A macroecological study of Caribbean parrotfishes

Wahyu A. Nugraha

A Thesis

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Abstract

Parrotfishes contribute to more than 80% of the biomass of herbivorous fishes in the Caribbean and they have been the dominant grazers on reefs since 1983. Maintaining healthy parrotfish populations is essential to help conserve benthic habitat cover which is suitable for the settlement and growth of reef building corals. However, the key environmental factors that currently affect local parrotfish abundance and population structure are scarcely known. Many reef studies are constrained to a limited geographical scale which may not be applicable at larger spatial scales. Parrotfish data across the wider Caribbean will help to overcome such issues.

This study investigates three relationships including parrotfish density and benthic habitat variables (Chapter 2); parrotfish density and fishing pressure (fisher density, human population, MPA protection) (Chapter 3); and parrotfish size at sex change and fishing pressure (Chapter 4). Fish and benthic habitat surveys at 7 to 15 sites were conducted in each of eight Caribbean countries including Antigua, Bonaire, Barbados, Curaçao, Dominican Republic, Jamaica, St. Lucia, and St. Vincent and the Grenadines.

Parrotfish abundance was positively correlated with coral cover and negatively correlated with macroalgal cover. Parrotfish abundance had a significant correlation with reef complexity (Chapter 2). Different sizes of parrotfish were associated with different habitats (Chapter 2). Fishing is likely to have reduced fish numerical abundance and biomass even at Caribbean scale (Chapter 3). While parrotfish biomass was significantly higher within MPAs, parrotfish numerical density was not significantly different (Chapter 3). The density of terminal parrotfish was significantly different (Chapter 4). Furthermore, fishing pressure was significantly correlated with the size at which phase change between initial and terminal phases occurs (Chapter 4).

This research demonstrates the major drivers of Caribbean parrotfish abundance and biomass which may help inform management of parrotfish and promote further coral reef ecosystem recovery.

For Insafitri, Ines, Emil

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Chapter 1. General introduction

The Caribbean region is a semi-enclosed sea bounded to the north by the Gulf of Mexico and to the east by the Atlantic Ocean, surrounded from north to south by the North American mainland, the east coast of Central America and north coast of South America. There are over 700 islands in this region, which are divided among 13 sovereign states and 17 dependent territories, including overseas territories of the United Kingdom, France, the Netherlands, and the United States of America (Figure 1.1).

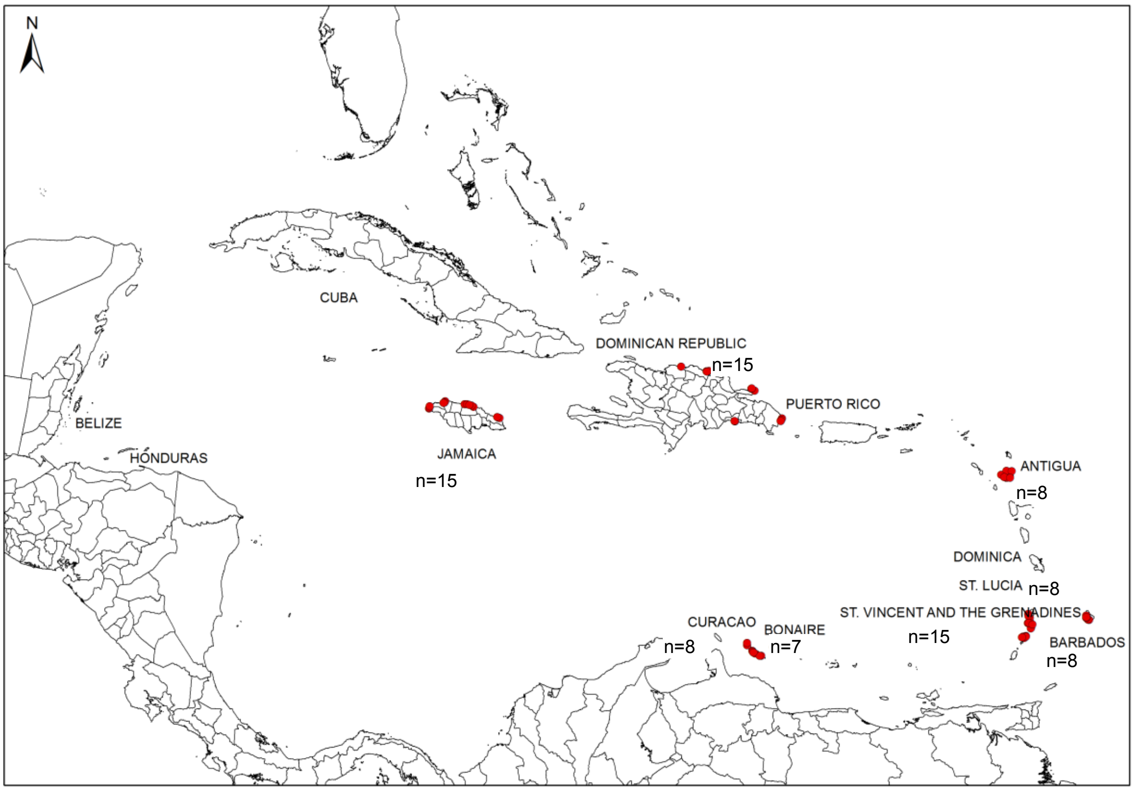

Figure 1.1 Map of the Caribbean showing the extant countries or territories. Red dot shows the study locations and number of sites.

The Caribbean marine environment includes some of the most productive and biologically complex ecosystems in the world, such as coral reefs, sea-grass beds, mangrove forests, and coastal lagoons. These tropical coastal ecosystems provide food, habitat, and nurseries for many marine and coastal species, including commercially valuable fishes and marine invertebrates. These ecosystems are vital to the economy of many communities and states in the region due to their association with activities such as fishing and tourism (Miller, 1996).

Connell (1977) likened coral reefs to “rain forests of the sea”, describing them as among the most biologically rich and productive ecosystems on earth, providing valuable ecosystem benefits to millions of coastal people, important as sources of food and income and nurseries for commercial fish species, attracting divers and snorkelers from around the world, generating the sand on tourist beaches, and protecting shorelines from the ravages of storms.

1.1 Caribbean coral reefs and fisheries

The importance of coral reefs in the Caribbean is evident from the map of social and economic dependency on coral reef resources (especially fisheries, tourism and nutrition) (Figure 1.2; Burke *et al.*, 2012).

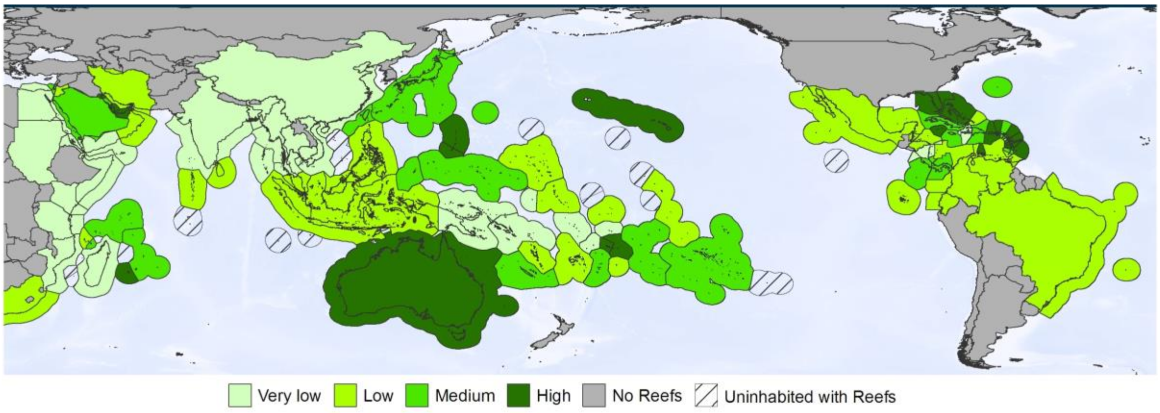

Figure 1.2 Social and Economic Dependence on Coral Reefs based on reef-associated population, reef fisheries employment, nutritional dependence on fish and seafood, reef-associated export value, reef tourism, and shoreline protection from reefs, with countries and territories categorized according to quartiles (Burke *et al.*, 2012).

Coral reefs are important to fisheries since they provide nursery grounds and habitat for commercially valuable fishes, such as Lutjanidae, Haemulidae, Lethrinidae, Scaridae, Siganidae, and several other families (Johannes, 1978; Munro, 1983; Andrews, 1990) and valuable invertebrates, such as molluscs, crustaceans and sea cucumbers, as well as seaweeds (Birkeland, 1997). Reef-related fisheries contributed over 10% of total world fisheries catch in the 1970’s (Smith, 1978). However, more than 6 million people worldwide can be classified as small-scale reef fishers, many of whom are not recorded in official data, and neither is their catch (Teh *et al.*, 2013). Coral reefs also provide ecological and other services such as shoreline protection and maintenance of species diversity (Moberg and Folke, 1999). In addition, they provide social and cultural services such as income from tourism activities (Birkeland, 1997), they sustain livelihoods and support cultural and religious values (Moberg and Folke, 1999).

The Caribbean fishing industry is characterized by a large artisanal sector. About 77% of fisheries in mainland countries and 95% of fisheries in insular countries are artisanal fisheries (Dunn *et al.*, 2010). Fishing boat sizes were almost all under 10 m with an average of 8.9m for artisanal fisheries, around 13.5m for semi-industrial fisheries, and on average around 20m for industrial fisheries, however 3% of the mainland fleet consisted of much larger "super-industrial" vessels. The average boat lengths for artisanal fisheries were found to be significantly different between insular and mainland countries, being smaller in the island countries especially in the southern Caribbean. Dunn *et al.* (2010) also found that fishing effort in terms of fishing vessel size and density varied greatly, ranging from 0.002 to 118.5 boat-meters/km^2. The highest fishing densities were mostly in coral reef areas around the chain of islands in the southern Caribbean from the Central American mainland (off Honduras and Nicaragua) to the Venezuelan coast. Hawkins and Roberts (2004a) studied fishing gear in six areas of the Caribbean and found that most fishers were using traditional fishing gears such as hook and line, spears, traps, and nets. Waite *et al.* (2011) report that such gears used in reef fisheries in Jamaica tend to be modified in such a way as to exacerbate the already prevalent overexploitation of reef fisheries, for example the use of fish pots or traps with small mesh sizes, and spear-fishing combined with compressor diving, and larger nets. It is likely that such practices are not confined to Jamaica. Dunn *et al.* (2010) also report the use of beach seines, trawls, longlines gear and diving equipment, with the majority of fishing vessels (62%) carrying more than one gear.

Coral reefs in the Caribbean comprise about 8% of the total coral reef area world wide (Bryant *et al.*, 1998) with a total area of around 26,000 km^2, most of which is in the form of shallow fringing reef systems (Burke and Maidens, 2004). The biological diversity or biodiversity of Caribbean coral reef communities is considered less than that of the Indo-Pacific region (Sheppard and Wells, 1988). Over 1,500 species of reef-building corals have been identified worldwide (Veron, 2000) of which over 1,400 are found in the Indian and Pacific oceans and approximately 70 in the Atlantic/Caribbean region (Spalding *et al.*, 2001). However, this disparity does not mean that Caribbean reefs are unimportant from a biodiversity point of view. Spalding *et al.* (2001) point out that although the Caribbean reefs may be considered "depauperate" compared to the much more diverse Indo-Pacific reefs, they are also unique with many endemic taxa, and the two regions share only seven coral genera. Furthermore, coral reefs are home to many organisms other than corals. Plaisance *et al.* (2011), focussing on crustaceans, highlight the fact that there are still many reef-associated species being discovered and many more as yet unknown to science in all the major coral reef areas of the world, including the Caribbean.

1.2 Threats to and decline of Caribbean coral reefs

Caribbean coral reefs have been under pressure for several decades, and large-scale environmental degradation had already occurred by the early 1990's as a result of both human and natural disturbances (Hughes, 1994). The direct and underlying causes of this decline include overfishing, climate change and disease (Hughes *et al.*, 2003), as well as other impacts due to rising human population densities (Burke and Maidens, 2004). In terms of relative magnitude, Burke *et al.* (2012) estimate that overfishing is the most pervasive threat, however they recognise that marine based pollution and damage, coastal development, and watershed-based pollution also pose significant threats. Hard coral cover declined by up to 80% over the past three decades (Gardner *et al.*, 2003; Alvarez-Filip *et al.*, 2011) but little changes since mid-1980s (Schutte *et al.*, 2010) and reef architectural complexity has been substantially reduced over the last 40 years (Alvarez-Filip *et al.*, 2009). Jackson *et al.* (2014) show a dramatic decline in average live coral cover in the Caribbean region from approximately 55% around 1970 to below 10% in the early 2000's. The most recent data in this report indicate a current average coral cover around 16%, with wide variation between sites. Burke *et al.* (2012) report that more than 75% of coral reefs in the Atlantic region (of which the majority are in the Caribbean) are under threat, with more than 30% in the 'high' or 'very high' threat category. For over 20 countries or territories in the region, all reefs were rated as threatened, including reefs in Florida (United States), Haiti, the Dominican Republic and Jamaica, while the Bahamas had the largest area of low threat rated reefs.

The decline in hard coral cover has been accompanied by an increase in macroalgal cover, and it is believed by some that the decline itself was a major cause of observed phase shifts from coral dominated substrate to predominantly fleshy algae cover (Done, 1992; Hughes, 1994; Nystrom *et al.*, 2000). Despite the massive increase in algal cover, if the term phase shift is defined as the event where macroalgae rise to over 50% of the total benthic cover, only about 4% of Caribbean reefs are actually dominated by macroalgae (Bruno *et al.*, 2009), and at some sites such as Dairy Bull, Jamaica (Idjadi *et al.*, 2006) increases in coral cover and dominance have been reported.

Reef biodiversity, ecosystem functioning and related environmental services are likely to be severely affected by extensive habitat loss (Alvarez-Filip *et al.*, 2009), with negative economic and social impacts. The people of the Caribbean region are highly dependent on the fisheries sector for economic and social development, which contributes significantly to food security, poverty alleviation, employment, foreign exchange earnings, development, and stability of rural and coastal communities, culture, recreation, and tourism. More than 120,000 fishers work directly in the fisheries sector and several thousand women work in the processing, marketing, boat building, net making, and other support services. Marine fisheries production in 2008 was estimated at 134,138.3 tonnes (Landell Mills Development Consultants, 2011). Waite *et al.* (2011) report that in Jamaica alone, reef-related fisheries support 15,000–20,000 mostly artisanal fishermen. In addition, fisheries provide an important “safety net” of food and employment for coastal communities, and contribute directly and indirectly to the livelihoods of more than 100,000 people (nearly 5% of the population) who are employed as wholesale and retail vendors, processors, gear makers, boat builders, and ice suppliers.

1.3 Parrotfish and their role in the coral reef

The parrotfishes (Family Labridae, Sub-family Scarinae) are a distinctive group of labroid fishes which can be found on coral reefs throughout the world with approximately 10 genera (Bellwood, 1994). Although primarily found in tropical waters, some species also inhabit subtropical waters (Choat and Bellwood, 1998). According to the most recent update of the Catalogue of Fishes (Eschmeyer and Fong, 2014), there are currently 99 recognised species in the Sub-Family Scarinae. The taxonomy of parrotfishes has undergone several revisions, and new species are still being discovered (Rocha *et al.*, 2012). Of the 10 parrotfish genera, only the genus *Scarus* has a pantropical distribution, while *Nicholsina* has representatives in both the Eastern Pacific and Caribbean/Atlantic regions, *Sparisoma* is only found in the Caribbean and SE Atlantic regions, *Cryptotomus* is limited to the Caribbean, and the remaining 6 genera are only found in the Indo-Pacific or Eastern Pacific regions (Bellwood, 1994). There are thus four genera of parrotfishes in the Caribbean region.

There are at least 14 recognised species of parrotfishes found in the Caribbean region, most of which belong to the *Scarus* and *Sparisoma* genera, with 6 species each. The two remaining species, *Cryptotomus roseus* and *Nicholsina usta* are uncommon (Robertson and Warner, 1978; Streelman *et al*., 2002). The most common species of parrotfishes in the Caribbean are *Scarus iserti, Sc. taeniopterus, Sparisoma aurofrenatum,* and *Sp. viride* (McAfee and Morgan, 1996; Hawkins and Roberts, 2004a). The Caribbean region is also home to the largest herbivorous fish in the Atlantic, the rainbow parrotfish *Sc. guacamaia* (Randall, 1967) which is currently listed as Near Threatened (NT) in the IUCN red list (Baillie *et al*., 2004).

In the Caribbean, parrotfishes are some of the most abundant fishes making up more than 80% of the biomass of herbivorous fishes (Mumby, 2009). Parrotfishes are divided into two groups referred to as herbivorous (Bruggemann *et al*., 1996; Mumby *et al*., 2006) and corallivorous fishes (Bruckner *et al*., 2000). Both groups include grazers, scrapers, and bioeroders (Bruckner *et al*., 2000; Ledlie *et al*., 2007; Alwany *et al*., 2009). The parrotfishes that consume coral (Bruckner *et al*., 2000; Rotjan and Lewis, 2008), also graze on algae and indirectly help coral recruitment on hard substrates (Steneck, 1988; Williams and Polunin, 2000; Mumby *et al*. 2006; Hughes *et al*., 2007b; Burkepile and Hay 2008; Mumby, 2009). As a result they can help avoid a shift from a coral to an algae dominated ecosystem (Ledlie *et al*., 2007, Mumby *et al*., 2007a; Bruckner *et al*., 2014). Contrary to the positive impacts of parrotfishes, Rotjan and Dimond (2010) found that corallivorous parrotfish predation on *Montastrea* had a negative impact in areas with low coral cover. Parrotfishes also graze seagrasses (Unsworth *et al*., 2007) which may further prevent seagrass growth on reefs.

Jackson *et al*. (2014) divide recent Caribbean coral reef history into three stages. Firstly 1970-1983, from the oldest data available up until and including the mass mortality of the formerly abundant sea urchin *Diadema antillarum* in 1983. This period also includes the first reports of White Band Disease (WBD) in the mid-1970s and early 1980s. The second stage is 1984-1998, from the aftermath of the *Diadema* die-off to the massive bleaching caused by the 1998 extreme heating event. The third period from 1999-2011 is called “the modern era of massively degraded coral reefs” (Jackson *et al*., 2014:13).

The role of parrotfishes as herbivores has become much more important in the Caribbean since the 1983 crash in populations of the herbivorous urchin *Diadema antillarum* (Lessios *et al*., 1984). Prior to this, *Diadema* urchins were the major algal grazers in the Caribbean (Morisson, 1988), and their mass mortality left the parrotfishes as the dominant algae grazers (Mumby *et al*., 2007a&b). After the disease outbreak, the algal community increased significantly in the shallow waters of Discovery Bay, Jamaica (Morrison, 1988). Edmunds and Carpenter (2001) reported that average macroalgal cover was 10 times higher in areas where *Diadema* were rare. However, a considerable increase in fish grazing intensity was also observed after the *Diadema* mass mortality (Morrison, 1988). Although *Scarus* was still the dominant grazer, it was observed that *Sparisoma*, not previously considered a habitual grazer on shallow reefs, extended its range into shallow reef areas (Morrison, 1988). Furthermore, Carpenter (1990) found that herbivorous fish population densities, with parrotfish as the major component, had increased about three-fold in shallow reefs four years after *Diadema* mass mortality. Parrotfishes could be taking over the role of dominant grazers and could have a significant effect on algal abundance in the absence of significant herbivory by *Diadema*.

The *Diadema* populations have in general not shown signs of significant recovery (Levitan *et al*., 2014; Lessios, 2015). For example, despite high fecundity, ten years after the outbreak of disease, *Diadema* density in the San Blas Archipelago (Panama) had only reached about 3.5% of the original population abundance (Lessios, 1995), even though historical comparisons show some increase in *Diadema* density in parts of the Caribbean (Edmund and Carpenter, 2001). With this ongoing low density of *Diadema* populations, the role of parrotfish as grazers, especially in controlling the distribution and abundance of algae, is increasingly considered an important issue (Jackson *et al*., 2014). However, Caribbean parrotfish populations are under threat from both environmental and fishing pressures (Choat *et al*., 2012), and it has been recognised that efforts are needed to maintain the abundance of these fishes.

In this context, it is essential to have a good understanding of the relationships between parrotfish abundance and environmental variables as well as with fishing activities in the wider Caribbean. Most parrotfish are protogynous hermaphrodites, being born female, achieving sexual maturity as females and eventually undergoing a sex change to the terminal male phase (Robertson and Warner, 1978), with each phase (juvenile, female, male) tending to have different colours and habits. It is thus important to compare parrotfish abundance between fished and unfished areas, explore the relationship between parrotfish life phase, environmental variables and fishing, as well as changes in size and other attributes associated with each life phase.

1.4 Parrotfish communities in the Caribbean and their relationships with environmental variables

The abundance and biomass of fish in the Caribbean, including parrotfish, experienced rapid changes during the last decade (Hutchings, 2000; Hutchings and Reynolds, 2004, Hutchings and Baum, 2005). Fish abundance has also varied both spatially and temporally (Kopp *et al.*, 2012). Several factors such as habitat characteristics, competition, predation, fishing pressure, and home range contribute to the variation in spatial fish population structure. Some regions in the wider Caribbean have limited larval connectivity (Cowen *et al.*, 2005). In addition connectivity appears to decline with decreasing coral cover and rugosity, as well as where a “stepping stone” between sites has been lost (Hughes *et al.*, 2005). The decline in connectivity within the Caribbean reef system may cause benthic (coral) cover and habitat complexity to become the main factors affecting fish abundance in many areas.

Parrotfish abundance and biomass data from various sites in the Caribbean are highly variable and are estimated in various ways. For example Lewis and Wainwright (1985) reported parrotfish abundance in Belize ranging from 25 to 128 fish/400m^2, while Rotjan and Lewis (2006) found the range to be 10-18 fish/240m^2 (Table 1.1). van Rooij *et al.* (1996) found parrotfish densities between 700 and 2500 fish/ha at various depths in Belize, while Nemeth and Appeldorn (2009) report parrotfish abundance in La Parguera, Puerto Rico of between 19.7 and 23.4 fish/100m^2, and according to Burkepile and Hay (2009) parrotfish species abundance in Conch Reef in the Florida Keys was 1-5 fish/100m^2, with *Sp. aurofrenatum* having the highest abundance and *Sp. chrysopterum* the lowest. Hawkins and Roberts (2004a) found parrotfish biomass in six locations in the Caribbean to be 20-80 g/m^2, the lowest parrotfish biomass in Jamaica and the highest in Bonaire; however Steneck *et al.* (2011) found parrotfish biomass in Bonaire was below 30 g/m^2. A historical analysis over the period from 1988 to 2012 stated that biomass was highly variable, however the average biomass of parrotfish was only about 14g/m^2 and even the highest value recorded in the Caribbean (71 g/m^2) was still much lower than in some Indo Pacific protected areas (Jackson *et al.*, 2014). The variation in parrotfish abundance among locations was considered likely to be due to survey methodologies used as well as differences in site and habitat characteristics for example reef depth topography and exposure, as well as the area of the reef surveyed (e.g. reef flat, crest or slope).

Table 1.1 Parrotfish abundance and biomass data from various sites in the Caribbean.

Location	Density (original)	Density (individual/ $100m^2$)	Sources
Belize	25 – 128 individual/$400m^2$	6.25 - 32	Lewis and Wainwright (1985)
Belize	700 – 2500 individual/ha	7 - 25	van Rooij *et al*. (1996)
Belize	10 – 18 individual/$240m^2$	4.17 – 7.5	Rotjan and Lewis (2006)
Florida Keys	1 - 5 individual/$100m^2$	1 - 5	Burkepile and Hay (2009)
Puerto Rico	19.7 - 23.4 individual/$100m^2$	19.7 – 23.4	Nemeth and Appeldorn (2009)

Newman *et al.* (2006) found that fish biomass in the North Caribbean varied extremely between sites, ranging from 14 to 593 g m^{-2}. Seven surveyed sites had biomass higher than the mean fish biomass found in Bonaire and Curacao (135 g m^{-2}) (Sandin *et al*., 2007). Sandin *et al.* (2007) argue that the difference in fish biomass between the North Caribbean and Bonaire and Curacao is attributable to depth and fishing pressure. Newman *et al*. (2006) surveyed the reef terraces in the North Caribbean, while Sandin *et al.* (2007) conducted surveys in Bonaire and Curacao on reef slopes with an inclination of around 20-50°, and fishing pressure in Bonaire and Curacao is believed to be lower than that of the North Caribbean. Bonaire and Curacao should have higher biomass because of low fishing pressure. This discrepancy make large-scale data collection in the wider Caribbean would be necessary to eliminate the effect of differences in methodology and researchers.

External factors may also change the proportion and composition of parrotfishes relative to other fishes. Mumby (2009) suggests that parrotfishes are the dominant herbivorous fishes in the Caribbean (about 80%), however, on the reef slopes in Guadeloupe, French West Indies, it was found that parrotfish contributed about 65% of herbivorous fish assemblage biomass (Kopp *et al*., 2012). Although perhaps such differences in the composition of herbivore fish maybe location specific, fishing practices which target some parrotfishes, but not other herbivorous fishes such as Pomacentridae, may have altered herbivorous fish assemblage compositions. The current composition of the herbivorous fish guild needs to be assessed, may reduce the ability of herbivorous fishes to promote reef resilience in the absence of the urchin *Diadema*.

The abundance of fishes on coral reefs is related to several benthic habitat factors, which include coral cover (Graham *et al.*, 2007; Tzadik and Appeldoorn, 2013), macroalgae (Sandin *et al.*, 2007), as well as reef complexity (Alvarez-Filip *et al.*, 2011; Bozec *et al.*, 2013). Turf algae (McClanahan *et al.*, 2000), and crustose coralline algae cover (Howard *et al.*, 2009) was correlated with fish abundance but no causation inferred. For example, decreases in coral cover and shifts in coral composition had an adverse effect on the associated reef fishes in the Seychelles (Graham *et al.*, 2007), while Brewer *et al.* (2009) found that in the Solomon Islands, sites with coral cover greater than 31% had more fish biomass (e.g. Acanthuridae, Scaridae, Lethrinidae, and Lutjanidae) than those with coral cover less than 31%. However, in the Caribbean the relationship between parrotfish abundance and environmental factors is not consistent among study sites and species (Table 1.2). In La Parguera, Puerto Rico, parrotfish abundance was positively correlated with coral cover and rugosity, although the abundance of *Sc. taeniopterus* specifically was negatively correlated with these factors and positively correlated with algal cover (Tzadik and Appeldoorn, 2013). The abundance of scarids in Oahu, Hawaii exhibited a weak positive correlation with habitat rugosity, live coral cover, and crustose coralline algae (CCA) cover (Howard *et al.*, 2009).

Table 1.2 Relationships between parrotfish and habitat variables.

Variable	Response		Location	Reference
	Abundance	Biomass		
Coral cover	+ (*)		La Parguera, Puerto Rico	(1)
	+		Oahu, Hawaii	(2)
	No	No	American Samoa	(3)
Algal cover	+ (*)		La Parguera, Puerto Rico	(1)
Rugosity index	+		Oahu, Hawaii; Belize	(2); (4)
	No	No	British Virgin Island; La Parguera, Puerto Rico	(5); (1)
Hole size	+		British Virgin Island	(5)

(*) shows only *Scarus taeniopterus*.

(1) Tzadik and Appeldoorn (2013); (2) Howard *et al.* (2009); (3) Sabater and Tofaeono (2007); (4) Bozec *et al.* (2013); (5) Gratwicke and Speight (2005a)

There is not always a clear relationship between fish abundance and benthic habitat variables. For example, herbivorous fish biomass in Curaçao and Bonaire was positively related with algal cover but not coral cover (Sandin *et al.*, 2007). In Belize, McClanahan *et al.* (2000) showed that removing algae (fleshy, calcareous and branching coralline algae) increased algal turf and coral canopy cover and in turn *Sp. viride* biomass increased six fold compared to the control site. In contrast, *Sp. viride* in the Florida Keys frequently occurred in areas of high macroalgal cover (Paddack and Sponaugle, 2008). In American Samoa no significant relationship between parrotfish abundance and coral cover was observed (Sabater and Tofaeono, 2007), and a number of other studies did not find a significant correlation between parrotfish abundance and the benthic habitat variables studied (Hart *et al.*, 1996; Ohman and Rajasuriya, 1998; and Gust, 2002).

Rugosity or complexity of the reef structure is often considered to be closely related to fish abundance and biomass. Bozec *et al.* (2013) showed that the abundance of parrotfish was asymptotically related to reef habitat complexity although the magnitude of the effect varied among species and sizes. In contrast, parrotfish biomass in Puerto Rico was not significantly correlated with rugosity (Nemeth and Appeldoorn, 2009) and the abundance of fish species on an artificial reef in the British Virgin Islands was not significantly correlated with rugosity, but was significantly correlated with hole sizes (Gratwicke and Speight, 2005a).

Coral cover can affect the abundance of both large and small fish species (Tolimieri, 1998; Halford *et al.*, 2004). Johansson *et al.* (2012) found that the density of small scraper and excavator parrotfish increased in areas with high coral cover. *Montastraea* (*Orbicella*) corals in Mexico support many small fish classes, and changes in *Montastraea* (*Orbicella*) cover could have important consequences for the abundance of small fish and subsequently affect adult fish (Alvarez-Filip *et al.*, 2011).

The relationship between habitat in terms of benthic cover and reef complexity with parrotfish abundance can vary between fish size classes or phases. Wilson *et al.* (2010) found that a decline in the slope of fish size spectra was associated with decreasing coral cover. However, Almany (2004) found that for small reef fish, abundance was only weakly correlated with an increase in habitat complexity, while for adult fish there was a strong correlation between abundance and increasing habitat complexity. It has been reported that large holes in reefs support more large fish than small fish (Hixon and Beets, 1999). An ontogenetic shift in parrotfish habitat was observed in Panama, with juvenile fishes found mainly in the lower reef slope zone and adult fishes primarily in the upper reef slope zone (McAfee and Morgan, 1996). Despite these and other studies, knowledge regarding the relationship between habitat cover and complexity with the abundance of parrotfish in relation to size and phase remains inadequate.

Various habitat characteristics or parameters can influence reef fish abundance and biomass at the same site, acting independently, interactively, or as confounding factors, so can intrinsic properties of the fish studied such as size/age or phase. Some conflicting results regarding the influence of coral cover, macroalgal cover and rugosity on fish may reflect regional variance in environment and behaviour or differences in methodology among study sites (Howard *et al.*, 2009). The results may also reflect spatial differences in size composition of the parrotfish. Bozec *et al.* (2013) found that different sizes of parrotfish had different relationships with rugosity. Friedlander and Parrish (1998) found that herbivorous fish abundance in Hawaii was influenced mainly by rugosity, turf cover, macroalgal cover, coral cover, while biomass is correlated with hole volume, CCA cover, and distance to the reef edge or crest. On the other hand, Howard *et al.* (2009) found only weak correlations between parrotfish abundance and rugosity, live coral cover, CCA cover, proportion of sand, and non-turf macroalgae, although fish size was not considered as a factor. The difference in the relationship between rugosity and abundance observed between parrotfish of different sizes (Bozec *et al.*, 2013) may also occur in other habitat types.

Most studies are conducted in a limited geographical area, the results often being extrapolated to the rest of the Caribbean (Hughes *et al.*, 2010). Large-scale data on parrotfish across the wider Caribbean will help address this problem of over-generalization. The data will be able to provide a better understanding of the factors that affect the Caribbean parrotfish populations, in particular their numerical abundance and biomass. This knowledge could then be used to identify actions which could help maintain healthy population status of these ecologically important fishes at large scale.

1.5 Parrotfish abundance and the effect of fishing pressure

Fish assemblages may in fact be influenced by many factors. These may include biotic (e.g. predation, competition, and recruitment), abiotic (e.g. depth and water quality), and historical factors (e.g. fishing pressure and hurricanes) (Adjeroud, 1998). Predation, both natural or due to human exploitation, has a considerable influence on prey community structure by altering survivorship and density (DeMartini *et al.*, 2008). One consequence of this is that elimination of predators may lead to an increase in their prey, such as herbivorous fish (Shurin *et al.*, 2002).

Growing human populations can affect fish abundance and community structure. The growing demand for food threatens parrotfish stocks. In the Mariana Archipelago, Richards *et al.* (2012) found that large bodied fish biomass was higher in areas where the human population was lower. Parrotfishes have increasingly become a target food fish because of the decline of the previous primary target species, which were mainly predators (Aswani and Sabetian, 2010; Thyresson *et al.*, 2011). In addition, parrotfish are very susceptible to capture in traps due to their wide body, even when they are not a target species (Rakitin and Kramer, 1996; Johnson, 2010). Indeed by the early 2000's parrotfish had become the most common fish caught in the multispecies fisheries in the Western Indian Ocean (McClanahan and Mangi, 2004). Since 2002, a rapid shift towards the capture of smaller herbivorous fish has occurred in the Caribbean due to overfishing of larger species as well as fishery-induced size reductions in average size of certain stocks (Mumby *et al.*, 2013).

Fishing pressure is widely regarded as a major threat to fish stocks (Bellwood *et al.*, 2011), and is considered responsible for the body-size decrease in the Caribbean (Hawkins and Roberts, 2004a, Valles and Oxenford, 2014) and the Canarian Archipelago (Tuya *et al.*, 2006). A compilation of data from 31 Indo-Pacific nations by Dulvy and Polunin (2004) suggested that the humphead parrotfish is increasingly rare outside marine protected areas. Parrotfish abundance has been found to decline rapidly when human population density increases, as evidenced by data from 18 reefs in the Indo-Pacific for the world's largest parrotfish *Bolbometopon muricatum* (Randall *et al.*, 1997) and for the parrotfish *Chlorurus sp.* (Bellwood *et al.*, 2011). Recent review on the global fishing effect to herbivorous fish showed a consistent biomass reduction trend of large-bodied functional group of fish (Edwards *et al.*, 2014). Based on observed trends it can be expected that the burgeoning human population will further depress parrotfish abundance and size.

Marine protected areas can play an important role in maintaining or increasing fish abundance. Hughes *et al.* (2007a) suggest that protected areas should increase parrotfish biomass as long as the predation pressure inside the reserve is lower than fishing mortality outside. For example in the cases of Saba Marine Park and Hol Chan Marine Reserve (Belize), after just four years of closure reef fish abundance, size, and biomass were higher inside than outside the protected areas. The biomass of non-cryptic demersal fish, including parrotfish, in both protected areas was double that in fished sites (Polunin and Roberts, 1993; Roberts *et al.*, 2001). Marine reserves may sometimes have a negative impact on parrotfishes because of increased large predatory fish abundance. Mumby *et al.* (2006) reported that small-bodied parrotfish (e.g. *Sc. iserti*) were smaller inside the protected area studied, with no difference in density. Conversely, for large-bodied parrotfishes there was no difference in size but density was twice as high inside the protected area.

Although it is widely accepted that fishing will reduce the average size of parrotfish through the extraction of larger individuals (Hawkins and Roberts, 2004a; Valles and Oxenford, 2014), the mechanisms operating on particular species or under a particular set of pressures and environmental variables are not well known. For example, how do various types and levels of fishing pressure affect parrotfish abundance, biomass, and size in the Caribbean? The relationships between these variables need further investigation, including the type of relationships (e.g. linear, exponential, or asymptotic). It is important to know these relationships as without intervention the increasing threat from fishing and human population growth is likely to lead to an ongoing decline in the abundance and biomass of parrotfish and likely knock-on effects to the habitat. The effect of protected areas on the parrotfish assemblages needs further investigation. One aim of this study is to improve knowledge and understanding of the ways in which parrotfish populations are affected and vary between protected (unfished) and unprotected areas (fished).

1.6 Parrotfish reproduction and life cycle

Choat and Bellwood (1998) describe the three stages or phases known in parrotfish, which typically have a distinctive appearance. The first phase is sexually immature juveniles of both sexes, generally characterized by drab colouration. The second, known as the initial phase (IP) may be either male or female, but in most species tends to be totally or predominantly female. The third stage is called the terminal phase (TP) and includes only mature males. Terminal males typically display bright colours and some may have other external signs such as a bulbous forehead shape. Some female parrotfishes can change into males before or after maturity depending on the species, but females of the genus *Scarus* cannot change sex before sexual maturity (Robertson and Warner, 1978).

Sex change in parrotfish can be affected by various factors. The onset of sex change in marine animals can be affected by variations in growth and mortality rate (Merot and Collin, 2012). One of the theories in fish sex change is called the size advantage model (Ghiselin, 1969). This theory suggests that under certain circumstances an individual with the ability to change its sex at a certain age or size will have a greater advantage in terms of reproductive success than an individual that remains a male or female. This model assumes that the age or size at which sex change occurs is genetically determined, however, environmental factors may also drive sex change (Charnov, 1982). Warner (1988b) suggests that there are at least two kinds of environmental factors which may prompt sex change in fish. The first type comprises extrinsic factors linked to physiological parameters, in which the optimal age and size for fish to change sex depends on the external environmental conditions. The second factor type relates to demography and male opportunity. For example a lack of mature males in the population may prompt a fish to change sex early (at a younger age or smaller size), or vice versa.

Based on Warner (1998b), fishing is one human activity that can affect fish sex change through at least two mechanisms. Firstly, fishers are likely to prefer large fish as targets. Removal of these larger fish, especially terminal males, may affect the size at which fish change sex, as in most parrotfishes terminal phase fish are considered to be reproductively mature and to have undergone sex change from female to male (Robertson and Warner, 1978). Thus, it is expected that increased fishing of parrotfishes will lead them to change sex early, shown by a decrease in the size of terminal phase fishes. Secondly, fishing increases mortality more generally, and thus reduces the chances of fish reaching reproductive maturity, which would also prevent them from subsequent sex change, making it advantageous for protogynous fishes to both mature early (as females) and change sex early (to provide males). There is indeed substantial evidence that parrotfishes can modify their reproductive strategy in response to environmental changes, for example adjust the age at which they change sex. Hawkins and Roberts (2004b) found that the size of terminal phase *Sp. viride* and *Sc. vetula* in the Caribbean, particularly in Saba, Bonaire, Puerto Rico, St. Lucia, Dominica, and Jamaica, decreased in line with increased fishing pressure.

Food availability may influence sex change in fish or other organisms as the growth rate affects the optimal size for sex change (Charnov, 1982), as observed for instance in *Crepidula spp.* (Gastropoda) (Merot and Collin, 2012). *Crepidula marginalis* was observed to initiate sex change earlier as well as to complete sex change later when raised with less food, while another species, *C. incurve,* changed sex later when raised with less food. Parrotfish sex change may also be influenced by food availability. Algae is the main source of food for majority of the parrotfishes, so that less food means increased competition between individuals, which will result in a size advantage model where extrinsic and physiological conditions may result in alterations of size during each life phase, including sex change (Warner, 1988a).

Herbivorous fishes often increase in abundance when algal cover increases, including following extensive coral loss (Wilson *et al*., 2006; Pratchett *et al*., 2009), however this is not always the case and may depend upon macroalgal community structure in terms of species and size (McClanahan *et al*., 2000). Declining coral cover in the Caribbean is considered to be a driver of as well as driven by shifts from coral to algal domination (Côté *et al*., 2005; Mumby, 2009). High coral cover areas typically have lower food availability for herbivorous fishes compared to low coral cover areas as herbivorous fishes feed on algae. This would seem to be the case for at least some parrotfish, as long as the algae present are palatable for the species and life stage considered (McClanahan *et al*., 2000). Thus the abundance and size of parrotfish during each life phase may be influenced by both habitat variables and fishing. Therefore, there is a need for research on relationships between abundance and size of parrotfish in each life phase with habitat and fishing. The results of such research could be used to develop options for management, thus supporting the conservation of these economically and ecologically valuable fishes as well as the welfare of the human communities in the Caribbean region.

1.6 Outline of the thesis

The goal of this thesis is to improve understanding of the macro-ecology of parrotfishes in the Caribbean. Large-scale data from 8 countries in the Caribbean will be used to help address the various research gaps mentioned above. The remainder of this thesis is organized into 4 further chapters as set out below.

Chapter 2 describes the relationships between parrotfish abundances and benthic habitat variables in selected sites in 8 countries during 2010-2011. Parrotfish abundance, biomass, and size were estimated using underwater visual census techniques. Habitat variables such as coral, macroalgae, turf, CCA cover, reef rugosity, hole density and size were quantified at the same time and sites as the data on parrotfish populations. The observed relationships between parrotfish abundance and habitat variables are discussed.

Chapter 3 addresses the relationships between parrotfish abundance and fishing pressure. Data on fish abundance, biomass and size were estimated and fishing pressure was assessed using three indices, namely: a human population index, a fisher per reef area index, and an index for MPA effectiveness. The relationships between parrotfish population parameters and the fishing pressure index were analysed using Spearman rank correlation tests. In addition, an abundance - biomass comparison (ABC) was used to study impacts of fishing pressure and the relationship between the w-statistic value from ABC and fishing pressure.

Chapter 4 presents data on the sizes at which parrotfishes change life phase and analyses the relationships between parrotfish life phase (Juveniles, Initial Phase, and Terminal Phase) and fishing pressure. In addition, parrotfish size at phase change are also estimated and described.

Finally, **Chapter 5** brings together the main findings from the previous chapters. These are discussed in the context of the wider literature especially to highlight the contributions made by this study.

Chapter 2. Relationships between parrotfish density and benthic habitat variables

2.1 Introduction

Parrotfishes (Labridae: Scarinae) are widely considered to play an important role in coral reef ecology. They make up more than 80% of the biomass of herbivorous fishes in the Caribbean (Mumby, 2009). Because they graze on algae they can indirectly promote coral recruitment on hard substrata (Williams and Polunin, 2000; Burkepile and Hay, 2006; Mumby *et al.*, 2006; Hughes *et al.*, 2007b; Burkepile and Hay, 2008; Mumby and Steneck, 2008; Mumby, 2009) and can reduce the risk of a shift from a coral to an algae-dominated ecosystem (Ledlie *et al.*, 2007). Some parrotfishes consume corals (Bruckner et al., 2000; Rotjan and Lewis, 2008) and hence they may play a major role in shaping the distribution and abundance of related coral species, as reported for *Porites* spp on the Great Barrier Reef (Bonaldo and Bellwood, 2011). In the Caribbean context, parrotfish corallivory has been related to benthic cover by corals of Genus *Montastraea* (*Orbicella* spp) (Rotjan and Dimond, 2010).

The decline of the herbivorous urchin *Diadema antillarum* since 1983 (Lessios *et al.*, 1984) has resulted in parrotfishes becoming the dominant grazers on Caribbean reefs (Mumby *et al.*, 2007a&b). In this situation, the capacity of reefs to maintain benthic habitat cover suitable for the settlement and growth of reef building corals is likely dependent on the presence of these herbivorous fish. Consequently, it is considered important to maintain healthy parrotfish populations, a view reinforced by a recent report on coral reef health in the Caribbean region (Jackson *et al.*, 2014). In order to do so, it is important, even vital, to have a good understanding of the key environmental factors that may affect parrotfish abundance.

Benthic cover types likely to significantly influence parrotfish assemblages, include hard (reef-building) corals (Gust, 2002; Graham *et al.*, 2007; Brewer *et al.*, 2009; Howard *et al.*, 2009; Johansson *et al.*, 2012; Tzadik and Appeldoorn, 2013), macroalgae (McClanahan *et al.*, 2000; Sandin *et al.*, 2007; Paddack and Sponaugle, 2008), algal turf (Friedlander and Parish, 1998; McClanahan *et al.*, 2000) and crustose coralline algae (Friedlander and Parish, 1998; Howard *et al.*, 2009). The structural habitat complexity, particularly the hard coral component, is also expected to be an important factor (Gratwicke and Speight, 2005a; Alvarez-Filip *et al*., 2011; Bozec *et al*., 2013).

Relationships between parrotfish abundance and environmental factors show marked variation between studies and study sites. For example Bozec *et al*. (2013) found that overall parrotfish abundance was positively correlated with reef habitat complexity, although the correlation varied between species and between size groups within the same species. In contrast, in Puerto Rico parrotfish biomass and rugosity were not correlated (Nemeth and Appeldoorn, 2009). Different measures of structural complexity can also lead to different results. For example, the abundance of fish species on an artificial reef in the British Virgin Islands could be predicted based on hole size but not on rugosity (Gratwicke and Speight, 2005a).

Benthic habitat cover and complexity may be differently related to parrotfish abundance at different spatial scales. While many studies have reported on the status of parrotfish and their relationships with habitat (Friedlander and Parish, 1998; Howard *et al*., 2009; Bozec *et al*., 2013), and some papers describe multi-scale spatial variability of fish abundance (Gust *et al*., 2001; Garchia-Charton *et al*., 2004), the relationships between benthic habitat cover, complexity and parrotfish abundance at different spatial scales are scarcely known. It has been suggested that the variability in observed relationships between habitat variables and fish abundance may not only reflect regional, environmental and human/societal factors or differences in methodology among study sites, but also the geographic scale of the study (Howard *et al*., 2009). For example, Sabater and Tofaeono (2007) found no significant relationship between parrotfish abundance and coral cover based on a study using a video camera to collect benthic habitat data. However underwater visual surveys by Howard *et al*. (2009) covered areas 7 times larger detected a relationship between coral cover and parrotfish abundance. These are just two of many other cases which indicate that large-scale surveys using uniform methodology are needed to determine the key environmental factors influencing parrotfish abundance and to test the general validity of perceived parrotfish/habitat relationships, and reinforce the importance of scale in research design.

The relationships between abundance, benthic cover and structural complexity on a given reef can vary significantly with fish body size and age for many reef fishes. For some fish taxa, population size/age spectrum or structure can vary with coral cover (Wilson *et al*., 2010). For some species the abundance of smaller juvenile fish may be only weakly related to coral cover while that of adult fish may be strongly related to benthic habitat complexity (Almany, 2004). In the US Virgin Islands, large holes in the reef structure tended to support more large than small fish (Hixon and Beets, 1989). Bozec *et al*. (2013) found *Sp. aurofrenatum* abundance was unrelated to rugosity in the 4-7cm and 13-20cm size classes, however there was a positive relation in the 8-12cm and 21-40cm size classes. An ontogenetic shift in parrotfish habitat was observed in Panama, where most juvenile fish were observed on the lower reef slope and adult fishes were seen primarily on the upper slope (McAfee and Morgan, 1996). Elucidating the relationships between abundance and habitat variables for different sizes of parrotfish is important, not least to provide information on habitat requirements during all stages or phases of parrotfish life history.

The two major parrotfish genera in the region, *Scarus* and *Sparisoma*, vary in their habits, for example the foraging and territorial areas of *Scarus* are typically much smaller than those of *Sparisoma* (Mumby and Wabnitz, 2002). *Scarus* species mostly consume algal turf and crustose coralline algae (Steneck and Dethier, 1994), while *Sparisoma* graze on fleshy macroalgae and have a more varied diet (Bruggemann *et al*., 1994). Observed relationships with reef rugosity differ between *Scarus* and *Sparisoma* (Bozec *et al*., 2013). While for both genera abundance was positively correlated with reef rugosity, the relationship for *Scarus* was linear in form, and that for *Sparisoma* was asymptotic. For small parrotfish (4-7cm), *Sc. iserti* abundance was correlated positively with rugosity, but for *Sp. aurofrenatum* there was no significant correlation (Bozec *et al*., 2013). The genera may also differ in their relationships to other habitat variables.

Surveys across geographical gradients and different habitat types should provide managers with relevant, robust data on relationships between parrotfish and their habitat at different spatial scales. To responds to this need, at least in part, the present study investigated large-scale relationships between parrotfish abundances and habitat in the Caribbean.

For this study, simple fish metrics of numerical density and biomass were used. Fish biomass is essentially a product of numerical density and fish size, and therefore can incorporate variations in size structure (Howard *et al*., 2009), while size can be considered as an indicator of or proxy for an individual’s role as a grazer (Bonaldo and Bellwood, 2008; Jayewardene, 2009). Both metrics are often strongly related to the physical condition of fish habitat (Howard *et al*., 2009; Graham and Nash, 2012; Bozec *et al*., 2013).

This study addressed the following specific questions: (1) What relationships exist between parrotfish abundance and benthic habitat variables at different spatial scales? (2) How do these relationships vary with fish size classes?

2.2 Methods

Fish and benthic habitat surveys were conducted in eight Caribbean countries (Antigua, Bonaire, Barbados, Curaçao, Dominican Republic, Jamaica, St. Lucia, St. Vincent and the Grenadines (SVG)) by the EU FORCE Project team. Seven to fifteen sites were surveyed in each country, with a total of eighty-four reef sites at depths of 10-15 m. Sites were generated by Hawth's Tool in *ArcGIS* using the stratified random point option, and then selected, again at random, based on the area of each country.

2.2.1 Fish surveys

Parrotfish abundance and size were recorded by Steven P. Newman, using an underwater visual census technique. At each site, four 10 x 4 m transects were placed to record fish <20 cm and eight 30 x 4 m transects for fish >20 cm total length (Figure 2.1). Transects were placed at random parallel to the shoreline in a uniform area of the reef and about 10-15m away from the boundary between reef and non-reef substrate. There was an interval of at least 10m between each transect. Data were gathered between October 2010 and December 2011. Surveys were conducted between 9 am and 3 pm local time for the best light conditions. Fish total length was estimated visually *in situ* to the nearest centimetre (cm). Parrotfish biomass was calculated using length-weight relationships between size and counts (Bohnsack *et al*., 1988; Eq. 2.1) with species-specific values from www.fishbase.org (Froese and Pauly, 2013).

$$\mathrm{W} = \mathrm{aL^b} \ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{(Eq. 2.1)}$$

Where W is Weight, a is species coefficient and b is species exponent (obtained from fisbase.org) and L is length.

2.2.2 Benthic surveys

Benthic habitat cover

Habitat cover data were collected by Stacey Williams on six 10m point intercept transects per site, with benthic cover recorded every 10cm thus totalling 101 data points per transect (Figure 2.1). Substrate categories recorded were coral, macroalgae, turf algae and crustose coralline algae (CCA). The benthic habitat transects were placed within the fish transects.

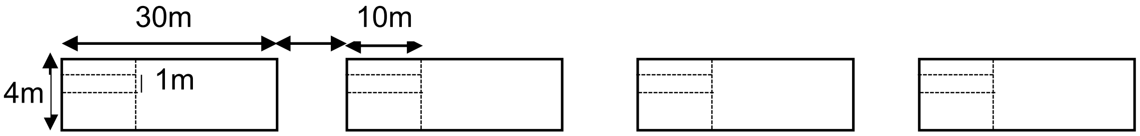

Figure 2.1 Transect layout per site of fish and benthic habitat. Four 10 x 4 m transects were placed inside 30 x 4 m transects. 10 m point intercept transect and 1 x 10 m transect for hole average size and density were also placed inside 30 x 4 m transect.

Rugosity

Reef rugosity was recorded by Charlie Dryden using a traditional chain-tape method (Risk, 1972) within the same sites as the fish surveys. A 10m, 8mm link chain was draped over the contour of the reef substrate and the straight-line distance between the ends was measured using a tape measure. In Bonaire, the Government of Bonaire did not permit the use of the chain, so a second tape was used instead. Although the use of the tape may have led to some underestimation of rugosity, Steven P Newman and Charlie Dryden were able to standardize the results by using comparative chain-tape data from reefs in SVG to adjust the rugosity measurements. They computed estimated chain lengths using a linear relationship between the chain and second tape length data from SVG, which yielded the following equation:

$\text{Chain length} = 0.8452 * \text{tape length} + 0.8982$ ($R^2 = 0.744$, n=20)

The Rugosity index was calculated using the following equation:

$$\text{Rugosity index} = \frac{\text{chain length}}{\text{straight line distance}} \text{ …………… (Eq. 2.2)}$$

Hole average size and density

Four 10m x 1m transects per site were used by Charlie Dryden to measure reef hole size and density at the same place and at the same distances apart as for the fish transects (Figure 2.1). A hole was defined as a cavity in the reef. Holes were counted and measured if they were > 20cm deep or deeper than their wider diameter. Holes were counted in 5cm size classes for holes < 50cm wide and the actual hole width was measured for holes > 50cm. The average size was then calculated. Hole density was calculated by dividing the hole frequency (the number of holes counted) by the area surveyed.

2.2.3 Data Handling

Data on numerical abundance and biomass were standardized based on transect area to calculate fish densities (individuals per 100m^2) and biomass (grams per 100m^2). Fish numerical abundance, biomass and habitat data were transformed to minimize departure from normality (Table 2.1). Parrotfish diversity was assessed by aggregating species abundance at country level. Analysis of Variance (ANOVA) tests were employed to determine significant differences in numerical abundance and biomass among countries and Tukey HSD post hoc tests were applied if the ANOVA found significant overall differences. Principal components analysis (PCA) ordination methods were used to assess the variation of parrotfish numerical abundance and biomass among sites and between countries. Benthic habitat variables were incorporated into the PCA using the *envfit* function in the *Vegan* package (Version 2.0-10; Oksanen *et al.*, 2013).

Fish numerical abundance and biomass were fourth root transformed to minimize the effect of dominant species. Habitat cover variables were arcsine square root transformed to reduce collinearity between proportional data (Sokal and Rolf, 1981; Zar, 1999). Habitat complexity variables were $\log_{10}$ or square root transformed (Table 2.1). In order to further reduce the effect of collinearity, benthic habitat cover data (coral, macroalgae, turf, and CCA cover) were combined using PCA. PC1 axis scores were used to represent benthic cover. The factor loading of PCA was also calculated (Appendix 1). Independent variables were tested for their collinearity using the Variable Inflation Factor (VIF). No variable was dropped because all variables had VIF values less than 2.5 (Allison, 1999).

Table 2.1 Available data, unit measurement, and transformation used.

Data	Measurement	Transformation
Fish numerical abundance	Individuals/100m^2	4th square root
Fish biomass	Grams/100m^2	4th square root
Coral cover	%	Arcsine square root
Macroalgae cover	%	Arcsine square root
Turf cover	%	Arcsine square root
CCA cover	%	Arcsine square root
Rugosity index	Index	-
Hole average size	cm	$\log_{10}$
Hole density	Number/m^2	$\log_{10}$

2.2.4 Statistical Analysis

Relationships between parrotfish abundance and habitat variables

Multiple linear regression (MLR) models were used to determine habitat factors affecting parrotfish abundance and biomass. MLR was used instead of Linear Mixed Effect Models because AIC was no difference between them. Numerical abundance and biomass of all parrotfish, *Scarus* spp and *Sparisoma* spp were tested against four habitat variables as independent variables. PC1, rugosity index, hole mean size and hole density were used as independent variables.

Relationships between habitat cover, habitat complexity, and parrotfish abundance were determined at country scale and at Caribbean regional scale. MLRs were used to examine these relationships in each country (n = 7-15 sites/country). At the regional scale, the parrotfish abundances across all sites (n = 84 sites) were used. The full model tested the following formula:

Y ~ PC1+ rugosity + hole density + hole mean size + noise ……… (Eq. 2.3)

where Y is fish numerical abundance or biomass.

The full MLR model was then subjected to a stepwise model selection test to find the minimal adequate model in *stepAIC* from the *MASS* package (version 7.3-29; Ripley *et al.*, 2013). The model with the lowest AIC value was chosen (Appendix 2). All tests and plots were conducted using the R software environment (version 3.0.2; R Core Team, 2013).

Relationships between parrotfish numerical abundance and habitat variables in the different size classes

To determine relationships of parrotfish abundance with benthic habitat variables at different fish size classes, linear mixed effect (LME) tests were employed because these allow missing value and unbalanced data to be analysed (Pinheiro and Bates, 2000). Unbalanced data usually come from field observations where the variables are uncontrollable by the observer. Moreover, LMEs allow the inclusion of random effect variables. Country was included as a random effect variable because initial data investigation showed parrotfish density and biomass variation among countries.

Parrotfish, *Scarus*, and *Sparisoma* numerical abundances were separately tested against the habitat variables as fixed effects. Biomass was not included because it is derived from abundance and fish size (Bohnsack *et al.*, 1988). PC1, rugosity index, hole average size, and hole density were modeled. Fish were grouped into total length

classes: (1) < 10cm, (2) 11-20cm, (3) 21-30, and (4) > 30cm. Parrotfish abundances at all sites (n=84 sites) were used.
The full model tested the following formula:
Y ~ PC1 score + rugosity + hole density + hole mean size + random effect + noise ………………………………………………………… (Eq. 2.4)
where Y is fish numerical abundance at size class

The full LMEs were subjected to stepwise model selection test to find the minimal adequate model using maximum likelihood in *stepAIC* in the *MASS* package (version 7.3-29; Ripley *et al.*, 2013; Appendix 3). The model with the lowest AIC value was chosen and then rerun using the restricted maximum likelihood (REML) method. LME models were analysed using the *nlme* package (version 3.1-113; Pinheiro *et al.*, 2013). R^2 (goodness-of-fit) marginal and conditional values were computed based on Nakagawa and Schielzeth (2013) and performed using the *r.squaredGLMM* function in the *MuMin* package (version 1.9.5; Barton, 2013). R^2_{marginal} is defined as the variation explained by a fixed variable, while $R^2_{\text{conditional}}$ is defined as variation explained by combination of a fixed and random variable. These R^2 values are good tests of fit of the mixed effect models equivalent to R^2 from linear models (Nakagawa and Schielzeth, 2013). To visualize the relationships between fixed and dependent variables, where these were significant, the data were plotted using the *visreg* package (version 2.0-4; Breheny and Burchett, 2013). All tests and plots were conducted using the R software environment (version 3.0.2; R Core Team, 2013).

2.3 Results

Ten species of parrotfishes were recorded within Caribbean with six to eight species present in each country (Table 2.2). Antigua, Bonaire, Dominican Republic and SVG had the highest number of parrotfish species, while Curaçao had the lowest with only six species. Four species of parrotfish were observed in all countries surveyed in the region namely *Sc. iserti, Sc. taeniopterus, Sp. aurofrenatum,* and *Sp. viride*, contributing 80-90% of total parrotfish abundance. The small-bodied parrotfishes such as *Sc. iserti, Sc. taeniopterus,* and *Sp. aurofrenatum* were present and dominated parrotfish abundance in most countries. In Bonaire and Curaçao, the large-bodied parrotfish *Sc. vetula* contributed 17.79% and 7.64% respectively to total parrotfish numerical abundance (Table 2.2).

Mean parrotfish (all species) densities by country varied from 17.89 ± 3.90 (value ± sd) to 62.28 ± 70.90 individuals/100m^2. The highest density was found in Antigua while the lowest density was found in Bonaire. There were significant differences in parrotfish numerical density among countries (ANOVA, F=3.015, $p < 0.05$) (Figure 2.2), the only difference being between Antigua and Barbados (Tukey HSD post-hoc, $p < 0.05$).

Biomass of parrotfish in the Caribbean ranged between 756.82 ± 391.90 and 3163.01 ± 845.37 g/100m^2, the highest mean biomass being in Bonaire and the lowest in Jamaica. There were significant differences in parrotfish biomass among countries (ANOVA, F=2.714, $p < 0.05$), the differences being between Bonaire and Dominican Republic and Jamaica ($p < 0.05$) and Bonaire and Jamaica ($p < 0.05$) (Figure 2.2B).

Table 2.2 Species abundance composition (in percent) in eight countries across the Caribbean.

Species	**Antigua**	**Barbados**	**Bonaire**	**Curaçao**	**Dominican Republic**	**Jamaica**	**St Lucia**	**SVG**
Scarus taeniopterus	18.76	20.92	35.57	39.67	20.21	7.99	44.58	22.66
Scarus iserti	33.77	16.31	1.08	7.02	22.21	40.55	2.50	10.14
Scarus coelestinus	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00
Scarus vetula	1.66	4.92	17.79	7.64	0.66	0.00	1.46	1.96
Scarus guacamaia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43
Sparisoma viride	12.36	21.23	28.63	22.31	16.49	5.22	16.46	32.79
Sparisoma aurofrenatum	29.47	33.23	15.18	21.69	34.04	40.40	33.13	30.49
Sparisoma chrysopterum	0.22	0.00	0.65	1.65	3.06	0.31	0.63	0.09
Sparisoma rubripinne	0.55	3.08	0.87	0.00	1.33	0.46	1.25	0.00
Sparisoma atomarium	3.20	0.31	0.00	0.00	1.99	5.07	0.00	1.45
Number of species	8	7	8	6	8	7	7	8

Mean numerical densities by country ranged from 7.37 ± 6.64 to 34.23 ± 63.67 fish/100m^2 (*Scarus*) and from 6.16 ± 1.46 to 28.05 ± 16.64 fish/100m^2 (*Sparisoma*), with the lowest density in Barbados and the highest in Antigua (Figure 2.2). *Scarus* numerical densities did not differ significantly among countries (ANOVA, F=1.105, $p > 0.05$) (Figure 2.2), however differences in *Sparisoma* numerical densities were significant (ANOVA, F=8.391, $p < 0.001$) (Figure 2.2). *Scarus* and *Sparisoma* mean biomass values ranged from 260 ± 161 to 1486 ± 791 and from 429 ± 215 to 1676 ± 245 g/100m^2, respectively, with the lowest biomass in Jamaica and the highest in Bonaire. There was no significant difference in *Scarus* biomass among countries (ANOVA, F=1.67, $p > 0.05$). There were significance differences in *Sparisoma* biomass among countries (ANOVA, F=4.165, $p < 0.001$). *Sparisoma* biomass differed significantly between Bonaire and Antigua, Barbados, Dominican Republic and Jamaica (Tukey HSD, $p < 0.05$) (Figure 2.2).

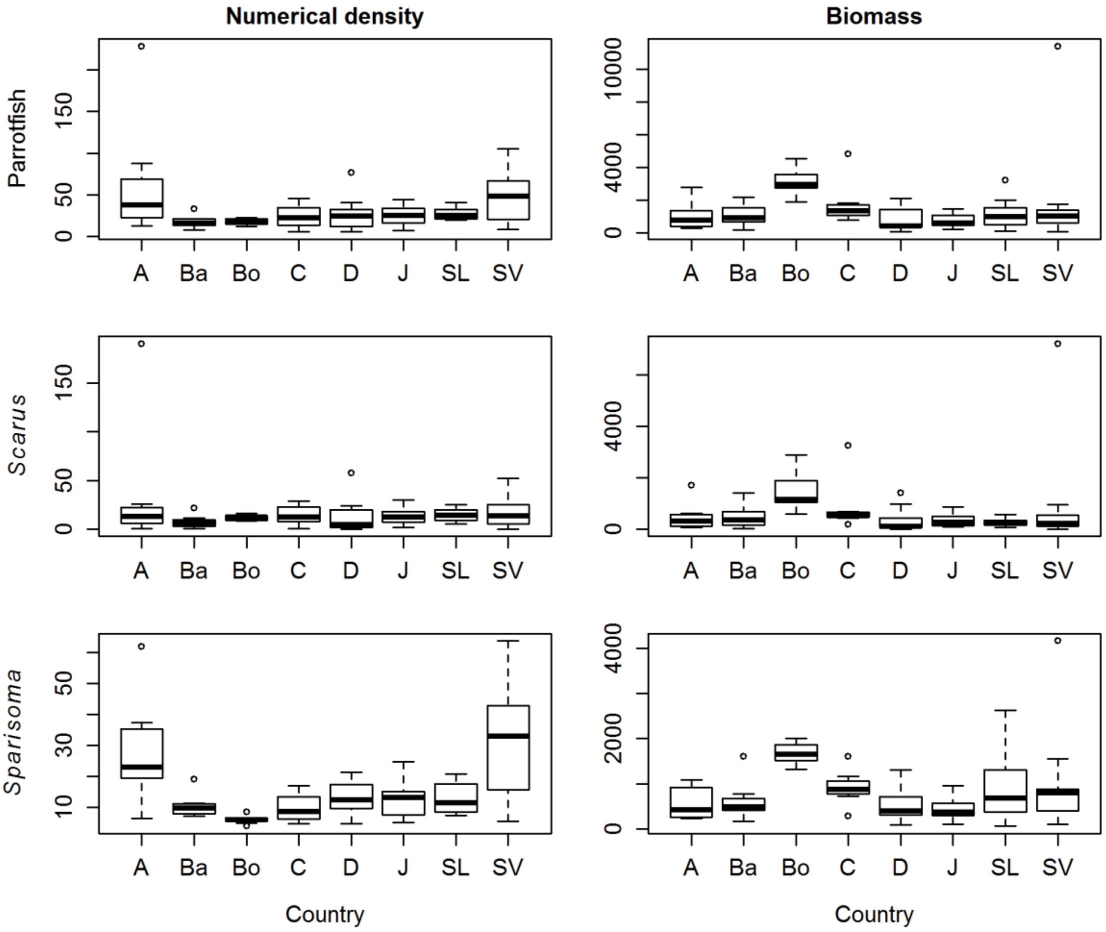

Figure 2.2 Parrotfish mean numerical abundance (individual/100m^2) and biomass (g/100m^2) per country. (A) Antigua, (Ba) Barbados, (Bo) Bonaire (C) Curacao , (D) Dominican Republic, (J) Jamaica, (SL) Saint Lucia, and (SVG) Saint Vincent and the Grenadines. The band inside box was median, whisker represent first and third quartiles, standard deviation (sd) was used as the error term.

Parrotfish assemblages were mostly composed of small and medium sized fish with the exception of Bonaire, where large parrotfish (more than 20 cm in size) were equally abundant with small parrotfish. Small and medium sized parrotfish were abundant in Antigua, St. Lucia, and SVG (Figure 2.3).

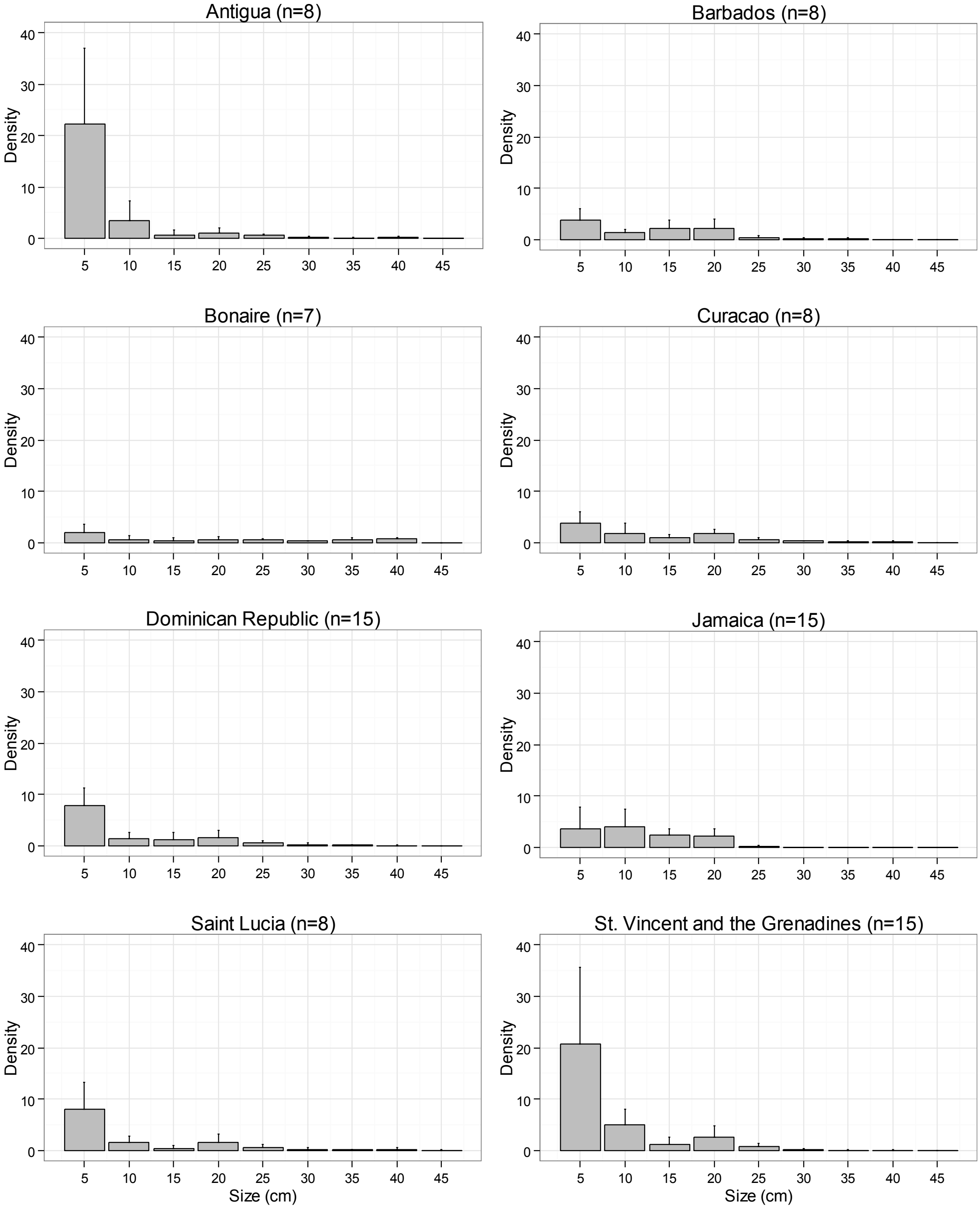

Figure 2.3 Size-frequency distributions of parrotfish by country. Values plotted as mean ± sd. Fish density is individual/100m^2.

A PCA with 2 dimension explained 50% of the benthic habitat cover variability, with each axis explaining 25% (Figure 2.4). There was clear separation between sites with higher coral cover and those with more macroalgae cover by PC1 axis. Coral, turf and CCA cover were found in the negative PC1 axis, while macroalgae cover was found in the positive axis. Sites in Barbados and Bonaire had low macroalgae cover, sites in Jamaica high macroalgae cover, and sites in other countries had mixed benthic cover. Benthic cover tended to be similar among sites within country (Figure 2.4).

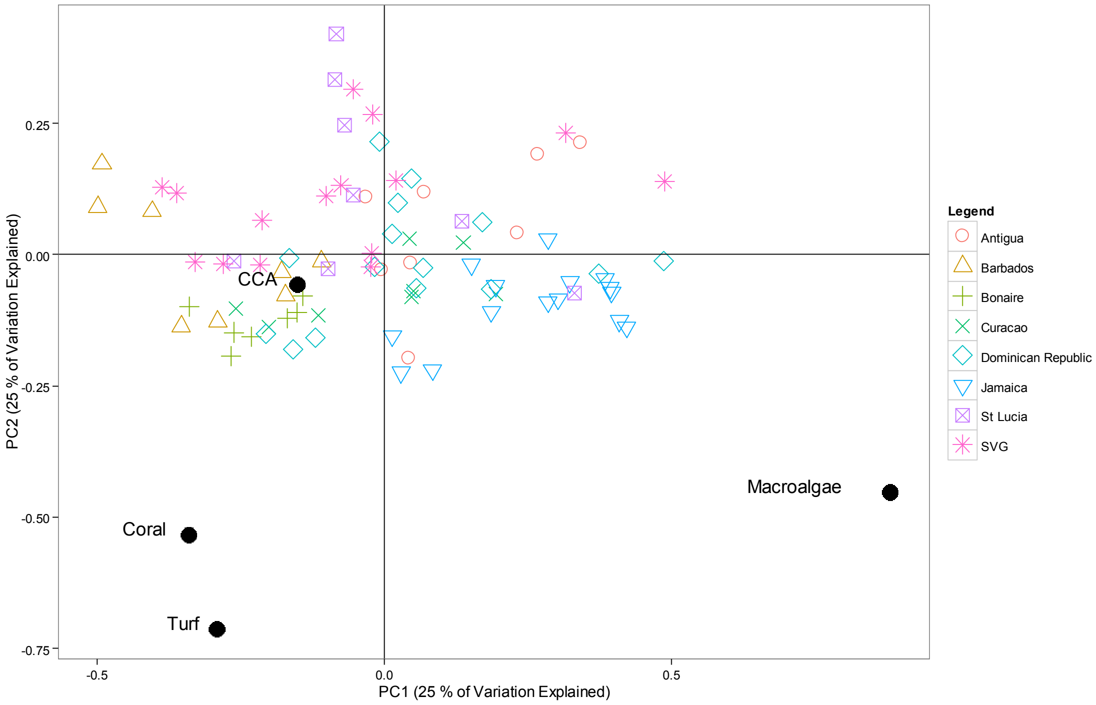

Figure 2.4 PCA of benthic habitat cover.

Over 70% of the variability in parrotfish numerical density was explained by two PCA dimensions (Figure 2.5), the first axis (PC1) explaining 45% and the second axis (PC2) 25% of the total variability. Sites with low parrotfish density had negative PC1 and positive PC2 values (top left), while those with higher parrotfish density had positive PC1 and negative PC2 values (bottom right, Figure 2.5; A). *Sp. viride* was the dominant species at the sites that had higher parrotfish density. The dominant small-bodied species, *Sc. iserti* and *Sp. atomarium* were most common at sites that had lower parrotfish numerical density. *Sp. aurofrenatum, Sp. crysopterum* and *Sp. rubrippine* were located near the centre of both axis. Higher parrotfish numerical abundance mainly corresponded with the complexity measures and lower parrotfish numerical abundance with benthic cover (PC1 score).

More than 88% of *Scarus* density was described by two PCA dimensions, *Scc. taeniopterus* being found predominantly in the sites with higher density and *Sc. iserti* mostly in sites with lower density (Figure 2.5, B). Lower *Scarus* density was correlated with benthic cover, while higher density was correlated with habitat complexity. The PCA with two dimensions described over 77% variability of *Sparisoma* numerical density (Figure 2.5; C). *Sp. viride* was found mostly in the sites with higher hole density. Lower *Sparisoma* density was also correlated with benthic cover, while higher density was correlated with habitat complexity.

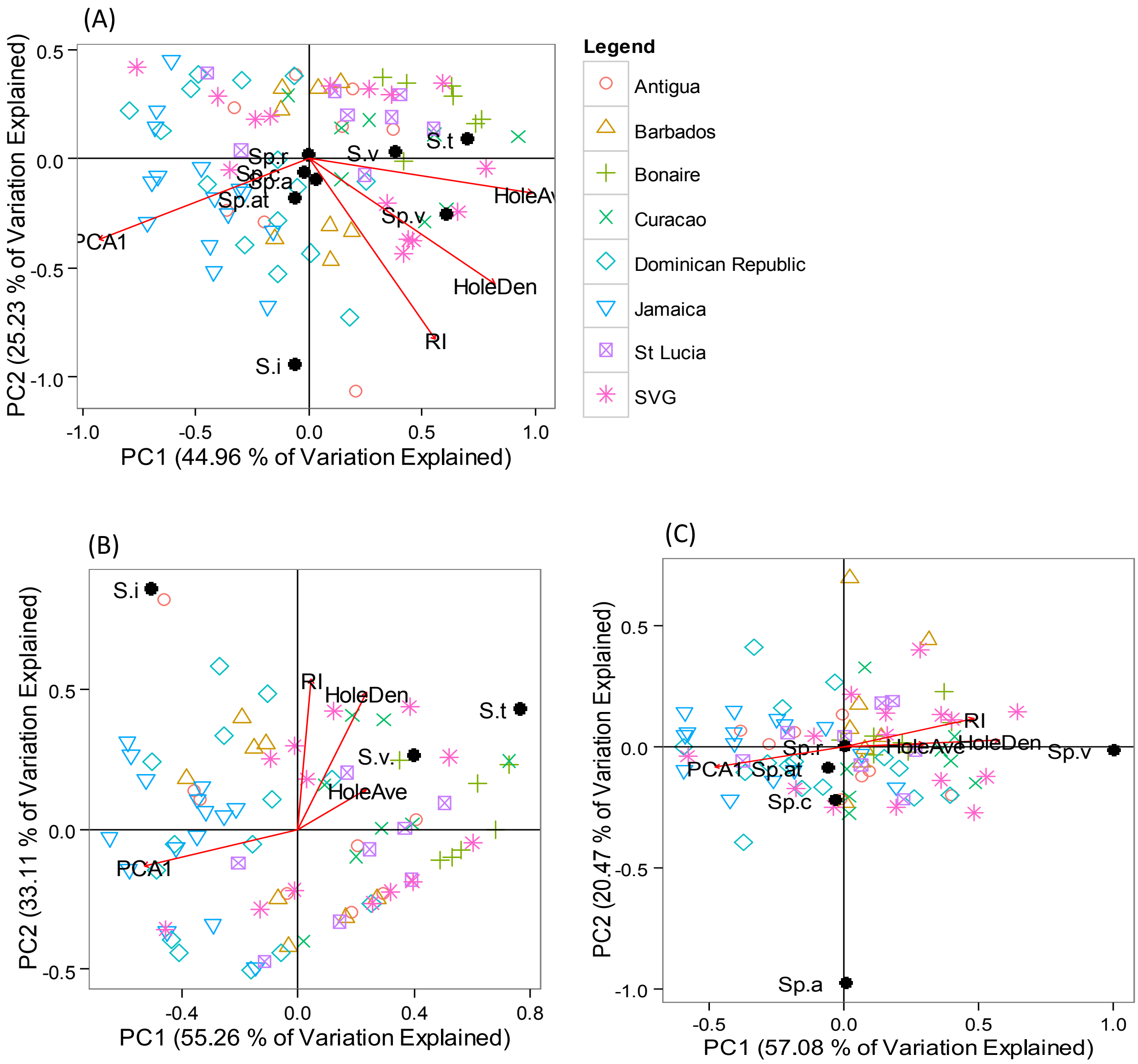

Figure 2.5 PCA of parrotfish assemblage numerical density. (A) Parrotfish, (B) *Scarus*, (C) *Sparisoma*. PCA1 = PCA1 score, RI = rugosity index, HoleAve = hole mean size, and Hole Den = hole density. S.i = *Sc. iserti*, S.t = *Sc. taeniopterus*, S.v = *Sc. vetula*, Sp.at = *Sp. atomarium*, Sp.a = *Sp. aurofrenatum*, Sp.c = *Sp. chrysopterum*, Sp.r = *Sp. rubiprinne*, and Sp.v = *Sp. viride*.

The PCA plots for *Scarus* and *Sparisoma* parrotfish biomass showed similar patterns to those for numerical density, however the first two components explained slightly more of the variability in the data (up to 82%) (Figure 2.6).

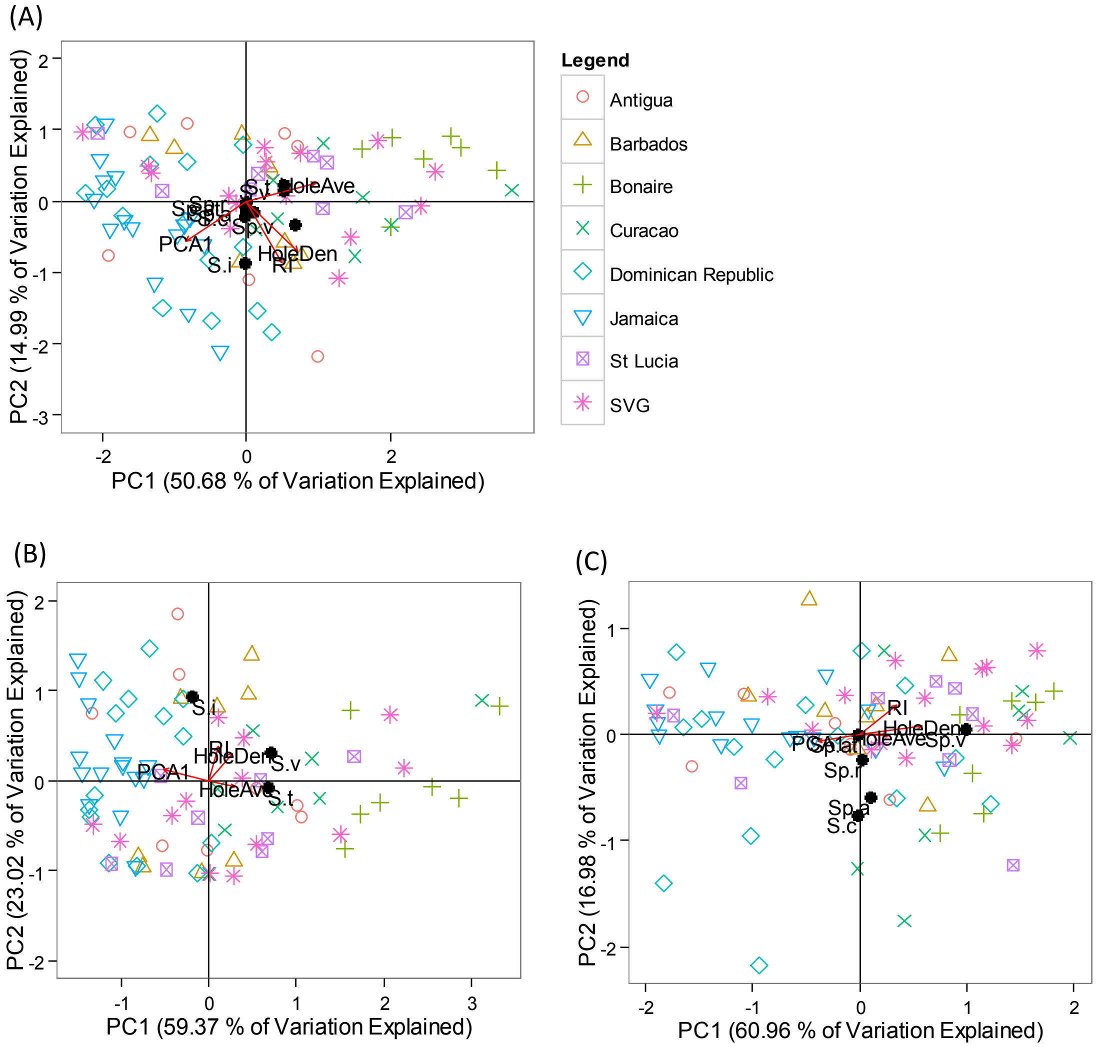

Figure 2.6 PCA of parrotfish assemblage biomass. (A) Parrotfish, (B) *Scarus*, (C) *Sparisoma*. PCA1 = PCA1 score, RI = rugosity index, HoleAve = hole mean size, and HoleDen = hole density. S.i = *Sc. iserti*, S.t = *Sc. taeniopterus*, S.v = *Sc. vetula*, Sp.at = *Sp. atomarium*, Sp.a = *Sp. aurofrenatum*, Sp.c = *Sp. chrysopterum*, Sp.r = *Sp. rubipinne*, and Sp.v = *Sp. viride*.

2.3.1 Relationships between parrotfish abundance and benthic habitat

Relationships of parrotfish numerical density and biomass to benthic habitat varied among countries and between spatial scales (Table 2.3). Parrotfish numerical density and biomass was mostly correlated with habitat complexity such as rugosity index and hole density.

Parrotfish numerical density in the Caribbean, Antigua, St. Lucia and SVG was positively correlated with rugosity index. Parrotfish numerical density was negatively correlated with the PC1 score in Curaçao (Table 2.3; Figure 2.7). Parrotfish numerical density had a positive correlation with hole density in the Dominican Republic. No significant relationship between parrotfish numerical density and benthic habitat was found in Barbados, Bonaire or Jamaica.

Parrotfish biomass was negatively correlated with the PC1 score in Curaçao and the Dominican Republic (Table 2.3). Parrotfish biomass was negatively correlated with rugosity index in Bonaire and positively correlated in Curaçao. Biomass was negatively correlated with hole mean size in Curaçao. Biomass was negatively correlated with hole density in Bonaire and Curaçao and positively correlated in the St. Lucia, and at the Caribbean. No significant relationship between parrotfish biomass and benthic habitat was found in Antigua, Barbados, Jamaica, or SVG (Table 2.3).

Table 2.3 Output from the multiple linear regression model between parrotfish numerical density, biomass and benthic habitat in eight countries and at the regional scale. "-" means no significant predictors.

Response	Group	Predictor	Slope	SE	t	p	R^2
Numerical density	Caribbean	Rugosity index	1.072	0.336	3.193	0.002	0.14
	Antigua	Rugosity index	2.605	0.936	2.782	0.049	0.87
	Barbados	-					
	Bonaire	-					
	Curaçao	PC1	-1.976	0.354	-5.580	0.001	0.87
	Dominican Rep	Hole density	0.673	0.307	2.195	0.047	0.27
	Jamaica	-					
	St. Lucia	Rugosity index	1.307	0.468	2.790	0.039	0.62
	SVG	Rugosity index	4.735	1.300	3.641	0.003	0.70
Biomass	Caribbean	Hole density	1.769	0.498	3.550	0.001	0.27
	Antigua	-					
	Barbados	-					
	Bonaire	Rugosity index	-4.182	0.865	-4.837	0.040	0.95
		Hole density	-1.859	0.385	-4.834	0.040	0.95
	Curaçao	PC1	-3.687	0.515	-7.155	0.000	0.98
		Rugosity index	6.629	1.050	6.312	0.008	0.98
		Hole mean size	-4.639	1.132	-4.097	0.026	0.98
		Hole density	-3.503	0.463	-7.568	0.005	0.98
	Dominican Rep	PC1	-3.219	1.185	-2.717	0.019	0.66
	Jamaica	-					
	St. Lucia	Hole density	6.634	1.272	5.216	0.020	0.82
	SVG	-					

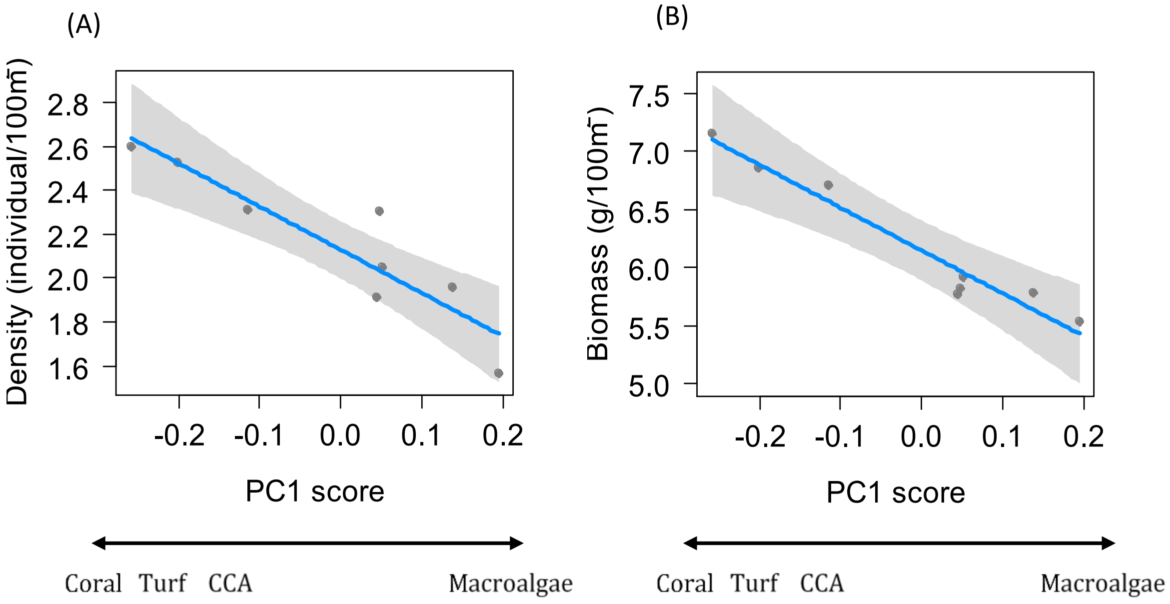

Figure 2.7 Parrotfish numerical abundance and biomass against PC1 score. (A) parrotfish numerical density in Curaçao, and (B) parrotfish biomass in Curaçao. Grey area indicates 95% confident interval (ci). The scale below figure (C) represents PC1 benthic cover loadings.

Scarus numerical density had a positive relationship with the PC1 score in Curaçao (Table 2.4). *Scarus* numerical density was positively correlated with rugosity index in Antigua, St. Lucia and SVG. There was a positive correlation with hole density in the Caribbean and St. Lucia. No significant relationship between *Scarus* numerical density and benthic habitat was found in Barbados, Bonaire, Dominican Republic or Jamaica (Table 2.4).

Scarus biomass was negatively correlated with the PC1 score in Curaçao and Dominican Republic, but positively correlated with the PC1 score in Barbados (Table 2.4). *Scarus* biomass was negatively correlated with hole mean size in Bonaire and Curaçao and positively correlated across all the Caribbean sites. *Scarus* biomass was negatively correlated with hole density in Bonaire and Curaçao and positively correlated in the whole Caribbean and St. Lucia. *Scarus* biomass was negatively correlated with the rugosity index in Bonaire and positively related in Curaçao. No significant relationship between *Scarus* biomass and benthic habitat was found in Antigua, Barbados, Jamaica or SVG (Table 2.4).

Scarus numerical density and biomass were mostly related to habitat complexity. *Scarus* numerical density and biomass showed a similar number of countries with significant relationships with habitat variables (Table 2.4).

Table 2.4 Output from the multiple linear regression model between *Scarus* numerical density and biomass and benthic habitat in eight countries and at regional scale. “-“ means no significant predictors.

Response	Group	Predictor	Slope	SE	t	p	R2
Numerical density	Caribbean	Hole density	0.724	0.242	2.996	0.004	0.30
	Antigua	Rugosity index	7.873	2.056	3.830	0.019	0.90
	Barbados	-					
	Bonaire	-					
	Curaçao	PC1	-2.443	0.524	-4.659	0.003	0.78
	Dominican Rep	-					
	Jamaica	-					
	St. Lucia	Rugosity index	1.882	0.499	3.772	0.020	0.94
		Hole density	0.805	0.252	3.199	0.033	0.94
	SVG	Rugosity index	3.237	1.141	2.836	0.015	0.80
Biomass	Caribbean	Hole mean size	5.292	1.507	3.512	0.001	0.30
		Hole density	2.144	0.569	3.768	0.000	0.30
	Antigua	-					
	Barbados	-					
	Bonaire	Rugosity index	-7.461	0.819	-9.106	0.003	0.98
		Hole mean size	-5.382	0.983	-5.474	0.012	0.98
		Hole density	-2.733	0.355	-7.706	0.005	0.98
	Curaçao	PC1	-5.339	0.784	-6.807	0.006	0.97
		Rugosity index	6.453	1.599	4.037	0.027	0.97
		Hole mean size	-7.149	1.724	-4.148	0.025	0.97
		Hole density	-4.057	0.705	-5.759	0.010	0.97
	Dominican Rep	PC1	-5.001	1.961	-2.554	0.024	0.33
	Jamaica	-					
	St. Lucia	Hole density	3.030	0.840	3.606	0.011	0.68
	SVG	-					

Multiple linear regression showed *Sparisoma* numerical density to be negatively correlated with the PC1 score in Curaçao (Table 2.5). *Sparisoma* numerical density was positively correlated with hole mean size in Antigua. *Sparisoma* numerical density had a positive correlation with rugosity index in SVG. No significant relationship was found between *Sparisoma* numerical density and benthic habitat in Barbados, Bonaire, Dominican Republic, St. Lucia, Jamaica or the Caribbean (Table 2.5).

Table 2.5 Output from the multiple linear regression model between *Sparisoma* numerical density and biomass and benthic habitat in eight countries and at regional scale. “-“ means no significant predictors.

Response	Group	Predictor	Slope	SE	t	p	R^2
Numerical density	Caribbean	-					
	Antigua	Hole mean size	4.123	1.388	2.971	0.031	0.69
	Barbados	-					
	Bonaire	-					
	Curaçao	PC1	-0.839	0.287	-2.924	0.043	0.82
	Dominican Rep	-					
	Jamaica	-					
	St. Lucia	-					
	SVG	Rugosity index	3.821	1.515	2.521	0.027	0.43
Biomass	Caribbean	Hole density	1.566	0.395	3.963	0.000	0.25
	Antigua	-					
	Barbados	-					
	Bonaire	-					
	Curaçao	Rugosity index	4.911	1.704	2.881	0.035	0.65
	Dominican Rep	PC1	-2.079	0.862	-2.414	0.033	0.68
		Hole density	1.555	0.574	2.706	0.019	0.68
	Jamaica	-					
	St. Lucia	Hole density	7.067	1.339	5.277	0.002	0.82
	SVG	-					

Sparisoma biomass was negatively correlated with the PC1 score at Dominican Republic (Table 2.5), being positively correlated with rugosity index in Curacao and with hole density in the Dominican Republic, St. Lucia, and the Caribbean. No significant relationship was found between *Sparisoma* biomass and benthic habitat in Antigua, Barbados, Bonaire, Jamaica or SVG. *Sparisoma* biomass was detecting higher number of countries which have significant relationship with habitat variable than those of numerical density (Table 2.5).

2.3.2 Relationships between parrotfish numerical abundance and habitat variables in the different size classes

Parrotfish numerical density relationships with benthic habitat varied across the different size classes (Table 2.6). Parrotfish, *Scarus* and *Sparisoma* numerical density in most size classes were positively related to habitat complexity. Small sized parrotfish numerical density was positively related with the rugosity index. Medium-size parrotfish numerical density was correlated significantly with the PC1 score and rugosity index. Parrotfish numerical density in the 11-20 cm size class was negatively correlated with the PC1 score. Parrotfish numerical density in the 21-30 cm and >30 cm size class showed a positive relationship with the hole density.

Scarus numerical density was correlated with habitat complexity in all size classes (Table 2.6). Small *Scarus* (0-10 cm) numerical density was positively correlated with the rugosity index and hole density. Medium *Scarus* (11-20cm) numerical density was positively correlated with the rugosity index and PC1. In the 21-30 cm size class, *Scarus* numerical density was positively related with hole density. *Scarus* numerical density in the > 30 cm size had a significant relationship with hole mean size.

Small *Sparisoma* numerical density was positively correlated with rugosity index, while for the 11-20 cm size class numerical density was negatively correlated with the PC1 score. In the 21-30 cm size class, *Sparisoma* numerical density was positively related with PC1 and hole density. Numerical density of *Sparisoma* > 30 cm exhibited a positive relationship with hole density (Table 2.6).

Table 2.6 Linear mixed effect model results for parrotfish numerical density versus benthic habitat in the different class sizes. Country was used as random effect in this model.

Group	Size (cm)	Predictor	Slope	SE	t	p	$R_{2\ conditional}$	$R_{2\ marginal}$
Parrotfish	0-10	Rugosity index	0.620	0.268	2.315	0.023	0.03	0.58
	11-20	PC1	-0.494	0.245	-2.011	0.048	0.06	0.30
	21-30	Hole density	0.276	0.094	2.929	0.005	0.17	0.30
	More than 30 cm	Hole density	0.418	0.148	2.823	0.006	0.09	0.48
Scarus	0-10	Rugosity index	0.998	0.383	2.578	0.012	0.22	0.45
		Hole density	0.526	0.191	2.751	0.008		
	11-20	PC1	-0.412	0.182	-2.265	0.027	0.30	0.49
		Rugosity index	0.931	0.321	2.905	0.005		
	21-30	Hole density	0.587	0.142	4.134	0.001	0.20	0.38
	More than 30 cm	Hole mean size	0.717	0.317	2.259	0.027	0.03	0.56
Sparisoma	0-10	Rugosity index	0.447	0.173	2.591	0.012	0.04	0.56
	11-20	PC1	-0.557	0.151	-3.691	0.000	0.15	0.50
	21-30	PC1	-0.242	0.113	-2.135	0.036	0.19	0.29
		Hole density	0.263	0.092	2.844	0.006		
	More than 30 cm	Hole density	0.313	0.141	2.228	0.029	0.08	0.40

2.4 Discussion

2.4.1 Relationships between parrotfish abundance and habitat variables

The density and biomass of *Scarus* and *Sparisoma* parrotfish genera in the Caribbean mostly showed a stronger correlation with the complexity of the benthic habitat than with benthic habitat cover. These findings are consistent with evidence from other studies. For example coral reef rugosity, the size of holes, and hole density were related to the abundance of fish in Hawaii (Friedlander and Parrish, 1998), and there are many reports indicating that fish abundance and biomass are associated with habitat complexity (Hixon and Beets, 1989; Friedlander and Parrish, 1998; Gratwicke and Speight, 2005b; Chong-Seng *et al.*, 2012; Bozec *et al.*, 2013). However, the results might be affected by other factors that are not included in the analysis such as fishing pressure and catastrophic events (i.e. hurricanes). Fishing pressure is known as one of the factors that reduce the abundance and biomass of fish (Hawkins and Roberts, 2004a; Valles and Oxenford, 2014).

The lack of significant relationships between parrotfish abundance and habitat cover may be due to the specific condition of the coral reefs in most places in the Caribbean. Parrotfish at La Parguera, Puerto Rico are known to prefer sites with both high rugosity and high coral cover (Tzadik and Appeldorn, 2013). However, at the present time, coral cover on reefs in the Caribbean is low (Gardner *et al.*, 2003; Edmunds and Elahi, 2007; Alvarez-Filip *et al.*, 2013; Perry *et al.*, 2013) and tends to be relatively uniform (Gardner *et al.*, 2003; Burkepile *et al.*, 2013; Jackson *et al.*, 2014). This could mean that the differences between sites are small, so small in fact that they do not reach thresholds where they would have a significant effect on fish abundance. The PCA results on benthic cover indicate that habitat cover across sites within countries was mostly similar (Figure 2.4). The abundance of fish in Moorea, French Polynesia gradually decreased when coral cover decreased to approximately 10% and then decreased sharply when coral cover fell below 10% (Holbrook *et al.*, 2008). Data indicate that coral cover in the Caribbean is between 3-47%, however most sites had coral cover >10%. Based on Holbrook *et al.* (2008), it is not surprising that the analysis did not find an association between benthic cover and parrotfish abundance and biomass of fish in most countries. This study's results are also consistent with the findings of Gratwicke and Speight (2005b) that the live coral cover is not a significant predictor for the abundance of fish in Tortola, British Virgin Islands.

The data also indicate that when benthic habitat cover is diverse, it is likely that there will be a correlation between parrotfish abundance and habitat cover. Data indicate that Curaçao had large ranges of 7-45% coral cover and 11-42% macroalgal cover, while other countries had smaller ranges. The gradient from low to relatively high coral cover among sites may explain why there was a relationship between parrotfish abundance and habitat type there. There were a negative relationships between parrotfish abundance and biomass and the PC1 axis (benthic habitat) in Curaçao, where negative values of the PC1 axis represent higher coral cover, while positive values meant a higher macroalgal cover (Figure 2.7). Thus, a negative relationship between the PC1 axis and abundance of parrotfish further indicates the importance of habitat type as well as structure with respect to the abundance of parrotfish. The relationship between parrotfish abundance and PC1 in Curaçao indicates that a relatively high coral cover may play an important role in maintaining the abundance of parrotfish or vice versa.

Although these are not conclusive findings, because the analysis is based on correlations which have yet to be proven to be causal, the results confirm previous evidence that parrotfish are found more easily and in greater abundance at sites with higher coral cover, lower macroalgal cover (Friedlander and Parish, 1998; Gratwicke and Speight, 2005a; Howard et al. 2009; Chong-Seng *et al*., 2012; Tzadik and Appeldorn, 2013), and a complex habitat structure (Tzadik and Appledorn, 2013). However, caution is required in connection with the fact that there may be a reciprocal relationship between the abundance of parrotfish and benthic habitat cover. First, increased coral cover may promote an increase in fish abundance or decreased coral cover may cause a decrease in fish abundance. There have been many studies on these relationships around the world (Syms and Jones, 2000; Pratchett *et al*., 2006; Holbrook *et al*., 2008; Pratchett *et al*., 2011). Second, an increase in the abundance of fish may increase coral cover. This is particularly true for parrotfish (Bellwood *et al*., 2006) which feed on algae, help to reduce macroalgal cover and thereby provide a hard substrate for coral recruitment (Burkepile and Hay, 2006; Mumby and Steneck, 2008). Furthermore, reef resilience increased 6-fold in Belize following parrotfish protection (Mumby *et al*., 2014).

While parrotfish abundance and biomass were associated with habitat complexity in most countries, the particular habitat complexity component varied. Interestingly, the habitat complexity parameters associated with parrotfish abundance were primarily reef rugosity and hole density, supporting results of Friedlander and Parrish (1998) on herbivorous fish biomass in Hawaii and Gratwicke and Speight (2005a) on artificial reefs in Tortola, British Virgin Islands, where fish abundance was significantly affected by hole size but was not significantly correlated to rugosity. Friedlander and Parrish (1998) also found a significant effect of hole size.

This study's results indicate that in most countries the abundance and biomass of parrotfish was significantly associated with rugosity, which is consistent with other studies within the region and elsewhere (Tzadik and Appeldorn, 2009; Bozec *et al.*, 2013; Hernandez-Landa *et al.*, 2015). In contrast, others found no relationships between reef rugosity and fish abundance (Gratwicke and Speight, 2005a; Nemeth and Appeldoorn, 2009) and this study's results also show that the abundance of *Scarus* was not associated with reef rugosity or any benthic habitat in Barbados, Bonaire and Jamaica (Table 2.3). The relationships between fish abundance and reef rugosity appears to be influenced by the size composition in each country, in which country that have the relationships such as Antigua, St. Lucia and SVG were dominated by small size parrotfish, mostly <20cm (Figure 2.3).

The differences in the relationship between the fish abundance and reef rugosity for *Sparisoma* and *Scarus*, may be explained by one or all of the following reasons: (1) different size classes may have different relationships with rugosity. (2) The low rugosity gradient among sites (1.2 to 1.7) may mean that the variability might not be sufficient to enable the detection of differences between sites. (3) Caution needs to be used because of differences in the shape and habitat function of different coral growth forms. The results show that the abundance of the small size class parrotfish had a significant relationship with rugosity, whereas in the larger fish abundance was associated with hole density (Table 2. 6). When *Scarus* and *Sparisoma* are not grouped by size, hole density is the only habitat variable that had significant relationship with overall parrotfish abundance. This implies that generalizing the parrotfish regardless of their size could result in inaccuracies in the detection of habitat factors predicting parrotfish abundance. Luckhurst and Luckhurst (1978) suggest that the branching coral growth forms provide more space for the protection of fish compared to rounded (glomerate) shapes, generally referred to as massive corals. Thus, sites with high rugosity may not necessarily have a particularly high abundance of fish, depending on the dominant type of coral growth form. To answer this question, further research is needed to compare the relationship between rugosity and the abundance of reef fish for each type of coral growth.

In general, there are similar trends in correlation with benthic habitat variables for parrotfish abundance and parrotfish biomass at regional scale in which they were correlated with reef complexity. However, there were differences in the way abundance and biomass respectively were correlated with habitat variables at the country scale. At a genus level, the present results indicate that *Scarus* abundance tended to be more closely related to habitat than biomass. In contrast, for *Sparisoma*, habitat was a better predictor of biomass than abundance. The genus *Sparisoma* is largely composed of bigger fish, while *Scarus* mostly consists of smaller fish (Bozec *et al.*, 2013). Fish biomass was obtained using a formula which involves multiplying the numerical density of fish with their total body length. Size describes the variation in size structure (Howard *et al.*, 2009), and it is not surprising that the use of *Sparisoma* biomass as the dependent variable provides more power in uncovering relationships with habitat variables and complexity. Meanwhile, species in the genus *Scarus* with a variety of smaller body sizes (mostly <20cm) did not contribute much to the total biomass, so the power to detect correlations is lower than using fish abundance.

This study findings support the conclusions of Bianchi and Hoisaeter (1992) that there may be significant differences in the patterns of abundance and biomass when individual fish sizes are significantly different. Thus, the findings indicate that fish biomass may be a good indicator if the body size of fish recorded during the survey varied greatly, but less useful if the parrotfish community consists largely of smaller fish.

Habitat factors that influence parrotfish abundance and biomass also differed between its genera. For example, *Scarus* abundance in Antigua was positively associated with rugosity index, while *Sparisoma* abundance correlated with hole size. This may be due to the composition of the species that dominate in Antigua. The genus *Scarus* in Antigua was dominated by *Sc. iserti* and *Sc. taeniopterus*, *Sparisoma* was dominated by *Sp. aurofrenatum* and *Sp. viride*. The *Scarus* species have small body size, maximum size of *Sc. iserti* and *Sc. taeniopterus* being 35cm (Lieske and Myers, 1994). This small size makes them very vulnerable to predation and thus they require a high rugosity for refuge.

Reef sites that have high rugosity are complex habitats, with a high availability of food such as suitable algae (Nemeth and Appeldorn, 2009). *Sc. iserti* also has a small foraging range (Mumby and Wabnitz, 2002), thus rugose reefs should help protect it from predation and ensure the availability of food. Meanwhile, the species in the genus *Sparisoma* have larger maximum sizes (Robins and Ray, 1986; Randall, 1978) and larger territories (Mumby and Wabnitz, 2002), enabling them to be more flexible in foraging, which in turn reduces dependency on rugosity. However, because of the threat of predators or fishing (Nemeth and Appeldorn, 2009), fish such as *Sp. viride* still benefit from refuge habitat, especially in inactive mode during evening (Sheppard, 1994), and thus seem to require holes in the coral reef.

The effect of fishing may mask potential relationships between fish abundance and benthic habitat. This is corroborated by Barbados and Bonaire (low fishing pressure) and Jamaica (high fishing pressure) which lacked such relationships. Possible relationships between fish abundance and fishing pressure gradient will be further investigated in Chapter 3. Similar level of coral cover and rugosity in Bonaire (high coral cover and rugosity) and Jamaica (low cover and rugosity) might also mask potential relationships.

The results also indicate that each parrotfish species had specific characteristics in relation to habitat variables. The abundance of *Sc. taeniopterus* was correlated with hole size, *Sc. iserti* abundance was positively associated with benthic habitat cover and rugosity, the abundance of *Sc. vetula* was associated with rugosity, *Sp. viride* abundance was correlated with hole density, but there was no significant relationship between the abundance of *Sp. aurofrenatum* and any habitat variable (Appendix 4). The results imply that species or genus specific discrimination may be needed when analysing relationships between parrotfish abundance and benthic habitat to avoid simplification and generalization as parrotfish vary in their responses to benthic habitat condition.

Parrotfish abundance and biomass and their relationship with benthic habitat at the regional scale are simply based on aggregate country-level data. Although not conclusive, the present findings suggest in particular that the abundance and biomass of parrotfish in the Caribbean were significantly correlated with rugosity, hole density and benthic habitat cover. However, caution is necessary when scaling down, as present results show there were differences between and within countries, that may be caused at least in part by parrotfish fish species composition in each country or site.

A major limitation of this study is that the survey was conducted over 10 months, which means that the data from each country were not collected in the same season. Thus, there is the possibility of temporal variation that is not taken into account in the analysis. This could be a significant confounding factor, for example Kopp *et al.* (2012) state that the highest herbivorous fish abundance and biomass in Guadeloupe were found during the rainy season. To limit the confounding effect of seasonal variations, simultaneous surveys would need to be done, which would require very considerable resources.

2.4.2 Relationships between parrotfish numerical abundance and habitat variables in the different size classes

The results on the relationship between the abundance of parrotfish and benthic habitat variables for different size classes showed that parrotfish have different relationships with their habitat according to body size. Parrotfish abundance was mainly associated with coral reef rugosity at a smaller body size (<20cm) while the abundance of larger sized parrotfish (> 20 cm) was predominantly associated with the density of holes. The findings are also corroborated by the Hixon and Beets (1989) experiment in which when hole size was constant, reefs with more holes supported more fish than reefs with fewer holes. Although parrotfish abundance was significantly associated with coral rugosity for *Sc. iserti* with small body size (similar to Bozec *et al.*, 2013), the results indicate that coral rugosity may not always provide more protection for parrotfish, especially for larger fish. Thus, the abundance of parrotfish with a larger body size could be better predicted by other habitat variables such as the density of holes that provide protection for fish.

Chapter 3. Relationships between fishing pressure and Caribbean parrotfish density

3.1 Introduction

Reef fish assemblages may be influenced by many factors, including biotic (e.g. predation, competition, recruitment), abiotic (e.g. depth, water quality) and historical (e.g. fishing pressure, hurricanes) factors (Adjeroud *et al*., 1998). Fishing clearly has a major influence on fish stocks and communities. For example, predation can have a considerable influence on prey community structure by altering survivorship and resultant density (DeMartini *et al.*, 2008), and the depletion of predatory fishes, often considered as prime target food fishes, can lead to an increase in herbivorous fish such as parrotfishes (Shurin *et al.*, 2002), at least in the short term.

The direct and indirect impacts of the increase in human population, in particular the growing demand for food, as well as various aspects of climate change pose threats to the abundance of parrotfishes (Scarinae), the main coral reef grazers (Hughes *et al*., 2003). Fishing is considered a major threat to parrotfish populations or stocks, and in particular overfishing of parrotfishes can lead to the impairment or loss of their functional roles, with negative impacts on tropical coastal ecosystem functions (Bellwood *et al.*, 2011).

Parrotfish have increasingly become a food fisheries target in all tropical oceans and the growing human population will likely further depress parrotfish abundances. In the Solomon Islands (Pacific Ocean) and Zanzibar (Indian Ocean), the increase in fishing pressure on parrotfish has been linked to the decline in populations of many traditional target species (Aswani and Sabetian, 2010; Thyresson *et al.*, 2011). Parrotfish are now the most common group of fishes caught in the multi-species fishery in the Western Indian Ocean (McClanahan and Mangi, 2004), and a rapid shift to smaller herbivorous fish has occurred in the Caribbean due to the overfishing of larger individuals (Mumby *et al.*, 2013).

Heavy fishing pressure can affect both overall fish biomass and the average size of individuals, and it is now widely accepted that excessive fishing pressure tends to reduce average parrotfish size through extraction of larger individuals. Richards *et al.* (2012) found that the biomass of large-bodied fish in the Mariana Archipelago was greater in areas with lower human population density, although the actual role of the human population or the mechanisms by which fish biomass was affected are unclear, since the causal mechanisms (e.g. fishing or other anthropogenic impacts) underlying the observed trends were not explained. In the Caribbean, overfishing, including excessive harvesting by artisanal fishers, is strongly correlated with reduction in parrotfish body-size, and in particular a reduction in the average size of terminal males (Hawkins and Roberts, 2004a&b; Valles and Oxenford, 2014). Indeed the average (assemblage level) parrotfish size has been proposed as a possible indicator of fishing effects under the conditions typical of most Caribbean shallow reefs (Valles and Oxenford, 2014).

There are at least two commonly used indices of fishing pressure. One of these is based on the number of fishers or fishing boats per unit area of coral reefs (Jennings *et al.*, 1995; Hawkins and Roberts, 2004a; Friedlander and Brown, 2004; Campbell and Pardede, 2006; Tuya *et al.*, 2006). The other index is based on the average human population density within a certain radius of the reef site surveyed (Jennings and Polunin, 1997; Dulvy *et al.*, 2004; Stallings, 2009; Wilson *et al.*, 2010; Valles and Oxenford, 2014). Both indices are widely considered capable of portraying fishing pressure and its relationship with fish abundance or biomass.

However, there is a lack of information on how well each of these fishing pressure indices relates to parrotfish abundance. While Hawkins and Roberts (2004a) and Valles and Oxenford (2014) both worked on parrotfish abundance, other differences in the methodologies used make it difficult to compare the indices and draw any conclusions regarding their respective merits. The uniform data sampling methods and personnel used in this study will allow us to compare the relationships between fisher density, human population size, and parrotfish abundance.

Marine protected areas (MPAs) tend to increase the abundance of marine fish (Roberts, 1995; Barrets *et al.*, 2007). After four years of protection from fishing, reef fish abundance, size, and biomass were greater in both the Saba Marine Park and Hol Chan Marine Reserve (Belize) than outside these MPAs. In each of the MPAs, the biomass of non-cryptic demersal fish, including parrotfishes, was twice that recorded at fished sites (Polunin and Roberts, 1993; Roberts *et al.*, 2001). Hughes *et al.* (2007a) suggested that the protection afforded by an MPA should increase parrotfish biomass as long as predation inside the MPA is lower than fishing mortality outside the MPA. Marine reserves may also have a negative impact on parrotfish body size due to an increase in the abundance of large predatory fish (Mumby *et al.*, 2006). Small-bodied parrotfishes (e.g. *Sc. iserti*) were smaller inside the Exuma Cays Land and Sea Park, Bahama, but there was no discernible difference in density within and outside the MPA.

While large-bodied parrotfishes did not differ in size, their density was double inside the reserve (Mumby *et al.*, 2006). The effect of MPAs on parrotfish assemblages needs further investigation. The present study will allow us to understand how parrotfish abundance and biomass vary between fished areas and unfished areas, particularly MPAs at large scale.

The impact of fishing pressure on fish assemblages can be assessed using the Abundance Biomass Comparison (ABC) method. Originally proposed by Warwick (1986) to detect the impact of pollution on macrobenthic communities, it was subsequently improved to detect effects of other disturbances, either physical or biological, on benthic invertebrates (Warwick *et al.,* 1987). The ABC method was also successfully applied to investigate disturbance on fish communities in Namibia (Bianchi *et al*., 2001), in the Bay of Biscay, France (Blanchard *et al*., 2004), and in South Africa (Yemane *et al*., 2005). The method has yet to be applied for assessing effects of fishing on reef fishes, but successfully applied on demersal fish. The applicability of ABC method to assess effects of fishing on parrotfish is needed. In the ABC plot, if the biomass curve is above the abundance curve this implies that the community is in an 'undisturbed' state. Conversely, if the abundance curve is above the biomass curve, this indicates that communities are in a 'disturbed' condition (Figure 3.1). The difference between the two curves is given by the W-index, a negative sign indicating that abundance curve lies above the biomass curve.

Despite considerable evidence that fishing pressure has a substantial impact on parrotfish populations, many questions remain unanswered. In view of the increasing threats from fishing and human population growth there is a need to determine how fishing pressure affects parrotfish abundance, biomass and size in the Caribbean. In particular, it is important to understand how these variables are related, as this will affect stock predictions and fishery management options.

The objectives of this chapter are to: (1) Compare relationships between fisher density, human population size and parrotfish abundance; (2) Determine how the W-index in the ABC method relates to, and might thus be used to predict fishing pressure; and (3) Assess effects of marine protected areas (MPAs) on parrotfish abundance and biomass.

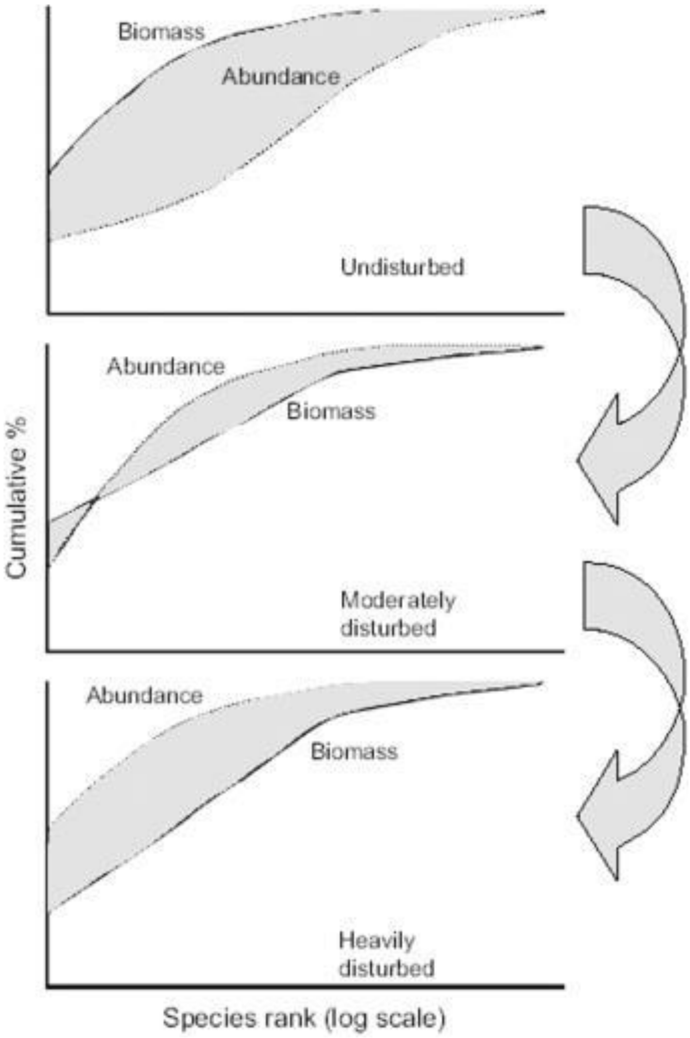

Figure 3.1 ABC plot showing various curves of abundance, biomass and community status (Yamane et al., 2005).

3.2 Method

Fish surveys were conducted in 8 Caribbean countries (Antigua, Bonaire, Barbados, Curaçao, Dominican Republic, Jamaica, St. Lucia and St. Vincent and Grenadines (SVG)) by the EU FORCE Project team. The methods used during the fish survey have been described in detail in Chapter 2.

3.2.1 Fishing Pressure

Fishing pressure was determined based on the number of fishers, the extent of the fishing area and the density of the human population; site within or outside MPA was taken into account.

Number of fishers

The number of fishers was determined from various sources, such as reports published by each country and research reports (Appendix 5). The number of fishers operating in each surveyed site was estimated from data from the coastal districts or towns in close proximity to the site, with a maximum distance of approximately 10km from it. Most fishers in the Caribbean are artisanal, operating close to shore (Dunn *et al.*, 2010). For example, reef fishers in Barbados operate on reefs with a maximum depth of 30m and a maximum distance of 5.3 nautical miles from the coast (Salas *et al.*, 2011). Therefore, the radius of 10km used in this study to calculate the human population and number of fishers affecting reef fish populations is appropriate. Some surveyed sites were very close to each other; hence, these had the same number of fishers and reef area. Due to difficulties in obtaining data, and in particular the frequent lack of recent data on the number of fishers, not all data were derived from the same year. However, in some countries the annual reports show that there were only small changes in the number of fishers over several years prior to the survey.

Fishing area

The reef area (in hectares), calculated within a 10km radius of each surveyed site, was obtained from the Global Distribution of Coral Reefs 2010 dataset produced by the United Nation Environmental Programme (UNEP) (http://data.unep-wcmc.org/datasets/13). This dataset was derived from satellite imagery data. This dataset provides estimates of coral reef coverage worldwide in the form of a polygon shaped layer. Reef area was calculated to the nearest hectare (ha) (Appendix 5) using ArcGIS v.10.1 software.

Human Population

The human population index was estimated by Iliana Chollett, based on human population size within a 10km radius of each reef site surveyed. To calculate the index, human population density was obtained from the Gridded Population of the World V.3, available at the Socio-economic Data and Application Center (SEDAC) of the University of Columbia (http://sedac.ciesin.columbia.edu/data/set/gpw-v3-population-density-future-estimates). Human population size was obtained through multiplying the human population density by the total land area within a 10km radius. Human population data for 2010 were used in these calculations, as fish surveys were conducted during that year. Human population size has been shown to correlate well with metrics of nominal fishing effort (Stewart *et al*., 2010). To further assess effect of of human population, human population size from the different radii (2 and 5km) were used. To further validate the effect, 2 and 5km coastal buffer were used to calculate human population size (Figure 3.2).

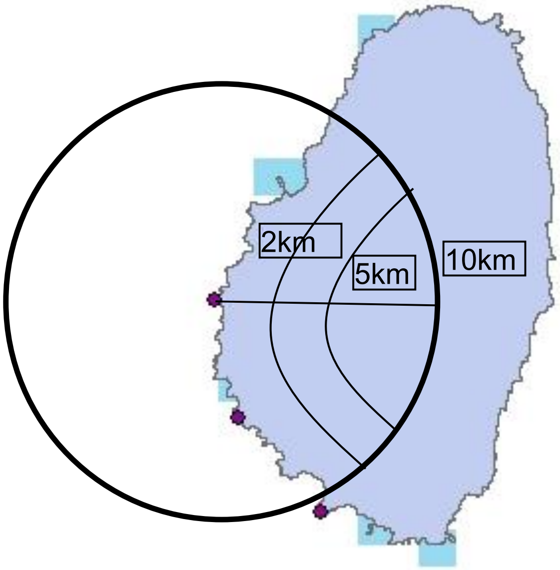

Figure 3.2 Illustration of radius and coastal buffer to calculate human population size showing 10km radius from site and 2 and 5km coastal buffer. Red dot represents transect site.

Marine Protected Areas

MPA data were obtained from the World Database of Protected Areas compiled by UNEP (http://protectedplanet.net). The shapefile with coordinates of the surveyed sites was overlaid onto the map of the MPA using ArcGIS v.10.1. The sites were classified as being within an MPA when they were within the boundaries of a legally designated MPA. Proposed MPA sites and the areas outside the legal MPAs were classified as non-protected areas. Due to lack of information on the effectiveness of each MPA, all designated MPAs were assumed to have a significant level of management.

3.2.2 Data Analysis

Fishing index and parrotfish abundance

The Spearman rank correlation test was used to examine potential relationships between human population size and parrotfish abundance and biomass, and to determine whether there was an association between fishing pressure and parrotfish abundance and biomass. The Spearman rank correlation test was used because the data was not normal even after transformation. To minimize the confounding effects of fishing protection (MPA), only data from sites outside the MPAs were used. The classification of the relationship strength was derived using Spearman rank correlation tests as described in Cohen (1988) (Table 3.1). The Spearman rank correlation tests were carried out using the R software (R Core Team, 2013).

Table 3.1 Rule of thumb of the strength of the relationship (Cohen, 1988)

Value of ρ	Strength of relationship
0.5 - 1.0	Strong
0.3 - 0.5	Moderate
0.1 – 0.3	Weak
0.0 – 0.1	None or very weak

MPA and parrotfish abundance

The differences between parrotfish abundance within and outside MPAs were assessed using the two-sample permutation test since data was not normal even after transformation, conducted within the *perm* package (version 1.0-0.0; Fay, 2010) in the R environment (R Core Team, 2013). Prior to the analysis, parrotfish abundance and biomass were fourth-root transformed to reduce the effect of extreme values.

Abundance Biomass Curve and fishing indices

The potential impact of fishing pressure was assessed using the ABC analysis for all sites. The W-index was calculated using equation 3.1. The W-index relationships with fishing index were then examined using the Spearman rank correlation test in the R environment (R Core Team, 2013). Only W-index values from sites outside MPAs were used. In order to determine the status of disturbance in each country, data on parrotfish density and biomass were aggregated at the country level. Trends in the W-index value obtained were assessed through regression with respect to fisher density (fishers/ha of reef) and human population density (human population/ha of reef) at the country level. The ABC plots and the calculation of the W-index were carried out using the *forams* package (version 2.0-4; Aluizio, 2014) in the R environment (R Core Team, 2013).

$$W=\frac{\sum_{i}^{s} 1(\text{Bi-Ai})}{50(\text{S-1})} \text{ .... (Eq. 3.1)}$$

Where W is W-index, Bi is biomass of i species, Ai is abundance of I species and S is the number of species.

3.3 Results

3.3.1 Human population and parrotfish abundance

Parrotfish numerical density had a weak negative correlation with human population size within a 10km radius of the sites (Spearman rank correlation test, ρ = -0.2793, p = 0.0495; Figure 3.3a). In contrast with parrotfish numerical density, parrotfish biomass was not significantly correlated with human population size although it exhibited a negative trend (Spearman rank correlation test, ρ = -0.0575, p = 0.6915; Figure 3.3b).

Scarus numerical density showed no significant relationship (Spearman rank correlation test, ρ = -0.1117, p = 0.4400, Figure 3.3c), while *Sparisoma* numerical density was negatively correlated with human population size (Spearman rank correlation test, ρ = -0.3456, p = 0.0140, Figure 3.3e). *Scarus* and *Sparisoma* biomass showed no significant relationship with human population size (Spearman rank correlation test, ρ = 0.0488, p = 0.7362 (*Scarus*), Figure 3.3d; ρ = -0.1511, p = 0.2950 (*Sparisoma*), Figure 3.3f).

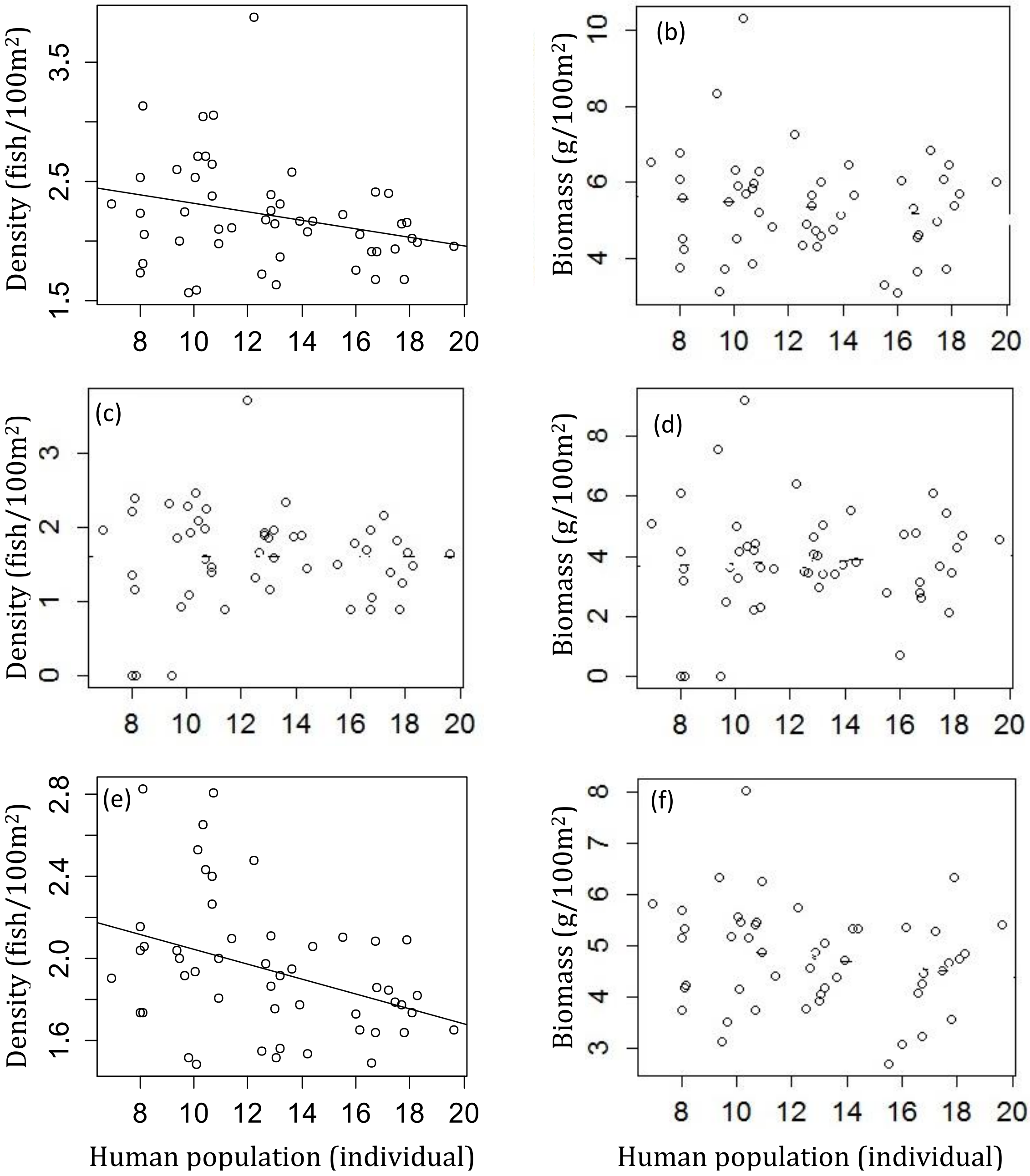

Figure 3.3 Relationships between human population size and parrotfish density (a) and biomass (b), *Scarus* density (c) and biomass (d), *Sparisoma* density (e) and biomass (f) across the Caribbean. Lines were fitted to the data to help visualize trends. Human population size, parrotfish abundance and biomass were fourth-root transformed.

Parrotfish numerical density had a negative correlation with human population size within a 2 and 5km radius of the sites (Spearman rank correlation test, ρ = -0.3056, p = 0.0309 (2km); ρ = -0.3020, p = 0.0330 (5km); Table 3.2). Parrotfish numerical density had a negative correlation with human population size within a 2, 5 and 10km radius of the sites and 5km coastal buffer (Spearman rank correlation test, ρ = -0.3583, p = 0.001 (2km); ρ = -0.3269, p = 0.0192 (5km); ρ = -0.3211, p = 0.0216 (10km); Table 3.3). In contrast with parrotfish numerical density, parrotfish biomass was not significantly correlated with human population size (Table 3.4).

Table 3.2 Correlation between human population size and parrotfish numerical density within various radii from the survey site.

Radius	**Parrotfish**		***Scarus***		***Sparisoma***	
(km)	**ρ**	**p-value**	**ρ**	**p-value**	**ρ**	**p-value**
2	-0.3056	0.0309	-0.1475	0.3068	-0.3415	0.0152
5	-0.3020	0.0330	-0.1250	0.3871	-0.3719	0.0078
10	-0.2793	0.0495	-0.1117	0.4400	-0.3456	0.0140
25	-0.1873	0.1928	-0.0566	0.6962	-0.2737	0.0545

Table 3.3 Correlation between human population size and parrotfish abundance within various radii from survey sites with 5 km coastal buffer.

Radius	**5 km buffer**	
(km)	**ρ**	**p-value**
2	-0.3583	0.0010
5	-0.3269	0.0192
10	-0.3211	0.0216
25	-0.0134	0.9254

Table 3.4 Correlation between human population size and parrotfish biomass within various radii from survey sites.

Radius (km)	**Without buffer**		**5km buffer**	
	ρ	**p-value**	**ρ**	**p-value**
2	-0.2043	0.1504	-0.2031	0.1528
5	-0.2202	0.1204	-0.2332	0.0995
10	-0.1653	0.2462	-0.2291	0.1059
25	-0.2078	0.1434	0.0371	0.9794

3.3.2 Fisher density and parrotfish abundance

Fisher density and parrotfish numerical density exhibited a negative relationship (ρ = -0.3682, p = 0.0080; Figure 3.4a). Similarly, fisher density was significantly correlated with parrotfish biomass (Spearman rank correlation test, ρ = -0.3382, p = 0.0163; Figure 3.4b).

Scarus numerical density showed no significant relationship (Spearman rank correlation test, ρ = -0.2503, p = 0.0796, Figure 3.4c), while *Sparisoma* numerical density was negatively correlated with fisher density (Spearman rank correlation test, ρ = -0.3783, p = 0.0067, Figure 3.4e). *Scarus* and *Sparisoma* biomass showed negative relationships with fisher density (Spearman rank correlation test, ρ = -0.2991, p = 0.0349 (*Scarus*), Figure 3.4d; ρ = -0.3653, p = 0.0091 (*Sparisoma*), Figure 3.4f).

3.3.3 Parrotfish abundance and protection against fishing

Mean parrotfish numerical density was slightly higher at MPA sites than at non-MPA sites but this was not significant (Permutation t-test, Z = 1.0259, p = 0.3049; Figure 3.5a). A significant difference was found between parrotfish biomass within and without the MPAs. Sites within an MPA had significantly higher parrotfish biomass than non-MPA sites (Permutation t-test, Z = 2.2429, p = 0.0059; Figure 3.5b).

Scarus numerical density was significantly different (Permutation t-test, Z = 2.7518, p = 0.0059, Figure 3.5c), while *Sparisoma* numerical density was no different between sites within and those outside MPA (Permutation t-test, Z = -0.8381, p = 0.4020, Figure 3.5e). *Scarus* and *Sparisoma* biomass were significantly different between sites within and outside MPA (Permutation t-test, Z = 2.4301, p = 0.0151 (*Scarus*), Figure 3.5d; Z = 2.1766, p = 0.0295 (*Sparisoma*), Figure 3.5f).

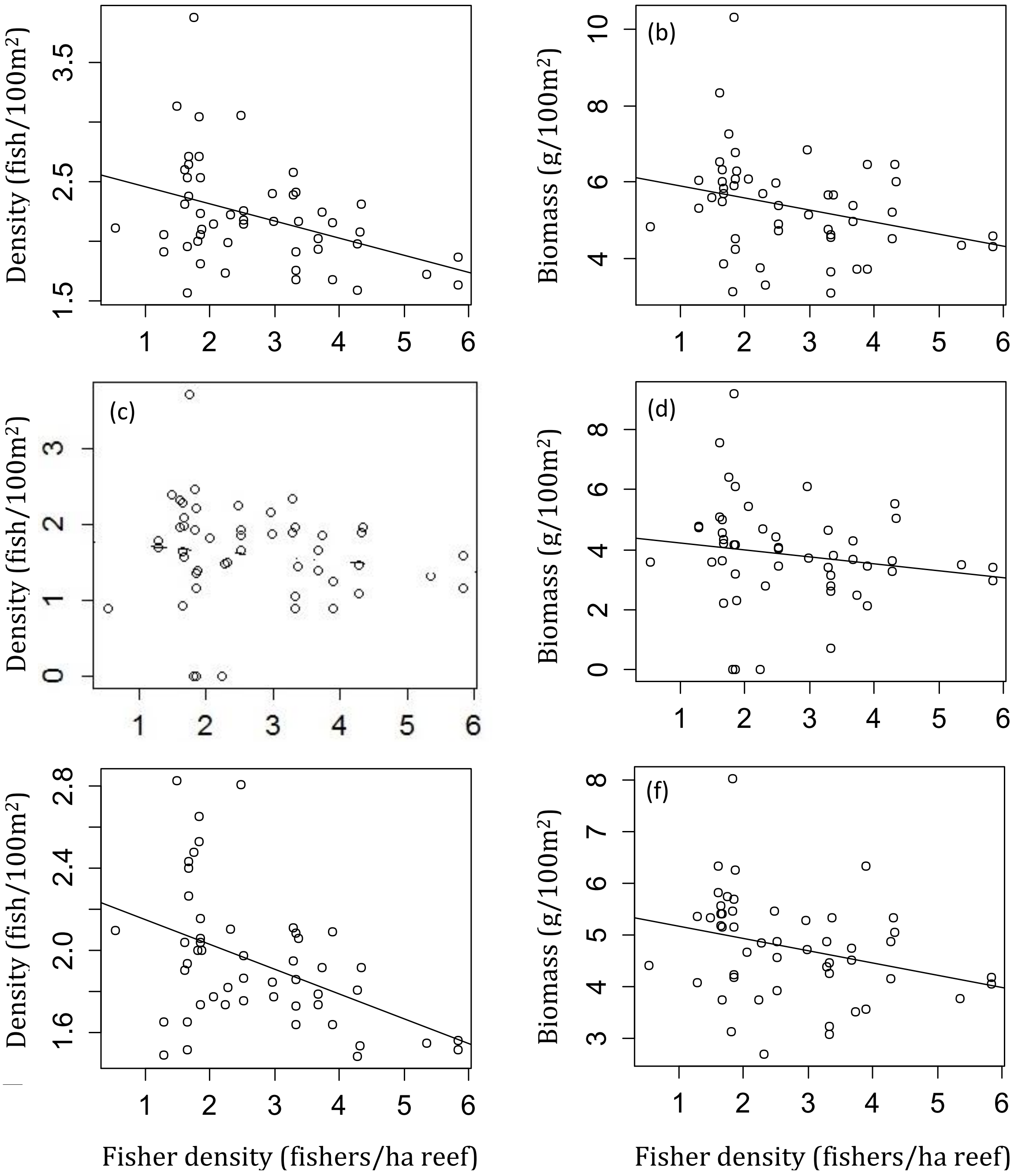

Figure 3.4 Correlation of parrotfish density (a) and biomass (b), *Scarus* density (c) and biomass (d), *Sparisoma* density (e) and biomass (f) and fisher density across the Caribbean. Lines were fitted to the data to help visualize trends. Fisher density, parrotfish abundance and biomass were fourth-root transformed.

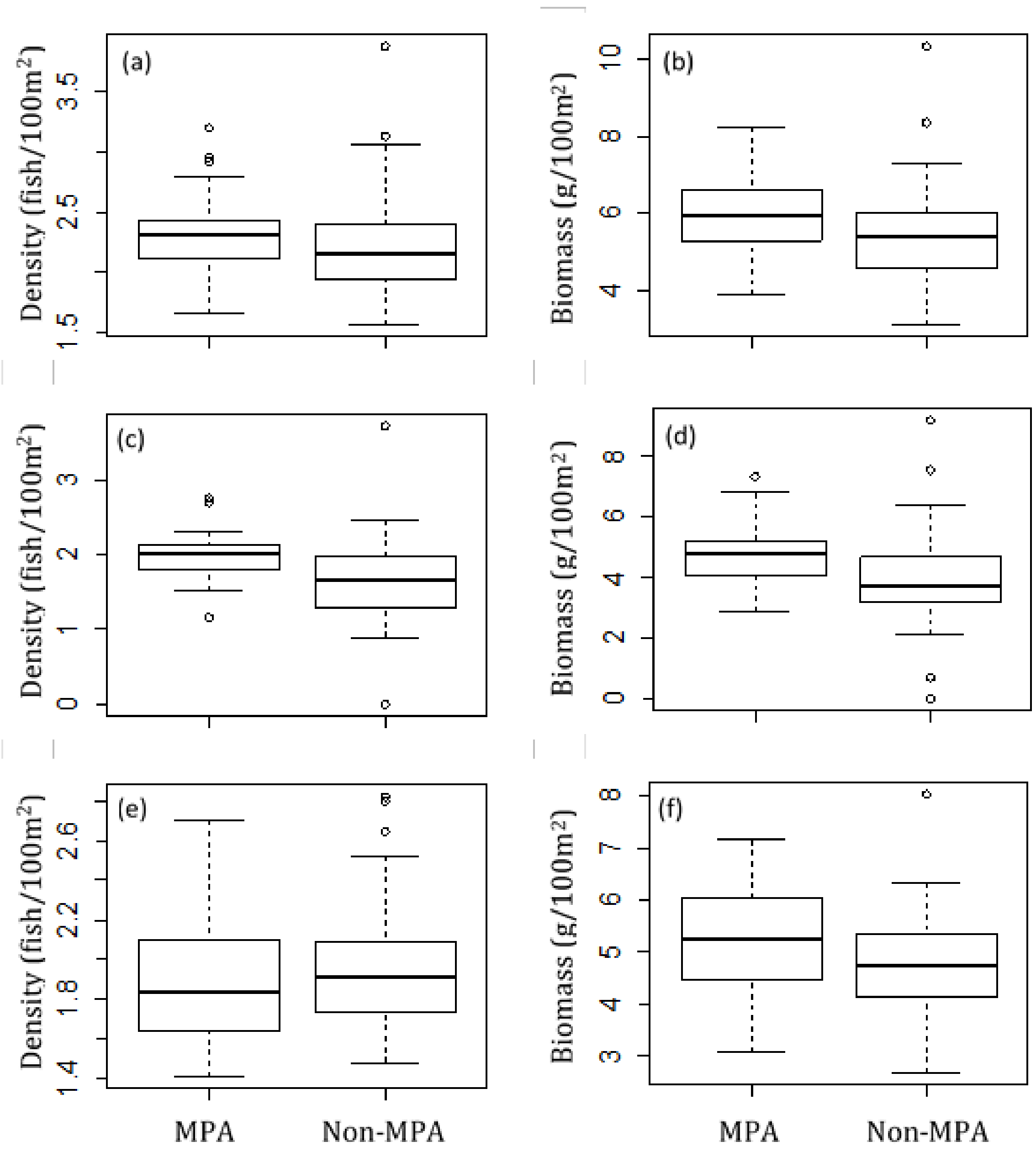

Figure 3.5 Differences between parrotfish density (a) and biomass (b), *Scarus* density (c) and biomass (d), *Sparisoma* density (e) and biomass (f) across the Caribbean within and outside MPA. Parrotfish abundance and biomass have been fourth-root transformed before plotting.

3.3.4 Fishing indices and Abundance Biomass Comparison

The ABC results showed that 61% of the 84 sites surveyed had a positive W-index. Out of 33 MPA sites, 79% had a positive index and 21% a negative W-index value. In contrast, only 49% (25/51) of non-MPA sites surveyed had a positive W-index (Figure 3.6). However no significant relationship was found between human population size and W-index (Spearman rank correlation test, ρ = -0.192, p = 0.178). Similarly, no relationship was found between fisher density and W-index (Spearman rank correlation test, ρ = -0.079, p = 0.583).

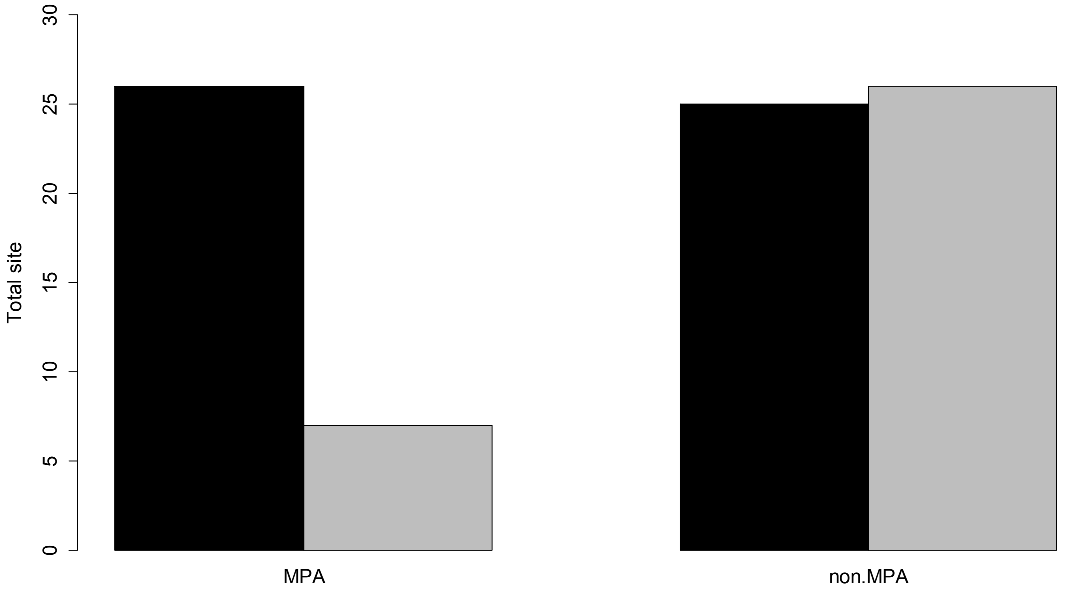

Figure 3.6 Number of MPA and non-MPA sites with positive and negative W-index values. Black bars represent positive W-index values. Grey bars represent negative W-index values.

For Bonaire and Curaçao the biomass curve was above that of abundance, so that both countries had a positive W-index (Figure 3.7c and 3.7d), indicating that the status of parrotfish assemblages in Bonaire and Curaçao could be described as relatively ‘undisturbed’. Meanwhile, SVG had a biomass curve both above and under the abundance curve with a negative W-index, which means that parrotfish assemblages in SVG were moderately ‘disturbed’ (Figure 3.7h). On the other hand, the other five countries had biomass curves beneath the abundance curve with negative W-indices, indicating parrotfish assemblages could be considered to be ‘disturbed’ (Figure 3.7).

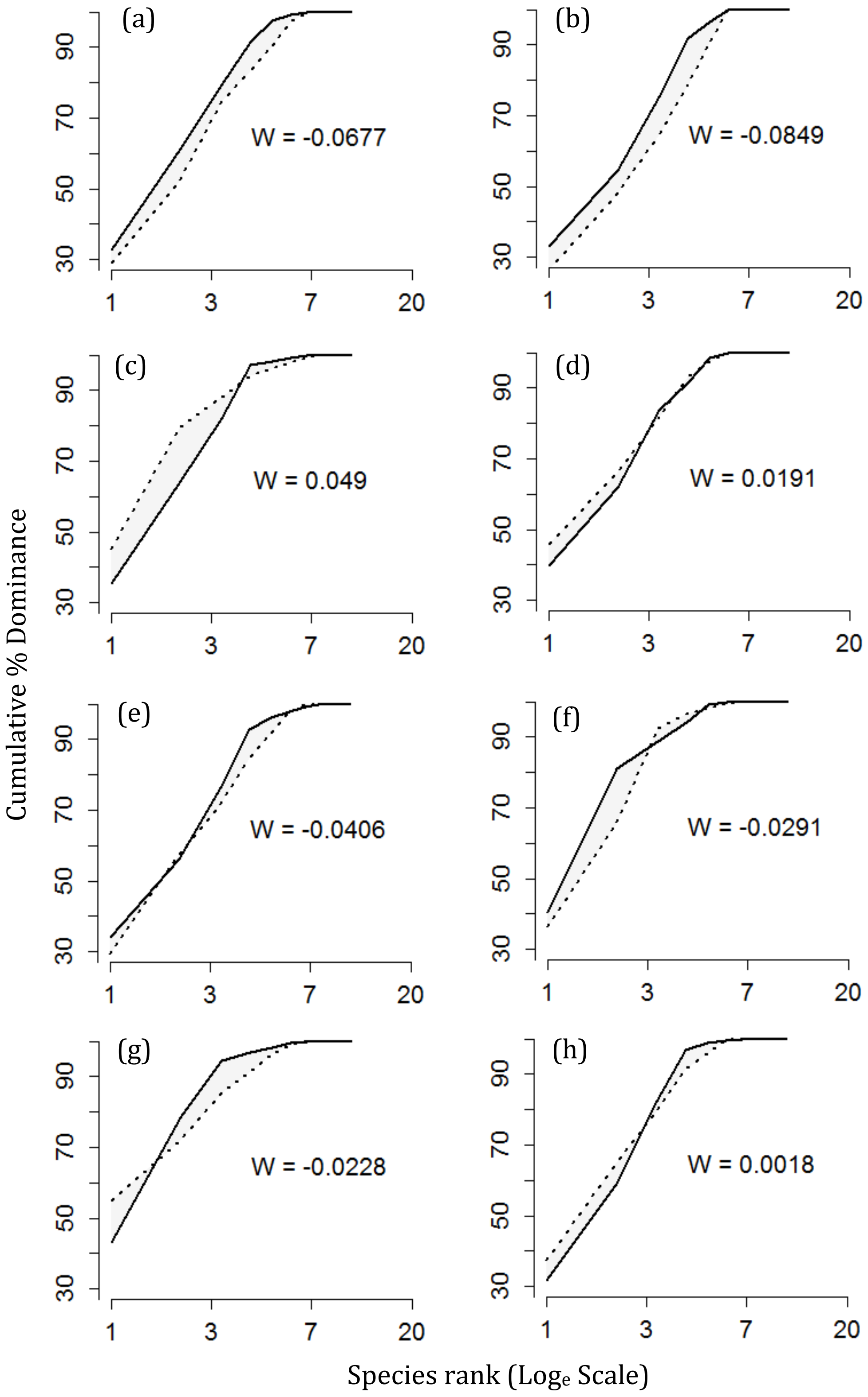

Figure 3.7 ABC curves of parrotfish in the Caribbean. Dashed lines represent parrotfish abundance, while solid lines represent biomass. (a) Antigua, (b) Barbados, (c) Bonaire, (d) Curaçao, (e) Dominican Republic, (f) Jamaica, (g) Saint Lucia, and (h) Saint Vincent and the Grenadines.

A negative relationship was found between fisher density and W-index at the country level (Spearman rank correlation, ρ = -0.857). The value of the W-index decreased exponentially with increasing fisher density (R^2= 0.737; Figure 3.8). A negative slope was found between human population size per ha reef and W-index by country level but the correlation was not significant (Spearman rank correlation, ρ = -0.429). The value of the W-index decreased exponentially with increasing human density (R^2= 0.177; Figure 3.8).

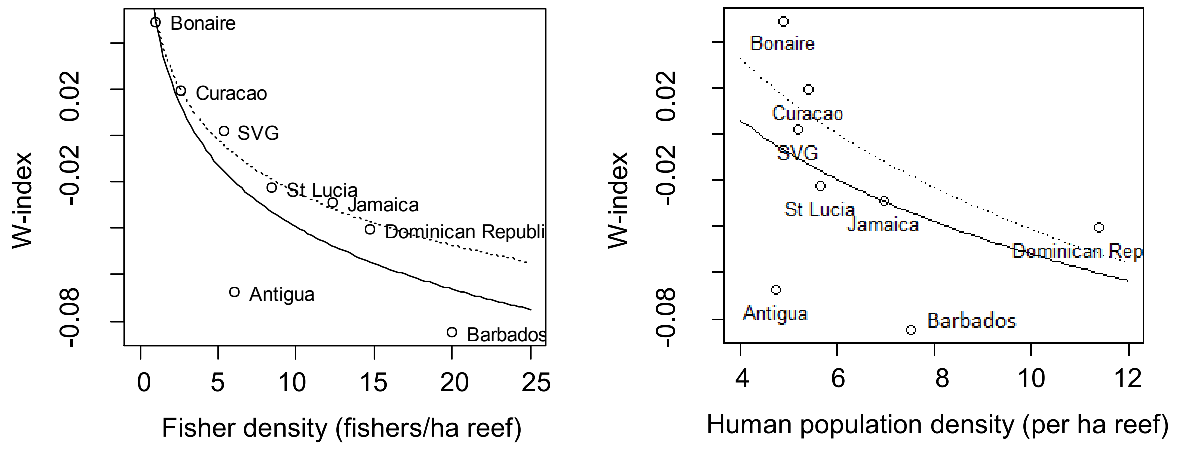

Figure 3.8 Non-linear regression between fishing pressure (fishers/ha reef) and W-index values from the ABC analysis. Solid lines represent an asymptotic relationship for all W-index values. Dashed lines represent asymptotic relationships for W-index values excluding Antigua and Barbados. Human population density was fourth-root transformed.

3.4 Discussion

3.4.1 Fishing pressure and parrotfish abundance

This study found that parrotfish numerical density in the Caribbean was negatively correlated with human population size but parrotfish biomass was not significantly correlated. These results differ from Valles and Oxenford (2014) who, using human population within a 25km radius, found that parrotfish abundance was not correlated with human population size but biomass was correlated. It is possible that the differences could be at least partially due to seasonal variation in parrotfish assemblages during extended survey periods. Valles and Oxenford (2014) analysed data from the Atlantic and Gulf Rapid Reef Assessment (AGGRA) conducted between 1998 and 2004. They found a relationship between human population size and parrotfish biomass, but the correlation was weak (p=0.048), and implied confounding effects due to seasonal variation were possible.

The lack of significant correlation between human population size and parrotfish biomass could be due to the choice of a 10km radius from the research site, which may be too great. The farther the distance from the study site, the smaller the percentage of human activities that may influence the marine environment. This is particularly true for sites near the big cities, for example La Bomba, Paisanito and Playa de Gollo that are close to Santo Domingo, capital city of the Dominican Republic (Appendix 5). In places where a majority of people are not working in marine related areas, using human population as a proxy for fishing activities will affect any analysis. When the research results were analysed using data on human populations within smaller radii of 2km and 5km of study sites, a negative correlation was found between parrotfish density and human population size, but still not with parrotfish biomass. The correlation between parrotfish density and human population was stronger using the 2km radius than the 5km radius. Furthermore, when applying a coastal buffer of 5km from the coastline, there was a significant correlation between parrotfish density and human population density within 10km radius of the sites. These results indicate that the highest anthropogenic impacts occur in coastal waters, especially close to human settlements. Such a spatial profile would be typical of artisanal fishing using small boats or even without boats.

A negative correlation with human population size was observed for parrotfish abundance but not for parrotfish biomass. Human populations affect marine fish populations directly and indirectly (Williams *et al*., 2008). One way in which humans directly affect fish assemblages is through fishing activities (Hawkins and Roberts, 2004a; Halpern *et al*., 2008; Aswani and Sabetian, 2010; Thyresson *et al*., 2011). It is possible that parrotfish populations are already so reduced that further impacts are negligible or too small to be detected with the methods used and the resolution of this study. Human indirect impacts include habitat loss (Williams *et al*., 2008) through coral mining (Brown and Dunne, 1988), loss of mangroves (Mumby *et al*., 2004), and pollution (Loya and Rinkevich, 1980; Hughes, 1994; Nystrom *et al*., 2000). To some extent at least, the correlation between human population size or proximity and parrotfish abundance may in fact be more of a proxy for habitat loss and degradation rather than a true indicator of the fishing pressure.

Although no significant correlation between human population size and parrotfish biomass was observed the trend was negative. There are several possible explanations for this non-significant correlation. For example, it has been shown that decreased coral cover can result in the decline of small fishes (Cheal *et al.*, 2008; Paddack *et al.*, 2009), while fishing tends to reduce populations of large-bodied fishes (Ruttenberg, 2001; Sala *et al.*, 2001). Thus, it is possible that fishing activities may have reduced the numbers of larger-size parrotfish while at the same time habitat degradation may have resulted in a decrease in the numbers of smaller-size parrotfish. Thus, while abundance would show a clear decline, the effect on biomass may be small, and largely due to chance. Such a situation could readily produce results indicating that by chance parrotfish biomass decreased as human population increased at some sites but with no strong trend, as was observed in this study.

Fisher density showed a significant correlation with parrotfish abundance and biomass across the Caribbean. The results are consistent with other studies which have shown that the extraction of large-bodied fish through fishing can result in the decline of fish numerical abundance and biomass including Caribbean parrotfish (Hawkins and Roberts, 2004a), Eastern Atlantic parrotfish (Tuya *et al.*, 2006), and other fishes elsewhere (Ruttenberg, 2001; William *et al.*, 2008; Sabetian, 2010; Bellwood *et al.*, 2011).

The results suggest that, at least in the case of Caribbean parrotfishes, fisher density appears to be a more powerful proxy for fishing pressure than human population size. These results support the findings of Dulvy *et al.* (2004) and Cinner and McClanahan (2006) that fisher density (representing fishing pressure) might provide a better metric of fishing pressure than indices based on human population size. One reason for this difference between the two proxies is that human population may tend to affect parrotfishes through habitat loss and not necessarily through fishing activities. The percentage of people who work as fishers varied between sites across the Caribbean, so that the direct effects of fishing activities were also varied. For example, data for the Asta site in Barbados showed that there were around 3000 inhabitants within a radius of 2km and around 180 fishers living in the nearest town. Meanwhile, at the Paynes Bay site in Barbados there was also a population of about 3000 people living nearby, but only about 30 of these were fishers. Both sites have similar areas of reef, so that although they have very similar human population sizes, the fisher density per reef area is very different. Consequently, the human population size may not be representative of fishing pressure, but could be a better descriptor for the level of general disturbance or stress to fish. It is also worth noting that the social and cultural differences within human populations across the region may cause bias when using the human population size as a proxy for fishing pressure (Williams *et al.*, 2008).

3.4.2 Parrotfish abundance and protection against fishing

Parrotfish abundance and biomass were both significantly different between sites within and those outside marine protected areas. These results were similar to those reported from the Western Solomon Islands (Aswani and Sabetian, 2010), with observed parrotfish abundance being lower outside than inside MPAs. The establishment of an MPA can enhance ecological processes and fisheries recovery (Roberts and Hawkins, 2000) and, over time, has been shown to increase the abundance of many marine fish (Roberts, 1995; Barrets *et al.*, 2007).

However, giving all MPA sites a similar protection status may have led us to underestimate the differences in parrotfish abundance and biomass between fished and unfished locations. Due to the difficulty in discriminating between sites based on the effectiveness of protection afforded by each MPA, all sites within MPAs were grouped together and considered as essentially unfished regardless of truly effective MPAs. It should be noted that because the MPA classification was extremely coarse, MPA sites might not have the same levels of protection and in addition reserve age varied substantially. Aswani and Sabetian (2010) found that parrotfish abundance in Nusa Hope, Western Solomon Islands (an effective MPA) was significantly higher than at Kida (a moderately effective MPA). The age of the reserve may also significantly enhance the abundance of fish (Molloy *et al.*, 2008), increasing with the length of time for which there has been (effective) protection. For example, Molloy *et al.* (2008) found that after protection for at least a decade fish abundance within MPAs was 3 times greater than abundance outside them, however when all MPAs were included in the analysis, regardless of their age, they found no significant difference overall between MPA and non-MPA sites.

The present results reinforce the belief that parrotfish abundance and biomass, where depleted by fishing, can be increased through applying significant levels of protection. However further research is needed on the effectiveness and duration of protection which are necessary to produce desired levels of improvement in parrotfish abundance and biomass.

3.4.3 Comparison between Fishing pressure and Abundance/Biomass (W-index)

The ABC results suggest that most MPAs in the Caribbean are or could be effective to protect parrotfish assemblages and to maintain them in a healthy status. Sites within an MPA were more likely to have parrotfish positive W-index values than non-MPAs which had equal numbers of sites with positive (undisturbed) and negative W-index values (disturbed), the former indicating significant number of larger parrotfish in the MPA sites compared to small ones. This is in keeping with the results from other studies; for example small-bodied parrotfish (e.g. *Sc. iserti*) density was not significantly different, while large-bodied parrotfish density was double inside the Exuma Cays Land and Sea Park, Bahamas (Mumby *et al.*, 2006).

No significant relationship was found between human population size and W-index value. It should be remembered that the W-index is a value representing the differences between the biomass and abundance curves (Warwick and Clarke, 1994). Thus, the lack of a significant relationship with the W-value is not surprising because the human population size metric (index) had failed to detect a relationship with fish biomass.

It was surprising that there was no significant correlation between fisher density and W-index, however the observed trend was negative. While this study found a significant relationship between fisher density and both parrotfish numerical abundance and biomass, this study also found an approximately equal number of sites with positive and negative W-index values in the fished areas. The lack of a significant correlation might indicate that fisher density has little or no impact on parrotfish assemblage status in some of the fished areas. Despite the low level of correlation, the negative trend indicates that the W-index may have potential as a proxy for fishing pressure on reef fish. Further research on a greater variety of fishes or on all reef fish at each site would be needed to confirm this possibility.

When the ABC analysis data were aggregated at country level, Bonaire and Curaçao had positive W-index values. Bonaire and Curaçao are island countries forming part of the Netherlands Antilles together with Aruba and Saba. These two small islands, especially Bonaire, are known to have above average reef condition (Wilkinson, 2008) and effective MPAs (Cooper, 2011; Relles, 2012). There are also few fishers operating the artisanal fisheries within Bonaire, mostly using hook and line (Hawkins and Roberts, 2004a). The economy of Bonaire is mostly reliant on the tourism industry, which has been reported as having a minimal effect in terms of degradation of the marine environment (Dixon, 1993; Parker, 1999). These factors are advantageous for marine fish communities, enabling them to grow to their full potential.

Jamaica, Dominican Republic and Barbados having negative W-values is unsurprising given the high number and density of fishers, and variety of fishing gears used in these countries (Hawkins and Roberts, 2004a). High fishing pressure can reduce the abundance of large-bodied fish either as target fish or because of by-catch (Mumby *et al*., 2006). Rakitin and Kramer (1996) found that a large number of *Sc. vetula* in Barbados were being caught in traps prior to them being an intended target. Since then the decrease in large-bodied parrotfish abundance has likely been accelerated by the inclusion of parrotfish as a target fish by fishers. For example, by 2001 ca. 39% of the total fish biomass captured using traps at Formigas Bank in Jamaica comprised parrotfishes. The volume of parrotfish caught using traps in 2001 was around 0.70kg/trap/haul at Formigas Bank, and approximately 0.36 and 0.96 kg/trap/haul in Discovery Bay and Morant Cay respectively, while parrotfishes also comprised about 3% of the total spearfishing catch (Grant, 2001).

The ABC results from this study at country level confirm previous findings (Blanchard *et al*., 2004; Yamane *et al*., 2005). The non-linear regression showed that the W-index value tends to decrease exponentially with increased fisher density, although the W-index value of Antigua was substantially below the regression line. Antigua has relatively low fisher density compared to other countries in the Caribbean, however this country suffers from the widespread use of illegal and unsustainable fishing practices (Horsford, 2004) and is considered at risk of overexploiting its marine resources (Carr and Heyman, 2009). The average finfish landings have been reported as 1509 t/year, to which parrotfish contributed about 225 t/year (FAO, 2008). There is also a thriving illegal market for parrotfish, which means that a substantial proportion of the parrotfish captured and sold are unrecorded (Carr and Heyman, 2009). This means that the available fisheries data are unlikely to reflect the true situation, with actual fishing pressure much higher than that reported.

The ABC method may have potential for use as a metric for fishing pressure, as an alternative to the fisher density index, at least at country scale. The use of fishing pressure indices in order to examine their relationships with fish assemblage structure is not without its drawbacks. The main problems include those related to the difficulty of obtaining accurate data and to the standardization of fishing effort across different gear types (Hawkins and Roberts, 2004a; Tuya *et al.*, 2006). These difficulties will be exacerbated where large-scale trends are being analysed. It could be possible to solve these difficulties through conducting a questionnaire survey in each location. However, such an activity would require time and incur considerable costs. Using the ABC method to derive the W-index values could be a simple and cost effective way to assess potential impacts of fishing pressure. However, this solution would need to be tested on other reef fish communities to ensure the validity of the method.

Chapter 4. Density and average size of parrotfish life phase in the Caribbean and their relationships with fishing

4.1. Introduction

Parrotfish have three distinct phases during their life, namely juvenile, initial and terminal, and can change sex between life phases (Choat and Bellwood, 1998). In most parrotfishes, the terminal phase is when the fish is considered mature and often assumed to have changed sex from female to male (Robertson and Warner, 1978). Female parrotfishes can become male before or after maturity depending on species or genus, however females of the genus *Scarus* cannot change sex before they are sexually mature (Robertson and Warner, 1978). Although many older or larger female parrotfish become terminal males, not all do so, and the prevalence and timing of this sex change is expected to vary in response to variations in growth and mortality rate (Merot and Collin, 2012).

One of the theories that aims to explain the evolutionary rationale for sex change in fishes is called 'the sex advantage model' (Ghiselin, 1969). It proposes the ability to change sex at a certain age or size will confer greater advantages on an individual in terms of reproductive success compared to an individual that remains male or female. This model is based on the assumption that the ability of a fish to undergo sex change at a given age or size is determined or at least substantially influenced by genetic factors, however it is possible and even likely that environmental factors can also drive sex change in fishes (Charnov, 1982). The size at which sex change occurs is frequently specific to each population of a given species, and may be determined by environmental factors reflected by local growth and mortality such as population density, competition for mates and predation (Alonzo and Mangel, 2004).

Warner (1988a) suggests that there are at least two ways in which environmental factors may affect fish sex change. The first is the effect on the individual of extrinsic factors which are related to physiological condition, so that the optimal age and size for a fish to change sex may depend on prevailing environmental conditions. The second is the impact of demography and male opportunity factors, for example the lack of sufficient mature males can drive female fish to change sex early in protogynous fishes or vice versa in protandrous species.

Mortality due to extraction by humans (fishing mortality) also influences the size at which sex change occurs in certain sequentially hermaphroditic fishes (Armsworth, 2001; Petersen and Warner, 2002). Fishing activities tend to target large mature fish, thus often preferentially selecting the terminal phase of protogynous or protandrous fishes, resulting in imbalance between the sexes. The removal of large fish may thus affect the size at which fish change sex, due to fishing pressure decreasing the chances of reaching size at which maturity and terminal phase historically occurred; therefore more fish will undergo sex change earlier in life or at smaller sizes. Hawkins and Roberts (2004b) reported decrease of terminal males size was linked to increased fishing pressure in *Sparisoma viride* and *S. vetula* at several sites in the Caribbean, particularly in Saba, Bonaire, Puerto Rico, St. Lucia, Dominica, and Jamaica. Loh and Pawlik (2014) also found that large terminal phase parrotfish were uncommon or absent on overfished reefs in the Caribbean. Although parrotfish behave differently during each life phase (Bonaldo *et al.*, 2006), and thus the response to habitat changes (degradation) and fishing pressure might vary between distinct life phases, it can be expected that increased fishing pressure on parrotfishes will most likely result in a tendency for them to change sex early.

One factor that can benefit sex-changing fish populations is the establishment of a well-managed marine protected area (MPA), with effective protection from fishing. A meta-analysis of sex-changing fish from several MPAs around the world showed that abundance was higher inside than outside the MPAs (Molloy *et al.*, 2008). Hawkins and Roberts (2004b) found that parrotfish terminal phase biomass and size were higher inside an MPA in St. Lucia than in the nearby fishing grounds. They further suggested that since mating success is likely to be influenced by the number of males, the relative density of each parrotfish life phase inside and outside the MPA should be determined.

The response of parrotfish to decrease in the size at which the sex change takes place affects species survival, however transition to the terminal phase at a small size will tend to cause a significant reduction in reproductive output, especially as fecundity tends to increase exponentially with body size (Bohnsack, 1990). To promote the recovery of parrotfish populations to a state where they mature and change sex at their original larger sizes, conservation efforts are needed. To measure the success of these conservation efforts, knowledge of the factors (i.e. fishing pressure) affecting abundance and average fish size at each life phase is important.

The average minimum sizes of each parrotfish life phase are widely known and published elsewhere for various species (Bruggemann *et al.*, 1994; Hawkins and Roberts, 2004b) and often used to infer response to different fishing pressure levels.

Minimum fish size as an indicator or a proxy for the effect of fishing pressure, while easy to use, might be misleading if there are one or a few individuals changing phase at sizes far different from the rest of the population. In order to infer effects of fishing, this study not only uses the change in mean size, but also explores the size at which fish shift to the next stage and uses these indicative phase shift sizes as predictors of response to fishing pressure.

This chapter focuses on the density and average size of different life phases of parrotfish in eight Caribbean countries, with particular attention to 4 species (*Sc. iserti, Sc. taeniopterus, Sp. aurofrenatum* and *Sp. Viride*) and to the relationships of these factors with fishing pressure. It addresses the following specific questions: (1) How are parrotfish abundance and size at each life phase related to fisher density; (2) How do parrotfish abundance and size in the different life phases differ between sites within MPAs and outside MPAs; and (3) what are the size ranges of each life phase and at approximately what size do parrotfish undergo life phase changes.

4.2 Methods

4.2.1 Fish survey

Fish surveys were conducted in eight Caribbean countries (Antigua, Bonaire, Barbados, Curaçao, Dominican Republic, Jamaica, St. Lucia and St. Vincent and Grenadines (SVG)) by the EU FORCE Project team. Underwater visual survey was used to collect data on parrotfish abundance and size from 84 sites across the Caribbean. In addition, fish life phase (juvenile (JP), initial (IP), and terminal (TP)) was determined *in situ* during the survey based on their coloration. Juveniles generally characterized by drab colouration, the initial phase (IP) by dull colouration and the terminal phase (TP) by bright colours. Since parrotfish change sex or not during phase change cannot determined based from their coloration, fish life phase were used in the analysis. The methods used during the survey have been described in detail in Chapter 2 of this thesis.

4.2.2 Fisher density and MPA status

The detailed method on how fisher density and MPA status were determined was described in Chapter 3. Fisher density was determined based on the number of fishers and the extent of the fishing area. The site location either inside or outside of

MPAs was also taken into account; out of 84 sites, 33 sites were inside MPAs and 51 sites were outside.

4.2.3 Data and statistical analysis

Data analysis was under taken in R (R core team, 2013). Abundance and biomass data were standardised by transect area to estimate fish densities (individuals per 100m^2). Fish numerical density was fourth-root transformed to minimise departure from normality (Table 2.1; Chapter 2). Fisher density was also fourth-root transformed to reduce the effect of extreme values.

To determine habitat and fisher density relationships with parrotfish density and mean size at different fish life phases, Spearman rank correlation tests were used. The Spearman rank correlation test was used because the data was not normal even after transformation. Numerical density and size were separately tested against fisher density for all parrotfish of the genera *Scarus* and *Sparisoma* (all 10 species identified were combined), and for 4 dominant species individually (*Sc. taeniopterus*, *Sc. iserti*, *Sp. aurofrenatum*, and *Sp. viride*). To minimize confounding effects of fishing protection (MPA), only data from sites outside the MPAs were used (*n*=51 sites).

The differences in parrotfish numerical density and mean size between sites inside and outside MPAs were assessed using two-sample permutation since the data was not normal even after transformation. Prior to the analysis, parrotfish density and mean size were fourth-root transformed to reduce the effect of extreme values. The two-sample permutation tests were conducted using the '*perm'* package (version 1.0-0.0; Fay, 2010)

To estimate the size range of each life phase and the size at life phase change, density curves of the three phases were plotted using the '*density'* and '*ggplot'* functions (Wickham, 2009). The intersections between pairs of density curves were examined and determined. Where there is more than one intersections, the biggest intersection size was used. Parrotfish (combined) and each of the two genera were analyzed by region and by country.

4.3 Results

The largest *Sc. taeniopterus* and *Sp. aurofrenatum* terminal phase mean size was found in Antigua, that of *Sc. iserti* was in Bonaire, and that of *Sp. viride* was in St.

Lucia, while the smallest terminal phase mean size was in Jamaica (Figure 4.1; Appendix 6). The proportion of terminal phase fish in the population also tended to be highest in Bonaire for each species, except for *Sc. teniopterus* which was found in Barbados (Figure 4.2; Appendix 7).

4.3.1 Correlation of fisher density with parrotfish density and mean size of each life phase

The correlation between fisher density and parrotfish numerical density varied between life phases, genera and species (Table 4.1). Juvenile phase parrotfish (JP) density was mostly significantly correlated with fisher density, while initial phase (IP) and terminal phase (TP) density was not significantly correlated.

In contrast with parrotfish numerical density, the mean sizes of IP and TP *Scarus* and *Sparisoma* were mostly significantly related to fisher density (Table 4.2). JP mean size was not significantly related to fisher density. In individual species, only the IP phase of *Sp. aurofrenatum* was significantly correlated with fisher density, while in other species this life phase were not found to be so correlated. In the terminal phase, a significant negative relationship between mean size and fisher density was found for *Sc. iserti* and *Sp. aurofrenatum* (Table 4.2).

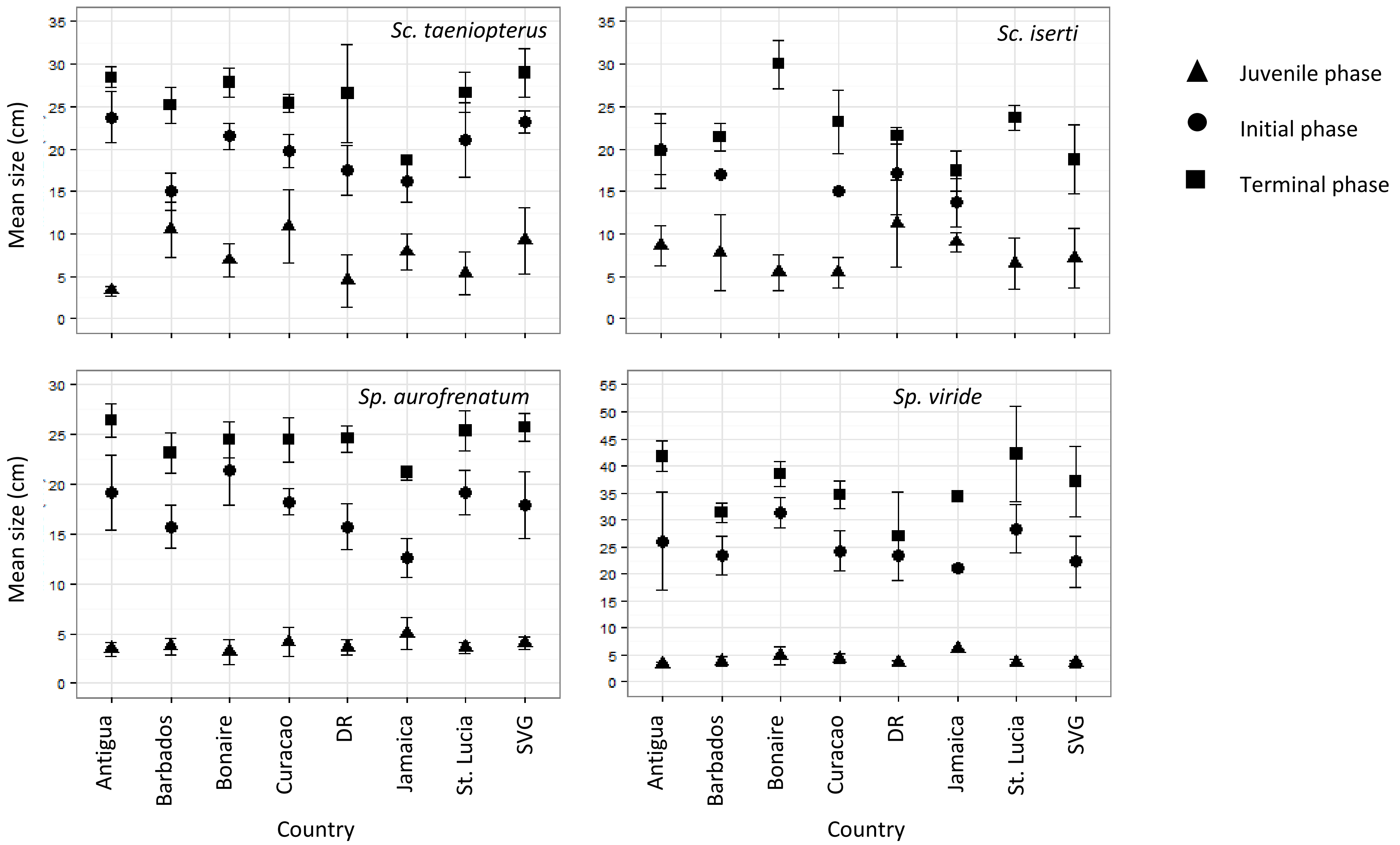

Figure 4.1 Mean size (in cm ± sd) of three different life phases (JP: juvenile phase, IP: initial phase, TP: terminal phase) of dominant parrotfish in the Caribbean.

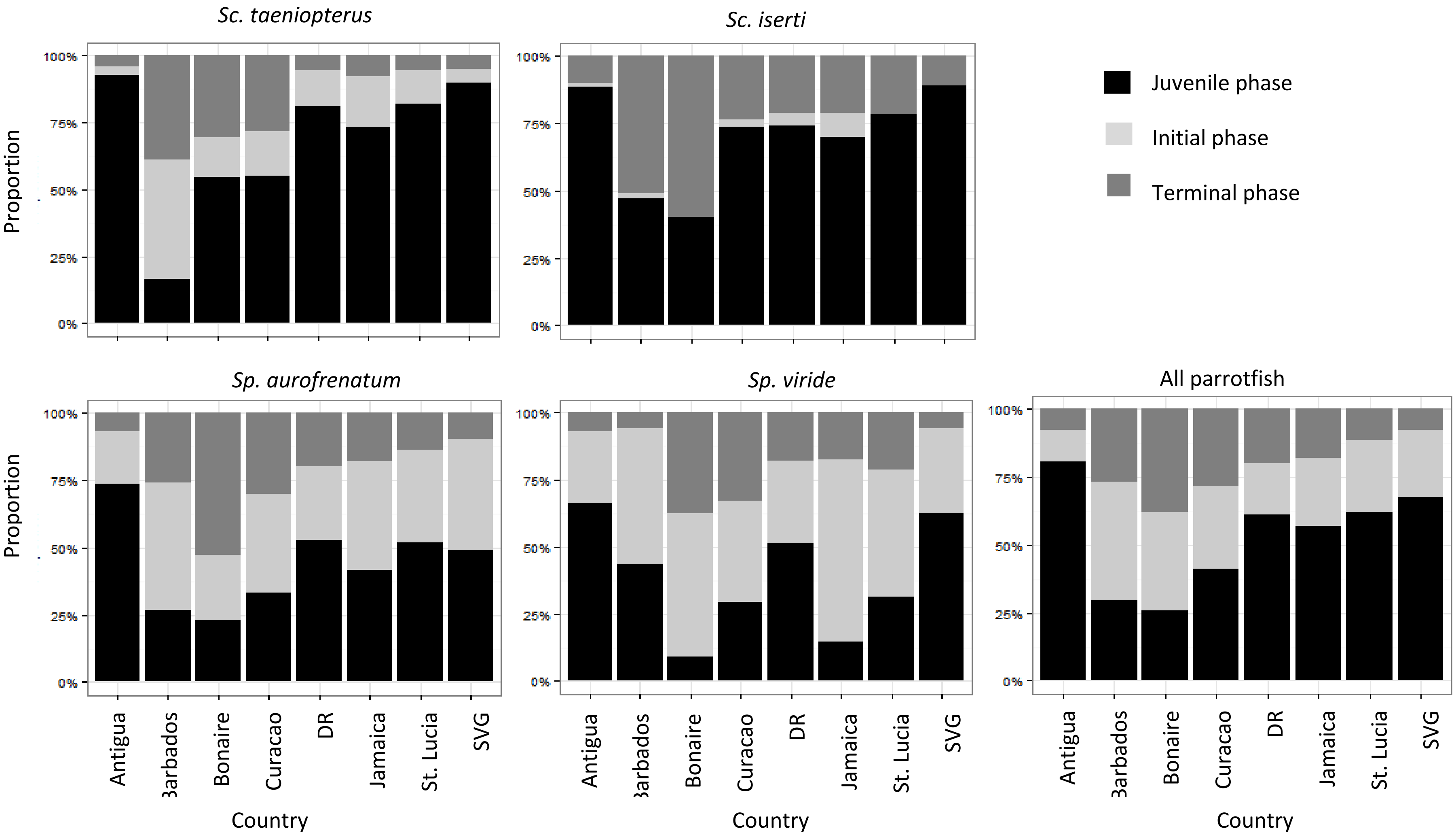

Figure 4.2 The proportion (%) of different life phases (JP: juvenile phase, IP: initial phase, TP: terminal phase) of dominant parrotfish in the Caribbean.

Table 4.1 Output from the Spearman rank correlation test of parrotfish numerical density and fisher density in eight countries in the Caribbean. * indicate significant value < 0.05, while ** indicate significant value < 0.005.

Life phase	Group	Rho	p value	
Juvenile	ALL	-0.420	0.0024	**
	Scarus	-0.468	0.0012	**
	Sparisoma	-0.429	0.0019	**
	Sc. taeniopterus	-0.389	0.0231	*
	Sc. iserti	0.167	0.3961	
	Sp. aurofrenatum	-0.331	0.0203	*
	Sp. viride	-0.347	0.0382	*
Initial	ALL	0.013	0.9301	
	Scarus	0.091	0.5961	
	Sparisoma	0.073	0.6203	
	Sc. taeniopterus	0.185	0.3750	
	Sc. iserti	0.307	0.4209	
	Sp. aurofrenatum	0.225	0.1366	
	Sp. viride	-0.058	0.7143	
Terminal	ALL	-0.144	0.3231	
	Scarus	-0.004	0.9812	
	Sparisoma	-0.121	0.4082	
	Sc. taeniopterus	-0.128	0.5245	
	Sc. iserti	0.220	0.3388	
	Sp. aurofrenatum	-0.034	0.8247	
	Sp. viride	-0.283	0.1605	

Table 4.2 Output from the Spearman rank correlation test of parrotfish mean size and fisher density in eight countries in the Caribbean. * indicates significant value < 0.05, ** indicates significant value < 0.005 and *** indicates significant value < 0.001.

Life phase	**Group**	**Rho**	**p value**	
Juvenile	ALL	0.097	0.5011	
	Scarus	-0.024	0.8748	
	Sparisoma	0.071	0.6252	
	Sc. taeniopterus	-0.058	0.7461	
	Sc. iserti	0.236	0.2258	
	Sp. aurofrenatum	0.114	0.4367	
	Sp. viride	-0.122	0.4797	
Initial	ALL	-0.411	0.0030	**
	Scarus	-0.335	0.0456	*
	Sparisoma	-0.420	0.0027	**
	Sc. taeniopterus	-0.373	0.0666	
	Sc. iserti	0.349	0.3573	
	Sp. aurofrenatum	-0.530	0.0002	***
	Sp. viride	-0.192	0.2238	
Terminal	ALL	-0.274	0.0569	
	Scarus	-0.386	0.0199	*
	Sparisoma	-0.315	0.0275	*
	Sc. taeniopterus	0.083	0.6802	
	Sc. iserti	-0.556	0.0089	**
	Sp. aurofrenatum	-0.367	0.0122	*
	Sp. viride	0.138	0.5001	

4.3.2 Relationship between parrotfish density and size in the different life phases and protection against fishing

In general, parrotfish density at each life phase was higher at sites inside MPAs than outside MPAs, except for individual species (Table 4.3). In the juvenile phase, densities were significantly higher in protected than not protected sites for *Sc. taeniopterus* (Permutation t-test; ρ=2.419, $p<0.05$; Table 4.3). In the terminal phase, the combined density of all parrotfishes was significantly different between sites within and outside MPAs (Permutation t-test; ρ=2.071, $p<0.05$; Table 4.3). No parrotfish, genus, or individual species initial phase (IP) had significantly different densities between MPAs and areas outside.

Sites within an MPA generally had higher mean parrotfish sizes than those outside the MPA, except for the juvenile phase. The mean sizes of the genus *Sparisoma* in juvenile (ρ=-2.154, $p<0.05$) and terminal phase (ρ=2.560, $p<0.05$) inside the MPAs were significantly different from those outside MPAs (Table 4.4).

Table 4.3 Output from a permutation t-test of parrotfish numerical density between MPA and non- MPA sites in eight countries in the Caribbean. * indicates significant value < 0.05.

Life phase	**Group**	**Z**	**p**	
Juvenile	All	0.9310	0.3519	
	Scarus	1.9559	0.0505	
	Sparisoma	-1.0181	0.3086	
	Sc. taeniopterus	2.4193	0.0156	*
	Sc. iserti	-0.1371	0.8909	
	Sp. aurofrenatum	-0.8418	0.3999	
	Sp. viride	-1.5945	0.1108	
Initial	All	0.1520	0.8791	
	Scarus	0.4493	0.6532	
	Sparisoma	-0.3508	0.7257	
	Sc. taeniopterus	-0.2831	0.7771	
	Sc. iserti	-	-	
	Sp. aurofrenatum	-1.1301	0.2585	
	Sp. viride	-0.1251	0.9005	
Terminal	All	2.0716	0.0383	*
	Scarus	0.7777	0.4367	
	Sparisoma	1.1293	0.2588	
	Sc. taeniopterus	0.6678	0.5043	
	Sc. iserti	-0.3620	0.7174	
	Sp. aurofrenatum	0.9378	0.3483	
	Sp. viride	-0.2895	0.7722	

Table 4.4 Output from a permutation t-test of parrotfish mean size between MPA and non-MPA sites in eight countries in the Caribbean. * indicates significant value < 0.05.

Life phase	Group	Z	p	
Juvenile	All	-0.8530	0.3937	
	Scarus	-1.7259	0.0846	
	Sparisoma	-2.1542	0.0312	*
	Sc. taeniopterus	-1.4467	0.1480	
	Sc. iserti	-0.6449	0.5190	
	Sp. aurofrenatum	-1.7831	0.0756	
	Sp. viride	-0.2576	0.7967	
Initial	All	1.5877	0.1124	
	Scarus	0.2663	0.7900	
	Sparisoma	1.3333	0.1824	
	Sc. taeniopterus	0.5537	0.5798	
	Sc. iserti	-	-	
	Sp. aurofrenatum	1.1841	0.2364	
	Sp. viride	1.6020	0.1092	
Terminal	All	1.3537	0.1758	
	Scarus	0.3586	0.7199	
	Sparisoma	2.5603	0.0105	*
	Sc. taeniopterus	-0.8558	0.3921	
	Sc. iserti	0.4564	0.6481	
	Sp. aurofrenatum	0.6068	0.5440	
	Sp. viride	1.6526	0.0984	

4.3.3 Size range of each life phase and estimation of size at phase change in parrotfish

Across the eight Caribbean countries, juvenile parrotfish had a minimum size of 1cm and maximum size of approximately 22cm. The initial phase size ranged from approximately 3 to 43cm, while the terminal phase ranged from 6 to 50cm (Figure 4.5). Initial phase parrotfish density was highest at a size of 19.73cm and terminal phase was at 20.20cm. Juvenile and initial phase parrotfish exhibited overlap in the size range between 6 and 22cm, with the intersection between the two occurring at approximately

8.62cm. Initial and terminal phase parrotfish exhibited overlap in the size range between 6 and 43cm, with the intersection between them at approximately 21.07cm.

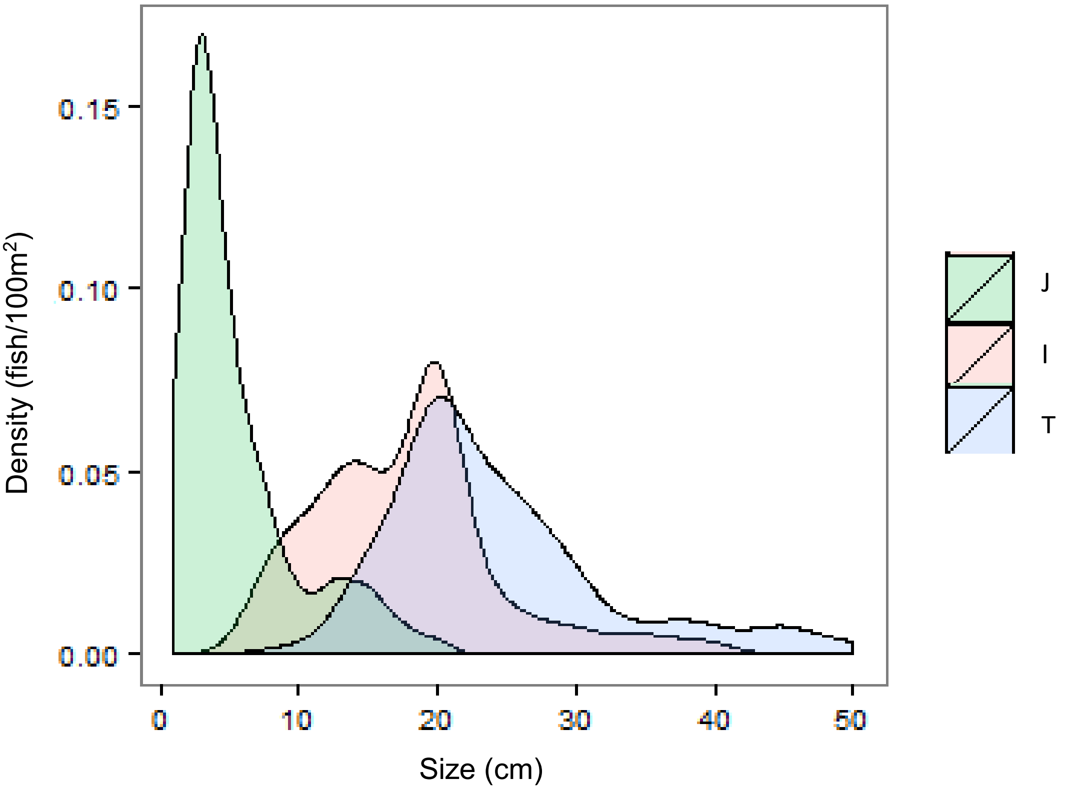

Figure 4.5 The density curve of parrotfish (combined) size for each life phase in the Caribbean. J: juvenile, I: initial and T: terminal phase.

Juvenile, initial and terminal *Scarus* size ranges were, respectively, from 1 to 24 cm, 4 - > 45 cm and 9 - > 45cm (Figure 4.6). Juvenile and initial phase of *Scarus* exhibited an overlap in size between 4 and 24cm, with the intersection point at approximately 12.61cm. Initial and terminal phase of *Scarus* overlapped in the size between 9 and 45cm, with the intersection point at approximately 21.68cm. The density of initial phase parrotfish peaked at a size of 19.82cm and terminal phase at 19.68cm.

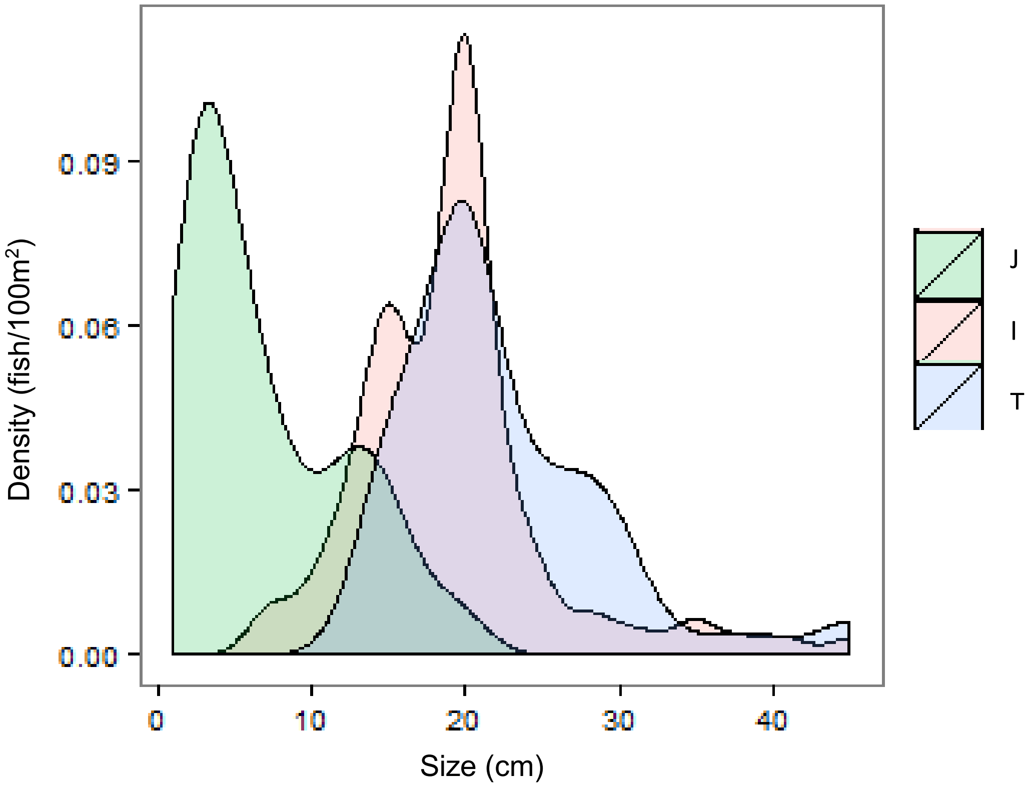

Figure 4.6 The density curve of *Scarus* size for each life phase in the Caribbean. J: juvenile, I: initial and T: terminal phase.

The highest density of initial and terminal phase *Sparisoma* occurred at 20 and 22cm, respectively (Figure 4.7). Juvenile and initial phases of *Sparisoma* exhibited overlap in the size range between 4 and 10cm, with the intersection between them at approximately 8.13cm. Initial and terminal phase *Sparisoma* size ranges overlapped between 8 and 42cm, with the intersection between them at approximately 21.11cm.

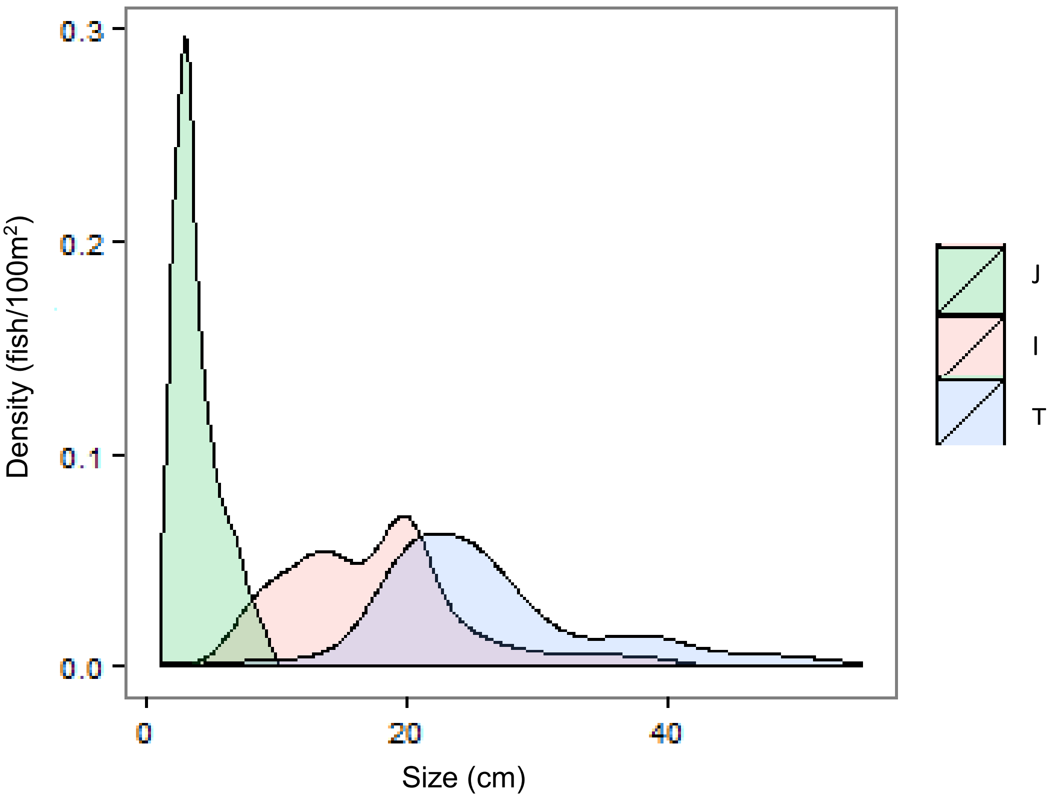

Figure 4.7 The density curve of *Sparisoma* size for each life phase in the Caribbean. J: juvenile, I: initial and T: terminal phase.

By country, the intersections between initial and terminal phase size density curves were at the following points: Bonaire 23.70cm, Curacao 17.32cm, SVG 22.74cm, Antigua 13.22cm, St. Lucia 22.85cm, Jamaica 14.49cm, Dominican Republic 18.36cm and Barbados 18.68cm. Those between juvenile and initial phase size density curves were: Bonaire 9.77cm, Curacao 9.81cm, SVG 8.04cm, Antigua 6.16cm, St. Lucia 7.23cm, Jamaica 8.92cm, Dominican Republic 9.64cm and Barbados 8.80cm (Figure 4.8). The size at which initial and terminal phases intersected tended to decrease with increasing fisher density (Spearman rank correlation test, $\rho = -0.69$, $p<0.1$; Figure 4.9). There was a negative trend in the relationship between the juvenile and initial phase intersect and fisher density, although the relationship was not significant (Spearman rank correlation test, $\rho = -0.331$, $p>0.1$; Figure 4.10).

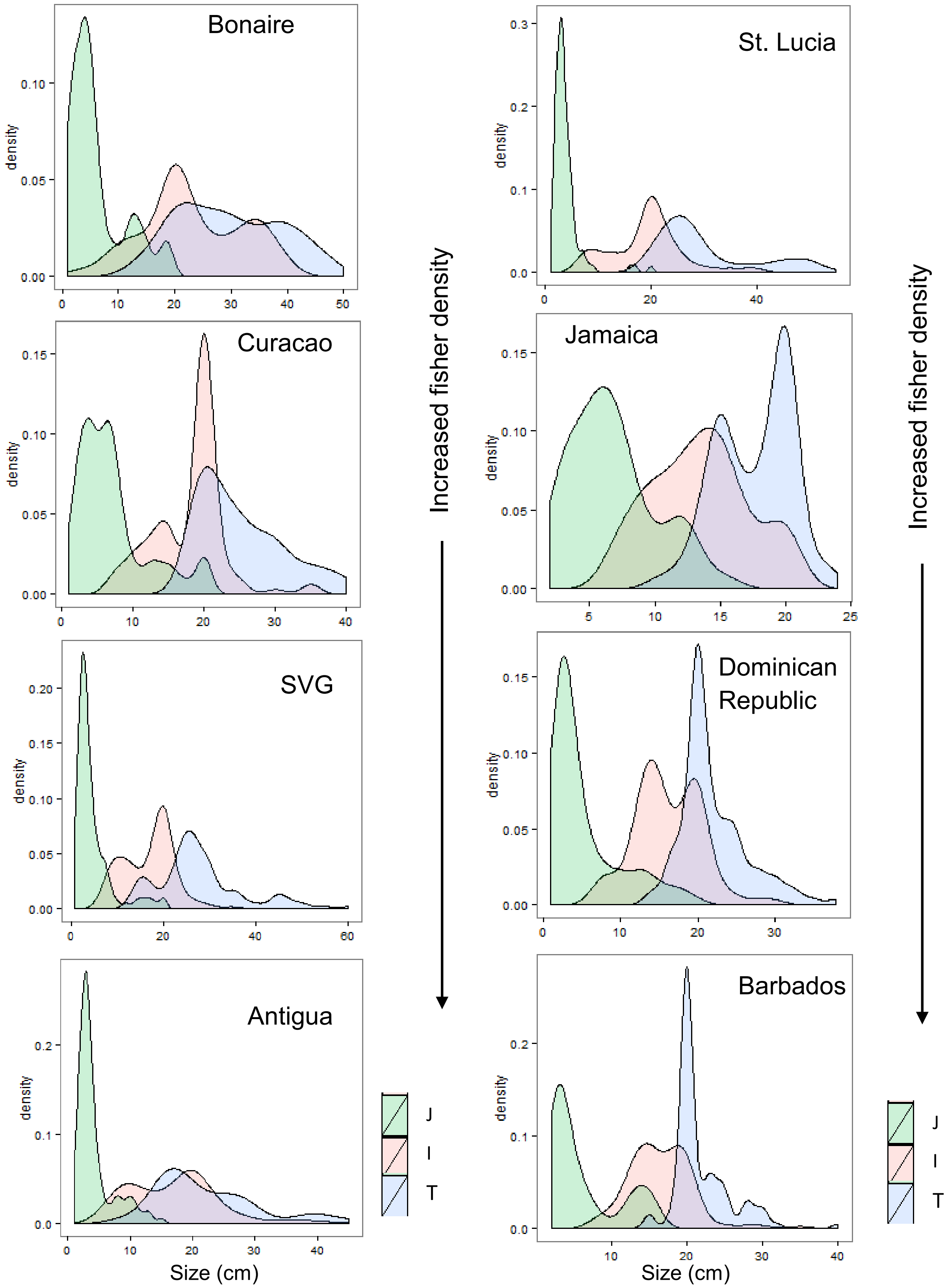

Figure 4.8 The density curve of parrotfish (combined) size of all life phase. J: juvenile, I: initial and T: terminal phase. Plots are ordered according to their fisher density (from lowest to highest). Density reflects probability of fish density in given fish size.

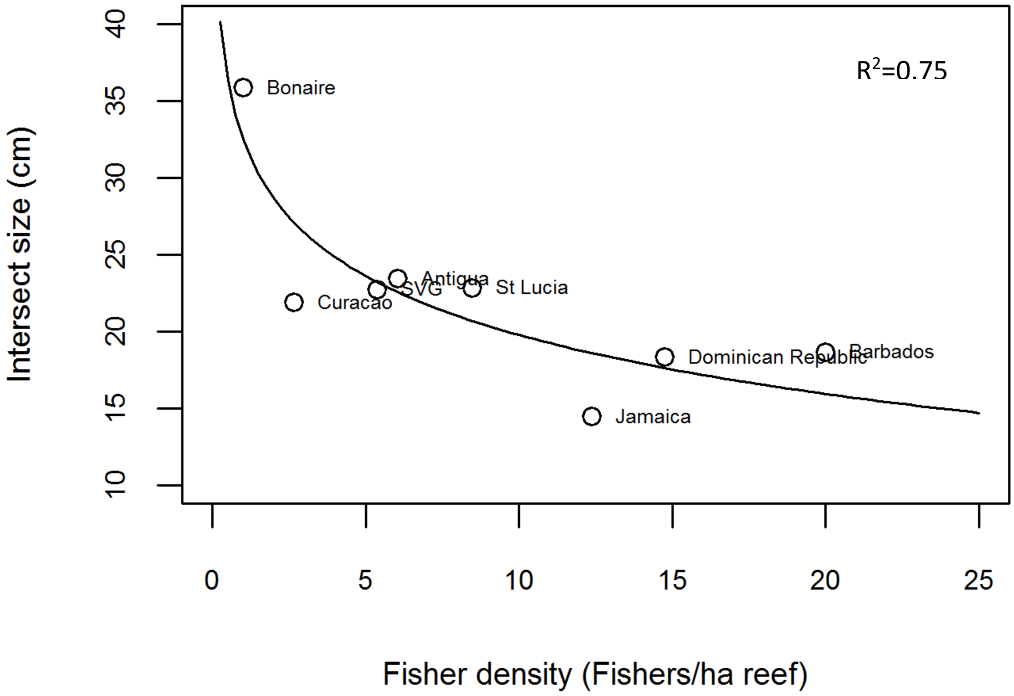

Figure 4.9 Fish size at intersect between initial and terminal phase against fisher density (fishers/ha reef). The line indicates a non-linear regression fit.

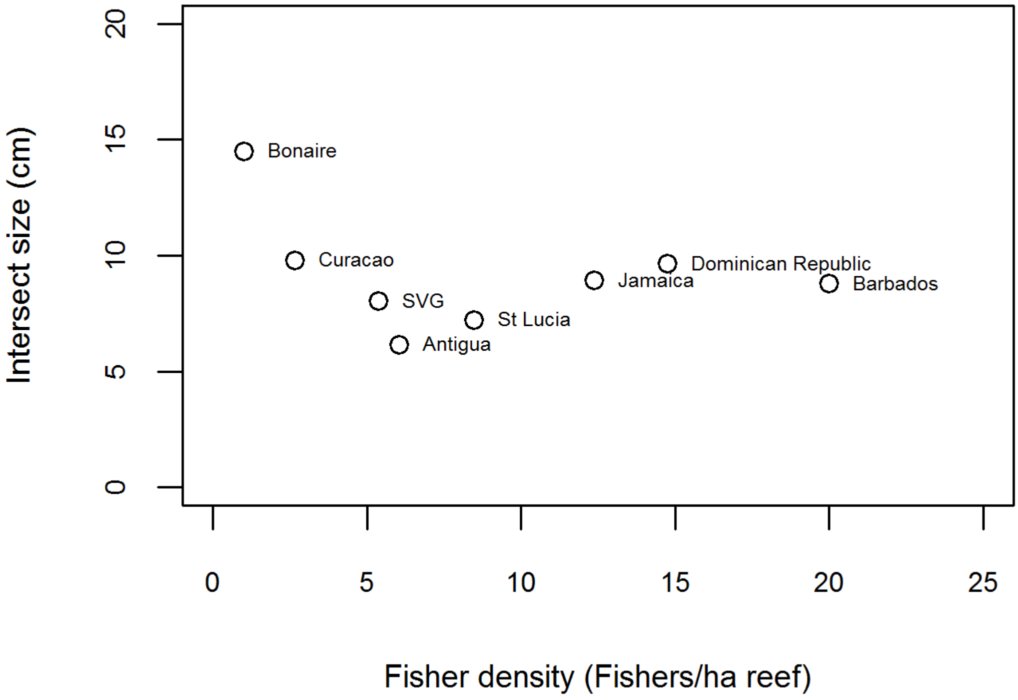

Figure 4.10 Fish size at intersect between juvenile and initial phase against fisher density (fishers/ha reef).

4.4 Discussion

In general, the density of parrotfish was negatively related to fisher density in the juvenile phase, although the initial and terminal phases did not have significant relationships. These results differ from those of Hawkins and Roberts (2004b) who showed the abundance of large fish tending to decrease with increasing fishing pressure. Hawkins and Roberts (2004b) did not explicitly state the terminal phase density decreased with increasing fishing pressure, but if most large fish are terminal phase fish, the terminal phase abundance was influenced by fishing pressure. However, the low density of large fish in the present study (Chapter 2), might be the reason why there was no relationship between initial and terminal phase fish density and fisher density.

Fishing selects large and mature individuals, and therefore influences the abundance of large fish (Ruttenberg, 2001; Hawkins and Roberts, 2004a; Tuya *et al.*, 2006; William *et al.*, 2008; Sabetian, 2010; Bellwood *et al.*, 2011). Parrotfish terminal phases usually have a size of more than 15 cm (Bruggemann *et al.*, 1994), so most likely fish in the terminal phase are targeted by fishing.

It is notable that the mean size of terminal phase parrotfish in St. Lucia was greater than the mean size in 1995-2001, during which period terminal phase parrotfish mean size increased; for example, *Sp. aurofrenatum* increased from ca. 18 to 19cm and *Sp. viride* from ca. 31 to 33cm (Hawkins and Roberts, 2004b). The present data (2010-2011) showed that mean sizes of terminal phase *Sp. aurofrenatum* and *Sp. viride* were 25.42±2.01 and 42.21±8.80cm, respectively. While fisher density may influence fish mean size, these data suggest that fishing pressure, at least in St. Lucia, might have decreased. The factor responsible for decreased fishing pressure is unclear at this stage. However, the perceived importance of parrotfish conservation to the coral reef ecosystem (Mumby *et al.*, 2006; Mumby, 2009; Jackson *et al.*, 2014) and rising awareness of people in the Caribbean to protect herbivorous fish (Organization of Eastern Caribbean States, 2009) may be partly responsible for relaxing fishing pressure on parrotfish. The numerical abundance of parrotfish in St. Lucia seems to have increased since 2001 (about 15 individual/100m^2; Hawkins and Roberts, 2004b) to about 30 individual/100m^2 in 2010 (this study) but the biomass has remained similar. This indicates a possible increase of small parrotfish abundance. It is however worth noting that different methodologies were used between studies. Hawkins and Roberts

(2004b) used a 10 m tape and surveyed 5 m on each side of it. This study used 10 x 4 m (small fish) and 30 x 4 m (large fish) transects. However, this cannot explain the large differences in size and density. The differences might come from varying accuracy of the fish estimate. Density estimates of fish from wider transect (10m) were 22 to 26% less than estimates from narrower (5m) transect (Cheal and Thompson, 1997). The increase in abundance of small fish and its mean size of terminal phase fish are good indications that parrotfish in St. Lucia have responded to changes in fishing pressure, however other factors could be involved (e.g. changes in growth and/or recruitment rate).

Surprisingly, this study found a significant negative relationship between juvenile density and fisher density. Although the juvenile phase is largely composed of small fish, some fish in this phase can attain a size above 15 cm, which is large enough to be caught by fishing activities. A significant relationship between fish density and fisher density could also result from indirect effects of fishing activities including reduction in large terminal phase fish (e.g. Robertson and Warner, 1978). Increasing fishing and natural mortality will normally reduce the number of terminal phase fish because most large fish are male. The low number of males may successively cause sex change occurs at a smaller size to increase their male abundance, as in the sparids *Chrysoblephus laticeps* and *C. cristiceps* (Buxton, 1990; Buxton, 1992), parrotfish (Hawkins and Roberts, 2004b), California sheephead, *Semicossyphus Pulcher* (Hamilton *et al*., 2007), and Northeast Arctic cod *Gadus morhua* (Jorgensen *et al*., 2009).

Reduced size at sex change and maturity stage will impact reproductive success. Fish fecundity is exponentially related to body length (Bohnsack, 1990). If the fish egg production is reduced, assuming no recruitment from adjacent areas, then the natural recruitment process will likely be affected overtime, which in turn will often reduce the number of juvenile phase fish. The non-existence of a relationship between fish density and fisher density in initial and terminal phases may indicate that the density was so low that fishing did not have any further effect. However, the low density of terminal phase may have reduced the recruitment process.

The plausibility of the situation described above is corroborated by the relationship between fish mean size and fisher density. The average size in all life phases of parrotfish, *Scarus* and *Sparisoma* was negatively related with fisher density.

There was a tendency for initial and terminal phase fish to have lower size at phase change. This represents a threat to parrotfish population resilience, the effectiveness of their ecological role and their value as fishery resources. This threat could be addressed by effective management intervention either using site protection such as MPAs or by regulation of fishing seasons to allow stock recovery (Roberts and Polunin, 1994; Roberts *et al.*, 2001; Barrets *et al.*, 2007; Molloy *et al.*, 2008). The need for management, either by MPA or fishing regulation is indicated by the greater density and mean size of terminal phase fish within MPAs, consistent with the results of Hawkins and Roberts (2004b), in which parrotfish biomass in St. Lucia increased after the creation of an MPA. Mean density of terminal phase *Sc. vetula* and *Sp. viride* doubled in the Exuma Cays Land and Sea Park (ECLSP, Bahamas; Mumby *et al.* 2006), while after a decade of protection, abundance of sex-changer fish within MPAs was higher than outside (Molloy *et al.*, 2008).

Well-managed MPAs, however, appear to have a negative effect on small parrotfish. Mumby *et al.* (2006) also found more small *Sc. iserti* and *Sp. aurofrenatum,* although not significant*,* in the ECLSP that was attributed to greater predator abundance inside the reserve. While larger-bodied parrotfish were released from fishing pressure and much less vulnerable to predation than the smaller-bodied species, fishing pressure was generally lower on the latter while they are a natural prey for the groupers and other large carnivorous fishes becoming much more abundant within the reserve. *Epinephelus striatus* in the reserve are able to consume between 60-90% of adults of *Sc. iserti* (Mumby *et al.*, 2006).

Various studies on the effects of fishing pressure on parrotfish life phase have typically used mean size as the response indicator (Hawkins and Roberts, 2004b; Valles and Oxenford, 2014). It is indeed possible to predict the size at sex change in the terminal phase by mean size, but this may not be able to confidently address whether parrotfish really change their phase at a smaller size. By using density curves, this study was able to plot the distribution of parrotfish fish size in each life phase and calculate the point where the two life phases intersected. This approach might allow improved understanding regarding the factors which cause parrotfish to modify the timing of their phase change.

In general, the size at which parrotfish changed their phase was bigger in areas with a lower fisher density than those with high fisher density. Fish size at phase change in Bonaire, Curacao, SVG, Antigua and St. Lucia was above average regional size across the 8 Caribbean countries, while that in Jamaica, Dominican Republic and Barbados was below the regional mean. These three countries have a large number of fishers and fishing occurs very intensively (Munro, 1983; Hawkins and Roberts, 2004a&b; Hardt, 2009). There was a negative correlation between phase-change size and fisher density, further indicating that fishing pressure is likely to affect the fish size at which phase change occurs. Fish in Jamaica had smaller size at initial and terminal phase change than in most other countries. This size was smaller than that from other countries that have a greater fisher density such as the Dominican Republic and Barbados. However it is worth pointing out that quantifying actual fishing pressure given a wide variety of fishing gears is difficult, the present findings being based only on the number of fishers per reef area as a proxy for all fishing activities.

Not differentiating between simple from sophisticated fishing equipment could lead to misleading measures of fishing pressure. The deviational fish mean size at phase change data in Jamaica from the trend line maybe attributable to this. There is need to find an effective way to better quantify fishing pressure activity. Nevertheless, the present results indicate that there was significant decrease of mean size of initial and terminal phase with increasing fisher density. Especially in Jamaica, Barbados and the Dominican Republic attention is needed to better manage parrotfish population in order to help restore the size at phase change to terminal phase close to the average size for the region, in which might help conserve parrotfish density in the long term. However, such management would need considerable effort to reduce the number of fishers, which would difficult considering poverty occurred in the said countries.

Chapter 5. Synthesis

This thesis focuses on the macroecology of Caribbean parrotfish. In particular, it investigates three relationships: between parrotfish density and benthic habitat variables (Chapter 2); between fishing pressure (fisher density, human population, MPA protection) and parrotfish density (Chapter 3); and between parrotfish size at sex change and fishing pressure (Chapter 4).

The present findings provide a novel contribution to the knowledge of parrotfish ecology in the Caribbean. Previous research has partly described their relationships with coral and algal cover (Tzadik and Appeldoorn, 2013), hole size (Gratwicke and Speight, 2005a), fishing pressure (Hawkins and Roberts, 2004a; Vales and Oxenford, 2014), the difference of parrotfish abundance inside and outside MPAs (Mumby *et al.*, 2006) and parrotfish sex change (Hawkins and Roberts, 2004b). However, these studies were invariably confined to small geographical areas which makes the extrapolation of findings to the Caribbean as a whole difficult or inappropriate. A strength of this thesis is its spatial scale and use of directly comparable data on parrotfish abundance, benthic habitat and fishing pressure from 8 countries across the Caribbean.

Parrotfish density and size at phase change and their relationships with habitat and fishing pressure were analysed both by country and at a regional scale. Parrotfish abundance was positively correlated with coral cover and negatively correlated with macroalgal cover. Parrotfish abundance had a significant correlation with reef complexity (Chapter 2). Different sizes of parrotfish were associated with different habitats (Chapter 2). Fishing is likely to have reduced fish numerical abundance and biomass even at Caribbean scale (Chapter 3). While parrotfish biomass was significantly higher within MPAs, parrotfish numerical density was not significantly different (Chapter 3). The density of terminal parrotfish was significantly different (Chapter 4). Furthermore, fishing pressure was significantly correlated with the size at which phase change between initial and terminal phases occurs (Chapter 4). The findings thus substantially contribute to the body of knowledge on parrotfish macroecology in each of the countries and Caribbean basin scale, and may therefore help inform the management of parrotfishes and their habitat, from local to regional scales.

5.1 Current state of knowledge

Understanding the relationship between parrotfish density and environmental factors is important in order to help the recovery of these fish. Parrotfish are considered an important functional group in the coral reef ecosystem, and parrotfish specific research has increased over the past decade.

5.1.1 Habitat

It is widely accepted that an increase in coral cover will tend to lead to an increase in parrotfish abundance, as abundance is positively correlated with coral cover and negatively correlated with macroalgal cover, although the strength and nature of this relationship vary between locations (Tzadik and Appeldoorn, 2013; Howard *et al*., 2009; Sabater and Tofaeono, 2007). Observed spatial variation is often thought to be at least partly due to differences in sampling methods, in the condition of habitat cover, or in the spatial scale of the study (Newman *et al*., 2006; Sandin *et al*., 2007). The present findings, however, suggest that variation in parrotfish density and its relationship with benthic habitat were not merely artefacts of sampling methodologies, but were most likely related to differences in benthic habitat and in fishing pressure (Chapter 2; Chapter 3). Lack of significant correlation between parrotfish density and benthic habitat cover was likely due to relatively uniform low percentage coral cover across many sites (Chapter 2). The initial decline in fish abundance due to a reduction in live coral cover is likely to have been swift (Graham, 2008) but fish population density will tend to stabilise when coral cover reaches or declines beyond a certain threshold (Holbrook *et al*., 2008). The spatial scale of a study can also affect the observed relationship. For example, there was no significant correlation between parrotfish density and benthic habitat variables in some countries, but these variables were significantly related at Caribbean scale (Chapter 2).

Parrotfish density and biomass were positively associated with habitat complexity. The impact of the loss of live coral and reduced reef structural complexity (loss of live coral have caused a dropping of reef carbonate production rates, possibly weakening reef growth, eventually directing to net reef erosion, and leading to reduction of reef structural complexity; Perry *et al.*, 2013) will be most noticeable on resident reef species (Chapter 2; Garpe *et al*., 2006; Graham *et al*., 2006). This study reinforces corroborates other studies showing significant correlations between fish abundance and reef complexity (Hixon and Beets, 1989; Friedlander and Parrish, 1998;

Gratwicke and Speight, 2005b; Chong-Seng *et al.*, 2012; Bozec *et al.*, 2013). One likely explanation for these is that parrotfishes become more reliant on the availability of suitable shelter as threats from predation and fishing increase. There is also possible that the fish that are not fished or predated are those that are more attached to reef complexity, e.g. less mobile fish. This implies that there will be a greater likelihood of success in maintaining parrotfish abundance if the structural complexity of the reef remains high, however it is very unlikely that this complexity alone will be sufficient to nullify or counteract the impact of fishing pressure (Chapter 3).

This study has advanced knowledge of the drivers of parrotfish density and biomass at various body sizes, and highlights the likelihood that parrotfish move between habitats during their life cycle. The results demonstrated that parrotfish of different size classes were associated with different habitats, a finding which also reinforces the importance of habitat cover and complexity (Chapter 2; Hixon and Beets, 1989; Bozec *et al.*, 2013).

Size-dependent habitat utilisation might be a strategy adopted by parrotfish in order to seek refuge from predators or fishing. This is evident from the differences in habitat complexity requirements between small and large parrotfish. Small parrotfish may need shelter from predatory fishes, e.g. grouper (Mumby *et al.*, 2006), while larger parrotfishes may need some form of refuge or protection from fishing and predator in the form of suitable hole density and size (Chapter 2; Hixon and Beets, 1989). Meanwhile, medium-sized fish (11-20cm) do not seem to require as much protection as they are most likely already large enough to have a good chance of avoiding becoming prey but still small enough to be less attractive to fishers; these fish seem to prefer sites with relatively high live coral cover in which generally has high habitat complexity. However, it is also likely that significant positive relationship between medium size parrotfish and coral cover is linked to increasing coral cover due to macroalgae grazing by parrotfish (Mumby *et al.*, 2007a; Mumby, 2009).

These results indicate that parrotfish depend on the presence of living coral (or vice versa) and high habitat complexity particularly during certain phases of their life cycle. The loss of live coral and reduced habitat complexity could affect parrotfish density and biomass, similarly to other fishes dependent on high structural complexity (Garpe *et al.*, 2006; Graham *et al.*, 2006; Pratchett *et al.*, 2008). Loss of habitat complexity would reduce habitat ability to provide refuge for fish and impairing fish become more vulnerable from predation and fishing, leading to the decline of fisheries productivity (Graham, 2014; Rogers *et al.*, 2014). Knowing and understanding the factors that drive changes in parrotfish density and biomass at different body sizes can provide additional information which could be taken into consideration in the protection and management of parrotfish. It is however clear that, due to the increasing threat of fishing targeting larger fish, there is an urgent need to reduce the fishing threat. One way to do this would be to enact fishing bans to allow parrotfish populations to recover.

5.1.2 Fishing pressure

There has been progress in understanding the relationship of parrotfish density and biomass with fishing pressure. It has been shown that the extraction of large-bodied fish through fishing can result in the decline of fish numerical abundance and biomass (Chapter 3; Ruttenberg, 2001; Hawkins and Roberts, 2004a; Tuya *et al.*, 2006; William *et al.*, 2008; Sabetian, 2010; Bellwood *et al.*, 2011). The present study has shown how parrotfish density and biomass may decrease with increasing fishing pressure over a large spatial-scale. It also confirms previous studies (Aswani and Sabetian, 2010; Mumby *at al.*, 2011; Thyresson *et al.*, 2011) indicating that parrotfish may have increasingly become a target for fishing, at least in some countries in the Caribbean.

There are at least two commonly used indices of fishing pressure: fisher density per unit of reef area (Jennings *et al.*, 1995; Hawkins and Roberts, 2004a; Friedlander and Brown, 2004; Campbell and Pardede, 2006; Tuya *et al.*, 2006) and human population density within a certain radius of the reef site surveyed (Jennings and Polunin, 1997; Dulvy *et al.*, 2004; Stallings, 2009; Wilson *et al.*, 2010; Valles and Oxenford, 2014). In this study, fisher density was significantly and negatively correlated with both parrotfish abundance and biomass, while a negative correlation with human population size was observed for parrotfish abundance but not for parrotfish biomass across the Caribbean (Chapter 3). These results suggest that for Caribbean parrotfishes, fisher density would seem to be a more powerful predictor and a more appropriate proxy for fishing pressure than human population size. This is consonant with the suggestions of Dulvy *et al.* (2004) and Cinner and McClanahan (2006) that fisher density may provide a better index of fishing pressure than indices based on human population size since fishing pressure directly affect parrotfish than human population index (Chapter 3).

The use of fishing pressure indices in order to examine their relationship with fish assemblages is not without its drawbacks. Obtaining accurate data can be a major challenge and there can be many difficulties in attempting some kind of standardization of fishing effort across different gear types (Hawkins and Roberts, 2004a; Tuya *et al.*, 2006). Using the ABC method to derive the W-index values could be one simple and cost effective way to assess impacts of fishing pressure in a data-poor situation. However, this solution would need to be tested on other reef fish communities to ensure the wider validity of the method.

Under the current scenario where herbivore (e.g. sea urchin) abundance is low (Levitan *et al.*, 2014; Lessios, 2015), and in which healthy parrotfish populations are needed in order to help the recovery of corals (Mumby, 2009; Bonaldo *et al.*, 2014), the fact that parrotfish have become a target for fisheries is concerning. Indeed, there would seem to be an urgent need to reduce the fishing pressure on parrotfish, for example by introducing MPAs in strategic locations.

MPAs are one method which has been proven potentially effective in providing protection and increasing fish density and biomass (Roberts, 1995; Barrets *et al.*, 2007; Lester *et al.*, 2009; Molloy *et al.*, 2008; Graham *et al.*, 2011; Edgar *et al.*, 2014). However, our results suggest that, although parrotfish biomass was significantly higher within Caribbean MPAs, parrotfish density did not differ significantly (Chapter 3). Parrotfish protected by a trapping ban in Bermuda showed a biomass 3.7 fold increase, but no increase in recruits, indicating no significant increase in numerical abundance (O'Farrell *et al.*, 2015). Indeed, in areas with low coral cover and structural complexity, the protection offered by some small MPAs has had no discernible effect other than higher biomass of fishery target species (Graham *et al.*, 2007; McClanahan *et al.*, 2007; Graham, 2008), which might be also the case for parrotfish. It has been suggested that MPAs may be able to provide protection for large parrotfish from fishing, but result in increased risk of predation for small parrotfish as an effect of increased large fish predators (McClanahan *et al.*, 2007; Mumby *et al.*, 2007a).

While the present study also found that juvenile parrotfish density did not differ significantly between sites inside and outside of MPAs, the density of terminal parrotfish was significantly different (Chapter 4). This result indicates that protection, in the form of an MPA, should at least be able to increase the density of large fish, which in turn is expected over time to increase recruitment, even though it is very likely that predation will have a substantial effect on population dynamics and size/age structure. Further research on the interaction between predator and parrotfish population abundances and structures inside MPAs is necessary. If this indirect effect has a negative impact which is greater than the direct effect of increasing large parrotfish abundance, it may be necessary to find more effective alternative or additional forms of protection, such as gear, species, or access restrictions (MacNeil *et al.*, 2015). MacNeil *et al.* (2015) further suggested that a combination of approaches might be needed to successfully manage fish recovery.

Without good planning and law enforcement, MPA formation will result in ineffective protection for either parrotfishes themselves, parrotfish habitat, or indeed parrotfish predators. The absence of significant differences in parrotfish density within and outside MPAs may well be an indication that some MPAs in the Caribbean are not effectively managed. There are many reasons why an MPA can be ineffective. Recently many large MPAs have been established, and there is some concern that this increase in size reflects a growing tendency to prioritize quantity over quality (Singleton and Roberts, 2014). Large scale MPAs are likely to promote holistic conservation and connectivity between ecosystems, however they also require expensive surveillance and monitoring activities (Wilhelm *et al.*, 2014) and may be unable to adequately protect parrotfish from unsustainable fishing. An MPA is also likely to be ineffective in protecting fish populations if the decline in their abundance is related to loss of habitat due to bleaching events (Graham *et al.*, 2007; Graham, 2008). MPAs is also cannot achieve their recovery potential when established less than 35 years before (MacNeil *et al.*, 2015).

Although some MPAs do not protect parrotfish fully, which might be because they were not long enough established to achieve their potential or they were setup in area where people depend on reef-based fisheries (MacNeil *et al.*, 2015), the data indicate that most of the MPAs were effective at least to some extent in protecting and maintaining parrotfish assemblages in a healthy state. This is confirmed by the ‘undisturbed’ status of parrotfish communities in 79% of the MPAs studied across the Caribbean, while only 49% of sites outside an MPA had ‘undisturbed’ status (Chapter 3). This difference provides a strong indication that a substantial number of MPAs are in fact helping to increase parrotfish biomass.

Out of the eight Caribbean countries included in this study, only Bonaire and Curaçao had country level 'undisturbed' parrotfish assemblage status. Given the important role of parrotfishes in shaping reef communities, there is a concern that reef recovery might be very difficult to achieve in the other six countries with ‘disturbed’ parrotfish populations. There is a need for serious attention from all stakeholders across the Caribbean in order to find ways to restore parrotfish populations and maintain them in a healthy state.

Fishing pressure can negatively affect parrotfish density and biomass (Chapter 4; Hawkins and Roberts, 2004b), however, the present study only found a significant relationship between juvenile parrotfish density and fishing pressure. Combined with other data, this result would seem to indicate that the abundance of large parrotfish is so low that it is no longer affected by the fishing (Chapter 2; Chapter 3). In such a situation, it has been shown that fishing pressure may result in an indirect effect on juvenile density due to reduced recruitment (Bohnsack, 1990).

Although fishing pressure was not significantly correlated with initial and terminal phase parrotfish density, there was a significant correlation with the mean size of these two phases. One explanation for this phenomenon is that Increased fishing pressure is likely to cause a reduction in the mean size of both the initial and terminal phases (Chapter 4; Hawkins and Roberts, 2004b). If fishing pressure is not reduced, it can be expected that the average size of terminal phase fish will continue to decrease. However in some countries, particularly St. Lucia, an increase in the average size of the terminal parrotfish was observed (Chapter 4; Hawkins and Roberts, 2004b), a trend which is thought to be due to an increase in public awareness and a reduction in fishing pressure (Mumby *et al*., 2006; Mumby, 2009; Organization of Eastern Caribbean States, 2009; Jackson *et al*., 2014). If this is indeed the case, then it is reassuring to think that, with appropriate conservation efforts, parrotfish density and average size can be increased, and population status improved.

Although the mean size at which the parrotfish terminal phase change occurs is often used as an indicator of the response to fishing (Bruggemann *et al*., 1994; Hawkins and Roberts, 2004b), the results of the present study indicate that size at phase change is not necessarily the phase mean size (Chapter 4). This study succeeded in estimating size at phase change by using a density plot. In Bonaire, Curaçao, SVG, Antigua and St. Lucia, fish size at phase change was above the regional average calculated across 8 countries in the Caribbean. Meanwhile in Jamaica, the Dominican Republic and Barbados the size at phase change was below the regional average size. This implies that conservation efforts are required to increase and restore the size at phase change in these three countries. This could most likely be achieved by reducing fishing pressure to allow fish to grow to their maximum size (Chapter 4).

In general, Bonaire was showed more intact habitat compared to other countries. Bonaire had highest parrotfish biomass, had positive W-index (undisturbed), had highest percentage of terminal phase parrotfish and had largest initial-terminal phase intersection size. Meanwhile, Jamaica was showed as degraded and disturbed parrotfish communities. Jamaica had lowest parrotfish biomass, had negative W-index (disturbed) and had smallest initial-terminal phase intersection size.

5.2 Management

With perceptible evidence of threats from loss of habitat and fishing pressure on parrotfish assemblages, it is clear that more effective management efforts are required to help reduce the impact of these threats and improve parrotfish and/or habitat recovery. One tool that could be used is the establishment of additional MPAs, with expectations of increasing fish density and average parrotfish size (Chapter 3; Chapter 4; Roberts, 1995; Barrets *et al.*, 2007; Lester *et al.*, 2009; Molloy *et al.*, 2008; Graham *et al.*, 2011; Edgar *et al.*, 2014; MacNeil *et al.*, 2015). However in order to obtain the desired results, many factors need to be considered such as choice of location and the size of the MPA as well as ensuring effective management, including law enforcement.

Providing protection for parrotfish via establishing an MPA may not produce rapid increases in fish density, as the abundance of fish tends to vary significantly with reserve age and condition (Molloy *et al.*, 2008). Typically, coral reef fish are anticipated on average to need 35 years of protection to achieve 90% recovery, while most depleted reefs would need 59 years (MacNeil *et al.*, 2015). In the current situation where benthic habitat has often become degraded, introducing an MPA to protect parrotfish may not have much success without some manipulation of habitat condition. When habitat complexity is very low at the MPA site, it will probably be necessary to increase habitat complexity, which tends to have a strong correlation with parrotfish abundance and population status (Chapter 2; Bozec *et al.*, 2013). One approach could be the introduction of one or more artificial reefs within the MPA. Artificial reefs increase habitat complexity, and can be used as a refuge by fishes, leading to an increase in fish abundance (Bohnsack, 1989; Hixon and Beets, 1989; Charbonnel *et al.*, 2002, Ferse, 2008; Ferse, 2009). However, the artificial reefs provided should have sufficient hole density and suitable hole size in order to be effective (Chapter 2; Hixon and Beets, 1989; Gratwicke and Speight, 2005a).

The combination of establishing MPAs, thus protecting parrotfish from fishing, with the deployment of artificial reefs, which could protect fish from predators, should have a beneficial effect on the abundance of various body sizes of parrotfish. If parrotfish density increases within a MPA, it can be expected to result in spillover effects across the MPA boundaries (McClanahan and Mangi, 2000; Abesamis and Russ, 2005; Perez-Ruzafa *et al*., 2008; Colleter *et al*., 2014). To further the protection of parrotfish, it has been stated that a moratorium on parrotfish fishing is necessary (Mumby, 2014). Other alternatives to MPAs are restrictions on some fishing gears, species or access to specific site. Fishing gear restrictions provide about 30%, restrictions on fish species that can be fished provide 40%, and restrictions to access specific site provide 50% biomass recovery (MacNeil *et al*., 2015). The prohibition of fishing could be advantageous because it would not require establishment of MPAs, but it would require very strong and vigilant law enforcement to ensure that the regulation is strictly implemented.

5.3 Conceptual model summarizing the major drivers of parrotfish abundance

This thesis and other studies make several advances in knowledge regarding parrotfish assemblages. Parrotfish abundance is positively correlated with coral cover and negatively correlated with macroalgal cover (Chapter 2; Sabater and Tofaeono, 2007; Howard *et al*., 2009; Tzadik and Appeldoorn, 2013). Parrotfish abundance also shows significant correlations with reef complexity (Chapter 2; Friedlander and Parrish, 1998; Hixon and Beets, 1989; Gratwicke and Speight, 2005b; Chong-Seng *et al*., 2012; Bozec *et al*., 2013). Parrotfish of different size classes were associated with different habitats (Chapter 2; Hixon and Beets, 1989; Bozec *et al*., 2013). Fishing can result in the decline of fish numerical abundance and biomass (Chapter 3; Ruttenberg, 2001; Hawkins and Roberts, 2004a; Tuya *et al*., 2006; William *et al*., 2008; Sabetian, 2010; Bellwood *et al*., 2011), even at large spatial-scales (Chapter 3). While parrotfish biomass was significantly higher within MPAs, parrotfish density did not differ significantly (Chapter 3), although the density of terminal parrotfish was significantly different (Chapter 4). However, MPAs could result in increased risk of predation for small parrotfish as an effect of increased abundance of large fish predators (McClanahan *et al*., 2007; Mumby *et al*., 2007a).

A simple conceptual model summarizing the known major drivers of parrotfish abundance and biomass can be developed (Figure 5.1). Such a model could be used to guide advice towards more general coral reef ecosystem recovery. Under the current scenario with low coral cover, low structural complexity and high fishing pressure, introducing a combination of effective MPAs, artificial reefs and fishing regulations (e.g. a selective fishing ban or moratorium) should substantially reduce fishing pressure on parrotfish. Reduced fishing pressure and artificial reefs to provide suitable shelter should in turn lead to an increase of parrotfish abundance. Although MPAs are believed to increase parrotfish predator abundance (McClanahan *et al.*, 2007; Mumby *et al.*, 2007a), the negative impacts on parrotfish abundance could be minimized through additional protection provided by artificial reef. Increased parrotfish abundance should then help regulate macroalgae (Steneck, 1988; Williams and Polunin, 2000; Mumby *et al.*, 2006; Hughes *et al.*, 2007b; Burkepile and Hay, 2008; Mumby, 2009); help provide suitable hard substrate for coral recruitment (Ledlie *et al.*, 2007, Mumby *et al.*, 2007a; Bruckner *et al.*, 2014); and promote higher structural complexity. These processes should lead to a positive feedback loop (Mumby and Steneck, 2008) and eventually to sustainable reef and parrotfish population recovery.

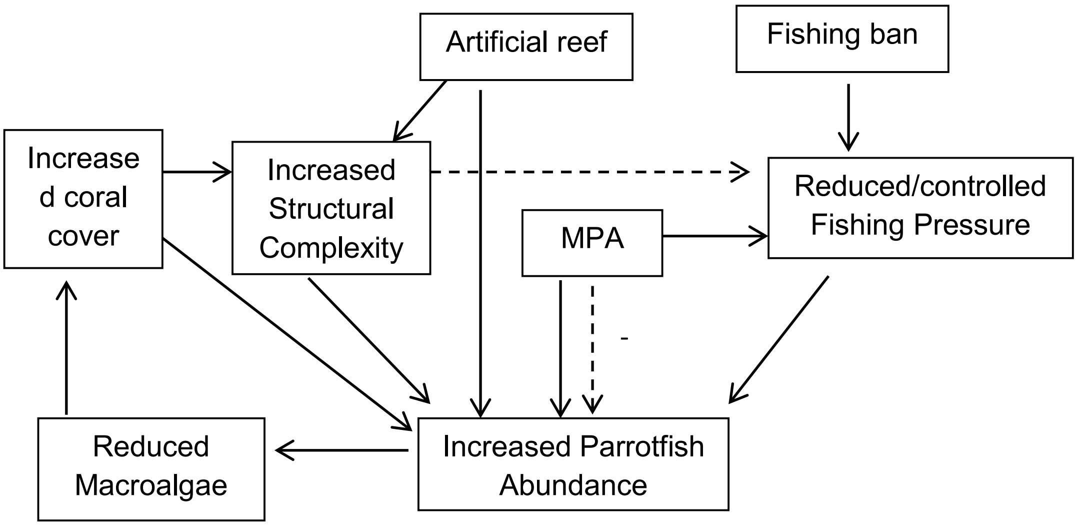

Figure 5.1 Simple conceptual model for enhancing parrotfish abundance and promoting coral cover and structural complexity. - indicates negative effect of MPA on parrotfish abundance. Solid lines represent direct, while dashed lines represent indirect effect.

Many fundamental questions on the ecology and conservation of parrotfish remain unanswered. There may be for example a reciprocal relationship between the abundance of parrotfish and benthic habitat cover. Firstly, it is likely that, all other factors held constant, increased coral cover will lead to an increase in fish abundance (Syms and Jones, 2000; Pratchett *et al.*, 2006; Holbrook *et al.*, 2008; Pratchett *et al.*, 2011). Secondly, again with other factors held constant, it is likely that an increase in the abundance of fish, including herbivorous fish, will lead to an increase in coral cover (Bellwood *et al.*, 2006). Parrotfish, which feed on algae, help reduce macroalgae cover and in turn provide a hard substrate for coral recruitment (Burkepile and Hay, 2006; Mumby and Steneck, 2008; Mumby *et al.*, 2014). However, this perceived impact of parrotfish abundance on coral cover has not yet been conclusively proven since most studies have been conducted on discrete occasion (short term) over small controlled areas or are based on correlative evidence (as here). There is need for further investigation into how parrotfish regulate benthic cover over long time periods and at different spatial scales.

While MPAs are believed to have positive effects on parrotfish abundance, it is suspected that there are often indirect effects due to increasing predators and competitors that may prevent parrotfish recovery (McClanahan *et al.*, 2007; Mumby *et al.*, 2007a). In this context, the extent to which predators and competitors affect parrotfish abundance, population structure (within species) and parrotfish community composition within an MPA is a matter which warrants further attention.

The use of artificial reefs as a fish-aggregating tool has been well studied (Bohnsack, 1989; Charbonnel *et al.*, 2002; Gratwicke and Speight, 2005b), however how parrotfish make use of or benefit from such reefs is unknown. As parrotfish abundance is correlated with habitat complexity (rugosity, hole density and size), they are likely to benefit most from artificial reefs with suitable hole numbers and sizes at degraded sites with low habitat complexity. Thus, research on how artificial reefs with variable hole density and size affect parrotfish abundance should be conducted over various time frames and at a number of spatial scales. Although at macroecological scales, the cost of such interventions would need to be considered in relation to the magnitude of such effects.

Food availability may influence sex change in fishes or other organisms as the growth rate affects the optimal size for sex change (Charnov, 1982). Algae is the main source of food for majority of the parrotfishes, so that less food means increased competition between individuals, which will result in a size advantage model where extrinsic and physiological conditions may result in alterations of size during each life phase, including sex change (Warner, 1988a). Thus, the effect of algal abundance and seasonality of algal abundance on parrotfish life phase or sex change need to be assessed.

Appendix 1 PCA loadings value of 4 benthic habitat (coral, CCA, macroalgae, turf).

Benthic habitat	Loadings value
Coral	-0.341
CCA	-0.151
Macroalgae	0.881
Turf	-0.291

Appendix 2 Example of multiple linear model selection based from AIC value.

Country	Model	AIC
Antigua	Sparisoma density ~ PCA1 + RI + HoleAve + HoleDen	-17.6
	Sparisoma density ~ PCA1 + HoleAve + HoleDen	-19.31
	Sparisoma density ~ PCA1 + HoleAve	-21.17
Curacao	Sparisoma density ~ PCA1 + RI + HoleAve + HoleDen	-31.41
	Sparisoma density ~ PCA1 + RI + HoleDen	-32.46
St. Vincent and the Grenadines	Sparisoma density ~ PCA1 + RI + HoleAve + HoleDen	-29.03
	Sparisoma density ~ PCA1 + RI + HoleAve	-30.88
	Sparisoma density ~ RI + HoleAve	-31.48

Appendix 3 Example of linear mixed effect model selection based from AIC value.

Size	Model	AIC
0-10cm	Parrotfish density ~ PCA1 + RI + HoleAve + HoleDen	58.27
	Parrotfish density ~ PCA1 + RI + HoleAve	56.29
	Parrotfish density ~ PCA1 + RI	55.42
	Parrotfish density ~ RI	55.11
11-20cm	Parrotfish density ~ PCA1 + RI + HoleAve + HoleDen	112.80
	Parrotfish density ~ PCA1 + RI + HoleDen	110.94
	Parrotfish density ~ PCA1 + RI	109.92
	Parrotfish density ~ PCA1	108.55
21-30cm	Parrotfish density ~ PCA1 + RI + HoleAve + HoleDen	-13.05
	Parrotfish density ~ PCA1 + RI + HoleDen	-15.04
	Parrotfish density ~ PCA1 + HoleDen	-16.97
>30cm	Parrotfish density ~ PCA1 + RI + HoleAve + HoleDen	65.90
	Parrotfish density ~ PCA1 + HoleAve + HoleDen	64.24

Appendix 4 Output from the multiple linear regression model between *Scarus and Sparisoma* numerical density and benthic habitat in SVG.

Species	Predictor	Slope	SE	t	p
Scarus					
S. iserti	PC1	1.329	0.544	2.445	0.033
	Rugosity index	5.985	2.050	2.920	0.014
S. taenioterus	Hole average size	1.753	0.666	2.633	0.023
S. vetula	Rugosity index	1.597	0.608	2.627	0.021
Sparisoma					
S. aurofrenatum	-				
S. viride	PC1	0.575	0.256	2.249	0.046
	Hole density	1.197	0.276	4.337	0.001

Appendix 5 Number of Fishers, estimated reef area (ha), fisher density, human population size, parrotfish abundance and biomass, and W-index at surveyed reef sites.

Country	Reef name	# fishers	Reef area (ha)	Fisher density	Human population	Protection	Abundance (fish/100m^2)	Biomass (g/100m^2)	W-index
Antigua	3 Fathom Bank	1	12.54	0.08	0	NON_MPA	19.79	541.26	-0.0191
	Ariadne	0	1	0.00	0	NON_MPA	49.69	1082.61	0.0388
	Big Sponge	38	4.04	9.41	226	MPA	30.42	332.45	-0.0324
	Cades Deep Force	38	4.04	9.41	0	MPA	45.21	454.75	0.0302
	Cades South	38	4.04	9.41	0	MPA	25.00	317.76	0.0270
	Hercules Pillars	24	6.68	3.59	1277	MPA	12.71	1464.35	0.0966
	Salt Fish Tail	10	1.04	9.62	0	NON_MPA	227.92	2781.14	-0.1194
	Shark Reef	38	1	38.00	0	NON_MPA	87.50	1275.36	-0.0569
Barbados	Asta	180	1	180.00	2934	NON_MPA	13.85	598.54	-0.0785
	Boot	232	1	232.00	3938	NON_MPA	21.46	1748.58	-0.0415
	Clarke's	115	1.5	76.67	878	NON_MPA	33.13	2178.10	0.0155
	Escape	27	1.5	18.00	2157	NON_MPA	20.94	1353.29	-0.0125
	Folkstone	27	1	27.00	3392	MPA	14.06	790.07	-0.0220
	Paynes Bay	27	1	27.00	3229	NON_MPA	15.73	1036.72	0
	Pieces of Eight	232	1	232.00	4326	NON_MPA	7.81	186.18	0.0398
	Welcome Inn	180	1	180.00	3938	NON_MPA	16.67	845.16	-0.0246
Bonaire	Aquarius	30	14.36	2.09	345	MPA	22.81	4544.31	0.1241
	Forest	30	10.05	2.99	152	MPA	22.08	2975.57	0.0386
	Kalabas	30	14.36	2.09	405	MPA	17.19	3664.73	0.0840
	Karpata	30	14.36	2.09	505	MPA	20.10	2907.87	0.0753
	Mi Dushi	30	10.05	2.99	767	MPA	12.29	2638.76	0.1183

	Oil Slick Leap	30	14.36	2.09	474	MPA	15.10	3521.39	0.0467
	Playa Funchi	30	11.64	2.58	177	MPA	15.63	1888.40	-0.0445
Curaçao	Boka	72	25.66	2.81	3483	NON_MPA	13.33	803.55	-0.0156
	Lagun Blanku	220	29.72	7.40	110	NON_MPA	40.94	1591.90	0.1099
	Marie Pampoen	220	29.72	7.40	8422	NON_MPA	14.58	1291.55	-0.0464
	Oostpunt	220	29.72	7.40	136	MPA	28.65	1424.15	0.0368
	Playa Grandi	220	29.72	7.40	1408	NON_MPA	5.94	896.64	-0.0275
	Playa Kalki	200	29.72	6.73	271	NON_MPA	28.23	1829.59	0.0973
	Playa Lagun	200	29.72	6.73	104	NON_MPA	45.73	4838.57	-0.0195
	Vaersenbaai	72	25.66	2.81	694	NON_MPA	17.60	1324.70	-0.0749
Dominican Republic	Cayo Arena	612	17.13	35.73	0	MPA	76.88	1759.30	0.0787
	El Muro	1232	10.07	122.34	3692	NON_MPA	13.13	446.82	-0.0814
	Elephant	1232	10.07	122.34	3692	NON_MPA	7.81	172.89	0.0417
	Fronton	2514	12.9	194.88	534	NON_MPA	25.21	191.03	0.0304
	La Bomba	228	4.86	46.91	10820	MPA	32.19	1665.81	0.1410
	Miniwall	1232	10.07	122.34	3629	NON_MPA	33.44	431.27	0.0764
	Paisanito	228	4.86	46.91	10820	MPA	32.50	1224.08	0.0484
	PC1	185	15.5	11.94	430	NON_MPA	17.92	320.60	-0.0644
	PC2	185	15.5	11.94	120	NON_MPA	41.25	2104.26	-0.0105
	PC3	185	15.58	11.87	195	NON_MPA	10.83	410.23	-0.0735
	PC4	185	15.58	11.87	74	NON_MPA	24.79	1355.36	-0.0119
	Playa de Gollo	228	4.86	46.91	9334	MPA	32.71	1553.80	-0.0273
	Puerto Malo	2514	7.56	332.54	901	NON_MPA	15.21	735.68	0.0802
	Tibisi	2514	7.56	332.54	480	NON_MPA	6.25	414.42	0.0620
	Zingara	1232	10.07	122.34	793	NON_MPA	9.48	89.70	0.2106

	Alligator West	1155	1	1155.00	324	NON_MPA	7.08	347.89	0.0184
	Christopher Cove	979	24.03	40.74	702	NON_MPA	25.83	840.25	-0.0343
	Coral Gardens	1420	18.55	76.55	0	MPA	40.42	781.28	0.0433
	Discovery Bay	979	24.03	40.74	680	NON_MPA	21.25	496.87	0.0202
	Dragon Point	1155	1	1155.00	335	NON_MPA	12.19	442.92	-0.0258
	Drax Hall	979	8.43	116.13	442	NON_MPA	32.29	1025.20	-0.0076
	East Montego Bay	588	31.85	18.46	790	MPA	30.62	1242.42	0.0334
Jamaica	Fairy Hill	1155	1.41	819.15	387	NON_MPA	8.85	351.34	-0.0298
	Lighthouse	1155	3.28	352.13	272	NON_MPA	28.33	1302.78	-0.0593
	Montego Bay Secrets	588	31.85	18.46	193	MPA	38.96	1114.37	0.0238
	Runaway Bay	979	24.03	40.74	470	NON_MPA	22.60	577.31	0.0579
	Shallow Plane	1420	18.55	76.55	20	MPA	23.33	630.76	0.0227
	South Negril	1420	18.55	76.55	819	MPA	7.71	220.41	0.0342
	Spanish Anchor	588	31.85	18.46	1462	MPA	35.31	1472.59	0.0346
	West Ochy	979	8.43	116.13	679	NON_MPA	44.38	505.86	0.0036
	Anse Cochon	2	1	2.00	852	MPA	19.69	931.83	0.0296
	Anse Jabet	3	1	3.00	923	MPA	20.63	1068.82	0.0050
	Blue Hole	8	1.57	5.10	1228	MPA	22.08	402.04	-0.1326
Saint Lucia	Coral Garden	8	1	8.00	1247	MPA	30.10	1111.94	0.0904
	Petite Piton Fish	8	1	8.00	1578	MPA	26.56	630.36	-0.0564
	Petite Piton Reserve	8	1	8.00	1578	MPA	40.62	3204.98	-0.0619
	Turtle Reef	8	1	8.00	826	MPA	35.10	2002.90	0.0214
	Vigie Beach	29	1	29.00	608	NON_MPA	24.48	115.44	0.0490
	Baliceaux	25	2.34	10.68	554	NON_MPA	15.83	95.99	0
	Boulders	26	3.3	7.88	673	NON_MPA	48.65	223.31	0.0754

	Byahaut Point	80	1	80.00	1842	NON_MPA	22.08	689.36	-0.0141
	Cane Garden Pt	130	1	130.00	1261	NON_MPA	22.19	1019.68	-0.0908
	Cathedral	26	3.3	7.88	1447	NON_MPA	32.19	1164.36	0.0089
	Horseshoe Reef	25	11.63	2.15	0	MPA	60.83	563.76	0.0377
	Marine Islands	350	1	350.00	1193	NON_MPA	18.44	1747.86	-0.0334
	Mayreau Gardens	25	11.63	2.15	395	MPA	73.23	1725.18	0.0320
	Mustique	25	5.07	4.93	928	NON_MPA	96.77	982.22	0.1116
	N Union	25	2.24	11.16	1166	NON_MPA	54.38	1204.08	0.0446
	Palm Island	25	2.07	12.08	183	NON_MPA	19.58	1573.40	0.1952
	Petit Mustique	25	1	25.00	0	NON_MPA	9.06	195.90	-0.0641
Saint Vincent and the Grenadines	Petit Tabac	25	11.63	2.15	0	MPA	105.52	1157.01	0.1253
	W Union	25	2.24	11.16	1487	NON_MPA	86.04	11374.44	0.1719
	West Cay	26	3.3	7.88	265	NON_MPA	53.96	1058.42	0.0028

Appendix 6 Mean size (in cm ± sd) of three different life phases (JP: juvenile phase, IP: initial phase, TP: terminal phase) of dominant parrotfish in the Caribbean.

	S. taeniopterus			***S. iserti***			***Sp. aurofrenatum***		
	JP	IP	TP	JP	IP	TP	JP	IP	TP
Antigua	3.30±0.60	23.75±2.96	28.43±1.20	8.60±2.36	20.00±3.00	19.79±4.36	3.41±0.76	19.22+3.79	26.43±1.68
Barbados	10.53±3.28	15.00±2.16	25.11±2.16	7.83±4.45	17.00±0.00	21.39±1.58	3.71±0.88	15.72+2.17	23.16±1.98
Bonaire	6.89±1.96	21.55±1.54	27.86±1.70	5.50±2.12	-	30.00±2.83	3.15±1.21	21.43+3.53	24.47±1.86
Curacao	10.85±4.30	19.78±1.96	25.41±1.06	5.44±1.81	15.00±0.00	23.20±3.77	4.16±1.48	18.24+1.29	24.50±2.25
Dominican Republic	4.49±3.06	17.50±2.92	26.55±5.79	11.27±5.14	17.17+4.82	21.54±0.92	3.62±0.74	15.75+2.33	24.61±1.32
Jamaica	7.87±2.12	16.11±2.35	18.67±0.00	9.01±1.08	13.70+2.83	17.45±2.38	5.05±1.62	12.59+1.99	21.16±0.73
Saint Lucia	5.35±2.55	21.09±4.34	26.62±2.35	6.50±3.04	-	23.67±1.53	3.61±0.55	19.19+2.26	25.42±2.01
SVG	9.25±3.91	23.20±1.33	28.97±2.82	7.20±3.53	-	18.73±4.07	4.01±0.64	17.97+3.35	25.76±1.35

Appendix 6. Continued

	Sp. viride		
	JP	IP	TP
Antigua	3.21±0.56	26.07+8.97	41.75±2.75
Barbados	3.80±0.84	23.40+3.51	31.34±1.89
Bonaire	4.81±1.69	31.27+2.78	38.53±2.34
Curacao	4.26±0.92	24.27+3.65	34.66±2.44
Dominican Republic	3.49±0.51	23.34+4.57	27.00±8.09
Jamaica	6.11±0.00	21.03+0.47	34.25±0.00
Saint Lucia	3.57±0.58	28.32+4.46	42.21±8.80
SVG	3.43±0.64	22.31+4.71	37.04±6.51

Appendix 7 The proportion (in percentage) of different life phases (JP: juvenile phase, IP: initial phase, TP: terminal phase) of dominant parrotfish in the Caribbean.

	S. taeniopterus			***S. iserti***			***Sp. aurofrenatum***			***Sp. viride***			**All**		
	JP	IP	TP	JP	IP	TP	JP	IP	TP	JP	IP	TP	JP	IP	TP
Antigua	92.91	3.19	3.90	88.44	1.52	10.04	73.90	19.14	6.95	66.37	27.02	6.61	80.79	11.50	7.71
Barbados	16.47	44.76	38.77	47.27	1.89	50.84	26.61	47.59	25.79	43.39	50.81	5.81	29.61	43.81	26.57
Bonaire	54.50	14.82	30.68	40.00	0.00	60.00	22.93	24.36	52.71	9.23	53.33	37.44	25.92	35.94	38.14
Curacao	55.00	16.72	28.29	73.68	2.96	23.36	33.44	36.72	29.84	29.40	37.66	32.94	41.10	30.62	28.28
Dominican Republic	80.95	13.72	5.33	74.18	4.74	21.08	52.94	27.07	19.99	51.30	30.94	17.76	61.15	19.22	19.62
Jamaica	73.08	19.23	7.69	70.05	8.74	21.21	41.75	40.31	17.95	14.71	67.65	17.65	56.78	25.36	17.85
Saint Lucia	81.97	12.76	5.27	78.57	0.00	21.43	51.84	34.31	13.85	31.54	47.06	21.40	62.14	26.35	11.51
SVG	90.07	4.95	4.98	89.10	0.00	10.90	49.09	41.21	9.71	62.40	31.67	5.93	67.81	24.27	7.92

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