

TOP-PREDATORS AS STRUCTURING AGENTS IN DYNAMIC MARINE ENVIRONMENTS

by

Jonathan Leo William Ruppert H.B.Sc.

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Department of Ecology and Evolutionary Biology
University of Toronto

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University of Toronto

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Thesis Abstract

Global declines in top-predators are occurring due established and ongoing fisheries throughout the world's oceans. In particular, dramatic declines have been observed for Atlantic cod (*Gadus morhua*) in the boreal sub-arctic and for reef sharks (mostly *Carcharhinidae spp.*) in coral reefs. The impact of these declines on marine communities still remains largely unclear due to food web complexity, interacting factors, confounding variables, and fluctuating ecosystem states. Furthermore, as the impact of disturbances on communities can be press (e.g. fisheries), pulse (e.g. environmental variability) or combine, fisheries contribute to disturbance regimes that can generate heterogeneity in communities, meaning that their effects are likely not uniform across space and time. Determining the ecological role of top-predators, as top-down structuring agents, alongside ecosystem disturbances is fundamental to understanding baseline conditions and ultimately may help to inform conservation efforts.

This thesis investigates the relative roles of top-predators and disturbances to build an understanding of how marine communities and food webs may be structured. This thesis aims to address: (i) how environmental variability may impact the role of top-predators, (ii) determine

the ecological role of top-predators in coral reef environments, (*iii*) how top-down and bottom-up structuring agents impact variability in food webs, and (*iv*) how humans are modifying the role of top-down and bottom-up structuring agents.

In this thesis I present three main findings: (*i*) top-predators have a strong top-down influence on marine communities and food webs alongside other disturbances, (*ii*) combined effects (between top-down and bottom-up structuring agents) can impact communities at broad and fine spatial scales, and (*iii*) spatial heterogeneity in structuring agents caused by human activities, impacts food web dynamics across multiple spatial scales. The findings in this thesis provide a foundation from which management decisions can be made to ultimately address restoration and conservation goals.

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Thesis Introduction

The role of structuring agents in marine ecosystems

Top-predators have the capacity to cause dramatic impacts in marine, freshwater and terrestrial ecosystems (Brashares *et al.* 2010; Estes *et al.* 2011). In marine ecosystems, top-predators are undergoing precipitous global declines in abundance due to the legacy and continual presence of fisheries (Myers *et al.* 1996; Ferretti *et al.* 2010). These declines in abundance are occurring against a background of alterations to natural disturbances (e.g. climate change) and the introduction of novel disturbances (e.g. habitat alteration, pollution; Guilderson & Schrag 1998; Burrows *et al.* 2011; Mora *et al.* 2011). A disturbance regime is being created in the Anthropocene where: (1) the ecological role of top-predators as top-down structuring agents is altered; (2) ecosystems need to contend with increased frequency and severity of disturbances (or environmental variability) that largely alter communities in a bottom-up manner; and, (3) top-down and bottom-up structuring processes can combine to impact communities and food webs (Darling & Côté 2008; Heithaus *et al.* 2010; Burrows *et al.* 2011).

Determining the role of top-predators and understanding how declines may alter ecosystems under current scenarios is essential for conservation and restoration goals (Estes *et al.* 2011). Top-predators either directly consume or cause costly behavioural responses in prey (Heithaus *et al.* 2008). It is for these reasons that top-predators are thought to structure prey populations and subsequently communities in a top-down manner. Atlantic cod (*Gadus morhua*) and reef sharks (mostly *Carcharhinidae spp.*) are top-predators found on the continental shelves of the north Atlantic and coral reefs of tropical waters, respectively (Cortes 1999; Worm & Myers 2003). Due to established and ongoing fisheries both species have experienced declines in abundance and in the case of cod (a managed fish stock), they have become overexploited in most regions (Myers *et al.* 1996; Ferretti *et al.* 2010). The impact of overexploitation of cod has lead to trophic cascades within the ecosystem, whereby declines in cod have had cascading effects on the trophic levels below (snow crab (*Chionoecetes opilio*) and shrimp (mainly

Pandalus borealis); Scheffer *et al.* 2005). A similar impact is thought to occur with sharks (Myers *et al.* 2007), however, for reef sharks this pattern remains largely unclear (Heithaus *et al.* 2010). Regardless of their relative role, it is clear that any impact these top-predators may have on fish communities has become altered due to their precipitous global declines in abundance.

Concurrent to top-predator declines, are alterations to disturbance and environmental variability regimes that structure communities in both the boreal sub-arctic and coral reef ecosystems. The chief cause of such changes is global warming, which creates: warmer oceanic waters, changes to primary productivity, and alters ocean chemistry (Greene *et al.* 2008; Burrows *et al.* 2011; Pandolfi *et al.* 2011). Pertinent to this thesis is the link between global climate change and the increase in severity and frequency of natural disturbances or environmental regimes (Guilderson & Schrag 1998; Donner *et al.* 2005; Emanuel 2005; IPCC 2007). In the boreal sub-arctic, a region located between the colder Arctic waters located to the north and the warmer temperate waters in the south, climate warming is thought to be beneficial for the distribution and abundance of species tolerant of warmer temperatures (e.g. cod; Castonguay *et al.* 1999) at the expense of species more tolerant of cooler temperatures (e.g. shrimp and crab; Tremblay 1997; Koeller 2000). In coral reefs, climate warming alters the frequency and intensity of bleaching and cyclones that degrade habitat and alter resources for species (Hughes *et al.* 2003; Donner *et al.* 2005; Emanuel 2005). In both ecosystems, alterations of abundance and distribution of species due to these novel regimes have the capacity to alter species interactions in the community (Scheffer *et al.* 2005; Estes *et al.* 2011). Further, because these disturbances and environmental variability events do not occur in isolation from top-predator declines, determining the relative strength and roles of processes that structure fish communities in a top-down and bottom-up manner can be difficult.

Interactions between the effects of top-down and bottom-up processes, which result in combined effects, remain largely unclear and undermine our ability to appropriately manage marine ecosystems (Darling & Côté 2008; Wilson *et al.* 2010a). In the absence of factorial experiments at the ecosystem scale, these impacts can be difficult to quantify (Borer & Gruner 2009). A combined effect, where both processes can interact, can be synergistic, antagonistic, or additive in its impact on fish species or communities. Combined effects that are synergies occur where the effect is greater than the algebraic sum of the impact of each stressor (Folt *et al.* 1999).

In comparison, antagonistic effects are less than the sum of the impact of each stressor and additive effects are equal to the sum of the impact of each stressor (Folt *et al.* 1999; Darling & Côté 2008). Previous work indicates that most combined effects are non-additive (synergies or antagonisms), making it more complicated to interpret combined effects for the management of ecosystems than a simple additive effect (Darling & Côté 2008). Thus, possible interactions between top-down and bottom-up processes are likely to be multiplicative or non-linear to create patterns in time and space that are distinct from the processes alone (Fortin & Dale 2005).

Interactions between disturbances are dynamic in space and time, which influences food web structure and can potentially impact the overall health of ecosystems (e.g. alternative stable states; Bellwood *et al.* 2004). This heterogeneity is creating variability in marine ecosystems that push them beyond traditional baseline conditions, which can have catastrophic consequences for economic and ecological viability of these systems. To manage marine ecosystems for the future we need a framework of understanding that includes knowledge of: (1) the relative roles of disturbances that structure marine communities in a top-down and bottom-up manner, and (2) how spatio-temporal variability in disturbances structure marine food webs. This thesis explores these concepts by using two focal ecosystems and capitalizing on unique sets of circumstances that control for many confounding variables (e.g. multiple species fisheries, pollution, etc.).

Disturbance

Oscillations in environmental conditions are a natural phenomenon that can also influence many terrestrial and marine ecosystems, however, there is evidence to support the notion that these oscillations are changing (Guilderson & Schrag 1998; Goodkin *et al.* 2008; Burrows *et al.* 2011). Using microchemistry techniques on large massive corals, studies have shown that the North Atlantic Oscillation (NAO) and the El Niño-Southern Oscillation (ENSO) in the Pacific have both increased in frequency and severity (Guilderson & Schrag 1998; Goodkin *et al.* 2008). In boreal sub-arctic marine ecosystems, environmental variability can be related to temperature tolerances of top-predators and prey that can alter their distribution and abundance (Perry *et al.* 2005a; Ruppert *et al.* 2009). Communities are then potentially subject to alternating roles of top-down and bottom-up control due to the altered distributions of top-predators (Ruppert *et al.* 2009). Further, studies have linked environmental variability to productivity within this region, which creates resources for primary consumers, altering how communities are structured in a

bottom-up manner (Greene *et al.* 2008). Hence, the role environmental variability plays in these boreal sub-arctic ecosystems is wide ranging and it remains largely unclear whether environmental variability can mediate top-down structuring in these communities via alterations in cod distribution and abundance.

In contrast, climatic events that impact coral reefs generally alter the benthic environment from largely coral dominated to algal dominated benthic habitats that structure communities in a bottom-up manner (e.g. cyclones, coral bleaching; Wilson *et al.* 2006; Graham *et al.* 2011). Coral cover is critical for reef fishes, because it is required for settlement, habitat and resources (Jones *et al.* 2004; Wilson *et al.* 2006). Further, similar to the plight of top-predators, coral cover is experiencing worldwide declines (Gardner *et al.* 2003; Bruno & Selig 2007; De'ath *et al.* 2012). As a result, changes in coral cover can alter the composition of primary consumer communities in a bottom-up manner, however, bottom-up structuring does not appear to be common across ecosystems for secondary consumers (mesopredators; Borer *et al.* 2006). This contrasts the impacts of top-down structuring by top-predators, where impacts appear to permeate throughout the food web (Scheffer *et al.* 2005; Borer *et al.* 2006; Estes *et al.* 2011). Thus, determining the relative roles of top-down and bottom-up processes in coral reef ecosystems is critical to provide insight for management goals.

Finally, marine ecosystems are experiencing the impact of fisheries that target multiple species (Pauly *et al.* 1998; Essington *et al.* 2006). A recent study found that 55% of coral fisheries are exploiting species in an unsustainable manner (Newton *et al.* 2007). As aforementioned, the consequence is evident for larger species, such as top-predators, which are declining in most regions of the world (Myers *et al.* 1996; Ferretti *et al.* 2010). Many studies have found that reefs impacted by fishing can have dramatically different fish community compositions that may arise from reduced top-down control (Friedlander & DeMartini 2002; Sandin *et al.* 2008). Further complicating this pattern, fishing gradients tend to occur alongside degradation in the benthic community that structures fish communities in a bottom-up manner (Friedlander & DeMartini 2002; Sandin *et al.* 2008). Thus, because fisheries remove multiple species and there are confounding gradients of degradation, the ecological role of top-predators in coral reef ecosystems remains unclear. One way to determine the ecological role of top-predators may be to investigate patterns of spatio-temporal heterogeneity, where patterns in

bottom-up and top-down structuring agents are competing gradients that can be subject to partial regression techniques (control; Fortin & Dale 2005). Another may be through factorial experiments to test for the independent and combined effects of each factor (Christensen *et al.* 1996; Borer & Gruner 2009). This thesis uses both approaches to achieve this objective.

Spatio-temporal variability

Biological interactions in a focal community are dynamic in space due to heterogeneity that results from landscape processes (Ricklefs 2008; Massol *et al.* 2011). Landscape processes in marine ecosystems arise from top-predator distributions and disturbance events that structure communities in a top-down and bottom-up manner. In boreal sub-arctic ecosystems, the range of influence of top-predators can be quite vast, as cod are a highly mobile and migratory species (deYoung & Rose 1993). Thus, their range of influence on community patterns is a reflection of not only density, but regions where they spend a large amount of time (e.g. the location of wintering and summer feeding grounds; Castonguay *et al.* 1999). Given that environmental variability influences cod distribution within many regions of the Northwest Atlantic (Loeng 1989; deYoung & Rose 1993; Vilhjálmsson 1997), the impact of top-down structuring by cod is likely not uniform within regions across contrasting environmental regimes. In contemporary coral reef ecosystems, higher densities and diversities of sharks are found in either managed or geographically isolated reefs (Robbins *et al.* 2006; Sandin *et al.* 2008; Field *et al.* 2009). For example, on the Great Barrier Reef (a multi-use managed marine park), densities of sharks appear to be maintained in no entry zones, whereas no take reserves and fished areas tend to have lower densities of sharks (Robbins *et al.* 2006). Management such as this can also create spatial heterogeneity in top-down structuring. The same can be said of bottom-up structuring where the scale of influence and severity of impact differs between cyclones and coral bleaching events (Mumby *et al.* 2011; De'ath *et al.* 2012). These natural disturbances will impact some reefs, but many others can be minimally impacted by the events.

Disturbances also operate at different temporal and spatial scales within the environment and it can be stated that no one disturbance is the same as another (Wilson *et al.* 2008). In particular, one of the biggest differences between disturbances is that they can be press (i.e. continuous) or a pulse event (i.e. short-term). Press disturbances often include activities such as: fisheries, pollution, and sedimentation (Pauly *et al.* 1998; Mora *et al.* 2011). However, these

disturbances can also become pulse events if their temporal impact is not continuous (i.e. an isolated event). Pulse disturbances are discrete; hence the event occurs at a point in time or over a particular period of time. Such events may include: environmental regimes (oscillations), cyclones, coral bleaching, and crown-of-thorns outbreaks (Moran *et al.* 1988; Guilderson & Schrag 1998; Donner *et al.* 2005; Emanuel 2005; Goodkin *et al.* 2008). These events can all have dramatic impacts on ecosystems that result in different recovery time frames (Wilson *et al.* 2006; Graham *et al.* 2011). The differences in time scales of impact and recovery alongside differences related to frequency and severity contribute to spatial heterogeneity in landscape processes that structure marine communities. Further, the influence of press and pulse disturbances can also have a profound influence on the variability in abundances of species (Minto *et al.* 2008; Mellin *et al.* 2010b). Higher variability in populations is thought to have a negative impact on species due to an increased risk of bottleneck and local species extinction (Melbourne & Hastings 2008). Thus, when considering the temporal stability of species abundances, stability is thought to be a good metric of resilience to disturbance events.

The concept that a food web's structure is dynamic in space and time is not novel. Communities are found within food webs of interactions that operate across multiple spatial and temporal scales (Ricklefs 2008; Massol *et al.* 2011). It is under the framework termed "metaecosystems" where attempts are made to unify the concepts of food web interactions (or metacommunity dynamics) and the concept of environmental variation that influences food web stability and compensatory dynamics (Gouhier *et al.* 2010; Massol *et al.* 2011). In this thesis I consider interactions between species in different trophic levels, where trophic level is positively associated with body size and range of movement (McCann *et al.* 2005). This implies that trophic levels in marine food webs are influenced by different scales of disturbances or environmental variability observed within the environment. This hierarchy creates even more complexity, resulting in likely non-additive community patterns related to the relative roles of top-down and bottom-up structuring agents.

Thesis outline

The overall objective of this thesis is to determine the ecological role of top-predators within marine food webs against a background of disturbances that structure communities in a top-down (fisheries and environmental variability) and bottom-up manner (cyclones and coral bleaching).

Focal ecosystems from the Northwest Atlantic, Northwest Australia and the Indo-Pacific are used to consider the role of top-predators in the context of long-term conservation and restoration management goals. Interactions between disturbances that may influence communities in a non-additive manner to contribute to spatio-temporal food web patterns are also considered to provide some clarity on the subject. This research contributes to a body of literature on marine food webs and community trophic structure that are used to formulate management decisions (Scheffer *et al.* 2005; Sandin *et al.* 2008; Wilson *et al.* 2010b; Williams *et al.* 2011). This thesis achieves this overall objective in four related, yet distinct chapters.

Chapter 1 presents a framework to investigate the role of environmental variability on food web structure using a combination of Multivariate Regression Tree (MRT) and Classification and Regression Tree (CART) modelling. In previous work, it has been identified that the distribution and abundance of Atlantic cod is dependent upon environmental variability (Loeng 1989; deYoung & Rose 1993; Vilhjálmsson 1997). Similar patterns are observed in the Northern Gulf of St. Lawrence, where dramatically different distributions are observed between two contrasting environmental regimes in 1991 - 1995 (cooler and less saline) and 1997 - 2003 (warmer and more saline; Ruppert *et al.* 2009). Here cod display increased fidelity for summer feeding grounds during the warmer period in comparison to the cooler period. In this chapter dynamics across the Gulf (North and South) are considered to address the following objectives: (1) how environmental variability impacts the trophic structure of communities, and (2) determine whether there are spatially discrete areas that are characterized by specific community structures. This chapter presents a novel framework to investigate community patterns through space and time while providing insight into the role of environmental variability on food web structure in a period of post cod decline.

In Chapter 2, I investigate the relative roles of processes that structure reef fish communities in a top-down and bottom-up manner. Many studies have shown that minimally impacted reefs have a fish trophic structure that differs significantly from those exposed to human activities (Friedlander & DeMartini 2002; Sandin *et al.* 2008; Williams *et al.* 2011). However, because these studies use comparisons based on gradients of human density, many factors contribute to this trend making it difficult to isolate the effects of structuring agents. Specifically, the role of top-predators in reef ecosystems remains unclear (Heithaus *et al.* 2010).

This chapter takes advantage of a unique set of events where reefs are subject to the removal of sharks (top-down) against a background of pulse disturbances (cyclone and coral bleaching; bottom-up) over the period of 1994 - 2008. This data set provides an opportunity to implement an ecosystem-scale BACI (Before/After – Control/Impact) design where I compare four treatments (fished/disturbed, fished/ non-disturbed, non-fished/disturbed, and non-fished/ non-disturbed) to isolate the impacts of each stressor (fishing and benthic disturbance). The objectives of this chapter include: (1) how changes to shark density impact the trophic structure of reef fishes, (2) what role disturbances play alongside changes to shark density, and (3) whether alterations to shark density and disturbances interact to produce a combined effect on coral reef fishes. The novelty of this chapter is the identification of the ecological role of sharks in reef ecosystems and whether combined effects are important to reef fish communities.

In Chapter 3, I consider how changes in the abundance of sharks may impact the temporal stability of coral reef food webs that are subject to environmental stochasticity. Fisheries that reduce the abundances of species (in an age truncated fashion) are thought to increase variability in species abundances, whereas predators act in more of a stabilizing fashion by reducing variability in abundances of prey species in marine ecosystems (Bax 1998; Hsieh *et al.* 2006). Thus, as top-predators sharks may contribute to the temporal stability of food webs to disturbance events, which is thought to be a good indication of resilience (Gonzalez & Loreau 2009; Mellin *et al.* 2010b). However, whether sharks directly structure food webs or if they impact food webs indirectly through an intermediary (mesopredators) remains an open question (Heithaus *et al.* 2010). This chapter builds upon the findings of the second chapter, using a causal food web model (top-predator, mesopredators, primary consumers and coral cover) to provide evidence of the strength and significance of structuring agents in coral reef food webs using structural equation models (Grace 2006). This achieved by using a fine scale differences (short gradient) of shark density and a gradient of disturbance (environmental stochasticity) at protected reefs. The objectives of this chapter include: (1) determining the role temporal variability plays in structuring reef fish communities, (2) investigate the role of top-down and bottom-up structuring agents to determine their strength and significance throughout the food web, and (3) ascertain whether sharks increase resilience on reefs by reducing temporal variability in trophic structure of fish communities. This chapter provides novel insight into the strength and significance of top-down and bottom-up structuring agents throughout the food web

and determines whether sharks play a critical role by increasing temporal stability and resilience in fish communities.

My thesis concludes with Chapter 4, where I investigate how patterns of top-down and bottom-up structuring agents are modified through space by human activities. Human density is associated with fisheries, nitrification and land-use change (causing increased sediment in runoff; Mora *et al.* 2011), which alter the roles of top-down and bottom-up structuring agents. To investigate these impacts through space, a top-down perspective is taken to apply a novel framework, using a combination of boosted regression tree modelling, geographically weighted regression and spatially constrained clustering, to determine if there are any distinct regions in the Pacific with similar processes that contribute to reef shark distributions. I also test for the significance and strength of interactions in a food web model throughout the Pacific and within each subregion using structural equation models (Grace 2006). The objectives for this chapter include: (1) determine how human activity is altering the role of sharks and disturbances at oceanic and regional scales, (2) whether structuring agents interact (human activity, sharks and disturbance) to impact fish communities, and (3) how these structuring agents contribute to spatial patterns in the trophic structure of reef fishes. The novelty of this chapter is the creation of a framework to determine how spatial heterogeneity in structuring agents contribute to food web patterns and it provides evidence of how reef fish communities are being altered by anthropogenic means at oceanic and regional scales.

Altogether these four chapters provide insight into the role of top-predators in environmentally dynamic marine ecosystems. Further, the chapters all provide insight into the current state of ecologically important ecosystems for long-term conservation and restoration goals.

Chapter 1

Environmental mediation of Atlantic cod on fish community composition: an application of multivariate regression tree analysis to exploited marine ecosystems

1.1 Abstract

Changes in species abundances caused by climatic variability have long been linked to alterations in community composition, species interactions and maintenance of biodiversity in marine ecosystems. Here I use multivariate regression tree (MRT) analyses to quantify how changes in species abundances and environmental variability contributed to observed patterns of community composition in the Gulf of St. Lawrence during two contrasting periods (the cooler and less saline period 1991 to 1995 and the warmer and more saline period 1997 to 2003).

Broad-scale patterns of community composition in both periods were consistently explained by the depth and salinity of the benthic environment, but biological factors differed. In the cold period, the previous year's catches of snow crab (*Chionoecetes opilio*) and northern shrimp (mainly *Pandalus borealis*) were most important, while in the warm period the previous year's catch of Atlantic cod (*Gadus morhua*) dominated. MRT models further identified spatially discrete areas where communities are characterized by relatively high abundances of these species. These results indicate that environmental variability leads to dynamic and spatially explicit responses not only of single species, but of marine communities. Applications of ecosystem management in the face of climate change must take this into account.

1.2 Introduction

Changes in species abundances, whether induced by environmental conditions or anthropogenic activities, have been linked to changes in community composition and interactions among species within many marine ecosystems (Myers & Worm 2003; Scheffer *et al.* 2005; Heithaus *et al.* 2008). These changes have the potential to disrupt ecosystem function and maintenance of biodiversity by influencing distributions, abundances, behaviour and population dynamics of species at multiple trophic levels (Frid *et al.* 2008; Sandin *et al.* 2010). Despite the importance of community dynamics to marine ecosystems, most studies have focused on single populations

with few studies emphasizing the effects of population changes at the community level (Benoît & Swain 2008). On the one hand, the common approach in fisheries science has been to conduct single-species management at the population level, with emphasis on managing the anthropogenic influences on abundance. In doing this, much of the information with regards to interactions among species may be lost, and, as a result, community level processes are not recognized (Beare *et al.* 2005). On the other hand, a historical approach in community ecology was to evaluate the impact of single ecological processes on community composition separately (Agrawal *et al.* 2007), despite ecology having transitioned to incorporating multiple processes that include competition, mutualism, predation, parasitism and the environment (Bronstein 1994; Wootton 1994; Stachowicz 2001). For example, predator declines may be occurring concurrently with changes in environmental conditions, with both influencing interactions between lower trophic level species and potentially altering community composition.

Substantial changes in the structure of fish communities have been documented throughout the north-western Atlantic for many shelf ecosystems (Benoît & Swain 2008). This boreal sub-arctic region experiences both ‘top-down’ structuring of community dynamics (e.g. Savenkoff *et al.* 2007b), where a predominant predator is Atlantic cod (*Gadus morhua*), and ‘bottom-up’ forcing, which is more tightly linked to environmental change (e.g. Greene *et al.* 2008). Cod stocks in this region were once among the most abundant worldwide and have been studied extensively, but due to overexploitation during a period of low productivity, declines were widespread in the late 1980s and early 1990s (Rose 2007; Halliday & Pinhorn 2009). In the Gulf of St. Lawrence during the last decade, a moratorium on cod fisheries reduced exploitation, and, with the poor environmental conditions of the early 1990s also abating, stock rebuilding has been slower than anticipated and biomass remains well below historic levels (DFO 2009, 2010a). Mechanisms contributing to low productivity in cod may be complex and accompanied by many other changes within the ecosystem and biological community. For example, cod declines occurred almost concurrently with increases in snow crab (*Chionoecetes opilio*) and shrimp (mainly *Pandalus borealis*; Savenkoff *et al.* 2007a) during the 1990s. Catch rates in 2008 and 2009 indicate major changes in the community, suggesting that crab and shrimp stocks in the Gulf are in decline (DFO 2010b, c) and cod stocks are showing modest increases in the northern Gulf, but modest declines in the southern Gulf (DFO 2009, 2010a). Such dynamics suggest not

only a strong environmental influence (Lilly *et al.* 2008), but second-order cascading effects, such as predation on lower trophic levels, with resultant community structural change.

Investigating spatio-temporal relationships between community structure and environmental variability can help to determine whether environmental influence and cascading effects on lower trophic levels are contributing to dramatic shifts in community composition throughout the Gulf. Environmental variability observed at smaller scales within the northern gulf throughout the 1990s and early 2000s was associated with a shift in site fidelity of cod, such that greater site fidelity to summer feeding grounds was demonstrated for warmer years compared to colder years (Ruppert *et al.* 2009). Although cod dynamics are clearly influenced by environmental variability, whether the change in environmental conditions throughout the Gulf (at a regional level) impacts the broader community is poorly understood. Further, if second-order cascading effects influence patterns of community composition, changes in cod site fidelity (as demonstrated at a smaller scale in the northern Gulf) may be inferred to have an effect on community composition patterns throughout the Gulf.

The relationship between community dynamics and the environment can also be scale dependent, such that environmental characteristics influence community dynamics at either regional and/or local spatial scales. Previous studies at broad continental scales have suggested that trophic dynamics and community composition within traditionally cod-dominated ecosystems in the Atlantic have a strong association with temperature and biodiversity gradients (Worm & Myers 2003; Frank *et al.* 2007). At finer scales Benoît & Swain (2008) have identified significant effects of fisheries and climate on the composition of the community within the southern Gulf of St. Lawrence. Further, the relationship between densities of species has also shown scale dependence between cod and capelin (predator and prey, respectively) within the northern Gulf of St. Lawrence (Rose & Leggett 1990). Hence, it is likely that the effects of environmental variability on community dynamics in the Gulf of St. Lawrence are scale dependent, and a multi-scale approach would be well suited for investigating community-environment relationships at a regional scale.

In this chapter I used a predictive community approach to investigate the dynamics in a portion of the community for which data were available (capelin presence/absence along with cod, shrimp and snow crab catch weight). This paper expanded upon a single-species and local-scale study published by (Ruppert *et al.* 2009) by investigating community dynamics at both

broad and fine spatial scales in the Gulf of St. Lawrence, in relation to environmental variability and the abundances of those species. The goal of this chapter was to ascertain how environmental conditions and species abundances can influence community composition during periods of differing ocean climate. I used a multi-scale, multivariate technique within a temporal framework, multivariate regression tree (MRT) analyses, to assess differences in the relationship between environmental variability and patterns of community composition.

1.3 Methods

1.3.1 Study Area

The Gulf of St. Lawrence is a semi-enclosed sea, forming the Northwest Atlantic Fisheries Organization (NAFO) management zones 4SRT and 3Pn (Figure 1.1). Some commercial species within the Gulf, such as cod, are managed as two separate units (northern and southern regions), but often the northern and southern units are viewed as subregions of a single, semi-enclosed Gulf ecosystem. The Gulf is characterized by highly variable bathymetry, to a maximum depth of about 500 m, and is dominated by shallow coastal shelves with deep trenches that bisect both the eastern and northern extensions. This chapter is concerned mainly with environmental conditions and community composition in the benthic environment, meaning that the variability in depth is likely to be a strong contributor to patterns in abiotic and biotic conditions throughout the region. Further, as a boreal marine ecosystem and semi-enclosed sea, the gulf experiences strong interannual variability in water and ice properties (Smith *et al.* 2006).

1.3.2 Data

Atlantic cod, snow crab and northern shrimp abundance data were obtained from Department of Fisheries and Oceans (DFO) Québec and Gulf Region annual bottom trawl surveys (BTS) spanning the years from 1991 to 1995 and from 1997 to 2003. The BTS for northern and southern Gulf regions follow a depth-stratified random survey design and were conducted during August and September of each year (Doubleday 1981; Gagnon 1991). Factors that could differ

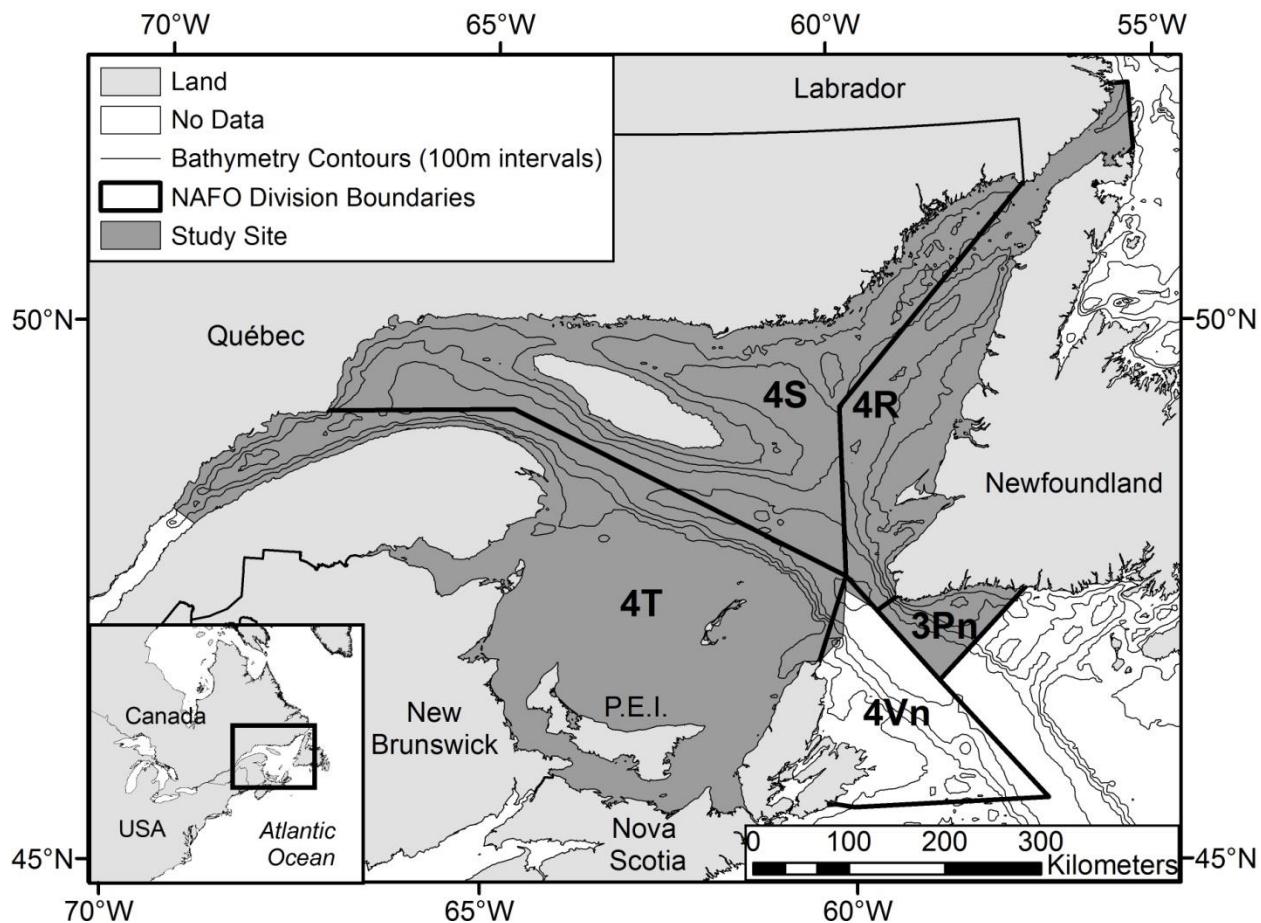


Figure 1.1. The Gulf of St. Lawrence and its NAFO management units. The study area (denoted in dark grey) includes management units 4SRT, 3Pn and a small portion of 4Vn. The contour lines delineate bathymetry at 100 m intervals in depth.

between the north and south regional BTS include: duration of tow, length of tow, the vessel and the type of gear used. All survey catches for the entire study region were standardized individually by tow duration to a 15 minute tow. Vessel and gear types were similar between regions, and changes among years have been subjected to standardization procedures (Fréchet *et al.* 2005; Benoît 2006).

BTS data also include information about the location (latitude and longitude), bottom temperature and bottom salinity (no salinity data were available for the northern area in 1996; hence, this year was not included). The BTS data also contain capelin (*Mallotus villosus*) catch weight, but, because capelin is a semi-pelagic species, the catch cannot be used to infer relative abundance. As a result any catch weight of capelin was used to only infer its presence. Depth, slope and orientation were derived from the 1 minute world bathymetric grid of the General Bathymetric Chart of the Oceans (GEBCO 2003). Surficial sediment data were provided by Natural Resources Canada, which coarsely classifies regions and represents the best available classification and coverage for the entire Gulf region (Fulton 1995). To account for lag responses to the abundance and distribution of a particular species, species catch weight measurements for the previous year were derived from interpolated BTS measurements by universal kriging for cod, shrimp and crab catch weights (Cressie 1993).

1.3.3 Analysis

To determine how the benthic fish community responds to contrasting environmental conditions that reflect a cooler, less saline (1991 to 1995) and a warmer, more saline (1997 to 2003) period I used an MRT approach (De'Ath 2002). Prior to the MRT analysis I verified whether or not temperature and salinity differ significantly between these two periods using the Wilcoxon-Mann-Whitney test, because the data are not normally distributed (Rosner 2000). I chose not to pool the data (i.e. all years of data) into a single regression tree, because this would remove much of the yearly variability, and I was interested in how and if community responses changed with respect to changes in environmental conditions through time. This means that a MRT model was created for each year of data analyzed.

MRT analysis is a data-mining technique that uses a recursive partitioning algorithm that subdivides sample sites into two groups based on the similarities in community composition (or the dependent variable) and environmental conditions (or the independent variables; Breiman *et*

al. 1984; De'Ath 2002). The final output is a tree structure with a root (with all samples together), branches that are formed by splits (based on the selection of an environmental variable and a threshold for that variable), and leaves that form the predictions (Figure 1.2). MRT analysis is an extension of the univariate regression tree analysis (i.e. classification and regression tree analysis or CART); with the difference being that it has a multivariate prediction. As a result MRT predictions can be viewed as the average response of each species to other species (i.e. a community) as opposed to the average response of a single species without consideration of any community responses (Figure 1.2). There are several advantages to MRT analysis, but the most important is that no assumptions are required regarding data structure, in contrast to many other multivariate techniques (De'Ath 2002). Non-targeted fisheries data are generally right skewed and zero-inflated, which means that values need to undergo log-transformation (i.e. $\log(x+1)$) prior to analysis to reduce large disparities between catch values (i.e. large and small catch values). The log-transformation improves the ability of MRT analysis to capture more subtleties of the community-environment relationships, because without the log-transformation MRT analysis strictly groups species abundances based on two categories: large catch weights and all other catch weights. This approach for regression techniques has proven to be quite robust for non-targeted fisheries data (Ruppert *et al.* 2009). Another useful property of MRT analysis with spatial data is that explanatory variables that operate at broader spatial scales are designated in trees within the first two splits, and variables used in subsequent splits in trees typically operate at finer spatial scales (Moore *et al.* 1991). This hierachal partitioning results in splits near the root of the tree having more observations than those below. This means that explanatory variables closer to the root of the tree explain more variation in the data than subsequent splits in the tree, which have inherently fewer observations. The MRT analyses were run in R Project for Statistical Computing, using the *mvpard* package (De'ath 2007b).

An important aspect of any analysis of multivariate ecological data is to determine how well a model explains variation in the data. With MRT analysis, prediction error is used to assess the fit of a model and to determine the appropriate tree size (i.e. initial MRT models created by this process are often over-sized). A measure of prediction error in this chapter was attained through cross-validation, which is not affected by small sample sizes (where $n < 1000$; De'Ath 2007a). To delineate an optimal tree size with a consistent minimum deviance (or prediction

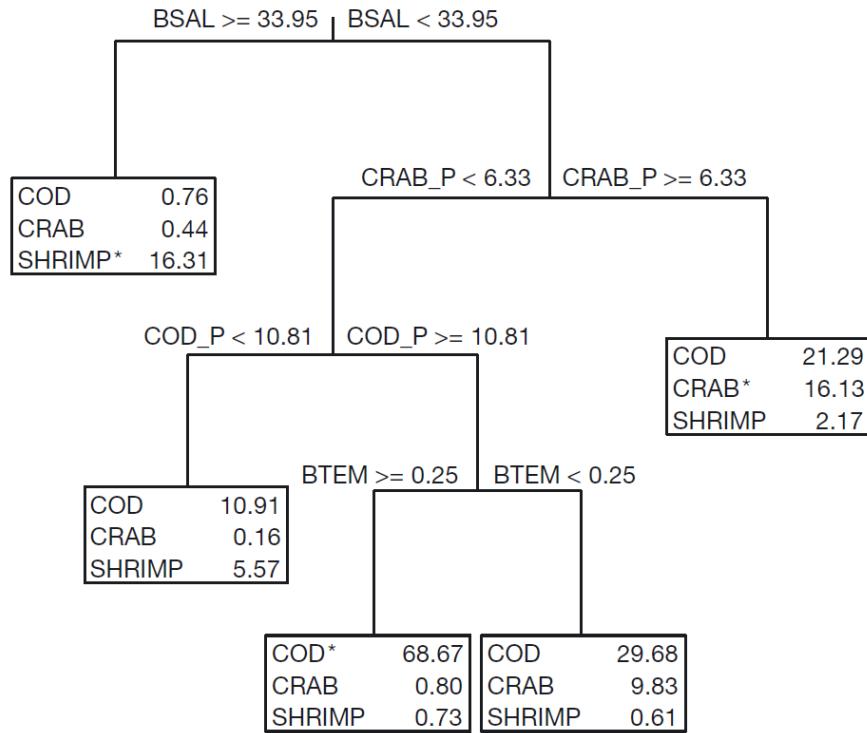


Figure 1.2. The multivariate regression tree for 1994 predicting the relative catch weight per tow (kg/tow) for cod (*Gadus morhua*), shrimp (*Pandalus borealis*) and crab (*Chionoecetes opilio*).

The leaves of the tree indicate the average catch weight per tow of each species given the conditions and thresholds stipulated by the splits. *Catch weights of species that were significantly higher, as per the indicator species index, than in other leaves

error), the 1 standard deviation rule was used to determine the appropriate tree size (Maindonald & Braun 2007). Despite the cross-validation analysis, the variability in the sample size and catch weights can present a problem in the ability of MRT analysis to determine appropriate community-environment relationships (Table 1.1). To test this, cross-validation was bootstrapped 1000 times to judge the precision of the final model (i.e. whether or not the tree and size of tree describe community-environment relationships). If consistency in a regression tree is demonstrated, this would indicate that the sample size or variability in catch weights does not present a problem for the finalized model.

When using MRT analysis there are several aspects to constructing a model that need to be investigated. To assess the degree of collinearity and hence redundancy among variables, Spearman correlation analysis was initially conducted on all variable pairs (Rosner 2000). As MRT is a method of constrained cluster analysis which chooses a tree structure with splits defined (or constrained) by environmental variables, a comparison with an unconstrained method of cluster analysis (i.e. partitioning methods that do not define splits by environmental variables) was conducted to determine whether MRT splits based on the variables used adequately accounted for the potential species variance (De'Ath 2002). Finally, to represent predictions of MRT analysis spatially, the multivariate responses or predictions need to be classified using a species indicator index. In the present chapter the indicator index developed by Dufrêne & Legendre (1997) was used. The index (d) is the product of the relative frequency (f) and relative average abundance (a) of species within clusters. Specifically, for a cluster c in set K the index would look as follows:

$$d_{i,c} = f_{i,c} \times a_i,$$

$$f_{i,c} = \frac{(\sum_{j \in c} p_{i,j})}{n_c}$$

$$a_{i,c} = \frac{(\sum_{j \in c} x_{i,j})/n_c}{\sum_{k=1}^K ((\sum_{j \in k} x_{i,j})/n_k)}$$

where $p_{i,j}$ is the presence/absence of species i in sample j , $x_{i,j}$ is the abundance of species i in sample j , and n_c is the number of samples in cluster c . Species that showed a higher MRT

Table 1.1. Sample size, number of splits and species variation explained by the multivariate regression tree models. The appropriate tree size for multivariate regression trees was determined by the 1 standard deviation rule (Maindonald & Braun 2007), based on 1000 cross-validation runs.

Year	Sample Size (<i>n</i>)	Number of Splits	Species Variation Explained
1991	365	7	63.46
1992	293	4	60.51
1993	341	8	61.89
1994	261	4	55.88
1995	231	11	71.61
1997	286	7	56.28
1998	352	13	61.02
1999	377	7	55.93
2000	390	11	63.83
2001	323	6	58.18
2002	314	27	76.42
2003	231	4	50.82

abundance value than expected by chance over 1000 iterations were used to classify the MRT prediction. This index has been used in previous work with MRT analysis and cluster analysis to provide an accurate means to classify and map MRT predictions (e.g. Claudet *et al.* 2006; DeVantier *et al.* 2006; Cappo *et al.* 2007; see Figure 1.2).

To summarize the similarities and differences between the variable selection of the MRT analysis in the early (1991 to 1995) and late (1997 to 2003) periods, I used CART (Breiman *et al.* 1984). CART is the univariate form of MRT analysis. For the CART models, the response variable is the period of the MRT model (i.e. early or late), and the explanatory variables are the variables selected by the MRT models to describe the responses of community composition. Using CART in this manner removes potential subjectivity of the interpretation of differences and similarities of variables selected by the MRT model predictions between the early and later period models.

1.4 Results

Bottom temperatures were significantly cooler in the Gulf of St. Lawrence between 1991 and 1995 compared to between 1997 and 2003 (Wilcoxon-Mann-Whitney $W = 1121171$ and $p < 0.001$; Figure 1.3). The bottom environment was also significantly less saline in the 1991 to 1995 period compared to the 1997 to 2003 period ($W = 1160747$ and $p < 0.001$; Figure 1.3). Hence, grouping the periods into 1991 to 1995 (colder, less saline) and 1997 to 2003 (warmer, more saline) was justified. Given the strong collinear properties of environmental variables in the marine environment, it was expected that the depth, salinity and temperature of the benthic environment would be redundant variables within the MRT analysis (Nybakken & Bertness 2003), but only depth and salinity had consistently significant Spearman correlation coefficients ($p < 0.001$; Figure 1.4). Neither was removed from the analysis, however, because both have the potential to independently describe important influences on the community dynamics in the Gulf.

Broad-scale variable selection by MRT analysis (i.e. variables assigned to the first two splits) during both the early 1990s (1991 to 1995) and the later period (1997 to 2003) were very different. During the early 1990s broad-scale species variation was explained mostly by salinity in the benthic environment and the previous year's catch weight of crab and shrimp (Figure 1.5). In contrast, during the later period, the previous year's catch weight of cod and salinity (with

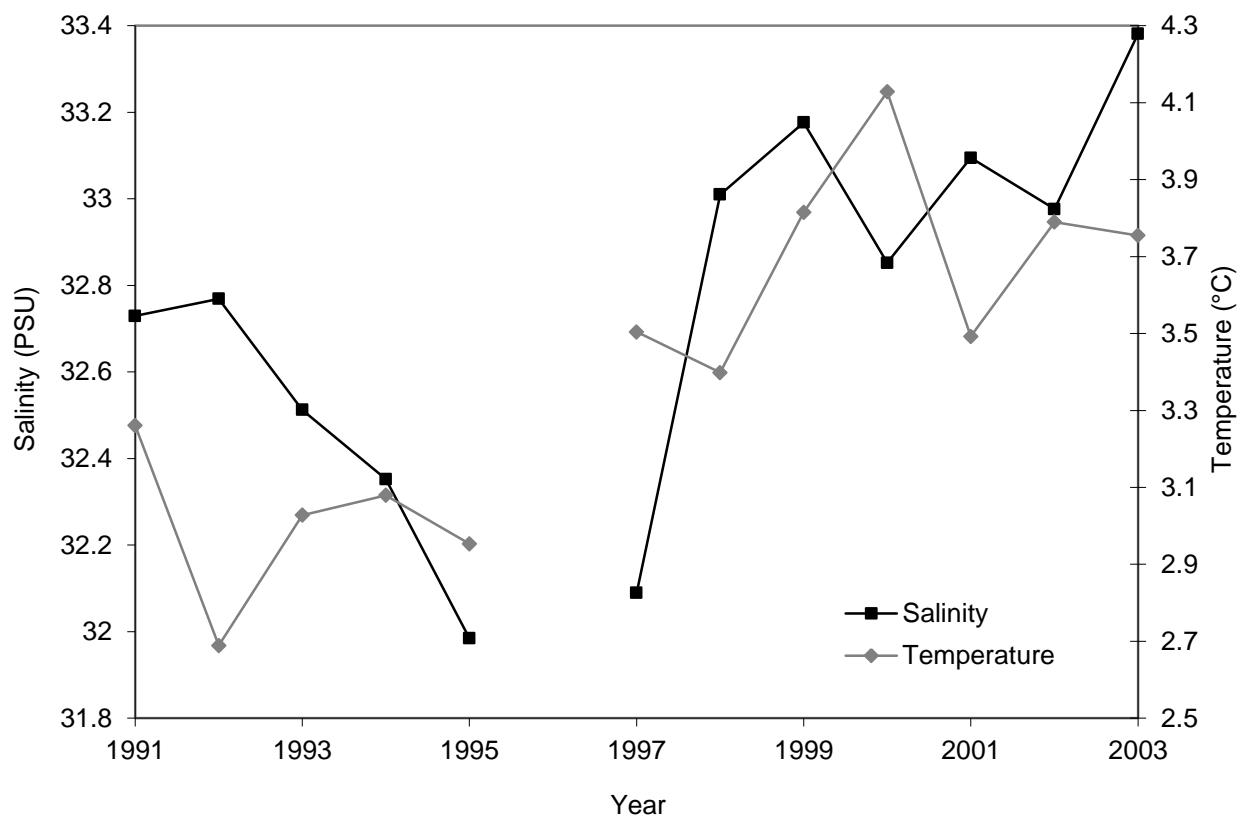


Figure 1.3. September/August average benthic temperature and salinity measurements recorded during bottom trawl surveys. The period from 1991 to 1995 displays significantly cooler temperatures and less saline conditions when compared to that from 1997 to 2003 ($W = 1121171$, $p < 0.001$; $W = 1160747$, $p < 0.001$, respectively).

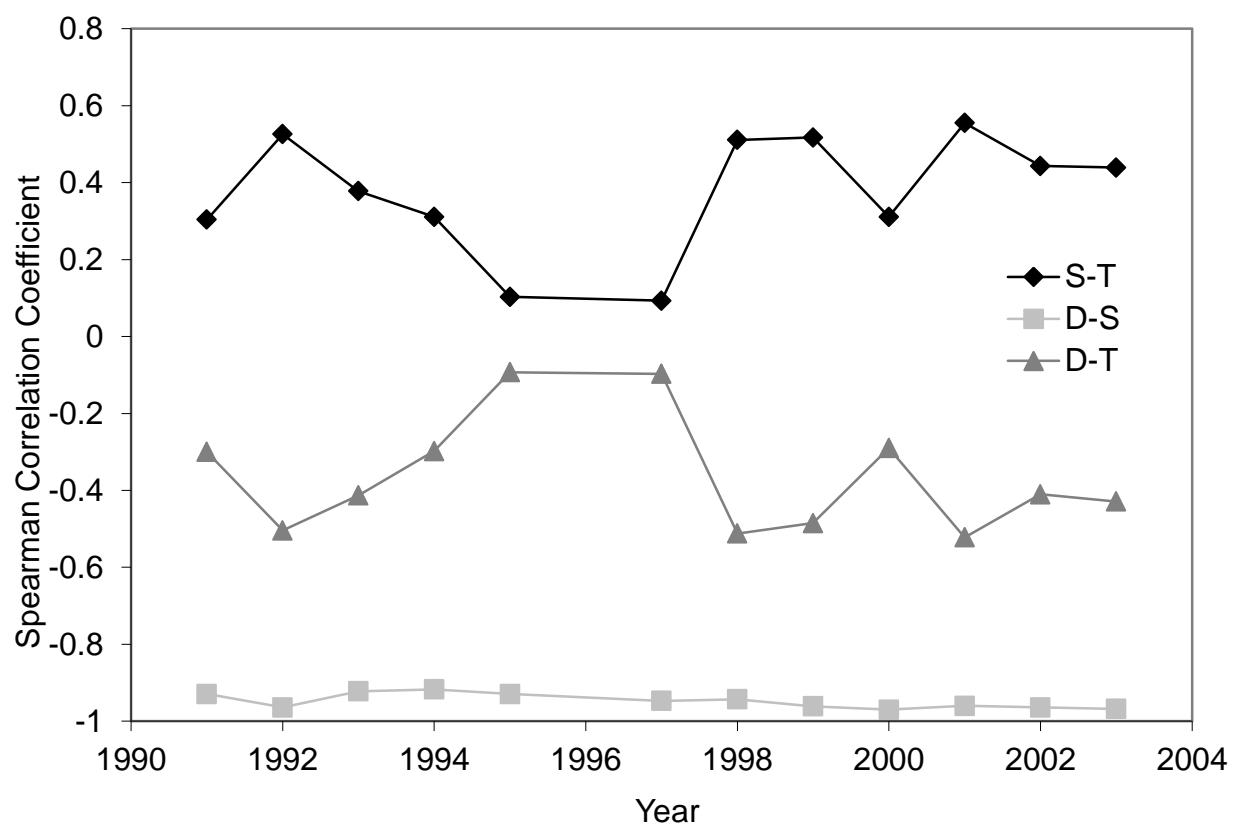


Figure 1.4. Spearman correlation coefficients between depth (D), temperature (T) and salinity (S) of the benthic environment in the Gulf of St. Lawrence. Only the coefficients between salinity and depth (D-S) are consistently significant ($p < 0.05$). Coefficients that have a magnitude greater than 0.8 are considered to be collinear.

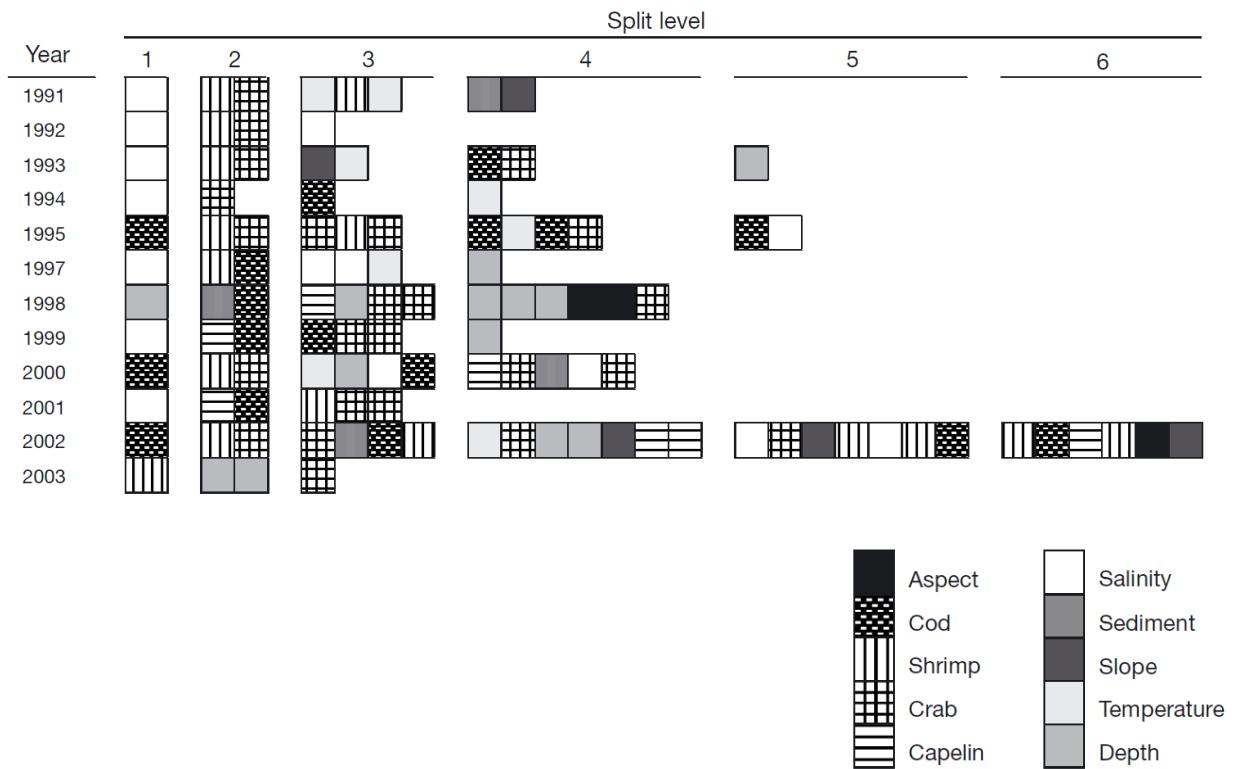


Figure 1.5. Variables selected for multivariate regression tree model splits based on bottom trawl surveys of Atlantic cod (*Gadus morhua*), shrimp (*Pandalus borealis*), crab (*Chionoecetes opilio*) and capelin (*Mallotus villosus*) catch weight per tow (kg). Splits are ranked (e.g. 1, 2) based on order of occurrence in the tree. See the legend for the classification of variables.

depth combined) were both the main determinants of broad-scale species variation for 6 out of 7 years (Figure 1.5). It was also notable that the previous year's catch weight for crab and shrimp, along with the presence/absence of capelin, were used in MRT models during the later period to explain broad-scale patterns of community composition, but none of these variables were used consistently.

MRT variable selection for finer scale species variation (i.e. the third, fourth, or fifth splits) displayed no consistent trends or patterns of variable selection between the early 1990s and the later period. The most prevalent finer scale variables in the models for the early 1990s included temperature and the previous catch weight of cod and crab (Figure 1.5). In the later period, the previous catch weight of crab was the most prevalent variable selected, but it only accounted for fine-scale species variation in 6 out of 7 years (Figure 1.5). Other variables that were prevalent in the later period included the previous catch weight of shrimp, cod, capelin, depth, and bottom salinity.

Classification tree analysis of the MRT variable selection between the periods showed two distinct groupings of the early and later period models by broad-scale variables. If the variable selection is analyzed by split level in the models, the previous catch weight of crab at the second split level and the bottom salinity at the first split level distinguish the models between the two periods with no misclassifications (Figure 1.6A). Crab catch weight in the previous year was the most important distinguishing variable between these periods, but it was a variable that was largely not selected in later period models (it was only selected by 2 out of 7 later period models; Figure 1.6A). In the instances where the previous catch weight of crab was chosen by models in the later period, the absence of bottom salinity at the first split level distinguished these later period models from the models of the early 1990s. If the MRT variable selection is interpreted as broad-scale (combining first and second splits) and fine-scale (combining third and fourth splits), then the classification tree changes (Figure 1.6B). The distinguishing variable between the early and later period models was the previous catch weight of cod at the broad scale. The previous catch weight of cod was consistently selected in the later period models, with the exception of the 2003 model, which was misclassified by the classification tree. The difference in the 2003 model was likely attributable to an upward bias in cod and shrimp abundance estimated by the DFO surveys in the Gulf compared to other abundance indices (DFO 2010a, b). Despite the single misclassification in the second model, the

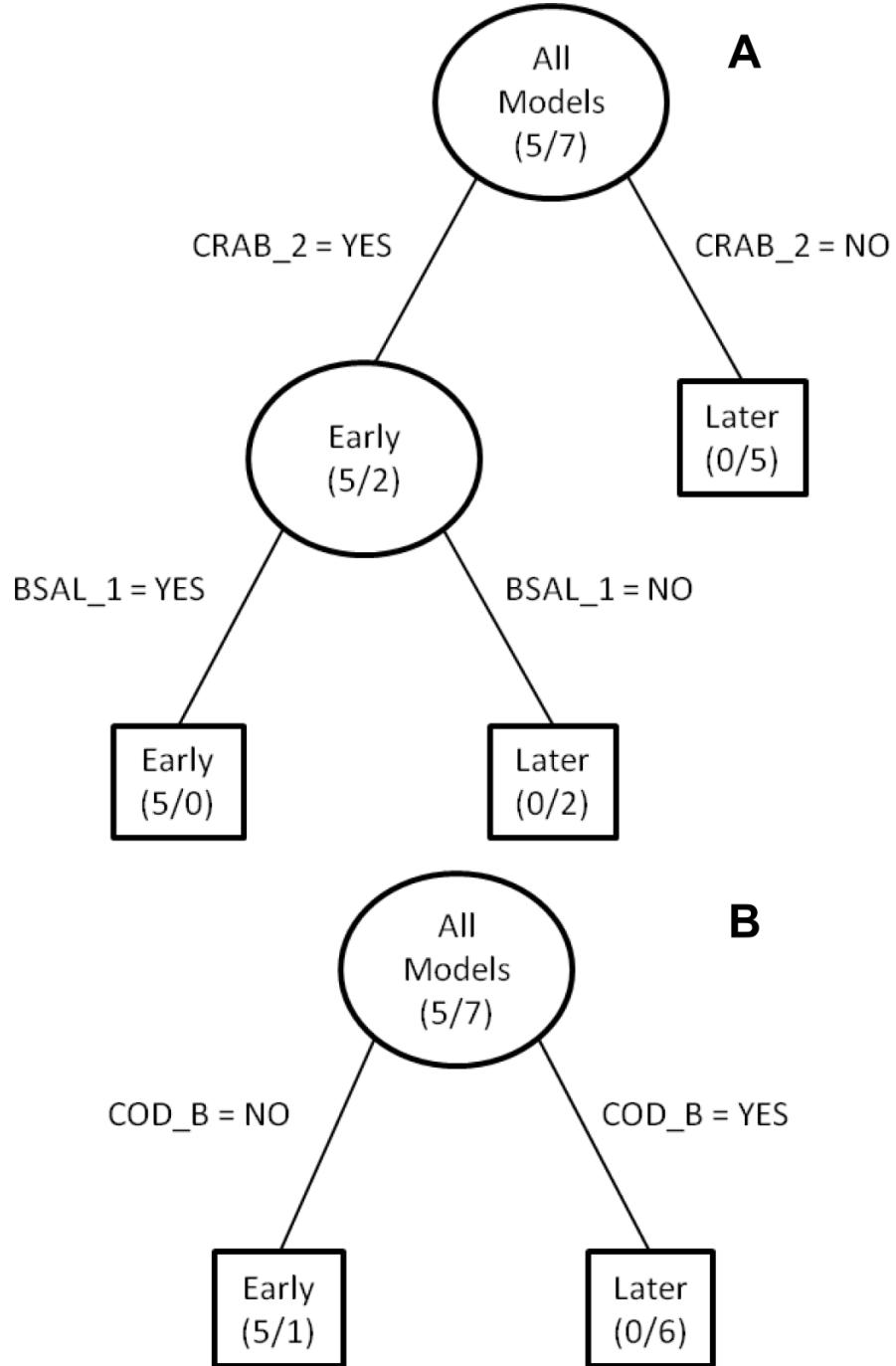


Figure 1.6. Classification tree analysis of multivariate regression tree variable selection by (A) split level and (B) broad- and fine-scale splits. '_B' denotes a broad-scale variable and '_1' and '_2' designate variables at the first and second split level, respectively. Predictions are the classification of models as either 1991 to 1995 (early) or 1997 to 2003 (late) based on variable selection. Numbers in parentheses indicate the ratio of early to late period models associated with a given node or split (e.g. early/late).

classification tree analysis suggested that there was a strong difference in the model variable selection between the periods that was largely attributable to the previous catch weight of crab and cod at the broad scale.

The cross-validation analysis showed a consistent result for MRT models, which indicated that variability in the sample size and in catch weights were not a major problem within this analysis (Table 1.2). Comparisons of MRT models with unconstrained cluster analysis revealed that the within-group variation for groups formed by MRT analysis were very similar to those formed by unconstrained clustering (Table 1.3), meaning that the environmental variables used to form trees in MRT analysis adequately accounted for the potential species variance that can be explained, and no other important unobserved variable was likely. Finally, the MRT models explained an average species variation across all years of 61%. None of the models displayed a poor ability to explain species variation in the data, with the variation explained ranging from 51 to 76% (Table 1.1).

Thus, applying the indicator species index to the MRT multivariate predictions revealed spatially explicit patterns of community composition throughout the study period (Figure 1.7). The indicator species index revealed that cod, crab and shrimp, which were sampled adequately in the BTS, each characterized spatially distinct multivariate response groupings for the majority of years analyzed. The patterns that emerged from these predictions were that regions characterized by shrimp occur within the deeper, more saline regions of the Gulf. Areas that were characterized by crabs were predominantly found throughout inshore regions of the southern Gulf. Cod were found to characterize the inshore regions throughout the Gulf, but these areas were fairly ubiquitous rather than continuous. Finally, the areas that were not characterized in abundance by a particular species or a combination of species in the analysis were the most spatially prominent (in area) as a prediction by the MRT models.

1.5 Discussion

A central objective of this chapter was to ascertain how community spatio-temporal dynamics may be influenced by abundances of a given species and changes in environmental conditions. Using MRT analysis, I am able to identify and link community dynamics in the Gulf of St. Lawrence to trends in salinity and temperature. A major advantage of this approach is that it provides a predictive framework of community composition and allows for multiple

Table 1.2. The number of times out of 1000 runs that a given tree size demonstrated a consistent minimum prediction error by the one-standard deviation rule. The grey boxes correspond to the tree size selected in the finalized models.

Number of Leaves	Year											
	1991	1992	1993	1994	1995	1997	1998	1999	2000	2001	2002	2003
4	-	259	-	198	-	-	-	-	-	-	2	-
5	-	546	23	535	-	2	4	-	-	-	22	505
6	8	-	8	230	1	-	2	147	5	-	13	28
7	163	40	88	-	-	2	40	159	20	710	25	59
8	372	65	183	30	5	181	82	198	6	2	25	9
9	36	26	485	6	51	130	-	191	6	-	18	7
10	28	23	50	1	87	80	58	124	12	4	8	6
11	47	22	18	-	119	94	59	103	84	6	14	14
12	66	8	21	-	155	80	74	28	412	13	-	10
13	-	2	21	-	120	-	134	8	192	68	30	22
14	-	2	14	-	102	66	163	9	80	-	28	29
15	67	3	17	-	67	73	100	2	37	-	20	16
16	-	-	20	-	106	124	48	3	-	87	25	5
17	66	-	17	-	49	49	38	3	41	12	36	16
18	34	-	-	-	35	21	28	7	26	-	46	22
19	33	-	7	-	28	30	25	6	15	7	44	36
20	15	-	-	-	14	24	15	11	-	9	-	23
21	9	1	-	-	12	-	32	1	4	22	41	29
22	-	-	2	-	10	11	30	-	-	11	53	-
23	14	-	3	-	14	7	25	-	-	9	-	15
24	8	-	1	-	1	10	11	-	4	15	61	17
25	-	-	-	-	7	2	12	-	4	8	60	30
26	5	-	-	-	2	4	7	-	-	5	58	33
27	-	-	-	-	1	-	2	-	7	-	54	25
28	6	-	-	-	-	2	5	-	3	4	86	10
29	9	2	3	-	7	3	4	-	1	6	86	6

Table 1.3. The constrained Multivariate Regression Tree error (MRT Cluster) and unconstrained clustering error (Cluster) for the most parsimonious tree size of all years analyzed. A similar resubstitution error or the product of the relative tree error and root node error between constrained and unconstrained clustering indicates coherence between the analyses.

Year	1991	1992	1993	1994	1995	1997	1998	1999	2000	2001	2002	2003	2004
Sample Size (<i>n</i>)	385	303	355	262	231	279	349	373	383	296	303	231	264
MRT	0.40	0.44	0.39	0.47	0.33	0.49	0.39	0.51	0.37	0.31	0.32	0.43	0.51
MRT Cluster	0.18	0.27	0.14	0.26	0.13	0.22	0.09	0.21	0.11	0.08	0.09	0.15	0.24
Cluster	0.17	0.33	0.13	0.28	0.14	0.22	0.09	0.22	0.12	0.08	0.09	0.17	0.24

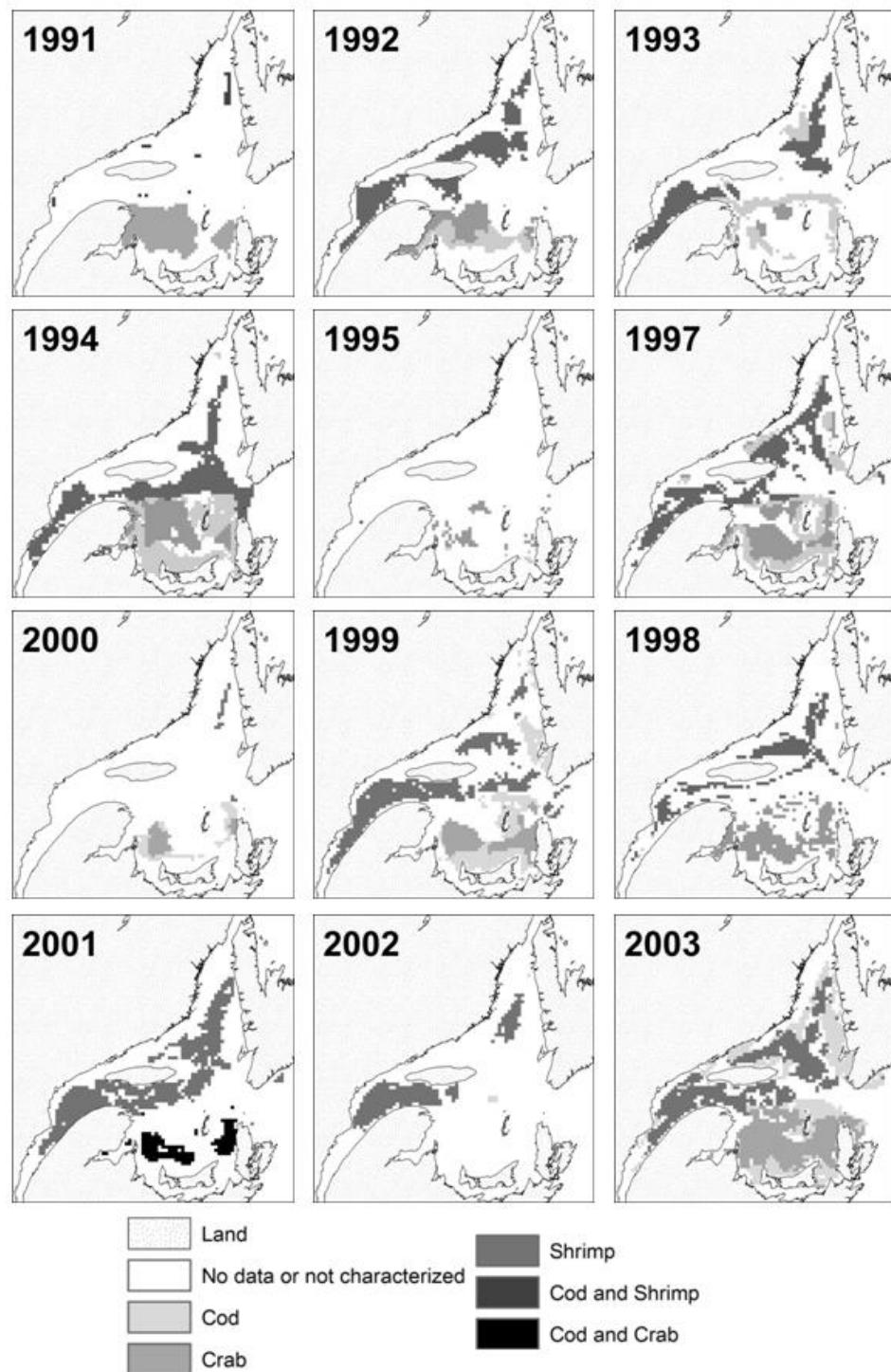


Figure 1.7. Maps of multivariate regression tree predictions spanning from 1991 to 1995 and from 1997 to 2003, based on species indicator index classification. These maps show areas with communities that are characterized by a given species (i.e. a species that has a significantly high abundance and frequency) at a 100 km² resolution.

interactions in dependent and independent variables that contribute to observed patterns (De'Ath 2002). Linking this technique with classification tree analysis is beneficial, because it aids in summarizing the differences in community dynamics between two different environmental regimes. Another important aspect was coupling of MRT analysis with the species indicator index (Dufrêne & Legendre 1997) to visualize spatio-temporal patterns of species with significantly high frequency and abundance, as predicted by the models. By taking these steps I am able to delineate which environmental factors characterize spatially explicit patterns of community composition without limiting the potential spatial or temporal scope.

1.5.1 Community Dynamics

The findings in this chapter demonstrate that well known long-term changes in environmental conditions (Benoît & Swain 2008; Ruppert *et al.* 2009) and the previous abundance of crab and cod contribute to spatio-temporal patterns of community composition at regional scales in the Gulf of St. Lawrence. In the cooler, less saline period (1991 to 1995), broad-scale community composition patterns were largely associated with benthic salinity and the previous year's catch weights of shrimp and crab. Whereas in the warmer, more saline period (1997 to 2003) community composition patterns were similarly associated with benthic salinity, however, in contrast are associated with the previous year's catch weight of cod. I interpret this to indicate that there is a strong and consistent pattern of community composition influenced by benthic salinity and depth gradients in the Gulf. This association likely reflects both the migration patterns of cod throughout the region and the more sedentary movement and habitat preference of snow crab and northern shrimp (Tremblay 1997; Castonguay *et al.* 1999; Koeller 2000). The MRT models show areas characterized by cod are typically found in the shallower inshore regions (summer distributions), which is consistent with earlier findings that cod in this region migrate annually between shallow summer feeding areas (largely feeding on capelin) and deeper over wintering grounds (Rose & Leggett 1988; Campana *et al.* 1999; Castonguay *et al.* 1999). Further, the MRT model predictions also consistently associate shrimp and crab with relatively deeper regions having cooler temperatures and more saline conditions, consistent with findings that shrimp prefer areas with bottom temperatures ranging from 1 to 6°C and that snow crab prefer even colder temperatures ranging from 1 to 2°C (Shumway *et al.* 1985; Tremblay 1997; Koeller 2000).

Environmental factors, however, did not underpin all MRT predictions. Perhaps the most novel finding of this chapter was that the previous year's crab abundance was the main biotic factor explaining patterns of community composition during the cold and less saline period of the early 1990s, whereas the previous year's cod abundance explained patterns of community dynamics in the warmer, more saline period that followed. These findings suggest that the influence of individual species on their community may not be constant, but will be mediated by the dynamics of environmental conditions, and, specifically in this case, that in cold periods the community structure will be most influenced by crab abundance, while in warmer periods it will be most influenced by cod. This is consistent with previous findings that cod behaviour may be influenced by the environment, in that fish tend to show less summer site fidelity in colder periods compared to warmer ones (Ruppert *et al.* 2009). Another factor potentially influencing range changes is abundance, with the expectation of range expansion in some species with increasing abundance (for cod, see Robichaud & Rose 2004). Over the period of this study, there were changes in the abundance of various species throughout the Gulf region. However, the changes appear to be shifts rather than expansions, which indicate that the spatial dynamics shown here reflect behavioural rather than abundance changes (unless asymmetrical range changes exist for various species that, in turn, influence community structure, which is possible but beyond the scope of the present analyses). Other studies have shown that cod and other species will modify their ranges under changing environmental conditions, independent of abundance (e.g. deYoung & Rose 1993; Nye *et al.* 2009). Another factor which could influence community dynamics is age structure of long-lived species (here only cod). This factor is unlikely to have been important to the analysis in this chapter as the age structures of Gulf cod populations did not change substantially between the two periods (DFO 2009, 2010a). What this and other studies demonstrate is that cod and snow crab can strongly influence at least some aspects of community dynamics when environmental conditions are favourable to them, but during unfavourable times their influence likely recedes.

1.5.2 Limitations

Given my approach and the data used within the analysis, I recognize that the findings are limited in several ways. The Gulf of St. Lawrence is a complex ecosystem with hundreds of species (Frank *et al.* 2006; Benoît & Swain 2008), and this chapter addresses questions of community composition with reference to only four (with capelin poorly sampled and only used

as a predictor of presence/absence). These four species, however, do represent some of the most ecologically important components of food web interactions and are also vital to the economic viability of the Gulf region (Worm & Myers 2003; DFO 2005). As no better data were available for this chapter, I believe that the interactions among these species can act as an index for wider community change within the gulf ecosystem. Another limitation of the data is that crab catch weight can be problematic as an index of abundance with the DFO bottom trawl surveys, because the gear used is biased towards catching larger individuals (generally large males). Thus, it should be noted that the crab abundance provides a sex-specific index of relative and not absolute abundance. In any event, the MRT methodology demonstrated here can accommodate additional and better data as they become available. Other important factors not considered in this chapter include changes in habitat quality (e.g. Nilsson & Rosenberg 2003), potential food resources (e.g. Savenkoff *et al.* 2006), and fisheries activities (e.g. Scheffer *et al.* 2005). I believe that the present work should be viewed as a demonstration of how community structures resulting from the dynamics of these factors can be linked among themselves and to environmental variation, and as a first step towards a more comprehensive community-based model.

1.5.3 Management applications and conclusions

Notwithstanding the limitations of the present analyses, the approach itself and its findings could be applied to fisheries management and conservation. Predictive outputs from the MRT analysis could allow fisheries managers to distribute fishing effort (or at least to know where effort is being exerted with respect to community distributions) for both economic and ecological viability of the stocks (Beare *et al.* 2005). With the understanding that community dynamics differ between cold and warm periods, the yearly MRT predictions could be combined to produce a ‘mode’ community prediction for each period (Figure 1.8). What emerges from this is an overall, spatially explicit assessment of community composition. In the present case, regions within the Gulf of St. Lawrence that are characterized by all 3 focal species (other species could be included if data were available) exhibited slightly different spatial arrangements when comparing the cooler, early 1990s with the warmer, late 1990s/early 2000s.

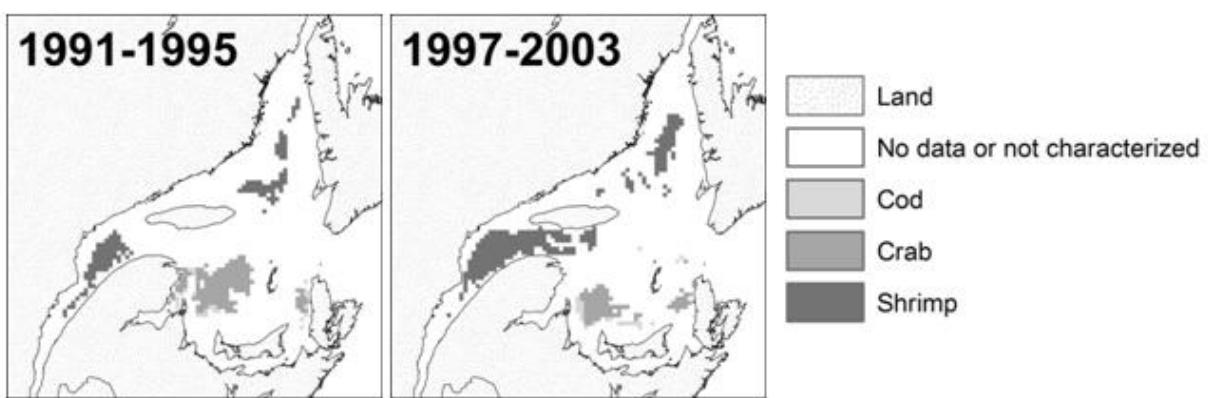


Figure 1.8. Combined multivariate regression tree predictions for the 1991 to 1995 and 1997 to 2003 periods. These maps show areas that are consistently characterized by a given species during each period (i.e. a species that has a significantly high abundance and frequency) at a 100 km² resolution.

As a final note, future predictions for the Gulf of St. Lawrence and the North Atlantic are that it will be subject to warmer conditions within the next century (IPCC 2007; Burrows *et al.* 2011). The present chapter has shown that there is a strong link between temperature and community dynamics in the Gulf; hence, temperature changes will expose species to novel conditions, and this could lead to local extirpations, alterations of migration patterns and/or dispersal from traditional sites, which, in turn, could disrupt spatio-temporal community composition patterns. In particular, this chapter emphasizes the importance of the link between environmental conditions (temperature and salinity) and the influences of specific species (here crab and cod) on community dynamics across broad spatial and temporal scales. Attempts to implement an ecosystem approach to management in fisheries ecosystems should consider the interactions of these environmental and single species effects on marine communities. MRT provides a relatively straightforward method to do that.

Chapter 2

Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs

2.1 Abstract

Due to human activities, marine and terrestrial ecosystems face a future where disturbances are predicted to occur at a frequency and severity unprecedented in the recent past. Of particular concern is the ability of systems to recover where multiple stressors act simultaneously. I examine this issue in the context of a coral reef ecosystem where increases in stressors, such as fisheries, benthic degradation, cyclones and coral bleaching are occurring at global scales. By utilizing long-term (decadal) monitoring programs, I examine the combined effects of press (removal of sharks) and pulse (cyclones, bleaching) disturbances on the trophic structure of coral reef fishes. I provide evidence that the loss of sharks as apex predators has an impact that propagates down the food chain, creating mesopredator release and altering the numbers of primary consumers. Simultaneously, I show how the effects of bottom-up processes of bleaching and cyclones propagate up the food chain through herbivores, planktivores and corallivores, but do not affect carnivores. Because the presence of sharks may promote the abundance of herbivores, their removal has implications for both natural and anthropogenic disturbances involving the loss of corals, as herbivores are critical to the progress and outcome of coral recovery.

2.2 Introduction

Marine and terrestrial ecosystems are assailed by disturbances that operate as regulators of system structure and function (Bellwood *et al.* 2004; Mouillot & Field 2005; Wilson *et al.* 2008; Pandolfi *et al.* 2011). For the most part, these are natural perturbations (for example storms or forest fires) that engender predictable cycles of destruction and recovery in ecosystem state (Connell 1997; Mouillot & Field 2005; Mumby *et al.* 2011). However, anthropogenic effects are

now so pervasive and far-reaching that it is predicted that the frequency and severity of these disturbances will increase, possibly challenging the ability of ecosystems to recover (IPCC 2007; Burrows *et al.* 2011). At the same time, we are subjecting many ecosystems to new types of anthropogenic disturbances. The combined effects of these events on ecosystem function and the ability of systems to recover where multiple and novel stressors act simultaneously remains unclear (Hughes & Connell 1999; Darling & Côté 2008).

Coral reef ecosystems offer an ideal model to explore this issue. Reefs are dynamic environments, where pulse disturbances such as coral bleaching, cyclones, crown-of-thorns (*Acanthaster planci*) outbreaks and coral disease are commonplace (Moran *et al.* 1988; Letourneur *et al.* 1993; Harvell *et al.* 2002; Graham *et al.* 2011; Pandolfi *et al.* 2011). Typically, these alter communities in a “bottom-up” manner by causing the death of live corals, which are then overgrown by algae in most places. In turn, this changes communities of reef fishes through effects on settlement, habitat type and rugosity (Jones *et al.* 2004). Where these disturbances are infrequent, corals recover through recruitment and regrowth, a process that can take around a decade to complete (Ninio *et al.* 2000; Graham *et al.* 2011).

Today, many reefs are afflicted with novel types of disturbances that are anthropogenic in origin and press in nature. One of the most pervasive of these is the removal of top-order predators such as sharks, a process that has been accelerating throughout the tropics in recent decades (Jackson *et al.* 2001; Baum & Myers 2004; Ferretti *et al.* 2010; Ward-Paige *et al.* 2010b). Because sharks have conservative life-history traits (slow growth rates, late sexual maturity, low reproductive output and long gestation), most cannot tolerate even moderate levels of fishing pressure and recovery of populations from over-exploitation is likely to require many years (Robbins *et al.* 2006; Dulvy *et al.* 2008). The impact of the loss of sharks on coral reefs is not clear (Heithaus *et al.* 2010). Ecosystem models give some insight, but provide contrasting evidence of whether reef sharks play a role in structuring fish communities that is important (Okey *et al.* 2004; Bascompte *et al.* 2005) or relatively minor (Stevens *et al.* 2000). Empirical work that has investigated the role of sharks in reef ecosystems has taken a “snapshot” approach when assessing the impact on the fish community, where trophic structure has been compared on reefs with and without sharks at a single instant in time (Friedlander & DeMartini 2002; Sandin *et al.* 2008; Williams *et al.* 2011). This ignores the fact that reef communities respond to a range

of disturbances that are both natural and anthropogenic in origin and operate at a variety of spatial and temporal scales. Such events usually occur at scales greater than entire reefs (10s-100s km) and re-structure reef communities in a “bottom-up” manner, in contrast to the “top-down” influence of reef predators (Ninio & Meekan 2002). Because in many cases reefs require over a decade to recover from disturbance events (Graham *et al.* 2011), any influence of top-down processes in structuring fish communities acts against a background of recovery from these bottom-up agents of change. Thus, if we are to understand the individual and combined effects of both natural and anthropogenic disturbances on reef ecosystems, we require studies with sufficient temporal and spatial scope to disentangle the effects of the loss of sharks as predators and natural disturbances on fish communities.

A second problem in examining the importance of sharks in reef ecosystems concerns the need for accurate and precise estimates of shark abundance. On non-fished reefs, sharks can make up the bulk of the biomass of top-order predators (DeMartini *et al.* 2008), even in shallow water (<20 m depth). However, traditional survey techniques, such as underwater visual censuses used to count sharks (Friedlander & DeMartini 2002; Robbins *et al.* 2006; Sandin *et al.* 2008) are restricted to depths accessible to divers (from the surface to around 30 m depth), which is only a fraction of the range occupied by reef-associated and oceanic sharks (Last & Stevens 2009). There are also well-documented biases in belt transect counts of large-bodied and faster-swimming fish by divers (Ward-Paige *et al.* 2010a; McCauley *et al.* 2012). Furthermore, the behaviour of both the diver and the shark are likely to have an effect on numbers recorded by underwater visual counts (McCauley *et al.* 2012). In some situations territorial reef sharks may be attracted by the presence of divers on the reef, particularly in locations where the entry of divers into reef waters is a relatively novel event (McCauley *et al.* 2012). Given that localities where large numbers of sharks remain are often characterized by their isolation and lack of accessibility to humans, this may be a problem for abundance estimates. Conversely, other places visited by many divers may be avoided by sharks (Ward-Paige *et al.* 2010a; McCauley *et al.* 2012). In either situation, the assumption that reef sharks are indifferent to the presence of divers may bias outcomes of visual censuses.

Here, I disentangle the relative and combined effects of the loss of sharks as top-order predators (a press disturbance) and the bottom-up, pulse disturbances of cyclones and bleaching

as processes structuring reef fish communities on remote atolls in the eastern Indian Ocean. Because the history of anthropogenic and benthic disturbances on these reefs is known, they provide an ideal ecosystem-scale (hundreds of km) natural experiment to investigate this subject. My objectives are to examine (1) how fishing changes shark assemblages in coral reef ecosystems, (2) if changes to shark assemblages impact the trophic structure of fish communities, (3) what role benthic disturbances have in structuring fish communities alongside shark removal, and (4) whether there are combined impacts of fishing and benthic disturbances? My study reefs have been the focus of long-term monitoring (1994 - 2008) of fish and coral communities using underwater visual censuses (UVC) and photo quadrat analysis, respectively. Shark numbers have been quantified on both reef systems using Baited Remote Underwater Video Stations (BRUVS), which collect data to depths of 50 m and are an effective means to sample reef-associated sharks without the use of divers. Indonesian fishermen target shark stocks on some of these reefs for the trade in shark fin (Rees *et al.* 2003; Field *et al.* 2009). In contrast, nearby atolls are protected from or subject to only very limited charter fishing that focuses on large pelagic species such as tuna and billfishes. The large differences in fishing pressure in concert with known pulse disturbance histories at these reefs offer a unique opportunity to quantify the relative and combined effects of top-down (sharks) and bottom-up (cyclones, bleaching) processes in structuring reef fish communities.

2.3 Methods

2.3.1 Study area

A unique combination of circumstances allowed for this chapter to examine the relative and combined effects of shark removal and benthic disturbances on the trophic structure of assemblages of coral reef fishes. Since 1994, changes in the abundance and diversity of benthic habitats and fishes have been monitored on the outer reef slopes of two groups of uninhabited, atoll-like coral reefs that lie off the coast of north-western Australia. The first of these, the Rowley Shoals (includes Mermaid, Clerke and Imperieuse Reefs; Figure 2.1) are marine protected areas (i.e. all forms of fishing are restricted), while the second, Scott Reefs (Seringapatam, North and South Scott Reefs; Figure 2.1) lie within the Australian-

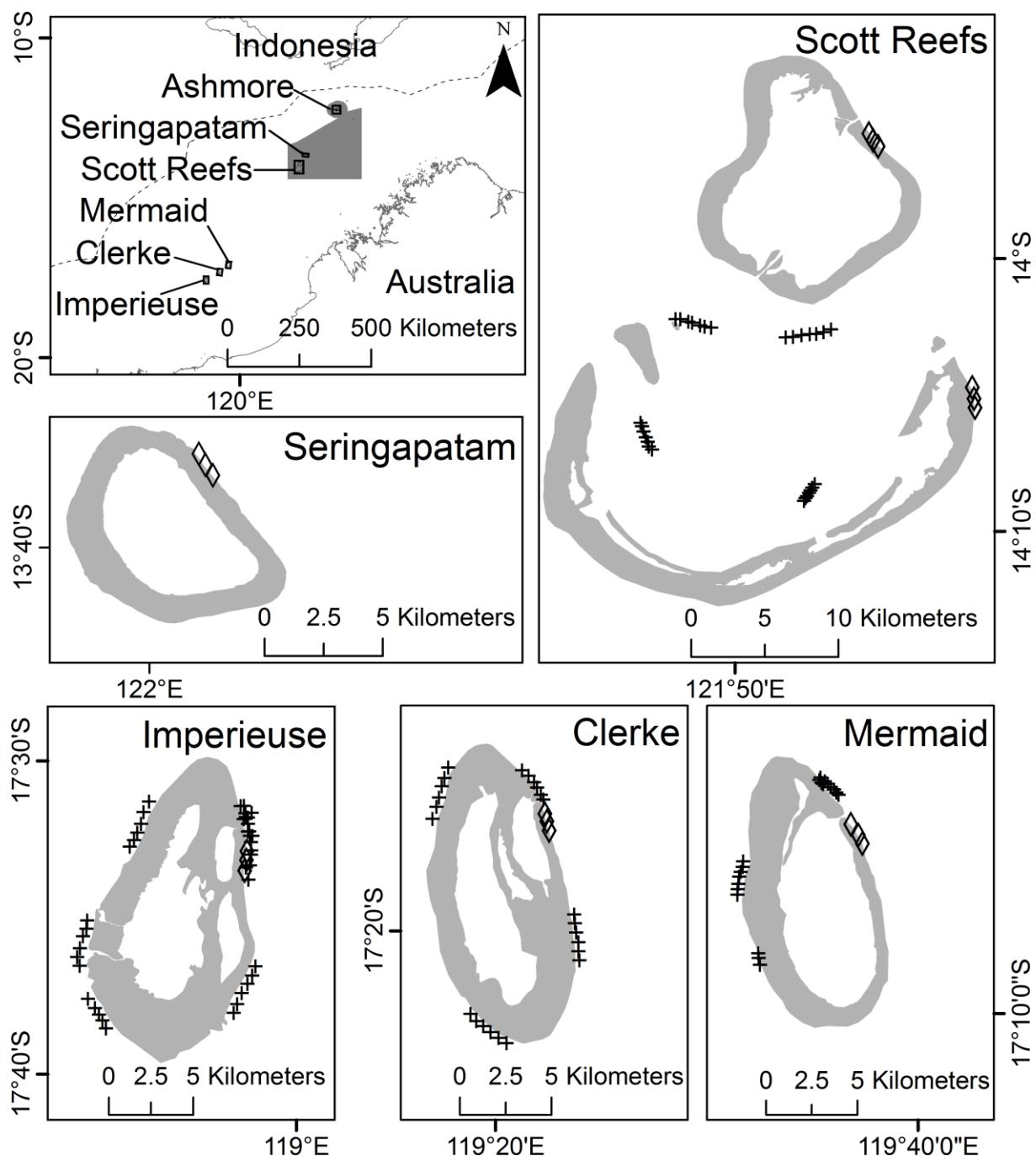


Figure 2.1. The protected Rowley Shoals (Imperieuse, Clerke and Mermaid Reefs) and fished Scott Reefs (Seringapatam, North Scott and South Scott Reefs). Shown are the locations of baited remote underwater video stations (crosses) and long term monitoring program sites (diamonds) on each reef (light grey). The dotted line shows the Australian Economic Exclusive Zone boundary and the dark grey area denotes the MoU Box 74.

Indonesian Memorandum of Understanding Box 74 (MoU74), an area of approximately 50,000 km², where Indonesian fishermen are granted access to the Australian exclusive economic zone to pursue fishing for sharks using traditional techniques (Field *et al.* 2009).

These Indonesian fishermen provide a press disturbance by targeting “banquet” species of high economic value, principally shark (for the shark fin soup trade), trepang (*Holothuroidea spp.*; sea cucumber) and trochus (*Trochidae spp.*; top snails) in a fishery that has historical origins dating to well before European settlement of Australia (Rees *et al.* 2003; Field *et al.* 2009; see Appendix for more details). Australian Customs and border patrol flights (2000-2007) confirm the presence of both legal and illegal Indonesian fishermen in the vicinity of the MoU74 Box, but not as far south as the Rowley Shoals (Field *et al.* 2009). Anthropogenic, biological and physical differences between Scott Reefs and the Rowley Shoals are summarised in Table 2A.1. There were only minor differences in chlorophyll-a and water temperatures (on average around 1°C) between the reefs and there is no evidence that this has led to greater productivity of coral or fish at either reef (See Table 2A.1). These reefs systems are also similar in size. However, there is a greater species richness of fishes at Scott Reef than the Rowley Shoals, which can be accounted for by the position of the Scott Reefs closer to Indonesia and the centre of reef fish diversity in the Coral Triangle than the Rowley Shoals. This difference in diversity is largely restricted to rare species (i.e. present in < 5% of sites) that make only a very minor contribution to patterns of abundance (Table 2A.1).

The Rowley Shoals and Scott Reefs are atoll-like reefs without any significant emergent land that lie over 300 km from the nearest coast. Distances between these groups of reefs and the coast limits any likelihood of larval exchange and genetic evidence suggests that fish communities on the reefs can be largely dependent on self-recruitment (Underwood *et al.* 2012). Additionally, tracking studies of grey reef sharks (*Carcharhinus amblyrhynchos*), at the Rowley Shoals have shown that there is little to no movement among reefs within the Shoals (Field *et al.* 2011). Thus, it is a reasonable assumption that atoll systems are independent of each other in terms of fish and shark stocks.

2.3.2 *Benthic Disturbance*

Both the Scott Reefs and Rowley Shoals experienced catastrophic pulse disturbances in the late 1990s (coral bleaching in 1998 and a Category 5 cyclone in 1996, respectively). Here, I

summarize differences in coral communities (*Isopora*, *Acropora*, massive, encrusting, soft, etc.), algae (crustose coralline turf and macro), abiotic (rubble, sand, etc.) and other cover (invertebrates, etc.) between reef systems. I focus primarily on coral cover as it provides an estimate of the frequency and strength of pulse disturbance events that in most cases do not directly impact fish communities through mortality, but alter benthic cover in coral reefs (Graham *et al.* 2008). At the Scott Reefs, bleaching reduced coral cover from *ca* 60% to <10%, while similar reductions in coral cover occurred at two of three reefs of the Rowley Shoals after a Category 5 cyclone (Figures 2.2A and 2.2B). Corals killed directly or indirectly by these pulse disturbances were overgrown by turfing algae, but coral cover returned to near pre-disturbance levels in the following decade. I used a threshold of <30% coral cover to classify reefs have been pulse disturbed (impacted and/or recovering) or >30% coral cover as non-disturbed (not impacted or recovered). This threshold was chosen because coral cover averaged around 30% for most reefs during the monitoring period (Table 2A.1) and this level of cover has been used to define “healthy” reefs worldwide (Bellwood *et al.* 2004; De’ath *et al.* 2012). Both fished and non-fished reefs had similar cover of hard and soft coral and algae prior to and after pulse disturbances.

2.3.3 *Shark and Fish Count Data*

Shark data were collected using BRUVS (Cappo *et al.* 2007) at Mermaid ($n = 28$) and Scott Reefs (North and South Scott only; $n = 28$) during June 2003 and at Clerke ($n = 24$) and Imperieuse ($n = 42$) Reefs in the Rowley Shoals in October 2004 (Figure 2.1). Generally, drops were located in 3-4 sites on the outer reef slope of each reef. At each site, six BRUVS were deployed on the reef slope during the day for approximately one hour of soak time, with each replicate being separated by at least 500 m (depth 10-60 m; Figure 2.1). All deployments were spread throughout daylight hours from 07:00 – 16:00 hrs. Interrogation of each tape provided the maximum number of each species seen together in any one time on the whole tape (MaxN). Here I report standardized shark abundances as MaxN per hour.

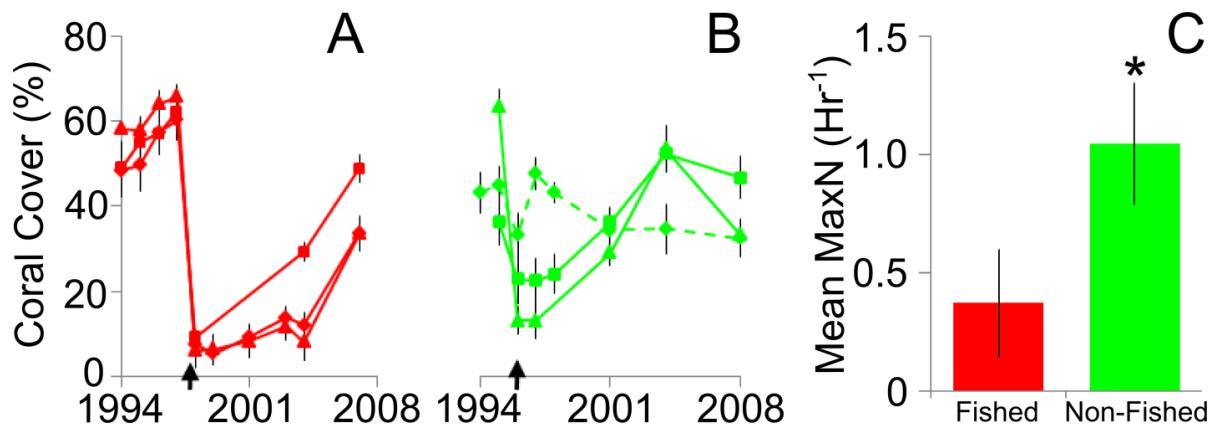


Figure 2.2. Coral cover for fished (red) and non-fished (green) reefs at (A) Scott Reefs and (B) Rowley Shoals, including reefs with (solid line) and without (dashed line) disturbance events. Arrows denote timing of disturbance. (C) Shark density at fished and non-fished reefs measured as the maximum number of each species seen together in any one time (MaxN) per hour of tape. Values are the means \pm 95% confidence intervals. * $p<0.05$ for permuted t -test.

Fish abundance and benthic cover data were collected by the Australian Institute of Marine Science Long Term Monitoring Program (LTMP) principally in October over the course of 1994-2008 (Halford & Thompson 1996; Jonker *et al.* 2008). Non-cryptic, adult (1+ year old) fishes were identified to species. Abundance surveys were conducted at 3 sites on each reef along 5 fixed transects that were each 50 m in length and deployed along the 6-9 m depth contour of the reef slope (Figure 2.1). This habitat type is widespread on each reef and extends around the reef perimeter. Larger and more mobile species (e.g. Lutjanidae, Lethrinidae) were counted within 2.5m either side of the transect tape and site-attached species (Pomacentridae) were counted on a return swim within 0.5 m either side of the belt transect. Species were classified into five trophic groups: carnivores, herbivores, planktivores, corallivores and detritivores (Table 2A.2). To reduce the influence of zeroes in multivariate analysis I removed rare species (defined as present in <5% of sites; Jackson & Harvey 1989). A total of 114 species remained of which the most diverse were carnivores (26 species including representatives of the families Chaetodontidae, Epinephelidae, Labridae, Lutjanidae, Lethrinidae, and Zanclidae) and herbivores (43 species including representatives of the families Acanthuridae, Pomacentridae, Sacridae and Siganidae), while corallivores (20 species, representatives of the Chaetodontidae and Pomacentridae), detritivores (7 species all from the Acanthuridae) and planktivores (18 species including representatives of the Lutjanidae, Pomacentridae and Acanthuridae) tended to be dominated by only one family (Table 2A.2). Benthic data along the same transects were determined from photographic or video frame analysis (Jonker *et al.* 2008).

2.3.4 Analysis

Principal Components Analysis (PCA) and Redundancy Analysis (RDA) were used to investigate differences in benthic and fish assemblages among four treatment groups: fished/disturbed ($n = 30$), non-fished/disturbed ($n = 21$), fished/non-disturbed ($n = 46$) and non-fished/non-disturbed ($n = 29$). In this case, fishing represents a press disturbance at Scott Reefs that has been occurring for centuries, while the Rowley Shoals are protected from any fishing pressure (Figure 2.1). A disturbance treatment refers to fish and benthic communities where coral was reduced below 30% cover after a cyclone that occurred on non-fished reefs in 1996 and bleaching that occurred on fished reefs in 1998 (Figures 2.2A and 2.2B). Species composition was described by the abundance of the five trophic groups (carnivores, herbivores, detritivores, corallivores and planktivores) in the RDA. This procedure involved using the *cca*

and *anova* libraries in the *vegan* package of R Statistical Language (Oksanen & Roberts 2010; see Appendix for more details).

Comparisons of shark abundance between fished (Scott Reefs) and non-fished (Rowley Shoals) reefs were conducted using R software with a one-tailed permuted *t*-test (Legendre 2005; $n = 9999$) that accommodated non-parametric data with unequal sample sizes. Shark abundances were surveyed only during the years 2003 and 2004. Patterns in shark density were similar across both sample periods despite the gap in sampling (results not shown). However, due to their conservative life history traits (longevity, late age of maturation, low fertility) a snapshot for this group may be more appropriate than for reef fishes that have much faster turn-over times of populations. Furthermore, very low abundances of reef sharks at the Scott Reefs were noted in surveys in 1998 near the start of this study (Skewes *et al.* 1999) and again in 2010-11 (Heyward *et al.* 2011a). Thus, I suggest that the abundance estimates of sharks shown here are representative of the period of 1994-2008. The Scott Reefs had fewer BRUVS samples, so I compared shark abundance at Scott with data available from BRUVS surveys of Ashmore Reef ($n=46$), another fished reef within the MoU74 box using a two-tailed permuted *t*-test ($t_{72} = 0.76$, $p = 1.0$). As there was no significant difference in shark abundance between these reefs, I used data from Scott Reefs for subsequent analyses.

Permuted ANOVAs were conducted using *adonis* function in the *vegan* package of R software (Oksanen & Roberts 2010). To test for the fixed-effects of fishing, disturbance and their interaction I used permuted ANOVAs ($n = 9999$). Further, pairwise comparisons using two-tailed permuted *t*-tests ($n = 9999$) were conducted to test for fishing and disturbance effects between the four treatment groups. As Euclidean distances were used in permuted ANOVAs, abundances were Hellinger transformed prior to testing (Legendre & Gallagher 2001). Bonferroni corrections were used to adjust significance levels for multiple tests (Legendre 2007).

2.4 Results

BRUVS sampling showed that the abundances of reef sharks (notably silvertip, *Carcharhinus albimarginatus* and grey reef, *C. amblyrhynchos*) at the protected Rowley Shoals were approximately three times those occurring on the fished Scott Reefs ($t_{96} = 3.86$, $p = 0.0175$; Figure 2.2C). Further, the PCA suggested that there were differences in the severity of

disturbances such that fished reefs had more algae and less coral following bleaching than non-fished reefs after the cyclone event (Figure 2A.1). This difference was not apparent in the other benthic groups (abiotic, other corals, and other benthos), which contributed far less to patterns in benthic composition (see Appendix for more details).

For both fished and non-fished reefs, the assemblage trophic structure of fishes after the recovery of coral cover was similar to that occurring prior to pulse disturbances (Gilmour *et al.* 2011). There were however, profound differences in assemblages and trophic structure between fished and non-fished reefs notably, in the abundance of carnivores and herbivores (Figure 2.3). Assemblages on the fished Scott Reefs had significantly greater numbers of mid-sized carnivores than the protected Rowley Shoals (Figure 2.4 and Table 2A.3). These differences were largely attributed to changes in numbers of Lutjanidae along with Lethrinidae, Serranidae and some Chaetodontidae. Multiple species from these families contributed to this pattern (Figure 2A.2). Densities of primary consumers also differed between reefs, so that herbivorous fishes were significantly more abundant at the protected Rowley Shoals than at the Scott Reefs following the pulse disturbance event (Figure 2.4 and Table 2A.3). Again, these differences were attributable to representatives of most of the major families of herbivores, including Scaridae, Acanthuridae, and Pomacentridae (Figure 2A.3).

I found no obvious differences in the densities of corallivorous and planktivorous fishes between fished and non-fished reefs (Figure 2.4 and Table 2A.3). For these families, variation in abundance was correlated with the timing of pulse disturbances (bleaching, cyclones) rather than the presence or absence of fishing.

The effects of bottom-up, pulse disturbances did not appear to propagate further up the food chain, as abundances of carnivores remained constant throughout the changes in coral cover (Figure 2.4). A possible synergistic effect of shark removal and coral loss was evident for detritivores, which increased during disturbance to a far greater degree on fished compared to unfished reefs (Figure 2.4).

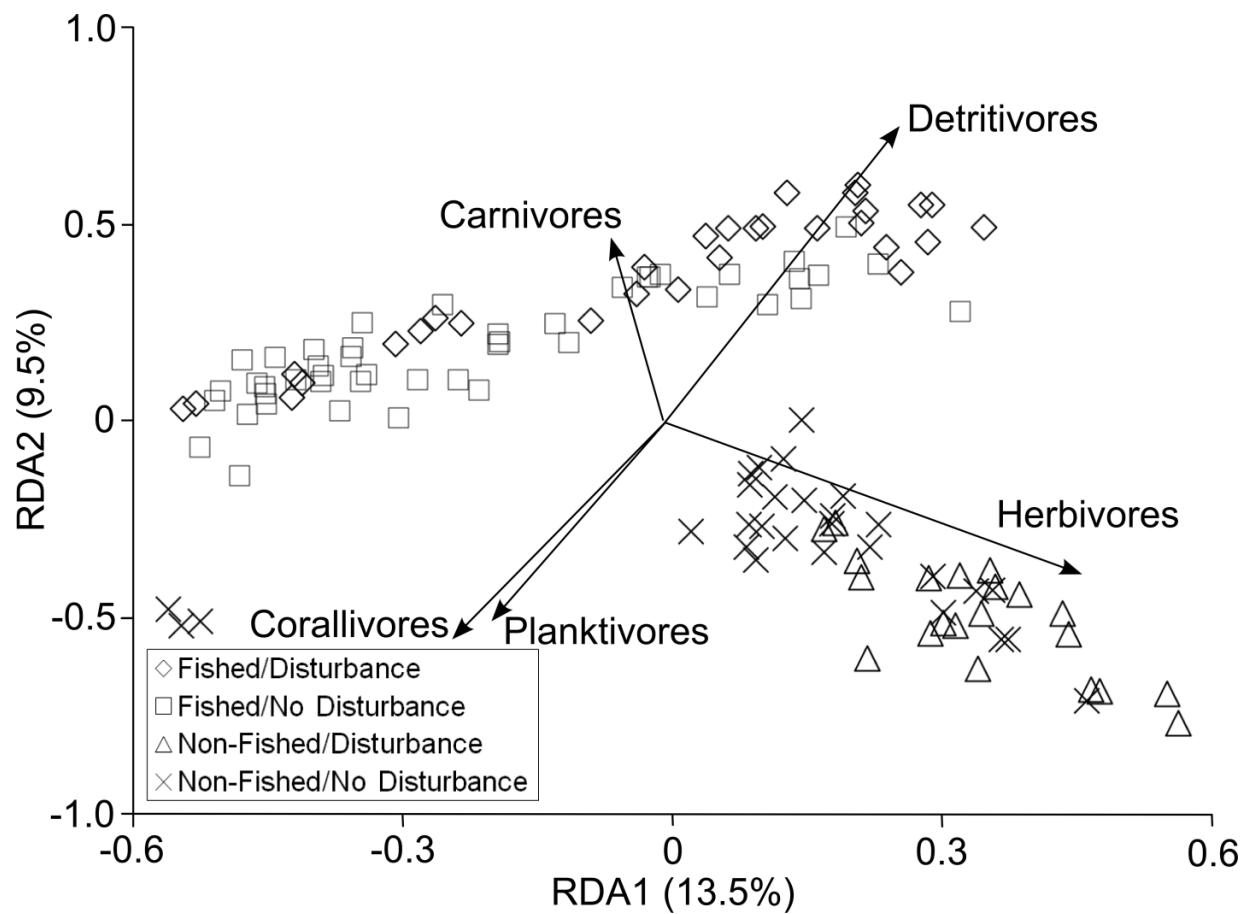


Figure 2.3. Redundancy analysis of species composition ($n=114$) for the five trophic groups (carnivore, herbivore, detritivore, corallivore and planktivore). Sites have been classified by the four treatments and the variation explained by each axis has been denoted.

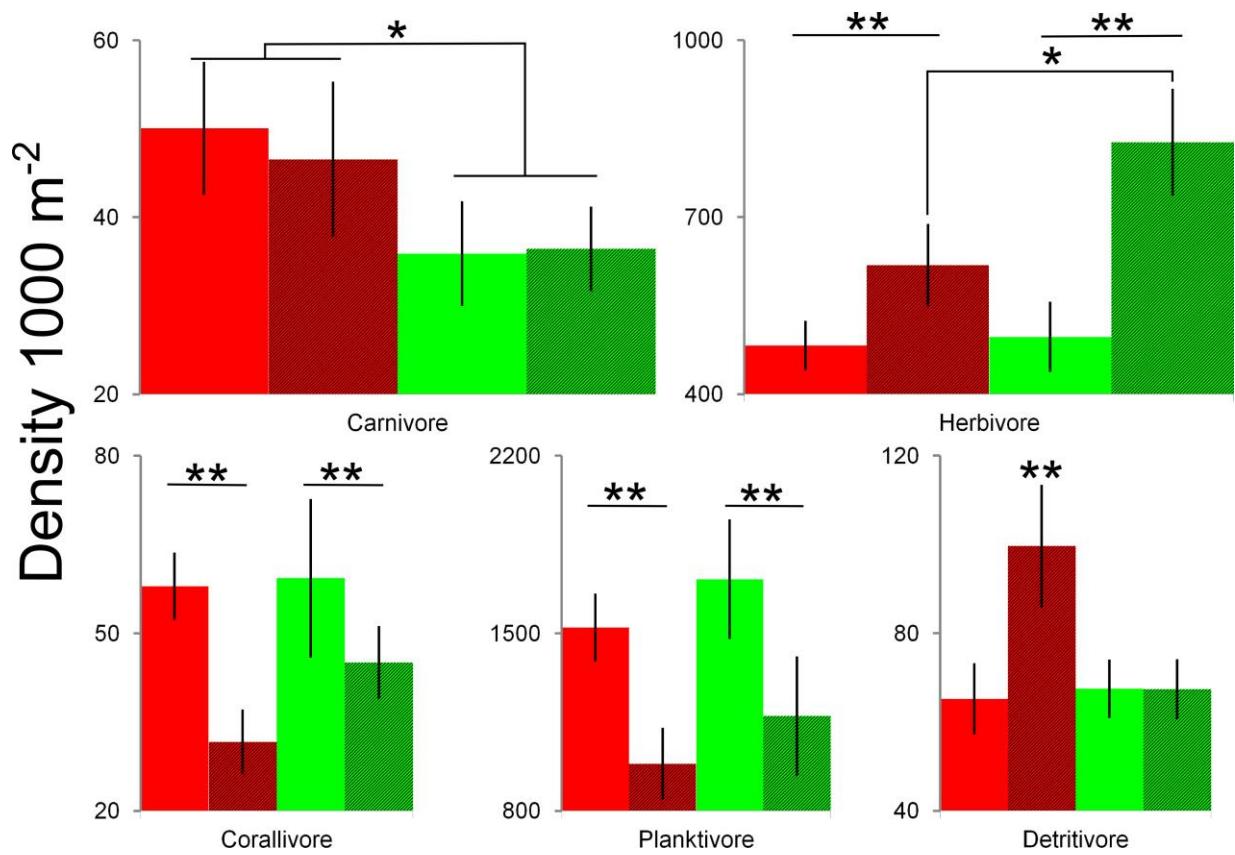


Figure 2.4. Mean density of trophic groups ($\pm 95\%$ confidence intervals) for fished (red) and non-fished (green) reefs. The density of trophic groups across fished, non-fished, disturbed (stippled bars) and non-disturbed (solid bars) reefs are shown. $^{**}p<0.01$ and $^{*}p<0.05$ for permuted ANOVAs and permuted *t*-tests.

2.5 Discussion

Sharks are apex predators (Cortes 1999) that have the capacity to affect fish community structure directly by consumption of prey or by inducing costly behavioural-risk effects (Heithaus *et al.* 2008). For these reasons, it is expected that sharks should have a strong influence on the species composition, biomass, and trophic structure of prey assemblages (Sandin *et al.* 2008; Williams *et al.* 2011). Nevertheless, demonstrating such effects has been problematic, usually because the loss of sharks is accompanied by a wide range of other anthropogenic disturbances. This is due to increased exploitation of fishes and invertebrates at lower trophic levels coined “fishing down the food chain” (Pauly *et al.* 1998) and ecosystem degradation through pollution, eutrophication and habitat loss, particularly where atolls are inhabited by growing human populations (Mora *et al.* 2011; Williams *et al.* 2011). Furthermore, many previous studies are limited in temporal scope and compare fish and benthic community structure across a gradient of shark abundance on reefs at only a single instant in time (Friedlander & DeMartini 2002; Sandin *et al.* 2008; Williams *et al.* 2011). This ignores the fact that coral communities are dynamic and that even pristine reefs are invariably in a state of flux between impact and recovery from natural, bottom-up disturbances that alter the structure of fish assemblages. Because the study atolls are uninhabited and the targets of fishing by Indonesians are largely limited to “banquet” species of high economic value, such as sharks (for the shark-fin soup trade; Field *et al.* 2009), I am able to investigate the effects of loss of sharks on community structure (mesopredator release, trophic cascade) without the confounding effects of other anthropogenic disturbances. Moreover, as changes in fish and benthic assemblages were monitored for more than a decade, I am able to extract the effects of the differences in shark numbers from the background of changes in benthic community structure caused by cyclones and bleaching.

2.5.1 *The trophic structure of fish communities*

Although this unique set of circumstances offers, for the first time, an opportunity to disentangle the effects of pulse and press disturbances on a coral reef ecosystem, my results must be considered within the context and limitations of a natural experiment. Because all such studies are correlative in nature, in most cases alternative explanations for patterns cannot be excluded. Bearing this caveat in mind, evidence that my interpretations are reasonable is that they are supported by a great number of earlier studies. For example, I found evidence that the loss of

sharks was correlated with an increase in the number of smaller, mesopredators on the study reefs (Figure 2.4). This phenomenon (termed “mesopredator release”) is a typical consequence of the removal of large apex predators from an ecosystem and examples occur throughout terrestrial environments, although there have been relatively few studies in marine habitats (Myers *et al.* 2007; Stallings 2008; Prugh *et al.* 2009; Brashares *et al.* 2010; Estes *et al.* 2011). At the Scott Reefs, mesopredators were generally mid-sized (15-40 cm; mostly *Lutjanidae* and *Lethrinidae*) species that consumed both fishes and invertebrates (Figure 2A.2). Abundances of mesopredators were independent of bottom-up changes in coral habitats, as numbers of this guild did not alter during the impact or recovery from the bleaching event at Scott Reef or the cyclone at the Rowley Shoals that removed up to 80% of the cover of live coral in shallow (< 30 m depth) water (see Figure 2.2).

I also found some evidence of a trophic cascade on the study reefs. The reduction in numbers of sharks as apex predators may have affected not only the smaller carnivores, but also herbivorous fishes (from multiple genera), as this guild was less abundant at the fished Scott Reefs than the unfished Rowley Shoals throughout the period of the study (Figure 2.4 and Figure 2A.3). However, in contrast to mesopredators, numbers of both herbivorous and detritivorous fishes also changed in response to bottom-up processes, increasing as algal cover replaced corals in the aftermath of the cyclone and bleaching events (Figure 2.4). I could find no evidence that corallivores and planktivores differed between fished and unfished reefs; changes in abundance of these trophic groups appeared to occur largely in response to bottom-up disturbance, with the removal of live coral likely to have negatively affected obligate corallivores and the settlement stages of many planktivores that preferentially recruited into live coral habitats. Similar responses to bottom-up disturbances have been recorded in these trophic groups by many other studies (Halford & Caley 2009; Emslie *et al.* 2011).

2.5.2 Future directions and limitations

Trophic cascades occur when changes in the abundance of higher-order predators directly and indirectly affect species at a number of lower trophic levels in a food chain. Such cascades are well-recognised in marine systems, with examples involving reductions in the numbers of sharks, lobsters, seastars and sea otters as apex predators causing fundamental changes in the structure and function of temperate marine ecosystems where they formerly occurred (Baum & Worm

2009; Salomon *et al.* 2010; Estes *et al.* 2011). In this chapter, I could not show the mechanism that linked trophic levels, however this is perhaps not surprising, given that high species diversity and wide niche-breaths of diet, which are typical traits of assemblages of coral reef fishes, are expected to make the precise impacts of mesopredators difficult to discern (Brashares *et al.* 2010). For example, in the Caribbean (Stallings 2008), an increase in coral reef mesopredators resulted in higher predation rates on fish recruits, with this effect not being limited to a single trophic group but expressed across all abundant species of recruits, ranging from mobile herbivores (*Scaridae*) to territorial damselfishes (*Pomacentridae*).

Disturbances can act synergistically, additively or antagonistically on the abundances of animals within an ecosystem (Darling & Côté 2008). In this chapter, bottom-up and top-down disturbances may have had a synergistic effect on abundances of detritivores. Fishes of this trophic group (mostly *Ctenochaetus*) were significantly more abundant on the fished Scott Reefs after the impact of bleaching than during undisturbed phases. In contrast, they did not differ in abundance during impact and undisturbed phases on the unfished Rowley Shoals. This result implies that the reduction in shark numbers may directly or indirectly allow these species to take advantage of the increase in detrital material trapped by turfing algae that overgrew dead corals during disturbance on Scott Reef. However, there are a number of alternative explanations of this pattern. For example, variation in numbers of detritivores might reflect fundamental differences in the nature of the disturbance between reef systems. Wave action caused by cyclones breaks up coral skeletons, reducing three-dimensional structure (Wilson *et al.* 2006). In contrast, bleaching removes only the outer layer of live coral, leaving the skeleton and the habitat intact. For this reason, bleaching may produce reefs that trap more detritus, increasing resources for detritivores. However, this effect is short-lived, lasting no more than a few months. After this time bioeroders create significant structural collapse of coral skeletons, so that the ultimate effects of both types of disturbance are very similar (Halford & Caley 2009). I found that increased abundances of detritivores at the Scott Reefs was not an ephemeral event, but was sustained over the many years that the reefs required to recover from severe bleaching. I did, however, find some evidence that the bleaching event at Scott Reefs was more severe in terms of removal of live coral than the cyclone at the Rowley Shoals. This may have benefitted detritivores at the Scott Reefs by creating more resources (Figure 2A.1). Again, such a hypothesis is difficult to reconcile with my observations, since I would expect that a greater loss of live coral and thus the presence

of more algae should also result in greater numbers of herbivores at the Scott Reefs than the Rowley Shoals. In fact, I recorded the opposite pattern, with fewer herbivores at Scott Reefs than the Rowley Shoals. Another possibility is that differences in abundance of detritivores between the Rowley Shoals and the Scott Reefs may be due to differential patterns of recruitment. Rare strong pulses in recruitment (greater by orders of magnitude than background levels) can be a feature of the biology of surgeonfishes on isolated reefs and atolls (Doherty 2002). Given that these fishes make up the majority of the detritivore group at both study reefs and I did not monitor recruitment, I cannot exclude the possibility that rather than a synergistic effect of the loss of sharks and pulse disturbance, the increase in abundance of detritivores at Scott Reef after the bleaching was due to one of these rare recruitment events.

2.5.3 *Conclusions*

Evidence for a link between the numbers of apex predators and herbivores has important implications for coral reef ecosystems. It is increasingly apparent that herbivorous fishes are fundamental to the dynamics of communities on reefs, since their feeding reduces algal cover and allows corals more space to colonise and grow in benthic habitats (Bellwood *et al.* 2004; Estes *et al.* 2011). This role is not limited to any particular type of herbivore (e.g. scraper, roving grazer, territorial grazer); rather all feeding modes are thought to be important (Thibaut *et al.* 2011). Because bottom-up disturbances that kill live coral result in an increased cover of algae, my results suggest that top-order predators may have a role in determining the rate of recovery of reefs from these events.

Although we may soon lack any practical ability to affect the frequency of bottom-up disturbances to coral reefs where these are driven by climate change, this is not the case with the loss of reef sharks. Tracking studies show that in many cases reef sharks maintain a high degree of site fidelity around coral reefs (Field *et al.* 2011; Barnett *et al.* 2012), so that options such as marine protected areas can be an effective means to conserve numbers of these apex predators (Speed *et al.* 2012). Healthy populations of reef sharks should be a key target of management strategies that seek to ensure the future resilience of coral reef ecosystems.

2.6 Appendix

2.6.1 Artisanal Fishing in the MoU74 Box

The Australian-Indonesian Memorandum of Understanding Box 74 (MoU74), allows Indonesian fishermen access to the Australian Exclusive Economic Zone to pursue fishing using traditional artisanal techniques (Field *et al.* 2009). Indonesian fishermen target “banquet” species of high economic value, principally shark (for shark fin), but also sea cucumber (*Holothuroidea spp.*) and trochus shell (top snails, *Trochidae spp.*; Skewes *et al.* 1999; Rees *et al.* 2003; Field *et al.* 2009). Studies conducted in 1998 corroborate my findings that fisheries activities in the MoU74 have reduced abundances of reef sharks (*Carcharhinidae*; Skewes *et al.* 1999). Recent studies in 2010 and 2011 confirm that this pattern has persisted to the present day (Heyward *et al.* 2011a; Heyward *et al.* 2011b).

Indonesian fishing techniques include snorkeling in shallow water for sea cucumber and top snails and longlining for sharks. Longlines are set at least 50 m off the reef edge to target sharks and avoid entanglement with corals (Skewes *et al.* 1999). Due to the distances to markets and a lack of on-board refrigeration, products are generally dried for transportation. Fishing for finfish other than sharks is generally limited to species that are caught for immediate consumption. Significant depletion of finfish stocks (other than sharks) by these fishermen was not detectable in my or previous studies (Skewes *et al.* 1999). Australian Customs and border patrol flights (2000-2007) also confirm the presence of Indonesian fishermen in the vicinity of the MoU74 Box throughout the period of the study, with a peak number of vessels spotted in the year 2006 (Field *et al.* 2009).

2.6.2 Physical and biological differences between Scott Reefs and Rowley Shoals

Physical, biological and anthropogenic factors that may have contributed to the differences I observed in fish communities between the Scott Reefs and Rowley Shoals have been summarized in Table 2A.1. Fishing is the main difference in anthropogenic activities between these reefs. All reefs are uninhabited and both have a similar area (Scott = 180 km²; Rowley = 174 km²), although they do differ in perimeters (Scott = 184 km; Rowley = 118 km; Table 2A.1). However, a large portion of the perimeter of South Scott Reef is effectively lagoon due to the horseshoe shape of the reef. Long-term monitoring sites within this lagoon were not included in

Table 2A.1. Anthropogenic and reef metrics between study site locations. Protected sites include Mermaid, Clerke and Imperieuse. Fished sites include South and North Scott, Seringapatam and Ashmore.

Reef	Anthropogenic Factors			Reef Metrics		
	Fishing	Management	Year Established	Population	Area** (km²)	Perimeter** (km)
Mermaid	Prohibited	Commonwealth Marine Reserve	1991	0	42.4	36.25
Clerke	Prohibited	DEC; Marine Park	1990	0	58.9	38.54
Imperieuse	Prohibited	DEC; Marine Park	1990	0	72.7	43.18
South Scott	Artisanal Fishing	MoU74 Box	1974	0	99.0	108.60
North Scott	Artisanal Fishing	MoU74 Box	1974	0	56.0	48.90
Seringapatam	Artisanal Fishing	MoU74 Box	1974	0	25.0	26.74
Ashmore	Artisanal Fishing	MoU74 Box; Marine Nature Reserve	1983	0	179.3	101.45

Table 2A.1 (Cont'd). Environmental and biotic factors between study site locations. Protected sites include Mermaid, Clerke and Imperieuse. Fished sites include South and North Scott, Seringapatam and Ashmore.

Reef	Environment Factors				Biota				
	Time-Averaged SST (°C)	Time-Averaged Chl a (mg/m³)	Recent Bleaching Events	Recent Cyclonic Events	Number of Fish Species	Rare Species (<5% of sites)	Mean Abundance (m²)	Mean Coral Cover ± SE	Mean Algal Cover ± SE
Mermaid	28.36	0.76		1996	84	0	2.84 ± 0.72	38.54 ± 6.82	32.6 ± 22.56
Clerke	28.26	0.90		1996	89	0	3.31 ± 1.0	29.95 ± 10.1	35.39 ± 22.78
Imperieuse	28.09	0.20		1996	86	0	3.04 ± 0.94	29.8 ± 18.9	49.41 ± 23.41
South Scott	29.04	0.28	1998		127	18	2.76 ± 0.73	32.81 ± 25.93	35.97 ± 26.18
North Scott	29.10	0.61	1998		117	19	2.65 ± 0.73	32.25 ± 21.78	32.73 ± 21.17
Seringapatam	29.10	0.31	1998		134	10	2.63 ± 0.53	45.15 ± 18.38	28.5 ± 18.56
Ashmore	-	-	-	-	-	-	-	-	-

* Sea Surface Temperature (SST; 2001 - 2008) and Chlorophyll a (Chl a; 1997 - 2008) were derived from remotely sensed imagery produced with the Giovanni online data system, developed and maintained by the NASA GES DISC at 4km resolution.

**Area and perimeter derived from ARCGIS layers.

this chapter. Small differences in chlorophyll-a concentration and sea surface temperature differences (reefs at the Rowley Shoals are on average one degree cooler than the Scott Reefs) may exist (Table 2A.1), however, given the resolution of chlorophyll-a measurements (pixel dimensions of 4km × 4km in remote sensing data), such estimates must be treated with caution. Furthermore, there is little evidence of differences in reef productivity since both reefs supported similar mean abundances of fish, coral cover and algal cover when compared over the entire sampling period (1994 – 2008; Table 2A.1). The most striking difference occurred in species diversity, with the Scott Reefs having a greater number of species than the Rowley Shoals (Table 2A.1). All the species that occurred exclusively at Scott Reefs were largely rare, occurring in less than 5% of transects. This difference reflects a latitudinal gradient of increasing species richness towards Indonesia and the Coral Triangle (Bellwood *et al.* 2005), a pattern recorded by other studies (Sandin *et al.* 2008; Williams *et al.* 2011).

2.6.3 *Benthic Disturbances*

Both the Scott Reefs and Rowley Shoals experienced catastrophic pulse disturbances in the late 1990s (coral bleaching in 1998 and a Category 5 cyclone in 1996, respectively). At the Scott Reefs, bleaching reduced coral cover from *ca* 60% to <10%, while similar declines in coral cover occurred at the Rowley Shoals after a Category 5 cyclone (Figure 2.2A and 2.2B). After the disturbance, corals were overgrown by turfing algae, but coral cover returned to near pre-disturbance levels for both reefs in the following decade.

Coral bleaching and cyclones are both acute, pulse disturbances that ultimately convert live coral to algal cover. There are, however, also some differences between these events. For example, cyclones physically break and reduce coral structure while bleaching leaves coral skeletons intact, at least for some months after the initial disturbance (Letourneur *et al.* 1993; Wilson *et al.* 2006; Pandolfi *et al.* 2011). Ultimately, bleaching also leads to the loss of coral structure as the dead coral is subject to bioeroding organisms and is reduced to rubble, a process that typically requires some months depending on the exposure of a reef to wave action. Despite each having a different initial effect on the structural complexity (or three-dimensional structure) of reefs, studies that have monitored these disturbances have found that both ultimately have very similar effects on fish communities. For example, Wilson *et al.* (2006) found that of five

trophic groups of reef fishes (carnivore, herbivore, detritivore, planktivore and corallivore), only planktivores differed in abundance between bleaching and cyclone events. Further, rates of recovery of coral cover after bleaching and cyclonic events also appear to be unrelated to disturbance type (Graham *et al.* 2011; Osborne *et al.* 2011).

In order to determine if differences in the major components of the benthic community might have contributed to my results, I compared communities among treatments in more detail using Principal Components Analysis (PCA). Here I interrogated cover using the dominant categories of benthic life forms found on the reef: hard (*Acropora* branching, tabulate and corymbose), *Pocillaporidae*, encrusting, massive, *Isopora* and “other” corals, soft coral, algae (macro and crustose coralline-turf), abiotic (e.g. rubble, sand, etc.), and other benthos (e.g. invertebrates, etc.). Prior to analysis the percent cover of each was arcsine and Hellinger transformed (Legendre & Gallagher 2001). This procedure used the *vegan* package of R Statistical Language (Oksanen & Roberts 2010).

The PCA biplot was able to explain 64.6% of variation in benthic community composition on the first two axes (Figure 2A.1). An overwhelming amount of this variation (48.7%) was explained across the first axis and was attributable to differences in algal (turf-crustose) and coral cover (hard and soft), such that sites following a pulse disturbance had more algal and less coral cover than sites prior to disturbance (Figure 2A.1). This analysis also showed that the bleaching event at the Scott Reefs resulted in a greater loss of coral cover and as a result more algal growth than the cyclone at the Rowley Shoals (Figure 2A.1). Although this may have benefitted detritivores at the Scott Reefs, I would also expect that the presence of more algae should have also resulted in greater numbers of herbivores. This was not the case, as numbers of herbivores were lower at Scott Reefs than the Rowley Shoals. Prior to disturbance all sites appeared to have similar amounts of algal and coral cover.

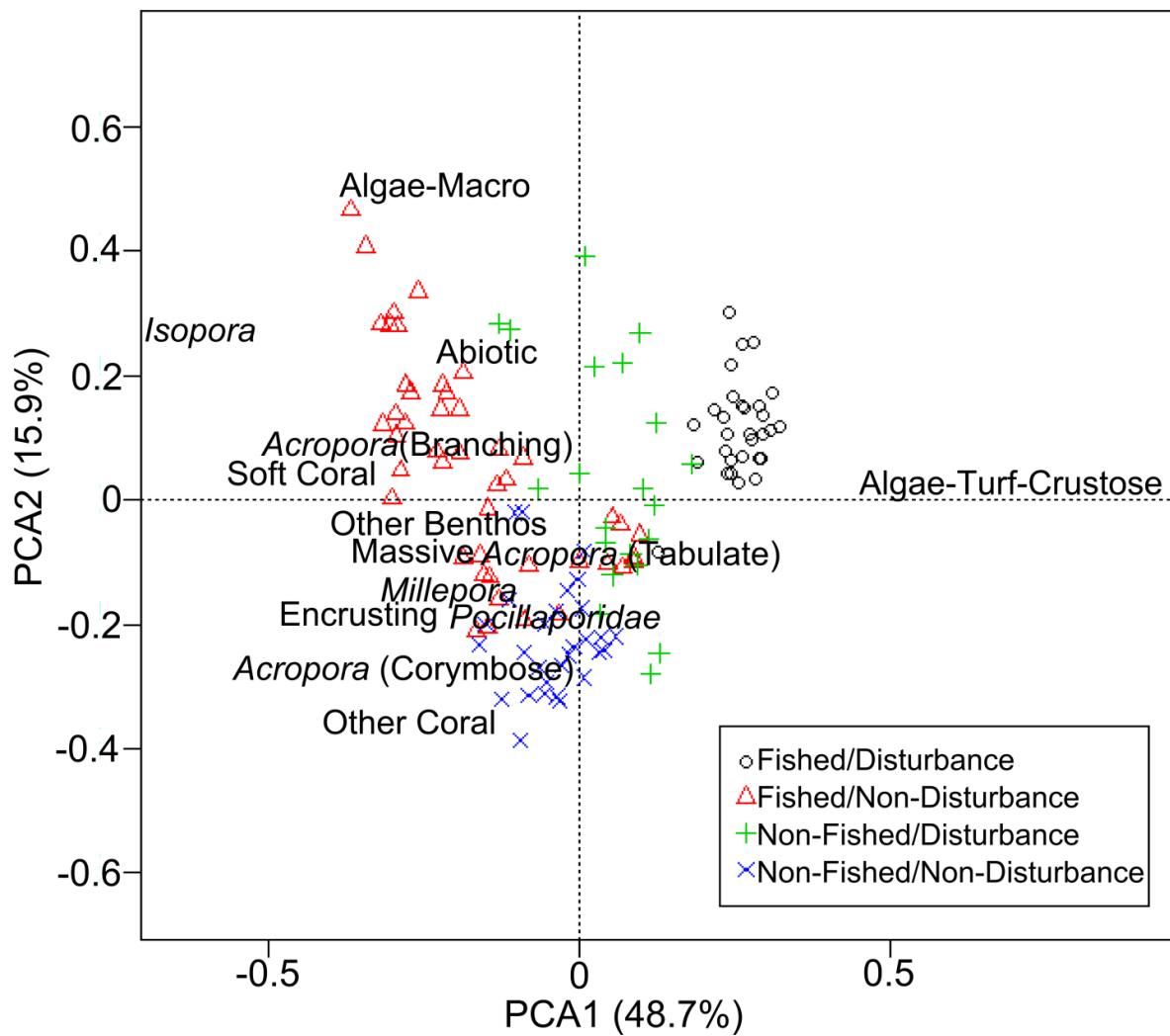


Figure 2A.1. Principal components analysis of benthic composition of hard coral (*Acropora* (Branching, Tabulate and Corymbose), *Pocillaporidae*, encrusting, massive, *Isopora*, and other coral), soft coral, algae (macro and crustose coralline-turf), abiotic (rubble, sand, etc.), and other benthos. Sites have been coded by the four treatments (see key). The amount of variation explained by each axis is shown.

Differences in types of coral cover between reefs contributed much less to overall patterns along the second axis of variation (15.7%; Figure 2A.1) and there was a large degree of overlap among the treatments. Regardless, there were some subtle differences between fished and non-fished reefs under non-disturbed conditions that were attributable to differences in the cover of macro algae and “other corals”, but these appeared to be driven by only a handful of sites (< 10). Furthermore, there was little evidence that the differences I observed between fished and non-fished reefs under non-disturbed conditions impacted the fish community. For example, the Scott Reefs had more macro algae under non-disturbed conditions (Figure 2A.1), a feature that should be expected to benefit abundances of herbivores, when in fact it did not (Figure 2.4). Thus, the principal variables in benthic composition that contributed to patterns of fish assemblages at the scale of the study appear to be related to differences in cover of algae and corals.

2.6.4 *Fish Community Composition Analysis*

Prior to analysis, I removed rare species (defined as present in <5% of sites; Jackson & Harvey 1989) and Hellinger transformed abundances (Legendre & Gallagher 2001). Collinearity between variables was assessed using variance inflation factors (VIF; VIF < 10 indicates non-collinearity). The significance of the Redundancy Analysis (RDA) model, RDA constraints and RDA axes were tested using a randomization procedure ($n = 9999$) where the data were permuted randomly and refitted to test for significance. This procedure involved using the *cca* and *anova* functions in the vegan package of R Statistical Language (Oksanen & Roberts 2010).

The RDA separated fished and non-fished reefs into two distinct groups (Figure 2.3). Fished sites tended to have higher abundances of carnivores and a lower abundance of herbivores in comparison to non-fished reefs. The overall model was significant (permutation analyses; $p < 0.01$), as were all 5 constraints ($p < 0.01$) and the first 4 axes of variation (or components; $p < 0.05$). The RDA was able to explain 29.5% of variation ($n = 114$ species). The first axis explained 13.5% of species variation and was related to the abundance of herbivorous fishes. The second axis of variation (which explained 9.5% of species variation) was related to the abundance of carnivores (Figure 2.3). Other trophic groups (corallivores, detritivores and

planktivores) showed changes in abundance that appeared to be more related to changes in benthic community structure than fishing.

Differences in the abundances of carnivores and herbivores between the Scott Reefs and the Rowley Shoals were the result of patterns occurring across multiple families, genera and species (Figures 2A.3, 2A.4 and Table 2A.2). Plots of the results of principal component analyses (PCA) show that differences in the abundances of carnivores ($n=15$ genera, 27 species) between these fished and non-fished reefs could be attributed to representatives of the genus *Lutjanus* and to a lesser extent on the genera *Forcipiger*, *Gnathodentex*, *Lethrinus*, *Plectropomus* and *Zanclus*, all of which tended to be more abundant at the Scott Reefs (Figure 2A.2). In contrast, the small wrasses *Gomphosus* and *Hemigymnus* tended to be more abundant at the protected Rowley Shoals (Figure 2A.2).

For herbivores, differences in the densities between the reef systems were driven by differences in the abundances of 12 genera (Figure 2A.3). In particular, representatives of the genera *Chlorurus*, *Naso*, *Pomacentrus* and *Zebrasoma* were more abundant at the Rowley Shoals than the Scott Reefs (Figure 2A.3). In contrast, the genera *Acanthurus*, *Chrysiptera*, *Plectroglyphidodon* and the rabbitfish *Siganus* characterised herbivores at the Scott Reefs (Figure 2A.3).

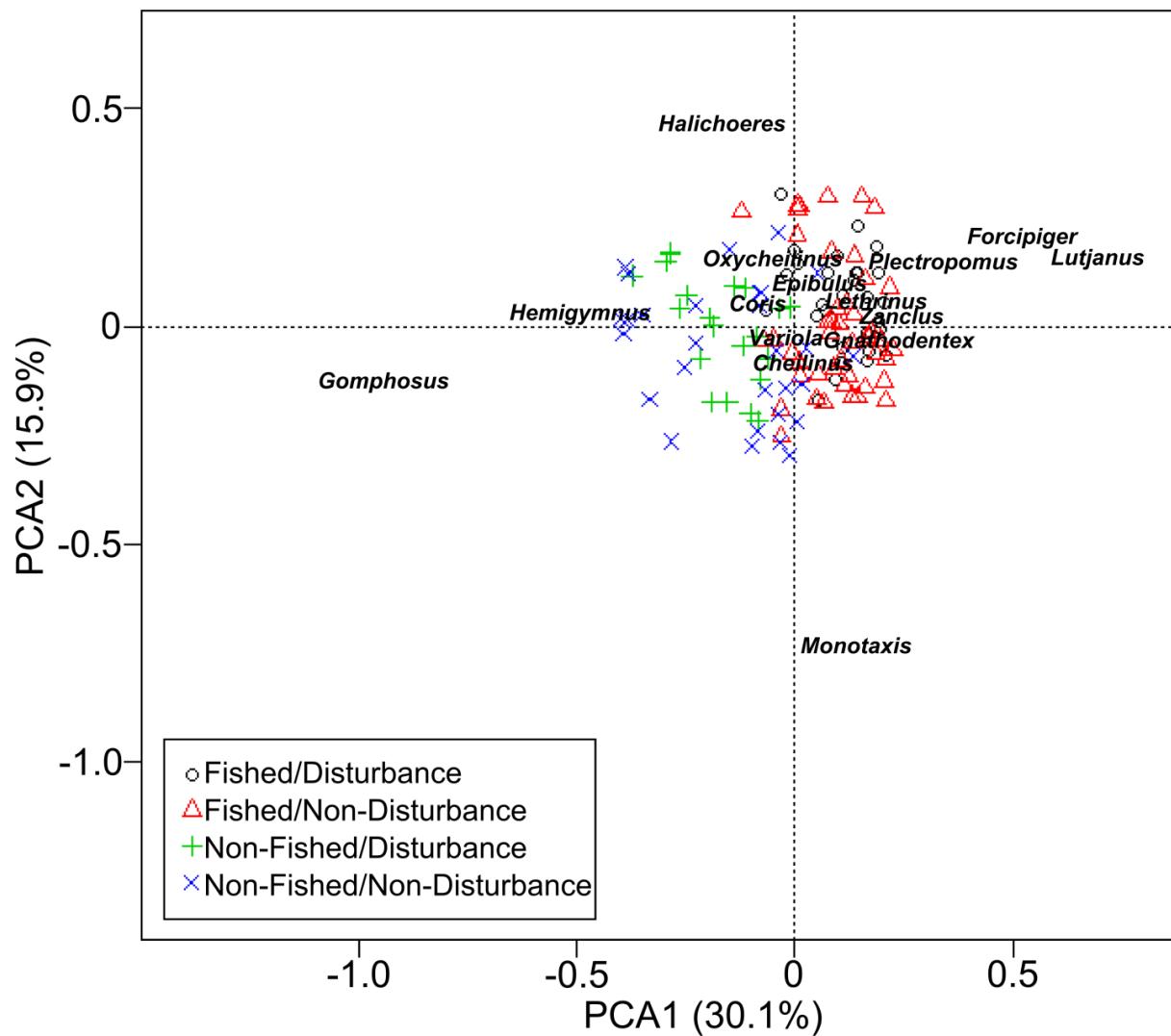


Figure 2A.2. PCA biplot of fish abundances by genus in the carnivore trophic group. The sites were coded by each of the four treatments and the 15 genera that made up the carnivore group are shown. The amount of variation explained by each axis is shown.

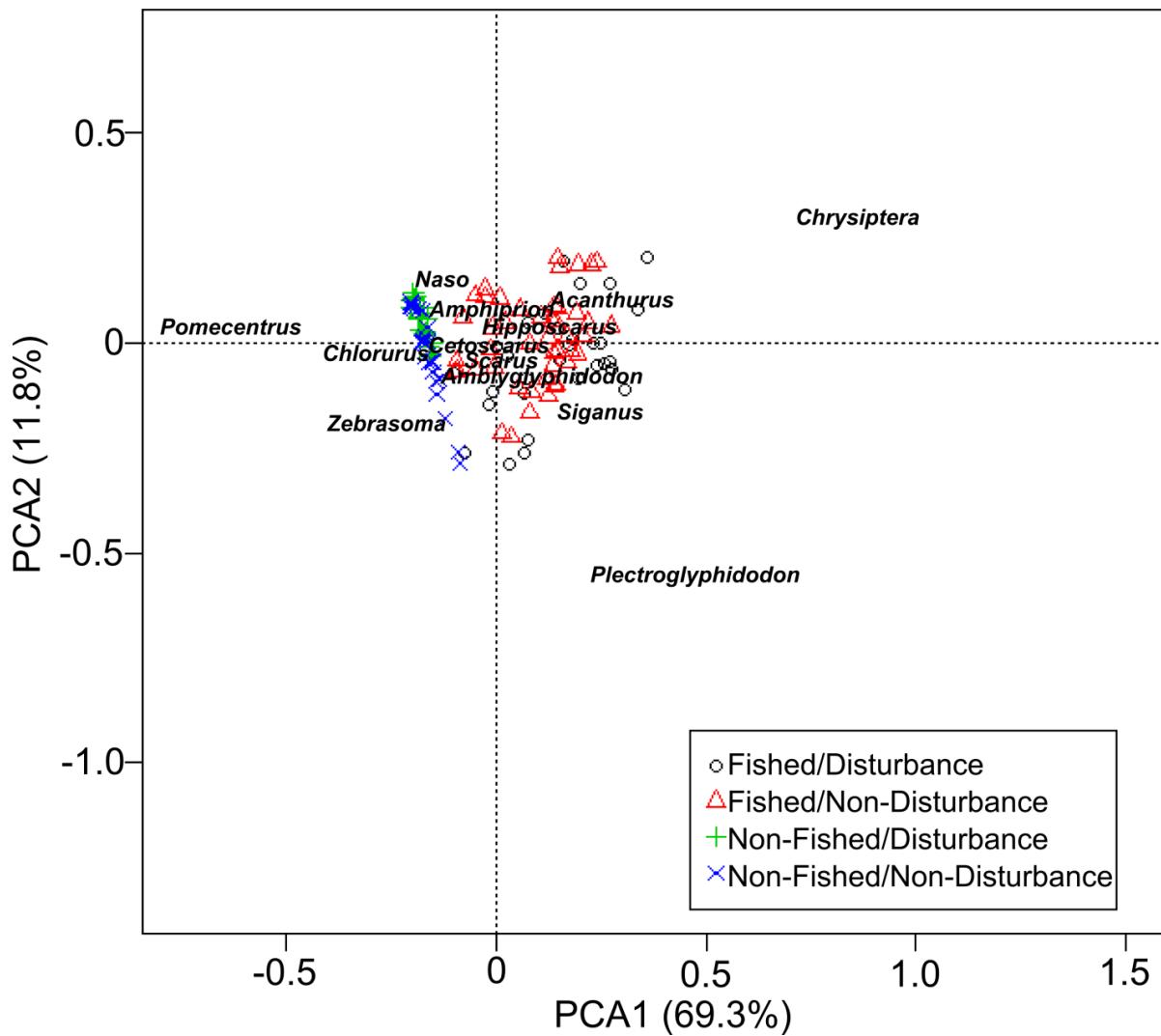


Figure 2A.3. PCA biplot of abundances of fish by genus in the herbivore trophic group. The 12 genera that make up the herbivore group are shown on the figure and the sites were coded by each of the four treatments. The amount of variation explained by each axis is shown.

Table 2A.2. Species composition of the five trophic groups (carnivore, herbivore, detritivore, planktivore and corallivore) used in the study. Species are listed alphabetically by family and species. Those classified as corallivores included both obligate and facultative coral feeders (Hughes *et al.* 2003; Wilson *et al.* 2006). Herbivores were classified according to Green and Bellwood (2009) while detritivores (including epilithic algal matrix feeders) followed Wilson *et al.* (2007). Planktivores and carnivores followed Froese and Pauly (2011). Only those species present in more than 5% of sites are included in this list.

Family	Species	Trophic Group
Acanthuridae	<i>Acanthurus auranticavus</i>	Herbivore
	<i>Acanthurus blochii</i>	Detritivore
	<i>Acanthurus dussumieri</i>	Detritivore
	<i>Acanthurus fowleri</i>	Herbivore
	<i>Acanthurus leucocheilus</i>	Detritivore
	<i>Acanthurus lineatus</i>	Herbivore
	<i>Acanthurus nigricans</i>	Herbivore
	<i>Acanthurus nigricauda</i>	Herbivore
	<i>Acanthurus nigrofasciatus</i>	Herbivore
	<i>Acanthurus olivaceus</i>	Detritivore
	<i>Acanthurus pyroferus</i>	Herbivore
	<i>Acanthurus thompsoni</i>	Planktivore
	<i>Ctenochaetus binotatus</i>	Detritivore
	<i>Ctenochaetus spp</i>	Detritivore
	<i>Ctenochaetus strigosus</i>	Detritivore
Naso	<i>Naso brevirostris</i>	Planktivore
	<i>Naso hexacanthus</i>	Planktivore
	<i>Naso lituratus</i>	Herbivore
	<i>Naso unicornis</i>	Herbivore
	<i>Naso vlamingii</i>	Planktivore

	<i>Zebrasoma scopas</i>	Herbivore
	<i>Zebrasoma veliferum</i>	Herbivore
Chaetodontidae	<i>Chaetodon adiergastos</i>	Corallivore
	<i>Chaetodon auriga</i>	Corallivore
	<i>Chaetodon baronessa</i>	Corallivore
	<i>Chaetodon bennetti</i>	Corallivore
	<i>Chaetodon ephippium</i>	Corallivore
	<i>Chaetodon kleinii</i>	Corallivore
	<i>Chaetodon lunula</i>	Corallivore
	<i>Chaetodon melannotus</i>	Corallivore
	<i>Chaetodon meyeri</i>	Corallivore
	<i>Chaetodon ornatissimus</i>	Corallivore
	<i>Chaetodon punctatofasciatus</i>	Corallivore
	<i>Chaetodon rafflesii</i>	Corallivore
	<i>Chaetodon semeion</i>	Corallivore
	<i>Chaetodon speculum</i>	Corallivore
	<i>Chaetodon trifascialis</i>	Corallivore
	<i>Chaetodon trifasciatus</i>	Corallivore
	<i>Chaetodon ulietensis</i>	Corallivore
	<i>Chaetodon unimaculatus</i>	Corallivore
	<i>Chaetodon vagabundus</i>	Corallivore
	<i>Forcipiger flavissimus</i>	Carnivore
	<i>Forcipiger longirostris</i>	Carnivore
Epinephelidae	<i>Plectropomus areolatus</i>	Carnivore
	<i>Plectropomus laevis</i>	Carnivore
	<i>Plectropomus oligacanthus</i>	Carnivore
	<i>Variola louti</i>	Carnivore

Labridae	<i>Cheilinus fasciatus</i>	Carnivore
	<i>Cheilinus undulatus</i>	Carnivore
	<i>Coris aygula</i>	Carnivore
	<i>Coris gaimard</i>	Carnivore
	<i>Epibulus insidiator</i>	Carnivore
	<i>Gomphosus varius</i>	Carnivore
	<i>Halichoeres hortulanus</i>	Carnivore
	<i>Hemigymnus fasciatus</i>	Carnivore
	<i>Hemigymnus melapterus</i>	Carnivore
	<i>Oxycheilinus digrammus</i>	Carnivore
	<i>Oxycheilinus unifasciatus</i>	Carnivore
Lethrinidae	<i>Gnathodentex aureolineatus</i>	Carnivore
	<i>Lethrinus erythracanthus</i>	Carnivore
	<i>Monotaxis grandoculis</i>	Carnivore
Lutjanidae	<i>Lutjanus bohar</i>	Carnivore
	<i>Lutjanus decussatus</i>	Carnivore
	<i>Lutjanus fulvus</i>	Carnivore
	<i>Lutjanus gibbus</i>	Carnivore
	<i>Lutjanus kasmira</i>	Carnivore
	<i>Macolor spp</i>	Planktivore
Pomacentridae	<i>Amblyglyphidodon aureus</i>	Planktivore
	<i>Amblyglyphidodon curacao</i>	Herbivore
	<i>Amblyglyphidodon leucogaster</i>	Herbivore
	<i>Amphiprion clarkii</i>	Herbivore
	<i>Chromis amboinensis</i>	Planktivore
	<i>Chromis atripeectoralis</i>	Planktivore
	<i>Chromis atripectoralis</i>	Planktivore

	<i>Chromis lepidolepis</i>	Planktivore
	<i>Chromis lineata</i>	Planktivore
	<i>Chromis margaritifer</i>	Planktivore
	<i>Chromis ternatensis</i>	Planktivore
	<i>Chromis weberi</i>	Planktivore
	<i>Chromis xanthurus</i>	Planktivore
	<i>Chrysiptera rex</i>	Herbivore
	<i>Dascyllus trimaculatus</i>	Planktivore
	<i>Plectroglyphidodon dickii</i>	Herbivore
	<i>Plectroglyphidodon johnstonianus</i>	Corallivore
	<i>Plectroglyphidodon lacrymatus</i>	Herbivore
	<i>Pomacentrus bankanensis</i>	Herbivore
	<i>Pomacentrus coelestis</i>	Herbivore
	<i>Pomacentrus lepidogenys</i>	Herbivore
	<i>Pomacentrus moluccensis</i>	Herbivore
	<i>Pomacentrus philippinus</i>	Planktivore
	<i>Pomacentrus vaiuli</i>	Herbivore
	<i>Pomachromis richardsoni</i>	Planktivore
Scaridae	<i>Cetoscarus bicolor</i>	Herbivore
	<i>Chlorurus bleekeri</i>	Herbivore
	<i>Chlorurus microrhinos</i>	Herbivore
	<i>Chlorurus sordidus</i>	Herbivore
	<i>Hipposcarus longiceps</i>	Herbivore
	<i>Scarus dimidiatus</i>	Herbivore
	<i>Scarus forsteni</i>	Herbivore
	<i>Scarus frenatus</i>	Herbivore
	<i>Scarus globiceps</i>	Herbivore

	<i>Scarus niger</i>	Herbivore
	<i>Scarus oviceps</i>	Herbivore
	<i>Scarus prasiognathos</i>	Herbivore
	<i>Scarus psittacus</i>	Herbivore
	<i>Scarus rubroviolaceus</i>	Herbivore
	<i>Scarus schlegeli</i>	Herbivore
	<i>Scarus spinus</i>	Herbivore
Siganidae	<i>Siganus corallinus</i>	Herbivore
	<i>Siganus puillus</i>	Herbivore
	<i>Siganus punctatissimus</i>	Herbivore
	<i>Siganus punctatus</i>	Herbivore
	<i>Siganus vulpinus</i>	Herbivore
Zanclidae	<i>Zanclus cornutus</i>	Carnivore

Table 2A.3. Summary of statistical tests to evaluate fishing, disturbance and interactive effects on densities of trophic groups. Fishing, disturbance and interaction effects were evaluated using a permuted two-way ANOVA. Permuted *t*-tests were used to conduct contrasts. *p*-values were Bonferroni corrected.

Trophic Group	Test-statistic	<i>p</i> -value	Contrast (permuted <i>t</i> -test)
Fishing Effects			
Carnivore	$F_{1,122} = 13.95$	0.0125	Disturbed=Non-Disturbed
Corallivore	$F_{1,122} = 0.0015$	1	
Planktivore	$F_{1,122} = 0.026$	1	
Herbivore	$F_{1,122} = 0.74$	1	
Detritivore	$F_{1,122} = 10.41$	0.001	
Disturbance Effects			
Carnivore	$F_{1,122} = 2.26$	1	
Corallivore	$F_{1,122} = 13.66$	0.0075	Fished=Non-Fished
Planktivore	$F_{1,122} = 70.25$	0.0025	Fished=Non-Fished
Herbivore	$F_{1,122} = 80.05$	0.0025	Fished<Non-Fished*
Detritivore	$F_{1,122} = 35.75$	0.0001	
Interaction Effects (Fishing x Disturbance)			
Carnivore	$F_{1,122} = 0.11$	1	
Corallivore	$F_{1,122} = 2.81$	1	
Planktivore	$F_{1,122} = 0.40$	1	
Herbivore	$F_{1,122} = 2.15$	1	
Detritivore	$F_{1,122} = 15.88$	0.005	

*Contrast significant only during disturbed phase ($t_{47} = 3.62$, $p = 0.001$)

Chapter 3

Spatio-temporal variability of food web structure on coral reefs

3.1 Abstract

Assessing the importance and significance of apex predators can be critical for long-term conservation and restoration goals. Reef environments are prone to environmental stochasticity (or temporal variability) in the form of benthic disturbances that structure coral reef fishes in a bottom-up manner. As apex predators, sharks likely play an important ecological role on coral reefs by reducing temporal variability in prey populations in a top-down manner. Here I use fish counts and benthic cover data from uninhabited and protected atolls to demonstrate that interannual variability (1995-2008) in coral cover is a major contributor to spatial patterns of reef fish trophic structure. I also provide evidence that sharks play a pivotal role in significantly structuring reef fishes. Specifically, higher shark densities result in strong significant decreases in the densities of carnivores, herbivores and corallivores. Given that all primary consumers are also structured by the benthic disturbances, the densities of primary consumers are a function of the combined effects of top-down and bottom-up structuring agents. Thus, higher shark densities have the capacity to reduce variability in the food web structure creating increased resilience for fish communities, stressing their important structuring role in reef ecosystems.

3.2 Introduction

Contemporary ecosystems are faced with disturbance regimes that are becoming increasingly more frequent and severe (Donner *et al.* 2005; Emanuel 2005; Burrows *et al.* 2011).

Disturbances on coral reefs impact the relative abundances of fish species in either a top-down (e.g. fisheries) or bottom-up (e.g. cyclones) manner by altering species interactions, resources, and habitat (Jones *et al.* 2004; Wilson *et al.* 2006; Wilson *et al.* 2008). However, increases in environmental (disturbances) or demographic stochasticity have the potential to push species below viable population sizes that subject them to bottlenecks and potentially local extinction events (Melbourne & Hastings 2008; Brook *et al.* 2011). Beyond the species level,

environmental stochasticity will impact food web stability and compensatory dynamics found within communities (Gouhier *et al.* 2010). Thus, temporal stability in abundances of species or groups of species is thought to be a metric of resilience to disturbance events. However, temporal stability in relation to food web structure, where some taxa may be more prone to environmental stochasticity on coral reefs, is largely unclear (Graham *et al.* 2006; Mellin *et al.* 2010b). Specifically, it is unknown what role apex predators play as potential top-down structuring agents (i.e. directly or indirectly interact) to reduce variability in prey species abundance (Heithaus *et al.* 2010). In this chapter, I take advantage of a unique set of circumstances over a long-term period (1995-2008), where uninhabited and protected reefs are subject to a gradient of shark density (apex predators) alongside a gradient of benthic disturbance (cyclone) to investigate how top-down and bottom-up processes combine to the structure reef fish food webs.

Coral reef fishes are increasingly impacted by the introduction of novel disturbances (e.g. pollution, fishing, etc.) and the alteration of natural disturbances (e.g. cyclones, bleaching, etc.) (Bellwood *et al.* 2004; Wilson *et al.* 2008; Burrows *et al.* 2011). This impact is evident in the continual global decline of coral cover and shark abundance, which can structure food webs in a bottom-up and top-down manner, respectively (Gardner *et al.* 2003; Bruno & Selig 2007; Ferretti *et al.* 2010; De'ath *et al.* 2012). Benthic degradation (the conversion of reefs from coral to algal dominated systems) is a concern for all coral reefs, because many species (in particular primary consumers) depend on coral cover for settlement, resources and habitat (Jones *et al.* 2004; Wilson *et al.* 2008). Coral degradation is a result of competition between coral and algae for space and is attributable to a suite of potential exogenous causes that include: cyclones, coral bleaching, crown-of-thorns outbreaks, disease and fishing (Moran *et al.* 1988; Letourneur *et al.* 1993; Harvell *et al.* 2002; Graham *et al.* 2011). What role these changes in benthic composition, and specifically variability in benthic composition, may have alongside alterations in apex predator and mesopredator densities is largely unclear (Darling & Côté 2008).

At the top of the food web, the density of sharks can be associated with dramatically different fish communities (Friedlander & DeMartini 2002; Sandin *et al.* 2008; Williams *et al.* 2011). However, shark densities are often altered by fisheries that target multiple species (Pauly *et al.* 1998; Essington *et al.* 2006). Thus, it can be difficult to evaluate the role of apex predators and ascertain what processes may be structuring fish food webs, because fisheries impacts can

overwhelm underlying direct and indirect species interactions in fish food webs. Many studies also utilize gradients of human density that represent a confounded gradient where many factors (e.g. fishing, pollution, sedimentation, etc.) could be structuring fish communities (Mora *et al.* 2011). Human density gradients are problematic, because they represent gradients of multi-species fisheries and benthic degradation that structure fish food webs in a top-down and bottom-up manner (Friedlander & DeMartini 2002; Sandin *et al.* 2008). Despite this problem, these studies provide important comparisons for management (impacted versus minimally impacted), but they fail to determine the role of specific drivers of change related to fish community trophic structure. They also overlook temporal variation in communities that arise from other environmental factors or interactions between trophic groups.

As top-predators, sharks likely have a role in structuring fish communities by impacting prey species directly through consumption or by inducing costly behavioural responses (Heithaus *et al.* 2008). Previous studies have also shown that interactions between sharks and prey are strong enough that decreases in the density of sharks can lead to community re-arrangements (Baum & Worm 2009; Prugh *et al.* 2009; Ferretti *et al.* 2010; Chapter 2). These studies suggest that sharks can be strong structuring agents, but they cannot preclude the fact that impacts on lower trophic level species are a function of either the effect of top-down, bottom-up or both processes. Further, these studies document changes throughout the ecosystem that have only been observed in circumstances where humans have played a major role to produce the resulting patterns. How top-down and bottom-up processes may combine to impact the trophic structure of fish communities under minimally impacted conditions is poorly understood.

I first investigate how interannual variability in reef fish trophic groups is impacted by fluctuations in bottom-up (coral cover) and top-down (mesopredator density) processes over a long-term period (1995-2008). Specifically, I address: (1) whether annual variability in benthic composition (coral cover), during a period of disturbance and recovery, is important to the variability in densities of all fish trophic groups and (2) determine if annual variability in mesopredator (carnivore) density impacts the variability of potential prey species (primary consumer densities; herbivores, corallivores, detritivores and planktivores). Based on these relationships, I then use a simplified food web model to determine the strength and significance of top-down and bottom-up processes that structure reef fish food webs (Figure 3.1). Using a

causal modeling framework (Structural Equation Models or SEMs; Grace 2006), I evaluate the strength and significance of interactions between apex predators, mesopredators, primary consumers and benthic cover. Specifically, I determine: (1) the relative roles of top-down and bottom-up structuring agents and (2) determine how pervasive the impacts are by top-down and bottom-up structuring agents are throughout the food web. Finally, I control for differences in the benthic community, which influence trophic patterns in a bottom-up manner, to determine if top-down control by sharks and carnivores on primary consumers may be partly independent of variability that originates from the benthic community.

3.3 Methods

3.3.1 Study area and sampling

I investigate patterns of coral reef food webs at the uninhabited and protected Rowley Shoals atoll reefs off the North-West coast of Australia (Figure 3.2). All three reefs are comparable in shape, size, and subject to very similar oceanographic conditions (see Table 2A.1 in Chapter 2). These reefs are spaced approximately 30-50km apart and are subject to long-term monitoring of fish and benthic communities since 1994. They are all protected reefs, meaning that they are free from artisanal fishing pressure from Indonesia, which impacts other reefs located to the north (Field *et al.* 2009). As remote reefs (approximately at 300km from coastal reefs), they are limited in terms of receiving large quantities of larval exchange from other reefs and this assertion has been confirmed through genetic evidence from other remote reefs within the region (Underwood *et al.* 2012). Further, movement studies of grey reef sharks (*Charcarhinus amblyrhynchos*) conducted at the Rowley Shoals and other remote reefs indicate that movement may be quite limited for reef sharks (i.e. they exhibit a high degree of site fidelity; Field *et al.* 2011; Barnett *et al.* 2012).

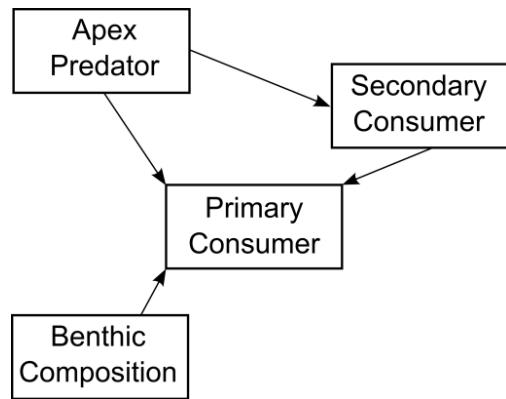


Figure 3.1. A conceptual model for testing the strength and significance of top-down and bottom-up structuring agents in coral reef ecosystems.

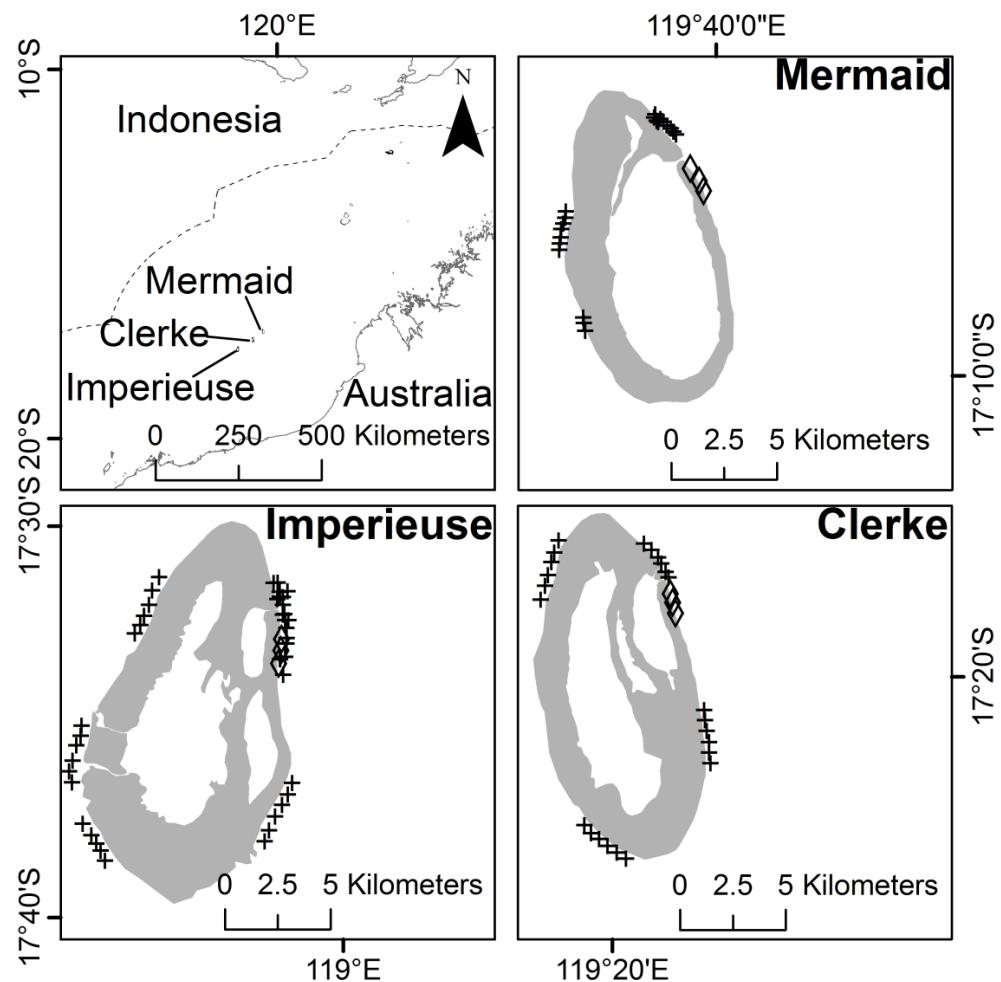


Figure 3.2. The protected Rowley Shoals which includes Mermaid, Clerke and Imperieuse reefs. Shown are the locations of long-term monitoring sites (diamonds) and baited remote underwater video stations (crosses). The dashed line represents the Australian economic exclusive zone.

A major category 5 cyclonic event in 1996 impacted all reefs at the Rowley shoals, however, due to proximity the impact was more severe for Imperieuse, followed by Clerke and Mermaid reefs (see Figure 2.2 in Chapter 2). Coral cover was dramatically reduced from well over 50% before the cyclonic event to less than 10% at some sites. As coral cover was reduced, dramatic changes in benthic cover on reefs were observed such that benthic communities became dominated by algae. Yet within a decade (1996 to 2007) coral cover recovered to pre-disturbance levels.

Shark abundances were sampled using Baited Remote Underwater Video Stations (BRUVS; Cappo *et al.* 2007). BRUVS consist of a camera in an underwater housing with a bait bag to attract carnivorous species. Sampling at Mermaid ($n = 28$) was conducted in June 2003, whereas Clerke ($n = 24$) and Imperieuse ($n = 42$) reefs were sampled in October 2004 (where n represents the number of drops; Fig 3.2). Deployments were during daylight hours, generally spaced by 500m with depths ranging from 10-60m on the reef slope (majority were conducted at 50m in depth). The maximum number of a given species of shark per tape (MaxN) was used as a measure of abundance and it is standardized at MaxN per hour of video. Counts show that there is variability in shark density throughout the reefs, which represents a natural gradient of shark density on the Rowley Shoals (Figure 3.3). As shark species all have very low rates of population turnover, I only use population estimates from the years 2003 and 2004 to estimate differences in density across the reefs for the period of 1995-2008 (Robbins *et al.* 2006; Ward-Paige *et al.* 2010b). These higher abundances of sharks appear to be maintained at the Rowley Shoals up until as recently as 2010-2011 (Heyward *et al.* 2011a).

Fish counts and benthic cover data are the subject to a long-term monitoring program conducted by the Australian Institute of Marine Science (AIMS), which is generally conducted in October. Here I use data collected from 1995-2008, of non-cryptic, adults (1+ year olds), where fish have been identified to species (Halford & Thompson 1996). Surveys were conducted with three sites on each reef located on the Northeast slope to reduce between-reef habitat biases (Figure 3.2). At each site, 5 permanent transects (spaced 10m apart) that are 50m in length are conducted at 6-9m in depth. Within 2.5m of the belt transect larger and more mobile species (e.g. *Lutjanidae*) are counted and site-attached species (e.g. *Pomacentridae*) are counted within 0.5m of the belt transect on a return swim. Alongside the fish counts, benthic cover data was collected

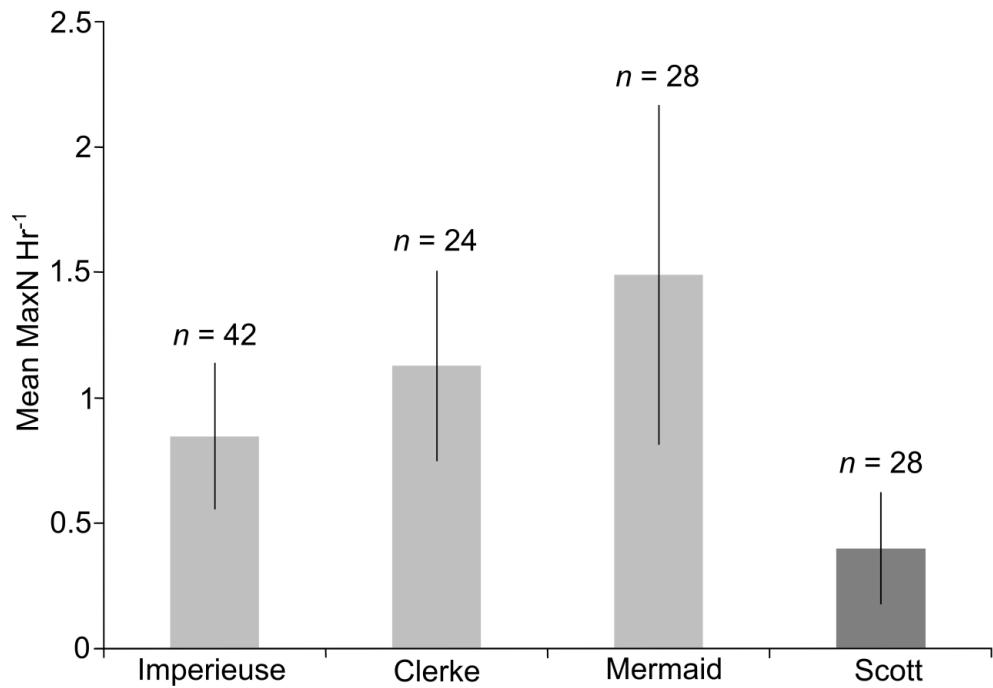


Figure 3.3. Abundance of sharks assessed by baited remote underwater video stations on outer slope sites. Abundances shown are the maximum number observed on screen during the sample period (MaxN) and standardized to per hour. The abundance for the protected Rowley Shoals (light grey) and the nearest (300km) fished reef (Scott reef; dark grey) is shown. Error bars represent 95% confidence intervals.

using photographic or video frame analysis (Jonker *et al.* 2008). The benthic cover data used in this chapter was grouped into two categories: coral (soft and hard) and algal (turf, macro, crustose coralline and sponges) cover. This reduced potential biases that may result from different benthic covers overlapping (e.g. macro algae on top of crustose coralline algae).

For the analysis, each fish species ($n = 95$) was classified into one of five trophic groups (carnivore, herbivore, corallivore, planktivore and detritivore) based on literature reviews (see Table 3A.1 and Appendix). Carnivores ($n = 24$; *Chaetodontidae*, *Epinephelidae*, *Lutjanidae*, *Lethrinidae*, *Labridae*, and *Zanclidae*) and herbivores ($n = 35$; *Acanthuridae*, *Pomacentridae*, *Scaridae*, and *Siganidae*) are the most species rich groups. Whereas, corallivores ($n = 16$; *Chaetodontidae* and *Pomacentridae*), planktivores ($n = 17$; *Acanthuridae*, *Lutjanidae* and *Pomacentridae*) and detritivores ($n = 3$; *Acanthuridae*) are dominated by a single family of fish and have fewer species in their groups.

3.3.2 Temporal variability of trophic structure

I first investigate interannual variability in benthic cover and each fish trophic group (carnivore, herbivore, corallivore, planktivore and detritivore) at the Rowley Shoals over a 13-year period, to determine how variability in benthic composition (bottom-up forcing) can influence community trophic structure. Using these broad groupings represents a trade-off between increasing uncertainty in models by increasing the number of parameters and biological realism. While size-based groupings would be ideal for food-web relationships, this information was not collected alongside counts and could not be incorporated. Here I test three possible mechanisms: (1) benthic composition is a direct competition for space between coral and algae, (2) alterations in coral cover directly impact herbivore, corallivore, planktivore and detritivore densities by altering resources, habitat and rugosity, and (3) changes to benthic cover do not impact densities of generalist carnivores (or mesopredators). I also investigate how variability in carnivores, may influence densities of potential prey in a top-down manner (primary consumers: herbivores, corallivores, planktivores and detritivores). Specifically, I test whether interannual variability in density of these mid-sized carnivores is related to annual variability in densities of species in lower trophic levels.

Standard deviations of yearly percent cover and densities of trophic groups over the 13-year period for each fixed transect ($n = 15$ at 3 reefs for $n = 45$) were used to investigate interannual variability. I used standard deviations to estimate temporal variability in absolute abundances, rather than using variance relative to the mean, which reflects that mechanisms are a result of changes in absolute rather than relative abundances (Arkema *et al.* 2009). Regression analysis was then used to determine whether temporal variability in coral cover (or benthic composition) can predict variation in algal cover and the densities of each trophic group. This procedure was repeated to test whether temporal variability in carnivore density (or mesopredators) can predict variation in the densities of other fish trophic groups. I compared the adjusted R^2 and significance of the relationship to evaluate whether there was any evidence for the mechanisms outlined. Significance was corrected for multiple tests using Bonferroni corrections in R software for statistical computing (Legendre 2007). I conducted this analysis to provide insight into what extent interannual variation in top-down and bottom-up structuring agents among transects and reefs contributes to resulting patterns of trophic structure.

3.3.3 *Direct and indirect interactions*

To determine the influence of top-down and bottom-up structuring agents on the trophic structure of fish communities I use a simplified food web framework (Figure 3.1). I assessed the relationship between apex predators, secondary consumers (carnivores), primary consumers (herbivores, corallivores, detritivores and planktivores) and benthic community composition (coral cover) using SEMs. Here I used long-term monitoring data ($n = 250$) over the period of 1995-2008 to investigate the strength and significance of interactions. Because fish data are collected over a long-term period, I incorporated time (or year of sample) into all of the SEMs to evaluate whether densities in trophic groups may result from temporal trends. From here I determined the relative roles and contribution of top-down and bottom-up structuring agents on reef fish food webs that are subject to a natural gradient in shark density and benthic disturbance.

The influence of top-down and bottom-up structuring agents on the composition primary consumer fishes is first evaluated. This is completed using Redundancy Analysis (RDA) on the densities of primary consumer species (herbivore, corallivore, planktivore, and detritivore) where the component scores for the two main axes of variation are used as response variables in the SEM model (see Appendix for more details; Figure 3A.1). I then investigate patterns of density

for each trophic group (herbivore, corallivore, detritivore and planktivore). However, I consider that potential patterns may arise from differences in variation related to disturbance regimes in the food web models. To control for this I re-run the six aforementioned models using the residuals from a linear regression where fish community composition and density of trophic groups are predicted by algal cover (which competes with coral and increases after cyclone events).

Parameter estimation and model fit are conducted in R software for statistical computing using the *lavaan* package (Rosseel 2012). Densities were log-transformed and benthic cover was arcsine transformed to adhere to SEM model assumptions. Path coefficients and whether coefficients were significantly different from zero were determined using maximum likelihood (see Appendix for more details). I standardized path coefficients to compare the magnitudes of interactions as there are several different units of measure in the same model (e.g. percent cover and density). Despite the reasonable sample size of transects ($n = 250$), model fit measures were bootstrapped ($n = 1000$) to attain 95% confidence intervals when assessing overall model fit (see Appendix). Finally, I assess the variation explained for mesopredators and primary consumers using the formula, $R^2 = 1 - V_e/V_o$, where V_e is the estimated variance and V_o is the observed variance (Arkema *et al.* 2009).

3.4 Results

3.4.1 Temporal variability of trophic structure

Yearly variability between algal and coral cover exhibits the strongest relationship, where variability in algal cover has 82% of variation explained by coral cover (Figure 3.4). I also demonstrate that annual variability in coral cover differs among transects by more than 5-fold (Figure 3.4). This pattern reveals that Mermaid and Clerke reefs have more similar annual variability in algae and coral cover; however, Imperieuse reef has by far the most variability. In general, these results suggest strong competition between cover types and that variability in benthic cover is dependent on site location.

Variability in coral cover is also a significant predictor of the annual variability of density in three trophic groups (Figure 3.4). Variability in corallivore density, a group that consumes

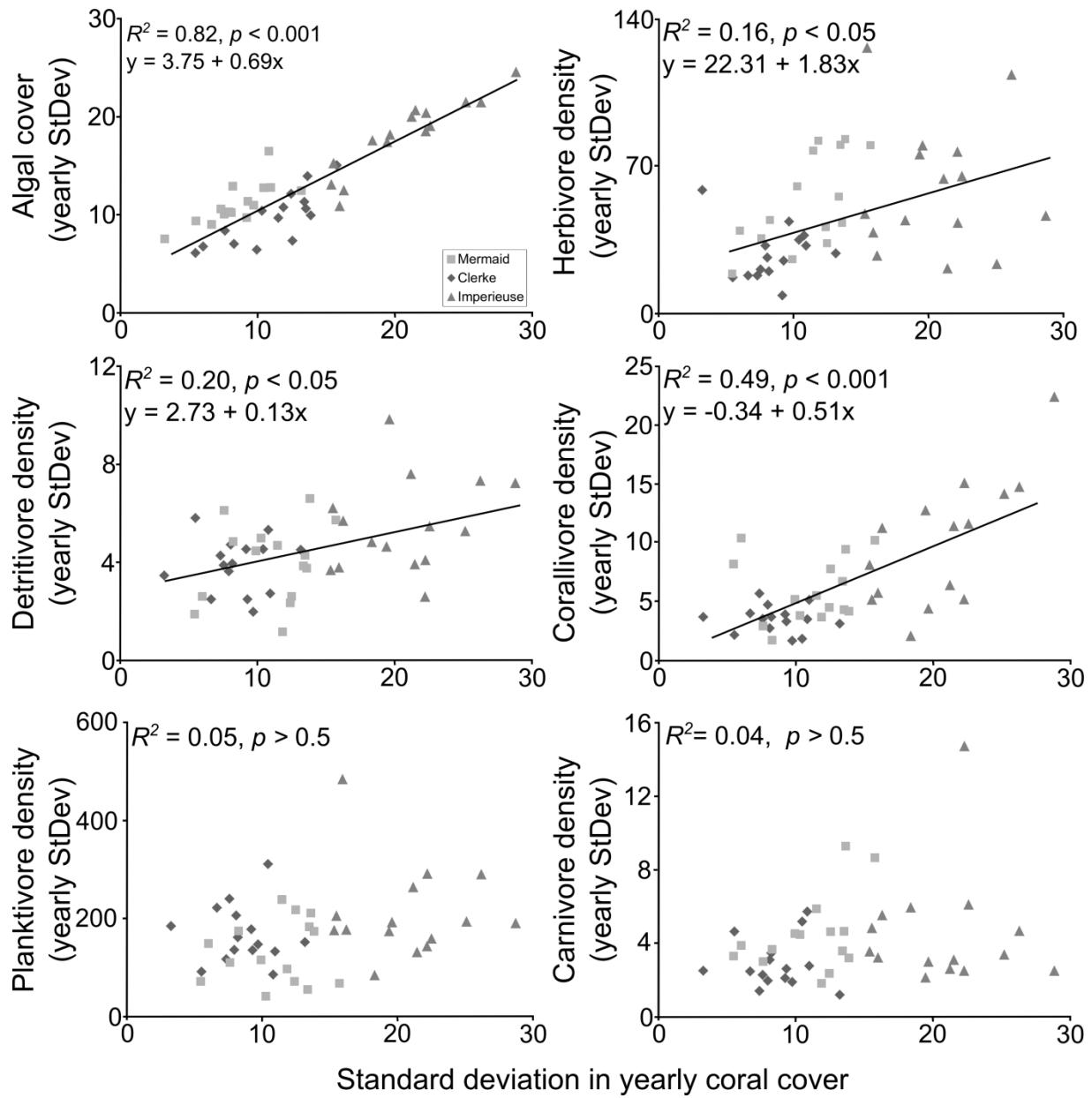


Figure 3.4. Interannual variation as measured by the standard deviation (StDev) in density at transects ($n = 45$) over the period of 1995-2008. Linear regression is used to predict algal cover and densities of five trophic groups by considering interannual variation in coral cover. Shown is the adjusted R^2 value and significance.

coral, shows the strongest relationship with 49% of variation explained by variability in coral cover (Figure 3.4). Annual variability in herbivore and detritivore density is also significantly associated with variability in coral cover (16% and 20% respectively; Figure 3.4). Other groups, planktivores and carnivores, have variability in density that is not significantly explained by variability in coral cover (Figure 3.4). This indicates that differences in annual variability of coral cover between reefs contribute to spatial patterns in density for corallivores, herbivores and detritivores. Finally, looking at variation in carnivore density I determine there are no significant associations (Figure 3A.1). This result indicates that bottom-up processes related to coral cover are more influential in structuring reef fish communities than top-down structuring via changes in carnivore density.

3.4.2 Direct and indirect interactions

To determine the strength and significance of structuring agents on fish communities I constructed SEMs and used site scores from a RDA biplot (Figure 3A.2). Constrained ordination is preferred as I am interested in composition patterns relative to trophic structural changes. The RDA is constructed using the densities of primary consumer species which are explained by trophic group classification (Table 3A.1 and see Appendix). The RDA explains 26.2% in species variation with a majority of variation attributable to the first axis of variation (15.4%; Figure 3A.2). For the SEMs, all had a reasonable variation explained (with the exception of planktivore models; Table 3.1). Further, all models had chi-square values where the covariance structure specified in the models was not significantly different from the covariance structure observed in the data (Table 3.1). Finally, all models displayed a good overall fit when considering multiple measures with bootstrapped confidence intervals ($n = 1000$; Table 3A.2 and see Appendix).

Shark density has a negative, direct and significant correlation with the density of carnivores across the Rowley Shoals (Figure 3.5 and Table 3A.3). However, this only represents 3.4% of variation explained for the density of carnivores. Thus, while increases in shark density appear to be significantly associated with reduced carnivore numbers, other factors are likely important to variation in carnivore density. I also found that sharks directly associated with the composition of the primary consumer community (Figure 3.5). In contrast, carnivores are not directly associated with alterations in the composition of the primary consumer community

Table 3.1. Variation explained by structural equation models for community composition (RDA1 and RDA2) and the densities of trophic groups (herbivore, corallivore, detritivore and planktivore) as the responses (endogenous variable) in the models. Also shown is the sample size (n), chi-square value (χ^2), degrees of freedom (df) and p -value.

Model	n	Chi-square	df	p -value	Non-Control Model Variation explained (R^2)	Control Model Variation explained (R^2)
RDA1	250	0.911	1	> 0.3	0.696	0.437
RDA2	250	0.911	1	> 0.3	0.530	0.493
Herbivore	250	0.911	1	> 0.3	0.442	0.144
Corallivore	250	0.911	1	> 0.3	0.243	0.182
Detritivore	250	0.911	1	> 0.3	0.162	0.125
Planktivore	250	0.911	1	> 0.3	0.117	0.032

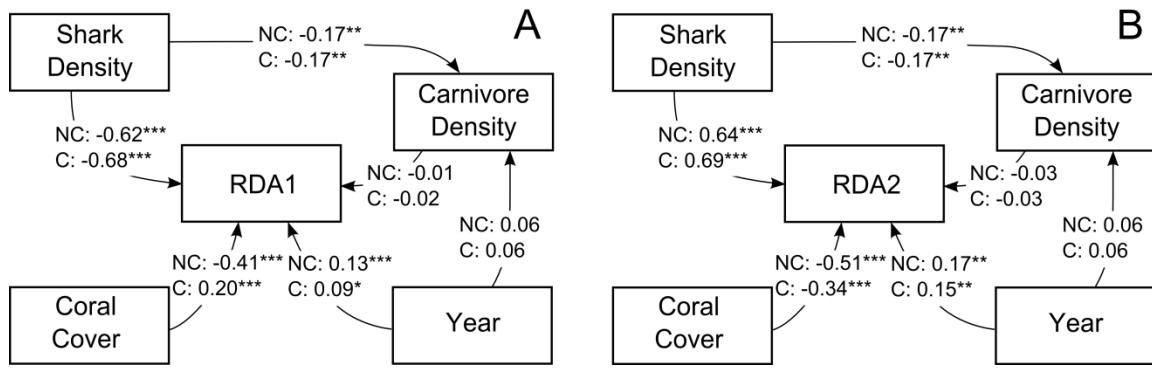


Figure 3.5. Structural equation models for primary consumer composition on (A) the first axis of variation (RDA1) and (B) second axis of variation (RDA2). The values are the magnitude of interaction, which are shown for models using the densities (NC) and models that control for differences in environmental variation (C). The level of significance for each magnitude has been denoted * $p<0.05$, ** $p<0.01$, and *** $p <0.001$.

(Figure 3.5). Hence, sharks do not appear to be indirectly associated with the composition of fish communities. I also found that time (or year) is a significant factor to the primary consumer community and specifically three trophic groups (herbivores, corallivores and detritivores; Figures 3.5 and 3.6). This indicates the existence of significant temporal trends in the abundance of these trophic groups that are likely related to the impact and recovery of the benthic community. Finally, I found that coral cover is a significantly associated with the composition patterns in the primary consumer community (Figure 3.5). Overall, a fair amount of variation in the composition of the primary consumers was explained by top-down and bottom-up structuring agents for both RDA axes of variation (70% and 53% for RDA1 and RDA2 respectively; Table 3.1). When the fish community composition is controlled by the amount of algal cover found at reefs, I observe that sharks are still a strong structuring agent, but the magnitude of impact for coral cover is reduced dramatically (44% and 49% for RDA1 and RDA2, respectively; Fig 3.5). Hence, despite a difference in benthic cover among transects, top-down processes related to shark densities are associated with different compositions of fish communities.

Variation explained by SEMs with the densities of herbivores and corallivores are some of the highest out of all of the models (44% and 24%, respectively). For both trophic groups increased shark density is significantly, negatively associated with their densities, while carnivore density is positively and significantly related to only the density of corallivores (Figure 3.6 and Table 3A.3). Further, herbivores are negatively and significantly impacted by coral cover, while corallivores are positively and significantly influenced by coral cover (Figure 3.6). When the density of herbivores is controlled by variation in algal cover, only the relationship with shark density is significant with a reasonable amount of variation explained (14%; Figure 3.6A). On the other hand, when corallivore density is controlled by variation in algal cover, all relationships are maintained and there is also a reasonable amount of variation explained by the SEM (18%; Figure 3.6B). Hence, both herbivore and corallivore densities appear to be negatively associated with shark density, while corallivores are strongly associated with differences in coral cover despite controlling for differences benthic cover.

Finally, I considered whether densities of detritivores and planktivores are associated with differences in shark density. Detritivore and planktivore SEMs had the lowest variation explained, especially when variation is controlled by algal cover (Table 3.1). Further, when

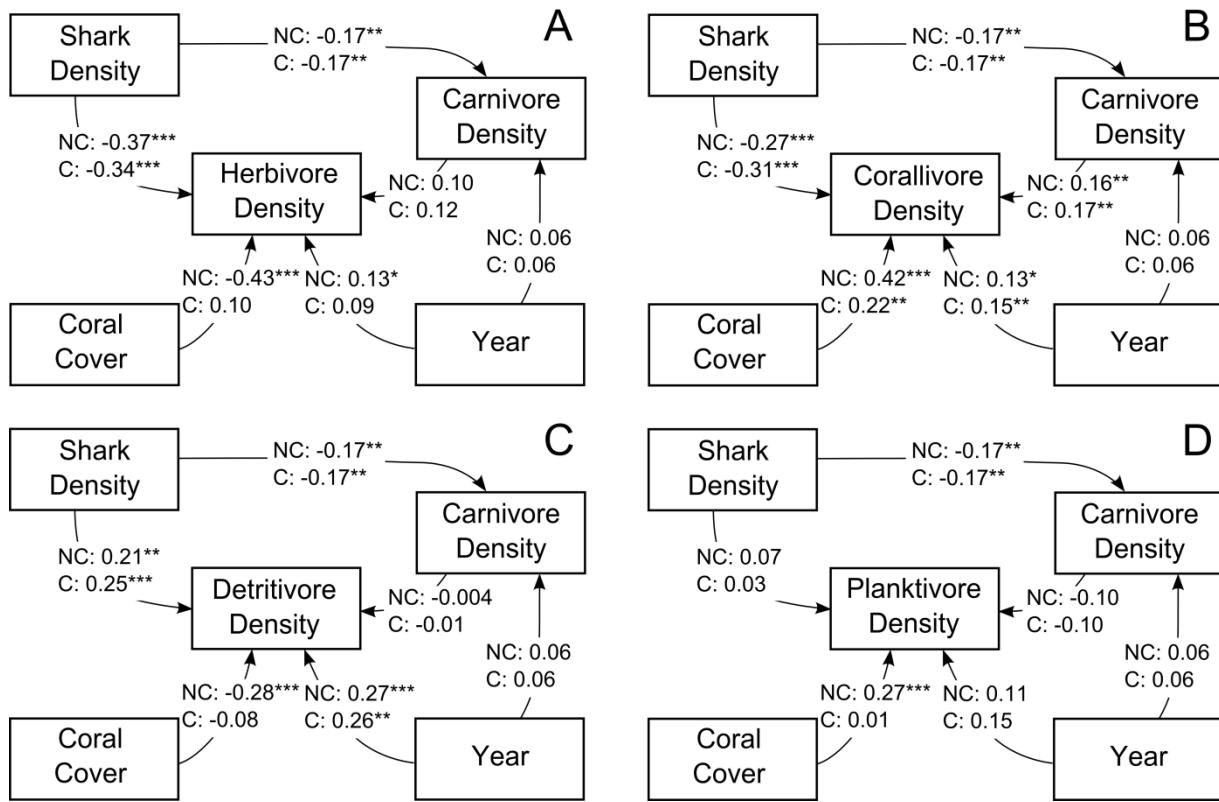


Figure 3.6. Structural equation models for primary consumers, (A) herbivores, (B) corallivores, (C) detritivores, and (D) planktivores. The values are the magnitude of interaction, which are shown for models using the densities (NC) and models that control for differences in environmental variation (C). The level of significance for each magnitude has been denoted * $p<0.05$, ** $p<0.01$, and *** $p < 0.001$.

examining interactions, only detritivore density appears to be associated significantly with shark density (Figure 3.6C and Table 3A.3). This positive association appears to maintain significance despite controlling for variation in algal cover (Figure 3.6C). Coral cover is also a strong structuring agent for both trophic groups when not controlling for differences in algal cover (Figures 3.6C and 3.6D). Thus, increases in the density of sharks may benefit detritivores, but other factors likely contribute to patterns of detritivore density due to the smaller amount of variation explained (Table 3.1). On the other hand, planktivores only appear to be correlated with processes that structure fish in a bottom-up manner.

3.5 Discussion

Sharks are top-predators and benthic cover provides resources and habitat for fish species (Cortes 1999; Jones *et al.* 2004). As a result, both are thought to be important structuring agents in coral reef food webs, however, understanding the relative roles of these structuring agents is difficult, because many studies utilize gradients of human density that are confounded by numerous variables (Friedlander & DeMartini 2002; Sandin *et al.* 2008; Wilson *et al.* 2010a). I provide evidence that annual variability in benthic cover can contribute significantly to spatial patterns of food web structure in a bottom-up manner. Hence the requirement in this chapter to control for patterns related to differences in benthic cover to better isolate apex predator impacts. I use uninhabited and protected reefs to demonstrate that shark density has a direct and strong magnitude of impact on the composition of fish communities even when variation related to benthic composition is controlled (Figure 3.5). Many studies across different ecosystems have shown that predators tend to exert strong top-down structuring throughout food webs, yet there is less evidence to support that bottom-up effects can have a similar impact throughout the food web (Borer *et al.* 2006). I demonstrate that in coral reefs, sharks occupy the role of top-down structuring agent (or top-predator), whereby the density of mesopredators (carnivores) and primary consumers (herbivores, corallivores and detritivores) are altered by shark density. Finally, I find that bottom-up structuring resulting from disturbance events causes dramatic changes only in primary consumer groups. In contrast to top-down structuring by sharks, bottom-up effects do not impact mesopredator density, suggesting that bottom-up effects have a limited impact further up the food web.

3.5.1 *Temporal variability*

Importantly, I demonstrate that differences in trophic patterns through space can result from differences in temporal variability related to benthic cover (here expressed as variability in algal cover predicted by variability in coral cover; Figure 3.4). Imperieuse reef has the highest variability due to a more severe impact from the 1996 cyclone event on the Rowley Shoals (Chapter 2). On the other hand, both Clerke and Mermaid reefs had similar variability in coral cover, yet Mermaid had more variability in algal cover than Clerke. These benthic patterns between variability in algae and coral cover are summarized nicely as a strong competitive relationship between them both. I find that differences in the variability of coral cover are linked to variability in densities of coral feeders and algal/detrital feeders. This reflects strong relationships with benthic cover as a resource and habitat for these groups (Hughes *et al.* 2003; Jones *et al.* 2004; Wilson *et al.* 2007). It also demonstrates that differences in the density of trophic groups across the reefs in space may result from differences in variability of benthic cover over a long-term period (1995-2008). Interestingly, I find that variability in the density of planktivores and carnivores is not related to variability in coral cover. This is despite the fact that coral is a critical habitat for many species in these groups and that coral cover has been linked with increased biomass of fish, which would equate to increased resources for carnivores (Wilson *et al.* 2008; McClanahan *et al.* 2011). Regardless, variability in benthic cover appears to be a strong structuring agent for most primary consumers and contributes to spatial heterogeneity in the trophic structure of coral reef food webs.

3.5.2 *Direct and indirect interactions*

Using SEMs I determine the strength and significance interactions involving sharks and benthic cover on the trophic structure of reef fish communities. I provide evidence that carnivore density is significantly and negatively associated with shark density (Figures 3.5 and 3.6). This result indicates that carnivores are structured in a top-down manner and provides evidence for the potential of mesopredator release in these systems (Prugh *et al.* 2009; Brashares *et al.* 2010). Yet, under the conditions I observe these communities there is rather weak evidence for this mechanism, because there is a low magnitude of interaction between sharks and carnivores, along with low variation explained in carnivore density. Carnivores also have a non-significant association with the composition of the primary consumer community (with the exception of a

weak positive interaction with corallivores), indicating the absence of a trophic cascade. This result confirms that carnivores appear to play a minimal role in this food web and that their abundances appear to be largely controlled in a top-down manner.

On the other hand, using SEMs I find strong evidence that higher densities of sharks are decreasing the densities of herbivores and corallivores despite controlling for differences related to benthic cover (Figure 3.6). These trophic groups are also significantly associated with processes that structure fish in a bottom-up manner suggesting that their densities are a function of the combined effects of top-down and bottom-up structuring agents. This result is important, because herbivores are central to the recovery of reefs from disturbances by aiding coral settlement (Bellwood *et al.* 2004). Further, this suggests that sharks may play an important role in altering survival probability of herbivores and corallivores, which can have dramatic effects on variability in their abundances (Hsieh *et al.* 2006; Minto *et al.* 2008). Thus, reefs with higher densities of sharks appear to have higher resilience to increased environmental stochasticity resulting from disturbances (Mellin *et al.* 2010b). In contrast to this pattern, I find that sharks may have a weak positive effect on detritivore density (Figure 3.6). Yet the poor variance explained by the SEMs for detritivores suggests that other factors not considered in this chapter are important to the densities of this trophic group.

I also find a strong significant temporal trend in the density of detritivores, but the magnitude is rather weak for the densities of herbivores and corallivores (Figure 3.6). This trend persists for corallivores and detritivores despite controlling for algal cover differences. However, in the case of corallivores this pattern is likely related to the impact and gradual recovery of coral over the study period (Chapter 2). For detritivores, there is the possibility that this trend may be related to differences in larval recruitment through time, which has been documented for species of this group (i.e. *Ctenochaetus*) on remote atolls (Doherty 2002). However, larval recruitment differences would arise through self-recruitment events at the Rowley Shoals rather than from external sources due to the extreme distances to nearby reefs (Underwood *et al.* 2012; Figure 3.2). Thus, temporal trends that arise from differences in recruitment, related to spawning and settlement, occur under the conditions observed at the study reefs and may be most important to trends in the density of detritivores. Another aspect to consider is that detritivores may compete with other trophic groups. In scenarios where herbivores may be less abundant, this may lead to

increases in algal cover that can trap detritus (Johnson *et al.* 1995; Chapter 2). As a result detritivores may benefit from increased resources leading to the observed patterns. Ultimately the mechanism responsible for this pattern is not clear and needs to be investigated in further studies.

3.5.3 Limitations and conclusions

Up until recently the ecological role of sharks in coral reef food webs has remained rather unclear (Heithaus *et al.* 2010). Attempts to quantify their role has come through the creation of ecosystem models, but results from these studies provide conflicting results where the role of sharks is assessed as minimal or important (Stevens *et al.* 2000; Okey *et al.* 2004; Bascompte *et al.* 2005). I am able to provide evidence via an empirical approach and a unique set of circumstances that sharks may play an important role in reef fish food webs. This is achieved through a trade-off, where I elected to forego the complexity of a complete food web species model ($n = 95$) in favour of a more parsimonious trophic model with 6 trophic groups to address the objectives. This approach overlooks potential competition between some trophic groups (primary consumers) and species compositional changes within trophic groups that can be important to food web dynamics (Borer & Gruner 2009). To some extent I do investigate compositional changes at the species level by using RDA scores in the SEMs, but these patterns are not interrogated in any detail (Figure 3.5). Further, I cannot account for differences in trophic structure that may arise due to the structural complexity found at the sites (Jones *et al.* 2004; Nemeth & Appeldoorn 2009; Pittman *et al.* 2009). However, coral cover and structural complexity can be related on coral reefs when coral cover is extensive (Wilson *et al.* 2007), such as the Rowley Shoals. Ultimately, these are mechanisms that need to be investigated in further studies.

I demonstrate the importance of considering temporal variability in trophic structure of reef fishes when working with fine spatial scales. Differences in temporal variability can contribute to resulting spatial patterns of trophic structure in reef fishes. Controlling for differences in this variability, I find that the trophic structure of reef fish communities is a function of the combined direct effects of top-down and bottom-up structuring agents. Specifically, sharks are directly associated with the composition of reef fish communities, such that fishes throughout the food web appear to be impacted. Whereas, changes to the benthic

community that directly structure primary consumer reef fishes in a bottom-up manner appear to only be important to primary consumers while having little impact on species further up the food web. Sharks also appear to be important regulators of the abundance of herbivores and corallivores, by reducing variability in their abundances in response to environmental stochasticity. Independent of anthropogenic impacts, I provide evidence that sharks are a pivotal apex predator on coral reefs that promote resilience through the top-down control of species composition and the densities of key trophic groups.

3.6 Appendix

3.6.1 Species composition and trophic groups

I classify species into five trophic groups that includes: carnivore, herbivore, detritivore, planktivore and corallivore (Table 3A.1). Corallivores included species that are either obligate or facultative coral feeders (Hughes *et al.* 2003; Wilson *et al.* 2006). Herbivorous species were classified utilizing specifications by Green & Bellwood (2009), while detritivores (including epilithic algal matrix feeders) followed Wilson *et al.* (2007), and planktivores and carnivores followed Froese & Pauly (2011).

Redundancy Analysis (RDA) is used to determine how interactions between top-down and bottom-up structuring agents may be related to changes in species composition of primary consumers. I excluded carnivores, as I am interested in their impact (alongside the impact of sharks) on species composition. Further, I find little evidence that carnivores play a major role within the food webs examined in this chapter, meaning that their exclusion here is warranted (Figure 3A.1). Prior to analysis, I removed rare species (present in <5% of sites) and species abundances ($n = 49$) were Hellinger transformed (Jackson & Harvey 1989; Legendre & Gallagher 2001). I also use permutation tests ($n = 9999$) to determine the significance of the RDA model, the model axes and constraints. This was conducted in R software for statistical computing using the *vegan* package (Oksanen & Roberts 2010).

The overall RDA was found to be significant ($F_{4,245} = 21.74, p = 0.005$) where 26.2% of species variation is explained (Figure 3A.2). All four axes of variation were significant (RDA1: $F_{1,245} = 51.26, p = 0.005$; RDA2: $F_{1,245} = 21.87, p = 0.005$; RDA3: $F_{1,245} = 11.67, p = 0.005$; RDA4: $F_{1,245} = 2.14, p = 0.033$) and all four constraints were significant in the model (Herbivore: $F_{1,245} = 48.22, p = 0.01$; Corallivore: $F_{1,245} = 20.29, p = 0.01$; Planktivore: $F_{1,245} = 14.14, p = 0.01$; Detritivore: $F_{1,245} = 4.29, p = 0.01$). The three reefs appear to have different species compositions that can be attributable to differences in trophic structure (Figure 3A.2). In particular, differences in the density of corallivores and herbivores appear to be contributing the most to the observed patterns of species composition.

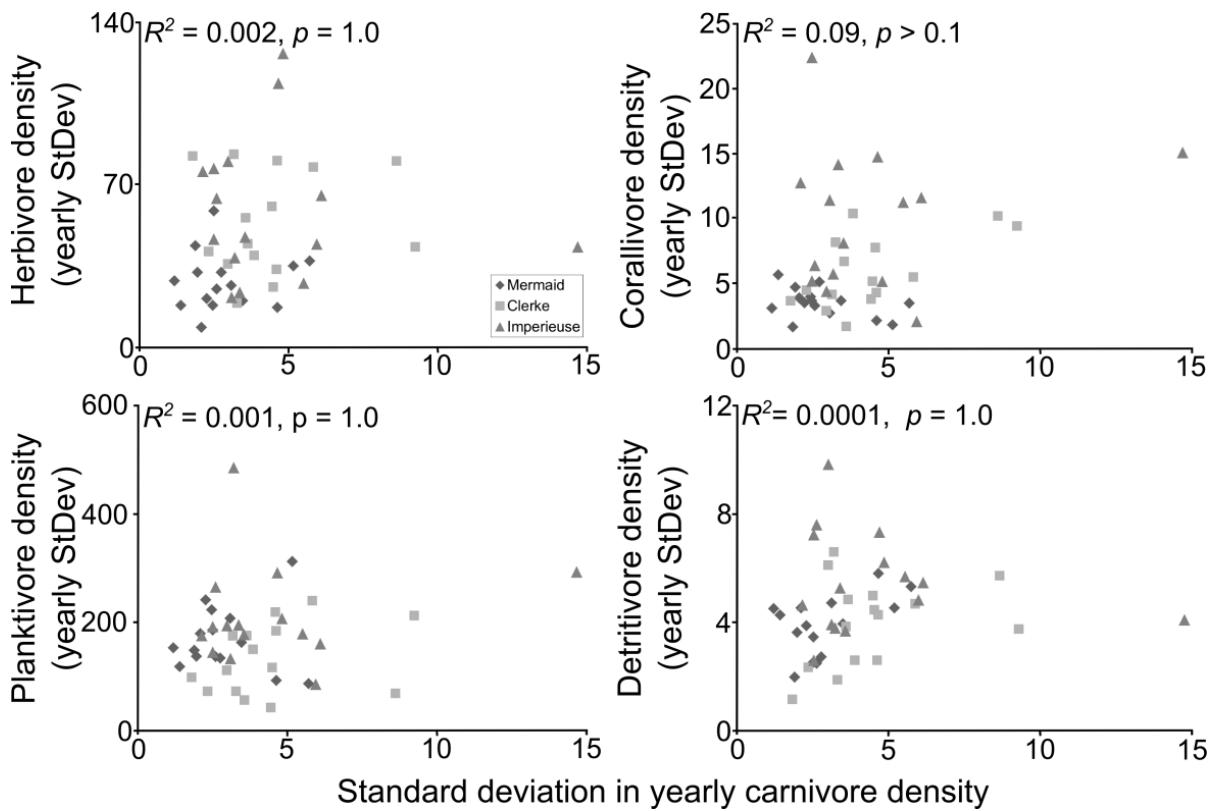


Figure 3A.1. Interannual variation as measured by the standard deviation (StDev) in trophic group density at transects ($n = 45$) over the period of 1995-2008. Here I use linear regression to predict interannual variation in the densities of four trophic groups by considering interannual variation in carnivore density.

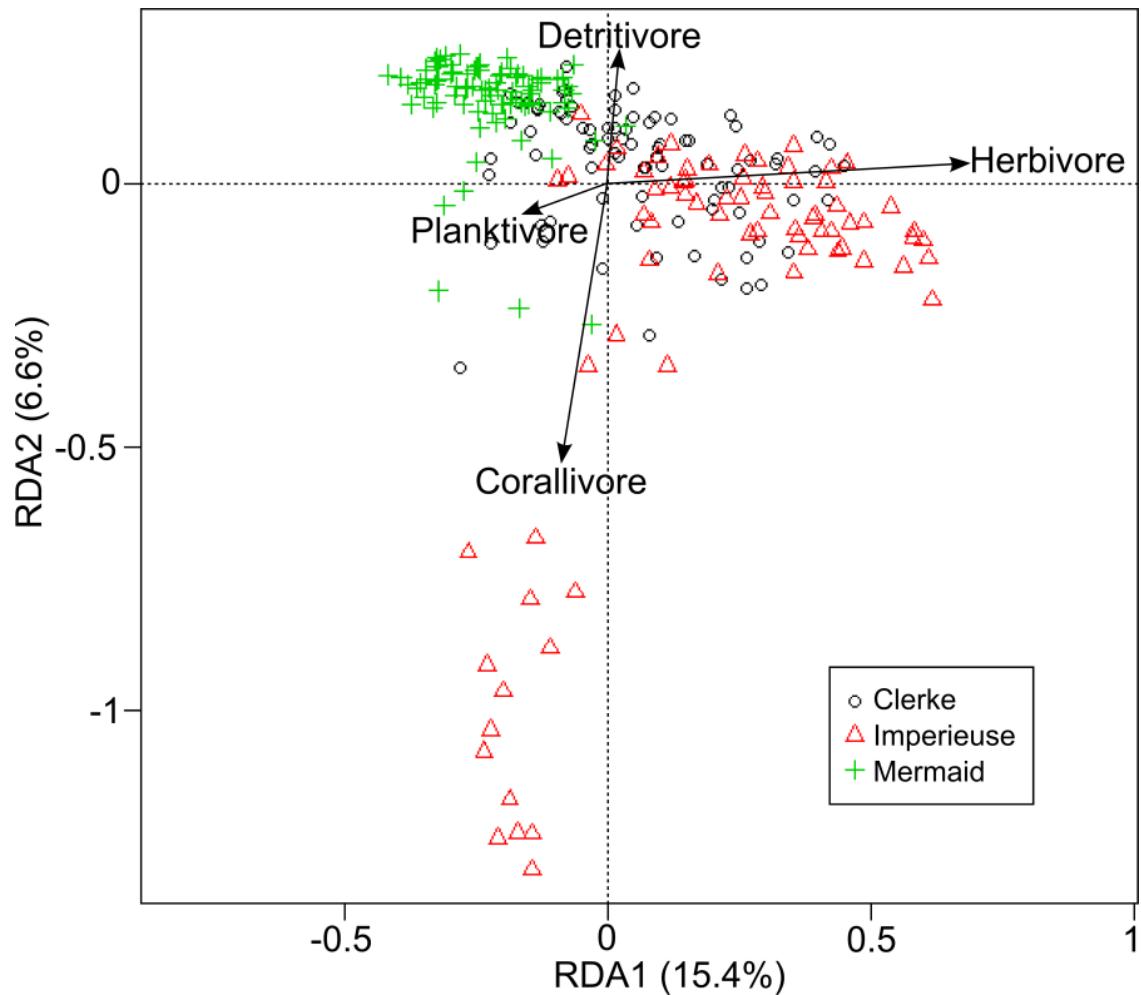


Figure 3A.2. Redundancy analysis of primary consumer species composition ($n=49$) on outer slope transects. Transects are classified by reef and the variation explained by each axis in the biplot is denoted.

Table 3A.1. Species classification into five trophic groups (carnivore, herbivore, detritivore, planktivore and corallivore). Species are listed alphabetically by family and species.

Family	Species	Trophic Group
Acanthuridae	<i>Acanthurus dussumieri</i>	Detritivore
	<i>Acanthurus lineatus</i>	Herbivore
	<i>Acanthurus nigricans</i>	Herbivore
	<i>Acanthurus nigrofasciatus</i>	Herbivore
	<i>Acanthurus olivaceus</i>	Detritivore
	<i>Acanthurus pyroferus</i>	Herbivore
	<i>Acanthurus thompsoni</i>	Planktivore
	<i>Ctenochaetus spp</i>	Detritivore
	<i>Naso brevirostris</i>	Planktivore
	<i>Naso lituratus</i>	Herbivore
Chaetodontidae	<i>Naso unicornis</i>	Herbivore
	<i>Naso vlamingii</i>	Planktivore
	<i>Zebrasoma scopas</i>	Herbivore
	<i>Zebrasoma veliferum</i>	Herbivore
	<i>Chaetodon adiergastos</i>	Corallivore
	<i>Chaetodon auriga</i>	Corallivore
	<i>Chaetodon bennetti</i>	Corallivore
	<i>Chaetodon ephippium</i>	Corallivore
	<i>Chaetodon lineolatus</i>	Corallivore
	<i>Chaetodon lunula</i>	Corallivore

	<i>Chaetodon semeion</i>	Corallivore
	<i>Chaetodon speculum</i>	Corallivore
	<i>Chaetodon trifascialis</i>	Corallivore
	<i>Chaetodon trifasciatus</i>	Corallivore
	<i>Chaetodon ulietensis</i>	Corallivore
	<i>Chaetodon unimaculatus</i>	Corallivore
	<i>Forcipiger flavissimus</i>	Carnivore
<i>Epinephelidae</i>	<i>Plectropomus areolatus</i>	Carnivore
	<i>Plectropomus laevis</i>	Carnivore
	<i>Variola louti</i>	Carnivore
<i>Labridae</i>	<i>Cheilinus chlorourus</i>	Carnivore
	<i>Cheilinus fasciatus</i>	Carnivore
	<i>Cheilinus undulatus</i>	Carnivore
	<i>Coris aygula</i>	Carnivore
	<i>Coris gaimard</i>	Carnivore
	<i>Epibulus insidiator</i>	Carnivore
	<i>Gomphosus varius</i>	Carnivore
	<i>Halichoeres hortulanus</i>	Carnivore
	<i>Hemigymnus fasciatus</i>	Carnivore
<i>Lethrinidae</i>	<i>Hemigymnus melapterus</i>	Carnivore
	<i>Oxycheilinus digrammus</i>	Carnivore
	<i>Oxycheilinus unifasciatus</i>	Carnivore
	<i>Gnathodentex aureolineatus</i>	Carnivore
	<i>Lethrinus erythropterus</i>	Carnivore
	<i>Monotaxis grandoculis</i>	Carnivore
	<i>Lutjanus bohar</i>	Carnivore
	<i>Lutjanus decussatus</i>	Carnivore

	<i>Lutjanus gibbus</i>	Carnivore
	<i>Lutjanus kasmira</i>	Carnivore
	<i>Macolor spp.</i>	Planktivore
<i>Pomacentridae</i>	<i>Amblyglyphidodon aureus</i>	Planktivore
	<i>Amphiprion akindynos</i>	Herbivore
	<i>Amphiprion clarkii</i>	Herbivore
	<i>Chromis amboinensis</i>	Planktivore
	<i>Chromis atripectoralis</i>	Planktivore
	<i>Chromis lepidolepis</i>	Planktivore
	<i>Chromis lineata</i>	Planktivore
	<i>Chromis margaritifer</i>	Planktivore
	<i>Chromis ternatensis</i>	Planktivore
	<i>Chromis weberi</i>	Planktivore
	<i>Chromis xanthura</i>	Planktivore
	<i>Dascyllus reticulatus</i>	Planktivore
	<i>Dascyllus trimaculatus</i>	Planktivore
	<i>Plectroglyphidodon dickii</i>	Herbivore
	<i>Plectroglyphidodon johnstonianus</i>	Corallivore
	<i>Plectroglyphidodon lacrymatus</i>	Herbivore
	<i>Pomacentrus bankanensis</i>	Herbivore
	<i>Pomacentrus coelestis</i>	Herbivore
	<i>Pomacentrus philippinus</i>	Planktivore
	<i>Pomacentrus vaiuli</i>	Herbivore
	<i>Pomachromis richardsoni</i>	Planktivore
	<i>Stegastes fasciolatus</i>	Herbivore
<i>Scaridae</i>	<i>Cetoscarus bicolor</i>	Herbivore
	<i>Chlorurus bleekeri</i>	Herbivore

	<i>Chlorurus microrhinos</i>	Herbivore
	<i>Chlorurus sordidus</i>	Herbivore
	<i>Hipposcarus longiceps</i>	Herbivore
	<i>Scarus dimidiatus</i>	Herbivore
	<i>Scarus forsteni</i>	Herbivore
	<i>Scarus frenatus</i>	Herbivore
	<i>Scarus globiceps</i>	Herbivore
	<i>Scarus niger</i>	Herbivore
	<i>Scarus oviceps</i>	Herbivore
	<i>Scarus prasiognathos</i>	Herbivore
	<i>Scarus psittacus</i>	Herbivore
	<i>Scarus rubroviolaceus</i>	Herbivore
	<i>Scarus schlegeli</i>	Herbivore
	<i>Scarus spinus</i>	Herbivore
<i>Siganidae</i>	<i>Siganus punctatus</i>	Herbivore
	<i>Siganus vulpinus</i>	Herbivore
<i>Zanclidae</i>	<i>Zanclus cornutus</i>	Carnivore

3.6.2 Structural equation model construction and evaluation.

I used results from interannual variability analysis, previous work at the Rowley Shoals (Chapter 2), and a review of the literature to build the conceptual model (Sandin *et al.* 2008; Brashares *et al.* 2010; Sandin *et al.* 2010; Figure 3.1). In particular, I used Chapter 2 to devise interactions between trophic groups in the fish community. This chapter demonstrates that shark density is negatively associated with carnivore density across a gradient of fishing pressure, implying mesopredator release. However, in the gradient used in this chapter I find little evidence that mesopredators play a major role within the food web (Figure 3A.1). Despite this result, I include mesopredators as a secondary consumer within the food web models to further examine what effects they may have in the food web. What is unknown from these studies is whether sharks or carnivores are the main structuring influence on the density of primary consumer trophic groups. I infer through their diet that sharks consume reef fish, and carnivores have the capacity to impact other carnivores and primary consumers (Cortes 1999; Froese & Pauly 2011). As such, sharks may impact primary consumer density directly or indirectly through alterations in carnivore density (Figure 3.1).

Primary consumers may have densities that are moderated by predators, but they are also influenced by the benthic community which provides habitat and resources (Figure 3.4; Jones *et al.* 2004). In contrast, changes in benthic cover seem to have little effect on mesopredators (or carnivores; Figure 3.4), which is consistent with many other studies (Borer *et al.* 2006). In the models I use only coral cover as an indicator benthic variability. Coral cover is often used as a means to quantify reef health (e.g. Mumby *et al.* 2007; McClanahan *et al.* 2011) and is a good proxy for disturbance severity, in particular for cyclones (e.g. Connell 1997; Mumby *et al.* 2011). Coral cover and algae are continually engaged in a competition for space as demonstrated in this chapter (Figure 3.3). I also chose to use coral cover in the models as opposed to algal cover, because rugosity (structural complexity) on the reef is more related to coral cover than algal cover on reefs where coral cover is extensive (Wilson *et al.* 2007).

Structural Equation Models (SEMs) were constructed and assessed using the *lavaan* package in R software (Rosseel 2012). The model was initially assessed using the chi-square statistic, where the covariance in the conceptual model is compared to the observed covariance in

the data (Grace 2006; Table 3.1). Overall model fit is not significant for all of the models constructed, which indicates that the expected covariance does not differ from observed covariance. Further, when I consider 95% confidence intervals for bootstrapped ($n = 1000$) values of chi-square I find that the confidence intervals for all models are also non-significant ($p > 0.05$; Table 3A.2). As all fit measures have drawbacks (chi-square can be considered too liberal), I assessed the fit of models by using three other fit measures which includes: root mean square error of approximation (RMSEA), standardised root mean square residual (SRMR), and comparative fit index (CFI). RMSEA fit measure demonstrates how well the model fits the covariance matrix (Hu & Bentler 1999; Steiger 2007). RMSEA adjusts for sample size (where chi-square does not) and favours parsimony. Models with $\Delta < 0.05$ are considered well fitting, while those < 0.03 have a great fit (Hu & Bentler 1999; Steiger 2007). SRMR is the square root difference between the residuals of the sample covariance and the expected model covariance (Hu & Bentler 1999). Here values < 0.05 are considered to be a good fitting model. Finally, CFI adjusts for sample size and compares the models chi-square value with that of a null model (all variables are uncorrelated; Hu & Bentler 1999). With a range of 0 to 1, values > 0.95 are considered to be good fitting models. All of the models (with the exception of the control planktivore model) had fit measures that indicate well fitting models (RMSEA < 0.05 ; SRMR < 0.05 ; CFI > 0.95 ; Table 3A.2).

Table 3A.2. The sample size (n) and bootstrapped ($n=1000$) model fit measures for structural equation models predicting community composition (RDA1 and RDA2) and the density of trophic groups. The models are sorted by those which do not control for variation in benthic composition (non-control) and those that do (control). Fit measures include Chi-Square (χ^2), the root mean square error of approximation (RMSEA), standardised root mean square residual (SRMR), and comparative fit index (CFI). Presented are the mean values \pm 95% confidence intervals in brackets.

Model	<i>n</i>	Non-Control Models				Control Models			
		Chi-Square	RMSEA	SRMR	CFI	Chi-Square	RMSEA	SRMR	CFI
RDA1	250	0.809 (0.069)	0.018 (0.002)	0.012 (0.001)	0.999 (0.001)	0.869 (0.075)	0.017 (0.002)	0.011 (0.001)	0.997 (0.001)
RDA2	250	0.853 (0.074)	0.017 (0.002)	0.013 (0.001)	0.998 (0.001)	0.809 (0.069)	0.017 (0.002)	0.012 (0.001)	0.998 (0.001)
Herbivore	250	0.862 (0.078)	0.019 (0.002)	0.012 (0.001)	0.998 (0.001)	0.922 (0.080)	0.017 (0.002)	0.011 (0.001)	0.992 (0.001)
Corallivore	250	0.832 (0.073)	0.018 (0.002)	0.012 (0.001)	0.995 (0.001)	0.826 (0.070)	0.018 (0.002)	0.012 (0.001)	0.994 (0.001)
Detritivore	250	0.832 (0.072)	0.018 (0.002)	0.011 (0.001)	0.994 (0.001)	0.846 (0.073)	0.018 (0.002)	0.012 (0.001)	0.991 (0.002)
Planktivore	250	0.899 (0.080)	0.018 (0.002)	0.012 (0.001)	0.992 (0.001)	0.907 (0.072)	0.019 (0.002)	0.012 (0.001)	0.977 (0.005)

Table 3A.3. Coefficient estimates, standard errors, test-statistic values, significance and standardized coefficients for all paths in structural equation models. Paths for models that do not control (non-control models) for variation in algal cover and those that do (control models) are shown.

Path	Non-Control Models					Control Models				
	Coefficient	Standard Error	Z-value	p-value	Standardized Coeficient	Coefficient	Standard Error	Z-value	p-value	Standardized Coeeficient
Shark Density -> Carnivore Density	-0.225	0.083	-2.73	0.006	-0.173	-0.225	0.083	-2.73	0.006	-0.173
Year -> Carnivore Density	0.008	0.009	0.872	0.383	0.062	0.008	0.009	0.872	0.383	0.062
Shark Density -> RDA1	-0.355	0.019	-18.431	< 0.001	-0.618	-0.297	0.019	-15.625	< 0.001	-0.68
Carnivore Density -> RDA1	-0.004	0.015	-0.293	0.769	-0.01	-0.008	0.015	-0.514	0.607	-0.023
Year -> RDA1	0.007	0.002	3.827	< 0.001	0.125	0.004	0.002	2.089	0.037	0.092
Coral Cover -> RDA1	-0.638	0.051	-12.605	< 0.001	-0.412	0.24	0.055	4.354	< 0.001	0.204
Shark Density -> RDA2	0.42	0.039	10.689	< 0.001	0.64	0.441	0.04	11.052	< 0.001	0.685
Carnivore Density -> RDA2	-0.015	0.023	-0.648	0.517	-0.029	-0.016	0.023	-0.685	0.494	-0.032
Year -> RDA2	0.011	0.003	3.477	0.001	0.167	0.01	0.003	3.061	0.002	0.153
Coral Cover -> RDA2	-0.895	0.137	-6.549	< 0.001	-0.505	-0.585	0.139	-4.206	< 0.001	-0.337
Shark Density -> Herbivore Density	-0.449	0.066	-6.81	< 0.001	-0.367	-0.338	0.066	-5.117	< 0.001	-0.339
Carnivore Density -> Herbivore Density	0.097	0.051	1.886	0.059	0.103	0.091	0.051	1.783	0.075	0.118
Year -> Herbivore Density	0.015	0.007	2.197	0.028	0.125	0.009	0.007	1.333	0.183	0.093
Coral Cover -> Herbivore Density	-1.411	0.168	-8.408	< 0.001	-0.426	0.277	0.172	1.605	0.108	0.103
Shark Density -> Corallivore Density	-0.419	0.084	-4.968	< 0.001	-0.268	-0.475	0.085	-5.582	< 0.001	-0.313
Carnivore Density -> Corallivore Density	0.193	0.058	3.294	0.001	0.161	0.196	0.059	3.334	0.001	0.168
Year -> Corallivore Density	0.02	0.008	2.449	0.014	0.13	0.023	0.008	2.829	0.005	0.154
Coral Cover -> Corallivore Density	1.756	0.259	6.782	< 0.001	0.416	0.908	0.265	3.428	0.001	0.222
Shark Density -> Detritivore Density	2.401	0.695	3.453	0.001	0.21	2.801	0.699	4.005	< 0.001	0.252
Carnivore Density -> Detritivore Density	-0.036	0.544	-0.067	0.947	-0.004	-0.059	0.541	-0.108	0.914	-0.007
Year -> Detritivore Density	0.3	0.083	3.601	< 0.001	0.269	0.278	0.083	3.358	0.001	0.256
Coral Cover -> Detritivore Density	-8.508	1.559	-5.457	< 0.001	-0.276	-2.439	1.561	-1.562	0.118	-0.081
Shark Density -> Planktivore Density	0.126	0.12	1.048	0.295	0.072	0.043	0.119	0.358	0.72	0.025
Carnivore Density -> Planktivore Density	-0.139	0.119	-1.175	0.24	-0.104	-0.135	0.119	-1.134	0.257	-0.105
Year -> Planktivore Density	0.019	0.015	1.299	0.194	0.113	0.024	0.015	1.603	0.109	0.146
Coral Cover -> Planktivore Density	1.292	0.251	5.14	< 0.001	0.273	0.032	0.249	0.129	0.897	0.007

Chapter 4

Coral reef food webs in a sea of human activity

4.1 Abstract

Effective ecosystem management requires knowledge of the influence of human activities on population dynamics and food web interactions. Here, I determine how coral reef food webs may be influenced by spatial heterogeneity in anthropogenic impacts that structure fish communities in a ‘top-down’ (i.e., fishing effects) and ‘bottom-up’ (i.e., degradation of benthic habitats) manner. I find that human activity is significantly and negatively linked to reef shark distribution, coral cover and ultimately the trophic structure of reef fish communities throughout the Pacific. This negative influence is not spatially uniform, but rather varies in strength, forming four regions in the Pacific where human activities act differently as a structuring agent of the food web across the regions. Furthermore, benthic community changes are significantly related to reef shark distributions throughout the Pacific, indicating possible interactions between human and natural processes on the abundances of apex predators in these ecosystems. As food webs are structured differently across four discrete regions in the Pacific, this chapter provides insight into the spatial variability in coral reef food web structure and emphasizes the need for conservation and management approaches to reflect and account for these patterns.

4.2 Introduction

The processes that underlie species interactions in the food webs of coral reefs have evolved over millions of years in the presence of environmental disturbances (such as cyclones, bleaching etc.) that have predictable patterns of impact and recovery (Connell 1997; Mumby *et al.* 2011). In the Anthropocene, the effects of human activities at global scales are predicted to change existing disturbance regimes so that impacts become more frequent and severe (Burrows *et al.* 2011). Furthermore, humans have introduced new types of disturbances to the reef environment that have coincided with the growth and spread of human populations across the globe (Bellwood *et al.* 2004; Wilson *et al.* 2008; Burrows *et al.* 2011; Mora *et al.* 2011).

One ubiquitous example of these (relatively) novel disturbances is fishing. In initial phases, the effects of fishing are concentrated on apex predators (species that are more mobile, larger in size, and carnivorous), such as sharks and large reef fishes (e.g. *Serranidae*, *Lutjanidae*, etc; Pauly *et al.* 1998; Essington *et al.* 2006; Field *et al.* 2009). Sharks are known to be particularly susceptible to over-fishing due their life-history traits of slow growth rates, late sexual maturity, low reproductive output and long gestation periods (Robbins *et al.* 2006; Dulvy *et al.* 2008). These large predators can have an important regulatory role in fish communities and their removal can elicit phenomena including mesopredator release, a situation where secondary consumers become highly abundant and trophic cascades, where changes occur in the structure and function of food chains at lower trophic levels (Baum & Worm 2009; Mumby *et al.* 2012; Chapter 2). At high levels of intensity, a process dubbed “fishing down the food chain” or “fishing through the food chain” occurs as the higher trophic groups are successively fished out, so that humans can ultimately target only the fastest-growing species at the base of the trophic pyramid (Pauly *et al.* 1998; Essington *et al.* 2006).

Human activity in the coastal zone adjacent to reefs also drives disturbances that act in a bottom-up manner. Overgrazing, forest removal, and agriculture in water catchments alter the nitrogen cycle, introduce pollutants, and increase rates of sedimentation on reefs (Mora *et al.* 2011). These alterations ultimately degrade benthic communities, reducing the amount of coral cover and changing the structure and turn-over of both benthic and fish assemblages (Bellwood *et al.* 2004; Mora *et al.* 2011). Thus, human activities can cause dramatic changes to reef communities by altering predation, resources and habitat.

Although the importance of humans as structuring agents in coral reef ecosystems is now well recognized, these impacts are not necessarily uniform in space or time. Notably, the susceptibility of reef ecosystems to anthropogenic disturbance will vary due to changes in the identity, demography, connectivity and productivity of organisms inhabiting each reef (Anderson *et al.* 2008; Melbourne & Hastings 2008; Mellin *et al.* 2010b). Furthermore, many nations have in place management strategies to mitigate or reduce human influences that can operate with varying degrees of success (e.g. Robbins *et al.* 2006). At present, no study has attempted to quantify how this variability in human influence and biological traits might interact to structure reef communities at broad spatial scales.

I address this issue using a modeling approach at both regional ($\sim 3,000,000$ - $14,000,000\text{km}^2$) and ocean basin scales ($\sim 37,000,000\text{km}^2$). I examine evidence for spatial heterogeneity in the influence of human activity and document how this may impact both fish and benthic communities. The coral reef ecosystems of the Pacific Ocean offer an ideal model to achieve these goals. Many enclaves of reefs still persist that are minimally impacted by human activities due to management and/or geographic isolation (Friedlander & DeMartini 2002; Williams *et al.* 2011). For example, isolated reefs, marine protected areas or places where fisheries are managed effectively can maintain high abundances of apex predators along with high cover of live coral (Robbins *et al.* 2006; Sandin *et al.* 2008; Williams *et al.* 2011; Nadon *et al.* 2012). In contrast, reefs near large human populations or with little to no management of human impacts tend to have lower densities of species that are components of the prey base for apex predators and have low cover of live coral. I use Structural Equation Models (SEMs; Grace 2006) and covariance structure to partition the impact of human activity and apex predators in order to investigate their relative strengths and significance to the food webs of coral reefs. The data sets for this task come from one of the world's largest surveys of coral reefs that recorded the identity and abundance of fishes and benthic communities on reefs from 17 countries and territories spanning the entire Pacific Ocean (Palau to French Polynesia). I test three hypotheses, that human activity on coral reefs in the Pacific Ocean: (1) is the strongest predictor of the distribution of reef sharks and amount of live coral cover, (2) interacts with shark distribution and coral cover to directly and indirectly impact the trophic structure of reef fish communities, and (3) that spatial variability in human impacts creates heterogeneity in the effects and influence of top-down and bottom-up structuring processes on reefs.

4.3 Methods

4.3.1 Study Region and Diver Surveys

Coral reefs throughout the Pacific were sampled using standardized underwater surveys by divers as a part of the Pacific Regional Oceanic and Coastal Fisheries project (PROCFish; Labrosse *et al.* 2002; Pinca *et al.* 2012). Counts were conducted in 17 different countries and territories (Figure 4.1) with 4-6 sites per country and 4-6 transects (50m) per site from 2002-2007 ($n = 1650$). Generally, 24 transects that are 50m in length, were stratified across four major reef types (fringing, intermediate, inner barrier, and outer barrier reefs) at each sample location.

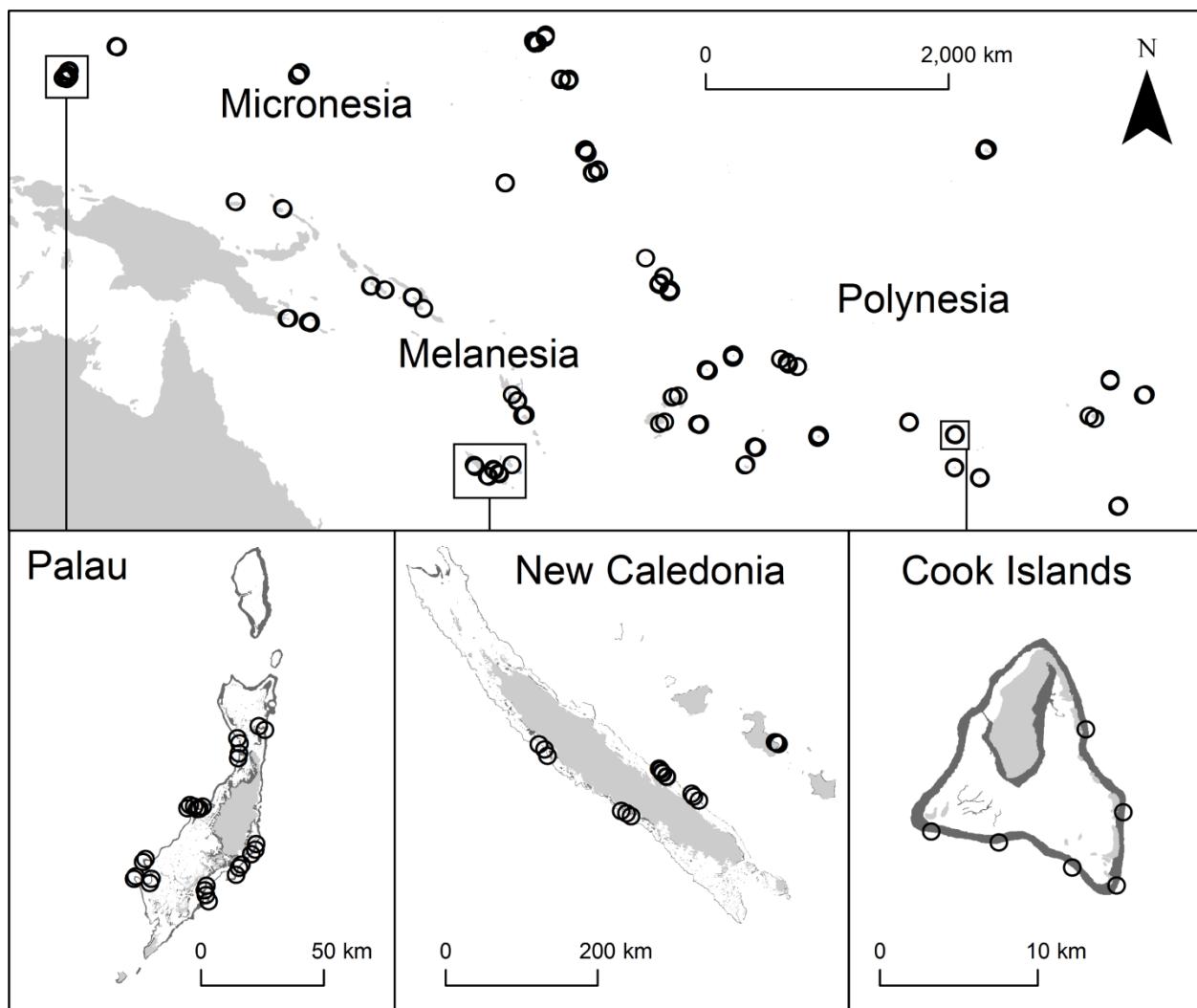


Figure 4.1. Study area throughout the Pacific Ocean. Sample sites are all from the outer reef slopes of islands and individual points mark the start of a transect ($n = 646$). Depending on the size of Island there may be either be several locations (Palau and New Caledonia) or a single location (Cook Islands) where transects were conducted.

Exact positions of sites were determined via satellite imagery in advance such that transects are spaced about 1-3km apart depending on the size and diversity of habitats found on the reef. To reduce inter-habitat variability in the analysis of counts, I only included sites from outer reef slopes and excluded all sites where visibility was less than 10m, giving a total sample size of 646 transects. Transects were generally conducted along 4-10m depth contour (7.3m average depth) but may range between 1-20m in depth on either side of the transect depending on the topography of the reef.

Counts of fish species included 11 major families that consist of: Acanthuridae, Ballistidae, Holocentridae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Scaridae, Epinephelinae, Siganidae and Zanclidae (Pinca *et al.* 2012). Counts were conducted using a distance-sampling technique (Labrosse *et al.* 2002). Briefly, this method involved two divers (one for each side of the transect), where each diver recorded the species, abundance, body length and distance to the transect line of each fish or group of fish on their side of the transect while swimming slowly down the line (Labrosse *et al.* 2002). All fish were counted within the range of visibility available to the diver. Prior to analysis, all size data was grouped into five classes (1-14, 15-24, 25-39, >40cm and sharks; see Appendix section 4.6.1). This approach allowed calculation of the appropriate width of transect for each size group necessary to reduce well-known biases associated with body size, behaviour, and cryptic colouration (Appendix 4.6.1Figure; Kulbicki 1998; Ward-Paige *et al.* 2010a; Bozec *et al.* 2011). For example, I calculated that the optimal transect width for detection of sharks on outer reef slopes was 20m (Figure 4A.1 and Table 4A.1), a value consistent with earlier studies (Robbins *et al.* 2006; Ward-Paige *et al.* 2010a; McCauley *et al.* 2012). All fishes were also classified into five trophic groups: sharks, carnivores, planktivores, herbivores and corallivores and I then calculated the wet biomass of each individual using length-weight conversions from the literature (Kulbicki *et al.* 2005; Froese & Pauly 2011; Kulbicki *et al.* 2011). In addition to fishes, 23 characteristics of the benthic habitat were recorded (e.g. coral, algae, rubble, etc.) within ten 5×5m quadrats arranged on each side completely along the length of the 50m transect (see Clua *et al.* 2006 for more details). These characteristics were then averaged across the 20 quadrats for each transect.

4.3.2 Model Covariates and Subregions

For the analysis I compiled benthic community, human activity and habitat variables known or thought to influence the distributions of coastal reef sharks. Benthic community variables included the percent cover of macro algae, turf algae, and coral, which were then arcsine and square root transformed to conform to assumptions of normality of data sets by the models. Similar to earlier studies (Ward-Paige *et al.* 2010b; Nadon *et al.* 2012), human activity was estimated as the number of people living within 20km of the site and the distance to a populated centre (with a density of 50 people per km²) based on gridded population count data available from the Socioeconomic Data and Applications Center (SEDAC 2005). Prior to analysis these data were log-transformed to comply with model assumptions. Finally, habitat variables included the average depth, visibility, type of reef (atoll, island with lagoon, and island with no lagoon), coastal reef (yes/no), water current (yes/no), slope (yes/no), vertical reef (yes/no) and habitat complexity (on a scale of 1-4).

I used an objective and spatially explicit modeling framework that utilized Boosted Regression Tree (BRT) analysis, Geographically Weighted Regression (GWR) and spatially constrained *k*-means cluster analysis (see Appendix sections 4.6.2, 4.6.3, and 4.6.4) to identify the variables contributing to distributions of sharks and to investigate how these relationships either changed or remained similar through space. Firstly, I identified the most influential variables that contributed to the distribution of grey (*Carcharhinus amblyrhynchos*), blacktip (*C. melanopterus*), whitetip (*Triaenodon obesus*) and all reef sharks using BRT models (Figure 4A.2 and Table 4A.2). Because sharks are a relatively rare component of the fish community (Table 4A.1), I pooled the datasets for all these species for further analysis. Following the BRT analysis, I examined how influential variables changed in space using GWR. The GWR model produced coefficients for each independent variable and standardized residual values for each sample location that allowed us to investigate spatial differences in the fit of the model (Fortin *et al.* 2012). I found that GWR was a better fit to the data than global regression (Table 4A.3) and that three of the influential variables had a significant amount of variability in space (Figure 4A.2 and 4A.3). Finally, a spatially-constrained cluster analysis was used to identify regions where coefficient values from the GWR had a maximized within-cluster similarity and between-cluster dissimilarity. This technique used Delaunay triangulation to constrain grouping spatially by neighbours and Ward's distance for similarity (Figure 4A.4). Using this approach, I was

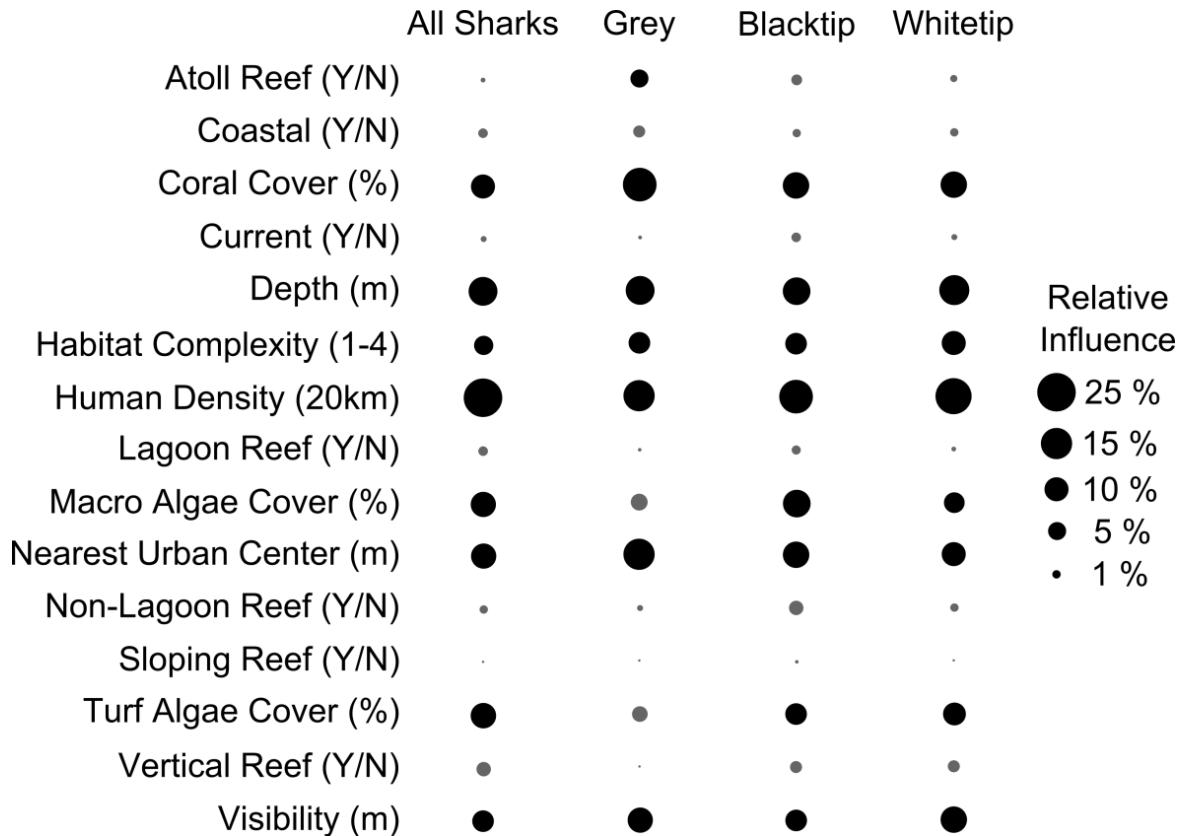


Figure 4.2. The relative influence of all variables on the distribution of all, grey, blacktip, and whitetip reef sharks. The size of the circles indicates the relative influence of the variables as determined by boosted regression tree analysis. Those with greater than 5% influence are denoted in black, others can be seen in grey.

Table 4.1. The sample size (n), reef shark prevalence across sites and variance explained by structural equation models (for endogenous variables) across the entire Pacific (all) and each identified region.

Region	n	% Variance Explained (R^2)				Coral
		Shark Prevalance (%)	Shark	Carnivore	Herbivore	
All	646	23.37	9.89	26.77	23.86	22.23
1	67	37.31	19.05	23.31	35.76	23.65
2	297	29.63	12.80	25.40	16.94	28.43
3	220	9.57	0.88	21.09	40.94	11.15
4	62	24.66	38.12	40.11	28.63	51.09
						11.19

able to demonstrate that there were four regions where processes that contributed to the distribution of sharks were spatially distinct (Table 4A.4 and Figure 4A.3).

4.3.3 *Causal Modeling*

Using the results of the analyses described above and earlier research on the influence of human activity on coral reef ecosystems, I investigated how human activity and the presence of sharks impacted communities of fishes. This was done by creating a model of direct and indirect interactions using Structural Equation Models (SEMs), to determine the relative strength and significance of human activity on the presence of sharks, coral cover and reef fish communities (Grace 2006; see also Appendix section 4.6.5). Firstly, I calculated principal component scores, which represented the biomass of four major trophic groups (carnivore, herbivore, planktivore, and corallivore). The principal component scores for sites were then used as the response variable in the SEMs to describe community-wide structural changes (Figure 4A.5). Habitat variables including depth and complexity, which influence the distribution of reef sharks and biomass of species in lower trophic levels were also included in the model. I then constructed SEMs based on interactions between the presence of top-order predators (sharks), mesopredator biomass (carnivores) and primary consumer biomass (herbivores) to determine whether underlying mechanisms (such as mesopredator release or trophic cascades) could be detected in response to spatial variability in human activity. This procedure was completed for reef fish communities across the entire Pacific Ocean and within each subregion identified by the spatially constrained *k*-means clustering analysis (Legendre & Fortin 1989).

Parameter estimation and testing of model fit for SEMs was completed using the *lavaan* library in R (Rosseel 2012). I used maximum likelihood to estimate path coefficients and examined whether coefficients were significantly different from zero using robust estimates of standard errors (Bentler & Dudgeon 1996). Estimations of model fit were bootstrapped ($n = 1000$) and 95% confidence intervals were used to evaluate the overall fit of the final models (see Appendix section 4.6.5). Standardized coefficients were used because the data in the models consisted of different units (presence/absence, coral cover and biomass) and I also needed to compare the magnitude of paths among several models. Finally, the amount of variation explained for each response (or endogenous variable in the SEMs) was determined using the

formula $R^2 = 1 - V_e/V_o$, where V_e was the estimated variance and V_o was the observed variance (Arkema *et al.* 2009).

4.4 Results

Divers observed seven species of sharks, the majority (>98%) of which were grey, blacktip and whitetip reef sharks. Sharks were present at 23.4% of outer reef sites although the prevalence of individual species was fairly low (Table 4.1). The number of people residing within 20km of sample locations (an inferred proxy for human activity) was the most influential variable driving the distribution of reef sharks throughout the Pacific Ocean (Figure 4.2). This was the case both for individual species and pooled data in the BRT analysis.

SEMs show a wide range in explained variation, where the variation explained in trophic structure (11-51%), coral cover (5-30%), and shark distribution (1-38%) had the largest ranges (Table 4.1). In contrast, herbivore biomass (17-41%) and carnivore biomass (21-40%) had the most consistent amount of variation explained across SEMs (Table 4.1). Finally, all SEMs demonstrated a very good fit using multiple measures of model fit (Table 4A.5 and 4A.6).

I found a statistically significant, negative association between human activity and reef shark distributions throughout the Pacific (-0.12 ± 0.024 [coefficient estimate \pm SE], $Z = -4.967$, $p < 0.0001$, standardized coefficient = -0.22; Figure 4.3). Other factors that were consistently significant correlates of shark distributions included the distance to urban center, cover of live coral and macroalgae, depth, habitat complexity and visibility (Figure 4.2). However, only three of these variables (human activity within 20km, cover of coral and macro algae) displayed a large amount of spatial variability (Figures 4A.2 and 4A.3). Further based on the SEMs, there is a statistically significant, negative correlation between human activity and the live coral cover throughout the Pacific (-0.036 ± 0.009 , $Z = -4.080$, $p < 0.0001$, standardized coefficient = -0.17; Figure 4.3). As human activities are negatively associated with shark distribution and live coral cover, I find that live coral was also significantly and positively correlated with the distribution of sharks at the scale of the Pacific (0.303 ± 0.097 , $Z = 3.125$, $p = 0.002$, standardized coefficient = 0.12; Figure 4.3).

SEMs indicated that human activity was significantly linked with changes in the trophic structure of reef fish communities throughout the Pacific (0.014 ± 0.006 , $Z = 2.287$, $p < 0.05$,

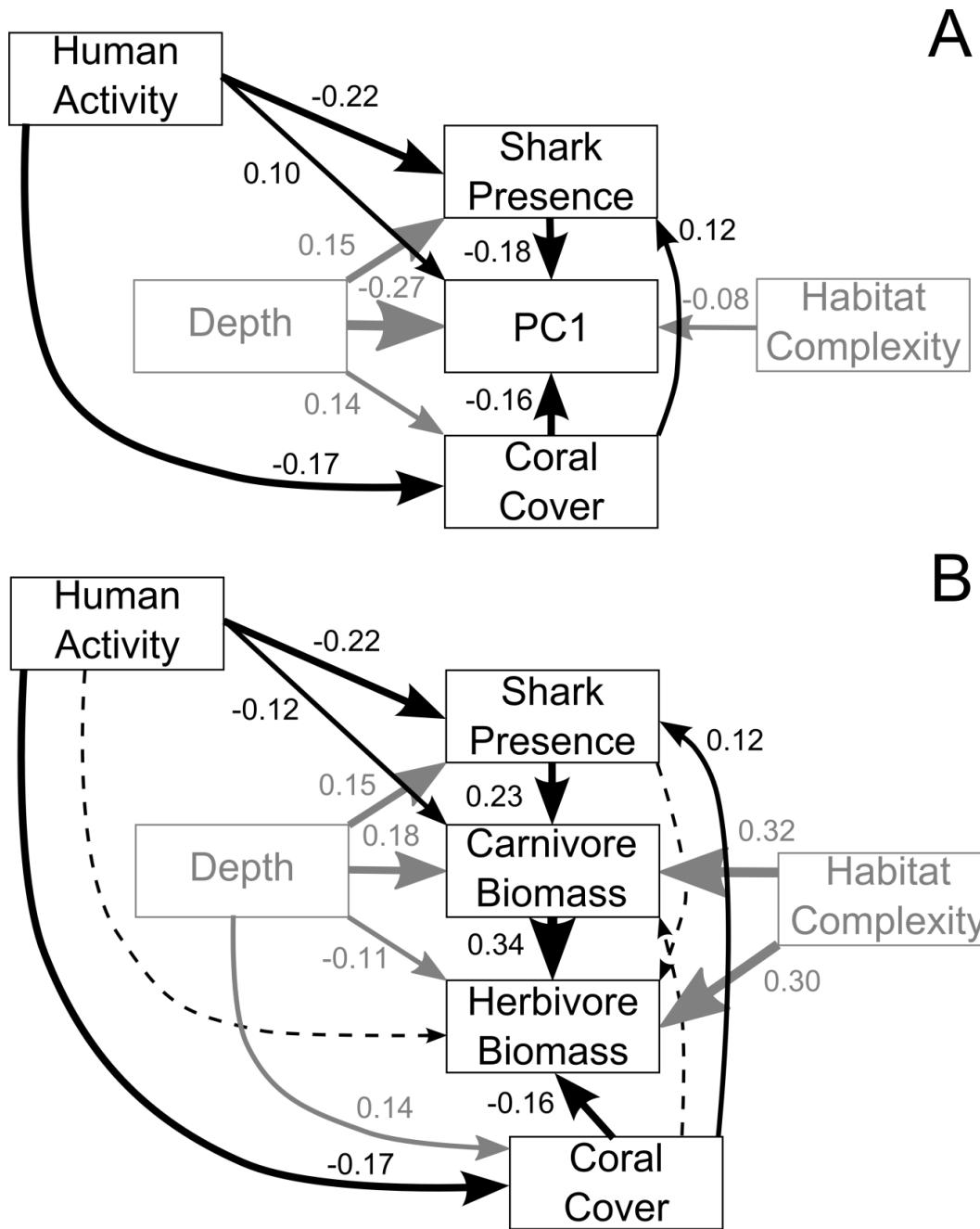


Figure 4.3. Structural equation models across all regions for the (A) trophic structure and (B) biomass of lower trophic levels (carnivores and herbivores). Interactions that are significant (solid) and non-significant (dashed) are shown by the arrows. Values associated with the arrows designate the magnitude of the interaction. Light grey colouring defines the habitat variables included in the models to improve fit. The overall fit of the models is also shown (R^2). Note: decreases in the principal component scores (PC1) indicate communities dominated by more carnivores and planktivores, alongside decreased dominance of herbivores.

standardized coefficient = 0.102; Figure 4.3A). Areas of intense human activity were significantly linked with decreases in the biomass of carnivores throughout the Pacific (-0.087 ± 0.032 , $Z = -2.692$, $p < 0.01$, standardized coefficient = -0.12; Figure 4.3B). In contrast, I could find no evidence that anthropogenic impacts were correlated with the biomass of herbivorous fishes lower down the food web (Figure 4.3B). I found weak positive link between the biomass of herbivores and human activity ($0.027 = -0.16 \times -0.17$) and a weak negative indirect association between the biomass of carnivores and human activity ($-0.056 = -0.22 \times 0.23$). Looking at changes in trophic structure, I found that increases in coral cover significantly decreased the biomass of herbivores, yet increased planktivore biomass (-0.106 ± 0.024 , $Z = -4.386$, $p < 0.0001$, standardized coefficient = -0.162; Figure 4.3A). In contrast, I found no evidence that changes in coral cover throughout the Pacific directly propagated up the food web to alter the biomass of carnivores (0.032 ± 0.13 , $Z = 0.248$, $p > 0.05$, standardized coefficient = 0.009; Figure 4.3B).

While human activity played a role in structuring the food webs of reef fishes, impacts varied dramatically across the four regions of the Pacific Ocean (Figure 4.4). In region 1 (including Palau, Chuuk, and Papua New Guinea), human activities had a significant, strong negative association with shark distributions (-0.108 ± 0.034 , $Z = -3.149$, $p < 0.01$, standardized coefficient = -0.331) and coral cover (-0.038 ± 0.012 , $Z = -3.052$, $p < 0.01$, standardized coefficient = -0.344; Figure 4.4). I was, however, unable to detect any link between these variables and the trophic structure of fish communities, with the exception of herbivore biomass, which was strongly and negatively linked to coral cover (-0.827 ± 0.288 , $Z = -2.869$, $p < 0.01$, standardized coefficient = -0.347; Figure 4.4). In region 2 (including New Caledonia, Vanuatu, and Marshall Islands) there were significant, negative and direct links between human activity and both shark distribution (-0.134 ± 0.040 , $Z = -3.389$, $p < 0.01$, standardized coefficient = -0.195) and coral cover (-0.046 ± 0.013 , $Z = -3.568$, $p < 0.0001$, standardized coefficient = -0.211; Figure 4.4). Both shark distribution and coral cover were linked to the trophic structure of fish communities in this region (-0.050 ± 0.015 , $Z = -3.407$, $p < 0.01$, standardized coefficient = -0.197 and -0.117 ± 0.040 , $Z = -2.884$, $p < 0.01$, standardized coefficient = -0.144; Figure 4.4). Of particular note, the analysis also identified effects of coral cover on herbivore biomass (-0.366 ± 0.132 , $Z = -2.770$, $p < 0.01$, standardized coefficient = -0.145; Figure 4.4). In region 3 (including

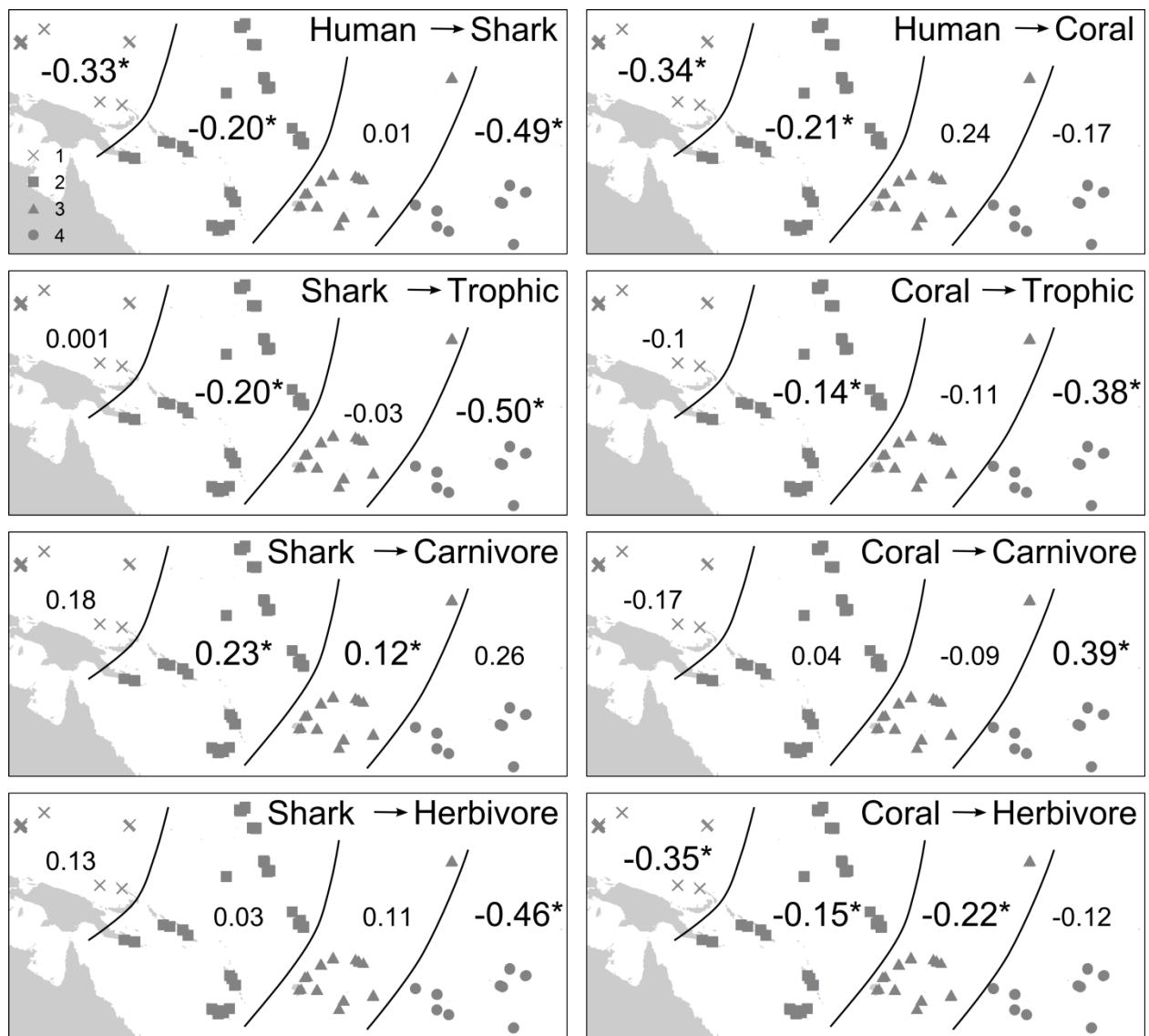


Figure 4.4. Structural equation model coefficients for each region in the Pacific (from left to right: region 1, 2, 3, and 4). I show significant ($*p<0.05$) interactions involving human activity (human), shark presence (shark), and coral cover (coral). Their direct effect on the biomass of carnivores, herbivores and the trophic structure (structure) of fish communities are shown. All direct impacts between human activity and carnivore biomass were non-significant (not shown).

Fiji, Kiribati, Samoa, and Tonga), both shark distribution and coral cover were not directly linked to human activities (0.005 ± 0.045 , $Z = 0.101$, $p > 0.05$, standardized coefficient = 0.008 and 0.084 ± 0.031 , $Z = 0.555$, $p > 0.05$, standardized coefficient = 0.041; Figure 4.4). Furthermore, shark distribution and coral cover did not appear to be significantly related to the trophic structure fish communities (0.010 ± 0.020 , $Z = 0.620$, $p > 0.05$, standardized coefficient = -0.031 and -0.060 ± 0.040 , $Z = -1.499$, $p > 0.05$, standardized coefficient = -0.110; Figure 4.4). However, I do observe positive associations between sharks and carnivore biomass (0.21 ± 0.102 , $Z = 2.053$, $p < 0.05$, standardized coefficient = 0.12; Figure 4.4). Also, coral cover and herbivore biomass appear to be negatively associated throughout this region (-0.439 ± 0.124 , $Z = -3.553$, $p < 0.0001$, standardized coefficient = -0.22; Figure 4.4). This region also has the highest mean human density and the lowest mean coral cover and shark prevalence per site out of all of the regions (Table 4A.7). Finally, in region 4 (French Polynesia and Cook Islands) there were strong negative links between human activity and the distribution of reef sharks (-0.24 ± 0.054 , $Z = -4.461$, $p < 0.0001$, standardized coefficient = -0.493; Figure 4.4). Shark distribution was also found to have a strong direct link to the trophic structure of fish communities (-0.134 ± 0.032 , $Z = -4.185$, $p < 0.0001$, standardized coefficient = -0.498; Figure 4.4). These combined effects meant that human activity had a strong indirect impact on the trophic structure of fish communities ($0.246 = -0.493 \times -0.498$), mainly through the increase of herbivore biomass ($0.227 = -0.493 \times -0.461$; Figure 4.4). Further, coral cover was impacted by human activities (-0.030 ± 0.019 , $Z = -1.589$, $p > 0.05$, standardized coefficient = -0.174) and coral cover appeared to also be a significant factor regulating the trophic structure (-0.295 ± 0.082 , $Z = -3.613$, $p < 0.0001$, standardized coefficient = -0.382; Figure 4.4).

All of these findings can be summarized by how key groups in the SEMs are structured (either via top-down, bottom-up, or both) in each of the four regions in the Pacific. I find dramatically different patterns depending on the group (Figure 4.5). For instance, in this chapter it appears that generally (3 out of 4 regions) sharks are structured by human activities in both a top-down and bottom-up manner (Figure 4.5A). The trophic structure of fish communities is also structured by both top-down and bottom-up processes throughout half of the Pacific (Figure 4.5B). However, for both carnivore and herbivore biomass there appears to be contrasting patterns in top-down and bottom-up structuring (with the exception of region 1 for carnivores; Figure 4.5).

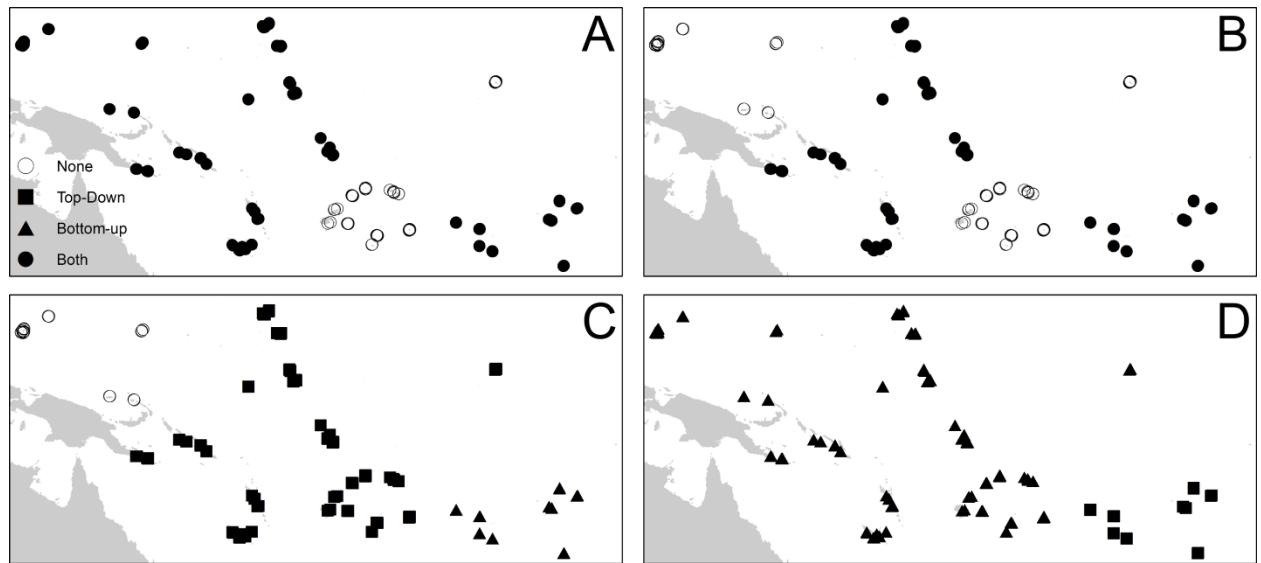


Figure 4.5. Top-down and bottom-up structuring resulting from human activities throughout the Pacific. Displayed is structuring based on the region for (A) reef shark distribution, (B) trophic structure (PC1 scores), (C) carnivore biomass, and (D) herbivore biomass.

4.5 Discussion

Biological communities exist in food webs that contain numerable species interactions, which operate across multiple spatial scales (Ricklefs 2008; Massol *et al.* 2011). The processes that underlie these interactions are important to both food web and ecosystem spatial dynamics. This has lead to the emergence of a unifying framework, termed ‘metaecosystems’ that incorporates both food web and ecosystem dynamics (Massol *et al.* 2011). In short, metaecosystems considers food web interactions under the context of environmental variation that influences food web stability and compensatory dynamics in communities (Gouhier *et al.* 2010). Both food web stability and compensatory dynamics can be critical for ecosystem health and resilience to disturbance events that operate at multiple spatial and temporal scales (Gonzalez & Loreau 2009). In this chapter I provide evidence that human activities are creating spatial heterogeneity in structuring agents throughout Pacific coral reefs. These anthropogenic impacts, in turn, are creating spatial dynamics that influence the food web structure of fish communities on coral reefs and ultimately impacting ecosystem resilience.

4.5.1 Anthropogenic impacts at the top and bottom of coral reef food webs in the Pacific

At the broad scale of the entire Pacific Ocean, the models identified a direct association between the absence of sharks and human activity (Figure 4.3), a result consistent with earlier studies in the Pacific and Caribbean (Ward-Paige *et al.* 2010b; Nadon *et al.* 2012). However, the magnitude of this link was not uniform throughout all regions of the Pacific (Figure 4.4) and for region 3 (Figure 4.4) I could find no relationship between human activity and shark presence. I suspect that the lack of a link between sharks and human activity occurred here simply because sharks had already largely been removed or reduced to very low numbers (only present at 9.6% of sites) by fishing prior to sampling (Newton *et al.* 2007). Despite this result, populations of reef sharks did occur throughout much of the remaining sampling locations (23.4% of sites have shark present) throughout the Pacific.

Strong links between patterns of human activity and coral cover were found. Cover of live coral was strongly and negatively associated with human activity throughout the Pacific, a pattern consistent with other studies globally, where human activity has been implicated in coral declines documented in the Pacific, Great Barrier Reef and Caribbean (Hughes *et al.* 2003;

Bellwood *et al.* 2004; Bruno & Selig 2007; De'ath *et al.* 2012; Pinca *et al.* 2012). This pattern was repeated at the regional scale, again with the exception of region 3, where I could find no link between these variables. Region 3 is afflicted by the highest mean human density per site, lowest presence of sharks (9.6%), lowest mean coral cover and is characterized by many over-exploited and collapsed fisheries (Newton *et al.* 2007; Table 4A.7). Further, many sites in this region (e.g. Fiji and Samoa) have been subject to devastating disturbances in late 1990s that have reduced live coral cover via coral bleaching and cyclonic events over the following decade. As a result, it appears that human activities are not currently driving changes in coral reef food webs within this region.

There was a positive, direct association between coral cover and shark distribution throughout half of the Pacific (Regions 2 and 4; Figures 4.3 and 4.5A). In these regions coral cover may be a proxy for ecosystem health, where reefs that sustain a greater biomass of resources tend to also be those reefs that have larger numbers of reef sharks (McClanahan *et al.* 2011). There is some indication that the reefs used in this chapter, maintain higher biomasses of fish when coral cover is also high (Table 4A.7). Regardless of the mechanism involved, this result suggests that bottom-up processes may possibly interact with the apex predators to influence food web dynamics in these regions of the Pacific. How such effects might operate (i.e. in a synergistic, antagonistic or additive manner), in coral reef ecosystems is not clear (Hughes & Connell 1999; Darling & Côté 2008), although this chapter provides the first evidence that they are detectable at very broad spatial scales of many thousands of kilometers.

4.5.2 Trophic structure of fish communities

Changes at the top and bottom of food webs have major impacts on fish communities. This chapter provides evidence that human activities are impacting the trophic structure of fish communities throughout the Pacific. Food webs in areas of high impact are characterized by an increased dominance of herbivores in the community that coincides with declines in the biomass of carnivores (Figure 4.3). Although evident at the scale of the entire ocean basin, these patterns were weaker at regional scales (Figure 4.4 and 4A.6). This weaker, non-significant result at regional scales (between human activity and trophic structure) may be due to either reduced power in the models or that human activities are largely structuring fish communities indirectly through shark distribution and coral cover (Figure 4.4). In contrast, shark presence and increases

to coral cover both coincide with increased dominance of carnivore and planktivore biomass throughout half of the Pacific (regions 2 and 4 in Figure 4.5B). This shift in trophic structure could be resulting from multi-species fisheries and/or bottom-up structuring due to changes in the benthic environment (Jones *et al.* 2004; Essington *et al.* 2006). Specifically, I identify that carnivore biomass is weakly, positively associated with shark presence throughout two of the largest regions (regions 2 and 3 in Figure 4.4). Generally, fisheries target apex predators (sharks and carnivores) that are larger in size and found higher in the food web (Pauly *et al.* 1998; Essington *et al.* 2006). Hence, if multi-species fisheries are occurring, I would expect that the biomass of sharks and carnivores to be positively associated with one another, which is the case throughout a majority of the Pacific (regions 2 and 3 in Figure 4.4). This confirmation of multi-species fisheries, explains why ecological mechanisms such as mesopredator release and trophic cascades are not common in coral reef ecosystems (Baum & Worm 2009; Estes *et al.* 2011; Chapter 2). Finally, coral cover is a preferred settlement site for many planktivore species and here I confirm this relationship by demonstrating that positive associations between coral cover and planktivore biomass (here shown as principal component scores or trophic structure) throughout most of the Pacific (regions 2 and 4 in Figure 4.4). Thus, it appears that multi-species fisheries alongside benthic degradation are promoting the dominance of herbivore species in coral reef food webs at regional and oceanic scales.

I further demonstrate that bottom-up forcing does not generally impact carnivore biomass, however, region 4 (French Polynesia; Figure 4.5C) provides an exception to that trend where I find a significant and positive relationship. Much like the interaction between shark distribution and coral cover, carnivores may benefit from resource rich areas where reefs have higher coral cover and fish biomass (i.e. higher densities of prey; McClanahan *et al.* 2011). This heterogeneity in structuring produces discrete patterns throughout the Pacific, where the importance of top-down and bottom-up structuring agents differ dramatically for carnivores (Figure 4.5C).

Although the biomass of herbivores is influenced by both human activity and coral cover (Figure 4.4), it appears that the benthic community is likely to be the most important agent structuring this component of the food chain throughout the Pacific (Figure 4.4). The relationship between coral and algal cover and herbivore biomass is well-recognised in coral reef ecosystems, where loss of coral results in an increase in algal cover and ultimately in numbers of herbivores

(Bellwood *et al.* 2004; Jones *et al.* 2004). However, I find that the presence of sharks was also linked to changes in herbivore biomass in region 4 (French Polynesia). Here herbivore biomass is negatively associated with presence of sharks, whereas throughout the rest of the Pacific herbivore biomass is tightly associated with changes to the benthic community (Figures 4.5D and 4A.6). This result indicates that where sharks are reasonably prevalent (present at 24.7% of sites) they may be strong top-down structuring agents on trophic groups lower down on the food chain. This final result is important, because it has only been previously suggested that sharks may structure communities at local scales (Sandin *et al.* 2008; Williams *et al.* 2011; Chapters 2 and 3). Further, because herbivore biomass is impacted, a group that is critical for allowing the establishment and recovery of coral cover, this result may be critical to resilience of reefs in the face of disturbances that cause degradation (Bellwood *et al.* 2004). In particular, sharks may be able to reduce variability in trophic groups lower down in the food web, leading to increases in the resilience of trophic structure to benthic disturbances (Melbourne & Hastings 2008; Brook *et al.* 2011; Chapter 3).

4.5.3 A future for coral reefs and the food web based approach

Processes that structure fish communities in a top-down manner operate at very different spatial and temporal scales than those that structure from the bottom-up. Both shark and coral populations operate at very different spatial and temporal scales in terms of life cycle, dispersal, home ranges, disturbances and species interactions which influence their abundance and distribution on reefs (Cortes 1999; Speed *et al.* 2010; Pinsky *et al.* 2012). Yet, using a top-down perspective I provide evidence that coral cover and shark distributions are important structuring agents in coral reef ecosystems. These results stress the need for management approaches to consider the combined effects between top-down and bottom-up structuring processes, while taking into consideration that both require very different conservation approaches given their ecologically relevant spatial and temporal scales. Further, impacts to shark and coral populations on Pacific reefs is creating fish communities where herbivores tend to make up a larger proportion of the community in the presence of higher human activity. While at first glance this might be viewed as advantageous for reef resilience, the group of herbivores that do well in the presence of human activity may not reflect the full diversity of feeding mechanisms in this guild (e.g. scraping, cropping, excavator, etc.; Thibaut *et al.* 2011). Without a full complement of feeding mechanisms, reef resilience may be compromised.

In this chapter I employ a data-driven approach that explicitly considers how food webs are dependent upon ecosystem dynamics that can be spatially heterogeneous. I demonstrate that coral reef food webs are structured quite differently among regions in the Pacific. However, other aspects related to biogeography, natural disturbances, management, among other factors may be important to consider. Here I indirectly account for biogeographic differences (longitude and latitude) by accounting for spatial variability in the models (GWR and spatially-constrained cluster analysis) and I also relate the findings to known patterns in natural or anthropogenic disturbances. Regardless, these factors may still add noise, underlie, or contribute to the patterns that I observe. For instance, Pinca *et al.* (2011) found that benthic cover is dependent on island (atoll, small island, complex island , and atoll) and habitat type (outer, back, lagoon, and coastal) throughout the Pacific. This relationship in turn can impact fish communities at the family and trophic level. However, here I only consider outer reefs (one habitat) to control for inter-habitat differences and find that island type is not a major factor influencing the distribution of sharks. Further, I account for benthic composition in the models (coral cover; related to island type) and am confident that I have, at the very least, accounted for some variation related to island types indirectly in this chapter. It should also be noted that I originally included management (distance of sites to marine protected areas) in the models, but no relationships were found to be significant with the biomass of fish or distribution of sharks (results not shown). I attribute this non-significant result to the increasing prevalence and frequency of illegal, unreported and unregulated fisheries throughout the Pacific (e.g. Field *et al.* 2009). This chapter would have also benefited from a broader temporal scale, which inhibits us from accounting for temporal variability in communities that can arise from human activities, reef size or connectivity (Anderson *et al.* 2008; MacNeil *et al.* 2009; Mellin *et al.* 2010a). Instead, here I use space as a substitute for the many factors that represent human activity (e.g. nitrification, commercial fisheries, subsistence fisheries, etc.) to demonstrate that anthropogenic impacts are highly variable throughout the Pacific. Finally, I also take a top-down view of food webs, but this can be completed from different perspectives depending on the study objectives.

4.5.4 Conclusion

Coral reef food webs have persisted for millions of years and require a management approach that incorporates ecosystem dynamics and food web interactions to insure long-term conservation and restoration goals are achieved. This chapter emphasizes that human activities

are a major contributor to shark declines, fish community structural changes and declines in coral cover throughout the Pacific. These activities have shifted communities towards a herbivore dominated trophic structure that has the potential to influence the resilience of coral reefs to natural disturbances. Given these results, reducing human activity that structures reef ecosystems directly (in a top-down and bottom-up manner) may provide the best management practice for reefs in the Pacific. However, the caveat is that this reduction needs to consider the spatial and temporal scales to which both top-down and bottom-up processes operate and combined effects that may be present between both. In the face of increased climate warming, reefs will only be assailed by more severe and frequent natural disturbances. Protecting reefscapes with managed marine reserves at ecologically relevant spatio-temporal scales will be vital for the long-term persistence of coral reef communities.

4.6 Appendix

4.6.1 Effective transect width

To insure the appropriate transect width is selected for fish counts I modeled the detection probability of fish counts across the perpendicular distances from the transect line. This was conducted to reduce potential error and bias that is present in the data if a single fixed width was chosen (Thomas *et al.* 2010). Previous work on the detection probabilities of coral reef fishes indicates that the body size of an individual can create the most bias with underwater visual counts (Ward-Paige *et al.* 2010a; Bozec *et al.* 2011). I used the estimated body size of fish to classify them into five groups including: 1-14cm, 15-24cm, 25-39cm, >40cm, and shark species. Using counts and the perpendicular distance from the belt transect line I modeled the detection probability of each group using software called *Distance* (Thomas *et al.* 2009). I used the four most common models to investigate detection probabilities (Uniform/Cosine, Half-Normal/Cosine, Half-Normal/Hermite polynomial and Half-Hazard/Simple polynomial; Thomas *et al.* 2010). Models were selected with the best fit (lowest Akaike Information Criterion (AIC) or overall visual assessment when models had similar AIC values). Fish were recorded in intervals, so I used 1m intervals for perpendicular distances for size groups between 1-39cm and 2m intervals for sharks and size groups > 40cm, because larger individuals do not necessarily fit within a single 1m interval. Otherwise, all recommended settings were used (Thomas *et al.* 2010) and I excluded transects where visibility was less than 10m from the transect line.

Frequency distributions of the five groups showed a dramatic difference in sightings across distance classes from the smaller to the larger size groups (Figure 4A.1). Sharks and >40cm sized fish had a more observations spread across 20m from the transect line. This was reflected in the larger effective transect width predictions (Table 4A.1). Smaller size classes had higher frequencies within the first 6m from the belt transect line (Figure 4A.1). This leads to smaller effective transect widths for the smaller size groups (1-39cm; Table 4A.1). Using the effective transect widths I rounded up to the nearest interval to specify the transect widths used in subsequent analyses. As this is only a single side of distance from the transect line this number was multiplied by two to reflect counts on both sides of the transect. Finally, all counts were standardized to densities of 500 m^2 (representing $50\text{m} \times 10\text{m}$ transect sizes) for subsequent analysis.

Table 4A.1. The Akaike Information Criterion (AIC) values for the models used to predict the effective transect width. The values are given for the four size classes and sharks. Bold denotes the best fit models and the effective distance is given for each class.

Model	1 -14 cm	15 - 24 cm	25 - 39 cm	> 40 cm	Sharks
<i>n</i>	21266	34286	19289	2576	260
Uniform/Cosine	80214.66	145694.5	88319.34	10340.92	1007.49
Half-normal/Cosine	79686.25	145391.2	88340.92	10340.61	1006.81
Half-normal/Hermite Polynomial	79675.3	145719.2	88658.55	10340.61	1006.81
Half-Hazard/Simple Polynomial	79821.66	145204.7	88195.72	10310.48	1007.18
Effective Distance (m)	3.65	5.4	6.58	9.92	8.6
Transect Width Used (m)	8	12	14	20	20

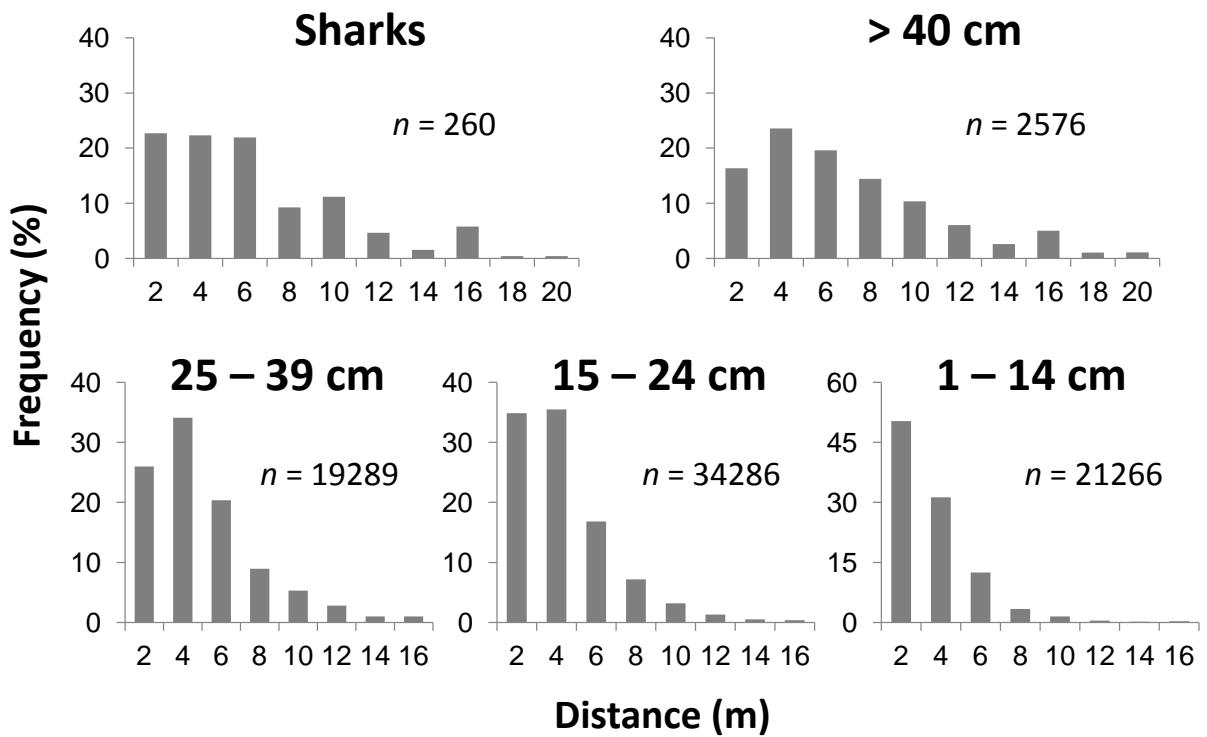


Figure 4A.1. Effect of body size on fish detectability on outer reef transects. Histograms are the relative frequency of the number of sightings of fish (in each class) at a given perpendicular distance from the transect belt line.

4.6.2 Influential covariates: Logistic boosted regression tree construction and evaluation

To determine the covariates that contribute to broad scale patterns of reef shark distribution I conducted logistic Boosted Regression Tree (BRT) analysis to determine the relative influence of each variable. BRT analysis is similar to classification and regression trees in that it creates subsets through binary partitioning that are increasingly homogenous based on a selection of predictors (Breiman *et al.* 1984). The difference is that a series of trees are constructed, rather than a single best fit tree, where the technique of boosting is used to combine large numbers of simple trees (Elith *et al.* 2008). Here many regression trees fit the data iteratively such that the focus is on fitting the residuals (or unexplained variation) for each subsequent tree until the model deviance is minimized. I constructed four models: grey (*Carcharhinus amblyrhynchos*), blacktip (*C. melanopterus*), whitetip (*Triaenodon obesus*), and all reef sharks.

I implement this analysis using R with the *gbm* library (Ridgeway 2012) and use guidelines specified in (Elith *et al.* 2008). Thus, I used a tree complexity of 5 (or 5 splits) and adjusted the learning rate from the suggested value of 0.01, to attain approximately 1000 trees or more for each model (Table 4A.2). An index of relative influence is used, which is defined as the number of times a variable is selected for splitting, weighted by the squared improvement of the model and averaged across all trees (Friedman & Meulman 2003). I define influential variables at broad spatial scales as those that have a relative influence of 5% or greater. All logistic BRT models showed reasonable AUC and deviance explained, with the exception of the model for whitetip reef shark distribution (Table 4A.2). This poor fit of the whitetip reef shark model could be due to some sort of sampling bias or perhaps important variables have been overlooked for this species. Regardless, due to the prevalence of individual species (Table 4.1) and the fact that subsequent analysis is not a data mining technique (high absence counts can be problematic creating zero inflation), I only focus on the results pertaining to the distribution of the pooled presence of all reef sharks.

Using BRT analysis, I demonstrate that human activity (i.e. number of people that reside within 20km of sample locations) is the most influential variable on the distribution of reef sharks (all sharks, blacktip and whitetip) throughout Pacific coral reefs (Figure 4.2). The distance to an urban center (50 people/km²), average depth of a transect, and benthic cover (coral, turf algae and macro algae) were also rather influential. The species models were similar, however,

Table 4A.2. The shark prevalence (%), number of trees (n), null deviance, cross-validated predictive deviance, percent deviance explained ,and cross-validated area under the receiver operator curve (AUC) for logistic boosted regression tree models. Models were conducted for all sharks, Grey (*Carcharhinus amblyrhynchos*), Blacktip (*C. Melanopterus*) and Whitetip (*Triaenodon obesus*) reef sharks.

Model	Shark Prevalence (%)	Learning Rate	# Trees	Null Deviance	CV Deviance \pm SE	% Deviance Explained	CV AUC \pm SE
All	23	0.0025	1450	1.09	0.95 \pm 0.042	13	0.746 \pm 0.026
Grey	7	0.001	1800	0.48	0.40 \pm 0.053	17	0.806 \pm 0.024
BlackTip	7	0.001	2800	0.51	0.45 \pm 0.041	11	0.794 \pm 0.023
WhiteTip	14	0.0025	950	0.80	0.75 \pm 0.068	6	0.703 \pm 0.031

grey reef sharks showed a different distributional response where coral cover is the most influential variable, followed by human activity, distance to urban center and depth (Figure 4.2). Factors such as visibility, habitat complexity, and whether or not the reef is an atoll for grey reef shark distribution, show more of a marginal influence on broad scale distributions. All other factors that show less than 5% influence likely do not contribute to broad spatial distributions through the Pacific.

4.6.3 *Spatially-dependent relationships: geographically weighted regression evaluation*

Using the results from the BRT analysis I investigate how the influential variables may have an influence on reef shark distribution that may change through space by implementing Logistic Geographically Weighted Regression (GWR). GWR was conducted in R using the *spgwr* library (Bivand & Yu 2012). In short, GWR works with the principal that points located closer to each other are more similar than those further apart. This is achieved by using a weighted Gaussian decay function, where relationships are fit at each sample location based on the bandwidth of a fixed kernel size (Fotheringham *et al.* 2002). I used corrected Akaike Information Criterion (AICc) optimization procedure to determine the most appropriate bandwidth size for the fixed kernel (Fotheringham *et al.* 2002). Here a fixed kernel of approximately 1350km is the most appropriate. I created a model with the pooled presence of all reef sharks, because the prevalence of individual species is too low to expect a reasonable model fit (Table 4.1). I also compared the overall fit of the logistic GWR model (local regression; spatial) to logistic generalized linear model (global; aspatial) to demonstrate model improvement (Table 4A.3). Model improvement in the GWR model can be seen with the reduction in log-likelihood and AICc model fit criteria. I then utilize the covariate coefficients of the GWR models to define regions where sharks have similar responses to their environment.

Three covariates (visibility, habitat complexity and turf algal cover) were found to be both globally and locally non-significant ($p>0.05$) to the distribution of reef sharks (Figure 4A.2). Some significant covariates had a minimal influence (depth and distance to population center) or greater local influence in the GWR model (human activity, coral cover, and macro algae cover) on shark distributions across the Pacific (Figure 4A.2). Overall, the fit of the GWR

Table 4A.3. Comparison between global logistic generalized linear model (GLM) and local logistic geographically weighted regression (GWR) models. Listed is the effective number of parameters (n), loglikelihood values (LL) and correct Akaike Information Criterion (AICc).

	n	LL	AICc
GLM	9.00	-317.26	652.80
GWR	33.58	-262.34	595.65

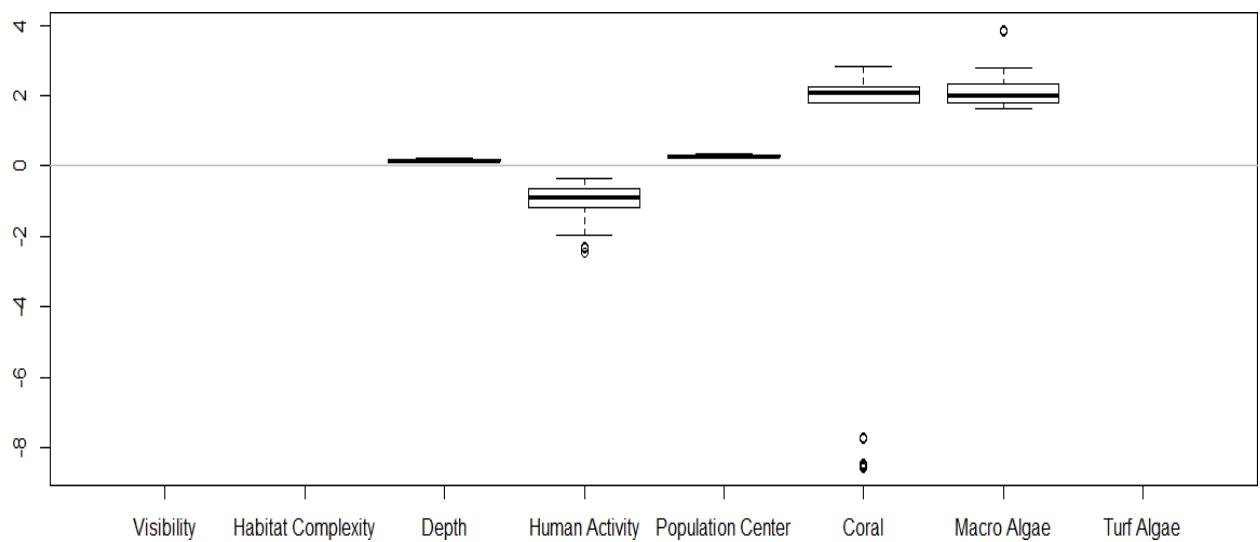


Figure 4A.2. Box and whisker plots of significant ($p < 0.05$) geographically weighted regression coefficients for the prediction of reef shark distribution in the Pacific. The plot shows the minimum, quartiles, median and maximum of values for each variable in the GWR model.

model (or the standardized residuals) was quite ubiquitous through space, with no particular areas or regions of better or poorer fit (Figure 4A.3A). Variables with greater local influence in the GWR model (human activity, coral cover, and macro algae cover) demonstrate that space is an important consideration with relationships between these covariates and shark distribution (Figures 4A.3B and 4A.3C; Fortin *et al.* 2012). However, the GWR model also indicates that coral cover and macro algal cover have a significant influence that is limited to smaller geographic areas (e.g. Figure 4A.3C). The density of people within 20km of sites, the most influential variable as designated by BRT models, has an overall negative influence on shark distribution with increasing influence from West to East throughout Pacific reefs (Figures 4A.2 and 4A.3B). On the other hand coral cover shows more of a ubiquitous influence on shark distributions, where there is an overall positive influence on shark distribution and coefficient values can range from negative to positive (Figures 4A.2 and 4A.3C).

4.6.4 Spatially constrained cluster analysis construction and evaluation.

To identify regions with similar interactions between the response and dependent variables I utilize a spatially constrained k -means clustering (Legendre & Legendre 1998). Spatially constrained cluster analysis differs from unconstrained clustering in that a contiguity relationship (here Delaunay triangulation; Figure 4A.4) along with a similarity (or distance) matrix is computed among objects (Legendre & Legendre 1998). Here I use the similarity of GWR coefficient values to define spatially explicit homogenous groupings. The groups identified represent regions where similar model fit could be found between covariates and shark distribution. Constrained cluster analysis was conducted in R using the *const.clust* library in R software (Legendre 2011).

Using Ward's distance (Ward 1963), I utilize cross-validated ($n=100$) fit measures (R^2 , corrected Akaike Information Criterion, Calinski-Harabasz Criterion and Cross-Validated Residual Error) to determine the optimal number of groups (Table 4A.5). Here I determine $k=5$ is the best size. Finally, I also require a minimum group size of 60 samples for structural equation modeling, so I combine two smaller subgroups ($n=21$ and $n = 46$ within the same spatial region) to ensure this criterion is met. Thus, I determine that there are 4 regions that are fairly distinct in the Pacific where relationships between dependent and independent variables differ dramatically (Figure 4A.3D).

Table 4A.4. Fit measures for each split (k) for spatially constrained cluster analysis. Listed is the variation explained (R-square), corrected Akaike Information Criterion (AICc), Calinski-Harabasz criterion (C-H), Calinski-Harabasz p-value (p), Cross-Validated Residual Error (CVRE), and minimum group size (n).

Groups (k)	R-Square	AICc	C-H	p (C-H)	CVRE	n (Min)
2	0.41	-6.00	452.89	1.65E-76	0.59	46
3	0.72	-6.73	817.02	2.78E-177	0.28	46
4	0.73	-6.77	579.98	2.90E-182	0.27	21
5	0.81	-7.14	700.90	2.30E-232	0.19	21
6	0.85	-7.36	734.52	2.47E-262	0.15	11
7	0.87	-7.49	709.43	1.14E-278	0.13	11
8	0.89	-7.62	708.62	5.25E-296	0.12	11

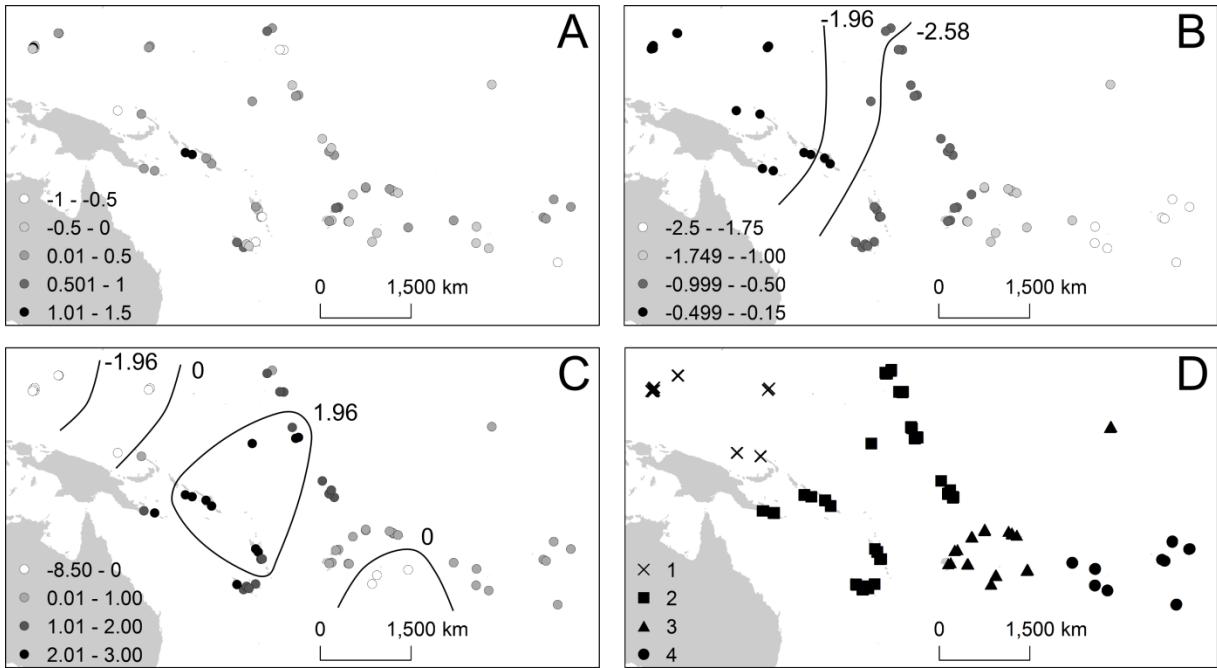


Figure 4A.3. Results from the geographically weighted regression (GWR) analysis and spatially constrained cluster analysis predicting the distribution of reef sharks. Displayed is (A) the mean standardized residuals, mean GWR coefficient values for (B) human activity and (C) coral cover at each site. Isolines designate the pseudo t-values which determine significance of the coefficient values ($t=\pm 1.96, p<0.05$; $t=\pm 2.58, p<0.01$). (D) The final groups from the spatially constrained cluster analysis.

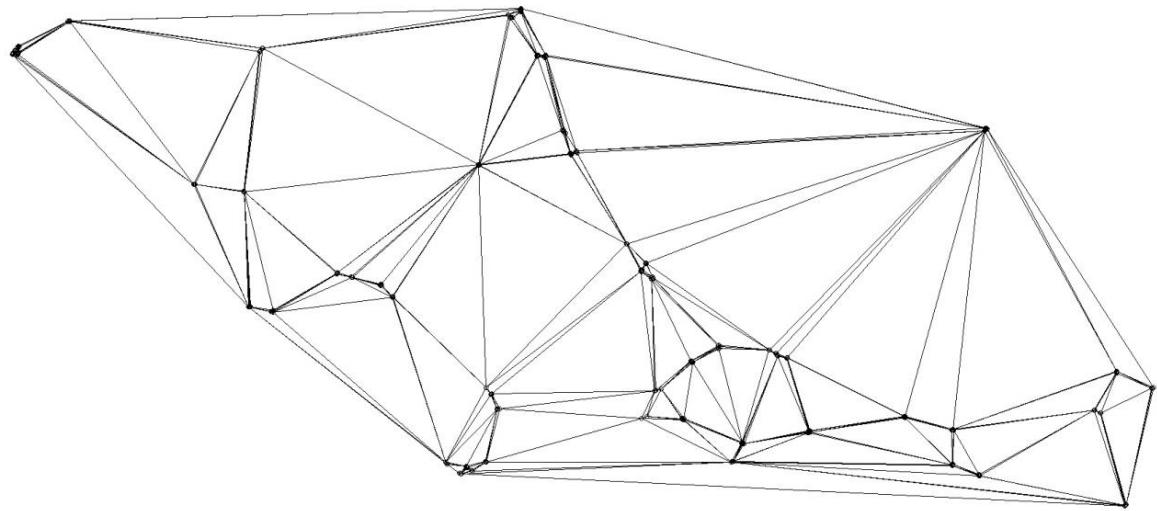


Figure 4A.4. The Delaunay triangulation links between sample sites used to form neighbour links (contiguity matrix) in the spatially constrained clustering method.

4.6.5 Structural equation model construction and evaluation

I created models describing direct and indirect relationships among shark presence, carnivore biomass, herbivore biomass and trophic structure. Model construction was based on models in this chapter (BRT and GWR), observational studies and literature on shark distribution (Robbins *et al.* 2006; Ward-Paige *et al.* 2010b; Nadon *et al.* 2012; Chapters 2 and 3) and coral reef food webs (Friedlander & DeMartini 2002; Okey *et al.* 2004; Bascompte *et al.* 2005; Sandin *et al.* 2008; Williams *et al.* 2011). To tease apart direct and indirect effects I used structural equation models (SEMs; Grace 2006) to parameterize the interactions and evaluate the hypothesized models to observed data.

Direct and indirect paths from human activity, through shark populations and benthic cover to the trophic structure of fish communities reflects well known associations at local and broad spatial scales on Pacific reefs (Mora *et al.* 2011; Williams *et al.* 2011; Nadon *et al.* 2012). In particular, changes to upper trophic levels are well studied, but whether the impact is stronger for sharks rather than carnivores is not clear (Friedlander & DeMartini 2002; Sandin *et al.* 2008; Williams *et al.* 2011; Chapters 2 and 3). Further, interactions between upper trophic levels allow us to investigate whether interactions between trophic groups are positive or negative implying either trophic cascades or multispecies fisheries throughout fish communities (Mumby *et al.* 2012; Chapter 2). Coral cover is the proxy used for the benthic community (bottom-up processes) and is a good indicator of reef health (Mumby *et al.* 2007; McClanahan *et al.* 2011) or can act as a proxy for natural disturbances (Connell 1997; Mumby *et al.* 2011). Coral cover is known to have a tight association with primary consumers and recruits (Jones *et al.* 2004), however, there is little evidence that coral cover is linked directly or indirectly to higher trophic levels (Wilson *et al.* 2010a). Habitat variables, such as depth and habitat complexity, are also important factors associated with the abundance and distribution of herbivores and carnivores (Nemeth & Appeldoorn 2009; Pittman *et al.* 2009; Friedlander *et al.* 2010), which influences community trophic structure. Further, depth may also be related to the amount of live coral cover seen at a specific location.

Using the biomass of four trophic groups (carnivore, herbivore, corallivore and planktivore) I classify fish community trophic structure using principal components analysis (PCA; Figure 4A.5; Legendre & Legendre 1998). I first Hellinger transform the biomass of these

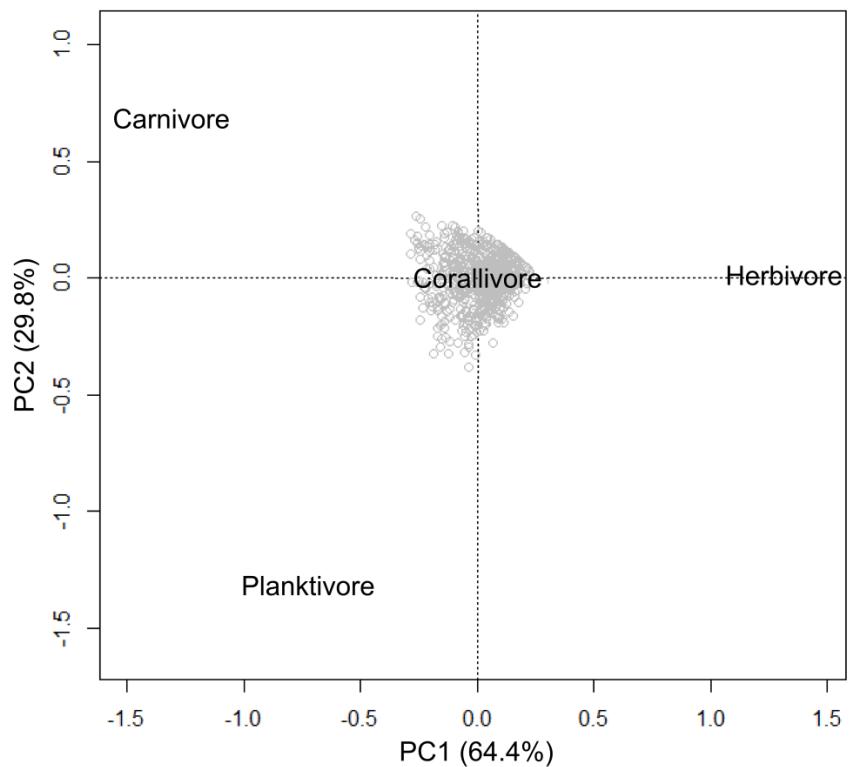


Figure 4A.5. Principal component analysis of the fish communities on outer reef slope sites ($n = 646$). Here the biomass of each trophic group is used to describe differences in fish community trophic structure. The percent variance explained by each axis is shown.

groups to allow values to be more amenable to linear gradient analysis (Legendre & Gallagher 2001). The first axis of variation explains 64.4% of variation and the second axis 29.8% of variation. Together this represents almost all of the variation between site locations. Because the first axis explains a majority of trophic structure differences I use this in the SEMs. Higher values on this axis indicate communities characterized by more herbivores (Figure 4A.5). On other hand, lower values indicate dominance of carnivores and to a lesser extent more planktivores within the fish community (Figure 4A.5). Corallivore biomass does not appear to show major differences across the sites.

SEMs were fit using R with the *lavaan* library (Rosseel 2012). I assessed the fit of models for the entire Pacific ($n = 646$) and for four subregions (Figure 4A.3D). SEM models were fit using a covariance matrix, specifying exogenous and endogenous variables and using maximum likelihood to estimate path coefficients. The fit of the model was initially assessed using a Chi-Square goodness of fit test, where expected covariance in the model was compared to observed covariance. All models were non-significant (Table 4A.5 and 4A.6) indicating that the expected model covariance was not different from the observed covariance. I also used bootstrapped ($n = 1000$) fit measures: root mean square error of approximation (RMSEA), standardised root mean square residual (SRMR), and comparative fit index (CFI). RMSEA is a value between 0 and 1, where well fitting models have values that are < 0.05 and models with a great fit <0.03 (Hu & Bentler 1999; Steiger 2007). Another good quality of RMSEA is that it is a fit measure that favours parsimony in models. SRMR is the square root difference between residuals of the sample covariance and expected model covariance. Values less than 0.05 are considered to be great (Hu & Bentler 1999). Finally, the CFI is a sample size corrected measure that compares the χ^2 value of the model to the null model (i.e. the worst case scenario where all variables are uncorrelated). It has a range of 0 to 1, with models with a good fit have >0.95 (Hu & Bentler 1999). All models had appropriate values of fit (RMSEA < 0.05 ; SRMR < 0.05 and CFI > 0.95), where all bootstrapped upper 95% confidence intervals do not overlap with the outlined values. Coefficient estimates and tests of significance of paths are presented in Figures 4A.5 and 4A.6 and the R^2 values in Table 4.1.

Table 4A.5. The sample size (n), shark prevalence (%), Chi-Square (χ^2), Chi-Square p -value, and bootstrapped ($n=1000$) model fit measures for structural equation models predicting shark presence, carnivore biomass and herbivore biomass. Fit measures include the root mean square error of approximation (RMSEA), standardised root mean square residual (SRMR), and comparative fit index (CFI).

Model	n	Shark Prevalance (%)	Chi-Square	p -value	Mean Bootstrapped Fit Measures ($\pm 95\% \text{ CI}$)		
					RMSEA	SRMR	CFI
All	646	23.37	0.27	0.874	0.011 (0.001)	0.01 (0.001)	0.999 (0.001)
1	67	37.31	0.441	0.802	0.035 (0.004)	0.032 (0.001)	0.994 (0.001)
2	297	29.63	3.713	0.156	0.017 (0.002)	0.015 (0.001)	0.997 (0.001)
3	220	9.57	2.225	0.329	0.032 (0.003)	0.021 (0.001)	0.996 (0.001)
4	62	24.66	2.155	0.34	0.044 (0.004)	0.034 (0.001)	0.992 (0.001)

Table 4A.6. The sample size (n), shark prevalence (%), Chi-Square (χ^2), Chi-Square p -value, and bootstrapped ($n=1000$) model fit measures for structural equation models predicting shark presence and trophic structure (principal component scores). Fit measures include the root mean square error of approximation (RMSEA), standardised root mean square residual (SRMR), and comparative fit index (CFI).

Model	n	Chi-Square	p -value	Mean Bootstrapped Fit Measures ($\pm 95\% \text{ CI}$)		
				RMSEA	SRMR	CFI
All	646	0.27	0.874	0.01 (0.001)	0.01 (0.001)	0.999 (0.001)
1	67	0.441	0.802	0.039 (0.004)	0.035 (0.001)	0.991 (0.001)
2	297	3.713	0.156	0.017 (0.002)	0.016 (0.001)	0.997 (0.001)
3	220	2.225	0.329	0.032 (0.003)	0.022 (0.001)	0.99 (0.001)
4	62	2.155	0.34	0.045 (0.004)	0.039 (0.001)	0.992 (0.001)

Table 4A.7. Summary statistics of variables used in structural equation models for the entire Pacific (All) and each region. Shown are the mean values of each variable with standard deviation in brackets. Biomass has been standardized to 500m².

Region	n	Human Density	Coral Cover (%)	Shark Biomass (g)	Habitat Complexity	Depth (m)	Carnivore Biomass (g)	Herbivore Biomass (g)	Total Biomass (g)
All	646	6509.84 (13060.62)	25.19 (15.95)	5341.92 (23564.63)	2.72 (0.75)	7.34 (3.10)	27310.32 (55527.43)	47905.29 (29936.46)	92874.59 (102052.92)
1	67	7745.59 (6434.62)	33.64 (17.86)	11459.92 (40432.33)	2.67 (0.64)	7.86 (3.25)	41953.37 (100501.59)	66258.91 (76893.81)	135650.78 (160111.54)
2	297	4845.79 (5131.14)	26.86 (14.62)	6287.28 (26837.53)	3.00 (0.57)	7.18 (3.55)	34915.25 (60194.64)	55319.73 (65805.92)	112734.48 (111170.67)
3	220	8033.67 (20107.79)	18.77 (14.78)	1431.04 (6223.241)	2.51 (0.83)	7.21 (2.69)	16535.81 (27398.24)	34537.16 (32100.07)	59869.72 (58539.95)
4	62	7738.67 (12428.09)	30.88 (15.85)	8079.27 (18986.15)	2.22 (0.77)	7.98 (1.55)	13288.45 (16142.28)	39989.25 (29936.46)	68627.44 (40694.15)

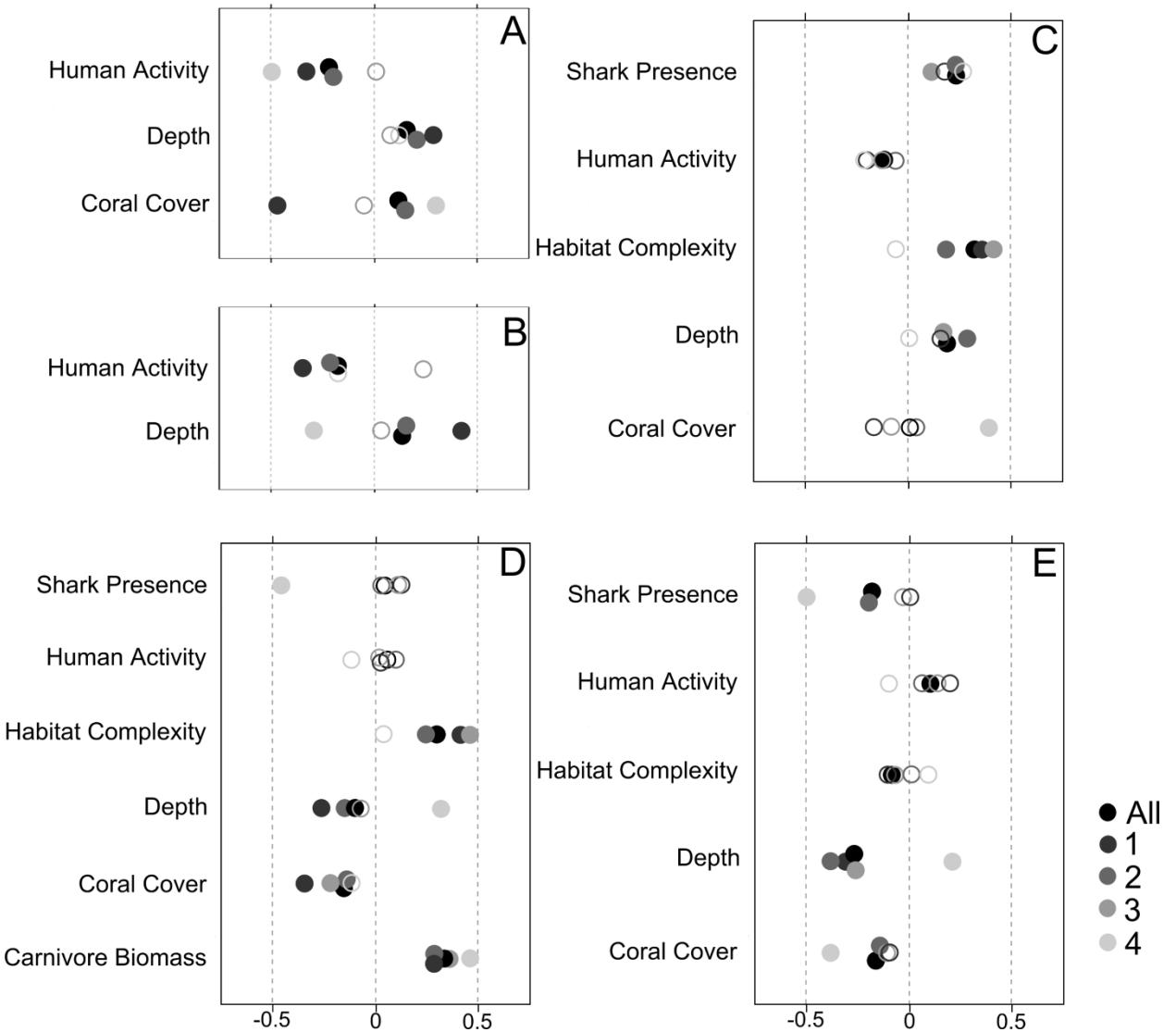


Figure 4A.6. The strength and significance of interactions in structural equation models (SEM) predicting (A) shark presence, (B) coral cover, (C) carnivore biomass, (D) herbivore biomass and (E) trophic structure. Standardized coefficient values for SEMs of the entire region (All) and all subregions are shown to make model comparisons. Both significant (solid) and non-significant (open) values are shown.

Chapter 5

Conclusions and future directions

5.1 Thesis summary

In this thesis, I investigated disturbance events that have the ability to alter fish communities as either a pulse (discrete) or press (continuous) effect through time. This impact can structure communities in either a top-down or bottom-up manner and originate from natural, anthropogenic, or a combination of both sources. Born out of these disturbance regimes are patterns in the trophic structure of fish communities, because species are involved with multiple interactions with other species in a food web, where food web stability and compensatory dynamics are altered by environmental stochasticity (Ricklefs 2008; Gonzalez & Loreau 2009; Massol *et al.* 2011). This legacy of impact, in turn, alters future resilience to disturbance events, impacting conservation and restoration management decisions (Christensen *et al.* 1996; Bellwood *et al.* 2004). In this thesis I considered how marine communities are structured, how disturbance regimes impact food-web stability, and considered the legacy of the disturbance regimes.

The use of human density gradients in many other studies has provided insight into how impacted and non-impacted communities may differ (e.g. Sandin *et al.* 2008; Williams *et al.* 2011). However, due to confounding gradients, disentangling and isolating impacts of specific structuring agents has proven elusive (Mora *et al.* 2011). Thus, isolating the ecological role of structuring agents, especially those species that are considered top-predators and prone to fisheries impacts, may provide valuable insights for future management decisions (Heithaus *et al.* 2010). Further, another uncertainty in marine ecosystems remains the threat that disturbances, which structure communities in a top-down and bottom-up manner, may interact to produce combined effects on the fish communities (Darling & Côté 2008). These communities are also nested in a the framework of food web interactions that are structured by multiple processes that can combine to be multiplicative or non-linear in time and space, which are distinct from the stressors by themselves (Fortin & Dale 2005). The main motivation of this thesis is to provide explicit insight into the relative roles of top-down and bottom-up structuring agents and

determine whether combined effects are important to the structuring of marine fish communities and food webs.

Each chapter investigated the relative role of structuring agents by utilizing a combination of fine and broad spatio-temporal scales. This is conducted in three distinct sections in this thesis. In the first section (chapter 1), the aim was to evaluate the role of contrasting environmental regimes (cooler and less saline versus warmer and more saline) on community patterns across a regional spatial scale and over a 13-year period (1991-2003). In the middle section (second and third chapter), community and food web patterns are interrogated across six remote reefs (fine spatial scale) subject to management and fishing, alongside benthic disturbances that occur over a 14-year period (1995-2008). The final section (chapter 4), a multi-scale spatial framework, is used to investigate how human activities alter top-down and bottom-up structuring agents of reef fishes from across 17 countries and territories in the Indo-Pacific Ocean. Together these sections offer a holistic perspective of how heterogeneity, produced by disturbances through space and time, impact patterns of fish communities and food web dynamics. Here I first describe the novelty and significance of each chapter, review the main results of each chapter, and provide insight for future research and management decisions.

Chapter 1 investigated the role of environmental variability and how it structured communities using a combination of Multivariate Regression Trees (MRT) and Classification and Regression Trees (CART). Given previous work by Ruppert *et al.* (2009), I hypothesized that differing site fidelity by top-predators (Atlantic cod; *Gadus morhua*) across contrasting environmental regimes in the Gulf may have an impact community trophic structure. Further, given the vast amount of variability in environmental conditions throughout the Gulf (Smith *et al.* 2006), community patterns may be spatially discrete due to thermal tolerances of each species (Perry *et al.* 2005b). This chapter provided a link between previous fisheries research that mainly focuses on single species (or stocks) to a community perspective, stressing the need for community or ecosystem scale approaches. Finally, it provided a case study for climate change scenarios for the Gulf of St. Lawrence, where valuable insight is gained into how communities may change when subject to warmer and more variable environmental conditions.

The objectives of the chapter were to: (1) assess whether environmental variability impacts the trophic structure of communities, and (2) determine whether there are spatially

discrete areas that are characterized by specific community structures. Here I found that community patterns differed between contrasting environmental regimes (cold, less saline versus warm, more saline) in the Gulf of St. Lawrence. Communities are structured by sedentary species (Northern shrimp (mainly *Pandalus borealis*) and snow crab (*Chinocetes opilio*)) during the cooler period and the more mobile top-predator species (Atlantic cod) during the warmer period in spatially distinct areas. This result indicates that environmental variability plays a critical role by impacting overall food web dynamics throughout the Gulf. Further, despite apparent sustained low abundances of cod since the early 1990s, cod maintain a community-wide influence during warmer, more amenable conditions.

In chapter 2, I take advantage of a unique set of circumstances where some fish communities are subject to the removal of sharks that structure communities in a top-down manner alongside benthic disturbances that structure fish communities in a bottom-up manner. Using long-term monitoring data (1995-2008) I implement a BACI (Before/After – Control/Impact) design where I isolate the impacts of each stressor (fishing and disturbance) and their potential combined effect on the trophic structure of fish communities. The motivation and novelty for this chapter was to provide insight into the ecological role of sharks as top-predators on coral reefs and ascertain how declines in sharks alongside coral declines (here disturbances) may combine to impact fish communities (Darling & Côté 2008; Wilson *et al.* 2010a).

In this chapter I ask: (1) how shark removal may impact the trophic structure of reef fishes, (2) what is the relative role of top-down and bottom-up structuring agents, and (3) whether there is any combined effect between shark removal and benthic disturbance on reef fishes? Previous work using ecosystem models or macroecological approaches have failed to provide conclusive evidence that sharks may be important to structuring fish communities (Heithaus *et al.* 2010). I was able to provide evidence that reefs subject to shark removal display properties of mesopredator release (increases in the abundance of carnivores) and that this activity also has impacts that cascade throughout the fish community (i.e. trophic cascade; Baum & Worm 2009; Prugh *et al.* 2009). This indicates that sharks may be an important structuring agent in coral reef communities. Moreover, sharks appear to structure the density of herbivores, a group central to the recovery of reefs after benthic disturbance events (Bellwood *et al.* 2004). Bottom-up effects from disturbances are also found to be important structuring agents for herbivores, corallivores and planktivores. Thus, the density of herbivores is a function of top-

down and bottom-up structuring agents. Finally, I also demonstrated that the combined effects of shark removal and benthic disturbance may impact detritivores in a synergistic manner.

These patterns in trophic structure prompted further questions regarding how reef food webs are structured. Specifically, (1) what role does temporal variability in benthic disturbance (environmental stochasticity) play in structuring reef fishes, (2) what is the strength and significance of direct and indirect interactions on reef fishes involving top-down and bottom-up structuring agents, and (3) do sharks increase resilience on reefs by reducing temporal variability in the trophic structure of fish communities? To address these questions in Chapter 3, I utilized uninhabited and protected reefs (fine scale and short gradients) that are subject to a natural gradient of shark density and a gradient of benthic disturbance. Further, I investigated annual temporal variability in structuring agents and implement a causal modeling framework built from a literature review of reef food webs and the results of chapter 2 using Structural Equation Models (SEMs). Here the novelty of the chapter was to determine how sharks structure reef fishes (directly or indirectly) and ascertain what ecosystem service this structuring may provide for fish communities.

I provided evidence that temporal variability in benthic cover over a long-term period (1995-2008) can produce spatial legacies of trophic structure across reefs. Coral cover is in strong competition for space with algae, where the densities of corallivores, herbivores and detritivores appear to be particularly altered by benthic cover differences. Across study locations the amount of variability in benthic cover differs almost 5-fold, meaning that this interannual variability is a main contributor to resulting trophic patterns across the reefs. This contrasts the annual variability in mesopredator density that appears to play a minimal role within these minimally impacted food webs. Previous work indicated that top-down structuring may be pervasive throughout most food webs, where bottom-up structuring is not (Borer *et al.* 2006). Here I confirmed this generality by showing that sharks have impacts that are throughout the food web, whereas bottom-up structuring is confined to only primary consumers. Specifically, I demonstrated that increases in shark density directly and significantly reduce the density in herbivores, corallivores and carnivores. Thus, under minimally impacted conditions it appears that sharks may increase food web stability and thereby confer resilience to reef ecosystems, which are prone to environmentally stochastic (disturbance) events.

In my final chapter, I applied a novel framework to determine how human activities are modifying top-down and bottom-up structuring agents in coral reef ecosystems. Using a combination of Boosted Regression Tree (BRT) models, Geographically Weighted Regression (GWR) and spatially-constrained cluster analysis, I determined spatially discrete regions throughout the Pacific where similar processes contribute to reef shark distribution. Subsequently, I interrogated interactions between structuring agents (human activity, shark distribution and coral cover) within a conceptual food web using SEMs within each subregion and throughout the Pacific. Here the framework allows researchers (via a top-down or bottom-up perspective) to investigate how spatially dynamic a food web may be over multiple scales.

Coral reef food webs are dynamic in space and may be directly impacted by human activities (e.g. fishing) or indirectly at the top (e.g. shark declines) and bottom (e.g. coral declines) of the food chain (Bruno & Selig 2007; Ferretti *et al.* 2010; Mora *et al.* 2011; De'ath *et al.* 2012). In this chapter I investigated: (1) how human activity is altering the role of structuring agents in coral reef ecosystems, (2) whether structuring agents combine to impact reef fishes, and (3) determine if there are spatially discrete food web structures throughout the Pacific. Human activity significantly and directly impacts shark distribution, coral cover and the trophic structure of Pacific reef fishes. In other words, human activity impacts are pervasive throughout the food web and throughout the Pacific. This result is similar to studies that look at the impact of one or two stressors (structuring agents) on structuring agents in coral reefs (Bellwood *et al.* 2004; Nadon *et al.* 2012). I also demonstrated that structuring agents may interact (coral cover and reef shark distribution) throughout the Pacific and within subregions. However, because both show the same response to human activity (a negative response to increasing human activity) I cannot say whether there may be interactions between them or whether the relationship is simply collinear. Finally, I provided evidence that there are four distinct regions within the Pacific where food web structure is unique. This chapter provides insight into the need to account for spatially relevant scales of structuring for both top-down and bottom-up processes that impact coral reef fishes. These findings also provide conclusive evidence that sharks are pivotal to coral reef food webs, not only as a structuring agent, but perhaps as an indicator of human impacts.

Defining the role of top-predators in marine ecosystems represents a major achievement of this thesis. In the boreal sub-arctic the impact of warming temperature on species, communities and ecosystems remains largely unclear (Perry *et al.* 2005b; Greene *et al.* 2008).

This is especially true for the post-cod decline era (1990s - present) where the role of cod as a top-predator in the community has come under question (Savenkoff *et al.* 2007a). In chapter 1, I was able to demonstrate that oscillations in environmental conditions (temperature and salinity) are linked to the distribution of cod (deYoung & Rose 1993; Vilhjálmsdóttir 1997; Ruppert *et al.* 2009), which structures communities throughout the Gulf of St. Lawrence. This is a likely result because cod are top-predators that tolerate warmer temperatures and in warmer temperatures they show higher fidelity to feeding grounds, which in turn structures communities in the Gulf. In contrast, lower fidelity to feeding grounds in the cooler period by cod creates communities that are structured in a bottom-up manner by more cold tolerant and sedentary species.

Previous to the work in this thesis there were many studies that compared the trophic structure between minimally impacted and impacted reefs alongside multiple confounding gradients (e.g. Sandin *et al.* 2008; Williams *et al.* 2011). This made it difficult to ascertain what factors may be the most important to structuring food webs on coral reefs. Further, ecosystem models offer what is arguably the best evidence of the ecological role of reef sharks, but they have produced conflicting results that indicate that sharks could play an important or minimal role in structuring fish communities (Stevens *et al.* 2000; Okey *et al.* 2004; Bascompte *et al.* 2005). Thus, the ecological role of sharks on coral reefs remains largely unclear (Heithaus *et al.* 2010). Here I provided evidence at multiple spatio-temporal scales that sharks are pivotal structuring agents on coral reefs. In particular, they appear to be an important regulator of the abundances of multiple trophic groups including: carnivores, herbivores, corallivores and detritivores. This is of particular interest in the case of shark removal on reefs (Chapter 2), where I found that lower densities of sharks decrease the densities of herbivores due to mesopredator release and cascade effects throughout the food web (i.e. trophic cascade). Further, I demonstrated that across multiple spatial and temporal scales sharks may be involved in combined effects (with bottom-up structuring agents) on reef fishes that can impact communities (Chapter 2 and 4). Finally, by investigating food web stability, I determined that reef food webs are dynamic in space and time, due to differences in environmental stochasticity and shark densities (Chapter 3 and 4). While the main cause of this heterogeneity may be human activities, I can assert that reductions in the density of sharks increase variability in reef food webs, thereby reducing resilience to environmental stochastic events.

In regards to the methods, another achievement of this thesis is development of the frameworks of analysis applied to meet the outlined objectives for Chapter 1 and 4. In chapter 1 the framework that is applied is entirely data-driven to determine the important factors that are structuring communities in the Gulf of St. Lawrence. Initially, MRT analysis is applied to a temporal data set to produce a model for every year of analysis. The MRT describes community patterns by exogenous factors, which creates a tree that summarizes variation attributable to each specific year (De'Ath 2002). You can then classify the trees as belonging to one of the contrasting environmental regimes (the warmer, more saline or colder, less saline period). These contrasting regimes are then differentiated by CART to determine what variables, selected in the MRT analysis, characterize each period. This simple procedure can be applied to any community where temporal data exists to summarize similarities and differences between contrasting regimes or impacts in a BACI fashion.

Also, there is currently no clear framework to evaluate how food webs may be impacted differentially through space by structuring agents. However, it is well established that food webs are not uniform in space and that food web stability and compensatory dynamics may be altered by environmental heterogeneity (Ricklefs 2008; Massol *et al.* 2011). In chapter 4, I developed a data-driven framework to determine discrete spatial regions where processes that impact a particular structuring agent are similar. In keeping with the main theme of this thesis, I took a top-down perspective and first determine the major factors that are contributing to reef shark distribution using BRT analysis (Elith *et al.* 2008). Focusing on broad scale patterns we use the most influential variables from the BRT to determine how the relationship between shark distribution and influential variables changes through space using GWR (Fotheringham *et al.* 2002). Finally, discrete areas of similarity are determined through a combination of Delaunay triangulation and cluster analysis to provide a spatially constrained cluster analysis (Legendre & Legendre 1998). This procedure allows researchers to interrogate how food web interactions may differ across regions where an important structuring agent responds differently to exogenous factors. In this thesis the application of SEMs provided the best option to investigate direct and indirect interactions in a food web (Grace 2006; Chapter 4), but other methods could also be used to compare interactions between the discrete regions. Using this framework in chapter 4 allowed me to provide evidence that not all reefs have food webs that are structured the same and that management plans, especially broad scale plans, need to take account of variation in food

web structure. Providing insight into the variability in food web structure can allow managers to make more informed decisions with regard to conservation and restoration goals.

5.2 Recommendations

There are several research recommendations where knowledge and understanding of how communities and food webs are structured may be improved. These include: (1) accounting for the range of movement of species in different trophic levels, (2) accounting for detection bias in species counts related to body size and movement, (3) incorporating recruitment dynamics into food web models, and (4) isolating specific mechanisms that induce community level responses in a bottom-up manner.

Food webs are structured in a hierachal manner, such that the higher up the food chain a species is found, the larger their body size and range of movement (McCann *et al.* 2005). In terms of range of movement, there is a general understanding that the home ranges of species lower in the coral reef food webs have much smaller home ranges (e.g. *Scaridae sp.*: ~ 250 m of linear reef) than those found at the top (e.g. reef sharks: ~ 10s km of linear reef; Barnett *et al.* 2012; Welsh & Bellwood 2012). The same can be said of boreal sub-arctic ecosystems where Atlantic cod have extensive movements in comparison to the more sedentary prey species (Tremblay 1997; Castonguay *et al.* 1999; Koeller 2000). This difference across the food chain (from top to bottom) impacts the range of influence (or interactions) a species may have with other species in the food web. Incorporating these movement dynamics and the subsequent relevant spatial scales that species or groups of species are structured into food web models may have a profound influence on results.

Related to this, using fixed transect widths or fishing gear, while a standard for many scientific surveys, is inherently bias where larger and more mobile species are under-represented in counts (Ward-Paige *et al.* 2010a; McCauley *et al.* 2012). For diver transects, one way to circumvent some of the detection bias is through the use of distance-based sampling methods, which are used in Chapter 4 of this thesis (e.g. Labrosse *et al.* 2002). In short, distance-based sampling is when two divers swim along a transect together and record the abundance, species, average body size, and distance to transect line for each fish seen. Previous work indicates that an appropriate transect width for fish species is largely dependent on body size (Bozec *et al.* 2011). Specific to this thesis, in chapter 4 I demonstrated that transects widths can range from 8

m to 20 m depending on body size. Further studies compliment this work and provide evidence that fixed width transects provide less reliable estimates of abundance (Kulbicki 1998; Ward-Paige *et al.* 2010a; Bozec *et al.* 2011). Thus, relevant transect widths based on body size can be quite variable. Further, using a distance-based sampling method to estimate density may address some of the bias with the aforementioned hierarchical problem when using counts in food web models. However, it falls short on accounting for the full range of movement of each species. Future comparative studies between fixed and distance-based surveys may prove useful in determining if results between sampling methods differ dramatically.

Another issue with marine macroecological studies is that generally most systems are open systems, where fish have a pelagic larval phase that can traverse large distances between reef environments (Sale 1991). To that end, the settlement of most fishes (some brooders and sharks are an exception) come from a mix of endogenous and exogenous sources (Doherty 1991; Sale 1991; Jones *et al.* 2004). Most surveys either use diver counts or fishing gear catches of older individuals, overlooking variation in densities that may result from larval recruitment dynamics that may impact the resulting trophic structure of fish communities (e.g. Halford & Thompson 1996). One way to circumvent some of the issues with larval recruitment is to use remote regions or isolated populations, where a large source of recruitment is a product of endogenous dynamics. Such is the case in Chapter 2 and 3, where genetic evidence indicates that self-recruitment is the major source for larval settlement on remote reefs in this region (Underwood *et al.* 2012). Thus, larval recruitment dynamics are solely the result of patterns on the reefs to which they originate. However, in these chapters the densities of detritivores show contrasting patterns whereby they have a positive response to fishing (low shark density) and disturbance (Chapter 2) and also appear to have higher densities in the presence of high densities in sharks (Chapter 3). This appears to be contrasting responses for detritivores, but it may reflect competition with herbivores, where detritivores have increased resources of detritus in the presence of high amounts of algae (which traps detritus). Higher algae cover may be present when herbivore densities are low (algae is a resource for herbivores), meaning that herbivores and detritivores indirectly interact (in manner such as the responses seen in Chapters 2 and 3). It could also reflect previous work on this trophic group on remote atolls (*Acanthuridae spp.*) that suggests that these patterns may be a result of strong pulses in recruitment (Doherty 2002). Thus,

to determine the specific mechanism, studies using adult counts (1+ year olds) need to be paired with juvenile/larval counts.

Settlement for fish on a reef is also related to the structural complexity of the benthic community (Jones *et al.* 2004; Wilson *et al.* 2007). A major contributor to structural complexity is coral cover due to its calcium carbonate skeletal structures that produce 3-dimensional structures on the reef. Coral cover is in decline in most regions including the Great Barrier reef (De'ath *et al.* 2012), Indo-Pacific (Bruno & Selig 2007) and the Caribbean (Gardner *et al.* 2003), which may have profound impacts on species diversity and ultimately trophic structure of reef fishes by impacting preferred settlement sites, habitat and resources (Jones *et al.* 2004). Thus, structural complexity impacts reef fish communities in a bottom-up manner similar to factors such as the amount of coral or algal cover. While coral cover as a measure may be a good indicator of structural complexity when coral cover is extensive (Chapter 2 and 3), it can also be poorly correlated with structural complexity (Wilson *et al.* 2007). In fact, in Chapter 4 and in previous work, structural complexity alongside other measures of the benthic habitat (percent cover) have both shown to be important factors contributing to the trophic structure of fish communities (Wilson *et al.* 2008). Therefore, incorporating measures of structural complexity via visual assessments (Chapter 4) or surveys that measure structural complexity may be necessary to determine the specific mechanisms involved with bottom-up structuring on reefs.

5.3 Conclusions

This thesis demonstrated that top-predators in coral reef and boreal sub-arctic marine ecosystems can have a profound influence on the trophic structure of communities and even increase food web stability. Further, I demonstrated that the impacts of top-predators as top-down structuring agents can interact with those that structure communities in a bottom-up manner. Bottom-up structuring agents that result from environmentally stochastic events, whether anthropogenic or natural in origin, will increase in severity and frequency in the future (e.g. Donner *et al.* 2005; Emanuel 2005). This will occur alongside human activities, where in this thesis, I demonstrated are directly altering the role of structuring agents over broad spatial scales, ultimately impacting fish communities and food webs. Further, in some cases it appears that ecosystems may be in an alternative stable state where traditional structuring agents do not play a role or their role has been diminished (Bellwood *et al.* 2004; Newton *et al.* 2007; Savenkoff *et al.* 2007a). Thus, there

is still a pressing need for conservation and restoration management to address the eventual or continual degradation of marine ecosystems from these global stressors.

There are many convincing examples where anthropogenic effects are homogenizing marine ecosystems. For instance, human activities are degrading benthic communities on reefs (from largely coral dominated to algal dominated) and selectively removing large and high trophic level species (e.g. Bellwood *et al.* 2004; Essington *et al.* 2006). However, these ecosystems are also prone to natural disturbances which are producing heterogeneous patterns of community and food web structure. This is leading to a scenario where multiple stressors that have the capacity to interact and impact ecosystems in a non-additive manner are also occurring against a background of main effects by stressors that operate at multiple spatial and temporal scales (Fortin & Dale 2005). Our ability to manage marine ecosystems effectively is only as good as our understanding of how these stressors impact structuring agents and underlying mechanisms of communities and food webs. This thesis stresses, through substantial evidence, that top-predators play a pivotal role in structuring marine communities against a background of environmental stochasticity and combined effects.

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