THE EFFECT OF BAIT ON FINE-SCALE HABITAT ASSOCIATIONS OF REEF FISH INVESTIGATED WITH REMOTE UNDERWATER VIDEO SYSTEMS

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ABSTRACT

Establishing the associations between fish and their habitats can aid in the monitoring of fish stocks and the design of effective marine protected areas (MPAs). Baited remote underwater stereo-video systems (stereo-BRUVs) are now commonly used to asses fish populations. The habitats seen in the video footage of stereo-BRUVs can be used to link fish fauna to preferred habitat types. However, the application of bait potentially attracts fish from surrounding habitats, and might result in a biased understanding of fish–habitat associations. A field study was conducted in the Tsitsikamma National Park MPA to determine the effect of bait on fine-scale fish–habitat associations, using remote photographic and video methods. The study was conducted over the summer season of 2015 and 2016. Data were collected within a 1x1 km shallow (9–44 m) reef complex. Within the sampling area, 944 photo-quadrats of the macrobenthos were taken 30 m apart by means of a drop camera. By separating the macrobenthos into broad taxonomic groups, five habitat types were identified, namely *Shallow Sand, Shallow Reef, Deep Reef, Deep Sand* and *Patch Reef*. The results show that even on a fine scale, depth is an important predictor of macrobenthic distribution and assemblage structure. Baited (stereo-BRUVs) and unbaited (stereo-RUVs) surveys were then conducted to sample the fish community in the same area during the period under study. Higher abundances of fish were observed in reef than in sandy habitats, and bait was seen to have a positive effect on species richness and fish abundance. When comparing habitats, fish abundance and composition on reef habitats were significantly different from sand habitats. This was observed in both the stereo-RUVs and stereo-BRUVs methods. High counts of roman (*Chrysoblephus laticeps*), fransmadam (*Boopsoidea inornata*) and steentjie (*Spondyliosoma emarginatum*) in reef habitats were contrasted by high counts of white sea catfish (*Galeichthys feliceps*), evil-eye puffer (*Amblyrhynchotes honckenii*) and lesser guitarfish (*Rhinecanthus annulatus*) in sandy habitats. Overall, the underlying patterns in fish diversity recorded with the two video methods were generally comparable. However, stereo-RUVs appeared to be unable to detect species that were present in sand habitats, while stereo-BRUVs increased the number and abundance of species recorded in all habitat types. In the stereo-RUVs footage, differences between reef habitats were dampened by the presence of highly abundant fish species. In the stereo-BRUVs footage, although bait appeared to have an effect on the observed fish assemblage, this manifested in an increase in species richness, higher fish abundances and a better overall ability to detect fish–habitat relationships. As such, stereo-BRUVs are considered a robust, effective and recommended method for detecting fish–habitat relationships, even over a fine scale.

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

CHAPTER 1

1 GENERAL INTRODUCTION

1.1 ECOSYSTEM APPROACH TO FISHERIES

Traditional management methods, such as single-species stock assessment, have been unsuccessful in preventing the overexploitation and decline of many fish stocks (Claudet et al., 2006; Pikitch et al., 2004). As such, there has been a shift in the management regime of fish stocks to include the protection of entire ecosystems, rather than focusing on endangered or exploited species (Claudet et al., 2006; Garcia and Cochrane, 2005). It is accepted that fish populations depend on a well-functioning, healthy ecosystem (Rosenberg et al., 2000), however, all ecosystems are subject to changes in environmental conditions, causing them to fluctuate naturally over time (George et al., 2007). Recognising that ecosystems change over time forms the basis of ecosystem-based fisheries management (EBFM), as well as the fact that ecosystems are driven by a range of complex biotic and abiotic interactions (George et al., 2007). The EBFM approach attempts to avoid the degradation of habitats caused by destructive fishing practices (Pikitch et al., 2004). Interactions between species (such as predator–prey relationships) as well as interactions between species and their habitat are crucial for a well-functioning ecosystem (Morishita, 2008). By protecting whole ecosystems, the protection of commercially important fish species is also ensured, as the interactions between both targeted and non-targeted species, as well as the immediate habitat, are all taken into consideration (George et al., 2007; Morishita, 2008). An ecosystem approach to fisheries (EAF) differs from EBFM in that EAF recognises the complexity and connectivity of ecosystems, and aims to meet human harvesting requirements while maintaining a healthy, functioning ecosystem (Garcia, 2003). The EBFM approach aims to manage human activities and considers the effects of fishing practices on both targeted and non-targeted fisheries, as well the subsequent consequences that may follow (George et al., 2007). Both management regimes, however, aim to take a broader approach to fisheries management, by considering the impacts of human intervention and the cascading effects on the environment, as well as the fisheries themselves. The goals of EBFM are therefore to ensure the long-term sustainable use of fish stocks while protecting ecosystem functioning and biodiversity, by realising a more holistic approach to fisheries management (Rosenberg et al., 2000).

Marine protected areas (MPAs) are considered to be one of the most effective tools in the protection of ecosystems, as exploited fish stocks are given refuge and degraded habitats are allowed to recover (Gell and Roberts, 2003). Furthermore, MPAs are able to reduce the broader, ecological impacts of fishing and are particularly advantageous to fisheries that target sedentary and less mobile fish species (Hilborn et al., 2004). No-take MPAs are able to offer full protection to a marine resource (Lester and Halpern, 2008) which is not only beneficial for the resource itself, but ensures a pristine environment and unaltered population. As such, MPAs can be considered to be ideal experimental sites for marine researchers, since functional links between organisms and their habitats can be defined from an unaltered ecosystem (Agardy, 1994). Once defined and understood, the links between organisms and their environment can aid in the management regimes of exploited fish stocks and degraded habitats. This is particularly beneficial in EBFM initiatives, as MPAs are able to accommodate the needs of multiple stakeholders, each with their own aims and objectives (Agardy, 1994). MPAs have, for instance, been shown to reduce the broader, ecological impacts of fishing, while being beneficial to fisheries that target sedentary and less mobile fish species (Hilborn et al., 2004; Kerwath et al., 2013). In South Africa, 23 MPAs have been established to date, protecting 21% of the coastline, with only 9% considered to be no-take areas (Sink et al., 2012). According to South Africa's 2011 National Biodiversity Assessment (Driver et al., 2012), 47% of marine and coastal habitat types in South Africa are threatened. Fishing remains the greatest threat to marine biodiversity, and is a key driver of change in marine and costal habitats. The majority of fish stocks in South Africa are overexploited and many are declining rapidly (Driver et al., 2012). This emphasises the need for, and importance of, accurate baseline data from which fish distribution patterns can be predicted, to support effective management and ensure the protection of South Africa's biodiversity.

Many initiatives in this country have aimed to establish additional no-take MPAs and review existing ones. To identify priority conservation and management areas, an understanding of the biogeographical patterns within an ecosystem is crucial (Turpie et al., 2000). Furthermore, once such areas are established, it is critical that they be suitably monitored, to keep track of their effectiveness in the protection of marine ecosystems and their potential benefits to adjacent fisheries.

1.2 LONG-TERM MONITORING

Marine ecosystems are undergoing rapid changes due to destructive fishing practices, water pollution and climate change (George et al., 2007). No management initiatives can, however, be put into effect without consistent information on the extent of environmental change (Vos et al., 2000). It is therefore essential that these changes be monitored, to assess whether the ecosystem is under threat and in need of protection. Long-term monitoring (LTM) of MPAs provides a baseline of near-pristine areas, to represent areas which are exempt from fishing pressure or other anthropogenic impacts. This baseline can be used as a target or reference point to ensure that the goals of newly established MPAs are achieved and to gauge the state of deterioration in exploited areas. LTM procedures must, however, be sensitive to change over time, appropriate in adequately representing the desired community, as well as cost effective, if they are to be meaningful and sustainable (Van Rein et al., 2011). Ideally, multiple components of an ecosystem should be monitored to detect long-term trends in its ecological status. This approach can, however, be time consuming and expensive, and could potentially jeopardise the objectives of monitoring or research initiatives. As such, alternative approaches to LTM may be employed. One such approach is the monitoring of surrogates, such as environmental conditions or specific species that can be used to represent the ecosystem as a whole (Lindenmayer et al., 2014). The protection of these surrogates will, in turn, provide protection for the entire ecosystem, but there is still much debate on the validity of the surrogates purported to accurately represent an ecosystem as a whole (Lindenmayer et al., 2014). Another approach is monitoring biological diversity, which allows for changes in the community structures of organisms to be perceived over time (Yoccoz et al., 2001). Long-term monitoring can be used to inform fisheries managers when developing management regimes (Ward and Jacoby, 1992). For LTM to be truly effective and efficient, the optimal method should be used, but, ideally, all available methods should be considered and examined.

1.3 ASSESSING MARINE FISH AND MACROBENTHIC ASSEMBLAGES

Over the years, various methods have been developed to sample ichthyofaunal and benthic invertebrate (macrobenthic) assemblages. Traditional methods of surveying fish involve extracting samples from fish populations by means of trawling, seine netting, gill netting, trapping and angling, and are often conducted in a fisheries-dependent manner (Cappo and Brown, 1996). Trawling and trapping methods have been used to sample fish communities (Travers et al., 2010, 2012), but these methods are destructive, and as such are inappropriate for use on vulnerable habitats and protected areas such as MPAs (Lowry et al., 2012). As a result, these traditional sampling techniques are becoming less common

in ecological studies, as they can further strain already over-exploited and depleted fish stocks. Eco-friendly methods of sampling fish communities and habitats have thus become more common in recent decades (e.g. Bozec et al., 2005; Heyns-Veale et al., 2017; Laidig et al., 2009; Wilson et al., 2010).

Underwater visual census (UVC) by SCUBA divers has been recognised as an appropriate way of sampling fish communities and habitats, as it is non-destructive and applicable to a wide range of different habitats (Samoilys and Carlos, 2000). The method has been used in a number of studies. For example, Bozec et al. (2005) and Wilson et al. (2008) used UVC to determine the effects of damaged coral reefs and habitat loss on reef fish assemblages. Most recently, the method has been used to measure the effect of structural complexity on reef fish assemblages (Darling et al., 2017). The UVC method has also been employed to measure habitat features through the use of quadrate surveys (Dethier et al., 1993; Leujak and Ormond, 2007; Ryan et al., 2007), providing data on fish–habitat associations and linkages (Murphy and Jenkins, 2010). Although this method is non-destructive, it is prone to observer bias and restricted to safe SCUBA-diving depths (Bernard et al., 2013; Harvey et al., 2007; Samoilys and Carlos, 2000). Remote photographic techniques such as remote-operated vehicles (ROVs; see Orange et al., 2002) and drop cameras (Roberts et al., 1994a) are able to provide habitat information of benthic marine environments in the form of photo-quadrats, which can be used to assess macrobenthic assemblages and formulate detailed habitat maps. Other means of obtaining habitat information involve using satellite imagery or hydroacoustics, such as sonar echo sounders and acoustic cameras (Murphy and Jenkins, 2010). These methods are non-invasive and able to sample a wide range of different habitat types at various depth ranges. The use of remote video methods is becoming globally recognised as an important tool in ecological studies (Bernard et al., 2014). Researchers wishing to gain unbiased fish population data have used RUVs) have been used by (Bernard and Götz, 2012; Cappo et al., 2003; Mallet and Pelletier, 2014). These systems have significant uses in terms of application and are mostly non-destructive to the environment (Bernard and Götz, 2012). The addition of a second camera to these (stereo-RUV) systems allows for three-dimensional information such as fish-size measurements to be extracted from the video footage (Harvey and Shortis, 1995; Mallet and Pelletier, 2014).

Baited remote underwater stereo-video systems (stereo-BRUVs) have recently gained much popularity as a means of implementing non-invasive sampling techniques for the monitoring of subtidal reef fish communities (Bernard and Götz, 2012; De Vos et al., 2014; Harvey et al., 2007; Mallet and Pelletier, 2014). The addition of bait to attract fish species makes these systems powerful tools in the monitoring of fish populations. Furthermore, they are appropriate for use in MPAs as they are non-invasive, can sample a

vast array of depths and are able to provide robust, quantitative data (Bernard and Götz, 2012; Cappo et al., 1999). Information can also be extracted from stereo-B/RUVs footage, providing information on fish–habitat relationships.

In the current study, the drop camera, stereo-RUVs and stereo-BRUVs methods were chosen as appropriate sampling methods, since they are considered to be feasible and sustainable tools for use in LTM. Stereo-BRUVs are gaining popularity on a global scale and are increasingly being used for applied management science (Bernard et al., 2014). To fully comprehend the nature of the data obtained from these systems, however, all biases pertaining to the method need to be understood, one such bias being the effect of bait on fish–habitat associations.

1.4 FISH–HABITAT ASSOCIATIONS

Assessing fish–habitat relationships plays an integral part in LTM, as changes in fish or macrobenthic assemblages over time can provide information on the state of the ecosystem (e.g. degraded or recovering). Fish–habitat associations refer to the preferences fish have for a certain environment or habitat. This harks back to the basic definition of ecology; of how an organism is related to its surrounding environment (Friederichs, 1958). An effective LTM needs to consider fish–habitat associations, as they provide a fundamental understanding of how reef communities are organised (Chittaro, 2002). The basis of many ecological studies in the marine environment is the ability to make accurate predictions regarding the relative abundance and distribution of fish communities (Willis et al., 2000). Perhaps the most effective way of making such predictions, is by understanding the association between fish and the habitat in which they are observed. Understanding the relationship between fish and their habitat is also key to well-developed fisheries management initiatives (Laidig et al., 2009). Once fish–habitat associations are understood, fish species distributions can essentially be predicted by looking at the structural and distributional components of habitats, allowing them to be managed more efficiently on larger spatial scales (Anderson et al., 2009). Predictive species modelling can also provide information on the environmental variables that play a role in the distribution of species (Monk et al., 2012), further identifying the habitat requirements of marine organisms (Johnson et al., 2013). The analysis of data at different spatial scales in ecological studies, using different statistical models, often results in different patterns being extracted, thereby affecting conclusions (Edmunds and Bruno, 1996; Monk et al., 2012). The strength of the relationship between fish and their habitat is highly scale dependent, and often different ecological processes and interactions are observable at different spatial scales (Nash et al., 2014; Syms, 1995). For example, larger-scale studies can often overlook fine-scale relationships between

organisms, providing only broader insight into the studied area. At these scales (hundreds of kilometres), regional-level information (such as species distribution structures) can be determined (Nash et al., 2014). While understanding the distribution patterns of fish species is vital to the management of fisheries (Gust et al., 2001), information gathered at a large scale may not contain relevant detailed information on species' specific home ranges or feeding preferences (Chittaro, 2004). At fine scales (tens to hundreds of metres), relationships between fish and habitat types are generally assessed (Syms, 1995) where processes occur more rapidly (Sale, 1998). At this scale, the influence of small changes in habitat structures or ecosystem dynamics can easily be observed as differing from the biogeographic processes observed over larger scales (Syms, 1995). It is therefore critical that the scale at which a study is conducted be taken into account, and the appropriate hypotheses be drawn up accordingly.

1.5 Problem identification and research questions

Invertebrate and reef fish communities have only recently been investigated with stereo-BRUVs in South Africa. This has proven to be a useful tool in describing the physical or ecological limits of subtidal reef fish species (Heyns-Veale et al., 2016). The use of bait in the stereo-BRUVs method has been shown to increase the abundance and number of fish species seen in the video footage (Bernard and Götz, 2012; Cappo et al., 1999; Harvey et al., 2007). The habitat information obtained using stereo-BRUVs can be linked to the observed fish fauna, thereby providing knowledge on fish–habitat associations. However, the very addition of bait to these systems may have an effect on the observed relationship between fish and their habitat. The effect of bait is thought be strongest at a fine scale (tens of metres), decreasing as scale increases. Bait attracts fish from nearby surrounding habitats that are not seen in the scope of the video footage, which can potentially lead to inaccurate assumptions regarding the relationship between the observed fish fauna and their habitats. If stereo-BRUVs are to be used as a reliable method to describe the relationship between fish and their habitats, an improved understanding of the methodological biases of bait is required.

This study therefore aimed to determine the effect of bait on fish–habitat associations over fine spatial scales (10s to 100s of metres). This was done by collecting photo-quadrats of the sea floor (benthos) using a drop camera which was subsequently used to identify habitat types within a given area. Fish data were then collected using stereo-RUVs and stereo-BRUVs within the same area. The effect of bait on fish–habitat associations was then quantified by comparing the fish diversity and assemblage structure sampled by the two methods. To achieve this, the following research questions were addressed:

- *What are the main habitat types and how are they distributed within the study area?*
- *What is the relationship between habitat (macrobenthos) and fish assemblages over fine spatial scales?*
- *If there is a relationship between habitat and fish assemblages, how does bait alter:*
    - *The observed fish assemblage*
    - *The observed relationship?*
- *Considering that habitats and macrobenthos are known to change over a depth gradient, how does bait alter:*
    - *The observed fish assemblage*
    - *The observed relationship?*

1.6 THESIS OVERVIEW

To achieve the aims and objectives of this study, the first step was to identify the distribution of habitat types within the study area. Chapter 2 focuses on defining the composition and distribution of macrobenthos within the study area. Detailed maps of the bathymetry and macrobenthic distribution of the study area are also provided in this chapter. Chapter 3 focuses on describing the fish community with the use of stereo-BRUVs and stereo-RUVs. In that chapter, distributional patterns in the fish community are described, as well as how those patterns are affected by the addition of bait. Finally, chapter 4 contains a synthesis of the core findings of the study and provides insight into the strengths and weaknesses of remote video methods, in addition to highlighting future considerations and recommendations.

CHAPTER 2

2 FINE-SCALE HABITAT CLASSIFICATION

2.1 INTRODUCTION

2.1.1 MACROBENTHOS

Reef habitat comprises a diverse biotic assemblage of mobile and sessile invertebrates (macrobenthos), as well as different types of substrate (Kostylev et al., 2001). Varying combinations of macrobenthos and substrate, along with factors such as temperature, depth and rugosity (a measure of surface roughness), result in the formation of a vast array of different habitat types. The diversity, structure and distribution of these reef habitats vary across different environmental conditions (Heyns-Veale et al., 2016; Pacheco et al., 2011). Macrobenthic invertebrates, such as various types of suspension feeders (e.g. sponges, corals and hydrozoans) dominate reef habitats, creating structural complexity (Gili and Coma, 1998; Heyns et al., 2016). This facilitates inter-specific trophic linkages between pelagic and benthic systems, such as creating habitats and food for fish species (Gili and Coma, 1998). Light intensity, flow rates, nutrient availability and temperature are key abiotic factors that influence the structure of macrobenthic communities (Garrabou et al., 2002). These abiotic factors change with increasing depth and, as such, shape and restructure macrobenthos communities (Garrabou et al., 2002; Heyns et al., 2016).

2.1.2 ESSENTIAL FISH HABITATS

Essential fish habitats are considered to be areas that are most favourable for fish populations to feed and reproduce (Valavanis et al., 2008). Macrobenthic biota are an integral part of habitat structure for fish, as larger species (e.g. sponges and corals) are able to structurally alter rugosity and profile, and may thereby dictate habitat type through ‘ecosystem engineering’ (Tissot et al., 2006). Colonial macrobenthos are able to form structure in low relief areas (Tissot et al., 2006), while other mobile invertebrate species provide additional food sources for fish species (Stoner et al., 2007). This amplifies fish–habitat associations, as fish make use of the enhanced habitat complexity provided by these ecosystem engineers. Many of these invertebrates are also prey for fish species (Choat and Kingett, 1982; Tissot et al., 2006), which ultimately influences fish community structures (Scharf et al., 2000). Sessile invertebrates are vulnerable to local

environmental changes such as water temperature and quality, in addition to anthropogenic impacts such as destructive fishing practices (Nelson, 2009). Macrobenthic assemblages have therefore been used as a measure of ecosystem condition, by monitoring their response to natural and anthropogenic stresses (Borja et al., 2000). The condition of a habitat will ultimately have an effect on the fish assemblage associated with that habitat, which can therefore indirectly be applied to the management of finfish fisheries (Caddy, 2004).

2.1.3 HABITAT ASSESSMENT

Local environmental conditions are of great importance to marine biota, as they shape the habitat in which an organism lives (Bain, 1999; Maddock, 1999). The physical and chemical conditions and processes found within a habitat can determine the spawning patterns, feeding habits and migratory routes of marine species (Hubert and Bergensen, 1999). Furthermore, the availability and variety of different habitat types found in an area influence the structure and composition of reef fish communities (Gratwicke and Speight, 2005; Maddock, 1999). Although fish are adaptable to some environmental change, they may move to select habitats that are most beneficial to their health and survival (Bellido et al., 2008). Environmental and physicochemical factors thus play a significant role in determining the distribution and structure of reef fish communities (Adjeroud et al., 1998). Depth, water temperature, habitat complexity and food availability have been highlighted as important factors in determining which fish species and age classes occur at different locations (Fitzpatrick et al., 2012; Heyns-Veale et al., 2016). The association between fish species and environmental conditions suggests that it is possible to predict fish and habitat distribution patterns based on key environmental parameters. These environmental parameters can subsequently be used to identify critical fish habitats and potential biodiversity hotspots at broader scales. Predicting spatial patterns of fish and habitat can also be considered useful in understanding key ecological processes, forming the basis of key EBFM initiatives such as policy-resource management (Garza-Pérez et al., 2004). Therefore, it is crucial to understand the environment in which fish occur, in order to predict their distributional patterns and, with that, to ensure their spatial protection and sustainable use as resources.

Habitat assessments are an important component of EBFM, as they contribute critical data for the assessment of ecosystem conditions and form the basis of biodiversity assessments (Thomson et al., 2001). Using these assessments to determine habitat quality and distribution can be useful in pinpointing which factors can limit fish abundance and distribution (Bain, 1999). The underlying assumption is that habitat type and availability are determinants of fish abundance and distribution (Johnston and Slaney,

1996). To truly determine fish–habitat associations, the habitat and fish community must be unaltered by human intervention: this, to ensure that these associations occur naturally, and not as a result of anthropogenic influences. Furthermore, by using pristine habitats as a reference or baseline, the condition and health of exploited habitats can be assessed (Johnston and Slaney, 1996). Thus, by gathering baseline data from pristine habitats, it can be assumed that true fish–habitat associations are being assessed. The extent to which these associations are altered by exploitation can then be measured and effectively managed (Edgar et al., 2004).

2.1.4 HABITAT MAPPING

With recent technological developments, a wide range of advanced tools has become available for gathering and representing geomorphological and biological data in the marine environment (Wright and Heyman, 2008). Geographic Information System (GIS) software has been implemented in various studies (Gonzalez-Mirelis et al., 2009; Kostylev et al., 2001; Sabater, 2010; Stevens and Connolly, 2003; Wright and Heyman, 2008) and is a highly beneficial tool to aid fisheries managers in visually mapping habitat distributions and assessing environmental change (Kostylev et al., 2001). Various field methods are applied to map marine benthos, such as acoustic mapping techniques including side-scan and multi-beam sonar (Kenny et al., 2003). Remote operated vehicle (ROV) data have also been used to create three-dimensional visualisations (McCann, 2003), but these methods are expensive as they require specialised training and equipment (Tanner et al., 2015). Photographic images and video techniques (such as drop cameras and BRUVs) have been shown to be both cost effective and relatively accurate, as well as capable of sampling the macrobenthos and fish communities (Deter et al., 2012; Tanner et al., 2015). When the photographs are geo-referenced, they can be visualised by GIS software. Simple, cost-effective, photographic assessment methods have therefore been used in a wide range of studies, varying from habitat assessment to studies on fish communities (Bennett et al., 2009; Deter et al., 2012; Garrabou et al., 2002; Harvey and Shortis, 1995; Parravicini et al., 2010; Roberts et al., 1994). Lastly, it is important that the appropriate spatial scale be applied when collecting and mapping habitat data. Different spatial scales will reveal different patterns and associations between related factors, which will consequently influence the overall outcome of a study (Chittaro, 2004).

2.1.5 AIMS

The overall aim of this chapter was to classify benthic habitat types based on substrate, depth and macrobenthic assemblage structure. To achieve this, the objectives of this research chapter were, amongst others, to:

- *Create a detailed bathymetric map of the selected study area within a large and well-established MPA and record fine-scale distributional patterns of the macrobenthic assemblages and substrate types*.

- *Define habitat types from the macrobenthic assemblage, depth and substrate-type data.*

- *Create habitat maps from the defined habitat types, to visualise the spatial distribution of the macrobenthic assemblages and substrate in the study area.*

2.2 METHODS AND MATERIALS

2.2.1 ECOREGION AND STUDY AREA

2.2.1.1 ECOREGION

The study was conducted in the Agulhas inshore ecozone, which forms part of the greater Agulhas Ecoregion (Sink et al., 2012; see Figure 2.1). The Agulhas Ecoregion stretches from Cape Point in the Western Cape to the Mbashe Estuary in the Eastern Cape of South Africa (Lombard et al., 2004; Sink et al., 2012). This area includes 11 MPAs, three of which are considered no-take MPAs (Bird Island, Tsitsikamma and De Hoop; see Sink et al., 2012). The Agulhas Ecoregion is an oceanographically complex area, as it encompasses warm water from the Agulhas Current and cold, nutrient-rich water from wind-induced upwelling cells (Lutjeharms et al., 2001; Roberts and Van den Berg, 2005). The inshore ecozone comprises a wide range of reef and expansive sand habitats (Sink et al., 2012). The shallow reefs in this area are prone to sand inundation, where sand transport periodically smothers low-profile reef structures, reducing biodiversity (Mcquaid et al., 1990; Sink et al., 2012). Reef habitats found in this area are often patchy and are dominated by sponges, ascidians, bryozoans and octocorals (Lombard et al., 2004; Sink et al., 2012).

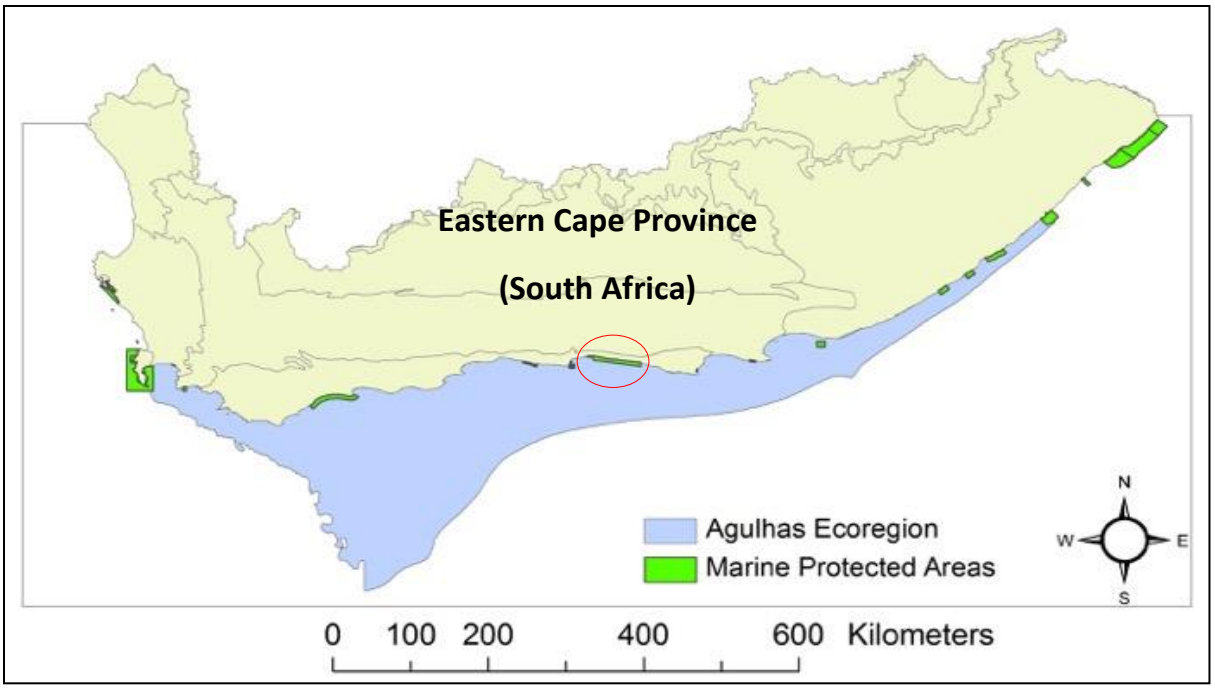

Figure 2.1: The Agulhas Ecoregion (shaded blue), showing the location of all MPAs (shaded in green) along the Eastern Cape coastline of South Africa, with the Tsitsikamma National Park MPA circled in red

2.2.1.2 STUDY AREA

Sampling was conducted in the Tsitsikamma National Park (NP) MPA (Figure 2.2). The MPA stretches 60 km along the South African coastline, from the Groot River East (34°04´S, 24°12´E) to Groot River West (33°59´S, 23°34´E) and extends 5.5 km offshore to a depth of about 100 m (Cowley et al., 2002; Roberts and Van den Berg, 2005). The park is located near the centre of the Agulhas Ecoregion and the benthic habitats consist of an array of steep rocky ridges, interlaying troughs and sandy patches that stretch throughout the length of the park (Hanekom, 2011; Kerwath et al., 2007).

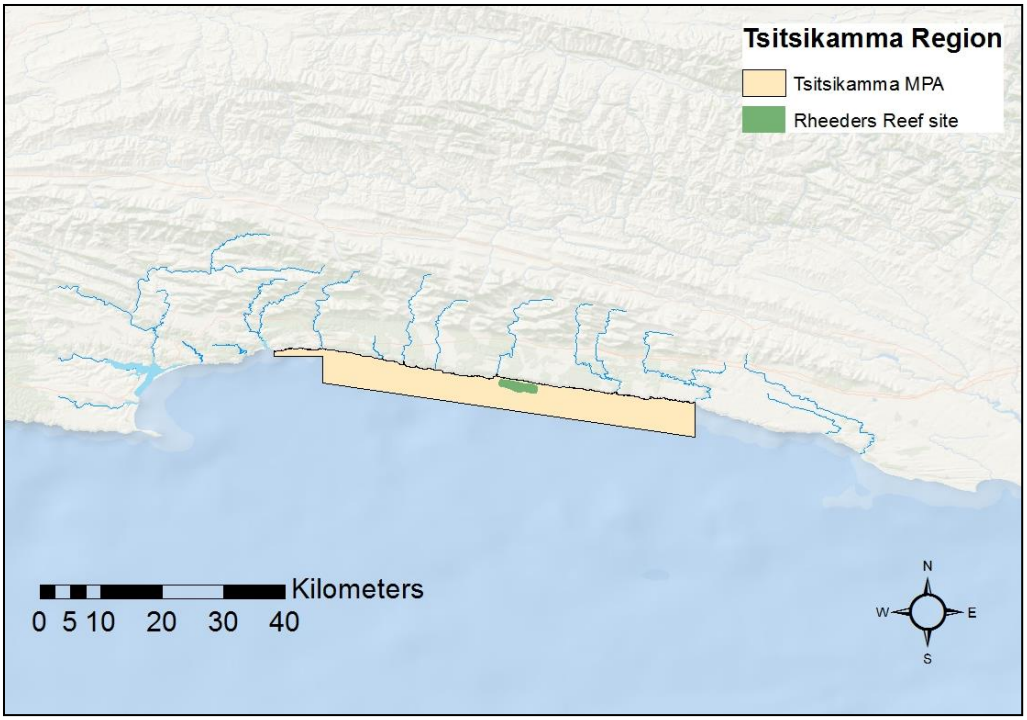

Figure 2.2: The Tsitsikamma NP MPA, showing the location of the study area (green shading), Rheeders Reef, within the MPA

Data were collected from Rheeders Reef, which is situated in the centre of the Tsitsikamma NP MPA (Figure 2.3). The Tsitsikamma NP MPA was chosen as it is South Africa's oldest no-take MPA (established in 1964) and assumed to be free of anthropogenic impacts. The data collected can therefore be considered unaltered by human intervention, and may be used as a baseline for future research. The site also encompasses a variety of different habitats, ranging from high- to low-profile rocky reefs with diverse macrobenthic assemblages and scattered sandy patches (Bernard and Götz, 2012). For the present research, an area of 1x1 km within Rheeders Reef was chosen as the study area (Figure 2.3). The area was deemed appropriate as it was a suitable size to enable comprehensive fine-scale sampling, it was easily accessible from the launch site and included different habitat types spanning a depth range of nine to 44 metres. The depth range was chosen to ensure that a representative range of habitat types and macrobenthic assemblages was incorporated in the study.

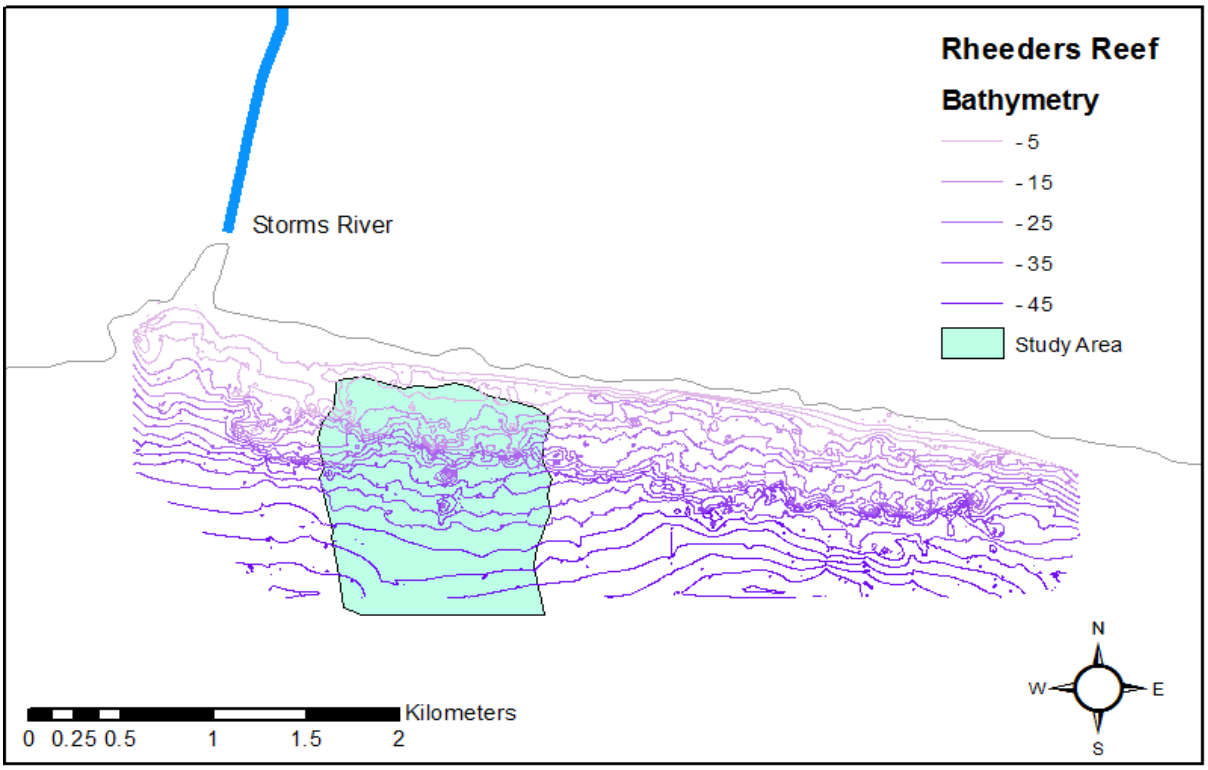

Figure 2.3: A bathymetric contour map of Rheeders Reef showing the location of the study area, shaded in blue, in relation to the launch site (Storms River Mouth) within the Tsitsikamma NP MPA

2.2.2 SAMPLING APPROACH

To obtain habitat information and data on the macrobenthic assemblages and their distribution, a drop camera was employed. A drop camera survey is a quantitative technique that allows for the efficient remote sampling of benthos across a broader range of depths that cannot be safely sampled using SCUBA surveys (Roberts et al., 1994). The drop camera system is primarily employed to collect downwards-facing photo-quadrats of the sea floor. The most commonly used approach for deploying/collecting photo-quadrats using this method is in the form of transects, allowing for the collection of data at various depths and scales (Munro, 2005; Parravicini et al., 2010).

The drop camera used in this study consisted of a circular stainless-steel frame, 65 cm in diameter, with an internal area of 0.33 m^2 (Figure 2.4). Mounted 50 cm above the frame was a stainless-steel camera housing enclosing a GoPro HERO 3 Black camera capable of taking high-definition photos (12 Megapixels). Lighting was provided by two LED (light-emitting device) dive torches attached to the steel frame, to illuminate the circular quadrat.

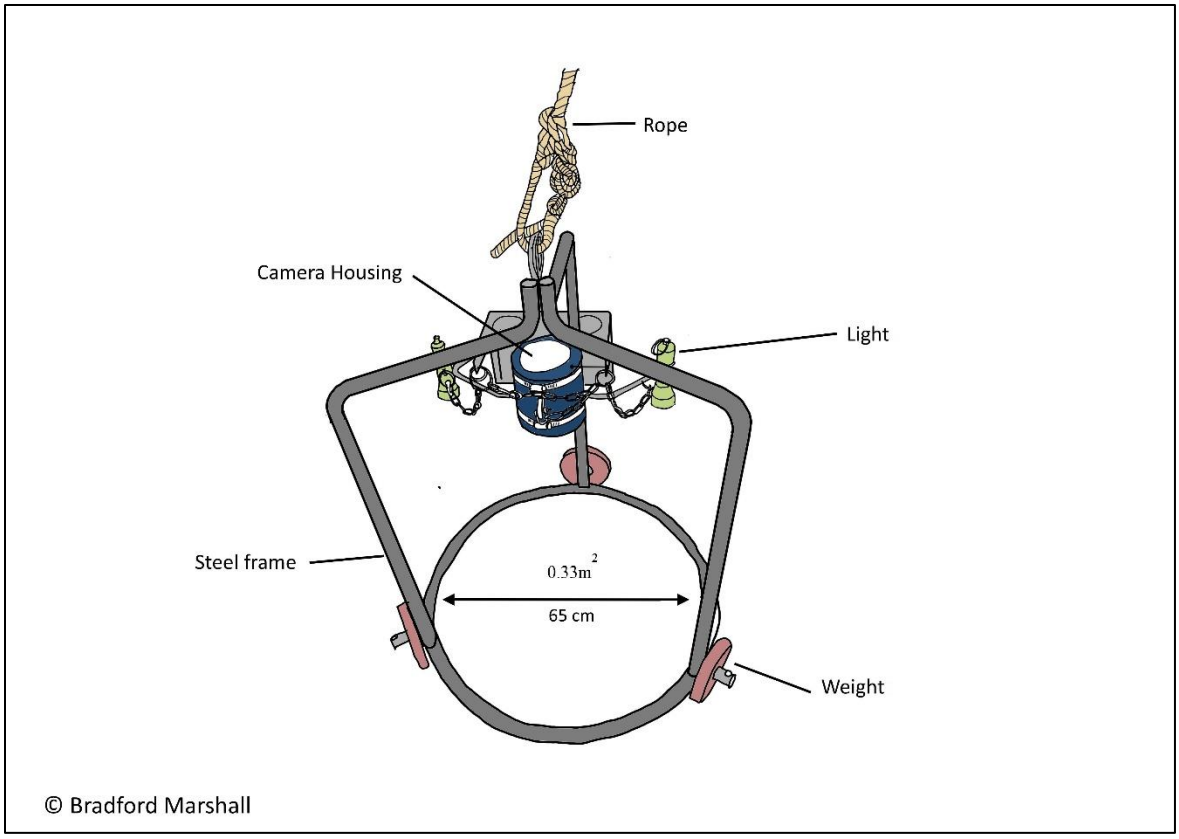

Figure 2.4: Annotated diagram of drop camera setup, with dimensions

Drawing by Bradford Marshall

Within the defined study area, samples (in the form of photo-quadrats) were collected along drop camera transects, with approximately 30 m between each sample, and 30 m separating adjacent transects. This allowed for the collection of fine-scale habitat information from which habitat maps could be produced. The drop camera was deployed off the side of an eight-metre semi-rigid inflatable boat utilising a davit and electric windlass winch to control the descent and ascent of the system. Once deployed, the system was lowered until it reached the substrate and was left for a period of five to eight seconds, after which it was raised approximately five metres above the sea floor whilst the boat moved to the next drop site on the transect. The GoPro camera was set to take a photo continuously every two seconds, resulting in at least two photo-quadrats while the drop camera was on the sea floor. At each drop site, the GPS coordinates, depth and time of day were recorded using a GPS-linked echo-sounder. The time on the GPS was synchronised with the time on the GoPro to allow for the matching of the photo-quadrats to the geographic coordinates and sample depth. To maintain maximum accuracy, the GPS coordinates were

recorded as soon as the system reached the sea floor. The boat's track log data were downloaded from the GPS-linked echo-sounder to verify the data, and were used to create a detailed bathymetric map of the study area.

2.2.3 IMAGE PROCESSING

The photo-quadrat samples were processed in Coral Point Count with extension for Microsoft Excel (CPCe 4.1; Kohler and Gill, 2006). In CPCe, the photo-quadrats were overlaid with an equidistant grid consisting of 100 points. Of these points, 32 which were inside the inner circle of the drop camera frame, were selected for analysis. Substrate type and macrobenthos that occurred under each point were identified according to a standardised hierarchical classification scheme, the Collaborative and Annotation Tools for Analysis of Marine Imagery (CATAMI, http://www.catami.org). The CATAMI classification scheme is a tool developed to provide a standardised classification method for scoring marine biota and physical characteristics from underwater imagery (Hill et al., 2014). The scheme is a hierarchal taxonomy-based system which includes morphological categories, thereby accounting for individuals that cannot be identified to species level (Ball et al., 1963; Hill et al., 2014). For data analysis, a subset of categories from the CATAMI classification scheme was chosen to determine the macrobenthos within the study area (Table 2.1). The major categories chosen were based on the most commonly occurring classes of macrobenthic species.

Table 2.1: Subset of major categories of macrobenthos and substrate type used, based on the CATAMI classification scheme

Biota	Substrate
Bryozoa: Hard	Rock
Bryozoa: Soft	Boulders and cobbles
Cnidaria: Anemones	Pebbles
Cnidaria: Corals: Fleshy Mushroom	Sand: Coarse (shell fragments)
Cnidaria: Corals: Non-Fleshy: Arborescent	Sand: Fine (no shell fragments)
Cnidaria: Hydrocorals	
Cnidaria: Hydroids	
Sponges: Crusts	
Sponges: Cup-Likes	
Sponges: Erect Forms	
Sponges: Massive Forms	
Macroalgae: Encrusting	
Macroalgae: Erect	
Ascidians: Stalked	
Ascidians: Unstalked	

2.2.4 DATA ANALYSIS

The data for this study were analysed in PRIMER (version 6) with the PERMANOVA add-on package (Anderson et al., 2008; Clarke and Gorley, 2006; Clarke and Warwick, 2001), after which habitat maps were created using GIS (ArcMap 10.3).

The percentage cover of the macrobenthos was estimated from the photo-quadrats analysed in CPCe. This was calculated by taking the relative frequency (number of points) of each identified taxa in the photo-quadrat and dividing it by the total number of points (32) analysed in the photo. From this, two sets of data were prepared: the first contained only biological data (percentage cover of macrobenthic taxa) while the second included the percentage cover of different substrate types, together with the water depth of each photo-quadrat (environmental data). In addition to percentage cover data, each site was further categorised as sand or reef, where sand sites consisted of 100% sand and sites that included some consolidated reef were classified as reef. Based on the CATAMI classification scheme, 20 major categories were identified from the photo-quadrats (five of which were substrate types) and used in the analyses to describe the habitat types (Table 2.1). In PRIMER the biological data were square-root transformed to down-weight the contributions of abundant macrobenthos, relative to rare macrobenthos (Clarke and

Warwick, 2001). A pairwise similarity matrix was then constructed based on a Bray-Curtis resemblance (Clarke and Warwick, 2001).

2.2.5 Classification of habitat types

The aim of this chapter was to identify habitat types from macrobenthos, substrate and depth data, and to map the distribution of these habitat types within the study area. This was achieved with the use of a linkage tree (LINKTREE procedure), a non-metric variation of the multivariate regression tree approach of De'Ath (2002), within the PRIMER software package (Clarke and Gorley, 2006). LINKTREE employs a cluster analysis to group biological data (in this case, macrobenthos) according to similarities between samples. At each split of the tree, the separation of groups is measured using the ANOSIM R-statistic, while the measure B% quantifies the absolute difference between groups, given as a percentage (Clarke and Gorley, 2006). The environmental variables (depth and substrate) associated with each cluster were then used to describe the physical habitat of the residing macrobenthos. The minimum group size of the clusters in the LINKTREE procedure was set to 70 samples, as preliminary analysis resulted in the formation of too many groups, making it difficult to extract general patterns (Clarke and Gorley, 2006).

The analysis was run in conjunction with a similarity profile analysis (SIMPROF) which uses permutations to test, statistically, whether clusters are truly present in unstructured data (Clarke and Gorley, 2006). The SIMPROF test examines whether similarities in the data are higher or lower than the mean of those that are expected to occur by chance. If similarities differ from the expected mean, it indicates evidence of true structure or groups in the data (Clarke et al., 2008). The significance of the split in the LINKTREE is thus given by the test statistic π and the corresponding p-value of the SIMPROF test.

2.2.6 Spatial analysis

The second analysis focused on creating fine-scale habitat maps in GIS (ArcGIS 10.3; ESRI, 2011). The produced maps included a bathymetric map and a map describing the distribution of habitat types identified from the LINKTREE procedure. The bathymetric map was created using the depth data gathered from the boat's track log, and the depth and GPS coordinate information from each photograph. The data from these points were converted into a raster layer and interpolated using the Natural Neighbour Technique (Boissonnat and Cazals, 2001). Contours were fitted to the interpolated map at one metre intervals. Following this, a fine-scale habitat map was created based on the habitat types defined by the LINKTREE procedure, to show the distribution of biota and substrate throughout the sampled area. This was achieved by creating a Thiessen polygon map in GIS, which defines a polygonal area around a sample

point, whereby any location within that polygon is characterised by the attributes of that point (Brassel and Reif, 1979).

2.3 RESULTS

In all, 944 photo-quadrats were collected using the drop camera. Of these, 709 (74.2%) were found on sand and had no visible macrobenthic biota, and 246 (25.8%) were classified as reef samples. The macrobenthos occurring on the reef samples consisted of sponges (30.94%) (found to be the most abundant biota), followed by cnidaria (18.25%), bryozoa (14.92%), macroalgae (12.39%) and ascidians (5.20%). The remaining 14.31% was found to contain no visible microbenthic organisms, and was classified based on the visible substrate type.

2.3.1 HABITAT TYPES

The LINKTREE cluster was split into four groups (A–D) and formed five different habitat types that were broadly defined as *Shallow Sand*, *Shallow Reef*, *Deep Reef*, *Deep Sand* and *Patch Reef* (figures 2.5 & 2.6). At split A, the sand-dominated habitats, with more than 62.5% sand, were separated from samples that contained less than 59.4% sand (ANOSIM R = 0.68; $\pi = 1.43$; $p < 0.001$; Figure 2.5). The sand-dominated samples were separated according to water depth at split D into *Deep Sand* (> 21.2 m) and *Shallow Sand* (< 21.2 m) habitats (ANOSIM R = 0.07; $\pi = 0.03$; $p < 0.005$). At cluster B, habitats that contained more than 3.1% coarse sand were split from those that contained less than 3.0% coarse sand (ANOSIM R = 0.2; $\pi = 6.97$; $p < 0.001$) separating the *Patch Reef* habitat from the reef habitats. The *Deep Reef* (> 14.7 m) and *Shallow Reef* (< 14.7 m) habitats were formed at split C (ANOSIM R = 0.12; $\pi = 6.88$; $p < 0.001$).

Patch Reef, found throughout the sampled depth range and classified according to substrate, contained only those samples where coarse sand and reef were present in the photo-quadrat. The total percentage cover of macrobenthos in the *Shallow Reef* and *Deep Reef* habitats was 85.8% and 92.9% respectively, while the *Patch Reef* habitat predominantly consisted of coarse sand (60.7%) and had 32.7% macrobenthos cover. The remaining cover in the *Shallow Reef* habitat consisted of bare rock (0.7%), boulders and pebbles (6.9%) as well as fine sand (6.6%). In the *Deep Reef*, 5.5% of the substratum consisted of bare rock and pebbles, and 1.6% of fine sand. The *Shallow Sand* habitat consisted of 99.2% fine sand with only 0.8% macrobenthic cover, while no macrobenthos was found in the *Deep Sand* habitat which consisted of 100% fine sand (Figure 2.6).

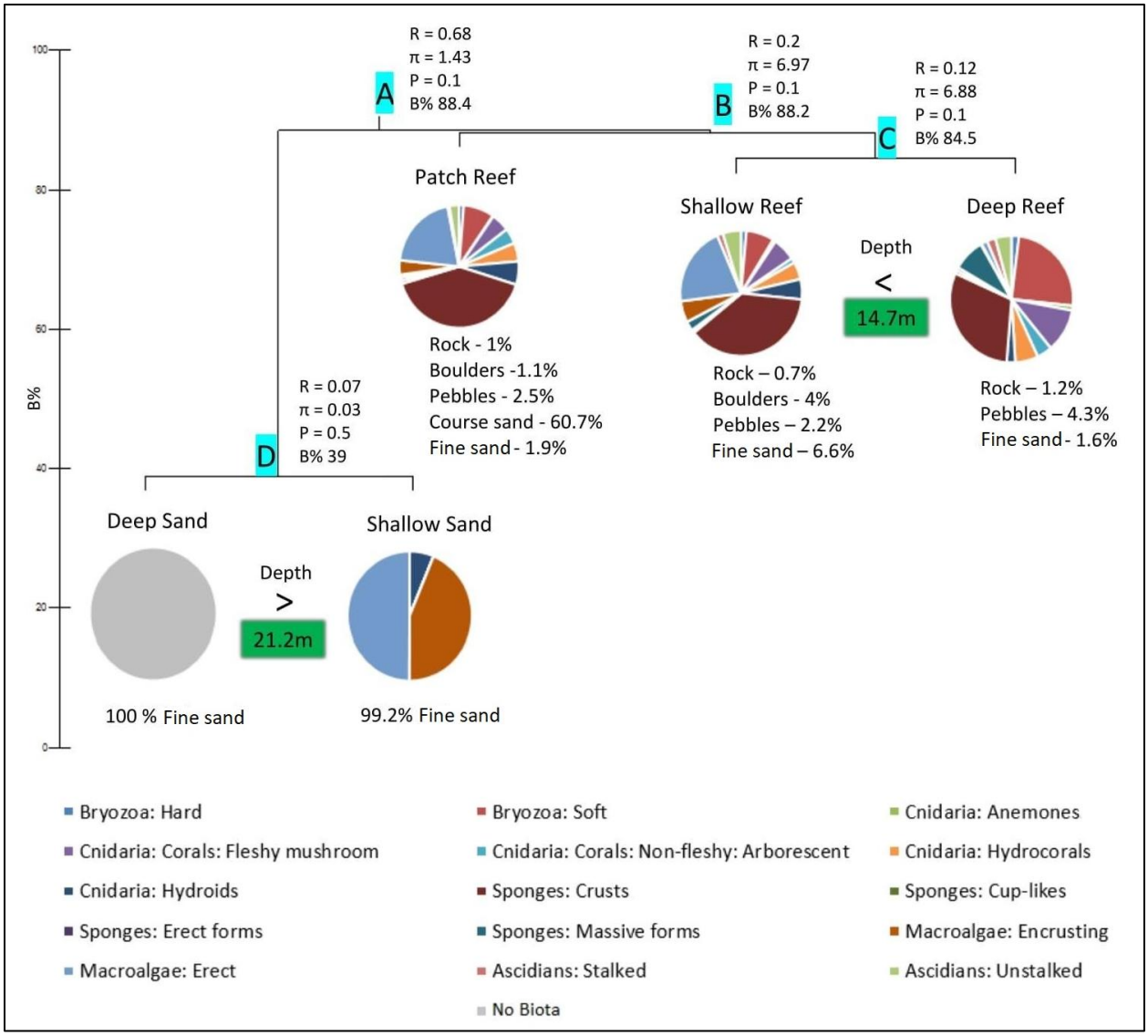

Figure 2.5: LINKTREE analysis showing the percentage contribution of macrobenthos (pie charts) and substrate (contribution indicated below respective pie charts) in each habitat type. The ANOSIM R measures the degree of separation between groups (R; 0–1; where 0 signifies no similarity and 1 complete similarity) and the absolute measure of difference between clusters (B%) is shown for each habitat type. The test statistic π and p-value (P) indicate the level of significance of the split between clusters (%)

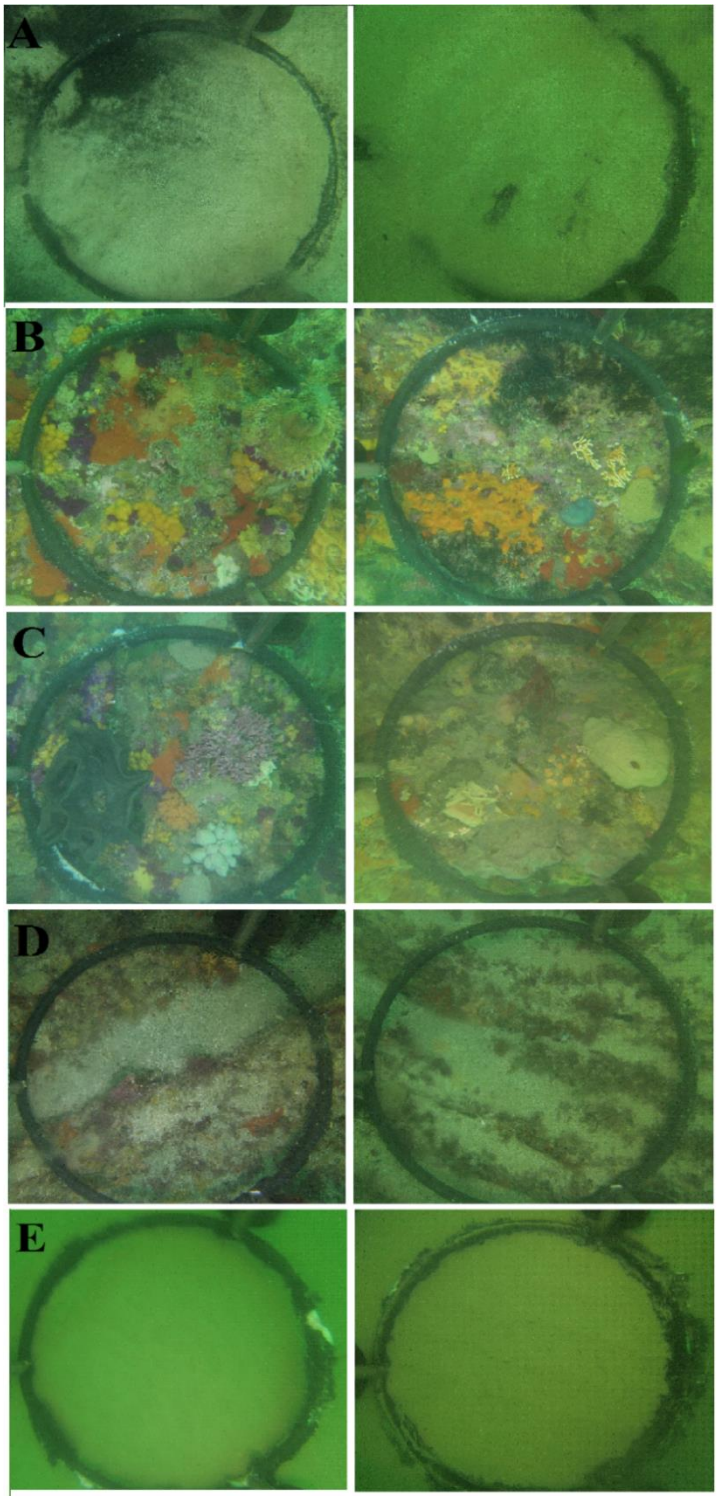

Figure 2.6: Photo quadrats of each habitat type. *Shallow Sand* (A), *Shallow Reef* (B), *Deep Reef* (C), *Patch Reef* (D) and *Deep Sand* (E)

2.3.2 MACROBENTHIC ASSEMBLAGE OF HABITAT TYPES

In the *Shallow Sand* habitat, the 0.8% macrobenthic cover contained three major macrobenthic biota groups and was dominated by the presence of erect and encrusting macroalgae (94%), with some intermittent hydroid cover (6%). The *Patch Reef* habitat type contained 14 of the 15 major macrobenthic biota groups, with the absence of anemones, and was characterised by a high percentage cover of sponges and macroalgae, which together accounted for 68% of the macrobenthos cover found in this habitat type. Since the *Patch Reef* habitat was not defined by depth, it is important to note that the macroalgae in this habitat were predominantly found in the shallow regions which correspond to the *Shallow Reef* habitat type (< 14.7 m), while sponges were found in both the shallow and deeper regions of the habitat type. The *Shallow Reef* habitat type was also dominated by sponges (41%) and macroalgae (27%), with considerably lower percentage contributions of cnidarians and bryozoans (17% and 8% respectively). In the *Deep Reef* habitat type, cnidaria and bryozoans were the most abundant taxa, together contributing 51% to the macrobenthic cover, while macroalgae only contributed 2% to the cover. Sponges, in their massive forms, were also found to be more abundant in the *Deep Reef* habitat than in other habitats (8% in the *Deep Reef*; 2% in *Shallow Reef*; 1% in *Patch Reef*). Ascidians were found in relatively low abundances when present in a habitat type, with the highest contribution of 7% in the *Shallow Reef* habitat and lower contributions of 6% and 3% in the *Deep Reef* and *Patch Reef* habitat types respectively. By contrast, encrusting sponges contributed most to the macrobenthic assemblages in all reef habitats, with a 41% contribution in the *Patch Reef* habitat, 38% in *Shallow Reef* and 31% in the *Deep Reef*.

2.3.3 GIS MAPS

The bathymetry map showed the formation of steep slopes and ridges in the shallower regions of the study area (between approx. seven and 24 m; see Figure 2.7 A), indicated by the bunching of contour lines. Most noticeable is the presence of a steep slope that stretches across the width of the study area. This steep slope is situated in the region where the bathymetry changes from 15–19 m to 20–24 m (as indicated by contour lines in close proximity to one another over a fine spatial scale). In the deeper regions, depth increases more gradually and the bathymetry of the region is relatively uniform, with no prominent ridges or deep troughs.

The generated habitat map showed a pattern in the distributions of the five habitat types (Figure 2.7 B). The inshore region of the study area is dominated by the *Shallow Sand* habitat, with the exception of some *Shallow Reef* and *Patch Reef* habitats found close to the coastline. The shallow and deep reef habitats form part of a contiguous reef system between depths of approximately 10 m and 20 m, with intermittent

patches of *Shallow Sand* and *Patch Reef* habitats. The latter is scattered throughout the study area, and predominantly found where reef habitats are nearby. Below the major reef complex lies the relatively homogenous large *Deep Sand* habitat, extending to a depth of approximately 40 m (Figure 2.7 B). The bathymetry of the sand habitats appears to be relatively flat, with a gentle depth gradient, while areas of high profile are found in the reef habitats. Two distinct shallow ridges are found within the *Shallow Reef* habitat, rising to an approximate depth of 9 m while a steep slope is found where the *Deep Reef* habitat borders the *Deep Sand* (Figure 2.7).

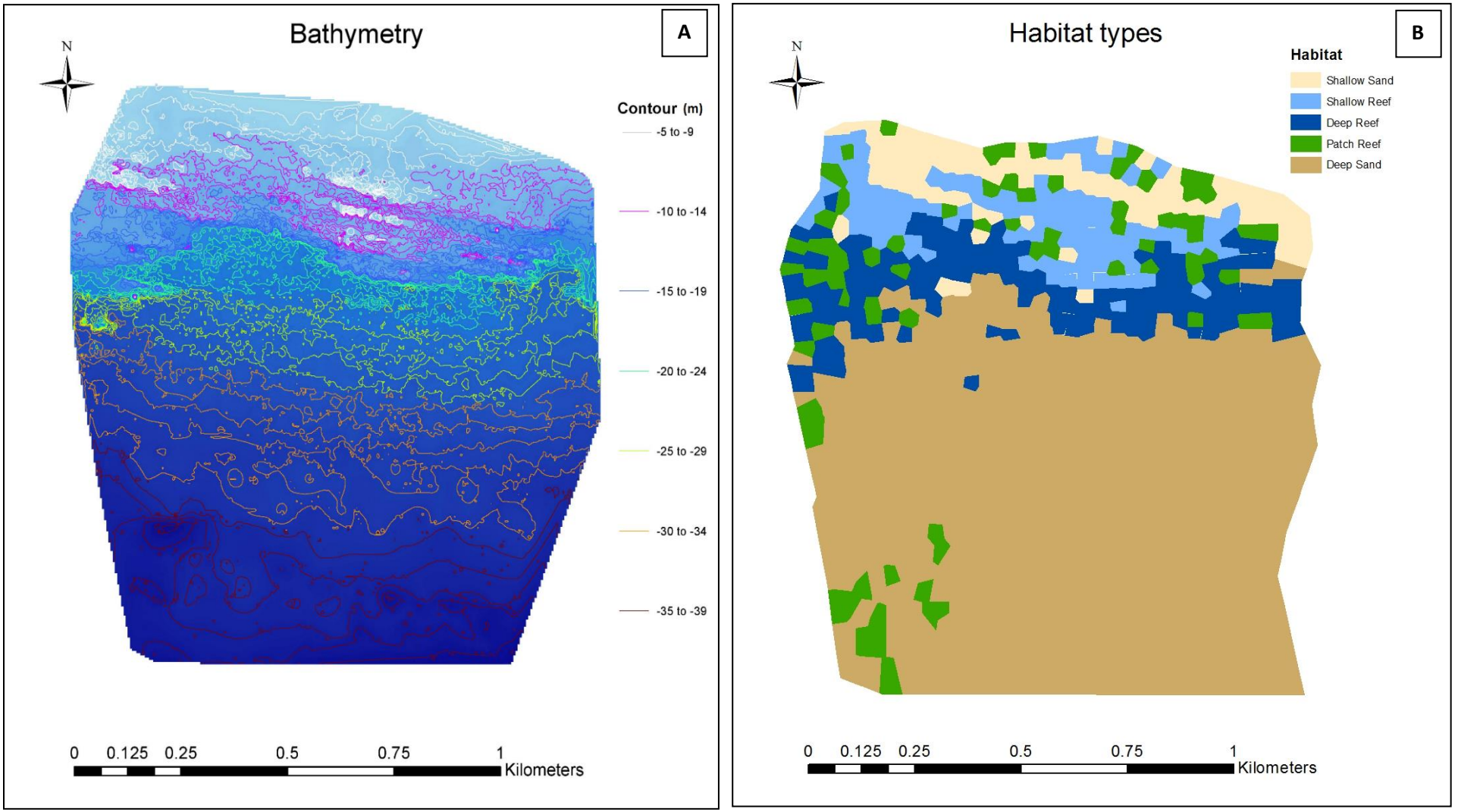

Figure 2.7: Bathymetric map of the study area situated in the Tsitsikamma NP MPA showing contour lines at 1 m intervals (A) and habitat map of the study area showing the distribution of the five habitat types (B).

2.4 DISCUSSION

The overall aim of this chapter was to identify and map the distribution of different habitat types within the study area, to establish and test fish–habitat relationships in the subsequent chapter. The habitat types defined by the LINKTREE analysis of the photo-quadrat data and abiotic variables corresponded well with the expected distribution of reef and sand sites indicated by the bathymetric map. The habitat map displayed the distribution of the different habitat types, and the bathymetry clearly indicated different depth zones within the study area. The LINKTREE analysis also indicated that depth-related patterns of macrobenthic distribution were evident in both the reef and sandy habitats. Low macrobenthic diversity was associated with the sandy habitats, while high diversity was found in the reef habitats.

2.4.1 MACROBENTHIC DISTRIBUTION PATTERNS

From the results, depth-related changes in macrobenthic distribution within the study area were evident. This was expected, as various studies have demonstrated that macrobenthic assemblages change with depth (Deter et al., 2012; Flach and De Bruin, 1999; Garrabou et al., 2002; Heyns et al., 2016; Macdonald et al., 2012). The reason for this depth-related zonation is thought to be explained by a number of factors: first, shallower areas receive more light, which enables benthic primary producers to grow in abundance (Gattuso et al., 2006); second, Heyns et al. (2016) suggest that differences in macrobenthic distribution related to the depth gradient can be attributed to sessile invertebrates occupying different niches. Under non-upwelling conditions, the Tsitsikamma coastline usually displays thermal stratification as well as high current velocities in shallower waters (Roberts and Van den Berg, 2005). Therefore, with an increase in depth, predictable changes in environmental variables such as light, water movement and temperature, are apparent. Different macrobenthic species respond to these environmental changes by adopting different resource management regimes (Heyns et al., 2016). Thus, a change in macrobenthic species composition over a depth gradient would be expected. Along with factors such as oxygen concentration, sediment type and topography (Howell et al., 2002), a range of different niches is created over a depth gradient which, in turn, causes a changeover of macrobenthic species.

Macrobenthic species distribution was concentrated on the main reef complex where steep slopes and high ridges were present. The habitat and bathymetric maps showed that the *Deep Reef* and *Shallow Reef* habitats cover the majority of these areas, and comprise 66.4% of the total macrobenthic cover. This is likely due to the fact that the majority of the substrate in this area consisted of hard rock or large boulders, providing suitable substrate for sessile and sedentary biota to attach to. Higher diversity and densities of

macrobenthos are expected to occur on hard substrate, as it allows species to firmly establish themselves (Barros et al., 2000). The *Shallow Sand* was the only one of the sandy habitats to contain any macrobenthic cover, although the macrobenthos accounted for less than 1% of the total cover in this habitat. The low abundance of macrobenthos in sandy habitats was also evident in other studies. Kostylev et al. (2001) found very low abundances and diversity of visible macrobenthos in shallow sandy habitats, with no macrobenthic species present over large sandy bedforms. The low abundance of macrobenthos in shallow, sandy waters could be attributed to the fact that these are high-energy environments, making it difficult for sessile invertebrates to establish themselves (Kostylev et al., 2001; Zea, 2001). This is particularly true in the Tsitsikamma area, as the coastline is associated with high wave energy and large-scale movements of sand (Roberts and Van den Berg, 2005). Sand movement would result in exposed low-profile reef being covered, smothering macrobenthos and inhibiting their ability to establish themselves in such an environment. At the same time it would inhibit the ability of macrobenthic species that prefer stable sand habitats to establish themselves.

2.4.2 MACROBENTHIC ASSEMBLAGE

Only three categories of visible macrobenthos were found in the *Shallow Sand* habitat, these being erect macroalgae, encrusting macroalgae and hydroids. Soft-bottom invertebrate communities generally consist of infaunal organisms that bury themselves into the sediment (Lardicci et al., 2004). To sample such infaunal communities, extractive methods such as grabs would possibly provide better insight into sandy habitat assemblage composition. This, and the expected instability of the soft sediments in shallow wave-dominated environments, would explain the low abundance of visible macrofauna detected on the surface of sandy substrates, especially when using photographic methods (as in this study). Macroalgae are usually associated with *Shallow Reef* communities (Heyns-Veale et al., 2016; Juanes et al., 2008). There are, however, instances where macroalgae were found in soft-bottom sediment (Albrecht, 1998; McKinnon et al., 2009; Pihl et al., 1999). The presence of encrusting macroalgae in the *Shallow Sand* habitat is a surprising result, which suggests that the sand layer in this habitat is patchy and dynamic. It is most likely that a thin layer of sand had moved onto the low-profile reef, allowing sessile invertebrates, which were attached to the rocky substrate, to stick out of the sand. As such, it is possible that sand in the area was deposited relatively recently, which might explain why no hard substrate was recorded within the habitat, and might account for the presence of erect macroalgae which would still be visible if covered with a thin layer of sand. Hydroid species also rarely settle on soft-bottom sediments, but have been closely associated with polychaetes, hermit crabs, parasitic copepods, bivalves, gastropods, tunicates and

some fishes (Boero, 1984), many of which are infauna sand-dwelling species (Lardicci et al., 2004). Kostylev et al. (2001) also found solitary hydroids in shallow sandy sediment, however, at the Tsitsikamma NP MPA, the presence of hard substrate covered with sand is the most likely explanation for the hydroid species observed. The research most comparable to the current study was also conducted in the Tsitsikamma NP MPA by Heyns et al. (2016). However, the deep reef habitat which those researchers surveyed was 45–75 m, i.e., deeper than the reefs in the current study (9–44 m). As such, the reefs surveyed in this study were only compared to the shallow habitat of Heyns et al. (2016).

The most noticeable difference between the reef habitats was the high abundance of macroalgae in the *Shallow Reef* and bryozoans in the *Deep Reef*. Heyns et al. (2016) observed similar patterns where bryozoans and sponges dominated deeper depths, while the macrobenthic assemblages of *Shallow Reef* habitats were populated by high abundances of macroalgae, ascidians and sponges. Although ascidian cover was generally low in the current study, cover was highest in the *Shallow Reef* habitat.

Bryozoans are colonial suspension feeders, and their feeding efficiency at different flow regimes can determine their distribution (Pratt, 2008). Shallow depths are usually associated with faster flow rates, greater turbulence and more frequent disturbance, while water velocity is expected to decrease as depth increases (Roberts and Van den Berg, 2005). Bryozoans in shallow waters are possibly outcompeted by faster-growing organisms (e.g. sponges and ascidians) that are better able to colonise disturbed shallow habitats which are exposed to strong wave action and storm damage. With an increase in depth, the associated decrease in currents, light and water movement may allow bryozoans to outcompete the light-dependent and faster-growing organisms typical of shallow environments (Heyns et al., 2016).

The broad distribution of sponges observed in this study was not surprising, as their extreme plasticity enables them to morphologically change their shape to adapt to different environmental conditions (Bell and Barnes, 2000; Heyns et al., 2016; Kaandorp, 1999; Okamura and Partridge, 1999). Sponges can feed on a large range of particle sizes (Heyns et al., 2016; Jackson and Winston, 1982). Thus, the lower flow rates of the *Deep Reef* habitat would suggest that sponges are able to feed in different environmental conditions, which explains their wide distribution (Zea, 2001).

2.4.3 Review of methodological approach

Multibeam echo-sounder technology has been used to determine detailed bathymetry map of the sea floor in multiple studies (Che Hasan et al., 2012; George et al., 2007; Kostylev et al., 2001; Tissot et al., 2006). This technology provides accurate and complete acoustic sea floor coverage, as well as depth

information (Che Hasan et al., 2012). Notably, multibeam echo-sounders need to be used in conjunction with other methods to survey macrobenthos (most often ROVs), which requires specialist skill to operate and are expensive to use (Tanner et al., 2015; Wright and Heyman, 2008). In the current study, photo-quadrats were the most suitable method to use, as additional habitat information could be extracted from the photographs, along with the depth and substrate type. Although the use of a multibeam echo-sounder would have produced a more accurate and detailed bathymetry map, the depth information gathered from the photo-quadrats and boat's tracklog data was able to accurately identify steep ridges and slopes within the study area. The method was relatively inexpensive and the equipment was easy to operate. The use of the CATAMI classification in conjunction with the drop camera method provided an "off-the-shelf" protocol, which required minimal adjustments to suit the application needs of the study. In South Africa, suitable photographic ID guides of reef macrofauna are lacking and there are many problems associated with identifying similar-looking organisms from photographs. The CATAMI protocol was, however, able to provide an adequate description of the macrobenthic community to delineate species clusters associated with environmental variables and define habitats.

2.4.4 Conclusion

The habitat types and their distribution corresponded well to the bathymetric maps, and general patterns evident in the macrobenthic assemblage correlate with previous studies. The relatively inexpensive drop camera method enabled the identification of distinct habitat types at an adequate scale, to allow for the assessment of the fish–habitat relationships in the following chapter. Future work on the current dataset could endeavour to conduct a multi-beam survey of the study area, to contrast against the single-beam echo-sounder data of the boat's GPS, incorporate the measure of bathymetric variability into the habitat-type descriptions, examine the effect of bathymetric variability on macrobenthic species diversity, and investigate patterns of spatial autocorrelation within the dataset.

CHAPTER 3

3 FISH–HABITAT ASSOCIATIONS AND THE EFFECT OF BAIT

3.1 INTRODUCTION

3.1.1 FISH AND THEIR HABITAT

A range of complex interactions occur between fishes and their environment. This facilitates their survival in a given habitat, and includes biotic and abiotic interactions such as predator–prey relationships or fish species utilising habitats for shelter (Garpe and Öhman, 2003; Valesini et al., 2004). These interactions are important when investigating the associations between fish and certain habitats, as they can determine the nature of the relationship between a fish and its environment. Understanding fish–habitat associations is, in turn, important for ecosystem-based fisheries management (EBFM). The ecosystem approach to fisheries emphasises the vulnerability of habitats and aims to protect the ecosystem as a whole, in turn protecting all fish species associated with the given habitat (Garcia et al., 2012; Pikitch et al., 2004). Commercially important fish species (e.g. roman (*Chrysoblephus laticeps*) or snoek (*Thyrsites atun*); see Griffiths, 2000) can occur in a variety of different habitat types. It is therefore important to accurately predict what fish species are likely to occur in certain habitat types. Knowing the habitat preferences of commercially important fish species enables fisheries managers to effectively manage such fish species, by protecting the areas where they are likely to occur in high abundances (Valesini et al., 2004). To achieve this, the nature of the associations between fish and their habitat needs to be determined.

Reef fish distribution is often patchy, with species usually irregularly dispersed over multiple spatial scales (Gust et al., 2001). In general, reef fish will often be observed in high abundance where the substratum suits their habitat preferences. This typically occurs in areas of high structural complexity where specific food items and shelter requirements are available (Fischer et al., 2007; Palma and Ojeda, 2002). Within such areas, fish assemblages are often separated across a depth gradient, with small herbivorous species being found in shallow habitats and larger predatory species at depth (Andradi-Brown et al., 2016; Heyns-Veale et al., 2016). Environmental conditions in different habitat types are also known to effect reef fish distribution, as many species vary in degrees of habitat specialisation (Fitzpatrick et al., 2012).

To date, various sampling techniques, each with its own set of advantages and limitations, have been used to survey fish populations (Mallet and Pelletier, 2014). Video techniques have gained popularity over recent years, as they are non-destructive (Unsworth et al., 2014) and able to sample fish communities in a range of different habitats (Samoilys and Carlos, 2000). One such technique is the baited remote underwater stereo-video system (stereo-BRUVs) which has been used in multiple studies around the world over recent years (Cappo et al., 2003; Harvey et al., 2007; Heyns-Veale et al., 2016; Parker, 2016). The stereo-BRUVs method employs bait to draw fish towards the camera's field of view. The application of bait with these systems has been shown to have a positive effect on species abundance, as well as species richness (Bernard and Götz, 2012; Dorman et al., 2012; Harvey et al., 2007). The stereo-BRUVs method provides data with low levels of variability, which reduces the level of sampling effort required to gather species abundance, richness and size data of reef fish over a wide range of depths and habitats (Bernard and Götz, 2012; Parker, 2016). Combined with the fact that stereo-BRUVs suffer from less observer bias than *in situ* methods such as UVCs whilst sampling (Bernard et al., 2014), the method is advocated as a highly robust and powerful tool to sample subtidal reef fish populations (Bernard and Götz, 2012; De Vos et al., 2014; Mallet and Pelletier, 2014). Despite this, issues have been raised regarding the potential biases introduced by the addition of bait (Dorman et al., 2012). Such biases include the fact that bait predominantly attracts predatory species, which could lead to an underestimation of the herbivorous species present in the area (Cappo et al., 2003). In areas where fish abundance is high, the presence of bait could lead to a saturation of the field of view, resulting in an underestimation of fish abundance in general (Cappo et al., 2004; Willis et al., 2000). On the other hand, in habitats where fish are scarce, abundances could be overestimated due to bait attraction from surrounding areas (Bernard and Götz, 2012; Willis et al., 2000). The unbaited configuration (stereo-RUVs) is able to provide data that are free from the effects of bait, assumed to depict a "natural" representation of the fish community. However, the use of stereo-RUVs, does not come with the advantages of stereo-BRUVs, and requires a considerably higher level of sampling effort to produce data that are comparable to those of stereo-BRUVs (Bernard and Götz, 2012; Watson et al., 2010). As such, they can be seen to be less cost effective than stereo-BRUVs and are therefore not ideal in long-term monitoring programmes. Given these uncertainties, the effect of bait on fish–habitat associations needs further clarification.

Research that aims to determine fish–habitat associations at large scales (hundreds of kilometres) typically focuses on broad-scale habitat variability and reef fish distribution (e.g. Williams and Bax, 2001). At broad scales, the effects of latitudinal gradients, temperature or water depth on species occurrence are commonly seen (Anderson and Yoklavich, 2007; Darling et al., 2017; Floeter et al., 2001; Heyns-Veale

et al., 2016; Poore et al., 2012). It is highly unlikely that the use of bait when sampling with stereo-BRUVs would influence the data collected at this broad scale, as fish species will not be attracted from different temperature regimes or major depth zones. This is simply because the size of the bait plume is not large enough and the deployment time is too short. It is likely that when looking at large-scale distribution patterns, the use of bait will rather provide a more complete assessment of the fish assemblages seen at a given site.

Fine-scale associations (tens of metres), on the other hand, may be influenced by bait as the bait plume may overlap with multiple habitat types. Although various habitats share many species (Williams and Bax, 2001), the addition of bait may attract fish from neighbouring habitat types. This could lead to an overestimation of certain fish species being seen in a habitat type, resulting in an inaccurate or even false assumption of those species being associated with that habitat type. Furthermore, given that bait is assumed to attract mainly predatory species, the lower detectability of non-predatory species may also reduce the ability of baited methods to detect habitat associations within this group.

To fully understand the potential biases caused by the addition of bait in the stereo-BRUVs method, the effect of bait on fine-scale fish–habitat associations needs further clarification. The findings of this research will contribute towards optimising the use of stereo-BRUVs data and provide baseline data on fine-scale fish–habitat associations in warm, temperate regions of South Africa.

3.1.2 AIM

The overarching aim of this chapter is to determine whether bait has an effect on the associations between fish and their habitats. The objectives are therefore to:

- *Describe the fish community within the study area mapped out in Chapter 2 and determine how it changes with increasing depth.*
- *Determine the associations between the fish community and habitat types from video samples.*
- *Determine the effect of bait on the type and strength of the observed associations.*

3.2 METHODS

3.2.1 ECOREGION, SAMPLING AREA AND STUDY SITE

The study site, Rheeders Reef, was chosen as it is situated in the centre of the Tsitsikamma NP MPA, which was established in 1964 (Sink et al., 2012), meaning its faunal assemblages have been free from exploitation for over 50 years. Rheeders Reef was considered to represent a close-to-pristine ecosystem, with fish distribution patterns being the result of natural, environmental and biological processes, rather than anthropogenic disturbances. Descriptions of the Agulhas Ecoregion, the Tsitsikamma NP MPA, Rheeders Reef and the fine-scale habitat in the study area are provided in Chapter 2.

3.2.2 SAMPLING APPROACH

To investigate the effect of bait on the rocky reef fish community, data were gathered using stereo-BRUVs (baited treatment) and stereo-RUVs (unbaited treatment). Within the area mapped out in Chapter 2, stereo-BRUVs and stereo-RUVs were deployed at separate sites that were randomly selected using the random point distribution function in ArcMap (version 10.3).

Bait acts as a fish attractant and thereby improves the sampling efficiency for the majority of fish species (Bernard and Götz, 2012; Harvey et al., 2007). This effect is, however, considered to bias the data collected by stereo-BRUVs, as bait has been shown to increase the counts of predatory species (Bernard and Götz, 2012). Since the unbaited configuration lacks this attractant effect, it is presumed to provide a more natural or unbiased representation of the reef fish community. The inclusion of both the stereo-BRUVs and stereo-RUVs methods in the sampling design therefore allowed the effects of bait on the fish–habitat interactions to be measured. To ensure that 95% of fish species are sampled at their maximum abundances, Bernard and Götz (2012) recommend a minimum deployment time of 35 minutes and 50 minutes for the unbaited and baited methods, respectively. To achieve the objective of determining whether stereo-BRUVs can be used to measure fish–habitat association, a deployment time of 60 minutes was applied for baited samples, as it is considered to be the global standard for BRUVs samples. For logistical reasons, and to maximise the potential MaxN/species richness in the stereo-RUVs footage, a deployment time of 40 minutes was applied.

To ensure that data collected by the two methods would be comparable in terms of variability, it has been suggested that the stereo-RUVs method requires a higher sampling effort (Bernard and Götz, 2012; Watson et al., 2010). Data that indicate a higher abundance of fish, such as found in the stereo-BRUVs method, and are less variable, are preferable since statistically significant trends are more likely to be in

evidence (Thompson and Mapstone, 1997). The stereo-RUVs method provides data that are highly variable and are generally zero inflated (Bernard and Götz, 2012). As such, to obtain data that are comparable with those of stereo-BRUVs with a similar statistical power, a higher sampling effort is required. Therefore, in the present study, the sampling effort of the stereo-RUVs method was increased by 30%. To account for the potential variability of the fish community over time, data were collected in the summer seasons, over two consecutive years (2015 and 2016).

The use of bait also poses the potential risk of pseudoreplication (Guisan and Zimmermann, 2000; Heffner et al., 1996), which may be the result of counting the same individual in separate but adjacent stereo-BRUVs deployments. To reduce the effect of pseudoreplication, the baited samples were either collected on separate days or separated by a minimum distance of 300 m, thus ensuring that the bait plumes of simultaneous stereo-BRUVs deployments did not overlap (Harvey et al., 2007). In contrast, unbaited samples were separated by at least 50 m, as stereo-RUVs were assumed to have a negligible attraction effect on the fish community. Furthermore, reef fish species are generally described as highly resident (Chapman and Kramer, 2000; Samoilys, 1997). In South Africa, Kerwath et al. (2007) found that roman (*Chrysoblephus laticeps*), a common sparid seen in stereo-BRUVs footage from the Tsitsikamma region (Bernard and Götz, 2012; Heyns-Veale et al., 2016) are resident, and rarely move more than 50 m within a given area.

Baited and unbaited systems were deployed off the same boat as described in Chapter 2, equipped with a davit and electric capstan winch for system retrieval. For each deployment, the system was lowered until it reached the benthos, at which point the time of day, GPS coordinates, depth (m) and treatment type were recorded. Water temperature (^{o}C) was recorded at five-minute intervals throughout the deployment time by a HOBO temperature logger attached to each stereo-BRUVs.

3.2.3 System setup and design

The stereo-BRUVs were based on the design of Harvey and Shortis (1995) and were similar to the configuration used by Unsworth et al. (2014). The systems (Figure 3.1) consisted of a stainless-steel frame supporting two stainless-steel waterproof housings mounted on a rigid base-bar and situated approximately 30 cm off the seafloor, when deployed. Each housing contained a high-definition video camera. The housings were separated by 0.7 m and orientated to face forwards with an inward convergence angle of 8°, such that the fields of view of the two cameras overlapped. Attached to the frame was a 1.5 m bait pole with a PVC bait container with 10 mm-diameter holes drilled into it. The bait container held approximately 0.8–1 kg of chummed pilchard (*Sardinops sagax*). For the unbaited systems,

the bait arm was detached to avoid fish being attracted to bait remains. Each system was attached with rope to surface buoys to mark its position and facilitate retrieval.

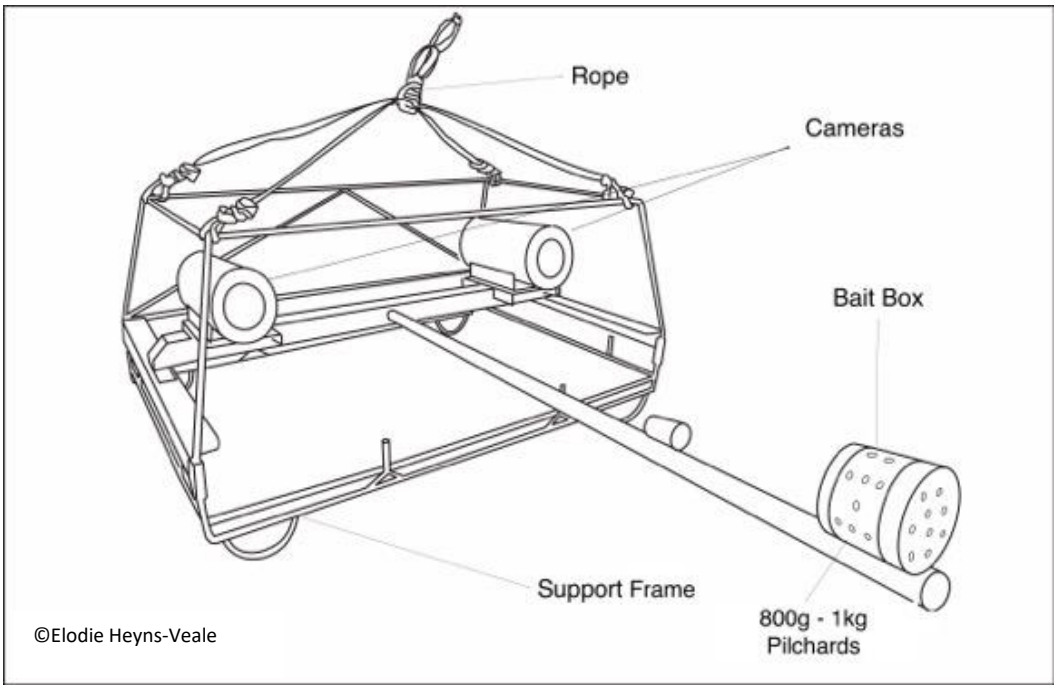

Figure 3.1: Annotated diagram of a baited stereo-BRUVs setup

3.2.4 VIDEO ANALYSIS

Videos were processed using EventMeasure software (SeaGIS) by a single observer. The camera systems were calibrated prior to and post deployment, using the calibration files derived from CAL v2.30 (SeaGIS, 2008) software (Harvey and Shortis, 1995). Fish seen in each video were identified to species level, where possible, and a measure of abundance – termed MaxN (i.e. the maximum number of individuals of a species seen in the field of view at a single moment [one video frame] during the video sample) – was determined for each observed species. The bottom type (sand or reef) was recorded for each video along with the depth (m), visibility (m) and treatment type (baited, unbaited) for that sample. Additional environmental data that were used as covariates in the statistical analyses, were also determined. These include sample depth, visibility, percentage water column and water temperature. Sample depth was taken from the echo-sounder on the boat as the stereo-BRUVs reached the sea floor, and visibility was estimated in EventMeasure by creating a 3D point at the furthest identifiable structure seen in the field of view of both cameras. Water column, expressed as a percentage of visible water column seen in the

video, was determined using the software package Vidana (MSEL) by measuring the percentage cover of water within the field of view of the cameras. Average water temperature (°C) was measured with HOBO temperature loggers attached to the system frame for each sample. Temperature recordings were taken at five-minute intervals over the course of the video sample. From this, an average water temperature from the middle 30 minutes of each deployment was calculated for each sample.

3.2.5 STATISTICAL ANALYSES

Multivariate statistical analyses were conducted in PRIMER (version 6) with the PERMANOVA add-on package (Anderson et al., 2008; Clarke and Gorley, 2006; Clarke and Warwick, 2001). Further, univariate analyses on species richness and roman abundance were conducted in R (R-Core Team, 2013) using the R Studio platform (R Studio Team, 2015).

3.2.5.1 MULTIVARIATE ANALYSIS OF FISH COMMUNITY

To test the effects of habitat and treatment type (bait) on community composition and species abundance, a sequential (type 1 sums of squares) permutational multivariate analysis of variance (PERNAMOVA) was conducted. The sequential PERMANOVA was based on a Modified Gower (log base 10) resemblance matrix of the MaxN data using 9999 permutations. The Modified Gower resemblance was deemed appropriate as it places greater emphasis on compositional change than MaxN values (abundance data), thereby accounting for less abundant, rare species by giving them the same weight as common ones (Clarke and Gorley, 2006). Visibility (*Visibility*) was added as the first covariate to the sequential model, followed by percentage water column (*Water Column*) and water temperature (*Temperature)*. These explanatory variables were added to the model, as they were independent of one another and could not be controlled for in the experimental design. Finally, the sequential PERMANOVA included the main effects and interaction between the categorical variables *Method* and *Habitat Type*. Pairwise comparisons were obtained to investigate any significant interactions (Anderson et al., 2008).

In addition, the MaxN data were transformed to presence/absence data using an S1 Simple matching resemblance. The PERMANOVA analysis was then run using the presence/absence data to test the effects of habitat and treatment type on fish community composition, following the same analytical approach as above.

A test for the homogeneity of multivariate dispersions using the PERMDISP routine was performed to determine whether differences in the dispersion of the data cloud between treatments (i.e. method) and habitat types was seen. This test used an ANOVA F statistic to compare the mean distance of functional

groups (i.e. habitat types) from their group centroid. The test, based on the Modified Gower remembrance, was run in conjunction with a canonical analysis of principalcoordinates (CAP).

A CAP analysis was conducted to illustrate the patterns in the multivariate data given the hypothesis that the interaction between bait and habitat type determines the fish assemblage structure. The CAP analysis was applied to reveal any underlying patterns in multivariate data that were potentially masked by overall patterns of dispersion of the data cloud (Anderson and Willis, 2003). The method is similar to a redundancy analysis (RDA), but allows for any distance or dissimilarity measure to be applied (Anderson and Willis, 2003; Legendre and Anderson, 1999). The CAP method uses a general discriminant analysis to maximise the difference between *a priori* groups (i.e. Habitat*Method) which are able to predict group allocation from principal coordinate (PCO) axes generated from the fish assemblage data (Anderson and Robinson, 2003; Anderson and Willis, 2003). The correct number of PCO axes (*m*) and their effectiveness of classifying fish assemblages into the correct grouping variable are determined by cross-validation tests. The leave-one-out procedure (Lachenbruch and Mickey, 1968) estimates the misclassification error, which is the proportion of samples that were placed in the wrong group. A high allocation success (correctly assigned samples) indicates a good fit of the model and can therefore be used to describe and predict patterns within the dataset.

The species responsible for the differences in treatments observed in the CAP analysis, were identified with the similarity percentages (SIMPER) analysis in PRIMER. A SIMPER analysis essentially breaks down similarities among samples within a group and displays them as percentage contributions for each species, in decreasing rank of such contributions (Clarke and Gorley, 2006). The cut-off for lower species contributions was set to 75%, thereby only showing the dominant species contributing to the dissimilarity between habitat types.

3.2.5.2 UNIVARIATE ANALYSES OF SPECIES RICHNESS AND ROMAN

The sparid species, roman (*Chrysoblephus laticeps*), was chosen for analysis as individuals were present in both the baited and unbaited treatments. Roman are strongly attracted by bait and show aggression around the bait container (Bernard and Götz, 2012). As such, roman abundance was used in the analysis to illustrate the effect of bait over a change in depth, as well as within each habitat type.

Species richness is the simplest measure of community and regional species diversity (Gotelli and Colwell, 2001) and, as such, was used to analyse changes in the fish community structure. Furthermore, since depth was found to influence the macrobenthic assemblage (see Chapter 2), the effect of depth and

habitat type on species richness and roman abundance was tested by means of generalised modelling techniques with the R Studio platform (R Studio Team, 2015).

Extensive data explorations were conducted following the protocol described by Zuur et al. (2010), which involved the determination of missing values, outliers, collinearity, and the relationships between the response variable and the covariates. Outliers were identified using Cleveland dot plots (Cleveland, 1993), while correlation between covariates was assessed with multi-panel scatterplots and Pearson correlation coefficients. To assess collinearity between continuous and categorical covariates, conditional boxplots were employed. Scatterplots then visualised the relationship between the response variable and each continuous covariate. Following data exploration, full or saturated models were formulated, after which point model validation and selection procedures were implemented. Model validation involved checking for over-dispersion and patterns in the residuals against the fitted values and all other covariates within the dataset. The model was then examined to determine whether any covariates could not explain the variation seen in the response variable. Such covariates were subsequently dropped from the model. Models were then selected based on an Akaike Information Criterion (AIC) approach, whereby the model with the lowest AIC score was chosen as the best fit model (Akaike, 1973). The AIC approach measures the goodness of fit of a model, as well as its complexity. The model that best fits the data, while still being reasonably simple, is the one with the lowest AIC score (Logan, 2010). Once model selection was complete, the validation process (see above) was repeated to ensure that any changes made to the model did not negatively influence the model fit.

Two full models that incorporated all necessary covariates were used to determine the effect of depth (Equ. 3.1) and habitat (Equ. 3.2) on species richness (*Richness*) and roman abundance (*Roman*), denoted as Y in the equations below. Since depth was incorporated into the description of habitat type (see Chapter 2), *Habitat* was excluded from the depth model so as to analyse the effect of depth separately. The variable bottom type (*Bottom*; reef or sand) was added to the depth model to account for the effect of reef and sand habitats on the fish community. The two full models are presented below as:

$$\eta(Y) \sim \alpha + \beta 1(Depth) + \beta 2(Method) + \beta 3(Bottom) + \beta 4(Method{:}\,Depth) + \beta 5(Method{:}\,Bottom) + \beta 6(Water\ column) + \beta 7(Temperature) + \beta 8(Visibility) + \varepsilon \quad (3.1)$$

The full-depth model above shows the variables, species richness or roman abundance $\eta(Y)$ in response to the predictors depth (*Depth*), method (baited or unbaited; *Method*), bottom type (reef or sand;

Bottom), the interaction between *Method* and *Depth* as well as *Method* and *Bottom,* water column (*Water Column*), temperature (*Temperature*) and visibility (*Visibility*). The interactions between *Method*:*Depth* and *Method:Bottom* were used to test whether the method changed the effect of depth or bottom type.

$$\eta(Y) \sim \alpha + \beta 1(Habitat) + \beta 2(Method) + \beta 3(Method{:}\,Habitat) + \beta 4(Water\ column) + \beta 5(Temperature) + \beta 6(Visibility) + \varepsilon \quad (3.2)$$

The full-habitat model above shows species richness or roman abundance $\eta(Y)$ in response to the predictors habitat type (*Habitat*), method, the interaction between method and habitat, water column, temperature and visibility.

3.2.5.3 Model selection for species richness

Data exploration revealed non-linear trends in the residuals, and generalised additive models (GAMs) were therefore employed in the 'mgcv' package v1.8 (Wood, 2016) in the R Environment (R-Core Team, 2013) using R Studio (R Studio Team, 2015). A Poisson distribution was first applied, as the response data were count data. The model validation, however, revealed that the data were over-dispersed (dispersion parameter = 2.31). A negative binomial distribution was therefore chosen, as it is well suited to over-dispersed non-normal count data (Logan, 2010; Zuur et al., 2009). To account for the non-linear trends observed in the residuals, smoothers were applied following the recommendations of Zuur (2012).

3.2.5.3.1 Effect of depth

To test for the effect of *Depth* on species richness, the model selection process indicated that the interaction between *Depth* and *Method* in the full model could be dropped. A smooth term (*f*) was added to those variables that showed a non-linear effect of species richness. This resulted in the best fit model (Equ. 3.1 AIC = 585.09; best fit model AIC =567.11), given as:

$$\eta(Richness) \sim \alpha + \beta 1(Depth) + \beta 2(Method) + \beta 3(Bottom) + \beta 5(Method{:}\,Bottom) + f1(Water\ column) + f2(Temperature) + f3(Visibility) + \varepsilon \quad (3.3)$$

3.2.5.3.2 EFFECT OF HABITAT

To examine the effect of habitat type on species richness, the model selection process revealed that the interaction between *Method* and *Habitat* could be dropped from the full model, as the effect of the interaction on species richness was negligible. Smoothers were again used on those variables that had a non-linear effect on species richness. This resulted in (Equ. 3.2 AIC = 642.80; best fit model AIC = 638.41) which was thus given as:

$$\eta(Richness) \sim \alpha + \beta 1(Habitat) + \beta 2(Method) + \beta 3(Temperature) + f1(Water\ column) + f2(Visibility) + \varepsilon \quad (3.4)$$

3.2.5.4 MODEL SELECTION FOR ROMAN ABUNDANCE

Data exploration showed non-linear trends in the residuals and, as such, GAMs were employed using the 'mgcv' package v1.8 (Wood, 2016) in R (R-Core Team, 2013) through R Studio (R Studio Team, 2015). Further exploration revealed that the roman abundance data was highly unbalanced between reef and sand sites, with very few observations of roman seen at sand sites. Therefore, for the analysis looking at the effect of depth on roman abundance, the data was subsetted to only contain samples that were deployed on reef. As such, bottom type was removed from the model.

3.2.5.4.1 EFFECT OF DEPTH ON ROMAN ABUNDANCE ON REEF

Model validation revealed that the subsetted data were not overdispersed, with no patterns seen in the residuals and, as such, a Poisson distribution was used. Model selection revealed that *Water Column* and *Bottom* could be dropped from the model, as well as the interaction between *Method* and *Bottom.* Smoothers were used on non-linear predictors (Equ. 3.1 AIC = 363.26; best fit model AIC = 362.22). The best fit model was therefore given as:

$$\eta(Roman) \sim \alpha + \beta 1(Depth) + \beta 2(Method{:}\,Depth) + f1(Temperature) + f2(Visibility) + \varepsilon \quad (3.5)$$

3.2.5.4.2 EFFECT OF HABITAT ON ROMAN ABUNDANCE

The model validation process revealed that the roman abundance data from the different habitat categories were over-dispersed (dispersion parameter = 1.99), therefore a negative binomial distribution

was applied. *Water Column* was dropped from the full model, along with the interaction between *Method* and *Habitat* (p = 0.21) following the model selection process (Equ. 3.2 AIC = 435.46; best fit model AIC = 433.23). The best fit model was therefore given as:

$$\eta(Roman) \sim \alpha + \beta 1(Habitat) + \beta 2(Method) + \beta 3(Temperature) + f1(Visibility) + \varepsilon \quad (3.6)$$

For more information on model validation details, please see Appendix A2, figures A2.1–A2.4.

3.3 RESULTS

3.3.1 ENVIRONMENTAL CONDITIONS

Over the duration of the study, the water temperature averaged (mean ± standard error) 16.9 ± 3.28°C, however the minimum and maximum water temperatures showed considerable variation and ranged from 9–22°C. The average water temperature in the stereo-RUVs and BRUVs samples was similar, with 17.15 ± 3.31°C recorded in the stereo-RUVs samples and 16.51 ± 3.21°C in the stereo-BRUVs samples. Overall, horizontal underwater visibility was low, showing high variability (1.72 ± 0.77m) in the unbaited samples and averaging 2.46 ± 0.89m in the baited samples. The visible reef seen in the video footage ranged from 0–100% with an average of 46.92 ± 34.20% and 53.78 ± 27.84% for the stereo-RUVs and BRUVs footage, respectively. The depth of sample deployments ranged from 9.6–33.0 m, with a mean depth of 19.1 ± 6.14 m. The mean depth of the unbaited deployments was 19.68 ± 6.40 m, while the baited sampleswere deployed at a mean depth of 18.33 ± 5.71 m. Representative samples of both methods were thus collected at all depths within the sampling area.

3.3.2 FISH COMMUNITY

A total of 143 samples (84 stereo-RUVs, 59 stereo-BRUVs) were collected within the five habitat types over the duration of the study (Table 3.1). From these, a total of 3 486 fish from 22 families and 60 species were recorded (Table A1.1). Using the baited method, 2 802 fish from 59 species were observed, while only 684 fish from 29 species were recorded in the unbaited footage. In the baited footage, 42 (70%) of the recorded species were teleosts, 16 (27%) were cartilaginous fish species, and one cephalopod species was seen. Of the 29 species seen in the unbaited footage, 22 (76%) were teleosts, 6 (21%) were cartilaginous and one cephalopod species, suggesting similarity in the proportional comparison (Table A1.1). The highest average number of individual fish and fish species was seen in the *Shallow Reef* habitat, using both video methods (Table 3.2). Noticeably fewer fish and fish species were recorded in the *Deep Sand* habitat, using the unbaited and baited video methods. High counts of roman, steentjie (*Spondyliosoma emarginatum*), fransmadam (*Boopsoidea inornata*) and two-tone fingerfin (*Chirodacylus brachydactulus*) were achieved in both the baited and unbaited samples (Table A1.2).

For more information on the observed fish community (such as percentage occurrence of species within each habitat and list of species) see Appendix A, tables A1.1 & A1.2.

Table 3.1: Number of baited stereo-BRUVs) and stereo-RUVs) sampled within each habitat

Habitat	**Stereo-BRUVs**	**Stereo-RUVs**	**Total**
Shallow Sand	6	9	**15**
Shallow Reef	12	18	**30**
Deep Reef	28	23	**51**
Patch Reef	3	7	**10**
Deep Sand	10	27	**37**
Total	**59**	**84**	**143**

Table 3.2: Average number of species (# Species) and average species abundance (MaxN) ± standard deviation (SD) per sample recorded in each habitat type using the stereo-RUVs) and baited stereo-BRUVs) methods

Habitat	**Stereo-RUVs**		**Stereo-BRUVs**	
	# Species	**MaxN**	**# Species**	**MaxN**
Shallow Sand	1.33 ± 2.55	2.56 ± 6.19	8 ± 5.25	38.67 ± 33.28
Shallow Reef	6.28 ± 3.64	19.11 ± 14.34	13.17 ± 3.59	58.5 ± 35.68
Deep Reef	3.87 ± 4.06	7.17 ± 10.46	12.5 ± 4.51	55.75 ± 38.08
Patch Reef	5 ± 2.94	15.14 ± 14.28	11.33 ± 4.16	50.33 ± 34.96
Deep Sand	0.78 ± 2.62	1.7 ± 6.74	4.4 ± 3.47	15.6 ± 18.92

The PERMANOVA revealed a significant effect of *Method* and *Habitat* and the interaction between them on both species composition (presence/absence analysis) and species abundance (tables 3.3 & 3.4). While *Temperature* had a significant effect on both species abundance and community composition, it was not a major contributor to the overall variability seen in the datasets (2.48 and 1.15% for community composition and species abundance respectively; Table 3.5). In the community composition data, *Method* (17.20%) contributed most to the variation seen within the data set, followed by *Visibility* (13.16%), *Habitat* (12.29%) and the interaction between *Method* and *Habitat* (9.22%). *Method* (17.58%) was found to contribute most to the variation seen in the species abundance data (MaxN), followed by *Habitat* (13.12%) and the interaction between *Method* and *Habitat* (10.83%). The covariate *% Water Column* contributed least to the variation seen in both the community composition and species abundance datasets (0.36% and 0.25% respectively).

Table 3.3: Sequential PERMANOVA based on species composition (presence/absence) resemblance data investigating fish community composition in response to covariates (visibility, % water column and water temperature) and treatment (*Method* and *Habitat*). Significant p-values are presented in bold (Df = degrees of freedom; SS = sum of squares; MS = mean squares; P(Perm) = probability level based on permutations)

Source	Df	SS	MS	Pseudo-F	P(Perm)	Unique Perms
Visibility	1	3676.7	3676.7	39.065	**0.0001**	9951
% Water Column	1	188.64	188.64	2.0043	0.0778	9938
Water Temperature	1	740.03	740.03	7.8627	**0.0001**	9941
Method	1	1928.8	1928.8	20.493	**0.0001**	9961
Habitat	4	2602.4	650.59	6.9125	**0.0001**	9914
Method *Habitat	4	1216.7	304.17	3.2318	**0.0001**	9935
Residual	112	10541	94.119			
Total	124	20895				

Table 3.4: Sequential PERMANOVA based on Modified Gower data investigating species abundance in response to covariates (visibility, % water column and water temperature) and treatment (*Method* and *Habitat*). Significant p-values are presented in bold (Df = degrees of freedom; SS = sum of squares; MS = mean squares; P(Perm) = probability level based on permutations)

Source	Df	SS	MS	Pseudo-F	P(Perm)	Unique Perms
Visibility	1	6.2323	6.2323	15.535	**0.0001**	9926
% Water Column	1	0.68061	0.68061	1.6965	0.0749	9937
Water Temperature	1	1.5684	1.5684	3.9094	**0.0002**	9924
Method	1	7.4123	7.4123	18.476	**0.0001**	9918
Habitat	4	10.459	2.6149	6.5179	**0.0001**	9889
Method *Habitat	4	5.3088	1.3272	3.3082	**0.0001**	9871
Residual	112	44.932	0.40118			
Total	124	76.594				

Table 3.5: PERMANOVA results for the estimates of components of variation to further investigate the contribution of each of the components of variation for both species composition and species abundance data (S = fixed term; V = random term; Prop = proportion of total variation explained by each variable)

Source	Composition			Abundance		
	Estimate	Prop (%)	Sq.root	Estimate	Prop (%)	Sq.root
S(Visibility)	28.661	13.64	5.3536	0.047	5.99	0.21598
S(% Water Column)	0.76519	0.36	0.87475	0.002	0.25	4.76E-02
S(Temperature)	5.2036	2.48	2.2811	0.009	1.15	9.70E-02
S(Method)	36.125	17.20	6.0104	0.138	17.58	0.37155
S(Habitat)	25.812	12.29	5.0806	0.103	13.12	0.32044
S(Method x Habitat)	19.372	9.22	4.4014	0.085	10.83	0.29223
V(Residuals)	94.119	44.81	9.7015	0.401	51.08	0.63339

3.3.3 THE EFFECT OF BAIT ON COMMUNITY STRUCTURE WITHIN HABITATS

Pairwise comparisons were conducted on the fish composition data to show the difference in the fish community between the different habitat types, using the baited and unbaited methods. The results show that the presence of bait significantly altered the fish communities found on the *Shallow Reef* ($p < 0.001$), *Deep Reef* ($p < 0.001$) and *Deep Sand* ($p < 0.005$) habitat types (Table 3.6).

Table 3.6: Pairwise comparisons showing the effect of bait on species composition, based on presence/absence resemblance data from within the five habitat types. Significant p-values are presented in bold (t = t statistic; P(Perm) = probability level based on permutations)

Habitat	T	P(Perm)	Perms
Shallow Sand	1.0738	0.355	9951
Shallow Reef	2.6284	**< 0.001**	9951
Patch Reef	1.7751	0.096	9950
Deep Reef	3.3344	**< 0.001**	9949
Deep Sand	2.9176	**0.003**	9947

To show the effect of bait on species abundance between different habitats, pairwise tests revealed that bait also significantly altered the fish abundance in the *Shallow Reef* ($p < 0.001$), *Deep Reef* ($p < 0.001$) and *Deep Sand* ($p < 0.001$) habitat types (Table 3.7).

Table 3.7: Pairwise comparisons showing the effect of bait on species abundance based on Modified Gower resemblance data, from within the five habitat types. Significant p-values are presented in bold (t = t statistic; P(Perm) = probability level based on permutations)

Habitat	t	P(Perm)	Perms
Shallow Sand	1.3095	0.076	9951
Shallow Reef	2.1147	**< 0.001**	9945
Patch Reef	1.4183	0.091	9950
Deep Reef	3.3894	**< 0.001**	9949
Deep Sand	3.2735	**< 0.001**	9947

Further pairwise comparisons were conducted on the species composition data to test for significant differences between habitat types within the sampling methods. With the unbaited data, significant differences ($p < 0.05$) were only seen between the *Shallow Reef* vs *Deep Sand* and *Patch Reef* vs *Deep Sand* habitat types (Table 3.8). With the baited method, significant differences were observed between the *Shallow Reef* vs *Deep Sand*, *Shallow Reef* vs *Deep Reef*, *Shallow Reef* vs *Shallow Sand*, *Patch Reef* vs *Shallow Sand, Deep Sand* vs *Deep Reef* and *Deep Reef* vs *Shallow Sand* (Table 3.8).

Table 3.8: Pairwise comparisons of species composition between different habitat types using the baited (stereo-BRUVs) and unbaited (stereo-RUVs) methods. Significant p values are shown in bold (t = t statistic; P(Perm) = probability level based on permutations)

Groups	Stereo-RUVs		Stereo-BRUVs	
	t	P(Perm)	T	P(Perm)
Shallow Reef, Patch Reef	0.876	0.510	0.928	0.465
Shallow Reef, Deep Sand	2.121	**0.015**	2.497	**<0.001**
Shallow Reef, Deep Reef	1.559	0.065	1.463	**0.036**
Shallow Reef, Shallow Sand	1.625	0.063	1.694	**0.040**
Patch Reef, Deep Sand	3.180	**0.003**	1.641	0.080
Patch Reef, Deep Reef	1.037	0.370	0.835	0.697
Patch Reef, Shallow Sand	1.867	0.055	2.066	**0.043**
Deep Sand, Deep Reef	0.845	0.530	3.758	**<0.001**
Deep Sand, Shallow Sand	1.192	0.246	1.222	0.252
Deep Reef, Shallow Sand	1.099	0.322	2.782	**<0.001**

Pairwise comparisons were then conducted on the species abundance data to test for significant differences between all combinations of habitat types using the two video methods. With the unbaited method, the pairwise comparisons of habitat type revealed significant differences ($p < 0.05$) in fish abundance between all groups, except for *Deep Reef* vs *Patch Reef* and *Patch Reef* vs *Shallow Reef* (Table 3.9). Comparisons with the baited samples revealed significant differences between the *Shallow Reef* vs *Deep Sand*, *Shallow Reef* vs *Deep Reef*, *Shallow Reef* vs *Shallow Sand*, *Deep Sand* vs *Deep Reef*, *Deep Sand* vs *Shallow Sand* and *Deep Reef* vs *Shallow Sand* habitat types (Table 3.9).

Table 3.9: Pairwise comparisons of species abundance between different habitat types using the baited (stereo-BRUVs) and unbaited (stereo-RUVs) methods. Significant p values are shown in bold (t = t statistic; P(Perm) = probability level based on permutations)

Groups	Stereo-RUVs		Stereo-BRUVs	
	t	P(Perm)	t	P(Perm)
Shallow Reef, Patch Reef	0.860	0.625	1.174	0.159
Shallow Reef, Deep Sand	5.101	**<0.001**	1.907	**<0.001**
Shallow Reef, Deep Reef	1.963	**0.009**	1.317	**0.026**
Shallow Reef, Shallow Sand	2.621	**0.001**	1.450	**0.018**
Patch Reef, Deep Sand	4.378	**<0.001**	1.333	0.079
Patch Reef, Deep Reef	1.351	0.093	1.079	0.277
Patch Reef, Shallow Sand	2.143	**0.002**	1.181	0.245
Deep Sand, Deep Reef	3.360	**<0.001**	2.922	**<0.001**
Deep Sand, Shallow Sand	1.934	**0.017**	1.444	**0.017**
Deep Reef, Shallow Sand	1.626	**0.025**	2.297	**0.000**

A PERMDISP test, for homogeneity of multivariate dispersions between methods on the fish composition and fish abundance data, revealed no significant differences in dispersion in the fish abundance data ($p = 0.879$; dispersion value $F = 0.002$). On the other hand, significant differences in dispersions from the centroid were identified in the fish composition data ($p = 0.001$; $F = 205.83$). Pairwise comparisons revealed significant differences in dispersion to be present between all habitat types ($p < 0.05$) within the species composition data (Table 3.10).

Table 3.10: Pairwise comparisons of tests for homogeneity of multivariate dispersions between methods within habitat types using the PERMDISP routine. Analyses were based on the fish composition (presence/absence) resemblance data. Significant p values are shown in bold (t = t statistic; P(Perm) = probability level based on permutations)

Habitat	t	P(Perm)
Shallow Sand	2,7723	**0.020**
Shallow Reef	4,6996	**0.001**
Patch Reef	4,0594	**0.007**
Deep Reef	8,7481	**0.001**
Deep Sand	5,0841	**0.002**

A CAP analysis was then conducted to determine whether bait had a significant effect on the fish community structure within the different habitat types in both the fish composition and abundance datasets. Baited and unbaited samples were analysed separately to highlight patterns within each method, rather than between methods.

Species composition

In the unbaited species composition data, two canonical axes (*m*) were used to explain the observed variation in the data. The first was able to explain 57% of the variation, while the second explained 43% (CAP 1 and 2 respectively; Figure 3.2 A). Here, there is no distinct pattern within the data cloud and it is difficult to determine which covariates are correlated with the axes (Figure 3.2 A).

In the baited data, the variation was explained using seven canonical axes (*m*). The first of the two axes is able to explain 83% of the observed variation, separating the data into reef and sand sites (CAP 1; Figure 3.2 B). The second of the two axes explains 49% of the variation and separates the data into deep and shallow sites (CAP 2; Figure 3.2 B). The allocation success in the species composition data was reported to be 42% for the unbaited CAP analysis, much lower than that of the baited CAP analysis with a 57% allocation success.

Species abundance

Seven canonical axes (*m*) were used to describe the variation in species abundance in the unbaited abundance data. Here, the first two canonical correlation values indicated the strength of correlation between species abundance, and habitat type was able to explain 73% and 58% of the observed variation in the unbaited data (CAP 1 and CAP 2 respectively; Figure 3.2 C). The first axis separated the data into

sand and reef sites, while the second separated the deep and shallow data. Within the baited method, the CAP best described the variation in species abundance using 14 canonical axes (*m*). The first two canonical correlation values were large, explaining 91% and 71% of the variation seen in the baited species abundance data (CAP 1 and CAP 2 respectively; Figure 3.2 D). The analysis clearly shows the formation of distinct groupings for the baited method, with the first canonical axis separating reef sites from sand sites and the second separating the different shallow and deep sand habitat types, while appearing to have little effect on the reef habitats (Figure 3.2 D). The allocation success for the unbaited CAP analysis was reported to be 52%, while the allocation of success for the baited analysis was approximately 10% higher (63%).

Although the pairwise comparisons from the PERMANOVA show that there is a clear effect of habitat type on fish abundance in the unbaited method (Table 3.9), the groupings seen in the data cloud in the unbaited method (although still distinct from one another) are not as clear as those seen in the baited method.

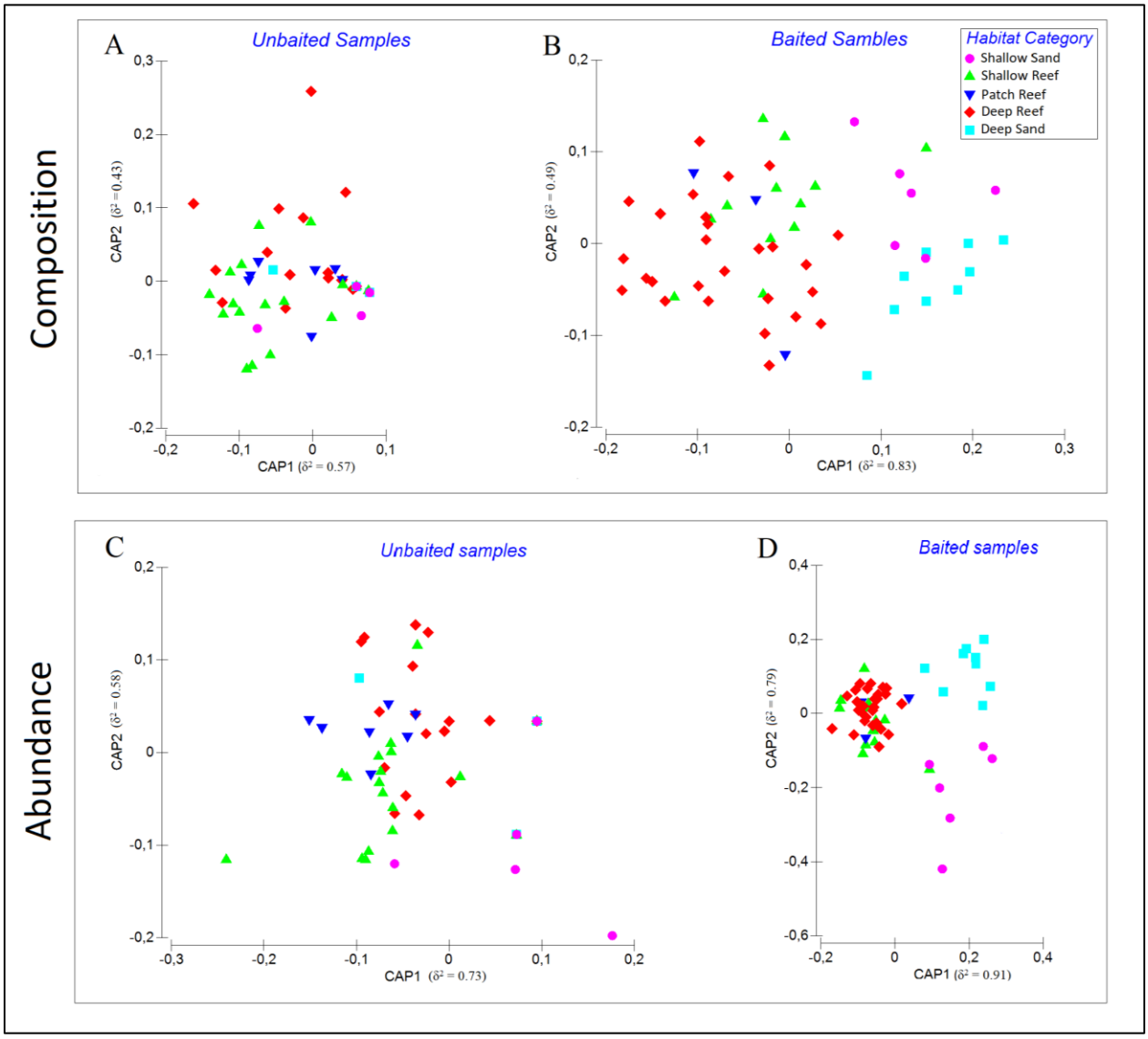

Figure 3.2: Canonical analysis of principal coordinates (CAP) on species composition data (A & B) and species abundance data (C & D) showing fish assemblages grouped by habitat type using the unbaited and baited methods

3.3.4 SIMPER ANALYSES

The species that contributed most to the differences in community composition between habitat types and methods were determined using a SIMPER analysis. The analyses were conducted only among those habitat types that showed significant differences in fish assemblages between the baited and unbaited methods, as well as the most relevant comparisons of different habitat types (*Shallow Reef, Deep Reef, Deep Sand*; Table 3.6).

The SIMPER results indicated that between methods within habitat type, the fish species steentjie, fransmadam and roman contributed most to the differences between the *Shallow Reef* and *Deep Reef* habitats (Table 3.11). Considerably higher abundances of these fish species were seen in the baited method in both habitats, with steentjie having the highest dissimilarity percentage contributions of 10.55% and 14.09% in the *Shallow Reef* and *Deep Reef* habitats respectively. In the *Deep Sand* habitat, the major contributing species were the evil-eye puffer (*Amblyrhynchotes honckenii*), smooth hound shark (*Mustelus mustelus*) and the white sea catfish (*Galeichthys feliceps*), all of which were associated with the baited method, with the evil-eye puffer having the highest dissimilarity contribution of 22.25%. The baited method in the *Deep Sand* habitat consistently yielded higher abundances of fish than the unbaited method. In contrast, in the *Shallow Reef*, the two-tone fingerfin was seen to have a higher average abundance in the unbaited method than the baited method. Similarly, in the *Deep Reef*, the barred fingerfin (*Chirodacylus pixi*) showed greater average abundance in the unbaited footage than in the baited footage (Table 3.11).

Table 3.11: SIMPER results showing average abundance of major species contributing to the dissimilarity between the stereo-RUVs and BRUVs methods (separated with "/") within habitat type. Major contributing species within each habitat type are highlighted, where significant differences (Table 3.7) between treatment were recorded. The percentage dissimilarity for each major contributing species is provided in brackets (%)

	Stereo-RUVs/Stereo-BRUVs				
Species	**Shallow Sand**	**Shallow Reef**	**Patch Reef**	**Deep Reef**	**Deep Sand**
Chrysoblephus laticeps	0.25/0.92 [1]	1.39/4.47 (6.17)	1.51/5.36	1.08/3.95 (7.66)	0.09/0.2 (4.51)
Spondyliosoma emarginatum	0.25/4.05	2.94/10.47 (10.55)	1.48/2.19	0.57/8.78 (14.09)	0/0
Boopsoidea inornata	0/0	2.35/6.17 (8.42)	1.2/10.02	1.1/8.39 (12.35)	0/0
Chirodactylus brachydactylus	0/0	1.29/0.82 (4.52)	1.03/0.45	0.35/0.88 (4.06)	0/0
Sarpa salpa	0/0	0.4/1.36 (5.92)	0/0	0.16/0.86 (3.72)	0/0
Pachymetopon aeneum	0/0	0.32/0.84 (3.81)	0/0.99	0.15/1.44 (5.3)	0/0
Haploblepharus edwardsii	0/0	0.08/0.93 (4.36)	0/0.26	0/0.54 (3.5)	0/0
Galeichthys feliceps	0.19/0.26	0/0.55 (2.96)	0/0.26	0/0.15	0/1.53 (12.77)
Pagellus bellottii natalensis	0.09/1.56	0/1.41 (5.24)	0/0	0/0.13	0/1.2 (8.84)
Amblyrhynchotes honckenii	0/1.1	0/0.97 (4.81)	0/0.58	0/0.34	0.05/1.44 (22.25)
Diplodus sargus capensis	0.09/1.48	0.25/1.72 (5.97)	0/1.34	0.21/1.59 (5.61)	0/0
Pomadasys olivaceum	0/0.95	0/0	0/1.08	0/0	0/0
Rhabdosargus holubi	0/1.51	0/0	0/0	0/0	0/0
Poroderma africanum	0/0	0/1.44 (5.87)	0/0.99	0.07/1.32 (7.01)	0/0
Trachurus trachurus	0/1.41	0/0	0/0	0/0	0/0
Cheilodactylus pixi	0/0	0/0	0.51/0.26	0.52/0.36 (3.28)	0/0
Cheilodactylus fasciatus	0/0	0.45/0.23 (2.62)	0/0	0.23/0.52 (2.79)	0/0
Gymnocrotaphus curvidens	0/0	0/0	0/0	0.19/0.42 (2.43)	0/0
Mustelus mustelus	0.19/0.7	0.08/0.86 (3.97)	0/0	0.03/0.4 (2.2)	0/0.93 (13.93)
Chrysoblephus cristiceps	0/0	0/0	0/0.58	0/0.42 (2.22)	0/0
Rhinecanthus annulatus	0/0	0/0	0/0	0/0	0/0.72 (6.79)

1: Unbaited (stereo-RUVs) / Baited (stereo-BRUVs)

SIMPER results comparing the stereo-RUVs and stereo-BRUVs methods between habitat types are presented for the most relevant comparisons: *Shallow Reef* vs *Shallow Sand*, *Shallow Reef* vs *Deep Reef*, *Deep Sand* vs *Deep Reef* and *Deep Sand* vs *Shallow Sand* (Table 3.12).

Shallow Reef vs *Shallow Sand*

In general, the average abundance of fish species was higher in the *Shallow Reef* than in the *Shallow Sand*, with the exception of the red tjor tjor (*Pagellus bellottii natalensis)* and cape stumpnose (*Rhabdosargus holubi*) which showed higher average abundances in the *Shallow Sand* habitat. In both the baited and unbaited comparisons, steentjie, fransmadam and roman contributed most to the dissimilarity between the *Shallow Reef* and *Shallow Sand* habitats. Steentjie contributed most to the dissimilarity in the unbaited comparison (21.28%), while fransmadam contributed most to the dissimilarity in the baited comparison (10.3%). In both habitats, the two-tone fingerfin was seen to have a higher average abundance in the unbaited method than in the baited method (Table 3.12).

Shallow Reef vs *Deep Reef*

A much greater number of species were seen when using the baited method in both these habitat types, with many species having small dissimilarity percentage contributions (Table 3.12). In the unbaited comparison between the *Shallow Reef* and *Deep Reef* habitat types, steentjie (19.17%), fransmadam (14.47%) and roman (11.4%) again had the highest dissimilarity percentage contributions. In contrast, in the baited comparison, roman had a considerably lower contribution of 1.4% and streepies (*Sarpa salpa*) had a higher dissimilarity contribution of 6.51%. Both steentjie and fransmadam had higher contributions of 7.92% and 7.33% respectively. The species roman, steentjie and fransmadam had higher average abundances in the *Shallow Reef* habitat in the unbaited method, but in the baited method, fransmadam demonstrated a higher average abundance in the *Deep Reef.*

Deep Sand vs *Deep Reef*

In the *Deep Sand* and *Deep Reef* comparison, steentjies, fransmadam and roman were again indicated as major contributors to differences between the two habitat types. Noticeably, the white sea catfish, red tjor tjor and lesser guitarfish (*Rhinecanthus annulatus*) did not appear in the unbaited footage in either habitat. However, these three species were seen in the baited footage in both habitats, with the exception of the lesser guitarfish which was only observed in the *Deep Sand* habitat (Table 3.12). The aforementioned species appeared to have a higher abundance in the *Deep Sand* in the baited comparison,

while the rest of the major contributing species had higher average abundances in the *Deep Reef* habitat type.

Deep Sand vs *Shallow Sand*

The fish species indicated as major contributors to differences seen in the baited comparisons between the *Deep Sand* and *Shallow Sand* habitats were the white sea catfish, red tjor tjor, smooth hound shark, cape stumpnose, maasbanker (*Trachurus trachurus*) and steentjie (Table 3.12). In the unbaited comparisons between the two habitats species abundances were generally low, with the white sea catfish contributing most to the dissimilarity (33.81%) and the smooth hound shark having the second highest contribution of 18.35%. In the baited comparison, steentjie had the highest dissimilarity contribution of 13.09% and was predominantly seen in the *Shallow Sand* habitat. The average abundance of the white sea catfish and lesser guitarfish was greater in the *Deep Sand*, while cape stumpnose and maasbanker recorded higher average abundances in the *Shallow Sand* habitat. The red tjor tjor was seen in both habitats, but with a slightly higher average abundance in the *Shallow Sand* habitat. The smooth hound shark was more abundant in the *Shallow Sand* habitat in the absence of bait, and was only observed in the *Deep Sand* when bait was present.

In general, the variations in the abundance of steentjie, fransmadam and roman played a significant role in the difference in fish assemblages observed between habitats. Steentjie and fransmadam, however, showed inconsistent patterns in abundance between habitat types when comparing the stereo-RUVs and stereo-BRUVs methods. Roman, on the other hand, demonstrated a fairly consistent pattern between methods in abundance across habitat types, and were always more abundant when the baited method was used.

Table 3.12: SIMPER results showing the average abundance of major species contributing to the dissimilarity between the stereo-RUVs (unbaited) and stereo-BRUVs (baited) methods between habitat types. Major contributing species in unbaited comparisons between habitat types are highlighted in blue, and major species in baited comparisons are highlighted in green. Dissimilarity percentage contributions for each major species are shown in brackets (%)

Species	Shallow Reef/Shallow Sand		Shallow Reef/Deep Reef		Deep Sand/Deep Reef		Deep Sand/Shallow Sand	
	Unbaited	Baited	Unbaited	Baited	Unbaited	Baited	Unbaited	Baited
Chrysoblephus laticeps	1.39/0.25 (11.5)	4.47/0.92 (7.12)	1.39/1.08 (11.4)	4.47/3.95 (4.1)	0.09/1.08 (22.85)	0.2/3.95 (8.01)	0.09/0.25	0.2/0.92 (5.04)
Spondyliosoma emarginatum	2.94/0.25 (21.28)	10.47/4.05 (9.63)	2.94/0.57 (19.17)	10.47/8.78 (7.92)	0.07/0.57 (12.17)	0.16/8.78 (11.74)	0.07/0.25	0.16/4.05 (13.09)
Boopsoidea inornata	2.35/0.22 (13.19)	6.17/0.2 (10.3)	2.35/1.1 (14.74)	6.17/8.39 (7.33)	0.05/1.1 (22.64)	0/8.39 (11.85)	0.05/0.22	0/0.2
Chirodactylus brachydactylus	1.29/0.09 (9.56)	0.82/0 (3.13)	1.29/0.35 (9.61)	0.82/0.88 (3.44)	0.05/0.35 (5.19)	0/0.88 (3.26)	0.05/0.09	0/0
Sarpa salpa	0.4/0	1.36/0.13 (4.38)	0.4/0.16 (4.19)	1.36/0.86 (6.51)	0/0.16	0/0.86 (2.58)	0/0	0/0.13
Pachymetopon aeneum	0.32/0	0.84/0 (3.21)	0.32/0.15 (3.81)	0.84/1.44 (4.44)	0/0.15	0/1.44 (4.28)	0/0	0/0
Haploblepharus edwardsii	0.08/0 (4.26)	0.93/0.35 (3.53)	0.08/0	0.93/0.54 (3.45)	0/0	0.26/0.54 (2.47)	0/0	0.26/0.35
Galeichthys feliceps	0/0.19 (5.2)	0.55/0.26	0/0	0.55/0.15 (2.85)	0/0	1.53/0.15 (4.78)	0/0.19 (33.81)	1.53/0.26 (7.07)
Pagellus bellottii natalensis	0/0.09	1.41/1.56 (5.49)	0/0	1.41/0.13 (4.97)	0/0	1.2/0.13 (3.98)	0/0.09 (16.91)	1.2/1.56 (8.88)
Amblyrhynchotes honckenii	0/0	0.97/1.1 (4.08)	0/0	0.97/0.34 (4.13)	0.05/0	1.44/0.34 (4.57)	0.05/0 (6.31)	1.44/1.1 (7.69)
Diplodus sargus capensis	0/0	1.72/1.48 (5.08)	0/0	1.72/1.59 (6.1)	0/0	0/1.59 (4.5)	0/0	0/1.48 (7.16)
Pomadasys olivaceum	0/0	0/0.95 (2.69)	0/0	0/0	0/0	0/0	0/0	0/0.95
Rhabdosargus holubi	0/0	0.58/1.51 (5.55)	0/0	0.58/0.16 (2.79)	0/0	0/0.16	0/0	0/1.51 (11.33)
Poroderma africanum	0/0	1.44/0 (4.98)	0/0	1.44/1.32 (3.94)	0/0	0/1.32 (5.4)	0/0	0/0
Trachurus trachurus	0/0	0/1.41 (3.87)	0/0	0/0	0/0	0/0	0/0	0/1.41 (4.96)
Cheilodactylus pixi	0.31/0	0.19/0	0.31/0.52 (5.94)	0.19/0.36 (2.21)	0.05/0.52 (8.91)	0/0.36	0.05/0	0/0
Cheilodactylus fasciatus	0.45/0	0.23/0	0.45/0.23 (4.55)	0.23/0.52 (2.65)	0.05/0.23 (4.35)	0.08/0.52 (2.17)	0.05/0	0.08/0
Gymnocrotaphus curvidens	0.52/0	0.26/0	0.52/0.19 (4.79)	0.26/0.42 (2.19)	0/0.19	0/0.42	0/0	0/0
Mustelus mustelus	0.08/0.19	0.86/0.7	0.08/0.03	0.86/0.4 (3.51)	0/0.03	0.93/0.4 (3.4)	0/0.19 (18.35)	0.93/0.7 (6.09)
Chrysoblephus cristiceps	0/0	0.39/0	0/0	0.39/0.42 (2.81)	0/0	0/0.42	0/0	0/0
Rhinecanthus annulatus	0/0	0/0.13	0/0	0/0	0/0	0.72/0 (2.63)	0/0	0.72/0.13 (3.9)

3.3.5 Univariate analyses on species richness and roman abundance

3.3.5.1 Effect of depth on species richness

The best-fit GAM run on the species richness data was able to explain 77.5% of the observed variability in the response variable. *Depth* did not to have a significant effect on species richness (χ^2 = 1.33, p-value = 0.25; Table 3.13), although a slightly negative relationship was indicated between species richness and depth in both methods (Table 3.14; Figure 3.3). The unbaited method had a highly significant negative effect on species richness ($p < 0.001$; Table 3.14). Similarly, the *Sand* bottom type had a significantly negative effect on species richness ($p < 0.001$; Table 3.14), with lower species richness than the reef bottom type for both the baited and unbaited methods (Figure 3.3). *Visibility, Water Column* and *Temperature* had a significant ($p < 0.05$) non-linear effect on species richness (effective degrees of freedom (EDF) > 1; Table 3.13), with *Visibility* and *Temperature* having a positive effect on species richness. *Temperature* had a positive effect on species richness up to 16°C, with further increases in water temperature having no noticeable effects on richness, while the visible percentage of *Water Column* had a slightly negative effect on species richness (see Appendix, Figure A2.1).

Table 3.13: Analysis of variance showing the effect of depth on species richness and significance of smooth terms (Model 3.3). Significant p-values are presented in bold (df = degrees of freedom; edf = effective degrees of freedom; Ref.df = residual effective degrees of freedom)

Coefficients	**df**	**Chi.sq**	**p-value**
Method	1	66.354	**< 0.001**
Depth	1	1.328	0.249
Bottom	1	20.684	**< 0.001**
Method: Bottom	1	20.763	**< 0.001**

Approximate significance of smooth terms	**edf**	**Ref.df**	**Chi.sq**	**p-value**
s(Visibility)	2.417	3.018	15.416	**0.001**
s(Water Column)	2.633	3.215	8.631	**0.045**
s(Temperature)	4.7	5.775	32.472	**< 0.001**

Table 3.14: The effect of depth and other covariates on species richness (Model 3.3). Intercept estimate = Method: Baited; Bottom: Reef. Significant p-values are presented in bold

Coefficients	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	2.689	0.166	16.166	**< 0.001**
Method Unbaited	-0.945	0.116	-8.146	**< 0.001**
Depth	-0.010	0.009	-1.153	0.249
Bottom Sand	-0.682	0.150	-4.548	**< 0.001**
Method Unbaited: Bottom Sand	-1.709	0.374983	-4.557	**< 0.001**

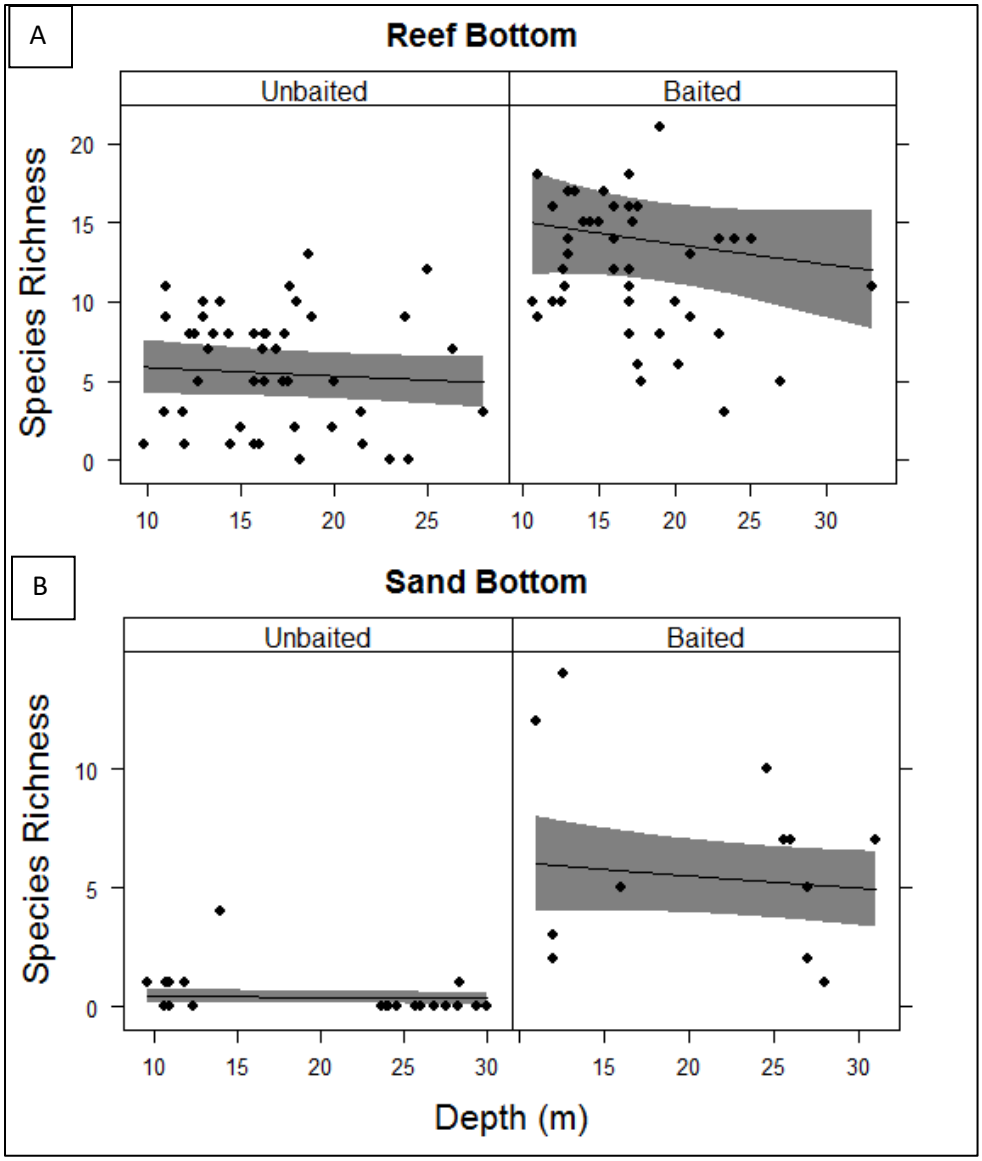

Figure 3.3: Output of Generalised Additive Model 3.3 testing the effect of depth on species richness. The plots display the observed data (black dots) collected on reef (A) and sand (B) sites using the baited and unbaited stereo-RUVs. The predicted species richness from the model (black line) with 95% approximate confidence intervals (grey shaded area) is overlaid and based on standardised values (mean) for water column (53.5%), temperature (17.2°C) and visibility (2.26 m)

3.3.5.2 Effect of habitat on species richness

The habitat model 3.4 was able to explain 60.9% of the variation observed in the species richness data. *Habitat* ($p < 0.001$) and *Method* ($p < 0.001$) were found to have a highly significant effect on species richness (Table 3.15). The interaction between *Habitat* and *Method* was dropped during the model selection process, indicating that the patterns in species richness between habitat types were consistent between sampling methods, with significantly fewer species recorded when bait was not used in each habitat type

Table 3.**16**; Figure 3.4). Fish species richness was significantly higher on the reef habitats than the sand habitats, in both the baited and unbaited methods (Figure 3.4). There was no significant difference in species richness between the three reef habitat types. Similarly, there was no difference in species richness between shallow and deep sand habitats (

Table 3.**16**; Figure 3.4). *Visibility* and *Water column* had non-linear effects on species richness (Table 3.15), with *Water Colu*mn having a negative effect and *Visibility* having a significantly positive effect (see Appendix, Figure A2.2).

Table 3.15: Analysis of variance showing the effect of habitat on species richness and the significance of smooth terms (Model 3.4). Significant p-values are presented in bold (df = degrees of freedom; edf = effective degrees of freedom; Ref.df = residual effective degrees of freedom)

Coefficients	**Df**	**Chi.sq**	**p-value**
Method	1	82.26	**< 0.001**
Habitat	4	24.54	**< 0.001**
Temperature	1	19.14	**< 0.001**

Approximate significance of smooth terms	**edf**	**Ref.df**	**Chi.sq**	**p-value**
s(Visibility)	2.793	3.485	24.599	**< 0.001**
s(Water Column)	1.365	1.634	1.538	0.264

Table 3.16: The effect of habitat and other covariates on species richness (Model 3.4). Intercept estimate = Method: Baited; Habitat: Patch Reef. Significant p-values are presented in bold

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.10193	0.33316	3.307	**< 0.001**
Method Unbaited	-1.02573	0.1131	-9.07	**< 0.001**
Habitat Deep Reef	-0.04279	0.18514	-0.231	0.817
Habitat Deep Sand	-0.66333	0.24341	-2.725	**0.006**
Habitat Shallow Sand	-0.58308	0.24188	-2.411	**0.016**
Habitat Shallow Reef	0.14018	0.1912	0.733	0.463
Temp	0.07669	0.01753	4.375	**< 0.001**

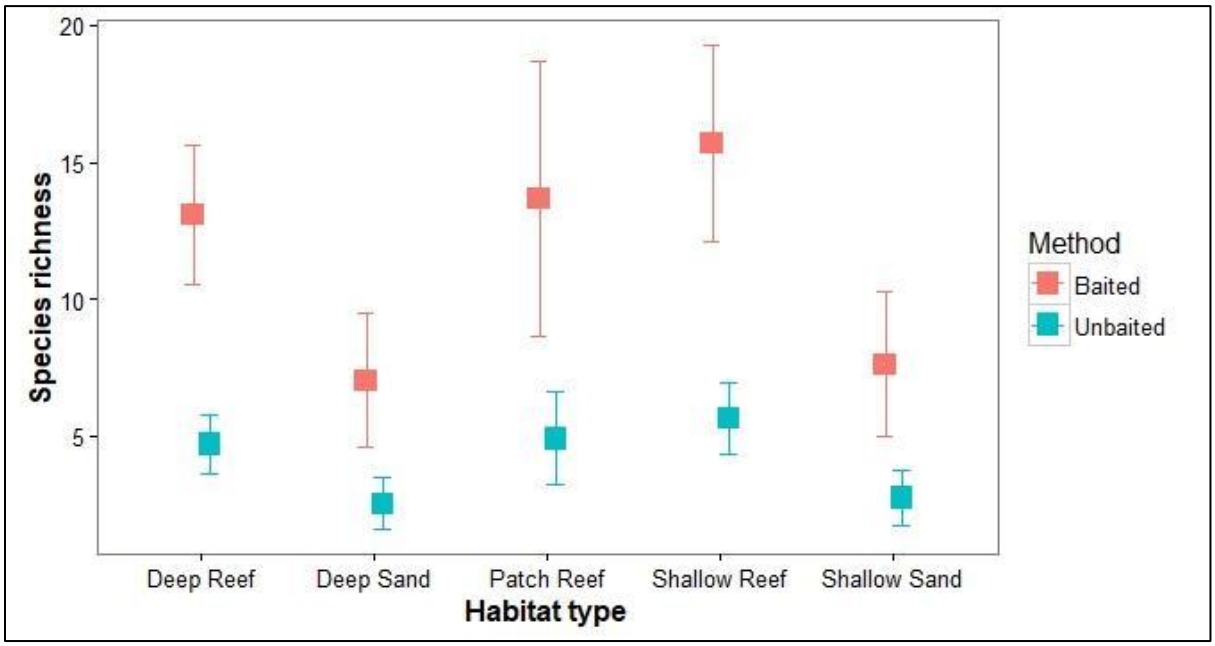

Figure 3.4: Output of Generalised Additive Model 3.4 testing the effect of habitat type on species richness, displaying predicted values of species richness (number of species) in response to change in habitat type. The predicted species richness data were based on standardised values (mean) for *Water Column* (53.50%), *Visibility* (2.26 m) and *Temperature* (17.2°C). The error bars represent the 95% confidence intervals

3.3.5.3 ROMAN ABUNDANCE

A total of 304 roman were observed in the study. Data exploration, however, revealed that only eight roman were seen on sandy sites, of which only one individual was observed using the unbaited method. As such, the data were subsetted to only contain reef sites for the depth analysis. In all, the subsetted data consisted of 89 reef sites of which 44 were baited and 45 were unbaited, with roman observed in 78 sites. When bait was used, 216 roman were recoded with an average (± SD) of 4.91 ± 3.21 roman per sample. Using the unbaited method, 80 roman were recorded on reef sites with an average of 1.70 ± 1.27 roman per sample.

3.3.5.3.1 EFFECT OF DEPTH ON ROMAN ABUNDANCE

The best-fit GAM was able to explain 54.2% of the variation in the roman abundance data. The results show that *Method* had a significant effect ($p < 0.01$; Table 3.17), with the unbaited method recording significantly fewer roman (Table 3.18). *Depth* had a slightly negative effect on roman abundance from the baited method, although the effect was not significant ($p = 0.87$; Table 3.18). For the unbaited method, however, depth had a slightly positive effect on roman abundance (Figure 3.5), but the effect was not significant either ($p = 0.33$; Table 3.18). *Temperature* and *Visibility* both had non-linear effects on roman abundance (EDF >1; Table 3.17) with temperature being significant ($p < 0.01$). An initial positive effect of *Visibility* (up to 2m) and *Temperature* (up to 12–13°C) was seen on roman abundance, after which the effects were more or less linear (see Appendix, Figure A2.3).

Table 3.17: Analysis of variance showing the effect of depth on roman abundance and the significance of smooth terms (Model 3.5). Significant p-values are presented in bold (df = degrees of freedom; edf = effective degrees of freedom; Ref.df = residual effective degrees of freedom)

Coefficients	**df**	**Chi.sq**	**p-value**
Method	1	7.59	**0.006**
Depth	1	0.029	0.865
Method: Depth	1	0.948	0.330

Approximate significance of smooth terms	**edf**	**Ref.df**	**Chi.sq**	**p-value**
s(Temperature)	6.547	7.663	21.324	**0.006**
s(Visibility)	4.806	5.816	7.608	0.293

Table 3.18: The effect of depth and treatment on roman abundance (Model 3.5). Intercept = Method: Baited. Significant p-values are presented in bold

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.676	0.325	5.162	**< 0.001**
Method Unbaited	-1.779	0.646	-2.755	**0.006**
Depth	-0.003	0.018	-0.17	0.865
Method Unbaited: Depth	0.034	0.035	0.973	0.330

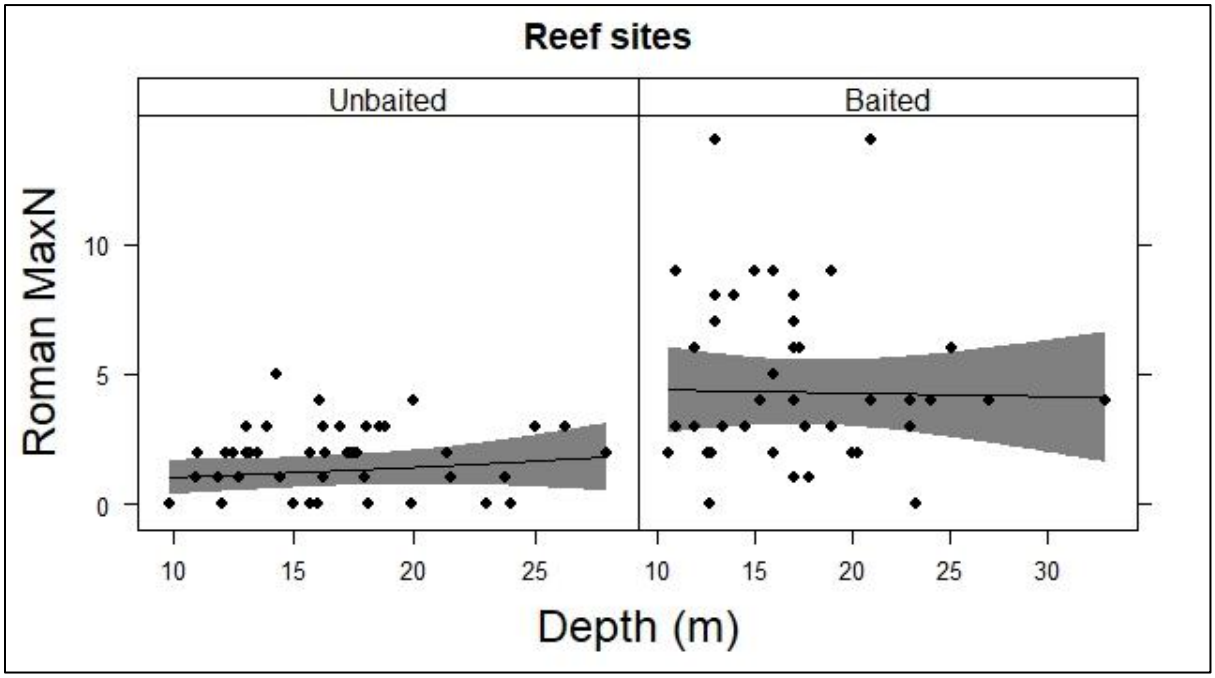

Figure 3.5: Output of the Generalised Additive Model 3.5 testing the effect of depth on roman abundance. The plots display the observed data (black dots) using the baited and unbaited stereo-RUVs methods on reef sites. The predicted species richness from the model (black line) with 95% confidence intervals (grey shaded area) is overlaid and based on standardised values (mean) for *Water Column* (54.29%), *Temperature* (17.08°C) and *Visibility* (2.45 m)

3.3.5.3.2 Effect of habitat on roman abundance

The habitat Model 3.6 was able to explain 56.4% of the variation in the roman abundance data. *Habitat* ($p < 0.001$) and the unbaited method ($p < 0.001$) were found to have a significant effect on roman

abundance (Table 3.19). The use of bait significantly increased the abundances of roman in all habitat types, relative to the unbaited stereo-RUVs, with the exception being the sand habitat types (Table 3.20). A slightly positive effect of habitat on roman abundance was seen in the *Patch Reef* and *Shallow Reef* habitat types, although the effect was not significant (Table 3.20). Significantly fewer roman were detected in the *Deep* and *Shallow Sand* habitats types, relative to the reef habitats (Table 3.20; Figure 3.6). However, in the sand habitats there was no marked effect of bait type (Figure 3.6). Bait did, however, increase the abundance of roman on sand habitats, to the point where there was no difference in the abundance of roman on reef habitats from the stereo-RUVs footage compared to sand habitats from the stereo-BRUVs footage (Figure 3.6). *Temperature* ($p < 0.05$) and *Visibility* ($p < 0.01$) were both found to have a significant effect on roman abundance, with visibility having an initial non-linear positive effect up to 2.5 m, after which the effect was generally linear (Table 3.20; see Appendix, Figure A2.4).

Table 3.19: Analysis of variance showing the effect of habitat on roman abundance and the significance of smooth terms (Model 3.6). Significant p-values are presented in bold (df = degrees of freedom; edf = effective degrees of freedom; Ref.df = residual effective degrees of freedom)

Coefficients	df	Chi.sq	p-value
Temperature	1	3.866	**0.049**
Method	1	35.705	**< 0.001**
Habitat	4	22.376	**< 0.001**

Approximate significance of smooth terms	**edf**	**Ref.df**	**Chi.sq**	**p-value**
s(Visibility)	4.238	5.206	17.36	**0.004**

Table 3.20: The effect of habitat and other covariates on roman abundance (Model 3.6). Intercept = Method: Baited; Habitat: Patch Reef. Significant p-values are presented in bold

Coefficients	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**

(Intercept)	0.463	0.484	0.958	0.338
Temp	0.051	0.026	1.966	**0.049**
Method Unbaited	-1.036	0.173	-5.975	**< 0.001**
Habitat Deep Reef	-0.107	0.264	-0.407	0.684
Habitat Deep Sand	-1.389	0.432	-3.214	**< 0.001**
Habitat Shallow Sand	-1.055	0.388	-2.720	**0.007**
Habitat Shallow Reef	0.047	0.272	0.171	0.864

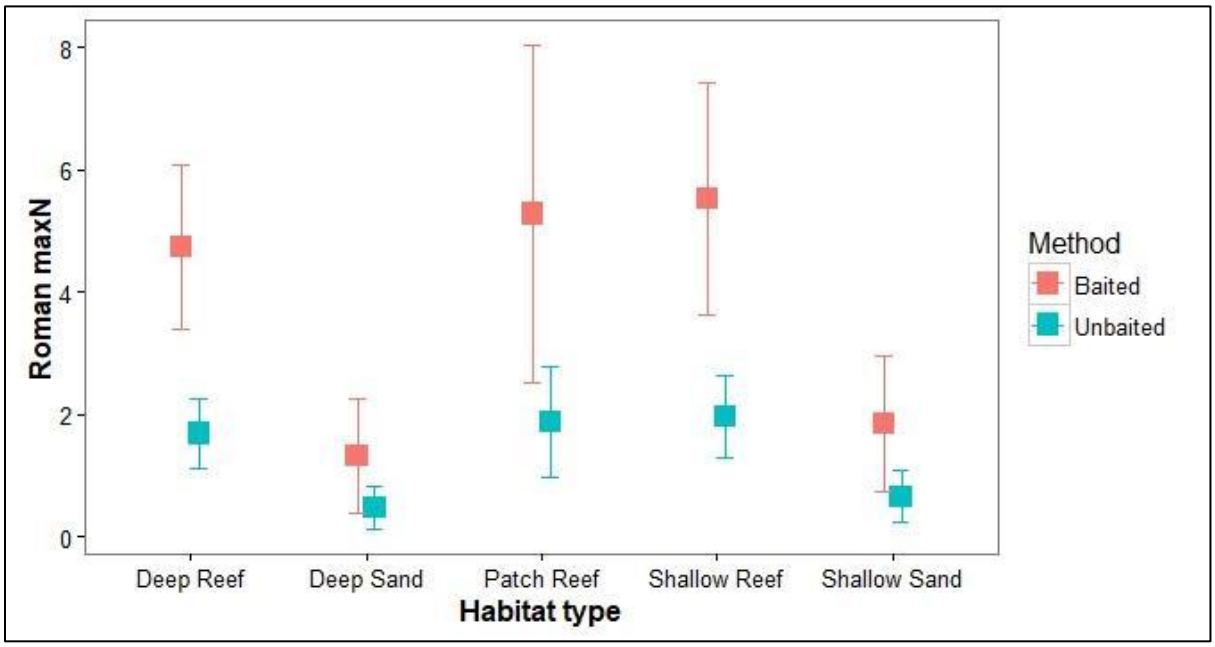

Figure 3.6: Output of Generalised Additive Model 3.6 testing the effect of habitat type on roman abundance, displaying predicted values of roman abundance (MaxN) in response to change in habitat types. The predicted abundance data are based on standardised values (mean) for *Water Column* (53.01%), *Visibility* (2.22 m) and *Temperature* (17.27°C). The error bars represent the 95% confidence intervals

3.4 Discussion

The aim of this chapter was to determine whether bait had an effect on the associations between the observed fish community and their habitats. This was done to determine whether the stereo-BRUVs method is appropriate to use when investigating fish–habitat associations. The specific objectives of this

chapter were to a) describe the observed fish community within the study area and how it changed with increasing depth, b) test whether the different fish assemblages could be associated with habitat types, and c) determine the effect of bait on the type and strength of those associations. The fish community observed with stereo-RUVs in the study area differed between reef and sand bottom types as well as among the five habitat types identified in Chapter 2, indicating that there was a definite association between the observed fish assemblages and bottom type, as well as the more finely (100s of metres) classified habitat types. In general, greater diversity and higher abundances of fishes were recorded by the baited video method than the unbaited method. The use of bait definitely had an effect on the observed fish assemblage, increasing fish–habitat associations, especially in sand habitats.

In the absence of bait, the sand habitats were not effectively sampled, while the presence of bait appeared to reduce the scale of the distinction between the fish communities found in the shallow (9–14 m) and deep (15–44 m) reef habitats. Habitat associations were, however, still apparent, indicating that stereo-BRUVs can be used to identify fine-scale patterns in fish assemblage structures.

3.4.1 FISH COMMUNITY STRUCTURE

The number of species detected in the present study was higher than that of previous studies conducted in the Tsitsikamma NP MPA. Both Bernard and Götz (2012) and Heyns-Veale et al. (2016) identified 48 fish species compared to the 60 species identified in the present study. The higher species richness can most likely be attributed to the greater sampling effort of the present study, where 143 samples were collected, compared to Bernard and Götz's (2012) 56 and Heyns-Veale et al's (2016) 51 samples.

Of the 60 species sampled during this study, 59 were recorded using the baited method and only 29 using the unbaited method. Previous research comparing the two methods, conducted by Bernard and Götz (2012), observed 46 species using the baited method and 34 using the unbaited method. The lower counts of species seen in the unbaited method in the current study could be attributed to the fact that the 2012 study by Bernard and Götz was conducted over a greater area (~3x1 km compared to 1x1 km). This could be related to the species–area relationship, which indicates that a greater number of species are expected to be observed as a sampled area increases (Conner and McCoy, 1979). The observed difference in species richness may also be attributed to the fact that only reef habitats were targeted in the 2012 research, while in the present study samples were spread across both reef and sand habitats. Although expanding the sampling scope to include sand habitats would be expected to increase species richness (as sand-associated species would be added to the species richness total), the results showed that stereo-RUVs were unable to effectively sample the sand fish assemblage.

3.4.2 PATTERNS IN THE FISH COMMUNITY STRUCTURE

To assess the effect of habitat and depth on the fish community, the results from the stereo-RUVs method were used. RUV systems are assumed to provide a more natural representation of the observed fish community, as they overcome most methodological biases associated with other sampling techniques (Bernard and Götz, 2012).

3.4.2.1 EFFECT OF HABITAT

In general, more species were found on reef habitats than sand habitats, which was expected since reef habitats provide food and shelter for many fish species typical to the Agulhas Ecoregion (Buxton and Smale, 1989; Guidetti, 2000; Luckenbach et al., 1999). Habitat and bottom type demonstrated a significant effect on the fish community composition and roman abundance. Reef habitats that contain areas of high relief (i.e. high-profile reef) have been positively associated with an increase in the abundance of fish species (Gratwicke and Speight, 2005; Guidetti, 2000). It is therefore not surprising that reef habitats and bottom type had higher richness and abundances of fish than sand habitats types. In the present study, the *Shallow Reef* habitat was predicted to have the highest species richness (Figure 3.4). Depth is considered to be a driving factor of fish species distribution and abundance (Brokovich et al., 2008; Heyns-Veale et al., 2016). Shallow habitats were also associated with high abundances of benthic primary producers (see Chapter 2) and warmer water temperatures. Benthic primary producers, such as macroalgae, are foundation species that directly support fish and other biotic communities by providing food and shelter (Poore et al., 2012). Thus, it is possible that the higher abundance of primary producers facilitated diversity and the abundance of fish species. In addition, warmer water temperatures affect fish metabolism, growth and movement (Green and Fisher, 2004), while shallow habitats are nursery areas for many juvenile fish species (Guidetti, 2000). As such, the high diversity and abundance of fish likely reflects numerous favourable abiotic and biotic conditions associated with shallow water reef habitats.

In terms of habitat use, certain fish species were present in all habitats in different abundances, while others were only observed in a particular habitat. Commonly occurring fish species that were recorded in all habitat types included roman, steentjie and fransmadam. Variation in the abundance of these fishes contributed strongly to the differences identified between habitat types. Although roman, steentjie and fransmadam are generally reef-associated species (Mann, 2013) and were more abundant in both the deep and shallow reef habitats, they were also seen on sandy habitats in low abundances. Roman occurred in similar abundances in the *Patch Reef* and *Shallow Reef* habitats, in both treatments. This suggests that roman may prefer to forage near reef habitats, to feed on sand-associated invertebrates.

Roman feed on a wide variety of prey items (echinoderms, cephalopods, small crustaceans and polychaetes; Mann, 2013), which allows them to actively seek out prey in all habitats (Heyns-Veale et al., 2016; Mann, 2013), potentially explaining why they were abundant in the *Patch Reef* habitat. This result might also be a territory-related effect, where definitive reef areas are strongly defended territories, deterring other roman from entering. While *Patch Reef* is a more marginal habitat, it might not be as strongly protected within a territory. Kerwath et al. (2007) observed territorial and aggressive behaviour among roman where the availability of food was spatially limited. However, the fact that roman abundance was similar in both the *Patch Reef* and *Shallow Reef* habitats in both treatments suggests that this pattern may be due to foraging behaviour. Fransmadam and steentjie are also considered to be habitat generalists (Heyns-Veale et al., 2016), with both species adopting an omnivorous lifestyle (Fairhurst et al., 2007; Mann, 2013).

In general, low diversity and abundances of fish were detected in the sand habitats, which were occupied by fish species that were adapted to fill that specific niche, most likely utilising different feeding strategies to avoid competition (for resources) or predators. For example, species such as the white sea catfish and the red tjor tjor were more abundant in the sandy habitats. While both roman and white sea catfish have similar diets (Mann, 2013), the catfish species usually prefer sandy bottoms where they are able to seek out benthic crustaceans and other infauna invertebrates (Tilney and Hecht, 1990).

3.4.2.2 Effect of depth

The effect of depth on fishes has been documented by multiple studies (Deter et al., 2012; Garrabou et al., 2002; Heyns-Veale et al., 2016; Howell et al., 2002) and depth is known to influence species distribution, richness and abundance (Brokovich et al., 2008; Heyns et al., 2016). However, in the present study, depth did not have a significant effect on species richness or abundance, although a slight decrease in species abundance was recorded with increasing depth (Figure 3.3). Andradi-Brown et al. (2016) and Heyns et al. (2016) found that a significantly negative effect of species richness and abundance was observed with an increase in depth. However, both studies considered depths that are less than 30 m to be shallow habitats, while deeper reefs were classified as > 30–35 m in depth. The present study was carried out within a narrow depth range (15–44 m), with reef habitats ranging from 9–25 m. This narrow depth range could be the reason why depth was not seen to have a significant effect on species richness or abundance. When comparing habitats, however, depth-related patterns become evident. The comparisons between *Shallow Sand* and *Deep Sand* habitats and *Shallow Reef* and *Deep Reef* habitats showed that fish occurred at lower abundances in the deep habitat types (tables 3.8 and 3.13). This

decline in abundance as depth increases is a commonly observed pattern (Brokovich et al., 2008; Heyns-Veale et al., 2016) and is likely attributable to more favourable ecological conditions found in the shallower depths supporting a higher abundance of fish, as discussed earlier.

Roman abundance was also observed to be independent of depth. Since the analysis excluded sand sites, this result suggests that, within the depth range sampled, roman are distributed relatively evenly across the contiguous reef complex.

3.4.2.3 Fish–habitat associations in the stereo-ruvs footage

The fish assemblages in the reef and sand habitats showed differences in both species richness and abundance, with noticeably more fish observed in reef habitats (Figure 3.7). The increased structural complexity provided by the macrobenthos found in the reef habitats likely explains this pattern. Structural complexity plays a vital part in reef fish distribution, as it can reduce predation rates by providing shelter for small fish species (Beukers and Jones, 1997). In the unbaited footage, the major contributing species associated with reef habitats were generalist and micro-invertebrate carnivores (Figure 3.7). Generalist carnivores, such as fransmadam and roman, have a very diverse diet consisting of a range of crustaceans, ascidians, algae, polychaete worms, bryozoans and molluscs (Mann, 2013). The *Deep Reef* habitat contained a high percentage of bryozoans and cnidaria, while the *Shallow Reef* consisted of a high percentage of macroalgae. The *Patch Reef* habitat mainly consisted of coarse sand, which would contain many infaunal invertebrates such as small crustaceans and polychaete worms. The abundance of food available in these habitats may explain why these species were seen in high abundances and showed a strong association with these habitat types. The *Shallow Sand* habitat appeared to be associated with species that are specifically adapted to living in sandy habitats, while no species appeared to be associated with the *Deep Sand* habitat in the data from the unbaited video systems (Figure 3.7). Although significant differences in fish abundance were seen between the reef habitats (Table 3.9), the major species associated with these habitats appeared to be very similar. This was indicated by the non-significant findings in the species composition analysis (Table 3.8), and can potentially be explained by the fact that, in most studies, ‘shallow’ habitat is classified as shallower than 25 m. Thus, it is evident that over the depth range and spatial scale considered, reef habitat preferences were reflected by higher abundances, rather than species turnover. There was, however, considerable difference in the species composition between the reef and sand habitats, highlighting the role of niche- based processes in structuring the fish community between these very distinct habitat types.

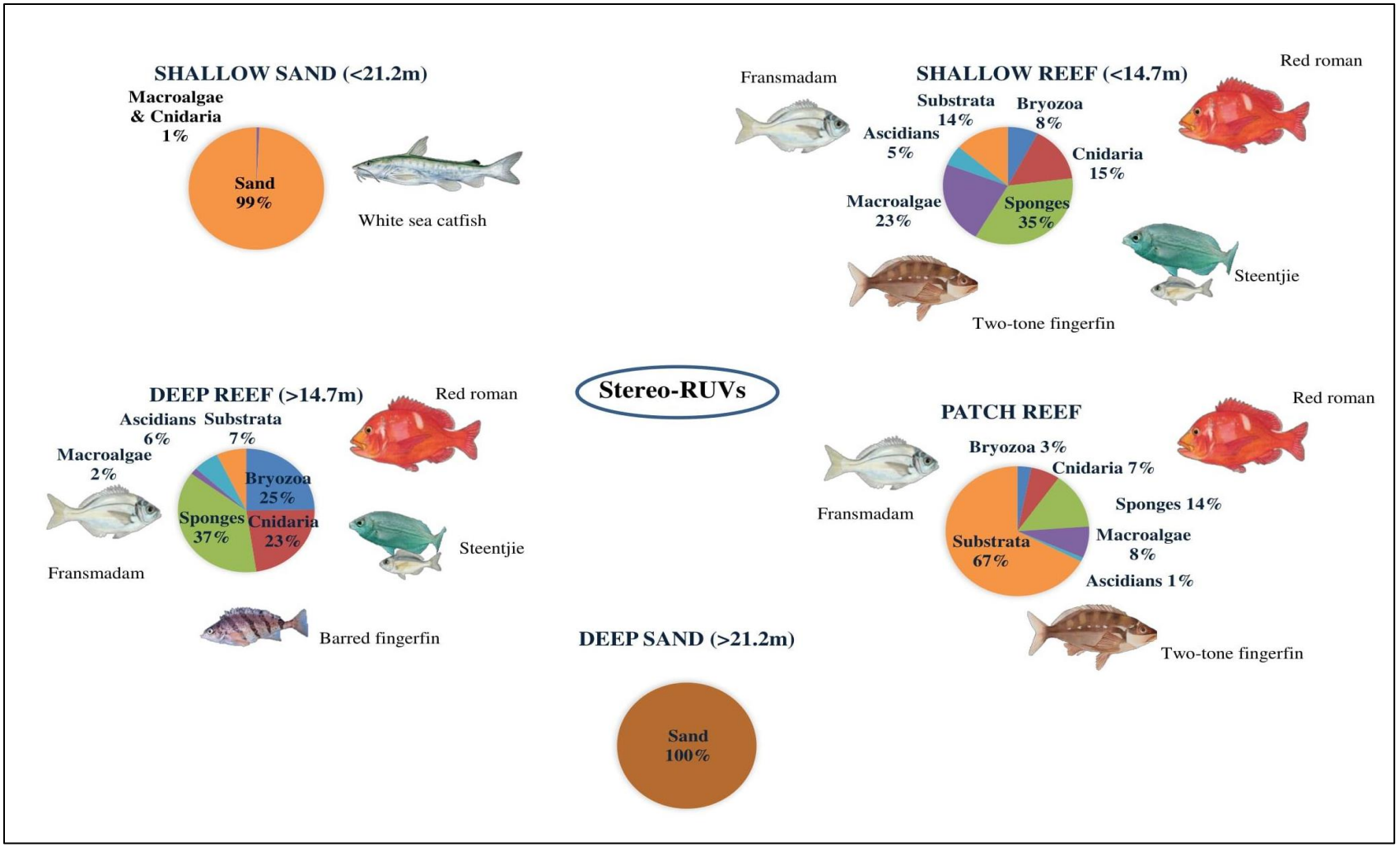

Figure 3.7: Fish-habitat associations showing the major contributing species from SIMPER analysis in each habitat type using the stereo-RUVs method

3.4.3 Effect of bait on the observed fish assemblage

Bait had a highly significant effect on both species richness and fish abundance. This was an expected result, as the baited method is known to attract a greater number and diversity of fish (Bernard and Götz, 2012; Dorman et al., 2012; Harvey et al., 2007). The addition of bait also appeared to attract a higher number of sparid species as well as higher trophic level species such as sharks. Bait did, however, have an inconsistent effect on the abundance of small micro-invertebrate carnivores (fingerfins) across habitat types and higher abundances of these species were found in the unbaited footage on reef habitats (Table 3.11). A consistent effect of bait was seen in roman abundance, where the baited method observed higher abundances in all habitat types. This suggests that species-specific biases may be present when using bait to detect habitat associations across fine spatial scales, especially when looking at smaller and abundant generalist carnivores.

The baited method was, however, able to sample fish species that were present in the sand habitats – species which were not detected using the unbaited method. For example, in the *Deep Sand*, the white sea catfish, red tjor tjor, smooth hound shark and lesser guitarfish were not present in the unbaited footage, while they were recorded in the baited footage (Table 3.12; Figure 3.8). The red tjor tjor, otherwise known as 'sand soldier', is a known sand-associated species which can be found in sandy habitats of up to 100 m in depth (Heemstra and Heemstra, 2004). In addition, the lesser guitarfish, white sea catfish and smooth hound shark are also known to be associated with sandy habitats (Espinoza et al., 2011; Mann, 2013; Tilney and Hecht, 1990). Similar patterns were observed in the *Shallow Sand*, where maasbanker, cape stumpnose and evil-eye puffer were not detected by the stereo-RUVS method (Table 3.12). Maasbanker is a pelagic species commonly found in midwater trawls (Barange et al., 1998; Kreiner et al., 2015), and is thus not part of the resident fish community, and not considered here. Cape stumpnose and the evil-eye puffer, on the other hand, are known to be associated with sand and shallow reef habitats (Mann, 2013).

Since the *Shallow Sand* did not contain much benthic cover or structural complexity, it can be assumed that the fish found in this habitat are lower-level trophic species, feeding on algae or infaunal invertebrates such as small molluscs, crustaceans and cnidarians. Therefore, the presence of fish species such as steentjie, cape stumpnose and black tail (*Diplodus sargus capensis*) would be expected to occur in this habitat type. Juvenile black tail and cape stumpnose are known to occur in shallow reefs and sandy habitats, and feed on a wide range of small prey items ranging from algae to small crustaceans (Heemstra and Heemstra, 2004). Juvenile cape stumpnose and steentjie predominantly feed on seagrass and algae,

changing to carnivory as they grow older (Fairhurst et al., 2007; Heemstra and Heemstra, 2004). As such, the stereo-BRUVs data appeared to provide a more complete assessment of the *Shallow Sand* fish assemblage, relative to the stereo-RUVs.

The *Deep Sand* habitat was the largest of the five habitat types but contained the least number of fish species. This is likely due to the absence of macrobenthic cover in this habitat, and a lack of structure from the reef. The absence of macrobenthos, such as algae that occurred in the *Shallow Sand* habitat, resulted in the loss of structural complexity, thereby reducing shelter and food for many fish species. While the data gathered by the stereo-RUVs footage indicated that no fish were associated with the *Deep Sand* habitat, the baited method identified numerous species with a close habitat association. These species included the lesser guitarfish, smooth hound shark, evil-eye puffer and white sea catfish (Figure 3.8). The findings suggest that the unbaited method is ineffective at sampling in sand habitat types, while the baited method is more effective.

A general trend in most ecological studies is that fish size and predator abundance increase with depth (Heyns-Veale et al., 2016; Macpherson and Duarte, 1991; Ryer et al., 2010). It can therefore be assumed that species that occur in the *Deep Sand* habitat are often predatory and are specifically adapted to live in sandy habitats. Furthermore, predatory species are expected to be attracted by bait, therefore it is not surprising that the addition of bait attracted larger predators such as the lesser guitarfish and smooth hound shark.

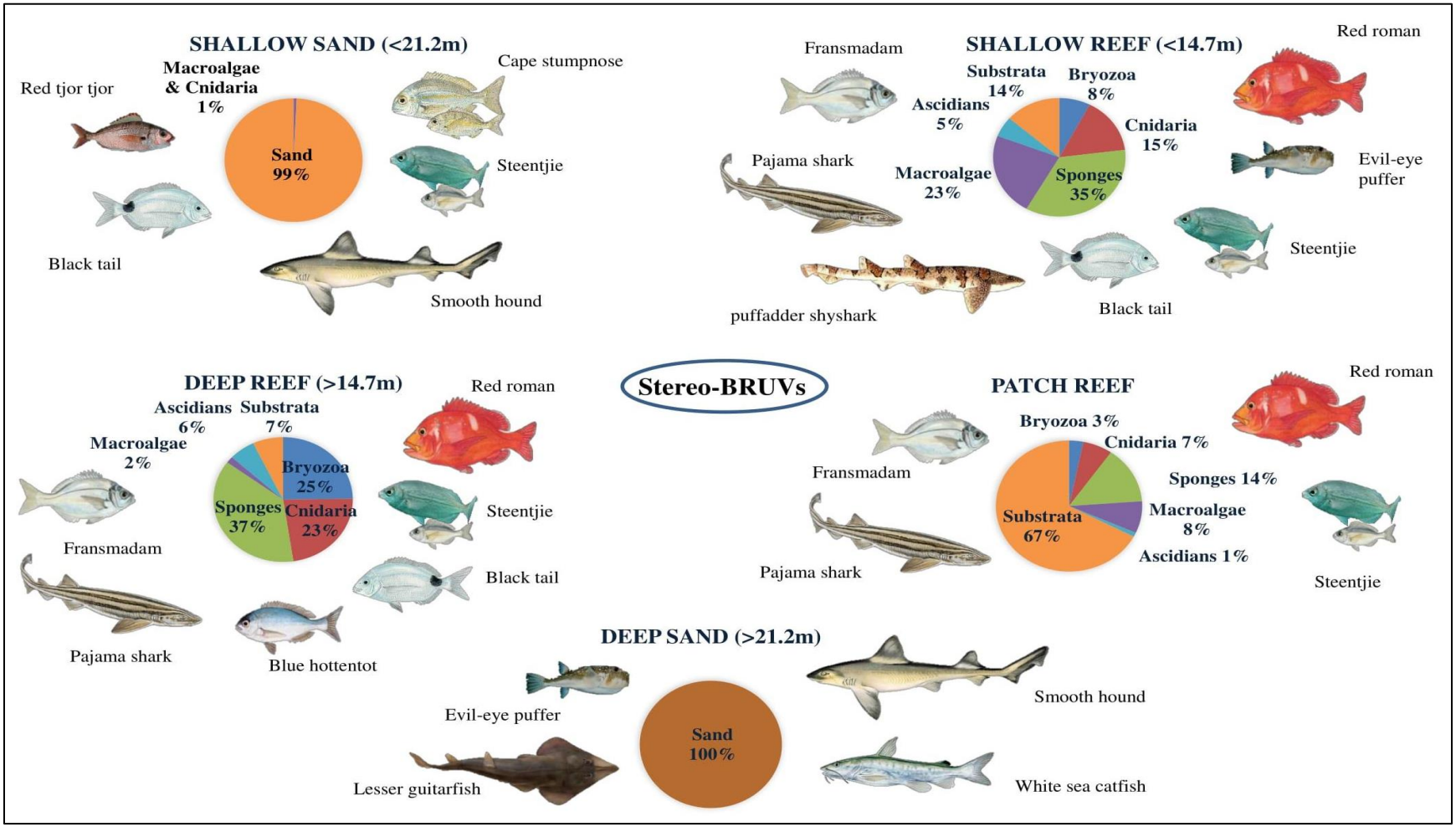

Figure 3.8: Fish–habitat associations showing the major contributing species from SIMPER analysis in each habitat type using the stereo-BRUVs method

The patterns seen in the CAP analysis (Figure 3.2) were more defined and had a greater allocation success in the baited than the unbaited method. A clear separation between the two sand habitats as well as between reef and sand habitats in both the species composition and abundance data were observed in the baited method. Bait seemed to reduce the difference in fish community structure between the shallow and deep reefs, when compared to the unbaited method. However, the pairwise test from the PERMANOVA run on the abundance data indicated that in both the baited and unbaited methods, the fish community structure differed significantly between the deep and shallow reef habitats, although the scale of the distinction was reduced when bait was present (P-value: stereo-RUVs = 0.009, stereo-BRUVs = 0.03). However, when considering the presence/absence data, the stereo-BRUVs method (not the stereo-RUVs method) was able to detect a difference in the fish assemblage structure. As such, the results from the multivariate analysis indicate that the use of bait in the stereo-RUV system emphasised the overall fish–habitat associations within the study area. This supports previous research from the same area that found distinct fish assemblages associated with different shallow reef habitats when sampling with stereo-BRUVs (Heyns-Veale et al., 2016). The 2016 study covered a slightly broader area (1.8 km^2), suggesting that stereo-BRUVs are capable of identifying fish–habitat associations across fine and medium scales. Undoubtedly, the stereo-BRUVs method should therefore also be capable of identifying fish–habitat associations over large spatial scales. Pairwise comparisons between methods within habitat type, of fish composition, show no significant differences in the *Shallow Sand* and *Patch Reef* habitats (Table 3.6), but pairwise comparisons between methods, within habitat type, in the PERMDISP analysis show significant differences in all habitat types (Table 3.10). This indicates that while the fish communities within the *Shallow Sand* and *Patch Reef* habitats appear to be similar in both the baited and unbaited methods, the methods differ in variability. The remaining three habitat types are characterised by different species with different levels of variability between samples. The lower allocation success for the unbaited samples in the CAP analysis (Figure 3.2), in combination with significant differences in dispersion (PERMDISP), implies that the unbaited method is more variable than the baited method. Bernard and Götz (2012) also found the unbaited method to be highly variable, concluding that a higher sampling effort is required for the data gathered by RUVs to be equivocal to those of BRUVs.

Although data collected by stereo-RUVs are more variable than those of stereo-BRUVs, the former method does have certain advantages. For example, two-tone fingerfin abundance was higher in the unbaited footage in the *Shallow Reef* relative to the baited systems. Similarly, in the *Deep Reef*, barred fingerfins (*Chirodactylus pixi*) were more abundant in the unbaited footage than the baited footage (Table 3.11). This result concurs with the findings of Bernard and Götz (2012), where a threefold increase in

fingerfins (Family *Cheilodactylidae*) was recorded in the absence of bait. The two-tone fingerfin is a micro-invertebrate carnivore found on rocky reefs in southern Africa (Heemstra and Heemstra, 2004), but it is not attracted to bait (Bernard and Götz, 2012). It could therefore be argued that the stereo-RUVs method is more suited for sampling herbivorous or micro-invertebrate feeders that are not attracted by bait, thereby obtaining more adequate fish–habitat associations. Watson et al. (2010), when comparing diver-operated stereo-video (stereo-DOV) and stereo-BRUVs methods, found very different fish assemblages when sampling with the two methods. Although species richness was significantly higher when using stereo-BRUVs than stereo-DOVs (a method that does not use the addition of bait), the study demonstrated that the choice of sampling method can lead to different interpretations of fish assemblage structures. However, Harvey et al. (2007) reported that herbivorous and lower-level trophic fish species were seen at 4–7 m, in the background of stereo-BRUVs footage, indicating that the stereo-BRUVs method is capable of sampling non-predatory fish species. Although the average visibility was not stipulated in the study by Harvey et al. (2007), 4–7 m is substantially greater than the average visibility of 2.1 m in the current study, enabling a greater number of species to be seen. It is possible that with poor visibility (< 2 m) unbaited methods could struggle to adequately sample the fish community. Therefore, unbaited methods (such as RUVs and DOVs) might perform better in clean water environments (e.g. tropical waters), where visibility is not a concern.

Pairwise comparisons of fish abundance between the *Patch Reef* and *Deep Sand* habitats and *Patch Reef* and *Shallow Sand* habitats showed that the differences between habitats was not consistent across methods (Table 3.9). In both instances, bait did not have a significant effect when comparing fish abundance between the two habitat types, indicating that when marginal reef and sand habitats are compared using the baited method, the fish–habitat association breaks down. *Patch Reef* can, however, be considered to be a marginal habitat type, as it was defined as a combination of coarse sand and reef. Therefore, similar fish species may be expected to be seen between the *Patch Reef* and sand habitat types. This would explain why no differences were observed within the baited method comparisons. Furthermore, it is possible that the significant differences in fish assemblages among the habitats, as identified by the stereo-RUVs, were potentially due to the method's inability to sample the fish on sand habitats. Comparisons between fish abundance in the *Deep Sand* and *Shallow Sand* habitats were significantly different using both the baited and unbaited methods (Table 3.9). It is most likely that depth is the factor driving the differences seen between these two habitats, where higher abundances and diversity of fish are likely to occur in shallow waters. In the stereo-RUVs data, species composition appears to be similar between habitat types (Table 3.8), while habitat types differ significantly in terms of species

abundance (Table 3.9). This suggests that variations in abundance, rather than species composition, drive the differences identified between habitats in the unbaited data.

3.4.4 Other considerations

Since samples were clustered close to one another, it is possible that the fish seen in the stereo-BRUVs footage were spatially autocorrelated. For example, fish communities on sand sites close to reef may have been biased by the presence of typically reef-associated species that were willing to travel onto the sand for an opportunity to forage. In this case, bait would appear to alter the true fish–habitat associations of those species. It was suggested by Hamylton (2013) that autocorrelation could provide useful information on how fishes are related to their surroundings (e.g. movement and feeding patterns). Future research should thus consider spatial autocorrelation when using stereo-BRUVs to sample across fine spatial scales.

The water temperature over the duration of the study was highly variable, which is typical of the Tsitsikamma area (Roberts and Van den Berg, 2005). Similar variations in water temperature were described in previous research studies conducted in the region by Bernard and Götz (2012) and Heyns et al. (2016), where temperatures ranged between 9 and 21°C. Temperature is one of the most important environmental factors influencing the well-being of fish (Morita et al., 2010) as it has an effect on metabolism (Hanna et al., 2008) as well as behaviour (Biro et al., 2010; Valdimarsson et al., 1997). Warmer water temperatures will cause an increase in the metabolic rate of fish in a given area, resulting in higher growth rates, increased mobility, as well as an increased food intake and foraging activities (Hanna et al., 2008). In the Tsitsikamma region, thermal vertical stratification is a common occurrence as a result of wind-driven coastal upwelling (usually in the summer months), where the difference in water temperature between surface and bottom layers can be greater than 4°C (Roberts and Van den Berg, 2005). Temperature was found to have a significant effect on species richness and roman abundance (Table 3.15; 3.19). The effect was, however, non-linear. Both species richness and roman abundance increased to a threshold after which further increases in water temperature had little influence on the fish community.

3.4.5 Conclusions

This research provides baseline information on the effect of bait on fine-scale fish–habitat associations in the warm, temperate Agulhas Ecoregion of South Africa. Bait had a positive effect on both species richness and abundance in all habitat types. Depth did not significantly affect the species richness or abundance of the observed reef fish community, but differences in the fish community were observable between

habitat types at different depths. The unbaited method appeared to be more efficient at sampling micro-invertebrate carnivores such as fingerfins, or species that are not attracted to bait. However, the stereo-RUVs methods were ineffective at sampling sand habitat types, and the structure of the fish communities within the different habitat types was highly variable. The stereo-BRUVs method, on the other hand, was able to sample the species expected to occur in sand habitats, as well as the reef habitats. The baited method was also less variable than the unbaited method, and able to detect a higher number of fish species. These findings provide support for the use of stereo-BRUV systems to detect fine-scale fish–habitat associations within the Agulhas Ecoregion of South Africa. Further analyses on this dataset should investigate the role of spatial autocorrelation and consider the effect of bait on the size of fish species.

CHAPTER 4

4 SYNTHESIS AND RECOMMENDATIONS

The principal goal of this research was to investigate whether stereo-BRUVs can be used as an appropriate method in determining fine-scale fish–habitat associations. This was achieved by conducting a field experiment that compared fish–habitat associations identified with stereo-BRUVs data to associations identified with unbaited stereo-RUVs data within a well-established MPA. This research was the first of its kind to attempt to understand the effect of bait on fine-scale fish–habitat associations.

4.1 DEFINING HABITAT TYPES

The collection of data beyond safe SCUBA-diving depths is often expensive and logistically challenging. The use of specialised equipment is needed, which often requires specialised training and vessels to operate. As such, information on deeper regions such as subtidal nearshore deep reefs is generally lacking. The drop camera method (described in Chapter 2 of this dissertation) was a relatively inexpensive method that enabled the cost-efficient collection of a high volume of benthic photo-quadrats, compared with other methods such as ROVs and multibeam echo-sounders. With this data, the benthos within the study area was classified into fine-scale habitat types, and detailed depth and habitat maps were made. However, when compared to multibeam echo-sounder surveys, the drop camera method provides lower resolution. Yates et al. (2016) used multibeam echo-sounder technology to collect habitat data over an area of 250 km^2 collecting points (pings) every 50–100 cm. When compared to the current study, which collected a point every 30 m, the multibeam echo-sounder method is able to produce maps of substantially higher resolution, and can cover a considerably larger area. The method does, however, require a significant amount of processing to obtain an end product. The use of photographs or video (as opposed to sonar) can provide a more accurate account of individual macrobenthic species found on the benthos. This results in the formation of more detailed habitat types from which greater inferences on fish–habitat associations can be made. The collection of photo-quadrats does, however, require data to be extracted from photographs before data analysis can be conducted –

this can be time consuming and difficult to sample over large areas. The drop camera method can therefore be said to be well suited for use over small areas (e.g. 1–2 km^2). The use of multibeam echo-sounder technology in conjunction with photographic methods would be able to provide a highly accurate representation of the sea floor. Yates et al. (2016) demonstrated this by using a multibeam echo-sounder in conjunction with the towed video method. In this way, high-resolution habitat maps were generated using the combined data from the two methods.

4.2 Determining fish–habitat associations

Various methods have been used to determine fish–habitat associations. A very common method is that of UVCs (these include DOVs as well as ROVs) which have been used in many studies (Bozec et al., 2005; Darling et al., 2017; Guidetti, 2000; Laidig et al., 2009; Wilson et al., 2008, 2010). The use of UVC is common in shallow coral reef studies, as it is able to provide a rapid assesment of reef fish populations (Samoilys and Carlos, 2000). This method is, however, prone to observer bias and limited by depth and, as such, the use of remote video methods is becoming more common (Bernard et al., 2014).

The current study demostrated the value of remote video techniques as an alternative to using UVC methods. The method has also succesfully been used in previous studies, such as those by Heyns-Veale et al. (2016) and Yates et al. (2016) to asses fish–habitat associations.

4.3 Concluding remarks

It was evident that a relationship between fish and their habitat is detectible using both the stereo-RUVs and stereo-BRUVs methods. This research indicated that over narrow depth ranges, fish communities can be predicted from reef and sand habitat types and vice versa, as distinctly different fish communities were present in each habitat type. The distribution of macrobenthos can thus be said to play an important role in the prediction of fish communities. Reef and sand habitats are crucial in the structuring of fish communities, with physical habitat structure seen as vital in increasing fish species' abundance and diversity. Depth did not have a significant effect on species richness, but did have a significant effect on fish abundance. Macrobenthic assemblages also changed over a depth gradient. Thus, over fine scales, it appears that depth has an effect on the distribution of fish communities.

4.4 Outcome and Recommendations

Overall, the stereo-BRUVs method was successful in determining fish–habitat associations on a fine scale. The use of bait appears to increase the spatial grain of each sample, strengthening the observed fish–habitat associations. Although significant differences in fish community structure between the respective reef habitats were seen in both the stereo-RUVs and stereo-BRUVs methods, it appears that, in the unbaited method, fine-scale differences are masked by the presence of highly abundant and schooling species. In the baited method, on the other hand, whilst being able to attract more species, bait may reduce the fine-scale differences seen between different reef habitat types. The stereo-RUVs method can, however, detect fish species that are not affected by the presence of bait. The abundance of these fish species (e.g. fingerfin family) is dampened in the presence of commonly occurring fish species that are attracted to bait. Care must thus be taken when using stereo-BRUVs as sampling tools, since certain species are under-sampled. The addition of bait in reef habitats increases the number of fish species and reduces variability in the data. The use of bait in sand habitats is highly effective in enhancing previously established fish–habitat associations. The stereo-BRUVs method can thus still be considered a robust and powerful tool for measuring fish–habitat associations.

The use of the stereo-BRUVs method can be considered to be an appropriate tool in long-term monitoring studies, as it is capable of observing whole fish communities including predatory fish, most of which are commercially important and thus necessary to monitor. By observing whole fish communities, changes in fish community structure can be detected over time. The method is also considered to be non-invasive (and thus suitable for use in sanctuary areas) as well as being cost effective. In turn, long-term research will be able to provide information on the state of marine ecosystems, thereby enabling fisheries managers to make informed decisions on the sustainable harvesting of fish stocks in South Africa.

4.5 Future research

This research was the first of its kind that specifically aimed to determine whether the use of bait-biased fish–habitat associations developed from data collected using stereo-BRUVs methods. While the results support the use of stereo-BRUVs data over stereo-RUVs data, additional research is needed from other sites, to more rigorously test the effect of bait on fish assemblages over fine spatial scales. The addition of another fine-scale sampling site in a different location, but at a

similar depth range, against which to compare the findings of the current study, would greatly improve our understanding of fish–habitat associations.

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6 APPENDIX

A.1. LIST OF SPECIES

Table A1.1: List of species seen in the video footage showing percentage occurrence (%) within each of the five habitat types

Species	Habitat				
	Patch Reef	Deep Reef	Sand Deep	Sand Shallow	Shallow Reef
A. aequidens	0	0	0	0	100
A. argyrozona	0	100	0	0	0
A. honckenii	6.67	30	23.33	13.33	26.67
A. sebastoides	0	75	8.33	0	16.67
B. inornata	8.33	52.78	2.78	2.78	33.33
C. brachydactylus	10.71	46.43	3.57	1.79	37.5
C. brachyurus	100	0	0	0	0
C. Clinidae spp	0	33.33	0	0	66.67
C. cristiceps	10	60	0	0	30
C. fasciatus	7.69	53.85	7.69	0	30.77
C. gibbiceps	0	100	0	0	0
C. grandis	100	0	0	0	0
C. laticeps	12.05	48.19	3.61	4.82	31.33
C. marleyi	0	50	0	0	50
C. nufar	0	66.67	0	8.33	25
C. pixi	11.11	55.56	5.56	0	27.78
C. superciliosus	0	100	0	0	0
C. Taurus	0	100	0	0	0
D. brevicaudata	10	50	10	20	10
D. sargus capensis	2.33	53.49	2.33	13.95	27.91
D. chrysonota	0	100	0	0	0
D. hottentotus	11.11	55.56	5.56	0	27.78
D. pastinaca	0	100	0	0	0
E. marginatus	0	100	0	0	0
E. whiteheadi	0	100	0	0	0
G. ater	0	72.73	18.18	0	9.09
G. curvidens	10.26	46.15	2.56	2.56	38.46
G. feliceps	4.76	23.81	23.81	19.05	28.57
G. natalensis	0	0	50	50	0
H. edwardsii	3.13	50	9.38	6.25	31.25

Table A1.1 continued

H. fuscus	0	20	20	0	60
L. mormyrus	0	0	0	40	60
M. Aquila	10	30	30	20	10
M. mustelus	2.78	36.11	16.67	16.67	27.78
N. cepedianus	25	75	0	0	0
O. conwayi	20	55	0	0	25
O. vulgaris	0	60	0	0	40
P. aeneum	4.88	58.54	2.44	2.44	31.71
P. africanum	8.11	64.86	0	0	27.03
P. bellottii natalensis	0	21.05	15.79	26.32	36.84
P. blochii	0	0	0	0	100
P. bovinus	0	50	50	0	0
P. dentata	100	0	0	0	0
P. grande	0	100	0	0	0
P. laniarius	0	16.67	50	0	33.33
P. olivaceum	25	50	0	25	0
P. pantherinum	0	66.67	0	0	33.33
P. rupestris	0	50	0	0	50
P. typus	0	33.33	66.67	0	0
R. acutus	0	0	0	0	100
R. annulatus	0	0	62.5	12.5	25
R. globiceps	12.5	75	0	12.5	0
R. holubi	6.67	40	0	26.67	26.67
S. durbanesis	0	50	0	0	50
S. emarginatum	8.11	45.95	4.05	6.76	35.14
S. knysnaensis	16.67	66.67	16.67	0	0
S. lalandi	0	75	0	0	25
S. salpa	6.67	46.67	0	6.67	40
T. megalopterus	0	0	0	50	50
T. trachurus	0	60	0	40	0

Table A1.2: List of species recorded using stereo-BRUVs and RUVs methods, sorted by class, showing the total number of samples where the species was seen (N) in both the baited and unbaited methods (n)

Class	Family	Common name	Scientific name	Total	Baited					Unbaited				
				N	n	Mean	SD	Min	Max	n	Mean	SD	Min	Max
Osteichthyes	Sparidae	Red roman	*Chrysoblephus laticeps*	84	46	4.87	3.12	1	14	38	2.16	0.97	1	5
Osteichthyes	Sparidae	Steentjie	*Spondyliosoma*	75	44	15.66	14.46	1	50	31	5.84	9.04	1	36
Osteichthyes	Sparidae	Fransmadam	*Boopsoidea inornata*	73	40	13.53	11.50	1	48	33	3.55	2.46	1	10
Osteichthyes	Cheilodactylidae	Twotone fingerfin	*Chirodactylus*	56	28	1.75	1.73	1	9	28	2.14	1.92	1	10
Osteichthyes	Sparidae	Blacktail seabream	*Diplodus sargus capensis*	43	31	4.26	3.18	1	12	12	1.25	0.45	1	2
Osteichthyes	Sparidae	Blue hottentot	*Pachymetopon aeneum*	41	30	2.47	2.13	1	10	11	1.45	0.52	1	2
Osteichthyes	Cheilodactylidae	Redfingers	*Cheilodactylus fasciatus*	39	19	1.16	0.37	1	2	20	1.05	0.22	1	2
Osteichthyes	Sparidae	Janbruin	*Gymnocrotaphus curvidens*	39	18	1.06	0.24	1	2	21	1.10	0.30	1	2
Osteichthyes	Cheilodactylidae	Barred fingerfin	*Cheilodactylus pixi*	36	14	1.29	0.61	1	3	22	1.36	0.66	1	3
Osteichthyes	Tetraodontidae	Evil-eye puffer	*Amblyrhynchotes honckenii*	30	29	2.07	1.49	1	6	1	1.00	-	1	1
Osteichthyes	Ariidae	White seacatfish	*Galeichthys feliceps*	21	19	2.53	3.17	1	12	2	1.00	0.00	1	1
Osteichthyes	Oplegnathidae	Cape knifejaw	*Oplegnathus conwayi*	20	11	1.00	0.00	1	1	9	1.11	0.33	1	2
Osteichthyes	Sparidae	Dageraad seabream	*Chrysoblephus cristiceps*	20	18	1.33	0.49	1	2	2	1.00	0.00	1	1
Osteichthyes	Sparidae	Red tjor tjor	*Pagellus bellottii natalensis*	19	18	6.89	12.19	1	50	1	1.00	-	1	1
Osteichthyes	Sparidae	Zebra seabream	*Diplodus hottentotus*	18	10	1.20	0.42	1	2	8	1.25	0.46	1	2
Osteichthyes	Sparidae	Cape stumpnose	*Rhabdosargus holubi*	15	15	2.33	1.84	1	7	-	-	-	-	-
Osteichthyes	Sparidae	Strepie	*Sarpa salpa*	15	11	20.18	18.98	1	57	4	18.25	3.77	13	22
Osteichthyes	Serranidae	Koester	*Acanthistius sebastoides*	12	12	1.00	0.00	1	1	-	-	-	-	-
Osteichthyes	Sparidae	Santer seabream	*Cheimerius nufar*	12	8	1.88	1.64	1	5	4	1.00	0.00	1	1
Osteichthyes	Ariidae	Black seacatfish	*Galeichthys ater*	11	10	1.40	0.70	1	3	1	2.00	-	2	2
Osteichthyes	Sparidae	White stumpnose	*Rhabdosargus globiceps*	8	8	1.13	0.35	1	2	-	-	-	-	-
Osteichthyes	Serranidae	African seabass	*Serranus knysnaensis*	6	6	1.33	0.52	1	2	-	-	-	-	-
Osteichthyes	Sparidae	Panga	*Pterogymnus laniarius*	6	5	1.80	0.84	1	3	1	2.00	-	2	2
Osteichthyes	Carangidae	Maasbanker	*Trachurus trachurus*	5	5	20.60	30.44	1	74	-	-	-	-	-

Table A1.2 continued

Class	Family	Common name	Scientific name	Total		Baited				Unbaited				
				N	n	Mean	SD	Min	Max	n	Mean	SD	Min	Max
Osteichthyes	Sparidae	Sand steenbras	*Lithognathus mormyrus*	5	5	3.00	4.4	1	11	-	-	-	-	-
Osteichthyes	Carangidae	Giant yellowtail	*Seriola lalandi*	4	2	1.5	0.7	1	2	2	6.5	7.7	1	12
Osteichthyes	Haemulidae	Olive grunter	*Pomadasys olivaceum*	4	4	16.75	25.	1	55	-	-	-	-	-
Osteichthyes	Hexanchidae	Spotted 7-gill cowshark	*Notorynchus cepedianus*	4	4	1	0	1	1	-	-	-	-	-
Osteichthyes	Clinidae	Klipfish	*Clinidae spp*	3	3	1.33	0.5	1	2	-	-	-	-	-
Osteichthyes	Parascorpididae	Jutjaw	*Parascorpis typus*	3	-	-	-	-	-	3	1	0	1	1
Osteichthyes	Chaetodontidae	Doublesash butterfly fish	*Chaetodon marleyi*	2	2	1	0	1	1	-	-	-	-	-
Osteichthyes	Sparidae	Red stumpnose	*Chrysoblephus gibbiceps*	2	2	1	0	1	1	-	-	-	-	-
Osteichthyes	Sparidae	Red steenbras	*Petrus rupestris*	2	2	1	0	1	1	-	-	-	-	-
Osteichthyes	Sparidae	White musslecracker	*Sparodon durbanesis*	2	1	2	-	2	2	1	1	-	1	1
Osteichthyes	Cheilodactylidae	Bank steenbras	*Chirodactylus grandis*	1	1	1	-	1	1	-	-	-	-	-
Osteichthyes	Clinidae	Super klipfish	*Clinus superciliosus*	1	1	1	-	1	1	-	-	-	-	-
Osteichthyes	Clupeidae	Round herring	*Etrumeus whiteheadi*	1	1	1	-	1	1	-	-	-	-	-
Osteichthyes	Sciaenidae	Geelbek	*Atractoscion aequidens*	1	1	2	-	2	2	-	-	-	-	-
Osteichthyes	Serranidae	Dusky grouper	*Epinephelus marginatus*	1	1	1	-	1	1	-	-	-	-	-
Osteichthyes	Sparidae	Carpenter seabream	*Argyrozona argyrozona*	1	1	2	-	2	2	-	-	-	-	-
Osteichthyes	Sparidae	Hottentot	*Pachymetopon blochii*	1	1	1	-	1	1	-	-	-	-	-
Osteichthyes	Sparidae	Bronze bream	*Pachymetopon grande*	1	1	1	-	1	1	-	-	-	-	-
Osteichthyes	Sparidae	Dane seabream	*Porcostoma dentata*	1	1	2	-	2	2	-	-	-	-	-
Condrichthye	Scyliorhinidae	Pajama catshark	*Poroderma africanum*	37	3	2.03	1.2	1	5	2	1	0	1	1
Condrichthye	Triakidae	Smooth-hound shark	*Mustelus mustelus*	36	3	1.52	0.9	1	5	5	1	0	1	1
Condrichthye	Scyliorhinidae	Puffadder shyshark	*Haploblepharus edwardsii*	32	3	1.27	0.5	1	3	2	1	0	1	1
Condrichthye	Dasyatidae	Short-tail stingray	*Dasyatis brevicaudata*	10	1	1.1	0.3	1	2	-	-	-	-	-
Condrichthye	Myliobatidae	Eagle ray	*Myliobatis aquila*	10	8	1.38	0.5	1	2	2	1	0	1	1
Condrichthye	Rhinobatidae	Lesser guitarfish	*Rhinobatos annulatus*	8	7	1.71	0.9	1	3	1	1	-	1	1

Table 1.2 continued

Class	Family	Common name	Scientific name	Total	Baited					Unbaited				
				N	n	Mean	SD	Min	Max	n	Mean	S	Min	Max
Condrichthye	Scyliorhinidae	Brown shyshark	*Haploblepharus fuscus*	5	5	1	0	1	1	-	-	-	-	-
Condrichthye	Scyliorhinidae	Leopard catshark	*Poroderma pantherinum*	3	3	1.33	0.	1	2	-	-	-	-	-
Condrichthye	Dasyatidae	Blue stingray	*Dasyatis chrysonota*	2	1	1	-	1	1	1	1	-	1	1
Condrichthye	Dasyatidae	Backwater butterfly	*Gymnura natalensis*	2	2	1	0	1	1	-	-	-	-	-
Condrichthye	Myliobatidae	Duckbill stingray	*Pteromylaeus bovinus*	2	2	1	0	1	1	-	-	-	-	-
Condrichthye	Triakidae	Spotted gully shark	*Triakis megalopterus*	2	2	1	0	1	1	-	-	-	-	-
Condrichthye	Carcharhinidae	Bronze whaler	*Carcharhinus brachyurus*	1	1	1	-	1	1	-	-	-	-	-
Condrichthye	Carcharhinidae	Milk shark	*Rhizoprionodon acutus*	1	1	1	-	1	1	-	-	-	-	-
Condrichthye	Dasyatidae	Common stingray	*Dasyatis pastinaca*	1	1	1	-	1	1	-	-	-	-	-
Condrichthye	Odontaspidida	Ragged-tooth shark	*Carcharias taurus*	1	1	1	-	1	1	-	-	-	-	-
Cephalopods	Octopodidae	Common octopus	*Octopus vulgaris*	5	4	1	0	1	1	1	1	-	1	1

A.2. RESIDUAL GAM PLOTS

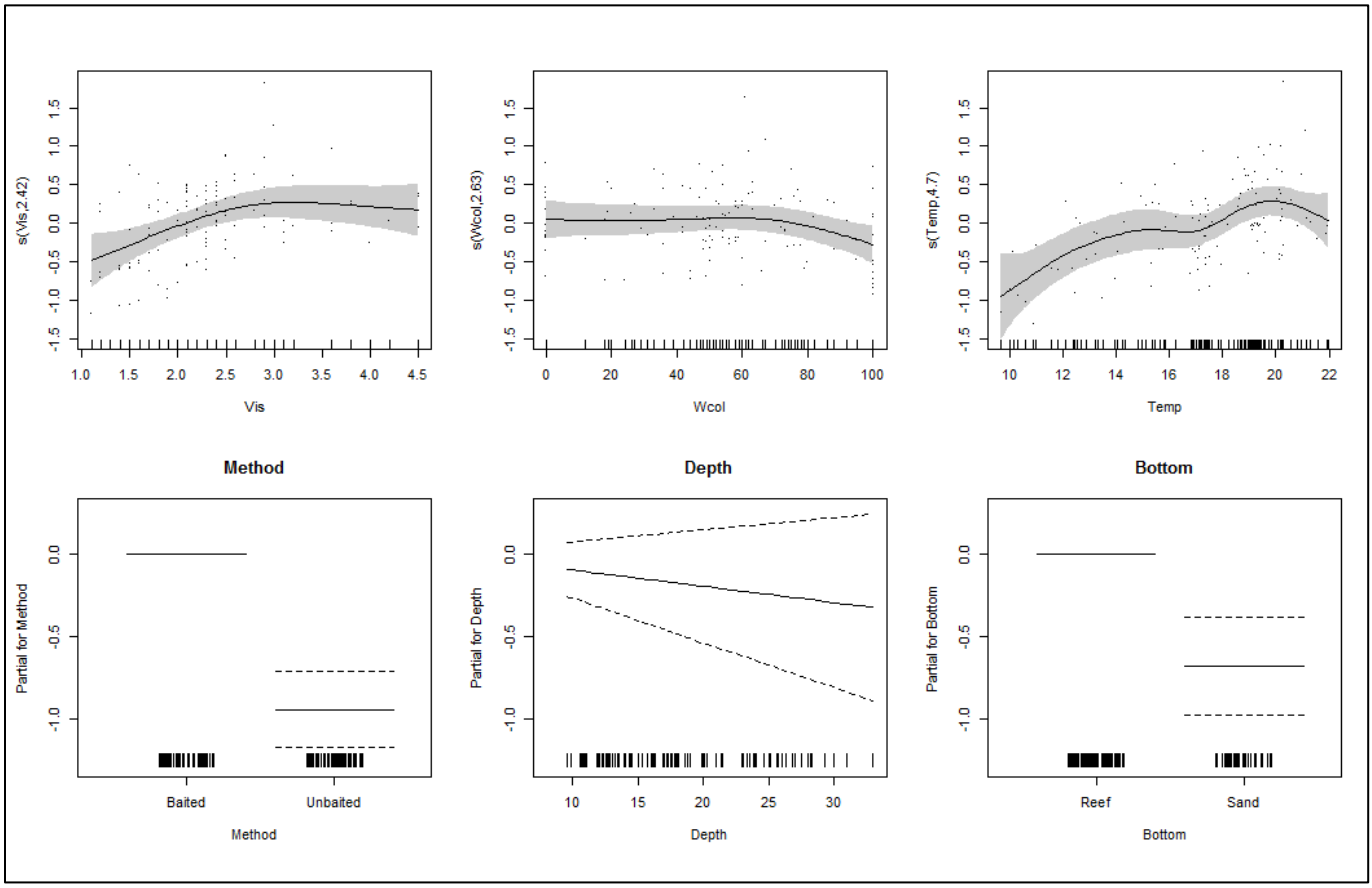

Figure A2.1: Residual plot of GAM model 3.3 testing the effect of depth on species richness, showing trends in residuals of smooth terms (visibility, water column and temperature) and parametric terms (method, depth and bottom type)

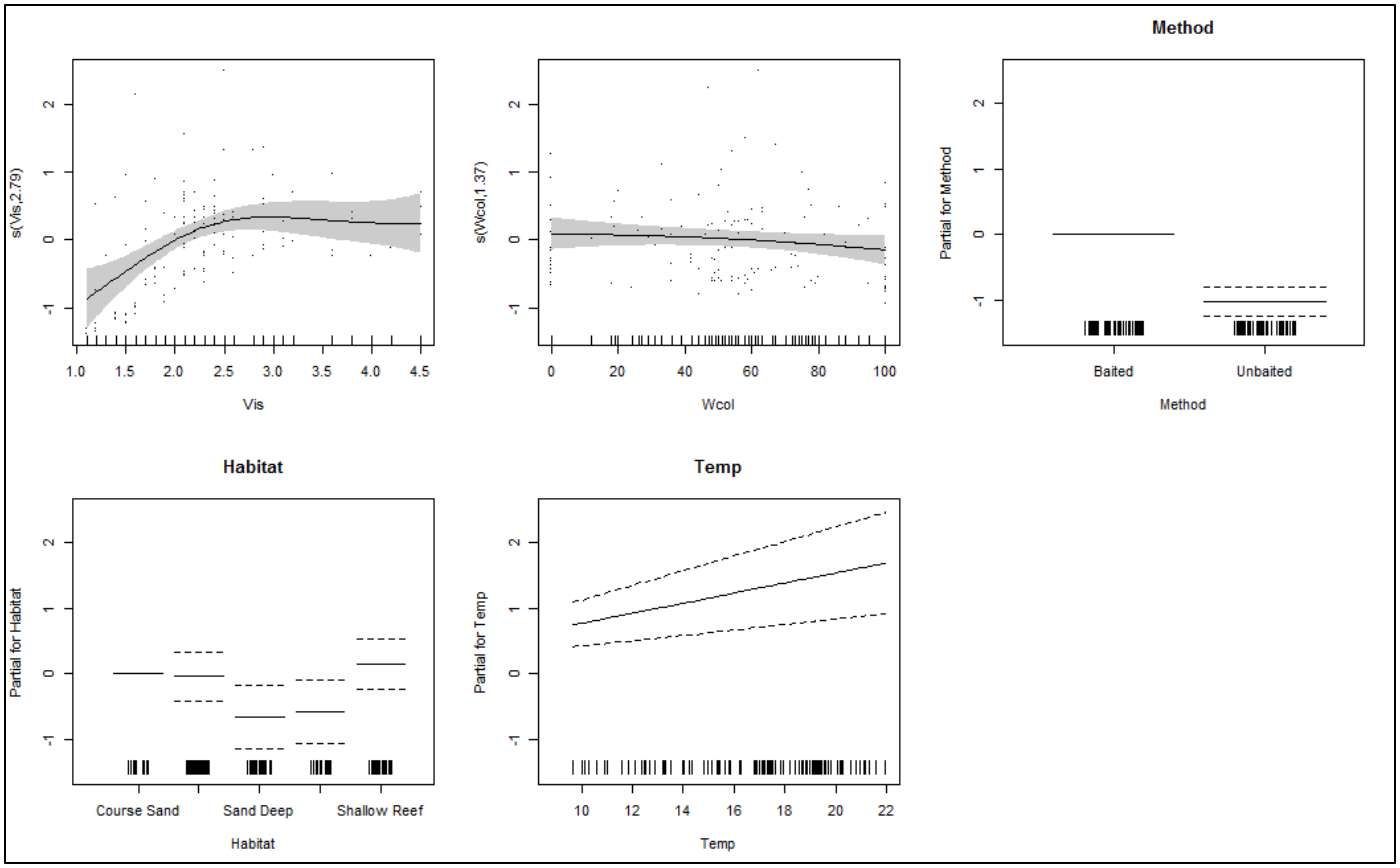

Figure A2.2: Residual plot of GAM model 3.4 testing the effect of habitat type on species richness, showing trends in residuals of smooth terms (visibility and water column) and parametric terms (method, habitat and bottom type)

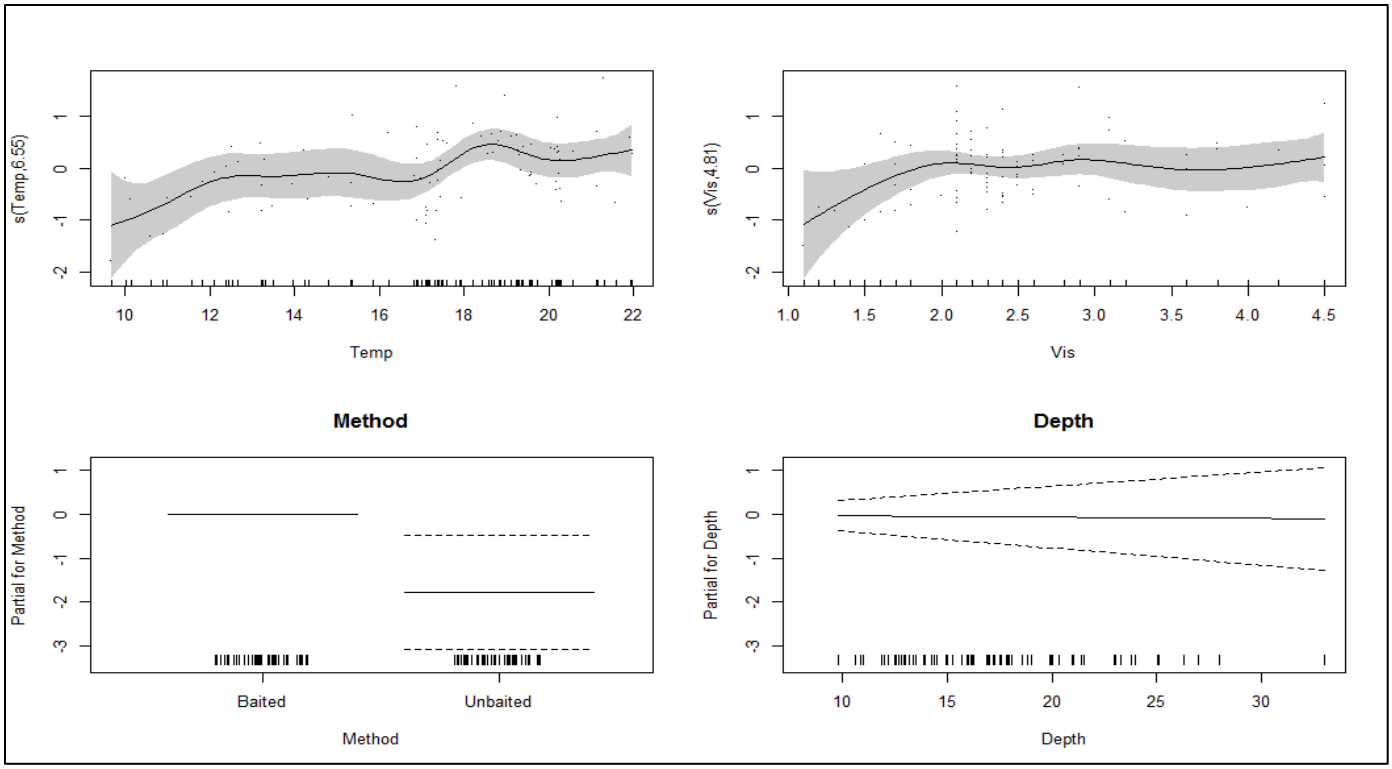

Figure A2.3: Residual plot of GAM model 3.5 testing the effect of depth on roman abundance, showing trends in residuals of smooth terms (temperature and visibility) and parametric terms (method and depth)

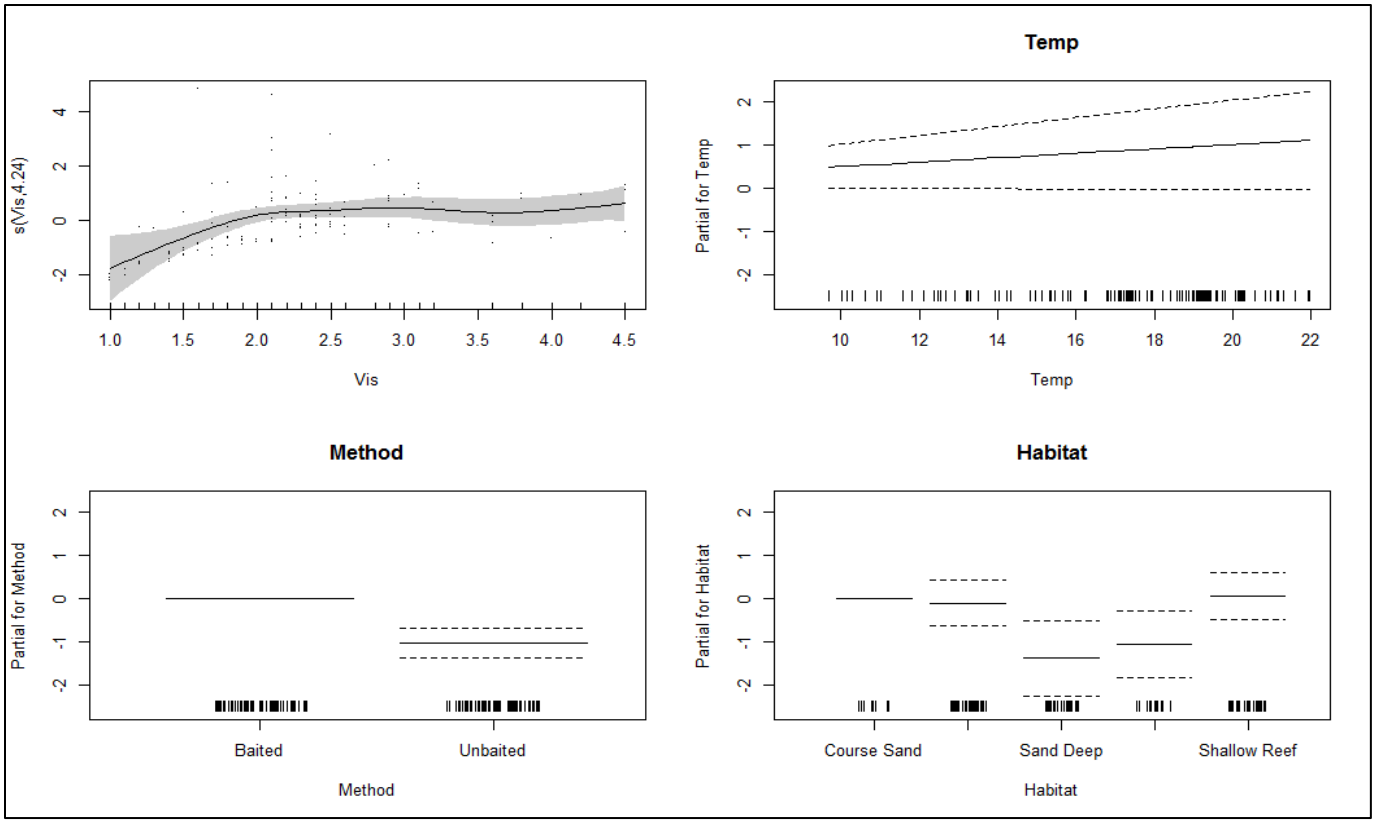

Figure A2.4: Residual plot of GAM model 3.6 testing the effect of habitat type on roman abundance, showing trends in residuals of smooth terms (visibility) and parametric terms (method and habitat)