Do submarine canyons influence the structure and diversity of benthic fish assemblages on the continental shelf edge?

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By

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ABSTRACT

Marine ecosystems play an important role in human welfare, such as providing food security and providing social, economic and environmental benefits to an increasing human population. However, due to the deleterious impact of overfishing as well as habitat degradation, pollution and climate change, many marine ecosystems and the substantial biodiversity they support, are under increasing threats. Submarine canyon ecosystems cut into the continental margin in all our oceans and are considered regions of enhanced diversity, abundance and biomass for many marine communities, including fish. In South Africa, the tropical Delagoa Ecoregion is characterised by numerous submarine canyons that are home to coelacanths *Latimeria chalumnae*, and a variety of commercially important line fish species. However, there is currently a lack of information on the ecological structure and functioning of these canyons, in relation to nearby non-canyon ecosystems. The aim of this thesis was to generate knowledge on the role of submarine canyons in influencing the benthic fish assemblage structure and diversity on the continental shelf and shelf edge within the high-latitude coral reef ecosystems in the tropical Delagoa Ecoregion of South Africa.

First, a systematic literature review was conducted to examine the current knowledge on the role of submarine canyons on the benthic fish assemblages occurring on continental margins, as well as outline the trends in canyon research. For the fieldwork component of this thesis, baited remote underwater stereo-video systems were utilised to gather data. The first research chapter, **chapter 3**, investigated the effect of ecosystem and depth on the diversity and structure of benthic fish assemblages within iSimangaliso Wetland Park in the Delagoa Ecoregion. Data were collected in 2017 from Wright Canyon (canyon ecosystem) and adjacent slope ecosystems around the canyon (non-canyon ecosystem) at depths ranging between 70 – 240 m. The second research chapter, **chapter 4**, data were collected in 2018, from

60 – 100 m depths in three submarine canyons (Wright, Diepgat, Levens) and their adjacent habitat within iSimangaliso Wetland Park to investigate the diversity patterns and community structure of benthic fish and consider location as a factor.

The systematic review showed that canyon research is still very much in its infancy, however more papers are expected to be published in the future. There were clear location associated biases detected, with more than 90 % of the canyon research being concentrated in the Mediterranean Sea, while only one study was published from South Africa. Most of the reviewed literature focused on invertebrates, with benthic fish (including cartilaginous fish) being the second most studied taxa. A wide range of methods from both fishery-dependent and fishery-independent categories were used to gather the data of benthic fish from the canyons and adjacent areas. With over 8500 submarine canyons mapped globally, the number of submarine canyon research published and the detected location bias is of great concern. More studies are needed in order to understand the role of submarine canyons on adjacent slope habitats

Overall, the results from the research chapters indicated that there were higher abundances in the canyon ecosystem compared to the non-canyon ecosystem. In contrast, evenness and beta-diversity were higher in the non-canyon ecosystem. Relief, bottom type as well as depth played a major role in explaining the observed abundance and diversity patterns. Both evenness and beta-diversity decreased with increase in depth. The canyon and non-canyon also differed in terms of habitat structure. The canyon ecosystem was characterised by patched reef and reef habitats with high relief whereas the non-canyon ecosystem was characterised by flat sand habitats, especially at shallower depths. Additionally, there were clear differences in terms of the fish community structure between the canyon and the non-canyon ecosystem. The heterogeneous and complex habitats of the canyon ecosystem were typified by species such as *Epinephelus poecilonotus, Polysteganus coeruleopunctatus and Chrysoblephus puniceus* in comparison to the less complex habitats outside the canyons that were preferred by species such as *Lagocephalus* *sceleratus*, and *Rhinobatos leucospilus*. The different locations sampled demonstrated that the canyon effect was not consistent at all locations, with varying results detected in the different sample locations.

This research demonstrates that clear differences exists between the benthic fish assemblages associated with canyon and non-canyon ecosystems and provides important information on the role of submarine canyons in the iSimangaliso Wetland Park. From this thesis, it is clear that a 'canyon effect' exists in the continental shelf and shelf edge. The results suggested that heterogeneity of habitats was the most important environmental factor that differed between the canyon and non-canyon ecosystems and these differences in the habitat were driving the observed patterns.

This thesis has provided a reference point, with regards to investigating the role and influence of these canyons on benthic fish assemblages occurring on the continental shelf edge. The information provided by this thesis can ultimately be used in other studies investigating benthic fish assemblages in other submarine canyons within iSimangaliso Wetland Park and the rest of South Africa.

Keywords; Submarine canyons, iSimangaliso Wetland Park, fish, diversity, continental shelf

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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.

CHAPTER 1

1 GENERAL INTRODUCTION

1.1 RATIONALE

Marine ecosystems play an important role in human welfare by providing food security and social, economic and environmental benefits to an increasing human population (Reid et al. 2005). However, many marine ecosystems, and the substantial biodiversity they support, are under increasing threats primarily due to the impact of overfishing, habitat degradation, pollution and climate change (Reid et al. 2005). Continental margin ecosystems are particularly susceptible to these threats because they are located adjacent to the heavily exploited coastal zone (Levin and Dayton 2009).

Continental margin ecosystems include submarine canyons, vertical walls, banks, ridges and seamounts. These habitats exhibit complex topographical heterogeneity, sharp environmental gradients and tectonic activities that combine to create suitable habitat that attracts diverse biological communities (Levin and Dayton 2009). Submarine canyons are sites of enhanced fish biomass and productivity on continental margins and current research indicates that anthropogenic activities such as overfishing impacts their overall ecological condition (De Leo et al. 2012, Fernandez-Arcaya et al. 2017). As such, recent interest has focused on the ecological importance of continental margins ecosystems such as submarine canyons, as they are one of the most widespread topographic features in all our oceans (Harris and Whiteway 2011).

In South Africa, the Delagoa Ecoregion is characterised by a narrow continental shelf that is cut by numerous submarine canyons of varying sizes and depths (Green and Uken 2008). Past research conducted on these canyons has been limited to their geology (Flemming 1980, Ramsay 1994, Green and Uken 2008, Green 2009), studies on the habitats and associated species as part of the search for coelacanths *Latimeria chalumnae* (Heemstra et al. 2006; Ramsay and Miller 2006; Sink et al. 2006) and brief oceanographic studies of some of the canyons (Roberts et al. 2006). Very little research has focused on the ecological functioning of these submarine canyons (Sink et al. 2006, Samaai et al. 2010) and no research has investigated if the canyons play an important role in enhancing local biodiversity. Therefore, it is important to conduct detailed research to improve our knowledge on submarine canyons to help better understand the importance of these canyons for both biodiversity conservation as well as the goods and services they support.

1.2 SUBMARINE CANYON BACKGROUND

Submarine canyons are valleys on the seafloor that are steep-sided and sculpted into the continental slope (Smith and Lindholm 2016). Canyons extend from canyon heads that cut the continental slope to several kilometres down the abyssal (Harris and Whiteway 2011). The distance from the head of a typical submarine canyon to the shore varies with faulting and local sedimentary processes, which places the head of the canyon anywhere from a few meters to over 50 km away from the shore (Lo Iacono et al. 2014). The depth of submarine canyons ranges from 150 m to 6542 m, with a global average of 1992 m, while the slope of a typical canyon wall varies from 2.9° to 23.7°(Harris and Whiteway 2011). The lowermost segment of the canyons tends to have a high concave profile compared to the uppermost segment that intersects the margins (Brothers et al. 2013). The uppermost segment of submarine canyons tend to be the steepest section and is mostly characterised by a linear to barely convex profile (Brothers et al. 2013). Canyons occur worldwide, with at least 5800 submarine canyons recorded globally (Harris and Whiteway 2011).

Due to the complex topographic features of canyons (Shepard and Dill 1966, Harris and Whiteway 2011), submarine canyons are characterized by numerous distinct physical oceanographic processes. The physical oceanographic processes within canyons include upwelling, where deep ocean water and nutrients are brought up onto the shelf (Howatt and Allen 2013) and high turbidity currents, which deposit large amounts of organic matter in the abyssal (Ingels et al. 2011). Additionally, complex topographic features result in accelerated dense-water cascades that increase the deposition of particulate organic matter and sediments from the coastal zones to the deeper regions (Canals et al. 2006). The variety of physical oceanographic processes and the inherent variability in the processes in submarine canyons can lead to the benthos being subject to strong spatial and temporal variability (Sabatés 1990, Danovaro et al. 1999, Ingels et al. 2012, Romano et al. 2013, 2017). Such, spatial and temporal variability is important as it results in high patchiness, which in turn support biodiversity and biological productivity (Vetter and Dayton 1998, De Leo et al. 2010).

1.3 CANYON EFFECT: ENVIRONMENTAL ALTERATIONS AND BIOLOGICAL RESPONSES

Less than 0.7 % of submarine canyons around the world have been studied to assess their effects on faunal diversity and structure (Tyler et al. 2009, McClain and Barry 2010, Vetter et al. 2010, Ingels et al. 2011, De Leo et al. 2012, 2014). However, the work that has been conducted has led to an understanding that an interplay of numerous factors occurring in submarine canyons regulates most, if not all, biological communities within canyons (McClain and Barry 2010). For example, complex currents resulting from upwelling events in canyons, increases the local concentration of particulate organic matter (POM) near the canyon heads, which in turn supports plankton production attracting fish, squid and adult crustaceans (Allen et al. 2001, Bosley et al. 2004). Additionally, unique current patterns along with down flushing events in submarine canyons generate increased nutrients and availability of food which then supports important fishes, suspension and deposit-feeding fauna and invertebrate assemblages (Quattrini et al. 2015). For example, Vetter and Dayton (1999), found that strong tidal currents transported considerable amounts of kelp and macroalgae from the canyon head throughout the Lajolla and Scripps canyons of Southern California. The kelp and macroalgae was then used as food by the residing benthic fauna and eventually resulted in increased richness and abundance of megafauna in the deeper parts of the canyons (Vetter and Dayton 1999).

Furthermore, the interplay of these numerous factors along with the extreme topography creates habitat heterogeneity within submarine canyons (Levin et al. 2010). Complex heterogeneous habitats provide more niches and different ways of exploiting environmental resources, thus increasing species diversity (Kovalenko et al. 2012). Habitat heterogeneity also increases biodiversity by providing spawning grounds (Hoff 2010), and refugia from predation (Vetter 1998). The interplay of these numerous factors within submarine canyons, compared to the adjacent slope habitat, is often referred to as “canyon effects” (Román et al. 2019).

1.4 BENTHIC FISH ASSEMBLAGES

There are many factors that influence the distribution of benthic fish in marine ecosystems. Benthic fish assemblages are often associated with specific benthic habitat types (Nakamura and Sano 2004, Fitzpatrick et al. 2012, Heyns-Veale et al. 2016). For example, a study conducted in Amitori Bay, in Japan reported higher species richness and abundance of fish in the coral area compared to the seagrass bed and sand area (Nakamura and Sano 2004). However, distribution patterns of benthic fish assemblages are not permanent and factors such as ontogenetic shifts in diet and habitat use are often related to depth (Fitzpatrick et al. 2012). As a result, depth is also an important factor that can explain fish assemblage structure in many marine habitats (Gaertner et al. 2013, Götz et al. 2014, Stefanoudis et al. 2019).

Fish assemblages are typically diverse in shallower depths, however, in depths of greater than 100 m, fish diversity tends to decreases with the increase in depth (Fitzpatrick et al. 2012, Zintzen et al. 2012, Götz et al. 2014), and a similar pattern is observed with fish abundance (Fitzpatrick et al. 2012, Zintzen et al. 2012). The distribution of benthos along the oceanic depth gradient is influenced by a number of factors. The alteration in environmental conditions, such as light and temperature with increasing depth, impacts primary production and food availability which in turn is thought to decrease relative fish biomass (Bergstad et al. 2008).

Within submarine canyons, the general trend of benthic fish assemblages along the depth gradient is not always consistent. Some studies have reported higher fish abundances and diversity in the deeper depth stratum (946 – 1100 m), in comparison to shallower depths (214 – 464 m) of the canyon (De Leo et al. 2012). Other studies reported a peak in fish abundance at intermediate depth and upper depth stratum (200 – 400 m) (Wellington et al. 2018). Depth zonation of benthic fish within submarine canyons has been suggested to be a result of the influence of many factors such as habitat complexity and heterogeneity, dissolved oxygen, upwelling and down welling processes (Currie et al. 2012a, De Leo et al. 2012). However, submarine canyons and adjacent slope habitats are difficult and expensive to sample and as such our understanding of submarine canyons and their ecological role to adjacent non-canyon habitats is still limited.

1.5 STUDY AIMS AND THESIS STRUCTURE

Submarine canyons are unique and important features of continental shelves which, through increased productivity, enhance biodiversity and support fisheries. However, the logistical constraints associated with sampling offshore and deep marine environments, means that our knowledge of the benefits of these systems to local biodiversity is limited. Therefore, the aim of this thesis is to generate an understanding of the role of submarine canyons in influencing the benthic fish assemblage structure and diversity at the continental shelf and shelf edge within the high-latitude coral reef ecosystems in the tropical Delagoa Ecoregion of South Africa.

To achieve this aim, fisheries independent surveys, employing baited remote underwater stereo-video systems (stereo-BRUVs), were conducted inside and adjacent to submarine canyons within the iSimangaliso Wetland Park. The data collected were used to answer the following research questions:

- What is the effect of ecosystem type (canyon ecosystem and non-canyon ecosystem) and depth on univariate metrics (abundance, biomass, species richness, Pielou's evenness and beta-diversity) of benthic fish population structure?
- What is the effect of ecosystem type and depth on the fish assemblage structure?
- Are the patterns observed consistent between different but nearby canyons?

In this thesis, these research questions will be addressed in two main research chapters. Each research chapter utilises a separate dataset collected from the same study area, one in 2017 and the other in 2018. However, the datasets differ in terms of the depth range covered (2017 = 70 – 240 m, 2018 = 60 – 100 m) and the replication of sampling localities within the study area (2017 = 1, 2018 = 3).

This thesis consists of five chapters, including chapter 1: **General introduction** and chapter 5: **General discussion**. Each of the remaining chapters (2 - 4) is written as a paper with the intention of submission to peer review journals and can thus be viewed as self-standing. Where methods are duplicated between chapters, the information is only provided in the chapter where the method first appears. Finally, the references cited in each chapter have been combined into a single reference list located at the end of the thesis.

Chapter 1 is the general introduction, which briefly outlines the rationale behind this research, provides background on submarine canyons and benthic fish assemblages and then highlights the main aims of each chapter included in this thesis.

Chapter 2 is a systematic review that will examine the current knowledge on the role of submarine canyons in structuring benthic fish assemblages occurring on continental margins. This review will also outline the trends in canyon research in terms of where the research is being carried out and what is being studied.

Chapter 3, which is the first research chapter, examines the effect of a submarine canyon and depth on benthic fish assemblages occurring on the continental shelf edge of iSimangaliso Wetland Park. This chapter will look at a canyon ecosystem and the adjacent area (non-canyon ecosystem) at a depth ranging from 70 – 240 m.

Chapter 4 is the second research chapter and will examine the differences in benthic fish assemblages between submarine canyons and their adjacent non-canyon habitats. This research chapter will be temporally different (sampled at a different year) from chapter three, and also take into account location (3 canyons and 3 non-canyon habitats) as a factor as there is variability amongst canyons (Harris and Whiteway 2011).

Lastly, **Chapter 5** will be the overall discussion of all the chapters. The chapter will mainly address the overall key findings, give concluding remarks and highlight the research gaps.

CHAPTER 2

2 TRENDS IN RESEARCH AND CURRENT KNOWLEDGE OF THE ROLE OF CANYONS IN STRUCTURING BENTHIC FISH ASSEMBLAGES OCCURRING ON THE CONTINENTAL MARGINS. A SYSTEMATIC REVIEW

2.1 ABSTRACT

Submarine canyons are widespread topographic features that cross continental margins in all oceans. Emerging research is pointing at submarine canyons as being hotspots for biodiversity and productivity. Employing the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) approach, this review documented trends in current literature focussing on “where”, “when”, “what” and “how” the research was carried out. Research on submarine canyons is still in its infancy stage; however, there is clear evidence that they are receiving more scientific attention. This said, there are clear locational biases, with more than 90% of the canyon research being concentrated in the Mediterranean Sea, while only one study was published from South Africa. Most of the published literature investigated the influence of canyons on benthic invertebrates. Benthic fish were the second most studied taxa with a wide range of methods employed to collect the benthic fish. Both extractive (bottom trawls, longline hauls) and non-extractive (diving, remote operated vehicles, baited remote underwater stereo-video systems) methods were used to gather fish data in submarine canyons and these methods have allowed us the knowledge of the role of canyons on fish assemblages. Submarine canyons are considered to be biodiversity hotspots relative to the open slope. This said, locational bias shown by the systematic review is of concern as there are at least 8500 submarine canyons mapped globally. Consequently, more studies are needed in other submarine canyons of the world in order to understand the influence of canyons on the benthic communities.

2.2 INTRODUCTION

Continental margins are complex physiographic, geological and biological environments that can be defined as transition zones between continents and oceans (Violante et al. 2017). One of the most widespread topographic features that cross continental margins in all oceans are the submarine canyons (De Leo et al. 2012). Submarine canyons were first properly defined by Shepard (1963), as “steep-walled, sinuous valleys with V-shaped cross sections, axes sloping outwards as continuously as river-cut land canyons and relief comparable to even the largest of land canyons”. Stated more plainly, submarine canyons are valleys on the seafloor that are steep-sided and sculpted into the continental slope (Smith and Lindholm 2016).

Research on submarine canyons began in the early 1900s (Shepard 1933, 1936, Daly 1936, du Toit 1940), at a time when important geological explorations of submarine canyons took place. The research expanded, and in the late 1960s and early 1970s, speculations began on what effect some of the geological processes such as movements of sediment via the canyon channel may have on the ocean life in canyons (Ross 1968, Rowe 1972). Since then, studies have documented differences in assemblage structure of benthic fauna such as macrofauna, cetaceans and fish between submarine canyons and adjacent slope habitats (Haedrich et al. 1980, Rowe et al. 1982, Houston and Haedrich 1984, Greene et al. 1988).

We now know that there are at least 8500 submarine canyons crossing continental margins globally (Harris et al. 2014). However, patterns of benthic community structure and productivity have been studied in relatively few submarine canyons (Houston and Haedrich 1984, Vetter and Dayton 1998, Sink et al. 2006, De Leo et al. 2010, Miller et al. 2012, Sion et al. 2019). This is primarily due to challenges of sampling within submarine canyons because of their location, steep slopes and rocky topography (Würtz 2012). Locally enhanced currents, as well as occasional down-flushing events within canyon systems add to the difficulties associated with data collection (Huvenne and Davies 2014). In the last few decades, submarine canyons have started gaining more attention because of several technological advances making them more accessible (Huvenne and Davies 2014). Advances in technologies such as Remotely Operated Vehicles (ROVs), submersibles and baited remote underwater stereo-video systems (stereo-BRUVs), have allowed scientist to gain insight about the ecological role of submarine canyons (Yoklavich et al. 2000, Miller et al. 2015, Quattrini et al. 2017, Wellington et al. 2018).

The existing research conducted in submarine canyons around the world has also advanced our understanding of the ecological functioning as well as the biological responses of these topographic features. Canyons are thought to play vital roles in the ocean, such as being the main conduits that connect shelf and coastal waters through the transportation of organic matter, water masses, particles and sediment to the bathyal and abyssal depths (Puig et al. 2014). In most cases, this vital link between bottom nutrient-rich water and coastal waters result in greater productivity which in turn supports greater abundance and biomass of marine species (Vetter and Dayton 1999). Submarine canyons have been found to harbour different and diverse faunal communities of fish, megafauna, corals, as well as other invertebrate species compared to their adjacent slope habitats (Vetter et al. 2010, De Leo et al. 2012, Gunton et al. 2015). Canyons also provide a heterogeneous set of habitats that range from rocky walls to soft sediments (De Leo et al. 2014). Complex heterogeneous habitats, like those provided by submarine canyons, create a greater variety of niches and offer different ways of exploiting the environmental resources thus increasing species diversity (Bazzaz 1975).

However, as important as the submarine canyon environments are, they are still susceptible to various anthropogenic activities and threats. Not only are the canyon heads targeted by fisheries (Puig et al. 2012), but submarine canyons are also threatened by the marine litter and pollution that is transported from the continental shelf to the deep sea (Koenig et al. 2013). Benthic fauna in submarine canyons are also subjected to physical processes that interact with the complex topography. Such processes include intensification of currents, variable intensity of disturbance events and sedimentary disturbances (Duros et al. 2011). Particularly, benthic fish assemblages in submarine canyons are influenced by depth (Domke et al. 2017). Depth may have an influence on the distribution and population structure of different species during their life stages, thus affecting the distribution of biomass and density of specific life stages (Fernandez-Arcaya et al. 2017). For example, a study conducted by Farrugio (2012), found that larger spawning fishes were commonly observed inside the canyon, in comparison to the adjacent open area.

With the growing levels of research interest, the growing knowledge on the importance of submarine canyons in structuring faunal communities and also understanding the increasing threats of human activities on marine ecosystems such as canyons, it is important to assess the recent trends in canyon research. By systematically assessing the current body of research this review will identify key trends (related to publication rates, where the research is being carried out, what aspects of canyons are being investigated, and the methods used) and main research gaps and priorities for future research. Considering this, the aims of this systematic review are to; 1) Examine and outline trends in canyon research, 2) Characterise the study locations, 3) Assess which taxa were investigated by the studies, and 4) focus on where the studies investigating the influence of submarine canyons on benthic fish assemblages are being carried out and identify the methods to survey the fish assemblages.

2.3 METHODS

2.3.1 LITERATURE SEARCH

This systematic review follows the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) method as a guide (Moher et al. 2015). A peer-reviewed literature search was conducted using the SciVerse Scopus (https://www.scopus.com) and Google Scholar (https://scholar.google.com) search engines. The search criteria included any papers, reviews, books and grey literature published between 1990 and the cut-off date 22 October 2018. This was done to "manage" the volume of literature to be reviewed, and also try to review only recent studies in order to obtain the most current knowledge of the role of canyons in structuring benthic assemblages occurring on the continental margins. The searching terms included "submarine canyons" AND "fish" OR "ecological role" OR "diversity" OR "benthic fish assemblages" OR "South Africa" in the title, keywords or abstract and the search was limited to the English language. This resulted in a total of 361 papers, without duplicates, being shortlisted from Scopus and Google Scholar (Figure 2.1). The process of selecting papers that were included in this review started with a screening of titles and abstracts (Figure 2.1). From this selection, literature was excluded if the study:

1. Did not investigate the influence of submarine canyons on marine biota (e.g. the study focussed on sediment transportation and submarine canyon evolution and mapping)
2. Only focused on the influence of submarine canyons on the structure and diversity of pelagic communities.
3. Mentioned "submarine canyons" in terrestrial and freshwater cases
4. Mentioned "submarine canyons" as to support the study area and not to address the ecological role of the canyons on the biota.

After the screening of titles and abstracts, approximately 66% of the literature was excluded with 122 papers advancing to the second selection process, which included a full-text reading. Using the same exclusion criteria (listed above), 57 papers were further excluded and the remaining 65 papers were used for this literature review.

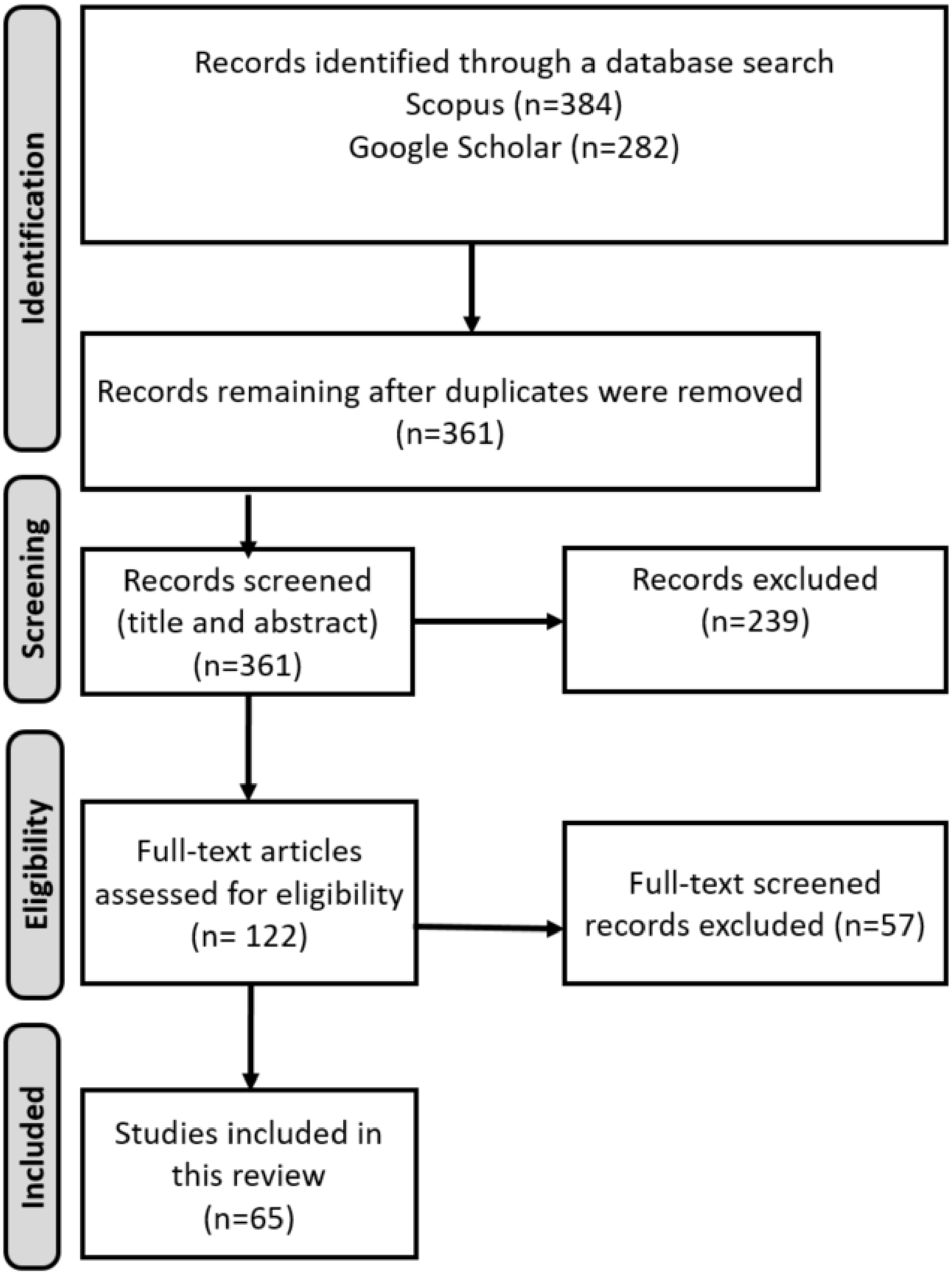


Figure 2.1: Methodology and selection criteria used in this systematic review

2.3.2 DATA ANALYSIS

The literature reviewed was categorised based on the year of publication, location of the study in terms of the global coastal realms and country (Spalding et al. 2007) and according to the different taxa investigated. Studies looking at the influence of canyons on fish (including cartilaginous fish) were further categorised based on their sampling methods, depth range and if the study was conducted during day or night.

2.4 RESULTS

2.4.1 ANNUAL TRENDS IN PUBLISHED LITERATURE

The literature reviewed here was published between 1994 and 2018. However, there were no publications from 1995 to 1997, 2002 to 2003 and 2005 (Figure 2.2). On an annual basis, the number of papers published from 2005 to the present has steadily risen, however, the inter-annual variability remains high (Figure 2.2). Based on the current trend in publications, it is expected that a greater number of papers on the ecological role of submarine canyons will be published in the future.

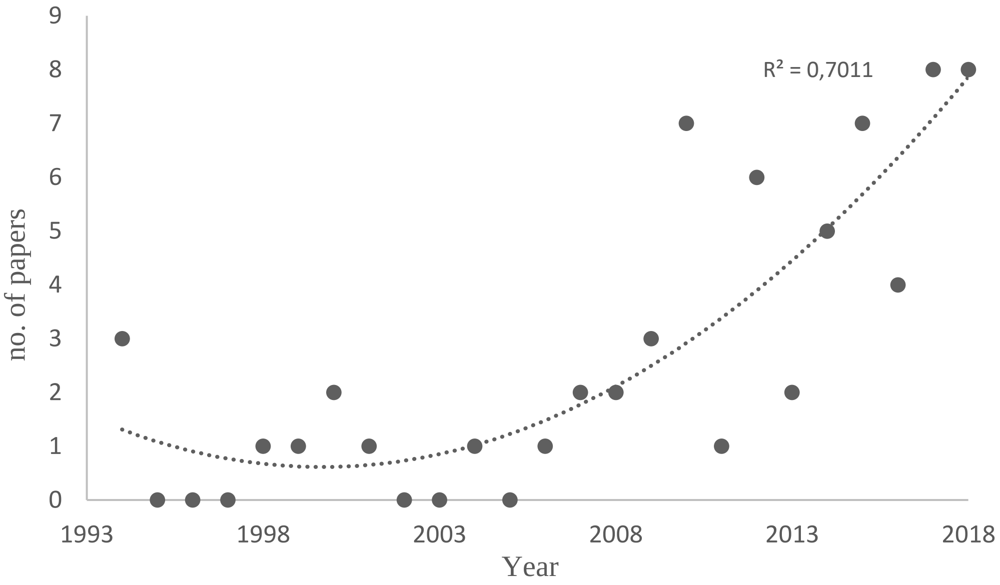


Figure 2.2: Published literature on submarine canyons influence on marine biota from 1994 to 2018

2.4.2 TAXA INVESTIGATED

Of all the literature in this systematic review, 46.8% looked at the influence submarine canyons on invertebrates. Invertebrates included corals, sponges, foraminifera, meiofauna and zooplankton. Only 18.08% of the reviewed literature focused on macrobenthos. Macrobenthos included species such as crustaceans and echinoderms but, in a few cases, also included fishes (Fanelli et al. 2018). Detritus was the least studied, with only 4.25% of the published literature looking at detritus in submarine canyons. Fish (including cartilaginous fish) were the second most studied taxa with 30.85% of the literature published focusing on the influence of submarine canyons on benthic fish assemblages.

2.4.3 GEOGRAPHIC DISTRIBUTION OF RESEARCH

Studies investigating submarine canyon's influence on marine biota were only conducted on three marine biogeographic realms (Spalding et al. 2007). The research from the Temperate Northern Atlantic constituted 94% of the total publications with only 4.76% conducted in Temperate Australasia and 1.19 % in Temperate Southern Africa. In the Temperate Northern Atlantic, studies were more common in the United States, Italy, Spain, France, Canada and the United Kingdom (n = 22, 16, 11, 8, 6 and 6 respectively) with fewer studies in the Netherlands, Germany and Belgium (n = 4, 4 and 2 respectively) (**Error! Reference source not found.**a). Only 4 studies were conducted in Australia (Temperate Australasia) and 1 study in South Africa (Temperate Southern Africa) (**Error! Reference source not found.**a).

2.4.4 BENTHIC FISH ASSEMBLAGES

2.4.4.1 GEOGRAPHIC DISTRIBUTION OF RESEARCH

When the literature investigating the canyon influence on only benthic fish were pulled out from the rest of the reviewed literature, a similar trend was observed where benthic fish assemblages in submarine canyons have been studied in only three biogeographic realms, namely Temperate Northern Atlantic (85.7%), Temperate Southern Africa (4.76%) and Temperate Australasia (9.52%). In the Temperate Northern Atlantic, the studies were most common in the United States (n = 11) and few studies were conducted in Spain, Italy, Canada and France (n = 3, 2, 1 & 1 respectively). In the southern hemisphere, only 1 study was conducted in South Africa (Temperate Southern Africa) and 2 studies in Australia (Temperate Australasia) (Figure 2.3b).

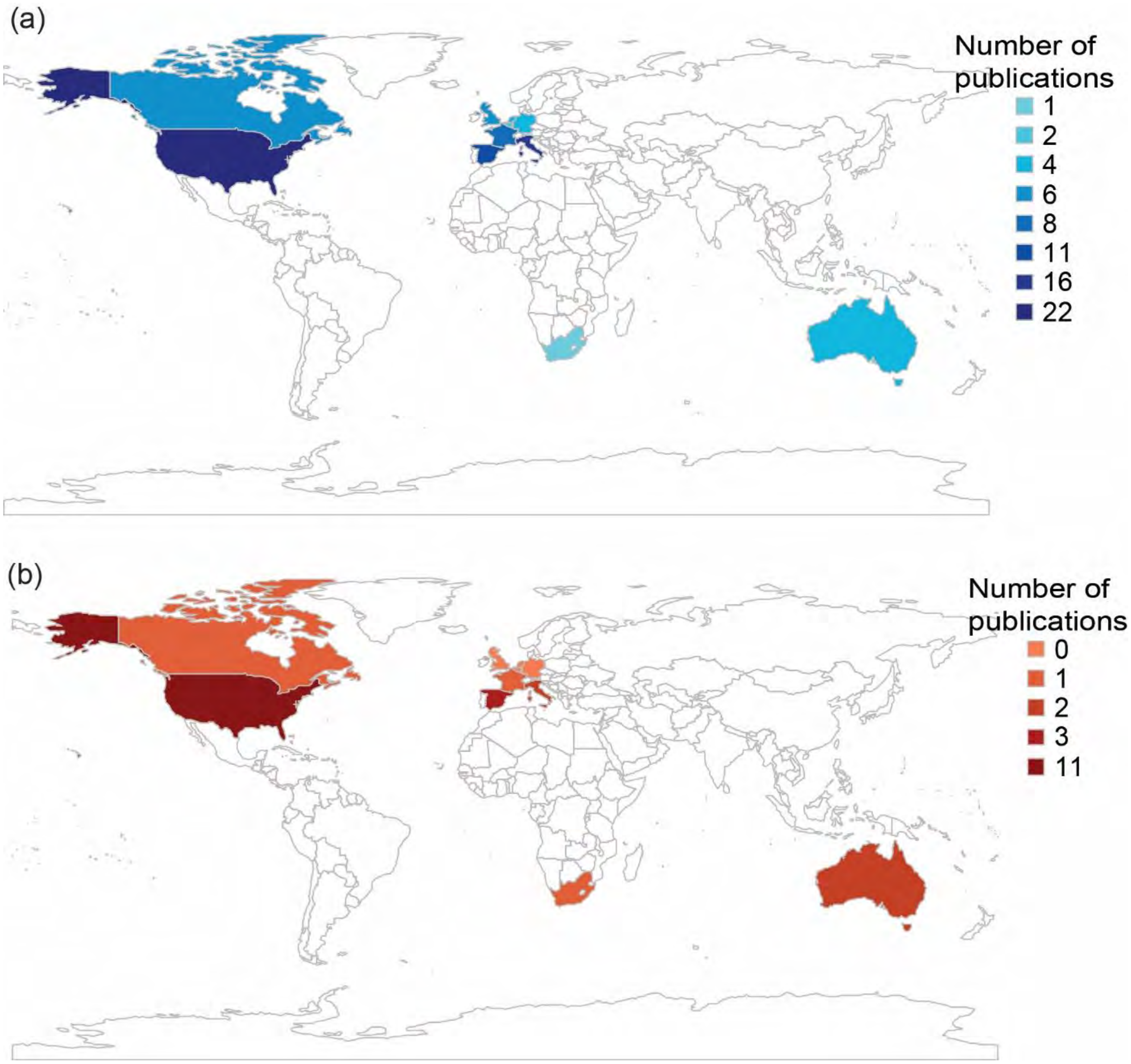


Figure 2.3: Map illustrating **(a)** the location and number of all the reviewed publications investigating the influence of submarine canyons on all the investigated taxa and **(b)** the location and number of literature investigating the influence of submarine canyons on fish assemblages.

2.4.4.2 SUMMARY OF THE RESEARCH METHODOLOGIES

A variety of methods were used to study fish in submarine canyons. For this review, the methodologies used to examine the influence of submarine canyons on benthic fish assemblages were extracted from the 30.85% studies focusing only on the assemblages of benthic fish. From these methodologies, two categories of sampling methods were identified. Category one is considered the non-extractive methods which included Diving, Landers, ROV's, stereo-BRUVs and submersibles. The extractive sampling methods were grouped into Category two and included longline hauls and trawling. Most of the reviewed literature conducted their surveys using bottom trawls (37.93 %) whereas diving, landers and stereo-BRUVs were the least used methods (Table 2.1). All of the surveys were conducted during the day regardless of the method used. The deepest surveys were carried out with an ROV (4060 m) and the shallowest were carried out with stereo-BRUVs (5 m) (Table 2.1)

Table 2.1: List of methods used to gather fish data extracted from the literature published focusing on the influence of submarine canyon on benthic fish assemblages. ROV, Remotely Operated underwater Vehicles; stereo-BRUVs, baited remote underwater stereo-video system.

Methodology	**Time (day or night)**	**Depth range (m)**	**% of published literature**	**Example of publication**
Category 1: Non-extractive				
Diving	Day	75 - 140	3.45	Sink et al., 2006
Landers	Day	443 - 788	3.45	D'Onghia et al., 2015
ROVs	Day	100 - 4060	20.69	Quattrini et al., 2017
stereo-BRUVs	Day	5 - 1000	3.45	Wellington et al., 2018
Submersibles	Day	160 - 700	20.69	Yoklavich et al., 1999
Category 2: Extractive				
Bottom trawls	Day	100 - 2000	37.93	Sabatini et al., 2007
Longline hauls	Day	200 - 635	10.34	Sion et al., 2018

2.5 DISCUSSION

According to Staples and Niazi (2007), a systematic review is a defined and methodical way to assess and analyse published primary studies in order to investigate a specific research question. In this chapter, I conducted a systematic review of literature published between 1990 and 2018 with the aim of investigating the trends in submarine canyon research in terms of when and where the research was carried out, what was investigated by the studies and how the data were collected. In this discussion, I will discuss the key findings of the review and highlight how this research has contributed to our ecological understanding of the role Canyon Ecosystems play for fishes.

Studies on submarine canyons are still highly location and region specific and, at the global scale, the ecological role of canyons is not well understood. This is despite the detailed study of mapping the world's canyons conducted by Harris and Whiteway (2011). Results obtained by this review illustrated that 95% of the reviewed literature was conducted in the Temperate Northern Atlantic (see supplementary Figure A.1), particularly in the Mediterranean Sea (Moranta et al. 2007, Koenig et al. 2013, D'Onghia et al. 2015, Fontanier et al. 2015, Capezzuto et al. 2018). The Mediterranean Sea is home to many submarine canyons (Harris et al. 2014) but these canyons are shorter, more closely spaced as well as very steep when compared to canyons of the rest of the world (Harris and Whiteway 2011). Most of the research carried out in the Mediterranean Sea is in the European sector. Submarine canyon research is concentrated in areas such as the European sector of the Mediterranean Sea as a result of the expensive equipment that is required to explore these ecosystems. This trend is also due to the comprehensive seafloor data that is made available through the European digital database, which is lacking in other parts of the world, for example, Africa (Ceramicola et al. 2015). However, one study was conducted in the Temperate Southern Africa region. Through the African Coelacanth Ecosystem Programme, Sink et al. (2006) looked at the habitats and biodiversity of the submarine canyons at Sodwana Bay in South Africa.

The results from this systematic review showed that most of the studies conducted on submarines canyons looked at the effect of canyons on invertebrates. Not only do invertebrates makeup 99% of all the species of animals on earth, but understanding and acknowledging their role in the marine ecosystems is important as they are at risk from human pressures such as habitat destruction and overfishing (Mather 2013). Additionally, the rapid response and recovery of benthic invertebrates, to natural and anthropogenic disturbances suggest that they can be used as proxy to study the effect of environmental change on aquatics habitats (Gresens et al. 2010, Ingels et al. 2011, Zeppilli et al. 2015).

The second most studied taxa were fish, including elasmobranchs. Fish play major role in their ecosystems and contribute substantially to global food security. A literature review conducted by Holmlund and Hammer (1999), reported the role of fish populations in their ecosystems. They suggested that some of the fundamental ecosystems services provided by fish populations include regulation of food web dynamics, maintaining sediment processes and maintaining genetic, species and ecosystem biodiversity. Fish are also an essential food resource for global human populations and, in many developing countries fish are the main or only source of protein (Holmlund and Hammer 1999, FOA 2000). Not only that, fish are very important economically and are source of income and employment to many developing countries (FAO 2000). Therefore, understanding the importance of different ecosystems in supporting fish population is important, as it will permit appropriate management of these essential resources.

Submarine canyons have been suggested to be beneficial to fisheries as they support high abundances of commercially valuable species (Company et al. 2012). It is thought that the higher abundances are facilitated by the complex habitats related to the high relief and structure forming biota, such as cold-water corals and sponges (Powell et al. 2018). The abundance of demersal fish is also enhanced by the high level of primary production that is a result of canyon-induced upwelling of nutrients (Fernandez-Arcaya et al. 2017).

Despite these important findings, research of submarine canyons to gather fish data still seems limited. Technological advances have made a range of techniques available for studying fish in submarine canyons, however traditional methods are still being used to gather fish data in canyons. Some of the traditional methods include trawling, gillnets and longlines (Stefanescu et al. 1994, Miller et al. 2015). Traditional methods provide a general understanding of fish and the association to their habitats and also provided estimates of species abundance, however, traditional methods like trawls do not capture the fine-scale accuracy that can be captured with modern techniques (Smith and Lindholm 2016). Trawls and nets are also extractive methods that remove biota from the ecosystem and this may limit the type of research that can be conducted using these methods, especially in Marine Protected Areas (MPAs) where rare and threatened species are investigated. Additionally, the impact of these extractive methods on the environment has been documented in many canyons. For example, Würtz (2012), reported that trawl nets and gillnets were mostly responsible for the degradation of the habitats in most canyons of the Mediterranean Sea.

Gathering fish data using imagery-based approaches in the marine environment has been conducted since the late 1900's (Grassle et al. 1975). Unlike the traditional methods, imagery based approaches give more understanding of fish populations in terms of diversity, relative abundance and depth distribution without the removal of species from their natural environments. Some of the non-extractive methods reported in this review included diving, remotely operated vehicles (ROVs), landers and stereo-BRUVs. Underwater Visual Censuses (UVC) by means of SCUBA has become the most used technique to survey and monitor fish assemblages in shallow water ecosystems (Holmes et al. 2013). While SCUBA based UVC in shallow ecosystems has numerous strengths, such as being cost affective and allowing a fast gathering of data (Holmes et al. 2013), these don't necessarily apply to deeper habitats like submarine canyons. No effective SCUBA survey can be undertaken in depths below 30 m, canyon depths are beyond this range therefore alternative techniques need to be evaluated. While SCUBA is not considered to be the optimal method to carry out assessments in canyons, past research has contributed to our understanding of canyon ecosystems (Sink et al. 2006).

To overcome the biases and also survey fish assemblages at depths outside of SUBA diving limits, video-sampling methods are being used to survey fish communities in marine ecosystems (Harvey et al. 2007, 2012, Hill et al. 2014, Ross et al. 2015). Remotely operated vehicles offers a robust survey tool for gathering fish data at a range of depths, including those inaccessible to most SCUBA methods (Sward et al. 2019). Remote operated vehicles have been used to gather fish data in many submarine canyon ecosystems (Ayma et al. 2016, Quattrini and Demopoulos 2016, Quattrini et al. 2017). For example, Ayma et al. (2016), compared ROV and Agassiz trawl methods for sampling deep water fauna of submarine canyons in the Northwestern Mediterranean Sea. These authors provided new insight on the behaviour of benthic fish inhabiting the Northwestern Mediterranean submarine canyons. The ROV performance was proven to be significantly better than trawls to obtain abundance indices for benthic fish and some motile crustaceans (Ayma et al. 2016).

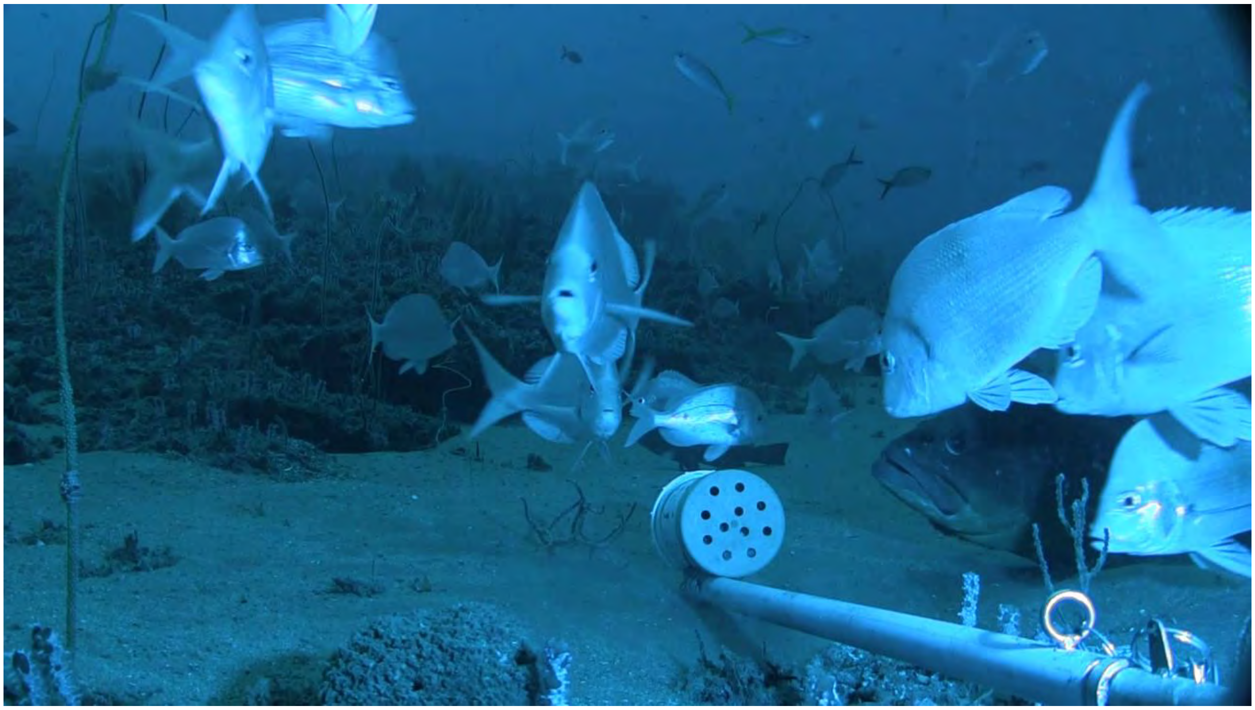
The benthic lander is considered as one of the historical method used to gather scientific data in deep-sea ecosystems (Ewing et al. 1967). Landers are deployed on the seafloor where they gather scientific data until commanded to return/flout to the surface via acoustic command from a ship (Bailey et al. 2007). Past research, employing benthic landers, has contributed to our understanding of the role of canyons in structuring benthic fish assemblages. For example, using a baited lander to explore the composition and behaviour of fish in the Bari Canyon, D'Onghia et al. (2015), recorded the first in situ documentation of fish fauna in this canyon ecosystem and concluded that their data suggest that the Bari Canyon could act as a refuge area for species that are vulnerable to fishing on the open slope. As most video sampling methods, benthic landers have some disadvantages like being highly selective as they only attract scavenging fish when baited (D'Onghia et al. 2015).

On the other hand, baited remote underwater stereo-video systems (stereo-BRUVs), are increasingly being employed over other sampling methodologies (Mallet 2014). Besides the advantage of being deployed in depths inaccessible to divers, stereo-BRUVs can be used in areas of high currents with the aid of additional weight to the system (Langlois et al. 2018) and most importantly in habitats with complex topographic features (Willis and Babcock 2000), such as submarine canyons (Hill et al. 2014, Wellington et al. 2018). Baited remote underwater stereo-video systems also record assemblages of a wide range of large and mobile species as well as species that are usually targeted by fisheries (Colton and Swearer 2010).

The importance of canyon ecosystems is now recognised in the scientific community and there is a growing level of research activity. Our overall results indicate a clear locational bias of existing research to the more developed countries in the Northern Hemisphere. This is of particular concern, as there are over 8500 active submarine canyons globally and greater effort should be placed in different geographic regions. A priority is to also expand on the taxa being investigated in submarine canyons, for example, more studies on fish assemblages should be conducted especially with the increase of overfishing in most parts of the world. Even though extractive methods are still being used to study fauna in these ecosystems, it is clear that remote methods are advancing research in this field. Importantly, researchers should aim to develop standardised best practices for the remote video sampling methods so that data from different projects and locations are comparable. While it is encouraging to see an increase in the output of canyon related research, there are still many knowledge gaps and there is still a need to better understand the effect that canyons have on the assemblage structure of fishes, and other biota, as well as the potential impact of anthropogenic threats on these ecosystems.

CHAPTER 3

3 THE EFFECT OF ECOSYSTEM AND DEPTH ON THE DIVERSITY AND STRUCTURE OF BENTHIC FISH ASSEMBLAGES FOUND IN WRIGHT CANYON, SOUTH AFRICA



Cover photo: Wright Canyon (70 m)

3.1 ABSTRACT

This research chapter investigated the effect of ecosystem (canyon and non-canyon) and depth on the diversity and structure of benthic fish assemblages found in Wright Canyon within the iSimangaliso Wetland Park. Using baited remote underwater stereo-video systems (stereo-BRUVs), fish assemblages were sampled from inside Wright Canyon and slope around the canyon at depths ranging between 70 and 240 m. Generalised Additive Models indicated a significant effect of ecosystem on total abundance, evenness and beta-diversity, with higher abundance and lower evenness and beta-diversity recorded in the canyon ecosystem, relative to the non-canyon ecosystems. Depth had a significant effect on the abundance, biomass, richness, evenness and beta-diversity in the non-canyon ecosystem, and only species richness and beta-diversity decreased significantly with depth in the canyon ecosystem. When considering the interaction between depth and ecosystem type, the effect of ecosystem on fish abundance was restricted to the shallow water samples (< 120 m), with higher fish abundance inside the canyon, while the effect of ecosystem on biomass and beta-diversity was strongest in the deeper water samples (>180 m). Species richness decreased with increasing depth in both ecosystems and beta-diversity showed a high species turnover on the shallower (70 to 100 m) and deeper (220 to 240 m) samples but low turnover in from depths of about 120 to 200 m. Similarly, multivariate analyses also revealed an effect of depth and ecosystem on the fish assemblage structure. Fish assemblages in the canyon and non-canyon ecosystem differed significantly where the canyon ecosystem was typified by patched reef and high relief whereas the non-canyon ecosystem was typified by flat sandy habitat. Overall, relief and depth were drivers of the difference in assemblage structure. These results highlight the influence of submarine canyons in structuring the benthic fish assemblages of Wright Canyon in the iSimangaliso Wetland Park.

3.2 INTRODUCTION

The fish communities in the shallow habitats of the iSimangaliso Wetland Park (IWP) have been well studied (Chater et al. 1995, Currie et al. 2012b, Floros et al. 2012, 2013). In contrast, there is very little research on the fish communities over the greater part of the offshore continental shelf of the IWP (Heemstra et al. 2006, Sink et al. 2006). However, several studies on the marine geology of the continental shelf on the east coast of South Africa has been published (Flemming 1980, Ramsay 1994, Ramsay and Miller 2006, Green and Uken 2008, Green 2009). Much of the continental shelf of the east coast is characterised by a steep slope and is found to be very narrow relative to the rest of the South African coastline (Flemming 1980). Specifically, the coastal plain of northern KwaZulu-Natal (KZN) is recognised for its steep and narrow shelf that is cut by numerous submarine canyons of varying sizes and depths (Flemming 1980, Ramsay 1994, Green and Uken 2008). The submarine canyons are situated within the IWP which is a Marine Protecting Area (MPA) protecting 78 km of the coastline of the northern KZN coast. The submarine canyons of IWP are oriented perpendicularly to the shoreline, cut the shelf at depths of 90 to 110 m and extend down a hundred kilometers to the bottom (Ramsay and Miller 2006, Sink et al. 2006). The very rugose heads emerge relatively close inshore, which suggests that the ecological role of these submarine canyons may be important not only to the deep-sea environment but also to the adjacent inshore areas.

The marine life within the submarine canyons of IWP received little scientific attention until the discovery of the coelacanths *Latimeria chalumnae* in the early 2000s (Venter et al. 2000). Since then, research interest in the oceanography and ecology of the area has grown (Roberts et al. 2006, Sink et al. 2006, Samaai et al. 2010). The main oceanographic feature of the IWP is the Agulhas current (Lutjeharms et al. 2001). The Agulhas current is warm, fast, strong and flows southwards, transporting warm tropical and sub-tropical waters and fauna (Beckley 2000, Beckley and Leis 2000). The oceanic environment of the canyons is characterised by strong currents. However, within the canyons, the currents may decrease significantly and in some places, there is little or no flow (Hissmann et al. 2006, Roberts et al. 2006). Roberts et al. (2006), observed down welling, upwelling and ripples on the canyon floor giving rise to a considerable variation on current flow within the canyons. There is also a high variability in temperature within the canyons. Depending on seasons, the temperature usually ranges between 15 to 27°C (Roberts et al. 2006).

Besides being home to coelacanths, submarine canyons of the IWP support distinct and diverse invertebrates that in turn support the vertebrates found within the canyons (Sink et al. 2006, Samaai et al. 2010). Most importantly, the canyon margins protect a variety of commercially important linefish species of the Sparidae, Serranidae and Lutjanidae families (Heemstra et al. 2006, Sink et al. 2006) as well as abundances of fish species that are rare and absent from the inshore ecosystem (Floros et al. 2012). These few studies conducted in the submarine canyons of the IWP have emphasised the uniqueness of these ecosystems in an otherwise quite sparse environment. There is still, however, a lack of knowledge on the influence and role of these canyons on the slope ecosystems.

It is then imperative to understand the influence of the submarine canyons of IWP on the local benthic fish assemblage structure and diversity. As a result, the aim of this study was to investigate the effect of ecosystem (canyon and non-canyon) and depth on the diversity and structure of benthic fish assemblages in Wright Canyon, South Africa. I hypothesised that there will be higher abundance, biomass and species richness in the canyon ecosystem because the canyon ecosystem is associated with greater topographical complexity which can positively impact these response variables (McClain and Barry 2010, De Leo et al. 2012). I expected to observe a difference in the fish assemblage structure between the canyon and non-canyon ecosystem due to environmental drivers including habitat complexity (relief) and habitat heterogeneity (bottom type).

3.3 MATERIALS AND METHODS

3.3.1 STUDY SITE

The video footage used in this study was collected from the Wright Canyon and the slope around the canyon (Figure 3.1) at depths ranging between 70 and 240 m. The Wright Canyon is located in the northern KwaZulu-Natal and forms part of the 23 mapped submarine canyons of the IWP (Ramsay and Miller 2006). Wright Canyon is the largest and most mature canyon in IWP (Ramsay and Miller 2006), with high rugose walls, many caves and overhangs that fall steeply towards the sediment-filled bottom (~700 m), which at its largest spans 2.2 km (Sink et al. 2006). Wright Canyon breaches the shelf edge at only about 2 km offshore and the canyon head is much closer to the shore (~ 40 m) compared to other canyons in the region (Ramsay and Miller 2006). The shelf habitat around the canyon is usually characterised by low profile sandy bottoms which progresivly become more reef dominated as you move closer to the shelf edge and slope.

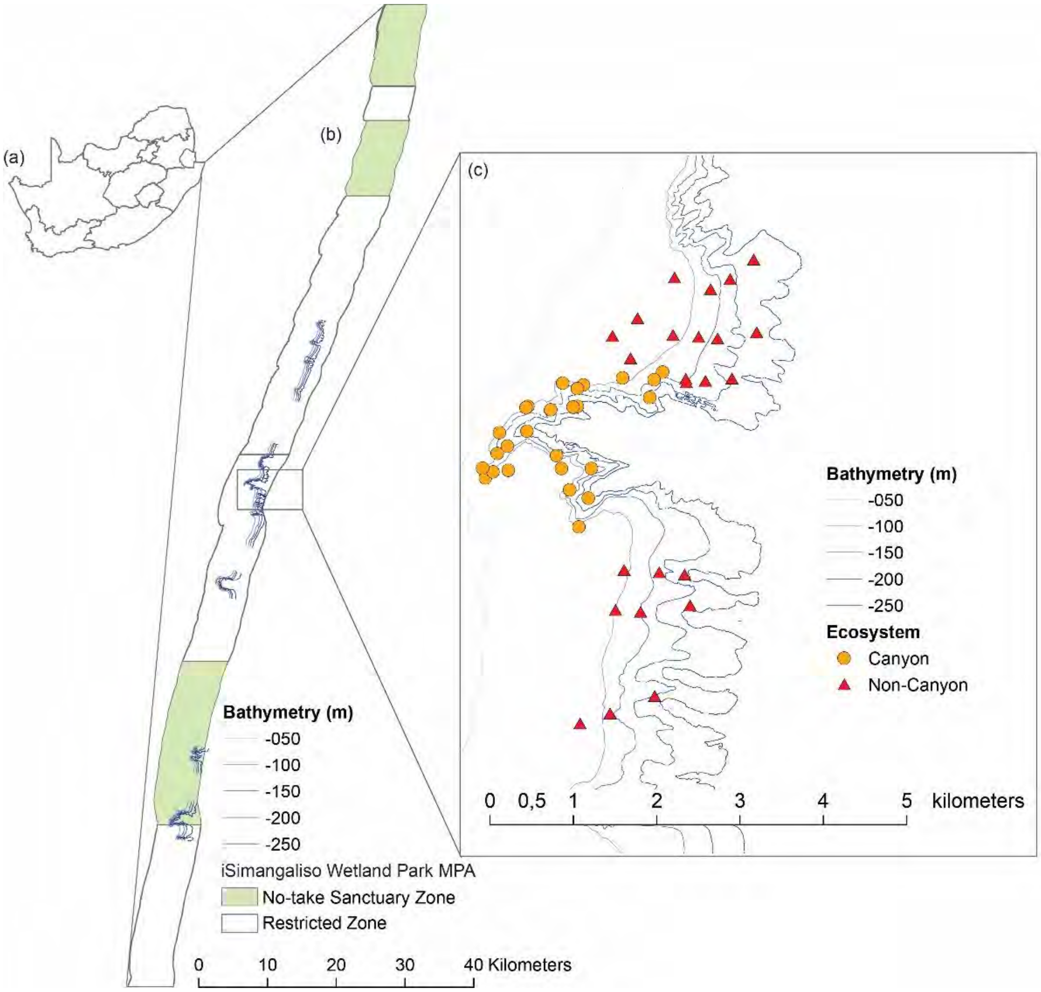


Figure 3.1: Map of study area. **(a)** Map of South Africa indicating the position of iSimangaliso Wetland Park Marine Protected Area, **(b)** location of Wright Canyon ecosystem and adjacent non-canyon ecosystem within the park, and **(c)** sampling locations of baited remote underwater stereo-video systems from the Wright canyon (yellow dot) and adjacent non-canyon (red triangle) ecosystems.

3.3.2 SAMPLING TECHNIQUE

Sampling was conducted using three baited remote underwater stereo-video systems (Stereo-BRUVs) (Figure 3.2), following the design of Harvey et al. (2012). Each system comprised two high-definition (1920 x 1080 pixels) video cameras within waterproof housings. Each housing was securely attached to a base bar, in a way that eliminated any potential movement, 0.7 m apart with an inward convergence angle of

8°, to gain an optimised overlapping field of view (FOV) (Watson et al. 2007, 2010, Harvey et al. 2012, Langlois et al. 2012). A blue LED light was mounted in the middle of the basebar to illuminate the area with a radius of approximately 5m within the FOV of the cameras. Blue colour was chosen as it travels furthest underwater and is thought to reduce behavioural biases in fishes (Fitzpatrick et al. 2013). The base bar was then mounted within a protective stainless steel frame that could be fitted with additional ballast to allow sampling in high current environments (Figure 3.2). The stereo-BRUVs were attached surface marker buoys using 4mm Dyneema GP12 rope to reduce drag on the systems. The rope length varied according to the water depth, but was always greater than twice the water depth in low current (< 1.5 knots) conditions and three times the water depth in high current (> 1.5 knots) conditions. Sampling was aborted when the water currents were greater than three knots. The stereo-BRUVs were baited with 1 - 0.8 kg of crushed sardines (*Sadinops sagax*) with an arm holding the bait within the cameras FOV and 1.5 m away from the system (Watson et al. 2010, Langlois et al. 2012).

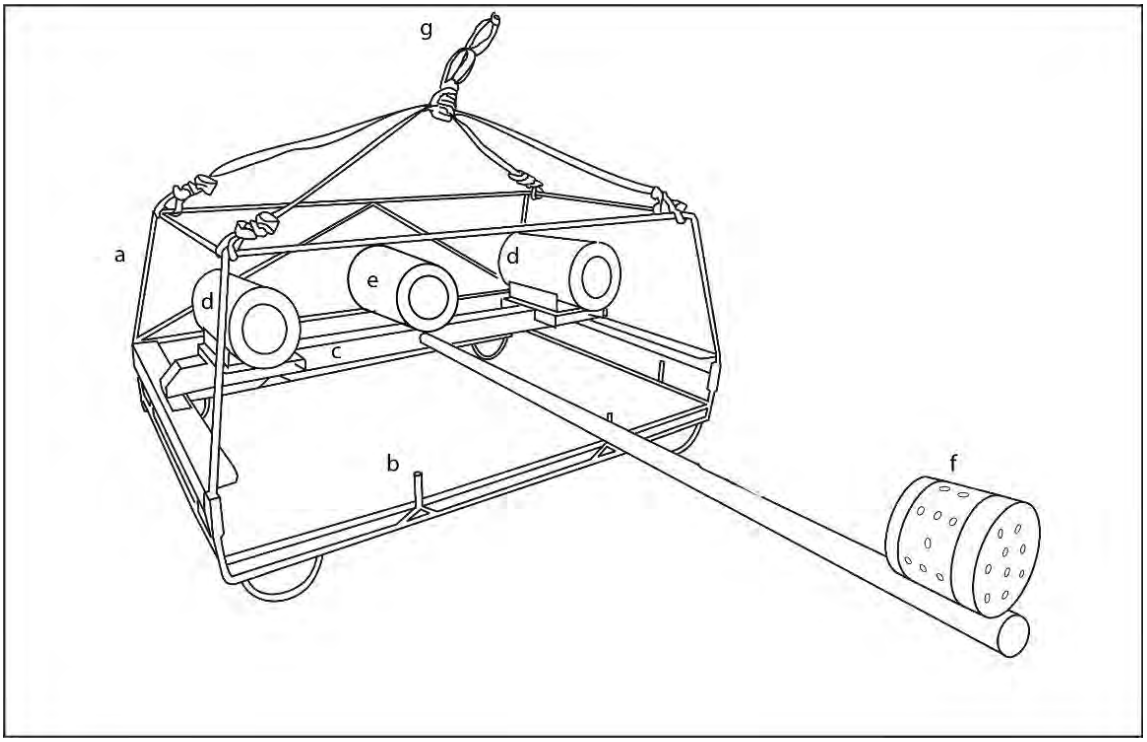


Figure 3.2: A schematic diagram of a baited remote underwater stereo-video system (stereo-BRUVs) showing a protective stainless steel frame **(a)** with pins to mount additional weights **(b)** and a base bar **(c)** that holds the housed high-definition video cameras **(d)** and blue LED light **(e)**. Extending perpendicular from the base bar is an arm that holds the bait canister **(f)** within the camera's Field of View. The system is linked to the surface by a buoy and rope system that attaches to the stainless steel frame **(g)**.

The use of stereo-video allowed for accurate length measurements when an individual fish was visible in the FOV of both cameras (Harvey et al. 2002). Prior to, and after the sample collection, each stereo-BRUVs was calibrated using a SeaGIS calibration cube and CAL software (the calibration procedure can be viewed in Harvey et al. 1996, Harvey and Shortis 1998). The generated calibration files were then used in the analysis to generate accurate length measurements of sighted fish species.

Sampling followed a stratified random approach. Strata included ecosystem type (Levels: canyon and non-canyon) and water depth (Levels: 70-120 m, 120-180 m, 180-240 m). Within the non-canyon ecosystem, samples were haphazardly distributed along transects to the north and south of the canyon. Within the canyon, stereo-BRUVs were deployed at randomly selected sites within each of the depth zones. As far as possible, all adjacent samples were separated by a minimum of 500 m. However, due to the steep nature of the canyon and slope, and the small size of the canyon ecosystem, this was not always possible. In these instances, adjacent samples, < 500 m apart, were collected of separate days or when the change in water depth between adjacent samples was greater than 30 m.

Each stereo-BRUVs was deployed off an 8.5 m rigid hulled inflatable boat and left to record on the seafloor for a minimum period of one hour (Watson, 2006). A total of 50 stereo-BRUVs deployments were collected (24 deployments in non-canyon ecosystem and 26 deployments in canyon ecosystem).

3.3.3 VIDEO ANALYSIS

Video samples were analysed using the EventMeasure (Stereo) software package (www.SeaGIS.com.au). Analysis of the video footage commenced after the system landed on the seafloor and the debris settled and continued for a period of one hour. Species were identified to the lowest taxonomic level. For each species identified, abundance was estimated at the maximum number of individuals sighted at one time (i.e., in one frame) (MaxN) (Cappo et al. 2004). MaxN has been found to be the conservative estimator of the relative abundance of species (Willis and Babcock 2000), but avoids replication of counts of individuals swimming in an out of the FOV of the cameras throughout the video analysis (Willis et al. 2003). Fork length measurements were measured at the time of MaxN. The length measurements were then used to calculate the weight of each individual fish species using the standard allometric length-weight relationship ($W = a \times L^b$) (De Robertis and Williams 2008), where a and b are constants for individual fish species found in FishBase (Froese and Pauly 2000) and L is the measured length. The individual weights were then summed for each species to obtain an estimate of biomass.

3.3.4 ESTIMATING COVARIATES

The following covariates were included in the models: habitat, average relief, water column (%), underwater visibility (m), obstruction (%), temperature (°C) and depth (m). Water column, underwater visibility and obstruction were included to account for differences in the field of view between samples. Visibility was estimated using Event Measure, by making a 3D point on an object at the edge of the visible distance that could be accurately identified from both cameras. Obstruction and water column were estimated from a still image of the FOV for each sample using the Vidana software package (www.marinespatialecologylab.org). For water column, the percentage of the visible water column, as opposed to the visible habitat, was measured. Obstruction was classified as anything in-between the camera and bait container that blocks a portion of the FOV and was measured following the same approach as water column. Habitat was classified into one of six categories which included (1) reef [only reef in the FOV], (2) patch-reef [a mixture of reef and sand in the FOV], (3) sand-inundated reef [reef covered with a thin veneer of sand], (4) sand [only sand in the FOV], (5) sand with cobbles [mixture of sand with larger cobbles/stones in the FOV] and (6) sand with sea pens [sand habitat with numerous sea pens]. The complexity of the habitat (relief, Wilson et al. 2007) was further measured using the Transect Measure software package (www.SeaGIS.com.au). The approach of measuring relief using Transect Measure employed a 5 x 4 (n = 20) grid overlaid onto a still image taken either at the beginning or end of each stereo-BRUVs sample, following the method of Collins et al. (2017). In each of the grid-cells, that included a portion of the seafloor, relief was estimated from 0 to 5 with 0 being no slope and 5 being large vertical walls (Wilson et al. 2007). Relief was then averaged to obtain a representative measure of relief for the sample. Average temperature data were obtained from Onset HOBO temperature loggers attached to each stereo-BRUVs and water depth was measured by the boat's echo-sounder.

3.3.5 STATISTICAL ANALYSIS

3.3.5.1 UNIVARIATE ANALYSIS

Univariate analyses were conducted with generalised additive models (GAMs) in R (R core team 2019), via the R-studio interface (R Studio Team 2019), using the MGCV package (Wood 2019). Prior to the GAM analysis, an unpaired two-sample Wilcoxon test (Wilcoxon 1945), was conducted to compare environmental parameters (*average relief*, *depth*, *temperature*, *visibility*, *water column* and *obstruction*) between the canyon and non-canyon ecosystem. The unpaired two-sample Wilcoxon test (also known as Wilcoxon rank sum test or Mann-Whitney test) is a non-parametric alternative to the unpaired two-sample t-test, which can be used to compare two independent groups of samples (Jacobi and Langevin 1996).

Generalised additive models are a semi-parametric extension of Generalised Linear Models (GLMs), that use smooth functions to model the effect of covariates on the data without assuming the parametric form of the relationship prior to the analysis, thus making them useful to model the non-linear response of the data to covariates (Wood and Augustin 2002). In this chapter, GAMs were chosen as exploratory data analysis revealed that the response variables had non-linear relationships with many of the continuous covariates included in the models (Zuur et al. 2013). Generalised additive models were used to test for the effect of *ecosystem*, *depth* and selected covariates (see section 3.3.4) on total abundance (sum of the MaxN for all species recorded in a single stereo-BRUVs sample), total biomass (sum of all mass of all fish measured in a single stereo-BRUVs sample) and the diversity indices which included species richness, Pielou's evenness index, and beta-diversity. The three different diversity indices modelled, measures a different component of species diversity. Species richness referred to the total number of species in the samples whereas evenness includes the abundances of the different species and is a measure of how close in numbers each species was in the samples (Vyas et al. 2012). Specifically, Pielou's evenness index was calculated using PRIMER v7 (Clarke and Warwick 2001). The value of Pielou's evenness ranges from 0 to

1 with larger values representing more even distribution in abundance among species (Pielou 1966). Lastly, beta-diversity was calculated using permutational analysis of multivariate dispersions in PRIMER (PERMDISP: Anderson 2006) and here considered to be an indication of species turnover and measured as the variation in species composition within each ecosystem.

Prior to constructing the models, the data were thoroughly explored to examine collinearity among the covariates (protocol can be viewed in Zuur et al. 2010). *Temperature* and *habitat* revealed a high correlation ($R > 0.7$) with *depth* and average *relief,* respectively, and were thus excluded from the models. *Percentage obstruction* was also excluded from the models as obstruction was limited to three samples and it had no discernible effects on the modelled response variables. For all GAMs, tensor product smooth terms (te), with the thin-plate regression splines basis-penalty (bs = tp) were used for the effects of the continuous covariates. *Ecosystem* was included as a parametric coefficient (Wood 2019). The GAMs were specified to allow for the effect of *depth* on the response variable to be modelled within each level of *ecosystem*, using the “by” function. The full GAM was specified as:

y = te(Visibility, k = 5, bs = "tp") + te(Water column, k = 4, bs = "tp") + te(Average relief, bs = "tp") + te(Depth, by = Ecosystem, bs = "tp") + Ecosystem Eq 3.1

where y represents the given response variable and k is the dimension of the basis used to represent the smooth term.

Different families of error distributions were used to model the response variables. Species richness was modelled using the Poisson distribution whereas abundance (MaxN) was modelled with a negative binomial distribution, to account for over-dispersion of the data (Zuur et al. 2013). Biomass, Pielou’s evenness, and beta-diversity were all modelled with Tweedie distribution for a case of $1 < p < 2$ (where $p = 1$ is a generalisation of a Poisson distribution and $p = 2$ is a gamma distribution) (Wood 2019). Model validation included assessment of residuals for spatial autocorrelation, and for patterns when plotted against the fitted values and covariates. To test for spatial autocorrelation, variograms were constructed with the model residuals, and all tests showed no evidence for spatial dependence within the dataset. For all models, the residuals showed no marked patterns and had an even distribution around zero, when plotted against the fitted values and the different explanatory variables. Wald's tests were carried out to test the significance of the explanatory variables included in each GAM (Wood 2011). Prediction plots from the GAM coefficients were generated to visualise the predicted patterns in the response variables in relation to (i) *ecosystem* and (ii) *depth* within *ecosystem*. Two types of prediction datasets were generated. To separate the effects of the continuous covariates from ecosystem, the predicted dataset for the effect of ecosystem were generated using standardised values (mean) for each covariate. To visualise the effect of depth within each ecosystem, while maintaining key ecosystem specific environmental traits, the data were predicted using the ecosystem specific mean value of average relief and the overall mean values for the remaining continuous covariates. Graphs of the predicted values from the model coefficients were created using ggplot2 (Wickham 2017).

3.3.5.2 MULTIVARIATE ANALYSIS

The multivariate analyses of the relative abundance (MaxN) and relative biomass were conducted using the statistical package PRIMER-E v7 (Clarke and Gorley 2015) with PERMANOVA+ add on (Anderson et al. 2008). Prior to transformation, shade plots of different levels of transformations were employed to aid the choice of the appropriate transformation (Clarke et al. 2014). Following this, the data were fourth-root transformed, to reduce the importance of the very abundant species and take the less common species into account (Clarke and Warwick 2001). A sequential permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis similarity index was used to test the hypothesis that benthic fish assemblages differed between ecosystems. The continuous covariates were fitted first, followed by the main factor *ecosystem* (fixed: canyon vs non-canyon). Prior to the analysis, the existence of highly correlated covariates was assessed using a draftsman plot (Clarke and Gorley 2015). *Temperature* was highly correlated with *depth* (r = 0.9). As a result *temperature* was excluded from the analysis. Additionally, *Percentage obstruction* was also excluded from the analysis as obstruction was limited to only three samples. *Habitat type* was also excluded from the analysis but rather overlaid as vectors on the Principal Coordinate Analysis (PCO). The model included interaction terms to determine if the effect of *average relief* and *depth* were consistent between the levels of *ecosystem*. The analysis was based on type I sum of squares using 9999 permutations under a reduced model (Anderson et al. 2008). Principal Coordinate Analysis was used to visualise the output given in PERMANOVA. Vector lines (Pearson's correlation coefficient, ≥ 0.4) for species and explanatory variable were overlaid onto the PCO to aid with the interpretation of the PCO output. Similarity percentages (SIMPER) for both abundance and biomass data were calculated to determine which fish species contributed most to within-group similarity and between-group dissimilarity within each ecosystem type (Clarke and Warwick 2001).

3.4 RESULTS

3.4.1 COMPARISON OF ENVIRONMENTAL PARAMETERS

Average relief was significantly (W = 478.5, p<0.01) greater in the canyon ecosystem (2.4 ± 1.1), compared to the non-canyon ecosystem (1.6 ± 1.0) (Table 3.1). For the remainder of the covariates measured, there was no significant (p>0.3, in all cases) effect of *ecosystem* on their values (Table 3.1).

Table 3.1: Mean and standard deviation (SD) for the continuous covariates measured in the canyon and non-canyon ecosystems and the results from unpaired two-sample Wilcoxon test comparing the continuous covariates between canyon and non-canyon ecosystem.

	Canyon		**Non canyon**				
Covariate	**Mean**	**SD**	**Mean**	**SD**	**W-value**	**p-Value**	
Average relief	2.4	1.1	1.6	1.0	478.5	<0.01	**
Depth	130.3	50.5	144.4	55.4	270	0.42	
Temperature	18.4	2.8	18.0	3.0	343	0.55	
Visibility	4.4	0.9	4.2	0.8	355.5	0.38	
Water column	55.4	23.6	56.0	13.6	321.5	0.86	
Obstruction	1.2	5.9	1.7	5.8	299	0.55	

P-value: 0 ‘***’, 0.001 ‘**’, 0.01 ‘*’, 0.05 ‘.’, 0.1 ‘ ’

The higher average relief recorded in the canyon ecosystem was driven by a greater proportion of reef habitats (n = 19) sampled, in comparison to the non-canyon ecosystem (n = 7) (Table 3.2). The sand habitat with fields of sea pens was unique to the canyon ecosystem (Table 3.2).

Table 3.2: Distribution of sampling effort (N) among the different habitat types and between the different ecosystems. The mean and standard deviation (SD) relief is provided for each habitat.

		Canyon			**Non-canyon**	
Habitat	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**
Patch-reef	9	2.9	0.8	3	2.8	0.3215
Reef	7	3.3	0.8	3	3.4	1.4012
Sand	3	1.1	0.1	14	1.0	0.1393
Sand inundated reef	3	2.4	0.6	1	1.3	-
Sand with cobbles	1	1.2	-	3	1.1	0.1732
Sand with sea pens	3	1.1	0.2	0	-	-

3.4.2 UNIVARIATE ANALYSIS

3.4.2.1 TOTAL ABUNDANCE

The GAM for the total abundance data explained 59.3% deviance. Results from the Wald's test, indicated that *visibility* and *average relief* had a significant effect on total abundance (Table 3.3). *Ecosystem* had a significant effect on total abundance (Table 3.3), with more fish recorded in the canyon ecosystem (mean ± standard deviation total MaxN/sample: 35.5 ± 18), in comparison to the non-canyon ecosystem (18.3 ± 17.1). However, the GAM predicted plots, based on standardised continuous covariates, indicated considerable overlap in confidence intervals between the two ecosystems (Figure 3.3a). *Depth* had a significant effect on abundance in the non-canyon ecosystem and no effect in the canyon ecosystem (Table 3.3). The GAM predicted plot, based on standardised values for *visibility*, *temperature*, *water column* and *obstruction*, and with *average relief* set for the *ecosystem* type average (Table 3.1), depicted an increase in abundance at mid-depths (160 m) in the non-canyon ecosystem (Figure 3.4a). When compared between the two ecosystems, a significant difference in abundance in the shallower depths was observed, but as depth increased, no difference was detected (Figure 3.4a).

Table 3.3: Results from the Wald's test run on the generalised additive models (GAMs) investigating patterns in total abundance from the study area. df = degrees of freedom; edf = estimated degrees of freedom.

Parametric Terms:	**df**	**Chi.sq**	**p-value**	
Ecosystem	1.00	6.03	0.014	*
Smooth Terms:	**edf**	**Chi.sq**	**p-value**	
te(Visibility)	4.00	5.70	0.008	**
te(Water column)	3.00	0.00	0.94	
te(Average relief)	4.00	16.7	<0.001	***
te(Depth): Canyon	4.00	2.39	0.063	.
te(Depth): Non-canyon	4.00	5.28	0.014	*

P-value: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' '

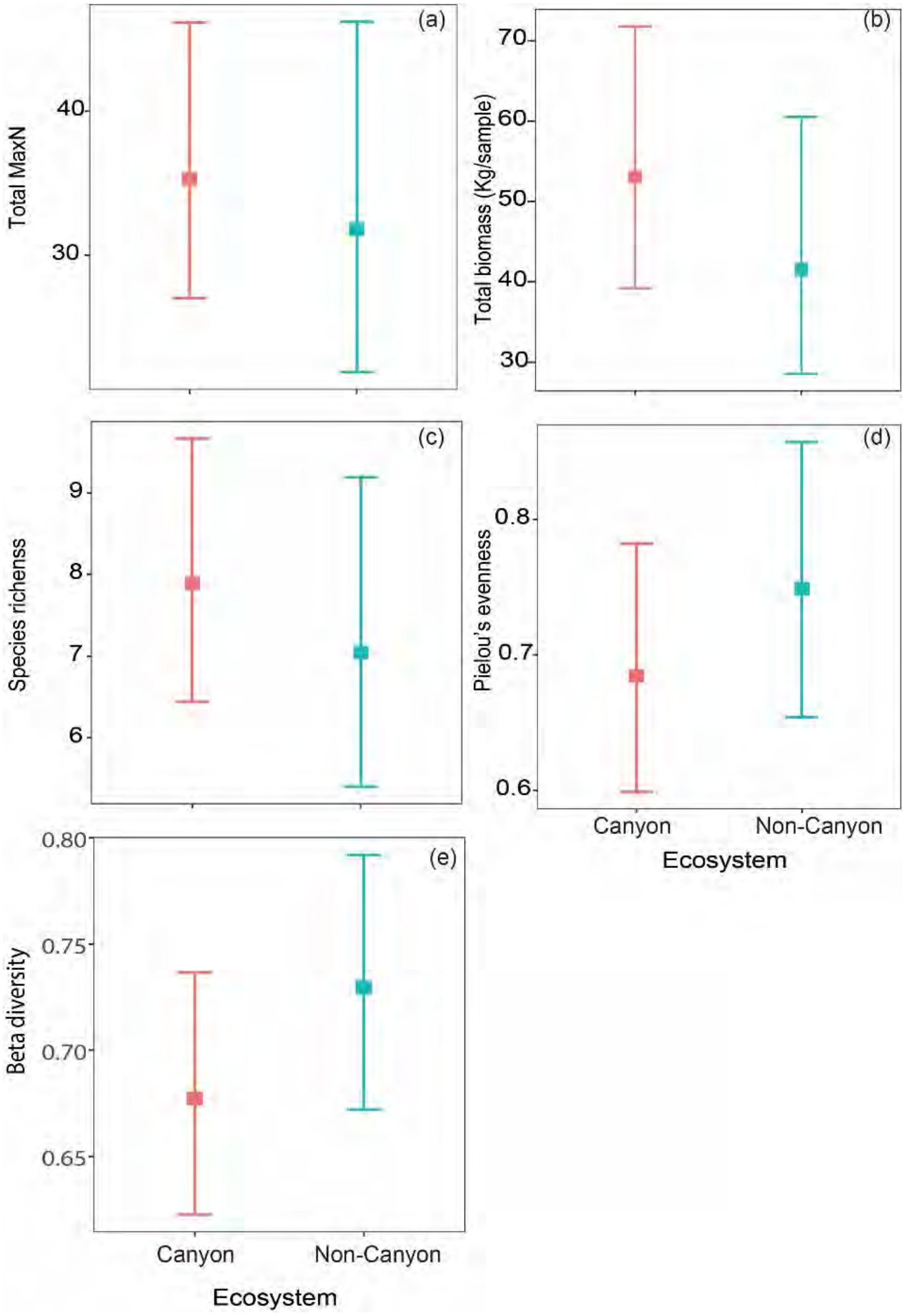


Figure 3.3: Relationship between predicted **(a)** total abundance (MaxN), **(b)** biomass (Kg/sample), **(c)** species richness, **(d)** Pielou's evenness, **(e)** beta-diversity and *ecosystem.* Predictions are based on standardised covariates for all the continuous covariates that were included in the Generalised Additive Models. The errors bars represent the 95% confidence intervals

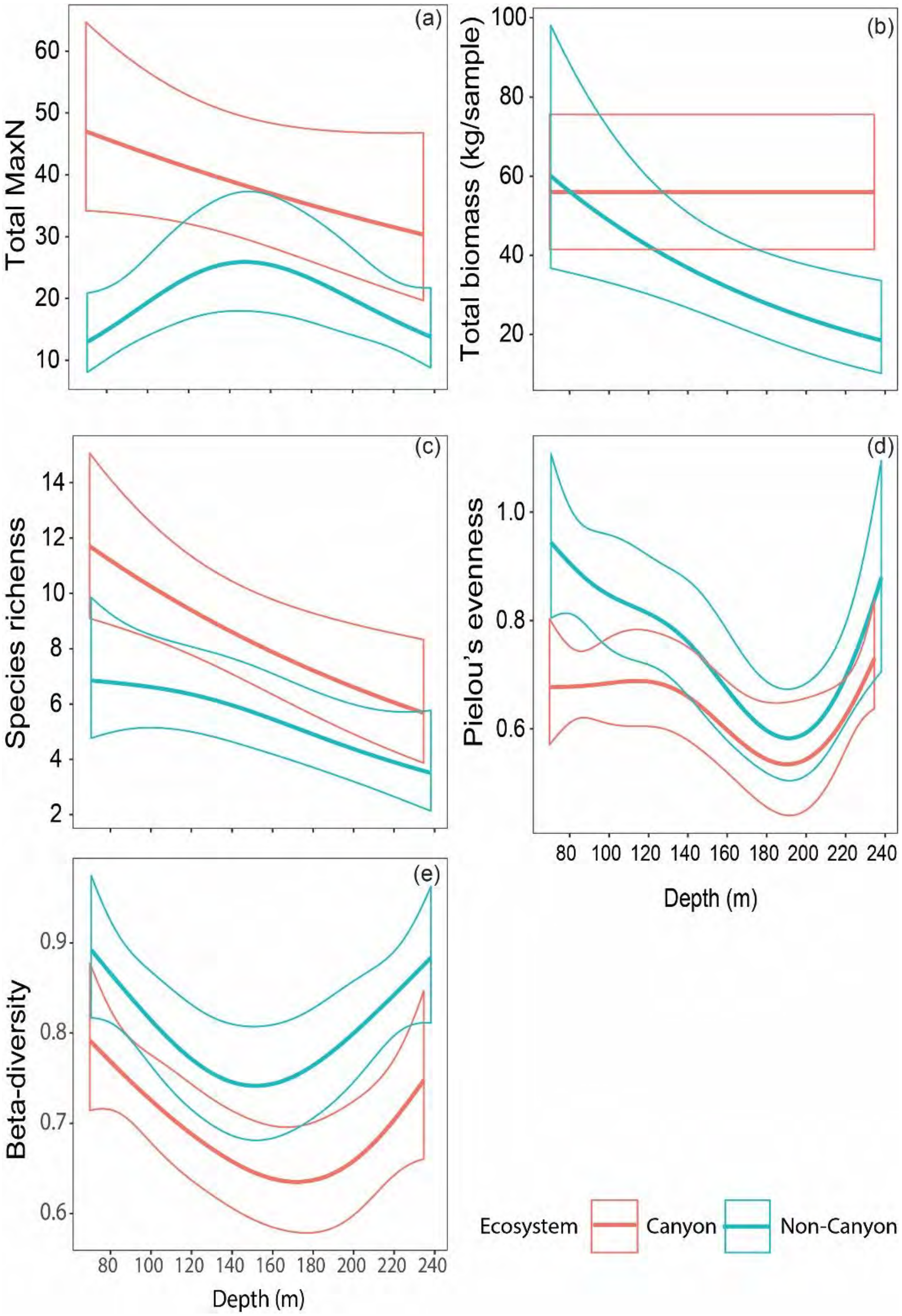


Figure 3.4: Predicted relationship between *depth* and **(a)** total abundance (MaxN), **(b)** biomass (Kg/sample), **(c)** species richness, **(d)** Pielou's evenness, **(e)** beta-diversity. Predictions were based on the estimates from the Generalised Additive Models using mean value of *average relief* for each ecosystem and standardised values (mean) for *visibility*, *temperature*, *water column* and *obstruction*. The error bars represent the 95% confidence intervals.

3.4.2.2 TOTAL BIOMASS

The GAM run on the total biomass data was only able to explain 39.9% deviance. *Visibility* had a significant effect on total biomass (Table 3.4). Total biomass was highly variable between samples and was greater in the canyon (57.1 ± 33.7 kg), compared to the non-canyon (37.1 ± 47.5). However, e*cosystem* had no significant effect on total biomass (Table 3.4). *Depth* had a significant effect on total biomass in the non-canyon ecosystem and no effect in the canyon ecosystem (Table 3.4). The GAM predicted plot, based on standardised values for *visability*, *temperature*, *water column* and *obstruction*, and with *average relief* set for the *ecosystem* type average (Table 3.1), depicted a steady decrease in total biomass with increase in depth in the non-canyon ecosystem (Figure 3.4b). When comparing the trend in total biomass over depth between the two ecosystems, a significant difference was evident at the deeper depths (> 180 m) with greater total fish biomass in the canyon, compared to the non-canyon (Figure 3.4b).

Table 3.4: Results from Wald's test run on the generalised additive models (GAMs) investigating patterns in total biomass from the study area. df = degrees of freedom; edf = estimated degrees of freedom.

Parametric Terms:	**df**	**F-value**	**p-value**	
Ecosystem	1.00	1.21	0.278	

Smooth Terms:	**edf**	**F-value**	**p-value**	
te(Visibility)	4.00	2.81	<0.001	***
te(Water column)	3.00	0.00	0.699	
te(Average relief)	4.00	0.64	0.079	.
te(Depth): Canyon	4.00	0.00	0.924	
te(Depth): Non-canyon	4.00	1.74	0.007	**

P-value: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' '

3.4.2.3 SPECIES RICHNESS

The GAM run on the species richness data explained 64.5% deviance. Results from the Wald's test (Table 3.5), indicated that *visibility* and *average relief* had a significant effect on species richness. *Ecosystem* had no effect on species richness (Table 3.5; Figure 3.3c), although a greater number of species were detected per sample in the canyon (8.4 ± 3.3), in comparison to the non-canyon (5.2 ± 3.5). *Depth* had a significant negative effect on species richness in both the canyon and non-canyon ecosystem (Table 3.5; Figure 3.4c).

Table 3.5: Results from the Wald's test run on the generalised additive models (GAMs) investigating patterns in species richness from the study area. df = degrees of freedom; edf = estimated degrees of freedom.

Parametric Terms:	**df**	**Chi.sq**	**p-value**	
Ecosystem	1.00	1.84	0.175	

Smooth Terms:	**edf**	**Chi.sq**	**p-value**	
te(Visibility)	4.00	9.31	0.001	**
te(Water column)	3.00	0.55	0.222	
te(Average relief)	4.00	16.52	<0.001	***
te(Depth): Canyon	4.00	7.97	0.002	**
te(Depth): Non-canyon	4.00	5.72	0.014	*

P-value: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' '

3.4.2.4 PIELOU'S EVENNESS

The GAM run on the Pielou's evenness data explained 59.2% deviance. *Average relief* and *water column* had a significant effect on Pielou's evenness (Table 3.6). *Ecosystem* had a significant effect on Pielou's evenness (Table 3.6), with higher evenness in the non-canyon ecosystem (0.77 ± 0.18), in comparison to the canyon ecosystem (0.66 ± 0.14). However, the GAM predicted plots, based on standardised for all continuous covariates included in the model, indicated an overlap in confidence intervals between the two ecosystems (Figure 3.3d), suggesting that it was the covariates that might be driving the ecosystem effect. *Depth* had a significant effect on Pielou's evenness only in the non-canyon ecosystem, and no effect on the canyon ecosystem (Table 3.6). The GAM predicted plot, based on standardised values for *visibility*, *temperature*, *water column* and *obstruction*, and with *average relief* set for the *ecosystem* type average (Table 3.1), indicated that the difference in evenness between ecosystems was restricted to shallow depths (< 100 m), and that in both ecosystems evenness decreased to a depth of about 190 m, followed by an increase with depth (Figure 3.4d)

Table 3.6: Results from the Wald's test run on the generalised additive models (GAMs) investigating patterns in Pielou's evenness from the study area. df = degrees of freedom; edf = estimated degrees of freedom.

Parametric Terms:	**df**	**F-value**	**p-value**	
Ecosystem	1.00	5.54	0.024	*
Smooth Terms:	**edf**	**F-value**	**p-value**	
te(Visibility)	4.00	0.19	0.256	
te(Water column)	3.00	1.48	0.029	*
te(Average relief)	4.00	1.51	0.012	*
te(Depth): Canyon	4.00	1.26	0.103	
te(Depth): Non-canyon	4.00	5.88	<0.001	***

P-value: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' '

3.4.2.5 BETA-DIVERSITY

The GAM fitted to the beta-diversity data explained 57.9% of the deviance. *Average relief* had a significant effect on beta-diversity (Table 3.7). There was a significant effect of *ecosystem* on beta-diversity (Table 3.7), with greater beta-diversity recorded in the non-canyon ecosystem (0.81 ± 0.15), relative to the canyon ecosystem (0.71 ± 0.1). However, the GAM predicted plot, illustrated that after accounting for ecosystem specific differences in the model covariates, there was little difference in beta-diversity between the two ecosystem types (Figure 3.3e). Depth had a significant effect in both ecosystem types (Table 3.7). The GAM predicted plot for the effect of depth within ecosystem, based on standardised values for *visibility*, *temperature*, *water column* and *obstruction*, and with *average relief* set for the *ecosystem* type average (Table 3.1), indicated that there was a high turnover of species at the shallower and deeper depths but low turnover in from depths of about 120 m to 200 m (Figure 3.4e). When comparing the trends between the two ecosystems, the greatest difference in beta-diversity between the canyon and non-canyon ecosystems was observed between depth of 170 m to 220 m (Figure 3.4e).

Table 3.7: Results from the Wald's test run on the generalised additive models (GAMs) investigating patterns in beta-diversity (multivariate dispersion) from the study area. df = degrees of freedom; edf = estimated degrees of freedom

Parametric Terms:	**df**	**F-value**	**p-value**	
Ecosystem	1.00	5.43	0.025	*
Smooth Terms:	**edf**	**F-value**	**p-value**	
te(Visibility)	0.0	0.00	1	
te(Water column)	0.5	0.16	0.32	
te(Average relief)	1	2.76	0.001	**
te(Depth): Canyon	2.3	2.78	0.004	**
te(Depth): Non-canyon	1.7	2.07	0.0099	**

P-value: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' '

3.4.3 MULTIVARIATE ASSEMBLAGES ANALYSIS

3.4.3.1 SPECIES COMPOSITION

A total of 1362 fish belonging to 27 families were identified from the 50 stereo-BRUVs deployments (Table A.1). Of these, 67.7 % were recorded in the canyon ecosystem with 28.5% only found in the canyon ecosystem. Some of the species only recorded in the canyon include: *Carcharhinus leucas* (zambezi shark), *Carcharhinus limbatus* (blacktip shark), *Epinephelus morrhua* (comet grouper), *Epinephelus tukula* (potato bass), *Seriola dumerili* (greater amberjack) and *Sphyrna lewini* (scalloped hammerhead shark). Of the species recorded in the non-canyon ecosystem (32.31 %), 12 % were only observed there and include: *Carcharhinus sealei* (blackspot shark), *Coris caudimacula* (spot-tail coris), *Himantura uarnak* (honeycomb stingray) and *Pagellus bellottii natalensis* (sand soldier). Species observed in both ecosystems (59.5%)

include, for example, *Argyrops spinifer* (king soldierbream)*, Cheimerius nufar* (santer)*, Chrysoblephus puniceus* (slinger)*, Epinephelus marginatus (*yellowbelly grouper), *Polysteganus coeruleopunctatus* (blueskin) and *Polysteganus praeorbitalis* (scotsman). Serranidae was the most diverse family with 14 species, followed by Carcharinidae, Lutjanidae and Sparidae with ten species respectively. The most abundant species in the entire study were *P. coeruleopunctatus (n =* 406), *C. puniceus* (n = 314) and *C. nufar* (*n* = 89) (Table A.1)

3.4.3.2 ABUNDANCE

Results from the PERMANOVA analysis of the fish abundance data indicated a significant effect of *ecosystem, depth, visibility, average relief* and the interaction between *depth* and *ecosystem* on the assemblage structure (Table 3.8). Additionally, the PCO showed a clear separation of the canyon and non-canyon samples (Figure 3.5). The first two PCO axes explained 45% of the total variation in abundance among fish assemblages (PCO1 = 27.4%, PCO2 = 17.6%; Figure 3.5). The separation of samples in the PCO according to *ecosystem*, co-varied strongly with relief and habitat type, with greater seafloor relief associated with the canyon ecosystem, in comparison to the non-canyon ecosystem samples which were more frequently on low relief sandy habitats (Figure 3.5b). Depth had an effect on the community structure (Figure 3.5b). The canyon ecosystem was typified by patched-reef with high relief, whereas the non-canyon ecosystem was highly correlated to sandy habitats (Figure 3.5b; Table 3.1). Fish species highly correlated with the non-canyon ecosystem were *C. sealei* and *Lagocephalus scleratus* (silver-cheeked toadfish) whereas the canyon ecosystem was characterised by *Epinephelus poecilonotus* (dot-dash grouper), *C. nufar*, *P. praeorbitalis* and *P. coeruleopunctatus* (Figure 3.5a). The SIMPER analysis by ecosystem showed the fish species that characterised each ecosystem (Table A.2). The average dissimilarity between the canyon and non-canyon ecosystem was 76%. The species that contributed most to the dissimilarity between the ecosystems were *P. coeruleopunctatus*, *E. poecilonotus*, *C. puniceus*, *C.*

nufar and *P. praeorbitalis*, all of which were more abundant in the canyon ecosystem (Table A.2), in agreement with the PCO (Figure 3.5a)

Table 3.8: Full model output of PERMANONA analyses on fish assemblage abundance data based on the fourth-root Bray-Curtis resemblance matrix. Bold values indicate significant difference (p<0.05). df, degrees of freedom; SS, sum of square; MS, mean squares; Pseudo-F, F-ratios; P (perm), probability level based on permutations.

Source	**df**	**SS**	**MS**	**Pseudo-F**	**P (perm)**
Visibility	1	10974	10974	5.493	**<0.001**
Water column	1	1887	1887	0.944	0.484
Average relief	1	15064	15064	7.541	**<0.001**
Depth	1	19366	19366	9.694	**<0.001**
Ecosystem	1	5452.7	5452.7	2.729	**0.003**
Depth x Ecosystem	1	5148.3	5148.3	2.577	**0.005**
Average relief x Ecosystem	1	1654.4	1654.4	0.609	0.609
Residual	42	83898	1997.6		
Total	49	143440			

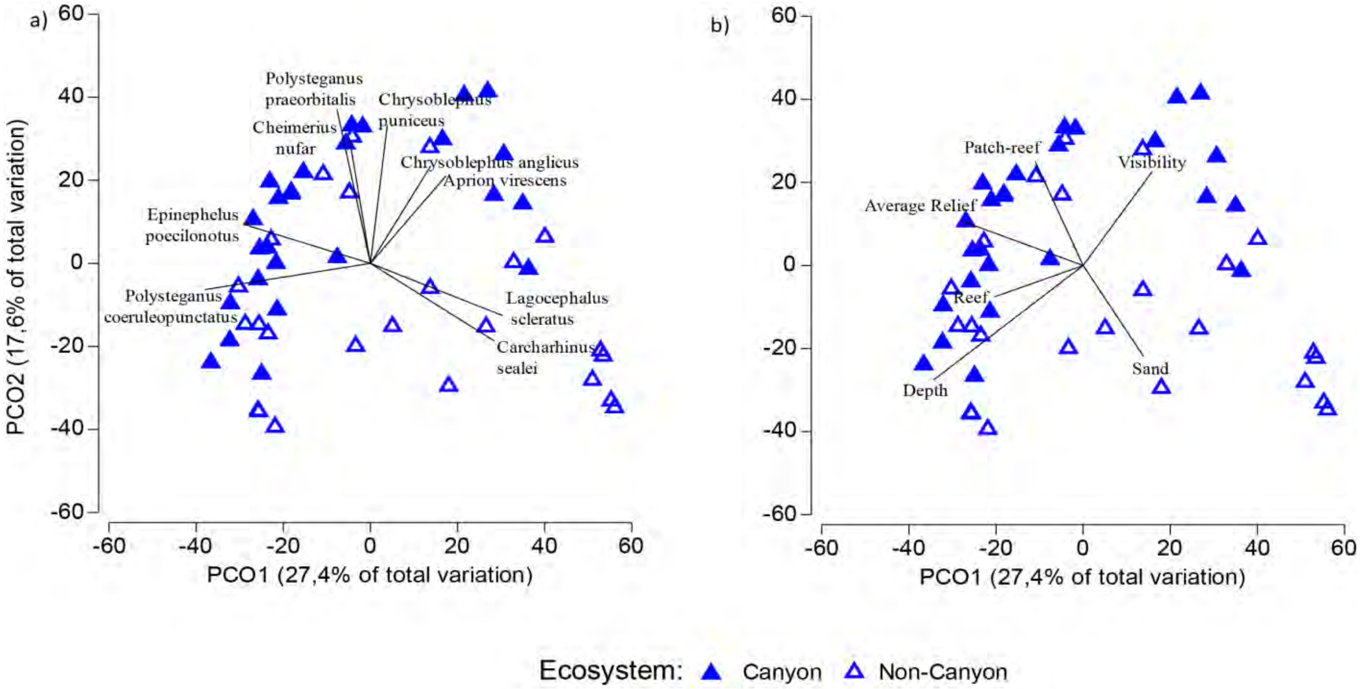


Figure 3.5: Principal coordinates analysis (PCO) of fourth-root transformed Bray-Curtis similarity fish abundance data indicating *ecosystems* with **a)** fish species vectors superimposed **b)** continuous covariates and habitat variables vectors. The length and direction of each vector indicate the strength of the correlation. Vectors are Pearson correlation ≥ 0.4.

3.4.3.3 BIOMASS

The PERMANOVA analysis of the fish biomass data showed a significant effect of *ecosystem*, *depth, visibility, average relief* and the interaction between *depth* and *ecosystem* on the assemblage structure (Table 3.9). The PCO showed a clear separation of the non-canyon and canyon ecosystem samples (Figure 3.6). The first two PCO axes explained 43.7% of the total variation in biomass among fish assemblages (PCO1 = 24.9%, PCO2 = 19.8%; Figure 3.6). As with the abundance data, the separation of samples according to ecosystem was strongly correlated with average relief (Figure 3.6b). Similar to abundance, the vectors on the PCO indicated that depth had an effect on the community structure (Figure 3.6b). Fish species highly correlated with the non-canyon ecosystem were *C. sealei* and *L. scleratus* whereas the canyon ecosystem was characterised by *E. poecilonotus*, *P. praeorbitalis*, *C. nufar* and *P. coeruleopunctatus* (Figure 3.6a). For biomass data, the SIMPER analysis showed that the average dissimilarity between the canyon and non-canyon ecosystem was 79.1%. The dissimilarity was mostly due to differences of higher biomass of the *E. poecilonotus*, *P. praeorbitalis*, *Seriola rivoliana* (longfin amberjack) and *C. nufar* in the canyon ecosystem (Table A.2).

Table 3.9: Full model output of PERMANONA analyses on fish assemblage biomass data based on the fourth-root Bray-Curtis resemblance matrix. Bold values indicate significant difference ($p<0.05$). df, degrees of freedom; SS, sum of square; MS, mean squares; Pseudo-F, F-ratios; P (perm), probability level based on permutations.

Source	**df**	**SS**	**MS**	**Pseudo-F**	**P (perm)**
Visibility	1	10181	10181	5.003	**<0.001**
Water column	1	2132.1	2132.1	1.048	0.408
Average relief	1	14060	14060	6.910	**<0.001**
Depth	1	17381	17381	8.542	**<0.001**
Ecosystem	1	4634.6	4634.6	2.278	**0.017**
Depth x Ecosystem	1	5730.9	5730.9	2.816	**0.002**
Average relief x Ecosystem	1	1542.3	1542.3	0.758	0.660
Residual	38	77313	2034.3		
Total	45	132970			

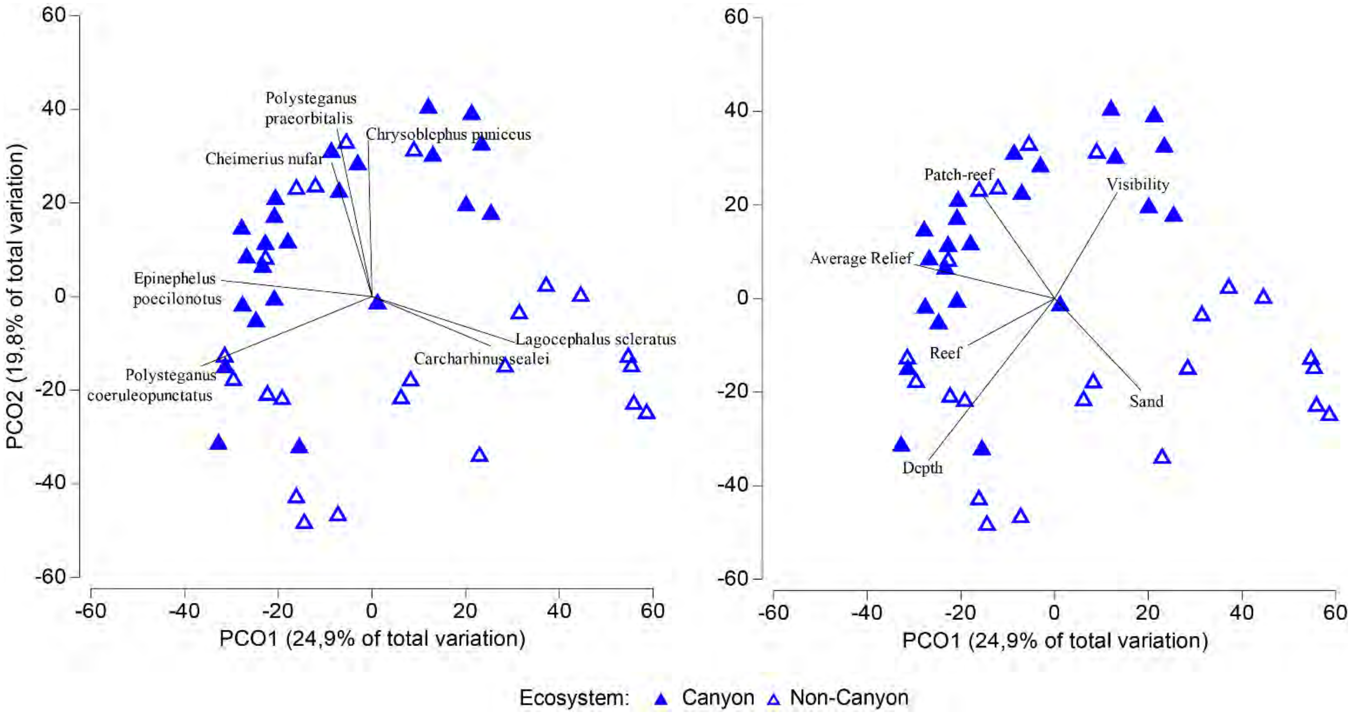


Figure 3.6: Principal coordinates analysis (PCO) of fourth-root transformed Bray-Curtis similarity fish biomass data indicating *ecosystems* with **a)** fish species vectors superimposed **b)** continuous covariates and habitat variables vectors. The length and direction of each vector indicate the strength of the correlation. Vectors are Pearson correlation ≥ 0.4.

3.5 DISCUSSION

The aim of this chapter was to compare the benthic fish assemblages of canyon and non-canyon ecosystems in an attempt to better understand how submarine canyons could influence fish assemblages and effect local patterns in biodiversity. Overall, the data suggested that the canyon ecosystem differs from the non-canyon ecosystem with different fish assemblages associated with each. The canyon ecosystem was characterised by higher abundances of benthic fish species and lower evenness and beta-diversity, relative to the non-canyon ecosystem. These patterns were strongly affected by the high relief habitats typical of canyon ecosystems. Although depth was important in structuring the fish assemblages in the non-canyon ecosystem, different responses to the depth gradient were observed within each ecosystem. Depth was a significant factor in structuring the fish abundance and biomass in terms of canyon vs non-canyon.

3.5.1 ECOSYSTEM

The results of this study showed that Wright Canyon of the IWP demonstrated clear differences in the fish assemblage structure when compared to the non-canyon ecosystem. From the univariate results, abundance, species evenness and beta-diversity demonstrated a significant effect of ecosystem. Multivariate analysis also demonstrated a significant effect of ecosystem since the fish assemblages differed at both ecosystems in both abundance and biomass values.

3.5.1.1 ABUNDANCE AND BIOMASS

The higher abundances of benthic fish species recorded in the Wright Canyon compared to the non-canyon ecosystem, is in agreement with previous studies (Stefanescu et al. 1994, De Leo et al. 2012). However, the absence of clear differences in the predicted plots from this study (Figure 3.3) highlights the importance of the significant covariates from the model (*visibility*, *average relief*) in enhancing abundances. As *average relief*, but not *visibility*, was found to be significantly higher in the canyon ecosystem, relative to the non-canyon ecosystem, it is possible that the more complex habitats associated with the canyons drove this difference. Interestingly, once the effect of average relief had been removed, the ecosystem effect was also negligible, and this suggests that other characteristics of canyons, such as upwelling or downwelling, may not strongly influence the demersal fish assemblages. The abundance and diversity of reef fish communities in many marine ecosystems have often been related to structural habitat complexity (Friedlander et al. 2003, Gratwicke and Speight 2005). For example, investigating the relationships between fish assemblages, their associated habitat, and degree of protection from fishing throughout the main Hawaiian Islands, Friedlander et al. (2003) recorded higher values for fish abundances as well as species richness and biomass in locations with higher substrate complexity. Relief may also promote high fish abundances because it provides more refuges and decreases the encounter rates between competitors as well as between predators and their prey (Almany 2004).

Our community analysis showed a significant difference in the abundance and biomass of benthic fish assemblages when compared between the canyon and the non-canyon ecosystems and is in agreement with previous studies (Stefanescu et al. 1994, Vetter and Dayton 1998, Ramirez-Llodra et al. 2010, Vetter et al. 2010). In contrast, some studies have reported no significant differences between benthic communities in the canyon and adjacent open slopes (Bianchelli et al. 2010). Differences in benthic communities between the canyon and the slope can be a result of many varying factors such as temperature variability, oxygen concentration as well as habitat heterogeneity (Vetter and Dayton 1998). From our results we suggest that depth and average relief were the most important factors structuring benthic fish assemblages. The canyon ecosystem was distinguished by patched reef and reef with high relief while the non-canyon ecosystem was distinguished by flat sandy bottoms with low relief. Similar results were reported by De Leo et al. (2012), when they investigated demersal fish assemblages in Pelukunu and Kawainui submarine canyons and their adjacent slope along the north shore of Moloka’i, Hawaii; the canyon ecosystems were characterised by a variety of habitats while the slope area was characterised by flat sandy bottoms. Habitat heterogeneity in submarine canyons and elsewhere has been found to be a key factor in contributing to the high faunal diversity (McClain and Barry 2010, De Leo et al. 2012, Fitzpatrick et al. 2012).

The typifying species in the non-canyon ecosystem were *C. sealei*, which was recorded only in this ecosystem and *L. scleratus* which is known to occur in high abundances on sand habitats (Kalogirou 2013). On the other hand, the canyon ecosystem was typified by species of the Sparidae and Serranidae families (abundance and biomass). Overall, the fish species composition reported by this study is a good representation of fish species found within the submarine canyons of the iSimangaliso Wetland Park (full species list: Table A.1) as most recorded species were also reported by Sink et al. (2006) and Heemstra et al. (2006). An interesting finding is that high abundances of various commercially important fish species of the Sparidae family were reported in both the canyon and non-canyon ecosystems. These included species such as *P. coeruleopunctatus* and *C. puniceus* which were also reported to be common in Wright Canyon by Sink et al. (2006).

3.5.1.2 DIVERSITY

In contrast to abundance, beta-diversity and evenness were lower in the canyon compared to the non-canyon ecosystem, suggesting a higher turnover and more even distribution of fish species in the non-canyon ecosystem, respectively. Lower evenness in canyon ecosystems have been noted for polychaetes in the Whittard and Portuguese Canyons (Paterson et al. 2011, Gunton et al. 2015) and macrofauna in the Scripps and LaJolla Submarine canyons (Vetter and Dayton 1998). In the Scrips and LaJolla submarine canyons, lower evenness in the canyon ecosystem was suggested to be linked to dominance by opportunistic species and deposits of detritus (Vetter and Dayton 1998). In the case of Whittard canyon ecosystem, the lower of evenness in the canyon ecosystem was due to high levels of physical disturbances in the canyon ecosystem (Gunton et al. 2015). The greater turn-over of species in the non-canyon ecosystem, compared to the canyon ecosystem, could be attributed to the proportion of different habitats sampled in the different ecosystems, with more consistent assemblages associated with reef related habitats (characteristic of the canyon), in comparison to sand related habitats (characteristic of the non-canyon).

3.5.2 DEPTH

Depth is frequently observed as an important factor that influences the change in diversity and structure of benthic fish in marine habitats (Gaertner et al. 2013, Götz et al. 2014, Stefanoudis et al. 2019). Depth is an important predictor of community structure because it acts as a proxy for several co-varying environmental factors such as light intensity, water temperature, water movement (Garrabou et al. 2002). From the univariate results presented here, it seems that the depth gradient had a greater impact on fish assemblages in the non-canyon compared to the canyon ecosystem as abundance, biomass, species richness, evenness and beta-diversity were significantly affected by depth. In contrast, only species richness and beta-diversity were significantly affected by depth in the canyon ecosystem.

Depth had a significant effect on both abundance and biomass. When the trends are compared between the two ecosystems, the results suggest that the head of the canyon was characterised by greater fish abundances in comparison to the deeper parts, where fish were less abundant (Figure 3.4a, b). Alternatively, in the non-canyon ecosystem, the shallow parts (or outer-shelf) were characterised by low abundances of large fish, while the deeper portion was characterised by low abundances of smaller fish. The bell-shaped curve evident in the abundance data when plotted against depth in the non-canyon ecosystem (Figure 3.4a) may be a sampling artefact, whereby those depths were characterised by greater relief habitats and thus higher abundances of fish.

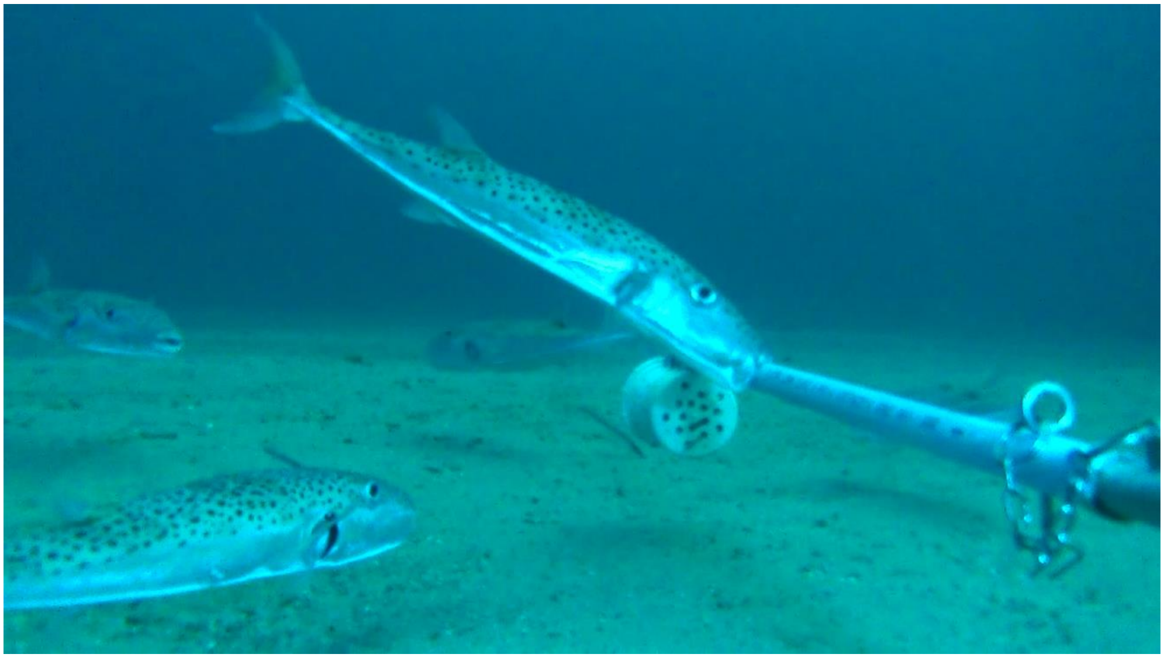
For diversity, species richness decreased progressively with increasing depth in both the canyon and non-canyon ecosystem (Figure 3.4c). At similar depths, Currie et al. (2012a) reported a decline in demersal fish species richness with depth in both the submarine canyon and non-canyon ecosystem off the Bonney Coast, South Australia. In this study, depth had a significant effect on evenness only in the non-canyon where evenness decreased to a depth of about 190 m followed by an increase with depth and had a significant effect on beta-diversity in the canyon ecosystem where beta-diversity decreased to a depth of about 140 m followed by an increase with depth (Figure 3.4d, e). The high diversity variability detected in this study seems to be linked with relief which was significant for richness, evenness and beta-diversity. Demersal fish diversity often shows inconsistent patterns across depth gradients in submarine canyons (McClain and Barry 2010, Currie et al. 2012a, De Leo et al. 2012). For example, McClain and Barry (2010), observed high species turnover of macrobenthic assemblages at depths of < 100 m in Monterey Canyon off the central California coast. These authors suggested that the observed results could be explained by increased habitat heterogeneity related to substrate patchiness and physical disturbances at these depths.

3.5.3 CONCLUSION

This study is unique in that it has highlighted differences in benthic fish diversity and community structure in both the canyon and the non-canyon ecosystem over a depth gradient, whilst previous research on IWP canyons primarily focused on the fish community within the canyon ecosystem. The data from this study suggest a “canyon effect” as the results indicated an effect of ecosystem on the structure and diversity of benthic fish assemblages of IWP. However, the “canyon effect” appears to be primarily driven by the greater habitat relief that is associated with the steep walls of canyons. In addition, depth was an important factor that structured the fish diversity within and outside Wright Canyon and also played a major role in the community structure within the canyon ecosystem.

CHAPTER 4

4 DIVERSITY AND COMMUNITY STRUCTURE OF BENTHIC FISH ON THE CONTINENTAL SHELF EDGE OF ISIMANGALISO WETLAND PARK: INFLUENCE OF SUBMARINE CANYONS AND DEPTH



Cover photo: Wright, non-canyon (60 m)

4.1 ABSTRACT

The continental shelf edge off iSimangaliso Wetland Park (IWP) is characterised by numerous shelf incising submarine canyons that harbour distinct biodiversity. However, there is still no understanding if these submarine canyons influence biodiversity occurring on the non-canyon continental shelf habitats. In June 2018, baited remote underwater stereo-video systems were deployed at 60, 80 and 100 m depth in three submarine canyons and their adjacent non-canyon habitat within the IWP to investigate the diversity patterns and community structure of benthic fish. The results indicated higher abundances of fishes in submarine canyons compared to the adjacent shelf habitat. Species evenness was higher in the non-canyon ecosystem compared to the canyons, with a decreased from the shallow to the deep sites. In both ecosystems, the shallower depth (60 m) contributed more to beta diversity compared to 80 m and 100 m samples. There were inconsistent patterns observed with abundance, biomass and diversity among the different sampled locations. Permutational multivariate analysis of variance indicated significant differences in the fish assemblage structure for both the abundance and biomass data. For both abundance and biomass, the pairwise comparisons revealed that the difference between the canyon and non-canyon ecosystem was restricted to the 100 m depth zone where the canyon ecosystem was typified by patch reef, reef, high relief and high abundances of Sparidae species. Overall, the results indicated that depth, relief and bottom type were important determinants of the difference in fish assemblage structure, but that the results were frequently not consistent among canyons.

4.2 INTRODUCTION

With the increase of anthropogenic disturbance, such as overfishing, in the marine environment, understanding and describing biodiversity has become a fundamental aim in marine biology. In particular, understanding and describing the distribution and diversity patterns of fish in marine ecosystems is very important. Fish are a key species in marine ecosystems because they occupy a high trophic level and a key position in cycling nutrients throughout the ecosystem (Xiujuan et al. 2011). The continental shelf, which can be described as a submerged margin of the continents, generates biological production that supports high levels of biodiversity in our oceans including over 90% of global fish catches (Pauly et al. 2002).

One of the most significant geomorphic features incising the continental shelf are submarine canyons. Submarine canyon ecosystems receive high levels of organic matter that is transported from inshore to the canyon heads, and this organic matter eventually travels down the canyon system as a result of turbidity and tidal currents (Ingels et al. 2011). Canyon ecosystems are also characterised by complex topographic features that result in habitat heterogeneity (McClain and Barry 2010). Both habitat heterogeneity and the input of high levels of organic matter can be fundamental drivers of biodiversity, and this suggests that submarine canyon ecosystems could be regions of enhanced diversity, abundance, biomass and biological productivity (Vetter 1994, Tews et al. 2004, De Leo et al. 2010). Considering this, submarine canyons may support fish assemblages that are unique from those of the surrounding shelf (Allen et al. 2001). However, spatial heterogeneity, in terms of size, shape, depth and functioning, and temporal variability both among different submarine canyons and within each system determine the ecology and the diversity of the systems benthic fauna (Cunha et al. 2011). Submarine canyon systems can be very different in terms of their morphology, and the different substrata allow settlement of a variety of benthic organisms (Cunha et al. 2011, Duffy et al. 2013), which in turn might support different fish assemblages.

Just like in most marine ecosystems, depth is also an important factor that can explain the variability in fish assemblages in submarine canyons (Sabatini et al. 2007, Currie et al. 2012a, De Leo et al. 2012, Fitzpatrick et al. 2012). Abundance and diversity patterns of fishes within submarine canyons have shown a varying trend along depth gradients. Abundance and diversity can either remain constant, peak at the canyon heads (Vetter and Dayton 1999), at intermediate depths (Quattrini et al. 2015) or at the deeper depths (De Leo et al. 2012).

The continental margin of iSimangaliso Wetland Park (IWP) marine protected area MPA) is characterised by submarine canyons that cut the continental shelf (Green and Uken 2008). The canyons support a heterogeneous set of habitat that ranges from sandy plains to rocky outcrops (Sink et al. 2006). The IWP submarine canyons are home to coelacanths *Latimeria chalumnae*, as well as distinct and diverse invertebrate communities that in turn support the epifauna found within the canyons (Sink et al. 2006, Samaai et al. 2010). At depth of 70 - 140 m, the canyon margins protect a variety of commercially important linefish species of the Sparidae, Serranidae and Lutjanidae families (Sink et al. 2006), and numerous fish species that are rare or absent from the inshore ecosystem (Floros et al. 2012). The few studies conducted to date inside the canyons of IWP have emphasised the uniqueness of these ecosystems as well as the unique biodiversity harboured within the canyons (Venter et al. 2000, Heemstra et al. 2006, Roberts et al. 2006, Sink et al. 2006, Samaai et al. 2010). However, no research has compared these canyons to adjacent non-canyon shelf-edge habitat, investigated the influence or role of these canyons on the continental shelf or assessed between canyon variability.

To address this gap, the present study aimed to investigate the patterns in diversity and community structure of benthic fish within and adjacent to the heads (60 to 100m depth) of submarine canyons on the continental shelf of iSimangaliso Wetland Park. Furthermore, the research aimed to identify if these patterns were consistent in different, but nearby canyons on the continental shelf. To address these aims, baited remote underwater stereo-video systems (stereo-BRUVs) were employed to gather fish data inside three submarine canyons (canyon ecosystem) and their adjacent shelf-edge habitat (non-canyon ecosystem) from three depth zones (60, 80, 100 m). I hypothesized that:

1. Abundances, biomass and diversity metrics (species richness, Pielou's evenness and beta-diversity) will be higher in the canyon ecosystem, compared to the non-canyon ecosystem, because of habitat complexity and habitat heterogeneity.
2. Patterns in diversity metrics and fish assemblage structure will be inconsistent between the canyons because different canyons are unique in terms of their morphology (Cunha et al., 2011; Huang et al., 2014).
3. The fish assemblage structure will differ significantly between the canyon and non-canyon ecosystem, because of expected difference in habitat complexity and habitat heterogeneity.

4.3 MATERIALS AND METHODS

4.3.1 STUDY AREA

This research was conducted in IWP which is a Marine Protected Area (MPA) enclosing 78 km of the coastline off the northern KwaZulu-Natal (KZN) and extending approximately 5.4 km out to sea (Mann et al. 1998) (Figure 4.1a). Throughout the MPA, boat-based bottom, or reef fishing, is prohibited, eliminating the confounding influence on fishing when testing the effect of ecosystem on fish assemblages. The IWP MPA is characterised by patches of hard substrates dominated by coral communities as well as areas of sandy substrates between the corals (Ramsay and Mason 1990). Up to a depth of 30 m, the coral communities are ahermatypic (Schumann 1987, Schleyer and Celliers 2003, Samaai et al. 2010). The continental shelf in this area is very narrow (2-5 km) and gradually slopes towards the shelf-edge, where numerous submarine canyons of varying sizes and shapes begin to appear between 60 - 110 m (Ramsay 1994). The canyon walls are highly rugose and contain caves and overhangs, whereas the continental shelf adjacent to the canyons is typified by a gradual slope with sandy plains (Sink et al. 2006). The environment outside the canyons is characterised by stronger currents, compared to the canyons where the current velocity has been found to decrease significantly (Roberts et al. 2006). The water temperature on the shallow inshore reefs has been found to range between 22°C and 27°C (mean 24.5°C), and decrease down to about 7°C at the canyon margins (Roberts et al. 2006).

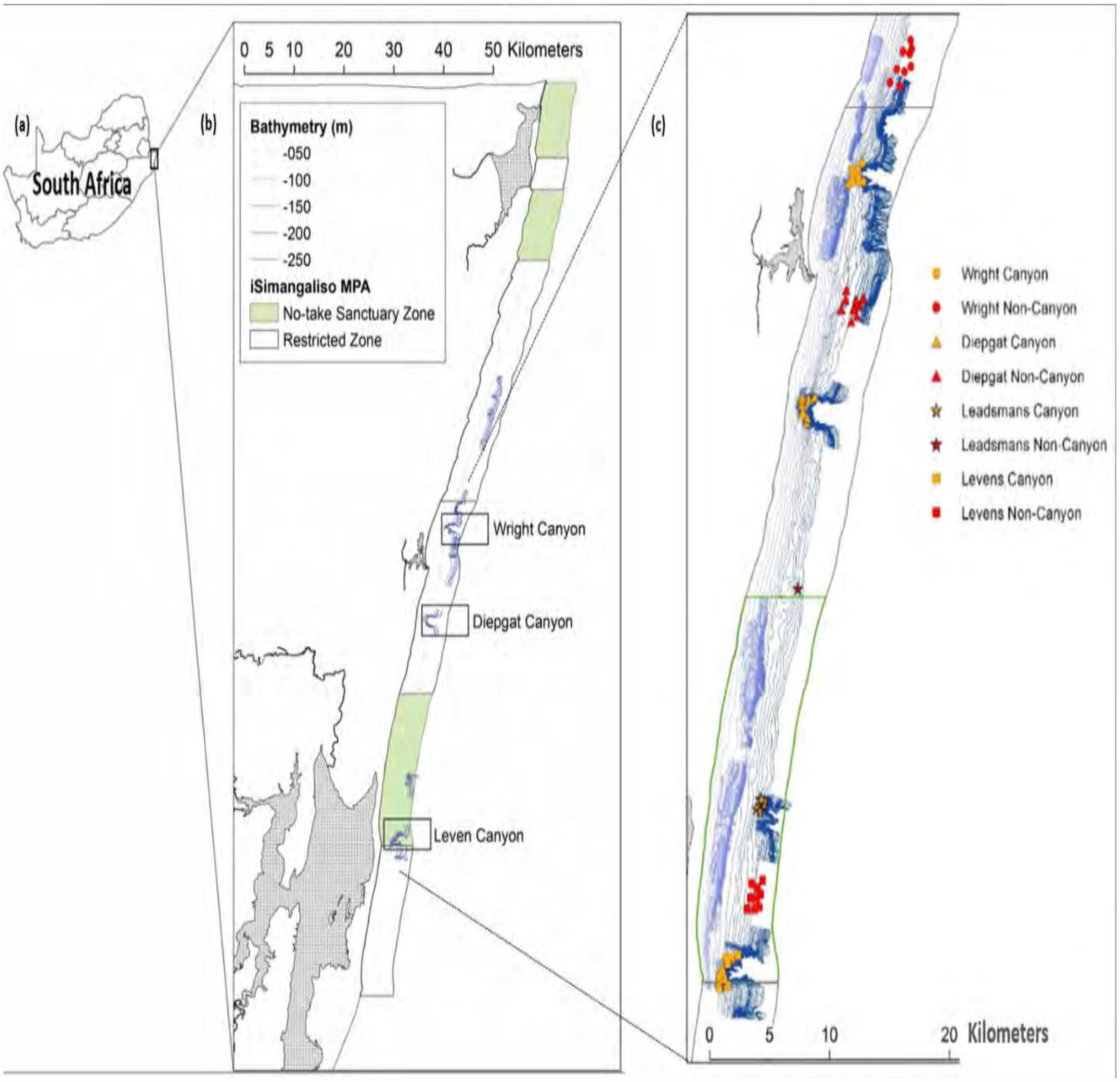


Figure 4.1: Map of study area. **(a)** Map of South Africa indicating the position of iSimangaliso Wetland Park Marine Protected Area, **(b)** location of the canyons within the park, and **(c)** sampling design indicating replicate sampling points inside the selected canyons and at the adjacent areas. The replicates within an ecosystem type were 500 m apart at each location.

4.3.2 SAMPLING DESIGN

For this study, sampling was conducted in June 2018 within three locations, where a location consisted of a submarine canyon (either Wright, Diepgat or Leven) and an adjacent area outside of the canyon and greater than 5 km from a neighbouring canyon (Figure 4.1b). Originally, the plan was to carry out surveys at four locations, however due to logistical and weather restrictions the sampling at the forth location (Leadsmans canyon) could not be completed (Figure 4.1c), and as such it was excluded from this chapter. Each of the canyons included here extend from the continental shelf to abyssal depth, but for this study, the fish data collections were limited to the canyon heads (60 – 100 m).

Wright Canyon is a large and mature canyon that starts at about 40 m depth. The canyon is located approximately 2 km from the coast and is 1.1 km wide where it cuts the shelf edge. Wright Canyon drops from 50 – 250 m over about 500 m. Compared to both Diepgat and Leven, Wright Canyon has a narrow canyon head and the walls are moderately incised with a few prominent tributaries (Figure 4.1c). Diepgat Canyon starts at about 80 m and is located approximately 1 km from the shore. The canyon drops from 50 – 250 m over about 1 km. Where it cuts into the shelf edge it is 1.8 km wide. Diepgat Canyon has fewer and smaller incisions into the canyon walls making the environment less dynamic than Levens Canyon (Figure 4.1c). Levens Canyon is also classified as a mature canyon. The canyon starts at about 50 m depth and at its closest is about 1.3 km from the shore. Where it cuts into the shelf edge (250 m depth) it is about 1.5 km wide. Levens Canyon drops from 50 – 250 m over about 800 m. Importantly, Levens is characterised by numerous smaller incisions/tributaries that have been cut into the canyon walls, making it a complex and dynamic topographic environment (Figure 4.1c).

The sampling design consisted of three factors: *ecosystem* (two levels; canyon and non-canyon; fixed), *depth zone* (three levels; 60, 80 and 100 m; fixed) and *location* (three levels; Diepgat, Wright and Levens; random). For each depth zone, three replicates were deployed at a randomly selected site in each location for both ecosystems resulting in a total of 54 deployments (three replicates x three depth zones x three locations x two ecosystems) (Figure 4.1c). Replicate stereo-BRUVs deployments were placed 500 m apart to avoid the overlap of bait plumes and reduce the likelihood of fish moving between sites during the sampling period (Watson et al. 2007).

4.3.3 SAMPLING TECHNIQUE

The sampling technique followed an identical approach described in Chapter 3, section 3.3.2 however sampling for this chapter was conducted using seven stereo-BRUVs instead of just three used in Chapter 3.

4.3.4 VIDEO ANALYSIS

Video analysis followed an identical approach described in Chapter 3, section 3.3.3.

4.3.5 ESTIMATING COVARIATES

Estimating covariates followed an identical approach described in Chapter 3, section 3.3.4.

4.3.6 STATISTICAL ANALYSIS

4.3.6.1 UNIVARIATE ANALYSIS

Univariate analyses were conducted with hierarchical generalised additive models (HGAMs) in R software (R core team 2019), via the R-studio interface (R studio Team 2019), using the MGCV package (Wood 2019). Hierarchical generalised additive models are an extension of the standard generalised additive models (GAMs). The HGAMs allow the modelling of non-linear functional relationships between the response and predictor variable, where the shape of the function can vary between group levels (Pedersen et al. 2019).

In this chapter, HGAMs were used to model the effect of *ecosystem, depth zone*, and selected covariates (*visibility*, *water column*, *obstruction*, *average relief*, *temperature, bottom type* [see Chapter 3, section 3.3.4 for more details on the covariates]) on total abundance, total biomass, species richness, Pielou’s evenness index and “local contribution to beta-diversity” (LCBD). To determine if the patterns were consistent among the three locations, the effect of *ecosystem*, *depth zone* and *location* was modelled for the same response variables listed above. Hierarchical generalised additive models were chosen to account for dependency within the dataset that could be associated with location and bottom type, for the first model, and with bottom type, for the second model (Pedersen et al. 2019). The three different diversity indices, which are species richness, Pielou's evenness and LCBD, were calculated because each index measured a different component of species diversity. Species richness referred to the total number of species in the sample, whereas species evenness expressed how evenly the individuals in the community were distributed over the different species (Vyas et al. 2012). Pielou's evenness index was calculated using PRIMER v7 (Clarke and Warwick 2001). The value of Pielou's evenness ranges from 0 to 1, with larger values representing more even distribution in abundance among species (Pielou 1966). Lastly, LCBD was calculated in R software following the method of Legendre and De Cáceres (2013). The local contribution to beta-diversity is the relative contribution of sampling units to beta-diversity and LCBD represents the degree of uniqueness of the sampling units in terms of species composition (Legendre and De Cáceres 2013). LCBD was used as an alternative to multivariate dispersion (used in Chapter 3) to measure beta-diversity.

Prior to constructing the models, the data were thoroughly explored to identify outliers and examine collinearity among the covariates (protocol can be viewed in Zuur et al. 2010). None of the covariates showed collinearity however, *obstruction* was excluded from the models as none of the samples were obstructed. For all HGAMs in the first analysis, looking at the effect of depth zone and ecosystems of diversity metrics, smooth terms (s) were specified with the thin-plate regression splines basis-penalty (bs = "tp") for the continuous covariates. *Location* and *bottom type* were included as random effects (bs = "re") (Pedersen et al. 2019). The main and interaction effects between *ecosystem* and *depth zone* were included as parametric coefficients. The full HGAM was specified as:

y = s(*Visibility*, bs = “tp” , k = 5) + s(*Water column*, bs = “tp”, k = 8) + s(*Temperature*, bs = “tp” , k = 5) + s (*Average relief*, bs = “tp” , k = 8) + *Depth zone* * *Ecosystem* + s(*Location*, bs = “re”) + s(*Bottom type*, bs = “re”) Eq 4.1

For the second analysis, *ecosystem*, *depth zone* and *location* were all included as parametric coefficients, and only *bottom* was included as a random effect. The full HGAM was specified as:

y = s(*Visibility* , bs = “tp” , k = 5) + s(*Water column*, bs = “tp”, k = 8) + s(*Temperature* , bs = “tp” , k = 5) + s (*Average relief* , bs = “tp” , k = 8) + *Depth zone* * *Ecosystem* * *Location* + s(*Bottom type*, bs = “re”) Eq 4.2

In both equations 4.1 and 4.2, y represents the given response variable and k is the dimension of the basis used to represent the smooth term.

Different families of distributions were used to model the response variables. Total biomass was modelled with Tweedie distribution for a case of $1 < p < 2$ (where $p = 1$ is a generalisation of a Poisson distribution and $p = 2$ is a gamma distribution) (Wood 2019), whereas total abundance and species richness were modelled with a negative binomial distribution to account for over-dispersion of the data (Barry and Welsh 2002). Lastly, evenness and LCBD were modelled using beta regression distribution. This was done because both evenness and LCBD are variables that assume values in the standard unit interval 0 and 1 (Cribari-Neto and Zeileis 2010). To validate the model, assessment of residuals for spatial autocorrelation and for the patterns when plotted against the fitted values and covariates were conducted. To test for spatial autocorrelation, variograms were constructed with the model residuals, and all tests showed no evidence for spatial dependence within the dataset. For all models, the residuals showed no marked patterns and had an even distribution around zero, when plotted against the fitted values and the different explanatory variables. Wald's tests were carried out to test the significance of the explanatory variables included in each HGAM. To separate the effects of the continuous covariates from *ecosystem, depth zone* and *location*, predicted dataset were generated using standardised values (mean) for each covariate. Plots based on the predicted values were then constructed using ggplot2 (Wickham 2017).

4.3.6.2 MULTIVARIATE ANALYSIS

The multivariate analysis was conducted using the statistical package PRIMER-E v7 (Clarke and Gorley 2015) with PERMANOVA+ add on (Anderson et al. 2008). To investigate whether multivariate abundance (MaxN) and total biomass data changed with *depth* and *ecosystem* as well as *location*, a three-way PERMANOVA analysis of *depth zone* (fixed: three levels, 60 m vs 80 m vs 100 m) by *ecosystem* (fixed: two levels, canyon vs non-canyon) by *location* (random: three levels, Diepgat vs Levens vs Wright) was used. *Visibility*, *water column*, *temperature*, *average relief* were included in the analysis as covariates. *Visibility* and *water column* were added as covariates to the analysis to account for differences in the field of view of the video samples. *Obstruction* was excluded from the analysis as no samples were obstructed. A modified Gower logbase 10 distance measure resemblance matrix was used to analyse the data (Anderson et al. 2006). For modified Gower logbase 10, an order of magnitude change in abundance is equal to a change in composition (Anderson et al. 2006). All the analyses were based on type I sum of squares using 9999 permutations under a reduced model (Anderson et al. 2008). *A Posteriori* pair-wise tests were conducted where a significant interaction effect was found (reporting only significant pair-wise results). Principal Coordinates Analysis (PCO) was used to visualise the abundance and biomass assemblage data. Furthermore, Pearson's correlation vectors (R > 0.3, for bottom type and environment variables and R > 0.5 for species data) were overlaid to identify the key assemblage attributes and environmental variables driving the patterns. Similarity percentages (SIMPER) for both abundance and biomass data were estimated to determine which fish species contributed most between-group similarity and dissimilarity (Clarke and Warwick 2001).

4.4 RESULTS

4.4.1 COMPARISON ON ENVIRONMENTAL CHARACTERISTICS

Water *temperature* decreased with increasing water depth and the pattern was consistent between *ecosystems* (Canyon - Non-canyon: 60 m = 20.8 ± 2.3 – 20.2 ± 1.3; 80 m = 18.0 ± 0.9 – 18.4 ± 1.0; 100 m = 16.8 ± 0.9 – 17.5 ± 1.2 ^{o}C). However, there was considerable variation among the three *locations,* particularly within the 60m *depth zone* (Table 4.1). Underwater *visibility* decreased slightly with depth, and was similar between the ecosystems (Canyon – Non-canyon: 60 m: 5.5 ± 1.6 – 5.3 ± 1.7; 80 m = 5.3 ± 1.7 – 4.5 ± 1.7; 100 m = 4.6 ± 2.2 – 4.5 ± 1.8 m). There was location specific variability, with lower visibility recorded at Levin, in comparison to wright and Diepgat (Table 4.1). Water column was consistent across depth within the non-canyon ecosystem (60 m = 53.0 ± 4.8; 80 m = 59.4 ± 11.9; 100 m = 51.7 ± 15.0 %), but varied in the canyon ecosystem (60 m = 51.7 ± 14.5; 80 m = 49.2 ± 16.8; 100 m = 36.2 ± 20.5 %).

Table 4.1: Summary statistic (mean and standard deviation [SD]) displaying trends in the continuous covariates associated with *depth zone*, *ecosystem* and *location*.

Depth Zone	Ecosystem	Location	Temperature (^{o}C) mean	SD	Visibility (m) mean	SD	Water Column (%) mean	SD	Average relief mean	SD
60	Canyon	Diepgat	20.3	0.7	5.9	0.2	41.7	24.0	1.1	0.1
60	Canyon	Levens	23.3	0.3	4.8	2.2	58.0	3.6	1.5	0.5
60	Canyon	Wright	18.8	2.1	5.8	1.9	55.3	5.0	1.1	0.1
60	Non-Canyon	Diepgat	19.3	0.3	5.5	1.9	52.0	7.9	0.0	0.0
60	Non-Canyon	Levens	21.1	1.9	4.5	1.1	56.3	1.5	1.4	0.3
60	Non-Canyon	Wright	20.1	0.8	5.8	2.2	50.7	1.5	1.0	0.0
80	Canyon	Diepgat	18.2	0.5	5.1	2.3	54.0	8.7	1.2	0.3
80	Canyon	Levens	18.1	1.7	4.1	1.0	41.3	29.7	1.8	0.7
80	Canyon	Wright	17.7	0.3	6.7	0.5	52.3	5.0	1.6	0.3
80	Non-Canyon	Diepgat	18.8	0.8	5.0	1.4	54.0	4.4	1.0	0.0
80	Non-Canyon	Levens	19.2	0.7	4.0	2.7	67.3	19.7	1.0	0.1
80	Non-Canyon	Wright	17.3	0.4	4.4	1.2	57.0	4.0	1.2	0.3
100	Canyon	Diepgat	17.6	0.2	5.7	2.3	33.0	23.3	1.4	1.4
100	Canyon	Levens	16.4	0.7	2.6	0.7	40.0	28.7	2.1	2.6
100	Canyon	Wright	16.4	1.3	5.5	2.3	35.7	16.6	2.9	0.1
100	Non-Canyon	Diepgat	16.9	0.8	3.9	1.1	56.0	1.0	1.0	0.0
100	Non-Canyon	Levens	18.0	0.2	3.9	1.8	41.7	24.4	1.1	1.0
100	Non-Canyon	Wright	17.7	2.0	5.8	2.1	57.3	9.0	1.1	0.1

Classification of bottom type from the still images captured in each sample revealed differences in *bottom type* and *average relief* between the two sampled *ecosystems* and amongst the sampled locations (Table 4.1). There was a high degree of variability in average relief within ecosystems and between depth zones and locations (Table 4.1). The canyon ecosystem being characterised by higher *average relief* (mean ± standard deviation = 1.64 ± 1.03) compared to the non-canyon ecosystem (0.97 ± 0.47). Amongst sampled locations*, average relief* was highest at Levens (1.49 ± 1.07) compared to Wright (1.47 ± 0.72) and Diepgat (0.95 ± 0.68). Average relief increased with depth in the canyons, but not in the non-canyon ecosystem (Table 4.1).

Reef and sand with sea pens were only encountered in the canyon ecosystem with a frequent occurrence of 11.11% and 29.63% respectively. High *average relief* patched reef was mostly encountered in the canyon ecosystem (33.33 %) compared to the non-canyon ecosystem (3.70%), whereas sand with low *average relief* was mostly encountered in the non-canyon ecosystem (25.92%), compared to the canyon ecosystem (11.11%). Sand with cobbles was the most encountered bottom type in the non-canyon ecosystem with a frequent occurrence of 44.44%.

4.4.2 UNIVARIATE RESULTS

4.4.2.1 TOTAL ABUNDANCE

a. Testing the effect of *ecosystem* and *depth zone*

The HGAM run on abundance data was able to explain 66% of the variability in the dataset. Results from the Wald's test, indicated *that ecosystem* had a significant effect on total abundance (Table 4.2a), with more fish detected in the canyon ecosystem (mean ± standard deviation: 38.22 ± 40.35 fish/sample) relative to the non-canyon ecosystem (16.67 ± 13.74 fish/sample). *Depth zone* and the interaction between *depth zone* and *ecosystem* had no effect on abundance (Table 4.2a). However, total abundance was considerably greater at depths of 60 m (mean ± standard deviation: 42.89 ± 65.90 fish/sample), relative to 80 m (36.0 ± 25.03 fish/sample) and 100 m (35.78 ± 16.87 fish/sample) in the canyon ecosystem. An opposite pattern was recorded in the non-canyon ecosystem with abundance greater at 100 m (23.0 ± 19.93 fish/sample), relative to 80 m (15.89 ± 9.89 fish/sample) and 60 m (11.11 ± 6.13 fish/sample). *Average relief* had a significant effect on abundance (Table 4.2a), with abundance increasing as habitats increase in complexity from low relief (0) to moderate relief (2-2.5), however further increases in relief didn't correspond to measurable increases in abundance (see supplementary Figure A.2). The random effects of *bottom type* and *location* significantly affected abundance (Table 4.2a). When plotting total abundance from the model, using standardised values for the covariates, the results indicated no clear difference (as indicated by the overlapping 95% confidence intervals) in abundance between ecosystems across the three depth zones (Figure 4.2a).

Table 4.2: Results from the Wald's test run on the hierarchical generalised additive models (HGAMs) investigating **(a)** the effect of *ecosystem* and *depth zone* and **(b)** the effect of *depth zone*, *ecosystem* and *location* on total abundance. Bold values indicate significant effect. df = degrees of freedom; edf = estimated degrees of freedom

	Parametric terms:	**df**	**Chi.sq**	**p-value**
(a) Effect of ecosystem and depth	Depth zone	2	0.34	0.843
	Ecosystem	1	6.99	**0.008**
	Depth zone: Ecosystem	2	1.81	0.41
	Smooth terms:	**edf**	**Chi.sq**	**p-value**
	s(Visibility)	0.00	0.00	0.603
	s(Water column)	0.00	0.00	1.000
	s(Temperature)	0.36	0.96	0.199
	s(Average relief)	1.49	10.26	**0.042**
	s(Location)	1.49	6.89	**0.023**
	s(Bottom type)	3.70	22.35	**<0.001**
	Parametric terms:	**df**	**Chi.sq**	**p-value**
(b) Effect of ecosystem, depth and location	Depth zone	2	4.71	0.095
	Ecosystem	1	15.55	**<0.001**
	Location	2	13.04	**0.001**
	Depth zone: Ecosystem	2	7.18	**0.027**
	Depth zone: Location	4	8.39	0.078
	Ecosystem: Location	2	12.16	**0.002**
	Depth zone: Location: Ecosystem	4	10.85	**0.028**
	Smooth terms:	**edf**	**Chi.sq**	**p-value**
	s(Visibility)	0.00	0.00	0.760
	s(Water column)	0.00	0.00	0.684
	s(Temperature)	0.00	0.00	0.496
	s(Average relief)	0.44	0.65	0.284
	s(Bottom type)	3.36	16.49	**<0.001**

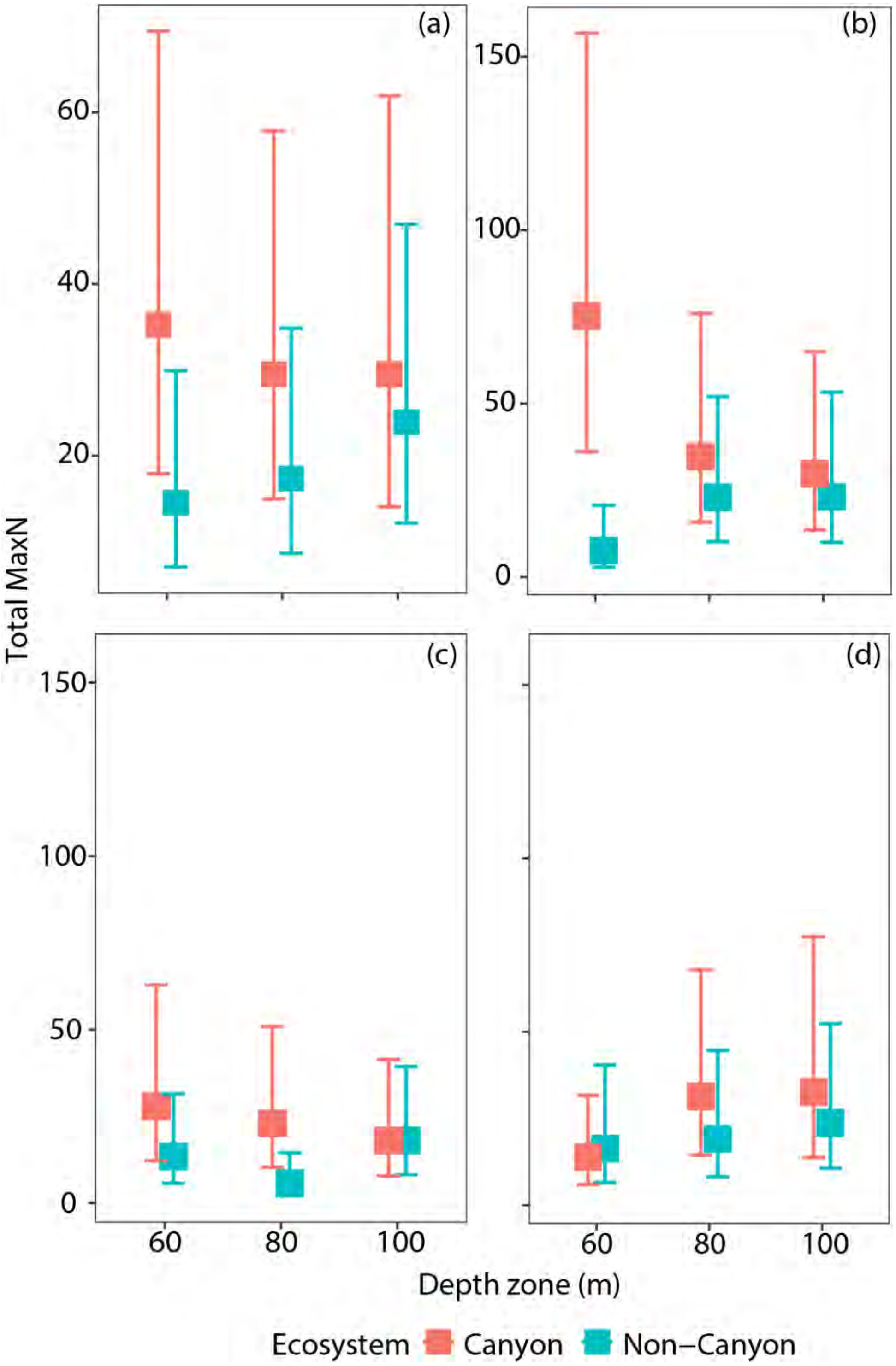


Figure 4.2: Predicted total abundance from the hierarchical generalised additive models (HGAMs) investigating **(a)** the effect of *ecosystem* and *depth zone* and the effect of *ecosystem* and *depth zone* at the different locations: **(b)** Diepgat **(c)** Levens and **(d)** Wright (*location*). The data presented are the predicted mean and 95 % confidence intervals (based on standardised mean values for all covariates included in the model).

b. Testing the effect of *ecosystem, depth zone* and *location*

The HGAM run on the total abundance data when *location* was considered as a factor along with *ecosystem* and *depth zone,* explained 75% of the variability in the dataset. Results from the Wald's test (Table 4.2b), indicated that *ecosystem* and *location* had a significant effect on total abundance, whereas *depth zone* showed no effect. The random effect of *bottom type* had a significant effect on abundance (Table 4.2b). The interaction between *ecosystem* x *depth zone* and *ecosystem* x *location*, as well as the three-way interaction between *ecosystem* x *depth zone* x *location*, also had a significant effect on abundance (Table 4.2b). To investigate these significant interactions, the predicted plot based on standardised covariates depicted that this pattern is driven by the differences between the ecosystems in the 60 m depth zone at Diepgat where higher abundances were recorded in the canyon ecosystem, relative to the non-canyon ecosystem (Figure 4.2b).

4.4.2.2 TOTAL BIOMASS

a. Testing the effect of *ecosystem* and *depth zone*

The HGAM run on total biomass data was able to explain only 5.53% of the variability in the dataset. Results from the Wald's test (Table 4.3a), indicated that both *ecosystem* and *depth zone*, as well as the interaction between *ecosystem* and *depth zone*, had no effect on total biomass. This suggests that, over the sampled depth zone and when treating *bottom type* and *location* as random effects, there was no underlying pattern in total biomass. When plotting total biomass from the model, using standardised values for the covariates, the results indicated no clear difference (as indicated by the overlapping 95% confidence intervals) in biomass between ecosystems across the three depth zones (Figure 4.3a).

Table 4.3: Results from the Wald's test run on the hierarchical generalised additive models (HGAMs) investigating **(a)** the effect of *ecosystem* and *depth zone* and **(b)** the effect of *depth zone*, *ecosystem* and *location* on total biomass. Bold values indicate significant effects. df = degrees of freedom; edf = estimated degrees of freedom

	Parametric terms:	**df**	**F-value**	**p-value**
(a) Effect of ecosystem and depth	Depth zone	2	0.91	0.410
	Ecosystem	1	0.04	0.845
	Depth zone: Ecosystem	2	1.61	0.211
	Smooth terms:	**edf**	**F-value**	**p-value**
	s(Visibility)	0.00	0	0.424
	s(Water column)	0.00	0	0.764
	s(Temperature)	0.00	0	0.692
	s(Average relief)	0.00	0	0.560
	s(Location)	0.00	0	0.546
	s(Bottom type)	0.00	0	0.697
	Parametric terms:	**df**	**F-value**	**p-value**
(b) Effect of ecosystem, depth and location	Depth zone	2	2.12	0.135
	Ecosystem	1	1.65	0.208
	Location	2	7.08	**0.003**
	Depth zone: Ecosystem	2	1.45	0.247
	Depth zone: Location	4	3.11	**0.027**
	Ecosystem: Location	2	3.50	**0.041**
	Depth zone: Location: Ecosystem	4	0.96	0.441
	Smooth terms:	**edf**	**F-value**	**p-value**
	s(Visibility)	0.47	0.19	0.219
	s(Water column)	0.00	0.00	0.573
	s(Temperature)	0.00	0.00	0.768
	s(Average relief)	0.00	0.00	0.464
	s(Bottom type)	0.00	0.00	0.966

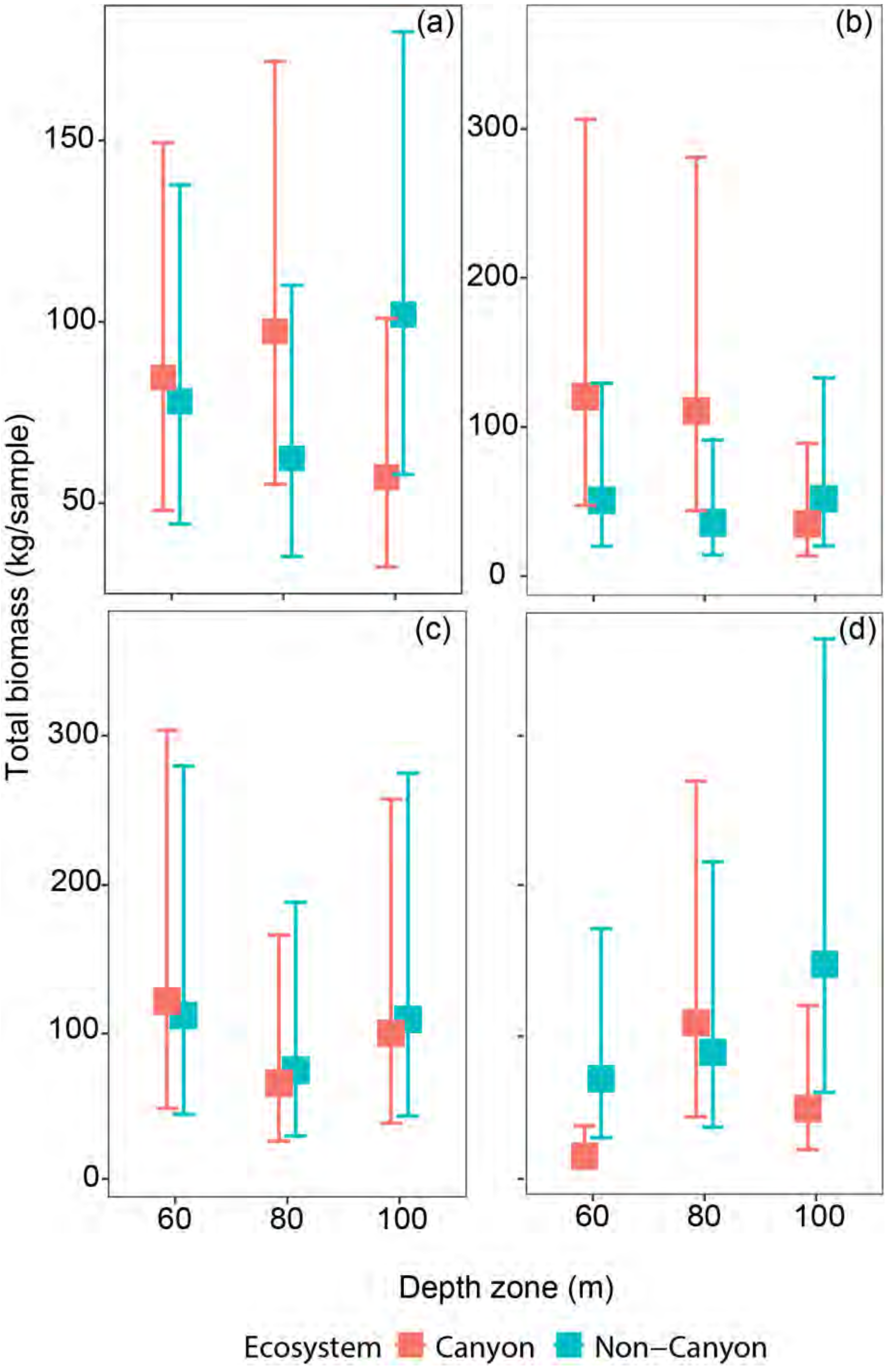


Figure 4.3: Predicted total biomass from the hierarchical generalised additive models (HGAMs) investigating **(a)** the effect of *ecosystem* and *depth zone* and the effect of *ecosystem* and *depth zone* at the different locations: **(b)** Diepgat **(c)** Levens and **(d)** Wright (*location*). The data presented are the predicted mean and 95 % confidence intervals (based on standardised mean values for all covariates included in the model).

b. Testing the effect of *ecosystem, depth zone* and *location*

The HGAM run on the total biomass data when *location* was considered as a factor along with *ecosystem* and *depth zone,* explained 35.7% of the variability in the dataset. The results showed that *location* had a significant effect on total biomass, whereas *ecosystem* and *depth zone* showed no effect (Table 4.3b). The interaction between *location* x *depth zone* and *location* x *ecosystem* had a significant effect on total biomass (Table 4.3b). The predicted plot, based on standardised covariates, depicted higher total biomass in the canyon ecosystem at the 60 m and 80 m depth zones at Diepgat (Figure 4.3b) and higher total biomass at the 60 m and 100 m depth zone in the non-canyon ecosystem at Wright (Figure 4.3d).

4.4.2.3 SPECIES RICHNESS

a. Testing the effect of *ecosystem* and *depth zone*

The HGAM run on species richness data was able to explain 37.2% of the variation in the dataset. Similar to total biomass, results from the Wald's test (Table 4.4a), indicated that both *ecosystem* and *depth zone*, as well as the interaction between ecosystem and depth zone, had no effect on species richness. *Average relief* had a significant effect on species richness (Table 4.4a), with richness increasing from low relief (0) to moderate relief (2-2.5). However further increases in relief, above 2.5, did not correspond to measurable increases in species richness (Figure A.3). When potting species richness from the model, using standardised values for the covariates included in the model, the results indicated no clear difference (as indicated by the overlapping 95% confidence intervals) in species richness between ecosystems across the three depth zones (Figure 4.4a).

Table 4.4: Results from the Wald's test run on the hierarchical generalised additive models (HGAMs) investigating **(a)** the effect of *ecosystem* and *depth zone* and **(b)** the effect of *depth zone*, *ecosystem* and *location* on species richness. Bold values indicate significant effects. df = degrees of freedom; edf = estimated degrees of freedom

	Parametric terms:	**df**	**Chi.sq**	**p-value**
(a) Effect of ecosystem and depth	Depth zone	2	1.25	0.534
	Ecosystem	1	0.52	0.472
	Depth zone: Ecosystem	2	1.54	0.462
	Smooth terms:	**edf**	**Chi.sq**	**p-value**
	s(Visibility)	0.00	0.00	0.413
	s(Water column)	0.18	0.23	0.266
	s(Temperature)	0.00	0.00	0.844
	s(Average relief)	1.60	7.45	**0.023**
	s(Location)	1.52	0.69	0.271
	s(Bottom type)	2.15	4.82	0.053
	Parametric terms:	**df**	**Chi.sq**	**p-value**
(b) Effect of ecosystem, depth and location	Depth zone	2	1.43	0.489
	Ecosystem	1	7.68	**0.006**
	Location	2	3.09	0.213
	Depth zone: Ecosystem	2	6.75	0.034
	Depth zone: Location	4	3.02	0.555
	Ecosystem: Location	2	7.33	**0.025**
	Depth zone: Location: Ecosystem	4	9.89	**0.042**
	Smooth terms:	**edf**	**Chi.sq**	**p-value**
	s(Visibility)	0.00	0.00	0.356
	s(Water column)	0.43	0.86	0.187
	s(Temperature)	0.00	0.00	0.630
	s(Average relief)	0.00	0.00	0.351
	s(Bottom type)	2.31	5.89	**0.029**

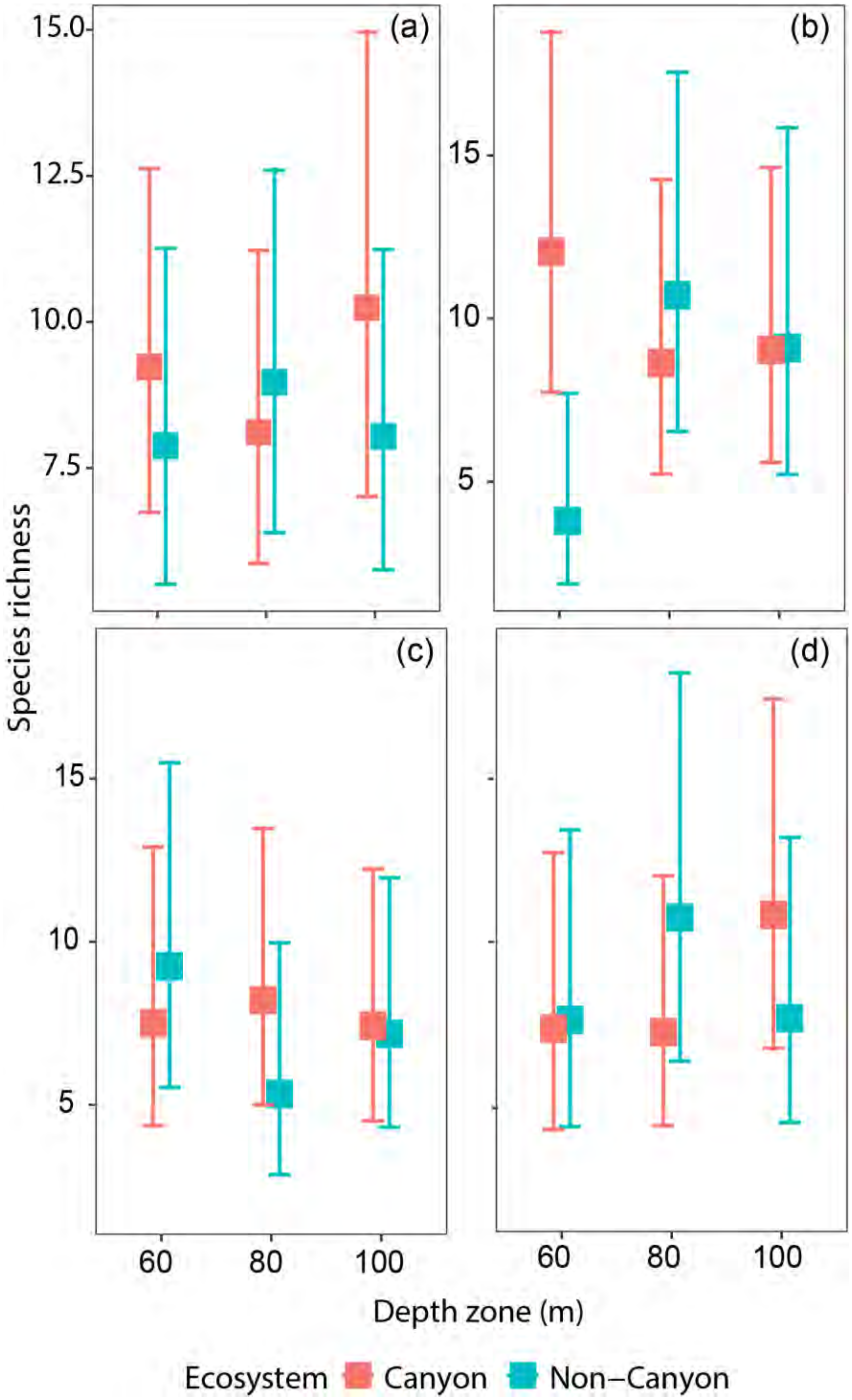


Figure 4.4: Predicted species richness from the hierarchical generalised additive models (HGAMs) investigating **(a)** the effect of *ecosystem* and *depth zone* and the effect of *ecosystem* and *depth zone* at the different locations: **(b)** Diepgat **(c)** Levens and **(d)** Wright (*location*). The data presented are the predicted mean and 95 % confidence intervals (based on standardised mean values for all covariates included in the model).

b. Testing the effect of *ecosystem, depth zone* and *location*

When *location* was considered as a factor along with *ecosystem* and *depth zone,* the HGAM run on the species richness data was able to explain 51.2% of the variation in the dataset. Results from the Wald's test (Table 4.4b), indicated that the random effect of *bottom type* had a significant effect on species richness. *Depth zone* and *location* showed no effect on species richness whereas *ecosystem* had a significant effect (Table 4.4b), with significantly higher richness detected in the canyon ecosystem relative to the non-canyon ecosystem (Figure A.4). The interaction between *location* x *ecosystem* and the three-way interaction between *ecosystem* x *depth zone* x *location* also had a significant effect on species richness (Table 4.4b). To investigate these significant interactions, the predicted plot based on standardised covariates depicted that this pattern is driven by significantly higher species richness in the canyon ecosystem of Diepgat at the 60 m depth zone (Figure 4.4b).

4.4.2.4 PIELOU'S EVENNESS

a. Testing the effect of *ecosystem* and *depth zone*

The HGAM run on Pielou's evenness data was able to explain 55.4% of the variability in the dataset. Results from the Wald's test (Table 4.5a), indicated that *ecosystem* had a significant effect on Pielou's evenness, with significantly higher values recorded in the non-canyon ecosystem (0.876 ± 0.118 species/sample) relative to the canyon ecosystem (0.727 ± 0.139 species/sample) (Figure A.5). *Water column* had a significant effect on Pielou's evenness. When keeping all of the covariates standard, the predicted data showed that the Pielou's evenness was higher in the non-canyon ecosystem in all depth zones (Figure 4.5a)

Table 4.5: Results from the Wald's test run on the hierarchical generalised additive models (HGAMs) investigating **(a)** the effect of *ecosystem* and *depth zone* and **(b)** the effect of *depth zone*, *ecosystem* and *location* on Pielou's evenness. Bold values indicate significant effects. df = degrees of freedom; edf = estimated degrees of freedom

	Parametric terms:	**df**	**Chi.sq**	**p-value**
(a) Effect of ecosystem and depth	Depth zone	2	0.89	0.640
	Ecosystem	1	6.87	**0.009**
	Depth zone: Ecosystem	2	1.10	0.577
	Smooth terms:	**edf**	**Chi.sq**	**p-value**
	s(Visibility)	0.00	0.00	0.487
	s(Water column)	0.84	6.10	**0.012**
	s(Temperature)	1.22	3.65	0.082
	s(Average relief)	0.00	0.00	0.574
	s(Location)	1.06	2.20	0.122
	s(Bottom type)	1.38	2.09	0.184
	Parametric terms:	**df**	**Chi.sq**	**p-value**
(b) Effect of ecosystem, depth and location	Depth zone	2	1.90	0.326
	Ecosystem	1	12.18	**<0.001**
	Location	2	12.16	**0.002**
	Depth zone: Ecosystem	2	4.75	0.093
	Depth zone: Location	4	13.58	**0.009**
	Ecosystem: Location	2	9.32	**0.009**
	Depth zone: Location: Ecosystem	4	15.29	**0.004**
	Smooth terms:	**edf**	**Chi.sq**	**p-value**
	s(Visibility)	0.81	1.49	0.175
	s(Water column)	0.00	0.00	0.611
	s(Temperature)	0.36	0.58	0.216
	s(Average relief)	0.86	1.65	0.218
	s(Bottom type)	2.90	11.15	**0.002**

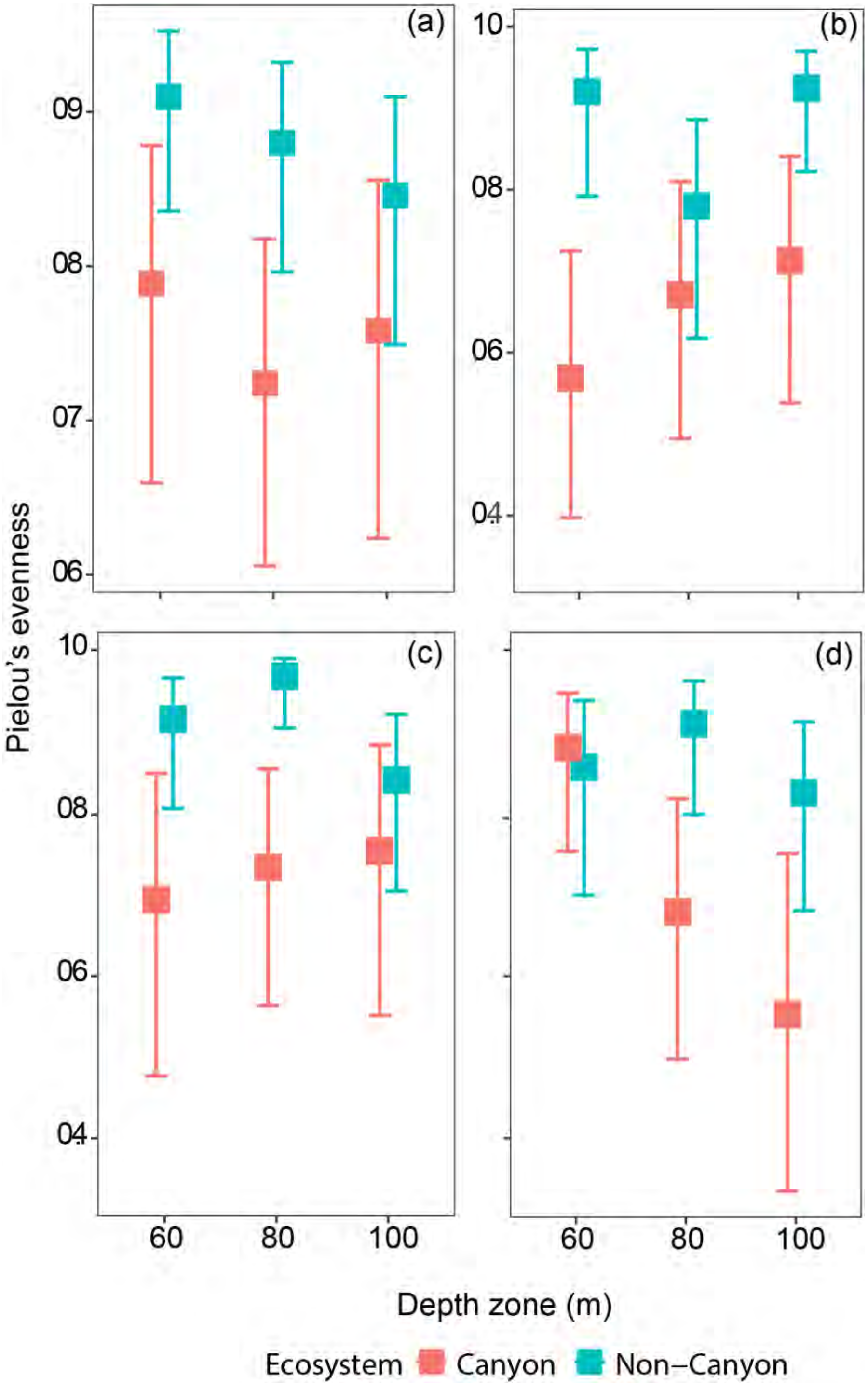


Figure 4.5: Predicted Pielou's evenness from the hierarchical generalised additive models (HGAMs) investigating **(a)** the effect of *ecosystem* and *depth zone* and the effect of *ecosystem* and *depth zone* at the different locations: **(b)** Diepgat **(c)** Levens and **(d)** Wright (*location*). The data presented are the predicted mean and 95 % confidence intervals (based on standardised mean values for all covariates included in the model).

b. Testing the effect of *ecosystem, depth zone* and *location*

When *location* was considered as a factor along with *ecosystem* and *depth zone,* the HGAM model run on Pielou's evenness data was able to explain 78.9% of the variability in the dataset. Results from the Wald's test (Table 4.5b), indicated that the random effect of *bottom type* had a significant effect on Pielou's evenness. *Ecosystem* and *location* showed a significant effect on evenness whereas, *depth zone* showed no effect (Table 4.5b). The interaction between *location* x *depth zone* and *location* x *ecosystem*, as well as the three way interaction between *ecosystem* x *depth zone* x *location*, also had a significant effect on evenness (Table 4.5b). The predicted plot based on standardised covariates depicted higher evenness in the non-canyon ecosystem in the 60 m depth zone at Diepgat (Figure 4.5b) and higher evenness in the 80 m depth zone at Levens (Figure 4.5c). Both Diepgat and Levens showed an increase in evenness with increase in depth in the canyon ecosystem (Figure 4.5b and c respectively) compared to the Wright where there was a decrease in evenness with increase in depth (Figure 4.5d).

4.4.2.5 LOCAL CONTRIBUTION TO BETA-DIVERSITY

a. Testing the effect of *ecosystem* and *depth zone*

The HGAM run on the LCBD data was able to explain 52% of the variability in the dataset and the results from the Wald's test (Table 4.6a) indicated that only *depth zone* had a significant effect on LCBD and this pattern was driven by the 60 m samples, which contributed more to beta diversity compared to 80 m and 100 m samples (Figure 4.6a).

Table 4.6: Results from the Wald's test run on the hierarchical generalised additive models (HGAMs) investigating **(a)** the effect of *ecosystem* and *depth zone* and **(b)** the effect of *depth zone*, *ecosystem* and *location* on local contribution to beta-diversity (LCBD). Bold values indicate significant effects. df = degrees of freedom; edf = estimated degrees of freedom

	Parametric terms:	**df**	**Chi.sq**	**p-value**
(a) Effect of ecosystem and depth	Depth zone	2	20.52	**<0.001**
	Ecosystem	1	0.07	0.798
	Depth zone: Ecosystem	2	1.12	1.572
	Smooth terms:	edf	Chi.sq	p-value
	s(Visibility)	0.47	1.00	0.164
	s(Water column)	0.97	2.52	0.077
	s(Temperature)	0.00	0.00	0.650
	s(Average relief)	1.15	2.00	0.195
	s(Location)	1.06	2.28	0.103
	s(Bottom type)	0.00	0.00	0.388
	Parametric terms:	df	Chi.sq	p-value
(b) Effect of ecosystem, depth and location	Depth zone	2	39.06	**<0.001**
	Ecosystem	1	3.73	0.054
	Location	2	7.64	**0.022**
	Depth zone: Ecosystem	2	14.88	**<0.001**
	Depth zone: Location	4	13.09	**0.010**
	Ecosystem: Location	2	6	**0.049**
	Depth zone: Location: Ecosystem	4	14.09	**0.007**
	Smooth terms:	edf	Chi.sq	p-value
	s(Visibility)	0.29	0.42	0.232
	s(Water column)	0.52	0.82	0.196
	s(Temperature)	0.00	0.00	0.809
	s(Average relief)	1.88	8.99	**0.009**
	s(Bottom type)	0.71	0.88	0.259

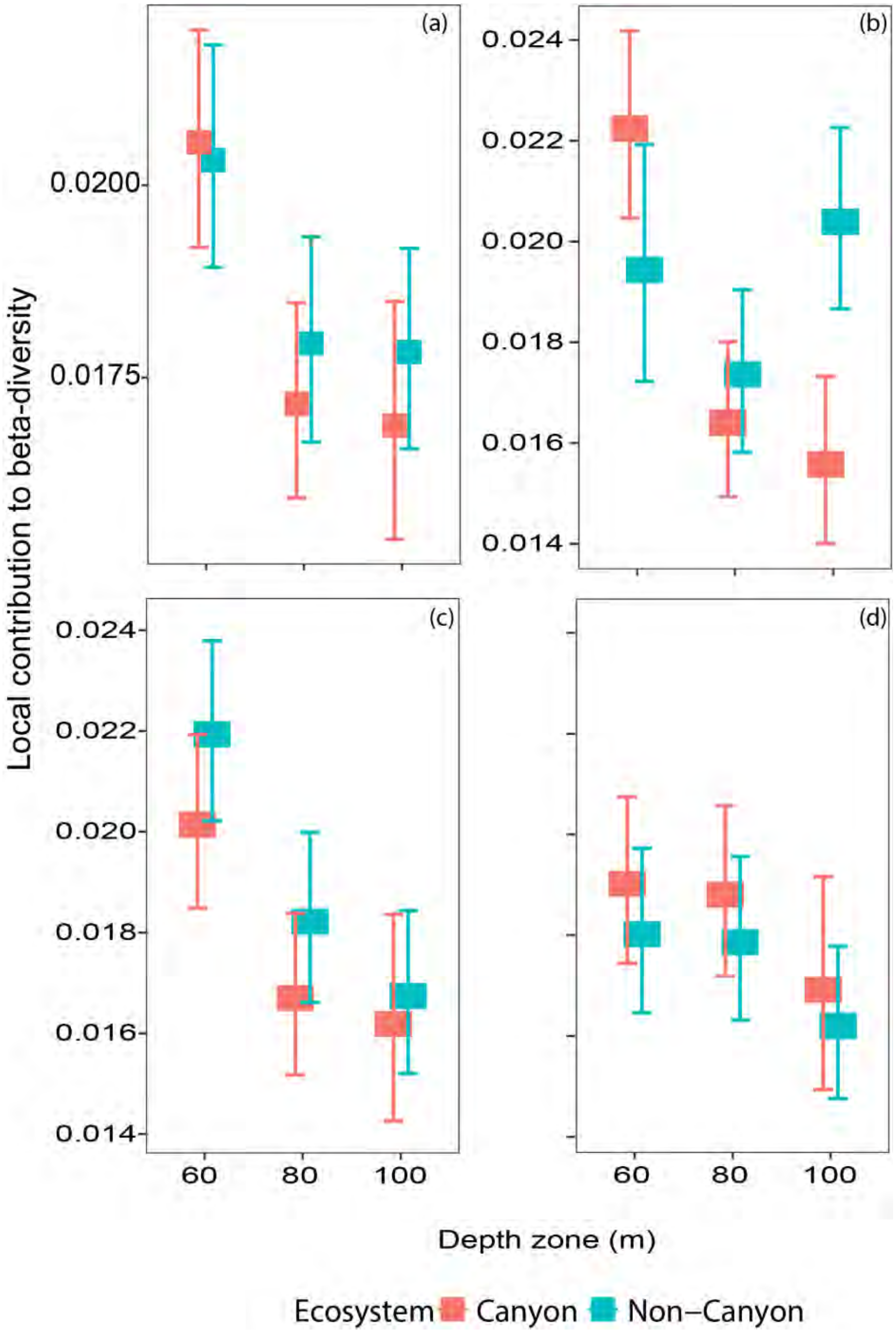


Figure 4.6: Predicted local contribution to beta-diversity (LCBD) from the hierarchical generalised additive models (HGAMs) investigating **(a)** the effect of *ecosystem* and *depth zone* and the effect of *ecosystem* and *depth zone* at the different locations: **(b)** Diepgat **(c)** Levens and **(d)** Wright (*location*). The data presented are the predicted mean and 95 % confidence intervals (based on standardised mean values for all covariates included in the model).

b. Testing the effect of *ecosystem, depth zone* and *location*

When *location* was considered as a factor along with *ecosystem* and *depth zone,* the HGAM run on the LCBD data was able to explain 78.6% of the variability in the dataset. Results from the Wald's test (Table 4.6b), indicated that *average relief* had a significant effect on LCBD. In contrast to all the above response variables, the results indicated a significant effect of *depth zone,* as well as *location* on LCBD, whereas *ecosystem* showed no effect (Table 4.6b). All the interactions (*depth zone* x *ecosystem*, *depth zone x location*, *ecosystem* x *location* and *depth zone* x *ecosystem* x *location*) also had an effect on LCBD (Table 4.6b). The predicted plot based on standardised covariates depicted significantly higher LCBD for the non-canyon ecosystem at the 100 m depth zone at Diepgat (Figure 4.6b). A decrease in LCBD with increase in depth at Levens was observed, suggesting that samples in the 60 m depth zone contributed more to beta-diversity compared to the samples in the 100 m depth zone (Figure 4.6c). An inconsistent pattern was observed at Wright (Figure 4.6d).

4.4.3 MULTIVARIATE RESULTS

4.4.3.1 SPECIES COMPOSITION

A total of 1479 fish belonging to 30 families were identified from the 54 stereo-BRUVs deployments (full species list in appendix Table A.3). Of the total fish recorded, 69.77% were recorded in the canyon systems. Species recorded only in the canyon ecosystem include *Caranx ignobilis* (giant kingfish), *Seriola dumerili* (greater amberjack) and *Epinephelus malabaricus* (malabar grouper). Species recorded only in the non-canyon ecosystem (30.22%) include species such as *Rhinobatos leucospilus* (grayspottted guitarfish) and *Pagellus bellottii natalensis* (sand soldier). The most abundant species in both the canyon and non-canyon ecosystem was

Chrysoblephus puniceus (slinger) with n = 233 and 85 respectively. More species were recorded in the 100 m depth zone (35.63%), relative to 60 m (32.86%) and 80 m (31.50%). The species recorded only in the 100 m depth zone include *S. dumerili* and *Polysteganus undulosus* (seventy-four). The species recorded only in the 80 m depth zone include *Aulacocephalus temminckii* (goldribbon soapfish) and recorded only in the 60 m depth zone was species such as *Carcharhinus sealei* (blackspot shark). *Chrysoblephus puniceus* was the most abundant species in in the 100 m and 80 m depth zones (n = 200 and 118 respectively) whereas the *Paracaesio xanthura* (yellowtail false fusilier) was the most abundant species in 60 m depth zone (n = 151). With Location, more species were recorded in Diepgat (44.89%) relative to Wright (31.84%) and Levens (23.25%). Species recorded only at Diepgat include *S. dumerili*. The species only recorded at Wright include *E. malabaricus* and *Sphyrna mokarran* (great hammerhead) and recorded only at Levens were species such as *P. undulosus*. *Paracaesio xanthura* was the most abundant species at Diepgat (n = 154) and *C. puniceus* was the most abundant species at both Wright and Levens with n = 147 and 75 respectively. In the entire study, Serranidae was the most diverse family with 13 species followed by Sparidae with ten species and Labridae with nine species. The most abundant species in the entire study were *C. puniceus* (n = 318), *P. xanthura* (n = 228), *Pristipomoides filamentosus* (rosy jobfish) (n = 130) and *Cheimerius nufar* (santer) (n = 105) (Table A.3).

4.4.3.2 ABUNDANCE

Results from the PERMANOVA run on the abundance data indicated that *ecosystem*, *depth zone*, *location, water column*, *temperature*, *average relief*, as well as the interaction between *ecosystem* and *depth zone* all significantly influenced the fish assemblage structure, whereas *visibility* showed no effect (Figure 4.7). Further, pair-wise comparisons revealed that the difference between the ecosystems was restricted to the 100 m depth zone (t = 1.4, P = 0.014). From the PCO plots, the results indicated that the canyon ecosystem at 100 m was typified by patched reef and reef with high relief whereas the 60 m depth zone was typified by sand with cobbles (Figure 4.7b). In contrast, the non-canyon ecosystem at 60 m was correlated with flat sandy habitats (Figure 4.7b). In this regard, patch reef and reef habitats with high relief at 100 m in the canyon were characterised by species such as the *Epinephelus poecilonotus* (dot-dash grouper), *Polysteganus coeruleopunctatus* (blueskin), *C. puniceus* and *Polysteganus praeorbitalis* (scotsman) (Figure 4.7a). In contrast, at 60 m the non-canyon ecosystem was correlated to *Lagocephalus sceleratus* (silver-cheeked toadfish) and the canyon ecosystem was correlated to *P. xanthura* (Figure 4.7a)

Table 4.7: Results from the sequential permutational multivariate analysis of variance (PERMANOVA) based on modified Gower (logbase10) distances testing the effect of *location, ecosystem* and *depth zone* together with selected covariates on the multivariate fish abundance data. Bold values indicate a significant effect. df = degrees of freedom; MS = mean square; Pseudo-F = F-ratios; P (perm) probability level based on permutations.

Source	**Df**	**SS**	**MS**	**Pseudo-F**	**P (perm)**
Visibility	1.00	0.75	0.75	1.45	0.051
Water column	1.00	1.51	1.51	3.14	**<0.001**
Temperature	1.00	2.27	2.27	4.51	**<0.001**
Average relief	1.00	1.08	1.08	2.16	**0.001**
Location	2.00	1.25	0.62	1.44	**0.019**
Ecosystem (Ec)	1.00	1.15	1.15	2.44	**<0.001**
Depth zone (DZ)	2.00	2.17	1.08	2.29	**<0.001**
Ec x DZ	1.00	1.05	1.05	2.22	**0.001**
Residual	43.00	20.38	0.48		
Total	53.00	31.74			

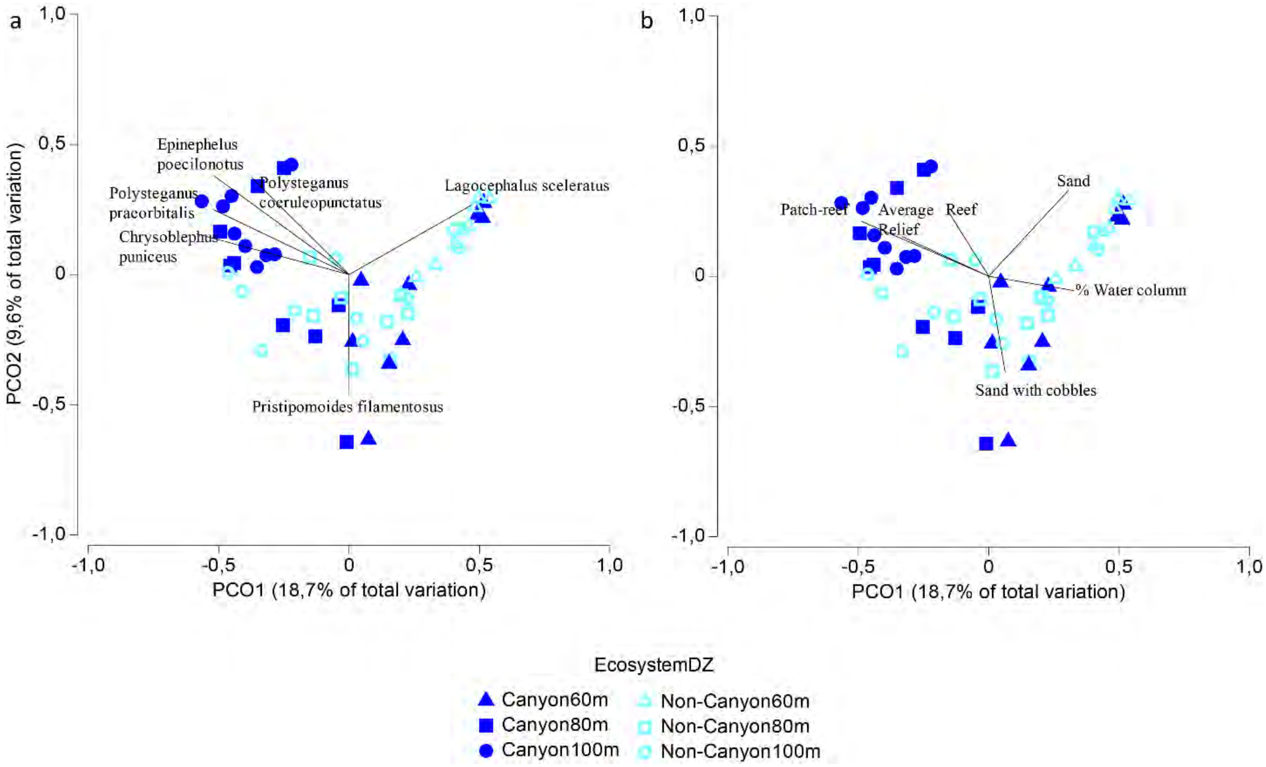


Figure 4.7: Results from the principle coordinate analysis (PCO) run on abundance data, showing the effect of *ecosystem* and *depth zone* on the fish community structure with Pearson's correlation vectors for **(a)** fish species (R = 0.5) and **(b)** bottom type and environmental (R=0.3) variables overlaid. The length and direction of each vector indicate the strength of the correlation.

According to the SIMPER analysis on the combined factors *ecosystem* and *depth zone*, *C. nufar* was very well represented, with contributions to all groups, whereas species such as *Echeneis naucrates* (shark remora) and *L. sceleratus* were typical high contributors to abundance at the 60 m depth zone, in both ecosystems (Table A.4). The dissimilarity was smallest between canyon 80 m and canyon 100 m (69.46%), and largest between canyon 100 m and non-canyon 60 m (97.68%) (Table A.5). The dissimilarity between canyon 80 m and canyon 100 m was due to differences in abundances of *C. puniceus*, *P. coeruleopunctatus*, *P. xanthura* and *C. nufar*, all of which decreased in abundance from canyon 100 m to canyon 80 m (Table A.5). Dissimilarity between canyon 100 m and non-canyon 60 m was due to differences in abundances of *C. puniceus*, *P.*

coeruleopunctatus, *P. xanthura* and *L. sceleratus*, all of which decreased in abundance from canyon 100 m to non-canyon 60 m except for *L. sceleratus* (Table A.5).

4.4.3.3 TOTAL BIOMASS

Similar to abundance, results from the PERMANOVA run on species biomass data indicated that *ecosystem*, *depth zone*, *location, water column*, *temperature*, *average relief*, as well as the interaction between *ecosystem* and *depth zone* all significantly influenced the fish assemblage structure, whereas *visibility* showed no effect (Table 4.8). For biomass, pairwise comparisons revealed no differences between the ecosystems at all sampled depth zones. However, from the PCO plots (Figure 4.8), the results indicated that the 100 m depth zone in the canyon was typified by patched reef with high relief (Figure 4.8b). At 60 m, the canyon ecosystem was typified by sand with sea pens while the non-canyon ecosystem at 60 m was highly correlated with sand (Figure 4.8b). In this regard, patched reef with high relief was characterised by species such as *P. praeorbitalis* (Figure 4.8a). At 60 m, the canyon ecosystem was typified by *Carcharhinus limbatus* (blacktip shark) and *Argyrops spinifer* (king soldierbream), while the non-canyon ecosystem was typified by *L. sceleratus* and *R. leucospilus* (Figure 4.8a).

Table 4.8: Results from the sequential permutational multivariate analysis of variance (PERMANOVA) based on modified Gower (logbase10) distances testing the effect of *location, ecosystem* and *depth zone* together with selected covariates on the multivariate fish biomass data. Bold values indicate a significant effect. df = degrees of freedom; MS = mean square; Pseudo-F = F-ratios; P (perm) probability level based on permutations.

Source	**Df**	**SS**	**MS**	**Pseudo-F**	**P (perm)**
Visibility	1.00	4.49	4.49	2.49	0.051
Water column	1.00	3.17	3.17	1.91	**0.010**
Temperature	1.00	5.08	5.08	2.85	**<0.001**
Average relief	1.00	3.72	3.72	2.08	**0.004**
Location	2.00	4.85	2.42	1.47	**0.025**
Ecosystem (Ec)	1.00	3.75	3.75	2.27	**0.002**
Depth zone (DZ)	2.00	4.52	2.26	1.37	**0.002**
Ec x DZ	2.00	4.86	2.43	1.47	**0.02**
Residual	37.00	60.96	1.65		
Total	48.00	95.44			

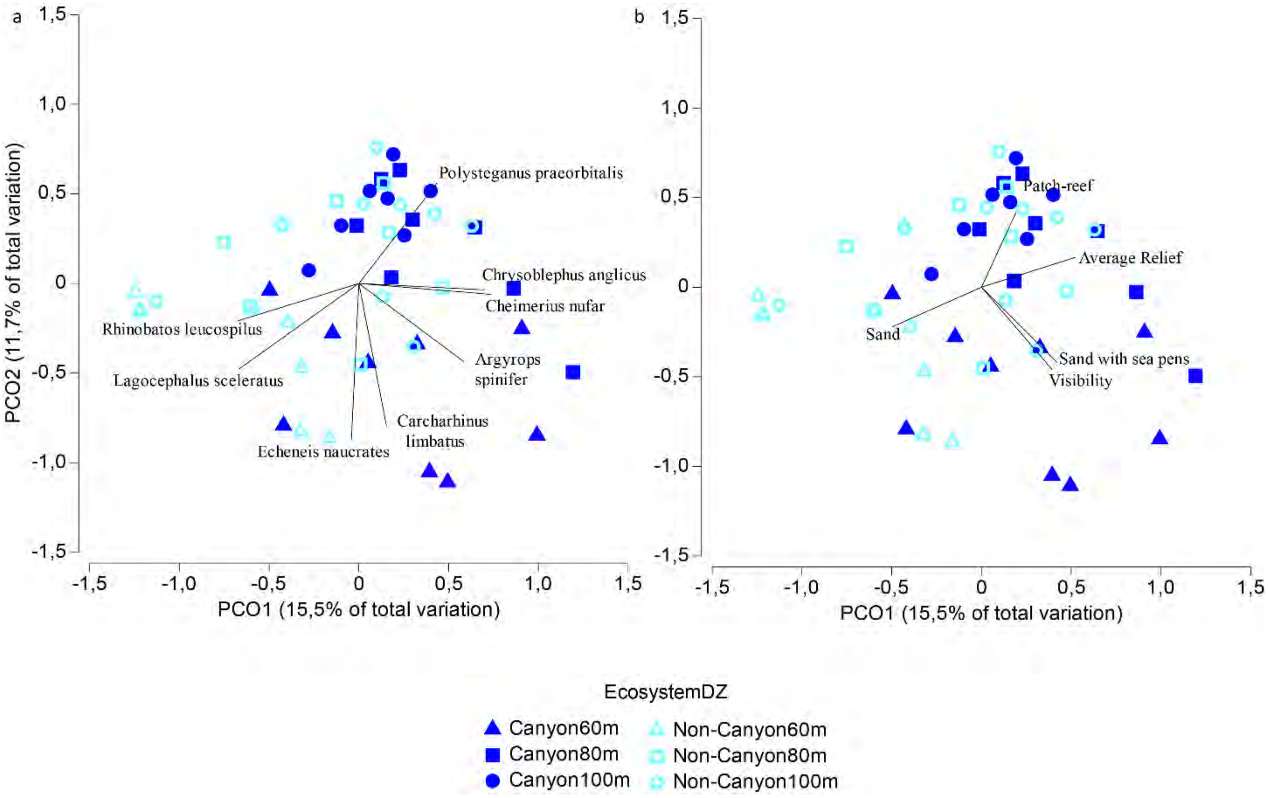


Figure 4.8: Results from the principle coordinate analysis (PCO) run on biomass data, showing the effect of *ecosystem* and *depth zone* on the fish community structure with Pearson's correlation vectors for **(a)** fish species (R = 0.5) and **(b)** bottom type and environmental (R=0.3) variables overlaid. The length and direction of each vector indicate the strength of the correlation.

For total biomass, the SIMPER analysis on the combined factors *ecosystem* and *depth zone* showed *C. nufar* was once again very well represented, with contributions to all groups except for the 60 m depth zone in the non-canyon ecosystem which was typified by higher biomasses of *C. limbatus*, *L. sceleratus* and *R. leucospilus* (Table A.6). Similar to abundance, the dissimilarity for biomass data was smallest between canyon 80 m and canyon 100 m (80.06%) and largest between canyon 100 m and non-canyon 60 m (97.21%) (Table A.7). The dissimilarity between canyon 80 m and canyon 100 m was due to differences in biomass of *Seriola rivoliana* (longfin amberjack), *Epinephelus marginatus* (yellowbelly grouper) and *C. puniceus*, all of which decreased in biomass from canyon

100 m to canyon 80 m. Dissimilarity between canyon 100 m and non-canyon 60 m was due to differences in biomass of *C. limbatus*, *C. puniceus* and *S. rivoliana*. *Carcharhinus limbatus* was only encountered at non-canyon 60 m, while both *C. puniceus* and *S. rivoliana* were only encountered in the canyon 100 m.

4.5 DISCUSSION

The main aims of this chapter were to investigate the patterns of diversity and community structure of benthic fish within the canyon and non-canyon ecosystems of the IWP MPA, and also characterise predictors that may explain the observed patterns. In addition to investigating these patterns, I assessed whether the patterns observed were consistent between different but nearby canyon ecosystems. Overall, there were higher abundances, and lower evenness and LCBD in the canyon ecosystem compared to the non-canyon ecosystem, and inconsistent patterns were observed at the different sampling locations. The benthic fish community in the study area differed significantly between the canyon and non-canyon ecosystem and among the sampled depth zones with evidence for bottom type and relief driving these differences.

4.5.1 PATTERNS IN ABUNDANCE, BIOMASS AND DIVERSITY

The results from this study indicated that location and the interaction of location with ecosystem and depth zone had a significant influence on the univariate metrics, with an exception of species richness. The sampled locations in this study were different in terms of habitat structure and average relief, both of which have been shown to result in high spatial variability of the benthic communities (Cunha et al. 2011). In the Portuguese submarine canyons, an effect of location on macrofaunal assemblages was observed by Cunha et al. (2011). The authors suggested that the influx of sediments in these very active canyon systems resulted in the canyons being different from the open slope which would have been able to explain the variability observed. Alternatively, the high variability observed within the canyons of IWP may be a result of a sampling artifact, linked to the low number of replicate samples (n = 3). The small sample size, when paired with patchy habitats within each ecosystem and among locations, would have increased variability in the dataset, and led to an inability to account for fine scale processes associated with specific habitats.

Species abundance was significantly different between the two ecosystems, with higher abundances observed in the canyon compared to the non-canyon ecosystem. However, when abundance was predicted based on standardised covariates, there were no clear differences between the ecosystems. Average relief was greater in the canyon ecosystems and also had a significant effect of abundance, with higher relief associated with higher abundance. Therefore, it is possible that the observed difference in abundance between the two ecosystems was driven by the difference in relief. Our findings of greater abundances in the canyons compared to the adjacent non-canyon ecosystem is consistent with findings from other studies investigating fish within canyons and adjacent slope. For example, when the influence of a submarine canyon on fish assemblages was investigated on the slope in the Catalan Sea (Western Mediterranean), higher fish abundances were found in the canyon compared to the slope habitat (Stefanescu et al. 1994). These authors concluded that higher abundances in the Catalan Sea submarine canyon were probably because of the role of the canyons in transporting sediments rich in organic matter from the shelf to deeper regions (Stefanescu et al. 1994). While it was possible that this process also contributed to greater abundance of fish in the canyons investigated here, the results suggest that the increased habitat complexity associated with canyons played a very important role in the observed pattern.

In contrast to abundance, evenness was higher in the non-canyon ecosystem compared to the canyon ecosystem. The trend of higher species evenness in the adjacent slope of submarine canyons has been documented in a range of systems and benthic taxa. For example, a study conducted by Gunton et al. (2015), found higher polychaete species evenness in the slope compared to the Whittard canyon system and suggested that this was a result of high physical disturbances within the canyon ecosystem. Greater nematode evenness was also recorded in the Nazaré non-canyon ecosystem, compared to the canyon ecosystem, when nematode diversity and association with the quantity and quality of sedimentary organic matter was investigated (Ingels et al. 2009). In the case of the canyon ecosystems within IWP, depressed evenness may be because of the greater variety of bottom type and relief observed in this ecosystem. The greater variety of bottom types and relief sampled in the canyon ecosystem would have increased the variability in the structure of the fish assemblage and, in turn, reduced the evenness.

The predicted HGAM plots showed that evenness decreased with increasing depth, meaning that species were more even in the 60 m depth zone compared to the 100 m depth zone, however, this pattern did not appear to be significant. A similar result was seen with LCBD data, where the 60 m samples contributed more to beta-diversity compared to the 80 and 100 m samples. This suggests that fish species at 80 and 100 m depth had a typically similar degree of uniqueness, compared to fish species at 60 m depth zone. Depth is an important factor that structures benthic fauna in marine ecosystems (De Leo et al. 2012, Piacenza et al. 2015, Heyns-Veale et al. 2016). However, bathymetric patterns of diversity for benthic fauna in submarine canyons and other marine ecosystems can be altered due to the complex interplay of multiple factors, such as increased nutrients input and habitat heterogeneity (McClain and Barry 2010, Vetter et al. 2010). Overall, the results in this study showed that depth didn’t have a strong influence on the predicted univariates metrics, with only LCBD showing a significant clear pattern along the depth gradient where LCBD decreased with the increase in depth. The lack of a clear influence of depth on the univariate metrics in this study may be attributed to the narrow sampled depth range (60 – 100 m).

In contrast, relief explained the greatest proportion of variance in the univariate data. Relief was greater in the canyon ecosystem, which was typified by reef and patched reef habitats and low in the non-canyon ecosystem which was characterised by mostly sandy habitats. The role of habitat complexity in shaping fish communities has been studied in a great number of marine ecosystems (Gratwicke and Speight 2005). It is hypothesised that habitat's complexity and heterogeneity may provide more niches and diverse ways of exploiting environmental resources thus increasing local species diversity (Willis et al. 2005). For this study, the results showed that species abundance and richness increased as the habitats increased from low to moderate complexity. Habitats complexity and heterogeneity have been found to explain fish biodiversity in other submarine canyons systems. For example, in the Hawaiian canyons Vetter et al. (2010) reported significantly higher faunal species richness and diversity was correlated with greater habitat heterogeneity. Vetter et al. (2010), suggested that different habitat features were essential structuring variables for the invertebrate megabenthos, yielding large dissimilarities between canyon and slope assemblages, and leading to higher invertebrate species richness and diversity in Hawaiian canyons.

4.5.2 COMMUNITY STRUCTURE

The results from the multivariate analysis, investigating patterns in fish assemblage’s structure between the ecosystems, depth zone and locations were similar to the results from the univariate analysis. The fish community structure differed significantly among the depth zones, between the canyon and non-canyon ecosystems and in the different locations. For community abundance and biomass, the pairwise comparisons revealed that the difference between the canyon and non-canyon ecosystem was within the 100 m depth zone. The physical nature of the canyon ecosystem at 100 m was high relief with a combination of reef and patched reef habitat. In comparison, the non-canyon habitats at 100 m were typified as a less complex habitat with low relief. It’s likely that the more complex nature of the canyon habitats was better suited for a distinct assemblage of fishes (including *P. coeruleopunctatus*, *C. puniceus* and *E. poecilonotus*), in comparison to the less complex habitats outside the canyons that were preferred by species such as *L. sceleratus* and *R. leucospilus*. At similar depths Sink et al. (2006), reported abundances of *C. puniceus* and *P. coeruleopunctatus* in rocky outcrops within these canyons suggesting species observed in this study are good representatives of the fish species found within the IWP canyons. *C. puniceus* and *P. coeruleopunctatus* were also responsible for the high dissimilarity between the canyon ecosystem at 100 m and the non-canyon ecosystem at 60 m. The non-canyon ecosystem at 60 m was characterised by low relief and sandy habitat with high abundances of *L. sceleratus*, a species which is known to occur in high abundances on sandy habitats (Kalogirou 2013). Conversely, at 60 m, the canyon ecosystem was characterised by sandy habitats with sea pens and cobbles which seemed to be preferred by high abundances of *P. filamentosus*.

The results from this study agree with previous studies that canyon ecosystems provide more complex benthic habitat compared to the adjacent non-canyon ecosystems, and this, in turn, alters the nature of the fish assemblage (Yoklavich et al. 2000, De Leo et al. 2010, Vetter et al. 2010). Different habitat types influence fish assemblages by providing many important functions such as food and shelter from predation (Bergström et al. 2016). The canyon ecosystems of IWP were typified by a range of bottom types (reef, patched reef, sand with sea pens) with high relief, in comparison to the non-canyon ecosystems, which was mostly typified by sandy bottoms with low relief. Bottom type has been found to be one of the key factors that influence fish assemblages in many marine ecosystems (Gonzalez-Sanson et al. 2009, Quattrini et al. 2015, Heyns-Veale et al. 2016), and it is likely that the increased complexity of the canyon seafloor played an important role in structuring the fish assemblage.

4.5.3 CONCLUSIONS

This chapter provides insight on the influence of submarine canyons on fish assemblages on the continental shelf edge within IWP. The results showed that at shallow depths of 60 – 100 m, the submarine canyons within IWP have an influence in fish assemblages on the continental shelf edge. The canyon ecosystem is characterised by heterogeneous habitats with high relief that support high abundances of fish compared to the non-canyon ecosystem. However, the patterns observed in the fish assemblage were not always consistent between replicate study locations, suggesting that local variability plays an important role in the structuring and functioning of the canyon and neighbouring non-canyon habitats. Future research in these canyons and their surrounding shelf habitats may be able to further isolate and understand the drivers of the observed results. This will likely require thorough oceanographic data collected within and around the submarine canyons together with measures of productivity and greater stereo-BRUVs sampling effort. Furthermore, investigating coexisting communities that have been found to differ between the canyon and slope habitat (Vetter and Dayton 1998; Ingels et al. 2009) may be able to explain the variability amongst these canyons. Overall, the results of this study suggest that the canyon heads are an important habitat for fish communities enhancing abundance and providing habitat for distinct fish assemblages.

CHAPTER 5

5 GENERAL DISCUSSION AND CONCLUSION

Marine ecosystems provide food security as well as social, economic and environmental benefits to a growing human population (Reid et al. 2005). However, due to overfishing, habitat degradation, pollution and climate change, many marine ecosystems are threatened (Reid et al. 2005). Submarine canyons are common geomorphic features that occur on the margins of all continents (Harris and Whiteway 2011, Harris et al. 2014), and the ecological significance of these ecosystems has been recognised as features associated with enhanced diversity, abundance and biomass of organisms (De Leo et al. 2012, Fernandez-Arcaya et al. 2017). In South Africa, iSimangaliso Wetland Park (IWP) in the Delagoa Ecoregion is characterised by numerous submarine canyons that are home to coelacanths *Latimeria chalumnae*, and a variety of commercially important line fish species. However, there is a lack of information on the ecosystem structure and the influence of these canyons on the continental shelf edge and slope ecosystems. The main aim of this thesis was to therefore to investigate the effect of submarine canyons on the benthic fish assemblage structure and diversity at the continental shelf and shelf edge within the high-latitude coral reef ecosystems in the tropical Delagoa Ecoregion of South Africa.

I hypothesized that fish abundances, biomass and diversity metrics (species richness, Pielou's evenness and beta-diversity) will be higher in the canyon ecosystems, compared to the non-canyon ecosystem, because of habitat complexity and habitat heterogeneity. Additionally, the fish assemblages structure will differ significantly between the canyon and non-canyon ecosystem because of the expected difference in habitat complexity and habitat heterogeneity. Finally, I hypothesized that patterns in diversity metrics and fish assemblage structure will be inconsistent between the canyons because different canyons are unique in terms of their morphology.

This thesis has substantially improved our knowledge of the influence of submarine canyons on the structure and diversity of benthic fish assemblages occurring on the continental shelf edge of IWP. Before the commencement of this research, an in-depth literature review was conducted, which revealed that submarine canyon research was still in its infancy and that there is still much to learn about the ecology and functioning of these ecosystems (**Chapter 2**). Using fisheries independent surveys techniques (**Chapter 3 and 4**), data were collected inside and adjacent to submarine canyons to determine abundance, biomass and diversity of benthic fish assemblages. This survey resulted in a comprehensive documentation of the benthic fish within the submarine canyons and adjacent non-canyon ecosystems. Environmental variables (such as ecosystem, depth, average relief and bottom type) that predicted fish distribution patterns within and adjacent to the canyons were also assessed.

5.1.1 SUMMARY OF KEY FINDINGS

In general, it is clear that a ‘canyon effect’ exists at the IWP since significantly higher total abundance and lower evenness and beta-diversity was observed in the canyon compared to the non-canyon ecosystems. The fish assemblage structure also differed with several species observed only within either of the ecosystems. Species such as *E. tukula*, *C. leucas* and *E. morrhua* were only detected in the canyon ecosystem whereas species such as *C. limbatus*, *H. uarnak* and *P. natalensis* were only detected only in the non-canyon ecosystem (**Chapter 3**). These differences in total abundance, evenness and the benthic fish assemblages were still evident even with the inclusion of different locations (**Chapter 4**). Over the depth range considered in Chapter 3 (70 - 240m), depth was an important predictor of the response variables, with most response variables decreasing with increasing depth. However, this pattern was not always consistent; for example, biomass decreased with increasing depth in the non-canyon ecosystem, but remained constant in the canyon. On the other hand, abundance decreased with increasing depth in the canyon, but displayed a bell-shaped curve (high abundance at mid-depths and low abundance at the shallow and deep extremes) in the non-canyon. In contrast to Chapter 3, the results from Chapter 4 indicated that depth did not obviously influence the univariate metrics, and this can mostly be attributed to the narrow depth range considered (60 – 100m), and potentially the high level of variability in the data. However, there was evidence that the assemblage structure varied according to depth zone, particularly in the canyon.

Average relief and bottom type appeared to be very important predictors of the univariate response variables and the multivariate fish assemblage. In this study, the canyons were characterised by more reef-associated habitats and greater relief, relative to the non-canyon ecosystems. Furthermore, the shallowest parts of the canyon ecosystems were characterised by a unique sea pen habitat that was not detected in any of the non-canyon locations. Relief seems to drive higher benthic fish abundances in other canyon and marine ecosystems (García-Charton and Pérez-Ruzafa 2001, Lingo and Szedlmayer 2006, De Leo et al. 2012, Ross et al. 2015). Relief or habitat complexity together with habitat heterogeneity provides more niches and diverse ways of exploiting environmental resources thus increasing local abundances and biodiversity (McClain and Barry 2010, Ross et al. 2015).

The assemblage structure differed significantly between the two ecosystems and once again the structure of the community was influenced by both relief and depth. Interestingly, there was also an effect of location in the community analysis which was also detected in the univariate analysis. Even though the univariate response variables did not always show the same trend at different locations, the multivariate results suggest that fish assemblage structures within the different locations were generally different.

5.2 RECOMMENDATIONS FOR FUTURE WORK AND CONCLUSION

Submarine canyons within IWP are well mapped and the processes that have formed them are well-documented (Ramsay and Miller. 2002, 2006). Upon the discovery of the coelacanth, in several submarine canyons within IWP, a considerable amount of work has been undertaken to study both the coelacanth and its relationship to the biophysical and chemical environment of the area (Heemstra et al. 2006, Hissmann et al. 2006, Ramsay and Miller. 2006, Roberts et al. 2006). No work has, however, looked at the influence of the canyons on faunal assemblage structure of shelf edge and slope ecosystems. Therefore, this thesis provides important insights into the role and influence of these canyons on benthic fish assemblages occurring on the continental shelf edge.

From the results presented here, it seems as if heterogeneity of habitat (profile and bottom type) was the most important environmental factor that differed between the canyon and non-canyon ecosystems and that these differences in habitat were driving the observed patterns. However, since we did not measure other potential important environmental processes such as upwelling and consequent increased productivity within the canyons, future research should focus on further comparing the oceanography and productivity within and outside the canyon ecosystems. An in-depth comparison of the oceanography between the ecosystems would determine if the differences between the ecosystems are mostly due to habitat heterogeneity or if additional processes are driving the patterns.

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7 APPENDIX

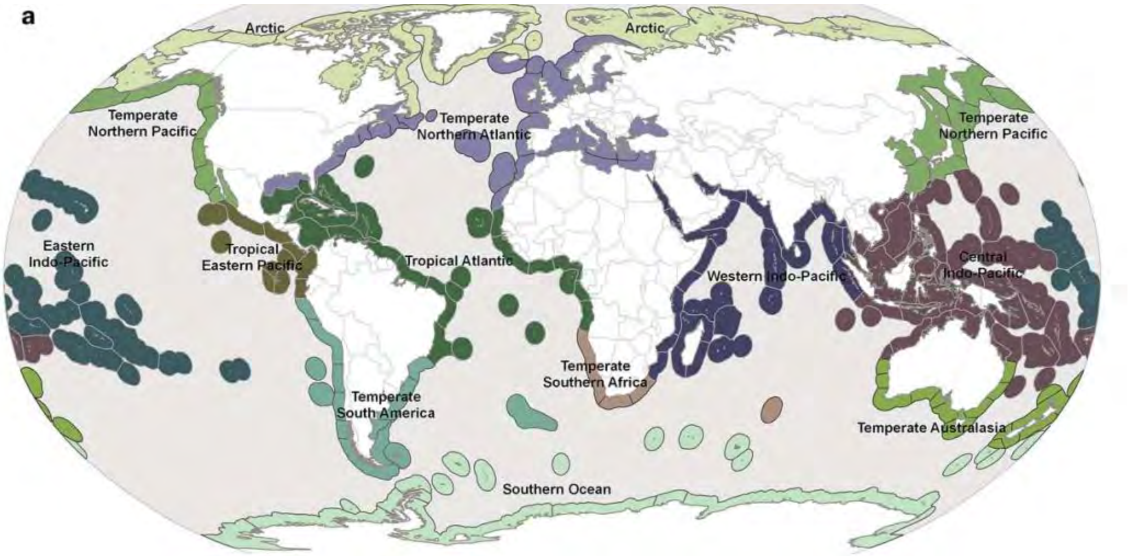

Figure A.1: The outline of the biogeographic realms of the world. (Figure extracted from Spalding et al., 2007)

Table A.1: List of all species, including mobile macro-invertebrates, recorded and the number of times each species was detected out of the 50 BRUVs samples analysed (N), together with the number of detection for each species in the two *Ecosystems* namely Wright canyon ecosystem and non-canyon ecosystem (**Chapter 3**)

Family	Species name	N	Canyon	Non-Canyon
Carangidae	*Carangoides coeruleopinnatus*	13	0	13
	Caranx ignobilis	1	1	0
	Seriola dumerili	6	6	0
	Seriola rivoliana	23	14	9
Carcharhinidae	*Carcharhinidae spp*	2	2	0
	Carcharhinus brachyurus	1	1	0
	Carcharhinus leucas	1	1	0
	Carcharhinus limbatus	2	2	0
	Carcharhinus obscurus	2	1	1
	Carcharhinus plumbeus	1	0	1
	Carcharhinus sealei	8	0	8
	Carcharhinus sp1	2	2	0
	Carcharhinus spp	1	0	1
Chaetodontidae	*Chaetodon dolosus*	4	4	0
Cheilodactylidae	*Chirodactylus jessicalenorum*	5	2	3
Dasyatidae	*Dasyatis thetidis*	4	1	3
	Himantura fai	1	0	1
	Pteroplatytrygon violacea	1	1	0
	Taeniura meyeni	2	1	1
Echeneidae	*Echeneis naucrates*	9	8	1
Hexanchidae	*Heptranchias perlo*	2	2	0
Labridae	*Bodianus bilunulatus*	2	2	0
	Bodianus leucosticticus	5	2	3
	Coris caudimacula	1	0	1
	Halichoeres bicolor	4	1	3
	Labridae sp1	1	0	1
	Labridae spp	4	0	4
Lethrinidae	*Gymnocranius grandoculis*	3	3	0
Lithodidae	*Lithodidae sp1*	4	0	4
Lutjanidae	*Aprion virescens*	7	6	1
	Apsilus fuscus	1	1	0
	Etelis carbunculus	7	4	3
	Etelis coruscans	1	1	0
	Lutjanidae spp	1	0	1
	Paracaesio xanthura	55	47	8
	Pristipomoides auricilla	1	1	0
	Pristipomoides multidens	1	1	0
	Pristipomoides spp	92	33	59
	Pristipomoides zonatus	2	2	0

Family	Species name	N	Canyon	Non-Canyon
Monacanthidae	*Aluterus monocerus*	2	0	2
Mullidae	*Parupeneus rubescens*	8	8	0
Muraenidae	*Gymnothorax johnsoni*	1	1	0
	Gymnothorax sp3	1	1	0
Palinuridae	*Palinurus delagoa*	1	1	0
Pinguipedidae	*Parapercis schauinslandii*	3	2	1
	Parapercis sp1	3	0	3
Polyprionidae	*Polyprion americanus*	1	1	0
Pomacentridae	*Chromis axillaris*	1	1	0
Rachycentridae	*Rachycentron canadum*	5	0	5
Scaridae	*Scaridae spp*	1	1	0
Scombridae	*Sarda orientalis*	1	0	1
	Scomberomorus commerson	4	3	1
Scyllaridae	*Scyllarides elisabethae*	1	0	1
Serranidae	*Epinephelus albomarginatus*	6	4	2
	Epinephelus chlorostigma	9	9	0
	Epinephelus coeruleopunctatus	2	2	0
	Epinephelus malabaricus	1	1	0
	Epinephelus marginatus	14	12	2
	Epinephelus morrhua	1	1	0
	Epinephelus poecilonotus	68	49	19
	Epinephelus tukula	2	2	0
	Hyporthodus octofasciatus	10	4	6
	Liopropoma spp	1	0	1
	Liopropoma spp.	2	0	2
	Serranidae spp	1	1	0
	Serranus knysnaensis	3	2	1
Sparidae	*Argyrops filamentosus*	7	1	6
	Argyrops spinifer	16	13	3
	Cheimerius nufar	89	59	30
	Chrysoblephus anglicus	10	4	6
	Chrysoblephus puniceus	314	275	39
	Cymatoceps nasutus	3	1	2
	Pagellus bellottii natalensis	16	0	16
	Petrus rupestris	4	4	0
	Polysteganus coeruleopunctatus	406	271	135
	Polysteganus praeorbitalis	32	26	6
Sphyrnidae	*Sphyrna lewini*	1	1	0
Squalidae	*Cirrhigaleus asper*	1	1	0
Tetraodontidae	*Amblyrhynchotes honckenii*	1	0	1
	Lagocephalus scleratus	25	7	18
	Tetraodontidae sp1	1	0	1

Table A.2: Output of Percentage Similarity (SIMPER) on **a)** abundance and **b)** biomass data from Wright canyon and adjacent non-canyon ecosystem. Abbreviations: Av.Abund (N-C), Average abundance (Non-canyon); AV.Abund (C), Average abundance (canyon); Av.Diss, Average dissimilarity; Diss/SD, Dissimilarity divided by the standard deviation; Contrib%, Percentage contribution; Cum.%, Cumulative percentage (**Chapter 3**). Table only shows the Cum % up to ± 50%

a) Abundance

Groups: Non-canyon & Canyon (Average dissimilarity = 76%)

Species	Av.Abund (N-C)	AV.Abund (C)	Av.Diss	Diss/SD	Contrib%	Cum.%
Polysteganus coeruleopunctatus	1.00	1.38	6.93	1.02	9.11	9.11
Epinephelus poecilonotus	0.32	0.87	5.61	1.13	7.38	16.50
Chrysoblephus puniceus	0.20	0.96	5.37	0.95	7.07	23.57
Cheimerius nufar	0.60	1.11	4.99	1.07	6.56	30.13
Polysteganus praeorbitalis	0.22	0.75	4.09	1.20	5.38	35.51
Pristipomoides spp	0.37	0.44	3.62	0.87	4.76	40.27
Lagocephalus scleratus	0.44	0.21	3.21	0.79	4.22	44.49
Seriola rivoliana	0.30	0.41	3.02	0.85	3.98	48.47
Paracaesio xanthura	0.11	0.35	2.24	0.59	2.95	51.42

b) Biomass

Groups: Non-canyon & Canyon (Average dissimilarity = 79.12%)

Species	Av.Abund (N-C)	AV.Abund (C)	Av.Diss	Diss/SD	Contrib%	Cum.%
Epinephelus poecilonotus	0.58	1.47	8.02	1.02	10.14	10.14
Polysteganus praeorbitalis	0.46	1.46	6.95	1.28	8.79	19.93
Seriola rivoliana	0.65	1.01	6.23	0.78	7.87	26.80
Cheimerius nufar	0.85	1.45	5.91	1.28	7.47	34.26
Polysteganus coeruleopunctatus	0.89	1.21	.65	1.09	7.15	41.41
Chrysoblephus puniceus	0.21	1.09	5.57	0.96	7.04	48.45
Dasyatis thetidis	0.57	0.18	3.05	0.43	3.85	52.30

Table A.3: List of all species, including mobile macro-invertebrates, recorded and the number of times each species was detected out of the 54 BRUVs samples analysed (N) in the canyon and non-canyon ecosystems of all locations (**Chapter 4**)

Family	**Species Name**	**N**	**Canyon**	**Non-Canyon**
Balistidae	*Abalistes stellaris*	1	0	1
	Odonus niger	5	5	0
	Sufflamen fraenatum	6	2	4
Carangidae	*Caranx ignobilis*	5	5	0
	Seriola dumerili	1	1	0
	Seriola rivoliana	24	20	4
Carcharhinidae	*Carcharhinus albimarginatus*	3	2	1
	Carcharhinus limbatus	10	6	4
	Carcharhinus obscurus	4	2	2
	Carcharhinus sealei	6	2	4
	Carcharhinus spp	6	4	2
	Galeocerdo cuvier	3	1	2
Chaetodontidae	*Chaetodon dolosus*	28	26	2
	Heniochus diphreutes	8	8	0
Cheilodactylidae	*Chirodactylus grandis*	1	1	0
Dasyatidae	*Dasyatis spp*	2	2	0
	Dasyatis thetidis	7	4	3
	Gymnura natalensis	1	1	0
	Himantura uarnak	2	1	1
	Taeniura meyeni	2	1	1
Dinopercidae	*Dinoperca petersi*	1	1	0
Echeneidae	*Echeneis naucrates*	20	9	11
Gobiidae	*Gnatholepis spp*	1	0	1
	Istigobius decoratus	7	7	0
Labridae	*Bodianus anthioides*	1	1	0
	Bodianus bilunulatus	2	1	1
	Bodianus bimaculatus	2	0	2
	Bodianus trilineatus	2	1	1
	Coris caudimacula	14	0	14
	Halichoeres leucoxanthus	3	3	0
	Iniistius pavo	8	2	6
	Labroides dimidiatus	1	0	1
	Thalassoma amblycephalum	2	0	2
Lethrinidae	*Gymnocranius grandoculis*	12	6	6
Lutjanidae	*Aphareus rutilans*	7	7	0
	Aprion virescens	27	18	9
	Paracaesio sordida	22	20	2
	Paracaesio xanthura	228	224	4
	Pristipomoides auricilla	1	1	0
	Pristipomoides filamentosus	130	63	67

Family	Species Name	N	Canyon	Non-canyon
Malacanthidae	*Malacanthus brevirostris*	2	0	2
Mullidae	*Parupeneus fraserorum*	6	0	6
	Parupeneus rubescens	6	6	0
Muraenidae	*Gymnothorax johnsoni*	1	0	1
	Gymnothorax nudivomer	1	1	0
Odontaspididae	*Carcharias taurus*	2	1	1
Oplegnathidae	*Oplegnathus robinsoni*	1	1	0
Ostraciidae	*Tetrosomus gibbosus*	2	0	2
Pinguipedidae	*Parapercis punctulata*	1	0	1
	Parapercis robinsoni	1	0	1
Pomacanthidae	*Pomacanthus rhomboides*	3	2	1
Pomacentridae	*Chromis woodsi*	2	0	2
Rhinobatidae	*Rhinobatos leucospilus*	7	0	7
	Rhynchobatus djiddensis	2	1	1
Sciaenidae	*Argyrosomus japonicus*	1	1	0
Scombridae	*Euthynnus affinis*	4	1	3
	Scomberomorus commerson	4	4	0
Serranidae	*Aulacocephalus temminckii*	1	1	0
	Cephalopholis sonnerati	5	4	1
	Epinephelus albomarginatus	19	6	13
	Epinephelus malabaricus	2	2	0
	Epinephelus marginatus	17	14	3
	Epinephelus multinotatus	1	1	0
	Epinephelus poecilonotus	28	25	3
	Epinephelus tukula	10	5	5
	Pseudanthias connelli	1	1	0
	Pseudanthias cooperi	1	1	0
	Pseudanthias gibbosus	22	18	4
	Serranus knysnaensis	17	0	17
	Variola louti	2	2	0
Sparidae	*Argyrops filamentosus*	19	5	14
	Argyrops spinifer	35	34	1
	Cheimerius nufar	105	69	36
	Chrysoblephus anglicus	30	15	15
	Chrysoblephus puniceus	318	233	85
	Cymatoceps nasutus	7	5	2
	Pagellus bellottii natalensis	14	0	14
	Polysteganus coeruleopunctatus	73	69	4
	Polysteganus praeorbitalis	29	21	8
	Polysteganus undulosus	1	0	1
Sphyrnidae	*Sphyrna mokarran*	4	4	0
Synodontidae	*Synodus myops*	6	2	4
	Synodus variegatus	1	1	0

Family	Species Name	N	Canyon	Non-canyon
Tetraodontidae	*Lagocephalus sceleratus*	48	18	30
Triakidae	*Mustelus mustelus*	1	0	0

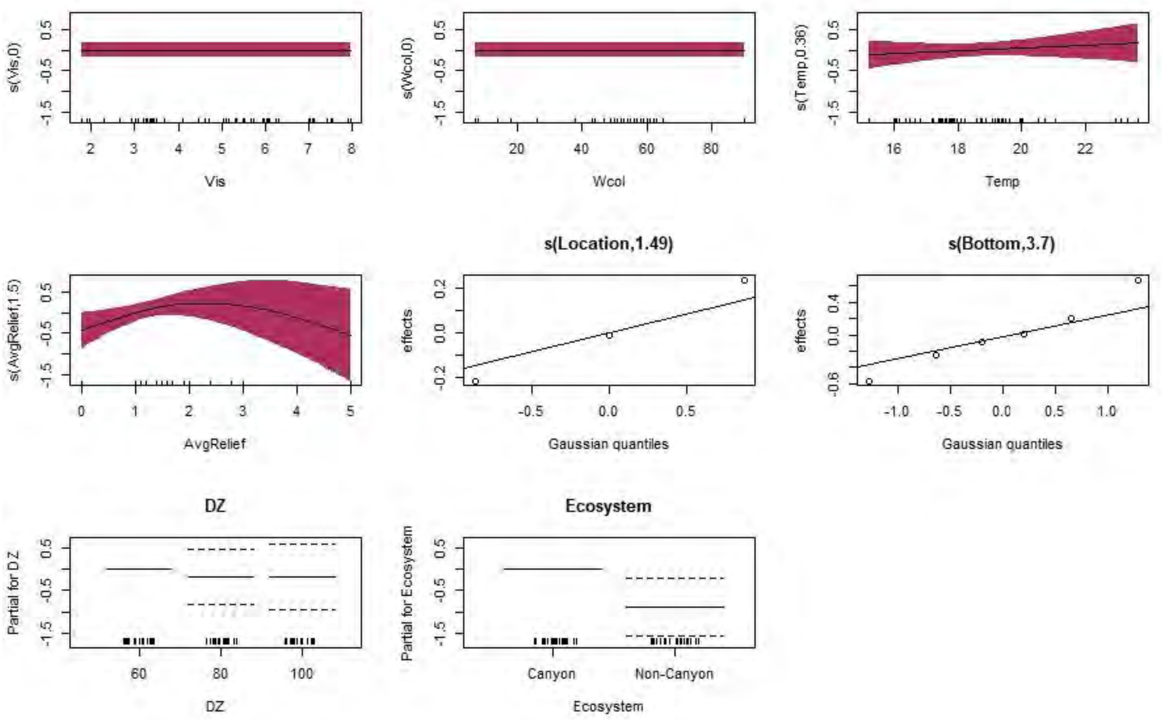

Figure A.2: Plots of the hierarchical generalised additive model fit for the response variable Total MaxN (abundance), showing the components smooth function on a scale of the linear predictor for the continuous covariates (*Visibility* (Vis), *water column* (Wcol), *Temperature* (Temp), *Average relief* (AvgRelief)), the plots for the random effect (*Location*, *Bottom type*) and the term plots for the parametric coefficient *Depth zone* and *Ecosystem*. In the smooth term plots, confidence intervals (gray bands) around the predicted mean are provided. Partial residuals (black dots) are provided for 1-d plots. The distribution of the predictor data is indicated by the short bars on the y-axis.

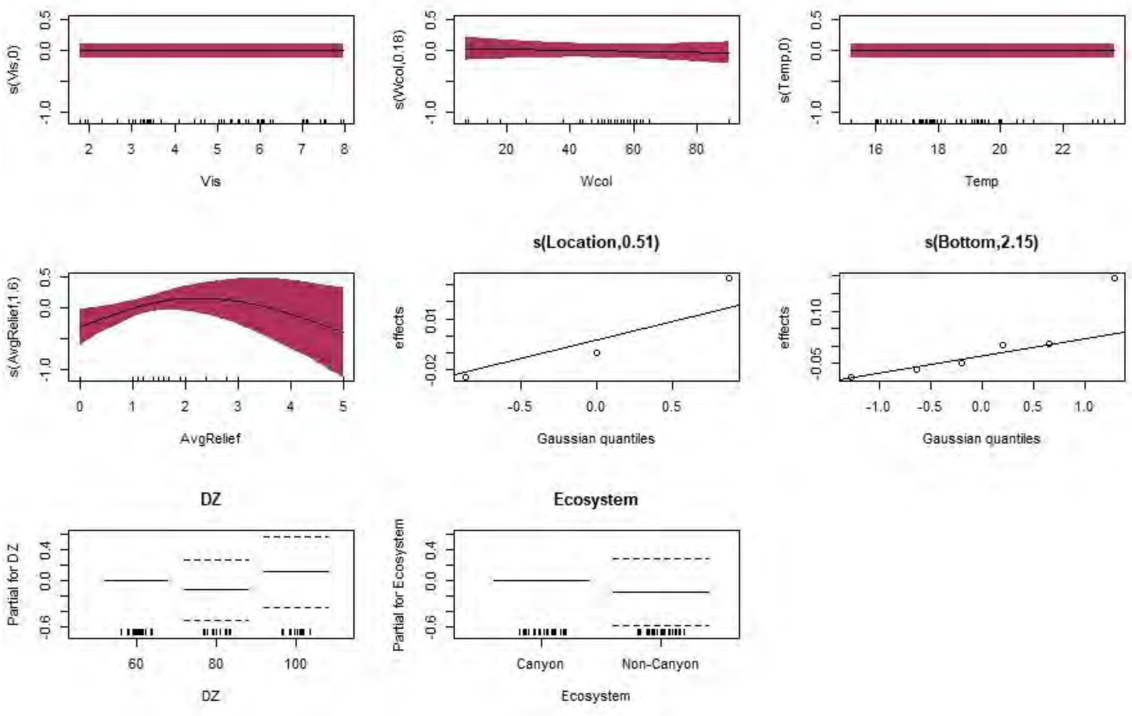

Figure A.3: Plots of the hierarchical generalised additive model fit for the response variable species richness, showing the components smooth function on a scale of the linear predictor for the continuous covariates (*Visibility* (Vis), *water column* (Wcol), *Temperature* (Temp), *Average relief* (AvgRelief)), the plots for the random effect (*Location*, *Bottom type*) and the term plots for the parametric coefficient *Depth zone* and *Ecosystem*. In the smooth term plots, confidence intervals (gray bands) around the predicted mean are provided. Partial residuals (black dots) are provided for 1-d plots. The distribution of the predictor data is indicated by the short bars on the y-axis.

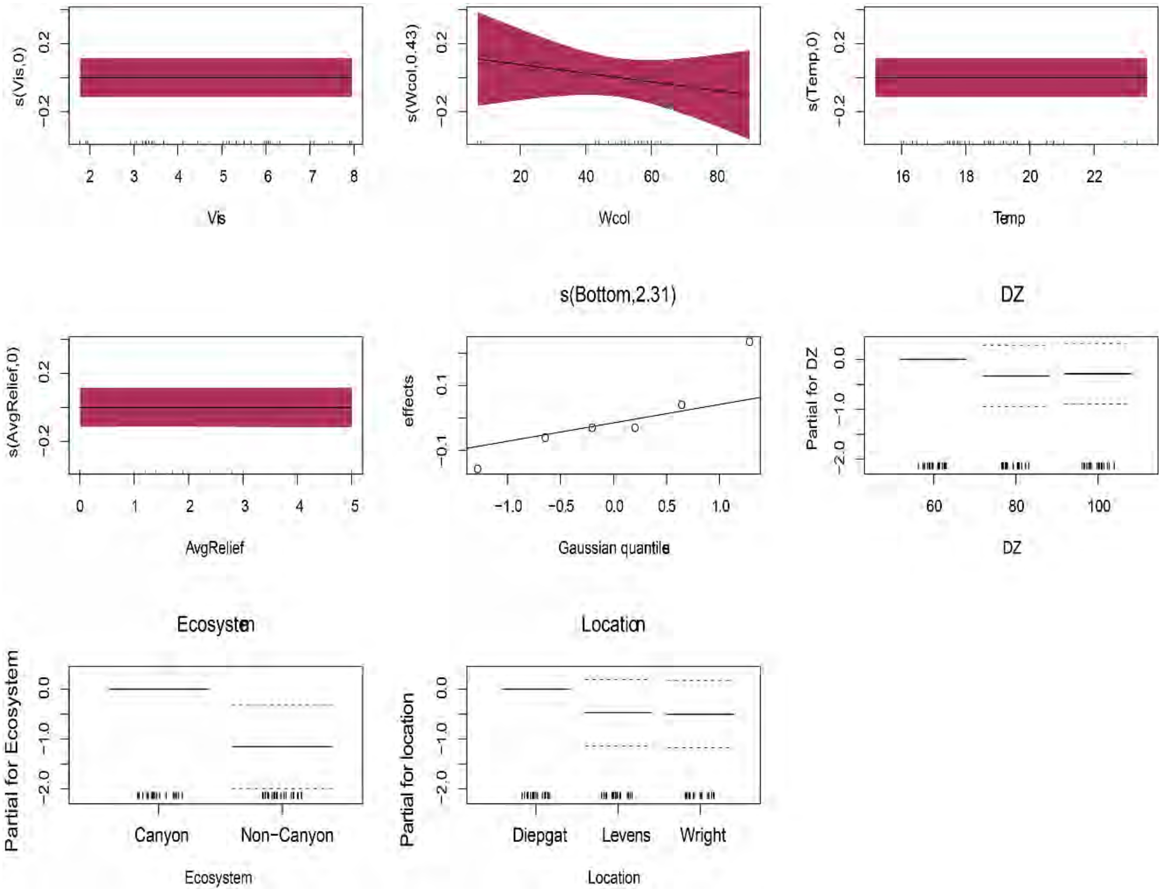

Figure A.4: Plots of the hierarchical generalised additive model fit for the response variable species richness, showing the components smooth function on a scale of the linear predictor for the continuous covariates (*Visibility* (Vis), *water column* (Wcol), *Temperature* (Temp), *Average relief* (AvgRelief)), the plots for the random effect (*Bottom type*) and the term plots for the parametric coefficient *Depth zone, Ecosystem* and *Location*. In the smooth term plots, confidence intervals (gray bands) around the predicted mean are provided. Partial residuals (black dots) are provided for 1-d plots. The distribution of the predictor data is indicated by the short bars on the y-axis.

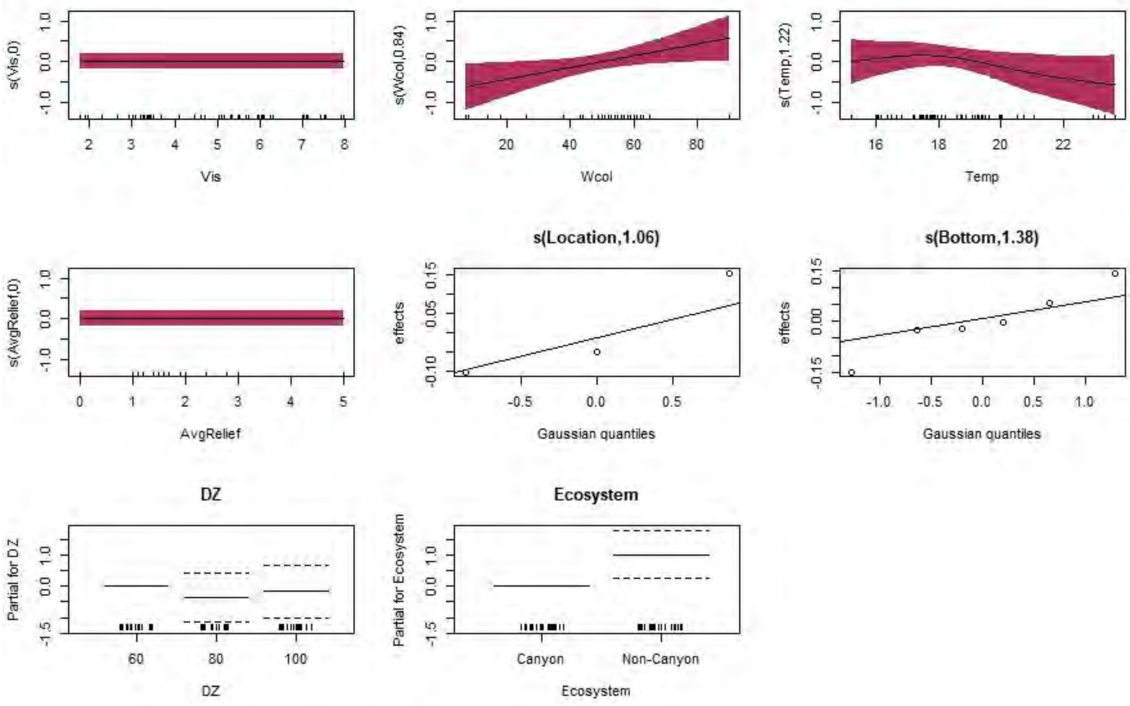

Figure A.5: Plots of the hierarchical generalised additive model fit for the response variable Pielou's evenness, showing the components smooth function on a scale of the linear predictor for the continuous covariates (*Visibility* (Vis), *water column* (Wcol), *Temperature* (Temp), *Average relief* (AvgRelief)), the plots for the random effect (*Location*, *Bottom type*) and the term plots for the parametric coefficient *Depth zone* and *Ecosystem*. In the smooth term plots, confidence intervals (gray bands) around the predicted mean are provided. Partial residuals (black dots) are provided for 1-d plots. The distribution of the predictor data is indicated by the short bars on the y-axis.

Table A.4: Summary of SIMPER analysis results on abundance data showing average abundance of typifying species in each *ecosystem* and *depth zone* group. Av. Abu, average abundance of each species; Av. Sim, the average similarity contributed by each species; Sim/SD, the ratio of similarity to standard deviation; Contrib%, the contribution of species to the overall similarity; Cum.%, additive overall similarity.

Species	**Av. Abu**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum %**
Canyon 60 m (Ave sim = 14.97%)					
Echeneis naucrates	1,00	4,04	0,92	27,00	27,00
Argyrops spinifer	2,56	3,47	0,42	23,16	50,17
Lagocephalus sceleratus	2,00	1,86	0,24	12,41	62,58
Cheimerius nufar	2,22	1,32	0,39	8,81	71,39
Aprion virescens	1,67	1,00	0,46	6,65	78,04
Carcharhinus limbatus	0,56	0,98	0,40	6,53	84,57
Canyon 80 m (Ave sim = 25.33%)					
Cheimerius nufar	3,33	7,19	1,14	28,40	28,40
Chrysoblephus puniceus	9,00	7,16	0,62	28,27	56,67
Chrysoblephus anglicus	0,78	2,20	0,92	8,68	65,35
Polysteganus praeorbitalis	1,00	1,96	0,97	7,74	73,09
Polysteganus coeruleopunctatus	2,78	1,69	0,21	6,68	79,77
Seriola rivoliana	0,78	1,35	0,39	5,33	85,10
Canyon 100 m (Ave sim = 38.65%)					
Chrysoblephus puniceus	16,89	18,65	1,06	48,26	48,26
Polysteganus coeruleopunctatus	4,89	6,95	0,75	17,97	66,23
Cheimerius nufar	2,11	3,18	1,18	8,22	74,45
Epinephelus poecilonotus	1,56	3,05	2,37	7,89	82,35
Polysteganus praeorbitalis	1,22	2,25	1,46	5,82	88,17
Epinephelus marginatus	1,00	1,09	0,77	2,82	90,99
Non-canyon 60 m (Ave sim = 23.91%)					
Lagocephalus sceleratus	2,44	11,64	0,93	48,70	48,70
Echeneis naucrates	1,11	2,61	0,55	10,91	59,60
Iniistius pavo	0,67	2,14	0,36	8,94	68,54
Rhinobatos leucospilus	0,44	2,02	0,41	8,47	77,01
Cheimerius nufar	0,56	1,44	0,44	6,01	83,02
Coris caudimacula	1,22	1,24	0,24	5,20	88,23

Species	Av. Abu	Av. Sim	Sim/SD	Contrib%	Cum %
Non-canyon 80 m (Ave sim = 22.52%)					
Serranus knysnaensis	1,44	5,82	0,95	25,86	25,86
Cheimerius nufar	1,56	4,50	0,63	19,99	45,85
Chrysoblephus anglicus	1,00	2,72	0,73	12,07	57,92
Pristipomoides filamentosus	3,00	2,02	0,40	8,96	66,88
Lagocephalus sceleratus	0,56	1,42	0,40	6,28	73,16
Aprion virescens	0,56	1,38	0,40	6,12	79,28
Non-canyon 100 m (Ave sim = 16.43%)					
Cheimerius nufar	1,89	4,39	0,77	26,70	26,70
Chrysoblephus puniceus	7,11	4,34	0,39	26,40	53,11
Pristipomoides filamentosus	4,44	2,14	0,41	13,03	66,13
Chrysoblephus anglicus	0,67	1,93	0,63	11,74	77,88
Serranus knysnaensis	0,44	0,93	0,17	5,64	83,51
Epinephelus albomarginatus	0,89	0,82	0,41	4,98	88,49

Table A.5: Summary of SIMPER analysis results on abundance data showing average abundance of discriminating species in each *ecosystem* and *depth zone* group, the contribution to the dissimilarity between the group and cumulative total of the contributions (90% cut-off). Contrib %, Percentage contribution; Cum %, Cumulative percentage; average dissi, Average dissimilarity between groups.

Species	**Average Abundance**		**Contrib %**	**Cum %**
	Canyon 60 m	Canyon 80 m (average dissi = 91.21%)		
Chrysoblephus puniceus	0,00	9,00	14,13	14,13
Pristipomoides filamentosus	4,89	1,33	10,50	24,63
Paracaesio xanthura	16,78	2,44	10,17	34,80
Cheimerius nufar	2,22	3,33	8,28	43,08
Polysteganus coeruleopunctatus	0,00	2,78	6,86	49,93
Argyrops spinifer	2,56	1,11	6,24	56,17
	Canyon 60 m	Canyon 100 m (average dissi = 95.03%)		
Chrysoblephus puniceus	0,00	16,89	24,12	24,12
Paracaesio xanthura	16,78	5,67	12,02	36,14
Polysteganus coeruleopunctatus	0,00	4,89	9,78	45,92
Pristipomoides filamentosus	4,89	0,78	6,91	52,83
Cheimerius nufar	2,22	2,11	4,62	57,45
Argyrops spinifer	2,56	0,11	4,48	61,93
	Canyon 80 m	Canyon 100 m (average dissi = 69.46%)		
Chrysoblephus puniceus	9,00	16,89	29,79	29,79
Polysteganus coeruleopunctatus	2,78	4,89	13,07	42,86
Paracaesio xanthura	2,44	5,67	10,40	53,26
Cheimerius nufar	3,33	2,11	5,41	58,67
Pristipomoides filamentosus	1,33	0,78	4,91	63,58
Paracaesio sordida	2,22	0,00	3,69	67,28
	Canyon 60 m	Non-canyon 100 m (average dissi = 92.28%)		
Pristipomoides filamentosus	4,89	4,44	14,15	14,15
Chrysoblephus puniceus	0,00	7,11	12,67	26,82

Species	Average Abundance		Contrib %	Cum %
Paracaesio xanthura	16,78	0,33	8,12	34,94
Lagocephalus sceleratus	2,00	0,33	7,78	42,72
Argyrops spinifer	2,56	0,00	7,08	49,80
Cheimerius nufar	2,22	1,89	7,07	56,87
	Canyon 80 m	Non-canyon 100 m (average dissi = 78.48%)		
Chrysoblephus puniceus	9,00	7,11	23,68	23,68
Pristipomoides filamentosus	1,33	4,44	12,19	35,87
Polysteganus coeruleopunctatus	2,78	0,44	9,90	45,77
Cheimerius nufar	3,33	1,89	8,07	53,85
Paracaesio sordida	2,22	0,22	4,47	58,32
Paracaesio xanthura	2,44	0,33	4,02	62,34
	Canyon 100 m	Non-canyon 100 m (average dissi = 78.10%)		
Chrysoblephus puniceus	16,89	7,11	30,91	30,91
Polysteganus coeruleopunctatus	4,89	0,44	12,92	43,82
Pristipomoides filamentosus	0,78	4,44	8,04	51,86
Paracaesio xanthura	5,67	0,33	7,64	59,51
Pseudanthias gibbosus	2,00	0,44	3,99	63,49
Cheimerius nufar	2,11	1,89	3,90	67,39
	Canyon 60 m	Non-canyon 80 m (average dissi = 90.58%)		
Pristipomoides filamentosus	4,89	3,00	3,00	14,31
Lagocephalus sceleratus	2,00	0,56	8,56	22,86
Paracaesio xanthura	16,78	0,11	8,26	31,12
Cheimerius nufar	2,22	1,56	7,90	39,03
Argyrops spinifer	2,56	0,00	7,72	46,74
Chrysoblephus puniceus	0,00	2,33	5,59	52,34
	Canyon 80 m	Non-canyon 80 m (average dissi = 83.24%)		
Chrysoblephus puniceus	9,00	2,33	19,43	19,43
Pristipomoides filamentosus	1,33	3,00	10,83	30,25
Polysteganus coeruleopunctatus	2,78	0,00	9,23	39,49

Species	**Average Abundance**		**Contrib %**	**Cum %**
Cheimerius nufar	3,33	1,56	8,51	48,00
Serranus knysnaensis	0,00	1,44	4,71	52,71
Paracaesio sordida	2,22	0,00	4,21	56,92
	Canyon 100 m	Non-canyon 80 m (average dissi = 86.35%)		
Chrysoblephus puniceus	16,89	2,33	29,88	29,88
Polysteganus coeruleopunctatus	4,89	0,00	13,06	42,93
Paracaesio xanthura	5,67	0,11	7,08	50,01
Pristipomoides filamentosus	0,78	3,00	6,30	56,31
Cheimerius nufar	2,11	1,56	4,01	60,32
Epinephelus poecilonotus	1,56	0,00	3,55	63,88
	Non-canyon 100 m	Non-canyon 80 m (average dissi = 78.38%)		
Chrysoblephus puniceus	7,11	2,33	21,08	21,08
Pristipomoides filamentosus	4,44	3,00	16,63	37,71
Cheimerius nufar	1,89	1,56	7,59	45,29
Serranus knysnaensis	0,44	1,44	5,96	51,25
Epinephelus albomarginatus	0,89	0,56	4,14	55,39
Argyrops filamentosus	1,00	0,56	3,76	59,15
	Canyon 60 m	Non-canyon 60 m (average dissi = 85.29%)		
Lagocephalus sceleratus	2,00	2,44	12,78	12,78
Pristipomoides filamentosus	4,89	0,00	10,35	23,13
Argyrops spinifer	2,56	0,11	9,19	32,32
Paracaesio xanthura	16,78	0,00	8,71	41,02
Cheimerius nufar	2,22	0,56	7,46	48,48
Aprion virescens	1,67	0,33	5,49	53,98
	Canyon 80 m	Non-canyon 60 m (average dissi = 96.65%)		
Chrysoblephus puniceus	9,00	0,00	16,92	16,92
Cheimerius nufar	3,33	0,56	9,13	26,04
Polysteganus coeruleopunctatus	2,78	0,00	8,84	34,88
Lagocephalus sceleratus	0,00	2,44	7,40	42,29

Species	**Average Abundance**		**Contrib %**	**Cum %**
Pristipomoides filamentosus	1,33	0,00	5,11	47,39
Paracaesio sordida	2,22	0,00	3,87	51,27
	Canyon 100 m	Non-canyon 60 m (average dissi = 97.68%)		
Chrysoblephus puniceus	16,89	0,00	29,48	29,48
Polysteganus coeruleopunctatus	4,89	0,00	12,70	42,18
Paracaesio xanthura	5,67	0,00	6,42	48,61
Lagocephalus sceleratus	0,00	2,44	5,42	54,03
Cheimerius nufar	2,11	0,56	3,77	57,80
Epinephelus poecilonotus	1,56	0,00	3,43	61,23
	Non-canyon 100 m	Non-canyon 60 m (average dissi = 93.66%)		
Chrysoblephus puniceus	7,11	0,00	16,29	16,29
Pristipomoides filamentosus	4,44	0,00	10,33	26,61
Lagocephalus sceleratus	0,33	2,44	9,76	36,37
Cheimerius nufar	1,89	0,56	6,15	42,52
Coris caudimacula	0,11	1,22	4,54	47,05
Echeneis naucrates	0,11	1,11	3,96	51,01
	Non-canyon 80 m	Non-canyon 60 m (average dissi = 89.43%)		
Pristipomoides filamentosus	3,00	0,00	9,89	9,89
Lagocephalus sceleratus	0,56	2,44	9,89	19,78
Chrysoblephus puniceus	2,33	0,00	7,76	27,53
Serranus knysnaensis	1,44	0,00	7,10	34,64
Cheimerius nufar	1,56	0,56	6,96	41,59
Coris caudimacula	0,22	1,22	5,40	46,99

Table A.6: Summary of SIMPER analysis results on biomass data showing average biomass of typifying species in each *ecosystem* and *depth zone* group. Av. Abu, average biomass of each species; Av. Sim, the average similarity contributed by each species; Sim/SD, the ratio of similarity to standard deviation; Contrib%, the contribution of species to the overall similarity; Cum.%, additive overall similarity.

Species	**Av.Abu**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum %**
Canyon 60 m (Ave sim = 14.32%)					
Carcharhinus limbatus	22,45	5,39	0,41	37,66	37,66
Aprion virescens	19,27	2,37	0,49	16,55	54,21
Caranx ignobilis	7,51	1,78	0,43	12,41	66,62
Argyrops spinifer	8,65	1,62	0,4	11,28	77,9
Cheimerius nufar	5,85	1,03	0,44	7,17	85,07
Dasyatis thetidis	17,67	0,65	0,17	4,52	89,59
Canyon 80 m (Ave sim = 19.91%)					
Seriola rivoliana	15,16	5,39	0,47	27,09	27,09
Cheimerius nufar	7,41	4,36	1,17	21,9	48,99
Polysteganus praeorbitalis	5,01	2,99	0,93	15	63,98
Chrysoblephus anglicus	3,94	2,07	0,66	10,38	74,37
Chrysoblephus puniceus	6,63	1,76	0,51	8,82	83,19
Argyrops spinifer	4,6	1,1	0,31	5,52	88,71
Canyon 100 m (Ave sim = 24.29%)					
Chrysoblephus puniceus	12,05	8,32	0,97	34,24	34,24
Cymatoceps nasutus	8,7	4,55	0,56	18,72	52,96
Polysteganus praeorbitalis	3,77	3,02	0,8	12,42	65,38
Cheimerius nufar	3,27	2,48	0,85	10,21	75,59
Polysteganus coeruleopunctatus	2,33	1,62	0,53	6,68	82,27
Seriola rivoliana	17,38	1,33	0,44	5,46	87,73
Non-canyon 60 m (Ave sim = 13.65%)					
Lagocephalus sceleratus	7,46	9,84	0,55	72,12	72,12
Carcharhinus limbatus	30,5	1,84	0,17	13,47	85,58
Rhinobatos leucospilus	1,32	0,77	0,27	5,64	91,22
Non-canyon 80 m (Ave sim = 11.45%)					
Cheimerius nufar	3,9	2,74	0,44	23,92	23,92

Species	**Av.Abu**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum %**
Polysteganus praeorbitalis	2,71	2,57	0,37	22,43	46,35
Lagocephalus sceleratus	1,83	2,23	0,46	19,49	65,84
Epinephelus albomarginatus	4,07	1,49	0,38	12,99	78,83
Chrysoblephus anglicus	2,55	1,2	0,54	10,47	89,29
Chrysoblephus puniceus	2,71	0,99	0,42	8,68	97,97
Non-canyon 100 m (Ave sim = 10.45%)					
Cheimerius nufar	4,85	2,76	0,94	26,37	26,37
Pristipomoides filamentosus	11	2,36	0,37	22,6	48,98
Chrysoblephus anglicus	2,58	1,78	0,7	17,04	66,02
Epinephelus albomarginatus	5,5	1,57	0,42	14,99	81
Chrysoblephus puniceus	3,34	0,81	0,43	7,79	88,79
Polysteganus praeorbitalis	2,64	0,74	0,41	7,07	95,86

Table A.7: Summary of SIMPER analysis results on biomass data showing average biomass of discriminating species in each *ecosystem* and *depth zone* group, the contribution to the dissimilarity between the group and cumulative total of the contributions (90% cut-off). Contrib %, Percentage contribution; Cum %, Cumulative percentage; average dissi, Average dissimilarity between groups.

Species	**Average Abundance**		**Contrib%**	**Cum %**
	Canyon 60 m	Canyon 80 m (average dissi = 91.58%)		
Carcharhinus limbatus	22,45	8,32	13,27	13,27
Seriola rivoliana	2,54	15,16	8,41	21,68
Aprion virescens	19,27	1,01	8,37	30,05
Dasyatis thetidis	17,67	8,63	8,24	38,29
Argyrops spinifer	8,65	4,6	5,71	44
Galeocerdo cuvier	20,12	0	5,67	49,67
	Canyon 60 m	Canyon 100 m (average dissi = 97.07%)		
Carcharhinus limbatus	22,45	0	11,75	11,75
Aprion virescens	19,27	0,99	7,97	19,72
Seriola rivoliana	2,54	17,38	7,56	27,28
Chrysoblephus puniceus	0	12,05	6,75	34,04
Epinephelus marginatus	0	11,08	6,33	40,36
Dasyatis thetidis	17,67	0	5,5	45,87
	Canyon 80 m	Canyon 100 m (average dissi = 80.06%)		
Epinephelus marginatus	4,19	11,08	11,35	29,05
Chrysoblephus puniceus	6,63	12,05	9,1	38,14
Cymatoceps nasutus	0	8,7	7,52	45,67
Carcharhinus obscurus	0	11,3	6,23	51,9
Cheimerius nufar	7,41	3,27	4,77	56,67
Carcharhinus spp	6,96	0	4,7	61,37
	Canyon 60 m	Non-canyon 100 m (average dissi =93.87%)		
Carcharhinus limbatus	22,45	14,39	17,19	17,19
Aprion virescens	19,27	0,74	8,72	25,91
Dasyatis thetidis	17,67	7,4	8,63	34,54

Species	**Average Abundance**		**Contrib%**	**Cum %**
Galeocerdo cuvier	20,12	2,09	7,02	41,55
Pristipomoides filamentosus	0,06	11	6,19	47,74
Argyrops spinifer	8,65	0	5,44	53,18
	Canyon 80 m	Non-canyon 100 m (average dissi = 86.47%)		
Seriola rivoliana	15,16	7,14	13,95	13,95
Carcharhinus limbatus	8,32	14,39	10,08	24,03
Dasyatis thetidis	8,63	7,4	8,55	32,58
Pristipomoides filamentosus	0,33	11	8,4	40,98
Cheimerius nufar	7,41	4,85	5,93	46,91
Chrysoblephus puniceus	6,63	3,34	5,64	52,55
	Canyon 100 m	Non-canyon 100 m (average dissi = 86.99%)		
Seriola rivoliana	17,38	7,14	12,44	12,44
Epinephelus marginatus	11,08	3,19	10,33	22,77
Chrysoblephus puniceus	12,05	3,34	9,64	32,41
Cymatoceps nasutus	8,7	2,83	8,97	41,38
Pristipomoides filamentosus	0,84	11	8,44	49,82
Carcharhinus limbatus	0	14,39	7,48	57,31
	Canyon 60 m	Non-canyon 80 m (average dissi = 92.68%)		
Carcharhinus limbatus	22,45	13,29	18,71	18,71
Aprion virescens	19,27	1,31	9,97	28,68
Dasyatis thetidis	17,67	6,57	9,53	38,21
Argyrops spinifer	8,65	0	6,32	44,53
Galeocerdo cuvier	20,12	0	6,18	50,72
Himantura uarnak	3,57	0	5,4	56,11
	Canyon 80 m	Non-canyon 80 m (average dissi = 85.11%)		
Seriola rivoliana	15,16	1,84	14,55	14,55
Carcharhinus limbatus	8,32	13,29	10,83	25,38
Dasyatis thetidis	8,63	6,57	9,49	34,87
Cheimerius nufar	7,41	3,9	7,08	41,95
Chrysoblephus puniceus	6,63	2,71	6,58	48,53
Carcharhinus spp	6,96	0	5,31	53,85

Species	Average Abundance		Contrib%	Cum %
	Canyon 100 m	Non-Canyon 80 m (average dissi = 86.37%)		
Seriola rivoliana	17,38	1,84	12,83	12,83
Chrysoblephus puniceus	12,05	2,71	11,31	24,14
Epinephelus marginatus	11,08	0	11,15	35,29
Cymatoceps nasutus	8,7	3,8	10,64	45,93
Carcharhinus limbatus	0	13,29	8,08	54,02
Carcharhinus obscurus	11,3	0	6,8	60,82
	Non-canyon 100 m	Non-canyon 80 m (average dissi = 84.05%)		
Carcharhinus limbatus	14,39	13,29	16,53	16,53
Pristipomoides filamentosus	11	0,84	11,93	28,46
Dasyatis thetidis	7,4	6,57	11,32	39,78
Cymatoceps nasutus	2,83	3,8	7,41	47,18
Cheimerius nufar	4,85	3,9	7,36	54,55
Seriola rivoliana	7,14	1,84	7,16	61,71
	Canyon 60 m	Non-canyon 60 m (average dissi = 92.72%)		
Carcharhinus limbatus	22,45	30,5	22,2	22,2
Aprion virescens	19,27	2,97	10,25	32,44
Himantura uarnak	3,57	2,64	6,31	38,75
Argyrops spinifer	8,65	0,35	6,31	45,06
Rhynchobatus djiddensis	6,66	5,48	6,25	51,31
Dasyatis thetidis	17,67	0	6,17	57,48
	Canyon 80 m	Non-canyon 60 m (average dissi = 96.73%)		
Carcharhinus limbatus	8,32	30,5	13,54	13,54
Seriola rivoliana	15,16	0	12,35	25,89
Lagocephalus sceleratus	0	7,46	6,04	31,94
Cheimerius nufar	7,41	2,23	5,88	37,81
Carcharias taurus	0	8,36	5,31	43,13
Chrysoblephus puniceus	6,63	0	5,13	48,26
	Canyon 100 m	Non-canyon 60 m (average dissi = 97.21%)		
Carcharhinus limbatus	0	30,5	11,52	11,52
Chrysoblephus puniceus	12,05	0	11,26	22,78

Species	**Average Abundance**		**Contrib%**	**Cum %**
Seriola rivoliana	17,38	0	9,78	32,56
Epinephelus marginatus	11,08	0	9,76	42,32
Carcharhinus obscurus	11,3	5,17	8,83	51,15
Cymatoceps nasutus	8,7	0	8,33	59,48
	Non-canyon 100 m	Non-canyon 60 m (average dissi =93.50%)		
Carcharhinus limbatus	14,39	30,5	18,25	18,25
Pristipomoides filamentosus	11	0	10,69	28,94
Lagocephalus sceleratus	0,45	7,46	7,86	36,8
Carcharias taurus	0	8,36	6,01	42,81
Cheimerius nufar	4,85	2,23	5,65	48,46
Dasyatis thetidis	7,4	0	5,26	53,72
	Non-canyon 80 m	Non-canyon 60 m (average dissi = 90.66%)		
Carcharhinus limbatus	13,29	30,5	20,83	20,83
Lagocephalus sceleratus	1,83	7,46	8,69	29,52
Aprion virescens	1,31	2,97	7,25	36,76
Carcharias taurus	0	8,36	7,1	43,86
Cheimerius nufar	3,9	2,23	6,7	50,56
Dasyatis thetidis	6,57	0	6,67	57,23