SHEDDING LIGHT ON THE FUTURE OF CARIBBEAN CORAL REEFS UNDER CLIMATE CHANGE

by

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Abstract

Coral reefs are important ecologically and socially but are threatened by local human impacts and future global climate change. Effective management promotes climate resilience but must take into account the unique multi-scale characteristics of coral reef ecosystems. This dissertation assessed historic trends in coral reef fish assemblages across the Caribbean, to determine the impacts of climate change and role of key environmental drivers in shaping these trends and investigated the influence of these drivers on future reef fish biodiversity. Firstly, using ecosystem indicators, I analyzed historical fisheries catches to assess the potential effects of ocean warming and habitat availability on Caribbean reef fish assemblages. I found that changes in community assemblages were higher than global average for all tropical fisheries and could be explained by increases in sea surface temperature and fishing effects. A negative interaction between reef habitats in each country and sea surface temperature in relation to changes in catch composition, suggesting that habitats may reduce the sensitivity of fish communities to warming. Secondly, using species distribution models, I projected changes in coral reefs under climate change in terms of their morphological complexity. Results showed that under a no-mitigation scenario reef complexity declines significantly, with the most morphologically complex species, *Acropora* sp., showing northward shifts in relative prevalence. Finally, I conducted multi-scale comparisons of the influence of reef complexity with other environmental variables on current and future Caribbean reef fish biodiversity. Reef fishes showed an affinity for higher temperatures, primary productivity and lower dissolved oxygen at the global scale, but tended toward more alkaline areas hosting reefs, with species showing mixed affinities toward dissolved oxygen. Regional models projected more rapid declines in biodiversity, though declines from global models were larger. Global and regional models projected similar magnitudes of range expansion, though invasions were projected mainly in higher latitudes for global models while regional models projected invasions in lower latitudes around reef-associated areas. Overall, my thesis provides new knowledge for climate-resilient conservation planning by highlighting the utility of multi-scale approaches and the role coral reef habitats may play in protecting reef fish assemblages against the impacts of climate change.

Lay Summary

Coral reef ecosystems are important to tropical nations but are being seriously impacted by climate change. It is important to understand the impacts of climate change on reef ecosystems to conserve the goods and services that they provide such as fisheries. In this thesis, I show that ocean warming has already affected Caribbean coral reef fisheries in the last few decades, while more extensive reef habitats may have helped reduce such impacts. However, my study also projects that Caribbean reef fishes and their habitats will be largely impacted by climate change, with southern Caribbean Sea being most at risk of such impacts. Effective strong mitigation of greenhouse gas emissions will reduce such impacts. Adaptation actions, such as habitat protection and fisheries management, are needed to deal with the unavoidable impacts of climate change on Caribbean fisheries.

Preface

This thesis represents my own work, with funding and guidance from my supervisor William Cheung throughout the process.

A version of Chapter 2 has been accepted for publication in Marine Ecology Progress Series. Maharaj, R. R., Lam, V. W., Pauly, D., & Cheung, W. W. (2018). Regional variability in the sensitivity of Caribbean reef fish assemblages to ocean warming. Marine Ecology Progress Series, 590, 201-209. I led the design, data analysis, visualization and writing of the manuscript with advice provided by WWL Cheung and D Pauly. The catch data used in this chapter were provided by Vicky Lam.

A version of chapter 3 is in preparation for submission for publication in a peer-reviewed journal, titled "Long-term effects of climate change Caribbean coral reef composition and structural complexity". I conceived and designed the study, visualized, and analyzed the data and wrote the first draft of the manuscript. Data and feedback were provided by Gabriel Reygondeau and William Cheung contributed toward writing the final manuscript.

For Chapter 4, I conceived and designed the study, collected, visualized, and analyzed the data and wrote the first draft of the manuscript. William Cheung and Gabriel Reygondeau provided feedback on the analysis while William Cheung contributed toward writing the final manuscript.

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First and foremost I thank William Cheung, who had just started his career as an assistant professor at the Fisheries Centre when he took the chance and recruited me, an unproven, wide-eyed and hugely naïve kid, as a student. It has only been through his immense patience, giving nature and the example set through his stalwart commitment to his work that I have made small steps toward becoming a slightly more capable scientist and human. Thank you for providing me the space to explore my own ideas, make my own mistakes and learn from them. Also thank you very much for supporting me through the time that I have been here. You provided all of the resources I needed to find success in my thesis, something that is hugely unprecedented in the part of the world I come from. I am immensely lucky to have benefitted from it.

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I want to thank my friends for making me feel at home in a foreign land. Most of us are not from here, but we managed to cut out our own odd little space in Vancouver. Thanks for all the great times over the years and for teaching me the importance of not taking myself too seriously. Stubborn as I am, I still do, but realize that this makes me a ridiculous person, and I'm fine with that just as well.

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Dedication

For my family,

This work would not be possible without the profound influence you’ve had on my life.

1 Introduction

1.1 Climate change poses a major threat to Marine Ecosystems

Marine organisms are biologically adapted through time to natural fluctuations and historical changes in global climate. However, rapid changes in atmospheric and oceanic chemistry, caused by greenhouse gas emissions from human activity since the industrial revolution in the late 19th century, are pushing many marine taxa closer to the limits of their biological functioning, threatening the structure and function of marine ecosystems (Doney et al., 2012). Coral reef ecosystems have shown large declines in recent history (Pandolfi et al., 2003) and are considered among the most heavily impacted marine ecosystems by human activities (Halpern et al., 2008). In the Pacific, the world's largest coral reef ecosystem, the Great Barrier Reef, saw a loss of ~50% of coral cover (from 28.0% to 13.8%) from 1985 to 2012 (De'ath et al., 2012). Caribbean reefs in the Western Atlantic saw a similar decline in coral cover during the same time period (Jackson et al., 2014). While the causes for these declines are mixed, the expected impacts of climate change threaten to worsen the state of modern coral reefs across the globe.

The future degradation of coral reefs from climate threats poses important consequences for the wellbeing of many coastal communities who depend upon them (Moberg and Folke, 1999). Global estimates suggest that between 5.2-6.8 million people participate in coral reef fisheries worth up to USD $5.7 billion per year (Cesar et al., 2003). Furthermore, reef fish are an important source of nutrition, providing more than half of the essential protein and mineral intake for over 400 million people across the globe (Dulvy and Allison, 2009). As such, climate change represents a clear and present threat to important components of society. Recent studies show that strong management programs are key to promoting healthy fisheries (Hilborn et al., 2020). In addition, well-managed coral reef ecosystems are more resilient to the impacts of climate change (Bates et al., 2014). However, effective ecosystem-based management for coral reefs should take into account the unique combinations of stressors and responses of coral reef ecosystems that exist across regions (Quentin Grafton, 2010).

In this chapter, I conduct a review of the primary scientific literature to examine our understanding of the major threats facing coral reef fish and their habitats under climate change. I attempt to show where the literature has made linkages between climate stressors at the global scale and ecological process relevant to fish communities at regional to local scales, underscoring important knowledge gaps that stand in the way of developing climate-proof fisheries policy. Finally, I pay special attention to coral reef ecosystems in the Caribbean region, my chosen area of study, noting the regional characteristics that set it apart from those in other parts of the world.

1.2 Climatic hazards facing coral reef ecosystems

Coral reef ecosystems are sensitive to physical and chemical conditions of the oceans that are being altered by anthropogenic greenhouse gases emissions, particularly through ocean warming, acidification, storms and sea level rises (Hoegh-Guldberg et al., 2017). Greenhouse gases have increased the amount of heat and CO_2 in the earth's atmosphere, much of which has been absorbed by the ocean (Cheng et al., 2017). The result of this has been a significant warming of the top 700 m of the global oceans estimated at 4.35±0.8 ZJ yr^{-1} between the periods of 1971–1990 and 1998–2017 (Pörtner et al., 2019). Anthropogenic carbon emissions also contribute to an increase in prevalence of marine heatwaves (MHWs), extremes of warm sea surface temperature that persist for days to months and across thousands of kilometers (Frölicher et al., 2018). These events rapidly transform optimal marine environments to ones that place life under high levels of metabolic stress (Liu et al., 2003). Climate models suggest that current trends of greenhouse gas emission will increase the probability (by a factor of 41 relative to the current day), duration (112 days), spatial extent (by a factor of 21 relative to the current day) and intensity (2.5 °C) of MHWs by the end of the 21st century (Frölicher et al., 2018).

The ocean is also a natural sink for atmospheric gases and excess atmospheric CO_2 has increased the rate of CO_2 uptake in the oceans. Because CO_2 is converted directly to carbonic acid when it is absorbed by the ocean, this increase in uptake has a profound impact on ocean chemistry, specifically in increasing its acidity. As a result, global ocean pH has declined by 0.013–0.03 pH units decade^{-1} over the past 25 years and is projected to decline a further 0.036–0.042 (Representative Concentration Pathway[1] or RCP 2.6) or 0.287–0.291 (RCP 8.5) pH units between the periods of 2006–2015 and 2081–2100 (Pörtner et al., 2019). Because of the increased exposure to glacial and ice cap melt, high altitude oceans are more diluted and have a lower buffering capacity against ocean acidification and associated declines in pH are expected to be the highest globally.

1.3 Climate change impacts on coral reef fishes

The impacts of climate change on reef fishes are associated with ocean warming and acidification and habitat loss (Munday et al., 2008). Like other marine fishes, the response of reef fishes to climate change is expected to be driven primarily by ocean warming in that they also have specific thermal windows within which they display optimal physiological performance (Pörtner and Farrell, 2008; Pauly, 2010). Though they are not thought to live very close to their thermal limits, climate impacts

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[1] Representative Concentration Pathways (RCP) are scenarios of climate forcing projected from a given atmospheric concentration of greenhouse gases. Four different concentrations result in three levels of additional energetic input (2.6, 4.5 and 8.6 W/m2) that produce distinct effects on global climate systems. Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.-F., 2011. The representative concentration pathways: an overview. Climatic change 109, 5..

still pose significant threats. While increases in temperature within thermal optima may potentially benefit coral reef fishes through increased juvenile settlement rates (Sponaugle et al., 2006), exceedingly high temperatures are associated with high pre- and post-hatching mortality (Gagliano et al., 2007). Warming may also affect reproductive output in adult fishes living in environment with temperature beyond their thermal preferences through lower mass-specific egg production (Ruttenberg et al., 2005). Reproductive effort may also be limited by reduced gonadal output in fishes that attain maturity at smaller body sizes due to restrictions on growth by lower oxygen availability (Pauly and Cheung, 2017; Barneche et al., 2018). These impacts on individual performance may cause shifts in distribution either through increased natural mortality in warmer areas or by migrating to more optimal areas (Fowler et al., 2017; Habary et al., 2017) causing a shift in community representation. . The manner in which distribution shifts occur would depend on a number of factors including, their thermal tolerances in relation to their current distribution range , the potential for acclimation and local adaptation, interactions with other species at the range boundary, dispersal capacity and the availability of suitable habitat outside the existing range (Munday et al., 2008).

While ocean acidification has been demonstrated to increase metabolic stress in reef fishes by disrupting cellular acid-base balance (Ishimatsu et al., 2008), effects are variable across species (Munday et al., 2009; Couturier et al., 2013; Sebastián and McClanahan, 2013). The most significant and consistent responses of reef fishes to ocean acidification lie in effects on their neuro-sensory functions, resulting in changes in behavior. Specifically, species show reduced sensitivity to homing (Devine et al., 2012; Devine and Munday, 2013) and predator olfactory cues (Cripps et al., 2011; Ferrari et al., 2011b; Allan et al., 2013), leading to riskier behavior and higher natural mortality (Munday et al., 2010; Ferrari et al., 2011a). On the other hand, the lack of observational studies (Munday et al., 2012) and recent laboratory evidence indicating little to no impact of acidification on fishes' ecophysiology and behavior (Clark et al., 2020) casts uncertainty on the cascading effects of ocean acidification from fishes to ecosystems.

Recent climate-driven declines in corals also pose a significant threat to the well-being of reef fish communities, specifically through the loss of refuge spaces for adult prey fish and juvenile settling habitat for larger predatory species (Holbrook et al., 2002; Jones et al., 2004). Corals within these assemblages compete for space on the coastal seascape and, among other biological traits, display a variety of skeleton growth forms that contribute to the competitive partitioning of this limited resource. Reefs with a variety of growth forms have greater overall structural complexity and an abundance and diversity of refuge spaces (Edinger and Risk, 2000; González-Barrios and Álvarez-Filip, 2018; Estrada-Saldívar et al., 2019). Such reefs have been shown to influence key aspects of reef fish ecology (Messmer et al., 2011; Graham, 2014; Rogers et al., 2014), including predation (Gilinsky, 1984; Gotceitas and Colgan, 1989; Hixon and Beets, 1993; Beukers and Jones, 1998), species coexistence (Holt, 1984) and juvenile recruitment (Gilinsky, 1984; Almany, 2004). As such, declines in coral cover and habitat complexity have been linked to declines in species richness (Newman et al., 2015), declines in small- to medium- bodied fishes (Alvarez-Filip et al., 2011c; Nash et al., 2013; Rogers et al., 2014), shifts in the representation of specific functional groups and the shortening of reef-associated food chains (Hempson et al., 2017).

Ocean warming and marine heatwaves (Oxenford et al., 2008; Eakin et al., 2010; Alemu I and Clement, 2014), storm impacts (Gardner et al., 2005) and acidification (Albright and Langdon, 2011) pose important threats to Caribbean corals. They are most vulnerable to climate change through heat stress and ultraviolet stress associated with MHWs, which disrupts the critical symbiosis they share with the algae *Symbiodinium* sp. which provide up to 90% of the nutrition for scleractinian corals (Muscatine and Porter, 1977). Up to 10% of coral declines on the Great Barrier Reef between 1985–2012 can be directly attributed to bleaching induced mortality (De'ath et al., 2012). While some corals show recovery following extreme warming events, both the frequency and intensity of MHWs are expected to increase under future climate change (Frölicher et al., 2018) providing narrower windows of recovery (Hughes et al., 2017b). In contrast to the acute impacts of warming, acidification is expected to affect corals in the long term and poses threats on two fronts: 1) it increases the rate of dissolution of coral's carbonate skeletons and 2) reduces the availability of aragonite below the concentrations required to activate key reactions associated with calcification. As a result, reefs are expected to display a shift from net accretion to net dissolution at the global scale by 2050 (Eyre et al., 2018), making them more brittle and susceptible to physical erosion. In addition, other environmental variables also play an important role in the persistence and integrity of coral reefs (Wilson et al., 2006). For instance, corals are sensitive to changes in water clarity and salinity (Kleypas et al., 1999), both of which are expected under climate change due to the amplification of the global hydrological cycle and resulting extremes in evaporation and precipitation (Durack et al., 2012). While these factors may not directly lead to coral mortality, they increase physiological stress on corals and their susceptibility to mortality inducing events such as bleaching and diseases (Harborne et al., 2017).

1.4 Region-specific biogeography and ecology may shape the way reef fish communities respond to climate change

While global status and trends in coral reef ecosystems have shown consistent degradation and declines, there are substantial variations between regions (Roff and Mumby, 2012), some of which may be linked to region-specific ecological characteristics. Modern reef fish assemblages across the globe have relatively similar taxonomic compositions at the family level, but show distinct regional identities as a result of their unique geological histories (Bellwood and Wainwright, 2002). The Caribbean basin consists of four large marine ecosystems (LMEs): the entirety of the Gulf of Mexico and Caribbean LMEs; the southern extent of the Southeast U.S. continental shelf LME; and the northernmost extent of the North Brazil Shelf LME. The basin itself is geographically complex with spatially heterogeneous physical environment that shapes the patterns and diversity in the function and distribution of marine organisms living there. Despite once being linked to the Pacific via the Tethys sea, vicariance events associated with the dissolution of the Tethys sea between the Cretaceous (97 – 124.5 Ma) and early Neogene (12-18 Ma), the closing of the Isthmus of Panama during the late Neogene (3.1 – 3.5 Ma) have contributed to the evolution of unique Caribbean marine biodiversity (Sale, 2002). Following this geographic isolation, Caribbean fish assemblages are a subset of the larger Tethys assemblage defined by lower diversity and a more temperate character compared to Indo-Pacific reef fishes assemblages (Bellwood, 1997). Previous studies on vulnerability of Caribbean reef fishes to human-related stressors such as over-fishing suggest that the species may be more vulnerable than their Pacific counterparts (Hughes, 1994) (Pandolfi et al., 2003). For example, as a result of overfishing, the density of Caribbean reef fishes (fish m^{-2}) declined by 2.7–6.0% $year^{-1}$ between 1955 to 2007 (Paddack et al., 2009).

At regional to local scales, climate-driven changes in the quality and availability of habitat may also influence the response of fish assemblages to climate change. Specifically, variations in future climate stress and differences in response to this stress may cause coral assemblages to be dominated by corals with simpler growth forms that support less complex reefs. The factors driving such variations are numerous, but the composition of coral assemblages is thought to be the most important factor (Van Woesik et al., 2012a). Generally speaking, species with boulder and weedy growth forms have shown lower rates of bleaching-induced mortality than those showing branching growth forms (Loya et al., 2001; McClanahan, 2004; van Woesik et al., 2012b). In addition, variations in the frequency and severity of environmental stress across space may cause some areas to be more heavily impacted than others. For instance, in East Africa, observed mortality during the 1998 and 2005 mass bleaching events was significantly related to differences in thermal regimes among sampling sites (McClanahan et al., 2007).

The potential interactions between habitat and climate change have not been extensively researched, primarily because of the difficulty in disentangling multiple confounding effects. However, recent evidence suggests that biological populations may be less vulnerable to climate stress when their preferred habitat is readily available (Mantyka-pringle et al., 2012; Maharaj et al., 2018). It is all but certain though that declines in species richness and shifts in community composition driven by warming, acidification and habitat loss will influence the overall productivity of coral reef ecosystems and fisheries, especially if functionally important species are among the most vulnerable (Graham et al., 2006; Halpern and Floeter, 2008; Messmer et al., 2014; Rogers et al., 2018).

While previous studies have identified the main climate threats facing coral reefs, the most vulnerable functional components and, to a lesser extent, projected their impacts under future climate scenarios (Buddemeier et al., 2011; Bozec et al., 2015), the consequences of these vulnerabilities and impacts on coral reef- associated fish assemblages are still not fully understood (Graham et al., 2011). As such, there still remains a sizeable gap in the knowledge required to build ecosystem-based fisheries management and conservation programs that are resilient to the impacts of climate change. In this thesis, I attempt to address this knowledge gap by exploring how climate-induced changes in the marine physical environment and availability of coral reef habitat in the Caribbean region may shape the response of reef fish communities to climate change. Specifically, I aim to answer the following questions:

What is the relative influence of climate change, habitat loss and fishing on Caribbean reef fish communities?

How might the response of coral reef assemblages to climate change affect the structural complexity of fish habitat in the future?

What is the relative influence of habitat loss and climate change on future reef fish biodiversity?

1.5 General approach

In this thesis, I explore the relative influence of physical environmental factors and habitat on the distribution of coral reef fishes in the context of climate change. Using historical fisheries catch data, I test the hypotheses that ocean warming has already affected coral reef fish assemblages and composition of fisheries catches in the Caribbean Sea; the variability in the detected shift may be explained by differences in exposure to ocean warming and habitat availability across the Caribbean (Chapter 2). I then use species distribution modelling algorithms to further explore the relationship between climate change, quality of coral reef habitats and biogeography of Caribbean coral reef fishes. Specifically, I use species distribution models to project the future distribution of Caribbean coral reef assemblages under future climate change, providing projections of climate impacts on habitat complexity based on the outputs from these models (Chapter 3). I apply the fundamental understanding and quantitative relationship between the physical ocean environmental conditions, coral reef habitats and the associated reef fish assemblages to project the fate of fisheries important species in the Caribbean under scenarios of climate change. Moreover, I test the relative importance of different environmental variables on the current and future distribution of Caribbean reef fishes. In addition, I explore the relative contribution of basin- and local- scale environmental factors in determining the future biogeography of Caribbean coral reef fishes (Chapter 4).

This thesis adds to the current understanding of climate impacts on marine biodiversity by exploring specific regional factors outlined in the established literature that may shape the response of reef fish communities in the Caribbean to climate stress. First, I show that climate impacts will vary significantly across the region. Second, I provide evidence to suggest that addressing local-scale factors may increase the resilience of coral reef assemblages under climate change. Finally, I show that regional-scale uncertainty in the impacts of climate change on Caribbean reef fish assemblages may be explained by considering biogeographical characteristics of Caribbean reef fish assemblages that distinguish them from global-scale factors.

2 Regional variability in the sensitivity of Caribbean reef fish assemblages to ocean warming

2.1 Introduction

Many tropical developing countries benefit from the wide array of ecological goods and services provided by coral reef ecosystems including nutrition, economic security, coastal protection and recreation (Moberg and Folke, 1999; Brander et al., 2007; Seenprachawong, 2016). Previous studies suggest that ocean warming could drive large-scale shifts in the distribution of fish species, with the potential to alter the composition, dynamics and productivity of local fish assemblages as well as their dependent fisheries (Cheung et al., 2013a; Jones et al., 2015). However, making predictions about the future state of local communities in the context of climate requires a better understanding of the role that small-scale heterogeneity in the broader ecosystem may play in shaping these impacts (Sherman, 2014). Here, we investigate the role played by two factors considered very influential in shaping reef fish assemblages: thermal exposure and habitat availability.

The relationship between thermal exposure and metabolic functioning across marine fishes through oxygen-limitation is well established (Pörtner and Knust, 2007; Pauly, 2010; Pauly and Cheung, 2017), as are the implications for their distribution and abundance (Dulvy et al., 2008; Cheung et al., 2011; Fernandes et al., 2013). Because thermal tolerance varies across fish assemblages, shifts in composition are likely, though the rate at which these changes occur may differ depending on their degree of thermal exposure. Cheung et al. (2013b) illustrated this using an ecological indicator, the Mean Temperature of the Catch (MTC), to demonstrate that species with higher thermal tolerances were increasing in dominance in fisheries catch across the Large Marine Ecosystems (LMEs) of the globe in accordance with rates of Sea Surface Temperature (SST) increase (Cheung et al., 2013b).

The impact of external environmental stressors has been shown to scale negatively with habitat size across a variety of spatial scales in terrestrial (Amundrud and Srivastava, 2015) and marine realms (Nagelkerken et al., 2015). While mechanisms seem to be specific to each system, they generally relate to the provision of habitat resources, which are understood to be more abundant on larger habitat tracts. In the case of coral reefs, most of the prominent literature focus on the importance of the number and density of refuge spaces (Messmer et al., 2011; Graham, 2014; Rogers et al., 2014) in mediating key ecological processes such as species coexistence (Holt, 1984), recruitment (Gilinsky, 1984; Almany, 2004) and predation (Gilinsky, 1984; Gotceitas and Colgan, 1989; Hixon and Beets, 1993; Beukers and Jones, 1998). In essence, more complex and extensive reef habitat will have greater numbers of fish refuge spaces and as a result, more diverse and abundant fish assemblages.

Fishing may exacerbate the sensitivity of marine populations and communities to climate change (Perry et al., 2010). Specifically, it has been shown to increase the variability of population size as the surplus production typically targeted by fisheries acts as a buffer against environmental variability (Hsieh et al., 2006). In addition, temperature may reduce the reproductive output of fish populations, and as such their regenerative capacity (Rijnsdorp et al., 2010). Given the importance of reef fisheries to the region, it is likely that such impacts are affecting the resilience of reef species against the effects of ocean warming.

In this study, we build on the findings of Cheung et al. (2013b) by assessing the strength of the relationship between SST and MTC trends focusing on the Caribbean LME and the associated coral reef fisheries. Furthermore, we assess the influence of habitat resources across this LME in shaping the impact of ocean warming on coral reef assemblages, with consideration of potential effects of fishing-induced changes in assemblages. Given the previously mentioned theoretical basis, here we establish our main assumptions regarding the interaction of climate with the mediating effects of habitat and fishing:

Habitat effects-

1. For two coral reefs A and B, with A being the larger of the two, reef A will have a greater quantity of habitat resources.
2. Habitat resources are important for various fish life history processes and increase the resilience of fish populations, particularly for less thermophilous species.

   Because of assumptions 1 and 2, changes in community structure in reef A in response to ocean warming are more likely to be slower than in reef B resulting in smaller values for ΔMTC.Fishing effects-

1. Reef fisheries tend to target large, high trophic level species over smaller lower trophic level species
2. Larger, higher trophic level species are slower growing, making them less sensitive to ocean warming compared to smaller, faster-growing species
3. Because of assumptions 1 and 2, for two fish communities A and B, with A being the less fished of the two, community A will show a smaller decrease in mean trophic level, indicating a greater presence of larger-bodied fish species and as such be less sensitive to the impacts of ocean warming.

2.2 Methods

2.2.1 Site Description

The Caribbean Large Marine Ecosystem (CLME) is an area of 3.2 million km^2 situated in the tropical western hemisphere and bounded by North America (South Florida), Central and South America and the Caribbean archipelago (Fig. 1). Since the closing of the Isthmus of Panama some 3.5 – 3.1 Mya, species and ecosystems within the region have taken on evolutionary pathways distinct from those of other similar regions of the world and as a result, contains numerous endemic species (Kuffner and Toth, 2016). Coral reef complexes within the region, which in total constitute ~7% of global coral cover, are distributed throughout the region, intimately associated with islands of the Caribbean archipelago. They range in size from smaller fringing reefs (e.g., the Buccoo reef complex off the southwestern coast of Trinidad & Tobago) to larger barrier reefs (e.g., the Meso-American barrier reef associated with the Yucatan Peninsula of Central America) (Cortés, 2003). Since the 1980s, many of these reefs have experienced significant declines in structural complexity, overall coverage and shifts to community dominance by macroalgae species (Alvarez-Filip et al., 2009; Jackson et al., 2014) .

The CLME has also experienced significant increases in ocean temperature (Hayes and Goreau, 2008; Jury and Winter, 2010), with negative consequences already observed for coral reef ecosystems across the region. The CLME is also located within the geographically complex Caribbean basin, the circulation patterns of which result in substantial spatial heterogeneity in the observed warming trend (Hayes and Goreau, 2008) (Fig. 1).

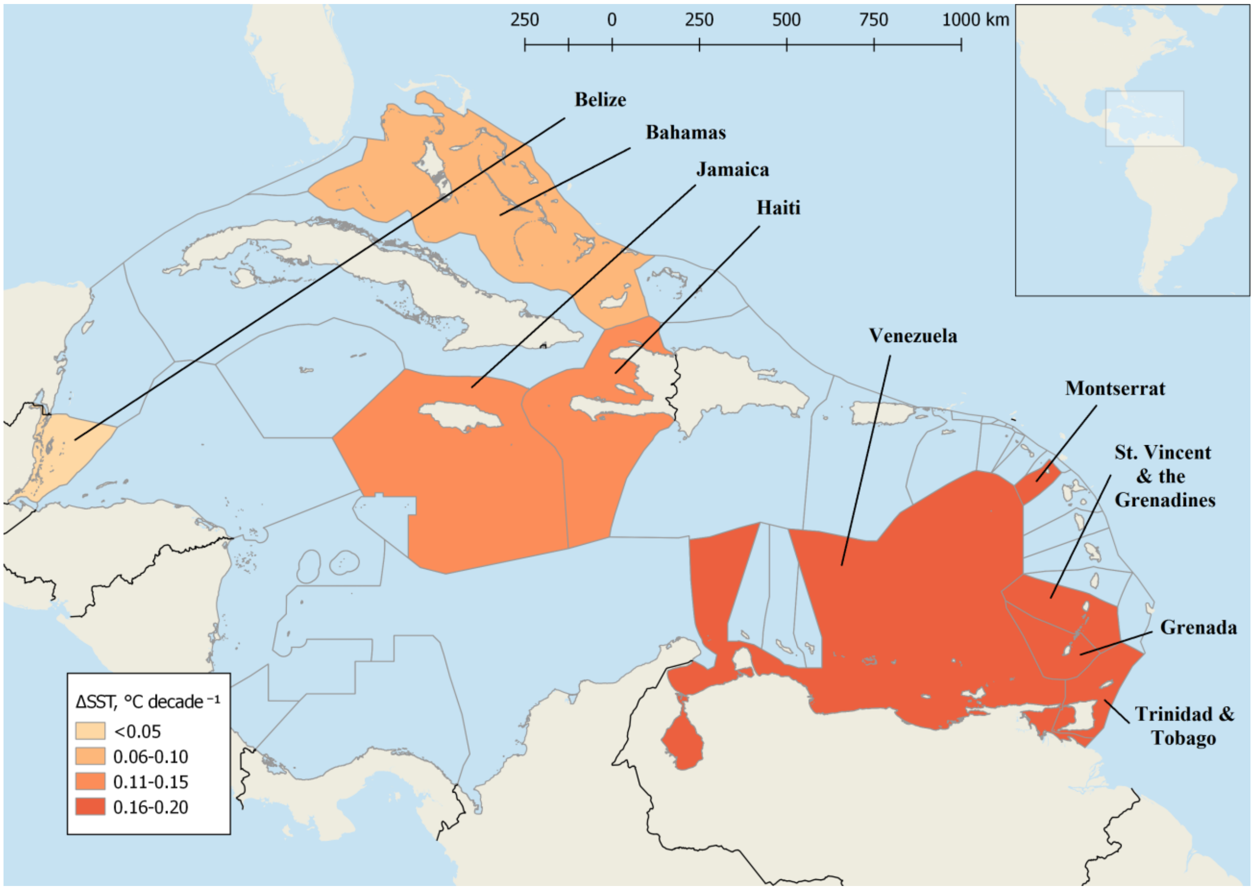

Figure 2.1 The Caribbean Large Marine Ecosystem; the EEZs of the 9 countries considered here are highlighted, with the colors reflecting the strength of ocean warming (ΔSST, from 1971-2010).

Fisheries in the CLME target a wide range of ecosystems from shallow reefs to open water pelagic systems, with coral reefs being the most socio-economically important, supplementing the income and nutrition of many local communities. More specifically, reef fisheries focus on a variety of species spanning the entire breadth of taxa represented in coral reef ecosystems. While these fisheries are generally considered overfished, fish landings and effort levels are thought to have stabilized in the early 1980s (Mahon, 2002). In this study, 9 countries were selected to represent the region (Table 1). We outlined the criteria for their selection in the following sections.

2.2.2 Fisheries and environmental data

Fisheries landings were obtained through the Sea Around Us catch reconstructions database (Pauly and Zeller, 2016). This database complements the Food and Agriculture Organization records of global fisheries landings (which is based on self-reports by member countries), using a variety of sources ranging from national archives to field reports to correct official estimates and increase the resolution of data around catch composition and fisheries sector. The resulting catch estimates were aggregated by each country's EEZ (Fig. 1). In this analysis, we obtained a subset of the catch from 1971-2010 containing only species with estimates of thermal preference and a non-zero value of coral affinity. Catch data were then processed further by removing taxa across the catch record that fulfilled at least one of three criteria:

1. Taxon comprised >20% of a single country's catch record;
2. Taxon is not included in FishBase (not a fish species);
3. Taxon is classified as 'pelagic-oceanic' according to FishBase.

Criterion 1 is implemented to remove a single taxon that may dominate the catch record, thus MTC can be more representative of the species assemblages and avoid trends that are disproportionately affected by one species. Criterion 2 is meant to remove taxa that are not fish and are not subject to the metabolic constraints of temperature and oxygen limitation. Criterion 3 on the other hand excluded coastal-migratory species that may have a non-zero value for coral affinity, but have abundance trends that are heavily influenced by the productivity of small pelagic fishes. Species fulfilling these criteria are documented in Tables A.1 and A.2. Following this, only countries with 5 or more taxa remaining in their respective catch records were selected for the study (Table 1).

Temperature and coral reef area data were obtained from published databases. SSTs were provided by the Hadley Center. This SST dataset is constructed by interpolating annual average SSTs onto a 0.5˚ x 0.5˚ grid using the nearest neighbor method, then averaging the SST of spatial cells within the EEZ boundary. Ideally, habitat availability is best represented using an index of habitat complexity collected through the study period. However, such data only exist for a small subset of Caribbean countries included in the analysis (Alvarez-Filip et al., 2009; Alvarez-Filip et al., 2011a; Alvarez-Filip et al., 2011b), precluding its use for our analysis. As such, we utilized data for coral reef area extracted from the UNEP World Conservation Monitoring Center's (UNEP-WCMC) database for the global distribution of coral reefs (UNEP-WCMC et al., 2010). While this database does not explicitly represent live coral cover, the authors assume that the area of the polygons is proportional to the likelihood that reef habitat exists. Furthermore, the database represents one of the best available databases for coral cover, especially considering its spatial coverage and the consistency of methods applied in its construction. Henceforth, we will refer to this predictor as 'Potential Reef Habitat' (PRH). PRH for each EEZ is estimated by first rasterizing WCMC shapefiles of potential coral distribution into a 0.5^o x 0.5^o spatial grid, determining the proportion of each cell that is covered by coral. This proportion was then multiplied by the estimated area of each cell, which are finally summed by EEZ and presented in Table 1.

Table 2.1 The 10 countries selected for the analyses, their potential reef habitat in km2 and the number of coral fish taxa present within the processed catch record.

Country	PRH (km^2)	Coral fish taxa in catch records
Bahamas	2869	8
Belize	1552	13
Jamaica	958	10
Venezuela	670	8
St. Vincent & the Grenadines	225	8
Grenada	213	7
Haiti	197	6
Montserrat	94	14
Trinidad & Tobago	40	6

The habitat preference index obtained from the Sea Around Us was based on qualitative descriptions of the species' degree of association to coral reef in published literature and databases (Pauly and Zeller, 2015) (see also Table A.1). It scales between 0 to 1, with 0 and 1 denoting no evidence of association and obligatory association with coral reef, respectively.

Thermal preference was estimated using the same method described in Cheung et al. (2013b), which combines the estimated relative abundance of each species with the climatology (averaged of 1971-2000) of SST data. Briefly, first the present (1971–2000) distribution of relative abundance of each species was estimated on a 0.5° latitude x 0.5° longitude grid of the world ocean. Temperature was not used in predicting species distribution to avoid circularity in subsequent analyses of which SST is an important component (Palomares et al., 2014). Second, each modelled species distribution was normalized and overlaid on the SST climatology from the Hadley Centre SST data set for 1971–2010. The temperature preference profile at SST bin i (p_i) of each species was calculated from the total relative abundance, K_i, and range area, A_i:

$$p_i = \frac{(K_i/A_i)}{\sum_i (K_i/A_i)}$$

The median value of the temperature preference profile is used as thermal preference of the species (Table A.1).

2.2.3 Calculating MTC by EEZ

We calculated annual MTC for each EEZ and the region as a while from 1971 to 2010 as the weighted average of temperature preference for taxa in the country annual catch record:

$$MTC_{yr} = \frac{\sum_i^n T_i . C_{i,yr}}{\sum_i^n C_{i,yr}} \qquad (1)$$

where MTC_{yr} is the Mean Temperature of the Catch for year yr, T_i is the estimated thermal preference for species i, $C_{i,yr}$ is the catch for species i in year yr, and n is the number of species in the catch record.

We calculated changes in SST (ΔSST) and MTC (ΔMTC) between 1975 and 2005 for each EEZ and the entire region by taking the difference between the average of 1971-1980 and 2001-2010. The formulation is as follows:

$$\Delta SST = \left(\frac{\sum_{t=2001}^{2010} SST_t}{10} - \frac{\sum_{t=1971}^{1980} SST_t}{10}\right)$$

2.2.4 Testing the relationship between SST, MTC, PRH and MTL

We examined the relationship between SST, PRH, MTL and MTC using a linear mixed-effects model. Specifically, we tested the hypothesis that SST is directly related to MTC while the available reef fish habitat, indicated by PRH, will reduce the positive relationship SST and MTC, with country's EEZ being a random effect. Prior to its inclusion in the analyses, PRH values are rescaled to a unit of thousand km^2 to increase the visibility of its associated regression parameters in the model statistics. The trends of catches may be influenced by the effects of fishing through the modification of species' population structure and their representation in the catch. We accounted for such potential effects by including changes in Mean Trophic Level (ΔMTL) in the model, an indicator that can be used to demonstrate the impact of fishing on fish assemblages (Pauly et al., 1998; Graham et al., 2017). MTL was calculated using the same formulation for MTC, by taking the weighted average of the estimated trophic level for taxa in the country annual catch record.

$$MTL_{yr} = \frac{\sum_i^n TL_i . C_{i,yr}}{\sum_i^n C_{i,yr}}$$

where MTL_{yr} is the Mean Trophic Level for year *yr*, TL_i is the estimated trophic level for species *i* obtained from FishBase (www.fishbase.org), $C_{i,yr}$ is the catch for species *i* in year *yr*, and *n* is the number of species in the catch record.

We used the R package nlme and function lme, with the full model taking the following form:

$$MTC \sim a \cdot SST + b \cdot PRH + c \cdot SST \cdot PRH + d \cdot MTL + \ z \cdot country$$

where a, b and c are matrices representing the fixed effects of *SST*, *PRH* and their interactions, while z is the random effects of different country's EEZs. Since we did not have any sub-sample of *PRH* for each country, the random effects of country's EEZs were specified for the intercept only.

We used backward elimination approach to explore the alternative hypotheses of simpler models. For each method, we sequentially removed non-significant predictors until we obtained the most parsimonious model. We also compared the goodness-of-fit and model performance based on R^2 and the Akaike Information Criterion (AIC) from alternative models.

2.3 Results

2.3.1 Trends in SST MTC and MTL

For the period of 1971-2010, the regional average of ΔSST of 0.13 ^{o}C decade^{-1} was found to be similar the global average for tropical LMEs of 0.14 ^{o}C decade^{-1}. MTC for coral reef catch across the Caribbean showed linear rates of increase of 0.19 ^{o}C decade^{-1}, on par with the global average of 0.19 ^{o}C decade^{-1} and higher than the global estimate of 0.14 ^{o}C decade^{-1} for tropical catches from all fisheries. Across EEZs, ΔSST ranged from 0.04 ^{o}C decade^{-1} to 0.18 ^{o}C decade^{-1} (Belize and Trinidad & Tobago respectively) while ΔMTC ranged from -0.10 ^{o}C to 0.62 ^{o}C decade^{-1} (Bahamas and Trinidad & Tobago respectively). More than half of the countries assessed produced estimates for ΔMTC exceeding the global mean for tropical ecosystems. Also, eight out of ten countries showed a decrease in MTL, Trinidad and Tobago having no change and Venezuela an increase in MTL. Table 2 provides a summary of these values. ΔSST and ΔMTC are seen to be significantly correlated with each other, with a glm (R function glm) returning an R^2 of 0.6. (Figure 3). Countries with smaller PRH seem to be underestimated by the simple linear relationship between ΔMTC and ΔSST.

Table 2.2 Estimates of ΔSST, ΔMTC and ΔMTL for the 9 countries assessed, along with corresponding regional and global tropical averages (* indicates values estimated by Cheung et al. 2013b)

Country	ΔSST	ΔMTC	ΔMTL
Trinidad & Tobago	0.18	0.62	0.00
Venezuela	0.17	0.16	0.05
Grenada	0.17	0.48	-0.08
Montserrat	0.16	0.49	-0.15
St. Vincent & the Grenadines	0.16	0.57	-0.11
Jamaica	0.13	0.04	-0.01
Haiti	0.11	0.00	-0.01
Bahamas	0.06	-0.10	-0.02
Belize	0.04	0.04	-0.01
Regional Average	0.14	0.19	0.01
Global Tropical Average*	0.14	0.14	-

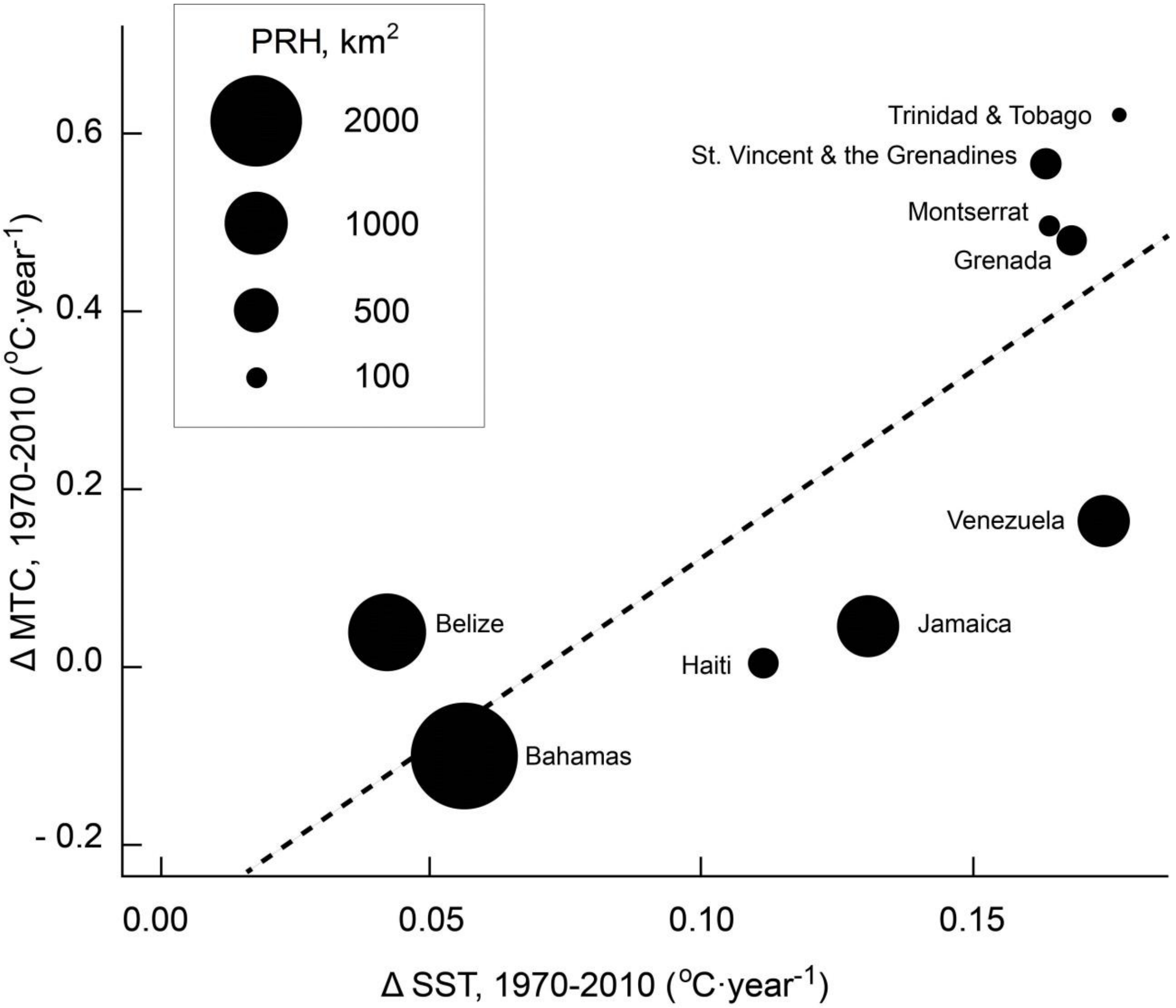

Figure 2.2 Scatterplot illustrating the positive correlation between ΔMTC and ΔSST. PRH for each country is represented by the size of each data point while the dotted line represents the linear relationship between ΔSST and ΔMTC.

2.3.2 The relationship between SST, PRH, MTC and MTL

Based on the results of the mixed effects modeling and backward elimination, the full model (with SST, PRH and their interactions, as well as MTL) was selected as the most parsimonious (Table 3). They suggest that SST is positively related to MTC and explains most of the variance. Though PRH explains a much smaller component of the variance in MTC, the interaction between SST and PRH is significant, and has a negative relationship with MTC which agrees with our *a priori* expectation. We sequentially removed the term representing the interaction between PRH and SST, and the PRH term altogether to test whether these would improve the performance of the model. The simpler models resulted in slight decreases in R^2 values and increases in AIC (Table 3). The predictor indicating fishing effect (MTL) is also significantly and negatively related to MTC, suggesting that the targeted removal of higher trophic level species may be increasing the vulnerability of reef fish assemblages to ocean warming.

Models without PRH and their interactions with SST in the model have a lower R^2 and higher AIC compared to the full model (Table 3). As PRH explained the smallest component of the variance in MTC, sequentially removed the term representing the interaction between PRH and SST, and the PRH term altogether to test whether these would improve the performance of the model. The simpler models resulted in slight decreases in R^2 values and increases in AIC.

Table 2.3 Statistics obtained from mixed effects modeling for our full model.

Model specification	Predictors	Coefficient	p-value	R^2	AIC
MTC ~ SST*PRH + MTL	SST	0.687	<0.001	0.901	308
	PRH	11.780	0.0023		
	SST*PRH	-0.422	<0.001		
	MTL	-3.200	<0.001		
MTC~SST + PRH + MTL	SST	0.430	<0.001	0.898	324
	PRH	0.232	0.4715		
	MTL	-3.272	<0.001		
MTC ~ SST + MTL	SST	0.438	<0.001	0.894	321
	MTL	-3.271	<0.001		

2.4 Discussion

Marine species are shifting their distribution ranges around the world in response to ocean warming, leading to changes in community structure (Poloczanska et al., 2016) and our study confirms that such a signature of ocean warming is robust, even at the regional and sectoral scale of Caribbean reef fisheries. They also suggest that the vulnerability of reef fisheries to ocean warming varies substantially across the region and is, for some countries, greater than previously estimated at the global scale (Cheung et al., 2013b). In addition, the negative relationship between MTL and MTC suggests that changes in trophic structure because of fishing and/or other human and natural drivers may exacerbate warming-induced changes in reef fish community structure (Hsieh et al., 2006; Rijnsdorp et al., 2010). Our findings highlight that the interactions between climate and non-climatic drivers of reef fish assemblages warrant further exploration in future studies. Finally, while the analysis is limited by the use of habitat proxy (PRH) and the relatively small sample size, the results support our main hypothesis that available habitat might play an important role in reducing the impact of ocean warming on reef fish communities. These findings add to the growing body of evidence for the important role of benthic habitat and vegetation play in moderating climate impacts on marine communities (Leonard, 2000; Mellin et al., 2010b; Mantyka-pringle et al., 2012).

While mechanisms underlying the combined effect of habitat and climate on biodiversity are better established on land compared to the ocean (Mantyka-pringle et al., 2012), thermal acclimation may serve as a possible point of intersection in the marine realm. Evidence suggests that while adults of some damselfish species show little to no capacity for acclimation (Nilsson et al., 2010; Donelson et al., 2011), juveniles display acclimation based upon the environmental conditions of their early developmental stages (Grenchik et al., 2013). This suggests that recruitment success, which complex habitat is known to facilitate (Almany, 2004), may be key to increasing the thermal resilience of reef fish across generational scales of time. On the contrary, our results suggest that even if such adaptive responses exist in some reef fishes, they may not be sufficient to fully counter the effects of warming across fish assemblages in these timescales. . Finally, with the decline of corals in recent years some scientists suggest that new configurations of reef habitat consisting of sponges, macroalgae, soft-corals and smaller amounts of slow-growing but stress tolerant hard corals, may arise in the future and continue to provide refuge spaces in some capacity (Done, 1992; Cruz et al., 2015). Due to the novel nature of such benthic configurations (Norström et al., 2009), their relative effect on the productivity of fisheries is yet to be properly understood.

Data availability and resolution were the main limiting factors in this study, affecting the number of countries included, our indices for the effect of fishing and reef habitat and finally the interpretation of our results. First, our analyses were limited to 9 EEZs since the taxonomic resolution of other country catch records did not fit the demands of our analysis. We repeated our analyses with a larger sample size by relaxing the threshold of taxonomic diversity required of a country's catch record (from 5 taxa to 3), but our conclusions remained unchanged from before (Tables A.5 and A.6). Second, the limited sample size and the use of a habitat proxy in PRH introduced some uncertainty in our statistical analyses. For example, we could have potentially avoided the apparent co-variance between exposure to ocean warming and reef habitat size if other Caribbean nations were included to increase our sample size. Furthermore, because PRH is ultimately a proxy for coral cover, it may not have properly represented the available habitat resources use by reef fish (Alvarez-Filip et al., 2011a). In addition, tropical reefs are part of a much larger coastal seascape that includes vast tracts of mangrove and seagrass habitat. Both of these play a significant role in the early life histories and survival of many of the species included in this analysis (Nagelkerken et al., 2000; Jones et al., 2010; Nagelkerken et al., 2017). As such, our analyses may be grossly underestimating the buffering effect of habitat through our limited sample size and use of PRH. Third, while MTL is a widely accepted indicator for detecting the influence of fishing on assemblages (Pauly et al., 1998; Pauly and Watson, 2005; Graham et al., 2017), its use is not an adequate replacement for effort data, which lack spatiotemporal consistency across the CLME. Future studies should expand the current analysis to test whether the effects of available reef habitat are robust when more sample EEZs from coral reefs in different part of the world area included. If the effect of available habitat area is real, it should also apply to other non-Caribbean reef fish assemblages, such as those in the Pacific and Indian Oceans. It would be useful to also use more direct observations of habitat area, as the remote sensing-based estimates of PRH used in this study may not represent habitat resources actually utilized by reef fish (Alvarez-Filip et al., 2011a). Other additional habitat-related variables that could be included in future studies include an index of reef complexity such as rugosity (Almany, 2004; Graham, 2014; Newman et al., 2015) as well as variables representing other components of the larger seascape within which corals exist. The findings from this study may help inform the design of field experiments to identify the mechanisms through which habitat availability may affect the sensitivity of reef fish communities to warming.

In conclusion, our study agrees with the growing consensus that climate change has and will continue to affect marine biodiversity, further underscoring the importance of slowing human impact on the myriad biological systems supporting important human activities. There is a dire need for effective traditional management mechanisms in the Caribbean region (Mahon, 2002), and other studies suggest that interactions between climate impacts and unmanaged fisheries are likely to weaken the resilience of fish populations (Hsieh et al., 2006; Rijnsdorp et al., 2010). Our results also agree with the growing consensus that increasing the resilience of fish populations to climate impacts will involve managing for the broader ecosystem (Levin and Lubchenco, 2008; Sherman, 2014), particularly through the designation and enforcement of marine protected areas (Agardy, 1994; Hyrenbach et al., 2000). The implementation of such plans though will also need to consider the impacts of climate on the distribution of critical reef fish habitat (Edgar et al., 2014), which have already and will undoubtedly continue to experience the greatest impacts from climate change (Hoegh-Guldberg, 2002; Orth et al., 2006; Gilman et al., 2008). It is only after measures, such as those previously mentioned, are considered will reef fisheries begin to receive thorough protection against the present and future impacts of climate change.

3 Climate change effects on the community composition and structural complexity of Caribbean reef fish habitat

3.1 Introduction

Caribbean coral reefs provide structurally complex habitat for large fish communities, providing crucial ecosystem services for countries in the region such as food supply, economic security and recreation (Moberg and Folke, 1999; Brander et al., 2007; Seenprachawong, 2016). However, in recent decades, human-driven changes of the marine environment have physically damaged coral reefs, contributed to increased intensity of coral bleaching and altered structure and functioning of coral reef ecosystems (Cheal et al., 2017; Hoegh-Guldberg et al., 2017; Hughes et al., 2017a). Particularly, change in ocean conditions impact the quality of habitat provided by coral reefs and the diversity, abundance and productivity of resident fish communities (Darling et al., 2017; Richardson et al., 2017). Attempts have been made to model the potential impacts of climate change on reef habitat quality, focusing on extreme events like bleaching and storm impact (Buddemeier et al., 2011; Bozec et al., 2015). However, a number of gaps still exist, specifically regarding the broader spatial trends of projected changes in the distribution and complexity of coral reef habitat resulting from long-term shifts in their environmental niche.

Structural complexity, defined as the physical three-dimensional configuration of a habitat (Darling et al., 2017), plays important roles in key life-history processes of fish living on coral reefs (Messmer et al., 2011; Graham, 2014; Rogers et al., 2014), including predation (Gilinsky, 1984; Gotceitas and Colgan, 1989; Hixon and Beets, 1993; Beukers and Jones, 1998), species coexistence (Holt, 1984) and juvenile recruitment (Gilinsky, 1984; Almany, 2004). Modeling the impact of climate change on the coverage and structural complexity of coral reefs is an important step to understanding the future of their associated fish communities (Wilson et al., 2010). Previous efforts have used models that investigated a number of climate impacts. For example, Buddemeier et al. (2011) compared sensitivities to long-term (growth, mortality and sensitivity of coral reefs to ocean acidification) and short-term (episodic bleaching) processes to model and simulate CO_2-related impacts on reefs of the Eastern Caribbean. Their analysis found significant declines in coral reefs in response to short-term bleaching, but not long-term acidification (Buddemeier et al., 2011). On the other hand, Bozec et al. (2015) estimated coral proliferation under climate change on the Caribbean coast of Central America by modelling coral growth dynamics under the impacts of tropical storms. These models also projected declines in coral reefs under scenarios of intense climate change through reduced structural complexity (Bozec et al., 2015). While these studies provide important first steps toward understanding the possible future changes to coral reef habitats, important gaps still exist. They include the interacting effects with broader range of abiotic environmental drivers, and the variations in the vulnerability of coral reefs due to variations in impact across space and coral assemblage structure.

While ocean warming (Oxenford et al., 2008; Eakin et al., 2010; Alemu I and Clement, 2014), storm impacts (Gardner et al., 2005) and acidification (Albright and Langdon, 2011) pose important threats to Caribbean corals, other environmental variables also play an important role in the persistence and integrity of coral reefs. For instance, corals are sensitive to changes in water clarity and salinity (Kleypas et al., 1999), both of which are expected under climate change due to the amplification of the global hydrological cycle and resulting extremes in evaporation and precipitation (Durack et al., 2012). While these factors may not directly lead to coral mortality, they increase physiological stress on corals and their susceptibility to mortality inducing events such as bleaching and diseases (Harborne et al., 2017).

In addition, these environmental variables show considerable spatial variability across regional scales. In the Caribbean basin, six broad physicochemical provinces based upon sea surface temperature, a proxy for water clarity, salinity, wind-driven exposure and hurricane incidence are identified (Chollett et al., 2012). Variability in environmental exposure is an important component of the vulnerability and, in some cases, adaptability of marine ecosystems to the impacts of climate change. Recent research suggests that spatial variability in the environmental stress imposed by climate change may create climate refugia for some corals in areas where climate stress is low relative to the other coral reef locations (Cacciapaglia and Woesik, 2015). The existence of such areas may provide restricted, local buffers against the near-term impacts of climate change on coral reefs while the society is transitioning towards a low carbon future.

Finally, coral species with skeletons of greater morphological complexity show greater sensitivity to bleaching conditions (van Woesik et al., 2012b). This means that areas with higher environmental stress should host coral communities with lower overall habitat complexity, due to the proliferation of more tolerant, but morphologically simpler, species. In the Caribbean, declines in structural complexity have been attributed to the region-wide loss of dominant, species such as *Acropora* spp.. While the role of disease and storm surges on these species are well documented, the role of climate change is not as well-understood. Thus, consideration of species-specific environmental tolerance and their contribution to the structural complexity of coral reefs help improve our understanding of the future state of reef ecosystems.

In this study, we attempt to incorporate multiple environmental drivers and spatial and taxonomic diversity in vulnerability and responses to climate change effects into projecting the future of coral reef habitats. Specifically, we apply species distribution models (SDMs) to project changes in biogeography of Caribbean corals. We use an ensemble of three algorithms, occurrence data for forty-three Caribbean coral species and six environmental variables from three Earth system models to train our models, which are then used to project biogeographical shifts for two future time periods and two contrasting scenarios of climate change. Then, we use the outputs of these SDMs to construct habitat metrics used to assess the impacts of climate change on coral reef habitat. We use the models and their simulation outputs to test three hypotheses:

H_1: The impacts of climate change on coral communities will cause significant declines in reef habitat quality by the end of the 21st century.

H_2: The impacts of climate change will result in significant differences in reef habitat quality across the Caribbean region, with a decline in habitat quality in lower latitudes and an increase in higher latitudes.

H_3: Changes in habitat complexity is linked to a decline in the prevalence of higher complexity coral species relative to lower complexity coral species.

Finally, we discuss the implications of our results for the adaptation of coral reefs, their dependent fish communities and societies in the Caribbean.

3.2 Materials and Methods

3.2.1 Study Area

The study area encompassed the Caribbean Large Marine Ecosystem between 8^{o}N and 33^{o}N and 99^{o}W and 58^{o}W. In this study, we sub-divided this area into three biogeographically distinct sub-regions based on the work of Chollett et al. (2012): the Northern, Southern and Central sub-regions (see Figure 1). The northern sub-region contains high-latitude areas within the exclusive economic zones (EEZs) of The Bahamas, Cuba and the United States of America (East coast and the Gulf of Mexico specifically). The southern sub-region contains regions near the South American continental land mass characterized by high riverine influence, i.e. low water clarity and low salinity. This sub-region encompasses the Economic Exclusive Zones (EEZs) of Trinidad & Tobago, Venezuela and Colombia. Finally, the central sub-region contains the inner Caribbean and regions "characterized by a mixture of relatively warm waters of high salinity and high water clarity" (Chollett et al., 2012). This sub-region includes the EEZs of Belize, Honduras, Mexico and Nicaragua.

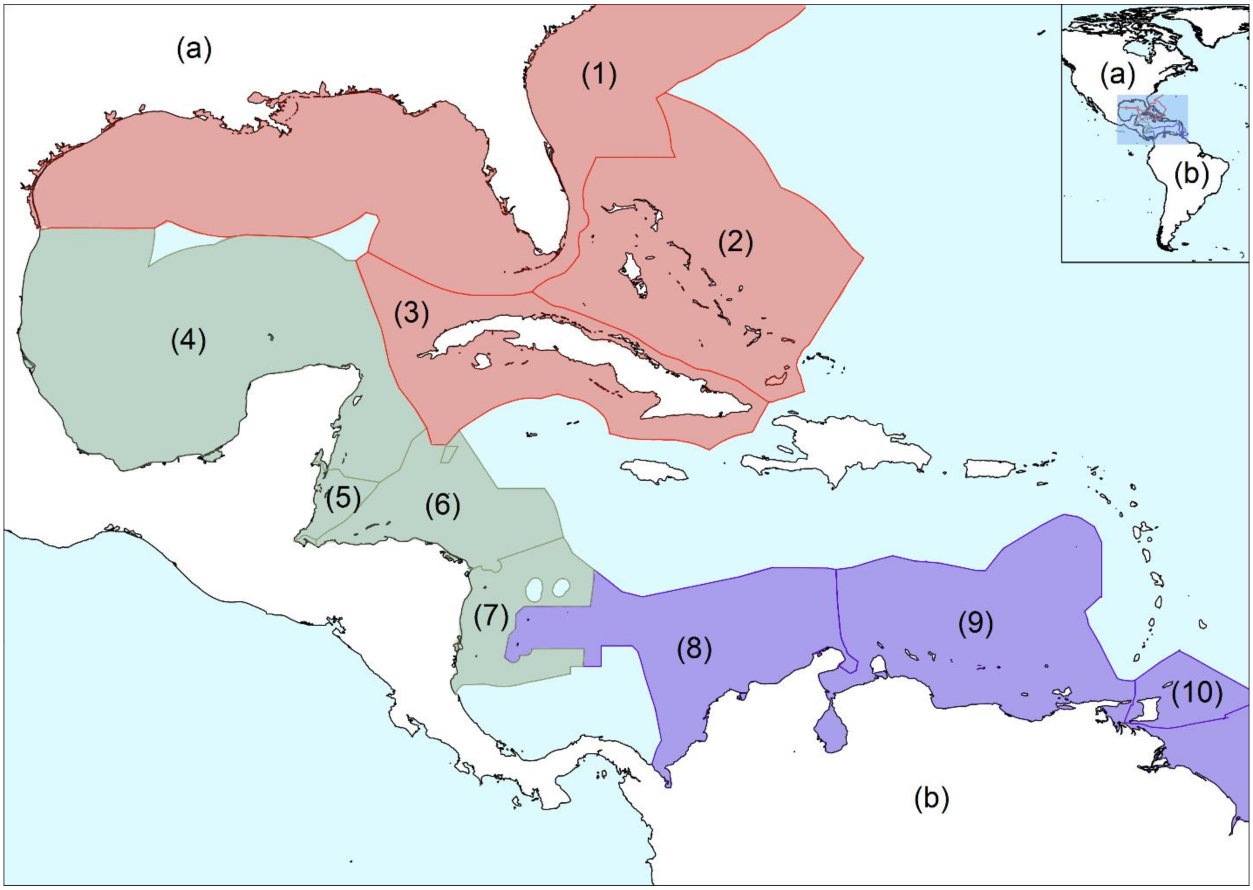

Figure 3.1 The countries with EEZs falling within our three selected sub-regions based upon the biogeographic zones of Chollett et al., (2012). Northern subregion (red): (1) USA (2) The Bahamas, (3) Cuba; Central subregion (green): (4) Mexico, (5) Belize, (6) Honduras, (7) Nicaragua; Southern subregion: (8) Colombia, (9) Venezuela, (10) Trinidad & Tobago. North (a) and South (b) America are labelled for reference.

3.2.2 Environmental data

Gridded data of environmental variables were obtained from outputs of three Earth system models: Geophysical Fluid Dynamics Laboratory-Earth System Model 2M (GFDL-ESM2M), Max-Planck-Institut fur Meteorologie-Earth System Model MR (MPI) and Institut Pierre Simon Laplace-CM5a-MR (IPSL). The environmental variables included sea surface temperature (^{o}C), pH, sediment, O_2

(mmol.m^{-3}) and salinity, all of which were interpolated from its native grid to a uniform grid system with a resolution of 0.5^{o} latitude x 0.5^{o} longitude (Cheung et al., 2017). In total 5 climatological averages were calculated, representing a baseline period from (1970~2000) and two future periods (2020~2050 & 2070~2100) under two Representative Concentration Pathways (RCPs) of carbon emissions including strong emissions mitigation (RCP 2.6) and no emissions mitigation (RCP 8.5)

3.2.3 Coral occurrence data

Geo-referenced occurrence records of coral species were extracted from online databases, specifically the Ocean Biogeographic Information System (OBIS, 2016) and Global Biodiversity Information Facility (GBIF.org, 2017). Though the GBIF database includes those from OBIS as well, querying occurrence records for all coral species for both databases ensured the complete coverage of occurrence across the region. Subsequent interpolation of the resulting combined data ensured the removal of replicates. Furthermore, points outside optimal depth ranges of warm-water corals reported in the literature of zero to 50m (Carpenter et al., 2008) were excluded (See Figure 2).

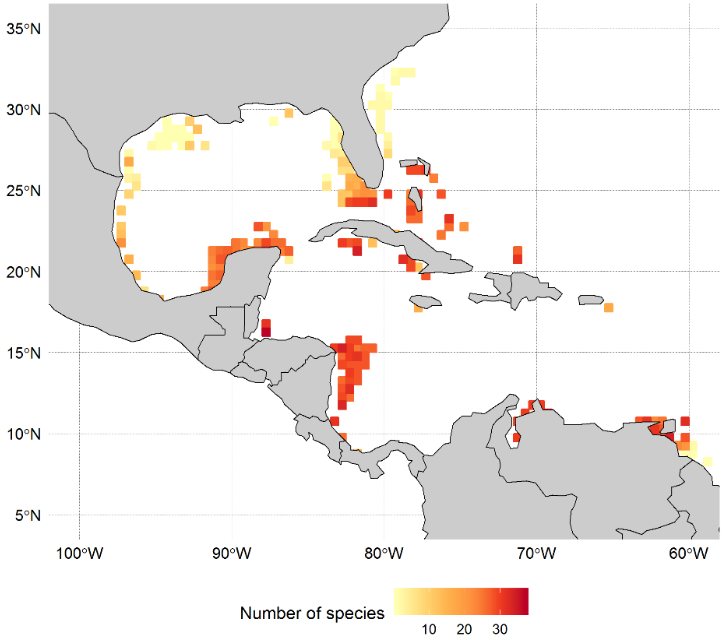

Figure 3.2 Georeferenced occurrence data for all coral species. The intensity of the color spectrum represents the number of species recorded per pixel.

3.2.4 Coral distribution models

Species distribution models (SDMs) were used to model the relationship between species occurrence and corresponding environmental variables. The methodology rests on the concept of ecological niche defined as a multidimensional environmental envelope defined by a set of evolutionarily determined environmental tolerances (Hutchinson, 1957). SDMs attempt to formalize the relationship between species occurrence records and environmental covariates to estimate species' fundamental niche and, in turn, approximate their past, present and future distribution. This approach is thought to be well-suited for marine organisms, the majority of which are ectotherms and thus expected to have spatial distributions that closely follow environmental gradients (Sunday et al., 2012; Pinsky et al., 2013). The use of species distribution models, though, requires that a distinction be made between areas of 'true absence' and those where data is lacking or 'pseudo-absence'. This is particularly difficult in the marine environment due to the difficulties and uncertainties associated with observational studies. As such most distribution models for marine species use presence-only models, which address ‘pseudo-absences’ by comparing the distribution of real occurrences along environmental gradients with that of a randomly generated dataset.

The distribution of each species was modelled using three algorithms: Boosted Regression Trees (BRT) (Elith et al., 2008), Maxent (Elith et al., 2011) and Artificial Neural Networks (ANN) (Olden et al., 2008). The algorithms were run using the Biomod2 modelling platform in the R statistical program v3.3.3 (R Development Core Team, www.r-project.org). These models were selected specifically because they use presence-only data. First, species with insufficient data for the algorithms used in this study were excluded resulting in a total of 37 species. Next, a random sample of 75% of each species’ occurrence data were selected to train the distribution models (training set). The remaining 25% were reserved for testing (testing set). The training data were correlated with the 1970 - 2000 climatology to create the baseline species distribution model. The 30-year climatology was then reapplied to the baseline model to produce an estimate for average distribution of coral fundamental niche for the period 1970 – 2000. The resulting estimate was then evaluated using the testing occurrence dataset, using the Area Under the Curve (AUC) as the performance metric. Future projections for each scenario were produced similarly by applying future climatologies to the baseline model.

3.2.5 Estimating habitat quality

Habitat quality was estimated using three indices, Species Richness (SR), a Habitat Complexity Index (HCI) and Acroporid Prevalence Ratios (APRs).

HCI is based on a classification scheme used by Edinger and Risk (2000) to assign conservation priority to reef habitats for the preservation of fish communities. This scheme ranked coral reefs based upon the relative composition of morphologically classified coral species such that reefs with higher diversity and greater proportion of morphologically complex species had a higher rank. For example, for 15 Indonesian coral reefs, their conservation classes were reliable predictors of a number of independently estimated habitat indices, including habitat complexity (Edinger and Risk, 2000).

To adapt this habitat classification scheme to the Caribbean, the species used in this study were grouped into growth morphologies comparable to those used in the Pacific (Figure 3). Growth morphologies for Caribbean species were made available through an online database of coral traits. Growth morphologies were described by two to four different classification schemes (See Tables B.1 & B.2). Specifically, the classifications available were the “Typical”, “Veron”, “Growth Form (GF)” and “Wallace” schemes. We applied each of the three classification schemes to describe the growth morphologies of coral species in the Caribbean. We had to exclude the “GF” and “Wallace” scheme because it could only classify less than 30% of the data; thus only the “Typical” and “Veron” classification schemes were used subsequently to assign the growth morphology of the recorded coral species. (See Table 3).

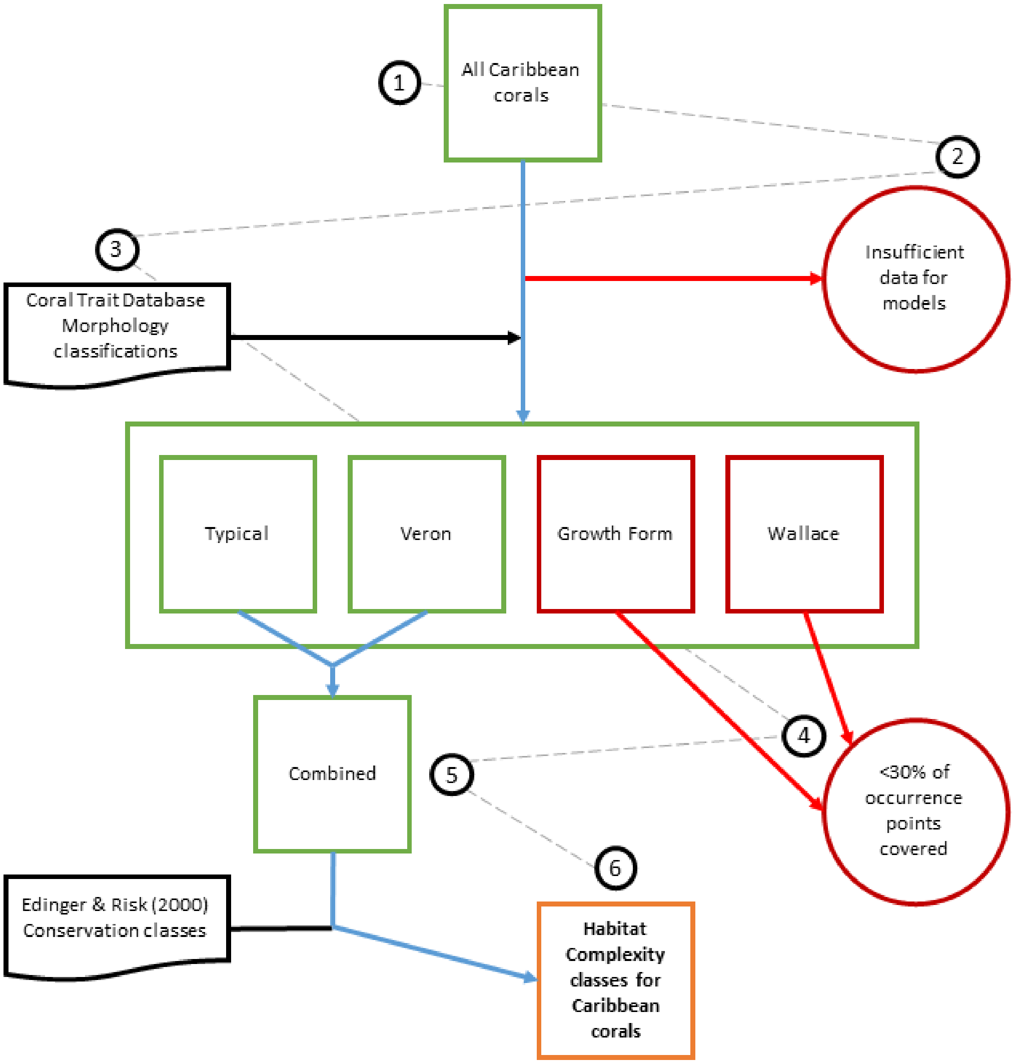

Figure 3.3 A flowchart outlining the classification of Caribbean coral reef species into habitat complexity classes adapted from the conservation classes of Edinger & Risk (2000).

We combined projections of species distribution with our morphology classification scheme to construct an index of habitat complexity for coral reefs. First, we found the probability of occurrence of a given morphological class by averaging the probability of occurrence of species falling in this class according to the following formulation:

$$\bar{p}_j = \frac{\sum_{k=1}^{n}(p_k)}{n}$$

Here the probability of occurrence of the j^{th} morphological class for a cell is given by the average probability of occurrence (p_k) of all n species of the j^{th} class that belong to that morphological class. Following this, the probability of occurrence for each morphology is then multiplied by its respective ordinal rank and summed to produce an estimate of habitat complexity as follows:

$$Habitat\ complexity_i = \sum_{j}^{N}\left(\bar{p}_j * r_j\right)$$

Equation 2 above illustrates that habitat complexity in the i^{th} cell is given by the sum of the probability of occurrence of all N morphological classes, weighted by their respective ordinal rank r given by our morphology classification scheme. The index ranges from 0 – 6 with larger values representing higher diversity habitats with greater structural complexity. We expect HCI to be lower at the end of the century (2070~2100), in the higher emissions scenario of climate change (RCP 8.5) and in the southern sub-region due to greater climate stress.

SR is simply calculated as the total number of species per cell that are predicted to occurrence by the models. We expect SR to be lower at the end of the 21st century (2070~2100), in the higher emissions scenario (RCP 8.5) and in the southern sub-region due to greater climate stress.

Finally, Acroporid Prevalence Ratios (APRs) were calculated and used to test for relative shifts in the prevalence of acroporids relative to other morphology categories. Specifically:

$$APR_{3,2} = \frac{p_{3,i}}{p_{2,i}} * \frac{n_3}{n_2}$$

Here $APR_{3,2}$ stands for the relative prevalence of acroporids to non-acroporid branching species, given by the ratio between the probability of occurrence of these species in cell *i*, multiplied by the ratio between the total number of cells in which they occur. The same is done for $APR_{3,1}$, or the relative prevalence of acroporids to massive and sub-massive species. These ratios are calculated for all sub-regions across all time periods and scenarios. We expect that climate change will result in lower APRs at the end of the 21st century (2070~2100), in the higher emissions scenario (RCP 8.5) and in the southern sub-region due to greater climate stress.

The relative change in all three habitat metrics (ΔHCI, ΔSR and ΔAPR) is calculated as follows:

$$Mid\ 21^{st}\ century\ change: \Delta X_{MC} = \frac{X_{MC} - X_{baseline}}{X_{baseline}}$$

$$End\ of\ 21^{st} century\ change: \Delta X_{EC} = \frac{X_{EC} - X_{baseline}}{X_{baseline}}$$

Here, the relative change in a habitat metric (ΔX) is given by the change observed to the middle or end of the 21st century (X_{MC} and X_{EC}), divided by that estimated for the start of the 21st century ($X_{baseline}$).

3.2.6 Illustrating the impacts of climate change on reef habitat

ANOVAs were used to test for differences among our estimated habitat metrics, using sub-regions, future periods and scenarios as blocking factors. Then Tukey's honestly significant difference posthoc test was then used to identify differences among combinations of blocking factors corresponding to our hypotheses, specifically time periods and scenarios for H_1 and sub-regions for H_2.

3.3 Results

Our model projections showed that the impact of long-term climate change on coral reef habitats, through changes in species richness, habitat complexity and community composition, were significantly different across sub-regions and between scenarios of climate change.

3.3.1 Species richness

Under RCP 2.6, species richness was projected to increase in all sub-regions (Figure 4), significantly so in the northern sub-region (Table SX, p= 0.011). On the other hand, under RCP 8.5, species richness was projected to decline significantly for all regions (Table B.3, $p_{Northern}$= 0.016, $p_{Central}$= 0.003, $p_{Southern}$< 0.001). Increases in species richness in the northern and central sub-regions were projected to be relatively similar, but significantly greater than the southern sub-regions under all RCPs and for the two the mid- and end of the 21st century (Table B.4, Tukey's HSD).

3.3.2 Habitat complexity index

Under RCP 2.6, habitat complexity index was projected to increase significantly by the end of the 21st century in the northern sub-region only (Figure 5; Table B.5, p= 0.03). In contrast, under RCP 8.5, habitat complexity index was projected to decline significantly across all sub-regions (Table B.5, $p_{Northern}$= 0.008, $p_{Central}$= 0.01, $p_{Southern}$< 0.001). The north was projected to show the greatest increases in habitat complexity for all RCPs (Figure 5), though this difference is more prominent under RCP 2.6 (Table B.6, Tukey's HSD). The southern and central sub-regions were relatively similar under RCP 2.6, though the south shows greater declines toward the end of the 21st century under RCP 8.5.

3.3.3 Changes in morphological composition

Contrary to our expectations, our models projected an overall increase in the prevalence of acroporids across the entire region, with the northern sub-region showing the greatest increase. Acroporids are projected to show significant increases relative to non-acroporid branching species for all sub-regions and RCPs (Figure 6b; Table B.7), with the northern sub-region showing the greatest increase (Figure 6b; Table B.8, Tukey's HSD). Acroporids only showed significant increases relative to massive and sub-massive species in the north under RCP 8.5 (Table B.7, $p_{\text{Northern, RCP 8.5}} < 0.001$). Acroporid prevalence showed conspicuous negative skew in estimated rates of change in both the southern and northern sub-regions under RCP 8.5 (Figure 6).

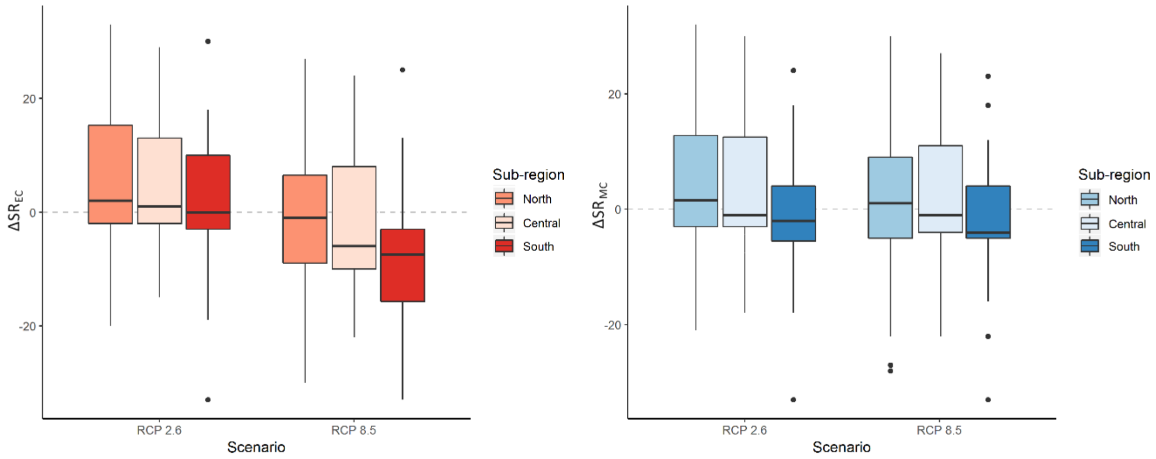

Figure 3.4 The change in species richness projected for the middle (blue) and end (red) of the 21st century for all sub-regions, under the RCP 2.6 and RCP 8.5 scenarios. Species richness was projected to increase toward the end of the century under RCP 2.6, but showed significant declines under RCP 8.5, especially in the south. For each set of estimates, box lengths represent the range between the first and third quartiles, whiskers represent the data within 1.5 times the length of the boxes and points represent all estimates outside of these ranges.

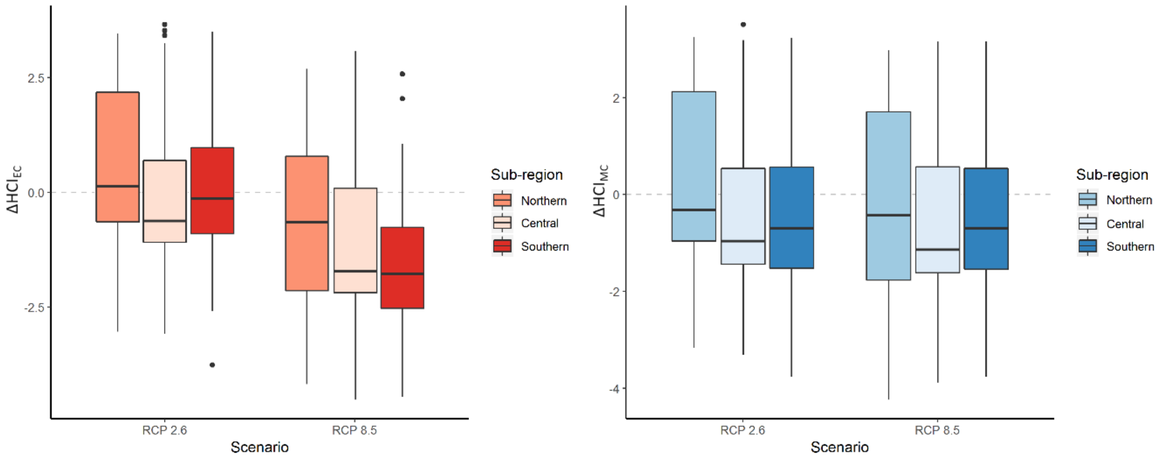

Figure 3.5 The change in reef habitat complexity projected for the middle (blue) and end (red) of the 21st century for all sub-regions, under the RCP 2.6 and RCP 8.5 scenarios. Reef structural complexity, expressed by the habitat complexity index (HCI), was projected to increase toward the end of the century under RCP 2.6, but showed significant declines under RCP 8.5, especially in the south. For each set of estimates, box lengths represent the range between the first and third quartiles, whiskers represent the data within 1.5 times the length of the boxes and points represent all estimates outside of these ranges.

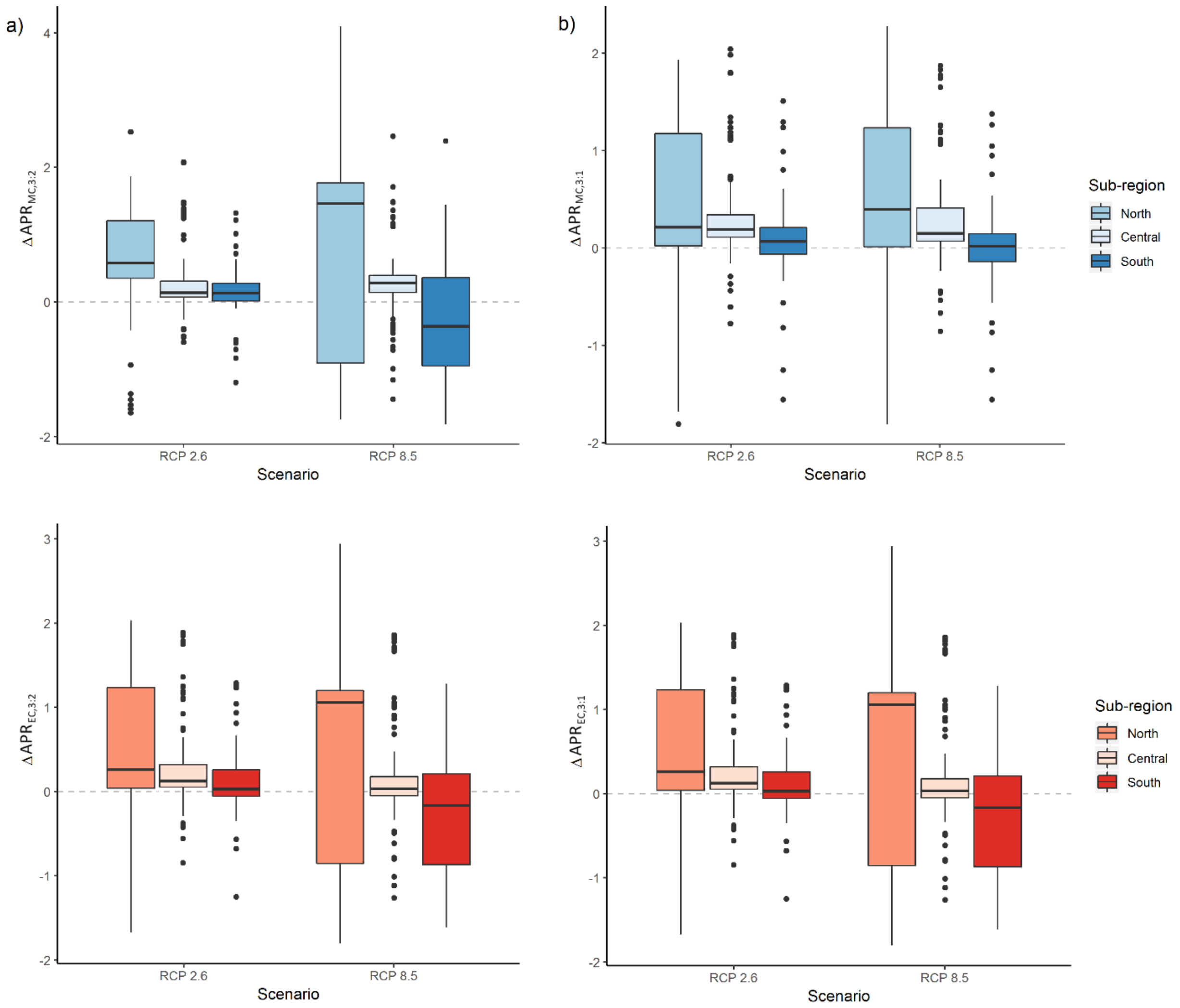

Figure 3.6 The change in the relative prevalence of acroporids projected for the middle (blue) and end (red) of the 21st century for all sub-regions, under the RCP 2.6 and RCP 8.5 scenarios. Acroporid prevalence is relative to that of non-acroporid branching species (a) and massive and sub-massive species (b), and expressed as acroporid prevalence ratios (APRs). Toward the end of the 21st century the prevalence of acroporids relative to non-acroporid branching and massive/sub-massive morphologies increased in all sub-regions under RCP 2.6. On the other hand, under RCP 8.5 relative prevalence increased in the north, but declined in the central and southern sub-regions. For each set of estimates, box lengths represent the range between the first and third quartiles, whiskers represent the data within 1.5 times the length of the boxes and points represent all estimates outside of these ranges.

3.4 Discussion

The results of our models agree with and add to the current understanding of climate change impacts on coral reef ecosystems. In line with the overall expectations of climate impacts on coral reefs, our models project a significantly more degraded future for reefs under RCP 8.5 compared to RCP 2.6 as indicated by the declines in species richness and habitat complexity. On the other hand, our projections show that declines in habitat complexity are not necessarily driven by changes in the morphological composition of reef communities, but instead general declines in the suitability of the marine environment for all three coral morphologies. Finally, our analyses projected a northward shift of suitable environmental conditions for all three coral morphologies under RCP 2.6 and specifically for acroporids under RCP 8.5.

The projected increase in the suitability of the marine environment for acroporids relative to other morphology groups in the central and northern sub-regions is largely unexpected given the history of Caribbean acroporid ecology in the Caribbean. In addition, recently published studies highlight the shift in community dominance from major framework builders (*Acroporia* spp. to *Orbicella* spp.) to historical non-framework builders (*Agaricia agaricites* and *Porites asteroids*) (Estrada-Saldívar et al., 2019; Toth et al., 2019). Since their large-scale decline in the early 1990s, acroporids have faced significant environmental and ecological barriers to their re-establishment (Rikki et al., 2006) and there is a justified expectation that reefs are likely to be structurally flatter in the future (Perry and Alvarez-Filip, 2019). However, recent studies provide evidence that acroporids may be recovering in some areas (Muller et al., 2014; Croquer et al., 2016). If such returns remain consistent and become more widespread, global efforts to mitigate climate emissions may yet play a positive role in preserving and facilitating the recovery of Caribbean coral reefs by improving the suitability of the marine environment for acroporids.

While it is difficult to compare exact values estimated among methods, the results of our analyses seem to agree with those of past modeling studies under the high emission scenario, but are more conservative for the low emission scenario. For instance, Bozec et al. (2014) also project significant declines in habitat complexity for reefs in Central America under RCP 8.5. On the other hand, Buddemeier et al. (2011) estimate that coral cover should drop below 5% across most southeastern Caribbean reefs by 2035, regardless of climate scenario (Buddemeier et al., 2011), while our results show a stark difference in the potential distribution of corals under the two scenarios tested. The difference in results between our study and that of Buddemeier et al. (2011) may be due to the different types of climate stress modelled. Their study simulates the impact of discrete, but severe, bleaching events on coral growth and mortality, which may impact coral prevalence more heavily than the long-term shifts the physical marine environment considered by our models. As such, their models suggest that recurring bleaching events may negate the benefits of mitigation. Reconciling this difference is an important next step in gaining a more complete understanding of future climate impacts on coral reefs through the Caribbean region.

These results also show that global climate mitigation efforts are necessary to preserve coral habitat. The RCP 2.6 scenario that we assessed represents a future that is close to (and not yet fully) the climate change level aspired under the Paris Agreement of limiting global warming to 1.5 ^{o}C relative to pre-industrial level. Although the projected impact under RCP 2.6 is much lower than RCP 8.5, our study shows that there will still be substantial residual impacts under this lower emissions pathway. Thus, our results highlight the need for a timely transition to a low emission pathway that may potentially provide a greater chance for reef-dependent communities to adapt to the impacts of anthropogenic climate change occurring beyond the 21st century. Our results also suggest that mitigation may help facilitate the return of acroporids in the central and northern Caribbean. Despite some evidence for their potential return in the Caribbean, acroporids are still encumbered by many ecological and environmental barriers in the Caribbean region. As such, global-scale mitigation of carbon emissions will need to be supported by improved local management to give acroporid populations the best chance of overcoming these barriers.

Niche models are not mechanistic models and rely upon the distribution of occurrence points as a proxy for structuring ecological processes. As such they may not capture processes such as connectivity (Figueiredo et al., 2016) and competition with other benthic taxa (McCook et al., 2001; González-Rivero et al., 2011), both of which heavily influence corals' ability to establish viable colonies. Connectivity among coral reef communities is important for the persistence of species' metapopulations (Jones et al., 2009). Connectivity may also contribute to the climate resilience of reefs by increasing the diversity of the genetic pool across regional metapopulations of coral species (Palumbi, 2003). On the other hand, the viability of coral populations that depend on externally sourced larvae will depend upon the reproductive potential of corals under climate stress (Baird and Marshall, 2002) and spatial reach of dispersal pathways (Underwood et al., 2007) relative to regional climate velocities.

The method of data splitting used in this study, while a common convention for many SDM applications, may increase spatial autocorrelation and decrease the independence of resulting training and testing datasets. As such, alternative methods, such as the use of broader spatial blocks as the basis for data splitting, should be investigated to address this issue. Coral cover and species composition from surveys would ultimately provide the best data to test our predictions since they would offer an independent measure of species distribution from our original dataset. Current databases do not provide the spatial coverage necessary to test a regional model, underscoring the need for better data availability for the Caribbean region. In addition, we did not include proxies for short-term stressors such as hurricane impacts and marine heatwaves as explanatory variables. Models including these variables, such as those used by studies highlighted earlier (Buddemeier et al., 2011; Bozec et al., 2015), may produce estimates for the prevalence of coral morphology groups and, by extension, habitat complexity lower than those predicted by our models. In addition, the resolution of our environmental data is quite broad, spanning spatial extents much larger than the coverage of individual coral reefs, heads and colonies. As such, the variability in environmental factors determining coral distribution at those finer spatial scales is lost. This may explain why our models fail to produce any projections for the eastern Caribbean as values for environmental variables in the coastal margins surrounding these islands are overshadowed by values from the oceanic space. The development of regional climate models will be useful to resolve estimates of coral prevalence at these smaller scales and be an important next step toward improving our habitat models. Finally, environmental variables associated with occurrence records would likely deviate from the values in the climatologies used, potentially affecting the range of environmental tolerances predicted by my models. On the other hand, my niche models assume that this variability is less important than the long-term climatological mean (standard deviation in the case of SST) for explaining regional distributions of corals.

3.5 Conclusion

Overall, this study advances our understanding on the future of Caribbean coral reefs under climate change by exploring the dimensions of the impacts of multiple environmental drivers on habitat complexity and their spatial variations. The findings provide insights for the conservation of coral reef ecosystems in the context of future climate change. We provide additional evidence for the benefits of global-scale emissions mitigation for Caribbean coral reef ecosystems. The modelling and analytical frameworks developed in this study can be applied to other coral reef ecosystem in the world. It can also be extended to examine the effects of changes in habitat structure and complexity of coral reefs on the associated biota under climate change.

4 The relative importance of different climate relevant environmental factors to the biogeography of coral reef fishes varies across spatial scales

4.1 Introduction

Coral reef ecosystems support important fisheries in tropical developing nations, but face a very high risk of impact from future climate change (Hoegh-Guldberg et al., 2017; Pörtner et al., 2019). The impacts of climate change on coral reef fishes have been a heavily researched topic (Munday et al., 2008; Hoey et al., 2016), but important knowledge gaps remain, making it difficult to link the global understanding of climate impacts to the management of reef fisheries. Most studies focus on the individual impacts of ocean warming, acidification and habitat loss. In addition, those looking at combined effects typically exclude biotic factors such as shifts in the distribution of coral habitat under climate change. Furthermore, little is known about the relative importance of these drivers to reef fish communities at different spatial scales (Mayor et al., 2009).

Ocean warming impacts the physiological performance and distribution of marine fishes (Pörtner, 2014; Pauly and Cheung, 2017). Marine ectotherms, including fishes, can be characterized by physiological ‘thermal windows’ (temperature ranges) within which they display optimal metabolic performance (Brett, 1971). Shifts in environmental temperature outside of their thermal windows severely limits their biological performance (Pörtner and Farrell, 2008). In response, fish populations shift their distributions to areas where environmental temperature falls within more optimal conditions (Perry et al., 2005; Fowler et al., 2017; Cheung, 2018). Reef fishes are no exception and some reef fish assemblages have shown ‘tropicalization’, or an increase in the prevalence of warm-adapted fishes, in response to changes in ocean temperature (Lloyd et al., 2012; Bates et al., 2014). However, poleward shifts in distribution may be limited by declines in coral habitats under climate change.

Ocean acidification may increase metabolic stress in reef fishes by disrupting cellular acid-base balance cardiorespiratory regulation (Ishimatsu et al., 2008), though laboratory studies show variable effects across species (Munday et al., 2009; Couturier et al., 2013; Sebastián and McClanahan, 2013). Ocean acidification may also affect the neuro-sensory system and behavior of reef fishes, for example, through reduced sensitivity to homing (Devine et al., 2012; Devine and Munday, 2013) and predator olfactory cues (Cripps et al., 2011; Ferrari et al., 2011b; Allan et al., 2013), leading to higher natural mortality in the wild (Munday et al., 2010; Ferrari et al., 2011a). However, the concentrations of CO_2 required to elicit behavioral responses in laboratory experiments often far exceed those expected in the near future (Munday et al., 2012). In addition, recent laboratory evidence indicating little to no impact of acidification (Clark et al., 2020) casts significant uncertainty on expected ecosystem-wide impacts.

Climate-induced habitat declines have important indirect impacts on coral reef fishes (Wilson et al., 2006; Pratchett et al., 2008). Previous research has shown that structurally complex reef habitats provide important refuges for a wide array of reef fishes (Alvarez-Filip et al., 2011c; Nash et al., 2013; Rogers et al., 2014), and influence key aspects of fish ecology such as recruitment and predator-prey interactions (Holt, 1984; Hixon and Beets, 1993; Almany, 2004). Consequently, habitat has been shown to explain current patterns of reef fish biodiversity at regional scales (Sandin et al., 2008; Mayor et al., 2009). In addition, some research has shown that contemporary patterns of reef fish biodiversity can be explained by coral reef habitat distributions as far back as the early quaternary (Pellissier et al., 2014). Furthermore, recent studies have highlighted evidence that biological populations may be less vulnerable to climate stress when their preferred habitat is readily available (Mantyka-pringle et al., 2012; Maharaj et al., 2018).

Understanding the combined direct and indirect impacts of warming, ocean acidification and other oceanographic changes on coral reefs and their relative contributions at different spatial scales is a critical component of developing climate-adaptive reef fisheries management. In this regard, this study aims to answer two questions regarding the effect of climate change on the distribution of reef fishes and the communities they comprise:

(1) What are the differences, if any, in the relative importance of the availability and complexity of coral reef habitats, temperature and other physical and oceanographic conditions for structuring reef fish communities between the global and regional scales?

(2) How will the combined effects of physical changes and habitat degradation may affect the future distribution of reef fish communities?

First, we use a species distribution model to analyze occurrence records of reef fish communities and datasets of the physical and chemical environmental conditions to elucidate the relative importance of environmental factors in determining the distribution of these reef fishes globally and in the Caribbean basin. We then apply the findings to project future distribution of Caribbean reef fish communities. Particularly, we explicitly model climate change effects on coral reef habitats and incorporate it into the projections for reef fishes. Finally, we discuss the implications of our results for climate-risks of reef fisheries and the development of climate-adapted reef fisheries management strategies to reduce such risks.

4.2 Methods

4.2.1 Study Area

This study focused on the Caribbean basin region while we also compared the model outputs with global-scale analysis. The Caribbean basin scale was by four large marine ecosystems (LMEs): the entirety of the Gulf of Mexico and Caribbean LMEs; the southern extent of the Southeast U.S. continental shelf LME; and the northernmost extent of the North Brazil Shelf LME. The basin itself is geographically complex leading to a spatially heterogeneous physical environment, likely contributing to patterns in the function and distribution of marine organisms living there.

The global scale analysis used the same grid resolution with a total of 172288 cells spanning all marine regions of the world. Our regional analysis used data from a subset of the global dataset, comprising 3244 cells of a 0.5° latitude x 0.5° longitude grid (from 8°N – 33°N latitude and 99°W – 58°W longitude).

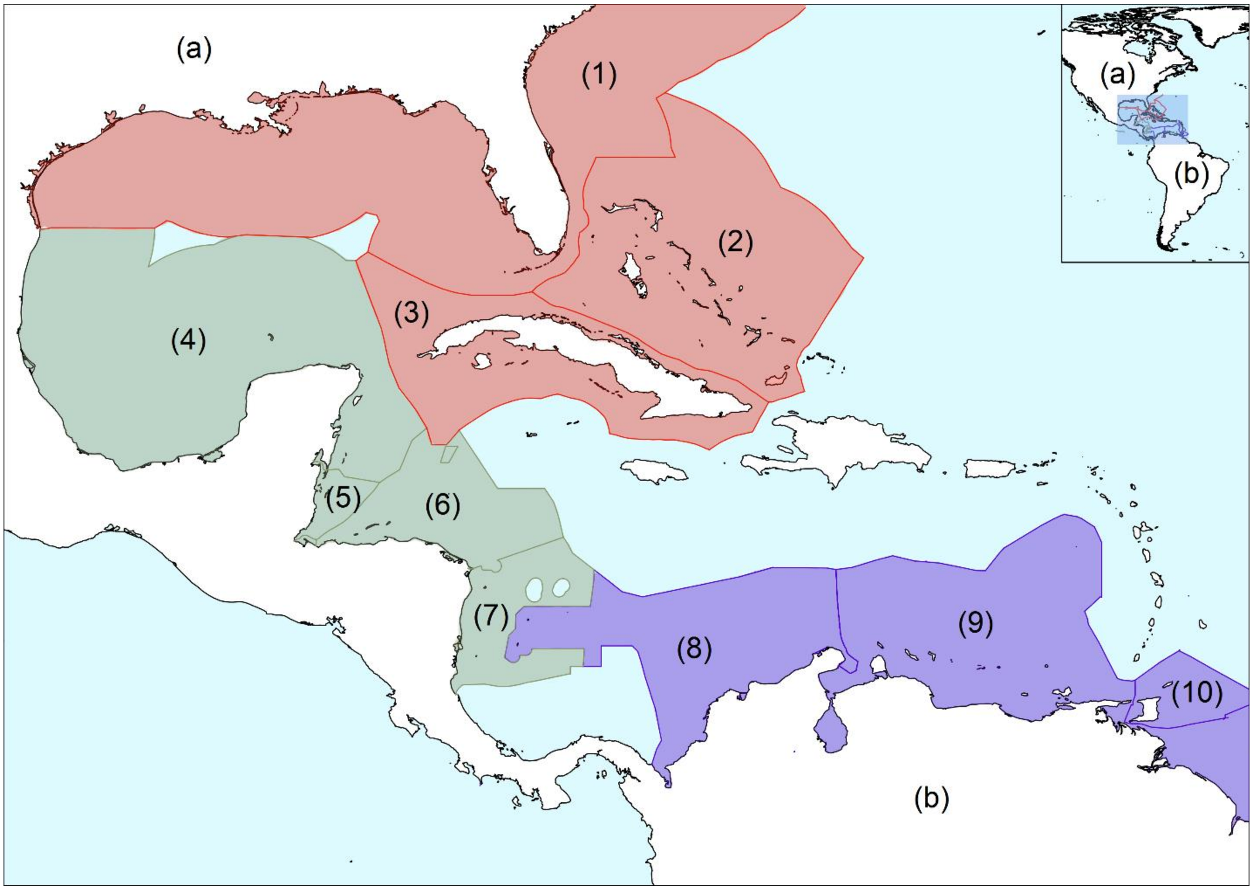

Figure 4.1 The countries with EEZs falling within our three selected sub-regions based upon the biogeographic zones of Chollett et al., (2012). Northern subregion (red): (1) USA (2) The Bahamas, (3) Cuba; Central subregion (green): (4) Mexico, (5) Belize, (6) Honduras, (7) Nicaragua; Southern subregion: (8) Colombia, (9) Venezuela, (10) Trinidad & Tobago. North (a) and South (b) America are labelled for reference.

4.2.2 Environmental data

We used simulated ocean conditions from Earth system models (ESMs) to project species distributions. We used outputs from three ESMs that were available from the Coupled Model Intercomparison Project Phase 5: Geophysical Fluid Dynamics Laboratory Earth System Model 2M, Max-Planck-Institut fur Meteorologie Earth system model and Institut Pierre Simon Laplace model CM5B-LR (referred to henceforth as GFDL, MPI and IPSL). The ocean variables included sea surface temperature (^{o}C), pH, benthic sediment thickness (a proxy for coastal sediment transport), O_2 concentration (mmol^{-1}m^{-3}) and salinity (psu), all of which were interpolated from their native grids to a uniform grid system with a resolution of 0.5^{o} latitude x 0.5^{o} longitude, matching that of the global grid (Cheung et al., 2016). In total, three climatological averages were calculated, including a baseline period (1970 – 2000) and two future periods (2020 – 2050 and 2070 – 2100). We considered two scenarios of greenhouse gas emissions, including 'strong emissions mitigation' and 'no mitigation policy' scenarios, i.e. Representative Concentration Pathways (RCP) 2.6 and RCP 8.5, respectively. Each of these scenarios correspond to environmental conditions expected under different levels of radiative forcing energy retained by the earth's atmosphere (2.6 and 8.5 Wm-^{2} respectively).

We also included the habitat complexity index (HCI) from the previous chapter as a proxy for the distribution and morphological complexity of coral reef habitat in the Caribbean. In summary, this index combines species' ranks of contribution to reef morphological complexity with their probability of occurrence from distribution models in a weighted average.

$$\bar{p}_j = \frac{\sum_{k=1}^{n}(p_k)}{n}$$

First the average probability of occurrence of the j^{th} morphological class, p_j, is calculated as the summed probability of occurrence, p_k of all species in the j^{th} class, divided by the total number of species:

$$HCI_i = \sum_{j}^{N}(\bar{p}_j * r_j)$$

HCI of the i^{th} cell is then given as the sum of average probability of each j^{th} morphological class multiplied by its respective rank, r_j.

4.2.3 Occurrence data for Caribbean reef fish

Geo-referenced occurrence records of 40 reef fish species were extracted from online databases including the Global Biodiversity Information Facility (GBIF) and Ocean Biogeographic Information System (OBIS, 2016). Though the GBIF database includes those from OBIS as well, querying occurrence records for all coral species for both databases ensured the complete coverage of occurrence across the region. Subsequent interpolation of the resulting combined data ensured the removal of replicates. In addition, while the Caribbean hosts a significantly larger number of reef fishes than those included in this study, this study attempted to mirror the species previously included in Chapter 2, to maintain consistency and comparability among the estimated trends. These occurrence points were filtered for the time period between 1970 and 2000, the same period as the baseline climatology used to train the operating model for species distribution. In addition, these occurrence records were rasterized to the same spatial grid used for the environmental data, the filtered for the depth and home ranges of each species using data from FishBase (See figure 2).

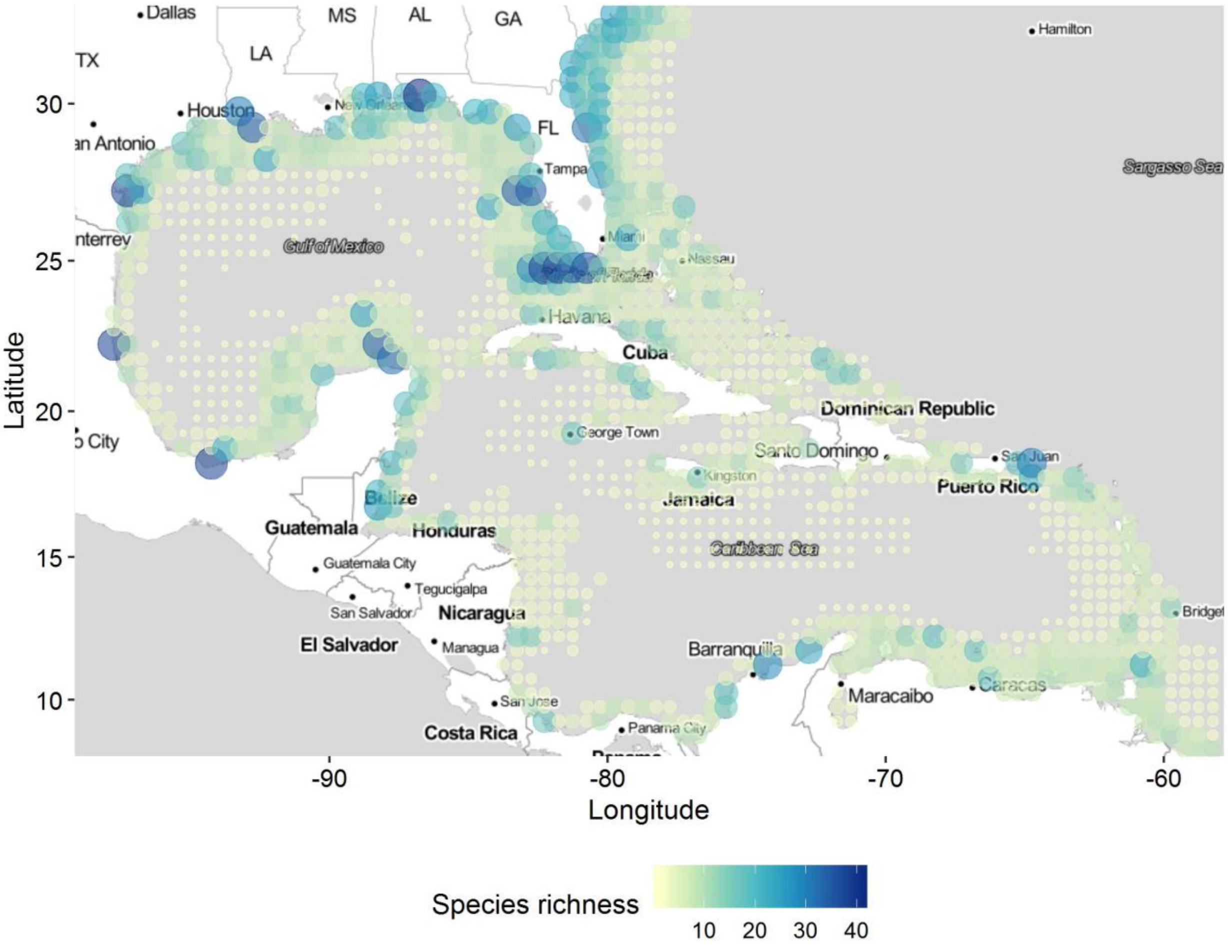

Figure 4.2 Rasterized occurrence data for all reef fish species. The color and size of the circles represent the number of species within a given 0.5^{o} x 0.5^{o} grid cell.

4.2.4 Comparison of the influence of environmental factors on reef fish distribution between spatial scales

We compared the relative influence of environmental factors on reef fish distribution between the regional and global scale using ecological-niche factor analysis (ENFA). ENFA is a method of quantifying a species' niche using presence-only data and environmental data by quantifying the n-dimensional hypervolume representing a species' niche within n-dimensional environmental space. In the process the method produces two indexes: marginality, which describes the location of a species' niche within the broader environmental space; and specialization, which describes the breadth of a species' niche compared to the breadth of the broader environmental space.

We use the marginality index for our comparison and calculated it using species occurrence and a climatology of five environmental variables (DO, SST, Salinity, pH and PP) for the period of 1970 – 2000, averaged over the three Earth system models. At the regional scale, we included the habitat complexity index (HCI) as a sixth variable representing potential available coral reef habitat. We could not do so at the global scale since HCI was not available in tropical regions outside of the Caribbean basin. To compare the effect of these different combinations of factors on fish distributions I used ENFA to construct three models:

i. Global model – Includes the entire global dataset of physical environmental parameters (172288 cells)
ii. Regional model 1 – A regional subset of of the global dataset of physical environmental parameters (3244 cells)
iii. Regional model 2 – The data for regional model 1, including HCI

Regional model 1 was compared to the global model to test the differences in relative importance of parameters between the scales. It was also compared to regional model 2 to test the importance of HCI on fish distribution relative to other physical environmental variables.

Marginality was calculated for each variable and ranges from -1 to 1 with the absolute value indicating the magnitude of influence and sign indicating the direction of influence each variable has on the location of a species' niche in the greater available environment. Because marginality is not comparable across the datasets used here, I instead ranked each variable according to their absolute marginality calculated for each species. Ranks took values from 1 to 5 at the global scale and 1 to 6 at the regional scale such that a higher rank indicated a greater influence of each variable on the marginality of a species' niche.

Finally, we tested the statistical differences in means and variances between global and regional sets of marginality for each environmental factor using t-tests and F-tests (excluding HCI which was not included in the global ENFA analysis).

4.2.5 Estimating changes in species richness, Extinctions and Invasions of reef fish communities under climate change

To project changes in species richness under climate change, we first used species distribution models to quantify the niches of 42 Caribbean reef fish species and project their distributions for the periods 1970-2000, 2020-2050 and 2070-2100, under RCP 2.6 and RCP 8.5 for the latter two periods. We used ENFA to select our environmental predictor variables, based on their contribution toward each species' niche marginality. As a result, our global model contained four physical environmental predictors while our regional model included HCI as a 5th predictor variable. Next, we modeled the distribution of species using three algorithms: Boosted Regression Trees (BRT), Maxent and Surface Range Envelope (SRE). The algorithms were available on the Biomod2 modelling platform in the R statistical program v3.6.2 (R Development Core Team, www.r-project.org). These models were selected specifically because they use presence-only data, the type of data that was available for the species included in our study.

A random sample of 75% of each species' occurrence data were selected for model training, while the remaining 25% were reserved for model testing. The training data were run through each algorithm with the baseline climatology to create the operating model. Finally, we produced estimates of a species' distribution by applying the appropriate climatology to the operating model. This was repeated for the three chosen algorithms, three sets of climatologies and two emissions scenarios resulting in a total of 18 projections for each species.

The performance of the operating models was quantified using the Area Under the Receiver Operating Characteristic Curve (AUC) with the ROCR package in R v3.6.2. This function compares the baseline projections of each operating model with the reserved testing data to produce the AUC metric. This metric has values ranging from 0 to 1, with 1 indicating the highest predictive power. The projections from models with AUC values less than or equal to 0.5 are excluded since they represent instances in which model predictions are theoretically as accurate as (or less than) a randomly generated result.

The projected HSI values were then used to estimate species richness, invasions and extinctions. Firstly, ensemble estimates of distribution for each species, a given emissions scenario and time period were produced by averaging the raw distribution projections from each algorithm, weighted by the AUC score generated from performance testing of the original operating models. The resulting model ensemble is then converted to species occurrence by changing the value of all cells with probabilities equal to and greater than a specified threshold to 1, and all others to 0. Following the methods of Jones and Cheung (2015), we tested a range of values (0.1, 0.3, 0.5 and 0.7) to determine the sensitivity of our results to our selection of thresholds, settling on a value of 0.3. The interpretation of this sensitivity analysis is discussed in our results.

Species Richness (SR)

SR was calculated by summing occurrence (*Occ*) in each k^{th} cell across all *l* species for all *i* time periods and *j* emissions scenarios.

$$SR_{i,k} = Occ_{i,k,1} + Occ_{i,k,2} \dots + Occ_{i,k,l-1} + Occ_{i,k,l}$$

$$SR_{i,j,k} = Occ_{i,j,k,1} + Occ_{i,j,k,2} \ldots + Occ_{i,j,k,l-1} + Occ_{i,j,k,l}$$

These were in turn used to calculate the change in species richness expected at the middle and end of the 21st century:

$$\Delta SR_{2050,j,k} = SR_{2050,j,k} - SR_{2000,k}$$

Extinctions and Invasions

For each species, cells in which species were present in a previous time period, but absent in the next were counted as extinctions. In contrast, cells in which species were absent in the previous time step, but present in the next were counted as invasions. First the difference in occurrence for each *l*th species in each *k*th cell between time periods was calculated.

$$\Delta Occ_{2050,j,k,l} = Occ_{2050,j,k,l} - Occ_{2000,k,l}$$

Then the result was filtered such that each of the k cells with values <0 were counted as extinctions while those >0 were counted as invasions.

$$Ext_{2050,j,l} = \left\{Ext_{2050,j,k,l} \subseteq \Delta Occ_{2050,j,l} \middle| Ext_{2050,j,k.l} < 0\right\}$$

$$Inv_{2050,j,l} = \left\{Inv_{2050,j,k,l} \subseteq \Delta Occ_{2050,j,l} \middle| Inv_{2050,j,k.l} > 0\right\}$$

Finally, these per-species estimates were then combined to produce estimates of extinction and invasion for each *k* cell, across the entire set of *l* reef fishes.

$$Ext_{i,k,j} = Ext_{i,j,k,1} + Ext_{i,j,k,2} \ldots + Ext_{i,j,k,l-1} + Ext_{i,j,k,l}$$

$$Inv_{i,k,j} = Inv_{i,j,k,1} + Inv_{i,j,k,2} \ldots + Inv_{i,j,k,l-1} + Inv_{i,j,k,l}$$

4.3 Results

4.3.1 Global versus regional-scale factors explaining patterns in the distribution of Caribbean reef fishes

At the global scale our analyses showed that the selected reef fishes were consistently distributed in areas with higher SST and PP, though the response to DO was mixed. These agreed with our expectations since tropical coastal regions tend to be characterized by these conditions relative to other parts of the global ocean though. Species that ranked DO the highest were associated with lower DO, while remaining species were mostly associated with higher DO. Salinity and pH both had very low explanatory power (Figure 3a). At the regional scale DO was the most important factor, though species' responses to environmental factors were significantly more varied in terms of direction and magnitude compared to the global scale (Figure 4.3b; Table C.2, $p<0.01$). In addition, at the regional level, while species that ranked DO the most important factor also showed low oxygen affinity, as in our global model, most of our species showed mixed affinities. pH was the second most important variable at the regional scale, contrasting with my global scale model which ranked it as the least important. In addition, the regional model estimated that species niches were defined by higher pH (lower acidity). SST was ranked as the third most important environmental factor with species showing a relatively mixed and significantly weaker response compared to the global scale ($p<0.01$, Table C.1). To add further contrast between global and regional scales, PP, the second highest globally ranked variable, held a much weaker overall rank at the regional scale (Figure 3b).

Rankings among regional variables showed two major changes when HCI was included in the analysis. First, HCI took the highest rank of all variables, showing a consistently positive effect (Figure 3c). Second, pH took on a higher rank over DO, showing consistently higher ranks and positive effects on fish distribution.

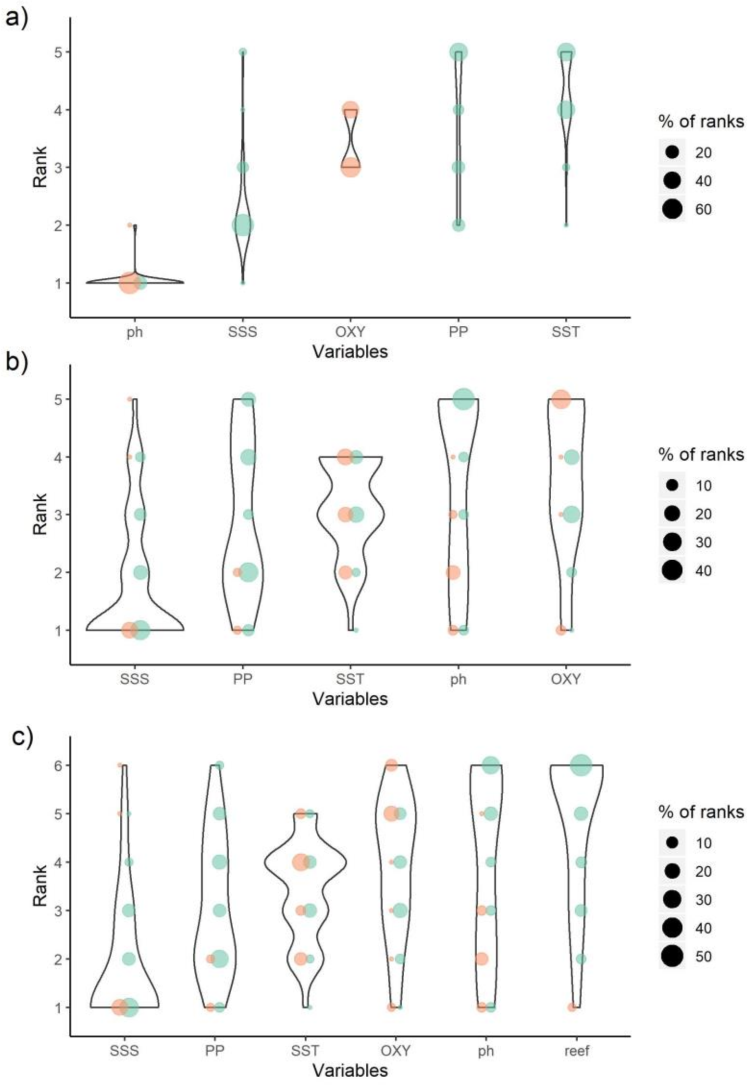

Figure 4.3 Violin plots illustrating the results of ENFA modeling, using the global (a), regional 1 (b) and regional 2 (c) datasets. Each violin plot displays the kernel probability density of ranks assigned to each environmental variable across all reef fishes. For each dataset they are arranged from left to right in order of increasing cumulative importance. Dot color represents the relationship of variables with each species' niche (green, positive; red, negative), while the size of each dot represents the percentage of all species at a given rank.

4.3.2 Estimates of species richness, extinction and invasion in coral reef fish communities under climate change

Regional-scale estimates of ΔSR indicated large relative declines of species richness across the region by 2050 for both scenarios of climate change (Figure 4). There was no further species loss by 2100. Species extinction drove these trends in ΔSR (Figure 5), though under both scenarios of climate change some small invasions contributed to small gains in species by 2100 within isolated areas along the Central American and south Cuban coasts (Figure 6; Figure C.3a). Areas showing species invasions were also associated with some of the last remaining coral reef habitat in the region (Figure C.4).

Global scale estimates of ΔSR also showed relative declines, but these were more limited in magnitude and extent at 2050, only showing increases by 2100 under the high emissions scenario (RCP 8.5) (Figure 4). Declines at 2050 were distributed around Central America, Cuba, southwestern Florida and The Bahamas under both climate change scenarios (Figure C.1b). By 2100 declines under RCP 2.6 increased only slightly in magnitude and northward extent, while under RCP 8.5 declines increased greatly in magnitude and extend in most areas. As with the regional-scale model, extinction seems to drive trends in ΔSR (Figure 5). However, in contrast to the regional-scale model, the global-scale model projected gains in species along the South American coast and northeastern Gulf of Mexico (Figure C.3b). Species invasion in these areas was projected to increase by 2100 under RCP 2.6, but decline under RCP 8.5 (Figure 6).

4.3.3 Sensitivity analysis

Estimates of invasion and extinction were relatively similar across thresholds, though there were some notable differences. Invasion at the regional scale followed the expected pattern, with $Thresh_{0.1}$

producing larger estimates followed by *Thresh*$_{0.3}$ and *Thresh*$_{0.5}$ (Figure C.5). There were no consistent trends in invasion estimates across thresholds at the global scale (Figure C.6).

At the regional scale *Thresh*$_{0.5}$ produced the smallest median estimates of extinction, but also the most variable. *Thresh*$_{0.1}$ produced the least variable and largest estimates of extinction. *Thresh*$_{0.3}$ produced extinction estimates of similar variance to *Thresh*$_{0.5}$, but with a slightly higher median value (Figure C.7). Extinction estimates were similar at the global scale. *Thresh*$_{0.1}$ consistently produced the lowest median estimates followed by *Thresh*$_{0.3}$ and *Thresh*$_{0.5}$, except in the south where this order is reversed (Figure C.8).

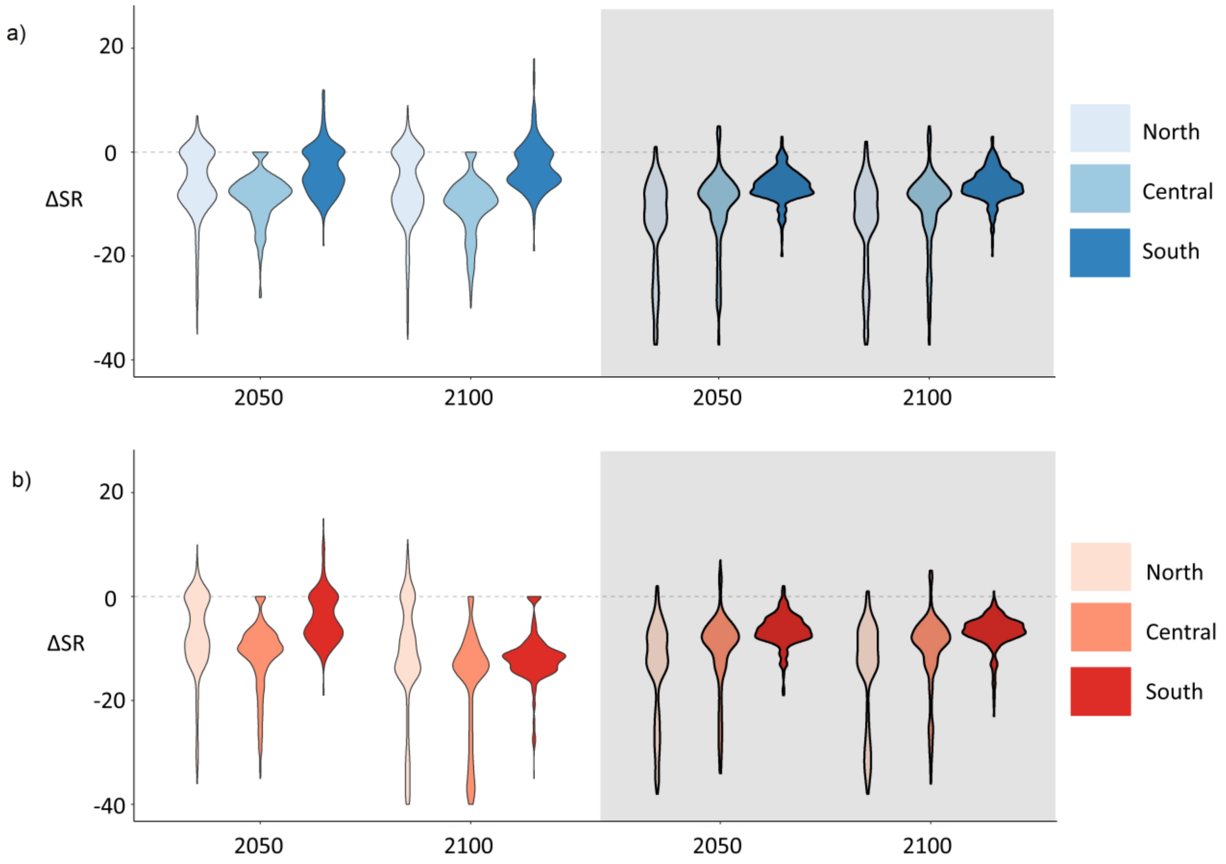

Figure 4.4 Global and regional (clear and shaded backgrounds, respectively) estimates of ΔSR for three sub-regions of the Caribbean basin under RCP 2.6 and RCP 8.5 scenarios [(a) and (b) respectively]. The width of the violin plot indicates the kernel probability density of data points at a given value.

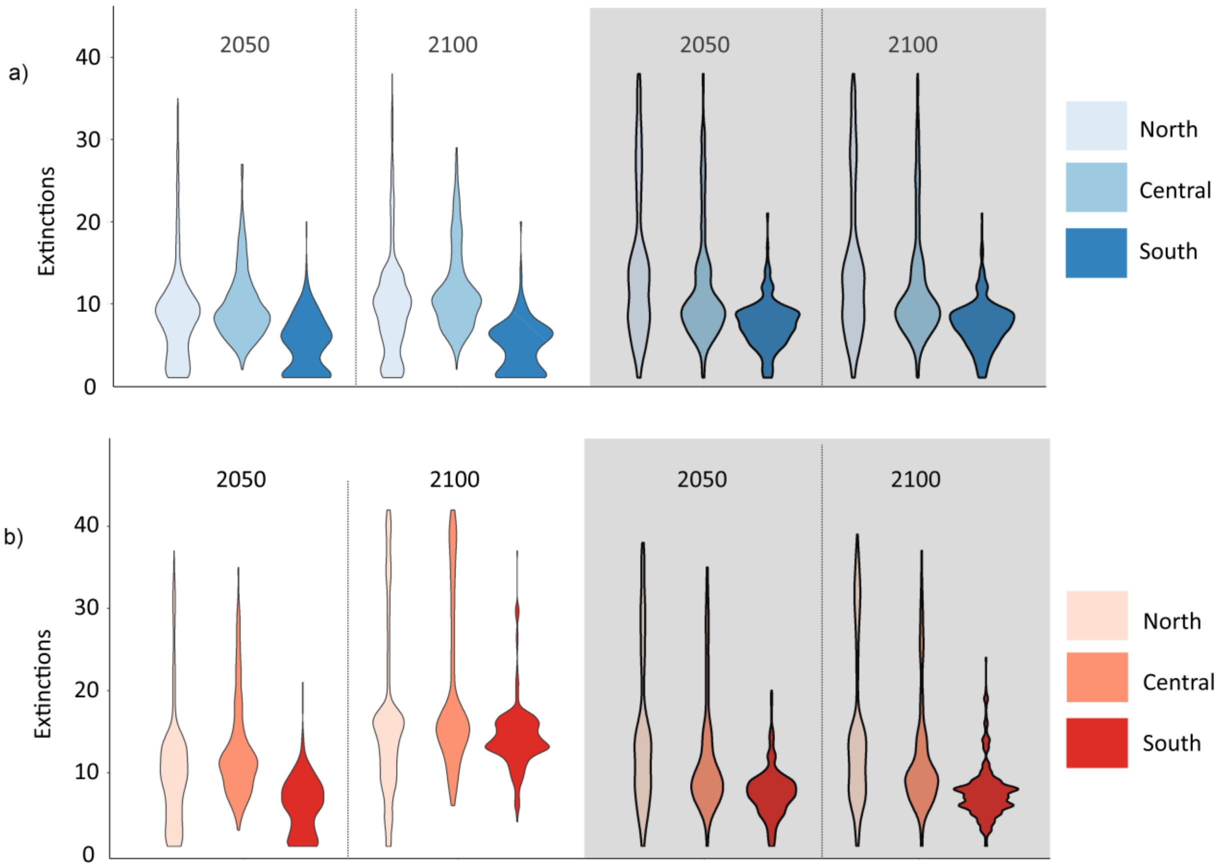

Figure 4.5 Global and region (clear and shaded backgrounds respectively) estimates of species extinctions for three sub-regions of the Caribbean basin under RCP 2.6 and RCP 8.5 scenarios [(a) and (b) respectively]. The width of the violin plot indicates the kernel probability density of data points at a given value.

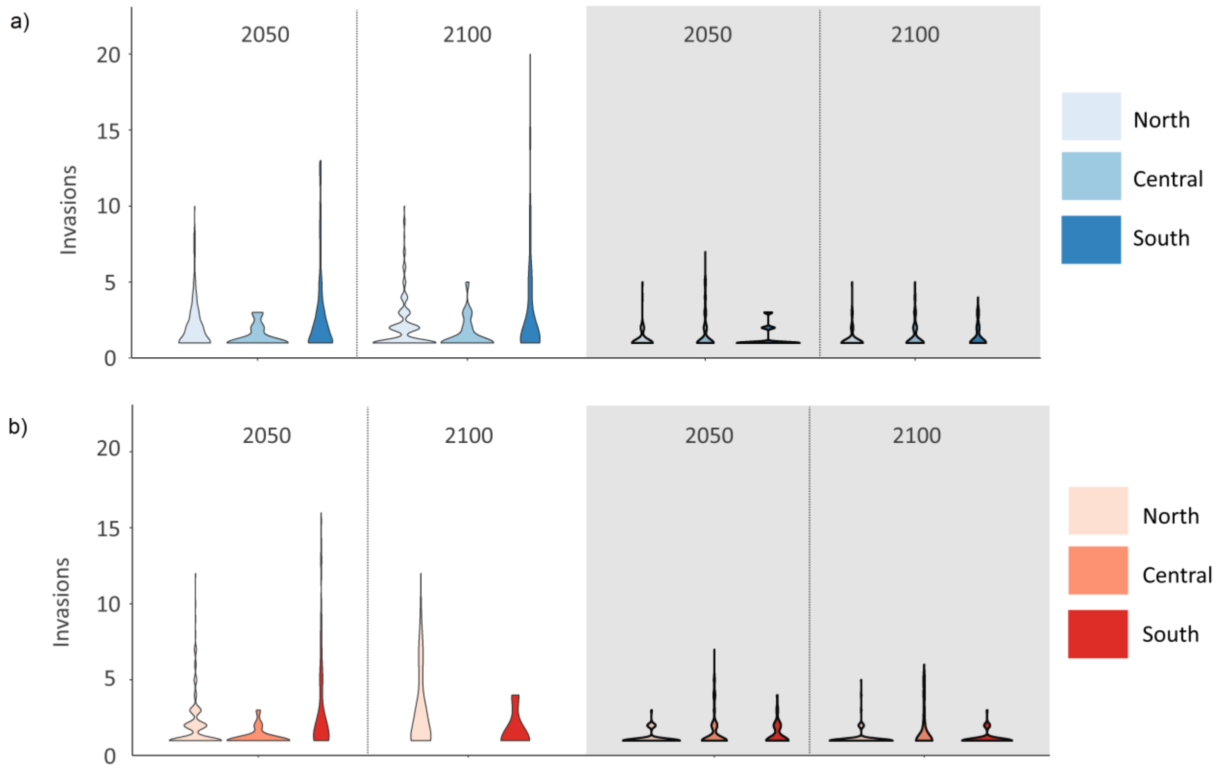

Figure 4.6 Global and regional (clear and shaded backgrounds respectively) estimates of species invasions for three sub-regions of the Caribbean basin under RCP 2.6 and RCP 8.5 scenarios [(a) and (b)]. The width of the violin plot indicates the kernel probability density of data points at a given value.

4.4 Discussion

Our study projected the future impacts of climate change on the future biodiversity of reef fish assemblages with explicit representation of climate effects on coral habitats. It assessed the predictions of global- and regional-scale models, providing insights into the influence of different environmental factors on the biogeography of reef fish under climate change at different spatial scales. Based on our results, we conclude that multi-scale analyses are necessary to deal with the uncertainty in downscaling the impacts of global climate change to regional contexts and provide further evidence that coral reef habitat may increase the resistance of reef fishes to the impacts of climate change. These findings contribute new insights into developing solution options to manage and conserve reef fish communities under climate change.

Our regional ENFA analysis showed that pH and HCI are important for defining reef fish niches at the regional scale. In particular, we show that invasions were restricted to areas projected to host coral reef habitats. Our regional models projected declines in biodiversity occurring sooner in the 21st century. Declines in complex coral habitat are a major threat to the persistence of reef fish assemblages (Wilson et al., 2006; Pratchett et al., 2008) because of its role in the maintenance of fish diversity and food web complexity (Newman et al., 2015; Hempson et al., 2017). The sensitivity of reef fishes to coral habitat changes varies as some reef fishes are known to inhabit marine ecosystems devoid of coral habitats. The shifts in composition of reef fishes under climate change due to their different dependency on the coverage and structural complexity of coral habitats may alter ecosystem structure and functions.

Our analyses suggested that reef fish niches are associated with areas of higher pH at the regional scale, a prediction consistent with the results of previous studies. However, further work is required to determine the mechanism behind such influences. Previous research suggests that declines in pH cause sensory disruption in fish, leading to riskier behavior and potentially increased levels of natural mortality in recruiting juveniles. Because our models did not explicitly represent these processes, we cannot directly relate laboratory observations of sensory impairment with the results of this study. In addition, recent research showing little to no effect of pH on fish behavior (Clark et al., 2020) casts further uncertainty on the consequences of ocean acidification for reef fishes and ecosystem productivity.

The results of this study agree with and add to previous findings regarding the importance of coral reef distributions for explaining biodiversity patterns in coral reef fishes (Parravicini et al., 2013; Pellissier et al., 2014). Parravicini et al. (2013) highlight the importance of including factors representing the paleontological record of habitat availability, such as shelf area, when assessing contemporary biodiversity trends. Furthermore, Pellisier et al. (2014) found that the isolation of contemporary reefs from climate refugia during periods of glaciation were important predictors of current reef fish biodiversity. Caribbean reef fish biodiversity is defined by extinctions due to habitat loss driven by declines in sea level associated with glaciation (Bellwood and Wainwright, 2002) and the inclusion of these factors may help explain regional biodiversity trends. On the other hand, the regional scale analyses in this study show that other environmental variables such as pH may be important in explaining reef fish distribution at a regional scale. As highlighted by Pellissier et al. (2014), future studies can expand from the modelling analysis presented in this chapter by including species traits to allows for a more informative interpretation of estimated trends of coral reef fish biodiversity.

Linking ecological principles at the regional and local scale to global analyses remains an important challenge in the development of climate proof policies for fisheries management. Previous research has proven the utility of multi-scale distribution modeling for explaining biodiversity patterns across coral reef ecosystems, providing a basis for their use in spatial resource management (Pittman et al., 2007; Mellin et al., 2010a). We add to this literature, showing that multi-scale approaches may highlight important characteristics of regional ecology that may shape the impacts of climate change on marine ecosystems. For example, our global model (broader spatial domain) projects significant biodiversity declines later than our regional model (narrower spatial domain) under a climate scenario of 'no mitigation'. Because our regional models are 'trained' on a smaller, regional subset of the global dataset, they represent local patterns, thus implicitly assuming that projected species' distributions reflect local adaptations. In contrast, estimates derived from our global models reflect the overall average adaptation across broader ranges of environmental gradients. Consequently, the estimated difference in rates of species loss may suggest that ecosystems with endemic species or locally adapted sub-populations filling a greater proportion of important functional roles are more likely to be more vulnerable to climate change. Such insights though, while potentially useful, require much deeper explorations in community composition than provided by the current analyses.

While distribution modeling provides an avenue to estimate the impacts of climate change on biodiversity, they must be interpreted in the context of their underlying assumptions.

- Niche models assume that current distributions represent the full range of species' environmental preferences through space and time, though the biogeographical history of reef fishes raises important questions about the appropriateness of such an assumption. The data used to train distribution models are based on species' presence within the period of 1970-2000 forcing the assumption that species entire range of preferences is represented by these distributions. The current environmental conditions may not capture the full range of conditions that the species prefer or are able to tolerate. Particularly, some reef fish may be restricted in some areas due to geographical barriers and thus the current distributions may only represent a portion of their full range of preferences.

- Statistical methods used to calculate the hypervolume representing a species' niche do not represent the mechanisms underlying species-habitat relationships, especially since dependency on reef habitats is known to vary across reef fish species. On the other hand, frameworks based on traits related to habitat use (Graham et al., 2011) may be employed to correct projections of reef fish distribution based on their fundamental niche, providing more accurate estimates of the impact of habitat changes on their distribution

- The niche models here did not capture the impacts of overfishing, a major cause of biodiversity decline on Caribbean reef fish assemblages. Similar to species-habitat interactions, projections of reef fish distributions may be corrected for fishing impact using trait-based frameworks for species' vulnerability to fishing (Cheung et al., 2005).

- Biotic interactions between species were not considered in our biodiversity projections. Species interactions can significantly affect species' responses to climate change (Gilman et al., 2010) and considering their effect is important for improving our understanding of climate impacts on biodiversity, particularly at smaller scales where these interactions have a greater influence.

In addition to these model assumptions, our data and methods provide sources of uncertainty that reduce the precision and accuracy of our projections. The cells within the 0.5° x 0.5 grid we use in our study cover large areas within which species occurrences, habitats and oceanic conditions vary significantly. In our database though, these variables are represented by single values and cannot capture local variability that may be important for capturing trends related to the small-scale processes we are testing for. Higher resolution data, though difficult to come by, could potentially assist in improving projections and management recommendations based on them. In addition, while occurrences sourced from OBIS and GBIF are sorted by life stage, occurrence records across all life stages were used to maximize the number of unique records available for model building and validation. Coral reef fishes display ontological shifts in coastal habitat use (Leis and McCormick, 2002) and, as a consequence, some occurrence points may be from the specific life stages of the species that are associated with areas that may not support coral reefs such as most coastal marshes and the open ocean. Based on these data, the model projections presented here may have overestimated reef fish distributions. As such, future studies should consider testing the effect of including only the specific life stages (e.g., adult stage) that are more closely associated with coral reefs.

The results of our study support the exploration of additional questions to increase our understanding of climate impacts on reef fisheries. First, they allow for a deeper exploration of estimates of biodiversity declines under climate change using trait-based approaches. Past studies have shown that species traits can help explain trends in reef fish biodiversity and the projections produced by species distribution models lend themselves well to these applications. For instance, differences in future invasion and extinction estimated by my regional and global models can be attributed to differences in life key history characteristics across reef fish assemblages. We show that declines projected by regional models including habitat distribution predict declines sooner than global models under a ‘no mitigation’ scenario, though it remains unclear whether this difference is due to declines in habitat availability, the impact of increasing pH, or the potential differences between regional and global models discussed previously. The effect of habitat on projections would be more clearly shown though within similar scales, i.e. global to global or regional to regional and the inclusion of projections from additional models would make the comparisons in this chapter more robust.. Working with smaller spatial domains will limit sample size, potentially affecting the performance of distribution models (Wisz et al., 2008). As such future studies should test more than just two models representing different spatial extents to provide a range of model sensitivity to scale selection. In addition, using higher resolution data could provide an avenue for increasing the data available to smaller spatial extents, though this may necessitate the inclusion of additional ecological characteristics known to influence reef fish distributions at more local scales (Mellin et al., 2010a; Pittman and Brown, 2011).

While further refinement is needed for these models to provide specific, robust advice for the management of reef fisheries under climate change, two main conclusions can be drawn. (1) Some countries may experience declines so drastic that it is unlikely local management interventions will help restore fish stocks to historic abundances. These countries should either focus on other target species that may be more resilient to climate change such as pelagic or estuarine stocks. (2) Pockets of optimal conditions may exist under milder scenarios of climate change and management resources should be invested into stewarding these as climate refugia. Area-based management tools (ABMTs) such as MPAs have proven quite effective for the protection of static areas of habitat and their accompanying marine assemblages when equipped with appropriate policies and enforcement. Discrepancies between regional and global projections indicate uncertainty in the exact location of potential refugia, but mobile MPAs show some promise as being dynamic enough to deal with the uncertainty in the changing distribution of marine fishes under the impacts of climate change. Furthermore, our projections show that this uncertainty is greater under more intense scenarios of climate change, reinforcing the important role mitigation can play in maintaining the productivity of coral reefs and their fisheries.

5 General conclusions

In this thesis I addressed questions related to the consequences of climate change on regional-scale coral reef fish ecology by exploring the relationship between biotic and abiotic factors and their influence on reef fish populations through the lens of ecological niche theory. Because ocean warming and habitat degradation are considered the two greatest threats to reef fish assemblages, I focused on exploring their combined effect on the composition of reef fish assemblages. Specifically, I investigated the impacts of climate change on reef fishes by comparing the indirect influence of changes in the distribution and quality of reef fish habitat with the influence of direct climate forcing on reef fishes and examining their combined effect through the analysis of empirical data and projections from ecosystem models.

5.1 Major findings and their implications

In chapter 2, I provided empirical evidence for the impact of ocean warming on coral reef fish communities, by showing that shifts in fish assemblages toward more thermally tolerant communities since the 1970s are well correlated with changes in sea surface temperature. In addition, I showed that a greater availability of reef habitat may reduce the sensitivity of reef fish assemblages to ocean warming. The results of this chapter provided evidence that ocean warming has already affected reef fish assemblage in the Caribbean, and that reef habitat might interact with temperature in affecting such effects.

In chapter 3, I explored the impacts of climate change on the distribution of habitat for coral reef fishes, showing that lowering carbon emissions from human activities could significantly reduce impacts on coral reef fish habitats. On the other hand, our results also showed that these impacts may vary significantly across the Caribbean. As such, while emissions mitigation may help some countries transition to a more sustainable, less-resource dependent state, other countries may require more drastic measures to adapt to the impacts of climate change on national fisheries.

Finally, in chapter 4, I projected the effects of climate change on the biogeography of reef fish assemblages in the Caribbean Sea. I also showed that reef fish biodiversity could be explained by different sets of environmental factors at the regional and global scales. Overall biodiversity is expected to decline across the region, but regional models project more immediate extinctions while global models project larger declines eventually. Invasions projected by global and regional models varied in latitude. Specifically, global models produced the expected trend of larger invasions at higher latitudes while regional models projected invasions at lower latitudes, but in areas likely to continue supporting architecturally complex reef habitats. These results show the importance of considering multiple scales for capturing a greater range of environmental influences on future reef fish assemblages.

5.2 Management implications

Due to sheer quantity of greenhouse gas emissions previously emitted, changes in ocean conditions under climate change are inevitable. As such, it is important to develop adaptation policies, particularly for species, ecosystems and the dependent human communities that are most vulnerable to climate change impacts. This thesis shows that the integrity of coral reef habitat structure contributes to reducing the sensitivity of the associated fish assemblages to ocean warming. Because of the importance of coral reef as habitat for the resilience of reef fish assemblages under climate change, protection of coral reefs such as through marine protected areas (MPA) appears to be an important adaptation measure. Currently, MPAs are popular in areas with limited formal fisheries management as they can achieve multiple management objectives and confer resilience to coastal ecosystems across multiple dimensions (Hopkins et al., 2016). The Caribbean hosts many MPAs, the majority of which protect coral reefs and other associated coastal habitats (Geoghegan et al., 2001; Guarderas et al., 2008). However, the effectiveness of protection they offer is contingent on a number of variables and remains a significant issue (Gill et al., 2017). In addition, shifts in the distribution of fish away from and reductions in their habitats within currently established MPAs threaten their efficacy (Bruno et al., 2018) and will require that these zones be periodically updated based on the best ecological science (Game et al., 2009).

Moreover, my study also showed that different species have different sensitivities to climate change impacts. Further works based on the methods produced here could help highlight the more vulnerable species and their associated habitats for greater emphasis on future research and management programs. In addition, such results suggest that fisheries may need target different species that may be more available or less sensitive to climate change impacts. However, because small-scale fisheries in the Caribbean are generally thought to be overexploited, policies prescribing shifts in target species must carefully consider their sustainability under fishing pressure.

In addition to maintaining biodiversity and supporting fisheries under climate change, there are many co-benefits for climate adaptation associated with maintaining the integrity of coral reefs. For example, the intensity of tropical storms is expected to increase under future climate change (Knutson et al., 2010), increasing the likelihood of destructive storm surges (Cheal et al., 2017). Coral reefs act as natural barriers to storm surges from tropical storms, reducing the damage they cause to coastal infrastructure, particularly those used by fishers (Guannel et al., 2016). In 2017, hurricane Maria devastated small islands in the Caribbean, such as Dominica, with fishing communities suffering significant infrastructural damage of up to US$2.4 million and losses in future catches of US$500,222 (CoD, 2017). The declines in coral reef coverage and complexity will only increase the susceptibility of Caribbean countries to storm surge impacts. Following hurricane Maria, the Commonwealth of

Dominica conducted a thorough review of impacts and potential means of addressing these to reduce the vulnerability of fishing communities to storm impacts including:

- Climate-proofing the fisheries sector
    - Build safe harbors, boat hauling equipment and boat shelters
    - Incorporate and improve early warning systems
    - Provide safety-at-sea training and equipment to fishers
    - Build institutional capacity to address disaster risk management and climate change adaptation
    - Investigate insurance programs to provide compensation for climate-related losses
    - Prepare a strategic action plan to implement measures
- Mainstreaming climate change in fisheries plans, policies and legislation
    - Require the use of biodegradable fishing gears to prevent ghost fishing in traps, nets and lines lost during storms
    - Carry out assessments on important ecosystems (e.g. coral reefs, seagrass beds, mangroves) and the services they provide (fisheries and tourism)
- Investigate opportunities for alternative livelihoods
    - Increased research and development in the aquaculture sector

This thesis also highlights the importance of global-scale carbon emission mitigation in affecting regional- to local-scale changes of coral reef fish assemblages. Specifically, the success of global efforts to mitigate carbon emissions can reduce the degree of adaptation and the associated financial investment required at the regional level (Fankhauser, 2010). Successful efforts toward reducing greenhouse gas emissions and sequestering excess carbon dioxide would result in mild decreases in the coverage and quality of reefs and diversity of fish assemblages across large areas of the Caribbean and allow for the persistence of reef fisheries. Such a scenario will require vast improvements in monitoring, assessment, research, policy development and enforcement for sustainable fisheries management (Hilborn et al., 2020). Because this will also involve a reduction of fishing effort, strategic interventions will be necessary to assist some fishers in their transition out of the fishery. However, if countries are less successful at mitigation, governments will expect to focus more on the imposition and enforcement of more drastic measures such as seasonal fisheries closures or even bans in an attempt to protect any limited remaining functions of coastal ecosystems. In this case, programs to help fishers transition into alternative livelihoods should also become a large focus of government efforts.

5.3 Future studies

I used ecosystem indicators based on catch reconstructions to provide evidence for the impact of climate change on fish assemblages and the influence of habitat on these trends. Ideally, these trends would be constructed using fisheries independent data, which would better represent fish community composition. However, though the spatial and temporal coverage of this type of data may not be as complete, presenting a different set of caveats. Ultimately, comparing both estimates would help reveal the effect of data biases on trends in overall community tolerances and contribute to dispelling the uncertainty around observed climate impacts. In addition, the distribution models used to compare the relative effect of climate change and habitat on biodiversity trends would benefit from higher resolution environmental data since habitat interactions occur at fine spatial scales.

Our distribution models did not include important ecological and biological factors that may influence the response of species to climate change. Past studies have used trait-based approaches to incorporate species interactions in projections of climate change on food web structure (Albouy et al., 2014). Distribution models generally assume evolution is static due to the time scales thought to be necessary for species to display tangible variation. On the other hand, rapid adaptations observed in some species due to phenotypic plasticity may influence their response to climate change and functional role in an ecosystem (Bush et al., 2016; Wade et al., 2017). Though chapter 4 provides some theoretical evidence for the influence of different types of adaptation (endemic vs global) on species' response to climate change, a better understanding will ideally require species-specific information on genetic and dispersal mechanisms that dictate the distribution of phenotypic plasticity of environmental tolerances across populations of species' (Kelly et al., 2012; Bush et al., 2016).

In conclusion, using a combination of ecosystem indicators and niche models, I have been able to test a number of questions relating to important knowledge gaps in our understanding of climate impacts on regional scale fish ecology, specifically in the context of Caribbean coral reefs. While our findings agree to great degree with the current scientific understanding of climate impacts on coral reef ecosystems, they also add additional nuance by showing that variability in impacts across spatial scales may relate to important ecological processes. These insights help build the knowledge required to develop climate-proof fisheries management policies and programs.

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Appendices

Appendix A: Chapter 2 supplementary tables

Table A.1 Estimated temperature preference and coral habitat affinity of taxa present in the catch records of the 9 countries used in the analyses.

Common Name	Median temperature preference, oC	Coral habitat affinity
Northern red snapper	22	0.50
Cero	24	0.75
Grey triggerfish	24	0.50
Sheepshead seabream	25	0.50
Bermuda sea chub	26	0.50
Lane snapper	26	0.75
Nassau grouper	26	0.25
Red hind	26	0.50
Tarpon	26	0.25
Atlantic tripletail	27	0.50
Black grouper	27	0.50
Cobia	27	0.50
Coney	27	0.75
Great barracuda	27	0.25
Vermilion snapper	27	0.50
Yellowfin grouper	27	0.50
Hound needlefish	28	0.25
Rainbow runner	28	0.75

Table A.2 Total catch and proportion contribution of the taxa included in the analyses for The Bahamas.

BAHAMAS		
Common Name	Total Catch	Catch Proportion
Nassau grouper	18590.648	0.320
Black grouper	8528.934	0.147
Yellowfin grouper	7257.586	0.125
Red hind	7112.919	0.122
Northern red snapper	5922.622	0.102
Lane snapper	5654.441	0.097
Great barracuda	4960.636	0.085
Cero	49.187	0.001
Blacktip shark	0.131	<0.001

Table A.3 Total catch and proportion contribution of the taxa included in the analyses for Belize.

BELIZE		
Common Name	Total Catch	Catch Proportion
Lane snapper	19863.562	0.269
Cero	18207.375	0.247
Great barracuda	8800.449	0.119
Nurse shark	7550.778	0.102
Scalloped hammerhead	6445.622	0.087
Northern red snapper	4354.632	0.059
Blacktip shark	3360.233	0.046
Cobia	1559.355	0.021
Sheepshead seabream	1559.355	0.021
Red hind	960.092	0.013
Nassau grouper	618.083	0.008
Black grouper	412.722	0.006
Tarpon	58.177	0.001
Yellowfin grouper	6.571	<0.001

Table A.4 Total catch and proportion contribution of the taxa included in the analyses for Grenada.

GRENADA		
Common Name	Total Catch	Catch Proportion
Red hind	11557.801	0.669
Cero	2356.453	0.136
Great barracuda	1399.169	0.081
Rainbow runner	975.343	0.056
Coney	958.482	0.055
Nassau grouper	7.399	<0.001
Yellowfin grouper	6.571	<0.001
Lane snapper	5.267	<0.001
Northern red snapper	3.781	<0.001
Scalloped hammerhead	0.292	<0.001
Blacktip shark	0.030	<0.001

Table A.5 Total catch and proportion contribution of the taxa included in the analyses for Haiti.

HAITI		
Common Name	Total Catch	Catch Proportion
Northern red snapper	13657.974	0.588
Hound needlefish	4632.673	0.199
Coney	3901.198	0.168
Cero	1026.285	0.044
Nassau grouper	7.399	<0.001
Yellowfin grouper	6.571	<0.001
Red hind	5.316	<0.001
Lane snapper	5.267	<0.001
Great barracuda	2.223	<0.001
Scalloped hammerhead	0.627	<0.001
Blacktip shark	0.131	<0.001

Table A.6 Total catch and proportion contribution of the taxa included in the analyses for Jamaica.

JAMAICA		
Common Name	Total Catch	Catch Proportion
Red hind	13188.152	0.536
Coney	3839.244	0.156
Great barracuda	2066.421	0.084
Cero	1790.494	0.073
Nassau grouper	1495.694	0.061
Black grouper	1407.737	0.057
Lane snapper	666.860	0.027
Yellowfin grouper	55.991	0.002
Rainbow runner	49.012	0.002
Sheepshead seabream	26.657	0.001
Northern red snapper	3.781	<0.001

Table A.7 Total catch and proportion contribution of the taxa included in the analyses for Montserrat.

MONTSERRAT		
Common Name	Total Catch	Catch Proportion
Cero	1333.500	0.537
Red hind	754.791	0.304
Coney	295.460	0.119
Bermuda sea chub	44.407	0.018
Great barracuda	19.038	0.008
Northern red snapper	15.579	0.006
Nassau grouper	7.911	0.003
Lane snapper	5.482	0.002
Blacktip shark	1.727	0.001
Sheepshead seabream	1.489	0.001
Grey triggerfish	1.279	0.001
Hound needlefish	0.949	<0.001
Tarpon	0.844	<0.001
Rainbow runner	0.259	<0.001

Table A.8 Total catch and proportion contribution of the taxa included in the analyses for St. Vincent & the Grenadines.

ST. VINCENT & THE GRENADINES		
Common Name	Total Catch	Catch Proportion
Red hind	7869.221	0.439
Coney	4551.188	0.254
Cero	3778.926	0.211
Rainbow runner	1275.201	0.071
Great barracuda	440.649	0.025
Northern red snapper	12.101	0.001
Nassau grouper	7.399	<0.001
Lane snapper	5.267	<0.001
Scalloped hammerhead	0.292	<0.001
Blacktip shark	0.007	<0.001

Table A.11 Total catch and proportion contribution of the taxa included in the analyses for Trinidad & Tobago.

TRINIDAD & TOBAGO		
Common Name	Total Catch	Catch Proportion
Tarpon	4131.093	0.515
Cero	3776.606	0.471
Blacktip shark	64.953	0.008
Nurse shark	7.918	0.001
Black grouper	7.573	0.001
Nassau grouper	7.399	0.001
Yellowfin grouper	6.571	0.001
Red hind	5.316	0.001
Lane snapper	5.267	0.001
Northern red snapper	3.781	<0.001
Atlantic tripletail	3.027	<0.001
Great barracuda	2.223	<0.001
Scalloped hammerhead	1.025	<0.001

Table A.12 Total catch and proportion contribution of the taxa included in the analyses for Venezuela.

VENEZUELA		
Common Name	Total Catch	Catch Proportion
Vermilion snapper	78461.924	0.566
Lane snapper	46195.683	0.333
Tarpon	7799.827	0.056
Cero	3178.824	0.023
Atlantic tripletail	2929.362	0.021
Blacktip shark	74.054	0.001
Nurse shark	7.918	<0.001
Black grouper	7.573	<0.001
Nassau grouper	7.399	<0.001
Yellowfin grouper	6.571	<0.001
Red hind	5.316	<0.001
Scalloped hammerhead	5.147	<0.001
Northern red snapper	3.781	<0.001
Great barracuda	2.223	<0.001

Table A.13 Species removed from the catch record and the respective taxon selection criteria used to justify their removal.

Common Name	Species Name	Criterion violated
Atlantic thread herring	Opisthonema oglinum	1
Bar jack	Caranx ruber	1
Black marlin	Istiompax indica	3
Caribbean spiny lobster	Panulirus argus	2
Common octopus	Octopus briareus	2
Greater amberjack	Seriola dumerili	1
Indo-Pacific sailfish	Istiophorus platypterus	3
King mackerel	Scomberomorus cavalla	1
Red grouper	Epinephelus morio	1
Yellowtail snapper	Ocyurus chrysurus	1

Table A.15 Countries assessed and the respective indicators produced when selection criteria for catch composition are relaxed to at least 3 taxa.

Country	PRH (km^2)	ΔSST	ΔMTC	ΔMTL
Trinidad & Tobago	40	0.18	0.62	0.00
Venezuela	670	0.17	0.16	0.05
Puerto Rico	267	0.17	0.02	-0.01
Grenada	213	0.17	0.48	-0.08
Montserrat	94	0.16	0.49	-0.15
St. Vincent & the Grenadines	225	0.16	0.57	-0.11
St. Lucia	129	0.16	0.72	-0.55
Dominican Republic	308	0.14	0.01	-0.02
Haiti	958	0.13	0.04	-0.01
Jamaica	197	0.11	0.00	-0.01
Bahamas	2869	0.06	-0.10	-0.02
Belize	1552	0.04	0.04	-0.01
Cuba	2229	0.04	0.00	-0.02

Table A.16 Statistics produced for generalized linear models including data from countries under the relaxed data selection criteria.

Model specification	Predictors	Coefficient	p-value	R^2	AIC
MTC ~ SST + PRH + SST * PRH + MTL	SST	0.635	<0.001	0.855	539
	PRH	10.993	0.001		
	SST*PRH	-0.389	<0.001		
	MTL	-1.159	<0.001		
MTC ~ SST + PRH + MTL	SST	0.425	<0.001	0.851	553
	PRH	0.303	0.221		
	MTL	-1.191	<0.001		
MTC ~ SST + MTL	SST	0.424	<0.001	0.845	551
	MTL	-1.192	<0.001		

Appendix B: Chapter 3 supplementary tables

Table B.1 21 of 37 Caribbean coral species included in our analyses showing total occurrence points as well as official and combined classifications. Individual morphology groups are color-coded to facilitate the identification of congruent groups across the classification schemes. Morphology abbreviations: ‘Brn (O)’ – Open-branching; ‘Brn (C)’ – Closed-branching; ‘Col’ – Columnar; ‘Enc’ – Encrusting; ‘S-Mas’ – Sub-massive.

Genus	Species	Occurrence	Classification Scheme			Combined
			Typical	Veron	Veron 2	
Acropora	cervicornis	862	Brn (O)	Brn (O)		Brn (O)
Acropora	palmata	870	Brn (O)	Brn (O)		Brn (O)
Oculina	diffusa	860	Brn (C)	Brn (C)	Brn (O)	Brn (C)
Cladocora	arbuscula	914	Brn (C)	Brn (C)		Brn (C)
Oculina	varicosa	970	Brn (C)	Brn (C)		Brn (C)
Porites	divaricata	846	Brn (C)	Brn (C)		Brn (C)
Porites	furcata	877	Brn (C)	Brn (C)		Brn (C)
Porites	porites	1178	Brn (C)	Brn (C)		Brn (C)
Madracis	auretenra	890		Brn (C)		Brn (C)
Dendrogyra	cylindrus	817	Col	Col		Col
Madracis	formosa	872	Col	Col		Col
Agaricia	tenuifolia	421	Lam	Lam		Lam
Leptoseris	cailleti	824	Lam	Lam		Lam
Mycetophyllia	reesi	761	Lam	Lam		Lam
Helioseris	cucullata	875	Lam			Lam
Agaricia	agaricites	1035	Lam	Lam	Enc	Lam
Agaricia	lamarcki	845	Lam	Lam	Enc	Lam
Agaricia	undata	626	Lam	Lam	Enc	Lam
Agaricia	humilis	857	Enc	Enc	S-Mas	Enc
Madracis	senaria	768	Enc	Enc		Enc
Solenastrea	hyades	891	S-Mas	S-Mas		S-Mas

Table B.2 16 of 37 Caribbean coral species included in our analyses showing total occurrence points as well as official and combined classifications. Individual morphology groups are color-coded to facilitate the identification of congruent groups across the classification schemes. Morphology abbreviations: ‘Enc’ – Encrusting; ‘Mas’ – Massive.

Genus	Species	Occurrence	Classification Scheme			Combined
			Typical	Veron	Veron 2	
Eusmilia	fastigiata	856	Mas	Mas		Mas
Isophyllastrea	rigida	832	Mas	Mas		Mas
Isophyllia	sinuosa	841	Mas	Mas		Mas
Manicina	areolata	851	Mas	Mas		Mas
Scolymia	cubensis	1036	Mas	Mas		Mas
Scolymia	lacera	844		Mas		Mas
Meandrina	danae	841	Mas			Mas
Orbicella	faveolata	889	Mas			Mas
Orbicella	annularis	893	Mas	Mas	Enc	Mas
Montastraea	cavernosa	1369	Mas	Mas	Enc	Mas
Porites	astreoides	1366	Mas	Mas	Enc	Mas
Colpophyllia	natans	901	Mas	Mas	Enc	Mas
Dichocoenia	stokesi	892	Mas	Mas	Enc	Mas
Diploria	clivosa	831	Mas	Mas	Enc	Mas
Mussa	angulosa	840	Mas	Mas	Enc	Mas
Stephanocoenia	intersepta	919	Mas	Mas	Enc	Mas

Table B.3 Combined morphologies assigned under classes adapted from the conservation priority framework devised by Edinger & Risk, 2000 showing the associated ranks and combined occurrence. Closed branching morphology is represented as ‘Branching (C)’ while open branching is represented as ‘Branching (O)’.

Combined morphology	Class	Rank	Combined occurrence
Open branching	Acroporid	3	1732
Closed branching	Non-acroporid branching & encrusting	2	15236
Columnar			
Laminar			
Encrusting			
Sub-massive	Massive & sub-massive	1	15892
Massive			

Table B.3: Statistics for the linear regression of species richness through the 21st century for all sub-regions and RCPs.

Group	Statistics				
North RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	-59.019	30.123	-1.959	0.051
	Year	0.037	0.015	2.545	0.011
North RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Intercept	78.267	26.363	2.969	0.003
	Year	-0.311	0.013	-2.418	0.016
Central RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	-13.839	30.290	-0.457	0.648
	Year	0.021	0.015	1.404	0.161
Central RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Intercept	110.395	28.108	3.928	<0.001
	Year	-0.041	0.014	-2.988	0.003
South RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	-16.381	34.174	-0.479	0.632
	Year	0.022	0.017	1.292	0.198
South RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Year	194.538	36.292	5.360	<0.001
	Residuals	-0.083	0.018	-4.697	<0.001

Table B.4: Statistics for ANOVAs and corresponding Tukey tests used to test differences in ΔSR among sub-regions for all future periods and RCPs.

Group	Test	Statistics					
RCP 2.6 2050	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	1460.000	730.000	5.711	0.004
		Residuals	277	35411.000	127.800		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.502	-3.096	4.099	0.942
			South - Central	-5.586	-10.247	-0.926	0.014
			South - North	-6.088	-10.454	-1.722	0.003
RCP 2.6 2100	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	1460.000	730.000	5.711	0.004
		Residuals	277	35411.000	127.800		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.502	-3.096	4.099	0.942
			South - Central	-5.586	-10.247	-0.926	0.014
			South - North	-6.088	-10.454	-1.722	0.003
RCP 8.5 2050	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	2049.000	1024.600	6.815	0.001
		Residuals	291	43750.000	150.300		
RCP 8.5 2050	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	-0.180	-3.915	3.554	0.993
			South - Central	-7.127	-12.090	-2.163	0.002
			South - North	-6.946	-11.710	-2.183	0.002
RCP 8.5 2100	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	2049.000	1024.600	6.815	0.001
		Residuals	291	43750.000	150.300		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	-0.180	-3.915	3.554	0.993
			South - Central	-7.127	-12.090	-2.163	0.002
			South - North	-2.081	-4.004	-0.157	0.030

Table B.5: Statistics for the linear regression of habitat complexity through the 21st century for all sub-regions and RCPs.

Group	Statistics				
North RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.152	0.041	27.962	<0.001
	Year	0.004	0.019	2.175	0.030
North RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.242	0.033	37.913	<0.001
	Year	-0.041	0.015	-2.674	0.008
Central RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.557	0.089	17.426	<0.001
	Year	0.003	0.041	0.079	0.937
Central RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.677	0.080	20.901	<0.001
	Year	-0.094	0.037	-2.533	0.011
South RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.282	0.068	18.755	<0.001
	Year	0.007	0.032	0.208	0.835
South RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.411	0.059	23.748	<0.001
	Year	-0.091	0.027	-3.316	<0.001

Table B.6: Statistics for ANOVAs and corresponding Tukey tests used to test for differences in ΔHCI among sub-regions for all future periods and RCPs.

Group	Test	Statistics					
RCP 2.6 2050	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	28.000	16.013	5.072	0.007
		Residuals	242	668.500	2.763		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.634	0.074	1.194	0.022
			South - Central	-0.134	-0.824	0.555	0.890
			South - North	-0.768	-1.451	-0.086	0.023
RCP 2.6 2100	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	25.000	12.524	4.714	0.010
		Residuals	243	645.600	2.657		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.673	0.125	1.221	0.011
			South - Central	0.080	-0.595	0.755	0.958
			South - North	-0.593	-1.262	0.076	0.094
RCP 8.5 2050	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	5.800	2.906	0.951	0.388
		Residuals	242	739.200	3.055		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.302	-0.287	0.891	0.449
			South - Central	-0.031	-0.755	0.692	0.994
			South - North	-0.333	-1.052	0.386	0.519
RCP 8.5 2100	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	26.500	13.252	5.295	0.015
		Residuals	236	728.100	3.085		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.323	-0.276	0.923	0.412
			South - Central	-0.585	-1.320	0.503	0.148
			South - North	-0.908	-1.639	-0.177	0.010

Table B.7: Statistics for the linear regression of APRs between acroporids and non-acroporid branching species through the 21st century for all sub-regions and RCPs.

Group	Statistics				
North RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.070	0.074	14.395	<0.001
	Year	0.131	0.033	4.024	<0.001
North RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Intercept	0.601	0.142	4.234	<0.001
	Year	0.543	0.065	8.374	<0.001
Central RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.124	0.041	27.628	<0.001
	Year	0.050	0.018	2.697	0.007
Central RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.093	0.050	21.953	<0.001
	Year	0.079	0.023	3.468	<0.001
South RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.122	0.066	17.095	<0.001
	Year	0.020	0.030	0.672	0.503
South RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.127	0.097	11.635	<0.001
	Year	0.021	0.047	0.442	0.660

Table B.8: Statistics for ANOVAs and corresponding Tukey tests used to test differences in ΔAPR between acroporids and non-acroporid branching species among sub-regions for all future periods and RCPs.

Group	Statistics				
North RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.113	0.054	20.483	<0.001
	Year	0.024	0.024	1.024	0.307
North RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Intercept	0.715	0.100	7.162	<0.001
	Year	0.322	0.046	7.021	<0.001
Central RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.169	0.041	28.802	<0.001
	Year	-0.001	0.018	-0.047	0.963
Central RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.086	0.041	26.269	<0.001
	Year	0.007	0.019	0.361	0.718
South RCP 2.6	Coefficient	Estimate	Std Error	t value	p
	Intercept	1.193	0.062	17.161	<0.001
	Year	-0.024	0.028	-0.844	0.400
South RCP 8.5	Coefficient	Estimate	Std Error	t value	p
	Year	1.131	0.075	15.028	<0.001
	Residuals	-0.027	0.036	-0.766	0.445

Table B.9: Statistics for the linear regression of APRs between acroporids and massive/sub-massive species through the 21st century for all sub-regions and RCPs.

Group	Test	Factor	Df	Sum Sq	Mean Sq	F value	p
RCP 2.6 2050	ANOVA	Spatial unit	2	16.060	8.032	14.940	<0.001
		Residuals	237	127.460	0.538		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.277	0.049	0.549	0.015
			South - Central	-0.397	-0.702	-0.091	0.007
			South - North	-0.696	-0.998	-0.393	< 0.001
RCP 2.6 2100	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	10.970	5.484	13.140	< 0.001
		Residuals	236	98.500	0.417		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Year	North - Central	0.350	0.129	0.571	< 0.001
			South - Central	-0.183	-0.453	0.086	0.246
			South - North	-0.533	-0.800	-0.267	< 0.001
RCP 8.5 2050	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	20.440	10.219	14.100	< 0.001
		Residuals	235	170.290	0.725		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.388	0.096	0.680	0.005
			South - Central	-0.390	-0.744	-0.036	0.027
RCP 8.5 2050	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	South - North	-0.778	-1.131	-0.425	< 0.001
RCP 8.5 2100	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	45.120	22.560	17.360	< 0.001
		Residuals	225	287.890	1.280		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.618	0.220	1.016	< 0.001
			South - Central	-0.536	-1.017	-0.055	0.025
			South - North	-1.154	-1.628	-0.681	<.001

Table B.10: Statistics for ANOVAs and corresponding Tukey tests used to test differences in ΔAPRs between acroporids and massive/sub-massive species among sub-regions for all future periods and RCPs.

Group	Test	Factor	Df	Sum Sq	Mean Sq	F value	p
RCP 2.6 2050	ANOVA	Spatial unit	2	2.770	1.385	2.863	0.059
		Residuals	237	242.000	117.060	0.484	
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.047	-0.187	0.282	0.883
			South - Central	-0.236	-0.525	0.052	0.132
			South - North	-0.283	-0.569	0.002	0.052
RCP 2.6 2100	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	2.660	1.329	2.931	0.055
		Residuals	243	110.180	0.453		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Year	North - Central	0.111	-0.115	0.338	0.477
			South - Central	-0.171	-0.450	0.108	0.318
			South - North	-0.283	-0.559	-0.006	0.044
RCP 8.5 2050	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	5.340	2.671	4.686	0.010
		Residuals	242	137.930	0.570		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.093	-0.161	0.347	0.665
			South - Central	-0.307	-0.619	0.006	0.056
			South - North	-0.400	-0.710	-0.089	0.007
RCP 8.5 2100	ANOVA	Factor	Df	Sum Sq	Mean Sq	F value	p
		Spatial unit	2	18.540	9.269	10.030	< 0.001
		Residuals	234	216.190	0.924		
	Tukey HSD	Factor	Comparison	Difference	Lower	Upper	p adj
		Spatial unit	North - Central	0.350	0.021	0.679	0.034
			South - Central	-0.405	-0.810	<0.001	0.050
			South - North	-0.754	-1.158	-0.351	<.001

Appendix C: Chapter 4 supplementary figures and tables

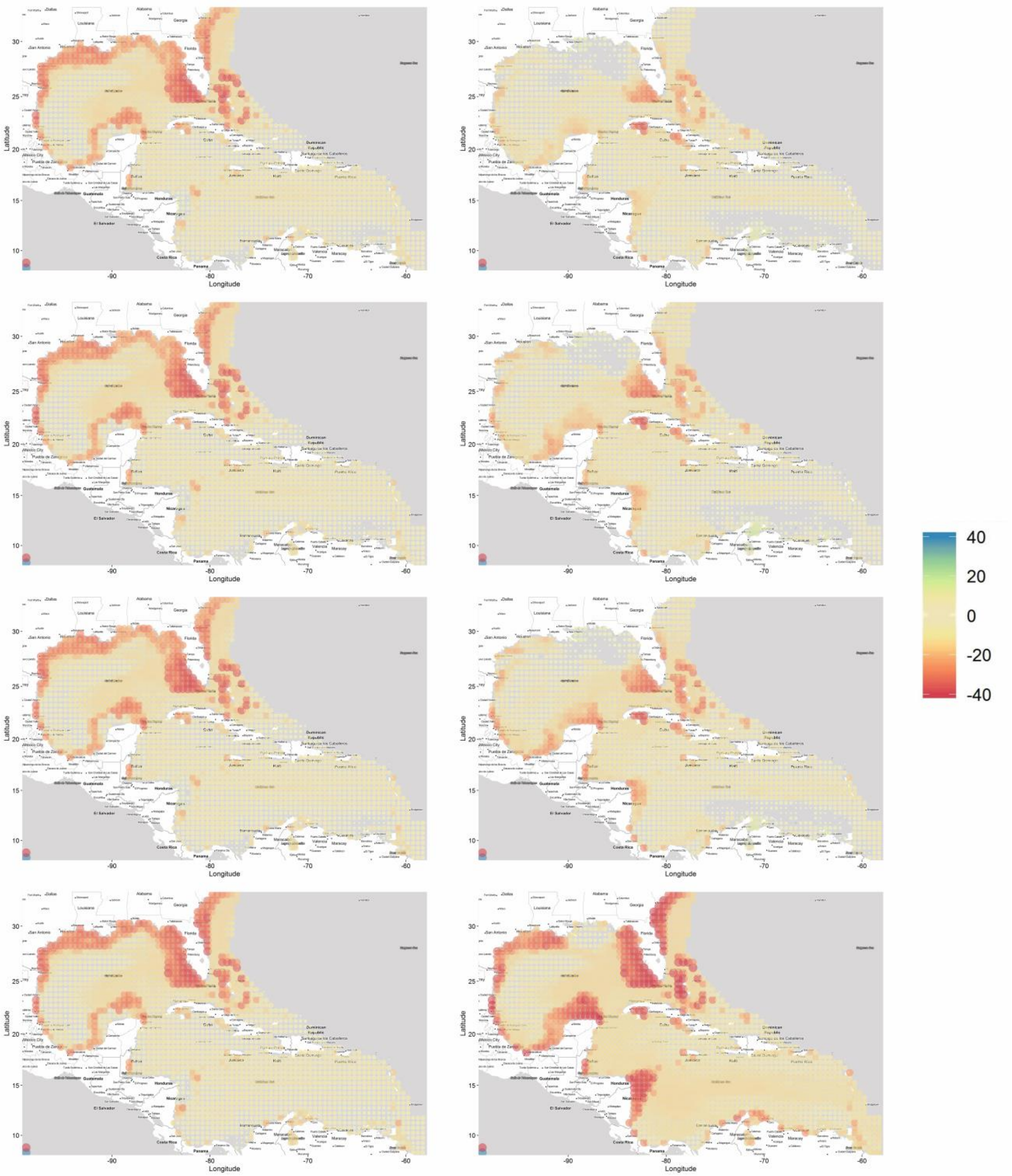

Figure C.1 The distribution of ΔSR estimated by global (left) and regional (right) models under two scenarios of climate change RCP 2.6 (a) and RCP 8.5 (b), at the years 2050 (i) and 2100 (ii).

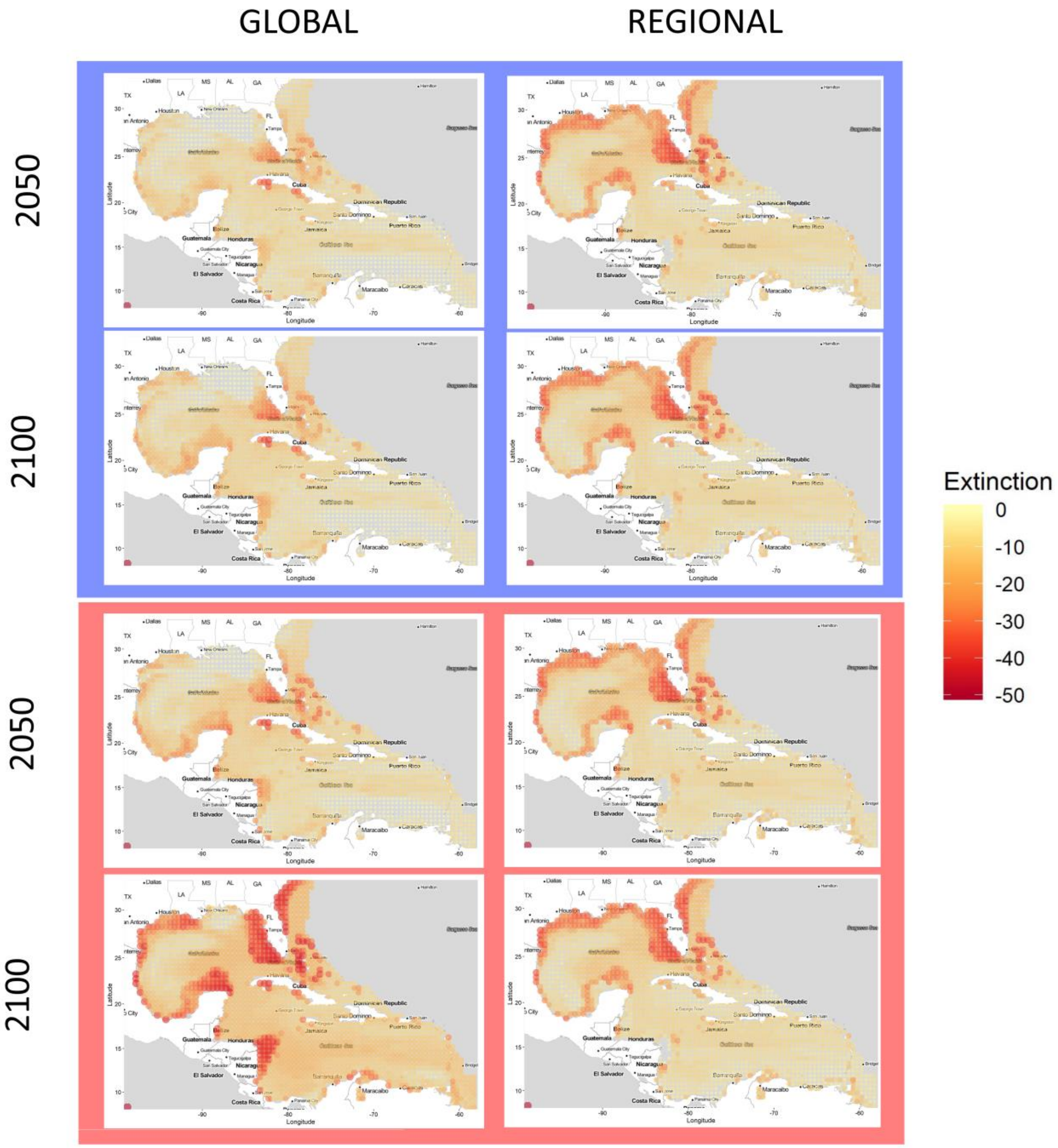

Figure C.2 The distribution of extinctions estimated by global (left) and regional (right) models at the years 2050 and 2100, under two scenarios of climate change RCP 2.6 (blue) and RCP 8.5 (red).

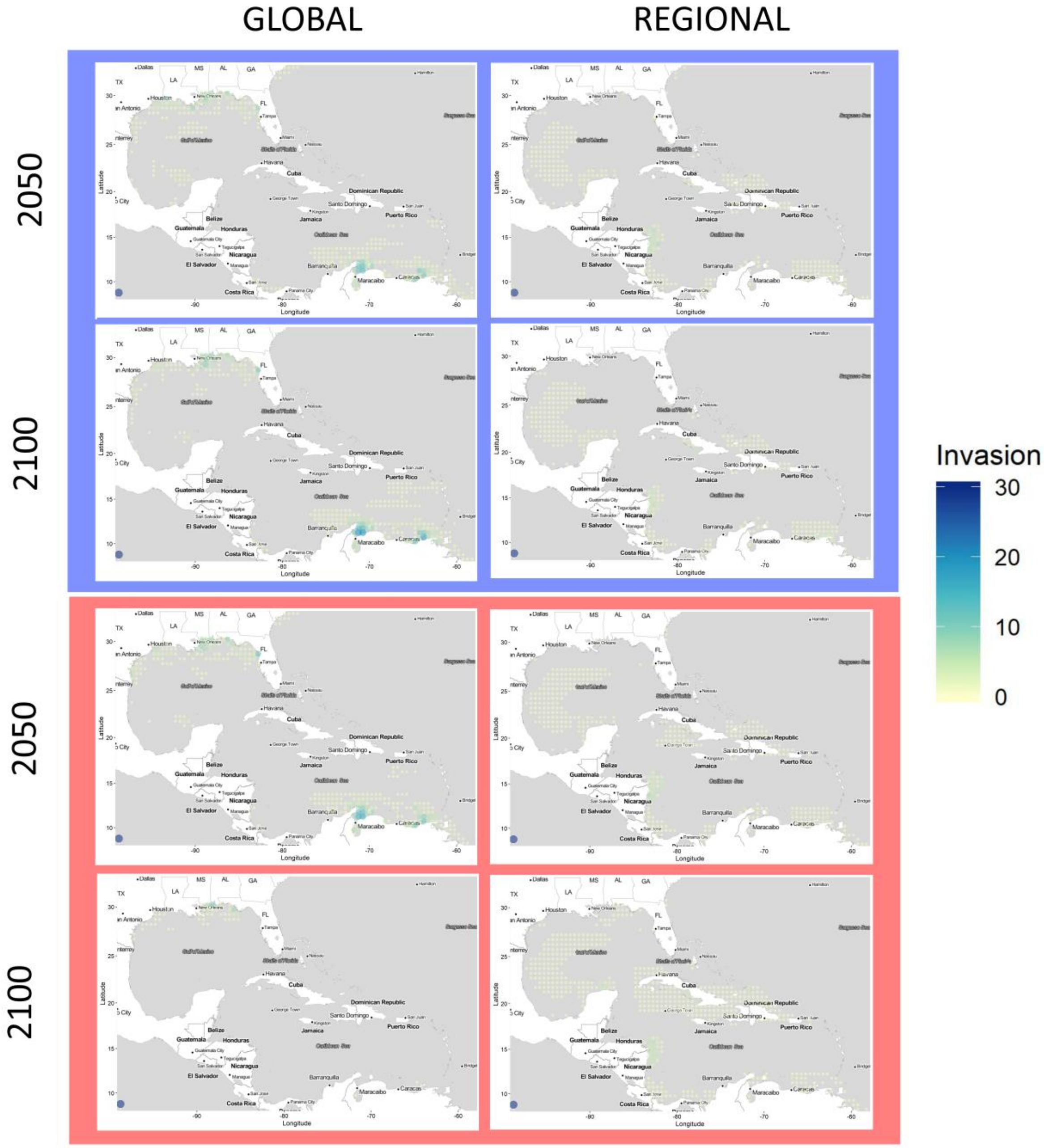

Figure C.3 The distribution of invasions estimated by global (left) and regional (right) models at the years 2050 and 2100, under two scenarios of climate change RCP 2.6 (blue) and RCP 8.5 (red).

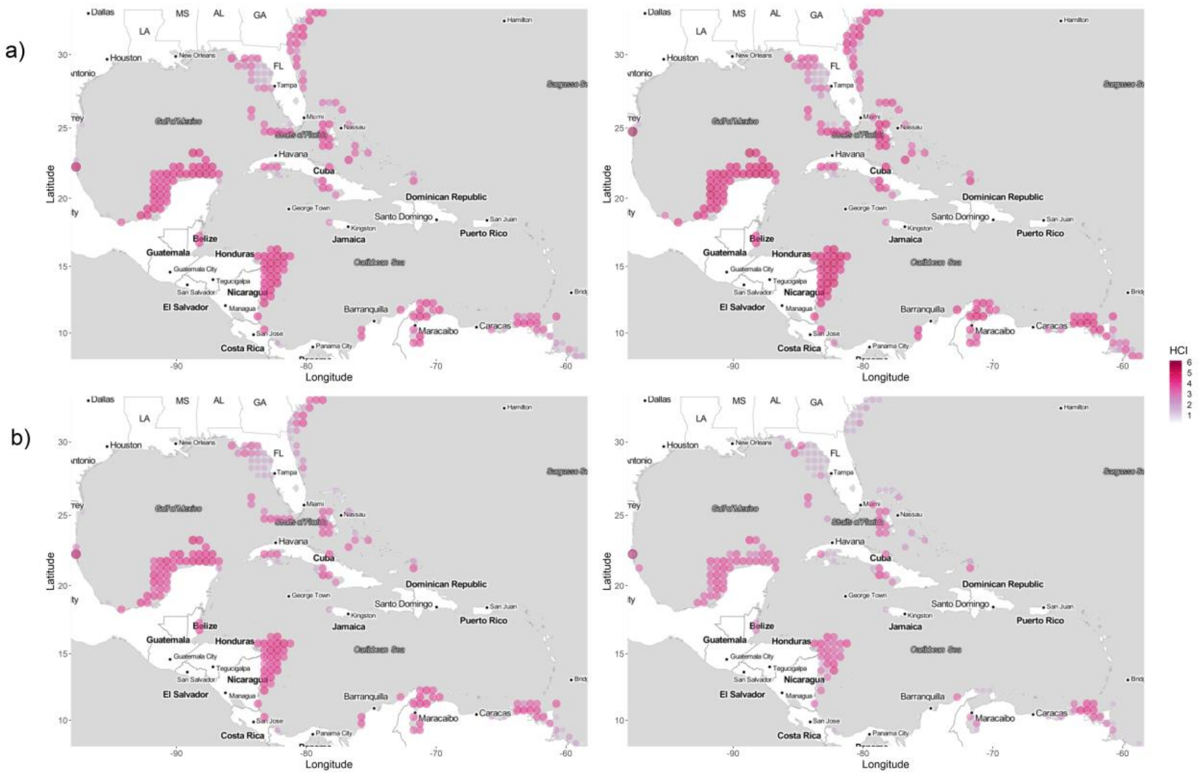

Figure C.4 The distribution of coral reef habitat in terms of HCI at 2050 (left) and 2100 (right) under two scenarios of climate change RCP 2.6 (a) and RCP 8.5 (b).

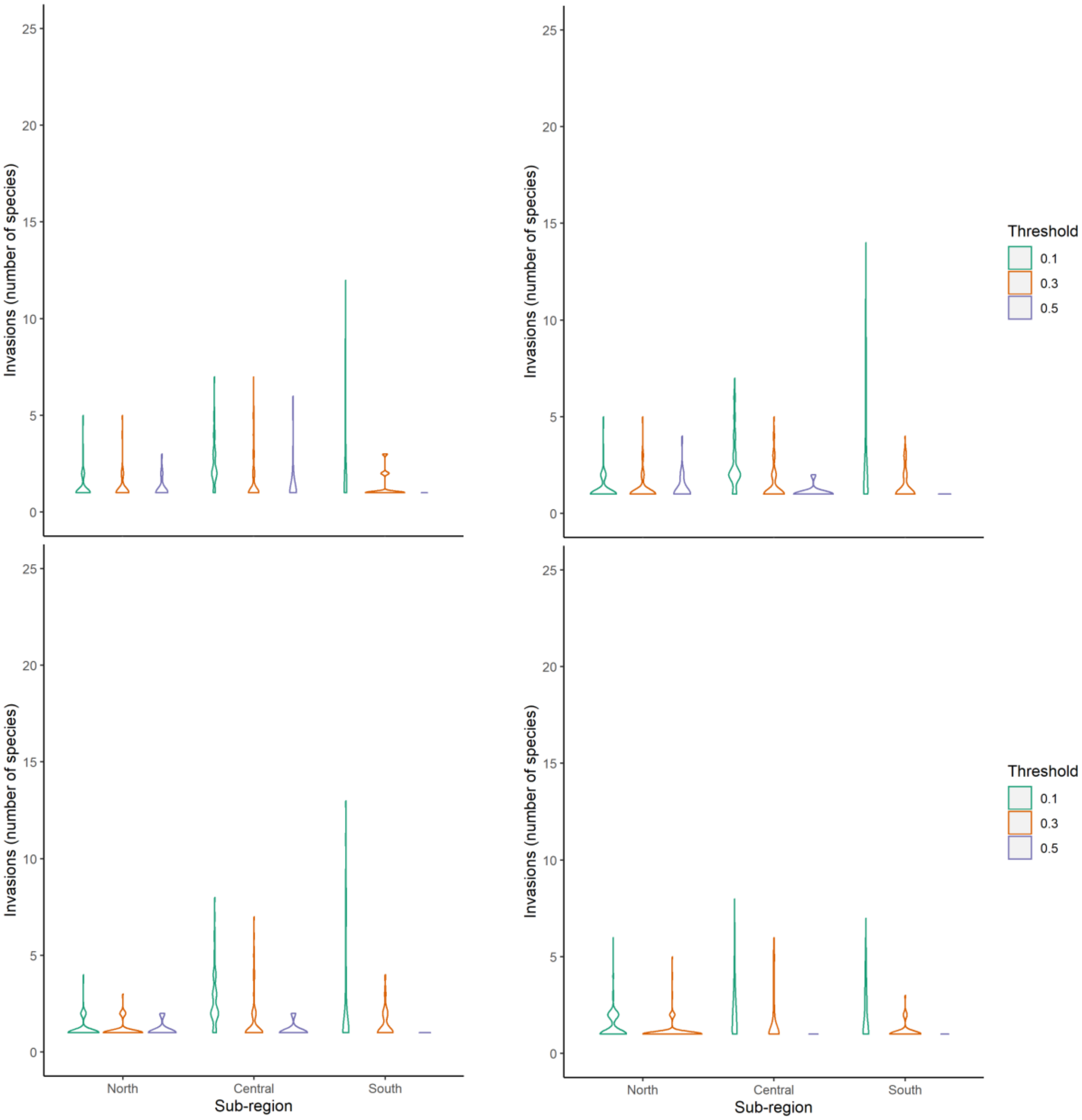

Figure C.5 Regional estimates of invasions using different threshold values at 2050 (left) and 2100 (right) under two scenarios of climate change RCP 2.6 (a) and RCP 8.5 (b).

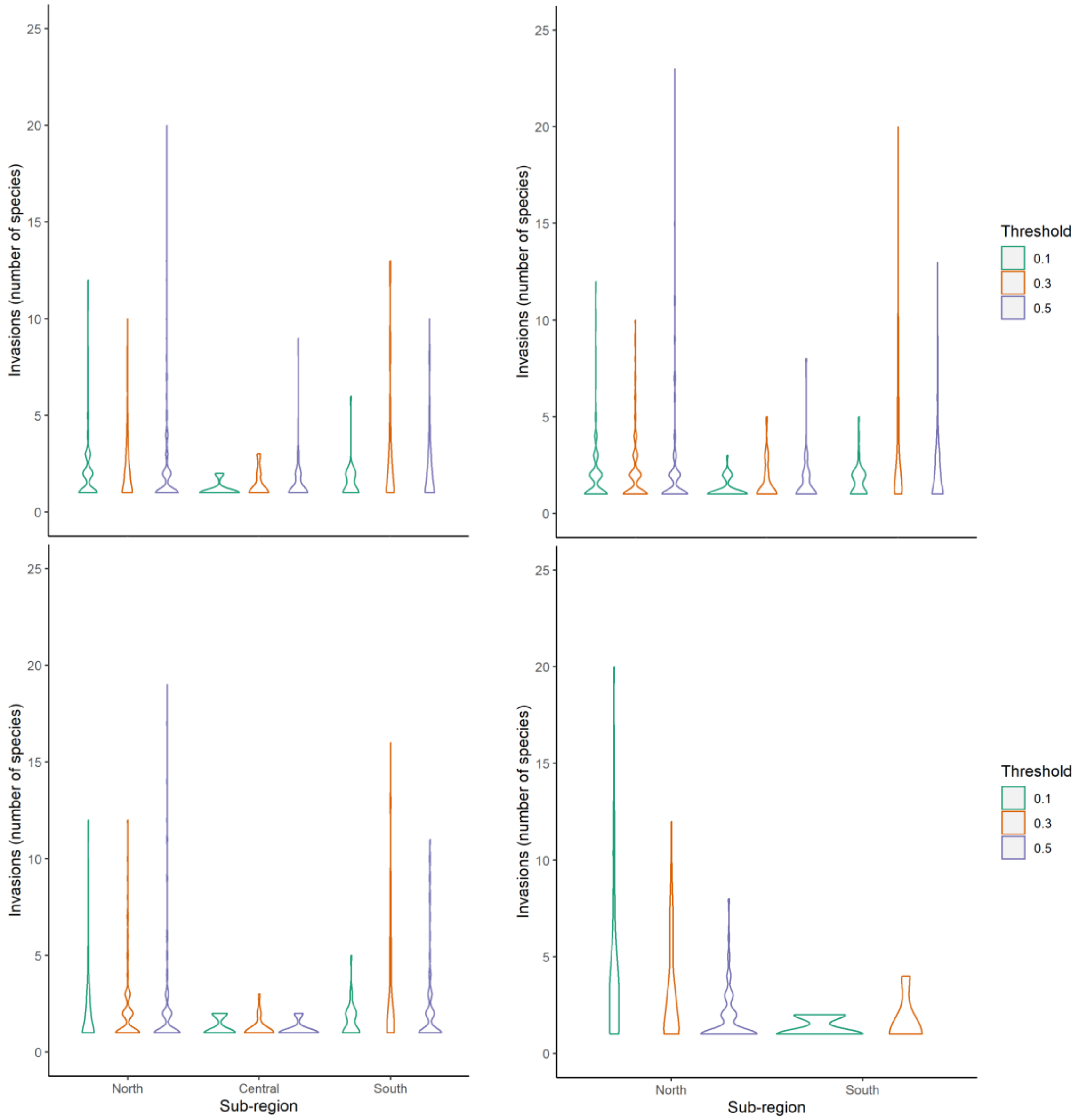

Figure C.6 Global estimates of invasions using different threshold values at 2050 (left) and 2100 (right) under two scenarios of climate change RCP 2.6 (a) and RCP 8.5 (b).

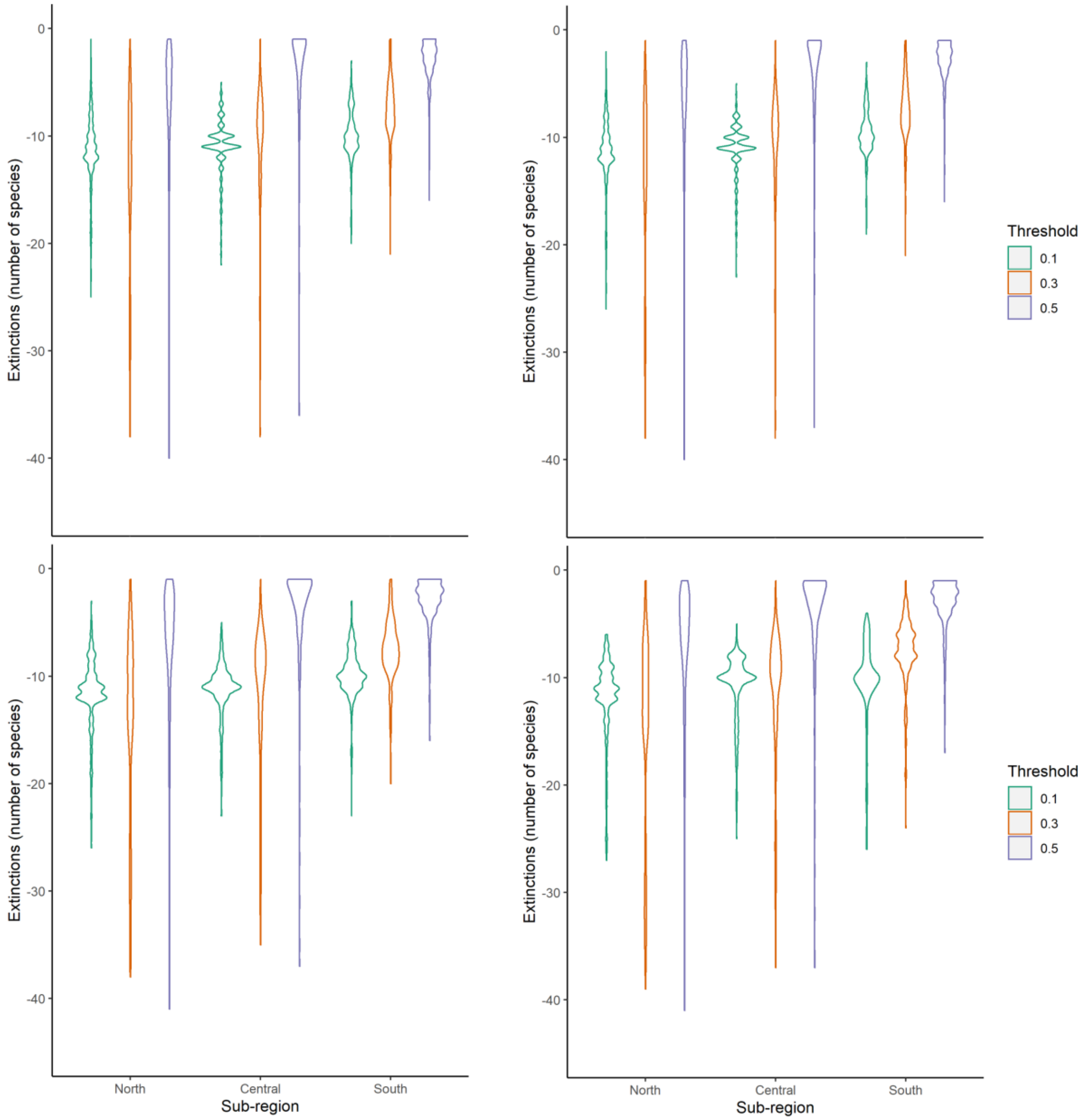

Figure C.7 Regional estimates of extinctions using different threshold values at 2050 (left) and 2100 (right) under two scenarios of climate change RCP 2.6 (a) and RCP 8.5 (b).

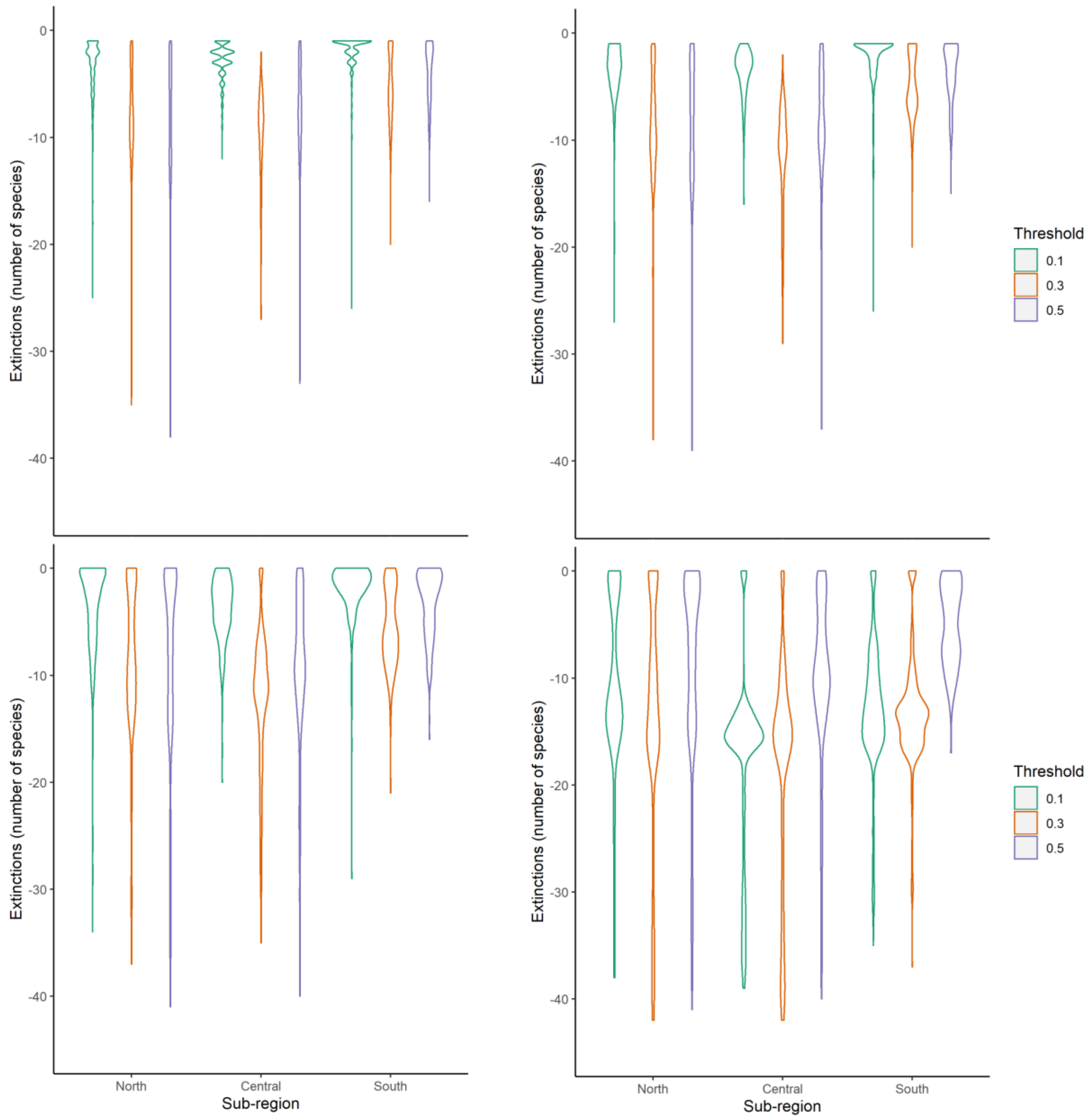

Figure C.8 Global estimates of extinction using different threshold values at 2050 (left) and 2100 (right) under two scenarios of climate change RCP 2.6 (a) and RCP 8.5 (b).

Table C.1 Statistics from t-tests comparing regional and global estimates of niche marginality for Caribbean coral reef fishes.

Variable	t-test	df	p
pH	10.61	41.8	<0.01
SSS	-2.46	72.59	0.02
OXY	1.01	52.95	0.32
SST	-7.49	80.1	<0.01
PP	-3.62	80.8	<0.01

Table C.2 Statistics from F-tests comparing regional and global estimates of niche marginality for Caribbean coral reef fishes.

Variable	F value	df	p
pH	102.56	41	<0.01
SSS	2.12	41	0.02
OXY	6.71	41	<0.01
SST	1.36	41	0.32
PP	1.28	41	0.437