The effect of habitat and spatial management on reef fish assemblages in an established marine protected area

A thesis submitted in fulfilment of the requirements for the degree of

MASTER OF SCIENCE

at

RHODES UNIVERSITY

By Vivienne Abigail Dames

July 2020

ABSTRACT

Coral reefs are global biodiversity hotspots and one of the most vulnerable ecosystems on the planet. Human disturbances, extractive overfishing and a changing climate threaten to collapse 75% of coral reefs by 2050. Marine Protected Areas (MPAs) which prohibit all forms of human activities are documented to achieve maximum conservation benefits; however, 94% of international MPAs still allow some form of fishing. This is the case in the iSimangaliso Wetland Park (IWP), which has protected South Africa's high latitude coral reefs (HLCRs) for over 30 years. The MPA within IWP is zoned to include No-Take Sanctuary Zones (NTSZs), which prohibit all activity, and a Controlled-Pelagic Zone (CPZ), which allow SCUBA diving and pelagic fishing but restrict all other human activities. While accommodating human needs within an MPA is essential for stakeholder acceptance, little is known about the effect of anthropogenic activity within the IWP MPA.

Along with anthropogenic drivers, previous studies have conveyed that latitude, depth and habitat type are some of the key drivers in shaping coral reef fish communities. Within habitat type, available habitat area and fine-scale benthic characteristics have been highlighted as key determinants of reef fish community ecology. Whether these drivers apply to high latitude coral reef (HLCR) ecosystems remains a gap in coral reef ecosystem research. Thus, this study aimed to identify important environmental variables and the effect of different management zones on reef fish populations and communities on the HLCRs within iSimangaliso Wetland Park.

This study used baited remote underwater stereo-video systems (Stereo-BRUVs) to survey habitats and fish assemblage structure within different management zones (From north to south: Maputaland NTSZ, CPZ and St Lucia NTSZ) of the IWP. Variation in the taxonomic and functional entities was defined according to three metrics, abundance, size (fork length) and abundance per maturity stage (juvenile or adult). The significant environmental drivers were then identified for both taxonomic and functional trait-based reef fish assemblages. Once habitat variability was accounted for, the effect of different management zones on assemblage structure was determined.

The taxonomic and functional structure of reef fish communities consistently responded to habitat variability, with functional indices and diversity increasing in habitats associated with higher relief stony coral habitats and decreasing in low relief sandy or macroalgal habitats. When looking at individual species populations, reef size played an important role in determining the average biomass of the dominant species, with larger individuals typically associated with larger reef patches. A similar pattern was detected with fish abundance, but the effect was less pronounced than with the biomass data. The significant effect of habitat variation and reef size on the fish populations and assemblages stresses the importance of accounting for habitat variability in spatial comparison studies. This finding also offers important insight into the benefit of protecting different habitat types to increase the overall diversity of fishes protected.

Both NTSZs supported unique predatory functional groups and species, whereas the CPZ was characterised by juvenile species and functional groups characterised by juveniles, suggesting that the CPZ may be impacted by the permitted anthropogenic activity. Alternatively, the CPZ may serve as a unique nursery ground for juveniles, but as the habitats in the CPZ were similar to those in the NTSZs, it is not clear why this might be the case. The Maputaland NTSZ appeared to support unique fish communities with greater functional richness, attributed to the additional presence of macroalgal habitats, which were absent from the other zones of the MPA. Single species analysis suggested that *Lethrinus crocineus* and *Epinephelus tukula*, which are both protected throughout the MPAs, were affected by the anthropogenic activity within the CPZ, as they were typically smaller and less abundant in the CPZ relative to the NTSZs. In agreement with my findings, previous studies in the area have identified that *E. tukula* is negatively influenced by high diving pressure that occurs in the CPZ. Alternatively, populations of *Caranx melampygus* and *Aprion virescens*, which are both permitted to be captured in the CPZ, appeared to benefit from the additional protection within the NTSZs and demonstrated direct impacts of past and present fishing pressure within the CPZ. The populations of *A. virescens*, *C. melampygus*, *E. tukula* and *L. crocineus* all displayed potentially greater abundance or biomass, or both, within the St Lucia NTSZ as compared to the Maputaland NTSZ. The fact that the St Lucia NTSZ is older than the Maputaland NTSZ may be the driving factor of this pattern. As for *Lutjanus bohar* and *Variola louti,* there were demonstrations of habitat preferences, however, there were no significant differences in the abundances and biomasses between different management zones when accounting for habitat variables.

These results demonstrate that the NTSZs, which encompass large reef complexes and a variety of benthic habitat types, is working as a management strategy for protecting unique assemblages and larger fish on HLCRs of the IWP. Nowadays, NTSZs often exist only because human needs are accommodated in other zones of an MPA. In the IWP example, the permitted activity in the CPZ generates substantial income for the local communities and as such generates local support for the MPA. However, my findings do demonstrate that the permitted activity in the CPZ is, directly and indirectly, affecting different species of fishes, and it is recommended that controlled zones within MPAs allow for adaptive management, long term monitoring and to enhance the conservation potential of these zones.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

This thesis is dedicated to my Dad ~ the grumpiest and most loving man I have ever known. There is nothing more special than the love that let us share a name.

I would like to express the deepest appreciation to my supervisor, Dr Anthony Bernard. You have demonstrated to me the attitude and substance of a true conservationist: by continually and convincingly conveying the spirit of adventure with regards to the ocean and research. Without his guidance, patience and enthusiasm this thesis would not have been possible. If I become only half the thinker, half the researcher, half the person that Anthony Bernard is, it will surely be one of my greatest accomplishments.

Some work tirelessly in the background. To Dr Camilla Floros and Dr Sean Porter my co-supervisors; Thank you for your inputs, corrections and steady guidance. You have helped to navigate me through the uncharted waters of academic publishing, multivariate land and thesis writing. I can only compare co-supervision to a long-distance relationship; not being able to bug you in person is a challenge, but not having you at all would be even harder.

To all those students, interns and technicians who participated on various field trips, thank you for helping to bring back some truly exciting footage. Without you, spying on the fish of iSimangaliso would not have been so easy.

Then there's *my* brother. If I had a different brother, I would punch him in the face and go find you. Thank you for being my first fishing buddy, and instilling in me an appreciation for all things scaled and finned. An ecologist I admire, Carl Safina, once said: "I fish to scratch the surface of those mysteries, for the nearness to the beautiful, and to reassure myself that the world remains". Safina may have said it, but you taught me that.

To the matriarch of our small tribe, Prof "Mom" Dames, you deserve poetry but the gratitude I have for you can hardly be expressed by sonnets. I couldn't have asked for a stronger woman to look up to. A true pioneer in your research field, and inspiring lecturer, an entrepreneur, a devoted mother and the one true love to my father. You taught me to never give up. You taught me to fight twice as hard as I thought I could. You are a testament to a phenomenal woman.

Lastly, to the fishes themselves. I want to thank you for your existence, for living out your fascinating intricate lives. Thank you for giving this girl a purpose. But also, I want to apologise. I'm sorry that your existence is threatened, that living has become such a challenge. The fight is not yet over. Just keep swimming.

DECLARATION

The following thesis has not been submitted to any university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author.

CHAPTER 1

GENERAL INTRODUCTION

1.1 PROBLEM STATEMENT

1.1.1 CORAL REEF ECOSYSTEMS

Coral reefs are unique and highly diverse marine ecosystems, supporting a multitude of spectacularly coloured fish, and high value social and economic activities. These productive shallow marine ecosystems are common along the tropical, equatorial regions within low latitudes (Barber and Bellwood, 2005). High latitude Coral Reefs (HLCRs), however, exists at the distributional limits for coral species often transitioning quickly into temperate systems (Schleyer and Celliers, 2005). These HLCRs are limited by the most powerful western boundary current in the Southern Hemisphere, constituted around 27° S, just south of the border between South Africa and Mozambique (Lutjeharms, 2006) These marginal coral ecosystems are often less diverse in terms of coral species and include macroalgae communities in their place (Schleyer and Celliers, 2003). However, to date HLCRs have received little research attention, in comparison to their low latitude counterparts, and we have a limited understanding of their ecological functioning and vulnerability. Nowadays there is a greater necessity to understand the structure and functioning HLCRs as this information may hold key information into the future of coral ecosystems in a changing global environment (Riegl, 2003; Schleyer et al., 2018).

Coral reefs are economically important and support the livelihoods of nearly 1 billion people either directly or indirectly (Wilkinson, 2002). It is estimated that nearly 30 million of the poorest people in the world depend entirely on coral reefs for their food and livelihoods (Wilkinson, 2002). At the same time, coral reefs provide shelter and nursery grounds for 25% of the world's marine fish species (Burke et al., 2011) and 32 out of the 34 described groups of extant organisms are found in coral ecosystems (Wilkinson, 2002). For example, there may be as many as 750 different species on one patch of coral reef (Panda assets assessments 2017). For comparative purposes, tropical rain forests are home to only nine groups of extant organisms (Wilkinson, 2002). As such, coral reef ecosystems are exceptionally valuable from a biodiversity and provisioning standpoint.

Threats to coral reefs can be divided into indirect climate-mediated changes (for example global warming and ocean acidification) or directly linked to destructive human practices (for example over-fishing, coral mining and irresponsible tourism); both of which have the potential to cause biodiversity loss and jeopardise the provision of ecosystem services. Despite their immense ecological, economic and aesthetic values, it is estimated that up to half of the world's coral reefs have been destroyed (The Nature Conservancy Rescue Reef Report 2017; Wilkinson, 2002), and it is predicted that 75% of these ecosystems will be experiencing long-term collapse as a result of human activities by the year 2050 (The Nature Conservancy Rescue Reef Report 2017; Wilkinson, 2002). If the present rate of destruction continues it is predicted that the world's coral reefs will be gone altogether by the year 2070 (Predictions based on Coral Specialist Group in the International Union for the Conservation of Nature; The Nature Conservancy Rescue Reef Report 2017). Due to the limited extent of research done on HLCRs, there is little understanding of how these ecosystems will respond to such threats in the future, and whether or not their existence at higher latitudes provides them with resilience to factors such as ocean warming (Schleyer et al., 2018). The HLCR of South Africa falls solely under one protected area, IWP, and has been identified as an endemism hotspot (Cowman et al., 2017). This makes monitoring and community assessments within this region imperative to protecting biodiversity within the country.

Impacts of disturbances such as exploitive or destructive fishing, ocean acidification and warming oceans are posing threats to the stability of coral ecosystems, hindering the provision of ecosystem services and reducing their biodiversity (Bellwood et al., 2004). Fishing reduces the abundance, biomass and mean size of targeted species and there is evidence that fishing can have significant negative impacts on the structure and function of reef ecosystems (Bellwood et al., 2004; Jennings and Polunin, 1996; Souter and Lindén, 2000). Over the last century, extensive exploitation of fisheries worldwide has resulted in changes to the ecological functioning of coastal ecosystems (Sims and Southward, 2006), and fish biomass has decreased by approximately two-thirds in comparison to historical baselines (Edgar et al., 2014).

In terms of the globally changing climate, the past five years have been the five warmest years on international record with the last decade has been the warmest decade (European Space Agency; Copernicus monitoring programme). An El Niño event occurring in 1997-98 which caused high sea surface temperatures, particularly in tropical areas resulted in the bleaching and die-off of corals over much of the world (Hoegh-Guldberg, 1999; Wilkinson, 2002). Massive coral mortalities were recorded for corals of the Indian Ocean, showing up to 50% coral mortality (Hoegh-Guldberg, 1999; Wilkinson, 2002). Sri Lanka, Maldives, India, Kenya, Tanzania and Seychelles were severely affected, losing up to 95% of corals (Wilkinson, 2002). In South Africa, reef corals escaped the mass mortalities observed across the tropics in the late 1990s (Heron et al., 2017; Gudka et al. 2018). Global bleaching events later occurred in 2010, 2014 and 2017 suggesting that the frequency of such phenomenon is increasing. South African coral reefs are protected by local small-scale upwelling events in summer that, if they occur at the right time, keep temperatures below bleaching levels (Riegl, 2003). Nevertheless, minor bleaching has occurred during the summer of 2000/2001 and in 2005 (Heron et al., 2017; Gudka et al., 2018; Porter and Schleyer, 2017). Worldwide, very few healthy and pristine coral reefs remain due to anthropogenic impacts, which makes modelling their baselines particularly challenging (Jackson et al., 2001).

1.1.2 FISH SPATIAL ECOLOGY

Ecological processes are somewhat excluded from fisheries models and management practices. The recognition of ecological process and habitat dependencies could have a profound positive impact on the recovery of exploited fish stocks, protection of biodiversity and support of ecosystem services (Link, 2002). Different fish species occupy various habitats, and such habitat preferences may change according to different life-history strategies. Some changes in life-history may be relatively minor, such as occupying shallow inshore environments when juvenile and moving to deeper offshore reefs with maturity (Edwards, 1992; Wheeler et al., 1986). Some changes can involve migrations and occupation of completely different marine environments such is the case for species that occupy estuaries as juveniles and move out to fully marine offshore environments (Ong et al., 2015). No matter how simple or how complex the relationship, species depend on particular habitat characteristics according to their life history (Ong et al., 2015), survival (Caley and John, 1996; Floros and Schleyer, 2017), and the niche they fulfil (Beukers and Jones, 1998; Wantiez and Chauvet, 2003). Environmental characteristics that have previously been identified as important included habitat complexity (Nash et al., 2013), available habitat size (Bellwood and Hughes, 2001), benthic cover type (Tuya et al., 2012), depth (Holbrook et al., 2002), temperature (Pankhurst and Munday, 2011) and seasonality (Daly et al., 2014), to name but a few. Within an ecosystem, fish communities are structured according to a range of environmental parameters, and experience stress should their physical environment change. For example, one of the leading causes of habitat variation is climate change. In coastal waters, sea surface temperatures are rising and even though warmer sea surface temperatures are likely to increase the growth rates of fishes living at sub-optimal temperatures (Rountrey et al., 2014), warmer waters might decrease growth rates for species living closer to their thermal optima (Neuheimer et al., 2011), resulting in range shifts and contractions. Research into fish spatial ecology and environmental drivers of fish communities have the potential to advance our fundamental understanding of the key ecological attributes and processes which create the complex ecosystems as we now know and experience them. It is only after we comprehend these processes that one can provide essential information to inform robust and efficient spatial management strategies (Brandl et al., 2019; Nash and Graham, 2016).

1.1.3 MARINE PROTECTED AREAS AS A FORM OF SPATIAL MANAGEMENT

Marine protected areas (MPAs) are defined by the IUCN in 2007 as 'a clearly delineated geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values.' Marine protected areas are a widely adopted management strategy as they mitigate the effects of overfishing and habitat degradation whilst simultaneously developing tourism revenue (Mora et al., 2006; Pomeroy et al., 2005). Since the establishment of MPAs worldwide, there have been numerous studies aimed at monitoring these areas and evaluating their efficacy. Studies have shown that MPAs do protect targeted species in terms of increasing abundance, size classes as well as overall ecosystem biodiversity (Barrett et al., 2007; Lester & Halpern, 2008; McClanahan & Arthur, 2001; Unsworth et al., 2007). The recovery of species populations and marine communities within protected areas is thought to create a spillover into neighbouring unprotected areas and in doing so support local and regional fisheries (Halpern et al., 2009). Marine protected areas are considered to be successful if they have twice as many large fish, five times more large fish biomass and fourteen times more elasmobranch biomass relative to fished areas (Barrett et al., 2007a; Edgar et al., 2014; McClanahan et al., 2007).

Marine protected areas do face challenges limiting their success in terms of conservation goals. Some challenges include difficulties in implementation and enforcement due to lack of governance, and a lack of adequate management guidance and evaluation (Alder, 1996; Fogarty et al., 2004). Most MPAs are disadvantaged by the severe lack of scientific knowledge and information regarding the ecosystem status as well as the effects of the various activities within the MPAs and different management zones (Fogarty et al., 2004). In cases where scientific information is provided, it is often incomplete, outdated and non-comparable restricting its ability to accurately define ecosystems and detect subtle changes (Bellwood et al., 2004; Knowlton and Jackson, 2008). The International Union for Conservation of Nature (IUCN) and the Convention on Biological Diversity (CBD) strongly recommend that MPAs incorporate a range of management approaches through the use of zones. Zonation which permits human activity is considered a solution to keep displaced people content and stimulate local support and stewardship for MPAs. Such management options that are commonly incorporated in MPAs are No-Take Sanctuary Zones and Restricted or Regulated Zones (UNEP-WCMC 2008). The use of different zones within MPAs allows the management approach to be customised according to ecological, cultural and social-economic factors in the area in which the MPA is established (Tunley, 2009). However, these factors commonly cause conflict between different stakeholders, as the implementation of one factor may cause a series of trade-offs. For example, it is thought that increased human access reduces the conservation potential of MPA (Costello and Ballantine, 2015). This has led to the establishment of "Paper Parks", a term given to MPAs which exist only in written regulations and but do not have the potential to contribute towards conservation goals. However, there is only limited published research demonstrating the effect of the zoned management effect of MPA effectiveness within South Africa and further research could provide valuable information to guide various management strategies and stakeholders.

1.2 RESEARCH GAP

To better understand the ecology and potential threats of disturbance to the fish communities inhabiting high latitude coral reefs there is a need to know more about how environmental drivers affect the spatial distribution of species and assemblages. This includes the need to investigate the relative importance of different environmental variables such as depth, macrobenthic habitat characteristics and available habitat size (Bellwood and Hughes, 2001; Darling et al., 2017a; Nash and Graham, 2016). Many studies based on spatial comparisons have overlooked environmental variables in the past, and there is no standard suite of variables developed for high latitude coral reef studies. To ensure the management measures that are put in place achieve their biodiversity conservation objectives there is a need for more research on the effects of different management zones within MPAs. The use of various levels of protection presents its challenges (Costello and Ballantine, 2015; Tunley, 2009). Restricted use of resources in regulated zones presents a biological compromise to accommodate human needs. Whereas, areas completely restricted and regarded as sanctuaries, receive the highest level of protection. The gap between the conservation potential of such zones has not received much attention in the literature, and given that zonation is a management strategy suggested by the IUCN and CBD it is important to try quantifying this biological compromise.

1.3 RESEARCH AIMS, OBJECTIVES AND QUESTIONS

1.3.1 THESIS AIM

The two aims of this thesis were to (1) identify the effect of habitat and key environmental drivers on the taxonomic and functional structure of reef fish assemblages and populations of key species, and (2) to determine the effect of the management zonation within the iSimangaliso Wetland Park MPA on reef fish communities as well as populations of key species, while accounting for the effect of important habitat variables.

1.3.2 OBJECTIVES

1) Conduct a Baited remote underwater stereo-video system (Stereo-BRUVs) field survey to sample the reef-associated fish assemblages within the St Lucia No-Take Sanctuary Zone, Maputaland No-Take Sanctuary Zone and the Controlled Pelagic Zone occurring between 8 and 40 m depth.

2) Quantify important environmental characteristics within the survey area.
    a. Determine the reef size, available habitat area, where each stereo-BRUVs sample was collected using existing multibeam sonar data.
    b. Using habitat images from stereo-BRUVs to characterise the relief and macrobenthic assemblage structure in the vicinity of each stereo-BRUVs sample
3) Classify the fish assemblages according to their taxonomic identities and functional traits.
4) Identify dominant species and determine the trait-based metrics of diversity.
5) Using multivariate statistics determine how the taxonomic and functional assemblage structure is influenced by the habitat variables and management zone.
6) Using univariate statistics determine how the habitat variables and management influence trait-based metrics and the abundance and biomass measures for the dominant species.

1.3.3 QUESTIONS

1.3.3.1 ASSEMBLAGE LEVEL QUESTIONS

i. What is the taxonomic and functional structure of reef fish assemblages in the iSimangaliso Wetland Park MPA?
ii. What are the most important environmental drivers of the taxonomic and functional structure of fish assemblages?
iii. How do functional indices of these reef fish communities respond to variation in macrobenthic communities?
iv. Are the taxonomic and functional reef fish assemblages significantly influenced by different management zones within the MPA, when fully accounting for habitat differences?
v. What are the characteristic fish species and functional groups in the iSimangaliso Wetland Park MPA?

1.3.3.2 SPECIES-LEVEL QUESTIONS

i. What is the population structure of the characteristic fish species (identified in question "v" above) within the iSimangaliso Wetland Park?

ii. What are the most important environmental drivers of the abundance and average biomass for the characteristic species within the iSimangaliso Wetland Park?

iii. Is there a significant difference in the abundance and biomass of these six study species according to the management zone strategy of iSimangaliso Wetland Park, when accounting for habitat differences?

iv. What is the effect of ignoring environmental drivers of population structure when carrying out spatial comparisons?

1.4 THESIS STRUCTURE

To achieve the aims and answer the proposed research questions this thesis includes four chapters:

1.4.1 CHAPTER 1: GENERAL INTRODUCTION

This first chapter provides the context and overall rationale for topics pertinent to this study, starting with a brief description of coral reefs, high latitude coral reefs and the relevant threats facing these delicate ecosystems. Next follows an introduction to the spatial ecology of reef fishes, relevant to a holistic and comprehensive ecosystem-based approach. Given the threats to these ecosystems an overview of protection, focusing on the use of Marine Protected Areas, the issues following this form of protection and the use of zoning strategies are also discussed. This information lays the foundation for the overall aim of the thesis and the research questions to be addressed.

1.4.2 CHAPTER 2: ASSEMBLAGE LEVEL RESEARCH

This second chapter details research done on the offshore reef fish communities of iSimangaliso Wetland Park from both a functional trait-based perspective and a traditional taxonomic (species level) community analysis. This study aimed to provide insight into key environmental drivers and the effect of MPA zonation on reef fish from a community perspective.

1.4.3 CHAPTER 3: DOMINANT SPECIES RESEARCH

This third chapter is an extended version of a paper published in the Journal of Ocean and Coastal Management (Dames et al., 2019). The only variation is that the work presented here includes data from the Maputaland No-Take Sanctuary Zone. The data from this zone was not yet available when the paper was published, therefore this chapter provides a more comprehensive version of the findings. The results do not significantly deviate from those which were published, but rather validate the published findings. This chapter investigated the effect of the environmental variables, used in Chapter 2, and zone, while taking into account habitat variability and reef size, on the abundance and biomass of six key fish species. Keeping in mind that reef size is often not available for most studies that conduct spatial comparisons, a follow-up investigation excluded reef size from statistical analyses to illustrate the effect of ignoring key environmental variables when carrying out spatial comparisons. Certain sections of the "Methods" are repeated from the previous chapter, given that the same data and approaches were used. In these instances, the reader is informed at the start of the paragraph that the content is the same and is directed to the chapter and section where the content was first provided.

1.4.4 CHAPTER 4: GENERAL DISCUSSION

The last chapter aims to summaries the key findings of this study concerning the overall aims. Also, the implications of the findings for the future management of iSimangaliso Wetland Park are considered and future research priorities are highlighted.

1.5 APPROACH OVERVIEW

1.5.1 ISIMANGALISO WETLAND PARK MPA

The iSimangaliso Wetland Park (IWP) MPA incorporates a multiple-use zone (termed the Controlled Pelagic Zone [CPZ]), and zones where all human activities are prohibited (termed No-Take Sanctuary Zones [NTSZs]). The IWP MPA is zoned to accommodate human needs, and the CPZ allows fishing for certain pelagic species and tourism. There are two NTSZs within this study, St Lucia and the Maputaland. The St Lucia NTSZ was established as such in 1979. The Maputaland NTSZ was proclaimed as a CPZ in 1986 but was changed to an NTSZ in 2001. The present CPZ, considered in this study is made up of zones established in both 1979 and 1986 and is located in between both NTSZs. The ST Lucia NTSZ is located over a large reef complex, consisting of few patch reefs. Whereas, the Maputaland NTSZ and CPZ consist of smaller reef complexes that are patchier in nature.

1.5.2 STEREO-BRUVS SURVEY

This study will incorporate a stereo-BRUVs survey conducted within the ST Lucia NTSZ, the CPZ and the Maputaland NTSZ reef complexes between a minimum depth of 8 m and a maximum depth of 40 m. This survey aimed to collect data on the relative abundance and biomass of reef-associated fish species. Secondarily these stereo-BRUV deployments were used to collect data on variation in habitat characteristics to be incorporated into statistical analyses.

1.5.3 ASSEMBLAGE LEVEL

The stereo-BRUVs data were used to build datasets of relative abundance, length and relative abundance of adults vs. juveniles for each species (named: stages). This was to address a secondary objective of establishing which data type is more informative and useful for research such as this. The datasets for abundance, lengths and stages were analysed from a standard taxonomic (using species identities perspective) and a trait-based functional approach. This was done according to the suggestions of Villéger et al. (2010) who suggested that the use of both approaches provides a comprehensive ecological understanding of fish communities. The abundance, lengths and stages of both taxonomic and functional communities were analysed using multivariate protocols to identify key environmental drivers and the significance of different management zones. Univariate analyses were also used to identify the effect of environmental variables and zonation on various metrics of functional diversity.

1.5.4 DOMINANT SPECIES

The results from the assemblage level analysis informed the selection of six characteristic species within the IWM MPA: *Aprion virescens* (Green jobfish), *Caranx melampygus* (Bluefin kingfish), *Epinephelus tukula* (Potato bass), *Lutjanus bohar* (Bohar snapper), *Lethrinus crocineus* (Yellowtail emperor) and *Variola louti* (Lyretail grouper). A series of univariate analyses were used to identify the important environmental drivers of the average biomass and abundance for each species, as well as the effect of different management zones on these metrics when fully accounting for habitat characteristics such as benthic cover and reef size. Reef size, in particular, has been highlighted by previous studies as a critical determinant of fish population structure (Bellwood and Hughes, 2001; Darling et al., 2017a; Nash and Graham, 2016). This data is typically unavailable and has only been collected for a limited number of ecosystems internationally. Fortunately, such data is available for iSimangaliso Wetland Park and thus a comparison of results was done to determine the effect of excluding reef size data from statistical models making spatial comparisons.

CHAPTER 2

HOW DOES THE TAXONOMIC AND FUNCTIONAL STRUCTURE OF FISH ASSEMBLAGES RESPOND TO VARIATION IN HABITAT AND SPATIAL MANAGEMENT?

2.1 ABSTRACT

Environment and management are important determinants of reef fish assemblage structure. Understanding environmental drivers of reef fish communities can enhance marine protected area (MPA) design and adaptive management. The iSimangaliso Wetland Park (IWP) MPA covers a diverse suite of habitats and consists of multiple management zones that permit different levels and types of anthropogenic activity. These zones include the Maputaland No-Take Sanctuary Zone (NTSZ) the Controlled Pelagic Zone (CPZ) and the St Lucia NTSZ. However, the structure of the fish assemblage among management zones and habitats is relatively unknown. Here, the effect of key environmental drivers and management zone on functional and taxonomic assemblage structures of reef fish was investigated within IWP. The benthic habitat within the study areas varied considerably consisting of mosaics of reef and sand habitat with variable seafloor relief and cover in corals. The habitat in Maputaland NTSZ was significantly different from the other two zones due mostly to the presence of macroalgal habitats in the Maputaland NTSZ. The three metrics used to define the multivariate fish assemblages (abundance, mean size and abundance within maturity classes) all provided meaningful information to advance our understanding of the structure of the IWP fish assemblages and the impact of the MPA zoning plan. The use of stages provided a comprehensive insight into the structure of juvenile populations within IWP and indicated the CPZ to be characterised by both juvenile of several species as well as functional groups made up of juveniles. Fish community structure was driven by the presence of reef, the seafloor relief, the cover of stony coral habitats, and to a lesser degree the presence of macroalgal habitats. The response of the fish assemblage structure to reef size, depth and the presence of habitats characterised by zoanthids was less consistent. The number of functional groups, along with functional richness, diversity and dispersion were higher in stony coral and high relief habitats, and lower in low relief, sand and macroalgae habitats. Assemblages in the Maputaland NTSZ had a significantly higher number of functional groups and richness, compared to the St Lucia NTSZ and Controlled Pelagic Zone, a result attributed to the addition of macroalgal habitats within this zone allowing for a different suite of species and functional niches. The CPZ was characterised by functional groups with immature life-stages whereas, the

two NTSZs were characterised by functional groups of large predators. These findings suggest that the NTSZ’s of the IWP are protecting mature higher trophic level assemblages of reef fishes and that assemblages in the CPZ may be impacted by the permitted anthropogenic activity. Additionally, high complexity reef habitats support the greatest diversity of fishes, but that marginal reefs or sandy habitats support unique fish assemblages and contribute towards local biodiversity.

2.2 INTRODUCTION

Globally, reefs are showing evidence of overfishing and habitat degradation from anthropogenic activity, and numerous studies have highlighted significant consequences on broader ecosystem functioning (see Bellwood et al., 2004; Brandl et al., 2019; Hoegh-Guldberg et al., 2007; Mumby et al., 2006; Sandin et al., 2008 for examples). High diversity ecosystems, such as coral reefs, are complex, making it challenging to understand the processes that determine their structure and functioning. To protect such high species numbers, along with their complex species-environment interactions, research must encompass the ecosystem as a whole. Such research would facilitate the Ecosystem-Based Fisheries Management (EBFM) and Ecosystem-Based Management (EBM) approaches (Crowder et al., 2008; Hall and Mainprize, 2004; Link, 2002; Thrush and Dayton, 2010).

Single species assessments using abundance and biomass, have contributed little to understanding the impacts of anthropogenic disturbances; in particular when trying to highlight the impacts of fishing pressure (Nash and Graham, 2016). In addition to this, data derived from single-species approaches cannot address questions on the knock-on effects of fisheries on ecosystem process, the condition of the benthos and the condition of the non-targeted fish community (Nash and Graham, 2016). Couple this with limited data on the ecosystem and we find that single-species stock assessments and management strategies fail to holistically and sustainably manage populations (Worm and Branch, 2012). Historic research has typically employed population-level stock assessments, but an acknowledgement of system-wide interactions and complex habitat relationships has resulted in a move towards more ecosystem-based approaches (Thrush and Dayton, 2010; Travisa et al., 2014). The nature of most fisheries is species-specific, and often these species populations are managed as a unit, for example, the coral trout fishery in Australia (see Mclean et al., 2011). However, coral reef fish communities are often subjected to multiple species being targeted, and thus there is a need to study the ecosystem as a whole, considering the entire fish community. Modern-day management of marine resources thus benefits from community-level knowledge (Fulton et al., 2005; Mangi et al., 2007; Mcclanahan and Hicks, 2011).

The effectiveness of management is further enhanced when it is based on a sound understanding of the broader ecosystem, such as fish and their habitat, and how different components are associated. Studies have demonstrated a high correlation between reef-associated fish species and the characteristics and condition of the benthic habitat (Bellwood et al., 2004; Graham and Nash, 2013). Management of reefs is limited in cases where broader ecosystem and habitat variables are not considered when studying the effects of human activities (Mcclanahan and Hicks, 2011; Mumby, 2014). The need for broader community assessments, which account for ecosystem processes, is mostly because reef systems present complex indirect relationships due to high levels of biodiversity (Done, 1992).

Further, investigation of different indicators for fish assemblage condition, or structure, and how they respond to different anthropogenic pressures and environmental gradients is a key gap to ensure effective management (Nash and Graham, 2016). Nash and Graham (2016) highlighted that this gap in our understanding of how fish communities respond to pressures is not surprising given that across all the studies they reviewed, the number of different indicators used was incredibly high, with very little consistency among studies. Consistency among studies and narrowing down suitable indicators would help to pinpoint how fish communities respond to different anthropogenic pressures and environmental gradients over broader scales and identify which indicators are best to address specific research questions.

2.2.1 DEFINING REEF FISH COMMUNITY STRUCTURE

Studies that examine the relationships between fish assemblages and environmental variables traditionally employ analyses on taxonomic species (Grossman et al., 1998), rather than functional trait-based groups. Studies that look only at the taxonomic identity of fish assemblages provide an incomplete perspective of biodiversity, as there is no recognition of the biological role and differences, or similarities, among species (Villéger et al., 2010). Assessments need to account for the ecosystem-based role of each species and the changes which may occur in species' roles due to changing environmental gradients. Taxonomic analysis on its own does prove useful when looking at local-scale variation in species presence (Gorman and Karr, 1978; Pyron et al., 2011); however, at larger spatial scales, variation in taxonomic communities are more reliant on species distributions and range-size factors. For this reason, large-scale assessments are considered more robust when using a trait-based functional approach which accounts for the structure and function of ecosystems (Pyron et al., 2011).

Trait-based functional ecology is "the use of functional traits, which are defined as biological attributes that influence organismal performances" to provide a holistic outlook on the complexity of ecosystems without the use of species taxonomic identities (Villéger et al., 2010). One of the key indices derived from this trait-based analysis is functional diversity, which indicates the diversity of traits within a fish community weighted by the abundance or size of individuals within each functional group (e.g. Petchey and Gaston, 2006). The use of trait-based groups was initially derived by plant ecologists (e.g. Garnier and Navas, 2012; Quétier et al., 2007; Verheyen et al., 2003) and before 2018 was mainly utilised in freshwater fish ecology (e.g. Eros et al., 2009; Frimpong and Angermeier, 2010; Hoeinghaus et al., 2007; Logez et al., 2013). Recently, the use of trait-based functional approaches in coral reef research has been gaining traction for benthic (e.g. Darling et al., 2017; Denis et al., 2017; Jain et al., 2014; Madin et al., 2016) and fish studies (e.g. Brandl et al., 2016; Plass-Johnson et al., 2016; Richardson et al., 2017).

The functional trait-based analysis incorporates a range of life-history traits and ecosystem roles within a community-level analysis and thus can provide an in-depth perspective into ecosystem structuring, the complexity of food webs and functional groupings (Díaz and Cabido, 2001; Hulot et al., 2000). The functional structure of reef fish assemblages is a product of the environment in which they prefer to occur. Anthropogenic impacts modify abiotic factors and the species biodiversity itself; thus, it is imperative to quantify differences and changes in the functional structure of fish communities due to human disturbance in addition to differences in taxonomic structure. The use of functional metrics is considered to be a part of the ecosystem-based approach to fisheries management, given that it is a metric that relies on how the environment shapes fish communities and how human disturbance may affect broader ecosystem structure and function (Friedlander and DeMartini, 2002; Henriques et al., 2014).

Analyses that incorporate functional metrics can identify the effect of a human disturbance on a specific ecosystem interaction, and from there, the consequence to the ecosystem as a whole can be gauged. For example, functional metrics have been used to identify critical losses in herbivorous functional groups that are important for mediating competition between coral and macroalgae (Cheal et al., 2013). The loss of this functional group consequently resulted in broader ecosystem regime shifts from coral to macroalgal dominated reefs (Cheal et al., 2013). Functional diversity weighted by abundance or biomass (Laliberte and Legendre, 2010; Villéger et al., 2008) may prove to be a useful alternative to metrics that depend solely on the presence and absence of species as functional diversity encompasses aspects of life history and ecosystem niche detail within a complex interactive community. The distribution and dominance of different functional groups within a community can also be used to identify anthropogenic impacts such as climate change (Graham et al., 2015). Depending on how functional metrics are defined and the information they utilise, they can prove to be useful as indicators of fishing pressure (Anand and Desrochers, 2004; Mouillot et al., 2014). When looking at the impacts of fishing on trophic level alone, fished areas usually display a noticeable decline in mean trophic level, given that fishing targets larger individuals which feed higher in the food chain (Britten et al., 2014; Laurans et al., 2004; Sala et al., 2004). However, when investigating trophic levels on coral reefs, this distinction is lost, given the large size of herbivorous species such as parrotfishes, and the complex nature of trophic cascades (Salomon et al., 2010). Therefore, while simple functional characteristics (e.g. trophic level) may be useful in certain scenarios, a more detailed functional approach, such as one that incorporates the maturity of individual fishes (e.g. stages), is critical to more accurately represent the effects of environmental or anthropogenic drives of change (Nash and Graham, 2016).

2.2.2 DRIVERS OF REEF FISH COMMUNITY STRUCTURE

One of the core faculties of ecology is to explain the distribution of biodiversity on earth, particularly in times when biodiversity is threatened by a range of human disturbances (Chapin et al., 2000; Roberts and Hawkins, 1999; Walther et al., 2002). An understanding of the patterns which determine biodiversity contributes immensely to successful management and conservation efforts. Biogeographers have determined that the key factors determining large scale patterns in biodiversity are available habitat area, temperature, environmental stability and geological activity (Cornell and Karlson, 2000; Gaston, 2000; Rosenzweig and Ziv, 1999), to name but a few. Community ecologists focus on more local scale patterns and have established that assemblages are determined by factors such as competition, predations, recruitment, disturbances, immigration and niche preference (Almany, 2004a; Bellwood and Hughes, 2001; Gaston, 2000; Leathwick et al., 2008; Lewis, 1998). Of the four variables latitude, longitude, habitat area and reef type, it has been found that habitat area accounts for 57% and 42% of the variation in fish and coral respectively (Bellwood and Hughes, 2001). Habitat area, however, is rarely included in marine ecological studies given that it is difficult to obtain and only available for a few reefs globally. Bellwood and Hughes (2001) found that once the habitat area was accounted for, latitude was identified as the next most important variable accounting for variation in offshore reef fish communities. Variation in shallow reef fish communities was attributed more to longitudinal variation, as this was a proxy for depth gradients in the particular region of study. Given the findings of this particular study (Bellwood and Hughes, 2001), latitude, depth, and habitat will be further discussed as possible variables accounting for differences in the reef fish assemblages.

2.2.2.1 LATITUDE

Variation in many environmental parameters (such as; temperature, seasonality and day length cycles) are correlated with latitude (Boyce et al., 2008; Conover, 1992; Ruttenberg et al., 2005; Tuya et al., 2012). Consequently, latitude often appears to drive variation in assemblage structure, as the environmental parameters impact distributions, life history and population demographics of fish assemblages. Several hypotheses have been put forward to explain the large scale patterns in the distribution of coral reef ecosystem biodiversity; the main theories being: centre of origin, the centre of overlap and centre of accumulation (Barber and Bellwood, 2005; Bellwood and Meyer, 2009; Gaither and Rocha, 2013; Hoeksema, 2007; Mora et al., 2003; Rosen, 1988). All three hypotheses have evidence to support them, based on phylogeographic studies of tropical marine fauna (Bernardi, 2005; Hodge et al., 2012; Rocha et al., 2008; Rocha and Bowen, 2008). Although tropical coral reefs display several central biodiversity hotspots, each with their gradients in fish diversity, there are multiple centres of endemism, which occur mostly on the periphery of these tropical hotspots (Bellwood and Hughes, 2001; Roberts et al., 2002). The high-latitude coral reefs (HLCRs) of the iSimangaliso Wetland Park (IWP) is one of these endemism hotspots (Cowman et al., 2017; Figure 2.1).

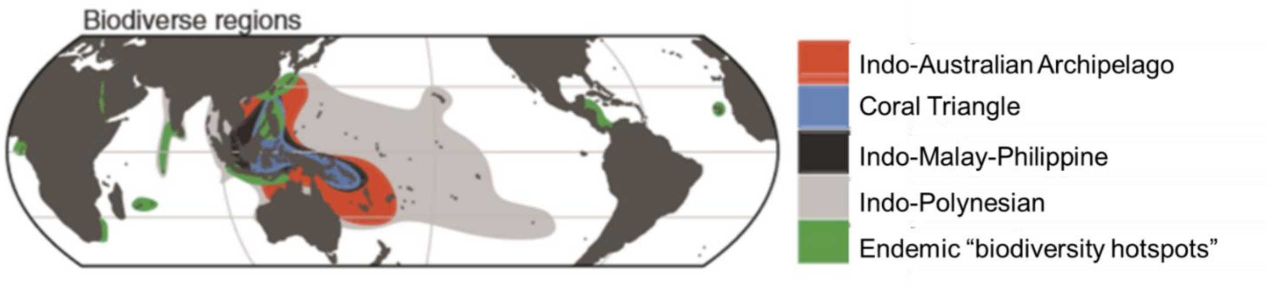


Figure 2.1: Map of biodiverse regions in the marine tropics (Cowman et al., 2017). Many of the endemic "Biodiversity hotspots" in green occur along the periphery of tropical hotspots. The high-latitude coral reefs of South Africa, within the iSimangaliso Wetland Park World Heritage Site, is one such endemic biodiversity hotspot.

2.2.2.2 DEPTH

The structure of fish assemblages has been shown to change according to depth (Friedlander and Parrish, 1998; Holbrook et al., 2002; Khalaf and Kochzius, 2002; Russ, 1984). This is especially true in coral reefs where substantial changes occur in physical and biotic components of the ecosystem over relatively short depth ranges (Brokovich et al., 2008, 2006; Lara and González, 1998; McGehee, 1994; Wantiez and Chauvet, 2003). Clear differences in coral community composition have been shown between shallow (< 10 m), mid-depth (~15 m) and deep reef (~30 m) attributed to substantial physical and biotic changes (Schleyer et al., 2018). For example, as depth increases, there is a decrease in light availability, decrease in temperature, a change in currents and depreciation of tidal effect, amongst other factors (Carter, 2013). Given that fish are ectotherms, the temperature is largely responsible for determining metabolism and behaviour and plays a dominant role in determining the spatial distribution of a fish species (Di Santo and Bennett, 2011; Pankhurst and Munday, 2011). The reduction in light may consequently hinder the ability of mobile organisms that rely on vision to forage (Rickel and Genin, 2005), decrease algae growth rates that would limit certain trophic groups of reef fish (Russ, 2002), and modify coral assemblages and resulting habitat structure on which many reef-associated species depend (Wilson et al., 2008a). It has been identified that fish assemblages of deeper reefs change more rapidly than on shallow reefs, and that separation in community structure occurs at 30 m deep. This 30 m depth was found to have the highest number of species, mostly due to an overlap between "deep" and "shallow" species (Brokovich et al., 2008).

2.2.2.3 HABITAT

Reef fish communities are dependent on niche related process (Mouillot et al., 2007), and thus the structure and functioning of the assemblages are influenced by habitat characteristics (Friedlander and Parrish, 1998; Komyakova et al., 2013; Trebilco et al., 2015). Animal populations will experience limitations imposed by the habitat in which they live. Regional-scale variation in habitat area stands out clearly as a major factor influencing reef fish populations of the Indo-Australian Archipelago and explains up to 42% of the variation in fish communities there (Bellwood and Hughes, 2001). The strong relationship between biodiversity, species composition, and habitat area offers direct evidence of the role which habitat area (reef size in the case of reef-associated species) plays in shaping patterns of biodiversity (Bellwood and Hughes, 2001; Mellin et al., 2010; Stier et al., 2014). Importantly, habitat associations can be more nuanced than just depending on habitat area. Reef fish may have complex interactions with the macrobenthos of a reef which is depending on their trophic relationships and shelter dependencies (Darling et al., 2017b). The abundances of some species, families and trophic groups are highly correlated with certain macrobenthic habitat characteristics. For example, the abundance of coral feeders has been shown to correlate with live coral cover, and the abundance of pomacentrid species that use branching corals for protection correlates with the density of *Acropora* spp. colonies (Chabanet et al., 1997; Darling et al., 2017b).

Different habitats are associated with different levels of complexity and structure, whether this structure is abiotic (consolidated and unconsolidated sediments and rock) or biotic (coral cover, oyster reef, submerged and emergent vegetation). Complexity can be considered as variation in the topographic structure of the habitat and can be measured by relief, interstitial space and surface area (Wilson et al., 2007). Habitat complexity influences the structuring of fish communities, whereby vegetated habitats support greater abundances and diversity of fish in comparison to sandy, unvegetated, areas (Heck and Crowder, 1991). The presence, diversity and percentage cover of corals have significant positive correlations with fish species richness and total fish abundances (Komyakova et al., 2013). The relationships between fish and their habitat are anything but clear cut, and can be driven by complex habitat selection processes (Edgar and Robertson, 1992; Levin and Hay, 2002, 1996; Tuya et al., 2009; Vega Fernández et al., 2007), hydrodynamics and larval supply (Jenkins et al., 1997; Jenkins and Hamer, 2001), and survival as a function of refuge provision and habitat complexity (Almany, 2004b, 2004a; Gratwicke and Speight, 2005; Wilson et al., 2007).

Approximately half of the studies looking at human disturbance do not account for the influence of habitat variables such as benthic cover, structural complexity and size of available habitat (Nash and Graham, 2016). Many of these studies also rely on spatial comparisons, where reef fish communities are studied across gradients of exploitation from areas of no-take to varying levels of human disturbance. The issue which arises with these studies is that the comparisons may include areas which have dissimilar habitat and therefore the results may be influenced by confounding habitat effects rather than just human disturbance. Because of the interactions between reef fish and their habitat, variables accounting for the macrobenthic variation and habitat complexity are included in this study.

2.2.2.4 ANTHROPOGENIC DRIVERS

As human populations increase, the pressure on fish assemblages from both fishing and habitat loss has increased, leading to increasing pressure on marine ecosystems (Newton et al., 2007). Fishing pressure removes individuals from a population, which results in a decline in the abundance and biomass of that species (Jennings and Kaiser, 1998). Slow growing, late maturing and highly resident individuals are more sensitive to extractive pressures compared to fast-growing, early maturing and highly mobile species (Bellwood et al., 2004; Pollock, 1995).

Size has been identified as the most important life-history parameter governing biological processes in marine ecosystems, as it gives insight into food intake, growth rates, predation and fishing pressure (Andersen and Beyer, 2006). Biomass has a more consistent response to fishing pressure, particularly in fisheries that selectively target larger individuals as there would be greater losses to the biomass of that species than to the abundance per unit area (Friedlander and DeMartini, 2002; Nash and Graham, 2016). Areas of poor habitat condition can be characterised by a dominance of fast-growing, rapidly maturing species and prevalence of juveniles of slow-growing species (King and McFarlane, 2003; Winemiller, 2005). Whereas, areas of good habitat condition can be characterised by the presence of adults and juveniles of slow-growing and late-maturing species (King and McFarlane, 2003; Winemiller, 2005). The additive effects of fishing and other human disturbances across many species will consequently lead to changes in the composition of species within a fish assemblage, as well as the relative dominance and rarity of species (Bellwood et al., 2006; Wilson et al., 2008b).

Just as fishing pressure alters fish assemblages, protection from fishing will also give rise to gradual changes in fish assemblages as recovery takes place. Marine protected areas (MPAs) are established to protect ecosystem biodiversity and targeted species to increase their abundance and size (Barrett et al., 2007; Lester et al., 2009; McClanahan and Arthur, 2001; Unsworth et al., 2007). However, 94% of MPAs internationally allow some degree of regulated fishing and thus fail to protect all aspects of biodiversity (Costello and Ballantine, 2015). Allowing some fishing within allocated MPA zones demonstrates a compromise to get selected elements of biodiversity protected while accommodating human needs. Although some degree of protection from human disturbance is better than no protection (Costello and Ballantine, 2015; Edgar et al., 2014), fish assemblages will likely be impacted to a certain degree within MPAs zoned to allow human activity, especially destructive activity such as fishing (Lester and Halpern, 2008).

2.2.3 iSIMANGALISO WETLAND PARK MARINE PROTECTED AREAS

The reef fishes within the Controlled Pelagic Zone (CPZ) of the iSimangaliso Wetland Park (IWP) are subject to anthropogenic pressure, namely fishing and diving pressures (Floros, 2010; Floros et al., 2013). The CPZ permits the capture of pelagic game fish species, with anglers typically targeting larger individuals and species at higher trophic levels and is most likely to affect top-down processes (Pauly, 1995). Consequently, one would expect to observe changes in both the taxonomic and the functional structure of fish assemblages. On the other hand, the No-Take Sanctuary Zones (St Lucia and Maputaland NTSZs) within the MPA allow no anthropogenic activity and the reef fish assemblage structure within these zones would be more in line with reference conditions.

The offshore reef fish assemblages which occur within the IWP remain relatively understudied, and the environmental drivers of these fish assemblages have not yet been fully described. These reef fish assemblages may be influenced by latitude, given that the MPA spans over 1.57^{o} in a roughly north-south orientation. Similarly, longitude, which may serve as a proxy for a depth gradient, could play a role in structuring fish communities. The iSimangaliso Wetland Park, like other high-latitude coral reefs (HLCRs), supports macroalgal habitats, but unlike other HLCRs also supports a high diversity of stony and soft corals. Along with multiple reef complexes of varying sizes, the IWP thus presents the opportunity to utilize natural habitat variation to identify patterns in reef fish communities. The zonation strategy implemented within the IWP, whereby some areas have been fully protected from human activity for 37 years (NTSZs; Floros, 2010) while others are regulated (CPZ), provides an opportunity to identify the effects of regulated fishing and diving pressure on reef fish assemblages.

2.2.4 AIMS AND OBJECTIVES

This chapter aims to describe the habitat associations and determine if the management zone affects the taxonomic and functional reef fish assemblage structure of the iSimangaliso Wetland Park.

The specific questions that I will aim to answer are:

vi. How are the fish assemblages of the IWP structured, both taxonomically and functionally?
vii. What are the most important environmental drivers of fish assemblages in the IWP?
viii. Is the fish assemblage structure influenced by the management zonation in the IWP, when accounting for habitat differences?
ix. What are the characteristic fish species and functional groups in the IWP?
x. How do functional indices of fish respond to variation in macrobenthic communities?

To achieve the research aims, this study employed a field survey to classify habitats and fish assemblage structure within multiple the Maputaland and St Lucia NTSZs and the CPZ of the IWP. Following this, all species recorded were classified according to a set of biological and behavioural traits, which provide insight into the functional role that each species serves within the reef ecosystem. Variation in the taxonomic and functional entities was defined according to three metrics, abundance, size (fork length) and abundance per maturity stage (juvenile or adult). The significant environmental drivers were then identified for both taxonomic and functional trait-based reef fish assemblages using multivariate and univariate statistical approaches. Once habitat variability was accounted for, the effect of different management zone on assemblage structure was determined.

Based on the approach followed in this chapter, the data allowed a comparison of the functional (trait-based) and taxonomic (species identity) approaches, and the abundance, lengths and stage metrics.

2.3 RATIONALE

The motivation for this study is based on the following literature findings:

i. Little is known about the offshore fish communities within iSimangaliso Wetland Park. The only studies done to date include the species lists developed by Chater et al. (1995, 1993) and the use of underwater visual census to identify effects of management styles by Currie et al. (2012), Floros (2010) and Floros et al. (2013).

ii. Little is known about the habitat associations between reef fishes and habitats in HLCRs. This is particularly true for iSimangaliso Wetland Park where the only association studied has been between *Acropora* coral species and juvenile reef fish (Floros and Schleyer, 2017). Previous studies mentioned in the above point were limited to diving depths, focused only on central reef habitats and did not fully account for habitat variation in their spatial comparisons.

iii. Fishing is known to disrupt natural patterns and habitat associations but MPAs provide a controlled ecosystem in which to carry out research. There are numerous documented cases of fishing altering life histories, reducing abundances and particularly the biomass of fishes (Andersen and Beyer, 2006; Bellwood et al., 2004; Jennings and Kaiser, 1998; Nash and Graham, 2016; Pollock, 1995). Such that protection from fishing in marine protected areas allows for recovery of fish populations (Barrett et al., 2007b; Lester et al., 2009b; McClanahan and Arthur, 2001; Unsworth et al., 2007). It is also stated that it takes an average of 35 years for coral reef fish populations to recover from historic fishing pressures (MacNeil et al., 2015). Considering that areas such as the St Lucia No-Take Sanctuary Zone has been protected for nearly 40 years, this area could likely serve as an ecological reference for a health community.

iv. Marine Protected Areas are often zoned to accommodate stakeholders needs and the impact of even minor disturbances in controlled access MPAs is relatively unknown (Lester et al., 2009a). There has been evidence supplied by Floros et al. (2013) of the direct impact of controlled pelagic game fishing of permitted target species (in particular *Aprion virescens*) and the suggested impact of diving pressure on sensitive species such as the iconic Potato bass, *Epinephelus tukula* within the Controlled Zone of iSimangaliso Wetland Park.

v. Human disturbances within the Controlled Pelagic Zone and complex habitat associations could act at both the taxonomic and functional level as suggested by Villéger et al. (2010) and could result in differences in the abundances (e.g. Mclean et al., 2011), biomass (e.g. Friedlander and DeMartini, 2002) or maturity structure (e.g. Shin et al., 2005) of fish populations. Based on the suggestions of Villéger et al. (2010) both a taxonomic and a functional trait-based approach were used to describe the fish communities of the IWP. Many fish assemblage studies have used either (or some combination of) relative abundance, biomass and maturity stage. This study implemented all three of these metrics to provide a comprehensive understanding of the IWP's fish assemblage structure, and further compare the usefulness of each metric.

2.4 METHODS AND MATERIALS

2.4.1 STUDY AREA AND SAMPLING APPROACH

Samples were collected during two separate field trips in November 2016 and June 2017, from three locations within the iSimangaliso Wetland Park (IWP) World Heritage Site MPA (Figure 2.2). The locations included the St Lucia No-Take Sanctuary Zone (NTSZ), St Lucia/Maputaland Controlled Pelagic Zone (CPZ) and the Maputaland NTSZ (Figure 2.2). Sampling was restricted to depths of 5-40 m and all samples were either on or in close proximity to available reef habitat (Figure 2.2). The exact sampling locations were pre-determined using Create Random Points in ArcGIS (10.4), with all points restricted to the known location of reef habitat (Ramsay et al., 2006) and the minimum allowed distance set at 500 m from its nearest neighbour within each reef patch. Each sample was collected *in situ* as near as possible to the predetermined locations and deployed on the seafloor for an analysis time of 60 minutes.

Relative abundance and length data were collected for all fish species using light-weight baited remote underwater stereo-video systems (stereo-BRUVs). Each stereo-BRUVs consisted of two High Definition (HD) video cameras mounted within a protective frame 70 cm apart with an inward convergence angle of 8^o degrees, to provide an overlapping field of view (Cappo et al., 2004; Ellis and DeMartini, 1995; Harvey et al., 2012; Langlois et al., 2010; Watson et al., 2010). Before, and after the field surveys, each stereo-BRUVs was calibrated using the software CAL (SeaGIS Pty Ltd), according to the procedure outlined in Harvey and Shortis (1998). The calibration of the stereo-BRUVs enabled accurate length measurements of the fish sighted in the video. Each stereo-BRUV was baited with 0.8-1 kg of crushed pilchards (*Sardinops sagax*), to attract fish into the field of view of the cameras, and deployed on the seafloor for one hour during daylight hours (07:00 – 15:00). A total of 105 stereo-BRUVs samples were collected, with 35 from each location.

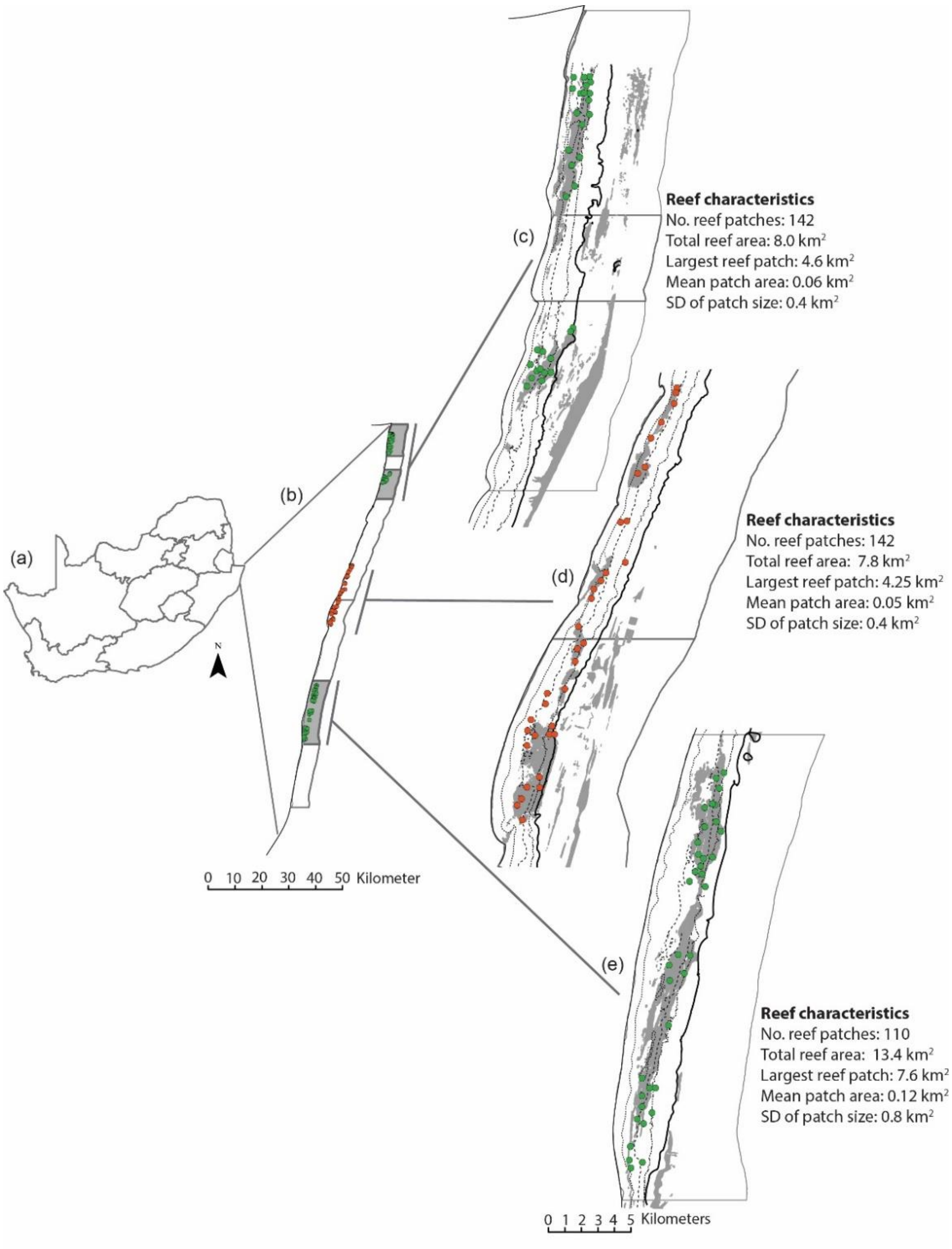


Figure 2.2: Map of the study area where a) shows the location of the iSimangaliso Wetland Park World (IWP) Heritage Site concerning South Africa; b) shows the management zonation layout of the IWP where grey indicates No-Take Sanctuary Zones (NTSZs) and white indicates Controlled Pelagic Zone (CPZ). Insets c-e give a detailed look at the zones included in this chapter and the locations of samples; Maputaland NTSZ along the Northern border of IWP (c), the combined Maputaland and St Lucia CPZ located between the two NTSZs (d) and the St Lucia NTSZ situated further South of IWP (e). Included alongside are reef characteristics for each zone. The St Lucia NTSZ (e) is characterised by fewer patches of larger reef complexes as compared to other zones. This said the CPZ (d) is characterised as having the most patches of smaller reef sizes compared to the two NTSZs.

2.4.2 DEFINING HABITAT VARIABLES

2.4.2.1 REEF AREA

Reef size was included as a proxy for available habitat and reef productivity (Mellin et al., 2010), and was calculated for each sample by measuring the total area (km^2) of the reef patch where the sample was collected using ArcGIS (10.4). Where samples were on sand, the reef size was defined as zero. The reef size data were obtained from side-scan sonar habitat maps (Ramsay et al., 2006) derived from the Innovation Fund Project developed by Dr P J Ramsay and Prof. M H Schleyer in 1998. Ramsay et al. (2006) aimed to produce highly specialised digital seafloor maps which can contribute to both tourism and conservation efforts within the IWP.

2.4.2.2 HABITAT STRUCTURE

Habitat and relief data were acquired from each stereo-BRUVs sample using the software program TransectMeasure (http://www.seagis.com.au). The approach employed a 5 × 4 m grid overlaid onto a screenshot image obtained from each stereo-BRUV sample, following the method of Collins et al. (2017). Each rectangle of the grid was analysed according to the standard (rapid) assessment of benthic composition, which includes descriptions of habitat type, relief, and field of view (Collins et al., 2017; see Appendix Table 6.1). The dominant habitat type was described based on the broad-scale Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification scheme (Hill et al., 2014). The relief described the topographic complexity or the height and angle of the substrate based on the approach proposed by Wilson et al. (2007).

The multivariate habitat data obtained for each habitat images was condensed into a reduced set of covariates that captured the majority of the habitat variability among samples, using the Direct Principal Component Method (DPCM), developed by Winker et al. (2014, 2013) (See Joo et al., 2015; Santos et al., 2017; Thorson et al., 2016 for examples). In the fisheries context, this approach uses continuous Principal Coordinate scores (PCs) derived from Principal Component Analysis (PCA) to replace categorical factors when describing catch composition data. In the context of this research, the PCs were used to describe habitats and habitat variation among samples. The scores were derived from a Principal Component Analysis (PCA) of the multivariate habitat data, carried out in Primer (Version 7 + PERMANOVA; Clarke and Gorley, 2015) using the Principal Coordinates Analysis (PCO) procedure, based on Euclidean distance (which is analogous to a PCA), (Anderson, 2001). Based on the results of the analyses, the first three PCO axes were selected as they described 79.4% of the variability in habitat among all stereo-BRUVs samples. Principal component analysis biplots showing the relationship between the three PCO axes were then created and Pearson correlation vectors (r > 0.4) were overlaid to identify the dominant habitat categories describing the variability (Figure 2.3). The results are presented here as they are required for the subsequent methods sections. The biplots showed that the first PCO axis (PCO1) described the variation among samples with high sand cover and low relief and those characterized by high relief stony coral dominated reefs (Figure 2.3 a, c); the second PCO axis (PCO2) captured the variation among habitats dominated by macroalgae and reefs with higher than normal detections of zoanthids and anemones (Figure 2.3 a, b); and the third PCO axis (PCO3) defined habitats dominated by macroalgae and reefs inhabited by stony corals (Figure 2.3 b, c). The three PCA axes were then regarded as unique 'habitat' covariates to be included in the analysis (named: PCO1, PCO2, PCO3).

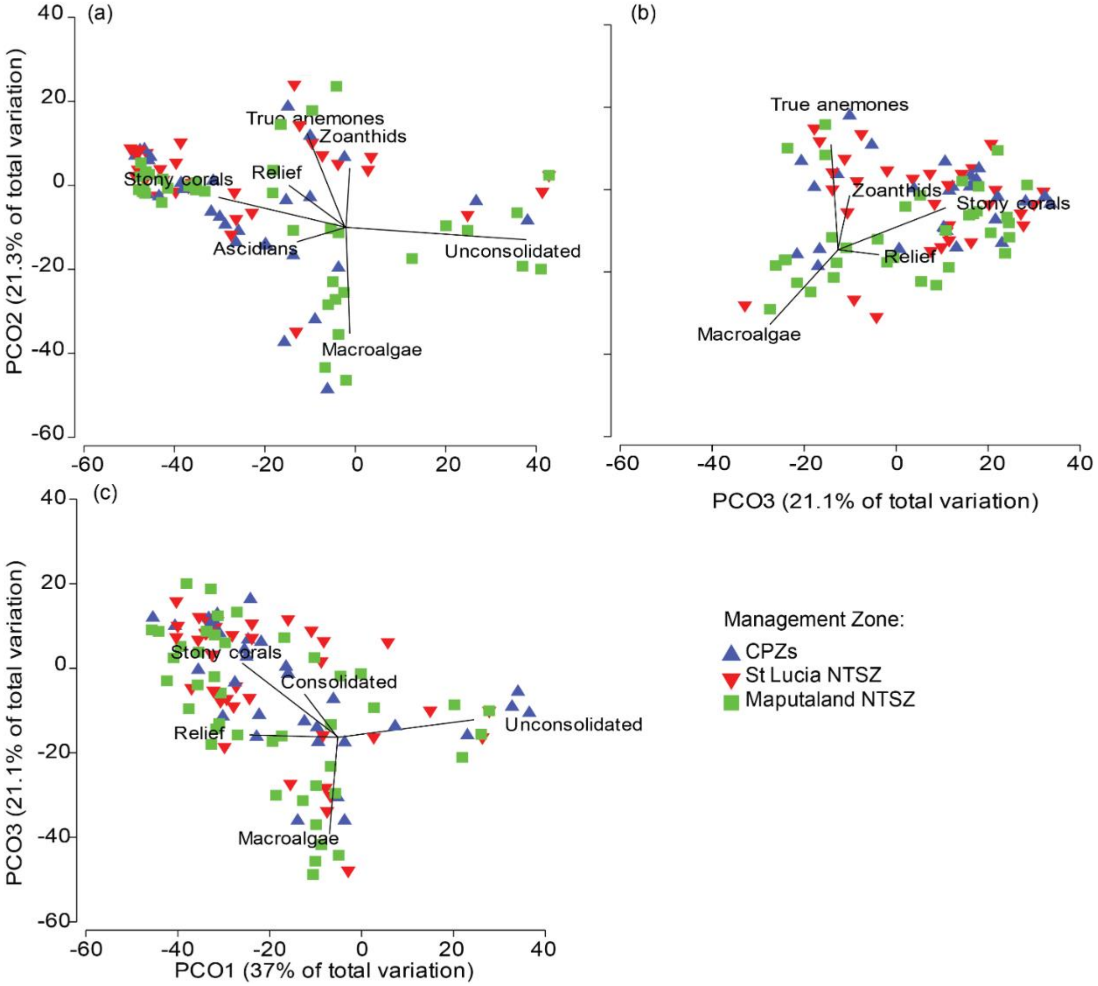


Figure 2.3: Biplots displaying variation in benthic characteristics derived from a principal component analysis (PCA). PCO1 describes habitat variation from high sand cover and low relief and those characterized by high relief stony coral dominated reefs (a, c); PCO2 captures the variation among habitats dominated by macroalgae and those that were inhabited by zoanthids and true anemones and those that are not (a, b) and PCO3 distinguishes habitats dominated by macroalgae and those dominated by stony corals (b, c). Drivers of variation were based on a cut off of 0.4 correlation.

2.4.2.3 ENVIRONMENTAL COVARIATES

In addition to reef area and the habitat descriptors (PCO1, PCO2 and PCO3) a suite of other environmental variables was included in this study to account for environmental variability and sampling biases. Water depth and temperature varied among samples and each sample was characterised by a distinct field of view determined by underwater visibility, different levels of water column and obstruction, given that each stereo-BRUVs lands differently on the seafloor due to habitat features. The list of all environmental variables included in this study is listed in Table 2.1 below, along with their descriptions and how these values were derived.

Table 2.1: Definitions, techniques and units for environmental variables (predictors) collected and included in statistical analyses.

Covariate	***Unit***	***Definition***	***Technique***
Visibility	m	The distance from the stereo-BRUVs within which a fish can be accurately identified.	Estimated using a 3D point on EventMeasure during video analysis.
Water column	%	The portion of the video sample dominated by the pelagic water column, relative to the seafloor.	Estimated using Vidana (freely available from www.marinespatialecologylab.org).
Obstruction	%	The portion of the camera lens blocked by a structure that reduces the area in which to see and count fish.	Estimated using Vidana.
Temperature	ºC	The bottom water temperature at the location where the sample was collected.	Onset HOBO Pro v2 loggers attached to stereo-BRUVs.
Depth	m	The distance from the sea surface to the ocean floor at the point where the stereo-BRUVs was deployed. For this study depths did not exceed 40 m.	GPS linked echo-sounder attached to the boat.
Habitat descriptor: PCO1	na	Distinguishes variation among samples with high sand cover and low relief and those characterized by high relief stony coral dominated reefs.	Derived from Direct Principal Component method preformed on benthic habitat and relief data.
Habitat descriptor: PCO2	na	Distinguishes variation among habitats dominated by macroalgae and those inhabited by zoanthids and anemones.	
Habitat descriptor: PCO3	na	Distinguishes habitats dominated by macroalgae and those that were characterised by stony corals.	
Reef size	km^2	The total area of the reef patch where the sample was collected measured using ArcGIS. Samples on the sand had a reef size of zero.	Side-scan sonar habitat maps (Ramsay et al., 2006)
X and Y	Decimal degrees	Latitude and Longitude for each sample.	Marked via GPS on board.

2.4.3 FISH ASSEMBLAGE DATA

2.4.3.1 SPECIES IDENTIFICATION

Each fish that was detected on the stereo-BRUVs samples was recorded to species level by one analyst, with all identifications being confirmed by an expert on tropical reef fish identification. Identifications were based on online databases, such as FishBase (Froese and Pauly, 2019), World Register of Marine Species (Mees et al., 2015) and FishWisePro (California Academy of Sciences 2019), and field guides, including The Reef Guide (King and Fraser, 2014), Two Oceans - A Guide To The Marine Life Of Southern Africa (Branch et al., 2017), Coastal Fishes of Southern Africa (Heemstra and Heemstra, 2004), Groupers of the World (Craig et al., 2012) and A Guide to The Common Sea Fishes of Southern Africa (van der Elst, 1981). All fish species recorded in this study were used to compile a species list.

2.4.3.2 ABUNDANCE, LENGTH AND STAGE OF MATURITY

Relative Abundance (MaxN) data were derived from the maximum number of individuals of each species observed within a single frame for each stereo-BRUVs sample for an analysis time of 60 minutes each (Langlois et al., 2010). Length was derived from point-to-point fork length measurements; this is possible using EventMeasure when both left and right videos are synchronised and calibrated, and the fish is fully visible in both cameras. Length measurements are sometimes limited given that some fish may only appear in one video of the stereo-pair, there may be obstruction, the fish may be too far away from the camera or the angle of the fish does not allow for an accurate measurement to be taken. As such, the number of length measurements is typically less than the estimated relative abundance (MaxN). Juveniles of a fish species typically occupy different habitats and trophic positions and fulfil different roles in an environment, in comparison to conspecific adults. Fishing regulation also typically restricts the catch of a species to the adult stages (King and McFarlane, 2003; Winemiller, 2005). As such, the immature component of a population could be regarded as functionally distinct from the adult portion. According to a study by Heyns-Veale et al. (2019), which looked at the traits of multiple species, modelling showed that length at maturity for most species and families was at 40% of the maximum attainable length. A third metric was produced to accommodate this, whereby the size data were used to classify a fish as adults (> 40 % of the maximum attainable size) or juveniles (< 40 % of the maximum attainable size), and the abundance of mature and immature individuals per species was estimated from the fish measured at MaxN.

2.4.3.3 TRAIT AND ASSEMBLY MATRICES

Using the fish species list generated across all samples analysed in EventMeasure, a trait-based matrix was built from the RFishBase package (Boettiger et al., 2012), and in-depth literature searches. The primary selection of traits was adapted from those chosen by Heyns-Veale et al. (2019) and Mouillot et al. (2014). Traits used in this study included information on maximum body size, diet preference, habitat preference, reproductive biology, preferred position in the water column, mobility and shoaling behaviour (defined in Table 2.2), which were all applied at the species level. Decisions on trait selection were also based on the availability of life history data, given that life-history characteristics of many species aren't as readily available as it is for others. In scenarios where there was no data available on a trait for a particular species in RFishBase (Boettiger et al., 2012), an in-depth literature search was conducted, and if that did not produce the information then the closest phylogenetic relative was chosen. To enable the functional diversity package (Laliberte and Legendre, 2010) to run successfully, there were no gaps and no blank spaces within the trait-based matrix.

The data obtained from video processing through EventMeasure produced three different metrics (see section 2.4.3.2 for more details) which from here on will be referred to as Abundance, lengths and stages. Each of these three metrics was processed to form an "Assembly Matrix" to accompany the "Trait Matrix" described above. The trait matrix and corresponding assembly matrices were then imported into RStudio and processed with the Functional Diversity (FD) Package (Laliberte and Legendre, 2010). The FD package was developed for measuring functional diversity and functional indices from multiple traits. Distance-based Functional Diversity (dbFD) implements a flexible distance-based framework to compute multidimensional functional diversity indices. The call for dbFD requires a "trait matrix" and corresponding "assembly matrix" which has the biological data. From these two matrices, the dbFD call can produce the three indices developed by Villéger et al. (2008): functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv); as well as functional dispersion (FDis; Laliberté and Legendre 2010), and *a posteriori* functional group richness (FGR) (Petchey and Gaston, 2006). Definitions for these five functional indices used in this study can be found in Table 2.3 below. Additional outputs of the dbFD call include Rao's quadratic entropy quotient (Q) (Botta-Dukát, 2005) and the community-level weighted means or proportions of trait values (CWM; e.g. Lavorel et al., 2008). Examples of the layout for trait and assembly matrices which are the required inputs can be seen in Figure 2.4 and the example of outputs from the dbFD call can be seen in Figure 2.5 below.

Table 2.2: Descriptions of traits selected for building a trait matrix to describe the functional role of each reef fish species. These traits were adapted from those chosen by Heyns-Veale et al. (2019) and Mouillot et al. (2014). The majority of information was collected using FishBase (Boettiger et al., 2012). Any gaps were filled using literature searches on the species, after which if the information was still unavailable the information for the next phylogenetic relative was used.

Trait	Notes	Trait Code	Description
Maximum attainable size	Maximum published length.	Continuous variable	Maximum recorded fork length (FL) in cm
Size Class	Based on categories generated by Haupt (2019).	Very small	0-18 cm FL
		Small	18-36 cm FL
		Medium	36-65 cm FL
		Large	65-200 cm FL
		Very large	> 200 cm FL
Maturity	Included only when analysing the relative abundance of adults vs. juveniles (Stages) (Heyns-Veale et al., 2019).	Juvenile	FL < 40% of Maximum attainable size
		Adult	FL > 40% of Maximum attainable size
Trophic Level	Represents the position of species within its food chain (Pauly et al., 1998).	Continuous variable (max value of 5)	Trophic level
Reproductive Mode	Sexual identity of individuals within a species (Smith and Wootton, 2016).	Dioecism	A species where males and females exist as separate individuals
		Protogyny	Sex changing: Born female and changes to male later in life
		Protandry	Sex changing: Born male and changes to female later in life
		Hermaphrodite	A species where one individual possesses both male and female gonads
Reproductive Guild 1	Type of parental care (Balon, 1990).	Guarders	Fish actively protect eggs and young

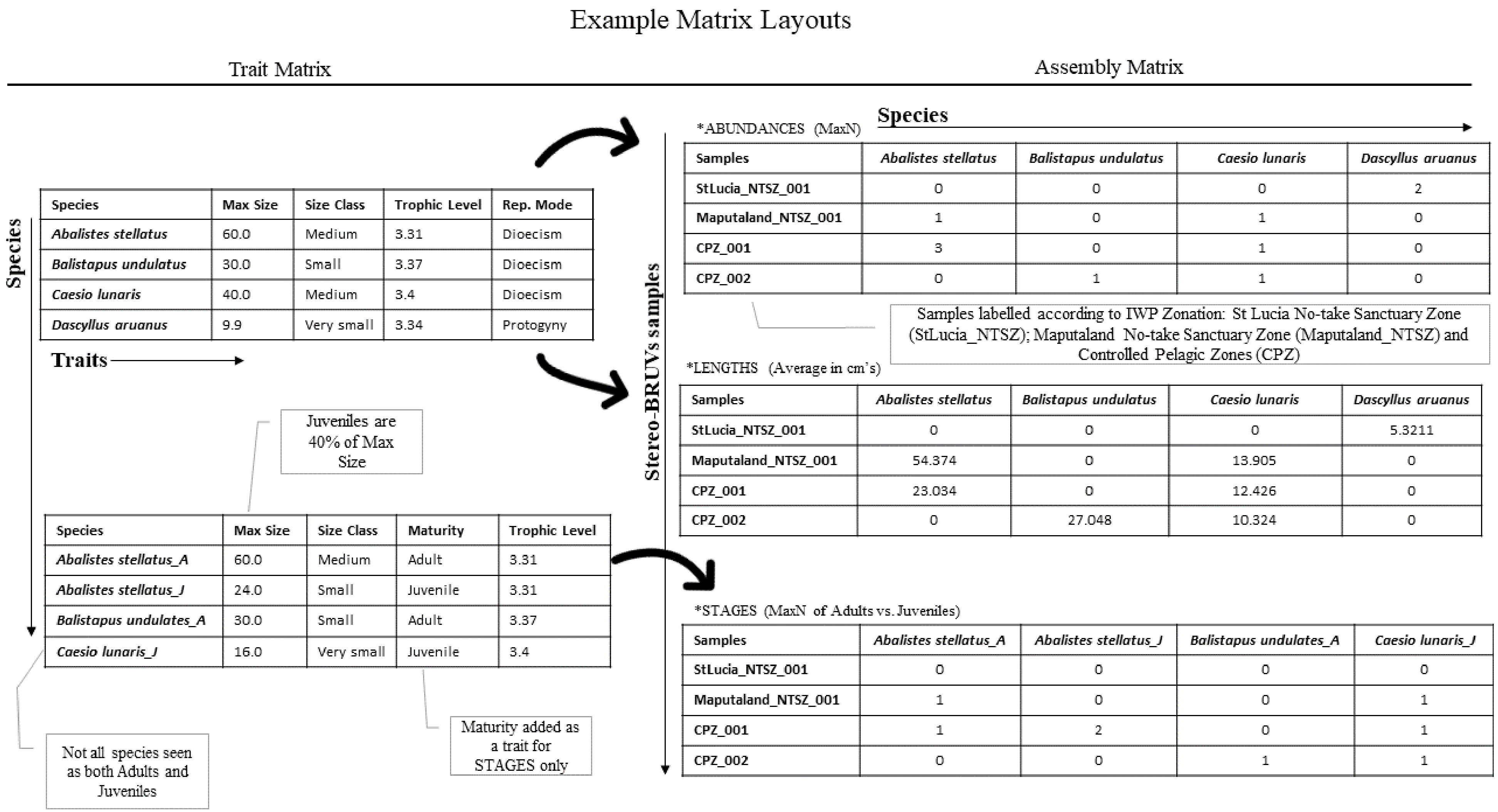
Trait	Notes	Trait Code	Description
		Nonguarders	Fish do not protect eggs and young
		Bearers	Fish carry their young with them for protection
Reproductive Guild 2	Additional information on the care of eggs and young (Balon, 1990).	External brooders	Eggs incubated externally on the parental body
		Internal livebearers	Eggs incubated within the parental body
		Nesters	Eggs guarded within a nest
		Open water/substratum egg scatterers	Non-guarders which abandon eggs after spawning
Gregariousness	Describes schooling and grouping activity (Pavlov and Kasumyan, 2000).	Solitary	Species is only encountered as individuals
	When information is unavailable can be quantified from MaxN.	Solitary, pairs or in groups	Species variably encountered as individuals, a pair or in groups of 5 individuals or less
		Pairs or small groups	Species encountered in pairs or small groups, rarely as individuals
		Small groups	Species encountered in groups of 5 to 20 individuals
		Medium groups	Species encountered in groups of 20 to 50 individuals
		Large groups	Species encountered in groups of more than 50 individuals
Feeding Guild	Describes the dominant food source for a species (Curtis-quick et al., 2012).	Planktivore	Species that feed on zooplankton and/or phytoplankton
		Herbivore	Species that feed on macroalgae and seagrasses
		Carnivore	Species that actively hunts and kills other fish (piscivorous)
		Higher carnivore	Species that actively hunts and kills a wide range of other animals
		Omnivore	Species which can be both herbivores and carnivorous
Feeding Behaviour	Describes observable feeding behaviour (Hobson, 1974).	Browsing on substrate	Species feeding off the seafloor or macrobenthos

Trait	Notes	Trait Code	Description
		Filtering plankton	Species in water column collecting planktonic food sources
		Grazing on aquatic plants	Species eating algae and other aquatic plants
		Hunting macrofauna (predator)	Species actively hunting other organisms
		Picking parasites off a host (cleaner)	Mutualistic, commensal or parasitic relationship between a fish and its host.
		Selective plankton feeding	Species employs specialised filtering mechanisms
		Variable	Omnivorous species and scavengers which are opportunistic
Habitat	Describes habitat preferences as well as dependency on stony corals (Komyakova et al., 2013).	Coral	Species that are dependent on corals, and are associated only with coral reefs
		Reef	Species that inhabit profiled reefs, even in the absence of corals
		Sand	Species that inhabit low profile sandy areas
		Coral/Reef	Species that will frequent both a coral reef and a bare rocky reef
		Reef/Sand	Species that will frequent bare high-profile reefs and sandy areas
		Coral/Reef/Sand	Somewhat of a habitat generalist, with no particular preference
Mobility	Describes the movement of a species and size of home ranges (Bellwood and Wainwright, 2001).	Within	Species that move only within one reef; a resident species with small home ranges
		Between	Species that move between reefs; nomadic species; large home ranges and highly mobile
Position in the water column	Describes the vertical movement of a species, and their associations according to the water column (Davis and Birdsong, 1973).	Benthic	Species that are closely associated with the seafloor and macrobenthos; bottom-dwelling species; demersal

Trait	Notes	Trait Code	Description
		Bentho-pelagic	Species that move freely between the seafloor and water column may be linked to behaviour and diel movements
		Pelagic	Species that patrols the upper water column, typical of game fish

Table 2.3: Definitions for the functional indices given as output from the FD package (Laliberte and Legendre, 2010) when processing a distance-based Functional Diversity call. These five indices were calculated for the Abundances, Lengths and Stages of reef fish.

Functional Indices	**Abbreviation**	**Definition**
Functional Groups	FGR	Uses trait-based similarities between species to form groups of species that serve similar ecological functions. Communities with more functional groups are characterised as less vulnerable, less functionally redundant and more ecologically diverse. The FD Package also produces a functional matrix which shows the abundances or average size (depends on whether abundance, lengths or stages was used) for each functional group within a sample, as well as the total number of different functional groups observed for each sample (Petchey and Gaston, 2006).
Functional richness	FRic	Estimated as the volume occupied in multidimensional space which contains all the trait values for the fish community within a sample (Villéger et al., 2008).
Functional diversity	FDiv	The proportion of the total relative abundance or size is supported by species with the most extreme functional traits, i.e. the value of the FDiv index changes as highly abundant species become closer or further away to the centre of gravity of the multidimensional functional space (Villéger et al., 2008).
Functional evenness	FEve	The regularity of the relative abundance or size distributed by all species within in multidimensional functional space (Villéger et al., 2008). The index is constrained between 0 and 1 and lower values represent a community where relative abundances or size are less evenly distributed among species.
Functional dispersion	FDis	The abundance-weighted deviation of species trait values from the centre of the multidimensional functional space (Laliberte and Legendre, 2010).



Species	Max Size	Size Class	Trophic Level	Rep. Mode
Abalistes stellatus	60.0	Medium	3.31	Dioecism
Balistapus undulatus	30.0	Small	3.37	Dioecism
Caesio lunaris	40.0	Medium	3.4	Dioecism
Dascyllus aruanus	9.9	Very small	3.34	Protogyny

Juveniles are 40% of Max Size

Species	Max Size	Size Class	Maturity	Trophic Level
Abalistes stellatus_A	60.0	Medium	Adult	3.31
Abalistes stellatus_J	24.0	Small	Juvenile	3.31
Balistapus undulates_A	30.0	Small	Adult	3.37
Caesio lunaris_J	16.0	Very small	Juvenile	3.4

Not all species seen as both Adults and Juveniles

Maturity added as a trait for STAGES only

*ABUNDANCES (MaxN)

Samples	*Abalistes stellatus*	*Balistapus undulatus*	*Caesio lunaris*	*Dascyllus aruanus*
StLucia_NTSZ_001	0	0	0	2
Maputaland_NTSZ_001	1	0	1	0
CPZ_001	3	0	1	0
CPZ_002	0	1	1	0

Samples labelled according to IWP Zonation: St Lucia No-take Sanctuary Zone (StLucia_NTSZ); Maputaland No-take Sanctuary Zone (Maputaland_NTSZ) and Controlled Pelagic Zones (CPZ)

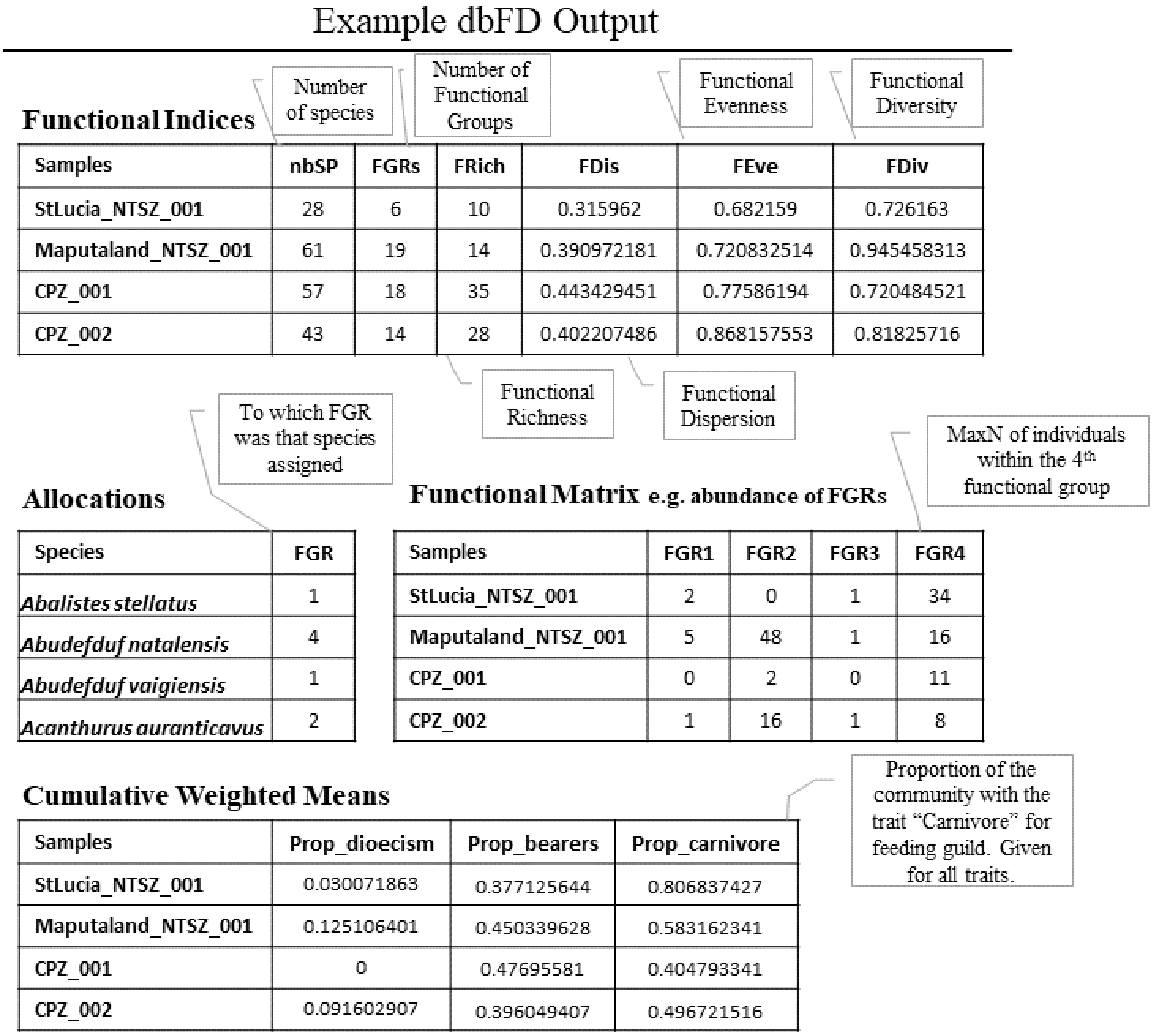
*LENGTHS (Average in cm's)

Samples	*Abalistes stellatus*	*Balistapus undulatus*	*Caesio lunaris*	*Dascyllus aruanus*
StLucia_NTSZ_001	0	0	0	5.3211
Maputaland_NTSZ_001	54.374	0	13.905	0
CPZ_001	23.034	0	12.426	0
CPZ_002	0	27.048	10.324	0

*STAGES (MaxN of Adults vs. Juveniles)

Samples	*Abalistes stellatus_A*	*Abalistes stellatus_J*	*Balistapus undulates_A*	*Caesio lunaris_J*
StLucia_NTSZ_001	0	0	0	0
Maputaland_NTSZ_001	1	0	0	1
CPZ_001	1	2	0	1
CPZ_002	0	0	1	1

Figure 2.4: Example of matrix input required for the FD Package and distance-based Functional Diversity. A trait matrix built according to a species list and the traits listed in Table 2.2 can be seen on the left. Where the bottom left trait matrix shows the addition of "maturity" when looking at abundances of adults and juveniles separately for the stages metric. On the right are the three assembly matrices used to process abundance, lengths and stages.



Example dbFD Output

Functional Indices

Number of species

Number of Functional Groups

Functional Evenness

Functional Diversity

Samples	nbSP	FGRs	FRich	FDis	FEve	FDiv
StLucia_NTSZ_001	28	6	10	0.315962	0.682159	0.726163
Maputaland_NTSZ_001	61	19	14	0.390972181	0.720832514	0.945458313
CPZ_001	57	18	35	0.443429451	0.77586194	0.720484521
CPZ_002	43	14	28	0.402207486	0.868157553	0.81825716

Functional Richness

Functional Dispersion

To which FGR was that species assigned

MaxN of individuals within the 4th functional group

Allocations

Species	FGR
Abalistes stellatus	1
Abudefduf natalensis	4
Abudefduf vaigiensis	1
Acanthurus auranticavus	2

Functional Matrix e.g. abundance of FGRs

Samples	FGR1	FGR2	FGR3	FGR4
StLucia_NTSZ_001	2	0	1	34
Maputaland_NTSZ_001	5	48	1	16
CPZ_001	0	2	0	11
CPZ_002	1	16	1	8

Cumulative Weighted Means

Proportion of the community with the trait "Carnivore" for feeding guild. Given for all traits.

Samples	Prop_dioecism	Prop_bearers	Prop_carnivore
StLucia_NTSZ_001	0.030071863	0.377125644	0.806837427
Maputaland_NTSZ_001	0.125106401	0.450339628	0.583162341
CPZ_001	0	0.47695581	0.404793341
CPZ_002	0.091602907	0.396049407	0.496721516

Figure 2.5: Example of data output from the distance-based Functional Diversity call of the FD Package. Above is a table where each sample has the number of species, the number of functional groups and the five functional indices, below which we see which species were allocated to which functional group. A functional matrix shows the relative abundance of individuals within each functional group for each sample. At the bottom is an example of Cumulative Weighted Means output which shows the proportions of each trait for each sample.

2.4.4 COMMUNITY ANALYSIS

As part of a comparison of methods, this study not only looked at the functional data derived for the iSimangaliso Wetland Park but also compared these to taxonomic community data. The same statistical analysis procedures described in the subsections below were conducted for the following datasets:

i. Relative abundances of functional groups
ii. Relative abundances of individual taxonomic species
iii. Average lengths of functional groups
iv. Average lengths of individual taxonomic species
v. The relative abundance of functional groups when maturity is incorporated as a trait.
vi. The relative abundance of adults and juveniles of individual taxonomic species

Where functional data for i, iii and v were produced by the Functional matrix output from the dbFD call of the FD Package and ii, iv and vi were the assembly matrices used as input into the dbFD call (Figure 2.4).

The multivariate analyses described in sections 2.4.4.1 to 2.4.5.1 were all done in Primer v7 + PERMANOVA (Clarke and Gorley, 2015). Shade plots were created to determine if data transformation and weighing were required, and which resemblance measure would best suit the data. For the relative abundance and relative abundance of adult and juvenile stages (datasets i, ii, v and vi) shade plots showed a high prevalence of zeros in the data, for this reason, a Modified Gower resemblance measure with Log base: 10 was used. Modified Gower is appropriate with zero-heavy data given that it accounts for highly abundant species, as it places greater emphasis on the compositional change of a community rather than actual MaxN or average biomass values (Anderson et al., 2006). As for the length data (datasets iii and iv), shade plots indicated that a square root transformation proved the most suitable for the data along with a Bray-Curtis similarity resemblance measure.

2.4.4.1 VISUALISATION OF DATA IN MULTIDIMENSIONAL SPACE

Non-metric multidimensional scaling (nMDS) was implemented to explore the datasets in all cases. These showed high levels of stress, indicative of unseen background structure and displayed minimal separation. As such, the resemblance matrices for the taxonomic and functional levels of abundance, lengths and stages were visualised using Canonical Analysis of Principal Coordinates (CAP), following the recommendation of Clarke and Gorley (2015). CAP is a constrained ordination technique that uses 9999 unique permutations to uncover patterns that are masked in nMDS, it does this by finding the angle at which maximum separation occurs among sampling groups, in this case, zone (Clarke and Gorley, 2015). The leave-one-out allocation was done to accompany each CAP analysis. This makes an inference about the hypothesis, giving and an indication of how unique each zone is, where values represent the percentage of samples correctly allocated to each zone.

2.4.4.2 ENVIRONMENTAL DATA AND CORRELATIONS

The environmental variables (see Table 2.1, above) considered in multivariate analyses were plotted with Draftsman plots to identify any problematic correlations between pairs of environmental variables. Longitude was excluded from all analyses given that high levels of correlation were found between Latitude and Longitude. However, when investigating potential environmental drivers via model optimisation procedures both longitude and latitude were included to determine if one had more of an influence than the other. All variables were pre-treated with suitable transformations and normalised. Normalisation was done on environmental data to place all variables on an equal scale (Clarke and Gorley, 2015). The environmental data were then processed into a resemblance matrix using Euclidean distance as a resemblance measure. Euclidean distance is advised for normalised environmental data (Clarke and Gorley, 2015). A principal component analysis (PCA) was then done on the environmental data, and correlation vectors with a cut-off of 0.4 correlation were overlaid on the biplot to display any relationships between management zones of the iSimangaliso Wetland Park and associated environmental variables.

The resemblance matrices for abundances, lengths and stages, at both the taxonomic and functional level, were then processed along with the environmental resemblance matrix using the Primer v7 RELATE function. This was done to test correlating patterns between environmental and biotic resemblance matrices (Clarke and Gorley, 2015). The correlation method used within RELATE was Spearman rank (not limited to linear relationships) and the analysis was done using 9999 permutations to calculate a Rho-statistic and level of significance. When significant correlations were found between the fish assemblage data and environmental data from the RELATE analysis, the BEST-analysis was employed. The BEST-analysis is a function in Primer v7 that identifies the subset of environmental variables which contribute the most to patterns and correlations seen in the biotic resemblance matrices (Clarke and Gorley, 2015). The BEST-analysis was done using Spearman rank correlations and 9999 permutations.

The resemblance matrices for abundances, lengths and stages for taxonomic and functional communities were then processed using distance-based linear models (DISTLM). This was done to fit a multivariate multiple-linear regression model of environmental (predictor) variables in the high-dimensional space defined by a measure of dissimilarity (Clarke and Gorley, 2015). This process is equivalent to fitting a linear regression model directly in the full Principal Coordinate (PCO) space, which is derived from a resemblance matrix (Clarke and Gorley, 2015). Additionally, the R^2 criterion produced by this analysis provides an indication of the proportion of variation explained by the linear model. The selection criteria used to find the best solution for the DISTLMs was the Akaike Information Criterion (AIC), which selects the best models by comparing model inaccuracies when predicting out of sample data (Clarke and Gorley, 2015).

2.4.5 EFFECT OF ZONATION ON FISH COMMUNITIES

Permutational multivariate analysis of variance (PERMANOVA) was done to test for significant differences in Abundances, Lengths and Stages at the functional and taxonomic level between the different zones (St Lucia NSTZ, Maputaland NTSZ and the CPZ) of the IWP. This was done according to a simple single factorial design including "zonation" as a fixed factor. The PERMANOVA was computed to run 9999 permutations of residuals under a reduced model with Type I sums of squares (sequential). The normalised environmental variables (Table 2.1) were included as the covariates worksheet. If the PERMANOVA showed significant differences between the different zones of the IWP, then this was followed up with a pair-wise PERMANOVA comparison to identify which zones were significantly different. To support the results of the PERMANOVA, a permutational test for homogeneity of dispersion (PERMDISP) was done. This shows whether significant differences identified by the PERMANOVA were due to significant differences in dispersion or because of differences in a location within multidimensional space. The PERMDISPs were done using 9999 permutations, based on distance from group centroids and included pairwise comparisons to identify between which pairs of zones dispersion differed significantly.

2.4.5.1 CHARACTERISTIC SPECIES AND FUNCTIONAL GROUPS

As an additional step, to assist in the interpretation of the multivariate results, similarity percentage breakdown (SIMPER) analyses were done on the untransformed Abundance, lengths and stages data, at both taxonomic and functional level (not the resemblance matrices). A SIMPER analysis is also referred to as "Similarity Percentages" and is done after hypothesis testing, in this case after a PERMANOVA (Clarke and Gorley, 2015). This analysis identifies the individual contributions of species (in this case species and functional groups) which contribute to the average similarity of samples within each group (in this case the grouping factor was zone) and also the average dissimilarity between all pairs within the grouping variable (Clarke and Gorley, 2015). The parameters for the SIMPER analyses were a Bray-Curtis similarity resemblance measure and the cut-off for low contributions of 50%.

2.4.6 EFFECT OF ZONES ON FUNCTIONAL INDICES

Generalized additive models (GAMs) were used to model functional indices derived from the FD Package for abundance, lengths and stages datasets. GAMs were used to accommodate non-linear relationships between the response variables and the continuous predictor variables (Zuur et al., 2009). As the values of the continuous PCOs were all centred on zero, all other continuous environmental variables (see Table 2.1) were standardized to zero means (Zuur et al., 2009). Prior to constructing the GAMs, the data were explored following the protocol of Zuur et al. (2009, 2013). These exploratory procedures included investigating interactions and collinearity between variables, checking for outliers, zero inflation and verifying spatial independence of samples using variograms [Gstat (Pebesm and Benedikt Graeler, 2020) and Sp (Hijmans et al., 2020) packages].

The FD package used to process the functional data produces five functional indices of interest: The number of functional groups in each sample (FGR), functional richness (FRich), functional diversity (FDiv), functional evenness (FEve) and functional dispersion (FDis). These five indices were produced on three separate metrics: for the abundance dataset, the lengths dataset and the stage of maturity dataset. It is also important to note that FGR and FRich are given as count data, whereas FDiv, FEve and FDis values are restricted to fall between 0 and 1 (See Figure 2.5 for example outputs). This will influence the distributions used to model these functional indices.

Model construction began by first exploring the appropriateness of generalised linear models (GLMs). However, in every case, the residuals from the GLMs indicated significant non-linear relationships and as such generalised additive models were used (GAMs) (Wood, 2017; Zuur et al., 2013). The GAMs were constructed for the indices, including smoothing terms for all variables and using “select=true” to only take into account the variables deemed necessary for that model (Wood, 2017). Tests of dispersion were used to decide on a suitable GAM distribution for FGR and FRich; being either Poisson or negative binomial. As for FDiv, FEve and FDis the GAMs were modelled using a beta distribution for proportional data, as was done by Almeida et al. (2018).

Each model was then processed using “summary.gam” to produce various summaries of the models, such as estimates of smoothing terms and “anova.gam” which implements a Wald’s test to make formal inferences with regards to the significance of variables (Zuur et al., 2009). The main aim of these inferences being to identify if the different zones of the IWP had a significant effect on a particular functional index. The GAM fit was inspected by plotting the model residuals versus fitted data and all other covariates included in the dataset. The relationship between the covariates included in the models and the response variable was first visualised using “plot.gam” and include shaded component-wise confidence intervals. Prediction plots from the GAM coefficients were generated to visualise the predicted patterns in the response variables with (i) management zone and (ii) the habitat descriptors (PCO1, PCO2, PCO3) within the management zone. Two types of prediction datasets were generated. To separate the effects of the environmental covariates from the management zone, the predicted dataset for the effect of the management zone was generated using standardised values (mean) for each covariate included in the model. To visualise the effect of the habitat descriptors (eg PCO1) within each management zone, the response variables were predicted for different values of the habitat descriptor (eg PCO1) within each management zone, while standardising all other covariates in the model to their mean values. These predictive plots allow for inference to be made on how functional indices vary across the different zones of the IWP as well as how they vary according to the habitat gradients captured by PCO1, PCO2 and PCO3.

All univariate modelling was conducted in the R environment for statistical computing (Version 3.6.0, R Development Core Team 2019) via the RStudio user interface (Version 1.1.456, RStudio Team 2015). Modelling via GAMs and GLMs were computed using the packages mgcv (Wood, 2017) and MASS (Ripley et al., 2019), respectively. Graphs were plotted using ggplot2 (Wickham, 2016).

2.5 RESULTS

2.5.1 GENERAL DESCRIPTION OF THE FISH ASSEMBLAGE

Of the 105 stereo-BRUVs samples included in this study, the shallowest sample was collected at 8 m and the deepest at 39.6 m. A total of 333 species from 62 families of teleost's and elasmobranchs were identified, with the average number of species per sample being 32.4 (±16.8). Of the 333 species detected, the Labridae family was the most diverse, with 50 species recorded, and followed by the Acanthuridae, Serranidae and Lutjanidae families (Table 2.4). Labridae, again, contributed most to the fish abundance, with 13 species contributing to 86.64% of all fish records (Table 2.4).

Table 2.4: The dominant families which had the greatest species diversity, as well as the greatest percentage contribution to relative abundances across all 105 samples within the iSimangaliso Wetland Park. Also included are the 10 most frequently occurring species (MaxN: relative abundance) displayed as a percentage of the total sample size (number of samples with at least one detection of the full 105 samples).

Number of species		% contribution to MaxN		The most frequently observed species	
Family	Species count	Family	Contribution	Species	Detection
Labridae	50	Labridae	16.92%	*Variola louti*	73.33%
Acanthuridae	28	Lutjanidae	10.22%	*Sufflamen fraenatum*	66.67%
Serranidae	26	Caesionidae	9.18%	*Aprion virescens*	65.71%
Lutjanidae	22	Acanthuridae	8.77%	*Lutjanus bohar*	65.71%
Pomacentridae	17	Lethrinidae	6.50%	*Bodianus bilunulatus*	62.86%
Carangidae	16	Chaetodontidae	6.30%	*Lethrinus rubrioperculatus*	60.95%
Chaetodontidae	15	Carangidae	5.36%	*Lethrinus crocineus*	60%
Sparidae	14	Balistidae	5.33%	*Labroides dimidiatus*	56.19%
Scaridae	13	Pomacentridae	5.12%	*Coris caudimacula*	52.38%
Balistidae	12	Serranidae	4.03%	*Gymnocranius grandoculis*	52.38%

The sum of relative abundances across all samples was 9160 fish with an average ± standard deviation (SD) of 87.2 ± 62.1 per sample. The total biomass of all measured individuals was 8 169 kg, with an average ± SD of 77.8 ± 67.5 kg per sample. When looking at elasmobranchs only, a total of 21 species across 8 families were recorded. In total 114 elasmobranchs were recorded, with an average of 1.11 ± 0.35 individuals per sample.

Table 2.5: Total number of functional groups for the abundance, lengths and stages datasets, as well as the average relative abundances within each functional group for Abundances and Stages or average size for the Lengths dataset. Also, sample averages for all five functional indices (± standard deviations) are provided.

	Dataset	**Abundance**	**Lengths**	**Stages**
	Total number of functional groups	31	21	39
	Average Abundance or Size	2.772 ± 6.56	40.956 ± 73.963	1.194 ± 2.462
Average per sample	*Functional Groups*	17.35 ± 6.772	11.659 ± 4.8	15.648 ± 7.525
	Functional Richness	32.72 ± 16.04	24.692 ± 13.869	26.67 ± 14.909
	Functional Diversity	0.758 ± 0.085	0.761 ± 0.062	0.818 ± 0.063
	Functional Evenness	0.794 ± 0.081	0.772 ± 0.067	0.835 ± 0.045
	Functional Dispersion	0.414 ± 0.055	0.397 ± 0.052	0.397 ± 0.038

A total of 31, 21 and 39 functional groups were identified for abundance, length and stage of maturity metrics, respectively (Table 2.5). The average (± standard deviation) relative abundances for each functional group was 2.77 ± 6.56 and 1.19 ± 2.46 for abundance and stage of maturity metrics, respectively. The average size of individuals within each functional group for the length metric was 40.96 ± 73.96 cm (Table 2.5).

2.5.2 ENVIRONMENTAL VARIATION

Before investigating the patterns in the fish assemblage a permutational multivariate analysis of variance (PERMANOVA) was used to determine if the habitats sampled with the stereo-BRUVs differed significantly between the No-Take Sanctuary Zones (NTSZs) and the Controlled Pelagic Zone (CPZ).

The PERMANOVA done on the multivariate habitat data showed that there was a significant difference in macrobenthos structure between the different management zones (Pseudo-F = 2.367; $P_{perm} = 0.011$). The pairwise PERMANOVA comparisons showed that these differences were due to the Maputaland NTSZ being different from both the St Lucia NTSZ ($t = 1.814$; $P_{perm} = 0.0115$) and the CPZ ($t = 1.622$; $P_{perm} = 0.038$). Whereas, there was no significant difference between the St Lucia NTSZ and the CPZ. Results from the PCA done on the normalised macrobenthic and abiotic data (Figure 2.6) indicated a clear separation of Maputaland NTSZ from the other two zones, attributed to a higher percentage cover of macroalgae in the Maputaland NTSZ than in the CPZ and St Lucia NTSZ. This pattern correlated strongly with latitude and longitude (Figure 2.6).

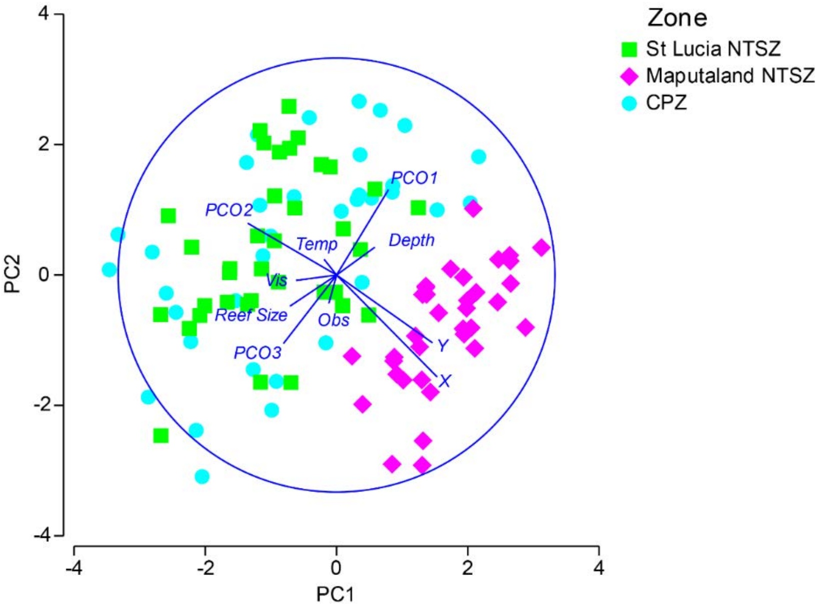


Figure 2.6: Principal Coordinate Analysis (PCA) of samples based on normalised environmental variables and macrobenthic data. Overlaid are the environmental vectors, where the length of the line corresponds to vector strength. The first axis of variation, PC1, accounts for 29.16% of total variation whereas, PC2 accounts for 21.27%. The environmental variables that correlate with the distribution of sampled habitats are overlaid as vectors (Pearson's correlation with the length corresponding to the correlation strength).

2.5.3 TAXONOMIC AND FUNCTIONAL COMMUNITY STRUCTURE

The clustering of communities based on their zones are also significantly distinct given that all P-values from the CAP analysis (derived from *a priori* hypothesis that communities between all zones are similar) were all well below 0.05 [Abundances: taxonomic trace-statistic = 1.05 P = 0.0002, functional trace-statistic = 0.63 P = 0.0002; Lengths: taxonomic trace-statistic = 0.664 P = 0.003, functional trace-statistic= 0.267 P = 0.008; Stages: taxonomic trace-statistic = 1.119 P = 0.0001, functional trace-statistic = 0.727 P = 0.0007].

When looking at reef fish communities from a taxonomic species level, CAP analyses indicated that samples showed some degree of clustering and separation of clusters based on their zone (Figure 2.7 a, c, e). When looking at fish communities from a functional level, clusters were less apparent, as is the case for the lengths data (Figure 2.7 d), or communities showed an increase in the overlap of clusters, compared to the taxonomic species level analyses (Figure 2.6 b, f).

The CAP analysis implements a leave-one-out allocation success as a means of cross-validating the clustering strengths. In a scenario where there were no distinct clusters and no differences in the fish communities found within the three zones the percentage of successful allocations, in theory, would be 33.3% due to randomising of allocations. Thus, any percentage of success greater than 33.3% indicates that clusters of fish communities are distinct between the three different zones. The results indicate that both taxonomic and functional fish communities had distinct differences between zones (Table 2.6). Furthermore, taxonomic communities were often more distinct between zones as compared to functional communities (Table 2.6, see colour scale).

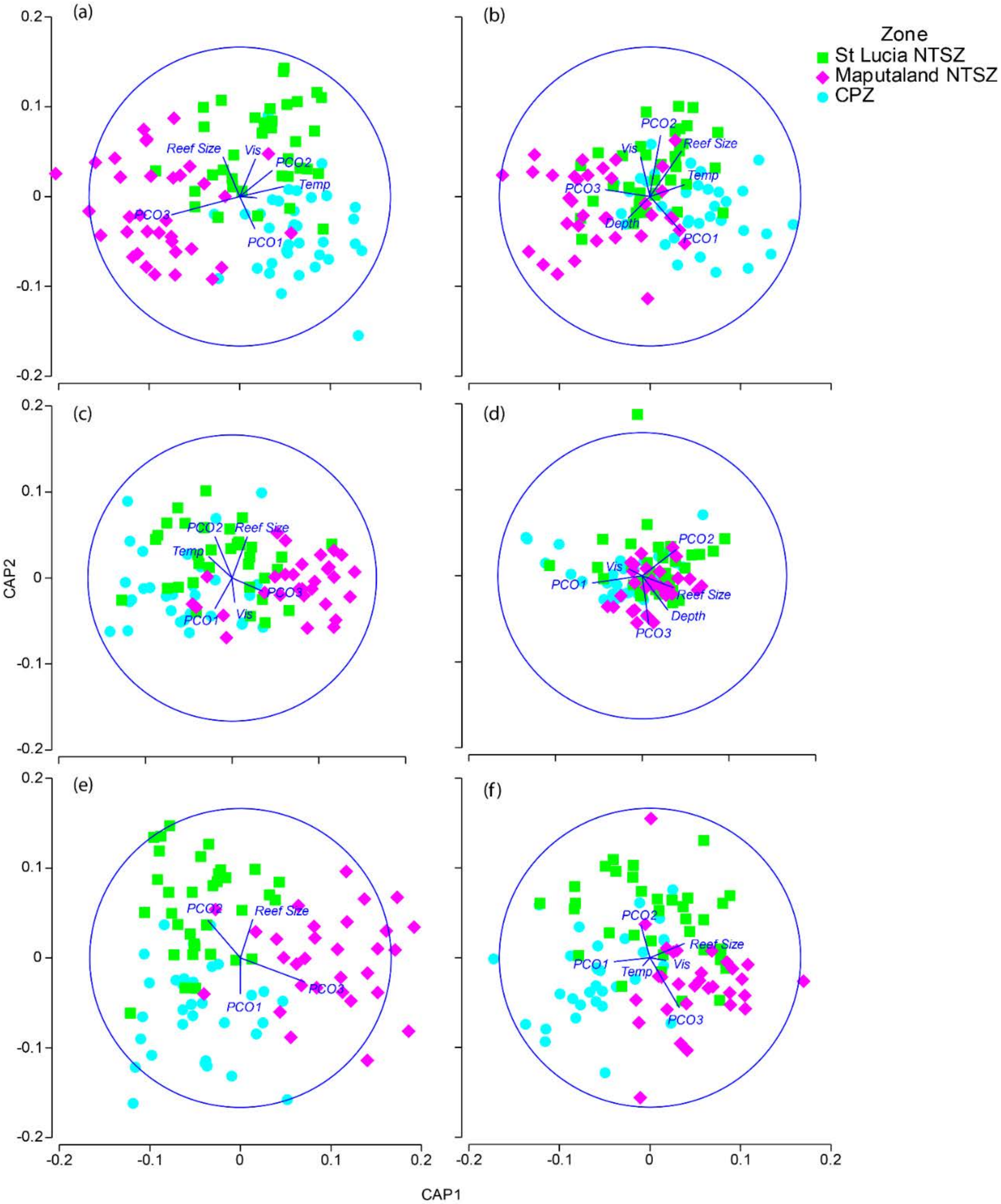


Figure 2.7: Canonical analysis of principal coordinates (CAP) for abundance (a, b), lengths (c, d) and stages of maturity (e, f) for reef fish in different management zones of the iSimangaliso Wetland Park (St Lucia No-Take Sanctuary Zone = green squares; Maputaland No-Take Sanctuary Zone = pink diamond; Controlled Pelagic Zone = blue dot). Graphs on the left (a, c, e) display analyses done on taxonomic community data. Graphs on the right display analyses done on the functional group-level data. Correlation vectors (R>0.4) for the environmental variables are overlaid, where the length of the line corresponds to the strength of the correlation and the direction to the correlated samples.

Table 2.6: Leave-one-out allocation success from the CAP analysis, where values represent the percentage of samples correctly allocated to each zone. Results are divided by both taxonomic (Tax.) and functional (Func) community analyses, as well as abundance (*A*), lengths (*L*) and stages of maturity (*S*) metrics. Included are the totals for the percentage of samples correctly allocated to each zone. Allocation percentages are ranked from high to low and colour coded according to the scale.

Leave-one-out Allocation			
		% correctly allocated	
Zone		**Tax.**	**Func.**
CPZ	*A*	65.714	57.143
	L	50	50
	S	56.25	53.125
St Lucia NTSZ	*A*	55.556	58.333
	L	47.059	35.294
	S	58.824	47.059
Maputaland NTSZ	*A*	68.571	62.857
	L	66.667	50
	S	56.667	63.33
Total correct for taxonomic and functional analyses.	*A*	0.63	0.59
	L	0.54	0.45
	S	0.57	0.54

Scale	69-65	64-60	59-55	54-50	49-45

2.5.4 ENVIRONMENTAL DRIVERS OF FISH ASSEMBLAGE STRUCTURE

Results from the RELATE analysis showed that every resemblance metric, derived from either abundance, length and stage of maturity at both a functional and taxonomic level, had patterns that significantly correlated with patterns in the resemblance matrix of the environmental data (Table 2.7). Results from the BEST-analysis identified that PCO1 (variation between low relief sand habitats and high relief stony coral habitats) and PCO3 (variation between stony coral dominated habitats and macroalgal dominated habitats) were the best subsets of variables to describe the patterns between biological and environmental data, with the taxonomic level length dataset being the only exception. For the taxonomic level length dataset, depth, PCO1 and PCO3 were identified as the best subset of covariates to explain the observed variation among samples (Table 2.7).

Table 2.7: Results from RELATE and BEST analyses to determine key potential environmental drivers of taxonomic and functional level communities where the first value indicates the Rho value followed by the corresponding P-value. The subset of variables identified by the BEST Analysis is also given along with their correlations derived from the BEST Analysis.

	RELATE	BEST	BEST Variables	Correlation
Abundance - Taxonomic	0.176; 0.02	0.501; 0.001	PCO1, PCO3	0.601
Abundance - Functional	0.176; 0.01	0.534; 0.001	PCO1, PCO3	0.634
Lengths - Taxonomic	0.137; 0.033	0.438; 0.001	Depth, PCO1, PCO3	0.538
Lengths - Functional	0.089; 0.004	0.471; 0.001	PCO1, PCO3	0.571
Stages - Taxonomic	0.132; 0.002	0.387; 0.001	PCO1, PCO3	0.587
Stages -Functional	0.121; 0.001	0.431; 0.001	PCO1, PCO3	0.531

The results from the DISTLMs (Table 2.8) reiterated the findings from the BEST-analysis (Table 2.7) where, in every scenario, PCO1 and PCO3 were prioritised as the first environmental variables to be added in the models using a step-wise procedure. The one exception being the taxonomic length metric, which sequentially added PCO1, depth and PCO3 in that order of importance (Table 2.8). In addition to PCO1 and PCO3 being consistent, depth came out as important in all datasets, with latitude and longitude important for two of the three datasets. In the functional data, many more explanatory variables explained variation in the data with latitude and longitude being important in all three datasets (Table 2.8).

Table 2.8: Sequential test results for Distance-Based Linear Models (DISTLM) where the selection criteria were Akaike information criterion (AIC score) and the selection procedure step-wise. In the step-wise selection procedure, variables are added in sequence until the AIC scores stop decreasing, with the most important variables added first. The model with the lowest AIC score is considered to be the best fitting model. Results are given for all datasets - abundance, lengths and stages of maturity at both a taxonomic and a functional level. Values given include the Trace Sum of Squares (SS(trace)), Pseudo-F, P-Value and residual degrees of freedom (res.df).

	Variable	**AIC**	**SS(trace)**	**Pseudo-F**	**P**	**res. df**
Abundance Taxonomic	PCO1	-61.258	4.316	7.838	0.000	104
	+PCO3	-62.776	1.870	3.476	0.000	103
	+X	-62.819	1.058	1.985	0.000	102
	+Y	-62.862	1.038	1.966	0.000	101
	+Depth	-62.941	1.035	1.981	0.001	100
Abundance Functional	PCO1	-86.987	10.388	24.046	0.000	104
	+PCO3	-88.881	1.828	4.494	0.000	103
	+X	-91.451	1.621	3.855	0.000	102
	+Depth	-92.785	1.284	3.227	0.000	101
	+Y	-93.858	1.149	2.942	0.000	100
	+Water Column	-94.402	0.926	2.404	0.002	99
	+PCO2	-94.885	0.883	2.323	0.004	98
	+Visibility	-95.180	0.798	2.124	0.007	97
Lengths Taxonomic	PCO1	769.250	26882.000	9.086	0.000	94
	+Depth	767.360	11051.000	3.848	0.000	93
	+PCO3	766.520	7793.300	2.766	0.001	92
Lengths Functional	PCO1	689.460	25608.000	19.874	0.000	94
	+PCO3	686.250	6403.200	5.191	0.000	93
	+X	684.940	3878.000	3.219	0.003	92
	+Y	681.830	5752.500	4.981	0.000	91
	+Water Column	681.170	2865.600	2.523	0.016	90
	+Visibility	680.850	2443.700	2.180	0.035	89
Stages Taxonomic	PCO1	-58.197	2.654	4.967	0.000	94
	+PCO3	-58.569	1.226	2.327	0.000	93
	+Depth	-58.213	3.193	3.978	0.000	92
Stages Functional	PCO1	-72.075	5.792	12.528	0.001	94
	+PCO3	-73.085	1.341	2.962	0.002	93
	+X	-74.272	1.376	3.106	0.001	92
	+Y	-75.136	1.198	2.755	0.001	91
	+Depth	-75.571	0.991	2.313	0.002	90
	+Water Column	-76.024	0.973	2.303	0.003	89

2.5.5 EFFECT OF ZONATION

The sequential PERMANOVA results showed that water column, obstruction and depth accounted for a significant amount of the variation in abundance, length and stage of maturity data for both the taxonomic and functional communities (Table 2.9). Similarly, variation in the habitat descriptors PCO1 and PCO3 both significantly influenced trends in all datasets at both the taxonomic and functional levels (Table 2.9). Latitude was found to significantly affect abundances at a taxonomic and functional level, and lengths and stages at a functional level. Once the effect of all these variables had been accounted for, the results indicated that the effect of the zone remained significant in every case (Table 2.9).

Table 2.9: Results (Pseudo-F; P_{perm}) of the permutational multivariate analysis of variance (PERMANOVA) run on the abundance, length and stage of maturity metrics for both taxonomic and functional communities. Each PERMANOVA was done according to a single factor design with zone, Type I Sequential sum of squares and 9999 permutations. The environmental variables added to the PERMANOVA included sampling bias variables such as visibility, water column and obstruction; other potentially important environmental factors such as temperature, depth, reef size and longitude; and lastly the three habitat gradients derived from the Direct Principal Component Method namely PCO1, PCO2 and PCO3. Cases where the P_{perm} infers a significant difference are given in bold.

Variables	**Abundance**		**Lengths**		**Stages**	
	Species	Functional	Species	Functional	Species	Functional
Visibility	1.198; 0.123	**3.117;** **<0.001**	**1.871;** **0.008**	**3.589;** **0.001**	1.251; 0.054	**2.474;** **<0.001**
Water column	**2.110;** **<0.001**	**4.205;** **<0.001**	**1.900;** **0.008**	**3.42;** **0.002**	**1.329;** **0.021**	**2.83;** **<0.001**
Obstruction	**2.096;** **<0.001**	**5.342;** **<0.001**	**2.959;** **<0.001**	**3.927;** **0.001**	**2.037;** **<0.001**	**4.032;** **<0.001**
Temperature	1.04; 0.336	**1.764;** **0.035**	0.959; 0.511	1.797; 0.085	0.915; 0.712	1.282; 0.162
Depth	**4.129;** **<0.001**	**5.761;** **<0.001**	**4.672;** **<0.001**	**2.782;** **0.01**	**2.662;** **<0.001**	**3.402;** **<0.001**
PCO1	**5.976;** **<0.001**	**18.486;** **<0.001**	**6.336;** **<0.001**	**15.321;** **<0.001**	**3.470;** **<0.001**	**8.638;** **<0.001**
PCO2	**1.846;** **0.001**	**2.332;** **0.003**	1.409; 0.085	0.713; 0.672	**1.513;** **0.004**	**1.625;** **0.041**
PCO3	**1.669;** **0.002**	**3.2512;** **<0.001**	**2.838;** **<0.001**	**5.199;** **<0.001**	**1.848;** **<0.001**	**2.596;** **0.001**
Reef size	1.218; 0.108	0.95; 0.497	0.772; 0.793	0.594; 0.757	1.028; 0.383	0.836; 0.682
Longitude	1.304; 0.058	1.603; 0.051	0.98; 0.561	**1.624;** **0.044**	1.267; 0.178	**1.635;** **0.039**
Zone	**1.601;** **<0.001**	**3.583;** **<0.001**	**1.926;** **<0.001**	**3.165;** **<0.001**	**1.541;** **<0.001**	**2.642;** **<0.001**

The *post hoc* pair-wise PERMANOVA showed that in every scenario it was the Maputaland NTSZ which was significantly different from the other management zones (Table 2.10). However, because PERMANOVA identifies a significant difference as either being due to locations in multidimensional space or due to differences in dispersion, a supplementary PERMDISP was done to identify if these significant differences were only due to a location effect and/or a dispersion effect. Length (Taxonomic: F = 3.236, $P_{(perm)} = 0.085$; Functional: F = 2.613, $P_{(perm)} = 0.173$) and stage of maturity (Taxonomic: F = 3.038, $P_{(perm)} = 0.091$; Functional: F = 3.03, $P_{(perm)} = 0.183$) showed no significant differences in homogeneity, suggesting that the significant results were due to differences in assemblage structure. On the other hand, the abundance metric showed a significant difference in the homogeneity of dispersion during the overall main test (Table 2.11).

Table 2.10: Pair-wise permutational multivariate analysis of variance (PERMANOVA) done to identify which management zones were significantly different from each other given that significance was found in the PERMANOVA analysis (Table 2.9). Values given in brackets indicate the t value and corresponding P_{perm} value. The pair-wise PERMANOVA was done using Type I sequential sum of squares and 9999 permutations. Cases where the P_{perm} infers a significant difference are given in bold.

	Abundance		**Length**		**Stage of maturity**	
	Species	Functional	Species	Functional	Species	Functional
CPZ vs. St Lucia NTSZ	1.105; 0.091	1.235; 0.082	1.133; 0.17	1.377; 0.076	1.074; 0.168	1.028; 0.37
CPZ vs. Maputaland NTSZ	**1.309; 0.004**	**2.376; 0.0001**	**1.447; 0.006**	**2.099; 0.001**	**1.26; 0.003**	**1.719; 0.0002**
St Lucia NTSZ vs. Maputaland NTSZ	**1.384; 0.0004**	**1.544; 0.006**	**1.423; 0.004**	**1.328; 0.008**	**1.313; 0.0006**	**1.778; 0.0003**

The PERMDISP pair-wise tests pinpointed these differences in dispersion to occur between the CPZ and the two NTSZs (Table 2.11), with greater levels of variability in the taxonomic and functional structure of the fish assemblages in the CPZ, relative to the NTSZs (see Figure 2.7a, b)

Table 2.11: Permutational test for homogeneity of dispersions (PERMDISP), where only the two abundance metrics showed significant differences in the overall main test and hence this table includes *post hoc* pairwise tests to identify which management zones had significant differences in dispersion. Main test results are given as (F; P_{perm}) and pairwise tests are given as (t; P_{perm}). Cases where the P_{perm} infers a significant difference are given in bold.

	Abundance Species	**Abundance Functional**
Deviations from Centroid: Main test	**F 9.249; P_{perm} 0.0001**	**F 11.42; P_{perm} 0.0001**
CPZ vs St Lucia NTSZ	**4.02; 0.0004**	**4.538; 0.0002**
CPZ vs Maputaland NSTZ	**2.356; 0.025**	**3.861; 0.001**
St Lucia NTSZ vs Maputaland NTSZ	2.05; 0.571	0.205; 0.861

2.5.5.1 CHARACTERISTIC SPECIES AND FUNCTIONAL GROUPS

While there was a notable variability in the makeup and contribution of the dominant species in terms of abundance within the different management zones, the SIMPER analysis indicated that four species were common (*Aprion virescens*, *Lutjanus bohar*, *Variola louti* and *Lethrinus crocineus*), however, they were all less abundant in the CPZ, relative to the NTSZs (Table 2.12). In addition, *Lethrinus rubrioperculatus* was highlighted as an important species within the NTSZs, but occurred in greater average abundance within the Maputaland NTSZ, relative to the St Lucia NTSZ (Table 2.12).

As for characteristic species based on the length dataset, there were three species common to all zones (*Lutjanus bohar*, *Variola louti* and *Aprion virescens*) once again all of which presented smaller average lengths within the CPZ. The two NTSZs also shared three species (*Epinephelus tukula*, *Lethrinus crocineus* and *Caranx melampygus*), of which only *L. crocineus* presented larger average lengths within the Maputaland NTSZ.

The SIMPER analysis run on the stage of maturity dataset indicated that the CPZ was largely characterised by juveniles, with only one adult stage listed for *Bodianus bilunulatus*. In contrast, the two NTSZs were characterised by adult fishes, with the St Lucia NTSZ being characterised by both adult and juveniles stages of *Aprion virescens* (Table 2.12).

Table 2.12 Results for taxonomic level SIMPER analysis to identify characteristic species for each management zone according to abundance, length and abundance per stage of maturity. Where X̄ represents the average value for each sample (Average MaxN or average length in cm's) and % shows the percentage which that species contributed towards the similarity of all samples within that zone. For the stage of maturity metric, 'A' indicates adults and 'J' indicates juveniles.

	CPZ			**St Lucia NTSZ**			**Maputaland NTSZ**		
	Species	x̄	**%**	**Species**	x̄	**%**	**Species**	x̄	**%**
Abundance	*Labroides dimidiatus*	1.49	9.79	*Lethrinus crocineus*	1.94	8.17	*Lethrinus rubrioperculatus*	3.43	7.27
	Lethrinus microdon	0.77	9.73	*Variola louti*	1.86	7.82	*Parupeneus macronemus*	1.29	7.15
	Gymnocranius grandoculis	1.04	6.51	*Lethrinus rubrioperculatus*	2.47	7.2	*Aprion virescens*	1.09	6.88
	Aprion virescens	0.74	5.95	*Bodianus bilunulatus*	1.42	6.31	*Coris caudimacula*	3.49	6.47
	Variola louti	0.83	4.86	*Aprion virescens*	1.17	6.12	*Lutjanus bohar*	2.09	6.46
	Lutjanus bohar	1.11	4.85	*Lutjanus bohar*	1.92	5.5	*Odonus niger*	3.89	4.83
	Lethrinus crocineus	1	4.75	*Acanthurus tennenti*	1.44	5.01	*Lethrinus crocineus*	1.89	4.5
	Sufflamen fraenatum	0.94	4.74	*Chaetodon auriga*	1.14	4.32	*Variola louti*	1.29	4.15
							Scarus rubroviolaceus	1.29	2.35
Length	*Lutjanus bohar*	274.12	9.69	*Epinephelus tukula*	1016.94	12.89	*Variola louti*	373.03	11.53
	Carcharhinus sealei	257.96	9.27	*Lutjanus bohar*	384.63	9.33	*Lutjanus bohar*	390.4	10.74
	Variola louti	253.74	8.99	*Variola louti*	357.08	8.73	*Aprion virescens*	438.06	9.65
	Sufflamen fraenatum	150.21	6.96	*Lethrinus crocineus*	264.67	8	*Epinephelus tukula*	961.94	7
	Bodianus bilunulatus	147.83	5.96	*Aprion virescens*	546.1	7.81	*Lethrinus crocineus*	405.76	5.42
	Aprion virescens	298.52	5	*Caranx melampygus*	501.92	7.49	*Caranx melampygus*	350.68	4.68
	Lethrinus rubrioperculatus	137.59	4.28				*Scarus rubroviolaceus*	264.16	4.25
Stage of maturity	*Lethrinus rubrioperculatus J*	1.13	8.02	*Lethrinus crocineus A*	1.79	12.88	*Lutjanus bohar A*	1.77	9.11
	Lutjanus bohar J	0.97	6.88	*Lethrinus rubrioperculatus A*	1.53	8.52	*Lethrinus crocineus A*	1.43	8.49
	Variola louti J	0.84	6.63	*Variola louti A*	1.21	7.02	*Lethrinus rubrioperculatus A*	1.83	7.89
	Sufflamen fraenatum J	0.66	6.49	*Lutjanus bohar A*	1.12	6.16	*Variola louti A*	1.1	7.13
	Bodianus bilunulatus A	0.53	6.44	*Sufflamen fraenatum A*	0.68	4.98	*Aprion virescens A*	0.67	5.86
	Carcharhinus sealei J	0.34	4.87	*Epinephelus tukula A*	0.71	4.11	*Coris caudimacula A*	1.13	5.16
	Gymnocranius grandoculis_J	0.56	3.99	*Aprion virescens A*	0.88	4.11	*Labroides dimidiatus A*	0.87	3.44
	Lethrinus crocineus J	0.72	3.76	*Aprion virescens J*	0.47	3	*Lethrinus microdon A*	0.57	3.04
	Aprion virescens J	0.59	3.55						

Table 2.13: Results from the SIMPER analysis to identify characteristic functional groups for each management zone according to abundance. The number of the functional group is given, along with the average relative abundance (MaxN), percentage (%) to which that group contributed and a representative species from that functional group (FGR).

	FGR	MaxN	%	Example species and common traits
CPZ	FGR_17	9.14	23.56	*Lethrinus microdon:* Medium, Protogynous, small groups, general habitats
	FGR_20	6.89	11.49	*Caesio teres:* Very small, lower carnivores, large shoals, mobile and pelagic
	FGR_16	3.2	7.84	*Lutjanus rivulatus:* Large, solitary carnivores, mobile, profile habitats
	FGR_13	2.94	5.95	*Plectorhinchus playfairi*: Medium, solitary hunting carnivores, profile habitats, bentho-pelagic
	FGR_31	2.37	4.66	*Sufflamen fraenatum*: Small, guarders, nesters, variable omnivores, solitary to groups
St Lucia NTSZ	FGR_17	8.97	20.14	*Lethrinus microdon*: Medium, Protogynous, small groups, general habitats
	FGR_13	4.56	9.57	*Plectorhinchus playfairi*: Medium, solitary hunting carnivores, profile habitats, bentho-pelagic
	FGR_28	2.92	7.05	*Epinephelus tukula*: Very large, protogyny, solitary carnivores, general habitats, bentho-pelagic
	FGR_5	4.08	6.6	*Acanthurus leucosternon*: Small, browsing herbivores, solitary to groups, profile habitats
	FGR_16	6.44	5.72	*Lutjanus rivulatus*: Large, solitary carnivores, mobile, profile habitats
	FGR_31	2.47	4.65	*Sufflamen fraenatum*: Small, guarders, nesters, variable omnivores, solitary to groups
Maputaland NTSZ	FGR_17	10.03	16.87	*Lethrinus microdon:* Medium, Protogynous, small groups, general habitats
	FGR_13	4.57	8.9	*Plectorhinchus playfairi*: Medium, solitary hunting carnivores, profile habitats, bentho-pelagic
	FGR_30	4.63	7.38	*Parupeneus indicus*: Small, nesters, small groups, mobile, profile habitats
	FGR_18	5.34	6.95	*Thalassoma herbracium*: Very small, solitary, mobile, coral-associated
	FGR_5	4.86	5.75	*Acanthurus leucosternon*: Small, browsing herbivores, solitary to groups, profile habitats
	FGR_11	3.71	5.33	*Labroides dimidiatus*: Very small, protogyny, cleaner, solitary or pairs, coral-associated

Table 2.14: Results from the SIMPER analysis indicating characteristic functional groups for each management zone according to length. The number of the functional group is given, along with the average cumulative length (Cum. Length), percentage (%) to which that group contributed and a representative species from that functional group (FGR).

	FGR	Cum. Length	%	Example species and common traits
CPZ	FGR_10	4401.18	25.02	*Lutjanus bohar*: Large, dioecism, hunting carnivore, gregarious, profile habitats
	FGR_13	3283.16	22.53	*Polysteganus praeorbitalis*: Large, protogyny, hunting carnivore, mobile, general habitats
	FGR_18	8552.57	9.46	*Rhynchobatus djiddensis*: Large, dioecism, internal live bearers, hunting carnivore, sand, solitary
St Luc NTSZ	FGR_10	5021.69	32.17	*Lutjanus bohar*: Large, dioecism, hunting carnivore, gregarious, profile habitats
	FGR_13	4390.59	22.55	*Polysteganus praeorbitalis*: Large, protogyny, hunting carnivore, mobile, general habitats
Map NTSZ	FGR_10	5259.54	33.64	*Lutjanus bohar*: Large, dioecism, hunting carnivore, gregarious, profile habitats
	FGR_13	5292.38	20.47	*Polysteganus praeorbitalis*: Large, protogyny, hunting carnivore, mobile, general habitats

Table 2.15: Results from the SIMPER analysis to identify characterising functional groups for each management zone according to the stage of maturity (stages). The number of the functional group is given, along with the average relative abundance (MaxN), percentage (%) to which that group contributed, whether the group is characterised by adults or juveniles (stage) and a representative species from that functional group (FGR).

	FGR	MaxN	%	Stage	Example species and common traits
CPZ	FGR_17	4.19	20.34	Juvenile	*Lethrinus microdon*: Small, Protogynous, small groups, general habitat
	FGR_11	2.97	10.67	Adult	*Plectorhinchus playfairi*: Medium, solitary hunting carnivores, profile habitats
	FGR_21	1.94	10.32	Juvenile	*Gymnocranius grandoculis*: Small, dioecism, solitary to small groups, variable omnivores
	FGR_16	3.53	9.99	Juvenile	*Lutjanus gibbus*: Small, dioecism, non-guarders, scatterers, lower carnivore, grouping
St Lucia NTSZ	FGR_17	6.94	28.85	Juvenile	*Lethrinus microdon*: Small, Protogynous, small groups, general habitat
	FGR_11	2.91	11.48	Adult	*Plectorhinchus playfairi*: Medium, solitary hunting carnivores, profile habitats
	FGR_30	2.32	8.55	Adult	*Epinephelus tukula*: Very large, protogyny, solitary carnivores, general habitats, bentho-pelagic
	FGR_9	1.38	5.5	Adult	*Caranx ignobilis* Very large, dioecism non-guarders, egg scatterers, hunting carnivore, Solitary, pelagic
Maputaland NTSZ	FGR_17	6.43	19.67	Juvenile	*Lethrinus microdon*: Small, Protogynous, small groups, general habitat
	FGR_11	3.57	12.55	Adult	*Plectorhinchus playfairi*: Medium, solitary hunting carnivores, profile habitats
	FGR_30	2.27	6.64	Adult	*Epinephelus tukula*: Very large, protogyny, solitary carnivores, general habitats, bentho-pelagic
	FGR_24	3.07	12.56	Adult	*Galeocerdo cuvier*: Very large, dioecism, internal live bearers higher carnivore, solitary

Functional community analysis on abundance data identified 10 functional groups that were characteristic of the IWP (Table 2.13). Two of the 10 functional groups were common to all zones: FGR_17, which is composed of medium to large Lethrinid (Emperors) species that are regarded as somewhat habitat generalists; FGR_13, which is composed of small to medium-sized Haemulid species (Rubberlips) which display solitary behaviours, as well as being carnivores which frequent high profile reefs (which are either bare or coral dominated). Four functional groups were unique to specific management zones: FGR_20, which consisted of small pelagic bait species (For example *Decapterus macarellus*), was found in the CPZ; FGR_28, which consisted of very large grouper (Serranidae) species, was specific to the St Lucia NTSZ; FGR_18 and FGR_11, which were both dominated by different assemblages of wrasse (For example *Bodianus bilunulatus*, *Coris Formosa*, *Halichoeres hortulans*), were restricted to the Maputaland NTSZ.

The number of length-based functional groups which contributed to 50% of similarity within a management zone, were far fewer than the number identified in the analysis of the abundance and stage of maturity metrics. Results (See Table 2.14) show two functional groups which are common to all zones; FGR_13 which is composed of Seabream species (Sparidae) are regarded as hunting carnivores with most species associated with sandy to reef habitats; and FGR_10 which is composed of Snappers (Lutjanids) which are seldom solitary and associate more with reef habitats. Interestingly, the CPZ has the addition of FGR_18 which is a small group of Wedgefishes (Rhinobatidae) and Rays (Dasyatidae) which frequents sandy habitats.

The SIMPER run on the stage of maturity functional data identified a juvenile Emperor (FGR_17) and an adult Rubberlip group (FGR_11) to be commonly characteristic of all zones (Table 2.15). The CPZ was characterised by juvenile functional groups, reiterating the presence of juveniles seen in the species level analyses (Table 2.12). The NTSZs saw the addition of a functional group composed of a few very large species of adult groupers (FGR_30). Lastly, the NTSZs had unique functional groups; whereby the St Lucia NTSZ had a characteristic group of large, solitary adult kingfish species (FGR_9) and the Maputaland NTSZ had a functional group composed of large, adult shark species (FGR_24).

2.5.6 THE RESPONSE OF FUNCTIONAL INDICES

2.5.6.1 EFFECT OF MANAGEMENT ZONE

The results from the Wald's test run on the GAMs showed that the number of functional groups (Table 2.16, 2.17, and 2.18) and the functional richness (Table 2.16, 2.17, and 2.18) were significantly affected by the management zone. When predictions were based on standardised estimates for model covariates, the results showed that the Maputaland NTSZ had a significantly higher number of functional groups and higher functional richness, relative to the St Lucia NTSZ and the CPZ (Figure 2.8 a, b). Functional dispersion was also significantly affected by the management zone, but this effect was only evident in the length and stage of maturity data (Table 2.17 and 2.18). When the mean values (± 95% confidence intervals) for functional dispersion based on the length data were estimated from the GAM coefficients using standardised values for the environmental covariates included in the Maputaland NTSZ had significantly higher functional dispersion, in comparison to both the St Lucia NTSZ and the CPA (Figure 2.8 e; Appendix Table 6.3). On the other hand, with the stages dataset, St Lucia and Maputaland No-Take Sanctuary Zones had similar functional dispersion, but both had significantly higher functional dispersion in comparison to the CPZ (Figure 2.8 e; Appendix Table 6.4). Management zone had a significant effect on functional evenness in the lengths dataset (Table 2.17), with significantly lower evenness in the Maputaland No-Take Sanctuary Zones, in comparison to the St Lucia NTSZ and the CPZ (Figure 2.8 d; Appendix Table 6.3). Management zone did not affect functional diversity in all cases (Table 2.16, 2.17, 2.18).

2.5.6.2 EFFECT OF REEF SIZE AND DEPTH

The effect of depth was inconsistent between the five functional indices or across the three metrics of abundance, lengths and stages. The Wald's test showed that depth had a significant effect on functional diversity based on abundance (Table 2.16). The GAM plots (Appendix Figure 6.14) showed the response of functional diversity with depth to be relatively linear and slightly negative. Functional richness was significantly influenced by depth based on lengths (Table 2.17). The response of functional richness oscillated with depth but overall showed a slightly negative trend (Appendix Figure 6.10). Both the number of functional groups and functional richness were significantly influenced by depth according to the stage of maturity (Table 2.18). The number of functional groups showed a relatively linear relationship; whereas functional richness had an oscillating trend with both indices generally increasing with a change in depth. (Appendix Figures 6.6 and 6.12 respectively).

The effect of reef size on the various metrics for assemblage structure was mostly negligible, with the only exception being evident with the measure of functional evenness from the multivariate length data (Table 2.17). The GAM Plots for this model showed that functional evenness decreased with an increase in reef size (Appendix Figure 6.22).

Table 2.16: Results from the Wald's test for generalised additive models for the functional indices (FGR= number of functional groups, Frich = functional richness, FDis = functional dispersion, FDiv = functional diversity and FEve = functional evenness) derived from functional analysis of abundance data. Degrees of freedom (df), Chi square (χ) and P values are given for parametric variables and estimated degrees of freedom (edf), Chi square (χ) and P values are given for non-parametric variables. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Abundances	**FGR**			**FRich**			**FDis**			**FDiv**			**FEve**		
	df	*χ*	*P*	*df*	*χ*	*P*	*df*	*χ*	*P*	*df*	*χ*	*P*	*df*	*χ*	*P*
Zone	2	23.400	<0.001***	2.000	15.870	<0.001***	2	1.193	0.384	2	1.805	0.406	2	4.002	0.134
	edf	*χ*	*P*	*edf*	*χ*	*P*	*edf*	*χ*	*P*	*edf*	*χ*	*P*	*edf*	*χ*	*P*
Visibility	1.979	11.540	0.001**	1.770	12.319	<0.001***	1.269	3.360	0.062	1.568	6.140	0.014*	0.281	0.392	0.238
Obstruction	0.487	0.942	0.122	1.064	2.471	0.083	0	0	1	0.882	7.248	0.003**	0	0	1
Water Column	1.577	1.743	0.284	0	0	0.914	0	0	0.329	0	0	0.383	0	0	0.416
Temperature	5.068	13.891	0.009**	3.955	5.440	0.206	1.267	3.205	0.067	1.321	2.677	0.112	0	0	0.392
Depth	0.393	0.537	0.229	0.725	1.703	0.115	0.271	0.315	0.277	1.780	14.026	<0.001***	0	0	1
PCO1	2.211	99.710	<0.001***	2.011	77.394	<0.001***	0.985	64.792	<0.001***	1.341	3.724	0.046*	0.422	0.729	0.019*
PCO2	1	6.887	0.003**	1	6.014	0.006**	1.373	4.854	0.022*	0.006	0.006	0.272	0	0	1
PCO3	2.869	22.557	<0.001***	2.919	22.547	<0.001***	1.573	6.128	0.014*	0.597	1.488	0.062	0	0	0.364
Reef size	3.012	5.577	0.107	0.811	0.856	0.321	0.102	0.114	0.284	0.306	0.393	0.243	0	0	0.900

Table 2.17: Results from the Wald's test for generalised additive models for the functional indices (FGR= number of functional groups, Frich = functional richness, FDis = functional dispersion, FDiv = functional diversity and FEve = functional evenness) derived from functional analysis of length data. Degrees freedom (df), χ (Chi-squared) and P values are given for parametric variables and edf (estimated degrees of freedom), Chi square (χ) and P values are given for non-parametric variables. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Asterisks indicate levels of significance; * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Lengths	**FGR**			**FRich**			**FDis**		
	df	*χ*	*P*	*df*	*χ*	*P*	*df*	*χ*	*P*
Zone	2	12.700	0.001**	2	7.803	0.02*	2	9.967	0.007**
	edf	*χ*	*P*	*edf*	*χ*	*P*	*edf*	*χ*	*P*
Visibility	1.447	6.282	0.011*	1.073	7.805	0.002**	1.077	2.583	0.085
Obstruction	0	0	0.371	1.360	4.048	0.03*	0	0	1
Water Column	0	0	1	0.000	0.000	0.684	0	0	0.225
Temperature	0	0	0.549	7.031	15.178	0.022*	0.502	1.006	0.151
Depth	0.679	2.107	0.072	3.578	9.175	0.025*	0.942	16.171	<0.001***
PCO1	1.833	74.253	<0.001***	0.980	47.613	<0.001***	1.776	58.297	<0.001***
PCO2	2.777	4.979	0.088	1	2.378	0.081	0	0	0.788
PCO3	2.932	24.006	<0.001***	3.263	17.402	<0.001***	2	16.535	<0.001***
Reef size	0	0	0.413	0.000	0.000	0.859	0	0	0.519

	FDiv			**FEve**		
	df	*χ*	*P*	*df*	*χ*	*P*
Zone	2	4.251	0.119	2	13.690	0.001*
	edf	*χ*	*P*	*edf*	*χ*	*P*
Visibility	0.794	1.537	0.140	0.000	0.000	0.615
Obstruction	0	0	0.574	0	0	1
Water Column	0	0	1	1	2	0.100
Temperature	0	0	1	0	0	1
Depth	0	0	0.475	0	0	1
PCO1	1.622	11.065	0.001**	1.855	11.067	0.001**
PCO2	0	0	0.504	0	0	1
PCO3	0	0	0.515	0	0	0.371
Reef size	0	0	0.469	1	4	0.029*

Table 2.18: Results from the Wald's test from the Generalised Additive Models for the Functional Indices (FGR= number of functional groups, Frich = functional richness, FDis = functional dispersion, FDiv = functional diversity and FEve = functional evenness) derived from functional analysis of Stage of maturity. Degrees freedom (df), χ (Chi-squared) and P values are given for parametric variables and edf (estimated degrees of freedom), Chi square and P values are also given for non-parametric variables. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Stages	**FGR**			**FRich**			**FDis**		
	df	χ	*P*	*df*	χ	*P*	*df*	χ	*P*
Zone	2	8.175	0.017*	2	22.140	<0.001***	2	11.230	0.004**
	edf	χ	*P*	*edf*	χ	*P*	*edf*	χ	*P*
Visibility	1.054	6.321	0.006**	1.797	12.971	<0.001***	1.185	3.459	0.048*
Obstruction	0.268	0.421	0.175	1.802	5.889	0.024*	0	0	1
Water Column	0	0	1	0	0	0.900	1	2	0.106
Temperature	7.301	15.330	0.02*	0	0	1	0.758	1.040	0.234
Depth	0.905	6.156	0.007**	2.413	6.430	0.039*	0	0	0.342
PCO1	1.966	68.027	<0.001***	0.994	40.945	<0.001***	2.314	56.401	<0.001***
PCO2	1	3.440	0.030*	3	6.639	0.049*	0	0	0.437
PCO3	2.836	22.712	<0.001***	3.337	21.794	<0.001***	0.676	2.083	0.041*
Reef size	0	0	0.654	0	0	0.961	0	0	0.903

	FDiv			**FEve**		
	df	χ	*P*	*df*	χ	*P*
Zone	2	0.939	0.625	2	0.475	0.788
	edf	χ	*P*	*edf*	χ	*P*
Visibility	0.793	1.281	0.186	0.615	1.010	0.182
Obstruction	0	0	0.333	0	0	1
Water Column	1.099	4.280	0.027*	0	1	0.206
Temperature	0.634	1.709	0.095	0	0	0.858
Depth	0	0	1	0	0	1
PCO1	2.006	3.098	0.041*	0.817	4.419	0.018*
PCO2	0	0	0.678	0	0	1
PCO3	0.732	2.706	0.039*	0	0	0.288
Reef size	0	0	0.419	1	3	0.053

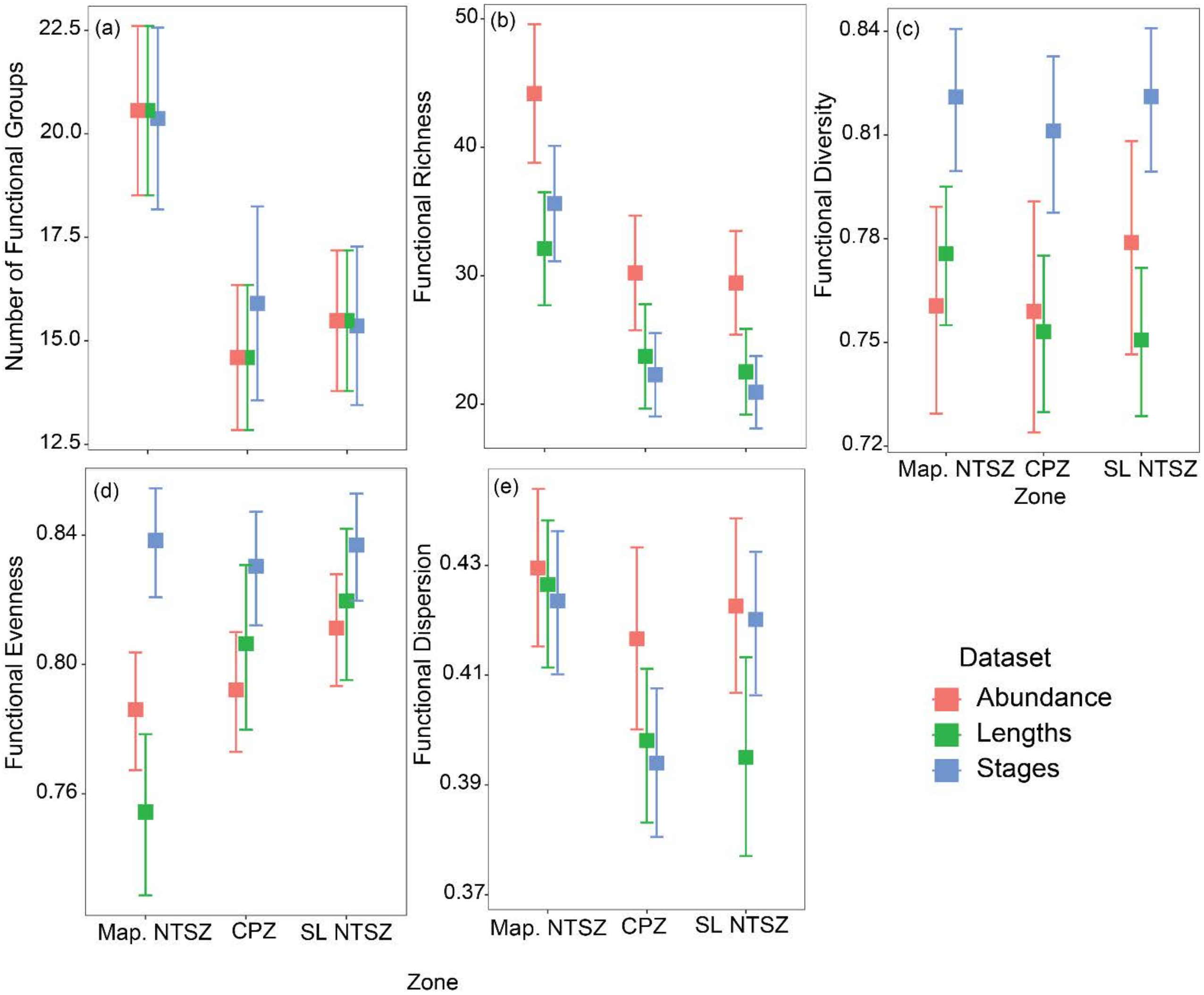


Figure 2.6: Predicted mean and 95 % confidence interval error bars from the generalized additive models for functional indices: (a) the number of functional groups, (b) functional richness, (c) functional diversity, (d) functional evenness and (e) functional dispersion; within different zones of the iSimangaliso Wetland Park (Map. NTSZ = Maputaland No-Take Sanctuary Zone, CPZ = Controlled Pelagic Zone and SL NTSZ =St Lucia No-Take Sanctuary Zone). Predictions were based on average values for all continuous covariates that were included in the models (see Table 2.16 to 2.18). The results from the abundance (red), lengths (green) and stages (blue) datasets have been combined to aid in visualisation.

2.5.6.3 EFFECT OF HABITAT COVARIATES: PCO1, PCO2 AND PCO3

The habitat covariates PCO1, PCO2 and PCO3 each captured a gradient of variation in the macrobenthic community within the iSimangaliso Wetland Park. The covariate PCO1 captured variation between habitats that are typically dominated by stony corals (low scores) to habitats that are sandy and have low relief (high scores). The Walds's test results indicated that the effect of PCO1 was significant for all five functional diversity indices derived from abundance, length and stage of maturity metrics (Table 2.16, 2.17 and 2.18). The predicted relationship between PCO1 and the functional indices, based on standardised values for the model covariates, indicated that the number of functional groups (Figure 2.9 a, f, k), functional richness (Figure 2.9 b, g, l), functional dispersion (Figure 2.9 c, h, m) and functional diversity (Figure 2.9 d, I, n) in general, displayed increasing values as the values of PCO1 increased. When looking at the general trends for functional indices concerning PCO1, values it was evident that these indices decreased as one moved from stony coral dominated habitats towards sandy low relief habitats. The opposite was true for functional evenness with a change in PCO1 (Figure 2.9 e, j, o), where overall positive trends are seen.

The Wald's test showed that only the number of functional groups and functional richness was significantly influenced by covariate PCO2 based on the abundance and stage of maturity metrics (Table 2.16, 2.18). Functional dispersion was also significantly influenced by PCO2 but only for the abundance dataset (Table 2.16). Low scores of PCO2 are associated with macroalgal habitats and high scores with habitats characterised by zoanthids and true anemones. The predicted relationship shows a general increasing trend in significant indices with an increase in PCO2 scores (Figure 2.10).

Lastly, habitat covariate PCO3 had a significant effect, according to the Wald's test, on the number of functional groups, functional richness and functional dispersion for abundance, lengths and stage of maturity (Table 2.16, 2.17 and 2.18). Functional diversity was also significantly affected by PCO3, but only for the stage of maturity metric (Table 2.18). Low scores of PCO3 were associated with macroalgal habitats and high scores with habitats characterised by stony corals. When indices showed significance with covariate PCO3, all overall trends were positive (Figure 2.11).

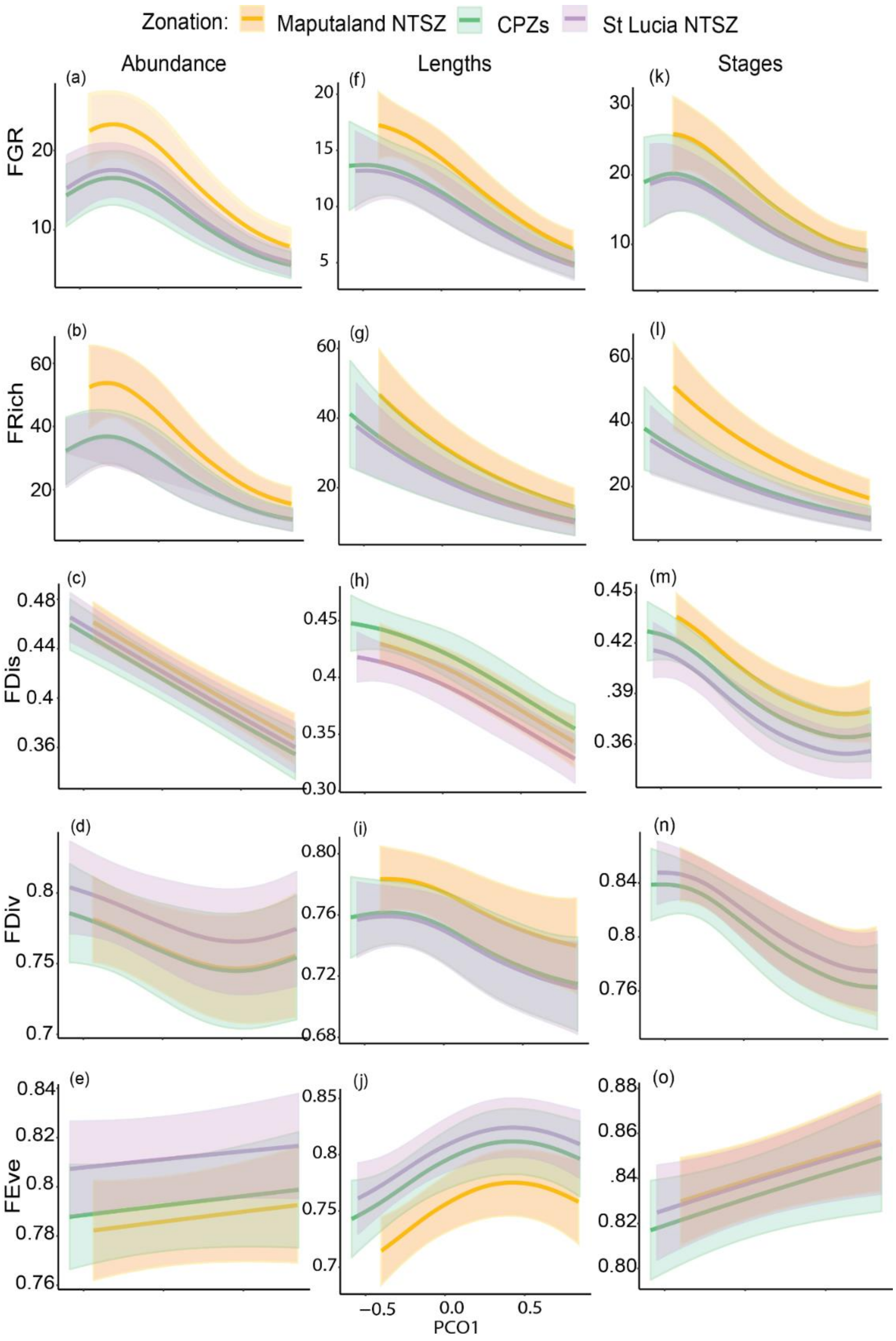


Figure 2.7: The predicted relationship between habitat variable PCO1 and number of functional groups (FGR a, f, k); functional richness (FRich b, g, l); functional dispersion (FDis c, h, m); functional diversity (FDiv d, I, n) and functional evenness (FEve e, j, o). Columns indicate which metric was used, such as abundance (a-e), length (f-j) or stage of maturity (k-o). Different colours represent the different management zones within the iSimangaliso Wetland Park (Yellow: Maputaland No-Take Sanctuary Zone; Green: Controlled Pelagic Zone and Purple: St Lucia No-Take Sanctuary Zone). The shaded area around each trend line indicates the approximate 95% confidence interval.

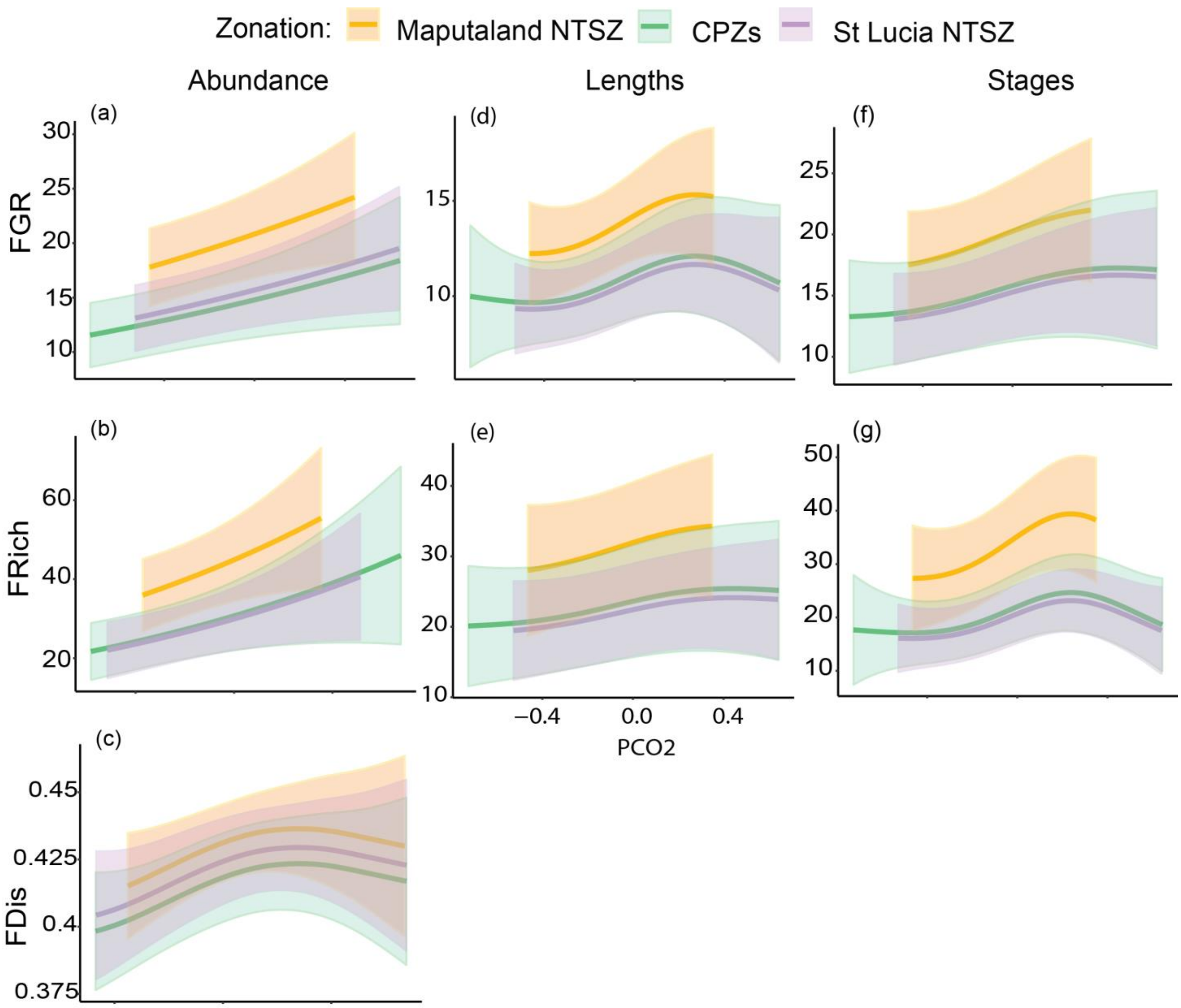


Figure 2.8: Predicted relationship curves between unique Habitat Variable PCO2 and number of functional groups (FGR a, d, f); functional richness (FRich b, e, g) and functional dispersion (FDis c). Columns indicate which dataset was used, such as abundances (a-c), lengths (d, e) or stages (f, g). Different colours represent the different zones within iSimangaliso Wetland Park (Yellow: Maputaland No-Take Sanctuary Zone; Green: Controlled Pelagic Zone and Purple: St Lucia No-Take Sanctuary Zone). The shaded area around each trend line indicates the approximate 95% confidence interval.

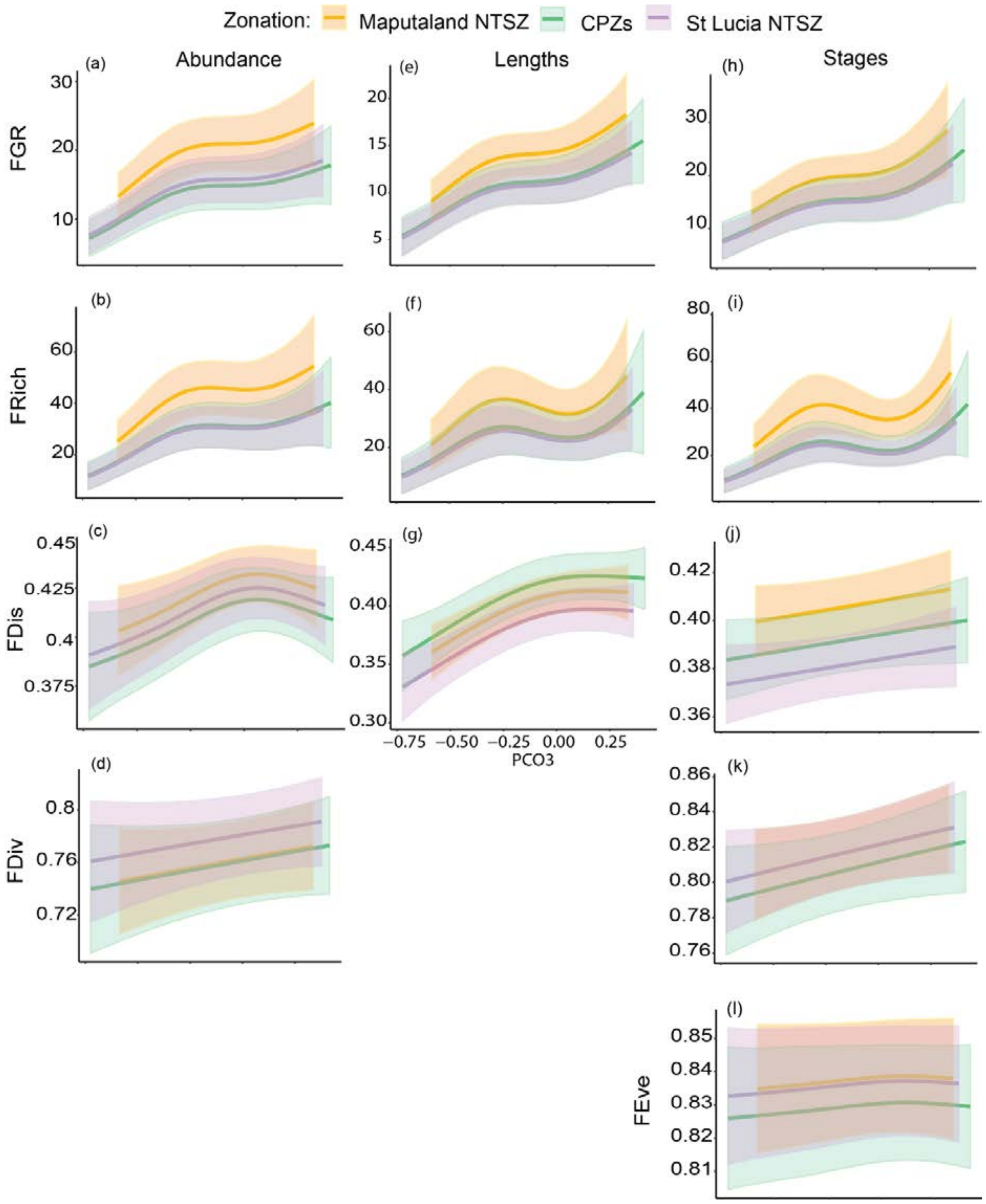


Figure 2.9: Predicted relationship curves between unique Habitat Variable PCO3 and the number of functional groups (FGR a, e, h); functional richness (FRich b, f, i); functional dispersion (FDis c, g, j); functional diversity (FDiv d, k) and functional evenness (FEve l). Columns indicate which dataset was used, such as abundances (a-d), lengths (e-g) or stages (h-l). Different colours represent the different zones within iSimangaliso Wetland Park (Yellow: Maputaland No-Take Sanctuary Zone; Green: Controlled Pelagic Zone and Purple: St Lucia No-Take Sanctuary Zone). The shaded area around each trend line indicates the approximate 95% confidence interval.

2.6 DISCUSSION

2.6.1 KEY FINDINGS

This chapter aimed to provide the first comprehensive assessment of the potential environmental drivers of the taxonomic and functional reef fish community structure within IWP MPA. Furthermore, the secondary aim of this study was to identify the potential difference in fish communities due to different management styles applied within the IWP MPA. To understand these dynamic fish communities better, both a taxonomic and functional analytical approach was used on three different metrics of population structure: abundance, lengths and stage of maturity.

The St Lucia NTSZ had the greatest reef area of the three zones, but the reef area was comparable between the CPZ and the Maputaland NTSZ. The habitat structure in the Maputaland NTSZ differed from that recorded in the St Lucia NTSZ and the CPZ, with a greater occurrence of macroalgae, relative to the other two zones. The taxonomic and functional reef fish community structure responded strongly to habitat type, with richer assemblages associated with high relief stony coral habitats, in comparison to low relief reefs and sandy habitats. Furthermore, the taxonomic and function fish assemblage structure differed between habitat characterised by macroalgae and those dominated by stony coral. Reef size had no measurable effect on the taxonomic and functional assemblage structure, as well as the univariate functional traits.

This study found that the Maputaland NTSZ differed significantly from the St Lucia NTSZ and the CPZ, with a greater number of species, functional groups and functional richness. Both the Maputaland and St Lucia NTSZ were identified as important areas for large predatory functional groups (large kingfish, groupers and shark species), whereas the CPZ was characterised by a higher abundance of immature fish from a variety of different species and functional groups.

2.6.2 VARIATION IN ASSEMBLAGES WITH HABITAT VARIABLES

The results from this research identified that the taxonomic and functional fish assemblage structure was primarily influenced by the environmental variables that captured the difference between low relief sandy and high relief stony coral habitats (PCO1) and between macro-algal and stony coral habitats (PCO3). High relief coral habitats have been shown to represent habitats with the most structural complexity (Gratwicke and Speight, 2005; McManus and Polsenberg, 2004). Vegetated macroalgal habitats, consisting mostly of broad laminate green macroalgae, although offering suitable nursery grounds for many species, provide substantially less structural complexity compared to coral habitats (Dahlgren and Eggleston, 2000; Jouffray et al., 2015), and unvegetated sandy habitat represents near-zero complexity for non-borrowing organisms (Jenkins and Hamer, 2001). Given that habitat complexity has been shown to structure fish communities in multiple studies (Beukers and Jones, 1998; Caley and John, 1996; Ferreira et al., 2001; Floros and Schleyer, 2017; Gorham and Alevizon, 1989; Gorman and Karr, 1978; Gratwicke and Speight, 2005; Gratwicke and Speight, 2005; Harding and Mann, 2001; Horan et al., 2000; Luckhurst and Luckhurst, 1978; McClanahan, 1994; Roberts and Ormond, 1987), it is not surprising then that PCO1 and PCO3 (which serve as proxies for different gradients of habitat complexity, productivity and food availability) are likely drivers of reef fish assemblages within the iSimangaliso Wetland Park (IWP).

When looking at the general trends displayed with PCO1, it was evident that the number of functional groups, functional richness, functional dispersion and functional diversity is lower in sandy habitats, relative to habitats with greater proportions of stony corals. This has implications when locating marine protected areas, indicating the importance of habitat selection during systematic conservation planning. To efficiently protect as much functional diversity as possible on reefs, high relief stony coral habitats need to be prioritised within protected areas. However, while reefs typically have greater diversity, the multivariate analyses showed that low relief and sand habitat support unique assemblages, of often important species (e.g. the wedgefishes). Thus, while prioritising conservation of reefs will maximise the alpha diversity protected, incorporating a range of habitats will enhance an MPAs ability to protect regional (or gamma) diversity.

The unique habitat variable PCO1 showed the opposite trend with functional evenness (Figure 2.12b). In this chapter, functional evenness gave insight into the regularity of the abundance and size distributions of species within a multidimensional functional space. The observed relationship with PCO1 suggests that functional communities in sandy habitats are more even in terms of abundances and sizes relative to those from stony coral habitats. Observations made during video analysis indicated that stony coral reefs can be home to solitary individuals which are either very large or very small, while simultaneously supporting incredibly large shoals and schools of either very small or very large individuals, making them characteristically uneven in terms of both abundance and size.

Apart from the main habitat variable, PCO1, the functional and taxonomic structure of fish assemblages also responded to more subtle differences in habitat structure among samples, associated with PCO2 and PCO3. The diversity metrics used in this study were typically lower in algal characterised habitats and higher in habitats with either Zoas and Anemones (PCO2) or Stony Corals (PCO3). Some studies have highlighted positive correlations between reef fish assemblages and habitat cover (Diaz-Pulido et al., 2009; Komyakova et al., 2013; McManus and Polsenberg, 2004) and these gradients have been shown to depend on human disturbances and levels of protection (McClanahan, 1997; McClanahan et al., 2002; McClanahan and Arthur, 2001). The vast majority of these studies focus mainly on coral and algal relationships, the interactions of reef fish assemblages and less dominant habitat covers like Zoas and Anemones remains a gap in coral ecology research.

This study has indicated that within the macroalgae habitats there are typically lower estimates for diversity metrics, relative to stony coral and areas with True Anemones and Zoas. The iSimangaliso Wetland Park (IWP) is considered to have relatively undisturbed macrobenthos as compared to reefs on a global scale (Porter and Schleyer, 2017; Schleyer et al., 2018; Schleyer and Celliers, 2005). The presence of macroalgae is often regarded as a sign of anthropogenic impacts and cause for concern with regards to ecosystem phase shifts (McManus and Polsenberg, 2004). However, the presence of laminate green macroalgae within the IWP forms part of the natural variation of the macrobenthos, occurring in areas where there is disturbance from sedimentation and deposition (Porter et al., 2017; Porter and Schleyer, 2017).

There is however the potential for an increase in the presence of macroalgae due to climate-mediated changes in herbivory and ecosystem phase-shift (Bruno et al., 2009; Done, 1992; Henrich Bruggemann et al., 2012; McManus and Polsenberg, 2004). The relevance of ecosystem phase shifts relates to the general trends observed for the unique habitat variable PCO3. Overall, the trends for the number of functional groups, functional richness, functional dispersion, and functional diversity were shown to decrease with an increase in values of PCO3, where high scores for PCO3 represented habitat dominated by stony corals and low scores represented macroalgal habitats. Based on the trends seen here, should climate change factors such as ocean acidification result in phase shifts toward an increase in laminate and foliose macroalgae, then there is potential for the decline in these functional indices. The boundaries of marine protected areas, unfortunately, have limited utility in mitigating the imminent threats posed by climate change. As the production of greenhouse gases produced by humans continues to increase, a changing climate promises increased ocean acidification, rising sea levels and sea surface temperatures and increased storm surges which may lead to phase shifts from stony coral dominated to macroalgal habitats (Carpenter et al., 2008; Hoegh-Guldberg and Bruno, 2010; Porter and Schleyer, 2019). Although storms facilitate the movement of nutrients into the canyon systems off iSimangaliso Wetland Park, they may contribute to increased variability on shallow reef systems. Future investigation into storm frequency off IWP's reefs is required, and monitoring reefs for potential shifts to macroalgae is imperative.

2.6.3 VARIATION IN ASSEMBLAGES AMONG MANAGEMENT ZONES

The IWP is zoned to include No-Take Sanctuary Zones (NTSZs), which protect reefs from all human activities, and Controlled Pelagic Zone (CPZ), which permit SCUBA diving, boating and pelagic game fishing with restrictions on species, size and bag limits. The results from this research demonstrated that the taxonomic and functional structure of the fish assemblages were different, with a significantly higher number of functional groups and greater functional richness in the Maputaland NTSZ, relative to the CPZ and the St Lucia NTSZ. The environment in the Maputaland NTSZ differed from the CPZ and the St Lucia NTSZ in terms of its spatial position and greater prevalence of macroalgae. The higher latitudinal situation possibly exposed the Maputaland NTSZ to more tropical conditions, similar to those characterising the bordering Ponta du Ouro Partial Marine Reserve (PPMR) in Mozambique to the north, and thus increased diversity. On the other hand, if latitude were the main factor driving the difference in assemblage structure, then one would expect the same pattern to be evident when comparing the St Lucia NTSZ (to the south) and the CPZ (to the north). However, the analyses suggested that there was no measurable difference in the taxonomic and functional structure of the fish assemblages between the CPZ and the St Lucia NTSZ. In this regard, the patterns observed in the fish assemblage correspond with those observed in the macro-benthos, which indicated that there was no difference between the CPZ and the St Lucia NTSC. While it is possible that spatial processes influenced the fish assemblage structure, the greater diversity of habitats, specifically the presence of macroalgae habitat, likely facilitated the presence of a different suite of fish species in the Maputaland NTSZ.

In the taxonomic analyses, a suite a characteristic species could be identified. Three species (*Aprion virescens*, *Variola louti* and *Lutjanus bohar*) were common to all three zones. To a lesser extent, *Lethrinus crocineus* was also common to all zones however, they were typically more abundance and larger in the two NTSZs, as compared to the CPZ. Two additional species which were characteristic of the NTSZs, but not the CPZ, were *Epinephelus tukula* and *Caranx melampygus*. A similar pattern was evident in the analysis for the functional groups. For example, FGR 17, defined as larger emperors which are mostly habitat generalists (e.g. species: *Lethrinus microdon*, *Lethrinus olivaceus* and *Lethrinus nebulosus*) contributed most to within-group similarity in the abundance data from all zones. Similarly, FGR 10 defined as mostly snappers (e.g. species *Lutjanus bohar*, *Lutjanus rivulatus* and *Aprion virescens*) contributed most to within-group similarity for all zones with regards to lengths data. On the other hand, FGR 13 was identified as the second most important group in both the abundance (e.g. species *Plectorhinchus playfairi*, *Plectorhinchus schotaf* and *Plectorhinchus chubbi*) and size (e.g. *Polysteganus praeorbitalis*, *Chrysoblephus puniceus* and *Chrysoblephus anglicus*) datasets.

The results of the SIMPER analyses identified that the Controlled Pelagic Zone (CPZ) was characterised by two functional groups defined by the presence of juvenile Lethrinids and Lutjanids, whereas NTSZs only had one functional group composed of juveniles. It has been shown that juvenile snappers and lethrinids are indicators of reefs with low predation pressure and high food availability (Lee et al., 2019). The CPZ of the

IWP may provide essential juvenile grounds because they provide the low predation pressure and high food availability necessary for the survival of these juvenile fishes. However, the habitat observed within the CPZ was similar to that of the St Lucia NTSZ, yet the St Lucia NTSZ s still characterised by larger fish. It is also possible that the juvenile functional stages prefer the mosaic of patch-reef habitats within the CPZ, in comparison to the expansive reef complexes in the St Lucia NTSZ. However, the reef structure in the CPZ is similar to that of the Maputaland NTSZ where juvenile functional stages were not prevalent. Furthermore, juveniles are often associated with algal habitats (Evans et al., 2014), and given the prevalence of macroalgal habitats in Maputaland NTSZ one would expect Maputaland NTSZ to be more of a nursery ground than the CPZ. Alternatively, the prevalence of juveniles within the CPZ could be attributed to the anthropogenic disturbance present within this zone. The non-destructive disturbances, such as boating and SCUBA diving, maybe proving enough of a disturbance to fish populations that larger adults avoid these reefs and concentrate in the NTSZs. The fact that game-fishing is also permitted in the CPZ could provide an additional threat of poaching as a result of lapsed compliance. Poaching is common in MPAs, even within the allocated Sanctuary Zones where any poaching is obvious. In situations where people are allowed to fish for certain target species in allocated zones there is evidence of lapsed compliance, especially in cases where enforcement is not sufficient (Chadwick et al., 2014). There is however no data to support this theory in the IWP MPA, and future monitoring of compliance, in the form of random spot-checks at sea and fish landings on the beach, should be carried out.

When looking at functional groups according to length, the CPZ was shown to be characterised by a functional group consisting mostly of wedgefishes, with a few sand-associated ray species. Recent studies have shown great concern for the status of wedgefishes (Rhinidae)(Kyne et al., 2019a). The dramatic decline of Wedgefishes in the western Indian Ocean is due to them being targeted for their high-value, and international demand for, ‘white’ fins (Dent and Clarke, 2015; Moore, 2017). These two families have now been classified as the two most imperilled marine fish families globally (Jabado, 2018; Moore, 2017). These species are particularly vulnerable given that they display limited biological productivity, are present in shallow waters where coastal fishing pressures peak and are vulnerable to both specific fisheries as well as being bycatch in other fisheries (Kyne et al., 2019b). Thus, the presence of a characteristic functional group consisting mostly of wedgefishes within the CPZ is of global conservation significance.

Apex predators are commonly defined as species with no predator, occupying the top of the food web and in the IWP include large species such as sharks and giant serranids (Floros, 2010). Functional groups which were composed of apex predators were only characteristic of the NTSZs. For example; FGR 30 which is a small group composed of very large Serranids (*Epinephelus tukula*, *Epinephelus malarbaricus* and

Plectropomus leopardus) was only characteristic of the two NTSZs and did not feature in the CPZ. Additionally, the St Lucia NTSZ was characterised by a functional group consisting of large carangids (FGR 9: *Caranx ignobilis*, *Gnathanodon speciosus*, *Scomberoides commersonnianus*, *Caranx melampygus* and *Caranx heberi*), while the Maputaland NTSZ was characterised by a functional group of large sharks (FGR 24: *Galeocerdo cuvier*, *Carcharhinus obscurus*, *Carcharhinus leucas*, *Carcharhinus amblyrhynchos* and *Carcharhinus albimarginatus*). The Maputaland NTSZ lies adjacent to the Ponta de Ouro Partial Marine Reserve, in Mozambique, which is known to be an important area for large shark species, in particular *G. cuvier* and *C. leucas* (Daly et al., 2018, 2014). The results presented here demonstrate that the Maputaland NTSZ provides additional protection to the large sharks that frequent the area and highlights the value of the transboundary marine protected area (Daly et al., 2018).

Floros (2010) discussed the absence of top predators within the CPZ of the iSimangaliso Wetland Park and suggested that human disturbances, in particular diving, had an adverse effect on the presence of predators. Floros (2010) identified at least three times as many *E. tukula* in the NTSZs using underwater visual census relative to the CPZ where diving and game fishing was permitted. To an extent, the results from my study further demonstrate the importance of NTSZs in supporting healthy populations of top predatory functional groups. Taxonomic level analyses revealed similar trends whereby *E. tukula*, was only characteristic of NSTZs. Similarly, *Caranx melampygus* which is currently on the permitted gamefish list was also only characteristic of NTSZs and not CPZ. Together, these results suggest that the NTSZs may be providing refuge for *E. tukula* and *C. melampygus* from diving and fishing pressure respectively. However, further species-level investigations are required.

2.6.4 APPROACHES AND DATASETS

The use of both a taxonomic and functional approach was based on the suggestions of (Villéger et al., 2010). It was suggested that biodiversity assessments require multifaceted functional and taxonomic approaches, particularly for communities under pressure. It is suggested that taxonomic and functional community structures respond to human disturbances in different ways, and often independently of each other (Villéger et al., 2010). Although both approaches used in this study behaved similarly, the inclusion of both approaches provided a comprehensive insight into the fish assemblages of iSimangaliso's high latitude reef, particularly since community analyses had not been done prior. Biodiversity assessments often entail various forms of datasets such as abundance, size and maturity structures of fish communities. The use of these datasets has each entail their pros and cons and thus depend on the aims of the study (Nash and Graham, 2016). Given that a comprehensive overview was the aim of this study, incorporation of all datasets proved useful. However, the consistency in the results suggests that it may not be necessary to include all three data types in future analyses. The only difference between datasets worth mentioning was that the stage of maturity metric gave additional insight into how adult and juvenile populations were structured throughout the IWP. The stage of maturity metric incorporates both the size and abundance of data and may represent a suitable single metric to capture the important size and abundance-based information. From a functional analysis perspective, expanding the trait database to accommodate ontogenetic shifts and trophodynamics and behaviour would add further value to the stage of maturity approach.

2.6.5 CONCLUDING REMARKS

The functional and species community analyses which were undertaken in my study have provided the first comprehensive community analysis of reef fish assemblages on offshore reefs in the iSimangaliso Wetland Park. Taxonomic and functional reef fish community structure responded strongly to habitat type and benthic cover. Richer and more diverse fish assemblages were associated with high relief stony coral habitats, in comparison to low relief reefs, sandy or macroalgal habitats. Importantly the sandy and macroalgal dominated habitats supported unique assemblages of fishes adding to the overall biodiversity in the IWP MPA. Reef size had no measurable effect on the taxonomic and functional assemblage structure except for functional evenness.

This study found that the Maputaland NTSZ differed significantly from the St Lucia NTSZ and the CPZ, with a greater number of species, functional groups and functional richness. This is potentially linked to the additional macroalgal habitats in this zone, whereas the St Lucia NTSZ and CPZ only have Reef and Sand habitats. The CPZ, which is characteristically made up of sand and small patch reef, was characterised by smaller fish and this needs further investigation to better understand the drivers and extent of human disturbance in this area. In terms of spatial planning of an MPA, this study demonstrates the importance of incorporating a habitat mosaic to enhance an MPAs ability to protect gamma diversity. Both the Maputaland and St Lucia NTSZ were identified as important areas for large predatory functional groups (large kingfish, groupers and shark species), highlighting the importance of sanctuary zones and transboundary protection, in the case of the Maputaland NTSZ, for highly mobile predatory species giving added value to this MPA.

Chapter 3

The effect of Management and Reef size on the Population Structure of key Reef Fish Species

3.1 ABSTRACT

The iSimangaliso Wetland Park (IWP) marine protected area (MPA) is an established (nearly 40 years old) multi-use MPA that protects South Africa's only coral reef habitats, however little is known about the habitat associations and the impact of the multi-use zonation plan for key fishes found in the MPA. To demonstrate conservation effects resulting from marine protected areas, many studies rely on spatial comparisons between areas afforded different levels of protection. These spatial comparisons can be confounded if the habitat and reef size are dissimilar and not accounted for in the statistical analysis. This study aimed to identify the key environmental drivers of the population structure (relative abundance and average biomass) of six fish species (*Aprion virescens, Caranx melampygus, Epinephelus tukula, Lutjanus bohar, Lethrinus crocineus and Variola louti*) common throughout the iSimangaliso Wetland Park. Taking into account reef size (obtained from multibeam sonar data) and benthic habitat structure, this research then tested the effect of management zone (St Lucia and Maputaland No-Take Sanctuary Zones = NTSZs; Controlled Pelagic Zone = CPZ) on the fish populations. Furthermore, this study tested the effect of ignoring reef size in spatial comparisons. The results showed that reef size had a consistent significant positive effect on the average biomass, but a negligible effect on the abundance of all six species. When reef size was included in the models, the results showed that two of the six species were not affected by the management zone, two appeared to be directly affected by the permitted (past and present) fishing activity in the CPZ, and the last two species appeared to be affected by the disturbance caused by the diving and/or boating activity in the CPZ. Excluding reef size from the analysis consistently resulted in the predicted average biomass increasing in the St Lucia NTSZ, but not the CPZ and the Maputaland NTSZ, because the latter two zones are characterised by similar reef sizes. When excluding reef size, the management zone effect changed from negligible to significant for three of the six species, and those which were significant when including reef size drastically increased the level of original significance when reef size was excluded. These results highlight the importance of accounting for the reef size, or area of suitable habitat, when conducting spatial comparisons among species and illustrate the potential impact of the trade-off required to accommodate human needs within protected spaces.

3.2 INTRODUCTION

3.2.1 VALUE OF CORAL ECOSYSTEMS

Coral reefs provide economic benefits and services, such as fisheries and tourism, to an estimated value of US$30 billion each year (Nellemann et al., 2009) and contribute to the livelihoods of approximately one billion people (Cesar et al., 2003; Nellemann et al., 2009). These ecosystem services are jeopardized by a range of anthropogenic impacts including climate change (Darling and Côté, 2018; Hoegh-Guldberg et al., 2007), fishing (Bellwood et al., 2004; Cesar et al., 2003; Jackson et al., 2001; Mous et al., 2000; Myers and Worm, 2003; Sale, 2008) and unsustainable tourism (Barker and Roberts, 2004; Hawkins and Roberts, 1992; Zakai and Chadwick-Furman, 2002).

3.2.2 MANAGEMENT PRACTICES

Many countries have imposed a management regime of marine protected areas (MPAs) as a strategy that seeks to mitigate the effects of overfishing and habitat degradation, while simultaneously supporting tourism and alternative livelihoods (Kelleher and Kenchington, 1991; Pomeroy et al., 2005). Research has shown that effective MPAs do protect resident fish species that are targeted by fisheries by increasing their abundance and biomass, while at the same time, enhancing overall biodiversity and delivering fisheries benefits (Barrett et al., 2007a; Edgar et al., 2014; Gell and Roberts, 2003; Heyns-Veale et al., 2019; Kerwath et al., 2013; Lester et al., 2009a; Lubchenco et al., 2003; McClanahan and Arthur, 2001; Richard K F Unsworth et al., 2007). Effective MPAs also serve as ecological reference sites, or benchmarks that scientists can use to determine the level of destruction or recovery of marine ecosystems in adjacent areas (McClanahan et al., 2007; Papworth et al., 2009; Sainsbury and Sumaila, 2003). However, the effectiveness of an MPA is not guaranteed as it is influenced by many factors, such as the condition of the ecosystem, level of protection, size, enforcement and compliance (Edgar et al., 2014; Gill et al., 2017; Nash and Graham, 2016). Although no-take MPAs provide the greatest level of protection, the approach adopted for the management of an MPA often reflects a compromise between conservation and societal needs, resulting in different levels of access to resources (i.e. zonation for multiple-use) within an MPA (Tunley, 2009). No-Take sanctuary zones are areas where all forms of extractive use of resources are prohibited. Other zones in multiple-use MPAs, such as Controlled Pelagic Zone, restrict extractive activities such as fishing, to a limited suite of species, or limit the types of fishing that may take place (or some combination of the two). For example, fishing can be limited to activities that target only pelagic gamefishes, whereas reef species are protected. Non-extractive activities, such as snorkelling and/or SCUBA diving, are also frequently accommodated within controlled zones. However, these permitted activities can cause disturbance and increase challenges in compliance and policing (Lester and Halpern, 2008), which impacts the extent of conservation benefits (Agardy et al., 2011). This issue is relevant to the management of MPAs in the coastal regions of South Africa, where several larger MPAs have been zoned for multiple uses and include controlled zones that allow for various forms of consumptive and non-consumptive activities, potentially limiting the conservation benefits of such MPAs and the entire MPA network (Bewana, 2009).

3.2.3 ISIMANGALISO WETLAND PARK MARINE PROTECTED AREA

The high-latitude coral reefs of the iSimangaliso Wetland Park (IWP) World Heritage Site, are the only coral reefs in South Africa (Floros, 2010; Schleyer et al., 2018) and they support unique biodiversity, important fisheries resources and numerous tourism businesses centred around SCUBA diving and recreational fishing (Schleyer and Celliers, 2005, 2003; Schleyer and Tomalin, 2000). The IWP World Heritage Site consists of two contiguous protected areas, St Lucia (proclaimed in 1979) and Maputaland (proclaimed in 1986). Both these MPAs are zoned to include No-Take Sanctuary Zones (NTSZs), where no extractive fishing or diving activities are permitted, and Controlled Pelagic Zone (CPZ) where recreational angling and spearfishing for pelagic gamefish are permitted, together with SCUBA diving (Mann et al., 2018, 2016). The CPZ is further zoned to permit recreational shore-based angling for all fishes. Fishing for offshore benthic and reef-associated fish has been prohibited throughout both the Maputaland and St Lucia section of IWP MPA for more than 30 years and it can thus be assumed that the populations and community structure of the reef fish should have recovered from historic fishing (MacNeil et al., 2015; Mann et al., 2016). It is, however, possible that the exploitation of pelagic species within the CPZ has impeded the recovery of reef fish abundance and biomass, particularly predatory species that may be caught and released as bycatch (Floros, 2010).

3.2.4 ENVIRONMENTAL VARIATION

Variation in environmental factors (e.g. habitat complexity and/or habitat area) among the different management zones in the IWP could also influence the reef fish populations. Although the available reef habitat within both zone types is patchy, the NTSZ in the St Lucia MPA is characterized by considerably greater area and larger patches of reef than in the adjacent CPZ and the Maputaland NTSZ (Figure 3.1). Larger reef areas support a greater diversity of fishes, exhibit lower rates of species turnover and are more resilient to disturbances, such as climate change (Mellin et al., 2010). In addition, larger reefs tend to have significantly higher biodiversity, abundance and biomass of reef-associated fish species (Bohnsack et al., 1994) and mean biomass has been shown to increase with reef size (Bohnsack et al., 1994; Hattori and Shibuno, 2015). Recent reviews have demonstrated that habitat complexity plays a vital role in determining fish community and fish population structure (Graham and Nash, 2013; Miller and Russ, 2014). In this regard, more complex habitats (i.e. those characterised by greater relief from physical or biogenic attributes) are typically associated with a greater diversity of fishes (Graham and Nash, 2013). Understanding how environmental variables alter the structure of fish populations is essential for ecosystem-based management and marine spatial planning as it permits the identification of essential habitats and priority conservation areas. Moreover, while many studies try to account for the effect of habitat complexity when testing MPA effectiveness through spatial comparisons (Claudet et al., 2006, 2011; Heyns-Veale et al., 2019; Miller and Russ, 2014; Shears et al., 2006, 2012), reef size is seldom included in these analyses (Mellin et al., 2010).

3.2.5 AIMS AND OBJECTIVES

While there is a growing body of research on the value of MPAs, further research demonstrating the effect of alternative management zones on the biota within MPAs is required to better inform decision-makers. The knowledge that habitat type, complexity, and size influence fish community and population structure, means that these drivers can't be ignored when implementing spatial comparisons to test MPA effectiveness. As such, this chapter aimed to test the combined effects of MPA zonation, reef size and habitat type on the abundance and average biomass of six species of reef fish collected from the NTSZs and CPZ of the IWP MPAs. Fine-scale reef size data are often not available due to the cost and logistics of carrying out side-scan sonar or multibeam echosounder surveys. As such, this chapter examined the impact that excluding reef size from the analysis had on the perceived effectiveness of the different zoning strategies.

Using abundance and biomass data for key species, together with the environmental data included from Chapter 2 (Section 2.4.2) the specific questions that I will aim to answer are:

i. How are the populations of *Aprion virescens*, *Caranx melampygus*, *Epinephelus tukula*, *Lutjanus bohar*, *Lethrinus crocineus* and *Variola louti* structured within iSimangaliso Wetland Park?

ii. What are the most important environmental drivers of the abundance and biomass for these six fish populations in the IWP?

iii. Is the abundance and biomass of these six study species influenced by the different zones within the IWP, when accounting for habitat differences?

3.3 MATERIALS AND METHODS

3.3.1 STUDY AREA AND SAMPLING APPROACH

The information provided here is the same as that provided in Chapter 2, Section 2.4.1.

Samples were collected within St Lucia and Maputaland No-Take Sanctuary Zones (NTSZ) and the Controlled Pelagic Zone (CPZ), all of which fall within MPAs and form part of the IWP World Heritage Site, during two separate field trips on November 2016 and June 2017 (Figure 3.1). Sampling was restricted to depths between 5-40 m and was either on or in close proximity to available reef habitat (Figure 3.1). The exact sampling locations were pre-determined using Create Random Points in ArcGIS (10.4), with the Minimum Allowed Distance set at 500 m from its nearest neighbour. Each sample was collected *in situ* as near as possible to the predetermined locations and deployed on the seafloor for an analysis time of 60 minutes.

Fish abundance and biomass data were collected with light-weight baited remote underwater stereo-video systems (stereo-BRUVs). Each stereo-BRUVs consisted of two high definition (HD) video cameras mounted within a protective frame 70 cm apart with an inward convergence angle of 8° to provide an overlapping field of view (Cappo et al., 2004; Ellis and DeMartini, 1995; Harvey et al., 2012; Langlois et al., 2010; Watson et al., 2010). Prior to, and after data collection, each stereo-BRUVs was calibrated using the software CAL (SeaGIS Pty Ltd) according to the procedure outlined in Harvey and Shortis (1998) to enable accurate measurements of the fish sighted in the video. Each stereo-BRUV was baited with 0.8-1 kg of crushed pilchards (*Sardinops sagax*) to attract fish into the field of view of the cameras and deployed on the seafloor for periods of one hour during daylight hours (07:00 – 15:00). A total of 96 stereo-BRUVs deployments were undertaken - 32 in each of the three management zones.

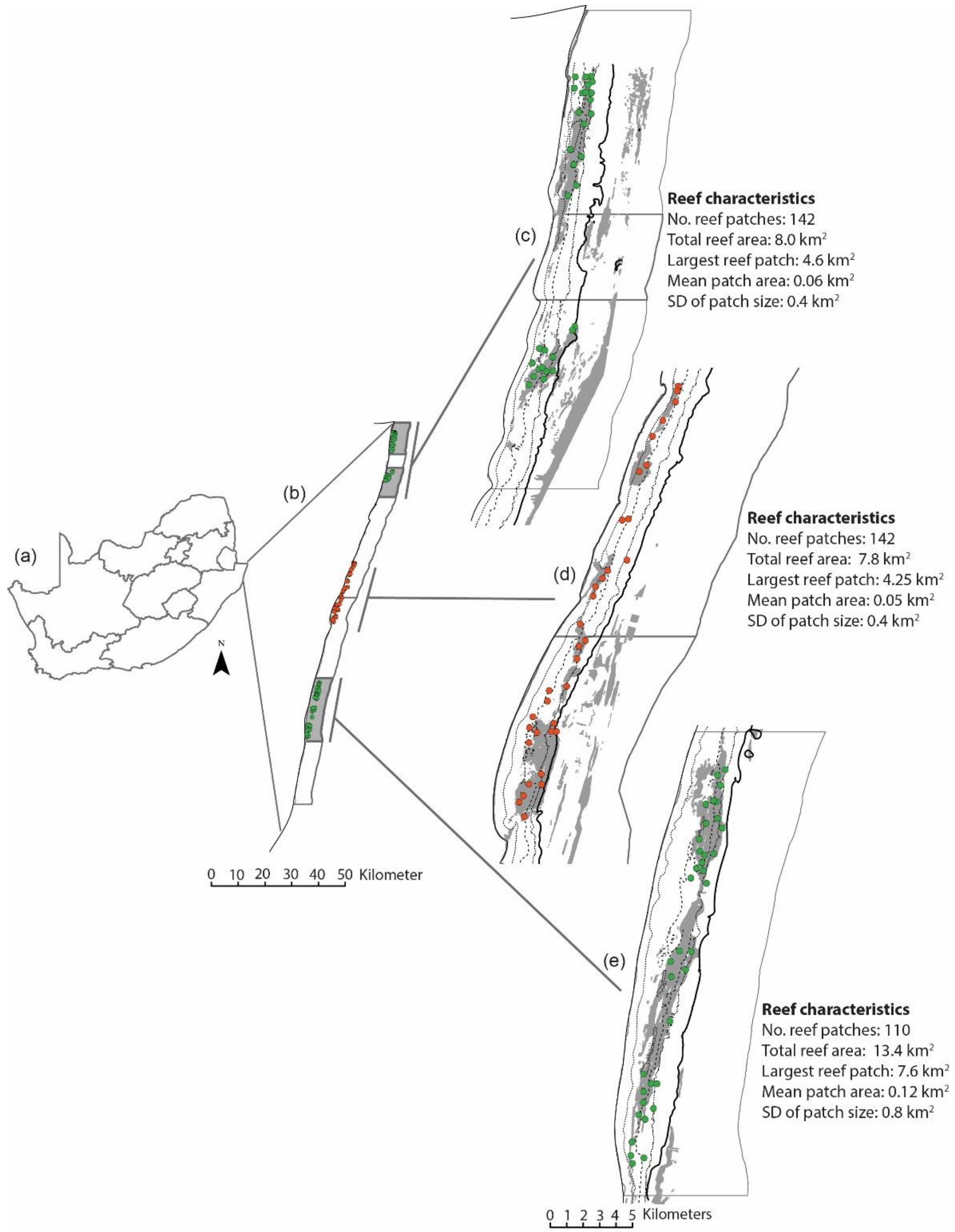


Figure 3.1: Maps showing (a) the location of the iSimangaliso Wetland Park Marine Protected Area (MPA) in South Africa, (b) the location of the No-Take Sanctuary Zones (NTSZs) seen as the darker shade and Controlled Pelagic Zone (CPZ) seen as the blocks with no shading. Expanded maps for each zone shows the distribution of sampling sites in (c) the Maputaland No-Take Sanctuary Zone (d) The Controlled Pelagic Zone and (e) the St Lucia No-Take Sanctuary Zone. Shaded areas in (c), (d) and (e) shows the actual location of the reefs with dotted lines showing depth profile. Data on the nature of the reef habitat within each survey area are provided alongside each sampling map (c-e).

3.3.2 HABITAT DESCRIPTIONS

The information provided here is repeated from Chapter 2, Section 2.4.2.

3.3.2.1 REEF AREA

Reef size was included as a proxy for available habitat and reef productivity (Mellin et al., 2010), and was calculated for each sample by measuring the total area (km^2) of the reef patch where the sample was collected using ArcGIS (10.4). Where samples were on sand, the reef size was defined as zero. The reef size data were obtained from side-scan sonar habitat maps (Ramsay et al., 2006) derived from the Innovation Fund Project developed by Dr P J Ramsay and Prof. M H Schleyer in 1998. Ramsay et al. (2006) aimed to produce highly specialised digital seafloor maps which can contribute to both tourism and conservation efforts within the IWP.

3.3.2.2 HABITAT STRUCTURE

Habitat and relief data were acquired from each stereo-BRUVs sample using the software program TransectMeasure (http://www.seagis.com.au). The approach employed a 5 × 4 m grid overlaid onto a screenshot image obtained from each stereo-BRUV sample, following the method of Collins et al. (2017). Each rectangle of the grid was analysed according to the standard (rapid) assessment of benthic composition, which includes descriptions of habitat type, relief, and field of view (Collins et al., 2017; see Appendix Table 6.1). The dominant habitat type was described based on the broad-scale Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification scheme (Hill et al., 2014). The relief described the topographic complexity or the height and angle of the substrate based on the approach proposed by Wilson et al. (2007).

The multivariate habitat data obtained for each habitat images was condensed into a reduced set of covariates that captured the majority of the habitat variability among samples, using the Direct Principal Component Method (DPCM), developed by Winker et al. (2014, 2013) (See Joo et al., 2015; Santos et al., 2017; Thorson et al., 2016 for examples). In the fisheries context, this approach uses continuous Principal Coordinate scores (PCs) derived from Principal Component Analysis (PCA) to replace categorical factors when describing catch composition data. In the context of this research, the PCs were used to describe habitats and habitat variation among samples. The scores were derived from a Principal Component Analysis (PCA) of the multivariate habitat data, carried out in Primer (Version 7 + PERMANOVA; Clarke and Gorley, 2015) using the Principal Coordinates Analysis (PCO) procedure, based on Euclidean distance (which is analogous to a PCA), (Anderson, 2001). Based on the results of the analyses, the first three PCO axes were selected as they described 79.4% of the variability in habitat among all stereo-BRUVs samples. Principal component analysis biplots of the habitat at each deployment, according to the three PCO axes, were then created with correlation vectors overlaid (Figure 2.3). These plots showed that the first PCO axis (PCO1) described the variation among samples with high sand cover and low relief and those characterized by high relief stony coral dominated reefs (Figure 2.3 a, c); the second PCO axis (PCO2) captured the variation among habitats dominated by macroalgae and reefs with higher than normal detections of zoanthids and anemones (Figure 2.3 a, b); and the third PCO axis (PCO3) defined habitats dominated by macroalgae and reefs inhabited by stony corals (Figure 2.3 b, c). The three PCA axes were then regarded as unique 'habitat' covariates to be included in the analysis (named: PCO1, PCO2, PCO3).

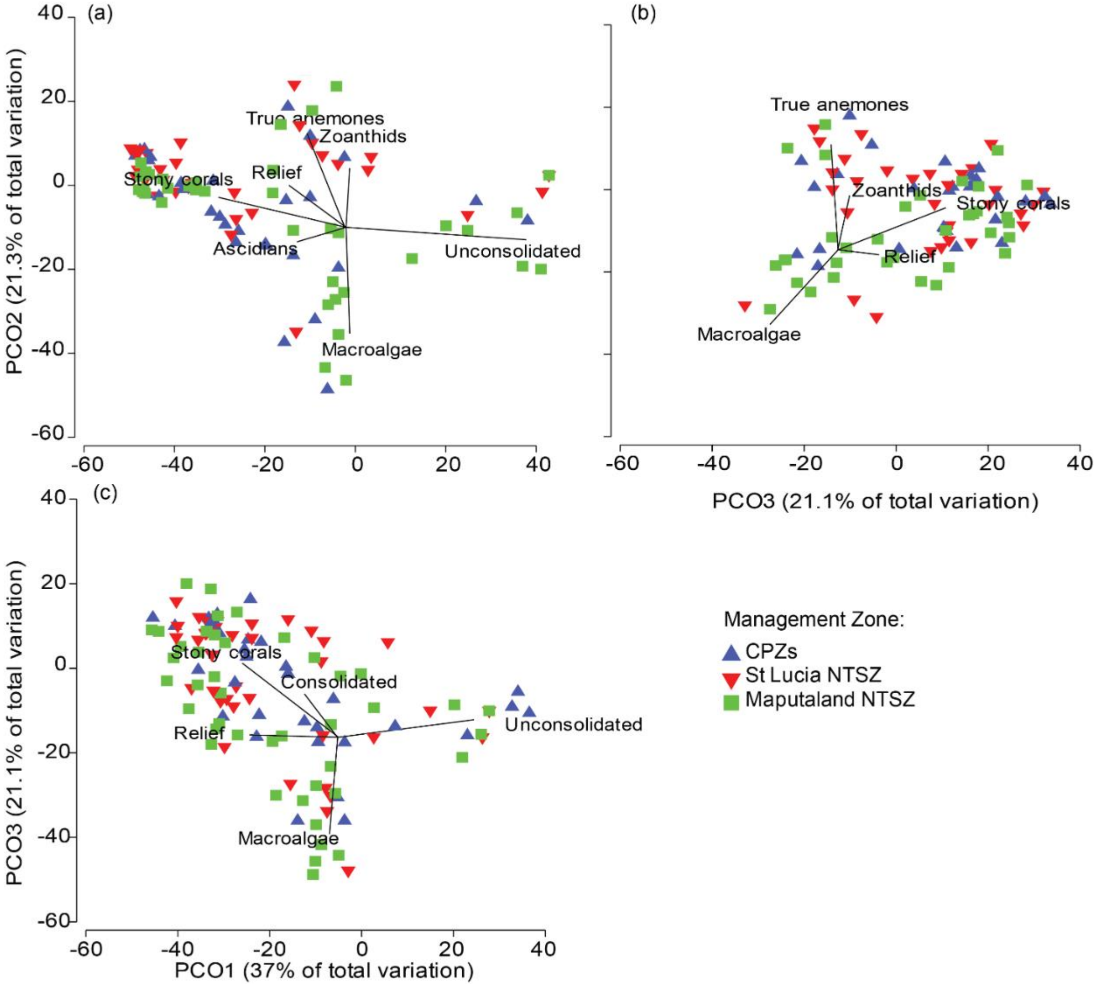


Figure 3.2: Biplots displaying variation in benthic characteristics derived from a principal component analysis (PCA). PCO1 describes habitat variation from high sand cover and low relief and those characterized by high relief stony coral dominated reefs (a, c); PCO2 captures the variation among habitats dominated by macroalgae and those that were inhabited by zoanthids and true anemones and those that are not (a, b) and PCO3 distinguishes habitats dominated by macroalgae and those dominated by stony corals (b, c). Drivers of variation were based on a cut off of 0.4 correlation.

3.3.2.3 ENVIRONMENTAL COVARIATES

In addition to reef area and the habitat descriptors (PCO1, PCO2 and PCO3) a suite of other environmental variables was included in this study to account for environmental variability and sampling biases. Water depth and temperature varied among samples and each sample was characterised by a distinct field of view determined by underwater visibility, different levels of water column and obstruction, given that each stereo-BRUVs lands differently on the seafloor, and different habitat features. The list of all environmental variables included in this study is listed in Table 3.1 below, along with their descriptions and how these values were derived.

Table 3.1: List of covariates recorded for each sample and included in the statistical analysis (generalised linear models). Each covariate is described in terms of its units, definition and the technique used to measure it or how it was derived.

Covariate	***Unit***	***Definition***	***Technique***
Visibility	m	The distance within which a fish can be accurately identified from the video samples.	Estimated using a 3D point on EventMeasure during video analysis
Water column	%	The portion of the video sample dominated by the pelagic water column.	Estimated using Vidana (freely available from www.marinespatialecologylab.org)
Obstruction	%	The portion of the camera lens blocked by a structure that reduces the area in which to see and count fish.	Estimated using Vidana
Temperature	ºC	The bottom water temperature at the location where the sample was collected.	Onset HOBO Pro v2 loggers attached to stereo-BRUVs
Depth	m	The distance from the sea surface to the ocean floor at the point where the stereo-BRUVs was deployed.	GPS linked echo-sounder attached to the boat
Habitat descriptor: PCO1		Distinguishes variation among samples with high sand cover and low relief and those characterized by high relief stony coral dominated reefs.	Derived from Direct Principal Component method preformed on benthic habitat and relief data.
Habitat descriptor: PCO2		Distinguishes variation among habitats dominated by macroalgae and those inhabited by Zoanthids and True Anemones.	
Habitat descriptor: PCO3		Distinguishes habitats dominated by macroalgae and those that were characterised by stony corals.	
Management zone	NTSZ/ CPZ	No-Take Sanctuary Zone (NTSZ): No boating, no diving, no fishing permitted. Controlled Pelagic Zone (CPZ): Controlled game fishing, diving permitted but no bottom fishing permitted.	These areas are located via a GPS onboard
Reef size	km^2	The total area of the reef patch where the sample was collected using ArcGIS. Samples on the sand had a reef size of zero	Side-scan sonar habitat maps (Ramsay et al., 2006)

3.3.3 SELECTED STUDY SPECIES

Based on the findings from Chapter 2, six species of fish (*Caranx melampygus*, *Lethrinus crocineus*, *Aprion virescens*, *Lutjanus bohar*, *Epinephelus tukula* and *Variola louti*) we selected for this chapter. Four of these species (*L. crocineus*, *A. virescens*, *L. bohar*, *V. louti*) were identified as being characteristic of all three management zones, while the remaining two species (*E. tukula* and *C. melampygus*) were identified as important from the NTSZs.

All of these species are regarded as common in the area and were historically targeted by fishermen before the establishment of the MPAs (van der Elst et al., 1996). Of the six species, *C. melampygus* is the only species of gamefish that could be harvested by line and spearfishers in the CPZ at the time that this study was conducted. Historically, *A. virescens* was a gamefish and could be harvested in the CPZ, but fishing for this species was prohibited in July 2011 (5 years before the sampling conducted for this thesis). The remaining four species (*L. crocineus, L. bohar, E. tukula* and *V. louti*) are all demersal reef fishes and have been protected in both the NTSZs and CPZ for more than 30 years. The relative abundance of each of the six species was measured using the MaxN metric (Cappo et al., 2004), defined as the maximum number of individuals of a species observed within a single frame during the one-hour deployment of the stereo-BRUVs. Where possible, length measurements (fork length, or total length in the case of *E. tukula*) were obtained for each fish counted in the MaxN frame. All samples were processed using the software package EventMeasure (Stereo) (SeaGIS 2015). Average-biomass values were then calculated by applying published length-weight relationships ($W_{(kg)}$ = a x Length^{b}) and averaging the weight per sample for each species (Mann, 2013).

3.3.4 STATISTICAL ANALYSIS

3.3.4.1 TESTING FOR VARIATION IN HABITAT STRUCTURE

A Permutational multivariate analysis of variance (PERMANOVA) was used to determine if the habitats sampled with the stereo-BRUVs differed significantly among the two NTSZs and the CPZ. The PERMANOVA was run on the multivariate habitat data derived from PCA using Primer v7 with PERMANOVA+ add-on (Clarke and Gorley, 2015). The PERMANOVA included *management zone* as a single factor with three levels and was run with 9999 unrestricted permutations of the raw data.

3.3.5 ASSESSING PATTERNS IN RELATIVE ABUNDANCE AND AVERAGE BIOMASS

3.3.5.1 MODELLING WITH GLMS AND GAMS

Generalized additive models (GAMs) were used to model the average relative abundance and average biomass of the six study species. GAMs were used to accommodate non-linear relationships between the response variables and the continuous predictor variables (Zuur et al., 2009). As the values of the continuous PCOs were all centred on zero, all other continuous environmental variables (see Table 2.1) were standardized to zero means (Zuur et al., 2009). Prior to constructing the GAMs, the data were explored following the protocol of Zuur et al. (2009, 2013). These exploratory procedures included investigating interactions and collinearity between variables, checking for outliers, zero inflation and verifying spatial independence of samples using variograms [Gstat (Pebesm and Benedikt Graeler, 2020) and Sp (Hijmans et al., 2020) packages].

Assessments of zero-inflation showed moderate frequencies (<30%) of zeros in the data for all species, except *E. tukula*, which had a high frequency (>40%) of zero-inflation. Furthermore, where *E. tukula* were present, they were most frequently recorded as single individuals (> 70 %), and for this reason, the abundance (MaxN) data were converted to presence/absence and analysed with the binomial distribution, thus results for this species indicate the probability of detection rather than abundances. The remaining abundance count data (MaxN) were modelled using the Poisson distribution if the tests of overdispersion were approximately 1, or negative binomial distribution if overdispersion was >1 (see Cameron and Trivedi, 1990). The biomass data were modelled using the Tweedie distribution for the case of $1<p<2$ (where $p = 1$ = equivalent to Poisson distribution; $p = 2$ = equivalent to gamma distribution) representing the class of Poisson mixtures of gamma distributions (Winker et al., 2014). The Tweedie distribution was selected as it is well suited for modelling data with a mass at zero (Tweedie, 1984). The GAMs were constructed for the indices (species abundance or average biomass) and included smoothing terms for all continuous variables and parametric terms for the factors (see Table 3.1). Model selection was carried out using “select=true” which automatically penalises the effect of unimportant variables allowing the model to only take into account the variables deemed necessary for that model (Wood, 2017). The GAM fit was inspected by plotting the model residuals versus fitted data and all other covariates included in the dataset.

Each model was processed using “summary.gam” to produce summaries of the model coefficients, such as estimates of smoothing terms, and “anova.gam” which implements a Wald’s test suitable for making formal inferences with regards to the significance of variables (Zuur et al., 2009). The main aim of these inferences being to identify if the different zones of the IWP had a significant effect on the average relative abundance or average biomass of the six study species. The relationship between the covariates included in the models and the response variable was first visualised using “plot.gam” and include shaded component-wise confidence intervals. Prediction plots from the GAM coefficients were generated to visualise the predicted patterns in the response variables concerning (i) management zone and (ii) the reef size within the management zone. Two types of prediction datasets were generated. To separate the effects of the environmental covariates from the management zone, the predicted dataset for the effect of the management zone was generated using standardised values (mean) for each covariate included in the model. To visualise the effect of the reef size within each management zone, the average abundances and biomasses for study species were predicted for different values of the reef size within each management zone, while standardising all other covariates in the model to their mean values. These predictive plots allow for inference to be made on how abundance and biomass for each species may vary across the different zones of the IWP as well as how they vary according to the reef size.

All univariate modelling was conducted in the R environment for statistical computing (Version 3.6.0, R Development Core Team 2019) via the RStudio user interface (Version 1.1.456, RStudio Team 2015). Modelling via GAMs and GLMs were computed using the packages mgcv (Wood, 2017) and MASS (Ripley et al., 2019), respectively. Graphs were plotted using ggplot2 (Wickham, 2016).

3.4 RESULTS

3.4.1 HABITAT COMPARISON

The PERMANOVA done on the multivariate habitat data showed that there was a significant difference in macrobenthos between different zones (Pseudo-$f_2 = 2.367$; $P_{perm} = 0.011$). Post hoc pairwise analyses showed that these differences were due to Maputaland NTSZ being different from both the St Lucia NTSZ and the CPZ (t 1.814; P_{perm} 0.0115 and t 1.622; P_{perm} 0.038 respectively).

Total reef area (km^2) was greatest in the St Lucia NTSZ, relative to the Maputaland NTSZ and CPZ, even after accounting for differences in the total survey area (St Lucia NTSZ: 13.4 km^2 reef / 31.3 km^2 total survey area; Maputaland NTSZ: 8 km^2 reef / 34 km^2 total survey area; CPZ: 7.8 km^2 reef / 22.3 km^2 total survey area) (Figure 3.1). In all zones, reefs were patchy, however, the St Lucia NTSZ had fewer but larger reef patches (Figure 3.1).

3.4.2 EFFECT OF REEF SIZE AND HABITAT ON ABUNDANCE AND BIOMASS

Of six species, the relative abundance of only *A. virescens* and *L. bohar* was significantly correlated with reef size (Table 3.2, Figure 3.3 and Appendix Table 6.6 and 6.12). However, the nature of the reef size effect was dependant on the management zone, with the abundance of *A. virescens* increasing with increasing reef size in the two NTSZs, and decreasing in the CPZ (Figure 3.3). The abundance of *L. bohar* increased with increasing reef size in both the CPZ and, to a lesser degree, in the St Lucia NTSZ (Figure 3.3), while in the Maputaland NTSZ *L. bohar* abundance displayed a bell-curve relationship with reef size, peaking on reefs approximately 2 km^2 in size (Figure 3.3).

For all six species, a significant relationship was identified between reef size and average biomass (Table 3.3, Figure 3.4 and 3.5 and Appendix Table 6.7, 6.9, 6.11, 6.13, 6.15, 6.17), with the majority of these relationships being positive. The average biomass of *A. virescens*, *L. crocineus* and *V. louti* increased significantly with increasing reef size within all three zones (Table 3.3, Figures 3.4 and 3.5). The average biomass of *C. melampygus* was only significantly related to reef size in the NTSZs, but not the CPZ (Table 3.3, Figure 3.4). *E. tukula* increased significantly in average biomass with increasing reef size within the Maputaland NTSZ and CPZ, but not the St Lucia NTSZ (Table 3.3, Figure 3.4 and 3.5). Lastly, the average biomass of *L. bohar* was only significantly related to reef size in the Maputaland NTSZ (Table 3.3, Figure 3.4).

Table 3.2: Results from the Wald's tests on the General Additive Models (GAMs) for the relative abundance (MaxN/sample) data. The table shows the results for the parametric term of Zonation (degrees freedom; Chi.sq; p-value) and the habitat covariates (estimated degrees freedom; Chi-sq; p-value). The "Analysis" column distinguishes among the models which included (Inc. RS) and excluded (Exc. RS) reef size. The "Distribution used" column indicates the distribution decided by a test of overdispersion, and presence/absence data used for *E. tukula*. Results for full models, including other covariates (e.g. temperature, depth, visibility) can be found in the appendix material for Chapter 3.

Species	**Analysis**	**Distribution used**	**Zonation**	**PCO1**	**PCO2**	**PCO3**	**Reef size: Map NTSZ**	**Reef size: CPZ**	**Reef size: St Lucia NTSZ**
A. virescens	Inc. RS	Poisson	2; 3.74, 0.154	1.453; 8.898; 0.002**	0.68; 2.1; 0.053	0.36; 0.462; 0.213	0.998; 3.211; 0.049*	0.742; 2.735; 0.053	0.608; 1.46; 0.117
	Exc. RS	Poisson	2; 1.317; 0.518	1.411; 6.757; 0.007**	0.62; 1.627; 0.08	0.001; 0; 0.368			
C. melampygus	Inc. RS	Poisson	2, 20.09; <0.001***	2.281; 16.627; 0.001***	0.001; 0; 0.344	1; 3.11; 0.0428*	0.001; 0; 0.402	0.001; 0; 0.414	1.028; 2.349; 0.093
	Exc. RS	Poisson	2, 27.85; <0.001***	2.22; 15.798; 0.001***	0.001; 0; 0.299	1.116; 3.292; 0.043*			
L. bohar	Inc. RS	Neg. Bin	2; 0.182; 0.913	0.001; 0; 0.583	0.317; 0.399; 0.253	0.677; 1.996; 0.082	1.811; 10.761; 0.003**	1.092; 3.721; 0.042*	0.46; 0.793; 0.187
	Exc. RS	Neg. Bin	2; 2.183; 0.336	0.001; 0; 0.451	0.001; 0; 0.403	0.772; 3.218; 0.039*			
L. crocineus	Inc. RS	Neg. Bin	2; 12.04; 0.002**	0.001; 0; 1	0.001; 0; 0.481	0.579; 0.887; 0.206	0.218; 0.275; 0.257	0.001; 0; 0.389	0.001; 0; 0.476
	Exc. RS	Neg. Bin	2; 11.93; 0.002**	0.001; 0; 1	0.001; 0; 0.473	0.639; 1.091; 0.172			
V. louti	Inc. RS	Poisson	2; 1.049; 0.592	0.908; 9.393; 0.001**	0.459; 0.889; 0.158	0.001; 0; 0.626	0.001; 0; 0.742	0.05; 0.052; 0.303	0.254; 0.329; 0.252
	Exc. RS	Poisson	2; 1.693; 0.429	0.909; 9.593; 0.001**	0.49; 1.006; 0.147	0.001; 0; 0.692			
E. tukula	Inc. RS	Binomial	2; 9.516;0.008**	0.001; 0; 0.344	0.001; 0; 0.79	0.001; 0; 0.843	0.001; 0; 1	0.001; 0; 0.748	0; 0; 0
	Exc. RS	Binomial	2; 9.516; 0.008**	0.001; 0; 0.6	0.001; 0; 0.344	0.001; 0; 0.829			

*Significance level: * = p < 0.05; ** = p <0.01, *** = p<0.001*

Table 3.3: Results from the Wald's tests run on the General Additive Models (GAMs) for the average biomass (kg/sample) data. The table shows the results for the parametric term of Zonation (degrees freedom; F value; p-value) and the habitat covariates (estimated degrees freedom; F; p-value). The "Analysis" column distinguishes among the models which included (Inc. RS) and excluded (Exc. RS) reef size. The "Distribution used" column indicates a Tweedie distribution and the corresponding P-value. Results for full models, including other covariates (e.g. temperature, depth, visibility) can be found in the appendix material for chapter 3.

Species	**Analysis**	**Distribution used**	**Zonation**	**PCO1**	**PCO2**	**PCO3**	**Reef size: Map NTSZ**	**Reef size: CPZ**	**Reef size: St Lucia NTSZ**
A. virescens	Inc. RS	Tweedie P: 1.4	2; 3.279; 0.043*	0.001; 0; 0.489	0.001; 0; 1	1.346; 1.028; 0.05*	0.892; 2.766; 0.004**	1.048; 1.301; 0.018*	0.804; 1.381; 0.026*
	Exc. RS	Tweedie P: 1.4	2; 8.207; <0.001**	0.001; 0; 0.999	0.001; 0; 0.385	1.604; 0.643; 0.027*			
C. melampygus	Inc. RS	Tweedie P: 1.1	2; 3.325; 0.041*	0.001; 0; 0.498	0.759; 0.924; 0.03*	0.001; 0; 0.848	0.955; 5.724; 0.001**	0.61; 0.459; 0.086	0.958; 8.587; 0.001**
	Exc. RS	Tweedie P: 1.1	2; 16.59; <0.001***	0.699; 0.25; 0.073	0.281; 0.043; 0.241	0.247; 0.033; 0.276			
L. bohar	Inc. RS	Tweedie P: 1.2	2; 0.128; 0.88	0.601; 0.372; 0.112	0.001; 0; 0.941	0.001; 0; 0.78	0.92; 2.773; 0.001**	0.232; 0.077; 0.25	0.748; 0.956; 0.052
	Exc. RS	Tweedie P: 1.2	2; 1.385; 0.026*	0.721; 0.322; 0.046*	0.001; 0; 0.999	0.122; 0.017; 0.27			
L. crocineus	Inc. RS	Tweedie P: 1.2	2; 0.787; 0.459	1.438; 0.947; 0.061	0.001; 0; 0.717	0.415; 0.188; 0.155	1.157; 2.634; 0.001**	0.86; 1.577; 0.008**	0.91; 3.506; 0.002**
	Exc. RS	Tweedie P: 1.2	2; 7.079; 0.001**	1.742; 0.425; 0.094	0.431; 0.077; 0.197	0.001; 0;1			
V. louti	Inc. RS	Tweedie P: 1.2	2; 0.708; 0.496	1.714; 2.334; 0.003**	0.001; 0; 0.568	0.596; 0.519; 0.054	0.791; 1.316; 0.012*	0.815; 1.556; 0.007**	1.723; 4.81; 0.001**
	Exc. RS	Tweedie P: 1.2	2; 8.498; <0.001***	2.344; 1.489; 0.001**	0.001; 0; 0.571	1.255; 0.582; 0.016*			
E. tukula	Inc. RS	Tweedie P: 1.1	2; 1.704; 0.049*	0.001; 0; 0.82	0.001; 0; 0.866	0.001; 0; 0.538	0.846; 1.817; 0.005**	0.742; 0.953; 0.026*	0.001; 0; 0.29
	Exc. RS	Tweedie P: 1.1	2; 3.012; <0.001***	0.718; 0.341; 0.037*	0.001; 0; 1	0.001; 0; 0.269			

Significance level: * = $p < 0.05$; ** = $p < 0.01$, *** = $p < 0.001$

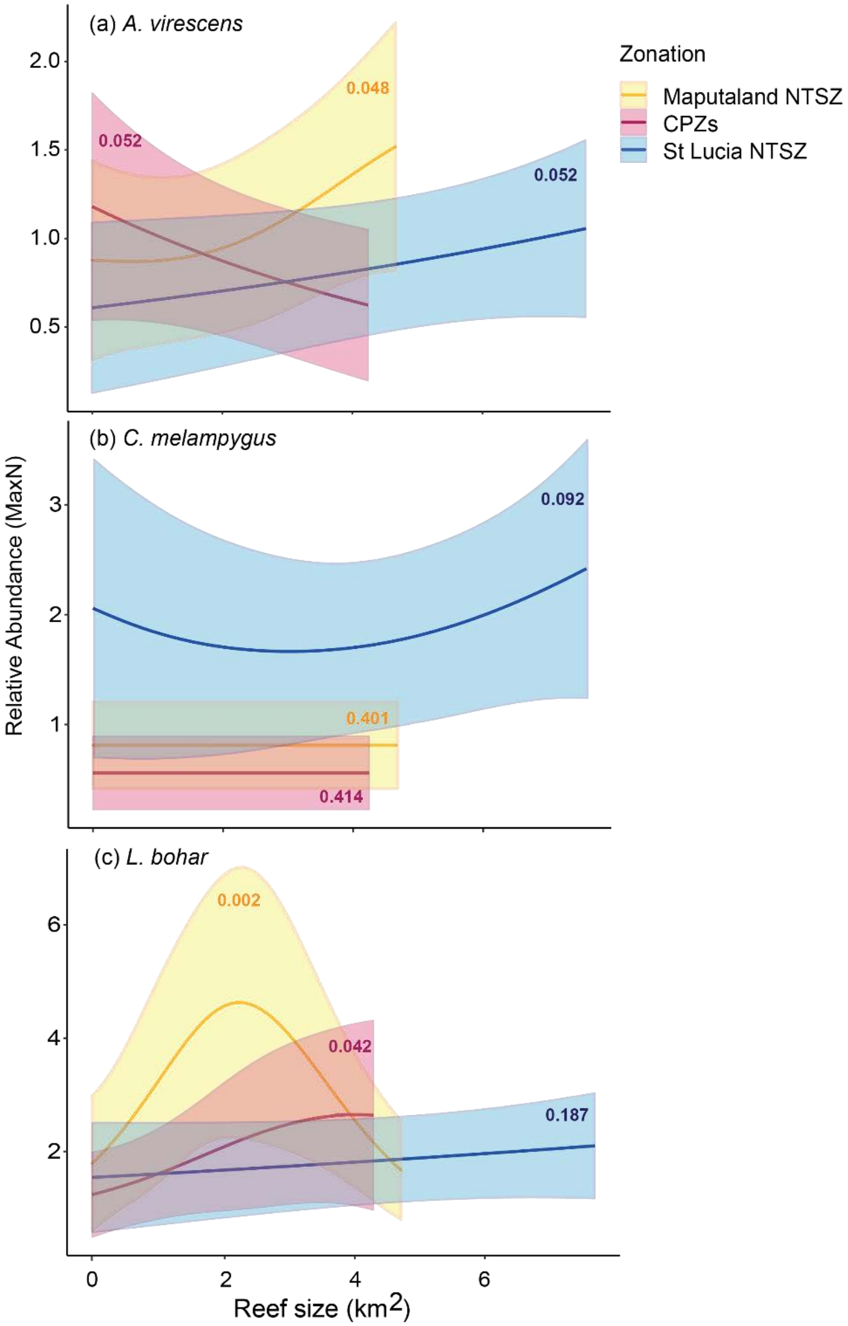


Figure 3.3: Relationship between reef size (km^2) and predicted relative abundance for *Aprion virescens* (a), *Caranx melampygus* (b) and *Lutjanus bohar* (c). Each plot shows the comparison between the Controlled Pelagic Zone (CPZ: Red) and the two No-Take Sanctuary Zones (Maputaland NTSZ: yellow and St Lucia NTSZ: Blue) within the iSimangaliso Wetland Park MPA. Numbers in colour correspond to the P-value for reef size within the respective zone. The area around each trend line indicates the approximate 95% confidence interval.

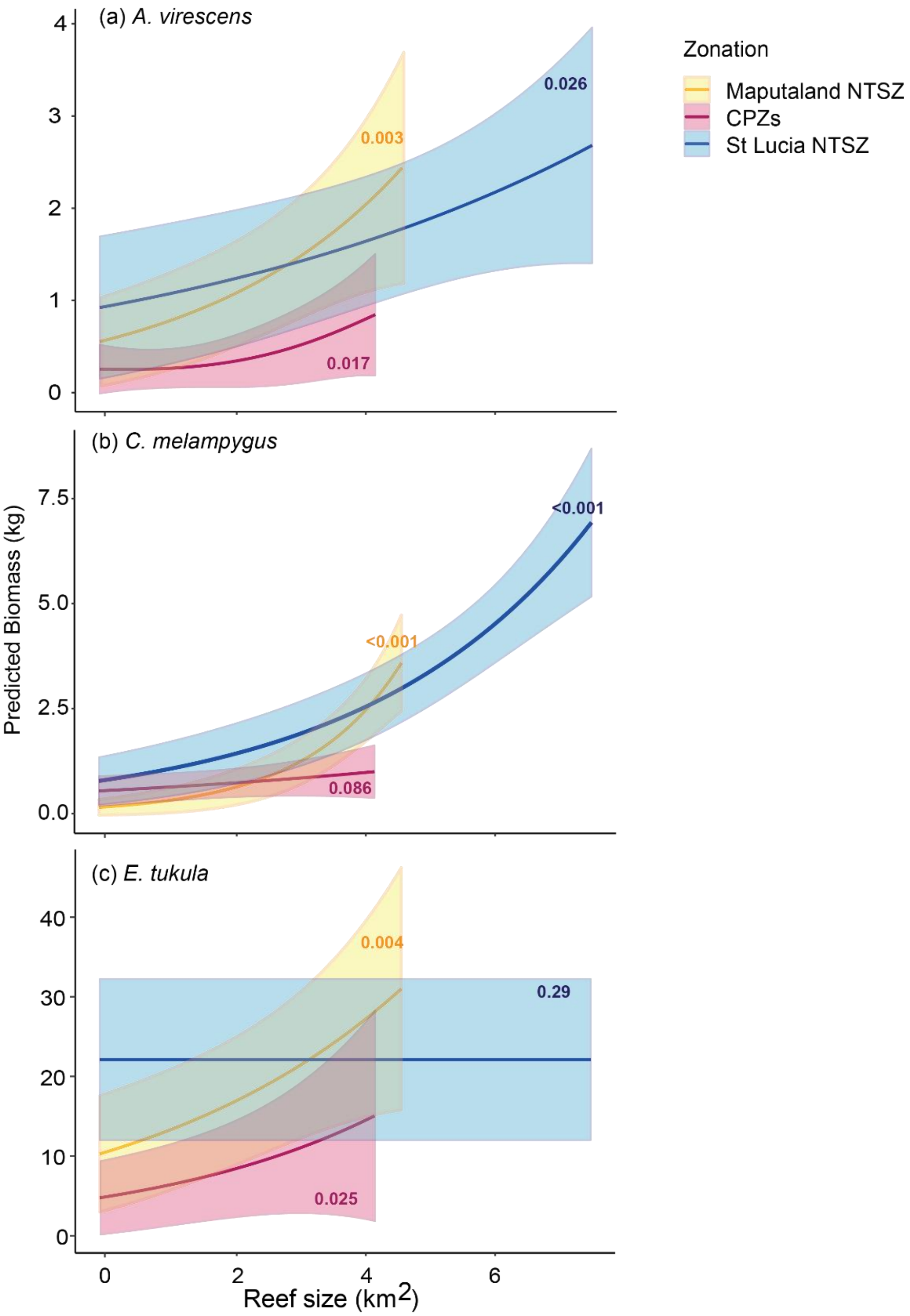


Figure 3.4: Relationship between reef size (km^2) and predicted average biomass for *Aprion virescens* (a), *Caranx melampygus* (b) and *Epinephelus tukula* (c). Each plot shows the comparison between the Controlled Pelagic Zone (CPZ: Red) and the two No-Take Sanctuary Zones (Maputaland NTSZ: yellow and St Lucia NTSZ: Blue) within the iSimangaliso Wetland Park MPA. Numbers in colour correspond to the P-value for Reef size within the respective zone. The area around each trend line indicates the approximate 95% confidence interval.

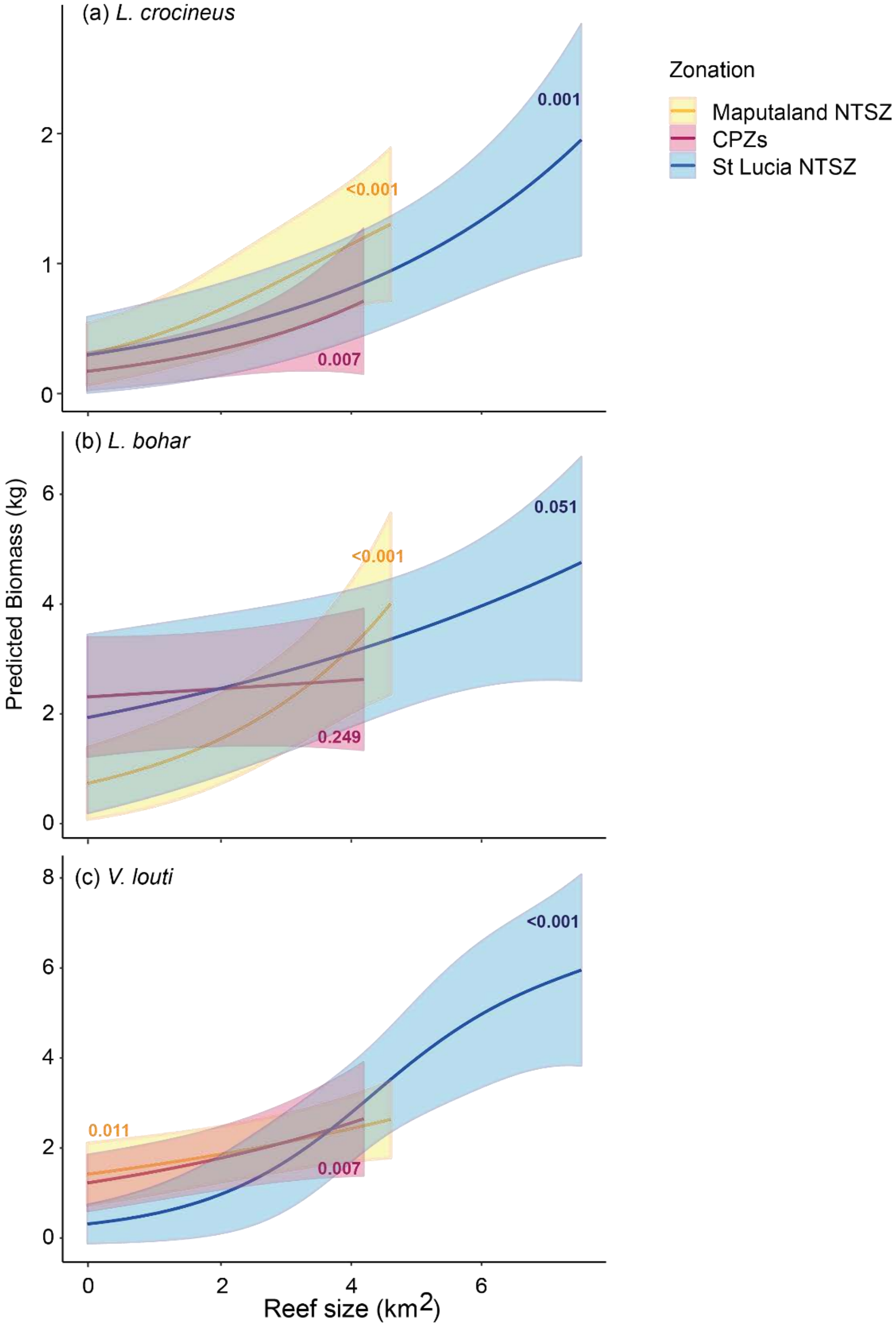


Figure 3.5: Relationship between reef size (km^2) and predicted average biomass for *Lethrinus crocienus* (a), *Lutjanus bohar* (b) and *Variola louti* (c). Each plot shows the comparison between the Controlled Pelagic Zone (CPZ: Red) and the two No-Take Sanctuary Zones (Maputaland NTSZ: yellow and St Lucia NTSZ: Blue) within the iSimangaliso Wetland Park MPA. Numbers in colour correspond to the P-value for Reef size within the respective zone. The area around each trend line indicates the approximate 95% confidence interval.

The relative abundance and average biomass per sample of *L. bohar*, *L. crocineus* and *E. tukula*, together with the average biomass of *C. melampygus,* were not influenced by the habitat covariates (PCO1, PCO2, PCO3) (Table 3.2 and 3.3). Habitat complexity (captured in PCO1) had a significant effect on the relative abundance of *A. virescens*, *C. melampygus* and *V. louti*, with greater abundances recorded in habitats with higher relief and dominated by stony corals (Table 3.2). Similarly, the average biomass of *V. louti* was significantly greater in habitats with higher relief (Table 3.3). The effect of PCO2 on the average biomass of *C. melampygus* was significant, with greater average biomass per sample associated with habitats which supported True anemones and Zoanthids and lower average biomass associated with habitats dominated by macroalgae (Table 3.3). The average biomass of *A. virescens* was significantly affected by variation in PCO3 with greater biomass occurring in areas dominated by stony corals relative to macroalgal habitats (Table 3.3).

The effect of depth on abundance and biomass was inconsistent across species and differed according to the inclusion and exclusion of reef size within the models. There were only four cases where the variable depth was significant. Depth had a significant negative effect on the average biomass of *Lethrinus crocineus* (F = 0.473, P = 0.032; Appendix Table 6.11) and a significant positive effect on the average biomass of *Epinephelus tukula* (F = 1.008, P = 0.007; Appendix Table 6.17) when reef size was included within the models. The relative abundance of *Lutjanus bohar* decreased significantly with increasing depth, both in models where reef size was included (F = 12.594; P = 0.001) and excluded (F = 8.568; P = 0.005) (see Appendix Table 6.12).

3.4.3 EFFECT OF ZONATION WHEN ACCOUNTING FOR REEF SIZE

There was no significant effect of zonation on the relative abundance and average biomass of *L. bohar* and *V. louti* (Table 3.2 and 3.3; Figure 3.6 d, e and 3.7 d, e). The relative abundance of *A. virescens* (Table 3.2, Figure 3.6 a) and biomass of *L. crocineus* (Table 3.3, Figure 3.7 c) also showed no significant effect of zonation. However, the predicted plots do indicate some degree of separation at the 95% confidence interval for the abundance of *A. virescens* and *L. bohar* (Figure 3.6 a and d respectively), and the biomass of *L. crocineus* (Figure 3.7 c). These separations occur due to greater average abundances of *A. virescens* and *L. bohar* within the Maputaland NTSZ, compared to the CPZ and St Lucia NTSZ respectively. Similarly, the predicted average biomass of *L. crocineus* appeared significantly greater in the Maputaland NTSZ, compared to the CPZ but not the St Lucia NTSZ (Figure 3.7 c). This does suggest that there is an element of a management zone effect for *A. virescens*, *L. bohar* and *L. crocineus*. The relative abundance for *C. melampygus* and the detection probability for *E. tukula* were predicted to be significantly higher in the St Lucia NTSZ, while there was no marked difference between the CPZ and the Maputaland NTSZ, in both cases (Figure 3.6 b, f). *Lethrinus crocineus* was predicted to have higher relative abundances in both NTSZs as compared to the CPZ (Figure 3.6 c), with Maputaland NTSZ having the greatest average abundance. The biomass of *A.* virescens, *C. melampygus* and *E. tukula* (Figure 3.7 a, b and f) were significantly higher in both of the NTSZs relative to the CPZ.

3.4.4 EFFECT OF ZONATION WHEN EXCLUDING REEF SIZE

Ignoring the covariate "reef size" in the GAMs run on the relative abundance data did not alter the significance of the effect of management zone on any of the species analysed (Table 3.2). This said, the before mentioned separations at the 95% confidence intervals for *A. virescens* and *L. bohar* abundances are no longer evident when reef size is excluded (Figure 3.6a and d). The interpretation of the effect of zonation on average biomass changed significantly for all six study species. When reef size was accounted for, three species showed no effect of zonation but later showed a significant effect when reef size was excluded, namely *L. crocineus* (Including reef size: P-value = 0.459; Excluding reef size: P-value = 0.001), *L. bohar* (Including reef size: P-value = 0.88; Excluding reef size: P-value = 0.026) and *V. louti* (Including reef size: P-value = 0.496; Excluding reef size: P-value = 0.0005 (see Figure 3.7 c, d, e). The biomass of *L. crocineus* and *L. bohar* (Figure 3.7 c and d) were subsequently predicted to be highest in the St Lucia NTSZ and lowest within the CPZ. The average biomass of *V. louti* (Figure 3.7 e) was predicted to be significantly higher in the St Lucia NTSZ, compared to the Maputaland NTSZ and CPZ. For the remaining species, which did originally show an effect of zonation when accounting for Reef size, P-values for zonation noticeably decreased in value (implying an increase in significance), especially for *A. virescens* (Including reef size: P-value = 0.043; Excluding reef size: P-value = 0.0005), *C. melampygus* (Including reef size: P-value = 0.046; Excluding reef size: P-value = <0.001) and *E. tukula* (Including reef size: P-value = 0.049; Excluding reef size: P-value = 0.0003) (Table 3.3; Figure 3.7 a, b, f).

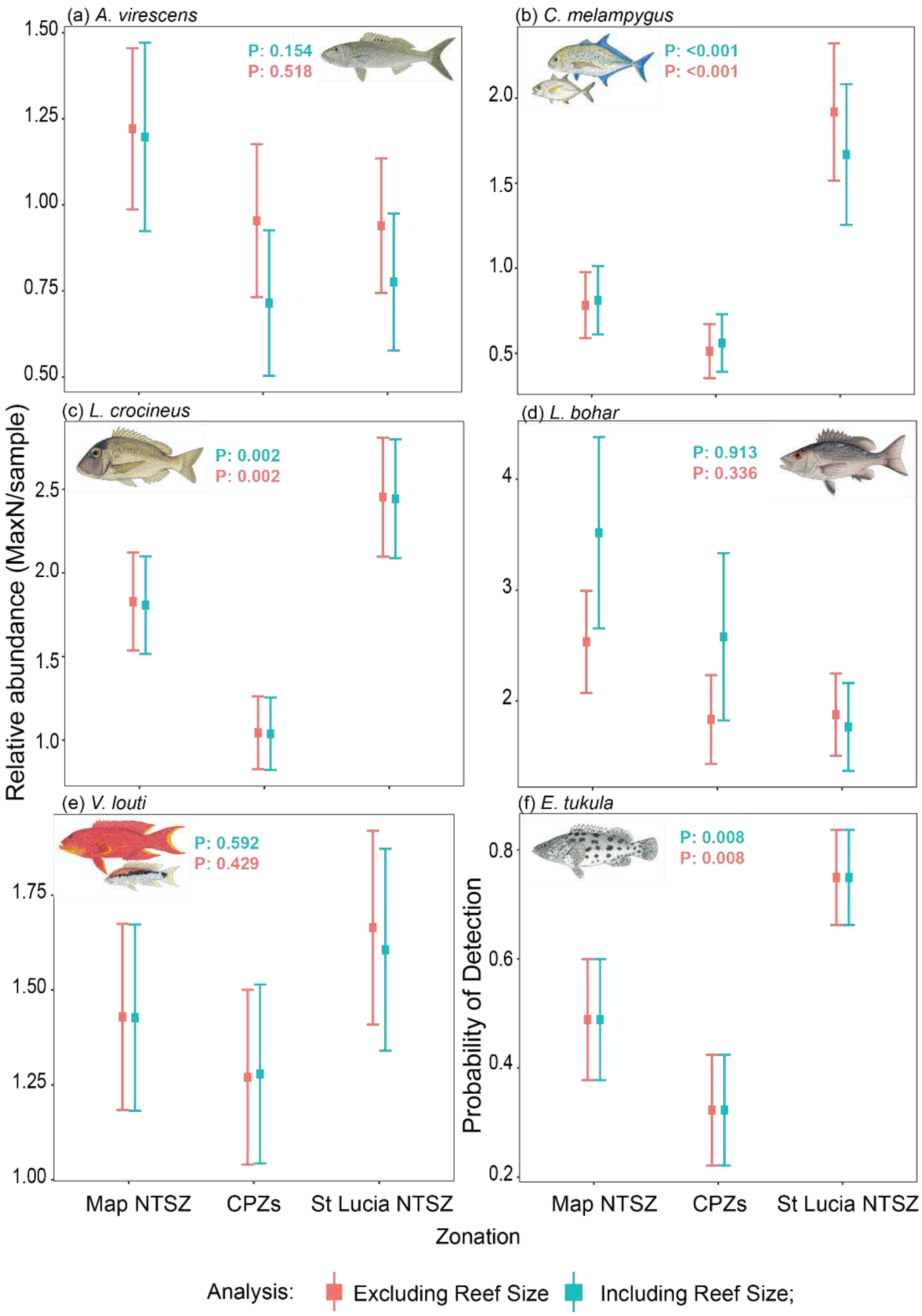


Figure 3.6: Comparison of predicted relative abundance (MaxN/sample) (a-e), probability of detection (f) for *Aprion virescens* (a), *Caranx melampygus* (b), *Lethrinus crocineus* (c), *Lutjanus bohar* (d), *Variola louti* (e) and *Epinephelus tukula* (f) between the Controlled Pelagic Zone (CPZ) and the two No-Take Sanctuary Zones (Map NTSZ: Maputaland and St Lucia NTSZ) for the general additive models that included reef size (blue) and excluded reef size (red). Predictions were based on average values for all continuous covariates that were included according to “select=true” (see Table 3.1). Error bars indicate approximate 95% confidence levels.

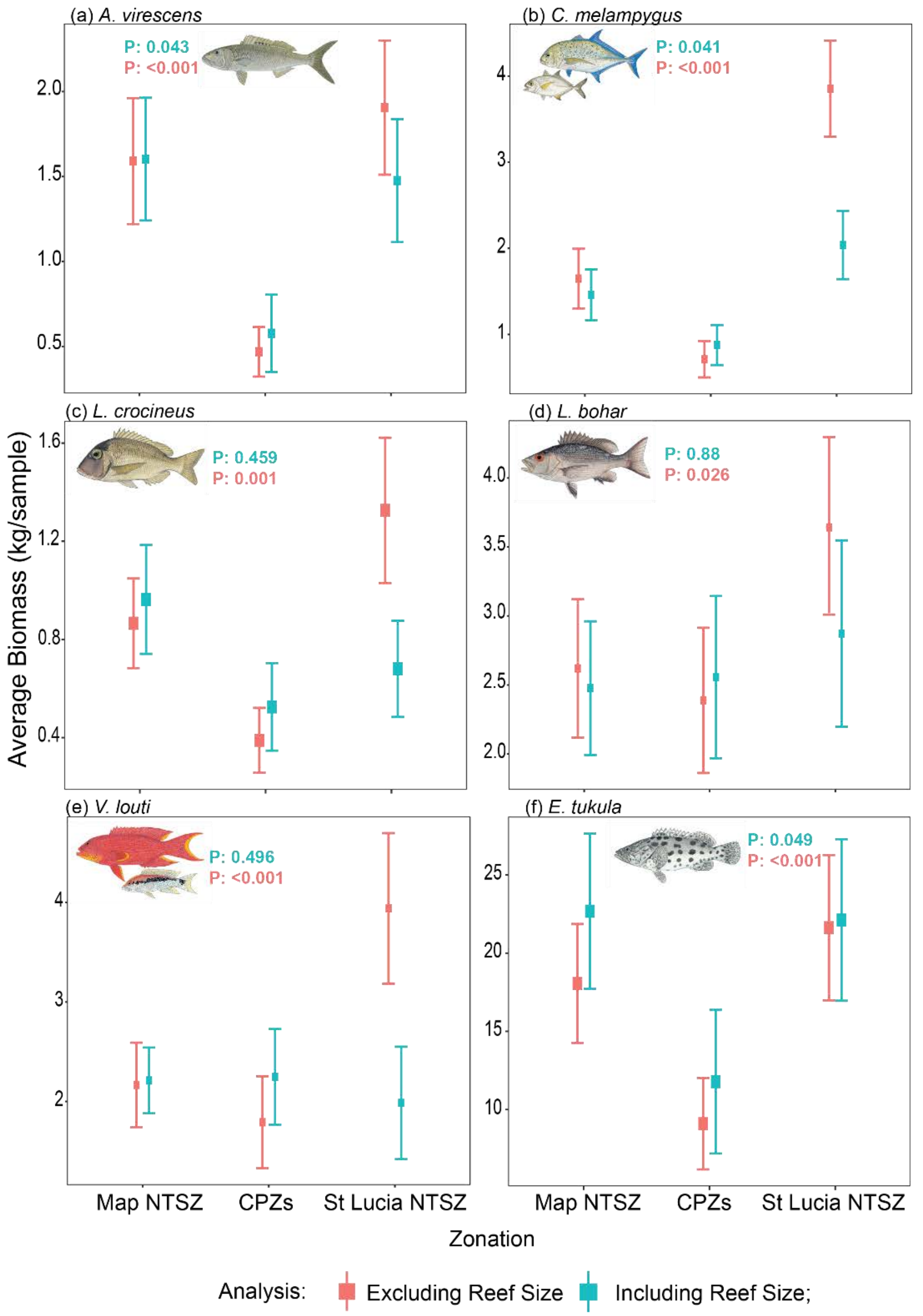


Figure 3.7: Comparison of predicted average biomass (kg/sample) for *Aprion virescens* (a), *Caranx melampygus* (b), *Lethrinus crocineus* (c), *Lutjanus bohar* (d), *Variola louti* (e) and *Epinephelus tukula* (f) between the Controlled Pelagic Zone (CPZ) and the two No-Take Sanctuary Zones (Map NTSZ: Maputaland and St Lucia NTSZ) for the general additive models that included reef size (blue) and excluded reef size (red). Predictions were based on average values for all continuous covariates that were included according to "select=true" (See Table 3.1). Error bars indicate approximate 95% confidence levels.

3.5 DISCUSSION

3.5.1 KEY FINDINGS

It was found that reef size had a consistently positive effect on the average biomass of the six species investigated, however, the effect was not strong on abundance data. As for other environmental variables considered, none were consistent among the different study species populations. When the differences in reef size were accounted for in the analyses, the effect of zonation on both the relative abundance and average biomass was significant for three of the six study species. Ignoring reef size increased the level of significance of the management zone for biomass models of all six species. This was most evident in the average biomass data when excluding reef size from the models as it changed the outcome of the management zone test from no effect to a significant effect for three species which previously showed no significant effect of management zone when reef size was accounted for.

3.5.2 VARIATION IN POPULATIONS WITH HABITAT VARIABLES

Reef size has been identified as an important factor determining reef fish assemblage structure (Bellwood and Hughes., 2001; Bohnsack et al., 1994). Other studies have provided detail on how larger reef areas provide higher levels of productivity, greater environmental diversity, greater holding capacities for fish populations, less limitation for species that have habitat to-body-size dependency and greater resilience of fish communities (Connor and McCoy, 2002; Cornell and Karlson, 2000; Davis et al., 2014; Hodgson et al., 2011; Huntington and Lirman, 2012; McIntosh et al., 2018; Mellin et al., 2010). These findings, where reef size was positively correlated with the average biomass of all six species, added further support to the importance of habitat size in structuring fish populations and size structure.

The relationship between reef size and abundance were typically weak, but when present, they were complex and inconsistent among the management zones. For example, the abundance of *Lutjanus bohar* showed positive relationships with increasing reef size, except in the Maputaland NTSZ where predictive plots showed this zone to have significantly higher average relative abundances, which peaked on intermediate-sized reefs. The relationship between the relative abundance of *A. virescens* and reef size changed according to the management zone, with greater abundance on smaller reefs in the CPZ and larger reefs in the NTSZs. The inconsistency between management zones suggests that other processes may be influencing the observed trends in abundance, rather than reef size. Habitat utilisation varies among different species (Munday, 2004; Rice, 2005), and different life-stages of a species (Dahlgren and Eggleston, 2000; Lecchini and Galzin, 2005; Wright et al., 1986). These features may create consistent abundances across different reef sizes, but foraging/energy requirements result in larger individuals occupying the more productive larger reefs.

Foraging distance has also been shown to scale positively with fish size (Nash et al., 2013). All the species considered in this chapter are relatively large and show a strong affinity to being attracted to stereo-BRUVs. As such it is possible that the lack of a relationship between reef size and abundance was attributed to large foraging areas, coupled with an attraction to the stereo-BRUVs, dampening any environmental associations.

Aprion virescens is considered to be a wide-ranging predator with a core activity area of up to 12 km in radius (Meyer, 2007), weak habitat preference and broad depth distributions (Asher et al., 2017). Although this could explain the absence of clear reef size associations with abundance, it does not explain why the associations identified in this research were different between the CPZ and NTSZ. Much of the anthropogenic pressure, such as the regulated game fishing, boating and diving are concentrated around the larger reef complexes in CPZ of the IWP MPA. Also, *A. virescens* was previously classified as a gamefish and could be harvested by line and spearfishermen in the CPZ before 2011. Research has shown that anthropogenic disturbances may influence the composition of fish communities, affecting the relative abundance of a species within certain areas (Floros, 2010; Nash and Graham, 2016). The apparent association with smaller reef patches in the CPZ may be attributed to the historical exploitation of *A. virescens*, and the continued anthropogenic disturbances on the larger reefs in the CPZ. Alternatively, in the NTSZs where no such pressures exist, more individuals can inhabit the larger reef areas without disturbance.

The effects of the other descriptive habitat variables, namely PCO1 (Sandy > Stony Coral habitats), PCO2 (Macroalgal > Zoas and Anenomes) and PCO3 (Macroalgal > Stony Coral) did not have any consistent patterns. The relative abundance and average biomass of *L. bohar*, *L. crocineus* and *E. tukula*, together with the average biomass of *C. melampygus*, did not respond to variation in any of the habitat variables. However, habitat complexity (captured in PCO1) was shown to have a significant effect on the relative abundance of *A. virescens*, *C. melampygus* and *V. louti*, with greater abundances recorded in habitats with higher relief and dominated by stony corals. Similarly, the average biomass of *V. louti* was significantly greater in habitats with higher relief. The structural complexity of these high relief and stony coral habitats provides sufficient available habitat area to support larger populations, reduce competition and provide sufficient productivity for predatory species (Caley and John, 1996; Friedlander and Parrish, 1998; Gratwicke and Speight, 2005; Lingo and Szedlmayer, 2006; Nash et al., 2013). The remaining habitat variables, PCO2 and PCO3, were only significant in singular cases. Greater average biomasses of *Caranx melampygus* were associated with habitats that supported true anemones and zoanthids and lower average biomass associated with habitats dominated by macroalgae. Greater average biomass of *Aprion virescens* was linked to areas dominated by stony corals, relative to macroalgal habitats. These interactions with habitat characteristics are most likely due to habitat preferences and the niche occupied by that species, both of which may change throughout its life history (Levin and Hay, 2002; Light and Jones, 1997; Lirman, 1994).

The effect of depth on relative abundance and average biomass was also inconsistent across species and depended on the inclusion of Reef size within the models. There were only three cases where the variable depth was shown to be significant when accounting for all habitat variables. Increasing water depth had a negative effect on the average biomass of *Lethrinus crocineus* and the abundance of *Lutjanus bohar*. On the other hand, the average biomass of *Epinephelus tukula* increased within increasing water depth. These results highlight how depth preferences, just like habitat, is species-dependent and may change according to life history (Brokovich et al., 2008, 2006; Lara and González, 1998; McGehee, 1994; Wantiez and Chauvet, 2003).

3.5.3 VARIATION IN POPULATIONS AMONG MANAGEMENT ZONES

When we accounted for reef size, populations of *A. virescens*, *C. melampygus*, *L. crocineus*, *Lutjanus bohar* and *E. tukula*, showed a significant effect of zonation on either average biomass or relative abundance, or both. The lack of any effect of zonation on the remaining species, *V. louti*, is perhaps not surprising since bottom or reef fishing has been banned in both the NTSZs and CPZ for more than 30 years, allowing ample time for the populations to recover (MacNeil et al., 2015).

The average biomass of *A. virescens* was predicted to be significantly greater in the NTSZs, compared to the CPZ. In contrast, the Wald's test indicated that management zone did not significantly affect the relative abundance of *A. virescens* however, the predictions based on the model coefficients indicated that Maputaland NTSZ did have a higher average relative abundance compared to the CPZ and St Lucia NTSZ at the 95% confidence interval level (Figure 3.6a). There are two changes in the management of the IWP MPA which are pertinent to understanding the impact of fishing on this species. The first being the promulgation of the Maputaland NTSZ, which before 2001 functioned as another CPZ where this species could be captured. Thus, the Maputaland NTSZ has afforded this species 16 years of full protection (2001 to sampling in 2017). The second change in management is the removal of this species of the pelagic gamefish list in the CPZ in 2011 based on the results released by Floros (2010). This means that *A. virescens* has been protected in the CPZ for five years (2001 to sampling in 2016). Considering the historical impact of exploitation (before 2011) on this species in the CPZ (Floros, 2010), our results suggest that the size structure of the population within the CPZ remains truncated, relative to both NTSZs. The significantly higher relative abundance of *A. virescens* in the Maputaland NTSZ, relative to the St Lucia NTSZ, may reflect a preference for lower latitude coral reef ecosystems. For example, Sancleme et al (2019) reported greater abundances of

A. virescens in heavily fished areas of the southern Mozambique (1.8 ± 0.3 individuals per BRUVs deployment), relative to the estimates from the Maputaland (1.2 individuals/sample) and St Lucia (0.8 individuals/sample) NTSZs. The average biomass predictions from this study suggested no significant differences for *A. virescens* within the two NTSZs and indicate that the effect of the historical exploitation within the Maputaland NTSZ may no longer be evident.

The average biomass of *C. melampygus* was similar between St Lucia and Maputaland NTSZs, and in both instances, the fish from the NTSZs were on average significantly larger than those recorded in CPZ. On the other hand, the relative abundance of *C. melampygus* in St Lucia NTSZ was significantly higher than that recorded in the Maputaland NTSZ and the CPZ. *Caranx melampygus* has strong site fidelity, well-defined home-ranges and a low occurrence of long-distance movements (Holland et al., 1996), making it vulnerable to fishing pressure and amenable to protection within a no-take MPA (Meyer et al., 2001). In the Hawaiian Islands, *C. melampygus* is frequently captured in fishing competitions (Meyer et al., 2001), and it has been demonstrated that individuals are smaller and less abundant in the fished areas compared to the more remote, less fished areas (Friedlander and DeMartini, 2002). The findings of this chapter are consistent with these earlier studies and suggest that *C. melampygus* may be particularly vulnerable to fishing pressure permitted in the CPZ. The inconsistent pattern in abundance between the NTSZs and the CPZ may reflect that fact that the Maputaland NTSZ is younger than the St Lucia NTSZ. Alternatively, the lower abundances in the Maputaland NTSZ, relative to the St Lucia NTSZ, may be attributed to an unmeasured factor.

Lethrinus crocineus was on average more abundant in both NTSZs, compared to the CPZ. However, the greatest average relative abundances were present within the St Lucia NTSZ. The population of *L. crocineus* is protected throughout the IWP MPA, indicating that fishing is unlikely to be the causal factor. Interestingly, the average biomass of *L. crocineus* was strongly influenced by habitat and the nature of the relationship was dependant on the management zone. Little is known about the ecology of *L. crocineus*; however, it is considered to be a benthic carnivore and somewhat of a habitat generalist, occurring on the sand and coral reef habitat (Carpenter and Allen, 1989). Although this does not explain why *L. crocineus* were more abundant in the NTSZs, compared to the CPZ. Previous *in situ* observations suggest that *L. crocineus* is a shy species that avoid divers (B. Mann pers. obs). The coral reefs within the CPZ of the IWP, particularly in the vicinity of Sodwana Bay, are among the most heavily dived reefs in the world (Barker and Roberts, 2004; Hawkins et al., 2005; Schleyer and Tomalin, 2000; Tratalos and Austin, 2001; Zakai and Chadwick-Furman, 2002). Consequently, there is a possibility that our result is driven by disturbance from SCUBA diving, which has impacted the population structure and habitat selection of *L. crocineus* in the CPZ.

The average biomass of *E. tukula* was significantly greater in the NTSZs, compared to the CPZ, and the probability of detecting *E. tukula* was significantly higher in the St Lucia NTSZ relative to the Maputaland NTSZ and CPZ. In terms of their relationship with reef size, the average biomass of *E. tukula* was positively correlated with reef size except in the case of the St Lucia NTSZ where reef size did not affect the biomass of *E. tukula*. A negative effect of diving pressure on *E. tukula* within the IWP MPA has been identified in previous studies (Floros, 2010; Floros et al., 2013). As this species is protected by fishing, and habitat associations were accounted for in the analyses, my findings may also reflect disturbance due to the diving activity permitted in the CPZ. As for the probability of detection, the CPZ and Maputaland NTSZ had significantly lower values, compared to the St Lucia NTSZ. The difference in detection probability between the two NTSZ is difficult to explain as the results account for site-specific differences in sampled habitat type. However, it is possible that explanatory variables not available for this study influenced the pattern. For example, the habitat offshore of the St Lucia NTSZ includes multiple canyons where large adult *E. tukula* and been previously documented (Nyawo, 2020), and these fish maybe contribute to local recruitment onto shallow inshore reefs. On the other hand, there are no canyons offshore from the areas sampled in the Maputaland NTSZ. However, this is a speculative explanation and warrants further investigation. Given the findings of Floros (2010) and Floros et al. (2013) and the territorial nature of this species, it is suggested that the lower probability of detection in the CPZ may be indicative of both historic and present diving pressure.

3.5.4 ACCOUNTING FOR HABITAT DIFFERENCES

The processes governing fish population and community structure are far more complex than just anthropogenic pressures, and the importance of habitat complexity and habitat size has been repeatedly demonstrated in the literature (Greenstreet and Rogers, 2006; Russ, 2002). However, in-depth literature reviews have shown that a large proportion of studies assessing fisheries and conservation impacts fail to adequately deal with confounding environmental factors (Miller and Russ, 2014; Nash and Graham, 2016), in particular, habitat size when making spatial comparisons. Most frequently, research investigating conservation and fishing effects rely on spatial comparisons, and for these comparisons to be valid, the environment at spatially distinct locations needs to be similar (Dulvy et al., 2004; Miller and Russ, 2014; Nash and Graham, 2016). The design and location of MPAs are often not random, and to maximise conservation benefits MPAs often deliberately incorporate highly productive areas (Miller and Russ, 2014). Consequently, it is often difficult to find similar habitats outside of MPAs to make valid comparisons. The IWP is a good example, with the St Lucia NTSZ encompassing the largest, most isolated reef complex in the area, and although the CPZ protects similar habitats, the reefs which support them are smaller in size. In contrast, the Maputaland NTSZ protects areas of distinct habitat, but the reef sizes are comparable to the CPZ.

The results of this chapter showed that reef size had a significant effect on the average biomass of most study species. This highlights the need to account for differences in reef size when conducting spatial comparisons, especially those focusing on the size structure of populations. Alternatively, the association between abundance and reef size was not clear for almost all of the species. For the most part, overlooking reef size did not change the significance of the outcome in this spatial assessment for the relative abundance data. The effect of ignoring reef size in the spatial comparison was much more apparent when considering data on average biomass, as the significance of the effect of management zone increased dramatically in all cases, and with three species (*L. crocineus*, *L. bohar* and *V. louti*) changed from no effect to a significant effect. In this example, the main changes always added weight to the perceived benefits of the area and management zone with the largest reef (the NTSZ's, and in particular the St Lucia NTSZ). Importantly, the direction of any effect would change if the exploited reef in the spatial comparison encompassed a larger area. For example, if larger reefs were found outside the MPA, then ignoring reef size would result in the perceived effectiveness of the MPA being negligible.

3.5.5 CONCLUSIONS

The results from this study reiterate those of previous studies that covariates describing the nature of habitats, in particular reef size, need to be considered when measuring the effects of management strategies in marine systems, as their omission may lead to spurious conclusions (Dulvy et al., 2004; Greenstreet and Rogers, 2006; Nash and Graham, 2016; Russ, 2002). Interestingly, while reef size had a consistent effect on the average biomass of different species, it had little to no effect on their relative abundance. This simultaneously highlights the sensitivity of fish size to environmental variables and the importance of fully accounting for environmental variables when conducting spatial comparisons with size data. This is especially true when arguing the case for or against MPAs and fisheries closures.

Increasingly, human needs must be accommodated (e.g. resource harvesting or recreation) within MPAs. In our example, the CPZ of the IWP MPA permitted fishing for pelagic species, SCUBA diving and the associated boating activity. Only two of the six reef-associated species examined here showed no effect on the management zone. Two of the remaining four appeared to be directly affected by the permitted (past and present) fishing activity, whereas the remaining two species might have been affected by disturbances due to diving and/or boating activity. There is also the potential that others (i.e. those not directly included in this study) environmental drivers of the fish populations influenced the observed patterns. For instance, differences in the age of the NTSZ may have contributed to the lower abundances of *E. tukula*, *L. crocineus* and *C. melampygus* in the Maputaland NTSZ, relative to the St Lucia NTSZ. On the other hand, preference for warmer lower latitude conditions may have contributed to the higher abundance of *L. bohar* and *A.*

virescens in the Maputaland NTSZ, relative to the St Lucia NTSZ. Overall, the results from this chapter identify key environmental associations at the species level and highlight the importance of No-Take Sanctuary Zones for the conservation and recovery of targeted species and illustrate some potential impacts of the trade-off required to accommodate human needs within protected spaces.

CHAPTER 4

GENERAL DISCUSSION

4.1 THESIS PURPOSE

This thesis aimed to identify the effect of habitat and key environmental drivers on the taxonomic and functional structure of reef fish assemblages and populations of key species, and determine the effect of the management zonation within the iSimangaliso Wetland Park (IWP) MPAs on reef fish communities as well as populations of key species while accounting for the effect of important habitat variables.

These aims were developed given that limited research has been done on the offshore fish communities within iSimangaliso Wetland Park, with only four published studies to date. Secondly, coral reef ecology research is also greatly focused on tropical lower latitude reefs, thus we have little understanding of their higher latitude counterparts. The Reef fish communities of IWP are also subject to selective game fishing, boating and SCUBA diving in allocated zones whereas other zones have been fully protected from human activity for nearly 40 years. This provides the opportunity for an investigation into the effect of zonation strategies on reef fish communities and single-species populations.

4.2 IWP MPA MANAGEMENT AND ENVIRONMENTAL GRADIENTS

This study involved three different management zones found within IWP. Two of which are No-Take Sanctuary Zones (NTSZs) but have been operating as such for different periods (St Lucia NTSZ = 37 years; Maputaland NTSZ = 16 years), and one Controlled Pelagic Zone (CPZ) which allows for restricted resource use. All three management zones have similar coral reef habitats, however, the Maputaland NTSZ has the addition of a macroalgae habitat, that is missing from the other two zones. Also, the St Lucia NTSZ has greater reef areas and larger reef patches, in comparison to the Maputaland NTSZ and the CPZ, which have similar-sized reefs and reef area.

The Maputaland No-Take Sanctuary Zone (NTSZ) lies on the northern border of the iSimangaliso Wetland Park (IMP), alongside the Mozambique border. In 2001, this area was declared a No-Take Sanctuary Zone, as prior it was a Controlled Pelagic Zone (CPZ), thus being subject to diving and recreational game fishing pressures. This area stands out in terms of its lower latitude, thus there is potential for slightly more tropical conditions and greater variation in habitat types given the prevalence of macroalgae in this region in addition to other habitat types. The St Lucia No-Take Sanctuary Zone, which occurs at a slightly higher latitude than the other management zones, was established in 1979 and has provided fish assemblages in this region with 37 years of protection (to the time it was sampled in 2016) from all human disturbances. The largest reef complexes fall within the St Lucia NTSZ, consisting of few reef patches. This is unlike other zones which have comparably smaller and patchier reefs. The controlled pelagic zone of iSimangaliso Wetland Park has been subject to controlled game fishing and intensive diving pressure since 1979 and 1986 within St Lucia and Maputaland MPA components, respectively. This macrobenthic habitat in this region is comparable to that of the St Lucia NTSZ, however, the reefs in this region are smaller and similarly sized to those within the Maputaland NTSZ.

4.3 FISHES OF THE ISIMANGALISO WETLAND PARK

This study identified a total of 333 confirmed species from 62 families of teleosts and elasmobranchs. A total of 9 160 observations of relative abundances were generated with a total observed biomass of 8 169 kg. Reef fish communities were further categorised into a total of 31, 21 and 39 functional groups for datasets of abundance, length and stage of maturity metrics, respectively.

4.4 THE EFFECT OF THE ENVIRONMENT ON THE FISHES IN THE ISIMANGALISO WETLAND PARK

Reef size at the species level is an important environmental variable, especially for average biomass data. However, reef size doesn’t appear to be an important driver of relative abundance and particularly for the taxonomic and functional assemblage structure. The biomass of all species positively correlated with reef size. Repeating these models to exclude the variable reef size, indicated how not including reef size leads to misinterpretation of results, and in most cases exaggerated the effects of the St Lucia NTSZ, where the biggest reefs were recorded. Reef size data are often unavailable, given the costs involved and the difficulty of obtaining such data. Nonetheless, this reiterates the importance of incorporating habitat characteristics when researching reef fish assemblages.

Reef fish assemblages throughout the IWP showed consistent correlations with two gradients in habitat variation, across various univariate and multivariate analyses. The first being PCO1, the gradient from stony coral habitats to low relief sandy habitats and the second PCO3, over a gradient from macroalgal habitats to those dominated by stony corals. It was found that a greater functional and taxonomic diversity was typically associated with high relief stony coral habitats, with low relief macroalgal and sandy habitats supporting less diversity but very different assemblages of species and juvenile groups. The importance of the habitat variation captured by these variables applied to both the taxonomic and functional structure of fish communities, however, were less consistent when looking at single-species populations. The importance of habitat variations to fish communities may be due to complex habitat selection processes (Edgar and Robertson, 1992; Levin and Hay, 1996), hydrodynamics and larval supply (Jenkins et al., 1997; Jenkins and Hamer, 2001) or survival as a function of refuge provision and habitat complexity (Almany, 2004a, 2004b; B. Gratwicke and Speight, 2005; Wilson et al., 2007). Most functional indices in this study were higher in stony coral habitats, and lower in habitats characterized by sand and macroalgae. This demonstrates the importance of stony coral habitats for supporting greater numbers of functional groups, functional richness and functional diversity (Thrush and Dayton, 2010; Travisa et al., 2014; Wilkinson, 2002).

Other environmental drivers considered in this study, in particular depth, did not show consistent patterns with communities and species analyses and thus was not deemed a key environmental driver over the depth range sampled (5 – 40 m). However, it is suggested that this variable be incorporated in studies given its highlighted importance in previous research (Bellwood and Hughes, 2001). In this study, the importance and nature of the relationship with depth appear to be species-specific and its significance is lost at the broader community scale.

Overall this study endorsed the incorporation of habitat variables when conducting spatial comparisons in reef fish communities on high latitude coral reefs. Of the environmental variables considered reef size was identified as a key variable to include when conducting size-based studies on single-species populations. This said, size-based data may be more sensitive to anthropogenic impacts, it is also more sensitive to environmental variables. As such, when environmental variables are missing, abundance data may still allow for unbiased, or reduce biased, spatial comparisons. The incorporation of macrobenthic data with the use of the Direct Principal Component Method (Winker et al., 2013) was identified as important when analysing multivariate community data as reef fish communities

4.5 THE EFFECT OF MANAGEMENT ZONE ON THE REEF FISHES

This study has highlighted the Maputaland NTSZ as a possible strong-hold for reef fish diversity in South Africa. This given that the area supports fish communities which are taxonomically and functionally unlike those found in other Zones, has a greater number of functional groups and functional richness with large predatory functional groups characterizing the area.

The St Lucia NTSZ has taxonomic and functional communities which are comparable to the CPZ, which allows for SCUBA diving and pelagic game fishing. In contrast to this, the St Lucia NTSZ is like that of Maputaland NTSZ as it too is characterized by large predatory functional groups.

The fish communities within the CPZ, although comparable to the St Lucia NTSZ, stood out in many ways. Characteristic functional groups in this region consisted mostly of juveniles. There was also a noted absence of characteristic predatory functional groups. These juveniles are most likely utilizing the small patch reefs and macroalgal habitats within the CPZ as nursery areas (Beets and Hixon, 1994; Light and Jones, 1997; Lirman, 1994). The prevalence of juveniles may also be due to favourable low predation pressure, indirectly liked to fishing pressures at high trophic levels (Lee et al., 2019). However, it is most likely that the prevalence of juveniles in the CPZ is attributed to the fishing pressure within this region, reduction of the mean trophic level by targeting predators and higher size classes as was documented previously by Floros (2010). Impacted areas are often associated with primarily juvenile fish communities and an absence of large adults (King and McFarlane, 2003; Winemiller, 2005). Functional analysis also showed that a functional group of wedgefishes were characteristic of the functional size structure within the CPZ. Given the conservation status of species within this family (Kyne et al., 2019b), the absence of bottom fishing in the CPZ may prove critical for their conservation.

The population structures of species sensitive to fishing (historically *A. virescens* and currently *C. melampygus*), and those sensitive to diving (*E. tukula* and *L. crocineus*) appear to be healthier in the NTSZs than in the CPZ. The absence of human disturbance within these zones has allowed for either greater abundances or biomasses, or a combination of both, in the NTSZs. It is for this reason that the St Lucia NTSZ may serve as a useful reference site for fish populations that may be subject to disturbances in the adjacent Controlled Pelagic Zone, given that habitats are comparable however, reef sizes will need to be accounted for. The key difference between the two NTSZs is that the probability of detecting *E. tukula* within the Maputaland NTSZ remains as low as those found with the CPZ, as was the case with *C. melampygus*. Suggesting that the 16 years of full protection offered by the Maputaland NTSZ (established as a Sanctuary 2001 and Sampled in 2017) has not allowed for the population of *C. melampygus* and *E. tukula* to fully recover. The smaller size and lower abundances of *A. virescens*, *C. melampygus*, *L. crocineus* and *E. tukula* within the CPZ highlights the potential consequence of accommodating human needs within a protected space. Management zones that allow for human activity cannot fully protect biodiversity in the same manner that No-Take Sanctuary Zones do (Mora et al., 2006).

4.6 LIMITATIONS

The use of baited remote underwater stereo-video systems may pose a “bait effect” that could select for specific taxonomic and functional groups of fish. However, the diversity figures in this study were high suggesting that this method provided a good general representation of the community as a whole. Chater et al. (1993) created a list of species, based on SCUBA and angling censuses and limited netting surveys, and recorded a total of 399 species (73 families) over a field sampling survey period of over two years. A study conducted over a decade later using UVC, amounting to 77 hours of underwater surveys over several trips and employing several divers (Floros 2010) recorded 284 species (50 families). Taking into account the shorter sampling period and sampling effort, the use of stereo-BRUVs in IWP produced 333 species, higher than what was accomplished with UVC. It is suggested that the use of pelagic stereo-BRUVs in IWP be incorporated into this dataset to account for pelagic game species, given that these are the species targeted in the CPZ.

The trait matrix for stages had some species where the adult and juveniles only varied according to their size classes and not according to any other traits. This is due to the lack of life history information available for these reef-associated species. The results are that I was unable to account for ontogenic shifts in habitat and niche usage within the stage based functional data. Had all this information been available, and the trait matrix for stages been fully populated with differences in juvenile traits, then the functional analysis for stages would have been far stronger. This should be emphasized as an important area to conduct further research.

The six selected study species were all quite large and while this worked to demonstrate the effect of habitat size at the scale of reefs, different sized fish will occupy different sized habitats and niches. In effect, this would break down the apparent association between smaller fishes and reef size at the scale I considered. It is possible that in this study, the smallest reef patch sampled was still bigger than the habitat requirements for many of the small species sampled. This might explain the patterns observed in the multivariate analysis, where reef size was not important, but finer-scale habitat characteristics were very important.

4.7 CONCLUSIONS

This study serves as a reference for future monitoring of reef fish assemblages within the iSimangaliso Wetland Park and provides insight for comparisons with future studies on high-latitude coral reefs. Considering that this ecosystem exists as an endemism hotspot (Bellwood and Hughes, 2001; Roberts et al., 2002 see figure 2.1), at the southern-most distributional limit of coral reefs on the east African coast, it has proven to be incredibly diverse in terms of the taxonomic and functional fish communities which exist along a spectrum of habitat variation. This study applied the suggestions of (Villéger et al., 2010), whereby the incorporation of both a taxonomic and functional approach described fish assemblages in implicit detail. The suggestions of (Nash and Graham, 2016) were also adhered to as habitat characteristics such as complexity, habitat type and size of available habitat were fully accounted for while conducting spatial comparisons. It is suggested that future spatial comparisons also incorporate these approaches into their study designs.

The contiguous marine protected areas within the iSimangaliso Wetland Park provides critical protection to an ecosystem that does not exist anywhere else in South Africa. Like other coral reefs, this is ultimately a vulnerable ecosystem that holds recreational, cultural and economic significance to local communities. The level of protection provided by iSimangaliso Wetland Park would not be possible if human needs were not accommodated and tourism not supported in allocated zones of the MPAs. However, it is important to recognize that such accommodation of human needs within protected space does come with ecological consequences. Given the plight of coral reefs in other African countries (Bellwood et al., 2004), both NTSZ, but the Maputaland NTSZ in particular, must be considered critical strongholds for tropical reef-associated species and predators.

REFERENCES

Agardy, T., di Sciara, G.N., Christie, P., 2011. Mind the gap: Addressing the shortcomings of marine protected areas through large scale marine spatial planning. Mar. Policy. https://doi.org/10.1016/j.marpol.2010.10.006

Alder, J., 1996. Have tropical marine protected areas worked? An initial analysis of their success. Coast. Manag. https://doi.org/10.1080/08920759609362285

Almany, G.R., 2004a. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. Oecologia. https://doi.org/10.1007/s00442-004-1617-0

Almany, G.R., 2004b. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? Oikos. https://doi.org/10.1111/j.0030-1299.2004.13193.x

Anand, M., Desrochers, R.E., 2004. Quantification of restoration success using complex systems concepts and models. Restor. Ecol. https://doi.org/10.1111/j.1061-2971.2004.00281.x

Andersen, K.H., Beyer, J.E., 2006. Asymptotic size determines species abundance in the marine size spectrum. Am. Nat. https://doi.org/10.1086/504849

Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. 9, 683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x

Asher, J., Williams, I.D., Harvey, E.S., 2017. An Assessment of Mobile Predator Populations along Shallow and Mesophotic Depth Gradients in the Hawaiian Archipelago. Sci. Rep. https://doi.org/10.1038/s41598-017-03568-1

Balon, E.K., 1990. Epigenetics of an epigeneticist: the development of some alternative concepts on the early ontogeny and evolution of fishes. Guelph Ichtyology Rev. 1, 1-48

Barber, P.H., Bellwood, D.R., 2005. Biodiversity hotspots: Evolutionary origins of biodiversity in wrasses (Halichoeres: Labridae) in the Indo-Pacific and new world tropics. Mol. Phylogenet. Evol. https://doi.org/10.1016/j.ympev.2004.10.004

Barker, N.H.L., Roberts, C.M., 2004. Scuba diver behaviour and the management of diving impacts on coral reefs. Biol. Conserv. 120, 481–489. https://doi.org/10.1016/j.biocon.2004.03.021

Barrett, N.S., Edgar, G.J., Buxton, C.D., Haddon, M., 2007a. Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. J. Exp. Mar. Bio. Ecol. https://doi.org/10.1016/j.jembe.2007.02.007

Barrett, N.S., Edgar, G.J., Buxton, C.D., Haddon, M., 2007b. Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. J. Exp. Mar. Bio. Ecol. https://doi.org/10.1016/j.jembe.2007.02.007

Beets, J., Hixon, M.A., 1994. Distribution, persistence, and growth of groupers (Pisces: Serranidae) on artificial and natural patch reefs in the Virgin Islands. Bull. Mar. Sci. 55(2-3), 470-483.

Bellwood, D.R., Hoey, A.S., Ackerman, J.L., Depczynski, M., 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Glob. Chang. Biol. https://doi.org/10.1111/j.1365-2486.2006.01204.x

Bellwood, D.R., Hughes, T.P., 2001. Regional-scale assembly rules and biodiversity of coral reefs. Science (80-.). 292, 1532–1534. https://doi.org/10.1126/science.1058635

Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. Nature. https://doi.org/10.1038/nature02691

Bellwood, D.R., Meyer, C.P., 2009. Endemism and evolution in the Coral Triangle: A call for clarity. J. Biogeogr. https://doi.org/10.1111/j.1365-2699.2009.02167.x

Bellwood, D.R., Wainwright, P., 2001. Locomotion in labrid fishes: Implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. Coral Reefs. https://doi.org/10.1007/s003380100156

Bernardi, G., 2005. Phylogeography and demography of sympatric sister surfperch species, Embiotoca jacksoni and E. lateralis along the California coast: Historical versus ecological factors. Evolution (N. Y). https://doi.org/10.1111/j.0014-3820.2005.tb00997.x

Beukers, J.S., Jones, G.P., 1998. Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia. https://doi.org/10.1007/s004420050419

Boettiger, C., Lang, D.T., Wainwright, P.C., 2012. Rfishbase: Exploring, manipulating and visualizing FishBase data from R. J. Fish Biol. https://doi.org/10.1111/j.1095-8649.2012.03464.x

Bohnsack, James A, Harper, D.E., Mcclellan, D.B., Hulsbeck, M., 1994. Effects of Reef Size on Colonization and. Bull. Mar. Sci. 55, 796–823.

Bohnsack, J. A., Harper, D.E., McClellan, D.B., Hulsbeck, M., 1994. Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, U.S.A. Bull. Mar. Sci. 55, 796–823.

Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J. Veg. Sci. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x

Boyce, D.G., Tittensor, D.P., Worm, B., 2008. Effects of temperature on global patterns of tuna and billfish richness. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps07237

Brandl, S.J., Emslie, M.J., Ceccarelli, D.M., 2016. Habitat degradation increases functional originality in highly diverse coral reef fish assemblages. Ecosphere. https://doi.org/10.1002/ecs2.1557

Brandl, S.J., Rasher, D.B., Côté, I.M., Casey, J.M., Darling, E.S., Lefcheck, J.S., Duffy, J.E., 2019. Coral reef ecosystem functioning: eight core processes and the role of biodiversity. Front. Ecol. Environ. https://doi.org/10.1002/fee.2088

Britten, G.L., Dowd, M., Minto, C., Ferretti, F., Boero, F., Lotze, H.K., 2014. Predator decline leads to decreased stability in a coastal fish community. Ecol. Lett. https://doi.org/10.1111/ele.12354

Brokovich, E., Baranes, A., Goren, M., 2006. Habitat structure determines coral reef fish assemblages at the northern tip of the Red Sea. Ecol. Indic. https://doi.org/10.1016/j.ecolind.2005.07.002

Brokovich, E., Einbinder, S., Shashar, N., Kiflawi, M., Kark, S., 2008. Descending to the twilight-zone: Changes in coral reef fish assemblages along a depth gradient down to 65 m. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps07591

Bruno, J.F., Sweatman, H., Precht, W.F., Selig, E.R., Schutte, V.G.W., 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology. https://doi.org/10.1890/08-1781.1

Burke, L., Reytar, K., Spalding, M., Perry, A., 2011. Reefs at Risk Revisited, Defenders. World Resources Report. https://pdf.wri.org/reefs_at_risk_revisited.pdf

Caley, M.J., John, J.S., 1996. Refuge Availability Structures Assemblages of Tropical Reef Fishes. J. Anim. Ecol. https://doi.org/10.2307/5777

Cameron, A.C., Trivedi, P.K., 1990. Regression-based tests for overdispersion in the Poisson model. J. Econom. https://doi.org/10.1016/0304-4076(90)90014-K

Cappo, M., Speare, P., De'Ath, G., 2004. Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. J. Exp. Mar. Bio. Ecol. https://doi.org/10.1016/j.jembe.2003.10.006

Carpenter, K.E., Abrar, M., Aeby, G., Aronson, R.B., Banks, S., Bruckner, A., Chiriboga, A., Cortés, J., Delbeek, J.C., DeVantier, L., Edgar, G.J., Edwards, A.J., Fenner, D., Guzmán, H.M., Hoeksema, B.W., Hodgson, G., Johan, O., Licuanan, W.Y., Livingstone, S.R., Lovell, E.R., Moore, J.A., Obura, D.O., Ochavillo, D., Polidoro, B.A., Precht, W.F., Quibilan, M.C., Reboton, C., Richards, Z.T., Rogers, A.D., Sanciangco, J., Sheppard, A., Sheppard, C., Smith, J., Stuart, S., Turak, E., Veron, J.E.N., Wallace, C., Weil, E., Wood, E., 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science (80-.). https://doi.org/10.1126/science.1159196

Carter, R.W.G., 2013. Coastal Environments: An Introduction to the Physical, Ecological, and Cultural Systems of

Coastlines, Coastal Environments: An Introduction to the Physical, Ecological, and Cultural Systems of Coastlines. https://doi.org/10.4319/lo.1989.34.4.0790

Cesar, H.J.S., Burke, L., Pet-Soede, L., 2003. The Economics of Worldwide Coral Reef Degradation. Cesar Environmental Economics Consulting, Arnhem, and WWF-Netherlands, Zeist, The Netherlands. 23 pp., Proceedings of the Royal Society of Medicine.

Chabanet, P., Ralambondrainy, H., Amanieu, M., Faure, G., Galzin, R., 1997. Relationships between coral reef substrata and fish. Coral Reefs. https://doi.org/10.1007/s003380050063

Chadwick, P., Duncan, J., Tunley, K., 2014. State of Management of South Africa's Marine Protected Areas. WWF South Africa Rep. Ser. 1–209.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S., 2000. Consequences of changing biodiversity. Nature. https://doi.org/10.1038/35012241

Chater, S.A., Beckley, L.E., Garratt, P.A., Ballard, J.A., van der Elst, R.P., 1993. Fishes from offshore reefs in the St. Lucia and Maputaland Marine Reserves, South Africa. Lammergeyer. Pietermaritzburg.

Chater, S.A., Beckley, L.E., Van der Elst, R.P., Garratt, P.A., 1995. Underwater visual census of fishes in the St. Lucia Marine Reserve, South Africa. Lammergeyer. Pietermaritzburg.

Cheal, A.J., Emslie, M., MacNeil, M.A., Miller, I., Sweatman, H., 2013. Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. Ecol. Appl. https://doi.org/10.1890/11-2253.1

Clarke, K.R., Gorley, R.N., 2015. Getting started with PRIMER v7. Prim. Plymouth, UK.

Claudet, J., García-Charton, J.A., Lenfant, P., 2011. Combined Effects of Levels of Protection and Environmental Variables at Different Spatial Resolutions on Fish Assemblages in a Marine Protected Area. Conserv. Biol. https://doi.org/10.1111/j.1523-1739.2010.01586.x

Claudet, J., Roussel, S., Pelletier, D., Rey-Valette, H., 2006. Spatial management of near shore coastal areas: The use of Marine Protected Areas (MPAS) in a fisheries management context. Vie Milieu. 56(4), 301-305.

Collins, D.L., Langlois, T.J., Bond, T., Holmes, T.H., Harvey, E.S., Fisher, R., McLean, D.L., 2017. A novel stereo-video method to investigate fish–habitat relationships. Methods Ecol. Evol. https://doi.org/10.1111/2041-210X.12650

Connor, E.F., McCoy, E.D., 2002. The Statistics and Biology of the Species-Area Relationship. Am. Nat. https://doi.org/10.1086/283438

Conover, D.O., 1992. Seasonality and the scheduling of life history at different latitudes. J. Fish Biol. https://doi.org/10.1111/j.1095-8649.1992.tb03876.x

Cornell, H. V., Karlson, R.H., 2000. Coral species richness: Ecological versus biogeographical influences. Coral Reefs 19, 37–49. https://doi.org/10.1007/s003380050224

Costello, M.J., Ballantine, B., 2015. Biodiversity conservation should focus on no-take Marine Reserves: 94% of Marine Protected Areas allow fishing. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2015.06.011

Cowman, P.F., Parravicini, V., Kulbicki, M., Floeter, S.R., 2017. The biogeography of tropical reef fishes: endemism and provinciality through time. Biol. Rev. https://doi.org/10.1111/brv.12323

Crowder, L.B., Hazen, E.L., Avissar, N., Bjorkland, R., Latanich, C., Ogburn, M.B., 2008. The Impacts of Fisheries on Marine Ecosystems and the Transition to Ecosystem-Based Management. Annu. Rev. Ecol. Evol. Syst. https://doi.org/10.1146/annurev.ecolsys.39.110707.173406

Currie, J.C., Sink, K.J., Le Noury, P., Branch, G.M., 2012. Comparing fish communities in sanctuaries, partly protected areas and open-access reefs in South-East Africa. African J. Mar. Sci. https://doi.org/10.2989/1814232X.2012.709963

Curtis-quick, J.A., Ahmadia, G.N., Smith, D.J., 2012. Feeding plasticity of reef fish. Proc. 12th Int. Coral Reef Symp. Cairns, Aust.

Dahlgren, C.P., Eggleston, D.B., 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology. https://doi.org/10.1890/0012-9658(2000)081[2227:EPUOHS]2.0.CO;2

Daly, R., Smale, M.J., Cowley, P.D., Froneman, P.W., 2014. Residency patterns and migration dynamics of adult bull sharks (Carcharhinus leucas) on the east coast of Southern Africa. PLoS One. https://doi.org/10.1371/journal.pone.0109357

Daly, R., Smale, M.J., Singh, S., Anders, D., Shivji, M., Clare, C.A., Lea, J.S.E., Sousa, L.L., Wetherbee, B.M., Fitzpatrick, R., Clarke, C.R., Sheaves, M., Barnett, A., 2018. Refuges and risks: Evaluating the benefits of an expanded MPA network for mobile apex predators. Divers. Distrib. https://doi.org/10.1111/ddi.12758

Dames, V., Bernard, A., Floros, C., Mann, B., Speed, C., Maggs, J., Laing, S., Meekan, M., Olbers, J., 2019. Zonation and reef size significantly influence fish population structure in an established marine protected area, iSimangaliso Wetland Park, South Africa. Ocean Coast. Manag. https://doi.org/10.1016/j.ocecoaman.2019.105040

Darling, E.S., Côté, I.M., 2018. Seeking resilience in marine ecosystems. Science (80-.). https://doi.org/10.1126/science.aas9852

Darling, E.S., Graham, N.A.J., Januchowski-Hartley, F.A., Nash, K.L., Pratchett, M.S., Wilson, S.K., 2017a. Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs. https://doi.org/10.1007/s00338-017-1539-z

Darling, E.S., Graham, N.A.J., Januchowski-Hartley, F.A., Nash, K.L., Pratchett, M.S., Wilson, S.K., 2017b. Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs 36, 561–575. https://doi.org/10.1007/s00338-017-1539-z

Davis, J.P., Pitt, K.A., Fry, B., Olds, A.D., Connolly, R.M., 2014. Seascape-scale trophic links for fish on inshore coral reefs. Coral Reefs 33, 897–907. https://doi.org/10.1007/s00338-014-1196-4

Davis, W.P., Birdsong, R.S., 1973. Coral reef fishes which forage in the water column. Helgoländer Wissenschaftliche Meeresuntersuchungen. https://doi.org/10.1007/BF01609520

de Arruda Almeida, B., Green, A.J., Sebastián-González, E., dos Anjos, L., 2018. Comparing species richness, functional diversity and functional composition of waterbird communities along environmental gradients in the neotropics. PLoS One 13, 1–18. https://doi.org/10.1371/journal.pone.0200959

Denis, V., Ribas-Deulofeu, L., Sturaro, N., Kuo, C.Y., Chen, C.A., 2017. A functional approach to the structural complexity of coral assemblages based on colony morphological features. Sci. Rep. 7, 1–11. https://doi.org/10.1038/s41598-017-10334-w

Dent, F., Clarke, S., 2015. State of the global market for shark products. FAO Fish. Aquac. Tech. Pap. No. 590.

Di Santo, V., Bennett, W.A., 2011. Effect of rapid temperature change on resting routine metabolic rates of two benthic elasmobranchs. Fish Physiol. Biochem. https://doi.org/10.1007/s10695-011-9490-3

Diaz-Pulido, G., McCook, L.J., Dove, S., Berkelmans, R., Roff, G., Kline, D.I., Weeks, S., Evans, R.D., Williamson, D.H., Hoegh-Guldberg, O., 2009. Doom and Boom on a Resilient Reef: Climate Change, Algal Overgrowth and Coral Recovery. PLoS One. https://doi.org/10.1371/journal.pone.0005239

Díaz, S., Cabido, M., 2001. Vive la différence: Plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. https://doi.org/10.1016/S0169-5347(01)02283-2

Done, T.J., 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia. https://doi.org/10.1007/BF00008211

Dulvy, N.K., Freckleton, R.P., Polunin, N.V.C., 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. Ecol. Lett. https://doi.org/10.1111/j.1461-0248.2004.00593.x

Edgar, G.J., Robertson, A.I., 1992. The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and process in a Western Australian Amphibolis bed. J. Exp. Mar. Bio. Ecol. https://doi.org/10.1016/0022-0981(92)90107-L

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature. https://doi.org/10.1038/nature13022

Edwards, A.J., 1992. FAO Species Catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. Mar. Pollut. Bull. https://doi.org/10.1016/0025-326x(92)90599-2

Ellis, D.M., DeMartini, E.E., 1995. Evaluation of a video camera technique for indexing abundances of juvenile pink snapper, Pristipomoides filamentosus, and other Hawaiian insular shelf fishes. Fish. Bull. 93, 67-77.

Eros, T., Heino, J., Schmera, D., Rask, M., 2009. Characterising functional trait diversity and trait-environment relationships in fish assemblages of boreal lakes. Freshw. Biol. https://doi.org/10.1111/j.1365-2427.2009.02220.x

Evans, R.D., Wilson, S.K., Field, S.N., Moore, J.A.Y., 2014. Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. Mar. Biol. https://doi.org/10.1007/s00227-013-2362-x

Ferreira, C.E.L., Gonçalves, J.E.A., Coutinho, R., 2001. Community structure of fishes and habitat complexity on a tropical rocky shore. Environ. Biol. Fishes. https://doi.org/10.1023/A:1011609617330

Floros, C., 2010. An evaluation of coral reef fish communities in South African marine protected areas (Doctoral dissertation).

Floros, C., Schleyer, M.H., 2017. The functional importance of Acropora austera as nursery areas for juvenile reef fish on South African coral reefs. Coral Reefs. https://doi.org/10.1007/s00338-016-1499-8

Floros, C., Schleyer, M.H., Maggs, J.Q., 2013. Fish as indicators of diving and fishing pressure on high-latitude coral reefs. Ocean Coast. Manag. 84, 130–139. https://doi.org/10.1016/j.ocecoaman.2013.08.005

Fogarty, B.M.J., Sci-, A.A., Hole, W., Sci-, N.F., Murawski, S. a, Spring, S., 2004. Do Marine Protected Areas Really Work ? Ocean. Mag. 43(2), 1-3.

Friedlander, A.M., DeMartini, E.E., 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps230253

Friedlander, A.M., Parrish, J.D., 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J. Exp. Mar. Bio. Ecol. https://doi.org/10.1016/S0022-0981(97)00164-0

Frimpong, E.A., Angermeier, P.L., 2010. Trait-based approaches in the analysis of stream fish communities. Am. Fish. Soc. Symp. (73) 109-136.

Froese, R., Pauly, D., 2019. Fishbase. World Wide Web electronic publication. [WWW Document]. FishBase.

Fulton, E.A., Smith, A.D.M., Punt, A.E., 2005. Which ecological indicators can robustly detect effects of fishing?, in: ICES Journal of Marine Science. https://doi.org/10.1016/j.icesjms.2004.12.012

Gaither, M.R., Rocha, L.A., 2013. Origins of species richness in the Indo-Malay-Philippine biodiversity hotspot: Evidence for the centre of overlap hypothesis. J. Biogeogr. https://doi.org/10.1111/jbi.12126

Garnier, E., Navas, M.L., 2012. A trait-based approach to comparative functional plant ecology: Concepts, methods and applications for agroecology. A review. Agron. Sustain. Dev. https://doi.org/10.1007/s13593-011-0036-y

Gaston, K.J., 2000. Global patterns in biodiversity. Nature. https://doi.org/10.1038/35012228

Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: The fishery effects of marine reserves. Trends Ecol. Evol. https://doi.org/10.1016/S0169-5347(03)00189-7

Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., Geldmann, J., Holst, S., Jensen, O.P., White, A.T., Basurto, X., Coad, L., Gates, R.D., Guannel, G., Mumby, P.J., Thomas, H., Whitmee, S., Woodley, S., Fox, H.E., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. Nature. https://doi.org/10.1038/nature21708

Gorham, J.C., Alevizon, W.S., 1989. Habitat complexity an the abundance of juvenile fishes residing on small scale artificial reefs. Bull. Mar. Sci. 44(2), 662-665

Gorman, O.T., Karr, J.R., 1978. Habitat Structure and Stream Fish Communities. Ecology. https://doi.org/10.2307/1936581

Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D., Wilson, S.K., 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature. https://doi.org/10.1038/nature14140

Graham, N.A.J., Nash, K.L., 2013. The importance of structural complexity in coral reef ecosystems. Coral Reefs. https://doi.org/10.1007/s00338-012-0984-y

Gratwicke, B., Speight, M.R., 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. J. Fish Biol. 66, 650–667. https://doi.org/10.1111/j.0022-1112.2005.00629.x

Gratwicke, Brian, Speight, M.R., 2005. Effects of habitat complexity on Caribbean marine fish assemblages. Mar. Ecol. Prog. Ser. 292, 301–310. https://doi.org/10.3354/meps292301

Greenstreet, S.P.R., Rogers, S.I., 2006. Indicators of the health of the North Sea fish community: identifying reference levels for an ecosystem approach to management. ICES J. Mar. Sci. https://doi.org/10.1016/j.icesjms.2005.12.009

Grossman, G.D., Ratajczak, R.E., Crawford, M., Freeman, M.C., 1998. Assemblage organization in stream fishes: Effects of environmental variation and interspecific interactions. Ecol. Monogr. https://doi.org/10.1890/0012-9615(1998)068[0395:AOISFE]2.0.CO;2

Hall, S.J., Mainprize, B., 2004. Towards ecosystem-based fisheries management. Fish Fish. https://doi.org/10.1111/j.1467-2960.2004.00133.x

Halpern, B.S., Lester, S.E., Kellner, J.B., 2009. Spillover from marine reserves and the replenishment of fished stocks. Environ. Conserv. https://doi.org/10.1017/S0376892910000032

Harding, J.M., Mann, R., 2001. Oyster reefs as fish habitat: Opportunistic use of restored reefs by transient fishes. J. Shellfish Res. 20(3), 951.

Harvey, E.S., Newman, S.J., McLean, D.L., Cappo, M., Meeuwig, J.J., Skepper, C.L., 2012. Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. Fish. Res. https://doi.org/10.1016/j.fishres.2012.01.026

Harvey, E.S., Shortis, M.R., 1998. Calibration Stability of an Underwater Stereo Video System : Implications for Measurement Accuracy and Precision. Mar. Technol. Soc. J. https://doi.org/10.1016/0306-4522(92)90504-U

Hattori, A., Shibuno, T., 2015. Total volume of 3D small patch reefs reflected in aerial photographs can predict total species richness of coral reef damselfish assemblages on a shallow back reef. Ecol. Res. https://doi.org/10.1007/s11284-015-1268-0

Hawkins, J.P., Roberts, C.M., 1992. Effects of recreational SCUBA diving on fore-reef slope communities of coral reefs. Biol. Conserv. https://doi.org/10.1016/0006-3207(92)91045-T

Hawkins, J.P., Roberts, C.M., Kooistra, D., Buchan, K., White, S., 2005. Sustainability of scuba diving tourism on coral reefs of Saba. Coast. Manag. https://doi.org/10.1080/08920750500217518

Heck, K.L., Crowder, L.B., 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. Habitat Struct. https://doi.org/10.1007/978-94-011-3076-9_14

Henrich Bruggemann, J., Rodier, M., Guillaume, M.M.M., Andréfouët, S., Arfi, R., Cinner, J.E., Pichon, M., Ramahatratra, F., Rasoamanendrika, F., Zinke, J., McClanahan, T.R., 2012. Wicked social-ecological problems forcing unprecedented change on the latitudinal margins of coral reefs: The Case of southwest Madagascar. Ecol. Soc. https://doi.org/10.5751/ES-05300-170447

Henriques, S., Pais, M.P., Vasconcelos, R.P., Murta, A., Azevedo, M., Costa, M.J., Cabral, H.N., 2014. Structural and functional trends indicate fishing pressure on marine fish assemblages. J. Appl. Ecol. 51, 623–631. https://doi.org/10.1111/1365-2664.12235

Heron, S.F., Eakin, C.M., Douvere, F., Anderson, K., Day, J.C., Geiger, E., Hoegh-Guldberg, O., Van Hooidonk, R., Hughes, T., Marshall, P., Obura, D., 2017. Impacts of Climate Change on World Heritage Coral Reefs: A First Global Scientific Assessment. Paris, UNESCO World Herit. Centre. 1–14.

Heyns-Veale, E.R., Richoux, N.B., Bernard, A.T.F., Götz, A., 2019. Protected nearshore shallow and deep subtidal rocky reef communities differ in their trophic diversity but not their nutritional condition. African J. Mar. Sci. https://doi.org/10.2989/1814232X.2019.1580614

Hijmans, R., Sumner, M., Macqueen, D., Lemon, J., Brien, J.O., Rourke, J.O., 2020. Package ‘ sp ’ R.

Hill, N.A., Barrett, N., Lawrence, E., Hulls, J., Dambacher, J.M., Nichol, S., Williams, A., Hayes, K.R., 2014. Quantifying fish assemblages in large, offshore marine protected areas: An Australian case study. PLoS One. https://doi.org/10.1371/journal.pone.0110831

Hobson, E.S., 1974. Feeding relationship of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull. 72(4), 915-1031.

Hodge, J.R., Read, C.I., van Herwerden, L., Bellwood, D.R., 2012. The role of peripheral endemism in species diversification: Evidence from the coral reef fish genus Anampses (Family: Labridae). Mol. Phylogenet. Evol. https://doi.org/10.1016/j.ympev.2011.11.007

Hodgson, J.A., Moilanen, A., Wintle, B.A., Thomas, C.D., 2011. Habitat area, quality and connectivity: Striking the balance for efficient conservation. J. Appl. Ecol. 48, 148–152. https://doi.org/10.1111/j.1365-2664.2010.01919.x

Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world’s coral reefs. Mar. Freshw. Res. https://doi.org/10.1071/MF99078

Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world’s marine ecosystems. Science (80-.). https://doi.org/10.1126/science.1189930

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A., Hatziolos, M.E., 2007. Coral reefs under rapid climate change and ocean acidification. Science. https://doi.org/10.1126/science.1152509

Hoeinghaus, D.J., Winemiller, K.O., Birnbaum, J.S., 2007. Local and regional determinants of stream fish assemblage structure: Inferences based on taxonomic vs. functional groups. J. Biogeogr. https://doi.org/10.1111/j.1365-2699.2006.01587.x

Hoeksema, B.W., 2007. Delineation of the Indo-Malayan Centre of Maximum Marine Biodiversity: The Coral Triangle. https://doi.org/10.1007/978-1-4020-6374-9_5

Holbrook, S.J., Brooks, A.J., Schmitt, R.J., 2002. Predictability of fish assemblages on coral patch reefs, in: Marine and Freshwater Research. https://doi.org/10.1071/MF01137

Holland, K.N., Lowe, C.G., Wetherbee, B.M., 1996. Movements and dispersal patterns of blue trevally (Caranx melampygus) in a fisheries conservation zone. Fish. Res. https://doi.org/10.1016/0165-7836(95)00442-4

Horan, D.L., Kershner, J.L., Hawkins, C.P., Crowl, T.A., 2000. Effects of Habitat Area and Complexity on Colorado River Cutthroat Trout Density in Uinta Mountain Streams. Trans. Am. Fish. Soc. https://doi.org/10.1577/1548-8659(2000)129<1250:eohaac>2.0.co;2

Hulot, F.D., Lacroix, G., Lescher-Moutoué, F., Loreau, M., 2000. Functional diversity governs ecosystem response to nutrient enrichment. Nature. https://doi.org/10.1038/35012591

Huntington, B.E., Lirman, D., 2012. Species-area relationships in coral communities: Evaluating mechanisms for a commonly observed pattern. Coral Reefs 31, 929–938. https://doi.org/10.1007/s00338-012-0917-9

Jabado, R.W., 2018. The fate of the most threatened order of elasmobranchs: Shark-like batoids (Rhinopristiformes) in the Arabian Sea and adjacent waters. Fish. Res. https://doi.org/10.1016/j.fishres.2018.03.022

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science (80-.). https://doi.org/10.1126/science.1059199

Jain, M., Flynn, D.F.B., Prager, C.M., Hart, G.M., Devan, C.M., Ahrestani, F.S., Palmer, M.I., Bunker, D.E., Knops, J.M.H., Jouseau, C.F., Naeem, S., 2014. The importance of rare species: A trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. Ecol. Evol. https://doi.org/10.1002/ece3.915

Jenkins, G.P., Black, K.P., Wheatley, M.J., Hatton, D.N., 1997. Temporal and spatial variability in recruitment of a temperate, seagrass-associated fish is largely determined by physical processes in the pre- and post-settlement phases. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps148023

Jenkins, G.P., Hamer, P.A., 2001. Spatial variation in the use of seagrass and unvegetated habitats by post-settlement King George whiting (Percoidei: Sillaginidae) in relation to meiofaunal distribution and macrophyte structure. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps224219

Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. https://doi.org/10.1016/s0065-2881(08)60212-6

Jennings, S., Polunin, N.V.C., 1996. Effects of Fishing Effort and Catch Rate Upon the Structure and Biomass of Fijian Reef Fish Communities. J. Appl. Ecol. https://doi.org/10.2307/2404761

Joo, R., Salcedo, O., Gutierrez, M., Fablet, R., Bertrand, S., 2015. Defining fishing spatial strategies from VMS data: Insights from the world's largest monospecific fishery. Fish. Res. https://doi.org/10.1016/j.fishres.2014.12.004

Jouffray, J.B., Nyström, M., Norström, A. V., Williams, I.D., Wedding, L.M., Kittinger, J.N., Williams, G.J., 2015. Identifying multiple coral reef regimes and their drivers across the hawaiian archipelago. Philos. Trans. R. Soc. B Biol. Sci. 370, 1–8. https://doi.org/10.1098/rstb.2013.0268

Kelleher, G., Kenchington, R., 1991. Guidelines for Establishing Marine Protected Areas. IUCN, Gland. Switz. https://doi.org/10.1017/S0376892901290304

Kerwath, S.E., Winker, H., Götz, A., Attwood, C.G., 2013. Marine protected area improves yield without disadvantaging fishers. Nat. Commun. https://doi.org/10.1038/ncomms3347

Khalaf, M.A., Kochzius, M., 2002. Changes in trophic community structure of shore fishes at an industrial site in the Gulf of Aqaba, Red Sea. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps239287

King, J.R., McFarlane, G.A., 2003. Marine fish life history strategies: Applications to fishery management. Fish. Manag. Ecol. https://doi.org/10.1046/j.1365-2400.2003.00359.x

Knowlton, N., Jackson, J.B.C., 2008. Shifting baselines, local impacts, and global change on coral reefs. PLoS Biol. https://doi.org/10.1371/journal.pbio.0060054

Komyakova, V., Munday, P.L., Jones, G.P., 2013. Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. PLoS One. https://doi.org/10.1371/journal.pone.0083178

Kyne, P.M., Jabado, R.W., Rigby, C.L., Dharmadi, Gore, M.A., Pollock, C.M., Herman, K.B., Cheok, J., Ebert, D.A., Simpfendorfer, C.A., Dulvy, N.K., 2019a. The thin edge of the wedge: extremely high extinction risk in wedgefishes and giant guitarfishes. bioRxiv 595462. https://doi.org/10.1101/595462

Kyne, P.M., Jabado, R.W., Rigby, C.L., Dharmadi, Gore, M.A., Pollock, C.M., Herman, K.B., Cheok, J., Ebert, D.A., Simpfendorfer, C.A., Dulvy, N.K., 2019b. The thin edge of the wedge: extremely high extinction risk in wedgefishes and giant guitarfishes. bioRxiv 595462. https://doi.org/10.1101/595462

Laliberte, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. https://doi.org/10.1890/08-2244.1

Langlois, T.J., Harvey, E.S., Fitzpatrick, B., Meeuwig, J.J., Shedrawi, G., Watson, D.L., 2010. Cost-efficient sampling of fish assemblages: Comparison of baited video stations and diver video transects. Aquat. Biol. https://doi.org/10.3354/ab00235

Lara, E.N., González, E.A., 1998. The relationship between reef fish community structure and environmental variables in the southern Mexican Caribbean. J. Fish Biol. https://doi.org/10.1111/j.1095-8649.1998.tb01028.x

Laurans, M., Gascuel, D., Chassot, E., Thiam, D., 2004. Changes in the trophic structure of fish demersal communities in West Africa in the three last decades, in: Aquatic Living Resources. https://doi.org/10.1051/alr:2004023

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A., Bonis, A., 2008. Assessing functional diversity in the field - Methodology matters! Funct. Ecol. https://doi.org/10.1111/j.1365-2435.2007.01339.x

Leathwick, J.R., Elith, J., Chadderton, W.L., Rowe, D., Hastie, T., 2008. Dispersal, disturbance and the contrasting biogeographies of New Zealand's diadromous and non-diadromous fish species. J. Biogeogr. https://doi.org/10.1111/j.1365-2699.2008.01887.x

Lecchini, D., Galzin, R., 2005. Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). Mar. Biol. https://doi.org/10.1007/s00227-004-1543-z

Lee, C.L., Wen, C.K.C., Huang, Y.H., Chung, C.Y., Lin, H.J., 2019. Ontogenetic habitat usage of juvenile carnivorous fish among seagrass-coral mosaic habitats. Diversity. https://doi.org/10.3390/d11020025

Lester, S.E., Halpern, B.S., 2008. Biological responses in marine no-take reserves versus partially protected areas. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps07599

Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S., Warner, R.R., 2009a. Biological effects within no-take marine reserves: A global synthesis. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps08029

Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S., Warner, R.R., 2009b. Biological effects within no-take marine reserves: A global synthesis. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps08029

Levin, P.S., Hay, M.E., 2002. Fish-seaweed association on temperate reefs: Do small-scale experiments predict large-scale patterns? Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps232239

Levin, P.S., Hay, M.E., 1996. Responses of temperate reef fishes to alterations in algal structure and species composition. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps134037

Lewis, A.R., 1998. Effects of experimental coral disturbance on the population dynamics of fishes on large patch reefs. J. Exp. Mar. Bio. Ecol. https://doi.org/10.1016/S0022-0981(98)00087-2

Light, P.R., Jones, G.P., 1997. Habitat preference in newly settled coral trout (Plectropomus leopardus, Serranidae). Coral Reefs. https://doi.org/10.1007/s003380050065

Lingo, M.E., Szedlmayer, S.T., 2006. The influence of habitat complexity on reef fish communities in the northeastern Gulf of Mexico. Environ. Biol. Fishes. https://doi.org/10.1007/s10641-006-9009-4

Link, J.S., 2002. What does ecosystem-based fisheries management mean? Fisheries , *27*(4), 18-21.

Lirman, D., 1994. Ontogenetic shifts in habitat preferences in the three-spot damselfish, Stegasees planifions (Cuvier), in Roatan Island, Honduras. J. Exp. Mar. Bio. Ecol. https://doi.org/10.1016/0022-0981(94)90080-9

Logez, M., Bady, P., Melcher, A., Pont, D., 2013. A continental-scale analysis of fish assemblage functional structure in European rivers. Ecography (Cop.). https://doi.org/10.1111/j.1600-0587.2012.07447.x

Lubchenco, J., Palumbi, S.R., Gaines, S.D., Andelman, S., 2003. Plugging a hole in the ocean: The emerging science of marine reserves. Ecol. Appl. https://doi.org/10.1890/1051-0761(2003)013[0003:PAHITO]2.0.CO;2

Luckhurst, B.E., Luckhurst, K., 1978. Analysis of the influence of substrate variables on coral reef fish communities. Mar. Biol. https://doi.org/10.1007/BF00455026

MacNeil, M.A., Graham, N.A.J., Cinner, J.E., Wilson, S.K., Williams, I.D., Maina, J., Newman, S., Friedlander, A.M., Jupiter, S., Polunin, N.V.C., McClanahan, T.R., 2015. Recovery potential of the world's coral reef fishes. Nature 520, 341–344. https://doi.org/10.1038/nature14358

Madin, J.S., Hoogenboom, M.O., Connolly, S.R., Darling, E.S., Falster, D.S., Huang, D., Keith, S.A., Mizerek, T., Pandolfi, J.M., Putnam, H.M., Baird, A.H., 2016. A Trait-Based Approach to Advance Coral Reef Science. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2016.02.012

Mangi, S.C., Roberts, C.M., Rodwell, L.D., 2007. Reef fisheries management in Kenya: Preliminary approach using the driver-pressure-state-impacts-response (DPSIR) scheme of indicators. Ocean Coast. Manag. https://doi.org/10.1016/j.ocecoaman.2006.10.003

Mann, B.Q., 2013. Southern African Marine Linefish Species Profiles, Biodiversity for Life.Special Publication No.9. https://doi.org/http://dx.doi.org/10.1016/j.marpol.2013.05.006

Mann, B.Q., Cowley, P.D., Dunlop, S.W., Potts, W.M., 2018. Is catch-and-release shore angling compatible with the conservation goals of marine protected areas? A case study from the iSimangaliso Wetland Park in South Africa. Fish. Res. https://doi.org/10.1016/j.fishres.2018.07.021

Mann, B.Q., Winker, H., Maggs, J.Q., Porter, S.N., 2016. Monitoring the recovery of a previously exploited surf-zone fish community in the St Lucia Marine Reserve, South Africa, using a no-take sanctuary area as a benchmark. African J. Mar. Sci. https://doi.org/10.2989/1814232X.2016.1224779

Marti J. Anderson, 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

McClanahan, T.R., 1997. Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. J. Exp. Mar. Bio. Ecol. https://doi.org/10.1016/S0022-0981(97)00069-5

McClanahan, T.R., 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. Coral Reefs. https://doi.org/10.1007/BF00303637

McClanahan, T.R., Arthur, R., 2001. The effect of marine reserves and habitat on populations of East African coral reef fishes. Ecol. Appl. https://doi.org/10.1890/1051-0761(2001)011[0559:TEOMRA]2.0.CO;2

McClanahan, T.R., Graham, N.A.J., Calnan, J.M., MacNeil, M.A., 2007. Toward pristine biomass: Reef fish recovery in coral reef marine protected areas in Kenya. Ecol. Appl. https://doi.org/10.1890/06-1450

Mcclanahan, T.R., Hicks, C.C., 2011. Changes in life history and ecological characteristics of coral reef fish catch composition with increasing fishery management. Fish. Manag. Ecol. https://doi.org/10.1111/j.1365-2400.2010.00768.x

McClanahan, T.R., Uku, J.N., Machano, H., 2002. Effect of macroalgal reduction on coral-reef fish in the Watamu Marine National Park, Kenya, in: Marine and Freshwater Research. https://doi.org/10.1071/MF01112

McGehee, M.A., 1994. Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps105243

McIntosh, A.R., McHugh, P.A., Plank, M.J., Jellyman, P.G., Warburton, H.J., Greig, H.S., 2018. Capacity to support predators scales with habitat size. Sci. Adv. 4, 1–8. https://doi.org/10.1126/sciadv.aap7523

Mclean, D.L., Harvey, E.S., Meeuwig, J.J., 2011. Declines in the abundance of coral trout (Plectropomus leopardus) in areas closed to fishing at the Houtman Abrolhos Islands, Western Australia. J. Exp. Mar. Bio. Ecol. https://doi.org/10.1016/j.jembe.2011.06.009

McManus, J.W., Polsenberg, J.F., 2004. Coral-algal phase shifts on coral reefs: Ecological and environmental aspects. Prog. Oceanogr. https://doi.org/10.1016/j.pocean.2004.02.014

Mees, J., Boxshall, G.A., Costello, M.J., Hernandez, F., Bailly, N., Boury-Esnault, N., Gofas, S., Horton, T., Klautau, M., Kroh, A., Paulay, G., Poore, G., Stöhr, S., Decock, W., Dekeyzer, S., Trias Verbeeck, A. Vandepitte, L. Vanhoorne, B., Adams, M.J., Adlard, R., Adriaens, P., Agatha, S., Ahn, K.J., Ahyong, S., Alvarez, B., Alvarez, F., Anderson, G., Angel, M., Arango, C., Artois, T., Atkinson, S., Barber, A., Bartsch, I., Bellan-Santini, D., Berta, A., Bieler, R., Bitner, M.A., Błażewicz-Paszkowycz, M., Bock, P., Böttger-Schnack, R., Bouchet, P., Boyko, C.B., Brandão, S.N., Bray, R., Bruce, N.L., Cairns, S., Campinas Bezerra, T.N., Cárdenas, P., Carrera-Parra, L.F., Carstens, E., Catalano, S.; Cedhagen, T., Chan, B.K., Chan, T.Y., Cheng, L., Churchill, M., Coleman, C.O., Collins, A.G., Crandall, K.A., Cribb, T., Dahdouh-Guebas, F., Daneliya, M., Dauvin, J.C., Davie, P., De Grave, S., Defaye, D., D'Hondt, J.L., Dijkstra, H., Dohrmann, M., Dolan, J., Doner, S., Eibye-Jacobsen, D., Eitel, M., Emig, C.; Epler, J., Faber, M., Fautin, D., Feist, S., Fernández-Rodríguez, V., Fišer, C., Fonseca, G., Foster, W., Frank, J.H., Fransen, C., Furuya, H., Galea, H., Gasca, R., Gaviria-Melo, S., Gerken, S., Gheerardyn, H., Gibson, D., Gil, J., Gittenberger, A., Glasby, C., Glover, A., González Solís, D., Gordon, D., Grabowski, M., Guerra-García, J.M., Guidetti, R., Guilini, K., Guiry, M.D., Hajdu, E., Hallermann, J., Harris, L., Hayward, B., Hendrycks, E., Ho, J. s., Høeg, J., Holovachov, O., Holsinger, J., Hooper, J., Hughes, L., Hummon, W., Iseto, T., Ivanenko, S., Iwataki, M., Janussen, D., Jarms, G., Jazdzewski, K., Just, J., Kamaltynov, R.M., Kaminski, M., Karanovic, I., Kim, Y.H., King, R., Kirk, P., Kolb, J., Kotov, A., Krapp-Schickel, T., Kremenetskaia, A., Kristensen, R., Lambert, G., Lazarus, D., LeCroy, S., Leduc, D., Lefkowitz, E.J., Lemaitre, R., Londoño Mesa, M.H., Lörz, A.N., Lowry, J., Lundholm, N., Macpherson, E., Madin, L., Mah, C., Manconi, R., Mapstone, G., Marshall, B., Marshall, D.J., McInnes, S., Meland, K., Merrin, K., Messing, C.G., Miljutin, D., Mills, C., Mokievsky, V., Molodtsova, T., Mooi, R., Morandini, A.C., Moreira da Rocha, R., Moretzsohn, F., Mortelmans, J., Mortimer, J., Nealova, L., Neubauer, T.A., Neuhaus, B., Ng, P., Nielsen, C., Nishikawa, T., Norenburg, J., O'Hara, T., Opresko, D., Osawa, M., Ota, Y., Parker, A., Patterson, D., Paxton, H., Perrier, V., Perrin, W., Pilger, J.F., Pisera, A., Polhemus, D., Pugh, P., Reimer, J.D., Reuscher, M., Rius, M., Rosenberg, G., Rützler, K., Rzhavsky, A., Saiz-Salinas, J., Salazar-Vallejo, S., Sames, B., Santos, S., Sartori, A.F., Satoh, A., Schatz, H., Schierwater, B., Schmidt-Rhaesa, A., Schneider, S., Schönberg, C., Schuchert, P., Self-Sullivan, C., Senna, A.R., Serejo, C., Shamsi, S., Sharma, J., Shenkar, N., Siegel, V., Sinniger, F., Sivell, D., Sket, B., Smit, H., Smol, N., Sterrer, W., Stienen, E., Strand, M., Suárez-Morales, E., Summers, M., Suttle, C., Swalla, B.J., Tabachnick, K.R., Taiti, S., Tandberg, A.H., Tang, D., Tasker, M., Tchesunov, A., ten Hove, H., ter Poorten, J.J., Thomas, J., Thuesen, E.V., Thurston, M., Thuy, B., Timi, J.T., Timm, T., Todaro, A., Turon, X., Tyler, S., Uetz, P., Vacelet, J., Vader, W., Väinölä, R., van der Meij, S.E., van Ofwegen, L., van Soest, R., Van Syoc, R., Vanaverbeke, J., Vonk, R., Vos, C., Walker-Smith, G., Walter, T.C., Watling, L., Whipps, C., White, K., Williams, G., Wyatt, N., Wylezich, C., Yasuhara, M., Zanol, J., Zeidler, W., 2015. World Register of Marine Species. Available from http//www.marinespecies.org. https://doi.org/10.14284/170

Mellin, C., Huchery, C., Caley, M.J., Meekan, M.G., Bradshaw, C.J.A., 2010. Reef size and isolation determine the temporal stability of coral reef fish populations. Ecology. https://doi.org/10.1890/10-0267.1

Meyer, C.G., 2007. The impacts of spear and other recreational fishers on a small permanent Marine Protected Area and adjacent pulse fished area. Fish. Res. https://doi.org/10.1016/j.fishres.2006.11.004

Meyer, C.G., Holland, K.N., Wetherbee, B.M., Lowe, C.G., 2001. Diet, resource partitioning and gear vulnerability of Hawaiian jacks captured in fishing tournaments. Fish. Res. https://doi.org/10.1016/S0165-7836(00)00285-X

Miller, K.I., Russ, G.R., 2014. Studies of no-take marine reserves: Methods for differentiating reserve and habitat effects. Ocean Coast. Manag. https://doi.org/10.1016/j.ocecoaman.2014.05.003

Mishal Gudka, David Obura, Jelvas Mwaura, Sean Porter, S.Y. and R.M., 2018. Impact of the 3rd Global Coral Bleaching Event on the Western Indian Ocean in 2016 I. Glob. Coral Reef Monit. Netw. (GCRMN)/Indian Ocean Comm. 1–72. https://doi.org/10.1016/j.ymeth.2011.08.008

Moore, A.B.M., 2017. Are guitarfishes the next sawfishes? Extinction risk and an urgent call for conservation action. Endanger. Species Res. https://doi.org/10.3354/esr00830

Mora, C., Andréfouët, S., Costello, M.J., Kranenburg, C., Rollo, A., Veron, J., Gaston, K.J., Myers, R.A., 2006. Coral reefs and the global network of marine protected areas. Science (80-.). https://doi.org/10.1126/science.1125295

Mora, C., Chittaro, P.M., Sale, P.F., Kritzer, J.P., Ludsin, S.A., 2003. Patterns and processes in reef fish diversity. Nature. https://doi.org/10.1038/nature01393

Mouillot, D., Dumay, O., Tomasini, J.A., 2007. Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. Estuar. Coast. Shelf Sci. https://doi.org/10.1016/j.ecss.2006.08.022

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender, M., Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L., Bellwood, D.R., 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc. Natl. Acad. Sci. U. S. A. 111, 13757–13762. https://doi.org/10.1073/pnas.1317625111

Mous, P.J., Pet-Soede, L., Erdman, M., Cesar, H.S.J., Sadovy, Y., Pet, J.S., 2000. Cyanide Fishing on Indonesian Coral Reefs for the Live Food Fish Market — What Is the Problem ?, in: Collected Essays on the Economics of Coral Reefs. 69-76.

Mumby, P.J., 2014. Stratifying herbivore fisheries by habitat to avoid ecosystem overfishing of coral reefs. J. Time Ser. Anal. https://doi.org/10.1111/faf.12078

Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C. V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., Buch, K., Box, S., Stoffle, R.W., Gill, A.B., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science (80-.). https://doi.org/10.1126/science.1121129

Munday, P.L., 2004. Competitive coexistence of coral-dwelling fishes: The lottery hypothesis revisited. Ecology. https://doi.org/10.1890/03-3100

Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. Nature. https://doi.org/10.1038/nature01610

Nash, K.L., Graham, N.A.J., 2016. Ecological indicators for coral reef fisheries management. Fish Fish. 17, 1029–1054. https://doi.org/10.1111/faf.12157

Nash, K.L., Graham, N.A.J., Wilson, S.K., Bellwood, D.R., 2013. Cross-scale Habitat Structure Drives Fish Body Size Distributions on Coral Reefs. Ecosystems 16, 478–490. https://doi.org/10.1007/s10021-012-9625-0

Nellemann, C., Corcoran, E., Duarte, C.M., Valdés, L., DeYoung, C., Fonseca, L., Grimsditch, G., 2009. Blue carbon. The role of healthy oceans in binding carbon, Environment. https://doi.org/10.1126/science.1210288

Neuheimer, A.B., Thresher, R.E., Lyle, J.M., Semmens, J.M., 2011. Tolerance limit for fish growth exceeded by warming waters. Nat. Clim. Chang. https://doi.org/10.1038/nclimate1084

Newton, K., Côté, I.M., Pilling, G.M., Jennings, S., Dulvy, N.K., 2007. Current and Future Sustainability of Island Coral Reef Fisheries. Curr. Biol. https://doi.org/10.1016/j.cub.2007.02.054

Ong, J.J.L., Nicholas Rountrey, A., Jane Meeuwig, J., John Newman, S., Zinke, J., Meekan, M.G., 2015. Contrasting environmental drivers of adult and juvenile growth in a marine fish: Implications for the effects of climate change. Sci. Rep. https://doi.org/10.1038/srep10859

Pankhurst, N.W., Munday, P.L., 2011. Effects of climate change on fish reproduction and early life history stages. Mar. Freshw. Res. https://doi.org/10.1071/MF10269

Papworth, S.K., Rist, J., Coad, L., Milner-Gulland, E.J., 2009. Evidence for shifting baseline syndrome in conservation. Conserv. Lett. https://doi.org/10.1111/j.1755-263X.2009.00049.x

Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol. Evol. https://doi.org/10.1016/S0169-5347(00)89171-5

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food webs. Science (80-.). https://doi.org/10.1126/science.279.5352.860

Pavlov, D.S., Kasumyan, A.O., 2000. Patterns and mechanisms of schooling behaviour in fish: A review. J. Ichthyol. 40(2), S163.

Pebesm, E., Benedikt Graeler, 2020. Package ‘ gstat .’

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: Back to basics and looking forward. Ecol. Lett. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Plass-Johnson, J.G., Taylor, M.H., Husain, A.A.A., Teichberg, M.C., Ferse, S.C.A., 2016. Non-random variability in functional composition of coral reef fish communities along an environmental gradient. PLoS One. https://doi.org/10.1371/journal.pone.0154014

Pollock, D.E., 1995. Changes in maturation ages and sizes in crustacean and fish populations. South African J. Mar. Sci. https://doi.org/10.2989/025776195095048 36

Pomeroy, R.S., Watson, L.M., Parks, J.E., Cid, G.A., 2005. How is your MPA doing? A methodology for evaluating the management effectiveness of marine protected areas. Ocean Coast. Manag. https://doi.org/10.1016/j.ocecoaman.2005.05.004

Porter, S.N., Branch, G.M., Sink, K.J., 2017. Sand-mediated divergence between shallow reef communities on horizontal and vertical substrata in the western Indian Ocean. African J. Mar. Sci. 39, 121–127. https://doi.org/10.2989/1814232X.2017.1303400

Porter, S.N., Schleyer, M.H., 2019. Environmental variation and how its spatial structure influences the cross-shelf distribution of high-latitude coral communities in South Africa. Diversity 11. https://doi.org/10.3390/d11040057

Porter, S.N., Schleyer, M.H., 2017. Long-term dynamics of a high-latitude coral reef community at Sodwana Bay, South Africa. Coral Reefs. https://doi.org/10.1007/s00338-016-1531-z

Pyron, M., Williams, L., Beugly, J., Jacquemin, S.J., 2011. The role of trait-based approaches in understanding stream fish assemblages. Freshw. Biol. https://doi.org/10.1111/j.1365-2427.2011.02596.x

Quétier, F., Lavorel, S., Thuiller, W., Davies, I., 2007. Plant-trait-based modeling assessment of ecosystem-service sensitivity to land-use change. Ecol. Appl. https://doi.org/10.1890/06-0750.1

Ramsay, P.J., Schleyer, M.H., Leuci, R., Muller, G.A., Celliers, L., Harris, J.M., 2006. The development of an expert marine geographical information system to provide an environmental and economic decision-support system for coastal tourism and leisure developments within the Lubombo Spatial Development Initiative 93.

Rice, J.C., 2005. Understanding fish habitat ecology to achieve conservation, in: Journal of Fish Biology. https://doi.org/10.1111/j.0022-1112.2005.00933.x

Richardson, L.E., Graham, N.A.J., Pratchett, M.S., Hoey, A.S., 2017. Structural complexity mediates functional structure of reef fish assemblages among coral habitats. Environ. Biol. Fishes 100, 193–207. https://doi.org/10.1007/s10641-016-0571-0

Rickel, S., Genin, A., 2005. Twilight transitions in coral reef fish: The input of light-induced changes in foraging behaviour. Anim. Behav. https://doi.org/10.1016/j.anbehav.2004.10.014

Riegl, B., 2003. Climate change and coral reefs: Different effects in two high-latitude areas (Arabian Gulf, South Africa), in: Coral Reefs. https://doi.org/10.1007/s00338-003-0335-0

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., 2019. MASS: support functions and datasets for venables and Ripley's MASS. R package version 7.3-51.5. Available from https://CRAN.R-project.org/package=MASS.

Roberts, C., Ormond, R., 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps041001

Roberts, C.M., Hawkins, J.P., 1999. Extinction risk in the sea. Trends Ecol. Evol. https://doi.org/10.1016/S0169-5347(98)01584-5

Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C., Werner, T.B., 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science (80-.). https://doi.org/10.1126/science.1067728

Rocha, L.A., Bowen, B.W., 2008. Speciation in coral-reef fishes. J. Fish Biol. https://doi.org/10.1111/j.1095-8649.2007.01770.x

Rocha, L.A., Rocha, C.R., Robertson, D.R., Bowen, B.W., 2008. Comparative phylogeography of Atlantic reef fishes indicates both origin and accumulation of diversity in the Caribbean. BMC Evol. Biol. https://doi.org/10.1186/1471-2148-8-157

Rosen, B.R., 1988. Biogeographic patterns: a perceptual overview. Anal. Biogeogr. https://doi.org/10.1007/978-94-009-1199-4_3

Rosenzweig, M.L., Ziv, Y., 1999. The echo pattern of species diversity: Pattern and processes. Ecography (Cop.). 22, 614–628. https://doi.org/10.1111/j.1600-0587.1999.tb00510.x

Rountrey, A.N., Coulson, P.G., Meeuwig, J.J., Meekan, M., 2014. Water temperature and fish growth: Otoliths predict growth patterns of a marine fish in a changing climate. Glob. Chang. Biol. https://doi.org/10.1111/gcb.12617

Russ, G., 1984. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps020023

Russ, G.R., 2002. Yet Another Review of Marine Reserves as Reef Fishery Management Tools, in: Coral Reef Fishes. https://doi.org/10.1016/B978-012615185-5/50024-4

Ruttenberg, B.I., Haupt, A.J., Chiriboga, A.I., Warner, R.R., 2005. Patterns, causes and consequences of regional variation in the ecology and life history of a reef fish. Oecologia. https://doi.org/10.1007/s00442-005-0150-0

Sainsbury, K., Sumaila, U.R., 2003. Incorporating ecosystem objectives into management of sustainable marine fisheries, including 'best practice'reference points and use of marine protected areas, in: Responsible Fisheries in the Marine Ecosystem. https://doi.org/10.1079/9780851996332.0343

Sala, E., Aburto-Oropeza, O., Reza, M., Paredes, G., López-Lemus, L.G., 2004. Fishing Down Coastal Food Webs in the Gulf of California. Fisheries. https://doi.org/10.1577/1548-8446(2004)29[19:fdcfwi]2.0.co;2

Sale, P.F., 2008. Management of coral reefs: Where we have gone wrong and what we can do about it. Mar. Pollut. Bull. https://doi.org/10.1016/j.marpolbul.2008.04.009

SALOMON, A.K., GAICHAS, S.K., SHEARS, N.T., SMITH, J.E., MADIN, E.M.P., GAINES, S.D., 2010. Key Features and Context-Dependence of Fishery-Induced Trophic Cascades. Conserv. Biol. https://doi.org/10.1111/j.1523-1739.2009.01436.x

Sandin, S.A., Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander, A.M., Konotchick, T., Malay, M., Maragos, J.E., Obura, D., Pantos, O., Paulay, G., Richie, M., Rohwer, F., Schroeder, R.E., Walsh, S., Jackson, J.B.C., Knowlton, N., Sala, E., 2008. Baselines and degradation of coral reefs in the Northern Line Islands. PLoS One. https://doi.org/10.1371/journal.pone.0001548

Santos, R.O., Rehage, J.S., Adams, A.J., Black, B.D., Osborne, J., Kroloff, E.K.N., 2017. Quantitative assessment of a data-limited recreational bonefish fishery using a time-series of fishing guides reports. PLoS One. https://doi.org/10.1371/journal.pone.0184776

Schleyer, M.H., Celliers, L., 2005. Modelling reef zonation in the Greater St Lucia Wetland Park, South Africa, in: Estuarine, Coastal and Shelf Science. https://doi.org/10.1016/j.ecss.2004.12.003

Schleyer, M.H., Celliers, L., 2003. Biodiversity on the marginal coral reefs of South Africa: what does the future hold? Zool. Verh. 345, 387-400.

Schleyer, M.H., Floros, C., Laing, S.C.S., Macdonald, A.H.H., Montoya-Maya, P.H., Morris, T., Porter, S.N., Seré, M.G., 2018. What can South African reefs tell us about the future of high-latitude coral systems? Mar. Pollut. Bull. https://doi.org/10.1016/j.marpolbul.2018.09.014

Schleyer, M.H., Tomalin, B.J., 2000. Damage on South African coral reefs and an assessment of their sustainable diving capacity using a fisheries approach. Bull. Mar. Sci. 67(3), 1025-1042.

Shears, N.T., Grace, R. V., Usmar, N.R., Kerr, V., Babcock, R.C., 2006. Long-term trends in lobster populations in a partially protected vs. no-take Marine Park. Biol. Conserv. https://doi.org/10.1016/j.biocon.2006.04.001

SHEARS, N.T., KUSHNER, D.J., KATZ, S.L., GAINES, S.D., 2012. Reconciling conflict between the direct and indirect effects of marine reserve protection. Environ. Conserv. https://doi.org/10.1017/s0376892912000082

Shin, Y.J., Rochet, M.J., Jennings, S., Field, J.G., Gislason, H., 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. ICES J. Mar. Sci. 62, 384–396. https://doi.org/10.1016/j.icesjms.2005.01.004

Sims, D.W., Southward, A.J., 2006. Dwindling fish numbers already of concern in 1883 [3]. Nature. https://doi.org/10.1038/439660c

Smith, C., Wootton, R.J., 2016. The remarkable reproductive diversity of teleost fishes. Fish Fish. https://doi.org/10.1111/faf.12116

Souter, D.W., Lindén, O., 2000. The health and future of coral reef systems. Ocean Coast. Manag. https://doi.org/10.1016/S0964-5691(00)00053-3

Stier, A.C., Hanson, K.M., Holbrook, S.J., Schmitt, R.J., Brooks, A.J., 2014. Predation and landscape characteristics independently affect reef fish community organization. Ecology 95, 1294–1307. https://doi.org/10.1890/12-1441.1

Thorson, J.T., Fonner, R., Haltuch, M.A., Ono, K., Winker, H., 2016. Accounting for spatiotemporal variation and fisher targeting when estimating abundance from multispecies fishery data [1]. Can. J. Fish. Aquat. Sci. https://doi.org/10.1139/cjfas-2015-0598

Thrush, S.F., Dayton, P.K., 2010. What Can Ecology Contribute to Ecosystem-Based Management? Ann. Rev. Mar. Sci. https://doi.org/10.1146/annurev-marine-120308-081129

Tratalos, J.A., Austin, T.J., 2001. Impacts of recreational SCUBA diving on coral communities of the Caribbean island of Grand Cayman. Biol. Conserv. https://doi.org/10.1016/S0006-3207(01)00085-4

Travisa, J., Coleman, F.C., Auster, P.J., Cury, P.M., Estes, J.A., Orensanz, J., Peterson, C.H., Power, M.E., Steneck, R.S., Wootton, J.T., 2014. Integrating the invisible fabric of nature into fisheries management. Proc. Natl. Acad. Sci. U. S. A. https://doi.org/10.1073/pnas.1305853111

Trebilco, R., Dulvy, N.K., Stewart, H., Salomon, A.K., 2015. The role of habitat complexity in shaping the size structure of a temperate reef fish community. Mar. Ecol. Prog. Ser. 532, 197–211. https://doi.org/10.3354/meps11330

Tunley, K., 2009. State of Management of South Africa ' s Marine Protected Areas. WWF South African Rep. Ser. 2009/Marin, 1–209. https://doi.org/10.1.1.69.962

Tuya, F., Cacabelos, E., Duarte, P., Jacinto, D., Castro, J.J., Silva, T., Bertocci, I., Franco, J.N., Arenas, F., Coca, J., Wernberg, T., 2012. Patterns of landscape and assemblage structure along a latitudinal gradient in ocean climate. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps09941

Tuya, F., Wernberg, T., Thomsen, M.S., 2009. Habitat structure affect abundances of labrid fishes across temperate reefs in south-western Australia. Environ. Biol. Fishes. https://doi.org/10.1007/s10641-009-9520-5

Unsworth, Richard K.F., Powell, A., Hukom, F., Smith, D.J., 2007. The ecology of Indo-Pacific grouper (Serranidae) species and the effects of a small scale no take area on grouper assemblage, abundance and size frequency distribution. Mar. Biol. https://doi.org/10.1007/s00227-007-0675-3

Unsworth, Richard K F, Wylie, E., Smith, D.J., Bell, J.J., 2007. Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. Estuar. Coast. Shelf Sci. https://doi.org/10.1016/j.ecss.2006.10.006

Vega Fernández, T., D'Anna, G., Badalamenti, F., Pérez-Ruzafa, A., 2007. Habitat connectivity as a factor affecting fish assemblages in temperate reefs. Aquat. Biol. https://doi.org/10.3354/ab00027

Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D.R., 2003. Response of forest plant species to land-use change: A life-history trait-based approach. J. Ecol. https://doi.org/10.1046/j.1365-2745.2003.00789.x

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology. https://doi.org/10.1890/07-1206.1

Villéger, S., Miranda, J.R., Mouillot, D., Hernandez, D.F., 2010. Contrasting changes in taxonomic vs . functional diversity of tropical fish communities after habitat degradation Author (s): Sébastien Villéger , Julia Ramos Miranda , Domingo Flores Hernández and David in taxonomic vs . functional of tropical diversit. Ecol. Soc. Am. 20, 1512–1522.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature. https://doi.org/10.1038/416389a

Wantiez, L., Chauvet, C., 2003. First data on community structure and trophic networks of Uvea coral reef fish assemblages (Wallis and Futuna, South Pacific Ocean). Cybium. 27(2), 83-100.

Watson, D.L., Harvey, E.S., Fitzpatrick, B.M., Langlois, T.J., Shedrawi, G., 2010. Assessing reef fish assemblage structure: How do different stereo-video techniques compare? Mar. Biol. https://doi.org/10.1007/s00227-010-1404-x

Wheeler, A., Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E., 1986. Fishes of the North-Eastern Atlantic and the Mediterranean. Vol. 1. Copeia. https://doi.org/10.2307/1444931

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. J. R. Stat. Soc. Ser. A (Statistics Soc. https://doi.org/10.1111/j.1467-985x.2010.00676_9.x

Wilkinson, C., 2002. *Status of Coral Reefs of the World : Coral Reefs*. Australian Institute of Marine Science.

Wilson, S.K., Burgess, S.C., Cheal, A.J., Emslie, M., Fisher, R., Miller, I., Polunin, N.V.C., Sweatman, H.P.A., 2008a. Habitat utilization by coral reef fish: Implications for specialists vs. generalists in a changing environment. J. Anim. Ecol. https://doi.org/10.1111/j.1365-2656.2007.01341.x

Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A., Cakacaka, A., Polunin, N.V.C., Rushton, S.P., 2008b. Exploitation and habitat degradation as agents of change within coral reef fish communities. Glob. Chang. Biol. https://doi.org/10.1111/j.1365-2486.2008.01696.x

Wilson, S.K., Graham, N.A.J., Polunin, N.V.C., 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Mar. Biol. https://doi.org/10.1007/s00227-006-0538-3

Winemiller, K.O., 2005. Life history strategies, population regulation, and implications for fisheries management, in: Canadian Journal of Fisheries and Aquatic Sciences. https://doi.org/10.1139/f05-040

Winker, H., Kerwath, S.E., Attwood, C.G., 2014. Proof of concept for a novel procedure to standardize multispecies catch and effort data. Fish. Res. https://doi.org/10.1016/j.fishres.2014.02.016

Winker, H., Kerwath, S.E., Attwood, C.G., 2013. Comparison of two approaches to standardize catch-per-unit-effort for targeting behaviour in a multispecies hand-line fishery. Fish. Res. https://doi.org/10.1016/j.fishres.2012.10.014

Wood, S.N., 2017. Generalized additive models: An introduction with R, second edition, Generalized Additive Models: An Introduction with R, Second Edition. https://doi.org/10.1201/9781315370279

Worm, B., Branch, T.A., 2012. The future of fish. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2012.07.005

Zakai, D., Chadwick-Furman, N.E., 2002. Impacts of intensive recreational diving on reef corals at Eilat, northern Red Sea. Biol. Conserv. https://doi.org/10.1016/S0006-3207(01)00181-1

Zuur, A.E., Ieno, E.N., Meesters, E.H.W.., 2009. Use R ! A Beginner's Guide to R, Media. https://doi.org/10.1007/978-0-387-93837-0

Zuur, A.F., Hilbe, J.M., Ieno, E.N., 2013. *A beginner'g guide to GLM and GLMM with R: a frequentist and Baysian perspective for ecologists.*, Beginner's Guide Series.

6 APPENDICES

List of Tables in Appendices Document:

List of Figures in Appendices Document:

6.1 APPENDIX FOR CHAPTER 2

Table 6.1: CATAMI (Collaborative and Annotation Tools for Analysis of Marine Imagery and Video) classifications employed in the analysis of the habitat images from the stereo-baited remote underwater video samples. The categories used to describe relief (Wilson et al., 2007) from the habitat images is also provided.

Classification	*Code*	*Description*
Relief		0 = 0 substrate slope 1=< 45 degree substrate slope 2 = 45 degree substrate slope 3 = > 45 degree substrate slope 4 = vertical wall with high structural complexity 5 = vertical wall with exceptional structural complexity
Ascidians	35000000	Commonly referred to as sea squirts these are sac-like marine invertebrate filter feeders. These organisms can occur as solitary and in colonial form, stalked and unstalked. Commonly occur in shallow waters.
Bryozoa	20000000	Also known as Polyzoa, Ectoprocta or commonly as lace corals. Bryozoans or 'lace corals'. There are two distinct forms; soft, articulated bryozoans and hard, rigid bryozoans. The organisms are usually found below the photic zone.
Consolidated	82001000	This describes a hard abiotic substrate which can either be rock, boulders or cobbles.
Crinoids	25001000	Commonly called feather stars. These organisms have many feathered arms radiating from a central disk and occurs in shallow water to great depths. There are two basic forms of crinoids: stalked and unstalked
Hydrocoral	11077000	A colonial organism with a calcareous skeleton resembling that of the true corals. Two forms exist; a hard, usually white, branching form and a massive or encrusting form.
Hydroids	11001000	These may appear feathery to fluffy, commonly planar and usually branched. The majority of hydroids are colonial, but when solitary they are usually translucent and can only be seen in images by their shadow.
Macroalgae	80300000	Commonly called seaweed, and includes all algae which is not unicellular. Can take on a variety of forms for example, filamentous, encrusting and sheet-like.
Mangrove	63345000	Mangroves are easy to distinguish and consist of shrubs or small trees that grow in coastal saline or brackish water. The term can also be applied to any tropical coastal vegetation consisting of such species. Their roots are typically exposed and become submerged on high tides.
Octocoral/ Black	11168901	The black corals and octocorals are combined as they share similar morphologies. Octocorals have often no skeleton (soft), but if a skeleton is obvious (e.g. gorgonians) it is typically covered by coloured tissue. Black corals often appear similar to gorgonians.
Seagrasses	63600901	These are flowering plants which occur in shallow and sheltered marine environments. Their elongate green leaves are easily distinguished from macroalgae. Seagrasses either have elliptical leaves or strap-like leaves

Classification	*Code*	*Description*
Sponges	10000000	Sponges are multicellular organisms with porous bodies and intricate channels which allow water circulation. Four morphologies exist; Encrusting, massive, hollow and erect.
Stony corals	11290000	Scleractinian stony corals or hard corals, are hexacorallids with an external skeleton. There are a wide variety of growth forms and may occur in cold-temperate to tropical marine habitats and at a wide range of depths.
True anemones	11229000	True anemones have a leathery body with a central mouth surrounded by a ring of tentacles and form close associations with clown fishes.
Unconsolidated	82001005	This describes a soft abiotic substrate which can either be mud, fine sand or course sand.
Zoanthids	11284000	Zoanthids fall under the same class as sea anemones, but differ by their colonial nature. There are variety of different colonizing formations and in numerous colours. These organisms have a leathery tissues, an obvious basal mat or stolons and individuals are often cylindrical.

Table 6.2: Results from the model summaries for Generalised Additive Models for the Functional Indices (FGR= Number of Functional Groups, Frich = Functional Richness, FDis = Functional Dispersion, FDiv = Functional Diversity and FEve = Functional Evenness) derived from functional analysis of Abundance data. Estimates, z and P values are given for parametric variables and edf (estimated degrees of freedom), Chi square and P values are also given for non-parametric variables. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Abundances	**FGR**			**FRich**			**FDis**		
	Estimate	*z*	*P*	*Estimate*	*z*	*P*	*Estimate*	*z*	*P*
Intercept	2.931	61.257	<0.001***	3.565	47.308	<0.001***	-0.321	-12.222	<0.001***
Zone CPZ	-0.343	-4.365	<0.001***	-0.380	-3.353	<0.001***	-0.053	-1.383	0.167
Zone St Lucia NTSZ	-0.283	-3.963	<0.001***	-0.406	-3.639	<0.001***	-0.028	-0.741	0.458
	edf	*Chi. Sq*	*P*	*edf*	*Chi. Sq*	*P*	*edf*	*Chi. Sq*	*P*
Visibility	1.979	11.540	<0.001***	1.770	12.319	<0.001***	1.269	3.360	0.062
Obstruction	0.487	0.942	0.122	1.064	2.471	0.083	0	0	1
Water Column	1.577	1.743	0.284	0.000	0.000	0.914	0	0	0.329
Temperature	5.068	13.891	<0.001***	3.955	5.440	0.206	1.267	3.205	0.067
Depth	0.393	0.537	0.229	0.725	1.703	0.115	0.271	0.315	0.277
PCO1	2.211	99.710	<0.001***	2.011	77.394	<0.001***	0.985	64.792	<0.001***
PCO2	1	6.887	0.003**	1	6.014	<0.001***	1.373	4.854	0.022*
PCO3	2.869	22.557	<0.001***	2.919	22.547	<0.001***	1.573	6.128	0.013*
Reef Size	3.012	5.577	0.107	0.811	0.856	0.321	0.102	0.114	0.284

	FDiv			**FEve**		
	Estimate	*z*	*P*	*Estimate*	*z*	*P*
Intercept	1.117	17.183	<0.001***	1.251	16.684	<0.001***
Zone CPZ	-0.009	-0.094	0.925	0.054	0.493	0.622
Zone St Lucia NTSZ	0.103	1.085	0.278	0.228	1.960	0.050*
	edf	*Chi. Sq*	*P*	*edf*	*Chi. Sq*	*P*
Visibility	1.568	6.140	0.014*	0.281	0.392	0.238
Obstruction	0.882	7.248	0.003**	0	0	1
Water Column	0	0	0.383	0	0	0.416
Temperature	1.321	2.677	0.112	0	0	0.392
Depth	1.780	14.026	<0.001***	0	0	1
PCO1	1.341	3.724	0.046*	0.422	0.729	0.018*
PCO2	0.006	0.006	0.272	0	0	1
PCO3	0.597	1.488	0.092	0	0	0.364
Reef Size	0.306	0.393	0.243	0	0	0.071

Table 6.3: Results from the model summaries for Generalised Additive Models for the Functional Indices (FGR= Number of Functional Groups, Frich = Functional Richness, FDis = Functional Dispersion, FDiv = Functional Diversity and FEve = Functional Evenness) derived from functional analysis of Length data. Estimates, z and P values are given for parametric variables and edf (estimated degrees of freedom), Chi square and P values are also given for non-parametric variables. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Lengths	**FGR**			**FRich**			**FDis**		
	Estimate	*z*	*P*	*Estimate*	*z*	*P*	*Estimate*	*z*	*P*
Intercept	2.532	44.583	<0.001***	3.248	35.155	<0.001***	-0.417	-14.451	<0.001***
Zone CPZ	-0.236	-2.756	0.006**	-0.302	-2.208	0.027*	0.053	1.292	0.196
Zone St Lucia NTSZ	-0.273	-3.395	<0.001***	-0.354	-2.709	0.007**	-0.065	-1.610	0.107
	edf	*Chi. Sq*	*P*	*edf*	*Chi. Sq*	*P*	*edf*	*Chi. Sq*	*P*
Visibility	1.447	6.282	0.0105*	1.073	7.805	0.002**	1.077	2.583	0.085
Obstruction	0	0	0.371	1.360	4.048	0.037*	0	0	0.461
Water Column	0	0	1	0	0	0.684	0.296	0.419	0.225
Temperature	0	0	0.549	7.031	15.178	0.022*	0.502	1.006	0.151
Depth	0.679	2.107	0.072	3.578	9.175	0.025*	0.942	16.171	<0.001***
PCO1	1.833	74.253	<0.001***	0.980	47.613	<0.001***	1.776	58.297	<0.001***
PCO2	2.777	4.979	0.088	1.019	2.378	0.081	0	0	0.788
PCO3	2.932	24.006	<0.001***	3.263	17.402	<0.001***	2.000	16.535	<0.001***
Reef Size	0	0	0.413	0	0	0.859	0	0	0.519

	FDiv			**FEve**		
	Estimate	*z*	*P*	*Estimate*	*z*	*P*
Intercept	1.218	22.874	<0.001***	1.044	17.234	<0.001***
Zone CPZ	-0.125	-1.677	0.094	0.224	2.492	0.013*
Zone St Lucia NTSZ	-0.138	-1.928	0.054	0.306	3.565	<0.001***
	edf	*Chi. Sq*	*P*	*edf*	*Chi. Sq*	*P*
Visibility	0.794	1.537	0.140	0	0	0.615
Obstruction	0	0	0.574	0	0	0.498
Water Column	0	0	1	0.627	1.681	0.100
Temperature	0	0	1	0	0	1
Depth	0	0	0.475	0	0	0.327
PCO1	1.622	11.065	<0.001***	1.855	11.067	<0.001***
PCO2	0	0	0.504	0	0	0.927
PCO3	0	0	0.515	0	0	0.371
Reef Size	0	0	0.469	0.785	3.652	0.029*

Table 6.4: Results from the model summaries for Generalised Additive Models for the Functional Indices (FGR= Number of Functional Groups, Frich = Functional Richness, FDis = Functional Dispersion, FDiv = Functional Diversity and FEve = Functional Evenness) derived from functional analysis of Stages data. Estimates, z and P values are given for parametric variables and edf (estimated degrees of freedom), Chi square and P values are also given for non-parametric variables. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Stages	**FGR**			**FRich**			**FDis**		
	Estimate	*z*	*P*	*Estimate*	*z*	*P*	*Estimate*	*z*	*P*
Intercept	2.793	38.301	<0.001***	3.451	41.198	<0.001***	-0.359	-16.506	<0.001***
Zone CPZ	-0.247	-2.231	0.026*	-0.469	-3.825	<0.001***	-0.058	-1.907	0.056
Zone St Lucia NTSZ	-0.282	-2.790	0.005**	-0.531	-4.432	<0.001***	-0.101	-3.351	<0.001***
	edf	*Chi. Sq*	*P*	*edf*	*Chi. Sq*	*P*	*edf*	*Chi. Sq*	*P*
Visibility	1.054	6.321	0.006**	1.797	12.971	<0.001***	1.185	3.459	0.048*
Obstruction	0.268	0.421	0.175	1.802	5.889	0.024*	0	0	0.847
Water Column	0	0	1	0	0	0.900	0.608	1.546	0.106
Temperature	7.301	15.330	0.027*	0	0	1	0.758	1.040	0.234
Depth	0.905	6.156	0.007**	2.413	6.430	0.039*	0	0	0.342
PCO1	1.966	68.027	<0.001***	0.994	40.945	<0.001***	2.314	56.401	<0.001***
PCO2	1.187	3.440	0.03*	2.868	6.639	0.049*	0	0	0.437
PCO3	2.836	22.712	<0.001***	3.337	21.794	<0.001***	0.676	2.083	0.051
Reef Size	0	0	0.654	0	0	0.961	0	0	0.903

	FDiv			**FEve**		
	Estimate	*z*	*P*	*Estimate*	*z*	*P*
Intercept	1.522	26.108	<0.001***	1.647	26.691	<0.001***
Zone CPZ	-0.066	-0.801	0.423	-0.058	-0.654	0.513
Zone St Lucia NTSZ	0	0.005	0.996	-0.011	-0.125	0.901
	edf	*Chi. Sq*	*P*	*edf*	*Chi. Sq*	*P*
Visibility	0.793	1.281	0.186	0.615	1.010	0.182
Obstruction	0	0	0.333	0	0	1.000
Water Column	1.099	4.280	0.027*	0.370	0.582	0.206
Temperature	0.634	1.709	0.095	0	0	0.858
Depth	0	0	1	0.002	0.002	0.313
PCO1	2.006	30.098	<0.001***	0.817	4.419	0.018*
PCO2	0	0	0.678	0	0	0.555
PCO3	0.732	2.706	0.039*	0.331	0.392	0.288
Reef Size	0	0	0.419	0.750	2.614	0.053

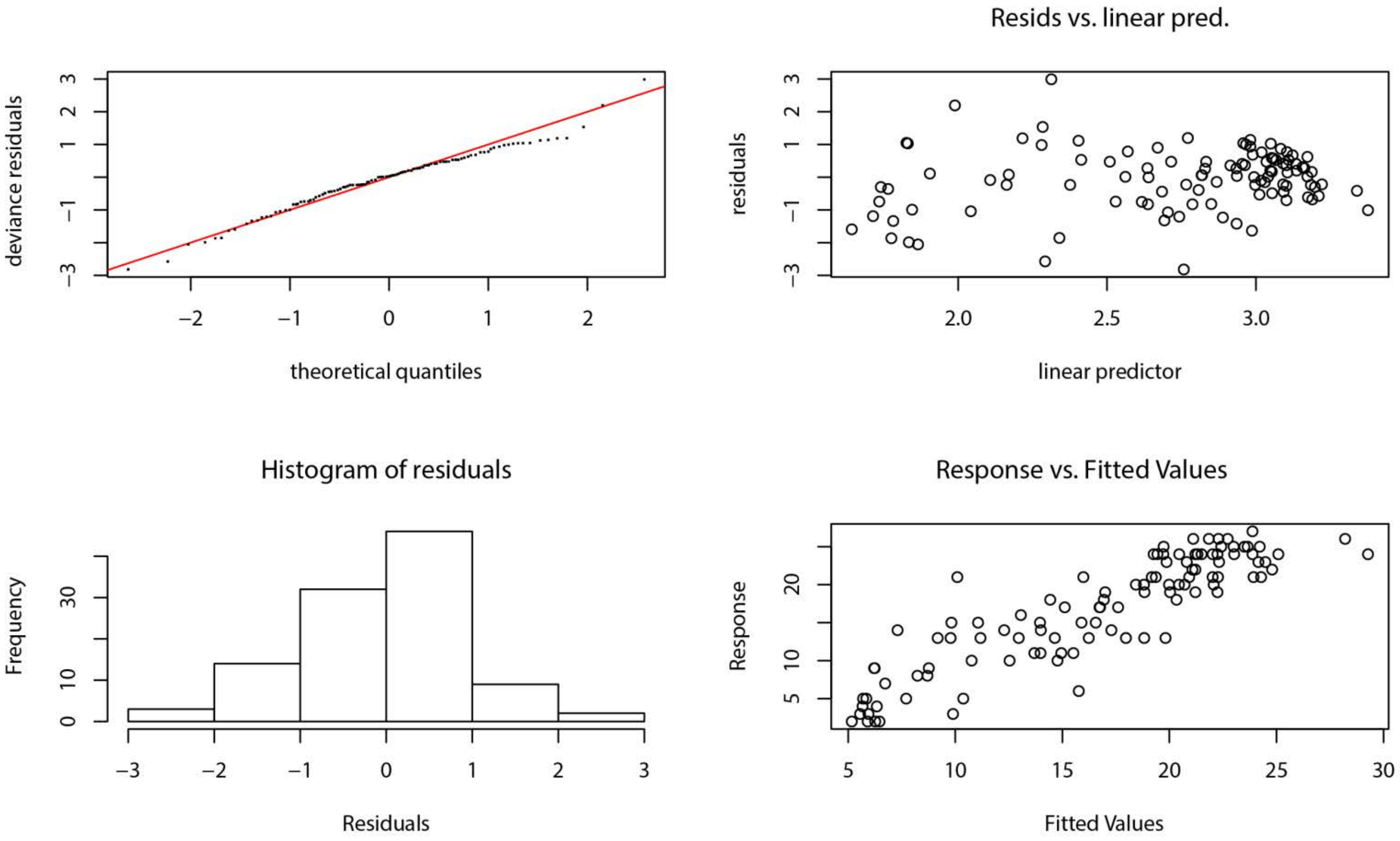


Figure: 6.1: Gam check for the number of functional groups modelled with the abundance data. Shows the deviance residuals versus fitted data for the Generalised Additive Model.

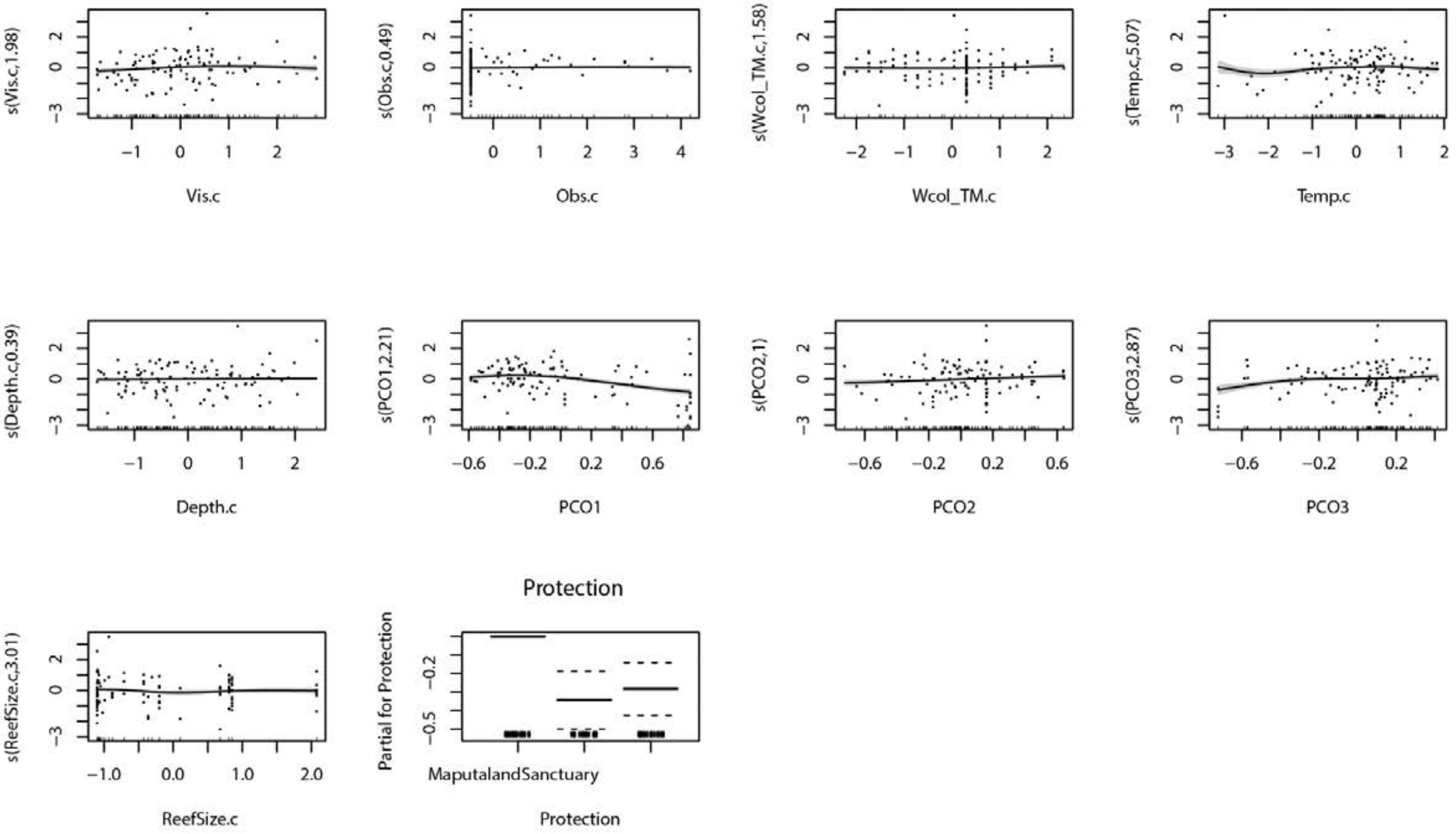


Figure 6.2: Gam plots for the number of functional groups modelled with abundance data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

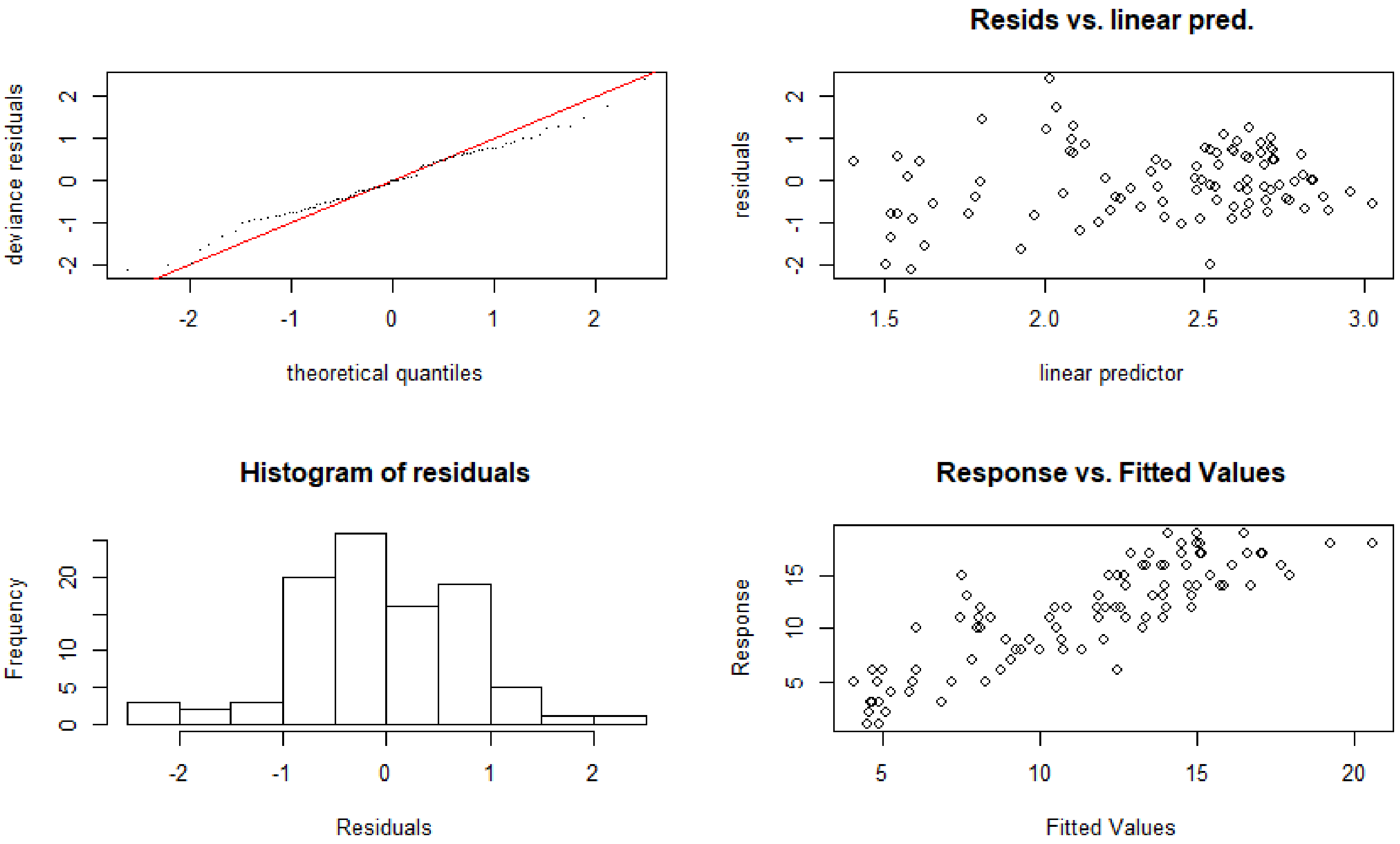


Figure 6.3: Gam check for the number of functional groups modelled with the length data. Shows the deviance residuals versus fitted data for the Generalised Additive Model.

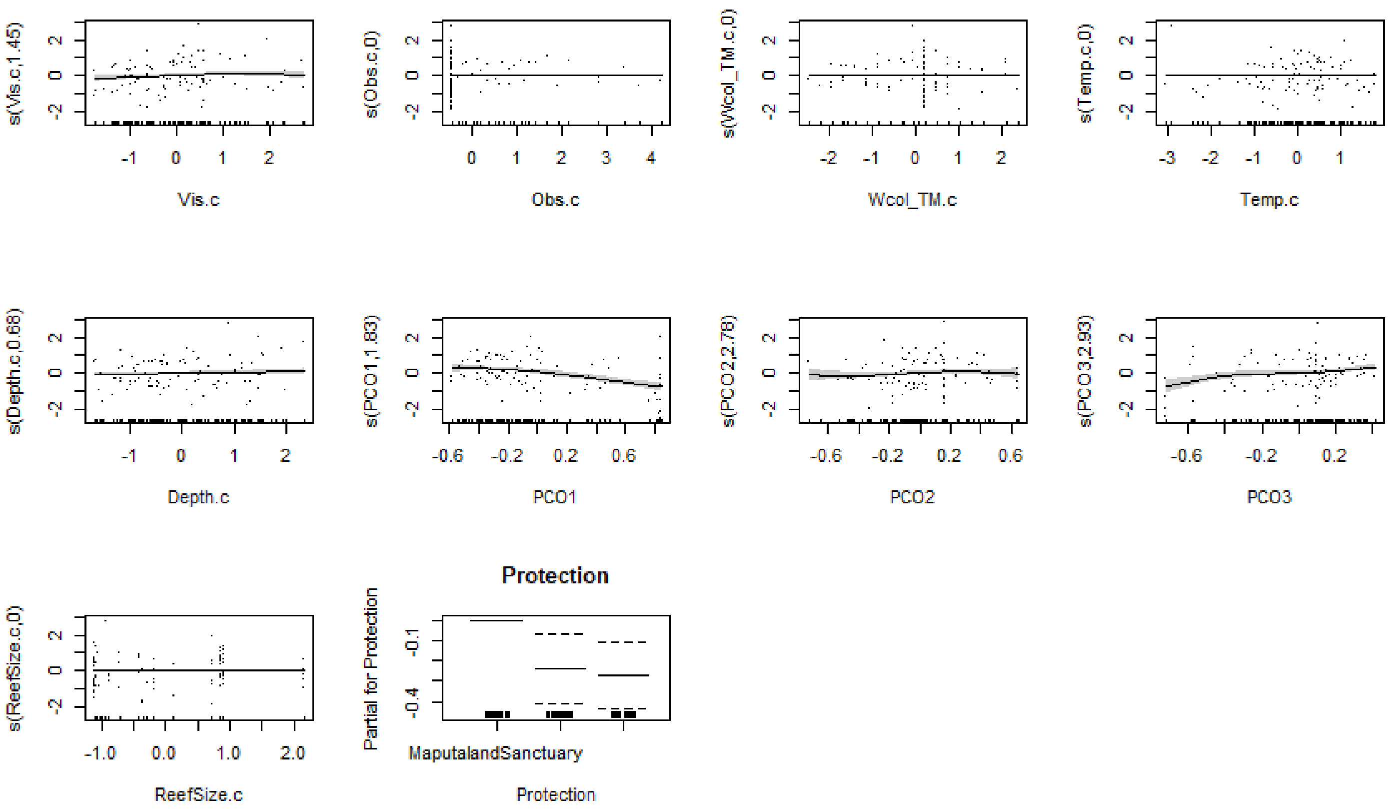


Figure 6.4: Gam plots for the number of functional groups modelled with length data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

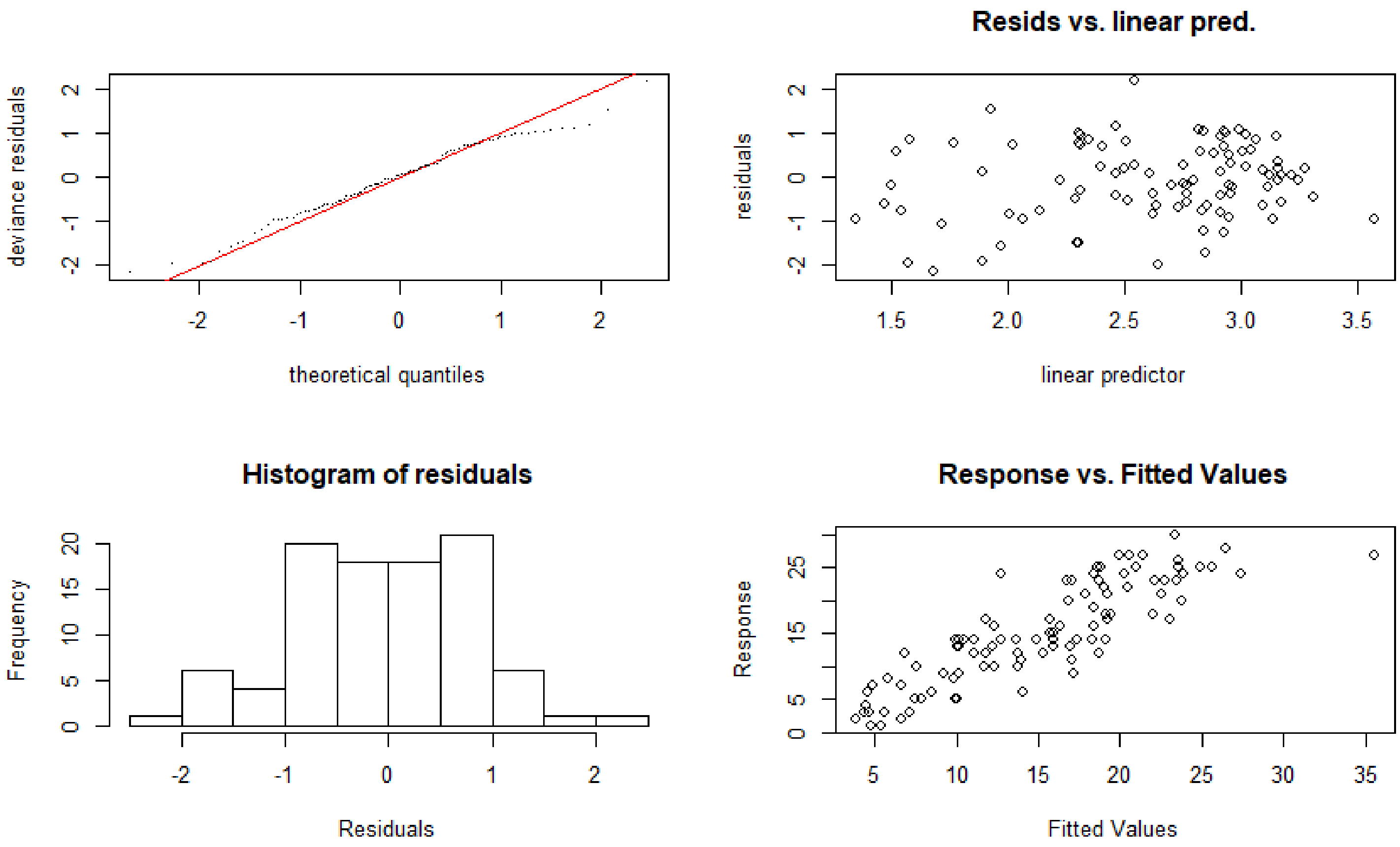


Figure 6.5: Gam check for the number of functional groups modelled with the stage of maturity data. Shows the deviance residuals versus fitted data for the General Additive Model.

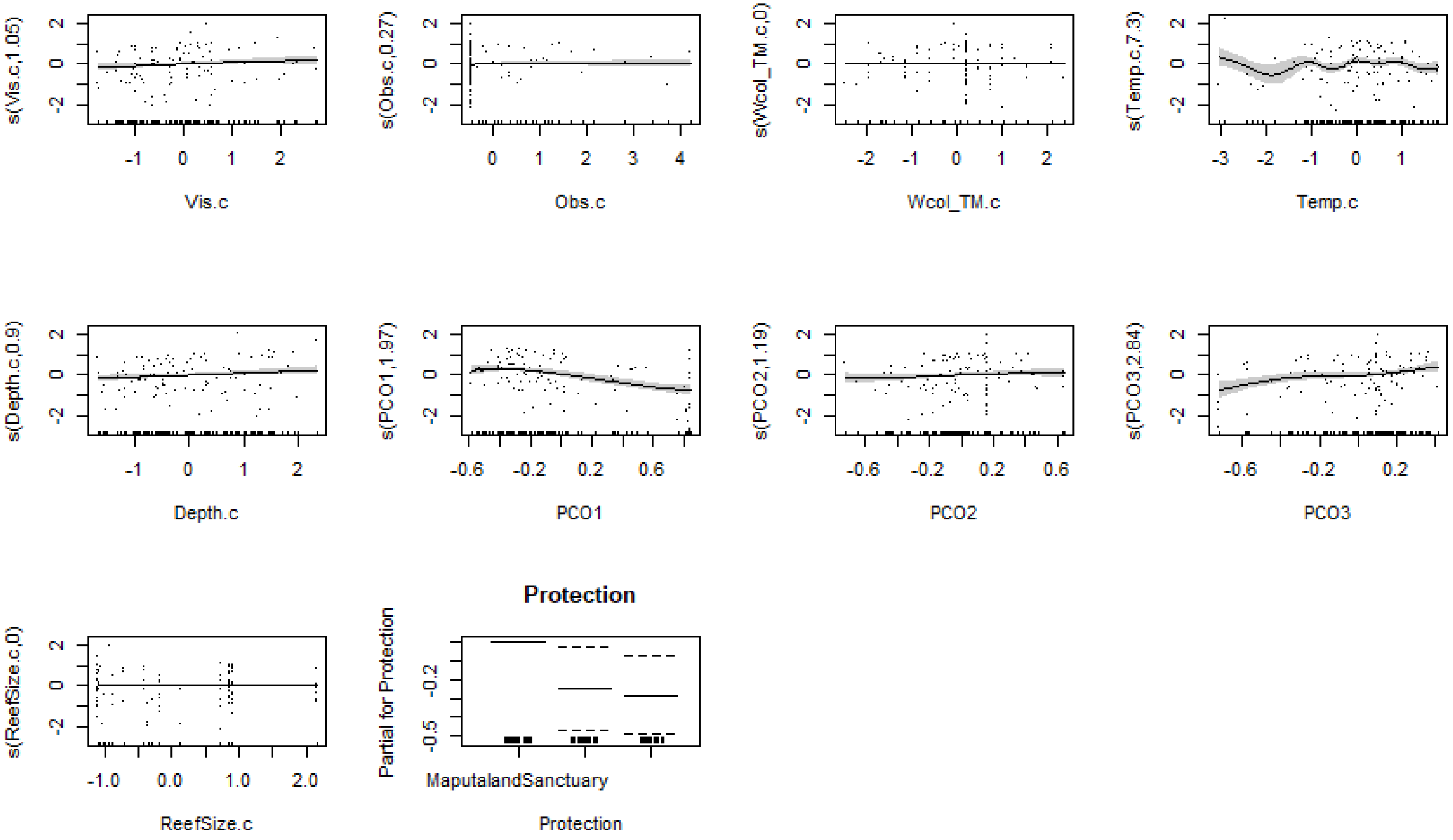


Figure 6.6: Gam plots for the number of functional groups modelled with stage of maturity data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

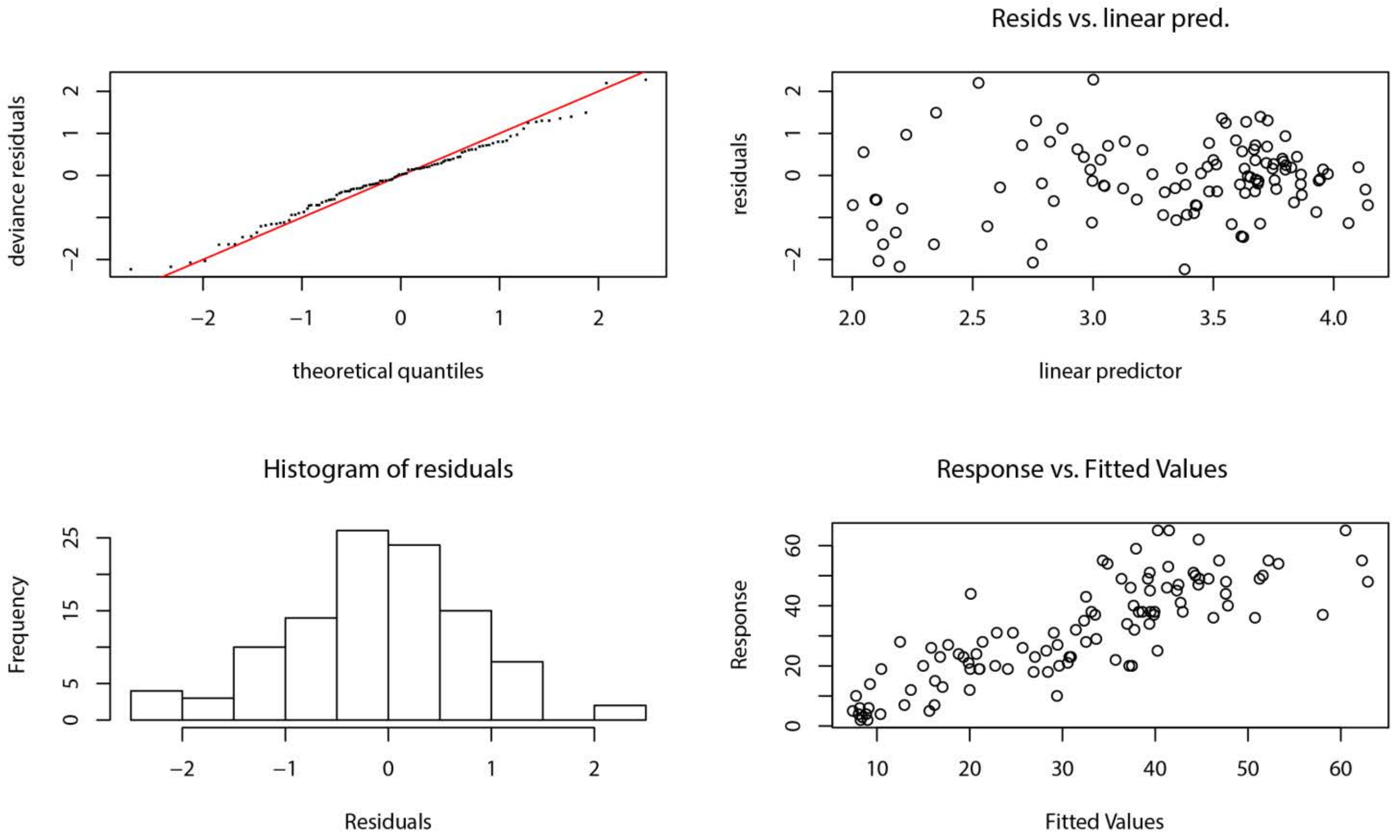


Figure 6.7: Gam check for the functional richness modelled with the abundance data. Shows the deviance residuals versus fitted data for the General Additive Model.

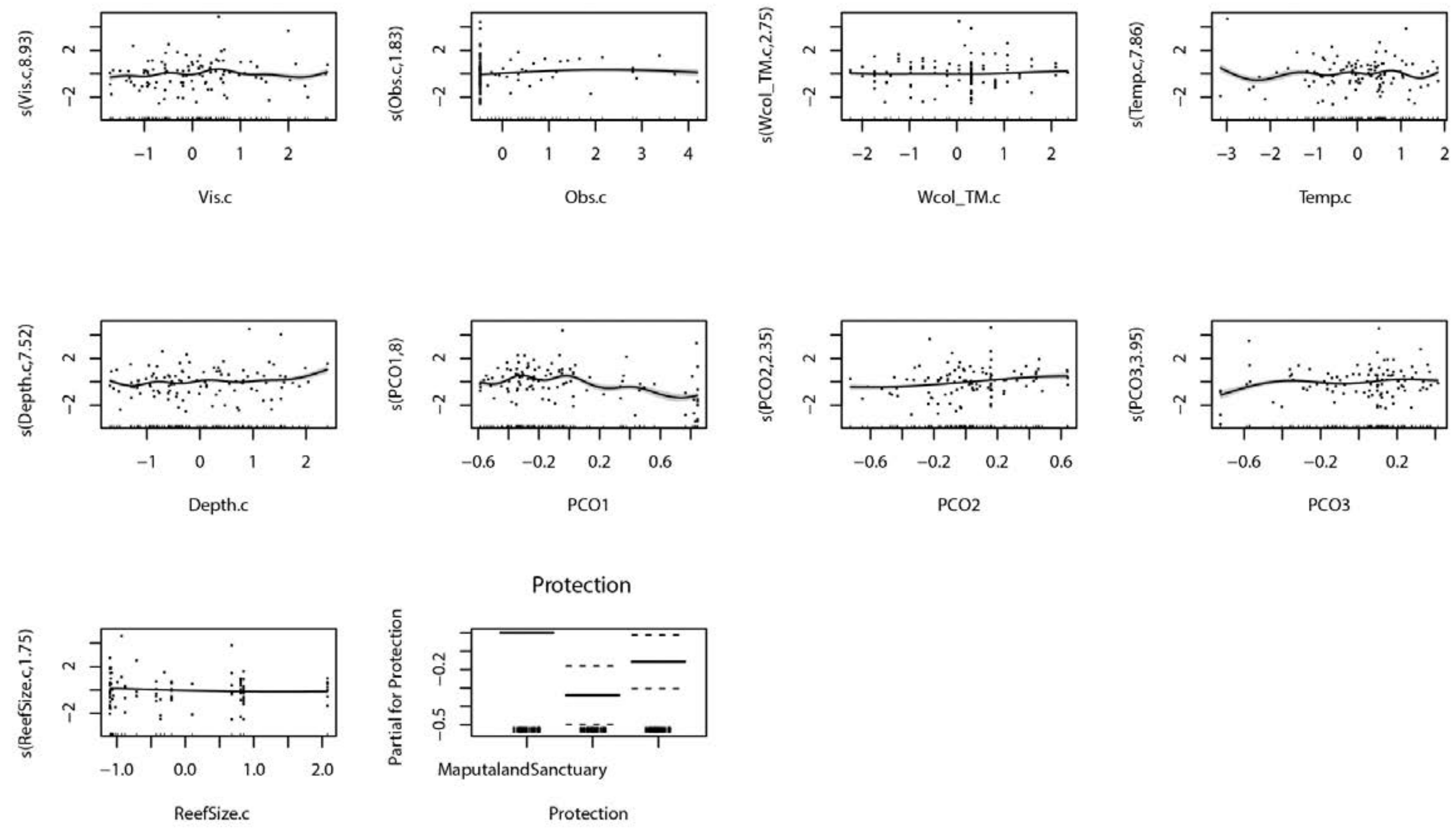


Figure 6.8: Gam plots for functional richness modelled with abundance data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

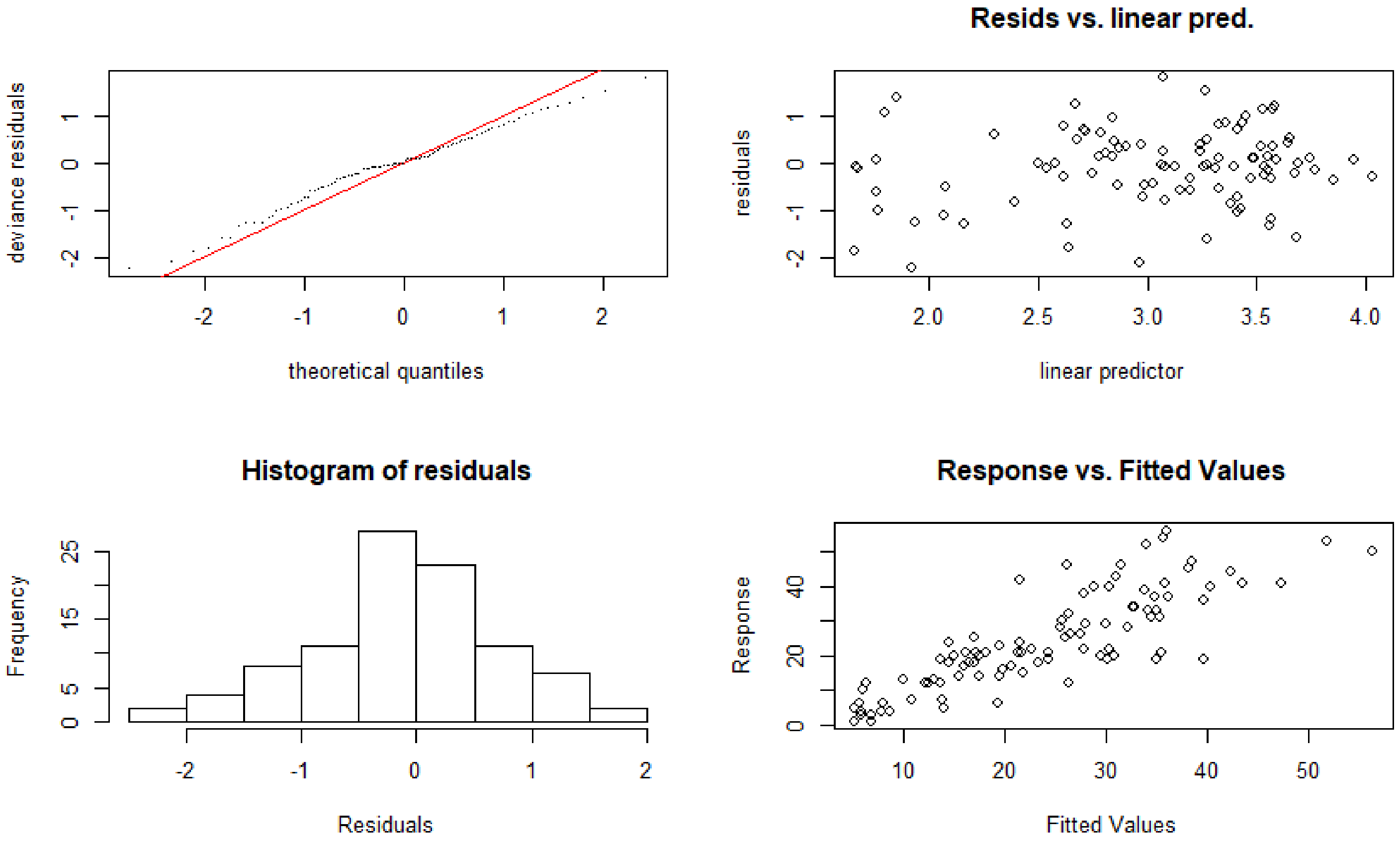


Figure 6.9: Gam check for functional richness modelled with the lengths data. Shows the deviance residuals versus fitted data for the General Additive Model.

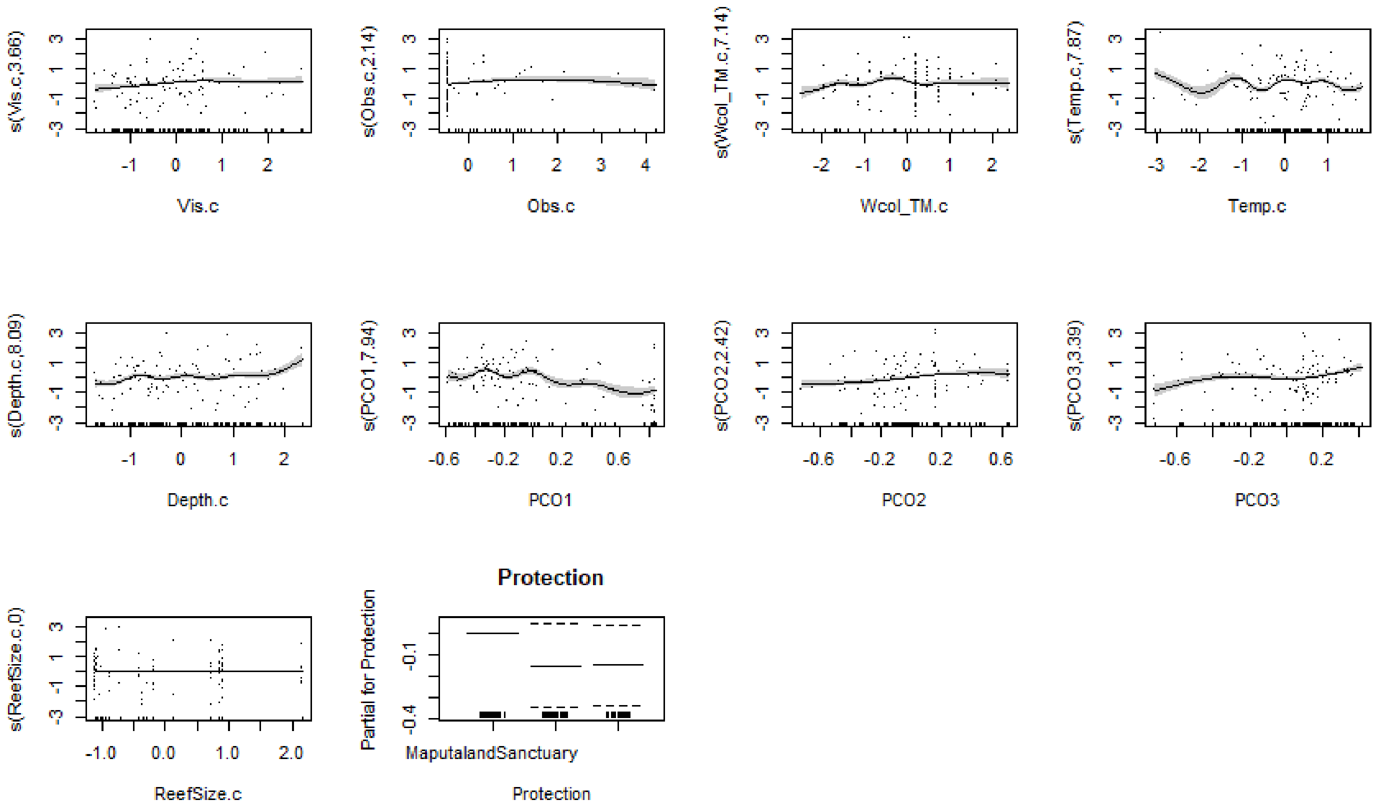


Figure 6.10: Gam plots for functional richness modelled according to lengths data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

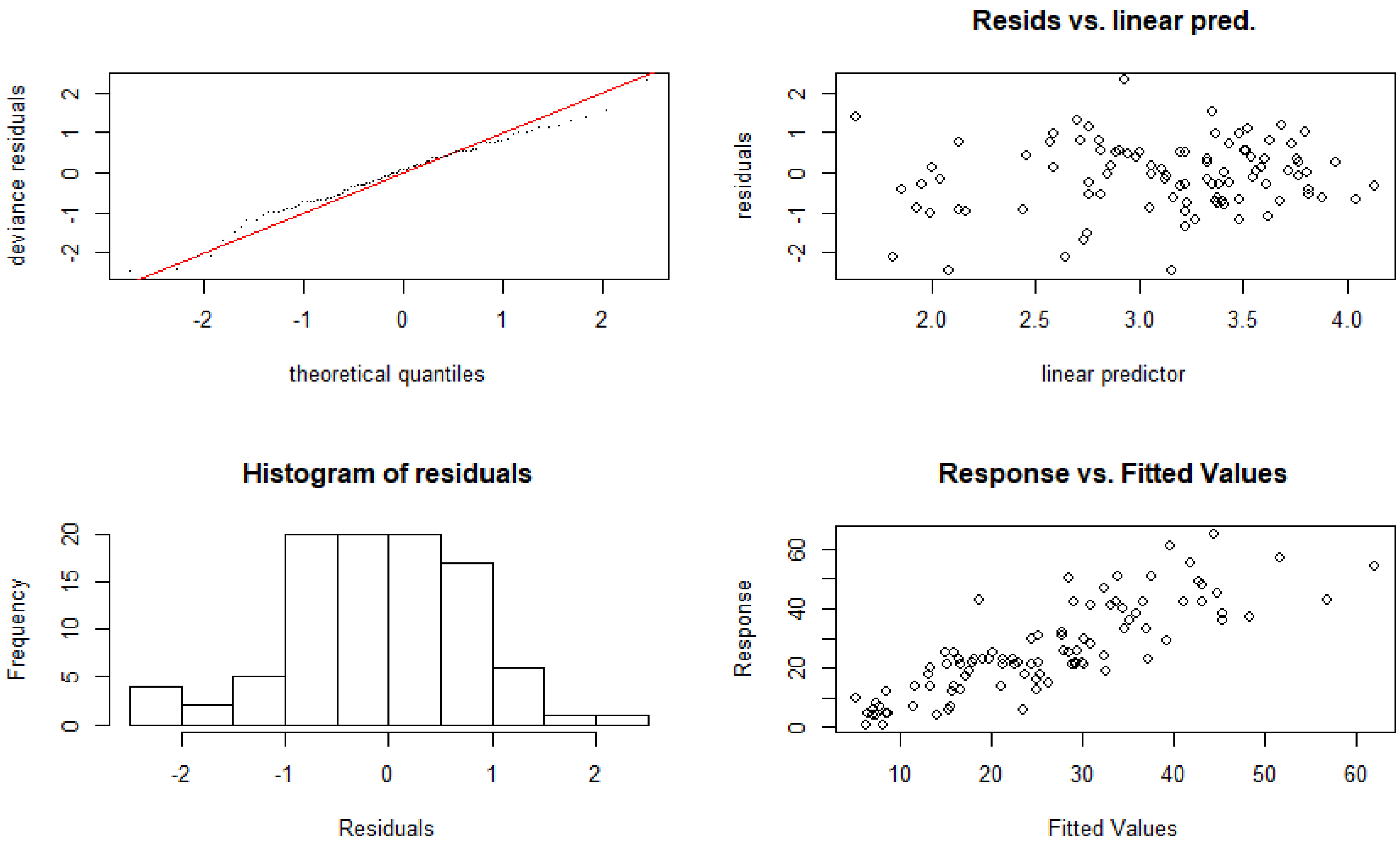


Figure 6.11: Gam check for functional richness modelled with the stage of maturity data. Shows the deviance residuals versus fitted data for the General Additive Model.

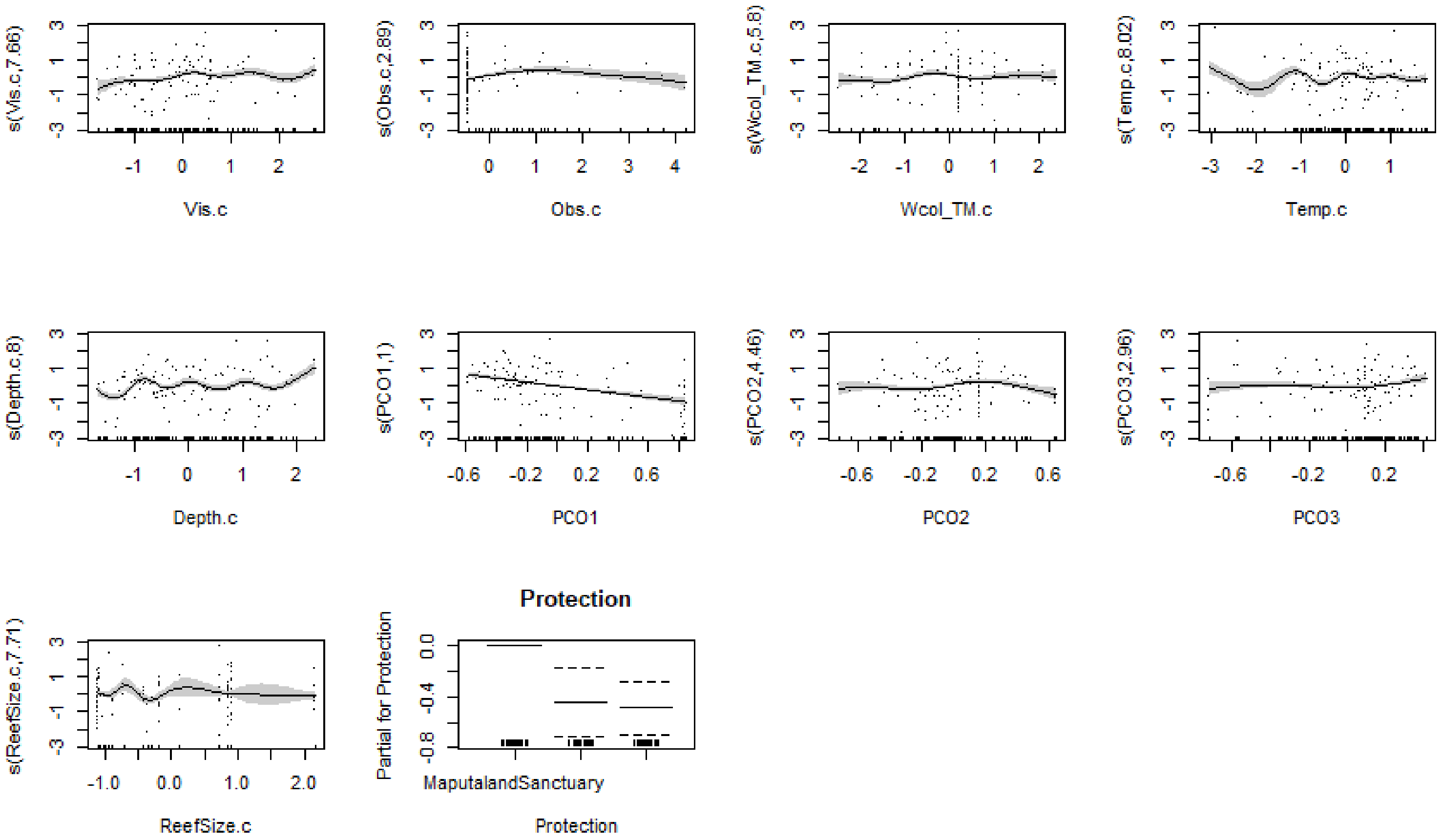


Figure 6.12: Gam plots for functional richness modelled with stage of maturity data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

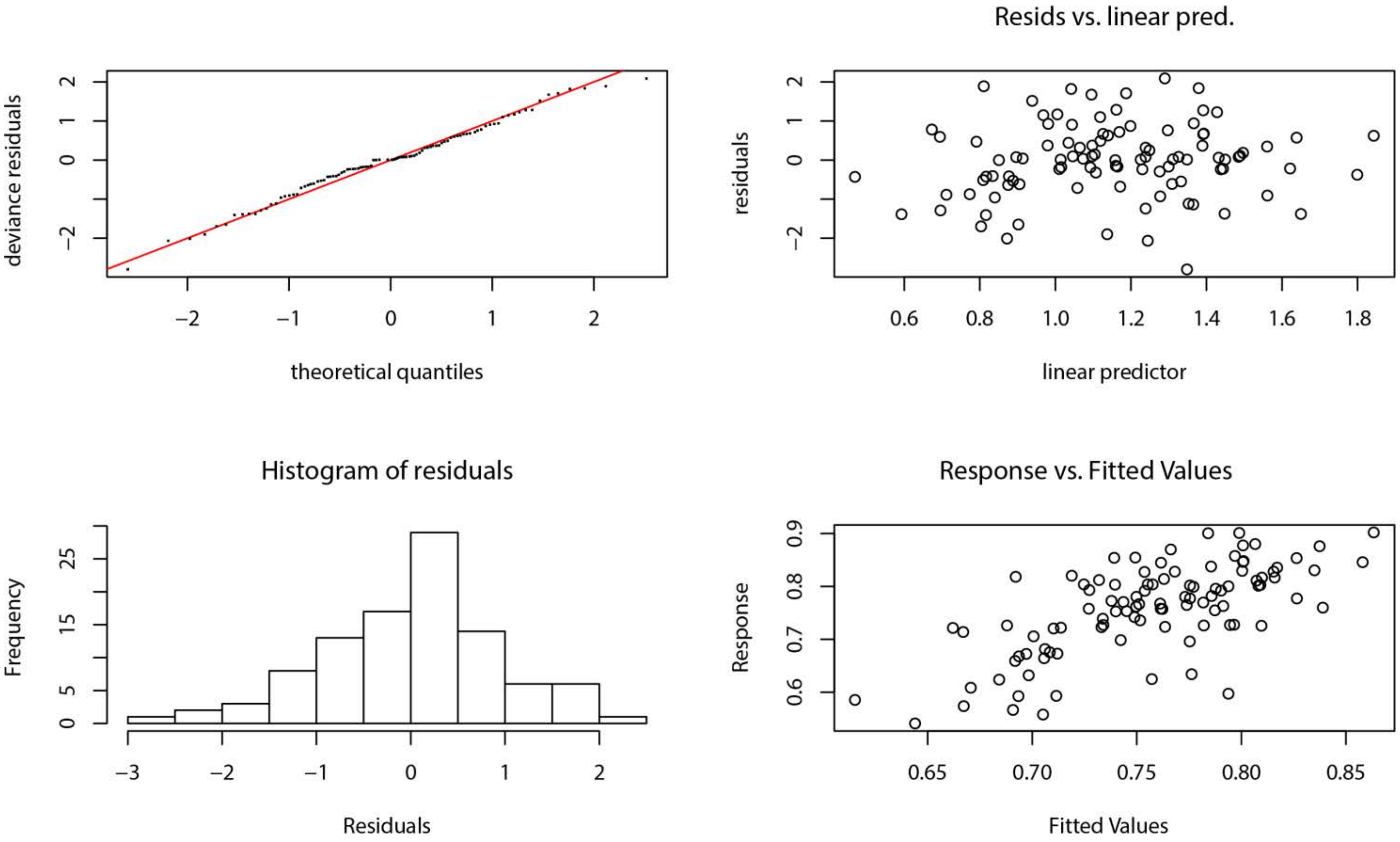


Figure 6.13: Gam check for functional diversity modelled with abundance data. Shows the deviance residuals versus fitted data for the General Additive Model.

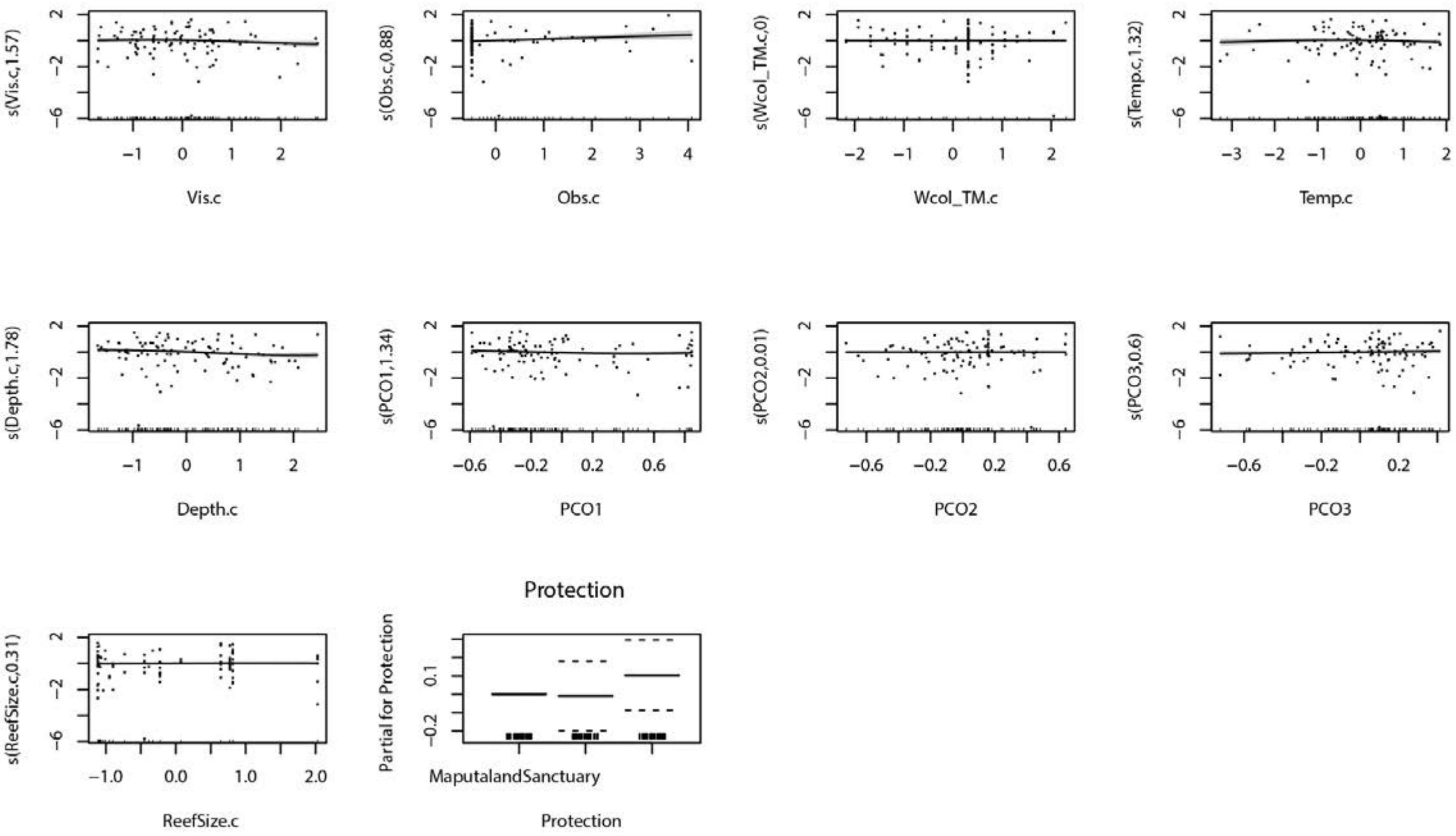


Figure 6.14: Gam plots for functional diversity modelled with abundance data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

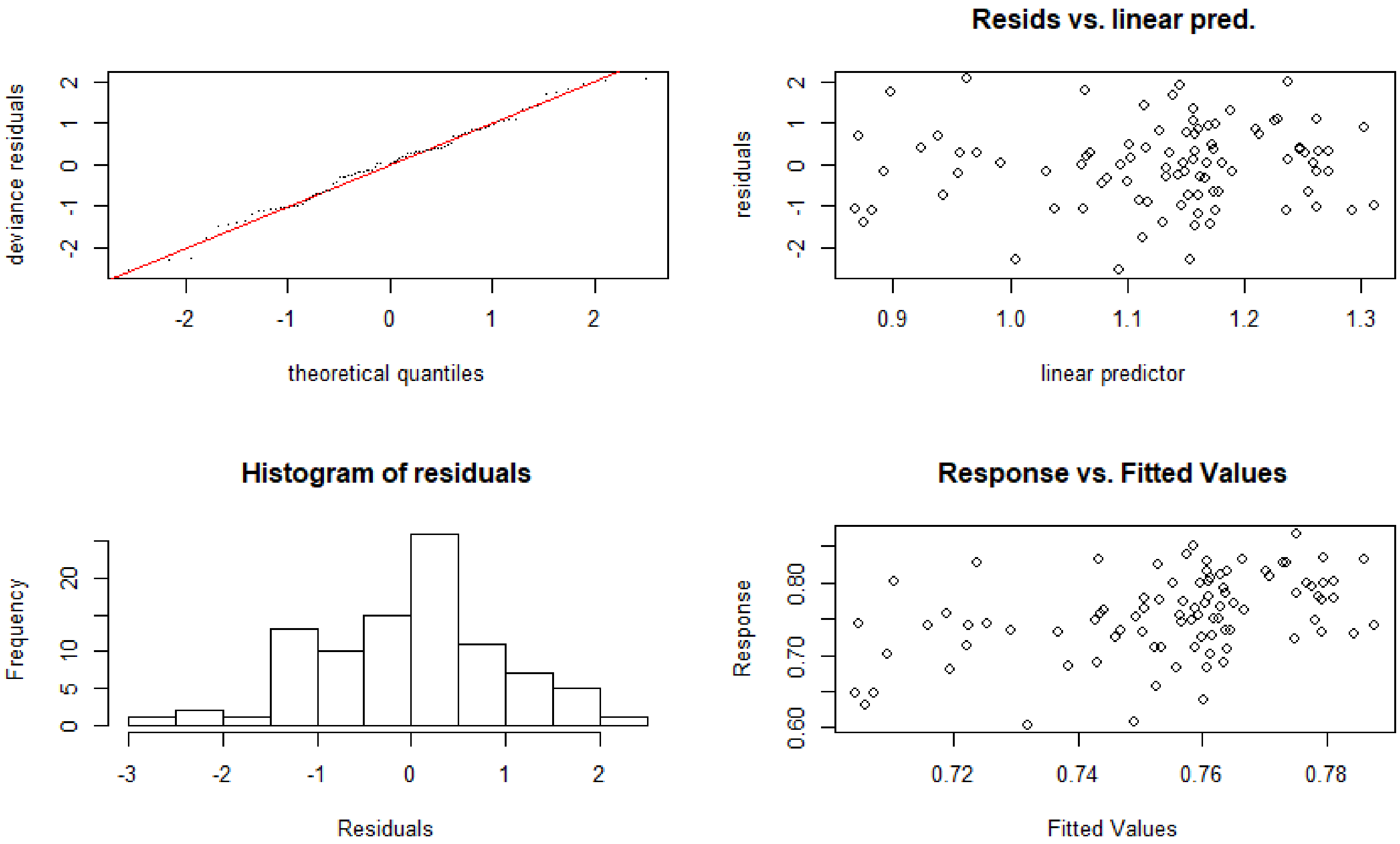


Figure 6.15: Gam check for functional diversity modelled with length data. Shows the deviance residuals versus fitted data for the General Additive Model.

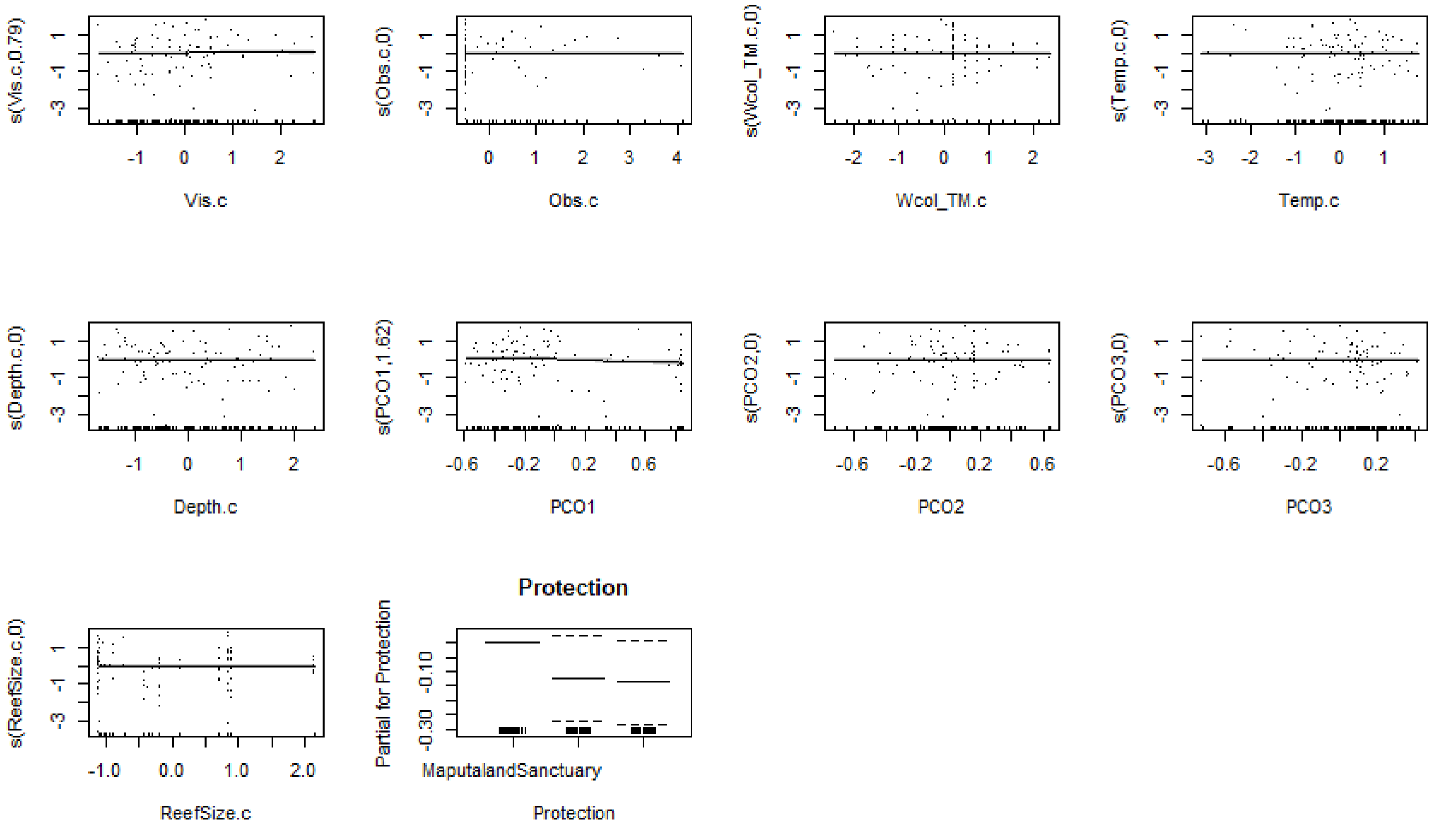


Figure 6.16: Gam plots for functional diversity modelled with thelengths data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

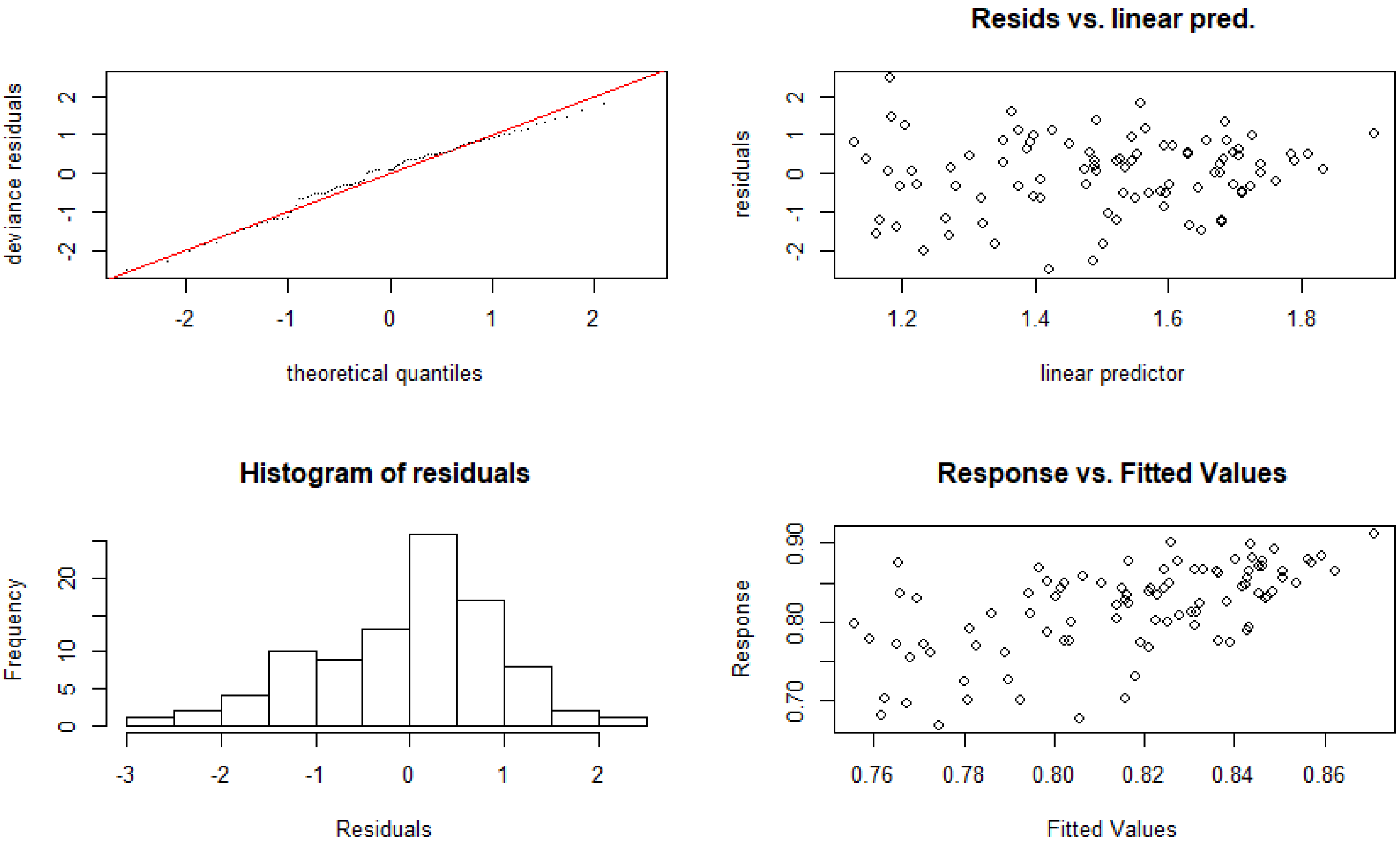


Figure 6.17: Gam Check for functional diversity modelled with the Stages data. Shows the deviance residuals versus fitted data for the General Additive Model.

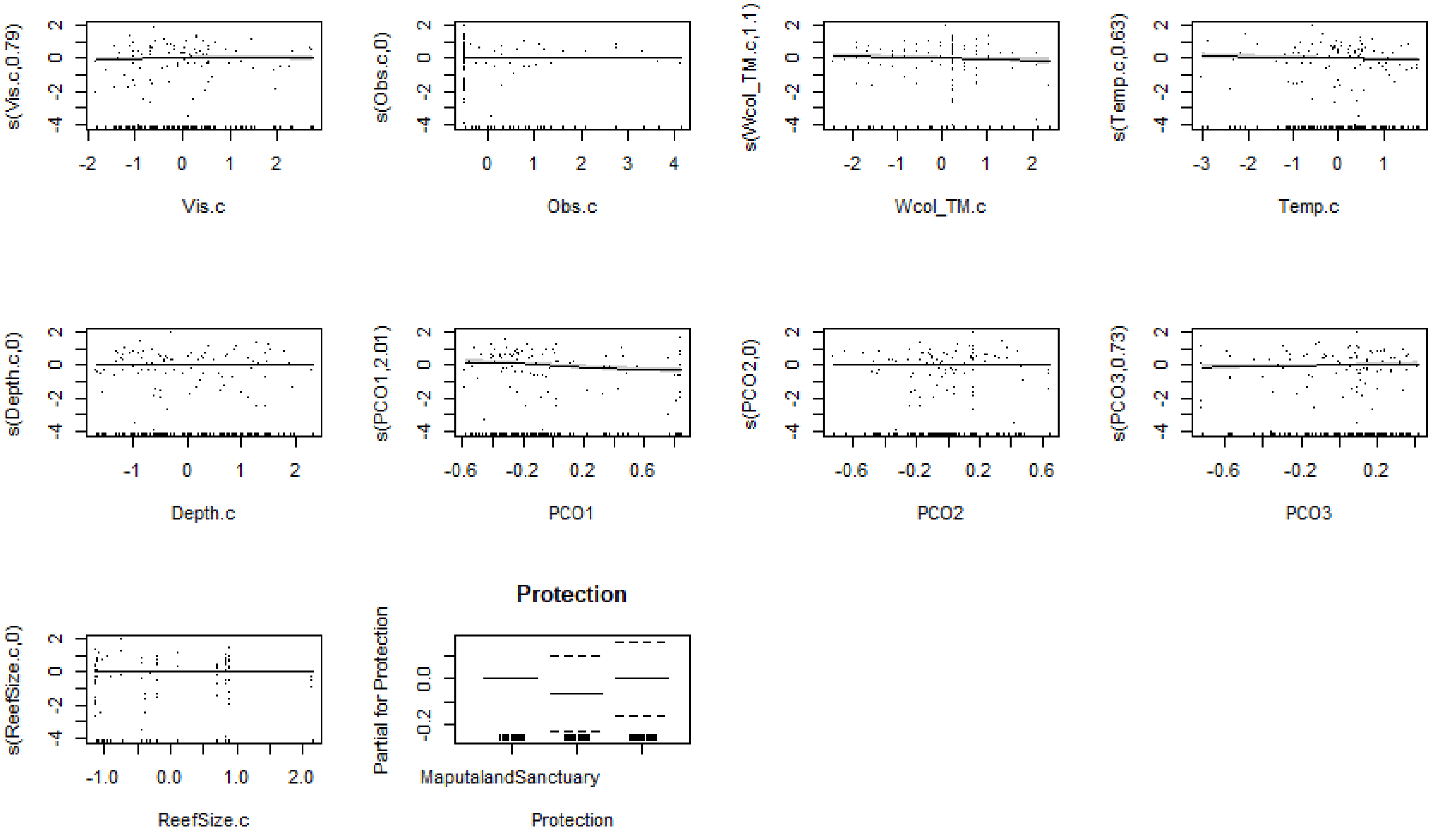


Figure 6.18: Gam Plots for functional diversity modelled with Stages data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

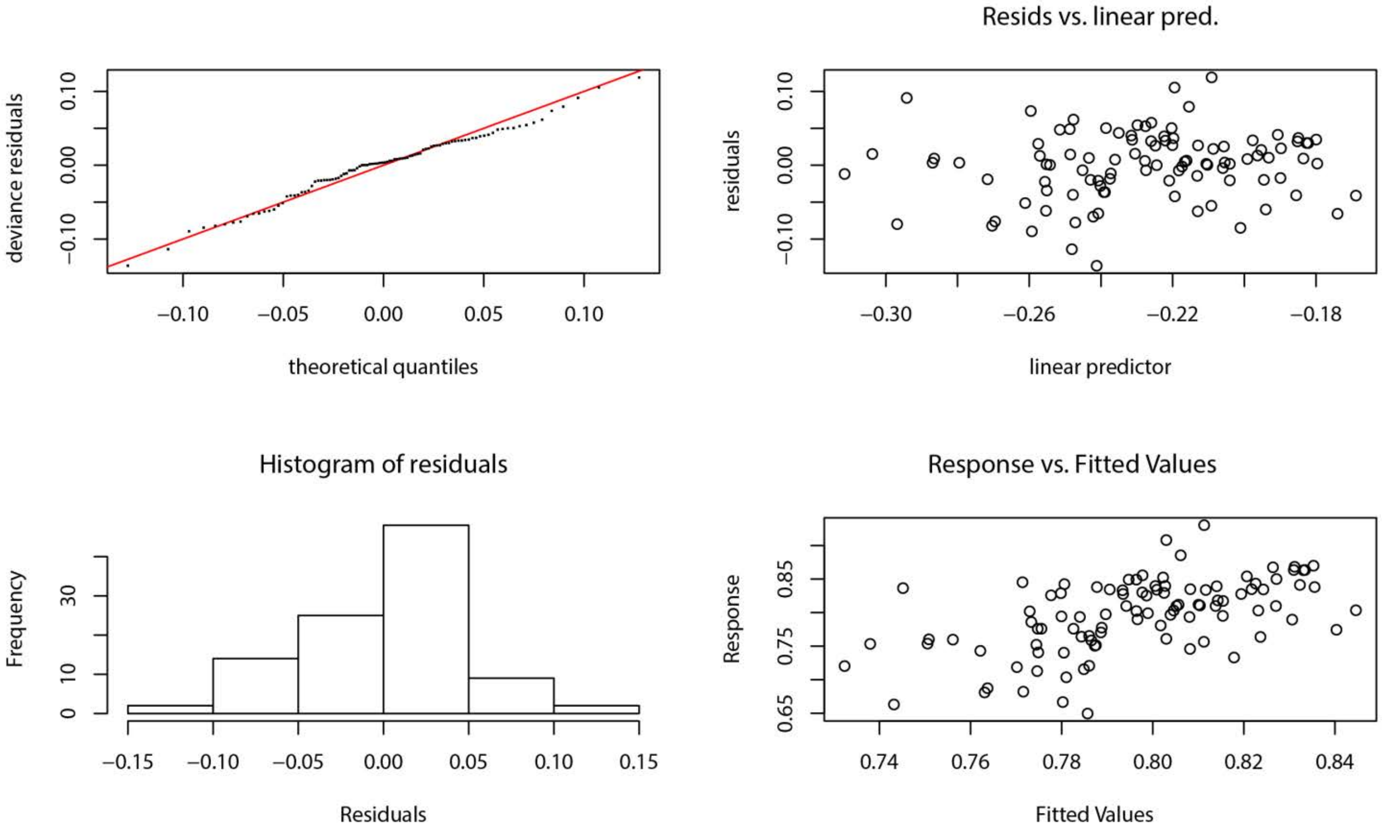


Figure 6.19: Gam Check for functional evenness modelled with the Abundance data. Shows the deviance residuals versus fitted data for the General Additive Model.

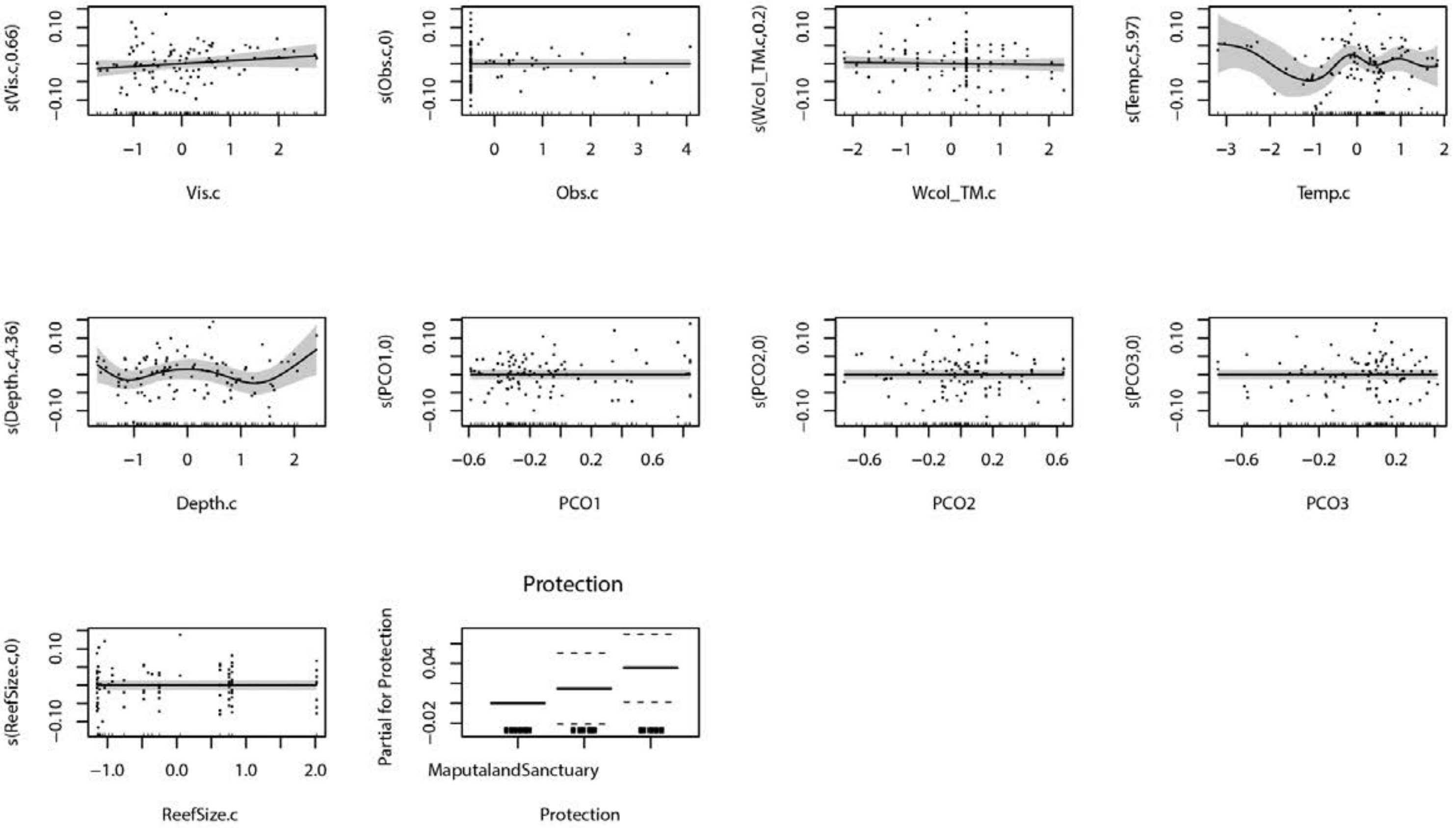


Figure 6.20: Gam Plots for functional evenness modelled with Abundance data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

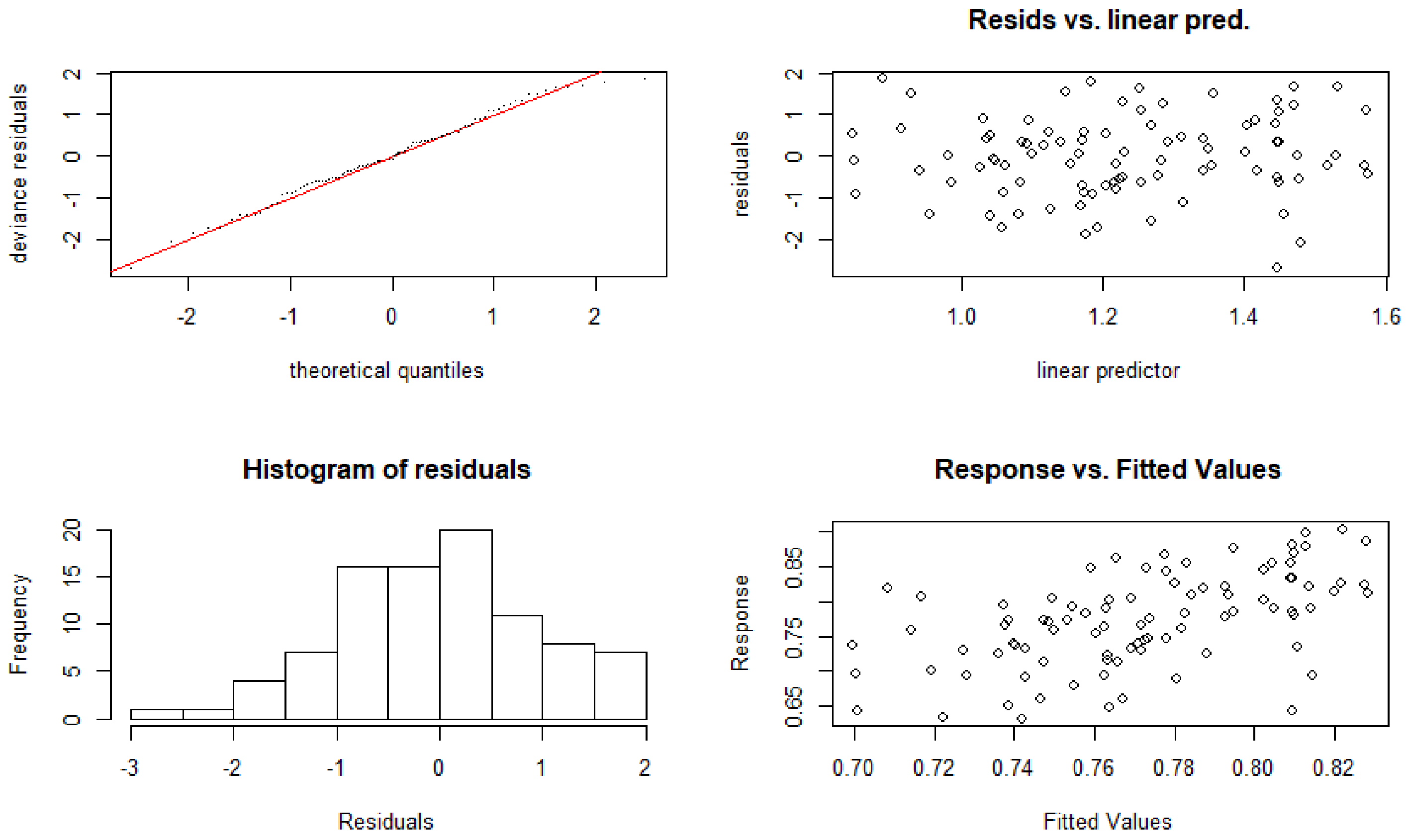


Figure 6.21: Gam Check for functional evenness modelled with the Lengths data. Shows the deviance residuals versus fitted data for the General Additive Model.

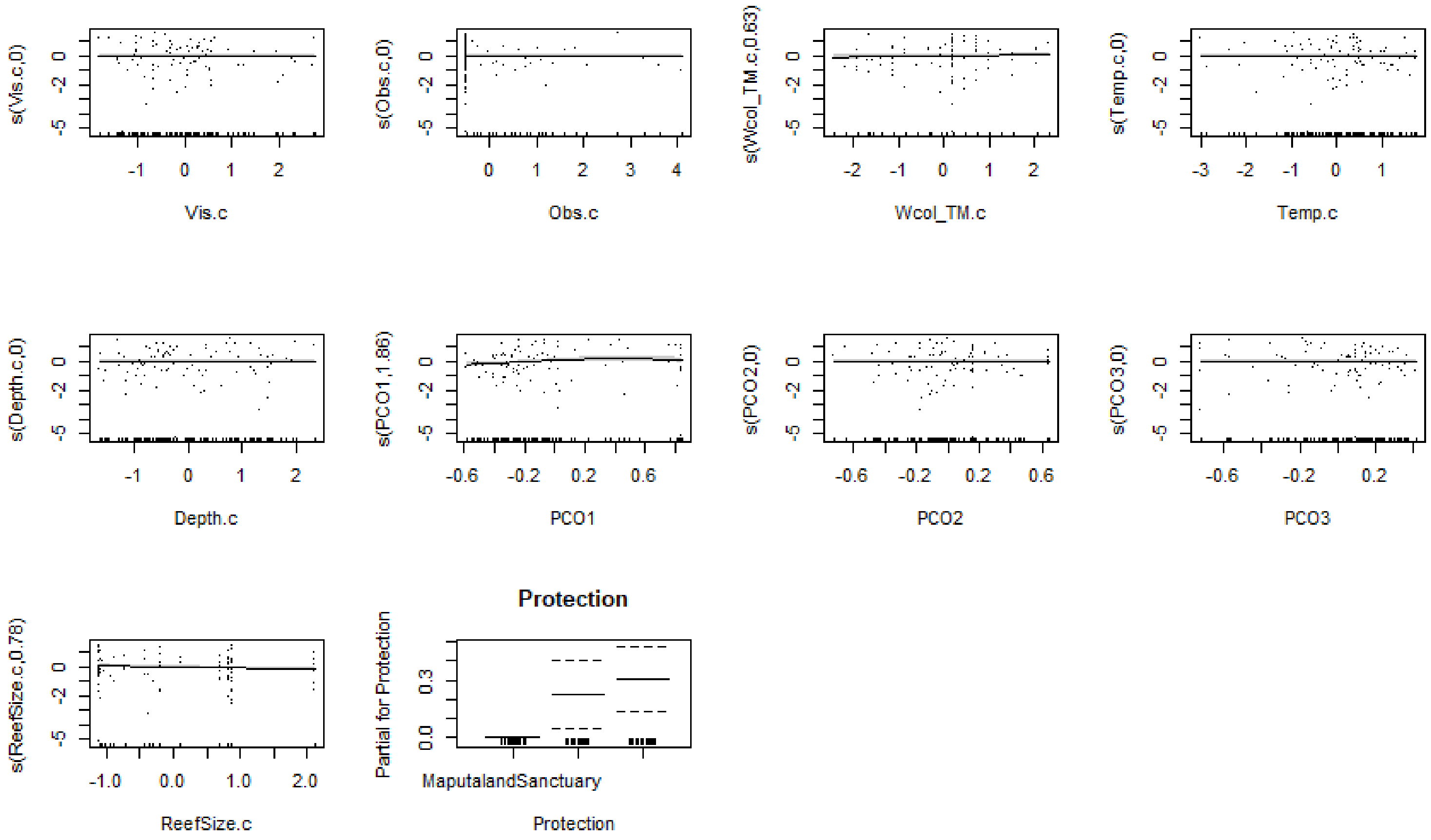


Figure 6.22: Gam Plots for functional evenness modelled with Lengths data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

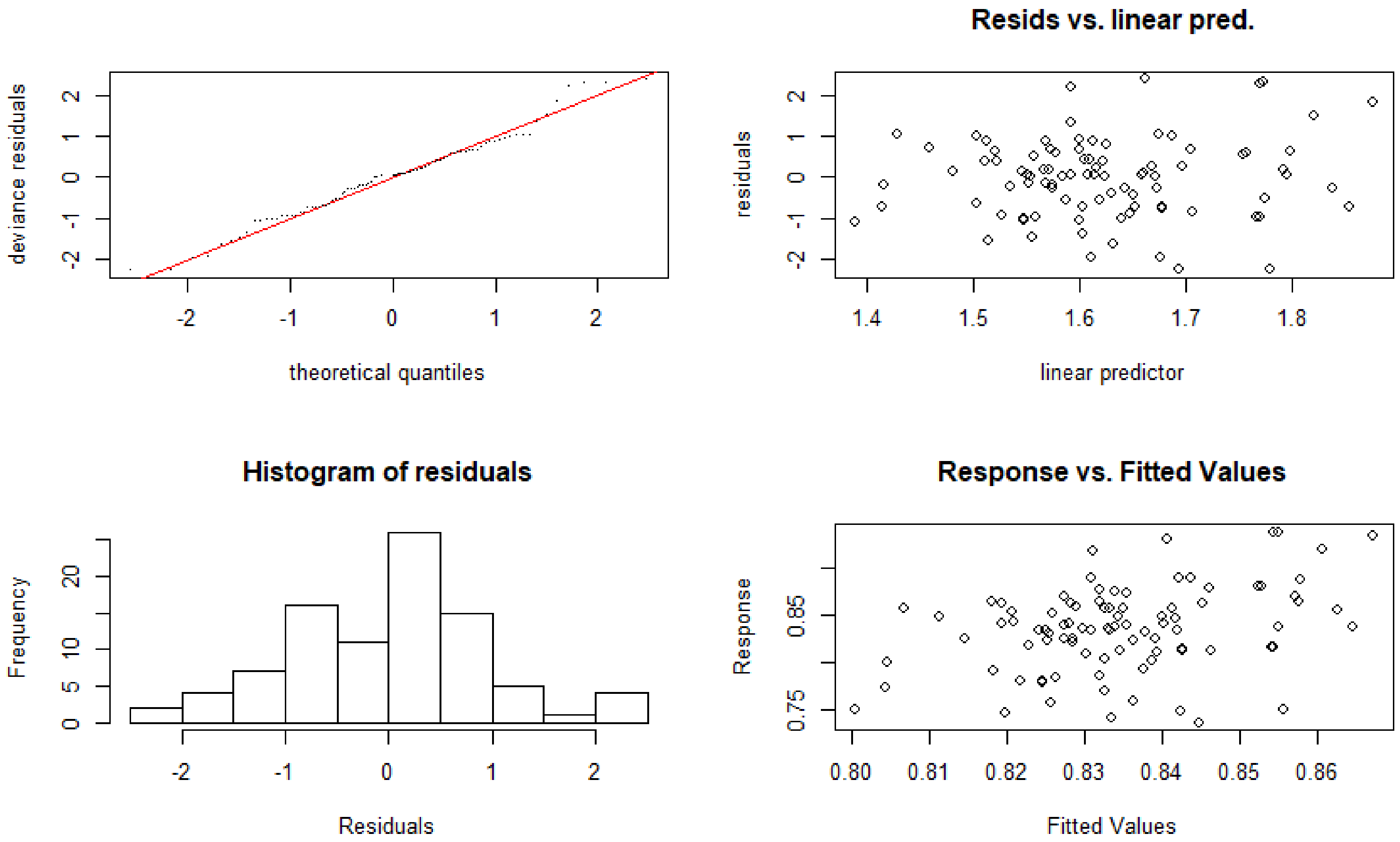


Figure 6.23: Gam Check for functional evenness modelled with the Stages data. Shows the deviance residuals versus fitted data for the General Additive Model.

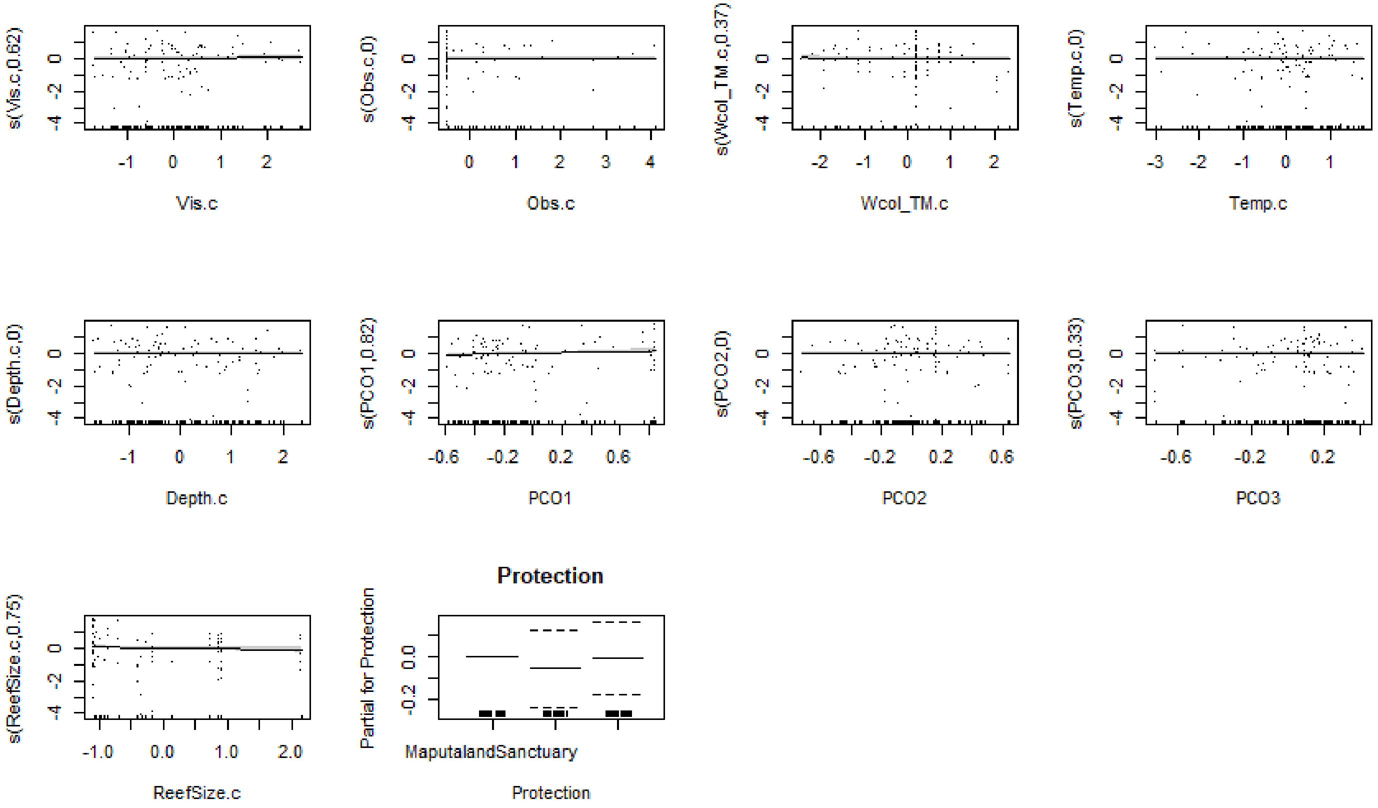


Figure 6.24: Gam Plots for functional evenness modelled with Stages data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

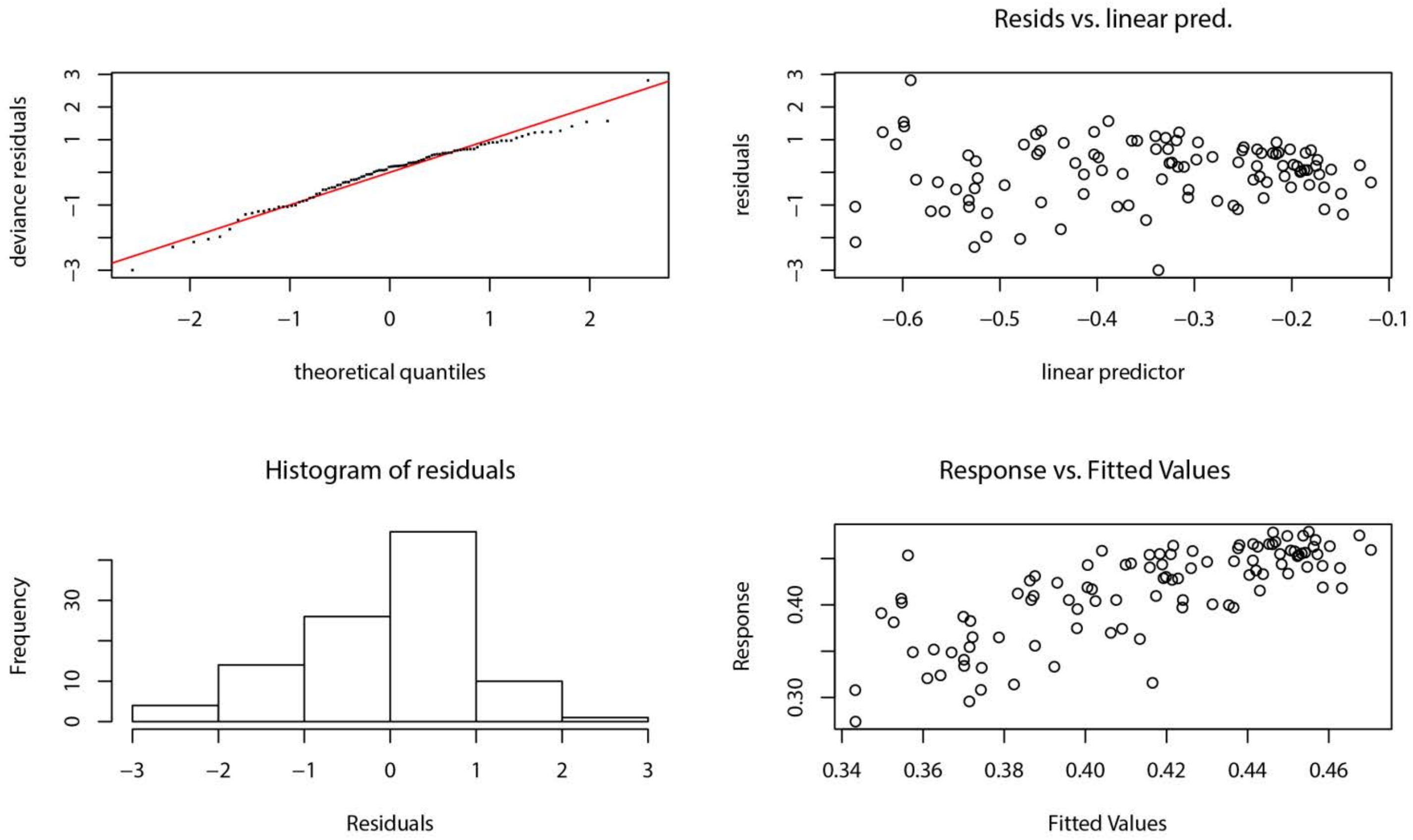


Figure 6.25: Gam Check for functional dispersion modelled with the Abundance data. Shows the deviance residuals versus fitted data for the General Additive Model.

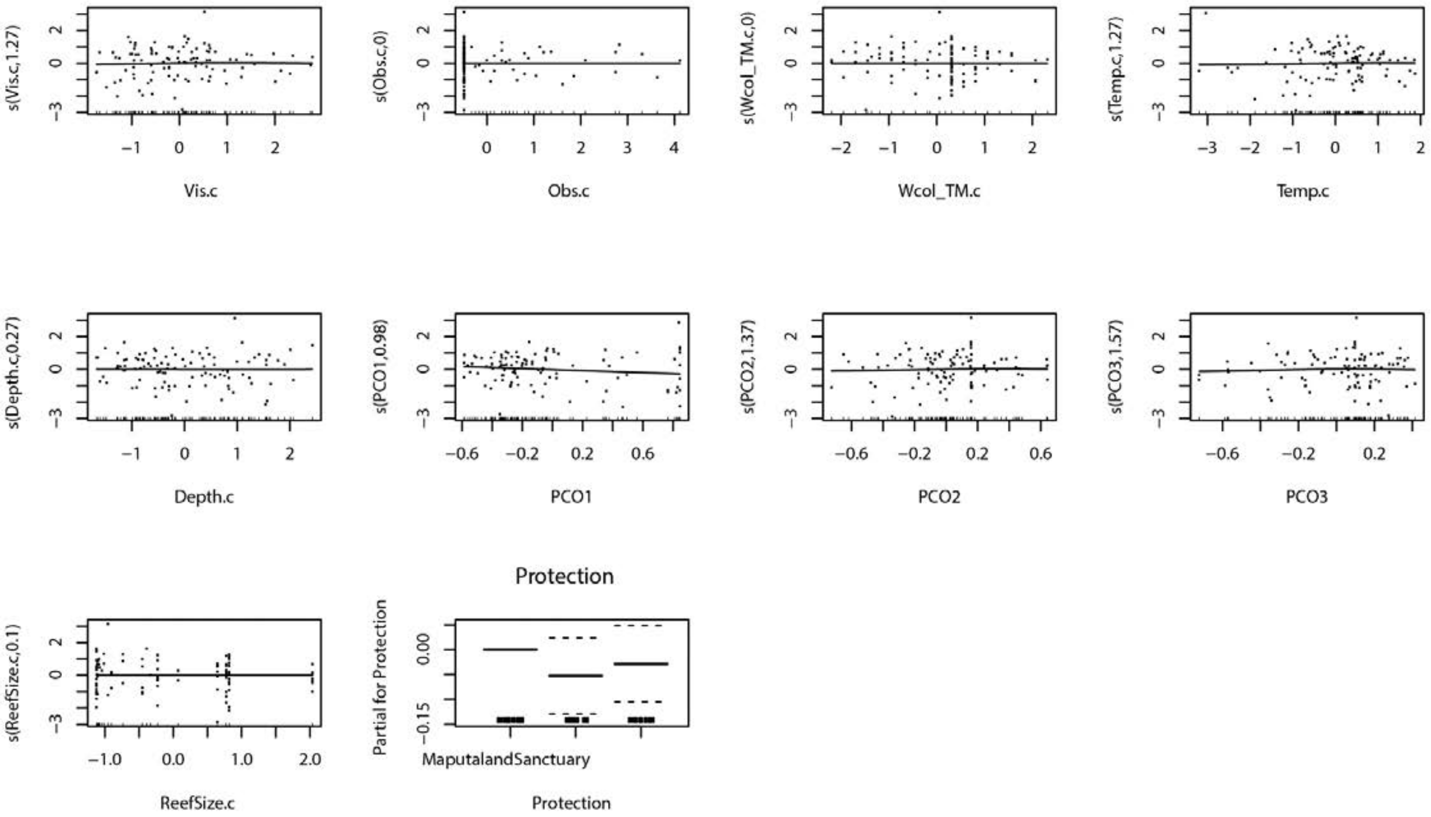


Figure 6.26: Gam Plots for functional dispersion modelled with Abundance data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

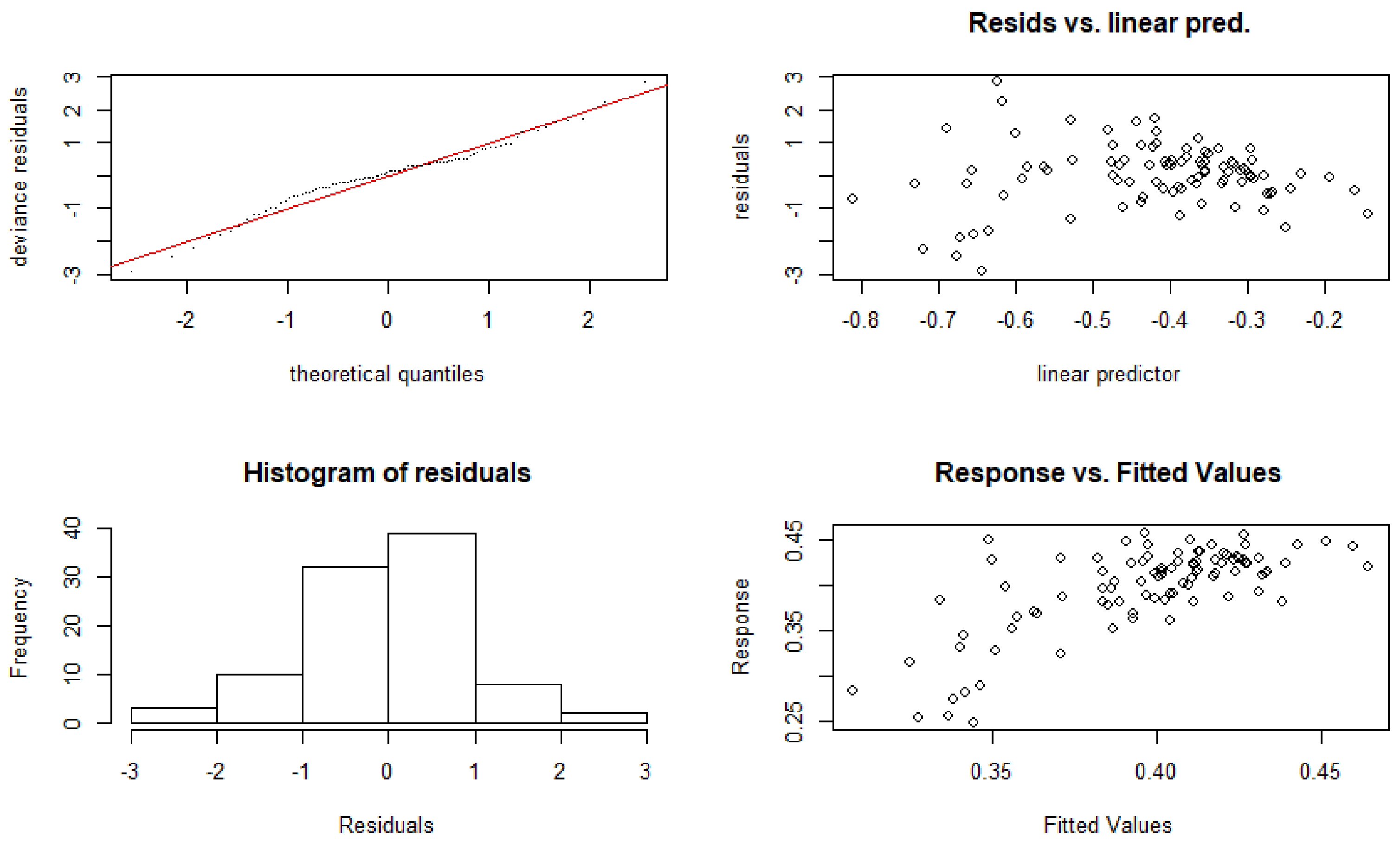


Figure 6.27: Gam Check for functional dispersion modelled with the Lengths data. Shows the deviance residuals versus fitted data for the General Additive Model.

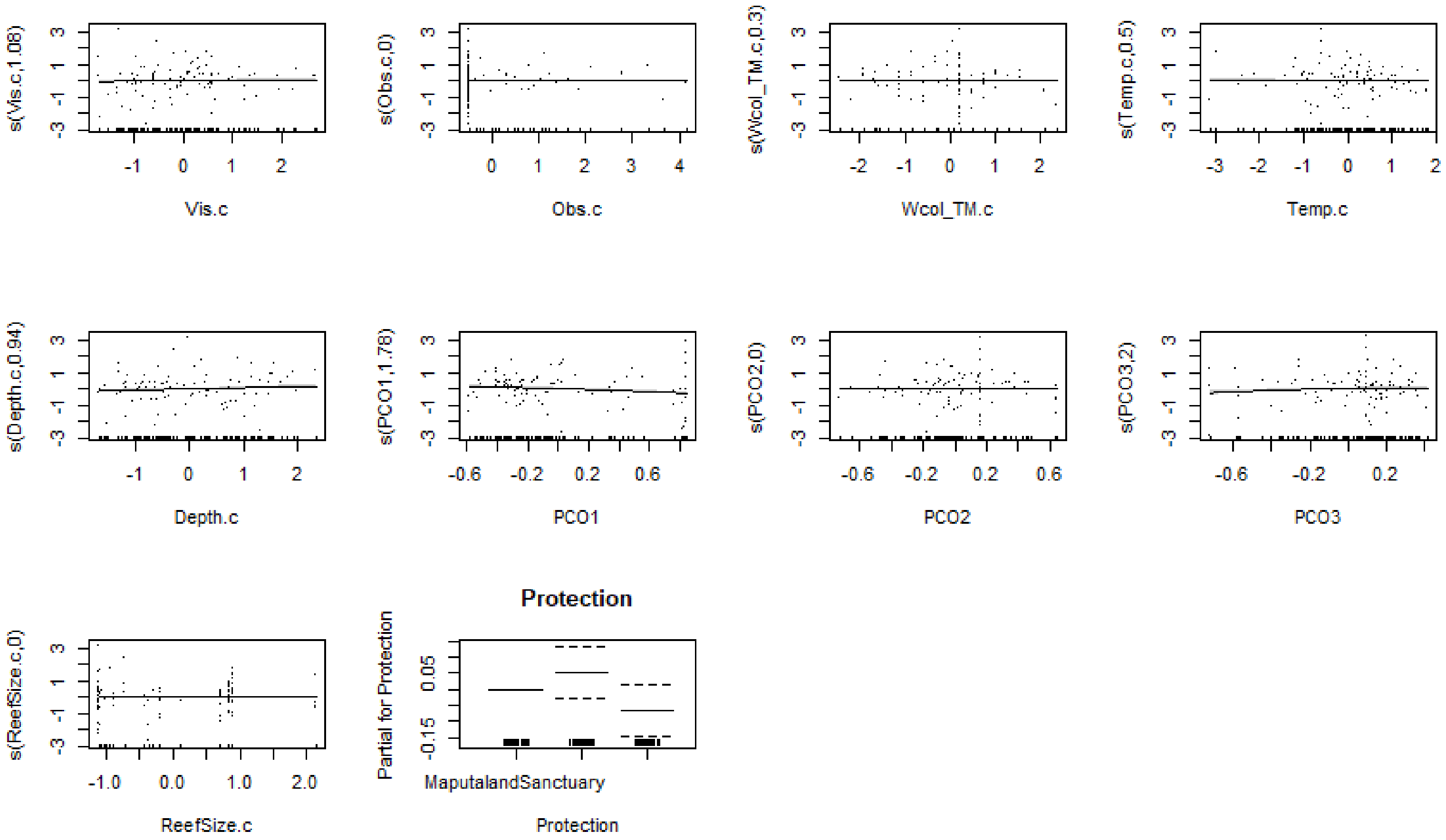


Figure 6.28: Gam Plots for functional dispersion modelled with Lengths data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

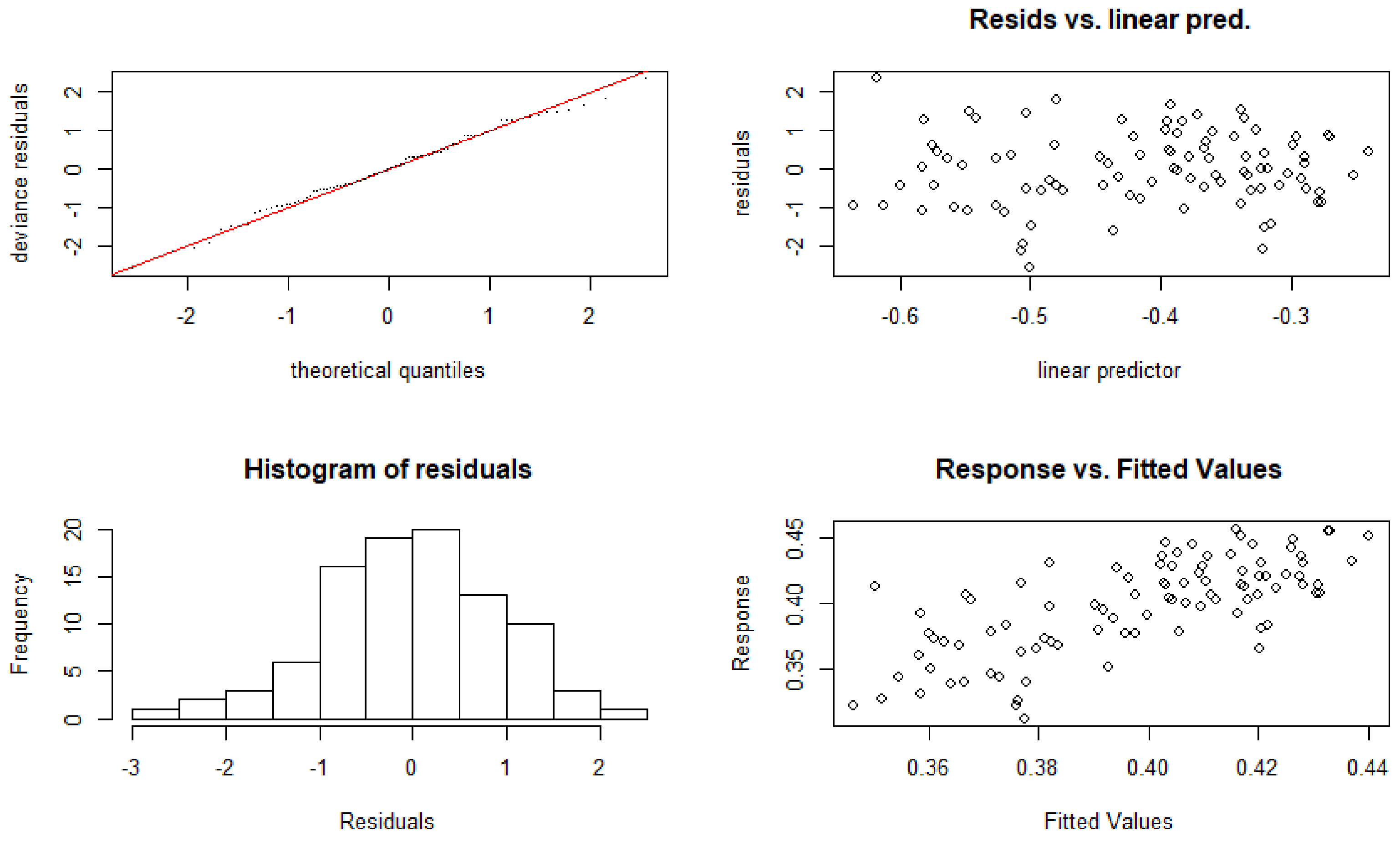


Figure 6.29: Gam Check for functional dispersion modelled with the Stages data. Shows the deviance residuals versus fitted data for the General Additive Model.

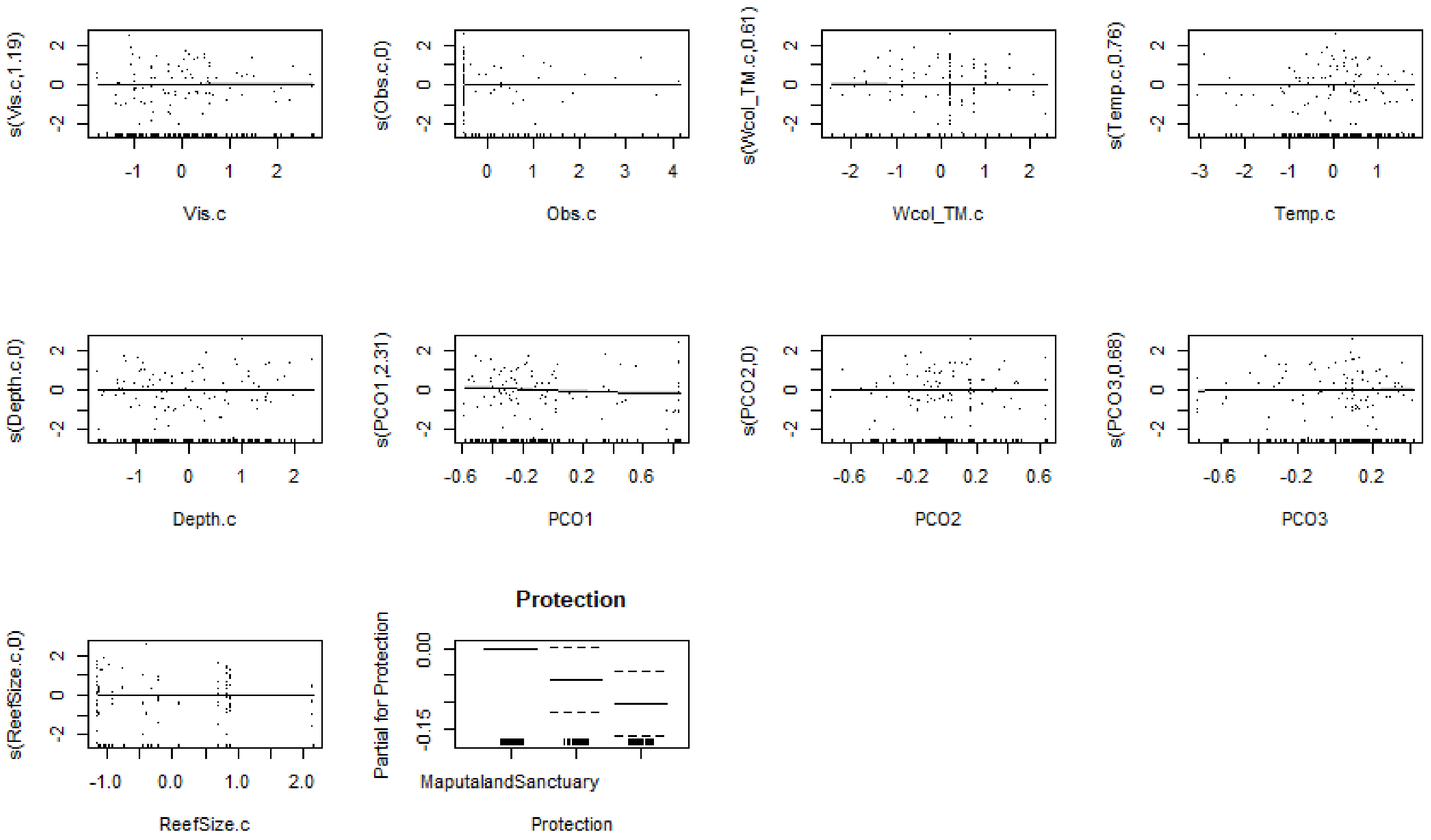


Figure 6.30: Gam Plots for functional dispersion modelled with Stages data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3.

Table 6.5 Averages and standard deviations for proportions of each trait within the different management zonations of the iSimangaliso Wetland Park. This was derived from FD Package, this is what is known as cumulative weighted means because proportions are weighted by the abundance of individuals with that trait.

		CPZs	**St Lucia NTSZ**	**Maputaland NTSZ**
Size Class	*very small*	0.171; 0.186	0.175; 0.153	0.236; 0.167
	small	0.181; 0.129	0.182; 0.127	0.24; 0.123
	medium	0.408; 0.23	0.276; 0.168	0.291; 0.163
	large	0.191; 0.155	0.265; 0.198	0.198; 0.184
	very large	0.051; 0.072	0.105; 0.232	0.038; 0.038
Maturity	*Adult*	0.761; 0.203	0.802; 0.203	0.784; 0.107
	Juvenile	0.239; 0.203	0.198; 0.203	0.216; 0.107
Trophic Level	*trophic 2<x<3*	0.362; 0.091	0.077; 0.072	0.082; 0.071
	trophic 3<x<4	0.537; 0.155	0.698; 0.189	0.751; 0.118
	trophic >4	0.101; 0.067	0.234; 0.217	0.167; 0.078
Rep. Mode	*dioecism*	0.694; 0.158	0.675; 0.142	0.716; 0.123
	hermaphrodite	0.001; 0.004	0.002; 0.005	0.002; 0.005
	protandry	0.013; 0.058	0.005; 0.01	0.021; 0.027
	protogyny	0.293; 0.149	0.32; 0.142	0.263; 0.117
Rep. Guild 1	*bearers*	0.042; 0.089	0.068; 0.195	0.03; 0.101
	guarders	0.166; 0.135	0.17; 0.155	0.17; 0.121
	Non-guarders	0.794; 0.136	0.764; 0.211	0.801; 0.135
	external brooders	0; 0	0; 0	0.001; 0.005
Rep. Guild 2	*internal live bearers*	0.042; 0.089	0.068; 0.195	0.029; 0.101
	nesters	0.202; 0.146	0.207; 0.155	0.224; 0.132
	open water substratum egg scatterers	0.757; 0.144	0.727; 0.2	0.748; 0.138
Gregariousness	*Solitary*	0.162; 0.155	0.215; 0.24	0.149; 0.136
	Solitary, pairs or in groups	0.19; 0.11	0.207; 0.103	0.216; 0.098
	Pairs or small groups	0.072; 0.077	0.072; 0.059	0.119; 0.096
	Small groups	0.139; 0.126	0.149; 0.104	0.118; 0.065
	Medium groups	0.236; 0.118	0.261; 0.146	0.258; 0.162
	Large groups	0.205; 0.226	0.099; 0.117	0.143; 0.155
Feeding Guild	*Planktivore*	0.155; 0.184	0.139; 0.157	0.175; 0.164
	Herbivore	0.101; 0.098	0.093; 0.089	0.104; 0.092
	Carnivore	0.522; 0.197	0.514; 0.197	0.523; 0.213
	Higher Carnivore	0.115; 0.072	0.196; 0.211	0.104; 0.078
	Omnivore	0.109; 0.086	0.06; 0.045	0.095; 0.063
Feeding Behaviour	*Browsing on substrate*	0.038; 0.034	0.037; 0.032	0.053; 0.05
	Filtering plankton	0.002; 0.005	0; 0	0; 0
	Grazing on aquatic plants	0.067; 0.085	0.058; 0.075	0.057; 0.074

		CPZs	**St Lucia NTSZ**	**Maputaland NTSZ**
	Hunting macrofauna (predator)	0.607; 0.222	0.67; 0.195	0.599; 0.218
	Picking parasites off a host (cleaner)	0.049; 0.089	0.04; 0.072	0.027; 0.04
	Selective plankton feeding	0.154; 0.184	0.139; 0.157	0.175; 0.164
	Variable	0.087; 0.075	0.06; 0.044	0.092; 0.062
Habitat	*Coral*	0.153; 0.155	0.166; 0.137	0.205; 0.126
	Reef	0.009; 0.022	0.003; 0.008	0.016; 0.049
	Sand	0.009; 0.018	0.009; 0.035	0.005; 0.015
	Coral/Reef	0.29; 0.182	0.242; 0.16	0.322; 0.157
	Reef/Sand	0.172; 0.276	0.075; 0.128	0.043; 0.103
	Coral/Reef/Sand	0.37; 0.26	0.508; 0.239	0.412; 0.208
Mobility	*Within*	0.664; 0.254	0.665; 0.231	0.549; 0.204
	Between	0.337; 0.254	0.336; 0.231	0.452; 0.204
Water Column	*Benthic*	0.521; 0.234	0.497; 0.206	0.581; 0.185
	Bentho-pelagic	0.299; 0.199	0.274; 0.147	0.339; 0.148
	Pelagic	0.182; 0.226	0.23; 0.257	0.081; 0.12

6.2 APPENDIX CHAPTER 3

Table 6.6: Results from the model summaries for Generalised Additive Models of the predicted relative abundance (Individuals/sample) of *Aprion virescens*. Estimates, standard errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as "Reef Size : Zone". Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

	Aprion virescens Abundance								
		Including Reef Size				**Excluding Reef Size**			
Parametric terms		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
	(Intercept)	0.194	0.186	1.041	0.298	0.1591	0.1707	0.932	0.351
	Management (CPZ)	-0.540	0.319	-1.690	0.091	-0.2465	0.2629	-0.938	0.348
	Management (St Lucia NTSZ)	-0.458	0.290	-1.579	0.114	-0.2619	0.2478	-1.057	0.291
Estimates for smooth terms		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
	Visibility	0.865	9	6.355	0.006 **	0.959	9	7.184	0.004 **
	Obstruction	0.000	9	0.000	0.661	0.000	9	0.000	0.680
	Water Column	0.893	9	8.285	0.002 **	0.893	9	8.218	0.002 **
	Temperature	0.000	9	0.000	0.853	0.001	9	0.001	0.327
	Depth	0.802	9	1.692	0.103	0.878	9	1.912	0.104
	PCO1	1.453	9	8.898	0.001**	1.411	9	6.757	0.006 **
	PCO2	0.679	9	2.100	0.052	0.619	9	1.627	0.079
	PCO3	0.360	4	0.462	0.213	0.000	9	0.000	0.368
	ReefSize : Maputaland NTSZ	0.997	3	3.211	0.048 *				
	ReefSize : CPZ	0.742	4	2.735	0.052				
	ReefSize : St Lucia NTSZ	0.607	3	1.460	0.117				

Table 6.7: Results from the model summaries for Generalised Additive Models the predicted biomass (kg/sample) of *Aprion virescens*. Estimates, Standard Errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), Residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as "Reef Size : Zone". Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Aprion virescens Biomass									
		Including Reef Size				**Excluding Reef Size**			
		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
Parametric terms	(Intercept)	0.537	0.209	2.569	0.012 *	0.567	0.213	2.663	0.009 **
	Management(CPZ)	-1.006	0.405	-2.485	0.015 *	-1.222	0.366	-3.333	0.001 **
	Management(St Lucia NTSZ)	-0.082	0.315	-0.262	0.794	0.181	0.283	0.637	0.525
		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
Estimates for smooth terms	Visibility	0.042	9	0.005	0.336	0.029	9	0.003	0.327
	Obstruction	0.000	9	0.000	0.322	0.000	9	0.000	0.779
	Water Column	0.000	9	0.000	1.000	0.000	9	0.000	0.909
	Temperature	0.000	9	0.000	0.943	0.000	9	0.000	0.595
	Depth	0.000	9	0.000	0.723	0.000	9	0.000	0.337
	PCO1	0.000	4	0.000	0.488	0.000	9	0.000	0.999
	PCO2	0.000	4	0.000	1.000	0.000	9	0.000	0.384
	PCO3	1.346	4	1.028	0.05 *	1.604	9	0.643	0.026 *
	ReefSize : Maputaland NTSZ	0.891	3	2.766	0.003 **				
	ReefSize : CPZ	1.048	4	1.301	0.017 *				
	ReefSize : St Lucia NTSZ	0.804	3	1.381	0.026 *				

Table 6.8: Results from the model summaries for Generalised Additive Models the predicted relative abundance (Individuals/sample) of *Caranx melampygus*. Estimates, Standard Errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), Residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that “Select = TRUE” regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as “Reef Size : Zone”. Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Caranx melampygus Abundance									
		Including Reef Size				**Excluding Reef Size**			
		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
Parametric terms	(Intercept)	-0.360	0.215	-1.673	0.094	-0.3306	0.2145	-1.541	0.123
	Management(CPZ)	-0.372	0.329	-1.129	0.259	-0.4232	0.3316	-1.276	0.201953
	Management(St Lucia NTSZ)	0.847	0.269	3.144	0.002 **	0.8966	0.2542	3.527	< 0.001 ***
Estimates for smooth terms		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
	Visibility	0.000	9	0.000	0.368	0.000	9	0.000	0.434
	Obstruction	0.000	9	0.000	1.000	0.000	9	0.000	1.000
	Water Column	1.205	9	4.204	0.028 *	1.428	9	5.841	0.014 *
	Temperature	0.869	9	6.547	0.005 **	0.860	9	6.124	0.007 **
	Depth	0.000	9	0.000	0.643	0.000	9	0.000	0.620
	PCO1	2.281	9	16.627	< 0.001 ***	2.220	9	15.798	< 0.001 ***
	PCO2	0.000	9	0.000	0.343	0.000	9	0.000	0.298
	PCO3	0.999	4	3.110	0.041 *	1.116	9	3.292	0.043 *
	ReefSize : Maputaland NTSZ	0.000	4	0.000	0.401				
	ReefSize : CPZ	0.000	4	0.000	0.414				
	ReefSize : St Lucia NTSZ	1.028	4	2.349	0.092				

Table 6.9: Results from the model summaries for Generalised Additive Models the predicted biomass (kg/sample) of *Caranx melampygus*. Estimates, Standard Errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), Residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that “Select = TRUE” regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as “Reef Size : Zone”. Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Caranx melampygus Biomass									
		Including Reef Size				**Excluding Reef Size**			
		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
Parametric terms	(Intercept)	0.378	0.202	1.875	0.064	0.574	0.200	2.874	0.005 **
	Management(CPZ)	-0.510	0.333	-1.533	0.129	-0.839	0.356	-2.355	0.021 *
	Management(St Lucia NTSZ)	0.334	0.280	1.191	0.237	0.850	0.250	3.399	0.001 **
		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
Estimates for smooth terms	Visibility	0.019	9	0.002	0.286	0.000	9	0.000	0.383
	Obstruction	0.000	9	0.000	0.586	0.000	9	0.000	0.409
	Water Column	0.000	9	0.000	0.339	0.000	9	0.000	0.581
	Temperature	0.000	9	0.000	0.657	1.282	9	0.315	0.103
	Depth	0.000	9	0.000	0.305	0.000	9	0.000	0.800
	PCO1	0.000	4	0.000	0.498	0.698	9	0.250	0.073
	PCO2	0.759	4	0.924	0.030 *	0.280	9	0.043	0.241
	PCO3	0.000	4	0.000	0.847	0.246	9	0.033	0.275
	ReefSize : Maputaland NTSZ	0.954	4	5.724	< 0.001 ***				
	ReefSize : CPZ	0.609	4	0.459	0.086				
	ReefSize : St Lucia NTSZ	0.957	3	8.587	< 0.001 ***				

Table 6.10: Results from the model summaries for Generalised Additive Models the predicted relative abundance (Individuals/sample) of *Lethrinus crocineus*. Estimates, Standard Errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), Residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that “Select = TRUE” regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as “Reef Size : Zone”. Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Lethrinus crocineus Abundance

		Including Reef Size				**Excluding Reef Size**			
		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
Parametric terms	(Intercept)	0.596	0.159	3.738	< 0.001 ***	0.605	0.158	3.831	< 0.001 ***
	Management(CPZ)	-0.555	0.261	-2.124	0.034	-0.562	0.261	-2.154	0.031 *
	Management(St Lucia NTSZ)	0.302	0.212	1.424	0.155	0.294	0.211	1.392	0.164
Estimates for smooth terms		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
	Visibility	0.000	9	0.000	0.747	0.000	9	0.000	0.760
	Obstruction	0.632	9	1.570	0.108	0.632	9	1.569	0.108
	Water Column	0.363	9	0.553	0.211	0.349	9	0.523	0.216
	Temperature	0.000	9	0.000	1.000	0.000	9	0.000	1.000
	Depth	0.000	9	0.000	0.417	0.000	9	0.000	0.394
	PCO1	0.000	9	0.000	1.000	0.000	9	0.000	1.000
	PCO2	0.000	9	0.000	0.481	0.000	9	0.000	0.473
	PCO3	0.579	4	0.887	0.206	0.638	9	1.091	0.172
	ReefSize : Maputaland NTSZ	0.217	4	0.275	0.257				
	ReefSize : CPZ	0.000	4	0.000	0.389				
	ReefSize : St Lucia NTSZ	0.000	4	0.000	0.476				

Table 6.11: Results from the model summaries for Generalised Additive Models the predicted biomass (kg/sample) of *Lethrinus crocienus*. Estimates, Standard Errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), Residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as "Reef Size : Zone". Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

		Lethrinus crocineus Biomass							
		Including Reef Size				**Excluding Reef Size**			
		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
Parametric terms	(Intercept)	-0.288	0.202	-1.424	0.159	-0.2779	0.1917	-1.449	0.151
	Management(CPZ)	-0.452	0.362	-1.250	0.215	-0.8002	0.3553	-2.252	0.027 *
	Management(St Lucia NTSZ)	-0.193	0.329	-0.587	0.559	0.4261	0.2573	1.656	0.1018
Estimates for smooth terms		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
	Visibility	0.612	9	0.186	0.100	0.686	9	0.230	0.085
	Obstruction	0.000	9	0.000	0.914	0.000	9	0.000	0.560
	Water Column	0.000	9	0.000	1.000	0.000	9	0.000	0.547
	Temperature	0.369	9	0.067	0.192	0.000	9	0.000	0.543
	Depth	1.312	9	0.473	0.032 *	0.947	9	0.166	0.198
	PCO1	1.438	4	0.947	0.061	1.742	9	0.425	0.093
	PCO2	0.000	4	0.000	0.716	0.431	9	0.077	0.196
	PCO3	0.414	4	0.188	0.154	0.000	9	0.000	1.000
	ReefSize : Maputaland NTSZ	1.157	4	2.634	0.001 **				
	ReefSize : CPZ	0.859	4	1.577	0.008 **				
	ReefSize : St Lucia NTSZ	0.910	3	3.506	0.001 **				

Table 6.12: Results from the model summaries for Generalised Additive Models the predicted relative abundance (Individuals/sample) of *Lutjanus bohar*. Estimates, Standard Errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), Residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as "Reef Size : Zone". Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Lutjanus bohar Abundance									
		Including Reef Size				**Excluding Reef Size**			
		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
Parametric terms	(Intercept)	0.313	0.221	1.418	0.156	0.748	0.161	4.656	< 0.001 ***
	Management(CPZ)	0.138	0.324	0.426	0.670	-0.323	0.247	-1.308	0.191
	Management(St Lucia NTSZ)	0.059	0.288	0.204	0.838	-0.300	0.235	-1.275	0.202
		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
Estimates for smooth terms	Visibility	0.000	9	0.000	0.573	0.000	9	0.000	0.501
	Obstruction	0.000	9	0.000	0.357	0.000	9	0.000	1.000
	Water Column	0.000	9	0.000	0.424	0.000	9	0.000	0.618
	Temperature	0.000	9	0.000	0.731	1.180	9	1.911	0.186
	Depth	2.216	9	12.594	0.001**	1.849	9	8.568	0.005 **
	PCO1	0.000	9	0.000	0.583	0.000	9	0.000	0.450
	PCO2	0.317	9	0.399	0.252	0.000	9	0.000	0.402
	PCO3	0.677	4	1.996	0.082	0.772	9	3.218	0.039 *
	ReefSize : Maputaland NTSZ	1.811	4	10.761	0.002				
	ReefSize : CPZ	1.092	4	3.721	0.042				
	ReefSize : St Lucia NTSZ	0.459	3	0.793	0.187				

Table 6.13: Results from the model summaries for Generalised Additive Models the predicted biomass (kg/sample) of *Lutjanus bohar*. Estimates, Standard Errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), Residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that “Select = TRUE” regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as “Reef Size : Zone”. Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

	Lutjanus bohar Biomass								
		Including Reef Size				**Excluding Reef Size**			
		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
Parametric terms	(Intercept)	0.890	0.193	4.621	< 0.001 ***	0.958	0.189	5.067	< 0.001 ***
	Management(CPZ)	0.032	0.294	0.107	0.915	-0.092	0.287	-0.322	0.748
	Management(St Lucia NTSZ)	0.148	0.300	0.495	0.622	0.329	0.259	1.273	0.207
		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
Estimates for smooth terms	Visibility	0.000	9	0.000	0.410	0.000	9	0.000	0.353
	Obstruction	0.000	9	0.000	0.760	0.000	9	0.000	0.752
	Water Column	0.742	9	0.149	0.157	0.409	9	0.070	0.204
	Temperature	0.000	9	0.000	1.000	0.000	9	0.000	0.854
	Depth	0.000	9	0.000	0.604	0.000	9	0.000	0.984
	PCO1	0.601	4	0.372	0.111	0.720	9	0.322	0.045 *
	PCO2	0.000	4	0.000	0.940	0.000	9	0.000	0.998
	PCO3	0.000	4	0.000	0.779	0.122	9	0.017	0.269
	ReefSize : Maputaland NTSZ	0.919	4	2.773	< 0.001 ***				
	ReefSize : CPZ	0.232	4	0.077	0.250				
	ReefSize : St Lucia NTSZ	0.748	3	0.956	0.051				

Table 6.14: Results from the model summaries for Generalised Additive Models the predicted relative abundance (Individuals/sample) of *Variola louti*. Estimates, Standard Errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), Residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that “Select = TRUE” regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as “Reef Size : Zone”. Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Variola louti Abundance									
		Including Reef Size				**Excluding Reef Size**			
Parametric terms		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
	(Intercept)	0.286	0.160	1.794	0.073	0.2867	0.1595	1.798	0.072
	Management(CPZ)	-0.110	0.238	-0.463	0.643	-0.1181	0.2353	-0.502	0.6158
	Management(St Lucia NTSZ)	0.118	0.223	0.530	0.596	0.1524	0.2135	0.714	0.4754
Estimates for smooth terms		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
	Visibility	1.485	9	3.597	0.078	1.489	9	3.624	0.077
	Obstruction	0.000	9	0.000	0.702	0.000	9	0.000	0.613
	Water Column	0.548	9	0.826	0.202	0.522	9	0.758	0.214
	Temperature	0.000	9	0.000	0.464	0.000	9	0.000	0.458
	Depth	0.000	9	0.000	0.637	0.000	9	0.000	0.658
	PCO1	0.907	9	9.393	0.001 **	0.909	9	9.593	0.001 **
	PCO2	0.459	9	0.889	0.158	0.490	9	1.006	0.147
	PCO3	0.000	4	0.000	0.626	0.000	9	0.000	0.691
	ReefSize : Maputaland NTSZ	0.000	4	0.000	0.742				
	ReefSize : CPZ	0.049	4	0.052	0.302				
	ReefSize : St Lucia NTSZ	0.254	3	0.329	0.252				

Table 6.15: Results from the model summaries for Generalised Additive Models the predicted biomass (kg/sample) of *Variola louti*. Estimates, Standard Errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), Residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that “Select = TRUE” regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as “Reef Size : Zone”. Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Variola louti Biomass									
		Including Reef Size				**Excluding Reef Size**			
		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
Parametric terms	(Intercept)	0.688	0.128	5.370	0.000	0.6443	0.1525	4.225	< 0.001 ***
	Management(CPZ)	0.016	0.219	0.074	0.941	-0.1902	0.2516	-0.756	0.45215
	Management(St Lucia NTSZ)	-0.330	0.294	-1.119	0.267	0.5981	0.1983	3.016	0.003 **
Estimates for smooth terms		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
	Visibility	1.244	9	0.662	0.009 **	1.497	9	0.813	0.007 **
	Obstruction	0.000	9	0.000	0.615	1.150	9	0.299	0.085
	Water Column	1.500	9	0.759	0.008 **	1.696	9	0.506	0.045 *
	Temperature	0.000	9	0.000	0.363	0.000	9	0.000	0.793
	Depth	0.000	9	0.000	1.000	0.001	9	0.000	0.307
	PCO1	1.714	4	2.334	0.003 **	2.344	9	1.489	0.001 **
	PCO2	0.000	4	0.000	0.567	0.000	9	0.000	0.570
	PCO3	0.596	4	0.519	0.054	1.255	9	0.582	0.015 *
	ReefSize : Maputaland NTSZ	0.790	4	1.316	0.011 *				
	ReefSize : CPZ	0.814	4	1.556	0.006 **				
	ReefSize : St Lucia NTSZ	1.723	4	4.810	< 0.001 ***				

Table 6.16: Results from the model summaries for Generalised Additive Models the probability of detection of *Epinephelus tukula*. Estimates, Standard Errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), Residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as "Reef Size : Zone". Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Epinephelus tukula Probability of detection									
		Including Reef Size				**Excluding Reef Size**			
		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
Parametric terms	(Intercept)	0.128	0.408	0.312	0.755	0.1275	0.4081	0.312	0.755
	Management(CPZ)	-0.696	0.615	-1.132	0.258	-0.6963	0.6151	-1.132	0.258
	Management(St Lucia NTSZ)	1.140	0.611	1.866	0.062	1.1395	0.6106	1.866	0.062
Estimates for smooth terms		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
	Visibility	1.158	9	2.766	0.085	1.158	9	2.766	0.086
	Obstruction	0.811	9	3.559	0.033 *	0.811	9	3.559	0.033 *
	Water Column	1.205	9	5.625	0.013 *	1.205	9	5.625	0.013 *
	Temperature	0.790	9	3.298	0.038 *	0.790	9	3.298	0.038 *
	Depth	0.000	9	0.000	0.629	0.000	9	0.000	0.583
	PCO1	0.000	9	0.000	0.599	0.000	9	0.000	0.599
	PCO2	0.000	9	0.000	0.343	0.000	9	0.000	0.343
	PCO3	0.000	4	0.000	0.789	0.000	9	0.000	0.828
	ReefSize : Maputaland NTSZ	0.000	4	0.000	0.843				
	ReefSize : CPZ	0.000	4	0.000	1.000				
	ReefSize : St Lucia NTSZ	0.000	4	0.000	0.747				

Table 6.17: Results from the model summaries for Generalised Additive Models the predicted biomass (kg/sample) of *Epinephelus tukula*. Estimates, Standard Errors, t and P values are given for parametric variables. Estimated degrees of freedom (edf), Residual degrees of freedom (Red.df), F and P values are also given for non-parametric variables for smooth terms. Where an edf of zero shows that "Select = TRUE" regarded the variable as having no effect, and an edf of 1 shows a linear relationship. Reef Size is given for each level of Management, indicated as "Reef Size : Zone". Models which included Reef size as a covariate are placed on the left of the table, and those excluding Reef Size on the Right. Asterisks indicate levels of significance; * P < 0.05, ** P < 0.01 and *** P < 0.001.

Epinephelus tukula Biomass									
		Including Reef Size				**Excluding Reef Size**			
		Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
Parametric terms	(Intercept)	2.889	0.180	16.013	< 0.001 ***	2.7484	0.1956	14.048	< 0.001 ***
	Management(CPZ)	-0.655	0.374	-1.751	0.084	-0.6854	0.3595	-1.907	0.0602
	Management(St Lucia NTSZ)	-0.025	0.256	-0.098	0.922	0.1801	0.2849	0.632	0.5292
Estimates for smooth terms		edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
	Visibility	0.009	9	0.001	0.233	0.000	9	0.000	0.413
	Obstruction	0.000	9	0.000	0.714	0.000	9	0.000	0.515
	Water Column	1.400	9	0.507	0.039 *	0.300	9	0.061	0.177
	Temperature	0.174	9	0.033	0.190	0.656	9	0.274	0.053
	Depth	2.044	9	1.008	0.007 **	1.279	9	0.325	0.098
	PCO1	0.000	4	0.000	0.820	0.718	9	0.341	0.037 *
	PCO2	0.000	4	0.000	0.866	0.000	9	0.000	1.000
	PCO3	0.000	4	0.000	0.538	0.000	9	0.000	0.268
	ReefSize : Maputaland NTSZ	0.845	4	1.817	0.004 **				
	ReefSize : CPZ	0.742	4	0.953	0.025 *				
	ReefSize : St Lucia NTSZ	0.000	3	0.000	0.290				

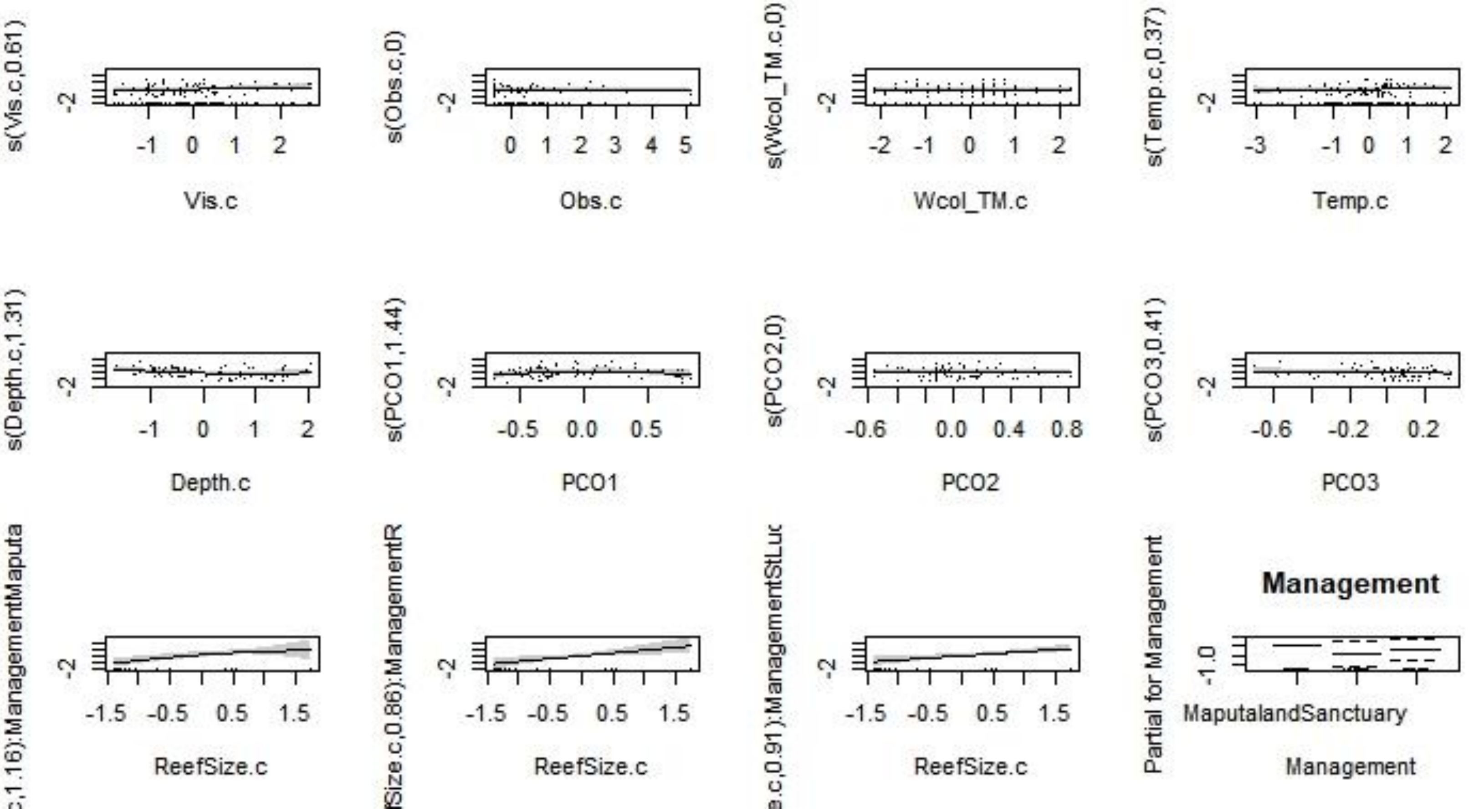


Figure 6.31 Gam Plots for the Biomass of *Lethrinus crocineus* modelled to include Reef Size data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3. Included in this appendix for the purpose of displaying the relationship with Depth (Depth.c).

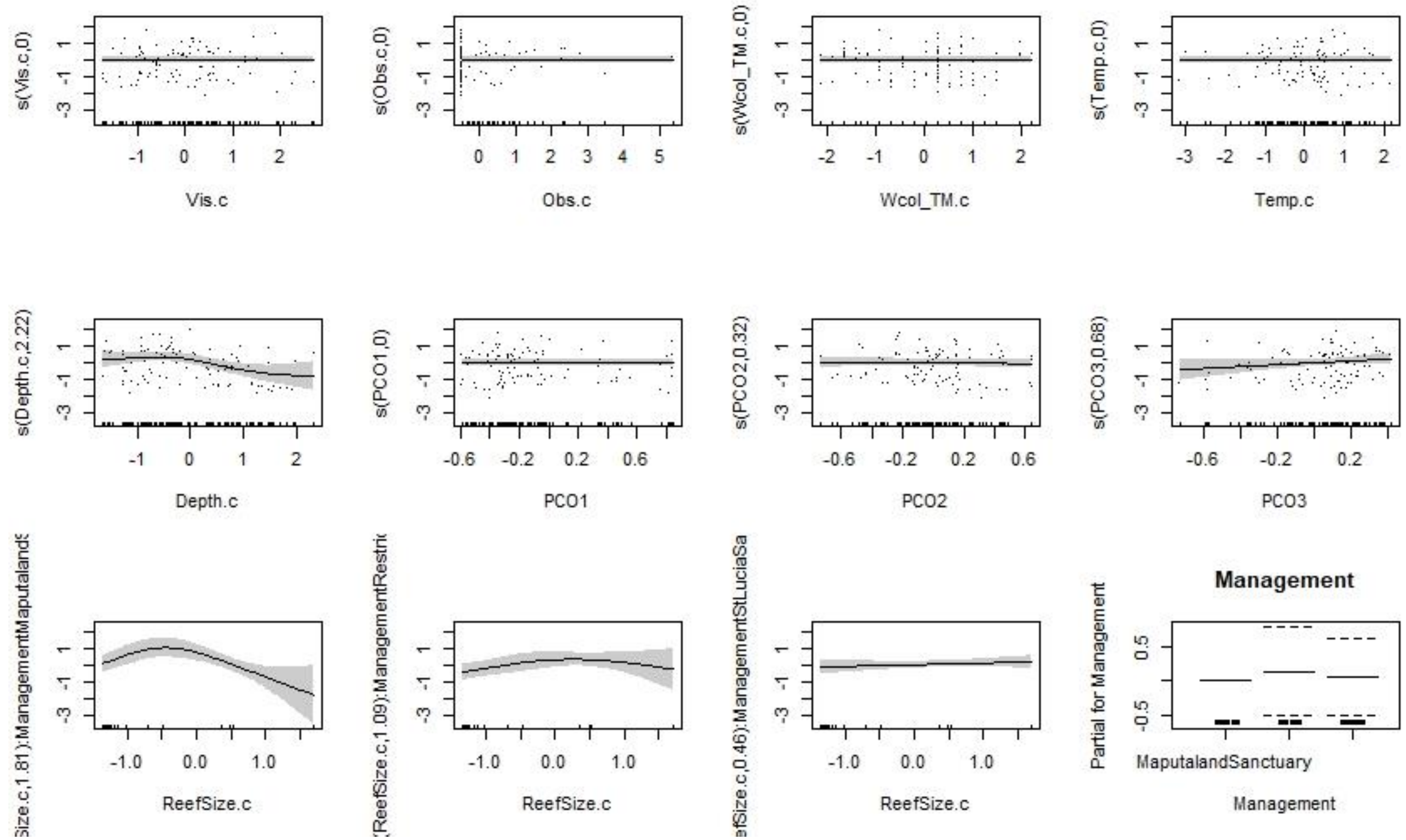


Figure 6.32: Gam Plots for the Abundance of *Lutjanus bohar* modelled to include Reef Size data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3. Included in this appendix for the purpose of displaying the relationship with Depth (Depth.c).

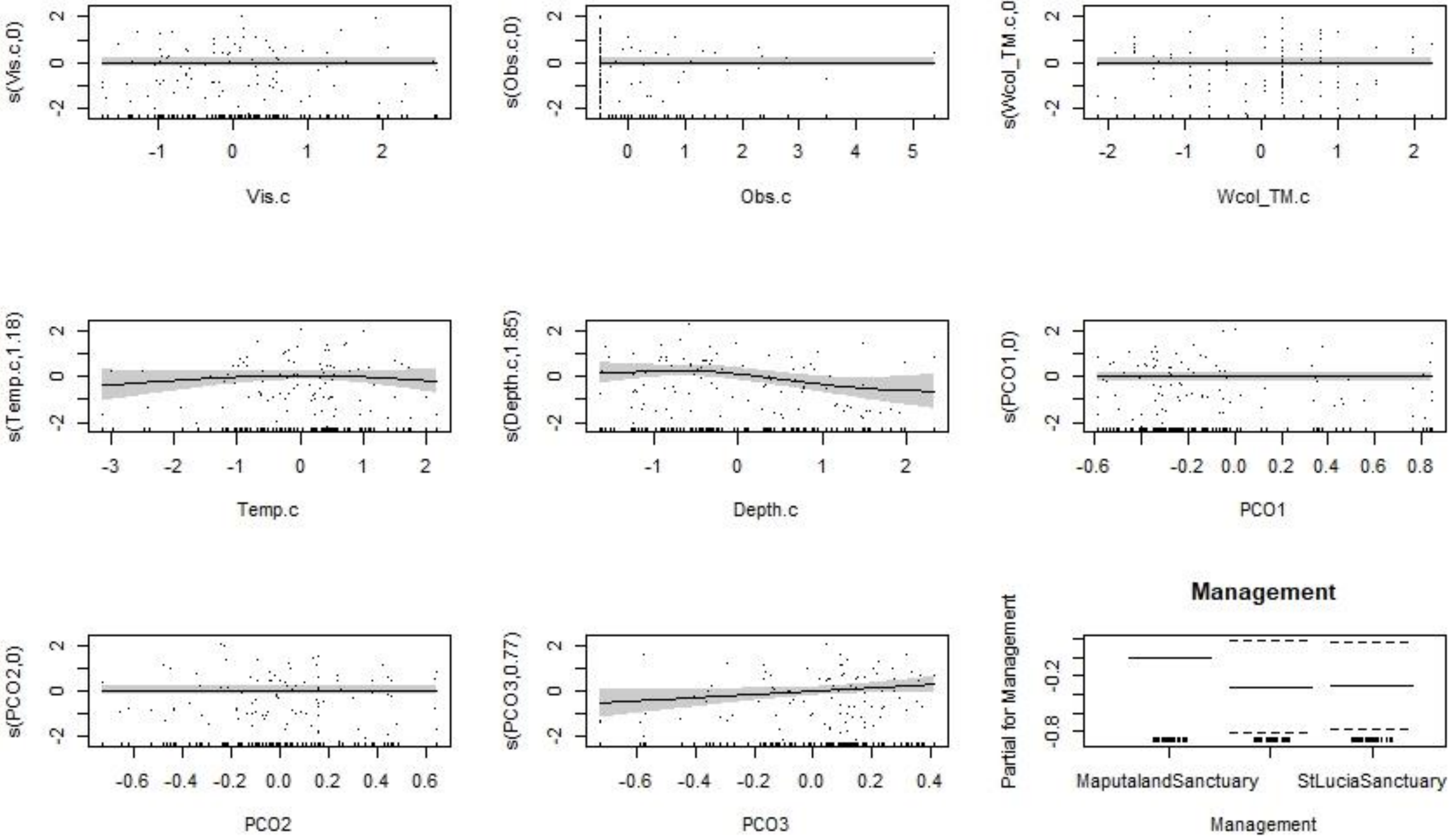


Figure 6.33: Gam Plots for the Abundance of *Lutjanus bohar* modelled to exclude Reef Size data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3. Included in this appendix for the purpose of displaying the relationship with Depth (Depth.c).

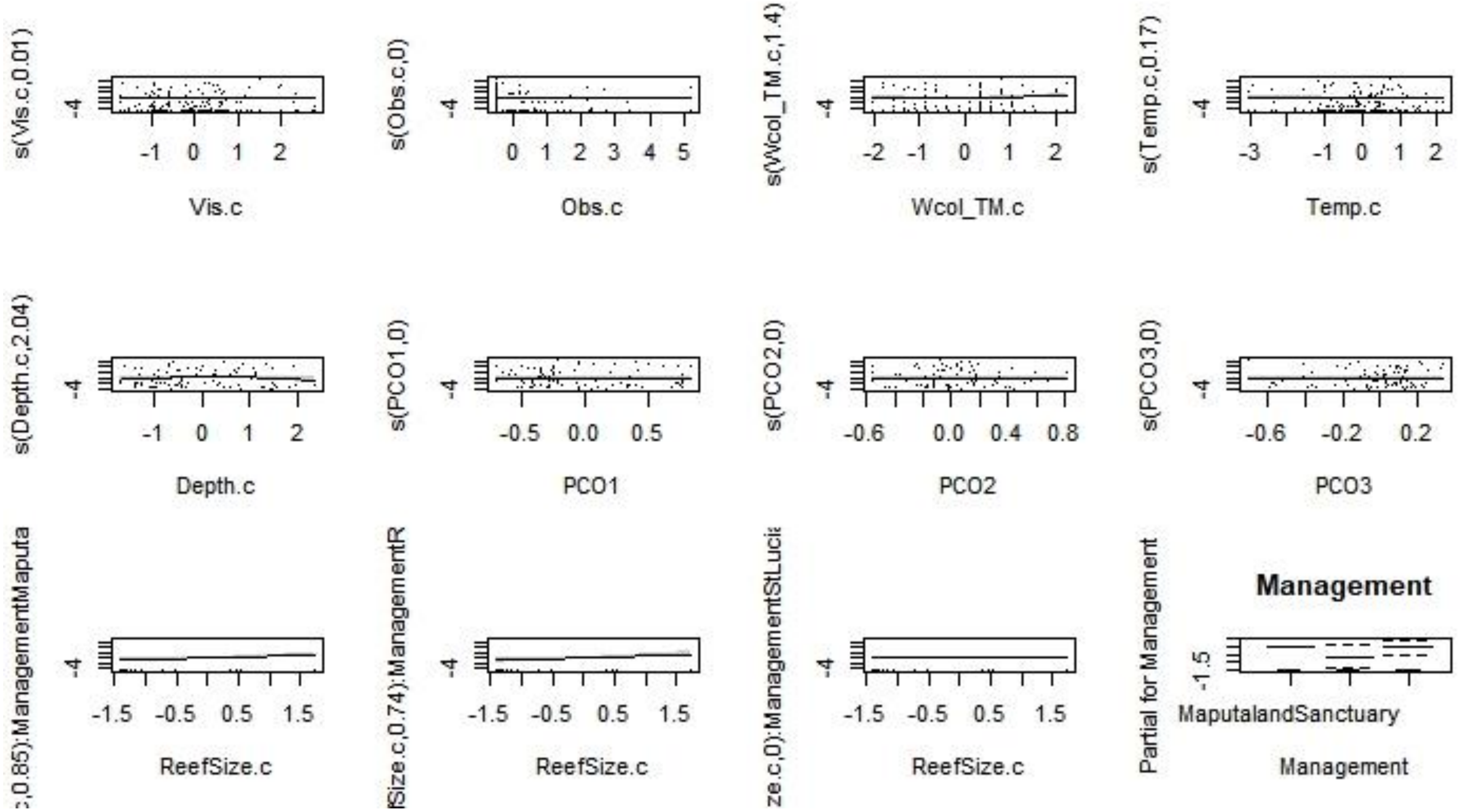


Figure 6.34 Gam Plots for the Biomass of *Epinephelus tukula* modelled to include Reef Size data. This shows the smoothing parameters for each covariate. Whereby Vis.c = Visbility, Obs.c = Obstruction, Wcol_TM.c = Water Column, Temp.c = Temperature, Depth.c = Depth, ReefSize.c = Reef Size then habitat variates generated via DPCM are listed PCO1, PCO2 and PCO3. Included in this appendix for the purpose of displaying the relationship with Depth (Depth.c).

6.3 SEASONAL COMPARISON

6.3.1 REASON FOR INVESTIGATION

Due to logistical constraints sampling within the iSimangaliso Wetland Park had to be done over two fieldtrips. The first fieldtrip was conducted in the austral summer of November 2016 and the second in the winter of June 2017. The first fieldtrip collected data from the St Lucia Sanctuary, and the St Lucia and Maputaland Restricted Zones. The second fieldtrip collected data from the Maputaland Sanctuary. High-latitude coral reefs are unique from equatorial reefs given that they will experience a marked difference in environmental conditions between seasons. This brief investigation aimed to establish if there was a significant difference in fish communities between seasons.

6.3.2 BRIEF METHODS

Eight Stereo-BRUV deployments from within the St Lucia Sanctuary were replicated at the same GPS coordinates for both the Summer (2016) field trip and the Winter (2017) field trip. These sixteen deployments were then analysed using EventMeasure to extract the relative abundance (MaxN) of all species present within each deployment. The abundance data were then placed into an assembly matrix of all 16 sample sites, along with a corresponding trait-matrix (See Chapter 2. The assembly and trait matrices were then processed in Rstudio using the FD Package (See Chapter 2 to build a matrix of abundances for functional groups across sample sites. The functional group abundances and raw species-level abundances were then analysed in Primer 7 + PERMANOVA. Shade plots indicated that there was no need for dispersion weighting and overall transformations. Resemblance matrices were then built using the Bray-Curtis resemblance measure for the functional group abundances and a modified Gower resemblance for the raw abundances given the prevalence of zeros in the data. Metric-multidimensional scaling (mMDS) was then used to visualise the functional and species-level abundances in both two- and three-dimensional space with corresponding Sheppard's plots. Both Sheppard's plots indicated the need for a non-zero intercept. The mMDS were then plotted with the season (Summer/Winter) as a factor. To test for a significant effect of season, PERMANOVAs were then done on the resemblance matrix using 9999 permutation, done according to unrestricted permutation of raw data with Type III Sum of Squares.

6.3.3 RESULTS

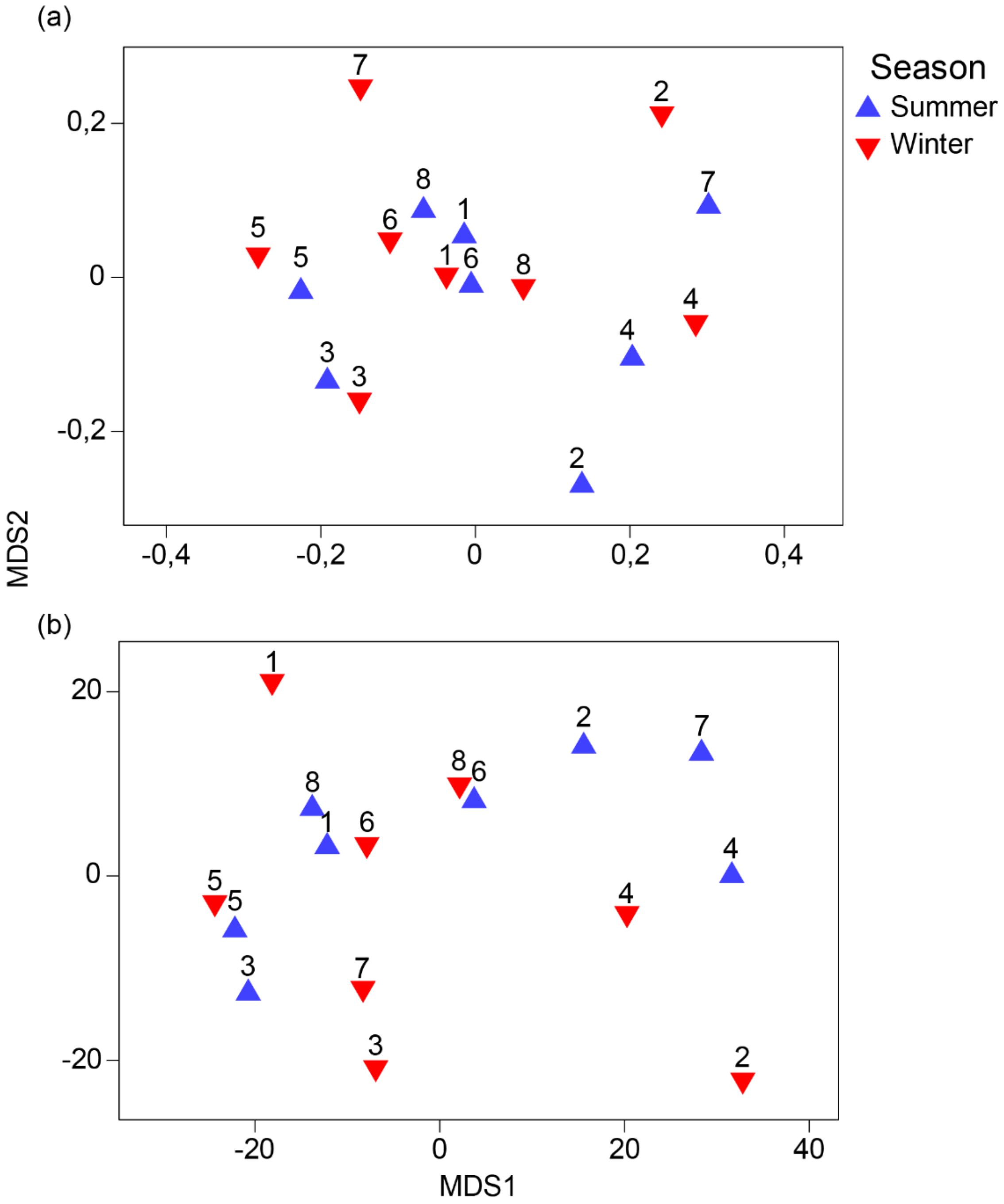


Figure 6.35 Metric-multidimensional scaling plots of a) Species Abundances with 0.17 2D Stress and b) Functional Group Abundances with 0.15 2D Stress both with non-zero intercept. This was based on a) Modified Gower and b) Bray-Curtis Resemblance matrices between eight samples collected in the St Lucia Sanctuary in Summer (2016) and their replicates collected in Winter (2017). Where numbering represents samples and their corresponding replicates and colour represents season.

Table 6.18 Output of PERMANOVA results to test level of significance for Season as a Factor. These PERMANOVAs were done using 9999 unrestricted permutations of raw data, and Type III Sum of Squares for both Species Abundances and Functional Group Abundances.

	PERMANOVA	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Species	Season	1	0.414	0.414	0.783	0.789	5025
	Residual	14	7.396	0.528			
	Total	15	7.81				
Functional Group	Season	1	540.9	540.9	0.308	0.978	5115
	Residual	14	24592	1756.6			
	Total	15	25133				

6.3.4 CONCLUSION

The mMDS plot shows no distinct groupings between winter and summer for both a Species and Functional Level of reef fish communities (Figure 6.1), this is then confirmed by the PERMANOVA which showed no significant difference between Season for Species and Functional Group Abundances ($_{\text{Pseudo-F}}$ 0.783; $_{\text{P(perm)}}$ 0.789 and $_{\text{Pseudo-F}}$ 0.308; $_{\text{P(perm)}}$ 0.978 respectively). Because there is no significant effect of Season the stereo-BRUV data collected from November 2016 and June 2017 can be analysed as a whole dataset.