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Functional roles of reef sharks on the Great Barrier Reef

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To the best of my knowledge and belief, the thesis contains no material previously published by any other person except where due acknowledgement has been made. Permission from external copyright holders and collaborators has been obtained when necessary.

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Abstract

Recent shifts in the understanding of ecological roles of reef sharks have brought questions about overlapping similarities in functional influence on coral reefs and potential outcomes of their removal. Co-occurring predators with dietary similarities (including reef sharks and large teleost fish) are thought to have redundant functional roles on coral reefs, providing a potential explanation as to why coral reef food webs lack evidence of trophic cascades when removal or exploitation occurs. However, there are gaps in this information where conclusions are derived from inference without observation or fine-enough detail to confirm assumptions. These gaps create areas of contention and a need to resolve uncertainty. Expanding knowledge of resource use and distribution can provide useful detail in areas previously undescribed among co-occurring mesopredators.

This thesis addresses gaps in understanding of reef sharks by identifying dietary relationships, spatial distribution, and abundance to better inform their functional roles in coral reef ecosystems. Integration of data collected using multiple methods from 2012-2017 addressed separate challenges in understanding ecology of reef sharks and other reef-dwelling species. Firstly, this thesis identified opportunities for improved application of trophodynamic studies on coral reefs (*Chapter 2*). I determined that trophodynamic studies will require more precise spatial and temporal data collection and analysis using multiple methods to fully explore the complex interactions within coral reef ecosystems. Based on this information, I used existing long-term survey data to characterize variability in diversity and abundance of fish and coral assemblages of coral reefs within the central Great Barrier Reef. Fish and benthic assemblages varied in density and diversity, but the proportion of fish functional groups was similar among reefs. While some post-disturbance recovery of the benthos was evident, changes in fish functional structure did not uniformly reflect benthic recovery patterns. (*Chapter 3*). This provided a view of potential reef resources for sharks, and verified that although reefs remain in degraded states, they are resilient to current pressures. By using fatty acid analysis, basal sources of nutrition and prey of mesopredators were identified to show important dietary differences between reef sharks and teleost fish within the study reefs (*Chapter 4*). Multivariate analysis identified significant dietary overlap between 2 shark species (whitetip reef sharks and grey

reef sharks), but whitetip reef sharks occupied a smaller niche area than grey reef sharks. Clear niche separation between sharks and teleost fishes (red throat emperor, coral trout and grass emperor) was also found. This dietary information was then used as a proxy to explore grey reef shark distribution related to specific prey abundance through use of acoustic telemetry and underwater surveys of prey resources (*Chapter 5*). From this chapter, caesionid and serranid distribution, both commonly reported in grey reef shark diet, were found to significantly influence the presence of grey reef sharks. Individual variation in proportion of grey reef shark detections and site use varied by specific receiver site across reefs within the array. Finally, a comparison of reef shark population abundances between management zones (open and closed to fishing) using both fishing and baited cameras were investigated to show potential resilience in the face of future negative impacts from increasing degradation pressures (*Chapter 6*). Grey reef sharks were the dominant species, with a proportional abundance of over 50 percent for each method used. BRUVS were more successful at capturing sightings of both whitetip and blacktip reef sharks. Our observations suggest that survey depths and probability of occurrence likely affect which species are detected or captured.

Overall, spatial and dietary inter-species partitioning of reef shark resources were found, where grey reef sharks were the most abundant and had the broadest distribution and dietary breadth. Niche partitioning was also observed between reef sharks and teleost fish, showing that functional redundancy is not as widespread as previously assumed. This research highlights a need for higher resolution in dietary detail to confirm prey and basal sources of nutrition for reef sharks. To monitor populations, structured multi-method approaches would likely best inform true abundance and distribution of reef sharks on the GBR. Further information is also needed on direct observation of predator-prey interactions and nocturnal behaviour without measures of baited influence, likely requiring extended monitoring and technological advancements. While this thesis provides essential detail that better informs functional roles, further research will be necessary to identify fully how loss or exploitation of reef shark species can impact coral reefs in the future.

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Chapter 1: General Introduction

Rapid marine biodiversity loss and habitat degradation as a result of human-influenced pressures such as fishing, pollution, and climate change (Hughes et al. 2003; Nyström 2006) has solidified the importance of understanding factors that maintain ecosystems. Some of the most threatened marine ecosystems, such as coral reefs, contain the highest levels of biodiversity (Bellwood et al. 2004). The concept of pristine ecosystems is fading, and research focus has been placed on understanding factors contributing to coral reef resilience and maintaining ecosystem function (Bellwood et al. 2019a, Bellwood et al. 2019b). These factors are based in functional ecology, where species performance is used to determine functional importance in an ecosystem (Jax 2005, Bellwood et al. 2019b). In light of unprecedented ecological changes that threaten all aspects of coral reef ecosystem functioning, conservationists and ecologists are asking questions of what to conserve and why. Thus, the importance of understanding the role of species in maintaining ecological processes and function on coral reefs is at the forefront of current ecological research.

However, definitions of ecosystem function and functional ecology are loosely expressed or poorly understood (S. Giller et al. 2004; Jax 2016, Bellwood et al. 2019b). Function is inherently linked to ecological processes and mechanistic patterns, where species traits are used to infer how an organism interacts with the environment. Species traits are defined as the “measurable features of an individual that potentially affect performance or fitness” (Cadotte et al. 2011). Hence, understanding these traits can assist in defining their ‘function’ or performance in an environment (e.g. functional role). These features or traits can relate to species morphology, biology, physiology, and behaviour, some of which are time dependent. Co-occurring species that share traits (regardless of taxonomy) can perform similar roles and are often categorised into groups or guilds that help generalise ecosystem structure and are considered functionally redundant (Steneck and Dethier 1994). These species are thought to share resources and overlap in ecological niche space. Alternatively, organisms with unique traits are considered functionally diverse from other species or groups, exploiting separate resources from other co-occurring species (Bellwood et al. 2004). The idea of functional redundancy infers ecological resilience as there are multiple species that perform similar roles within the environment. Hence, if biodiversity loss occurs, there species occupying the same niche able to maintain that role or process within an ecosystem. However, research definitions of species (functional) roles can dramatically change depending on knowledge of species traits (Bellwood et al. 2003; Lucifora et al. 2009; Bierwagen et al. 2017) and the spatial or behavioural nature (Meyer et al. 2010; Streit et al. 2019) of their performance. Without understanding species performance in a specific environment, it is difficult to determine their influence on an ecosystem. Thus, detailed understanding of function is crucial in determining the influence of a species or guild and has direct links to how these species should be managed.

The classification or functional organisation of fish communities are mostly trophic (dietary) in nature, where functional groups or guilds (e.g. herbivores, piscivores) identify trophic position of species in food webs (Bellwood et al. 2004; Aguilar-Medrano and Calderon-Aguilera 2016). The construct of functional groups helps to simplify and organise the understanding of food web links based off a guild's contribution to energy flow in an ecosystem (trophodynamics). A more in-depth description and background of the use of trophodynamics in coral reef study is given in *Chapter 2*, where specific focus is placed on methods used to interpret diet and energy flow as well as important gaps to consider for future research. While dietary contribution is important in defining functional roles or species or groups, it is only one aspect of functional ecology. Some reef-dwelling species are known to derive energy from multiple trophic levels and shift diet in response to disturbance which complicates assignment of functional groups (Nyström 2006; Brandl et al. 2016). Additionally, the semi-open nature of reef systems allows for input from alternate source pools such as pelagic systems, further adding complexity to dietary roles as seen with mobile predators (McCauley et al. 2012b). As a result, interpreting species influence based on trophic roles can result in over-generalisation of species performance in ecosystems, and can ignore aspects such as differences in life history, biogeography, spatial distribution, and differing temporal scales (*Chapter 2*). Additionally, assumptions of functional similarity of species performance based solely on trophic position can overlook key differences in the role species play for ecosystems (Chalcraft and Resetarits Jr 2003). Hence, trophic studies can help inform functional roles, but cannot entirely define the influence or contribution of a species to an ecosystem.

The ecological uncertainties that come with defining species roles or importance to ecosystems unsurprisingly stimulates debate between researchers. One of the more debated species groups on coral reefs in both trophic and functional space are reef sharks. Reef sharks are assumed to play a vital role in the functioning of marine ecosystems as predators and, like most other species in coral reef habitats, are under increasing pressure from human stressors (Sandin et al. 2008; Chin et al. 2013; Roff et al. 2016a). Reef sharks until recently were classified as apex predators, where their ecological role and influence on an ecosystem was assumed to sit at the top of the food chain (Opitz 1996; Friedlander and DeMartini 2002). The authors suggested that removal of these apex predators could potentially trigger top-down cascading effects on ecosystems (Mumby et al. 2006; Sandin et al. 2008; Casey et al. 2017). Heupel et al (2014) originally challenged this notion by providing evidence that traditional classification of reef shark species is insufficient in recognizing factors such as dietary differences in ontogeny, feeding behaviour, and habitat characteristics. Following this research, others suggested reef sharks (*Carcharhinus amblyrhynchos*; grey reef shark, *Triaenodon obesus*; whitetip reef shark, *Carcharhinus melanopterus*; blacktip reef shark) be re-classified to mesopredator level based on trophic position estimates; below more mobile, larger bodied sharks such as bull sharks (*Carcharhinus leucas*) and tiger sharks (*Galeocerdo cuvier*) that also occur on reefs (Frisch et al. 2016; Roff et al. 2016b). These authors also suggested that based on evidence of functional redundancy with reef teleost mesopredators such as coral trout (*Plectropomus leopardus*), that their ecological influence is likely less than previously thought. However, results of these studies are limited and focus mainly on the trophic influence of reef sharks, ignoring potential indirect behavioural effects such as feeding suppression (Rizzari et al. 2014b; Rasher et al. 2017), and direct effects such as combined or cooperative hunting (Mourier et al. 2016; Robbins and Renaud 2016). There is growing evidence in the literature that non-consumptive effects and landscapes of fear from sharks impact food-web links by altering prey selection of other predators in the presence of high-risk scenarios (Lester et al. 2020; Mitchell and Harborne 2020). This literature highlights that functional roles should not purely be measured from diet and other factors should be considered when describing their ecological ‘importance’ or influence.

The functional importance of sharks for coral reefs is also dependent on their abundance and distribution. For some areas, optimal habitat and population status is unclear due to limited research with differing methods, creating another area of debate surrounding reef sharks. Additionally, human activity can have large impacts on both the abundance and distribution of reef sharks and functioning of coral reef systems (Ferretti et al. 2010). These impacts can vary significantly by location (Nadon et al. 2012). For example, in the Caribbean there are strong declines in reef shark populations as a result of human activity (Ward-Paige et al. 2010). However, in remote locations such as Fakarava, French Polynesia, reef sharks occur in near-pristine conditions where high abundance has the potential to change the top-down influence of reef sharks based on differences in biomass pyramid structure (Mourier et al. 2016). In Australia, research within the Great Barrier Reef Marine Park (GBRMP) has aimed to explore the life history, ecology, and effects of management and human activity on population size of mobile species such as sharks (McCook et al. 2010; Ceccarelli et al. 2014). In the GBRMP, reef sharks have been found to remain resident to specific reefs (Espinoza et al. 2015), are genetically well mixed (Momigliano et al. 2015), and are associated with complex habitat such as coral cover (Espinoza et al. 2014; Rizzari et al. 2014c). Some research has indicated dramatic declines in reef shark populations in the past two decades (Robbins 2006; Robbins et al. 2006; Hisano et al. 2011; Rizzari et al. 2014a), whereas other research indicates more stability (Heupel et al. 2009). Even after recent reef shark re-classification to as mesopredators, population models to investigate ecosystem stability are still using reef sharks in an apex framework which produces potentially conflicting arguments about status and functional roles (Casey et al. 2017). Much of this contention is based around methods used which identifies a need to standardise approaches to assessing populations. Although reef sharks are clearly linked to areas with high coral cover, there is not enough data on fine-scale distribution to determine what influences distribution for these species and whether niche partitioning and effects of resource competition occur. In teleost predators, sympatric species have been found to partition resources by depth segregation (Matley et al. 2016), and spatial partitioning has also been observed between reef shark species on the Southern GBR likely due to competitive effects (Heupel et al. 2018).

Even with improved understanding of functional roles and population status of resident reef shark populations, it would be difficult to measure influence or contributions without also understanding the whole of the reef community. This is of importance as history of human disturbance coupled with climate change and natural acute disturbance events such as cyclones/hurricanes has left many reefs in degraded states (Hoegh-Guldberg 1999; De'ath et al. 2012; Hughes et al. 2018). Since most reefs have been perturbed at some level, it is important to understand how this impacts community structure and function. This information can give insight into resource availability and competition, as well as post-disturbance (human or natural) recovery potential of fish and coral assemblages where reef sharks occur. For example, do fish and coral assemblages change over time and how may that affect reef shark occurrence? Is there variability between reefs, particularly relative to recovery potential? Therefore, in order to understand functional roles of reef sharks within coral reef ecosystems, it is also important to know the resource availability predators have to sustain healthy populations. This can be accomplished by categorising the reef community assemblage as well as identify potential underlying competitive effects from other predators sharing that resource. Lack of robust data in these areas (Heupel et al. 2019) presents an opportunity to refine our understanding of reef shark species using a combination of methods to gain a comprehensive picture of how sharks use coral reefs and what resources are available to them.

In general, without clear definitions of functional roles, population status, and relative distribution of reef sharks, it is difficult to interpret their influence and role on coral reefs. This thesis used a multi-method approach to fill gaps in the understanding of reef community structure and the spatial distribution and trophic roles of reef predators on coral reefs of the Central Great Barrier Reef (GBR). The study region was chosen due to availability of long-term data as well as similarity in shape, size and aspect to prevailing winds and other known environmental patterns in the region. Four main reefs

(Rib, Helix, Knife, and Chicken) were the focus of reef-scale research within this thesis, with specific chapters also examining a larger suite of reefs to investigate the effects of reef zoning (i.e. open or closed to fishing) on predator populations. Grey reef sharks were the focal predator species for this work since they are commonly encountered and there is previous research in similar areas in the GBR to compare to. Other reef shark and large teleost species are included in some chapters where relevant.

The overarching aims of the thesis are to use existing long-term data and multiple field methods to fill gaps in our understanding of the functional ecology and population status of grey reef sharks at focal reefs on the Central GBR by:

(1) Identifying the necessary tools to fill gaps in energy flow in reef systems.

(2) Using reef-scale data to describe variability of reef resources across a range of degraded states.

(3) Resolving areas of uncertainty in the trophic ecology of reef sharks.

(4) Determining whether prey availability influences grey reef shark activity space around reefs.

(5) Assessing the persistence and relative abundance of reef shark populations over time.

These aims will attempt to overcome previous limitations in interpretation of grey reef shark behaviour and ecology in the Central GBR. Thesis chapters (Chapters 2 - 6) address the above-mentioned aims and are integrated to address the overarching aim to better understand functional roles and resource use of reef sharks. The chapter content is summarised briefly below. This thesis is structured as stand-alone scientific manuscripts of which some have been published in peer-reviewed journals. Any repetition in the chapters will be mostly limited to the study area and sampling methods.

Chapter 1 (this chapter) introduces the broad importance of appropriately defining trophic roles and species-specific influence species on coral reef ecosystems. It introduces the aims of the research and approach as well as outlines thesis structure.

Chapter 2 is a literature review of traditional approaches in the study of trophodynamics of coral reef ecosystems. This review identifies the importance of appreciating the complexity of coral reefs in study design and approaches to investigating energy flow of coral reefs. This review also shows a need for multiple methods, collaboration, and long term-data within the same spatial scales are most appropriate for future study. This review has been published in *Frontiers in Marine Science.*

Chapter 3 examines variability of reef resource by showing the capacity for reefs within the study site to recover and reassemble in both fish and coral assemblages post-disturbance. This study also determines the response of fish functional groups compared to benthic recovery. This data chapter defines the scale of the thesis and the importance of reef-scale information for ecological study. This chapter has been published in *Marine Biology.*

Chapter 4 identifies differences in mesopredator diet through use of fatty acid analysis. Muscle tissue and blood plasma samples were used to determine dietary niche similarity and differences in co-occurring large bodied teleost fish and reef sharks. This chapter also provides method validation for faster processing and extraction techniques on tropical fish species. This chapter has been published in *Marine Ecology Progress Series.*

Chapter 5 uses passive acoustic telemetry to determine long-term movement and activity space of grey reef sharks and underwater visual surveys to measure site-specific resource availability by quantifying prey abundance. This manuscript is in preparation for publication.

Chapter 6 combines traditional angling methods and baited remote underwater video surveys to examine abundance and distribution of reef sharks and the effectiveness of zoning restrictions within the Central GBR. This manuscript is in preparation for publication.

Chapter 7 consists of the general discussion which synthesises the components of each chapter in the context of ecological implications

Chapter 2: Trophodynamics as a tool for understanding coral reef ecosystems

2.1 Introduction

Understanding the biological organization and physical nature of an environment has enabled ecological research to play a central role in providing management and conservation advice for important ecosystems. While ecology comprises a wide array of components, food web structure and trophic links are fundamental aspects of biological organization (Odum and Barrett 1971; McIntosh 1986) and encompass a large body of literature. Trophodynamics, “the dynamics of nutrition or metabolism”, was first proposed by Lindeman (1942) and is fundamental in understanding the flow of energy through food webs. Relationships within a community, energy flow, and linkages between biota and the environment are all encompassed in Lindeman’s approach. The idea of energy flow in an ecosystem strengthened earlier studies such as biomass pyramids (Elton 1927; Turney and Buddle 2016), opening the way for incorporation of food webs into ecology to understand ecosystem processes (McIntosh 1986; Sale 2002). Definition of ecosystem processes is crucial to trophodynamic studies because they encompass biological, physical and chemical mechanisms that link species and facilitate energy flow. These processes explain the contribution of decomposition, production, and nutrient cycling to ecosystem function (i.e. the way an ecosystem distributes energy) (Libralato et al., 2014). Although trophodynamics was not originally defined for marine ecosystems, researchers have applied this concept to marine food webs including coral reef ecosystems (Paine 1966; Ryther, 1969). Contemporary trophodynamic analyses integrate ecosystem processes and food webs within a spatially and temporally explicit context to understand energy flow and trophic relationships in coral reefs. In a conservation and management context, trophodynamics can be used to predict the ecological effects of disturbances or fishing, and trophodynamic patterns are used as indicators for the state of coral reef systems.

Incorporating trophodynamics in marine studies is difficult due to the degree of uncertainty in describing interactions within highly complex marine food webs. Traditionally, marine food webs were thought to be resource-driven systems based on phytoplankton availability to lower-level consumers (Verity and Smetacek 1996; Frank et al. 2007). For example, Odum and Kuenzler (1955) used trophodynamics to study coral reefs and identified energy pathways through both turf algae and fish to consumers, demonstrating that energy can be derived from both benthic and pelagic sources in a single system. Complex interactions among species also increase challenges in characterizing ecological functions within coral reefs (Huston 1983; Pinnegar et al. 2000; Hubert et al. 2011). This complexity increases the difficulty in defining the trophic position of an individual or species within a food web (Choat and Bellwood 1991; Choat et al. 2002; Frisch et al. 2014).

An additional complicating factor is the high level of spatial and temporal variation in coral reef systems, adding to the complexity of mapping ecological functionality on larger scales (Newman et al. 1997). Interpretation of these interactions can be difficult without long-term data (McIntosh 1986; Sale 2002) and are challenging to apply in conservation and management (Alva-Basurto and Arias-Gonzalez 2014). Physical and biological factors change over space and time in reef ecosystems (Sale 2002). Therefore, even if trophic interactions have been well described for a species and reef system in one location, the key processes that regulate ecosystem dynamics can be missed if the system is not observed over appropriate temporal (Scheffer et al. 2008) or spatial scales (Heymans et al. 2016). While quantitative analytical techniques have improved, complexity of trophic variability within populations, tissue turnover rates, and limited understanding of source pools (e.g. benthic versus pelagic sources) can significantly affect interpretation of results (Layman 2007a; Layman 2007b; Layman et al. 2012). Furthermore, scaling issues limit the interpretability of trophodynamic data. Due to the complexity and variability of coral reef ecosystems, simplifications are often applied. For example, global databases [e.g. Fishbase (Froese and Pauly 2003)] may be used to source available data in lieu of extensive field collection to obtain site specific data (Bauman et al. 2010; Alva-Basurto and Arias-González 2014; Ashworth et al. 2014; Ceccarelli et al. 2014; Aguilar-Medrano and Barber 2016). However, information within these databases is often limited to specific regions. Similarly, reef fish feeding habits and trophic position can differ by population, so modelling over broad areas may not reflect interactions for an entire region unless spatial variation is understood and included (Michener et al. 2007).

Current trends in coral reef management highlight both biodiversity and biomass as indicators of reef health (Huston 1983; Bellwood et al. 2004; Aguilar-Medrano and Calderon-Aguilera 2016; Turney and Buddle, 2016). Documented declines in top predators and keystone species from anthropogenic disturbance (Dulvy et al. 2004; Sandin et al. 2008; Estes et al. 2011) has resulted in exploration of trophic cascades and assessment of ecological roles of predators in coral reef reefs (Heupel et al. 2014; Boaden and Kingsford 2015; Rizzari et al. 2015; Weijerman et al. 2015; Thillainath et al. 2016). However, identifying trophic cascades is difficult in reef ecosystems. Only recently has there been evidence of a predator driven coral reef trophic cascade, but this was linked to tidal effects reducing predator occurrence rather than fishing effects (Rasher et al. 2017). Given the lack of examples of trophic cascades in coral reef habitats, it is necessary to ensure an appropriate framework is used to interpret data for these ecosystems. While applied research is a necessary step for improved conservation, misinterpretation of ecological roles can lead to poor conservation and management outcomes (Grubbs et al. 2016).

This review explores: (1) the variables most considered in trophodynamics studies, (2) critiques the adequacy of methods used, and (3) contemplates whether recent publications applied methods suitable to support prominent theories in coral reef ecology. We discuss how recent research on drivers of coral reef trophodynamics often do not account for spatial and temporal variation and methodological issues and provide recommendations for future trophodynamic research.

2.2 Article selection

Searches were performed through different bibliographic platforms to ensure access to the widest range of literature available. Web of Science, Scopus, and Google Scholar were used to explore and extract available published material (Falagas et al. 2008). Google Books NGram Viewer (Lin et al. 2012), Scopus (Kähler 2010), and SciVal (Colledge and Verlinde 2014) metrics were used to analyse trends in keywords and publications to select articles for review (Table S2-a). Selection of publications was similar to Libralato et al. (2014) who showed increased frequency of key phrases such as "food chains", "food webs", and "trophic level" in publications since 1960 from Scopus and NGram searches. They established an historical timeline for the development of trophodynamics in research but did not link keyword searches to coral reefs. For this review, 347 abstracts were chosen from 1942 to 2016 and filtered for keywords with highest relevance to trophodynamics in coral reef ecology. To evaluate recent trends in publications, additional searches were performed through Scival for "food web" and "trophic" relative to coral reefs to determine the top 50 keywords based on 291 publications from 2011 to 2016. Herbivores and predators were the two most common trophic groups studied (Table S2-b). Predators outnumbered herbivores in the literature in the past 5 years with up to 24 publications in 2016 (Table S2-b). For percent scholarly output, habitat, community structure, trophic level, and stable isotopes were among the top-ranking keywords in publication growth.

2.3 Ecological concepts, trophodynamics, and coral reefs

The foundation of trophodynamics is the understanding of how food webs contribute to energy flow. In ecology, food web dynamics are typically based on a hierarchical, pyramid structure where organisms requiring more energy are less abundant than lower level consumers and producers (Libralato et al. 2014). This structure is seen across terrestrial and aquatic environments and is attributed to biomass scaling where resource availability limits the number of large-bodied organisms and higher trophic levels (Trebilco et al. 2013; Hatton et al. 2015). Coral reefs typically follow this classical food pyramid structure, however, due to complex food webs (Choat and Bellwood 1985) and variability in habitat structure (Cox et al. 2000), it has been difficult to define generalized ecological relationships.

Identification of pathways linking sources of nutrition to consumer is essential for understanding ecological relationships in food webs (Table 1). Low-level organisms in a food web, known as producers (such as phytoplankton), provide energy to higher levels through consumption and assimilation. Large-bodied organisms typically hold higher positions in food pyramids as their energetic requirements require consumption of lower level producers and consumers (Lindeman 1942). In biochemical ocean cycling, production occurs through: (1) fixing inorganic source pools of dissolved gases from nitrogen (i.e. nitrates, ammonia), carbon (CO_2), and other essential elements (sulphur and hydrogen), or (2) particulate organic food uptake from nitrogen substrate, detritus (marine snow), and carbon into biological cycles (Michener et al. 2007). These sources of primary production are considered food-web baselines in trophic ecology and their availability is largely dependent on environmental and hydrodynamic variables unique to a region (Paulay 1997). Producers are the origins of bottom-up forcing which influence resource limitation and carrying capacity of higher trophic levels (Terborgh 2015). Biogeographic differences in reef resource availability are explained by factors such as: latitudinal and longitudinal gradients (Harmelin-Vivien 2002), distance from human disturbance, position on the continental shelf, degrees of isolation, and oceanographic variables such as sea surface temperature, upwelling, and currents (Paulay 1997). How each of these components affect food web production and resource availability should be considered in trophodynamic studies.

Within a marine food web, an organism’s role in energy transfer is assigned a trophic position (Bowen 1997; Layman et al. 2012). Interactions among organisms and energy flow are typically defined by resource control or “trophic forcing,” where energy flow within a system can be consumer-driven (top-down), resource-driven (bottom-up), or middle-driven (mid-level consumers) (Verity and Smetacek 1996; Frank et al. 2007; Young et al. 2015). The type of resource control can have major impacts on communities at localized and/or large-scales via cascades or pyramid structures (Sandin et al. 2008; Estes et al. 2011; Sandin and Zgliczynski 2015). Therefore, it is important to examine how trophodynamics influence a community at a defined scale. Contributions from benthic and pelagic sources limit understanding of bottom-up processes on coral reefs because biogeochemical cycles are not well described over spatiotemporal scales (Young et al. 2015). Nutrient enrichment and herbivory have been recognized as crucial bottom-up and top-down processes respectively; influencing ecosystem function and community structure and providing competing hypotheses (Smith et al. 2010). Meanwhile some researchers describe the influence of multiple controlling forces on coral reefs (Lapointe 1999; Terborgh 2015), and others report higher importance of specific trophic groups on resource availability (Lewis and Wainwright 1985; Hughes et al. 1987; Hughes et al. 2007). Disruption of trophic levels through loss and mortality of organisms in a community alter the stability of a food pyramid which can lead to trophic cascades.

For example, pressure exerted by higher trophic levels can control abundance of lower trophic groups preventing cascading effects across food webs. This assumes that keystone species and apex predators are the strongest controlling forces on food web dynamics (McClanahan and Branch 2008). A few cases have described inverse pyramids where the biomass of predators is greater than that of lower level consumers (DeMartini et al. 2008; Sandin et al. 2008; Sandin and Zgliczynski 2015), which is uncharacteristic of a typical marine environment. These examples have only been documented in near-pristine environments (Sandin and Zgliczynski 2015; Mourier et al. 2016; Simpfendorfer and Heupel 2016) and to date have not been reported outside of steep-sided, isolated atolls exposed to upwelling. Whether productivity subsidies supporting inverse pyramids in smaller isolated reefs can be possible for larger, continental environments is unknown. Continental reefs are also exposed to human activity, where high predator abundance is less common (Sandin and Zgliczynski 2015). Without long-term data, it is unclear whether inverse pyramids are more representative of a natural, balanced state than bottom-up pyramids.

Additionally, functional redundancy and diffuse predation may prevent degradation under disturbance, masking the potential controlling effects of trophic groups or individual species (Bascompte et al. 2005). For example, many reef ecosystems have multiple mesopredators feeding at a similar trophic level. Interactions within and among these species and available prey complicate the ability to define trophic pathways. Aside from the concept of "mesopredator release" caused by removal of apex predators (Stallings 2008; Ruppert et al. 2013; Roff et al. 2016a; b; Ruppert et al. 2016), mesopredator influence on communities is largely unknown. Middle-driven systems caused by intermediate consumer influence have only been described for oceanic environments where small pelagic fish control the abundance of both the predator and their prey (Cury et al. 2000; Young et al. 2015). To our knowledge, middle driven systems have not been explored for coral reefs. Beyond defining trophic position, the importance of understanding specific interactions between and among trophic groups is necessary to interpret ecological roles (Figures 2.1-2.2).

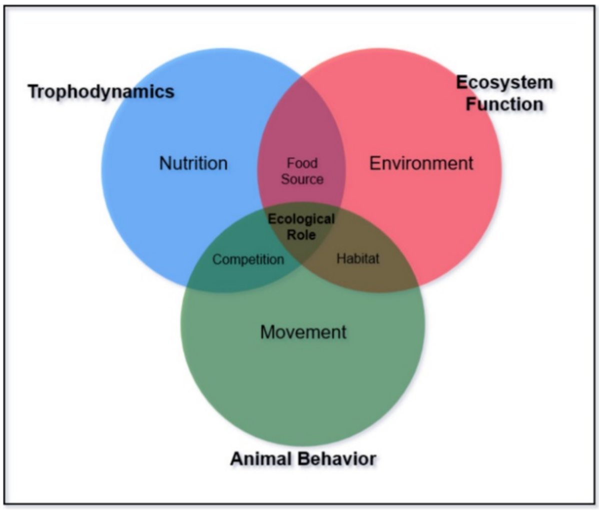


Figure 2.1: Diagram of how necessary concepts contribute to informing ecological roles of a species

The presence of multiple-food webs within coral reefs decreases our ability to understand mechanisms that regulate stability. Based on present knowledge, it is still unclear whether coral reefs behave similar to other marine ecosystems from a trophodynamic perspective. Defining which ecosystem processes contribute to the abundance and biodiversity of coral reefs is controversial (Karlson and Hurd 1993). While it is generally accepted that coral reef communities are stable, the interactions among communities and connectivity from larval dispersal and recruitment are less well known (Forrester et al. 2002). More research is needed to outline consumer-resource interactions and identify knowledge gaps in food webs. While energy availability is an indicator of reef health evidenced by species richness, habitat is also an influential factor (Bellwood et al. 2005). Even at the reef scale, community food web length can differ with habitat (Kolasinski et al. 2016). The importance of understanding spatial dynamics within the study area, whether local or regional, is crucial to assessing ecological roles and energy contribution of a species to a population, community, or ecosystem. Additionally, more attention should be directed toward the influence of under-studied groups such as non-target, cryptic, nocturnal, and benthic macrofauna (Young et al. 2015). For instance, parasites are rarely included in trophodynamic study despite being the most common consumer type in ecological food webs (Demopoulos and Sikkel 2015). Recent reef food web models that include parasitism show insignificant changes to overall flow of models but can dramatically affect specific trophic pathways (Arias-González and Morand 2006). Parasites are also thought to affect feeding behaviour of herbivorous grazers (Fox et al. 2009). Other cryptic organisms can affect trophic links in consumer species with commonly accepted ecological roles. For example, consumption of copepods (Kramer et al. 2013) and high concentration of autotrophs (Clements et al. 2016) sourced within the epilithic algal matrix (EAM) by parrotfish raises questions about the main components of their nutrition. Exclusion of other trophic links such as connectivity to mangrove or seagrass habitats is also common, where grazers are known to make nocturnal migrations off coral reefs to avoid micropredation (Sikkel et al. 2017), or exploit foraging opportunities (Nagelkerken et al. 2000). Limited time and resources prevent incorporation of every component of a food web into a study, but the composition of components included, or excluded, requires consideration when interpreting results.

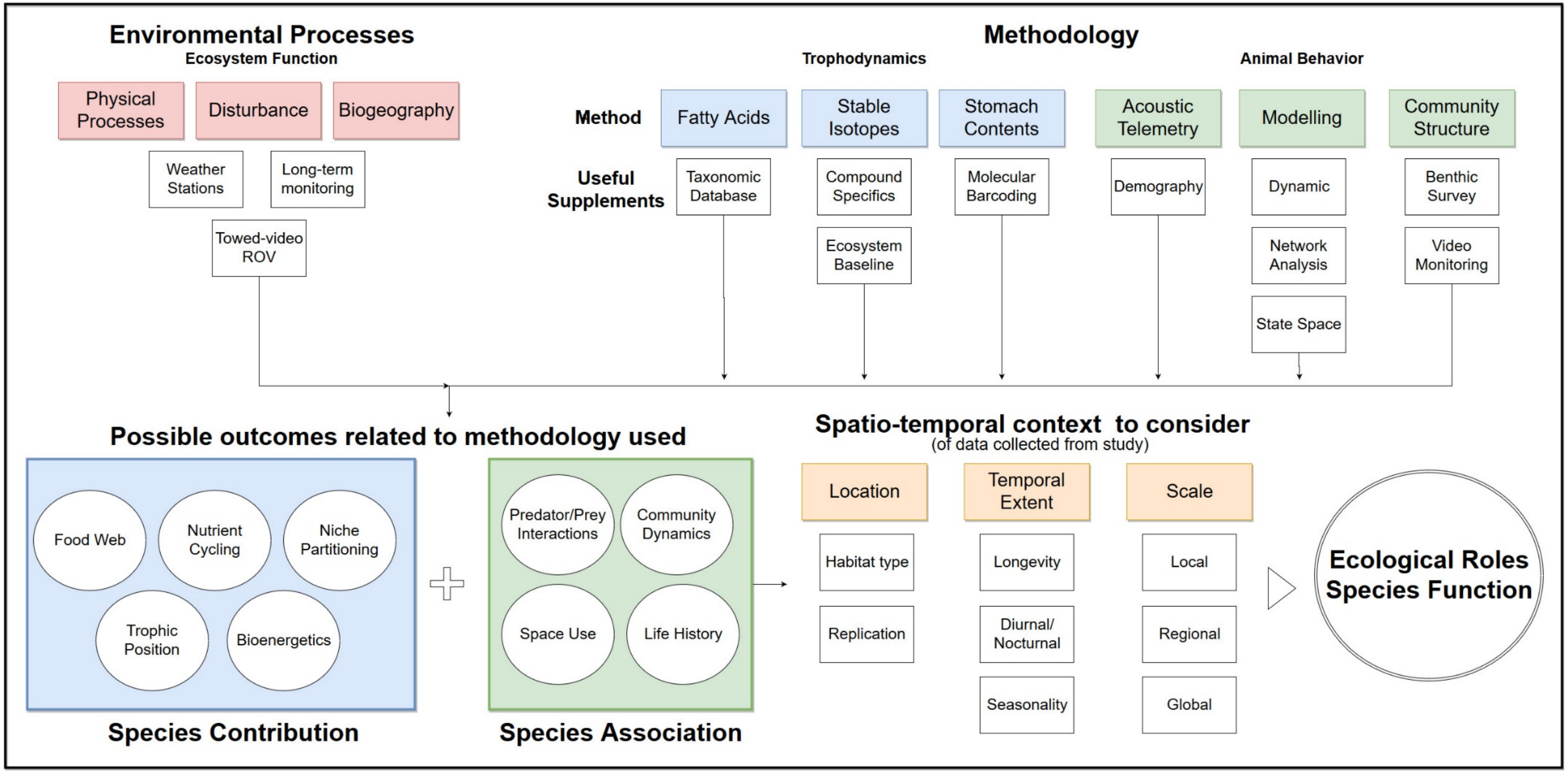


Figure 2.2: Flow chart of suggested process to inform ecological roles from common methodology used in trophodynamic study for a species in coral reefs

Table 2.1: Benefits and disadvantages of methods commonly used in trophodynamic study and which ecological concepts they most relate to

Type	Method	Benefits	Disadvantages	Ecological Concepts
Diet Analysis	Stomach Contents	▪Accurate interpretation of diet composition ▪Offers some taxonomic resolution compared to other methods ▪Can identify life stage of prey	▪Biased towards what has been eaten recently ▪Empty contents are common in larger animals, can lead to misinterpretation ▪Biased towards identification of larger prey items ▪May require lethal sampling	Food web dynamics, food web pathways, consumer resource interactions, functional redundancy
	Molecular Barcoding	▪High taxonomic accuracy in degraded or digested samples ▪Assists resolution of stomach content analysis ▪Possible to be non-lethal ▪(from fecal samples)	▪Can't interpret without sequence database ▪DNA extraction bias ▪Does not distinguish size or life stage	Food web dynamics, food web pathways, consumer resource interactions, functional redundancy
	AA-CSIA	▪Accounts for diet assimilation (tissues) in addition to recent diet (blood) ▪Possible to be non-lethal ▪Does not require ecological baseline for source	▪More expensive than traditional SIA	Trophic position, species biogeographic differences, diffuse predation, functional redundancy
	Stable Isotope Analysis	▪Accounts for diet assimilation (tissues) in addition to recent diet (blood) ▪Possible to be non-lethal	▪Need ecological baseline with temporal consideration	Primary Production, trophic position, biogeographic differences
	Fatty Acid Analysis	▪Can be used to compare diet profiles ▪Does not require ecological baseline for source ▪Possible to be non-lethal	▪Low taxonomic resolution without extensive reference database	Primary Production, trophic interactions, diffuse predation, functional redundancy
	Total Lipid Content	▪Interprets energy allocation and life-history strategy ▪Community metabolic processes	▪Composition can differ between tissues and species ▪Requires greater understanding of metabolic roles of a species ▪Best sample type is liver which requires lethal sampling	Ecosystem health, trophic cascades, functional redundancy, diffuse predation
Ecological Modelling	Multi-species Dynamic Models (i.e. Ecopath)/ Aggregate Models	▪Good for predictions ▪Accommodate for multi-species ▪Can account for behavior over a ▪time-series	▪Difficult for heterogeneity in data ▪Increases untestable assumptions ▪Often includes averaged categorical data	Trophic cascades, diffuse predation, functional redundancy, ecosystem processes
	Individual-based models	▪Explores underlying mechanisms ▪May include predator-prey interactions with a defined spatial scale ▪Ease in coupling with physical models	▪Difficult to incorporate whole ecosystem ▪Statistical cost to increased coupling	Trophic cascades, diffuse predation, functional redundancy, ecosystem processes
	Process-based/Mechanistic models	▪Founded in ecological theory which makes for easy application to known systems ▪Clearly defined assumptions	▪Compromises in scale and resolution in spatial-temporal processes ▪Experimental design may not match management scales	Trophic cascades, diffuse predation, functional redundancy, ecosystem processes
Telemetry	Acoustic electronic tagging	▪Accurate assessment of movement of organisms within the environment, leads to understanding habitat use and predator-prey interactions	▪Expensive, which limits sample size ▪Limited battery life ▪Increased model performance from more robust analytical tools available	Consumer resource interactions, nocturnal organisms

2.4 Methods used to study trophodynamics in tropical coral reefs

The main focus of trophodynamic research is determining spatially and temporally appropriate consumption and interactions across trophic groups (Figure 2.2). Paine (1980) demonstrated the effect of interaction strength of food webs on communities in aquatic systems, and new techniques are constantly being developed to better describe these interactions. Most methods for identifying food web relationships are limited by spatiotemporal scales and variable biological and environmental conditions (Sale 2002; Chabanet et al. 2010; Layman et al. 2012; Young et al. 2015). Fortunately, new techniques in methodology and analysis are available to enhance ecological study (Table 2.1). Most of the methods in this section have already been well reviewed or described by other authors (Layman 2007a; Ilves et al. 2011; Layman et al. 2012; McCauley et al. 2012b; Gilby and Stevens, 2014; Young et al., 2015), so this text highlighted publications that used these methods to describe common ecological roles and functions of coral reef ecosystems. Much of the current research focuses on specific groups such as higher trophic levels or herbivores. While this focus helps define the roles of certain aspects of the food web, research is still needed to incorporate under-represented components of ecosystems to develop a more comprehensive view of coral reef ecosystems.

2.4.1 Diet analyses

Diet analysis is one of the most common methods in trophodynamic study along with direct observation of predator prey-relationships (Choat et al. 2004; Fox et al. 2009; Kramer et al. 2013; Young et al. 2015; Wen et al. 2016). Stomach contents can directly inform what a consumer ingests by examining the frequency of occurrence of species in stomach samples (Cortes 1999). This method can work well to uncover trophic interactions for commonly occurring and abundant species. However, there is often uncertainty in prey identification and metabolic requirements of a consumer (Young et al. 2015). For species of conservation concern, sample sizes for study can be low as there are limitations to lethal sampling. Non-lethal methods such as gastric lavage show what has been recently consumed (Cortes 1997; Frisch et al. 2016), but may be unreliable for determining the full scope of the diet of an individual. For larger species such as sharks, angling may also induce gastric emptying before landing (Frisch et al. 2016), which can affect results. In fact, many studies using gastric lavage and baited capture report high proportions of empty stomachs in predators. Due to these limitations, biochemical tracers and immunological testing through molecular identification of prey (Symondson 2002) have been used to supplement stomach content studies. Taxonomic molecular barcoding can supplement gut content study and assist in characterization of diet (Paula et al. 2016). Molecular barcodes designed to identify diet specialization on invasive macroalgae by coral reef grazers has uncovered trophic links previously unknown in herbivorous fishes in Hawai'i (Stamoulis et al. 2017). Combination of multiple methods in diet analysis can identify trophic position and food web links for trophodynamics, but care is needed when using these methods to identify ecological roles. Habitat is known to be an important consideration in most ecological studies, and it is mentioned most frequently in studies examining stomach contents (98 percent, Table 2.2). Yet even recent studies have ignored potential effects of habitat by combining samples across regions without understanding community composition and available prey. Spatial scale and habitat variables are crucial elements to defining diet analysis in trophodynamics research. Seasonal (i.e. temporal) variability in prey abundance or availability must also be considered. While these aspects are present in some studies, they must be more widely applied to help define ecological processes and trophodynamics in coral reefs and other marine habitats.

2.4.2 Biochemical tracers

Biochemical tracers identify dietary sources in a food web and what individuals directly consume (Post 2002; Young et al. 2015). Tracers quantitatively measure assimilation through tissues to define the diet of an individual without the uncertainty of species identification of stomach content studies (Post 2002; Layman et al. 2007a). Nitrogen and carbon isotopic enrichment in bulk tissue are examined through stable isotope analysis to define the relationship between a predator and its prey

(Post 2002; Layman et al. 2007b; McClanahan et al. 2011; Layman et al. 2012). For producers, carbon isotope proportions vary due to different methods of energy production through photosynthesis (Michener et al. 2007). Carbon ($\delta^{13}C$) is used to identify source pools as there is limited variation in values after trophic transfer, while nitrogen ($\delta^{15}N$) is used to identify trophic position as enrichment is progressive across trophic levels (Kolasinski et al. 2016). Spatiotemporal comparison of diet is also possible with fatty acid analysis. When a predator consumes a species, fatty acids are absorbed with little change in the unique signature, meaning that prey can be identified from adipose tissue and blood samples (Budge et al. 2006). Without a known database of fatty acid profiles, these studies can be limiting. For biochemical tracers, food web limitations mainly come from time and resources available to define an appropriate ecological baseline. Without understanding carbon sources, studies may lack context. For example, carbon flow is challenging to elucidate in coral reefs due to multiple end-members feeding from both benthic and pelagic sources. Application of compound specific amino acid analysis (AA-CSIA) and Bayesian mixing-model techniques can assist in defining these baselines (McMahon et al. 2015). AA-CSIA can provide better baselines by looking at specific amino acids that fractionate with each trophic step (Bradley et al. 2016). AA-CSIA can also reduce the number of samples for analysis by eliminating the need for an exhaustive baseline. But tissue turnover rates, functional redundancy, and complications in retention of nitrogen in certain organisms can also limit analysis (Post 2002; Layman et al. 2007a; McClanahan et al. 2011; Layman et al. 2012). Without species-specific study, improved techniques, and time-series baselines, it is difficult to get a true estimate of trophic position (Layman et al. 2012). Recently, Matley et al. (2016) showed that diet tissue determination factors and turnover rates measured for temperate species may not apply to tropical species, as $\delta^{15}N$ enrichment was lower than published values for a slow-growing predatory reef fish. In larger predatory species such as sharks, care in sample preparation is also necessary as urea retention without extraction can severely affect values, which is often not a common method employed for stable isotope analysis (Li et al. 2016). The physical and biogeochemical nature of a habitat can also have large effects on trophic community structure even at a fine scale. For example, Kolasinksi et al. (2016) studied macro-invertebrate communities of coral reefs and found significant temporal and spatial differences in food web lengths indicating a variety of energy pathways which complicate trophic level definition. Therefore, consideration should be given to understanding the data sources that may limit research to specific habitats or time periods. Recent studies use large-scale spatial and temporal differences in sample collection as caveats in the discussion (Frisch et al. 2016), as opposed to incorporation into the study design. From reviewed publications, only 42 percent of stable isotope analyses included a reference to carbon sources, and 21 percent for fatty acid analyses; 50 percent of studies used a combination of stable isotopes and stomach contents, while 25 percent used a combination of fatty acid and stomach contents (Table 2.2). Stable isotopes contributed to 58 percent of studies that assessed trophic levels of organisms and have been used in 39 percent of Ecopath studies. Refined analysis of trophic levels through biochemical tracers is likely to strengthen and improve trophodynamics research as applications of these methods expand.

2.4.3 Ecological modelling

Statistical models are widely used in ecological studies to understand energy flow and provide a whole of system interpretation. Due to the complexities of marine food webs, trophic relationships are often used to categorize interactions between trophic levels and among individuals within models (Bozec et al. 2005). While linear models often show patterns in specific relationships from quantitative study, they are not robust enough to handle complex food webs such as those on coral reefs (Evans et al. 2013). Dynamic models are required to describe ecosystem organization through networks of species that interact (Liu et al. 2009). In trophodynamic studies, species abundance and diversity are typically categorized by functional groups where diet and habitat similarities are shared by multiple species. This allows simplification of models to a tractable level where input parameters are determined by functional group and often include known values of productivity, biomass, and metabolic efficiency.

While there are multiple dynamic food web models available, Ecopath (Polovina 1984) is the most commonly used for marine and aquatic study (Heymans et al. 2016) and has been applied to coral reefs. Under the assumption of energy equilibrium, Ecopath uses mass balance equations to determine trophic relationships of biomass and productivity (Polovina 1984). Ecopath can be fitted for time series with Ecosim (EwE) (Gotelli and Entsminger 2001) and account for spatial differentiation of habitat with Ecospace (Opschoor 1995). While Ecopath is a popular method, few studies using this model in marine research include time series and spatial data, and even fewer are applied to coral reef ecosystems (Heymans et al. 2016).

Table 2.2: Proportion of reviewed publications that use additional methods for trophodynamic study or mention common keywords in related literature (N=398). EndNote® (Thompson Reuters) was used to annotate documents for searches. [PUBS=proportion of total reviewed publications, ECOPATH (n= 22), LM: linear model (n=42), M=model (n=218), SIA=stable isotope analysis (n=72), SC=stomach content (n=44)]

			Analytical Techniques				
Complementary Methods							
	N	**PUBS**	**ECOPATH**	**LM**	**M**	**SIA**	**SC**
Stable Isotope Analysis	72	0.21	0.39	0.71	0.26	NA	0.50
Ecological Baseline	96	0.28	0.54	0.45	0.39	0.42	0.27
Fatty Acid Analysis	26	0.07	0.14	0.10	0.12	0.21	0.25
Stomach Content	44	0.13	0.11	0.19	0.18	0.18	NA
Model	218	0.63	NA	NA	NA	0.78	0.86
Telemetry	33	0.10	0.04	0.17	0.14	0.18	0.11
Common Keywords in Reviewed Literature							
	N	**PUBS**	**ECOPATH**	**LM**	**M**	**SIA**	**SC**
Abundance	228	0.66	0.79	0.95	0.84	0.65	0.95
Fishbase	70	0.20	0.39	0.43	0.28	0.08	0.25
Ecological Role	47	0.14	0.36	0.19	0.18	0.28	0.27
Habitat	238	0.69	0.89	0.90	0.86	0.71	0.98
Community Structure	162	0.47	0.61	0.64	0.61	0.42	0.57
Trophic Level	131	0.38	0.86	0.50	0.51	0.58	0.57
Trophic Cascade	82	0.24	0.39	0.29	0.32	0.22	0.25
Top-Down	59	0.17	0.39	0.21	0.24	0.22	0.23
Bottom-Up	44	0.13	0.39	0.10	0.18	0.15	0.09
Top-Down+Bottom-Up	35	0.10	0.25	0.10	0.14	0.13	0.07
Caribbean	177	0.51	0.68	0.71	0.69	0.53	0.68
Great Barrier Reef	166	0.48	0.54	0.69	0.61	0.44	0.68
Management	174	0.50	0.93	0.76	0.68	0.50	0.52

For Ecopath to be effective, thermodynamics and ecological knowledge behind fitting a model are required to prevent misuse (Evans et al. 2013; Young et al. 2015). Thirty-nine percent of reviewed Ecopath studies (Table 2.2) for coral reefs used Fishbase (Froese and Pauly 2003) as a source of data for the model. While this resource is a reputable data repository with relevant diet and productivity information, there is considerable uncertainty in empirical data and regional species variation. Without understanding ontogenetic diet change, temporal and biological shifts in behaviour and foraging of a species, responses to disturbance may be poorly interpreted (Young et al. 2015). Even if an organism has a highly specialized diet and small home range, external stressors and biogeography vary (Sale 2002). Ecopath relies upon the strength of interactions between predators and prey and requires extensive knowledge of each species fitted into the model. While these models take diet into account, predator avoidance is less well described and parameters such as refuge availability and niche occupation are difficult to fit into a model. For mobile, large predators, effects on lower trophic groups are poorly understood as top-down forces often result in diffuse predation that is difficult to characterize with Ecopath parameters. Predator-prey structure in ecological models was recently examined and researchers found that more complex models do not necessarily invalidate predicted behaviours in simpler models, but care must be used when employing the latter (Walters et al. 2016). The authors showed how assumptions of feeding rates of predators, prey availability and other factors drastically change isocline patterns in predator-prey models. They note that uniform spatial assumptions should be avoided when using trophic models. Of the reviewed studies, habitat was referenced in 89 percent of Ecopath studies focused on coral reefs (Table 2.2), but many were not specific to a single area and assumed homogenous habitat across regional scales. Testing underlying assumptions is critical when employing predator-prey models (Heymans et al., 2016), and understanding interactions at an appropriate spatial scale will assist in increasing the efficacy of these models.

While some scientists have urged that more process-based ecological models be developed to identify the underlying mechanistic behaviour of an ecosystem (Evans et al. 2013; Turney and Buddle 2016), recent articles still often ignore dynamics of spatial and temporal variability as well as historical baselines (Lamy et al. 2016). Some authors have moved past dynamic models such as Ecopath and explored individual-based predator-prey population models to account for spatiotemporal heterogeneity (Thierry et al. 2015). Others have tested vulnerability of reef ecosystems by measuring overall entropy from bioenergetics (Arreguín-Sánchez and Ruiz-Barreiro 2014), interaction strength between trophic levels (Bascompte et al. 2005) and applied network analysis (Navia et al. 2016). Integration of unified models may also be beneficial. While unified models often are used to explain theories of biodiversity, recent developments of metacommunity analysis between labrid fishes and corals have identified patterns of species associations (Connolly et al. 2017). Species associations are critical in integration of trophodynamics into management. Critics of food web models for coral reefs highlight that any model will be a simplified version of real-time processes and caution should be taken when using them to inform management. Although management is mentioned in 98 percent of reviewed publications (Table 2.2), few articles using Ecopath in marine environments have been used for management purposes (Heymans et al. 2016). To better inform management, research is needed on spatiotemporal variability to better fit models. As Ecopath provides an informed snapshot of behaviour of a system, including variability over space and time may assist in reducing uncertainty.

2.4.4 Telemetry

Acoustic telemetry is widely used in aquatic ecology, but rarely incorporated into trophodynamic studies. Telemetry can be used to better understand the distribution, residency, and behavioural patterns of species and applied to understanding how predators interact with prey (McCauley et al. 2012b; Young et al. 2015; Matley et al. 2016). Matley et al. (2016) determined that although two species of co-occurring reef fish had overlapping diets, space use differed between the two species suggesting niche separation. Studying movement can also show how behaviour may be affected by environmental stressors and conditions. Telemetry can also be used to supplement other methods to identify behavioural adaptions to resources such as targeting invasive species (Bierwagen et al. 2017). Improved analytical methods for ecology such as network analysis (Espinoza et al. 2015), Bayesian statistics (Johnson et al. 2010) and state-space models (Jonsen et al. 2005) are assisting predictive capability of movement relative to environmental variability. For example, telemetry has helped define population dynamics through focused mark-recapture models (Dudgeon et al. 2015). Other applications such as identifying feeding patterns from movement and prey associations that may influence food web dynamics may play a role in future trophodynamic analyses. Despite the advantages of telemetry, the time and financial investment required may limit sample sizes and application to trophodynamics (Young et al. 2015). Telemetry was used in less than 10 percent of reviewed studies and less than 20 percent in combination with other empirical methods (Table 2.2).

2.5 Challenges and Discussion

The key challenges in trophodynamic study in coral reefs come from logistical difficulties, methodology limitations, and context of study design. Whether a study intends to identify an energy pathway, or consider management decisions relating to a species, the conclusions should not go beyond the limitations derived from the study. Sufficient information of reef ecology such as spatiotemporal abundance, distribution, habitat associations, environmental inputs, diet, and life history of a species is necessary to inform ecological roles and function (Figure 2.2). While recent examples of poor management decisions have created a need for standardizing approaches in the field of trophodynamics (Grubbs et al. 2016), studies are still omitting key concepts before implementing applied research. We have highlighted such studies in relation to popular methods, but also identified recent research that is incorporating and combining new methods to account for some of the challenges faced within the field. In addition to using combined methodology, researchers should consider concepts that better explain the organizational structure of coral reefs and how multiple food webs or communities interact.

2.5.1 Accounting for variation in studies

Habitat and community structure are well-documented to be important variables in ecosystem processes, particularly when examining trophodynamics. Yet, scientists often take a “one size fits all approach" to food-web studies. Dornelas et al. (2006) demonstrated that coral reefs cannot be explained by widely-accepted theories of biodiversity, which suggests that spatiotemporal stochasticity observed in coral reefs is not well understood. This validates the need to understand process-based interactions. Most trophodynamic studies of coral reefs come from the Caribbean and Great Barrier Reef, which cover large spatial scales and latitudinal gradients. While biogeographic variability is constantly acknowledged, publications link conservation concern to broad topics such as management zones irrespective of reef variability or geographic position (Frisch et al. 2014; Rizzari et al. 2014; Boaden and Kingsford 2015), and perform large scale analyses based on databases that do not account for fine-scale variation (Campbell and Pardede 2006; Graham et al. 2008; Campbell et al. 2011; Barneche et al. 2014; Alonso et al. 2015; Aguilar-Medrano and Barber 2016). While management zones are important to understanding human disturbance, many studies exploring fishing effects lack historical baselines, movement data, and diet relative to changing diversity and community structure (Greenwood et al. 2010; Edgar et al. 2011). Additionally, the influence of natural cycles is rarely considered (Kruse et al. 2016) although they can play an important role in ecosystem function. A review by Bijou et al. (2013) discussed the effect of natural cycles (diurnal, tidal, lunar, and seasonal variation) on fish movement where the authors found that studies ignoring natural cycles increased unexplained variation in the data thereby reducing their effectiveness in defining ecosystem processes.

2.5.2 Controlling forces in trophodynamics

In addition to lacking spatiotemporal context, researchers may be misinterpreting controlling forces in coral reefs. Across all ecosystems, biomass pyramids and the role of trophic subsidies are not well understood (Trebilco et al. 2013). Top-down versus bottom-up organization of coral reefs is debated in the field, particularly regarding the focus of conservation efforts (herbivore focused, or predator focused). Pyramids are the primary structure used to argue resource control but may oversimplify the unique and fine-scale interactions that occur at the reef level. Marine food webs have been described as “ecological road maps” and the varying networks that link different trophic levels in coral reefs could explain their resilience to cascading effects (Turney and Buddle 2016). In coral reefs, the semi-open nature of communities increases the difficulty in mapping food webs from source to consumer and the influence mesopredators may have on lower trophic levels. Trophic cascades were mentioned in 24 percent of reviewed publications, yet there is little empirical evidence documenting cascading effects in coral reefs. Even in the few cases documenting trophic cascades, the results are inconclusive. Estes et al. (2011) used the Northern Line Islands as an example of trophic cascade, but the original research by Sandin et al. (2008) showed no evidence of trophic cascade through use of principle component analysis. The work by Sandin et al. (2008) reflects conclusions made by Bascompte et al. (2005) who showed strength of trophic interactions on coral reefs buffer cascading effects but become weaker under pressure of external perturbations such as overfishing. This does not mean that cascading effects do not exist, but evidence is limited, and little is known outside of correlative associations regarding herbivore biomass increases due to predator removal or other effects of disturbance.

In trophic cascades, if a trophic level is added or removed, coral-algal phase shifts and changes in ecosystem stability can occur (Terborgh 2015). The strongest evidence of cascades found in coral reef systems come from herbivory, where depletion of grazers such as echinoderms from overfishing or pathogens allowed for explosive population growth of macroalgae in the Caribbean (Hughes et al. 1987, Mumby et al. 2005). Rasher et al. (2017) also described a trophic cascade via reduced exposure of herbivores to predators which resulted in variation in feeding patterns based on fear effects. Though the expected negative effects of cascades in reefs aren’t always clear. In cases where conservation efforts have maintained predator populations via reduced fishing, the expected cascading effect of macroalgal increase from a depletion of grazers as prey doesn’t always occur (Mumby et al. 2007). Keystone species and functional redundancy are not always present in reefs with high biodiversity (Hoey and Bellwood 2009), which makes comparison across spatial scales all the more difficult. Even if assumed cascading events are observed such as phase shift, finding the cause of such patterns at large spatial scales is challenging (Dulvy et al. 2004). Attention should also be paid to temporal gradients over which cascades occur, considering life-history and growth capabilities of populations as well as lagged effects from perturbations that can occur over extended time periods (Dulvy et al. 2004, Grubbs et al. 2016). The difficulty in linking trophic levels to the same event that categorizes a trophic cascade is difficult to support empirically, particularly when most reefs are already in a degraded state from external stressors. The fact that cascades have not yet been effectively documented for coral reefs undermines the assumed organization of coral reef food webs. High biodiversity complicates ecosystem models and trophodynamics but may be key to the functionality of reef ecosystems in a changing environment.

Although pyramid structure is evident in coral reefs, there are high numbers of mesopredators representing intermediate trophic levels that are thought to exhibit functional redundancy. Mesopredators are considered to have less of an effect on the trophic structure of a system (Paine 1980; Estes et al. 2011), but there is little empirical evidence to support this due to difficulty in defining predator-prey relationships. A recent meta-analysis of food web studies found that aquatic models produced a strong pyramid pattern, suggesting scale variance in predator-prey ratios according to biomass power laws consistent with Hatton et al. (2015) (Turney and Buddle 2016). The analysis also showed that on average aquatic communities have a higher diversity of mesopredator species than herbivores, with low abundance of top predators. Intermediate effects of mesopredators on aquatic systems are largely unknown and often grouped within many ecosystem types such as intertidal, pelagic, and reef (Hatton et al. 2015). Elasmobranchs and other fishes are known to feed at different trophic levels based on stage of maturity, where they exhibit high functional redundancy as mesopredators and limited redundancy as apex (Navia et al. 2017). Thus, assigning a single ecological role to a species is limiting and can affect the predictive nature of model capability. The role and effects of mesopredators requires further exploration and definition to refine where greatest predation and productivity sources occur in reef systems. Many researchers believe that coral reefs are influenced by both top-down and bottom-up processes, and it should not be a question of one versus the other (Terborgh 2015). Further exploration of middle-driven systems and consideration of the driving interactions between trophic groups should be considered.

2.5.3 The contributions of trophodynamics to coral reef ecology

There are many components of trophodynamics that we are beginning to understand which can be used to inform ecosystem function and changes over time. Many of these components are shared among marine systems, but discretion should be used when assuming similar trophodynamics processes that are not fully described for coral systems. Current research validates that coral reefs fundamentally have:

(1) Highly complex, semi-open systems (Sale 2002).

(2) Resident species and mobile visitors that utilize reef habitats (Dudgeon et al. 2015).

(3) Influence from both benthic and pelagic productivity sources (Michener et al. 2007).

(4) High abundance and diversity which play a large role in ecosystem function (Choat et al. 2004).

(5) Spatiotemporal variability which is essential to assessing trophic position (Heymans et al. 2016).

(6) Small areas with high diversity exhibiting functional redundancy between producers and consumers (Aguilar-Medrano and Calderon-Aguilera 2016).

(7) Food web omnivory that can weaken chance of trophic cascades, even in the presence of exploitation of predators (Bascompte et al. 2005).

(8) Predators that are known to exhibit diffuse predation, although their effect on lower trophic levels is still poorly understood (Heupel et al. 2014).

(9) Cryptic, invertebrate, and nocturnal organisms which are often ignored in food webs (Marnane and Bellwood, 2002; Kolasinski et al. 2016).

(10) Pyramids of species richness that are not generated by chance. (Turney and Buddle 2016).

These concepts need to be explicitly considered in study designs of trophodynamic research and uncertainty should be acknowledged before drawing conclusions regarding the ecological role of any species. Additionally, the underlying trophodynamic processes describing these observations should incorporate long-term datasets that accurately reflect the scope of data used. Before describing ecological roles of reef organisms, it is necessary to determine which interactions may have the highest influence on the trophic structure of these complex systems. For researchers, this space is still largely under-studied, and collaborative efforts are likely needed to elucidate the mechanisms that contribute to the stability of these ecosystems.

There are still many ecological unknowns in coral reef systems and there will likely never be a perfect approach to fully describe coral reef trophodynamics, but we can strive for better empirical data collection and analysis of patterns. Standardizing the approach to applied questions may help create a more cohesive space for collaboration in future studies. There is a need to apply multiple methods and clear definitions of spatial and temporal scale to meet the needs of trophodynamic research (Figure 2.2). How a species contributes energetically and how they interact with other species within a community take different methodological approaches and clear synthesis between the two to identify ecological roles. Arguably, coral reef systems do not appear to energetically behave the same as other marine food webs, such as intertidal or pelagic systems, and trophodynamic study should consider different scenarios and models. Based on concepts in this paper, we suggest recent literature may not adequately acknowledge the unique differences in coral reef food webs against the broader literature in marine trophodynamics, particularly over varying spatiotemporal scales. While theories for coral reefs are constantly being modified, conclusions of many articles still resort to generic descriptions of standard pyramid structure to explain biodiversity. Predation and competition within predator-prey interactions should be further considered in addition to exploring the effects of both bottom-up and top-down approaches. Without a better understanding of essential reef processes that affect ecological roles of species over both space and time, caution should be used in applying results to management and conservation efforts.

Chapter 3: Reef-scale variability in fish and coral assemblages on the central Great Barrier Reef

3.1 Introduction

Coral reefs host nearly a third of worldwide marine fish species and despite widespread degradation, remain some of the most productive and diverse marine ecosystems (Moberg and Folke 1999; Sheppard et al. 2017). Yet, the persistence of reef productivity is reliant on recovery from disturbance, which have both natural and anthropogenic causes. The increasing frequency and severity of events are leading to widespread coral loss and degradation of coral reef ecosystems (De'ath et al. 2012, Cheal et al. 2017; Hughes et al. 2017). The compounding effects of disturbance are seen at varying scales across systems such as the Great Barrier Reef (GBR). Previous research shows most coral and reef fish communities on the GBR recover following disturbance (Halford et al. 2004; Emslie et al. 2008; Johns et al. 2014), with relatively few experiencing phase shifts (Cheal et al. 2010). While the GBR has a positive record of recovery and re-assembly (Done et al. 1991; Halford et al. 2004; Emslie et al. 2008; Johns et al. 2014), future disturbance may negatively influence recovery through increasing severity of disturbances (Cheal et al. 2017; Hughes et al. 2017). Additionally, research has also shown that reefs at the sub-regional (10-100km) scale show variable recovery to localized disturbance events (Osborne et al. 2011). Amidst ongoing climate change, the coupled effects of natural disturbance with anthropogenic stressors impedes recovery potential. Even though reefs on the GBR thus far have remained relatively stable through disturbance pulses, it is important to monitor areas that may be most vulnerable to persistent stressors.

The GBR is subject to acute and chronic disturbances that directly affect the biological organization of reefs and can cause structural damage that degrade essential habitat for associated fauna. Key acute disturbances include mass coral bleaching (the expulsion of symbiotic zooxanthellae), tropical cyclones (including hurricanes and typhoons) and outbreaks of the corallivorous crown-of-thorns starfish (COTS), *Acanthaster* cf. *solaris* (Osborne et al. 2011; De'ath et al. 2012; Hughes et al. 2017). Important chronic disturbances include higher sea surface temperatures (linked to coral bleaching and disease), reduced water quality from terrestrial runoff, coastal development and dredging, and overfishing. The primary negative effect of disturbance is coral mortality generally measured as reduction in percent hard (Scleractinian) coral cover, a common metric of reef health. Additionally, most disturbances cause differential mortality among coral taxa, which then fundamentally alters the composition of coral assemblages. The return of hard coral cover and re-assembly of coral communities back to pre-disturbance levels and configurations are important in determining reef recovery following acute disturbances.

One way to determine whether habitats become degraded or remain healthy is to categorize their present status and susceptibility to changing conditions. Several biological and physical features can be quantified to determine reef condition and vulnerability to disturbance. In general, coral reproduction, recruitment and growth, habitat availability, and the presence of abundant and diverse herbivorous fish assemblages all contribute to maintaining a coral-dominated state (Graham et al. 2011). For instance, herbivore grazing limits algal overgrowth, creating space for coral recruitment, which also provides more complex habitat for reef-dwelling fishes (Burkepile and Hay 2008). These features can be quantified into common metrics for determining reef condition through measure of percent hard and soft coral cover, algal cover, structural complexity (e.g. rugosity) species abundance, and species diversity (Smith et al. 2016).

A growing literature on threats to coral reef stability highlights the need to assess mechanisms that maintain reef condition between disturbance events. As reefs are inherently dynamic systems punctuated by perturbations, recovery from disturbances requires the full range of processes be preserved. However, the strength and direction of change in a given process is determined by the response diversity (the spread of change in numerical abundance of individual species) and functional redundancy (the number of species performing a given function) (Elmquist et al. 2003). Coral reefs have been well studied in recent decades, yet we still have limited understanding of the underlying interactions important to ecosystem stability.

Fishes are a diverse component of coral reefs and perform many ecological functions, such as energy transfer (McMahon et al. 2016), bioerosion (Bellwood 1995), and herbivory (Green and Bellwood 2009). Individual species perform ecological functions which drive ecosystem processes, where a greater array of functions (functional diversity) equate to a greater diversity of processes which promote reef health (Nyström 2006; Pratchett et al. 2011). Degradation of benthic communities can affect fish populations following acute disturbance (Pratchett et al. 2008; Graham et al. 2011), but long-term effects on community structure need to be identified. Few studies have examined functional differences in communities with similar habitat and disturbance exposure (but see Emslie et al. 2010, 2012, 2017, Mellin et al 2016). Without long-term observations of functional group diversity within assemblages, recovery and productivity remain unknown (Berkstrom et al. 2013).

Large scale studies of coral reefs on the GBR have shown general patterns in ecological response to degradation (Osborne et al. 2011; De'ath et al. 2012), but such studies tend to average over dynamics at coarse spatial scales and can miss impacts of disturbance to individual reefs (Done et al. 1991). Therefore, it is important to assess disturbances at different spatial and temporal scales. Understanding spatio-temporal differences among reefs is necessary to define how the response to disturbance varies among individual reefs and what effect local changes have on broad scale patterns. For example, reefs vary in size and shape, and are subject to differing environmental drivers and disturbance regimes (Williams 1982; Bellwood et al. 2004), which influence variability in community structure. Thus, the role distinct disturbance events have on individual reef community structure and composition can be variable (Houk et al. 2014).

Here we explore the functional structure of fish assemblages to determine spatial reef-level variability relative to benthic structure and community patterns associated with response to disturbance. The aims of this paper were to: (1) assess reef variability and community structure over time at four reefs with similar geomorphology and exposure to local disturbance, (2) investigate whether certain functional groups in reef assemblage structure contributed to variability and recovery among reefs; and (3) if any observed change in functional assemblage variation post-disturbance is an indicator of reef vulnerability or reassembly. We hypothesize that fish functional abundance and diversity differs with distance across the continental shelf position due to differences in human exposure and physical oceanographic features. Thus, we expect that reef reassembly post-disturbance will not be uniform across all reefs in the study area. Based on recent research showing large-scale study can mask fine-scale changes (Ceccarelli et al. 2016), we also predict that fish functional changes reveal more detail about reef recovery than fish abundance and diversity.

3.2 Materials and Methods

3.2.1 Study Site and Surveys

To quantify reef-scale community composition and the impact of disturbance, four individual reefs were surveyed biennially from 2006-2016 by the Long Term Monitoring Program (LTMP) at the Australian Institute of Marine Science (AIMS). Reefs were selected to be of similar size, orientation, location in the central section of the GBR (~18°S), and position across the continental shelf. Reefs were also paired depending on management zone (open or closed to fishing – Figure 3.1). Rib and Helix Reefs are on the mid-continental shelf, while Chicken and Knife are situated on the outer-shelf.

Distance from the coast (kms) was calculated for each reef. The LTMP surveys three sites in shallow reef-slope habitat (<15m) on the northeastern flank of each reef (Figure 3.1). Each site comprises five permanently marked 50 m transects between 6 and 9m depth (n = 15 per reef per year). The abundance of 216 species of diurnally active, conspicuous fishes were recorded using underwater visual census (Halford and Thompson 1994) and converted to density/1000m^2. Pomacentrid fishes were counted on 1m belt transects while all other fishes were counted on 5m belt transects. The observer swam the transect recording the abundance of all 216 species encountered at a standard swimming speed of approximately 10m/minute, while a second diver deployed the transect tape behind the observer. Percent cover of corals and other benthic biota were then estimated from digital images taken concurrently along the same transects by separate observers following the fish surveys (Jonker et al 2008). Benthic organisms were subsequently identified to the highest taxonomic level possible under five points per image (n = 200 points per transect) with ‘ReefMon’ software and the data were converted to percent cover (Jonker et al 2008). In addition to survey data, environmental data is also taken. The LTMP collects water temperature (VEMCO temperature loggers), wind speed, tide, underwater visibility and depth for each survey site. During the study period, some reefs were impacted by COTS and severe TC Yasi (2011), which passed just to the north of study area.

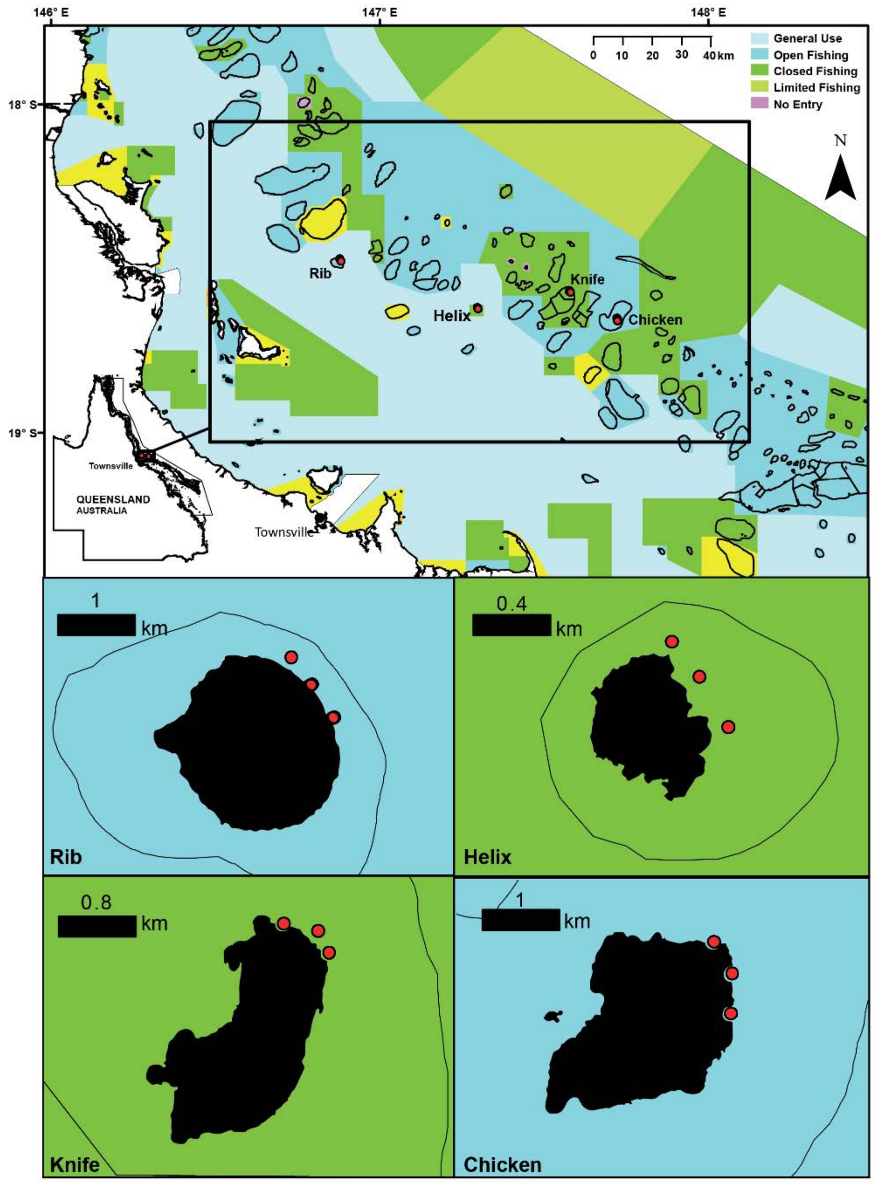


Figure 3.1: Map of the Townsville sector of the central Great Barrier Reef (Queensland, Australia) overlaid with GBRMPA zoning information: Light blue=general use zone (open to all fishing), Dark Blue= habitat protection zone (open to fishing except trawling)-, Dark Green= marine national park zone (closed to fishing), Yellow= conservation park zone (limited fishing), Pink= preservation zone (no entry), marine park boundary, and locations of LTMP survey sites (red markers) on northeast reef slope habitat

3.2.2 Reef Community Characteristics

Percent cover of benthic communities were recorded in seven categories; hard coral (*Acropora* and non-*Acropora*), soft coral, abiotic (i.e. dead coral, rubble, sand), coralline algae, macroalgae (e.g. *Halimeda*), turf algae, sponges, and other (Table S3-a). Fishes were assigned to one of 11 functional groups similar to previous studies (Emslie et al. 2008; MacNeil et al. 2015) including, planktivores (some Pomacentridae), grazers (some Acanthuridae, Siganidae), detritivores (Acanthuridae, some Pomacentridae), omnivorous Pomacentrids (some Pomacentridae), Piscivores (Serranidae), excavators/scrapers (Scarine Labridae), browsers (some Acanthuridae), piscivorous invertivores (some Lethrinidae, Lutjanidae), corallivores (Chaetodontidae), micro-invertivores (some Pomacentridae, Labridae), and macro-invertivores (some Lethrinidae) (Table S3-a). Density of functional groups was calculated by summing the density of all species assigned to that group.

3.3.3 Data Analysis

Multivariate Analysis

All analyses were conducted in R version 3.5 (R Core Team 2018). Multivariate analyses were used to examine spatial differences in (1) benthic cover and (2) fish community density to determine the most influential explanatory variables that contributed to community dissimilarity among reefs. To examine spatial variability in community structure among reefs, we used separate constrained distance-based redundancy analyses (db-RDA) based on a Bray-Curtis dissimilarity matrix using ‘vegdist’ and ‘capscale’ functions in the ‘vegan’ package (Oksanen et al. 2017) for benthic and fish groups. Dissimilarity values from ordinations were tested for collinearity using ‘vif.cca’ diagnostic canonical correspondence analysis (CCA) and ‘ordistep’ model with pseudo-Aikake Information Criterion (AIC). The diagnostic function assessed potential linear dependencies among constraints before running the ‘ordistep’ model. Partial effects for each factor were used as predictors to determine the best performing model. The initial ‘ordistep’ models were used as an exploratory tool to see if any unexpected community variables may explain drivers of dissimilarity in assemblage of both benthic and fish groups. This involved including density of all fish functional groups as variables for benthic models and all benthic groups as variables for multivariate fish models. Additionally, constrained ordinations included reef characteristics and environmental explanatory variables such as tide, water temperature, shelf position, site and management zone. While we would have preferred to include additional physical variables such as wave exposure, this information was unavailable.

However, distance from land was used as a proxy as outer-shelf reefs are known to be areas that have stronger wave action and exposure to deeper depths. After running the initial model, any variable that did not make ecological sense or was determined to be collinear with other variables was dropped. Then, the ‘ordistep’ models were re-run with limited variables until the best model (with the lowest pseudo-AIC) was determined for both benthic group dissimilarity and fish functional group dissimilarity (Tables S3-b, S3-c).

Ordination bi-plots associated with the best performing model of constrained variables were produced with canonical analysis of principal components (CAP), where the axes represent the distance and direction of higher abundance for site and species scores. Trajectory arrows in the bi-plot were fit for highest influence of reef variability from explanatory variables. Centroids were also plotted to visualize average assemblage differences between pre- and post- disturbance periods per reef. Permutational analysis of variance (PERMANOVA) using ‘adonis’ was used to characterize multivariate differences in benthic and fish assemblage structure among reefs and years (Table S3-d). Variance partitioning (‘varpart’) was also used to look at variance (adjusted R^2) of each exploratory variable in the models.

For benthic groups, multivariate analyses were performed with a community matrix of percent cover. Because the benthic groups were proportional data versus count data for fishes, they were not transformed prior to performing ordinations. Explanatory variables for the constrained ordinations initially included all fish functional groups, survey site, distance from land, and the reef and year interaction term. Management zone and shelf position were dropped due to collinearity and lower effect on variance than other factors. Fish functional groups were included as predictor variables to determine if any had potential top-down influence on benthic cover.

For fishes, multivariate analyses were performed for two separate community matrices; one based on individual species and one based on functional groups. The mean density of fish species and functional groups were fourth root transformed to reduce the influence of highly abundant species and functional groups before conducting ordinations (Andradi-Brown et al. 2016). The species ordination explained less variation than the functional group ordination and was dropped from further analysis. Explanatory variables for the functional constrained ordination initially included all benthic groups, survey site, distance from land, and the reef and year interaction term. Management zone and shelf position were dropped due to collinearity and lower effect on variance than other factors. Benthic groups were included as predictor variables to determine if any had potential bottom-up influence on fish density.

Pearson's correlation was then used to examine pairwise relationships among trophic groups and benthic habitat by reef. Correlations were measured between fish and benthic groups to determine potential dependencies fish may have to benthic cover and vice-versa. Correlations were statistically tested with 'cor.mtest' function to generate Rho and p-values between each fish functional group and benthic cover per reef.

Linear Models

Spatio-temporal variation

Linear modelling was used to determine the spatio-temporal effects of most influential explanatory variables on the distribution of each individual benthic and functional group. To compare spatial and temporal variation of percent cover of benthic groups, we used restricted maximum likelihood (REML) with the 'lmer' function in the 'lme4' package (Bates et al. 2013). Linear models were based on the best model derived from the multivariate analysis but with the addition of a random term of site nested within reef with the intercept conditional on categorical year (i.e. Year | Reef/Site). All models included the fixed terms of reef and year interaction, and distance from land. In the seven benthic models (one for each benthic group), corallivorous fishes were included as a fixed terms of were added for some groups (non-*Acropora,* coralline algae) to test for top-down effects on benthic assemblages (Table S3-e).

To compare spatial and temporal variation in overall fish density, species richness, and density of each fish functional group we used Poisson generalized linear mixed effect models (glmer) with 'lme4' package (Bates et al. 2013). For each of the thirteen models (one for total density, species richness, and one each for the density of each fish functional group), reef and year interaction, distance from land, and hard coral (*Acropora* and non-*Acropora*) were fixed terms and site nested within reef with the intercept conditional on year (i.e. Year | Reef / Site) was included as a random term (Table S3-e). Hard coral was included to account for habitat complexity, which has been shown to be important driver of reef fish assemblage structure (Gratewick and Speight 2005; Graham et al. 2009; Emslie et al. 2014). Additionally, for models investigating herbivorous fishes (i.e. detritivores, grazers, excavator/scrapers), macroalgae, and turf algae were added as fixed terms in the model comparison. These fishes graze on algae which may be reasonably be expected to exert bottom-up control of their populations.

For both benthic and fish models, tests for temporal auto-correlation were performed with the 'acf' function on residuals in the "BASE" package. Overall, no temporal auto-correlation was found for benthic or fish groups. For each benthic and fish group, models were tested with AIC to choose the most parsimonious fit before choosing the most optimal for post-hoc testing. Tests of statistical significance of pairwise terms (Reef |Year) were conducted for benthic and fish groups using a Tukey's post-hoc test adjusted for multiple comparison of means with 'lsmeans' (Lenth 2016).

Disturbance

Linear modelling was also used to look at the impacts of disturbance on each benthic and functional group, comparing benthic cover and fish functional density pre- and post- disturbance. To test for effects of disturbance on overall assemblage structure, benthic cover and fish densities were separately categorized as "pre" (2006-2010) and "post" (2012-2016) disturbance by aggregating transects within each time period (15 transects/reef per sampling year totalling n=45 per reef pre/post) to determine differences in community assemblage as a response to severe Tropical Cyclone Yasi. To investigate interaction terms, Tukey's post-hoc in 'lsmeans' was used as a measure of statistical significance, where the pairwise term (disturbance | reef) was compared for each benthic group (Table S3-e).

For each benthic group, a generalized linear mixed effect model using restricted maximum likelihood (REML) was performed to examine benthic cover differences pre- and post- disturbance. All models had fixed terms of reef and year interaction, and distance from land with an included random term of site nested within reef with the intercept conditional on categorical year (i.e. Year | Reef/Site) (Table S3-g).

Generalized linear mixed effect models with a Poisson distribution were performed for overall mean fish density, species richness, and the density of each fish functional group to examine pre- and post-disturbance differences. For each model (13 total- one for overall mean fish density, species richness, and the density of eleven fish functional groups), reef and year interaction, distance from land, and hard coral (*Acropora* and non-*Acropora* as a proxy for structural complexity) were fixed terms and site nested within reef with the intercept conditional on year (i.e. Year | Reef/Site) was included as a random term (Table S3-h). Additionally, similarity of percentages (SIMPER) analysis was used to determine which species per functional group had the highest contributions to decline or increases in density post- disturbance (Table S3-i).

3.3 Results

3.3.1 Spatial and temporal patterns in benthic assemblages

There were distinctions in benthic assemblages among the four reefs with main differences between mid-shelf and outer-shelf reefs (Figure 3.2). Management zone had little effect on assemblage structure of the benthos from ordination models and was dropped from subsequent linear models. The biggest driver in distinction of benthic assemblages was the reef and year interaction ($R^2=0.30$, $p<0.001$, Table S3-d) followed by distance from land ($R^2=0.14$, $p<0.001$, Table 3.1, Table S3-d). *Acropora sp.* and turf algae were characteristic of mid-shelf reefs while coralline, non-*Acropora sp.* and soft coral characterized outer-shelf reefs (Figure 3.2, Table 3.1). All other benthic categories had minimal influence on reef variability except for soft coral cover which contributed to community differences between Knife and Chicken. Spatially, the most dissimilar reefs were Rib and Knife Reefs and temporally the years 2012 (year immediately following disturbance) and 2016 were most influential in distinction among sites. Corallivores had a small significant effect on percent cover of benthos between sites ($R^2=0.02$, $p<0.001$, Table S3-d) contributing to vertical separation between Rib Reef and outer-shelf reefs. Chicken and Knife reefs had the strongest structural changes pre- and post-disturbance compared to Rib and Helix reefs (Figure 3.2, Table 3.2).

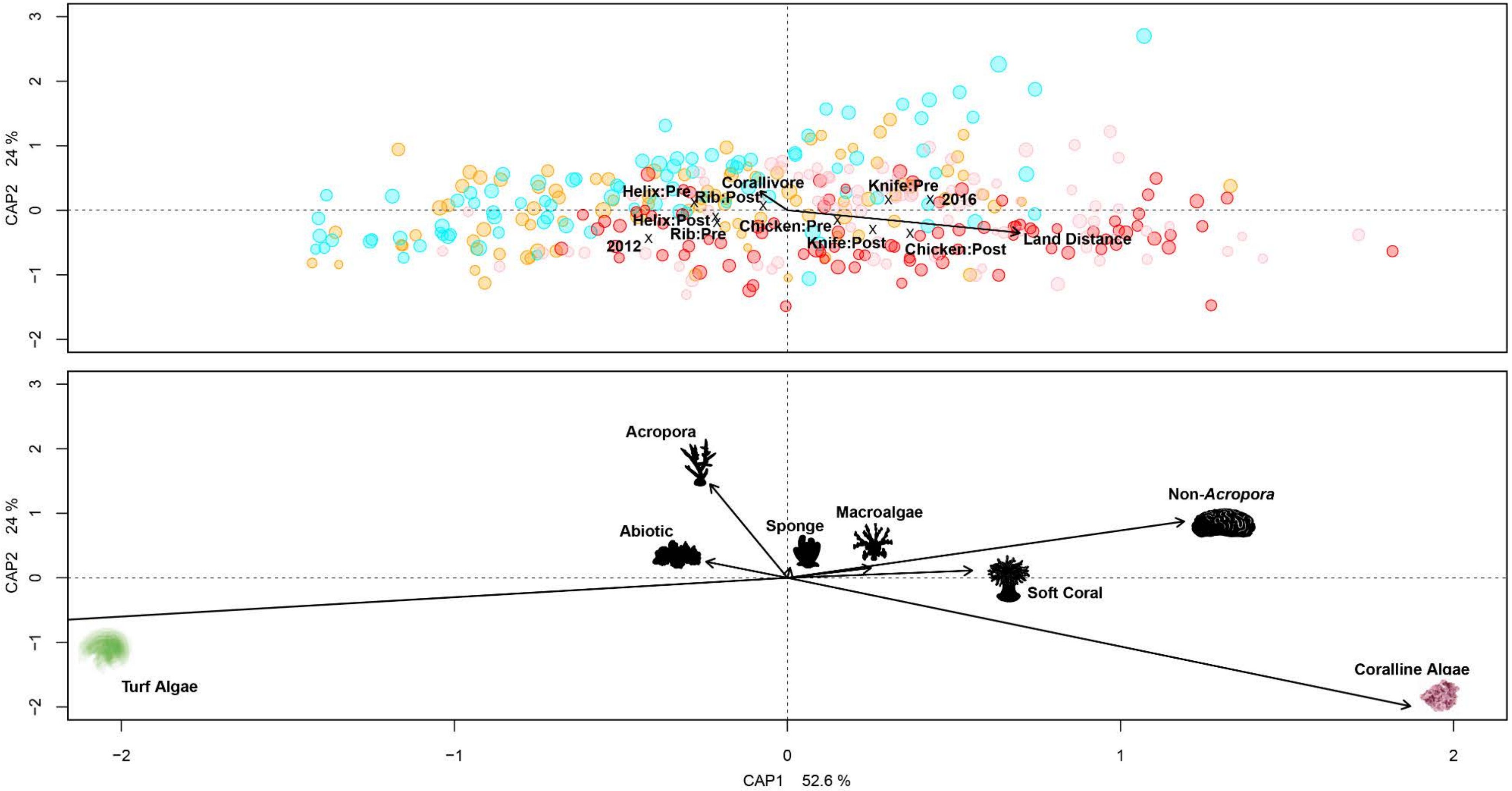


Figure 3.2: Distance based constrained ordination biplot using Bray Curtis capscale dissimilarity. Benthic groups divided between *Acropora* and Non-*Acropora* hard coral to view recovery versus re-assembly. See Table 3.1 for dissimilarity scores. Top panel includes site ordination with arrow trajectory fit for multivariate model explanatory variables and years with the highest percent cover dissimilarity. Each "X" denotes centroids for percent cover pre- and post-disturbance of each reef. Each point is a transect survey (~N=360) where sizes indicate species richness and colour indicates Reef (Yellow: Helix, Blue: Rib, Red: Knife, Pink: Chicken). Bottom panel represents the benthic group percent cover

Overall, there were no significant differences in percent cover between reefs at each year during the survey period (Table S3-e), but the structure of benthic assemblages changed through time and the nature of change varied among reefs due to the differential impact of disturbances. These include a crown-of-thorns outbreak at Helix Reef and the passage of a severe Tropical Cyclone Yasi in 2011. Changes were strongly driven by declines in hard and soft coral cover (Table S3-g) pre- and post- disturbance, although the magnitude varied among reefs (Figure 3.3). For example, *Acropora* spp. was significantly higher post-disturbance at Rib Reef than all other reefs (Table S3-g). The strong recovery of both tabulate and branching *Acropora* and branching Non-*Acropora* at Rib Reef were the strongest contributors to hard coral cover differences between Rib and other reefs (Figures S3-a, S3-b). Similarly, coralline algae increased following Cyclone Yasi on the outer-shelf reefs (Table S3-e), but there was no detectable difference on mid-shelf reefs. There were also marked declines in branching *Acropora* at Helix Reef and sub massive *Acropora* at Knife Reef post-disturbance (Figures S3-a). Additionally, significant differences in soft coral cover on Helix and Chicken Reefs were evident pre-disturbance but were indistinguishable post-disturbance. Turf algae was the only benthic component to show no difference pre- and post- disturbance (Table S3-g). There was evidence of rapid recovery following Tropical Cyclone Yasi, particularly in hard coral cover (Figure 3.3).

Table 3.1: Capscale (canonical analysis of principal components) benthic scores (8 benthic groups) for best performing model explaining dissimilarity for distance-based redundancy plots (Fig 2). Dissimilarity for explanatory variables and centroids are also listed

Benthic Explanatory	CAP1	CAP2	Benthic Group	CAP1	CAP2
Land Distance	0.71	-0.31	**Turf_Algae**	-3.50	-1.05
Corallivore	-0.07	0.30	**Coralline**	1.87	-1.99
2012	-0.41	-0.39	**Non-*Acropora***	1.19	0.87
2016	0.44	0.21	***Acropora***	-0.23	1.45
Chicken.post	0.22	-0.18	**Soft Coral**	0.55	0.11
Chicken.pre	0.16	-0.11	**Abiotic**	-0.24	0.25
Helix.post	-0.21	-0.06	**Macroalgae**	0.25	0.15
Helix.pre	-0.27	0.16	**Sponge**	0.01	0.16
Knife.post	0.26	-0.25			
Knife.pre	0.31	0.21			
Rib.post	-0.25	0.26			
Rib.pre	-0.22	0.06			

Table 3.2: Capscale (canonical analysis of principal components) fish functional scores (11 fish groups) for best performing model explaining dissimilarity for distance-based redundancy plots (Fig 4). Dissimilarity for explanatory variables and centroids are also listed

Trophic Explanatory	CAP1	CAP2	Trophic Group	CAP1	CAP2
Land Distance	0.89	-0.02	**Planktivore**	-1.96	-1.79
Acropora	-0.30	-0.14	**Grazer**	1.16	-0.05
Non-*Acropora*	0.05	-0.22	**Omniv_Pom**	-1.06	-0.20
2012	0.06	0.24	**Excavator/Scraper**	-0.22	0.03
2016	-0.06	-0.58	**Corallivore**	-0.10	0.02
Chicken.post	0.07	-0.09	**Macro-invertivore**	-0.05	0.01
Chicken.pre	0.16	0.08	**Detritivore**	-0.01	0.03
Helix.post	0.13	-0.06	**Piscivore**	0.03	-0.01
Helix.pre	-0.29	0.33	**Pisci-invertivore**	-0.02	0.00
Knife.post	0.34	-0.08	**Micro-invertivore**	-0.01	0.00
Knife.pre	0.47	0.11	**Browser**	-0.01	0.00
Rib.post	-0.48	-0.10			
Rib.pre	-0.18	-0.01			

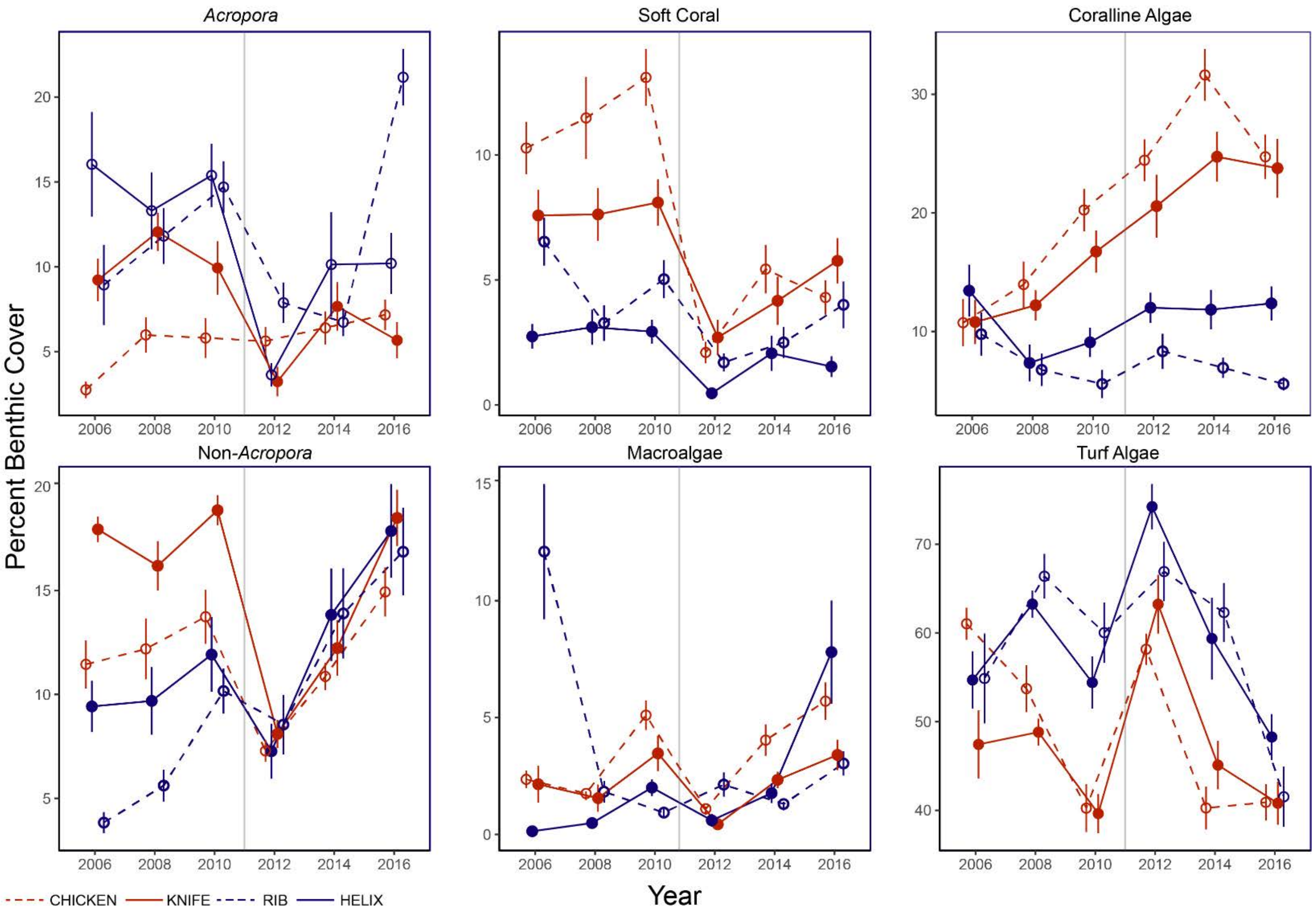


Figure 3.3: Percent benthic cover by year (95% CI). Red: Outer-Shelf, Blue: Mid-Shelf. Dashed line & open circles: Open Fishing, Closed line & closed circles: Closed Fishing. Grey mid-line: disturbance event Cyclone Yasi. Each reef was impacted by severe Cyclone Yasi in 2011. The only reef with an active crown of thorns outbreak (*Acanthacaster plancii)* during survey years was Helix. See Tukey's results for multiple comparisons of benthic groups for interactions (Reef x Year, Disturbance x Reef) (Tables S3-e, S3-g)

3.3.2 Spatial and temporal patterns in reef fish assemblages

Despite substantial overlap in reef fish assemblage among individual reefs, differences in assemblage structure were largely attributed to distance from the coast (land distance, R^2:0.09, $p<0.001$), reef and year interaction (R^2:0.18, $p<0.001$). Hard coral cover also had a small contribution to assemblage dissimilarity (*Acropora:* R^2:0.01, $p<0.001$, non-*Acropora:* R^2:0.02, $p<0.001$ (Figure 3.4, Table 3.1, Table S3-d). Management zone contributed little to variation in fish assemblage (Table S3-c). Mid-shelf reefs tended to have higher total density and species richness than outer-shelf reefs (Figure 3.5). Additionally, the density of five out of eleven functional groups of fishes showed significant differences among reefs. For example, planktivores were the most abundant functional group at all reefs, with density highest at Rib Reef (Figure 3.4, Table S3-f). Similarly, omnivorous pomacentrids and excavator/scrapers were more abundant on mid-shelf reefs, and while grazers were a conspicuous component of fish assemblages at all reefs, their density was higher on outer-shelf reefs (Figure 3.4). Browsing fishes, piscivores, and piscivorous-invertivores were observed in low numbers and formed a small proportion of density in the total assemblage at all reefs (Figure 3.6, Table 3.3).

While the structure of reef fish assemblages was indicative of a reef's position across the continental shelf (Figure 3.4), there were temporal fluctuations in the density of functional groups that varied among reefs (Table S3-f). Moreover, there were significant changes in the mean total density and species richness of fishes through time which varied among reefs (two-way ANOVA density: Reef*Year df=15, F=4.1, $p<0.05$, species richness: Reef*Year df=15, F=3.3, $p<0.05$) (Figure 3.5). Total density generally declined at all reefs until 2012, after which there were strong increases to the highest levels recorded at all reefs except Helix (Figure 3.5). Similar patterns were apparent for species richness, although the year of lowest richness varied among reefs and there was no recovery at Helix Reef (Figure 3.5).

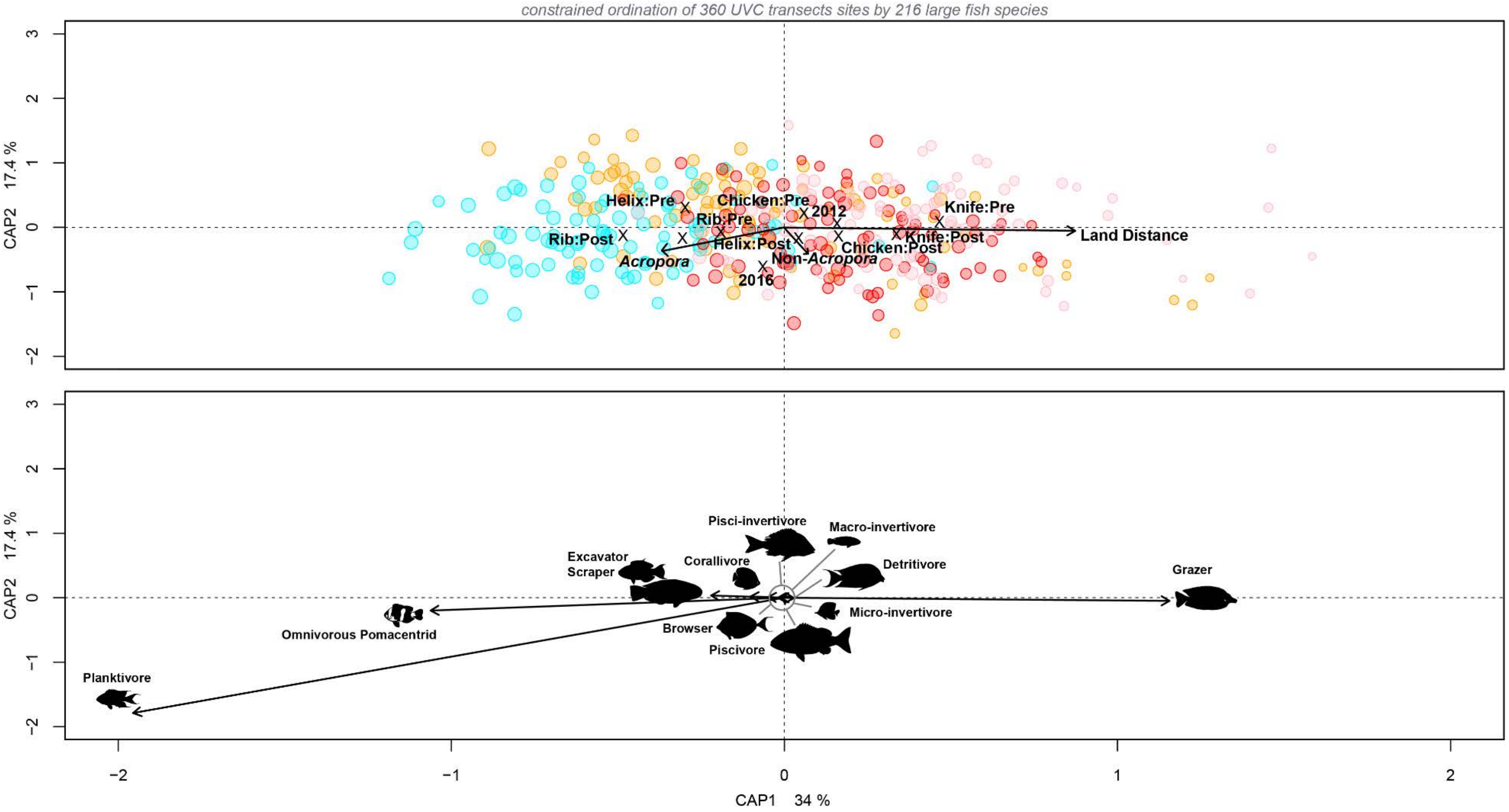


Figure 3.4: Distance based constrained ordination biplot using Bray Curtis capscale dissimilarity for fish communities. See Table 3.2 for dissimilarity scores. Top panel includes spatial ordination with arrow trajectory fit for multivariate model explanatory variables. Each “X” denotes centroids for percent cover pre- and post-disturbance of each reef and years with the highest abundance dissimilarity. Each point is a transect survey (~N=360) where sizes indicate species richness and colour indicates Reef (Yellow: Helix, Blue: Rib, Red: Knife, Pink: Chicken). Bottom panel represents the fish group (~11 total) abundance dissimilarity. Scale of fish is not related to ordination importance, but to general differences in body size

Multiple comparisons of means using Tukey's test showed densities of excavators/scrapers, detritivores, and planktivores had the strongest significant differences among reefs through time (Table S3-f), where there were no general patterns in density among reefs and years. Planktivore density varied among reefs and through time (Table S3-f) and appeared closely related to changes in hard coral cover (rho>0.6, $p<0.05$) (Figure 3.3). Furthermore, hard coral cover had a significant effect on all functional groups except for excavators/scrapers and browsers (Table S3-f). The strongest effect of excavator/scraper abundance was driven by macroalgae cover, while turf algae was the strongest driver for detritivores. Planktivores were the only group to consistently have higher mean density post-disturbance across all reefs (Table S3-f). Disturbance effects were considerably greater at Helix reef with impacts evident in 6 out of 11 functional groups post-disturbance (Table S3-h). Of these functional groups, planktivore and corallivore density significantly increased post-disturbance at other reefs, and most prominently for Rib and Chicken reefs. Rib fish densities of corallivores, omnivorous pomacentrids, planktivores, and micro-invertivores were higher than all other reefs in 2016.

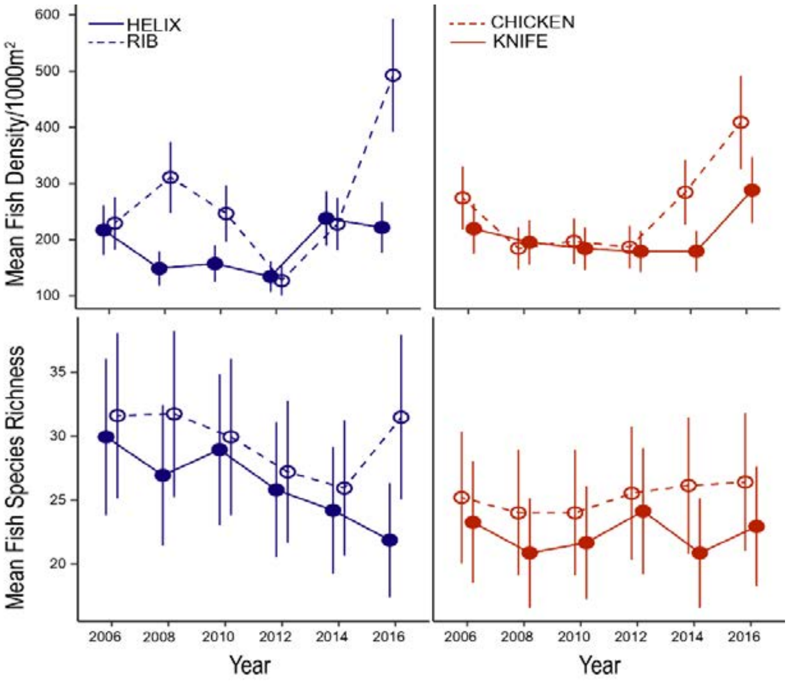


Figure 3.5: Local variation of mean fish density/1000m^2 and (95% CI). Red: Outer-Shelf, Blue: Mid-Shelf. Dashed line & open circles: Open Fishing, Closed line & closed circles: Closed Fishing. Grey mid-line: disturbance event Cyclone Yasi. ANOVA (formula=Density~Reef*Year) df=15, F=4.05, $p<0.01$ and mean fish species richness ANOVA (formula=Species Richness~Reef*Year) df=15, F=3.26, $p<0.01$ by year

Differences in fish assemblage structure among reefs and through time resulted from variation in the proportion of individual functional groups (Fig. 4, Table 3.3). Planktivores, grazers, and excavator/scrapers were the most abundant functional groups across all reefs. While changes in mean density of functional groups occurred during the study period, most proportions of abundance stayed relatively stable through time with a few exceptions. Grazers remained dominant at all reefs except Rib Reef where their proportional abundance declined from 2006-2016 (14.3-4.98%) (Table 3.1). Additionally, at Helix Reef, numbers of piscivores, excavator/scrapers, macro-invertivores, piscivorous-invertivores, and detritivores decreased between 2014 and 2016. Conversely, some functional groups became more dominant in the years post-disturbance. Percent of total abundance of planktivores increased from 2012 (~25-36%) to 2016 (~56-65%) at all reefs. At mid-shelf reefs, omnivorous pomacentrids increased from 2012 (~6-12%) to 2016 (~8-17%), but percent of abundance did not change for outer-shelf (Figure 3.4, Table 3.1). From the SIMPER analysis, the highest combined contribution (59.9%) to omnivorous pomacentrid recovery at Rib stemmed from increase in abundance of two species; *Acanthochromis polyacanthis* (21.59) and *Pomacentrus moluccensis* (38.28). Planktivore recovery at all reefs except Helix was due to an increase in *Neopomacentus azysron*. Conversely, decline in abundance at all reefs for macro-invertivores were mainly from *Hemigymnus fasciatus* and *Hemigymnus melapterus*, and decline in grazers was due to *Plectroglyphidodon lacrymatus* (Table S3-i).

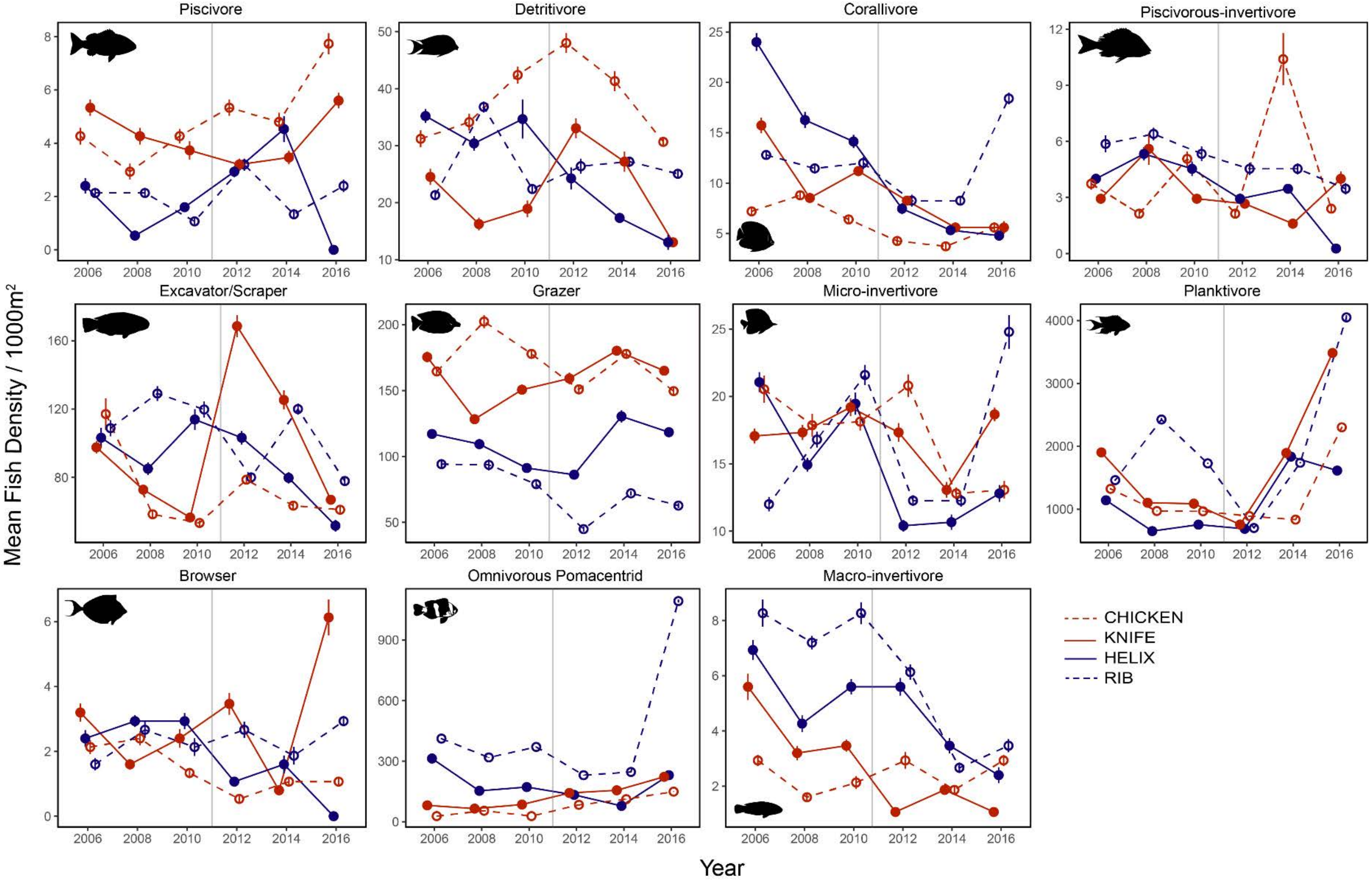


Figure 3.6: Mean fish density/1000m^2 of functional groups by year (95% CI). Red: Outer-Shelf, Blue: Mid-Shelf. Dashed line & open circles: Open Fishing, Closed line & closed circles: Closed Fishing. Grey mid-line: disturbance event Cyclone Yasi. See Tukey's results for multiple comparisons of functional groups for pairwise interactions (Reef*Year, Disturbance*Reef) (Table S3-f , S3-h)

Table 3.3: Functional group relative proportions (% of total abundance) by reef and year for study site

Functional Group	**2006**	**2008**	**2010**	**2012**	**2014**	**2016**	**2006**	**2008**	**2010**	**2012**	**2014**	**2016**
	Rib						**Chicken**					
Planktivore	44.45	55.73	48.98	36.1	53.03	64.34	50.37	42.98	40.46	25.3	46.85	65.94
Grazer	14.3	10.75	11.18	11.53	10.98	4.98	23.21	25	28.01	26.64	22.29	15.62
Detritivore	3.24	4.23	3.17	6.79	4.15	1.99	4.13	6.65	7.88	8.03	5.11	2.9
Omnivorous Pomacentrid	12.52	7.32	10.5	11.87	7.52	17.37	2.15	2.55	3.17	4.77	3.86	4.21
Piscivore	0.32	0.24	0.15	0.82	0.2	0.19	0.56	0.57	0.79	0.89	0.59	0.73
Excavator/Scraper	16.53	14.82	16.96	20.59	18.3	6.18	12.91	14.19	10.51	28.2	15.5	6.33
Browser	0.24	0.31	0.3	0.69	0.28	0.23	0.42	0.31	0.45	0.58	0.1	0.58
Piscivorous Invertivore	0.89	0.73	0.76	1.17	0.69	0.28	0.49	0.42	0.94	0.36	1.29	0.23
Corallivore	1.94	1.32	1.7	2.13	1.26	1.46	0.95	1.72	1.19	0.71	0.46	0.53
Micro-invertivore	1.82	1.93	3.06	3.16	1.87	1.97	2.26	3.38	3.57	2.9	1.62	1.77
Macro-invertivore	1.26	0.83	1.17	1.58	0.41	0.28	0.74	0.62	0.64	0.18	0.23	0.1
	Helix						**Knife**					
Planktivore	36.81	29.62	31.12	32.78	56.41	56.14	41.55	36.4	38.87	35.29	33.98	60.68
Grazer	18.86	24.83	18.8	20.52	20.03	20.58	25.82	37.89	35.76	29.9	36.21	19.71
Detritivore	5.67	6.9	7.15	5.78	2.66	2.27	3.85	3.05	3.81	6.55	5.54	1.72
Omnivorous Pomacentrid	10.09	6.97	7.09	6.35	2.42	8.02	0.88	2.05	1.13	3.33	4.56	3.94
Piscivore	0.39	0.12	0.33	0.7	0.7	0	0.84	0.8	0.75	0.63	0.71	0.74
Excavator/Scraper	16.62	19.32	23.47	24.59	12.25	8.99	18.37	10.93	10.72	15.58	12.92	8.05
Browser	0.39	0.67	0.6	0.25	0.25	0	0.33	0.45	0.27	0.11	0.22	0.14
Piscivorous Invertivore	0.64	1.21	0.93	0.7	0.53	0.05	0.46	1.05	0.59	0.53	0.33	0.53
Corallivore	3.87	3.69	2.91	1.78	0.82	0.83	2.47	1.6	2.25	1.64	1.14	0.74
Micro-invertivore	3.39	3.39	4.01	2.48	1.64	2.23	3.22	3.34	3.65	4.12	2.61	1.72
Macro-invertivore	1.12	0.97	1.15	1.33	0.53	0.42	0.46	0.3	0.43	0.58	0.38	0.39

3.3.3 Reef Community Relationships

Changes in the proportions of fish functional groups were not uniformly correlated with changes in benthic habitat characteristics. Most comparisons within and among functional groups and benthic habitats demonstrated low levels of correlation (rho<0.3, Figure S3-c), but there were some exceptions. Links between species and biota varied, but some patterns were consistent across reefs. For example, there was an inverse relationship between turf algae and non-*Acropora* coral cover (Rho=|0.46-0.58|) at all reefs (Figure 3.3 & Figure S3-c), and similarly, between turf algae and *Acropora* coral cover (rho: |0.35-0.64|) at all reefs except Knife (Figure 3.3 & Figure S3-c). Also, turf algae showed significant inverse relationships with coralline algae (Rho=|0.37-0.67|) and macroalgae (rho=|0.31-0.54|). While there were consistent relationships across reefs for some benthic taxa, the relationships between the benthos and fish functional groups were more variable. For instance, planktivores were positively related to *Acropora* at Rib Reef, to non-*Acropora* at Chicken and Knife, but showed no relationships with any form of hard coral at Helix (Figure 3.3 & Figure S3-c). Omnivorous pomacentrids had a significant positive correlation with hard coral cover, but only at reefs open to fishing (rho=|0.35-0.47|). Rib Reef represents the highest number of significant correlations between omnivorous pomacentrids and planktivores and their relationships to benthic *Acropora/*non-*Acropora.* Fish functional groups were not strongly related to each other, but corallivores had a positive association with omnivorous pomacentrids at Rib and micro-invertivores at Helix. Whether these underlying relationships in the reef community contributed to strong recovery post-disturbance rather than similar patterns in temporal abundance at these sites are unclear.

3.4 Discussion

As coral reef ecosystems continue to be exposed to disturbance regimes, increased and improved data are required to define recovery potential. Our detailed study of four similar size and shape reefs at varying distances across the shelf revealed reef-level differences in community composition and response to disturbance. This suggests reef-scale (i.e. single individual reefs) data may be crucial to understanding the capacity of reefs to recover from ongoing disturbance and that this level of examination should be nested within large-scale or regional analyses.

Benthic assemblages were variable among reefs and years, with a strong distinction between mid- and outer-shelf sites. This distinction could be explained largely by natural variations in wave exposure, water clarity, and sources of productivity consistent with large-scale studies on the GBR (Halford et al. 2004; Emslie et al. 2008; Johns et al. 2014). However, more clearly defined shelf separation occurred in higher fish density and species richness on mid-shelf reefs, with clearest spatial differences in the density of functional groups such as planktivores and grazers. Distance from coast was also stronger predictor than mid- and outer- shelf position on benthic and fish assemblages. As shelf position is an arbitrary categorical predictor, use of a continuous distance variable of reef position more readily explained distinctions across the shelf. While cross-shelf variation in fish density on the GBR was incorporated in early studies of community assemblages (Done 1982; Williams 1982), recent studies focus on specific guilds (e.g. herbivores; (Hoey and Bellwood 2008) or use categorical shelf variables (Emslie et al. 2012). This study highlights observation of spatial differences in functional density from an across-shelf perspective may provide detailed information about which functional groups are most influential in variation among reefs.

Natural variability of bio-physical conditions is a prime driver of benthic community dynamics (Done 1982; Emslie et al. 2010), and some components of the fish assemblage responded to that variation. For instance, Rib Reef exhibited the highest *Acropora* coral cover and planktivore density of all reefs. This result was surprising since strong wave exposure and proximity to pelagic upwelling at outer-shelf sites (Fabricius 1995) increase plankton and nutrient availability. Since planktivores were most prominent at a mid-shelf reef, density was likely driven by dependence on *Acropora* coral cover, particularly for tabulate and bottlebrush. Hard coral cover has previously been reported as a strong driver of planktivore density and diversity due to the shelter it affords (Pratchett et al. 2014). Recovery of *non-Acropora* at all reefs post-disturbance could explain the high density of *Pomacentrus* *lepidogenys* and *Neopomacentrus azysron,* as non-*Acropora* dominated reef-scape has been found to be associated with high abundance of these two fish species (Arias-González et al. 2006). Although planktivores were highest at Rib reef, they recovered strongly at all reefs. This could be due to their smaller body size leading to faster growth rates and recruitment pulses than larger fish. Though other small-bodied fish such as omnivorous pomacentrids did not uniformly recover across all reefs. Browsing fishes were observed in low numbers across all reefs despite their known commonality in shallow reef slope habitats (Russ 1984), and low numbers may reflect the lack of macroalgae at these sites.

While there was an observable link between some benthic assemblage components with functional groups, other relationships between benthic biota and fish assemblage were not as apparent. Results indicate environmental drivers had more influence on some functional groups than benthic relationships. For example, large-bodied predators showed no significant correlation with any other functional group or benthic category. While some studies have revealed fish population declines following coral loss (Jones et al. 2004; Wilson et al. 2006), others present evidence that specific functional groups remain stable or increase post-disturbance (Ceccarelli et al. 2016; Hempson et al. 2017). For instance, herbivore abundance is commonly linked to algal availability (Wilson et al. 2006), and corallivores are known to decrease following coral loss (Pratchett et al. 2014). Here results show that characteristics contributing to individual reef variability may promote stability as there was no common pattern in decline post-disturbance among reefs, particularly for piscivores, excavator/scrapers, and detritivores.

Despite global coral loss (Hughes 1994; Jackson et al. 2014), this study shows recovery of hard coral equal to or surpassing pre-disturbance levels consistent with large-scale studies for the GBR (Halford et al. 2004; Emslie et al. 2008; Johns et al. 2014). Although all reefs showed benthic recovery, grazers, detritivores, corallivores, and macro-invertivores continued to decline post-disturbance. Few studies link loss of fish functional density (outside of herbivory) with increasing coral cover, a key bottom-up finding from the present study generally and for Helix Reef specifically. Loss of density of functional groups showed no clear pattern across reefs, which could mean that unknown stressors are a stronger influence on decline. Alternatively, this decline could mean that some of the larger fish groups have moved to areas outside of survey sites in response to changes in environmental conditions outside of acute stressors (Currey et al. 2015); such as deeper reef areas, or areas that provide greater refugia. Further study is required to delineate some of these differences.

Helix Reef had the largest changes in fish functional group density relative to disturbance. For instance, the density of functional groups such as corallivores, micro-invertivores, and detritivores had significant differences in mean density pre- and post- disturbance and showed general overall patterns in decline throughout the study period. This could mean that patterns in settlement and density are more dependent on the level of food resources than total habitat availability for some functional groups. Alternatively, lack of specific coral types that are preferred habitat for some fish functional groups could deter settlement. The loss of branching coral at Helix Reef over the duration of the study could explain decreased density of corallivores. For example, Brooker et al. (2013) found that corallivorous fish abundance was more significantly associated with *Acropora* branching coral over any other coral morphology or preferred prey. This aligns with conclusions from Pratchett et al. (2014) that ecological specialization predominantly contributes to response variability of fishes to disturbance. Those authors also concluded that corallivores will be most affected by habitat loss over other fish functional groups which is consistent with these results. Even though hard coral recovery occurred for Helix Reef, there has been re-assembly of the benthic community with changes to the dominant species from loss of branching *Acropora* to recovery of tabulate *Acropora* and sub massive non-*Acropora*, which could explain why previously dominant benthic dwelling groups such as corallivores have declined post-disturbance.

The Rib Reef fish assemblage was distinct from outer-shelf reefs due to variation in density of planktivores, omnivorous pomacentrids, corallivores, and cover of *Acropora* corals. Despite marked declines in these functional groups post-disturbance, recovery of density at Rib Reef surpassed the other reefs. The disproportionately high density of some benthic dwelling fish functional groups such as corallivores and omnivorous-pomacentrids at Rib Reef may be due to the higher reassembly of tabulate and bottlebrush *Acropora* coral and branching non-*Acropora* than other reefs. This could also explain lagged recovery of omnivorous pomacentrids at other reefs since *Acropora* had not yet recovered. Omnivorous pomacentrid recovery at Rib Reef appears related to an increase of *Acropora* as this benthic group creates suitable habitat for *Acanthochromis polyacanthus* and *Pomacentrus moluccensis* (Arias-González et al. 2006). Results from this study also suggest tabulate and foliaceous coral re-assembly post-disturbance is stronger at mid-shelf than outer-shelf reefs (Johns et al. 2014).

Outer-shelf reefs may have sustained more structural damage from Cyclone Yasi due to higher exposure to swells than mid-shelf reefs, which might explain lagged recovery of fishes at those sites. However, all reefs sustained similar levels of damage to benthic groups, so fish functional differences could be explained by other factors such as loss of complex structure, though rugosity was not collected for the study period. Research by Gilmour et al. (2013) showed that distance from human stressors contributed to rapid benthic recovery and coral recruitment at isolated reefs. Here we show that while distance from land is a strong driver of variation in both benthic and fish communities in the central GBR, benthic and fish community recovery can occur in areas closer to human activity such as mid-shelf reefs. Moreover, expectations for faster recovery from disturbance, such as reef depth and high density of herbivores (Graham et al. 2015), did not increase fish density at outer-shelf sites. Additionally, particular fish groups (larger fish such as piscivores and pisci-invertivores) showed no pattern of response to disturbance and may carry greater resistance towards acute stressors than others. Detritivore and some invertivore densities declined at all reefs post-cyclone and it is too early to determine whether any long-term recovery will take place. Hence, it is not clear whether these are lagged effects in recovery occurring in the study area which will require future monitoring.

Other factors that have been attributed to reef recovery, such as management zone (Mellin et al 2016), did not influence this study. For example, recovery of both benthic and fish groups was not distinctive between management zone showing recovery potential is not uniform for protected areas. This somewhat contradicts findings from Mellin et al (2016) who showed that marine protected areas on the GBR are more resilient to effects of disturbance. The difference in findings may be to the large latitudinal area of coverage in these studies or the fact that in the early periods of their study reefs were subject to a broader range of disturbance types. In another study, Emslie et al. (2015) showed that while reef protection status does not affect some fish groups, it had a large impact on abundance of large piscivores, a result not reflected in the present study. However, those authors also noted that Townsville reefs showed the lowest biomass of piscivores in their study on the whole of the GBR. Thus, it is possible that the low overall density of piscivorous fishes in the Townsville sector may not be large enough to tease out differences by protection status. The reef level variation in functional group responses to disturbance in our study also shows that drivers in density and functional stability may vary across biogeographic areas even at the local scale. Since our study takes a fine-scale approach on a small number of reefs, future study should consider a larger sample size.

While this study shows that benthic communities have recovered post-disturbance, it is unclear whether fish communities will also recover functionally post-disturbance. Although environmental effects drive some functional variability among reefs, there is a need to understand factors beyond benthic recovery to interpret community response to future disturbance events. This study provided evidence that reef–level data produce a different level of detail in community dynamics than seen at regional and large-scales. This aligns with sub-regional results from Osborne et al (2011) showing that there is no net decline post- disturbance on the GBR as a whole, but there was substantial variability in recovery from disturbance at finer spatial scales. This can be important to the application of management strategies, which are often implemented at the reef level (e.g. zoning). While regional studies identify variation between locations, more subtle ecological processes may be missed that could reveal future resilience to disturbance. It was interesting to note that there was recovery of some benthic groups at Rib Reef compared to other reefs. Rib Reef is closest to shore and is open to fishing. Future studies should compare a larger number of reefs that are open and closed to fishing and collect additional environmental characteristics such as structural complexity (e.g. rugosity) or water quality, to test the generality of the patterns in recovery identified in this study. This could assist in identifying more specific contributors to variation in communities between management areas and provide guidance on how directed management may improve and promote resilience and recovery.

When examining total density of fishes pre- and post-disturbance, there were no significant differences among reefs, which masked the underlying effects of disturbance to individual functional groups. Furthermore, without including interactions between reef and year, the level of impact to individual reefs would be missed in large scale approaches. From this study, it is clear that Helix Reef has undergone a level of functional degradation that is not reflected in other focal reefs, potentially showing increased vulnerability to future disturbance events. This may warrant further study as to whether species carrying a high degree of specialization were differentially impacted at Helix Reef (Villéger et al. 2010; Plass-Johnson et al. 2016). This result exposes questions about the level of detail and scale applied to defining reef variability, community patterns and recovery. With some acute disturbances (e.g. cyclones and bleaching) expected to increase in frequency and severity in the future Hoegh-Guldberg 1999, Rosenzweig et al 2008; IPCC 2014; Wolff et al. 2018), it is important to examine the response of coral reefs to such disturbances at various spatial scales. While broad scale approaches (e.g. 10s to 100s kilometres) will generalise the responses of reef communities to acute disturbances, fine scale (e.g. 100s metres to kilometres) appraisals will give a more nuanced understanding of the reef level variability in fish and benthic community dynamics following acute disturbances.

Chapter 4: Trophic niches determined from fatty acid profiles of sympatric coral reef mesopredators

4.1: Introduction

Despite a large body of trophic research about coral reef ecosystems, surprisingly little is known about ecological processes (i.e. nutrient cycling, energy flow) among high-order predators. These knowledge gaps are derived from difficulty in identifying dietary sources and predator-prey interactions of mobile species such as sharks. High-order predators are assumed to limit population growth of lower trophic (dietary) levels through consumption (direct effects) and suppressed predatory activity (indirect effects) via top-down influences (Heithaus et al. 2008; Ripple et al. 2016). Due to the complexity of reef systems, it is difficult to characterise discrete trophic levels above primary consumers due to high-levels of omnivory (Thompson et al. 2007). Generally, fishes are categorized into functional groups (Root 1967) or guilds which cluster species based on ecological traits in relation to diet, morphology, and competition (Reecht et al. 2013). Previous studies have hypothesized that the semi-open nature of reefs (connectivity, energy subsidies) and functional redundancy (species sharing similar functional roles) are the reason disruptions such as predator-mediated trophic cascades are uncommon in reef systems, a topic regularly debated among researchers (Roff et al. 2016; Ruppert et al. 2016). Moreover, omnivory (Bascompte et al. 2005) and diffuse predation (consumers feeding on multiple dietary resources) among predators (Heupel et al. 2014) are thought to weaken cascading effects that can be observed with low functional diversity (trait-based species richness) in degraded reefs (Thompson et al. 2007). Fish ecological function in general can often be defined in one-dimension (discrete groupings based on a specific ecological trait) or equated solely to trophic (dietary) position (Rosenfeld 2002) which can lead to oversimplification of an organism's influence on a community, particularly when relying on functional redundancy to maintain an ecosystem after a loss in diversity (Reecht et al. 2013; Mouillot et al. 2014). Conceptually, if multiple species in a community share ecological roles or prey on multiple resource types, there is a greater opportunity for dietary gaps to be filled if there is a loss of biodiversity.

However, the functional roles of some reef fishes have been shown to transition following persistent habitat degradation (Brandl et al. 2016). Additionally, trophic roles for many reef-dwelling species is limited or context-dependent (small spatial scales, limited methods), meaning that without this information, functional roles of similar species remain largely unknown. For these reasons, it is important to understand functional redundancy at all trophic levels in a community and their relationship to ecosystem stability, particularly when such ecosystems are already vulnerable to degradation.

Biochemical tracers are increasingly used in a range of ecosystem types to determine the energy flow through a system and the functional role of species. While stable isotope analysis is most commonly used in trophic studies, lipid and fatty acid (FA) analysis is gaining traction largely due its greater ability to identify basal food chain dependencies and quantify carbon-based energy flows (Bierwagen et al. 2018b; Pethybridge et al. 2018). For example, Arai et al. (2015a) found functional redundancy in three species of parrotfish in coral reefs in the South China Sea due to similar FA profiles. In the same study area, FA profiles showed bigeye snapper (*Lutjanus lutjanus*) may undergo diet and habitat shifts with changing stages of ontogeny (Arai et al. 2015b). In northern Australia, Nichols et al. (2001) revealed inter-specific polyunsaturated FA (PUFA) differences in liver oils between shark species. The authors also determined intra-specific spatial and seasonal differences in FA profiles in blacktip reef sharks (*Carcharhinus melanopterus*), while tiger sharks (*Galeocerdo cuvier*) showed less variability. Application of FA analysis to tropical shark species is limited but has been used to distinguish species and populations in subtropical areas such as the southeast United States (Ackman 2000) and South Africa (Davidson et al. 2011). These spatial, temporal, and species level differences are important in distinguishing functional roles and understanding how organismal responses to impacting factors such as environment may change due to anthropogenic pressures and natural variability. Despite FA applicability to these types of studies and the higher level of detail over stable isotope analysis due to number of potential tracers, sample processing takes time and often comes at a high cost. Due to recent research by Parrish et al. (2015), faster methods have been applied to analysis of fish tissues of pelagic species such as albacore tuna (*Thunnus alalunga*) and white sharks (*Carcharadon carcharias*) that have been found to be comparable to traditional FA extraction methods. However, the method of direct transmethylation has yet to be applied to tropical fish species, presenting an opportunity to explore potential differences in approach.

The Great Barrier Reef (GBR) is under threat and vulnerable to degradation due to various pressures, including climate change impacts (e.g. coral bleaching) amplified by disturbance events (De'ath et al. 2012; Hughes et al. 2017). These pressures that may negatively impact the reef such as anthropogenic (fishing, runoff) and natural (cyclones, crown of thorns starfish, *Acanthacaster plancii*) fuel the need for better understanding of the ecological factors that contribute to stable, healthy reefs. Near-pristine reef ecosystems often have trophic structures connecting energy pathways flowing from primary producers to top-level consumers, supporting biodiversity and populations (Houk & Musburger 2013). In general, coral reef food webs, like most ecosystems, are thought to be structured as pyramids of species richness where each subsequently higher trophic level reduces in biomass and richness due to energy availability (Trebilco et al. 2013; Hatton et al. 2015). This type of structure implies that a smaller number of high-level predators such as sharks with large biomass can be supported by reefs over smaller-bodied teleost predators. Species can be distinguished into functional groups (i.e. detritivores, herbivores, invertivores, piscivores, omnivores) based on dietary and morphological traits. Functional characteristics of reef-dwelling species have been shown to change spatially (Hemingson & Bellwood 2016) and with ontogeny (Tilley et al. 2013). Reef sharks and large-bodied teleost fish are often categorized as piscivores and pisci-invertivores with a high degree of generalized feeding in some species (Emslie et al. 2008; Speed et al. 2012; MacNeil et al. 2015; Frisch et al. 2016). Therefore, it is important to determine if there is similarity or separation in diets of organisms classified with similar functional roles.

Reef sharks have often been assumed to be apex predators in coral reef systems (Friedlander & DeMartini 2002; Rizzari et al. 2014; Casey et al. 2017), but the significance of their functional role is not well defined. Reef-associated sharks most common to the GBR are blacktip reef (*Carcharhinus melanopterus*), whitetip reef (*Triaenodon obesus*), and grey reef (*Carcharhinus amblyrhynchos*) (Chin et al. 2010). Conclusive dietary studies of reef sharks are minimal (but see Cortes 1999, Papastamatiou et al. 2006; Frisch et al. 2016), where different methods can lead to different interpretations about long-term diet, basal source dependencies, and nutrient pathways (*Chapter 2*; Pethybridge et al. 2018). Recent research using stable isotope and stomach content analyses (Frisch et al. 2016; Roff et al. 2016; Bond et al. 2018) re-classified reef sharks as mesopredators having similar trophic levels as large predatory teleosts (e.g. coral trout (*Plectropomus leopardus*), red throat emperor (*Lethrinus miniatus*)). These results raise questions about the ecological importance and top-down influence of reef sharks compared to other smaller-bodied mesopredators, such as snappers, groupers, and emperors (i.e. teleost fish) (Roff et al. 2016). Researchers have assumed a degree of functional redundancy occurs among reef sharks and predatory teleost fish. However, these conclusions are the subject of contention (Ruppert et al. 2016) warranting the need for further research. Ecological models also show weak top-down effects from reef sharks on the GBR (Casey et al. 2017), but these models characterize sharks as apex predators which may contradict recent findings of their ecological roles as mesopredators. Since species such as grey reef and whitetip reef sharks are found to be more resident (Espinoza et al. 2015) than larger bodied transient predators such as tiger sharks (Meyer et al. 2010) and bull sharks (*Carcharhinus leucas*) (Heupel et al. 2015), it is possible that reef sharks are more dependent on reef-derived resources than larger apex predators. Conversely, some studies show that grey reef sharks are more dependent on pelagic carbon resources (Frisch et al. 2016; Williams et al. 2018). Furthermore, assumptions about the inter-specific trophic interactions of high-order predators on coral reefs are rarely backed by empirical evidence; behavioural influence and activity space have only recently been compared among predators (Speed et al. 2012; Rizzari et al. 2014; Matley et al. 2016b; Heupel et al. 2018).

Here, we apply FA analysis to a selection of reef-dwelling mesopredators on the GBR to compare basal source, habitat dependencies and dietary preferences among species. The aims of this study were to: (1) determine applicability of FA analysis, including a new rapid extraction method, to tissues of tropical mesopredators, and (2) determine the degree of inter- and intra-specific dietary overlap among reef mesopredators. Based on previous research showing overlaps in both diet (Frisch et al. 2016) and space use (Heupel et al. 2018), we test the hypothesis that functional redundancy occurs for mesopredators on the GBR.

4.2 Methods and Materials

4.2.1 Sampling

Samples were collected from four reefs on the central GBR (~18° S) between May 2016 and April 2017 (Figure 4.1). Benthic habitat of these reefs is generally comprised of high hard coral cover (~30-50%) (Sweatman et al. 2008), but recent disturbance and bleaching events have since affected these areas. At the time of the study, reefs were comprised mainly of turf algae (42.9%), *non-Acropora* (branching) hard coral cover (17%), crustose coralline algae (16.6%), and *Acropora* (tabulate) coral cover (11.1%) (*Chapter 3*).

Muscle tissue and blood samples from 51 reef-dwelling individuals representing six families (2 carcharhinids, 2 lethrinids, and 1 serranid) were used for analysis (Table 4.1). Additional species were sampled (1 carcharhinid, 5 teleosts), however due to their low sample size they were not included in the statistical analysis (Table S4-a). Individuals were captured using traditional angling methods on rod and reel, hand line, or float lines. Any individual captured regardless of size or sex within permit requirements were sampled. For reef shark samples, captured individuals were placed in tonic immobility and a section of dorsal muscle tissue taken with scalpel and forceps from the base of the dorsal fin or anal fin. For a subset of sharks, blood was taken ventrally from the caudal vein. Sharks were released in good condition post capture. For bony teleost reef fish, dorsal muscle biopsies of up to 1.5 g were performed post-lethal capture and blood (1-3 mL) was taken from the caudal vein or gills. Due to poor condition of bony teleost fish post-sampling, all individuals for the study were retained after capture. All muscle samples were immediately frozen on board the vessel and stored at -20°C until lipid extraction. Blood plasma was separated with a portable centrifuge and extracted on the vessel and subsequently frozen.

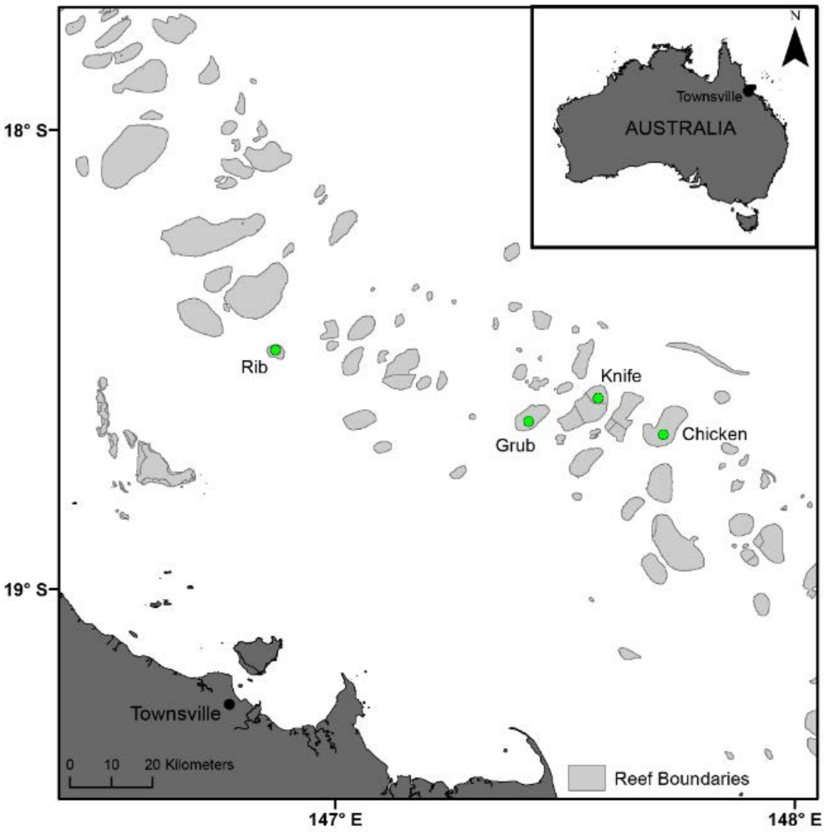


Figure 4.1: Map of the four sampling locations off Townsville reefs on the central Great Barrier Reef. Light grey polygons are reef outlines. Green circles are study locations

Wet tissues were used for analysis based on recent research from Sardenne et al (2019) which concluded that lipid degradation occurs in dry tissue samples stored longer than one month. Parrish et al. (2015) also demonstrated that FAs of wet tissue of bony fish and sharks can be extracted through direct transmethylation and are commonly used in full extraction. Any remaining dermal and connective tissue from samples were removed from muscle tissue prior to extraction. FA methyl ester (FAME) extractions from a subset of 36 samples (21 white muscle tissue, 15 blood) were compared through two processes for method validation: (1) total lipid extraction followed by transmethylation (traditional), and (2) direct transmethylation (Figures S4-a, S4-b). An additional 42 samples were thereafter processed only with direct transmethylation. We compared these processes as the direct transmethylation method is a relatively new approach for determining fatty acids in fish tissues. Research stating this is a viable method was performed by Parrish et al (2015) but was only performed for albacore tuna and white sharks. Since this study examines tropical fish species, method validation was necessary to support use of direct methylation.

4.2.2 Traditional Method: Total lipid extraction of fish tissue and transmethylation

Samples of wet tissue (0.01-1.5 g) were extracted according to a modified Bligh and Dyer (1959) method. Before extraction all clean glassware was rinsed with nanograde dicloromethane (DCM). Tissues were mixed in 100 mL separatory funnels with a solvent mixture of DCM:methanol (MeOH):milliQ H_2O (10:20:8 mL), shaken and left overnight. The following day, a second solvent mixture of DCM: saline milliQ H_2O (9g NaCl/L) (10:10 mL) was added and left for at least two hours. The lower aqueous layer was then drained into a 50-100 mL round bottom flask and rotary-evaporated in a 40 °C hot water bath. DCM was added to the extract and transferred into a pre-weighed glass 2 mL vial. Each vial was placed on a heated block and blown down under nitrogen gas where the extract was rinsed twice with DCM and transferred into the vial. After the extract was thoroughly dried, an internal standardized solvent of 1,000 µl 23:0 FAME:DCM was added and stored in -20 °C until processing.

Table 4.1: Species included the study with common names, sample size (N), sample size per study site, and fork length range of samples

Order	*Family*	*Species*	Common Name	N	*Rib*	*Grub*	*Knife*	*Chicken*	Fork Length Range (cm)
Carcharhiniformes	Carcharhinidae	*Carcharhinus amblyrhynchos*	Grey reef shark	26	*2*	-	*18*	*6*	61-151
		Triaenodon obesus	Whitetip reef shark	6	-	-	-	*6*	100-123
Perciformes	Lethrinidae	*Lethrinus miniatus*	Red throat emperor	26	-	-	*9*	*17*	31-52
		Lethrinus laticaudus	Grass emperor	6	-	-		*6*	10-50
	Serranidae	*Plectropomus leopardus*	Common coral trout	12		*1*	*5*	*6*	38-56

4.2.3 Fast Method: Direct transmethylation

For each sample, 0.01-0.4 g wet fish tissue or plasma was transferred into clean pre-weighed and tared glass test tubes. The direct transmethylation method described above was then used to extract FAs from the lipid backbone, protein, and carbohydrates.

Fatty acid analysis

FA peaks were identified through gas chromatography using an Agilent Technologies 6890N GC (Palo Alto, California, USA), with an HP-5 cross-linked methyl silicone fused silica capillary column (50 x 0.32 mm i.d.), an FID, a splitless injector, and an Agilent Technologies 7683 Series auto-sampler and injector. Helium was used as the carrier gas. Selected FA samples were further analysed using gas chromatography-mass spectrometry (GC-MS) to validate peak identifications. A Finnigan Thermoquest system fitted with an on-column injector was used to perform GC-MS with Thermoquest Xcalibur software (Austin, Texas, USA). Analytical (GC) error, using replicate analysis of an internal (tuna oil) standard, was low with a mean coefficient of variation (CV) of 12% (ranging from 0 – 92% for different FAs). Error associated with the direct transmethylation method, based on the GC analysis of replicate tissue sub-samples taken for a subset of individuals was slightly higher with a mean CV of 28% (ranging 0-97% for individual FAs).

4.2.4 Statistical Analysis

From the 58 FAs detected through GC, 32 FAs (average proportion of total FAs >0.1%) were used for analysis. For direct transmethylation versus traditional full extraction methods, linear regressions were used to compare cross-validity of methods for specific FA groups that were the principle drivers in dissimilarity among species. As values for each principle FA detected varied in significance between the direct transmethylation method and the traditional method (total lipid extraction followed by transmethylation), only extractions through direct transmethylation were used for comparison in multivariate analysis for consistency. The sum of saturated FAs (SFA), mono-unsaturated FAs

(MUFA), polyunsaturated FAs (PUFA), and branched isomer saturated FAs (Iso-SFA) were calculated for each species and sample type.

Because of low sample size of some species, proportional mean percentages of essential FAs relative to each species were compared only between grey reef sharks, whitetip reef sharks, coral trout (*Plectropomus leopardus*), red throat emperor (*Lethrinus miniatus*), and grass emperor (*Lethrinus laticaudis*) using 'vegan' in R (R Core Team 2018; Oksanen et al. 2016). These species comprised the main focus of the study. FA profiles were compared between extraction (direct and total) and tissue type (muscle and blood). Additionally, due to limited size and volume of some samples, only three species (grey reef shark, coral trout, red throat emperor) were used for tissue type comparison. Analysis of similarities (ANOSIM), similarity of percentages (SIMPER), and redundancy analysis (RDA) were used to define species differences in basal dietary sources by identifying the primary FAs that contribute to sample variation. RDA was chosen to constrain FA explanatory variables on distance-based (Euclidean) ordinations over principal components. Additionally, RDA was used to compare the degree of separation of each species based on FA profiles obtained by the direct transmethylation method compared to traditional full-extraction method. Statistical differences between the analytical methods were tested using PERMANOVA in vegan. Due to the spatial and sampling limitations of the study, no environmental variables were fit to the ordinations as constraints. Variance was measured from dissimilarity matrix values and tested for significance with permutational analysis of variance (adonis-PERMANOVA) using tissue type cross-compared with species. Fork length (all) and sex (reef sharks only) were tested as response variables. Niche overlap and width were calculated between species FA profiles in R using SPAA (species association analysis; Zhang 2016) and EcoSimR packages (Gotelli et al. 2015) to determine the degree of similarity or separation in ecological niche space. Niche overlap was calculated using *Pianka* variance derived from competition coefficients that determine shared resource by multiple species returning values between 0 and 1; where 0 suggests no shared resources and 1 as complete overlap in resource utilization (Gotelli et al, 2015). Niche width was determined using the *Shannon* Index which is the main index to quantitatively measure diet diversity (Petraitis 1979; Brower et al. 1998).

Post-hoc multilevel comparisons on PERMANOVAs including comparisons between tissue type (i.e. blood plasma versus muscle tissue) were tested using a pairwise adonis function with Bonferroni correction (Martinez 2017). Additionally, regressions were performed by species including summed proportions of all essential FAs. Finally, FA trophic biomarkers (FATM) commonly seen as indicators of differences in primary production and basal dietary sources were plotted as ratios by muscle and blood type of directly transmethylated samples. Some accepted markers in literature indicative of diatoms are 16:1ω7 and 18:1ω7, and markers of dinoflagellates are 16:0 and 22:6ω3 (Dalsgaard et al. 2003; Parrish 2013). While all species can biosynthesise 16:0, separation between species can also show habitat differences (Meyer et al. 2019). Certain biomarker ratios can provide information on long-term diet. For instance, a ratio of 16:1ω7/16:0 can distinguish between diatom and dinoflagellate feeding (Pethybridge et al. 2014). Ratios have also been used to interpret differences in trophic position (20:5ω3/22:6ω3) and degree of carnivory (18:1ω7/18:1ω9) (Dalsgaard et al. 2003).

4.3 Results

4.3.1 Traditional Full Extraction versus Direct Methods

No statistical differences were found in mean overall FA profiles of muscle tissue between traditional and direct transmethylation methods (PERMANOVA, perm=999, $p>0.05$, $r^2=0.04$). However, FA proportions of blood plasma samples between methods were statistically different ($p<0.05$, $r^2=0.19$). These differences were principally derived from high concentrations of 16:0 (palmitic acid) (SIMPER 14.1% dissimilarity contribution), 22:6ω3 (DHA, docosahexaenoic acid, 13.6%) and 18:0 (10%) (stearic acid) estimated from direct compared to traditional methods (Tables 4.2 & 4.3). Muscle tissue FA profiles for both methods consisted primarily of PUFA (mainly DHA and ARA, 20:4ω6 arachidonic acid) for each species except grey reef sharks, where PUFAs comprised less than SFA and MUFAs using direct methods (Table 4.2). PUFA proportions (percent ± standard deviation) were also higher using traditional extraction methods (37 ± 4 – 56 ± 6 %) over direct methods (28 ± 3 – 47 ± 5%) except in whitetip reef sharks. Blood plasma FA profiles showed generally higher concentrations of SFA, MUFA, and PUFA with direct methods (39± 5 – 48 ± 7%) compared to traditional (38 ± 5 – 42 ± 4%) (Table 4.2). PUFAs were generally found in the highest proportions in both methods followed by SFAs (28 ± 5 – 40 ± 8%).

Linear regressions of overall mean FA profiles (essential FAs) by species (grey reef shark, coral trout, red throat emperor) between traditional and direct methods (for both blood plasma and muscle tissue) showed high statistical significance passing through the origin ($p<0.005$) with r^2 values ranging from 0.82 - 0.91 and slopes from 0.63 - 1.03 (Figure 4.4). However, regressions for six of the major FA contributors varied in statistical significance (p value range >0.5 - <0.001) with r^2 values ranging from 0.04 - 0.4 and slopes from 0.02 - 0.7 for muscle tissue (Figure S4-a). Furthermore, regressions of essential FAs comparing extractive methods for blood plasma were not statistically significant (S4-b). These results indicate that for this study estimation of essential FA contributions to muscle resulting in high concentrations are less reliable for direct comparison between methods and that blood plasma methods could not be compared.

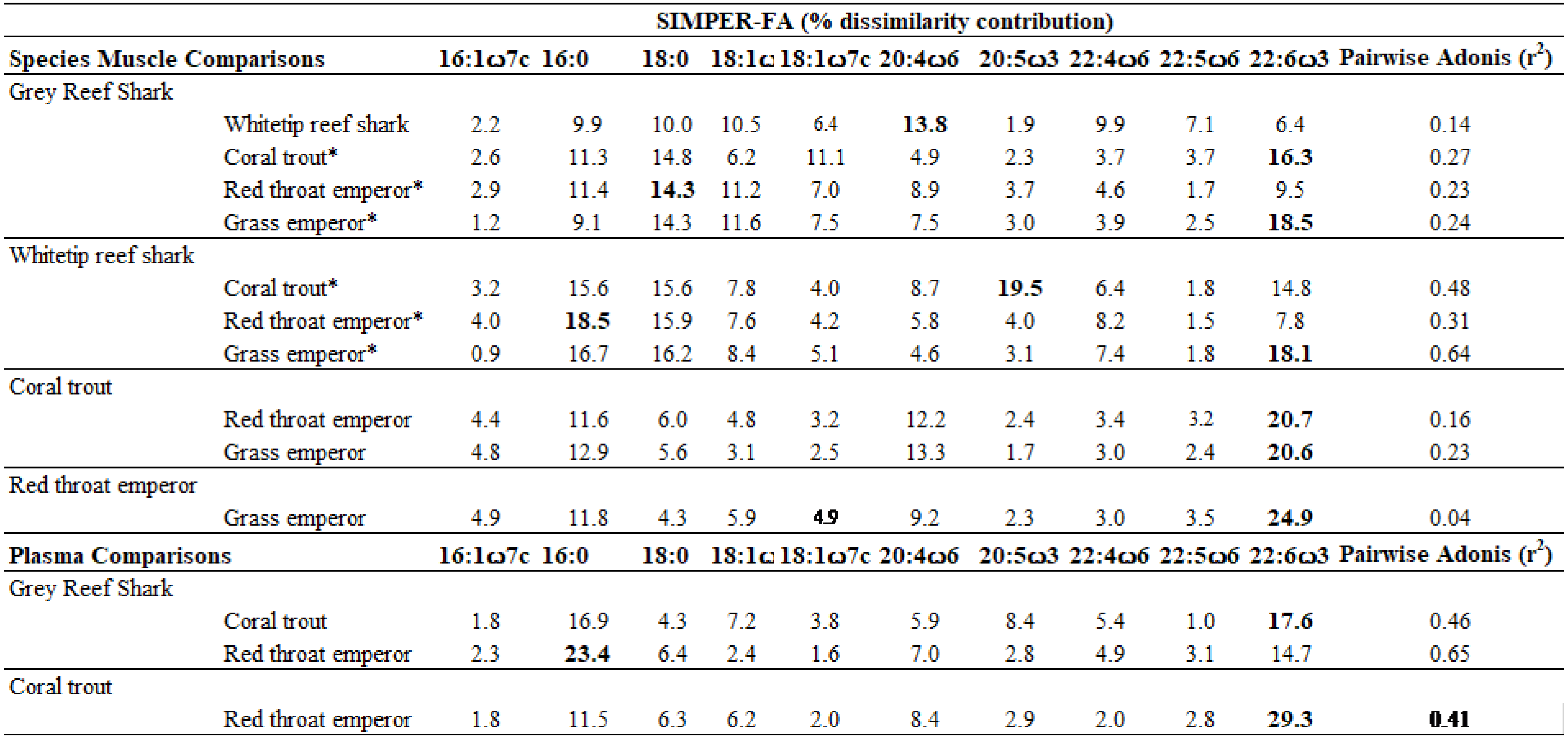
4.3.2 Muscle versus Plasma Tissue

Muscle and blood plasma were analysed using only direct transmethylation results due to concern around cross-comparison based on the extraction method used. Additionally, muscle and blood plasma comparisons were only tested for grey reef sharks, coral trout and red throat emperor due to volume of the sample and availability. There was a statistical difference in overall mean FA profiles between muscle and plasma using direct transmethylated (PERMANOVA, perm=999, $p=0.05$, $r^2=0.20$). Furthermore, crossed PERMANOVAs showed a significant effect from the interaction between species and tissue sample type ($p<0.005$, $r^2=0.42$) prompting further post-hoc pairwise comparisons. There were no statistical differences between muscle and blood FA profiles for red throat emperor (pairwise Adonis, perm=999, $p>0.05$, $r^2=0.09$) and coral trout ($p>0.05$, $r^2=0.12$), but grey reef sharks were statistically distinct ($p=<0.05$, $r^2=0.22$). ANOSIM tests also showed that FA profiles of individual grey reef sharks overlapped but showed statistical separation between muscle and blood plasma (ANOSIM-R=0.49, $p<0.005$), whereas coral trout (R=0.15, $p>0.05$) and red throat emperor (R=-0.08, $p>0.05$) were difficult to separate between tissue types. The differences in tissue type of grey reef sharks were mainly from 18:0 (SIMPER dissimilarity, 17.3%), DHA (16.8%), and 18:1ω9 (13.8%) (Table 4.3).

Table 4.2: Mean relative proportions (% ± standard deviation) of essential fatty acids (FAs) (>0.1%). TLEFA: total lipid extraction followed by transmethylation, TMFA: extraction by direct transmethylation. Bold indicates FAs with high concentrations greater than 3

	Common Coral Trout				Grey Reef Shark				Red Throat Emperor				Whitetip Reef Shark		Grass Emperor
	Muscle		Plasma		Muscle		Plasma		Muscle		Plasma		Muscle		Muscle
FA	TLEFA	TMFA	TLEFA	TMFA	TLEFA	TMFA	TLEFA	TMFA	TLEFA	TMFA	TLEFA	TMFA	TLEFA	TMFA	TMFA
14:0	0.2 ± 0.2	1.4 ± 1.6	0.2 ± 0.5	0.6 ± 0.4	0.2 ± 0.3	0.3 ± 0.5	0.1 ± 0.1	0.5 ± 0.2	0.0 ± 0.0	1.4 ± 0.9	0.1 ± 0.2	0.5 ± 0.2	0.2 ± 0.2	0.2 ± 0.1	0.3 ± 0.3
15:0	0.1 ± 0.1	0.5 ± 0.2	0.1 ± 0.1	0.6 ± 0.1	0.1 ± 0.1	0.2 ± 0.3	0.2 ± 0.2	0.4 ± 0.1	0.1 ± 0.1	0.7 ± 0.4	0.2 ± 0.3	0.8 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.5 ± 0.3
16:0	**10.3 ± 6.0**	**18.7 ± 6.5**	**9.1 ± 3.2**	**20.9 ± 2.8**	**11.0 ± 3.6**	**11.5 ± 3.1**	**10.3 ± 5.4**	**15.5 ± 1.6**	**9.3 ± 3.8**	**18.0 ± 5.0**	**13.2 ± 8.6**	**23.9 ± 3.0**	**7.7 ± 0.8**	**6.9 ± 0.7**	**17.7 ± 3.5**
16:0(FALD)	0.2 ± 0.2	0.9 ± 0.7	1.1 ± 1.6	1.2 ± 0.3	0.3 ± 0.5	0.7 ± 0.4	0.3 ± 0.2	0.8 ± 0.3	0.2 ± 0.1	0.6 ± 0.4	0.1 ± 0.1	0.6 ± 0.1	0.8 ± 0.6	2.4 ± 2.7	1.2 ± 0.6
17:0	0.7 ± 0.2	0.9 ± 0.3	1.2 ± 0.2	1.3 ± 0.4	0.6 ± 0.3	0.6 ± 0.5	1.2 ± 0.2	1.2 ± 0.2	1.0 ± 0.2	1.2 ± 0.4	2.0 ± 0.6	1.9 ± 0.2	0.5 ± 0.2	0.5 ± 0.1	1.0 ± 0.4
18:0	**11.0 ± 4.4**	**8.8 ± 2.6**	**12.1 ± 4.1**	**9.8 ± 1.8**	**16.3 ± 4.5**	**20.1 ± 6.4**	**11.7 ± 1.8**	**9.1 ± 0.6**	**12.3 ± 1.1**	**11.6 ± 2**	**16.7 ± 6.5**	**11.3 ± 1.1**	**22.8 ± 2.0**	**21.3 ± 0.8**	**10.7 ± 1.4**
19:0	0.4 ± 0.1	0.4 ± 0.1	0.8 ± 0.5	0.4 ± 0.1	0.5 ± 0.4	0.2 ± 0.1	0.5 ± 0.2	0.3 ± 0.0	0.5 ± 0.1	0.4 ± 0.1	0.4 ± 0.4	0.4 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.4 ± 0.1
20:0	0.3 ± 0.1	0.3 ± 0.2	0.6 ± 0.3	0.3 ± 0.1	1.6 ± 3.30	0.9 ± 1.0	0.7 ± 0.1	0.5 ± 0.1	0.5 ± 0.2	0.4 ± 0.2	0.7 ± 0.6	0.4 ± 0.1	0.3 ± 0.2	0.4 ± 0.0	0.2 ± 0.1
22:0	0.4 ± 0.2	0.2 ± 0.1	3.6 ± 6.8	0.4 ± 0.1	1.0 ± 1.0	0.6 ± 0.2	1.6 ± 1.1	1.3 ± 0.3	0.5 ± 0.2	0.4 ± 0.3	1.7 ± 2.4	0.5 ± 0.1	0.6 ± 0.2	0.5 ± 0.1	1.2 ± 0.3
24:0	0.4 ± 0.1	0.4 ± 0.1	1.0 ± 0.8	0.5 ± 0.1	0.6 ± 0.3	0.5 ± 0.4	1.7 ± 0.5	2.6 ± 0.9	0.4 ± 0.1	0.4 ± 0.3	0.9 ± 0.9	0.4 ± 0.1	0.3 ± 0.2	0.3 ± 0.0	0.4 ± 0.1
16:1ω7c	**0.9 ± 0.7**	**3.4 ± 2.6**	**0.7 ± 0.3**	**1.8 ± 0.5**	**1.2 ± 0.7**	**1.9 ± 1.0**	**1.3 ± 1.3**	**1.6 ± 0.6**	**0.8 ± 0.4**	**3.2 ± 2.1**	**0.6 ± 0.9**	**2.3 ± 0.2**	**0.9 ± 0.6**	**0.8 ± 0.1**	**1.4 ± 0.6**
17:1ω8c+a17:0	0.4 ± 0.3	0.6 ± 0.3	0.7 ± 0.6	0.5 ± 0.2	0.6 ± 0.4	0.5 ± 0.2	0.5 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.7 ± 0.2	0.4 ± 0.4	0.8 ± 0.2	0.5 ± 0.3	0.4 ± 0.1	0.7 ±0.3
18:1ω7	**2.2 ± 1.1**	**2.7 ± 2.2**	**2.4 ± 0.5**	**2.2 ± 0.2**	**4.8 ± 2.8**	**6.8 ± 3.1**	**3.5 ± 0.7**	**3.4 ± 0.2**	**2.4 ± 0.2**	**2.8 ± 1.5**	**2.4 ± 2.1**	**2.8 ± 0.2**	**5.0 ± 0.5**	**5.2 ± 0.7**	**1.9 ± 0.4**
18:1ω9	**9.6 ± 2.3**	**8.6 ± 0.8**	**7.1 ± 3.3**	**5.9 ± 1.2**	**11.7 ± 4.1**	**17.2 ± 5.8**	**8.9 ± 0.9**	**8.2 ± 0.9**	**8.7 ± 0.9**	**10.6 ± 2.7**	**9.4 ± 5.1**	**7.8 ± 0.7**	**15.8 ± 2.2**	**14.8 ± 1.4**	**9.3 ± 1.5**
20:1ω9	0.6 ± 0.3	0.5 ± 0.4	1.0 ± 0.9	0.4 ± 0.1	1.4 ± 0.7	1.4 ± 1.0	1.0 ± 0.1	0.6 ± 0.4	0.6 ± 0.2	0.6 ± 0.4	0.3 ± 0.4	0.6 ± 0.4	0.9 ± 0.2	1.1 ± 0.2	0.2 ± 0.2
24:1ω11	**2.4 ± 0.4**	**1.5 ± 0.9**	**3.3 ± 1.6**	**3.0 ± 0.7**	**1.7 ± 0.3**	**2.0 ± 0.9**	**1.7 ± 0.3**	**2.1 ± 0.6**	**1.4 ± 0.5**	**1.3 ± 1.0**	**2.8 ± 1.6**	**1.9 ± 0.7**	**1.3 ± 0.2**	**1.7 ± 0.2**	**1.2 ± 0.3**
16:4	**0.1 ± 0.1**	**0.1 ± 0.4**	**3.5 ± 3.4**	**0.0 ± 0.0**	**0.4 ± 03**	**0.2 ± 0.3**	**4 ± 6.0**	**0.1 ± 0.2**	**0.3 ± 0.3**	**0.1 ± 0.1**	**1.8 ± 2.7**	**0.1 ± 0.2**	**0.1 ± 0.1**	**0.0 ± 0.0**	**0.0 ± 0.0**
17:1	1.6 ± 0.5	0.7 ± 0.4	0.9 ± 0.4	0.2 ± 0.1	0.9 ± 0.6	1.0 ± 0.5	0.8 ± 0.3	0.5 ± 0.3	0.8 ± 0.4	0.9 ± 0.7	1.2 ± 2.5	0.1 ± 0.2	1.6 ± 0.4	0.9 ± 0.4	0.7 ± 0.2
18:2ω6	1.5 ± 0.6	2.3 ± 1.3	0.9 ± 0.2	1.1 ± 0.3	1.0 ± 0.3	1.0 ± 0.7	1.9 ± 1.1	1.2 ± 0.2	2.6 ± 1.2	2.2 ± 1.0	0.8 ± 0.8	1.8 ± 0.3	1.3 ± 0.1	1.3 ± 0.1	1.7 ± 1.1
20:2ω6	0.5 ± 0.1	0.5 ± 0.4	0.7 ± 0.4	0.3 ± 0.1	0.7 ± 0.2	0.5 ± 0.2	0.9 ± 0.1	0.6 ± 0.2	0.7 ± 0.2	0.5 ± 0.3	0.3 ± 0.4	0.4 ± 0.1	0.5 ± 0.3	0.6 ± 0.1	0.4 ± 0.2
18:3ω3	0.5 ± 0.2	0.7 ± 0.4	0.3 ± 0.1	0.4 ± 0.1	0.3 ± 0.3	0.2 ± 0.6	0.6 ± 0.2	0.5 ± 0.1	0.8 ± 0.4	0.7 ± 0.4	0.2 ± 0.3	0.5 ± 0.2	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.2
20:4ω3	0.5 ± 0.2	06 ± 0.2	0.5 ± 0.4	0.3 ± 0.1	0.5 ± 0.3	0.4 ± 0.3	0.6 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.2	0.2 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0.5 ± 0.1
20:3ω6	0.8 ± 0.3	0.7 ± 0.3	0.8 ± 0.5	0.4 ± 0.1	0.8 ± 0.3	0.5 ± 0.2	0.9 ± 0.0	0.7 ± 0.2	0.7 ± 0.1	0.6 ± 0.3	0.3 ± 0.3	0.3 ± 0.1	0.6 ± 0.3	0.9 ± 0.2	0.6 ± 0.1
20:4ω6	**10.0 ± 3.2**	**7.4 ± 4.1**	**8.2 ± 4.0**	**10.5 ± 2.2**	**8.0 ± 3.0**	**7.4 ± 33**	**9.4 ± 5.1**	**10.3 ± 1.4**	**18.0 ± 2.7**	**12.0 ± 4.1**	**10.7 ± 5.4**	**12.2 ± 2.6**	**13.8 ± 3.4**	**13.8 ± 2.1**	**12.2 ± 2.8**
20:5ω3	**2.6 ± 0.7**	**2.3 ± 0.7**	**3.3 ± 0.9**	**4.2 ± 1.0**	**2.2 ± 2.0**	**1.5 ± 2.0**	**2.3 ± 0.7**	**3.7 ± 1.2**	**4.3 ± 0.7**	**3.2 ± 1.1**	**3.6 ± 0.4**	**3.4 ± 0.4**	**0.6 ± 0.2**	**0.8 ± 0.1**	**2.8 ± 0.5**
20:1ω11c	0.3 ± 0.4	0.2 ± 0.2	0.8 ± 0.6	0.4 ± 0.4	0.3 ± 0.4	0.5 ± 1.0	0.8 ± 0.3	0.7 ± 0.5	0.7 ± 0.5	0.6 ± 0.5	0.4 ± 0.4	0.6 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.4 ± 0.2
22:1ω7	0.4 ± 0.3	0.2 ± 0.1	1.6 ± 1.8	0.3 ± 0.1	1.1 ± 1.3	0.3 ± 0.1	1.5 ± 1.2	0.6 ± 0.6	0.5 ± 0.3	0.2 ± 0.1	0.3 ± 0.3	0.5 ± 0.1	0.3 ± 0.3	0.1 ± 0.0	0.2 ± 0.1
22:1ω9	0.4 ± 0.4	0.2 ± 0.1	1.0 ± 1.5	0.1 ± 0.1	1.0 ± 0.9	0.4 ± 0.2	1.3 ± 0.6	0.6 ± 0.6	0.4 ± 0.3	0.1 ± 0.1	0.2 ± 0.2	0.0 ± 0.0	0.3 ± 0.5	0.2 ± 0.0	0.1 ± 0.0
22:4ω6	**3.5 ± 1.5**	**3.2 ± 1.5**	**2.6 ± 1.1**	**2.2 ± 0.8**	**6.2 ± 3.8**	**4.6 ± 3.5**	**3.8 ± 2.0**	**3.9 ± 0.7**	**4.1 ± 0.4**	**3.5 ± 1.8**	**1.9 ± 1.2**	**2.2 ± 0.4**	**6.4 ± 2.9**	**8.4 ± 1.8**	**3.5 ± 0.6**
22:5ω3	**3.1 ± 0.7**	**4.8 ± 6.5**	**2.2 ± 0.9**	**2.2 ± 0.4**	**2.5 ± 0.9**	**2.2 ± 2.0**	**3.0 ± 1.1**	**2.9 ± 0.6**	**3.6 ± 0.6**	**2.5 ± 0.5**	**2.5 ± 1.3**	**2.1 ± 0.3**	**1.7 ± 0.5**	**1.9 ± 0.3**	**3.3 ± 0.9**
22:5ω6	**4.8 ± 2.7**	**3.5 ± 1.1**	**1.8 ± 0.7**	**2.1 ± 0.3**	**2.7 ± 1.3**	**1.6 ± 0.9**	**2.0 ± 0.8**	**2.3 ± 0.3**	**2.9 ± 0.9**	**2.3 ± 1.0**	**1.2 ± 1.1**	**1.2 ± 0.3**	**2.0 ± 1.0**	**2.4 ± 0.5**	**3.2 ± 1.0**
22:6ω3	**27.4 ± 13.6**	**19.9 ± 9.5**	**16.8 ± 7.8**	**24.3 ± 3.5**	**13.8 ± 8.7**	**8.4 ± 3.7**	**14.9 ± 5.9**	**19.5 ± 3.8**	**17.8 ± 5.7**	**13 ± 5.7**	**16.5 ± 8.7**	**14.7 ± 2.3**	**9.6 ± 1.6**	**9.7 ± 1.3**	**20.9 ± 7.0**
24:1ω7	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.4	0.0 ± 0.0	0.2 ± 0.3	0.1 ± 0.2	0.3 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.6 ± 0.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
i17:0	0.3 ± 0.2	0.2 ± 0.1	2.3 ± 4.3	0.4 ± 0.2	0.9 ± 0.7	0.8 ± 0.2	0.4 ± 0.1	0.4 ± 0.1	0.2 ± 0.1	0.4 ± 0.2	2.4 ± 5.1	0.6 ± 0.3	1.0 ± 0.1	0.7 ± 0.3	0.3 ± 0.1
ΣSFA	23.8 ± 4.5	31.6 ± 6.3	28.8 ± 4.4	34.7 ± 7.1	32.1 ± 5.9	35.0 ± 7.1	28.1 ± 4.5	31.4 ± 5.3	24.7 ± 4.6	34.5 ± 6.4	36.0 ± 6.3	40.3 ± 8.1	32.6 ± 7.6	30.2 ± 7.1	31.4 ± 6.3
ΣMUFA	19.7 ± 2.0	19.7 ± 1.8	27.8 ± 1.5	14.9 ± 1.3	26.5 ± 2.4	33.3 ± 3.6	28.7 ± 1.8	19.5 ± 1.7	17.8 ± 1.7	21.7 ± 2.2	21.9 ± 1.9	17.9 ± 1.7	27.4 ± 3.2	25.6 ± 3.1	16.3 ± 2.0
ΣPUFA	55.3 ± 7.3	46.6 ± 5.2	38.5 ± 4.6	48.2 ± 6.6	38.8 ± 4	28.5 ± 2.8	41.5 ± 4.2	46.4 ± 5.4	56.4 ± 6.1	41.5 ± 4.2	38.6 ± 4.8	39.3 ± 4.7	37 ± 4.3	40.2 ± 4.4	49.7 ± 5.9
ΣIso-SFA	0.5 ± 0.2	0.5 ± 0.1	2.7 ± 1.2	0.5 ± 0.2	1.3 ± 0.4	1.3 ± 0.3	0.7 ± 0.2	1.1 ± 0.3	0.4 ± 0.1	0.8 ± 0.2	3.1 ± 1.1	1.0 ± 0.3	1.6 ± 0.5	1.1 ± 0.3	0.5 ± 0.1
ΣOther	0.8 ± 0.1	1.7 ± 0.5	2.2 ± 0.5	1.7 ± 0.7	1.3 ± 0.2	1.9 ± 0.4	1.1 ± 0.1	1.6 ± 0.4	0.6 ± 0.1	1.5 ± 0.3	0.5 ± 0.1	1.5 ± 0.4	1.4 ± 0.4	3.00 ± 1.4	2.1 ± 0.7

Table 4.3: SIMPER (Similarity of Percentages) % dissimilarity contribution between species and pairwise PERMANOVA (Adonis-vegan R, perm=999) r^2 values of muscle tissue and blood plasma. Global statistical significance between species determined by pairwise PERMANOVA denoted by *adjusted p value<0.05, bold values indicate strongest FA contribution to dissimilarity per species group comparison. Bold values indicate primary FA contribution to dissimilarity for each species comparison



		SIMPER-FA (% dissimilarity contribution)										
Species Muscle Comparisons		**16:1ω7c**	**16:0**	**18:0**	**18:1c**	**18:1ω7c**	**20:4ω6**	**20:5ω3**	**22:4ω6**	**22:5ω6**	**22:6ω3**	**Pairwise Adonis (r^2)**
Grey Reef Shark												
	Whitetip reef shark	2.2	9.9	10.0	10.5	6.4	**13.8**	1.9	9.9	7.1	6.4	0.14
	Coral trout*	2.6	11.3	14.8	6.2	11.1	4.9	2.3	3.7	3.7	**16.3**	0.27
	Red throat emperor*	2.9	11.4	**14.3**	11.2	7.0	8.9	3.7	4.6	1.7	9.5	0.23
	Grass emperor*	1.2	9.1	14.3	11.6	7.5	7.5	3.0	3.9	2.5	**18.5**	0.24
Whitetip reef shark												
	Coral trout*	3.2	15.6	15.6	7.8	4.0	8.7	**19.5**	6.4	1.8	14.8	0.48
	Red throat emperor*	4.0	**18.5**	15.9	7.6	4.2	5.8	4.0	8.2	1.5	7.8	0.31
	Grass emperor*	0.9	16.7	16.2	8.4	5.1	4.6	3.1	7.4	1.8	**18.1**	0.64
Coral trout												
	Red throat emperor	4.4	11.6	6.0	4.8	3.2	12.2	2.4	3.4	3.2	**20.7**	0.16
	Grass emperor	4.8	12.9	5.6	3.1	2.5	13.3	1.7	3.0	2.4	**20.6**	0.23
Red throat emperor												
	Grass emperor	4.9	11.8	4.3	5.9	**4.9**	9.2	2.3	3.0	3.5	**24.9**	0.04
Plasma Comparisons		**16:1ω7c**	**16:0**	**18:0**	**18:1c**	**18:1ω7c**	**20:4ω6**	**20:5ω3**	**22:4ω6**	**22:5ω6**	**22:6ω3**	**Pairwise Adonis (r^2)**
Grey Reef Shark												
	Coral trout	1.8	16.9	4.3	7.2	3.8	5.9	8.4	5.4	1.0	**17.6**	0.46
	Red throat emperor	2.3	**23.4**	6.4	2.4	1.6	7.0	2.8	4.9	3.1	14.7	0.65
Coral trout												
	Red throat emperor	1.8	11.5	6.3	6.2	2.0	8.4	2.9	2.0	2.8	**29.3**	**0.41**

4.3.3 Species-Specific Differences in FA Profiles

Blood plasma comprised mainly PUFA (DHA and ARA) for grey reef sharks (46 ± 5%) and coral trout (48 ± 7%). Grey reef shark muscle composition was primarily SFA (35 ± 7%) and MUFA (33 ± 4%), whereas PUFA was still dominant for coral trout. Red throat emperor composition was dominated by PUFA and SFA, but SFA was slightly higher in plasma(40 ± 8%) than in muscle (34 ± 6.4%) (Table 4.2).

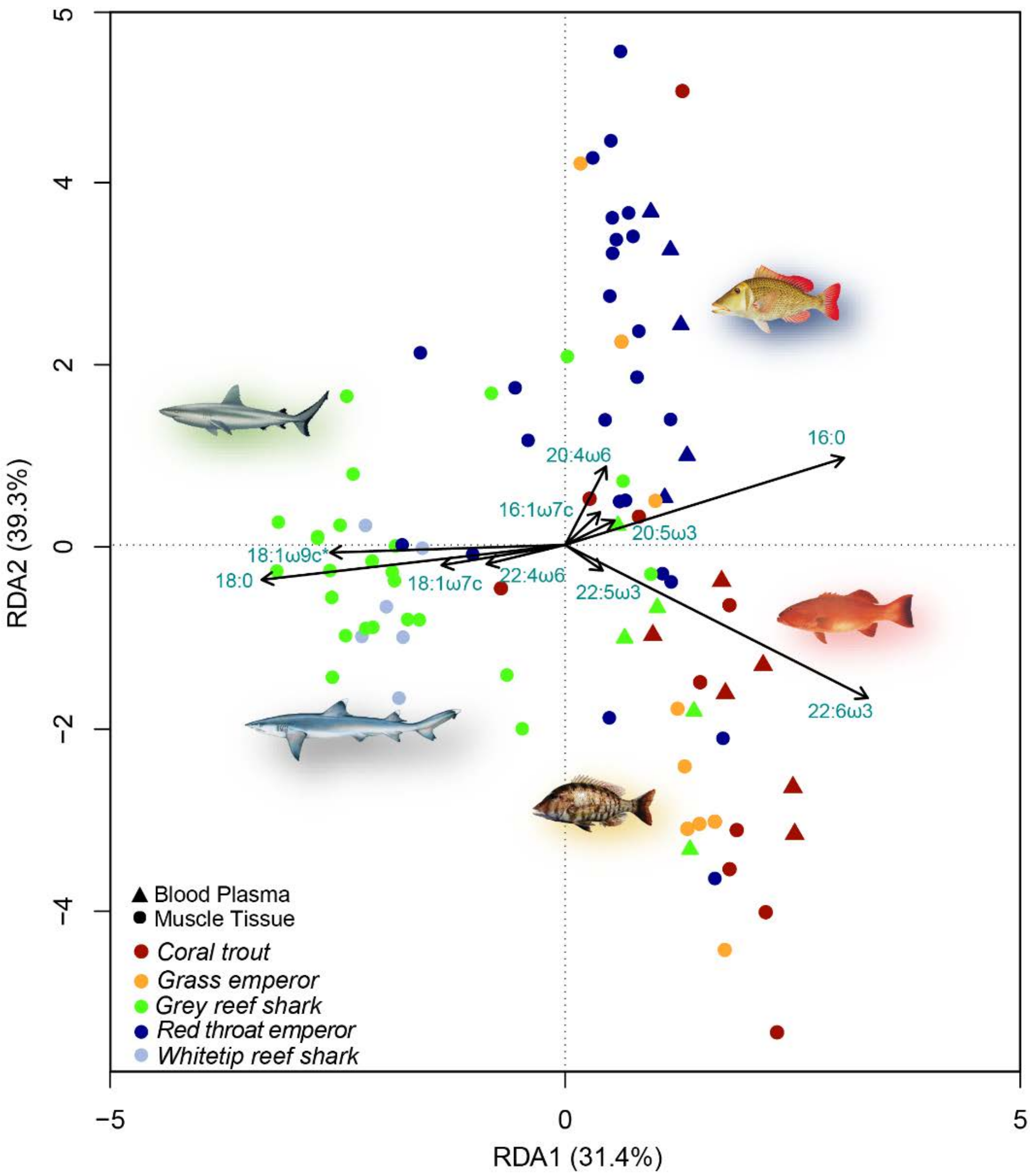


Figure 4.2: Redundancy analysis (rda) of fatty acid profiles from muscle tissue across sampled reef fishes. Eigenvalues are the total variance (%) explained by each axis (RDA1/RDA2)

Of the 32 FAs (average proportion of total FAs >0.1), those commonly found with highest concentrations in all species and tissue types were DHA, ARA, 16:0, and 18:0 (Table 4.2). ANOSIM tests showed that samples were more related within tissue type (muscle vs. plasma). Shark muscle tissue FA contributions for both grey reef and whitetip reef sharks were statistically different from muscle tissue of bony teleost fishes (coral trout, red throat emperor, grass emperor) (pairwise PERMANOVA, perm=999, adjusted p><0.05, r^2 range=0.2 - 0.6), but not statistically distinct from each other (adjusted p>0.05, r^2=0.14) (Table 4.3, Figure 4.2). However, whitetip reef shark muscle occupied a smaller niche space than grey reef sharks even though there was a degree of overlap (Figure 4.2). Differences in grey reef shark muscle tissue compared to coral trout and red throat emperor were largely driven by concentrations of DHA (SIMPER dissimilarity 16.3 and 18.5% respectively), whereas red throat emperor separated out based on 18:0 (14.3%). Conversely, whitetip reef shark differences in muscle were primarily from 16:0 acid when compared to coral trout and red throat emperor (15.6 and 18.54% respectively) and DHA for grass emperor (18.1%). Overall, 16:0 values were lowest for sharks and highest in red throat emperor and coral trout. Redundancy analysis showed that clustering was driven by species differences in FA concentrations [coral trout/grass emperor (DHA), red throat emperor (16:0 and ARA), grey reef/whitetip reef sharks (18:0, 18:1ω9, 18:1ω7) (Figure 4.2)]. The percent overlap calculations ranged from 0.62-0.92 with the closest niche space between coral trout and grass emperor, and the most distinct were between whitetip reef sharks and coral trout (Table 4.4). Comparing the RDA of fatty acid values derived from the traditional method, this same clustering was observed per species (df=3, F=2.3, p<0.005). This shows that even though there are degrees of variation in proportional values of FA groups between the FA analytical methods, the ecological distinctions are the same. There was no effect of fork length or sex on FA composition in any of the Adonis models.

Blood plasma FA profiles were not statistically distinct between grey reef shark and coral trout (pairwise Adonis, perm=999, p>0.05, r^2=0.46), indicating differences in relatedness between tissue types for certain species. For blood plasma in red throat emperor, similar contributions of SFAs dominated by 16:0 acid (40.34±8.1) and PUFAs (mainly DHA and ARA, 39.27±4.65) were found.

There were no statistical differences between plasma FA profiles of coral trout and red throat emperor.

Table 4.4: FA niche breadth calculations for each of the five species compared using 'spaa' and EcoSimR. Niche overlap percentage (spaa; Pianka variance), Niche widths (EcoSimR; Shannon diversity index).

Niche Overlap Percentage

	Common coral trout	Grass emperor	Grey reef shark	Red throat emperor
Grass emperor	0.92			
Grey reef shark	0.72	0.75		
Red throat emperor	0.88	0.90	0.79	
White-tip reef shark	0.62	0.69	0.86	0.73

Niche Widths

Common coral trout	Grass emperor	Grey reef shark	Red throat emperor	White-tip reef shark
2.00	1.99	2.06	2.06	1.99

4.3.4 Trophic Biomarkers

FATM ratios varied among species where muscle ratios of whitetip reef sharks showed tight groupings indicative of smaller dietary niches while the other species had a broader range of values (Figure 4.3). Mean muscle and plasma ratios differed between species, as did the degree of separation. For the 16:1ω7/16:0 (diatoms/zooplankton), there was clear separation and in general, tight grouping within species. The 16:0/18:0 biomarker was higher in sharks than in teleosts within this study. DHA/EPA ratios also clustered in tight groupings within species with low ratios in sharks compared to teleosts with the main differences coming from the proportion of DHA. Finally, there was a linear trend in the 18:1ω7/18:1ω9 ratio, where sharks had higher concentration in these FAs than teleosts.

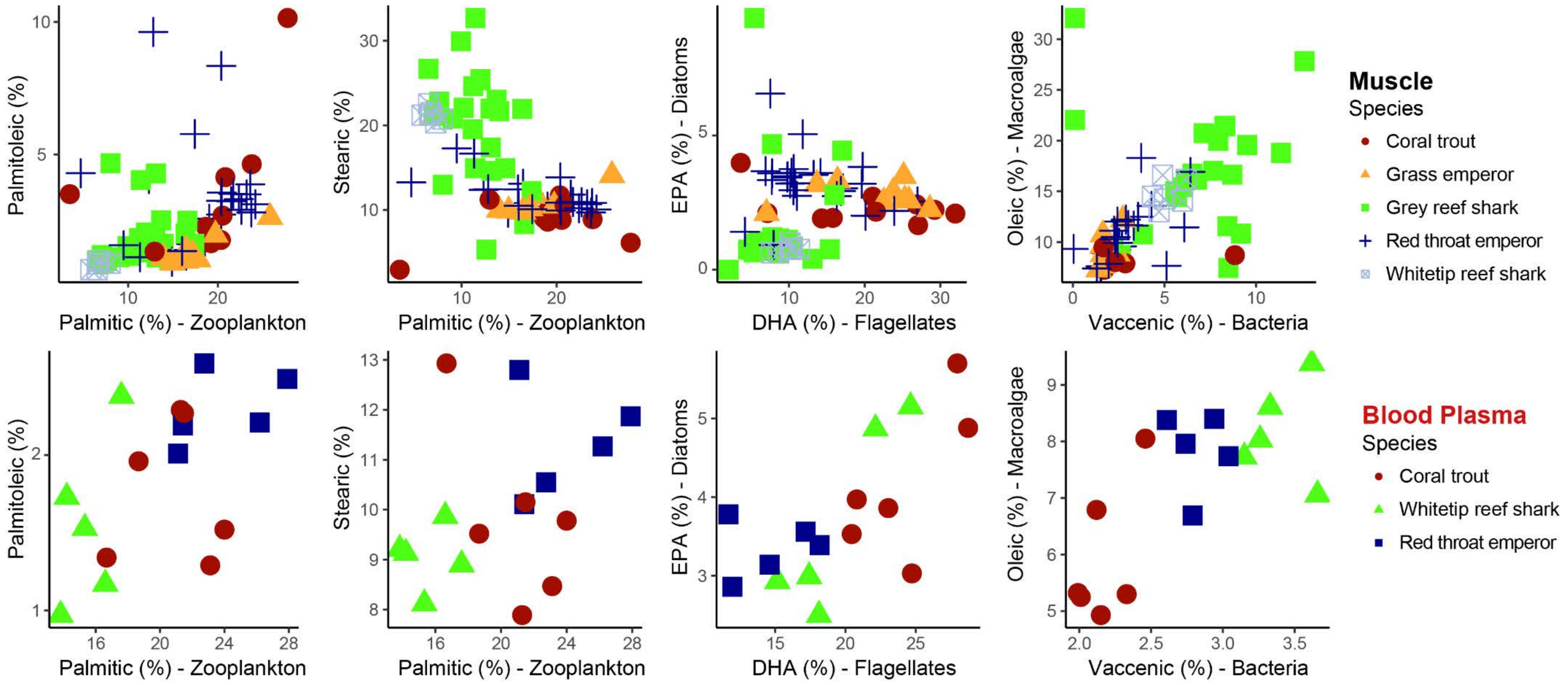


Figure 4.3: Common trophic biomarker ratio comparisons between species by muscle (top) and blood plasma (bottom)

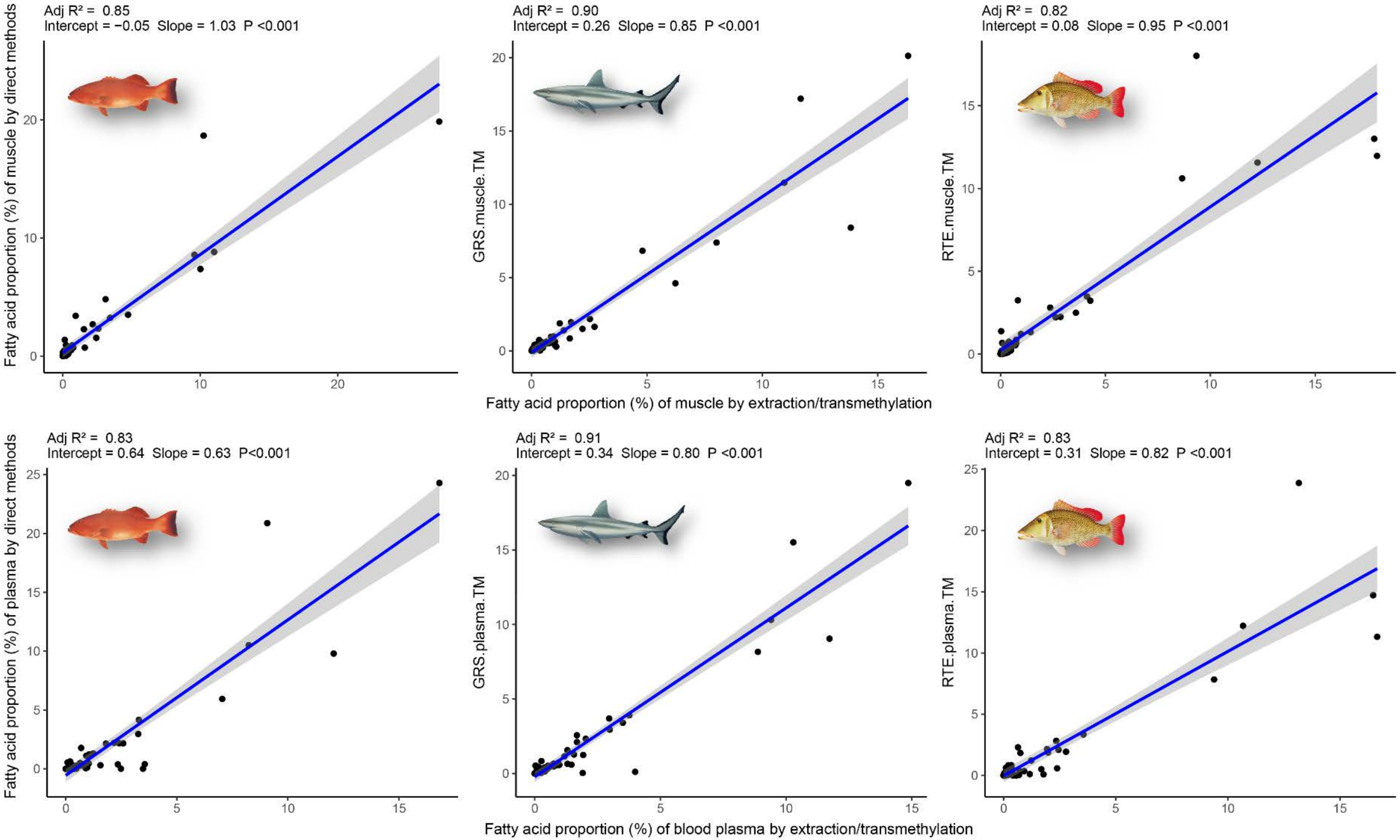


Figure 4.4: Linear regressions comparing traditional to direct methods of extraction of 32 FA values for muscle (top row) and plasma (bottom row) of coral trout (left), grey reef shark (middle), red throat emperor (right). Grey area are smoothed confidence intervals and p-values are the difference to the 1:1 line ratio

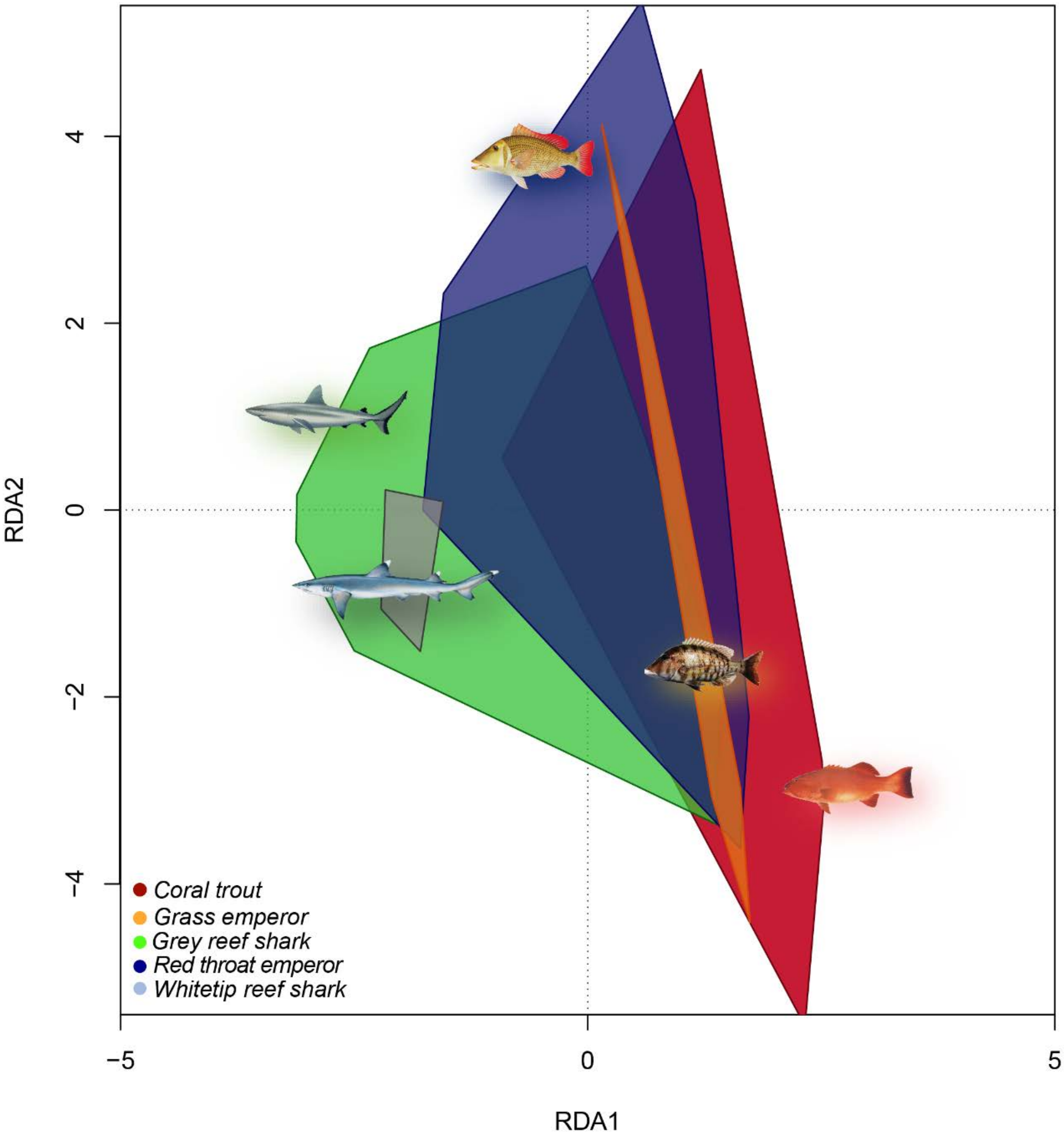


Figure 4.5: Convex hulls distinguishing total FA niche breadth of each species

4.4 Discussion:

This study demonstrated that there were differences in trophic niches, from calculating degree of overlap, between five species of coral reef mesopredators as indicated by FA profiles and biomarkers. Reef shark FA profiles (grey reef shark, whitetip reef shark) were found to be distinct from teleosts. These results offer a higher resolution of dietary distinction than stable isotope analysis between species due to a larger number of potential markers. However, results from our study can help supplement stable isotope analysis which gives a better understanding of trophic position (Post 2002). Recent research by Espinoza et al (2019) using stable isotope analysis in the Townsville region showed similar dietary overlap to our study (Figure 4.5) between whitetip reef sharks, grey reef sharks, red throat emperor, and coral trout. Additionally, grey reef sharks were found to occupy a higher relative trophic position than whitetip reef sharks, coral trout, and red throat emperor. This is converse to findings by Roff et al. (2016) and Frisch et al. (2016) who showed significant overlap in isotopic niche space among sharks and high-order teleosts on coral reefs. The authors also found trophic redundancy among grey reef sharks, whitetip reef sharks, and blacktip reef sharks (*Carcharhinus melanopterus*). The distinction between mesopredators in our study was driven primarily by prevalence of 18:1ω9 and 18:1w7 in sharks compared to prevalence of 16:0 in teleosts. All species occupied a similar FA niche breadth. However, grass emperor and whitetip reef sharks occupied the smallest breadth which may be characteristic of a more specialized diet range. This can be further verified by more specific resource utilization and least amount of niche overlap of whitetip reef sharks. Previous stomach content studies of whitetip reef sharks reveal high numbers of teleost fishes (~80-91%) (Cortes 1999; Frisch et al. 2016) supporting our results that whitetip reef sharks are possibly less generalist feeders than grey reef sharks.

We also demonstrated the direct transmethylation procedure is appropriate for trophic studies of tropical species, but more research is necessary before comparing analyses across tissue types. This result contributes to a growing pool of literature that validates direct transmethylation methods and questions future use of blood plasma. Studies incorporating cross-tissue differences in the future should include an experimental phase in order to investigate an individual's trophic ecology at shorter time scales compared to muscle. For example, this type of study would need knowledge of potential effects such as timing of last meal for better interpretation of differences between blood plasma and muscle turnover rates related to FA.

We found the main FAs separating species were DHA, 16:0, and 18:0. These three FAs have been used in other studies as strong indicators of prey differences (Iverson et al. 2001, Beckmann et al. 2013). Additionally, differences in FA profiles between mesopredators found in this study can be linked to specific basal sources that have not previously been documented for coral reef species. For example, DHA is linked to symbiotic dinoflagellates in some species of coral (Zhukova & Titlyanov 2003), suggesting that fishes with high levels of DHA (such as coral trout) in their tissues are supported by coral derived carbon. Such differences can help to characterise sympatric species, but also give insights into habitat use and basal sources of food webs (Piché et al. 2010; Arai et al. 2015b).

Other FAs important in characterizing species in this study were 18:1ω9, 18:1ω7, and ARA which are the principal components separating fish and sharks. ARA has been found to be high in omnivores and benthivores in Australia (Dunstan et al. 1988). Furthermore, ARA is a primary component of coral, mucus and crustose coralline algae (CCA) on coral reefs in the Caribbean (van Duyl et al. 2011) and soft coral in the South China Sea (Imbs et al. 2009). These inferences can assist in determining prey types that utilize these specific benthic resources. Piscivorous reef fish such as coral trout (Emslie et al. 2008) largely consume labrid, pomacentrid and caesionid fishes (Frisch et al. 2014, Matley et al. 2018), which is reflective of high DHA found for planktivores in the Northwestern Hawaiian Islands (NWHI) (Piché et al. 2010) as well as coral trout in our study. Other large reef fish such as grass and red throat emperors are often considered piscivorous-invertivores (MacNeil et al. 2015), and the high proportion of ARA found in these species align with a diet consisting of cephalopods and crustaceans (Piché et al. 2010). Conversely, variable results have been reported for indicator types of other FAs. For example, 18:1ω9 has been used as an indicator for carnivory (Pethybridge et al. 2011) but has also been linked to macroalgae in other instances (Parrish 2013). Though more research is needed to identify specific prey resources for predatory fishes on coral reefs, high levels of ARA and DHA in teleosts could indicate a stronger link to prey that rely on coral and algal habitat types than for sharks. Studies have also found that some reef dwelling sharks, such as grey reef sharks, can bring pelagic inputs (nutrients) to reefs (McCauley et al. 2012; Frisch et al. 2016, Williams et al. 2018). MacCauley et al. (2012) determined that reef sharks differ in derived carbon resources (pelagic) and habitat use from large teleost fish (reef-based) on Palmyra Atoll. The dominant FAs characteristic of pelagic clupeids is 18:1ω9 in sprat and 18:1ω7 in herring (Keinänen et al. 2017), aligning with both stomach contents and FA profiles of reef shark species. As 18:1ω9 and 18:1ω7 were two of the most distinguishing FAs between sharks and teleost fish in our study, it is possible that these FAs could be a dietary indicator for clupeids as well as some reef fish and cephalopods; which have all been found in previous stomach content analysis of reef sharks (Cortes 1999, Frisch et al. 2016). Given that these linkages are important to identify in ecological interpretation, focus on basal sources will benefit future study.

While research on FA composition on coral reefs in Australia is minimal, results for FA profiles here were similar to a study on the Southern GBR (~23°S) where high proportions of PUFA in coral trout (mainly DHA) were reported (Belling et al. 1997). Only one other study has reported FA profiles of reef sharks (liver samples) in northern Australia (Nichols et al. 2001) where whaler sharks off Townsville reefs showed similarly high proportions of 18:1ω9 and 16:0 as observed in the current study. A study on coral reefs in the Northwestern Hawaiian Islands (NWHI) found that five FAs accounted for ~60% of total FA found in reef fish (Piché et al. 2010). Four of these FAs (16:0, 18:1ω9, ARA, and DHA) were the strongest indicators for distinction between species in our study. The authors found 18:1ω9 (marker for production) to be highest in conspicuous fishes such as armourhead (~26%) and squirrelfish, unicornfish, squid, some eels, and shrimp compared to other species. 16:0 was highest in herbivores (~30%) while planktivores and cephalopods were high in DHA (~26%) and EPA (~10%). Crustaceans and cephalopods also contained the highest proportion of ARA (~11%). This information from the NWHI is useful as their results align with stomach content studies (Wetherbee et al. 1997; Cortes 1999) that have revealed potential prey items for our study species. In the GBR and NWHI reef sharks have consistently been found with a high proportion of largely unidentifiable teleost (including remains of cardinalfish, surgeonfish, and parrotfish) with cephalopods, clupeids, eels, and crustaceans also identified (Wetherbee et al. 1997; Cortes 1999, McCauley et al. 2012b; Frisch et al. 2016). These results specifically for sharks can help to refine our interpretation of distinction from teleost predators. For example, the main dietary components of stomach contents of coral trout sampled in Townsville reefs (same to our study) are pomacentrids and clupeids (Matley et al. 2018). Though we found limited functional redundancy between reef sharks and teleosts in our study, the varying degree of overlap could be due to species in families such as Caesionidae of which are known to be a common prey type between reef sharks and coral trout.

In addition to dietary differences, results of this study also indicate potential functional differences between mesopredators. Reef sharks are more mobile than red throat and coral trout based on previous habitat and movement studies indicating that they have access to a broader range of prey types (Currey et al. 2015; Espinoza et al. 2015; Matley et al. 2016). Therefore, sharks likely occupy different habitats in addition to dietary distinctions. This is corroborated by a recent study from Meyer et al (2019) showing that 16:0, 18:0 and DHA indicate different habitat types which are the main components of distinction between sharks and teleost fish in this study. A conceptual representation of the reef food web, including habitat and dietary differences between the study species, based on this and existing research are displayed in Figure 4.6.

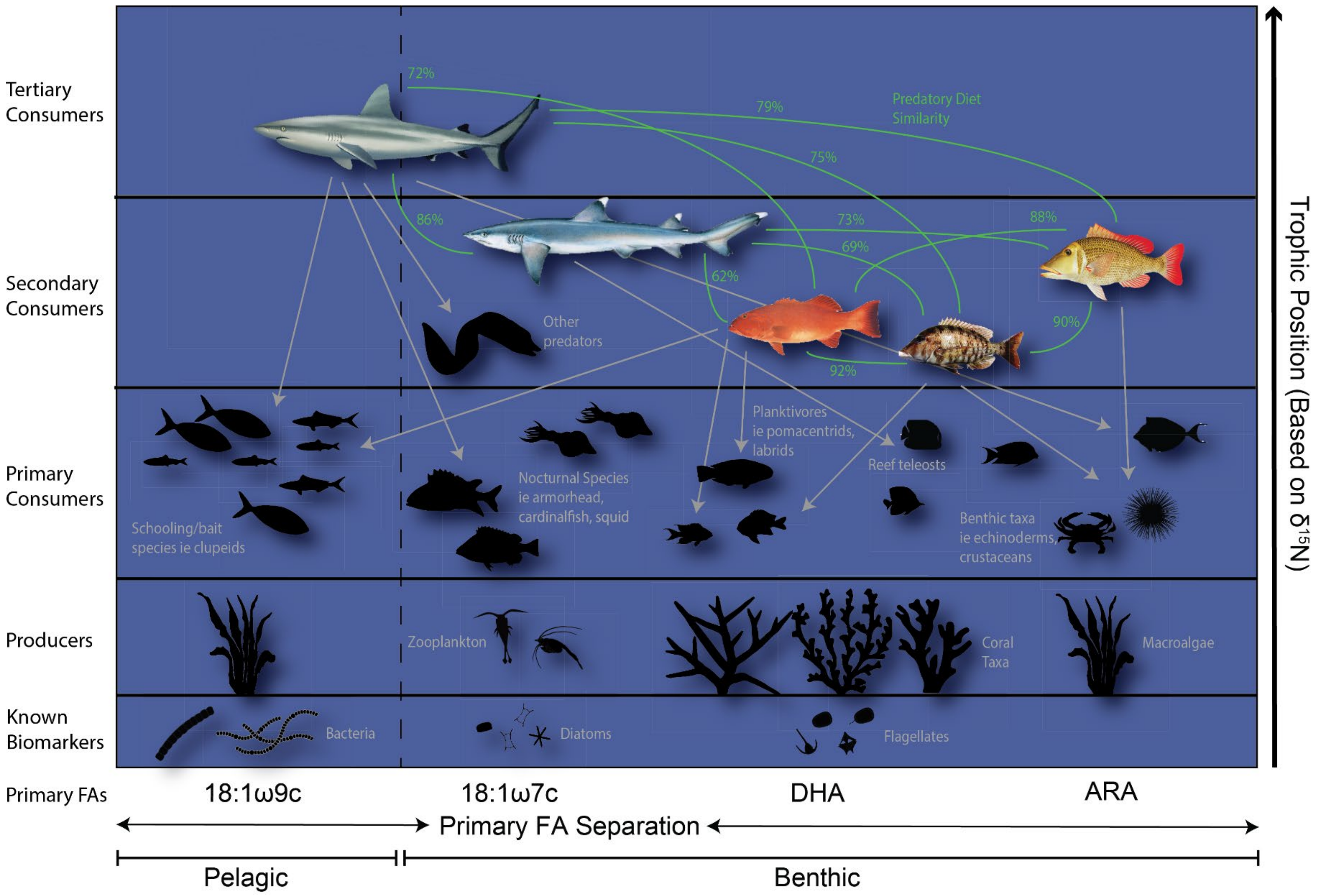


Figure 4.6: Conceptual food web diagram of the study species combining the results of this study with current research drawn from both biochemical and dietary studies in the GBR region (Frisch et al. 2016; Matley et al. 2018, Espinoza et al. 2019) as well as broader understanding of basal sources and trophic levels from FA (Pethybridge et al. 2018, Meyer et al. 2019) and stable isotope study (Layman et al. 2012; Munroe et al. 2018). Grey lines indicate diet, green lines indicate niche similarity between study species, silhouettes indicate potential dietary pathways

In addition to exploring the trophic ecology of reef mesopredators, this study also examined the utility of using different analytical methods and tissues for future work. We determined that full FA profiles of muscle tissue (but not blood plasma) are directly comparable between traditional full extraction and direct transmethylation methods, although certain FAs (including 16:0 and DHA) are statistically variable. This result differed from Parrish et al. (2015) who showed that direct transmethylation was a viable method to assess specific individual FAs in muscle tissue in addition to FA profiles of two pelagic marine species (albacore tuna and white sharks). Differences in lipid class composition between tropical and pelagic species (not determined in this study) may be a driving factor for these inter-study differences given that the same laboratories and procedures were used. These results indicate that species level responses to the direct method compared to the traditional method should be performed, particularly for blood plasma. Though there was statistical variation with some individual FAs, analysing samples only from the traditional method showed the same FA separation by species as the direct method. Hence, there are no differences in the overall ecological implications of species distinction seen between analytical methods for muscle tissue extraction

The statistical distinctions between FA profiles of muscle and blood plasma for most species in this study further demonstrate the need for more research into use of blood plasma in FA trophic studies. However, similarity in plasma profiles to muscle between red throat emperor and coral trout compared to the distinct plasma profile relative to muscle of grey reef sharks is an interesting observation. Matley et al. (2016a) examined differences in blood plasma to muscle tissue in stable isotope ratios of coral trout and found that differences in nitrogen tissue turnover rates were mainly due to metabolism. Additionally, blood plasma discrimination factors were indicators of recent diet versus long-term assimilation in muscle.

The difference between muscle and plasma of grey reef sharks could be due to different functional roles the tissues play with plasma thought to transport newly obtained FA throughout the body. Hence, plasma profiles may be more closely related to FAs from recent feeding compared to long-term assimilation in muscle tissue. Furthermore, the opportunistic nature of grey reef shark feeding and access to a broader range of diet over teleosts could also be a reason plasma is distinct from muscle. For example, if grey reef sharks successfully forage an area not often visited, the recent diet may differ from that assimilated. Alternatively, considering these results in relation to our study, the differences between FA muscle and blood plasma of grey reef sharks could also mean that reef sharks are metabolising PUFA at a greater rate than teleosts. This result is similar to findings from Meyer et al. (2019) who showed that physiological distinctions among species should be accounted for in diet studies when comparing across species. Future studies with experimental validation should incorporate blood plasma of multiple species of sharks and teleosts to determine whether this was an isolated occurrence based on a small sample size of grey reef shark plasma or commonly seen across elasmobranchs.

4.4.1 Conclusions

A broader suite of literature is available for FA trophic biomarkers in coastal and pelagic habitats than for tropical coral reefs making our research an important contribution to understanding reef-specific FA composition. This study greatly expands our limited knowledge of the functional role of coral reef mesopredators and can be used as a baseline for future work on the GBR and other tropical reef systems. FA analysis is being increasingly applied in ecological studies, and while more validation of methods is needed, our study shows that FA profiles can be used to identify distinctions at the mesopredator level on coral reefs. These results can offer a finer degree of dietary detail than other biochemical tracers, although ideally FA profiles would be used in combination with other methods such as stable isotopes or molecular metabarcoding, to further improve our understanding of the ecology of mesopredators. Ecologically, there was a degree of overlap among species compared in this study, but the distinct clustering observed indicates varied habitat and dietary use within reef systems. This needs to be considered when describing the trophic organization of food webs and more research should be done to fully define the roles of mesopredators in coral reef systems before inferring ecological importance of species and implications for ecosystem stability.

Chapter 5: Activity space and residency of a coral reef mesopredator reveal influence of prey density on reef-scale distribution

5.1 Introduction

A fundamental aspect of ecology is understanding physical and biological factors that influence movement of organisms (Baker 1978; Nathan et al. 2008). These factors are key in understanding habitat selection and can be used to improve the expectations and outcomes of how changes in such factors may impact spatial distribution of a species (Robinson et al. 2011). Activity space is the spatial extent of an animal's movement in a given time period and is a measurable feature that can be used to infer movement behaviour of a species. Ecological factors such as competition, prey availability, and predation risk can influence habitat selection (McCauley et al. 2012b). Therefore, small activity space must satisfy needs of the individual including resource availability, predator avoidance, and reproductive behaviour. Inevitably, if some individuals are using small areas, there is an expectation that specific factors influence site-selection and fidelity to that area. Reef-associated sharks on the Great Barrier Reef (GBR) have been well-studied in certain locations, showing variation in movement capacity and behaviour based on underlying environmental and biological factors. Common areas of occurrence and residency variation have been explained for grey reef sharks (*Carcharhinus amblyrhynchos*) through influence of some extrinsic (e.g. hard coral cover, degree of isolation) (Heupel et al. 2010; Espinoza et al. 2014) or intrinsic factors (e.g. sex, life stage) (Espinoza et al. 2015a), affecting abundance and movement behaviour of this species. However, understanding movement behaviour and activity space in the context of resource availability is rarely applied to such approaches (Speed et al. 2012). This information can be useful to expand predictive capability of defining movement and hence spatial ecology, as well as designing appropriate conservation approaches.

For example, grey reef sharks occurring on the GBR have generally been shown to remain highly resident to specific reefs across the continental shelf throughout the year (central and Southern GBR)

(Heupel and Simpfendorfer 2014b; Espinoza et al. 2015a). However, grey reef sharks are also genetically well-mixed on the GBR (Momigliano et al. 2015), meaning that some degree of movement outside of resident reefs occurs for reproductive purposes. A single incidence of a grey reef shark moving over large-scale distance has been recorded in the GBR (~134km, Coral Sea - Northern GBR) (Heupel et al. 2010). This example shows the capability of the species to move relatively large distances even though populations mostly remain resident to small-scale features. However, many parameters have not been tested, particularly at the reef-scale. While environmental factors can help explain larger-scale patterns, ecological level factors such as prey distribution and habitat are likely to explain more of the variation in home ranges than other factors.

Productive habitats with high availability of prey resources are likely attractive to marine predators (Sih 2005; Dupuch et al. 2009), however, these predator-prey dynamics have rarely been tested empirically outside of ecological theory predictions (Sih 2005). Theory such as the ideal free distribution (IFD) dictates that predator distribution is proportional to prey availability (Fretwell and Lucas 1969). However, this concept is difficult to test as there are additional factors to this theory that can influence distribution. For instance, indirect predator avoidance effects and capture probabilities due to habitat structure can affect spatial distribution of prey resources. IFD also relies on the concept that predators have perfect knowledge of the best resources in their environment (Hakoyama 2003). In order to formally test this theory directly, distribution and direct observation of predator-prey interactions *in situ* across a time series would be needed. As coral reef environments contain a complex array of habitat features with high species diversity (Bellwood and Wainwright 2002; Hughes et al. 2002), this type of ecosystem would be difficult to directly test IFD hypotheses but is ideal to apply basic concepts of foraging theory in terms of distribution of predators and prey. For example, IFD also states that optimal habitat or high resource areas are distributed in patches where predators compete. As patches deplete or become overrun with competition, predators are expected to utilize the next best resource. To test these concepts, it is important to first see whether the predator can freely move between resources as well as gain an idea of what resources are available within a home range. Understanding these features would assist in examining whether prey availability is a primary influencing factor in the distribution of predators and provide insight as to whether predators commonly occur in areas that have a high density of resources.

Complex habitats such as coral reefs support a higher abundance of reef fish species; meaning that foraging and competition of reef sharks should be considered as factors influencing distribution. Yet, correlative study between predator and prey abundance are often mentioned as possible drivers in the literature, but rarely tested (Torres et al. 2006). Even though these biological parameters are difficult to test *in situ* for mobile species, strong correlations have been found between seabird predators and prey distribution at fine scales in marine environments (Parrish et al. 1998; Heithaus 2005). Some studies have aimed to explore whether prey abundance influences shark distribution. Prey abundance was found to have little effect on shaping inshore shark distribution within a known nursery (Heupel and Hueter 2002), or at small spatial scales for inshore mature sharks (Torres et al. 2006) in bay areas of Florida, USA. However, Torres et al. (2006) noted that there were likely regional effects of teleost abundance on shark distribution. The strongest predictor of grey reef shark distribution on the GBR to date has been found to be complex habitat from hard coral cover (Espinoza et al. 2014), which is also known to provide shelter and food for many reef-dwelling fishes (Friedlander and Parrish 1998; Wilson et al. 2008). Thus, studies that examine the relationship between the distribution of key groups of teleosts that are prey for reef sharks could improve predictions of reef shark distribution and movement.

To understand predator distribution in relation to prey, detail is also needed on predator diet. Reef-associated sharks are often found with a large percentage of unidentifiable teleost fish in their diet in addition to molluscs and cephalopods (Wetherbee et al. 1997; Cortes 1999; Frisch et al. 2016). However, stable isotope studies have revealed conflicting importance in the level of dietary partitioning found between reef sharks (grey reef shark, whitetip reef shark, and blacktip reef shark) and other large bodied teleost predators such as red throat emperor (*Lethrinus miniatus*) and coral trout (*Plectropomus leopardus*) (Frisch et al. 2016; Roff et al. 2016; Espinoza et al. 2019). Grey reef sharks are often classified as generalist and opportunistic feeders, but little is known about how prey seeking behaviour affects their movement patterns. Therefore, it is necessary to understand how their distribution compares to potential prey abundance to better understand how sharks use their environment.

On the GBR, indirect predatory effects from grey reef sharks have been previously shown to affect herbivore foraging behaviour (Rizzari et al. 2014), but the literature does not address whether overall predator density is affected by prey distribution. Hence, one of the difficult issues with predator-prey comparison is the ability to determine prey resource availability and distribution in time and space. Here we examined the spatial ecology of grey reef sharks using passive acoustic telemetry at the reef-scale level on the central Great Barrier Reef and compared their activity space and distribution to prey density from surveys conducted during the same time period to show: (1) relationship of predator distribution to prey distribution, (2) whether grey reef sharks display common areas of use, and (3) whether any patterns in distribution are reproducible across multiple reefs in similar areas. We hypothesize that grey reef shark movements are influenced by prey resources and hence specific sites with higher prey abundance around the reef are subject to common use by the population.

5.2 Methods

5.2.1 Study Design

Acoustic Telemetry

An array of 33 VR2W acoustic receivers (Vemco, Bedford, Nova Scotia, Canada) were used to observe grey reef shark movements (n=46) across four semi-isolated coral reefs from January 2012 to February 2017. Based on the assumption that maximum detection range of each acoustic receiver in this area is 250 m (Espinoza unpubl. data), the total possible detection area covered for the four reefs was ~6,480 km^2 These reefs (Figure 5.1) are of similar latitudinal position (~18°S), located on the mid- and outer-shelf regions of the Townsville (TSV) Coastline (Queensland, Australia). These reefs are also subject to different fishing management through zoning by the Great Barrier Reef Marine Park Authority (GBRMPA). Two reefs (Rib and Chicken) are open to fishing, and two are closed to fishing (Helix and Knife). Receivers were deployed at depths between 12 and 20 m, anchored directly to hard substrate with a chain and suspended in the water column using a mooring rope (1-1.5 m) connected to a buoy. Receivers were placed around the perimeter of each reef, positioned away from substrate that could potentially limit detection range. Receivers were downloaded every 6 months and mooring materials were replaced if needed.

Sharks were captured using drop lines and rod and reel fishing. Drop lines consisted of 20-40 m polypropylene float lines attached to a 5-15 m sinking lead line (based on fishing depth) connected to a surface buoy. Tackle consisted of single gangions per drop line with 16/0 or 14/0 Mustad tuna circle hooks. Gangions were constructed with nylon cord, one metre wire leader, and stainless-steel snap longline clips that connect to spliced eyes from the sinking line. Hooks were baited with thawed fish (e.g. squid, pilchard, butterfly bream). Individuals targeted with rod and reel were captured using monofilament line attached to leader line or wire trace. Hooks used were 7/0 and 8/0 octopus or circle hooks baited with smaller offcuts from drop line fishing. Upon capture, individuals were immediately placed in tonic immobility, measured (pre-caudal length; PCL, fork length; FL, and stretch total length; STL), sexed, internally implanted with a coded Vemco V16P-4H (69 kHz) acoustic transmitter equipped with depth-sensing, and externally tagged with a unique rototag in the dorsal fin. Individual condition was noted as well as sexual maturity of males (calcified claspers). Acoustic transmitters were surgically placed into the peritoneal cavity through a small incision (2 cm) along the ventral midline and closed with dissolvable surgical sutures. Animal capture and surgical methods were performed by trained individuals under the James Cook University Animal Ethics permit (A1933). Total processing time of each individual in tonic immobility was a maximum of 10 minutes. Transmitters were programmed to stop after 835 days to eliminate the possibilities of error close to the end of battery life.

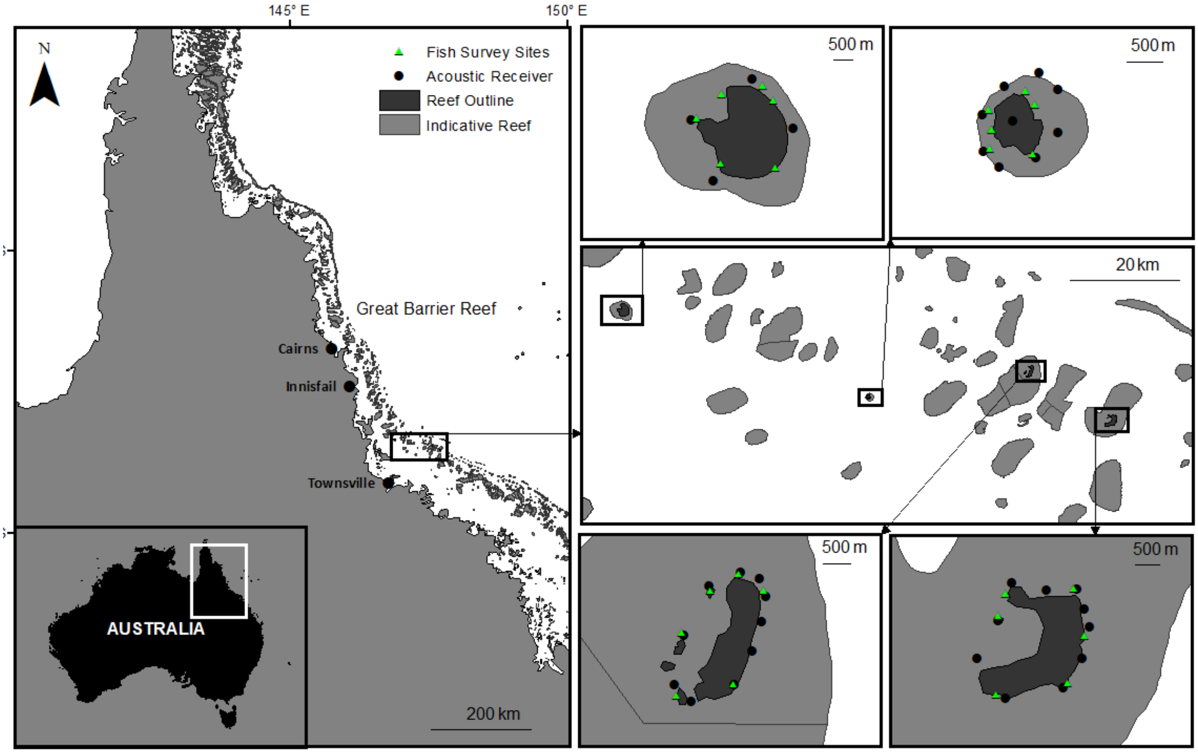


Figure 5.1: (a) Map of Queensland, Australia showing the location of fish survey locations and acoustic receiver array in (b) Townsville mid- and outer-shelf reefs (c) Rib Reef, (d) Helix Reef, (e) Chicken Reef, (f) Knife Reef

Underwater Surveys

Fish surveys were conducted through simultaneous underwater surveys of belt transects by a pair of divers over two seasons. One diver conducted a visual census of fish (UVC) and the other performed a diver-operated stereo video (DOV) survey. The camera system of the DOV consists of two GoPro® Hero 4 Silver cameras mounted inside waterproof underwater housings at fixed angles to an aluminium bar with handles (manufacturer SeaGIS), allowing accurate measurements of fish lengths that were used to estimate biomass. The diver conducting UVC applied the fish counting Standard Operating Procedures of the Australian Institute of Marine Science Long Term Monitoring Program (AIMS LTMP). The AIMS LTMP counts 216 species of diurnal fish that associate with the benthos (Halford and Thompson 1994; Bierwagen et al. 2018). The DOV video acts as a video record of the fish counted for future reference for a UVC counter. Additionally, given SOP limitations on actively counting of schooling and other fishes that aggregate in the water column, DOV surveys for this study were used to include these types of water column fishes as they are not normally included in the standard UVC.

UVC and DOV surveys were conducted at six sites around each of four focal reefs (Rib, Helix, Knife, Chicken Reefs; Figure 5.1). At each site, three (50 m) belt transects were deployed, totalling 18 surveys per reef. Of the six sites per reef, two were at AIMS LTMP locations for the purposes of comparison and standardisation of fish counts. For each survey, the fish counter laid the belt transect while counting large fish 2.5 m either side of the transect. The second diver swam beside and to the left of the UVC diver angling the DOV horizontally across the transect. On return, the UVC diver counted small fish 0.5 m either side of the transect and the second diver followed angling the DOV downward to record the benthos. Two separate survey periods were conducted at the same sites in January and July 2016.

5.2.2 Video Processing

Before each sampling period, the DOV system was calibrated using a calibration cube, measurement bar, camera parameters, and CAL software package (SeaGIS) that calibrates DOV measurement lengths to high accuracy (SE ± 5mm). Calibrated files were then loaded into Event Measure (stereo) (hereafter EM) software (SeaGIS) allowing the user to count abundance and complete length measurements. A user-defined species code file allowed for appropriate logs and identification of individuals on the transect. To stay consistent with UVC standards, identification and measurement limits were defined to 2.5 m either side of the transect within the software. Videos were synchronised in EM and fish were identified to the highest taxonomic level possible. While the UVC fish counter limited surveys to the LTMP SOP, the DOV video reviewer counted and measured every individual within the 5 m transect area. Individuals swimming into the frame behind the cameras were not counted to reduce double counting. For schooling species, up to 40 individuals were measured in single or multiple frames that contained the entire school, and each individual in the frame were identified and marked for appropriate counts.

5.2.3 Statistical analysis

Residency Patterns and Shark Movement

Residency and roaming indices were calculated for all individuals at each reef. A shark was considered present in an area if greater than five detections were recorded in a single day. Residency index was calculated by dividing the number of days detected by the total monitoring days of each individual. Roaming index was calculated by dividing the number of receivers an individual was detected on by the total number of receivers in the array (Espinoza et al. 2015a). Residency index was calculated for two levels at the reef-scale (reef residency); by individual and averaged by sex for each reef. Per Espinoza *et al.,* (2015), residency and roaming indices (± SD, standard deviation) range from 0 to 1, where high residency and high roaming is indicated by values closest to 1. Maximum number of days detected were also calculated by determining the highest number of consecutive days recorded for each individual and average by sex per reef for the monitoring period (± SD). Analysis of variance (ANOVA) in R software version 3.5.2 (R Core Team 2018) was used to determine differences in residency by sex per reef.

A previous study conducted by Espinoza *et al*. (2015) overlapped with the acoustic array and time period used for this study, so certain temporal environmental factors such as water temperature, wind speed and tidal height were removed from final models as no significant effects were found in the previous study. This allowed us to limit explanatory variables, reducing the degree of uncertainty in our model structure. Generalised linear mixed effect models (GLMER) using "*lme4*" (Bates et al. 2013) were used to determine influencing factors in weekly and monthly reef residency of grey reef sharks. Capture depth and biological factors (sex, size) were tested against weekly and monthly residency patterns of individuals tracked over a six-year period (2012-2017). Current strength was also considered but removed as preliminary analysis showed no direct association with movement. Days monitored were determined by the maximum life of the transmitter (835 days) or number of days possible if the array was removed before the life of the transmitter ended. Models were fitted with a binomial distribution due to the proportional nature of indices in this study. In order to account for variation in sample size among reefs and years, a random term of (Year | Reef / Tag ID) was included in each model. Models were tested against a null model including the same random term.

Activity space was determined using centres of activity (COA) defined by the mean position of latitude and longitude binned into hourly detections per receiver (Heupel and Simpfendorfer 2014a; Espinoza et al. 2015a; Udyawer et al. 2018). Reef-level, Brownian Bridge 2-dimensional kernel utilization distributions (KUD, 50 and 95%) and inter-reef trajectories were calculated from Universal Transverse Mercator projection (UTM) converted COAs (m) using "*adehabitatHR*" and "*adehabitatLT*" packages in R (Calenge 2006). Data filtering and date/time conversions were completed with "*TidyR*" (Wickham 2017) and "*lubridate*" (Grolemund and Wickham 2011) packages. Mapping was performed with both "*ggmap*" using Google® satellite imagery (Kahle et al. 2019) with "*ggplot2*" (Wickham 2016) for graphical KUD output (Figures S5-a - S5-d) and ArcMap 10.6.1 (*ESRI*) for additional graphics. Percent KUD overlap of individuals per reef was also calculated in ArcMap 10.6.1.

Site specific use was examined using a Chi-Squared test of independence to test the null assumption that there is no difference in distribution of sharks by receiver location. Additionally, mean proportion of total shark detections per receiver at each reef were calculated. To further investigate influence of specific sites on space use, weekly residencies by receiver site per reef were modelled with binomial GLMER using the explanatory variables (capture depth, size, sex) and random term (Year | Reef / Tag ID) as with previous models to account for variability in sample size among reefs and years.

Fish abundance and biomass

Fish abundance was determined by collating data from the UVC and DOV surveys. The UVC surveys were used as the main dataset and the DOV supplemented this dataset by adding species (such as water column and schooling fishes) that were not counted on the AIMS LTMP UVC standard surveys to give a much larger basis for determining fish abundance and diversity at study locations. To determine differences in abundance between survey periods, a Chi-Squared test of independence was performed against the null assumption that there is no difference in fish abundance and community composition between survey times. A Chi-Squared test was also used to determine fish differences (by family) between 2016 data from the AIMS LTMP surveys and fish surveys from this study for that year for standardisation purposes. To determine the most influential species that contribute to dissimilarity among sites and reefs, constrained distance-based redundancy analysis (db-RDA) based on a Bray-Curtis dissimilarity was performed using the “vegan” package in R (Oksanen et al. 2016). Fish abundance was fourth root transformed to account for naturally abundant species. Fish communities were modelled against explanatory variables such as survey site, reef, zone, and sampling period using a permutational analysis of variance (PERMANOVA).

Fish biomass was calculated using only the DOV data from the length-weight relationship equation $W = aL^b$ (Froese and Binohlan 2000), where W=weight (g), L = length (cm), and ‘a’ and ‘b’ are coefficients of standardized regression equations taken from Kulbicki et al. (2005) representing the intercept and the slope respectively for each species surveyed. The UVC data was not used for biomass as lengths were not estimated. Length calculations were taken from average lengths measured per species from the EM software. Biomass was determined by the summed weights of each number of individuals (N) per species in each survey site (6 per reef) and averaged by fish family and converted to kg/1000 m^2.

To determine inter-reef variability, generalized linear models were used for overall abundance and biomass between sites and reefs. Fish family abundance and biomass were compared by reef and survey site. Tukey's post-hoc pairwise comparisons with survey site conditional on reef were performed using "*lsmeans*" in R (Lenth and Lenth 2018).

Predator distribution and prey availability

Due to location and limited surveys of prey availability, survey sites were treated as patches and paired to the closest receiver. By using similar metrics of receiver detections of sharks as a proxy to compare to fish abundance, relationships between prey density and predator distribution were calculated. These were fitted with a GLMER by maximum likelihood using a Poisson distribution to compare detection frequency with overall fish abundance, fish family, reef, and distance from tag location. Receiver location and tag ID were included as random terms conditional on the intercept to account for variation in number of receivers and individuals per reef. Overdispersion was calculated by dividing the residual sum of squares by the number of observations subtracted from fixed effects and random effects. Autocorrelation was tested for using the auto-correlation function '*acf*' in R. To determine the effect of significance of fish families on individual receiver sites per reef, a Poisson model of total receiver detections per shark were fitted with an interaction between each fish family and receiver serial number using reef and tag ID as random terms.

Table 5.1 Residency of *Carcharhinus amblyrhynchos* monitored in the central Great Barrier Reef

Tag	Sex	FL	Tagging Date	Tagging Reef	Days Monitored	Days Detected	Max *d* detected	Reefs Detected	Roaming Index	Residency Index
GR1	M	80	15/01/2012	Helix	835	670	441	1	0.89	0.80
GR2	M	69	15/01/2012	Helix	835	19	18	1	0.44	0.02
GR3	F	72.7	24/04/2012	Helix	835	829	742	1	0.89	0.99
GR4	M	84	24/04/2012	Helix	835	538	21	2	0.11	0.64
GR5	M	66.5	24/04/2012	Helix	835	696	382	1	0.89	0.83
GR6	F	139	12/02/2013	Helix	835	604	223	1	1.00	0.72
GR7	M	118	14/02/2013	Rib	835	590	69	1	0.75	0.71
GR8	M	107	15/02/2013	Rib	835	785	262	1	0.75	0.94
GR9	M	59	20/02/2013	Helix	835	162	161	1	0.56	0.19
GR10	M	51.9	20/02/2013	Helix						
GR11	F	62.8	21/02/2013	Helix	835	241	141	1	0.89	0.29
GR12	F	146	17/06/2015	Helix						
GR13	F	132	17/06/2015	Helix	595	224	138	1	0.89	0.38
GR14	F	59	18/06/2015	Helix	594	177	118	2	0.11	0.30
GR15	M	55.5	18/06/2015	Helix	594	215	93	1	0.78	0.36
GR16	F	135	19/06/2015	Knife						
GR17	F	88	19/06/2015	Knife	593	577	123	1	0.40	0.97
GR18	F	71.5	19/06/2015	Knife	593	182	132	1	0.80	0.31
GR19	F	67	19/06/2015	Knife						
GR20	F	61	19/06/2015	Knife	593	110	57	1	0.90	0.19
GR21	F	59	19/06/2015	Knife	593	286	16	1	0.90	0.48
GR22	F	0	19/06/2015	Knife	593	196	28	1	1.00	0.33
GR23	M	89	19/06/2015	Knife	593	82	4	1	0.20	0.14
GR24	M	65	19/06/2015	Knife	593	587	308	1	1.00	0.99
GR25	M	64	19/06/2015	Knife	593	148	52	1	0.90	0.25
GR26	F	135	20/06/2015	Chicken	592	521	92	1	0.80	0.88
GR27	F	134	20/06/2015	Chicken	592	548	115	1	0.70	0.93
GR28	F	123	20/06/2015	Chicken	592	279	91	2	0.20	0.47
GR29	F	122	20/06/2015	Chicken	592	527	135	1	0.90	0.89
GR30	F	122	20/06/2015	Chicken	592	437	109	2	0.60	0.74
GR31	F	60	20/06/2015	Chicken	592	66	21	2	0.20	0.11
GR32	F	10	20/06/2015	Chicken	592	205	34	1	0.90	0.35
GR33	M	102	20/06/2015	Chicken	592	424	67	1	1.00	0.72
GR34	M	58	20/06/2015	Chicken	592	285	155	2	0.40	0.48
GR35	M	113	21/06/2015	Rib	591	138	12	1	1.00	0.23
GR36		120	22/06/2015	Rib	590	475	69	1	1.00	0.81
GR37	M	135	17/05/2016	Chicken	260	261	260	1	0.90	1.00
GR38	F	123	18/05/2016	Chicken						
GR39	F	90	19/05/2016	Knife	258	157	13	1	0.40	0.61
GR40	F	82	19/05/2016	Knife	258	6	1	1	0.20	0.02
GR41	M	88	19/05/2016	Knife	258	61	5	1	0.50	0.24
GR42	M	73	19/05/2016	Knife	258	29	3	1	0.20	0.11
GR43	M	66.5	19/05/2016	Knife	258	206	25	1	0.30	0.80
GR44	F	61	20/05/2016	Knife	257	82	6	1	0.30	0.32
GR45	F	61.5	17/06/2015	Helix	595	307	241	1	1	0.52
GR46	M	66	24/04/2012	Helix						

Sex: M males, F females. FL: Fork Length. Max d: maximum number consecutive days detected in monitoring period.
Residency Index: the number of days a shark was detected divided by the number of days monitored in the reef tagging array
Roaming Index: the number of receivers detected per reef divided by the total number of reef receivers

5.3 Results

5.3.1 Shark Movement

A total of 46 grey reef sharks (26 female, 20 male) were implanted with acoustic transmitters. Size of individuals (FL) ranged from 52- to 146 cm, with no significant differences found between FL of males (80.5 ± 23.5 cm) and females (88.7 ± 40.4 cm; *t* test = 1.68, df = 40, $p > 0.05$). One shark was never detected (GR19) and five individuals were detected less than five days (GR10, G12, GR16, GR38, GR46). The remaining 40 individuals represented a variable residency index range from 0.02 to 1.00 within the tagging array (Table 5.1) with high mean residency to single reefs (0.48 ± 0.11 SE). Eighteen individuals were detected on greater than 50 percent of days monitored. Chicken and Rib reefs (open fishing, 0.62 ± 0.32 – 0.81) displayed higher mean residency of individuals than Knife and Helix (closed fishing, 0.4 ± 0.29 – 0.54 ± 0.31) (Table 5.2). Additionally, six individuals were recorded moving to other reefs in the study area, with three never returned to their tagging reef (Figure 5.2). Individuals that did not return were recorded at their original reef up to 20 days prior to moving away.

Some sharks were found to use the whole reef (Table 5.1) with mean roaming activity >0.5 for all reefs (Table 5.2), which is comparable to extent of activity space (95% KUD) range of all individuals (0.27 - 7.53 km^2). However, core activity space (50% KUD) of sharks stayed within a significantly smaller activity area (0.01 – 0.91 km^2; *t* test=1.67, df=74, $p<0.005$) (Figures S5-a to S5-d). There were no significant differences in core or extent of activity space between FL and sex of grey reef sharks. However, there were reef-related differences in core and extent of activity space. Grey reef sharks exhibited lower core activity at Chicken Reef compared to others (glm; SE=0.64, t=3.5, $p<0.005$). Additionally, Rib Reef had the highest extent of activity space over other reefs (glm; SE=0.53, t=2.66, $p<0.05$). Despite high roaming activity at each reef, grey reef sharks occupied separate core activity space (50% KUD) with minimal mean overlap (0.05 - 0.14 km^2) indicating partitioning at each reef by tagged individuals (Table 5.3, Figures S5-a to S5-d). The proportion of overlap to overall mean core activity space was between 24 - 60 % showing reef-level differences in shared activity space (Table 5.3). However, the mean overlap of extent (95% KUD) of activity space was significantly higher (0.45 - 1.93 km^2; t test=1.65, df=233, $p<0.005$) revealing areas of common use around each reef. Percent overlap of individuals in the mean extent of activity space across reefs ranged from 37 – 64 %. Overall, the lowest percent overlap of individual core and extent of activity space was at Knife Reef.

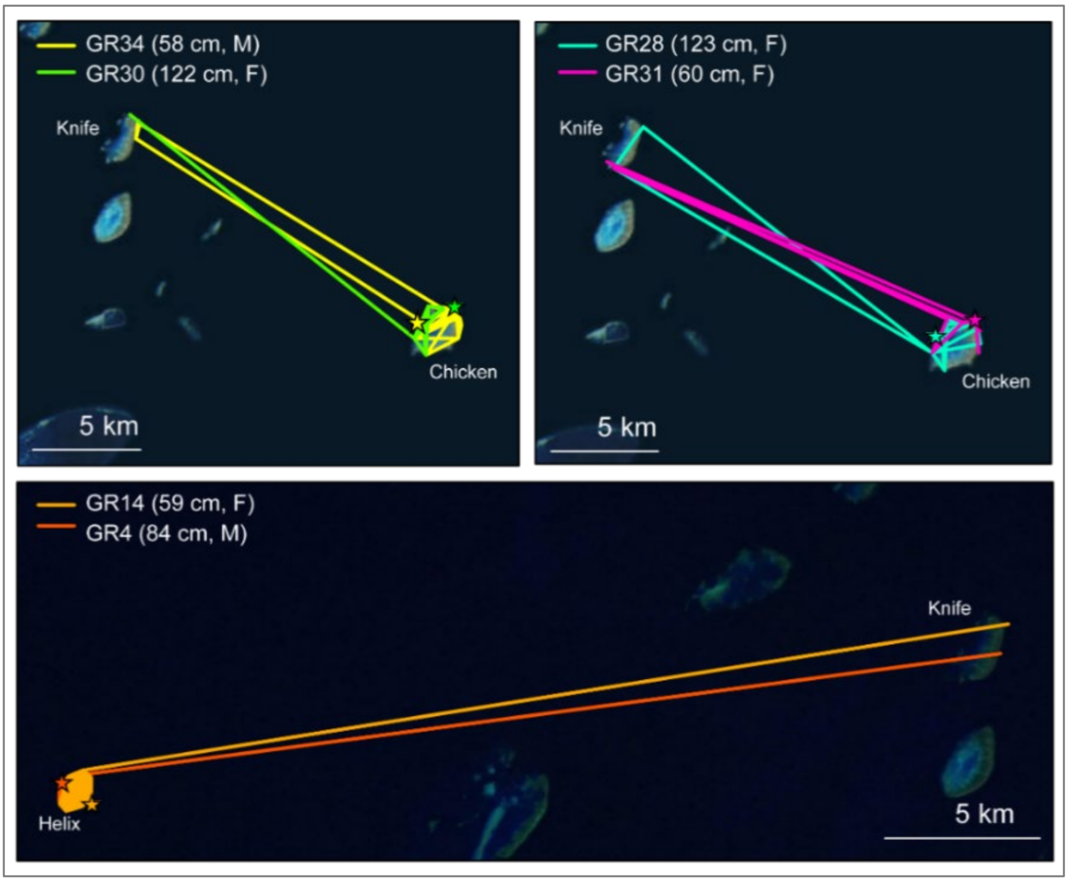


Figure 5.2: Movement trajectories from the 6 tagged individuals that visited more than one reef in the acoustic receiver monitoring array (Townsville Reefs, central GBR). Stars are tagging locations coloured by individual. *Individuals GR30, GR14, and GR4 did not return to their tagging reef once foraying to the other reef

Table 5.2: Reef-level activity by sex for residency and roaming

N (46)	Reef	Sex	FL (cm)	Days Detected	Max *d.* detected	Roaming	Residency
8	Chicken	F	100.86 ± 47.56	369 ± 187.77	85.29 ± 42.34	0.61 ± 0.3	0.62 ± 0.32
3		M	98.33 ± 38.63	323.33 ± 88	160.67 ± 96.62	0.77 ± 0.32	0.73 ± 0.26
7	Helix	F	93.1 ± 39.11	415 ± 287.45	272.4 ± 265.58	0.76 ± 0.36	0.54 ± 0.31
8		M	69 ± 11.26	383.33 ± 287.72	186 ± 183.39	0.61 ± 0.31	0.47 ± 0.33
10	Knife	F	64.06 ± 28.71	199.5 ± 173.77	47 ± 52.61	0.61 ± 0.32	0.4 ± 0.29
6		M	74.25 ± 11.48	185.5 ± 206.75	66.17 ± 119.98	0.52 ± 0.35	0.42 ± 0.38
1	Rib	F	120	475	69	1	0.81
3		M	112.67 ± 5.51	504.33 ± 331.9	114.33 ± 131.02	0.83 ± 0.14	0.63 ± 0.36

N: number of individuals. Sex: M males, F females. FL: Mean Fork Length. Max d: mean maximum number consecutive days detected in monitoring period.
Residency Index: the mean number of days a shark was detected divided by the number of days monitored in the tagging array
Roaming Index: the mean number of receivers detected per reef divided by the total number of reef receivers

Table 5.3: Mean percent Brownian Bridge KUD area and Overlap (±SD) for core and extent of activity space of grey reef shark individuals per reef

	KUD Area (km^2)		**KUD Overlap (km^2)**			**Proportion of Total KUD**	
Reef	**50% (Core)**	**95% (Extent)**	***N***	**50% (Core)**	**95% (Extent)**	**50% (Core)**	**95% (Extent)**
Chicken	0.09 ± 0.04	1.09 ± 0.58	34	0.05 ± 0.03	0.45 ± 0.29	0.60	0.41
Helix	0.17 ± 0.10	1.07 ± 0.32	66	0.06 ± 0.04	0.68 ± 0.24	0.37	0.64
Knife	0.24 ± 0.22	1.96 ± 1.72	28	0.06 ± 0.04	0.73 ± 0.52	0.24	0.37
Rib	0.33 ± 0.39	4.53 ± 2.66	6	0.14 ± 0.05	1.93 ± 1.36	0.41	0.43

There were no significant effects in overall weekly and monthly reef residency by size and sex of individual (month; p>0.05, AIC =417.4 week; p>0.05, AIC=1507, Supp Table 5.1). While the modelling approach to examine reef-level biological factors overall revealed 21 models higher than the null model for month and 8 models for week, the best performing model only included week and month as meaningful factors (Table S5-a). However, the second-best performing model for each included size (FL). Contrary to reef residency of sharks over the entire study period, significant effects of size and sex were found for weekly residency of individuals by receiver site (Table S5-b, Figures S5-e to S5-h), indicating potential fine-scale interactions linked to biological factors. For example, there were higher proportions of females than males during certain weeks of the year at specific receiver locations at each reef (Figures S5-e to S5-h). Additionally, all models performed better than the null model for weekly residency to specific sites.

In addition to reef-level patterns, site use at the receiver level was also compared. The mean proportion of detections of individuals per receiver site for each reef ranged from 0.0-0.69 (± 0.17 SD), where the proportion of detections was significantly different from the expected null uniform distribution surrounding each reef (χ^2=60 , p > 0.05, df = 54). There were significant differences in mean intra-reef proportion of detections of all individuals present between receiver sites, indicating that certain locations were subject to higher site use than others (Figure 5.3). However, residency and roaming indices (Figure 5.4) show that there was a large degree of variation in site use among individuals across all reefs. For example, there was a significantly larger mean proportion of total shark detections at the NW aspect of Rib Reef (>50%), but at Knife Reef the largest amount of mean total detections (>50%) occurred at the Western aspect (SE=0.01, z=3.32, p<0.005, Figure 5.3). These results in proportion of detections are consistent with KUD activity space (Figures S5-a to S5-d).

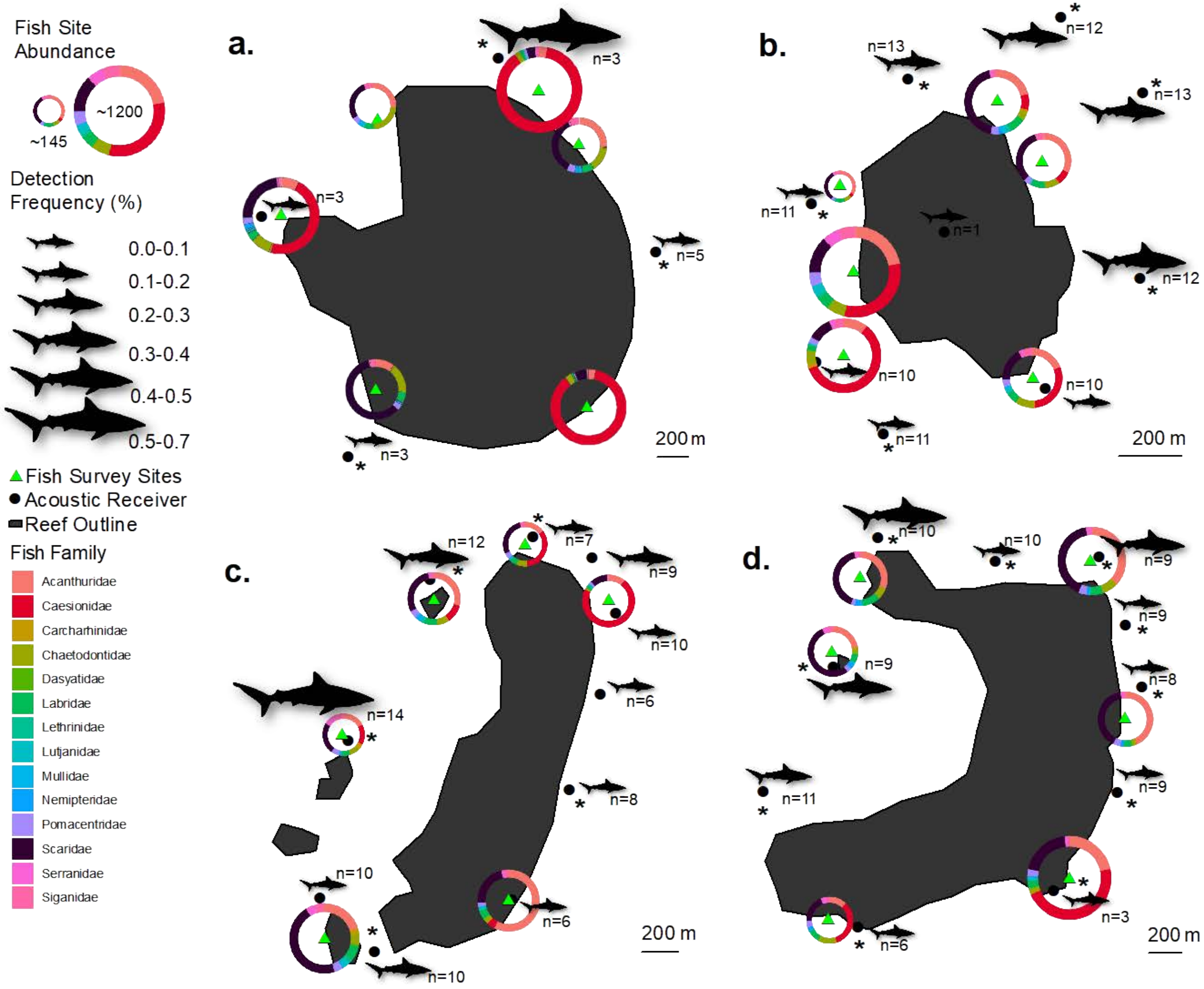


Figure 5.3: Fish abundance by survey site compared to shark receiver use (mean proportion of total detections) around reefs (a) Rib, (b) Helix, (c) Knife, (d) Chicken. Fish are scaled by fourth-root transformation. * indicates significant difference in receiver detection frequency of tagged individuals for each reef (Poisson GLMER: Receiver Detections ~ Family*Abundance + Tag Distance + Receiver + (1 | Tag ID / Reef). n=number of individuals detected per site. Ring plots surrounding survey sites indicate teleost family abundance where size of the ring is proportional to abundance. Size of shark is proportional to detection frequency

5.3.2 Fish Surveys

The most abundant fish species were consistent through time across the survey area (Figure 5.5) and no significant differences in community composition or species abundance were found between the two survey periods. Based on this finding, abundance and biomass were averaged over the two survey periods. Additionally, there was no difference in fish abundance between the AIMS LTMP survey data for 2016 and the surveys for this study (X^2=63, df=56, p>0.05) indicating fish abundance was consistent throughout a single year. Caesionids and pomacentrids were the main contributors to dissimilarity among sites and reefs with higher abundance on mid-shelf reefs compared to outer-shelf reefs (Figure 5.5). When comparing survey data between reefs, differences were apparent in community structure (df=3, F=2.46, p=0.05) and fish family biomass (df=58, F=2.91, p<0.05), showing reef-scale variability in assemblages. Biomass ranged from ~905-1775 kg/km^2 per reef. Families Acanthuridae, Caesionidae, and Scaridae accounted for the highest biomass of fishes at each reef (Figure S5-i). When comparing sites across reefs, there were differences in total biomass and fish families (df=5, F=2.5, p<0.005), meaning that distribution of prey was specific to each reef. Additionally, within each reef, significant differences were found between sites in both abundance and biomass by fish family meaning that intra-reef community composition and biomass was not uniformly distributed. For example, the location of highest fish abundance for reefs were located at sites 2 (NE aspect, Rib Reef), 6 (W aspect, Helix Reef), 4 (SE aspect, Chicken Reef), and 5 (SW aspect, Knife Reef) (Figure 5.3). Site-specific differences in biomass were different to sites of highest abundance (Figure 6, Tables S5-c & S5-d)

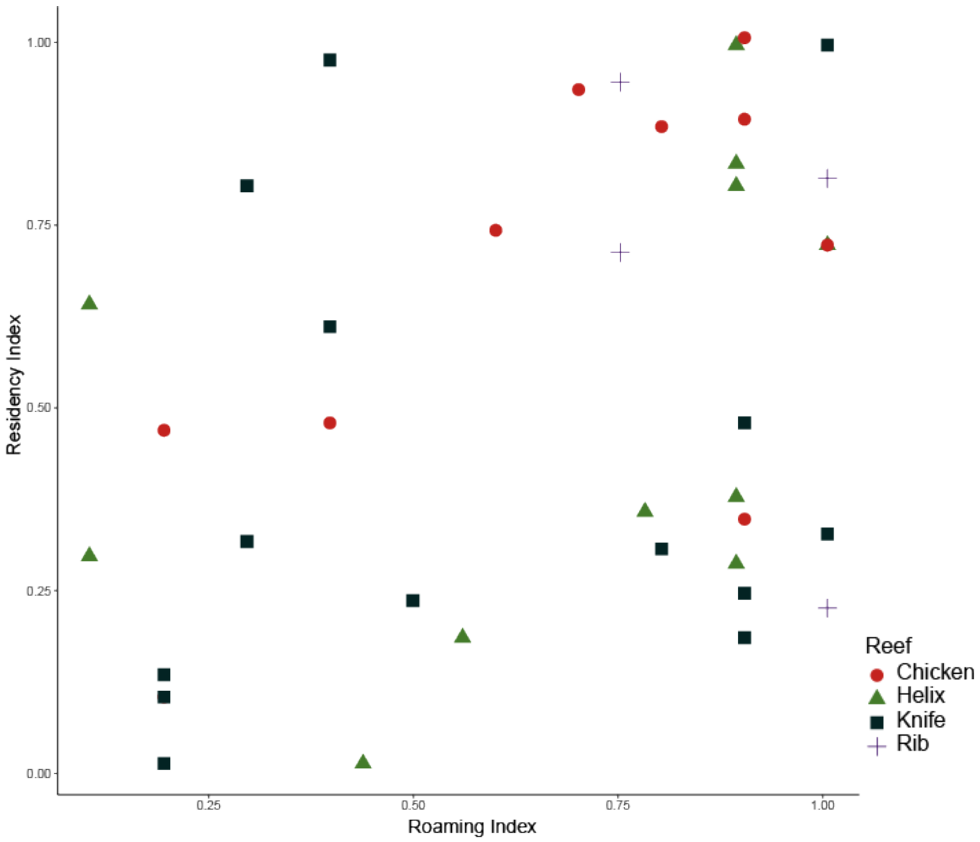


Figure 5.4: Residency-roaming indices for grey reef sharks per reef in TSV. Each symbol represents a value for an individual shark. Residency Index=number days detected/number of days monitored, Roaming Index=number of receivers detected/total number of receivers in reef array

5.3.3 Predator distribution and prey availability

Mixed effect models revealed significant interactions between fish family and receiver detections of grey reef sharks in the study area. The strongest positive relationship between shark presence and fish family was with caesionids (glmer; z=2.5, p<0.05). Additionally, there were weak positive interactions with high serranid abundance and shark presence (z=1.9, p=0.06). These relationships were neither autocorrelated nor over dispersed. Significant differences in abundance and biomass of these two families between sites were present for each reef in the study area. There were no significant differences found for overall fish abundance and grey reef shark presence (z=0.02, p=0.98) or other highly abundant fish families such as pomacentrids. Significant negative effects of distance from tagging location and number of detections (z value=-2.13, p=0.03) were also found which show that grey reef sharks captured are often within their core areas of activity (Supp Figs 1-4). This result implies that bait is most effective for sharks closest to the fishing area and suggests that sharks are spending time foraging in their core areas, linking shark presence to prey availability.

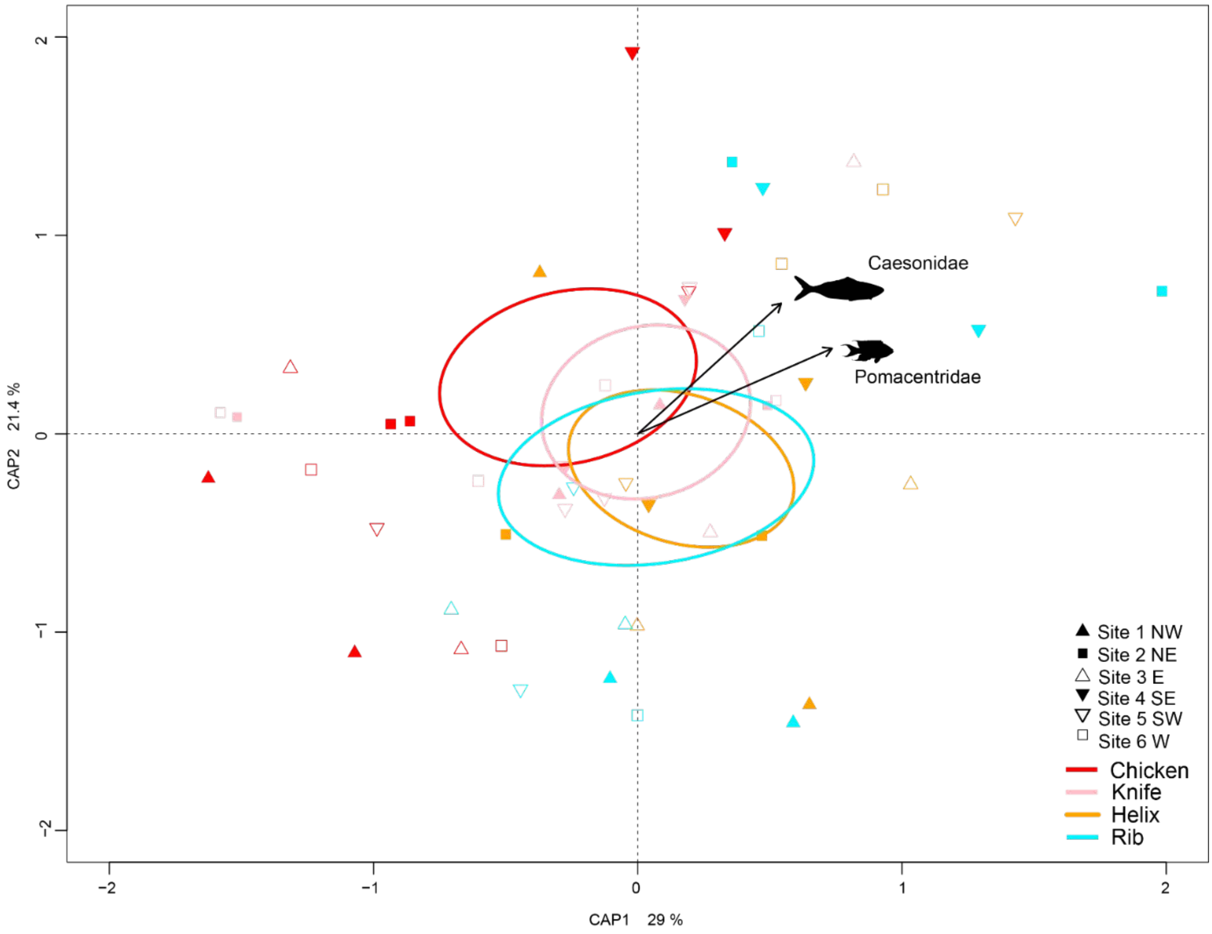


Figure 5.5: Constrained ordination (Capscale dbRDA) of fish survey sites showing abundance dissimilarities among reefs and the two largest fish families contributing to differences. PERMANOVA(capscale : Fish Community Matrix ~ Reef + Site+ Sample Period + Reef : Site)

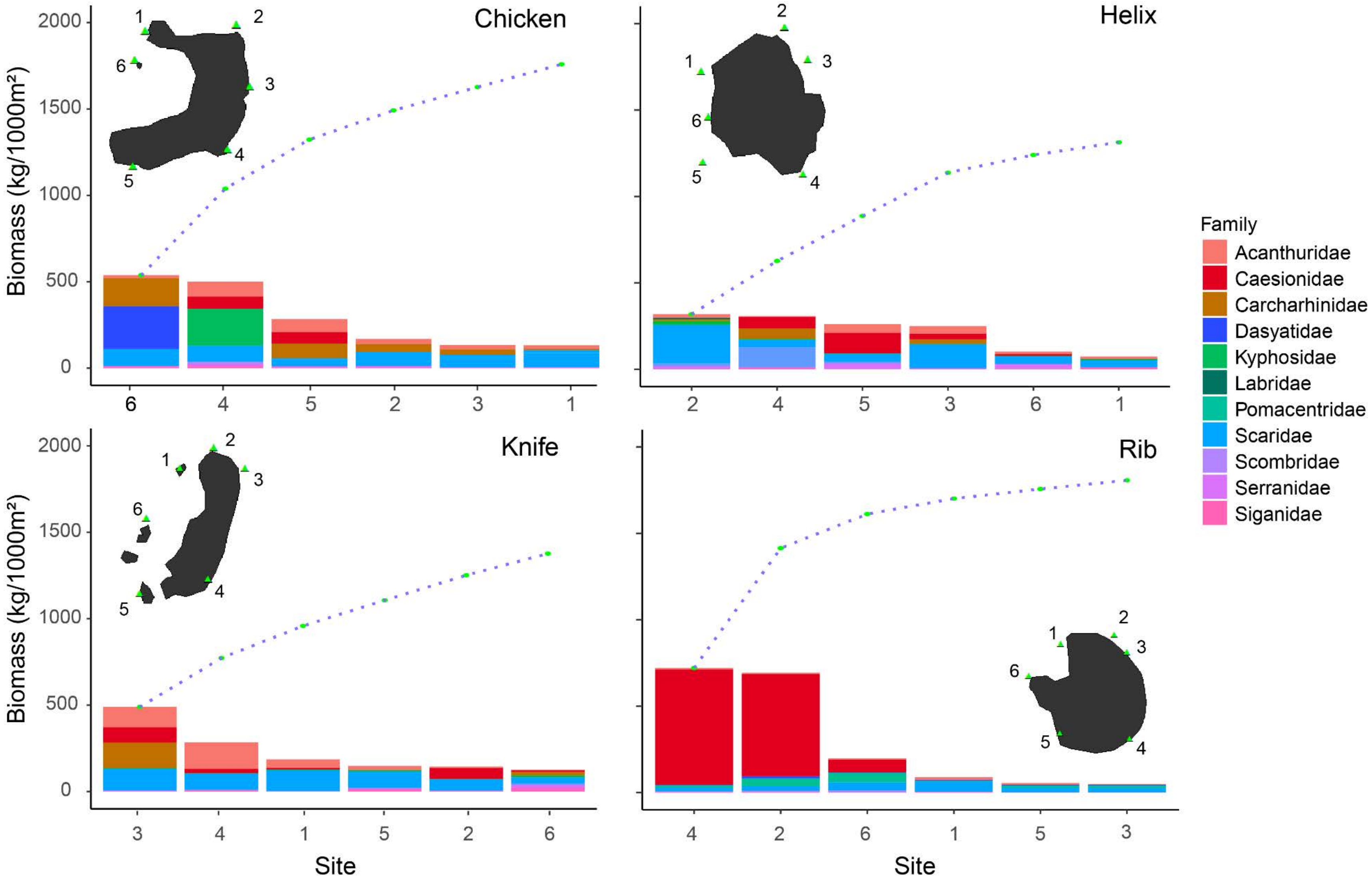


Figure 5.6: Fish biomass$^{\text{-Site/Reef}}$ (kg/1000 m^2) Pareto barplot by fish family with cumulative biomass curve

5.4 Discussion

Overall, this study examined predator and prey distribution to explore potential interactions and drivers of movement and habitat use by grey reef sharks at four similar reefs on the GBR. The variability in site distribution and abundance found in this study for both prey species and grey reef sharks indicate that neither predator nor prey are uniformly distributed, yet there are no obvious patterns in the variation among reefs. It should be noted that quantifying this variation is limited due to the small sample size (n=4 reefs). There was no evidence that distribution of predators and prey were influenced by environmental/oceanographic features that affect all reefs in the study area. Prey distribution data also suggested that areas of high productivity are not consistent between reefs. Hence, site-specific variation should be considered in future surveys, particularly when a general assumption exists that reefs in regional areas and of similar sizes are the same in the terms of ability to support prey and predator populations. While there were differences at each reef in individual shark movement and site-use, there were also areas grey reef sharks used more consistently than the rest of the reef. These areas were significantly related to some fish families such as schooling species (caesionids) and reef-dwellers (serranids). However, future study will be needed to confirm these relationships.

From this study we show that resident grey reef sharks can use the whole reef outlined by roaming activity, yet some individuals remain in smaller areas identifying potential costs of moving to other patches. Additionally, the level of intra-species partitioning found in this study supports that a population is well distributed around the reef in relation to general resource availability. This study also highlights some potential strategy as shark distribution was related to known abundant prey such as caesionids. This result differs from Heupel and Heuter (2002) who determined prey abundance was not an influential factor in juvenile blacktip reef shark (*Carcharhinus limbatus*) distribution. Future study should include more comparisons between predator and prey abundance as well as behavioural interactions between the two as there are not many that currently do so (Heithaus et al. 2009; Rizzari et al. 2014). More research into this area could confirm potential hunting strategy and knowledge of prey distribution which can support or differ from IFD. The concept behind spatial dynamics of populations that meet IFD is that individuals are capable of selecting the best habitat suitable to occupy until some level of carrying capacity of the population is achieved (MacCall 1990; Sullivan et al. 2006). Other individuals in the population will then subsequently choose lower quality habitats to occupy. While the data in this study did not directly test IFD, we can use basic concepts to explore the relationships between predators and prey as well as competition. This study revealed reef patches with varying abundance and biomass, indicative of habitat-rich and poor areas. Grey reef shark distribution reflected this in some part by the differences in proportion of the population at each patch.

Reef-level data revealed that sharks were highly resident to a single reef, with limited movement outside array areas. For example, mean residency from each reef showed that most sharks spent at least 50% of their time at a single reef. This finding is lower than the overlapping study by Espinoza et al (2015b) that found grey reef sharks spent approximately ~80% of their time within a tagging array. This is possibly due to differences in specific reefs included in the author's study and ours. Converse to Espinoza et al.'s findings, however, less inter-reef movements were documented during this study showing high attachment to individual reefs. It is possible that underlying environmental factors were influencing reef residency for our study, but no common inter-reef theme emerged. Future research should look into untested abiotic factors (Schlaff et al. 2014) as well as wave energy and currents to explore whether difference in these dynamics at the fine-scale level alter shark distribution and movement. Fish surveys taken during crepuscular or night hours at different depths would also benefit future research to complement patterns seen in passive telemetry studies (Vianna et al. 2013) compared to foraging and additional behavioural modes.

The finding of individual variability in distribution of reef shark populations is consistent with many other studies of coral reef predators (Speed et al. 2011; Espinoza et al. 2015a; Espinoza et al. 2015b; McCauley et al. 2016; Shipley et al. 2018), yet our study builds on these findings to also show individual variability in site-specific distribution at the reef-level that was not consistent across all reefs. Although reef sharks were found to be capable of using entire reefs, as seen by the extent of activity space and roaming, their core areas of use were small, and their location differed among reefs. For example, at Rib Reef the area with the highest proportion of shark use was the NE aspect of the reef. Yet, for Knife Reef it was the Western aspect. This suggests there are unexplained reef scale factors that should be investigated to explain the variability found in reef distribution. Additionally, mean size of activity space varied per reef. For instance, the mean extent of activity space ranged from 1.0 (Helix Reef) to 4.5 km^2 (Rib Reef). These differences did not directly correlate with reef size and as such suggest there are specific areas at each individual reef that are subject to higher areas of use by grey reef sharks which relate to higher prey abundance. This result shows that future directed study may provide evidence to show grey reef sharks are conforming to IFD.

The differences found between proportion of area used between sites within a reef was linked to both sex and size of individuals showing the benefit of investigating at fine-scales across multiple locations to better interpret movement of reef shark populations. While many studies indicate inter-reef and regional sex and size-based differences in spatial distribution (Klimley 1987; Sims 2005; Papastamatiou et al. 2010; Bansemer and Bennett 2011), small-scale presence and absence of these biological factors could potentially indicate sex-specific behaviours. Individual behaviour of reef sharks was also apparent based on degree of overlap in core areas of activity, showing partitioning of core home ranges. However, the overlap found in extent of activity space (95% KUD) could indicate areas where individuals commonly forage outside their core areas of activity. Future research could determine level of activity and foraging behaviour within and outside of core areas through the addition of tools such as accelerometers in telemetry study (e.g. Meese and Lowe 2020). Though there is limited research into spatial differences between shark species (Speed et al. 2011), inter-specific partitioning of reef sharks was identified in the Southern GBR (Heupel et al. 2018). Additionally, Heupel, Lédée *et al.* (2018) revealed grey reef sharks had larger space use and less clustering than other species such as blacktip reef sharks (*Carcharhinus melanopterus*). This finding, in conjunction with distinct separation in depth use indicated inter-species partitioning. The authors concluded that competition for prey was likely a factor in separation. The results of our study showed that individual grey reef sharks are using small ecological spaces to satisfy their biological needs which may reflect niche separation among individuals along the lines of that described between species by Heupel, Lédée *et al.* (2018). However, further direct testing of this hypothesis is required.

The reef-level variability of fish assemblages found in our study is consistent with the AIMS LTMP surveys from this area and shows reef-level differences in community structure. Community structure was consistent from reef to reef outside of highly abundant species (Bierwagen et al. 2018). This variation between reefs was largely driven by caesionids and pomacentrids showing that the most abundant schooling and reef-dwelling species can drive changes in community structure. Acanthurids, caesionids, and scarids were the largest contributors to biomass and also well-distributed around each reef. This showed that there is potential prey availability for predators surrounding the entire reef. Each of these families have been found to be in the diet of grey reef sharks (Frisch et al. 2016), so there is potential that their variability in surrounding reef environments may shape grey reef shark presence. Both abundance and biomass of fish families occurring in the study area were found to vary from site to site surrounding each reef, furthering the potential of prey to shape shark distribution. There has long been an assumption that areas of high productivity are found on the most exposed side of GBR patch reefs due to wave exposure maintaining diversity (Huston 1985; Hamner et al. 1988) and influencing structure providing complex habitat (Duce et al. 2014). Considering long-term research on the GBR by the AIMS LTMP uses only the NE flank in their surveys (believed to be the most productive), our findings contradict this assumption. However, intra-reef site variation was not consistent among reefs, meaning areas of productivity potentially change between reefs, revealing no evidence of regional patterns in distribution of prey. These findings also indicate that distribution and abundance of fish communities are reef-specific and should be considered in future surveys. Caesionids were found in high numbers at different directional aspects of reefs in our study area, thus including them in future surveys could help to indicate most productive areas around the reef perimeter. These fishes often occur in areas of high pelagic inflow (Hamner et al. 1988; Munday et al. 2007) and could potentially be used as an indicator species of areas outside windward locations that receive pelagic input.

The findings from our study support the hypothesis that predator movement is directly related to prey abundance and distribution. For example, a direct association between high numbers of caesioinids and shark presence was found. Additional weak effects were found for serranids suggesting their distribution is also important to shark occurrence and movements. These findings were interesting because there was no direct association with shark distribution and overall fish abundance or biomass, meaning that finer detail is necessary to tease out important relationships with potential prey. Additionally, as caesionids and serranids have been shown to be prey of grey reef sharks through stomach contents and direct observation, (Cortés 1999; Frisch et al. 2016; Mourier et al. 2016), the correlation in distribution revealed in our study provide a basis for directly testing IFD on the GBR. However, due to the high diversity of potential prey, these associations likely do not paint the entire picture of distribution and movement of sharks resident to these areas. Additionally, a potential caveat resulting from this portion of the study is that the most optimal model selected through AIC comparing total detections to fish abundance is a cruder metric than other models tested for predator-prey influence. This metric may be more vulnerable to effects of error resulting in false detections, but are still considered rare with the equipment used (Simpfendorfer et al. 2015). Total detections also limit interpretation of high use of one individual over another, but results compare to other metrics such as total proportion of detections in this sudy (Figure 5.3).

Presence of grey reef sharks upon capture within or near their core areas of activity could mean that food resources are sufficient within their activity space, where an increase or patches of higher prey density outside an individual's normal foraging area do not have a significant impact on movement. However, there is limited research in this area (Sims 2003; Heupel et al. 2019). Alternatively, even though the biomass of fishes is well-distributed surrounding the reefs in this study, the biomass reported in this study falls far below pristine biomass (~1000-1400 kg/ha) considered to be benchmarks for reef carrying capacity (MacNeil et al. 2015; McClanahan 2019). It is possible that smaller activity space in this area could be related to limiting energy expenditure based on food availability (McNab 1963). Though the residency of individuals is high for a semi-open system, it is also possible that sharks forage away from detection areas to search for food. The larger extent of activity space of individuals supports this possibility. Considering that recent bioenergetics models suggests that reef sharks need approximately ~1.5% body weight totalling approximately 110-180 kg fish per year per shark (Mourier et al. 2016), larger activity space would fit that model particularly when considering that total biomass reported for this study was less than 1000 kg per 1000 m^2 at each site in the study area. Another possibility is that competition could limit the amount of opportunistic foraging, which would be consistent with the observation of small amounts of overlap in core areas of activity. However, evidence showing a non-uniform distribution around each reef and larger overlap in extent of activity space makes this conclusion unlikely. Recent research has shown support that competition may influence movement based on species niche partitioning on a reef in the Southern GBR (Heupel et al. 2018). These findings show there are other potential behavioural reasons there are higher proportions of grey reef sharks around some areas of the reef. Other possibilities include influence of large predators such as great hammerheads (*Sphyrna mokkaran*) which are known to target grey reef sharks as prey (Mourier et al. 2013). Future studies would also benefit from use of hydrodynamic models (McInturf et al. 2019) and additional biologging tools such as accelerometers and animal-borne cameras (Carrier et al. 2018; Andrzejaczek et al. 2019) to better understand foraging mode, energy expenditure, and fine-scale movement of this species.

5.4.1 Conclusion

Here we examined the fine-scale spatial distribution of sharks and their potential prey surrounding four reefs on the central GBR. We found that shark distribution was related to abundance of specific prey species such as caesionids and serranids, suggesting they may conform to the IFD. We also determined that there were no consistent patterns in distribution of sharks and teleost fish among reefs revealing variation in dynamics of reefs with similar size and exposure. The small core home ranges of grey reef sharks showed small levels of overlap among individuals at each reef indicating partitioning within local populations. Future research should formally test concepts of IFD and prey-seeking behaviours. Even with the results of this study it would be difficult to dictate whether partitioned intra-reef core activity space mixed with broader common areas of use of reef sharks is related strictly to prey distribution, habitat suitability, or other unknown underlying factors without further investigation.

Chapter 6: Reef shark occurrence and population trends revealed from fishing and baited remote underwater video on the Great Barrier Reef

6.1 Introduction

Sharks play a vital role in ecological processes and provide socioeconomic benefit through tourism and food security (Dulvy et al. 2017). Despite this importance, many shark populations are in decline worldwide, and status of other shark populations remain unknown or data deficient (Heupel and Simpfendorfer 2010; Dulvy et al. 2014; Campana et al. 2016; IUCN 2019). Based on global concerns, surveys are being conducted to assess shark population vulnerability due to increased pressures from fishing, habitat degradation and climate change. Coral reefs are highly diverse and threatened with such pressures, creating a need to understand ecological roles and vulnerability of sharks in these ecosystems.

Globally, species such as grey reef sharks (*Carcharhinus amblyrhynchos*), whitetip reef sharks (*Triaenodon obesus*) and blacktip reef sharks are listed as Near Threatened by the International Union for Conservation of Nature and Natural Resources (IUCN) (Heupel 2009; Smale 2009b; Smale 2009a) and require more research to clarify their ongoing status given the age of these assessments and recent evidence of decline in some regions. For example, in some areas such as Indonesia, reef shark populations have been heavily depleted from fishing activity, where their rare occurrence suggests ecological extinction (Sembiring et al. 2015). Compared to developing coastal nations where reef sharks contribute to economic gain and food security (White 2007; Sembiring et al. 2015), Australian reef shark landings are often a result of bycatch (Gribble et al. 2005; Heupel et al. 2009), and therefore may not be as threatened as other countries that target them directly. However, there is little detail outside of fisheries logbooks that can inform long-term reef shark population trends in Australia, and some research shows evidence of depletion and rapid annual decline (Robbins et al. 2006; Rizzari et al. 2014a). In Australia many commercially targeted elasmobranchs are fished sustainably according to current management practice (Simpfendorfer and Dulvy 2017). However, compared to some pelagic and inshore sharks and rays, reef sharks are not a common fishery-targeted species group (Gribble et al. 2005; Heupel et al. 2009), and need local information about their status in relation to human activity. Additionally, other human-mediated pressures may increase their vulnerability in the future. For instance, temperature increase from climate change, or degradation of habitat and prey availability can impact distribution and movement and amplify negative effects from fishing (Chin et al. 2010). These findings have increased the need to understand vulnerability of reef shark populations to potential threats and assess population status.

The number of studies to estimate shark population status have increased over the years yet methods used to monitor populations are limited in capacity to determine population size and trend over time. For example, the most common methods are extractive through line, net, and trawl fishing (Simpfendorfer and Dulvy 2017). While these methods provide valuable indices for population status and trends of species, line fishing relies on bait attraction and proximity, and all methods can result in mortality post-release or involve lethal sampling (Dapp et al. 2016; Musyl and Gilman 2019). Additionally, fishery-dependent data sources such as logbook information depend on the expertise and credibility of the recorder (Wetherbee et al. 1997; Heupel et al. 2009). Traditional angling also ignores behavioural factors such as avoidance of capture (Mourier et al. 2017). Due to limitations associated with catch data from traditional fishing methods, underwater survey techniques such as underwater visual census (UVC) are commonly applied (Friedlander and DeMartini 2002; Sandin et al. 2008; Rizzari et al. 2014b). These methods can both over- and under-estimate population trends based on encounter rates at different locations and are affected by factors such as visibility (Willis et al. 2000; Ward-Paige et al. 2010). Other non-extractive methods are now applied using both baited and non-baited remote camera systems to count animals (Cappo et al. 2003; Cappo et al. 2006; Cappo et al. 2007; Langlois et al. 2018). These methods provide indices of relative abundance and distribution, but only recently have provided metrics for identifying individuals (Sherman et al. 2018) and hence the ability to generate absolute abundance. These authors showed that baited remote underwater video stations (BRUVS) can underestimate populations of elasmobranchs using the standard relative abundance 'MaxN' metric, which counts only the maximum number of individuals of each species in a single video frame. Due to the advantages and limitations of many survey methods, calls for future study indicate that multiple methods should be employed to provide a more comprehensive understanding of shark population status.

Recent evidence suggests that no-take marine reserves are successful in leading to recovery of reef shark populations in Western Australia (Speed et al. 2018) and provide successful conservation measures for sharks within the Great Barrier Reef Marine Park (GBRMP) where abundance was found to increase after re-zoning of specific areas to be no-take (Espinoza et al. 2014; Rizzari et al. 2014c). However, management effectiveness and population assessments within the GBR are still an area of debate where reported rates of decline are highly variable (Robbins et al. 2006; Heupel et al. 2009; Hisano et al. 2011; Rizzari et al. 2014a). The main debate regarding population estimates and decline from these studies stem in part from the type of survey method used. For example, Robbins et al. (2006) using underwater diver surveys suggested that grey reef and whitetip reef sharks were at risk from overfishing and in severe decline from previously unfished states. This notion was contradicted by findings from Heupel et al. (2009) who used fishery logbook data to show stable reef shark populations on the Great Barrier Reef (GBR) over a ~17-year period. Additional studies then compared these findings with multiple underwater survey techniques (Rizzari et al. 2014a) and demographic models (Hisano et al. 2011) to show contradictory evidence to Heupel et al. (2009) of population decline. Despite ongoing controversy over population status, it is generally agreed by all authors that restricted fishing zones assist in supporting populations.

While many studies have examined distribution of coral reef associated shark species and population status on the GBR (Heupel et al. 2009; Espinoza et al. 2014; Heupel and Simpfendorfer 2014; Rizzari et al. 2014a; Rizzari et al. 2014c; Espinoza et al. 2015b), there is a need for continued monitoring of populations particularly when considering fishing management zones. In recent years, multiple shark survey studies have taken place in the region off Townsville, QLD on the central GBR (Espinoza et al. 2014; Espinoza et al. 2015a; Bierwagen et al. 2019). These studies employed traditional fishing methods as well as BRUVS deployments which create an opportunity to examine fishing catch rates to understand relative population size as well as estimate relative abundance and distribution in the same area from BRUVS. Reef sharks are often highly resident (Papastamatiou et al. 2009; Barnett et al. 2012; Vianna et al. 2013; Espinoza et al. 2015a) and are closely associated with complex coral habitat (Espinoza et al. 2014; Shipley et al. 2018). By employing multiple methods in a region over a number of years changes in reef shark abundance over time, and how they are locally distributed, can be determined. The aims of this paper were to determine whether fishing restrictions have had an impact on distribution and abundance of reef sharks, whether populations remained stable over the sampling period, and the likelihood of encountering reef sharks within the Townsville study region. Additionally, we looked to identify any localised sites where reef shark species are more likely to occur. Given recent increases in disturbance to coral reefs in the GBR (bleaching, storm frequency, etc.) we hypothesised that these may have resulted in population declines at reefs where these disturbances are more frequent.

6.2 Methods

6.2.1 Study Site

This study was performed with data collected from 2012-2017 in the Townsville sector of the central GBR including sampling at 14 reefs (14 fishing, 4 BRUVS) ranging from the mid-shelf to the outer-continental shelf (Figure 6.1). The central GBR is a patch reef system with depths between reefs reaching ~60m. The Townsville sector is within the GBRMP and reef zones regulate levels of fishing and entry which vary among study reefs.

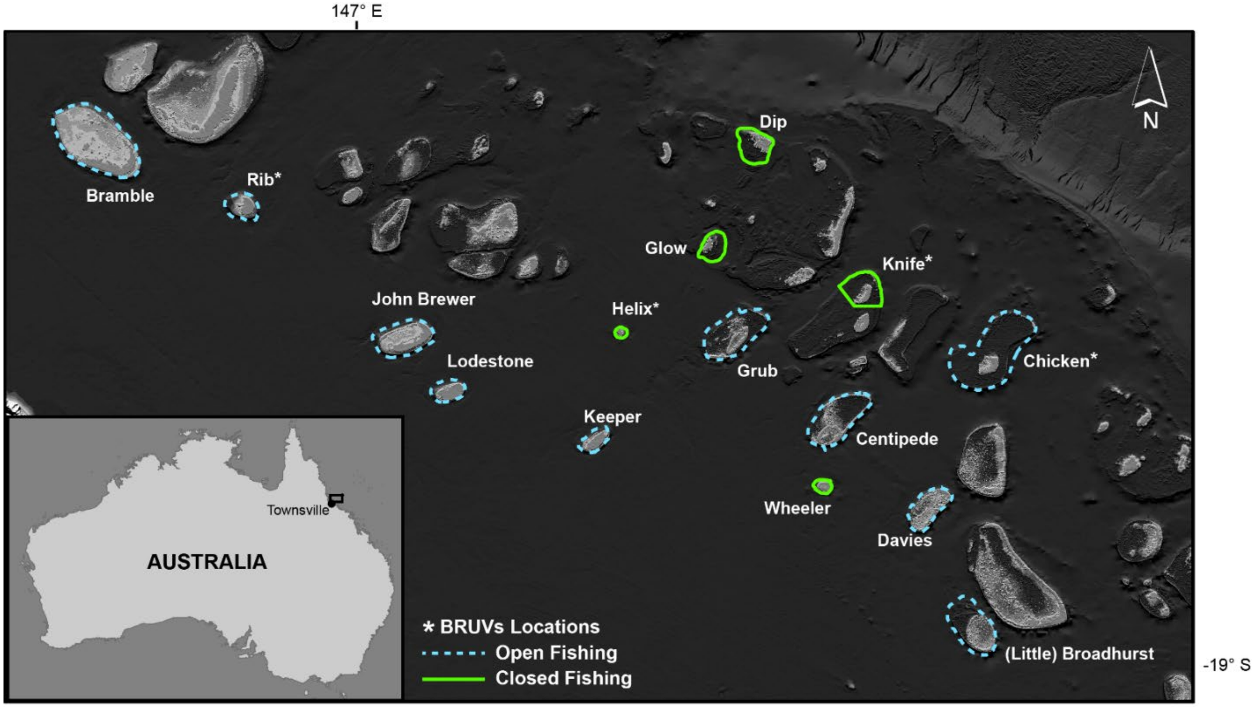


Figure 6.1: Study Location in the Townsville Sector (~18 S) of the Great Barrier Reef. Each reef outlined indicates the fishing locations for the study. Colours indicate management status where BRUVS deployments are also located at specific reefs (*Rib, Helix, Knife, Chicken)

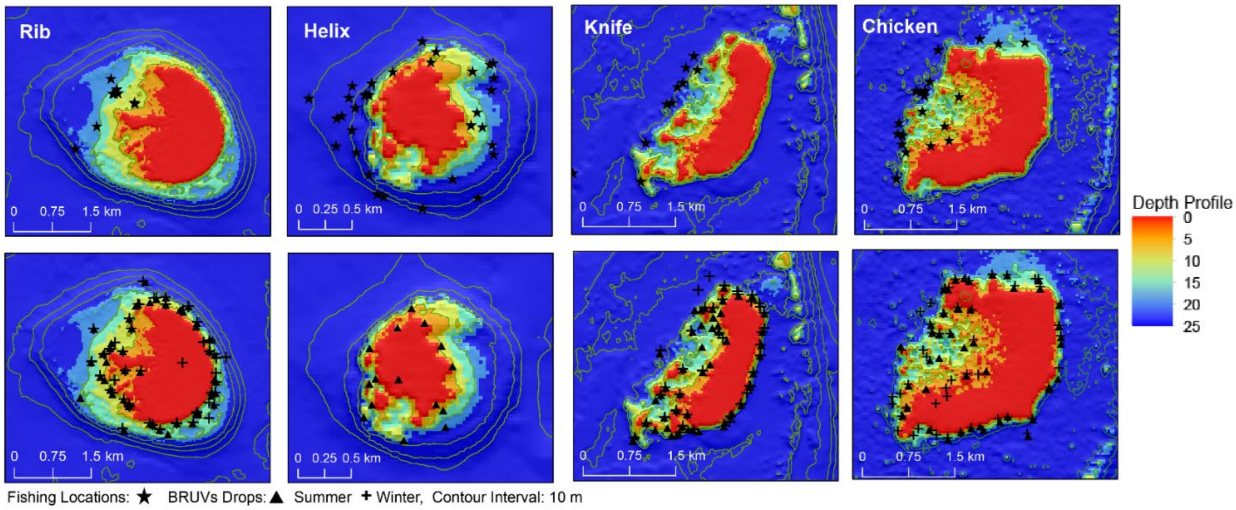


Figure 6.2: Fishing locations represented as stars (top) and BRUVS deployments as triangles (bottom) for each reef in the study area. Bathymetry and hill shade data were obtained from the Deep Reef Explorer website. Depth (m) (http://deepreef.org; Beaman 2018).

6.2.2 Fishing

Fishing methods were similar to (Espinoza et al. 2015a). Sharks were caught using traditional angling methods, mainly from use of drop lines and rod and reel fishing. Drop lines were 20-40 m in length and consisted of polypropylene float line with a Styrofoam buoy attached to a lead line between 5 and 15 m depending on depth and location. Single gangions were attached to each drop line equipped with a Mustad tuna circle hook (14/0, 16/0) connected to wire leader. Hooks were baited with frames or offcuts of fresh (e.g. red throat emperor, coral trout, finger mark, grass emperor) and thawed fish (e.g. squid, butterfly bream, pilchard). Sharks were also captured through rod and reel fishing with monofilament line attached to leader line or wire trace. Captured sharks were processed in tonic immobility, measured, sexed, and externally tagged using a rototag on the dorsal fin. Condition of individual and maturity was also recorded. Animal capture and processing was performed under James Cook University Animal Ethics (A1933) as well as GBRMPA (G37987.1) and Queensland Fisheries (187250) permits.

6.2.3 Baited Remote Underwater Video

Baited remote underwater video systems (hereafter BRUVS) were deployed at three reefs (Rib, Knife, and Chicken) over two sampling seasons in 2016; one in January (summer) and the other repeating deployments at the same locations in July (winter). Additional deployments in January also occurred at Helix Reef for one sampling season. The BRUVS were deployed during diurnal hours in reef habitat less than 40 m at all areas surrounding a reef. Housings for the BRUVS units were comprised of a GoPro Hero 4 Silver® camera in wide angle view (1920 x 1080 format, 30 frames s^{-1}) secured in custom housings designed by the Australian Institute of Marine Science. Housings consisted of polyvinyl chloride (PVC) cylinders with a fixed internal mount for the camera facing a clear acrylic Perspex® window equipped with an O-Ring seal rated to a depth of 100 m. This housing was attached to a 4-leg lightweight collapsible aluminium frame. To reduce possibility of BRUVS impact to substrate and recovery potential, legs were attached with cable ties that break under pressure if snags occurred. Dive weights of up to 16 kg were attached evenly to the base to ensure upright placement and reduce impact of strong currents during deployment. The BRUVS contained an attachment for a bait arm 1 m in length extending outward in line with the camera and a mesh bag at the end used for bait. Bait used was approximately 1 kg of crushed pilchards (Clupeidae, *Sardinella* spp). Using surface boats, BRUVS were manually deployed to the seafloor bottom with a polypropylene floating rope attached to a surface buoy. BRUVS were randomly deployed in groups of five, spaced at least 500 m apart and left to soak for a minimum of one-hour as is standard for the Global FinPrint project (www.globalfinprint.com). Up to 24 BRUVS were deployed in a single day, with a minimum of 50 deployments surrounding each sampling reef. Deployment methods were similar to (Sherman et al. 2018). As a component of the Global FinPrint project, many species are recorded and documented for later viewing. For the purposes of this study to understand shark relative abundance, datasets for the BRUVS drops were limited to shark species only.

6.2.4 Annotation

Video footage from BRUVS was observed by two independent, trained annotators using either Event Measure (www.seagis.com, v.4.43) or Annotator (www.globalfinprint.com) software. The highest number of individuals captured in a frame per species and sex is a standard measurement technique in video-analysis where underestimation is likely but limits re-counting of the same individual (see Willis and Babcock 2000; Cappo 2010). To annotate a video, the observer marked entry into the frame of individuals for every new shark species and only re-marked a frame if the number of individuals per species increased, creating a maximum number of individuals per species (MaxN) of each BRUV drop. Habitat, approximate current strength, visibility, and time of first entry was also recorded by the video observer and marked.

6.2.5 Data Analysis

Fishing

Catch per unit effort (CPUE) was calculated from fishing data where effort was measured in the form of fishing hours for each survey trip. CPUE was averaged over each survey trip for aggregate shark catch as well as per species and compared by management zone and plotted using ‘ggplot2’ (Wickham 2016) in R version 3.5.1 (R Core Team 2018). Gaussian linear mixed effect models (‘lmer’) by maximum likelihood with a response variable of log-transformed CPUE with a constant [log10(CPUE+0.001)] to account for zeros (Butterworth 1995; Maunder and Punt 2004) were used in ‘lme4’ (Bates et al. 2015) to assess influence management zone and time on catch. An interaction term of zone and year as well as a distance from land were included as fixed effects and a random effect of reef conditional on year was added to account for variability in number of reefs visited per survey year. For the purposes of this study, we grouped Great Barrier Reef Marine Park (GBRMP) management zones (Figure 6.1) to compare between no-take restricted (Marine National Park, hereafter green, N=5) and open (Habitat Protection

Area/Conservation Park, hereafter blue, N=10) zones as they are most common to the Townsville Region. During model selection, residuals were investigated for overdispersion by dividing the residual sum of squares by residual degrees of freedom. Autocorrelation was tested with the acf function in the ‘MuMIn’ (Barton 2019) package in R. Interaction effects were determined with “lsmeans” (Lenth and Lenth 2018) with management zone conditional on year.

Mixed Effect Models

To determine the effect of biological and environmental drivers on successful catch, logistic regressions by maximum likelihood (Laplace Approximation) were performed at the hook level using binary data (catch/no-catch) with the ‘glmer’ function in the “lme4” package (Bates et al. 2015) in R. An interaction term of management zone and year, land distance, depth, season, and wind were modelled against hook success of all shark species as well as grey reef sharks, whitetip reef sharks, bull sharks, blacktip reef sharks, and silvertip sharks. All models included the random terms of the intercept conditional on hook size to account for gear variability and “Reef/year” to account for variation in differences in reefs visited per year. Random terms of hook size and soak time were excluded from the models based on AIC performance. Post-hoc interaction effects were determined with “lsmeans.” Models were plotted using ‘sjPlot’ (Ludecke 2019) in R. Model residuals were investigated by testing predicted values and were measured for overdispersion using the DHARMa package in R (Hartig 2017). Autocorrelation was tested by using the ‘acf’ function.

BRUVS

To determine the effect of biological and environmental drivers on relative abundance, conditional Poisson (log link) and zero inflated negative binomial generalised linear mixed models were performed with ‘glmmTMB’ (Mollie E. Brooks 2017) in R. Management zone, visibility, hard coral cover, land distance, depth, and season were modelled against MaxN of total aggregate shark species as well as grey reef sharks, whitetip reef sharks, blacktip reef sharks, and tiger sharks. All models included the random term of the intercept conditional on soak time/reef name to account for variation in duration of BRUVS deployments and reef location. Model residuals were also investigated using the DHARMa package and ‘acf’ function.

Survey method comparison

To compare abundance from fishing to BRUVS deployments, data was filtered for the same sampling season (summer) in 2016. Fishing sites were also filtered to only include the four reefs surveyed with BRUVS deployments. Species accumulation curves were constructed for each survey method using the ‘vegan’ package (Oksanen et al. 2016) in R. For summer 2016, 40 fishing locations were used compared to 164 BRUVS deployments. One accumulation curve only used the first 40 locations of each survey method and a second included all location sites.

Local Distribution (Reef-Scale)

For BRUVS deployments, mean relative abundance per hour (Mean MaxN h^{-1}) was calculated per species for each deployment reef and tested for reef level differences with log-transformed linear models. A minimum curvature spline interpolation with barriers and hotspot analysis with the Getis-Ord Gi* statistic in ArcMap (version 10.6) were used to analyse local distribution of aggregate and common species surrounding each reef based on BRUVs deployments. A fixed distance band with Euclidean distance was used where neighbouring features exert influence on the target feature to identify statistically significant hot and cold spots for the Getis Ord Gi* statistic. To reduce type I error (false positives), a false discovery rate correction was used (similar to Bonferonni). Moran’s I statistic was used to measure spatial autocorrelation. Distribution was analysed with BRUVS data due to a more uniform coverage of deployments surrounding each reef compared to fishing effort distribution.

6.3 Results

A total of 1820 lines and 310 BRUVS were deployed for this study (Figure 6.2), comprising1062 hours of fishing effort and 453 hours of BRUVS footage. Nine different shark species (N=327, Table 6.1) were captured with traditional fishing whereas seven shark species were recorded on BRUVS (Sum of MaxN=413 occurrences, Table 6.2). Grey reef sharks were the most commonly occurring species with a total of 191 fishing captures, and MaxN sum of 213 on BRUVS (133 summer [164 drops], 80 winter [146 drops]). Proportion of grey reef sharks was 55 and 52 percent of total for fishing and BRUVS observations, respectively. The highest mean relative proportion of abundance from the BRUVS data for grey reef sharks was at Knife Reef (59 %) and lowest at Rib Reef (9 %).

Table 6.1: Fishing captures of species from 2012-2017 with mean fork length (FL), mean depth, and count of sex

Common Name	Species	Captures	FL (cm) ± SD	Depth (m)	M	F
Silvertip Shark	*Carcharhinus albimarginatus*	35	116.7 ± 37.4	32.1 ± 8.5	14	20
Grey Reef Shark	*Carcharhinus amblyrhynchos*	191	107.6 ± 60.3	27.1 ± 7.7	87	103
Bull Shark	*Carcharhinus leucas*	38	203.7 ± 24.8	29.7 ± 10.0	8	30
Blacktip Reef Shark	*Carcharhinus melanopterus*	13	111.3 ± 5.8	24 ± 5.4	8	8
Tiger Shark	*Galeocerdo cuvier*	8	165.4 ± 60.8	33 ± 9.3	1	7
Lemon Shark	*Negaprion acutidens*	10	217.7 ± 11.7	27.1 ± 7.7	1	8
Great Hammerhead	*Sphyrna mokarran*	4	213 ± 54.3	29.7 ± 10.5	1	3
Whitetip Reef Shark	*Triaenodon obesus*	28	103.6 ± 18.2	23.8 ± 5.7	8	20

Fishing data showed no significant differences in CPUE between fishing zones overall for aggregate and species CPUE (Figure 6.3, Table S6-a). Annual trends showed there were no significant differences in CPUE between open and closed zones for aggregate catch, where catch rates of each zone fluctuated year to year in a similar pattern (Figure 6.4, Table S6-a). Annual CPUE varied by species (Figure 6.4, Table

S6-a). For example, there were no significant differences in CPUE between zones for grey reef, bull, and silvertip sharks. However, annual CPUE was significantly higher in green zones for whitetip and blacktip reef sharks in certain years such as 2014 (whitetips) and 2014 and 2015 (blacktips). There was also no strong pattern in decline in CPUE for any species for either green or blue zones. The greatest effects of variability from random terms were observed in bull sharks (Table S6-a), where changes in fishing location between years likely influenced CPUE over time. Comparison of species accumulation curves between open and closed zones (Figure 6.5), indicate no difference in the number of species captured, meaning species richness was similar between management areas.

Table 6.2: Counts for species encountered on an averaged 226 hours of baited remote underwater video (BRUVS), mean BRUVS depth, and counts for 342 total hours of fishing survey effort in the same sampling year (2016)

Common Name	Species	Summer	Winter	Depth (m)	Fishing
Grey Reef Shark	*Carcharhinus amblyrhynchos*	133	80	15.8 ± 7.5	24
Bull Shark	*Carcharhinus leucas*	0	0	-	0
Blacktip Reef Shark	*Carcharhinus melanopterus*	34	19	12.6 ± 5.8	3
Tiger Shark	*Galeocerdo cuvier*	1	2	21.5 ± 3.3	0
Nurse Shark	*Nebrius ferrugineus*	5	0	9.2 ± 1.5	0
Lemon Shark	*Negaprion acutidens*	4	3	20.1 ± 7.0	0
Great Hammerhead	*Sphyrna mokarran*	1	0	10.2	0
Whitetip Reef Shark	*Triaenodon obesus*	91	40	15.0 ± 7.3	7

When considering successful capture of species (catch/no catch) at the hook level compared to abundance CPUE measures, species-specific logistic regressions (except grey reef sharks) produced wide confidence interval ranges and odds ratios so were excluded due to uncertainty in predicting and interpreting outcomes. For grey reef sharks, catch was most successful overall in green zones and during periods of moderate winds (Figure 6.6, Table S6-b). These results were affected by survey year where capture was more likely in blue zones. There were no zonal differences of aggregate species at the hook level except for 2016 where capture was more successful in green zones. Shallower depths also had a positive influence on grey reef shark capture success. Catch success of combined shark species was strongly influenced by the random term of hook size and reef fished (Table S6-b), likely due to size differences between species. There was minimal influence of random terms for grey reef sharks which is likely due to their high abundance within the study site. No other factors had an impact on the response variable of catch success of each species. These models were neither auto-correlated nor over dispersed.

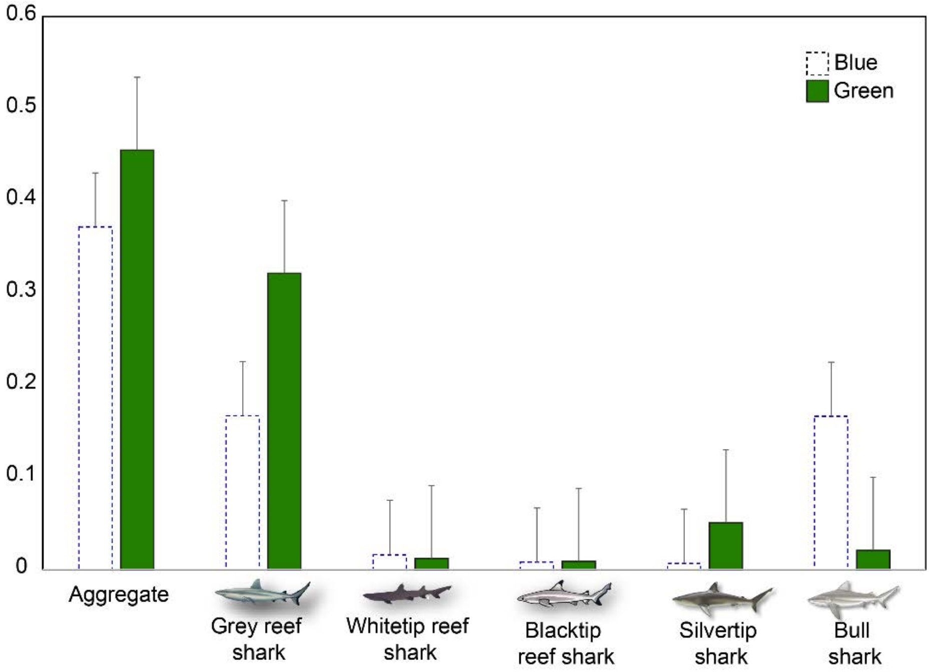


Figure 6.3: Mean CPUE abundance from 2012-2017 separated by management zones. Bars: Standard Error. Images sourced from IAN Image Library (https://ian.umces.edu/imagelibrary/)

Compared to fishing data, ZINB models for relative abundance of BRUVS deployments showed significantly higher MaxN proportional abundance of aggregate, grey reef, and whitetip reef sharks in closed zones (Figure 6.7, Table S6-c). Additionally, the winter season was an influencing factor for higher relative abundance of aggregate total and whitetip reef sharks. Distance from land and depth had a negative significant influence on grey reef shark relative abundance. Compared to other species, blacktip reef shark abundance was not affected by fishing zone but was significantly higher in depths lower than mean occurrence (Figure 6.7). As with the fishing data, models were not auto-correlated or over-dispersed (dispersion range 0.01-1.4).

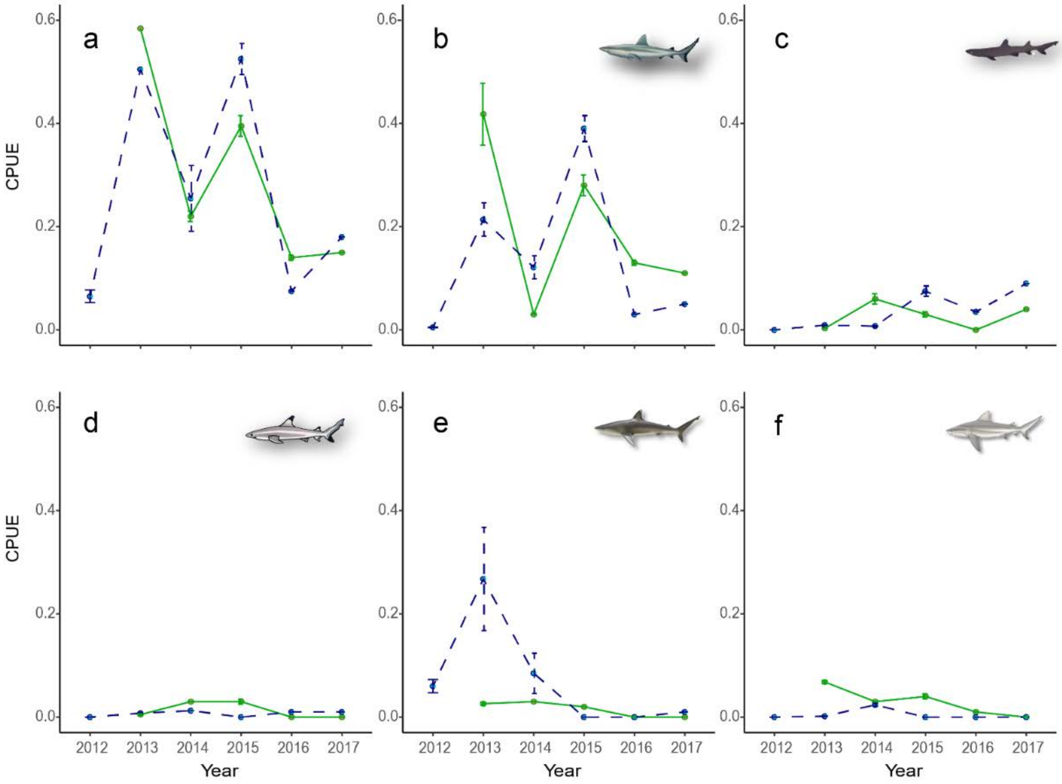


Figure 6.4: Mean annual CPUE from total fishing catch data from 2012-2017 separated by primary management zones (green: closed, blue: open, bars: standard error)

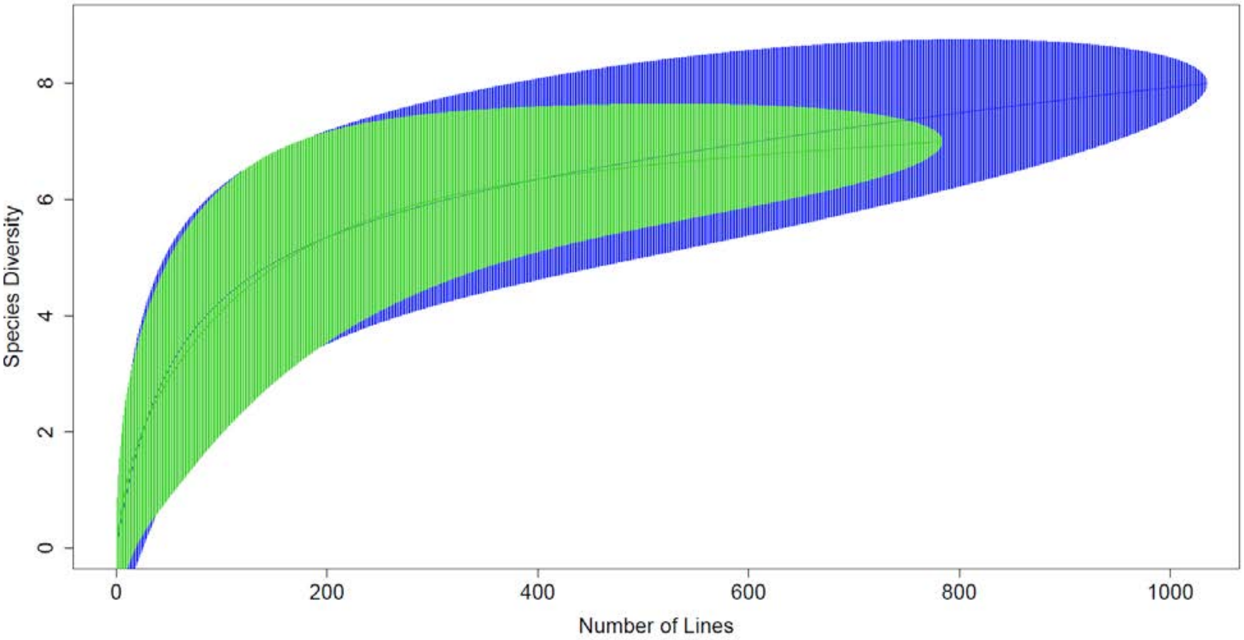


Figure 6.5: Species accumulation curves by fishing zone (green closed, blue open) for total fishing lines deployed from 2012-2017, bars=95 % confidence intervals

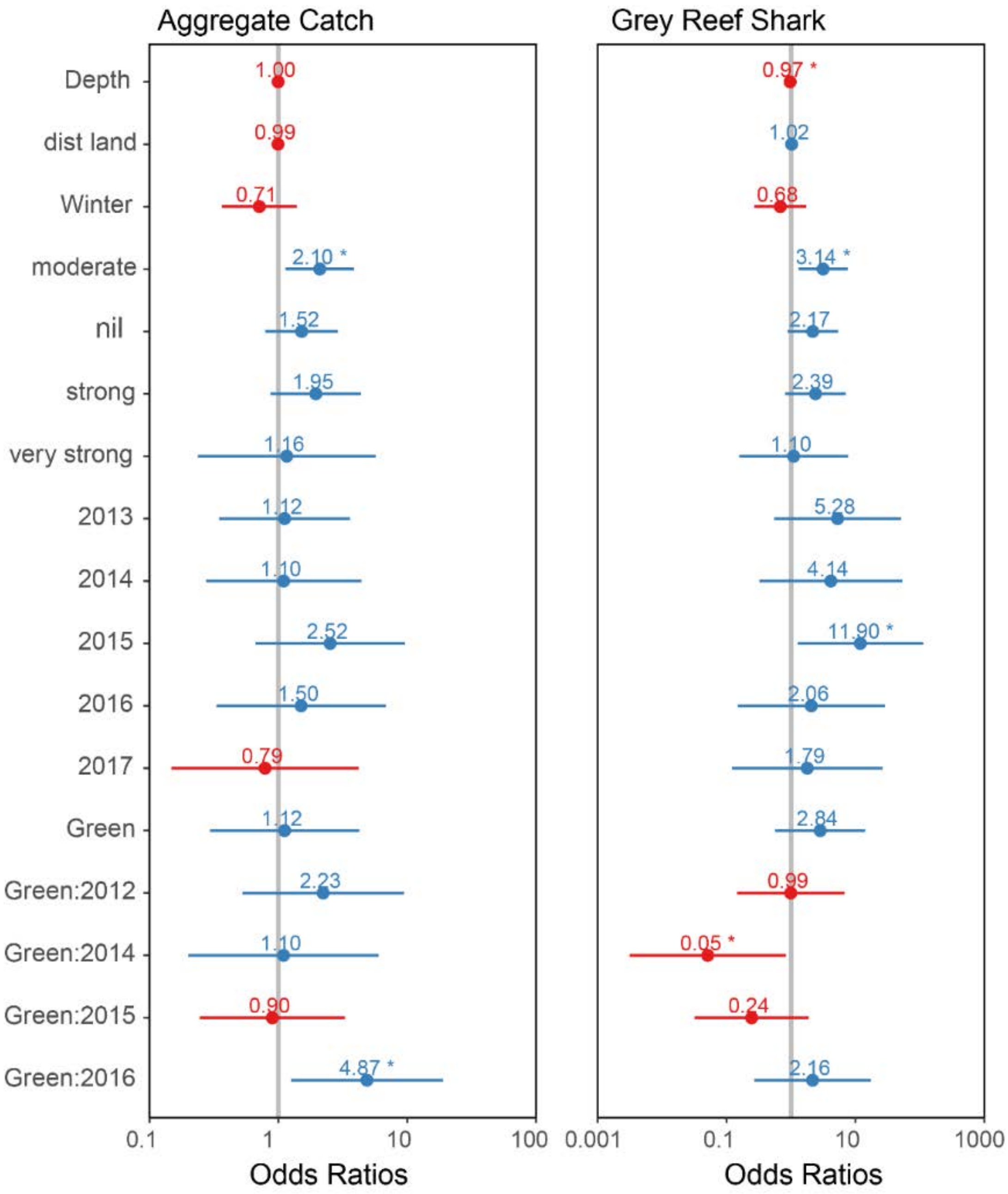


Figure 6.6: Binomial logistic regressions (logit link) odds ratios of fishing data for total catch and species with significant fixed effects (random term conditional on Reef/Year). Red: Negative effect, Blue: Positive effect, * indicates significance with p<0.05

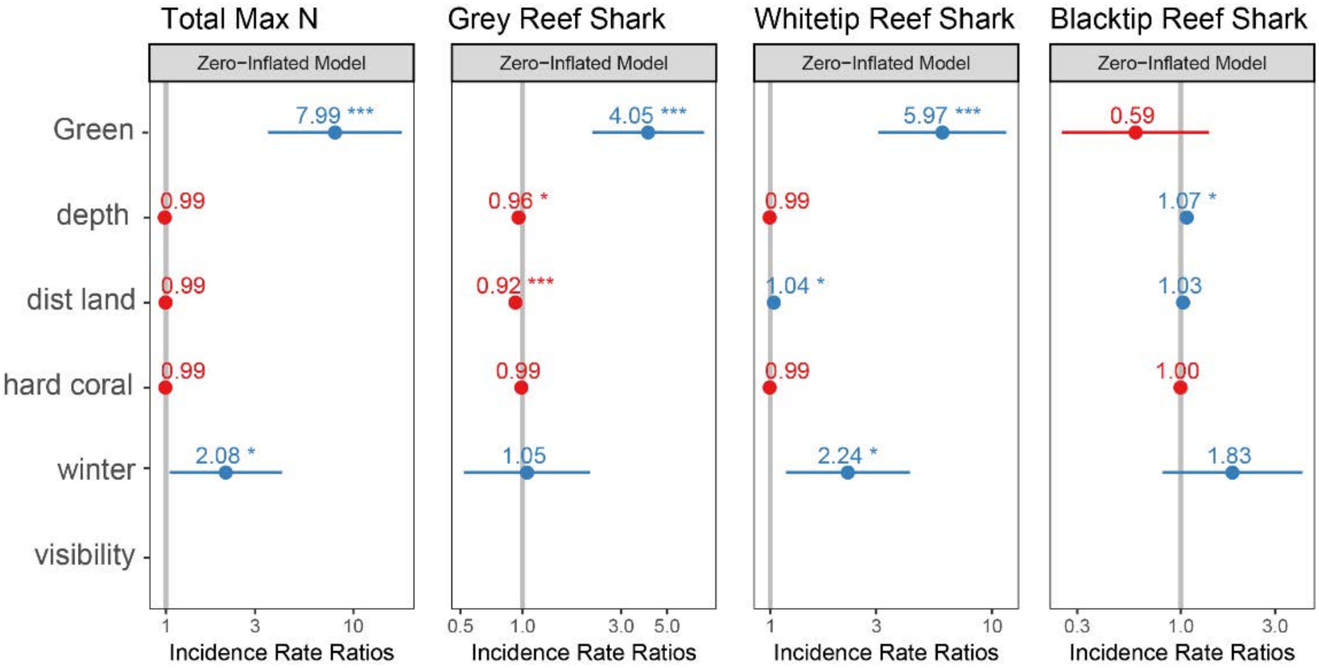


Figure 6.7: Zero-inflated negative binomial generalised linear mixed models for BRUVS deployments over two sampling seasons in 2016 showing significant fixed effects with a random term conditional on soak time/reef**.** Red: Negative effect, Blue: Positive effect, * indicates significance with p<0.05

When comparing survey methods, BRUVS deployments were more effective at measuring species diversity based on total deployments in the same sampling season (Figure 6.8). In one sampling season, seven total species were recorded on BRUVS compared to four species captured in fishing surveys. It should be noted however, that BRUVS survey periods were subject to better weather which enabled researchers to access the entirety of each reef compared to limited locations for fishing (Figure 6.2). BRUVS also, on average, were placed in shallower locations than fishing sites (Tables 6.1, 6.2).

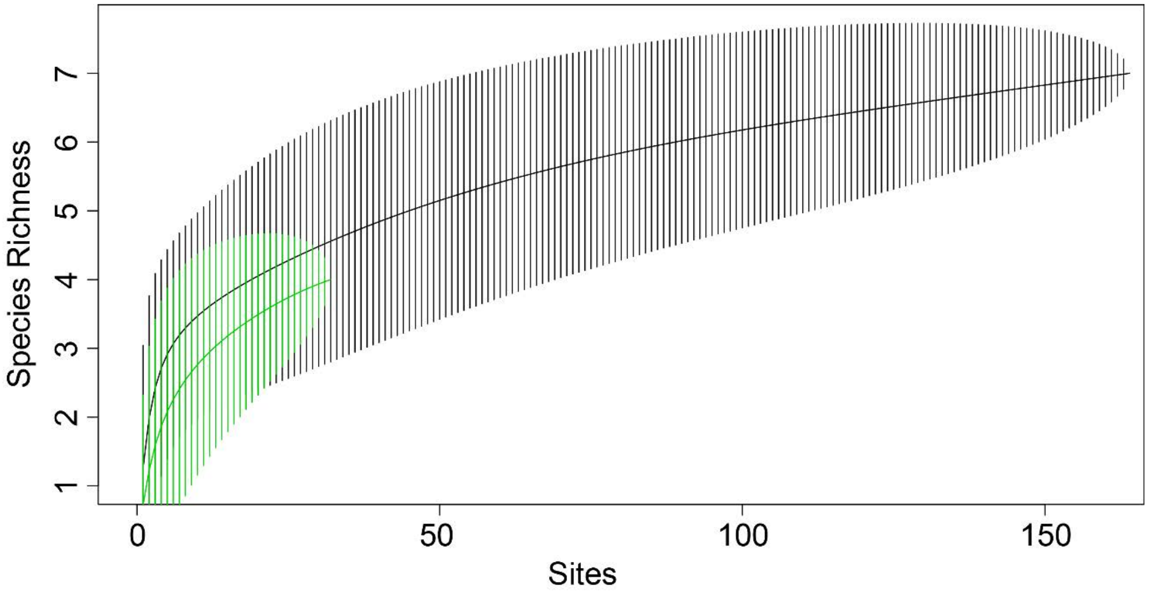


Figure 6.8: Species accumulation curves for total BRUVS drops (black) and fishing sites (green) in the same sampling season (Summer) in 2016, bars= 95% confidence intervals

Reef-level analysis showed grey reef sharks were most abundant on Knife reef with a relative abundance of 1.57 MaxN h^{-1} but were not significantly different between reefs (Figure 6.9). BRUVS observations also showed whitetip reef sharks were most prominent in closed zones 0.65 – 0.93 MaxN h^{-1} and positively related to hard coral cover (SE=0.46, df=157, $p<0.001$). Blacktip reef sharks were reported in low numbers across all reefs (0.09 - 0.25 MaxN h^{-1}). Spline interpolation with the Getis-Ord Gi* and Global Moran's I statistics at the reef scale showed significant hotspots and spatial autocorrelation (non-random clustering) at various locations surrounding each reef, particularly for aggregate species, whitetip reef and blacktip reef sharks (Figure 6.10).Grey reef sharks showed no significant clustering as they were well dispersed across all reefs.

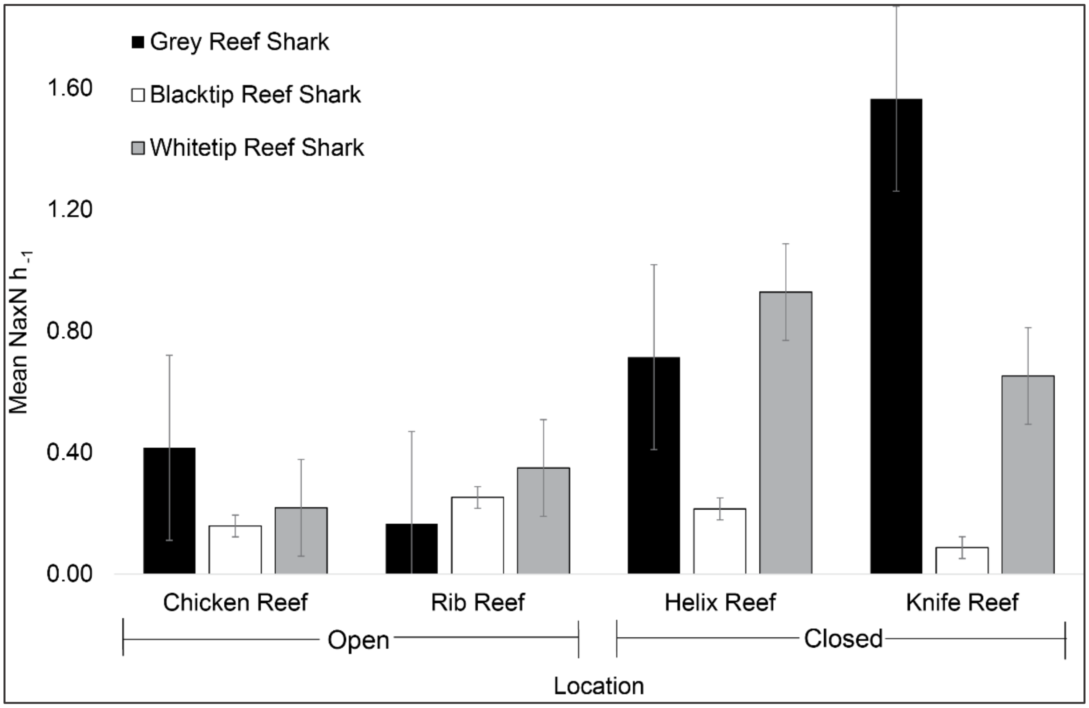


Figure 6.9: Mean abundance per hour (MaxN h^{-1}) of sharks per reef at BRUVS locations

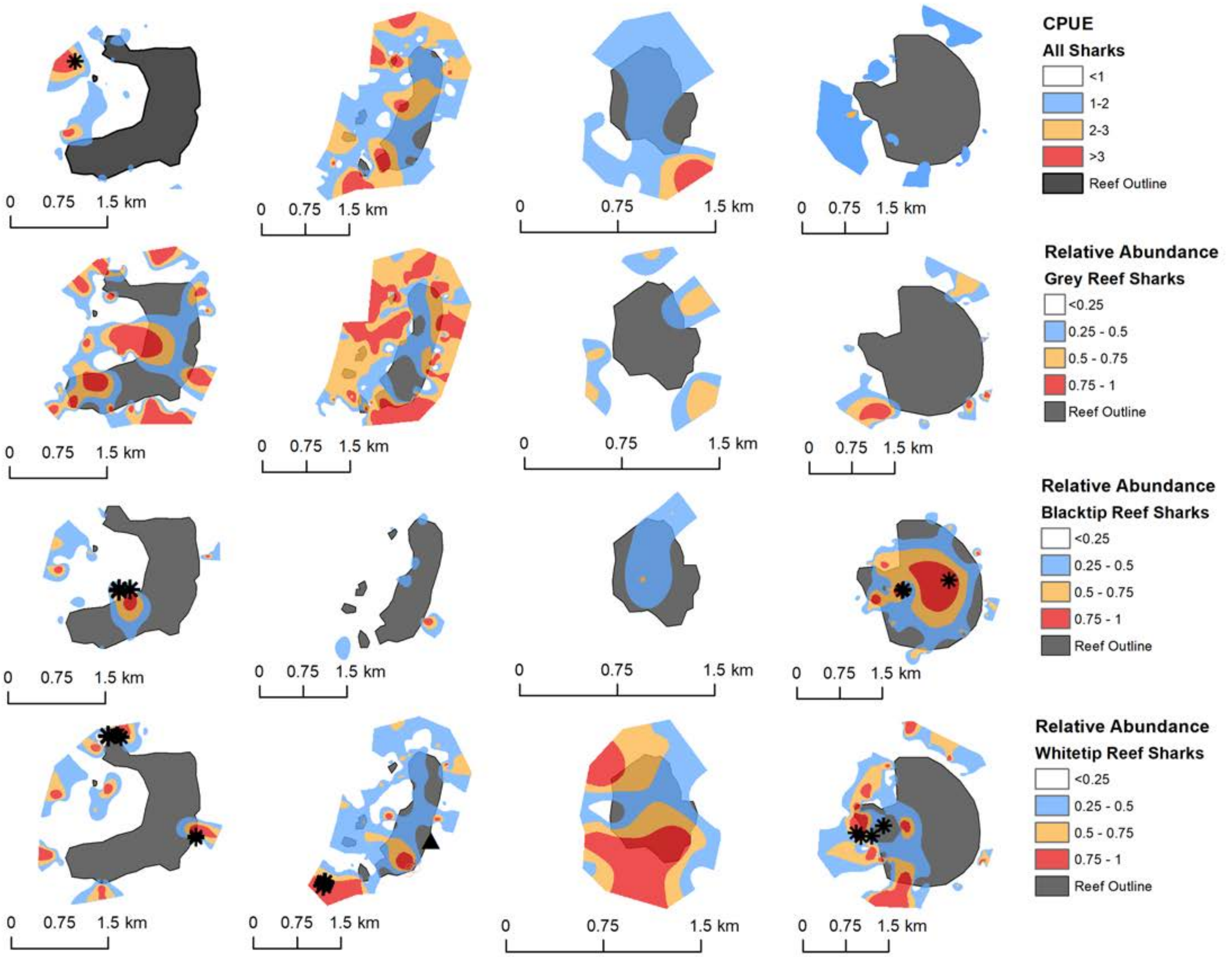


Figure 6.10: CPUE and species distribution models from BRUVS data using minimum curvature spline interpolation and hotspot analysis with the Getis-Ord G statistic using false discovery rate correction. * indicates statistically significant hotspots and Δ indicates a single cold spot with $p<0.05$.

6.4 Discussion

Through use of two different survey methodologies, we have shown that non-extractive BRUVS provide similar measures of species richness to fishing, yet BRUVS add insights to species occurrence that catch data did not reveal. BRUVS were more effective for identifying the occurrence of whitetip and blacktip reef sharks over traditional fishing methods with low CPUE. This is likely due to BRUVS dropped on average in shallower depths than fishing sites, which is consistent with the significant clustering of species like whitetips and blacktips in shallower areas. Heupel et al (2018) found strong evidence of species partitioning on a coral reef through use of telemetry, showing that species such as blacktips use shallower areas on the edge of reef crests. BRUVS also revealed differences in relative abundance between management zone and seasonal abundance for grey reef and whitetip reef sharks. This finding is consistent with studies that have better success in BRUVS for measuring diurnal relative abundance of species compared to fishing measures (Willis and Babcock 2000; Cappo et al. 2003), but whether baited scenarios reflect real-world presence is something to also consider.

Neither BRUVS nor traditional fishing in later years of the survey has successfully observed bull and silvertip sharks, both of which had overall been low in catch numbers throughout the sampling period. This corresponded with changing reef sampling sites over time. However, low rates of observing bull sharks on BRUVS is consistent with findings by Espinoza et al. (2014) who also reported low numbers in the GBR. From movement studies, bull and silvertip sharks have been found to be more mobile than resident shark species such as grey reefs, either by making large scale coastal migrations (bulls) or moving between reefs (silvertips) (Espinoza et al. 2015b). This means the probability of occurrence of these species within fishing/BRUVS areas is likely less than other species such as grey and whitetip reef sharks that are resident in these areas. However, Espinoza et al. (2014) observed high numbers of silvertip sightings, particularly offshore. In their study, silvertips were consistently reported in depths deeper (21.2 - 76.1 m) than most BRUVS deployments from our study (averaging ~14 m with a maximum depth of 37 m), which may also account for the disparity. These results highlight the need to understand space use and habitat preferences of species when conducting surveys that consider their abundance and stability over time and between open and closed areas.

Analysis at the hook level showed that in one year more reef sharks were more successfully captured in open zones compared to closed zones. While this result could be due to a number of factors, hook level data shows that it is possible that blue zones create increased potential for shark behaviour to shift towards targeting hooks regardless of risk. For example, Mitchell et al. (2017) found that shark depredation (consumption of fish off hooks before capture) was greater in areas with greater recreational fishing pressure off Western Australia. However, due to an isolated year and to adequately understand our findings, more information is needed from fishing sectors to see if catch susceptibility is higher in blue zones, particularly in heavily fished areas. There is little information regarding whether sharks are more attracted to live fish caught by recreational fishers compared to dead bait (used in our fishing methods), New South Wales gamefish anglers who target sharks were more successful with dead bait then live (Lowry et al. 2006). Within the GBRMP, there is little data on recreational fishing activity particularly for depredation. Most information on landings come from the commercial fishery (Chin et al. 2019), where the annual Queensland Fisheries summaries report low catch for reef sharks as they are not targeted species and have bag limits, creating a knowledge gap in reporting on reef shark landings or interactions.

Based on results from the central GBR collated here, reef shark CPUE showed no pattern of decline from 2013 to 2017. Catch rates fluctuated between years, with low reported numbers for some species particularly in recent years such as blacktip reef, bull, and silvertip sharks. This study indicates that there were no differences in fishing based CPUE of any species between zones except in specific years for whitetip and blacktip reef sharks (2014/2015). Additionally, similar species richness between zones was observed. The differences in sampling effort and locations over the years could be a factor in low catch rates of these species, or a result of fishing in areas that species are not likely to be found, as previously mentioned. These findings are backed by high abundance from the last year of survey from BRUVS. These trends contradict previous results presented by Robbins et al (2006) who estimates of ~17 percent annual decline rate of grey reef sharks and evidence of rapid decline using population growth estimates by Hisano et al (2011). The differences in results between studies suggest that there may be complex issues related to reef shark abundance with the potential that population size and trend varies by location and is thus not uniform across the GBR. However, these differences also show that there is still limited information as to how well survey methods reflect true levels of abundance (Willis et al. 2000; McCauley et al. 2012a, Rizzari et al. 2014a). The lack of difference in CPUE between blue and green zones for aggregated species data and particularly for grey reef sharks does contrasts findings from UVC surveys by Ayling and Choat (2008), who sighted grey reef sharks were four times more often in green zones than blue in the central GBR which was used as a proxy for abundance. Additionally, there were no differences in CPUE between blue and green zones for blacktip reef sharks and whitetip reef sharks except in specific years, also which differs from Ayling and Choat (2008) who found two times as many whitetip reef sharks in green zones over blue. This contradiction highlights that care should be used when comparing between studies that employ different survey methods of measuring abundance (e.g. SCUBA observations versus fishing versus BRUV) (McCauley et al. 2012a). It should be noted that catch of some species such as blacktip reef and silvertip sharks were minimal among years meaning that populations at the study location may have been low for a long period, were naturally low in abundance for these areas, or that fishing areas do not reflect preferred habitat of these species. Interspecific competition could also be a factor in low abundance estimates of some reef shark species (Heupel et al. 2018; Matich et al. 2017). The CPUE was also highly variable between years in both open and closed zones, making determination of trends over time difficult.

The observed year to year fluctuations in CPUE likely reflect other factors causing variation. For instance, the central region of the GBR was impacted by cyclones, crown of thorns (*Acanthacatser plancii*) outbreaks, and mass coral bleaching during the survey period of this study. These disturbances resulted in coral cover being reduced to its lowest reported level (~14 percent) in 2017 (Sweatman et al. 2018). However, the GBR has a documented capacity to recover and reassemble post disturbance (Emslie et al. 2008; Bierwagen et al. 2018). This means that while faced with disturbance pressures, reefs in the study area are likely to also have recovered to some degree during this period. Coral cover provides essential complex habitat for many reef-associated species (Graham et al. 2007; Pratchett et al. 2008; Bierwagen et al. 2018) including reef sharks (Espinoza et al. 2014) and their prey (Wilson et al. 2006; Komyakova et al. 2018). It is possible that changes in coral cover over the years influenced sharks to move from degraded areas to seek more optimal habitat and that shark occurrence may fluctuate with reef state and rates of reef recovery. If these redistributions are occurring, they could explain reported reef-level changes in CPUE which are unlikely be due to mortality given the rapid increases observed in some year, but rather a change of presence in certain years. Conversely, results in our study from BRUVS data and hotspot distribution analysis showed grey reef sharks consistently occurred around the entire reef area including back reef habitat with low reported coral cover. This would suggest habitat type may not be a key driver for their distribution. Hence, reef sharks do not always associate solely with complex structure, relating back to their mobility potential. Another interesting result was that wind speed was an influential factor in capture success which partly aligns with grey reef shark telemetry data from (Heupel and Simpfendorfer 2014) that found wind speed to have weak effects on shark presence however the authors suggested wind speed may affect detectability of sharks on acoustic receivers rather than their occurrence. This result also differs from Espinoza et al (2015a) who found no positive effects of wind strength on shark occurrence on BRUVS. These finding highlights differences in the potential for a range of factors to influence catch success which ultimately may lead to variability of CPUE.

The mixed effect models for both catch data and BRUVS showed that fishing zone had the highest impact over other factors on species relative abundance for aggregate catch, grey reef sharks, and whitetip reef sharks. However, this factor did not influence blacktip reef shark abundance. While the effect of sampling season (summer/winter) was negligible for catch data, relative abundance of aggregate species and whitetip reef sharks was higher in winter months for BRUVS. When considering total catch as well as relative abundance from BRUVS in our study, the Townsville region appears to support high reef shark species richness and areas of high use by reef shark species. Grey reef sharks were uniformly distributed across all reefs in the BRUVS study with no significant clustering in any one area. Their abundance was higher than expected with one reef (Knife) recording one shark for every BRUVS deployment with the highest MaxN of five individuals. Compared to low reported MaxN h^{-1} numbers for limited Townsville reefs from 2000-2010 reported by Espinoza et al (2014) (supporting information), shark presence may have increased in recent years. Our study also showed that whitetip reef shark presence in the study region differs between MaxN h^{-1} and CPUE. These findings indicate that a single method may not be optimal for fully understanding abundance and distribution of these species, where survey location as well as capture method (extractive or non-extractive) likely influences understanding of relative abundance. Similar findings in CPUE versus BRUVS accuracy for fish populations have been reported (Parker et al. 2016). We recommend future research in establishing baselines for population assessment using stereo-BRUVS which can accurately identify individuals based on size (Harvey et al. 2012; Langlois et al. 2018). We also show that different methods more accurately reflect species trends, meaning it is best to understand which method will work best for target species within a study. Employing multiple methods is likely the most optimal route as some are able to capture a clearer picture of distribution and abundance over others. Multiple methods would also make it easier to compare to other studies that incorporate one over another.

Another interesting component of this study shows that local distribution from BRUVS surveys indicate species clustering for whitetip reef sharks, blacktip reef sharks, and total aggregate catch indicating that there are common areas of use around specific reefs. Although, no consistent pattern can be seen in reef aspect. Interestingly, blacktip reef sharks seemed to cluster in more central, shallow reef locations compared to other reef sharks which is supported by a study by Heupel et al. (2018) in the Southern GBR. Future study may benefit from targeting specific areas for surveys based on individual species distribution. Considering that abundance between fishing zones may vary by species, it is important to structure management strategies to accommodate less abundant species that do not follow overall aggregate trends. This has been important when highlighting that aggregation of individuals within populations has been found to lead to loss of complex detail in species movement (Mourier et al. 2019). As such, similar approaches when considering abundance may not be beneficial for interpreting species trends as they tend to follow the most abundant species as seen in this study with grey reef sharks.

6.4.1 Conclusions

This study found that restricted fishing (closed) zones on the GBR are effective for supporting higher abundances of reef shark species overall, but low reported numbers of some species will need further investigation. We also found that species residing in open zones may be more susceptible to capture. This study demonstrated that angling estimates alone may not provide a true picture of population trends, and other methods such as BRUVS can be beneficial in determining presence and distribution of species. Our results contradict some previous findings of population decline, by indicating specific reefs support high numbers of species such as grey reef and whitetip reef sharks and there were no differences between open and closed zones. As this study presents findings that show a degree of uncertainty in trends, future study should incorporate continued long-term monitoring of abundance and species-specific distribution using multiple methods to more fully capture the status and trends of populations.

Chapter 7: General discussion

7.1 Challenges in defining functional roles of reef sharks using trophodynamics

In recent years there has been a shift away from oversimplification of marine food webs by realizing the potential of feeding interactions; such changes have altered previous perceptions of trophic influence in marine ecosystems (Bascompte et al. 2005; Trebilco et al. 2013; Hussey et al. 2014). This shift is apparent in research relating to coral reefs where reef shark species have been re-categorised as mesopredators, leaving the apex classification for larger-bodied species such as tiger, bull, and hammerhead sharks (Heupel et al. 2014; Frisch et al. 2016; Roff et al. 2016a; Espinoza et al. 2019). From a trophic ecology standpoint, evidence supports this shift through use of methods such as stable isotope and gut content analysis (Frisch et al. 2016; Espinoza et al. 2019), showing that reef sharks occupy a lower trophic position than apex predators, are functionally redundant and potentially exhibit diffuse predation (Heupel et al. 2014; Roff et al. 2016a). This conclusion is of importance as it provides possible explanations for why there is limited evidence for trophic cascades on coral reefs. Additionally, with this re-categorisation comes the assumption that the magnitude of top-down controlling influences of some reef sharks is much lower than previously considered, recognising that their functional role is different than hypothesized (Frisch et al. 2016; Roff et al. 2016a).

These conclusions, however, come with a few caveats. Firstly, re-defining functional roles of reef sharks has placed three of the most common species in redundant feeding niches (grey reef, whitetip reef, and blacktip reef sharks) (Frisch et al. 2016). Secondly, there is a suggestion of functional redundancy with other reef predators such as larger teleost fish (coral trout, red throat emperor, Spanish mackerel; *Scomberomorous commersoni*) based on similar stomach contents and predictions from isotope mixing models which provide low resolution on specific diet (Roff et al. 2016a). Thirdly, this re-categorization comes from direct predatory feeding effects since there is limited data on indirect behavioural effects such as feeding suppression of lower trophic organisms (i.e. herbivores) (Rizzari et al. 2014b). Lastly, there is lack of context in how these roles can change from a biogeographic or spatial standpoint. As identified in *Chapter 2*, substantial information is needed to identify functional or ecological roles of organisms, particularly when pertaining to complex systems such as coral reefs. Moreover, there is a need for clarity in population status and how feeding may influence movement and distribution of reef sharks. This thesis aimed to fill gaps in these areas where there has been no previous research, or where more detailed definition was required. Acquiring these details were nested in consideration of how the rest of the ecosystem is structured. Existing research relating to these factors is not often available within the same spatial scale over extended periods and require more detail (Figure 7.1).

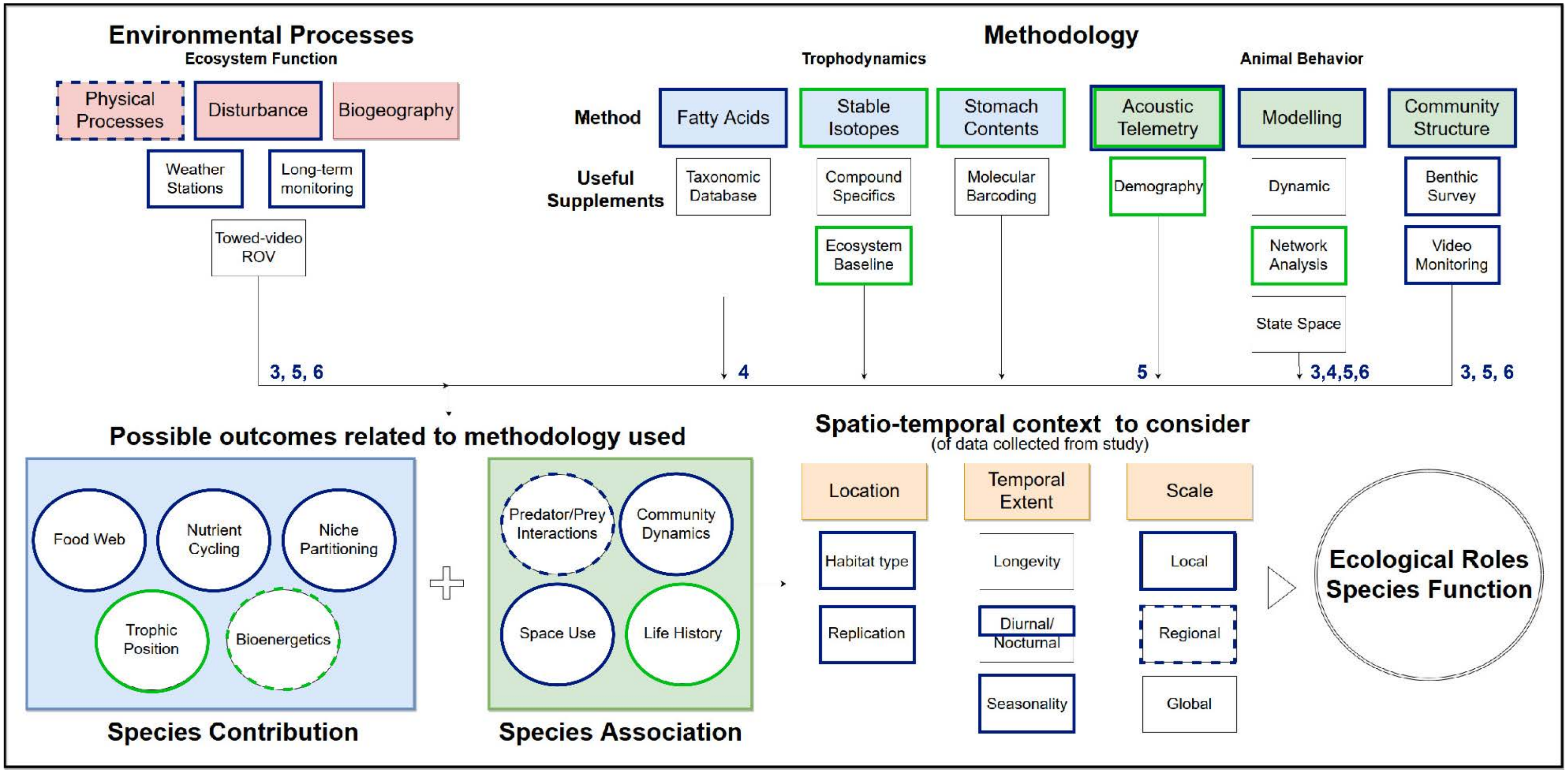


Figure 7.1: Graphic showing how achieved aims and data chapter considerations of the thesis (numbered, blue) relate to gaps identified in *Chapter 2* (Figure 2.2) leading to outcomes that will assist in informing functional roles of reef sharks. (Blue outline– thesis elements; Green outline – taken from existing literature in same spatial scale; dashed outlines – Incomplete information)

7.2 Reef resilience and implications for predators

Understanding how reef sharks fit in their current environment is essential to creating baselines to address implications of future changes to ecosystems. Without knowledge of the resources reef sharks require, it is difficult to determine whether potential resource depletion will impact survival and residence. This creates questions around how many predators degraded or non-pristine reefs can support. Therefore, it is necessary to measure the reef community and resilience to disturbance events as well as determine spatiotemporal variability in reef recovery. Reef recovery capacity can then be examined in the context of resilience of reef shark habitat. *Chapter 3* revealed that coral re-growth at all reefs studied equalled or surpassed pre-disturbance levels, yet reef-level differences drove recovery of some fish functional groups. Additionally, some functional group abundance such as grazers, corallivores and macro-invertivores were not correlated with benthic recovery as their density continued to decline after coral recovery. This result highlights the need to understand lagged recovery effects and that coral health cannot always be used as a proxy for fish abundance and species richness.

There were also unexpected findings framed around coral reef recovery and nutrient availability. For example, tabulate and bottlebrush coral species on mid-shelf reefs were found to have a higher capacity to recover over outer-shelf reefs, creating habitat and recruitment potential for species groups such as planktivores. This result was surprising as outer-shelf reefs are more exposed to upwelling and pelagic nutrients (Fabricius 1995). These nutrients such as nitrogen are utilised by coral for re-growth which promotes recruitment of fish species. *Chapter 4* showed that reef sharks are a source of these essential pelagic nutrients to reefs, where other research shows that reef sharks are egesting them at much higher rates than previously considered (Williams et al. 2018). Hence, as nutrient dynamics are primarily regulated by animal biomass on coral reefs (Allgeier et al. 2017) presence of sharks around mid-shelf reefs (*Chapters 5, 6*) could potentially assist in recovery of lower trophic organisms and benthic structure post-disturbance that were previously thought to have lower resource potential compared to outer-shelf habitats. While other nutrient inputs such as terrestrial runoff should be considered, they reach mid-shelf regions of the GBR in much lower levels than inshore (Brodie et al. 2005). Overall, while *Chapter 3* revealed reef-variability, recovery potential was seen across all reefs with similar abundance proportions of fish functional groups among them. This is a promising finding in terms of reef resilience.

7.3 Dietary separation among reef mesopredators

This thesis aimed to first understand reef resources, and second, confirm which components reef sharks utilise. While there has been an inference of evidence for functional redundancy from gut content and stable isotope studies, these findings lack fine detail and resolution. Reef sharks are found to have high percentages of teleost fish in their diet (Cortes 1999; Frisch et al. 2016), which is why most are considered to be functionally redundant. However, for some species such as grey reef sharks, teleost prey taxa are largely unidentifiable (Papastamatiou et al. 2006; Frisch et al. 2016). Stable isotope studies also employ a small number of tracers (δ^{15}Nitrogen, δ^{13}Carbon), limiting the level of resolution to identify basal food chain dependencies in isotopic niche space (*Chapter 2*). In *Chapter 4*, fatty acid analysis was used to gain a finer level of dietary detail for reef mesopredators. The main fatty acids that separated each species have been used in other studies as strong indicators of prey differences, where niche partitioning was found between reef sharks and teleost fish as well as tighter niche space for whitetip reef compared to grey reef sharks. Whitetip reef sharks have been previously suggested to be highly generalist feeders with the ability to target keystone species such as unicornfish (*Naso* spp) (Frisch et al. 2016). Findings from *Chapter 4* suggest that whitetip reef sharks may be more specialist feeders than previously indicated and in addition to small niche space, whitetip reef shark trophic biomarkers for basal sources were provided to further support evidence of dietary specialisation. Conversely, grey reef sharks have long been shown to be generalist feeders which is consistent with findings here, providing support for diffuse predation. However, assumed functional redundancy with teleost reef fish (particularly for those such as coral trout that also feed from pelagic resources) was shown in *Chapter 4* to have less overlap than anticipated. This is of importance as both grey reef sharks and coral trout have been found to target similar species such as fusiliers. *Chapter 4* shows that there is also some level of specialisation and a larger basis for pelagic inputs by grey reef sharks over reef-dwelling teleosts. When combining results from *Chapter 4* and existing stable isotope and gut content work, there is a much clearer picture in dietary specialisation between mesopredator species (*Chapter 4*, Figure 4.6). Stable isotope study confirms that there is redundancy with some basal separation from carbon isotopes between benthic and pelagic derived nutrients of mesopredators (Frisch et al. 2016; Roff et al. 2016b; Espinoza et al. 2019). Stable isotopes are highly effective at identifying trophic levels but are less beneficial in determining basal sources of nutrition and diet composition (Pethybridge et al. 2018). The benefit from adding fatty acids to this work is that a higher level of detail is seen in prey resources, showing significant differences in species consumed. Thus, while predatory reef sharks and teleost species remain at similar trophic levels, they likely have different functions. Functional differences have also been shown in movement studies, where co-occurring reef sharks and teleost species have differing movement patterns and habitat use. One study on the southern GBR showed spatial separation between five shark species (Heupel et al. 2018). This has also been observed at Palmyra between species such as grey and blacktip reef sharks (Papastamatiou et al. 2018). On the GBR, co-occurring teleost species of coral trout also undergo depth and dietary niche partitioning revealing different functions within the same species complex (Matley et al. 2016). These results are not surprising due to complexity of reef systems and feeding opportunities. Though redundancy among mesopredators has been previously considered to limit cascading effects on reef systems, *Chapter 4* shows that there are still possible negative consequences of predatory removal on coral reefs.

7.4 Space use and relative abundance of reef sharks

The results of this thesis show that reef sharks were found to be distributed across all study reefs, with spatial separation of some species such as whitetip and blacktip reef sharks. Blacktip reef, silvertip, and bull sharks were reported in low numbers compared to whitetip reef and grey reef shark species (*Chapter 6*). As a case example, distribution and space-use of grey reef sharks was found in part to be related to prey abundance (*Chapter 5*). Grey reef sharks exhibited residency to the study reefs and individuals often overlapped in both core and extent of space use. While grey reef sharks were distributed around each reef, there were also areas where individuals were detected more often which was related to prey availability. Though there were shifts in abundance over time creating difficulty in identifying patterns in abundance, there was no evidence of decline in any species during the survey period. Additionally, there were no differences in CPUE of species between no-take and open management zones. These results differ from other studies on the GBR which have shown increase in shark abundance since re-zoning of the marine park in 2004 (Espinoza et al. 2014), and a significantly higher abundance of sharks in no-take or no access zones (Ayling and Choat 2008; Espinoza et al. 2014; Rizzari et al. 2014a). These differences may depend on survey method use (e.g. fishing, BRUVS, diver survey), or scale of study. It is also possible that due to low reported take of reef sharks from Queensland fisheries in recent times (Heaven 2018), that the lack of difference between management zones reflects that strict fishing regulations (bag limits) offer similar protections for sharks in areas open to fishing. Additionally, shark distribution was found to differ from other studies that show importance of habitat type as an influence (Rizzari et al. 2014c; Papastamatiou et al. 2018). *Chapter 6* demonstrates that species such as grey reef sharks are not only concentrated in reef slope habitats, and hard coral may not be the best predictor for abundance of reef sharks. The spatial separation and abundance differences observed between species shows there are differences in how reef sharks utilise reefs regardless of management zoning, where functional distinctions cannot be over-generalised. Spatial separation has also been observed in areas of the Southern GBR (Heupel et al. 2018) which indicates that spatial partitioning among reef mesopredators is not isolated to specific regions of the GBR. Hence, probability of occurrence and distribution should always be considered when describing function of species on coral reefs.

7.5 Ecological implications

Overall, this thesis provides a snapshot of what reef shark populations look like on degraded reefs with differing recovery potential over time. In their current state, these coral reefs have a capacity to recover post-disturbance, yet some lagged effects should be considered for future study. This is important due to coupled effects from future stressors such as potential increased climate-mediated ecosystem impacts mixed with natural disturbance. This thesis shows that some shark populations (e.g. silvertip, blacktip reef sharks) are reported in much lower in numbers over time than others (e.g. grey reef sharks) and therefore may not contribute the same level of functional influence due to their limited abundance. Habitat and resource use also differed between reef shark species. Species such as whitetip reef sharks had tight feeding niches and were distributed around the reef differently to grey reef and blacktip reef sharks. So even though they remain at the mesopredator level, their marginal niche and limited spatial overlap with other species at the same dietary position shows they may be more functionally distinct than other reef shark species. Grey reef sharks also have low dietary overlap with some mesopredators, but their isotopic niche space deriving nutrients from both pelagic and benthic resources give a much broader range of diet (*Chapter 4*), leading to possible feeding effects such as diffuse predation. Additionally, their common presence around all reefs within the study likely has behavioural implications for lower trophic organisms that have not yet been identified. As such, combined effects of direct predation by grey reef sharks mixed with indirect behavioural effects on lower trophic levels may carry a larger functional influence than other mesopredator species lower in abundance and less widely distributed. In some isolated near-pristine systems, grey reef sharks feed at a higher trophic position compared to more degraded systems due to their high abundance, changing their feeding capability beyond gape limitations due to cooperative hunting of high-level mesopredators such as gropers (Mourier et al. 2016). Adaptive feeding also relates to food availability in this area where spawning aggregations subsidise local food webs, creating higher carrying capacity of predators compared to places such as the Great Barrier Reef where large spawning aggregations are rare. These spatial differences must be considered in describing species function in future studies. Species function should also be investigated in areas that are underrepresented by research such as Indonesia, where reef sharks are targeted and are heavily depleted (Momigliano 2016; Jaiteh 2017). Gaining insights into how reefs are affected in these areas from their loss compared to stable and pristine populations would help to understand functional influence of reef shark species. However, despite extensive research on the trophic ecology of reef sharks, it is incredibly difficult to link singular effects of whether loss of predatory species or human pressures has greater impact on the health of reef systems as seen in Caribbean reefs (Ward-Paige et al. 2010) and reefs outside the GBR in Australia (Ruppert et al. 2013).

7.6 Future Directions

While there are still areas of uncertainty, findings from this thesis have highlighted questions that require more information to resolve. One of which is whether roving or transient apex predators or species with low abundance on the central GBR have the same functional influence as resident and highly abundant mesopredators. For example, bull sharks are migratory and less resident than mesopredatory reef sharks (Espinoza et al. 2015). While they have been found to return to tagging reefs using acoustic telemetry, their movement networks are more complex than species such as grey reef sharks. Bull sharks were found to spend less than 20% of their time in habitats within the monitoring array and reported in low numbers for this thesis in certain locations (*Chapter 6*). Hence, for specific reefs within the GBR, are bull sharks resident enough to regulate abundance of lower trophic levels and are landscapes of fear from larger predators occurring? Existing suggestions of size-based functional classification (Heupel et al. 2014) may also need to look at how abundance and presence of species over time impacts these views. Conversely, the most abundant sharks on the sampled reefs were grey reefs that were also highly site attached. This raises questions as to whether their ability to limit release of lower trophic levels is more influential than transient predators, where exploitation or mortality could have a larger impact on cascading effects on reef ecosystems. However, as apex predators such as bull sharks are highly mobile with higher energetic needs their influence on grey reef sharks and other mesopredators is not well known. Isolated cases of predation observations with hammerhead sharks feeding on reef sharks (Mourier et al. 2013) are rare and more information is needed in this area. Previous studies have been clear in the fact that functional redundancy of mesopredators with teleost fish possibly limits cascading effects when shark exploitation occurs (Frisch et al. 2016; Roff et al. 2016a; Casey et al. 2017), but often do not consider that loss of both mesopredator and apex sharks could create large areas where specialist roles are not filled and provide opportunities for release of faster growing mesopredators. Cryptic organisms on reefs are also understudied (Heupel et al. 2019), and their functional importance to limit cascading effects and trophodynamics (*Chapter 2*) should also be considered in the future.

Additionally, care should be used when classifying sharks as mesopredators when considering trophic cascade models and mesopredator release. Reef sharks have slower growth rates (Chin et al. 2013) and lower fecundity (Hisano et al. 2011) than some larger bodied predators such as tiger sharks (Meyer et al. 2014). In cases where there is suggested mesopredator release, loss of apex predators such as tiger, bull, and hammerhead sharks are not sufficient to cause rapid growth of reef shark populations based on life history traits. Hence, population and biomass increases at the mesopredator level from cascading effects and lower-level prey suppression cannot be attributed specifically to reef sharks and other slow-growing elasmobranchs. This is a factor that has been ignored relative to cascading effects suggested to be caused between other elasmobranchs (Grubbs et al. 2016). There is also potential that loss of larger sharks (or transience) may in fact allow reef sharks to adaptively fill an apex role with lower risk of predation by larger shark species.

While this thesis addresses some gaps in the literature, there are many areas to direct future research which can further inform functional roles of reef sharks. These are based mainly on interactions among predators and between predator and prey. These interactions are difficult to observe *in situ,* but this information would help to understand behavioural effects predators may have on their prey. With new technologies, possibilities are arising to include non-consumptive effects such as landscapes of fear outside of experimental stages and may be beneficial to include in future food web and ecosystem models (Lester et al. 2020; Mitchell and Harborne 2020). Further analysis of the BRUVS data collected (*Chapter 6*) in this thesis may give insights into this area (Bierwagen, unpublished observations). However, baited influence can alter true natural behaviours and needs to be considered in the interpretation of these types of observations. Behavioural interactions have also helped to clarify instances where morphological traits such as gape size were assumed to limit capacity of reef sharks to consume large bodied mesopredators such as grouper (Mourier et al. 2016). New techniques in analysis of animal monitoring such as network analysis and individual based models will also help to reveal individual and species-level distinctions in behaviour around reefs. These analysis techniques have benefited the understanding of potential consequences of exploitation and social networks in areas such as French Polynesia (Mourier et al. 2017) and spatial separation of species in Palmyra (Papastamatiou et al. 2018) and the Great Barrier Reef (Heupel et al. 2018).

Use of new techniques can also expand our understanding of the ecology of reef sharks (Carrier et al. 2018; Heupel et al. 2019). Methods such as analysis of stomach contents through DNA metabarcoding combined with fatty acid or compound specific stable isotope analysis will provide a better picture of dietary preferences between and among reef-dwelling species. DNA barcoding has been used in other mesopredator species such as coral trout, giving much greater detail on diet composition (Matley et al. 2018). Application of this methodology would greatly improve our understanding of food web linkages as well as potential spatial differences in diet based on prey availability. One other area that is understudied is nocturnal behaviour and activities of reef-dwelling species. Nocturnal observations of reef sharks have provided new information on how reef sharks feed both mechanistically and opportunistically (Mourier et al. 2016). Future efforts in researching diet and behaviour of reef sharks should consider including nocturnal data in their framework.

7.7 Concluding Statement

Overall this thesis provides evidence of both trophic and spatial separation of reef shark species with varying degrees of abundance across reefs in the central GBR. This provides new insights into how reef sharks use resources from a fine-scale perspective, indicating areas of more specialisation than previously considered. The range of variability found in many aspects of this thesis for reef communities and associated shark species should be considered in the future as they may have implications for management. Additionally, employing multi-method approaches as described in this thesis will be beneficial in the future to understand how to best manage resilience of species and systems considering the compounding effects of negative climate impacts in the future. Finally, this thesis provides some positive conclusions that reefs under current pressure remain resilient, and abundance of some reef shark species are not declining at rates previously reported for the central GBR. However, future threats should be examined with caution as reef sharks are in decline in many regions across the world.

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Appendices – Supplementary Materials

Chapter 2

Table S2-a: *Table of search keywords and resulting numbers of publications from a search within: "tropical"*

Search Engine	Search Terms	**Publications
Google Scholar	trophic + coral reef + tropical	19600
	trophic forcing or trophic control + coral reef	5
	trophic role or trophic position + coral reef	98
	trophic dynamic or trophodynamic + coral reef	28
Web of Science	trophic + coral reef + tropical	97
	trophic forcing or trophic control + coral reef	10
	trophic role or trophic position + coral reef	685
	trophic dynamic or trophodynamic + coral reef	88
Scopus	trophic + coral reef + tropical	7409
	trophic forcing or trophic control + coral reef	216
	trophic role or trophic position + coral reef	784
	trophic dynamic or trophodynamic + coral reef	250

**Initial searches took place October 6, 2015 and were re-performed on February 15, 2016 to include recent publications

Table S2-b: *Number of publications (N=291) by year of top keywords returned from "food web" and "trophic" searches relative to coral reefs from 2011-2016*

Keyword	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**
Fish	22	19	24	22	34	34
Habitat	12	10	16	17	15	23
Herbivore	4	11	5	8	9	15
Predator/s	8	3	9	13	29	24
Caribbean	4	3	3	7	11	8
Trophic Structure	4	6	3	10	1	10
Community Structure	4	6	5	5	8	3
Pomacentridae	3	5	4	1	6	6
Trophic Cascade	3	3	0	1	3	9
Trophic Interaction	2	3	6	3	4	0
Great Barrier Reef	1	2	2	4	3	4
Sponge	1	1	1	0	6	2
Habitat Use	0	1	2	2	2	1
Red Sea	0	0	1	2	3	2

Chapter 3

Table S3-a: *Fish taxa listed by genus/species, family, and trophic group used in analysis.*

Species	Family	Trophic Group
Acanthurus albipectoralis	Acanthuridae	Planktivore
Acanturhus auranticavus	Acanthuridae	Grazer
Acanthurus blochii	Acanthuridae	Grazer
Acanthurus dussumeri	Acanthuridae	Grazer
Acanthurus grammoptilus	Acanthuridae	Grazer
Acanthurus lineatus	Acanthuridae	Grazer
Acanthurus mata	Acanthuridae	Planktivore
Acanthurus nigricans	Acanthuridae	Grazer
Acanthurus nigriofuscus	Acanthuridae	Grazer
Acanthurus nigricauda	Acanthuridae	Grazer
Acanthurus olivaceus	Acanthuridae	Detritivore
Acanthurus pyroferus	Acanthuridae	Grazer
Acanthurus thompsoni	Acanthuridae	Planktivore
Acanthurus triostegus	Acanthuridae	Grazer
Acanthrus xanthopterus	Acanthuridae	Grazer
Acanthrochromis polyacanthus	Pomacentridae	Omnivorous Pomacentridae
Amblyglyphidodon aureus	Pomacentridae	Planktivore
Amblyglyphidodon curacao	Pomacentridae	Omnivorous Pomacentridae
Amblygliphidodon leucogaster	Pomacentridae	Omnivorous Pomacentridae
Amphiprion akindynos	Pomacentridae	Omnivorous Pomacentridae
Amphiprion chrysopterus	Pomacentridae	Omnivorous Pomacentridae
Amphiprion clarkii	Pomacentridae	Omnivorous Pomacentridae
Amphiprion melanopus	Pomacentridae	Omnivorous Pomacentridae
Amphiprion percula	Pomacentridae	Omnivorous Pomacentridae
Amphiprion perideraion	Pomacentridae	Omnivorous Pomacentridae
Anyperodon leucogrammicus	Serranidae	Piscivore
Bolbometapon muricatum	Scaridae	Excavator/Scraper
Calotomus carolinus	Scaridae	Browser
Cephalopholis argus	Serranidae	Pisci-invertivore
Cephalopholus boenak	Serranidae	Pisci-invertivore
Cephalopholus cyanostigma	Serranidae	Pisci-invertivore
Cephalopholus microprion	Serranidae	Pisci-invertivore
Cephalopholus miniata	Serranidae	Pisci-invertivore
Cephalopholus urodeta	Serranidae	Pisci-invertivore
Cetoscarus bicolor	Scaridae	Excavator/Scraper
Chaetodon aureofasciatus	Chaetodontidae	Corallivore
Chaetodon auriga	Chaetodontidae	Micro-invertivore
Chaetodon baronessa	Chaetodontidae	Corallivore
Chaetodon bennetti	Chaetodontidae	Corallivore
Chaetodon citrinellus	Chaetodontidae	Micro-invertivore
Chaetodon ephippium	Chaetodontidae	Micro-invertivore
Chaetodon falcula	Chaetodontidae	Micro-invertivore
Chaetodon kleinii	Chaetodontidae	Micro-invertivore
Chaetodon lineolatus	Chaetodontidae	Micro-invertivore
Chaetodon lunula	Chaetodontidae	Micro-invertivore
Chaetodon melannotus	Chaetodontidae	Corallivore
Chaetodon mertensii	Chaetodontidae	Micro-invertivore
Chaetodon meyeri	Chaetodontidae	Corallivore
Chaetodon ornatissimus	Chaetodontidae	Corallivore
Chaetodon pelewensis	Chaetodontidae	Micro-invertivore
Chaetodon plebeius	Chaetodontidae	Corallivore
Chaetodon puncatofasciatus	Chaetodontidae	Micro-invertivore
Chaetodon rafflesii	Chaetodontidae	Micro-invertivore
Chaetodon rainfordi	Chaetodontidae	Corallivore
Chaetodon reticulatus	Chaetodontidae	Corallivore
Chaetodon speculum	Chaetodontidae	Micro-invertivore
Chaetodon trifascialis	Chaetodontidae	Corallivore
Chaetodon trifasciatus	Chaetodontidae	Corallivore

Chaetodon ulitensis	Chaetodontidae	Micro-invertivore	*Coris gaimard*	Labridae	Micro-invertivore
Chaetodon unimaculatus	Chaetodontidae	Corallivore	*Cromileptes altivelis*	Serranidae	Piscivore
Chaetodon vagabundus	Chaetodontidae	Micro-invertivore	*Ctenochaetus spp*	Acanthuridae	Detritivore
Chelinus fasciatus	Labridae	Macro-invertivore	*Dascyllus aruanus*	Pomacentridae	Planktivore
Chelinus undulatus	Labridae	Macro-invertivore	*Dascyllus melanurus*	Pomacentridae	Planktivore
Chelmon rostratus	Chaetodontidae	Micro-invertivore	*Dascyllus reticulatus*	Pomacentridae	Planktivore
Choerodon fasciatus	Labridae	Micro-invertivore	*Dascyllus trimaculatus*	Pomacentridae	Planktivore
Chromis agilis	Pomacentridae	Planktivore	*Dischistodus melanotus*	Pomacentridae	Detritivore
Chromis amboinensis	Pomacentridae	Planktivore	*Dischistodus perspicillatus*	Pomacentridae	Detritivore

Species	**Family**	**Trophic Group**	**Species**	**Family**	**Trophic Group**
Chromis atripectoralis	Pomacentridae	Planktivore	*Dischistodus prosopotaeinia*	Pomacentridae	Detritivore
Chromis chrysura	Pomacentridae	Planktivore	*Dischistodus pseudochrysopoecilus*	Pomacentridae	Detritivore
Chromis iomelas	Pomacentridae	Planktivore	*Epibulus insidiator*	Labridae	Pisci-invertivore
Chromis lepidolepis	Pomacentridae	Planktivore	*Epinephelus coioides*	Serranidae	Piscivore
Chromis lineata	Pomacentridae	Planktivore	*Epinephelus cyanopodus*	Serranidae	Piscivore
Chromis margaritifer	Pomacentridae	Planktivore	*Epinephelus fasciatus*	Serranidae	Piscivore
Chromis nitida	Pomacentridae	Planktivore	*Epinephelus fuscoguttatus*	Serranidae	Piscivore
Chromis retrofasciata	Pomacentridae	Planktivore	*Epinephelus lanceolatus*	Serranidae	Piscivore
Chromis ternatensis	Pomacentridae	Planktivore	*Epinephelus macrospilos*	Serranidae	Piscivore
Chromis vanderbilti	Pomacentridae	Planktivore	*Epinephelus merra*	Serranidae	Piscivore
Chromis weberi	Pomacentridae	Planktivore	*Epinephelus ongus*	Serranidae	Piscivore
Chromis xanthura	Pomacentridae	Planktivore	*Epinephelus quoyanus*	Serranidae	Piscivore
Chlorurus bleekeri	Scaridae	Excavator/Scraper	*Epinephelus spilotoceps*	Serranidae	Piscivore
Chlorurus frontalis	Scaridae	Excavator/Scraper	*Epinephelus tauvina*	Serranidae	Piscivore
Chlorurus japanensis	Scaridae	Excavator/Scraper	*Epinephelus undulosus*	Serranidae	Piscivore
Chlorurus microrhinos	Scaridae	Excavator/Scraper	*Forcipiger flavissimus*	Chaetodontidae	Micro-invertivore
Chlorurus sordidus	Scaridae	Excavator/Scraper	*Forcipiger longirostrus*	Chaetodontidae	Micro-invertivore
Chrysiptera flavipinnis	Pomacentridae	Planktivore	*Gnathodon aureolineatus*	Lethrinidae	Pisci-invertivore
Chrysiptera rex	Pomacentridae	Omnivorous Pomacentridae	*Gomphosus varius*	Labridae	Micro-invertivore
Chrysiptera rollandi	Pomacentridae	Micro-invertivore	*Halichoeres hortulanus*	Labridae	Micro-invertivore
Chrysiptera talboti	Pomacentridae	Planktivore	*Hemigymnus fasciatus*	Labridae	Macro-invertivore
Hemigymnus melapturus	Labridae	Macro-invertivore	*Lutjanus vitta*	Lutjanidae	Pisci-invertivore
Hemiglyphidodon plagiometopon	Pomacentridae	Grazer	*Macolor spp*	Lutjanidae	Pisci-invertivore
Hipposcarus longiceps	Scaridae	Excavator/Scraper	*Monotaxis grandoculus*	Lethrinidae	Macro-invertivore

Hemitaurichthys polyepis	Chaetodontidae	Planktivore	*Naso lituratus*	Acanthuridae	Broswer
Lethrinus atkinsoni	Lethrinidae	Pisci-invertivore	*Naso tuberosus*	Acanthuridae	Planktivore
Lethrinus erythropterus	Lethrinidae	Pisci-invertivore	*Naso unicornis*	Acanthuridae	Browser
Lethrinus erythracanthus	Lethrinidae	Pisci-invertivore	*Neoglyphidodon melas*	Pomacentridae	Micro-invertivore
Lethrinus harak	Lethrinidae	Pisci-invertivore	*Neoglyphidodon nigroris*	Pomacentridae	Planktivore
Lethrinus miniatus	Lethrinidae	Pisci-invertivore	*Neoglyphidodon polyacanthus*	Pomacentridae	Planktivore
Lethrinus nebulosus	Lethrinidae	Pisci-invertivore	*Neopomacentrus azysron*	Pomacentridae	Planktivore
Lethrinus obsoletus	Lethrinidae	Pisci-invertivore	*Neopomacentrus bankieri*	Pomacentridae	Planktivore
Lethrinus olivaceus	Lethrinidae	Pisci-invertivore	*Neopomacentrus cyanomos*	Pomacentridae	Planktivore
Lethrinus ornatus	Lethrinidae	Pisci-invertivore	*Pomacrhomis richardsoni*	Pomacentridae	Planktivore
Lethrinus rubrioperculatus	Lethrinidae	Pisci-invertivore	*Paracanthurus hepatus*	Acanthuridae	Planktivore
Lethrinus xanthochilus	Lethrinidae	Pisci-invertivore	*Plectroglyphidodon dickii*	Pomacentridae	Micro-invertivore
Lutjanus adetti	Lutjanidae	Pisci-invertivore	*Plectroglyphidodon jonstonianus*	Pomacentridae	Corallivore
Lutjanus argentimaculatus	Lutjanidae	Pisci-invertivore	*Plectroglyphidodon lacrymatus*	Pomacentridae	Grazer
Lutjanus bohar	Lutjanidae	Piscivore	*Plectropomus areolatus*	Serranidae	Piscivore

Species	**Family**	**Trophic Group**	**Species**	**Family**	**Trophic Group**
Lutjanus carponotatus	Lutjanidae	Pisci-invertivore	*Siganus doliatus*	Siganidae	Grazer
Lutjanus fulviflamma	Lutjanidae	Pisci-invertivore	*Siganus lineatus*	Siganidae	Grazer
Lutjanus fulvus	Lutjanidae	Pisci-invertivore	*Plectropomus laevis*	Serranidae	Piscivore
Lutjanus gibbus	Lutjanidae	Pisci-invertivore	*Siganus punctatissimus*	Siganidae	Grazer
Lutjanus kasmira	Lutjanidae	Pisci-invertivore	*Siganus punctatus*	Siganidae	Grazer
Lutjanus	Lutjanidae	Pisci-invertivore	*Siganus puellus*	Siganidae	Grazer
Lutjanus lutjanus	Lutjanidae	Pisci-invertivore	*Siganus vulpinus*	Siganidae	Grazer
Lutjanus monostigma	Lutjanidae	Pisci-invertivore	*Stegastes apicales*	Pomacentridae	Grazer
Lutjanus quinquelineatus	Lutjanidae	Pisci-invertivore	*Plectropomus maculatus*	Serranidae	Piscivore
Lutjanus rivulatus	Lutjanidae	Pisci-invertivore	*Pomacentrus adelus*	Pomacentridae	Grazer
Lutjanus russeli	Lutjanidae	Pisci-invertivore	*Pomacentrus amboinensis*	Pomacentridae	Omnivorous Pomacentridae
Lutjanus sebae	Lutjanidae	Pisci-invertivore	*Pomacentrus australis*	Pomacentridae	Omnivorous Pomacentridae
Pomacentrus moluccensis	Pomacentridae	Omnivorous Pomacentridae	*Pomacentrus bankieri*	Pomacentridae	Grazer
Pomacentrus nagasakiensis	Pomacentridae	Omnivorous Pomacentridae	*Pomacentrus brachialis*	Pomacentridae	Omnivorous Pomacentridae
Pomacentus philippinus	Pomacentridae	Planktivore	*Pomacentrus chrysura*	Pomacentridae	Grazer
Pomacentrus vaiuli	Pomacentridae	Grazer	*Pomacentrus coelestis*	Pomacentridae	Planktivore

Pomacentrus wardi	Pomacentridae	Grazer
Premnas biaculeatus	Pomacentridae	Omnivorous Pomacentridae
Scarus altipinnis	Scaridae	Excavator/Scraper
Scarus chameleon	Scaridae	Excavator/Scraper
Scarus dimidiatus	Scaridae	Excavator/Scraper
Scarus flavipectoralis	Scaridae	Excavator/Scraper
Scarus forsteni	Scaridae	Excavator/Scraper
Scarus frenatus	Scaridae	Excavator/Scraper
Scarus ghobban	Scaridae	Excavator/Scraper
Scarus globiceps	Scaridae	Excavator/Scraper
Scarus longipinnis	Scaridae	Excavator/Scraper
Scarus niger	Scaridae	Excavator/Scraper
Scarus oviceps	Scaridae	Excavator/Scraper
Scarus psittacus	Scaridae	Excavator/Scraper
Scarus rivulatus	Scaridae	Excavator/Scraper
Scarus rubrioviolaceus	Scaridae	Excavator/Scraper
Scarus schlegeli	Scaridae	Excavator/Scraper
Scarus spinus	Scaridae	Excavator/Scraper
Siganus argenteus	Siganidae	Grazer
Siganus corallinus	Siganidae	Grazer
Pomacentrus grammnorhyncus	Pomacentridae	Grazer
Pomacentrus lepidogenys	Pomacentridae	Planktivore
Stegastes fasciolatus	Pomacentridae	Grazer
Stegastes gascoynei	Pomacentridae	Grazer
Stegastes nigricans	Pomacentridae	Grazer
Variola louti	Serranidae	Piscivore
Zanclus cornutus	Acanthuridae	Micro-invertivore
Zebrasoma scopus	Acanthuridae	Grazer
Zebrasoma veliferum	Zanclidae	Grazer

Table S3-b: *Benthic Stepwise ordination model with pseudo-AIC output of constrained capscale ordination methods. Bold model is the best performing model (LTMP.diss~Reef:Year+Site+Corallivore+Land Distance, AIC: 819.97)*

Start: LTMP.diss ~ 1

		Df	AIC	F	Pr(>F)	
+	Reef:Year	23	828.12	11.9157	0.005	**
+	Dist_Land	1	943.51	59.4782	0.005	**
+	Corallivore	1	990.26	8.638	0.005	**
+	Site	2	996.02	2.4077	0.03	*

Step 1: LTMP.diss ~ Reef:Year

		Df	AIC	F	Pr(>F)	
-	Reef:Year	23	996.84	11.916	0.005	**
		Df	AIC	F	Pr(>F)	
+	Site	2	823.31	4.1355	0.005	**
+	Dist_Land	1	825.88	3.969	0.01	**
+	Corallivore	1	826.3	3.5674	0.015	*

Step 2: LTMP.diss ~ Site + Reef:Year

		Df	AIC	F	Pr(>F)	
-	Site	2	828.12	4.1355	0.01	**
-	Reef:Year	23	996.02	12.1381	0.005	**
		Df	AIC	F	Pr(>F)	
+	Corallivore	1	821.17	3.8533	0.015	*
+	Dist_Land	1	822.42	2.6856	0.07	.

Step 3: LTMP.diss ~ Site + Corallivore + Reef:Year

		Df	AIC	F	Pr(>F)	
-	Corallivore	1	823.31	3.8533	0.03	*
-	Site	2	826.3	4.2788	0.01	**
-	Reef:Year	23	989.43	11.7758	0.005	**
		Df	AIC	F	Pr(>F)	
+	**Dist_Land**	**1**	**819.97**	**2.9642**	**0.04**	*

Step 4: LTMP.diss ~ Site + Corallivore + Dist_Land + Reef:Year

		Df	AIC	F	Pr(>F)	
-	Dist_Land	1	821.17	2.9642	0.055	.
-	Corallivore	1	822.42	4.1294	0.02	*
-	Site	2	823.68	3.5962	0.005	**
-	Reef:Year	23	936.32	8.2258	0.005	**

Table S3-c: *Fish Stepwise ordination model with AIC output of constrained capscale ordination method. Bold model is the best performing model (LTMP.diss~Reef:Year+Acropora+Non-Acropora+Land Distance, AIC 680.84)*

Start: LTMP.diss ~ 1						
		Df	AIC	F	Pr(>F)	
+	Reef:Year	23	689.28	5.2842	0.005	**
+	Dist_Land	1	722.16	35.749	0.005	**
+	Zone	1	743.47	13.1194	0.005	**
+	Acropora	1	750.09	6.3566	0.005	**
+	Non_Acropora	1	750.28	6.1662	0.005	**
+	Turf_Algae	1	751.29	5.1419	0.005	**
+	Soft_Coral	1	753.07	3.3517	0.005	**
+	Site	2	754.29	2.0623	0.025	*
+	Macroalgae	1	755.37	1.0486	0.46	

Step 1: LTMP.diss ~ Reef:Year						
		Df	AIC	F	Pr(>F)	
-	Reef:Year	23	754.43	5.2842	0.005	**
		Df	AIC	F	Pr(>F)	
+	Non_Acropora	1	683.8	7.0325	0.005	**
+	Site	2	687.63	2.6384	0.005	**
+	Dist_Land	1	687.47	3.5615	0.015	*
+	Acropora	1	689.15	1.9858	0.12	
+	Soft_Coral	1	689.66	1.5069	0.18	
+	Turf_Algae	1	689.82	1.3549	0.24	
+	Macroalgae	1	689.92	1.2677	0.31	
+	Zone	0	689.28			

Step 2: LTMP.diss ~ Non_Acropora + Reef:Year						
		Df	AIC	F	Pr(>F)	
-	Non_Acropora	1	689.28	7.0325	0.005	**
-	Reef:Year	23	750.28	5.342	0.005	**
		Df	AIC	F	Pr(>F)	
+	Dist_Land	1	681.13	4.3597	0.005	**
+	Site	2	682.86	2.2989	0.03	*
+	Acropora	1	683.53	2.113	0.06	.
+	Macroalgae	1	684.35	1.3446	0.285	
+	Soft_Coral	1	684.57	1.1357	0.375	
+	Turf_Algae	1	685.29	0.4737	0.76	
+	Zone	0	683.8			

Step 3: LTMP.diss ~ Non_Acropora + Dist_Land + Reef:Year						
		Df	AIC	F	Pr(>F)	
-	Dist_Land	1	683.8	4.3597	0.005	**
-	Non_Acropora	1	687.47	7.8287	0.005	**
-	Reef:Year	23	716.14	3.6647	0.005	**
		Df	AIC	F	Pr(>F)	
+	**Acropora**	**1**	**680.84**	**2.1237**	**0.07**	.
+	Soft_Coral	1	681.64	1.3819	0.26	
+	Site	2	682.37	1.2778	0.28	
+	Macroalgae	1	681.67	1.3468	0.285	
+	Turf_Algae	1	682.63	0.4589	0.81	
+	Zone	0	681.13			

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table S3-d: *Adonis PERMANOVA model output of benthic and fish communities formula: from best performing model produced by the ordination method*

*Benthic: formula: adonis(Benthic Diss~Reef*Year+Site+Land Distance+Corallivore)*

*Fish: adonis(Fish Diss~Reef*Year+Land Distance+Acropora+non-Acropora*)

Benthic Community Dissimilarity

Predictors	**df**	**SumsOfSqs**	**MeanSqs**	**F.Model**	**R2**	**Pr(>F)**	
Reef:Year	23	4.771	0.20743	8.226	0.30009	0.001	***
Land Distance	1	2.2651	2.26506	89.821	0.14247	0.001	***
Site	2	0.2099	0.10493	4.161	0.0132	0.001	***
Corallivore	1	0.2804	0.28036	11.118	0.01763	0.001	***

Fish Community Dissimilarity

Predictors	**df**	**SumsOfSqs**	**MeanSqs**	**F.Model**	**R2**	**Pr(>F)**	
Reef:Year	23	1.4276	0.06207	3.613	0.17608	0.001	***
Acropora	1	0.0814	0.08136	4.736	0.01003	0.001	***
non-*Acropora*	1	0.1427	0.14268	8.306	0.0176	0.001	***
Land Distance	1	0.7361	0.73614	42.854	0.09079	0.001	***

Table S3-e: *Tukey's post-hoc results from generalized linear mixed effect models (Poisson distribution) for overall mean fish density, species richness, and 11 functional groups with a reef conditional on year pairwise comparison. Model structures, estimates, and p-values are listed in the table (p-value significance: 33 *=<0.05, **=<0.01)*

Benthic Cover

Function	**Reef**	**Comparison**	**2006**	**2008**	**2010**	**2012**	**2014**	**2016**
lmer(Acropora~Reef:Year+Land Distance+(1|Reef/Site)								
Acropora	Chicken	Helix	-4.90	1.07	-1.20	10.38	4.65	5.35
		Knife	-9.16	-8.75	-6.82	-0.29	-3.95	-1.18
	-	Rib	9.77	10.12	7.05	13.69	15.61	1.94
	Helix	Knife	-4.25	-9.82	-5.62	-10.67	-8.60	-6.54
		Rib	14.67	9.05	8.25	3.31	10.96	-3.41
	Knife	Rib	18.92	18.87	13.87	13.99	19.57	3.12
lmer(Acropora~Reef:Year+Land Distance+Corallivore+(1|Reef/Site)								
Non-Acropora	Chicken	Helix	-25.56	-25.54	-26.21	-28.23	-31.29	-31.38
		Knife	3.01	5.07	4.20	8.47	7.81	5.52
	-	Rib	-46.12	-47.30	-50.16	-55.08	-56.82	-55.32
	Helix	Knife	28.57	30.61	30.40	36.70	39.10	36.90
		Rib	-20.56	-21.76	-23.95	-26.85	-25.52	-23.94
	Knife	Rib	-49.12	-52.37	-54.35	-63.54	-64.63	-60.84
lmer(Soft Coral~Reef:Year+Land Distance+(1|Reef/Site)								
Soft Coral	Chicken	Helix	46.5	47.3	49.1	40.6	42.3	41.7
		Knife	-9.8	-8.6	-7.5	-13.1	-11.2	-13.9
	-	Rib	77.7	82.2	82.1	74.4	76.9	74.3
	Helix	Knife	-56.2	-55.9	-56.5	-53.6	-53.5	-55.6
		Rib	31.3	34.9	33.0	33.8	34.6	32.6
	Knife	Rib	87.5	90.8	89.5	87.5	88.1	88.2
lmer(Macroalage~Reef:Year+Land Distance+(Year|Reef/Site)								
Macroalgae	Chicken	Helix	2.06	1.11	2.94	0.34	2.11	-2.26
		Knife	0.26	0.25	1.68	0.71	1.75	2.35
	-	Rib	-10.04	-0.37	3.87	-1.33	2.44	2.37
	Helix	Knife	-1.80	-0.86	-1.26	0.37	-0.36	4.61
		Rib	-12.10	-1.48	0.93	-1.67	0.33	4.62
	Knife	Rib	-10.30	-0.62	2.19	-2.04	0.69	0.02

Function	**Reef**	**Comparison**	**2006**	**2008**	**2010**	**2012**	**2014**	**2016**
lmer(Coralline~Reef:Year+Land Distance+Corallivore+(Year|Reef/Site)								
Coralline Algae	Chicken	Helix	-63.47	-54.31	-49.76	-48.56	-41.23	-48.70
		Knife	19.62	21.28	23.13	23.48	26.47	20.50
	-	Rib	-115.02	-108.85	-101.31	-99.90	-91.31	-96.70
	Helix	Knife	83.10	75.59	72.89	72.04	67.69	69.20
		Rib	-51.55	-54.54	-51.55	-51.34	-50.08	-48.00
	Knife	Rib	-134.65	-130.12	-124.44	-123.38	-117.77	-117.20
lmer(Turf Algae~Reef:Year+Land Distance+(Year|Reef/Site)								
Turf Algae	Chicken	Helix	52.66	36.79	32.17	30.25	27.23	38.96
		Knife	-1.22	-9.92	-14.21	-19.90	-19.66	-14.72
	-	Rib	94.25	75.41	68.29	79.32	66.05	87.46
	Helix	Knife	-53.88	-46.72	-46.38	-50.15	-46.88	-53.68
		Rib	41.59	38.61	36.13	49.07	38.82	48.50
	Knife	Rib	95.47	85.33	82.50	99.22	85.70	102.18
lmer(Sponge~Reef:Year+Land Distance+(Year|Reef/Site)								
Sponge	Chicken	Helix	4.30	4.35	4.44	5.14	5.21	5.11
		Knife	-1.94	-1.87	-2.14	-1.50	-1.97	-1.47
	-	Rib	8.19	8.16	8.56	9.39	8.13	7.86
	Helix	Knife	-6.24	-6.22	-6.57	-6.64	-7.17	-6.57
		Rib	3.90	3.81	4.12	4.26	2.92	2.75
	Knife	Rib	10.14	10.03	10.70	10.90	10.10	9.33

Table S3-f: *Tukey's post-hoc results from generalized linear mixed effect models for benthic cover of 6 categories with a reef conditional on year pairwise comparison. Model structures, estimates, and p-values are listed in the table (p-value significance: *=<0.05, **=<0.01)*

						Fish Densities								
Function	**Reef**	**Comparison**	**2006**		**2008**		**2010**		**2012**		**2014**		**2016**	
glmer(Fish Density~Reef:Year+Land Distance+Acropora+Non Acropora+(Year|Reef/Site), family=poisson)														
Overall Mean Fish Density	Chicken	Helix	-1.63		-1.47		-1.45		-1.29		-1.39		-1.03	
		Knife	0.82		0.60		0.58		0.71		1.04		0.89	
		Rib	-3.13		-3.72		-3.42		-2.71		-2.97		-3.24	
	Helix	Knife	2.45		2.07		2.03		2.00		2.43		1.92	
		Rib	-1.50		-2.25		-1.97		-1.41		-1.59		-2.21	
	Knife	Rib	-3.95		-4.32		-3.99		-3.41		-4.02		-4.13	
glmer(Species Richness~Reef:Year+Land Distance+Acropora+Non Acropora+(Year|Reef/Site), family=poisson)														
Species Richness	Chicken	Helix	0.75		0.80		0.73		0.92		1.04		1.15	
		Knife	-0.15		-0.12		-0.14		-0.24		-0.06		-0.12	
		Rib	1.47		1.43		1.52		1.72		1.81		1.62	
	Helix	Knife	-0.90		-0.91		-0.88		-1.16		-1.10		-1.27	
		Rib	0.73		0.63		0.79		0.80		0.76		0.47	
	Knife	Rib	1.63		1.54		1.66		1.95		1.86		1.74	
glmer(Detritivore~Reef:Year+Land Distance+Acropora+Non Acropora+Turf Algae+Macroalgae+(Year|Reef/Site), family=poisson)														
Detritivore	Chicken	Helix	9.27	**	9.51	**	9.95	**	10.39	**	10.42	**	10.46	**
		Knife	-2.70	**	-2.35		-1.91	**	-2.71	**	-2.60	**	-2.01	
		Rib	18.17	**	17.90	**	18.76	**	18.70	**	18.63	**	18.32	**
	Helix	Knife	-11.96	**	-11.86	**	-11.86	**	-13.09	**	-13.01	**	-12.47	**
		Rib	8.90	**	8.39	**	8.81	**	8.31	**	8.21	**	7.86	**
	Knife	Rib	20.87	**	20.25	**	20.67	**	21.41	**	21.22	**	20.33	**
glmer(Planktivore~Reef:Year+Land Distance+Acropora+Non Acropora+(Year|Reef/Site), family=poisson)														
Planktivore	Chicken	Helix	-3.38	*	-3.83	**	-3.93	**	-4.25	**	-4.26	**	-3.60	**
		Knife	2.09	**	1.69	**	1.70	**	1.28		2.28	**	1.84	**
		Rib	-8.25	**	-9.19	**	-8.82	**	-8.30	**	-8.35	**	-8.35	**
	Helix	Knife	5.47	**	5.52	**	5.63	**	5.53	**	6.54	**	6.54	**
		Rib	-4.87	**	-5.37	**	-4.89	**	-4.06	**	-4.09	**	-4.09	**
	Knife	Rib	-10.34	**	-10.88	**	-10.53	**	-9.58	**	-10.63	**	-10.63	**
glmer(Grazer~Reef:Year+Land Distance+Acropora+Non Acropora+Turf Algae+Macroalgae+(Year|Reef/Site), family=poisson)														
Grazer	Chicken	Helix	-0.29		-0.44		-0.08		-0.02		-0.28		-0.39	
		Knife	0.20		-0.23		0.06		0.30		0.28		0.33	
		Rib	-0.78		-0.79		-0.51		-0.07		-0.31		-0.35	
	Helix	Knife	0.49		0.21		0.14		0.32		0.56		0.72	
		Rib	-0.49		-0.35		-0.43		-0.05		-0.03		0.05	
	Knife	Rib	-0.97		-0.56		-0.57		-0.37		-0.59		-0.68	
glmer(Omniv Pom~Reef:Year+Land Distance+Acropora+Non Acropora+(Year|Reef/Site), family=poisson)														
Omnivorous Pomacentrid	Chicken	Helix	2.36		2.84		3.06		3.91		4.76		3.87	
		Knife	0.01		-0.92		0.05		-0.55		-0.81		-0.69	
		Rib	5.37		5.46		5.64		6.84		7.04		5.59	**
	Helix	Knife	-2.35		-3.76		-3.01		-4.46		-5.57		-4.57	
		Rib	3.01		2.61		2.59		2.93		2.28		1.72	**
	Knife	Rib	5.36		6.38		5.59		7.39		7.85		6.29	**
glmer(Piscivore~Reef:Year+Land Distance+Acropora+Non Acropora+(Year|Reef/Site), family=poisson)														
Piscivore	Chicken	Helix	-4.5		-3.3		-4.0		-4.4		-4.9		13.9	
		Knife	1.4		1.2		1.7		2.1		1.9		1.9	
		Rib	-8.8		-9.2		-8.1		-9.0		-8.2		-8.3	
	Helix	Knife	5.8		4.5		5.8		6.5		6.9		-12.1	
		Rib	-4.4		-5.9		-4.1		-4.6		-3.3		-22.3	
	Knife	Rib	-10.2		-10.4		-9.9		-11.1		-10.1		-10.2	
glmer(Excavator/Scraper~Reef:Year+Land Distance+Turf Algae+Macroalgae+(Year|Reef/Site), family=poisson)														
	Chicken	Helix	-6.67	**	-6.81	**	-7.21	**	-6.28	**	-6.30	**	-6.55	**

Excavator/Scraper		Knife	2.19	**	2.44	**	2.28	**	2.89	**	2.84	**	2.35	**
		Rib	-13.28	**	-13.41	**	-13.48	**	-12.20	**	-12.81	**	-12.89	**
	Helix	Knife	8.86	**	9.25	**	9.49	**	9.17	**	9.14	**	8.90	**
		Rib	-6.61	**	-6.61	**	-6.27	**	-5.92	**	-6.50	**	-6.33	**
	Knife	Rib	-15.47	**	-15.86	**	-15.76	**	-15.09	**	-15.64	**	-15.23	**

Function	**Reef**	**Comparison**	**2006**		**2008**		**2010**		**2012**		**2014**		**2016**	
glmer(Browser~Reef:Year+(Year|Reef/Site), family=poisson)														
Browser	Chicken	Helix	0.29		-0.61		-0.26		1.17		-0.68		17.78	
		Knife	0.39		-0.42		0.49		1.86		-0.36		1.72	*
		Rib	0.68		-0.52		0.03		0.25		-0.85		0.71	
	Helix	Knife	0.10		0.20		0.75		0.69		0.32		-16.05	
		Rib	0.40		0.09		0.29		-0.92		-0.17		-17.06	
	Knife	Rib	0.30		-0.10		-0.46		-1.61		-0.49		-1.01	
glmer(Pisc Invert~Reef:Year+Land Distance+Acropora+Non Acropora+(Year|Reef/Site), family=poisson)														
Piscivorous Invertivore	Chicken	Helix	-1.40		-2.36		-1.43		-2.02		-0.59		0.59	
		Knife	0.90		-0.08		1.17		0.27		2.31		0.43	
		Rib	-3.45		-4.04		-3.14		-3.87		-2.46		-3.18	
	Helix	Knife	2.30		2.28		2.60		2.29		2.90		-0.17	
		Rib	-2.06		-1.68		-1.71		-1.84		-1.86		-3.77	
	Knife	Rib	-4.36		-3.96		-4.31		-4.14		-4.77		-3.60	
glmer(Corallivore~Reef:Year+Land Distance+Acropora+Non Acropora+(Year|Reef/Site), family=poisson)														
Corallivore	Chicken	Helix	6.64		7.24		7.04		7.40		7.67		8.22	*
		Knife	-3.06	*	-2.25		-2.88	*	-3.27	*	-2.86	*	-2.35	
		Rib	14.08		14.41		14.17		14.09		14.05		13.70	
	Helix	Knife	-9.69		-9.49		-9.92		-10.67	*	-10.53	*	-10.57	*
		Rib	7.45	*	7.17	*	7.13	*	6.68		6.37		5.49	
	Knife	Rib	17.14	*	16.66		17.05	*	17.36	*	16.91	*	16.06	
glmer(Micro-invert~Reef:Year+Land Distance+Acropora+Non Acropora+(Year|Reef/Site), family=poisson)														
Micro-invertivore	Chicken	Helix	-2.43		-2.08		-2.24		-1.74		-2.09		-1.91	
		Knife	0.46		0.75		0.76		0.54		0.73		1.14	
		Rib	-3.84		-4.19		-4.36		-3.94		-4.27		-4.57	
	Helix	Knife	2.89		2.83		2.99		2.28		2.82		3.05	
		Rib	-1.41		-2.11		-2.12		-2.21		-2.18		-2.66	
	Knife	Rib	-4.30		-4.94		-5.12		-4.48		-5.00		-5.71	
glmer(Macro-invert~Reef:Year+Land Distance+Acropora+Non Acropora+(Year|Reef/Site), family=poisson)														
Macro-invertivore	Chicken	Helix	1.60		1.55		1.34		0.23		1.36		1.10	
		Knife	0.03		0.08		-0.12		-1.61		-0.60		-1.62	
		Rib	3.13		2.71		2.66		1.79		3.22		2.32	
	Helix	Knife	-1.58		-1.47		-1.46		-1.84		-1.96		-2.72	
		Rib	1.53		1.16		1.32		1.56		1.86		1.22	
	Knife	Rib	3.10		2.63		2.78		3.40		3.82		3.94	

Table S3-g: *Tukey's post-hoc results from generalized linear mixed effect models generalized linear mixed effect models (Poisson distribution) overall mean fish density, species richness, and 11 functional groups with a reef conditional on disturbance comparison. (Pre: years <2011, post years>2011) Model structures, estimates, and p-values are listed in the table (p-value significance: *=<0.05, **=<0.01)*

Benthic Disturbance							
Function	Reef	Pre/Post		Function	Reef	Pre/Post	
lmer(Acropora~Reef:Year+Land Dist+(1|Reef/Site)				lmer(Coralline~Reef:Year+Land Distance+(1|Reef/Site)			
Acropora	Chicken	1.55		**Coralline Algae**	Chicken	11.96	**
	Helix	-6.92	**		Helix	2.11	
	Knife	-4.88	**		Knife	9.78	**
	Rib	0.11			Rib	-0.42	
lmer(Non_Acropora~Reef:Year+Land Distance+(1|Reef/Site)				lmer(Turf Algae~Reef:Year+Land Distance+(Year|Reef/Site)			
Non-Acropora	Chicken	-1.43		**Turf Algae**	Chicken	-8.21	
	Helix	2.64	*		Helix	1.12	
	Knife	-4.72	**		Knife	0.66	
	Rib	6.57	**		Rib	-0.14	
lmer(Soft Coral~Reef:Year+Land Distance+(1|Reef/Site)				lmer(Sponge~Reef:Year+Land Distance+(1|Reef/Site)			
Soft Coral	Chicken	-7.68	**	**Sponge**	Chicken	0.22	
	Helix	-1.58	*		Helix	-0.57	
	Knife	-3.56	**		Knife	-0.12	*
	Rib	-2.21	**		Rib	0.06	
lmer(Macroalage~Reef:Year+Land Distance+(Year|Reef/Site)							
Macroalgae	Chicken	2.09					
	Helix	1.17					
	Knife	0.56					
	Rib	-4.63	*				

Table S3-h: *Tukey's post-hoc results from generalized linear mixed effect models for benthic cover of 6 categories with a reef conditional on disturbance comparison. (Pre: years <2011, post years>2011) Model structures, estimates, and p-values are listed in the table (p-value significance: *=<0.05, **=<0.01)*

Function	Reef	Pre/Post	Sig	Function	Reef	Pre/Post	Sig	Function	Reef	Pre/Post	Sig
Mean Fish Density	Chicken	0.37	*	**Omnivorous Pomacentrid**	Chicken	0.88	**	**Corallivore**	Chicken	-0.5	**
	Helix	0.03			Helix	-0.23			Helix	-1.09	**
	Knife	0.22			Knife	0.94	**		Knife	-0.46	**
	Rib	-0.2			Rib	0.05	**		Rib	-0.15	
Species Richness	Chicken	0.54		**Piscivore**	Chicken	0.44	*	**Micro-invertivore**	Chicken	-0.1	
	Helix	-0.28	**		Helix	-0.02			Helix	-0.44	
	Knife	0.01			Knife	-0.13			Knife	-0.16	
	Rib	-0.17			Rib	0.23			Rib	-0.02	
Detritivore	Chicken	0.07		**Excavator Scraper**	Chicken	0.66	*	**Macro-invertivore**	Chicken	-1.12	**
	Helix	-0.54	*		Helix	-0.11			Helix	-0.38	*
	Knife	0.51			Knife	0.17			Knife	0.15	
	Rib	-0.13			Rib	-0.4	*		Rib	-0.66	**
Planktivore	Chicken	0.78	**	**Browser**	Chicken	0.37					
	Helix	0.66	**		Helix	-1.13	*				
	Knife	0.56	**		Knife	-0.79	*				
	Rib	0.08			Rib	0.15					
Grazer	Chicken	-0.1		**Piscivorous Invertivore**	Chicken	0.01					
	Helix	0.05			Helix	-0.65	*				
	Knife	-0.21	*		Knife	-0.36					
	Rib	-0.43			Rib	-0.28					

model structures

<table>
<tr><td>Mean Fish Density</td><td>glmer(AB~Reef*disturb+Dist_Land+Acropora+Non_Acropora+(Year|Reef/Site),data=data.1, family=poisson)</td></tr>
<tr><td>Species Richness</td><td>glmer(SR~Reef*disturb+Dist_Land+Acropora+Non_Acropora+(1|Reef/Site),data=data.1, family=poisson)</td></tr>
<tr><td>Detritivore</td><td>glmer(Detritivore~Reef*disturb+Dist_Land+Acropora+Non_Acropora+Macroalgae+Turf_Algae+(Year|Reef/Site),data=data.1, family=poisson)</td></tr>
<tr><td>Planktivore</td><td>glmer(Planktivore~Reef*disturb+Dist_Land+Acropora+Non_Acropora+(Year|Reef/Site),data=data.1, family=poisson)</td></tr>
<tr><td>Grazer</td><td>glmer(Grazer~Reef*disturb+Dist_Land+Acropora+Non_Acropora+Macroalgae+Turf_Algae+(Year|Reef/Site),data=data.1, family=poisson)</td></tr>
<tr><td>Omnivorous Pomacentrid</td><td>glmer(Omniv_Pom~Reef*disturb+Dist_Land+Acropora+Non_Acropora+(Year|Reef/Site),data=data.1, family=poisson)</td></tr>
<tr><td>Piscivore</td><td>glmer(Piscivore~Reef*disturb+(1|Reef/Site),data=data.1, family=poisson)</td></tr>
<tr><td>Excavator/Scraper</td><td>glmer(Exc_Scraper~Reef*disturb+Dist_Land+Macroalgae+Turf_Algae+(Year|Reef/Site),data=data.1, family=poisson)</td></tr>
<tr><td>Browser</td><td>glmer(Browser~Reef*disturb+(1|Reef/Site)</td></tr>
<tr><td>Pisc-invertivore</td><td>glmer(Pisc_invert~Reef*disturb+Dist_Land+Acropora+(1|Reef/Site),data=data.1, family=poisson)</td></tr>
<tr><td>Corallivore</td><td>glmer(Corallivore~Reef*disturb+Dist_Land+Acropora+Non_Acropora+(Year|Reef/Site),data=data.1, family=poisson)</td></tr>
<tr><td>Micro-invertivore</td><td>glmer(Micro_invert~Reef*disturb+Dist_Land+Acropora+(1|Reef/Site),data=data.1, family=poisson)</td></tr>
<tr><td>Macro-invertivore</td><td>glmer(Macro_invert~Reef*disturb+(1|Reef/Site),data=data.1, family=poisson)</td></tr>
</table>

Table S3-i: *SIMPER (Similarity of Percentages) comparisons by species with greatest contribution to decline or recovery post disturbance per fish functional group by reef*

		Rib			Helix			Knife			Chicken		
Functional Group	**Species**	**Pre**	**Post**	**Contribution (%)**	**Pre**	**Post**	**Contribution (%)**	**Pre**	**Post**	**Contribution (%)**	**Pre**	**Post**	**Contribution (%)**
Detritivore	*Acanthurus olivaceus*	0.02	0.86	14.45	1.49	1.55	21.31				0.00	0.18	1.64
	Ctenochaetus spp.	6.40	5.70	77.08	5.64	3.38	58.51	5.87	6.85	97.75	9.40	9.82	98.36
	Dischistodus melanotus	0.22	0.11	6.59	0.98	0.08	14.59						
	Dischistodus prosopotaenia	0.04	0.00	0.89	0.02	0.03	0.64	0.00	0.03	0.99			
	Dischistodus pseudochrysopocilus	0.02	0.02	0.99	0.22	0.10	4.95	0.03	0.00	1.26			
Piscivore	*Lutjanus bohar*	0.00	0.12	10.32	0.63	0.21	30.34	0.53	0.60	36.37	0.13	0.10	10.13
	Plectropomus laevis	0.06	0.29	34.44	0.13	0.36	20.27	0.12	0.25	14.73	0.42	0.23	27.52
	Plectropomus leopardus	1.06	0.88	55.24	0.88	1.36	49.39	1.35	0.80	48.90	1.21	1.77	59.74
	Variola louti										0.00	0.03	2.61
Omnivorous Pomacentrid	*Acanthachromis polyacanthus*	4.27	6.84	21.59	3.50	3.32	31.46	1.85	4.95	63.27	2.67	5.31	56.75
	Amblygliphidodon curacao	4.89	4.11	21.46	2.39	1.68	21.15	0.21	0.02	4.70			
	Amphiprion akindynos				0.20	0.08	2.25	0.06	0.20	6.33	0.16	0.13	3.81
	Chrysiptera rex				0.05	0.24	4.10	0.21	1.07	19.38	1.21	3.20	38.94
	Pomacentrus amboinensis	0.36	1.16	4.64									
	Pomacentrus brachialis	0.87	1.24	6.49									
	Pomacentrus moluccensis	6.98	11.62	38.28	4.36	3.16	36.69						
Browser	*Calotomus carolinus*	0.00	0.05	4.37							0.11	0.00	6.64
	Naso lituratus	0.27	0.05	29.42	0.05	0.14	22.11	0.13	0.30	37.79	0.22	0.81	38.03
	Naso unicornis	1.33	1.30	66.21	1.43	1.29	77.89	1.33	0.70	62.21	1.17	1.63	55.33
Excavator/Scraper	*Chlorurus microrhinos*				1.91	1.56	8.71	1.00	1.76	9.39	1.33	4.80	13.15
	Chlorurus sordidus	4.47	3.20	10.85	4.02	3.36	13.94	3.07	4.22	16.54	2.80	3.71	10.12
	Scarus frenatus				2.76	2.22	9.36	1.53	1.47	8.12			
	Scarus globiceps				1.93	1.62	8.93	5.07	1.76	14.37	2.53	4.42	13.20
	Scarus niger	3.89	2.84	8.21	5.31	3.78	16.94						
	Scarus psittacus	3.24	2.33	12.23				3.53	1.09	13.30	4.33	5.64	17.78
	Scarus rivulatus	6.62	2.69	17.20									
	Scarus schlegeli	2.64	4.24	12.68							0.67	3.36	9.85
Corallivore	*Chaetodon aureofasciatus*	0.17	0.31	8.83									
	Chaetodon baronessa	0.88	0.43	19.23	1.12	0.81	23.62	1.24	0.37	26.68	0.47	0.27	19.86
	Chaetodon melannotus							0.08	0.30	8.62	0.22	0.04	8.79
	Chaetodon plebeius				0.51	0.23	11.14	0.16	0.44	9.90			
	Chaetodon rainfordi	0.68	1.17	22.92	1.39	0.62	22.88	0.55	0.11	13.64	0.89	0.77	27.89
	Chaetodon trifascialis	0.41	0.17	9.18	0.54	0.04	12.32						
	Chaetodon trifasciatus	0.83	1.20	25.34	1.24	0.81	26.17	0.97	1.37	30.49	0.50	0.62	27.58
	Plectroglyphidodon johnstonianus										0.17	0.08	8.62
Micro-invertivore	*Chaetodon citrinellus*				0.80	0.38	15.32	1.88	1.27	29.71	1.80	1.53	30.04
	Chaetodon citrinellus	0.40	0.36	8.80									
	Chaetodon ulietensis							0.48	0.00	7.38	0.20	0.31	8.12
	Chaetodon vagabundus	0.45	0.48	9.39									
	Choerodon fasciatus				0.16	0.30	7.18	0.07	0.17	4.41	0.24	0.22	7.08
	Chrysiptera rollandi	1.14	1.57	22.91	0.38	0.20	7.64						
	Gomphosus varius	1.02	0.57	14.70	1.22	0.40	19.09	1.26	0.63	19.11	0.82	0.40	15.05
	Halichores hortulanus	0.62	0.69	12.57	1.22	0.90	17.97	1.00	1.46	21.79	0.91	1.18	21.36

	Plectroglyphidodon dickii												
Macro-invertivore	*Hemigymnus fasciatus*	1.14	0.83	47.75	1.21	1.19	50.40	0.83	0.67	42.08	1.18	0.64	49.08
	Hemigymnus melapterus	0.49	0.42	35.19	0.59	0.14	32.07	0.44	0.33	30.61	0.11	0.36	26.53
	Monotaxis grandoculis	0.16	0.17	17.06	0.10	0.29	17.53	0.11	0.44	27.31	0.36	0.18	24.39
Pisci-invertivore	*Epibulus insidiator*	0.90	0.21	31.86	0.52	0.31	27.08	0.23	0.13	26.78			
	Lethrinus erythracanthus										0.00	0.10	5.75
	Lethrinus miniatus	0.05	0.16	7.75	0.29	0.77	34.86	0.00	0.07	6.33	0.53	0.50	25.91
	Lethrinus nebulosus				0.14	0.00	4.33				0.11	1.50	20.03
	Lutjanus carponotatus	0.15	0.21	12.43									
	Lutjanus fulviflamma							0.08	0.00	6.66	0.00	0.30	6.18
	Lutjanus fulviflamma							0.08	0.20	15.18			
	Lutjanus lutjanus	0.35	0.16	11.83									
	Lutjanus russelli				0.24	0.08	8.75						
	Macolor spp	0.00	0.16	7.16	0.19	0.23	14.49	0.62	0.93	45.05	0.58	1.50	32.78
Planktivore	*Chromis atripectoralis*				23.24	0.51	12.09	9.93	0.00	4.34			
	Chromis weberi										2.67	1.93	4.58
	Neoglyphidodon nigroris	4.96	2.33	5.22									
	Neopomacentrus azysron	18.93	38.47	26.24	14.96	25.84	25.46	15.31	9.58	22.09	32.91	45.09	46.76
	Pomacentrus coelestis	3.24	8.18	9.89	4.40	21.07	24.63	0.16	6.82	9.09	0.24	4.16	5.09
	Pomacentrus lepidogenys	53.62	49.58	38.66	15.69	15.24	23.23	33.09	44.09	47.50	27.51	44.62	32.93
	Pomacentrus phillipinus	7.67	6.27	8.48	3.04	3.42	6.95	3.00	3.58	7.87	4.20	3.40	5.92
Grazer	*Acanthurus lineatus*							1.93	2.20	6.92			
	Acanthurus nigrofuscus				1.00	1.96	6.37	7.09	7.53	13.74	7.64	9.16	17.11
	Acanthurus triostegus							3.51	0.00	6.17			
	Plectroglyphidodon lacrymatus	3.71	1.53	15.01	7.31	4.02	17.57	13.13	8.82	23.89	9.02	4.71	15.05
	Pomacentrus bankanensis	1.76	1.96	11.55	6.62	7.24	21.15	14.09	15.04	27.27	0.96	0.47	5.63
	Pomacentrus wardi	10.29	6.62	31.19	3.44	4.62	12.64						
	Siganus corallinus	2.07	0.82	8.78									
	Stegastes apicalis				1.22	1.47	6.65				3.40	2.53	11.36
	Stegastes fasciatus										1.36	1.69	6.01
	Zebrasoma scopus	0.96	0.47	5.63									

Figure S3-a: *Percent benthic cover of Acropora coral sub-species by year (95% CI). Red: Outer-Shelf, Blue: Mid-Shelf, Dashed Line/Open Circles: Open Fishing, Dashed Line/Closed Circles: Closed Fishing, grey mid-line:disturbance event Cyclone YasiEach reef was impacted by severe Cyclone Yasi in 2011. The only reef withan active crown of thorns outbreak (Acanthacaster plancii) during survey years was Helix.*

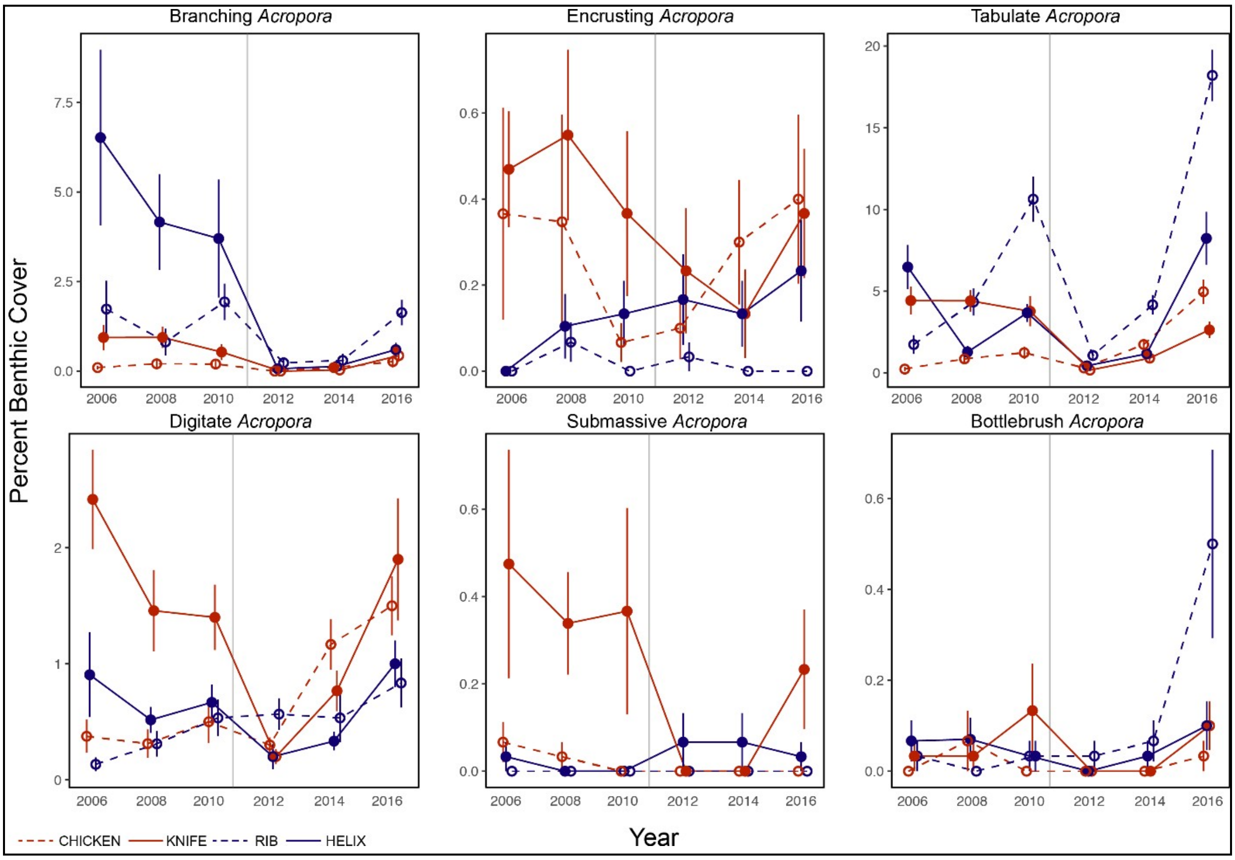


Figure S3-b: *Percent benthic cover of Non-Acropora coral sub-species by year (95% CI). Red: Outer-Shelf, Blue:Mid-Shelf, Dashed Line/Open Circles: Open Fishing, Dashed Line/Closed Circles: Closed Fishing, grey mid-line: disturbance event Cyclone Yasi. Each reef was impacted by severe Cyclone Yasi in 2011. The only reef with an active crown of thorns outbreak (Acanthacaster plancii) during survey years was Helix.*

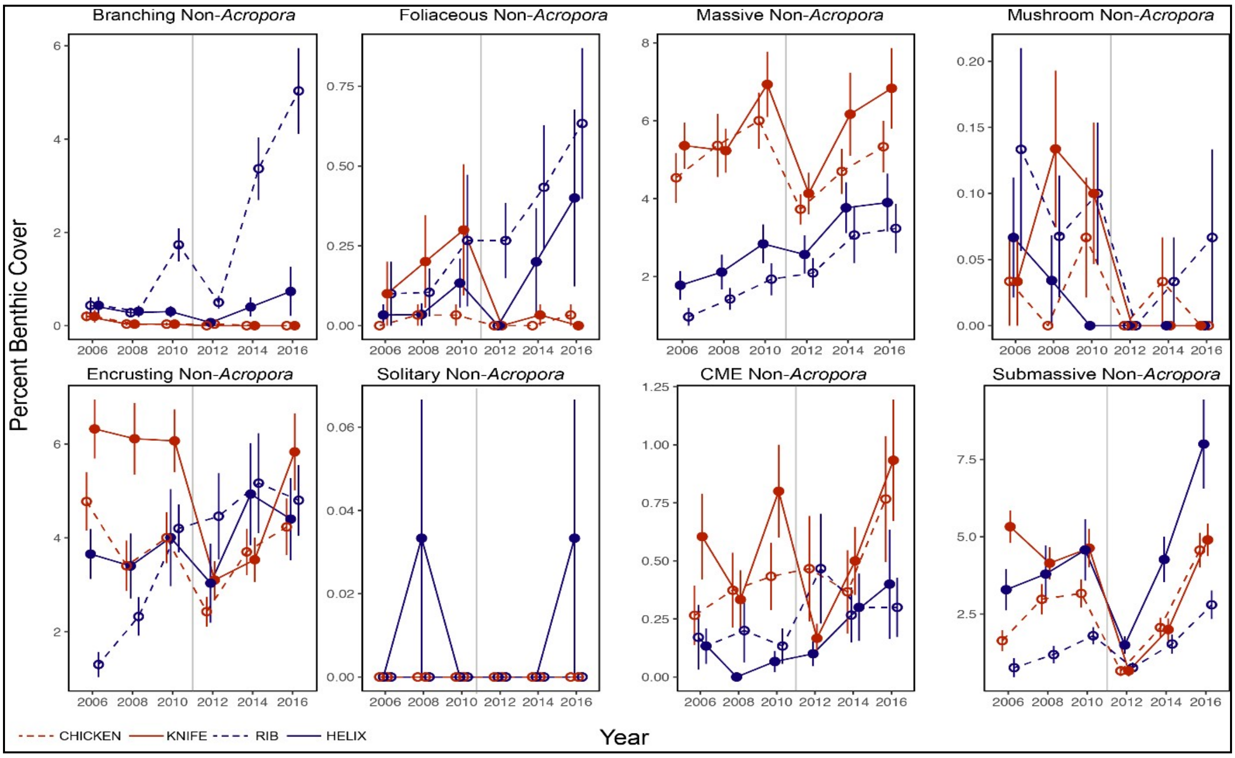
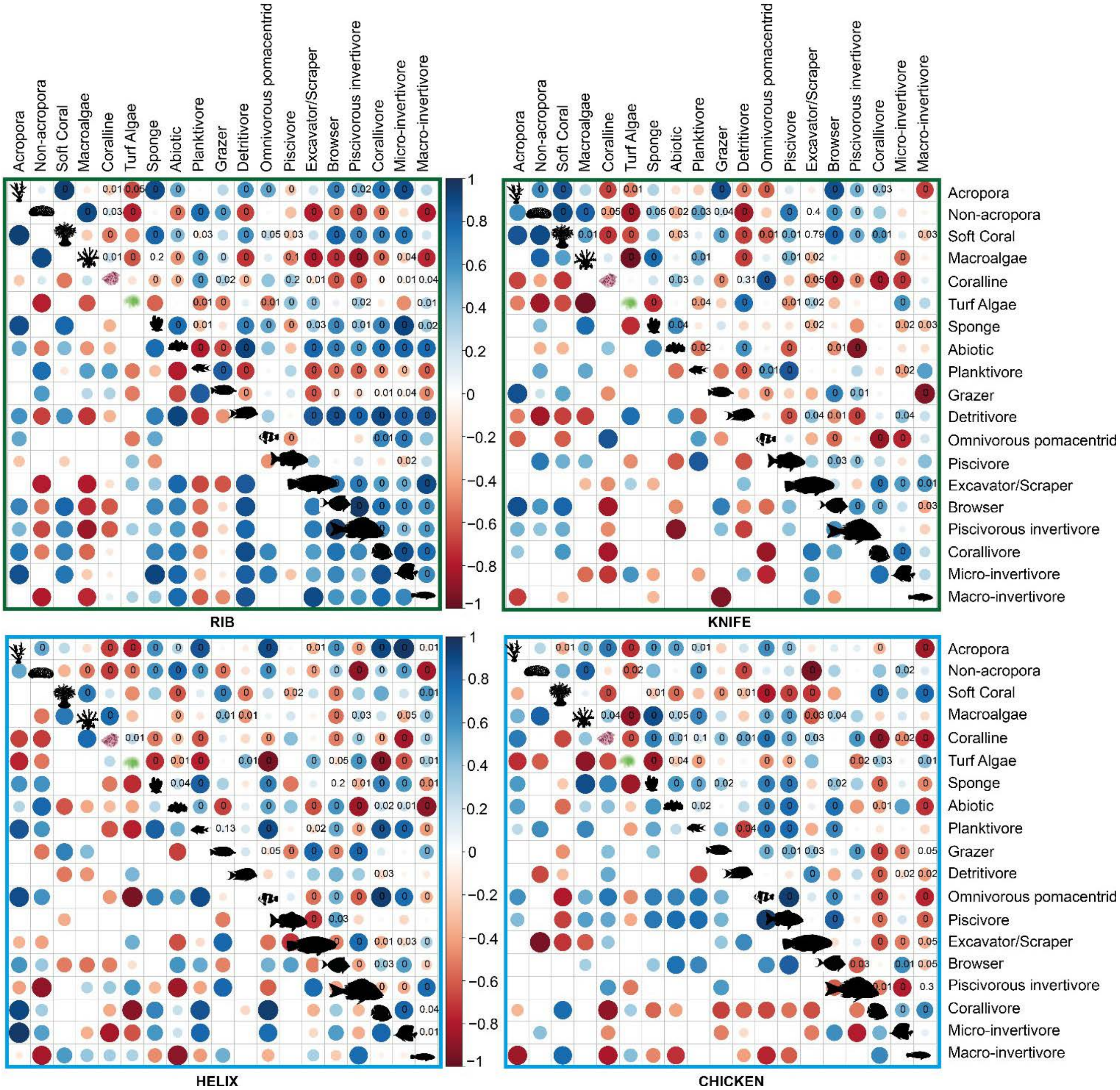


Figure S3-c: Pearson's correlations between relative density of trophic groups and benthic habitat. Biggest circles have the strongest rho values. Inversely related=Red gradient, Positive=Blue. P-Values (upper-half), Insignificant Blank (lower-half)



Chapter 4

***Table S4-a**: Additional species sampled that were not included in the analysis*

	Passionfruit coral trout	Spangled emperor	Spanish mackerel	Blue-stripe snapper	Blacktip reef shark	Yellow spotted trevally	
	P. aerolatus	*L. nebulosus*	*S. commerson*	*L. kasmira*	*C. melanopterus*	*C. fulvogutattus*	
	n=1	*n=3*	*n=2*	*n=1*	*n=1*	*n=2*	
	Muscle	Muscle	Muscle	Muscle	Muscle	Muscle	Plasma
14:0	0.46±0	0.8±1.07	0.38±0.16	0.42±0	0.24±0	3.41±2.46	2.79±0.43
15:0	0.59±0	1.04±0.87	0.45±0.08	0.41±0	0.4±0	1.04±0.83	0.83±0.42
16:0	17.23±0	19.65±5.02	20.06±0.52	17.28±0	22.89±0	34.73±1.45	13.54±5.9
16:0(FALD)	2.03±0	0.44±0.3	0.74±0.09	1.07±0	0.64±0	0.81±0.61	0.71±0.33
17:0	1.06±0	1.53±0.77	1.08±0.19	0.8±0	0.79±0	1.54±0.84	1.6±0.58
18:0	10±0	10.1±0.56	10.68±1.19	10.14±0	10.2±0	13.42±0.35	13.58±0.31
19:0	0.4±0	0.45±0.11	0.36±0.03	0.34±0	0.26±0	0.65±0.16	0.42±0.18
20:0	0.14±0	0.36±0.23	0.2±0.02	0.14±0	0.2±0	0.69±0.19	0.41±0.4
22:0	1.93±0	1.07±0.57	1.3±0.43	1.13±0	1±0	1.45±0.74	1.42±0.04
24:0	0.38±0	0.36±0.15	0.28±0.11	0.31±0	0.25±0	0.42±0.09	0.36±0.23
16:1ω7c	1.14±0	3.18±1.89	2.07±0.47	1.5±0	1.95±0	5.26±2.78	8.27±8.68
17:1ω8c+a17:0	0.84±0	1.18±0.63	0.69±0.27	0.59±0	0.54±0	0.52±0.07	0.66±0.49
18:1ω7	1.28±0	2.5±0.9	1.82±0.11	1.72±0	1.63±0	3.11±0.61	3.8±2.57
18:1ω9	8.84±0	10.53±1.13	9.01±0.3	9.16±0	10.26±0	13.06±4.91	7.07±2.86
20:1ω9	0.09±0	0.42±0.18	0.26±0.19	0.07±0	0.23±0	0.51±0.05	0.71±0.68
24:1ω11	1.93±0	1.07±0.57	1.3±0.43	1.13±0	1±0	1.45±0.74	1.42±0.04
16:4	0±0	0.03±0.05	0±0	0±0	0±0	0±0	0.03±0.04
17:1	0.87±0	1.06±0.82	0.83±0.12	0.59±0	0.73±0	0.24±0.12	0.07±0.1
18:2ω6	1.23±0	1.5±0.55	2.06±0.16	1.1±0	2.13±0	0.69±0.16	1.35±0.99
20:2ω6	0.25±0	0.43±0.17	0.37±0.12	0.23±0	0.26±0	0.18±0.02	0.28±0.18
18:3ω3	0.26±0	0.88±0.7	1.06±0.1	0.2±0	0.83±0	0.2±0.21	0.55±0.42
20:4ω3	0.44±0	0.51±0.2	0.63±0.08	0.39±0	0.5±0	0.27±0.22	0.36±0.12
20:3ω6	0.47±0	0.51±0.2	0.82±0.27	0.51±0	0.7±0	0.19±0.11	0.18±0.08
20:4ω6	14.73±0	10.86±5.75	9.75±5.58	12.75±0	17.02±0	1.27±0.49	3.22±0.49
20:5ω3	1.96±0	2.96±1.05	3.58±0.94	3.38±0	3.8±0	1.49±0.67	4.95±0.91
20:1ω11c	0.17±0	0.79±0.73	0.52±0.2	0.22±0	0.27±0	0.05±0.07	0.25±0.06
22:1ω7	0.36±0	0.23±0.14	0.26±0.16	0.17±0	0.19±0	0.14±0.04	0.17±0.06
22:1ω9	0.1±0	0.08±0.02	0.07±0.07	0.03±0	0±0	0.06±0.08	0.21±0.19
22:4ω6	4.61±0	3.42±1.81	3.01±0.85	3.37±0	3.65±0	0.33±0.11	1.94±1.51
22:5ω3	2.6±0	3.41±0.89	3.15±0.48	3.76±0	2.72±0	0.9±0.16	4.39±3.2
22:5ω6	4.18±0	2.17±1.32	2.73±0.46	3.43±0	1.83±0	1.02±0.52	1.49±0.25
22:6ω3	19.42±0	13.39±7.79	19.43±4.91	22.82±0	12.48±0	10.28±4.5	21.02±12.83
24:1ω7	0±0	0±0.01	0±0	0.03±0	0.02±0	0±0	0.01±0.01
i17:0	0.27±0	0.48±0.24	0.3±0.1	0.3±0	0.21±0	0.28±0.13	0.29±0.13
ΣSFA	30.51±6.08	34.75±6.7	33.76±7	30.08±6.15	35.49±7.82	56.32±11.46	33.88±5.61
ΣMUFA	15.87±1.81	21.73±2.19	17.12±1.85	15.59±1.87	16.7±2.1	24.57±2.83	23.5±2.21
ΣPUFA	50.38±5.98	40.66±4.11	47.15±5.26	52.14±6.44	46.24±5.09	16.98±2.65	40.59±5.46
ΣIso-SFA	0.38±0.13	1.03±0.21	0.45±0.14	0.46±0.14	0.21±0.11	0.77±0.1	0.56±0.12
ΣOther	2.86±1.17	1.82±0.21	1.52±0.41	1.73±0.6	1.36±0.33	1.38±0.45	1.48±0.38

Figure S4-a*: Linear regressions of muscle tissue comparison of traditional (x-axis) and direct (y-axis) methods for essential fatty acids . Symbols are unique species categories. Grey area are smoothed confidence intervals.*

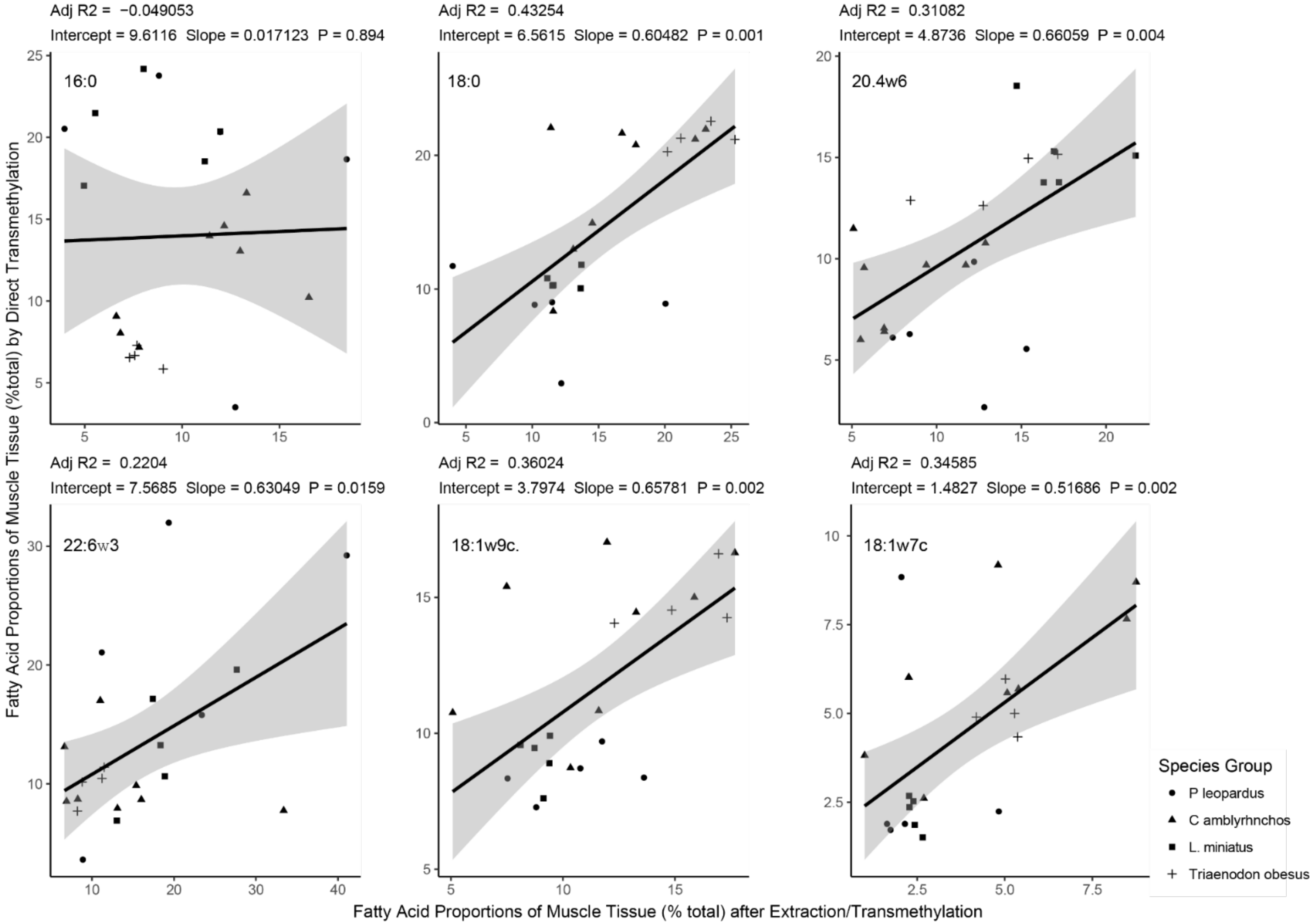
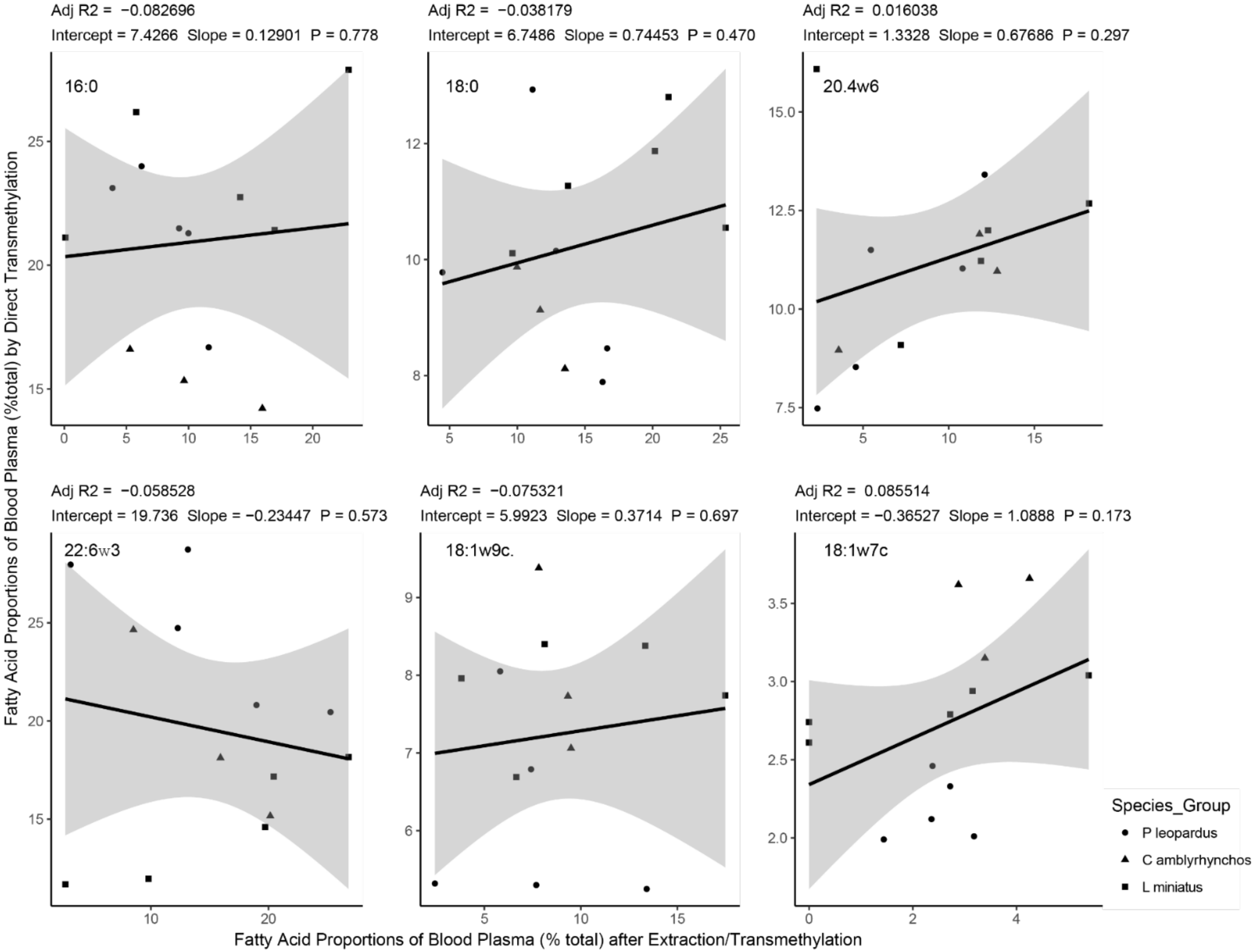


Figure S4-b*: Linear regressions of blood plasma comparison of traditional (x-axis) and direct (y-axis) methods for essential fatty acids. Symbols are unique species categories. Grey area are smoothed confidence intervals.*



Chapter 5

Table S5-a: *Binomial glmer AICc ranked model selection based on monthly and weekly reef residencies. RI = residency index, FL = fork length, depth= capture depth. All models have a random term of (Year | Reef / Tag ID) and were compared to the null model RI ~ 1 + (Year | Reef / Tag ID) (Monthly null; df=30 , logLik=-277.8, AICc=567.7) (Weekly null; df=70, logLik=-801.6, AICc=1609.2)*

Rank	Monthly	df	logLik	AICc	Rank	Weekly	df	logLik	AICc
1	RI ~ month	14	-191.9	412.7	1	RI ~ Week	55	-694.2	1501.3
2	RI ~ FL + month	15	-190.8	412.7	2	RI ~ FL + week	56	-693.9	1502.9
3	RI ~ month + depth	15	-191.4	413.9	3	RI ~ Sex + Week	57	-693.6	1504.5
4	RI ~ FL + month + depth	16	-190.8	414.8	4	RI ~ FL + Sex + Week	58	-693.5	1506.4
5	RI ~ month + sex	16	-191.7	416.7	5	RI ~ Sex + Depth + Week	69	-683.7	1510.1
6	RI ~ FL + month + sex	17	-190.7	416.8	6	RI ~ Depth + Week	68	-685.3	1511.3
7	RI ~ month + sex + depth	17	-191.2	417.9	7	RI ~ FL + Sex + Depth + Week	70	-683.5	1511.9
8	RI ~ month + sex + FL:Sex	18	-190.4	418.5	8	RI ~ FL + Depth + Week	69	-685.2	1513.1
9	RI ~ FL + month + sex + depth	18	-190.7	418.9	9	RI ~ FL	4	-801.5	1611.0
10	RI ~ FL + month + sex + depth + FL : sex	19	-190.4	420.4	10	RI ~ Sex	5	-801.0	1612.1
11	RI ~ FL + month + FL:month	26	-184.0	423.2	11	RI ~ FL + Sex	6	-800.9	1613.9
12	RI ~ FL + month + depth + FL : month	27	-183.7	425.0	12	RI ~ Sex + Depth	17	-791.1	1616.5
13	RI ~ FL+ month + sex + FL : month	28	-183.3	426.5	13	RI ~ FL + Sex + Depth	18	-790.6	1617.5
14	RI ~ FL+ month + sex + depth + FL : month	29	-183.2	428.4	14	RI ~ Depth	16	-793.2	1618.7
15	RI ~ FL + month + sex + FL : month + FL : sex	29	-183.2	428.5	15	RI ~ FL + Depth	17	-792.8	1619.8
16	RI ~ FL + month + sex + depth + FL : month + FL : sex	30	-182.9	430.2					
18	RI ~ FL	4	-214.2	436.4					
19	RI ~ depth	4	-214.6	437.3					
20	RI ~ FL + depth	5	-214.1	438.3					
21	RI ~ Sex	5	-214.9	439.9					
22	RI ~ FL+ Sex	6	-214.1	440.3					
23	RI ~ Sex + depth	6	-214.4	440.9					
24	RI ~ FL + Sex + FL : sex	7	-213.9	442.0					
25	RI ~ FL + Sex + depth	7	-214.0	442.2					
26	RI ~ FL + Sex + depth + FL : sex	8	-213.7	443.8					

***Table S5-b**: Binomial glmer AICc ranked model selection based on weekly residencies by individual receiver site (Serial). RI = residency index, FL = fork length. All models have a random term of (Year | Reef / Tag ID) and were compared to the null model RI ~ 1 + (Year | Reef / Tag ID) (df= 70, logLik=-3846.4, AICc=7706.7)*

Rank	Weekly	df	logLik	AICc
1	RI ~ FL + Serial + Sex + Week + FL : Serial + Sex : Serial	149	-2782.3	5870.6
2	RI ~ FL + Serial + Sex + Week + FL : Sex + FL : Serial + Sex : Serial	150	-2781.8	5871.7
3	RI ~ FL + Serial + Sex + FL : Serial + Sex : Serial	97	-2870.2	5937.8
4	RI ~ FL + Serial + Sex + Week + FL : Serial	122	-2933.1	6115.5
5	RI ~ FL + Serial + Week + FL : Serial	120	-2937.4	6119.9
6	RI ~ FL + Serial + Sex + Week + FL : Serial	122	-2940.8	6130.9
7	RI ~ FL + Serial + Sex + Week + FL : Sex + FL : Serial	123	-2942.0	6135.4
8	RI ~ FL + Serial + Sex + FL : Sex + FL : Serial	71	-3032.1	6208.0
9	RI ~ FL + Serial + Sex + FL : Serial	70	-3033.3	6208.4
10	RI ~ Serial + Sex + Week + Sex : Serial	120	-3028.6	6302.4
11	RI ~ FL + Serial + Sex + Week + Sex : Serial	121	-3028.1	6303.4
12	RI ~ FL + Serial + Sex + Week + FL : Sex + Sex : Serial	122	-3040.0	6329.3
13	RI ~ Serial + Sex + Sex : Serial	68	-3109.8	6357.3
14	RI ~ FL + Serial + Sex + Sex : Serial	69	-3110.5	6360.7
15	RI ~ FL + Serial + Sex + FL : Sex + Sex : Serial	70	-3109.6	6361.0
16	RI ~ Serial + Week + FL : Serial	89	-3311.0	6802.9
17	RI ~ FL + Serial + Week	90	-3314.6	6812.0
18	RI ~ FL + Serial + Sex + Week	92	-3313.8	6814.6
19	RI ~ FL + Serial + Sex + Week + FL : Sex	93	-3313.6	6816.2
20	RI ~ Serial + Sex + Week	91	-3317.5	6820.0
21	RI ~ Serial	37	-3395.8	6866.1
22	RI ~ Serial + Sex	39	-3394.1	6866.8
23	RI ~ FL + Serial	38	-3395.6	6867.6
24	RI ~ FL + Serial + Sex	40	-3394.2	6869.0
25	RI ~ FL + Serial + Sex + FL : Sex	41	-3394.3	6871.1
26	RI ~ Serial + Sex + FL : Sex	41	-3397.5	6877.6
27	RI ~ 1	8	-3776.4	7568.8
28	RI ~ FL	9	-3775.8	7569.5
29	RI ~ FL + Sex + Week	63	-3729.5	7586.4
30	RI ~ Sex	10	-3784.0	7588.1
31	RI ~ Sex + Week	62	-3731.9	7589.3
32	RI ~ FL + Sex	11	-3785.2	7592.4
33	RI ~ FL + Sex + Week + FL : Serial	64	-3731.7	7592.9
34	RI ~ Week	60	-3737.8	7596.9
35	RI ~ FL + Sex + FL : Sex	12	-3788.1	7600.3
36	RI ~ FL + Week	61	-3740.5	7604.3
37	RI ~ Sex + FL : Sex	11	-3800.4	7622.8
38	RI ~ FL + Sex + Week + FL : Sex	63	-3750.0	7627.4

***Table S5-c:** Post hoc reef site comparisons of abundance for common fish families from generalized linear models per reef using 'lsmeans'*

			Caesioinidae								Acanthuridae								Lethrinidae								Labridae				
Reef	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Chicken	1	2	-2.86E-08	631.7919	Inf	0	1	1	2	5.60E-02	0.118309	Inf	0.473	0.9971	1	2	-1.82E+01	5442.46	Inf	-0.003	1	1	2	8.60E-01	0.254333	Inf	3.382	**0.0094**
	1	3	-2.50E-08	706.3648	Inf	0	1	1	3	1.54E-01	0.136775	Inf	1.127	0.8703	1	3	-3.24E-09	8605.284	Inf	0	1	1	3	1.24E+00	0.345286	Inf	3.6	**0.0043**
	1	4	-1.88E+01	446.7443	Inf	-0.042	1	1	4	1.78E-01	0.1222	Inf	1.459	0.6907	1	4	-1.59E-09	7696.8	Inf	0	1	1	4	1.12E+00	0.279382	Inf	4.002	**0.0009**
	1	5	-1.76E+01	446.7443	Inf	-0.04	1	1	5	1.56E+00	0.197638	Inf	7.875	**<.0001**	1	5	-1.89E+01	5442.46	Inf	-0.003	1	1	5	9.07E-01	0.258553	Inf	3.507	**0.006**
	1	6	-1.93E-08	706.3648	Inf	0	1	1	6	5.60E-01	0.157035	Inf	3.564	**0.0049**	1	6	-4.89E-08	8605.284	Inf	0	1	1	6	9.07E-01	0.301097	Inf	3.011	**0.0312**
	2	3	3.52E-09	706.3648	Inf	0	1	2	3	9.82E-02	0.138199	Inf	0.711	0.9808	2	3	1.82E+01	6665.625	Inf	0.003	1	2	3	3.83E-01	0.381374	Inf	1.004	0.9167
	2	4	-1.88E+01	446.7443	Inf	-0.042	1	2	4	1.22E-01	0.123791	Inf	0.988	0.922	2	4	1.82E+01	5442.46	Inf	0.003	1	2	4	2.58E-01	0.322921	Inf	0.798	0.9679
	2	5	-1.76E+01	446.7443	Inf	-0.04	1	2	5	1.50E+00	0.198626	Inf	7.554	**<.0001**	2	5	-6.93E-01	1.224745	Inf	-0.566	0.9932	2	5	4.65E-02	0.30508	Inf	0.152	1
	2	6	9.25E-09	706.3648	Inf	0	1	2	6	5.04E-01	0.158276	Inf	3.182	**0.0183**	2	6	1.82E+01	6665.625	Inf	0.003	1	2	6	4.65E-02	0.341882	Inf	0.136	1
	3	4	-1.88E+01	547.1478	Inf	-0.034	1	3	4	2.41E-02	0.141545	Inf	0.17	1	3	4	1.65E-09	8605.284	Inf	0	1	3	4	-1.25E-01	0.398516	Inf	-0.314	0.9996
	3	5	-1.76E+01	547.1478	Inf	-0.032	1	3	5	1.40E+00	0.21015	Inf	6.673	**<.0001**	3	5	-1.89E+01	6665.625	Inf	-0.003	1	3	5	-3.36E-01	0.384201	Inf	-0.876	0.9524
	3	6	5.73E-09	773.7838	Inf	0	1	3	6	4.05E-01	0.172516	Inf	2.35	0.1742	3	6	-4.56E-08	9426.617	Inf	0	1	3	6	-3.36E-01	0.414029	Inf	-0.813	0.9653
	4	5	1.15E+00	0.124483	Inf	9.225	**<.0001**	4	5	1.38E+00	0.200968	Inf	6.858	**<.0001**	4	5	-1.89E+01	5442.46	Inf	-0.003	1	4	5	-2.11E-01	0.326255	Inf	-0.648	0.9873
	4	6	1.88E+01	547.1478	Inf	0.034	1	4	6	3.81E-01	0.161206	Inf	2.366	0.1684	4	6	-4.73E-08	8605.284	Inf	0	1	4	6	-2.11E-01	0.360905	Inf	-0.585	0.992
	5	6	1.76E+01	547.1478	Inf	0.032	1	5	6	-9.97E-01	0.223864	Inf	-4.453	**0.0001**	5	6	1.89E+01	6665.625	Inf	0.003	1	5	6	7.70E-14	0.345033	Inf	0	1
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Helix	1	2	-1.29E+00	0.399353	Inf	-3.225	**0.0159**	1	2	-1.08E-01	0.16464	Inf	-0.657	0.9864	1	2	-1.61E+00	1.095445	Inf	-1.469	0.684	1	2	-3.57E-01	0.284521	Inf	-1.254	0.8101
	1	3	-1.14E+00	0.406202	Inf	-2.805	0.0566	1	3	-3.57E-01	0.155839	Inf	-2.289	0.1985	1	3	6.28E-15	1.414214	Inf	0	1	1	3	-2.14E-01	0.293395	Inf	-0.728	0.9786
	1	4	-2.59E+00	0.366532	Inf	-7.075	**<.0001**	1	4	1.44E-02	0.169642	Inf	0.085	1	1	4	-6.93E-01	1.224745	Inf	-0.566	0.9932	1	4	-9.10E-02	0.301823	Inf	-0.301	0.9997
	1	5	-3.75E+00	0.357701	Inf	-10.474	**<.0001**	1	5	1.38E-01	0.175155	Inf	0.786	0.97	1	5	-1.10E+00	1.154701	Inf	-0.951	0.9329	1	5	4.05E-01	0.345033	Inf	1.175	0.8489
	1	6	-2.47E+00	0.368139	Inf	-6.721	**<.0001**	1	6	5.88E-02	0.171573	Inf	0.343	0.9994	1	6	-1.10E+00	1.154701	Inf	-0.951	0.9329	1	6	4.05E-01	0.345033	Inf	1.175	0.8489
	2	3	1.48E-01	0.272915	Inf	0.544	0.9943	2	3	-2.48E-01	0.151065	Inf	-1.645	0.5687	2	3	1.61E+00	1.095445	Inf	1.469	0.684	2	3	1.43E-01	0.267946	Inf	0.534	0.9948
	2	4	-1.31E+00	0.209353	Inf	-6.236	**<.0001**	2	4	1.23E-01	0.165267	Inf	0.742	0.9767	2	4	9.16E-01	0.83666	Inf	1.095	0.8835	2	4	2.66E-01	0.277149	Inf	0.959	0.9308
	2	5	-2.46E+00	0.193475	Inf	-12.708	**<.0001**	2	5	2.46E-01	0.170921	Inf	1.438	0.7035	2	5	5.11E-01	0.730297	Inf	0.699	0.9821	2	5	7.62E-01	0.323669	Inf	2.355	0.1725
	2	6	-1.19E+00	0.212153	Inf	-5.593	**<.0001**	2	6	1.67E-01	0.167248	Inf	0.999	0.9185	2	6	5.11E-01	0.730297	Inf	0.699	0.9821	2	6	7.62E-01	0.323669	Inf	2.355	0.1725
	3	4	-1.45E+00	0.222139	Inf	-6.545	**<.0001**	3	4	3.71E-01	0.156502	Inf	2.371	0.1665	3	4	-6.93E-01	1.224745	Inf	-0.566	0.9932	3	4	1.23E-01	0.286251	Inf	0.428	0.9982
	3	5	-2.61E+00	0.207243	Inf	-12.58	**<.0001**	3	5	4.94E-01	0.162461	Inf	3.043	**0.0284**	3	5	-1.10E+00	1.154701	Inf	-0.951	0.9329	3	5	6.19E-01	0.331497	Inf	1.867	0.4224
	3	6	-1.34E+00	0.224781	Inf	-5.939	**<.0001**	3	6	4.16E-01	0.158592	Inf	2.62	0.0924	3	6	-1.10E+00	1.154701	Inf	-0.951	0.9329	3	6	6.19E-01	0.331497	Inf	1.867	0.4224
	4	5	-1.15E+00	0.110886	Inf	-10.4	**<.0001**	4	5	1.23E-01	0.175745	Inf	0.701	0.9819	4	5	-4.05E-01	0.912871	Inf	-0.444	0.9978	4	5	4.96E-01	0.338979	Inf	1.465	0.687
	4	6	1.19E-01	0.140968	Inf	0.844	0.9593	4	6	4.45E-02	0.172175	Inf	0.258	0.9998	4	6	-4.05E-01	0.912871	Inf	-0.444	0.9978	4	6	4.96E-01	0.338979	Inf	1.465	0.687
	5	6	1.27E+00	0.116087	Inf	10.958	**<.0001**	5	6	-7.88E-02	0.177609	Inf	-0.444	0.9978	5	6	-8.14E-15	0.816497	Inf	0	1	5	6	-1.11E-16	0.377965	Inf	0	1
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Knife	1	2	-1.12E+00	0.210245	Inf	-5.33	**<.0001**	1	2	6.56E-01	0.19248	Inf	3.408	**0.0086**	1	2	1.89E+01	5442.46	Inf	0.003	1	1	2	3.83E-01	0.334845	Inf	1.144	0.863
	1	3	-2.91E+00	0.18747	Inf	-15.535	**<.0001**	1	3	-2.50E-02	0.158126	Inf	-0.158	1	1	3	6.93E-01	1.224745	Inf	0.566	0.9932	1	3	3.18E-01	0.328564	Inf	0.969	0.9277
	1	4	1.82E-01	0.270801	Inf	0.673	0.9849	1	4	-1.46E+00	0.124863	Inf	-11.712	**<.0001**	1	4	1.89E+01	5442.46	Inf	0.003	1	1	4	-2.41E-01	0.284901	Inf	-0.846	0.9587
	1	5	1.66E+01	446.7443	Inf	0.037	1	1	5	1.07E-01	0.163532	Inf	0.653	0.9868	1	5	-1.25E+00	0.801784	Inf	-1.562	0.6234	1	5	-8.70E-02	0.295163	Inf	-0.295	0.9997
	1	6	3.39E-02	0.260415	Inf	0.13	1	1	6	9.04E-01	0.209543	Inf	4.313	**0.0002**	1	6	6.93E-01	1.224745	Inf	0.566	0.9932	1	6	6.06E-01	0.35887	Inf	1.689	0.5391
	2	3	-1.79E+00	0.112611	Inf	-15.911	**<.0001**	2	3	-6.81E-01	0.191666	Inf	-3.552	**0.0051**	2	3	-1.82E+01	5442.46	Inf	-0.003	1	2	3	-6.45E-02	0.359398	Inf	-0.18	1
	2	4	1.30E+00	0.225543	Inf	5.777	**<.0001**	2	4	-2.12E+00	0.165296	Inf	-12.815	**<.0001**	2	4	-4.99E-11	7696.8	Inf	0	1	2	4	-6.24E-01	0.31997	Inf	-1.951	0.3712
	2	5	1.77E+01	446.7443	Inf	0.04	1	2	5	-5.49E-01	0.19615	Inf	-2.799	0.0575	2	5	-2.01E+01	5442.46	Inf	-0.004	1	2	5	-4.70E-01	0.32914	Inf	-1.428	0.7099
	2	6	1.15E+00	0.212961	Inf	5.421	**<.0001**	2	6	2.48E-01	0.235882	Inf	1.051	0.9006	2	6	-1.82E+01	5442.46	Inf	-0.003	1	2	6	2.23E-01	0.387298	Inf	0.576	0.9926
	3	4	3.09E+00	0.204479	Inf	15.134	**<.0001**	3	4	-1.44E+00	0.123605	Inf	-11.629	**<.0001**	3	4	1.82E+01	5442.46	Inf	0.003	1	3	4	-5.60E-01	0.313392	Inf	-1.786	0.475
	3	5	1.95E+01	446.7443	Inf	0.044	1	3	5	1.32E-01	0.162574	Inf	0.811	0.9657	3	5	-1.95E+00	1.069045	Inf	-1.82	0.4526	3	5	-4.05E-01	0.322749	Inf	-1.256	0.8087
	3	6	2.95E+00	0.190511	Inf	15.465	**<.0001**	3	6	9.29E-01	0.208796	Inf	4.448	**0.0001**	3	6	7.62E-15	1.414214	Inf	0	1	3	6	2.88E-01	0.381881	Inf	0.753	0.9751
	4	5	1.64E+01	446.7443	Inf	0.037	1	4	5	1.57E+00	0.130449	Inf	12.029	**<.0001**	4	5	-2.01E+01	5442.46	Inf	-0.004	1	4	5	1.54E-01	0.278174	Inf	0.554	0.9938
	4	6	-1.48E-01	0.272915	Inf	-0.544	0.9943	4	6	2.37E+00	0.184885	Inf	12.798	**<.0001**	4	6	-1.82E+01	5442.46	Inf	-0.003	1	4	6	8.47E-01	0.345033	Inf	2.456	0.1375
	5	6	-1.66E+01	446.7443	Inf	-0.037	1	5	6	7.97E-01	0.212919	Inf	3.743	**0.0025**	5	6	1.95E+00	1.069045	Inf	1.82	0.4526	5	6	6.93E-01	0.353553	Inf	1.961	0.3653
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Rib	1	2	-2.05E+01	446.7443	Inf	-0.046	1	1	2	2.97E-01	0.183075	Inf	1.624	0.5828	1	2	1.10E+00	1.154701	Inf	0.951	0.9329	1	2	-2.01E-01	0.317821	Inf	-0.631	0.9887
	1	3	1.41E-08	631.7919	Inf	0	1	1	3	-9.53E-02	0.165145	Inf	-0.577	0.9925	1	3	1.10E+00	1.154701	Inf	0.951	0.9329	1	3	-1.05E-01	0.324893	Inf	-0.324	0.9995
	1	4	-2.09E+01	446.7443	Inf	-0.047	1	1	4	-1.08E-01	0.16464	Inf	-0.657	0.9864	1	4	4.05E-01	0.912871	Inf	0.444	0.9978	1	4	-1.05E-01	0.324893	Inf	-0.324	0.9995
	1	5	1.41E-08	631.7919	Inf	0	1	1	5	4.42E-01	0.191071	Inf	2.312	0.1889	1	5	4.05E-01	0.912871	Inf	0.444	0.9978	1	5	-2.45E-01	0.314696	Inf	-0.779	0.9711
	1	6	-1.88E+01	446.7443	Inf	-0.042	1	1	6	4.42E-01	0.191071	Inf	2.312	0.1889	1	6	4.05E-01	0.912871	Inf	0.444	0.9978	1	6	-1.05E-01	0.324893	Inf	-0.324	0.9995
	2	3	2.05E+01	446.7443	Inf	0.046	1	2	3	-3.93E-01	0.179493	Inf	-2.187	0.2437	2	3	-5.77E-15	1.414214	Inf	0	1	2	3	9.53E-02	0.308957	Inf	0.308	0.9996
	2	4	-4.27E-01	0.033576	Inf	-12.706	**<.0001**	2	4	-4.05E-01	0.179029	Inf	-2.265	0.2086	2	4	-6.93E-01	1.224745	Inf	-0.566	0.9932	2	4	9.53E-02	0.308957	Inf	0.308	0.9996
	2	5	2.05E+01	446.7443	Inf	0.046	1	2	5	1.45E-01	0.2036	Inf	0.71	0.9808	2	5	-6.93E-01	1.224745	Inf	-0.566	0.9932	2	5	-4.45E-02	0.298216	Inf	-0.149	1
	2	6	1.67E+00	0.065715	Inf	25.466	**<.0001**	2	6	1.45E-01	0.2036	Inf	0.71	0.9808	2	6	-6.93E-01	1.224745	Inf	-0.566	0.9932	2	6	9.53E-02	0.308957	Inf	0.308	0.9996
	3	4	-2.09E+01	446.7443	Inf	-0.047	1	3	4	-1.29E-02	0.160647	Inf	-0.08	1	3	4	-6.93E-01	1.224745	Inf	-0.566	0.9932	3	4	-2.44E-15	0.316228	Inf	0	1
	3	5	-6.48E-12	631.7919	Inf	0	1	3	5	5.37E-01	0.187641	Inf	2.863	**0.0482**	3	5	-6.93E-01	1.224745	Inf	-0.566	0.9932	3	5	-1.40E-01	0.305742	Inf	-0.457	0.9975
	3	6	-1.88E+01	446.7443	Inf	-0.042	1	3	6	5.37E-01	0.187641	Inf	2.863	**0.0482**	3	6	-6.93E-01	1.224745	Inf	-0.566	0.9932	3	6	2.22E-16	0.316228	Inf	0	1
	4	5	2.09E+01	446.7443	Inf	0.047	1	4	5	5.50E-01	0.187197	Inf	2.938	**0.0388**	4	5	1.62E-14	1	Inf	0	1	4	5	-1.40E-01	0.305742	Inf	-0.457	0.9975
	4	6	2.10E+00	0.063887	Inf	32.872	**<.0001**	4	6	5.50E-01	0.187197	Inf	2.938	**0.0388**	4	6	-6.30E-15	1	Inf	0	1	4	6	2.66E-15	0.316228	Inf	0	1
	5	6	-1.88E+01	446.7443	Inf	-0.042	1	5	6	-7.08E-16	0.210819	Inf	0	1	5	6	-2.25E-14	1	Inf	0	1	5	6	1.40E-01	0.305742	Inf	0.457	0.9975

	Pomacentridae							Scaridae							Serranidae						
Reef	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Chicken	1	2	-0.786269	0.045374	Inf	-17.329	**<.0001**	1	2	0.23742	0.108123	Inf	2.196	0.2395	1	2	8.70E-02	0.417424	Inf	0.208	0.9999
	1	3	-0.365056	0.053733	Inf	-6.794	**<.0001**	1	3	0.518588	0.134691	Inf	3.85	**0.0016**	1	3	6.93E-01	0.57735	Inf	1.201	0.8368
	1	4	-1.184405	0.042978	Inf	-27.558	**<.0001**	1	4	0.54047	0.118339	Inf	4.567	**0.0001**	1	4	4.05E-01	0.456436	Inf	0.888	0.9494
	1	5	-0.151926	0.051279	Inf	-2.963	**0.0361**	1	5	1.376038	0.159884	Inf	8.606	**<.0001**	1	5	8.70E-02	0.417424	Inf	0.208	0.9999
	1	6	-0.016135	0.059179	Inf	-0.273	0.9998	1	6	-0.027956	0.112576	Inf	-0.248	0.9999	1	6	-1.18E-01	0.440959	Inf	-0.267	0.9998
	2	3	0.421213	0.046012	Inf	9.154	**<.0001**	2	3	0.281167	0.139725	Inf	2.012	0.3351	2	3	6.06E-01	0.583874	Inf	1.038	0.9051
	2	4	-0.398136	0.032818	Inf	-12.132	**<.0001**	2	4	0.30305	0.124038	Inf	2.443	0.1415	2	4	3.18E-01	0.46466	Inf	0.685	0.9836
	2	5	0.634344	0.043121	Inf	14.711	**<.0001**	2	5	1.138618	0.164147	Inf	6.937	**<.0001**	2	5	1.39E-16	0.426401	Inf	0	1
	2	6	0.770134	0.052269	Inf	14.734	**<.0001**	2	6	-0.265376	0.118553	Inf	-2.238	0.2201	2	6	-2.05E-01	0.449467	Inf	-0.456	0.9975
	3	4	-0.819349	0.043652	Inf	-18.77	**<.0001**	3	4	0.021883	0.147772	Inf	0.148	1	3	4	-2.88E-01	0.612372	Inf	-0.47	0.9972
	3	5	0.21313	0.051844	Inf	4.111	**0.0006**	3	5	0.85745	0.182744	Inf	4.692	**<.0001**	3	5	-6.06E-01	0.583874	Inf	-1.038	0.9051
	3	6	0.348921	0.059669	Inf	5.848	**<.0001**	3	6	-0.546544	0.143199	Inf	-3.817	**0.0019**	3	6	-8.11E-01	0.600925	Inf	-1.349	0.7572
	4	5	1.032479	0.040593	Inf	25.435	**<.0001**	4	5	0.835568	0.171049	Inf	4.885	**<.0001**	4	5	-3.18E-01	0.46466	Inf	-0.685	0.9836
	4	6	1.16827	0.050204	Inf	23.271	**<.0001**	4	6	-0.568426	0.127939	Inf	-4.443	**0.0001**	4	6	-5.23E-01	0.485913	Inf	-1.077	0.8908
	5	6	0.135791	0.05747	Inf	2.363	0.1695	5	6	-1.403994	0.167114	Inf	-8.401	**<.0001**	5	6	-2.05E-01	0.449467	Inf	-0.456	0.9975
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Helix	1	2	-1.737957	0.064804	Inf	-26.819	**<.0001**	1	2	-0.864212	0.145653	Inf	-5.933	**<.0001**	1	2	-2.23E-01	0.67082	Inf	-0.333	0.9995
	1	3	-1.028343	0.069632	Inf	-14.768	**<.0001**	1	3	-0.400478	0.157878	Inf	-2.537	0.1136	1	3	1.66E+01	1214.377	Inf	0.014	1
	1	4	-1.992268	0.063706	Inf	-31.273	**<.0001**	1	4	0.030305	0.174098	Inf	0.174	1	1	4	-6.93E-01	0.612372	Inf	-1.132	0.8682
	1	5	-2.02391	0.063587	Inf	-31.829	**<.0001**	1	5	0.127155	0.178534	Inf	0.712	0.9805	1	5	-1.10E+00	0.57735	Inf	-1.903	0.4003
	1	6	-2.147184	0.063155	Inf	-33.998	**<.0001**	1	6	0.541131	0.201411	Inf	2.687	0.0779	1	6	-1.50E+00	0.552771	Inf	-2.721	0.0711
	2	3	0.709614	0.04365	Inf	16.257	**<.0001**	2	3	0.463734	0.12763	Inf	3.633	**0.0038**	2	3	1.68E+01	1214.377	Inf	0.014	1
	2	4	-0.254311	0.033395	Inf	-7.615	**<.0001**	2	4	0.894517	0.147221	Inf	6.076	**<.0001**	2	4	-4.70E-01	0.570088	Inf	-0.824	0.9631
	2	5	-0.285953	0.033167	Inf	-8.622	**<.0001**	2	5	0.991367	0.152442	Inf	6.503	**<.0001**	2	5	-8.75E-01	0.532291	Inf	-1.645	0.5687
	2	6	-0.409227	0.032332	Inf	-12.657	**<.0001**	2	6	1.405343	0.178691	Inf	7.865	**<.0001**	2	6	-1.28E+00	0.505525	Inf	-2.534	0.1143
	3	4	-0.963925	0.042003	Inf	-22.949	**<.0001**	3	4	0.430783	0.159326	Inf	2.704	0.0744	3	4	-1.73E+01	1214.377	Inf	-0.014	1
	3	5	-0.995567	0.041822	Inf	-23.805	**<.0001**	3	5	0.527633	0.164162	Inf	3.214	**0.0165**	3	5	-1.77E+01	1214.377	Inf	-0.015	1
	3	6	-1.118841	0.041162	Inf	-27.181	**<.0001**	3	6	0.941609	0.188788	Inf	4.988	**<.0001**	3	6	-1.81E+01	1214.377	Inf	-0.015	1
	4	5	-0.031642	0.030968	Inf	-1.022	0.9108	4	5	0.09685	0.179816	Inf	0.539	0.9946	4	5	-4.05E-01	0.456436	Inf	-0.888	0.9494
	4	6	-0.154916	0.030071	Inf	-5.152	**<.0001**	4	6	0.510826	0.202548	Inf	2.522	0.1176	4	6	-8.11E-01	0.424918	Inf	-1.908	0.3968
	5	6	-0.123274	0.029818	Inf	-4.134	**0.0005**	5	6	0.413976	0.206374	Inf	2.006	0.3388	5	6	-4.05E-01	0.372678	Inf	-1.088	0.8864
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Knife	1	2	0.168166	0.04715	Inf	3.567	**0.0049**	1	2	0.025642	0.160141	Inf	0.16	1	1	2	6.93E-01	0.707107	Inf	0.98	0.9244
	1	3	0.0185	0.04534	Inf	0.408	0.9986	1	3	-0.025001	0.158126	Inf	-0.158	1	1	3	1.82E-01	0.60553	Inf	0.301	0.9997
	1	4	-0.369525	0.041498	Inf	-8.905	**<.0001**	1	4	-0.498087	0.142655	Inf	-3.492	**0.0064**	1	4	-2.88E-01	0.540062	Inf	-0.533	0.9949
	1	5	-0.434899	0.040958	Inf	-10.618	**<.0001**	1	5	-0.711957	0.137366	Inf	-5.183	**<.0001**	1	5	-9.81E-01	0.478714	Inf	-2.049	0.3146
	1	6	0.404956	0.050448	Inf	8.027	**<.0001**	1	6	0.562785	0.186763	Inf	3.013	**0.031**	1	6	-8.47E-01	0.48795	Inf	-1.736	0.5075
	2	3	-0.149666	0.047351	Inf	-3.161	**0.0196**	2	3	-0.050644	0.159163	Inf	-0.318	0.9996	2	3	-5.11E-01	0.730297	Inf	-0.699	0.9821
	2	4	-0.53769	0.043687	Inf	-12.308	**<.0001**	2	4	-0.523729	0.143803	Inf	-3.642	**0.0037**	2	4	-9.81E-01	0.677003	Inf	-1.449	0.697
	2	5	-0.603064	0.043174	Inf	-13.968	**<.0001**	2	5	-0.737599	0.138558	Inf	-5.323	**<.0001**	2	5	-1.67E+00	0.629153	Inf	-2.661	0.0833
	2	6	0.23679	0.052264	Inf	4.531	**0.0001**	2	6	0.537143	0.187641	Inf	2.863	**0.0482**	2	6	-1.54E+00	0.636209	Inf	-2.421	0.1488
	3	4	-0.388025	0.041726	Inf	-9.299	**<.0001**	3	4	-0.473085	0.141556	Inf	-3.342	**0.0108**	3	4	-4.70E-01	0.570088	Inf	-0.824	0.9631
	3	5	-0.453399	0.041189	Inf	-11.008	**<.0001**	3	5	-0.686955	0.136224	Inf	-5.043	**<.0001**	3	5	-1.16E+00	0.512348	Inf	-2.27	0.2063
	3	6	0.386456	0.050637	Inf	7.632	**<.0001**	3	6	0.587787	0.185925	Inf	3.161	**0.0196**	3	6	-1.03E+00	0.520988	Inf	-1.976	0.356
	4	5	-0.065374	0.036918	Inf	-1.771	0.4848	4	5	-0.21387	0.117913	Inf	-1.814	0.4567	4	5	-6.93E-01	0.433013	Inf	-1.601	0.598
	4	6	0.774481	0.047228	Inf	16.399	**<.0001**	4	6	1.060872	0.172958	Inf	6.134	**<.0001**	4	6	-5.60E-01	0.443203	Inf	-1.263	0.8054
	5	6	0.839855	0.046754	Inf	17.963	**<.0001**	5	6	1.274742	0.168622	Inf	7.56	**<.0001**	5	6	1.34E-01	0.365963	Inf	0.365	0.9992
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Rib	1	2	-1.325021	0.039902	Inf	-33.207	**<.0001**	1	2	0.292136	0.176608	Inf	1.654	0.5624	1	2	-2.08E+00	1.06066	Inf	-1.961	0.3653
	1	3	-0.646807	0.043779	Inf	-14.774	**<.0001**	1	3	-0.336472	0.151186	Inf	-2.226	0.2259	1	3	-1.10E+00	1.154701	Inf	-0.951	0.9329
	1	4	-0.821081	0.042559	Inf	-19.293	**<.0001**	1	4	-0.572861	0.144403	Inf	-3.967	**0.001**	1	4	-1.10E+00	1.154701	Inf	-0.951	0.9329
	1	5	-0.572293	0.044357	Inf	-12.902	**<.0001**	1	5	-1.243194	0.131071	Inf	-9.485	**<.0001**	1	5	-6.93E-01	1.224745	Inf	-0.566	0.9932
	1	6	-1.152481	0.040684	Inf	-28.328	**<.0001**	1	6	-0.624154	0.143095	Inf	-4.362	**0.0002**	1	6	-1.39E+00	1.118034	Inf	-1.24	0.8172
	2	3	0.678214	0.031513	Inf	21.521	**<.0001**	2	3	-0.628609	0.165472	Inf	-3.799	**0.002**	2	3	9.81E-01	0.677003	Inf	1.449	0.697
	2	4	0.50394	0.029795	Inf	16.914	**<.0001**	2	4	-0.864997	0.159298	Inf	-5.43	**<.0001**	2	4	9.81E-01	0.677003	Inf	1.449	0.697
	2	5	0.752728	0.032312	Inf	23.296	**<.0001**	2	5	-1.53533	0.14732	Inf	-10.422	**<.0001**	2	5	1.39E+00	0.790569	Inf	1.754	0.4962
	2	6	0.17254	0.027049	Inf	6.379	**<.0001**	2	6	-0.916291	0.158114	Inf	-5.795	**<.0001**	2	6	6.93E-01	0.612372	Inf	1.132	0.8682
	3	4	-0.174274	0.034816	Inf	-5.006	**<.0001**	3	4	-0.236389	0.130547	Inf	-1.811	0.4587	3	4	-9.44E-16	0.816497	Inf	0	1
	3	5	0.074513	0.036993	Inf	2.014	0.334	3	5	-0.906721	0.115629	Inf	-7.842	**<.0001**	3	5	4.05E-01	0.912871	Inf	0.444	0.9978
	3	6	-0.505674	0.032497	Inf	-15.561	**<.0001**	3	6	-0.287682	0.129099	Inf	-2.228	0.2246	3	6	-2.88E-01	0.763763	Inf	-0.377	0.999
	4	5	0.248788	0.03554	Inf	7	**<.0001**	4	5	-0.670333	0.106607	Inf	-6.288	**<.0001**	4	5	4.05E-01	0.912871	Inf	0.444	0.9978
	4	6	-0.3314	0.030833	Inf	-10.748	**<.0001**	4	6	-0.051293	0.121085	Inf	-0.424	0.9983	4	6	-2.88E-01	0.763763	Inf	-0.377	0.999
	5	6	-0.580187	0.033272	Inf	-17.438	**<.0001**	5	6	0.619039	0.104828	Inf	5.905	**<.0001**	5	6	-6.93E-01	0.866025	Inf	-0.8	0.9675

Table S5-d: *Post hoc reef site comparisons of biomass for common fish families from generalized linear models per reef using 'lsmeans'*

	Caesionidae							**Acanthuridae**							**Labridae**							**Pomacentridae**						
Reef	**Site**	**Contrast**	**estimate**	**SE**	**df**	**z.ratio**	**p value**	**Site**	**Contrast**	**estimate**	**SE**	**df**	**z.ratio**	**p value**	**Site**	**Contrast**	**estimate**	**SE**	**df**	**z.ratio**	**p value**	**Site**	**Contrast**	**estimate**	**SE**	**df**	**z.ratio**	**p value**
Chicken	1	2	7.66E-08	1.62E+05	Inf	0	1	1	2	-0.405465	0.204124	Inf	-1.986	0.3501	1	2	-9.10E-02	0.301823	Inf	-0.301	0.9997	1	2	-8.02E-01	0.333775	Inf	-2.404	0.1548
	1	3	7.42E-08	1.62E+05	Inf	0	1	1	3	-0.262364	0.210311	Inf	-1.248	0.8133	1	3	-3.89E-01	0.282625	Inf	-1.378	0.7403	1	3	-7.41E-02	0.385164	Inf	-0.192	1
	1	4	-2.92E+01	1.15E+05	Inf	0	1	1	4	-1.458615	0.175539	Inf	-8.309	**<.0001**	1	4	1.25E+00	0.46291	Inf	2.706	0.074	1	4	-1.22E+00	0.315674	Inf	-3.862	**0.0016**
	1	5	-2.85E+01	1.15E+05	Inf	0	1	1	5	-1.3284	0.177827	Inf	-7.47	**<.0001**	1	5	6.47E-01	0.372194	Inf	1.737	0.5069	1	5	-3.79E-01	0.359937	Inf	-1.054	0.8993
	1	6	6.01E-08	1.62E+05	Inf	0	1	1	6	0.133531	0.231455	Inf	0.577	0.9925	1	6	1.10E+00	0.436436	Inf	2.517	0.119	1	6	4.86E-01	0.449359	Inf	1.08	0.8893
	2	3	-2.44E-09	1.62E+05	Inf	0	1	2	3	0.143101	0.189466	Inf	0.755	0.9748	2	3	-2.98E-01	0.275202	Inf	-1.085	0.8877	2	3	7.28E-01	0.32544	Inf	2.238	0.2204
	2	4	-2.92E+01	1.15E+05	Inf	0	1	2	4	-1.05315	0.149935	Inf	-7.024	**<.0001**	2	4	1.34E+00	0.458416	Inf	2.931	**0.0396**	2	4	-4.17E-01	0.239186	Inf	-1.743	0.5031
	2	5	-2.85E+01	1.15E+05	Inf	0	1	2	5	-0.922935	0.152608	Inf	-6.048	**<.0001**	2	5	7.38E-01	0.366589	Inf	2.012	0.3353	2	5	4.23E-01	0.295151	Inf	1.433	0.707
	2	6	-1.65E-08	1.62E+05	Inf	0	1	2	6	0.538997	0.212693	Inf	2.534	0.1142	2	6	1.19E+00	0.431666	Inf	2.756	0.0648	2	6	1.29E+00	0.399353	Inf	3.225	**0.0159**
	3	4	-2.92E+01	1.15E+05	Inf	0	1	3	4	-1.196251	0.158255	Inf	-7.559	**<.0001**	3	4	1.64E+00	0.44601	Inf	3.682	**0.0032**	3	4	-1.15E+00	0.306848	Inf	-3.732	**0.0026**
	3	5	-2.85E+01	1.15E+05	Inf	0	1	3	5	-1.066036	0.16079	Inf	-6.63	**<.0001**	3	5	1.04E+00	0.350952	Inf	2.952	**0.0372**	3	5	-3.05E-01	0.352222	Inf	-0.867	0.9543
	3	6	-1.40E-08	1.62E+05	Inf	0	1	3	6	0.395896	0.218637	Inf	1.811	0.4587	3	6	1.49E+00	0.418468	Inf	3.556	**0.0051**	3	6	5.60E-01	0.443203	Inf	1.263	0.8054
	4	5	7.37E-01	1.49E-01	Inf	4.961	**<.0001**	4	5	0.130215	0.111519	Inf	1.168	0.8523	4	5	-6.06E-01	0.507519	Inf	-1.194	0.8398	4	5	8.40E-01	0.274516	Inf	3.059	**0.027**
	4	6	2.92E+01	1.15E+05	Inf	0	1	4	6	1.592146	0.185433	Inf	8.586	**<.0001**	4	6	-1.54E-01	0.556349	Inf	-0.277	0.9998	4	6	1.70E+00	0.384353	Inf	4.435	**0.0001**
	5	6	2.85E+01	1.15E+05	Inf	0	1	5	6	1.461932	0.187601	Inf	7.793	**<.0001**	5	6	4.52E-01	0.483494	Inf	0.935	0.9376	5	6	8.65E-01	0.421464	Inf	2.052	0.3127
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Helix	1	2	-2.08E+00	1.06E+00	Inf	-1.961	0.3653	1	2	-0.465363	0.245546	Inf	-1.895	0.405	1	2	-1.28E+00	0.32648	Inf	-3.909	**0.0013**	1	2	-3.51E-01	0.299447	Inf	-1.173	0.8496
	1	3	-3.47E+00	1.02E+00	Inf	-3.413	**0.0084**	1	3	-1.1815	0.220002	Inf	-5.37	**<.0001**	1	3	6.93E-01	0.5	Inf	1.386	0.7354	1	3	-1.00E-01	0.316624	Inf	-0.316	0.9996
	1	4	-4.22E+00	1.01E+00	Inf	-4.189	**0.0004**	1	4	1.909543	0.535758	Inf	3.564	**0.0049**	1	4	8.75E-01	0.532291	Inf	1.645	0.5687	1	4	-5.13E-02	0.320362	Inf	-0.16	1
	1	5	-5.46E+00	1.00E+00	Inf	-5.452	**<.0001**	1	5	-1.299283	0.217113	Inf	-5.984	**<.0001**	1	5	5.39E-01	0.475595	Inf	1.133	0.8676	1	5	-5.21E-01	0.289623	Inf	-1.8	0.4657
	1	6	-3.00E+00	1.02E+00	Inf	-2.924	**0.0405**	1	6	-0.071459	0.267432	Inf	-0.267	0.9998	1	6	1.39E+00	0.645497	Inf	2.148	0.2628	1	6	1.72E-01	0.33931	Inf	0.506	0.9959
	2	3	-1.39E+00	3.95E-01	Inf	-3.507	**0.006**	2	3	-0.716137	0.186063	Inf	-3.849	**0.0017**	2	3	1.97E+00	0.435801	Inf	4.519	**0.0001**	2	3	2.51E-01	0.290957	Inf	0.864	0.955
	2	4	-2.14E+00	3.74E-01	Inf	-5.725	**<.0001**	2	4	2.374906	0.522739	Inf	4.543	**0.0001**	2	4	2.15E+00	0.4725	Inf	4.554	**0.0001**	2	4	3.00E-01	0.29502	Inf	1.017	0.9124
	2	5	-3.38E+00	3.60E-01	Inf	-9.414	**<.0001**	2	5	-0.83392	0.182639	Inf	-4.566	**0.0001**	2	5	1.82E+00	0.40757	Inf	4.454	**0.0001**	2	5	-1.70E-01	0.261318	Inf	-0.65	0.9871
	2	6	-9.16E-01	4.18E-01	Inf	-2.19	0.2422	2	6	0.393904	0.240289	Inf	1.639	0.5723	2	6	2.66E+00	0.597151	Inf	4.459	**0.0001**	2	6	5.23E-01	0.315495	Inf	1.658	0.5595
	3	4	-7.54E-01	2.14E-01	Inf	-3.516	**0.0058**	3	4	3.091042	0.511237	Inf	6.046	**<.0001**	3	4	1.82E-01	0.60553	Inf	0.301	0.9997	3	4	4.88E-02	0.312441	Inf	0.156	1
	3	5	-2.00E+00	1.88E-01	Inf	-10.607	**<.0001**	3	5	-0.117783	0.146508	Inf	-0.804	0.9669	3	5	-1.54E-01	0.556349	Inf	-0.277	0.9998	3	5	-4.21E-01	0.280836	Inf	-1.5	0.6644
	3	6	4.70E-01	2.85E-01	Inf	1.649	0.5659	3	6	1.110041	0.214118	Inf	5.184	**<.0001**	3	6	6.93E-01	0.707107	Inf	0.98	0.9244	3	6	2.72E-01	0.331842	Inf	0.819	0.9641
	4	5	-1.24E+00	1.38E-01	Inf	-9.042	**<.0001**	4	5	-3.208825	0.510001	Inf	-6.292	**<.0001**	4	5	-3.36E-01	0.58554	Inf	-0.575	0.9927	4	5	-4.70E-01	0.285044	Inf	-1.649	0.5659
	4	6	1.22E+00	2.54E-01	Inf	4.811	**<.0001**	4	6	-1.981001	0.533369	Inf	-3.714	**0.0028**	4	6	5.11E-01	0.730297	Inf	0.699	0.9821	4	6	2.23E-01	0.33541	Inf	0.665	0.9857
	5	6	2.47E+00	2.33E-01	Inf	10.598	**<.0001**	5	6	1.227824	0.211149	Inf	5.815	**<.0001**	5	6	8.47E-01	0.690066	Inf	1.228	0.8233	5	6	6.93E-01	0.306186	Inf	2.264	0.209
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Knife	1	2	-1.84E+00	3.40E-01	Inf	-5.407	**<.0001**	1	2	0.926762	0.271044	Inf	3.419	**0.0083**	1	2	2.88E-01	0.763763	Inf	0.377	0.999	1	2	1.82E-01	0.60553	Inf	0.301	0.9997
	1	3	-2.87E+00	3.25E-01	Inf	-8.841	**<.0001**	1	3	-1.588385	0.158394	Inf	-10.028	**<.0001**	1	3	-2.23E-01	0.67082	Inf	-0.333	0.9995	1	3	-4.05E-01	0.527046	Inf	-0.769	0.9727
	1	4	-8.75E-01	3.76E-01	Inf	-2.326	0.1835	1	4	-1.159237	0.165437	Inf	-7.007	**<.0001**	1	4	6.93E-01	0.866025	Inf	0.8	0.9675	1	4	4.05E-01	0.645497	Inf	0.628	0.989
	1	5	2.66E+01	1.15E+05	Inf	0	1	1	5	0.693147	0.25	Inf	2.773	0.0619	1	5	-5.60E-01	0.626783	Inf	-0.893	0.9484	1	5	-4.05E-01	0.527046	Inf	-0.769	0.9727
	1	6	1.05E-01	4.59E-01	Inf	0.229	0.9999	1	6	3.178054	0.721688	Inf	4.404	**0.0002**	1	6	-9.16E-01	0.591608	Inf	-1.549	0.6325	1	6	1.10E+00	0.816496	Inf	1.346	0.7595
	2	3	-1.03E+00	1.47E-01	Inf	-7.042	**<.0001**	2	3	-2.515147	0.23851	Inf	-10.545	**<.0001**	2	3	-5.11E-01	0.730297	Inf	-0.699	0.9821	2	3	-5.88E-01	0.557773	Inf	-1.054	0.8994
	2	4	9.65E-01	2.40E-01	Inf	4.023	**0.0008**	2	4	-2.085999	0.243244	Inf	-8.576	**<.0001**	2	4	4.05E-01	0.912871	Inf	0.444	0.9978	2	4	2.23E-01	0.67082	Inf	0.333	0.9995
	2	5	2.84E+01	1.15E+05	Inf	0	1	2	5	-0.233615	0.30708	Inf	-0.761	0.974	2	5	-8.47E-01	0.690066	Inf	-1.228	0.8233	2	5	-5.88E-01	0.557773	Inf	-1.054	0.8994
	2	6	1.95E+00	3.56E-01	Inf	5.461	**<.0001**	2	6	2.251292	0.743392	Inf	3.028	**0.0296**	2	6	-1.20E+00	0.658281	Inf	-1.829	0.4469	2	6	9.16E-01	0.83666	Inf	1.095	0.8835
	3	4	2.00E+00	2.18E-01	Inf	9.186	**<.0001**	3	4	0.429148	0.103881	Inf	4.131	**0.0005**	3	4	9.16E-01	0.83666	Inf	1.095	0.8835	3	4	8.11E-01	0.600925	Inf	1.349	0.7572
	3	5	2.95E+01	1.15E+05	Inf	0	1	3	5	2.281532	0.214294	Inf	10.647	**<.0001**	3	5	-3.36E-01	0.58554	Inf	-0.575	0.9927	3	5	-7.84E-16	0.471405	Inf	0	1
	3	6	2.98E+00	3.42E-01	Inf	8.718	**<.0001**	3	6	4.766438	0.710109	Inf	6.712	**<.0001**	3	6	-6.93E-01	0.547723	Inf	-1.266	0.8039	3	6	1.50E+00	0.781736	Inf	1.924	0.3873
	4	5	2.75E+01	1.15E+05	Inf	0	1	4	5	1.852384	0.219551	Inf	8.437	**<.0001**	4	5	-1.25E+00	0.801784	Inf	-1.562	0.6234	4	5	-8.11E-01	0.600925	Inf	-1.349	0.7572
	4	6	9.81E-01	3.91E-01	Inf	2.509	0.1213	4	6	4.337291	0.711713	Inf	6.094	**<.0001**	4	6	-1.61E+00	0.774596	Inf	-2.078	0.2989	4	6	6.93E-01	0.866025	Inf	0.8	0.9675
	5	6	-2.65E+01	1.15E+05	Inf	0	1	5	6	2.484907	0.73598	Inf	3.376	**0.0096**	5	6	-3.57E-01	0.492805	Inf	-0.724	0.9791	5	6	1.50E+00	0.781736	Inf	1.924	0.3873
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Rib	1	2	-3.14E+01	1.15E+05	Inf	0	1	1	2	0.757686	0.312916	Inf	2.421	0.1488	1	2	-1.02E+00	0.38873	Inf	-2.628	0.0905	1	2	-2.30E+00	0.349603	Inf	-6.586	**<.0001**
	1	3	-1.28E-09	1.62E+05	Inf	0	1	1	3	1.067841	0.349513	Inf	3.055	**0.0273**	1	3	1.18E-01	0.485913	Inf	0.242	0.9999	1	3	-1.13E+00	0.383178	Inf	-2.962	**0.0361**
	1	4	-3.15E+01	1.15E+05	Inf	0	1	1	4	0.632523	0.300123	Inf	2.108	0.2832	1	4	5.88E-01	0.557773	Inf	1.054	0.8994	1	4	-1.17E+00	0.381568	Inf	-3.066	**0.0264**
	1	5	-9.47E-12	1.62E+05	Inf	0	1	1	5	1.163151	0.362284	Inf	3.211	**0.0167**	1	5	8.11E-01	0.600925	Inf	1.349	0.7572	1	5	-4.42E-01	0.427247	Inf	-1.034	0.9065
	1	6	-2.86E+01	1.15E+05	Inf	0	1	1	6	0.900787	0.328897	Inf	2.739	0.0678	1	6	5.88E-01	0.557773	Inf	1.054	0.8994	1	6	-2.53E+00	0.346353	Inf	-7.305	**<.0001**
	2	3	3.14E+01	1.15E+05	Inf	0	1	2	3	0.310155	0.396958	Inf	0.781	0.9707	2	3	1.14E+00	0.406202	Inf	2.805	0.0566	2	3	1.17E+00	0.216392	Inf	5.396	**<.0001**
	2	4	-1.22E-01	3.99E-02	Inf	-3.051	**0.0277**	2	4	-0.125163	0.354246	Inf	-0.353	0.9993	2	4	1.61E+00	0.489898	Inf	3.285	**0.013**	2	4	1.13E+00	0.213527	Inf	5.304	**<.0001**
	2	5	3.14E+01	1.15E+05	Inf	0	1	2	5	0.405465	0.408248	Inf	0.993	0.9203	2	5	1.83E+00	0.538517	Inf	3.403	**0.0087**	2	5	1.86E+00	0.287297	Inf	6.477	**<.0001**
	2	6	2.78E+00	1.21E-01	Inf	23.087	**<.0001**	2	6	0.143101	0.378932	Inf	0.378	0.999	2	6	1.61E+00	0.489898	Inf	3.285	**0.013**	2	6	-2.28E-01	0.141282	Inf	-1.611	0.5913
	3	4	-3.15E+01	1.15E+05	Inf	0	1	3	4	-0.435318	0.386953	Inf	-1.125	0.8712	3	4	4.70E-01	0.570088	Inf	0.824	0.9631	3	4	-3.51E-02	0.264947	Inf	-0.132	1
	3	5	1.27E-09	1.62E+05	Inf	0	1	3	5	0.09531	0.436931	Inf	0.218	0.9999	3	5	6.93E-01	0.612372	Inf	1.132	0.8682	3	5	6.93E-01	0.327327	Inf	2.118	0.278
	3	6	-2.86E+01	1.15E+05	Inf	0	1	3	6	-0.167054	0.409673	Inf	-0.408	0.9986	3	6	4.70E-01	0.570088	Inf	0.824	0.9631	3	6	-1.40E+00	0.211102	Inf	-6.609	**<.0001**
	4	5	3.15E+01	1.15E+05	Inf	0	1	4	5	0.530628	0.398527	Inf	1.331	0.7675	4	5	2.23E-01	0.67082	Inf	0.333	0.9995	4	5	7.28E-01	0.32544	Inf	2.238	0.2204
	4	6	2.91E+00	1.20E-01	Inf	24.162	**<.0001**	4	6	0.268264	0.368438	Inf	0.728	0.9785	4	6	8.88E-16	0.632456	Inf	0	1	4	6	-1.36E+00	0.208164	Inf	-6.534	**<.0001**
	5	6	-2.86E+01	1.15E+05	Inf	0	1	5	6	-0.262364	0.420622	Inf	-0.624	0.9893	5	6	-2.23E-01	0.67082	Inf	-0.333	0.9995	5	6	-2.09E+00	0.283334	Inf	-7.371	**<.0001**

	Scaridae							Serranidae							Siganidae						
Reef	**Site**	**Contrast**	**estimate**	**SE**	**df**	**z.ratio**	**p value**	**Site**	**Contrast**	**estimate**	**SE**	**df**	**z.ratio**	**p value**	**Site**	**Contrast**	**estimate**	**SE**	**df**	**z.ratio**	**p value**
Chicken	1	2	0.405465	0.123091	Inf	3.294	**0.0127**	1	2	-2.23E-01	4.74E-01	Inf	-0.47	0.9971	1	2	4.05E-01	9.13E-01	Inf	0.444	0.9978
	1	3	0.480973	0.125954	Inf	3.819	**0.0019**	1	3	2.88E-01	5.40E-01	Inf	0.533	0.9949	1	3	3.44E-15	8.16E-01	Inf	0	1
	1	4	0.178692	0.115356	Inf	1.549	0.6323	1	4	-1.10E+00	4.08E-01	Inf	-2.691	0.077	1	4	-1.20E+00	6.58E-01	Inf	-1.829	0.4469
	1	5	0.978811	0.148962	Inf	6.571	**<.0001**	1	5	-6.29E-01	4.38E-01	Inf	-1.436	0.7051	1	5	-9.81E-01	6.77E-01	Inf	-1.449	0.697
	1	6	-0.098061	0.107495	Inf	-0.912	0.9435	1	6	-1.18E-01	4.86E-01	Inf	-0.242	0.9999	1	6	-1.73E+00	6.26E-01	Inf	-2.77	0.0624
	2	3	0.075508	0.137458	Inf	0.549	0.9941	2	3	5.11E-01	5.16E-01	Inf	0.989	0.9216	2	3	-4.05E-01	9.13E-01	Inf	-0.444	0.9978
	2	4	-0.226773	0.127817	Inf	-1.774	0.4825	2	4	-8.75E-01	3.76E-01	Inf	-2.326	0.1835	2	4	-1.61E+00	7.75E-01	Inf	-2.078	0.2989
	2	5	0.573346	0.158808	Inf	3.61	**0.0041**	2	5	-4.05E-01	4.08E-01	Inf	-0.993	0.9203	2	5	-1.39E+00	7.91E-01	Inf	-1.754	0.4962
	2	6	-0.503526	0.12077	Inf	-4.169	**0.0004**	2	6	1.05E-01	4.59E-01	Inf	0.229	0.9999	2	6	-2.14E+00	7.48E-01	Inf	-2.863	**0.0482**
	3	4	-0.302281	0.130577	Inf	-2.315	0.1879	3	4	-1.39E+00	4.56E-01	Inf	-3.037	**0.0288**	3	4	-1.20E+00	6.58E-01	Inf	-1.829	0.4469
	3	5	0.497838	0.161037	Inf	3.091	**0.0244**	3	5	-9.16E-01	4.83E-01	Inf	-1.897	0.404	3	5	-9.81E-01	6.77E-01	Inf	-1.449	0.697
	3	6	-0.579034	0.123687	Inf	-4.681	**<.0001**	3	6	-4.05E-01	5.27E-01	Inf	-0.769	0.9727	3	6	-1.73E+00	6.26E-01	Inf	-2.77	0.0624
	4	5	0.800119	0.15289	Inf	5.233	**<.0001**	4	5	4.70E-01	3.29E-01	Inf	1.428	0.7099	4	5	2.23E-01	4.74E-01	Inf	0.47	0.9971
	4	6	-0.276753	0.112876	Inf	-2.452	0.1388	4	6	9.81E-01	3.91E-01	Inf	2.509	0.1213	4	6	-5.31E-01	3.99E-01	Inf	-1.331	0.7675
	5	6	-1.076872	0.147049	Inf	-7.323	**<.0001**	5	6	5.11E-01	4.22E-01	Inf	1.212	0.8315	5	6	-7.54E-01	4.29E-01	Inf	-1.758	0.4932
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Helix	1	2	-1.878988	0.134207	Inf	-14.001	**<.0001**	1	2	-2.69E+01	1.15E+05	Inf	0	1	1	2	1.79E+00	5.40E-01	Inf	3.318	**0.0117**
	1	3	-1.374506	0.13992	Inf	-9.824	**<.0001**	1	3	-2.50E+01	1.15E+05	Inf	0	1	1	3	9.81E-01	3.91E-01	Inf	2.509	0.1213
	1	4	1.067841	0.247143	Inf	4.321	**0.0002**	1	4	-2.61E+01	1.15E+05	Inf	0	1	1	4	1.10E+00	4.08E-01	Inf	2.691	0.077
	1	5	0.09844	0.181291	Inf	0.543	0.9944	1	5	-2.85E+01	1.15E+05	Inf	0	1	1	5	2.08E+00	6.12E-01	Inf	3.396	**0.009**
	1	6	-0.184922	0.169151	Inf	-1.093	0.8843	1	6	-2.82E+01	1.15E+05	Inf	0	1	1	6	6.93E-01	3.54E-01	Inf	1.961	0.3653
	2	3	0.504481	0.079619	Inf	6.336	**<.0001**	2	3	1.95E+00	7.56E-01	Inf	2.574	0.1036	2	3	-8.11E-01	6.01E-01	Inf	-1.349	0.7572
	2	4	2.946828	0.218726	Inf	13.473	**<.0001**	2	4	8.47E-01	4.88E-01	Inf	1.736	0.5075	2	4	-6.93E-01	6.12E-01	Inf	-1.132	0.8682
	2	5	1.977428	0.1401	Inf	14.114	**<.0001**	2	5	-1.54E+00	2.95E-01	Inf	-5.211	**<.0001**	2	5	2.88E-01	7.64E-01	Inf	0.377	0.999
	2	6	1.694066	0.123991	Inf	13.663	**<.0001**	2	6	-1.25E+00	3.03E-01	Inf	-4.134	**0.0005**	2	6	-1.10E+00	5.77E-01	Inf	-1.903	0.4003
	3	4	2.442347	0.222277	Inf	10.988	**<.0001**	3	4	-1.10E+00	8.16E-01	Inf	-1.346	0.7595	3	4	1.18E-01	4.86E-01	Inf	0.242	0.9999
	3	5	1.472946	0.145581	Inf	10.118	**<.0001**	3	5	-3.48E+00	7.18E-01	Inf	-4.849	**<.0001**	3	5	1.10E+00	6.67E-01	Inf	1.648	0.5665
	3	6	1.189584	0.130152	Inf	9.14	**<.0001**	3	6	-3.20E+00	7.21E-01	Inf	-4.434	**0.0001**	3	6	-2.88E-01	4.41E-01	Inf	-0.652	0.9869
	4	5	-0.969401	0.250392	Inf	-3.872	**0.0015**	4	5	-2.38E+00	4.27E-01	Inf	-5.584	**<.0001**	4	5	9.81E-01	6.77E-01	Inf	1.449	0.697
	4	6	-1.252763	0.241747	Inf	-5.182	**<.0001**	4	6	-2.10E+00	4.33E-01	Inf	-4.855	**<.0001**	4	6	-4.05E-01	4.56E-01	Inf	-0.888	0.9494
	5	6	-0.283362	0.173863	Inf	-1.63	0.5787	5	6	2.83E-01	1.89E-01	Inf	1.494	0.6685	5	6	-1.39E+00	6.45E-01	Inf	-2.148	0.2628
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Knife	1	2	-0.09844	0.128192	Inf	-0.768	0.9729	1	2	2.43E+01	1.15E+05	Inf	0	1	1	2	-1.39E+00	1.12E+00	Inf	-1.24	0.8172
	1	3	-0.050431	0.129682	Inf	-0.389	0.9989	1	3	-1.79E+00	1.08E+00	Inf	-1.659	0.5592	1	3	2.23E+01	4.22E+04	Inf	0.001	1
	1	4	0.253781	0.14047	Inf	1.807	0.4613	1	4	-6.93E-01	1.22E+00	Inf	-0.566	0.9932	1	4	-1.95E+00	1.07E+00	Inf	-1.82	0.4526
	1	5	0.287682	0.141827	Inf	2.028	0.326	1	5	-1.61E+00	1.10E+00	Inf	-1.469	0.684	1	5	-2.77E+00	1.03E+00	Inf	-2.69	0.0772
	1	6	1.257083	0.197291	Inf	6.372	**<.0001**	1	6	-2.83E+00	1.03E+00	Inf	-2.753	0.0652	1	6	-3.04E+00	1.02E+00	Inf	-2.975	**0.0348**
	2	3	0.048009	0.126528	Inf	0.379	0.999	2	3	-2.61E+01	1.15E+05	Inf	0	1	2	3	2.37E+01	4.22E+04	Inf	0.001	1
	2	4	0.352221	0.137563	Inf	2.56	0.1072	2	4	-2.50E+01	1.15E+05	Inf	0	1	2	4	-5.60E-01	6.27E-01	Inf	-0.893	0.9484
	2	5	0.386122	0.138949	Inf	2.779	0.0609	2	5	-2.59E+01	1.15E+05	Inf	0	1	2	5	-1.39E+00	5.59E-01	Inf	-2.48	0.13
	2	6	1.355523	0.195232	Inf	6.943	**<.0001**	2	6	-2.71E+01	1.15E+05	Inf	0	1	2	6	-1.66E+00	5.46E-01	Inf	-3.04	**0.0286**
	3	4	0.304211	0.138953	Inf	2.189	0.2426	3	4	1.10E+00	8.16E-01	Inf	1.346	0.7595	3	4	-2.42E+01	4.22E+04	Inf	-0.001	1
	3	5	0.338113	0.140325	Inf	2.41	0.1528	3	5	1.82E-01	6.06E-01	Inf	0.301	0.9997	3	5	-2.51E+01	4.22E+04	Inf	-0.001	1
	3	6	1.307513	0.196214	Inf	6.664	**<.0001**	3	6	-1.04E+00	4.75E-01	Inf	-2.193	0.2408	3	6	-2.53E+01	4.22E+04	Inf	-0.001	1
	4	5	0.033902	0.150351	Inf	0.225	0.9999	4	5	-9.16E-01	8.37E-01	Inf	-1.095	0.8835	4	5	-8.27E-01	4.53E-01	Inf	-1.824	0.45
	4	6	1.003302	0.203505	Inf	4.93	**<.0001**	4	6	-2.14E+00	7.48E-01	Inf	-2.863	**0.0482**	4	6	-1.10E+00	4.36E-01	Inf	-2.517	0.119
	5	6	0.969401	0.204444	Inf	4.742	**<.0001**	5	6	-1.22E+00	5.09E-01	Inf	-2.405	0.1542	5	6	-2.72E-01	3.32E-01	Inf	-0.819	0.9641
	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value	Site	Contrast	estimate	SE	df	z.ratio	p value
Rib	1	2	0.736822	0.162494	Inf	4.534	**0.0001**	1	2	-1.10E+00	8.16E-01	Inf	-1.346	0.7595	1	2	-3.36E-01	4.14E-01	Inf	-0.813	0.9653
	1	3	0.870354	0.170162	Inf	5.115	**<.0001**	1	3	6.93E-01	1.22E+00	Inf	0.566	0.9932	1	3	1.20E+00	6.58E-01	Inf	1.829	0.4469
	1	4	1.000974	0.178333	Inf	5.613	**<.0001**	1	4	2.50E+01	1.15E+05	Inf	0	1	1	4	-3.36E-01	4.14E-01	Inf	-0.813	0.9653
	1	5	1.504077	0.216815	Inf	6.937	**<.0001**	1	5	2.50E+01	1.15E+05	Inf	0	1	1	5	2.30E+00	1.05E+00	Inf	2.195	0.2397
	1	6	0.229574	0.138923	Inf	1.653	0.5635	1	6	-1.70E+00	7.69E-01	Inf	-2.218	0.2294	1	6	9.16E-01	5.92E-01	Inf	1.549	0.6325
	2	3	0.133531	0.195615	Inf	0.683	0.9839	2	3	1.79E+00	1.08E+00	Inf	1.659	0.5592	2	3	1.54E+00	6.36E-01	Inf	2.421	0.1488
	2	4	0.264152	0.202763	Inf	1.303	0.7837	2	4	2.61E+01	1.15E+05	Inf	0	1	2	4	1.11E-16	3.78E-01	Inf	0	1
	2	5	0.767255	0.237316	Inf	3.233	**0.0155**	2	5	2.61E+01	1.15E+05	Inf	0	1	2	5	2.64E+00	1.04E+00	Inf	2.55	0.1101
	2	6	-0.507248	0.169144	Inf	-2.999	**0.0324**	2	6	-6.06E-01	5.08E-01	Inf	-1.194	0.8398	2	6	1.25E+00	5.67E-01	Inf	2.21	0.2331
	3	4	0.13062	0.208959	Inf	0.625	0.9892	3	4	2.43E+01	1.15E+05	Inf	0	1	3	4	-1.54E+00	6.36E-01	Inf	-2.421	0.1488
	3	5	0.633724	0.242631	Inf	2.612	0.0943	3	5	2.43E+01	1.15E+05	Inf	0	1	3	5	1.10E+00	1.15E+00	Inf	0.951	0.9329
	3	6	-0.640779	0.176524	Inf	-3.63	**0.0038**	3	6	-2.40E+00	1.04E+00	Inf	-2.296	0.1956	3	6	-2.88E-01	7.64E-01	Inf	-0.377	0.999
	4	5	0.503104	0.24843	Inf	2.025	0.3279	4	5	5.58E-10	1.62E+05	Inf	0	1	4	5	2.64E+00	1.04E+00	Inf	2.55	0.1101
	4	6	-0.771399	0.184414	Inf	-4.183	**0.0004**	4	6	-2.67E+01	1.15E+05	Inf	0	1	4	6	1.25E+00	5.67E-01	Inf	2.21	0.2331
	5	6	-1.274503	0.221843	Inf	-5.745	**<.0001**	5	6	-2.67E+01	1.15E+05	Inf	0	1	5	6	-1.39E+00	1.12E+00	Inf	-1.24	0.8172

***Figure S5-a**: 50% (red) and 95% (white) Brownian Bridge KUDs (KUD areas in km^2) for each tagged individual shark at Rib Reef. Yellow point=tagging location. KUDs were only plotted if there were more than 5 detections of an individual*

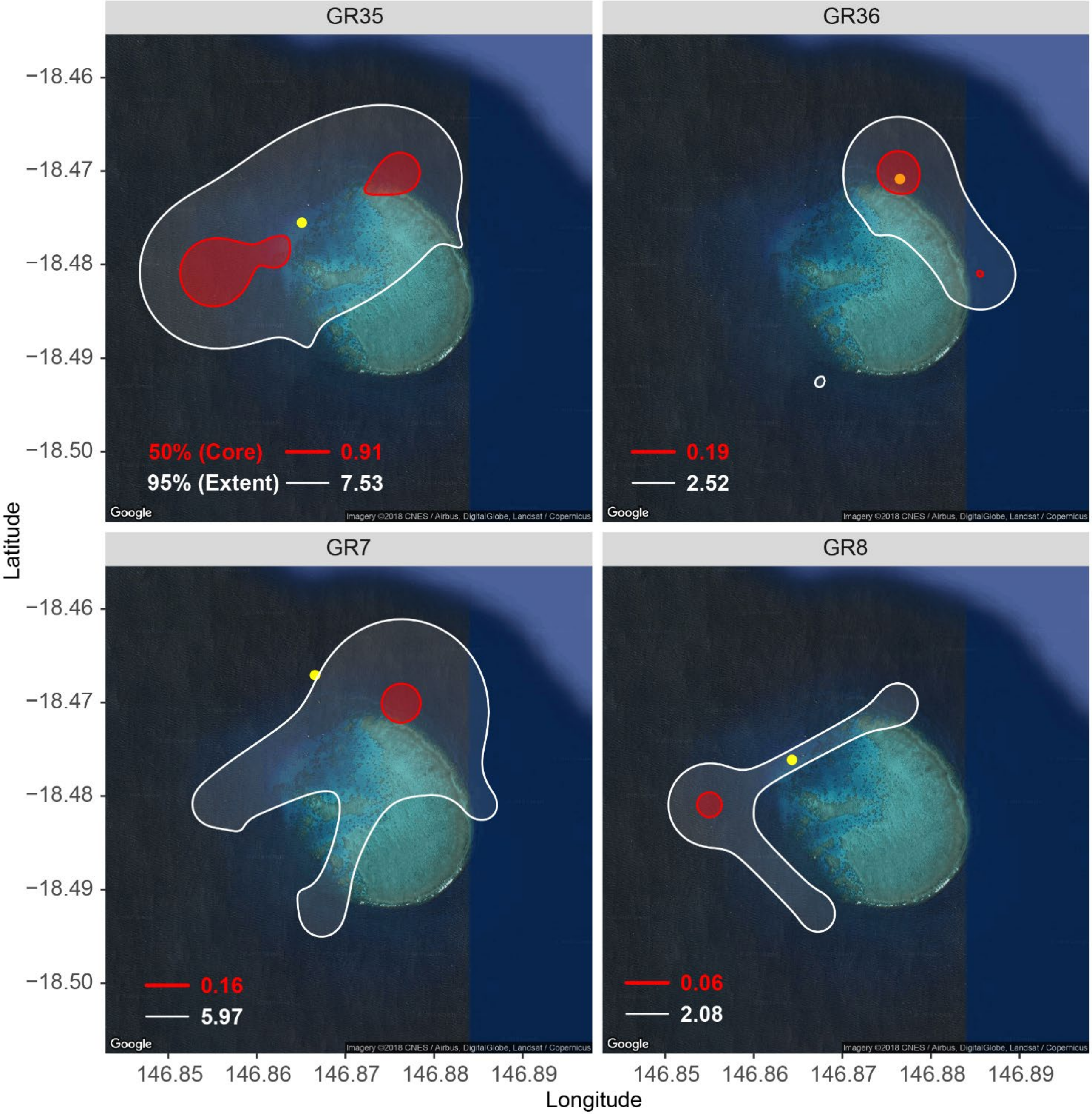


Figure S5-b: *50% (red) and 95% (white) Brownian Bridge KUDs (KUD areas in km^2) for each tagged individual shark at Helix Reef. Yellow point=tagging location. KUDs were only plotted if there were more than 5 detections of an individual*

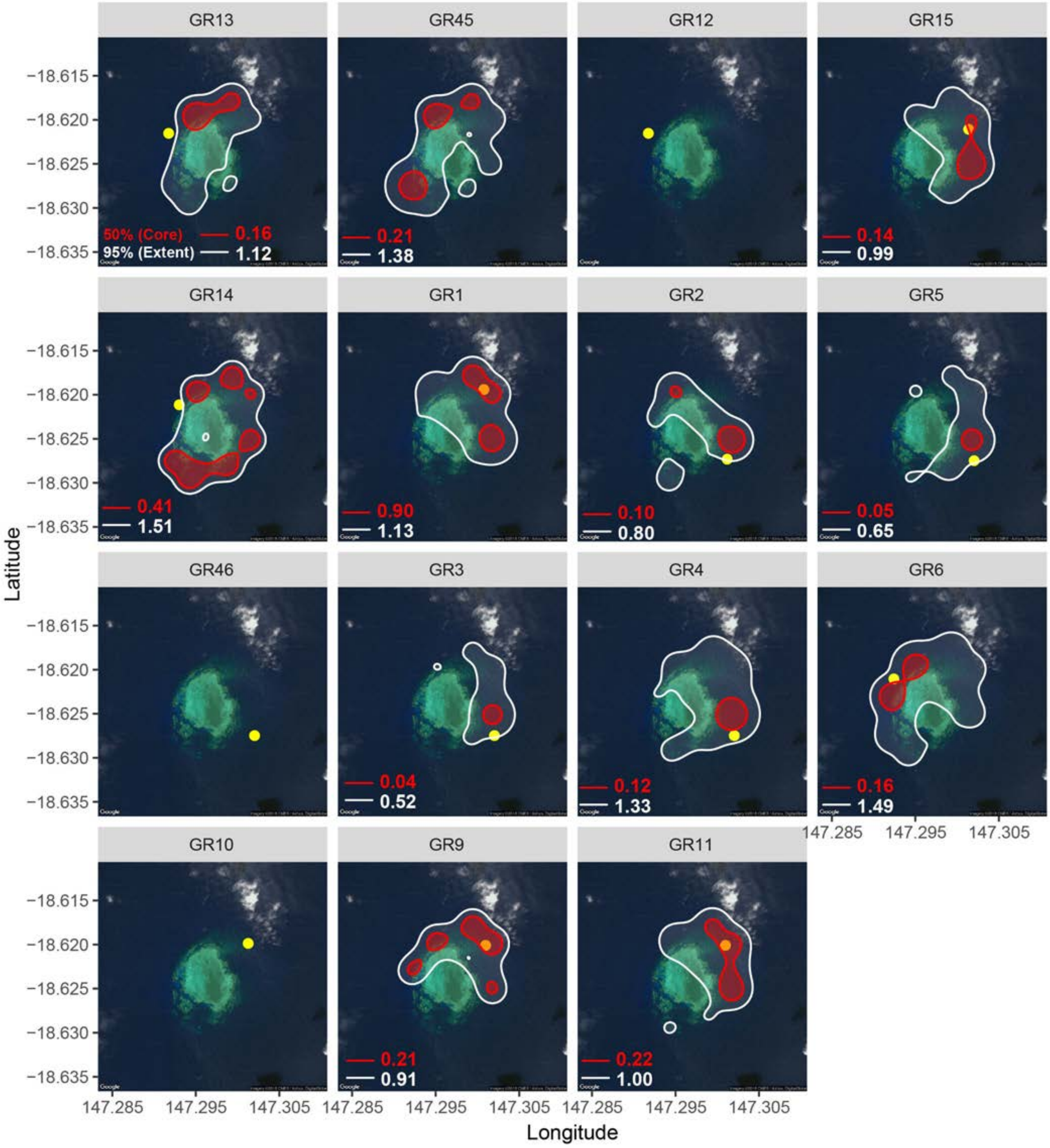


Figure S5-c*: 50% (red) and 95% (white) Brownian Bridge KUDs (KUD areas in km^2) for each tagged individual shark at Knife Reef. Yellow point=tagging location. KUDs were only plotted if there were more than 5 detections of an individual*

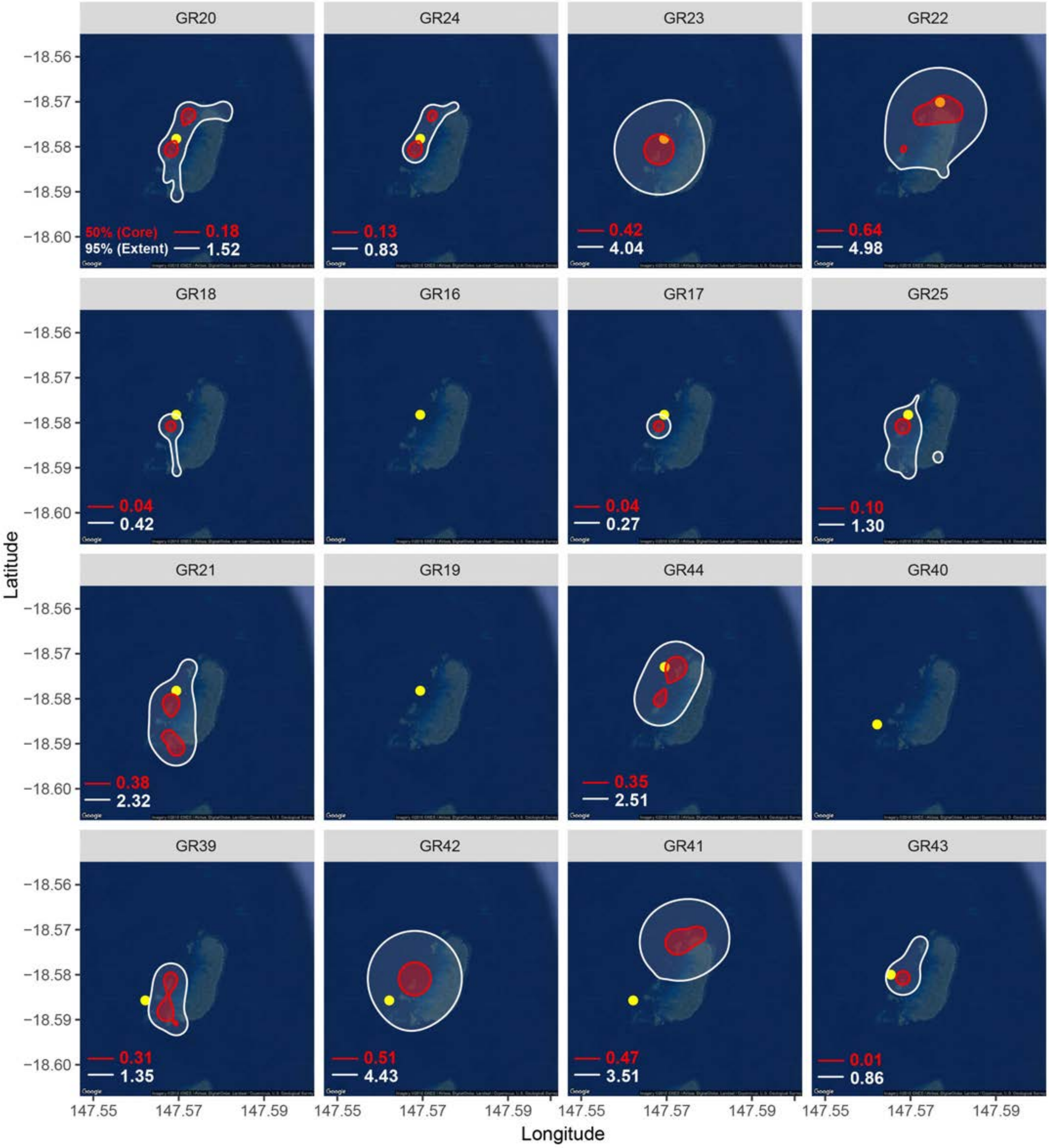


***Figure S5-d :** 50% (red) and 95% (white) Brownian Bridge KUDs (KUD areas in km^2) for each tagged individual shark at Chicken Reef. Yellow point=tagging location. KUDs were only plotted if there were more than 5 detections of an individual*

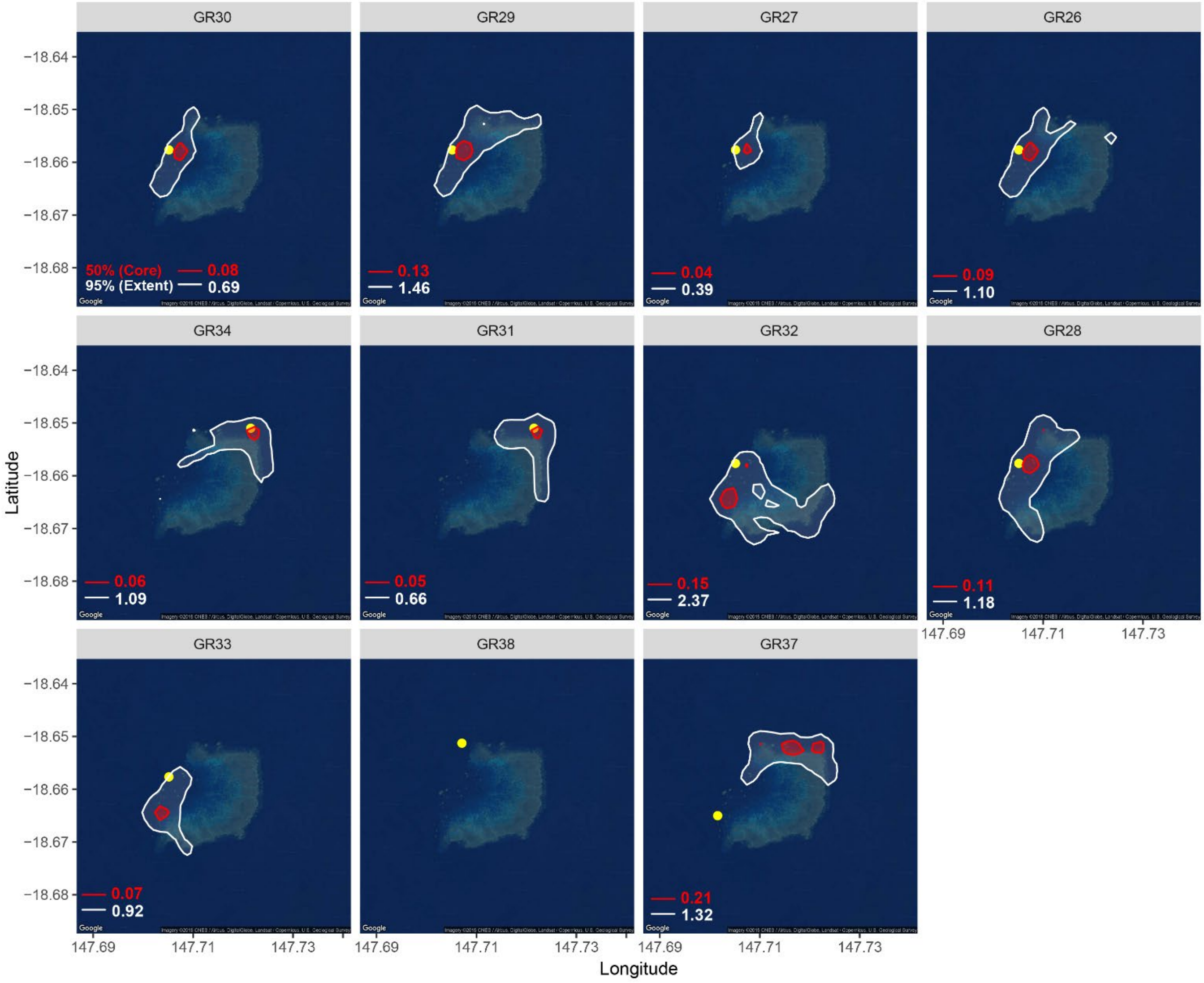


Figure S5-e*: Differences in weekly residency by sex for Rib reef*

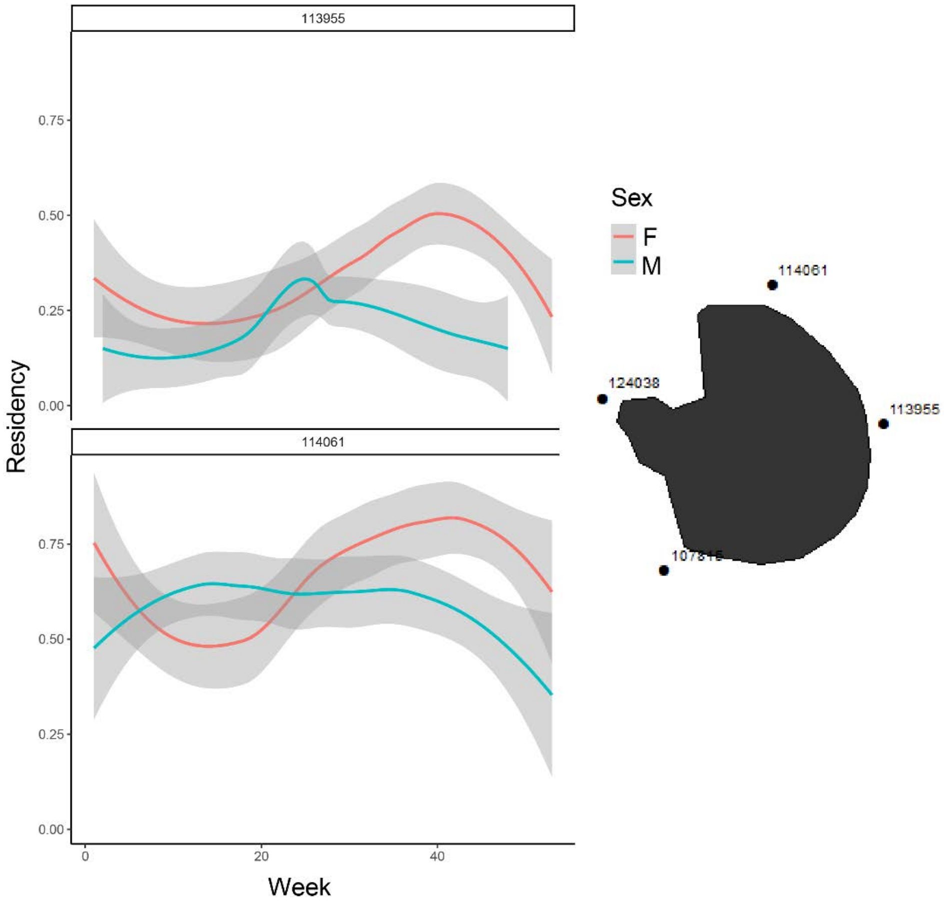


Figure S5-f*: Differences in weekly residency by sex for Helix reef*

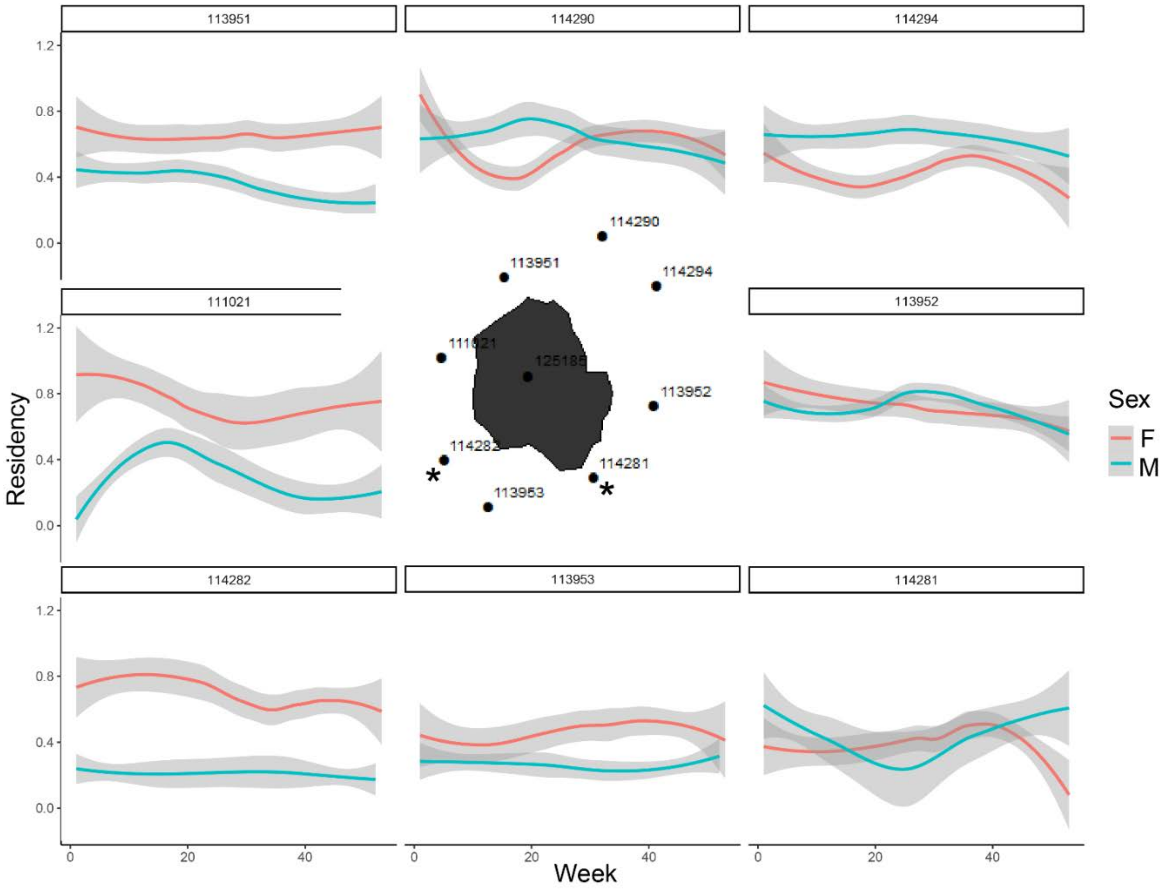


Figure S5-g*: Differences in weekly residency by sex for Chicken reef*

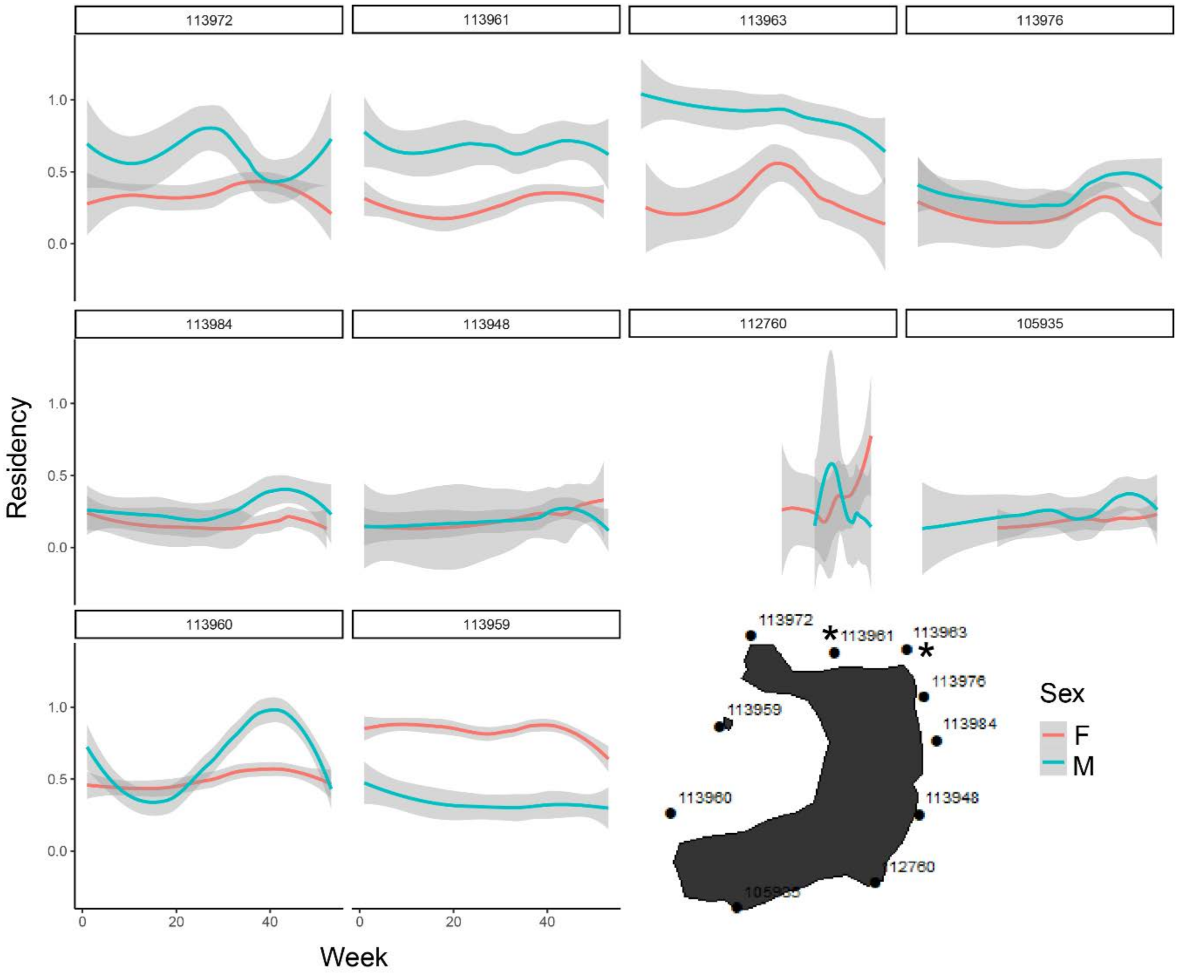


Figure S5-h*: Differences in weekly residency by sex for Knife reef*

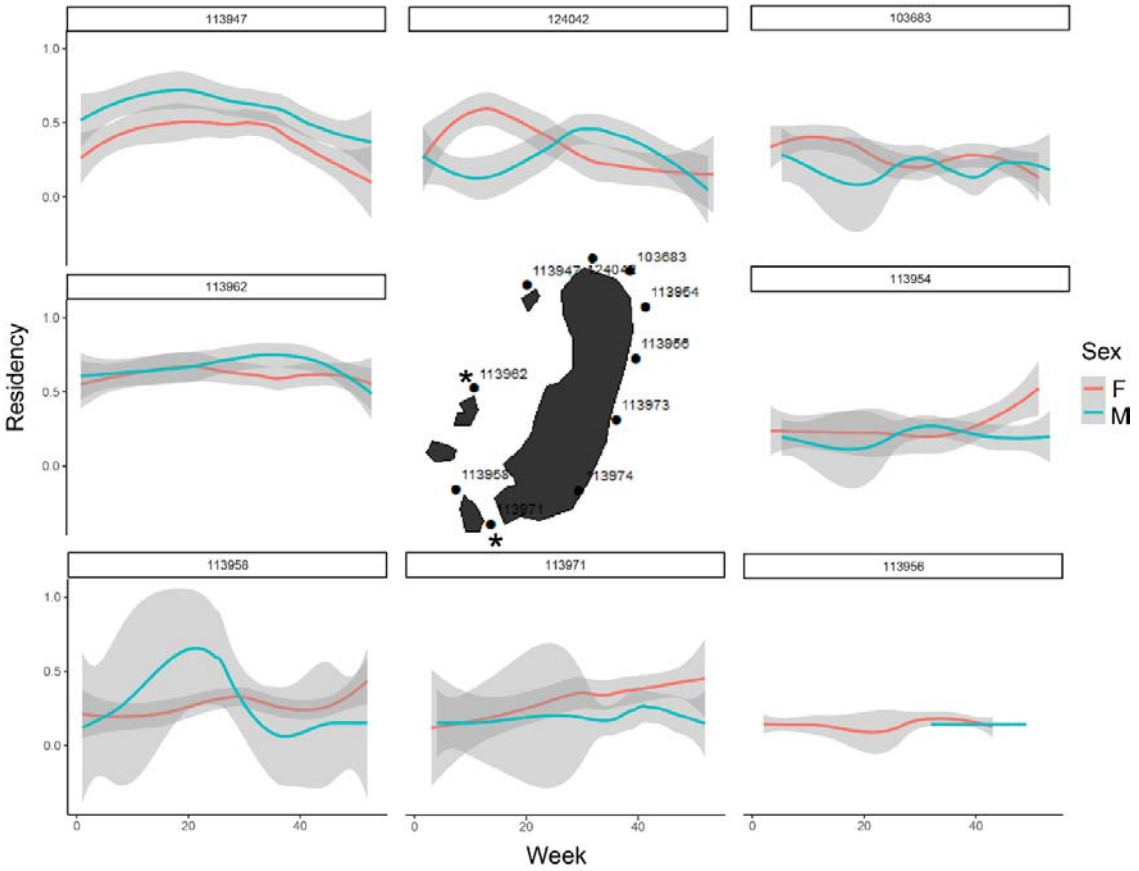


Figure S5-i*: Fish biomass*$^{-Reef}$ *(kg/1000 m*^{2}*) Pareto barplot with cumulative biomass curve by family*

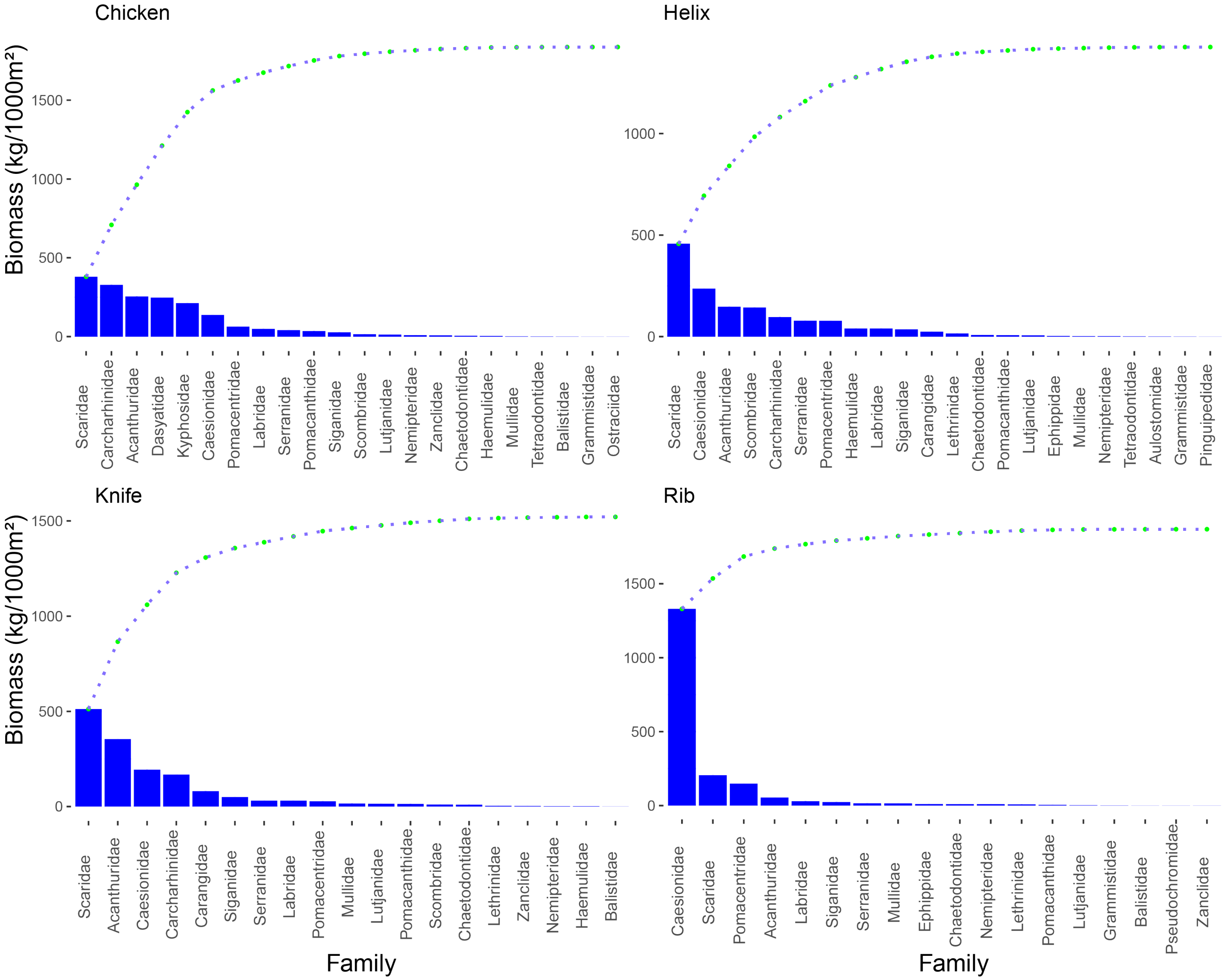


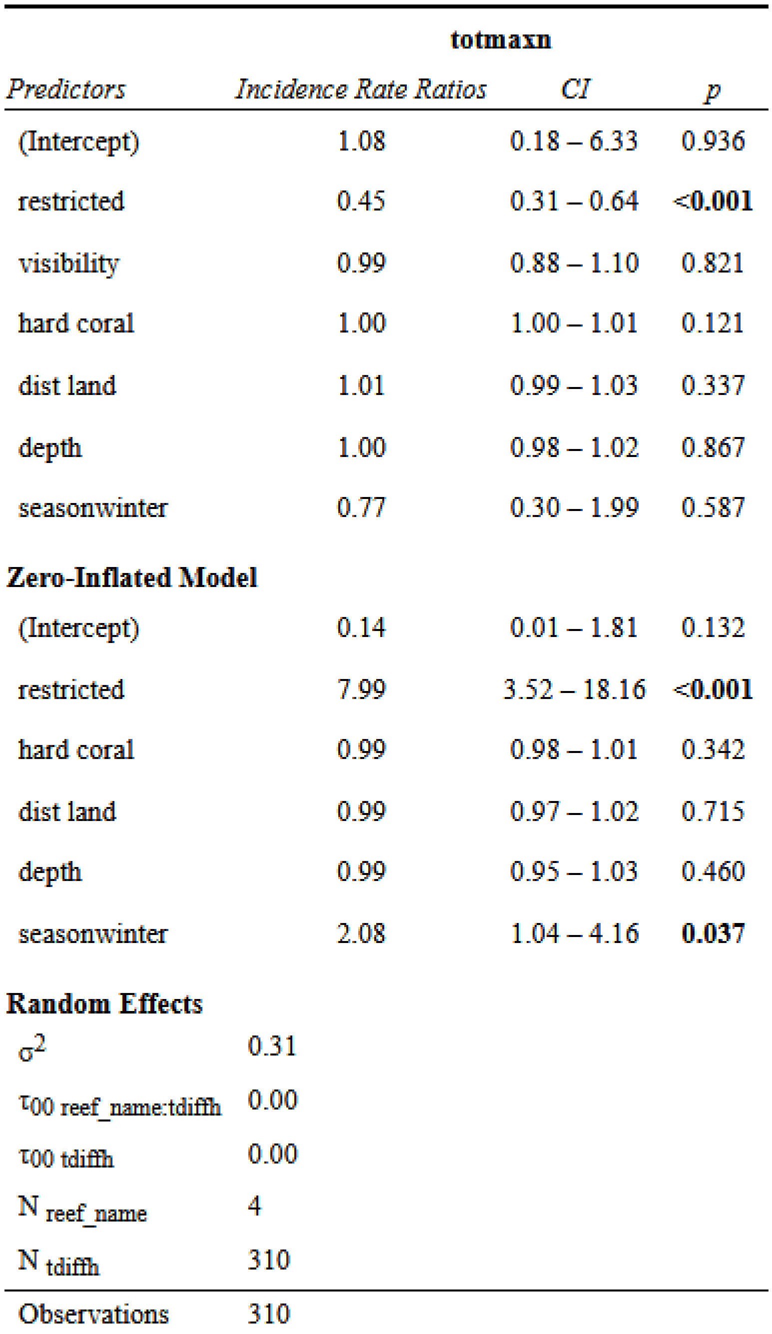
Table S6-a: *Generalised linear models of log-transformed CPUE data for total catch and species by primary management zone and year*

	log 10(CPUE+0.001)			**log 10(BTS+0.001)**			**log 10(GRS+0.001)**			**log 10(WTS+0.001)**			**log 10(BUL+0.001)**			**log 10(STS+0.001)**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	-2.44	-5.14 – 0.26	0.077	-4.23	-6.01 – -2.46	**<0.001**	-3.37	-6.85 – 0.11	0.057	-3.77	-5.34 – -2.19	**<0.001**	-1.88	-4.91 – 1.15	0.224	-1.79	-3.84 – 0.25	0.086
Open	0.11	-2.17 – 2.39	0.925	1.06	-0.46 – 2.57	0.173	-0.19	-2.95 – 2.57	0.893	0.38	-0.97 – 1.72	0.582	0.96	-1.63 – 3.54	0.467	-0.42	-2.10 – 1.26	0.624
Year 2013	1.61	-0.96 – 4.17	0.220	1.14	-0.53 – 2.81	0.182	1.61	-1.41 – 4.64	0.296	0.33	-1.15 – 1.81	0.662	1.15	-1.69 – 4.00	0.426	0.43	-1.41 – 2.27	0.646
Year 2014	1.24	-1.68 – 4.17	0.405	2.48	0.53 – 4.42	**0.013**	0.81	-2.56 – 4.18	0.638	2.01	0.29 – 3.73	**0.022**	1.81	-1.50 – 5.13	0.284	1.37	-0.74 – 3.48	0.202
Year 2015	1.39	-1.32 – 4.11	0.314	1.86	0.06 – 3.66	**0.043**	1.45	-1.56 – 4.46	0.346	1.08	-0.51 – 2.68	0.183	1.22	-1.84 – 4.29	0.435	1.07	-0.83 – 2.97	0.271
Year 2016	1.00	-1.72 – 3.71	0.473	0.96	-0.84 – 2.77	0.295	1.24	-1.78 – 4.25	0.422	0.18	-1.42 – 1.77	0.829	0.45	-2.62 – 3.53	0.773	0.80	-1.10 – 2.71	0.409
Year 2017	0.97	-0.94 – 2.89	0.319	0.94	-0.33 – 2.20	0.146	0.95	-1.25 – 3.15	0.397	1.73	0.61 – 2.85	**0.002**	0.60	-1.56 – 2.76	0.585	0.42	-0.95 – 1.79	0.550
Distland	0.01	-0.01 – 0.03	0.493	0.00	-0.01 – 0.02	0.620	0.02	-0.01 – 0.05	0.262	0.01	-0.00 – 0.02	0.220	-0.02	-0.04 – 0.00	0.090	-0.02	-0.03 – 0.00	0.069
ZoneOpen:Year2013	-0.45	-2.91 – 2.01	0.719	-0.95	-2.54 – 0.64	0.242	-1.02	-3.96 – 1.92	0.497	-0.17	-1.58 – 1.23	0.808	-0.54	-3.24 – 2.17	0.698	-0.31	-2.07 – 1.45	0.731
ZoneOpen:Year2014	-0.81	-3.66 – 2.05	0.579	-2.10	-3.99 – -0.20	**0.030**	-0.25	-3.55 – 3.06	0.884	-1.87	-3.55 – -0.19	**0.029**	-1.94	-5.17 – 1.30	0.240	-0.57	-2.63 – 1.49	0.590
ZoneOpen:Year2015	0.05	-2.74 – 2.85	0.972	-1.93	-3.78 – -0.07	**0.042**	0.39	-2.56 – 3.35	0.794	0.65	-1.00 – 2.29	0.440	-1.89	-5.05 – 1.28	0.243	-0.75	-2.66 – 1.15	0.439
ZoneOpen:Year2016	-0.32	-3.12 – 2.48	0.823	-0.37	-2.23 – 1.49	0.697	-0.26	-3.21 – 2.70	0.864	1.23	-0.41 – 2.87	0.142	-1.11	-4.27 – 2.06	0.494	-0.48	-2.38 – 1.43	0.622
Random Effects																		
σ^2	0.38			0.30			0.30			0.23			0.87			0.30		
τ_{00}	0.29 Year:Reef			0.00 Year:Reef			0.40 Year:Reef			0.00 Year:Reef			0.00 Year:Reef			0.00 Year:Reef		
	0.00 Reef			0.00 Reef			0.40 Reef			0.00 Reef			0.00 Reef			0.08 Reef		
ICC	0.43						0.73									0.21		
N	6 Year			6 Year			6 Year			6 Year			6 Year			6 Year		
	17 Reef			17 Reef			17 Reef			17 Reef			17 Reef			17 Reef		
Observations	50			50			50			50			50			50		
Marginal R^2 / Conditional R^2	0.274 / 0.589			0.349 / 0.823			0.298 / 0.448											

Table S6-b: *Negative binomial generalized linear mixed effect models (logit link) of fishing data for total catch and species with significant effects of management zone (random term conditional on month/Reef)*

	Catch			GRS		
Predictors	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*
(Intercept)	0.03	0.00 – 0.37	**0.005**	0.00	0.00 – 0.05	**<0.001**
Green	1.12	0.29 – 4.26	0.868	2.77	0.68 – 11.31	0.155
year 2013	1.12	0.35 – 3.60	0.851	6.21	0.73 – 52.91	0.095
year 2014	1.10	0.28 – 4.41	0.892	5.37	0.49 – 58.89	0.169
year 2015	2.52	0.66 – 9.59	0.174	11.13	1.27 – 97.47	**0.029**
year 2016	1.50	0.33 – 6.82	0.597	0.71	0.07 – 7.57	0.779
year 2017	0.79	0.15 – 4.20	0.781	1.17	0.09 – 14.89	0.905
dist land	0.99	0.97 – 1.02	0.654	1.03	1.00 – 1.06	0.091
Depth	1.00	0.97 – 1.02	0.790	0.97	0.94 – 1.00	0.065
Winter	0.71	0.37 – 1.39	0.320	0.64	0.26 – 1.58	0.331
moderate	2.10	1.14 – 3.87	**0.018**	3.23	1.37 – 7.60	**0.007**
nil	1.52	0.79 – 2.90	0.208	2.48	1.03 – 5.94	**0.042**
strong	1.95	0.87 – 4.38	0.104	3.12	1.13 – 8.57	**0.028**
very strong	1.16	0.24 – 5.69	0.852	1.45	0.21 – 9.89	0.706
ZoneGreen:year2013	2.23	0.53 – 9.42	0.277	0.80	0.16 – 3.98	0.785
ZoneGreen:year2014	1.10	0.20 – 6.01	0.914	0.06	0.00 – 0.84	**0.037**
ZoneGreen:year2015	0.90	0.25 – 3.29	0.872	0.29	0.06 – 1.50	0.139
ZoneGreen:year2016	4.87	1.26 – 18.90	**0.022**	1.75	0.35 – 8.71	0.493
Random Effects						
σ^2	3.29			3.29		
τ_{00}	$0.00_{\text{year:Reef}}$			$0.00_{\text{year:Reef}}$		
	0.19_{Reef}			0.05_{Reef}		
	$2.16_{\text{Hook.size}}$					
ICC	0.42			0.02		
N	$6_{\text{Hook.size}}$			6_{year}		
	6_{year}			16_{Reef}		
	16_{Reef}					
Observations	1819			1819		
Marginal R^2 / Conditional R^2	0.092 / 0.470			0.229 / 0.241		

Table S6-c: *Poisson (log link) and zero inflated negative binomial generalised linear mixed models for BRUVS deployments over two sampling seasons in 2016 showing significant effects of management zone and season with a random term conditional on soak time/reef.*



	totmaxn		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	1.08	0.18 – 6.33	0.936
restricted	0.45	0.31 – 0.64	**<0.001**
visibility	0.99	0.88 – 1.10	0.821
hard coral	1.00	1.00 – 1.01	0.121
dist land	1.01	0.99 – 1.03	0.337
depth	1.00	0.98 – 1.02	0.867
seasonwinter	0.77	0.30 – 1.99	0.587
Zero-Inflated Model			
(Intercept)	0.14	0.01 – 1.81	0.132
restricted	7.99	3.52 – 18.16	**<0.001**
hard coral	0.99	0.98 – 1.01	0.342
dist land	0.99	0.97 – 1.02	0.715
depth	0.99	0.95 – 1.03	0.460
seasonwinter	2.08	1.04 – 4.16	**0.037**
Random Effects			
σ^2	0.31		
τ_{00} reef_name:tdiffh	0.00		
τ_{00} tdiffh	0.00		
N reef_name	4		
N tdiffh	310		
Observations	310		