VIDEOGRAPHIC ANALYSIS OF THE COELACANTH, *LATIMERIA CHALUMNAE*, AND ASSOCIATED HABITATS IN THE ISIMANGALISO WETLAND PARK, KWAZULU-NATAL, SOUTH AFRICA

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Abstract

Videography is a valuable tool in biological and ecological studies. Using video footage obtained during previous coelacanth surveys, this thesis investigated coelacanths and their associated habitats in the submarine canyons of iSimangaliso Wetland Park, South Africa. This thesis aimed to (1) describe the biological habitats within the submarine canyons, (2) determine coelacanth distribution within these habitats, and (3) assess the use of computer-aided identification to successfully identify individual coelacanths. Seven different habitat types were noted with the most distinctive being the canyon margins that consisted of dense agglomerations of gorgonians, wire and whip corals, and sponges. Results suggested that although substratum type has a great influence on invertebrate community structure in the canyons, depth is the principal factor. Coelacanths were associated with cave habitats within the steep rocky canyon walls. Habitat analyses allowed predictive classification tree models to be constructed. Depth, underlying percentage of rock, and percentage cover of gorgonians and sponges were the most important variables for determining coelacanth presence and absence. The overall correct classification rate for the model was estimated at 96.6%, correctly predicting coelacanth absence (> 99%) better than presence (60%). Because coelacanths have a unique spot pattern it was possible to quickly and accurately identify specific individuals photographically using computer-aided identification software. Without any manual intervention by an operator the software accurately identified between 56 and 92% of the individuals. Identification success increased to 100% if the operator could also manually select from other potential matching photographs. It was also shown that fish exhibiting a yaw angle not exceeding 60˚ could be accurately identified in photographs. Each of the sections presented in this thesis represent a possible step towards analysing coelacanth-related habitats, locating and then analysing new habitats. Steps include first locating a population and then performing a habitat analysis. Coelacanth location within the different habitats can then be determined allowing the development of predictive models to potentially identify possible locations of new populations. The final step is to identify individual fish within the population for assessing demographic parameters and population monitoring.

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List of acronyms and abbreviations

ACEP	African Coelacanth Ecosystem Programme
ADCP	Acoustic Doppler Current Profiler
AUV	Autonomous Underwater Vehicle
BRUV	Baited Remote Underwater Video
CART	Classification and Regression Trees
CBD	Convention on Biological Diversity
CITES	Convention on International Trade in Endangered Species
CTD	Conductivity, Temperature, Depth
CV	Coefficient of Variation
EFH	Essential Fish Habitat
GAM	Generalised Additive Models
GLM	Generalised Linear Models
IUCN	International Union for Conservation of Nature
IWP	iSimangaliso Wetland Park
LDA	Linear Discriminant Analysis
MVA	Multivariate Analysis
OOB	out-of-bag
PCA	Principal Components Analysis
PIT	Passive Integrated Transponder
RF	Random forest
ROV	Remotely Operated Vehicle
SAEON	South African Environmental Observation Network
SCUBA	Self Contained Underwater Breathing Apparatus
SHEBI	SHE analysis for Biofacies Identification
SLDA	Stepwise Linear Discriminant Analysis
SST	Sea Surface Temperature

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Chapter 1

General Introduction

1.1 Videography within the marine environment

Underwater photography has been used since the 1850s where simple glass plates were used to protect cameras and provide a medium through which to capture images. The introduction of O-ring seals in the 1930s facilitated the development of effective waterproof housings that resulted in a surge in the use of underwater imaging. The increase in popularity of SCUBA diving further stimulated the demand for underwater imaging (Barnes 1952). Underwater imaging equipment advanced rapidly and by the 1960s there were a large number of underwater cameras and housings available that enabled underwater imaging to become accessible to both enthusiasts and scientists. In 1983 Sony released its first portable camcorder that resulted in videography being quickly adopted by scientists as a sampling tool that could be applied within a wide range of marine experiments due to the ease with which camcorders could be used by both divers (Boland and Lewbell 1986) and Remotely Operated Vehicles (ROVs) (Vrana and Schwartz 1989). Recent developments in digital imaging and the rapid reduction in equipment costs allow even novice divers to capture and manipulate high-resolution imagery. Digital technology has less noise and interference, and is now considered to be more reliable than the original analogue recording or signal transmission cameras (Shortis et al. 2009).

1.2 Videography as an ecological sampling tool

Videography is now used routinely in various underwater applications ranging from seabed mapping (Hale and Cooke 1962), shipwreck surveys (Hohle 1971, Pollio 1971), oil and gas exploration (Leatherdale and Turner 1983), and ecological studies (Hewitt at al. 2004). As it is a non-destructive sampling method (Voght et al. 1997, Parry et al. 2003, Tkachenko 2005) videography is now widely used to monitor marine communities (Page et al. 2001, Houk and Van Woesik 2006, Nadon and

Stirling 2006, Lirman et al. 2007, Shortis et al. 2007) and to sample rare or endangered species with minimal disturbance (Lewis et al. 2004, Watson et al. 2005).

A significant advantage over most other sampling gears is that videography is non-destructive and the study site is not physically altered. A consequence is that the same site can be sampled repeatedly over time if required which is particularly useful in long-term monitoring studies (Collie et al. 2000, Hewitt et al. 2004, Tkachenko 2005, McDonald et al. 2006). As videography allows for the direct detection of impacts on benthic communities it therefore eliminates the need to physically sample the sea floor. Physical sampling methods can introduce sampling bias in future samples from site degradation due to previous destructive sampling methods (Collie et al. 2000, Hewitt et al. 2004). This allows for the preservation of underwater habitats and enables sampling in sensitive areas (Douglas 1993, Parrish et al. 2000).

Sampling underwater is usually constrained by time that can be spent underwater collecting data (Aronson et al. 1994, Lam et al. 2006). As videography enables rapid data capture (Leonard and Clark 1993, Aronson et al. 1994, Voght et al. 1997, McDonald et al. 2006) this reduces the time required to be spent underwater (Lam et al. 2006). A larger area can also be sampled (Brown et al. 2004) in the same amount of time than when recording data *in situ* (Aronson et al. 1994). It has also been found that studies utilising video are more likely to detect cryptic or rare species as the video footage covers a continuous, large area of the sea floor (Lam et al. 2006).

The versatility of modern day video cameras has removed the constraint of manual operation when diving with SCUBA. Cameras can be attached to a variety of underwater equipment such as ROVs (Parry et al. 2003, Solan et al. 2003, Lam et al. 2006, Pacunski et al. 2008), sleds that can be towed along the sea floor (Hewitt et al. 2004), and manned submarines (Solan et al. 2003, Heemstra et al. 2006a, 2006b). This sampling flexibility has allowed for sampling at greater depths (Parry et al. 2003, McDonald et al. 2006) and sampling areas that are difficult or dangerous for diving (McDonald et al. 2006). Examples include the documentation and exploration of new, unexplored habitats such

the Mariana Trench where Takagawa (2005) filmed benthic fauna that had not been previously observed.

Videography, if used correctly, minimises disturbance of the behaviour of the study animals (Lewis et al. 2004, Watson et al. 2005). Fish have been shown to show biased behaviour towards divers, furthermore, time constraints associated with SCUBA diving make acclimatization difficult (Cole 1994, Willis and Babcock 2000, Watson et al. 2005).

Videography has been shown to be cost effective in the long-term (Aronson et al. 1994, Brown et al. 2004, Hill and Wilkinson 2004) because although initial set up costs are high, running costs tend to be low.

Video cameras are simple to operate and although surveys need to be designed by trained scientists, the videographers capturing footage underwater need only be experienced divers (Hill and Wilkinson 2004, Lam et al. 2006). Methods where divers collect information *in situ* require observers to be both divers and scientists in order to correctly identify marine organisms. This introduces additional costs and logistical constraints to a research study.

From an ecological sampling perspective, a significant advantage of videography is that as it can be archived a permanent visual record can be kept of the sample (Leonard and Clark 1993, Voght et al. 1997, McDonald et al. 2006, Lirman et al. 2007). This allows processing at a later date (Leonard and Clark 1993), reanalysis of footage at will when more information is needed (Rogers and Miller 2001, Lam et al. 2006), and facilitates collaborative research due to the ease of duplicating and sharing digital footage (Rogers and Miller 2001). In long-term monitoring studies, series of reference images can be compared and re-compared making changes, which can be small in magnitude, easier to detect.

Images are also a powerful tool in education and have a much greater impact on the general public than sets of data and statistics (Hill and Wilkinson 2004, Lam et al. 2006).

Detailed quantitative information as well as visual qualitative information can be captured from video footage (Hill and Wilkinson 2004) through careful sampling design and replication (Lam et al. 2006). For example, through the use of point count data from video footage, simple univariate statistical treatments can be applied as well as complex multivariate ordinations and tests (Aronson et al. 1994).

As with any sampling method there are limitations to videography (Hill and Wilkinson 2004) but as long as one is aware of these, the sampling design can be conceptualised to reduce their effects (Porter and Meier 1992). The two dimensional nature of video footage means that organisms sheltering under structures or covered by the benthos will not be visible on the footage (Rogers and Miller 2001). Any diversity studies will show some bias in this respect. Limitations in footage resolution mean that small and cryptic species may be difficult to distinguish (Voght et al. 1997, Hill and Wilkinson 2004). Taxonomic resolution in video footage is limited and *in situ* identification by a taxonomist will almost inevitably be more accurate (Rogers and Miller 2001). The rapid advance in digital technology has reduced this effect as still images with high megapixel counts can now be taken to supplement the video footage (Lam et al. 2006). Lastly, initial start-up and maintenance costs may be high, especially for small scale studies with budgeting constraints (Hill and Wilkinson 2004).

1.3 A review of the uses of videography in marine biology and ecology

Epibenthic studies

Videography is one of the most commonly used sampling methods to obtain data on epibenthic biota (Jaap et al. 1994, Voght et al. 1997, Shortis et al. 2009). Sampling designs are varied and range from simple transect counts to more complex experiments where measurements of size and biomass are estimated from metrics such as volume or surface area using stereo-video (Harvey and Shortis 1996, Harvey et al. 2002, Watson et al. 2005, Shortis et al. 2009, Langlois et al. 2010). Video transect methods can also be used to monitor epibenthic abundance and distribution through the detection of

spatial and temporal changes and patterns in community structure (Maliao et al. 2009). Other videographic epibenthic studies have focused on estimating the abundance of individual organisms or species (Harriott 1995, Vetter and Dayton 1999, Willis and Babcock 2000, Langlois et al. 2010) through simple censuses of organisms encountered within the video transects (Labrosse et al. 2002) using ROV-mounted cameras (Barry and Baxter 1993, Pacunski 2008), hand-held cameras with SCUBA (Alevizon and Brooks 1975, Potts et al. 1987, Aronson et al. 1994, Parker et al. 1994, Shortis et al. 2007, Friedlander and Parrish 1998), and point counts, usually with the aid of Baited Remote Underwater Video (BRUV) cameras (Babcock et al. 1999, Willis and Babcock 2000, Willis et al. 2000, Westera et al. 2003).

Using video data to conduct underwater censuses is not limited to estimating abundance. Other physical data can be collected as these can be analysed after the surveys have been conducted. For example, in those studies documenting the effect of different habitat types on fish assemblages the number and types of fish visible in the video transect are recorded and then quantitative measurements are taken from the archived still frames of the habitat (Friedlander and Parrish 1998, Maliao et al. 2009).

Monitoring

Another application of underwater census techniques is for monitoring where the number of individuals in different areas can be counted and compared either spatially or temporally to determine the impacts on abundance (Magorrian and Service 1998) and/or species richness patterns (Watson et al. 2005). Community composition changes, particularly over time, can be effectively monitored using videography (Page et al. 2001, Houk and Van Woesik 2006, Nadon and Stirling 2006, Lirman et al. 2007, Shortis et al. 2007) through repeated sampling allowing analysis of changes that have occurred between sampling trips. Videographic-based monitoring schemes have also highlighted effects of external anthropogenic pressures (Riegl 2001) such as coral bleaching (Riegl et al. 2001,

Rogers and Miller 2001, Hill and Wilkinson 2004) and fishing practices (Norrisa et al. 1997, Heifetz et al. 2009, Armstrong et al. 2008) on benthic ecosystems.

Behavioral studies

The ability to capture video footage in real-time and then archive it for later analysis has greatly facilitated behavioural studies of fish (Dunlap and Pawlik 1996, Friesen and Chivers 2006, Hammerschlag et al. 2006), marine mammals (Dudzinki et al. 1995a, 1995b, Herzing 1996, Mann 1999) and invertebrates (Coen et al. 1981). Studying the interactions within and between groups of animals is facilitated by repeatedly observing the same sequence of footage observing a different individual with each playback (Mann 1999, Brâger et al. 1999). Video playback methods are another powerful tool in behavioural research (Fleishman and Endler 2000) and involve pre-recorded video sequences being played back to animals to artificially mimic behaviour and observe reactions (Fleishman et al. 1998, Fleishman and Endler 2000).

Fish communities and assemblages

The use of videography in studying fish assemblages has grown in popularity because populations of large fish can be effectively and accurately sampled with video transects. However, studies are limited to areas with sufficient visibility as fish abundance can be easily underestimated (Davis and Anderson 1989, Langlois et al. 2010). Remote cameras, both baited (Willis and Babcock 2000, Willis et al. 2000, Cappo et al. 2006, Langlois et al. 2010) and unbaited (Watson et al. 2005), deployed underwater have been found to reduce this underestimation (Shortis et al. 2009) and efficiently determine relative densities (Willis and Babcock 2000, Willis et al. 2000) and species richness of both reef fish (Watson et al. 2005) and fish in deeper habitats such as submarine canyons (Heemstra et al. 2006a, 2006b).

Measurements

Additional measurements can be taken using underwater video (Spitz et al. 2000, Waite et al. 2007) and can be used to study growth patterns, swimming speeds (Ridoux et al. 1997), school density (Harvey et al. 2001a, 2001b), dispersion (Klimley and Brown 1983), and three-dimensional structure (Dill et al. 1981). Single cameras can be effectively used as long as a form of calibration is used to correct for different camera angles (Eleftheiou and McIntyre 2005), however, the most common technique involves the use of stereo-video which combines images from two cameras taken simultaneously (Harvey and Shortis 1996, Harvey et al. 2002, Eleftheiou and McIntyre 2005, Abdo et al. 2006, Shortis et al. 2009, Langlois et al. 2010). The ability to derive three-dimensional data from raw footage enables standardisation of unit sample size, enabling much greater accuracy in the detection of spatial and temporal changes (Harvey et al. 2004).

1.4 Videography within a South African context

Within South Africa, videography was first applied in the 1970s to supplement real-time observations in the laboratory (Berry 1970, Wallace 1972). It is now a common sampling method particularly in areas with good water visibility. With the trend towards investigating climate change and coral bleaching, videography in South Africa has been extensively used for reef monitoring (Riegl 2001, Celliers and Schleyer 2002, Schleyer and Celliers 2005, Schleyer et al. 2006, Celliers and Schleyer 2008, Schleyer et al. 2008), assessing the impacts of crown of thorns starfish *Acanthaster planci* predation, investigating physical damage from large swell conditions and recreational diving (Celliers and Schleyer 2008), and factors inhibiting reef formation (Riegl 2001). At the Aliwal Shoal, near Durban, videography was the main sampling tool to conduct a benthic survey and to assess the effects of effluent from a wood pulp factory (Schleyer et al. 2006). Other monitoring studies include BRUV used to monitor benthic fish stocks in Castle Rock reserve, Cape Town (D'agata 2010), and in an ongoing long-term monitoring study of benthic invertebrates and fish in Tsitsikamma National Park and Table Mountain National Park (Götz, A., SAEON, *pers. com.*). On a larger scale, in the Greater

St. Lucia National Park, now the iSimangaliso Wetland Park (IWP), reef zonation was assessed (Schleyer and Celliers 2005) and the colonization rates of invertebrates and fish on artificial reefs is the focus of ongoing research (Bailey, S., SAEON, *pers. com.*).

The use of videography in South African studies is not limited to shallow reefs. Chokka squid *Loligo vulgaris reynaudii* is an important fisheries resource along the Eastern Cape coast, South Africa between Port Alfred and Plettenberg Bay. Several studies have utilised videography as it minimizes disturbances and provides the most suitable sampling methods for ethological studies including spawning behaviour (Sauer et al. 1993, Smale et al. 2001) and predator-prey interactions. Other behavioural studies that have utilised videography in South Africa include the nursing behaviour of Cape fur seals (Kirkman 2010) and the predatory tactics of white sharks *Carcharodon carcharias* (Martin et al. 2005). Video footage from the East Kleinemonde Estuary using remote underwater cameras allowed the use of the littoral habitats and behaviour of the fish in relation to the different habitats to be assessed (Becker et al. 2010). Video footage has also been used to supplement observations made during laboratory studies on behaviour. The mating behaviour of spiny lobster *Panulirus homarus* (Berry 1970) as well as the reactions of bull and raggedtooth sharks to gill nets set in tanks (Wallace 1972) were investigated using video footage in addition to real-time observations.

Video data from deep reefs is usually captured from ROVs or submersibles because of depth and time constraints when SCUBA diving. Videography is thus an ideal sampling tool in deep water environments and was utilized to study coelacanths *Latimeria chalumnae* in the IWP (Venter et al. 2000, Hissmann et al. 2002a, Heemstra et al. 2006b, Hissmann et al. 2006, Sink et al. 2006) and the Comoros (Hissmann et al. 1998, Fricke et al. 2011) as well their associated fish (Heemstra et al. 2006a, 2006b) and deep water invertebrate fauna (Hissmann et al. 2002b, Sink et al. 2006, Samaai et al. 2010). Due to the coelacanths's protected status (IUCN 2011), videography remains one of the only practical means by which these fish and associated deep water habitats can be studied.

1.5 An introduction to the coelacanth and its habitat

The coelacanth *Latimeria chalumnae* Smith 1939 has rapidly become an icon for conservation and marine research since the discovery of the "living fossil" by Marjorie Courtenay Latimer from a fishing trawler operating off East London. It has sparked intense scientific and media interest as it was widely considered to be a tetrapod ancestor (Smith 1939a, 1939b, Romer 1966, Campbell 1987). Coelacanths represent one of the original primitive sarcopterygians (SAPPI 2001) and are the only extant relative of an ancient lineage of lobe-finned fishes (Fricke and Hissmann 2000).

Figure 1.1: Coelacanth *Latimeria chalumnae* photographed at the head of Jesser Canyon off Sodwana Bay, South Africa (© Andromède Oceanology, Eric Bahauet)

Coelacanths are IUCN listed as critically endangered (IUCN 2011) due to their restricted distribution and low population size (Bruton and Stobbs 1991). They are slow growing (Fricke and

Hissmann 2000), have a low fecundity (with a maximum 67 eggs per female) and are late-maturing (Froese and Palomares 2000). These life history characteristics make them particularly vulnerable to external disturbances and warrants their protection wherever possible.

Isolated populations have been found off the east coast of Africa, from the holotype collected off the Chalumna River, South Africa (Smith 1939a, 1939b) in the south**,** northwards through Mozambique (Bruton et al. 1992), Tanzania (Schartl et al. 2005, Benno et al. 2006, Nywandi 2006) to as far north as Kenya (Vos and Oyugi 2002). They have also been found off the southwest coast of Madagascar (Heemstra et al. 1996) and unconfirmed reports suggest that they have been also caught on its east coast. The Comoros Islands contain the best studied and perhaps largest population with over 200 individuals caught as artisanal fisheries bycatch and a similar number observed alive in scientific surveys (Bruton and Stobbs 1991, Stobbs and Bruton 1991, Fricke et al. 2000, Fricke et al. 2011). In South Africa, a viable population was recently discovered in the IWP (Venter et al. 2000).

The habitat ranges of coelacanths appear to be largely determined by both their physiology (Wood et al. 1972) and proximate oceanographic factors. Temperature, light intensity, ocean currents and oxygen availability (Ribbink and Roberts 2006) have all been found to have varying effects on the limits of vertical and horizontal distribution of these fish and their activity levels (Fricke and Plante 1988, Hissmann et al. 1998, Hissmann et al. 2006). Coelacanths require high dissolved oxygen concentrations as they have low oxygen uptake efficiency due to both their blood physiology (Hughes and Itazawa 1972, Hughes 1976, Hughes 1995) and low gill surface area relative to their body size (Hughes 1980). Coelacanths have both short gill filaments and gill lamellae with a thick epithelial layer that both pose passive diffusion constraints. In addition, their blood is more viscous than other fishes (Hughes 1980).

In both the Comoros and South Africa, the normal temperature range of coelacanths has been found to be between 16 and 20˚C, although fish have been shown to tolerate temperatures up to 24˚C (Fricke et al. 1991, Hissmann et al. 1998, Hissmann et al. 2006, Roberts et al. 2006). The lower temperature limit of these fish has not yet been determined. It is assumed that they can tolerate

relatively large fluctuations in seasonal and daily temperatures (Ribbink and Roberts 2006) as there has been documented evidence of a 6˚C change within a single day in Sodwana Bay (Roberts et al. 2006). The coelacanth's metabolic rates therefore need to be kept low to avoid respiratory stress (Hughes 1980). Furthermore, as coelacanths are assumed to be weak swimmers (Fricke and Hissmann 1992, Ribbink and Roberts 2006) and have eyes that are sensitive to bright light (Yokoyama et al. 1999) they are thought to avoid moving waters by taking shelter in caves (Fricke et al. 1991) even though oxygen concentrations are higher in waters with strong currents. In Sodwana Bay, surface currents are strong and can reach 120 cm s^{-1}, decreasing to between 20 and 60 cm s^{-1} at depths of 100-140 m. Current velocity further decreases within the canyons themselves and can be virtually non-existent due to both shelter and boundary effects (Roberts et al. 2006). It is within this physical environment that coelacanths are found (Venter et al. 2000) at depths from 96 to 133 m (Hissmann et al. 2006) where the strong surface currents are virtually absent (Roberts et al. 2006). Temperatures at these depths are low enough to accommodate the required dissolved oxygen concentrations.

1.6 Problem identification and thesis outline

From 2002 to 2004 video footage was collected onboard the German submersible *JAGO* during coelacanth surveys at the heads, edges and within the canyons in the IWP at depths ranging from 46 to 359 m. During these expeditions, a total of 47 dives were undertaken where the primary focus was to simply locate coelacanths and document them. The video footage recorded was mainly of these caves with sporadic recordings of the benthos made along the search tracks. Only one dive was dedicated to recording the habitat at the bottom and along the steep walls of the southern arm of Wright Canyon. Preliminary reports detailing the megabenthos (Hissmann et al. 2002b), geomorphology and distribution of caves (Hissmann et al. 2002a) observed were produced, however, few peer reviewed articles have resulted from analysis of this footage. Records of fish observed during the surveys contributed towards a fish species list for the region (Heemstra et al. 2006b) and observations of coelacanths encountered allowed 24 individuals to be identified (Hissmann et al. 2006) and

catalogued, contributing to knowledge on coelacanth demographics, behaviour and movements. Video footage from experienced Trimix divers allowed distinct habitat types to be recognised within the canyons (Sink et al. 2006) and were confirmed by preliminary analysis of the *JAGO* footage (Hissmann et al. 2002b). A qualitative analysis of the canyon habitats is however lacking.

The deepwater habitats favoured by coelacanths complicate locating and studying them. In order to study coelacanths, they must first be located. Defining their habitat requirements would therefore assist in expediting the searching process. The physical habitat requirements of coelacanths are reasonably well-documented and predictive models have been developed to determine their potential distribution ranges outside of their known localities (Green et al. 2009, Owens et al. 2011). Their biological requirements still remain relatively unknown.

This thesis will make extensive use of this archived video footage. Data will be reanalysed to contribute towards answering specific research questions pertaining to the coelacanth and its habitat. The three main aims of this thesis are: (1) to describe coelacanth habitat in the IWP, (2) to quantify the relationship of coelacanths and their associated habitats in order to predict coelacanth distribution, and (3) to assess the suitability of computer-aided identification software to identify individual coelacanths. The thesis is structured into six chapters.

Chapter 1 reviews the use of videography in marine ecology and biology and its advantages and disadvantages. The coelacanth and its habitats are introduced and the suitability of video footage for studying this fish discussed. Chapter 2 describes the study area and the oceanography around the canyons in the IWP and the data used are described. A combination of multivariate and univariate SHE analyses is presented in Chapter 3 to describe and identify coelacanth habitat in the IWP and determine in which of these habitats coelacanths are located. Using the data from Chapter 3, Chapter 4 develops a classification tree model that predicts coelacanth distribution in relation to depth, habitat and their associated macroinvertebrate communities. Chapter 5 describes the use of computer-aided identification to successfully identify individual coelacanths. To conclude, Chapter 6 presents a

general discussion in which the results of the different chapters are discussed and recommendations for further research are provided.

Chapter 2

Study area

The submarine canyons situated within the IWP (formerly the Greater St Lucia Wetland Park), a marine protected area enclosing 78 km of the coastline off the northern KwaZulu-Natal coast, South Africa constituted the study area for this thesis. The KwaZulu-Natal continental shelf is comparatively narrow between 2 and 5 km compared to the global average of 75 km and is cut through by numerous canyons (Ramsay 1994). There are 23 canyons in total, with six in a mature-phase and 17 in a youthful-phase (Ramsay and Miller 2006). This phase classification is based on morphometric features such as size and the degree to which the canyon has encroached on the continental shelf (Farre et al. 1983). Mature phase canyons tend to be large features cutting into the continental shelf with steep sides whereas the youthful-phase canyons occur in deeper water near the continental margin and are generally smaller.

This thesis investigated 10 canyons namely - Island Rock, Mabibi, White Sands, Wright, Jesser, Deepgat, Leadsman, Leven, Chaka, and a small unnamed canyon between Jesser and Wright canyon, named “Small Canyon” (Figure 2.1). The canyon heads are precipitous and have steep cliffs in some areas where overhangs and caves are frequent due to the presence of carbonate rock cement that was dissolved away during low sea levels in the Pleistocene period when the surf zone was at this level (Ramsay and Miller 2006).

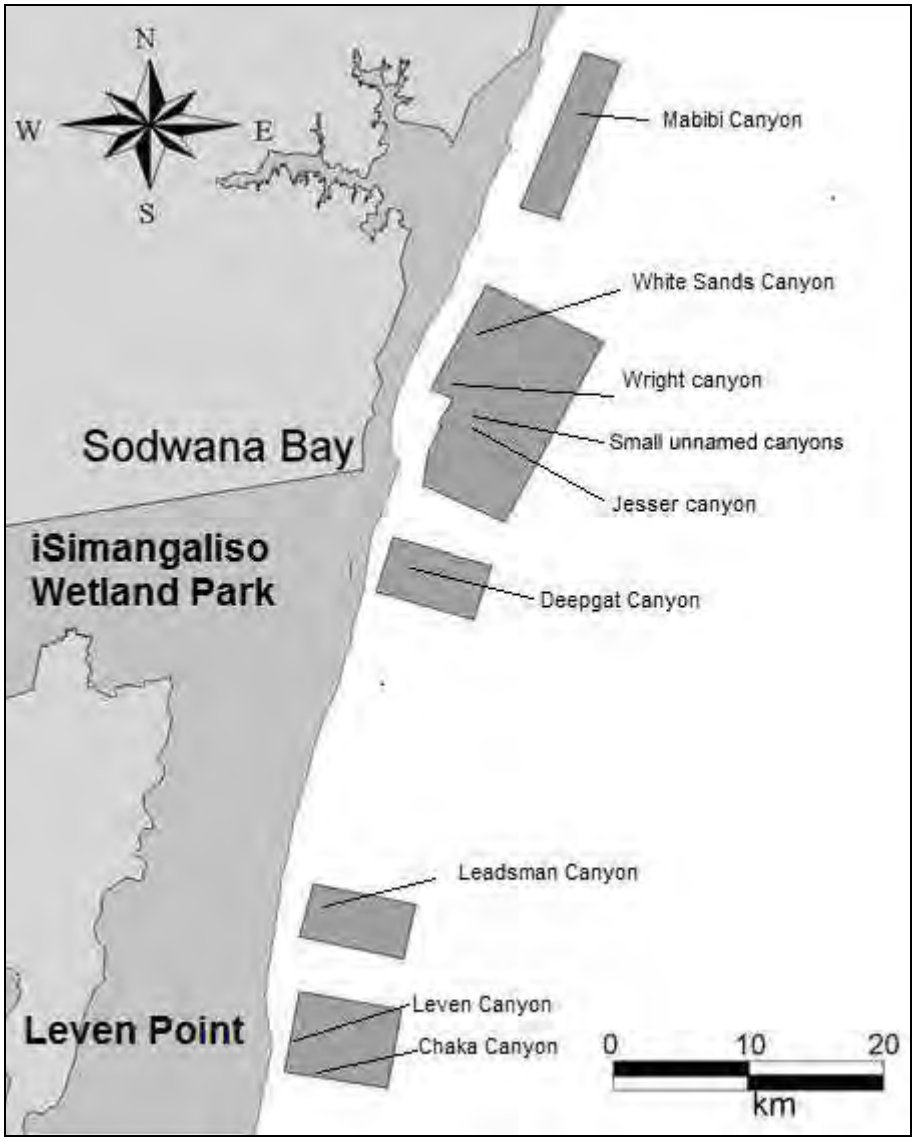


Figure 2.1: Map showing the location of nine of the canyons off the KwaZulu-Natal coast where the raw video footage used in this study was obtained (Island Rock is not shown). The heads of the canyons are indicated by the black lines (Modified from Ramsay and Miller 2006)

In general, the northern margins of the mature canyon heads tend to be steeper and more stable than those in the south where there are sediment slumps. A deep "thalweg" occurs in the bottom of the mature canyons and slopes down with an angle of around 3° to over 700 m in depth. The gradients of the head margins range from 17° to up to 61° in areas (Ramsay and Miller 2006).

Jesser canyon is the most developed of the youthful-phase canyons (Ramsay and Miller 2006) and is where the first South African coelacanth was observed (Venter et al. 2000). This canyon has encroached on the continental slope to 90 m and has a maximum width of 696 m. The sides of the thalweg are steep with gradients from 21° to 50° reaching a depth of over 580 m with a gentle slope of 4.6°. The head of this canyon has sides varying in steepness from 12.3° to 43°. The other youthful-phase canyons have a similar structure in that they are linear, narrow and steep-sided with small heads with margin gradients ranging from 10.6° to 51.3°. Their thalwegs slope downwards with an average gradient of 5.1° (Ramsay and Miller 2006).

Bathymetric maps (Figure 2.2 and 2.3) illustrate examples of the structure of mature and youthful phase canyons. Off Sodwana Bay, two mature canyons are Wright Canyon and White Sands Canyon, and two youthful-phase canyons are Jesser Canyon and Small Canyon (Figure 2.2). Off Leven Point there is one mature canyon, Leven Canyon and one youthful phase canyon, Chaka Canyon (Figure 2.3).

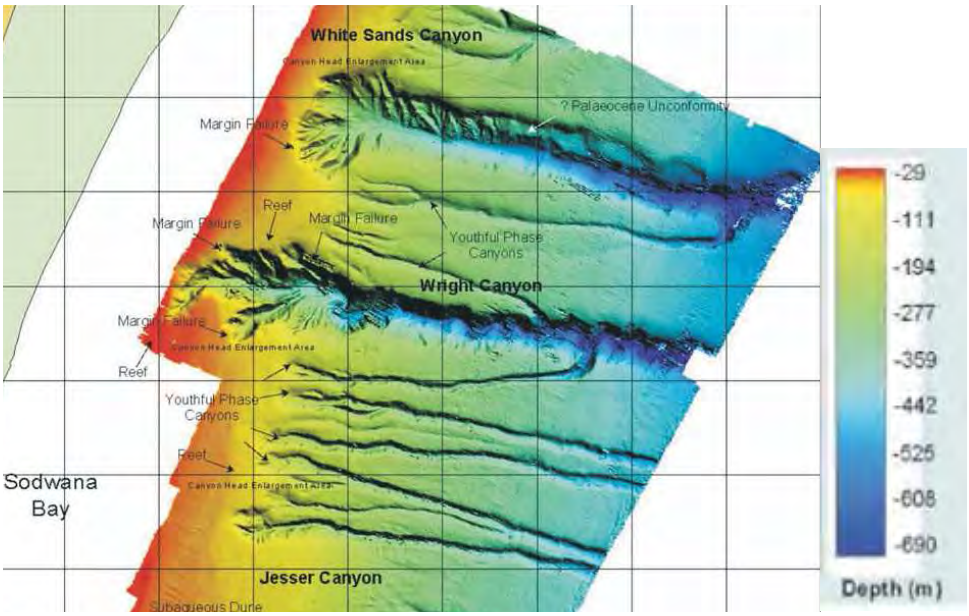


Figure 2.2: A colour-draped bathymetry map of four of the surveyed canyons off Sodwana Bay - Jesser, Wright, White Sands and the small canyon between Wright and Jesser (Ramsay and Miller 2006)

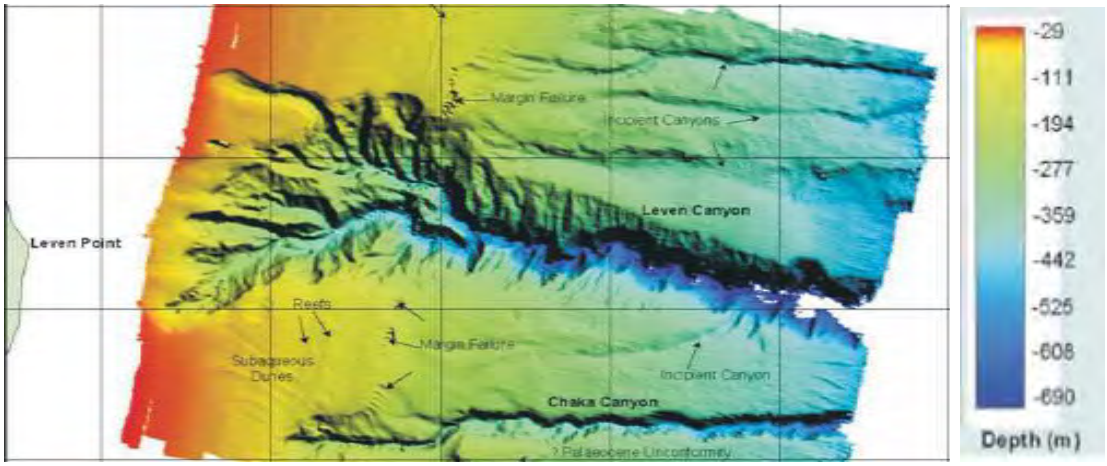


Figure 2.3: A colour-draped bathymetry map of the canyons off Leven Point (Ramsay and Miller 2006)

2.1 Oceanographic environment

The main oceanographic feature of the IWP is the Agulhas Current (Figure 2.4) that 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 then flows in shore, parallel to the coastline all the way to Port Elizabeth (Lutjeharms 2006).

The northern Agulhas Current system is the section found in the region off the KwaZulu-Natal coastline. Current speeds of 1.5 m s^{-1} along the current edge prevail in this section, sea surface temperatures (SST) range from 20˚ to 28˚C, and salinities are usually in the region of 35.0 to 35.5 that are typical of Tropical Surface Water. In this region, Subtropical Surface Water flows 60 km offshore at depths between 150 and 250 m. These two waters mix along the shelf to form the shelf water due to upwelling of the deeper Subtropical Surface Water inshore of the main Agulhas Current due to the continental shelf's morphology (Lutjeharms 2006).

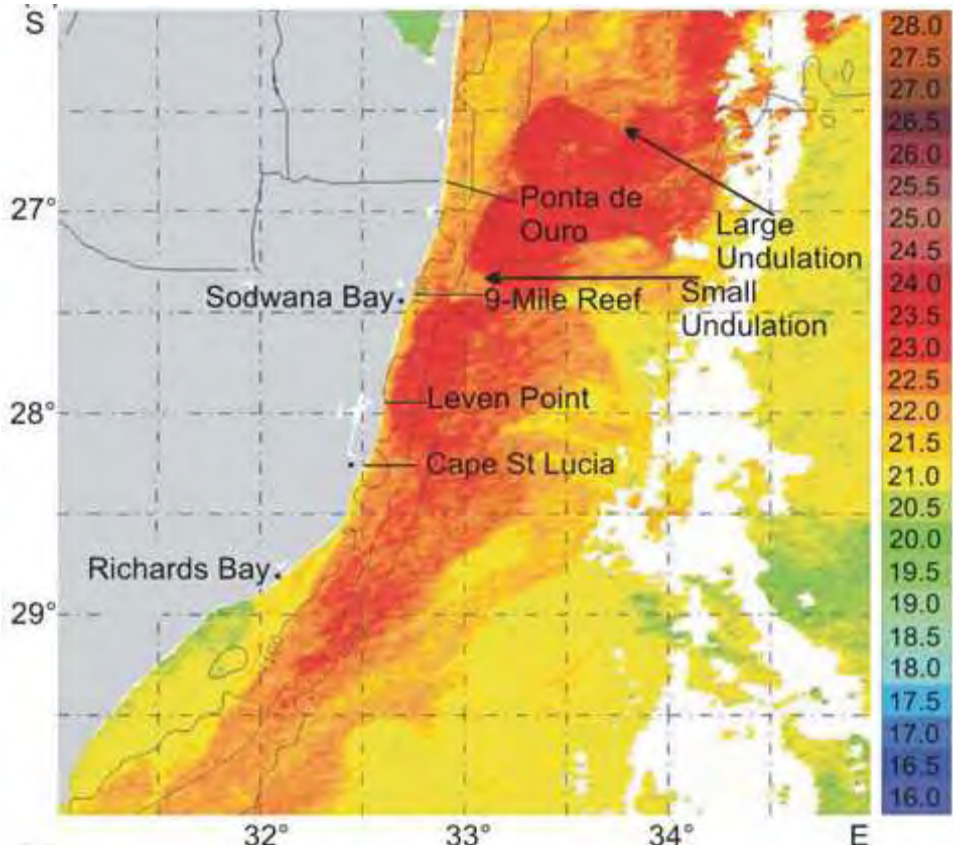


Figure 2.4: A sea surface temperature image shows a snapshot of the location of the warm core of the Agulhas current (red) past the study area. Scale in ˚C (Roberts et al. 2006)

The oceanic environment off the canyons is characterised by strong currents. Within the canyons, however, the currents decrease significantly and there is little or no flow velocity in places (Hissmann et al. 2006, Roberts et al. 2006). There is considerable variation in current flow within the canyons as downwelling, upwelling and ripples on the canyon floor have been observed (Roberts et al. 2006). A boundary layer between the sea floor in the canyons and the fast moving Agulhas Current has been observed where virtually no current has been observed at times (Ribbink and Roberts 2006). Currents at 100 - 140 m show considerable variation and were measured between 20 and 60 cm s^{-1} (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 (Figure 2.5) (Roberts et al. 2006) and also coincides with the depth in the canyons where numerous caves and overhangs are found. There is high temperature variability within the canyons. While temperature usually ranges between 15 to 22˚C seasonally, an 8˚C difference was observed in a single day by Roberts et al. (2006). This variation is due to changes in flow regime which cause upwelling cells (Figure 2.5) as well as tides and daily water movements up and down the continental slope (Ribbink and Roberts 2006).

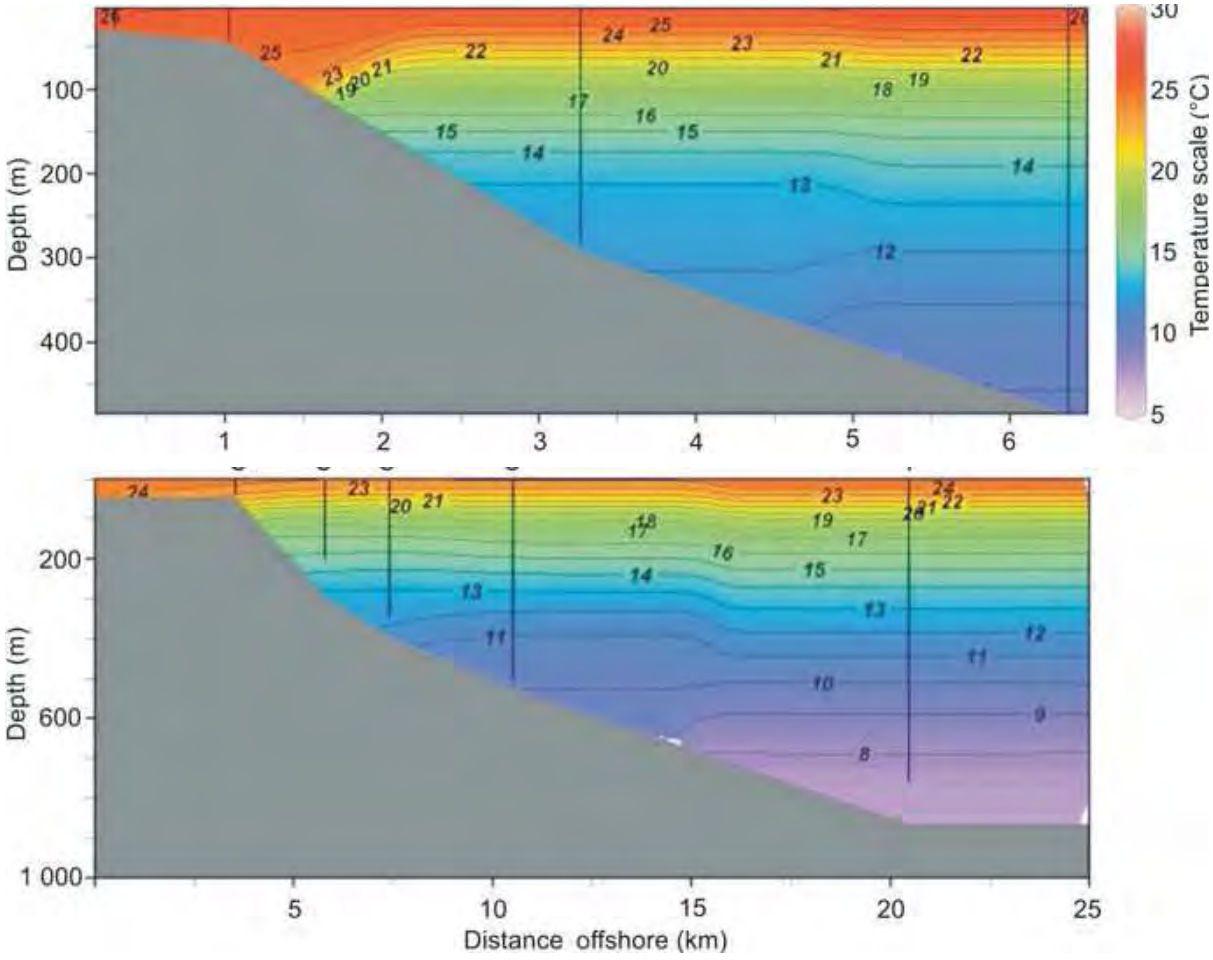


Figure 2.5: The isothermal structure off the study area showing two extremes with the thermocline dipping down onto the slope (top) and shelf-edge upwelling (bottom) (Roberts et al. 2006)

2.2 Videographic material available

The German research submersible *JAGO* was used to survey the coelacanths in the IWP with 13 canyons explored from between 2002 until 2004 on three sampling trips where the submersible was operated off the *FRS Algoa*. During these surveys the research objective was to locate coelacanths within the canyons (Table 2.1). Surveys focussed on areas, such as caves and rocky overhangs, which could potentially support coelacanths. The videographic footage from these surveys constituted the research material for this thesis.

Table 2.1: Details of the *JAGO* dives and the videographic footage available from 2002 to 2004

Canyon	Year	Bottom Time (hours)	Min/Max Depth (m)	Useable footage (min)
Chaka	2004	6.3	70–124	80.7
Diepgat	2002, 2004	12.6	50–359	134.7
Island Rock	2002, 2003, 2004	10.0	61–198	143.3
Jesser	2002, 2003, 2004	54.3	70–255	333.0
Leadsman	2003, 2004	10.6	91–184	56.8
Leven	2004	10.8	71–125	90.7
Mabibi	2002, 2004	9.6	110–139	99.0
Small	2002, 2004	8.9	95–193	77.4
White Sands	2002, 2004	6.6	91–152	67.8
Wright	2002, 2003	35.9	46–345	166.0
TOTAL		166.4		1249.4

Chapter 3

A multivariate analysis of coelacanth, *Latimeria chalumnae*, daytime habitat in South Africa

3.1 Introduction

The importance of taking a holistic approach when conserving sensitive species is widely recognized and is premised on the whole ecosystem being managed rather than focusing on one particular organism (Peterson et al. 2000, Gislason 2001, Hewitt et al. 2004, George et al. 2007, Sanchirico and Mumby 2009, Pace 2010). An ecosystem approach to management has now been legislated in several countries (EPBC 1999, Gaines et al. 1999, Apitz et al. 2006, Belgrano et al. 2006, Borja et al. 2009, Styring 2010). For example, in the USA, the Magnuson-Stevens Fishery Conservation and Management Act (NOAA 1999) includes a section termed "Essential Fish Habitat (EFH)" that defines EFH as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity". Substrate is further defined as "sediment, hard bottom, structures underlying the waters and associated biological communities" (NOAA 1999, p4). This act illustrates the need to investigate all aspects of a rare or endangered species' habitat together with its relationships with sympatric biota (Rieser 2000, Rosenberg et al. 2000, NOAA 1999, 2007) thus allowing the whole ecosystem to be conserved and managed (Agardi 2000). Understanding EFH of sensitive or rare species and their relationships with their proximate environment is complex (Schulze and Mooney 1993) and it is clear that ecosystem biodiversity needs to be quantified, monitored and maintained to ensure proper ecosystem functioning (Lovejoy 1994, EPAP 2006).

The Convention on Biological Diversity (CBD) requires that its member nations quantify their biodiversity and monitor its changes in order to produce and implement conservation plans (Grey 2000). Identifying specific habitats and biodiversity patterns will therefore improve the understanding of the different ecological components such that the development of more comprehensive management strategies can be facilitated (Gaines et al. 1999). Defining specific

habitats also allows for a more refined definition of a species' EFH within the broader ecosystem (NOAA 1999, Rosenberg et al. 2000) and will facilitate further investigation into the relationships between the species and its associated fauna (Peterson et al. 2000, Auster 2007).

Species classified as rare and/or endangered by the IUCN require immediate conservative action as they are at risk of extinction. Within South Africa, coelacanths *Latimeria chalumnae* are classified as critically endangered (IUCN 2011) prompting the need to determine their EFH. While videographic data relating to coelacanths and their submarine canyon habitat have been collected in the IWP (Hissmann et al. 2006) only an unpublished checklist of biota observed has been reported (Hissmann et al. 2002b). Additional amateur videographic material from Wright and Jesser Canyons, also within the IWP, was analysed by Sink et al. (2006) to determine invertebrate diversity and composition.

There is a need for a more rigorous analysis of the diversity and habitat types within submarine canyons in the IWP that are inhabited by the most southerly distributed population of coelacanths such that more complex questions of how coelacanths utilise these different habitats and the extent to which they are dependent upon them can then be addressed. This chapter therefore aims to both define and describe the different habitats in the canyons and to determine where coelacanths are distributed within these habitats.

3.2 Materials and methods

Sampling protocol

All data were obtained from the video footage obtained during eighteen *JAGO* submersible surveys operating within the submarine canyons of the IWP between 2002 and 2004 (Table 3.1). The video footage was sampled by stratifying the video footage by year and by canyon.

The primary objective of the *JAGO* surveys was to simply locate coelacanths. As a result, the resultant video footage consists mainly of the submersible moving along an *ad hoc* transect to locate caves that have been identified as the primary habitat of coelacanths. Once a cave was located it was

searched for coelacanths and possibly investigated for other invertebrates or fishes of interest. To account for this search-and-stop survey design, this study only included video footage when the submersible was moving to standardise the time spent within each canyon each year. A total of 50 still frames, now referred to as samples, were then extracted from each survey determined by dividing the time surveyed by the required sample number. This reduced both temporal, in terms of the progression of the submersible, and spatial, in terms of the area covered along the seafloor, autocorrelation within the data. In the case of two surveys that were too short in duration fewer than 50 samples were collected. All samples were extracted from the video footage with *MovAvi Video Suite v8*. A total of 839 frames were sampled (Table 3.1). Once all samples were extracted from the video footage, they were pre-processed by cropping out those areas where the substratum and/or biota were poorly visible due to poor illumination.

Table 3.1: Summary of *JAGO*'s total searching time and still photograph frame spacing to sample the submarine canyons off iSimangaliso Wetland Park, South Africa

Canyon	Year	Number of still frames	Total time (min)	Frame spacing (sec)
Chaka	2004	50	80.7	97
Deepgat	2002	50	40.7	49
	2004	50	94.0	113
Island Rock	2003	50	94.5	113
	2004	50	24.7	30
Jesser	2002	50	111.5	134
	2003	50	121.1	145
	2004	50	100.5	121
Leadsman	2003	13	4.9	22
	2004	50	51.9	62
Leven	2004	50	90.7	109
Mabibi	2002	50	7.2	9
	2004	50	91.8	110
Small	2004	50	77.4	93
White Sands	2002	26	12.6	29
	2004	50	55.2	66
Wright	2002	50	120.8	145
	2003	50	45.2	54
TOTAL		839	1225.3	

Each sample was analysed using a random stratified sampling design by digitally overlaying random points and identifying the substratum type or biota under each point using *Coral Point Count with Excel Extensions* (*CPCe v3.6*) (Kohler and Gill 2006). Each sample was different in area due to differential zooming of the camera that was mounted at an angle to the substratum. To standardise the number of randomly allocated points for each sample such that the relative proportion of substratum and biota were comparable between samples, all samples were previewed and the ratio of the size of the obvious and common invertebrates relative to the total area of the still frame estimated. This ratio was used to increase or decrease the number of randomly allocated points. For example, if the camera zoomed in and the ratio was double that of a reference frame, then the number of randomly allocated points was halved. It was assumed that all reference invertebrates were identical in size. In this way the number of samples was not affected by zooming but only the number of random points allocated. Due to the angle of the sample, all randomly generated points that fell off the substratum were excluded from the analyses. The final data collected from each sample included the proportional cover of the different invertebrates, proportional cover of uncolonised substratum, and depth.

Taxon and substratum identification

Any diversity analysis investigates the changes in proportions of identifiable taxa that could be resolved to the lowest taxonomic level. The inability to correctly identify a species does not, fortunately, constrain the analysis if the species, or taxa, can be consistently differentiated from each other. The biota identified in the analysis included corals, gorgonians, hydroids, sponges, sea pens, echinoderms, fishes, coelacanths, ctenophores, bryozoans, urchins, anemones, algae, gastropods, crustaceans, live cover and unknown animals. Three substratum types were identified. These were rock, sand and silt.

Fishes were identified to species level wherever possible (Table 3.2, Figure 3.1) using Smith (2003), Heemstra and Heemstra (2004) and Heemstra et al. (2006a, 2006b). Due to differential photograph quality if a fish was completely unidentifiable to at least family level they were classed as

an “unknown fish” and in cases where species identification was impossible were classified as the genus and a numeric species identifier.

Table 3.2: Species list of fishes identified in the still frames from the *JAGO* footage

Common Name	Scientific Name
Glassy	*Ambassis* sp. 1 and 2
Blue cardinalfish	*Apogon fukuii*
Goldribbon soapfish	*Aulacocephalus temmincki*
Fusilier	*Caeseo* sp.
	Symphysanodon sp.
Doublesash butterflyfish	*Chaetodon marleyi*
Santer	*Cheimerius nufar*
Slinger	*Chrysoblephus puniceus*
Brindle bass	*Epinephelus lanceolatus*
Dot dash grouper	*Epinephelus poecilonotus*
Flagtail	*Kuhlia* sp.
Coelacanth	*Latimeria chalumnae*
Monkfish	Lophiiformes
Pineapple fish	*Monocentris japonica*
Yellowfin soldier	*Myripristis chryseres*
Yellowtail blue snapper	*Paracaesio xanthura*
Spotted grunter	*Pomadasys commersonii*
Crescent tail bigeye	*Priacanthus hamrur*
Japanese bigeye	*Pristigenys niphonia*
Goldie	*Pseudanthius* sp.
Wrasse	Unknown Labrid
Sweeper	Unknown Pempherid
Scorpionfish	Unknown Scorpionids 1 and 2
Grouper	Unknown Serranids 1 - 3
Blaasop	Unknown Tetraodontid
John dory	*Zeus faber*
Unknown	Unknown 1 - 6

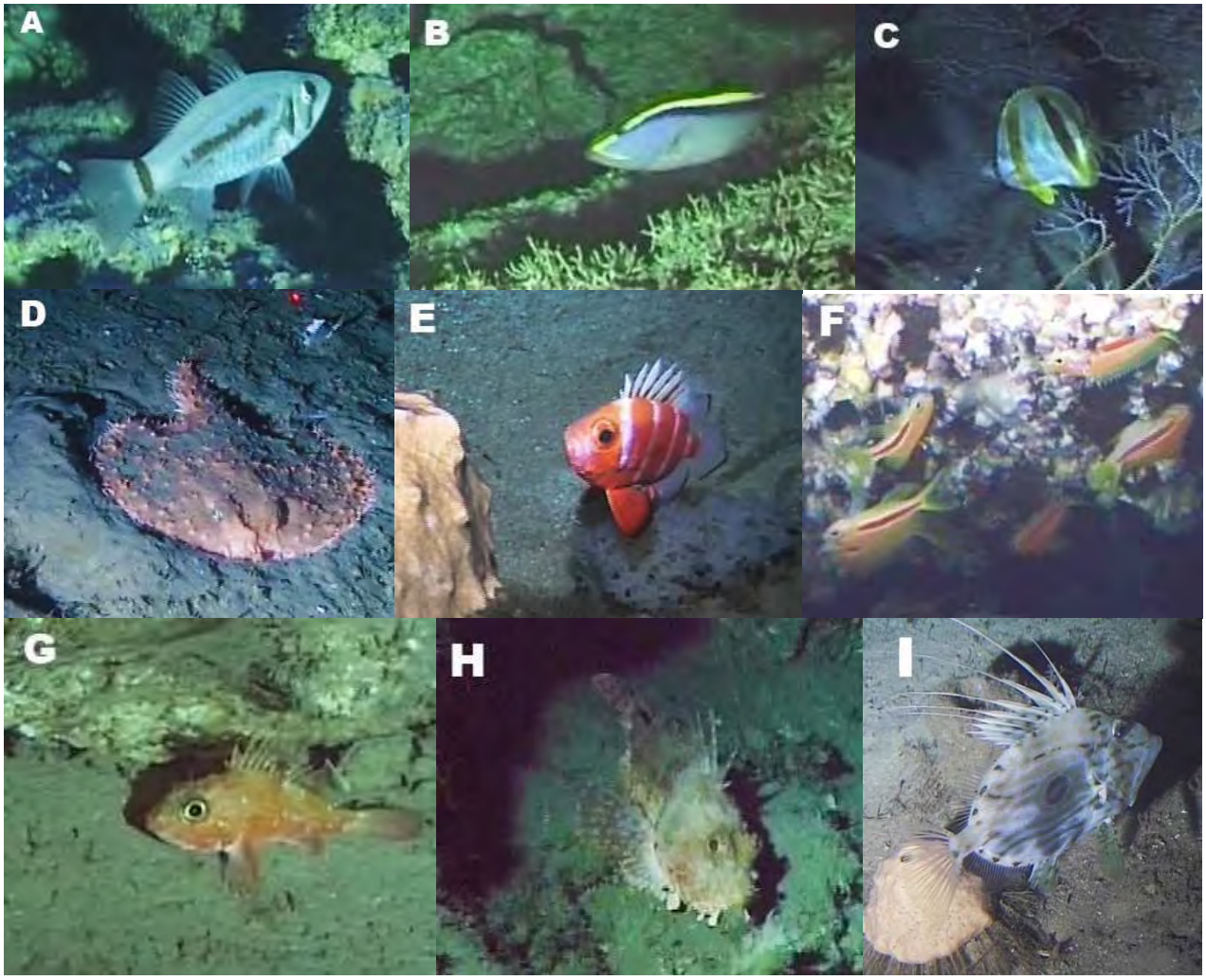


Figure 3.1: Various fish identified from the *JAGO* Videographic footage. (A) Unidentified glassy *Ambassis* sp., (B) gold ribbon soapfish *Aulacocephalus temmincki*, (C) doublesash butterflyfish *Chaetodon marleyi*, (D) monkfish, (E) Japanese bigeye *Pristigenys niphonia*, (F) female red-banded anthias *Pseudanthias fasciatus*, (G and H) scorpionfish *Scorpionid* spp, and (I) John Dory *Zeus faber*

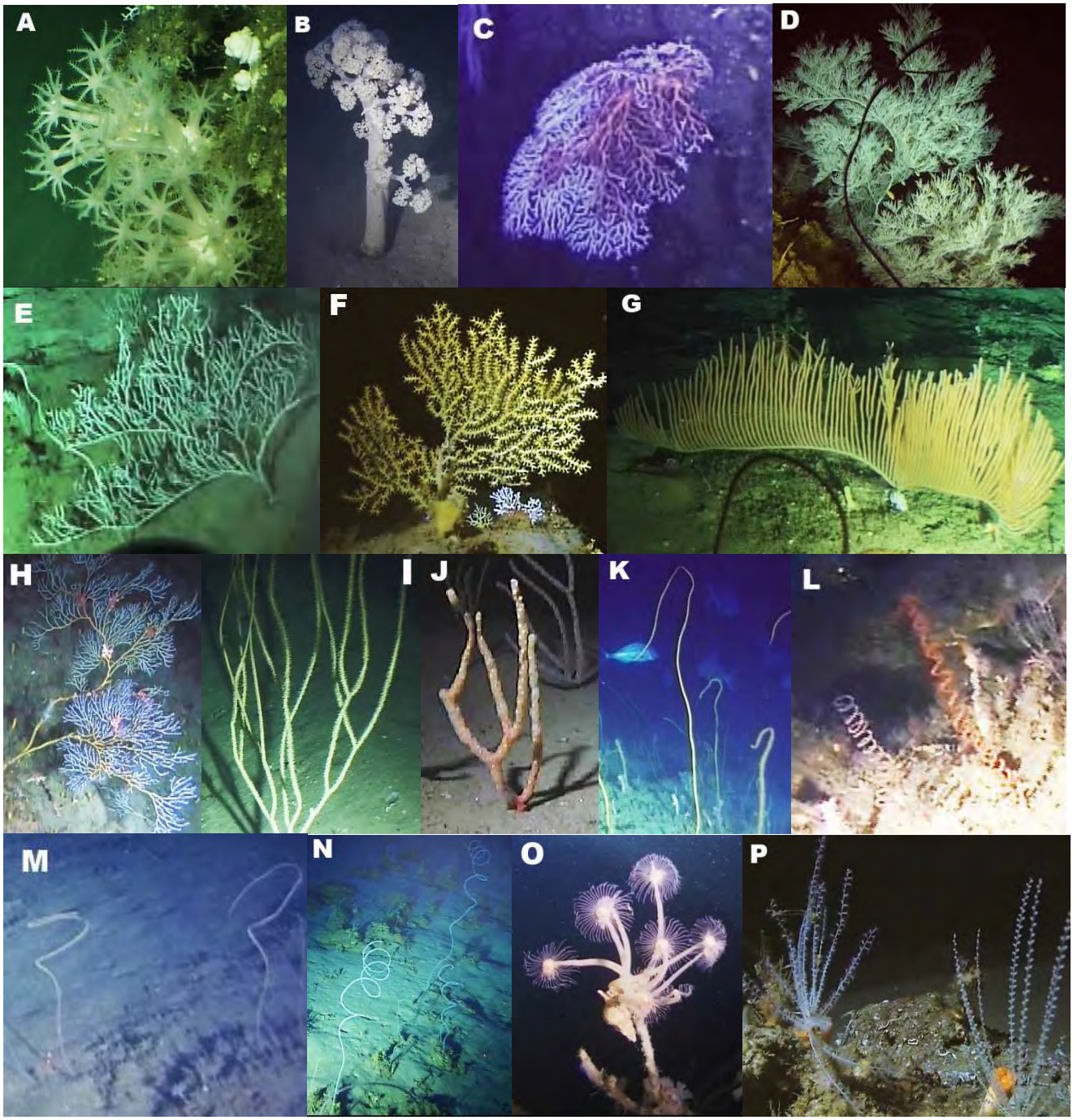


Figure 3.2: Examples of cnidarians identified from the *JAGO* submersible footage that include corals, gorgonians, black corals, whip and wire corals and hydroids. (A) Alcyonacea, (B) *Dendrophyta* sp., (C) lace coral *Stylaster* sp., (D) black coral *Antipathes* sp., (E) *Rumphella* sp., (F) *Eunicella* sp., (G) *Ctenocella* sp., (H) *Nicella dichotoma*, (I) *Echinogorgia* sp., (J) *Homophytum verrucosum*, (K) *Juncella* sp., (L) *Simpsonella spiralis*, (M) *Simpsonella squanifera*, (N) *Cirripathes* sp., (O) *Hydroia* sp., and (P*)* *Hydroia* sp. with an unidentified gastropod

Invertebrates were identified to phylum from Gosliner et al. (1996) and Branch et al. (2010). In particular, the Cnideria (Figure 3.2 and 3.3) were identified from Williams (1990, 1992a, 1992b, 1993) and the Echinodermata (Figure 3.4) from Mortensen (1916). The Porifera (Figure 3.6) were classified according to their morphology (Boury-Esnault and Rutzler 1997) and colour (Samaai et al. 2010) because the low resolution of the video footage often made species identification impossible. Sink et al. (2006) was finally used to cross-reference and identify common species. Invertebrates which could not be identified due to poor quality still frames were classified as "unknown invertebrates".

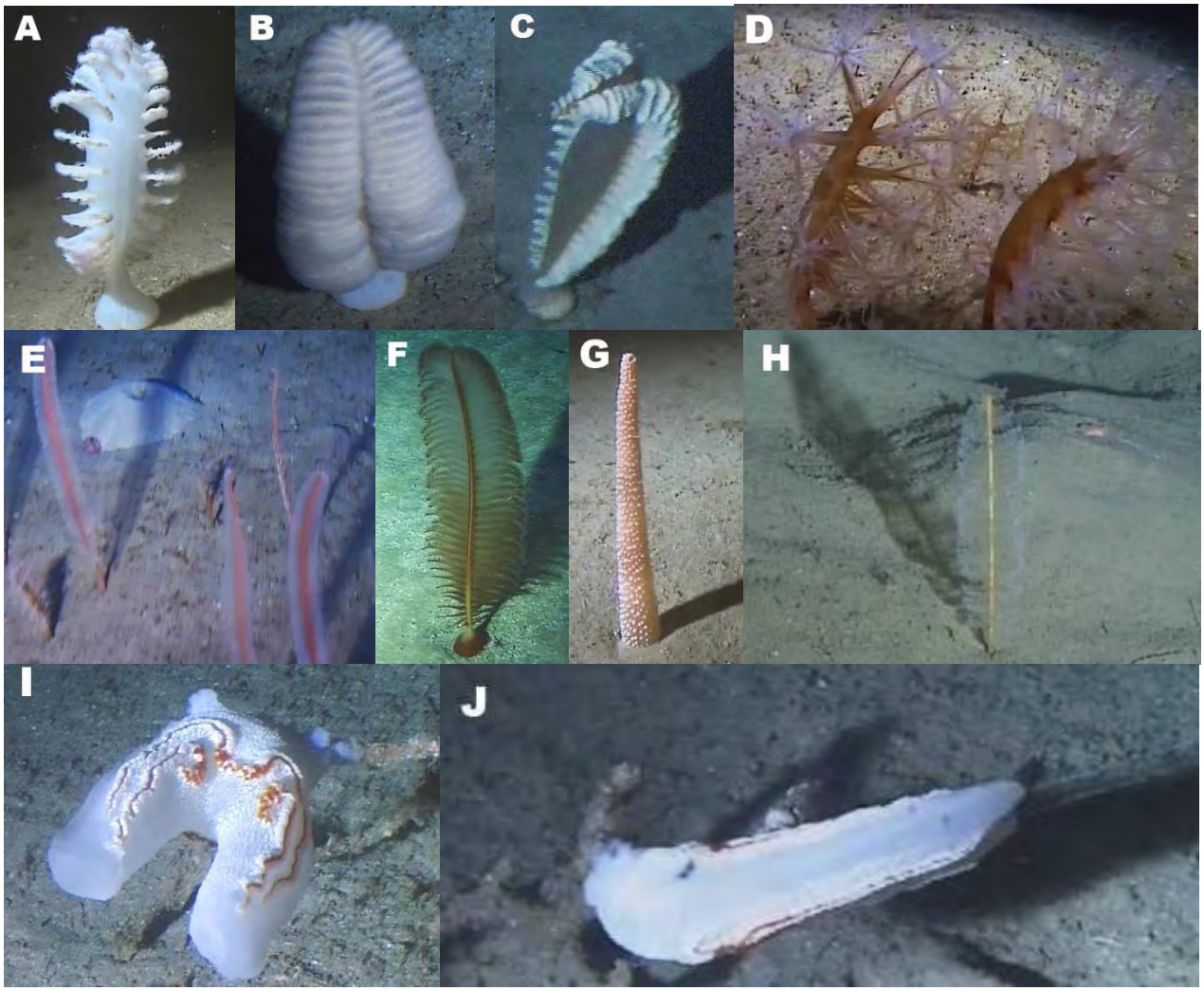


Figure 3.3: Additional Cnidaria, Pennatulacea and Ctenophora identified from the *JAGO* footage. (A, B, C) *Pteriodes* sp., (D) *Sclerobelemnon* sp., (E, F) *Virgulria* sp., (G, H) unidentified Pennatulacea, (I) sessile ctenophore inactive and (J) feeding

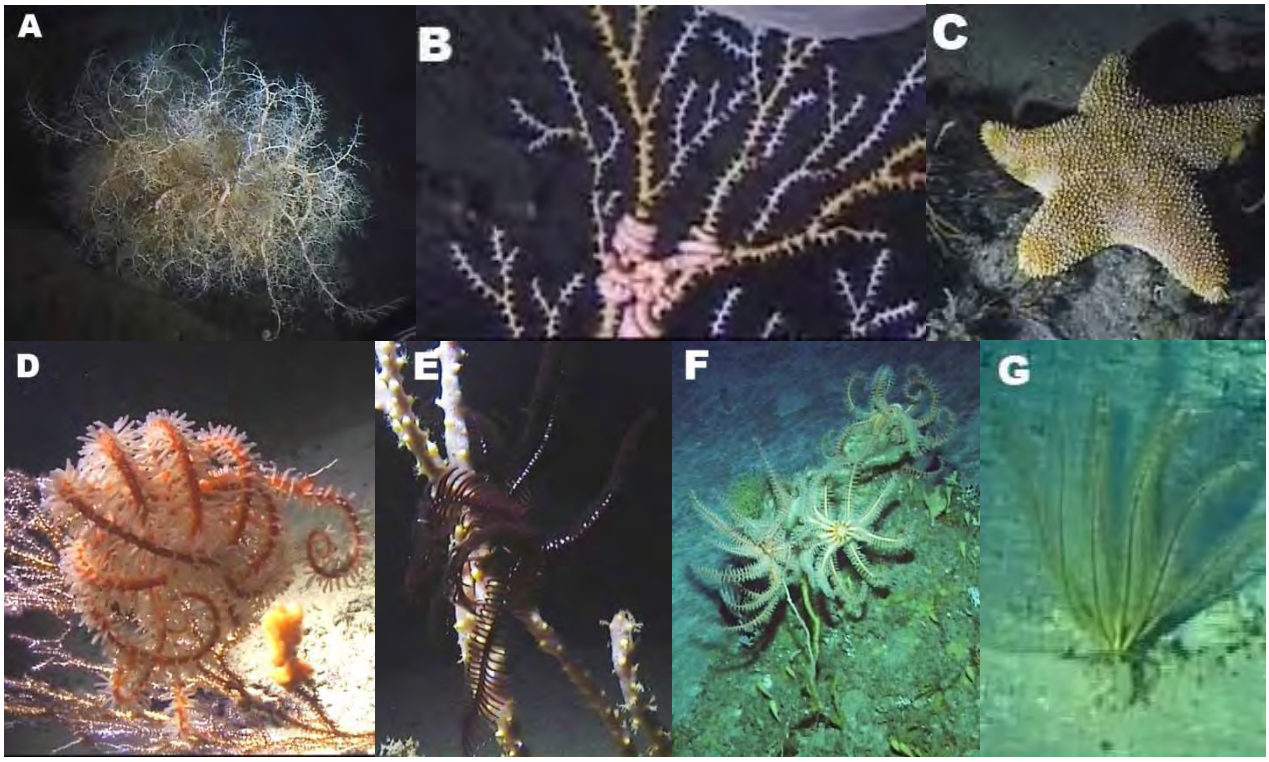


Figure 3.4: Examples of Echinodermata identified from the *JAGO* footage. (A) Basket star, *Astroba nuba*, (B) brittlestar, *Asteroschema capensis*, (C) unidentified asteroid starfish, and (D-G) unidentified crinoid feather stars

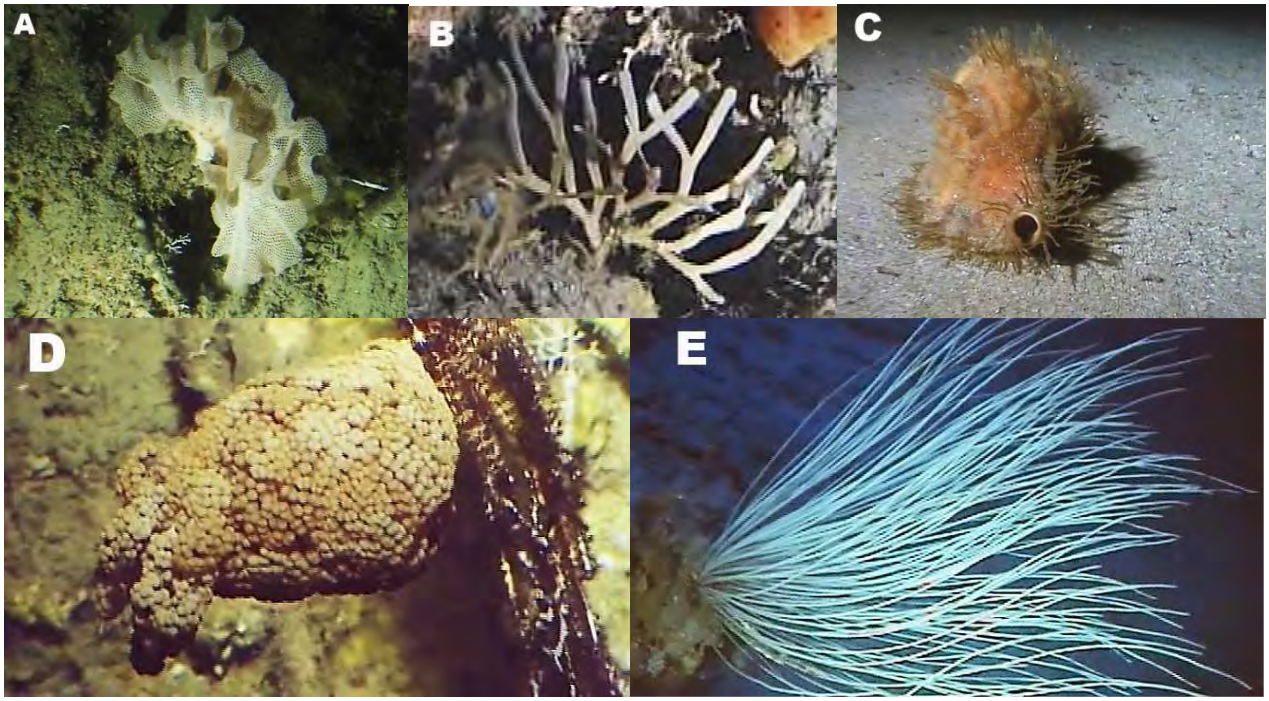


Figure 3.5: Examples of Bryozoa, Gastropoda and unidentified invertebrates from the *JAGO* footage. (A) False lace coral, *Idiocytum* sp., (B) unknown bryozoan, (C) *Cypraeidae* sp., and (D and E) unidentified invertebrates

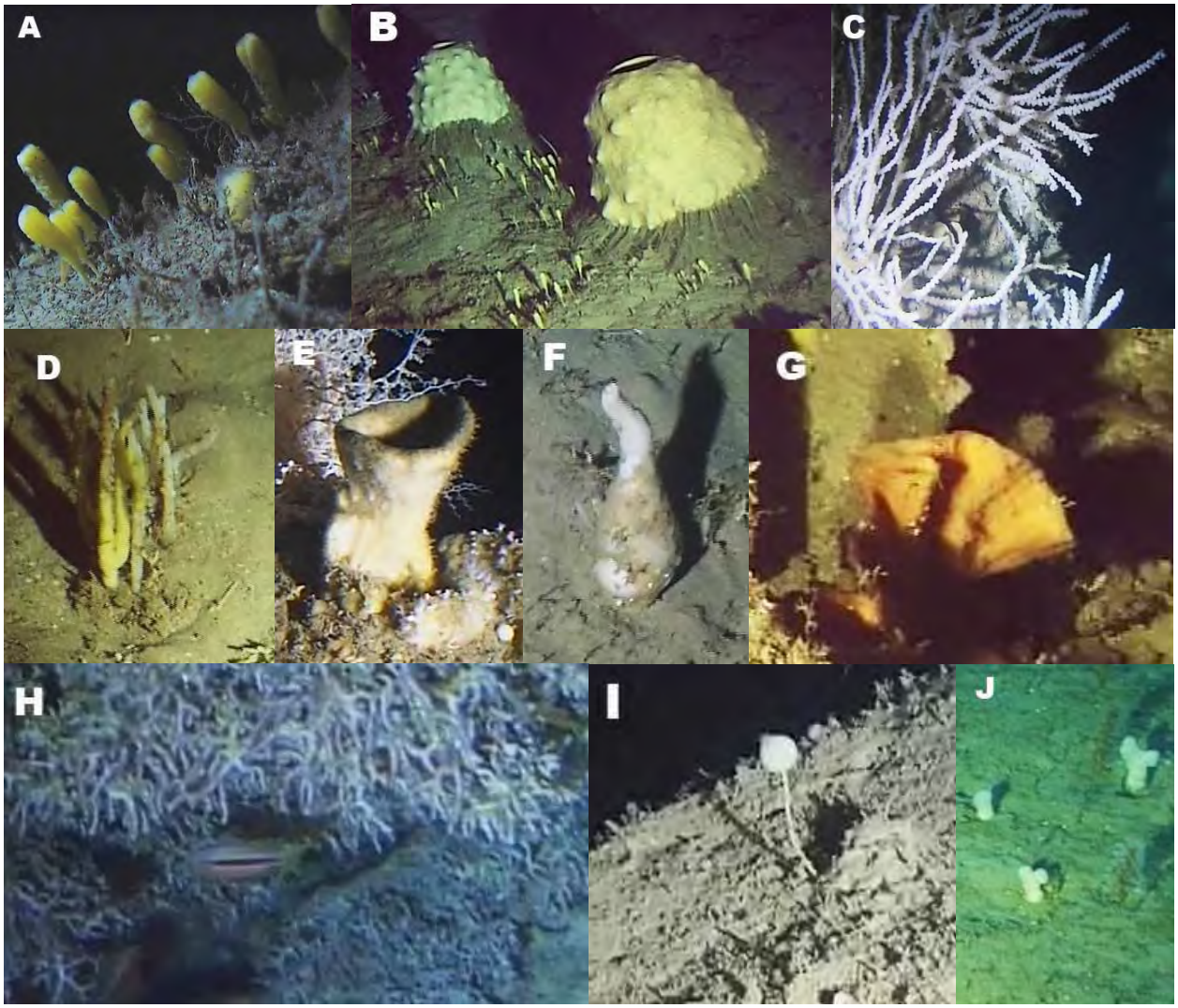


Figure 3.6: Examples of Porifera identified from the *JAGO* footage illustrating their different morphometry. (A) *Echinostylos* sp., (B) *Pheronema* sp., (C) *Sclerothamnus* sp., (D) aborescent-shaped sponge, (E) caliculate-shaped sponge, (F) conical-shaped sponge, (G) foliaceous-shaped sponge, (H) digitate-shaped sponge, (I) stipitate-shaped sponge, and (J) unidentified globular sponges found in a sea pen forest

Data analysis

Three datasets were analysed. These were (1) the proportion of different biota within each sample per canyon per year, (2) the proportion of different biota and depth within each sample per canyon per year, and (3) the proportion of different biota and uncolonised substratum and depth within each sample per canyon per year. These three datasets were used to investigate biotic structure, biotic structure related to depth, and biotic structure related to both depth and underlying substratum.

Table 3.3: The different invertebrate taxa identified in the still frames from the *JAGO* footage

Phylum	Main Categories	Sub Categories	Phylum	Main Categories	Sub Categories
Cnidaria	Corals		Echinodermata		
		Alcyonacea			*Asteroschema capensis*
		Dendronephyta sp.			*Astroba nuba*
		Scleraterinia			Asteroidea
		Stylaster sp.1 and 2			Crinoidea type 1 - 4
		Antipathes sp.			Holothuroidea
	Gorgonacea			Echinoidea	
		Juncella sp.			Echinoidea type 1 and 2
		Nicella dichotoma	Porifera	Sponges	
		Leptogorgia sp.			*Schlerothalmnus* sp.
		Homophytum verrucosum			*Pheronema* sp.
		Rumphella sp.			*Echinostylinos* sp.
		Acanthogorgia sp.			Aborescent sp.
		Echinogorgia sp.			Caliculate sp.
		Eunicella sp.			Columnar white sp.
		Antipathes sp.			Columnar yellow sp.
		Ctenocella sp.			Conical sp.
		Stichopathes sp.			Digitate sp.
		Simpsonella spiralis			Encrusting white sp.
		Simpsonella squanifera			Encrusting yellow sp.
	Hydrozoa				Foliaceous sp.
		Hydroia type 1 and 2			Globular blue sp.
	Pennatulacea				Globular sp.
		Pteroides sp. 1 - 3			Stipitate white sp.
		Sclerobelemnon sp.			Tubular orange sp.
		Virgularia sp. 1 and 2	Other	Algae	
		Virgularia sp. 2			Rhodophyta
		Unknown sp. 1 and 2		Gastropoda	
	Actiniaria				Cypraeidae sp.
		Actinaria type 1			Unknown gastropod
	Zoanthidea			Crustacea	
		Zoanthid type 1			Majidae
	Ctenophora		Unknown	Unknown Invertebrates 1-6	
		Sessile Ctenophore			
Bryozoa	Bryozoans				
		Idiocytum sp.			
		Bryozoan type 1-6			

SHE analysis

SHE analysis (Hayek and Buzas 1997) attempts to integrate several indices developed to quantitatively estimate species diversity. The analysis is based on the relationship between species

richness and taxa abundance and how this relationship relates to both diversity and dominance. Mathematically this relationship is expressed as $H = \ln S + \ln E$ which links species richness (S = number of species), the Shannon-Wiener diversity index (H), and dominance or evenness ($E = e^H/S$). A change in either species richness or abundance indicates a change in diversity. The relationship remains constant only if species richness remains constant. As with any sampling approach, the value of S usually increases with an increase in sampling effort. Due to the relationship between ln$S$, ln$E$ and H, if either ln$E$ or H remain constant between samples the other will exhibit a linear change with an increase in ln$S$. The statistical relationship between S and the number of individuals (N) is such that as N increases with sampling effort so does S. Due to this relationship, a plot of ln$N$ versus ln$E$ can be used to define sequential diversity changes through time or space through the identification of "biofacies". These biofacies are recognised by a change in the linear relationship between ln$N$ versus ln$E$ as "slope breaks" on the resulting graph, since any deviation from a linear trend indicates either a change in proportions of species or evenness (Hayek and Buzas 1997).

Not all biofacies can be identified by a single plot. To separate out the subsequent biofacies an iterative procedure is employed whereby subplots are created by a stepwise deletion of samples that have already been analysed. For example, those samples that were analysed prior to a slope break are removed and S, N, H and E recalculated. This iterative process is repeated until all samples have been separated into biofacies. This process is known as SHE analysis for Biofacies Identification (SHEBI) (Hayek and Buzas 1997, Osterman et al. 2002, Mana 2005, Buzas et al. 2007).

In this study for each of the samples, species richness and number of individuals were manually counted. The number of individuals in the sample, Shannon-Wiener's diversity index (H), the evenness (E) and their natural logarithms were then calculated as described in detail by Buzas and Hayek (1996). The ln$N$ for each canyon was plotted against ln$E$ to produce a "hollow curve" (Hayek and Buzas 1997) after which the iterative SHEBI procedure was applied to determine biofacies for each canyon (Figure 3.7).

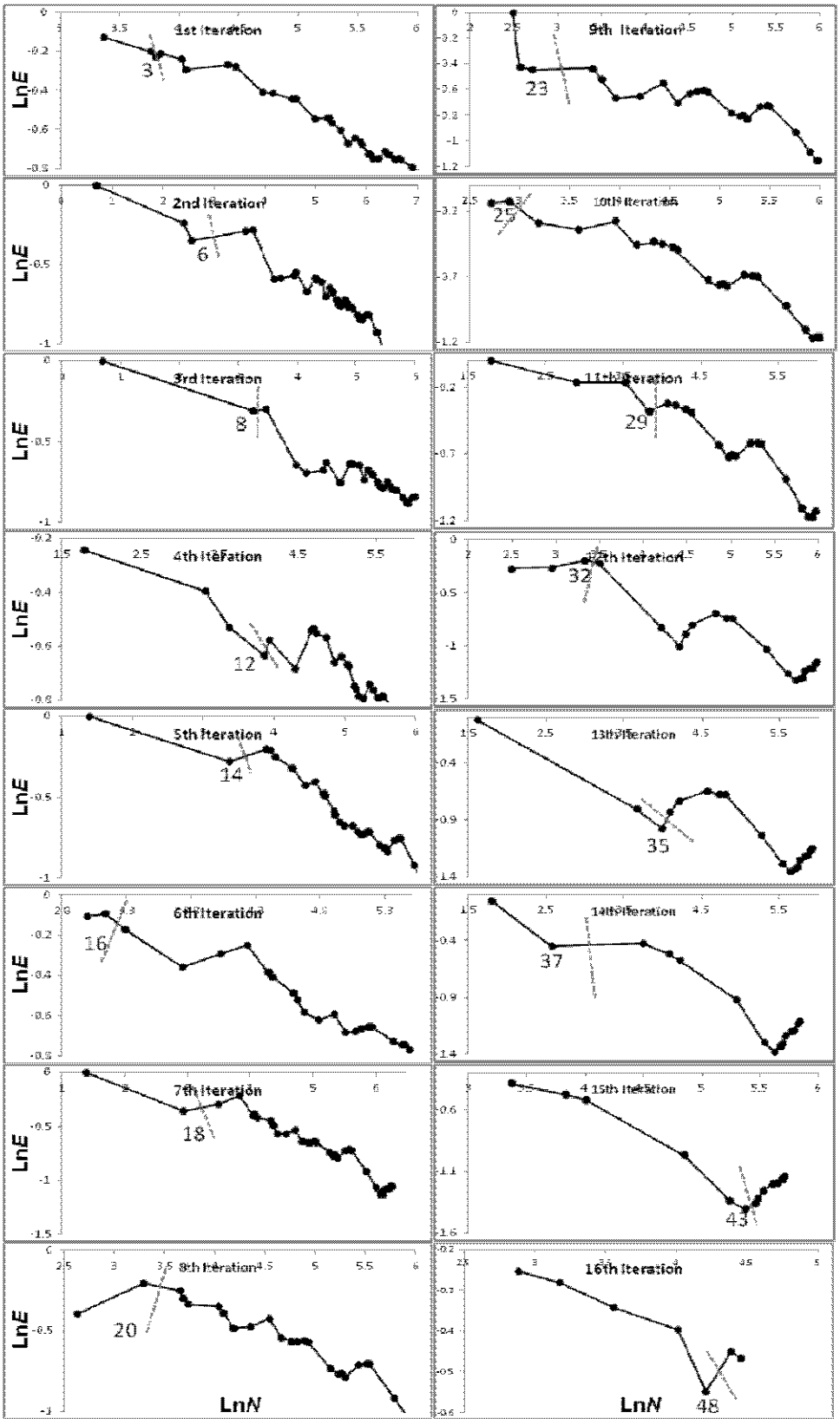


Figure 3.7: An example of the sequence of plots of calculated ln*E* (y-axis) versus ln*N* (x-axis) for the 2004 transect in Chaka canyon. The top graph shows the values calculated from the entire transect. The dotted lines indicate a slope break and thus a new biofacie. Proceeding graphs illustrate recalculated values of ln*N* and ln*E* for all samples after the slope break

Multivariate analyses (MVA)

Parametric multivariate analyses were used to both explore and classify the samples. A multivariate approach was considered appropriate as it provided a rigorous statistical framework for investigating the joint relationships between variables within the data. One particular strength of a multivariate approach is it can reduce the patterns in those data to a smaller number of dimensions while preserving most of the information in the original, higher-dimensional data. The data were subjected to both Principal Components Analysis (PCA) and Linear Discriminant Analysis (LDA).

PCA assumes that there is no structure within the data and there are no hypothesised relationships. PCA, therefore, simply studies the inter-correlations of a number of variables by clustering them into common factors. PCA reduces the dimensionality of the data by recombining different variables together and constructing new factors, which are, in turn, considered to be new variables. Each of these estimated factors then explain a component of the total variance within the data. Factor scores can also be visualised and used to investigate the existence of any underlying structure within the data that might describe groups (or classes) of observations with similar characteristics. Percentages rather than proportions were used in all analyses such that all the data, that included depth, were of similar magnitudes. A covariance matrix was used for all the PCAs.

For each PCA the biotic components of the substratum flora/fauna that were identified were allocated into 17 taxa categories. These categories included corals, gorgonians, hydroids, sponges, sea pens, echinoderms, coelacanths, other fish, ctenophores, bryozoans, urchins, anemones, algae, gastropods, crustaceans, live cover and unidentified fauna (Table 3.3).

Samples for the PCA were initially classified according to the identified SHE biofacies (Table 3.4). When the first two principal components from the PCA were visualised, the SHE biofacies were further classified from the clusters on the biplot and separate biofacies with similar invertebrate assemblages were grouped together to produce a final set of “biozones” for classification. Frames were also classified based on published habitat types of Sink et al. (2006) (Table 3.4, Figure 3.8) and according to presence or absence of coelacanths.

Table 3.4: Habitat types after Sink et al. (2006) and their descriptions, together with the seven biozone types identified from visual analysis of the still frames in different biofacies as defined by the SHE analysis and PCA, and the dominant invertebrates in each

Code	Habitat Type/Biozone	Description
		Sink et al. (2006)
1	Sand flats	Flat areas of sand above the canyon slope
2	Rocky outcrops	Rocky areas in the sand flats
3	Large rocky structures	Large isolated rocks, mainly on the canyon slopes
4	Overhangs and caves	Overhangs and caves usually within the canyon walls
5	Steep walls and cliffs	Canyon walls
6	Canyon bottom/Thalweg	Thick sediment and chipping boulders from slopes above
		This study
1	Sea pens	Sea pens dominant, mainly on sand
2	Cave invertebrates	Cave invertebrates
3	Sponges	Sponges dominant, mainly large glass sponges (*Pheronema* sp.)
4	No invertebrates	Bare sand
5	Mixed, small invertebrates	Mixture of small invertebrates. Mainly sponges, gorgonians and anemones
6	Gorgonians and sponges	Gorgonians and sponges (*Echinostylos* sp.) dominant. Wire and whip corals present.
7	Deep-water glass sponges	Deep water glass sponges (*Sclerothamnus* sp.) dominant

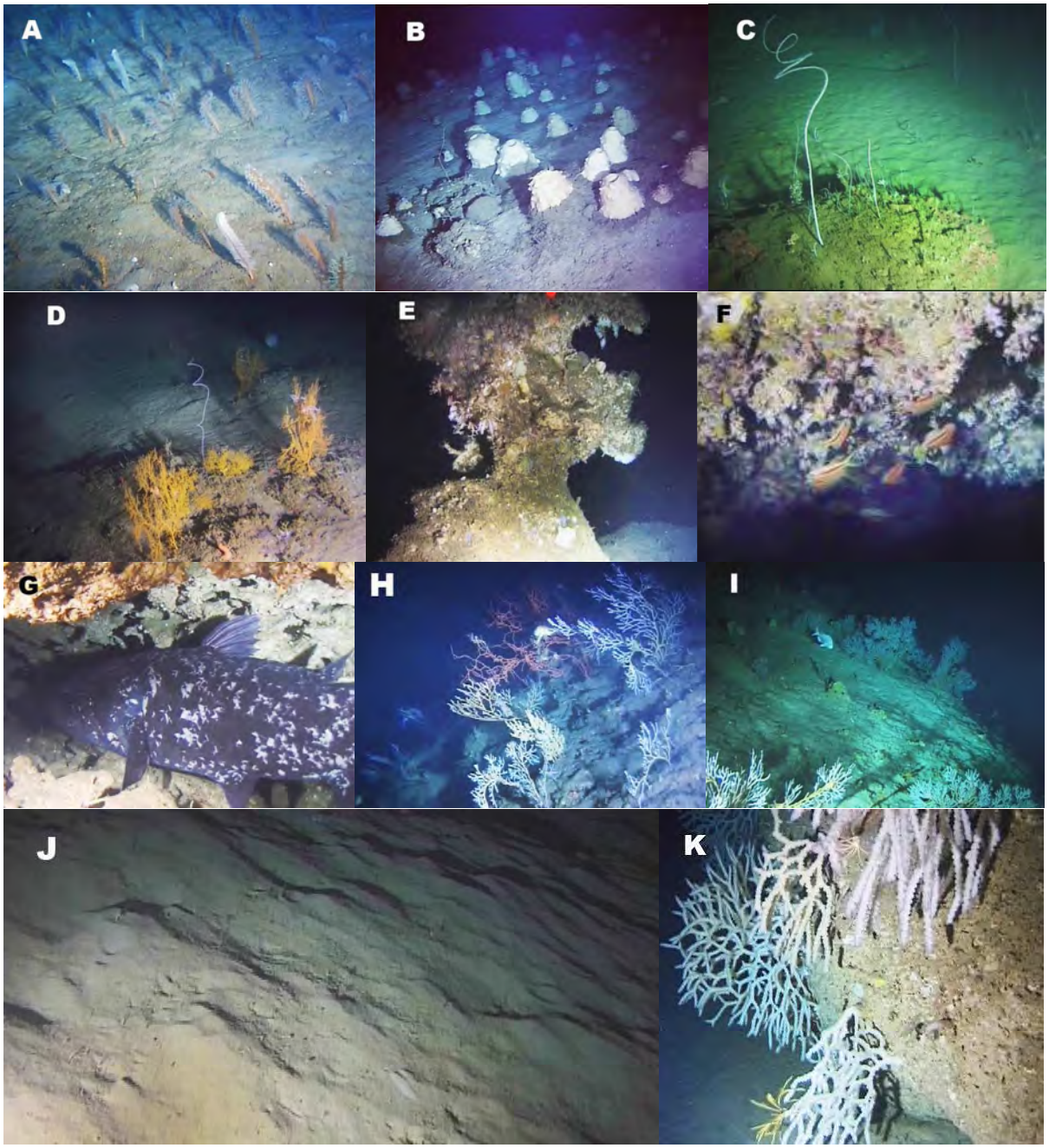


Figure 3.8: Typical examples of the pre-defined habitat types according to Sink et al. (2006) (Table 3.4). Sand flats of Habitat Type 1 (A) with sea pen forests and (B) *Pheronema* sponges, (C and D) rocky areas within the sand flats with gorgonians and corals characteristic of Habitat Type 2, (E) isolated rock structures of Habitat Type 3, (F and G) sponge encrusted roof and bare walls of the caves in Habitat Type 4, (H and I) dense growth of invertebrates on the canyon walls of Habitat Type 5, (J) bare silt and (K) chipping boulders with *Sclerothamnus* spp. sponges in the deep thalweg of Habitat Type 6

To assess whether these observed, or predefined clusters from the PCA, are indeed distinct and identifiable, they need to be statistically classified. LDA is a commonly used multivariate classification technique that assesses the statistical strength of predefined groups by means of a discriminant function. The discriminant function is a linear combination of the original variables that best separate groups such that a coefficient for each variable and a constant is calculated. SLDA results in *k*-1 discriminant functions, *k* being the number of groups, or classes, analysed. The importance of each discriminant function in the analysis is given by its canonical correlation and the total variance explained by each function. An extension to LDA is a stepwise linear discriminant analysis (SLDA). In SLDA, all possible variables are added to the discriminant function sequentially to assess the strength of the variable in being able to discriminate the different groups. Wilks' λ is used to assess the discriminatory effectiveness of the analysis (Wilks 1932). A SLDA approach can also be used as an exploratory tool to identify the good predictor variables from a range of good and weak variables. Variable selection terminates when no further increase in the accuracy of the discriminant function can be achieved. This approach singles out the significant variables which can best classify the data.

Once a set of variables has been defined, LDA is usually followed by the formulation of cross-validation classification matrices that show the number of correct categories classification success and error rates for each discriminant function. Cross-validation procedures omit the individual group being classified (i.e. n - 1) to classify the other groups, thus creating an unbiased classification matrix.

SLDA with cross validation was used to determine the classification success of the biozones, the published habitats according to Sink et al. (2006) and to assess the discriminatory effectiveness of each data set to predict coelacanth presence or absence.

The statistical environmental R (R Development Core Team 2009) was used for all analyses.

3.3 Results

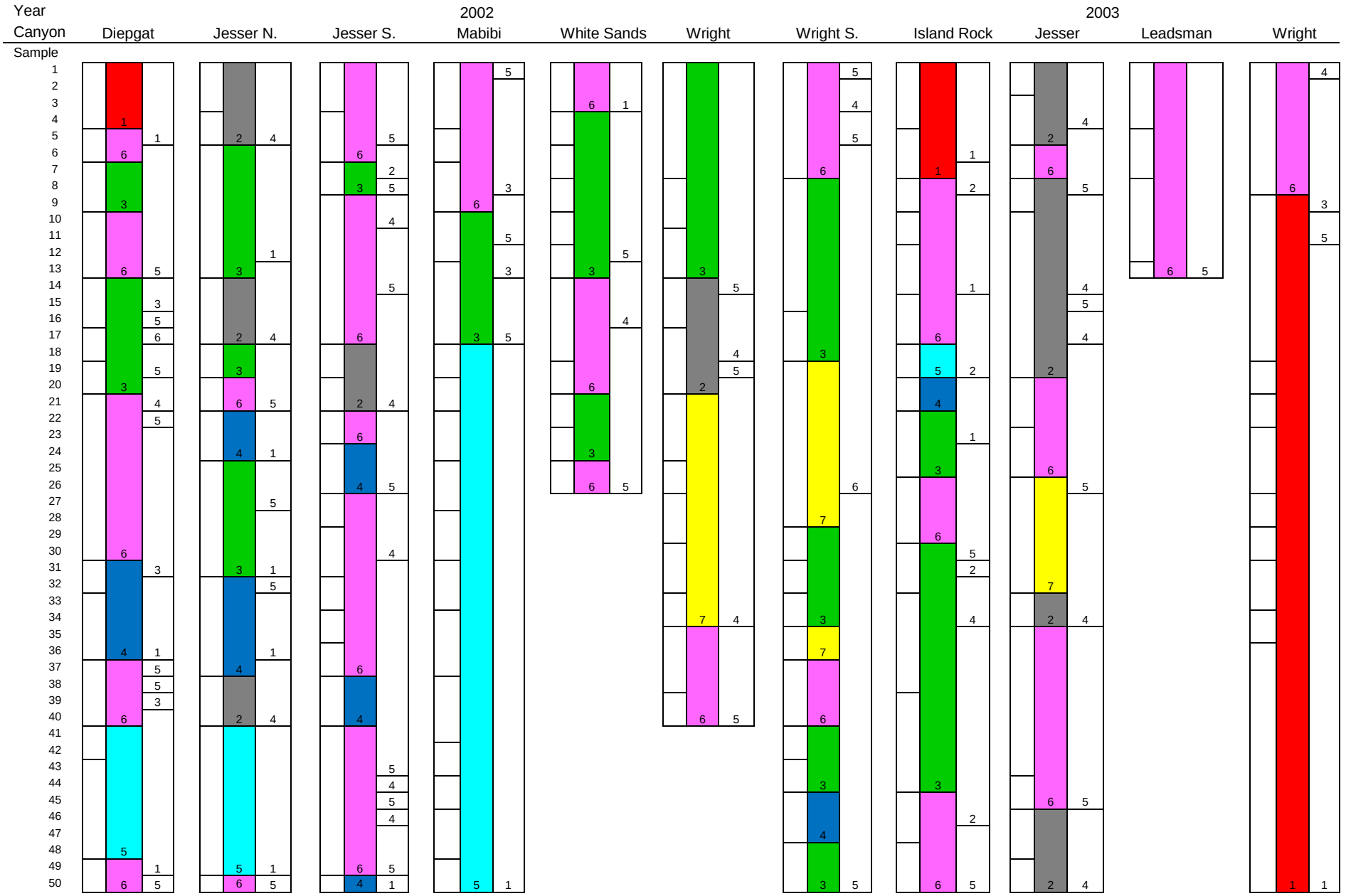
SHE Analysis

The SHE analysis was found to be particularly sensitive to changes in invertebrate composition, both in terms of changes in abundance and composition of the community assemblage. It was clear that the introduction or removal of a single species caused a slope break and therefore constituted a new biofacie (Table 3.4). While fifteen initial habitats were determined from SHEBI these were consolidated into seven final biozones after PCA by combining several similar biofacies into the same biozone according to their grouping in the ordinated plots (Table 3.5).

Principal Component Analysis

PCA was applied to each of the three different datasets. When the biotic variables were included without depth or substratum type, the first two Principal Components explained 52% of the variance within the data (Table 3.6). The strongest loadings in the first Principal Component were sponges, gorgonians and sea pens, and in the second Principal Component gorgonians, sponges and sea pens. After the inclusion of depth, the first two Principal Components explained 85% of the variance, with depth being the strongest loading in the first Principal Component. The second Principal Component's strongest loadings were sponges, gorgonians and sea pens. With the additional inclusion of substratum type, the variance explained by first two Principal Components dropped to 74%. Depth loaded strongly in the first Principal Component, with sand, rock and sponges having the next strongest loadings. In the second Principal Component, the strongest loadings were sand, rock and depth.

Table 3.5: The "biofacies" from SHE analysis, the Biozones 1 to 7 (corresponding to Table 3.4) determined by PCA in the middle columns and the pre-defined habitat types after Sink et al. (2006) in the right hand columns. Canyons were sampled from 2002 to 2005. Samples refer to consecutive still frames



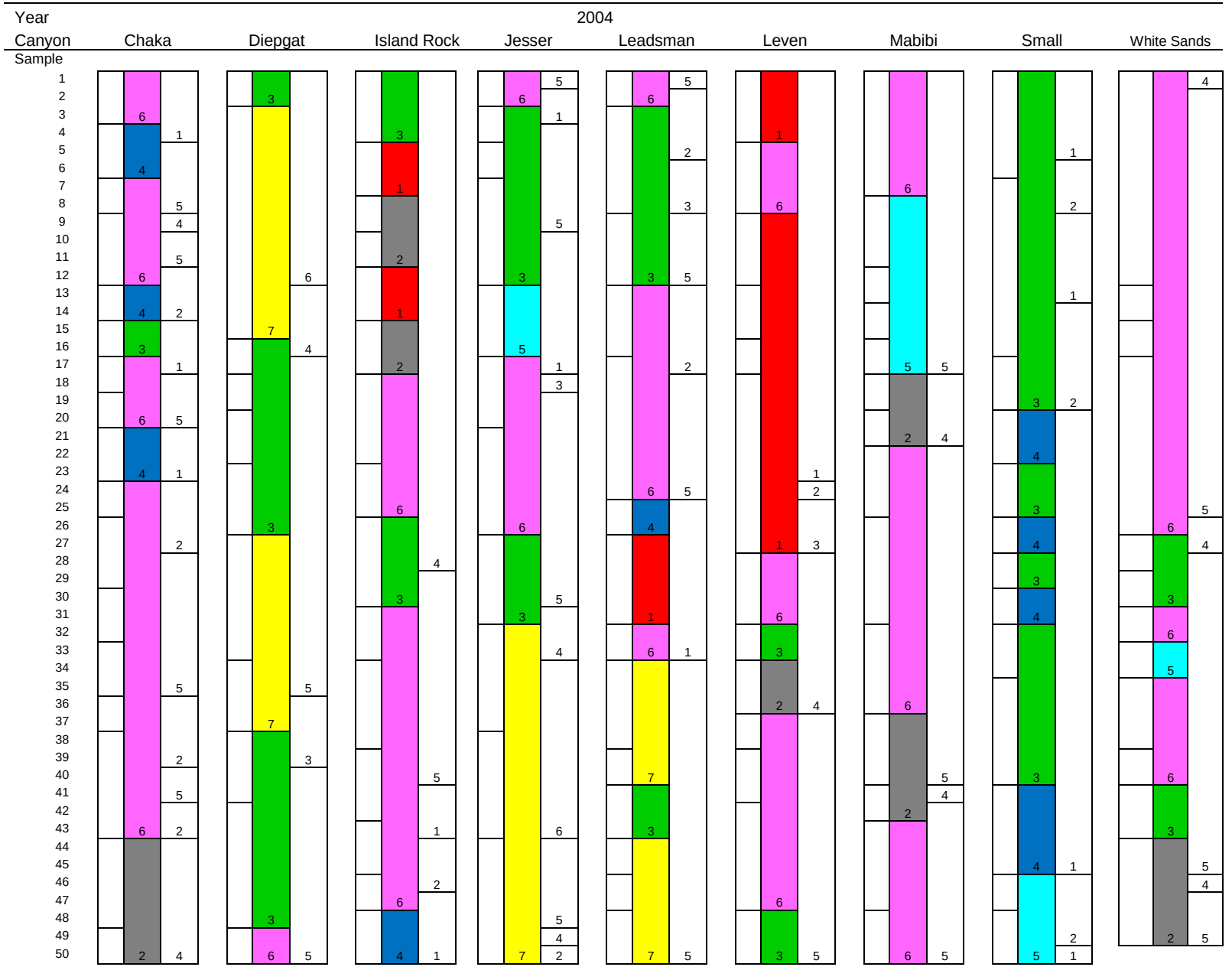

Year
2004
Canyon
Chaka
Diepgat
Island Rock
Jesser
Leadsman
Leven
Mabibi
Small
White Sands
Sample

Table 3.6: Principal Component (PC) loadings, standard deviations, eigenvalues and explained variance of the first two Principal Components from the three different datasets analysed. Bold values indicate major (> |0.10|) loadings

	Dataset 1		Dataset 2		Dataset 3	
Variable	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
Depth	-	-	**1.00**	0.08	**0.95**	**0.25**
Coral	0.04	-0.01	-0.01	0.04	-0.01	0.00
Gorgonians	**0.35**	**-0.89**	-0.04	**0.32**	-0.03	-0.06
Hydroids	0.00	0.00	0.00	0.00	0.00	0.00
Sponges	**-0.93**	**-0.30**	0.06	**-0.94**	0.07	**-0.12**
Sea Pens	**0.13**	**0.29**	-0.05	0.10	-0.05	0.05
Echinoderms	0.02	-0.03	-0.01	0.01	0.00	0.00
Fish	0.00	0.00	0.00	0.00	0.00	0.00
Coelacanth	-0.01	0.07	-0.01	-0.02	-0.01	-0.03
Ctenophore	0.00	0.00	0.00	0.00	0.00	0.00
Bryozoans	0.00	0.03	0.00	-0.01	0.00	-0.01
Urchins	0.00	0.00	0.00	0.00	0.00	0.00
Anemones	0.00	0.00	0.00	0.00	0.00	0.00
Algae	0.00	0.00	0.00	0.00	0.00	0.00
Gastropods	0.00	0.00	0.00	0.00	0.00	0.00
Crustaceans	0.00	0.00	0.00	0.00	0.00	0.00
Live cover	0.03	**-0.14**	-0.01	0.02	-0.01	0.01
Unknowns	0.01	0.00	0.00	0.00	0.00	0.00
Rock	-	-	-	-	**0.13**	**-0.64**
Sand	-	-	-	-	**-0.22**	**0.70**
Silt	-	-	-	-	**0.15**	**0.11**
Standard deviation	17.9	13.5	55.3	17.5	56.8	41.1
Eigenvalues	322	182	3056	305	3225	1689
Total variance (%)	36.5	20.6	78.1	7.8	48.6	25.4
Cumulative variance (%)	36.5	57.2	78.1	85.9	48.6	74.0

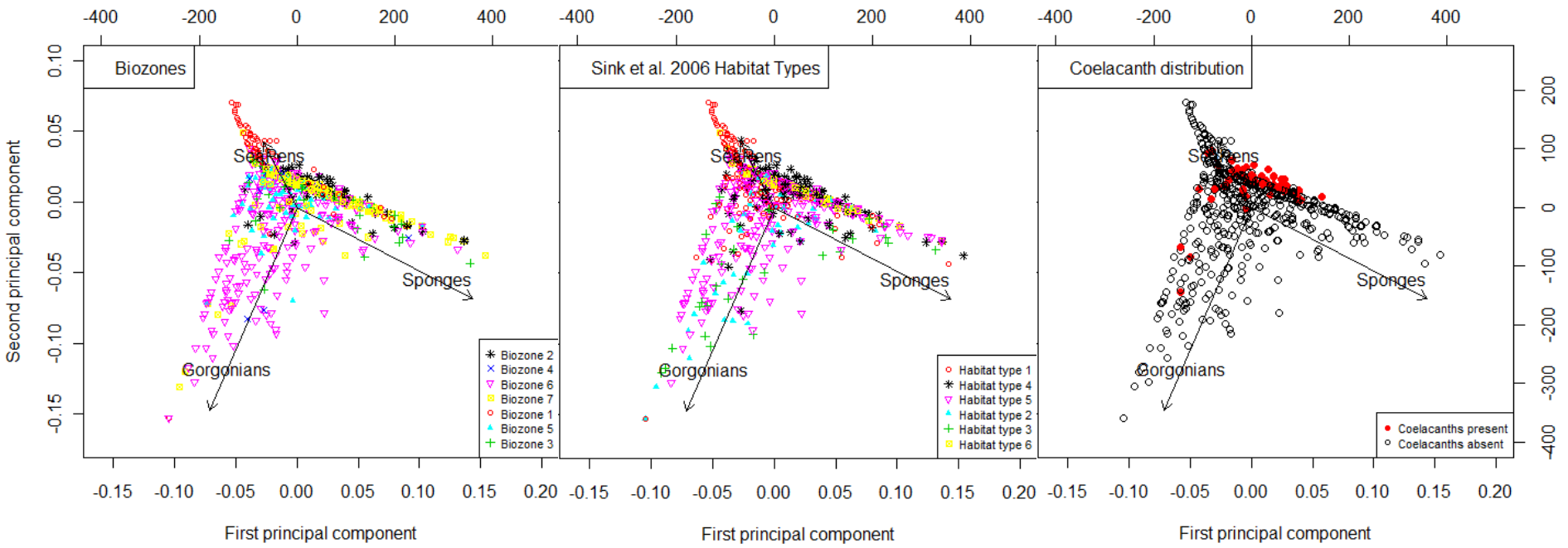


Figure 3.9: Principal Components Analysis of the proportional cover of different invertebrate taxa from the ten canyons in iSimangaliso Wetland Park (IWP). The ordinated plots illustrate sample scores and the seven different Biozones obtained from either SHEBI (left), the six habitat types defined by Sink et al. (2006) (middle), and coelacanth presence or absence (right). The arrows represent those variables with the highest loadings that, when combined, explain the most variation within the data

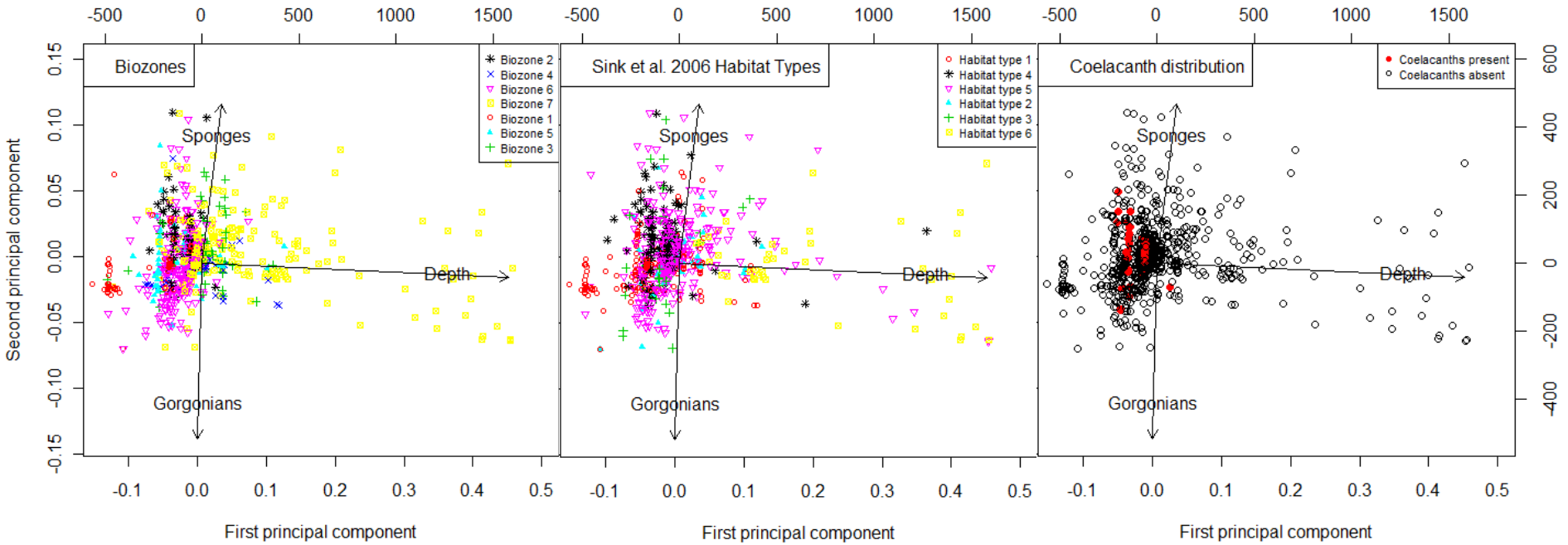


Figure 3.10: Principal Components Analysis of only the biotic variables with depth included from the ten canyons in iSimangaliso Wetland Park (IWP). The ordinated plots illustrate individual sample scores and the seven different Biozones obtained from either SHEBI (left), the six habitat types defined by Sink et al. (2006) (middle), and coelacanth presence or absence (right). The arrows represent those variables with the highest loadings that, when combined, explain the most variation within the data

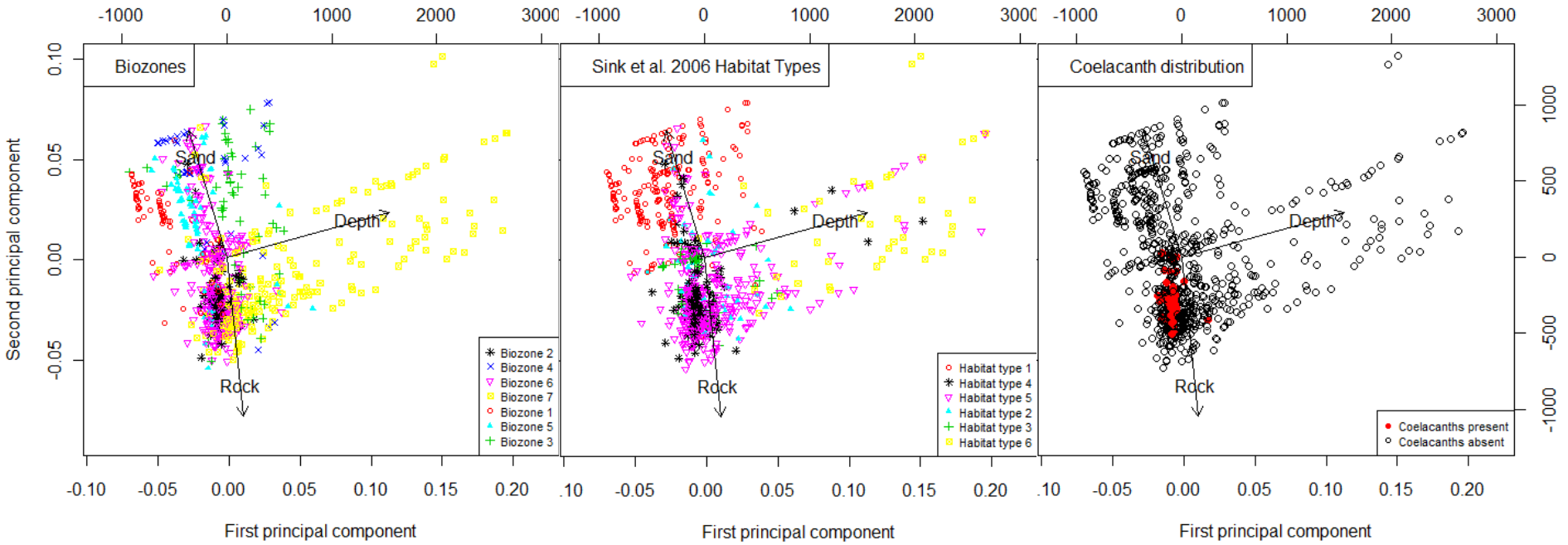


Figure 3.11: Principal Components Analysis of only the biotic, abiotic variables and depth from the ten canyons in iSimangaliso Wetland Park (IWP). The ordinated plots illustrate individual video still frame scores and the seven different Biozones obtained from SHEBI (left), the six habitat types defined by Sink et al. (2006) (middle), and coelacanth presence or absence (right). The arrows represent those variables with the highest loadings that, when combined, explain the most variation within the data

When the first two Principal Components were ordinated according to the Biozones, the importance of the substratum type and depth was apparent. In Figures 3.10 and 3.11, Biozones 3, 5, 6 and 7, corresponding to habitats dominated by sponges, mixed and small invertebrates, gorgonians and deep-water sponges, clustered together biologically (Figure 3.9) separated out into more defined groups with the addition of depth in the analysis. The addition of substratum type further defines Biozones 4 (invertebrateless sand) and 5 (mixed small invertebrates) from Biozone 6 (gorgonians and sponges), pulling Biozone 5 upwards corresponding with the loadings for sandy substratum and 6 downwards, corresponding with the loadings for rocky substratum (Figure 3.10). Biozone 1, sea pen-dominated sand flats, clustered in all three of the PCA models as there was a biotic and substratum component to the biofacie. Biozone 7, deep-water sponges, shows a clear separation corresponding with the loadings for depth (Figures 3.10 and 3.11).

With the habitats classified according to Sink et al. (2006), most habitats show some degree of overlap except for Habitat Type 1, sand flats, which is well-defined in all three of the PCAs. Habitat Types 2 (rocky outcrops), 3 (large isolated rocks), 4 (overhangs and caves) and 5 (canyon walls) are clustered together and were indistinguishable by either substratum type. However when depth is included as an additional variable, Habitat Type 6, the thalweg, and Habitat Type 1, sand flats, both ordinated out as well-defined clusters corresponding with the strong loadings on depth and sand, respectively (Figure 3.11).

When the first two Principal Components were ordinated according to coelacanth presence or absence it is apparent and not surprising that coelacanths were found in the caves of Biozone 2 that are dispersed amongst Biozone 6 along the canyon margin and upper walls. These are rocky environments and all three datasets clearly show the association of coelacanth presence with Biozone 2, regardless of inclusion of depth or substrate (Figures 3.9 to 3.11).

Table 3.7: Wilk's λ values associated with individual biotic and abiotic variables that were identified by stepwise linear discriminant analyses having the greatest influence to discriminate between classes, both for the Biozones and the Habitat types defined by Sink et al. (2006). The three most important variables are denoted in bold. All statistics were significant at $p < 0.01$

	Dataset 1		Dataset 2		Dataset 3	
Variable	SHE	Sink et al.	SHE	Sink et al.	SHE	Sink et al.
Depth	-	-	**0.27**	**0.52**	**0.17**	**0.17**
Coral	0.22	0.37	0.15	0.19	0.11	0.09
Gorgonians	**0.25**	0.49	0.17	0.26	0.10	0.09
Hydroids	0.16	0.36	0.11	0.19	0.08	0.07
Sponges	0.19	0.44	0.14	0.23	0.09	0.08
Sea Pens	**0.41**	**0.63**	**0.41**	**0.33**	**0.41**	0.11
Echinoderms	0.16	0.41	0.11	0.22	0.08	0.09
Fish	0.16	0.37	0.12	0.20	0.08	0.08
Coelacanths	**0.29**	**0.75**	**0.20**	**0.39**	0.12	**0.13**
Ctenophores	0.15	0.38	0.11	0.20	0.08	0.08
Bryozoans	0.17	0.42	0.12	0.22	0.08	0.08
Urchins	0.16	0.36	0.12	0.19	0.08	0.08
Anemones	0.17	0.36	0.12	0.19	0.09	0.08
Algae	0.18	0.38	0.13	0.20	0.09	0.08
Gastropods	0.15	0.36	0.11	0.21	0.08	0.08
Crustaceans	0.15	0.40	0.11	0.19	0.08	0.08
Live cover	0.15	**0.54**	0.11	0.29	0.08	0.10
Unknown biota	0.16	0.39	0.11	0.21	0.08	0.08
Rock	-	-	-	-	0.08	0.08
Sand	-	-	-	-	**0.25**	**0.32**
Silt	-	-	-	-	0.08	0.08

Linear Discriminate Analysis

The results from the substratum type classification using SLDA (Table 3.7) were similar to those from the PCA with the most significant variables corresponding with those with the strongest loadings in the PCA. For example, Biozone 1 and Sink et al.'s (2006) Habitat Type 1 were the most easily discriminated from the general data cluster due to a dominance of sea pens. Depth was overwhelmingly dominant in the second and third PCA and was similarly important to the SLDAs (Table 3.7).

For the classification of the Biozones (Table 3.8), Biozones 6 and 7 appeared to have to most successful classification for all three datasets. The most successful dataset included abiotic, biotic variables and depth, averaging a 62% success rate, where the most important variables for discriminating between Biozones were gorgonians, sea pens and coelacanths. In the second dataset, the most important variables were gorgonians, echinoderms, coelacanths, algae, and depth. For the third dataset, the important biotic variables were gorgonians and coelacanths, and the abiotic variables were depth and sand.

The highest success rate overall was seen for the habitats defined by Sink et al. (2006) in the third model with a 69% classification success rate. Habitat Types 1 (sand flats) and 5 (canyon walls) showed the best classification in all three models investigated (Table 3.8). In the first and third dataset, the habitats defined by Sink et al. (2006) had a higher success rate than the Biozones determined through SHEBI and PCA. The second dataset explained the most variance from the PCA (Table 3.6) with the Biozones being better classified (Table 3.8).

Table 3.8: Classification success rate for the stepwise linear discriminant analysis (SLDA) performed on the different pre-defined habitat types. The seven Biozones and six habitat types as defined by Sink et al. (2006) for the three datasets and the overall classification success for both Biozones and Sink et al. (2006) habitat types classification schemes for each dataset. The two most successfully classified classes for each set of habitats are denoted in bold

		Dataset 1		Dataset 2		Dataset 3	
		Biozones	Sink et al.	Biozones	Sink et al.	Biozones	Sink et al.
Per Habitat type (%)	1	6.5	**6.7**	6.8	**7.9**	6.2	**23.6**
	2	4.6	0.0	4.7	0.0	4.7	0.0
	3	0.0	2.3	0.0	2.3	0.7	0.0
	4	0.0	6.1	0.0	6.1	4.1	6.1
	5	0.0	**39.1**	0.8	**36.8**	2.7	**35.7**
	6	**18.0**	0.0	**32.1**	3.6	**28.7**	3.6
	7	**21.8**		**14.2**		**14.9**	
Overall (%)		51.0	54.1	58.6	56.7	62.0	69.0

Table 3.9: Classification matrix of the final stepwise linear discriminant analysis (SLDA) performed on the coelacanth presence/absence data using all variables (all biotic variables, depth and substratum type). The correct classifications are on the diagonal (in bold)

	Absent	Present	Total
Absent	**759**	9	768
Present	12	**46**	58
Proportion correct (%)	98.8	79.3	

When the data were classified according to coelacanth presence or absence, the results from the SLDA indicated that coelacanth presence cannot be classified by biotic variables and depth alone as the data from datasets where substratum was not included in the analyses could not be classified. The inclusion of the underlying substratum, however, has a classification success rate of 97.5% (Table 3.9). The most significant variables in discriminating between coelacanth presence and absence were either geological (sand, rock and silt) or biological (gorgonians and sponges) (Table 3.10). Depth was also an important variable.

Table 3.10: Wilk's λ values associated with individual habitat variables that were identified by stepwise linear discriminant analyses having the greatest influence to discriminate between coelacanth presence and absence. The six most important variables are denoted in bold. All statistics were significant at $p < 0.01$

Variable	Coelacanth presence/absence
Depth	**0.95**
Coral	0.52
Gorgonians	**0.93**
Hydroids	0.39
Sponges	**0.92**
SeaPens	0.67
Echinoderms	0.4
Bryozoans	0.84
Urchins	0.39
Anemones	0.4
Livecover	0.79
Rock	**0.88**
Sand	**0.97**
Silt	**0.91**

3.4 Discussion

The structure of the physical habitat plays an important role in structuring invertebrate communities in submarine canyons (Friedlander and Parrish 1998, Ramirez-Llodra et al. 2010) and on deep reefs (Rivero-Calle et al. 2008). Depth is also known to structure benthic communities on a larger spatial scale (Cartes et al. 2009). When the physical structure of the IWP's canyons was investigated, there are three clear structural components - shallow areas outside the canyons, the canyon walls and margins, and the deep thalweg that was characterised by thick sediment and large boulders (Sink et al. 2006). Sink et al.'s (2006) habitat classification was based mainly on these geological differences in substratum type. The biofacies determined through SHE analyses were based primarily on biological structure, with depth and substratum type included in the MVA. This explains why Sink et al.'s (2006) habitat types generally showed better classification success than the Biozones. The results of both the PCA and the SLDA suggest that although substratum type significantly influences invertebrate community structure in the canyons, it is depth that is the principal factor. Biozones also separate out into the three canyon zones when depth is accounted for. Biozones dominated by sea pens and a mixture of small invertebrates were found in the shallower areas outside the canyons. Biozones displaying a mixture of gorgonians and sponges occurred on the canyon margins and walls and the Biozone sparsely colonized by the deep water *Sclerothamnus* spp. sponges were found mainly in the deeper thalweg. When substratum type is included in the analysis, better division is noted between the four Biozones found around the canyon margin. Generally classification success according to the SLDA increased when abiotic factors and depth were included, showing the importance of both these factors in structuring invertebrate distribution within the canyons. Coelacanth presence and absence showed the best classification success of 97.5% and illustrated those habitats associated with coelacanths to be mainly within rocky caves and surrounding steep slopes, dominated by gorgonians and sponges.

SHE analysis has been shown to be sensitive to small changes in species composition (Mana 2005). This was noticeable in this study where the addition or removal of even a single species from the analysis produced a slope break and thus a new biofacie. Fortunately, these changes were often

not significant enough to warrant classification of a new biozone. The use of multivariate analysis in conjunction with SHEBI provided a more rigorous analytical framework whereby similar biofacies from the SHEBI can be ordinated into the same biozone using PCA, thus clarifying where slope breaks were representing significant biozone changes or simply a change in species within a biozone.

Both the published habitat types according to Sink et al. (2006) and the Biozones were poorly classified with a success rate of between 54% to 69%, and 51% to 62%, respectively. The best classification success was recorded with the inclusion of both depth and substratum type in the analyses despite the PCA explaining less variability in the data. This was probably due to the high degree of overlap in invertebrate types within the different classified habitat types, and as with most statistical analysis, the inclusion of additional covariates. For example, the rocky areas amongst the shallow sand flats supported the same community structure as the canyon margins and isolated rocky structures within the canyons. In addition, sea pens were found mainly along the sandy flats, but were also encountered throughout the depth distribution in the study such as on the thalweg, the floor of the underwater canyons, and in the sandy substratum forming the bottom of some caves within the canyons.

The most successful classified habitat types were Sink et al.'s (2006) Habitat Type 5 with a success rate of between 35 and 39%, and SHE's Biozone 6 with between 18 and 32% success rate over all three models. Both these habitats refer to the canyon margin where dense agglomerations of invertebrates are found. The percentage invertebrate cover on the canyon margin of Wright canyon was estimated as high as 80% (Sink et al. 2006). Although classified according to its distinct invertebrate assemblages, the canyon margins where these habitats typically occur are at a standard depth throughout the canyons.

The deep regions of the canyons were characterised by thick, unstable sediments. The influx of large amounts of sediments from the upper regions of the canyon has been found to greatly reduce the diversity in the deep sections of canyons (Rowe 1971). This habitat is dominated by the massive glass sponges *Sclerothamnus* sp. that are found only on rock but encountered through a wide depth

range from 128 - 380 m on the lower canyon walls and boulders in the deep thalweg, depths below the typical distribution of the filter feeders of the canyon margin. The lack of other species at these depths could be due to the reduced feeding effectiveness of filter feeders from upper regions when covered by sediment at frequent intervals.

Depth and substratum type are not the only factors driving distribution of invertebrates in canyons as the current regimes within submarine canyons have been found to have both direct and indirect effects on invertebrate distribution patterns (Rowe 1971) through the distribution of particulate organic matter (Hughes et al. 1999). Although submarine canyons vary in their structural complexity, they act as traps for detrital material from both the continental shelf and further offshore and can, as a result, support high densities of filter feeders (North 1964, Vetter and Dayton 1999, UNEP 2006, Christiansen 2010, Ramirez-Llodra et al. 2010). A dense community of gorgonians, echinoderms, wire corals and sponges was typically distributed along the canyon margins and walls. Previous studies also indicate that these filter feeders (Branch et al. 2005) are significantly more abundant in this region of the IWP canyons than on the shallower scattered reef outcrops outside the canyons (Sink et al. 2006). The concentration of these species along canyon margins could be indicative of some upwelling from the canyons causing a rise in primary production and thus an increase in food concentrations in the water column.

Gorgonians and sponges are believed to be out-competed by scleractinian corals and zooxanthellate octocorals in shallower reefs (Williams 1993, Sink et al. 2006) because they rely only on organic matter in suspension in the water column whereas shallow water species have zooxanthellae and can utilize both sunlight and filter feeding (Ramirez-Llodra et al. 2010). The reduced sunlight associated with increasing depth in the canyons would hinder photosynthetic species thus allowing the gorgonians and sponges, taxa that do not rely on sunlight, to take advantage of filter feeding and thus dominate.

Weak currents have been recorded in the caves within the canyons (Ribbink and Roberts 2006). Gorgonians, echinoderms and sponges were the most common invertebrates found around the

caves and on the surrounding slopes although gorgonians and echinoderms were virtually absent from the caves. This could be explained by their filter feeding habits as they are passive feeders which rely on either water movements or the sinking of particles due to gravity to supply them with food (Branch et al. 2005). With the virtual absence of water movements within the caves, the amount of nutrients available for filter feeders would be reduced.

Mobile species such as echinoderms can take advantage of temporal and spatial variations in nutrient levels within canyons (Cartes et al. 2009, Ramirez-Llodra et al. 2010). While little or no current has been observed during submersible dives by Roberts et al. (2006), ripples were observed on soft substratum along the canyon margins and floor suggesting the presence of occasional strong currents, similar to those observed in Oceanographer Canyon on the Georges Bank, USA (Valentine et al. 1980). It has been noted that canyons, in general, have complex hydrographic regimes that influence their invertebrate communities (Ramirez-Llodra et al. 2010). The observed patchy distribution of these organisms, especially crinoids and ophiuroids along some areas of the canyon walls suggests that these species may move to take advantage of varying food availability. These fluctuations in water flow through the canyons would also determine prey availability for filter feeders and could drive the short term distributions of mobile organisms such as echinoderms.

Coelacanths were only associated with caves within the steep rocky canyon walls. It is known that coelacanths shelter in caves during the day (Fricke et al. 1991, Venter et al. 2000) possibly to reduce their metabolism to avoid respiratory stress (Hughes and Itazawa 1972, Hughes 1976, 1980) and to avoid bright light. Although coelacanths are known to make excursions to greater depths to search for prey during the night (Fricke et al. 1991, Fricke and Hissmann 2000, Hissmann et al. 2000) no coelacanths were found in the deepwater thalweg or along the deeper parts of the canyon walls. This could possibly be a sampling artifact as most of the video footage was recorded during the day when coelacanths are usually sheltering in caves (Fricke et al. 1991). During the night when coelacanths are more active and forage at deeper depths (Uyeno and Tutsumi 1991, Fricke and Hissmann 2000) no video footage was available.

It is apparent that there are several clear community types associated with the submarine canyons in the IWP. In terms of this study it would appear that the EFH for coelacanths would be constrained to caves and the steep canyon slopes surrounding the caves. To define caves as the complete EFH for coelacanths, fulfilling all the physical and biological requirements for "spawning, breeding, feeding, or growth to maturity" that define the requirements of an EFH (NOAA 1999, p4) would be inaccurate and myopic given the lack of information regarding their spawning, breeding and feeding requirements. Although one individual coelacanth was recorded at 54 m during an upwelling episode (Hissmann et al. 2006), generally the higher temperatures and greater current velocities (Roberts et al. 2006) associated with the shallower sand flats outside the canyons regions would restrict coelacanths to within the canyons, thus potentially allowing regions outside the canyons to be excluded from coelacanth-specific EFH.

To conclude, it is recommended that future studies investigating coelacanth habitat should concentrate on more rigorous sampling of invertebrates in order to better understand the distribution, abundance and biodiversity of animals within the deeper reef habitats. A statistically defensible sampling design should facilitate better analyses of the relationships between the habitats and their associated biodiversity. These future studies should include multiple depth strata and within these, all representative habitat types should be sampled. Transects should also be standardised between canyons. Areas in the same regions where coelacanths are not found need to be sampled in order to compare presence and absence data. In terms of further "coelacanth" research, it is important that a comprehensive analysis of their habitat and associated invertebrates, as well as interspecific relationships is performed, to both aid the search for new populations and to help to determine management plans for the conservation of ecosystems where known populations of coelacanths exist.

Chapter 4

Predicting coelacanth, *Latimeria chalumnae*, daytime distribution using classification trees

4.1 Introduction

Understanding the relationship between a species and its environment such that its distribution can be predicted is important particularly with respect to contemporary research being focussed on climate change (Guisan and Zimmermann 2000, De'ath 2002, Elith et al. 2006). For sensitive or endangered species occupying narrow niches an understanding of this species-environment relationship can assist in conservation planning and management (Pearce and Ferrier 2000a, Rushton et al. 2004, Elith et al. 2006), and for determining those factors affecting its present and future distribution patterns (Ricklefs 2004, Elith et al. 2006). Several predictive statistical models have been used to predict a species' occurrence or distribution. Applications include models applied to wildlife (Buckland and Elston 1993, Mace et al. 1999, Manel et al. 1999, Mladenoff et al. 1995, 1999, Pearce and Ferrier 2000b), fish (Lek et al. 1996, Mastrorillo et al. 1997, Guisan and Zimmermann 2000), benthic invertebrates (Bailey et al. 1998) and to both terrestrial (Carpenter et al. 1993, Guisan et al. 1999, Guisan and Zimmermann 2000) and aquatic plants (Lehmann et al. 1997, Lehmann 1998, Guisan and Zimmermann 2000).

Statistical models range from classical techniques such as generalised linear models (GLM, McCullagh and Nelder 1983), generalised additive models (GAM, Hastie and Tibshirani 1990) and generalised regression analysis (Lehmann et al. 2003), environmental envelopes, and machine learning methods that synthesise classification functions (Garzón et al. 2006). Machine learning methods and classification and regression trees (CART, Breiman et al. 1984), are used to predict the value of a dependent variable based on a set of explanatory variables (Džeroski and Drumm 2003) using a series of binary splits utilising one variable at a time and have been found to produce more

accurate predictions than either GLM or GAM when applied to complex data (Franklin 1998, Vayssiéres et al. 2000). Their strengths include them being better suited to processing the non-linear relationships, lack of balance and high-order interactions that often arise between environmental variables (De'ath 2002). Different CART techniques have been successfully used in a variety of ecological studies (Usio et al. 2006) with applications including the determination of habitat preferences of marine invertebrates (Džeroski and Drumm 2003), mammals (Debeljak et al. 2001), birds (Seoane et al. 2005), plants (Franklin 1998, Vayssiéres et al. 2000), and in predicting species distribution (Olden and Jackson 2002, Usio et al. 2006), composition (Magnuson et al. 1998) and richness (Pittman et al. 2007). Predictive CART models have also been employed in plant pathology (Baker 1993) and wildlife management (Grubb and King 1991).

Coelacanths are critically endangered (IUCN 2011) and need to be conserved. Owing to their dispersed distribution and preference for depths >100 m they are also both difficult and expensive to locate and investigate within their natural environment. If coelacanths are to be easily and quickly located, those areas with suitable coelacanth habitat must be determined to narrow down searching areas. The physical characteristics of suitable coelacanth habitats have already been determined. What is known is that they prefer areas with rugged topography and numerous caves in which to shelter from currents (Fricke et al. 1991) and within water temperatures between 16 and 20˚C (Fricke et al. 1991, Hissmann et al. 1998, Hissmann et al. 2006). Based on this information, Green et al. (2009) suggested potential areas where they might be located based on shelf topography. These areas include between Olumbe and Port Amelia in northern Mozambique, and the coastline from Port St John's to Port Shepstone in South Africa (Green et al. 2009). Owens et al. (2011) extended the analysis using an ecological niche model that incorporated the realised niches of coelacanths and oceanographic data. Additional predicted coelacanth habitat included the Seychelles, the Mascarene archipelago, and the Malay Archipelago. These areas are still, unfortunately geographically large areas to search. An alternative approach would therefore be to predict their distribution within these predicted localities.

Including biological requirements in terms of associated invertebrates and fish would enable search areas to be better defined. In this chapter depth, substratum type and densities of associated biota will be used to predict coelacanth presence and absence in the canyons in the IWP using CART. CART was considered to be the preferred predictive method as tree models produce better predictions than GLM or GAM when modelling complex data with multiple variables (De'ath 2002) as they use non-parametric models which, unlike parametric models, do not rely on assumptions of variable distribution patterns or require transformations of data (Usio et al. 2006).

4.2 Materials and methods

Data

Data used the analysis were the set of still frames extracted and analysed in Chapter 3.

Data analysis

Classification and regression trees (CART)

Classification and regression trees (Breiman et al. 1984) explain the effect of one or more explanatory variables on a single response variable that can either be categorical, where a classification tree is constructed, or numeric, where a regression tree is constructed. CART models are produced by repeatedly splitting the dataset into two mutually exclusive groups based on a single explanatory variable at each split. Each group is labelled by the categorical response variable, or mean value of the numeric response variable, together with the size of the group and the values of the defining explanatory variable (De'ath and Fabricius 2000) as measured by the Gini index (Breiman et al. 1984). Splitting continues until further splits no longer reduce the Gini index. The Gini index is defined as $G = \sum_{k=1}^{K} p_k (1 - p_k)$ where p_k is the proportion of observations at the node in

the k^{th} class of K classes. The index is minimised when one p_k is 1 and all other are 0 (when the node is "pure"), and is maximised when all p_k values are $1/K$ (when all observations are spread equally across all K classes). The resulting model is in the form of a tree with binary splits along each variable forming nodes (Garzón et al. 2006). There are two steps to constructing the model. A complex or "overfitted" tree is initially constructed from the entire dataset. This complex tree is then "pruned" into a simpler form containing only those explanatory variables that best describe the response variable using cross-validation (Usio et al. 2006).

Random forests (RF, Breiman 2001) is an alternative classification tree approach where many trees are fitted to a dataset to produce a "forest" and then the predictor values from all the trees are combined, using different bootstrapped replicates of the data, to produce nodes that are split according to the best split of all the variables tested. RF characteristically produces accurate predictions without overfitting the data (Prasad et al. 2006, Cutler et al. 2007). Bootstrap samples leave out sections of the original data, termed "out-of-bag" (OOB) observations. Because these OOB observations are not used in the fitting of the tree, they can be used as accuracy estimates for cross-validation of the tree. Through this, RF can produce a value for variable importance, calculated from the contribution each variable makes at each of the nodes in the tree where it is used (Cutler et al. 2007).

Coelacanth presence or absence was used as the classification response variable. Percentage cover of the biotic habitat, percentage substratum type and depth were the explanatory variables.

The analysis approach taken in this chapter was to calculate the importance of the explanatory variables by constructing a RF for each of the datasets. The most appropriate model was selected based on the lowest OOB error rate and *k*-statistic, and the highest predicted class-dependent accuracy (Cohen 1960). The *k*-statistic was calculated through confusion matrices (Table 4.1) as:

$$k = \frac{D - Q}{n - Q} \quad \text{where} \quad D = TP + TN\,, \quad Q = \frac{(TP + FP)(TP + FN) + (FN + TN)(FP + TN)}{n},$$

TP are the true positives, FP are the false positives, TN are the true negatives, FN are the false negatives, and n the overall number of classes.

Variable importance was assessed using the OOB observations and the Gini index. As the Gini index indicates the impurity of a tree, the decrease in the Gini index was used as an additional measure of variable importance. Every time a split of a node is made on a certain variable the Gini index decreases and the tree becomes more "pure". The Gini index for the two resulting nodes is less than the original node. Variable importance can thus be assessed by adding up the Gini index decreases for each individual explanatory variable over all trees in the forest where the most important variable will show the greatest overall decrease in Gini index.

A classification tree was then constructed from the set of variables that produced the most accurate RF model with cross-validation used to determine the optimal number of terminal nodes for the pruned tree. Optimal tree size, or the number of terminal nodes, was determined following leave-one-out cross-validation where the dataset is split into subsets that are left out one at a time to determine average deviance along increasing tree size (Venables and Ripley 1999).

All analyses were conducted in *R* (R Development Core Team 2009) with the packages *randomForest* (Liaw and Wiener 2002) and *tree* (Ripley 2011).

4.3 Results

Random forests

A total of 400 base models, aggregated with three variables used at each split, were constructed from two datasets – the full data and one excluding substratum type. The best model was obtained using the full data set based on the OOB error rate, *k*-statistic, and class-dependent accuracy (Table 4.1).

Table 4.1: Confusion matrix and class-independent error, OOB error rate and *k*-statistic for the two datasets tested with RF. Classes are coelacanth presence "P" and absence "A". The correct classifications for each class are on the diagonal (in bold)

	Biotic variables and depth			Biotic variables, depth and substratum type		
	P	A	Class error	P	A	Class error
P	**764**	4	0.01	**766**	2	<0.01
A	37	**21**	0.64	23	**35**	0.40
OOB error rate			3.03%			4.96%
K statistic			0.48			0.72

Table 4.2: Class specific variable importance computed as mean decrease in accuracy. Classes are coelacanth presence "P" and absence "A" and variables are ranked according to importance for each class, mean decrease in accuracy over both classes and mean decrease in the Gini index. The 4 most important variables are denoted bold in each case

	Variable Importance			
	Mean Decrease in Accuracy			Mean Decrease in
Variable	A	P	Both Classes	Gini index
Depth	**0.61**	**3.90**	**0.95**	**27.63**
Algae	0.00	0.00	0.57	3.87
Anemones	0.03	-0.23	**0.94**	**10.97**
Bryozoans	0.57	1.54	**0.79**	**12.95**
Coral	0.21	2.48	0.20	0.45
Crustaceans	0.00	0.00	0.43	0.94
Ctenophore	0.00	0.00	0.00	0.01
Echinoderms	0.31	1.59	0.62	2.96
Gastropods	0.00	0.00	0.03	0.04
Gorgonians	**0.92**	**3.30**	0.00	0.27
Livecover	0.13	0.98	0.00	0.00
Sea Pens	-0.16	1.45	0.00	0.00
Sponges	**0.64**	2.77	0.00	0.00
Unknowns	0.18	-0.02	0.24	0.87
Urchins	0.00	0.24	0.17	2.82
Rock	**0.58**	**3.46**	**0.84**	**18.12**
Sand	0.38	**3.08**	0.59	3.47
Silt	0.41	2.30	0.55	4.69

Variable selection

Depth was consistently identified as the most important variable except in terms of coelacanth absence where it was ranked third (Table 4.2). The two most important biotic variables were gorgonians and sponges. Rock was the most important substratum type.

Classification trees

The predictor variables used in the classification tree were depth and rock and the biotic variables gorgonians and sponges which corresponded to the four variables found to be most important by RF (Table 4.2). The optimal number of terminal nodes determined through cross-validation was found to be seven. The overall correct classification rate for the model was 96.6%. The final classification tree model indicated that coelacanths were associated with depths between 116.5 and 110.5 m, regardless of substratum type or percentage cover of invertebrates (Figure 4.1). Within this depth range, subsequent splits were determined by gorgonians, rock and sponges with coelacanths associated with percentage cover of gorgonians of < 11.2% where rock cover was ≥ 1.2% but are generally absent from areas of low rock cover (< 1.2%). Coelacanths were also associated with areas of percentage cover of sponges of < 27.4% and rock cover of < 70.7%.

4.4 Discussion

Within the IWP submarine canyons coelacanths have been found sheltering within sandstone caves that are encrusted with sponges, corals and gorgonians at depths between 104 and 144 m. These variables were subsequently found to be important in predicting their presence while variables associated with non-cave related habitats such as sea pens on the shallow canyon-margin sandflats or the deep water *Sclerothamnus* spp. sponges found in the thalweg predicted their absence. The overall correct classification rate for the model was estimated at 96.6%, correctly predicting absence (> 99%) better than presence (60%).

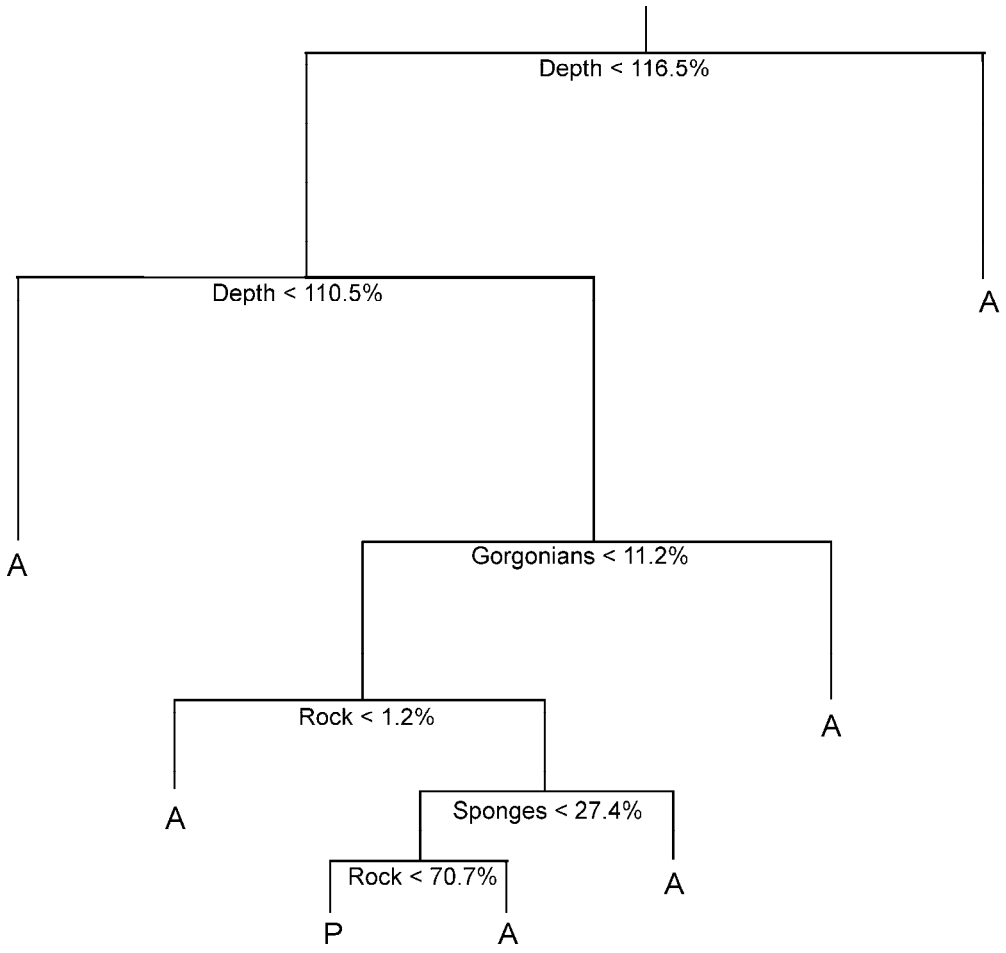


Figure 4.1: Classification tree for coelacanth presence "P" and absence "A" in the 11 submarine canyons off Sodwana Bay. The length of each vertical line below each split corresponds to variable importance. Values and labels at each split correspond to threshold values of the labeled variable

The classification tree showed that depth was the primary factor in determining coelacanth distribution. According to the model the optimal depth distribution for coelacanths in IWP would be between 110.5 and 116.5 m that corresponds to the location of the caves where coelacanths have been documented (Hissmann et al. 2006). The average depth at which coelacanths were observed was 113 m and 75% of the observations were recorded within the predicted range. It must be noted that all dive surveys were conducted during the day resulting in coelacanths only being found in caves despite evidence to suggest that they leave the caves to forage at deeper depths at night (Uyeno and Tutsumi 1991, Fricke and Hissmann 2000, Hissmann et al. 2000).

In the IWP submarine canyons, the 20ºC isotherm is generally found at around 100 m. As a result, caves inhabited by coelacanths are found within a temperatures range of between 16 and 22.5ºC (Roberts et al. 2006). Coelacanths require a high dissolved oxygen concentration as they have low oxygen uptake efficiency due to their blood physiology (Hughes and Itazawa 1972, Hughes 1976, 1995) together with a low gill surface area to body size ratio that physiologically restricts them to temperatures below 22.8ºC. The physiological requirements of coelacanths would therefore confirm the depth range estimated by the classification tree. Although depth is the principal indicator factor, it is important to note that the depth range where coelacanths are likely to be found is influenced by the temperature at that depth. Thus the model should be adjusted if used for areas with different temperature profiles such as in the Comoros where the same temperatures are found more than 100 m deeper than in the IWP (Fricke et al. 1991, Roberts et al. 2006).

Sponges and gorgonians were found to be the most important biota that explain coelacanth presence. Coelacanths are not known to prey on these sessile invertebrates, with only fish and cephalopods being found in their stomachs (Uyeno and Tutsumi 1991). Sponges were the dominant invertebrate taxa within the caves which were fringed by dense communities of gorgonians (Sink et al. 2006). Although gorgonians were also found to be an important indicator variable, coelacanths were associated with a relatively low percentage cover of gorgonians (< 11.2%) with gorgonians almost absent from inside the caves where coelacanths were found. Low gorgonian density in caves could be explained by their feeding habits as gorgonians are passive filter feeders that rely on either water movements or the sinking of detritus for nutrition. Coelacanths shelter in caves as there are reduced currents (Ribbink and Roberts 2006) together with increased shelter from potential predators (Green et al. 2009). With the virtual absence of water movements within the caves, the amount of food available for filter feeders would be reduced. The co-distribution of sponges and coelacanths in caves could therefore be due to both species relying on the physical aspects of the cave for shelter, rather than any co-dependence.

Substratum type was important in predicting coelacanth distribution with rock showing a high variable importance in all analyses. Coelacanths were associated with substratum composing of between 1.19 and 70.7% rock. Caves utilized by coelacanths could show a low percentage cover of rock due to encrusting sponges colonizing most of the surface area, resulting in the broad range of rock cover shown by the classification tree.

The application of predictive models is not necessarily limited to predicting a species' current distribution but can also be used to investigate historical (Peterson et al. 2004) or future (Skov and Svenning 2004, Thomas et al. 2004) patterns in relation to past and future climatic conditions. There is considerable debate over the original point of dispersion of the coelacanth (Schliewen et al. 1993, Stobbs 2002, Green et al. 2009), originally thought to be in the Comoros (Balon et al. 1988, Schliewen et al. 1993) where the largest population has been recorded. Once predictive models have been determined for coelacanths throughout their known distribution ranges, they could be used to help map historic distributions of the coelacanth, and perhaps provide better insight into the founder population locality. Classification trees have been shown to provide a simple and efficient method for modeling coelacanth presence and absence given habitat data. The model developed suggests that if additional coelacanths are to be found within the IWP then surveys should concentrate at depths between 110 and 120 m in rocky areas with high concentrations of gorgonians. Coelacanths' nocturnal foraging habitat also suggests that the optimal time to search for coelacanths initially would be during daylight hours when they are constrained to caves (Fricke et al. 1991) and not dispersed in deeper, less accessible areas, which could then be searched once a population has been located.

Chapter 5

Computer-aided identification of coelacanths, *Latimeria chalumnae,* using scale patterns

5.1 Introduction

Coelacanths *Latimeria chalumnae* Smith, 1939 are large-bodied fish that are listed as endangered by CITES (UNEP-WCMC 2005) and critically endangered by the IUCN (2011). They have a limited distribution range, low population sizes, low fecundity, late maturation and a long lifespan (Hissmann et al. 1998, Froese and Palomares 2000). These are all life history characteristics that predispose them to be vulnerable to external disturbances. Coelacanths live at depths in excess of 100 m that makes both locating and studying them inherently difficult (Hissmann et al. 2006). Developing alternative methods by which individual fish can be identified will therefore facilitate future research and conservation initiatives.

In the situation of rare and endangered species, such as coelacanths, the ability to recognize an individual within a population is essential for estimating demographic parameters such as population size and mortality rates. Individual identification can be achieved by applying an artificial mark, such as inserting a coloured or numbered tag (Kohler and Turner 2001, Arzoumanian et al. 2005) externally or a passive integrated transponder (PIT) internally (McCutcheon et al. 1994, Gibbons and Andrews 2004), injecting dye subcutaneously (Kelly 1967), clipping fins (Johnsen and Ugedal 1988, Lukey et al. 2006), or using the individual's natural markings (Ullas Karanth and Nichols 1998, Dixon 2003, Arzoumanian et al. 2005, Foster et al. 2006, Frisch and Hobbs 2007, Speed et al. 2007, Kitchen-Wheeler 2010).

Artificial tags have been shown to have detrimental effects upon the tagged individuals. Apart from being stressful and potentially exposing the animal to infection that may reduce survival, the tagging process itself may disrupt natural behavior (Bergman et al. 1992, Bridger and Booth 2003, Speed et al. 2007). There are also ethical considerations concerning the animal's welfare (Wilson and

McMahon 2006, McMahon et al. 2006), especially in the case of rare species where any increase in mortality is problematic.

The use of photographs as a visual "marking" method (Arzoumanian et al. 2005, Speed et al. 2007) rather than the physical tagging of the animal is showing considerable promise as it reduces the initial stress related with the marking procedure and is known to be reliable over a longer time period (Beaumont and Goold 2007, Speed et al. 2007, Van Tienhoven et al. 2007, Barker and Williamson 2010). Coelacanths' spots have been found to remain the same over at least a nine year period (Hissmann et al. 1998). This is particularly relevant when investigating rare and sensitive species during population monitoring studies where individuals need to be re-identified over a number of years (Seber 1982). Another disadvantage of physical tags is potential tag loss. If natural markings are retained for the duration of the experiment then the loss of "marks" is also avoided. The use of natural marks to identify individuals is now widely used in marine species such as seals (Beaumont and Goold 2007), cetaceans (Smith et al. 1999, Fujiwara and Caswell 2001), sea turtles (Schofield et al. 2008), great white sharks (Gubili et al. 2009) and raggedtooth sharks (Van Tienhoven et al. 2007, Barker and Williamson 2010).

Computer-aided identification of natural marks has been successful in identifying the spot patterns of cheetah *Acinonyx jubatus* (Kelly 2001), head shapes of green *Chelonia mydas* and hawksbill *Eretmochelys imbricate* turtles (Reisser et al. 2008), the characteristic shapes and patterns on flukes of marine mammals such as dorsal fin shape in bottlenosed dolphin (Lapolla 2005), fluke patterns in humpback whales *Megaptera novaeangliae* (Kniest et al. 2010), spot patterns of raggedtooth sharks (Van Tienhoven et al. 2007, Barker and Williamson 2010), whale sharks (Arzoumanian et al. 2005, Speed et al. 2007) and manta rays (Kitchen-Wheeler 2010), and even the stripes of zebras (Foster et al. 2006).

Coelacanths possess a unique pattern of white and blue scales (Figure 1.1) that can be used to identify specific individuals from photographs (Hissmann et al. 1998, Fricke and Hissmann 2000, Sink et al. 2006). The ability to identify individual coelacanths from their spot pattern has allowed

population monitoring of the Comoros populations (Fricke et al. 1991, Hissmann et al. 1998, Fricke et al. 2000) and a count of 24 South African coelacanths (Ribbink and Roberts 2006), allowing lifespan (over 20 years) and growth rates to be estimated (Hissmann et al. 1998). The combination of lasting individual-specific patterning together with its endangered status (UNEP-WCMC 2005, IUCN 2011) makes coelacanths potential candidates for photoidentification.

This chapter assesses the use of computer-aided identification to successfully identify individual coelacanths by assessing operator precision and accuracy, and through estimating the effect that the angle of photograph yaw has on identification success.

5.2 Materials and Methods

Data available

A catalogue of digital photographs, produced by the African Coelacanth Ecosystem Project (ACEP) (Ribbink and Roberts 2006), was used as the reference photographs for this study. The catalogue was extracted from submersible video footage that was collected between 2002 and 2004. The raw video footage from this period was also used to obtain additional test photographs. The reference catalogue consists of a list of 24 individual fish that have been previously identified by experienced observers by manually identifying each individual fish from photographs, and contains photographs of both sides of the fish, where available, and a description of additional characteristic features such as deformities. A digital database containing different photographs of previously identified individual coelacanths from the ACEP Coelacanth Catalogue was created. Photographs of the right and/or left hand sides of the coelacanths were treated as "different" individuals for this study. This reference database was comprised 29 photographs of 24 different fish. For each fish within the reference database 60 of the most obvious and diagnostic spots were selected to geometrically define the individual.

Software

I^3*S* (*Interactive Individual Identification System* v 2.0[1]) was used in this study. The software uses affine mapping to geometrically transform positions of points (or lines) on one plane to another plane if each plane has a set of three reference coordinates. Any co-ordinate(s) (such as scale patterns denoted as dots) on the source plane are therefore mapped to their relative position in the destination plane. A coelacanth example is illustrated in Figure 5.1. For this study, the three reference coordinates were (1) the anterior base of the first dorsal fin, (2) the anterior base of the epicaudal fin, and (3) the anterior base of the pectoral fin (Figure 5.2). Once the software is open, a user opens a photograph and selects the three reference coordinates by clicking the mouse on the appropriate areas on the photograph. The software then allows for a maximum of 80 of the most obvious and diagnostic spots within the reference coordinates using the computer mouse. For this study only 60 spots were selected as we wanted to assess the lower bound of the software's ability to accurately identify new photographs. When comparing a new photograph to a database of reference photographs, the software sequentially affine maps the new photograph to each of the reference photographs (Figure 5.1) and ranks the potential matches based on the squared Euclidean distance between matching spots. A final, manual check is made possible by the operator cross-referencing the highest ranked possible match against the new photograph. For a more detailed description refer to Speed et al. (2007) and Van Tienhoven et al. (2007).

[1] http://www.reijns.com/i3s/

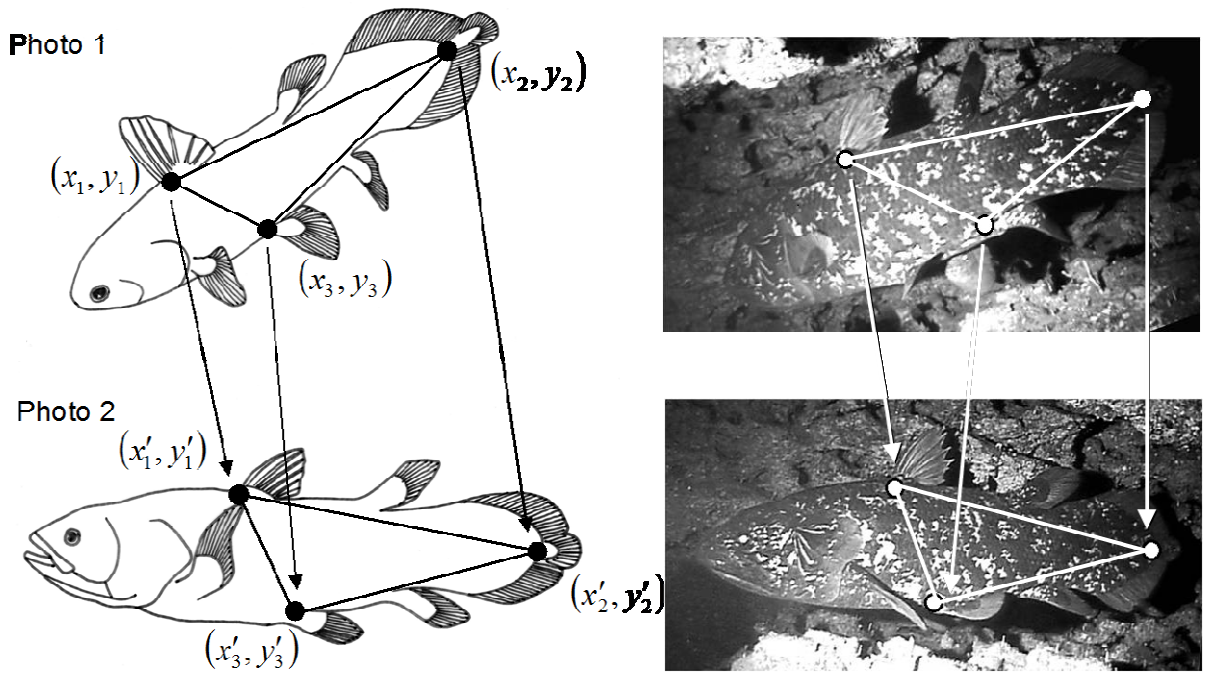


Figure 5.1: An example of an affine map that transforms the plane of Photo 1 to a plane in Photo 2. An affine map requires three reference points $\{(x_1, y_1), (x_2, y_2), (x_3, y_3)\}$ from Photo 1 that correspond to those $\{(x'_1, y'_1), (x'_2, y'_2), (x'_3, y'_3)\}$ for Photo 2. The spots within these reference points on Photo 1 are geometrically transformed

Operator accuracy

Twelve different, novice operators performed an experiment to estimate operator precision and accuracy. The experiments were conducted 'blind' in that the operators did not know the identity of the coelacanths in the photographs. In this experiment operators were provided with 25 photographs that were different from the reference database. These additional photographs were obtained by extracting still frames of fish from the submersible video footage at their most perpendicular orientation to the camera. All operators were instructed to use the defined reference points but could use their own discretion in selecting those scale patterns which, in their opinion, would be considered obvious and diagnostic. Each digitized photograph from each operator was then compared against the

reference database. Identification was considered to be correct if the correct photograph was ranked first on the list of closest matching photographs.

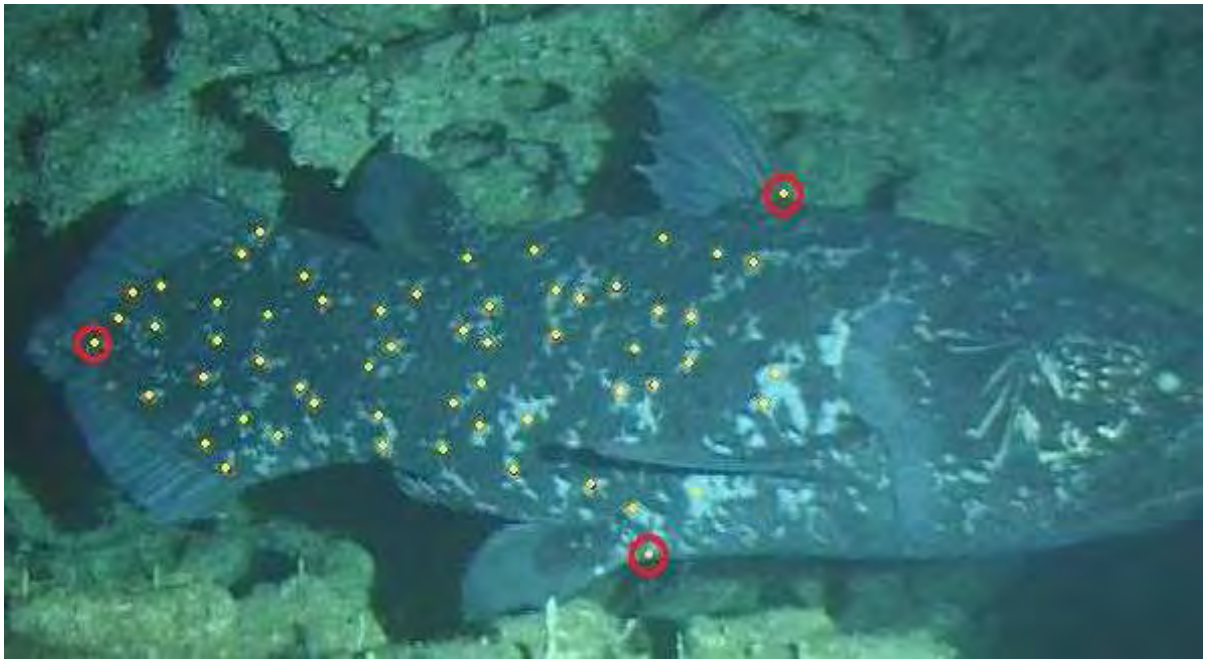


Figure 5.2: Typical reference photograph of a coelacanth, *Latimeria chalumnae,* with three circled reference coordinates and 60 yellow spots that indicate the position of diagnostic white scales

Estimation of the effect of angle of yaw

In another experiment, 141 still photographs of 26 different coelacanths exhibiting yaw (the rotation of a fish around its vertical axis) angles between 0 and 80˚ were extracted from the video footage. The photographs were categorized by yaw angle and compared against fish within the reference database by a single operator. Yaw angle (θ) was calculated as $\theta = \sin^{-1}\left(\frac{ROLTD}{3.95}\right)$ where $ROLTD$ is the ratio of total length to body depth of a new fish, and 3.95 is the average total length to depth ratio of all reference fish that were photographed perpendicular to the camera.

5.3 Results

Creating the reference database of 29 photographs with reference spots took under 35 min. For each new photograph it took, on average, 69.8 s to define 60 reference points and to search the database for the correct match.

Software testing

The first experiment showed that coelacanth individuals could be efficiently and successfully identified with a success rate of between 56 and 92% of correct photographs being ranked first on the list, and a 100% success rate if the photographs were then identified manually. The average rank of the correct photograph was between 1.4 and 3.8. Despite the high identification success rate variability was high in the average number of shared spot pairs (CV = 15.9 – 30.0%) and high in the average squared distance between spots (CV = 67.0 – 90.8%) (Table 5.1).

Estimation of the effect of angle of yaw

The software could successfully identify coelacanths in photographs where fish exhibited a yaw angle of up to 60º (Table 5.2). Although the percentage of photographs ranked first on the list decreased with an increase in angle, all fish could be identified by manually viewing the fish in the database and matching them to the photograph of the unknown fish, even at angles of up to 80˚.

Table 5.1: Percentage of the 25 coelacanth, *Latimeria chalumnae,* photographs correctly identified and ranked first on the list of most closely matched individuals, the average number of shared spot pairs, and their mean squared distance between spots in the test and reference photographs. Average rank denotes the mean placing of the correct photographs on the list of the most closely matched fish. A total of 60 spots was selected for both the test and reference photographs. Coefficients of variation are in parentheses

Operator	Percentage Correct	Average Rank	Spot Pairs	Mean squared distance
1	92	1.4	36.2 (20.9%)	0.22 (70.1%)
2	88	3.4	31.2 (17.9%)	0.27 (67.0%)
3	72	2.7	30.0 (20.7%)	0.30 (76.7%)
4	80	2.1	37.0 (16.6%)	0.24 (71.4%)
5	64	3.2	31.8 (30.0%)	0.27 (80.7%)
6	68	3.8	28.8 (29.9%)	0.31 (83.8%)
7	68	2.8	32.8 (29.9%)	0.26 (71.5%)
8	72	2.2	36.0 (20.9%)	0.24 (77.4%)
9	56	2.2	32.4 (24.6%)	0.27 (83.6%)
10	72	2	37.9 (15.9%)	0.24 (73.5%)
11	64	3.3	34.4 (24.4%)	0.26 (90.8%)
12	80	2.3	37.4 (18.0%)	0.22 (78.6%)

Table 5.2: Percentage correctly identified coelacanth, *Latimeria chalumnae,* photographs, the mean squared distance between spots in the test and reference photographs, and the average number of shared spot pairs for different categories of yaw angle. Average rank denotes the mean placing of the correct photograph on the list of the most closely matched fish. A total of 60 spots was selected for both the test and reference photographs. Coefficients of variation are in parentheses

Angle of yaw (°)	n	Percentage Correct	Average Rank	Matching Pairs	Mean squared distance
0 - 9.9	14	71.4	1.8	35.5 (21.0%)	0.30 (70.2%)
10 - 19.9	16	75	3.8	37.1 (16.5%)	0.19 (69.4%)
20 - 29.9	29	62.1	4.7	35.4 (22.9%)	0.18 (43.0%)
30 - 39.9	27	48.1	5	34.0 (22.6%)	0.18 (38.0%)
40 - 49.9	33	42.4	6	33.6 (21.7%)	0.17 (32.0%)
50 - 59.9	16	31.3	6.5	30.1 (14.2%)	0.21 (34.3%)
60 - 80	6	0	12.8	28.2 (12.8%)	0.23 (20.1%)

5.4 Discussion

Traditionally identification of coelacanths has been conducted by manually identifying each individual from a photograph and comparing it against a catalogue of known individuals (Sink et al. 2006). This has been successfully applied in the Comoros (Fricke and Hissmann 1994) and IWP populations (Ribbink and Roberts 2006). This approach is time consuming and becomes more onerous the more referenced fish there are in the catalogue. This study shows that computer-aided identification can be used to quickly and accurately identify individual coelacanths given still photographs from underwater video footage. The advantage of computer-aided identification is that it is not completely automated as the operator can define the reference points, select diagnostic spots and then have the additional option of using a visual match to check the database results. This two-stage process speeds up the short-listing of candidate individuals before manually selecting the correct individual. Computer-aided identification is therefore faster than identifying individually from a reference catalogue manually.

The ability of using computer-aided identification software to efficiently identify individual coelacanths with only one reference photograph in the database is advantageous. Van Tienhoven et al. (2007) found that the accuracy of identifying a correct individual increased as additional photographs of the same individual were added to the database. This shows future promise as when more fish are re-sighted and "tagged" with a photograph, the database will grow and the probability of finding a match will increase.

It was found that the size of individual fish did not change over a period of 9 years (Hissmann et al. 1998), and since maximum life span has been estimated at 103 years (Fricke et al. 2011) it can be expected that spot pattern should remain the same for long periods of the fishes' lifespan. The ability to add additional photographs to the existing database allows for individual's spot pattern to be updated as new photographs are acquired during future studies and can be used to validate and improve the use of spot patterns to identify individual fish.

Van Tienhoven et al. (2007), when using computer-aided identification on raggedtooth sharks, noted that the largest source of error in identification occurred when the shark's body was bent. Coelacanths are fortunately less sinuous than sharks due to their specialized form of locomotion (Fricke et al. 1987) and even if the video stills were imperfect, individuals could still be identified. Most computer-aided software that relies on a two-dimensional affine transformation assumes that the subject is a rigid, two-dimensional plane. This means that the "perfect" photographs for the database would be taken directly perpendicularly to the animal. The allocation of standard reference points facilitates the comparison of photographs that are angled as long as the reference points are still visible.

Coelacanths habitually shelter in caves during the day (Fricke et al. 1991, Venter et al. 2000). It is often impossible to obtain a "perfect" photograph taken perpendicular to the fish and, due to the additional difficulty of locating the fish, there are a limited number of photographs available for identification. The results of the yaw tests show that coelacanths can be correctly identified at an angle of up to 60º although the need for operator-intervention in order to select the correct fish from the ranked list increases with an increase in angle. Although manual identification through comparison of pictures is still needed, the time spent is greatly reduced due to the ranking system where the most likely matches can be viewed first. The ability to recognize photographs of coelacanths showing moderate yaw is advantageous as this increases the number of useful photographs which can be obtained from video footage.

Speed et al. (2007) predicted that species with irregular spots would be unsuitable for computer-aided identification due to inter-user variability in spot choice. This study showed that despite coelacanths having irregular shaped spots they could be accurately identified. In this study 60 spots per individual were selected from a potential 80-120 per individual with approximately half being matched between photographs. This may explain Speed et al.'s (2007) later comments that by increasing the number of reference spots there should be a commensurate increase in identification rate.

Coelacanths are listed by CITES (UNEP-WCMC 2005) and the IUCN (2011) as either "endangered" or "critically endangered", respectively. Coelacanths must therefore be disturbed as little as possible during scientific observations limiting any data collection for studies to non-invasive methods such as video and photography. Computer aided identification could facilitate future research on these fish through greater efficiency and accuracy of identification and reduced stress on the animals.

One of the main criteria for assessing an animal's conservation status is the quality of information available regarding its population size (Mace 1995, Collar 1996, Robbirt et al. 2006, ITTO and IUCN 2009). For small populations, population size is often estimated using a mark-recapture experiment where animals are caught, identified and released at least twice. Population size is estimated based on the numbers of animals caught and the ratio of previously marked to unmarked individuals in the samples (Seber 1982). While various mark-recapture estimators have different assumptions (Pollock et al. 1990), one common assumption is that "marks" are permanent over the duration of the experiment and that the "marks" are easily recognized on recaptured individuals (Stevick et al. 2001). Computer-aided identification can be used to facilitate the re-identification of individual coelacanths, facilitating future population studies.

To conclude, computer aided identification of coelacanths allows for a more efficient use of photoidentification which is essential given the coelacanth's endangered status. The application of this tool with regards to coelacanth populations could be used to identify other individuals in larger populations such as those in the Comoros where 115 individuals have been identified (Fricke et al. 2011), allowing the application of mark-recapture methods. This would facilitate assessments on the movements and residency status of individual coelacanths, both which are essential for its conservation and management.

Chapter 6

General Discussion

Coelacanths are large-bodied, reclusive fish that inhabit deep water environments and have a restricted distribution range (Hissmann et al. 1998, Fricke and Hissmann 2000, Hissmann et al. 2006). Coelacanths are also critically endangered (IUCN 2011). Within South Africa they are protected (DAFF 2011) and have been identified as having a high research priority (Anon 2000, Ribbink and Roberts 2006). The high costs and logistical hurdles associated with using highly skilled manned underwater submersibles deployed from ships have hampered coelacanth-specific research efforts. As a consequence there is incomplete information regarding their distribution, life history and ecological relationships. The populations resident in the Comoros (eg. Fricke and Hissmann 2000, Fricke et al. 2000) and South Africa (Hissmann et al. 2006) have attracted the most research attention. Unfortunately little research into the broader aspects of their biological and physical environment has been conducted. An ecosystem-based management approach dictates that the whole ecosystem needs to be managed rather than focusing on one particular species (Peterson et al. 2000, Pace 2010). Given the coelacanth's iconic status it is surprising that these broader research topics have received little attention. In 2001 South Africa initiated the African Coelacanth Environment Programme (ACEP) to conduct extensive ecosystem-based research in the northern KwaZulu-Natal including the Western Indian Ocean subsequent to discovery of a population of coelacanths in the IWP. Its successor, ACEP II, was initiated in 2008 for another 4 years. In 2012 the programme is planned to start its third phase.

Considerable quantities of data were collected during ACEP I that have been archived. Archived material presents several research opportunities. For example, as video footage provides a permanent visual record of a sample (Rogers and Miller 2001, Lirman et al. 2007) it can be reanalysed whenever necessary (Lam et al. 2006) even if the original footage was recorded for a different purpose. In addition the ease with which digital material can be shared facilitates collaborative

research (Rogers and Miller 2001). Videography is one of the only ways in which coelacanths and their habitat could be sampled in IWP because it is safe and non-invasive. The archived digital video footage recorded from *JAGO* from 2002 to 2004 therefore provides an invaluable research resource. This thesis was based on utilising this pre-recorded video footage to gain additional insight into the coelacanth and its associated habitats within the IWP. Three research aims were to (1) describe the submarine habitat of the canyons within the IWP to describe coelacanth-specific EFH, (2) determine coelacanth distribution within these habitats, and finally (3) assess the potential of computer-aided identification to successfully identify individual coelacanths.

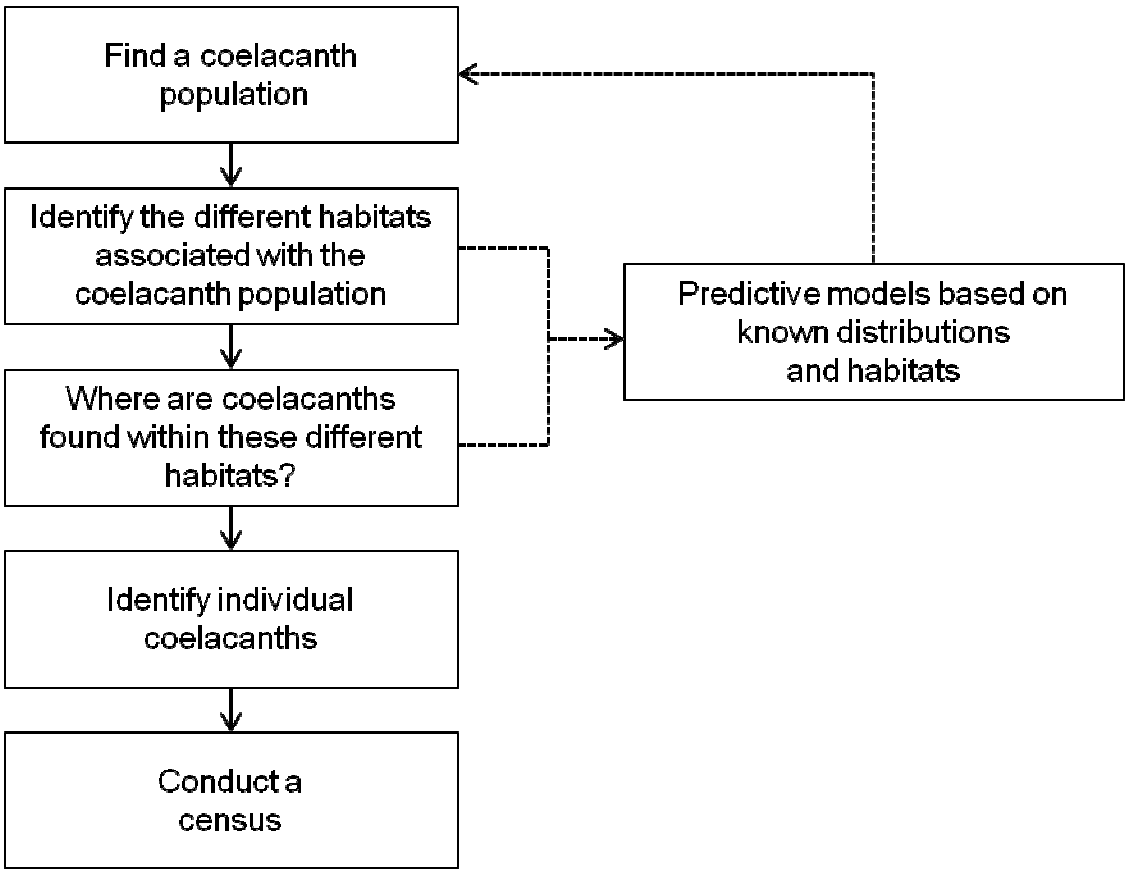


Figure 6.1: Flow diagram of research steps taken to analyse coelacanths and their habitats. Dotted arrows indicate a feedback loop representing the steps towards locating new populations

This thesis was structured into three chapters each outlining a possible step taken towards analysing coelacanth-related habitats, locating and then analysing new habitats. A flow chart is presented in Figure 6.1 indicating the progression of these possible steps and how they are interrelated in terms of this thesis and future application.

In the case of coelacanths, as with all rare species, the first step is to locate a population, the second step is to conduct a habitat analysis to determine the different habitats and the biotic community. Once different habitats types have been determined, it is necessary to determine those habitats utilized by, and possibly preferred, by coelacanths (Figure 6.1). In order to conserve a sensitive species all aspects of that species' habitat together with its relationships with sympatric biota must be determined (Rieser 2000, Rosenberg et al. 2000). It is therefore necessary to define its EFH (NOAA 1999). Chapter 3 concentrated on identifying and quantifying the habitats within the submarine canyons of the IWP using multivariate and SHE analyses. Seven different habitats were distinguished and invertebrate distribution was found to be strongly influenced by physical canyon structure. Coelacanths were found in caves and on surrounding steep slopes. From these results it would appear that only caves in the submarine canyons in the IWP form the coelacanths' EFH. It is known, however, that coelacanths do make excursions into deeper waters to forage during the night (Fricke et al. 1991, Fricke and Hissmann 2000, Hissmann et al. 2000) and information is needed on all aspects of coelacanth life history before a definite EFH can be defined.

Previous predictive models for coelacanths have been based on coelacanths' physical requirements (Green et al. 2009, Owens et al. 2011). Habitat analysis on areas identified by these models would allow the application of the predictive models to narrow down search areas. Chapter 4 showed that classification trees can efficiently predict coelacanth presence and absence based on depth, invertebrate structure and substratum type. Based on this information an analysis of coelacanths and their associated habitats would then allow for future prediction of coelacanths within the IWP and potentially other populations. Classification trees could refine areas defined by Green et al. (2009). The region between Olumbe and Port Amelia in Northern Mozambique has submarine

canyons similar to those in IWP (Green et al. 2009) and would be a potential target zone. Once a new population is located, these research steps could be applied to that area and possibly allow for comparisons between populations.

The forth step is to identify individual coelacanths within the population. The ability to recognize an individual within a population is essential for estimating demographic parameters (Kohler and Turner 2001, Arzoumanian et al. 2005), especially when dealing with endangered species. Chapter 5 showed that computer computer-aided identification of coelacanths allows for a more efficient use of photoidentification of individuals unique spot patterns. This would be especially useful for identifying individuals within large populations such as that in the Comoros where 115 coelacanths have been identified (Fricke et al. 2011). A mark-recapture study would be the next logical step as this enables population estimates to be made. Reliable population estimates, especially for endangered species, are crucial for population monitoring (Johnson et al. 2006), developing management strategies (Staples 2006) and assessing conservation status (Mace 1995, Collar 1996, Robbirt et al. 2006, ITTO and IUCN 2009). Although the number of individuals identified to date in the IWP population is too small for a mark-recapture study to be applied, there is an ongoing study of this nature in the Comoros (Fricke et al. 2011).

Recommendations for future studies

In this thesis samples were taken only from archived video footage that was collected during the ACEP I surveys between 2003 and 2005 where the objectives of the surveys were to find and catalogue coelacanths. Although this thesis presents an analysis of these data to generate information on coelacanths and their associated habitats, there were several constraints because the footage was not intended for a habitat study. No sampling design is perfect (Edgar 2004) but if these constraints are recognised and identified steps can be taken to extract data that are meaningful. .

The first constraint was poor filming technique. In terms of filming, camera speed, elevation and angle should ideally be kept constant within and between transects (Aronson et al. 1994). This is necessary if qualitative estimates such as percentage cover are to be obtained from the video footage.

However, external factors such as the unpredictable topography (Sink et al. 2006) and currents (Roberts et al. 2006) encountered within the IWP canyons often confounds filming. This results in images with differential resolution (Pilgrim et al. 2000). Although these hurdles can be overcome to some extent during analysis, processing is considerably simpler and faster if they can be reduced or accounted for in the field. This can be achieved with the use of a laser-scaling system consisting of a known array of lasers projected onto the substratum beneath the camera that allow for computerized scaling of images through analysis of the laser spot positions on the video footage (Pilgrim et al. 2000).

The second constraint was sampling design. Sampling design is one of the core aspects of any monitoring programme as it influences not only the data that can be obtained from a study but also its application to future programmes (Van der Meer 2007). Designing a sampling strategy is a complex procedure that needs to take into account the desired outcomes of the study and constraints arising from the physical properties of the area being sampled (Ryan 2004). To produce an exhaustive sampling protocol for surveying and monitoring coelacanth habitats, both within the IWP and other regions, falls outside the scope of this thesis. However, what is clear is that there is a need for a detailed habitat analysis within the canyons in the IWP with a sampling strategy designed specifically for that purpose. Videographic footage for this study had no specific sample design and as a result some habitats were either over or underrepresented. The majority of footage was of caves with coelacanths and there was limited footage available of the deeper canyon regions. Although this was compensated for in the selection of still frames, future studies would benefit from a more statistically robust sampling design. Sampling should include multiple depth strata, not only concentrating on depths where coelacanths have been observed, but also in the deeper regions of the canyons. Care should also be taken to sample all representative habitat types and transects should be standardised between canyons. Areas in the same regions where coelacanths are not found need to be sampled in order to compare presence and absence data. Finally, standardisation will allow for comparisons to be made, not only between IWP canyons but on a larger scale between habitats of different populations such as those in the Comoros and Tanzania.

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