

Building the foundation for efficient monitoring of mesophotic fishes to support management of the uThukela Banks marine protected area

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Thembelihle Dube

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ABSTRACT

Long-term monitoring (LTM) is essential to assess the ecological benefits of marine protected areas (MPAs), and baseline data are required as a foundation of an effective monitoring programme. However, to be successful, LTM programmes must be feasible, in terms of costs and resources, and rigorous, to ensure statistical trends are detectable. The uThukela Banks MPA is a relatively new (established in 2019) large conservation area on the North-East coast of KwaZulu-Natal, South Africa. uThukela Banks MPA protects important demersal fisheries species found on mesophotic reef systems in the mid- and outer-continental shelf (30-150 m depth). Mesophotic reefs are particularly important for larger sexually mature fish that undertake ontogenetic habitat shifts from shallow nursery grounds. Few studies, especially in the context of South Africa, have investigated fish population and community structure on mesophotic reefs or on method optimization for LTM of mesophotic reef ecosystems. As such, this study aimed to provide a description of the fish communities and propose a feasible and robust LTM programme for the mesophotic reef fishes in the uThukela Banks MPA. To do this, 11 mesophotic reefs were mapped with multi-beam echo-sounder and fish were surveyed with baited remote underwater stereo-video systems (stereo-BRUVs) following a stratified random sampling approach, informed by the reef maps.

Fish assemblage structure on the mesophotic reefs was significantly influenced by depth, benthic habitat type and habitat complexity. Reef habitats hosted higher species richness and abundance than adjacent sand habitats. Slinger *Chrysoblephus puniceus* abundance was greatest on moderate-depth reefs with higher structural complexity. Multivariate analyses identified distinct fish assemblages among the management zones, with restricted and controlled-pelagic zones supporting different assemblages than adjacent fished sites. However, this was driven by habitat and depth gradients rather than management measures. Species accumulation curves, power analysis and cost-benefit analysis were used to identify the sampling parameters for a feasible and robust LTM programme. Species accumulation curves had very high variability with between 8 and 38 samples required to detect 90 % of the observed fish species. The power analysis showed that 36 samples per location are required to detect a 10 % annual increase in slinger abundance over five years. Sample size requirements to detect the same changes in the abundance of all fish, biomass of all fish and abundance of species caught by commercial fisheries (sexually mature fisheries targets) was 16, 28, and 32, respectively. The results from the cost-benefit analysis showed that

the costs for collecting stereo-BRUVs data per reef was R42 450 including boat fuel, bait, consumables, skipper, accommodation etc. The cost per stereo-BRUVs sample was R1 180.56 and the cost of surveying one mesophotic reef in each of the four zones of the uThukela Banks MPA and an adjacent fished reef site would be R212 500. A cost of R467 500 was estimated to survey the 11 reef systems originally included in this study.

These results highlighted the importance of cost-considerations in an LTM programme. The priorities of a LTM programme must be refined and predetermined, because financial constraints tend to restrict the scope of monitoring. The study's outcome is an optimally designed LTM that can be used by Ezemvelo KZN Wildlife (the management authority for the uThukela Banks MPA). These comprehensive baseline data and their inclusion into a monitoring framework will help them to monitor changes in fish assemblages in the study area. The study also serves as a template that can be used to inform mesophotic fish population monitoring throughout the KwaZulu-Natal MPA network.

Key words: marine protected areas, stereo-BRUVs, baseline data, LTM, mesophotic fish

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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.

1 GENERAL INTRODUCTION

1.1 GLOBAL STATE OF FISH POPULATIONS AND THEIR IMPORTANCE TO HUMANS

Marine fish stocks worldwide across a variety of species, taxonomic groups, and trophic levels, are in decline (Pauly et al., 2002; Pauly, 2008). The Peruvian anchoveta population, for instance, collapsed in 1971-1972; the first collapse to have global repercussions and perceived to have been caused by an El Niño event (Pauly et al., 2002). However, several studies show that overfishing was also the cause of the collapse in addition to what has been labelled as “environmental effects”, the increase in actual catches was determined to be approximately 18 million tonnes, which far exceeded the reported catches of 12 million tonnes (Pauly et al., 2002). Overfishing is one of the biggest threats to fish populations (Myers and Worm, 2005; Pauly et al., 2005; Brander, 2007; Sink et al., 2019; Sadovy de Mitcheson et al., 2020; Dulvy et al., 2021; Sherman et al., 2023). With reductions (to a tenth or less) in the biomass of large fish and high-value fish species that are traditionally targeted by fisheries (Jennings and Kaiser, 1998; Hsieh et al., 2008; Pauly, 2008; Asche et al., 2025). This is especially true regarding the removal of higher trophic level fishes such as sharks and rays (Sherman et al., 2023; Jabado et al., 2024). This disproportionate collapse of fish stocks at a particular trophic level compromises productivity of ecological communities.

Marine biodiversity is essential for human well-being and survival. Many people who live along the coast depend on fishing to support their livelihoods; providing them with jobs, recreational opportunities, a food source, and various cultural and spiritual connections (Mathiesen, 2015; Jabado et al., 2024). Recreational fisheries are one example of a fisheries sector that help improve the financial status of people. South Africa (SA) is one of the countries whose marine recreational fishing sector is regarded as an economically important component of its fisheries (Baust et al., 2015; Potts et al., 2022). Successful marine tourism in SA is underpinned by healthy ecosystems, of which well-managed fish stocks form an integral part; whether whale watching, shark cage diving or dive tourism, and plays a key recreational and economic role (Geldenhuys et al., 2019; Munien et al., 2019). However, growing human populations

accelerates the loss of biodiversity (Hockey and Branch, 1997; Jackson et al., 2001; Dalton et al., 2021). For example, the South African linefishery has been growing since the middle of the 1800s to include different fisheries sectors, including recreational, small-scale, and commercial fishers (Mann, 2013).

1.2 ANTHROPOGENIC IMPACTS ON FISH POPULATIONS

Anthropogenic impacts such as overfishing results in habitat loss, this threatens the persistence of marine fish biodiversity (Turner et al., 1999; Yan et al., 2021). Sediment loads generated by construction may be deposited in shallow ecosystems and estuaries. Resulting in high turbidity levels which limits light penetration thus preventing growth of rooted aquatic plants (Islam and Tanaka, 2004). Fine sediment may inhibit fish spawning which in turn disrupts the aquatic ecosystem habitat (Thrush and Dayton, 2002; Islam and Tanaka, 2004; Petersen et al., 2015; Brown et al., 2022). Pollution also leads to a decline in fish population, for example, filter-feeding megafauna; particularly, manta rays, are more susceptible to ingesting pollutants such as microplastics and heavy metals (Stewart et al., 2018). Pesticides used for pest control reach the ocean through runoff into coastal waters. These have harmful effects on marine life, including tumours, lesions, cancers, and immune system suppression, and excessive slime on the gills and scales of fish (Islam and Tanaka, 2004; Stewart et al., 2018). In addition, anthropogenic-induced climate change, reflected by an increase in ocean acidity (Doney et al., 2009) and temperatures (Bindoff et al., 2007; Ortega-Cisneros et al., 2021) negatively affect fish populations. Ocean warming reduces subsurface oxygen and causes marine species to suffocate and die. In addition, it may change the behaviour, demographic traits (for example productivity), and physiological functioning, and the behaviour of fish thus resulting in shifts in spatial range, seasonal abundance, and size structure of populations (Doney et al., 2012).

1.3 ANTHROPOGENIC PRESSURES IN THE UTHUKELA BANKS MPA

The eThekweni Metropolitan has 3.9 million people, accounting 34.7 % of the total population of the KZN province (eThekweni metropolitan and DCoG, 2020). The eThekweni Metropole has highest coastal accessibility due to nearby ports and harbours. Greater accessibility to marine resources on the KZN coast leads to increased exploitation as more people settle in the region (Sink et al., 2019). For example, uThukela river is a conduit for sediment delivery to both near and offshore ecosystems of the KZN Bight, acting as a critical link between land and sea (Sink et al., 2019). Therefore, population growth may

negatively affect the KZN Bight and uThukela River, leading to poor conditions in the uThukela Banks MPA, which is located near the largest harbours in Africa (Richards Bay and Durban harbour).

Anthropogenic activities on the shelf edge in the KZN include midwater trawl fishery, offshore hake trawling, large pelagic long linefishery (Petersen et al., 2015). These activities compromise species environmental cues, food web processes, and nursery functions, degrading the overall ecological condition of marine ecosystem types (Petersen et al., 2015; Lagabriele et al., 2018). Commercial fishing gear can negatively impact fish populations, especially larger non-target species. For example, commercial prawn trawling in uThukela MPA Banks harms sharks and various fish species due to high bycatch levels (Fennessy, 1994). Offshore pipelines extend over 155 km from land to offshore platforms, connecting gas-to-liquid plants and this pose a risk to the ecosystem (DFE, 2022). Understanding these pressures is vital for improving marine conservation efforts. uThukela Banks MPA was proclaimed to protect unique and threatened benthic ecosystem types and associated ecological processes of the area contained within this area of the Natal Bight (DEA SA, 2019). Including reef, gravelly, and submarine canyon habitats. Among these important ecosystems was the protection of mesophotic reefs, which host important, abundant and diverse marine organisms, including mesophotic reef fishes. Therefore, research and monitoring are needed to track recovery and the outcomes of different management measures.

1.4 MANAGEMENT OF FISH POPULATIONS

Fisheries management aims to ensure sustainability by providing food, supporting economic activities, while conserving fish populations (Claudet et al., 2006). A key conservation challenge today is managing ecosystems, marine resources, and resource users amid climate change and growing human populations (Carlisle et al., 2019).

1.4.1 TRADITIONAL SPECIES MANAGEMENT

Single species management is the traditional approach for managing fish populations. It focuses on individual species, without considering their relationships with the environment (Mace, 2001; Aïramé et al., 2003). Traditional fisheries management can rebuild depleted fisheries, maintain healthy stock sizes, and achieve target fishing rates (Hilborn and Ovando, 2014). However, it costs up to 15 % of the stock's landed value and requires skilled fisheries scientists and personnel to manage and enforce fishery regulations (Arnason et al., 2000). It relies mostly on single species stock assessments (Claudet et al., 2006)

and stock status (Jennings et al., 1996) which necessitates extensive and expert analysis (Hilborn and Ovando, 2014). It has also failed to prevent fish stock declines and overfishing (Claudet et al., 2006). This management tools include gear restrictions, catch shares, total allowable catch reductions, closed areas, total fishing effort reductions, fisheries certification, capacity reductions, and community co-management (Hilborn and Ovando, 2014). These tools can only be implemented over large spatial scales (Palumbi, 2004). Rising biodiversity threats requires donors and conservation managers to develop advanced , transparent and efficient tools for prioritising conservation actions (Edgar et al., 2007). Which speaks to fisheries management both locally and globally. Traditional management alone had little historical success in halting marine biodiversity loss, highlighting the need for alternative and more realistic approaches to sustainably manage heavily exploited fish stocks (Shannon et al., 2010).

1.4.2 ECOSYSTEM APPROACH TO FISHERIES MANAGEMENT

The ecosystem-based approach to fisheries management (EBFM), synonymous with the ecosystem approach to fisheries (EAF), is an approach developed and implemented by managers for the sustainable use of biodiversity (Jennings et al., 1996; Garcia and Cochrane, 2005). The EBFM is recommended for addressing a holistic, effective and adaptive management approach that not only consider the ecosystem, but consistently manages fish catches (Jennings et al., 1996; Pikitch et al., 2004a). It addresses growing direct and indirect effects of fishing on targeted populations, essential habitats, trophic connections, and ecosystem functions (George et al., 2007; Kellner et al., 2011). The basis of EBFM is recognising that ecosystems fluctuate and change naturally over time (George et al., 2007). It seeks to prevent habitat degradation caused by destructive fishing methods (Pikitch et al., 2004a).

Marine protected areas (MPAs) are one of the EBFM tools for mitigating the impacts of anthropogenic activities on the ocean and designated specifically for conserving fish stocks in the light of changes in marine ecosystems. They are defined as spatially demarcated areas with restrictions to control or reduce human activity, and promote marine biodiversity conservation and management (Edgar et al., 2007; Dando, 2020). They are often divided into zones, a spectrum which includes extractive zones where certain activities are permitted, and no-take zones offering full protection of marine resources because extractive use such as fishing is not permitted (Field et al., 2025). They supplement traditional fisheries management, their objectives includes managing and protecting sensitive, threatened, and essential habitats (i.e. nursery grounds and spawning sites) (Agardy, 2000; Palumbi, 2004); conserving endangered

species (Roberts et al., 2021; Faure-Beaulieu et al., 2023); supporting the recovery of depleted stocks (Heyns-Veale et al., 2019a); recovering age, size classes and sex ratios, and to benefit the recovery of fisheries (Rieser, 2000). They also play a huge role in improving fish yields while conserving biological diversity by reducing fishing effort and hence overall mortality (Jennings and Kaiser, 1998; Aïramé et al., 2003; Stevens and Connolly, 2004; Kerwath et al., 2013).

Some MPAs have been proven to be effective in fish stock recovery and demonstrated a beneficial spillover effect into adjacent areas (Jennings et al., 1996; Agardy, 2000; Adams and Kowalski, 2021). A spillover effect is when fish eggs and larvae enhance stocks in the adjacent (typically unprotected) areas (Bohnsack et al., 1994; Kerwath et al., 2013; Bennett et al., 2017; Kirkman et al., 2021). In the United States of America, two reserves Banana Creek and the North Banana River reserve experienced intense commercial and recreational fishing prior to their closure for national security reasons due to their proximity to Kennedy Space Center. The nearby fisheries significantly benefitted from these reserves with high proportion of trophy fish (record size), 62 % of black drum *Pogonias cromis*, 54 % of red drum *Sciaenops ocellatus*, and 50 % of spotted seatrout *Cynoscion nebulosus* (Kenchington et al., 2003) indicating a spillover effect. The most cited example of spillover effect is one from the Philippines, where an increase in fish yields was observed outside the boundaries of a small protected area at Apo Island, less than a decade after it was established (Russ and Alcala, 1996). A direct example of spillover success which increased the catches in adjacent areas in the SA context, is the recovery of Roman *Chrysoblephus laticeps*, a SA endemic seabream inside the Goukamma MPA (Kerwath et al., 2013). Another study of a no-take zone in the De Hoop MPA plays a significant role in providing protection for protected and threatened species of sharks, the findings showed higher relative abundance of sharks inside the MPA compared to areas outside the MPA (Albano et al., 2021).

The success of MPAs lies in their ability to accomplish their aims, and to adapt management where these objectives require revision. Success can be measured by evaluating and measuring an MPAs' effects (Ban et al., 2017) and comparing them against their goals (OECD, 2016; Mann-Lang et al., 2021). This can be done by comparing both biological and ecological measures such as density and biomass of fish assemblages, organism sizes, benthic habitat health, and species richness (Giakoumi et al., 2018). Additionally, MPAs' success can be judged using indicators that include but not limited to stakeholder participation in management, maintenance and establishment of features required for an MPA to function, compliance with rules, time after declaration and increases in biodiversity (Francis et al., 2002;

Soler et al., 2015). According to Edgar et al., (2014) effective MPAs include characteristics such as no-take zonation, enforced, old age, large size and isolation (called the NEOLI principles). Marine protected areas designed with the ecology of target species in mind have also proven to be successful (Rudd et al., 2001). However, MPAs' efficacy is influenced by budget, governance and buffer size (Edgar et al., 2014; Gill et al., 2017).

Many marine protected areas have failed in achieving their aims and objectives. One of the reasons being a lack of funding, which hinders the achievement of MPAs' aims and objectives (Halpern, 2014). For example, a study conducted in East Africa where MPAs that lacked funding did not perform well compared to MPAs that received funding from external funders (Francis et al., 2002). Inadequate inclusion and involvement of stakeholders during decision-making and planning processes hinders success (Jentoft et al., 2012; Sowman and Sunde, 2018). Leading to resistance by local communities as a result of negative impacts linked with the MPAs. The rationale for taking into account social and economic factors is that these have influence on long-term resilience and biological diversity of MPAs as a form of conservation initiative (Kelleher, 1999; Kirkman et al., 2021). In addition, both social and economic factors are one of the reasons the MPAs fail.

Marine protected areas that are officially designed but have poor enforced regulations, lack monitoring, and compliance by resource users are known as 'paper parks' (Halpern, 2014; Field et al., 2025). Other factor contributing to some MPAs becoming 'paper parks', include the rushed designation and the preference for areas that are politically convenient to establish (Relano and Pauly, 2023). Poor implementation is due to a lack of human capacity, equipment, and due to lack of funds (Field et al., 2025) as already discussed in the above paragraph. Even the perfectly designed MPAs will not succeed without adequate enforcement (Faure-Beaulieu et al., 2023), an example is Coco Island National Park, one of the world's oldest MPAs, where there was a decrease in elasmobranch species, with eight of 12 species declining over two decades (White et al., 2015). This decline was a result of illegal fishing pressure within and outside the MPA, which resulted from the lack of enforcement (White et al., 2015). A decline in fish populations within MPAs will continue unabated unless adequate enforcement is put in place to reduce fishing pressure.

Enforcement is currently lacking in many of the South African MPAs (Tunley, 2009; Adams and Kowalski, 2021; Kirkman et al., 2021). An example is that of the Aliwal Shoal MPA which highlighted the lack of law

enforcement among other issues such as poor fisheries management and lack of trained MPA management staff. All these compromises the ecological performance of MPAs (Gill et al., 2017). South Africa (SA) declared 20 new MPAs in 2019 after considerable consultation, planning and negotiation; this expansion included some existing coastal MPAs (Sink et al., 2019) leading to 42 MPAs in 2019. This expansion increased coverage within SA's continental Exclusive Economic Zone (EEZ) from 0.4 % to 5.4 % as part of the Operation Phakisa economy programme aimed at unlocking economic potential of SA and enhancing marine conservation (Kirkman et al., 2021).

The design of MPAs must be based on how they can be used to improve fisheries yields, this includes the use of evaluation using adaptive management techniques (Hilborn et al., 2004). They are designed using social, economic, and ecological (Ban et al., 2011; OECD, 2016) criteria to decide where they will be located. Some criteria include ranking methods (Hockey and Branch, 1997), biogeographic distributions hotspots and home range (Hockey and Branch, 1997; Turpie et al., 2000; Rudd et al., 2001; Fox et al., 2012; Kirkman et al., 2021) features such as reefs (Schéré et al., 2020). Marine protected area networks are also designed in a way that will enhance marine biodiversity, considering replication (Kirkman et al., 2021), connectivity, alignment of boundaries, and size as variables (Margules and Pressey, 2000). However, MPAs tend to respond differently to fishing restrictions as a result of factors that are species-specific, and include fecundity, larval dispersal, mobility, exploitation level prior to and after MPA establishment, environmental context and indirect interactions between species (Babcock et al., 2010). An MPA's design directly or indirectly shapes how humans perceive MPAs, their interactions with marine resources and ultimately MPAs' performance (Mascia, 2004).

There are several challenges associated with the presence of MPAs, and it can be costly and difficult to manage them (Driver et al., 2012). It must be ensured that funding is available to effectively manage the MPA following its establishment. Using MPAs for fisheries management can lower transactional costs such as those for monitoring, enforcement, and gathering of information, because MPAs require less detailed information compared to other fishery management tools that are more information-intensive (Fox et al., 2012). The implementation of MPAs may result in costs associated with the potential displacement of fishers (OECD, 2016). Both the costs and benefits of MPAs depends on their different objectives, location, and degree of protection (OECD, 2016). In addition, MPA design, zonation, socio-economic context, monitoring and enforcement are the main determinants of operating costs of MPAs (Ban et al., 2011). A global study by Brander et al., 2015 on net benefits of protecting marine habitats through expanding

coverage of no-take MPAs to 10 % and 30 %. It found that the benefits exceeded the costs with ratios ranging from 3.17 to 19.77, meaning that for every unit of cost invested in designing and managing the MPAs there would be 3.17 units of benefits. An understanding of the costs and benefits of an MPA is crucial as it assist evaluation of benefits of an MPA to society by decision makers and enable prioritization of efforts to other MPAs in cases where there are limited resources (OECD, 2016). Furthermore, the understanding of costs and benefits can help in budgeting for funds that will be used to effectively and efficiently monitor the MPA (Jameson et al., 2002; OECD, 2016).

1.5 BASELINE ASSESSMENT

The continued exploitation of fish stocks and a decline of many species increase the need for more research on MPAs to support their design, expansion, and monitoring. Many fish species are valued resources and assessing the assemblage composition within MPAs will provide data to support their management. Marine protected area evaluation will increase accountability and assist managers to determine resource prioritization and communicate with the public (Leverington et al., 2010).

There is a need for baseline data that can be used for protection and effective management of fish assemblages in MPAs. Baseline data will provide vital ecological, conservation, and management insights that ensures adaptive management strategies. This is particularly important for the uThukela Banks MPA which is relatively new (established in 2019) and lacks historical data. It is vital to provide baseline descriptions of marine biodiversity at different scales, together with concurrent explanations of the physical parameters of the ocean system that underlie and drive these patterns and processes (De Vos, 2020). Information on the density, diversity, and size classes of fish populations needs to be collected in order to examine how fishing and other disturbances affect fish populations (Langlois et al., 2006). Additionally, quantitative baseline data including a range of key processes and variables (Fox et al., 2012) before management must be obtained to assist assess whether the MPA is meeting its objectives and goals (Francis et al., 2002) and to inform the design of future monitoring and management efforts (Dames et al., 2020). Knowledge on species distribution can assist managers make decisions about which areas to protect (De Vos, 2020). To sustain biodiversity, it is generally believed that protecting major sites and their associated habitats as protected areas or by other management measures is the best course of action (Edgar et al., 2007). More in-depth synthesis of knowledge and accurate primary research is needed to offer a solid foundation for management and policy implementation to ensure MPAs are effective and

useful (Heyns-Veale et al., 2019a). To demonstrate the benefits of MPAs to society, it is critical to conduct long-term ecological research to determine how the marine ecosystems change following the proclamation of an MPA (Dames et al., 2020). Non-destructive methods are preferred especially for investigating fish within ecologically sensitive areas or highly protected marine reserves (Langlois et al., 2006). These monitoring tools need to be optimized to enhance accuracy, efficiency, and cost-effectiveness for fish management.

1.6 LONG-TERM MONITORING AND OPTIMIZATION

Marine protected areas can be an appropriate tool for ecosystem protection by reducing ecological fishing impacts. However, to achieve the desired conservation benefits they need to be monitored and evaluate their success.

Therefore, long-term ecological monitoring (LTEM) (thereafter referred to as LTM) programmes are needed to monitor and evaluate the efficacy of MPAs, and they need to be robust and well designed to efficiently and effectively monitor the MPAs. Monitoring is critical to adequately manage threatened marine biodiversity and in the context of this study to support MPA management of mesophotic reef fish assemblages. However, LTM is resource intensive and sometimes fails because the monitoring requirements are too much. The skills and considerations required to detect the long-term trends in ecosystem ecological condition include labour, equipment, knowledge of resource systems and time (Langlois et al., 2010; OECD, 2016). The costs and expectations faced during LTM do not remove the need for adequate monitoring. These challenges can be mitigated by determining the minimum monitoring requirements to achieve a set of conservation objectives (Carwardine et al., 2012). The minimum requirements can take the form of identification of key monitoring location or specific species (species-based surrogates), the minimum number of locations, and identifying optimal sample size to detect the diversity (e.g. species accumulation curves). Identification of a minimum required sample size will assist to achieve statistical power, which ensures that monitoring agencies can detect change in abundance over time (Brown et al., 2004; Lindenmayer et al., 2014). However, the technique of assessing statistical power prior to settling on a sample size is not widely practised (Brown et al., 2004). In addition, a cost-benefit analysis can be run to measure the financial versus statistical implications of different monitoring programmes. Cost-benefit analysis is aimed at assessing the time needed to gather and process information, as well the quantity of data collected per survey (Brown et al., 2004).

Monitoring of MPAs is essential to obtain ecological and socio-economic baseline data (Kirkman et al., 2021; Mann-Lang et al., 2021; OECD, 2016). The focus of the current study is ecological monitoring to assess the performance of the uThukela Banks MPA, which currently lack a monitoring plan. This type of monitoring is aimed at keeping track of changes in organism size, species abundance, and community structure over time, and signal which strategies need to be revised based on observed trends in the data. Long-term biological data is essential as it helps to track ecosystem changes and distinguish between anthropogenic stress-driven and natural change (Dando, 2020). Therefore, it's essential to understand population biology in marine settings (Dando, 2020). Identifying the most suitable (sampling) method is key to efficient monitoring of the mesophotic reef fishes of the uThukela Banks MPA: choosing a method that is cost-effective, represents the community being studied, and one that detects ecosystem or population changes.

1.7 FISH HABITAT ASSOCIATION

The benthic environment influences marine processes that in turn determine the spatial distribution (Wilson et al., 2008), species richness, species abundance (Goodsell and Connell, 2005; Anderson et al., 2009; Fitzpatrick et al., 2012; Heyns-Veale et al., 2016; Hill et al., 2018a; Borland et al., 2021; Kirkman et al., 2021) and composition of demersal fish assemblages (Dames et al., 2020). This influences the ability of fishes to locate their prey. Fishes use multiple types of habitats to reproduce, feed and frequently congregate in areas where terrain complexity and seascape connectivity are elevated, because of this the spatial characteristics are deemed significant (Borland et al., 2021). The habitat preferred by mobile animals can change with ontogeny which leads to variation in the degree of habitat specialization among life stages (Chatfield et al., 2010; Fitzpatrick et al., 2012). Furthermore, species composition, size and trophic structure of targeted fish communities can be altered by fishing (Wilson et al., 2008).

Knowledge of fish-habitat associations helps ecologists and conservationists to design appropriate cost-effective monitoring programmes for assessing fish assemblages. Mapping seabed habitats is vital in terms of measuring habitat availability across resource management scales (Anderson et al., 2009; Baynes et al., 2023). Habitat maps (fish-habitat association) can then be used by managers and researchers to assess biodiversity metrics of the assemblages, where significant and predictable species-habitat associations exist (Anderson et al., 2009). Understanding how fish interact with their environment helps with the identification of important conditions influencing fish stocks' abundance (Fitzpatrick et al., 2012)

and evaluate how well reefs and particularly mesophotic reefs are represented in MPAs. Moreover, this knowledge allows for stratified sampling based on benthic habitat types, for example, sand or mesophotic reefs, which will ensure scientifically robust and cost-effective monitoring. Establishing these associations creates baseline data that allow comparisons in the future. This is important, particularly for the uThukela Banks MPA that lacks a long-term ecological monitoring plan across all management zones and habitats. As well as comprehensive mapping of all habitat types. These associations are critical for this MPA, given that its mesophotic reefs were historically important fishing grounds (Driver et al., 2012).

1.8 STUDY AIMS AND THESIS STRUCTURE

The uThukela Banks MPA protects important demersal fisheries species found on mesophotic reef systems in the mid- and outer-continental shelf (30-150 m depth). In particular, fish assemblages important to commercial hook and line fisheries (linefish). Mesophotic reefs are particularly important for larger sexually mature fish that undertake ontogenetic habitat shifts from shallow nursery grounds (Turner et al., 2017).

The uThukela Banks MPA is zoned with an inshore and offshore area (Figure 2.1), two inshore controlled zones and two inshore restricted zones which form part of the inshore area. The offshore area consists of one offshore restricted zone, three offshore controlled zones, and one controlled-pelagic linefish zone (DEA SA, 2019). The offshore zones of the MPA were specifically designed to protect the mesophotic reefs which are ecologically important as they provide refugia from anthropogenic pressures (Button et al., 2021). The inshore reefs are characterised by very low water clarity, due to high sediment load of the uThukela River (Lamberth et al., 2009) and are not considered to be viable sites for monitoring using non-destructive video-based sampling technique. Although the inshore portion of this MPA is primarily sandy, but there are important reef habitats on the coastline and the offshore mesophotic reefs. The latter have greater tolerance of disturbance (Dames et al., 2020) and support diverse fish assemblages as shown in the current study. Furthermore, offshore reef sites are characterised by cleaner water, but were also historically important fishing sites (Lamberth et al., 2009) so ideal for monitoring the recovery of impacted fish diversity.

There is growing efforts to improve the representativity and extent of protection of marine biodiversity in South Africa, with increasing studies focussed on evaluating the efficacy of MPAs (Kirkman et al., 2021). The information above is essential to generate a baseline knowledge of the mesophotic ecosystems and

their importance for biodiversity and fisheries species. Because the uThukela Banks MPA is a newly established MPA, baseline assessments are required to assess whether the MPA is meeting its objectives and goals (Francis et al., 2002; Fox et al., 2012). Currently, there are no established monitoring programmes in the MPA, and it is therefore important to design feasible and effective programme to monitor the mesophotic reef fish through time to measure the ecological response to protection and zonation. Few studies, especially in the context of South Africa, have investigated fish population and community structure on mesophotic reefs or on method optimization for LTM of mesophotic reef ecosystems.

As such, this study aims to build the foundation for the efficient monitoring of mesophotic fishes to support management in the uThukela Banks MPA. By providing a description of the fish communities and propose a feasible and robust LTM programme for mesophotic reef fishes in the uThukela Banks MPA. The study used baited remote underwater stereo-video system (stereo-BRUVs) sampling, a technique which has been increasingly widely adopted (Watson et al., 2005; Fitzpatrick et al., 2012; Harvey et al., 2012; Bernard et al., 2014; De Vos et al., 2014; Langlois et al., 2018, 2020; Schramm et al., 2020; Dalton et al., 2021; Smit et al., 2023).

The research questions were addressed in three research chapters using data collected from the same study site (uThukela Banks MPA). The following questions were addressed for each of the three objectives:

Objective 1

- How do environmental variables (depth, relief, and benthic habitat) influence demersal fish assemblages on univariate metrics (abundance, size composition, alpha and beta diversity)?

Objective 2

- How do fish assemblages (using metrics investigated in objective 1, vary between management zones in the uThukela MPA and reef complexes within management zones?

Objective 3:

- Use rarefaction and extrapolation to determine the number of samples required to detect 95% of available species on each of the reef systems?

- Use power analysis to determine the number of samples required to detect a 10% change in the abundance of fishes over a period of five years with a statistical power of 0.8 at the $\alpha = 0.05$ level.
- Determine the cost of surveying each mesophotic reef within and adjacent to the MPA based on required sample size
- Use a cost-benefit analysis to investigate how the optimal sampling programme looks like and what are the cost benefit implications of different versions of this plan.

Guided by three main hypotheses:

- higher species richness, abundance, and diversity in high-relief reef habitats than low relief reef and sand habitats;
- depth to have a stronger influence on fish assemblage structure and diversity than location and the different management zones of the uThukela Banks MPA; and
- no measurable effect of management zone to be observed on fish assemblages because of the MPA being relatively new.

This thesis consists of five chapters:

Chapter 1 is the general introduction which contains the study context and rationale behind the research, a review of relevant literature and highlights the thesis aims and objectives. This chapter also provides a reader with a summary of the thesis structure.

Chapter 2 includes the study region uThukela, anthropogenic pressures in the study area, and the general methodology and approach to achieving the thesis aim (sampling technique, field surveys and sampling design, video processing and analytical approach).

Chapter 3 is research chapter 1 based on the first objective of the study; this chapter quantifies the environmental variables to understand how they influence fish assemblages and diversity. This chapter was also based on the second objective of the study, which focused on how the fish assemblages vary among the different zones of the MPA and areas outside the MPA. This chapter provides insight on the effect of zonation of reef fishes. The focus is also on “baseline” comparison of assemblages among different management zones, determining which sites have higher diversity/abundance/fish biomass.

Spatial differences will be detected taking into account habitat differences, and key sites for biodiversity in the MPA will be identified in this chapter.

Chapter 4 is research chapter 2 and is based on the third objective of the study; this chapter focused on identifying key areas for long-term ecological monitoring, identifying optimal sample size to detect and monitor changes in fish assemblages through time.

Chapter 5 is the general discussion, it relates the findings from the two research chapters to the overall aim of the thesis, provides a critical assessment of the research conducted and highlights important outcomes, the strengths and research gaps. In addition, this chapter highlights future recommendations, considerations, and their implications for management of the uThukela Banks MPA.

2 GENERAL MATERIALS AND METHODS

2.1 STUDY SITE

2.1.1 UTHUKELA BANKS MPA

The study was conducted on the continental shelf of central KwaZulu-Natal (KZN) inside and adjacent to the uThukela Banks MPA (Dalton et al., 2021; Green et al., 2022) (Figure 2.1). KwaZulu-Natal is the province on the east coast of South Africa and spans both the subtropical Natal and the tropical Delagoa biogeographic provinces (Sink et al., 2019). The uThukela Banks MPA was declared in 2019 after stakeholder engagement identified it as a priority for conservation (DEA SA, 2019: gazette no. 42479). The MPA is located in central KZN, between Richards Bay and Durban (30.5° - 32.5° E, 28° - 30.5° S) and has a total size of 4 094 km² (Lamberth et al., 2009). This MPA extends to depth of 500 m and has an offshore extent of 37 km in the north and 50 km in south (Lamberth et al., 2009; DEA SA, 2019: gazette no. 42479). The uThukela Banks MPA is zoned with an inshore and offshore area, with the inshore zones extending from the high-water mark to the 2 m depth contour and the offshore zone from here to the MPAs seaward boundary (Figure 2.1). Two inshore controlled zones and two inshore restricted zones form part of the inshore area. The offshore area consists of one offshore restricted zone, three offshore controlled zones, and one controlled-pelagic linefish zone (CPLF) (DEA SA, 2019: gazette no. 42479) (Figure 2.1). In the restricted zones all forms of extraction are prohibited, this includes activities such as fishing (harvesting of intertidal organisms and invertebrates) and all gear types are prohibited; including nets, lines, hooks, traps etc. The CPLF is a controlled zone that only permits pelagic fishing and spearfishing and prohibits fishing of any shark species, fishing from a vessel between sunset and sunrise, and collecting broodstock for aquaculture or undertaking aquaculture (DEA SA, 2019). In the controlled zones fishing is only permitted to the people in possession of permits and only species specified in sub-regulation may be fished (DEA SA, 2019). The controlled zones prohibits recreational fishing within the MPA between 17h00 and 06h00, as well as having fishing gear onboard a vessel (DEA SA, 2019).

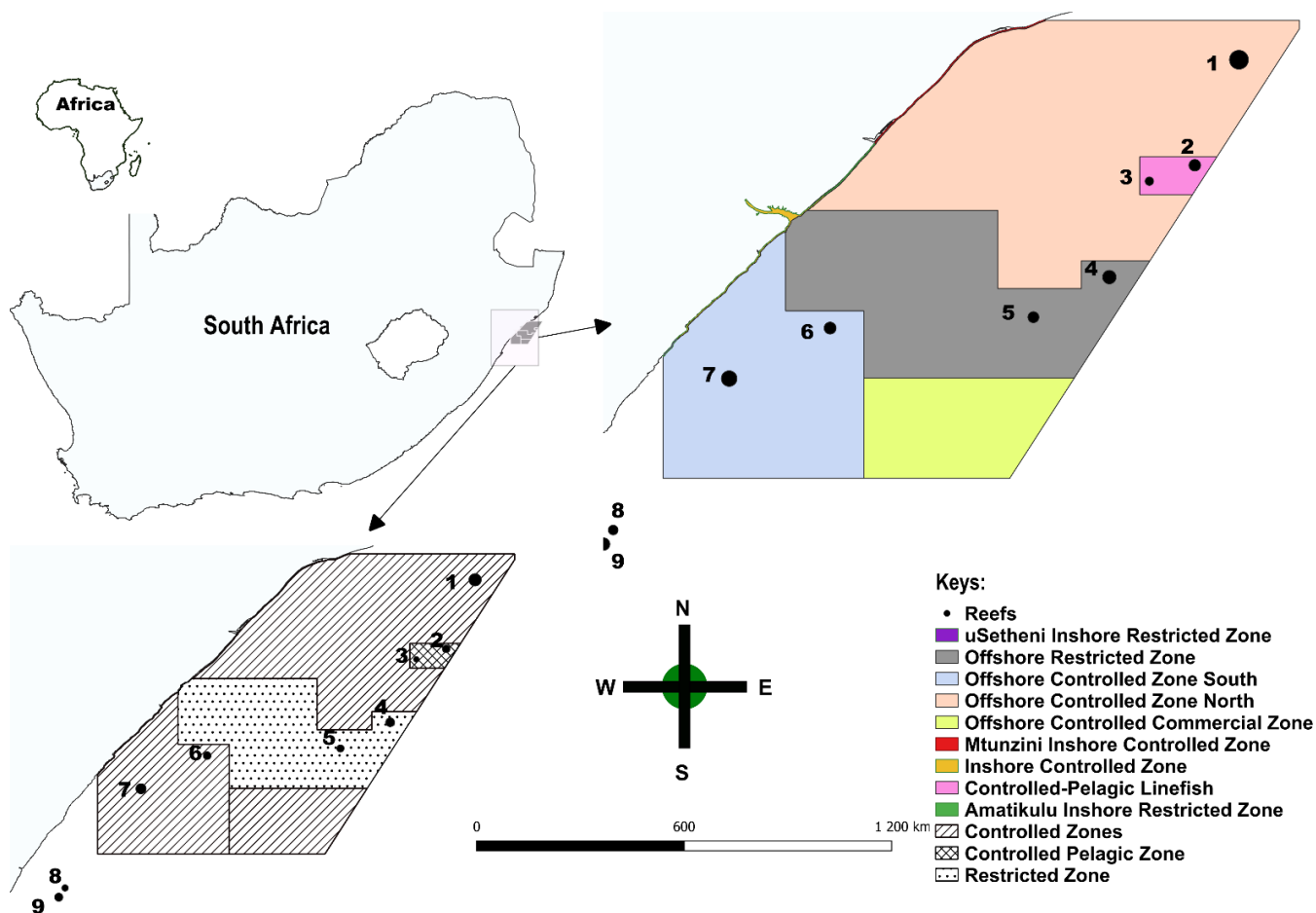


Figure 2.1: Map of study area: the uThukela Banks marine protected area (MPA) showing mesophotic reef sites (black circles) nested within and outside the MPA. The management zones in the uThukela MPA includes controlled, restricted, and controlled-pelagic linefish with list zones. The mapped sites that were investigated include (1) Durnford Hats, (2) Zini Hard Edge, (3) Pat's Paradise, (4) Carpenter, (5) Sundowner, (6) Zinkwazi, (7) Ballito Tongaat, (8) uMdloti and (9) Rosie Snow. Both uMdloti and Rosie Snow (represent exploited zones).

2.2 UTHUKELA BANKS ENVIRONMENT

The uThukela Banks MPA is located within the KZN Bight on the south-east coast of South Africa (Heye et al., 2021). This MPA is approximately 160 km long between Durban and Richards Bay (Meyer et al., 2002; Fennessy et al., 2016). The KZN Bight includes the shoreline, uThukela river estuary, and waters offshore, where the continental shelf is wider than the remaining coast and extends approximately 50 km wide, extending to the boundary of the Agulhas current in KZN (Fennessy et al., 2016). This Bight is an example of a river-influenced bight, with the uThukela river dominating freshwater discharge (in this bight) (Lutjeharms et al., 2006; Lamberth et al., 2009; De Lecea and Cooper, 2016). The uThukela river contributes more than 38 % of provincial freshwater flow (Lagabriele et al., 2018). As such, the uThukela river contributes a lot to the environmental dynamics of this region, including the shelf waters being classified as oligotrophic in the central and northern regions (Meyer et al., 2002).

The KZN Bight is ecologically significant for recruitment of many species due to higher nutrient availability from freshwater inflow and from upwelling, which enhances productivity in the northernmost region of the Bight (Hutchings et al., 2002; Lutjeharms et al., 2006; Heye et al., 2021). The Agulhas current strongly influences the KZN Bight on its seaward boundary as it follows the continental shelf edge and generates the inshore eddies and drives the upwelling (Lutjeharms et al., 2001). In general, the KwaZulu-Natal's waters are oligotrophic with low productivity (Lagabriele et al., 2018); the Agulhas current, therefore, plays a vital role in supporting productivity and drives species distribution throughout the KZN region by transporting salty, warm, tropical waters southward along coastline of KZN (Lutjeharms et al., 2001).

The uThukela River plays an important role in the functioning of the KZN Bight and uThukela Banks as it contributes nutrients and sediments into the adjacent marine system. The nutrients support productivity, especially in the shelf area (which is a limited nutrient region). The uThukela river is known as the greatest source of sediment for the shelf region, evidenced by the offshore Thukela cone, the major depocenter of the region (Lutjeharms et al., 2006). The river's sediment load plays an important role in shaping the benthic environment of the uThukela Banks MPA and provides nutrients thus benefiting marine organisms that are dependent on sediment rich environments. The southern portions of the MPA offshore of the uMvoti estuary consist mostly of mud on the seafloor, giving way to coarser sandy and gravelly material in the central and northern areas (Green et al., 2022).

2.3 STUDY FOCUS

The study focused primarily on mesophotic reefs (40 – 150 m) but sampling took place between 36.5 m and 192.5 m depth (Figure 2.1). These mesophotic reefs were selected, firstly, because they were key fishing areas for the recreational and commercial line fishing sector in the region. In addition, they provide home to threatened linefish such as the Seventy four *Polysteganus undulosus* and blackmussel cracker *Cymatoceps nasutus* (Mackay, 2018). According to Lamberth et al (2009), the most important fishery in KZN is both the commercial and recreational line fishery, accounting for 40 % of the landed mass. As such, the offshore zones of the MPA were designed specifically to protect these mesophotic reefs. Furthermore, mesophotic reefs are reefs in the mesophotic depth zone which is ecologically significant, supporting high endemism (Lindfield et al., 2016), higher abundance, biomass and biodiversity (Bohnsack et al., 1994). Lastly, higher water clarity on the mesophotic reefs in this MPA permitted the use of baited remote underwater stereo-video system (stereo-BRUVs) for sampling; this method can be successfully employed in the clearer water offshore than on reefs where inshore water is influenced by incoming turbid freshwater from the uThukela estuary.

2.4 SAMPLING TECHNIQUE

2.4.1 SAMPLING METHOD

The sampling was conducted using stereo-BRUVs following nationally and globally accepted best practice guidelines (Langlois et al., 2020). Baited remote underwater stereo-video systems are a fisheries-independent, standardised approach for estimating size distributions and relative abundances of fish assemblages (Heyns-Veale et al., 2016). The stereo-BRUVs used in this study had a standardised construction and comprised of three stainless-steel housings (depth rating: 350 m): two (Figure 2.2, d) with high definition (HD: 1920 x 1080 pixels) Go Pro Hero Black 7 cameras mounted on a base bar 70 cm apart and converging inward at an angle of 8° to gain a field of view (FOV) that overlaps optimally (Ellis and DeMartini, 1995; Cappelletti et al., 2004; Harvey et al., 2012; Langlois et al., 2012). The two cameras filmed simultaneously to enable precise fish length measurements (Harvey and Shortis, 1998; Heyns-Veale et al., 2016) during video analysis. The Go Pro Hero 7 was set to record with a linear FOV, phase alternating line (PAL), 50 frames per second (FPS).

The third housing contained a white light emitting diode (LED) light unit mounted in the middle of the base bar to provide additional lighting required for the deeper depths where light levels are low (Figure 2.2, e). White LEDs were used to deliver the finest image quality possible to facilitate species identification (Dalton et al., 2021). Upon deployment, lighting was delayed for 10 minutes so that a sensor (Wildlife Computers TDR-MK9) could measure the ambient light concentration at the sampling depth. The basebar with housings was secured within a protective stainless-steel frame (Figure 2.2, a) to which additional weights could be mounted to ensure that the stereo-BRUVs remained stationary when on the seafloor. The bait arm (1.5 m polyvinyl chloride tube [PVC]) extended perpendicular from the middle of the base bar with a perforated PVC bait canister (Figure 2.2, f) attached to the end. The bait container was designed to hold at least 1 kg of crushed sardine *Sardinops sagax* bait. The stereo-BRUVs were deployed to the seafloor using 4 mm Dyneema GP12 rope (Figure 2.2, g) (two to three times water depth to account for strong currents) and connected to surface marker buoys to mark its position and enable recovery. The water depth (m), temperature (°C) and light concentration (lux) for each stereo-BRUVs deployment was recorded using Wildlife Computer TDR-MK9 loggers (Wildlife Computers, 2012) attached to the basebars and set to take measurements at one minute intervals.

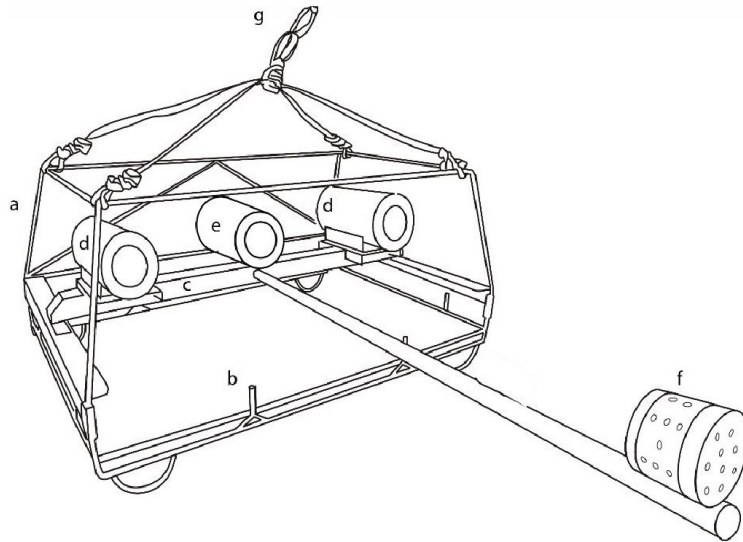


Figure 2.2: A diagram of the type of baited remote underwater stereo-video system (stereo-BRUVs) used in this study, showing a protective stainless-steel frame (**a**) with pins that allow mounting of weights (**b**), a base bar (**c**) holding two high-definition video cameras (in waterproof aluminium housings) (**d**) and a white LED light (**e**). Perpendicular to the base bar is a perforated polyvinyl chloride (PVC) bait canister attached to a 1.5 m-long plastic bait arm (**f**) and a rope connected to a surface marker buoy links the stainless-steel frame to the ocean surface and (**g**) showing a rope that attaches to surface marker buoys to allow the recovery of the stereo-BRUVs.

2.4.2 SAMPLING APPROACH

A total of 130 stereo-BRUVs were deployed inside and adjacent to the uThukela MPA. For each deployment, the geographic position (Latitude and Longitude) was recorded using the boat's Geographic Positioning System (GPS). A total of six variables were recorded during each stereo-BRUVs deployment: depth, water temperature, visibility, bottom type, percentage water column and percentage obstruction (Table 2.1). Four replicate stereo-BRUVs were used, with each deployed at randomly selected stations within a reef complex for at least 60 minutes repetitively throughout a sampling day, 07h00 and 16h00 (Langlois et al., 2020). The stereo-BRUVs were deployed at least 500 m apart to reduce the chance of fish travelling between locations (counting and attracting the same individuals) during the collection time and to avoid bait plume overlap (Wilson et al., 2007). Each stereo-BRUVs was baited with between 0.8-1 kilogram of crushed sardine to attract fish into the camera's FOV (Langlois et al., 2020). Although using bait to attract fish is known to introduce bias by underrepresenting herbivores, it has been shown to improve the precision of count data and therefore, provides one of the most effective methods of surveying the entire fish community (Harvey et al., 2007; Bernard and Götz, 2012). The descent and

recovery of the stereo-BRUVs from the research vessel (*Hispidus*) and seafloor was controlled by using a winch system. Each stereo-BRUVs was calibrated prior to and after data collection using CAL software and a SeaGIS calibration cube (SeaGIS Pty Ltd). Calibration was done to ensure accurate measurement of individual fish appearing in the FOV during the analysis (Harvey and Shortis, 1998; Harvey et al., 2002b; Heyns-Veale et al., 2016).

The study was conducted on reef complexes at the uThukela Banks MPA and adjacent unprotected areas, with all samples collected in June-July (winter) 2022. Study was conducted in winter due to uThukela Banks MPA being located within the KZN Bight which is associated with nutrient rich water due to upwelling. The upwelling events influence phytoplankton productivity which would lead to water being murky and therefore reduce visibility (Roberts and Nieuwenhuys, 2016). Therefore, making it difficult to observe species using stereo-BRUVs. In addition, nutrient rich water is important for life-history phases (breeding, nursery, and feeding). Therefore, this might lead to high abundances and diversity estimates than what would normally occur, leading to skewed LTM trends (Roberts and Nieuwenhuys, 2016). A multibeam echosounder (MBES) survey of each reef was done prior to the stereo-BRUVs sampling to create detailed bathymetric maps. Multibeam echosounder data was used to obtain measures of seafloor slope, depth and rugosity to help inform site selection. The African Coelacanth Ecosystem Programme (ACEP)'s Geophysics and Mapping Platform (GeMap) was used to collect the MBES data. In addition, SBG system (Navsight Apogee inertial navigation system) and Seabat reason 7101 were used to collect the MBES data (Wanda et al., 2023). The difference between the live sound velocity was measured at intervals less than three metres. Qinertia (v.30.5966) and HYPAC (2022) were used to process raw data (Wanda et al., 2023). Data and derivatives were interpolated and visualised using ESRI's ArcMap 10.1 (Kirkman et al., 2021) and Golden Software Surfer to raster files for later use (Wanda et al., 2023). Reef complexes were then classified by slope using QGIS (version 3.42.0) according to the following procedure: (1) For each reef complex, slope rasters were created from the depth rasters files; (2) slope contour lines were created from the slope rasters for the 4° and 10° slopes; and (3) the contours were then converted into polygons that showed two categories of reef complexes: sand (< 4° slope), low-profile reef (4-10° slope) and high-profile reef (> 10° slope). These maps were then used to inform a stratified random sampling design with an even allocation of samples between the low (10 samples) and high (10 samples) profile reef sites. In the planning process sand was avoided; however, some points during the survey included both reef and sand. The location of the sampling sites was determined using the Generate Random Point tool in QGIS

with a minimum distance of 500 m between sampling sites (within each reef patch) (Watson et al., 2007). This design ensured the equitable distribution of sampling locations within habitat strata (Kermorvant et al., 2019). While sampling in the field, it was ensured that each sample was collected *in situ* as near as possible to the randomly created points.

Additionally, the MBES data were used to measure the terrain heterogeneity using the Terrain Ruggedness Index (TRI) (Riley et al., 1999). This index offers a standardised and efficient measure of terrain heterogeneity useful for objectively assessing habitat complexity and comparisons between areas (Riley et al., 1999). This index was calculated for every sample site, by summarising the change in elevation within the 3 x 3-pixel grid from the Multibeam echo-sounder seafloor data (Riley et al., 1999; Jenness, 2004; Hogg et al., 2016). This was achieved using a terrain analysis function implemented in the QGIS software. The extent of terrain roughness was calculated as the mean and variance in TRI scores (μ -TRI and var-TRI, respectively) within a circular area around each sampling point at two scales, 10 m and 50 m radii. This allowed us to test if the observed fish assemblage was influenced by TRI at different scales.

2.4.3 VIDEO PROCESSING

The EventMeasure (stereo) software package (www.SeaGIS.com.au) was used to analyse video samples to record fish diversity, estimate relative abundance and measure lengths of individuals recorded during each deployment. Videos were analysed for 60 minutes from the time the stereo-BRUVs settled on the seafloor (time on seafloor) and debris settled and the light turned on. The stereo-BRUVs samples that had poor visibility were excluded in the analysis. The time of first sighting and MaxN abundance (Cappo et al., 2003) were recorded for each species during the 60-video analysis period. The value MaxN is the highest number of individuals for a species sighted in one video frame (Cappo et al., 2004; Heyns-Veale et al., 2016; Stobart et al., 2015) throughout the 60 minutes footage sample. Videos were analysed by one analyst to avoid inter-observer variability (Mallet and Pelletier, 2014) and species were identified to the lowest taxonomic levels using online databases such as FishBase (Froese and Pauly, 2022) and field guides, including Coastal fishes of Southern Africa (Heemstra and Heemstra, 2004) and More Reef Fishes and Nudibranchs (King and Fraser, 2014). A species identification image catalogue was compiled using all species found in this study.

Abundance for each species was estimated using the measure MaxN, because individual fish can be recounted when they come in and out of the camera's FOV during the 60-video analysis period. Continuous counting would result in over-estimating abundance. MaxN is a conservative measure of abundance because there are probably more fish in the vicinity of the camera than are visible in the frame at the same time; however, it avoids recounting, and it is thus the preferred relative abundance metric for stereo-BRUVs. It is widely used as the abundance estimate which reduces the likelihood that an observer counts the same individuals more than once (Ellis and DeMartini, 1995; Cappelletti et al., 2004; Watson et al., 2005; Harvey et al., 2007; Stobart et al., 2007).

Fork length measurements were obtained for the fish present in the MaxN video frame. Fork length is the distance from the top of the snout to the end of the centre of the caudal fin rays. This is widely used and standardised ecological and fisheries studies. For some individuals observed at MaxN it was not possible to obtain lengths because they were not fully visible in both cameras. In these cases, it was ensured that at least 75 % of the individuals counted in MaxN were measured to obtain accurate size structure data.

2.4.4 DATA PROCESSING

Length measurements were used to calculate the weight of each individual species using a standard allometric length-weight relationship equation ($W = a \times L^b$) (De Robertis and Williams, 2008), where W is the fish weight (g), a and b are species-specific conversion constants that were obtained from FishBase (Froese and Pauly, 2022), and L is measured fish length (fork length) (cm). The final step was to export data from EventMeasure in a textfile format (.txt) and import it into Microsoft Excel for thorough cleaning prior to statistical analysis.

2.4.5 ESTIMATING COVARIATES

Numerous environmental variables influence the observed patterns in fish assemblage structure and composition. Furthermore, sampling methods are associated with parameters that may influence the species and abundances detected. For stereo-BRUVs, the species assemblage structure and abundance are influenced by parameters that determine the FOV such as visibility, percentage water column and percentage obstruction (Table 2.1). The environmental variables measured during this study included latitude and longitude, temperature, depth, ambient light concentration, seafloor rugosity and habitat type (Table 2.1).

Table 2.1: Environmental variables (covariates), units and data source collected and included in statistical analyses.

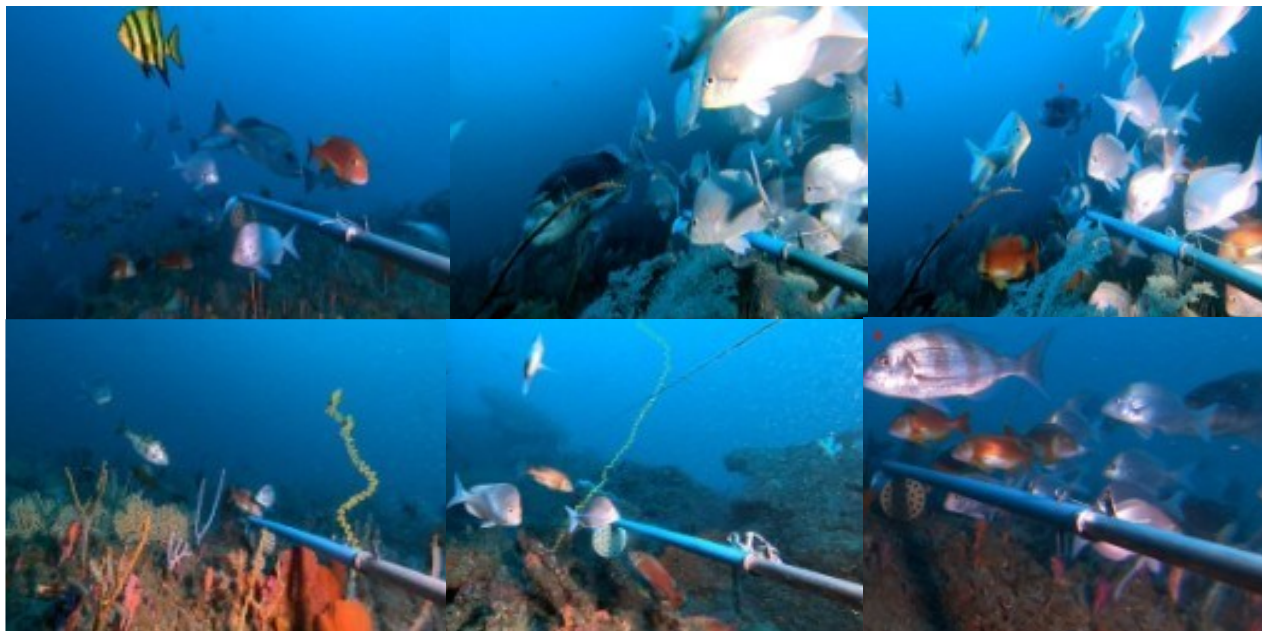
Covariate	Unit	Data source	Description
Visibility	m	Estimated in EventMeasure during video analysis.	Underwater visibility determined for each stereo-BRUVs sample when analysing videos. Visibility was obtained by calculating the distance observed by creating a 3D point at the farthest identifiable fish visible in the FOV of both cameras at a single frame.
Water column	%	Estimated using Vidana software (www.marinespatialecologylab.org) during video analysis.	Percentage water column was determined for each sample during video analysis to account for differences in species composition due to differences in FOV. It was obtained by calculating the percentage of visible water column in the FOV of the camera as opposed to visible seafloor.
Obstruction	%	Estimated using Vidana.	The percentage of obstruction from structures within 1 m of the cameras blocking the FOV thus reducing the area where fish can be seen and counted.
Latitude and Longitude	Decimal degrees	Marked using GPS on board.	Latitude and Longitude for each stereo-BRUVs sample collected.
Temperature	°C	Wildlife Computers TDR-MK9 logger attached on the stereo-BRUVs frame	Measured at each deployment site every five minutes with the average over the deployment duration taken as the temperature.
Depth	m	GPS linked echosounder attached on the boat.	It is the distance from the surface of the seafloor at the site where the stereo-BRUVs was deployed.
Ambient Light concentration	Lux	Wildlife Computers TDR-MK9 logger attached on the stereo-BRUVs frame	The amount of light that penetrates the water at the site of stereo-BRUVs deployment. Taken before the stereo-BRUVs light switched on at the start of the deployment.

Table 2.1: Continued.

Covariate	Unit	Data source	Description
Seafloor rugosity	Terrain ruggedness index (TRI), calculated as mean and variance TRI scores	Multibeam echo-sounder seafloor data.	TRI is a measure of seafloor roughness structure and variance in slope within 10, 25, and 50 m radius obtained around each stereo-BRUVs site.
Seafloor type	N/A	Visual classification of habitat based on field of view in sample.	Type of habitat observed in the FOV of the stereo-BRUVs at each deployment site. Six categories: Reef low 100% reef characteristics with height variations of <1 m Reef high 100% reef with height variations >1 m Patch-reef low mixture of sand patches (>30% of FOV) and reef with height variations <1 m Patch-reef high mixture of sand patches (>30% of FOV) and with height variations >1 m Sand inundated reef reef covered with a thin layer of sand Sand 100% sand in the FOV

CHAPTER 3

3 ENVIRONMENTAL AND SPATIAL DRIVERS OF MESOPHOTIC FISH ASSEMBLAGE STRUCTURE IN THE UTHUKELA BANKS MPA



3.1 ABSTRACT

Environmental variables strongly influence fish distribution and abundance. An understanding of the variables is essential to support marine spatial planning and the design of effective marine protected areas (MPAs). Therefore, this chapter investigated the influence of environmental variables (depth, seafloor relief, and benthic habitat) on demersal fish assemblage structure and diversity of mesophotic reef fish in the uThukela Banks MPA. This MPA includes multiple-use zones ranging from extractive and fully protected areas and was designed to in part to protect offshore mesophotic reefs historically targeted by linefisheries.

Baited remote underwater stereo-video systems (stereo-BRUVs) were used to collect fish assemblage data at depths ranging between 36 and 192 m. Reef habitats were initially mapped using multibeam echosounder and categorised based on relief. A stratified-random sampling design was followed incorporating relief as a key factor in sample selection. Generalised Additive Mixed Models (GAMMs) were used to analyse univariate metrics (abundance, species richness, Shannon and beta diversity, and slinger *Chrysoblephus puniceus* abundance. Multivariate assemblage patterns were examined using ordination techniques.

Results highlighted the importance of reef habitats which has higher species richness and abundance. They also showed different diversity in terms of species occurring in sand and reef habitats. Fish diversity decreased with increase in water depth. The slinger, an ecologically and economically important species in the commercial linefishery, was the most abundance fish recorded, with higher abundances on reef habitats in upper mesophotic depths. Multivariate analysis showed that depth, habitat type, and relief significantly influenced assemblage composition.

The study findings highlight the importance of complex reef habitats in supporting fish abundance and diversity. The results also emphasise the importance of the range of habitats in supporting overall biodiversity. The findings provide important baseline data for monitoring and suggest that the uThukela Banks MPA may support the recovery of key exploited species such as slinger. Understanding how fish communities vary across environmental gradients is essential for effective adaptive MPA management.

Key words: mesophotic reefs, fish diversity, depth, habitat, baseline assessment

3.2 INTRODUCTION

3.2.1 BACKGROUND

3.2.1.1 *MARINE PROTECTED AREAS*

Marine protected areas (MPAs) are a viable tool in marine conservation and biodiversity protection (Edgar et al., 2014; Lubchenco and Grorud-Colvert, 2015; Sala and Giakoumi, 2018; Kerwath et al., 2019; Strain et al., 2019; Turnbull et al., 2021). This mostly applies to, but is not limited to, well-managed MPAs where there is strong enforcement, and where resource use or extractive activities are either prohibited or permitted with restrictions (Edgar et al., 2014; Pendleton et al., 2018; Sala and Giakoumi, 2018). Well designed and managed MPAs tend to have a high species richness, diversity, abundance, large fish biomass, and they promote ecosystem health and population recovery through protection (Edgar et al., 2014; Leenhardt et al., 2015; Sherman et al., 2018; Turnbull et al., 2021). They also help to maintain the genetic diversity of fished species (Sink, 2016). In the face of climate change and anthropogenic perturbations, MPAs play a crucial role in promoting ecosystem resilience (Costello and Ballantine, 2015; Roberts et al., 2017; Bates et al., 2018; Benedetti-Cecchi et al., 2024). Furthermore, MPAs play a significant role in fisheries management, preserving critical habitats for important species and contributing to the sustainable use of resources (Benedetti-Cecchi et al., 2024; Di Franco et al., 2016; Edgar et al., 2014; Laffoley et al., 2019; Leenhardt et al., 2015). Research has shown that MPAs can support fisheries management by protecting and restoring fish stocks (Di Franco et al., 2016; Carr et al., 2017; Lenihan et al., 2021). When appropriately situated, MPAs can also protect vital habitats, like spawning aggregations and nursery grounds for fish species (Rieser et al., 2013; Loffler et al., 2015; McConnaughey et al., 2020).

3.2.1.2 *DEMERSAL FISH ASSEMBLAGES*

Demersal fish live in close association with the seafloor and play an important role in the functioning of benthic ecosystems (Leis, 2006; Graham and Nash, 2013; Aune et al., 2018). Demersal fish species display a variety of feeding behaviours (e.g. corallivores, planktivores, herbivores, omnivores, carnivores) through which they facilitate nutrient recycling and control populations of lower trophic level organisms (e.g. algae, benthic invertebrates) thereby enhancing benthic ecosystem health and resilience (Bellwood et al., 2003; Graham and Nash, 2013; Villéger et al., 2017; Petrik et al., 2019; Loiseau et al., 2023). Many species of demersal fish, especially those that are large, are subject to extensive fisheries pressure. Furthermore,

the majority of these species have life-history traits that make them vulnerable to fisheries exploitation. For example, they exhibit slow growth rates, late sexual maturity, low fecundity and have restricted home ranges (Griffiths et al., 1999; Penney et al., 1999; Mann, 2013). Therefore, understanding their diversity and assemblage structures is crucial for adaptive management and supporting effective MPA management.

3.2.1.3 MESOPHOTIC REEFS

Mesophotic reefs, found between 30 and 150 m depth, play a vital role as critical habitats for demersal fish, often important as breeding sites, and are rich fishing grounds (Lesser et al., 2009; Hinderstein et al., 2010; Kahng et al., 2010, 2014; Bongaerts et al., 2017; Harris et al., 2021; Bell et al., 2024; Rocha et al., 2024). For example, many species of demersal fish occupy broad depth ranges and show ontogenetic depth distributions with immature fish found on shallow reefs and adults on mesophotic reefs (Bongaerts et al., 2017). Therefore, MPAs that incorporate mesophotic reefs can help protect spawner biomass and re-seed areas adjacent to MPAs in a phenomenon known as the “spillover effect” (Bohnsack et al., 1994; Kerwath et al., 2013; Bennett et al., 2017; Kirkman et al., 2021). That being said, mesophotic reefs also act as nursery sites for other fish species, and they show higher resilience to perturbations associated with climate change (Bongaerts et al., 2017). In the face of overfishing, mesophotic reefs hold great potential for being a refuge for demersal fish. Integrating mesophotic reefs into MPA networks and MPA design is critical (Loiseau et al., 2023), as it will help maintain ecological connectivity, and enhance marine biodiversity resilience to environmental changes.

The mesophotic zone is typically classified as upper and lower mesophotic zones; 30-50 and 50-150 m, respectively (Bell et al., 2024). However, this depth classification varies by location due to site-specific environmental factors such as light, temperature (Kahng et al., 2010; Kahng et al., 2014; Pyle and Copus, 2019), and seasons (Campoy et al., 2023). They are also characterised by low temperatures and low light; whilst the light intensity is low, it is the primary driver for productivity, facilitating the growth of algae, corals, and sponges, which dominate the mesophotic zone (Puglise et al., 2009; Harris et al., 2021). Community patterns on mesophotic reefs are shaped by environmental factors such as nutrients, sedimentation, temperature, topography, dissolved organic carbon, depth, and water movement (Bridge et al., 2011). These environmental conditions are key biological drivers of community composition and ecosystem functioning (Harris et al., 2021; Bell et al., 2024).

3.2.2 ROLE OF ENVIRONMENTAL VARIABLES IN SHAPING DEMERSAL FISH ASSEMBLAGES

To be able to protect fish communities in the South African context, one needs to understand how they interact with their environment and the factors that influence their distribution. This can be achieved through ecological research that generates comprehensive data to inform policy, management, and conservation efforts in South Africa and similar marine environments (Friedlander et al., 2003; Neves et al., 2016; Cheal et al., 2021). Knowledge of fish-habitat associations is essential to aid our understanding of the processes that drive patterns in fish diversity and abundance (McLean et al., 2016; Collins et al., 2017; Wines et al., 2020; Cheal et al., 2021). This aligns with broader conservation goals such as sustainable fisheries management, biodiversity conservation, and resilience.

3.2.2.1 BENTHIC HABITAT COMPLEXITY AND RELIEF

In general, habitat type plays a vital role in structuring associated ecological communities (Brokovich et al., 2008; Komyakova et al., 2013; Collins et al., 2017; Williams et al., 2019; Martin et al., 2024). For example, there is a strong link between benthic habitat type such as corals reefs, sand flats or mangroves, and fish assemblage composition, which is linked to the habitat preferences, foraging behaviour and food availability (Abdul Wahab et al., 2018; Hill et al., 2018a; Dalton et al., 2021). In particular, three-dimensional habitats, such as coral reefs, increase structural complexity of the environment and support greater reef fish abundance and diversity (McCormick, 1994; Christensen et al., 2003; Currey-Randall et al., 2021; Komyakova et al., 2013). Structural complexity is defined as a measurement of variation in a habitat's topographic structure, which can be measured by using relief, interstitial space, and surface area (Grigg, 1994; Wilson et al., 2007; Komyakova et al., 2013). Structurally complex habitats offer broader range of living spaces, thereby reducing competition and predation (Cheal et al., 2008). These structurally complex habitats also enhance fisheries productivity (Rogers et al., 2014) thus disproportionately contributing to fisheries yields for associated species.

Seafloor relief is a critical determinant shaping the distribution and fish assemblage (Dames et al., 2020; Borland et al., 2021). Relief and structural complexity are similar however relief typically refers to variation in the vertical structure of the seafloor of habitat, while structural complexity incorporates the 3-dimensional features. Typically, features of the seafloor that are characterised by high rugosity, supporting a diverse range of fish populations with high abundance (Borland et al., 2021). Rocky reef habitats are often associated with diverse fish assemblages, with higher relief areas attracting higher

abundances and diversity of species. A study by Friedlander and Parrish (1998) in Hawaii showed that high fish biomass is usually associated with high and complex relief, whereas low relief habitat harbours low reef fish biomass. This is because rugose areas on the seafloor provide greater niche diversity, refuge from predation, reduced effects of competition, diverse foraging environments and favourable spawning sites (Gratwicke and Speight, 2005; Kostylev et al., 2005; Komyakova et al., 2013; Rogers et al., 2014; Smith et al., 2014; Collins et al., 2017; Bracewell et al., 2018; Friedlander et al., 2003; Borland et al., 2021).

3.2.2.2 DEPTH

Depth is one of the environmental variables affecting life below the water's surface that is considered a reliable and important predictor of community structure (Götz et al., 2014; Tornabene et al., 2016; Williams et al., 2019; Prabowo and Christian, 2024;). This is especially true for fish abundance and fish assemblage structure (Friedlander and Parrish, 1998). The general pattern is a decline in fish assemblage diversity with increase in water depth (Friedlander and Parrish, 1998; Brokovich et al., 2008; Garcia-Sais, 2010; Kahng et al., 2010; Bejarano et al., 2014; Pinheiro et al., 2016; Campoy et al., 2023), however, this trend is not uniform. For example, in the mesophotic zone, diversity of some taxa, such as groupers, lanternfishes, anthias, and colonial anemones appears to peak at greater depths (Soares et al., 2019). In addition, a study by Abdul Wahab et al., (2018) showed that fish diversity, abundance and biomass increased with depth up to 60 m in the upper mesophotic zone. However, depths below 60 m usually have lower diversity; this is attributed to the relationship between benthic habitat-forming taxa and the environment, depth and substrate type (Abdul Wahab et al., 2018). In contrast, other studies have shown that there is higher fish diversity and abundance at shallower depths (5-30 m), compared to deeper areas (Fitzpatrick et al., 2012; Götz et al., 2014).

Depth can also act as a proxy for a number of parameters such as water temperature, light intensity and wave energy (Dalton et al., 2021). In the above examples, this is due to a strong correlation between the variables with deeper water associated with low temperatures, and light intensity.

3.2.3 HISTORICAL IMPORTANCE OF MESOPHOTIC REEF FISHERIES IN THE UTHUKELA BANKS MPA

The uThukela Banks MPA is a newly established MPA, declared in 2019 as priority for conservation after stakeholder engagement (Green et al., 2022). "As per NEM: PAA section 38(1) and through the Management Agreement, the management of uThukela MPA was delegated to the provincial conservation agency, Ezemvelo KZN Wildlife". Mesophotic reefs in the uThukela Banks MPA were

historically important fishing grounds supporting economically valuable demersal reef fish species. Prior to the promulgation of the MPA, fishing on these reefs had intensified due to technological advancements, including GPS and echosounders for mapping fishing sites, slipway facilities for vessel maintenance, onboard freezers, and the use of larger, faster vessels with increased crew capacity (Penney et al., 1999; Mann, 2013). These advancements led to overfishing, habitat degradation (Haupt et al., 2017), and dramatic changes in fish community structure. This is particularly true for the demersal reef-dwelling sparids, most of which are resident (Griffiths et al., 1998; Penney et al., 1999; Mann, 2013). Sparid species are especially vulnerable to overfishing due to their complex life histories, including late maturity, slow growth, and sex changes (Griffiths et al., 1999; Penney et al., 1999; Mann, 2013;). Among the sparids is the red steenbras *Petrus rupestris*, world largest seabream, which played a significant role in both commercial and recreation boat-based hook and linefishery (Mann, 2013). However, it is now considered collapsed or heavily depleted (Kerwath et al., 2019). Other important species include catface rockcod *Epinephelus andersoni* which is a resident and endemic species in South Africa (Haupt et al., 2017). Other high value species targeted by the hook and line fishery include resident reef fishes such as slinger *Chrysoblephus puniceus*, Scotsman *Polysteganus praeorbitalis*, black musselcracker *Cymatoceps nasutus* and Englishman *Chrysoblephus anglicus* (Penney et al., 1999). The populations of many of these species are also considered overexploited (Mann, 2013).

Due to the history of fishing on the mesophotic reefs and the life history characteristics of demersal fish species that occur on the reefs, it is expected that the populations of these now protected species given protection while in the restricted zone of the MPA will recover, given sufficient time. As such, monitoring of these populations should be prioritised to build the case for the MPA and support its management. Slinger is considered to be a key species for monitoring fisheries impacts and MPA effectiveness within KZN. It is the most important species in southern Mozambique and KwaZulu-Natal's commercial linefishery and recreational boat-based linefishery (Maggs et al., 2017), comprising 66 % of commercial catch in the offshore KZN linefishery since 1994 (Penney et al., 1999; Dunlop and Mann, 2013).

3.2.4 PROBLEM STATEMENT

Currently there is a knowledge gap about reef fish assemblages (Turner et al., 2017) in the mesophotic zone and deeper reefs (Tornabene et al., 2016). The lack of information and understanding of these ecosystems leads to generalised assumptions about mesophotic reefs; their structure, connectivity, and

role as refugia (Turner et al., 2017). The depletion of fish stocks inshore has impelled traditional shallow-water fisheries to move offshore. As such, it is vital that fish assemblages in deep waters be assessed to supplement our understanding of these critical habitats to help account for the distribution of fish assemblages and diversity.

There are very few studies that have looked at the influence of environmental variables on demersal fish assemblages on the mesophotic reefs, particularly in the Western Indian Ocean. This research gap is due to the difficulties and costs associated with carrying out surveys at deeper depths. Furthermore, there is no baseline data on the diversity and structure of fish assemblages particularly in the uThukela Banks MPA. The lack of baseline studies makes it difficult to provide context for the interpretation of changes and the variability in fish assemblages (Currie et al., 2020), thus preventing informed decision making. Preliminary exploration of these reefs show that they have rich diversity of fish (Dalton et al., 2021), however, comprehensive sampling within the MPA is yet to be completed. This highlights the urgent need of investigating the environmental factors influencing fish distribution in this MPA. The baseline datasets will also provide a starting point for determining the extent of fish populations decline or recovery within the MPA, thus supporting effective and adaptive management of the conservation area.

3.2.5 OBJECTIVES OF THE CURRENT STUDY

The aim for this chapter is to determine how environmental variables (depth, relief and benthic habitat) influence demersal fish assemblage diversity and structure on mesophotic reefs in the uThukela Banks MPA. In addition, this chapter will explore how fish assemblages vary between different management zones and reef complexes within the MPA. Lastly, the implications of these findings for conservation and management practices within the MPA will be discussed.

It was hypothesised that there will be higher species richness, abundance, and diversity in high relief reef habitats than low relief reef and sand habitats. It was also hypothesised that depth would have a stronger influence on fish assemblage structure and diversity than location and the different management zones of the uThukela Banks MPA. As the MPA is relatively new, it was hypothesised that there would be no measurable effect of management zone on the observed fish assemblages.

3.3 METHODS AND MATERIAL

The study site (section 2.1), sampling technique (section 2.4), video processing (section 2.4.3), and estimating covariates (section 2.4.5) can be found in the main methods (General materials and Methods).

3.3.1 ANALYTICAL APPROACH

3.3.1.1 UNIVARIATE ANALYSIS

Generalised regression techniques were used to determine the relationship between the environmental variables and the fish abundance and diversity metrics. The fish abundance and diversity metrics included: total abundance, slinger abundance, species richness, Beta-diversity and Shannon diversity. Total abundance is the sum of MaxN for every species recorded in a single stereo-BRUVs sample including that of slinger. The abundance (MaxN) of slinger was included as a metric for these analyses as slinger is one of the most important fisheries species in the region and a dominant component of reef ecosystems (Maggs et al., 2017). Species richness is the count of all unique species identified in each stereo-BRUVs samples. Beta-diversity quantifies the differences in species composition between sample units for a specific region at a specific spatial scale (Anderson et al., 2006). Shannon diversity index was used to evaluate variation in diversity because this index accounts for both species richness and total abundance (Bracewell et al., 2018). Species richness and Shannon-diversity were both calculated in PRIMER v7. Beta-diversity was measured as the multivariate dispersion score for each sample using the PERMDISP (permutational multivariate dispersion) routine in Plymouth Routines in Multivariate Ecological Research (PRIMER v7) + Permutational Multivariate Analysis of Variance (PERMANOVA) add-on software (Anderson et al., 2006).

All modelling was conducted in R software (R core team 2022) via R studio interface (R Development Core Team 2024). The ‘mgcv’ (Wood, 2008), ‘MASS’ (Ripley et al., 2019) and ‘nlme’ (Pinheiro et al., 2023) packages were employed for the modelling (Wood, 2008), and plots were produced using ‘ggplot2’ (Wickham and Wickham, 2016). Zuur et al. (2010) outlines the importance of data exploration before conducting any statistical analysis. Consequently, prior to model construction, detailed data exploration was done to check for outliers in the response and explanatory variables, examine collinearity among the covariates, and plot the relationships between response and explanatory variables (Williams et al., 2019; Zuur et al., 2010). The observed relationships between explanatory and response variables showed a non-linear effect of depth and visibility on the diversity indices (species richness and total abundance) thus,

necessitating the use of Generalised Additive Models (GAMs). The risk of overfitting models was minimised by examining the collinearity between the variables (Williams et al., 2019). Pearson correlation was used for assessing the collinearity among predictors, the highly correlated variables with correlation (>0.75) were removed (Maciel et al., 2024). Spatial autocorrelation was tested by constructing variograms with model residuals, this accounted for spatial aspects of sampling design used in the current study. Statistical modelling was conducted upon the completion of the data exploration. Furthermore, the exploration of data revealed that there were strong non-linear relationships between the dependent and continuous, independent variables. Furthermore, the sampling design resulted in samples being spatially clustered at different sampling locations (i.e. on separate reef systems) (section 2.4.2). Therefore, to account for the spatial dependency in the dataset, generalized additive mixed effects models (GAMMs) were used, with location included as a random effect.

Generalised additive models are an extension of Generalised linear models (GLMs), which includes smoothers in the regression function (Venables and Ripley, 2002), to model covariate effects and account for nonlinear relationships. They are valuable for capturing the shape of the relationship between covariates and the response variables without making a prior assumption about its parametric form (McLean et al., 2016). Mixed effect structures extend the capabilities of GAMs by incorporating random effects, which allow for the modelling of complex, hierarchical data and account for spatial dependency in ecological datasets. Therefore, GAMMs enable the partitioning of variation due to spatial autocorrelation or site-specific factors, improving model accuracy and inference in ecological studies (Zuur et al., 2010). GAMMs also help to account for overdispersion, a common problem in ecological research that is spatially structured (Williams et al., 2019). The relationship between the response variable and the covariates were visualised using 'plot.gam' function that included confidence intervals.

The data exploration demonstrated high collinearity (> 0.75) between the mean and variance scores for the terrain ruggedness index (TRI), at both scales (10 and 50m), and thus only the mean TRI scores were used. Similarly, light-level was excluded from the modelling because it was strongly correlated with depth (negative correlation). For each response variable the full GAMM was specified in R as:

$$Y \sim s(\text{Visibility}) + s(\text{Water column}) + s(\text{Temperature}) + s(\text{Depth}) + s(\text{TRI.10}) + s(\text{TRI.50}) + \text{Habitat} + s(\text{Location}, \text{bs} = \text{"re"})$$

Eq 3.1

All continuous variables were modelled with thin plate regression splines. The categorical variable 'habitat' was modelled as a parametric term. The categorical variable 'location' was modelled with a random effect spline basis to account for the grouping structure in the data. To identify the best-fit model for each response variable full-subset model selection was performed using the dredge function in the 'MuMIn' package (Barton, 2023). This process involved fitting all possible sub-models of the full-model and ranking them based on the Akaike information criterion (AIC; Akaike, 1974) to identify the most parsimonious model that best explained the data while avoiding overfitting.

Model assumptions were tested using '*performance*' package (Lüdecke et al., 2021). The Poisson error distribution, which assumes that the mean is equal to the variance, was used to model the metrics based on count data (species richness, total abundance, slinger abundance). All assumptions were met for species richness and environmental variables. However, the assumptions of normality, overdispersion and homogeneity were violated in the models for the slinger abundance and total abundance; therefore, a negative binomial family of error distribution was used. Tweedie error distributions were used to fit the GAMMs for Shannon and Beta Diversity.

To measure if there was any effect of management zone on the abundance and diversity metrics, the above modelling approach was replicated with the inclusion of 'management' as a parametric term in the GAMM. Management modelled as a categorical fixed effect, allowing the model to estimate whether different management zones have effect on metrics. To prevent pseudo-replication leading to overestimation of significance levels of model parameters and precision (Weltz et al., 2013), location (reef complex) where the stereo-BRUVs landed was treated as a random effect using the *bs="re"* term to account for location being nested within the management zones of the uThukela Banks MPA. This was done to accommodate for the clustering (lack of independence) of samples within each reef.

To illustrate the effect of significant environmental variables, the mean ($\pm$ 95 CI) abundance and diversity estimate were predicted from the model coefficients and plotted using '*ggplot2*'. The predictions were made for the range of values for each environmental variable of interest while keeping all the other variables included in the best-fit model standard to their mean scores. The random effect of location was excluded during the prediction process.

3.3.1.2 MULTIVARIATE ANALYSIS

All species abundance data were analysed as a multivariate dataset in PRIMER V7 with the PERMANOVA add-on package (Anderson et al., 2008) to determine the effect of spatial and environmental variables on fish community structure. The data were log transformed and a Bray-Curtis similarity resemblance measure between samples was calculated (Anderson et al., 2011). Log transformation was done to down weight the effect of highly abundant species on the outcomes, relative to rare species.

A shade plot is a simple matrix visualisation that shows species abundance at different sampling sites (Clarke et al., 2014). It was employed before data transformation to help select an appropriate transformation (Clarke et al., 2014). Prior to the analysis, Draftsman plot was used to identify highly correlated environmental variables. The following environmental variables were removed from the multivariate analysis because they highly correlated with each other: light level which negatively correlated with depth ($r=0.84$), TRI10m variance which correlated with TRI10m ($r=0.78$); and TRI50m variance which correlated with TRI50m ($r=0.77$) and longitude which highly correlated with latitude ($r=0.96$).

Species composition and abundance comparisons between management zones, location and benthic habitat covariates was performed with a PERMANOVA. Statistical significance was tested with 9999 residual permutations with type 1 (sequential) sum of squares. Independent variables were included as factors and as covariates in the PERMANOVA and were specified in sequential order in the model to first take into account the sampling related `noise` covariates and then the environmental and spatial variables. The order was: visibility, water column, temperature, depth, habitat (fixed factor), TRI10m, TRI50m, latitude, management (fixed factor) and location (random factor). After removing the highly correlated variables, obstruction was excluded as no samples were obstructed.

Multivariate community data was visualised using non-metric multidimensional scaling (nMDS) plots with points displayed according to the zones of the MPA using the same pre-treatment from PERMANOVA. Pre-treatment are steps taken to prepare data prior to the analysis; they include data transformation/normalisation and data cleaning (Clarke et al., 2014). Pre-treatment addresses problems such as outliers and missing values, and this improves the reliability and data accuracy. The nMDS was done to visualize the patterns of differences in community structure (fish species detected) (Zintzen et al., 2012; Arreola et al., 2024) among different zones at different sampling depths. This ordination technique

was appropriate because the data used is ecological data which has zeros in most samples because of the absence of certain species in the sample (Clarke and Warwick, 2001). Canonical analysis of principal coordinates was performed to evaluate the effect of significant factors: habitat, management zones and location; and identify species driving the observed differences. The CAP is a constrained ordination technique that uncover patterns masked by the nMDS and it does this using 9999 unique permutations (Anderson and Willis, 2003; Clarke and Gorley, 2015). For both CAP and nMDS the correlation between dominant species and canonical analysis was done using a Pearson's correlation ($R=0.4$). To determine the misclassification error cross validation tests were performed. Cross validation gives an insight about the model's predictive performance and stability. Accompanying each CAP a leave-one-out allocation was done. This method draws an inference regarding the hypothesis, by evaluating model's performance on the excluded data points (Berrar, 2018). Higher allocation percentage success indicates that the model has good predictive power.

PERMDISP is a distance-based test for homogeneity of multivariate dispersion that compares the variability within factors. A PERMDISP based on Bray-Curtis similarity measure was conducted to check if the levels of the factors: habitat, management, and location differed in terms of variability within each level. The Similarity percentage breakdown (SIMPER) for abundance data was performed in PRIMER to estimate the contribution of fish species to the average similarity and dissimilarity of within and between management zones and habitats for observed differences in the CAP analysis. Prior to conducting SIMPER, data were transformed using $\text{Log}(X+1)$ transformation to reduce the contribution of abundant species in the data in relation to less abundant species (Clarke et al., 2006). The cut-off for lower species contributions was set to 80 %, this was done to ensure that only dominant species that contributed to the dissimilarity between management zones and habitat types were shown. A non-Euclidean similarity measure, Bray-Curtis resemblance measure was used to calculate similarity between replicate samples (Clarke et al., 2006).

3.4 RESULTS

3.4.1 GENERAL DESCRIPTION OF SPECIES ASSEMBLAGE COMPOSITION

A total of 127 species from 42 families with 5 753 individuals (sum of MaxNs) were identified from the 126 stereo-BRUVs samples deployments (Table 7.1). Samples covered habitat types including sand, sand inundated reef, and reef. Sand habitats were sampled between 50.5-192.5 m and reef habitats were sampled from depths of 36.5-172.5 m. There was higher proportion of Osteichthyes (105 species), relative to Chondrichthyes (22 species) in shallower depths. From the collected video samples, the majority of fish were identified to the species level and only 3 % were identified to the level of genus and family. The most abundant species included slinger ($n = 1230$), santer *Cheimerius nufar* ($n = 639$), sand soldier *Pagellus natalensis* ($n = 497$). Sparidae was the most diverse family with 25 species, followed by Serranidae which had 11 species (Appendix Table 7.1A). The three metrics presented in the tables below correspond to instances where habitat and management had significant effects on diversity and fish assemblage structure. The following number of samples fell into each habitat type: sand (27), SIR (36), and reef (63).

3.4.2 UNIVARIATE ANALYSIS

3.4.2.1 EFFECT OF ENVIRONMENTAL VARIABLES ON TOTAL ABUNDANCE

The best-fit GAMM run on total abundance explained 71.3 % variability in the response variable. The results showed the significant effect of habitat, visibility, temperature, depth, and location on total abundance (Table 3.1, a). Total fish abundance was significantly higher on reef habitats than sand habitats, however, there was no measurable difference between sand and sand inundated reef (SIR); sand inundated reef and reef habitat benthic environments (Figure 3.1, a). Temperature showed a significant linear trend (effective degrees of freedom (edf) = 1), with total fish abundance decreasing with increase in water temperature (Appendix Figure 7.2). Visibility and depth had a significant non-linear effect (edf>1) on total abundance (Table 3.1, a). Total fish abundance initially increased with increasing visibility but plateaued and remained relatively constant at higher levels of visibility (Appendix Figure 7.2). The effect of depth showed an exponential decay pattern with highest abundances observed between 35-80 m declining rapidly before plateauing past 80 m (Figure 3.2, a). The random effect of location was highly significant indicating a high degree of variability in total abundance between the different mesophotic reefs in the MPA (Table 3.1, a).

Table 3.1: Wald's test results of the generalised additive mixed models investigating the effect of environmental variables on total abundance, species richness, Shannon diversity, beta diversity, and slinger abundance. The df = degrees of freedom; edf = estimated degrees of freedom; Ref. edf = residual effective degrees of freedom; Chi.sq/ X^2 = Chi square, F = test statistic. TR10 m and TR150 m = Terrain ruggedness index at 10 metre and 50 metre radiuses. The P-values are given for both parametric and smooth terms. Significant p-values are represented by an asterisk (*).

(a)Total abundance	Parametric Terms	df		Chi.sq	p-value	Symbol
	Habitat	2		17.47	0.000	***
	Smooth Terms	edf	Ref.edf	Chi.sq	p-value	
	s(Visibility)	3.082	3.395	18.637	0.000	***
	s(Water column)	1.613	1.997	1.044	0.603	
	s(Temperature)	1.000	1.000	6.003	0.014	*
	s(Depth)	2.460	3.030	38.071	0.000	***
	s(TR10m)	1.000	1.001	0.355	0.551	
	s(TR150m)	1.442	1.738	1.455	0.538	
	s(Location) random effect	5.057	8.000	20.999	0.000	***
(b) Species richness	Parametric Terms	df		Chi.sq		Symbol
	Habitat	2		21.46	0.000	***
	Smooth Terms	edf	Ref.edf	Chi.sq	p-value	
	s(Visibility)	2.803	3.545	8.862	0.041	*
	s(Temperature)	1.000	1.000	13.929	0.001	**
	s(Depth)	2.968	3.672	94.687	0.000	***
	s(TR10 m)	2.644	3.289	8.169	0.052	.
	s(TR150 m)	2.042	32.531	1.478	0.478	
	s(Location) random effect	2.125	8.000	3,205	0.139	
(c) Beta diversity	Parametric Terms	df		F-value		Symbol
	Habitat	2		0.601	0.55	
	Smooth Terms	edf	Ref.edf	F-value	p-value	
	s(Visibility)	1.000	1.000	0.202	0.654	
	s(Temperature)	3.111	3.784	1.424	0.227	
	s(Depth)	2.179	2.680	5.631	0.003	* *

(c) Beta diversity	Smooth Terms	edf	Ref.edf	F-value	p-value	Symbol
	s(TRI10 m)	1.000	1.000	2.781	0.098	.
	s(TRI50 m)	1.058	1.108	1.393	0.225	.
	s(Location) random effect	4.852	8.000	2.137	0.000	***
(d) Shannon diversity	Parametric Terms	df		F-value		
	Habitat	2		1.133	0.326	
	Smooth Terms	edf	Ref.edf	F-value	p-value	Symbol
	s(Visibility)	1.046	1.089	7.199	0.006	**
	s(Water column)	1.577	1.950	0.653	0.561	.
	s(Temperature)	1.000	1.000	14.222	0.000	***
	s(Depth)	2.531	3.118	14.285	0.000	***
	s(TRI10 m)	1.855	2.305	1.221	0.235	.
	s(TRI50 m)	2.607	3.259	2.685	0.054	.
	s(location) random effect	4.182	8.000	1.521	0.006	**
(e) Slinger abundance	Parametric Terms	df		Chi.sq		
	Habitat	2		17.56	0.000	***
	Smooth Terms	edf	Ref.edf	Chi.sq	p-value	
	s(Visibility)	3.027	3.819	11.614	0.018	*
	s(Water column)	1.000	1.000	3.810	0.051	.
	s(Depth)	3.181	3.950	11.397	0.024	*
	s(TRI10 m)	1.000	1.000	0.003	0.961	.
	s(TRI50 m)	1.681	2.056	1.391	0.518	.
	s(Location) random effect	4.310	8.000	10.188	0.015	*

*P-value: *** < 0.001; ** < 0.01; * < 0.05; '.' < 0,1*

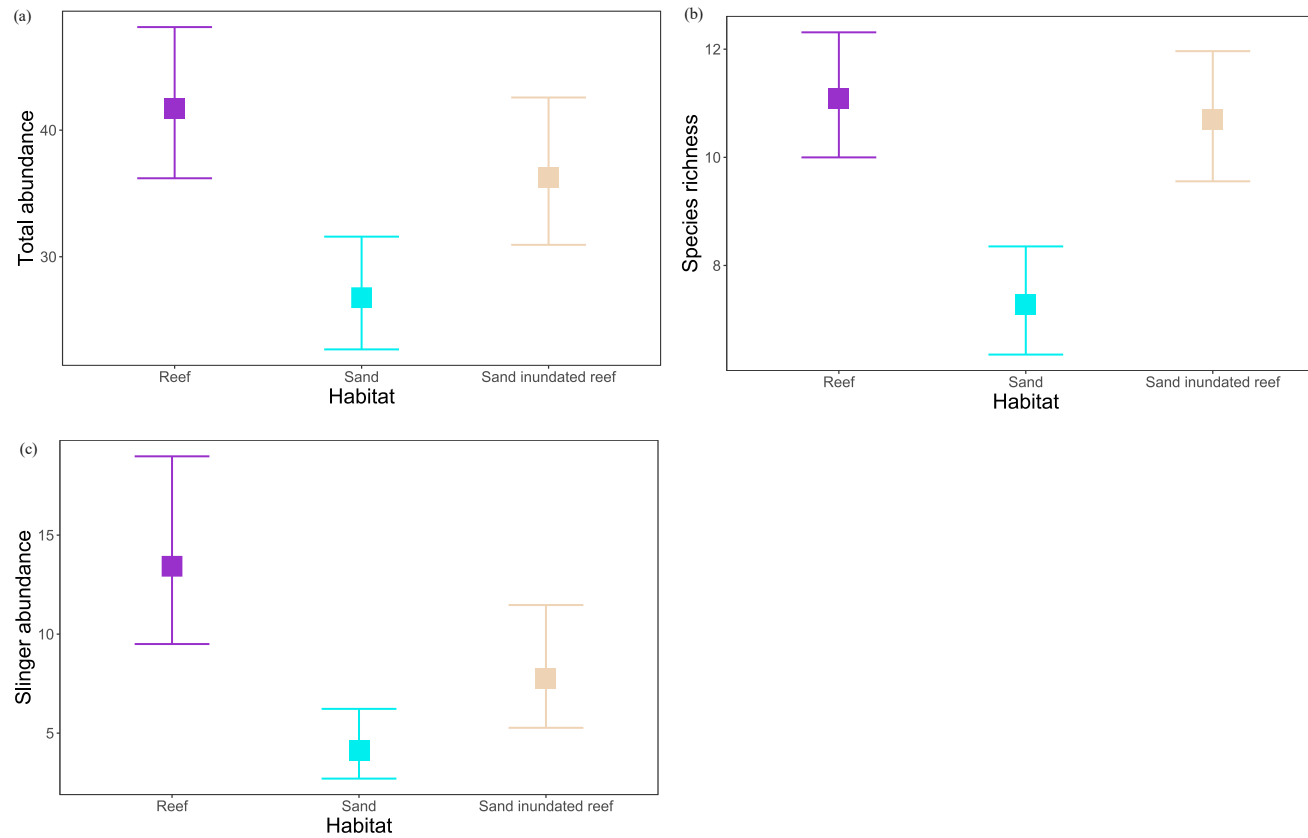


Figure 3.1: Results from generalised additive mixed effect models (GAMMs) showing the effect of benthic habitat type on the (a) total abundance, (b) species richness and (c) slinger abundance. The predictions within each habitat class are based on standardised mean values for all explanatory variables included in the best-fit GAMMs. The error bars represent 95 % confidence interval.

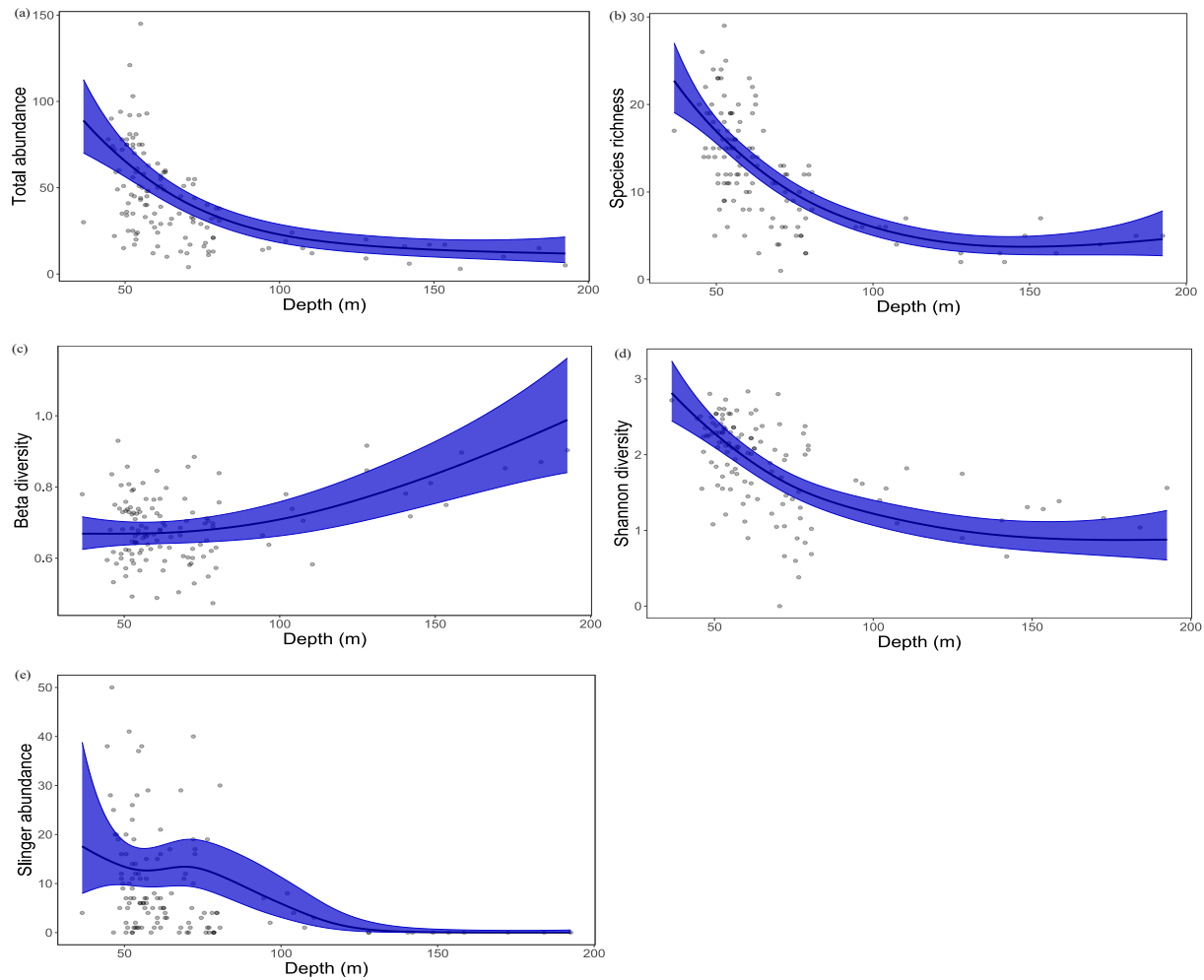


Figure 3.2: Results from generalised additive mixed effect models (GAMMs) showing the effect of depth on the (a) total abundance, (b) species richness, (c) beta diversity, (d) Shannon diversity and (e) slinger abundance. The predictions are based on standardised mean values for all explanatory variables included in the best-fit GAMMs. The error bars represent 95 % confidence interval.

3.4.2.2 EFFECT OF ENVIRONMENTAL VARIABLES ON SPECIES RICHNESS

The best-fit GAMM for species richness data was able to explain 72.3 % variability in response variable. The results showed a significant effect of habitat, visibility, temperature, and depth on species richness ($p < 0.05$). Temperature had a linear effect ($\text{edf} = 1$) on species richness with richness decreasing with increasing temperature, higher species richness between 16-17 °C and lowest species richness between 21-22 °C (Appendix Figure 7.3). Visibility and depth showed a non-linear relationship ($\text{edf} > 1$) with species richness (Table 3.1, b). There was no significance difference between reef habitats (reef and SIR); this was indicated by a considerable overlap in the confident intervals (Figure 3.1, b). Sand habitat had significantly lower species richness than reef and SIR habitats (Figure 3.1, b). Species richness showed a similar pattern to total abundance, decreasing with increasing water depth before levelling off deeper than 80 m depth (Figure 3.2, b).

3.4.2.3 EFFECT OF ENVIRONMENTAL VARIABLES ON BETA DIVERSITY

The best-fit GAMM run on beta diversity explained 43% of the variability in the response variable. Wald's test run on GAMM results showed that visibility, temperature, TRI10m, TRI50m, and habitat had no effect on beta diversity (Table 3.1, c). There was a significant effect of depth ($F = 5.631$, $p = 0.003$) and location ($F = 2.137$, $p = 0.001$) on beta diversity. Beta diversity increased significantly with the increase in water depth, with higher beta diversity past 100 m compared to lower diversity below this depth (Figure 3.2, c) (Appendix Figure 7.4). The significant effect of location indicated that beta diversity between the reef systems.

3.4.2.4 EFFECT OF ENVIRONMENTAL VARIABLES ON SHANNON DIVERSITY

The best-fit GAMM run on Shannon diversity explained 52.8 % variability in the response variable. Wald's test results showed no effect ($p > 0.05$) of habitat, water column, TRI10m, and TRI50m on Shannon diversity. Depth had the significant effect on Shannon diversity ($F = 14.285$, $p < 0.001$) (Table 3.1, d) with trend that mirrored the pattern observed in species richness and total abundance (Figure 3.2 d). Shannon diversity decreased with increasing water temperature (Appendix Figure 7.4). Visibility had a non-linear effect, with highest diversity at intermediate levels of visibility (Appendix Figure 7.4). Shannon diversity varied significantly among the survey locations (Table 3.1, d).

3.4.2.5 EFFECT OF ENVIRONMENTAL VARIABLES ON SLINGER ABUNDANCE

The best-fit GAMM run on slinger abundance data was able to explain 54.4 % variability in the response variable. Wald's test results run on GAMM showed that habitat, visibility, depth, and location had a significant effect on slinger abundance (Table 3.1, e). A non-linear trend was observed for visibility and depth. There was no effect ($p > 0.05$) of water column, TRI10m, and TRI50m on slinger abundance. The plot based on the model estimates showed higher slinger abundance at lower water depth between 40-70 m declining rapidly to 120m depth below which they were absent (Figure 3.2, e). A slight negative relationship was observed between slinger abundance and visibility (Appendix Figure 7.5). The habitat effect indicated significantly lower slinger abundance on sand compared to reef habitat (Figure 3.1 c). However, there were no significant differences between the reef habitats (reef and SIR) indicated by overlapping confidence intervals of these habitats (Figure 3.1, c).

3.4.2.6 THE EFFECT OF MANAGEMENT ZONE ON DIVERSITY AND ABUNDANCE METRICS

Results from the Wald tests run on GAMMs showed that there was a significant effect of management on total abundance ($X^2 = 8.036$, $P = 0.040$), species richness ($X^2 = 20.64$, $p < 0.001$), Shannon diversity ($F = 3.196$, $p = 0.002$), and slinger abundance ($X^2 = 10.44$, $P = 0.015$) (Table 3.2). There was no effect of management only on Shannon diversity (Table 3.2, d). Total abundance was significantly higher in the exploited zone than the restricted zone (Figure 3.3 a). Species richness and Shannon diversity was significantly higher in the exploited zone than both the restricted zone and the CPLF (Figure 3.2, b and c). Slinger abundance was significantly higher in the CPLF than the restricted zone (Figure 3.2, d).

Table 3.2: Wald's test results of the generalised additive mixed models investigating the effect of management on total abundance, species richness, Shannon diversity, beta diversity, and slinger abundance in the uThukela Banks marine protected area. df = degrees of freedom; edf = estimated degrees of freedom; Ref.edf = residual effective degrees of freedom; Chi.sq/ X² = Chi square, F = test statistic. TRI10 m and TRI50 m = Terrain ruggedness index at 10 metre and 50 metre radiuses. The P-values are given for both parametric and smooth terms. Significant p-values are represented by an asterisk (*).

(a) Total abundance	Parametric Terms	df		Chi.sq	p-value	Symbol
	Management	3		8.306	0.040	*
	Smooth Terms	edf	Ref.edf	Chi.sq	p-value	
	s(Visibility)	3.737	4.670	31.608	0.000	***
	s(Water column)	2.935	3.633	4.050	0.259	
	s(Depth)	2.242	2.805	29.507	0.000	***
	s(TRI10m)	1.000	1.000	0.281	0.596	
	s(TRI50m)	1.000	1.000	0.012	0.911	
	s(Location) random effect	2.914	5.000	8.803	0.009	**
(b) Species richness	Parametric Terms	df		Chi.sq	p-value	Symbol
	Management	3		20.64	0.000	***
	Smooth Terms	edf	Ref.edf	Chi.sq	p-value	
	s(Visibility)	4.64	5.684	25.570	0.000	***
	s(Water column)	3.000	3.698	4.034	0.257	
	s(Depth)	2.770	3.459	67.770	0.000	***
	s(TRI10m)	2.830	3.503	6.884	0.129	
	s(TRI50m)	1.913	2.384	1.758	0.427	
	s(Location) random effect	0.000	5.000	0.001	0.520	
(c) Beta diversity	Parametric Terms	df		Chi.sq	p-value	Symbol
	Management	3		0.616	0.606	
	Smooth Terms	edf	Ref.edf	Chi.sq	p-value	
	s(Visibility)	1.000	1.000	0.003	0.953	
	s(Depth)	1.440	1.747	5.538	0.026	*
	s(TRI10 m)	1.000	1.000	3.377	0.068	.

(c) Beta diversity	Smooth Terms	df		Chi.sq	p-value	Symbol
	s(TRI50 m)	2.742	3.431	1.425	0.193	
	s(Location) random effect	4.011	5.000	4.869	0.000	***
(d) Shannon diversity	Parametric Terms	df		Chi.sq	p-value	Symbol
	Management	3		3.196	0.026	*
	Smooth Terms	edf	Ref.edf	Chi.sq	p-value	
	s(Visibility)	1.757	2.210	6.048	0.003	**
	s(Depth)	1.968	2.467	4.187	0.013	*
	s(TRI10 m)	2.544	1.621	0.965	0.507	
	s(TRI50 m)	2.544	3.179	2.486	0.068	.
	s(Location) random effect	2.629	5.000	1.571	0.013	*
	Parametric Terms	df		Chi.sq	p-value	Symbol
	Management	3		10.44	0.015	
(e) Slinger abundance	Smooth Terms	edf	Ref.edf	Chi.sq	p-value	
	s(Visibility)	3.075	3.894	12.811	0.011	*
	s(Water column)	1.000	1.000	2.241	0.134	
	s(Temperature)	1.000	1.000	0.418	0.518	
	s(Depth)	3.169	3.983	13.930	0.009	**
	s(TRI10 m)	1.000	1.000	0.004	0.951	
	s(TRI50 m)	1.000	1.000	0.321	0.571	
	s(Location)	2.219	5.000	4.408	0.070	.
	Parametric Terms	df		Chi.sq	p-value	Symbol
	Management	3		10.44	0.015	

*P-value: *** < 0.001; ** < 0.01; * < 0.05; '.' < 0.1*

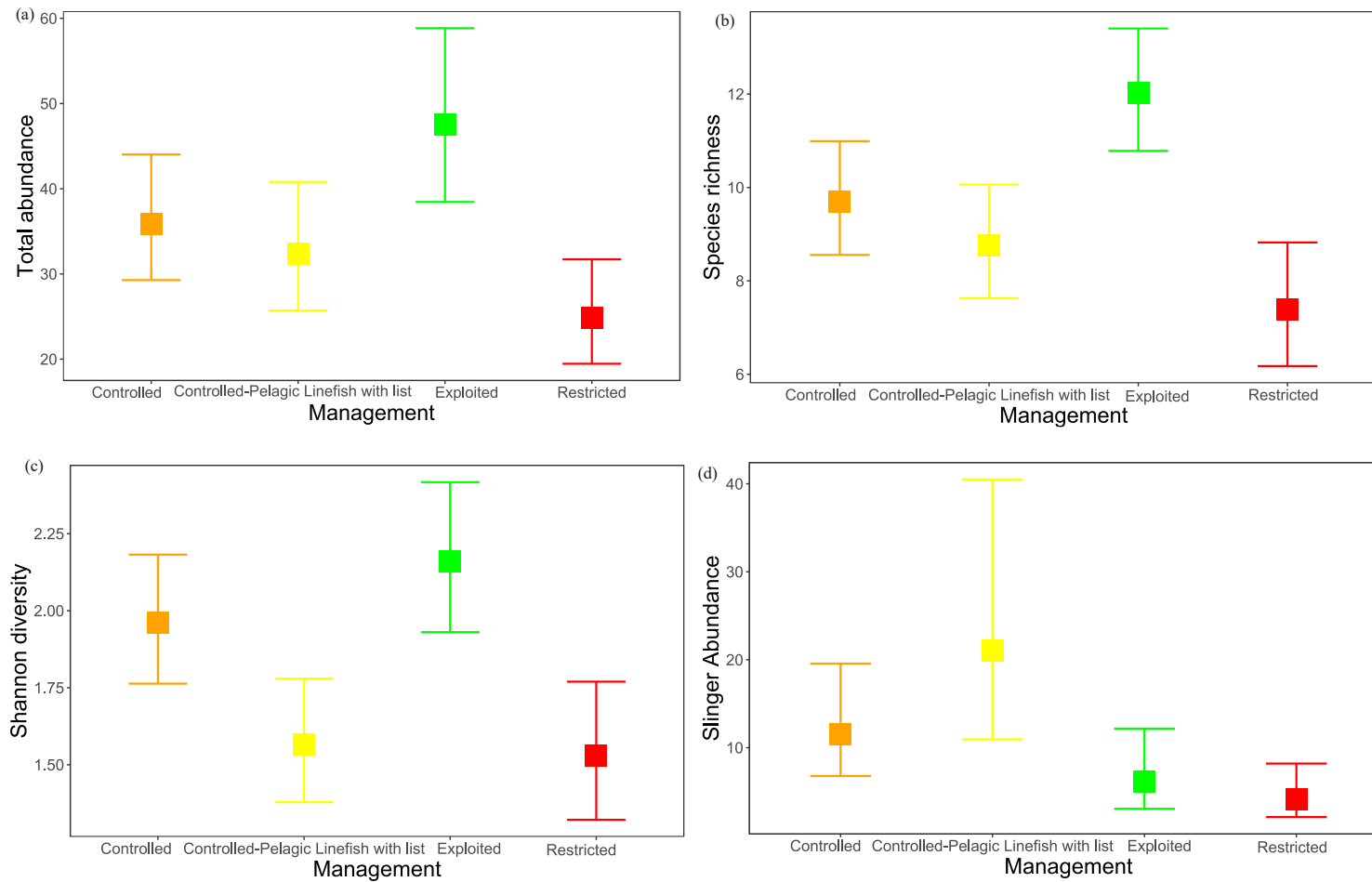


Figure 3.3: Results from generalised additive model (GAM) output testing the effect of management zonation in the uThukela Banks MPA on the (a) total abundance, (b) species richness, (c) Shannon diversity, (d) slinger abundance. The predictions based on standardised mean values for all explanatory variables included in the GAM. The error bars represent 95 % confidence interval.

3.4.3 MULTIVARIATE ANALYSIS OF FISH ASSEMBLAGE ABUNDANCE

Results from sequential PERMANOVA indicated that all variables accounted for a significant ($p < 0.05$) amount of variation in fish assemblage abundance (Table 3.3). In addition to this, a significant interaction was observed between habitat and management (pseudo-F = 1.6965, $p = 0.0002$) on fish assemblage abundance. A PERMDISP test for homogeneity of multivariate showed that dispersion among samples was significantly influenced by habitat, management zone and location this was indicated by a PERMDISP ($p = 0.0193$, $p = 0.0001$ and $p = 0.0001$) respectively.

Table 3.3: Full model output of the sequential permutational multivariate analysis of variance (PERMANOVA) run on log (X+1) transformed fish species abundance resemblance data in response to covariates (visibility, % water column, temperature, depth, mean terrain rugosity index at 10 (TRI10m) and 50 meter (TRI50m) radius), and the factors: management, habitat and location) based on Bray-Curtis similarities. Significant p-values ($p < 0.05$) are given in bold, and they indicate significance difference. Degrees of freedom (df), sum of square (SS), mean squares (MS), pseudo-F, probability level based on permutations (P perm).

Source	df	SS	MS	Pseudo-F	P (perm)
Visibility	1	8611.1	8611.1	4.3256	0.0001
Water column	1	11136	11136	4.6643	0.0001
Temperature	1	18478	18478	3,8587	0.0001
Depth	1	47631	47631	9.2895	0.0001
Habitat	2	15298	7649.2	4.34	0.0001
TRI10m	1	7211	7211.3	4.0245	0.0001
TRI50m	1	5098.7	5098.7	2.9602	0.0004
Management	3	20406	6802.1	1.5342	0.0297
Latitude	1	13603	13603	2.3864	0.0008
Location	5	27885	5576.9	2.4868	0.0001
Habitat x Management	6	13559	2259.9	1.6965	0.0002
Residual	102	42.325	1309.6		
Total	125	71.179			

The pairwise PERMANOVA comparisons showed significant differences between sand and reef ($t = 2.5746$, $P = 0.0001$); sand and SIR ($t = 1.5596$, $P = 0.005$) and between reef and SIR ($t = 1.3835$, $P = 0.0201$). The differences in fish assemblages between different management zones was due to the controlled-pelagic linefish with list being different in terms of species composition to the exploited zone ($t = 1.8228$, $p = 0.0009$), the controlled zone different from restricted zone ($t = 1.5763$, $p = 0.0065$) and restricted different from exploited zone ($t = 2.3294$, $p = 0.0001$). The differences in fish assemblages between different

locations was due to Durnford Hat being different from Ballito Tongaat ($t = 2.3486$, $P = 0.0001$) and Zinkwazi ($t = 1.4621$, $P = 0.0175$); and uMdloti being different from Rosie Snow ($t = 1.5419$, $P = 0.0084$). For habitat, the results from non-metric multidimensional scaling showed the distinct clustering of reef and sand samples, with SIR occupying an intermediate space between the other two habitats (Figure 3.4, a). The spread of samples along the x-axis of the biplot was strongly correlated with depth, suggesting there were more sand samples in the deep waters. The species correlation vectors (Figure 3.4, b) showed that deeper samples were characterised by blueskin *Polysteganus coeruleopunctatus* seabream and largehead hairtail *Trichiurus lepturus* while the shallow reef samples had more than fifteen species with ($R=0.4$) correlations threshold (Figure 3.4, b).

The nMDS plots for management zone showed a partial separation between the restricted and CPLF zones of the MPA and these were distinct from the controlled zone and exploited zone which were characterised by similar fish assemblages (high degree of overlap). The observed pattern was strongly correlated with depth and latitude (Figure 3.4, c). Restricted and CPLF were typified by a deep-water fish blueskin seabream and largehead hairtail. The following species typified controlled and exploited zone: sand soldier, African scad *Trachurus Delagoa*, steentjie *Spondylus emarginatus*, cavebass *Dinoperca pertersi*, zebra seasbream *Diplodus hottentotus*, striped grunter *Pomadasys striatus*, German seasbream *Polyamblyodon germanum*, and dane seabream *Pocorstoma dentata*. The controlled zones (controlled-pelagic linefish with list and controlled) were typified by Englishman *Chrysoblephus anglicus*, slinger, halfmoon rockcod *Epinephelus vivulatus*, fourline hogfish *Bodianus trilineatus*, and scotsman *Polysteganus praeorbitalis* (Figure 3.4, d).

When looking at the nMDS in terms of the Location variable, it is evident that the samples are clustered according to latitude with the northern reefs (Carpenters, Sundowners, Zini Hard Edge, Pat's paradise and Durnford Hat) clustered above the southern reefs (Ballito-Tonga, Zinkwazi, Umdloti and Rosy Snow) (Figure 3.4, e). The effect of depth was also evident in the northern reefs with the fish assemblages from the shallower Pats Paradise and Durnford Hat being different from Carpenters, Sundowners and Zini Hard Edge reefs (Figure 3.4, e). Lastly, the dispersion of samples in the NMDs plots varied according to latitude, with the southern reefs clustered tightly together and the northern reefs showing greater variation in species assemblages (Figure 3.4, e). The northern deep reefs were characterised by blueskin seabream and largehead hairtail. The northern shallow reefs were characterised Natal emperor *Lethrinus scoparius*, rosy goatfish *Parapeneus rubescens*, halfmoon rockcod, fourline hogfish, African butterfly fish *Chaetodon*

dolusus, slinger and Englishman (Figure 3.4, e). The southern reefs were characterised by natal pandora, African scad, steentjie, stripped grunter, dane seabream, cavebass, German seabream, and zebra seabream (Figure 3.4, f).

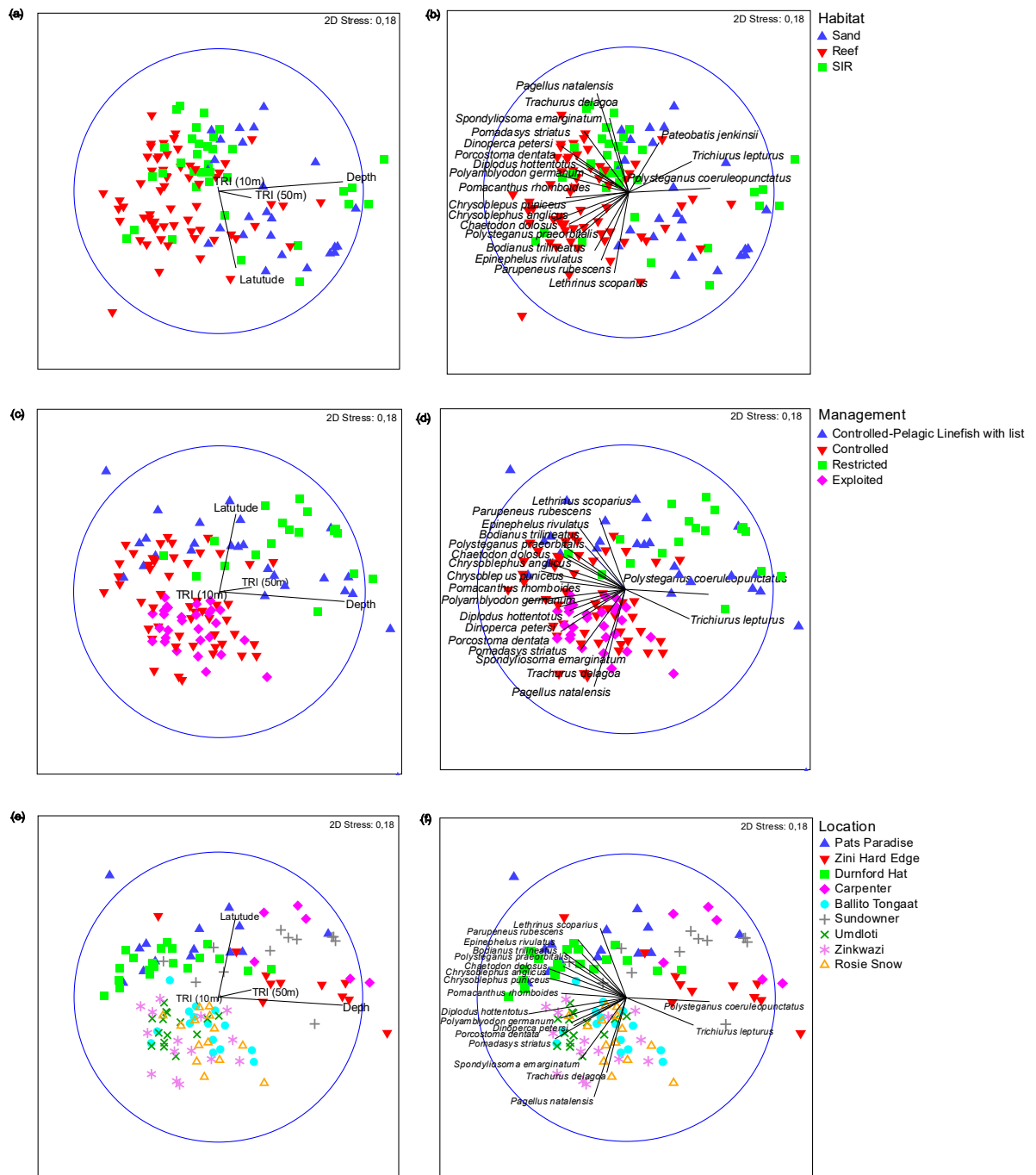


Figure 3.4: Non-metric multidimensional scaling (nMDS) plots of $\log(X+1)$ transformed fish abundance data from stereo-BRUVs samples based on Bray-Curtis resemblance matrix. The first row representing environmental variables vectors and second row representing fish species vectors superimposed on an nMDS plot correlating with the distribution of habitat (a,b); management (c,d) and location (e,f). Environmental variables and species vectors overlaid, the line length of each vector indicate the direction and correlation strength. Pearson correlation for species vectors ($R = 0.4$) and environmental vectors selected.

A CAP analysis was conducted to determine whether benthic habitat types, management and location had a significant effect on fish community and fish abundance based on *a priori* hypotheses that fish communities between different habitats and management zones are similar. The CAP analysis showed a significant separation between benthic habitats ($\text{tr}(\mathbf{Q}_m' \mathbf{H} \mathbf{Q}_m)$: 0.489, $p=0.0001$); and management ($\text{tr}(\mathbf{Q}_m' \mathbf{H} \mathbf{Q}_m)$: 1.644, $p=0.0001$) for the abundance data. Twenty-three species contributed to observed differences ($R=0.04$) in the abundance data (Figure 3.5, a). The analysis showed clustering of reef and SIR, and 19 species were shared between them. Partial clustering was observed between the three habitats the following species were shared: santer, blueskin seabream, and African scad (Figure 3.5, a).

The leave-one-out cross validation from a CAP analysis evaluated how well each observation for each group habitat classified from all the samples in which only a test set is removed from the model fitting process. The cross-validation analysis predicted which habitat sample was collected based on species assemblage with overall accuracy of 60 %. Reef habitat group had the highest classification (74.2 %) compared to both sand and SIR which had classification percentages of 53.6 % and 52.8 % respectively. Only seven and nine observations were misclassified as SIR and sand respectively, in the reef habitat group. This indicated that the group reef was well distinguished as there were fewer misclassifications (Appendix Table 7.2B).

There was no clear separation of management zones, however, the exploited and controlled zone were partially clustered and had shared species among them. The restricted zone and controlled-pelagic linefish with list were typified by santer. Dane seabream strongly correlated with the controlled zone. Eighteen species contributed to the observed differences ($R=0.04$) in distinguishing fish species in different management zones (Figure 3.5, b).

The leave-one-out cross validation of observation from four groups: CPLF, controlled, restricted and exploited management zones. Overall accuracy of 78.6 % and 99 out of 126 total observations were correctly classified. Across all samples only 21.4 % of the observations were misclassified. The restricted group showed high classification of 93.1 % with only two and 27 observations misclassified as controlled and exploited group, respectively. Furthermore, the restricted group showed lowest correct percentage (66.7 %) compared to the rest of other groups. Only 12 observations were classified as restricted and three were misclassified as controlled and three as the CPLF. This indicated the difficulty of a model in

differentiating the restricted group especially between the two controlled management zones (controlled and CPLF) (Appendix Table 7.3C).

There was a clear separation of the Zini Hard Edge (location) reef system, being the deepest reef system, and it was strongly correlated with blueskin seabream. There was a clustering of the southern reefs Rosie Snow, Zinkwazi, Ballito Tongaat and Umdloti and the following species were shared between these locations: African scad, steentjie, sand soldier, Cape stumpnose *Rhabdosargus holubi*, false Englishman *Chrysoblephus lophus*, zebra seabream, German seabream, old woman angelfish *Pomacanthus rhomboides*, dane seasbream, slinger and African butterfly fish. Similarly, there was a clustering pattern of the northern reefs of Durnford Hat, Carpenter and Pat's Paradise, the shared species between them included Natal emperor *Lethrinus scoparius*, halfmoon rockcod, rosy goatfish *Parupeneus rubescens* and fourline hogfish (Figure 3.5, c). In addition, carpenter reef showed greater dispersion than the other locations. The leave-one-out cross validation of observation from nine groups of locations showed an overall accuracy of 70.6 % and 89 out of 126 total observations were correctly classified. Across all samples only 29.4 % of the observations were misclassified. Both Zini Hard Edge and Umdloti both showed highest classification of 80 % with only a few observations misclassified. Furthermore, Carpenter location showed lowest correct percentage (50 %) compared to the rest of other groups, one observation from Carpenter was misclassified into Pat's Paradise and two misclassified into Zini Hard Edge (Appendix Table 7.4D).

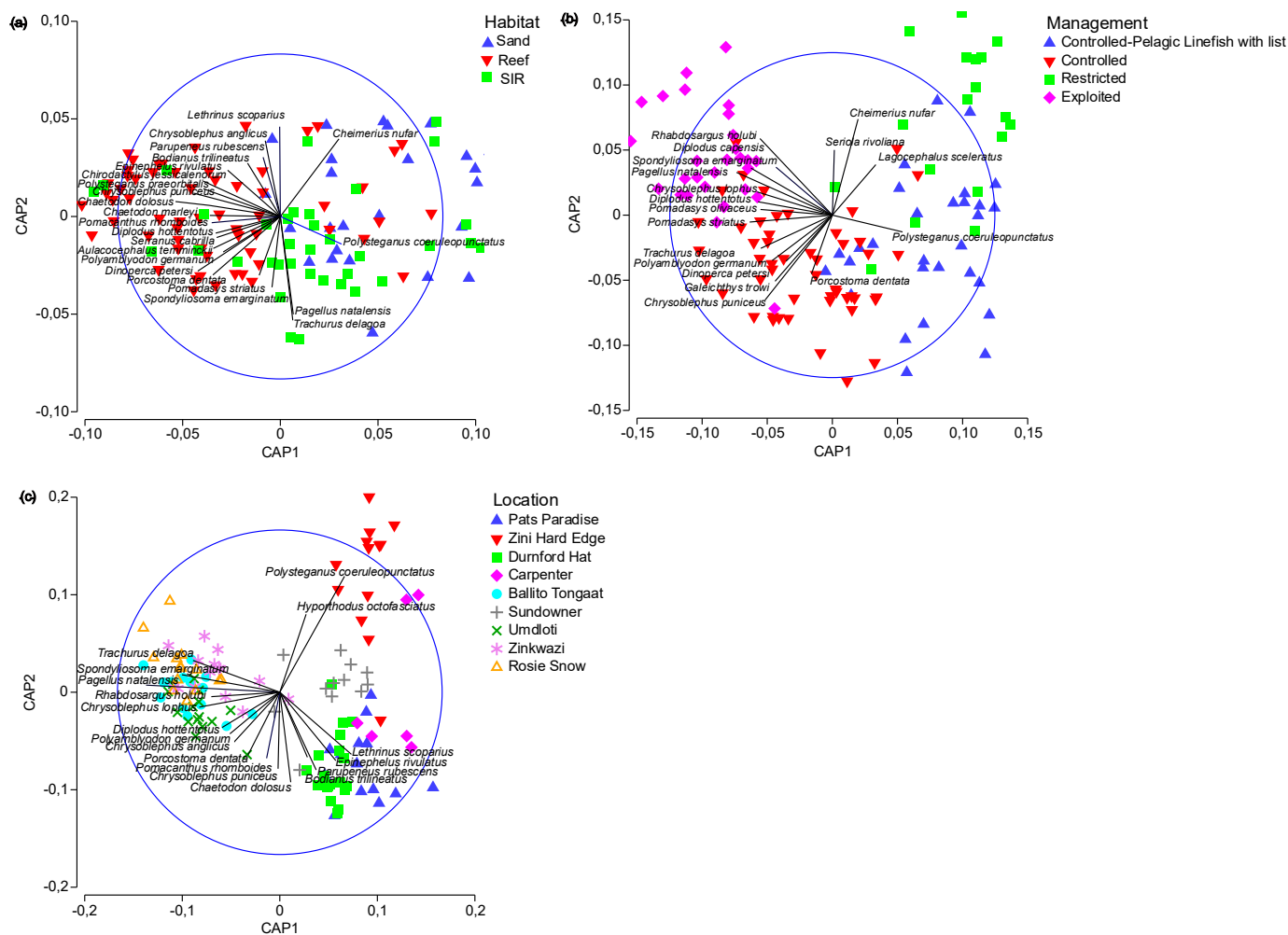


Figure 3.5: Results from the canonical analysis of principal coordinates (CAP) ordination of samples based on Bray-Curtis similarities for fish abundance, grouped by habitat type (a), management (b) and location (c). Overlaid fish vectors with Pearson correlation ($R=0.4$). The strength of the correlation is shown by each vector's length and direction.

A SIMPER analysis was used to further investigate the community similarity in fish community composition between sand, reef and SIR habitats. The results showed the key patterns in fish assemblages across the three habitats and very few species contributed to the observed patterns. Santer (44.02 and 24.22 %) and slinger (21.12; 20.77 and 29.88 %) were responsible for explaining the average similarity in sand, reef and SIR habitat type respectively. Indicating an overlap in the dominant species. The species that had the least contribution in the similarity includes Englishman (5.53 %) in sand habitat, sand soldier (4.66 %) in reef and African scad (4.61 %) in the SIR habitat (Figure 3.6). In addition, reef habitat (33.32 %) had the highest average similarity compared to sand and SIR. The dissimilarity in demersal fish assemblages between reef and sand averaged 70.148 % and species contributing to this dissimilarity included slinger (5.95 %), sand soldier (3.97 %), dane seabream (3.90 %), santer (3.54%) and striped seabream (4.69 %). Sand and sand inundated reef also represented higher levels of dissimilarity (70.13 %), this dissimilarity was mostly due to differences in higher abundances of slinger contributing 8.00 %, natal pandora (6.89 %), santer (5.40 %), dane seabream (5.38 %) and steentjie (4.93 %). Lastly, the dissimilarity between reef and sand inundated reef was 68.23 % in demersal fish assemblage. Species contributing to this dissimilarity included slinger (7.33 %), sand soldier (5.98 %), striped grunter (4.93 %), *dane seabream* (4.86 %), and steentjie (4.74 %) (Figure 3.6).

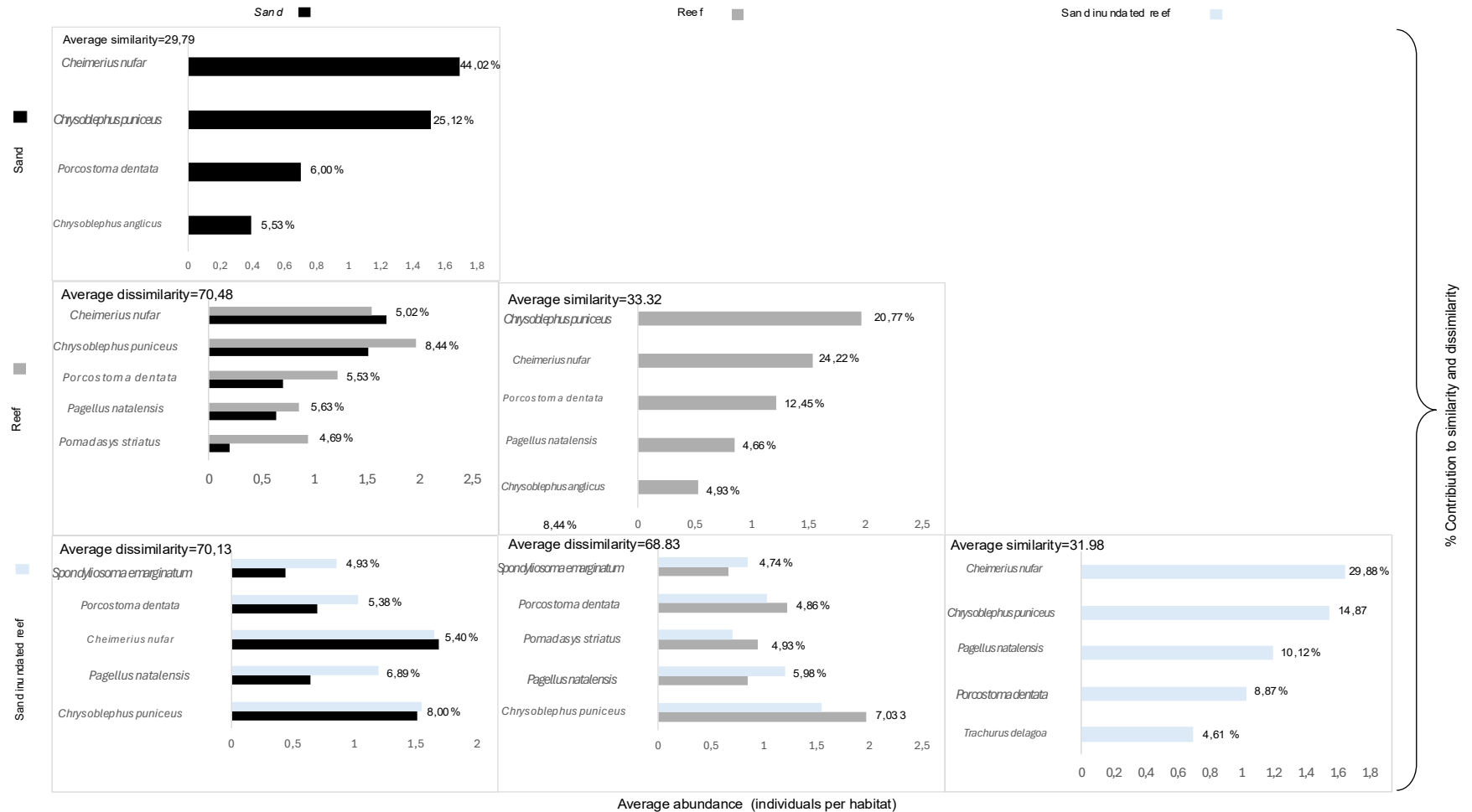


Figure 3.6: Results from similarity percentage (SIMPER) analysis on abundance data according to habitat type. Average similarity blocks represent average abundances of the five most abundant species (average number of each species per habitat type/within group), and the species that contributed to average (dis)similarity (differences in community composition between the three habitat types). With sand habitat having only four most abundant species. The percentages on top of the bars indicate percentage dis(similarity) contribution of each species. Cut-off a cumulative % dissimilarity of 80%, log(X+1) transformation.

The species contributing significantly to the differences in community structure between locations within the uThukela Banks MPA were determined using a SIMPER analysis. The findings indicated that Rosie Snow had the highest average similarity (54.94 %), with sand soldier (16.93 %), santer (16.84 %), and slinger (16.78 % being the main contributors to similarity). Zini Hard Edge showed lowest average similarity (30.25 %) compared to the rest of other locations, santer (29.16 %) and blueskin (50.89 %) stood out as the main contributors to similarity within this group (Table 3.4).

Zini Hard Edge and uMdloti reefs had the highest average dissimilarity (84.38 %) compared to the rest of other reefs. The most species that contributed to this dissimilarity include sand soldier (9.04 %), blueskin (6.78 %) and steentjie (6.55 %). Ballito Tongaat and Rosie Snow reefs had the lowest average dissimilarity, and the major contributor to this pattern was steentjie (8.51 %), followed by African scad (7.04 %). Slinger was the most represented species across all groups (Appendix Table 7.5).

Table 3.4: Results from SIMPER analysis on abundance data showing average abundance of the typifying species in each of the nine locations, calculated from Log(X+1) transformed abundance data. Av.Abu, average abundance of individual species; Av.Sim, the average similarity that individual species contribute; Sim/SD, the similarity ratio to standard deviation; Contrib%, individual species contribution to the overall similarity; Cum.%, accruing overall similarity. Fish species appearing for the first time in the thesis are italicised.

Species	Av.Abu	Av.Sim	Sim/SD	Contrib %	Cum %
Pat's Paradise (Ave sim = 38,57)					
Santer	1,48	10,24	1,27	26,56	26,56
Slinger	2,36	9,69	1,06	25,13	51,69
Natal emperor	0,98	3,69	1,06	9,57	61,26
dane sea bream	0,90	2,97	0,76	7,71	68,97
Halfmoon rockcod	0,65	2,28	0,90	5,92	74,89
Zini Hard Edge (Ave sim = 30,25)					
Blueskin	1,62	15,40	1,07	50,89	50,89
Santer	1,22	8,82	0,89	29,16	80,05
Durnford Hat (Ave sim = 41,98)					
Slinger	2,60	11,50	1,75	27,39	27,39
Santer	1,43	7,54	1,60	17,95	45,34
Dane seabream	1,58	5,11	1,35	12,17	57,51
African butterflyfish	1,12	2,59	0,79	6,17	63,68
Englishman	0,79	2,58	1,13	6,15	69,83
Carpenter (Ave sim = 39,35)					
Santer	1,84	27,13	3,32	68,95	68,95
Natal emperor	0,66	5,59	0,77	14,20	83,15
Ballito Tongaat (Ave sim = 47,03)					
Santer	1,86	10,51	2,44	22,34	22,34

Species	Av.Abu	Av.Sim	Sim/SD	Contrib %	Cum %
Sand soldier	1,93	8,11	1,37	17,23	39,58
Dane seabream	1,41	6,14	2,03	13,05	52,62
Slinger	1,52	5,10	1,29	10,84	63,46
African scad	1,34	3,76	0,84	7,99	71,45
Sundowner (Ave sim = 38,64)					
Santer	2,46	23,57	1,97	61,00	61,00
Slinger	1,07	2,56	0,52	6,62	67,62
Longfin yellowtail <i>Seriola rivoliana</i>	0,59	2,27	0,58	5,88	73,50
Englishman	0,46	2,22	0,81	5,74	79,24
Blue stingray <i>Dasyatis chrysonota</i>	0,41	1,36	0,51	3,51	82,74
Umdloti (Ave sim = 50,79)					
Sand soldier	2,25	7,49	1,65	14,75	14,75
Slinger	2,08	7,43	2,31	14,63	29,38
Santer	1,64	6,11	2,54	12,03	41,41
Dane seabream	1,27	3,97	1,46	7,82	49,23
Steentjie	1,76	3,88	0,86	7,63	56,86
Zinkwazi (Ave sim = 46,75)					
Dane seabream	1,45	6,75	1,71	14,45	14,45
Danter	1,12	5,75	3,11	12,30	26,74
Slinger	1,77	5,65	0,88	12,09	38,84
African scad	1,14	5,63	1,71	12,03	50,87
Sand soldier	1,23	5,38	1,45	11,51	62,38
Rosie Snow (Ave sim = 54,94)					
Sand soldier	1,87	9,30	2,91	16,93	16,93
Santer	1,77	9,25	3,62	16,84	33,76
Slinger	1,82	9,22	3,73	16,78	50,55
Steentjie	2,02	8,38	1,61	15,25	65,80
Dane seabream	1,19	4,48	1,11	8,15	73,95

3.5 DISCUSSION

A rich diversity of fish was recorded within the study area and the environmental variables had a significant influence on demersal fish assemblage structure. This was demonstrated by a higher abundance and diversity of fishes in reef habitats, compared to sand habitats. Abundance and diversity decreased with increasing depth; however, beta diversity was higher in the deep samples. This was supported by community analysis which showed that the species composition changed over the depth gradient. The terrain ruggedness index (TRI), calculated from the multi-beam mapping data, had minimal influence on the diversity metrics, but was an important variable when looking at the community structure. The spatial variables, location and latitude, played a significant role in determining the diversity and the assemblage structure with deep reefs separating from shallow systems and the northern reefs being distinct from the southern reefs. The spatial variability was also evident when comparing the different MPA zones, with the restricted zone having lower abundance and diversity, however this result may be a sampling artefact. Although temperature was not a primary variable of interest in the current study, it significantly affected total abundance, species richness, and Shannon diversity, likely due to its correlation with depth. This is corroborated by Dalton et al., (2021) who lists temperature as one of the parameters that depth can serve as a proxy.

3.5.1 HABITAT

Habitat was a significant driver of fish abundance and species richness, and of slinger abundance. Reef habitats are more complex than sand habitats for benthic epifauna and demersal fishes: they provide higher availability of physical (e.g. rocky outcroppings and cracks) and biogenic (eg. Stony corals and sponges) microhabitats, which provide shelter from predation and increase the availability of food for a variety of species (Gomes et al., 2024). In addition, reef ecosystems are known to support numerous commercially important fish species. The significance of reefs in the distribution of fish species is well documented (Friedlander et al., 2003; Gratwicke and Speight, 2005; Edgar et al., 2014; Hall and Kingsford, 2021; Gomes et al., 2024). In contrast, sand habitat showed the lowest fish abundances, and this is tied to the lower physical and biogenic structural complexity. Fishes at different life stages use mosaic habitats as foraging grounds habitats such as seagrass, sandy and rock habitats (Christensen et al., 2003; Hall and Kingsford, 2021). Mosaic habitats give fish the opportunity to also feed in sand habitat and take refuge on nearby reefs if needed, satisfying both biological imperatives, feeding and surviving. For example, most

diversity on sand habitats is the infauna (organisms living in the sand itself). This makes it an important foraging ground for many species like rays and skates (Ebert and Bizzarro, 2009; Jacobsen and Bennett, 2013; Costa et al., 2015); such as the ones observed in the current study e.g blue stingray, broad stingray *Bathytoshia lata*, short-tail sting ray *Bathytoshia brevicaudata*. Therefore, whilst diversity is lower on sand than on reefs if we compare by the square metre, sand habitats are still important when it comes to diversity in general, and likely host diversity that is more mobile over a larger area. The current study showed that sand habitats shared a number of species with adjacent reefs demonstrating connectivity among reef habitats and sand habitats. This was indicated by the overlaps in species composition in the nMDS and CAP analysis among sand and reef habitat, among sand and sand inundated reef (SIR) as well as in the management zones. These low relief habitats play an important role as foraging grounds for reef-dependent fishes (Hewitt et al., 2005; Sievers et al., 2020; Dance et al., 2021; Hall and Kingsford, 2021).

Two species were unique to SIR, including largehead hairtail and blueskin seabream. This could indicate the unique role of unstructured habitats on local fish diversity, and this is important for overall ecosystem health. The largehead hairtail is a highly commercial species and blueskin seabream is also of commercial importance. Especially in the context of KZN, commercial fisheries is important for socio-economical, recreational, and as a food source (Penney et al., 1999). Depth also contributed to observed differences in fish diversity and structure, as these two species were not found in the upper mesophotic but only in the lower mesophotic. At the same time, the sand habitats were more frequently sampled in deeper waters. Therefore, these findings could be due to correlation and not causation effect. However, the presence of largehead hairtail and Blueskin seabream on the deep sandy habitat still suggest that sand is an important habitat for protection. In addition, their protection may contribute to maintaining mesophotic reef fish diversity, productivity, and further sampling of these habitats may lead to the uncovering of additional unique species. As such, sand habitats should also be considered for management and must be protected. Moreover, different biotic communities exist in each of these habitats, and individual or community-level processes vary at distinct scales within these communities; therefore, excluding any kind of habitat will undoubtedly create a “bottleneck” thus significantly affecting population growth (Christensen et al., 2003). However, as already stated above, the priority must be reef habitats, because these ecosystems harbour endemic and severely exploited species such as seventy four *Polysteganus undulosus* (critically endangered), black mussel cracker *Cymatoceps nasutus* (vulnerable) according to International Union for Conservation of Nature (IUCN) Red List of Threatened Species

(Comeros-Raynal et al., 2016). Mesophotic reef in the uThukela Banks MPA are historically important fishing sites, therefore, studying them will help inform management decisions and provide baseline data to track changes in fish populations over time. In addition, while sand habitats were not the focus of the study design, the emerging results emphasized the need to also monitor sand habitats.

Habitat specificity could also be the cause of observed differences in mesophotic reef fishes' abundance in different habitat types. Different fish tend to be attracted to different habitats, for example, fish may prefer a habitat because of resource availability such as shelter and food (Williams and Bax, 2001; Loffler et al., 2015). In addition, behavioural differences can influence habitat preference, potentially due to variations in prey capture ability or predator avoidance (Rypel et al., 2007). Higher species richness, abundance and diversity in reef habitats could be due to the present of complex structures that provide refuge and predator avoidance. However, there was still a considerable overlap in habitat use by some species, with species such as santer, Blueskin seabream, and African scad shared between the three habitats. This overlap could be associated to the preference at different life stages and trade-off among predator avoidance, resource use and resource availability which may result in species occupying multiple habitat types (Wilson et al., 2008; Green et al., 2015). Habitat specificity could also be linked to ontogenic shifts in habitat use. For instance, some species move between habitat types as they grow and develop e.g. some fish spend time in mangroves and sea grasses at juvenile stages and spend their adult stages on reefs (Green et al., 2015; Sievers et al., 2020).

The nMDS analysis showed clear separation between the reef and sand habitats with the sand inundated reef appearing to be a transition habitat between the two. Sand inundated reefs were predominantly encountered on the reef margins, so this result makes sense and reiterates the finding that there is connectivity across the low and high relief habitats sampled in this study. SIMPER results show that four species (slinger, santer, sand soldier, and dane seabream) dominated across all habitats. This could suggest that these are habitat generalists that show an ability to forage and utilise all habitats within the vicinity of reef complexes. However, slinger and sand soldier also contributed to the observed dissimilarity between different habitats indicating ecological role of these habitats. This can be attributed to variation in abundance between the different habitats with higher santer abundance on sand than reef, and higher slinger abundance on reef than sand.

The most dominant species in this study was slinger, a resident schooling species with a very localised specificity (Maggs et al., 2017). It was significantly influenced by high relief habitat, which is not surprising given that it is known to occur in such habitat (Maggs et al., 2017). However, the SIMPER analysis in this study also showed that slinger was one of the few species occurring in abundance across all habitats. This again suggest that they utilise a wide variety of habitats within reef systems exploiting foraging opportunities across all habitats while at the same time relying heavily on the complexity of reefs for refuge. Higher MaxN of slinger compared to the rest of reef fishes in the uThukela Banks MPA was not surprising as previous studies also found slinger to be the most abundant fish captured in the KZN and Mozambique commercial, boat-based line fisheries (Garra, 1985; Lichucha, 2001; Maggs et al., 2017). Slinger belongs to the family Sparidae, which includes species that are vulnerable to exploitation by both recreational and commercial fisheries due to their large size, long lifespan, and status as resident species (Maggs, 2011). However, based on fisheries catch data, slinger seems to be more resilient to fishing pressure than other Sparidae species, due to large scale spawning and increased survival due to protection thus protecting adult spawning slinger population (Maggs, 2011; Penney et al., 1999). Therefore, the abundance of slinger together with santer, sand soldier, and dane seabream (abundant species across all habitats) in the new uThukela Banks MPA indicates that this MPA will play an important role in management and protection of these species and potentially contribute to fisheries viability in the areas outside of the MPA.

3.5.2 HABITAT COMPLEXITY

Habitat complexity is used synonymously with the terms rugosity, topography or architecture, and the habitat complexity concept encompasses both the diversity of substratum types (species or life forms) and that of vertical relief (McCormick, 1994; Collins et al., 2017;). In both marine and terrestrial habitats, topographically complex habitats are known to harbour higher biodiversity, and therefore become regions of higher conservation value (Loke and Chisholm, 2022). Results from this study found that habitats that are more complex (e.g. reefs), support high abundances and diversity than sand habitats. This is congruent with a study by Dalton et al (2021) where reef substrates had higher species richness and diversity in contrast to sandy sites. This is because benthic habitat influences seafloor relief and consequently influences the kind of species found in that area (Hewitt et al., 2005; Kostylev et al., 2005; Button et al., 2021). The significance of habitat complexity in structuring fish assemblages is increasingly recognised by a number of studies that found higher species abundance and diversity to be associated

with a high degree of complexity (Friedlander and Parrish, 1998; Friedlander et al., 2003; Cappo et al., 2004; Gratwicke and Speight, 2005; Kostylev et al., 2005; Watson et al., 2005; Harvey et al., 2013; Smith et al., 2014; McLean et al., 2016; Collins et al., 2017; Bracewell et al., 2018; Hall and Kingsford, 2021; Sih et al., 2017). Structurally complex habitats (reefs) provides a wide range of distinct niches and microhabitats which ensures species-coexistence, therefore promoting within habitat diversity (Friedlander et al., 2003; Kostylev et al., 2005; Williams et al., 2019).

However, results from the univariate analyses showed that terrain ruggedness index (TRI) had no effect on univariate metrics, meaning that abundances and diversity at both TRI10m and TRI50m scale are not influenced by terrain roughness. This was surprising as one would expect TRI to be significant as it is related to habitat complexity and influences fish distribution and assemblage structure. While TRI was measured and tested over two scales, small ($TRI_{10} = 8 \text{ m}^2$) and large ($TRI_{50} = 199 \text{ m}^2$), it is possible that these were not meaningful for the sampled fish assemblages and did not accurately capture the habitat variability. Alternatively, it is possible that the highly summarised diversity and abundance metrics (species richness, Shannon diversity, or total abundance) were not sensitive enough to detect the effect on assemblage structure. This is supported by the fact the multivariate analysis indicated that TRI was an important predictor of fish assemblage structure at both small and large scales. As such TRI should be included for planning purposes. This is for a number of reasons, firstly, because TRI is a proxy for habitat complexity that can be used to understand direct controls for species distribution (Austin, 2002). The latter can be used to map species occurrence and targeted conservation. Secondly, it can be used to measure microhabitat diversity and habitat's ability to provide shelter for a number of species and help provide escape terrain from predation (Graham and Nash, 2013). Higher habitat complexity provides support to diverse biological communities. Thirdly, TRI can be used to assess the quality of habitat (Dilts et al., 2022), habitat mapping where ecological hotspots are identified and this may aid in directing funding and improve planning (De Vos, 2020). From a planning perspective, incorporating TRI can help map hotspots, this will ensure areas to be prioritised for protection. Lastly, in the context of the mesophotic reefs which may support species targeted by fisheries, their ecological significance to fisheries is one reason they should be protected. Secondly, their diversity is another important reason they should be protected, acknowledging that mesophotic reefs extends beyond fishing value, and their role should be assessed within a broader biodiversity and ecosystem function. Therefore, an understanding TRI can

help manage fishing pressure in these reefs and reduce habitat degradation in the important management zones within the uThukela Banks MPA.

3.5.2.1 DEPTH

Depth played a significant role in structuring fish assemblages and diversity. It influenced fish assemblage patterns and was associated with high beta diversity. However, the general pattern was a decline in richness, diversity, and abundance of fish with increasing water depth. The findings by Gaertner et al., (2013) also showed this general pattern where both species richness and evenness decreased with an increase in water depth. These results are congruent to the current study, which found the negative trend. However, it is worth noting that this study was undertaken at different depth range (200 m to 800 m) as the one by Gaertner et al., (2013). A number of studies have found similar results to the current study where both depth and habitat type were the most important factors contributing to fish distribution patterns (Christensen et al., 2003; Baker et al., 2012). In addition, this study's results are congruent with those from a study by Komyakova et al. (2013) which demonstrated that depth and habitat influences species composition as well as fish species abundance and richness.

Mesophotic reefs are divided into two main zones: the lower and the upper mesophotic zones. The upper mesophotic zone (shallower) is an extension of the shallow (30-60 m) water reef; the lower mesophotic zone (deeper) and is approximately between 60-150 m (Kahng et al., 2017). Fish assemblages at upper mesophotic zones were characterized by high total abundances, species richness, beta diversity, Shannon diversity, and slinger abundance compared to lower mesophotic zone, which was characterized by lower abundances and diversity. This general pattern is consistent with a previous study by Arreola et al., (2024), which observed higher species richness of 16 at 50 m and low species richness (seven) at 70 m. A lot of other studies revealed that depth strongly influences the community structure of demersal fish (Williams and Bax, 2001; Garrabou et al., 2002; Friedlander et al., 2003; Brokovich et al., 2008; Goetze et al., 2011; Pearson and Stevens, 2015; Heyns-Veale et al., 2016; Dalton et al., 2021).

There is limited information on the lower mesophotic zone with a number of studies focussing on mesophotic zone at depths shallower than 80 m (Pinheiro et al., 2016). This study bridged that gap as it examined both the upper and the lower mesophotic zones, therefore contributing to the growing body of research on the lower mesophotic zone. Slinger seemed to get replaced by blueskin when moving from the upper to the lower mesophotic zone. It is possible that this is due to habitat preference and

physiological constraints. Previous research has shown that a decline in habitat heterogeneity with depth may also be the cause of a decline in fish abundance and diversity (Zintzen et al., 2012). Although sampling was intended to occur on reefs, there was a greater probability of sampling on sand in the lower mesophotic zone. This was due to more low relief habitat in the deeper areas making it harder to land on reef. In addition, the relative precision of stereo-BRUVs deployment naturally decreased with increasing water depth due to factors such as current driven drift, rope length variability, and reduced control during deployment. The results suggest that slinger prefer reef habitat and blue skin prefer sand, and this habitat preference could have contributed to the observed results. Physiological preferences would also have a strong effect, and it is possible that blueskin are better suited for foraging in lowlight cool water environments, compared to slinger. Both temperature and light intensity decrease with increasing depth, hindering mobile species capacity for foraging and the reduction in resource availability (Brokovich et al., 2008). Changes in depth are also associated with other important abiotic conditions such as water movement, oxygen levels, and changes in sediment deposition on reef structures, as well as biotic features like sessile organisms (Garrahou et al., 2002; Pearson and Stevens, 2015; Heyns-Veale et al., 2016; Heyns et al., 2016;). These abiotic factors lead to modification of habitat available to fish (Heyns-Veale et al., 2016) and are most likely have a cumulative effect in driving the changes in fish community structure (Dalton et al., 2021).

3.5.3 FISH ASSEMBLAGES AMONG DIFFERENT MANAGEMENT ZONES AND LOCATIONS

Both the univariate and multivariate analyses showed a significant effect of management zone on fish assemblage structure in contrary to the hypothesis stating there would be no measurable effect of management on fish assemblages. These highlights baseline spatial variability in fish assemblages among the zones. These results were surprising because the uThukela Banks MPA is a newly established MPA (2019), meaning it is too new to have an effect. Therefore, the observed results were likely a correlation, rather than causation scenario. Meaning the observed results are more to do with the natural differences among the management zones, i.e spatial variability and other variables that may influence population status such as fisher access.

With an effective MPA, one would expect highest abundances and diversity in restricted (no-take) zones, followed by controlled zones and then exploited zones. However, interesting results were found in the current study where total abundance, species richness and Shannon diversity showed significantly higher

abundances in the exploited zone compared to the restricted zone, and to a lesser degree the 'CPLF' zone. During this survey, sampling was informed by comprehensive multi-beam echo-sounder maps for all reefs, except those found in the restricted zone. This was due to logistical constraints that prohibited mapping from taking place before the biological sampling. Due to this, there was a much greater proportion of sand sites sampled in the restricted zone compared to the other zones of the MPA. As the results have shown, sand habits were associated with lower richness, diversity and abundance, and it is likely that the observed results are a sampling artefact. Subsequent to this study, the restricted zone reefs were mapped and structured sampling was undertaken, however the data were not available for this thesis. However, all data will be merged to form a comprehensive baseline dataset for the MPA.

Another possible explanation could be that the reefs in the CPLF (depth range: 36.5-192.5 m; mean depth: 74.6 m), and to a lesser degree the restricted zone (depth range: 62.5-142 m; mean depth: 77.8 m), were considerably deeper than those in the controlled zones (depth range: 44.5-64.5 m; mean depth: 55.7 m), and exploited zone (depth range: 48.5-79.5 m; mean depth: 59.5 m). As already discussed above, the shallower upper mesophotic zone was associated with high abundance and diversity, compared to the deeper lower mesophotic zone. Further monitoring and research should take into account these differences and work to ensure adequate sampling design.

The variable location, which refers to the different reef complexes included in this study, had a highly significant effect on the observed fish assemblages. There are a number of potential reasons for this. Firstly, some reefs were deeper than others, while others were characterised by more sand habitat than reef. These have been discussed in the previous paragraph. In addition, there appeared to be a strong effect of latitude on the fish assemblage structure, with a northern grouping and a southern grouping. This was most evident at the locations with similar depth and habitat. Latitudinal variation in fish assemblage structure is a common occurrence (Williams and Bax, 2001; Malcolm et al., 2007; Langlois et al., 2012), however the latitudinal scale covered in this study was relatively small, <200 km. It is possible that this is attributed to the shape of the continental shelf, with the northern areas closer to the shelf edge and the warm clean Agulhas Current, and the southern areas further onto the Tugela Bank. Future studies will need to address the issue of capacity and resource limitation through engaging with human stakeholders and users, and through citizen science. This could include training of students and interns to analyse data, which will build capacity. In addition, collaborations between Universities and NGOs for shared equipment will reduce financial constraints.

3.5.3.1 THE VALUE OF BATHYMETRY MAPPING

This study used novel multibeam echosounder (MBES) bathymetry data to map and classify relief at the different locations in the uThukela Banks MPA. These maps were essential for informing the sampling design and provided additional valuable data to measure the terrain ruggedness index. This is consistent with a number of studies that found advancements in the use of GIS to be very useful in quantifying species habitat usage patterns across the seascape using bathymetric Digital elevation models (DEM) and identifying ontogenetic changes in species preferred habitat (Christensen et al., 2003; Friedlander et al., 2003; Cameron et al., 2014). There is a growing use of MBES for biological applications in marine habitat. Including seafloor characterisation (Hasan et al., 2011), fish habitat suitability estimation (where species are located and distributed as well as for MPA planning (Christensen et al., 2003; Friedlander et al., 2003; Ierodiaconou et al., 2007; Cameron et al., 2014; Lecours et al., 2015; Ilich et al., 2021; Wanda et al., 2023). The results from this study provide another example of how detailed bathymetry maps can support ecological surveys and in term marine spatial planning and management.

3.5.3.2 LIMITATIONS

There were several limitations of this study that need to be considered. Like all other sampling techniques, stereo-BRUVs are not without limitations, including the effects of bait, light, and field of view (Sih et al., 2017; 2019). The use of bait is one of the limitations of stereo-BRUVs that may lead to biases as it may attract predatory species and exclude herbivorous or omnivorous species and cryptic species compared to un-baited remote underwater video systems (RUVs) (Cappo et al., 2004; Watson et al., 2005; Harvey et al., 2007; Stobart et al., 2007). However, this limitation did not bias the interpretation of fish-habitat association because there was a consistent use of bait for all samples collected across the three habitat types (sand, reef and sand inundated reef). Therefore, any bias would be consistent among different habitats (Hall and Kingsford, 2021). In addition, there was little risk of overlap in species moving from one sampling location to another since all sampling locations were separated by 500 m. This means that the interpretation of fish-habitat association was not confounded. The use of bait in underwater video systems helps attract fish into the field of view of the camera and increase precision in count data, differentiating fish communities in different habitats (Harvey et al., 2007; Bernard and Götz, 2012). A growing body of research has used bait (Ellis and DeMartini, 1995; Willis and Anderson, 2003; Cappo et al., 2004; Watson et al., 2005; Harvey et al., 2007; Bernard and Götz, 2012; Bernard et al., 2013; Langlois et al., 2020).

Water visibility is known to influence BRUVs performance, where low visibility lessens the sensitivity of data gathered using this visual technique and potentially limits identification to species level (Cappo et al., 2003). This effect was accounted for during data analysis, where visibility with the rest of other covariates were included in the analysis. Other limitations that need to be acknowledged includes the interpretation of TRI which must be done with caution, considering that TRI depends on the resolution and accuracy of seafloor bathymetry (Gomes et al., 2024). However, this limitation was not a problem for the current study because highly accurate MBES survey data was used to generate the TRI. Although finer scale data could have been used, the fish that were surveyed were generally large and, therefore, are unlikely to associate with habitat features at spatial scales than those employed in this study. However, future research should test this to provide a more complete picture of habitat associations. Stereo-baited remote underwater proved to be very efficient in improving the knowledge and providing insight on the role of environmental variables on mesophotic reef fish community structure and distribution. This insight is essential for conservation and management of mesophotic reef fishes.

3.5.3.3 CONCLUSION

The current study highlighted the pivotal role of environmental variables in shaping the distribution patterns of fish communities in uThukela Banks MPA. The first hypothesis stating that there will be higher species richness, abundance, and diversity in high relief reef habitat than low relief habitat was met. This has implications for management of the uThukela MPA, including the assessment of important habitats within the MPA and strategies for prioritising long-term monitoring. The second hypothesis stating that depth would have stronger influence on fish assemblage structure and diversity than location and the different management zone was met. It was clear that depth indeed did have a strong influence of fish assemblages, but this was also the case for the management zone with total abundance, species richness, and Shannon diversity being significantly higher in the exploited zone compared to the restricted zone. Importantly, the deeper sites appeared to be associated with different fish species from those in the upper mesophotic, highlighting the value of protecting broad depth ranges and diverse habitats.

From a practical standpoint, this study is the first of its kind, providing comprehensive baseline data on the effect of depth, benthic habitat and rugosity on mesophotic reef fish assemblages in the uThukela Banks MPA. This is important in the understanding of the distribution, composition and structure of mesophotic reef fishes of the study area. The current study also highlighted the importance of using bathymetric maps for LTM programmes given that fish assemblages are closely linked to localised habitat.

In addition, it contributes to growing knowledge and evidence of the role of environmental variables such as depth, habitat and rugosity in structuring fish communities, which is information that now needs to be integrated into the planning, design, and adaptive management for prioritized monitoring in MPAs.

Establishing robust baselines and research approaches for monitoring marine species populations and distributions is crucial for spatial and fisheries management (Christensen et al., 2003; Harvey et al., 2013). Results from this study can be used as a baseline data on demersal mesophotic reef fish assemblages of the uThukela Banks MPA and allow tracking change in diversity and abundance of fish through time (Christensen et al., 2003; Magurran et al., 2010; Gomes et al., 2024) and strengthening our understanding of temporal variations in biodiversity within fish communities. However, prior to undertaking any long-term monitoring, it is essential to design an effective and feasible long-term monitoring strategy. This will be the focus on the next research chapter.

CHAPTER 4

4 OPTIMAL SAMPLING PROGRAMME FOR MESOPHOTIC REEF FISH ASSEMBLAGE MONITORING IN THE UThukela BANKS MPA



4.1 ABSTRACT

A long-term monitoring (LTM) programme is a vital element in understanding how fish assemblages in marine protected areas (MPAs) respond to protection. Despite its significance, LTM can be costly and labour intensive. If LTM programmes are not properly designed or financially feasible, they may fail. Therefore, this study was aimed at developing an optimal and efficient sampling programme using baited remote underwater stereo-video systems (stereo-BRUVs) to monitor mesophotic reef fish assemblages in the uThukela Banks MPA. To do this, a multimethod approach was used which integrates species accumulation curves, power analysis, and cost-benefit analysis to assess the feasibility of different monitoring scenarios.

Species accumulation curves showed that samples between 8 and 38 were required to detect 90 % of species richness in each reef system. Power analyses showed that 36 samples per location were required to detect 10 % increase in slinger *Chrysoblephus puniceus* abundance over a five-year period with 80 % power. Based on the findings, a sample size of 16 was recommended to detect meaningful change in total fish abundance, while 32 samples were required to measure similar magnitude of change in abundance of mature fisheries targets over a period of five years. A cost-benefit analysis showed that a single stereo-BRUV sample costs an estimated amount of R1 180.56.

It is recommended that 36 stereo-BRUVs samples should be collected to ensure that sufficient information is gathered to address questions about the abundance of important fishery species and different life stages, as well as capturing fish diversity. This was based on slinger abundance power analysis, as slinger was the species with high abundances in the current study. An LTM programme that samples all 11 reefs that were included in the present study would cost approximately R467 500, and 297 days of video annotations by a single analyst to complete. While an LTM programme that samples one reef from each of the four offshore management zones, one northern and one southern fished reef would cost R254 707 and 162 days of video annotation. In terms of costs and time, a comprehensive LTM would not be practically feasible, a minimal LTM scenario would also not provide adequate information. However, a minimal LTM would be feasible and allow sufficient time for video annotation and reporting to be completed if it is conducted on a five-year cycle. Ideally a comprehensive sampling of all reef systems should be monitored for

detecting long-term trends in mesophotic reef fish ecological status. Therefore, the LTM needs to be feasible, however, comprehensive sampling is not always feasible. As such, it can be expensive and time consuming and could jeopardise research monitoring objectives. Alternative approaches to LTM include monitoring of surrogates (e.g representative reefs in the current study or environmental variables), which can be used to represent the whole ecosystem. However, there is a debate as to whether the surrogates accurately represent the whole ecosystem.

These results demonstrate that optimising LTM design requires balancing statistical power, ecological representativeness, and financial constraints. This chapter provides a replicable framework for planning cost-effective monitoring in data-limited MPAs. The study findings are intended to guide evidence-based management decisions in the uThukela MPA and can be applicable in designing feasible monitoring programmes for reef fishes across the KwaZulu-Natal MPA network.

Keywords: marine protected areas, optimal sampling, monitoring, uThukela Banks, cost-benefit analysis

4.2 INTRODUCTION

4.2.1 THE IMPORTANCE OF LONG-TERM MONITORING IN MARINE PROTECTED AREAS

Monitoring is essential for biodiversity conservation, marine spatial planning and determining the ecological effectiveness of marine protected areas (MPAs) (Vos et al., 2000; Yoccoz et al., 2001; Mascia et al., 2017; Kirkman et al., 2021; Kennedy, 2023). Vos et al., (2000) defines monitoring as “the repetitive measurement of a specified set of variables at one or more locations over an extended period of time according to prearranged schedules in space and time”. Long-term monitoring (LTM) contributes to the knowledge and understanding of ecosystems, thus allowing decision makers to deal effectively with the changes in the marine environment, and help them make informed decisions (Ward and Jacoby, 1992; Vos et al., 2000; Yoccoz et al., 2001; Addison, 2011; Mascia et al., 2017; Jansen et al., 2024). This also aids the assessment of the status of the MPA effectiveness. For example, before-after control-impact studies can be used to compare the current fish assemblages to their previous status, prior the establishment of an MPA (Giakoumi et al., 2018). Effective management requires current data that can provide immediate insight into the status of the species, as this will allow the detection of any changes in the environment and permit adaptive management. Effective LTM programmes are those that are implemented and sustained with the goal of measuring biota to support management and successful management of MPAs (Yoccoz et al., 2001). Long term monitoring programmes that are successful are those that have predefined objectives, collect statistically robust data, and regularly assess the programme’s viability using available and sustainability of funds (Caughlan and Oakley, 2001; Perkins et al., 2021). Therefore, management requires a long-term monitoring (LTM) programme that is well designed, robust and suggests alternative management strategies that can be implemented, if necessary (Ward and Jacoby, 1992; Willis and Babcock, 2000).

4.2.2 THE CHALLENGES OF LONG-TERM MONITORING PROGRAMME DESIGN

Designing an LTM programme comes with several challenges that need to be addressed to ensure its efficacy, reliability and sustainability. These include constraints in human capacity and skills as well as high cost (financial capacity) of setting up and maintaining LTM programmes, which restricts the ability to gather enough data (Vos et al., 2000; Caughlan and Oakley, 2001; Yoccoz et al., 2001; Morris et al., 2024). Monitoring programmes require sustainable funding, with

programmes only becoming valuable after a period of time (Vos et al., 2000). This means that benefits from the initial investments will only be evident once enough temporal data has been collected to detect changes that are not related to general environmental variability. The design of an LTM programme is also important (Spellerberg, 1991), with poorly designed programmes being those that operate at unsuitable spatial and temporal scales, have unclear objectives, use inappropriate sampling methodologies, or being excessively expensive, which compromises their long-term feasibility (Ward and Jacoby, 1992; Caughlan and Oakley, 2001; Yoccoz et al., 2001; Addison, 2011). Poor design is a result of improper planning, not identifying what it is that the programme should monitor, why, and how to monitor (Yoccoz et al., 2001). These challenges are the reason why many LTMs fail to detect effects, thereby limiting their potential impact (Vos et al., 2000). Consequently, monitoring programmes must consider what is logistically and financially feasible (Langlois et al., 2010). In particular, South African MPAs are poorly resourced; therefore, their monitoring needs to be cost-effective. The cost-effectiveness of a monitoring programme determines its long-term success (Caughlan and Oakley, 2001).

4.2.3 METHODOLOGICAL CONSIDERATIONS

Various monitoring tools are used in MPAs to survey reef fish populations. These sampling methodologies vary in terms of their costs, logistical constraints, sampling biases, and the fish assemblages that they observe. Examples of these methods include visual survey techniques which are less invasive and are grouped as underwater visual census (UVC), remotely operated vehicle (ROV), remote underwater video (RUV), baited remote underwater stereo- video system (stereo-BRUVs), or stereo-RUV (Murphy and Jenkins, 2010). Remote underwater video is free of biases caused by altered fish behaviour due to the presence of bait and the absence of divers in the water (Bernard and Götz, 2012). The laboratory protocols (i.e video analysis) allow for quality control to ensure accurate identification and counting of fish from the recorded videos (Stobart et al., 2007; Bernard and Götz, 2012). However, RUV are susceptible to significant spatial and temporal variability since changes in abundance brought on by habitat variability are not mitigated by bait's attraction effect (Watson et al., 2005). Consequently, they require higher sampling effort to generate data with similar statistical power to stereo-BRUVs, for example (Watson et al., 2005; Harvey et al., 2007). Moreover, RUVs are more expensive compared to baited systems in that more expensive equipment is required to increase the chance of obtaining statistically robust

results (Willis et al., 2000). Techniques such as UVC are subject to observer bias (since fish can be disturbed by or attracted to SCUBA divers) (Watson and Harvey, 2007), require large teams of divers to conduct sufficient replicate transects, and are limited to water depth shallower than 30 m due to safety considerations (Williams et al., 2006; Stobart et al., 2007; Langlois et al., 2012, 2010). Sampling methods such as controlled angling (CA) and fish-trapping (FT) have lower financial costs and are greater logistical feasibility compared to UVC and stereo-BRUVs. Their logistical advantages include reduced training requirements (limited to anglers trained in fish identification, catch-release protocols, and handling); as they do not involve post-survey video analysis with specialised software, there is minimal laboratory time, and they require simpler equipment (Bennett et al., 2009; Colton and Swearer, 2010; Bernard, 2012). The coverage and frequency of UVC is therefore restricted by the availability of skilled divers and environmental conditions (Langlois et al., 2010). Furthermore, research has shown that UVC can underestimate population densities relative to angling and BRUV techniques (Willis et al., 2000). This suggests that UVC method is less likely reliable, than BRUVs to sample reef fishes (Harvey et al., 2002a). The advantages of using UVC include repeatability, non-invasiveness, and the ability to collect quantitative data on abundance (Harvey and Mladenov, 2001). While all sampling methods have their biases, the depth limitation associated with UVC is of particular concern as you are unable to collect data over full depth distribution of a species or within deeper areas in MPAs resulting in incomplete assessments.

Extractive sampling methods are generally not considered suitable for monitoring inside MPAs as they go against the conservation objectives of many MPAs, to protect biodiversity and ecosystems. For example, demersal trawling damages the seafloor ecosystems; this makes it an unsuitable technique for ecological monitoring as it compromises management objectives in MPAs. In recent times, the use of stereo-BRUVs has grown because of their ability to sample a broad suite of species, identify key predator species (including large piscivorous fish and sharks), having higher statistical power than UVC, no depth restrictions, generating precise data resulting in lower required sampling effort, and the broad-scale availability (Willis and Babcock, 2000; Cappo et al., 2004; Malcolm et al., 2007; Langlois et al., 2010; Bernard et al., 2013; Harvey et al., 2012; Langlois et al., 2012; Stobart et al., 2007, 2015). Moreover, they record a number of variables including species composition, size structure, relative abundance, and seafloor habitat

characteristics and these make them well suited to be used in MPAs (Stobart et al., 2007; Langlois et al., 2018). In addition, stereo-BRUVs provide accurate measures of fish length, which is a key metric for monitoring recovery of fish species and is valuable for informing the management of fish populations because of their comparability to fisheries-dependent data sources (Harvey and Shortis, 1996; Harvey et al., 2012; Langlois et al., 2012; Schramm et al., 2020).

Despite their bias, stereo-BRUVs are generally considered as a suitable tool for LTM, supporting data collection for MPA management decision making. Sampling programmes must take biases into consideration while designing the LTM programmes and interpreting findings. For example, stereo-BRUVs limitations and biases include the use of bait, light, and limitations in the field of view (Sih et al., 2019, 2017). Bait attracts predatory species and may deter herbivorous or omnivorous species and cryptic species compared to un-baited remote underwater video systems, which may therefore lead to biases (Cappo et al., 2004; Watson et al., 2005; Harvey et al., 2007; Stobart et al., 2007). Even though stereo-BRUVs are free from in-water observer bias that may alter fish behaviour, observer bias can be encountered during video footage analysis. This bias can be overcome by reanalysing the video footage if errors are detected during the analysis (Harvey et al., 2013). Huge amounts of data obtained from video footage creates a bottleneck in the processing of data (Cappo et al., 2003; Colton and Swearer, 2010). In addition, water visibility affects stereo-BRUVs performance; for instance, lower visibility lessens sensitivity if data gathered using this visual technique (Cappo et al., 2003).

When considering the financial implications of LTM, high statistical power of stereo-BRUVs data means that fewer samples will be required to collect statistically robust data, thereby reducing the cost relative to other methods. Furthermore, the ability of stereo-BRUVs to sample predatory species targeted by fisheries means that data are useful for management and reporting.

4.2.4 OPTIMIZING A MONITORING PROGRAMME

Despite the challenges of designing a LTM programme, there are ways that they can be streamlined and optimised to ensure that are fit for purpose and cost-effective. This optimisation process involves decisions about how data will be collected and how many samples will be collected in a way that minimises the costs, while maximizing the value of the monitoring programme (Vos et al., 2000). One of the most important steps when designing the LTM

programme is to select the most appropriate method (Vos et al., 2000; Yoccoz et al., 2001). This has been considered in detail in the previous section. Once a suitable method has been identified, a pilot study can be used that allows researchers to test the suitability of a sampling methodology, measure the power of the data to detect change in ecological metrics, and estimate the cost of monitoring requirements (Ward and Jacoby, 1992).

A power analysis can be used to determine the optimal number of samples required to detect change with a desired level of probability (Harvey et al., 2001) and investigate the ways in which differences in experimental design will affect the ability to answer research questions (Bolker, 2008). In addition to power analysis, species accumulation curves, and sampling coverage can be used to estimate the number of samples to adequately detect alpha diversity at a site (Hsieh et al., 2016). In cases where financial resources are limiting, optimising sample size plays an important role in ensuring efficient use of resources in order to meet LTM objectives (Maxwell and Jennings, 2005).

Once the sampling requirements have been identified, a cost-benefit analyses (CBA) can be implemented to determine the costs of a LTM programme under various scenarios (Caughlan and Oakley, 2001; Elphick, 2008). Taking into account cost considerations plays an important role when designing a LTM, as it allows monitoring programme managers to develop realistic costs and benefits expectations (Vos et al., 2000; Caughlan and Oakley, 2001; Elphick, 2008). The costs could include how much time is spent in the field collecting data, the size and skill level of the research team, the costs of vessel operations, the amount of data that has to be collected, and the laboratory costs to process the collected samples. There is a close relationship between the costs and statistical considerations in a LTM programme (Caughlan and Oakley, 2001). This implies that the available financial resources are closely linked to the statistical decisions made during the design and implementation of an LTM. For example, higher costs may allow for the collection of larger sample sizes and yield higher statistical power. A cost-effective LTM programme can address the stated objectives; this is important for results interpretation.

4.2.5 AIMS AND OBJECTIVES

Building on the results from the first chapter, the premise for this chapter is to design an optimal LTM programme for mesophotic reef fish populations in the uThukela Banks MPA. The outcome

of this study will be an optimally designed LTM programme for Ezemvelo that will allow them to monitor changes in fish assemblages and populations through time. The following objectives were addressed:

- Use rarefaction and extrapolation to determine the number of samples required to detect 90 % of available species on each of the reef systems.
- Use power analysis to determine the number of samples required to detect a 10% change in the abundance of fishes over a period of five years with a statistical power of 0.8 at the $\alpha = 0.05$ level.
- Determine the cost of surveying each mesophotic reef within and adjacent to the MPA
- Use a cost-benefit analysis to investigate how the optimal sampling programme looks like and what are the cost benefit implications of different versions of this plan.

4.3 MATERIALS AND METHODS

The study site (section 2.1), sampling method (section 2.4.1), sampling approach (section 2.4.2), video processing (section 2.4.3), and estimating covariates (section 2.4.5) can be found in the main methods (General materials and Methods).

4.3.1 SAMPLING TECHNIQUE

4.3.1.1 DATA PROCESSING

Sexual maturity was estimated for each commercially and recreationally important linefish species observed in the stereo-BRUVs data. For this, size at 50 % maturity was taken from the Southern African Marine Linefish Species Profile (Mann, 2013) or Fishbase (Froese and Pauly, 2022) if the data was not there. In cases where maturity data were not available in the above sources, length at maturity was estimated from fish measured at MaxN (where fish >40 % of maximum attainable size was classified as mature and that <40 % of maximum attainable size classified as immature (Heyns-Veale et al., 2019b). Using the length data and the size at 50 % maturity, each measured individual was classified as mature or immature and the proportion of mature individuals per sample was then calculated. The abundance of mature fisheries target was then calculated by multiplying the MaxN by the proportion of mature individuals for each fisheries target species and then summing this value for all fisheries targets seen in a sample.

Overall, the stereo-BRUVs data were used to create the following univariate response variables:

- (1) Total relative abundance (sum of MaxN for all species)
- (2) Total relative biomass (sum of biomass for all species)
- (3) Relative abundance of mature fisheries targets
- (4) Relative abundance of slinger (slinger MaxN)

4.3.2 ANALYTICAL APPROACH

4.3.2.1 SPECIES ACCUMULATION CURVES

The first step of the statistical analysis was to conduct sample size-based extrapolation and rarefaction analysis in R using the 'iNEXT' package (Hsieh et al., 2016). The analyses were run to compare species accumulation among the different mesophotic reefs (Ballito Tongaat, Carpenter,

Durnford Hat, Pat's Paradise, Rosy Snowball, Sunflower, uMdloti, Zini Hard Edge, and Zinkwazi) surveyed in this study. The analysis was run using bootstrapping based on 100 replications to determine species richness at asymptote ($\pm$ 95% confidence intervals) and sampling effort was extrapolated to a maximum of 60 samples per reef system (Chao et al., 2014; Hsieh et al., 2016). Any extrapolation beyond this threshold is unreliable because of prediction bias (Chao et al., 2014). Sample size-based rarefaction and extrapolation curves were plotted for species richness ($q=0$) and the number of samples required to detect 90 % of the extrapolated species richness was recorded.

4.3.2.2 POWER ANALYSIS

A Monte Carlo simulation ($n = 500$ iterations) power analysis was used to determine the minimum annual sample size to detect a 10 % change in population size over a period of five years at a significance level of $\alpha < 0.05$. Detecting a 10 % change in population size was importance as 10 % represents a biologically meaningful threshold for monitoring fish populations especially for slow-growing, long-lived reef fish (De Vos et al., 2014). This followed the approach developed by De Vos et al., (2014), where MaxN counts were first modelled using a generalised linear model (GLM) to obtain mean and variance parameter estimates. The fitted GLM parameters were then used to generate simulated datasets by drawing random samples from the selected error distribution for each year. Following this, a new GLM was fitted to each simulated dataset to test if the effect of year was significant. From these results, a statistical power was calculated as the proportion of simulations, which successfully detected significant trends ($p < 0.05$). Lastly, the sample size required to achieve 80 % statistical power was determined by fitting asymptotic growth functions to the observed relationship between sample size and statistical power.

The metrics used in the analysis were total fish abundance, total fish biomass, abundance of sexually mature fisheries targets (referred to as abundance of mature targets from this point forward) and slinger abundance. Total fish biomass was fitted with a Tweedie error distribution with the variance power set to 1.25. The abundance metrics (total fish abundance, abundance of mature targets and slinger abundance) were fitted with a negative binomial error distribution. All power analyses were conducted in R software (R core team 2022) via R studio interface (R Development Core Team 2022) following the approach of De Vos et al (2014).

4.3.2.3 *COST BENEFIT ANALYSIS*

Using results from a pilot study, a cost-benefit analysis can be conducted to optimise the allocation of effort and determine a feasible LTM programme structure (Langlois et al., 2010). Based on the outcomes and costs of this study, the costs associated with data collection in the field using stereo-BRUVs technique were calculated in terms of field work costs (travel, research consumables, skipper time, vessel fuel, number of sea days to collect required samples, accommodation and subsistence during the field trip) and video annotation fees (cost required to annotate video samples). Results from the rarefaction and extrapolation analysis and the power analysis were used to determine the optimal sample size, which was in turn used to estimate fieldtrip duration, taking into account bad weather days, and the overall costs.

Using the results from the cost-analysis, the costs for two LTM scenarios were calculated. Scenario-1 represented a comprehensive scenario where replicate reefs were surveyed in each of the management zones of the uThukela Banks MPA (the same reefs considered in this preliminary study), while Scenario-2, represented a minimum LTM programme where only one reef was included from each of the management zones, together with a Southern and Northern fished reefs.

4.4 RESULTS

4.4.1 SPECIES ACCUMULATION CURVES

There was considerable variability in the rate of species accumulation among the different reefs, with Rosy Snowball and Durnford Hats Reefs having the highest species richness and Carpenters reef the lowest (Figure 4.1 a). The analysis of sampling completeness showed that sample coverage was estimated at 87 % for Pat's Paradise, 77 % for Zini Hard Edge, 92 % for Durnford Hats, 58 % for Carpenter, 91 % for Ballito Tongaat, 86 % for Sundowner, 94 % for uMdloti, 90 % for Zinkwazi, and 94 % for Rosy Snowball. All curves reached their asymptote at sampling levels greater than what was achieved during this study. The sampling completeness curves indicated that between eight (Umdloti Reef) and 38 (Zini Hard Edge) samples were required to detect 90 % of available species (Figure 4.2 b).

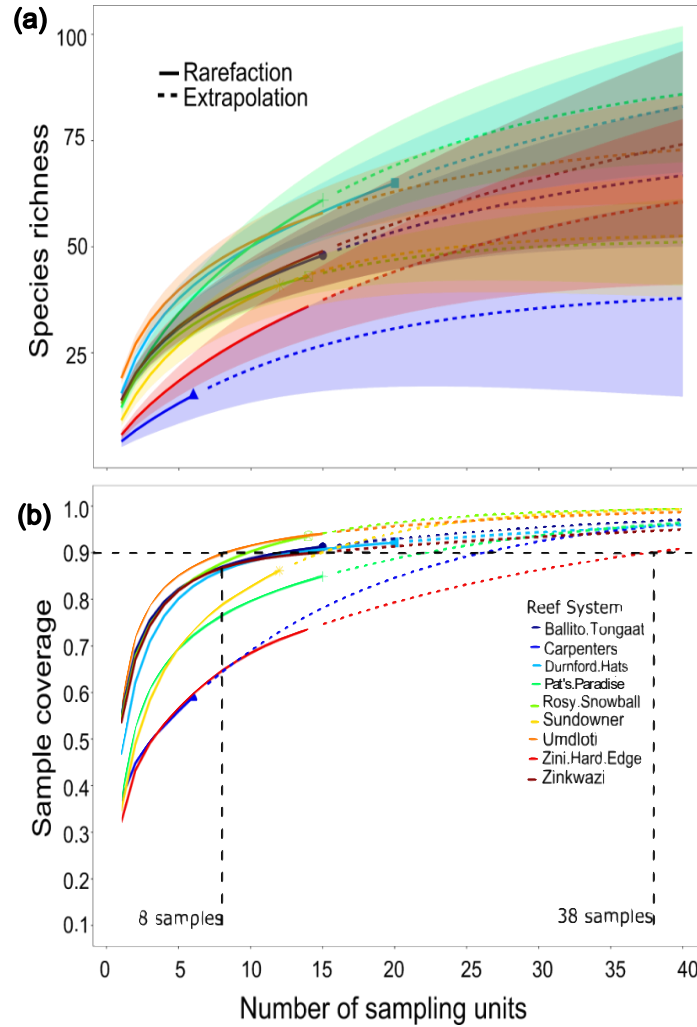


Figure 4.1: Comparison of sample-size-based curves (rarefaction = solid lines, extrapolation = dashed curves) up to the base sample size of 40, plotted for the species richness ($q=0$) recorded at the mesophotic reef systems (Ballito Tongaat, Carpenter, Durnford Hat, Pat's Paradise, Rosy Snowball, Sundowner, uMdloti, Zini Hard Edge, and Zinkwazi) in the uThukela Banks MPA (a). Sample coverage plot for rarefaction and extrapolation samples as a function of sample size for mesophotic reef fish data among the different mesophotic reef systems (locations) (b). Shaded areas indicate the 95 % bootstrapped confidence intervals (CI) with significant differences indicated by overlapping CI. Symbols on the lines indicate the sample size achieved during this study.

4.4.2 POWER ANALYSIS

Power analysis was done to consider a sampling size necessary to detect changes in fish assemblage through time (effect size). It indicated that 36 samples will be required per location to be able to detect a 10 % change in slinger abundance over a five-year period, with a statistical power of 0.8 at a significance level of 0.05. Sample size requirements for abundance of all fish, biomass of all fish and abundance of fish caught by commercial fisheries would be 16, 28, and 32, respectively (Figure 4.2).

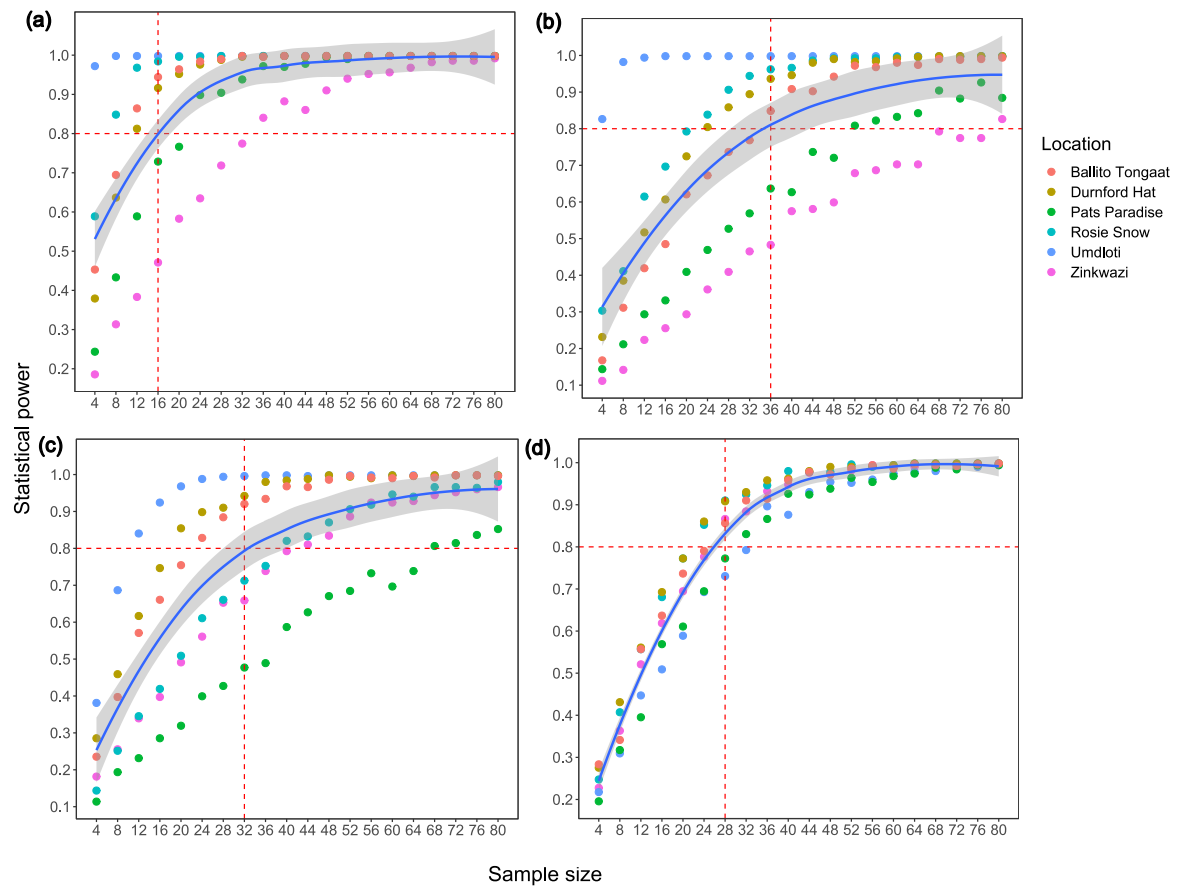


Figure 4.2: The required annual sample size to detect a 10 % increase in (a) abundance of all fish (total abundance) (b) slinger abundance (c) abundance of fish caught by commercial fishers and (d) biomass of all fish with 80 % power and a significant level of $\alpha = 0.05$ over a period of five years.

4.4.3 COST BENEFIT ANALYSIS

Based on the presented results, it is recommended that 36 samples are collected per reef system within the uThukela Banks MPA over a period of 5 years. This was based on the power analysis results which showed that a maximum number of samples required to detect change to be 36 (which was for slinger abundance). This will ensure that the data can be confidently used to answer questions on the abundance of key fisheries species (slinger = 36 samples) and life-stages (abundance of mature fisheries targets = 32 samples), while at the same time capturing the diversity of fishes (max = 38 samples) over a period of 5 years.

The cost analysis took into account the required number of samples, the time taken to collect the samples in the field, human resources, consumables (e.g. bait, fuel cable ties, spares), fieldtrip general costs (e.g. accommodation, transport, subsistence) and the data storage. Based on the experience of conducting the stereo-BRUVs surveys during this study, it is estimated that three sea-days are required to collect 36 samples with on average 130 km being covered and 130 litres of petrol being used each day (Table 4.1). Due to weather constraints, it is estimated that 5 days (6 nights) in the field will be required to get the three weather windows. Best practice indicated that between 0.8 and 1 kg of sardine bait is used for each stereo-BRUVs sample, indicating the 30 kg of bait is adequate for the 36 samples, 0.83 kg/sample (Table 4.1). The minimum team size to carry out the surveys was set at four people, including the skipper.

It is estimated that 36 stereo-BRUVs samples require 1.5 TB of data storage space, requiring 2 x 2 TB hard drives for the main and back up data storage (Table 4.1). The cost of video annotation was not included in the analysis, but it is estimated that this will cost R 1200/sample (6 hours/sample x R200/hour), totalling R 43 200/reef. The video annotation was not included in the cost analysis as this can be done by interns or students. Based on these costs, one stereo-BRUVs sample will cost R 1 179.2 for the field work costs, or R2 379.2 for both the field work and the video annotation.

These costs and sampling estimates were then used to develop two monitoring scenarios for the MPA – a comprehensive option, where all reefs included in this study are incorporated in to the LTM programme; and a minimal option, where only one reef per offshore management zone (4

Zones: Southern controlled, Restricted, Northern controlled, CPLF) and one southern and one northern fished reef (6 reefs in total).

Table 4.1: Results from the cost analysis for the uThukela Banks MPA using stereo-BRUVs with cost per reef indicated as total cost.

Consumables	Quantity	Cost per unit	Total cost
Boat fuel	130 L/day x R25/L x 3 days	R3 250	R9 750
Skipper	3 days	R2 500	R7 500
Bait	30 kg x R40 x 36 samples	R40	R1 200
Consumables	Per day	R500	R1 500
Accommodation	R500/prs x 4prs x 6 nights	R2 000	R12 000
Subsistence and travel cost	R250/prs x 4prs x 6 days	R1 000	R6 000
Car fuel	R5/km mileage x 50 km/day x 6 days	R250	R1 500
Data storage	2 x 2 Hard drives	R1 000	R3 000
		Total	R42 450

The total cost to comprehensively survey the 11 reefs included in this study would be R467 500 giving a total of 396 samples and 297 days for a single video analyst to annotate the videos. The cost of the annotation, if required, would be R 475 200, bring the total cost of the survey to R942 700 (Table 4.2). It is estimated that the minimal survey of the MPA would cost R254 707 with video annotation taking 162 days and costing an additional R259 200, if required (Table 4.2).

Table 4.2: Results from the co-efficiency analysis for the uThukela Banks MPA reef systems (locations) and three management zones plus a reef system in the fished region of the MPA (adjacent site).

Scenario	Comprehensive	Minimal
Reefs	11	6
Sea days (field work)	33	18
Bad weather days	33	18
Samples	396	216
Survey cost	R467 500	R254 707.2
Video annotation time (8 hour days)	297	162
Video annotation costs	R475 200	R 259 200
<i>Combined cost</i>	<i>R942 700</i>	<i>R513 907</i>

4.5 DISCUSSION

Information on the optimisation of LTM monitoring programmes is scarce, especially in South Africa. The General introduction has addressed the importance of LTM programmes, their evaluation, and optimization. Following up on that, this chapter was aimed at designing an optimal LTM monitoring programme to monitor the mesophotic reef fishes of the uThukela Banks MPA. Species accumulations were highly variable with eight to 38 samples required to detect 90 % of available species, depending on the reef system being sampled. The results from the power analysis indicated that 36 samples were required to monitor trends in slinger abundance, however fewer samples were required for the less variable metrics such as total MaxN. The cost analysis showed that the cost per stereo-BRUVs sample was R1 180.56 with an additional R1 200 required for the video annotation per sample.

4.5.1 STEREO-BRUVS AS A TOOL FOR MPA LONG-TERM MONITORING

Baited remote underwater stereo-video systems were employed as a suitable tool for the MPA LTM in the current study owing to their ability to provide adequate sampling success rate. The study focused on mesophotic reefs, necessitating the use of a method that is non-invasive, cost-effective and specifically suited to surveying these ecosystems and supporting future management of mesophotic reef fishes in the uThukela Banks MPA. Bait inclusion allowed us to observe significantly more fish species than would have using non-baited systems. The use of stereo-BRUVs for LTM in the uThukela Banks MPA provided a permanent record of fish assemblages of the entire sample that can be re-analysed for validation or if there are any errors in data. This is one of the benefits of using stereo-BRUVs and is crucial for assessing the effectiveness of the study area in response to management actions. The standardisation of stereo-BRUVs as a monitoring tool for reef fishes ensured data collection across different reef systems and produced comparable data with low variability compared to other methods. Low variability of stereo-BRUVs in the current study is in agreement with previous work (Langlois et al., 2020; Willis et al., 2000; Bernard, 2012; De Vos et al., 2014) and to the use and knowledge of LTM programmes for surveying mesophotic reef fish communities using stereo-BRUVs.

4.5.2 SAMPLING OPTIMIZATION

No previous studies have attempted to design an optimised fish LTM programme for the fish in the uThukela Banks MPA and few other MPAs in South Africa. As such, the current study can provide valuable information to support the management of the Thukela Banks MPA. Furthermore, the optimization process followed aimed to calculate and reduce the costs associated with monitoring mesophotic reef fish populations, improving feasibility and providing a decision-making tool. As ecosystem based approach guides ecological research, it is important that the sampling method is thorough and comprehensive to effectively understand and manage fish populations (Pikitch et al., 2004).

The power analysis indicated that optimised sampling effort to measure the abundance of mature fisheries targets was 32 samples, and 36 samples for slinger abundance required to detect population increase of 10 % annually over a period of five years. The greater number of samples required correlates with higher levels of variability in the data that is driven by lower abundances and natural patterns in habitat preferences and foraging behaviour. Power analysis has been used by a number of studies to inform the design of LTM programmes. For example, in the context of South Africa, studies that have optimised sampling methods all concluded that stereo-BRUVs or BRUVs significantly sample more species (Bernard, 2012; Bernard et al., 2013; De Vos et al., 2014; Parker, 2015), however these studies were comparing different sampling methods such as UVC, CAS and BRUVs in detecting common fish species, red roman *Chrysoblephus laticeps*, abundance. Whereas this study employed stereo-BRUVs (two synchronised cameras) which provided additional benefits of obtaining size data. It is worth noting that data for total abundance and slinger abundance would be exactly the same if it was collected with BRUVs (has a single underwater video camera). A study by Bernard and Götz (2012) also used power analysis in a similar way to this study and found that eight samples are required to monitor red roman populations but higher numbers of samples to monitor rare species. This finding also motivated the selection of slinger in the current study. The power analysis run of four metrics varied in their content and specificity. The most summarised metric was total abundance, followed by total biomass, the abundance of mature fisheries targets and the abundance of slinger. The results indicated that greater sampling effort was required to detect change for more specific metrics.

The generalised metrics may be appealing from a cost perspective; however, they lack sensitivity to detect meaningful changes in key species or groups of species.

Optimised sampling has diagnostic capability, constantly collect high species abundances and would provide better and more reliable data in LTM (Bernard, 2012). MacNeil et al (2020) highlighted the importance of standardising stereo-BRUVs to enable comparisons across locations, studies and years, especially for data used for LTM programmes. Research carried out outside of South Africa, which utilised power analysis for sampling optimisation (using stereo-BRUVs), includes a study by Hill et al (2018b). It found that < 100 samples are required to detect change in fish abundance. Cundy et al (2017) also found that between 20-30 samples will be required to detect the number of species. These findings show that the number of samples required to detect change in fish abundance are area specific. For example, the current study results showed that between eight to 38 samples are required to detect changes in abundance. Another study from Australia by Harvey et al., (2012) evaluated the number of deployments required to detect effect sizes of 50 %, 100 %, and 200 % increase in the abundance of target species. Power analysis results for this study showed that stereo-BRUVs required fewer replicates than fish traps to detect change in abundance with between 15 to 25 samples for stereo-BRUVs and more than 40 samples for fish traps. This study is different from the current study in that it compared sample sizes to detect change in fish populations between two sampling techniques. Sampling effort is an important element to consider when optimising the sampling protocol, and how it is implemented is also important (Hsuan et al., 2025).

Another study from South Africa used power analysis, and found that the use of stereo-BRUVs required a small sample size to detect 10 % change in abundance over a 5 year period (Parker, 2015). Those were the findings on evaluation of sampling methods in Tsitsikamma National Park MPA, the oldest SA's MPA (established 1954) and largest (320 km²) no take MPA in Africa. However, the current study is different from that of Parker (2015) in that it explored cost-benefit analysis of using stereo-BRUVs to assess reef fish assemblages.

The use of CBA from this study enabled us to propose different LTM scenarios as a framework that will be applicable to uThukela Banks MPA, also adaptable for other MPAs in KZN and elsewhere. The MPAs in KZN have existing datasets so sampling optimisation can be carried out and costs

calculated. The stereo-BRUVs significantly observed higher species abundances in the uThukela Banks MPA than would have with un-baited systems. The use of stereo-BRUVs is shown to provide an added benefit of size data, which is often a better indicator for MPA effectiveness than an index of abundance on its own, and this is corroborated by findings from (Langlois et al., 2010; Bernard et al., 2013; De Vos et al., 2014).

The motivation for using stereo-BRUVs is based on their ability to be concurrently deployed in different habitats, making efficient use of boat time (Harvey et al., 2007; Langlois et al., 2010; Santana-Garcon et al., 2014; Whitmarsh et al., 2017). Multiple stereo-BRUVs deployments in diverse environments from shallow to deeper reefs broadened the research scope and ensured that we achieved adequate sampling success rate, cover large spatial area, maximise efficiency, and achieve high statistical power in a short period of time. Furthermore, this approach minimises costs and time spent in the field by making use of available resources, such as boats and personnel (Langlois et al., 2018). The use of stereo-BRUVs also allowed successful collection of fish data past the conventional 30 m depth limit set by SCUBA diving. The use of non-destructive monitoring tools such as stereo-BRUVs are recommended in MPAs and need to be critically examined and optimised to ensure that they fully describe mesophotic fish assemblages. Data from the current study contributes to management and conservation of reef fishes across the continental shelf of South Africa (Bernard et al., 2014).

Species accumulation curves had very high variability with between eight and 38 samples required to detect 90 % of the observed fish species using stereo-BRUVs. This suggests that some reef systems require fewer samples to achieve species saturation, while other require extensive replication. This also ensured that data collected met the required statistical power (Ward and Jacoby, 1992; Vos et al., 2000; Yoccoz et al., 2001). Fish assemblage estimates can be affected by high variance among samples and is influenced by species-specific traits (e.g. behaviour) as well as sampling conditions such as gear type and habitat features (Kwak and Peterson, 2007). High variance can be overcome by increasing the sample size (Kwak and Peterson, 2007), this also increase or improves the likelihood of detecting rare species. This could also explain why slinger abundance required higher sampling effort to detect change and this is likely to do with lower stability in abundances as it's a single species, rather than a group.

4.5.3 OBSERVED PATTERNS IN SPECIES RICHNESS AND SAMPLING COMPLETENESS

Species accumulation curves showed that species richness was greater at Durnford Hat reef system and species richness was observed at Carpenter reef and Zini Hard Edge. Zini Hard Edge was the deepest station and the reason for lowest richness could be attributed to depth. This is corroborated by a number of studies that found higher species richness at shallower depths and lower species richness with increase in water depth (Brown et al., 2022; Garcia-Sais, 2010; Heyns et al., 2016; Zintzen et al., 2012).

Based on the number of samples collected in this study, there was high variation in sampling coverage among different reef systems, with some reef systems showing incomplete coverage (Figure 4.1, b). This is a concern as it indicates inconsistency across different reef systems. What incomplete coverage means is that the dataset did not provide a complete representation of fish species in the reef systems. Reef systems such as Carpenter, which had the lowest number of samples, had incomplete coverage (58 %) which was the lowest coverage among all reef systems of the uThukela Banks MPA. This was also indicated by steep species accumulation curve (SAC) in reef plots not reaching the asymptote. The main reason for incomplete coverage at the different reefs was insufficient samples. There were time constraints; time was not sufficient to survey all the identified reefs at the required intensity. The other reasons were mostly linked to weather (poor sea conditions) which made it unfeasible to carry out sampling as initially planned. A lack of appropriate sampling map for some of the reef systems (locations) such as Carpenter was also the cause of incomplete coverage. The lack of a proper map indicating the location of the reef led to collecting more sand samples than from other reefs. Knowing that sand has lower species richness, this could have also contributed to observed species richness differences. Therefore, increasing sampling effort will ensure better representation of fish populations in this reef system. Another limitation was water visibility, poor visibility led to incomplete coverage as some samples had to be omitted due to poor visibility, and this could be the reason for the underestimation of species in some reef systems. As such, samples collected within the reef systems in the uThukela Banks MPA had poor visibility, as a result they were excluded in the analysis.

The species accumulation curves (rarefaction and extrapolation curves) run on species richness showed no significant differences among the reef systems. This could suggest that species richness

across the reef systems is relatively uniform. It could also indicate similar habitats and environmental conditions within the MPA (this was discussed in Chapter 3). Additionally, the non-significant results could also indicate species interchange between these reef systems and a high level of connectivity. These findings are consistent with results from a previous study addressing the use of species richness to infer ecological connectivity between the ecosystem (Chavez-Hidalgo et al., 2010). A study by Steinitz et al (2006) also provided evidence for connectivity between communities of geographical and environmental distance, where the communities closest to each other were more similar than those farthest from each other due to lower connectivity. High connectivity among reef systems could mean that one reef provides similar information as others. Therefore, a high level of connectivity could benefit monitoring efforts by supporting a reduction in the number of reefs that needs to be monitored, thereby reducing financial costs. However, from a conservation perspective, the sampling effort needs to be directed towards preserving the overall integrity of the uThukela Banks MPA rather than focusing of specific reefs. It should be noted that comprehensive monitoring can be a challenge with practical limitations like time (more travel time) and financial resources (costs of the survey).

In an LTM context, the observed results from the sampling conducted in this study highlight the value of running analyses to determine suitable sample sizes to achieve sampling completeness. The results from the power analyses and sampling completeness indicated that 36 samples are required to adequately sample populations and fish diversity on a single reef. This is over double the maximum what was achieved during this study and the incomplete sampling will have implications for the certainty around the ecological findings presented in this thesis. However, this does not detract from the value of this research as it was a preliminary study where sampling effort was spread among a large number of reefs to improve the spatial footprint and allow the comparative analyses implemented in Chapter 3.

4.5.4 ECOLOGICAL METRICS & INDICATORS

Ecological metrics are variables that reflect the state of an ecosystem or community, and ideally correlate with environmental variables (e.g. depth, water temperature) or anthropogenic disturbances (e.g. interventions and fishing pressure). Metrics that are sensitive to changes in the environment or level of disturbance are considered to be ecological indicators. A good ecological

indicator is one that is easy to measure, repeatable, informative and sensitive to change. Selecting suitable ecological indicators is an essential step in the design of an LTM programme as the sampling programme needs to be able to collect the required data in a standardised way.

In this Chapter, total abundance of all fish, total biomass of all fish, abundance of mature targets, and the abundance of slinger were used as metrics to determine the required sampling effort. The results from the power analysis showed that total abundance required the lowest number of samples ($n = 16$) to detect change with a power of 80 %. While fewer samples are required for this metric, total abundance will not be sensitive to changes in the fish assemblage structure or key species populations. This is because total abundance, and to a degree total biomass, are highly summarised metrics that use data from all observed fish without considering the importance or ecological role of the species. For example, fishing has been shown to remove large high trophic level, high value species which are in turn replaced by smaller low trophic level species (Pauly, 2008; Sherman et al., 2018; Jabado et al., 2024). In these instances, total abundance may stay the same, or even increase, obscuring important ecological patterns (i.e. masking the decline of the larger more vulnerable species). Furthermore, if sampling requirements are set to detect change in highly summarised metrics, then it is unlikely that the data collected could be used to detect change in the more specific (information rich) metrics, such as the abundance of key groups (e.g. fisheries targets) or species (e.g. slinger), as they require higher sampling effort because they are more variable. The importance of ecological metrics is supported by Pinna et al., (2023) who stressed the importance of selecting the most appropriate indicators and metrics for ensuring the effectiveness of an ecosystem under study. In addition, each MPA should have a priority list which takes into consideration the ecological importance, IUCN status or stock status, value to fisheries, and contribution if the MPA in conserving the species.

Slinger abundance showed the highest number of samples required to detect change ($n = 36$). This species was selected because it was the most abundant species (MaxN) in the uThukela Banks MPA dataset and is the primary species targeted by the commercial line fisheries (Penney et al., 1999). Slinger is from Sparidae family, and most of the species from this family are resident species and are targeted by fisheries. They are generally slow growing species, with high residency, long life expectancy, and large size at maturity relative to maximum size (Griffiths et al., 1999; Penney et al., 1999; Mann, 2013). Due to their high abundance and fisheries importance, slinger will play

an important role as an indicator of mesophotic reef fish health in the uThukela Banks MPA and conservation efforts should focus on slinger.

The abundance of mature fisheries targets is another information rich and specific indicator that will be sensitive to fisheries pressures and useful for LTM in MPAs. Abundance of mature individuals in fish populations is thought to be critical for monitoring fish productivity and long-term sustainability of the species, and understand reproductive potential (Bris et al., 2015; Perkins et al., 2021). Most fisheries have minimum size limits and also preferentially target larger higher value fish (Asche et al., 2015; Heyns et al., 2016). On the other hand, MPAs are well known to promote the recovery of large sexually mature individuals, particularly those with restricted home ranges, within their boundaries (Russ and Alcala, 1996; Kerwath et al., 2008; Maggs, 2011; Götz et al., 2013). As such the abundance of mature fisheries target provides useful data to support MPA and fisheries monitoring and management. This metric could easily be extended to be the biomass of mature fisheries targets. Furthermore, reproductive potential is exponentially correlated with size and larger sexually mature fish produce more gametes than smaller ones (Kirkman et al., 2021). Therefore, the biomass of mature fisheries targets should be able to better capture the reproductive potential of a species.

Lastly, pooling total biomass (of all species) can be an important indicator for detecting the role of an MPA and its effectiveness (Caselle et al., 2015). As with total abundance, total biomass is a highly summarised metric with lower information content than those based on specific species or groups of species. However, total biomass can be used alongside total abundance to determine if the average fish size is increasing or decreasing in an area.

4.5.5 COST-BENEFIT CONSIDERATIONS AND LTM SCENARIOS

There is an increasing need for LTM programmes that are able to measure change in species diversity in a cost-effective manner. Cost-benefit analysis is one way to evaluate trade-offs between costs and benefits of using different sampling techniques. This effective tool can establish general recommendations on the most suitable method for addressing specific set of questions laid out in the LTM objectives (Elphick, 2008). In this study, costs were identified and include both direct (boat time, personnel, consumables etc) and time taken to analyse video footage) costs.

From a cost perspective, the results showed that the cost per stereo-BRUVs sample would be R1 180.56, while R42 450 was required to collect the recommended 36 samples on each reef system. It is worth noting that although these figures were derived from SAIAB resources, there may be slight variations in the context of the Ezemvelo due to differences in human capacity and other resources. The amount of time required for one analyst to process the fish data from the 36 samples is estimated to be seven weeks (~ 1 sample/day). When this is scaled up across all 11 reefs surveyed during this study, a total of 396 stereo-BRUVs are required at a cost of R 467 500 and requiring 297 workdays for a single analyst to process the videos. The time taken to process the videos can be reduced by assigning the responsibility to more analysts; however, this would incur additional costs, as it would prevent those employees from performing their other job functions. If contracted video analysts were required, then the total cost would double (Table 4.2). The amount of time spent in the field when conducting a full survey is high, especially considering that there is typically a one-to-one ratio of bad weather days to sea-going days (Bernard, 2012). Time is considered an important factor in an LTM programme as it influences the amount of data collected and analysed, as well as financial costs (Mantelatto et al., 2013). As such, it is unlikely that a comprehensive survey of multiple reefs inside and outside the MPA and across all management zones is feasible. Most of monitoring initiatives in MPAs have limited resources (Gill et al., 2017). This is true of the Ezemvelo and other MPA management authorities in south Africa which have significant constraints on financial and human resources. Consequently, a reduced sampling protocol is more practical.

The uThukela Banks MPA has four offshore management zones and within these there are one or more mesophotic reef systems. The restricted zone is in the centre of the MPA with a controlled zone to its north and south. In the northern controlled zone, there is a smaller controlled zone with stricter rules on the type of fishing and species that can be captured. To assess the conservation effectiveness of the MPA, data should be collected from each of the management zones. When measuring the effectiveness of an MPA, it is common practice to compare trends inside the MPAs to adjacent areas that are open to fishing. The results from Chapter 3 showed there was a significant effect of latitude on the fish assemblage structure with northern communities being different from southern communities. Therefore, in the case of the uThukela

Banks MPA, it would be beneficial to compare trends observed inside the MPA to fished reefs in the North and South.

The second scenario considered in the CBA followed this logic, with one reef selected from each management zone and one adjacent fished reef to the North and South (6 reefs in total). This approach halves the cost, in terms of finances (R 254 707) and time (36 days in the field, 162 days for video annotation). The benefit of this approach is focussed on the cost saving while maintaining the statistical power by collecting sufficient samples from each reef. The cost, or compromise, is that there are no replicate reefs within each management zone, which limits the ability to generalise the observed results from one reef across all reefs within a management zone. This is particularly relevant when the sampled reef is unique or anomalous from other sites within the management zone. An alternative monitoring design would be to half the number of samples per reef ($n = 18$) and survey two reefs per management zone (maintaining 36 samples at the management zone scale). However, this would jeopardise the statistical power of the data at the reef scale potentially hiding temporal and spatial patterns in the data. Furthermore, the results from Chapter 3 (see Figure 3.5) and the rarefaction analysis performed in this chapter provided evidence of high connectivity among adjacent and nearby reef systems due to similarities in the species assemblages. As such selecting one reef from which to collect the optimal number of samples can be justified.

The exception in this study was the reef called Zini Hard Edge (see results from Chapter 3, Figure 3.5). Zini Hard Edge was by far the deepest reef and had a unique fish assemblage, in comparison to the shallower mesophotic reefs. Because it is not comparable with other reefs included in this study, it might be better to exclude it from the long-term monitoring programme and focus the efforts on reefs that would allow for better spatial comparisons. Furthermore, Zini Hard Edge is situated on the shelf edge and is prone to high current conditions. This will complicate sampling and often result in failure to obtain the data required for the LTM programme.

While the second scenario with the minimal number of reef sites is the more feasible of the two options, the financial and time implications are still considerable. This is especially true as sampling will be conducted on an annual basis over a period of five years as a large research team will be required to collect, process and report on the data before the next survey takes place.

Addison, (2011) acknowledged the importance of report writing as an important and final step of a properly designed monitoring framework, allowing adaptive management and improved monitoring. In addition, reporting of monitoring data is a reflection of a LTM programme success (Caughlan and Oakley, 2001) and its value. An effective monitoring programme is more than just data collection but also includes analysis and data interpretation (Vos et al., 2000). Therefore, any monitoring cycle must incorporate time for the reporting process thereby permitting responsive management. With one video analyst it is estimated that the monitoring cycle could be completed within a 16-month period (Figure 4.3). Therefore, repeating the monitoring cycle over a longer interval would improve the feasibility of the LTM programme and ultimately reduce the costs on an annual basis.

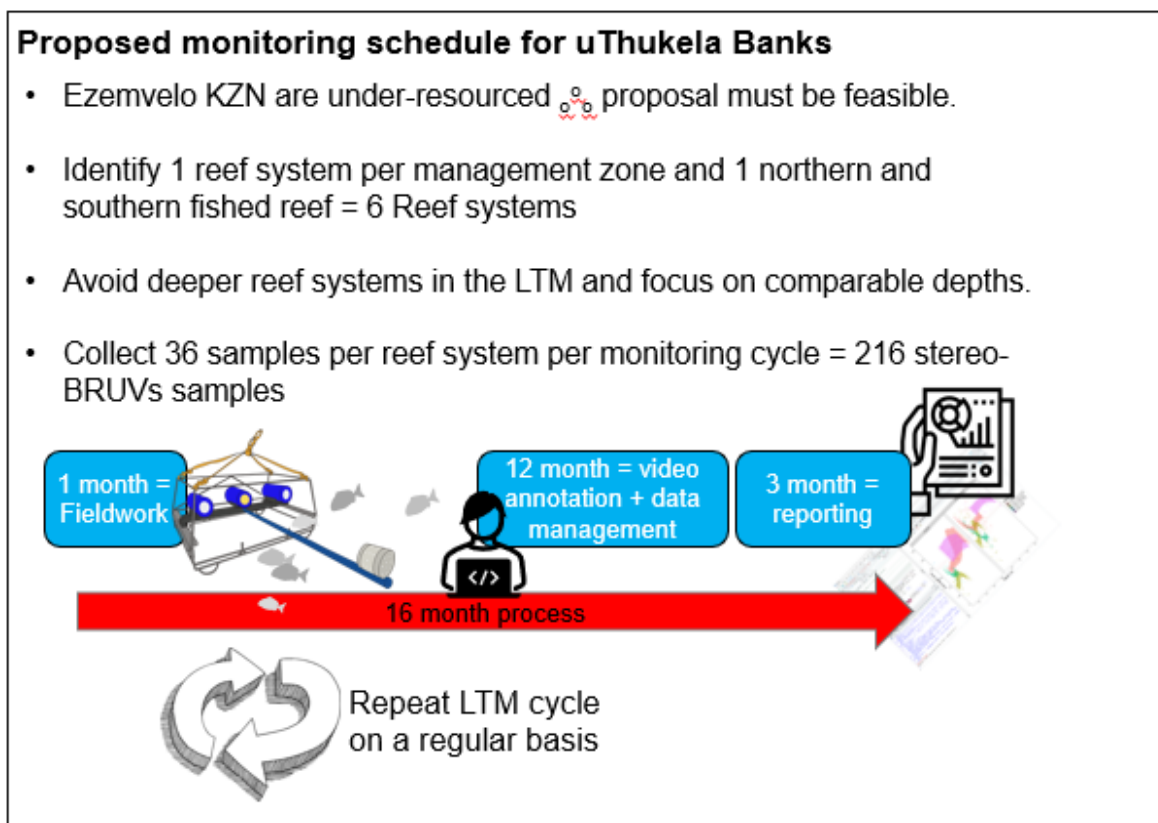


Figure 4.3: Proposed monitoring schedule for the uThukela Banks MPA for the six reef systems.

4.6 CONCLUSION

The current study is the first of its kind to provide a comprehensive baseline data on mesophotic reef fishes of the uThukela Banks MPA and an optimal sampling method. The study assessed cost-effectiveness and conclusions and recommendations are based on alternative scenarios. The findings illustrated the role of stereo-BRUVs in surveying high fish abundances with fewer samples and higher statistical power in detecting change. A minimum of 36 samples were required to adequately sample populations and fish diversity in the study area. Identifying the required sample size for detecting change in fish population was found to be very important for optimizing sampling method (stereo-BRUVs) and ensure their adequate replication and their effectiveness.

The study addressed the challenge of balancing comprehensive ecological monitoring with practical limitations such as time and financial costs. By evaluating the sensitivity of different metrics, the study identified indicators that were more sensitive to ecological change and those that were not as sensitive. Slinger abundance proved to be more sensitive to changes in fish assemblage populations and therefore was proven more effective in detecting important ecological patterns in mesophotic reef fish monitoring. In contrast metrics such as total abundance and total biomass required fewer samples to detect change, however, may obscure meaningful patterns that could help inform management.

The baseline data collected from the mesophotic reefs of the uThukela Banks MPA provide a foundation for assessing the magnitude of change in the adjacent (fished) areas that lack natural baseline data. This study supports a very strategic approach to monitoring that is ecosystem based and adaptive management combining specific and non-sensitive metrics thus ensuring a cost-effective monitoring.

An additional consideration when designing an LTM programme is the use of multiple sampling methods to better sample the fish population. The use of multiple methods is usually recommended to show the entire fish community and its population trends (Watson et al., 2005; Colton and Swearer, 2010). However, most studies ignore logistical feasibility; therefore, it is important that LTM programmes are sustainable and realistic. A LTM may be effective if it focusses its efforts on using a single method and understanding its limitations, and using indicator species that demonstrate direct and indirect fishing effects on reef communities (Bernard, 2012; Dunham

et al., 2024). Bernard, (2012) acknowledges the importance of comprehensive knowledge on biodiversity and species richness in the LTM programme. However, this extensive sampling comes at an increased cost (financial costs, more time to be dedicated in the field, and analysis of video footage). As such, the use of a single method is advisable. This study showed the use of stereo-BRUVs to have potential in sampling fish assemblages not in conjunction with other sampling techniques.

This work has focussed on uThukela Banks MPA, however, Ezemvelo manages a network of four large MPAs in KwaZulu-Natal, and the feasibility of monitoring programmes should be considered across their management network. This will be considered in the final discussion.

5 GENERAL DISCUSSION

The goal of this study was to build a foundation for efficient monitoring of the mesophotic reef assemblages in the uThukela Banks MPA. This was achieved by using stereo-BRUVs to obtain data from the reefs of this MPA, to identify the effect of the environmental variables on fish species abundance and diversity. Following this, an optimal LTM programme was designed that would allow Ezemvelo to monitor change in fish assemblages and populations through time. The purpose of this discussion chapter is to summarise the main findings of this study and then discuss a potential long-term monitoring programme for the MPA as well as other MPAs in KZN.

5.1 HABITAT, DEPTH AND RELIEF DRIVE REEF FISH STRUCTURE IN THE UTHUKELA BANKS MPA

Habitat played a crucial role in structuring fish communities of the uThukela Banks MPA, with more structurally complex habitats showing high species abundance and diversity. This finding is attributed to the higher availability of microhabitats, providing shelter from predation, and increase food availability for a variety of species (Friedlander et al., 2003; Edgar et al., 2014; Hall and Kingsford, 2021; Gomes et al., 2024). In contrast, low profile habitats, such as sand, had lower fish diversity and abundance, but were characterised by unique fish species, such as blueskin seabream and largehead hairtail. Furthermore, there was evidence to show that the dominant fish species recorded in this study, slinger and santer, utilised both the reef and sand environments highlighting the ecosystem connectivity. These findings also indicate that management and conservation efforts can be improved by protecting a mosaic of habitats, not only the ones with the highest diversity. Terrain ruggedness index which is habitat complexity proxy had no effect on univariate metrics, meaning that abundances and diversity at both TRI10m and TRI50m scale are not influenced by terrain roughness. This was unexpected, because terrain roughness is known to influence fish distribution and assemblage structure. Rugose areas on the seafloor provide greater

niche diversity, refuge from predation, reduced effects of competition, diverse foraging environments and favourable spawning sites (Gratwicke and Speight, 2005; Komyakova et al., 2013; Kostylev et al., 2005; Smith et al., 2014).

Depth also played an important role in fish assemblage structure. Lower species richness and abundance was observed with increase in water depth. However, opposite pattern was observed for beta diversity which has higher species richness and abundance in the lower mesophotic. Even though shallower reefs supported richer fish assemblage the deep reefs were characterised by unique assemblages. It is likely that a number of environmental and physiological factors contribute to this pattern, such as an increase in the prevalence of low relief habitats in deep water and a decrease in water temperature and light availability. This is corroborated by previous studies which also found higher species richness and diversity at shallower depths (Friedlander and Parrish, 1998; Williams and Bax, 2001; Friedlander et al., 2003; Zintzen et al., 2012; Komyakova et al., 2013; Sih et al., 2019, 2017). The observed higher abundances of slinger in the upper mesophotic showed that the uThukela Banks MPA has potential to play an important role in the recovery of this important fisheries species in KZN.

It was surprising to find no significant effect of terrain ruggedness (TRI) on fish diversity and abundance. Terrain ruggedness index is related to habitat complexity (Riley et al., 1999); and is known to influence fish assemblages due to its relationship with habitat complexity. However, the GAMMs showed that TRI at both scales (TRI10m and TRI50m) did not have a significant effect on fish abundance and diversity; but less refined categories of habitat types (sand, sand inundated reef, and reef) were more reliable descriptors at the level of fish diversity in the uThukela Banks MPA. However, TRI was important in describing the multivariate fish assemblage structure. This suggests that the more summarised diversity metrics hide the more fine scale species specific. Lastly, location had an important effect, with fish assemblages from lower mesophotic reef complexes being different to upper mesophotic reef complexes. There was also a strong latitudinal gradient in fish communities of the uThukela Banks MPA, with northern upper-mesophotic reefs having different assemblages to southern upper mesophotic reefs. Due to the limited spatial scale of this study, this finding likely reflects difference in environmental conditions between the northern and southern regions of the uThukela Banks MPA region. In most instances, this location specific variation was the likely cause of the differences in fish assemblages observed

between the different management zones of the MPA. In the case of the restricted zone, the low diversity and abundance of fish is likely a sampling artefact linked to limitations in the sampling design at Carpenters and Sundowners reefs.

5.2 A MONITORING PROGRAMME FOR THE UTHUKELA BANKS MPA

The stereo-BRUVs appeared to be a highly effective tool to survey the fish assemblages in the region. Furthermore, their ability to non-destructively sample both shallow and deep sites in the marine environment make them an ideal survey method for sampling mesophotic reef fishes of the uThukela Banks MPA. Previous research has shown that they are a suitable tool for LTM as fewer samples are required to produce statistically robust data, in comparison to other visual census methods (Willis et al., 2000; Cappo et al., 2004; Langlois et al., 2010; Gardner and Struthers, 2013). High statistical power at smaller sample sizes is important because it allows for cost-effective and accurate identification of ecological trends within MPA and permits appropriate management responses (Morris et al., 2024). Furthermore, the statistical power is a crucial component of an effective monitoring programme (Perkins et al., 2021).

The power analysis and species accumulation curves used in this study provided a statistical foundation for selecting optimal sample size required to detect change in diversity and populations through time. The species accumulation curves varied considerably among locations requiring between eight (at Umdloti) and 38 (at Zini Hard Edge) to detect 90 % of the available species. This variation likely reflects depth range and variation in habitat types at each location, as the species sampled will change according to habitat and depth. There was an increase in species richness with sampling effort. High species richness across the nine locations reflects the structural complexity of the reef systems with some locations requiring more effort to sample effectively than others. High structurally complex habitats support more niches and requiring more samples to detect 90 % of available species. For example, the sample coverage was estimated at 91 % for Ballito Tongaat, 92 % for Durnford Hat, and 94 % Rosy Snow which were more structurally complex. In contrast to Zini Hard Edge (77 %) and Pat's Paradise (87 %) which showed lower estimated coverage as they were associated with habitats that had low structural complexity. Carpenter reef system had the lowest estimated coverage of 58 % and this was due

to a lack of proper sampling map for this reef system. Therefore, increasing sampling size in future will ensure better representation of mesophotic reef fishes in this reef system.

The power analysis was run on four different metrics that varied in their information content and specificity. Total abundance was the most summarised metrics, followed by total biomass, the abundance of mature fisheries targets and the abundance of slinger. The results showed that the more specific metrics required greater sampling effort to collect statistically robust data. While this might make the generalised metrics appealing from a cost perspective, they lack the sensitivity to detect early and meaningful changes in key species or groups of species. Based on this, the sample size required for monitoring slinger populations (36 samples/reef) was proposed as a target effort for monitoring. This sample size is within the sampling effort required to detect 90 % of available species in the mesophotic reefs of the uThukela Banks MPA.

The cost analysis indicated that on average a stereo-BRUVs sample would cost R1 180 to collect, with an additional R1 200 required if paid video analysts were used. Based on this cost and the required sample size, monitoring multiple reefs within each management zone is not a feasible option for management authorities with limited budgets and staff. Therefore, the proposed monitoring programme for the uThukela Banks MPA is based on scenario-2 which included one reef per management zone ($n = 4$), with a focus on selecting reefs that were comparable in terms of depth and environmental conditions. In addition, it is recommended that a northern and southern exploited reef be included in the programme to allow for the relative effectiveness of the MPA to be assessed while acknowledging the latitudinal variation observed in this study. This gives a total of six zones reef systems (6 reef systems x 36 samples as a baseline per year = 216 samples). The data collection for this scenario would cost approximately R 255 000 and require about 5 weeks to complete the surveys. Video annotation would take approximately 162 days, if using a single video analyst, and cost approximately R260 000, if using paid video analysts. Based on this a 16-month monitoring cycle was proposed that provide additional time for data analysis and reporting. This approach will provide comprehensive and statistically robust data for each reef during each monitoring cycle (16-month) over 5 years. The 16-month breakdown (1 month of fieldwork, 12 months of video annotation and data management, and 3 months of report writing. However, the frequency of repeated visits also needs to be considered.

5.3 PROPOSED NETWORK SCALE LTM FOR THE EZEMVELO KZN MPA

From a management authority perspective, regular monitoring is important for adaptive management strategies allowing for adjustments to be made timeously when changes are observed in the ecosystem. But Ezemvelo must consider monitoring all their MPAs. Unless they have substantial budgets and teams of field technicians and video analysts, monitoring annually or biannually will not be feasible. Ezemvelo manages four main MPAs, three of them under a management agreement with the Department of Forestry, Fisheries and the Environment (DFFE). Those include Protea Banks, Aliwal Shoal, and uThukela Banks. The fourth MPA, iSimangaliso is managed under a management agreement with the iSimangaliso Authority. These MPAs play a critical role in the sustainable management of resources and for conserving marine biodiversity in KZN.

A possible scenario would be to implement a monitoring cycle over a four-year period (Figure 5.1). In this scenario, Ezemvelo could carry out field surveys of two MPAs per year in year one and year two. To ensure effectiveness and efficiency, their monitoring should consider grouping MPAs by size. For instance, they could monitor Protea Banks (smaller MPA) together with uThukela Banks (bigger MPA), and the same with iSimangaliso (bigger) together with Aliwal Shoal (smaller). This would be followed by a two-year break from field work where videos are processed and reports written (Figure 5.1). Based on the cost estimates for uThukela Banks MPA and assuming comparable costs at each MPA, Ezemvelo would need in excess of R 1 000 000 per four-year period for the data collection from the KZN MPAs, and double that if video analysts were paid for the annotation process.

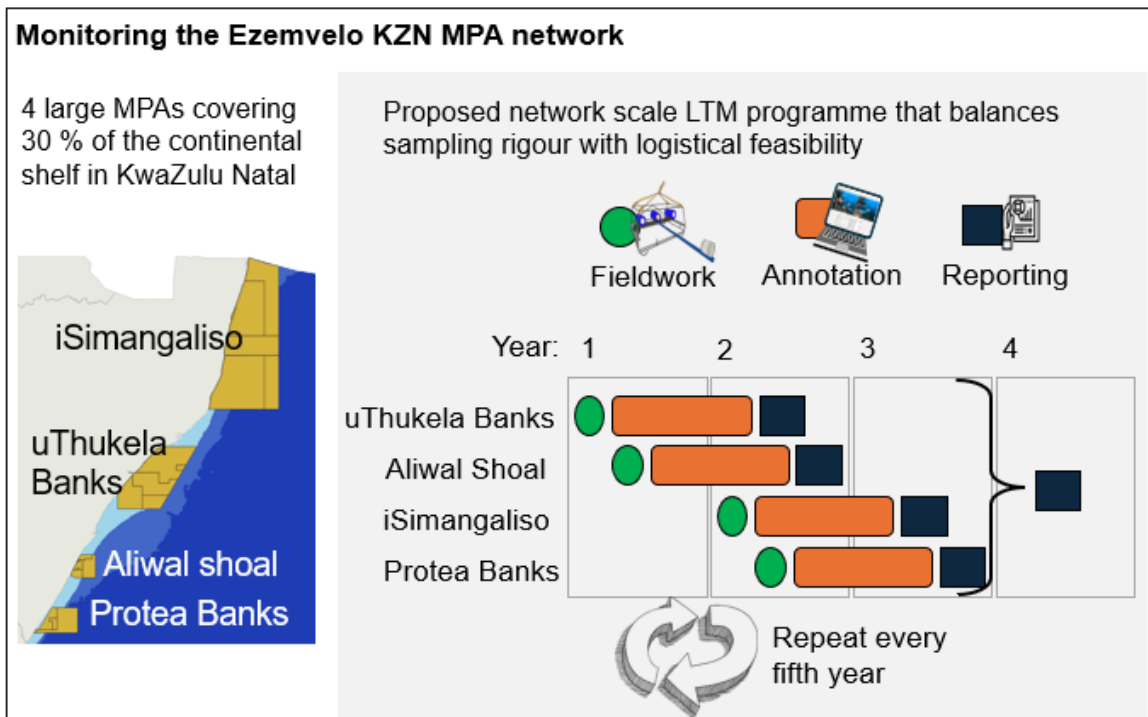


Figure 5.1: Proposed network scale for LTM programme for the Ezemvelo KZN MPAs including time taken in the field and for analysing video footage as well as reporting to ensure that the programme meets its objectives.

This is still a substantial financial outlay and potentially not within the budget of the any MPA management authority. While there are cost-cutting options, such as reducing the sample size and/or the number of sampling locations, the implications need to be carefully considered by the management authority. For example, reducing the sample size might compromise the ability to detect meaningful changes in diversity and/or populations of key fish species, while reducing the number of sites within each MPA would limit the ability to compare between different management zones and relate the MPAs performance to areas open to fishing. An alternative option would be to repeat the process carried out in this thesis at each of the MPAs to determine the specific monitoring requirements at each site. The results from this study showed that there was a considerable amount of spatial variability and as such the other MPAs might require reduced sampling effort. This hypothetical scenario provides a useful starting point for the conceptualisation of a monitoring programme, and further research within each of the MPAs would be required to optimise the total costs and ensure that all datasets are statistically robust.

Time is such an important factor when monitoring activities in the long-term as it influences financial costs and the amount of data that can be collected and analysed (Mantelatto et al., 2013). Time taken to process video footage when extracting MaxN is one of BRUVs weaknesses (Colton and Swearer, 2010). However, time taken to extract data (MaxN) should not only be viewed as a drawback, particularly if the outcome is increased diagnostic power, since gathering precise and accurate data is a fundamental component of biological monitoring (Bernard, 2012). That being said, future studies will benefit from applying machine learning algorithms that will reduce time spent extracting data (Button et al., 2021). This will support the use of stereo-BRUVs as an LTM programme.

From a management perspective, it is important to understand how long it might take to detect effects of reduced fishing pressure. This is essential in choosing right indicators to monitor MPAs. In addition, it helps managers track changes in the environment and assess MPA performance over realistic time frames (Perkins et al., 2021). However, monitoring and evaluation is dependent on the MPAs long-term monitoring plan. Time frames could also be influenced by life history of species, where records appear earlier for short-lived species and at a later stage for long-lived ones (Franceschini et al., 2024). It is also dependent on the initial condition of an MPA (i.e if heavily exploited, it might take long to recover), the size of an MPA and the degree of protection as outlined by Edgar et al., (2014) based on the “NEOLI” principle.

A study by Mann et al., (2022) at a duration of 10 years was able to detect trends in selected indicator species over time, where the four main species that were caught in the no-take area all showed an increase in average between 2006 and 2016. Those species include, slinger, Scotsman, *Epinephelus marginatus*, and black musselcracker. Whereas, Perkins et al., (2021) showed that to detect change for species using ROV, a sampling technique ranged from 13 to over 25 years. The estimated recovery timescales for reef fish biomass under protection is 35 years on average and less than 60 years in heavily depleted cases MacNeil et al., (2015).

The success of management plan implementation depends on the capacity of the management authorities (Jameson et al., 2002). There is great value of management authorities partnering with other organisations, NGOs, and scientists. In South Africa, there are strong examples of this: for instance, SANParks has partnered with SAEON and secured external funding to support video

processing through NGOs. In addition, interns and students can be trained to provide valuable support. Non-Governmental Organisations such as WWF South Africa and Endangered Wildlife Trust can provide technical support, fill capacity and resource gaps, and promote stakeholder engagement. Such multi-stakeholder collaborations are critical for the successful implementation of effective, long-term ecological monitoring ensuring that it is financially sustainable and scientifically rigorous.

5.4 CONCLUSION

This study is the first to obtain a standardised measure of mesophotic fish diversity and abundance across reef habitats in the uThukela Banks MPA, and to decipher the key environmental drivers of observed patterns in reef fish community assemblage structure. The study establishes a baseline record for Ezemvelo and further illustrates the efficacy of evaluating mesophotic reef fish assemblages with stereo-BRUVs. Their ability to non-destructively obtain data in a standardised manner will ensure that future monitoring of mesophotic reef fishes in the uThukela Banks MPA is feasible and can support their adaptive long-term management. The stereo-BRUVs were efficient and afforded the potential to detect changes in fish assemblages in the study area. Maximizing the efficiency of a sampling technique should be a primary goal in monitoring programmes designed to detect change (Brown et al., 2004; Schramm et al., 2020). The cost-benefit analysis was a valuable exercise and demonstrated that the costs attached to this monitoring programme are substantial, and it is expected that further compromises might need to be made. However, the LTM programme outlined in this study, as well as the discussion around a range of potential scenarios, is a framework that can be built on not only within the KZN MPA network, but more broadly across the South African MPA network as it expands and as monitoring becomes both essential and more challenging. Existing collaborations between research institutes, such as the South African Institute for Aquatic Biodiversity and management authority (Ezemvelo KZN Wildlife) will benefit future management of mesophotic reef fishes within the KZN MPA network.

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7 APPENDIX

Table 7.1A: The species list for demersal fish communities investigated in the uThukela Banks marine protected area. Species were obtained from stereo-BRUVs footage and are arranged in alphabetical order (family). Sum of maxN is the total of the maximum number of each fish, shark, and ray species observed in the field of view of the stereo-BRUVs camera from the uThukela Banks dataset.

Family	Species name	Common name	Sum of Max N
Acanthuridae	<i>Acanthurus mata</i>	Elongate surgeonfish	11
Ariidae	<i>Galeichthys trowi</i>	Natal seacatfish	99
Balistidae	<i>Abalistes stellatus</i>	Starry triggerfish	1
	<i>Sufflamen fraenatum</i>	Masked triggerfish	4
Berycidae	<i>Centroberyx spinosus</i>	Short alfonsino	2
Carangidae	<i>Caranx heberi</i>	Blacktip trevally	1
	<i>Caranx ignobilis</i>	Giant trevally	1
	<i>Pseudocaranx dentex</i>	White trevally	5
	<i>Seriola dumerili</i>	Greater amberjack	9
	<i>Seriola lalandi</i>	Yellowtail amberjack	30
	<i>Seriola rivoliana</i>	Longfin yellowtail	72
	<i>Trachurus delagoa</i>	African scad	199
Carcharhinidae	<i>Carcharhinidae spp.</i>	Carcharhinidae spp.	1
	<i>Carcharhinus brachyurus</i>	Bronze whaler	3
	<i>Carcharhinus obscurus</i>	Dusky shark	6
	<i>Carcharhinus spp</i>	Carcharhinus spp.	1
	<i>Galeocerdo cuvier</i>	Tiger shark	6
	<i>Carcharhinus limbatus</i>	Blacktip shark	2
	<i>Carcharhinus plumbeus</i>	Sandbar shark	1
Chaetodontidae	<i>Chaetodon auriga</i>	Threadfin butterflyfish	2
	<i>Chaetodon blackburnii</i>	Brownburnie	14
	<i>Chaetodon dolosus</i>	African butterflyfish	114
	<i>Chaetodon kleinii</i>	Sunburst butterflyfish	1
		Doublesash	
	<i>Chaetodon marleyi</i>	butterflyfish	20
	<i>Heniochus acuminatus</i>	Coachman	10
	<i>Heniochus diphreutes</i>	Schooling coachman	2

Family	Species name	Common name	Sum of Max N
Cheilodactylidae	<i>Chirodactylus brachydactylus</i>	Two-tone fingerfin	2
	<i>Chirodactylus jessicalenorum</i>	Natal fingerfin	34
Dasyatidae	<i>Bathytoshia brevicaudata</i>	Short-tail stingray	2
	<i>Bathytoshia lata</i>	Brown stingray	5
	<i>Dasyatis chrysonota</i>	Blue stingray	25
	<i>Taeniurops meyeri</i>	Round ribbon tail ray	1
	<i>Pateobatis jenkinsii</i>	Sharpnose stingray	1
	<i>Dasyatis spp</i>	Dasyatis spp.	1
	<i>Dinoperca petersi</i>	Cavebass	40
Echeneidae	<i>Echeneis naucrates</i>	Shark remora	5
Fistulariidae	<i>Fistularia commersonii</i>	Smooth flutemouth	1
Gymnuridae	<i>Gymnura natalensis</i>	Butterfly ray	10
Haemulidae	<i>Plectorhinchus chubbi</i>	Dusky rubberlip	51
	<i>Plectorhinchus playfairi</i>	Whitebarred rubberlip	1
	<i>Pomadasys olivaceus</i>	Piggy	91
	<i>Pomadasys striatus</i>	Stripped grunter	430
Labridae	<i>Anchichoerops natalensis</i>	Natal wrasse	2
	<i>Bodianus bilunulatus</i>	Tarry hogfish	4
	<i>Bodianus trilineatus</i>	Fourline hogfish	25
Lethrinidae	<i>Gymnocranius grandoculis</i>	Blue-lined large-eye bream	3
	<i>Lethrinus scoparius</i>	Natal emperor	55
Lutjanidae	<i>Aphareus furca</i>	Blue small toothed jobfish	1
	<i>Aprion virescens</i>	Green jobfish	3
	<i>Lutjanidae spp</i>	Lutjanidae spp.	2
	<i>Paracaesio xanthura</i>	Yellowtail blue snapper	15
	<i>Pristipomoides filamentosus</i>	Crimson jobfish	4
Mullidae	<i>Parupeneus rubescens</i>	Rosy goatfish	35
Muraenidae	<i>Gymnothorax chilospilus</i>	Lipspot moray	3
	<i>Gymnothorax elegans</i>	Elegant moray	7
	<i>Gymnothorax favagineus</i>	Honeycomb moray	1
	<i>Gymnothorax flavimarginatus</i>	Yellow-edged moray	1
	<i>Gymnothorax griseus</i>	Geometric moray	2
	<i>Gymnothorax johnsoni</i>	White-spotted moray	7
	<i>Muraenidae spp</i>	Muraenidae spp.	1
Myliobatidae	<i>Myliobatis aquila</i>	Common eagle ray	2
Odontaspidae	<i>Carcharias taurus</i>	Sand tiger shark	1
Oplegnathidae	<i>Oplegnathus conwayi</i>	Cape knifejaw	11
	<i>Oplegnathus robinsoni</i>	Natal knifejaw	8
Pinguipedidae	<i>Parapercis punctulata</i>	Spotted sandperch	20

Family	Species name	Common name	Sum of Max N
Pomacanthidae	<i>Apolemichthys kingi</i>	Tiger angelfish	2
	<i>Pomacanthus rhomboides</i>	Old woman angelfish	49
Pomacentridae	<i>Chromis woodsi</i>	Spiny chromis	8
	<i>Chromis xanthura</i>	Yellowtail chromis	2
Pomatomidae	<i>Pomatomus saltatrix</i>	Bluefish	1
Priacanthidae	<i>Priacanthus hamrur</i>	Moontail bullseye	2
Rhinobatidae	<i>Rhinobatos austini</i>	Austin's guitarfish	15
	<i>Acroteriobatus leucospilus</i>	Grayspotted guitarfish	4
Sciaenidae	<i>Argyrosomus japonicus</i>	Dusky kob	2
	<i>Atractoscion aequidens</i>	Geelbeck croacker	21
	<i>Umbrina ronchus</i>	Slender baardman	10
Scombridae	<i>Sarda orientalis</i>	Striped bonito	1
	<i>Scomberomorus commerson</i>	King mackerel	1
Scorpaenidae	<i>Pterois miles</i>	Devil firefish	2
	<i>Scorpaena scrofa</i>	Red scorpionfish	4
	<i>Scorpaenopsis spp</i>	Scorpaenopsis spp.	1
Serranidae	<i>Aulacocephalus temminckii</i>	Goldribbon soapfish	20
	<i>Cephalopholis sonnerati</i>	Tomato rockcod	6
	<i>Epinephelus albomarginatus</i>	White-edged rockcod	19
	<i>Epinephelus andersoni</i>	Catface rockcod	58
	<i>Epinephelus coioides</i>	Orange-spotted rockcod	2
	<i>Epinephelus fasciatus</i>	Black-tipped rockcod	3
	<i>Epinephelus malabaricus</i>	Malabar rockcod	1
	<i>Epinephelus marginatus</i>	Yellowbelly rockcod	6
	<i>Epinephelus rivulatus</i>	Halfmoon rockcod	77
	<i>Hyporthodus octofasciatus</i>	Eightbar grouper	3
	<i>Liopropoma spp</i>	Liopropoma spp.	1
	<i>Pseudanthias gibbosus</i>	Redstripe basslet	32
	<i>Serranus cabrilla</i>	Comber	47
Sparidae	<i>Argyrops spinifer</i>	King soldierbream	2
	<i>Cheimerius nufar</i>	Santer	639
	<i>Chrysoblephus anglicus</i>	Englishman	94
	<i>Chrysoblephus gibbiceps</i>	Red stumpnose	1
	<i>Chrysoblephus lophus</i>	False Englishman	62
	<i>Chrysoblephus puniceus</i>	Slinger	1230
	<i>Cymatoceps nasutus</i>	Black musselcracker	13
	<i>Diplodus capensis</i>	Blacktail	32
	<i>Diplodus hottentotus</i>	Zebra	89
	<i>Pachymetopon aeneum</i>	Bluehottentot	5
	<i>Pachymetopon grande</i>	Bronze seabream	2

Family	Species name	Common name	Sum of Max N
Sparidae	<i>Pagellus natalensis</i>	Sand soldier	497
	<i>Polyamblyodon germanum</i>	German seabream	52
	<i>Polyamblyodon gibbosum</i>	Knife-back seabream	7
	<i>Polysteganus coeruleopunctatus</i>	Blueskin	104
	<i>Polysteganus praeorbitalis</i>	Scotsman	31
	<i>Polysteganus undulosus</i>	Seventyfour	8
	<i>Porcostoma dentata</i>	Dane seabream	378
	<i>Rhabdosargus globiceps</i>	White stumpnose	3
	<i>Rhabdosargus holubi</i>	Cape stumpnose	65
	<i>Rhabdosargus sarba</i>	Goldlined seabream	4
	<i>Rhabdosargus thorpei</i>	Bigeye stumpnose	21
	<i>Spondyliosoma emarginatum</i>	Steentjie	405
	<i>Trachurus delagoa</i>	African scad	18
Sphyrnidae	<i>Sphyrna lewini</i>	Scalloped hammerhead	9
Squalidae	<i>Squalus spp</i>	Squalus spp.	7
Synodontidae	<i>Synodus indicus</i>	Indian lizardfish	1
Tetraodontidae	<i>Lagocephalus sceleratus</i>	Silver-cheeked toadfish	6
	<i>Tylerius spinosissimus</i>	Spiny blassop	1
Trachichthyidae	<i>Trachichthyidae spp</i>	Trachichthyidae spp.	1
Triakidae	<i>Mustelus mosis</i>	Hardnose smooth-hound	3
	<i>Mustelus mustelus</i>	Smooth-hound	28
Zeidae	<i>Zeus faber</i>	John dory	3
Trichiuridae	<i>Trichiurus lepturus</i>	Largehead hairtail	2

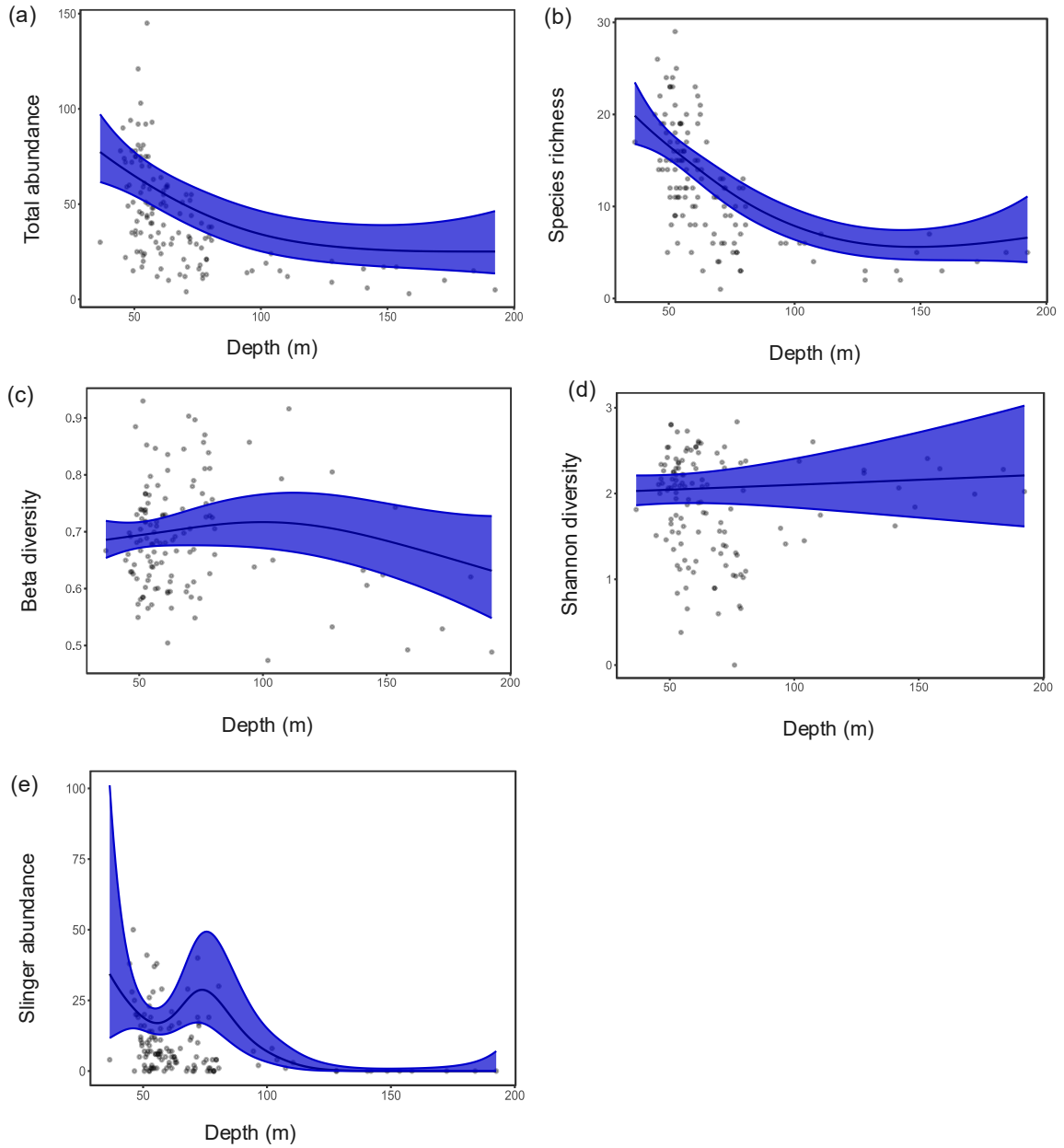


Figure 7.1: Results from generalised additive mixed model output for management, testing the effect of depth on the predicted values of (a) total abundance, (b) species richness and (c) slinger abundance. The predictions based on standardised mean values for all explanatory variables included in the GAM. The error bars represent 95 % confidence interval.

Table 7.2B: Leave-one-out cross validation from Canonical analysis of principal components, where allocations of observations from three groups (sand, reef and sand inundated reef habitat) to predicted categories are shown. The % correct, represents the percentage of samples correctly allocated to each habitat.

Habitat type (Original group)	Classified as				
	Sand	Reef	SIR	Total	% Correct
Sand	15	2	11	28	53.4
Reef	9	46	7	62	74.2
SIR	10	7	19	36	52.8

Table 7.3C: Leave-one-out cross validation (LOOCV) from Canonical analysis of principal components, where allocations of observations from four groups (controlled-pelagic linefish with list, controlled, restricted and exploited) to predicted categories are shown. The % correct, represents the percentage of samples correctly allocated to each management zone.

Management zones (Original group)	Classified as					% Correct
	Controlled-Pelagic Linefish with list	Controlled	Restricted	Exploited	Total	
Controlled-Pelagic Linefish with list	21	3	5	0	29	72.4
Controlled	2	39	2	7	50	78.0
Restricted	3	3	12	0	18	66.7
Exploited	0	2	0	27	29	93.1

Table 7.4D: Leave-one-out cross validation from Canonical analysis of principal components, where allocations of observations from nine groups (Pats Paradise, Zini Hard Edge, Durnford Hat, Carpenter, Ballito Tongaat, Sundowner, Umdloti, Zinkwazi, and Rosie Snow) to predicted categories are shown. The % correct, represents the percentage of samples correctly allocated to each management zone.

	Classified as										
Locations (Original group)	Pats Paradise	Zini Hard Edge	Durnford Hat	Carpenter	Ballito Tongaat	Sundowner	Umdloti	Zinkwazi	Rosie Snow	Total	% Correct
Pats Paradise	9	0	3	2	0	0	0	0	0	14	64.3
Zini Hard Edge	1	12	0	0	0	2	0	0	0	15	80.0
Durnford Hat	4	0	15	1	0	0	0	0	0	20	75.0
Carpenter	1	2	0	3	0	0	0	0	0	6	50.0
Ballito Tongaat	0	0	1	0	8	0	3	2	1	15	53.3
Sundowner	0	0	2	0	1	9	0	0	0	12	75.0
Umdloti	0	0	0	0	1	0	12	0	2	15	80.0
Zinkwazi	0	0	0	0	4	0	0	10	1	15	66.7
Rosie Snow	0	0	0	0	1	0	2	0	11	14	78.6

Table 7.5E: Results from SIMPER analysis on abundance data showing average abundance of the species contributing to dissimilarity between the nine locations, calculated from Log(X+1) transformed abundance data. Av.Abu, average abundance of individual species; Av.Diss, the average dissimilarity between groups; Diss/SD, the dissimilarity ratio to standard deviation; Contrib%, individual species contribution to the overall dissimilarity; Cum.%, accruing overall dissimilarity.

Species	Average Abundance		Av.Diss	Diss/SD	Contrib %	Cum. %
	Pat's Paradise	Zini Hard Edge	average dissim= (81,48)			
Slinger	2,36	0,87	9,93	1,27	12,18	12,18
Blueskin	0,00	1,62	8,75	1,25	10,74	22,92
Santer	1,48	1,22	5,24	0,98	6,44	29,36
Natal emperor	0,98	0,00	4,53	1,36	5,56	34,92
Dane seabream	0,90	0,12	3,92	1,23	4,82	39,73
	Pat's Paradise	Durnford Hat	average dissim= (63,31)			
Slinger	2,36	2,60	5,40	0,99	8,54	8,54
Dane seabream	0,90	1,58	3,16	1,23	5,71	14,24
African butterflyfish	0,44	0,95	3,20	0,84	5,05	19,29
Natal emperor	0,60	1,12	3,02	1,24	4,78	24,07
Halfmoon rockcod	0,98	0,25	2,90	1,15	4,58	28,65
	Zini Hard Edge	Durnford Hat	average dissim= (82,17)			
Slinger	0,87	2,60	8,70	1,54	10,59	10,59
Blueskin	1,62	0,00	7,38	1,25	8,98	19,57
Dane seabream	0,12	1,58	5,66	1,77	6,89	26,46
Santer	1,22	1,43	4,18	1,01	5,09	31,55
African butterflyfish	0,00	1,12	3,76	1,24	4,57	36,12
	Pat's Paradise	Carpenter	average dissim= (70,27)			
Slinger	2,36	0,61	10,94	1,30	15,58	15,58
Blueskin	0,00	0,65	4,59	0,57	6,53	22,10
Dane seabream	0,90	0,12	4,20	1,26	5,98	28,08
Natal emperor	0,98	0,66	4,13	1,11	5,88	33,96
Santer	1,48	1,84	3,97	1,19	5,65	39,96
	Zini Hard Edge	Carpenter	average dissim= (70,86)			
Blueskin	1,62	0,65	11,23	1,34	15,84	15,84
Santer	1,22	1,84	9,54	1,24	13,46	29,30
Slinger	0,87	0,61	8,02	1,01	11,32	40,63
Natal emperor	0,00	0,66	5,19	1,32	7,32	47,94
Halfmoon rockcod	0,07	0,30	2,69	0,72	3,80	51,74
	Durnford Hat	Carpenter	average dissim= (76,19)			
Slinger	2,60	0,61	9,80	1,58	12,86	12,86
Dane seabream	1,58	0,12	5,99	1,79	7,86	20,72

Species	Average Abundance	Av.Diss	Diss/SD	Contrib %	Cum. %	Species
Blueskin	0,00	0,65	3,68	0,58	4,83	30,71
Striped grunter	0,95	0,00	3,64	0,77	4,77	35,49
	Pat's Paradise	Ballito Tongaat average diss= (70,94)				
Sand soldier	0,00	1,93	6,65	1,57	9,38	9,38
Slinger	2,36	1,52	5,71	1,22	8,05	17,43
African scad	0,05	1,34	4,28	1,16	6,03	23,46
Steentjie	0,16	1,07	3,20	1,01	4,51	27,97
African emperor	0,98	0,07	3,05	1,33	4,29	32,26
	Zini Hard Edge	Ballito Tongaat average diss= (82,30)				
Sand soldier	0,05	1,93	8,35	1,70	10,15	10,15
Blueskin	1,62	0,00	7,23	1,47	8,79	18,94
Slinger	0,87	1,52	5,59	1,44	6,79	25,73
Dane seabream	0,12	1,41	5,51	2,23	6,69	32,42
African scad	0,18	1,34	5,19	1,23	6,31	38,73
	Durnford Hat	Ballito Tongaat average diss= (67,98)				
Sand soldier	0,15	1,93	5,78	1,50	8,51	8,51
Slinger	2,60	1,52	4,58	1,25	6,74	15,25
African scad	0,11	1,34	3,90	1,14	5,73	20,99
Striped grunter	0,95	0,58	3,11	0,90	4,58	25,56
Steentjie	0,03	1,07	2,89	0,98	4,26	29,82
	Carpenter	Ballito Tongaat average diss= (77,15)				
Sand soldier	0,00	1,93	9,03	1,70	11,70	11,70
African scad	0,00	1,34	5,86	1,22	7,60	19,30
Dane seabream	0,12	1,41	5,81	2,25	7,53	26,83
Slinger	0,61	1,52	5,73	1,49	7,42	34,26
Steentjie	0,00	1,07	4,22	1,05	5,47	39,73
	Pat's Paradise	Sundowner average diss= (82,30)				
Slinger	2,36	1,07	8,26	1,15	11,65	11,65
Santer	1,48	2,46	4,61	1,38	6,50	18,15
Natal emperor	0,98	0,12	3,68	1,24	5,18	23,33
Dane seabream	0,90	0,62	3,60	1,19	5,07	28,41
Longfin	0,38	0,59	2,86	0,96	4,03	32,44
yellowtail						
	Zini Hard Edge	Sundowner average diss= (78,78)				
Blueskin	1,62	0,00	9,98	1,39	12,67	12,67
Santer	1,22	2,46	9,21	1,11	11,69	24,36
Slinger	0,87	1,07	6,76	1,05	8,58	32,94
Longfin yellowtail	0,09	0,59	3,37	0,98	4,28	37,22
Dane seabream	0,12	0,62	2,90	0,86	3,68	40,89
	Durnford Hat	Sundowner average diss= (72,00)				
Slinger	2,60	1,07	7,26	1,28	10,09	10,09
Dane seabream	1,58	0,62	4,54	1,41	6,31	16,40
Santer	1,43	2,46	4,22	1,34	5,86	22,26

Species	Average Abundance	Av.Diss	Diss/SD	Contrib %	Cum. %	Species
Capenter Sundowner average diss= (68,99)						
Slinger	0,61	1,07	6,46	1,01	9,37	9,37
Santer	1,84	2,46	6,13	1,18	8,89	18,26
Blueskin	0,65	0,00	5,27	0,68	7,64	25,90
African emperor	0,66	0,12	4,04	1,18	5,85	31,75
Longfin yellowtail	0,00	0,59	3,68	0,95	5,33	37,08
Ballito Tongaat Sundowner average diss= (68,73)						
Sand soldier	1,93	0,23	6,83	1,51	9,94	9,94
Slinger	1,52	1,07	4,83	1,35	7,03	16,97
African scad	1,34	0,20	4,82	1,19	6,13	23,99
Dane seabream	1,41	0,62	4,21	1,50	5,11	30,12
Steentjie	1,07	0,09	3,51	1,03	3,93	35,23
Pat's Paradise Umdlotti average diss= (70,70)						
Sand soldier	0,00	2,25	6,32	1,90	8,94	8,94
Steentjie	0,16	1,76	4,48	1,30	6,33	15,27
Slinger	2,36	2,08	4,21	1,27	5,95	21,22
Striped grunter	0,44	1,51	3,97	1,23	5,62	26,84
Zebra seabream	0,05	1,06	2,75	1,53	3,88	30,72
ZiniHard Edge Umdlotti average diss= (84,38)						
Sand soldier	0,05	2,25	7,63	2,00	9,04	9,04
Blueskin	1,62	0,00	5,72	1,49	6,78	15,82
Steentjie	0,00	1,76	5,53	1,35	6,55	22,37
Slinger	0,87	2,08	5,44	1,69	6,45	28,82
Striped grunter	0,19	1,51	4,69	1,33	5,55	34,37
Durnford Hat Umdlotti average diss= (64,59)						
Sand soldier	0,15	2,25	5,51	1,77	8,53	8,53
Steentjie	0,03	1,76	4,15	1,27	6,42	14,96
Striped grunter	0,95	1,51	3,66	1,27	5,66	20,62
Slinger	2,60	2,08	2,83	1,13	4,38	25,00
Dane seabream	1,58	1,27	2,41	1,23	3,73	28,73
Carpenter Umdlotti average diss= (81,89)						
Sand soldier	0,00	2,25	8,14	2,01	9,94	9,94
Steentjie	0,00	1,76	5,77	1,35	7,05	16,99
Slinger	0,61	2,08	5,75	1,60	7,02	24,01
Striped grunter	0,00	1,51	5,11	1,30	6,24	30,25
Dane seabream	0,12	1,27	4,26	1,81	5,20	35,45
Ballito Tongaat Umdlotti average diss= (55,79)						
Steentjie	1,07	1,76	3,85	1,37	6,90	6,90
Striped grunter	0,58	1,51	3,71	1,30	6,66	13,55
African scad	1,34	0,43	3,29	1,24	5,89	19,44
Sand soldier	1,93	2,25	3,00	1,05	5,38	24,82
Slinger	1,52	2,08	2,83	1,14	5,07	29,89

Species	Average Abundance	Av.Diss	Diss/SD	Contrib %	Cum. %	Species
Sundowner Umdloti average diss= (70,66)						
Sand soldier	0,23	2,25	6,37	1,77	9,02	9,02
Steentjie	0,09	1,76	4,89	1,32	6,92	15,94
Slinger	1,07	2,08	4,56	1,34	6,45	22,39
Striped grunter	0,00	1,51	4,37	1,28	6,18	28,57
Dane seabream	0,62	1,27	3,23	1,39	4,57	33,14
Pat's Paradise Zinkwazi average diss= (70,81)						
Slinger	2,36	1,77	5,92	1,17	8,36	8,36
Sand soldier	0,00	1,23	4,51	1,38	6,37	14,73
Striped grunter	0,44	1,14	4,00	1,05	5,64	20,38
African scad	0,05	1,14	3,96	1,68	5,59	25,97
Dane seabream	0,90	1,45	3,35	1,07	4,73	30,70
Zini Hard Edge Zinkwazi average diss= (83,58)						
Blueskin	1,62	0,00	7,28	1,53	8,71	8,71
Slinger	0,87	1,77	6,85	1,31	8,20	16,91
Dane seabream	0,12	1,45	6,23	1,83	7,45	24,36
Sand soldier	0,05	1,23	5,65	1,45	6,76	31,12
Striped grunter	0,19	1,14	4,72	1,07	5,64	36,76
Durnford Hat Zinkwazi average diss= (66,43)						
Slinger	2,60	1,77	4,66	1,23	7,02	7,02
Sand soldier	0,15	1,23	4,09	1,37	6,16	13,18
Striped grunter	0,95	1,14	3,86	1,16	5,81	18,98
African scad	0,11	1,14	3,65	1,72	5,50	24,48
Dane seabream	1,58	1,45	2,95	1,14	4,44	28,92
Carpenter Zinkwazi average diss= (80,13)						
Slinger	0,61	1,77	7,25	1,29	9,05	9,05
Dane seabream	0,12	1,45	6,62	1,83	8,26	17,31
Sand soldier	0,00	1,23	6,21	1,50	7,75	25,06
African scad	0,00	1,14	5,73	2,00	6,45	32,21
Striped grunter	0,00	1,14	5,17	1,03	4,98	43,64
Ballito Tongaat Zinkwazi average diss= (57,03)						
Slinger	1,52	1,77	4,26	1,30	7,47	7,47
Sand solier	1,93	1,23	3,77	1,43	6,61	14,07
Striped grunter	0,58	1,14	3,69	1,13	6,46	20,54
Steentjie	1,07	0,63	3,24	1,19	5,67	26,21
African scad	1,34	1,14	3,15	1,49	5,52	31,73
Sundowner Zinkwazi average diss= (75,00)						
Slinger	1,07	1,77	5,85	1,18	7,80	7,80
Santer	2,46	1,12	5,53	1,84	7,37	15,17
Dane seabream	0,62	1,45	4,70	1,36	6,27	21,44
African scad	0,20	1,4	4,63	1,88	6,18	27,62
Sand soldier	0,23	1,23	4,60	1,31	6,13	33,75

Species	Average Abundance	Av.Diss	Diss/SD	Contrib %	Cum. %	Species
	Umdloti	Zinkwazi average dissi= (59,07)				
Steentjie	1,76	0,63	3,96	1,34	6,70	6,70
Sand soldier	2,25	1,23	3,53	1,53	5,97	12,67
Striped grunter	1,51	1,14	3,35	1,27	5,68	18,35
Slinger	2,08	1,77	3,35	1,27	5,67	24,02
African scad	0,43	1,14	2,93	1,78	4,96	28,98
	Pat's Paradise	Rosie Snow average dissi= (59,07)				
Steentjie	0,16	2,02	6,46	1,70	9,05	9,05
Sand soldier	0,00	1,87	6,45	2,32	9,03	18,08
Slinger	2,36	0,96	5,05	1,52	7,07	25,15
Striped grunter	0,44	0,93	3,36	1,26	4,70	29,85
Piggy	0,00	0,00	3,29	1,24	4,60	34,46
<i>Pomadasys olivaceus</i>						
	Zini Hard Edge	Rosie Snow average dissi= (81,36)				
Steentjie	0,00	2,02	8,53	2,09	10,48	10,48
Sand soldier	0,05	1,87	8,02	2,70	9,85	20,34
Blueskin	1,62	0,00	6,97	1,58	8,57	28,91
Slinger	0,87	1,82	6,10	1,63	7,50	36,41
Dane seabream	1,12	1,19	4,91	1,51	6,04	42,45
	Durnford Hat	Rosie Snow average dissi= (67,48)				
Steentjie	0,03	2,02	5,97	1,75	8,85	8,85
Sand soldier	0,15	1,87	5,61	2,23	8,32	17,17
Slinger	2,60	0,96	3,42	1,66	5,07	22,24
Striped grunter	0,95	1,19	3,38	1,28	5,01	27,25
Dane seabream	1,58	0,05	2,98	1,28	4,42	31,67
	Carpenter	Rosie Snow average dissi= (77,62)				
Steentjie	0,00	2,02	9,05	2,09	11,65	11,65
Sand soldier	0,61	1,87	8,72	2,88	11,23	22,89
Slinger	0,12	1,82	6,55	1,54	8,44	31,33
Dane seabream	0,12	1,19	5,21	1,53	6,71	38,04
Striped grunter	0,00	0,93	4,19	1,25	5,40	43,43
	Ballito Tongaat	Rosie Snow average dissi= (54,03)				
Steentjie	1,07	2,02	4,60	1,41	8,51	8,51
African scad	1,34	0,60	3,80	1,26	7,04	15,55
Striped grunter	0,58	0,96	3,17	1,29	5,87	21,42
Slinger	1,52	1,82	3,03	1,19	5,61	27,03
Sand soldier	1,93	1,87	2,98	1,23	5,51	32,54
Piggy	0,00	0,93	2,94	1,31	5,44	37,98
	Sundowner	Rosie Snow average dissi= (70,41)				
Steentjie	0,09	2,02	7,24	1,84	10,29	10,29
Sand soldier	0,23	1,87	6,38	1,93	9,06	19,35
Slinger	1,07	1,82	5,17	1,35	7,35	26,70

Species	Average Abundance	Av.Diss	Diss/SD	Contrib %	Cum. %	Species
	Sundowner	Rosie Snow average dissi= (70,41)				
Dane seabream	0,62	1,19	3,94	1,29	5,60	32,30
Piggy	0,00	0,93	3,64	1,28	5,16	37,46
	Umdloti	Rosie Snow average dissi= (52,03)				
Steentjie	1,76	2,02	3,62	1,26	6,69	6,69
Striped grunter	1,51	0,96	3,19	1,43	6,13	13,09
Sand soldier	2,25	1,87	2,67	1,38	5,14	18,23
Piggy	0,56	0,93	2,52	1,34	4,84	23,07
Zebra seabream	1,06	0,26	2,29	1,50	4,40	27,47
	Zinkwazi	Rosie Snow average dissi= (56,82)				
Steentjie	0,63	2,02	5,14	1,57	9,05	9,05
Slinger	1,77	1,82	3,84	1,58	6,76	15,81
African scad	1,14	0,60	3,38	1,74	5,94	21,76
Striped grunter	1,14	0,96	3,23	1,28	5,69	27,45
Sand soldier	1,23	1,87	2,80	1,35	4,93	32,38

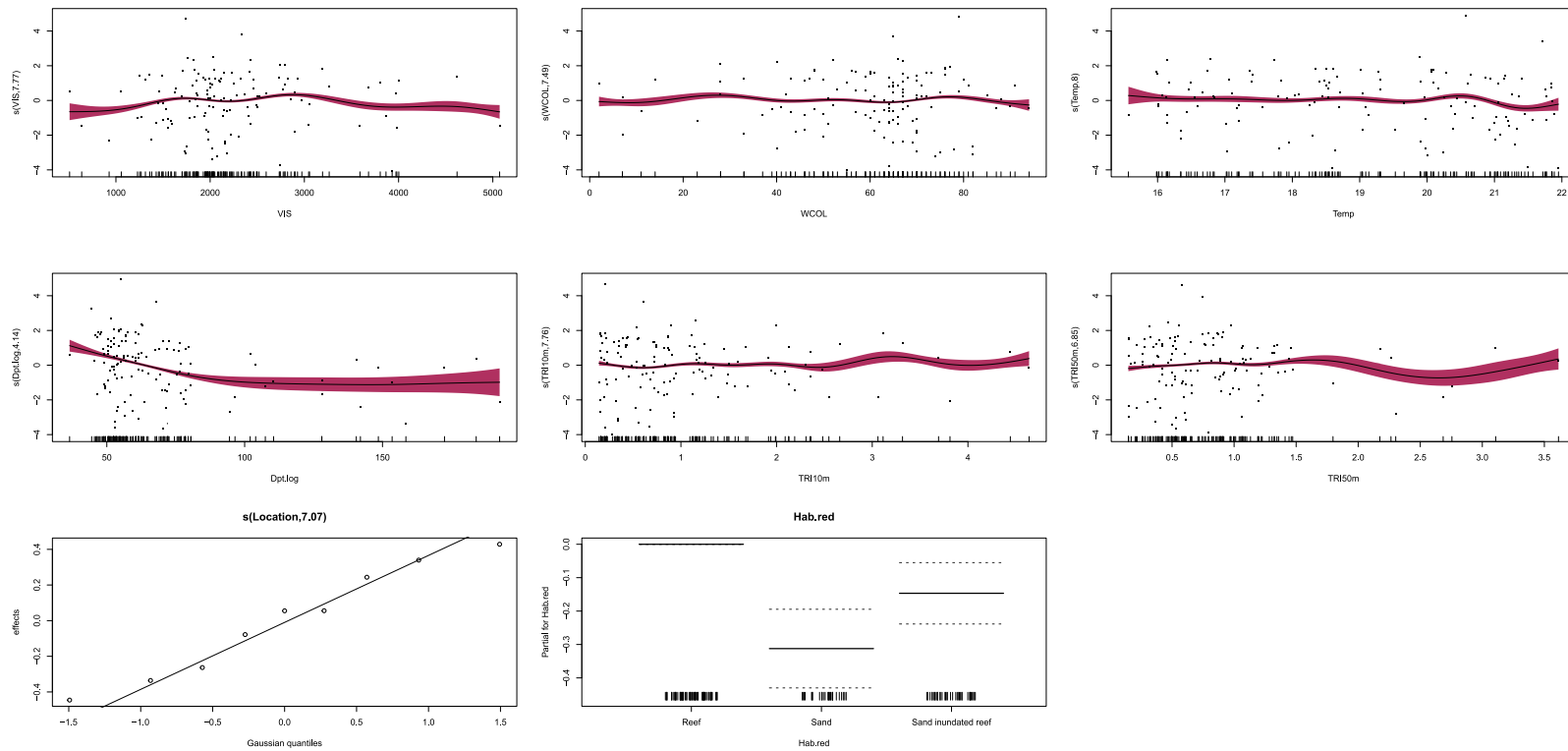


Figure 7.2: Generalised additive mixed model plots with the panel showing the estimated smooth effect of a predictor on the response variable Total abundance (MaxN). The continuous covariates shown include Vis= visibility, WCOL= water column, Temp= temperature, Dpt.log= depth, TRI10m and TRI50m = terrain ruggedness index (TRI) at 10m and 50m, scale respectively. The plots for parametric term= habitat and location as random effect. The shaded regions represent the 95 % confidence intervals (CI).

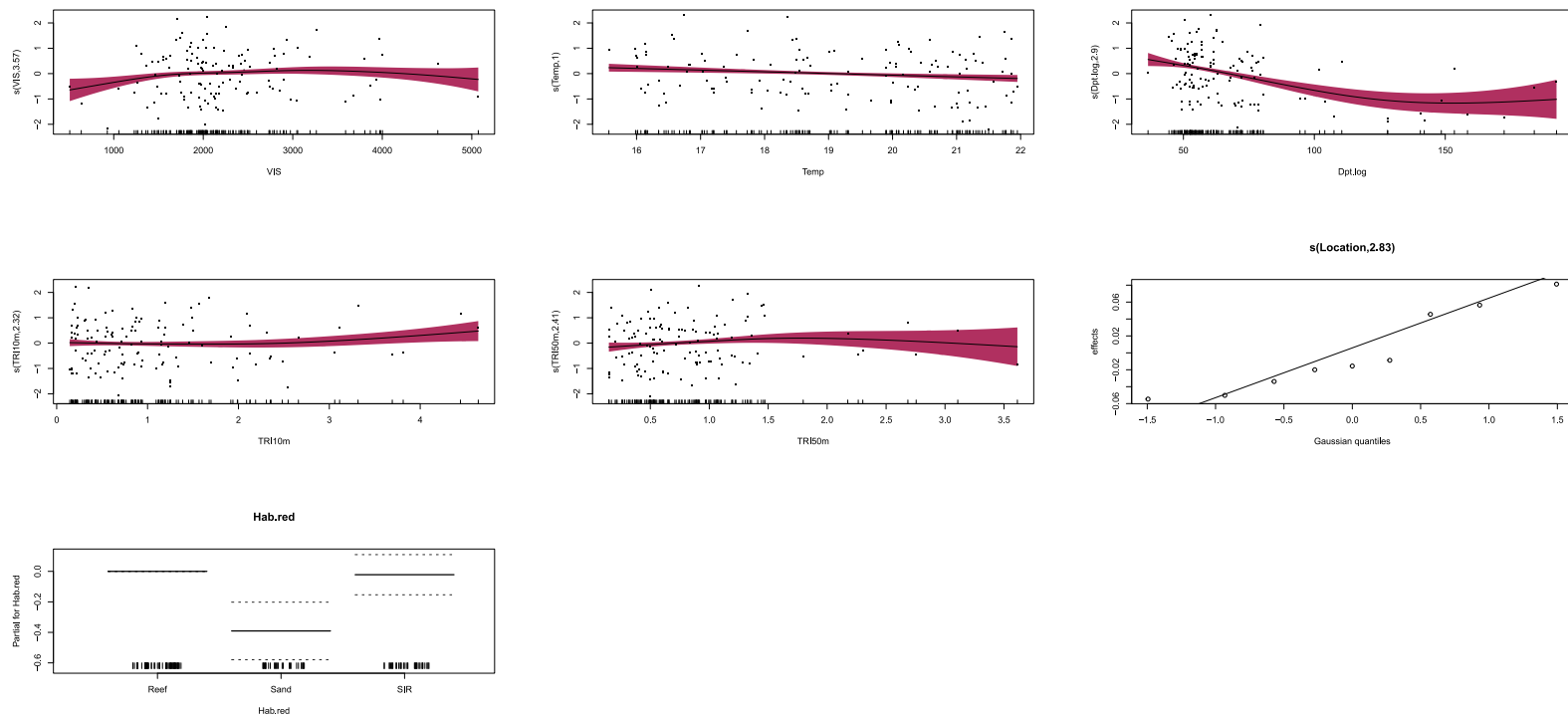


Figure 7.3: Generalised additive mixed model plots with the panel showing the estimated smooth effect of a predictor on the response variable Species richness. The continuous covariates shown include Vis= visibility, Temp= temperature, Dpt.log= depth, TRI10m and TRI50m = terrain ruggedness index (TRI) at 10m and 50m, scale respectively. The plots for parametric term= habitat and location as random effect. The shaded regions represent the 95 % CI.

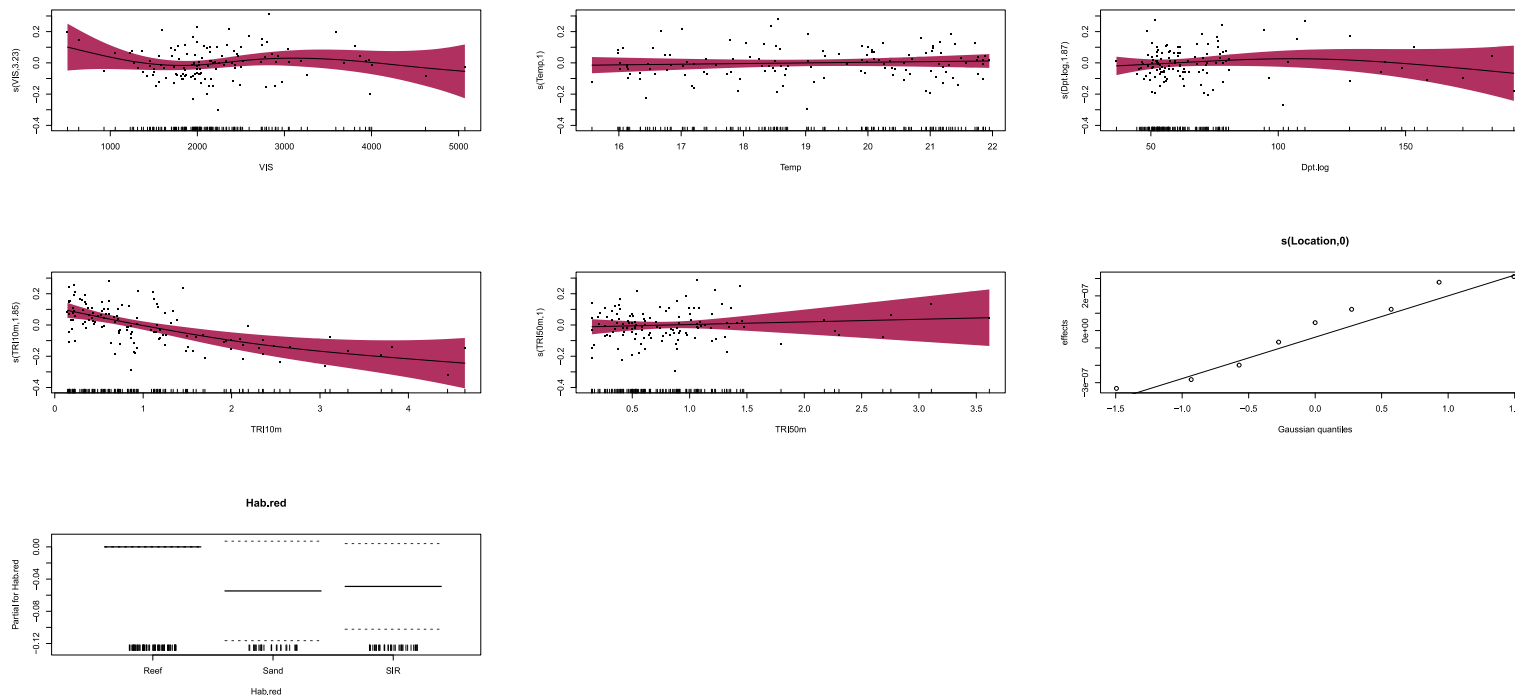


Figure 7.4: Generalised additive mixed model plots with the panel showing the estimated smooth effect of a predictor on the response variable Beta diversity. The continuous covariates shown include Vis= visibility, Temp= temperature, Dpt.log= depth, TRI10m and TRI50m = terrain ruggedness index (TRI) at 10m and 50m, scale respectively. The plots for parametric term= habitat and location as random effect. The shaded regions represent the 95 % parametric term= habitat and location as random effect. The shaded regions represent the 95 % CI.

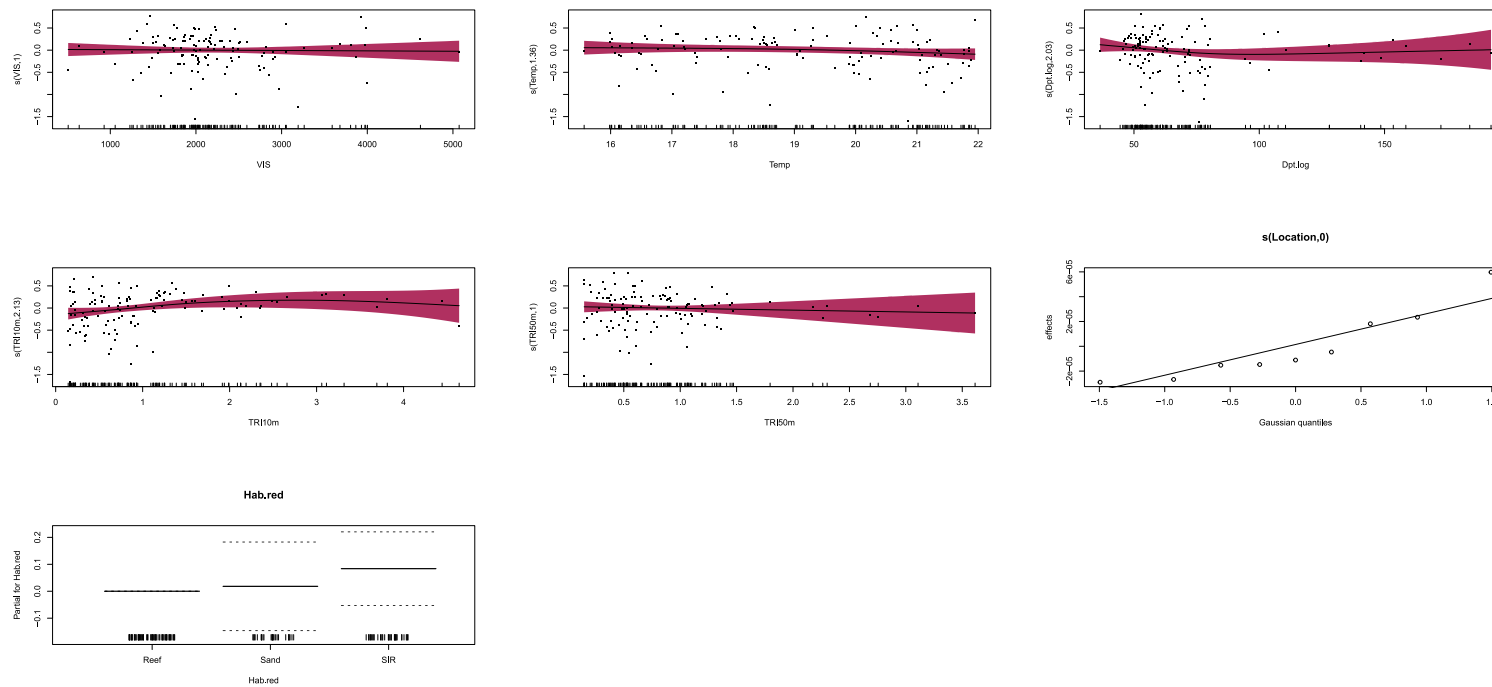


Figure 7.5: Generalised additive mixed model plots with the panel showing the estimated smooth effect of a predictor on the response variable Shannon diversity. The continuous covariates shown include Vis= visibility, Temp= temperature, Dpt.log= depth, TRI10m and TRI50m = terrain ruggedness index (TRI) at 10m and 50m, scale respectively. The plots for parametric term= habitat and location as random effect. The shaded regions represent the 95 % parametric term= habitat and location as random effect. The shaded regions represent the 95 % CI.

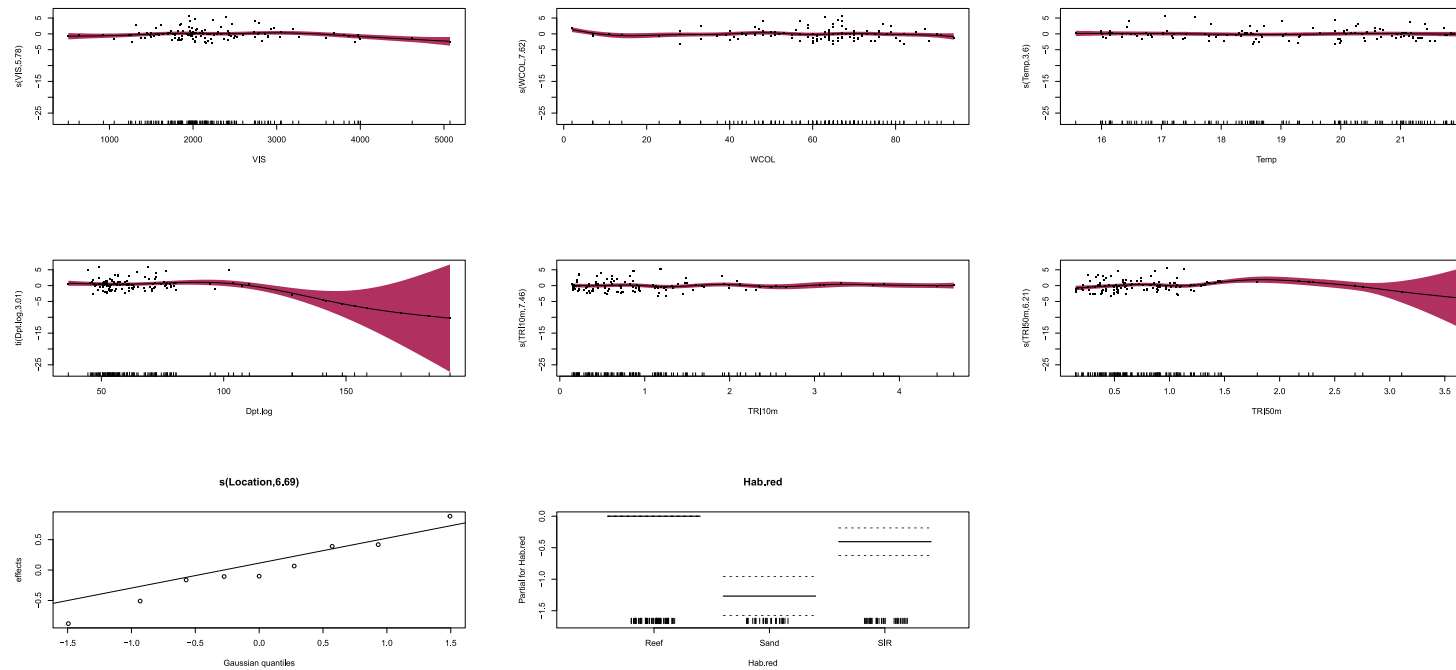


Figure 7.6: Generalised additive mixed model plots with the panel showing the estimated smooth effect of a predictor on the response variable Slinger abundance. The continuous covariates shown include Vis= visibility, WCOL= water column, Temp= temperature, Dpt.log= depth, TRI10m and TRI50m = terrain ruggedness index (TRI) at 10m and 50m, scale respectively. The plots for parametric term= habitat and location as random effect. The shaded regions represent the 95% CI.

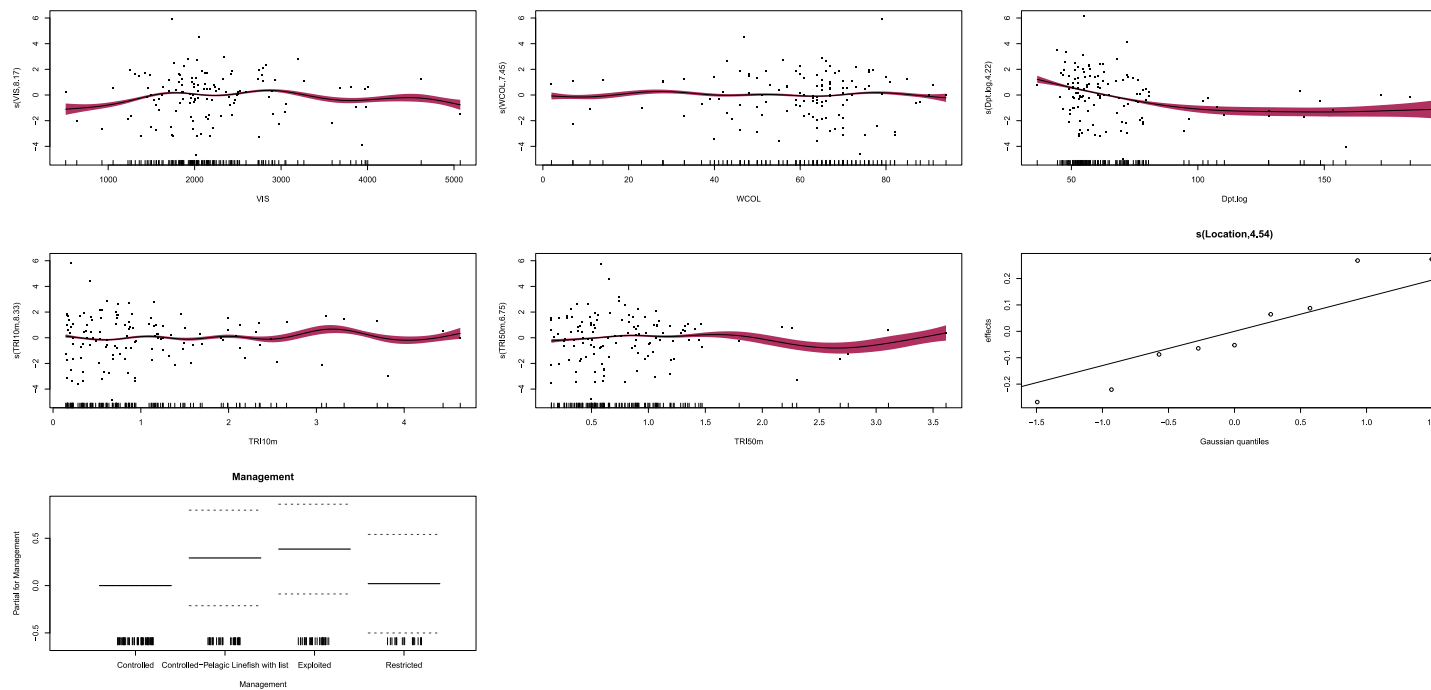


Figure 7.7: Generalised additive mixed model plots with the panel showing the estimated smooth effect of a predictor on the response variable Total abundance (MaxN). The continuous covariates shown include Vis= visibility, WCOL= water column, Temp= temperature, Dpt.log= depth, TRI10m and TRI50m = terrain ruggedness index (TRI) at 10m and 50m, scale respectively. The plots for parametric term=management and location as random effect. The shaded regions represent the 95 % CI.

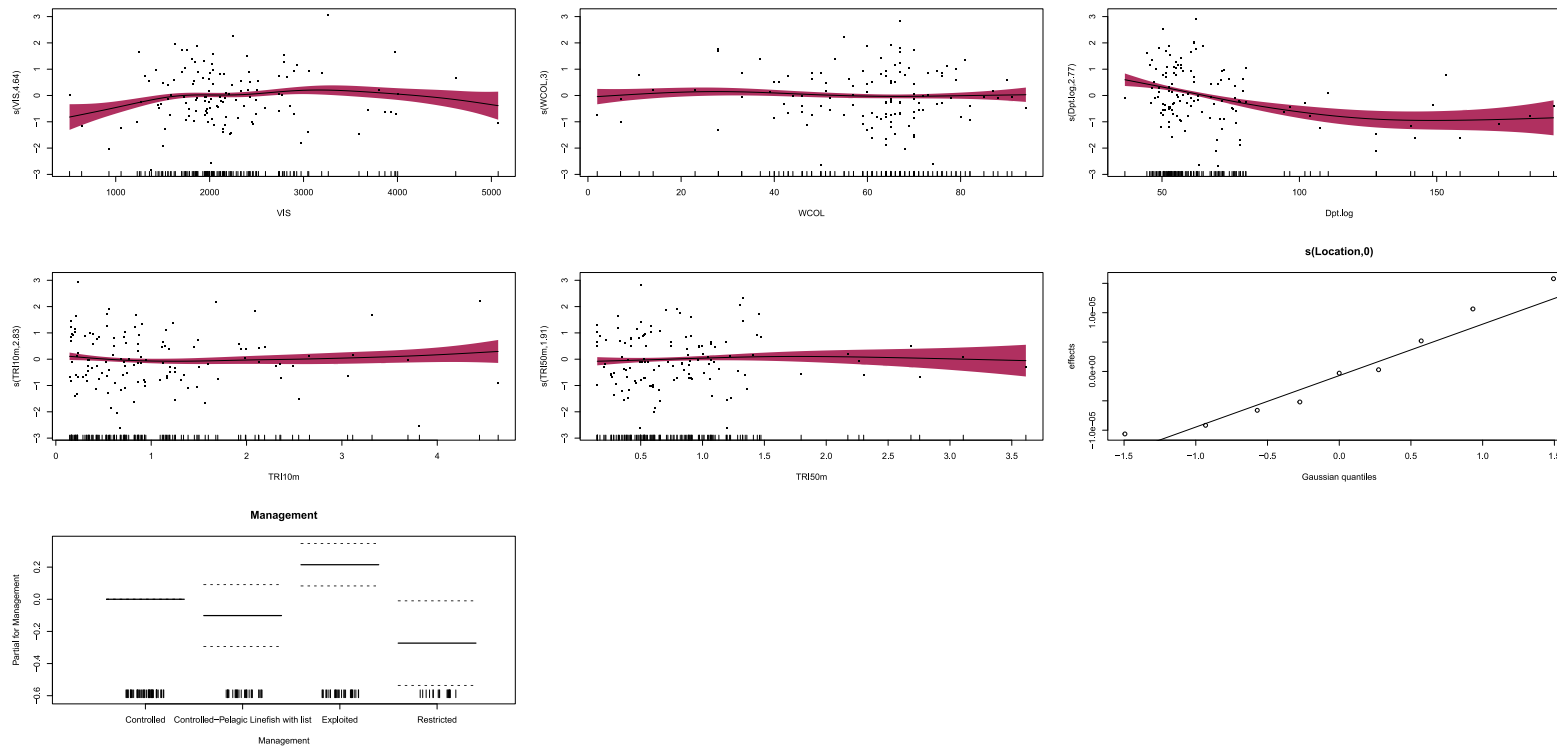


Figure 7.8: Generalised additive mixed model plots with the panel showing the estimated smooth effect of a predictor on the response variable Species richness. The continuous covariates shown include Vis= visibility, WCOL= water column, Temp= temperature, Dpt.log= depth, TRI10m and TRI50m = terrain ruggedness index (TRI) at 10m and 50m, scale respectively. The plots for parametric term=management and location as random effect. The shaded regions represent the 95 % CI.

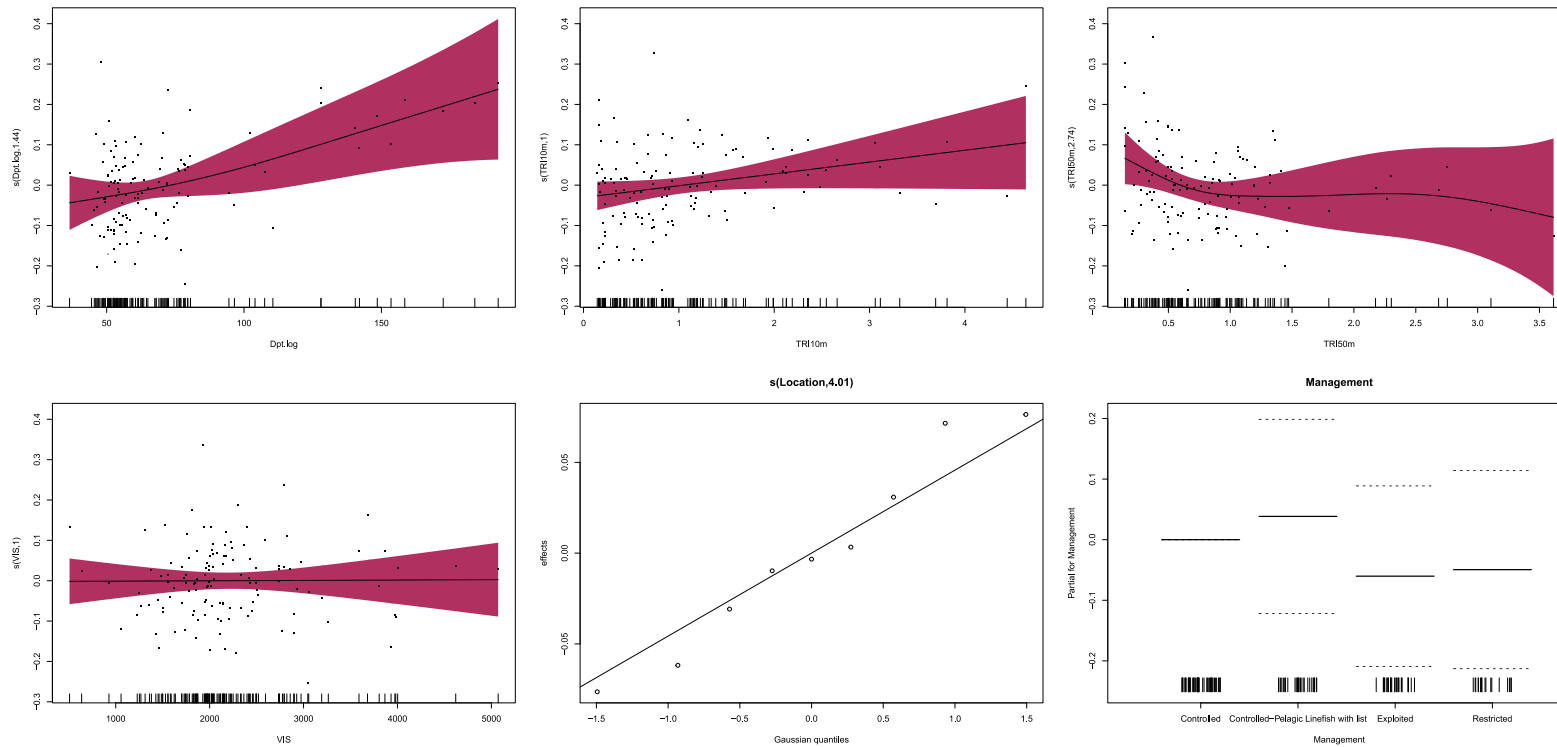


Figure 7.9: Generalised additive mixed model plots with the panel showing the estimated smooth effect of a predictor on the response variable Beta diversity. The continuous covariates shown include Vis= visibility, WCOL= water column, Temp= temperature, Dpt.log= depth, TRI10m and TRI50m = terrain ruggedness index (TRI) at 10m and 50m, scale respectively. The plots for parametric term=management and location as random effect. The shaded regions represent the 95 % CI.

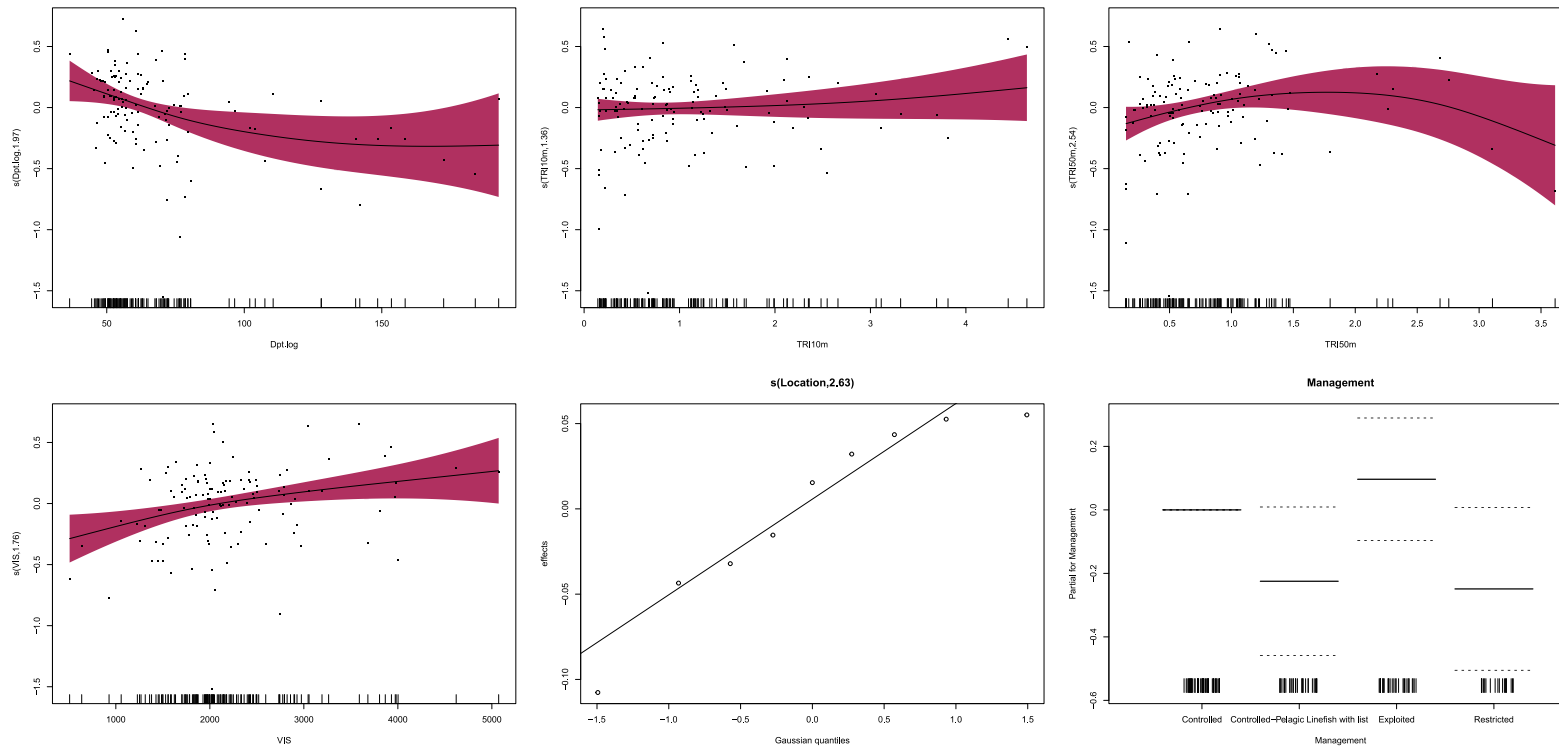


Figure 7.10: Generalised additive mixed model plots with the panel showing the estimated smooth effect of a predictor on the response variable Shannon diversity. The continuous covariates shown include Vis= visibility, WCOL= water column, Temp= temperature, Dpt.log= depth, TRI10m and TRI50m = terrain ruggedness index (TRI) at 10m and 50m, scale respectively. The plots for parametric term=management and location as random effect. The shaded regions represent the 95 % CI.

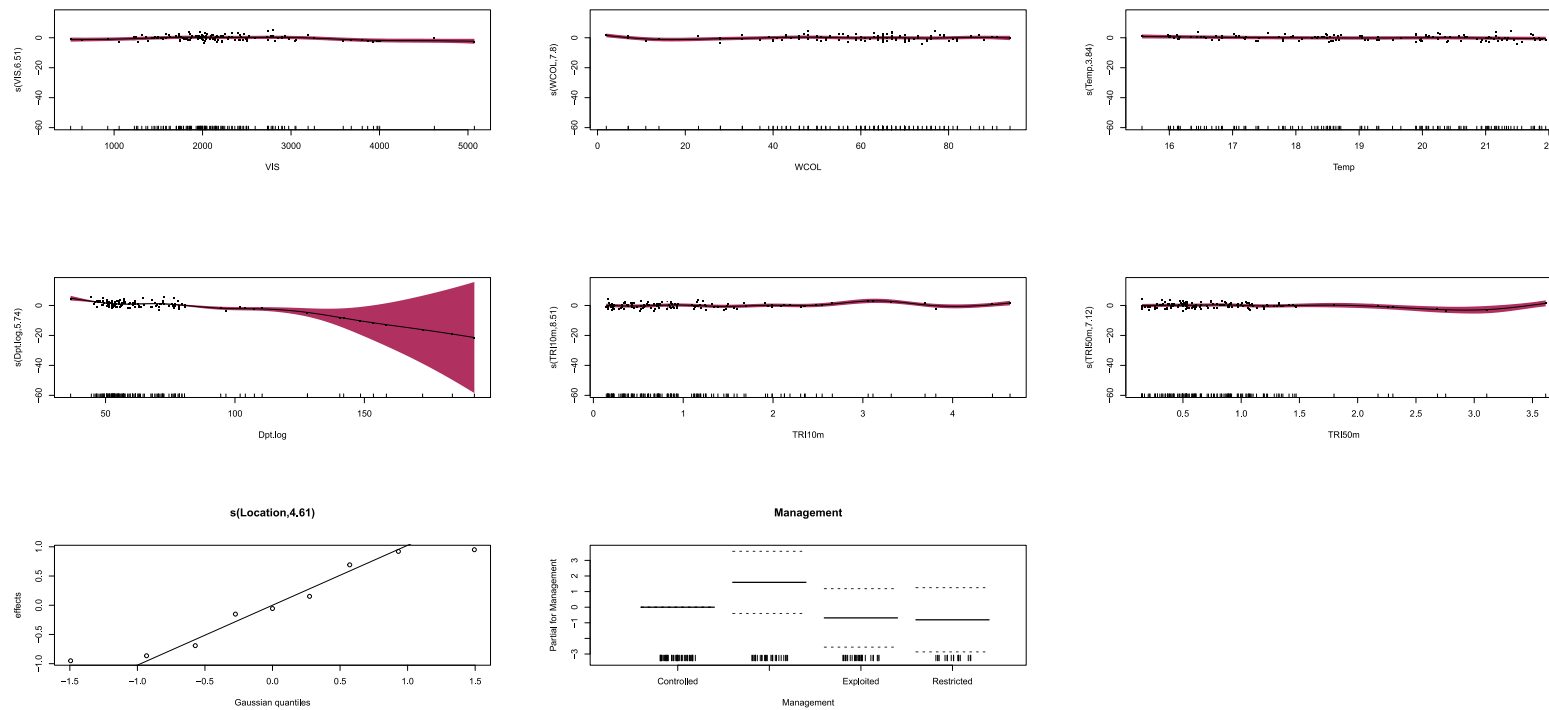


Figure 7.11: Generalised additive mixed model plots with the panel showing the estimated smooth effect of a predictor on the response variable Slinger abundance. The continuous covariates shown include Vis= visibility, WCOL= water column, Temp= temperature, Dpt.log= depth, TRI10m and TRI50m = terrain ruggedness index (TRI) at 10m and 50m, scale respectively. The plots for parametric term=management and location as random effect. The shaded regions represent the 95 % CI.