habitat for ambush predatory tactics often used by reef predators (Shpigel and Fishelson 1989, Almany 2004a, Morris Jr and Akins 2009).The very mixed group of 11 (large, mobile invertivores) contains a range of species and sizes, which utilise a mix of survival strategies (Helfman 1986, White and Warner 2007, Harborne et al. 2012) and have a broad diet (Randall 1967). There is a relationship for small size classes with site refuge which may indicate a close relationship with the substratum at early life stages but above 10 cm there is no relationship. Group 13 (large, reef piscivores) had positive relationships with site refuge but negative relationships with hole sizes. This group contains some of the key predators on coral reefs and their mixed relationship with refuge potentially reflects the relationships exhibited by their prey and the presence of refuge on reefs may allow for a broader diet (Crowder and Cooper 1982).

Conflicting results have been found regarding relationships between fish size and shelter use in many other studies. A detailed study looking at the relationship between shelter size and fish occupancy found large holes to be disproportionately more important (Ménard et al. 2012). However studies examining the numerical relationship between fish populations and shelter counts have found a match between fish size and shelter size (Hixon et al. 1989, Friedlander and Parrish 1998). The differences in the results might be reflected by the communities or species surveyed. Small shelters physically exclude larger species making these permanent refuges from predation (Caley and St John 1996). Larger shelters provide a temporary refuge, removing prey from the sight and decreasing the chance of predation (Rilov et al. 2007).

Increasing understanding about the interchange between the habitat and the fish community means beginning to understand potential feedback systems and how changes in one can lead to changes in another. By analysing the functional community, it is possible to understand this in greater detail. Functional diversity metrics provide information about the stability and resilience of a community. The findings presented here show that increased site refuge and shelter hole frequencies of a range of sizes at a site will increase functional diversity and have a positive influence on a range of functional groups. This study reveals that homogenisation of reef structure in the Caribbean (Alvarez-Filip et al. 2009) will continue to drive changes in fish community structure, eventually altering the habitat function of contemporary Caribbean reefs.

Large and diverse communities such as coral reef fish exhibit a variety of relationships and responses. The aim of this study has been to examine this community at a functional level and to understand the potential relationships between this community and shelter on reefs. Despite the variety of responses, it is possible to draw valuable conclusions from this work. Firstly, we can state that the functional diversity of the Caribbean reef fish community is related to the refuge characteristics of coral reefs. Secondly, many functional groups exhibit a relationship with refuge availability on reefs. Finally, the relationship with refuge is likely to change over the duration of a species' and functional group's life history, as fish grow, alter their diet or change their preferred habitat (de la Morinière et al. 2003). Identifying these patterns enables a better understanding of the relationship between reef community functioning and the habitat the reef matrix provides. Additionally, with the future for coral reefs far from certain it adds a necessary piece of information to the toolbox scientists and managers are able to use to identify areas most at risk or most at need of management.

The findings here are among the first to identify a specific habitat characteristic which relates to the fish functional community on Caribbean coral reefs. This result is in contrast the findings of Guillemot et al. (2011) who found that small-scale habitat factors had little or no effect on the functional-species relationship. However it is in support of work that has found relationships between the habitat structure and species composition (Hixon and Menge 1991b, Caley and St John 1996, Harborne et al. 2012, Graham and Nash 2012). Further knowledge about the factors which influence the functional health on coral reefs, particularly those at risk of severe degradation, is important both in understanding the elements key to maintaining resilient and functional reef systems, and for the efficacy of management of these systems.

This analysis shows the use of functional community analysis to assess changes in the fish community reveals trends in the way fish respond to changing habitat characteristics which is of direct relevance to the health and resilience of coral reefs.

5. Influence of the diel cycle on fish – habitat structural complexity relationships

5.1. Introduction

Evidence for relationships between species diversity and abundances and habitat structural complexity comes from a range of habitats including: forests (MacArthur and MacArthur 1961, McElhinny et al. 2005), grassland (August 1983, Rosenzweig 1992), rocky shores (Kostylev et al. 2005), seagrass beds (Stoner and Lewis III 1985, Verweij et al. 2006) and coral reefs (Gratwicke and Speight 2005a, Graham and Nash 2012). However studies have almost exclusively focused on relationships with the diurnal faunal community, yet animals change their activity patterns over the diel cycle, and are often active during one period and shelter during the other (van Schaik and Griffiths 1996, Reebs 2002). Broadening the scope of research to include the nocturnal community will significantly improve understanding as to the scale and causative pathways of this relationship. It is therefore necessary to understand whether relationships identified from diurnal surveys are the same nocturnally.

Coral reefs are ecosystems where the relationship between habitat structural complexity and the fish community has begun to be extensively researched (Sale 1991, Beukers and Jones 1998, Graham and Nash 2012, Alvarez-Filip et al. 2015). Habitats formed of highly complex corals such as *Acropora* spp. and *Orbicella* spp. promote both diversity and abundance of fish species (Lirman 1999, Alvarez-Filip et al. 2011c, Harborne et al. 2012). Habitat variability or changes in habitat condition can alter the diversity, abundance and spatial distribution of fish on coral reefs (Sale 1991, Alvarez-Filip et al. 2015). However, these relationships have been primarily found during the day and little is known about if and how they may change at night. Examining these relationships will yield a more complete understanding of the underlying mechanisms of fish community response to change on coral reefs (Holzman et al. 2007).

Many reef fishes are active during either day or night and fish assemblages on coral reefs vary significantly over the diel period. At dusk there is vertical migration down into the reef by fish diurnally-active in the water column, and movement in the opposite direction by nocturnally-active species (Hobson 1972, 1973, Marnane and Bellwood 2002). Other species migrate horizontally across the reef between feeding grounds; many scarids move from algae-dominated areas to more complex areas to shelter at night, whereas some Holocentridae and Haemulidae species move to flatter habitats to forage (Hobson 1972, Helfman 1986). There are therefore, likely to be a range of structure use patterns amongst groups as behavioural and physiological adaptations cause them to respond differently to changing light levels. The relationship between the fish community and habitat structural complexity will be better understood when the nocturnal relationships are studied.

Through the investigation of nocturnal communities, this study aims to fill gaps in the knowledge of relationships between the fish community and coral reef habitat structural complexity. The specific objectives were to: (1) compare the relationships between abundance, biomass and species of the fish community during the day and night., (2) examine the relationship between functional diversity and habitat structural complexity during the day and night, (3) examine the relationships between the biomass of coral reef fish functional groups and habitat structural complexity during the day and night.

5.2. **Methods**

All underwater visual censuses (UVCs) of the fish community were performed on the sheltered western coast of Bonaire (12.16° N, 68.28° W) within the Bonaire National Marine Park[4]. Surveys were performed within an 8 km linear distance (Figure 5.1), on the fringing

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[4] All habitat structural complexity and fish community data in this chapter was collected by Tom Sparke as part of an MSc project supervised by C. Dryden, S. Newman and N. Polunin. This work was not affiliated with the FORCE project.

reef running parallel to the shoreline at 8 - 15 m depth. This geographically constrained study area was selected so as to constrain environmental spatial variability and increase the chances of correctly attributing any differences to structural complexity. Surveys were performed using 5 x 5 m plots, the locations of which were selected based on a visual estimation of complexity. Plots were assigned a level of complexity based on a three-point scale (low, medium and high) where low complexity plots were flat with minimal vertical relief or refuge; medium plots had significant vertical relief in the form of short (<50 cm tall) towers or mounds and a number of refuge holes; high complexity plots were characterised by high relief and high numbers of refuge created by fissures, overhangs and coral structures. Each complexity level had 15 replicates Plots were at least 5 m apart. Surveys were performed by a single trained observer (Tom Sparke). Diurnal surveys were conducted between 08:30 and 16:40 hours and nocturnal surveys of the same plots took place a minimum of one hour after sunset between 20:05 and

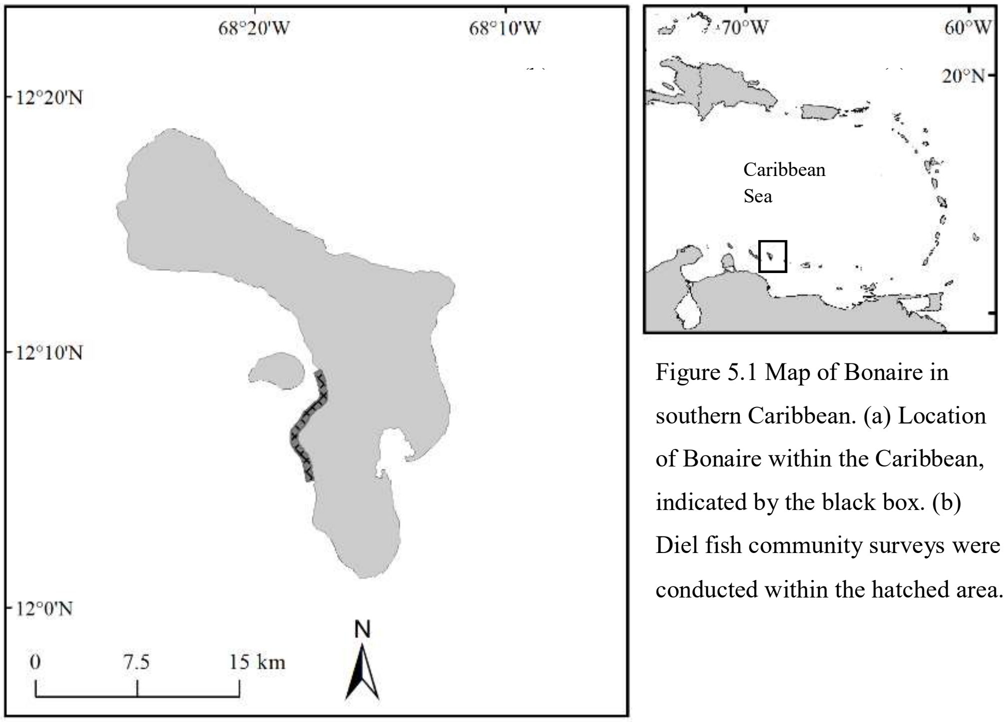

Figure 5.1 Map of Bonaire in southern Caribbean. (a) Location of Bonaire within the Caribbean, indicated by the black box. (b) Diel fish community surveys were conducted within the hatched area.

22:50 allowing the changeover to the nocturnal assemblage to be completed (Hobson 1972). Surveys were performed using SCUBA. Plot areas were measured using a transect tape first. All fish were counted and identified to species and total length (TL) was estimated to the nearest centimetre. Nocturnal plots were surveyed using a red light (Light and Motion GoBe Red Focus Light 165 Lumens 60° beam). Only larger nocturnal fish appeared to be significantly disturbed by this and were counted first. All species observed were assigned a value or category in each of the six fish functional traits (Table 4.1) following the same process outlined in chapter 4. The survey procedure was the same for both diurnal and nocturnal plots; large mobile fish were counted first followed by smaller site attached species and finally a detailed search of holes and refuge areas to locate cryptic or sheltering species. Plots took between 15 – 25 minutes to survey with more complex plots taking longer due to a greater surface area and increased number of refuge areas.

Effects of habitat structural complexity on abundance, biomass, species richness and functional diversity of the fish community were examined using univariate permutational analysis of variance (PERMANOVA) reduced models with pairwise tests using Euclidean similarity matrices. Abundance and biomass data were fourth-root transformed to conform to normality and homoscedasticity assumptions and to reduce effects of dominant species. All analyses of diel changes in the fish community were performed in PRIMER-Ev6 with PERMANOVA extension (Anderson et al. 2008). Functional richness, functional evenness and functional divergence (Mouchet et al. 2010, Schleuter et al. 2010) were calculated using the FD package (Laliberté et al. 2014) in R version 3.0.1. (R Core Team 2014). Species were assigned to functional groups (Table 4.2). The functional groups present in both the diurnal and nocturnal surveys were then examined further for their structural complexity relationships using the univariate PERMANOVA approach.

5.3. **Results**

Total fish abundance, biomass and species richness all had significant positive relationships with structural complexity both diurnally and nocturnally (Table 5.1 and Figure 5.2), although the biomass (pairwise PERMANOVA, t = 0.465, $p > 0.05$) and richness (pairwise PERMANOVA, t = 0.507， $p > 0.05$) of the nocturnal community was not significantly different between medium and high structural complexities. The functional diversity indices showed a mixed relationship with structural complexity. Functional richness had a positive relationship with complexity both diurnally and nocturnally. High structural complexity plots had a significantly greater diurnal functional richness then either low or medium (pairwaise PERMANOVA, $p < 0.05$) and medium and high structural complexity plots were greater than low structural complexity plots (pairwise PERMANOVA, $p < 0.05$) at night. Functional divergence had a significant positive diurnal relationship with structural complexity, however there was no significant nocturnal relationship. Functional evenness had no significant diurnal or nocturnal relationship with structural complexity.

Table 5.1 Differences in fish abundance, biomass, species richness and functional diversity indices comparisons between structural complexity levels in diurnal and nocturnal surveys from PERMANOVA tests. Significance level: - = non-significant, * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$

Fish community metric	Diurnal		Nocturnal	
	Pseudo-F	significance	Pseudo-F	significance
Total abundance	29.97	***	13.14	***
Total biomass	8.01	***	2.27	**
Species richness	18.83	***	8.32	***
Functional richness	4.77	*	7.02	**
Functional evenness	0.98	-	0.44	-
Functional divergence	5.52	**	0.02	-

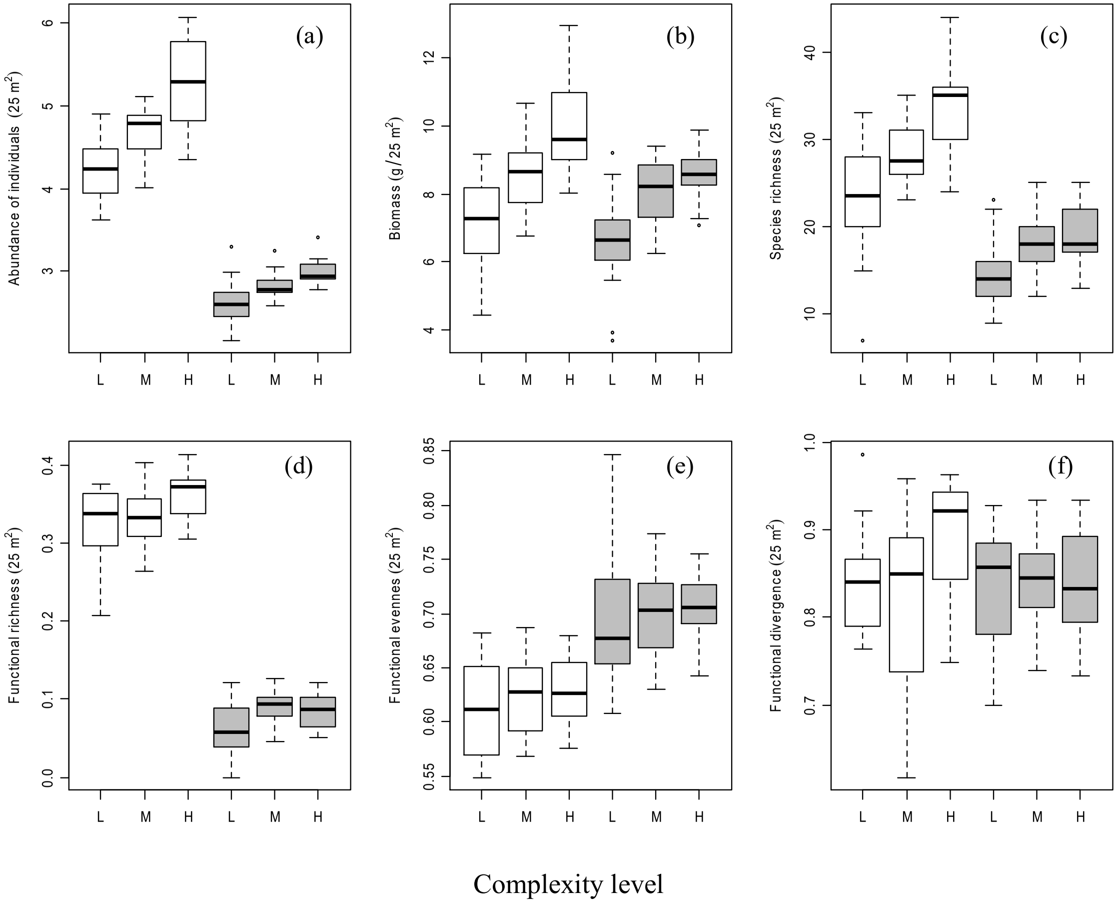

Figure 5.2 Plots of diurnal (white) and nocturnal (grey) of (a) total numerical abundance, (b) total biomass (c) species richness, (d) functional richness, (e) functional evenness and (f) functional divergence in 25 m^2 plots against reef structural complexity levels (low (L), medium (M) and high (H)). Boxes show the interquartile range and the black line within the box represents the median value.

Functional group 14 (large, solitary, pelagic piscivores) was absent from all surveys and functional group 9 was absent from the nocturnal community and was therefore not included in the analysis. The biomass of all of the remaining groups varied significantly with structural complexity either diurnally and/or nocturnally. The biomass of 10 groups displayed significant diurnal differences in biomass with structural complexity and eight groups had significant nocturnal relationships with complexity (Table 5.2). The presence and direction of the relationships varied by functional group (Figure 5.3). Functional group 1 (small, sessile, benthic individuals) biomass had a negative relationship with structural complexity both diurnally and nocturnally. There were significant differences between all structural complexity levels during the day and between low and medium, and low and high at night.

Four functional groups had positive diurnal relationships with structural complexity and no significant nocturnal relationship. Functional group 2 (small, invertivores) biomass increased during the day with significant differences between low and both medium and high. Functional group 8 (large, mobile herbivores) had a significantly higher biomass at medium structural complexities than at either low or high structural complexities. The biomass of functional group 10 (medium, schooling reef piscivores) had a significantly higher biomass at high structural complexity than at either medium or low. Functional group 11 (large, mobile invertivores) diurnal biomass varied significantly among all structural complexity levels. However, both groups 10 and 11 were virtually absent from the nocturnal community and their biomass at all structural complexity levels did not differ significantly from 0.

The biomass of three functional groups had positive diurnal and nocturnal relationships with structural complexity. All three of these functional groups - 3 (small, territorial herbivores), 5 (small, schooling, pelagic planktivores) and 13 (large, solitary, reef piscivores) - had a significantly greater diurnal biomass at high and medium than at low structural complexities and a significantly different nocturnal biomass at all three structural complexity levels. Functional groups 4 (medium, solitary invertivores) and 7 (mobile, schooling invertivores) had positive diurnal relationships; biomass was significantly greater at medium and high structural complexities than low structural complexities. Nocturnal biomass of these two groups had a significant peak at medium structural complexities.

Functional group 6 (small, roaming, invertivores) did not differ significantly with structural complexity during the day, however it had a higher nocturnal biomass at both low and high complexities than medium structural complexity where they were virtually absent. Functional group 12 (benthic piscivores) was largely absent from the diurnal surveys, however biomass was significantly greater at high structural complexities in nocturnal surveys.

Table 5.2 Differences in biomass of functional groups between structural complexity levels in diurnal and nocturnal surveys from univariate PERMANOVA analysis. Significance level: - = non-significant, * = p <0.05, ** = p <0.01 and *** = p <0.001

Functional group	Diurnal		Nocturnal	
	Pseudo-F	Significance	Pseudo-F	Significance
1	37.23	***	4.015	*
2	27.40	***	2.359	-
3	12.68	***	44.934	***
4	36.52	***	5.682	**
5	13.72	***	79.374	***
6	3.35	*	2.654	-
7	7.27	***	4.149	*
8	3.46	-	2.134	-
10	5.52	**	0.120	-
11	8.47	**	0.101	-
12	2.86	-	2.865	-
13	5.08	**	3.764	*

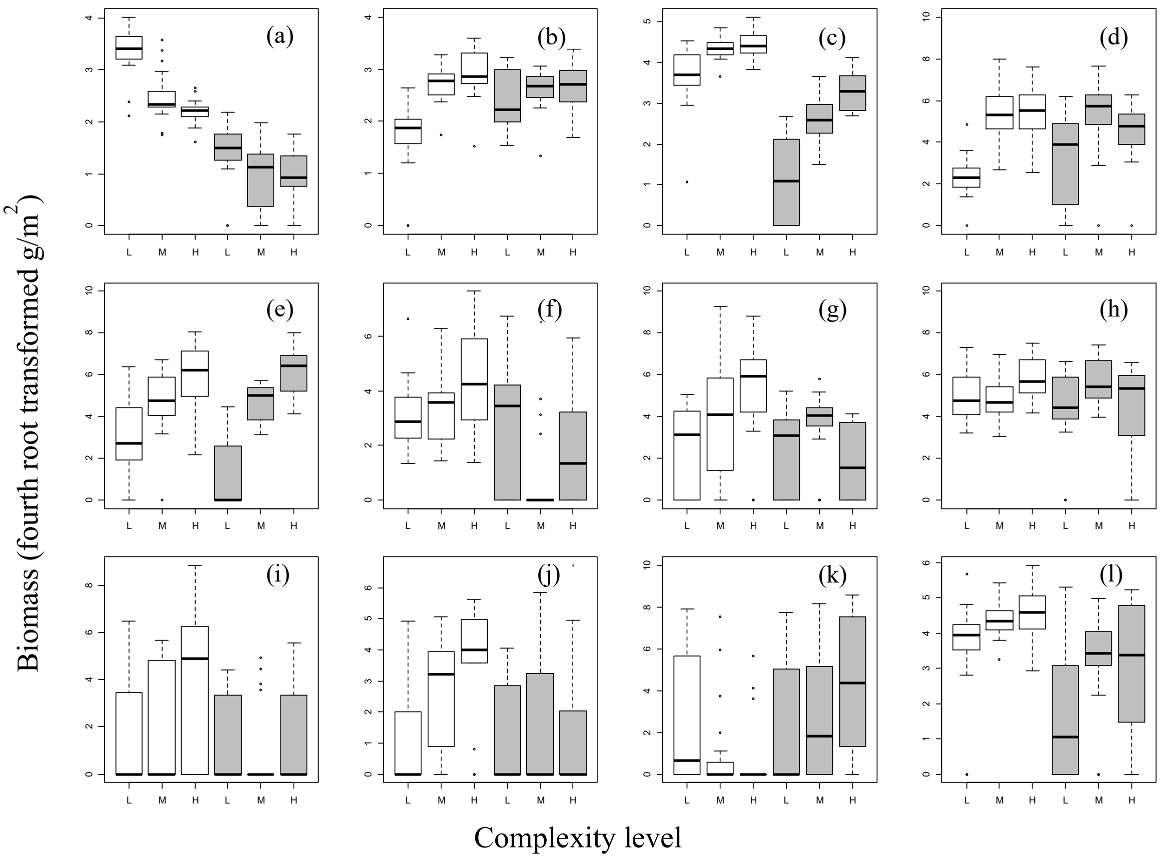

Figure 5.3 Total fourth-root transformed biomass of diurnal (white) and nocturnal (grey) relationships of (a) functional group 1, (b) functional group 2 (c) functional group 3, (d) functional group 4, (e) functional group 5, (f) functional group 6, (g) functional group 7, (h) functional group 8, (i) functional group 10, (j) functional group 11, (k) functional group 12 and (l) functional group 13 in 25 m^2 plots across the three reef structural complexity levels; low (L), medium (M) and high (H). Boxes show the interquartile range and the black line within the box represents the median value.

5.4. **Discussion**

This study is the first to examine nocturnal relationships between the fish community and habitat structural complexity, and the first diel comparison, therefore the findings represent a significant advancement in understanding the role of coral reef structural complexity. Positive diurnal relationships between habitat structural complexity and fish abundance, biomass and species richness community were maintained over the nocturnal period. This shows that habitat structural complexity continues to plays a significant role for fish communities throughout the diel period. The relationship between functional diversity and structural complexity appears to be less straightforward. Functional richness increased with structural complexity both diurnally and nocturnally, however functional divergence only had a positive relationship during the day while functional evenness was unrelated to structural complexity. This suggests that while there is an increase in number of traits present, and therefore a greater filling of the functional space at higher structural complexities, the utilisation of niche space within the habitat is unaffected by changes in complexity. The increase in functional divergence with structural complexity suggests a greater degree of niche separation at high structural complexities, and thus lower resource competition. The increase in traits present and the greater niche separation at higher structural complexities indicate that habitat structure promotes a more functionally diverse community; this may result in increased productivity which could buffer them against environmental fluctuations or species invasions (Mason et al. 2005).

The significant positive relationships with habitat structural complexity at night suggests that predator avoidance is likely to be a key driver of nocturnal reef space use. Other potential drivers of space use, such as territoriality (Bay et al. 2001) and avoidance of UV light (Sweet et al. 2012) are unimportant at night. Fish are at significant risk of predation while relatively immobile and less sensitive to external stimuli (Cerri 1983, Holbrook and Schmitt 2002, Yokogawa et al. 2007). Fish on coral reefs are most at risk from predation at night when outside shelter (Holbrook and Schmitt 2002) emphasising the continued importance of structure throughout the diel cycle. It is not evident what causes the plateauing of the relationship at medium and high structural complexities for biomass and richness. It may be related to shelter suitability at higher complexities where, although shelter density increases diversity decreases potentially creating less refuge for larger fish (Hixon and Beets 1993). It may also be due to prey movement as many nocturnally active fish groups are invertivores (Hobson 1973), and though many coral reef invertebrates are known to nocturnally active (Glynn and Enochs 2011) their night time movement on reefs is not yet fully understood.

This positive relationship was not seen in all functional groups. The twelve groups studied revealed a diverse combination of positive, curvilinear and negative diurnal and nocturnal relationships between total biomass and reef structural complexity. The group-specific responses to structural complexity over the diel cycle are likely to result from differences in diurnal and nocturnal behaviour and activity patterns (Hobson 1965). Functional groups 3 (small, territorial herbivores), 5 (small, schooling, pelagic planktivores) and 13 (large, solitary, reef piscivores) all had positive diurnal and nocturnal relationships with structural complexity. Fish from groups 3 and 5 are either territorial (Robertson 1996) or feed in the water column over structurally complex reefs (Friedlander and Parrish 1998) and they refuge within their territories or seek shelter in the reef directly below at night (Hobson 1972), as a result these groups are reliant on structural complexity across the diel cycle. Group 13 consists of many of the important piscivorous predators on coral reefs. They are often visual ambush predators, the majority of which are diurnally and crepuscularly active (Hobson 1965, Gibran 2007) and therefore utilise coral reef structure to hide from prey. At night when they are less active they may seek shelter in more structurally complex reefs.

Functional groups 2 (small invertivores), 4 (medium, solitary invertivores), 7 (medium, schooling invertivores) and 12 (benthic piscivores) contained many of the nocturnally active species. However, these groups all had different nocturnal relationships with structural complexity from each other. Apogonidae, which account for much of the biomass in group 2 are nocturnally active and disperse horizontally across the reef to forage with dietary differences leading species to different areas of the reef (Marnane and Bellwood 2002). During the day they display cryptic behaviour and make use of shelters (Gardiner and Jones 2005), however at night they are able to feed in the water column when their physiological adaptations make them better suited to environmental conditions (Fishelson et al. 2004). The nocturnally active invertivores in groups 4 and 7 utilise the reef matrix during the day for schooling and refuge in medium and structurally complex reefs (Helfman et al. 1982, Ménard et al. 2007). However, much like apogonids, they disperse across the reef to feed at night, resulting in increased utilisation of less structurally complex areas and a weaker relationship with structural complexity. The diurnal biomass of group 12 was low across all complexities; this may be related to their cryptic behaviour (Gilbert et al. 2005). However active hunting at night and an attraction to areas of high prey density may explain the greater nocturnal biomass at more structurally complex reefs (Hobson 1975).

The diurnal biomass of functional group 6 (small, roaming invertivores) had non-significant positive relationships with structural complexity, however there was a significant trough at medium complexities in the nocturnal surveys. This group consists of a mix of diurnally and nocturnally active roaming invertivores. The mixed nature of this group means that the relationship with structural complexity may be split over the diel cycle. Those active during the day may have little relationship with structural complexity as they roam over the reef (Cole and Pratchett 2013), however at night these species use refuges (Robertson and Sheldon 1979), and are therefore likely to have a closer relationship with the structure. However mullids feed over the diel cycle, foraging in areas of rubble and sand (Krajewski et al. 2006). This use of less structurally complex patches for foraging is likely to account for the bimodal relationship with structural complexity at night within this group.

Fish community abundance, biomass, species richness, and functional richness data provide some of the first evidence that habitat structural complexity plays an important role in structuring fish communities over the entire diel cycle. Functional groups were found to vary in their response to structural complexity over the diel cycle. For some groups the importance of structure as a refuge is maintained at night, whereas for others there may be a release from predation as they move to flatter areas to forage. This array of relationships highlights the need for further study into species or functional group relationships with reef structure over the diel cycle.

6. Fish behavioural interactions with coral reef structural complexity

6.1. Introduction

Environmental condition plays a key role in organisation of animal communities in a given habitat. Though the relationship between coral reef habitat and the abundance and diversity of the community has received significant attention (Hixon and Menge 1991b, Sale 1991, Gratwicke and Speight 2005a, Graham and Nash 2012, Alvarez-Filip et al. 2015), how these communities respond over small spatial scales has been somewhat overlooked. Spatial heterogeneity over these scales often relates to variations in habitat quality which in turns results in variations in species distribution. A key component of habitat quality which can vary over these scales is habitat structural complexity with more structurally complex areas typically associated with higher abundances and diversities of fish than flatter areas (Wilson et al. 2007), even when separated by only short distances (Newman et al. 2015).

Advances have been made in measurement of habitat structural complexity, with attempts to capture a greater amount of the variability associated with the reef habitat (Wilson et al. 2007, Harborne et al. 2012, Nash et al. 2013, Newman et al. 2015), which are likely to be more relatable to the fish community. However, identifying behavioural associations between fish and their physical habitat may help elucidate causal relationships. A number of behavioural associations with habitat structure have been identified. Fish use habitat structure and landmarks for navigation as they move (Ogden and Quinn 1984, Reese 1989). Areas of very low complexity such as sand or rubble patches can act as a barrier to movement between reefs (Afonso et al. 2008a, Turgeon et al. 2010) because they lack features necessary to provide shelter from predators (Sweatman and Robertson 1994). Tethering experiments have shown these flatter areas, especially in close proximity to the reef edge, have higher predation risks (Shulman 1985a, Sweatman and Robertson 1994), although these areas may be important for small fish which are able to utilise small holes in the rubble which larger fish cannot (Schrandt et al. 2012).

Many smaller reef fish, such as *Gramma loreto* and *Stegastes* spp are territorial around specific features such as vertical relief or nesting sites (Freeman and Alevizon 1983, Robertson 1996, Cheney and Côté 2003). This is likely to be an important characteristic in fish whose size and behaviour leads them to perform relatively restricted movements in close proximity to the substrate, where any significant movements away from the reef may leave them at a greater risk of predation. A number of species compete intra- and inter-specifically over features (e.g. shelter sites) which are not part of a territory but may be important for food or shelter (Robertson and Sheldon 1979, Shulman 1985b). Behaviour can also vary within species across levels of complexity. As complexity increased, aggression and shelter use decreased in a damselfish (Schrandt et al. 2012), potentially due to greater availability of shelter, which reduced competition and thus the number of antagonistic encounters.

Coral reef fishes can exhibit habitat-associated intraspecific variation in traits such as territoriality (Afonso et al. 2008b), reproductive performance (Pankhurst et al. 2008) and growth (Feary et al. 2009). This shows the potential relationships that habitat structure can have with the fish community. Behaviour can be closely linked with changes in habitat condition, potentially resulting in behaviourally different approaches as the fish respond to locally disparate challenges (Foster 1999). Such changes may have far-reaching consequences for the dynamics of communities when population dynamics can be affected by variations in the behaviour in individuals (Anholt 1997, Sutherland and Norris 2002, Schrandt et al. 2012). Understanding the way in which fish utilise the reef matrix for daily processes, and how changes in reef structure may affect these and potentially decrease a species' ability to persist, need greater attention.

This study aims to understand the role fish behaviour and preference plays in the previously identified numerical relationships between habitat structural complexity and the coral reef fish community. The specific objectives were to: (1) examine whether behaviour varies systematically across the fish community, (2) which behaviours vary within species at different structural complexities and (3) determine whether the availability of structural features varies among complexities and whether certain species show a preference for specific habitat features on reefs.

6.2. **Methods**

All underwater visual censuses (UVCs) and behaviour observations of the fish community were performed on the sheltered western coast of Bonaire (12.16° N, 68.28° W) within the Bonaire National Marine Park[5]. Surveys were performed within an 8 km linear distance (Figure 6.1), on the fringing reef running parallel to the shoreline at 8 - 15 m depth. This geographically constrained study area was selected to limit environmental spatial variability and increase the chances of correctly attributing any differences to structural complexity. All surveys were performed using 5 x 5 m plots, the locations of which were selected based on a visual estimation of complexity. Plots were surveyed using SCUBA at six different complexity levels, with 0 being flat reefs with little structure and 5 being highly complex (Wilson et al. 2007, Newman et al. 2015). These were grouped into low, medium and high structural complexities because no significant differences were found in feature availability between 0-1, 2-3 and 4-5. The feature selection analysis only used data from plots of high structural complexity plots to preclude any confounding effects of structural complexity on feature availability or behaviour. In order to assess the feature space within the plots, counts were taken of the numbers and types of structural features available in each plot. A feature

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[5] All habitat structural complexity, fish community and fish behaviour data in this chapter were collected by C. Dryden and C. Skinner. This work was not affiliated with the FORCE project

was considered as any distinct structure available for utilisation by reef fish species (Figure 6.2).

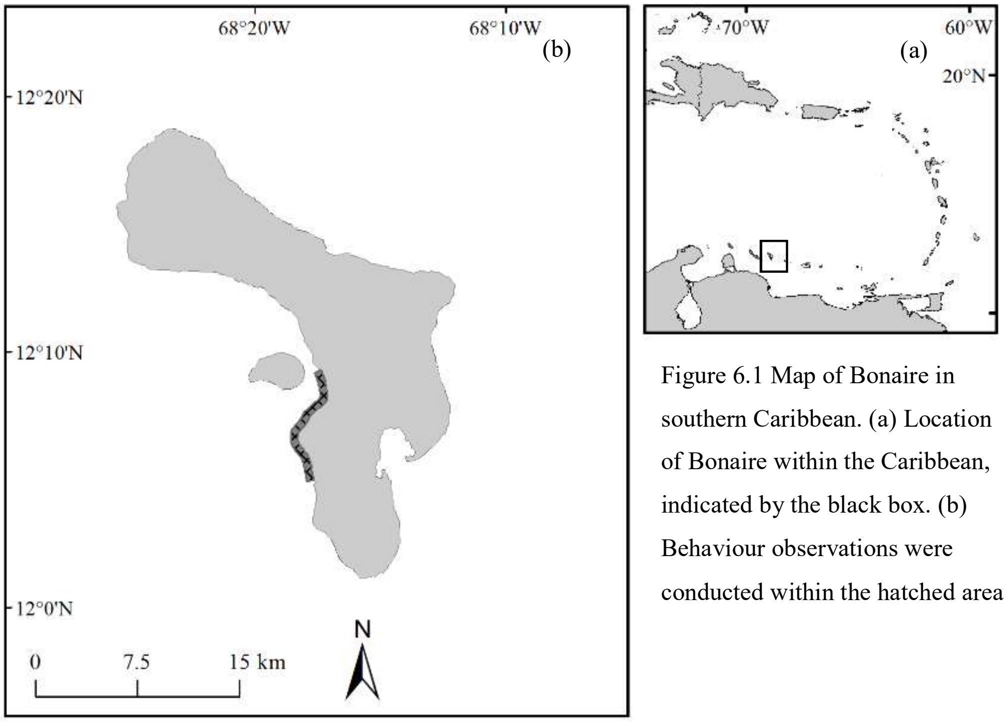

Figure 6.1 Map of Bonaire in southern Caribbean. (a) Location of Bonaire within the Caribbean, indicated by the black box. (b) Behaviour observations were conducted within the hatched area.

Fish species to be observed were chosen through a combination of the functional group analysis and preliminary field observations of behaviour. Chapter 4 identified specific fish functional groups (Table 4.2) and their relationships with structure in the form of refuge. In preliminary observations, individuals from multiple species in these functional groups were observed for 10 minute periods, during which the start time, duration and frequency of behaviours performed and features interacted with were noted and the distance moved from original location was recorded. An individual was deemed to be interacting with a feature based on distance from and orientation to a feature and its pattern and speed of movement (Figure 6.2). Through this preliminary work seven species from six functional groups were selected based on representativeness and observability (Table 6.1). A behavioural ethogram for each species and time budget analysis were developed. This information was used to create a catalogue of behaviours for each species (Table 6.2) and to elucidate the duration of each behaviour and the length time required to observe all the behaviours. Based on this information a focal observation period of three minutes was selected. Behaviours were classified based on distinct patterns of movement, feeding or conspecific interactions which had the potential for some feature association.

All fish behavioural observations were conducted between 08:00 and 15:00. Once the estimate of structural complexity and the count of features were completed on a plot, the observer then moved a minimum of 5 m away from the plot and waited 3 minutes for fish to resume normal behaviour and movement. After this period an individual from one of the study species was selected at random within the plot, its size (TL to nearest centimetre) and life phase (if determined by obvious colouration) were recorded, and the three-minute observation period would begin. The start time of all changes in behaviour and feature associations were recorded allowing for the calculation of durations spent performing behaviours or at specific reef features. After the observation period the observer then moved away from the plot to identify a different individual from one of the study species and the observation process was repeated. This was performed for a maximum of five individuals at each plot. If at any point during the observation period, the focal individual moved outside of the plot, the observation was stopped and another individual inside the plot was selected and the observation started again from the beginning.

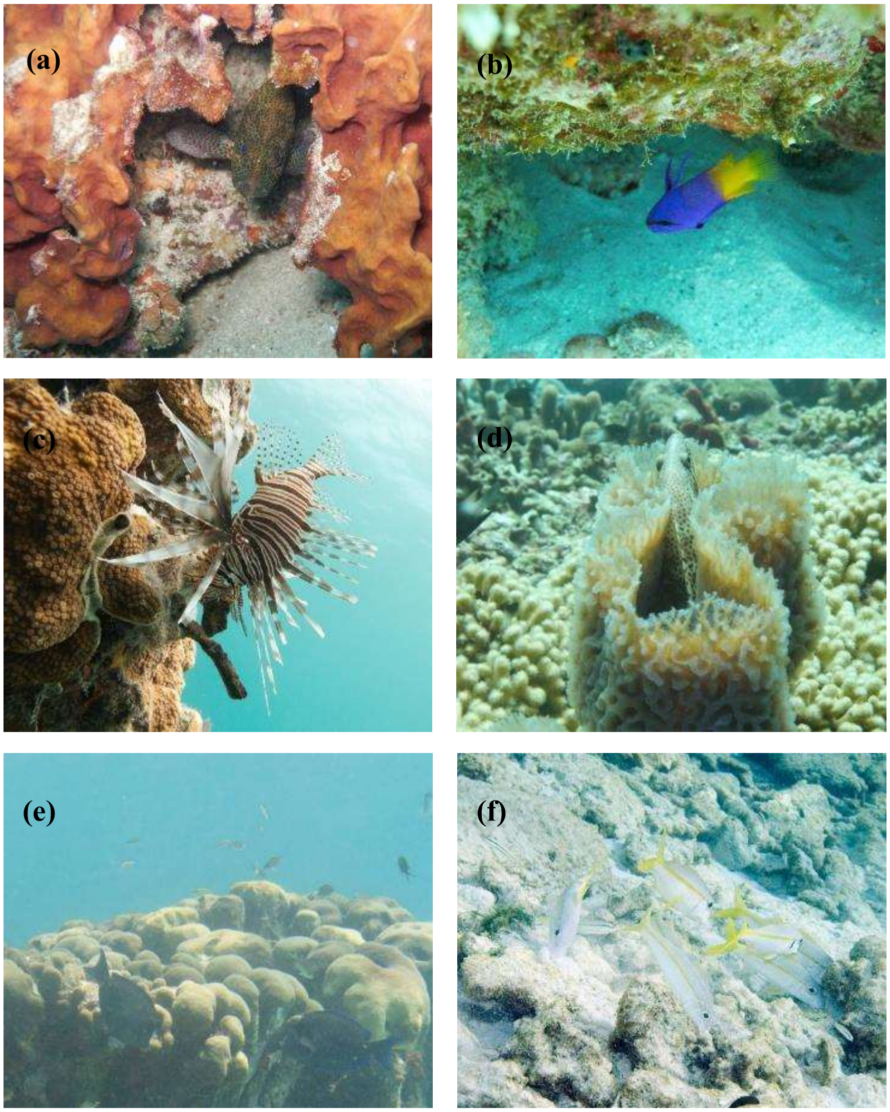

Figure 6.2 Coral reef fish species utilising a range of reef features. (a) *Cephalopholis. cruentatus* in refuge, (b) *Gramma loreto* under overhang, (c) *Pterois volitans* beside vertical relief, (d) *C cruentatus* in sponge, (e) *Chromis multilineata,* above *Orbicella annularis* head and (f) *Mulloidichthys martinicus* foraging in uncolonised substrate. All photos taken by C Dryden

Table 6.1 Species observed for this study. Functional group was identified through the analysis in chapter 4.

Functional Group	Species	Common name	Functional Group Description
2	*Gramma loreto*	Fairy basslet	Small, site attached relatively immobile invertivores
3	*Stegastes planifrons*	Threespot damsel	Small territorial herbivores with close interaction with the substrate
4	*Myripristis jacobus*	Blackbar soldierfish	Small - Medium invertivores. Mobile, most nocturnal utilising the reef matrix during the day
6	*Thalassoma bifasciatum*	Bluehead wrasse	Small-medium roaming invertivores which form pairs or small schools
6	*Mulloidichthys martinicus*	Yellow goatfish	Small-medium roaming invertivores which form pairs or small schools
7	*Haemulon flavolineatum*	French grunt	Medium, mobile, schooling invertivores utilising the reef matrix during the day and hunting elsewhere are night
13	*Cephalopholis cruentatus*	Graysby	Large mobile piscivores, utilise the reef matrix for hunting

Table 6.2 The six fish behaviours observed in this study

Behaviour	Description
Slow swim	Moves slowly across the reef or structure
Fast Swim	Moves quickly across the reef or structure
Slow swim/ Hover	Moving very slowly switching between swimming slowly and hovering
Feed	Any behaviour associated with eating e.g. biting at turf algae or foraging in sand
Hover	Rest motionless above the benthos or beside/above a structure
Perch	Rest motionless on the benthos or a structure

Table 6.3 Classification of features available to fish on Caribbean coral reefs

Feature	Description
Bowl	A depression surrounded by higher walls. Wider than deep. May have one large side entrance.
Coral	An individual coral colony. This includes encrusting, foliose and small digitate corals.
Orbicella annularis head	Characteristic columnar coral head of *O. annularis*
Overhang	A section of rock or coral which extends outward creating a sheltered or shaded area underneath.
Refuge	A hole in reef matrix with an approximately circular opening
Soft or Fire coral	Stands of soft or fire coral
Sponge	All sponges. Including barrel, finger, tube, rope and vase sponges
Uncolonised substrate	Any patch of sand, rubble or bare rock on the reef bed
Vertical Relief	Any significant elevation above the benthic substrate with vertical or near vertical sides

To test for systematic changes in behaviour across complexities multiple regression on distance matrices (MRMs) were used. First a Bray-Curtis distance matrix of all species' combined behaviour durations was regressed against a Euclidean distance matrix of the six-point visual scale of complexity. A binary species matrix was then added to the regression enabling a test for species level differences in behaviour, based on the approach described in Legendre et al. (1994). All analysis on distance matrices was perform using the 'ecodist' package (Goslee and Urban 2007) in R 3.0.1. (R Core Team 2014).

To test for within-species changes in behaviour, the proportion of time spent moving and proportion of time performing the most common behaviour (by species) were tested among complexities. Proportion data was arcsine transformed and analysis performed using PERMONOVA in PRIMER-Ev6 with PERMANOVA extension (Anderson et al. 2008).

A principal coordinates analysis (PCA) was performed using the PERMANOVA+ add on (Anderson et al. 2008) to identify how the availability of features differed between complexities. Compositional analysis was used to examine feature selection by fish. A matrix of habitat usage was created using the proportion of time spent at a feature and a second matrix of habitat availability was created using the counts of features within a plot. The analysis was performed using the ‘compana’ function in the package ‘adehabitatHS’ (Calenge 2006) in R 3.0.1. (R Core Team 2014). Compositional analysis was chosen over selection ratios because normality of distributions is important when using selection ratios such as those of Manly or Jacob (Aebischer et al. 1993). Additionally, the high numbers of zeros in the data would have greatly affected the selection ratios, whereas compositional analysis can handle this using its “randomisation” procedure. Given the high number of features available for use on coral reefs, there also exists an inherent issue with the use of selection ratios as the more habitat types that are distinguished, the lower the sample sizes for observed use of each type; this reduces the power of statistical tests to identify relationships between use and availability (Garshelis 2000). Furthermore, in resource selection ratios, the proportional uses of the various resources are not independent of each other. If one habitat type has a low proportional use, others will naturally have a higher use which may lead to the apparent selection of other types because total proportion must sum to one (unit sum constraint). This problem can be overcome in compositional analysis by using a log-ratio transformation making them linearly independent (Pendleton et al. 1998). Not all habitat features were available to, or utilised by each animal, therefore the initial list of 23 features was reduced by pooling similar features; nine features were used in the final analysis (Table 6.3). This reduced the number of null proportions and improved the accuracy of the analysis and comparisons across the dataset (Aebischer et al. 1993).

6.3. **Results**

6.3.1. Behavioural relationships

There were no significant systematic differences in the behaviour of the fish observed among structural complexities when all species were grouped (Table 6.4). When the species matrix was added to the regression formula, the result became significant, indicating differences among species in their behaviour, however the coefficient for complexity remained low. When species were examined separately there were no significant changes in their overall behaviour (i.e. all behaviours combined) among complexity levels.

Three species displayed variations in the durations of specific behaviours among structural complexities (Table 6.5), however, there were no significant behavioural changes in the other four. The three species which differed in behaviour durations were *S. planifrons* (functional group 3), *T. bifasciatum* (functional group 6) and *C. cruentatus* (functional group 13). All three species spent a greater amount of time moving around the survey area at low structural complexity than at medium or high structural complexities (pairwise PERMANOVA, $p < 0.05$). Both *S. planifrons* and *T. bifasciatum* spent a significantly greater amount of time feeding at medium and high structural complexities than at low structural complexity (pairwise PERMANOVA, $p < 0.01$). *C. cruentatus* spent significantly more time perched on the substrate or on structures at high and medium structural complexities than in low structural complexity reef plots (pairwise PERMANOVA, $p < 0.05$), where they spent more time hovering above the benthos.

Table 6.4 Results of analysis of systematic differences in behaviour across structural complexity levels with MRM analysis. All species tested for differences across the six-point scale of complexity (0-5) and between species. Species then tested separately for differences across structural complexity. Species are ordered by functional group. Significance level: - = non-significant, * = p <0.05 and ** = p <0.01.

	Coefficient	F-value	Significance	R - squared
All Species combined				
Complexity	-0.86	1614.07	**	0.10
Species	48.73			
Focal Species				
G. loreto	4.83	0.69	-	-
S. planifrons	1.95	0.74	-	-
M. jacobus	1.01	0.05	-	-
T. bifasciatum	-0.06	0.07	-	-
M. martinicus	5.23	0.37	-	-
H. flavolineatum	1.66	0.82	-	-
C. cruentatus	0.69	0.27	-	-

Table 6.5 Significant differences in durations of specific behaviours across the three structural complexity levels determined by univariate PERMANOVAs. ** = p <0.01, * = p <0.05.

Species	Pseudo-F	p-value	significance
S. planifrons			
Mobile	4.885	0.006	**
Feeding	6.324	0.002	**
T. bifasciatum			
Mobile	3.714	0.025	*
Feeding	4.303	0.019	*
C. cruentatus			
Mobile	2.884	0.044	*
Perch	2.226	0.017	*

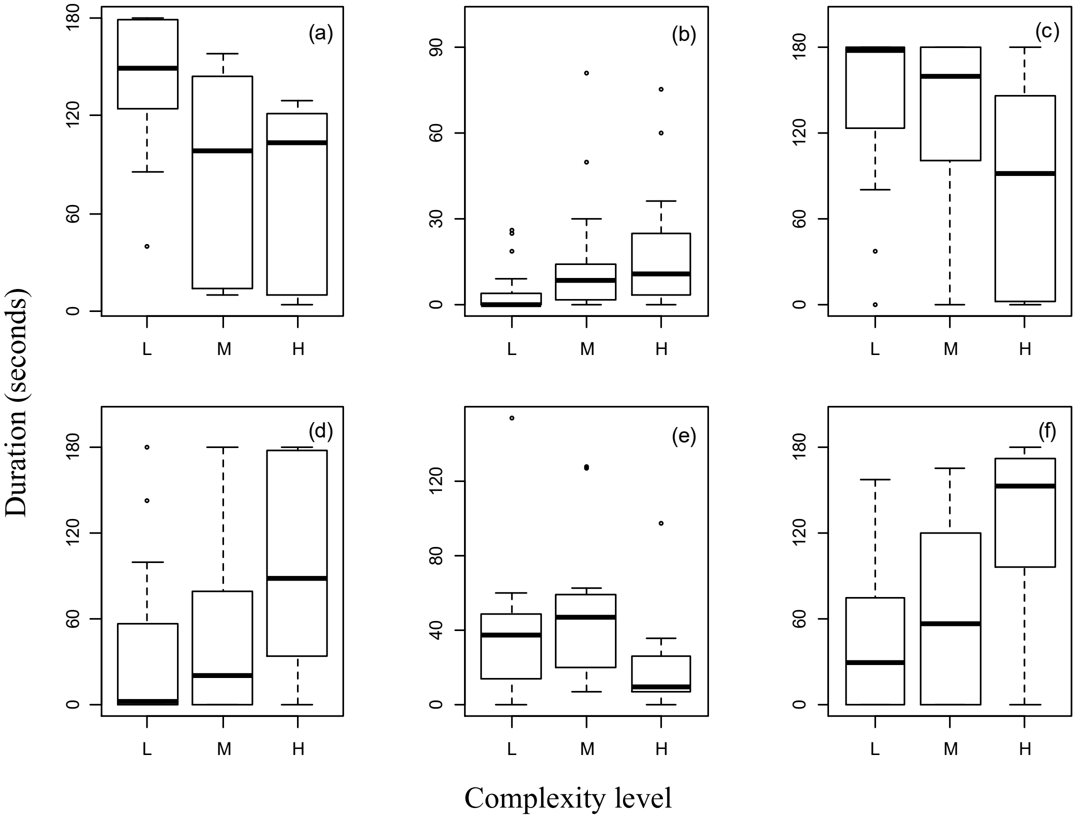

Figure 6.3 Box plots of durations of the species' behaviours that differed significantly across structural complexity levels. (a) *S. planifrons* time spent moving, (b) *S. planifrons* feeding, (c) *T. bifasciatum* moving, (d) *T. bifasciatum* feeding, (e) *C. cruentatus* and (f) *C. cruentatus* perched on features. Boxes show the interquartile range and bold black lines show median value.

6.3.2. Feature space and preference

There was a significant difference in the feature space between high and medium (R statistic = 0.067, significance level 3.1%), high and low (R statistic = 0.001, Significance level 0.001%), and medium and low (R statistic = 0.001, significance level 0.0015%), structural complexity plots. The first two PC axes explained 50.8% and 20.7% of the variation respectively (Figure 6.4). The PCA indicated that the main differences between the structural complexities were: the availability of uncolonised substrate and sponge, which had greatest cover on low structural complexity plots; and vertical relief, *O. annularis* coral heads and bowls, which were greatest on the higher structural complexity plots. All species observed showed significant preferences for features (Table 6.6). All primarily selected vertical relief, both when grouped and separated by species, however this was not always significantly greater than the second or even third feature in the ranking. Five species (*G. loreto, S. planifrons*, *M. jacobus, M. martinicus* and *C. cruentatus*) significantly selected for only the first one or two features with no significant differences between the other features. The remaining two species (*T. bifasciatum* and *H. flavolineatum*) showed significant selection only over the least preferred features, suggesting a broader range were utilised.

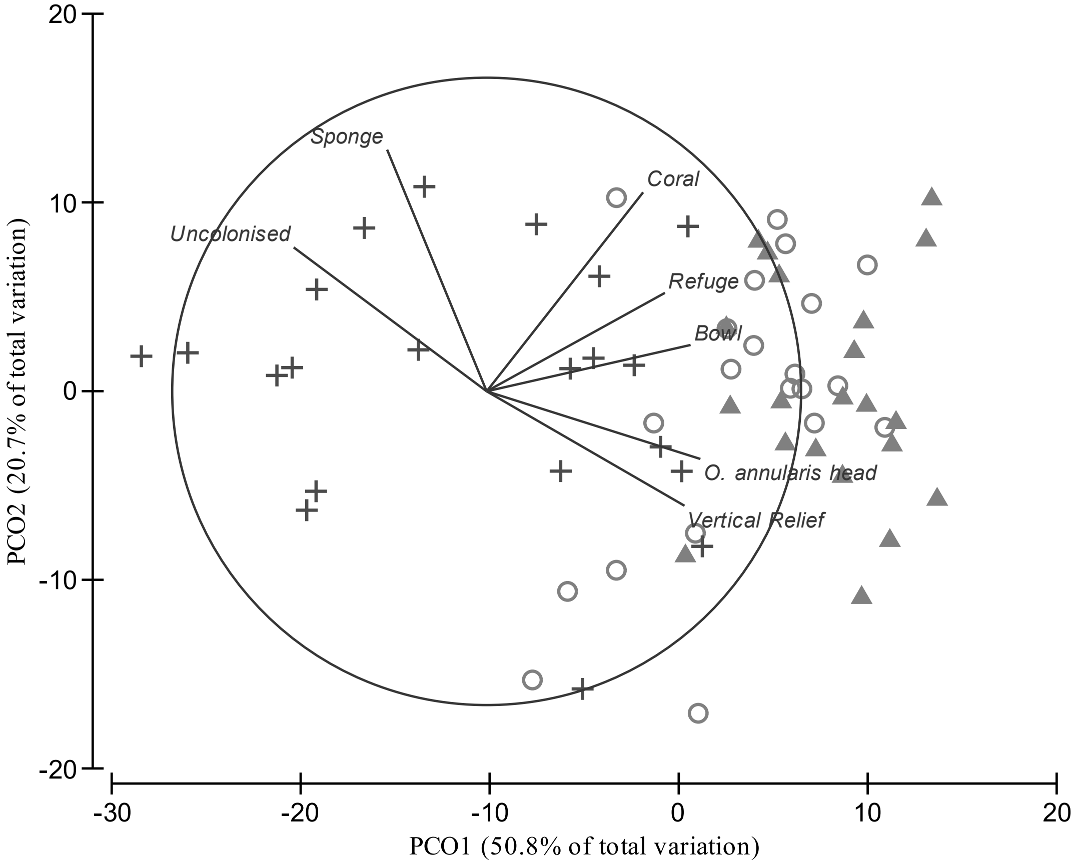

Figure 6.4 Principal coordinates analysis of the frequency of reef features across low (+), medium (O) and high (▲) complexity plots.

Table 6.6 Feature selection ranking (most selected [1] to least selected [5]) of the five most selected features for each of the seven species resulting from the compositional analysis approach to feature selection. ** = $p < 0.01$, * = $p < 0.05$. Within each row, features with the same superscript letter do not differ significantly in relative selection (t test, $p > 0.05$)

Species	Habitat ranking					λ	Significance
	1	2	3	4	5		
All Species	Vertical relief	Overhang^{a}	Bowl^{a}	Refuge^{a}	Soft and fire Coral^{a}	0.265	**
G. loreto	Vertical relief	Overhang^{a}	*O. annularis*^{ab}	Bowl^{ab}	Uncolonised^{c}	0.017	*
S. planifrons	Vertical relief	*O. annularis*^{a}	Coral^{a}	Sponge^{a}	Soft and fire Coral^{a}	0.041	*
M. jacobus	Vertical relief^{a}	Overhang^{ab}	Refuge^{abc}	Soft and fire Coral^{bc}	Bowl^{c}	0.033	**
T. bifasciatum	Vertical relief	Coral^{a}	Sponge^{a}	Bowl^{a}	*O. annularis*^{a}	0.006	**
M. martinicus	Vertical relief^{a}	Bowl^{a}	Overhang^{ab}	Uncolonised^{b}	Sponge^{b}	0.033	**
H. flavolineatum	Vertical relief	Uncolonised^{ab}	Bowl^{ab}	Overhang^{ab}	Soft and fire Coral^{b}	0.037	*
C. cruentatus	Vertical relief^{a}	Uncolonised^{ab}	Soft and fire Coral^{bc}	Refuge^{c}	Bowl^{c}	0.053	*

6.4. **Discussion**

6.4.1. Behavioural relationships

There was no systematic change in behaviour across structural complexities however there were significant interspecific differences. The species observed were specifically selected to cover a range of functional ecological roles and are therefore likely to utilise the habitat differently. Different behavioural responses to changes in structural complexity were thus expected. Of the seven species observed, three (*S. planifrons*, *T. bifasciatum* and *C. cruentatus*) displayed changes in behaviour among structural complexities.

C. cruentatus was more mobile at low structural complexities and spent more time hovering above rather than sitting on the substrate. Given the historical release from predation on most Caribbean coral reefs (Mumby et al. 2012), *C. cruentatus*, along with other similar-sized meso-predators such as *C. fulvus* and the invasive *Pterois volitans* have become the dominant piscivores and as such are likely to have experienced fear release (Ritchie and Johnson 2009). Therefore, they are required to be inconspicuous only when hunting. *C. cruentatus* is an ambush predator, preferring to hunt from the substrate where they are least visible (Shpigel and Fishelson 1989). Less structurally complex areas are less conducive for this as they have fewer structures to hide in, under or behind (Sluka et al. 2001). *C. cruentatus* is also territorial, often overlapping with territories of conspecifics (Popple and Hunte 2005), and may chase competing individuals from favourable ambush spots (pers. obs; see also Shpigel and Fishelson 1991). The higher mobility and greater time above the substrate at lower structural complexities may result from temporary displacement from preferred structurally complex areas. Hovering or swimming above the substrate may allow individuals to identify a more favourable habitat nearby to which they can move. This is supported by the observation that individuals frequently left the survey area during focal surveys on low complexity plots.

S. planifrons spent a greater proportion of time moving at low structural complexities. This may result from increased risk of predation in low complexity areas. *S. planifrons* alter their behaviour in the presence of predators, reducing non-avoidance activities such as territory defence or feeding (Helfman 1989). The continuous movement could be a way of increasing the chances of observing an approaching predator. This is supported by a reduction in time spent feeding on low structural complexity reefs (Figure 6.5), suggesting these individuals might have been prioritising predator avoidance; the biomass of this group was also lower at low structural complexities. Living on less complex or degraded reefs increases the concentration of the stress hormone cortisol in another Caribbean damselfish *S. partitus* (Schrandt and Lema 2011); such a response may underlie the observed behavioural changes, indicating an ability to respond to changes in habitat condition. Though specific antagonistic behaviours were not examined in this study, an increase in aggressive behaviours has been observed as a response to changing habitat conditions (Schrandt et al. 2012). The increased mobility detected here may also suggest an increase in territorial behaviour.

T. bifasciatum spent a greater amount of time moving across the reef and less time feeding on less structurally complex plots. This species was possibly foregoing behaviours which enhance fitness in order to enhance survivorship in the more degraded environment. Most of its feeding is in the water column (Clifton and Motta 1998) and in the absence of vertical structures on reefs of low structural complexity; this a riskier strategy because individuals must travel further from the safety of the reef structure in order to reach food in the water column. Cleaning behaviour was included in the category of feeding; this likely also represents a reduction in cleaning of other fishes by this species, juvenile *T. bifasciatum* being one of the few cleaners on Caribbean reefs (Johnson and Ruben 1988) and servicing a range of fish species (Darcy et al. 1974). *T. bifasciatum* is a coral reef ecological generalist and is almost ubiquitous across the Caribbean region having been found in 115 out 116 sites surveyed at a range of complexities across the Caribbean region (Newman et al. unpublished). Therefore, it is likely to be amongst the species least affected by degradation or flattening of the reefs. The changes in behaviour may indicate the ability of this species to adapt to the changing environment.

The four species which showed no change in behaviour were *H. flavolineatum*, *M. jacobus, M. martinicus* and *G. loreto***.** Both *H. flavolineatum* and *M. martinicus* are nocturnally active (Helfman et al. 1982, Krajewski et al. 2006); during the day they commonly occur in mixed schools (Pereira et al. 2011) hovering in association with structures (Helfman and Schultz 1984). *M. jacobus* and *G. loreto* were only present on medium and high structural complexity reefs, and most of the behavioural differences observed across the species were between low and/or high or medium complexity plots. *M. jacobus* is a nocturnally-active species and during the day utilises the same shelter sites over long periods (Luckhurst and Luckhurst 1978b); here they were observed to hover either at the entrance or deeper within these shelters. *G. loreto* followed a very simple pattern of behaviour consisting of slow swimming close to vertical relief or under overhangs occasionally feeding on small items in the water column. The presence and behaviour of these two species were more closely tied to the specific features themselves than to overall reef structural complexity.

6.4.2. Feature space and preference

There was a significant difference in the features available between low and both medium and high structural complexity reefs. The features most associated with high and medium structural complexities were vertical relief, *Orbicella annularis* coral heads, bowls and refuge. The variety of structures indicates greater habitat heterogeneity in these areas, a characteristic which is conducive to highly diverse communities (Tews et al. 2004). The low structural complexity areas were characterised by uncolonised substrate and sponges. Uncolonised substrate could be made of rubble, sand or bare rock which provide little in the way of shelter for most fish, and such flat areas adjacent to reef habitat are a greater predation risk (Shulman 1985a). However low structural complexity areas within the reef mosaic are important for a number of species as foraging grounds (Burke 1995, Krajewski et al. 2006) and also for juvenile recruitment (Sponaugle and Cowen 1996, Wilkes et al. 2008). Though medium structural complexity areas contained many of the same features as high complexity areas there were fewer of these features present in each plot. Though not examined here, the features in medium structural complexity areas tended to be smaller e.g. lower vertical relief or narrower holes, creating different habitat conditions.

Given positive relationships between aspects of the fish community and habitat structural complexity, those features which characterise higher complexities are evidently those which were most selected for by the species observed. When all species were grouped, vertical relief was the feature most preferred and flatter features such as uncolonised substrate and coral patches were the least preferred. The significant preference of *C. cruentatus* for vertical relief followed by uncolonised substrate, with no other significant selections, accords with the species' dominant behaviours, which are either perching or hovering, commonly waiting in ambush for prey or being cleaned by gobies or *Periclimenes* spp. shrimp. *C. cruentatus* were most commonly observed displaying camouflaged colours on top or at the base of towers. *G. loreto* had a strong preference for vertical relief over all other features. The only other feature selected for was overhangs. In the limited literature on this species, vertical development of a coral structure was found to be important in determining presence (Freeman and Alevizon 1983). *G. loreto* was absent from all low complexity reefs surveyed here, and occurred in only 5 of 49 (10%) of low complexity sites in a Caribbean wide survey (Newman et al. unpublished), suggesting they are associated almost exclusively with habitats with sufficient vertical relief.

S. planifrons selected vertical relief, however there was no significant preference for other features over each other. Preference for *Acropora* spp. has been previously identified for *S. planifrons* (Precht et al. 2010), however in the absence of this, use of vertical structure such as that created by *O. annularis* has been documented (Precht et al. 2010). Given the territorial nature of *S. planifrons*, the lack of preferences for multiple features indicates it is a complexity generalist, utilising most of the features on the reef habitat. *S. planifrons* territories can therefore be expected to contain many of these features. *S. planifrons* swims slowly in circuits around its territory, disrupting this behaviour only to feed in algal gardens (Ceccarelli 2007), to defend its territory or retreat from a predator. More work would be needed to determine if all these features play a key role within the territories and thus the loss of these features would result in negative effects, or whether there are a few important features within the territory which are key to the survival of the individual. *T. bifasciatum* had a strong preference for vertical relief; all other features were selected for equally except refuge or overhangs which were significantly less utilised. During the day this species swims relative freely and feeds within the water column (Clifton and Motta 1998). Vertical relief allows an individual to remain close to the relative safety of the reef matrix whilst feeding, reducing potential predation risks. In addition, juvenile *T. bifasciatum* frequently clean other fish and prominent vertical features are often used as cleaning stations (Johnson and Ruben 1988). These findings suggest this species is a structure generalist, able to persist at a range of reef structural complexities even where a limited selection of features may be present. This species utilises shelters within the reef to avoid predation at night (Robertson and Sheldon 1979), however during the day, shelter use was not witnessed.

H. flavolineatum selected for four features: vertical relief, uncolonised substrate, bowl and overhang. During the day this species forms schools frequently associated with reef structures (Helfman and Schultz 1984). The structures preferred in this study were ones which could potentially be used as landmarks on the reef. *H. flavolineatum* and other haemulids return to the same features on reefs after nocturnal foraging and may remain within close proximity to them, often as part of a school during the day (Helfman and Schultz 1984). This highlights the potential importance of these features to this group. In addition rather than utilising shelter when approached by a predator, haemulids elicit antipredator schooling behaviours (Hein 1996). *M. jacobus* had a preference for vertical relief, overhangs and refuge. This is a nocturnally active species (Ménard et al. 2007), which uses the reef matrix primarily for shelter during the day, remaining in close proximity to complex structures which afford it shelter from predation. *M. martinicus* has similar preferences to *H. flavolineatum*, having a preference for vertical relief and bowls followed by non-significant preferences for uncolonised substrate and overhangs. This reflects the diurnal behaviours, where it forms mixed schools with *H. flavolineatum* at prominent features or it forages in patches of sand or rubble.

6.4.3. Conclusion

Observations of behaviour and feature preferences were able to identify potential drivers behind the numerical relationships between the fish community and habitat structural complexity. It appears that habitat structural complexity on coral reefs creates a specific milieu which may change with changes in complexity. Those species which have the ability to adapt their behaviours may therefore be those which are able to be successful at lower complexities. Small non-fisheries target species such as wrasse and damsels, with less specialist physical ties to the habitat structure are those most likely to persist after habitat degradation (Newman et al. 2015). Despite the lower biomass of these functional groups, they were present in all diurnal surveys of low complexity reefs.

There are a number of specialist species in the Indo-Pacific which rely on the presence of certain corals (Wilson et al. 2008a, Kerry and Bellwood 2015a). These coral obligates experience significant declines in response to live coral loss, which if severe enough can lead to extirpations (Graham et al. 2006, Feary et al. 2007a, Wilson et al. 2008a). This study has indicated that despite the lack of coral obligates, some species of Caribbean fish may be structural obligates. These specialist species could be at risk of local extinctions where reef flattening results in the loss of key structures. The findings presented here are among the first to identify key fish and habitat relationships that are outside of the traditional numerical and diurnal relationships previously focused on.

7. Synthesis

7.1. Overview

The subject of coral reef habitat structural complexity has received significant attention over the last 4 years. As of 01/08/2016 163 articles (keyword search: coral reef structural complexity on Google Scholar (www.scholar.google.com)) have been published in peer review journals since 2012 which either explicitly examine complexity or use it as an explanatory variable. Through this discussion I will reflect on how and where the work performed in this thesis fits within the wider field and how it might add insight into how changes in habitat structural complexity have occurred and how it has affected the associated fish communities. I will then suggest what the future for these reefs might be in light of this research and current knowledge on the impacts of climate change. Finally, I will discuss the potential management implications of the findings presented here and identify future directions for research into habitat structural complexity and its relationship with associated communities.

A key strength of this project is the logical pathway the thesis has followed. This created a structure where each chapter has been able to build upon the last and allowed the combination of findings to contribute to an overall conclusion. The spatial scale, level of detail of the dataset and the effort taken to collect it mean it is likely to be challenging to replicate. Early in the project it became clear an understanding of the many direct and indirect processes which interact to build the framework of coral reefs must be accounted for in the analyses. Therefore, the use of pathway analysis became a major component of the analysis in Chapters 2, 3 and 4, performed through structural equation modelling (SEM). Developing an *a priori* pathway structure which is both logical and justifiable requires first understanding the system at a level not necessary for many other analytical approaches. Hopefully the concepts which have formed the basis for this analysis are replicable and the work performed here will provide a source of both ideas and comparison for future research across a range of scales. Finally, the examination of nocturnal and behavioural associations has revealed important community and mechanistic associations with habitat which are two themes in this topic which have received far too little attention.

Recent work examining the impacts of environmental and human drivers of temporal change in Caribbean habitat structural complexity had identified hurricanes and bioerosion the significant processes (Alvarez-Filip et al. 2011d). However, a study which was able to examine the influence of these drivers across space was lacking. The Alvarez-Filip et al. (2011) study was also limited in the number of drivers analysed (3) and in the number of sites examined (49). The research performed in Chapter 2 was able to build on this study by using a greater degree of spatial resolution and greater range of drivers. Additionally, the approach taken in this chapter was also based on the concept that corals, being fixed in space, are inevitably subject to a number of drivers which are almost certain be co-related. Therefore, they will interact both directly and indirectly to dictate the range and magnitude of their impacts to reef habitat structural complexity. For this reason, the use of SEM analysis, or an alternative pathway approach, is necessary in order to attempt to model such a system. The findings presented in Chapter 3 confirm the importance of hurricanes in driving Caribbean habitat structural complexity at both the basin and region scales. There is a clear role of physical disturbance driving contemporary habitat structural complexity following a number of severe disturbance events such as the *Diadema* die-off (Carpenter 1990) and coral disease (Aronson and Precht 2001).

These findings are an important step in understanding the drivers of biogenic structures globally. Typically, structure creating organisms are fixed and subsequently subject to a range of pressures which will affect their growth and survivorship, from which they are unable to escape. The suite of drivers which influence woodland growth leads to boreal forests in the arctic (Thompson et al. 2004) and rainforests in the tropics (Higgins et al. 2015). Within these ecosystems variations in drivers on a smaller spatial scale impact structural development. In the arctic a range of site characteristics result in increasing structural complexity along a gradient from tundra to boreal forest (Thompson et al. 2004). Localised increases in structural complexity influence albedo and net radiation which on large scales may influence the climate. Therefore, the ability to understand the environmental and spatial characteristics which drive forest growth will be important in regional climate modelling (Beringer et al. 2001). British broadleaved woodlands have undergone a significant change in ecological structure as a result of factors including: pollution, grazing pressures, alien species and changes in land use (Hopkins and Kirby 2007). This has resulted in a significant decline in high complexity forest. Continued loss of this structurally complex habitat will have severe impacts on Britain's flora and fauna, thus maintaining and protecting the remaining structure will rely on a detailed understanding of the direct and indirect effects of the broad range of driving factors which made possible through pathway analyses which can examine these. Where monospecific formations create structurally complex habitats it may be of even greater importance to understand the drivers of the system given the absence of structural redundancy available in more diverse systems. Examples of this include: kelp forests (Wernberg et al. 2011), mussel beds and oyster reefs (Lawrie and McQuaid 2001, Beck et al. 2011).

In order to understand the impact that changes in habitat structural complexity will have on associated fish communities it is important to understand the links between the two. A large body of literature exists examining this relationship. However, a step which has been frequently overlooked in this process is where we examine how the human derived construct, usually a component of an ecosystem, such as structural complexity, reflects the characteristics of the habitat in which the organisms are found. Habitat structural complexity is a multidimensional construct and must be treated as such. However until recently the measures being used to capture it were relatively simplistic and accounted for little of this dimensionality (Kostylev et al. 2005, Dustan et al. 2013). A range of contemporary methods has begun to better incorporate multiple aspects of complexity to reflect species-habitat associations such as: multiple properties of refuges (Ménard et al. 2007), targeted meso-scale metrics (Harborne et al. 2012), a size-scale focussed assessment (Nash et al. 2013) or visual assessment based on numerous characteristics (Wilson et al. 2007, Newman et al. 2015). However, a quantitative examination of how multiple measures interact to form the complex reef structural was still lacking. Combining the measures used through direct and indirect pathways accounts for many of the things which may be related to the associated reef communities to be examined together (Chapter 3). This sheds new light on how the community is related to the whole structural matrix, whilst reducing the bias of the observer which comes about through the selection of specific perceived aspects of the habitat which may not have any relevance to the community itself. For example the widely used measure of rugosity using a tape or chain (Risk 1971) contains little information about features of the habitat which may be of direct use to fishes.

The dataset used in this study covers a range of reef types and complexities from across the Caribbean region which adds robustness to the analysis, allowing for a broad assessment of the relationships between the measures and diversity of the Caribbean fish community. More detailed information about habitat structural complexity components, such as those of refuge characteristics on reefs (Ménard et al. 2007) or stand structure in woodlands (McElhinny et al. 2005) may be used improve understanding about the specific structural characteristics which influence faunal communities. The advent of photogrammetry or stereo videography is a major step forwards in the study of habitat structural complexity. Through these approaches it is possible to re-create natural 3-dimesional habitats, potentially changing the way we measure structural complexity (Storlazzi et al. 2016). However, it is important that continued research identifies and examines the components of a habitat which are relevant to animals and how these parts combine to create the whole habitat (Chapter 3).

Examining specific components of habitat structural complexity (e.g. Chapter 4) has improved understanding about the relationships between the reef habitat and different facets of the fish community. This is a logical approach to studies as it is apparent that small gobies will not perceive the reef structure in the same way as a large grouper and thus approaches which can account for this polychotomy within the fish community must be employed. When examined at intermediate scales fish communities can be separated by their relationships with different aspects of the reef structure (Harborne et al. 2012). Rugosity metrics were found to be generally poor predictors of the multivariate fish assemblage, but when separated, coral height (damselfish and parrotfish) and number of corals (surgeonfish and wrasse) were found to be significant predictors of specific components of the fish community (Harborne et al. 2012). Chapter 4 builds on this using both the SEM generated site refuge variable and separated refuge sizes. Through this approach it was possible to account for both the holistic refuge characteristics of the reef and the different cross-scale patterns of refuge. The availability of refuges of different sizes correlates with fish body sizes (Nash et al. 2013, Chapter 4). Changes in reef structural complexity or stable state (e.g. to algal dominated) are likely to result in a homogenisation of the substratum (Alvarez-Filip et al. 2009, Edwards et al. 2011) which may in turn lead to decreases in the range of fish body sizes (Nash et al. 2013) and functional diversity (Chapter 4) on coral reefs. By taking a functional approach to the analysis in Chapter 4 it was possible reveal novel relationships between the fish community and habitat structural complexity. Previous analyses of the coral reef fish functional community in relation to habitat structural complexity have rarely looked beyond diet (but see

Mouillot et al. 2013). However, the trait-based approach used in Chapters 4 and 5 made it possible to examine how changes in the reef structure will affect community function.

Changes in activity and behaviour between day and night is a feature of the coral reef fish community (Hobson 1972, Helfman 1986) and yet nocturnal usage of the reef matrix has surprisingly received little attention. It has been shown that shelter occupation changes as diurnally active fish seek refuge and nocturnally active fish disperse from diurnal shelters (Helfman 1986). Utilisation of available resources also changes with the diel cycle, as some nocturnally active families, such as Haemulidae and Lutjanidae, which aggregate on reefs during the day, nocturnally migrate away from the protection of the complex reef to forage on less structurally complex reefs or alternative habitats, such as seagrasses (Burke 1995, Hitt et al. 2011). Community level analyses revealed the maintenance of a positive diurnal relationship between habitat structural complexity and the fish community over the entire diel cycle (Chapter 5). However, there were changes within certain groups of fish. Such changes include a shifts from linear to curvilinear relationships where medium structural complexities become more important (e.g. functional group 5) or where the relationship with complexity is lost as fish forage in low structural complexity areas (e.g. functional group 2). Incorporating this knowledge into future models assessing the effects of changes in reef structural complexity will improve accuracy and predictive power.

Though relationships between the fish community and habitat structural complexity have been identified both here and in other studies the causative pathways are only beginning to be understood. Behavioural associations between fish and the habitat reveal how changes in reef structure will affect fish. Bicolour damselfish (*Stegastes partitus*) became more aggressive in low structural complexity habitats and used shelter more frequently (Schrandt et al. 2012). Behavioural adaptations were observed in some species during this study (Chapter 6). The species which did show significant changes in behaviour represent the most successful functional groups across the region representing habitat and dietary generalists (*T. bifasciatum*), territorial herbivores (*S. planifrons*) and piscivorous meso-predators (*C. cruentatus*) (Paddack et al. 2009, Mumby et al. 2012). Those species which have the ability to adapt their behaviours appear to also be those which are most successful when confronted with exploitation and habitat degradation (Wilson et al. 2008b, Newman et al. 2015). This work has barely scratched the surface of the role behavioural studies will have in developing our understandings about responses to habitat degradation. In the future, a comprehension of both the proximate and ultimate causes (Tinbergen 1963) of habitat associated behaviours and behavioural changes will greatly enhance understanding about the impacts of habitat degradation and how best to conserve species (Buchholz 2007).

7.2. **Temporal significance**

A significant array of environmental and human pressures which influence coral reef structural complexity persistence and development have been documented (Hoegh-Guldberg 1999b, Bellwood et al. 2004) many of which have been increasing in frequency and severity over the past 50 years (Hoegh-Guldberg et al. 2007, IPCC 2014a). Caribbean reefs have been particularly affected by these impacts (Hughes 1994, IPCC 2014b), which have led to significant declines in live coral cover across the region (Gardner et al. 2003, Schutte et al. 2010). As a result of the changes the Caribbean region has undergone and its predicted future trajectory, it is of use to interpret the findings of this project in a temporal setting.

The earliest record of quantitative study using a measure of habitat structural complexity in the Caribbean was a solitary survey in 1969, followed by a gap six years to 1974, after which studies including complexity measures featured increasingly regularly in the literature (Alvarez-Filip et al. 2009). An analysis of these studies documents a non-linear decline in structural complexity across the region (Alvarez-Filip et al. 2009). The spatial analysis (Chapter 2) suggests that there has not been a homogenous decline in structural complexity on reefs throughout the region, otherwise there would there would likely have been spatial autocorrelation in the data. Instead different reefs have been degraded at different rates leaving the countries interspersed with reefs of differing structural complexities. This is supported by the differential effects of disturbances found in both region (Edwards et al. 2011, Chapter 2) and site level studies (Mumby 1999).

There have been a number of disturbance events, such as outbreaks of coral disease (Aronson and Precht 2001), *Diadema* die-off (Lessios et al. 1984, Carpenter 1990) or coral bleaching (Eakin et al. 2010, Alemu and Clement 2014) which have affected the Caribbean almost ubiquitously. However, the resulting impacts these events have on the structural complexity of reefs may be more related to the physical disturbance regime. Where bleaching and hurricanes have been studied simultaneously, bleaching alone had no measurable effects on recruitment or community structure (Mumby 1999). However the combination of bleaching and hurricanes have been shown to lead to significant declines in coral cover (Edwards et al. 2011) which were positively related to reef structural complexity (Chapter 2). Chapter 2 identified hurricanes and wave exposure to be the two strongest predictors of reef complexity, both having negative direct and/or indirect effects and the variation in declines in coral reef structure across the Caribbean may be largely attributable to the range in the intensity of these two drivers.

Strong relationships exist between fish communities and coral reef structural complexity (Graham and Nash 2012). The impacts of structural degradation in the Caribbean are therefore likely to have resonated through the Caribbean reef fish community. There has been a decline in the overall density of Caribbean reef fishes since the late 1990s (Paddack et al.

2009) and this decline was in part attributed to declines in coral reef structural complexity. When the fish community was examined in detail it was found that specialist species (those found only on coral reefs) and generalist species (those found in a broader range of habitats e.g. gorgonian fields or sea grass beds) responded differently to changes in the degree of degradation of Caribbean coral reefs (Alvarez-Filip et al. 2015). The use of traits to examine the relationship of the fish functional community (Chapter 4) gives further insight into this decline. The positive relationship between functional diversity and refuge on reefs suggests that reductions in structural complexity will decrease the number of functional traits present, and these results will lead to the simplification of the fish community found by Alvarez-Filip et al. (2015) and on less complex reefs in this thesis (Chapters 4 & 5).

Previous studies which have examined reefs of different structural complexities, rather than examined temporal trends support this finding as lower structural complexities support less abundant and species rich communities (Gratwicke and Speight 2005b, Chong-Seng et al. 2012). Though this relationship has been found previously to be important for fish during the day we can now say with confidence that this positive relationship is true across the diel cycle (Chapter 5). This study provided some of the first evidence that habitat structural complexity plays an important role in structuring fish communities over the entire diel cycle.

Temporal studies looking at how relationships between habitat structural complexity and fish populations have provided insight as to how Caribbean reefs have changed over the past 60 years (Hughes and Tanner 2000, Gardner et al. 2003, Paddack et al. 2009, Alvarez-Filip et al. 2009). While contemporary studies are able to elucidate the more detailed relationships between structural complexity and fish communities (Graham and Nash 2012, Alvarez-Filip et al. 2015). Combining temporal information with that from spatial studies it is possible to imagine how the Caribbean was once a mosaic of structurally complex reefs interspersed with less structurally complex areas created by local scale discrepancies in the disturbance regime or geology. This suggests that a highly diverse fish community would predominate in the structurally complex areas and more generalist species would predominate in the low complexity patches. Using knowledge about the trajectory of Caribbean coral reef structural complexity and the relationship with the fish community it is possible to speculate to some degree about the future of structural complexity and fish communities on reefs in the region.

The latest Intergovernmental Panel on Climate Change (IPCC) report predicts that continued anthropogenic driven climate change will lead to global mean sea surface temperature (SST) increase relative to the period 1986 - 2005 in the range of 0.3°C - 0.7°C and this could be as great as 4.8°C by the end of the 21st century in worst-case scenarios (IPCC 2014a). However the Paris climate change agreements states that countries will aim to keep warming of the earth's climate to below 2°C (Burleson 2016). The release of greenhouse gases has also driven decreases in the pH of the oceans which are predicted to be between 15 - 109% lower by the end of the century. The impacts of increasing temperatures and CO_2 have been extensively reviewed (Hoegh-Guldberg et al. 2007, Baker et al. 2008, Veron et al. 2009) and models have been used to predict the impacts of their continued increase to coral reefs (Evenhuis et al. 2015). However, with the knowledge gained from this project and other recent studies it is possible to infer how these changes will affect the structural complexity of Caribbean reefs.

Coral cover was found to have a positive relationship with structural complexity (Chapter 2, Alvarez-Filip et al. 2011b, Graham and Nash 2012). The declines in live coral cover perpetuated by the predicted increases in frequency and severity of bleaching events (Baker et al. 2008) may result in a temporary decoupling of this relationship. This will be due to the persistence of structure after coral death in the short-term. In the long-term if coral cover does not regenerate, and instead the structure is eroded the structure that persists may instead be created by non-coral organisms, such as sponges and the coral cover may be formed of hardier, less complex corals (e.g. *Porites* spp. and *Siderastrea* spp.). The 2015/16 El Niño event is one of the strongest on record (Allen 2016) and has sustained high sea surface temperatures across the oceans (Hansen et al. 2016). The full impacts of this on coral reefs are yet to be understood at the time of writing, however monitoring their trajectories will further indicate the future of tropical coral reefs. There is evidence of adaptation to the effects of climate change within coral populations (Hoey et al. 2016), however the ability of corals to match the pace of these effects is unknown, especially in areas impacted by the additive effects of local scale degradation.

One of the predicted results of a warmer climate is an increase in the frequency and severity of hurricanes (Emanuel 2005, Bender et al. 2010). Therefore the negative effects of these events (Alvarez-Filip, Gill, et al. 2011, Chapter 2) on structural complexity are likely to drive further flattening of Caribbean reefs. A troubling observation is that a number of high complexity reefs surveyed in this project consisted of dead coral skeleton (Figure 7.1). These reefs are at risk of near-term structural collapse, which will result in sudden declines in complexity in these areas. An increase in bleaching events will likely leave additional reefs in this precarious situation. However, coral reefs which are more structurally complex are both more resistant to bleaching events, and more likely to rebound following a bleaching event (Graham et al. 2015) which may help buffer these reefs against disturbance in the short-term.

No significant change in hurricane tracks has been predicted for the Caribbean (Bender et al. 2010), therefore reefs in countries afforded protection by their geographic location e.g. Bonaire and Curaçao (Meyer et al. 2003) are likely to fare better in a future with increasing hurricane frequency and intensity. Bleaching and storms can have different impacts across relatively small scales (Bythell et al. 1993, Mumby 1999) which suggests that some reefs which, through their position in space, may be more resilient to rapid change. However, these remnant, structurally complex coral reefs could potentially provide the framework for other less complex species to grow on. This may provide additional resilience to the reef structure as live coral growth formed of encrusting species, such as *Porites astreoides* is less likely to erode than dead skeleton. Examples of this occurring can be seen in figure 7.1 There are also examples of complex corals providing shelter for remnant cryptic patches of coral allowing them to survive a bleaching event and, if conditions are favourable, significantly regenerate a virtually dead colony (Roff et al. 2014).

Figure 7.1 Examples of complex structure persisting after the death of *Acropora palmata* in Anguilla (top left), *Orbicella annularis* complex in Anguilla (bottom left) and Orbicella spp. complex in Jamaica (right).

To fully understand the future of habitat structural complexity it is necessary to combine the models focussing on environmental drivers of structural complexity (Chapter 2) with more detailed information about local carbonate budgets. Net carbonate production/loss is likely to vary greatly across the region given the range of factors which influence it (Perry et al. 2012). However, where this has been examined on a local scale it appears that Caribbean reefs may be shifting to a system of net loss (Perry et al. 2014a). Where information about bleaching and hurricanes have been included in models with carbonate budgets in order to forecast the future of Caribbean reefs, there was a predicted decline of habitat structural complexity in a warming climate (Bozec et al. 2014).

The predicted changes in structural complexity will likely yield further changes in the Caribbean coral reef fish community. The decline in the proportion of fish which are coral reef specialists (Alvarez-Filip et al. 2015) is likely to continue as coral dominated reefs flatten and shift to alternative states (Graham et al. 2014). Declines in structural complexity are likely to favour smaller generalist species, with groups such as labrids, gobies and damsels likely to profit (Newman et al. 2015). The functional community approach used in Chapters 4 and 5 suggests that less structurally complex reefs in the future will be less functionally diverse and dominated by species with overlapping traits. Consequently, many of the reefs in the Caribbean will be populated by fish which feed on invertebrates, live in small schools and are unlikely to be site attached (Chapter 4) e.g. many labrid species. Maintaining structural complexity on reefs has also been found to retain functional diversity and functional redundancy on coral reefs (Emslie et al. 2014). Particularly important might be the positive relationships found between herbivores and structural complexity (Harborne et al. 2012; Graham & Nash 2013; Chapter 4). Herbivorous fishes have an important role in the maintenance of healthy reefs and their grazing of algae creates a positive feedback loop whereby their removal of algae allows coral settlement and growth, which in turn increases structural complexity (Bozec et al. 2013). Herbivore populations increase reef resilience in the face of hurricane and coral bleaching (Edwards et al. 2011). The declines which are likely to be perpetuated by structural complexity losses may cause a switch to a negative feedback loop (Mumby and Steneck 2008) resulting in shifts to flatter reefs and alternative states (Nyström et al. 2012). Monitoring factors which indicate reef resilience, such as the functional fish community will enable the prediction of potential adverse effects (McClanahan et al. 2012, Bozec and Mumby 2015) and better opportunity for directed coral reef management strategies (Anthony et al. 2015). Habitat structural complexity is another such factor which can be monitored with relative ease, yet can reveal much about the functioning (Chapters 4 & 5), and fisheries potential (Nash and Graham 2016) of a reef and its potential response to disturbance in the future (Graham et al. 2015).

7.3. **Caveats**

In this study the term coral reef has been used indiscriminately to discuss sites surveyed. It should therefore be noted that a recent study by Williams et al. (2015) suggested it was important to differentiate between Caribbean reef types when making ecological assessments. However given the aim of the project was primarily to examine structural complexity the inclusion of multiple reef types allows for a better understanding of relationships across the region, especially given a reef future which is likely to involve an increase in the number of these alternative reef types (Graham et al. 2014). Second, given the degradation that has occurred on Caribbean reefs over the past 60 years, surveys of truly high structurally complex reefs were lacking. A visual assessment of all reefs surveyed throughout this project by both the author and S. Newman, found only four reefs of the highest category. This may limit the scope of some of the conclusions. For example, Chapters 5 and 6 grouped reefs into low, medium and high structural complexities. Few significant differences in the fish community were found between medium and high structural complexity reefs. This may be in part because the dissimilarity between the two reef types is no longer as great as it was historically. Therefore these findings are likely confounded by shifting baselines (Knowlton and Jackson 2008) and an acknowledgement of this limitation is important when discussing the findings presented here.

Though the data utilised in this project covered a large proportion of the region (15 countries) there are some significant geographical gaps in the dataset. No data were obtained from the north Coast of South America (Venezuela or Columbia) or the southern section of Central America (Nicaragua, Costa Rica or Panama). Though data was offered from Cuba (by Elena de la Guardia) unfortunately it could not be incorporated into the study due to methodological differences. This meant that both a spatial region and the largest island of the Caribbean were not accounted for. Therefore, the description of processes driving Caribbean coral reef structural complexity is somewhat incomplete despite this being the most comprehensive study to date.

7.4. **Implications for management**

With clear evidence for the long-term impacts of habitat structural complexity loss on the fish community there is a need to assess how effective management can help reduce these impacts and maintain the reef structure. There has been a change in emphasis of research over the last 50 years from examining how reefs were structured and functioned ecologically, to contemporary work on how disturbances will affect reef ecosystems (Mumby and Steneck 2008). This has allowed scientific research to better inform management on the impact of disturbance, and how to mitigate impacts. However, in order for this to be of use to management there needs to be a coherent output from this work which can make recommendations about what is important and what approaches may work best. Managers are limited in their resources and their toolbox for interventions which can include habitat protection, fisheries management, coastal planning and direct restorative strategies (Mumby and Steneck 2008), many of which differ in their efficacy depending on the current state of the habitat (Rogers et al. 2015). Social conditions will also have a significant effect on the implementation of reef management (McClanahan et al. 2008). However, monitoring of habitat structural complexity is likely to be an rapid and economical way of identifying which areas are most at risk from future climate change impacts (Graham et al. 2015).

It is becoming increasingly recognised that the variety of processes impacting coral reefs are likely to lead to systems which will look and function differently in the future (Hobbs et al. 2009, Graham et al. 2014). Future reefs which may be either degraded or represent novel systems (Graham et al. 2014) are unlikely to support the same level of services, however they will still be able to provide many of the key services which are required to sustain coastal communities and livelihoods (Rogers et al. 2015). There is unlikely to be one cure-all strategy which works for all reef ecosystems and therefore future management should be tailored to maximise the benefits to a particular habitat. Currently marine protected areas (MPAs) are widely used in an effort to manage coral reefs, and where they are well positioned and managed, these have been shown to have significant positive effects for fish communities (Russ 2002, Halpern 2003, Edgar et al. 2014). However, studies examining MPAs have focused on structurally complex areas as these tend to the areas selected for protection. When the effects of protection have been modelled for less structurally complex areas the benefits have proven to be limited (Rogers et al. 2015). Chapter 2 did not identify any positive relationship between MPAs and complexity. This could be interpreted in two ways, either that protection has no effect on structure, an assertion supported by Alvarez-Filip et al. (2011), or that areas are being protected based on reasons unrelated to the promotion or management of coral reef structural complexity (Appeldoorn and Lindeman 2003). If the first scenario is true then it is time to explore different management strategies; if it is the second, then given the positive relationships with habitat structural complexity it will be worth addressing this and making increasing structural complexity a key target of reef protection.

The trajectory of reefs in different locations and under different pressures will also vary, which will also lead to different management frameworks for different circumstances (Mumby et al. 2014). Therefore, the first step in targeting management strategies is identifying areas of differing structural complexity through spatial analysis and examining the drivers which will affect the potential future of structural complexity in a given area such as in Chapter 2. Reefs with low structural complexity are predicted to be positively affected by a broader suite of tool including: creating artificial complexity, coral restoration and herbivore management (Rogers et al. 2015). There is evidence to show artificial reefs can promote healthy populations (Baine 2001, Abelson and Shlesinger 2002) and have additional ecosystem services (Ng et al. 2015). The findings documented in Chapters 3, 4, 5 and 6 can be used to guide design as a better understanding of how different components of structural complexity combine to create a reef habitat containing the key characteristics of most importance to the functional fish community. There remain number of problems associated with artificial reef use such as longevity, cost and toxin leach (Broughton 2012) however given the importance of habitat structural complexity to the reef community found in this project and elsewhere artificially creating structural complexity is likely to an important area of future research and development.

It was observed that all countries surveyed possessed range of reef structural complexities (Chapter 2), suggesting that managers will be required to manage both high and low structural complexity reefs simultaneously. Simply declaring protected areas will not work for all of these habitats. The lack of spatial auto-correlation found in Chapter 2 suggests that areas of high structural complexity exists in pockets across the region. Some of these, created by

Acropora may be transitional in nature. Their fragility and susceptibility to disturbance (Lirman and Fong 1997, Aronson and Precht 2001) and fast growth rates could lead them to appear and disappear on a regular basis, moving from site to site over decadal timescales. However the structure created by more massive, slow growing corals such as *Orbicella* spp. may provide a stable state given their slow growth and generally high resilience (Edmunds and Elahi 2007, Edmunds 2015). It may be the loss of this species which should most concern scientists and managers. Therefore, protection of this habitat should be a management priority.

Coral reefs globally are undergoing shifts to alternative states, which are no longer dominated by corals but instead by algae, sponge or soft corals (Norström et al. 2009, Bell et al. 2013). Therefore, the role of non-coral biogenic structure in these habitats must also be examined. An analysis of the role of these structures by Newman et al. (2015) revealed relationships with sponges was confined to a few specialist fish species and octocorals frequently exhibited negative relationships with fish species presence. However total species richness for the wider reef community was positively related to both sponge and octocoral height, though to a lesser degree than coral generated structure. Relationships with non-coral structure may be an important future research area in light of these findings, and given the ongoing transition of many coral reefs.

The Caribbean region has the opportunity to lead the way in developing adaptive and effective management if it acts now. The variety of impacts faced means a range of management strategies are required, many of which are currently available. If targeted management approaches are utilised, well monitored and reported, then scientists and managers working in the region will be able to provide a significant contribution to society's attempts to maintain functioning ecosystems which are still able to provide a range of ecosystem goods and services in the face on ongoing local and global pressures.

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