Quantitative fish survey of the submarine canyons of the iSimangaliso Wetland Park

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Abstract

There have been no quantitative studies of fish species associated with the submarine canyons of the north east coast of South Africa. These canyons offer protection to coelacanths *Latimeria chalumnae*, fish of commercial importance, and a number of protected and endemic species. A fish survey was conducted by remotely operated vehicle (ROV) that captured video footage at depths between 60 m and 160 m. Seven canyons (Island Rock, South Island Rock, Wright, Jesser, Diepgat, Leadsman and Chaka) and one deep reef (Diepgat Deep Reef) spread along 78 km of shelf break were surveyed. Fish were identified and counted in 1143 30-second video segments. Patterns in diversity and abundance were investigated with respect to canyon, depth, and habitat type. The survey found 52 fish species from 23 families. The families Serranidae and Sparidae were well represented. The first submarine images of the critically endangered Seventy-Four seabream are particularly noteworthy. Only three Myliobatidae species represented the Chondrichthyans. Variation in Shannon-Wiener species diversity (H') was influenced by the diversity of habitat (Kruskall-Wallis p<0,0001) and depths (Kruskall-Wallis p<0,0001). Mann-Whitney post hoc tests showed cave to have a higher H' than sandy plain (p<0,001) and wall (p<0,001). H' for margin was greater than sandy plain (p=0,001) and wall (p<0,001). H' for rock outcrop was greater than sandy plain (p=0,006). Fish diversity increased with increasing depth until 90m, thereafter diversity decreased with subsequent depths. Habitat (Permanova p=0,0031) had the strongest influence on fish community composition. No north-south separation in terms of fish diversity (H') among canyons was detected. The results were consistent with similar studies. All canyons were adequately sampled as the rate of discovery of additional species per sample was ≤1%. A minimum of 80 30-second samples per canyon is recommended to survey fish. The survey methods employed during this study are recommended for surveying deep reef fish to allow for meaningful comparative studies.

1. Introduction

Prior to 2000 very little research had been conducted into marine life in the submarine canyons of the iSimangaliso Wetland Park (IWP), in north-eastern South Africa. The discovery of coelacanths *Latimeria chalumnae* in Jesser canyon off Sodwana in 1999 (Venter et al. 2000), sparked enormous interest in the oceanography and ecology of the area.

The deep reefs of the submarine canyons in the IWP are home to coelacanths and diverse animal communities that are distinct from those in shallow (less than 40m) reefs (Sink et al. 2006). The canyon margins are also thought to be home to large numbers of commercially important fish species of the Sparidae, Serranidae and Lutjanidae families. The presence of the critically endangered coelacanth (Musik 2000) and commercially important fish species warrants the efforts to protect the area, but existing zoning arrangements may require further refinement to protect the canyons.

The implementation of Marine Protected Areas (MPAs) has become a popular management option for the conservation of marine species. MPAs such as the IWP have been shown to enhance reef fish abundance and diversity in various parts of the world (Halpern 2003). In South Africa there are a number of examples that demonstrate the effectiveness of MPAs in protecting species (Buxton and Smale 1989, Bennett and Attwood 1991, Currie et al. 2012b, Kerwath et al. 2013, Floros et al. 2013).

In 2010, South Africa had approximately 23% of its coastline protected by MPAs, however this constitutes only ~1% of the exclusive economic zone (Griffiths et al. 2010). Additionally, despite good coverage by MPAs, approximately 50% of fish species that are commercially exploited receive protection in this way (Solano-Fernandez et al. 2012).

Most of the benthic species (~83%) that have been recorded in South Africa are found at depths less than 100 m (Griffiths et al. 2010). An indication of the importance of protecting deep reefs and their associated species is that they are largely excluded from conservation areas (Solano-Fernandez et al. 2012).

Through the application of the maximum likelihood model of Solow and Smith (2005), it has been estimated that approximately 94 southern African endemic fish species remain to be described. These are likely to inhabit the subtropical waters along the east coast of

South Africa (von der Heyden 2011). The submarine canyons of the IWP fall within the middle of the east coast biogeographical zone. This zone is reported to have the highest diversity of fish in South Africa (Turpie et al. 2000, Solano-Fernandez et al. 2012).

Given the limited knowledge of species in the submarine canyons, a significant portion of these undescribed species may be found in these canyons. Heemstra et al. (2006) conducted a survey by submersible of the fish in these canyons at depths between 100 m and 400 m. The results of this survey showed that possibly only one third of the potential species of the submarine canyons of the IWP were recorded.

1.1. Survey techniques

A number of fishery-independent techniques for studying reef fish assemblages have been developed. These include *inter alia* controlled angling, trawl sampling, underwater visual census (UVC) and a variety of videography techniques.

The advantages of controlled angling techniques are that they are cost-effective and highly skilled personnel are not needed. Accurate fish measurements can be made of fish captured in inaccessible, turbulent environments (Cowley et al. 2002, Attwood 2003). Trawl sampling is a useful technique for obtaining data on small, cryptic species. This technique is able to record high species richness, irrespective of visibility (Cappo et al. 2004).

Unlike controlled angling census techniques (Götz et al. 2011, Götz et al. 2014) and trawl sampling (Cappo et al. 2004), UVC and videography are non-destructive techniques, allowing for them to be used repeatedly in sensitive areas. Since its development by Brock (1954), UVC by means of SCUBA has been used extensively. Dive transects have been found to efficiently record absolute abundances (Stobart et al. 2007). Cryptic species are more likely to be sampled by UVC as divers actively search for these species (Watson et al. 2005). However, the submarine canyon environments below 50 m are difficult to survey by SCUBA. Conventional SCUBA diving is restricted to depths less than 30 m. Below 30 m SCUBA is possible by using mixed gas, but this is expensive, dangerous and physiological constraints limit bottom time (Stobart et al. 2007). Errors in species identification, incorrect estimations of fish measurements and inter-observer bias are disadvantages of using this method (Harvey et al 2002, Harvey et al. 2004, Watson et al. 2010).

The advent of video sampling techniques has meant that observer bias could be reduced as a number of observers could check images repeatedly. Reliable abundance, species richness, size and behaviour data could be recorded (Willis and Babcock 2000). Diver operated video (DOV) surveys reduce biases, however the differential attraction to divers by certain fish species and disturbance of fish by divers, are still obstacles (Watson et al. 2010).

Baited remote underwater video (BRUV) techniques have been found to complement UVC by sampling species that normally shy away from divers (Willis et al. 2000). BRUVs are able to quantify mobile species and they have the additional benefit of providing important information on species behaviour (Lowry et al. 2012). Videographic studies are said to be limited to areas with sufficient visibility as fish abundance can be easily underestimated (Davis and Anderson 1989, Cappo et al. 2004, Langlois et al. 2010). Remote cameras, both baited (Willis and Babcock 2000, Willis et al. 2000, Cappo et al. 2006, Langlois et al. 2010, Bernard and Götz 2012) and unbaited (Watson et al. 2005), deployed underwater have been found to reduce this underestimation (Shortis et al. 2009, Bernard and Götz 2012) and efficiently determine relative densities (Willis et al. 2000). Under-reporting of herbivorous fish and cryptic fish species are disadvantages of the BRUV technique (Colton and Swearer 2010, Watson et al. 2005)

Advances in UVC have seen the addition of stereo video to the BRUV technique. Three-dimensional data enable this technique to take fish measurements with improved accuracy. Changes in the survey area are more likely to be detected, thereby vastly increasing the amount and value of data per sample (Harvey et al. 2004). This is particularly useful when studying the effects of fishing on fish populations (Langlois et al. 2012). Techniques such as high-resolution, nondestructive and in-situ stereo-BRUVs can provide improved understanding of ecology on deep and shallow reef habitats. In addition, such techniques can produce data that support effective ecosystem-based fisheries management (EBFM). Preliminary work in South Africa has shown stereo-BRUVs to be cost-efficient (Bernard et al. 2014) thus making their use a viable option.

Given the protected status of the coelacanth *Latimeria chalumnae*, the most feasible method for researching this species and its associated habitat in the deep submarine canyons from deep reefs is by video census. Video footage captured by remotely operated vehicles (ROVs) and submersible has been used extensively in the IWP.

Research on coelacanths (Venter et al. 2000, Heemstra et al. 2006, Hissmann et al. 2006, Sink et al. 2006), associated fish (Heemstra et al. 2006) and deep-water invertebrate fauna (Sink et al. 2006, Samaai et al. 2010, Thornycroft 2012) has been carried out in this way. Depth and time constraints when SCUBA diving are overcome by these methods. Below 150 m, research has typically been conducted by submersible (Heemstra et al. 2006, Stein et al. 1992, Ross and Quattrini 2009) however, some research below this depth has been conducted by ROVs (Ross and Quattrini 2009, McClain et al. 2010). The use of ROVs and submersibles is expensive (Bernard et al. 2014) and require deployment from research vessels and skilled operators. However, ROVs are less expensive and carry less risk than submersibles.

1.2. Fish diversity and assemblage patterns

In a number of shallow subtropical water studies (<100 m), benthic habitat type been found to separate fish communities (Currie et al. 2012b, Friedlander and Parish 1998, Ribeiro et al. 2005). A study by Malcolm et al. (2011) found depth to have the strongest effect, although a strong habitat effect was also evident. BRUVs were used by Malcolm et al. (2011) to sample a wider depth range (>60 m) than the other studies (<25 m).

In deep (>100 m) habitats, depth has been found to be the main cause of differentiation in fish assemblages (Yemane et al. 2010, Zintzen et al. 2012, Currie et al. 2012a). None of these studies tested for habitat effects. The study by Currie et al. (2012a) was conducted in a south east Australian submarine canyon to a depth of 1500 m. No significant differentiation by depth was seen between sampling stations at 100 m and 200 m. However, below 200 m strong depth effects were observed. The studies by Yemane et al. (2010) and Zintzen et al. (2012) were conducted along continental slopes of the south coast of South Africa and northern New Zealand, respectively. Both of these studies sampled up until at least 500 m.

Species diversity is highest in shallow water and it has been shown to decrease with increasing depth (Götz et al. 2014, Yemane et al. 2010). Species richness follows a similar pattern to diversity and also decreases with depth (Smith and Brown 2002; Yemane et al. 2010; Reum and Essington 2011; Follesa et al. 2011, Zintzen et al. 2012).

Given the aforementioned trends with depth, one would expect substantially lower species richness and diversity in the submarine canyons compared to the shallow environments. However, submarine canyons have been shown to be hotspots of regional productivity through canyon upwelling (De Leo et al. 2010). A variety of zooplankton have been found to maintain position within canyons (Macquart-Moulin and Patriti 1996, Allen et al. 2001), which may influence the fish assemblages and result in geographically different assemblage patterns from one area to another. One can therefore not assume that trends observed in other deep marine habitats will be consistent with those in shelf-edge canyons, particularly in areas of strong currents.

Habitat effects on fish diversity and assemblage patterns has been linked to heterogeneity of the benthic substrate (Friedlander and Parrish 1998). The substrate along the edges of the submarine canyons of the IWP is known to be diverse (Sink et al. 2006; Thornycroft 2012). Therefore, a strong habitat effect on the fish diversity and assemblages is expected.

1.3. Fish species of the iSimangaliso Wetland Park

The shallow habitats of the IWP have been extensively studied (Chater et al. 1995; Celiers and Schleyer 2008, Floros et al. 2013). The most notable recent study is that of a baseline assessment of the coral reef fish communities by Floros et al. (2012) who found 284 species belonging to 50 families being recorded at 12 to 15 m.

Between 1987 and 1990, Chater et al. (1993) conducted fish surveys of shallow (<45 m) reefs in the IWP by UVC. Fishery-independent angling surveys were also conducted. Only 10% of fish caught were not recorded during SCUBA surveys. This indicates that the species associated with deep habitats were not well represented here.

The first attempt to obtained baseline quantitative data on distribution and abundances of fishes in the IWP was by Chater et al. (1995). UVCs were conducted to assess abundances of fish species from 13 families of reef fish inside the IWP. A number of species of the Serranidae, Lutjanidae and Lethrinidae were recorded. These are commercially important species further north in Mozambique.

No quantitative surveys of the deep reef fish have been conducted. A list of fish species encountered during a submersible expedition was compiled by Heemstra et al. (2006). During this expedition 54 species were recorded between 100 m and 359 m. Additionally, Sink et al. (2006) conducted 19 Trimix dives from 1998 to 2001. The survey depth was between 75 m and 140 m. A number of species of the Lutjanidae and Sparidae families were recorded. One previously unrecorded fish species was documented, the coelacanth *Latimeria chalumnae.*

1.4. Aims of this study

In this study I make use of video footage collected by ROV in the submarines canyons of the IWP. It is the first quantitative study of canyon fish abundance. The aim of this study is, firstly to provide a survey of the deep reef fish of the submarine canyons of the IWP that will build upon the fish species list compiled by Heemstra et al. (2006) and Sink et al. (2006). Research into such habitats where so little is known has revealed species that were not previously recorded in southern Africa or are new to science (Sink et al*.* 2006).

Secondly, patterns in the fish assemblages among habitat and along depth and latitude gradients will be investigated. The fish assemblages among canyons will also be compared. An understanding of these patterns will facilitate effective conservation planning (i.e. zoning of MPAs) and contribute towards a better understanding of coelacanth behaviour.

An assessment as to the suitability of ROV for sampling the submarine canyons of the IWP will be also made. It is hoped that this study will aid in the development of an effective, standardised sampling method for these deep habitats.

2. Study area

This study was conducted in the submarine canyons in the iSimanagaliso Wetland Park, a marine protected area enclosing 78 km of the coastline off Sodwana on the northern KwaZulu-Natal coast, South Africa (Figure 1). The KwaZulu-Natal continental shelf varies between 2 and 5 km, which is very narrow compared to the global average of 75 km. It is cut through by 23 canyons (Ramsay 1994). The canyon heads (Figure 2) have steep sides. Overhangs and caves are common due to the presence of carbonate rock cement that was eroded during low sea levels in the Pleistocene period when the surf zone was at this level (Ramsay and Miller 2006).

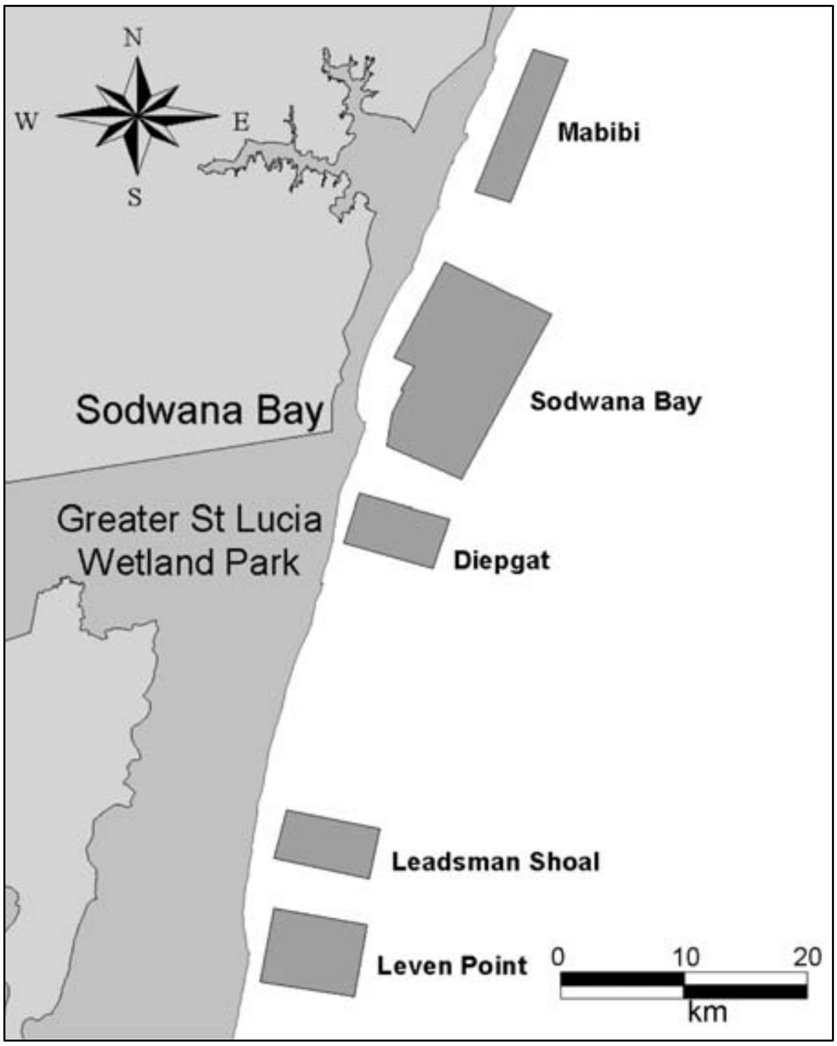


Figure 1. Locality map of five survey blocks off the northern KwaZulu-Natal continental shelf and slope

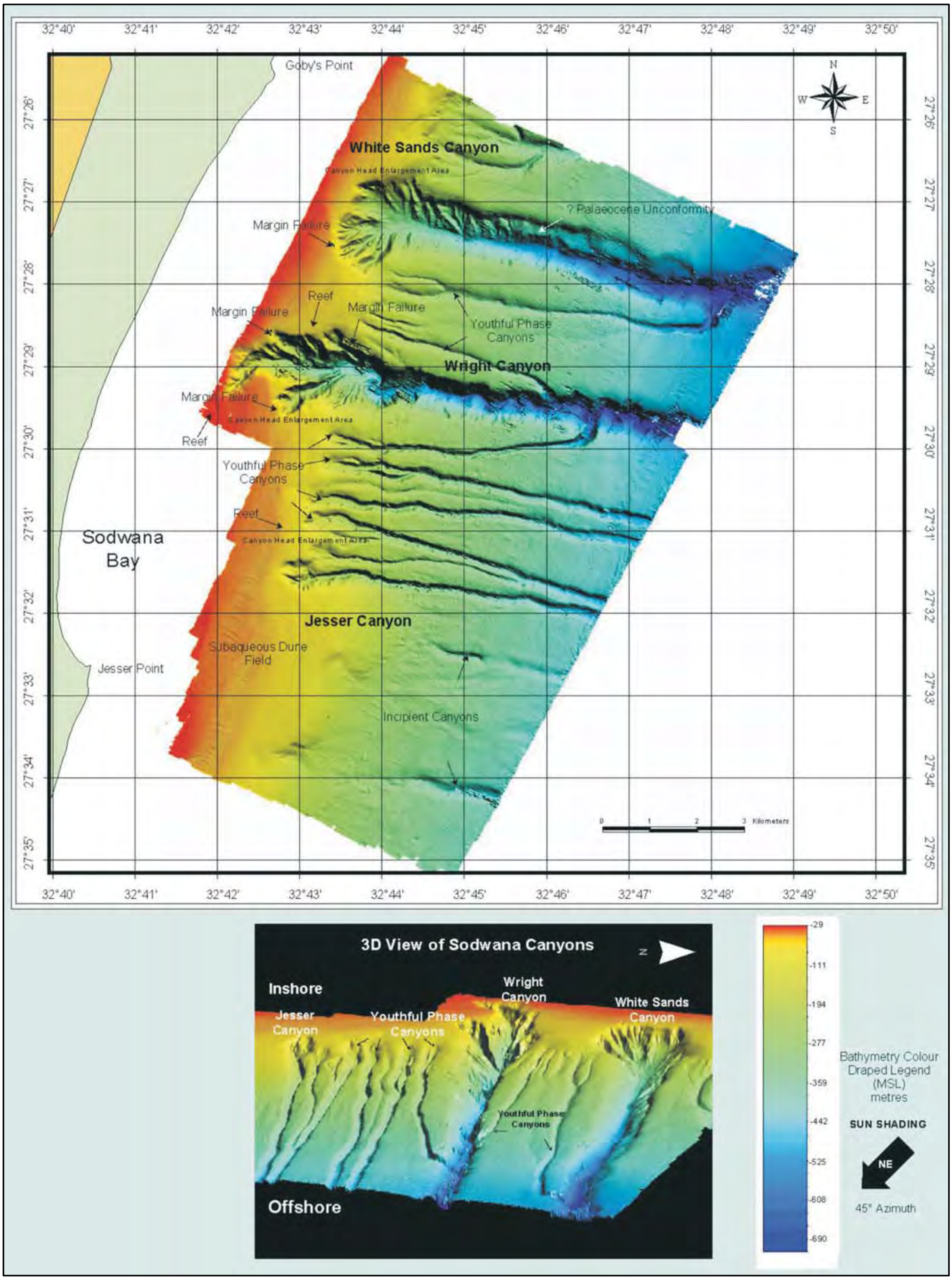


Figure 2. Bathymetric map of a number of submarine canyons off Sodwana Bay (Ramsay & Miller 2006)

Oceanographic environment

The main oceanographic feature of the IWP is the Agulhas Current, which is one of the world's major southward flowing currents (Ramsay 1994, Lutjeharms et al*.* 2001). Recirculation from a South-West Indian Ocean Gyre (Lutjeharms 2006) and waters following complex routes south of Madagascar and in the Mozambique Channel between Maputo and Durban, South Africa (Ramsay 1994) are the main source of water. The Agulhas Current flows parallel to the coastline all the way to Port Elizabeth (Lutjeharms 2006).

The oceanic environment off the canyons is characterised by strong currents. However, within the canyons, the current velocity decreases significantly and in places there is little or no flow (Hissmann et al. 2006, Roberts et al. 2006). Upwelling, downwelling and ripples on the canyon floor have been observed giving rise to considerable variation in current flow within the canyons (Roberts et al. 2006).

The 20°C isotherm, which is within the tolerable temperature range for coelacanths (Hissmann et al. 1998, Ribbink and Roberts 2006), is situated at approximately 100 m depth (Roberts et al. 2006), coincidentally the depth where numerous caves and overhangs are found. Within the canyons there is high variability in temperature. Temperature between 104 m to 140 m ranges between 15°C and 22°C seasonally. This variation is due to changes in flow regime, which cause upwelling cells as well as tides and daily water movements up and down the continental slope (Ribbink and Roberts 2006).

This dissertation surveyed fish in seven submarine canyons (Island Rock, South Island Rock, Wright, Jesser, Diepgat, Leadsman and Chaka) and one deep reef (Diepgat Deep Reef) that is associated with a shallow canyon margin.

3. Materials and Methods

3.1. Remotely Operated Vehicle Survey

In 2013, the Isimangaliso Coelacanth Expedition took place as part of the African Coelacanth Ecosystem Programme (ACEP). The expedition ran from 10 April to 13 May 2013. Video footage was captured during 17 survey dives by a remotely operated vehicle (ROV). The primary goal of these ROV surveys was to investigate the population size, and habitat use of the coelacanth *Latimeria chalumnae*. This study of the icthyofaunal assemblages and their habitat and depth patterns forms part of the research into the broader offshore diversity of the iSimangaliso Wetland Park (IWP) and marine ecosystems associated with the coelacanth.

The ROV conducted randomly stratified surveys across the IWP, and inspected known coelacanth caves. The ROV surveys focused on the margin habitat of shelf-indenting and shelf-breaching canyons (Green et al. 2009). Using ArcMap10, the margin habitat was selected based on the bathymetric data for canyons as delineated by Ramsay and Millar (2006). Using the 100 m depth contour, the total length of the margin habitat was determined (32.57 km) and zoned into 61 survey areas of approximately 500 m, covering a total of 31.1 km. This included three survey areas that were between 400 and 500 m in length. Three areas of less than 400 m survey length were excluded from the survey area (one per canyon in Island Rock, White Sands, Wright, and Diepgat).

The Seaeye Falcon Remotely Operated Vehicle (ROV) System was used to undertake survey dives on the submarine canyons and deep reefs within the iSimangaliso Wetland Park (IWP). The ROV system included a surface power supply unit, a surface control unit, a hand control unit and a system monitor and keyboard. It was equipped with a high definition video camera also capable of 10 megapixel digital photographs, laser scaling (6 cm laser distance) and optical zoom. The ROV system was setup onboard the research vessel M/V *Angra Pequena,* attached by 300 m of umbilical and launched and recovered using a crane.

Video footage was captured continuously from the time that the ROV started the dive until the time that it exited the water. The ROV speed was not constant along transects as it would slow down to investigate caves and crevices and to keep the umbilical clear of obstacles.

3.2. Video analysis

The video footage of each dive was split into 30-second segments. Each segment was analysed separately. A segment of 30 seconds was found to be more manageable than a longer time frame, as it would require less replaying of video to make sure that data had been accurately recorded. Habitat and depth could also be more accurately recorded in this way. The data recorded included: fish species and abundance, depth and habitat type.

To avoid the potential problem of counting the same fish multiple times as it enters and exits the field of view, abundance was recorded as the maximum number of fish of each species seen in a particular video frame during a 30s segment (Ellis and DeMartini 1995, Parker et al. 1997, Menza et al. 2007).

The depth and time of day were displayed during video playback and recorded at the start of each video segment. The depth of each observation was later assigned to a depth class. The change in depth during a video segment was normally not more than five meters. Ten-meter intervals were used to categorise depths to ensure that any rapid change of depth during a 30s interval still fell within one depth class.

Habitat types (Table 1) were classified as Sandy Plain, Rock Outcrop, Margin, Wall, Cave or Thalweg. These habitat types were classified according to studies by Sink et al. (2006) and Thornycroft (2012). Flat, sandy areas dominated by sea pens above the canyon slope were classified as "Sandy Plain". This habitat type was normally above 90 m. Rocky patches within these plains were classified as "Rock Outcrop". The rocky canyon edges between 90 m and 120 m with a variety of invertebrate species and dense cover were classified as "margin". If the substrate had very little invertebrate cover and was over 100 m deep it was classified as "wall". This included any vertical rock structure below 100 m. If a vertical rock structure had a slope of more than 90 degrees it was classified as habitat type "cave". The "thalweg" habitat classification was assigned to the silt habitat on the floor of the canyon at depths below that of the "wall". In this study, the "thalweg" habitat was only ever identified below 125 m. Examples of the appearance of these habitats can be seen in figure 3.

Table 1: Criteria for habitat classification within canyons of the iSimangaliso Wetland Park

Habitat type	Depth	Description
Sandy Plain	<90m	Bare sand or dominated by sea pens. No invertebrates that require rock to attach to.
Rock Outcrop	<90m	Rock structure surrounded by sand. Numerous invertebrates.
Margin	<120m	Rocky canyon edge. Numerous invertebrates.
Cave	>90m	Caves or overhangs. Usually within the margin or wall habitats. Few invertebrates.
Wall	>120m	Rocky slopes, sometimes vertical. Little to no invertebrate cover.
Thalweg	>120m	Silt bottom of canyons below wall habitat. Occasionally strewn with dislodged boulders. No invertebrate cover.

Video footage that was obscured (i.e. disturbed sediment), unfocused, or where the habitat could not be identified, was excluded from the analysis. If the ROV remained stationary for more than 60s then only the first 30s was included.

Fishes were identified to species level wherever possible using Smith & Heemstra (1986), Heemstra et al. (2006), King and Fraser (2014) and Froese et al. (2014).

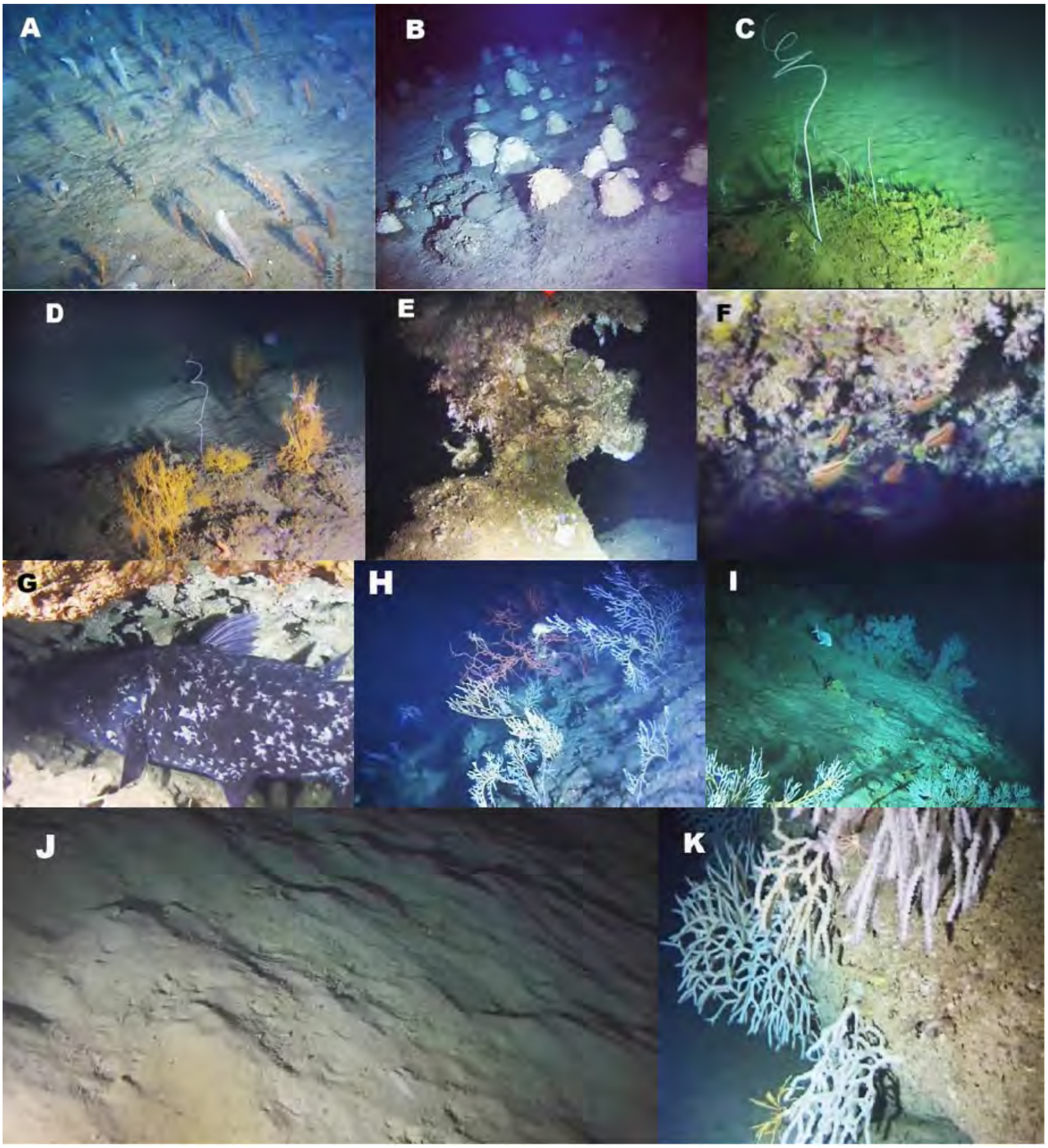


Figure 3. Habitat types according to Thornycroft (2012): Sandy Plain (A and B), Margin (C and D), Rock Outcrop (E), Cave (F and G), Wall (H and I) and Thalweg (J and K)

3.3. Statistical methods

To determine whether fish assemblages differed among canyons, habitat types or depth classes, the data were subjected to multivariate analyses. These analyses were conducted in PRIMER 6 according to the guidelines in Clarke and Warwick (2001) and Clarke and Gorley (2006). The relative abundances and a ranking technique that allows for comparisons of unequal sample sizes were used for all analyses. This type of analysis was selected because it is appropriate for this dataset, which is not normally distributed.

The DIVERSE function in PRIMER-E (Clarke and Warwick 2001) was used to calculate the Shannon-Wiener (H') diversity indices per canyon, habitat type and depth class. The commonly used logarithmic base 10 was selected for calculating H' (Zar 1996). Differences in mean H' among canyons and habitats were tested by means of Kruskal-Wallis. Pairwise comparisons were conducted by means of the Mann-Whitney test with the Bonferonni correction.

The possibility that the habitat composition of the samples could explain the species richness or species diversity patterns among canyons was tested in two ways. Firstly, it was hypothesised that the evenness of habitats in canyons would correlate with either species richness or diversity. This was tested by least squares linear regressions, in which the information index $H = \Sigma p_i \ln(p_i)$, where p is the proportion of the habitat i in the samples of the canyon. Secondly, it was hypothesised that the species richness and diversity was related to the proportion of samples that fell in the habitats that had the highest species richness. This was tested by least squares regression in which the independent variable was the proportion of samples in cave and rock outcrop. Cave and rock outcrop were the two habitats with the highest diversity.

The fish abundance count data were then standardised and thus converted into relative abundances, expressed as percentages. This new data set was then square-root transformed in order to down-weight the influence of very abundant fishes. This transformation was considered sufficient, as there is only one order of magnitude between the highest and lowest number of individuals counted. Similarities between samples were calculated using a Bray-Curtis similarity coefficient. The resulting similarity matrices were used when performing non-metric multidimensional scaling (MDS) analyses.

Permutational multivariate analysis of variance (PERMANOVA) was conducted in PRIMER (Anderson et al. 2008). A three-factor design was used with canyon, habitat type and depth class as factors. The PERMANOVA table was constructed using Type III sums of squares. The number of permutations was set at 9999 for calculating statistical differences between factors and for exploring the interactions between factors.

Similarity percentage (SIMPER) analyses in PRIMER-E (Clarke and Warwick 2001) were used to determine which species contributed to 90 percent of the differences between canyons, habitat type and depth class.

4. Results

4.1. Species recorded

Video footage from 17 ROV dives in 8 canyons produced 10.5 hours of usable footage (Table 2). The footage was divided into 1143 segments. The margin was sampled the most, followed by the wall and cave habitats (Figure 4). Little sampling focus was directed at sandy plain, rock outcrop or thalweg.

Table 2: Remotely operated vehicle survey time for each of the iSimangaliso Wetland Park canyons

Location	Survey time (min)	Usable footage (min)
Island Rock	157	57
South Island Rock	90	30
Wright	590	144
Jesser	253	51
Diepgat Deep Reef	92	21
Diepgat	346	151
Leadsman	216	42
Chaka	285	123,5
Total	2029	619,5

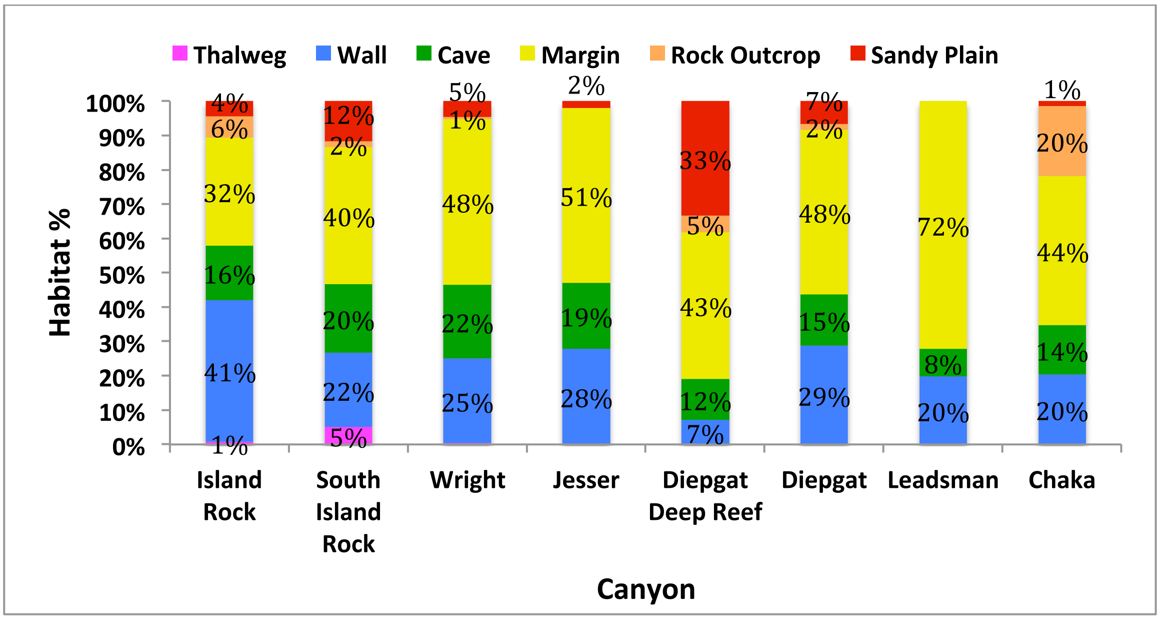


Figure 4: Percentage of samples collected from each habitat in each canyon

The depth range over which samples were collected in each canyon ranged from 68 m to 161 m (Figure 5). The smallest depth range was sampled on Diepgat Deep Reef, with most samples obtained at shallow depths (i.e. <100 m). Chaka canyon had a similar depth range, but mostly at depths greater than 100 m. Diepgat and Wright canyons had the largest depth range sampled. Only Island Rock and Diepgat had samples collected from depths greater than 150 m.

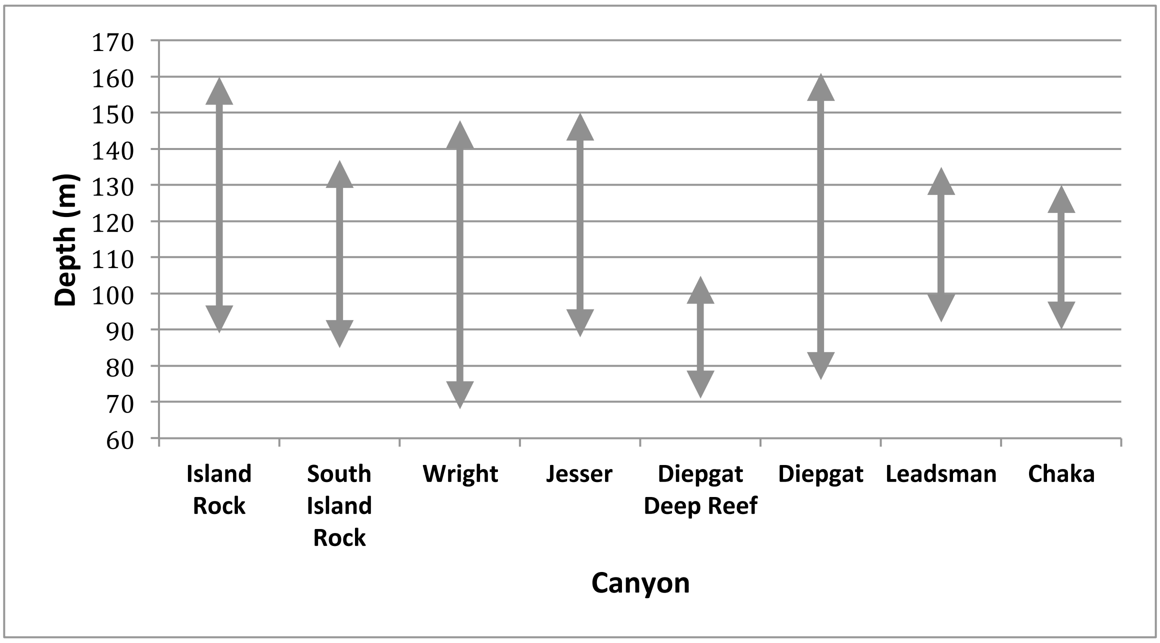


Figure 5: Depth range of samples collected in each canyon

During this study 52 species of fish from 23 families were identified (Table 3). The most commonly encountered species were the One-stripe Goldie *Pseudanthias gibbosus* (Serranidae) followed by Slinger *Chrysoblephus puniceus* (Sparidae). The commercially important Sparidae family was also well represented by Blueskin *Polysteganus coeruleopunctatus.* Other noteworthy sightings include a number of protected Red Steenbras *Petrus rupestris* sightings, and the first *in situ* sighting of the Seventy-four *Polysteganus undulosus.*

Myripristis chryseres (Holocentridae)*, Epinephelus morrhua, Odontanthias borbonius, Pseudanthias gibbosus* (Serranidae) and *Chrysoblephus puniceus* (Sparidae) were the only species that were encountered in all of the canyons.

Table 3 shows that the most species recorded in any canyon was 33. This was in Jesser canyon where the most usable footage was recorded (302 segments = 2.52 h). This was similar in Wright canyon with 30 species (288 segments = 2.4 h). Substantially less usable footage was available from the rest of the canyons due to poor visibility caused by adverse weather conditions.

Table 3: List of species, species richness, and sampling effort in each of the iSimangaliso Wetland Park canyons

Family	Species	Island Rock	South Island Rock	Wright	Jesser	Diepgat Deep reef	Diepgat	Leadsman	Chaka
Ambassidae	*Ambassis sp.*	✓	✓	✓	✓		✓		✓
Apogonidae	Apogon fukuii	✓	✓	✓	✓		✓	✓	✓
Apogonidae	*Ostorhincus apogonoides*		✓				✓		
Apogonidae	*Pristiapogon kallopterus*						✓		
Berycidae	*Centroberyx druzhinini*	✓	✓	✓	✓		✓	✓	✓
Carangidae	*Seriola rivoliana*	✓		✓	✓	✓	✓	✓	✓
Chaetodontidae	*Chaetodon dolosus*	✓					✓		
Chaetodontidae	*Chaetodon marleyi*	✓	✓	✓	✓		✓		✓
Chaetodontidae	*Chaetodon sp.*	✓		✓	✓		✓		✓
Chaetodontidae	*Heniochus acuminatus*					✓			
Cheilodactylidae	*Chirodactylus jessicalenorum*				✓				✓
Dasyatidae	*Himantura jenkinsii*	✓							
Haemulide	*Dinoperca petersi*						✓		
Haemulide	*Pomadasys striatus*				✓				
Holocentridae	*Myripristis chryseres*	✓	✓	✓	✓	✓	✓	✓	✓
Labridae	*Anampses lineatus*			✓					
Labridae	*Bodianus trilineatus*	✓	✓	✓	✓		✓		✓
Labridae	*Suezichthys sp.*	✓	✓	✓	✓		✓		✓
Lutjanidae	*Aprion virescens*						✓	✓	
Lutjanidae	*Paracaesio sordida*	✓				✓	✓	✓	
Lutjanidae	*Paracaesio xanthura*	✓	✓	✓	✓	✓	✓	✓	
Mobulidae	*Manta alfredi*						✓		
Monacanthidae	*Aluterus monoceros*				✓		✓		
Monacanthidae	*Thamnaconus fajardoi*			✓					✓
Monocentridae	*Monocentris japonica*		✓		✓		✓		✓
Muraenidae	*Gymnothorax favagineus*	✓							
Pomacanthidae	*Apolemichthys kingi*							✓	
Pomacanthidae	*Pomacanthus rhomboides*			✓		✓			
Pomacentridae	*Chromis woodsi*	✓	✓		✓		✓	✓	
Priacanthidae	*Priacanthus hamrur*	✓		✓					
Priacanthidae	*Pristigenys niphonia*	✓			✓		✓		✓
Sciaenidae	*Argyrosomus japonicus*		✓						✓
Sciaenidae	*Umbrina robinsoni*				✓				✓
Scorpaenidae	*Scorpaenopsis venosa*	✓		✓			✓	✓	
Serranidae	*Aulacocephalus temminckii*	✓	✓	✓	✓		✓	✓	✓
Serranidae	*Epinephelus marginatus*			✓	✓	✓	✓	✓	✓
Serranidae	*Epinephelus morrhua*	✓	✓	✓	✓	✓	✓	✓	✓

Serranidae	*Epinephelus tukula*					✓		✓	✓
Serranidae	*Liopropoma sp.*	✓	✓	✓	✓		✓	✓	✓
Serranidae	*Odontanthias borbonius*	✓	✓	✓	✓	✓	✓	✓	✓
Serranidae	*Plectranthias sp.*			✓			✓		
Serranidae	*Pseudanthias gibbosus*	✓	✓	✓	✓	✓	✓	✓	✓
Serranidae	*Serranus knysnaensis*	✓					✓		✓
Sparidae	*Chrysoblephus anglicus*	✓	✓	✓	✓			✓	✓
Sparidae	*Chrysoblephus puniceus*	✓	✓	✓	✓	✓	✓	✓	✓
Sparidae	*Petrus rupestris*			✓	✓				✓
Sparidae	*Polysteganus coeruleopunctatus*			✓	✓	✓	✓	✓	✓
Sparidae	*Polysteganus praeorbitalis*	✓		✓	✓				✓
Sparidae	*Polysteganus undulosus*	✓							
Symphysanodontidae	*Symphysandon sp.*	✓		✓			✓	✓	✓
Tetraodontidae	*Arothron immaculatus*		✓						
Tetraodontidae	*Canthigaster inframacula*			✓	✓				
Unidentified	*Ray 1*			✓					
Total Diversity		29	20	30	29	13	33	21	29
No. of 30s segments		114	60	288	104	42	302	86	147

The majority of the ROV surveys were spent in the margin habitat followed by the wall habitat, then cave (Table 4). The number of species recorded per habitat was highest in the margin habitat. The cave habitat had the next highest number of species.

Table 4: Species richness in each habitat type across all iSimangaliso Wetland Park canyons

Habitat type	Species richness	Number of segments
Sandy Plain	10	63
Rock Outcrop	27	47
Margin	41	541
Wall	29	297
Cave	33	190
Thalweg	2	5
Σ		1143

C. puniceus was the only species that was found in all habitats while *P. gibbosus* and *Paracaesio xanthura* were found in five of the six habitat types. *Myripristis chryseres* and *Monocentris japonica* were species that were frequently encountered during dives. *M. chryseres* was only ever seen in margin and cave habitats while *M. japonica* was only seen in wall and cave habitats.

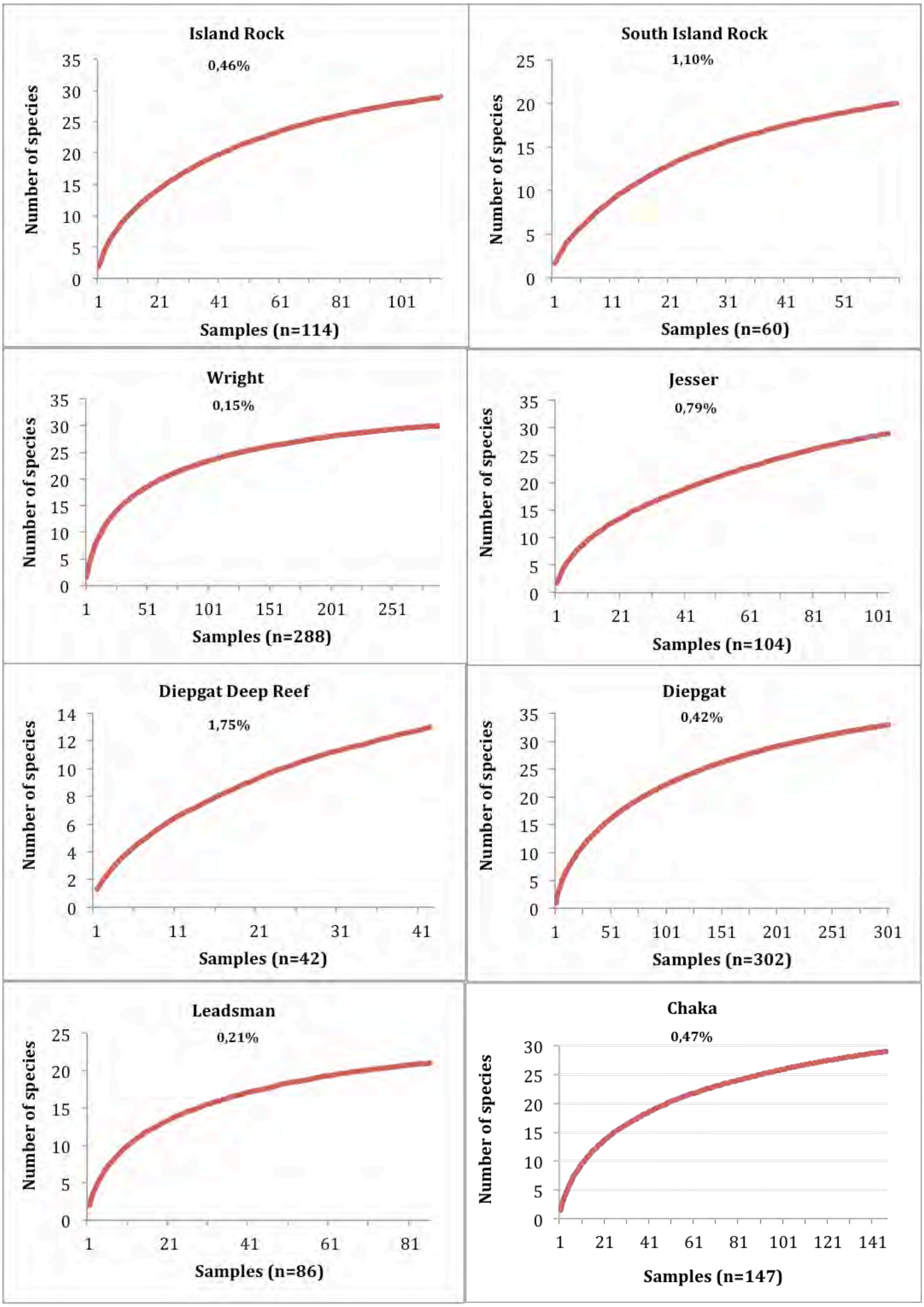
A comparison of species composition at the various depth classes (Appendix 1) showed *Chrysoblephus puniceus* to have the greatest depth range and was encountered at all depth classes from 60 m to 150 m. *Pseudanthias gibbosus* (70 m to 150 m) and *Symphysanodon sp*. (80 m to 160 m) were second in this respect and were encountered in one depth class less than *C. puniceus*. *Centroberyx druzhinini* and *Aulacocephalus temminckii* were frequently encountered, but only between the depth classes of 90 m and 130 m. *Myripristis chryseres* was frequently encountered between depth classes 80 m and 110 m.

4.2. Species accumulation

Species accumulation plots (Figure 6) show that on the whole there were sufficient sample numbers to document the fish assemblages of each submarine canyon in the IWP. Sample sizes were deemed sufficient if an additional sample failed to improve the species richness by 1%. The sample size of 60 for South Island Rock resulted in a rate of discovery very close to 1% (1,1%). Figure 6 shows Diepgat Deep Reef to be the only site with a rate of discovery over 1%.

In terms of habitat type, species accumulation plots (Figure 7) show evidence of thorough sampling of the Margin, Cave and Wall habitats. All three habitats exhibited rates of discovery well below 1%. Sandy Plain, Rock Outcrop and Thalweg were not sufficiently sampled. The rate of discovery of new species could not be calculated for the Thalweg habitat type as the number of samples was too low.

Species accumulation plots (Figure 8) show that the depths of 90 m to 120 m were adequately sampled. In each instance the marginal rate of discovery was well below 1%. Depth categories outside this range were not sampled sufficiently.



Island Rock

South Island Rock

Wright

Jesser

Diepgat Deep Reef

Diepgat

Leadsman

Chaka

Figure 6: Species accumulation plots for each canyon using the "Sobs" routine in PRIMER (Clarke and Gorley 2006). The rate of new species discovery (%) is shown for each canyon

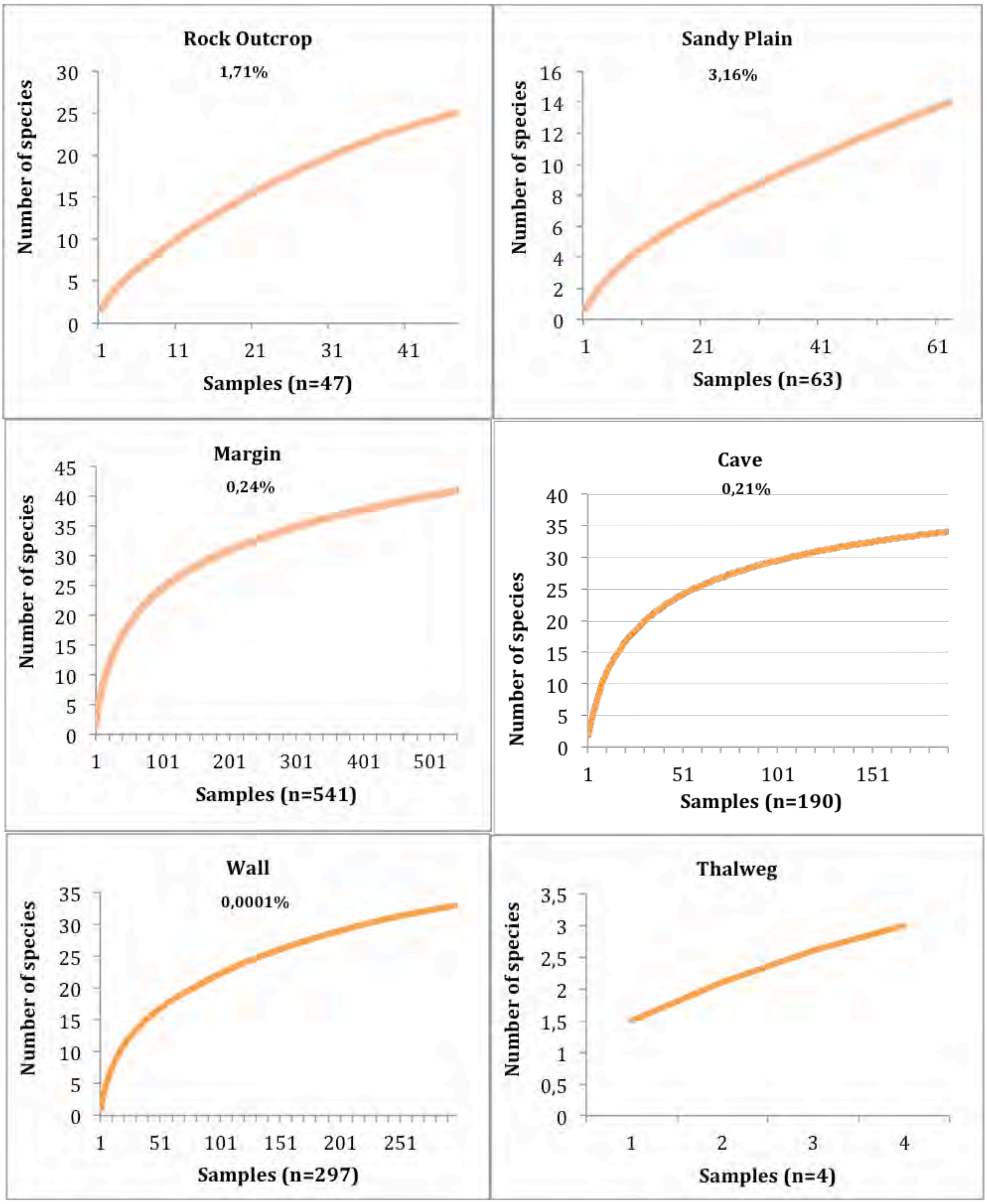


Figure7. Species accumulation plots for each habitat using the "Sobs" routine in PRIMER (Clarke and Gorley 2006). The rate of new species discovery (%) is shown for each habitat

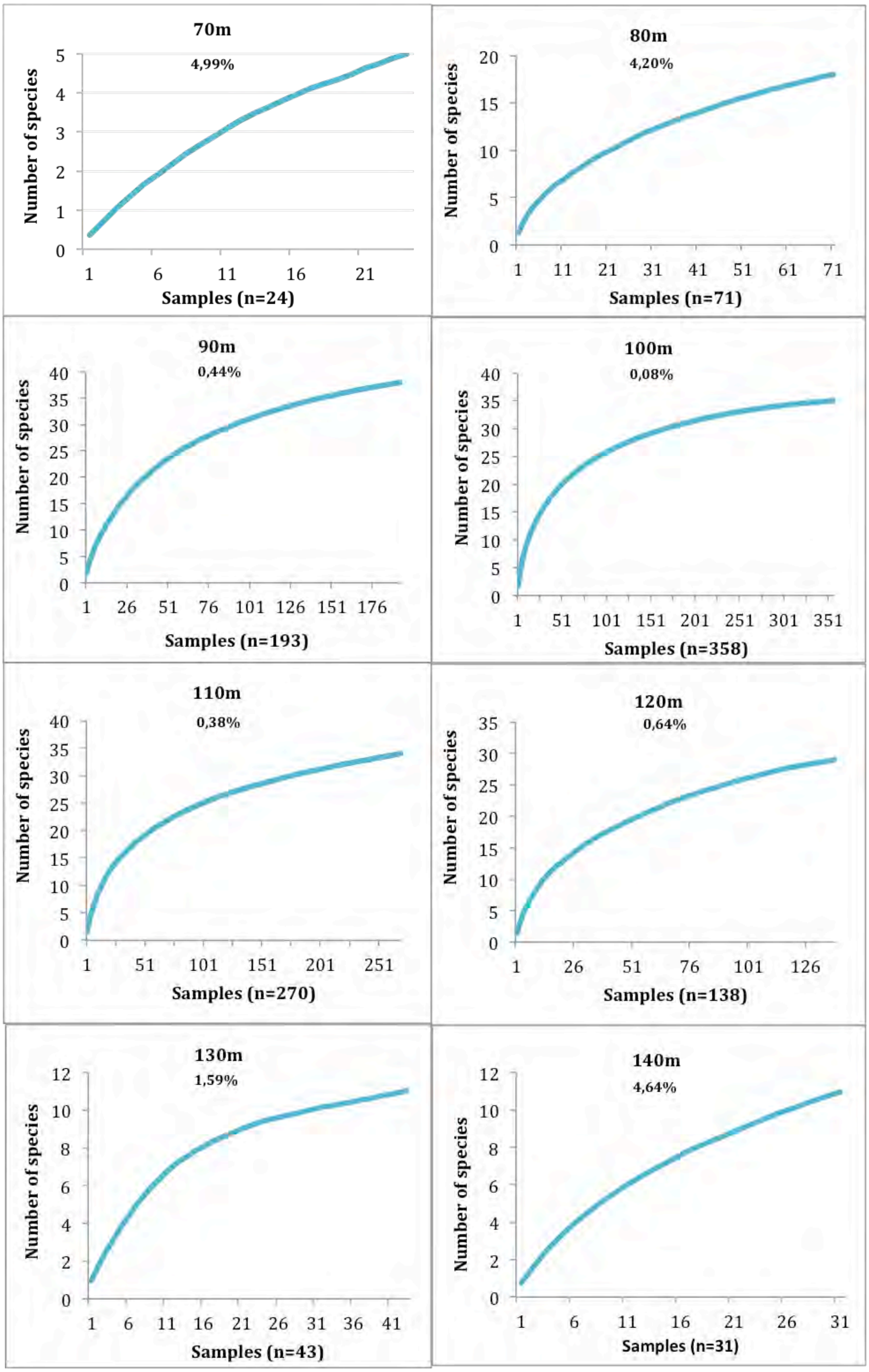


Figure 8. Species accumulation plots for each depth using the "Sobs" routine in PRIMER (Clarke and Gorley 2006). The rate of new species discovery (%) is shown for each depth

4.3. Assemblage patterns

The MDS plot in Figure 9 shows a fair amount of overlap in ordinal space between the canyons, but no clear pattern of separation is evident. Wright canyon appears to have very little overlap with Diepgat, Island Rock and Leadsman Canyons. Jesser and Chaka Canyons seem to overlap slightly while Diepgat Deep Reef appears to be quite distinct from all canyons.

Figure 9: Non-metric multidimensional scaling ordination for samples between each iSimangaliso Wetland Park canyon, ordered from north to south in the legend

The MDS ordination plot with habitat as the chosen factor (Figure 10) shows clear separation of the habitats in ordinal space with very little overlap. This indicates that distinct fish assemblages are found in each habitat.

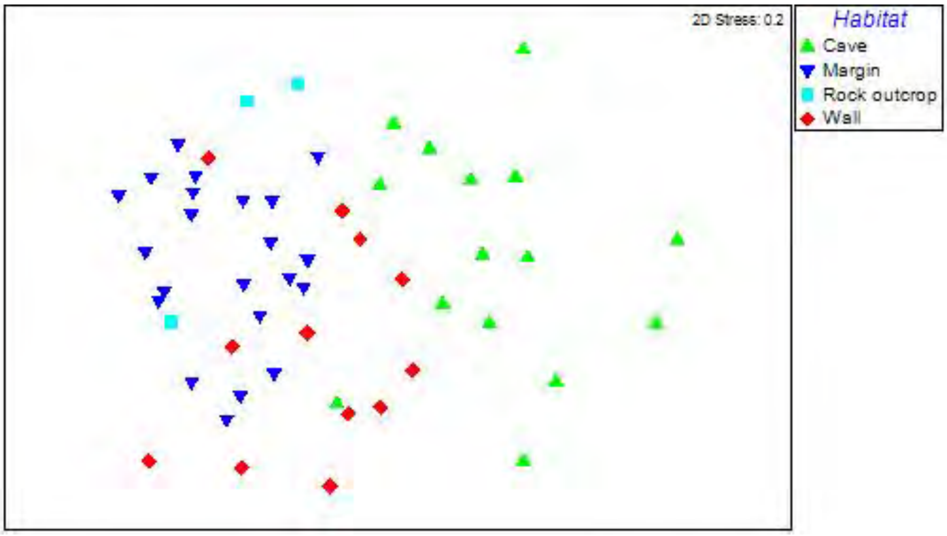


Figure 10: Non-metric multidimensional scaling ordination of samples between each habitat type in the iSimangaliso Wetland Park canyons

There is some overlap between the shallower depth classes in the MDS plot in figure 11. The pattern of changing fish assemblage with increasing depth is still visible. Looking at the top left of the plot and moving towards the red dot at the bottom there appears to be a pattern of change in fish assemblage with increasing depth. Depth classes 7, 14, 15 and 16 (i.e. 70, 140, 150 and 160 m) were excluded from this analysis. There were too few fish recorded for the few segments analysed, which resulted in errors being reported in the PRIMER analysis while constructing the resemblance matrix.

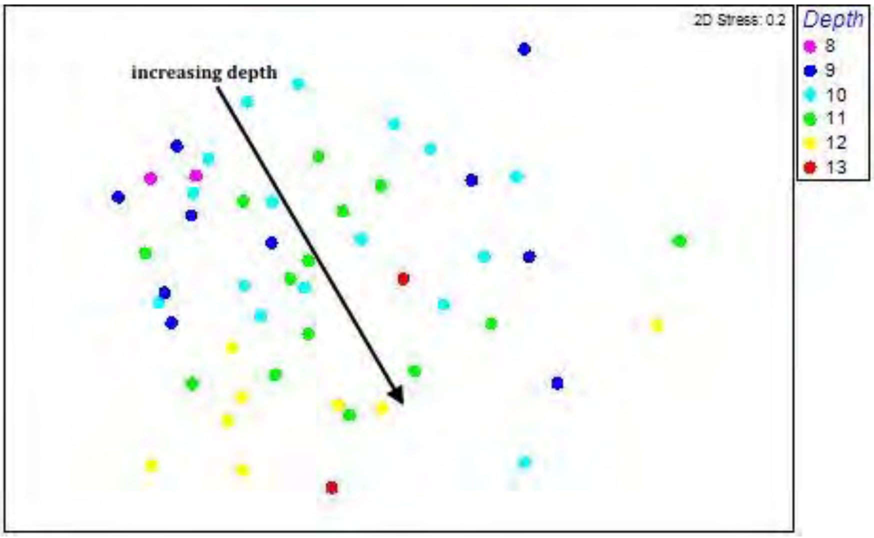


Figure 11: Non-metric multidimensional scaling ordination of samples between each depth class sampled in the iSimangaliso Wetland Park canyons. Depth classes are abbreviated such that 8 represents 80-89 m, 9 represents 90-99 m and so on

4.4. Factors responsible for fish assemblage patterns

The PERMANOVA analysis (Table 5) shows significant differences in fish assemblages for the factors of habitat and canyon. Habitat type was found to have the most significant effect on the fish assemblage pattern (P=0,0031). When the factors were tested for their combined effects, habitat and canyon together (P=0,0001) were found to be the most significant contributing factor to the fish assemblage patterns in this study. Interestingly, although in isolation depth was not found to have a significant influence (p=0,6628), the combination of depth and canyon (p=0,0018) had a stronger effect than habitat. The effect of canyon on fish assemblages is significant (0,0224), but weakly so.

Table 5: PERMANOVA of the relative abundance of 52 fish species (square-root transformed) in response to depth class (De), habitat type (Ha), canyon (Ca) and their interactions

Source	df	MS	Pseudo-F	P(perm)
De	8	2891,4	0,89984	0,6628
Ha	3	7148,3	2,2247	0,0031
Ca	5	5095,4	1,5858	0,0224
DexHa	17	3828,5	1,1915	0,0922
DexCa	33	4242,3	1,3203	0,0018
HaxCa	24	4865,1	1,5141	0,0001
DexHaxCa	29	3817,6	1,1881	0,0464
Res	762	3213,2		
Total	889			

4.5. Diversity comparisons

The Shannon-Wiener species diversity was found to be significantly different between the canyons (Kruskal-Wallis chi-squared = 49,4641, df = 7, p<0,0001). Pairwise comparisons (Table 6) revealed significant differences in diversity between Island Rock and Diepgat (p<0,001), Jesser and Diepgat (p<0,001), Leadsman and Diepgat (p<0,001) and between Leadsman and Wright (p=0,03031).

The species diversity between canyons (Figure 12) shows that Leadsman canyon followed by Island Rock has the highest species diversity. Diepgat was found to have the lowest diversity, followed by Diepgat Deep Reef. There is no apparent north-south trend with regards to species diversity.

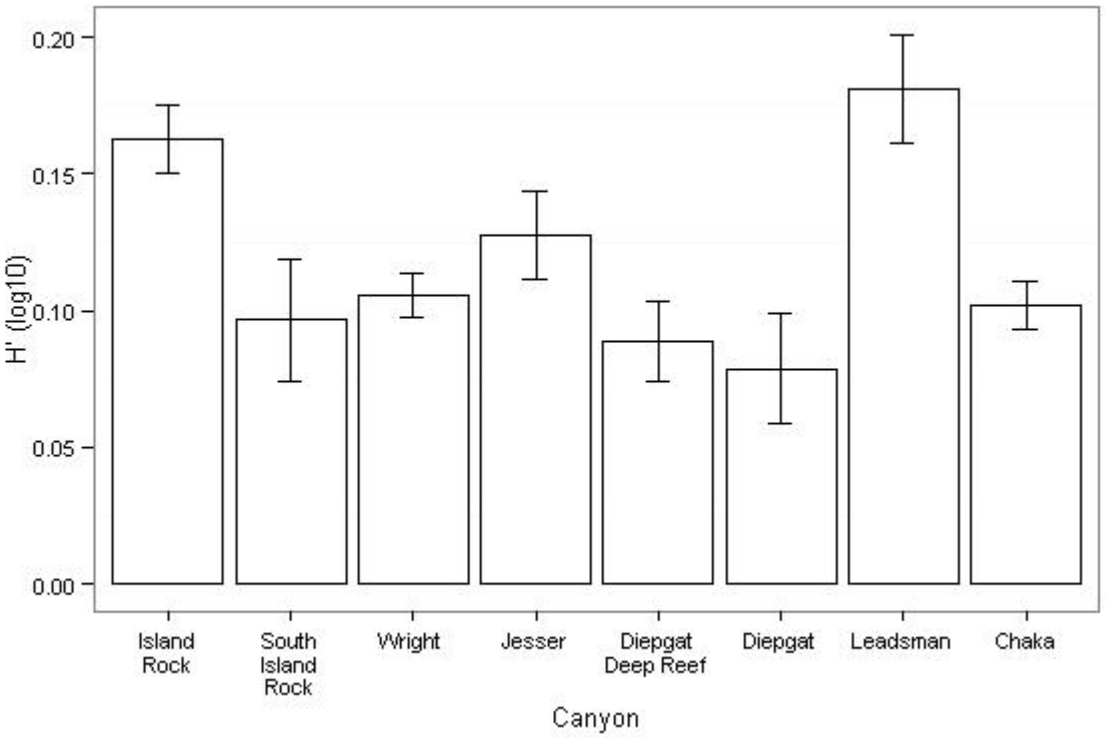


Figure 12: Mean (± 1 SE) Shannon-Wiener diversity indexes (H') for each canyon arranged from north (Island Rock) to south (Chaka)

There were no significant correlations between either species richness or diversity per canyon and either the evenness of habitat or the proportion of cave and rock outcrop.

Table 6. Adjusted p-values resulting from pairwise comparisons of H' between canyons. Values in bold reflect where differences are significant

	Chaka	Diepgat	Diepgat Deep Reef	Island Rock	Jesser	Leadsman	South Island Rock
Diepgat	0,672	-	-	-	-	-	-
Diepgat Deep Reef	1,000	1,000	-	-	-	-	-
Island Rock	0,104	**<0,001**	0.419	-	-	-	-
Jesser	1,000	**<0,001**	1,000	1,000	-	-	-
Leadsman	0,079	**<0,001**	0.302	1,000	1,000	-	-
South Island Rock	1,000	1,000	1,000	0,631	1,000	0,409	-
Wright	1,000	0,063	1,000	0,058	1,000	**0,030**	1,000

The species diversity between habitats was found to be significantly different (Kruskal-Wallis chi-squared = 44,7098, df = 5, p <0,001). Pairwise comparisons (Table 7) showed the species diversity of Sandy Plain to be significantly different to that of Cave (p<0,001) and Margin (p=0,001). The difference in H' was found to be significant between Wall and Cave (p<0,001), Rock Outcrop and Sandy Plain (P=0,006), and between Wall and Margin (p<0,001).

When diversity was compared between the habitat types (Figure 13), “Cave” was found to be the most diverse followed closely by “Rock outcrop”. “Thalweg” had the lowest diversity followed by “Sandy plain”. “Margin” was sampled 541 times compared to 297 samples (“Wall”) and 190 samples (‘Cave”). “Margin” recorded the third highest diversity.

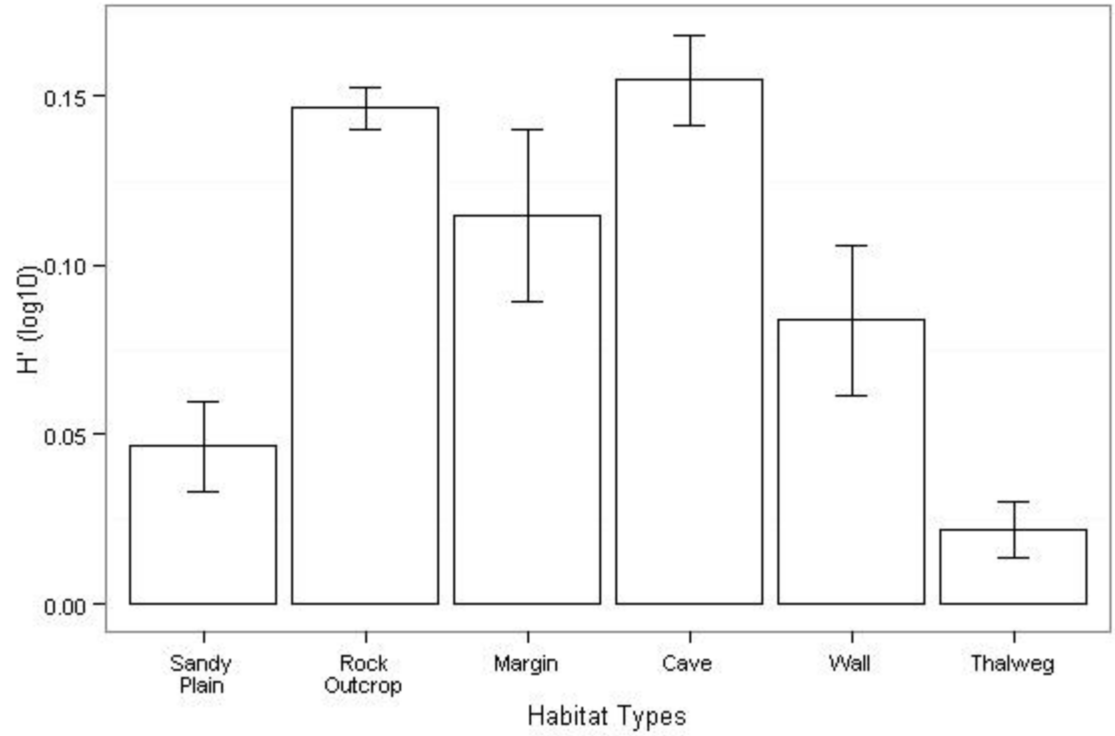


Figure 13: Mean (± 1 SE) Shannon-Wiener diversity indexes (H’) for each habitat type

Table 7. Adjusted p-values resulting from pairwise comparisons of H’ between depth categories. Values in bold reflect where differences are significant

	Cave	Margin	Rock Outcrop	Sandy Plain	Thalweg
Margin	0,768	-	-	-	-
Rock Outcrop	1,000	1,000	-	-	-
Sandy Plain	**<0,001**	**0,001**	**0,006**	-	-
Thalweg	1,000	1,000	1,000	1,000	-
Wall	**<0,001**	**<0,001**	0,337	1,000	1,000

The species diversity between depth classes was found to be significantly different (Kruskal-Wallis chi-squared = 54.9141, df = 9, p<0,0001). Pairwise comparisons (Table 8) support what is shown in Figure 14. Depth class 9 and 10 (i.e. 90 m and 100 m) were the most diverse. Species diversity increased between classes 7 and 9, and then decreased from 90 m with each depth class.

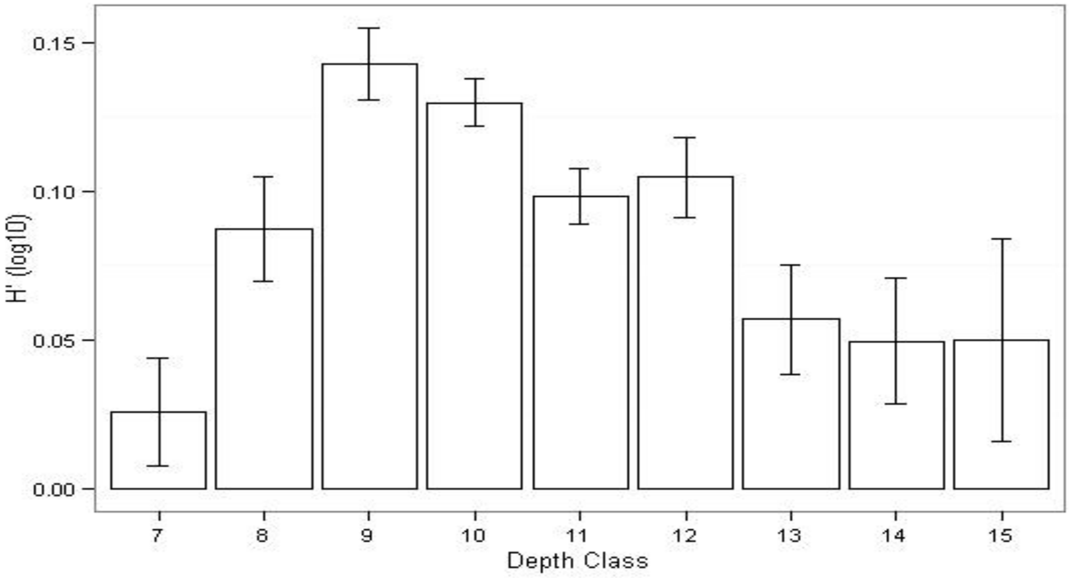


Figure 14: Mean (± 1 SE) Shannon-Wiener diversity indexes (H') for each depth class. Depth classes are abbreviated such that 8 represents 80-89m, 9 represents 90-99m and so on

Table 8. Adjusted p-values resulting from pairwise comparisons of H' between depth categories. Values in bold reflect where differences are significant

	10	**11**	**12**	**13**	**14**	**15**	**16**	**7**	**8**
11	**0,047**	-	-	-	-	-	-	-	-
12	1,000	1,000	-	-	-	-	-	-	-
13	**0,023**	1,000	1,000	-	-	-	-	-	-
14	**0,037**	1,000	1,000	1,000	-	-	-	-	-
15	1,000	1,000	1,000	1,000	1,000	-	-	-	-
16	1,000	1,000	1,000	1,000	1,000	1,000	-	-	-
7	**0,008**	0,290	0,348	1,000	1,000	1,000	1,000	-	-
8	0,961	1,000	1,000	1,000	1,000	1,000	1,000	0,446	-
9	1,000	**0,015**	0,419	**0,009**	**0,016**	1,000	1,000	**0,003**	0,350

4.6. Characteristic species

The SIMPER analysis by canyon (Table 9) shows the species that characterise each one. In all canyons *Pseudanthias gibbosus* and *Chrysoblephus puniceus* are the species contributing the most to the similarity. With the exception of Wright and Leadsman canyons, *P.gibbosus* contributed the most. In the case of South Island Rock and Jesser canyons, these two species on their own contributed to 90% of the similarity in each canyon. The contribution percentages were very similar too. Diepgat, Island Rock and Leadsman canyons each had *Paracaesio xanthura* as the third highest contributor to the assemblage. The presence of *Symphysanodon sp.* in the SIMPER analysis further characterises the fish assemblage of Leadsman canyon.

Chaka and Wright canyons show fewer similarities to the other canyons and each other. Chaka canyon is characterised by *Centroberyx druzhinini* and *Odontanthias borbonius* as the third and fourth highest contributors, respectively, to the canyon's fish assemblage. *Symphysanodon sp.* and *Epinephelus morrhua* were the third and fourth most important discriminatory species in Wright canyon.

Table 9: Characteristic species identified by similarity percentage analysis (SIMPER) for each canyon

Group	Species	Av.Abund	Contrib%	Cum.%
Island Rock	*Pseudanthias gibbosus*	4,8	67,8	67,8
	Chrysoblephus puniceus	2,4	18,5	86,2
	Paracaesio xanthura	1,7	7,8	94,0
South Island Rock	*Pseudanthias gibbosus*	5,3	77,9	77,9
	Chrysoblephus puniceus	2,0	13,2	91,2
Wright	*Chrysoblephus puniceus*	3,1	46,3	46,3
	Pseudanthias gibbosus	2,8	36,8	83,0
	Symphysandon sp.	1,1	5,4	88,4
	Epinephelus morrhua	0,7	2,8	91,2
Jesser	*Pseudanthias gibbosus*	5,0	75,8	75,8
	Chrysoblephus puniceus	2,1	14,8	90,6
Diepgat Deep Reef	*Pseudanthias gibbosus*	6,1	84,3	84,3
	Chrysoblephus puniceus	2,2	11,9	96,2
Diepgat	*Pseudanthias gibbosus*	3,8	62,7	62,7
	Chrysoblephus puniceus	2,1	21,6	84,3
	Paracaesio xanthura	1,2	7,2	91,5
Leadsman	*Chrysoblephus puniceus*	3,0	38,5	38,5
	Pseudanthias gibbosus	2,3	22,9	61,4
	Paracaesio xanthura	2,1	17,8	79,3
	Symphysandon sp.	1,7	12,9	92,2
Chaka	*Pseudanthias gibbosus*	3,4	60,5	60,5
	Chrysoblephus puniceus	1,7	16,3	76,8
	Centroberyx druzhinini	1,4	10,2	87,0
	Odontanthias borbonius	1,0	5,2	92,2

The SIMPER analysis by habitat type (Table 10) showed *Pseudanthias gibbosus* to be the greatest contributor to the similarity, except in "Thalweg". Out of four segments in this habitat type fish were only once recorded in one segment. *Centroberyx druzhinini* was the only species seen, so this cannot really be referred to as a species that characterises this habitat. This species did however contribute the second highest percentage in the "cave" habitat type, and fourth highest in "wall". The species that really distinguish "cave" from other habitats are large contributions from *Myripristis chryseres* (17,22%), *Epinephelus morrhua* (5,84%) and *Aulacocephalus temminckii* (2,47%). The "wall" habitat type is characterised by a large contribution by *Odontanthias borbonius* (9,88%).

It is difficult to say which species characterise the "sandy plain", "rock outcrop" and "margin" habitats as all three are dominated by *Pseudanthias gibbosus* and *Chrysoblephus puniceus.* However, *Pseudanthias gibbosus* contributed towards 85,64% of the fish similarity of "sandy plain". This was substantially less in "rock outcrop"(55,96%) and "margin"(57,42%).

Table 10: Characteristic species identified by similarity percentage analysis (SIMPER) for each habitat type

Group	Species	Av.Abund	Contrib%	Cum.%
Margin	*Pseudanthias gibbosus*	4,4	57,4	57,4
	Chrysoblephus puniceus	3,4	35,7	93,2
Cave	*Pseudanthias gibbosus*	2,3	32,7	32,7
	Centroberyx druzhinini	2,1	29,4	62,1
	Myripristis chryseres	1,6	17,2	79,3
	Epinephelus morrhua	0,9	5,8	85,2
	Chrysoblephus puniceus	0,7	3,1	88,3
	Aulacocephalus temminckii	0,6	2,5	90,7
Wall	*Pseudanthias gibbosus*	3,2	53,6	53,6
	Chrysoblephus puniceus	1,8	17,8	71,3
	Odontanthias borbonius	1,3	9,9	81,2
	Centroberyx druzhinini	1,3	8,0	89,2
	Symphysanodon sp.	0,8	3,2	92,4
Sandy Plain	*Pseudanthias gibbosus*	6,3	85,6	85,6
	Chrysoblephus puniceus	2,0	9,9	95,6
Rock outcrop	*Pseudanthias gibbosus*	4,1	56,0	56,0
	Chrysoblephus puniceus	3,5	40,0	95,9
Thalweg	*Centroberyx druzhinini*	6,6	100,0	100,0

The SIMPER analysis by depth (Table 11) showed a gradual change with depth in the discriminatory species until depth class 11 (i.e. 110 m). Depth classes 7, 8, 9, 10 and 11 were dominated by *Pseudanthias gibbosus* and *Chrysoblephus puniceus*. In classes 7, 8, and 9 these two species together were responsible for 90% of the fish assemblage. *P.gibbosus* contributed the most each time. At depth class 10 the aforementioned two species were joined by *Paracaesio xanthura* (6,6%). This species was replaced by *Centroberyx druzhinini* (4,9%) in depth class 11.

The change in fish assemblages seemed to be quite dramatic from depth class 12 (i.e. 120 m) onwards. In depth class 12 the contribution by *P. gibbosus* (35,76) was substantially lower than it had been for the depth classes 9,10, 11. It was still the leading contributor, but second now was *Odontanthias borbonius* (16,94%). A further four species contributed to this assemblage.

Depth class 13 was characterised by a large contribution by *Centroberyx druzhinini* (23,72%) that came close to replacing *P.gibbosus* (24,62%) as the top contributor to this assemblage.

The fish assemblage of depth class 14 was very distinct with neither *C.puniceus* nor *P. gibbosus* included in the list of species that contributed to 90%. *Polysteganus* *coeruleopunctatus* made up half the assemblage with *Epinephelus morrhua* (28,35%) and *Symphysanodon sp.* (12,85%) the second and third highest contributors.

Depth class 15 was once again dominated by *Pseudanthias gibbosus* (69,1%) and *Chrysoblephus puniceus* (30,9%), with only *Pseudanthias gibbosus* in depth class 16 (100%).

Table 11: Characteristic species identified by similarity percentage analysis (SIMPER) for each depth class. Depth classes are abbreviated such that 8 represents 80-89 m, 9 represents 90-99 m and so on

Group	Species	Av.Abund	Contrib%	Cum.%
6	*Less than 2 samples in group*			
7	*Pseudanthias gibbosus*	5,8	88,6	88,6
	Chrysoblephus puniceus	2,6	11,4	100,0
8	*Pseudanthias gibbosus*	5,0	71,6	71,6
	Chrysoblephus puniceus	2,8	23,7	95,4
9	*Pseudanthias gibbosus*	4,2	56,5	56,5
	Chrysoblephus puniceus	3,4	38,5	95,0
10	*Pseudanthias gibbosus*	4,4	60,3	60,3
	Chrysoblephus puniceus	3,0	24,8	85,1
	Paracaesio xanthura	1,3	6,6	91,7
11	*Pseudanthias gibbosus*	3,7	60,1	60,1
	Chrysoblephus puniceus	2,3	25,2	85,3
	Centroberyx druzhinini	1,1	5,0	90,2
12	*Pseudanthias gibbosus*	2,3	35,8	35,8
	Odontanthias borbonius	1,5	16,9	52,7
	Chrysoblephus puniceus	1,5	15,1	67,7
	Centroberyx druzhinini	1,3	11,2	79,0
	Symphysanodon sp.	1,1	7,8	86,8
	Epinephelus morrhua	1,1	7,8	94,6
13	*Pseudanthias gibbosus*	1,9	24,6	24,6
	Centroberyx druzhinini	1,8	23,7	48,3
	Odontanthias borbonius	1,6	17,4	65,7
	Chrysoblephus puniceus	1,5	15,3	81,0
	Symphysanodon sp.	1,2	9,2	90,2
14	*Polysteganus coeruleopunctatus*	2,9	50,0	49,6
	Epinephelus morrhua	2,3	28,4	77,9
	Symphysanodon sp.	1,6	12,9	90,8
15	*Pseudanthias gibbosus*	3,2	69,1	69,1
	Chrysoblephus puniceus	2,4	30,9	100,0
16	*Pseudanthias gibbosus*	6,7	100,0	100,0

5. Discussion

5.1. Suitability of ROV to canyon survey

The ROV was able to sample a variety of habitats to a depth of 160 m. SCUBA surveys have previously reached a depth of 140 m (Sink et al. 2006). However, the ROV employed in this study was able to conduct surveys for several hours. SCUBA surveys can only be conducted over less than one hour. The ability of the ROV to explore caves and crevices enabled the recording of less mobile species and species that dwell in caves during the day. This would not have been the case if a BRUV technique had been used and the ROV was also able to explore smaller cavities in the substrate than would be possible by a manned submersible vehicle. The deep reef studies off the southeastern coast of the United States by Ross and Quattrini (2009) was conducted predominantly by submersible, but ROV was also used to survey small cavities that the submersible could not enter.

By dividing the video footage into short 30-second segments, sampled fish could be accurately placed at a particular depth or habitat type. The patterns that were subsequently discovered based on high-resolution data were therefore a realistic reflection of the fish associations made with regards to depth and habitat.

5.2. Were canyons adequately sampled for fish

Sample sizes over 80 would be an unnecessary use of resources as every additional sample would produce < 1% of the species richness. Apart from Diepgat Deep Reef, sample sizes of each canyon were sufficient to meet this criterion. A review of the literature did not provide any recommended sample sizes for surveying fish in submarine canyons.

Depth categories that did not fall between 90 m and 120 m were not sampled adequately. The ROV was focused primarily on this depth range. The Sandy Plain and Rock Outcrop habitats generally occur at less than 90 m and Thalweg at greater than 120 m depth. Consequently, sampling of these habitats was not adequate. A minimum of 80 samples per depth category is also recommended.

The rates of discovery calculated from the species accumulation curves for each habitat suggest that each habitat requires a different amount of sampling effort. Further investigation into the amount of effort is required to sample each habitat is required.

5.3. Species assemblage

A similar number of fish species (54) to this survey (52) were recorded by Heemstra et al. (2006) along a larger depth range (100 m to 400 m) by submersible. Video images from 47 dives, each 4 hours long, were recorded by Heemstra et al. (2006). Less than 34 hours of video footage in 17 dives were recorded during this survey. It is likely that if this study had a greater depth range, more species would have been encountered as the two species lists differ considerably. There were only 26 species in this study common to that of Heemstra et al. (2006). Species such as *Pseudanthias gibbosus, Aulacocephalus temminckii, Epenephelus morrhua* and *Symphysanodon sp*, which are common to that of Heemstra et al. (2006) are deep-water species and therefore not found in shallow-water surveys.

The species composition of this study bore a strong resemblance to that recorded by Sink et al. (2006). That particular study identified 18 species in 40 minutes of amateur video. Trimix divers surveyed a depth range of 74 m to 140 m (similar to this study). This study recorded 14 of the species in the survey by Sink et al. (2006).

As in this study, one of the most common species encountered by Sink et al. (2006) was *Pseudanthias gibbosus.* This species is considered rare in inshore areas shallower than 35m (King and Fraser 2014) and was absent from the surveys conducted by Chater et al. (1995 and 1993) and Floros et al. (2012). *Epinephelus morrhua* was also frequently encountered in this study but it is absent from shallow-water surveys (Chater et al. 1993, 1995, Floros et al. 2012). However, this species was encountered frequently by Sink et al. (2006) and Heemstra et al. (2006). This may suggest that this species is restricted to deeper reefs. Prior to these studies there had been few recorded sightings of *Aulacocephalus temminckii* (Smith and Heemstra 1986). In this study this species was frequently encountered, often in caves between 90 m and 100 m.

This study on deep reefs recorded high abundances, compared to shallow reef environments (Floros et al. 2012, Chater et al. 1993 Chater et al. 1995) of various commercially important members of the Sparidae family. In this study Slinger

Chrysoblephus puniceus was the most abundant, followed by Blueskin *Polysteganus coeruleopunctatus*, Englishman *Chrysoblephus anglicus* and Scotsman *Polysteganus praeorbitalis.* These species were also common in studies by Heemstra et al. (2006) and Sink et al. (2006). The members of the Sparidae family have a general preference for cooler water temperatures. Most Sparidae species recorded in this study were at the northern extent of their distributions (Smith and Heemstra 1986).

Chater et al. (1993) recorded 21 Lutjanid species, while Floros et al. (2012) found the Lutjanidae family to be one of six families that contributed more than 50% towards the fish community in shallow habitat. This study recorded high abundances of *Paracaesio xanthura*, and low abundances of two other Lutjanids. Similarly, few Lutjanids were recorded by Heemstra et al. (2006) and Sink et al. (2006). The southern limit for most Lutjanid distribution is believed to be northeastern South Africa (Smith and Heemstra 1986). A preference for warmer water is a likely explanation for so few recorded Lutjanids in deeper water.

With the exception of a few myliobatids, chondrichthyans were absent from this study and that of Sink et al. (2006). A few species were recorded by Heemstra et al. (2006), while numerous chondrichthyans were recorded by Chater et al. (1993). Most of these records were from dive surveys. The dive survey by Floros et al. (2012) also made no mention of recording chondrichthyans. An explanation for these results is unavailable.

The SCUBA survey by Floros et al. (2012) produced 284 species from 50 families while that of Chater et al. (1993) recorded 399 species from 73 families. There are a number of explanations for the disparity in number of fish taxa between the shallow and deep reef studies. Firstly, controlled angling census by Chater et al. (1993) enabled recording of pelagic species in addition to the benthic species. Therefore pelagic species are poorly represented in this study. Secondly, these deep reefs may well have a lower diversity than those reefs above 40m. However, certain cryptic species of families such as Gobidae and Blenidae were not encountered at all during this study. Future studies may well do so as this study was not primarily focused on seeking these out and the low visibility in these deep environments adds an extra challenge.

A number of noteworthy species that are currently under threat were recorded during this study. These included a number of sightings of Red Steenbras *Petrus rupestris*, a species endemic to South Africa (Smith and Heemstra 1986). This species is currently listed as endangered on the IUCN Red List (Mann et al. 2014b).

There was also a sighting of the Seventy-four Seabream *Polysteganus undulosus*, another South African endemic (Smith and Heemstra 1986). This species is currently listed as critically endangered on the IUCN Red List (Mann et al. 2014a) and it is the first time that in-situ images have been obtained for this species in the submarine canyons of the IWP.

5.4. Species diversity

Two possible explanations for the difference in fish diversity among canyons are offered. Firstly, habitat diversity varied greatly between the canyons. Habitat was the factor that had the greatest effect on species composition. Therefore, one would expect habitat diversity to result in different diversities among canyons. There was, however, no correlation between evenness of habitat sampled and either the species richness or diversity.

Secondly, it is possible that the habitat with the most species varies in representation among canyons. However, no correlation could be found between species richness of diversity and the relative proportion of samples that were either cave or rocky outcrop habitat.

Other factors might therefore be responsible for the variability of species diversity among canyons. For example, there is known to be high variability in temperature between canyons (Roberts et al. 2006). It is natural that the fish assemblages would then differ as species attempt to stay within their preferred temperature range. The variation of depth ranges sampled between canyons would therefore mean that different temperature ranges would be present between canyons. Additionally, Roberts et al. (2006) found that a temperature change of as much as 8°C could take place in 24 hours at a single location.

In terms of species diversity per habitat type, rock outcrop was expected to be the most diverse, followed closely by margin (Sink et al. 2006). These habitats were thought to be the most diverse in invertebrate cover and in morphology. However, cave was shown to have the highest diversity. This habitat was well sampled and there is little chance that this habitat could be confused for another. The shelter offered against currents meant that the visibility was high enough to allow for more cryptic species to be identified (e.g. various members of the Apogonidae family).

Rock outcrop was severely under sampled, but the second highest species diversity was recorded in this habitat. H' has been known to underestimate diversity at times, but this decreases with increasing sample size (Zar 1996). Therefore, with more focus on this habitat in future surveys it may well prove to be the habitat with the highest fish diversity.

The margin habitat type was the most thoroughly sampled of all habitat types. However, the distinguishing line between wall and margin is not always definite. Invertebrate cover and topographical changes are, at times, gradual within the submarine canyons of the IWP, resulting in overlapping habitat types. By observation of the footage, it is thought that margin should have reported a higher diversity than it did, and wall a lower diversity.

The diversity and species richness patterns in the IWP submarine canyons fit the expected patterns. From 90m depth (where the margin habitat starts) species richness and diversity decreases with depth. The 60 m to 80 m depths showed lower species richness and diversity in this study compared to the 90 m depth class. The substrate is simply less diverse in terms of structure and invertebrate cover in the sandy plain habitat than is typical at depths less than 80 m. Similar to the submarine canyon study by Currie et al. (2012a), species richness was found to be highest at 90 m, followed by a steady decrease. Currie et al. (2012a) found elevated benthic chlorophyll levels at that depth.

5.5. Fish assemblage patterns

Canyon comparisons

Canyons vary in terms of their morphology. Some canyons may have steep sides and reach greater depths than others, and may present a deeper incision in the continental slope than others. Gradients also vary among canyons. Topography would likely affect turbulence and upwelling in the canyon and that would in turn have an effect on the invertebrate and fish species composition. Topography might explain the significant differences in species composition among canyons.

The significant interaction between canyon and habitat, and between canyon and depth shows that habitat and depth associations of species vary among the canyons, again suggesting an influence of topography.

There was no correlation between latitude and species assemblage.

Depth

The depth range that was surveyed was too narrow to detect differences in fish assemblages with depth. The Permanova results reveal differences in fish community due to depth only when the effect is combined with that of canyon. This is likely to be due to differences in temperature with depth between canyons. Other studies of deep-water habitats have revealed depth to be the most important factor. Malcolm et al. (2011) found that fish assemblages differ significantly according to depth and are only moderately affected by the benthic community. In that study three depth classes with a broader depth range (i.e. <25 m, 25-60 m, >60 m) than this study were used. Currie et al. (2012a) surveyed fish in a submarine canyon in Australia between 100 m and 1500 m. Depth was also found to best explain the fish assemblage patterns. Fish were sampled at 100 m, 200 m, 500 m, 1000 m and 1500 m depths. The Currie et al. (2012a) survey only detected a depth effect below 200 m. This study did not cover depths beyond 160 m.

Habitat

The result showing habitat to have the strongest influence on fish communities is not surprising. This is consistent with the studies by Currie et al. (2012b) as well as Friedlander and Parish (1998). The latter study showed that a large amount of variability between fish assemblages was explained by measures of holes in the substrate. These are thought to be important for shelter and could also explain why in this study the cave habitat was shown to have the highest diversity as fish took shelter from the strong currents. The visibility in the caves was the clearest and certainly made it possible for more species to be identified, so this result may be partially biased.

Ross and Quattrini (2009) surveyed deep reef fish along the southeastern United States between 366m and 770m. Their findings showed that patterns were affected by a combination of depth and habitat-type. Given that the depth range studied here was very narrow, it is likely that future studies with broader depth ranges will prove depth to have a stronger effect on the fish assemblages as the range increases. It is likely then that habitat will have less of an influence on these assemblages with increasing depth. Further testing of this hypothesis is required in future studies.

6. Conclusion

There is a need for a standardised method for surveying deep reef fish to allow for meaningful comparative studies. The ROV survey method used here was found to be effective for this study. The method for analysing footage is highly recommended in order to accurately interpret patterns in fish communities. A sample size of 80 30-second samples of video footage is the recommended minimum. It should be noted that at least three times this effort is needed for future surveys. In this study, approximately two thirds of video footage was unusable. This guideline could be used to develope a standard survey method for deep reef studies. This method can be improved by sampling comparable depth ranges among canyons.

This survey found habitat to have the most influence on fish composition. However, deeper habitat and depth patterns should be investigated in future.

Although no coelacanths were encountered during this survey, two other IUCN Red Data species were seen. Red Steenbras are seldom seen and this was the first time that a Seventy-Four was seen in the submarine canyons of The IWP. This highlights the importance of protecting marine life in these deep habitats of the IWP.

In terms of habitat diversity the most important canyons are Island Rock, South Island Rock, Diepgat Deep Reef and Chaka. The most important canyons in terms of species diversity are Island Rock, Wright, Jesser and Leadsman. The apparent mismatch between these lists would suggest that additional studies on habitat classification, perhaps using better oceanographic data are needed.

This survey recorded 26 species of fish not previously recorded by Heemstra et al. (2006) or Sink et al. (2006) in the submarine canyons of the IWP.

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Appendix 1

Table 1: Species observed at each depth class and the number of video segments for each depth class

Family	Species	60 m	70 m	80 m	90 m	100 m	110 m	120 m	130 m	140 m	150 m
Ambassidae	*Ambassis sp.*				✓	✓	✓				
Apogonidae	Apogon fukuii			✓	✓	✓	✓	✓			
Apogonidae	*Ostorhincus apogonoides*				✓	✓					
Apogonidae	*Pristiapogon kallopterus*				✓						
Berycidae	*Centroberyx druzhinini*				✓	✓	✓	✓	✓		
Carangidae	*Seriola rivoliana*			✓	✓	✓	✓	✓			
Chaetodontidae	*Chaetodon dolosus*				✓						
Chaetodontidae	*Chaetodon marleyi*			✓	✓	✓				✓	
Chaetodontidae	*Chaetodon sp.*				✓	✓	✓	✓			
Chaetodontidae	*Heniochus acuminatus*		✓								
Cheilodactylidae	*Chirodactylus jessicalenorum*						✓	✓			
Dasyatidae	*Himantura jenkinsii*					✓					
Haemulide	*Dinoperca petersi*			✓	✓						
Haemulide	*Pomadasys striatus*					✓					
Holocentridae	*Myripristis chryseres*			✓	✓	✓	✓				
Labridae	*Anampses lineatus*			✓							
Labridae	*Bodianus trilineatus*				✓	✓	✓	✓			
Labridae	*Suezichthys sp.*			✓	✓	✓	✓	✓			
Lutjanidae	*Aprion virescens*			✓	✓	✓	✓				
Lutjanidae	*Paracaesio sordida*			✓	✓	✓	✓				
Lutjanidae	*Paracaesio xanthura*			✓	✓	✓	✓	✓		✓	
Mobulidae	*Manta alfredi*			✓							
Monacanthidae	*Aluterus monoceros*					✓	✓				
Monacanthidae	*Thamnaconus fajardoi*					✓	✓				
Monocentridae	*Monocentris japonica*				✓	✓	✓	✓			
Muraenidae	*Gymnothorax favagineus*				✓						
Pomacanthidae	*Apolemichthys kingi*						✓				
Pomacanthidae	*Pomacanthus rhomboides*			✓							
Pomacentridae	*Chromis woodsi*				✓	✓	✓				
Priacanthidae	*Priacanthus hamrur*				✓	✓	✓				✓
Priacanthidae	*Pristigenys niphonia*				✓	✓	✓	✓			
Sciaenidae	*Argyrosomus japonicus*				✓		✓				
Sciaenidae	*Umbrina robinsoni*					✓		✓			
Scorpaenidae	*Scorpaenopsis venosa*					✓	✓	✓		✓	
Serranidae	*Aulacocephalus temminckii*				✓	✓	✓	✓	✓		
Serranidae	*Epinephelus marginatus*					✓					
Serranidae	*Epinephelus morrhua*				✓	✓	✓	✓	✓	✓	
Serranidae	*Epinephelus tukula*		✓		✓		✓	✓			
Serranidae	*Liopropoma sp.*				✓	✓	✓	✓		✓	
Serranidae	*Odontanthias borbonius*			✓	✓	✓	✓	✓	✓	✓	✓
Serranidae	*Plectranthias sp.*				✓		✓				

Serranidae	*Pseudanthias gibbosus*		✓	✓	✓	✓	✓	✓	✓	✓	✓
Serranidae	*Serranus knysnaensis*			✓	✓			✓			
Sparidae	*Chrysoblephus anglicus*				✓	✓	✓	✓			
Sparidae	*Chrysoblephus puniceus*	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Sparidae	*Petrus rupestris*				✓	✓	✓	✓	✓		
Sparidae	*Polysteganus coeruleopunctatus*				✓	✓	✓	✓	✓	✓	✓
Sparidae	*Polysteganus praeorbitalis*		✓		✓	✓	✓	✓			
Sparidae	*Polysteganus undulosus*					✓					
Symphysanodontidae	*Symphysanodon sp.*			✓	✓	✓	✓	✓	✓	✓	✓
Tetraodontidae	*Arothron immaculatus*				✓						
Tetraodontidae	*Canthigaster inframacula*				✓			✓			
Unidentified	*Ray 1*							✓			
Species richness		1	5	17	38	36	34	27	9	10	6
No. of 30s segments		1	24	71	193	358	270	138	43	31	10