BIODIVERSITY PATTERNS IN FALSE BAY: AN ASSESSMENT USING UNDERWATER CAMERAS

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DECLARATIONS

PLAGIARISM DECLARATION

I know the meaning of plagiarism and declare that all the work in this thesis, save for that which is properly acknowledged, is my own. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed by candidate

Signature: Date: 31 October 2020

RESEARCH DECLARATION

Research was conducted inside the Table Mountain National Park (TMNP) marine protected area (MPA) with permission from South African National Parks (SANParks). Permit Number: CRC-2014-012.

Portions of the fish baited remote underwater mono-video system (mono-BRUVs) data, those pertaining to chondrichthyans, used in this thesis are published in De Vos, L., Watson, R.G.A., Götz, A. & Attwood, C.G. 2015. Baited remote underwater video system (BRUVs) survey of chondrichthyan diversity in False Bay, South Africa. *African Journal of Marine Science*. 37(2): 209-218. doi: 10.2989/1814232X.2015.1036119.
Nothing in this publication is repeated here, neither the analyses nor the text. My thesis presents an entirely new interpretation of the data.

Angle versus Range data were provided by Andrew Murray from Underwater Surveys Ltd.

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I started this project because I was curious about the communities under the sea. What I did not expect was that I would learn much more about my community on land, and the power of their support. To everyone who played a role, many of whom I will inevitably omit to mention here, I am truly thankful.

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ABSTRACT

Understanding how marine biodiversity is distributed, and what drives these patterns, relies on good descriptions of marine ecosystems. This information should inform the protection of biodiversity and guide its management. Relationships between marine landscapes and biodiversity therefore need to be described at scales that are useful to regional management. Simultaneous sampling of marine biodiversity and the seafloor is challenging, so baseline ecosystem descriptions are often mismatched in their abiotic and biotic components. Cameras can sample the seafloor and its associated biodiversity concurrently, with good coverage and at low cost. These are important considerations for sustainable monitoring to inform conservation management in resource-limited regions. Terrestrial landscape characterisations cannot simply be translated to the ocean because interpreting remote ocean terrain assessments in a manner relevant to ecological analysis is complicated by depth, circulation, light attenuation, and other oceanographic variables. The integration of some of these concepts into rapid marine biodiversity assessments therefore needs ground-truthing where they are applied in new regions, to advance sustainability in long-term marine monitoring.

This thesis investigated the relationship between landscape composition and benthic marine biodiversity in False Bay, South Africa using novel methods that extended biodiversity sampling across more depths and habitats than any single, previous survey of the bay. This study’s approach piloted sampling and interpreting the marine landscape and biodiversity over matching spatial and temporal scales. The coverage, repeatability and ecosystem-level scale applied to this study make it a useful basis to develop monitoring protocols that are appropriate to conservation management at relevant regional scales. New insights for the region include a) a new description of the seafloor using classifications that explain the variation in epibenthic megafauna and ichthyofauna communities, b) a quantitative account of the epibenthic megafauna on the eastern reefs where species diversity was highest, and c) the synthesis of seafloor descriptions with the epibenthic megafauna and ichthyofauna to describe nine regions of False Bay, relative to two previous descriptions of "grounds".

Photographs and multibeam bathymetry characterised the seafloor on eight transects across the bay and were ground-truthed by grab samples repeated at representative sites. Two new classifications were applied to describe the seafloor. Horizontal seafloor heterogeneity was

highest in the east, and reef was distributed along the eastern and western margins. The Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) scheme captured accurate broad-scale descriptions of the physical landscape when applied to photographs. Grabs are still needed to provide fine-scale particle size data on soft sediments where most invertebrate diversity is likely infauna. However, CATAMI abstracts fine-scale sediment variation into simpler groupings more useful for rapid ecosystem assessment. Photographic sampling is repeatable, which is useful for long-term ecosystem monitoring.

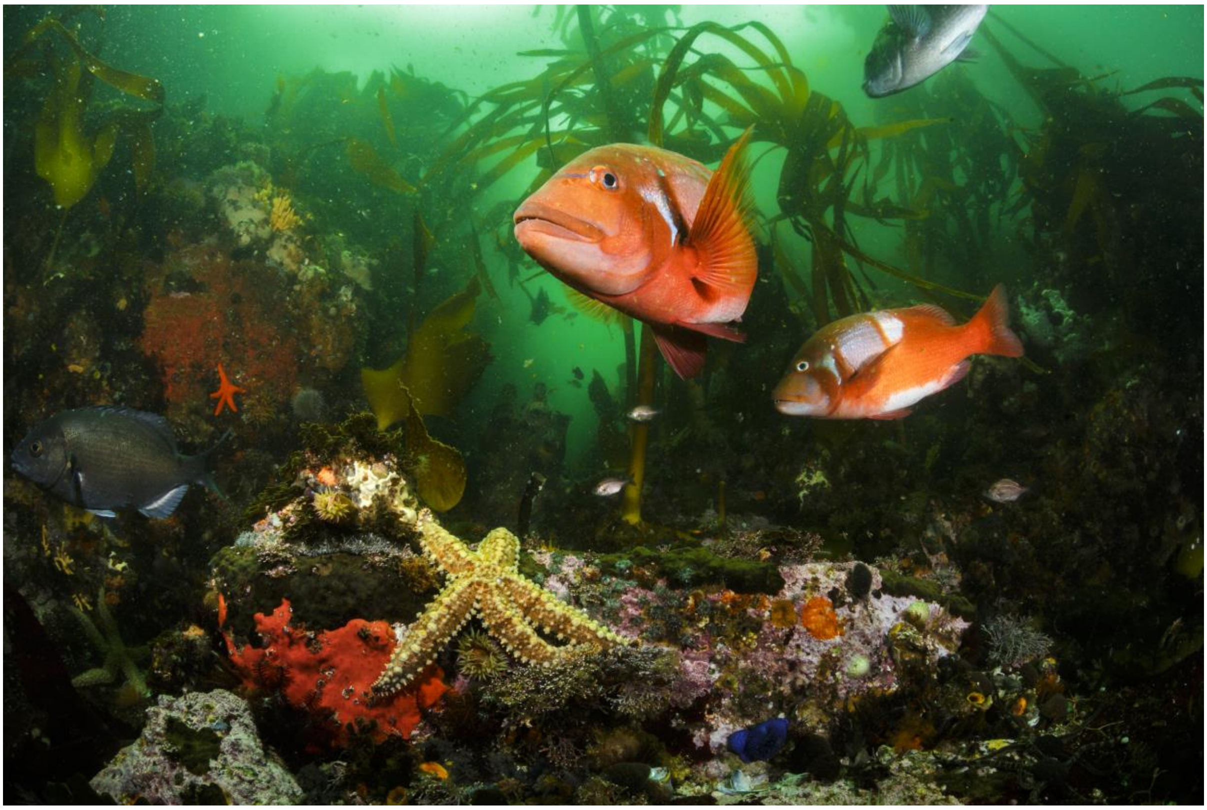
Photographs taken using a jump camera rig assessed the epibenthic megafauna across habitats and along depth gradients. Rényi diversity showed that species diversity increased in shallow waters up to 40 m, reaching a peak between 30 and 40 m, before decreasing with increasing depth. Species diversity was highest in the east, where seafloor heterogeneity was also highest. This result is interesting because eastern False Bay falls mostly outside the current marine protected area (MPA) network and has been relatively under-represented in previous surveys. The jump camera documents ecosystem-level biodiversity patterns and processes, and the random point count method in Coral Point Count (CPCe) is useful to assess community composition and cover on reefs.

The relative abundance and distribution of ichthyofauna were assessed using baited remote underwater video systems (BRUVs). Fifty-seven fish species from 30 families were recorded between 4 and 84 m. Rényi diversity showed that species richness was similar for reef and sand overall, but the Shannon-Wiener diversity index (H') was significantly higher on reef sites than on sand sites ($t = 1.972$, $p < 0.0001$). Species richness for the whole bay was similar in winter and summer, which indicates that the same species are likely present year-round; however, the Shannon-Wiener diversity index was significantly higher in winter ($t = 1.973$, $p < 0.013$) and evenness was greater in winter at the level of the site. These findings highlight the difficulty in protecting sufficient sand habitat to encompass the patchy distribution of sand-associated species and highlight seasonal differences in optimal visibility for future camera monitoring surveys by conservation management.

There are clear patterns in the marine biodiversity of False Bay, at various scales, that can be detected using novel methods for the region. The study’s approach to classifying both the landscape and its associated biodiversity creates a framework for future ecosystem threat assessment that can be applied elsewhere, especially along the South African coastline.

CHAPTER 1

GENERAL INTRODUCTION



Roman (*Chrysoblephus laticeps*) and Cape seabream (*Pachymetopon blochii*) hover over colourful reefs in the kelp forests of the Table Mountain National Park (TMNP) marine protected area (MPA) in False Bay. Photo: Joris van Alphen**.**

1.1. Understanding patterns in marine biodiversity

Marine biodiversity is arranged in patterns that can be analysed at a variety of spatial scales (Gray 1997; Roberts et al. 2002; Tittensor et al. 2010). Describing the distribution of biodiversity is a challenge that is central to the field of ecology (Lawton 1999; Gaston 2000). Our observations lead naturally to an investigation of the drivers that structure these patterns: which processes predict the heterogeneity that we observe (Tilman 1999)? Are there general trends that we can extrapolate to explain the distribution of biodiversity? At which scales, and at what resolution (Lawton 1999)? The composition and functioning of biodiversity, with the ecosystem processes it supports, have a direct bearing on human-beings by delivering ecosystem services central to our wellbeing (Sandifer et al. 2015). Understanding how biodiversity is distributed, and which landscape factors drive this distribution, underpins how we integrate ecological and social information to plan for ecosystem service provision (Gaston 2000; Cumming et al. 2013).

The description of biodiversity patterns and our understanding of its predictors have developed from a conservation imperative. Our growing human population has accelerated biodiversity loss through species overexploitation (Jackson et al. 2001; Dulvy et al. 2014), habitat loss (Lotze et al. 2006), pollution (Gall & Thompson 2015), alien invasive species (Bax et al. 2003) and climate change (WWF 2016). Of these threats, species overexploitation accounts for the highest number of declining marine populations (WWF 2016) and threatens adequate ecosystem functioning (Jackson et al. 2001; Worm et al. 2006). Descriptions of distribution can inform which regions should be protected and help guide management action.

1.2. Understanding patterns and processes to inform protection

The range of threats to the ocean requires a spectrum of solutions. The diverse approaches divide loosely into species-focused and spaces-focused solutions, with the gradual shift over 20 years from species towards spaces (Roff & Zacharias 2011). Part of the implementation of an ecosystem-based approach to fisheries (EAF) is the delineation of marine protected areas (MPAs) and zoning of marine spaces to manage biodiversity while addressing the needs of multiple stakeholders (Lauck et al. 1998). There are increasing calls for more strategic planning during MPA design and implementation (Chuenpagdee et al. 2013) so that MPAs are created with explicit goals (Foley et al. 2010). Their performance must also be evaluated once implemented (Hockey & Branch 1997). The MPA network can then be adapted and refined to ensure that goals are being met (Pomeroy et al. 2005). There are also calls for strategic MPA implementation that is inclusive, transparent, and scientifically informed (Tallis & Lubchenco 2014). To achieve this, ocean ecosystems - their landscapes and the biodiversity they harbour - need to be sufficiently understood (Stevens & Connolly 2004; Kendall et al. 2005).

Our capacity to describe marine biodiversity at sea requires consideration if we are to improve our understanding of what drives marine biodiversity patterns and processes (McArthur et al. 2010). Issues of cost, logistics, time, access, and technological development make sampling biological communities at local, regional, and global scales unrealistic (Zajac 2008; McArthur et al. 2010). In the absence of complete biological datasets, abiotic data can inform suitable proxies to infer and extrapolate biodiversity information (Stevens & Connolly 2004; Post 2008; Buhl-Mortensen et al. 2012). Baseline descriptions of marine biodiversity at a variety of scales are necessary, as are concomitant descriptions of the physical characteristics of the ocean system that support and drive these patterns and processes (Sale 1998, Lecours et al. 2015). There is still insufficient resolution of the abiotic and biotic elements of ocean landscapes, and drivers at a variety of scales need to be described and tested (McArthur et al. 2010, Lecours et al. 2015). Ground-truthed abiotic assessments form the basis of valuable information that can guide descriptions and conservation planning in under-sampled, or under-resourced, regions (Tittensor et al. 2010; SANBI & UNEP-WCMC 2016).

1.3. Assessing patterns of marine biodiversity across spatial and temporal scales

The consideration of scale is essential in ecology: the patterns we observe may change according to the resolution and extent of our analysis in both space and time (Turner et al. 1989; Levin 1992; Cumming & Collier 2005, Lecours et al. 2015). Biodiversity itself is structured, defined and functions at many scales; from genetic, to functional, phyletic, species and community (Gray 1997). Much work has been done to understand the distribution of marine biodiversity, and the drivers of biodiversity patterns, at a global scale (Gray 1997; Tittensor et al. 2010). Species diversity increases on hard substrates from the Arctic to the tropics (Kendall & Aschan 1993), and it is relatively higher in the Antarctic than the Arctic (Dayton et al. 1994). Diversity is higher in benthic systems and inshore coastal environments than pelagic and open ocean ecosystems (Gray 1997). Coral reefs support species diversity that peaks around the Indonesian archipelago and decreases as one moves away from this biodiversity hotspot (Gray 1997; Roberts et al. 2002). However, drivers of diversity will differ in their importance from global to regional to local scales (Turner et al. 1989; Levin 1992). Indeed, the factors identified at a global or regional scale might not be as useful or powerful to describe patterns in diversity at a local scale (Turner et al. 1989; Sale 1998).

Considering the scales at which to assess biodiversity patterns is critical because management and monitoring also differ in their resolution and extent. Identifying global hotspots for marine biodiversity may help to direct funding, improve planning, and focus efforts for the stakeholders involved at that scale. However, the on-the-ground implementation of many conservation strategies falls to regional, or more often, local governance. We know that biodiversity in coastal regions is high and that the proximity to human populations drives the high levels of threat to that diversity (Gray 1997). The nature of both biodiversity and its threats will, however, differ in coastal regions around the globe. It is here that regional and local assessments become key: regional analysis can guide policies and strategy country-by-country, informing spatial planning and conservation priorities (Margules & Pressey 2000; Driver et al. 2012). After prioritisation and implementation, the enforcement and monitoring of many conservation management tools, especially that of marine protected areas (MPAs), happens at a local scale. There is a case to assess patterns of biodiversity at local scales that may guide local conservation management.

There is, moreover, a temporal aspect to scale: the elements of an ocean landscape will change in their structure and function through time (Turner et al. 1989). The implementation of ecosystem-based management strategies such as MPAs requires ongoing assessments of whether these tools are meeting their biodiversity protection goals (Katsanevakis et al. 2011). Marine biodiversity monitoring is an integral part of ongoing adaptive management, and there is a need to monitor changes over time.

1.4. The logistics of biodiversity mapping and monitoring in under-resourced regions

The regions where marine biodiversity is rich are often the same regions where human impacts on the ocean are high (Tittensor et al. 2010). There is also some agreement that these regions of critical concern coincide with those that are most under-resourced (Pauly 2006; Moran & Kanemoto 2017). More than half the global fish exports by value originate in developing nations (FAO 2016). Where the end of the supply chain is in countries such as the United States of America (USA) and those of the European Union, the cost of product demand is often outsourced (Moran & Kanemoto 2017) to global biodiversity hotspots; those centres of rich biodiversity where overfishing, land-based agricultural run-off and changing sea surface temperatures are counted among some of the primary threats (Roberts et al. 2002). At the same time, developing nations are regions of heightened dependence on jobs and food security from marine fisheries (FAO 2018). Indeed, while their relative fish consumption is considered low, the proportion of fish protein in their diet is higher for people in developing nations than elsewhere (FAO 2018).

Monitoring and mapping, which are critical to adequately managing threatened biodiversity, involve labour, skills, equipment, logistics and time that incur a significant cost (Langlois et al. 2010). The cost and labour implications for sustainable, long-term assessments are daunting (Stobart et al. 2007). In many instances, baseline descriptions of biological communities are missing. This consideration does not remove the need for adequate monitoring, nor detract from the relevance of scientific accuracy. It highlights the necessary consideration of tools that address biodiversity conservation goals within the constraints of logistics and costs. Taking logistics and costs into account is particularly relevant where biodiversity threat is high and humans are especially ocean-dependent, but where resource availability is low, as is so often the case in developing nations.

1.5. Remote underwater photography and video for long-term monitoring

Biodiversity monitoring should track community structure, species abundance and organism size over time (Cappo et al. 2003) and signal where strategies need revision (Lubchenco & Grorud-Colvert 2015). The kind of information of interest would, aside from the baseline presence and changing abundance of species over time, include the presence and relative abundance of rare or threatened species, some measure of habitat condition, records of breeding populations and an indication of shifts from adjacent areas (Cappo et al. 2003). "Rapid Assessment Techniques" for baseline assessments and long-term monitoring have evolved out of the need to balance costs and logistics with adequate data quality and long-term data series (e.g. Samoilys & Carlos 2000; Samways & Hatton 2001).

The development of affordable camera technology has made remote camera surveys a prominent part of rapid assessments, particularly where non-destructive sampling is required across a range of depth gradients and habitat-types (Bernard et al. 2014). Baited remote underwater video surveys (BRUVs) and jump cameras are independent of SCUBA divers and afford sampling at greater depths and in lower water visibility conditions (Bernard et al. 2014; Heyns-Veale et al. 2016). Remotely-operated vehicles (ROVs), towed cameras and autonomous underwater vehicles (AUVs) achieve the same and may extend the spatial scale of surveys (Solan et al. 2003; Williams et al. 2015; Heyns-Veale et al. 2016), but not overcome cost considerations and the need for skilled operators.

A permanent video or photographic record of surveys is an improvement that achieves several goals. It lowers observer bias (Langlois et al. 2010; Bernard & Götz 2012) and reduces the need for specialists in the field and during analysis (Cappo et al. 2003). It is a standardised data collection method (Bernard et al. 2014), providing a visual archive that can be revisited, assessed by other observers, and reviewed by experts (Willis et al. 2000). It also makes data transparent to the various stakeholders involved in ocean conservation and management, providing a record that can be shared, re-analysed to address different questions or used to interrogate at different resolutions (Cappo et al. 2003; Bernard et al. 2014).

1.6. South African marine biodiversity

The total regional marine diversity in South Africa to date has been recorded as 12, 194 species, a number that is expected to rise as sampling effort and taxonomic attention increase (Griffiths et al. 2010). The species diversity and range of ecosystems represented in three oceans managed by South Africa support various human activities, from mining, tourism, and fishing, to recreation and infrastructure development (Sink et al. 2011; Driver et al. 2012). Upwelling encourages high biological productivity in the cool, temperate Atlantic Ocean in the west where the Benguela current dominates, which in turn supports important fisheries (Griffiths et al. 2010). In the Indian Ocean in the east, species diversity is high, but biological productivity is lower where the Agulhas current dominates. The relative importance of commercial fisheries is therefore much lower in the east, but dense human populations still exert a strong influence on marine resources here (Griffiths et al. 2010). Coastal development is a critical threat to coastal ecosystems, and fishing is the most significant pressure in most inshore and offshore ecosystems (Sink et al. 2011).

There have been a number of biogeographic descriptions at various spatial scales and across taxonomic groups that integrate the distribution of marine biodiversity and drivers of its patterns along the South African coastline (Brown & Jarman 1978; Emanuel et al. 1992; Stegenga & Bolton 1992; Bustamante & Branch 1996; Turpie et al. 2000; Sink 2001; Bolton et al. 2004). More recently, biological, and physical patterns and processes have been integrated across the full extent of the South African exclusive economic zone (EEZ) into the description of nine bioregions, with five inshore regions (Sink et al. 2004). The combination of a significant number of surveys, over a long history of study on the coastline, has informed the delineation of a MPA network that protects biodiversity across several bioregions (Turpie et al. 2000; Tunley 2009) and the generation of an expanded protected area network (Sink 2016). The adaptive management of MPAs, as well as the continued management of marine resources along the entire South African coastline, requires ongoing description and monitoring of its biodiversity (Anderson 2000; Griffiths 2000; Willis et al. 2003).

The management of South Africa's marine biodiversity relies on the continued capacity to describe, monitor and evaluate the impact of its growing human population; all of whom are reliant on the ocean for ecosystem services (Sink et al. 2011; Driver et al. 2012; WWF 2012). Significant gaps still exist in our understanding of ecosystem functioning across some systems in South Africa (Anderson 2000). There is a need to address ecosystem-level surveys and monitoring on subtidal reefs (Anderson 2000) and soft subtidal sediments (Leslie 2000). Many of the existing gaps are the result of the constraints of funding, labour, and capacity to implement long-term monitoring programmes (Anderson 2000; WWF 2012). The addition of methods to survey biological communities and the physical seafloor in a manner that is repeatable and sustainable would serve to address some of these gaps and strengthen long-term biodiversity monitoring in South Africa.

1.7. False Bay as a case study

Lying south of the city of Cape Town, False Bay is South Africa's largest bay (Spargo 1991) (**Figure 1**). The bay is surrounded by the Cape Peninsula Mountain Chain in the west, and the Hottentots-Hollands mountains in the east. Estimations of the bay's area vary between 1082 and 1091 km^2 and place its volume at approximately 44.6 km^3 (Spargo 1991). The mouth of the bay opens to the Atlantic Ocean between Cape Point and Cape Hangklip at a depth of just over 80 m, where the distance between the two peninsula points is 30 km (Spargo 1991) (**Figure 1**). There are several smaller bays within False Bay; for example, Simon's Bay on the north-western coastline, and Gordon's Bay in the north-east (Mallory 1970).

The northern reaches of the False Bay coastline are characterised by a sandy beach, unbroken except for sandstone cliffs at Strandfontein and Swartklip (Mallory 1970) (**Figure 1**). This area of shoreline extends northwards into vegetated dunes that neighbour the Cape Flats: a populated region of flat, deep sand that divides False Bay from Table Bay to the north (Spargo 1991). The Cape Flats Aquifer is a large, underground store of freshwater that is recharged by rainfall and which flows into False Bay, discharging an estimated 10^6 $m^3.y^{-1}$ (Spargo 1991). By contrast, the eastern and western margins are more mountainous, rising to the highest point of 678 m at Swartkop on the western shore and 1269 m at Kogelberg in the east (Mallory 1970; Spargo 1991). The coastline from the Strand to Cape Hangklip in the east is typified by cliffs and a narrow sandy beach, while that from Muizenberg to Cape Point in the west comprises a mix of lower Table Mountain Group sandstone and Cape Granite Suite boulders (Spargo 1991). A total of eleven streams and rivers feed into False Bay (**Figure 1**), including the Buffels, Silvermine, Eerste, Lourens, Steenbras and Rooi Els (Morant 1991). Of these eleven rivers, four have estuaries: the Zand, Eerste, Lourens and Rooi Els, while the rest drain into the bay with few estuarine characteristics (Morant 1991).

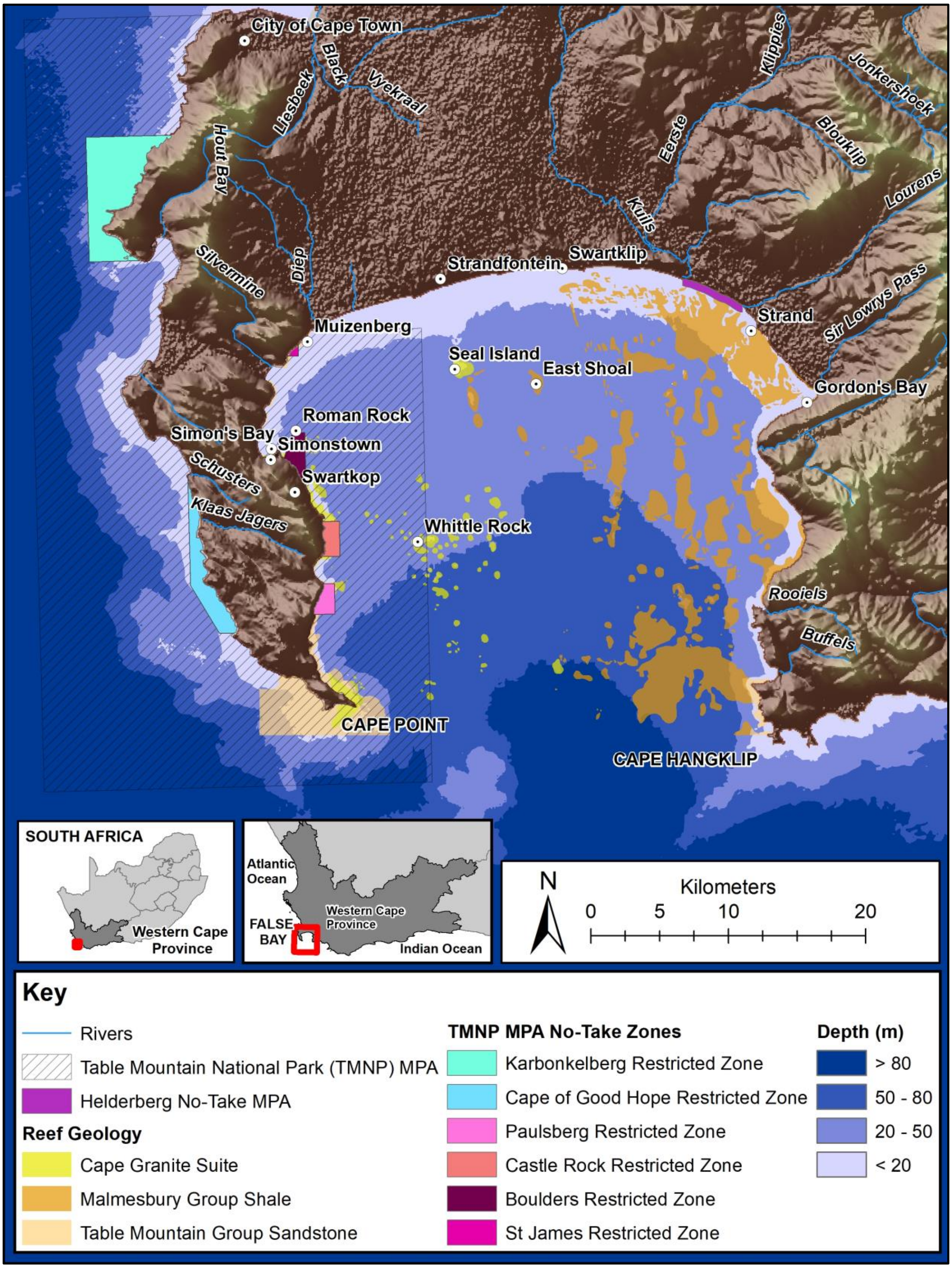


Figure 1. The location of False Bay in the context of South Africa (inset map) and the Western Cape Province (inset map). Key sites are shown to give geographical context in relation to the terrestrial topography (EKZNW 2015), river network (SANBI 2011), subtidal reef geology (Van Zyl 2011) and ocean depth (m) (Van Zyl 2011) of the region. All the no-take zones (restricted zones) are shown for the Table Mountain National Park (TMNP) marine protected area (MPA) (DEA 2019a). The TMNP no-take MPAs in False Bay are the Paulsberg, Castle Rock and St James Restricted Zones. The Helderberg MPA, managed by the City of Cape Town, is shown separately (DEA 2019a).

1.7.1. Geology and seafloor morphology

The “Challenger” expedition of 1873 – 1876 marked the first foray into geological research in False Bay, with a single sediment sample taken at Simonstown (Murray & Renard 1891). Since then, numerous bathymetric and geological surveys have ascertained that the floor of False Bay slopes gradually from its northern shore to a maximum depth at just over 90 m at its mouth (Mallory 1970; Spargo 1991). Any high, rocky relief dwindles moving away from the mountainous coastlines in the east and west and moving into deeper waters to the south (Simpson et al. 1970). The majority of the bay comprises sand varying in grain size from very fine (0.06 – 013 mm) to very coarse (1.0 – 2.0 mm), with the finest sediment evident near the deepest reaches of False Bay at its mouth (Bowie et al. 1970). The relief deviates from its sandy uniformity to give way to rock pinnacles and the Cape Granite Suite outcrops of Whittle Rock, Roman Rock and the bay’s only true island, Seal Island (Simpson et al. 1970; Du Plessis & Glass 1991). Malmesbury Group shale predominates in the east of the bay, where York and East shoal rise as outcrops that have been more resistant to erosion than the surrounding landscape (Du Plessis & Glass 1991).

1.7.2. Weather, wind, and ocean currents

The Mediterranean climate of the south-western Cape region prevails in False Bay: winter rainfall and summer “Cape Doctor” winds, with fine-scale variation in different regions of the bay itself mediated by features like the eastern mountains (Spargo 1991). On a synoptic scale, False Bay is influenced by the South Atlantic high-pressure cell, which governs the predominantly south-easterly wind regime that is typical of the greater Cape region (Gründlingh & Largier 1991; Jury 1991). Rain and cold temperatures are brought with north-westerly winds in winter, and orographic lift over the mountains causes local variation in rainfall (Spargo 1991). Summer anticyclonic conditions and cyclonic winter conditions influence the physical oceanography of the bay: summer south-easterly winds are characteristic and most important, while north-westerly winds typify winter (Atkins 1970a).

The prevailing wind conditions during the year vary around the bay, with south-easterly winds dominant almost year-round in the south-west near Cape Point, where highest wind speeds are also recorded (Atkins 1970a; Gründlingh & Largier 1991). The fine-scale variability around the extent of False Bay is evident in what Atkins (1970a) has summarised as the prevailing southerly wind at the northern coastline, south-easterly wind in the south-western reaches of the bay, and south-westerly or south-easterly wind direction in the far north-east of the bay. Sea surface temperatures vary around 15°C in winter and 19°C in summer (Atkins 1970b). In summer, temperature stratification lowers water temperatures at the bottom to 1-3°C less than in winter (Atkins 1970b). These temperatures are also affected by cold water that extends north-west across the bay from its origin at Cape Hangklip because of wind-induced upwelling (Cram 1970).

1.7.3. Subtidal biodiversity

Its location at the confluence of the Benguela and Agulhas oceanographic regimes means that False Bay hosts biodiversity representative of both the cold west coast and the warmer south coast (Day 1970). There are over 200 fish species recorded in the bay (Day et al. 1970), including 37 chondrichthyans (Best et al. 2013), one agnathan, 172 teleosts and 1629 benthic invertebrates (Day et al. 1970). Commercial fishing in the region dates to the 17th century, and the bay has seen all major fishing techniques used (Bekker 1991; Penney 1991). Currently, the commercial and recreational line fisheries, commercial beach-seining by a limited number of permitted operators and recreational spearfishing are the primary forms of fishing (Penney 1991; Lamberth 1994; Lechanteur 2000; Best et al. 2013).

1.7.4. Conservation and management

The Table Mountain National Park (TMNP) marine protected area (MPA) was declared in 2004 under the Marine Living Resources Act of South Africa (RSA 1998; Tunley 2009). The MPA encompasses an area of 956 km^2 and 5.9% of its subtidal area is in six no-take zones where fishing is prohibited (Tunley 2009; Chadwick et al. 2014). The MPA wraps around the Cape Peninsula, such that four of the six no-take zones are in the western half of False Bay (which is the eastern side of the Cape Peninsula) (**Figure 1**). Two of the no-take zones in False Bay; namely, St James and Castle Rocks, were in place before the declaration of TMNP in its current format (Lechanteur 2004). Castle Rocks Marine Reserve and a portion of the Kalk Bay Marine Reserve (KBMR) (as they were previously named) were no-take zones; the remainder of the KBMR was a marine reserve where shore-angling was permitted (Clark 2001). The Castle Rocks no-take zone, therefore, represents the oldest sanctuary area in the current TMNP MPA in False Bay (Tunley 2009).

The objectives outlined for this MPA are to protect populations of commercially important fish and invertebrate species, including linefish, abalone and west coast rock lobster (DEAT 2004; Lechanteur 2004; TMNP 2015). The TMNP MPA is a suitable candidate for the expansion of its no-take zones, according to an assessment of the state of the management of South Africa's MPAs, under the proviso that additional scientific advice informs such an expansion (Chadwick et al. 2014). The primary issues highlighted for the TMNP MPA were compliance, law enforcement, poaching and a general lack of awareness of the boundaries of the MPA and its regulations (WWF 2012). South African National Parks (SANParks) manages the TMNP MPA (Chadwick et al. 2014).

In the north-east of False Bay, the Helderberg MPA (HMPA) incorporates 4 km of sandy beach habitat and protects the subtidal environment to a maximum of 500 m out to sea (Tunley 2009) (**Figure 1**). The HMPA is located between the Eerste river and the Lourens river (Sparks & Mullins 2017). Promulgated in 2000, the MPA protects 14 km of coastline and 24.6 km^2 of subtidal habitat (Tunley 2009). The City of Cape Town manages the Helderberg MPA (Tunley 2009). The primary threats identified in this MPA are pollution and coastal development that impact the active littoral zone and the beach dunes (Tunley 2009). There is evidence of accumulated heavy metals in the sediment and mussels *Mytilus galloprovincialis* in the HMPA (Sparks & Mullins 2017). The MPA is classified as a "no-take" zone where fishing is prohibited (Tunley 2009).

1.8. False Bay: the need for synthesis, update, and the application of new methods

False Bay presents a useful case study to develop monitoring and mapping methods to apply to temperate, coastal ecosystems where logistics and funding are constrained. The bay has a long history of human-use (Spargo 1991; Harris 2017) with a growing, urban human population that relies on its ecosystem services in the form of jobs, food, and recreation (Spargo 1991). It is also a microcosm that reflects the challenges along the length of the South African coast and presents important considerations for the future of highly utilised coastal areas. A synthesis and update of subtidal biodiversity and habitat information in False Bay are therefore considered important to inform the implementation of research and monitoring in the region.

Most of the baseline descriptions of the subtidal invertebrate biodiversity of False Bay were published over 40 years ago (Morgans & Day 1959; Morgans 1962; Field 1970; Field 1971; Day et al. 1970). Trends in some of its fish populations and catches have been assessed on more recent timescales (Bennett 1991; Penney 1991; Lamberth 1994; Clark et al. 1994; Lamberth et al. 1994; Lamberth et al. 1995a; Lamberth et al. 1995b; Lamberth et al. 1995c; Clark et al. 1996a; Lechanteur 2000; Lamberth 2006; Best et al. 2013; Sanguinetti 2013; Hewitt et al. 2018), but no single synthesis updates the bay's subtidal ichthyofauna across various habitats and depths. There has been no previous attempt to understand the distribution patterns of the ichthyofauna of False Bay in relation to environmental drivers at the scale of the entire bay. The development of underwater camera survey methods for use on the South African coastline (Bernard & Götz 2012; Bernard 2012; De Vos et al. 2014) represents a new opportunity to assess the biodiversity of False Bay, across a greater range of depths and habitats, on a scale that has to date not been achieved.

1.9. AIMS OF THESIS

This thesis aims to update and improve the current state of knowledge of the epibenthic megafauna and ichthyofauna across False Bay. In doing so, the overarching aim is to contribute to the information needed to manage a highly utilized bay that has significant historical, cultural, commercial, and recreational importance. A key theme underpinning this study's approach was that the sustainable monitoring of South Africa's marine resources has often been hindered by logistical and financial constraints. Therefore, the introduction of novel methodologies that overcome some of the current sampling limitations was important, and all sampling was conducted by the author across methodologies and novel engineering to assess repeatability and long-term feasibility.

1.10. SPECIFIC OBJECTIVES

i. Describe the physical seafloor, and derive a description of subtidal habitats, at the same spatial and temporal scale as the biological communities.
ii. Test novel classification systems to integrate abiotic and biotic factors to gain an ecological view of the seafloor.
iii. Survey the relative abundance and distribution of epibenthic megafauna along a depth gradient, and assess potential drivers of this distribution, at the scale of False Bay.
iv. Survey the relative abundance and distribution of the ichthyofauna across depths and seafloor geology and assess potential drivers of this distribution at the scale of False Bay.
v. Assess whether remote surveys will be useful to future monitoring efforts in False Bay.
vi. Derive a new description of ecosystem regions across False Bay, with key characteristics that highlight zones that may require different management objectives, sampling approaches and survey methods.

1.11. OUTLINE OF THESIS STRUCTURE

This thesis presents data collected from three assessments of False Bay in three data chapters and a final synthesis chapter that highlights the primary conclusions.

An understanding of the landscape of False Bay is underpinned by the adequate description of its seafloor, combining insights from techniques that are typically used separately for either geological surveys or biological assessments. Chapter 2 synthesises the available habitat information from previous surveys and provides an updated assessment of the physical seafloor of False Bay using multibeam bathymetry, photographs, and sediment samples. Two new classification schemes are applied to describe the physical landscape of the bay to provide a landscape characterisation relevant to biological descriptions in False Bay. Physical seafloor measures (depth, rugosity, and slope) are presented from bathymetry data in conjunction with descriptions of the seafloor at two scales (the entire bay, and eight localised transects) that provide the basis for linking biological communities to environmental (landscape) factors in the subsequent chapters.

The epibenthic megafauna community of False Bay is described in Chapter 3 using a jump camera technique that is novel for the region. A new classification scheme is applied to characterise biological communities for the first time at the full extent of the bay. The relationship between key environmental factors in the physical landscape and the distribution of epibenthic megafauna communities are presented. The findings from this study are discussed in relation to findings from previous subtidal invertebrate surveys by Morgans (1962) and Field (1970, 1971).

The first description of the relative abundance and diversity of the ichthyofauna of False Bay across various depths and habitats at the scale of the entire bay using baited remote underwater mono-video systems (mono-BRUVs) and baited remote underwater stereo-video systems (stereo-BRUVs) is presented in Chapter 4. This chapter explores the relationship between ichthyofauna community composition and key environmental factors in the physical landscape and assesses the relative importance of these factors.

The results from the data chapters are synthesised in Chapter 5. The epibenthic megafauna and ichthyofauna species that typified different regions of False Bay are used to describe nine “regions” of the bay that incorporate the new descriptions of depth, habitat type and species groups. These regions are synthesised and contrasted with the “grounds” first presented by Morgans (1962) and stations described by Field (1971). The main conclusions from this thesis are discussed, with particular attention to those findings relevant to the future application of the new methodologies used in this study.

CHAPTER 2

A NEW SYNTHESIS OF THE PHYSICAL SEAFLOOR OF FALSE BAY FROM PHOTOGRAPHS, MULTIBEAM BATHYMETRY AND SEDIMENT SAMPLES

False plum anemones (*Pseudactinia flagellifera*) and coralline algae compete for a place among the life that carpets the Cape Granite Suite boulders in western False Bay Photo: Joris van Alphen.

2.1. ABSTRACT

Maps that characterise the physical seafloor are important to integrate biodiversity information with an understanding of the ocean landscape. These maps facilitate the identification of key drivers of patterns in biodiversity distribution. The geology of False Bay has been mapped at various resolutions, but there has been no integration from an ecological perspective of the seafloor across all habitats and depths. Remote cameras offer a cost-effective means of mapping the seafloor, matching biodiversity samples with a seafloor description to refine our understanding of biodiversity distribution. Multibeam sonar improves the extent and resolution of seafloor surveys over other geological sampling methods. The application of new methods in ocean landscapes requires ground-truthing relative to known geological information before their interpretation is sound. A jump camera was used to take 400 photographs of the seafloor along eight transects in False Bay. The photographs were described using the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification scheme (Althaus et al. 2013). A multibeam sonar survey recorded spatially referenced depth soundings along the same eight transects and measures of slope, aspect and seafloor roughness were calculated from bathymetry data. Thirty-two sediment samples were collected using a Van Veen grab to ground-truth the new CATAMI and Angle Range Analysis (ARA) seafloor classifications of unconsolidated sediments. Six CATAMI and 11 ARA seafloor types were detected across False Bay. Roughness and slope were correlated, and orthogonal to depth. The CATAMI classification collated particle size information into straightforward groupings and reflected finer-scale seafloor heterogeneity than the broad-scale geological delineation of reef and sand. The ARA classification distinguished reef from sand but reflected high seafloor variation that is too uncertain to inform ecological surveys without further ground-truthing. Both classifications showed horizontal seafloor heterogeneity to be highest in the east. The jump camera method is a useful addition to rapid sampling that can extend coverage across reef and sand habitat. All survey methods characterised False Bay as largely sand, with reef along the margins.

2.2. INTRODUCTION

Managing ocean landscapes has become a priority as anthropogenic threats to marine ecosystems and the services they provide are better understood (Worm et al. 2006). The magnitude of these threats requires that human impacts on ecosystem composition and functioning are mitigated (Lubchenco et al. 2003). Describing, monitoring, and managing anthropogenic impacts on marine systems, particularly marine biodiversity, underpins an ecosystem approach to ocean management (Levin et al. 2009). One key strategy in managing marine biodiversity is the declaration of marine protected areas (MPAs). Marine protected areas are a means to mitigate direct human impacts on biological communities (Agardy 1994; Lauck et al. 1998; Roberts et al. 2005), the physical ocean landscape (Fernandes et al. 2005) and indirectly on biological communities in an altered or changing physical environment (Lindholm et al. 2001). Landscapes need to be adequately understood to effectively design, enforce, and defend spatial plans (Stevens & Connolly 2004; Kendall et al. 2005).

Other biodiversity management interventions also require an understanding of the marine landscape to inform their implementation. Baseline landscape information is needed to track climate change impacts (Selkoe et al. 2009) and monitor the effects of pollution (Johnston & Roberts 2009), coastal construction (Rogers 1990), aquaculture (Diana 2009) and the development of renewable energy infrastructure (Garcia et al. 2007). The implementation of any management strategies relies on a baseline understanding of what the physical and biological elements of the ocean landscape are, and how they are distributed (Shumchenia & King 2010).

Despite the need for benthic maps, less than 10% of the seafloor is mapped to the same extent and resolution as terrestrial landscapes (Wright & Heyman 2008). The reason for this disparity lies in the logistical challenges the ocean presents to sampling: cost, water turbidity and sheer scale limit the extent of mapping. This is especially true at local or regional scales where conservation management authorities are often additionally limited by labour, equipment, and capacity constraints. It is at precisely these same scales that many management questions are posed (Huang et al. 2011). Whereas bathymetry data were historically collected for navigational purposes, there is now a need to link descriptions of marine biodiversity to seafloor topography. Understanding the physical nature of the seafloor is a first step towards interpreting interactions between the landscape and biological communities (Kendall et al.

2005; Shumchenia & King 2010). The distribution of benthic biological communities has been linked to ocean depth and the nature of the seafloor (Sahade et al. 2004; Heyns et al. 2016). Reliable seafloor maps that describe the physical landscape are therefore critical for biodiversity management (Wilson et al. 2007).

Firstly, reliable seafloor maps can improve our understanding of the link between the abiotic and biotic variables in the marine landscape, which helps refine suitable abiotic proxies for spatial planning (Post 2008). An understanding of abiotic proxies is particularly important where abiotic sampling might be cheaper and logistically easier than biological sampling. Baseline physical data can be used to extrapolate patterns of biodiversity where biological sampling is limited (Wilson et al. 2007). Biological communities and their associated habitat can be identified in this way (Post 2008). An understanding of the extent of sensitive or underrepresented habitats can refine management priorities and spatial planning (Kendall et al. 2005; SANBI & UNEP-WCMC 2016).

Secondly, seafloor surveys can generate measures of physical variables that influence the distribution of biological communities. Sonar surveys generate depth data, and benthic invertebrate communities vary along depth gradients (Sahade et al. 2004; Heyns et al. 2016). The structural complexity of the seafloor influences benthic invertebrate colonisation and establishment (Keough & Downes 1982). Slope, a measure of seafloor steepness, may influence local currents that supply food, and invertebrate settlement (Bekkby et al. 2002). Rugosity or “roughness”, a measure of seafloor substrate and texture, is useful to describe areas that support distinct communities (McArthur et al. 2010). Aspect, a measure of the seafloor orientation, may reflect patterns in water movement and indicate the degree of exposure to wave energy; these factors influence the growth of suspension feeders (Eckman & Duggins 1993), invertebrate colonisation and settlement of larvae and the formation of suitable biogenic habitat (Wilson et al. 2007).

However, a temporal and spatial disconnect often exists between the geophysical description of the seafloor, and biological sampling in the same region (Shumchenia & King 2010). It is essential to refine the ability to map seafloor characteristics at a scale, extent and resolution that is relevant to both the scientific or management question at hand, and the biodiversity of interest (Shumchenia & King 2010). Morgans (1959; 1962) completed the first survey of the False Bay benthos at limited discrete locations and noted that the integration of geological information into ecological studies without suitable adaptation to specific ecological requirements is problematic (Morgans & Day 1959). A synthesis of current knowledge must be matched with some adaptation of methods to suit the study (Morgans & Day 1959). Strictly geological classifications may not adequately address ecological interpretation (Shumchenia & King 2010).

With the field of seafloor mapping rapidly developing, a variety of instruments can be deployed to map landscapes at various scales and resolutions (Brown et al. 2011). Equally numerous ways to characterise the seafloor have developed (Erdey-Heydorn 2008; Du Preez 2015). How useful these data are to answer questions depends on the data collection methods, and how they are processed (Le Bas & Huvenne 2009). The choice of which methods to use is a question of scale and context (Shumchenia & King 2010). The introduction of new methods offers potentially useful additions to an existing suite of techniques: they extend the range of scales at which the seafloor is characterised, extract new physical variables to test relative to biological communities, match physical and biological descriptions in time and space, and address logistical challenges (Dolan & Lucier 2013).

The advent of multibeam sonar technology to map benthic habitats represents a move towards the kind of terrain analysis available to terrestrial ecologists, generating bathymetry data detailed enough to derive digital terrain models (DTM) (Wilson et al. 2007). Multibeam sonar provides a measure of depth over large areas of the seafloor (Fonseca & Mayer 2007). The bathymetry data from multibeam surveys can be used to extract measures of aspect, slope, and rugosity in addition to high-resolution depth data (Wilson et al. 2007; Shumchenia & King 2010). Acoustic backscatter data from multibeam bathymetry can also be used to classify the seafloor based on the combined influence of sediment grain size, seafloor slope and roughness (Dartnell & Gardner 2004; Shumchenia & King 2010). The application of new technology requires ground-truthing to assess whether we can detect variability at relevant scales (Stevens & Connolly 2004). The use of multiple methods can refine the interpretation of acoustic backscatter (Dartnell & Gardner 2004) and tease apart which geological measures may be biologically meaningful, scientifically rigorous and expedient for management (Shumchenia & King 2010).

Photographs sample biodiversity and its associated habitat simultaneously. This method extends sampling below depths that limit SCUBA surveys (Roberts et al. 1994) and pairs biodiversity with landscape characteristics in time and space. The pairing of biodiversity data with an *in-situ* landscape description is an advantage where repeat sampling by other methods might not precisely match the original samples spatially and provides a logistically simple method for obtaining two datasets in one survey. Photographs, however, present a challenge to the accuracy of seafloor mapping without ground-truthing. A broad classification scheme such as the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) (Althaus et al. 2015) is specific to photographic and video sampling. Classification schemes standardise ways of dealing with poor visibility, low resolution and limited ground-truthing. An assessment of how this classification scheme compares to findings from previous surveys would indicate whether new methods are helpful.

False Bay's bathymetry and physical seafloor characteristics have been described by surveys that detail depth contours (Mallory 1970; Simpson et al. 1970), geological formation (Simpson et al. 1970; Flemming 1982; Du Plessis & Glass 1991) and sediment properties (Bowie et al. 1970; De F. Retief 1970; Terhorst 1987; Du Plessis & Glass 1991). The first survey was the "Challenger" expedition of 1873 – 1876 which sampled in Simon's Bay (Murray & Renard 1891). The seafloor of False Bay was first mapped in 1869 by Lieut. W. Deacon, R.N., who provided sounding data using a hand lead line that would later be used to compile bathymetric charts of the whole bay (Mallory 1970). Dredgings were initiated in 1946 by Day and continued by Morgans (1962), who collected dredge samples between 8 m and 88 m depth. Five grain sizes between very coarse sand and very fine sand (after Wentworth 1922) were recorded, where most samples were medium or fine sand (Morgans 1962). The British Admiralty charts 636 and 2095 showed that reef decreases with depth, and mud occurs from 56 m depth downwards (Morgans 1962).

Dredge and grab sampling show that False Bay comprises primarily fine to medium-grained sands (Bowie et al. 1970). Grain size decreases with depth, with finest sands found at the mouth of the bay and south of Seal Island (Bowie et al. 1970). Very coarse sands (1.0 – 2.0 mm) are concentrated in the west from Simonstown to Cape Point, and the east from the Eerste River mouth to Cape Hangklip (Bowie et al. 1970). Sampling by bathymetric and seismic reflection profiles, rock samples and side-scan sonar show that False Bay is underlain by Cape Granite Suite in the west and Malmesbury Group shale in the east (Du Plessis & Glass 1991). Seven "physiographic terrains" were described by comparing data from bathymetric contour maps and sidescan sonar sonographs with rock and sediment samples to characterise the relief and composition of the seafloor (Du Plessis & Glass 1991).

False Bay presents a relevant case study to ground-truth new methods and classification schemes that introduce an ecological perspective to how we characterise ocean landscapes. Baseline information on the geology and sediment from previous surveys provides a useful sounding board to compare new methods that could be expanded to novel areas of the South African coastline. It is important to test the accuracy of remote camera methods and assess what should be refined in an Australian classification scheme (Althaus et al. 2015) to be effective in South Africa.

False Bay has a long history of human use (Spargo 1991) and represents significant biological diversity (Day 1970; Brown & Jarman 1978; Griffiths et al. 2010) that requires monitoring. The City of Cape Town where the bay is located balances population growth and post-Apartheid urban planning (Van der Merwe et al. 1991; Quick & Thornton 1991) with environmental protection and ecosystem service delivery (De Wit et al. 2012). The geology and bathymetry of False Bay will not change over the same timescales as biological communities, nor human populations and their impacts on biodiversity. However, other aspects of the landscape will change on a timescale relevant to current management and monitoring in False Bay, and this is important to understand in connection with the biological communities. Mapping the seafloor at scales that can be adapted to integrate in future with other abiotic data to classify ecosystem types, matched with biodiversity information to map ecological condition, informs ecosystem threat classification and management prioritisation (SANBI & UNEP-WCMC 2016).

In False Bay, conserving subtidal biodiversity is not limited to managing fishing. Siltation has been documented on the seafloor at Gordon’s Bay harbour (De F. Retief 1970), a host of alien invasive species may affect sediment bioturbation (Robinson et al. 2005; Robinson et al. 2016), kelp beds have moved eastwards (Bolton et al. 2012; Blamey et al. 2015) and documented land use changes (Chingombe 2012; Mwangi 2014) influence freshwater outflow at the Zandvlei estuary, the Zeekoevlei outfall, the Eerste River estuary, Lourens River, Sir Lowry’s River and stormwater drains along the shoreline (Skibbe 1991). A means of assessing this scale of change is not currently captured in the existing descriptions of the physical seafloor of False Bay. New methods offer an opportunity to simultaneously capture ecosystem pattern and process, which may improve the integration of abiotic and biotic elements of the ocean landscape. If the methods applied in this study generate data comparable to previous surveys but extend coverage that helps us understand patterns of biodiversity across a range of depths and habitats, we can improve our understanding of the status and distribution of biodiversity. This establishes a basis for subtidal ecosystem monitoring. An update to our knowledge of False Bay using novel methods is pertinent to simplify long-term monitoring, inform management in a region that has experienced significant social change and mitigate the consequences for its biodiversity.

Finally, it is important to bear in mind that in developing nations like South Africa, context necessarily underpins the applicability of applied science. A paucity of funding and human resources can limit sampling. There is a need to identify which methods can meet both the rigour of scientific scrutiny and overcome the limitations of capacity. It could be argued that in striking this balance lies some of the most pressing work to be done in applied ocean science. Much of the world's oceans are managed by developing nations or fall under the classification of High Seas, where the capacity for monitoring is arguably most limited (Ban et al. 2014). There is relevance, therefore, in testing methods deployed at greater extent and frequency in developed nations, in regions that present both oceanographic and logistical challenges representative of much of the world's most threatened oceans. False Bay presents a case study to apply methods that may overcome logistical constraints, and in doing so, address how we survey other coastal regions in South Africa.

This chapter characterises the seafloor of False Bay using multibeam bathymetry, photographs, and sediment samples along eight transects where biological samples were collected. The aim was to i) assess whether these methods adequately detect patterns in the seafloor and characterise the region favourably compared to known geological surveys and ground-truthed sediment samples, ii) characterise the seafloor of False Bay according to two new classification schemes for the region and describe the physical environment at two scales: that of the bay, and along individual transects and iii) derive physical measures from multibeam bathymetry data that can be used to interpret patterns of biodiversity across False Bay.

2.3. MATERIALS AND METHODS

2.3.1 Study area

The floor of False Bay slopes gradually southward from its northern shore to a maximum depth of around 90 m at its mouth (Mallory 1970; Spargo 1991) (**Figure 2**). Sediments in much of the bay vary in grain size from very fine (0.06 – 013 mm) to very coarse (1.0 – 2.0 mm), with the finest sediment in the deepest reaches (Bowie et al. 1970). Table Mountain Group sandstone rock is found in the north-west and south-west (Du Plessis & Glass 1991) (**Figure 2**). Malmesbury Group shale rock is visible at the surface in the east, and at the York and East shoal outcrops (Du Plessis & Glass 1991). Cape Granite Suite outcrops rise to the surface in the west and central bay (Du Plessis & Glass 1991). High profile reef dwindles with distance from the coastlines in the east and west (Simpson et al. 1970). The relief deviates from its sandy uniformity to form rock pinnacles and Cape Granite Suite outcrops at Whittle Rock, Roman Rock and Seal Island (Simpson et al. 1970; Du Plessis & Glass 1991).

2.3.2 Remote photographic seafloor description: CATAMI classification of samples

GPS-referenced depth measurements provided by the Council for Geoscience were interpolated in ArcMap™ (Maps throughout this study were created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com) to make a contour map of False Bay (Van Zyl 2011) (**Figure 2**). The digital terrain model (DTM) was constructed from naval fair chart data, and sidescan sonar covering the area from Cape Point to Simonstown (from the 10 m isobath out to approximately 30 m) (Van Zyl 2011). The "shape area" of the different geological types was calculated from these data layers and the percentage coverage of each type (sand, Malmesbury Group shale, Table Mountain Group sandstone, Cape Granite Suite) was calculated by dividing the total shape area for each geological type by the total bay area. Eight transects were delineated perpendicular to the prevailing depth contours to cover the bay and sample the changes in seafloor type with increasing depth, following the methods and findings outlined by Morgans (1962) and Field (1970) (**Figure 2**). This ensured that each transect covered changing depth and habitat-type from north to south, and east to west. Transects were chosen over random points to sample the change in community composition along a depth gradient (*sensu* Götz 2006; Heyns et al. 2016). Reef habitat is limited to shallow depths in False Bay, so the distribution of reef and sand habitat could not be sampled equally while using transects sampling along a depth gradient. Future research can use a grid design to test reef and sand equally.

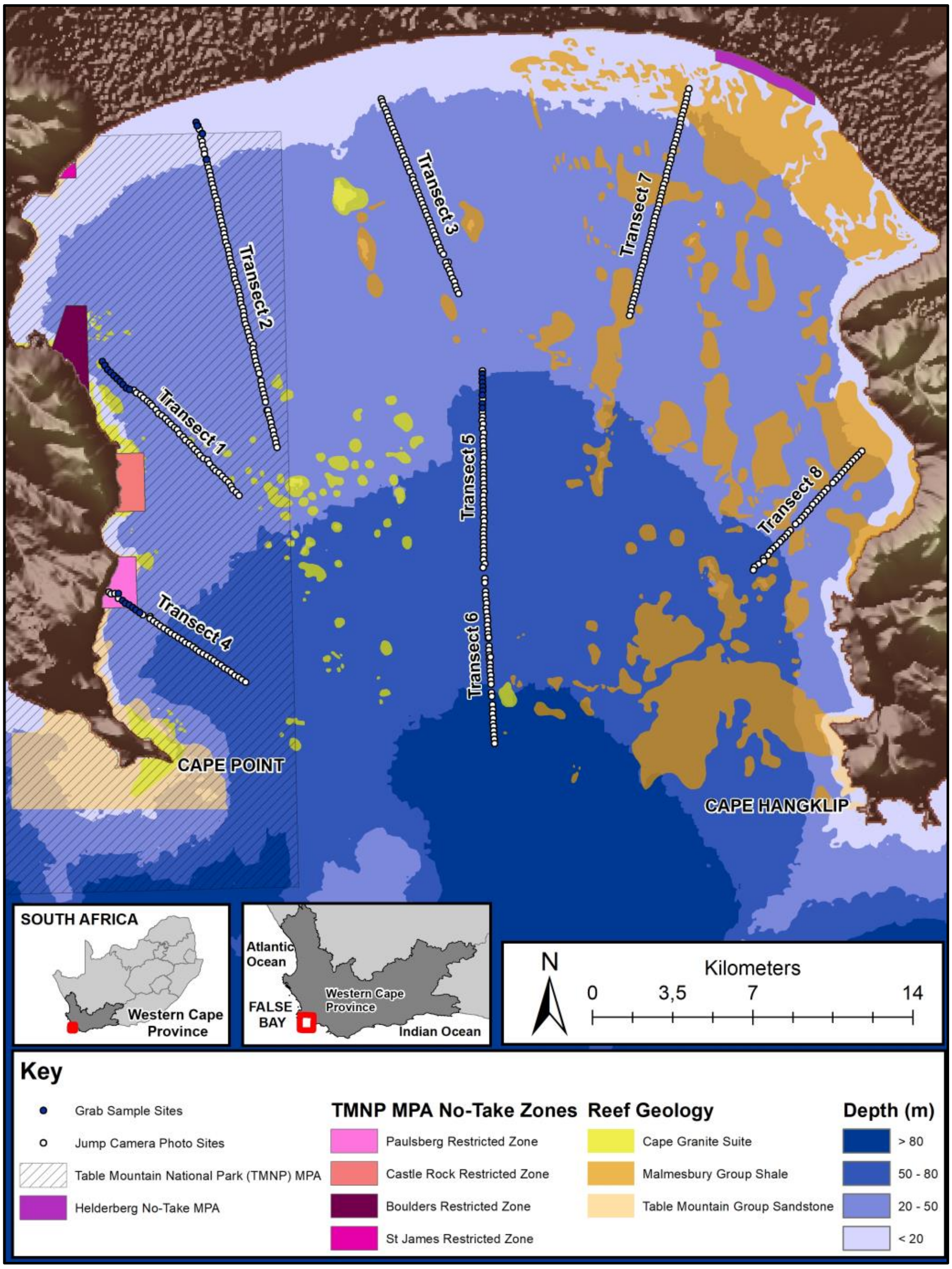


Figure 2. The location and name of eight study transects delineated for jump camera photographic sampling, perpendicular to the prevailing depth (m) contours (Van Zyl 2011) in False Bay, South Africa. Multibeam sonar tracks, jump camera photographs and sediment grab samples were collected on separate sampling occasions on these same transects. False Bay is shown in the context of the surrounding terrestrial topography (EKZNW 2015), subtidal reef geology (Van Zyl 2011) and marine protected areas (MPAs) (DEA 2019a).

A GoPro Hero 3™ camera attached to a jump camera rig took 400 photographs of the seafloor along eight transects in False Bay (**Figure 2**). The jump camera rig consisted of a downward-facing camera in a housing, set 1 m above the seafloor (**Figure 2**). Two LED dive torches lit the view in the circular base with an internal area of 0.3 m^2. Each transect was sampled separately and completed in a single day. The jump camera rig was lowered to the seafloor at intervals of 0.1 nautical miles (185 m) along the length of each transect and the GoPro camera set to take one photograph every five seconds. The rig was deployed to the seafloor for 35 seconds, such that the photograph with the clearest field of view could be selected in analysis afterwards.

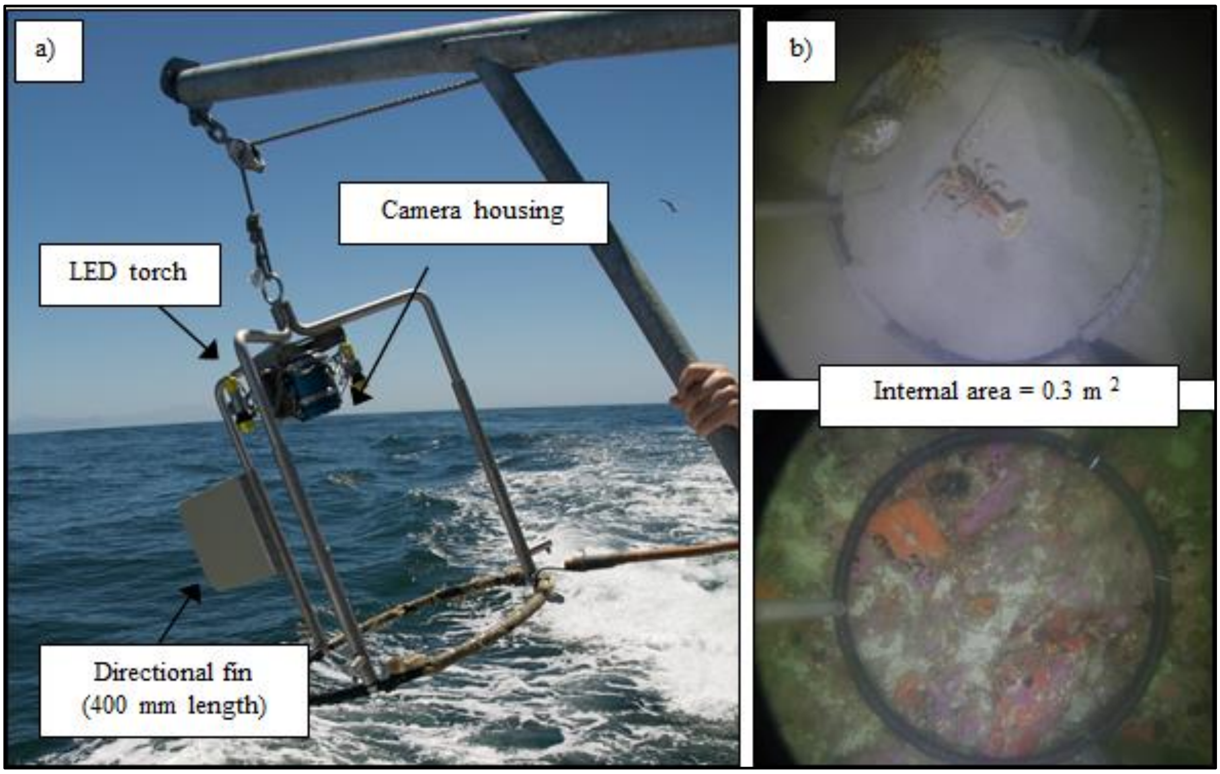


Figure 3. a) A stainless-steel jump camera rig with GoPro camera in housing and LED torches, **b)** the internal area of the jump camera rig "quadrat" and photographic sample used for the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification.

While 400 photographs were collected at sea, visibility and lighting were suitable for adequate visual assessment to detect substrate type in 373 photographs. Therefore, 373 photographs across eight transects were used in the final analysis. Each photograph was assigned a single CATAMI code (**Table 1**) for each of the following descriptors: substrate type, bedform, relief and visibility.

Table 1. Description of the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification codes used for 316 samples in this study (from Althaus et al. 2013).

CATAMI	Description
SCC	Substrate: consolidated (hard): cobbles
SCR	Substrate: consolidated (hard): rock
SUSM	Substrate: unconsolidated (soft): sand/mud (<2 mm): mud/silt (< 64 µm)
SUP	Substrate: unconsolidated (soft): pebble/gravel
SUPBS	Substrate: unconsolidated (soft), pebble/gravel: biogenic (screwshells)
SUSC	Substrate: unconsolidated (soft): sand/mud (<2 mm): coarse sand (shell fragments)
SUSF	Substrate: unconsolidated (soft): sand/mud (<2 mm): fine sand (no shell fragments)

2.3.3. Sediment sampling: percentage clay, sand, and gravel

Thirty-two sediment samples were collected using a Van Veen grab with a grab area of 250 cm^2 (**Figure 4**). Transects 1, 2, 4 and 5 were selected for grab sampling (**Figure 4**). Transects with sufficient unconsolidated seafloor type (sand) were selected to directly compare grab samples (grain size classification) with the CATAMI classification of the photographic sample taken at the same location.

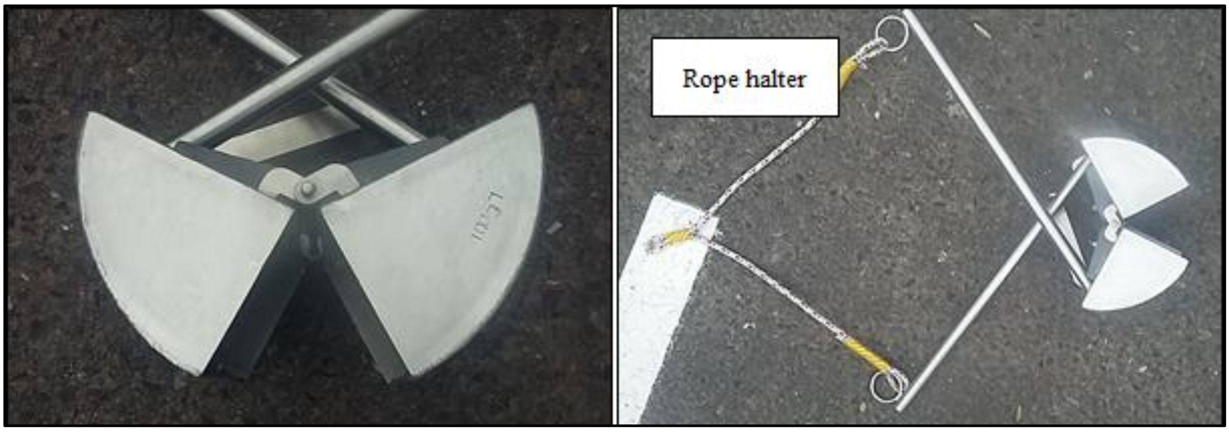


Figure 4. Van Veen grab from Lwandle Marine Environmental Services with grab area of 250 cm^2 used to collect 32 sediment samples from four transects in False Bay, South Africa.

The sediment was processed according to the method developed by Woodborne (1991) and MacHutchon (2013). Samples were dried for 24 hours to remove the seawater from the sediment. A sediment splitter subsampled each bulk sample equally: half was retained for carbonate analysis and the remainder was dried in an oven at 60 C for 24 hours to remove any remaining seawater. To calculate the percentage of fine sediment, 100 g was weighed and then wet sieved through a 63 µm mesh. With the finest sediment sieved out, the remaining sediment was dried in an oven at 60° C and the final dry weight recorded. The percentage of fine sediment was calculated as follows:

$$Fine\ sediment\ (g) = initial\ dry\ sediment\ (g) - final\ dry\ sediment\ (g) \ldots\ldots\ldots\ldots \text{(2.1)}$$

$$Fine\ sediment\ (\%) = fine\ sediment\ (g) /\ initial\ dry\ sediment\ (g) \times 100 \ldots\ldots\ldots\ldots \text{(2.2)}$$

The dried sediment was then sieved through a 2000 µm SABS approved and ISO 3310-1 certified stainless-steel test sieve (with a fixed diameter of 200 mm) in a Fritsch vibratory sieve shaker set to three minutes per sample. Sediment that did not pass through the 2000 µm mesh was considered gravel. To calculate the percentage of gravel, sediment that passed through the 2000 µm mesh was weighed and calculated as follows:

$$Gravel\ sediment\ (g) = initial\ dry\ sediment\ (g) - sieved\ sediment\ (g) \ldots\ldots\ldots\ldots \text{(2.3)}$$

$$Gravel\ sediment\ (\%) = gravel\ sediment(g) \div initial\ dry\ sediment\ (g)\ \times\ 100 \ldots \text{(2.4)}$$

The sediment sieved through the 2000 µm mesh was considered sand and was used for settling tube processing. The percentage of sand was calculated as follows:

$$Sieved\ sediment\ (g) /\ initial\ dry\ sediment\ (g)\ \times\ 100 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{(2.5)}$$

The proportion of gravel, sand and fine sediment in each grab sample taken from transects 1, 2, 4 and 5 were plotted in a ternary diagram using the XLSTAT data analysis extension (XLSTAT 2017) for Microsoft Excel (2011). The diagram represented the proportion of these three variables for every sample as a position on the sides of an equilateral triangle. The proportion of these three variables summed to a constant of 1.0 for every sample.

2.3.4. Sediment sampling: grain size classification

The Council for Geoscience sediment settling tube (**Figure 5**) was used to generate grain size curves. The settling tube sorted sediment size on the principle that differently sized sediment particles have different settling velocities (MacHutchon 2013). When a known quantity of sediment is placed at the surface of a water column in a settling tube, each sediment particle in the sample falls under the weight of gravity until it reaches terminal speed.

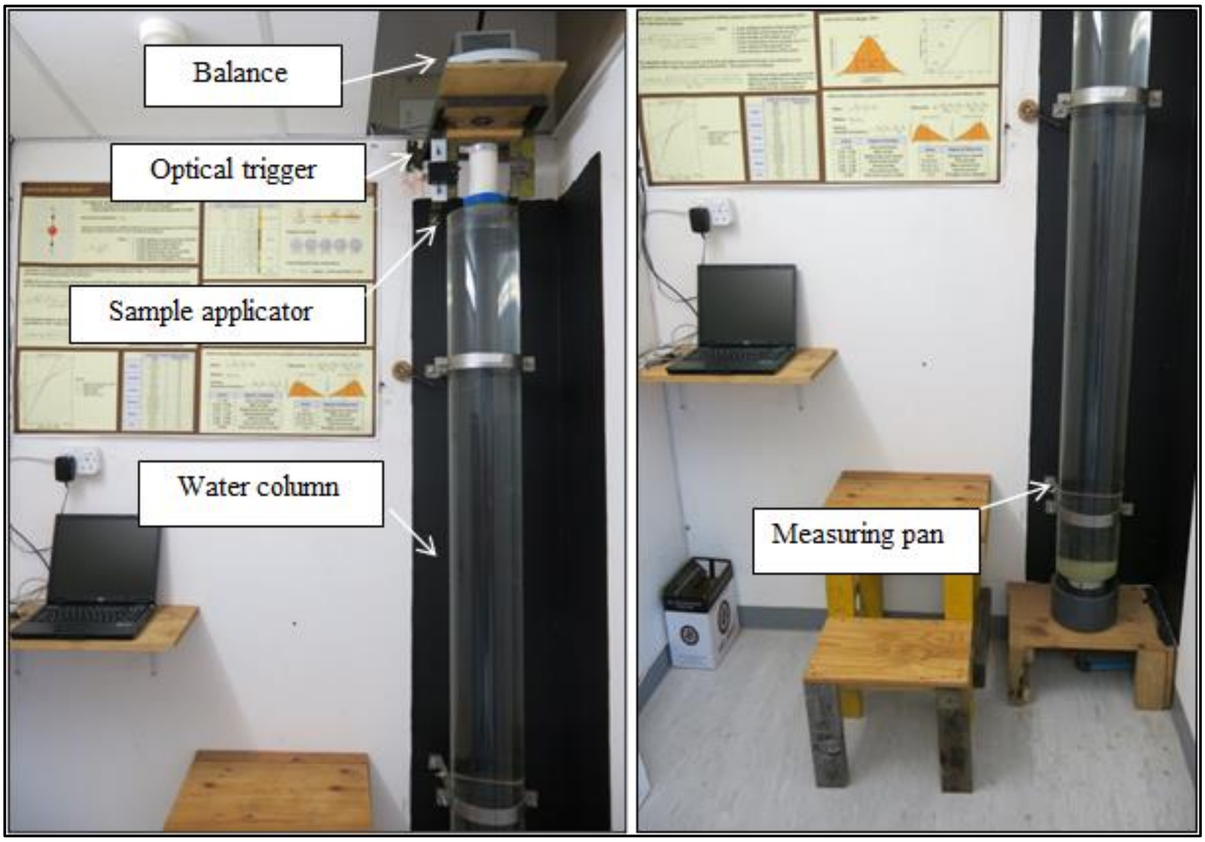


Figure 5. Settling tube and associated equipment to process sediment samples [photographs courtesy: Michael MacHutchon, Council for Geoscience (Bellville, South Africa)].

Different particles vary in grain size, and according to Stoke's Law, reach different terminal speeds. Larger grains fall faster than small ones and, in this way, the sample is sorted. The software associated with the settling tube uses a formula that calculates the velocity of the particle as a function of the density and radius of the particle, its acceleration due to gravity, and the density and dynamic viscosity of the water (Gibbs et al. 1971):

$$V = \frac{-3\mu + \sqrt{9\mu^2 + gr^2\rho_f(\rho_s - \rho_f)(0.015476 + 0.19841r)}}{\rho_f(0.011607 + 0.14881r)} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2.6)$$

Approximately 5 g of sediment was adhered to 38 µm gauze on an applicator using Extran®. The applicator was lowered to the water surface in the 2 m long PVC settling tube. On contact with the water, the applicator broke the surface tension and the sediment particles fell through the water column to a collection pan where the weight of the accumulated sediment was logged by an Adam Equipment PGL 203 balance. The balance recorded the accumulated weight of the grains on a computer. Sediment size distributions were graphed as cumulative weight percentage (Boggs 2001). Mean and median grain size, skewness, and sorting (after Folk & Ward 1957) were derived from these curves as follows:

For the mean μ_1:

$$\mu = \frac{\phi_{16} + \phi_{50} + \phi_{84}}{3} \quad \text{……………………………………………………………………….}(2.7)$$

For the median Md_1:

$$M_d = \phi_{50} \quad \text{………………………………………………………………………...... } (2.8)$$

For the degree of sorting (standard deviation):

$$\sigma = \frac{\phi_{84} + \phi_{16}}{4} + \frac{\phi_{95} - \phi_5}{6.6} \text{……………………………………………………………………….}(2.9)$$

where the degree of sorting is classified according to the following thresholds:

Table 2. Sorting (standard deviation) (after Folk & Ward 1957).

Value	**Degree of sorting**
< 0.35	Very well sorted
0.35 – 0.50	Well sorted
0.50 – 0.71	Moderately well sorted
0.71 – 1.00	Moderately sorted
1.00 – 2.00	Poorly sorted
2.00 – 4.00	Very poorly sorted
> 4.00	Extremely poorly sorted

Skewness:

$$sk = \frac{\phi_{84}+\phi_{16}-2\phi_{50}}{2(\phi_{84}-\phi_{16}} + \frac{\phi_{95}+\phi_{5}-2\phi_{50}}{2(\phi_{95}-\phi_{5})} \text{ ....} (2.10)$$

where the degree of skewness is classified according to the following thresholds:

Table 3. Degree of skewness (after Folk & Ward 1957).

Value	**Degree of skewness**
> 0.3	Strongly fine skewed
0.3 to 0.1	Fine skewed
0.1 to -0.1	Near symmetrical
-0.1 to -0.3	Coarse skewed
< -.03	Strongly coarse skewed

2.3.5. Multibeam sonar survey: bathymetry

A multibeam sonar survey recorded spatially referenced depth soundings along eight transects (**Figure 2**). Underwater Surveys Pty Ltd (A Matthew, Underwater Surveys Pty Ltd, Cape Town) processed the 200 kHz multibeam bathymetry data as a 3-column XYZ ASCII file with positive depth values (m). These data were gridded at 4 x 4 m, which was interpolated as a raster in ArcMap™ 10.5.1 (www.esri.com) to represent depth values across eight transects, ranging between six and 84 m depth.

2.3.6. Bathymetric derivatives: slope, aspect, and roughness

Aspect was calculated using the Calculate Aspect tool in the Benthic Terrain Modeler (BTM) in ArcMap™ 10.5.1 (Wright et al. 2012; Walbridge et al. 2018). This measure identifies the compass direction of the downhill slope for each cell of a raster surface. In this case, the depth raster surface from the results of the multibeam survey was used as the input, and a raster was generated with an aspect value for every cell. The tool works using a three by three moving cell window; if the processing cell has no data, the output is “Null”. Likewise, the tool requires seven of the eight neighbouring cells to have data to generate a value for the processing cell. Where a neighbouring cell is missing data, or along the boundaries of the input dataset (in this case, the boundaries of each of the eight transects), the output value is “Null”. This was deemed permissible because the multibeam swathe along each of the transects was much wider (between 90 and 150 m) in extent than the point for each jump camera photo site. Where jump camera photo sites fell outside or at the very edge of the multibeam data swathe, measures of aspect were not calculated. Aspect values were generated in positive degrees between 0 and 360, measured clockwise from north, and those cells with zero slope were assigned an aspect value of -1.

The slope was calculated using the Calculate Slope tool in the BTM for ArcMap 10.5.1 (Wright et al. 2012; Walbridge et al. 2018). A single slope value (calculated as the gradient, or rate of maximum change in z) was processed for every cell based on the bathymetric raster surface input, and the result was expressed in degrees. The tool used a three by three scanning window of grid cells where the average gradient in the horizontal and vertical direction was found based on the centre processing cell and its eight neighbours. Where there were insufficient neighbouring cells, the result was “Null”. Wherever cells were surrounded by neighbours, where at least seven contained data, the slope was calculated as the inverse tangent of the hypotenuse of the horizontal and vertical gradients.

A measure of the structural complexity of the seafloor (called roughness) was derived for each cell using the Surface Area to Planar Area tool in the BTM toolbox in ArcMap™ 10.5.1 (Wright et al. 2012; Walbridge et al. 2018). This technique was developed by Jenness (2004) and used a three by three cell window to calculate the ratio between the three-dimensional surface area and the planar area of a raster surface. The surface area was calculated using the triangulated area of each neighbouring cell and applied the Pythagorean Theorem. In this way, the surface grid was triangulated. The projected area of each triangular grid was calculated, and this was compared to the surface planar area. The resulting values typically range from one (flat) to four (high variation) (Jenness 2004). In this version of the BTM toolbox, the planar area is corrected for slope (Du Preez 2015).

2.3.7. Angle Range Analysis: multibeam acoustic backscatter data

Multibeam sonar data provide beam-by-beam time-series data of the acoustic backscatter that were gridded at 0.5 m and 0.25 grid size, and displayed as tiff images for each transect with red green blue (RGB) values at 0.5 m grid size in Appendix 1. These data were used to characterise the seafloor based on the Angle Range Analysis (ARA) method (QPS, n.d.) using the QPS Fledermaus Geocoder Toolbox (FGMT) by Underwater Surveys Pty Ltd (A Matthew, Underwater Surveys Pty Ltd, Cape Town). No sample data from False Bay were available during processing, so the default values for a Reson 7125, 200kHz MBES were used for classification. The 4D geo-spatial processing and analysis tool FMGT used the Jackson Model (Jackson et al. 1996) to compare the actual backscatter response to the expected acoustic response curves, rather than a single threshold to determine the sediment classification. The Jackson Model generated an expected acoustic response curve as a function of grazing angle versus returned backscatter intensity. The grazing angle is the angle (corrected) at which the sound wave hits the seafloor (QPS, n.d.). The response curve is analysed to generate the sediment model. This analysis generated a series of 20 ARA classification seafloor types to characterise the substrate (**Table 4**).

Table 4. Angle Range Analysis (ARA) classifications.

ARA classification	Description
1	Gravel
2	Gravelly coarse sand
3	Coarse sand - sandy gravel
4	Coarse sand - gravelly sand
5	Medium sand - gravelly muddy sand
6	Medium sand
7	Fine sand
8	Silty sand
9	Muddy sand
10	Very fine sand
11	Clayey sand
12	Coarse silt
13	Sandy silt
14	Medium silt
15	Sandy mud
16	Fine silt
17	Sandy clay
18	Very fine silt
19	Silty clay
20	Clay

ARA classifications were not calibrated for False Bay. The actual sediment type classified by this analysis was considered less important than the ability to detect seafloor variation. The relative classifications were deemed important; that is, one sample was distinguished from another by the assignation of a code (*sensu* Edwards et al. 2003). For the rest of the document, ARA classification types are referenced as ARA1 – ARA20. This assessed whether backscatter data would be useful in detecting seafloor variation, to calibrate region-specific sediments in future.

The XY positions for each jump camera photograph were added to the bathymetric raster in ArcMap™ and a measure of aspect, slope and rugosity was extracted for every photograph using Extract Multipoints to Layer in Spatial Analyst Tools. An ARA code was assigned to each photograph site using a Spatial Join in ArcMap™ to identify the nearest value from the bathymetric dataset to each photo. The XY positions for each grab sample were added to the project in ArcMap™ to check the degree of spatial overlap for the surveys. The results from the grain size analysis were associated with each XY point and joined by means of a Table Join in the Coverage toolbox in ArcMap™. Grab samples that fell >29 m from a jump camera photograph site were excluded from subsequent analysis. A table was generated that returned a measure of aspect, slope, surface roughness, grain size, an ARA and CATAMI classification for every jump camera photograph. Thirty-two samples were used in subsequent analyses that each had corresponding grain size, CATAMI and ARA classifications. The variance and standard deviation of depth across all samples was checked and considered insignificant, so that 316 samples with corresponding CATAMI and ARA classifications, depth, roughness, slope, and aspect values were used in analysis.

Depth, roughness, slope, and aspect were assessed using principal components analysis (PCA) in PRIMER 7 (Clarke & Gorley 2006). The interactions between variables are expressed in a combination that assesses the "total variance between fractions" (Davis 1973). Variables are plotted onto a best fitting plane and weighted based on their contribution to the variance between samples, representing patterns in the data such that the first principal component (PC1) explains most of the variability in the data, and each subsequent component explains as much of the remaining variability in the data as possible (Clarke & Gorley 2015). The Eigenvectors indicate the orientation of the variables and the Eigenvalues indicate the length of the variables (Abdi 2007). Variables weighted closer to zero are less related to the variation than variables weighted away from zero (East 1987, reported in Escott 2011). The CATAMI and ARA classifications for each jump camera sample were displayed on the bathymetric raster in ArcMap™. Each transect was displayed according to the same reference scale, and each one presented on its own as one map out of a series eight maps. This way of presenting the maps visualised the comparison of CATAMI and ARA classifications for every sample along that transect.

2.3.8. Depth distribution across samples

The distribution of depth across eight transects, six CATAMI and 11 ARA classifications was graphed as a separate box and whisker plot using the boxplot function in the statistical platform R (R Core Team 2017) for each factor. The function plots the median depth (m) and the first and third quartiles as lower and upper limits of the box, respectively. The minimum and maximum values (that are not outliers) are plotted as the lower and upper whiskers, respectively. Outliers are equal to any value less than Q_1 – 1.5 X IQR or greater than Q_3 + 1.5 X IQR, where Q_1 = the first quartile, Q_3 = the third quartile and IQR = the interquartile range.

2.4. RESULTS

The interpolation of data from Van Zyl (2011) and calculation of shape areas showed that the seafloor of False Bay is 83% unconsolidated substrate (sand) and 17% rocky reef (**Figure 6**).

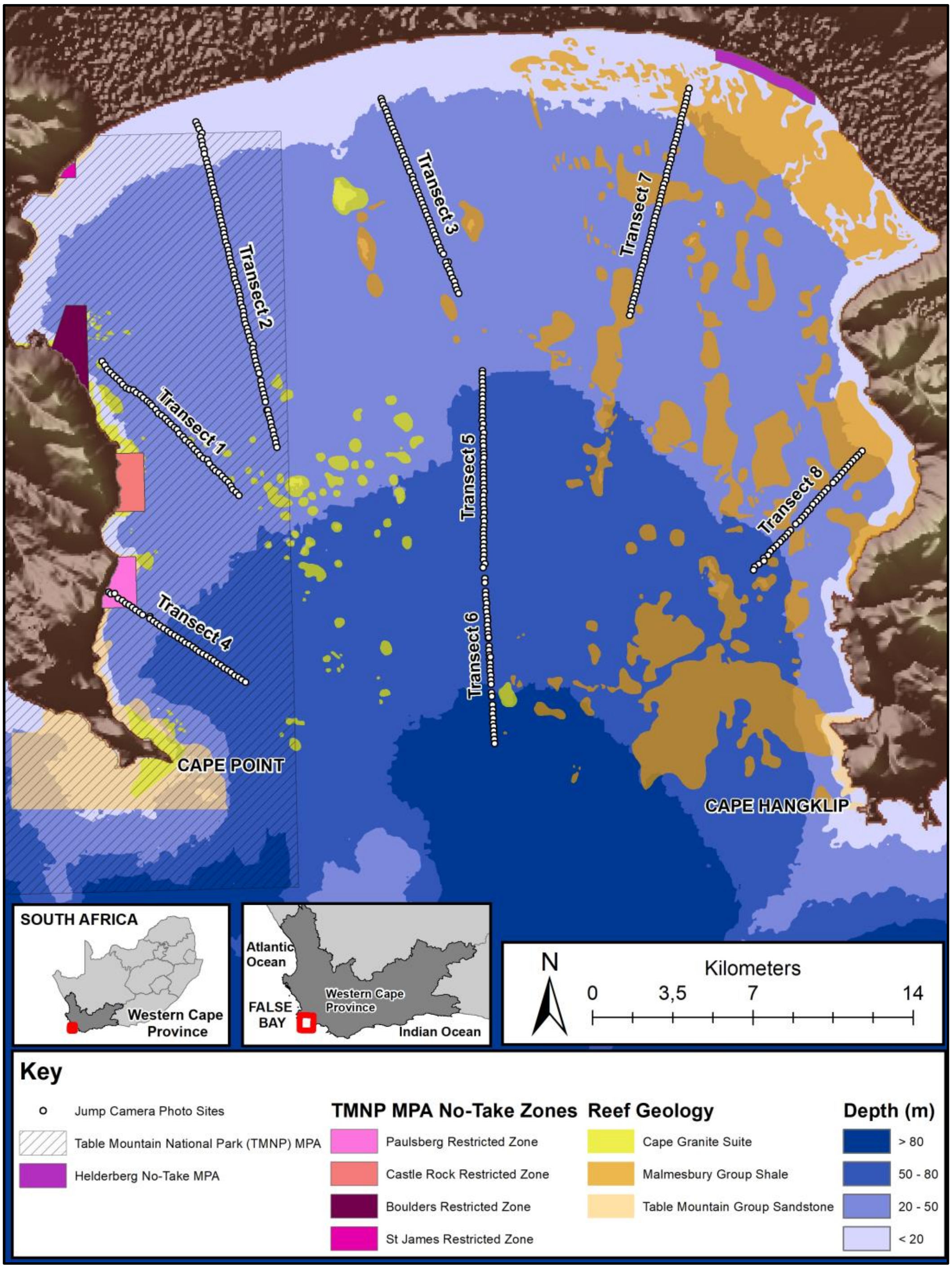


Figure 6. The location of 316 jump camera sampling sites, where CATAMI and multibeam ARA data are available at the same site, along eight transects that are perpendicular to the prevailing depth (m) contours (Van Zyl 2011) in False Bay, South Africa. The bay is shown in the context of the surrounding terrestrial topography (EKZNW 2015), subtidal reef geology (Van Zyl 2011) and marine protected areas (MPAs) (DEA 2019a).

Of the rocky reef component, 14 % was Malmesbury Group shale, 2% was Cape Granite Suite, and 1% was Table Mountain Group sandstone. Malmesbury Group shale was predominant in the eastern half of False Bay, extending from Swartklip east, and south to Cape Hangklip (**Figure 6**). A few patches of Malmesbury Group shale were also evident at York shoal (south of Seal Island) and East shoal. Malmesbury Group shale was found at all depths. Cape Granite Suite was concentrated along the western margin of False Bay, from Simon's Bay and at Roman Rocks, along the coast to Cape Point. Outcrops were also evident in the western half of the bay's centre, including Whittle Rock and some deeper rock at the mouth of the bay. Table Mountain Group sandstone was evident as a very narrow band at the coast at St James and Kalk Bay. Another band extended from Smitswinkel Bay southwards, around Cape Point. Another isolated band was evident in the east, south of Pringle Bay towards Cape Hangklip. Table Mountain Group sandstone was only found close inshore at the coastline within False Bay, up to 50 m deep.

2.4.1. Number and distribution of deployments

Three hundred and sixteen sites that had matching jump camera and multibeam sonar data were sampled at depths between 8 m and 84 m (average of 44 m) across eight transects.

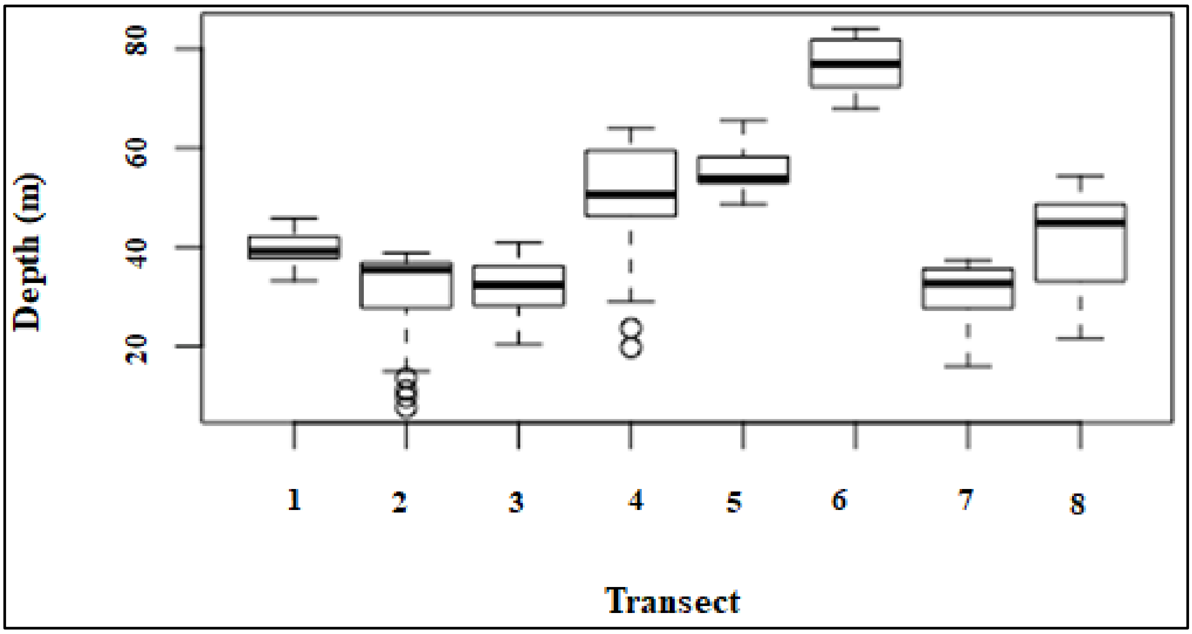


Figure 7. The distribution of depth (m) across eight transects sampled in False Bay, South Africa. The central line represents the median depth (m). The lower and upper limits of the box represent the first and third quartiles, respectively. The lower and upper whiskers represent the minimum and maximum values. Outliers are represented by the symbol O.

Transect 6 was the deepest transect on average (**Table 5**) with a maximum depth of 84 m. Transect 1 had the lowest range (12.6 m) and transect 4 had the highest range (44. 2 m). There were no outlier values on transect 1, where the maximum depth was 46 m, and the minimum depth was 33 m. The minimum depth of transect 4 (20 m) was considered an outlier (**Figure 7**). Transect 2 was the shallowest transect on average (mean depth = 30.9 m) with a minimum depth of 8 m, which was considered an outlier (**Figure 7**).

Table 5. Summary depth (m) values for 316 samples on eight transects in False Bay, South Africa.

		Depth (m)		
Transect	**Minimum**	**Maximum**	**Mean**	**Range**
1	33	46	39.8	12.6
2	8	39	30.9	31.2
3	20	41	32.0	20.6
4	20	64	50.2	44.2
5	49	66	55.4	16.9
6	68	84	76.8	16.0
7	16	37	31.2	21.4
8	22	54	41.3	32.8

2.4.2. Sediment characteristics from grab samples

2.4.2.1. Number and distribution of samples

Thirty-three grab samples were collected from transects 1, 2, 4 and 5. Transect 1 constituted 10 samples between 35 m and 40 m depth. Transect 2 constituted 9 samples between 7 m and 27 m depth. Transect 4 constituted 6 samples between 33 m and 48 m. Transect 5 constituted 7 samples between 52 m and 57 m.

2.4.2.2. Sediment sample characteristics

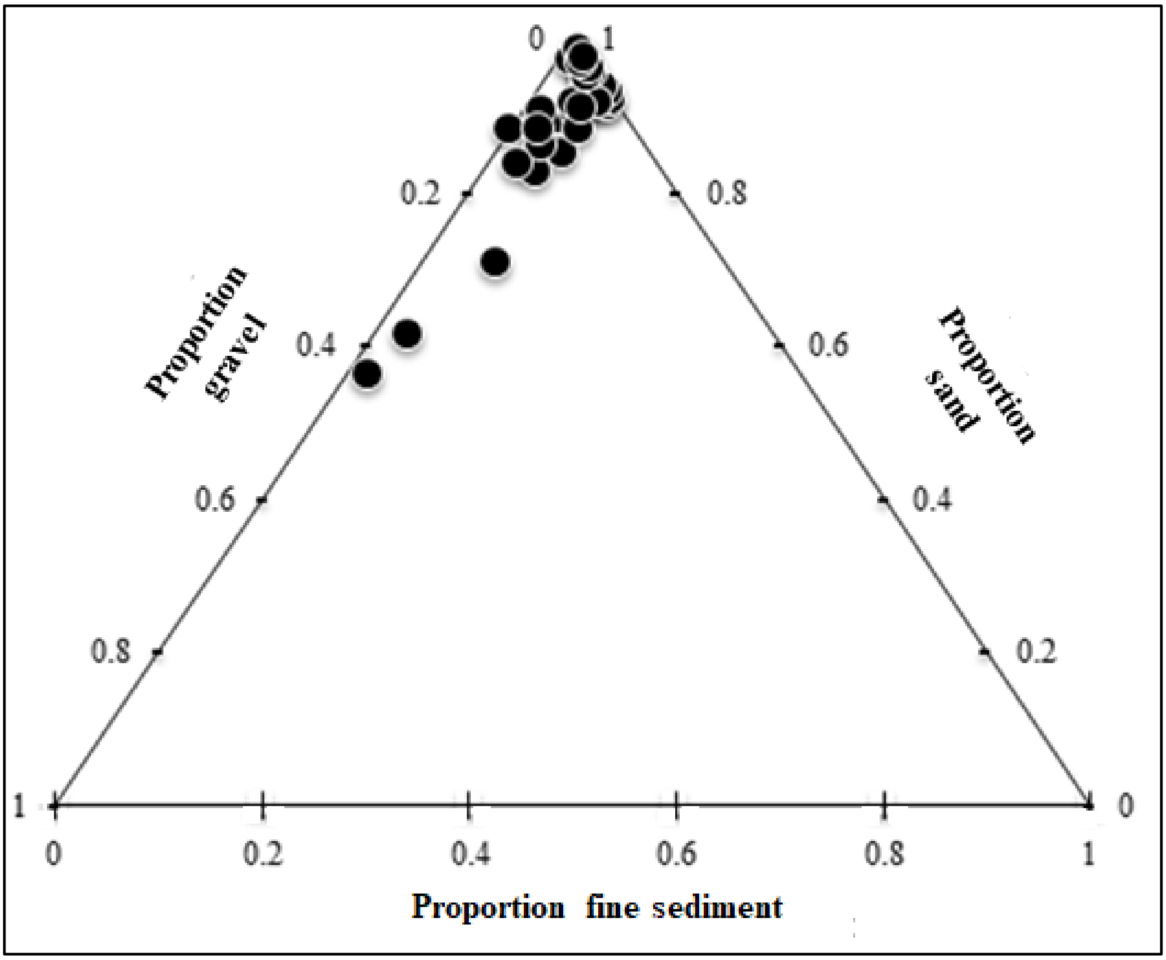


Figure 8. The proportion of gravel, sand and fine sediment in each grab sample taken from transects 1, 2, 4 and 5 in False Bay, South Africa.

All sediment samples constituted at least 55.8% sand (**Figure 8**). All samples constituted very little fine sediment. One sample (depth = 52 m) from transect 5 constituted the highest proportion of fine sediment (0.7% gravel, 91% sand, 8% fine sediment). Three samples constituting at least 22% gravel were outliers. One sample (depth = 55 m) from transect 5 constituted the highest proportion of gravel (42% gravel, 56% sand, 3% fine sediment). Two samples from transect 4 (depth = 40 m and 48 m) constituted 35% gravel, 61% sand, 4% fine sediment and 22% gravel, 71% sand, 7% fine sediment, respectively.

2.4.2.3. Particle size data (after Morgans & Day 1959 and Bowie et al. 1970)

The sand component of 32 sediment samples was processed for transects 1, 2, 4 and 5. Samples were classified according to four different grain sizes, following Wentworth (1922). The majority (75%) of samples were classified as medium sand (mean size = 0.25 – 0.50 mm) (**Table 6**) and 13% of samples were classified as coarse sand (mean size 0.50 – 1.0 mm). Nine percent of samples were classified as fine sand (mean size = 0.125 – 0.25 mm) and 3.1% as very coarse sand (mean size 1 – 2 mm).

Samples on transect 1 were all classified as medium sand. Samples on transect 5 fell into four grain size categories: namely, very coarse sand (1 sample), coarse sand (1 sample), medium sand (4 samples) and fine sand (2 samples). Transect 2 had two grain sizes (coarse, medium) and transect 4 had two grain sizes (fine, medium).

2.4.2.4 Sorting (standard deviation) and skewness

The degree of sorting for all samples varied widely with depth. Most samples were well sorted (standard deviation ranged between 0.35 - 0.5) or moderately well sorted (standard deviation ranged between 0.5 - 0.71) (Table 2.6). Eight samples were moderately sorted (standard deviation ranged between 0.71 - 1.0). A minority of samples were either poorly sorted (standard deviation ranged between 2.0 - 4.0) or very well sorted (standard deviation < 0.35).

Table 6. Grain size data and summary sedimentary statistics calculated from cumulative grain curves (after Folk & Ward 1957) for 32 grab samples collected from four transects in False Bay, South Africa.

Degree of Sorting	**Transect**			
	1	**2**	**4**	**5**
Poorly sorted	3	-	-	-
Moderately sorted	6	1	-	1
Moderately well sorted	1	1	4	3
Well sorted	-	5	2	3
Very well sorted	-	1	-	1
Mean grain size (mm)	0.4	0.5	0.4	0.5
Median grain size (mm)	0.3	0.4	0.4	0.3
Mean grain size (phi)	1.5	1.2	1.6	1.4
Median grain size (phi)	1.6	1.2	1.4	1.6

Most samples (32%) were strongly coarse skewed and 26% of samples were near symmetrical. A minority of samples were fine skewed (9%) or strongly fine skewed (12%); 20% of samples were coarse skewed.

2.4.3. CATAMI classification of seafloor substrates

Six different CATAMI seafloor types (**Table 1**) were detected as the primary cover for a CATAMI classification of 316 photographs (**Figure 9**). Fine sand (SUSF) and coarse sand (SUSC) were most common across all sites (67.4% and 13.6% respectively) (**Figure 9**). Most samples (88.9%) were unconsolidated seafloor (SUP, SUPBS, SUSC, SUSF) and 11.1% of samples were consolidated seafloor (SCC, SCR).

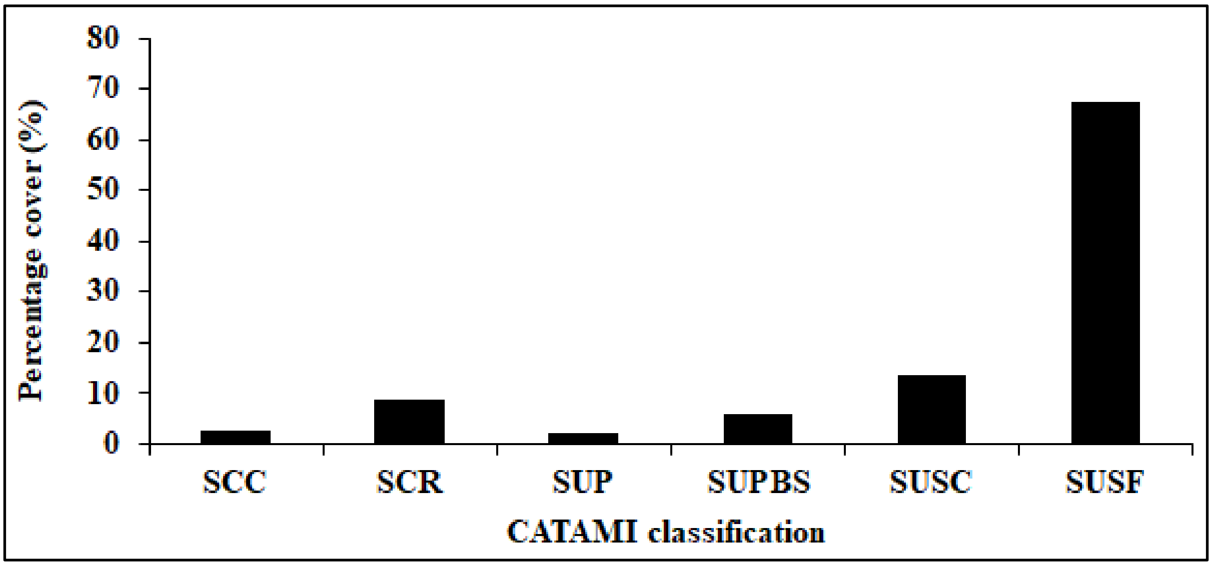


Figure 9. Percentage cover (%) of seafloor types classified according to the CATAMI classification scheme on eight transects in False Bay, South Africa. Seafloor types fell under the broad CATAMI categories consolidated (rock = SCC, SCR) and unconsolidated (sand = SUP, SUPBS, SUSC, SUSF).

Fine sand (SUSF) was the primary seafloor type for samples on seven out of the eight transects (**Table 7**). Only on transect 7 was biogenic screwshell material (SUPBS) the primary seafloor type (48%). Fine sand (SUSF) was the only seafloor type recorded on transect 6 (100%).

Table 7. Percentage cover (%) of seafloor types classified according to the CATAMI classification scheme on eight transects in False Bay, South Africa.

	CATAMI classification					
Transect	**SCC**	**SCR**	**SUP**	**SUPBS**	**SUSC**	**SUSF**
1	-	-	-	2	48	50
2	-	8	-	-	8	85
3	8	-	-	-	3	89
4	-	-	-	48	17	34
5	2	-	2	7	2	87
6	-	-	-	-	-	100
7	9	33	15	-	12	30
8	3	32	3	-	16	46

Transects 7 and 8 showed the most variation in seafloor classifications with five CATAMI seafloor types recorded each. Biogenic sediment (screwshells, SUPBS) was recorded at 51.4 m depth on average (**Table 8**).

Table 8. Summary depth (m) values for six CATAMI classification seafloor types from 316 samples on eight transects in False Bay, South Africa.

CATAMI	**Maximum**	**Minimum**	**Mean**	**Standard Deviation**	**Range**
SCC	57	16	37.1	12.4	41.0
SCR	46	10	28.8	8.8	35.8
SUP	51	27	38.1	7.9	23.3
SUPBS	64	42	51.4	6.2	21.9
SUSC	60	8	39.7	10.0	52.2
SUSF	84	14	46.8	17.3	70.4

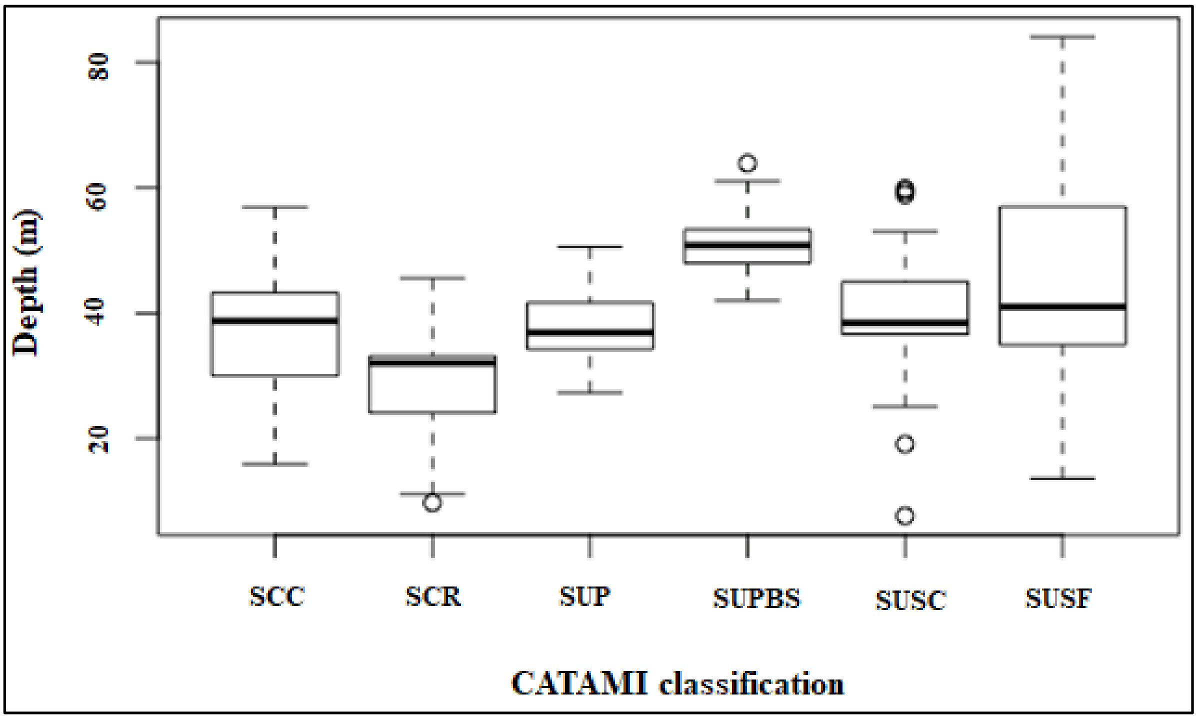


Figure 10. The distribution of depth (m) for six CATAMI classification seafloor types on eight transects in False Bay, South Africa. The central line represents the median depth (m). The lower and upper limits of the box represent the first and third quartiles, respectively. The lower and upper whiskers represent the minimum and maximum values. Outliers are represented by the symbol O.

The deepest sample (63.87 m) recorded as biogenic was considered an outlier (**Figure 10**). Fine sand (SUSF) was recorded at 47.0 m depth on average. Rock (SCR) was recorded at 29.0 m depth on average. The shallowest sample was recorded as coarse sand (SUSC) but was considered an outlier. Samples classified as fine sand (SUSF) covered the greatest range of depths (70.4 m) (**Figure 10**). Samples classified as fine sand (SUSF) were recorded at the greatest depth (84.0 m).

2.4.4. ARA classification of seafloor substrates

Eleven different ARA classifications were detected for 316 sites across eight transects (**Figure 11**). Classification ARA20 was most common across all sites (50%). Most samples were classified ARA12 (12%), ARA13 (10%) and ARA11 (8%). The few remaining samples were scattered across seven ARA classifications.

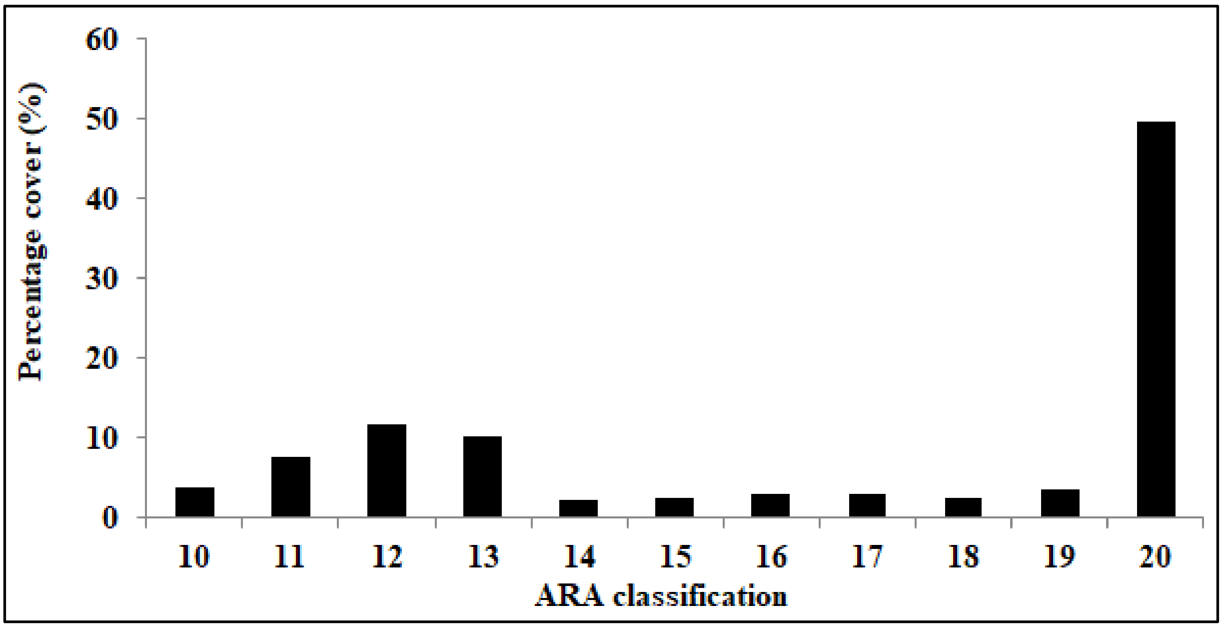


Figure 11. Percentage cover of seafloor substrate types classified according to the ARA classification scheme along eight transects in False Bay, South Africa.

ARA20 was the primary seafloor type for samples on 5 out of the 8 transects (**Table 9**). Most samples on transect 3 (86.5%) were ARA20. On transect 4 ARA20 was the primary seafloor type (27.6%). Most samples on transect 6 were ARA13 (41.7%). Transects 5 and 6 showed the most variation in seafloor classifications with 11 ARA seafloor types recorded each. Transect 3 showed the least variation in seafloor classifications with 3 ARA seafloor types recorded.

Table 9. Percentage cover (%) of seafloor types classified according to ARA classification on eight transects in False Bay, South Africa.

	ARA classification										
Transect	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
1	-	-	6.5	2.2	4.4	4.4	6.5	2.2	2.2	4.4	67.4
2	-	-	1.9	1.9	1.9	1.9	-	5.8	3.9	5.8	76.9
3	-	2.7	10.8	-	-	-	-	-	-	-	86.5
4	27.6	20.7	-	3.5	-	3.5	3.5	10.3	3.5	6.9	20.7
5	6.5	8.7	6.5	4.4	2.1	4.4	4.4	4.4	2.2	4.4	52.2
6	2.8	11.1	11.1	41.7	2.8	5.6	2.8	2.8	2.8	5.6	11.1
7	-	18.2	33.3	18.2	3.0	-	9.1	-	6.1	-	12.1
8	-	8.1	29.7	16.2	2.7	-	-	-	-	-	43.2

ARA classifications were spread across samples at a variety of depths (**Figure 12**). The deepest sample (84 m) was classified ARA17 (**Table 10**). Five other samples were similarly deep, but all classified with a different ARA classification. The most common classification across samples (ARA20) was recorded across a wide range of depths (63.2 m) where the deepest samples were considered outliers. Samples classified as ARA10 were found across the smallest depth range (20.0 m).

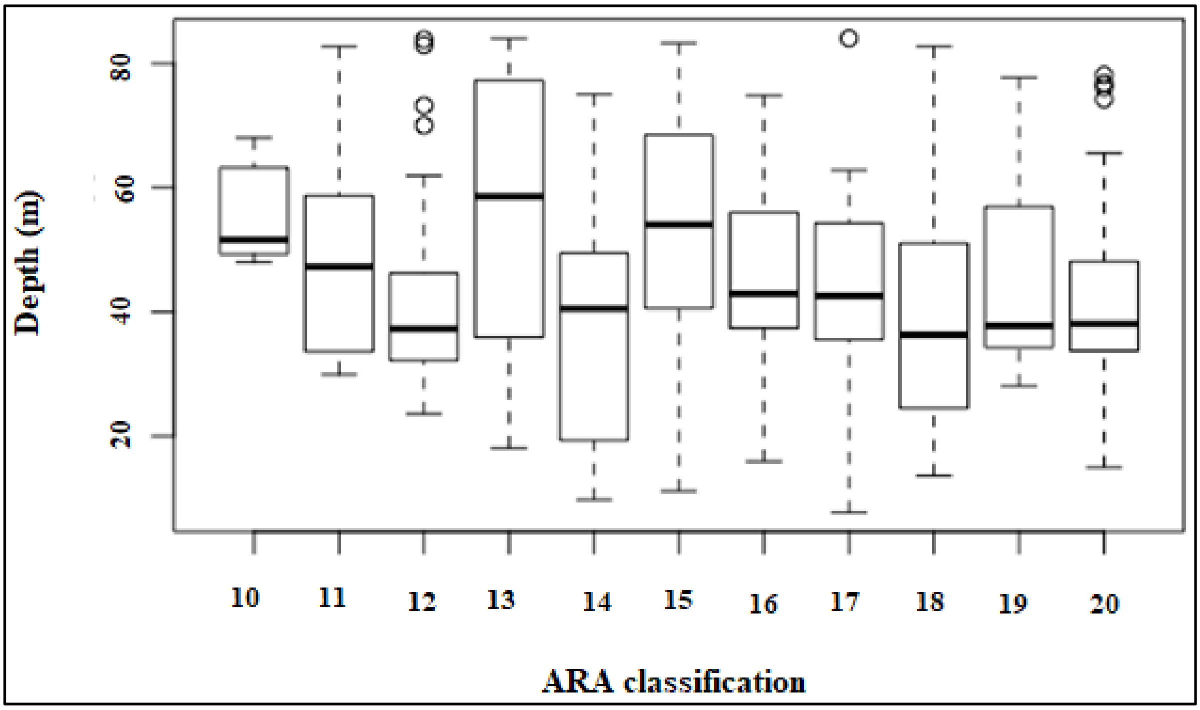


Figure 12. The distribution of depth (m) for 11 ARA classification seafloor types on eight transects in False Bay, South Africa. The central line represents the median depth (m). The lower and upper limits of the box represent the first and third quartiles, respectively. The lower and upper whiskers represent the minimum and maximum values. Outliers are represented by the symbol O.

Table 10. Summary depth (m) values for 11 ARA classification seafloor types from 316 samples on eight transects in False Bay, South Africa.

ARA	Maximum	Minimum	Mean	Standard Deviation	Range
10	68	48	55.0	7.4	20.0
11	83	30	48.8	14.9	52.8
12	84	24	42.3	15.8	60.2
13	84	18	55.7	22.3	66.0
14	75	10	37.5	23.1	65.3
15	83	11	52.6	22.8	72.1
16	75	16	44.8	17.0	58.9
17	84	8	44.3	21.2	76.4
18	83	14	40.0	22.7	69.1
19	78	28	47.2	18.2	49.7
20	78	15	40.5	11.9	63.2

2.4.5. Grain size comparison with CATAMI and ARA classifications

2.4.5.1. Grain size versus CATAMI

The CATAMI classification of 32 jump camera photographic samples from transects 1, 2, 4 and 5 resulted in five different seafloor classifications (SCR, SUP, SUPBS, SUSC, SUSF). The grain size analysis of 32 grab samples of sediment collected at the same location as the photographic (CATAMI) samples resulted in four different Wentworth (1922) grain size classifications. Most grab samples (75%) were medium sand (0.25 – 0.50 mm) (**Table 11**). Most photographic (CATAMI) samples (29%) were fine sand (SUSF, < 2 mm with no visible shell fragments). The remaining CATAMI samples were primarily (25%) coarse sand (SUSC, < 2 mm with visible shell fragments) and biogenic screwshell material (13%) (SUPBS, pebble/gravel: biogenic [screwshells]).

A direct comparison shows that most grab samples were classified as medium sand and most photographic samples were classified according to three CATAMI unconsolidated seafloor types (SUSF, SUSC and SUPBS). Where grain size analysis was classified as medium sand, the majority of CATAMI samples were classified as either SUSF or SUSC (56%). One instance of rock (SCR) corresponds with a grain size classification of coarse sand and two instances of rock correspond with a grain size classification of medium sand. Two samples classified as SUSC corresponded with a grain size of coarse sand and very coarse sand, respectively.

Table 11. Comparison of grain size classification (Wentworth 1922) and CATAMI (Althaus et al. 2013) classifications of 32 samples taken at the same location along four transects in False Bay, South Africa.

	CATAMI classification				
Grain size	**SCR**	**SUP**	**SUPBS**	**SUSC**	**SUSF**
Coarse sand	1	2	-	1	-
Fine sand	-	-	-	-	3
Medium sand	2	-	4	8	10
Very coarse sand	-	-	-	1	-

One grain size and two CATAMI classifications were detected on transect 1. The grain size classification of all samples on transect 1 was medium sand. The CATAMI classification of samples on transect 1 was 80% coarse sand (SUSC) and 20% fine sand (SUSF).

Two grain sizes and four CATAMI classifications were detected on transect 2. The grain size classification of samples on transect 2 was 62% medium sand and 38% coarse sand. The CATAMI classification of samples on transect 2 was 37.5% rock (SCR), 12.5% pebble/gravel (SUP), 12.5% coarse sand (SUSC) and 37.5% fine sand (SUSF).

Two grain sizes and two CATAMI classifications were detected on transect 4. The grain size classification on transect 4 was 83% medium sand and 17% coarse sand. The CATAMI classification of samples on transect 4 was 50% coarse sand (SUSC) and 50% fine sand (SUSF).

Four grain sizes and four CATAMI classifications were detected on transect 5. The grain size classification on transect 5 was 50% medium sand, 25% fine sand, 12.5% coarse sand and 12.5% very coarse sand. The CATAMI classification of samples on transect 4 was 62.5% fine sand (SUSF), 12.0% pebble/gravel (SUP), 12.5% biogenic (SUPBS) and 12.5% coarse sand (SUSC).

2.4.5.2. Grain size versus ARA

The ARA classification of 32 multibeam sonar samples from transects 1, 2, 4 and 5 resulted in eight different seafloor classifications (11, 14, 15, 16, 17, 18, 19, 20). The grain size analysis of 32 grab samples of sediment collected at the same location as the multibeam sonar (ARA) samples resulted in four different Wentworth (1922) grain size classifications. Most grab samples (75%) were medium sand (0.25 – 0.50 mm) (Table 2.12). Most multibeam sonar (ARA) samples (50%) were classified as ARA20.

A direct comparison shows that where most grab samples were classified as medium sand, the majority of multibeam sonar samples were classified according to one predominant ARA classification (ARA20) (**Table 12**). Where grain size analysis classified medium sand, most ARA samples were also classified ARA20 (44%). The remaining samples were scattered widely among ARA classifications and grain sizes.

Table 12. Comparison of grain size classification (after Wentworth 1922) and Angle Range Analysis (ARA) classifications for 32 samples taken at the same location along four transects in False Bay, South Africa.

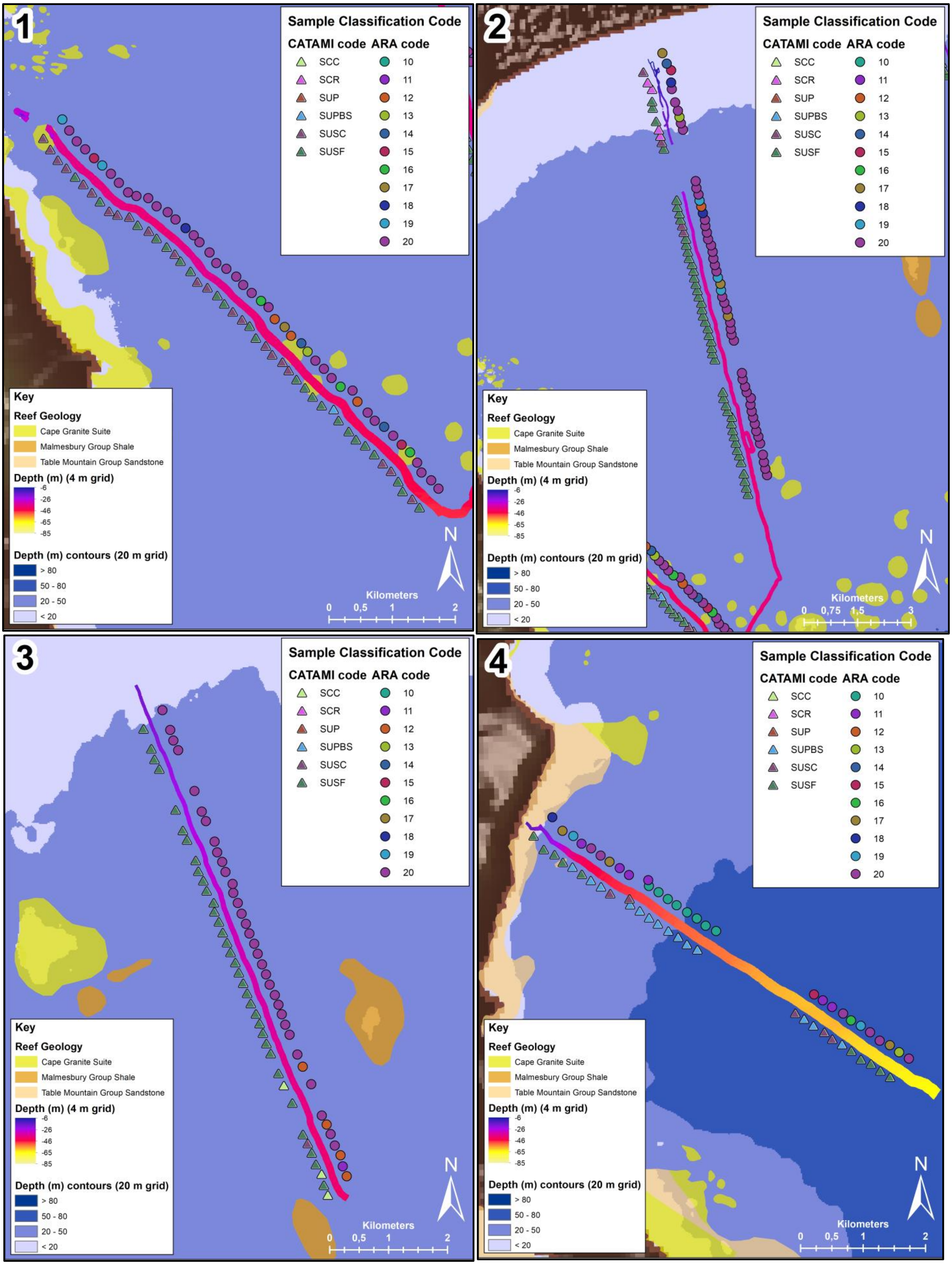
	ARA classification							
Grain size	**ARA11**	**ARA14**	**ARA15**	**ARA16**	**ARA17**	**ARA18**	**ARA19**	**ARA20**
Coarse sand	1	-	1	-	1	-	1	-
Fine sand	-	-	-	1	-	-		2
Medium sand	2	1	1	-	1	1	4	14
Very coarse sand	1	-	-	-	-	-	-	-

2.4.6. Characterising the seafloor of False Bay according to CATAMI and ARA classification

2.4.6.1. Comparison of CATAMI and ARA classifications

There were more ARA classifications assigned to samples on all transects than CATAMI classifications (**Figure 13**). Samples on transect 1 were assigned to three CATAMI and nine ARA classifications. Samples on transect 2 were assigned to three CATAMI and eight ARA classifications. The two classification methods represent equal variability in seafloor types for samples on transects 3 and 8 (**Figure 13**). Samples on transect 3 were assigned to three CATAMI and three ARA classifications. Samples on transect 8 were assigned to five CATAMI and five ARA classifications. The difference in the number of classifications assigned by both methods was highest for samples on transects 5 and 6. Samples on transect 5 were assigned to five CATAMI and 11 ARA classifications. Samples on transect 6 were assigned to one CATAMI and 11 ARA classifications. Samples on transect 7 were assigned to five CATAMI and seven ARA classifications.

Transects 2, 3 and 8 show that where the CATAMI classification changed, the ARA classification typically changed too (**Figure 13**). In many instances, the changes were on a simple interruption of continuity of SUSF and SUSC.


1
Sample Classification Code
CATAMI code
ARA code
SCC
SCR
SUP
SUPBS
SUSC
SUSF
10
11
12
13
14
15
16
17
18
19
20
Key
Reef Geology
Cape Granite Suite
Malmesbury Group Shale
Table Mountain Group Sandstone
Depth (m) (4 m grid)
-6
-26
-46
-65
-85
Depth (m) contours (20 m grid)
> 80
50 - 80
20 - 50
< 20
N
Kilometers
0
0,5
1
2
2
Sample Classification Code
CATAMI code
ARA code
SCC
SCR
SUP
SUPBS
SUSC
SUSF
10
11
12
13
14
15
16
17
18
19
20
Key
Reef Geology
Cape Granite Suite
Malmesbury Group Shale
Table Mountain Group Sandstone
Depth (m) (4 m grid)
-6
-26
-46
-65
-85
Depth (m) contours (20 m grid)
> 80
50 - 80
20 - 50
< 20
N
Kilometers
0
0,75
1,5
3
3
Sample Classification Code
CATAMI code
ARA code
SCC
SCR
SUP
SUPBS
SUSC
SUSF
10
11
12
13
14
15
16
17
18
19
20
Key
Reef Geology
Cape Granite Suite
Malmesbury Group Shale
Table Mountain Group Sandstone
Depth (m) (4 m grid)
-6
-26
-46
-65
-85
Depth (m) contours (20 m grid)
> 80
50 - 80
20 - 50
< 20
N
Kilometers
0
0,5
1
2
4
Sample Classification Code
CATAMI code
ARA code
SCC
SCR
SUP
SUPBS
SUSC
SUSF
10
11
12
13
14
15
16
17
18
19
20
Key
Reef Geology
Cape Granite Suite
Malmesbury Group Shale
Table Mountain Group Sandstone
Depth (m) (4 m grid)
-6
-26
-46
-65
-85
Depth (m) contours (20 m grid)
> 80
50 - 80
20 - 50
< 20
N
Kilometers
0
0,5
1
2

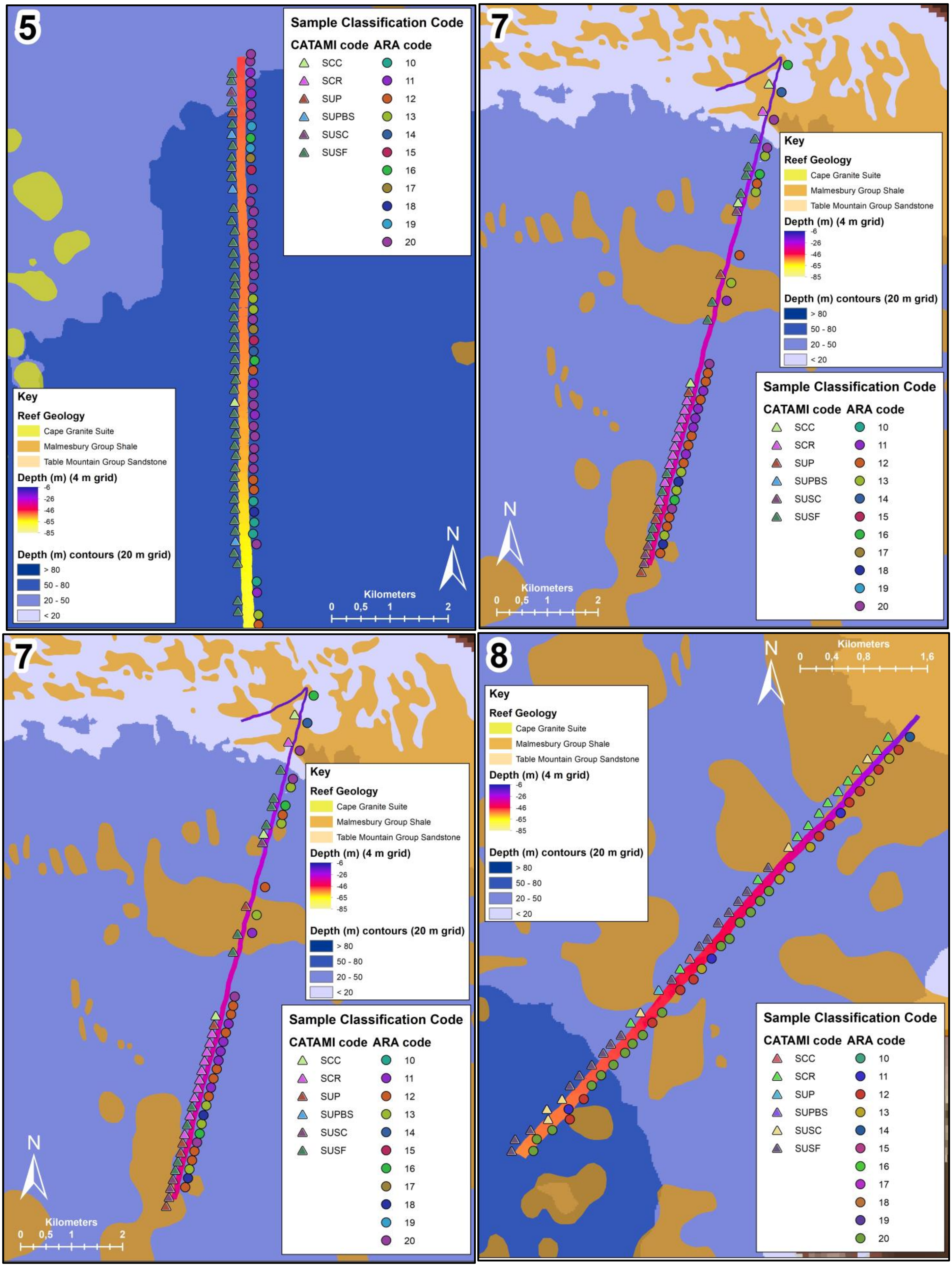


Figure 13. CATAMI and ARA classification of 316 samples on eight transects in False Bay, South Africa. Each panel shows the transect number (1 – 8), and high-resolution depth (m) collected using multibeam sonar (gridded at 4 m) runs along each transect. All transects are shown in the context of subtidal reef geology (Van Zyl 2011) and depth (m) gridded at 20 m and visualised in contours (Van Zyl 2011).

2.4.6.2. CATAMI classification by depth

Samples on transect 1 alternated between fine sand (SUSF) and coarse (SUSC) with no clear trend with depth (**Figure 13**). Samples on transect 2 showed variation in CATAMI classification in shallow water (**Figure 13**). Coarse sand (SUSC) was recorded up to 29 m depth. Rock was recorded up to 18 m depth. All samples deeper than 29 m were uniformly fine sand (SUSF). Samples on transect 3 showed variation in CATAMI classification in deeper water (**Figure 13**). All samples from 20 m depth to 36 m depth were uniformly fine sand (SUSF). Cobble (SCC) samples were recorded between 37 m and 41 m. Samples are variable in CATAMI classification on transect 4. The transect is predominantly biogenic (SUPBS) recorded from 42 m depth (**Figure 13**). The remaining majority of samples were fine sand (SUSF) recorded from 20 m. Depth dropped sharply from 29 m to 37 m on transect 4, after which the remainder of samples were between 42 m and 64 m depth, classified as coarse sand (SUSC), biogenic (SUPBS) and fine sand (SUSF).

Samples on transect 5 were almost uniformly fine sand (SUSF) from 49 m to 66 m depth (**Figure 13**). Samples on transect 6 were uniformly fine sand (SUSF) from 68 m to 84 m depth (**Figure 13**). Samples on transect 7 showed variation in CATAMI classification with no clear trend with depth, except where rock (SCR) was recorded along the transect where depth was uniform and varied little with distance (all nine samples were 33 m deep). Samples on transect 8 showed some pattern with depth. Rock (SCR) was predominantly recorded for samples between 22 m and 33 m depth (**Figure 13**). Most samples between 38 m and 54 m depth were fine sand (SUSF).

2.4.6.3. Classification by depth and ARA

Samples on transect 1 were predominantly classified as ARA20 from 33 m to 46 m depth (**Figure 13**). There was some variation in classification and samples classified as ARA10 were only recorded between 33 m and 39 m depth. Samples classified as ARA12 were only recorded from 40 m depth. Samples on transect 2 were almost uniformly classified as ARA20 from 15 m to 39 m (**Figure 13**). Five ARA classification types were recorded between 8 m and 18 m. Samples on transect 3 were uniformly classified as ARA20 from 20 m to 36 m depth (**Figure 13**). Between 37 m and 41 m, three ARA classification types were recorded. Samples on transect 4 showed no clear pattern with depth, except where samples were classified as ARA10 between 48 m and 52 m depth (**Figure 13**). Samples on transect 5 showed no clear pattern with depth, except that samples classified as ARA20 were predominant on this transect and were recorded at all depths between 49 m to 68 m (**Figure 13**).

Samples classified on transect 6 showed no pattern with depth (**Figure 13**). Eleven ARA classification types were distributed widely between 68 m and 84 m depth. Samples classified on transect 7 corresponded to seven ARA classification types that were distributed widely between 16 m and 36 m depth (**Figure 13**). Samples classified as ARA12 on transect 8 were distributed widely between 24 m and 53 m depth (**Figure 13**). Samples classified as ARA20 were recorded from 40 m to 54 m depth.

2.6.3.4. CATAMI classifications across all transects

Transects where samples were classified almost uniformly as fine sand (SUSF) were recorded in the shallow north of False Bay (transect 2 and transect 3) (**Figure 13).** Samples were recorded at an average depth of 30.9 m and 32.0 m on transect 2 and transect 3 respectively (**Table 5**). Samples were also classified almost uniformly as fine sand (SUSF) on transects in the deep, middle reaches of False Bay (transect 5 and transect 6) (**Figure 13**). Samples were recorded at an average depth of 55.4 m and 76.8 m on transect 5 and transect 6 respectively (**Table 5**).

Transect 4 and transect 7 (on the far western and eastern margins of False Bay respectively) recorded the highest heterogeneity of seafloor types (**Figure 13**). Transect 4 also showed the highest range of depths (44.2 m) with a steep drop over a short distance (< 200 m) from 29 m to 37 m depth. Transects 1 and 8 recorded some heterogeneity of seafloor types on the western (33 m – 46 m depth) and eastern (22 m – 54 m depth) margins of the bay respectively (**Figure 13**).

2.4.6.5. ARA classifications across all transects

Transects where samples were classified almost uniformly as ARA20 were recorded in the shallow north of False Bay (transect 2 and transect 3) (**Figure 13**). Samples were mostly classified as ARA20 in the deeper, middle reaches of False Bay (transect 5). Samples on transect 6 showed heterogeneity in seafloor types where 11 ARA classification types were recorded (**Figure 13**). One seafloor type (ARA13) predominated on transect 6 (42%).

The ARA results were similar to CATAMI classification results for transect 4 and transect 7 and transect 1 and transect 8. The western and eastern margins of False Bay showed more heterogeneity in the number of ARA classifications across samples than the northern and central reaches of the bay (**Figure 13**).

2.4.7. Principal components analysis (PCA) of samples

Fifty-six percent of the variation was explained by PC1 (**Figure 14**). In PC1, the Eigenvectors slope (-0.660) and roughness (-0.658) were more related to the variation than depth (0.363). Thirty percent of the variation was explained by PC2. In PC2, depth (-0.932) is more related to the variation than slope (-0.248) and roughness (-0.266). Slope, roughness, and depth cumulatively account for 86% of the variation in the data.

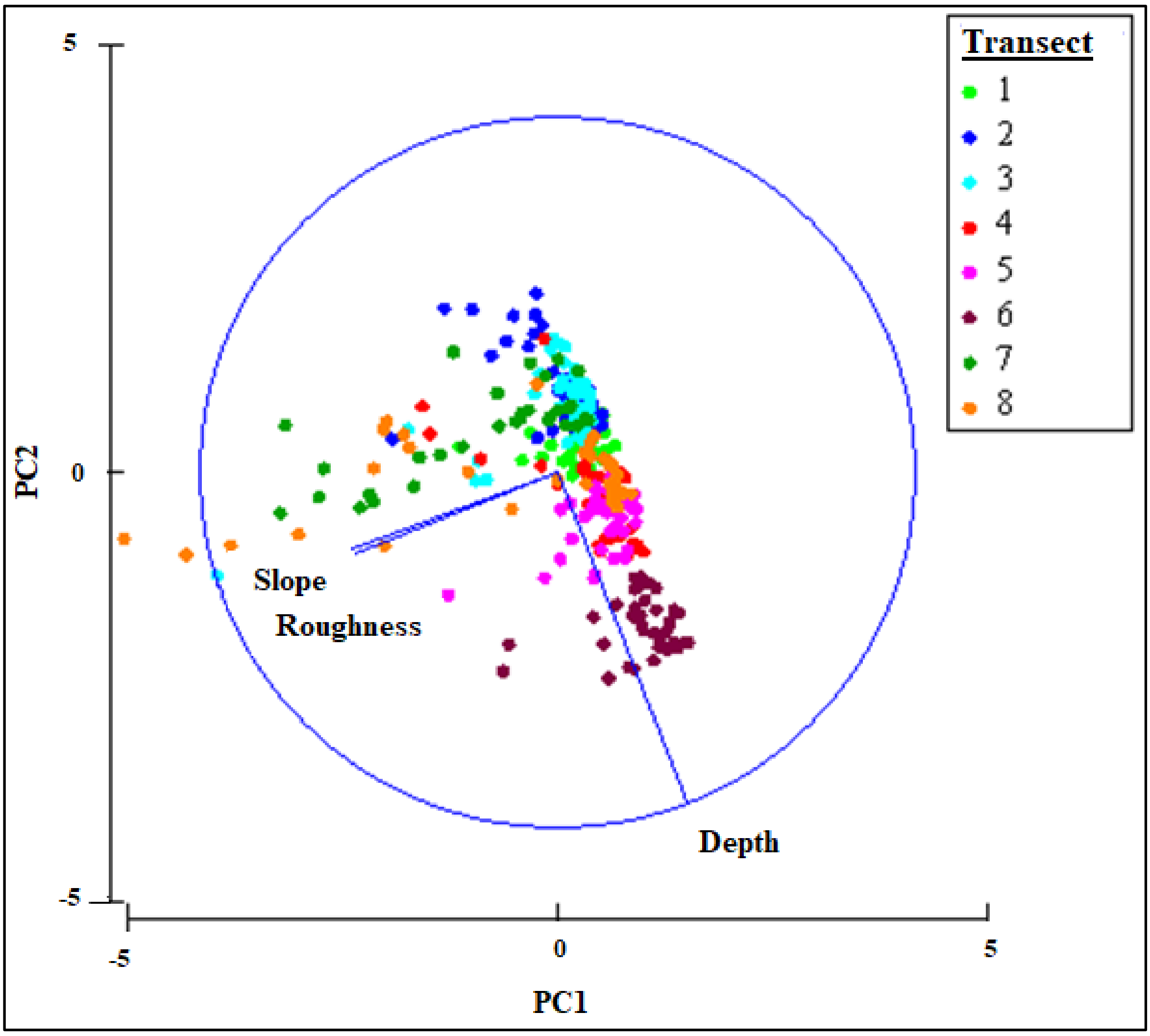


Figure 14. Principal components analysis (PCA) of 316 samples across eight transects with variables depth (m), roughness and slope according to the factor transect. Eigenvalues: PCA1 = 1.68, PCA2 = 0.897, PCA3 = 0.424.

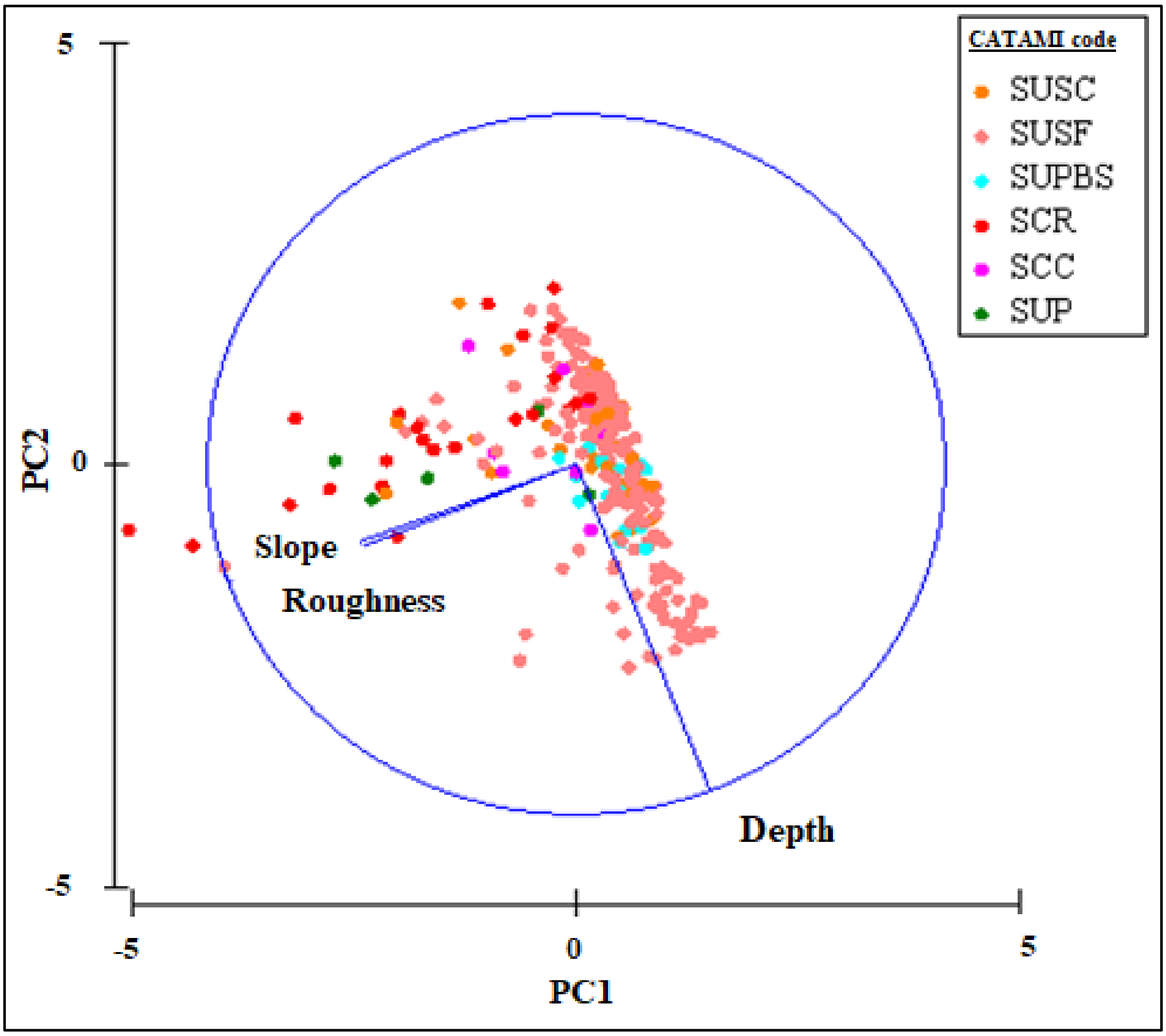


Figure 15. Principal components analysis (PCA) of 316 samples across eight transects with variables depth (m), roughness and slope according to the factor CATAMI classification. Eigenvalues: PCA1 = 1.68, PCA2 = 0.897, PCA3 = 0.424.

The variables roughness and slope were not correlated with depth (**Figure 15**). Their influences were orthogonal: there was variation in seafloor topography across the full range of sampled depths. Samples on transect 7 and transect 8 showed the highest variation in roughness and slope values, and the highest roughness and slope values. There was some variation in roughness and slope on transects 3, 5 and 6. Transects were grouped according to depth. Samples on transect 5 and 6 were deeper than most samples on all other transects. Samples on transect 2 were the shallowest of all samples.

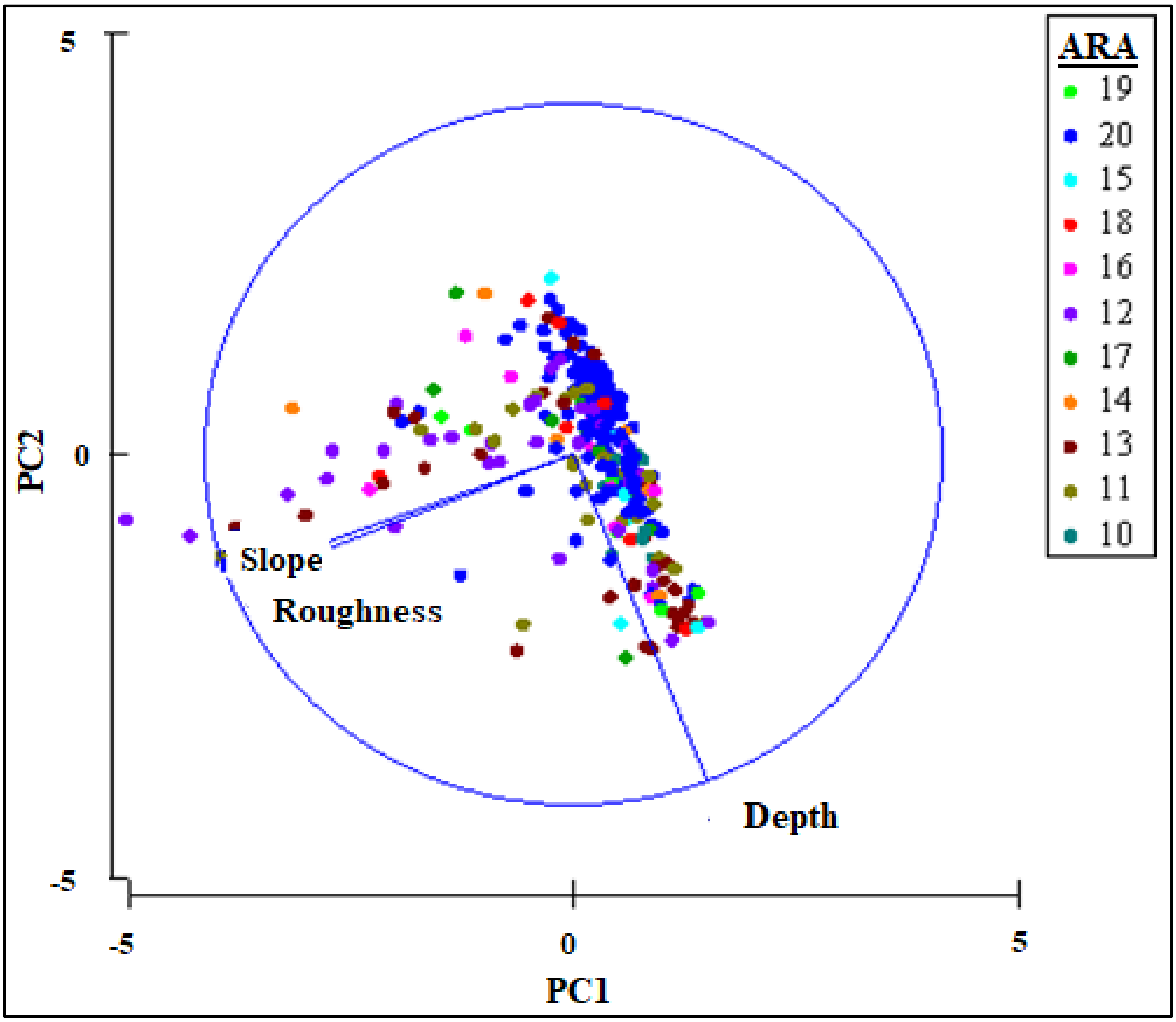


Figure 16. Principal components analysis (PCA) of 316 samples across eight transects with variables depth (m), roughness and slope according to the factor ARA classification. Eigenvalues: PCA1 = 1.68, PCA2 = 0.897, PCA3 = 0.424.

The highest slope and roughness values were on samples classified at SCR (**Figure 16**). Samples classified as rock (SCR), cobbles (SCC) and coarse sand (SUSC) varied the most in roughness and slope values. Most of the consolidated seafloor types (SCR, SCC) were found at shallower depths. Samples classified as fine sand (SUSF) showed no correlation with depth, distributed across a range of sampled depth values. The deepest samples were all classified as fine sand (SUSF).

ARA12 shows the greatest range of slope and roughness values and shows some of the highest slope and roughness values (**Figure 16**). ARA20 was found across a wide range of depths and had low slope and roughness values. Some of the deepest samples were classified ARA13. Most samples had low roughness and slope values.

2.5. DISCUSSION

2.5.1. A synthesis of depth, geology, and sediment cover patterns in False Bay

Multibeam bathymetry along the transects in this study detected a maximum depth of 84 m on transect 6 at the mouth of False Bay. The addition of multibeam bathymetry data gridded to 4 by 4 m improves the resolution of the naval data interpolation (Van Zyl 2011) along this study's transects. Patterns in this study were similar to previous surveys, with the lowest slopes on transects 2, 3, 5 and 6 in the north and centre of the bay. Mallory (1970) showed that depth changed gradually in the northern and central bay, with a gradient of 1 in 400 on a bathymetric map where depth contours are spaced at 9 m intervals. A sharp drop off on transect 4 in the south-western in the Paulsberg no-take zone of the TMNP MPA is the continuation of the peninsula mountain slope. The slope was greatest along the western and eastern margins close to Cape Point and Cape Hangklip. The portion of the bay in the depth range of 20 – 50 m was greater than other depth intervals (Van Zyl 2011).

The calculation of seafloor substrate cover from data provided by Van Zyl (2011) showed that False Bay comprises predominantly unconsolidated sediment (83% sand), except where rocky reef is evident at the seafloor surface (17%). This finding matches patterns from previous surveys (Morgans 1962; Bowie et al. 1970; Mallory 1970; Simpson et al. 1970; Du Plessis & Glass 1991). Malmesbury Group shale (14%) dominated the eastern half of False Bay (from Van Zyl 2011). Samples from transects 7 and 8, in north-eastern and south-eastern False Bay, showed the most variation in roughness and slope calculated from bathymetry data. These match findings from echosounder bathymetric profiles that seafloor roughness increases in the eastern half of the bay (Simpson et al. 1970). Cape Granite Suite (2%) in the west was visible as un-weathered tors in the form of Whittle Rock, Roman Rock and Seal Island (Simpson et al. 1970; Du Plessis & Glass 1991). Table Mountain Group sandstone only constituted 1% of the bay and was apparent in the west against the coastline and near Cape Hangklip in the south-east.

2.5.2. Can measures derived from bathymetry be used for future investigation of biodiversity patterns?

Lack of correlation between roughness and depth, and between slope and depth, presents these variables as suitable joint independent variables in predicting biological patterns. All three variables have been collected in other surveys (Wedding & Friedlander 2008; Foster et al. 2009), but slope and roughness were correlated with each other in False Bay, and it may be possible to use just one of these variables to analyse biodiversity data. Roughness is a measure of the texture or rugosity of the seafloor, indicating its complexity (Jenness 2003; Jenness 2004; Wright & Heyman 2008). Seafloor complexity has been shown to predict differences in benthic communities (Buhl-Mortensen et al. 2012). Seafloor roughness may indicate sediment mobility, which influences the composition of benthic communities (Post 2008). Wave action and currents influence the movement of sediment in False Bay (De F. Retief 1970), as does the dispersion of sediment near the Eerste and Lourens river mouths (Bowie et al. 1970). Whether variation in seafloor roughness at this scale is relevant to biological communities has not been tested in False Bay.

Slope is a measure of the topography and profile of the seafloor (Wright & Heyman 2008). The slope of a site will influence its exposure to currents or the influx of water, which is another influence on the composition of benthic communities (Post 2008). Most samples in this study had low roughness and slope values, matching the characterisation of False Bay as a largely sand-covered seafloor with medium to fine-grained sand and with gradual depth variation from north to south (Mallory 1970; Bowie et al. 1970; Du Plessis & Glass 1991). Depth is an important variable to include on its own to assess biodiversity patterns. This result matches conclusions from surveys by Morgans (1962), and to a lesser extent, by Field (1970, 1971).

Roughness and slope varied most along transects 7 and 8, where samples were classified as SCR (reef) using CATAMI and as ARA12. The CATAMI classification SCR and the ARA classification ARA12 both related to the highest roughness and slope values in this study. The samples classified as SUSF (fine sand) using CATAMI showed the same patterns in the principal components analysis as ARA20. This broad delineation of reef and sand habitat appears to have been detected in both CATAMI and ARA classification, with ARA12 possibly representing reef and ARA20 possibly representing sand. This result gives more confidence to the interpretation that ARA12 represents rocky reef and reflects findings elsewhere that ARA distinguishes between consolidated and unconsolidated seafloor (Kloser et al. 2010). Ground-truthed samples on these transects at the same locations where multibeam data have now been collected could form the basis of future tests to assess the accuracy of these linkages. It is reasonable to use the results of this study as a basis to test this same broad delineation first, using samples classified as ARA12 and ARA20 to distinguish reef and sand (Kloser et al. 2010).

2.5.3. False Bay described by CATAMI classification versus previous surveys

Results from this study not only detected patterns described at the scale of the bay, but also reflected the character of the seafloor according to different “grounds” and “terrains” described across different surveys (Morgans 1962; Du Plessis & Glass 1991). An 89% majority of samples across all transects were assigned to unconsolidated sediment using CATAMI, close to the 83% calculated from interpolated data (Van Zyl 2011). This result indicates two things: firstly, the sampling design covers a suitable representation of the habitats of False Bay. Secondly, the CATAMI classification method recorded habitat variation that reflected patterns at the scale of the bay’s extent.

The seafloor in the northern and central regions of False Bay was homogenous with a gradual depth gradient. At its deepest at the mouth of the bay, the seafloor was fine sand (SUSF) less than 2 mm in grain size with no visible shell fragments. The seafloor on the eastern and western margins of the bay was heterogeneous. This was particularly apparent in the east, from Macassar beach southwards, and in the region of Kogelbaai. Here, rock (SCR) and cobble (SCC) seafloor comprising visible Malmesbury Group shale reef was interspersed with sand. This region ranged in roughness and slope values, where the rock and cobble seafloor varied in its rugosity and profile over a gentle depth gradient. The south-western margin of False Bay had a unique habitat in the form of biogenic screwshells (SUPBS) at depths below 42 m.

These findings match descriptions of a smooth, gently sloping seafloor for much of the bay, except where rugged rocky reef emerges on the margins in the west and east (Morgans 1962; Mallory 1970; Du Plessis & Glass 1991). Transect 4 in this study was characterised by a predominantly sand and biogenic screwshell seafloor with relatively low roughness and slope values. There was some variation in roughness and slope values, but not nearly as much as transects 7 and 8 in the east. A sharp drop in depth on transect 4 mirrored the steeply sloping but smooth seafloor of "physiographic terrain" number 10 as described by Du Plessis and Glass (1991). Transect 1, 2 and 3 coincide with "physiographic terrain" number 11 as described by Du Plessis and Glass (1991). The seafloor is almost uniformly sand; in this study, classified as fine (SUSF) and coarse (SUSC) sand less than 2 mm in grain size. This classification covers the full range of grain size described for these regions by Bowie et al. (1970) because the CATAMI classification scheme distinguishes sand at a coarser resolution than grab sampling. Transects 2 and 3 intersect "physiographic terrain" number 9 described by Du Plessis and Glass (1991), where the seafloor is generally sand, but some rocky patches are detected in waters shallower than 30 m. In this study, rock was classified on transect 2 in waters between 10 m and 18 m depth.

Classification using CATAMI introduced new descriptions of biogenic screwshell material south of Smitswinkel Bay and detected variation in unconsolidated sediment that would otherwise have been grouped as "sand". Where geological surveys distinguish rock from sand, and rock type (Cape Granite Suite, Malmesbury Group shale and Table Mountain Group sandstone), the CATAMI classification incorporates measures beyond physical seafloor descriptions a modifiers: biogenic material, veneer, kelp beds and other descriptors that are useful to broaden a purely descriptive seafloor survey into an ongoing baseline for benthic habitat classification, threat status analysis and ecosystem threat assessments (Levin et al. 2009; SANBI & UNEP-WCMC 2016). Arkema et al. (2006) highlight the need for operational tools to implement ecosystem-based management, translating theory into practice: the CATAMI classification represents a compromise between fine-scale interrogation of the physical environment and a relatively simpler method to deploy and interpret for biodiversity management.

2.5.4. CATAMI versus grain size from grab samples

A direct comparison of samples collected at the same location using two different methods (grab and photographs) recorded 4 different grain sizes and 5 different CATAMI seafloor types, respectively. The two methods of sampling differ in their intrinsic resolution and extent of detection. It is therefore important to first discuss what exactly each method is sampling. Grab samples are very specific in what portion of the seafloor they assess. Grain size classification results only deal with unconsolidated sediment captured by the grab's "bite". Sediment samples are then processed by sieving, and by the time we consider the grain size classification according to Wentworth (1922), it is only the sand component of the entire grab sample that is discussed.

By contrast, the CATAMI classification of the jump camera photographs considers all visible seafloor habitats and would include visible rock, and larger-grained sediment (cobbles, pebbles, shell) together with sand. The Van Veen grab obtains a subsurface sample, digging into the sediment and recording a shallow sample of the nature of the seafloor beyond its surface appearance. The photographs consider only the seafloor surface that is visible to the assessor's eye. The Van Veen grab samples a relatively small area of 0.025 m^2, whereas the camera captures 0.3 m^2.

It is therefore not useful to compare the number of grain sizes classified according to Wentworth with the number of CATAMI seafloor types classified for the same samples; we are in fact not comparing like with like. The majority of False Bay is classified as medium sand (Bowie et al. 1970). The same pattern was detected in this study from both grab samples and CATAMI classification. We can then directly compare those grab samples classified as medium (0.25 – 0.55 mm) sand (24 samples) with the CATAMI classification for those same samples. Seventy-five percent of these samples were classified as fine and coarse sand (SUSF and SUSC). The titles assigned to these classifications are misleading when compared to Wentworth's geological terminology; both CATAMI classifications describe sand that is less than 2 mm grain size. This very broadly covers the threshold for medium sand according to the Wentworth scale (0.25 mm – 0.50 mm). Indeed, it covers all grain sizes up to 2 mm, which are effectively all 5 grain sizes detected by Morgans (1962) and Bowie et al. (1970). Both methods are effectively detecting the same habitat; it is their resolution that differs. The difference in grain size at the scale of mm would be impossible to detect visually on a photograph. Therefore, CATAMI identifies sand, with or without visible shell fragments, where grab samples distinguish fine-scale differences in grain size within those CATAMI groupings.

A small proportion (13%) of those same samples classified as medium sand according to Wentworth (1922) was classified as biogenic shell material using CATAMI. A likely explanation for this is that some of the sample is often lost at various stages of sampling and processing, altering slightly the grab sample that goes to grain size classification – a sampling issue that is raised by Field (1970, 1971) as a shortcoming in some of the False Bay samples, where contextual habitat information that would be applicable to biological surveys may be missed. Often, fine sediment is lost during grab sampling, and pre-treatment of samples before sieving and processing by settling tube can alter the natural aggregation of particles (Morgans & Day 1959; Bowie et al. 1970). Biogenic shell material would have been sieved out by the time samples were processed in the settling tube and assigned to the percentage of gravel sediment for those samples. The presence of shell fragments that would be visible on a photograph would not be present in the sediment processed in the settling tube and classified according to Wentworth (1922). CATAMI detects the nature of the seafloor at its visible surface and the grab samples reflect a vertical profile (the screwshell cover of the seafloor is shallow).

The most useful way to detect heterogeneity in unconsolidated sediment is by means of grab samples to assess grain size. The CATAMI classification does not detect variation on sand at a scale as fine as grain size from grab samples, which is an anticipated limitation of photograph sampling (Jørgensen & Gulliksen 2001). The method does not improve on fine-scale sediment surveys because its groupings SUSF and SUSC are broad, but where this has been ground-truthed using grain size analysis, these two categories can be revised and modified where higher resolution is required. Grab sampling is necessary for fine-scale sediment data; this would be important for studies on the infauna where particle size is likely important (Field 1971). However, the broad-scale landscape description with visible seafloor characteristics from CATAMI may be sufficient for epibenthic megafauna communities (Sahade et al. 2004) and for fish populations (Moore et al. 2011; Gilby et al. 2016). Where benthic communities are too variable relative to the fine-scale descriptions of particle size, it may be more important to use CATAMI as a means to integrate seafloor characteristics so that habitats and communities are useful to interpret and delineate for management, zonation and assessment (Hewitt et al. 2004). For surveys where broad habitats need to be differentiated and logistics are constrained, a photographic method such as the jump camera is a viable consideration (Sahade et al. 2004).

2.5.5. False Bay described by ARA versus previous surveys

The seafloor in the northern section of False Bay is largely homogenous as detailed by the ARA classification. The region south of Roman Rocks and Simon’s Bay (transect 1) was predominantly one ARA classification type (ARA20, 67%), a finding that mirrors the most uniform “physiographic terrain” number 11 detailed by Du Plessis and Glass (1990). Results from grain size analysis also showed the region along this transect to be predominantly medium sand (Bowie et al. 1970). That the ARA classification results in 11 seafloor types for this same region, albeit with most of these occurring at very low levels, indicates two possibilities. Firstly, the method would do better to group descriptions according to the actual sampled sediment recorded (ground-truthed). That is, several description categories on the coarse end of the scale (ARA10 – ARA13) could be lumped to reflect coarse sand (0.5 mm – 1.0 mm). Samples from ARA14 – ARA20 might better be grouped as medium sand (0.25 mm – 0.5 mm). This would result in fewer seafloor types for the same region, which might be easier to interpret.

It may, therefore, be unnecessary to ground-truth sediment at every sampling site where the ARA classification shows more variation than CATAMI. Rather, it may be useful to work within the spectrum of consolidated seafloor (ARA10 – ARA13) and unconsolidated sediments (ARA14 – ARA20). In this case, grab sampling and sediment grain size analysis for the samples classified by ARA would be the only certain way to ground truth this classification. This ground-truthing exercise would need to revisit the sites sampled in this study, because the previous grab and dredge samples from False Bay used to characterise the sediment do not match the multibeam sonar transects spatially or temporally. Kloser et al. (2010) discuss how comparing ARA to physical samples is complicated, especially where geolocations may be inaccurate or mismatched at such fine scales. Their recommendation is for a basis of well described referenced sites, which this study presents as a first step.

Secondly, it is possible that the multibeam sonar is accounting for a number of combined variables that are described separately in each of the other surveys by Morgans (1962), Bowie et al. (1970) and Du Plessis and Glass (1991). This method would therefore detect the highest heterogeneity because it integrates several measures of the seafloor environment; namely, roughness, sediment volume variation and acoustic impedance (Fonseca et al. 2002). Indeed, Fonseca et al. (2004) and Fonseca and Mayer (2007) discuss how ARA parameters incorporate orthogonal distance, which is related to the sediment volume. That is, the volume of free fluid or gas in the sediment (Fonseca et al. 2004). Gas in sediments affects the backscatter response in a manner that indicates interactions with both grain size and water depth (Fonseca et al. 2002). This means that the response will vary between sediments that contain gas between shallow and deep-water samples, and between fine and coarse grain sizes (Fonseca et al. 2002). Each sample classified by both ARA and CATAMI in this study would vary not only in the grain size of its sediment, but in the roughness of the seafloor, its slope and aspect, any biogenic cover and organic content within the sediment (i.e. $CaCO_3$). The organic content in the sediment would affect the gas and free fluid volume, which indicates that this “biological” factor may well be incorporated in the ARA classification of sediments. Both grain size and organic content explain variation in infauna biological communities in unconsolidated sediments in False Bay (Field 1971).

The seafloor south of Strandfontein beach (transect 2) and to the south-west of Kapteinsklip (transect 3) between Seal Island and East Shoal is much more uniform in its ARA classification. This result not only matches the findings from Du Plessis and Glass (1991) in terms of classification to “physiographic terrain” number 11, but some heterogeneity at the start of transect 2 matches that described by “physiographic terrain” number 9 (Du Plessis & Glass 1991), which the transect intersects. These results confirm that the ARA classification does not represent grain size on its own. If this were the case, we would expect variation on transect 2 and transect 3, where grain size varies from coarse sand, to medium sand, to very coarse sand (Bowie et al. 1970).

Heterogeneity in the seafloor was apparent once again on transect 7 and transect 8 in the eastern half of the bay. On transect 7, a range of ARA classifications was more equitably distributed along its length. ARA12 was dominant (33%), but samples were also classified ARA11 (18%), ARA13 (18%), ARA20 (12%) and ARA16 (9%). This contrasts with transect 1, transect 2 and transect 3 where only one ARA classification (ARA20) accounted for more than 60% of the seafloor. This result reflects the same heterogeneity in the seafloor that was apparent from the CATAMI classification of samples. This transect showed the greatest variation in seafloor roughness and slope values, which is reflected in the number of ARA classifications detected. It is therefore apparent that the seafloor along the eastern margin of False Bay shows much variation in its seafloor topography and substrate, despite the gradual variation in depth from north to south. Du Plessis and Glass (1991) describe much of the eastern half of the bay as “physiographic terrain” number 6: this study shows that the transects in this section of the bay vary along their length, alternating predominantly between rock and sand, with a range of roughness and slope values for what amounts to the same rock type (Malmesbury Group shale, Du Plessis & Glass 1991).

The eastern half has sediment that ranges from very coarse to coarse to medium and even fine sand (Bowie et al. 1970) and, while the overall profile of Malmesbury Group shale reef is low relative to other geological formations in the region (Du Plessis & Glass 1991), this study shows that the rocks and cobbles from this reef vary in roughness. As a result, this transect indicates more clearly that the ARA classification is possibly integrating several variables into its delineation of seafloor types relative to other surveys and classifications. However, the descriptions of each classification type are not useful as they currently stand for False Bay. This reiterates a need to refine the thresholds for descriptions, and revisit the terminology applied, but suggests that the factors involved in doing so are more complex than the scope of this study.

The idea of any straightforward grouping of ARA classifications according to grain size thresholds (increasing from coarse to fine grain sizes from classification ARA1 to ARA20) is shown to be more complex based on patterns from transect 6. Most samples on this transect were assigned ARA13. According to previous surveys, and the CATAMI classification, this region is characterised by fine and medium grained sands (Bowie et al. 1970). The classification ARA13 would not be, according to this study, the finest grained classification to assign. This is again an indication that the model is accounting for a more complex complement of variables on the seafloor, and that using the classification, at this stage, for anything more than an indication of variability in the nature of the seafloor, is ill-advised without spatially and temporally matched grab samples to ground-truth the classification. However, transect 6 would represent a suitable transect to revisit to refine the ARA classification system. More variation in the seafloor is detected by the ARA classification in this deepest region of False Bay. By contrast, Du Plessis and Glass (1991) classify this area as “physiographic terrain” 11, which is largely homogenous. There is some variation of sand grain size described by Bowie et al. (1970), whereas Morgans (1962) describes the area as largely poorly sorted, fine sand.

The bathymetry data from multibeam sonar surveys are clearly useful in extracting measures of roughness and slope, and the multibeam technique is useful for fine-scale depth measures. The method also distinguishes variation in the nature of the seafloor, but there is no clear pattern to discern a useful break in groupings of ARA classification from this analysis. Broadly, ARA20 appears to agree with the distribution of fine sand, and ARA12 with the distribution of reef, where ARA10 also appears to conform to the distribution of biogenic screwshell material. This study indicates that there is merit to interrogating multibeam sonar acoustic backscatter data, and refining an ARA classification that is based on a regionally-relevant data set: it is perhaps here that further integration of a geophysical description of the seafloor can be incorporated in the biological interpretation of ocean landscapes, where these components of landscape analysis are typically kept separate.

2.5.6. Is ARA a useful classification scheme for False Bay?

The ARA classification might be more sensitive to seafloor variation because it is incorporating more variables than sediment grain size alone (Fonseca et al. 2002; Fonseca & Mayer 2007). Grab samples, and ARA classification of multibeam sonar backscatter data at the same sites, recorded four different grain sizes and eight different ARA seafloor types, respectively. In this instance, it may be that a variable such as organic carbon content in the sediment is detected and incorporated into the reading (Fonseca et al. 2002). Organic carbon and calcium carbonate content of the sediment varies across the bay (Bowie et al. 1970). The incorporation of this variable into a suite of other measurements that are accounted for in ARA (including seafloor roughness, depth, and sediment grain size) would introduce a useful biological measure of the seafloor into a single method. Given the current cost and complexity of achieving multibeam sonar surveys, ARA would need to account for more variables than a much cheaper, logistically simpler method such as the CATAMI classification of photographs.

False Bay is described as homogenous sand across most of its extent, and data that can distinguish variability in the seafloor at fine scales may help understand patterns that likely describe higher variability than what is currently captured. Indeed, many acoustic data describe the seafloor and its sediment such that biological communities show high variability when assessed at this scale (Hewitt et al. 2004). Fine-scale habitat information would be useful to understand the relationship between biodiversity and the physical seafloor, especially to assess localised patterns or species. Still, it would be less useful to identify broad-scale patterns needed to inform management, regional zonation, or threat assessments (Hewitt et al. 2004). However, even where information on fine-scale variability and the relationship between (particularly soft-sediment) fauna and the seafloor is necessary, acoustic backscatter data is still too uncertain for adequate ecological interpretation (Edwards et al. 2003). Grab samples and CATAMI classification of photographs would better integrate fine and broad-scale descriptions of the ocean landscape until acoustic backscatter data is adequately ground-truthed.

2.5.7. Is the addition of new methods useful?

All classification types characterise the seafloor of False Bay as more homogenous in the north and in central regions, whereas the margins of the bay in the west and east show more seafloor heterogeneity. This is despite expectations that the results of each classification would differ in their general characterisation of False Bay because they assess the seafloor at slightly different resolutions and incorporate different components of the seafloor. Wentworth grain size shows variation in the sediment where other surveys do not: delineating the bay according to grain size gives a fine-scale account of heterogeneity within the habitat classified more uniformly by other methods as “sand”. Seismic profiling also distinguished a range of sand types across False Bay (Du Plessis & Glass 1991). Grain size has been shown as important in determining benthic community composition, affecting factors such as larval settlement (Whitlatch 1977). This method of classification facilitates analysis of benthic community variation at a very fine scale, where samples may differ from one another with less than 200 m between them.

The CATAMI classification scheme captures patterns of seafloor character at the scale of the bay. The method gives a more broad classification of grain size, with two sand classifications (SUSF and SUSC) effectively encapsulating all the grain sizes, from very coarse sand to very fine sand, that have been recorded for False Bay by Morgans & Day 1959, Morgans 1962 and Bowie et al. 1970. Heterogeneity within these two classifications is effectively masked. This classification extends beyond one measure of sediment type, however, and captures a range of substrate types from consolidated to unconsolidated, considering the entire visible surface of the seafloor. While it might appear too broad to capture fine-scale heterogeneity within one substrate type like sand, it does classify a greater range of substrate types across the entire extent of the ecosystem. The method also offers a standardised system that can be applied at a global scale, which facilitates comparison at several scales.

Angle Range Analysis (ARA) appears to capture variation in the seafloor with the greatest sensitivity, which may overestimate the actual variability in the physical environment. Whilst the general patterns are comparable to findings from grain size and CATAMI classification, this method will be more useful with proper future interrogation of the model and the introduction of terminology in the classification output that better pertains to the geology of False Bay. This study provides spatially matched grab samples with data on sediment characteristics, grain size and calcium carbonate content that can be used to refine the ARA. Currently, multibeam sonar data only exists from this study and along transects that are matched by samples of the benthic, macroinvertebrate fauna. Future, more extensive coverage of the bay using multibeam sonar can extend the use of ARA classification to a physical description of the seafloor where data also exists for the ichthyofauna of False Bay. For this reason, CATAMI classification is potentially most applicable across multiple biodiversity datasets, because it is specifically designed to address visual (photo and video) surveys. The refinement of the ARA classification was considered beyond the scope of this study, but it is introduced here for the first time for this region, together with the requisite, spatially-aligned data to effectively ground-truth the analysis.

Three different survey methods were used to obtain samples which could classify the seafloor and calculate the variation in sediment type, grain size, substrate cover, roughness, depth, slope, and aspect. False Bay has previously been surveyed using grab, dredge and rock samples (Morgans & Day 1959; Morgans 1962; Bowie et al. 1970; Du Plessis & Glass 1991), bathymetric profiles from sounding surveys (Mallory 1970; Simpson et al. 1970; Du Plessis & Glass 1991), side-scan sonar and seismic reflection profiles (Du Plessis & Glass 1991). There are several points to consider in assessing whether the introduction of new survey techniques is valid and useful, and whether camera and multibeam sonar surveys improve the type of information currently available for the seafloor. Firstly, do the survey methods provide insights at a refined resolution or add new measures of the seafloor to our understanding? Secondly, do they offer any improvement in coverage (to increase the extent of surveys) and repeatability (to be used across habitats and a range of regions)?

Jump camera sampling provides a visual record that can reference previous surveys and ground truth results to describe substrate types that are not clearly identified or discussed, referencing the biogenic screwshells in the south-west of False Bay by way of example. For instance, the distribution of the screwshells, and the density of the beds makes it seem likely that this region might have been missed in the grid design of the previous surveys. The species does not appear to be alien, but future grab sampling could aim for species identification. The greatest addition of new insights is offered by multibeam sonar, which contributes several measures of seafloor variation at a very fine scale. The relevance of data at this scale to biological science and biodiversity management needs to be tested (Wedding & Friedlander 2008; Foster et al. 2009). Both sampling methods detected roughly the same patterns as what is currently known for the seafloor of False Bay, with the addition of some new descriptions and indices. This might not be where the greatest advantage of these methods lies; rather, it confirms that their scientific accuracy is within the realm of acceptability relative to other survey methods.

The type of information currently available for False Bay is comprehensive at a variety of scales, considering that the physical environment is relatively uncomplex for much of the region. However, this would not be the case along the entire coast of South Africa. Geological sampling gives an accurate description of the nature of the seafloor at a reasonably fine scale. The disadvantage lies in the labour-intensive nature of sampling and sample-processing, which reduces the extent of coverage by grab and dredge samples across the bay. This means a fair amount of interpolation happens in the description of general patterns across the bay. It is important to consider the logistical improvements offered by jump camera sampling, and the coverage capabilities of multibeam sonar surveys. The advantage of jump camera sampling lies in the spatial and temporal match of abiotic and biotic elements of the ecosystem in a single dataset. This is also advantageous where logistics make repeat sampling with several survey techniques expensive and labour-intensive, and therefore likely unsustainable over long timescales or difficult to roll out to every region of interest at a coast-wide scale.

The advantage of multibeam sonar surveys lies in the ability to detect geological information with potentially wider spatial coverage than previous geological surveys like grab and dredge sampling, with a higher resolution than the CATAMI classification of jump camera photographs. The multibeam sonar survey presented significant cost to this study and required some expert processing and computing of the initial outputs, before mapping, interpolation and the calculation of indices was possible. Given that different survey methods capture data that provides insights at a variety of different scales, the addition of new methods simply means that a potentially greater variety of questions can be asked. The new survey methods and the classification of the seafloor according to new techniques introduced in this study detect known patterns for False Bay, where every level of interpretation of the physical environment is a question of scale.

2.5.8. Conclusion

With little oceanographic variation, characterising the landscape of False Bay in terms of depth and the nature of the seafloor is important to investigate biodiversity distribution. There is no topographic influence on current or tide, no tidal race, and few barriers to dispersal in current, salinity or temperature. The composition of the ocean landscape in terms of depth and habitat has been shown to be important to describe epibenthic communities (Sahade et al. 2004) and demersal fish (Moore et al. 2011). The CATAMI classification provides a broad-scale landscape description that will be useful to explore not only the structuring of communities, but is an archived, standardised description of the seafloor surface that can be revisited over time to assess ecosystem change. The ARA classification provides fine-scale measures of variation in the seafloor, but its application is uncertain and requires much more ground-truthing to interpret adequately (Edwards et al. 2003).

Finding a line of interpretation somewhere between a geological approach, and what ecological investigation later requires, is complex. Morgans (1962) outlined the necessity of more interdisciplinary interrogation of marine landscapes, where ecologists can interpret geological information such that the most ecologically relevant interpretation is carried through to ecosystem understanding (Shumchenia & King 2010). No single measure incorporates all indices, from grain size (mm) to substrate type (sand, rock), to the nature of the underlying bedrock to the organic content of the sediment, to the slope, aspect and roughness of the seafloor at a particular location, to give a single, definitive classification type. What is useful is to assess whether these methods are detecting seafloor variation in the same regions, and uniform seafloor in the same regions. This study shows that, with varying degrees of resolution, the same broad patterns for the bay are detected across all methods. This is promising for the non-extractive, time-efficient jump camera method that would be repeatable over time, and the high resolution multibeam sonar method, that both extend sampling coverage across the full extent of the bay.

CHAPTER 3

A REMOTE PHOTO ASSESSMENT OF THE RELATIVE COVER AND DISTRIBUTION OF EPIBENTHIC MEGAFAUNA IN FALSE BAY

Kelp (*Ecklonia maxima*) and Cape urchins (*Parechinus angulosus*) are part of the riot of colour on a reef in the Castle Rocks no-take zone of the Table Mountain National Park (TMNP) marine protected area (MPA). The rocky reefs are typically high-profile, granite boulders and are protected in parts of western False Bay. Photograph: Joris van Alphen.

3.1. ABSTRACT

Sessile, epibenthic megafauna communities that cannot move to evade disturbance are often most vulnerable to anthropogenic impacts. Adequate management of benthic communities requires information on their distribution, and an understanding of what key environmental factors explain observed patterns. However, repeat sampling of the seafloor is often logistically taxing and so the addition of a rapid biodiversity assessment method to detect broad-scale patterns in species distribution, and to monitor change in pattern and process, needs to be tested. The infauna of False Bay's soft sediments was previously surveyed using 222 dredge samples and 89 grab samples, and 13 dive surveys limited to a maximum depth of 26 m have described biodiversity on reefs in western False Bay. These surveys were conducted in the 1950s and 1960s. There has been no previous baseline description of epibenthic megafauna communities across all depths and habitats at the full extent of the bay, nor has there been any updated biodiversity survey to address repeated sampling to detect changes in biodiversity abundance and distribution over time. Four hundred photographs were taken using a novel jump camera rig on eight transects across False Bay that covered a range of depth gradients, and habitat types. Eighty-nine species were recorded in 373 photographs in this first remote camera survey, and their distribution assessed in relation to the physical ocean landscape. The featherstar *Comanthus wahlbergi* was most frequently detected across all samples. Encrusting sponges were most common on the eastern reefs of False Bay. Species diversity was highest between 30 – 40 m and decreased with depth. Species diversity was highest on the eastern and western margins on False Bay, where habitat heterogeneity was highest. Depth explained more of the variation in community composition than roughness or slope (BIOENV, $\alpha = 0.001$). Separation among samples was low, but one-way ANOSIM tests showed that depth (Global R = 0.013; p = 0.01), CATAMI habitat (Global R = 0.02; p = 0.002) and transect (Global R = 0.037; p = 0.001) were significant predictors of similarity among samples. The study confirmed patterns from elsewhere in South Africa, and globally, that depth and habitat structure epibenthic communities and provide useful, stable delineators for future zonation and monitoring. The novel jump camera method greatly extended the coverage of samples that could be achieved by a single diver and were most useful for providing a repeatable quantification of cover on reefs. This is important for future monitoring in False Bay, where regions of highest epibenthic megafauna diversity are outside the marine protected area (MPA) network and have been under-represented in previous surveys.

3.2. INTRODUCTION

Understanding biodiversity patterns underpins focused management of human activities (Vanderklift & Ward 2000). However, describing and monitoring the biodiversity of the seafloor is logistically challenging (Zajac 2008; Williams et al. 2015). Before we can predict biodiversity patterns based on acoustic signatures, or infer species' distributions using physical seafloor descriptions as a proxy, we have to understand the relationship between the abiotic and biotic components of the ecosystem (Elith & Leathwick 2009; Howell et al. 2010).

Epibenthic megafauna – those visible species that occupy the seafloor surface - are especially vulnerable to the impacts of human activities, because sessile or slow-moving animals often cannot evade disturbance (Solan et al. 2003). Bottom-trawling (Olsgard et al 2008), dredging (Thrush & Dayton 2002), pollution (Johnston & Roberts 2009; Gall & Thompson 2015) and the introduction of alien species (Occhipinti-Ambrogi 2007) affect these organisms directly (Solan et al. 2003). Invertebrate biodiversity loss is problematic because these species often play a structuring role in their ecosystems: they increase habitat heterogeneity (Bradshaw et al. 2003; Buhl-Mortensen et al. 2010) and influence primary production and energy transfer (Coma et al. 1994). The impact of human activities on benthic invertebrates translates to community pattern, process and function: placing at risk processes such as bioturbation from burrowing invertebrates (Solan et al. 2003), and functions such as providing attachment sites (Wahl 2009), shelter (Bradshaw et al. 2003; Buhl-Mortensen et al. 2010) and food (Snelgrove 1998).

Benthic invertebrates have been sampled using various methods. Dredges, grabs (Morgans 1962; Field 1970; Field 1971; Buhl-Mortensen et al. 2012) and box corers are designed for soft sediments and capture both infauna and epifauna (Beisiegel et al. 2017). Benthic sledges (Buhl-Mortensen et al. 2012; Williams et al. 2015) and SCUBA surveys (Edgar et al. 1997) record benthic invertebrates living on the seafloor surface. The methods chosen for a particular survey will depend on the nature of the seafloor: dredges and trawls are unsuited to high profile reefs (Zajac 2008), and grabs and box corers do not work efficiently in coarse-grained or consolidated sediments. The scale of the question and the extent of the survey region are important: remote sensing, including aerial photography, can detect changes in shallow-water invertebrate populations at a large scale, such as coral bleaching events (Yamano & Tamura 2004; Kutser et al. 2006), but may not resolve species classifications to address fine-scale management questions (Alquezar & Boyd 2007); for example, alien species invasions (Peters et al. 2017) and the effect of pollution on organisms' physiology (Spark & Mullins 2017).

Destructive sampling may be undesirable where habitats are considered sensitive, species are rare or where protected area stipulations prohibit disturbance. Sampling by dredge, trawl and grabs are all destructive (Solan et al. 2003). However, may not be possible to eliminate destructive sampling: these methods may help ground-truth sediment type and grain size data, and biological collections inform taxonomy (Althaus et al. 2015). However, non-destructive alternatives may increase the scope and frequency of sampling, but other challenges limit their application (Goffredo et al. 2010). Underwater visual censuses (UVC) using SCUBA involve significant cost and labour (Goffredo et al. 2010), are limited by depth and water turbidity (Beisiegel et al. 2017) and may miss contextual data such as substrate type (Solan et al. 2003).

A non-destructive method that can overcome some logistical constraints, sample across habitat types and to greater depths, would be a useful addition to invertebrate biodiversity monitoring. Overcoming logistical challenges is particularly necessary where survey capacity is limited. A method that lowers cost and increases coverage may advance monitoring survey consistency in resource-limited regions. Photographic surveys provide an archived record of species abundance and distribution, and associated sediment, that can be reassessed (Piepenburg & Schmid 1997; Solan et al. 2003). While some camera surveys are still diver operated (Solan et al. 2003; Preskitt et al. 2004; Beisiegel et al. 2017), remote imagery surveys facilitate sampling at greater depths because they are independent of divers (Heyns et al. 2016). Remotely operated vehicles (ROVs), towed cameras and autonomous underwater vehicles (AUVs) all offer a solution to improving the scale of benthic surveys (Solan et al. 2003; Williams et al. 2015; Heyns et al. 2016). They are still, however, expensive to construct and may require skilled operators.

A downward-facing jump camera that collects still and video imagery facilitates non-destructive sampling over large areas, across variable topography and habitats, without the skilled labour required for either SCUBA or ROV surveys (Beisiegel et al. 2017). A jump camera is designed to operate like a SCUBA photo quadrat survey, but the rig is lowered from a boat and moved sequentially along transects, taking photos of the seafloor at set intervals (Roberts et al. 1994; Sahade et al. 1998). The jump camera method provides data on species relative cover, habitat type and species-associations for benthic communities (Sahade et al.

1998). Camera surveys are limited by the quantity and speed of data processing to identify and count species from photographs that have been captured in the field. Computer-based analysis of photographs is more time-consuming than in-field identification (Roberts et al. 1994; Preskitt et al. 2004), but the images provide an archived record of the ecosystem, and their identification can be verified by experts, which might mean they are more reliable than UVC.

As imagery surveys are increasingly used, classifying the biodiversity and landscape data in images using standardised terms make data more broadly applicable (Althaus et al. 2015). Classification systems are also a step towards automated image-processing, which will reduce the post-field analysis time, increase spatial coverage, and reduce labour (Beijbom et al. 2015). Many systems have been developed around the world (Strong et al. 2018). The European Union Nature Information Systems (EUNIS; Davies et al. 2017) encompassed surveys in the Northeast Atlantic (Gomes-Perreira et al. 2016). The Coastal and Marine Ecological Classification Standard (CMECS) encompasses coastal and deep waters in the United States of America (Gomes-Perreira et al. 2016). The World Register of Marine Species (WoRMS; Costello et al. 2013) provides a list of names for classification; however, an annotation system that considers the nature of image-based surveys is necessary. This study uses the Collaborative and Automation Tools for Analysis of Marine Imagery and Video (CATAMI; Althaus et al. 2013), an Australian classification scheme specifically developed for quantifying and classifying the seafloor and its biodiversity in marine image-based surveys.

South African invertebrate research has been concentrated in regions of significant effort to understand species’ distributions (Gibbons 1999; Awad et al. 2002). The need to implement ecosystem-based management of marine resources, and to expand the current network of marine protected areas (MPAs) (Sink 2016), highlights the importance of addressing sampling gaps in the remaining under-surveyed areas. The Challenger research expedition marked the start of the earliest invertebrate collections in False Bay in 1873 in Simon’s Bay (Morgans & Day 1959). The government-appointed biologist JDF Gilchrist worked on the shallow seabeds of South Africa’s coastline from 1902 until the focus of government research shifted primarily to fisheries during the world wars (Morgans & Day 1959). The emphasis for invertebrates moved from the continental shelf to the intertidal zone (Stephenson 1939, 1944, 1947). Dredging was started again by JH Day in 1946 and continued until early SCUBA diving supplemented surveys.

False Bay is in a region of overlap between the faunistic provinces defined as the south and west coasts of South Africa (Stephenson 1939, 1944, 1947). Influences from the Benguela upwelling regime and Agulhas current are apparent in the oceanography and resultant biota (Day 1970; Awad et al. 2002; Griffiths et al. 2010). There are 1116 invertebrate species recorded in False Bay, which represents the site with third highest invertebrate species diversity in South Africa (Awad et al. 2002). Forty-four percent (449 species) of the total diversity in False Bay is endemic to South Africa (Awad et al. 2002). Some of these results may be the consequence of sampling bias (the bay is located near to three major South Africa universities) and its long history of study relative to elsewhere in South Africa (Day 1970; Field 1970, 1971; Griffiths & Branch 1991; Awad et al. 2002). At exposed locations in the bay itself, species typical of the west coast are recorded in higher abundance, whereas the more sheltered areas harbour a higher proportion of species typical of the south coast (Day 1970). Invertebrate diversity patterns in intertidal and rocky shore habitats are especially well studied (Stephenson 1944; Morgans & Day 1959; Griffiths & Branch 1991). Subtidal invertebrate sampling in False Bay has been conducted by dredging (Morgans 1962, Field 1970), dive surveys to a maximum depth of 26 m (Morgans 1962) and grab sampling in deeper water (Day et al. 1970; Field 1971).

The first attempt to link benthic invertebrates to their associated habitat and describe ‘faunistic grounds’ was made by Morgans (1962). Dredge samples supplemented by diving observations gave a preliminary description of reef and sand communities (Morgans 1962). Patterns of invertebrate distribution were different on rocky and sand seafloor surfaces, and species richness was higher on rock than on sand. Morgans ascribed the difference in species richness and distribution to the nature of the substrate, but limitations in sampling methods at the time prevented any further correlation or description (Morgans 1962). Slope, aspect, and rugosity were posited to influence sunlight illumination and water turbulence, which in turn affect the biodiversity of shallow rocky habitats, but the actual influence of these variables was not tested (Morgans 1962).

Morgans (1962) sampled to a maximum depth of 26 m by diving, and a maximum depth of 36 m by dredging. Dredge sampling aboard the RS Africana II increased that effort to depths below 40 m (Morgans 1962). Morgans collected 72 dredge samples across rock, sand, and mixed seafloor habitats. He added to these data by diving, collecting a further seven samples on rock and six on sand. Some of these data informed the delineation of seven “grounds” on soft sediment. According to his descriptions, the polychaete *Diopatra neapolitana*, seastar

Marthasterias africana and gastropods *Nassarius speciosa* and *Bullia laevissima* characterise a sandy seafloor between 7 – 23 m from Fish Hoek south to Glencairn. Coarse sands with broken shell fragments characterise the northern and north-western regions of False Bay between 10 – 40 m, dominated by *D. neapolitana* tubes and *Astropectan* and *Marthasterias* seastars. The mouth of False Bay between 78 – 88 m depth was described as green mud comprising faecal pellets and dominated by the clam *Dosinia pubescens*. To the west between 62 – 82 m, the seafloor is silty sand with broken shell matter and characterised by the sea urchin *Spatangus capensis* (Morgans 1962). Six of the seven proposed “grounds” are drawn, but the descriptions are extrapolated over large areas from as few as two samples.

Day et al. (1970) discuss species distribution patterns in relation to water temperature in False Bay. Where upwelling occurred at the more exposed Danger Point and Cape Hangklip at the south-eastern point of the bay, the proportion of species typical of the west coast was higher than elsewhere in the bay. Where it was more sheltered, there were more species typical of the south coast than elsewhere in the bay. A total of 1629 species are listed: 68 echinoderms, 392 molluscs, 76 decapod crustaceans, 324 polychaetes, 84 hydrozoans and 685 other invertebrates in a synthesis of records published up to 1970 and unpublished catalogues from the University of Cape Town (Day et al. 1970). This exceeds the 1116 invertebrates listed by Awad, Griffiths & Turpie (2002), and includes intertidal and subtidal species.

Field (1970) confirmed that benthic community composition changed with depth and habitat in False Bay. He selected 20 samples representing 150 species from 150 dredge samples and 89 grab samples (Field 1970). Sand-associated species between 5 – 24 m were distinct from the remaining biota. Species in mud and shell seafloor habitats deeper than 70 m were distinct from other biota. The urchin *S. capensis* inhabited an area larger than Morgans (1962) outlined. Field (1970) suggested that the “grounds” described in his and Morgans’s work may contain different communities. Within a limited depth range, statistically significant differences between samples pointed to more variation than either study reflected (Field 1970). Grab samples along a single depth gradient on sand classified six faunistic groups, two of which were associated with the surf zone (Field 1971). This study suggested that sediment type and grain size mediated the depth trend observed in the first survey (Field 1971).

Field (1970) pointed out several field sampling shortcomings that constrained inferences about biodiversity patterns in False Bay. Firstly, grab and dredge samples lacked contextual information. Could the seafloor habitat be patchy, and if so, did the sample represent an isolated patch? Secondly, dredging may combine different communities in a single sample. Every sampling technique has shortcomings: for instance, a camera survey will not detail the benthic infauna, planktonic forms, or microscopic species. It is therefore important to consider the purpose of a new sampling method: does it describe community composition and distribution, and can it assess change over time? Morgans, Field and Day all proposed further work based on their benthic surveys, especially to understand patterns of distribution and characterise "grounds" (Morgans & Day 1959; Morgans 1962; Field 1970; Day et al. 1970; Field 1971). Dredge and grab samples described a significant proportion of the infauna, but little has been published since 1971 to understand epibenthic megafauna in False Bay. The effort required to collect and interpret these data may have prevented further work.

Distribution patterns in the rocky intertidal zone have been well-studied in the region (Morgans & Day 1959; Field & MacFarlane 1968; Kruger & Griffiths 1998; McQuaid & Branch 1984). There has also been discussion of the distribution of known biota from False Bay at a coast-wide scale (Awad et al. 2002; Sink et al. 2004; Griffiths et al. 2010; Driver et al. 2012; Scott et al. 2012). Commercially important invertebrates; notably, west coast rock lobsters (*Jasus lalandii*) (Cockcroft et al. 2008; Blamey et al. 2010), common octopus (*Octopus vulgaris*) (Smith & Griffiths 2002; Smith 2003; Oosthuizen et al. 2004), abalone (*Haliotis midae*) (Tarr et al. 1996; DAFF 2016) and scallops (*Pecten sulcicostatus*) (De Villiers 1976) have been surveyed. Divers surveyed the status of *J. lalandii*, *H. midae*, alikreukel (*Turbo sarmaticus*) and Cape urchins (*Parechinus angulosis*) between 3 – 10 m depth around the Cape Peninsula in the west of False Bay (Mayfield et al. 2001). Descriptions of the distribution of alien invasive species set False Bay in context of the South African coastline (Robinson et al. 2005; Hampton & Griffiths 2007), and there has been some investigation into such anthropogenic impacts as pollution on invertebrate species (Reineke et al. 2012).

Much has changed in False Bay since these surveys, with potential direct and indirect impacts on benthic marine communities. A growing human population, particularly along the northern shoreline, has increased coastal development (Van Herwerden & Griffiths 1991; WWF 2012). Intensifying construction affects pollution, habitat alteration and degradation (Day & Gardiner 1991; Molden 1991; Schoonees & Bartels 1991; Quick & Thornton 1991; Rundgren 1992). The need to sustain more people around False Bay has changed industrial, stormwater and wastewater discharge (Quick 1993). These changes affect marine invertebrate biodiversity:

sewage effluent from the Cape Flats Wastewater Treatment Works increased meiofauna numbers on sandy beaches at Zeekoevlei (Skibbe 1991). The heavy metal cadmium, introduced to the marine environment through industrial work, paint and fertilizers, accumulated in the grey volcano barnacle (*Tetraclita serrata*), the pink-lipped topshell (*Oxystele sinensis*), the goat's eye limpet (*Cymbula oculus*) and the mussel (*Choromytilus meridionalis*) (Reineke et al. 2012). There is evidence of nutrient and pollution loading in the Eerste and Kuilsriver catchment (Chingombe 2012; Mwangi 2014), pesticides in the Lourens catchment (Schulz & Peal 2001) and heavy metals in the Helderberg marine protected area (MPA) (Sparks & Mullins 2017). Land and sea systems are linked in False Bay and impacts on the subtidal biodiversity cannot remain divorced from the influence from terrestrial land-use changes.

The south-eastward shift of the west coast rock lobster (*Jasus lalandii*) in the early 1990s has changed benthic community composition at Cape Hangklip (Blamey et al. 2010). Benthic herbivores have declined by 99.3%, but sessile invertebrates and macroalgae have increased by 2600% and 453% respectively, post *J. lalandii* invasion (Blamey et al. 2010). Regime shifts are important to monitor to inform an ecosystem-approach to management in the region, especially where ecosystem changes have economic consequences (Blamey et al. 2010). The proximity of Cape Hangklip to False Bay itself places the bay in a region of possible *J. lalandii* invasion. Ongoing monitoring of commercial species of interest, but also of the ecosystem, is essential to capture temporal changes in community composition. The eastward movement of the macroalgae *Ecklonia maxima* since 2006 has been linked to inshore water temperature changes and general cooling (Bolton et al. 2012). In the long term, these changes affect both ecology and livelihoods, altering benthic communities that have been otherwise stable for around 70 years (Bolton et al. 2012).

Environmental management and conservation strategies have also changed. The new boundaries of the Table Mountain National Park (TMNP) MPA were delineated in 2004 (Tunley 2009). The indirect impacts of fisheries management and possible recoveries in no-take zones require assessment. There is also reason to look to the future of False Bay and its benthic invertebrates. An experimental octopus fishery (Smith & Griffiths 2002), the application for an experimental whelk fishery and potential aquaculture ventures (WWF 2012) illustrate the changing nature of resource-use, and how impacts may shift to as-yet unconsidered species. Desalination plants constructed in 2018 at Strandfontein and Monwabisi during an extended drought exemplify how the region will continue to change. Brine dispersion models help predict where the marine environment will be impacted (Advision 2018a, 2018b), but there has been no updated quantification of the biota. Sufficient biodiversity data pre- and post-infrastructure development would facilitate sound monitoring of benthic invertebrates.

Carr (2014) used baited remote underwater mono-video system (mono-BRUVs) data to explore macroinvertebrate distribution in False Bay in 5 – 50 m depth. The study recorded 67 species and confirmed differences in macroinvertebrate communities on reef and sand. While the results are useful for mobile, predatory invertebrate species such as *J. lalandii*, BRUVs sampling limited accurate identification and abundance estimates for poriferans and echinoderms (in particular, crinoids) (Carr 2014). The survey design was optimised for fish sampling and focused on reefs key to linefish species (De Vos et al. 2015). A quantitative update of sessile epibenthic megafauna across all habitats and depths at the extent of the bay, spatially and temporally paired with a seafloor classification, is missing.

Improvements in technology to sample the seafloor and associated biodiversity make it pertinent to revisit invertebrate distribution in False Bay. The results of previous surveys afford comparison with results from new methods, which is useful for validation before integration into monitoring programmes. This chapter characterises the epibenthic megafauna of False Bay using a novel jump camera survey across depth gradients. The aim was to use a novel photographic technique to i) determine the relative cover, diversity and distribution of epibenthic megafauna, ii) employ the CATAMI classification scheme to describe biodiversity and iii) to use the physical seafloor characteristics determined in Chapter 2 to assess which environmental factors best explain differences in community composition.

3.3. METHODS AND MATERIALS

3.3.1. Study area

False Bay (**Figure 17**) is located in the Western Cape province of South Africa between 34° 04’ and 34° 23’ S and 18° 26’ and 18° 52’ E, east of the Stilbaai MPA (**Figure 17** inset map) which is located at 34° 23’S and 21°25’E and the Tsitsikamma MPA (**Figure 17** inset map) which is located at 34° 01’S and 23°53’E in both the Western and Eastern Cape provinces.

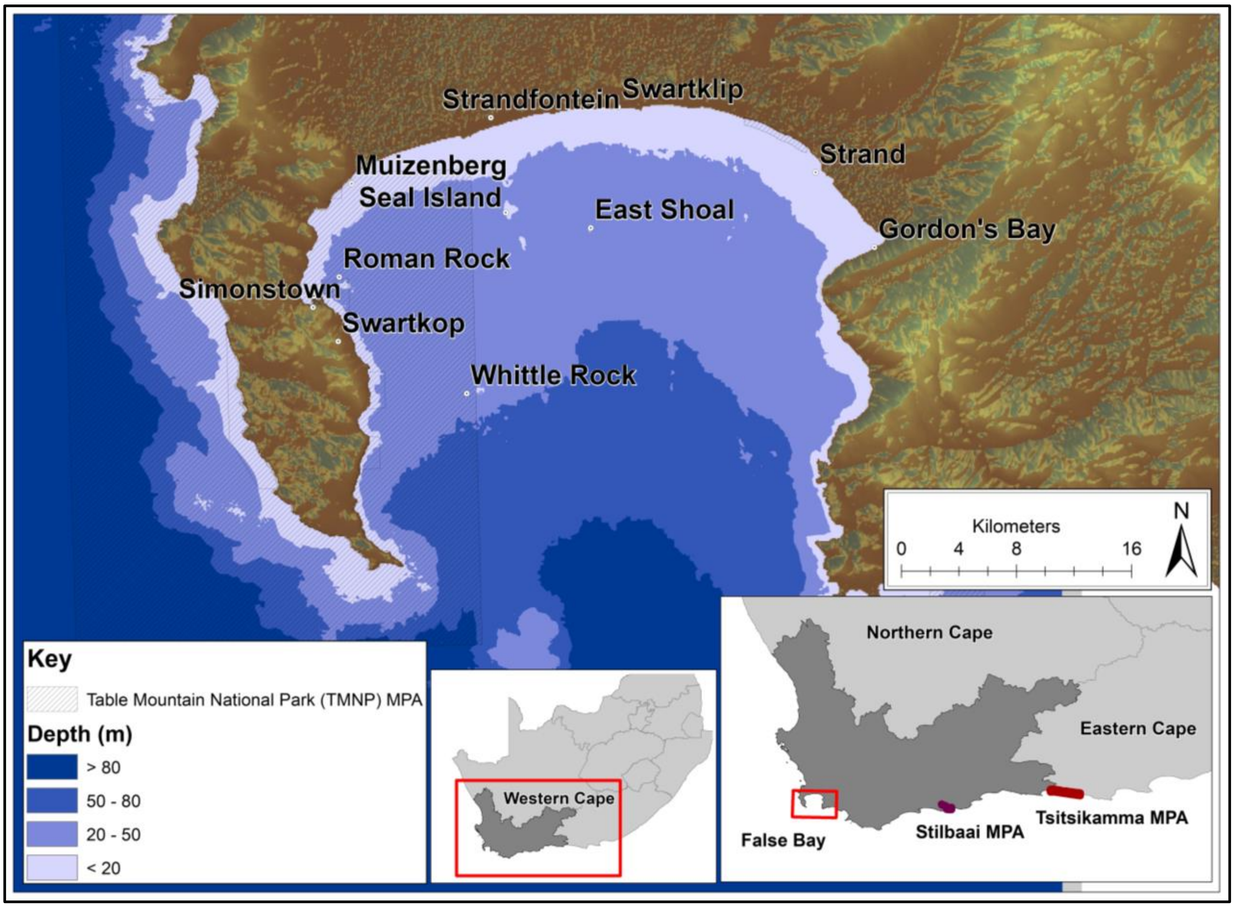


Figure 17. Key topographical features (EKZNW 2015) and depth (m) contours (Van Zyl 2011) of False Bay, in the context of South Africa (inset map) and the Western Cape province where the Tsitsikamma marine protected area (MPA) and Stilbaai MPA are shown (inset map).

3.3.2. Jump camera photo survey

Eight linear transects were designed in ArcGIS (Chapter 2) to achieve three sampling aims. First, to assess changes in epibenthic megafauna community composition, the transects needed to cover a range of depths across the bay. Transects were plotted perpendicular to the prevailing depth contours: this ensured that depth changed maximally along each transect and avoided pseudoreplication of sites where settlement of benthic invertebrates might follow the prevailing currents within a single depth contour. Depth was split into three categories: shallow (0 – 30 m), medium (30 – 60 m) and deep (60 – 90 m) to be tested as a factor in the design (**Figure 17**). These categories covered the broad depth categories outlined by Morgans (1962) and Field (1970) in delineating "grounds" and changes in community composition. All eight transects covered this range of depths; however, no single transect covered depths 0 – 90 m (**Figure 18**).

It was important to achieve the maximum coverage of the bay using a single method across all habitat types and depths. Previous subtidal surveys of the benthic biota relied on grab and dredge samples spaced widely apart (Morgans 1962; Day 1970; Field 1970; Field 1971), and on dive surveys limited to depths less than 26 m (Morgans & Day 1959). Therefore, the second aim was to plot transects widely apart to cover all different sections of False Bay (**Figure 18**). Transects were chosen over random points to sample the change in community composition along a depth gradient (*sensu* Götz 2006; Heyns et al. 2016). However, reef habitat is limited to shallow depths in False Bay, so the distribution of reef and sand habitat could not be sampled equally while using transects sampling along a depth gradient. Future research can use a grid design to test reef and sand equally. Lastly, the nature of this study differed from previous surveys in that only the visible, epibenthic megafauna were assessed. Previous surveys assessed the infauna in sand substrata (Morgans 1962; Field 1970; Field 1971). However, where relevant, the comparison of a new technique to previous findings was considered important and transects were delineated to achieve reasonable coverage of the previous survey areas outlined by Morgans (1962) and Field (1970, 1971), especially where a major change in benthic community and the nature of the seafloor is mentioned between 5 m – 24 m and again at 70 m (Field 1970).

Four hundred photographs were selected from the series taken over eight transects [transect 1 (46 samples), transect 2 (80 samples), transect 3 (51 samples), transect 4 (40 samples), transect 5 (48 samples), transect 6 (40 samples), transect 7 (56 samples) and transect 8 (40 samples)] in False Bay (**Figure 18**).

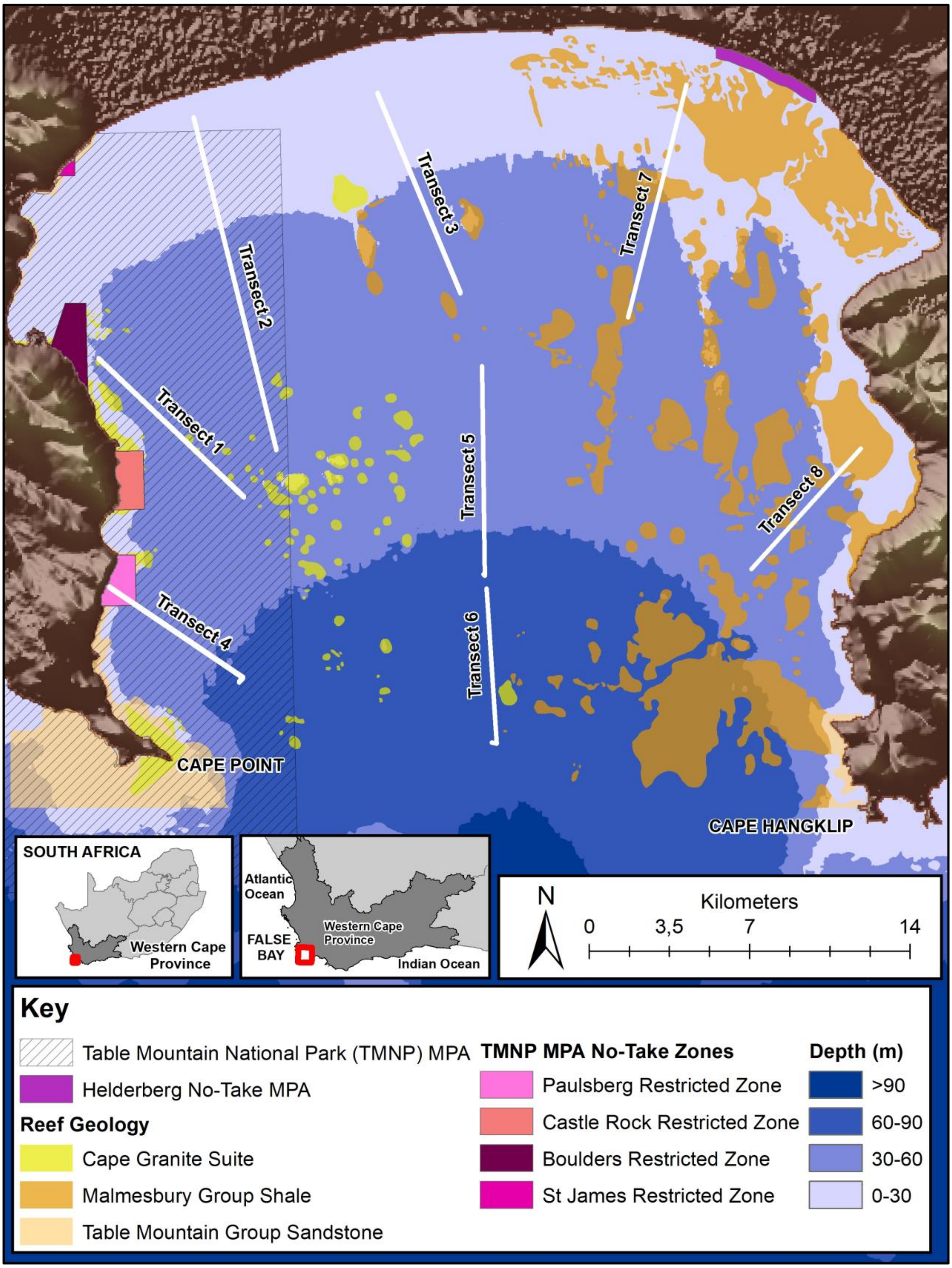


Figure 18. The location and name of eight transects delineated for jump camera photographic sampling, perpendicular to the prevailing depth (m) contours (Van Zyl 2011) [categorised according to accommodate the broad depth categories outlined by Morgans (1962) and Field (1970)] in False Bay, South Africa. False Bay is shown in the context of the surrounding terrestrial topography (EKZNW 2015), subtidal reef geology (Van Zyl 2011) and marine protected areas (MPAs) (DEA 2019a).

A GoPro Hero© 3 in a custom-built underwater housing rated to 200 m depth was set to take one photograph every five seconds along the length of each transect at intervals of 0.1 nautical miles (185 m). A jump camera rig (**Figure 19**) holding the downward-facing camera and underwater housing (described in depth in Chapter 2, and illustrated in **Figure 19** in this chapter) set to 1 m above the seafloor, was manually deployed to the seafloor for 35 seconds so that any disturbance of the seafloor sediment on deployment that clouded photographs could settle. Two LED dive torches lit the view in the circular base with an internal area of 0.3 m^2. Each transect was sampled separately and completed in a single day.

Figure 19. Jump camera housing rated to 200 m depth capability containing a GoPro Hero 3 © set to take still photographs of the seafloor. On either side of the housing is an LED dive torch to illuminate the seafloor within the quadrat.

Seven photographs were taken at each site during this time and the single photograph with the clearest field of view was selected in analysis afterwards, so that only one photograph per site was used in processing and analysis. The jump camera rig was hauled to the surface using a capstan winch and re-deployed every 0.1 nautical miles (185 m) for the length of each transect. Each transect was sampled in a single day aboard the University of Cape Town vessel *Sargasso* (**Figure 20**).

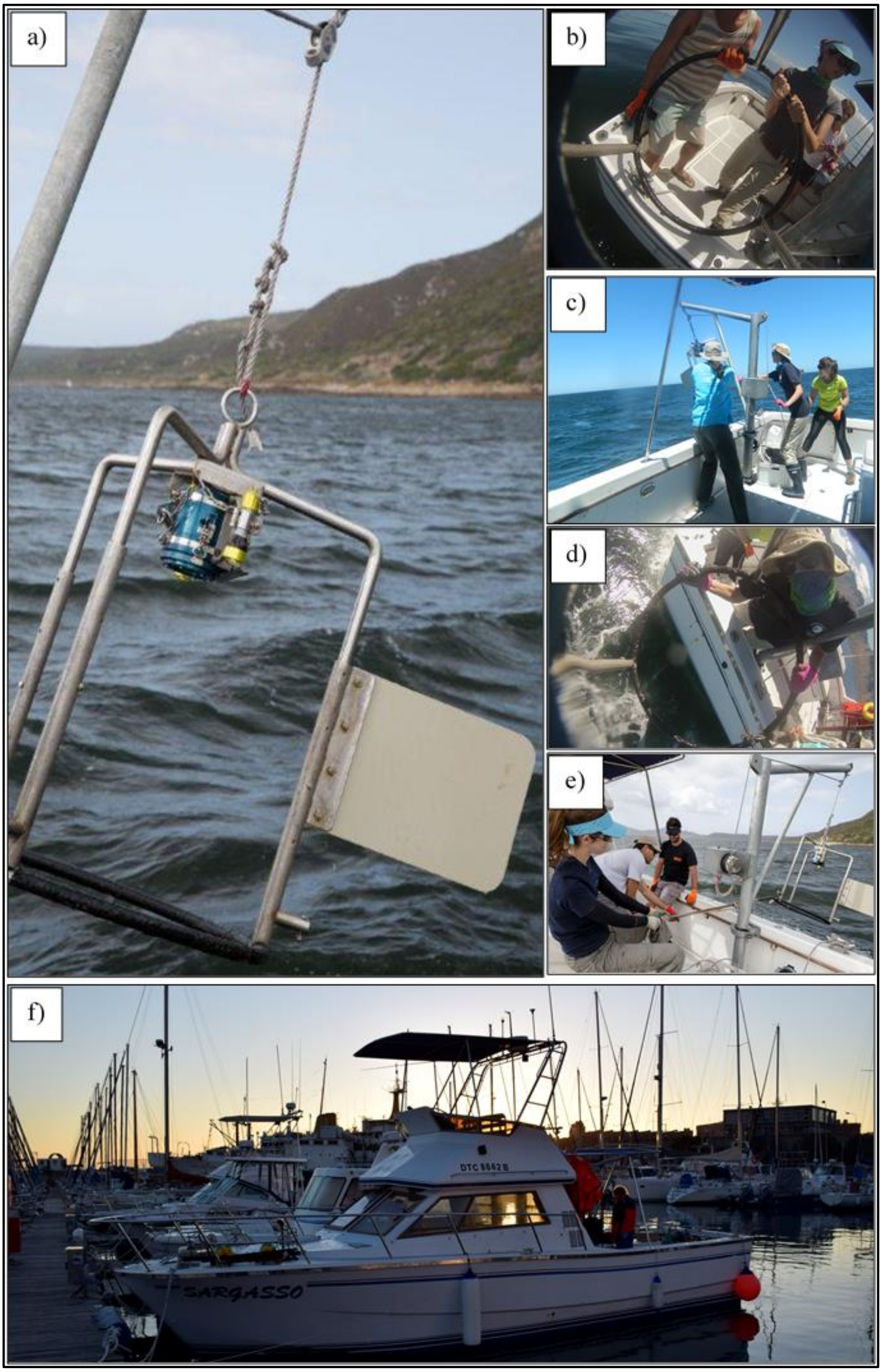


Figure 20. Deployment of the jump camera rig (a), with camera housing and lights (a) from the vessel Sargasso (f) using a capstan winch (e). A plastic fin attached to the metal frame of the jump camera prevented the rig from spinning in the water column upon deployment (a and e). The circular base (b and d) had an internal area of 0.3 m^2.

3.3.3. Presence/absence assessment of photographs and identification to species level

Three hundred and seventy-three photographs were suitable for visual assessment, after samples classified as zero visibility were rejected from the 400 samples collected in the field. “Zero visibility” was determined where samples had low water clarity and were too dark to see the biota or the nature of the seafloor; this was usually where dinoflagellates during a red tide event had clouded the entire field of view. All 373 samples were assessed individually and all taxa visible in the 0.3 m^2 circular frame of the jump camera were identified as species or nominal species. Any taxa outside the 0.3 m^2 frame were discounted. Species were identified using reference guides (Jones 2008; Marais 2011; Branch et al. 2017). Every sample was then independently re-assessed together with an invertebrate expert for False Bay, first with Georgina Jones (Southern Underwater Research Group) and then with Professor Emeritus George Branch (University of Cape Town). This was the first remote photographic survey of the benthos of False Bay, so experts were called on to help with two elements: the identification of species from a photograph rather than from a physical sample, and familiarity with the known biota of the region.

The final species identifications and taxonomic nomenclature were the result of the following process:

- A single observer (the author) assessing all photographs using reference guides for identification and the CATAMI scheme (Althaus et al. 2013) for classification
- Expert consultation and data checking of all photographs and classification
- Confirmation of valid names on the World Register of Marine Species (WoRMS 2018)
- Cross-referencing final species identifications and classifications with the species list for False Bay compiled by Day et al. (1970)

Table 13. Additional identification references per phylum.

Phylum	**Reference**
Arthropoda	Griffiths, C.L., Landschoff, J. & Atkinson, L.J. 2018. Phylum Arthropoda. In *Field Guide to the Offshore Marine Invertebrates of South Africa.* Atkinson, L.J. & Sink, K.J. Eds. Pretoria, South Africa: Malachite Marketing and Media. 133-226. Dawson, J. & Griffiths, C.L. 2012. Revision of the crown crabs, genus Hymenosoma (Crustacea: Hymenosomatidae), of South Africa. *African Natural History*. 8: 16-29. [Online] ISSN 2305-7963.
Annelida	Karenyi, N. & Atkinson, L.J. 2018. Phylum Annelida. In *Field Guide to the Offshore Marine Invertebrates of South Africa*. Atkinson, L.J. & Sink, K.J. Eds. Pretoria, South Africa: Malachite Marketing and Media. 121-132. Hewitt, C. L., Martin, R. B., Sliwa, C., McEnnulty, F. R., Murphy, N. E., Jones, T., & Cooper, S. 2002. National introduced marine pest information system. [Accessed 19/09/2017] [Online] *http://crimp. marine. csiro. au/nimpis,* Knight-Jones, P. & Perkins, T. H. 1998. A revision of Sabella, Bispira and Stylomma (Polychaeta: Sabellidae). *Zoological Journal of the Linnean Society*. 123(4): 385-467. doi: 10.1111/j.1096-3642.1998.tb01370.x
Bryozoa	Florence, W.K., Hayward, P.J. & Gibbons, M.J. 2007. Taxonomy of shallow-water Bryozoa from the west coast of South Africa. *African Natural History.* 3: 1-58. Boonzaaier, M.K. 2017. Diversity and Zoogeography of South African Bryozoa. PhD thesis. University of the Western Cape, Cape Town, South Africa.
Echinodermata	Atkinson, L.J., Mah, C., Filander, Z., Olbers, J. & Thandar, A. 2018. Phylum Echinodermata. In *Field Guide to the Offshore Marine Invertebrates of South Africa*. Atkinson, L.J. & Sink K.J. Eds. Pretoria, South Africa: Malachite Marketing and Media. 393-476.
Porifera	Samaai, T. 2006. Biodiversity" hotspots", patterns of richness and endemism, and distribution of marine sponges in South Africa based on actual and interpolation data: A comparative approach. *Zootaxa*. 1358(1): 1-37. Samaai, T. & Gibbons, M.J. 2005. Demospongiae taxonomy and biodiversity of the Benguela region on the west coast of South Africa. *African Natural History*. 1(1): 1-96. [Online] https://hdl.handle.net/10520/EJC17340.

3.3.4. Presence/absence classification of biota and the seafloor using CATAMI

The Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification scheme (Althaus et al. 2013) was used to assign a code for the dominant seafloor substrate in each of the same 373 photographs (**Table 1**). Along these transect sections, the classification Substrate: Unconsolidated (soft): Sand / mud (< 2 mm): Mud/silt (< 64 µm) (SUSM) was added, and the code SHA assigned where a point was un-scorable or indistinguishable (Althaus et al. 2013). Every species identified in every sample was assigned a CATAMI species code (**Table 14**). All CATAMI species codes were assigned in consultation with Georgina Jones and Professor Emeritus George Branch.

Table 14. Description of the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification codes used for 373 samples in this study (from Althaus et al. 2013).

CATAMI	Description	CATAMI	Description
ASC	*Ascidians: Stalked: Colonial*	EFU	*Echinoderms: Feather stars: Unstalked crinoids*
AUC	*Ascidians: Unstalked: Colonial*	EOBSS	*Echinoderms: Ophiuroids: Brittle/snake stars*
AUS	*Ascidians: Unstalked: Solitary*	ESC	*Echinoderms: Sea cucumbers*
BRYHM	*Bryozoa: Hard: Massive*	ESS	*Echinoderms: Sea stars*
BRYS	*Bryozoa: Soft*	ESUI	*Echinoderms: Sea urchins: Irregular urchins*
BRYSF	*Bryozoa: Soft: Foliaceous*	FB	*Fishes: Bony fishes*
CBBFM	*Cnidaria: Corals: Black & Octocorals: Branching: Fleshy: Mushroom*	MAENRC	*Microalgae: Encrusting: Red: Calcareous*
CBBNA	*Cnidaria: Corals: Black & Octocorals: Branching: Non-Fleshy: Arborescent*	MOB	*Molluscs: Bivalves*
CBFFS	*Cnidaria: Corals: Black & Octocorals: Branching: Fleshy: Arborescent*	MOG	*Molluscs: Gastropods*
CBQ	*Cnidaria: Corals: Black & Octocorals: Fan (2D): Fern-frond: Simple*	SPC	*Sponges: Crusts*
CNCAZ	*Cnidaria: Colonial anemones: Zoanthids*	SPCCR	*Sponges: Crusts: Creeping/ramose*
CNHYD	*Hydroids*	SPCE	*Sponges: Crusts: Encrusting*
CNTR	*Cnidaria: True anemones*	SPCLCC	*Sponges: Cup-likes: Cups/goblet*
CNTU	*Cnidaria: Tube anemones*	SPEL	*Sponges: Erect forms: Laminar*
CRCT	*Crustacea: Crabs: True crabs*	SPES	*Sponges: Erect forms: Simple*
CRLR	*Crustacea: Lobsters: Rock lobsters*	SPM	*Sponges: Massive forms*
CSSOA	*Cnidaria: Corals: Sony corals: Solitary: Attached*	SPMSI	*Sponges: Massive forms: Simple*
		WPOT	*Worms: Polychaetes: Tube worms*

3.3.5. Functional feeding groups

Every species was assigned a food source (epibenthic, surface, subsurface), diet (carnivore, omnivore, herbivore), food type/size [sediment, particulate organic matter, benthic microfauna (single-celled organisms), benthic meiofauna (organisms <500 µm), epibenthic megafauna (organisms >500 μm), phytoplankton, zooplankton] and feeding mode (deposit feeder, detritus feeder, suspension/filter feeder, predator, scavenger) after the classification system devised by MacDonald et al. (2010). Information was compiled using reference guides (Jones 2008; King & Fraser 2014; Branch et al. 2017) and literature (**Table 15**). The information was combined to create a final feeding guild code (*sensu* MacDonald et al. 2010; MacDonald et al. 2012) and cross-referenced with Heyns (2016). Mobile predatory species = “Predators”, sessile species feeding passively from matter in suspension = “Suspension feeders”, sessile species feeding actively from matter in suspension = “Filter feeders”, photosynthesizing species = “Autotrophs”, species feeding from dead organic material on the seafloor = “Detritivores”, species actively searching for dead organic material = “Scavengers” and species feeding from settled, dead organic material in the sediment = “Deposit feeders”. Where a species’ feeding behaviour was not available, information from a congeneric species was applied.

Table 15. Additional references for trophic information by major group.

Phylum	Reference
Porifera	Samaai, T. & Gibbons, M.J. 2005. Demospongiae taxonomy and biodiversity of the Benguela region on the west coast of South Africa. *African Natural History*. 1(1):1-96. [Online] https://hdl.handle.net/10520/EJC17340. Van Soest, R.W., Boury-Esnault, N., Vacelet, J., Dohrmann, M., Erpenbeck, D., De Voogd, N.J., Santodomingo, N., Vanhoorne, B. et al. 2012. Global diversity of sponges (Porifera). *PLoS One*. *7*(4): p.e35105. doi: 10.1371/journal.pone.0035105.
Bryozoa	Bullivant, J.S. 1968. The method of feeding of lophophorates (bryozoan, phoronida, Brachiopoda). *New Zealand Journal of Marine and Freshwater Research*. 2(1): 135-146. doi: 10.1080/00288330.1968.9515231. Winston, J.E. 1977. Feeding in marine bryozoans. In *Biology of bryozoans*. Woollacott, R.M. & Zimmer, R.L. Eds. New York, United States of America: Academic Press. 233-271.

3.3.6. Relative cover photograph assessment and CATAMI identification of species

The relative cover of biota and seafloor substrata was calculated for 373 photographs in Coral Point Count with Excel Extensions (CPCe 4.1) using the random point count method (Kohler & Gill 2006). A 0.2 m^2 quadrat was overlain in CPCe 4.1 inside the circular frame of the jump camera rig (*sensu* Heyns et al. 2016). Fifty-four random points were assigned within the quadrat, based on results from species accumulation curves published in a study from the Tsitsikamma MPA further east along the South African coast, which would be a comparable temperate region (Heyns et al. 2016). The CATAMI classification scheme was used to assign a species code for all biota assessed (Althaus et al. 2013), wherever a point landed on an organism. Wherever a point landed on seafloor substrate rather than a macroinvertebrate species or algae, a CATAMI substrate code was assigned (**Table 1**). The average relative cover (%) was calculated for each CATAMI biota and substrate type, across all sites, for each transect. To classify broad-scale habitat (reef and sand), the substrate was grouped according to the CATAMI distinction of "consolidated" and "unconsolidated" sediment. Since the transects were plotted along a changing depth gradient to test the effect of depth, there were naturally fewer reef samples because this habitat is restricted to the shallow start of any transect. Using "consolidated" and "unconsolidated" could account for rock cover (reef) and include cobbles and boulders, which were more evenly distributed along transects.

3.3.7. Species diversity and community composition using presence/absence data

The number of different phyla, species and feeding modes was counted per transect and depth category and recorded as "count". To assess species ubiquity, the number of samples in which a species was recorded was calculated and tabulated as 'frequency of occurrence' per transect and depth category.

3.3.8. Indices of species diversity

Frequency data based on presence/absence records for 373 samples across False Bay were used to calculate Rényi's diversity, which was plotted for depth categories and transects, using the function renyi (Oksanen et al. 2017) in the R package *vegan* version 2.4-5v (R Core Team 2017). The Rényi curve moves along the axis from species richness (does not account for relative abundance or evenness), through indices that increasingly incorporate abundance and evenness in their measure, to the relative abundance of a single, dominant species. The Rényi plot uses Trellis (lattice) graphics with a separate panel for each transect and depth category (Oksanen et al. 2017). Presence/absence records of each species were obtained for every sample in each category (depth and transect). Abundance was taken to be the frequency of occurrence across all records in a category. The proportion of species (p_i) in a category is the frequency of occurrence of species *i* divided by the frequency of occurrence of all species.

Rényi's diversity is a generalization of the Shannon-Wiener (H') diversity index given as follows:

$$H.a = \frac{1}{(1-a)} log \sum_{i=1}^{S} p_i^a \text{ .... } (3.1)$$

where a = scale parameter, and p_i^a = proportion of species i.

The species richness is given where a = 0 in Equation 3.1. Species richness can be gamma (γ) diversity or a diversity. In this study, a = 0 reflects the species richness in the aggregated sites for that category (depth or transect) on the Rényi curve. The H' diversity is given where a = 1 in Equation 3.1. H' diversity accounts for both species richness and evenness, and is typically written as:

$$\mathrm{H}' = -\sum_{i=1}^{s} p_i \, ln \, p_i \text{ .... } (3.2)$$

The Simpson's diversity index (D) is given where a = 2 in Equation 3.1. The D index gives more weight to dominant species and accounts for the number of species present together with their relative abundance. This index is not discussed in the results. At a = ∞, the Rényi number reflects the relative abundance of the dominant species.

3.3.9. Assessment of assemblage composition

Differences in species composition were analysed to test the effect of depth, transect, CATAMI habitat type and broad-scale habitat (unconsolidated and consolidated sediment) using one-way Analysis of Similarity (ANOSIM) tests performed on each factor separately with 999 permutations (Clarke 1993) using CATAMI relative cover data. Data were root-root transformed and the ANOSIM analysis in PRIMER-E version 6 (Clarke & Gorley 2006) tested whether patterns in the data were the result of those categorical factors, or chance. Multidimensional scaling (MDS) plots were plotted for significant factors ($p < 0.05$) that were determined with ANOSIM. When ANOSIM results detected significant differences ($p < 0.05$), a Bray-Curtis similarity percentage (SIMPER) analysis identified the contribution of an individual species or CATAMI group towards these differences (Clarke 1993; Clarke & Warwick 2001). SIMPER was performed for root-root transformed relative cover data and presence/absence data. A cut-off criterion of 75% similarity was selected for species of interest.

3.3.10. Environmental predictors of differences in community composition

Environmental data were normalised to ensure the comparability of different measures. A BIOENV procedure in PRIMER-E version 6 (Clarke & Gorley 2006) assessed which combinations of continuous environmental variables best explain differences in species composition among sites (Clarke & Warwick 2001). Slope, roughness, and depth were variables calculated from multibeam bathymetry data (**Figure 14**, **Figure 15** and **Figure 16**) and were tested in this analysis.

3.4. RESULTS

3.4.1. Species diversity and community composition based on presence/absence data

Eighty nine species were recorded in 373 samples on eight transects across False Bay (Appendix). Transect 1 had 46 sites, transect 2 had 62 sites, transect 3 had 50 sites, transect 4 had 31 sites, transect 5 had 48 sites, transect 6 had 40 sites, transect 7 had 56 sites and transect 8 had 40 sites. Species in the phylum Porifera (77 records), Echinodermata (74 records) and Cnidaria (64 records) were most frequently recorded across all samples.

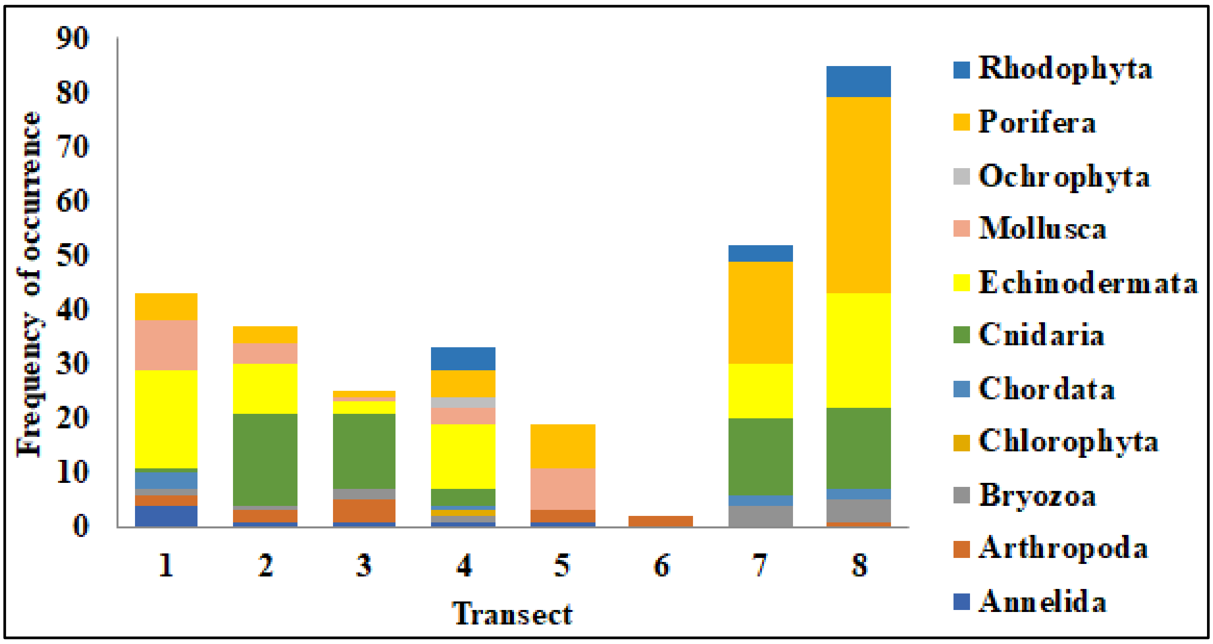


Figure 21. The frequency of occurrence of 11 phyla across eight transects in False Bay, South Africa.

The highest number of phyla was recorded on transect 4 (10 phyla) (**Figure 21**). One phylum (Arthropoda) was recorded on transect 6. Most species on transects 1 and 4 were in the phylum Echinodermata. Most species on transects 7 and 8 were in the phylum Porifera. Most species on transects 2 and 3 were in the phylum Cnidaria. Algae were recorded on transects 4, 7 and 8, but all three algal phyla were only recorded on transect 4. Seven feeding modes were recorded on 373 samples on eight transects in False Bay (**Figure 22**). Active suspension feeders (filter feeders, 117 records) and passive suspension feeders (suspension feeders, 127 records) were the most frequently recorded feeding modes across all samples. Suspension feeders were differentiated here as filter feeders (active) and suspension (passive) feeders. Predators were recorded everywhere except transect 7. Only predators were recorded on transect 6. The highest number of different feeding modes was recorded on transect 1 (6 modes). Autotrophs were recorded on transects 4, 7 and 8. Detritivores were recorded on transects 1, 7 and 8. Scavengers were recorded on transects 1, 2, 3 and 5. On no single transect were all seven feeding modes recorded.

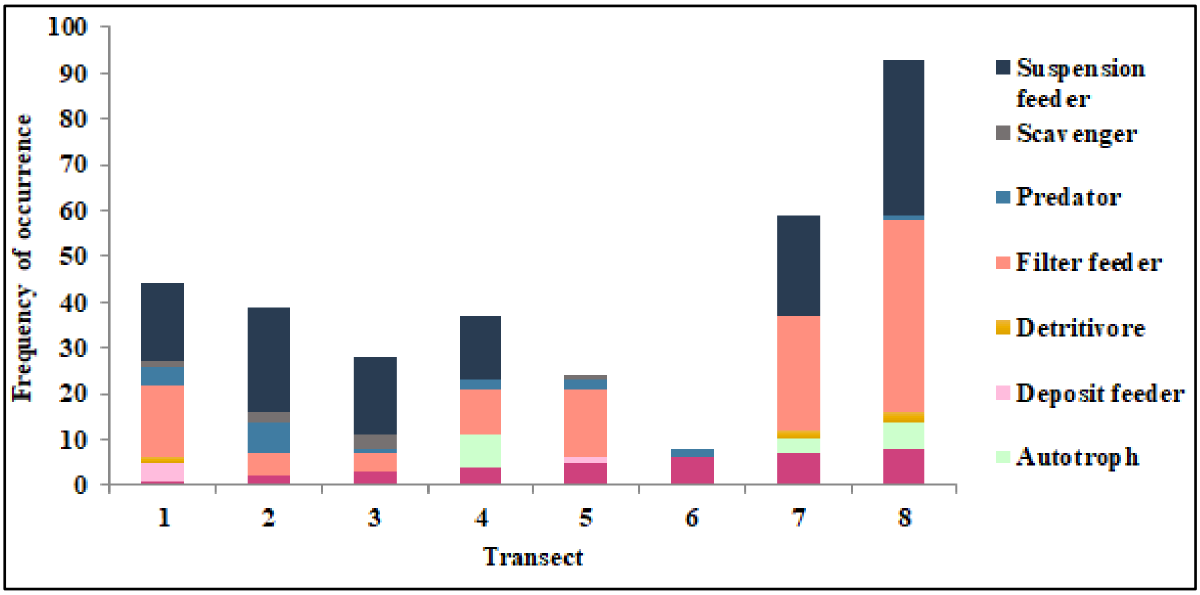


Figure 22. The frequency of occurrence of species categorised according to each feeding mode across eight transects in False Bay, South Africa.

The common featherstar *Comanthus wahlbergi* (**Figure 23**a) was the most frequently found species across 373 samples (27 records). The highest number of species was recorded on transect 8 (37 species) (**Table 16**). Transect 8 was dominated by the phylum Porifera (36 records) and characterised by *C. wahlbergi* (10 records). Species diversity was lowest on transect 6 where the west coast rock lobster (**Figure 23**d) *Jasus lalandii* (two records) was the only species recorded (**Table 16**). The highest number of species was recorded between 30 – 40 m depth (**Table 17**). *Comanthus wahlbergi* (12 records) was most frequently recorded between 30 – 40 m depth. Filter feeders were most frequently recorded in the 30 – 40 m depth category (**Table 17**). *Jasus lalandii* was the only species found deeper than 60 m. The horse mussel *Atrina squamifera* (**Figure 23**b) dominated between 40 – 60 m depth (**Table 17**). The red encrusting sponge *Clathria oudekraalensis* (**Figure 24**c) was most frequently recorded between 10 – 20 m depth.

Table 16. The total count of phyla, species and feeding modes for 373 samples on eight transects in False Bay, South Africa. The phylum, species and feeding mode most commonly recorded on each transect are listed as "most frequently found" (after Morgans 1962). The number of samples where the most frequently found phylum was recorded is listed in brackets. Where phylum frequency was tied (or very close to tied), all phyla are listed, and the number of samples is in brackets at the end. The number of samples where the most frequently found species was recorded is listed in brackets. Where species' frequency was tied, all species are listed, and the number of samples is in brackets at the end.

Count				***Most frequently found***		
Transect	**Phyla**	**Species**	**Feeding modes**	**Phylum**	**Species**	**Feeding modes**
1	8	21	6	Echinodermata (18)	*Atrina squamifera* (8), *Comanthus wahlbergi* (6)	Suspension feeder
2	7	19	4	Cnidaria (17)	*Ceriantheopsis nikitai* (5), *Anthopleura michaelseni* (4)	Suspension feeder
3	7	13	4	Cnidaria (14)	*Virgularia schultzei* (5), *Ceriantheopsis nikitai* (4)	Suspension feeder
4	10	24	4	Echinodermata (12)	*Comanthus wahlbergi*, *Atrina squamifera* (3)	Suspension feeder
5	4	12	4	Mollusca, Porifera (8)	*Atrina squamifera* (7)	Filter feeder
6	1	1	1	Arthropoda (2)	*Jasus lalandii* (2)	Predator
7	6	26	5	Porifera (19)	*Clathria oudekraalensis* (7)	Filter feeder
8	7	37	5	Porifera (36)	*Comanthus wahlbergi* (10)	Filter feeder

Table 17. The total count of phyla, species and feeding modes for 373 samples in nine depth categories (10 m increments) on eight transects in False Bay, South Africa. The phylum, species and feeding mode most commonly recorded on each transect are listed as "most frequently found" (after Morgans 1962). The number of samples where the most frequently found phylum was recorded is listed in brackets. Where phylum frequency was tied (or very close to tied), all phyla are listed, and the number of samples is in brackets at the end. The number of samples where the most frequently found species was recorded is listed in brackets. Where species' frequency was tied, all species are listed, and the number of samples is in brackets at the end.

Count					***Most frequently found***		
Depth (m)	**Transects**	**Phyla**	**Species**	**Feeding modes**	**Phylum**	**Species**	**Feeding modes**
0 - 10	2	4	4	3	Cnidaria, Echinodermata, Mollusca, Porifera (1)	*Pseudactinia flagellifera, Clathria oudekraalensis, Nucella squamosa, Roweia stephensoni (1)*	Suspension feeder
10 - 20	2, 7	9	26	4	Echinodermata (14)	*Clathria oudekraalensis (5)*	Filter feeder
20 - 30	1,2,3,4, 7, 8	9	39	6	Cnidaria (28)	*Comanthus wahlbergi (10)*	Suspension feeder
30 - 40	1,2,3,4,7,8	9	47	7	Porifera (33), Echinodermata (32)	*Comanthus wahlbergi (12)*	Filter feeder
40 - 50	1,3,4, 5,8	7	20	4	Mollusca, Porifera (10)	*Atrina squamifera (9)*	Filter feeder
50 - 60	4,5,8	4	4	4	Mollusca (5)	*Atrina squamifera (5)*	Filter feeder
60 - 70	4,5,6	0	0	0	-	-	-
70 - 80	6	1	1	1	Arthropoda (1)	*Jasus lalandii (1)*	Predator
80 - 90	6	1	1	1	Arthropoda (1)	*Jasus lalandii (1)*	Predator

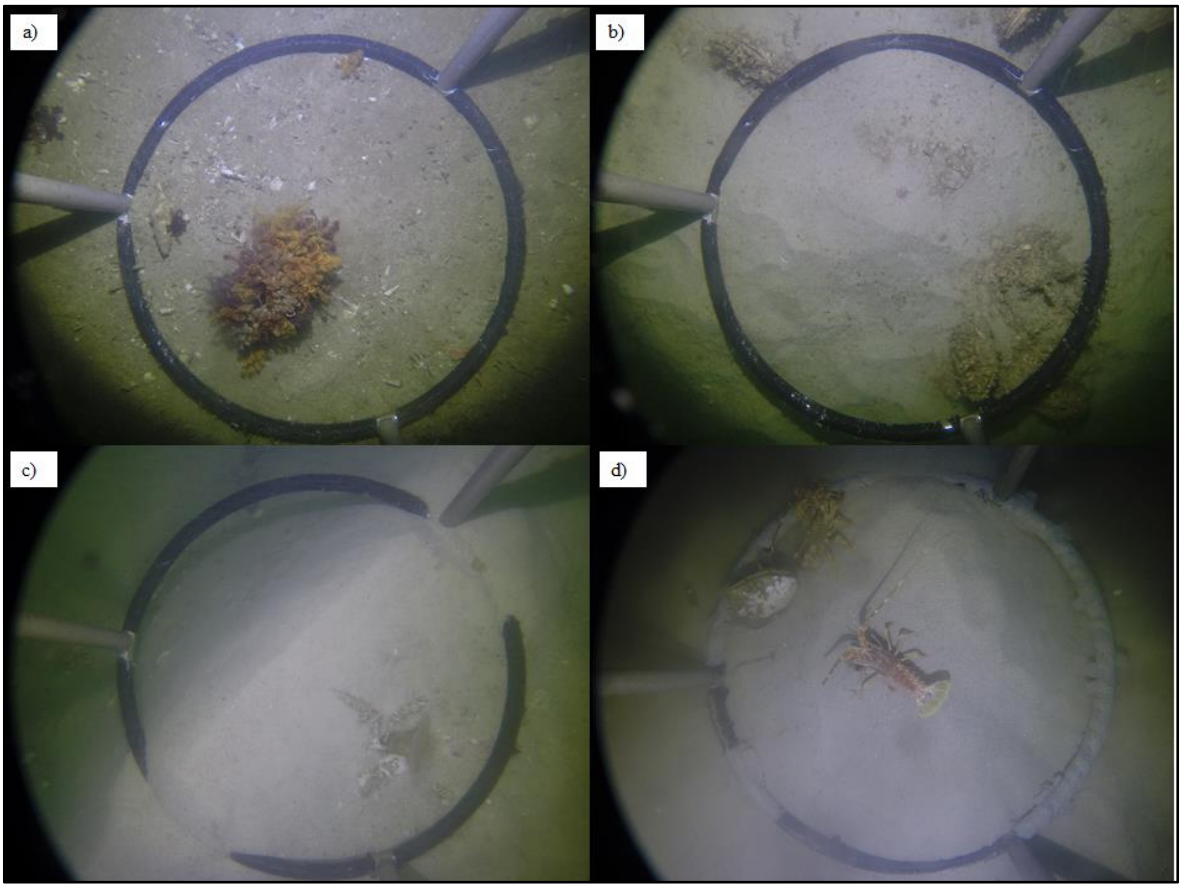


Figure 23. Jump camera photograph examples of a) *Comanthus wahlbergi*, b) *Atrina squamifera*, c) *Ceriantheopsis nikitai* and d) *Jasus lalandii.*

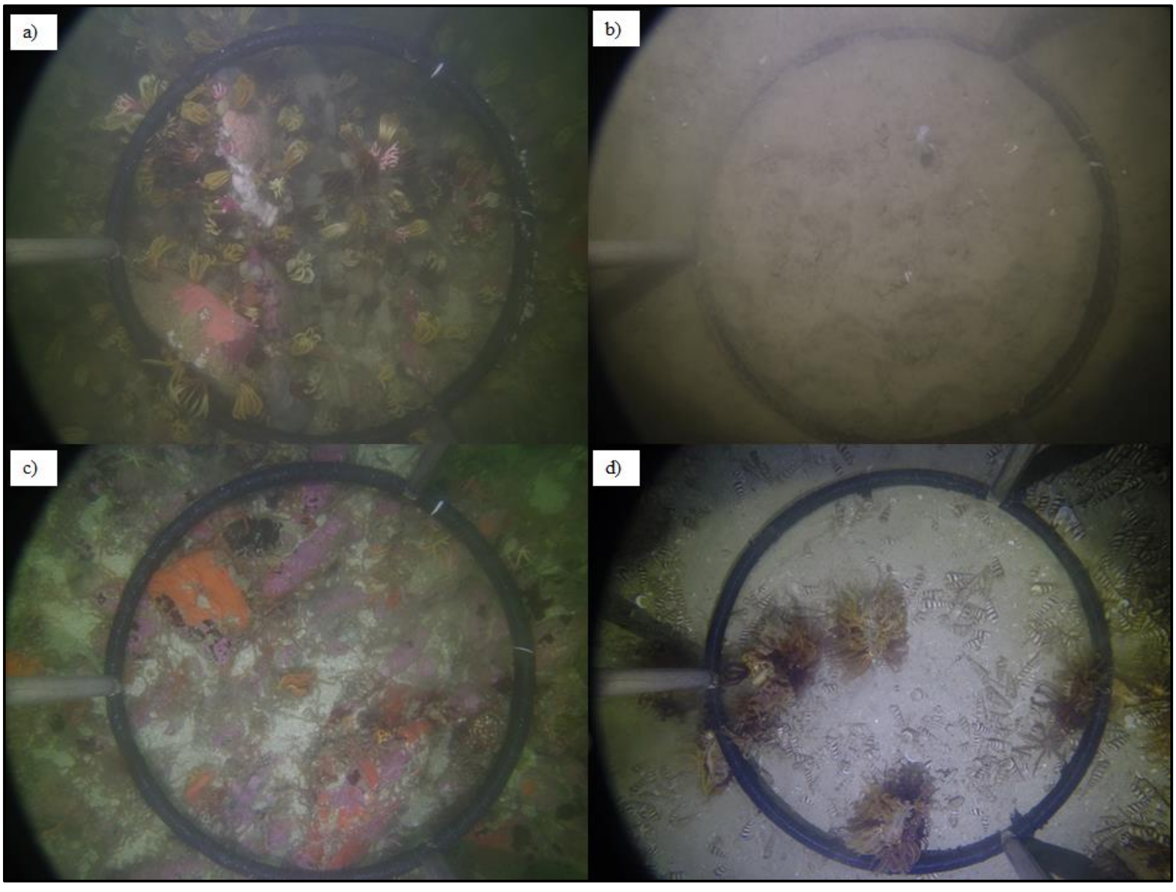


Figure 24. Jump camera photograph examples of a) Tropiometra carinata b) Virgularia schultzei, c) Clathria oudekraalensis and Ophiothrix fragilis, and d) Atrina squamifera covered with Comanthus wahlbergi.

3.4.2. Species diversity indices

Frequency data based on presence/absence records for 373 samples and across False Bay were used to calculate Rényi's diversity, which was plotted for depth categories and transects. There were nine depth categories at 10 m increments.

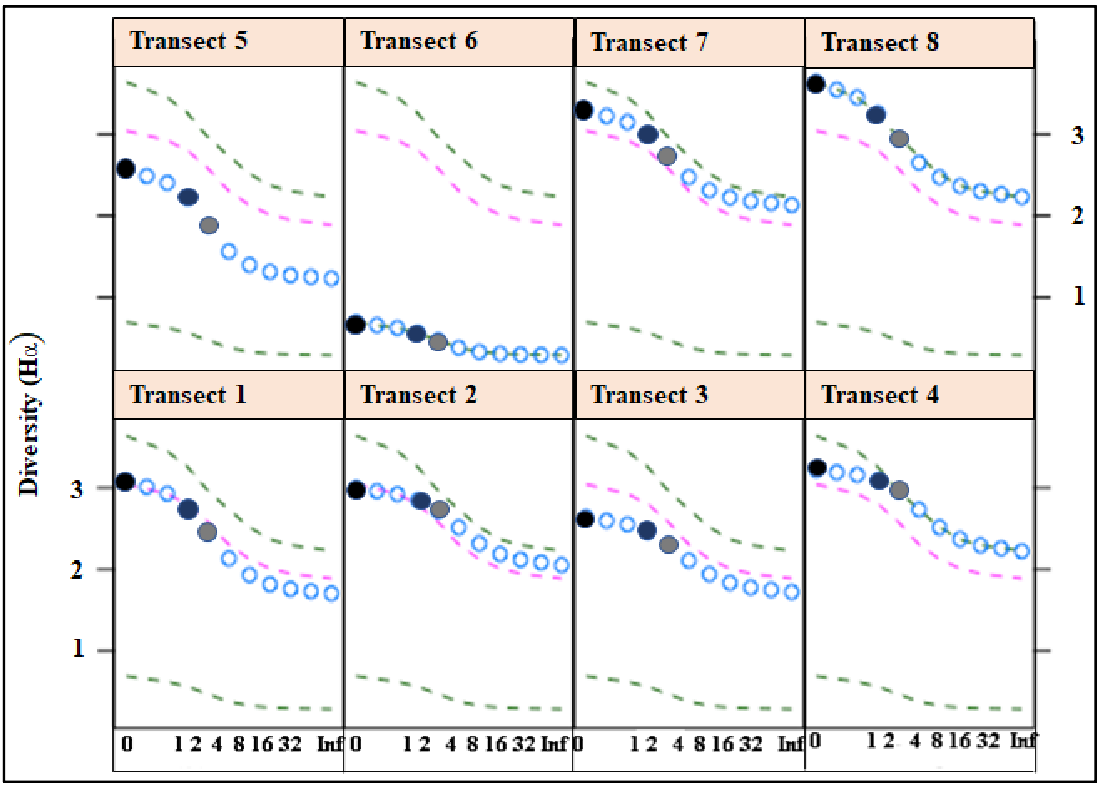


Figure 25. The Rényi diversities for eight transects in False Bay. The plot uses Trellis graphics with a separate panel for each transect. The x-axis shows the α value of the Rényi formula, where species richness (black dot) is α = 0, Shannon-Wiener Diversity (H') (blue dot) is α = 1, and the Simpson's diversity index (D) (grey dot) is α = 2. The last dot in the curve is the relative abundance of the dominant species. The y-axis shows Rényi diversity profile values (Hα). The green lines indicate the extremes, and the pink line indicates the median in the data set (Oksanen et al. 2017).

Species diversity is highest on transect 8, where the upper extreme of the dataset is represented (**Figure 25**). Species diversity is lowest on transect 6, where the lower extreme of the dataset is represented. Transects 4 and 7 reflect the second highest diversity overall, above the median diversity values for the dataset. Transects 1 and 2 have diversity trends that follow closely the median for the dataset. Evenness was similar for all transects except 6, where evenness was highest.

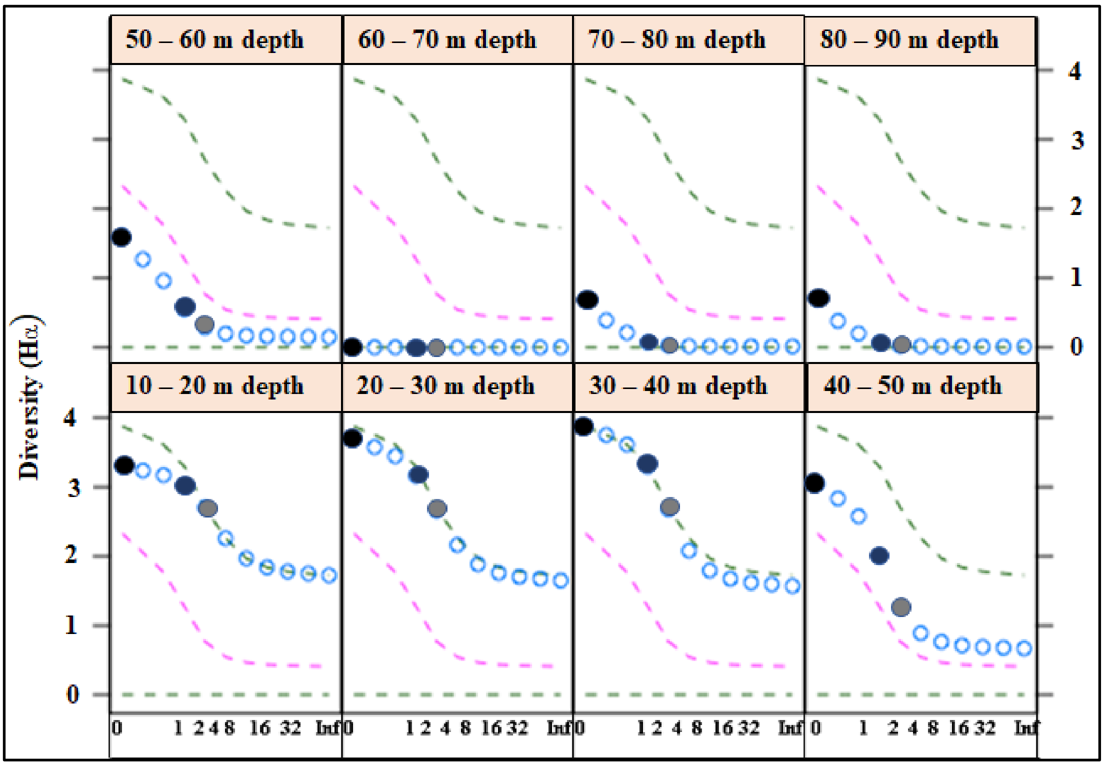


Figure 26. The Rényi diversities for eight depth categories (10 m increments) in False Bay. The plot uses Trellis graphics with a separate panel for each depth category. The x-axis shows the α value of the Rényi formula, where species richness (black dot) is α = 0, Shannon-Wiener Diversity (H') (blue dot) is α = 1, and the Simpson's diversity index (D) (grey dot) is α = 2. The last dot in the curve is the relative abundance of the dominant species. The y-axis shows Rényi diversity profile values (Hα). The green lines indicate the extremes, and the pink line indicates the median in the data set (Oksanen et al. 2017).

Species diversity was highest between 30 – 40 m (**Figure 26**). Diversity was more even between 0 – 10 m and 10 – 20 m than between 30 – 40 m. All species diversity indices (α, H' and D) increased between 0 – 40 m, and then decreased with increasing depth. No species were detected between 60 – 70 m depth, where the lower extreme of the dataset is represented. Species diversity was low on transects 7 and 8. Species diversity was close to the median value of the dataset between 40 – 50 m.

3.4.3. CATAMI diversity based on presence/absence data

Forty CATAMI classifications were assigned to 373 presence/absence samples on eight transects in False Bay. The most common groups were encrusting sponges (SPCE) (48 records) and unstalked featherstars (EFU) (39 records). The highest diversity of CATAMI groups was classified on transects 8 (21 records) and 4 (18 records) (**Table 18**). The lowest diversity of CATAMI groups was classified on transect 6. Rock lobsters (CRLR) were the only group recorded on transect 6 (2 records). Transects 4 (5 records), 7 (15 records) and 8 (19 records) were dominated by encrusting sponges (SPCE). The frequency of occurrence of unstalked featherstars (EFU), bivalve molluscs (MOB) and brittlestars (EOBSS) was equal on transect 1 (8 records each). True anemones (CNTR) were most frequently recorded on transect 2 (9 records). Seapens (CBQ) were most frequently recorded on transect 3 (5 records). Bivalve molluscs were most frequently recorded on transect 5 (7 records).

Table 18. The total count of the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classifications and the most frequently recorded CATAMI group on eight transects in False Bay, South Africa where EFU = *Echinoderms: Feather stars: Unstalked crinoids,* EOBSS = *Echinoderms: Ophiuroids: Brittle/snake stars* , MOB = *Molluscs: Bivalves* , CNTR = *Cnidaria: True anemones,* CBQ = *Cnidaria: Corals: Black & Octocorals: Fan (2D): Fern-frond: Simple* , SPCE = *Sponges: Crusts: Encrusting,* CRLR = *Crustacea: Lobsters: Rock lobsters* and SPCE = *Sponges: Crusts: Encrusting.* The number of samples a CATAMI group was recorded in is given in brackets.

Transect	CATAMI groups	Frequency of occurrence
1	17	EFU (8), EOBSS (8), MOB (8)
2	13	CNTR (9)
3	13	CBQ (5)
4	18	SPCE (5)
5	9	MOB (7)
6	1	CRLR (2)
7	14	SPCE (15)
8	21	SPCE (19)

3.4.4. CATAMI diversity based on relative cover data

Twenty-nine CATAMI classifications were assigned to 373 relative cover samples on eight transects in False Bay, including macroalgal groups. The most common groups with the highest cumulative relative cover were encrusting sponges (SPCE, 8.6%) and unstalked featherstars

(EFU, 6.1%). The highest diversity of groups was classified on transects 1 and 8 (11 and 13 groups, respectively) (**Table 19**). No CATAMI biotic groups were recorded on transect 6, where samples were mostly fine sand (SUSF, 98%) (**Figure 27**).

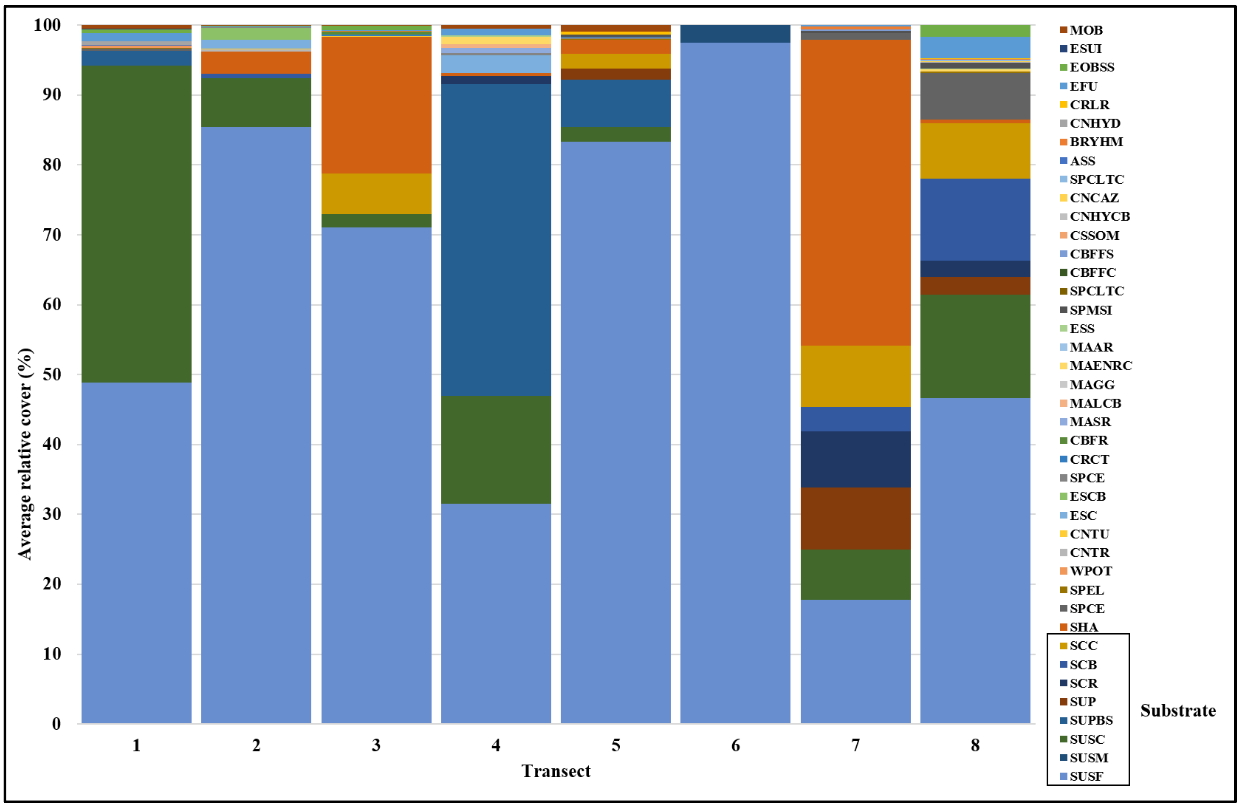


Figure 27. The average relative cover (%) of all biota and substrate types across all sites on each transect, for eight transects in False Bay, South Africa.

Transects 7 (3.7% total average cover by all biota) and 8 (13.5% total average cover by all biota) were dominated by cover of encrusting sponges (SPCE) (1.0% and 6.7%, average cover across sites on each transect, respectively). Cover on transects 1 (3.7% total average cover by all biota over 46 sites) and 3 (1.6% total average cover by all biota over 50 sites) was highest for unstalked featherstars (EFU) (1.2% and 2.5% average cover across sites on each transect, respectively). Cover on transect 2 (3.7% total average cover by all biota over 62 sites) and 4 (6% total average cover by all biota over 31 sites) was highest for benthic sea cucumbers (ESCB) (3.0% and 2.5% average cover across sites on each transect, respectively). Cover on transect 5 (2.0% total average cover by all biota over 48 sites) was highest for bivalve molluscs (0.9% average cover across sites).

Table 19. The total count of CATAMI classifications and the CATAMI group with the highest average relative cover (%) over all sites (N) on each of the eight transects in False Bay, South Africa. The number of sites where that group was recorded is listed as frequency for that transect. The number of sites on each transect is listed as N.

Transect	N	CATAMI groups	Average relative cover (%)	Frequency
1	46	11	EFU (1.2)	6
2	62	8	ESCB (1.7))	2
3	50	7	EFU (0.7)	2
4	31	10	ESCB (2.5)	2
5	48	7	MOB (0.9)	7
6	40	0	-	-
7	56	8	SPCE (1.0)	4
8	40	13	SPCE (6.7)	11

3.4.5. Patterns and predictors of community composition

To assess the effect of depth, transect, CATAMI habitat type and broad-scale habitat (unconsolidated and consolidated sediment) on species composition, multivariate analyses of species relative cover and some presence/absence data are presented in this section. A multidimensional scaling (MDS) plot shows similarity among sites based on species composition, where sites are characterised according to depth category (m), CATAMI habitat type and transect.

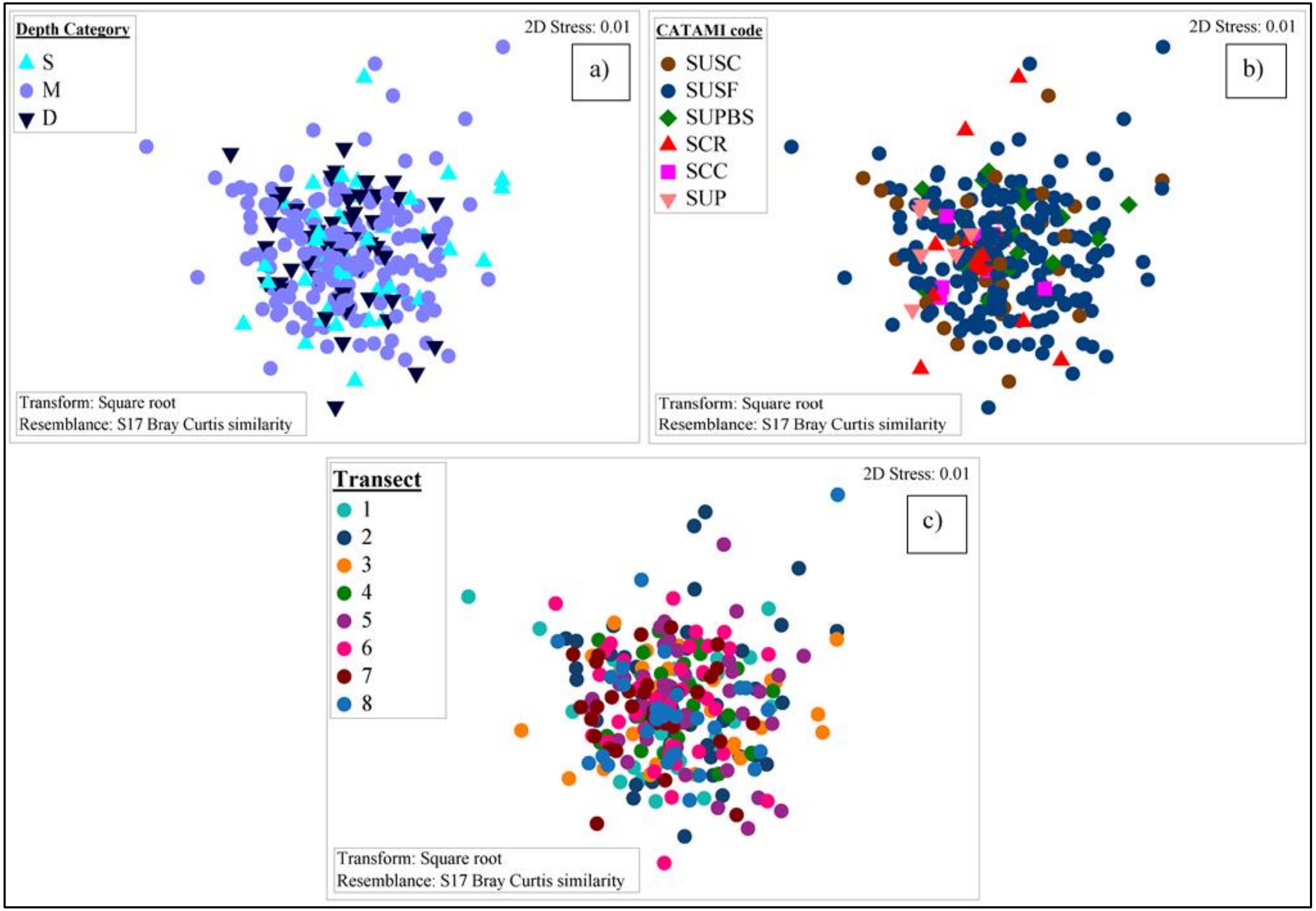


Figure 28. Similarity among sites based on species composition. Sites are characterised according to a) depth category [S = shallow (0 - 30m), M = medium (30 - 60m), D = deep (60 - 90m)], b) CATAMI habitat type and c) transect (1 – 8).

Separation among samples was low for all factors (**Figure 28**). A one-way ANOSIM confirmed that there was very low separation among samples in different depth categories, but any differences were significant (Global R = 0.015; p = 0.01). A one-way ANOSIM confirmed that there was very low separation among samples between CATAMI habitat types, but what differences there were, were significant (Global R = 0.02; p = 0.002). A one-way ANOSIM analysis showed that transect (Global R = 0.031; p = 0.001) was a significant predictor of similarity between samples, with low separation of samples. Of these significant factors, the relatively higher R-values make transect the strongest predictor, followed by depth and CATAMI habitat. The ARA classification was not significant (Global R = 0.009; p = 0.06). Habitat (unconsolidated and consolidated) was not significant (Global R = 0.006; p = 0.22).

The pair-wise ANOSIM results for depth showed that medium (30 – 60 m) sites were significantly different from deep (60 – 90 m) samples (R = 0.027; p = 0.001) and that shallow (0 – 30 m) sites were significantly different from deep samples (R = 0.063; p = 0.001). Medium sites were not significantly different from shallow sites (R = 0.004; p = 0.23).

3.4.6. Environmental predictors of community composition

Depth is the most significant predictor of differences in visible, epibenthic megafauna and algal community composition across False Bay (**Table 20**). The strength of this correlation is weak (Rho = 0.096), but the result is highly significant (p = 0.01).

Table 20. The combinations of environmental variables that best explain variation in species assemblage (relative cover) among 316 sites in False Bay, South Africa (BIOENV, α = 0.01).

Number of variables	**Correlation**	**Selections**
1	0.096	Depth
2	0.032	Roughness, depth
2	0.026	Slope, depth
3	0.009	All
1	-0.032	Slope
2	-0.043	Slope, roughness
1	-0.058	Roughness

Depth appears consistently as an explanatory variable in the three subsequent BIOENV selections, contributing to four combinations in total. Roughness and slope also contribute to four combinations each but are only positively correlated when they are considered in combination with depth. The positive correlation is weakest when all four environmental factors are considered in combination. Where roughness and slope are considered individually, or in combination with each other, the correlation is negative and only appears as the last three combinations.

3.4.7. Species that typify samples in each habitat type and depth category

Comanthus wahlbergi (**Figure 23**a) was typical of coarse sand sites (SUSC) (**Table 21**). The species also contributed to 22.85% similarity between rock (SCR) samples. The cup coral *Balanophyllia bonaspei* typified cobble habitats (SCC). *Atrina squamifera* (**Figure 23**b) accounted for nearly 50% of the similarity between samples collected on fine sand (SUSF) and 100% similarity between samples where the seafloor was classified as biogenic screwshell material (SUPBS). All similarities were zero for SUP because each of the 10 species recorded in this habitat type was recorded the same number of times (1 record each). The CATAMI group EFU typified coarse sand sites (SUSC), contributing 80% to similarity between sites in the CATAMI habitat category. Fine sand (SUSF) sites were characterised by MOB (80% similarity) and rock (SCR) sites were typified by SPCE (68%).

Table 21. The results of a Similarity Percentage (SIMPER) analysis show the percentage contribution (%) of these species to similarity between sites in each CATAMI habitat type, where similarities were not zero or one. Cumulative species percentage (%) contribution was cut off at 75% to list species in the table. Where a single species' contribution exceeded this, the percentage contribution is listed as greater than 75 %.

CATAMI habitat	**Species**	**Percentage contribution (%)**
SUSC	*Comanthus wahlbergi*	73.64
SUSF	*Atrina squamifera*	49.30
	Ceriantheopsis nikitai	21.32
SUPBS	*Atrina squamifera*	100.00
SCR	*Clathria oudekraalensis*	34.30
	Comanthus wahlbergi	22.95
	Balanophyllia bonaspei	18.00
SCC	*Balanophyllia bonaspei*	100.00

The presence of the burrowing anemone *Ceriantheopsis nikitai* (**Figure 23**c) and *C. wahlbergi* contributed to 69% of the similarity between samples in the shallow depth category (0 – 30 m) (**Table 22**). *Atrina squamifera* and *C. wahlbergi* contributed to 68% of the similarity between samples in the medium depth category (31 – 60 m). The only species recorded in the deep depth category (61 – 90 m) was *J. lalandii* which contributed 100% to the similarity between sites in this category. Overall, similarity between samples in all three depth categories was low (3%, 2% and 1% for shallow, medium, and deep sites respectively). The CATAMI classification group EFU were typical of shallow depth (0 – 30 m) contributing 44% to the similarity between sites in that depth category. Medium depths (30 – 60 m) were typified by MOB (56% similarity).

Table 22. The species that typify samples in each depth category, contributing up to 75% to the similarity between samples in a depth category, are listed in the shaded boxes on the diagonal. Species that contribute up to 50% of the dissimilarity between samples between different depth categories are listed in the unshaded boxes off the diagonals. Species are common in the depth category listed in the column, but rare in the depth category listed in the row. Shallow = 0 – 30 m, medium = 30 – 60 m, deep = 60.

		Common		
		Shallow	**Medium**	**Deep**
	Shallow	*Ceriantheopsis nikitai* *Comanthus wahlbergi*	*Atrina squamifera* *Balanophyllia bonaspei* *Mursia cristiata*	*Jasus lalandii*
Rare	**Medium**	*Ceriantheopsis nikitai* *Comanthus wahlbergi* *Virgularia schultzei*	*Atrina squamifera* *Comanthus wahlbergi*	*Jasus lalandii*
	Deep	*Ceriantheopsis nikitai* *Comanthus wahlbergi* *Virgularia schultzei*	*Atrina squamifera* *Comanthus wahlbergi* *Balanophyllia bonaspei*	*Jasus lalandii*

3.5. DISCUSSION

3.5.1. False Bay in context

The common featherstar (*Comanthus wahlbergi*) was most frequently recorded across all sites in this study. Crinoids are particularly common in False Bay, with *C. wahlbergi* most abundant on reefs (Jones 2008; Lanterbecq et al. 2009; Branch et al. 2017). Morgans (1962) recorded *C. wahlbergi* as "common" between 15 – 25 m depth at seven sites. As suspension feeders that grip to rock using cirri, they were most frequently recorded in this study on transects 1, 4 and 8. They typified transect 8, a region of rock and fine sand with some cobble, pebble and coarse sand habitat in the east of False Bay between 22 – 54 m depth. This was suitable habitat for crinoids to cling to rocks where they form dense coverage (Jones 2008; Lanterbecq et al. 2009). Conservation priorities are typically focused on rare species, but there is a case to monitor common species, particularly as a reference for ecosystem change. Common species are also easier to sample and are often suitable indicators to assess change. *Comanthus wahlbergi* formed part of the diet of roman seabream (*Chrysoblephus laticeps*), a fish listed as Near Threatened (Mann et al. 2014a), and part of the diet of red stumpnose seabream (*Chrysoblephus gibbiceps*) (Van Zyl 2013), listed as Endangered (Mann et al. 2014b). Evidence of trophic effects from overfishing are difficult to assess using community data (Rochet & Trenkel 2003; Fulton et al. 2005). However, monitoring across the ecosystem can better track changes where there is competition and predation within macroinvertebrate communities (Blamey et al. 2010), and doing so over time can monitor trophic impacts on the benthos (Frid et al. 2000).

Two other species typical of reefs were frequently recorded. The red encrusting sponge [*Clathria (Isociella) oudekraalensis*] is an endemic sponge described between 6 – 24 m on both sides of the Cape Peninsula (Samaai & Gibbons 2005; Jones 2008). It was most commonly recorded on transect 7 and typified samples on rocky reef. Transect 7 is west of Strand and Gordon's Bay, on Malmesbury Group shale between 16 – 37 m depth. *Clathria oudekraalensis* is described as a shallow water sponge (Samaai & Gibbons 2005), its encrusting form more typical of regions of high water flow. The most frequent records of the elegant featherstar (*Tropiometra carinata*) came from transect 8, and it was also recorded on transect 1, 4 and 7. This species was not captured in surveys by Morgans and Day (1959) or Morgans (1962), an indication that this study extends coverage of the bay and that doing so adds to our ecosystem level picture of False Bay. *Tropiometra carinata* is also not discussed in Field (1970) as typical of any of the habitats or regions described. It is documented in Day et al. (1970) and well known to divers who frequent the eastern reefs of False Bay (Jones 2008). It was recorded using baited remote underwater video systems (BRUVs), typically at intermediate (16 – 30 m) depths on reef in the eastern region of False Bay (Carr 2014).

The most frequently recorded species on unconsolidated seafloor (including fine sand, coarse sand, biogenic screwshell and cobble habitat) was the horse mussel *Atrina squamifera*. Higgo (2015) hypothesized that *A. squamifera* distribution could be explained by sediment type and grain size; in this study, the species was most often recorded on fine sand. It was sampled on all transects except in the east and was most frequent in the north-west and central False Bay. *Atrina squamifera* typified fine sand and biogenic screwshell habitat between 20 – 64 m depth just south of Smitswinkel Bay and in the Paulsberg no-take zone of the TMNP MPA. While there were more records of *A.* s*quamifera* on fine sand, it was also recorded on coarse sediments and always recorded as single individuals rather than aggregations. *Atrina squamifera* was recorded in the same "grounds" characterised by the polychaete *Diopatra neapolitana* and the heart urchin *Spatangus capensis* (Morgans 1962). *Atrina squamifera* did not characterise regions described either by Morgans and Day (1959), Morgans (1962) or Field (1970, 1971) and does not appear in their published species lists. It is recorded in Day et al. (1970). The species was not captured on BRUVs data which were limited to 50 m depth (Carr 2014).

This study confirms findings by Higgo (2015) that *A. squamifera* is found distributed as single individuals, as opposed to the aggregations typical for a similar species in the same genus, *A. zelandica*, in New Zealand (Cummings et al. 2001, Miller et al. 2002). Higgo's (2015) estimations around Roman Rock showed the density of *A. squamifera* to be one individual per 3 m^2, a pattern of distribution similar to observations of *A. zelandica* on a "featureless" seafloor (Mattern et al. 2013). As a filter feeder, the distribution of *A. squamifera* is likely linked to patterns of circulation in False Bay. It was hypothesised that where current speeds are high, *A. squamifera* appear as individuals, and that *A. zelandica* form dense aggregations where currents are low and there is relative shelter from wave action (Warwick et al. 1997; Cummings et al. 1998). No aggregations of *A. squamifera* were observed in this study; all records were upright individuals visible on the seafloor. It is difficult to assess *A. squamifera* densities without data on the bottom currents at the same sites, but the species was absent on transects 7 and 8. Here, surface current speeds are high (Atkins 1970a); however, the prevalence of reef habitat would make this an unlikely habitat for *A. squamifera*. Relative surface current speeds are lower where *A. squamifera* was most frequent. Patterns of circulation around False Bay are variable and complicated, with fine-scale patterns and some seasonal variation; the "patchiness" in the distribution of *A. squamifera* that is raised by Higgo (2015) is matched by variation in its associated sediment type, grain size and location in the bay (which accounts, in part, for circulation). Improved data on circulation, especially the bottom currents, will further investigation of this species' distribution.

Atrina squamifera was detected across depth categories in False Bay, which suggests that the species is widely distributed. It was suggested that surveys covering the bay's full extent should confirm whether any dense aggregations of *A. squamifera* exist (Higgo 2015). This study indicates that they do not. However, patchy distribution and solitary formation of the species might require an area-by-area approach to understanding its actual densities in False Bay. The jump camera is helpful for rapid biodiversity assessment and detected *A. squamifera* at a broader extent across the full False Bay ecosystem. It is possible, however, to miss localised areas of dense aggregations on sand in False Bay that are better tested using gridded sampling design. Higgo (2015) suggests that *A. squamifera* is less an ecosystem engineer (as suggested for *A. zelandica*) than a foundation species that hosts an associated biological community. The jump camera method improved the detection of a species that, while of relatively low commercial interest, is of ecological significance and was underrepresented in previous surveys.

3.5.2. Are any important species missing?

Several invertebrates constitute commercial interest or conservation concern, or both, in False Bay (DAFF 2016; Okes et al. 2018). The study did not adequately quantify mobile, predatory species like the west coast rock lobster (*Jasus lalandii*) that would be important for long-term monitoring. The species was recorded at six sites, which was more than expected for a mobile species that was anticipated to move if deterred by the quadrat descending to the seafloor from the boat, but not to the extent that it dominated reef sites as shown in the invertebrate dataset analysed from the BRUVs survey (Carr 2014). The use of bait and horizontal-facing video cameras is evidently more useful to draw individuals into the field of view to quantify, and a focus on reef habitats and kelp beds would be a more targeted design to capture a species of interest such as *J. lalandii* (Roberson et al. 2017).

Jasus lalandii was recorded in the deepest reaches of False Bay, on fine sand between 49 – 84 m. The species has been described in the region from the intertidal zone to 46 m depth (Day et al. 1970), to at least 30 m (Jones 2008) and to at least 50 m depth (Pollock & Beyers 1981). Carr (2014) highlighted *J. lalandii* distinguishing reef from sand sites, and Morgans and Day (1959) recorded the species on shallow reefs and kelp beds on the western margin of False Bay. While the number of records is insufficient to draw any conclusions or describe patterns, it is interesting to note that *J. lalandii* was detected using an unbaited method, and on sand habitat because the depths surveyed could be extended by using cameras.

A quadrat and downward-facing camera should suit cover estimates of species such as the abalone *Haliotis midae*. However, this species was absent from this study. *Haliotis midae* was not recorded by BRUVs or discussed by Morgans and Day (1959): if the species were more abundant, it would be expected to at least have been sampled using the jump camera on flatter reef. *Haliotis midae* is significantly depleted as a result of poaching, which may account for its absence (Okes et al. 2018). However, this might signal the need to target species of interest with other sampling methods. This study encompassed both the habitat and depth range of *H. midae*, but it was expected that the gastropod would inhabit crevices and overhangs which are not easily sampled using the jump camera or remain cryptic for identification from photographs. Future jump camera sampling should focus a gridded design that increases the number of reef samples, rather than a transect design that is useful for assessing changing depth but constrains the number of reef samples. Perhaps of more importance is that photographs give a broad ecosystem overview of predominant taxa and their coverage (Hewitt et al. 2004). This is particularly evident on rocky reef habitat, where biodiversity is high and sampling with camera-based methods can more adequately represent the visible, sessile epibenthic megafauna (Kipson et al. 2011; Guinda et al. 2012). This would be useful for long-term monitoring of ecosystem change, especially where increases in certain species (Tarr et al. 1996; Mayfield & Branch 2000; Cockcroft et al. 2008), shifts in species distribution (Blamey et al. 2010) or species declines (Griffiths 2000) have impacts on the benthic biota (Mayfield & Branch 2000; Blamey et al. 2010).

The scallop *Pecten sulcicostatus* was absent from this study. De Villiers (1976) discussed the commercial interest in this species, and investigation into its viability as a resource in False Bay. Aggregations of *P. sulcicostatus* were found at commercial densities near the centre of False Bay and were more broadly distributed at lower densities throughout the western half of the bay (De Villiers 1976). This distribution coincides to some degree with transects 1, 4 and 5 in this study. Its absence from the jump camera records is not unexpected: *P. sulcicostatus* swims (Arendse & Pitcher 2012) and would likely move away from an object that descends onto the seafloor, evading detection by the camera. However, the same could be said for mobile species such as *J. lalandii*, which was detected, albeit under-represented in this study. More likely is the possibility that the sampling design was not optimised to detect unevenly distributed concentrations of a particular species. A gridded sampling design in known regions of preference; that is, sand at about 40 m depth (Arendse & Pitcher 2012) that targets *P. sulcicostatus* would a) be more representative of the jump camera's suitability to detect the species at all and b) revisit whether these concentrations still exist in False Bay. Overall, the density of *P. sulcicostatus* was deemed too low in False Bay to support a viable fishery (Arendse & Pitcher 2012), but the detection of the full scope of biodiversity would be useful to long-term monitoring of ecosystem change.

3.5.3. Trends in species diversity

Epibenthic megafauna species diversity was highest between 30 – 40 m depth. Diversity increased with depth up to a maximum of 40 m depth, after which species diversity declined. This mirrors findings on reefs in the Tsitsikamma MPA (Heyns et al. 2016), for Arctic epibenthic communities (Sahade et al. 2004) and on coral reefs where species diversity increased with increasing depth in the shallows (Loya 1972), only to decrease after 30 m (Sheppard 1980). The intermediate disturbance hypothesis (Connell 1978; Fox 1979; Dial & Roughgarden 1998) was proposed as an explanation for patterns in Tsitsikamma (Heyns et al. 2016). According to this theory, wave action, light intensity and water movement would be highest in shallow depths where conditions favour fast-growing algae on reefs (Osman 1977; Dial & Roughgarden 1998). With increasing depth, light intensity diminishes, and water movement slows enough to reduce the competitive advantage of algae; slower-growing and suspension feeding species have space to colonize (Heyns et al. 2016). As depth continues to increase, light attenuates enough to exclude algae and water movement slows such that particle sediment becomes problematic for clogging low-growing and encrusting suspension feeders (Eckman & Duggins 1993). Results with depth or habitat need to be discussed with their relationship in mind: reefs in False Bay are shallow, and their visible diversity will be linked to depth results. It is therefore difficult to separate the two, unless future assessments target an equal number of reef and sand sites in comparable depth zones, or if the sampling design is such that the different probabilities of sampling reef or sand can be accounted for in the analysis.

Species diversity was highest on the eastern and western margins of False Bay, which represented the greatest variety of CATAMI habitats. Diversity was highest on transect 8, on the eastern Malmesbury Group shale reefs between 22 – 54 m depth. The seafloor on transect 7 and 8 was patchy: a mixture of consolidated rock, cobble, pebble, and coarse and fine sand. The east does not include the high-profile Cape Granite Suite reefs of the western bay (Du Plessis & Glass 1991). What the underlying Malmesbury Group shale rock type in this region lacks in vertical profile, might promote epibenthic megafauna diversity by its horizontal seafloor heterogeneity. Transect 7 and 8 also reflected the greatest variation in roughness and slope. This diversity in habitat is accompanied by a gentle depth gradient, with both transects covering the 30 – 40 m depth zone for most of their extent, which is the optimal depth for maximum diversity.

Species diversity was also high on transect 4 in the south-west between 20 – 64 m depth. This transect covered the greatest range in depth and species diversity may reflect the different depth zones covered over a relatively short distance. The transect covered a mixture of fine and coarse sand, and biogenic screwshell material. The rock in its shallowest reaches would be Cape Granite Suite (Du Plessis & Glass 1991), which is some of the highest profile reef in False Bay. Reef profile offers habitat complexity, increasing the availability of niches for different species in the form of crevices and overhangs (Kohn 1967). The combination of these variables promotes diversity (Kovalenko et al. 2012; Heyns et al. 2016). This was the only transect where all three algal phyla and six algal species were recorded.

Species diversity was lowest on transect 6, which is the deepest region between 68 – 84 m. This fits the pattern of decreasing diversity with increasing depth (Sheppard 1980; Heyns et al. 2016). Water movement is important to sessile suspension feeders (Eckman & Duggins 1993) which were absent at depth. Low current speeds at depth at the mouth of the bay (Atkins 1970a) may contribute to lower diversity at depth (Heyns et al. 2016). However, Field (1971) points to the paucity of data for bottom currents in False Bay and found that sediment grain size mediated depth-related patterns found in previous work (Field 1970). The region is also characterised by uniform, fine sand. It is tempting to explain low diversity on sand at depth with expected higher diversity on reefs where there is food, shelter, and light (Götz 2006;

Heyns et al. 2016). This result is difficult to interrogate, because reefs decrease with depth in False Bay (Du Plessis & Glass 1991). Field (1970) notes that the differences observed between reef and sand communities at depths less than 25 m become less marked with depth. It is most likely that sand habitats, especially at greater depths, comprise predominantly infauna that are undetected in photographs (Jórgensen & Gulliksen 2001).

Currently, the TMNP MPA protects the western margin of the bay (Tunley 2009). Helderberg MPA only covers a small area in the north-east. Most research to date has focused on the west, and in particular, its rocky shores and infratidal areas rather than deeper water. There are two important elements to explore: firstly, what does this diversity in horizontal seafloor habitat and epibenthic megafauna mean for fish in eastern False Bay? Secondly, what is the aim of management, monitoring and even dive tourism with regards to regions of high biodiversity? The threats to epibenthic megafauna are as high in the east as in the west: siltation at Gordon’s Bay harbour (De F. Retief 1970), pollution from the Eerste, Kuilsriver and Lourens catchments (Schulz & Peal 2001; Chingombe 2012; Mwangi 2014) and petroleum hydrocarbons from land- and sea-based sources (Moldan 1991) will affect epibenthic megafauna. Fishing activity on the eastern reefs will also affect the seafloor, where boat anchors and fishing gear (west coast rock lobster traps and octopus traps) could alter habitat complexity (Auster et al. 1996) and the composition of benthic invertebrates communities (Collie et al. 2000; Collins et al. 2010), but the exact impacts and severity are unclear (Backhurst & Cole 2000) unless monitored.

3.5.4. Frequency of feeding modes across habitat and depth

Autotrophs were only recorded on transects 4, 7 and 8. On these shallow reefs, wave action, light intensity and water movement would be highest and support algal growth (Osman 1977; Dial & Roughgarden 1998). These transects had minimum depths of between 16 – 22 m, shallow enough for light to penetrate the water column to support photosynthesis necessary for algal growth. Autotrophs were not detected along the extent of these transects but were limited to their shallowest reaches. No autotrophs were recorded deeper than 30 m. It is expected that autotrophs and their associated grazers would be among the first feeding groups to disappear from invertebrate communities as light diminishes with increasing depth, and this result mirrors findings along depth gradients further east in Goukamma (Götz 2006) and Tsitsikamma (Heyns et al. 2016).

However, no autotrophs were recorded on any other transects, even those that covered more shallow regions of False Bay. For instance, the minimum depth of transect 2 was 8 m but the seafloor sampled there was coarse sand. Therefore, the nature of the seafloor on these transects is an important consideration in a suite of explanatory factors. The south-west where transect 4 is located covers some rock in the shallowest reaches, and the seafloor is heterogeneous on transects 7 and 8. Algae would encrust over consolidated reef habitats with rocks, cobbles and boulders or anchor by means of a holdfast to areas of rough seafloor more easily than on sand (Velimirov et al. 1977). The distribution of autotrophs therefore not only follows a pattern with depth, but also habitat type: the rocky regions where autotrophs such as kelp can anchor are predominantly found along the western and eastern margins of False Bay (Chapter 2).

The south-western and south-eastern margins are also regions of upwelling (Van Ballegooyen 1991). Species of kelp grow rapidly where essential nutrients, light and suitable water temperatures are found in conjunction with a rocky seafloor where holdfasts can take hold (Van Den Hoek 1982). Where other transects may have covered shallow depths, reef habitats, or a combination of both, current direction and possibly upwelling in the south-west and south-east help distinguish why no autotrophs were recorded on other transects in this study. The cold ocean temperatures and nutrient-rich waters associated with upwelling events would support kelp species in the east - predominantly *Ecklonia maxima* and *Laminaria pallida* (Velimirov et al. 1977) - that are typical of the west coast and the Benguela upwelling regime (Anderson et al. 2007). The kelp *E. maxima* has been documented moving east into False Bay, first by Day (1970) after it was not present in surveys by Eyre (1939). The species was further recorded in False Bay by Bolton and Anderson (1987) and was discussed as part of the evidence for change in the intertidal biota of the bay over time (Mead 2011). Given that cooling sea surface trends have facilitated the extension of *E. maxima's* range further east (Bolton et al. 2012), the ability to track resultant ecosystem change using cameras may be important. While the jump camera would work best for encrusting algae, or small kelp, changes to the current configuration might facilitate better future sampling in kelp beds. Jump cameras facilitate the kind of repeat photography comparisons over time that can track what other change might result in the ecosystem (Reimers et al. 2014) and introduce landscape level monitoring of biodiversity impacts, such as is increasingly documented for vegetation cover (Hoffman & Rohde 2011) and the effects of land use change (Kull 2005; Moseley 2006) on land.

The eastward shift of *J. lalandii*, and their consequent predation on grazing species such as *Parechinus angulosus* (Mayfield et al. 2001, Blamey et al. 2012), has also encouraged the growth of macroalgae in regions where seaweeds were previously scarce (Blamey et al. 2010). Carr (2014) showed that *J. lalandii* were commonly recorded in the south-western and south-eastern margins of False Bay, where transects 4, 7 and 8 are located. In this study, *J. lalandii* were not recorded on transects 4 and 7, but this likely reflects that BRUVs are more suitable than a jump camera to sample this species. The jump camera method was useful for quantifying algal cover: change at the ecosystem level is important to monitor, and methods need to encapsulate information more broadly than single-species' focus.

Most mobile predators were found on sand in northern False Bay. A general clockwise surface current rotation was recorded in summer for False Bay, but no clear pattern was distinguished for bottom currents that were highly variable wherever measurements were attempted (Atkins 1970a). However, surface current vectors were slower in north-western False Bay from Simonstown to Muizenberg (Atkins 1970a). Here, predators able to move around to hunt may have an advantage, where water movement is insufficient to support active filter feeders, and suspension feeders that may require lower current flow to avoid damaging their feeding structures (Heyns et al. 2016).

Filter feeders and suspension feeders dominated across most transects and were especially apparent in the east. Circulation patterns have only been modelled at a very limited and fine scale in the east at Gordon's Bay, where water movement and seafloor topography are the result of a complex mix of longshore wave energy, wind transport, tidal, wave and rip transport and current transport from the south-west, south-east and north-west (De F Retief 1970). Understanding patterns of current velocity in this region is therefore complicated. However, optimal water movement and current flow are key to the feeding strategies of each different filter and suspension feeder, depending on their mode of food capture (Eckman & Duggins 1993). Most different kinds of filter and suspension feeders were found on transects 1, 4, 7 and 8 where upwelling and the flow of currents bringing nutrients from adjacent regions would supply particulate matter in suspension. This matches findings on coral reefs, where turbid reefs inshore supported filter feeders with particulate matter in suspension (Anthony 2000).

Mobile predators and scavengers were recorded on the deepest transects. Autotrophs and filter feeders were absent at depth. Bottom currents in False Bay are small and variable (Atkins

1970a) and have not been adequately modelled to fully explain patterns in feeding group distribution with depth (Field 1971). However, prevailing clockwise surface currents show that current vectors are lower at the mouth of False Bay (Atkins 1970a). Wave energy would be highest in the shallows, and surface and midwater currents would dissipate with depth (Bretschneider 1957). There is no influence of tidal race, draining or tidal current that would impact deeper regions of False Bay. Where current rates slow, rates of sedimentation increase, which is problematic for the clogging of the feeding structures of filter and suspension feeders (Heyns et al. 2016). While current flow was not measured in this study, studies elsewhere in South Africa have shown that filter and suspension feeders decrease with decreasing current speed (Heyns et al. 2016). Where light is too low to support autotrophs, and water movement too slow to support filter and suspension feeders, hunting and scavenging would be advantageous.

The absence of grazing herbivores on transects 7 and 8 is notable: the invasion of *J. lalandii* to Cape Hangklip and further east has been linked to the decline of herbivores in the same region, and an increase in filter and suspension feeders in their stead (Blamey et al. 2010). The jump camera was most useful for sampling reef, and reef in this area was well covered. However, expected grazers on reef such as the Cape urchin *Parechinus angulosus* were absent from this study. This absence matches findings from Blamey et al. (2012) that predatory *J. lalandii* have eliminated *P. angulosus* in parts of eastern False Bay. The interactions between species within communities, from competition and grazing to predation, will structure patterns of biodiversity as much as environmental factors (Lubchenco 1978; Branch 2008). These ecological interactions take place within the framework set out by environmental factors (McQuaid & Branch 1984). It is difficult to understand the nature of these relationships and predict their impacts in advance. Therefore, methods that detect and confirm regime shifts or species' absence are important for monitoring. The jump camera samples epibenthic megafauna biodiversity distribution and key environmental factors (Beisiegel et al. 2017), but it is easily repeated to detect regime shifts and the ecosystem effects of competition and predation over time. Targeted jump camera sampling in a grid format on reef should be a priority to track the consequences of this regime shift (Blamey & Branch 2012; Blamey et al. 2015; Blamey & Bolton 2018) on False Bay's western and eastern reefs.

3.5.5. Sampling across reef and sand habitats

The CATAMI description of community composition was applied using both presence/absence and relative cover data. It was expected that random point count estimates in CPCe might be useful for reef habitats, where benthic cover is high (Deter et al. 2012), but that they may underrepresent species presence on sandy habitats where it was expected that visible macrobenthic species would be sparsely distributed on the seafloor surface (Jørgensen & Gulliksen 2001; Sahade et al. 2004). This was the case for transect 6, where no data were recorded from random points dropped in CPCe. By chance, the 54 points dropped in photographs along that transect did not detect the rock lobsters that were recorded in the presence/absence description. This was, however, the lowest diversity region and even using presence/absence counts of all visible species, only rock lobsters were recorded.

A range of insights into the ecosystem offers different planning opportunities, and the consideration of factors for different questions. On transect 2, south of Simon's Bay and near Noah's Ark on the western margin of False Bay, anemones were most frequently recorded. The area is predominantly fine sand, which accounts for the repeated presence of *Ceriantheopsis nikitai* and *Anthopleura michaelseni*. Sea cucumbers represented higher abundance by relative cover on the same transect. On limited rocky seafloor between 11 – 20 m depth, the red-chested sea cucumber *Pseudocnella insolens* was recorded at such densities that it accounted for the highest relative cover. This result highlights that the size and behaviour of different specie will determine how well sampled they are using a random point count method (Perkins et al. 2016). Sea cucumbers, especially *P. insolens*, tend to aggregate or form dense groups over a relatively small area (Jones 2008). By contrast, the solitary anemones in this study represented a smaller size footprint in each image. Processing this baseline image data using both presence/absence of all visible biota in the jump camera frame and the point count method in CPCe was important so that a species' behaviour or size footprint in a photograph did not eliminate it from the dataset because it was not suited to point count analysis. The combination of both datasets in this study therefore provides a reliable baseline from which monitoring work can begin to ask specific, and often species-specific questions (Perkins et al. 2016).

Sea pens were recorded most frequently in the north, but featherstars accounted for higher relative cover. *Comanthus wahlbergi* form dense mats (Jones 2008; Branch et al. 2017) which means that even though the species was only recorded at two sites, it dominated relative cover.

On transect 4, encrusting sponges most frequently recorded but sea cucumbers had the highest relative cover. Red chested sea cucumbers (*Pseudocnella insolens*), golden sea cucumbers (*Thyone aurea*) and mauve sea cucumbers (*Pentacta doliolum*) were all only recorded at one site each on this transect, but the tendency of *P. insolens* to form dense groups (Jones 2008) increased their relative cover.

3.5.6. Environmental drivers of species distribution

Transect, depth and CATAMI habitat were the factors that best explained differences in community composition. The relative importance of these factors differed, and the consideration of one or two key factors may be more useful to direct monitoring and planning. The term transect is essentially a proxy for location in the bay, which incorporates different levels of factors, some of which were measured in this study as part of a landscape composition approach (e.g. CATAMI habitat, depth) and many that were not (e.g. localised circulation patterns). This helped delineate the bay into monitoring units, which facilitates later discussion of patterns in False Bay based on location and will be useful to highlight regions previously under-represented in other surveys, or that would merit monitoring focus in the future.

Depth was an important factor that explained differences in epibenthic megafauna communities. This confirms some predictions by Morgans (1962) and Field (1970), and mirrors findings elsewhere in South Africa (Götz 2006; Heyns et al. 2016), as well as for epibenthic megafauna in global seas (Callaway et al. 2002; Sahade et al. 2004; Deter et al. 2012). The correlation is relatively weak; perhaps explained by the generally gradual depth gradients across much of False Bay, and the fact that much of the region sits within 30 – 60 m depth. *Comanthus wahlbergi* was common on reefs between 30 – 60 m, and *A. squamifera* was common on sand in the same depth range. Sahade et al. (2004) showed that where the prevalence of hard bottom substrates increased with depth, species diversity increased. In this study, species diversity decreases with depth, as does the prevalence of reefs. Differences in particle size, the nature of the seafloor and sediment organic content vary with depth, and these factors will complicate any simple delineation of communities based on depth alone (Sheldon et al. 1972). Depth will form part of complicated interactions that determine benthic, macroinvertebrate community composition; including, habitat, circulation, sediment grain size and organic content, as well as competition, predation, and disturbance (Piepenburg et al. 2001).

Broad-scale habitat (unconsolidated and consolidated sediment) was not a significant factor. The transects in this study followed the natural proportion of habitats in False Bay, but in future a survey design that samples an equal number of reef and sand sites in comparable depth zones could investigate trends on reef sites. However, CATAMI seafloor classifications were significant, and these incorporate more fine-scale descriptions of habitats along the length of each transect. It may therefore be that these seafloor classifications more accurately capture the level of seafloor heterogeneity that is most important to invertebrate communities; that is, the CATAMI description captures more detail on sediment type and grain size, which have been shown to influence invertebrate community composition (Field 1971). The ARA classifications capture most seafloor heterogeneity, but this was not a significant factor in differentiating community composition across False Bay. The level of variability may in fact be too high to be significant in distinguishing communities at this scale (Hewitt et al. 2004), and acoustic data might be more useful in the future to understand patterns for specific species of interest. Certainly, at this stage, the level of uncertainty in acoustic data (Edwards et al. 2003), especially for a first description in False Bay, makes this factor currently the least useful for monitoring in the future.

While depth was the most important variable that explained differences along each transect, roughness and depth together were the next best explanation of differences in community composition, followed by slope and depth. Neither roughness nor slope were adequate predictors on their own. Roughness and slope values varied little across transects in this study, with the highest variation in the east. In effect, roughness corresponds to seafloor hardness and reflects reef coverage. This result helps separate depth as the variable that drives most of the observed variation, rather than the fact that reefs are shallow, and sand is deep in False Bay. Roughness and slope only explain differences in combination with depth, which confirms the pattern discussed previously that depth is a more important factor than CATAMI habitat, but both were significant. Depth, and only then the physical nature of the seafloor, are useful to distinguish macroinvertebrate communities across False Bay.

This study suggests that depth can predict differences in community composition at fine scales (4 m bathymetry resolution) but that roughness and slope at the same scale are not useful as factors on their own. It is important to know that there are differences with depth, even if the cause of those differences is more difficult to interrogate and can likely not be ascribed to depth alone. The differentiation of communities or the presence of key species with depth is useful for monitoring and planning at broad scales (Callaway et al. 2002). This is especially true in False Bay where there is no obvious oceanographic variation, and the physical ocean landscape (depth and habitat) represents the most reasonable means to distinguish biodiversity patterns.

3.5.7. A consideration of scale for environmental drivers

There are factors besides the ones measured here that influence species diversity and distribution. The question is, given that we now have an extensive range of insights into the biodiversity of the bay, which of these factors are useful for implementation in spatial planning or future management of False Bay. The other consideration is that, while these variables attempt to integrate a geological and a biological perspective to explaining patterns, they are all imposed on a complex and nuanced system that operates at a range of scales in time and space (Barry & Dayton 1991). It is important that the aims of surveys, and consequently, the methods they employ and the variables they superimpose, need revisiting. We need to understand ecological systems for any number of reasons: in False Bay, improved understanding guides the management of a changing system. While we cannot describe exactly how organisms are distributed based on their perception of their environment, we can choose variables that help us better meet our own intention.

Depth, roughness, and slope influence benthic invertebrate communities elsewhere, at a variety of scales (Dartnell & Gardner 2004). However, the methods to derive this resolution of information can be expensive and logistically challenging for other regions in South Africa. The question remains: what is the minimum necessary to measure that helps distinguish benthic communities at a scale relevant to future planning and management? Given that False Bay has been delineated as its own entity for the National Ecosystem Assessment 2019 (K Sink, South African National Biodiversity Institute (SANBI), Cape Town, personal communication), it makes most sense to consider scale at the extent of the bay. At the scale of the bay, False Bay varies little in roughness and slope, such that further refining our understanding of communities based on this resolution of information seems unnecessary. Depth, location (transect) and CATAMI habitat, as significant predictors of community composition, are more easily measured in the field to describe biodiversity across False Bay. These factors match findings elsewhere that substrate, location, and depth distinguished epibenthic megafauna communities (Sahade et al. 2004) and can be easily obtained using jump cameras if deployed elsewhere on the South African coastline.

3.5.8. A description of epibenthic megafauna communities across False Bay

The mouth of False Bay is deep and almost uniformly fine sand, with the lowest records of macroinvertebrate diversity and abundance. Only the mobile predator *Jasus lalandii* was detected here, between 68 – 84 m. This coincides with the *Spatangus/Epizoanthus* ground described by Morgans (1962). This study did not detect the "many large, purple sea urchins, *Spatangus capensis*" (Morgans 1962). Field (1970) proposes that the area characterised by *S. capensis* is even larger than indicated by Morgans (1962). That these urchins were not detected in our survey may be the result of their habit of burying in sandy substrate (Branch et al 2017), which highlights a limitation of the visual sampling for such species.

The northern, sandy seafloor of the bay was characterised by Cnidarians, and predators. Here, shallow sand is churned by wave action and siltation likely makes clogging filter-feeding apparatus problematic (Pihl 1986). The burrowing anemone *Ceriantheopsis nikitai* was most frequently recorded on transect 2, on almost uniform sand between 8 – 39 m depth. The crevice anemone (*Anthopleura michaelseni*) and the feathery sea pen (*Virgularia schultzei*) were recorded on a gentle depth gradient and homogenous seafloor south of Muizenberg. This area coincides with *D. neapolitana* ground (Morgans 1962), stretching northwards from Miller's Point to Muizenberg, and east across Strandfontein almost to Gordon's Bay along the northern reaches of False Bay. This study, like Field (1970), indicates that there is fine-scale variation within the broader *D. neapolitana* ground.

A unique region south of Smitswinkel Bay encompassed shallow reef inshore, near the cliffs of the Paulsberg no-take zone for fish within the TMNP MPA (Tunley 2009). Autotrophs, filter, and suspension feeders were all recorded here. Species diversity was high, and *C. wahlbergi* and *A. squamifera* were the most frequently found species. This region was not described or surveyed previously by Morgans and Day (1959) or Morgans (1962).

Diversity was highest in the eastern half of False Bay from Monwabisi south towards Kogelbay. Encrusting sponges dominated in occurrence and relative cover. Filter and suspension feeders were most common; in a region known for its seasonal upwelling (Atkins 1970a, Atkins 1970b). The red encrusting sponge *Clathria oudekraalensis* and common featherstar *C. wahlbergi* were most frequently recorded here. Transect 7 falls within the *D. neapolitana* ground (Morgans 1962). This study, however, recorded higher diversity in seafloor heterogeneity and community composition here. This kind of information, paired with a repeatable method, is important: Blamey et al. (2010) have reported significant changes to benthic communities along South Africa's south-western coast after a shift in the distribution of predatory rock lobsters *J. lalandii*. They report increases in sessile Cnidaria, Porifera, Scleractinia and Bryozoa, which translates to a shift from herbivore-dominated communities to an ecosystem of macrophytes and sessile cnidarians (Blamey et al. 2010). The dominance of sponges is evident along the eastern region of False Bay sampled in this study.

The eastern extent of False Bay falls largely outside of any formal protected area network, and as such, is subject to a variety of anthropogenic pressures. A consideration for the future is how this, in combination with ecosystem level changes (of which the invasion of *J. lalandii* may be one), will a) affect species at all levels of the trophic system and b) be managed. This study greatly extended the coverage of all previous assessments, and has captured ecosystem patterns further north than what was sampled by Blamey et al. (2010), who from their study could already assess that the benthic community at Cape Hangklip had been altered.

3.5.9. Advantages and disadvantages of the jump camera sampling method

The jump camera method extended non-extractive sampling to the reefs across the extent of False Bay, where previously only the western reefs up to 26 m depth that were accessible to SCUBA divers were sampled (Morgans & Day 1956, Morgans 1962). Relative to SCUBA surveys, the jump camera underrepresented cryptic and camouflaged species, and those species found in crevices, caves, and overhangs. The abalone *Haliotis midae* was notably absent from this study but may be corrected by targeted sampling in a grid format on reefs in False Bay, especially where low profile reefs could be sampled using a jump camera. Future reef-focused monitoring would increase the number of samples on the western and eastern margins of False Bay and thereby improve detection of reef-associated species. The description of sponges using cameras limits the taxonomic accuracy for identification, except where common species are well recognised and documented. However, using the CATAMI classification scheme captures the diversity in sponge growth forms rather than concentrating on species-level identification, which may be a more useful way to monitor changes in the cover of this group, particularly on the eastern reefs of False Bay where there is some indication of regime shifts that favour sponge cover (Blamey et al. 2010).

The random point count method of analysing jump camera photographs was more useful to characterise the epibenthic megafauna species diversity and composition on reefs than on sand. For reef samples, a method that quantifies cover is useful to monitor changes in species such as encrusting sponges and algae, as well as species such as *C. wahlbergi* and the red-chested sea cucumber (*Pseudocnella insolens*) that aggregate in high densities. The jump camera method provides a means to calculate the relative cover of subtidal macroinvertebrate species and substrate type, which improves on presence/absence species inventories. The cover of encrusting or aggregating reef species may change over time, and this would provide indicators by which to monitor ecosystem change. However, presence/absence analysis of jump camera photographs was suitable for both habitats, and more useful for sand sites where species are more sparsely distributed.

Relative to dredge and grab sampling, the jump camera method increased the number of samples achieved over a shorter survey timeframe, achieving 400 deployments by a single researcher in eight sampling days. Time efficiency is important for rapid biodiversity assessments, and long-term monitoring where capacity is limited. However, most of the invertebrate diversity on unconsolidated sediments in False Bay is in the infauna, which is largely, if not entirely, lost in jump camera sampling. For this reason, extractive sampling by dredge and grab is necessary to adequately describe the full complement of subtidal invertebrate communities on soft sediments.

The jump camera method nevertheless recorded visible predators and detritivores on unconsolidated sediments, photographing *Jasus lalandii* below 80 m depth on fine sand where it is absent from all previous surveys. Variation in epibenthic megafauna communities was still detected on soft sediments, especially in the north west of False Bay, where both Morgans (1962) and Field (1971) describe fine scale variation in invertebrate diversity both on the surface and in the infauna. The capacity the jump camera provides to collect more samples in the region also likely captures more of the variation in the habitat with which the epibenthic megafauna are associated. The horse mussel *Atrina squamifera* was detected on unconsolidated seafloor sediments, where it did not appear as a species that characterised any grounds described previously (Morgans 1962; Field 1970; Field 1971). The scallop *Pecten sulcicostatus* was absent from this survey, but there was little spatial overlap with the regions where this species was previously described in high concentrations (De Villiers 1976). Future sampling designs where the effect of a depth gradient is not being tested could target these *P. sulcicostatus* grounds in a grid format using the jump camera.

Jump cameras do not offer an all-in-one solution to describing the full complement of invertebrate biodiversity, and where a foundation of baseline species information is needed, dredge and grab sampling of soft sediments must accompany jump camera sampling. However, the jump camera method does provide a few key improvements to give a complementary view of the invertebrate communities in False Bay. An *in-situ* habitat description was paired with the biological sample, matching exactly in space and time, which provides ecosystem context that was previously noted as lacking in grab and dredge samples (Field 1970). This archived, shareable information is particularly useful to track ecosystem change over time, especially where photographs can be re-analysed and provide comparative datasets akin to those used in terrestrial vegetation (Rohde 1997; Hoffmann & Rohde 2011) and land use cover (Hoffman et al. 2018) repeat photography studies. An ecosystem view of the epibenthic megafauna in False Bay establishes a baseline for ecosystem threat status classification and long-term monitoring, particularly on reefs and where the habitat associated with invertebrate communities will change. The jump camera method is also non-destructive, which may be important in regions where there is conservation imperative to reduce the impact of sampling in sensitive habitats or on threatened species. This is particularly important for a monitoring method, which would be repeated over time. Whereas extractive sampling has limited applicability for repeated surveys, the jump camera can be used as often as necessary for a monitoring programme.

3.5.10. Conclusion

Patterns in epibenthic megafauna community composition across False Bay reflect changes with depth, and then with the physical nature of the seafloor. This study corroborates findings that the jump camera method is useful to detect sessile, epibenthic megafauna that are visible on the seafloor (Sahade et al. 2004; Beisiegel et al. 2017) but will under-sample mobile species and miss the infauna (Jørgensen & Gulliksen 2001). The jump camera offers a standardised, repeatable method that detects pattern and process across a greater extent (Roberts et al. 1994; Jørgensen & Gulliksen 2001; Sahade et al. 2004), covering more depths than most diver-dependent survey methods, and achieving coverage across more habitats than previous survey methods employed in False Bay. Depth, CATAMI habitat and location (transect) provide spatially and temporally stable factors that are baseline proxies for other factors, enough to guide future monitoring efforts and inform spatial planning. It is also possible to match these factors in space and time to the biological communities because they can all be recorded in the same survey.

Each of the eight transects could be described in terms of community composition and characterising species; however, low separation among samples and relatively weak correlations with predictors of community composition indicates that delineation of grounds at the scale of the bay is more useful to future management. A distinction between east, west, north, and south based on depth and habitat may be a useful start. The CATAMI classification explained more variation in community composition than broad habitat (consolidated and unconsolidated). The repeatability of this method, especially on rocky reef habitat, provides a platform for further investigation, especially into patterns of benthic community change in the east of False Bay where formal protection does not exist, but species diversity was highest. A pre-emptive rather than a reactive approach to long-term monitoring at the ecosystem level is beneficial not only at the community level but also, ultimately, at the species level. This is particularly important given indications of spatio-temporal changes in intertidal community composition in False Bay (Mead 2011) and the climate-related shift of species into False Bay that restructure entire communities (Blamey et al. 2010) that will pertain to currently unprotected regions of False Bay

CHAPTER 4

THE DISTRIBUTION AND RELATIVE ABUNDANCE OF ICHTHYOFAUNA IN FALSE BAY FROM MONO- AND STEREO-BAITED REMOTE UNDERWATER VIDEO SYSTEM SURVEYS

Cape seabream (*Pachymetopon blochii*) cluster around the stereo-BRUVs deployed to the seafloor in the Table Mountain National Park (TMNP) marine protected area (MPA). Photograph: Joris van Alphen

4.1. ABSTRACT

Conservation management relies on a sound understanding of how fish are distributed in marine systems. Conservation planning often relies on information on the key environmental drivers of these same distribution patterns. There is a need to understand the influence of marine landscape composition on demersal fish, especially where the extent of regional habitat heterogeneity and its effect on community composition is poorly understood. False Bay has a long history of fishing activity, and standardised, repeatable methods are needed to monitor fish populations at an ecosystem level. This was the first assessment of fish diversity and distribution on both reef and sand, and across a range of depth strata, using a standardised, non-extractive video method in False Bay. Two hundred and thirteen samples were analysed from baited remote underwater mono- and stereo-video systems (BRUVs) deployments. Videos were analysed to calculate the MaxN relative abundance of fish species and assign habitat descriptions at various scales. Fifty-seven species from 30 families were recorded between 4 m and 84 m depth. Habitat (reef and sand), depth, season and CATAMI habitat explained most of the variation in community composition. Of these factors, the CATAMI classifications were weakest, but helped understand fine-scale patterns in species associations. One-way ANOSIM tests showed that reef type (Global $R = 0.189$, $p < 0.001$), seafloor profile (Global $R = 0.169$, $p < 0.001$) and region in the bay (Global $R = 0.248$, $p < 0.001$) were also significant. Species groups were formed at 20% Bray-Curtis similarity, where associations were clear for groups typical of shallow reef and shallow sand sites. The Shannon-Wiener diversity index (H’) was higher on reef than on sand at the site level ($t = 1.972$, $p < 0.0001$), but the overall species richness for False Bay was similar for both habitats. Forty-three species were recorded specifically on sand, 10 of which were of conservation concern. These records included several batoids that are typically inadequately identified in fisheries catch data. Research in South Africa has typically focused BRUVs on reefs, but this study demonstrates that their application on soft sediments is useful to detect patterns for sand-associated species. This is especially true where soft sediments are not homogenous, and where species do not strictly associate with either reef or sand. This study gives ecosystem-level insights into the distribution of False Bay’s ichthyofauna and provides a basis for long-term monitoring using a non-extractive, repeatable method.

4.2. INTRODUCTION

Anthropogenic impacts in the coastal zone are direct and pervasive, with the result that marine biodiversity is highly threatened here (Gray 1997). Global declines in populations of coastal fishes are primarily linked to overfishing, pollution, and habitat destruction (Myers & Worm 2005; Pauly et al. 2005; Dulvy et al. 2008). The identification of these threats, together with information from biodiversity surveys of the populations they impact, drive efforts to critically assess approaches to systematic conservation planning and ecosystem-based fisheries management (Chatfield et al. 2010; Pittman & Brown 2011). Adequate fisheries regulation requires species-specific information (Maxwell et al. 2009). These data exist for some species of economic value, but are rarely adequate and are entirely lacking for most non-target species that are nonetheless taken as bycatch or impacted by cascading trophic effects and habitat destruction (Malcolm et al. 2007; Chatfield et al. 2010). This paucity of sufficient, basic ecological information across a broader range of species in ecosystems limits the efficacy of conservation efforts (Mellin et al. 2009; Pittman et al. 2009; Pittman & Brown 2011).

Primary among the information required to address these gaps is the identification of key environmental drivers and the extent of their influence on biodiversity in a region (Chatfield et al. 2010; Tittensor et al. 2010; Pittman & Brown 2011). These data inform predictions of the effect of habitat loss on biodiversity, direct protected area designation and conservation planning (Margules & Pressey 2000; Fernandes et al. 2005; Tittensor et al. 2010) and inform habitat-related fisheries management (Chatfield et al. 2010). Information on the distribution of fish, their patterns of abundance and key environmental relationships, directs long-term ecosystem level monitoring programmes and assessments, and informs evidence-based marine spatial planning. The relationships between biodiversity and the relevant environmental factors tend to be complex (Gray 1997; Worm et al. 2006), and the collection of adequate data to explore these links in temperate ecosystems is limited.

What we do know about the distribution patterns of demersal fish is that they are linked to several key environmental factors that exist at a variety of spatial and temporal scales (Knudby et al. 2010). Habitat type and complexity, seafloor rugosity, and depth are important influences on tropical fish species richness, community composition and abundance, especially on coral reefs (Friedlander & Parrish 1998; Pittman et al. 2007). These environmental factors influence food availability, shelter from predators and the availability of suitable nurseries, and are the most important predictors of species' distributions (Friedlander & Parrish 1998; Pittman et al. 2007). Water temperature, light availability and visibility have been shown to influence fish activity rates and movement patterns (Buxton & Smale 1989; Kerwath et al. 2007).

Prey availability, competition and stability are also important determinants of distribution patterns for most fish species (Knowlton 1992; Hixon & Beets 1993). The distribution and movement patterns of predatory species such as roman (*Chrysoblephus laticeps*), red steenbras (*Petrus rupestris*) and dageraad (*C. cristiceps*) are linked to the abundance of suitable prey, which is determined by environmental factors (Buxton & Smale 1989). The extension of this type of information is needed across a broader complement of species as a baseline for informed management of fish communities in regions that are under increasing human pressure. Whereas logistical constraints previously limited the collection of these ecological data, improvements in marine technology now facilitate the mapping of biodiversity on much broader scales (White et al. 2013).

In this context, baited remote underwater video systems (BRUVs) are particularly useful for data collection within larger depth ranges and across diverse habitat types to assess species' distributions at broad spatial scales (White et al. 2013; Bernard et al. 2014). The improvements that BRUVs offer over traditional survey techniques lies in their cost-efficiency through high data quality and the practice of simultaneous deployments, increasing sampling effort while lowering fieldwork time (Langlois et al. 2010). Coastal zone assessments in South Africa require improvement in both the spatial and temporal extent, while negotiating limited conservation resources (Tunley 2009). Baited remote underwater video systems appear to provide a complementary method for dealing with large areas, widely distributed species, and the sustainability constraints of long-term programmes (Bernard & Götz 2012; White et al. 2013). They also facilitate the kind of landscape analysis that is well-established for terrestrial systems, investigating the relationship between ocean landscape features and species distribution that is developed in conjunction with improved capacity for high resolution seafloor mapping and descriptions of landscape composition (Moore et al. 2011).

False Bay is classified as part of the Agulhas Bioregion, a warm-temperate bioregion typical of the southern Cape coast (Lombard et al. 2004). This classification is based on large-scale patterns in ocean currents, productivity, temperatures, and biological variation (Lombard et al. 2004). Cape Point in the south-west of False Bay is a place of overlap for two ecotones; namely, the South Western Cape bioregion to the west and the Agulhas bioregion (Lombard et al. 2004). While there is a trend of decreasing ichthyofaunal diversity from east to west along the South African coast, False Bay represents species typical of two major oceanographic regimes, the Benguela and the Agulhas (Griffiths et al. 2010). The fish community comprises many species that are found around the Cape from the west to the south coast (Day 1970). Smith (1953, reported in Day 1970) suggested that 230 fish species distributed on the south and west coasts of South Africa were feasibly present in False Bay; since most of these are oceanic or deep-dwelling species, only 200 of these have actually been recorded inside the bay (Day et al. 1970).

Sixty-five percent of the species found in False Bay are typical of both the west and south coasts of South Africa. A remaining 30.5% is typical of the south coast, 3.9% is typical of the west coast, and 0.8% is found only in False Bay (Day et al. 1970). For these reasons, it is considered an important region for ichthyofaunal diversity (Day et al. 1970; Griffiths et al. 2010). Of the 200 species recorded inside False Bay, 41.4% are endemic, 14.8% of Indo-Pacific origin and 43.8% are considered from elsewhere (Day et al. 1970). It was suggested that the sandy seafloor would be depauperate of fish relative to the reefs, and that fish distribution would be associated with the distribution of reef habitat, water temperatures (ocean species avoid the cooler waters of the western shores in False Bay) and the prevailing currents (Day 1970).

Fishing in a variety of forms has long been important to False Bay (Richards & Pasquier 1989; Harris 2017), and the first recorded, commercial fishing activity dates to the seventeenth century (Penney 1991). The region supports commercial beach-seine and linefisheries and a recreational fishery, with all three often competing for the same species (Penney 1991). Multi-species commercial linefishery operations focus on the bay’s reefs, targeting resident reef fish such as Cape seabream (*Pachymetopon blochii*) and *C. laticeps*. The linefishery also targets more nomadic, predatory species that utilise the bay; notably, snoek (*Thyrsites atun*), yellowtail (*Seriola lalandi*), geelbek (*Atractoscion aequidens*) and carpenter (*Argyrozona argyrozona*) (Penney 1991). A range of fishing methods have been employed in the bay that impact the chondrichthyan population and these are detailed in a study by Best et al. (2013). This study recorded 37 species in the bay and showed populations of soupfin sharks (*Galeorhinus galeus*) and *Raja* species to be declining (Best et al. 2013).

Penney (1991) notes that linefish catches in False Bay are strongly seasonal and linked to environmental factors. Fluctuations in the appearance of *T. atun* and *S. lalandi* in the bay are the result of shifting migratory patterns linked to environmental factors and prey availability. Observed declines in the populations of resident reef fishes of False Bay, however, are the result of overfishing in both the commercial and recreational sectors (Penney 1991). The life histories of many endemic reef fish make them vulnerable to overexploitation, and with increased effort in the linefishery in the past century, many of these populations are considered collapsed (Griffiths et al. 2000). Declines in red stumpnose (*C. gibbiceps*) have reduced its prevalence in local catches (Mann & Wilke 2013), and the closure of the *P. rupestris* fishery highlights the critical need to prioritise long-term monitoring of species of concern in the bay. An evidence-based approach to describing the distribution of species across habitat types in the region is necessary to inform current fisheries management and protected area planning in the bay.

This study is a first assessment of species diversity and relative abundance of the ichthyofauna of False Bay at the full scale of the bay between 4 and 90 m in relation to key landscape descriptors. The aim is to i) describe species relative abundance and distribution across the full range of depths, habitats and across seasons, ii) identify key environmental factors that differentiate community composition in the region and iii) assess the relative importance of these environmental factors to provide a basis for ongoing surveys and assessments.

4.3. METHODS AND MATERIALS

4.3.1. Study area

False Bay (**Figure 29**) extends to a maximum depth of over 80 m at its mouth between Cape Point and Cape Hangklip (Spargo 1991). The bay is roughly square and extends approximately 30 km in length on either side (Spargo 1991). The Stilbaai MPA (**Figure 29** inset map) located at 34° 23'S and 21°25'E in the Western Cape province, and the Tsitsikamma MPA (**Figure 29** inset map) located at 34° 01'S and 23°53'E in both the Western and Eastern Cape provinces, were comparable sites where previous sampling times had been tested.

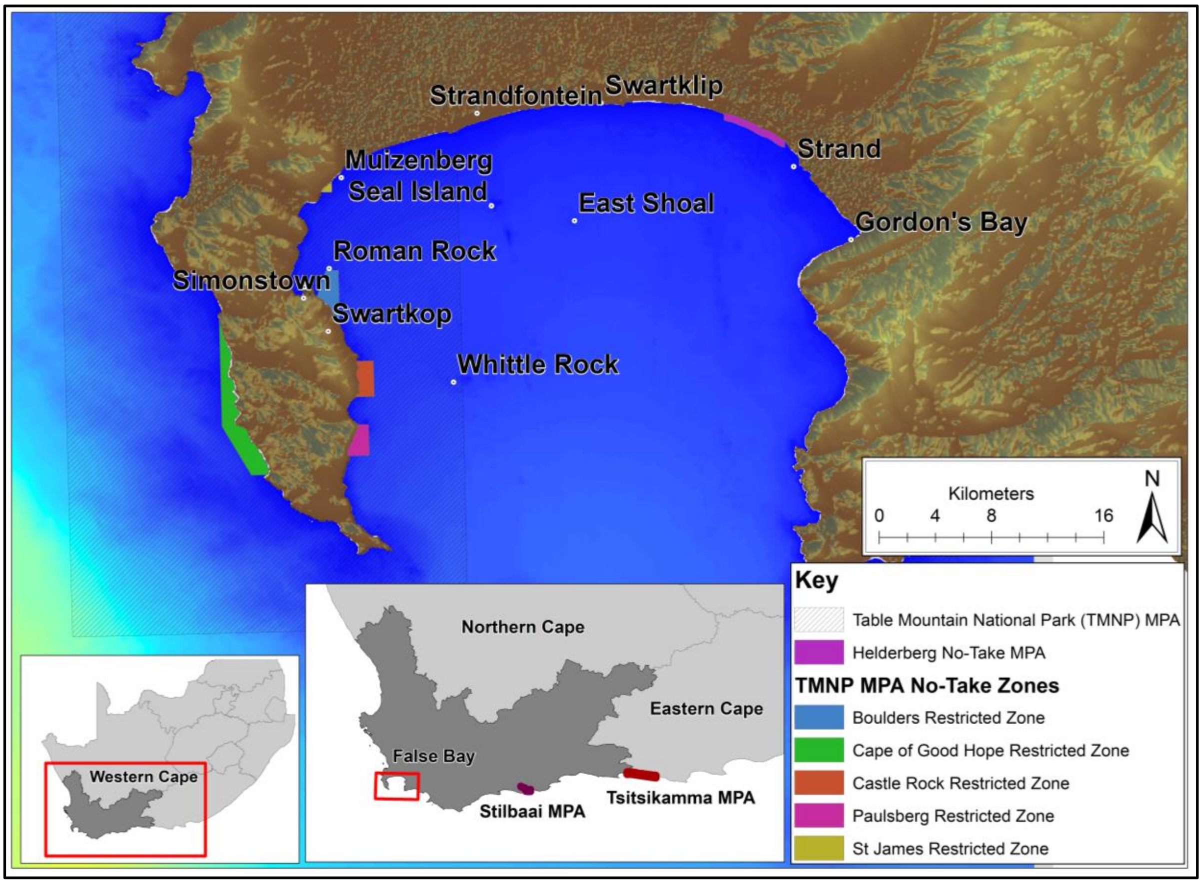


Figure 29. Key topographical features (EKZNW 2015) and marine protected areas (MPAs) (DEA 2019a) of False Bay and the Cape Peninsula, in the context of South Africa (inset map) and the Western Cape province where the Tsitsikamma marine protected area (MPA) and Stilbaai MPA are shown (inset map). Bathymetric depth (m) is gridded at 20 m (Van Zyl 2011).

4.3.2. Baited remote underwater video systems (BRUVs)

Two hundred baited remote underwater mono-video system (mono-BRUVs) hours were collected between July and December in 2012. This dataset was limited by camera housing and light capability to a maximum of 50 m water depth. To increase coverage of False Bay as the technological and logistical development of BRUVs unfolded in South Africa and facilitated deeper sampling (Bernard et al. 2014), a further 138 baited remote underwater stereo-video system (stereo-BRUVs) hours were collected between March and December in 2015. From a total of 338 video hours, 15 mono-BRUVs videos had zero visibility or field of view (FOV). Repeated red tide algal blooms reduced visibility to zero in 110 stereo-BRUVs videos. The usable stereo-BRUVs video sample size (28 samples) was therefore too low to use the size measuring capability that stereo-BRUVs offer to achieve length-frequency information for species across the bay. These samples were consequently treated the same as mono-BRUVs samples because 1) the same random, stratified survey design had been used to designate stereo-BRUVs sample sites and 2) diversity and relative abundance could be derived from the MaxN measures (described later) from both mono- and stereo-BRUVs data. Datasets were combined to a total of 213 usable samples as the single most extensive survey of the ichthyofauna of False Bay, across a range of habitats and depths to achieve suitable coverage of the bay (**Figure 30**).

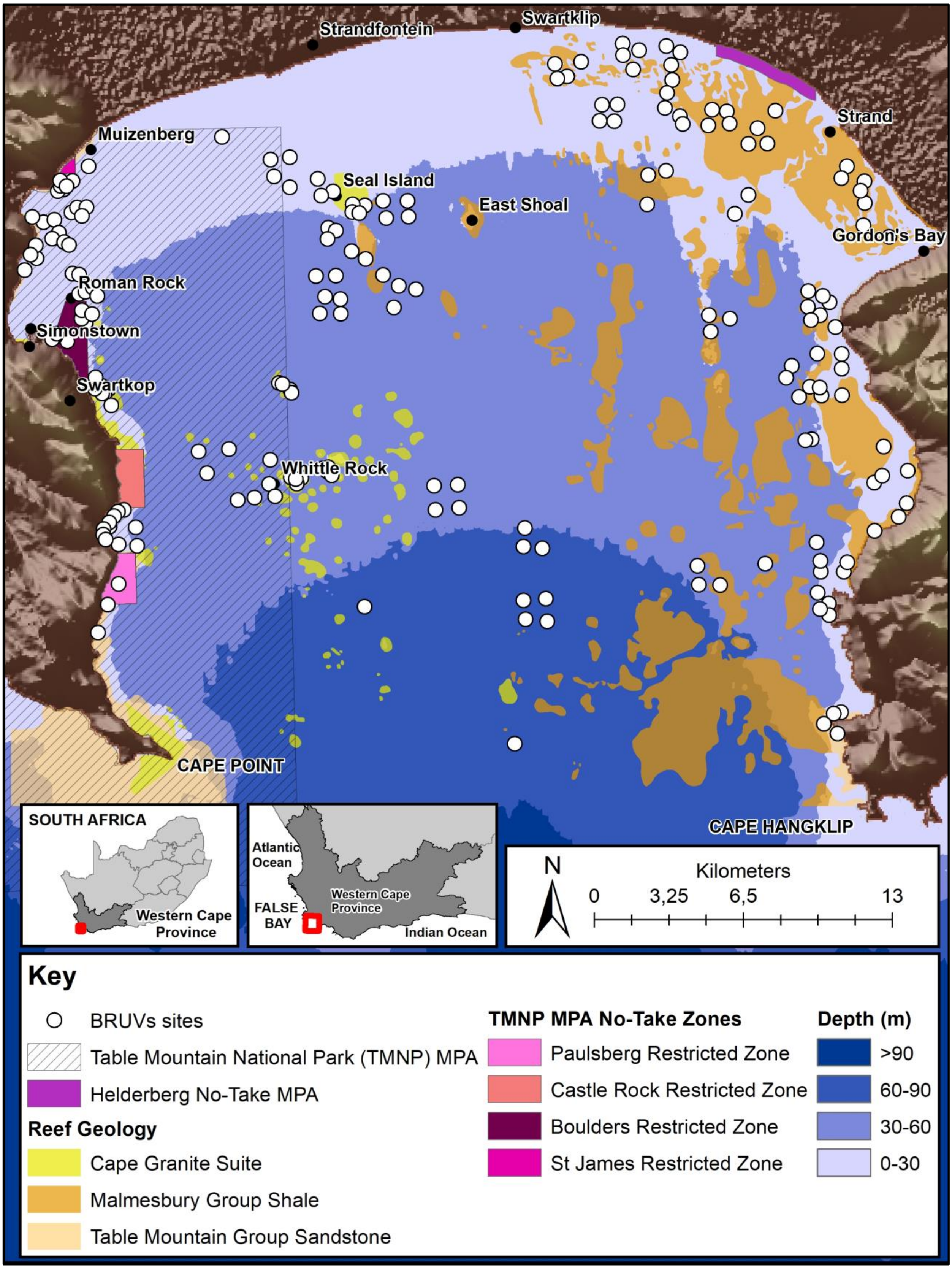


Figure 30. The location of 185 baited remote underwater mono-video system (BRUVs) and 28 baited remote underwater stereo-video system (stereo-BRUVs) sampling sites across False Bay. Sites were selected according to a random, stratified design based on subtidal reef geology (Van Zyl 2011) and depth (m) contours (Van Zyl 2011). The terrestrial topography (EKZNW 2015) and marine protected area (MPA) (DEA 2019a) network are shown for context.

4.3.3. Baited remote underwater mono-video systems (mono-BRUVs) sampling

4.3.3.1 Sampling sites

Spatially referenced depth measurements provided by the Council for Geoscience marine geoscience programme were interpolated in ArcMap™ (www.esri.com) to create a contour map of False Bay (Van Zyl 2011). Nine sampling zones, each with a range of depths and habitat types, divided the bay (**Figure 31**). Each sampling zone incorporated different factors and different levels of these factors. Some of these factors were measured in this study: chiefly, habitat and depth (and nested within these, reef type and reef profile). Some of these factors were not: for instance, local circulation patterns. However, nine zones ensured that a cross-section of all these factors was integrated into the survey design to achieve maximum representation across False Bay. These sampling zones also considered the distance from the nearest slipway to each survey region and facilitated fieldwork planning. The combination of both considerations was important as a basis for other monitoring programmes. Achieving coverage of the bay's different habitats and depths, and planning vessel capacity, fuel costs, and survey distances for repeat sampling over multiple days by a single surveyor formed the same basis for planning that other conservation management and monitoring would have to consider. Sampling zones were restricted to 5 - 50 m depth (60% of the bay) using the buffer geoprocessing tool in ArcMap 10.1™ (www.esri.com). Deployments could not be achieved from the sampling vessel in the turbulent waters shallower than 5 m and the cameras needed lights and customized housings in waters below 50 m. The stereo-BRUVs (which have camera housings pressure rated to greater water depth and additional lights built into the system) were therefore used to sample deeper waters later in this survey to meet these requirements.

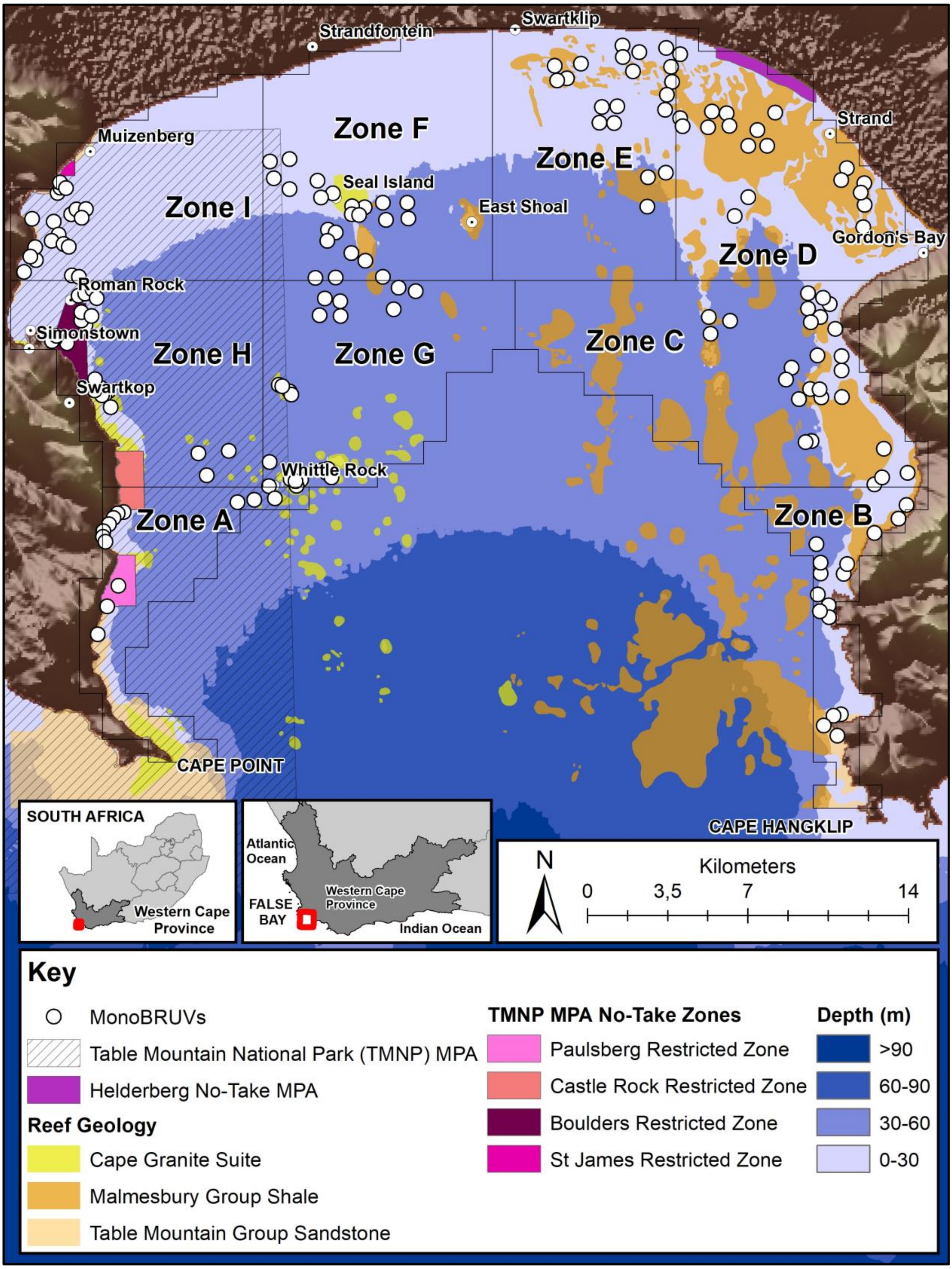


Figure 31. The location of baited remote underwater mono-video (mono-BRUVs) sites in False Bay. The number of sites was allocated proportional to the size of the sampling zone (A – I) and distributed proportional to the depth (m) (Van Zyl 2011) and subtidal reef geology (Van Zyl 2011) represented in each sampling zone. The terrestrial topography (EKZNW 2015) and marine protected areas (MPAs) (DEA 2019a) are shown for context.

A random stratified design distributed samples such that each zone encompassed a range of depths and habitat types, and these zones were sampled in winter (June - July) and summer (December). The number of samples per zone was proportional to the size of the zone (**Figure 31**). The relative proportion of sand and reef was calculated for each sampling zone. Reefs constituted 17% of False Bay (Van Zyl 2011) (**Figure 31**), so a deliberate bias was introduced to ensure that 50% of the samples were on this habitat type. The bias was considered necessary because reefs represented different types (Cape Granite Suite, Malmesbury Shale Group, Table Mountain Sandstone Group) and profiles, were considered to host higher species richness and were of particular monitoring interest as they formed part of the current no-take zones in the TMNP MPA. Fifty percent of samples per zone was allocated to reef, and 50% were assigned to sand. Reef samples were further distributed in proportion to reef type (Malmesbury Group shale, Cape Granite Suite and Table Mountain Group sandstone) in zones which included more than one reef type.

The ‘Create Random Points’ tool, part of the ‘Data Management Tool’ in ArcMap 10.1™ (www.esri.com), was used to designate sampling sites for each zone. The average distance to the nearest neighbouring site was approximately 500 m. This distance was increased from the minimum distance of 250 m that each sample was initially buffered from its nearest neighbour using the ‘Minimum Distance Allowed’ tool in ArcMap 10.1™. Minimum distances were based on research in the Tsitsikamma MPA (**Figure 29**), a comparable region further east along the South African coast, to retain statistically independent samples and reduce the likelihood of overlapping bait plumes (Bernard & Götz 2012).

4.3.3.2 Baited remote underwater mono-video systems (BRUVs)

The mono-BRUVs used GoPro Hero2^{TM} HD cameras in standard housings pressure-rated to a maximum of 50 m water depth (**Figure 32**). Cameras focused on a perforated PVC bait canister (130 mm by 110 mm with 10 mm perforations) positioned 1 m away from the lens. Sardines (*Sardinops sagax*) were used for bait (1 kg per sample). The camera rigs were lowered by hand to the seafloor from the sampling vessel, and the start time was recorded after five minutes. Each sample was 60 minutes in video duration, based on research globally (Harvey et al. 2007) and in the Tsitsikamma and Stilbaai MPAs (**Figure 29**), which are comparable regions further east in South Africa (Bernard & Götz 2012; De Vos et al. 2014).

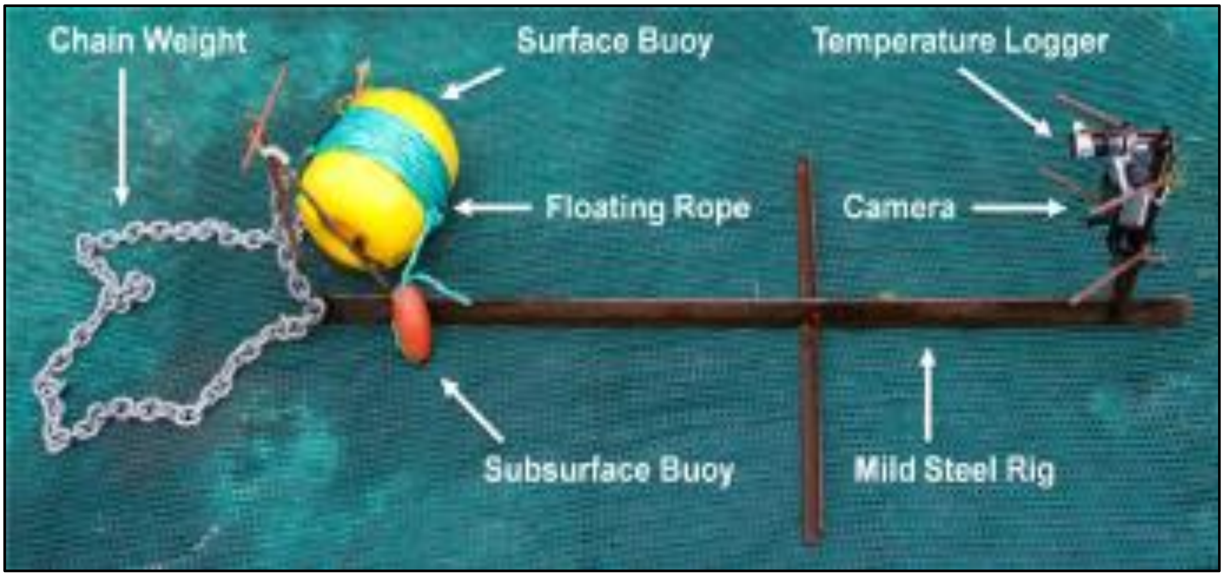


Figure 32. Baited remote underwater mono-video systems (mono-BRUVs) configuration used to collect the data in the first part of this study.

4.3.3.3. Environmental variables

Depth was verified at each site from the sampling vessel's echo sounder. Broad-scale habitat was classified as either 'reef' or 'sand'. Habitat (reef or sand) was ground-truthed for each sample during video analysis, and some samples that were incorrectly designated as reef on the interpolated geological data from Van Zyl (2011) were reclassified. Reef-type was classified from the naval fair chart data and geological classifications from the Council for Geoscience and recorded as 'Cape Granite Suite', 'Malmesbury Group shale' or 'Table Mountain Group sandstone' (Van Zyl 2011).

4.3.3.4. Video analysis

Videos were analysed by the author using Apple QuickTime 7.7.1. The MaxN measure of abundance was recorded for every species identified in each sample (Cappo et al. 2003). Max N is the maximum number of individuals of a species in a single frame for the duration of a video. It avoids re-counting individuals swimming in and out of the camera's field of view (FOV) (Willis & Babcock 2000). Species were all identified to species level based on reference guides (Smith & Heemstra 1991; Heemstra & Heemstra 2004; Jones 2008; Branch et al. 2017; Ebert et al. 2013; King & Fraser 2014). Any uncertain species identifications were sent for verification by other experts who either a) knew the species typical of the region, b) were experts on a specific taxonomic group or c) were familiar with identification from video or photos. *Haploblepharus edwardsii* and *H. pictus* were the only species grouped and identified to genus level. They are discussed throughout this study as *Haploblepharus spp.*, based on discussions about the ongoing genetic research into distinguishing these two species (K Gledhill, South African Shark Conservancy (SASC), Hermanus, personal communication). *Clinus superciliosis* is included as one species until there is clarity with distinguishing *Clinus ornatus* (C Attwood, University of Cape Town (UCT), Cape Town, personal communication). Once a species list was compiled, all records were cross-referenced with the list compiled by Day et al. (1970).

The dominant seafloor substrate (**Table 23**) and the seafloor relief (**Table 24**) visible in each of the 185 videos (and stereo-BRUVs samples) was described using the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification scheme (Althaus et al. 2013). Important habitat modifiers were recorded in addition to the dominant seafloor substrate in accordance with the CATAMI scheme (Althaus et al. 2013). A habitat modifier was an addition to the dominant seafloor substrate that would influence the species community present, form a habitat-type of its own, or inform anecdotal reference for later analysis. The most important modifier that was later included in discussion was kelp (*Laminaria pallida* and *Ecklonia maxima* were not differentiated to species level). Kelp only appeared on consolidated rock seafloor habitat (SCR in **Table 23**) and was quantified in terms of presence or absence. Other habitat modifiers included biogenic cover and any habitat veneer, where sand may have inundated underlying reef (sand veneer in this study).

Table 23. The Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) seafloor classifications used in this study (Althaus et al. 2013).

Classification	Description
SCB	Substrate: consolidated (hard): boulders
SCC	Substrate: consolidated (hard), cobbles
SCR	Substrate: consolidated (hard), rock
SUPB	Substrate: unconsolidated (soft): pebble (10 – 64 mm)
SUPG	Substrate: unconsolidated (soft): gravel (2 – 10 mm)
SUSC	Substrate: unconsolidated (soft): sand/mud (<2 mm): coarse sand (shell fragments)
SUSF	Substrate: unconsolidated (soft): sand/mud (<2 mm): fine sand (no shell fragments)

Table 24. CATAMI seafloor relief classifications used in this study (from Althaus et al. 2013).

Classification	**Description**
RF	Relief: flat
RLL	Relief: low (<1 m)
RLM	Relief: moderate (1 – 3 m)

4.3.4. Baited remote underwater stereo-video systems (stereo-BRUVs) sampling

4.3.4.1. Sampling sites

Nine sampling zones were plotted on the interpolated contour map of False Bay described in section 4.3.3.1 (**Figure 33**). These zones extended data collection across the full range of depths represented in False Bay. The stereo-BRUVs configuration was more suited to sampling at depth than the mono-BRUVs. The stereo-BRUVs camera housings were pressure rated to 200 m water depth, and a single, white light gave suitable illumination where light penetration through the water column became limiting. The mono-BRUVs camera housings were pressure-limited to a maximum of 50 m water depth. Sampling zones were restricted to depths between 4 and 90 m using the buffer geoprocessing tool in ArcMap 10.1™ (www.esri.com), covering 100% of False Bay that could be accessed using the sampling vessel *Sargasso*. A random stratified design described in 4.3.3.1 distributed samples to ensure that each zone, depth range and habitat type was sampled from March through to December. The stereo-BRUVs sampling zones formed the basis for the factor that would become “Region” used later in this study. The

“Regions” incorporated both mono-BRUVs (where they occurred) and stereo-BRUVs samples (where they extended sampling to greater depths and into the central mouth of False Bay). The species typifying each of these nine “Regions” were derived from the combined coverage of mono-BRUVs and stereo-BRUVs across False Bay. These regions ensured that all samples were randomly allocated within a stratified design that considered the proportional distribution of different depths and habitats within each zone. Their designation also integrated the logistical considerations (distance from the slipway, survey time, vessel costs and fuel use for single-day sampling) that are necessary to integrate into any long-term monitoring programme. Ultimately, this delineation allowed this study to consider three crucial factors: 1) adequate survey coverage of the bay’s depths and habitats, 2) planning considerations for conservation management and 3) a bay-wide basis for comparison with previous surveys across different survey methods and biodiversity focus. This would allow for all methods, and all levels of the sampled ecosystem, to be integrated and provide a landscape-level means of interpreting False Bay.

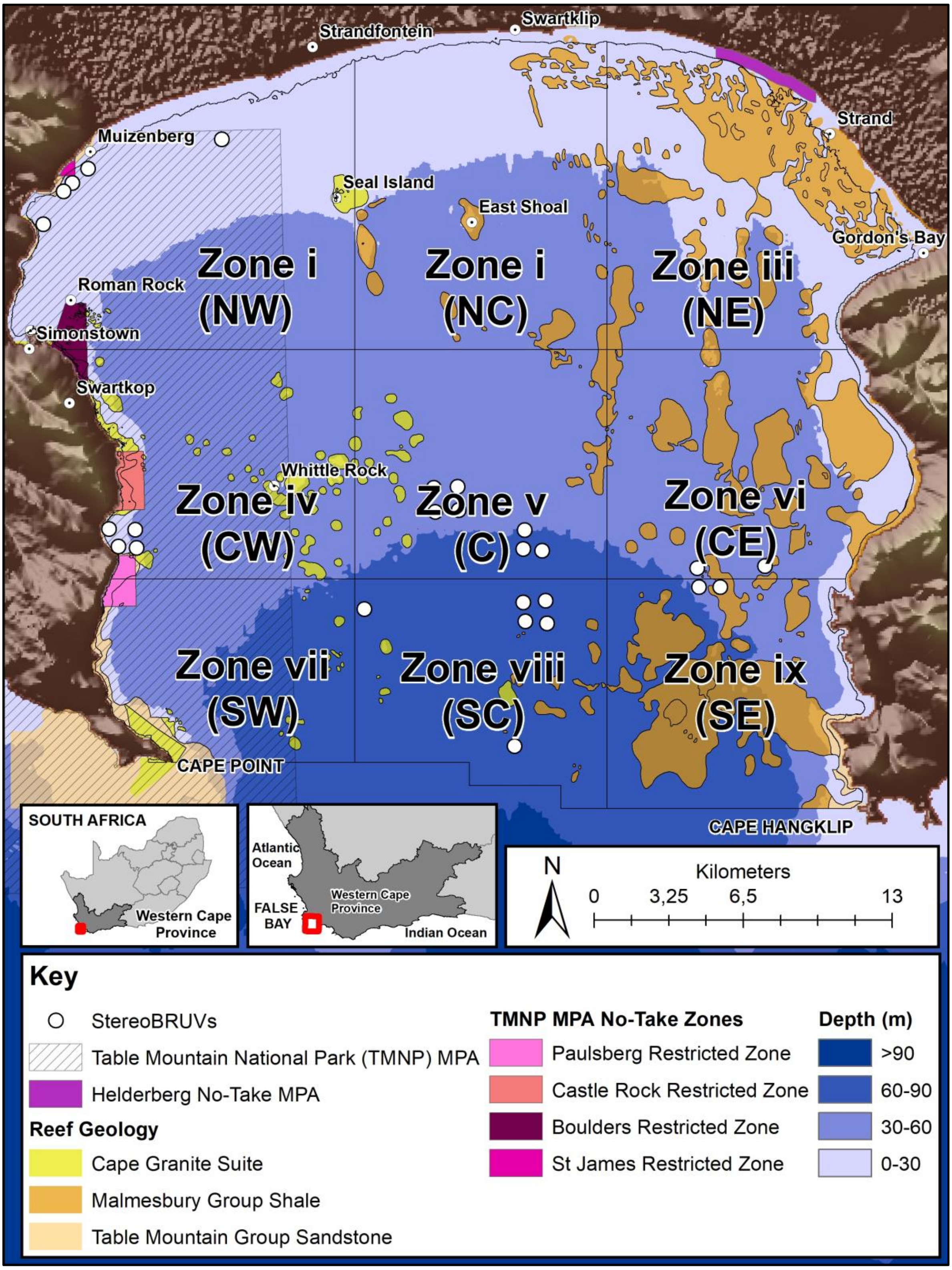


Figure 33. The location of baited remote underwater stereo-video (stereo-BRUVs) sites in False Bay, South Africa in relation nine sampling zones allocated for the survey design that are later referred to as regions. Zone i = North West, Zone ii = North Central, Zone iii = North East; Zone iv = Central West, Zone v = Central, Zone vi = Central East; Zone vii = South West, Zone viii = South Central, Zone ix = South East. Data shown include terrestrial topography (EKZNW 2015), subtidal reef geology (Van Zyl 2011), marine protected areas (MPAs) (DEA 2019a) and depth (m) (Van Zyl 2011).

4.3.4.2. Baited remote underwater stereo-video systems (stereo-BRUVs)

Baited remote underwater stereo-video systems (stereo-BRUVs) used two video cameras (Canon Legria HFM 506) mounted 70 cm apart on a horizontal centre bar on a stainless-steel frame (Bernard et al. 2014). The camera housings (pressure rated to 200 m water depth) were mounted on baseplates that converged inwards at an angle of seven degrees so that the cameras' fields of view overlapped (**Figure 34.**). A rigid arm held a bait container 1.2 m ahead of both cameras, within their field of view. Bait canisters were filled with 1 kg of chopped sardines (*Sardinops sagax*). Lights were required in this study because the stereo-BRUVs were deployed to a maximum depth of 84 m. White lights were used based on findings that this colour maximised species attraction and detection for diurnal fish surveys (Harvey et al. 2012).

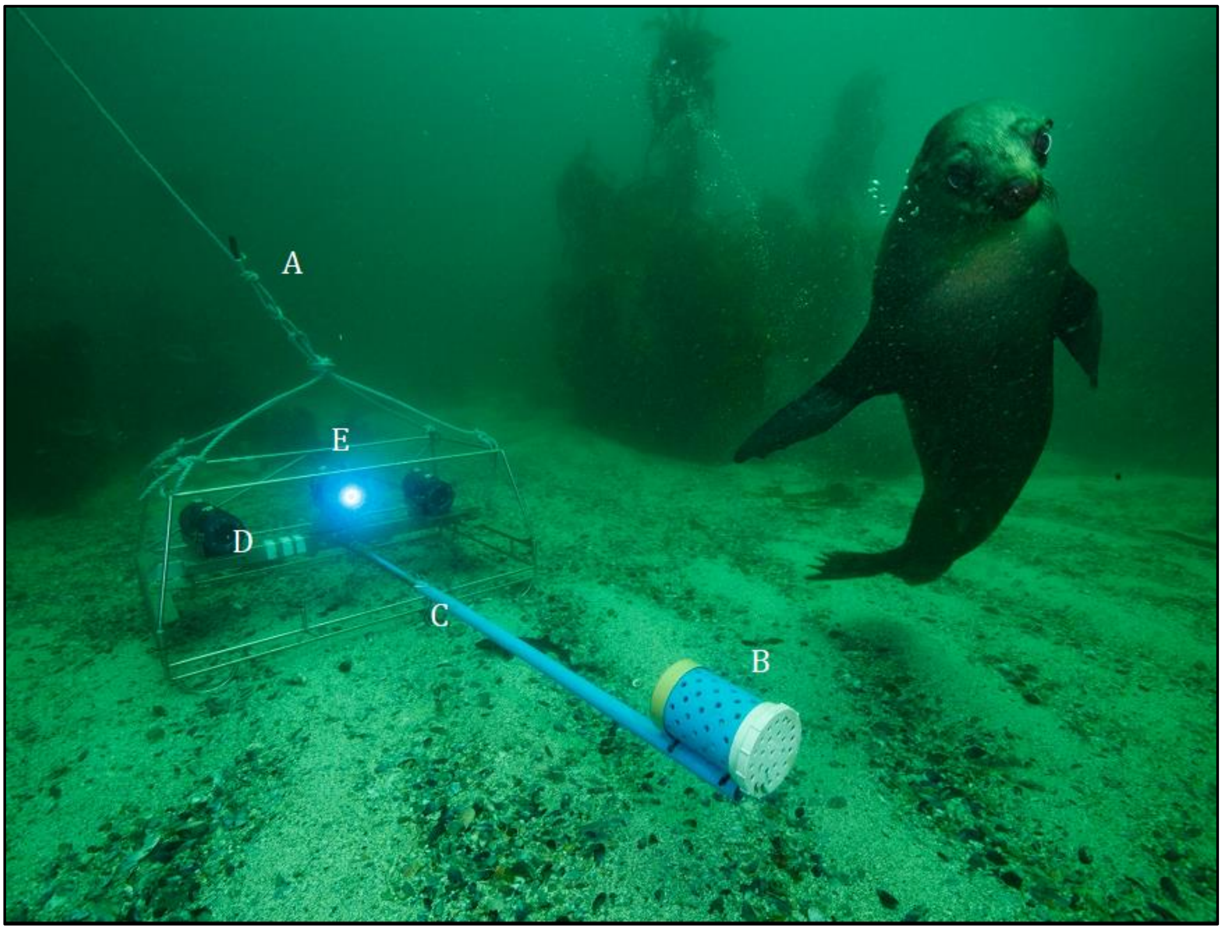


Figure 34. A baited remote underwater stereo-video system (stereo-BRUVs) deployed to the seafloor in the Table Mountain National Park (TMNP) marine protected area. The stereo-BRUVs were linked to the surface by means of a rope (A) to a surface buoy, such that 4 systems could be deployed to film simultaneously. A bait canister (B) was held 1.2 m from the cameras on a rigid arm (C). The two cameras are fixed to a centre bar (D), angled inwards, and a light was used at all depths (E) (photograph: Joris van Alphen).

4.3.4.3. Video analysis

Videos were recorded in the MPEG transport stream (.mts) format and a single video hour is split across multiple files. Videos were therefore concatenated into a single file using the EventMeasure analysis software (SeaGIS 2017) and then converted into high definition Audio Video Interleave (.avi) files using Xilisoft Video Converter Ultimate v.6.5.5. All videos were analysed by the author and each species in the hour-long video was identified, and its MaxN measure of relative abundance (Cappo et al. 2003) recorded using the EventMeasure analysis software. EventMeasure captures species identification, MaxN value and the video time at MaxN. The overlapping field of view of the two cameras in a stereo-BRUVs frame configuration facilitates size measures to be taken for species visible in synchronised footage analysed in EventMeasure. The video footage was synchronised using the synchronising diode (**Figure 34**) before each stereo-BRUVs was deployed to the seafloor. Length measurements and distance from the camera (range) could therefore be made at the time at MaxN for each species. Cameras were calibrated (Harvey & Shortis 1998) before the survey using a calibration cube and CAL software (SeaGIS 2017). The total number of stereo-BRUVs samples achieved in this survey (110 samples) would usually allow for length-frequency measures to be taken across the bay. However, the low number of usable stereo-BRUVs samples precluded the length-frequency component. All stereo-BRUVs data were therefore treated the same as mono-BRUVs data (see section *4.3.2*) The same protocol outlined in *4.1.3.4* was observed for species identification and description. Videos with zero visibility were rejected. Repeated red tide algal blooms in the False Bay region persisted for several months, with the result that senescing dinoflagellates sank to the seafloor and were not visible from the surface but often clouded the FOV of videos.

The same landscape environmental variables were applied as described for the mono-BRUVs survey. Three depth categories: shallow (0 – 30 m), medium (30 – 60 m) and deep (60 – 90 m) followed those used for the epibenthic megafauna survey (Chapter 3). Broad-scale habitat was classified as either reef or sand. The Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification scheme (Althaus et al. 2013) was used to describe the dominant seafloor substrate and the seafloor relief visible in each of the 28 videos used in the final analysis.

4.3.4. Species abundance indices

The total number of sites where a species was recorded was tabulated as ‘frequency’. Relative frequency was calculated as the frequency of a species divided by the total number of all sites sampled. Relative abundance for each species was calculated as the sum of all MaxN values for each species divided by the total number of sites sampled. Mean MaxN gave the average maximum abundance at which a species was recorded, calculated as the sum of all MaxN values for each species divided by the number of sites where a species was recorded. Standard deviation was calculated to assess the level of dispersion from each mean MaxN value for each species because it was presumed that shoaling behaviour would impact the variation in MaxN values between sites for certain species. Each species was assigned a feeding guild (**Table 25**) based on descriptions of their biology from reference guides and the literature. The description of guilds was based on an expansion of those delineated by Stergiou and Karpouzi (2002). Those species classified as omnivores were typically species with a preference for animal prey, and both carnivores and omnivores are discussed concerning their preference for either fish prey or invertebrate prey based on their specific descriptions in the literature.

Table 25. Description of feeding guilds (*sensu* Stergiou & Karpouzi 2002) used to divide species according to their feeding biology (Smith & Heemstra 1991; Heemstra & Heemstra 2004; Branch et al. 2017).

Feeding guild	**Feeding preferences**
Carnivore	Decapods, cephalopods, fish
Omnivore	Algae, molluscs, worms, crustaceans, hydrozoans
Planktivore	Phytoplankton and zooplankton
Herbivore	Algae
Scavenger	Dead tissues

Species of conservation concern that were recorded in this study were selected if they were classified according to either one or a combination of the listings outlined in **Table 26**.

Table 26. Definitions used as selection criteria to determine species of conservation concern for inclusion in this study's analysis.

Source	**Criterion**	**Definition**
IUCN[1]	Vulnerable	High risk of extinction in the wild.
	Endangered	Very high risk of extinction in the wild.
	Critically Endangered	Extremely high risk of extinction in the wild.
WWF[2]	Red	Unsustainable harvest, environmental concerns with harvest methodologies, poor fishery management, 'no-sale' species (illegal to buy or sell in South Africa).
Linefish Species Profiles[3]	Stock status	Declining or collapsed

Listings for species on the Threatened or Protected Species regulations (TOPS) and Convention on International Trade in Endangered Species of Wildlife and Flora (CITES) were considered, but not tabulated. Only pipefish (*Sygnathus temminckii* in this study) and *Poroderma pantherinum* were species in addition to the table that are listed as "Protected" by TOPS (DEA 2017). These species were not included because the risk of extinction was not considered as a requirement for TOPS Protected species listing (Pfabb 2014). The great white shark (*Carcharodon carcharias*) was listed as Vulnerable on TOPS (DEA 2017) and on CITES Appendix II (assessed in 2005). These measures were not included because the *C. carcharias* already appears in the table according to IUCN listing, and CITES listing is specific to trade regulations. It therefore incorporates some of the same considerations that inform the other criteria.

To highlight where targeted surveys would best detect species of conservation concern in long-term monitoring programmes, these species were tabulated separately with information on their a) likelihood of detection, b) average abundance at a site and c) overall detection in the bay which were recorded as relative frequency (frequency/total sites sampled), mean MaxN and relative abundance (sum of MaxN/frequency), respectively. The total number of sites where each species was recorded in each depth category, on each habitat and each CATAMI habitat was calculated. Where species frequency of occurrence was equal on different habitats, both

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[1] International Union for Conservation of Nature (IUCN) Red List of Threatened Species ™

[2] World Wildlife Fund (WWF) South African Sustainable Seafood Initiative (SASSI)

[3] Southern African Marine Linefish Species Profiles (Mann 2013)

habitat types were tabulated. Where there was a clear majority or preference (>5), the majority habitat was recorded. The IUCN and SASSI (SASSI 2018) listing for individual species was tabulated, and the date of assessment included.

To highlight where targeted surveys would best detect species of commercial value in long-term monitoring programmes, species that were listed as targets for the False Bay linefishery (Bennett 1991; Mann 2013; DAFF 2016), beach-seine (Lamberth et al. 1994) and spearfishery (Lechanteur 2000) were tabulated separately with information on their a) likelihood of detection, b) average abundance at a site and c) overall detection in the bay which were recorded as relative frequency (frequency/total sites sampled), mean MaxN and relative abundance (sum of MaxN/frequency), respectively. The total number of sites where each species was recorded in different depth categories, on different habitats and different CATAMI habitats was calculated. Where species frequency of occurrence was equal on different habitats, both habitat types were tabulated. Where there was a clear majority or preference (>5), the majority habitat was recorded.

4.3.5. Species diversity indices

MaxN relative abundance was used to calculate Rényi's diversity, which was plotted for 213 samples (185 mono-BRUVs and 28 stereo-BRUVs) for depth categories at 10 m increments and habitat (reef and sand) using the function renyi in the R package *vegan* version 2.4-5v (Oksanen et al. 2017). The Rényi curve follows from species richness that does not account for relative abundance or evenness, through indices that increasingly incorporate abundance and evenness in their measure, to end with the relative abundance of a single, dominant species. The Rényi plot uses Trellis (lattice) graphics with a separate panel for each transect and depth category (Oksanen et al. 2017). Rényi's diversity was plotted for 185 mono-BRUVs samples for season (winter and summer).

Rényi diversity is a generalization of the Shannon-Wiener diversity index (H') and given as follows:

$$H.a = \frac{1}{(1-a)} log \sum_{i=1}^{S} p_i^a \text{ ....} (4.1)$$

where a = scale parameter, and p_i^a = proportion of species i.

The species richness is given where a = 0 in Equation 4.1. In this study, a = 0 reflects the species richness in the aggregated sites for that category (depth, habitat, or season) on the Rényi curve. The H' diversity is given where a = 1 in Equation 4.1. H' diversity accounts for both species richness and evenness, and is typically written as:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i \quad \text{.........} \quad (4.2)$$

The Simpson's diversity index (D) is given where a = 2 in Equation 4.1. The D index gives more weight to dominant species and accounts for both the number of species present and their relative abundance. This index is not discussed in the results. At a = ∞, the Rényi number reflects the relative abundance of the dominant species.

A two-sample equal variance Student's t-test tested separately the assumption that the species richness (α diversity) of sites did not differ between reef and sand, and between seasons. Using MaxN relative abundance, the Shannon-Wiener diversity index (H') was calculated for each sample site using the DIVERSE function in the Plymouth Routines in Multivariate Ecological Research (PRIMER) Version 6+ software package (Clarke 1993; Clarke & Warwick 2001). A two-sample equal variance Student's t-test tested separately the assumption that the H'(loge) of sites did not differ between habitats, and between seasons.

4.3.6. Environmental factors and community composition

Using MaxN relative abundance, data were root-root transformed to promote the influence of rare species and analysed using PRIMER Version 6+ software package (Clarke 1993; Clarke & Warwick 2001).

The Bray-Curtis similarity index was calculated among 209 samples to reflect similarity in relative abundance and species composition. Samples were included if they all had Max N relative abundance and environmental data. Environmental data were normalised. A multi-dimensional scaling (MDS) plot represented similarity among samples and displayed the effects of depth category (shallow = 0-30 m, medium = 30-60 m and deep = 60-90 m), habitat type (reef and sand), CATAMI habitat type, reef type (Cape Granite Suite, Table Mountain Group sandstone and Malmesbury Group shale), seafloor profile (RF, RLL, RLM) and region (North West, North Central, North East, Central West, Central, Central East, South West, South

Central, South East) on community composition. A one-way Analysis of Similarity (ANOSIM) test assessed separately the influence of each of these factors with 999 permutations (Clarke 1993). The mono-BRUVs dataset was then taken as a subset to assess separately and a one-way ANOSIM tested the influence of season (summer and winter) on species composition and abundance.

The Bray-Curtis similarity index was calculated among 57 species over the 209 samples to reflect similarity in relative abundance and species composition. A cluster diagram displayed groupings of species at 20%, 40%, 60%, 80% and 100% similarity. A MDS plot represented similarity among species and 20% similarity ovoids were superimposed.

Permutational multivariate analysis of variance (PERMANOVA) was used to test for differences in assemblage structure among habitats and depth categories using combined stereo-BRUVs and mono-BRUVs data. The mono-BRUVs dataset was taken as a subset to assess individual and interaction effects of habitat, depth, and season. These were represented in models 1 and 3 in the results. In total, four PERMANOVA models with different combinations of these variables and their interactions were constructed. PERMANOVA models were evaluated using the pseudo-F statistic with 999 random permutations of the data using the extension software PERMANOVA+ in PRIMER-E v6 (Clarke & Gorley 2006).

The similarity percentage (SIMPER) routine identified the contribution of each species towards differences among depth profiles, habitats, CATAMI habitat types, region and seasons, and distinguished which species were typically associated with each set of environmental factors (Clarke 1993; Clarke & Warwick 2001). For region, the two species that had the highest individual contribution to percentage similarity in the group were tabulated.

4.4. RESULTS

A total of 213 mono- and stereo-BRUVs samples were analysed in this study. Samples were distributed such that 129 samples were on sand, and 84 samples were on reef. Given that the natural proportion of depth contours in False Bay fall into the < 50 m depth range, most samples were in the shallow (0 – 30 m) and medium (30 – 60 m) depth categories (147 and 61 samples, respectively). Ninety-five mono-BRUVs samples were recorded in winter, and 90 mono-BRUVs samples were recorded in summer. Twenty-eight stereo-BRUVs samples fell into the intermediate season (August to October) between winter (July) and summer (December) A total of 57 fish species from 30 families were recorded across 213 analysed sites in False Bay (**Table 27**). Thirty-eight species from 18 families were from the class Actinopterygii. Eighteen species from 11 families were from the class Chondrichthyes. Only one species, *Eptatretus hexatrema*, was from the class Myxiniformes.

4.4.1. Species frequency across all sites

Haploblepharus spp. (**Figure 37**) were frequently recorded (82% of total sites). *Poroderma africanum* (**Figure 37**) (36% of total sites) and *Mustelus mustelus* (23% of sites) were the next most frequently recorded chondrichthyans across all sites. *Trachurus capensis* (**Figure 38**) (48% of total sites), *Spondyliosoma emarginatum* (**Figure 38**) (44% of total sites) and *Chelidonichthys capensis* (**Figure 38**) (41% of total sites) were the most frequently recorded actinopterygians across all sites.

The family Sparidae represented the highest number of species of the actinopterygians (14 species). The most frequently recorded species in this family were *Spondyliosoma emarginatum* (44% of total sites), *Chrysoblephus laticeps* (**Figure 37**) (34% of total sites), *Pterogymnus laniarius* (31% of total sites) and *Pachymetopon blochii* (**Figure 37**) (32% of total sites).

The family Scyliorhinidae was the most frequently recorded of the chondrichthyans, with three species identified to species level and *Haploblepharus edwardsii* and *Haploblepharus pictus* considered together as *Haploblepharus spp.* (172 total sites).

4.4.2. Species frequency *across depths*

A random, stratified design designated total of 200 mono-BRUVs samples in the 0 – 50 m depth range (which is the majority of the bay’s natural depth range), and a total of 138 stere-BRUVs samples in the 0 – 90 m depth range. Of the 213 analysed samples, most (69%) were in the shallow depth category (0 – 30 m) (**Figure 35**). Twenty-nine percent of samples were in the medium depth category (30 – 60 m) and 2% were in the deep depth category (60 – 90 m).

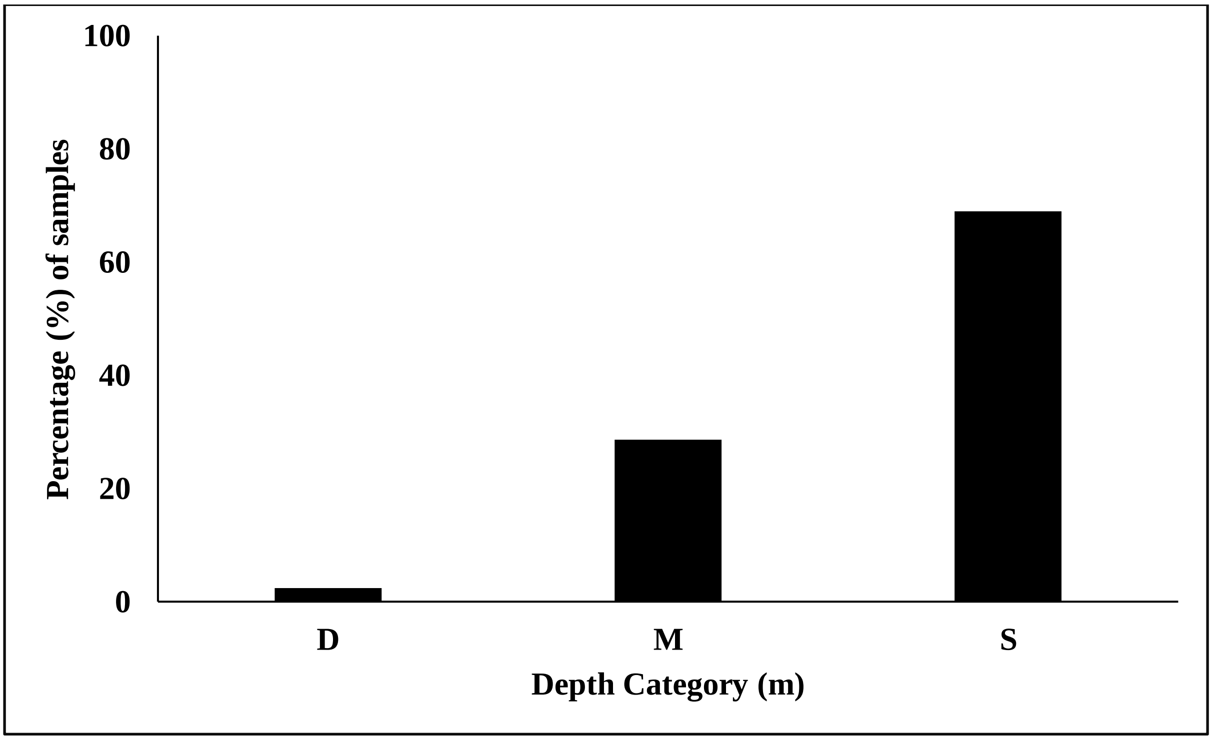

Figure 35. The percentage distribution of 213 analysed samples among different depth categories (m) in False Bay, where S = shallow (0 – 30 m), M = medium (30 – 60 m), D = deep (60 – 90 m).

Haploblepharus spp. were most frequently recorded in shallow depths between 0 – 30 m (66% of total sites). *Chelidonichthys capensis* was the most frequently recorded species in intermediate depths between 30 – 60 m (20% of total sites) and deep sites between 60 – 90 m (2.4% of total sites).

4.4.3. Species frequency across broad and fine-scale habitats

Reefs constituted 17% of False Bay (Van Zyl 2011), so a deliberate bias designated 50% of the 338 samples filmed (200 mono-BRUVs and 138 stereo-BRUVs) on this habitat type. The bias was considered necessary because reefs represented different types (Cape Suite Granite, Malmesbury Group shale, Table Mountain Group sandstone) and profiles. In the final distribution of the 213 analysed samples, most (129 samples) were on sand (61%) and 84 samples (39%) were on reef (**Figure 36**).

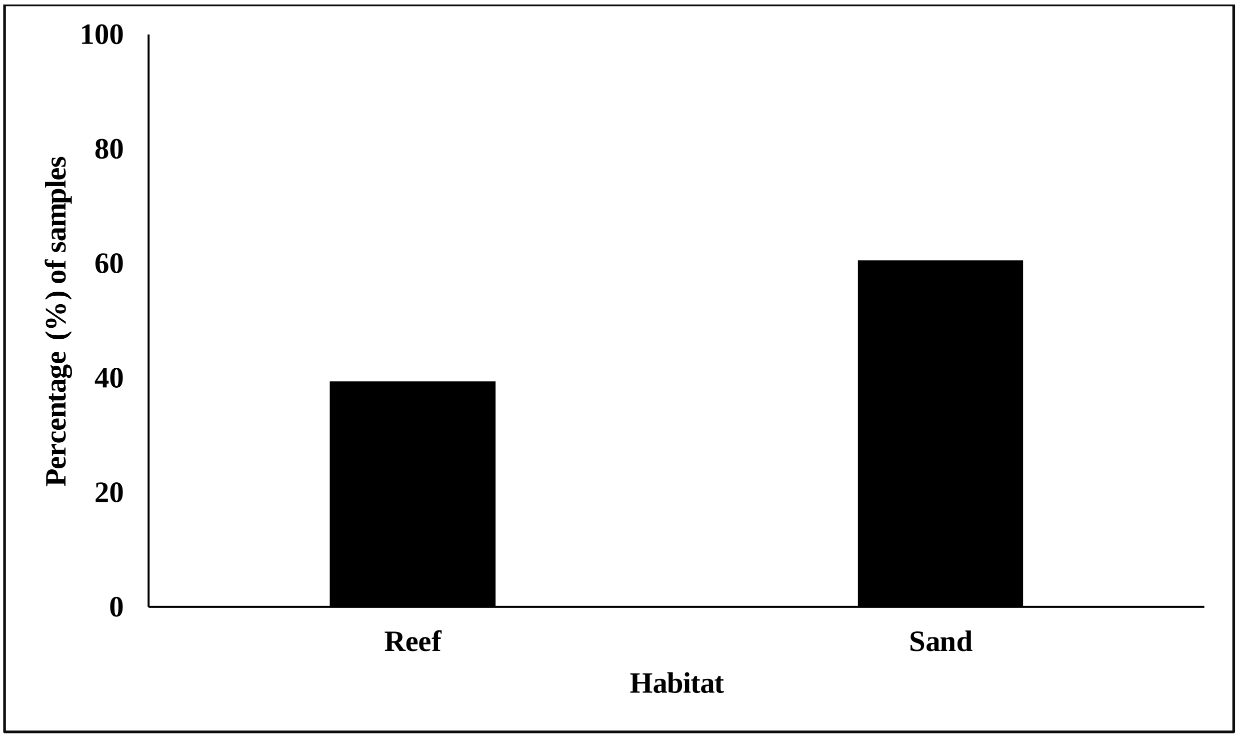

Figure 36. The percentage distribution of 213 samples across habitat type in False Bay.

Haploblepharus spp. and *C. capensis* were the most frequently recorded species on sand (41% and 38% of total sites, respectively; 70% and 64% of sand sites, respectively). *Haploblepharus spp.* were most frequently recorded on reef (41% of total sites; 100% of reef sites). *Chrysoblephus laticeps* was the second most frequently recorded species on reef (29% of total sites; 72% of reef sites).

Samples were further refined into different CATAMI habitat types, and most samples were distributed across fine sand (SUSF) and coarse sand (SUSC) (72 and 47 samples, respectively). Of the reef-designated samples, most (64 samples) were on consolidated rock (SCR), and 7 samples were on cobble habitat (SCC) and 3 samples were on boulder reef (SCB). A minority of the remaining analysed samples where visible habitat could be refined into a CATAMI classification type were recorded as pebble (SUPB) and gravel (SUPBG) habitat (1 and 2 samples, respectively).

Chelidonichthys capensis was the most common species on SUSF (23% of total sites; 70% of SUSF sites) and *Haploblepharus spp.* were most common on SUSC (20% of total sites; 96% of SUSC sites). Species were more even in their frequency across all other CATAMI habitat types. *Chrysoblephus laticeps*, *Haploblepharus spp.* and *P. africanum* (1% of total sites; 50% of SCB sites) were slightly more common than other species on SCB. *Haploblepharus spp.* were slightly more common than other species on SCC (3% of total sites; 86% of SSC sites).

The distribution of samples across different reef types followed the natural proportion of those types in False Bay. Most (21% of samples) were on Malmesbury Group shale, 13% of samples on Cape Granite Suite and 6% of samples on Table Mountain Group sandstone. Of the analysed samples where relief could be assessed, most were classified as flat (54% of total samples, 67% of classified samples), 15% of total samples (18% of classified samples) were distributed across moderate relief (1 – 3 m) and 12% of total samples (15% of classified samples) across low relief (< 1 m). Twelve sites were recorded where kelp was obvious. These sites corresponded to SCR reef habitat.

Haploblepharus spp. were recorded across all reef types and reef profiles, as well as were kelp was recorded (6% of total sites; 100% of kelp sites). *Pachymetopon blochii* (4% of total sites; 75% of kelp sites), *C. laticeps* (4% of total sites; 67% of kelp sites) and *Clinus superciliosis* (3% of total sites; 58% of kelp records) were also recorded in kelp.

4.4.6. Frequency of feeding guilds across depth and habitat

Most species were either omnivores (40% of total sites) or carnivores (53% of total sites) (**Table 27**). These feeding guilds dominated communities in shallow depths (0 – 30 m). Omnivores and carnivores were recorded across a wide range of depths but decreased in frequency with increasing depth. The scavenger *E. hexatrema* was recorded in all three depth categories. The herbivore *Sarpa salpa* was only found in the shallow depths, between 0 – 20 m depth. Planktivores were only recorded up to a maximum of 50 m depth.

The herbivore *S. salpa* was only recorded on reef habitat. More omnivores that preferred invertebrate prey were recorded on reef (21 species) than on sand (12 species). Thirteen carnivores that preferred both invertebrate prey and some fish were recorded on reef and 16 on sand. Ten carnivores that preferred fish prey were recorded on reef and 13 on sand. Planktivores (2 species on reef, 1 species on sand) and the scavenger *E. hexatrema* were more evenly recorded across both habitats.

Omnivores that preferred invertebrate prey were more frequently found on rocky reef habitat (SCR) (51% of records) than on any other CATAMI classified habitat type, but they were present on all seven different habitat types. Carnivores that preferred invertebrates were the most frequently recorded feeding guild on fine sand habitat (SUSF) (11% of total records) and coarse sand habitat (SUSC) (8% of total records). Within the rocky reef habitat (SCR), all feeding guilds were recorded in kelp beds where most species were either carnivores that preferred fish (35% of kelp sites), carnivores that preferred invertebrates (30% of kelp sites) and omnivores that preferred invertebrates (29% of kelp sites).

Figure 37. Species typical of False Bay, and frequently recorded in this study are shown in panels: b) roman seabream (*Chrysoblephus laticeps*), c) Cape seabream (*Pachymetopon blochii*), d) pyjama catshark (*Poroderma africanum*) and e) *Haploblepharus* spp. Species identified as of conservation concern and recorded in this study are shown in panels: a) red stumpnose (*Chrysoblephus gibbiceps*) and d) *P. africanum*. Other interesting, and typical species, shown in the context of their habitat are f) broadnose sevengill shark (*Notorynchus cepedianus*), g) spotted gully shark (*Triakis megalopterus*) and h) *C. laticeps with P. blochii*. Photos courtesy: Mac Stone and Joris van Alphen.

Table 27. Ichthyofauna diversity and relative abundance (the sum of all MaxN values for each species divided by the total number of sites sampled) recorded for 213 samples in False Bay. Species are ordered alphabetically by family, and then by species. CV = co-efficient of variation. Frequency is the total number of sites where a species was recorded. Relative frequency was calculated as the frequency of a species divided by the total number of all sites sampled. Mean MaxN is the average maximum abundance at which a species was recorded, calculated as the sum of all MaxN values for each species divided by the number of sites where a species was recorded. Each species was assigned a feeding guild (**Table 25**) based on descriptions of their biology from reference guides and the literature.

						MaxN		
Feeding Guild	**Family**	**Scientific name**	**Common name**	**Frequency**	**Relative frequency**	**Mean**	**Relative abundance**	**CV**
Carnivore	Ariidae	*Galeichthys feliceps*	White seacatfish	90	0.42	3.03	1.29	5.43
Parasite	Blenniidae	*Aspidontus taeniatus tractus*	Mimic blenny	1	0.00	1.00	0.00	3.45
Omnivore	Blenniidae	*Parablennius cornutus*	Horned blenny	2	0.01	1.00	0.01	3.11
Carnivore	Callorhinchidae	*Callorhinchus capensis*	Elephantfish	6	0.03	1.00	0.03	2.28
Carnivore	Carangidae	*Seriola lalandi*	Yellowtail	4	0.02	1.75	0.03	0.00
Planktivore	Carangidae	*Trachurus capensis*	Maasbanker	101	0.48	33.04	15.73	0.00
Omnivore	Cheilodactylidae	*Cheilodactylus fasciatus*	Redfinger	20	0.09	1.60	0.15	1.74
Omnivore	Cheilodactylidae	*Cheilodactylus pixi*	Barred fingerfin	4	0.02	1.25	0.02	0.00
Omnivore	Cheilodactylidae	*Chirodactylus brachydactylus*	Two-tone fingerfin	10	0.05	1.20	0.06	7.38
Omnivore	Cheilodactylidae	*Chirodactylus grandis*	Bank steenbras	2	0.01	1.00	0.01	0.00
Omnivore	Clinidae	*Clinus agilis*	Agile klipfish	1	0.00	1.00	0.00	0.00
Omnivore	Clinidae	*Clinus superciliosis*	Super klipvis	27	0.13	1.15	0.15	2.45
Omnivore	Congiopodus	*Congiopodus torvus*	Horsefish	6	0.03	1.00	0.03	0.00
Carnivore	Dasyatidae	*Dasyatis brevicaudata*	Short-tailed ray	11	0.05	1.00	0.05	0.00
Omnivore	Dasyatidae	*Dasyatis pastinaca*	Blue stingray	2	0.01	1.00	0.01	0.00
Piscivore	Gempylidae	*Thyrsites atun*	Snoek	3	0.01	12.67	0.18	0.00
Omnivore	Gobiidae	*Caffrogobius saldanhae*	Commafin goby	3	0.01	1.33	0.02	0.00

Omnivore	Gobiidae	*Psammogobius knysnaensis*	Knysna sand goby	16	0.08	1.13	0.09	4.24
Omnivore	Gonorynchidae	*Gonorynchus gonorhynchus*	Beaked sandfish	2	0.01	15.00	0.14	0.00
Carnivore	Gymnuridae	*Gymnura natalensis*	Diamond ray	5	0.02	1.00	0.02	0.00
Carnivore	Hexanchidae	*Notorynchus cepedianus*	Broadnose sevengill shark	10	0.05	1.00	0.05	0.00
Carnivore	Lamnidae	*Carcharodon carcharias*	Great white shark	3	0.01	1.00	0.01	0.00
Omnivore	Myliobatidae	*Myliobatis aquila*	Eagle ray	9	0.04	1.00	0.04	0.00
Scavenger	Myxinidae	*Eptatretus hexatrema*	Sixgill hagfish	9	0.04	1.22	0.05	0.00
Planktivore	Parascorpididae	*Parascorpis typus*	Jutjaw	2	0.01	1.00	0.01	0.00
Carnivore	Pomatomidae	*Pomatomus saltatrix*	Elf	3	0.01	1.33	0.02	0.00
Carnivore	Rajidae	*Raja straeleni*	Biscuit skate	9	0.04	1.00	0.04	0.00
Carnivore	Rajidae	*Rostroraja alba*	Spearnose skate	3	0.01	1.00	0.01	0.00
Carnivore	Rhinobatidae	*Acroteriobatus annulatus*	Lesser guitarfish	1	0.00	1.00	0.00	0.00
Carnivore	Sciaenidae	*Argyrosomus inordorus*	Silver kob	4	0.02	1.00	0.02	0.00
Carnivore	Sciaenidae	*Atractoscion aequidens*	Geelbek	3	0.01	1.00	0.01	0.00
Carnivore	Scyliorhinidae	*Halaelurus natalensis*	Tiger catshark	21	0.10	1.19	0.12	3.38
Carnivore	Scyliorhinidae	*Haploblepharus spp.*	Shyshark	172	0.81	2.64	2.15	0.80
Carnivore	Scyliorhinidae	*Poroderma africanum*	Pyjama catshark	75	0.35	1.61	0.58	7.00
Carnivore	Scyliorhinidae	*Poroderma pantherinum*	Leopard catshark	26	0.12	1.27	0.16	0.00
Omnivore	Soleidae	*Cynoglossus capensis*	Sand tonguefish	2	0.01	1.00	0.01	0.00
Carnivore	Sparidae	*Argyrozona argyrozona*	Carpenter	20	0.09	3.10	0.30	9.88
Omnivore	Sparidae	*Boopsoidea inornata*	Fransmadam	4	0.02	1.00	0.02	0.00
Carnivore	Sparidae	*Chrysoblephus gibbiceps*	Red stumpnose	4	0.02	1.00	0.02	7.50
Omnivore	Sparidae	*Chrysoblephus laticeps*	Roman	71	0.33	2.14	0.72	0.00
Omnivore	Sparidae	*Diplodus hottentotus*	Zebra	2	0.01	1.00	0.01	0.00
Omnivore	Sparidae	*Diplodus sargus capensis*	Blacktail	2	0.01	2.00	0.02	0.00
Omnivore	Sparidae	*Gymnocrotaphus curvidens*	John Brown	2	0.01	1.00	0.01	5.83

Omnivore	Sparidae	*Pachymetopon aeneum*	Blue hottentot	9	0.04	1.89	0.08	0.00
Carnivore	Sparidae	*Pachymetopon blochii*	Cape seabream	67	0.32	6.19	1.98	0.00
Carnivore	Sparidae	*Petrus rupestris*	Red steenbras	9	0.04	1.11	0.05	0.00
Carnivore	Sparidae	*Pterogymnus laniarius*	Panga	66	0.31	4.80	1.51	1.56
Omnivore	Sparidae	*Rhabdosargus globiceps*	White stumpnose	31	0.15	2.61	0.39	8.16
Herbivore	Sparidae	*Sarpa salpa*	Strepie	4	0.02	108.50	2.07	0.00
Omnivore	Sparidae	*Spondyliosoma emarginatum*	Steentjie	92	0.43	5.51	2.41	2.80
Carnivore	Squalidae	*Squalus megalops*	Spiny dogfish	1	0.00	1.00	0.00	0.00
Omnivore	Sygnathidae	*Sygnathus temminckii*	Longsnout pipefish	3	0.01	1.00	0.01	3.62
Carnivore	Tetraodontidae	*Amblyrhynchotes honckenii*	Evil-eye pufferfish	50	0.24	1.58	0.38	0.00
Carnivore	Triakidae	*Galeorhinus galeus*	Soupfin shark	16	0.08	1.07	0.08	3.39
Carnivore	Triakidae	*Mustelus mustelus*	Smooth hound shark	48	0.23	1.19	0.27	2.10
Carnivore	Triakidae	*Triakis megalopterus*	Spotted gully shark	4	0.02	1.00	0.02	0.00
Carnivore	Triglidae	*Chelidonichthys capensis*	Cape gurnard	87	0.41	2.70	1.12	1.47

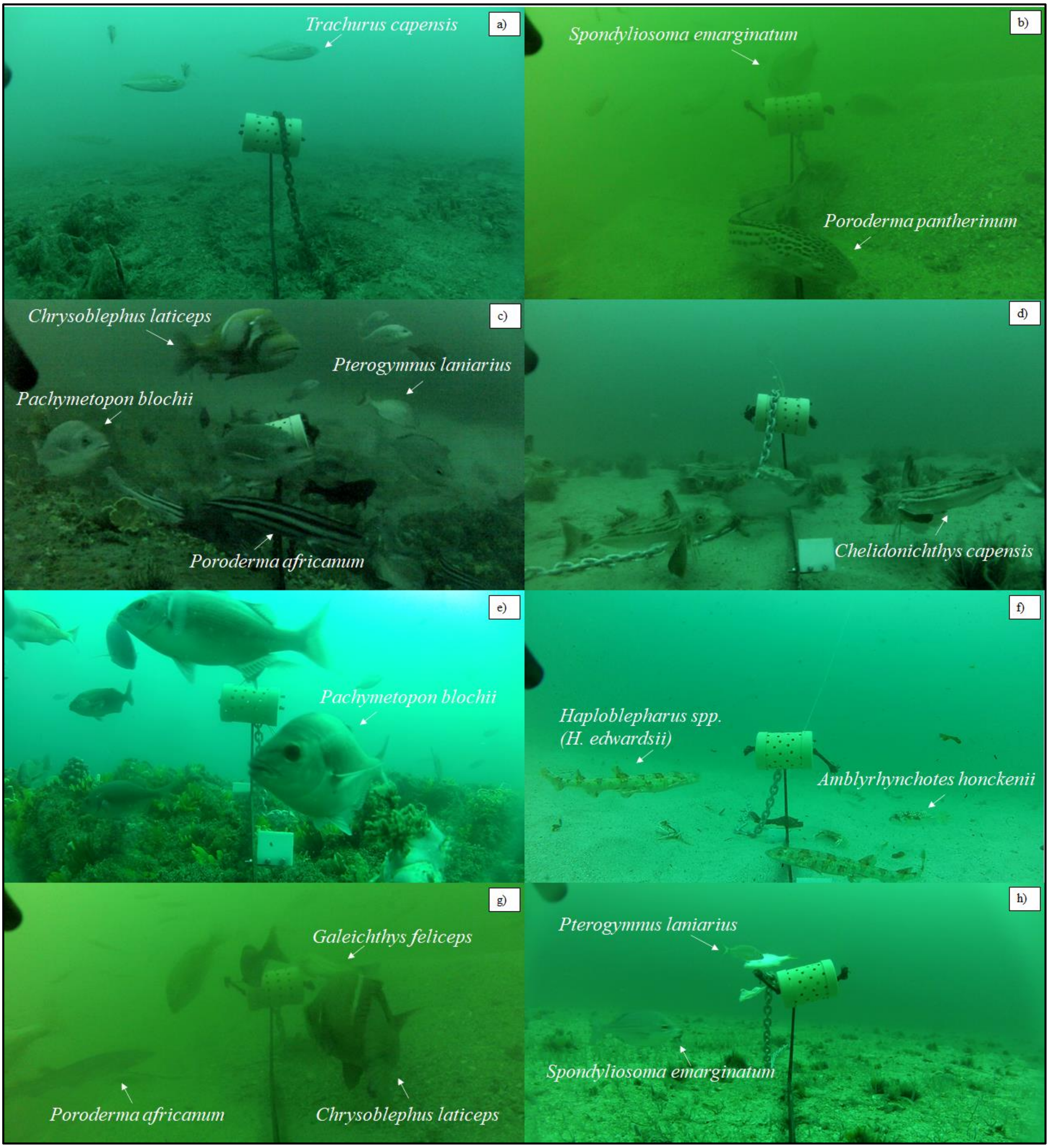

Figure 38. A series of mono-BRUVs screengrab representations of the ten most frequently recorded species across 213 samples from False Bay. These, in order of the frequency they appear in **Table 27**, include: *Haploblepharus spp*., maasbanker (*Trachurus capensis*), steentjie (*Spondyliosoma emarginatum*), Cape gurnard (*Chelidonichthys capensis*), white seacatfish (*Galeichthys feliceps*), pyjama catshark (*Poroderma africanum*), roman (*Chrysoblephus laticeps*), Cape seabream (*Pachymetopon blochii*), panga (*Pterogymnus laniarius*) and evil-eye pufferfish (*Amblyrhynchotes honckenii*).

4.4.7. Species of conservation concern

Fifteen species out of the 57 total species recorded from 213 samples in this study were identified as of conservation concern (**Table 28**), based on their classification according to the criteria outlined in the methods (**Table 26**). Three of these 15 species had specific considerations. *Raja straeleni* was data deficient for the IUCN listing, but had been classified as red by SASSI, and *Argyrosomus inodorus* has not been listed by the IUCN. *Rostroraja alba* was not listed according to SASSI but was Endangered on the IUCN list.

Among the species of conservation concern that would merit special monitoring attention, *Poroderma africanum* (35% of sites) was recorded more frequently across all sites than all other species of conservation concern (**Table 28**). The species was most recorded in shallow depths between 0-30 m, on reef habitat. *Mustelus mustelus* (23% of sites), *Rhabdosargus globiceps* (15% of sites) and *Galeorhinus galeus* (8% of sites) were more frequently recorded than all other species.

Atractoscion aequidens, *Carcharodon carcharias*, *P. africanum*, *Chrysoblephus gibbiceps*, *A. inodorus*, *M. mustelus* and *R. globiceps* were recorded on more than one CATAMI habitat type. Of these, *C. carcharias* and *R. globiceps* were recorded equally on both reef and sand habitat. *Diplodus hottentotus* was recorded in kelp on reef habitat. All species were predominantly recorded in shallow (0-30 m) depth. Eight species were more frequently recorded on sand and five species were more frequently recorded on reef.

Petrus rupestris, *C. gibbiceps* and *R. alba* were recorded as Endangered by the IUCN. Fourteen species were classified as red on the SASSI list. *Sygnathus temminckii* and *Poroderma pantherinum* (not tabulated) were listed as Protected on TOPS (DEA 2017). *Carcharodon carcharias* was listed as Vulnerable on TOPS (DEA 2017) and on CITES Appendix II.

Table 28. Targeted habitat (S = sand, R = reef, K = kelp), depth (shallow = S, medium = M, deep = D) and CATAMI habitat (SUSF = fine sand, SUSC = coarse sand, SCC = cobbles, SCR = rock) highlighted for focused monitoring of species of conservation concern, with observed MaxN relative abundance and relative frequency recorded in this study. The International Union for Conservation of Nature (IUCN) (DD = data deficient, LC = least concern, NT = near threatened, V = vulnerable, E = endangered) and World Wildlife Fund (WWF) South African Sustainable Seafood Initiative (SASSI) (R = red, O = orange) listings are given with the date of assessment for each species in brackets. NT = not listed.

				MaxN						
Family	**Scientific name**	**Common name**	**Relative frequency**	**Mean**	**SD**	**Habitat**	**Depth**	**CATAMI**	**IUCN**	**SASSI**
Rajidae	*Raja straeleni*	Biscuit skate	0.04	1.00	0.00	S	S, M	SUSF	DD (2003)	R
Sparidae	*Diplodus sargus capensis*	Blacktail	0.01	2.00	1.4	R	S	SCR	LC (2009)	R
Pomatomidae	*Pomatomus saltatrix*	Elf	0.01	1.33	0.58	S	S	SUSF	V (2014)	O, R
Sciaenidae	*Atractoscion aequidens*	Geelbek	0.01	1.00	0.00	S	S	SUSF, SUSC, SCR	V (2014)	R
Lamnidae	*Carcharodon carcharias*	Great white shark	0.01	1.00	0.00	R, S	S	SCC, SCR, SUSF	V (2005)	R
Sparidae	*Gymnocrotaphus curvidens*	John Brown	0.01	1.00	0.00	R	S	SCR	LC (2009)	R
Scyliorhinidae	*Poroderma africanum*	Pyjama catshark	0.35	1.61	0.9	R	S	SCR, SUSC, SUSF	NT (2005)	R
Sparidae	*Petrus rupestris*	Red steenbras	0.04	1.11	0.33	R	S	SCR	E (2009)	R
Sparidae	*Chrysoblephus gibbiceps*	Red stumpnose	0.02	1.00	0.00	S	S, M	SUSF, SUSC, SCR	E (2009)	R
Sciaenidae	*Argyrosomus inodorus*	Silver kob	0.02	1.00	0.00	S	S	SUSF, SUSC, SCR	NL	R
Triakidae	*Mustelus mustelus*	Smooth hound shark	0.23	1.19	0.57	S	S	SUSF, SUSC, SCR	V (2004)	O, R
Triakidae	*Galeorhinus galeus*	Soupfin shark	0.08	1.07	0.26	S	S	SUSF	V (2006)	O, R
Rajidae	*Rostroraja alba*	Spearnose skate	0.01	1.00	0.00	S	S	SUSF, SUSC	E (2006)	NL
Sparidae	*Rhabdosargus globiceps*	White stumpnose	0.15	2.61	3.15	R, S	S	SUSF, SUSC, SCR	V (2009)	R
Sparidae	*Diplodus hottentotus*	Zebra	0.01	1.00	0.00	R, K	S	SCR	LC (2009)	R

4.4.8. Species of commercial interest

Ten species out of the 57 total species recorded from 213 samples in this study were summarised in **Table 29** as of value to commercial fisheries, and therefore meriting targeted monitoring. *Trachurus capensis* (48% of sites) was the most frequently recorded species of commercial interest (**Table 29**). The species was recorded on both reef and sand habitat, and on fine (SUSF) and coarse (SUSC) sand CATAMI habitat. After *T. capensis*, *Chelidonichthys capensis* (41% of sites), *Chrysoblephus laticeps* (33% of sites), *Pachymetopon blochii* (32% of sites) and *Pterogymnus laniarius* (31% of sites) were more frequently recorded than all other commercial species. *Seriola lalandi* (2% of sites), *Thyrsites atun* (1% of sites) and *Atractoscion aequidens* (1% of sites) were rarely recorded across all sites.

Trachurus capensis and *T. atun* had the highest mean MaxN values. *Seriola lalandi, A. inodorus* and *A. aequidens* had the lowest mean MaxN values.

All commercial species were recorded most frequently in shallow (0-30 m) depths, except for *C. capensis*, which was found more equally across shallow and medium (30-60 m) depths.

Four species were found predominantly on sand habitat. Two species were found predominantly on reef habitat. Four species – *T. capensis*, *A. aequidens*, *Argyrozona argyrozona* and *P. laniarius* - were recorded on both reef and sand habitat. Only three CATAMI habitat types (SCR, SUSF, SUSC) were represented for commercial fish.

Table 29. Targeted habitat, depth and CATAMI habitat highlighted for focused monitoring of species of commercial interest, with observed MaxN and relative frequency recorded in this study.

				MaxN				
Family	**Scientific name**	**Common name**	**Relative frequency**	**Mean**	**SD**	**Habitat**	**Depth**	**CATAMI**
Carangidae	*Seriola lalandi*	Yellowtail	0.02	1.75	1.50	Sand	Shallow	SUSC, SCR, SUSF
Carangidae	*Trachurus capensis*	Maasbanker	0.48	33.04	56.94	Reef & sand	Shallow	SUSF, SCR, SUSC
Gempylidae	*Thyrsites atun*	Snoek	0.01	12.67	10.41	Sand	Shallow	SUSC, SUSF
Sciaenidae	*Argyrosomus inodorus*	Silver kob	0.02	1.00	0.00	Sand	Shallow	SUSF
Sciaenidae	*Atractoscion aequidens*	Geelbek	0.01	1.00	0.00	Reef & sand	Shallow	SCR, SUSC
Sparidae	*Argyrozona argyrozona*	Carpenter	0.09	3.10	2.92	Reef & sand	Shallow	SCR, SUSC
Sparidae	*Chrysoblephus laticeps*	Roman	0.33	2.14	1.26	Reef	Shallow	SCR
Sparidae	*Pachymetopon blochii*	Cape seabream	0.32	6.19	6.15	Reef	Shallow	SCR
Sparidae	*Pterogymnus laniarius*	Panga	0.31	4.80	5.21	Reef & sand	Shallow	SCR, SUSC
Triglidae	*Chelidonichthys capensis*	Cape gurnard	0.41	2.70	1.65	Sand	Shallow, Medium	SUSF, SUSC

4.4.9. Species diversity indices

The MaxN relative abundance values for 57 species recorded in 213 samples were used to calculate Rényi's diversity. This was plotted for depth categories at 10 m increments. Most samples were in 11 – 20 m water depth (30%) and 21 – 30 m water depth (27%). The remaining samples were distributed across 0 – 10 m depth (13%), 31 – 40 m depth (17%), 41 – 50 m depth (6%) and 51 – 60 m depth (7%). One percent of samples were in 61 – 70 m and 70 – 80 m depth, respectively, and 0.5% of samples were in 80 – 90 m depth.

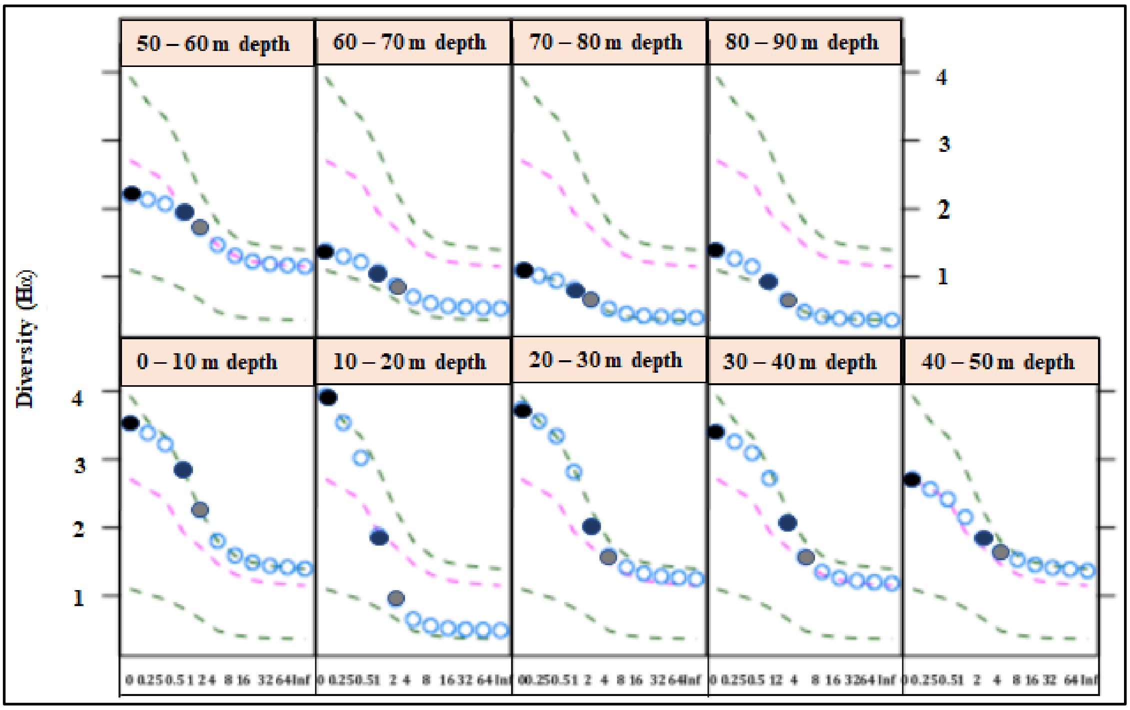

Figure 39. The Rényi diversities for all sites in nine depth categories (10 m increments) combined for 213 mono-BRUVs and stereo-BRUVs samples across False Bay. The plot uses Trellis graphics with a separate panel for each depth category. The x-axis shows the α value of the Rényi formula, where species richness (black dot) is α = 0, Shannon-Wiener Diversity (H') (blue dot) is α = 1, and the Simpson's diversity index (D) (grey dot) is α = 2. The last dot in the curve is the relative abundance of the dominant species. The y-axis shows Rényi diversity profile values (Hα). The green lines indicate the extremes, and the pink line indicates the median in the data set (Oksanen et al. 2017).

Species diversity was highest between 0 – 10 m, 20 – 30 m and 30 – 40 m depth (**Figure 39**). The Shannon-Wiener diversity index (H') and the Simpson's diversity index were highest in these depth intervals. Species richness in the aggregated sites was highest between 10 – 20 m depth, but evenness was lower than other shallow depths. Evenness increased with increasing depth, where 40 – 50 m depth was more even than 30 – 40 m depth and 50 – 60 m depth was more even than 40 – 50 m depth. Below 30 – 40 m depth, diversity decreased with increasing depth. Species diversity was lowest between 70 – 80 m depth, representing the lower extreme of the dataset.

Rényi's diversity was plotted for (reef and sand), where 61% of samples were on sand and 39% of samples were on reef (**Figure 36**).

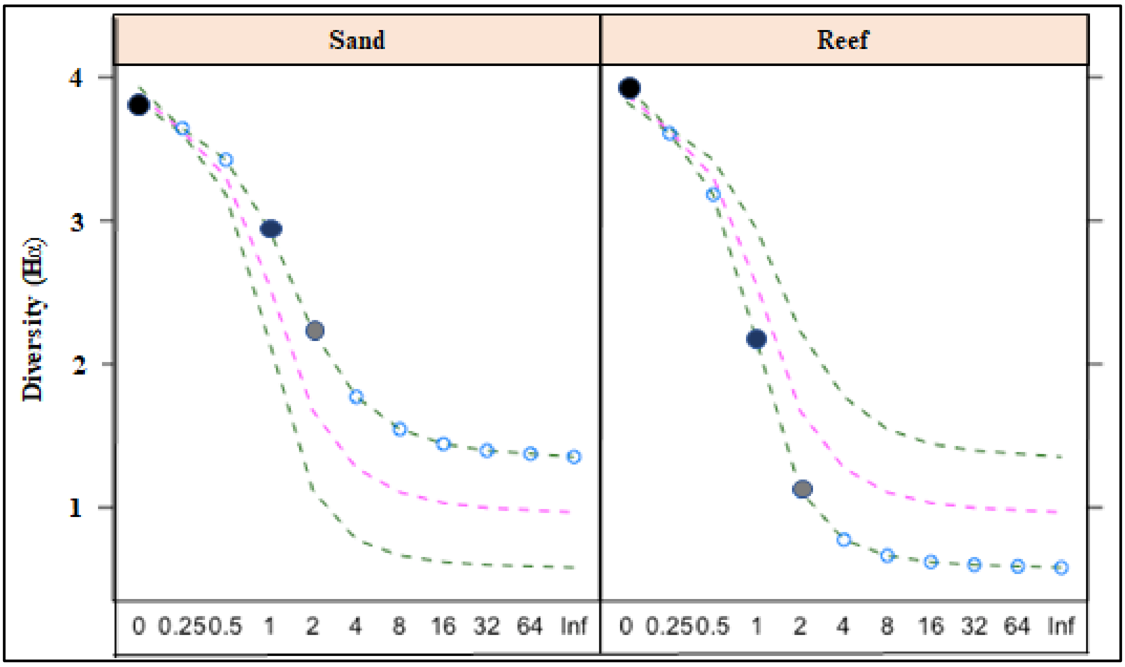

Figure 40. The Rényi diversities for all sand and reef sites combined for 213 mono-BRUVs and stereo-BRUVs samples across False Bay. The plot uses Trellis graphics with a separate panel for each habitat type. The dots in each panel show the values for sites in that habitat. The x-axis shows the α value of the Rényi formula, where species richness (black dot) is α = 0, Shannon-Wiener Diversity (H') (blue dot) is α = 1, and the Simpson's diversity index (D) (grey dot) is α = 2. The last dot in the curve is the relative abundance of the dominant species. The y-axis shows Rényi diversity profile values (Hα). The green lines indicate the extremes, and the pink line indicates the median in the data set (Oksanen et al. 2017).

Species richness was similar for reef and sand overall (**Figure 40**). Evenness was greater on reef than on sand. The relative abundance of a dominant species on reef was higher than on sand. Although species richness in the aggregated sites was similar between reef and sand, the average diversity per site was not.

The two-sample t-test with equal variances found that species richness differed significantly between reef and sand sites (reef mean = 7.810, sand mean = 4.832, df = 207, t = 1.971, p < 0.0001), and the Shannon-Wiener diversity index (H’) differed significantly between reef and sand sites (reef mean = 1.390, sand mean = 1.033, df = 192, t = 1.972, p < 0.0001). At the level of the site, reef was more diverse and had greater evenness than sand.

Rényi’s diversity was plotted for 185 mono-BRUVs samples for season (winter and summer), where 51% of samples were in July (winter) and 49% of samples were in December (summer).

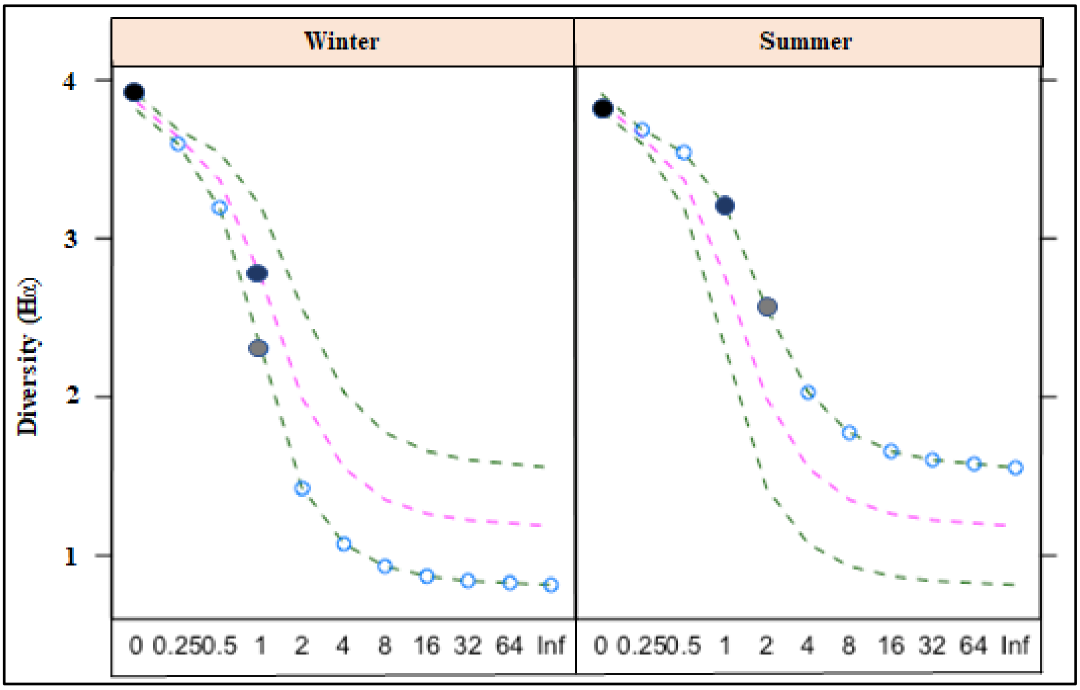

Figure 41. The Rényi diversities for all winter and summer sites combined for 185 mono-BRUVs samples across False Bay. The plot uses Trellis graphics with a separate panel for each season. The dots in each panel show the values for sites in that season. The x-axis shows the α value of the Rényi formula, where species richness (black dot) is α = 0, Shannon-Wiener Diversity (H’) (blue dot) is α = 1, and the Simpson’s diversity index (D) (grey dot) is α = 2. The last dot in the curve is the relative abundance of the dominant species. The y-axis shows Rényi diversity profile values (Hα). The green lines indicate the extremes, and the pink line indicates the median in the data set (Oksanen et al. 2017).

Species richness for the whole bay was similar for winter and summer (**Figure 41**). Evenness was greater in winter than in summer. The two-sample t-test with equal variances found that species richness did not differ significantly in summer and winter (summer mean = 6.322, winter mean = 6.589, df = 183, t = 1.973, p < 0.0001). The two-sample t-test with equal variances found that Shannon-Wiener diversity (H') differed significantly in summer and winter (summer mean = 1.115, winter mean = 1.320, df = 183, t = 1.973, p < 0.013). At the level of the site, winter was more diverse and had greater evenness than summer.

4.4.10. Environmental factors and community composition

To reflect similarity in relative abundance and species composition, the Bray-Curtis similarity index was calculated among the 209 samples that had both MaxN relative abundance and environmental data, out of the 213 analysed samples. The effects of different environmental factors on community composition were displayed in multidimension scaling (MDS) plots.

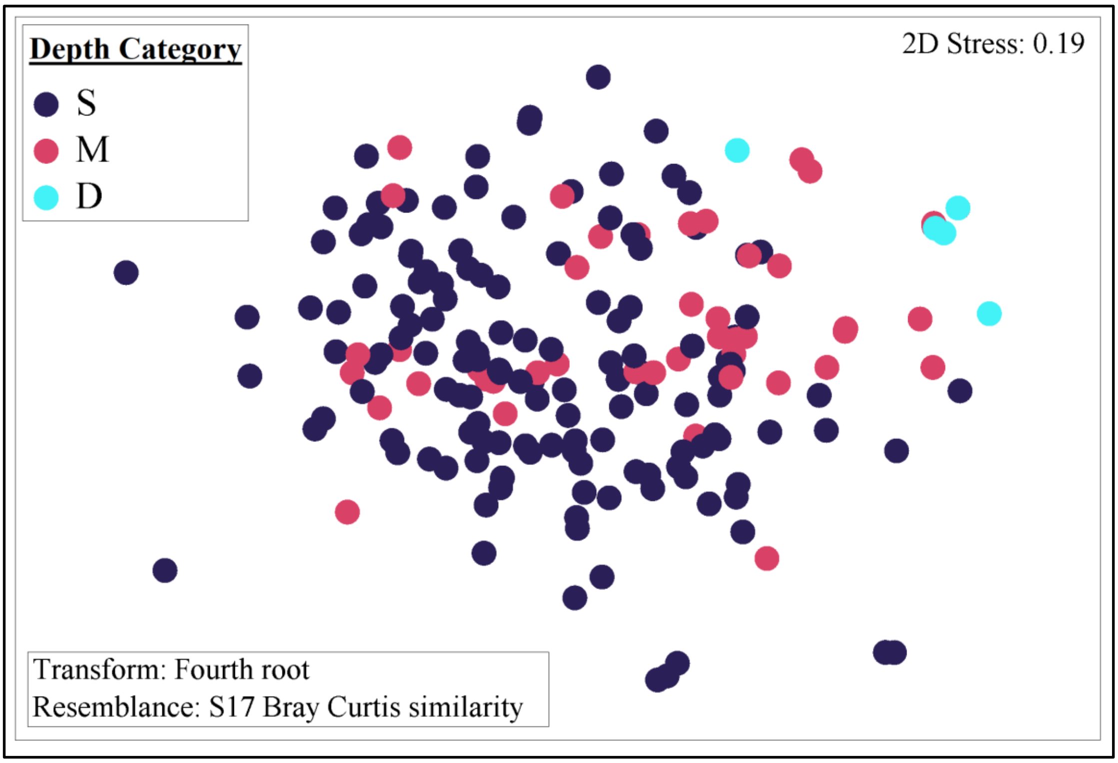

Figure 42. Similarity among sites based on species composition. Sites are characterised according to a) depth category [S = shallow (0 – 30 m), M = medium (30 – 60 m), D = deep (60 – 90 m)].

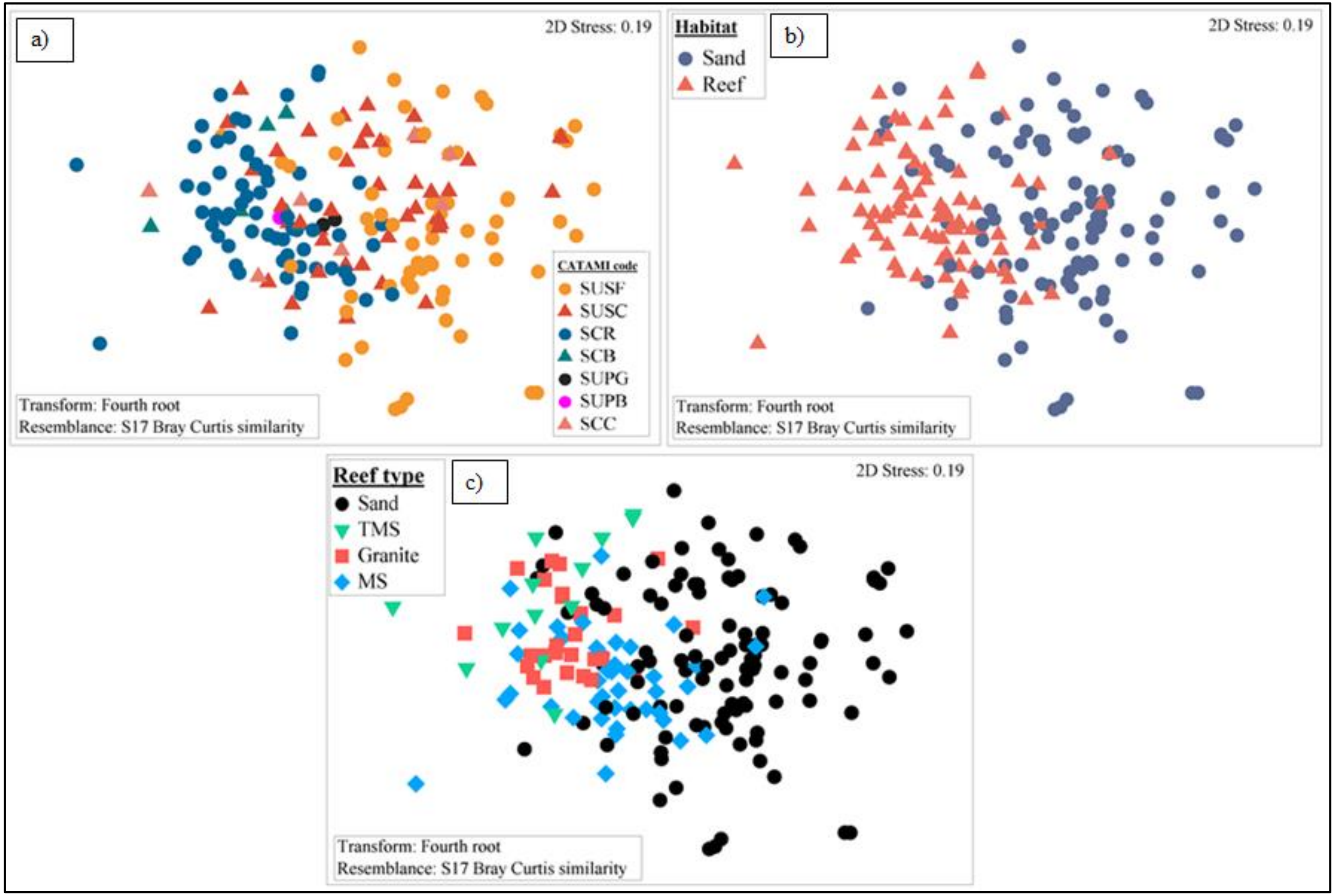

Figure 43. Similarity among sites based on species composition. Sites are characterised according to CATAMI habitat type (SUSF = fine sand, SUSC = coarse sand, SCR = rock, SCB = boulders, SUPG = gravel, SUPB = pebbles, SCC = cobbles), habitat (reef and sand) and reef type (TMS = Table Mountain Group sandstone, MS = Malmesbury Group shale)

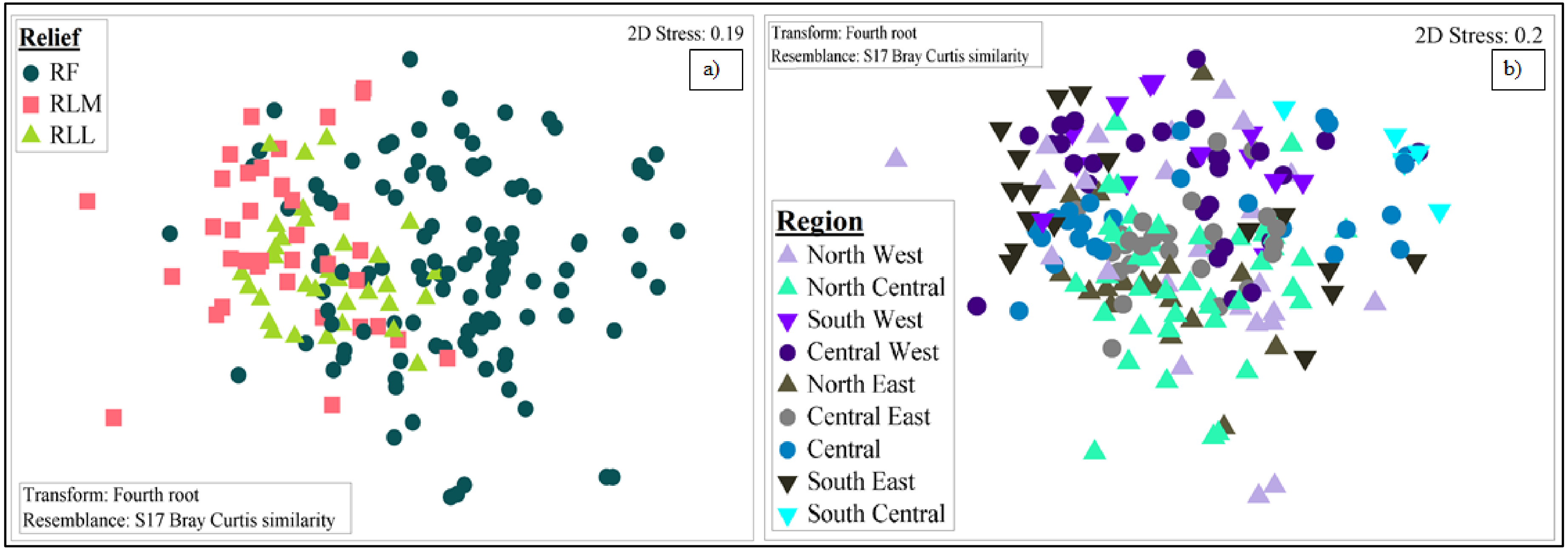

Figure 44. Similarity among sites based on species composition. Sites are characterised according to seafloor profile (RF = flat, RLL = < 1 m, RLM = 1 – 3 m) and according to region in the bay.

There was moderate separation among samples for all factors (**Figure 42 - Figure 44**). A one-way ANOSIM showed that depth (Global R = 0.193, $p < 0.001$), habitat (reef and sand) (Global R = 0.294, $p < 0.01$), CATAMI habitat type (Global R = 0.242, $p < 0.001$), reef type (Global R = 0.189, $p < 0.001$), seafloor profile (Global R = 0.169, $p < 0.001$) and region (Global R = 0.248, $p < 0.001$) were important predictors of species abundance and community composition. Of these, the relatively higher R-values make habitat (reef and sand), region and CATAMI habitat type the stronger predictors of fish assemblage structure.

The mono-BRUVs dataset was then taken as a subset to assess separately and a one-way ANOSIM tested the influence of season (summer and winter) on species composition and abundance. This ANOSIM on 185 mono-BRUVs samples showed that season (Global R = 0.125, $p < 0.001$) was an important predictor of similarity among samples, with relatively lower separation among samples than all other environmental variables tested.

Two factor PERMANOVA models showed that habitat, season, depth and CATAMI habitat type explained differences in species composition (**Table 30**). All factors were significant, as were their interaction terms. In all cases, the interaction term was considerably less significant than the model main effects. Habitat (Pseudo-F_1 = 27.11; $p < 0.001$) explained more differences in community composition than season ((Pseudo-F_2 = 6.7887; $p < 0.001$) in model 1, which was calculated using mono-BRUVs data. Habitat (Pseudo-F_3 = 20.555; $p < 0.001$) explained more differences in community composition than depth (Pseudo-F_4 = 6.4832; $p < 0.001$) in model 2. Season (Pseudo-F_5 = 12.199; $p < 0.001$) explained only slightly more of the differences in community composition than depth (Pseudo-F_6 = 11.046; $p < 0.001$) in model 3, which was calculated using mono-BRUVs data. CATAMI habitat type (Pseudo-F_7 = 4.6262; $p < 0.001$) explained the least of the differences in community composition compared to habitat and season, and explained only slightly more of the differences than depth (Pseudo-F_8 = 4.0384; $p < 0.001$) in model 4.

Table 30. Results of four Permutational Multivariate Analysis of Variance (PERMANOVA) models testing the effect of habitat (reef and sand), season (summer and winter), depth category (shallow, medium and deep), CATAMI habitat type and their interactions on species composition in False Bay. Df = degrees of freedom. Significant p-values are denoted by (*). Models 1 and 3 represent mono-BRUVs datasets, and models 2 and include the stereo-BRUVs datasets.

Model Design	Model Input Factors	Df	Pseudo-F	P (perm)
1	Habitat	1	27.11	0.001*
	Season	1	6.7887	0.001*
	Habitat X Season	1	2.8476	0.001*
2	Habitat	1	20.555	0.001*
	Depth category	2	6.4832	0.001*
	Habitat X Depth category	1	2.8407	0.005*
3	Season	1	12.199	0.001*
	Depth category	1	11.046	0.001*
	Season X Depth category	1	4.6774	0.001*
4	CATAMI	6	4.6262	0.001*
	Depth category	2	4.0384	0.001*
	CATAMI X Depth category	5	2.0126	0.002*

4.4.11. Community composition and species that typified community types

Species that grouped together into communities at 20% Bray-Curtis similarity were displayed in a MDS plot and in a cluster diagram. The Bray-Curtis similarity index was calculated among 57 species from 209 samples where ichthyofauna were recorded (MaxN relative abundance and environmental data were both available in all these samples), out of the total of 213 samples analysed.

Rhabdosargus globiceps, *Mustelus mustelus*, *Amblyrhynchotes honckenii*, *Halaelurus natalensis* and *Chelidonichthys capensis* formed a group at 20% similarity (**Figure 45**). These species were frequently found on sand and in shallow depth (0 – 30 m).

Pachymetopon blochii, Chrysoblephus laticeps, Spondyliosoma emarginatum, Galeichthys feliceps, *Pterogymnus laniarius, Haploblepharus spp.*, *Trachurus capensis*, *Poroderma pantherinum*, *Poroderma africanum* and *Argyrozona argyrozona* formed a group at 20% similarity (**Figure 45**). These species were frequently found on reef and in shallow depth (0 – 30 m).

Triakis megalops, *Cynoglossus capensis*, *Parablennius cornutus* and *Clinus agilis* formed a group at 20% similarity (**Figure 45**). These species were recorded on sand and in shallow depth (0 – 30 m).

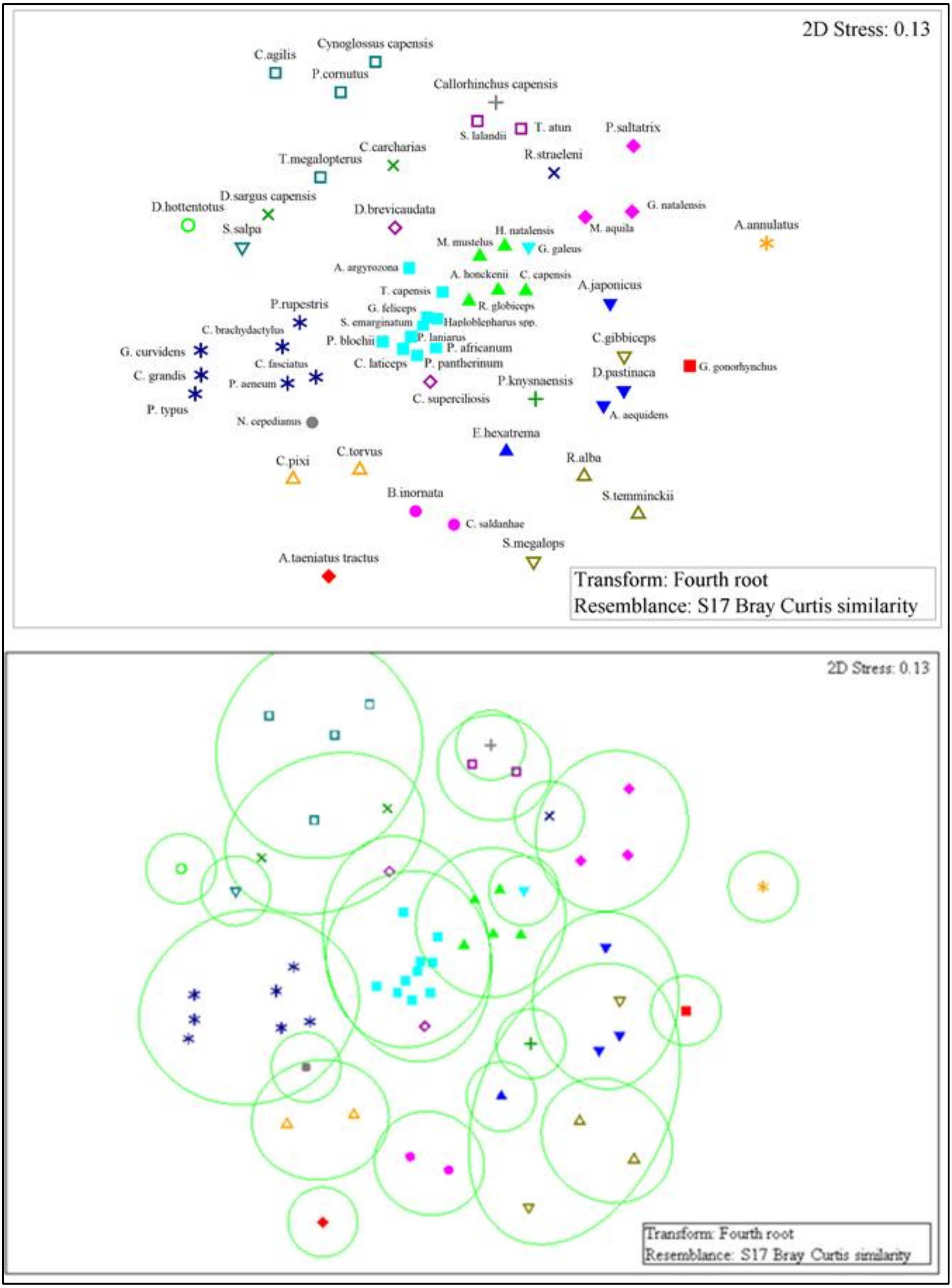

Figure 45. Bray Curtis similarity among species at 20% resemblance level. Species that are similar at 20% are indicated by the same symbol and are grouped by an ellipse. Species that share a symbol colour form groups at < 20% similarity.

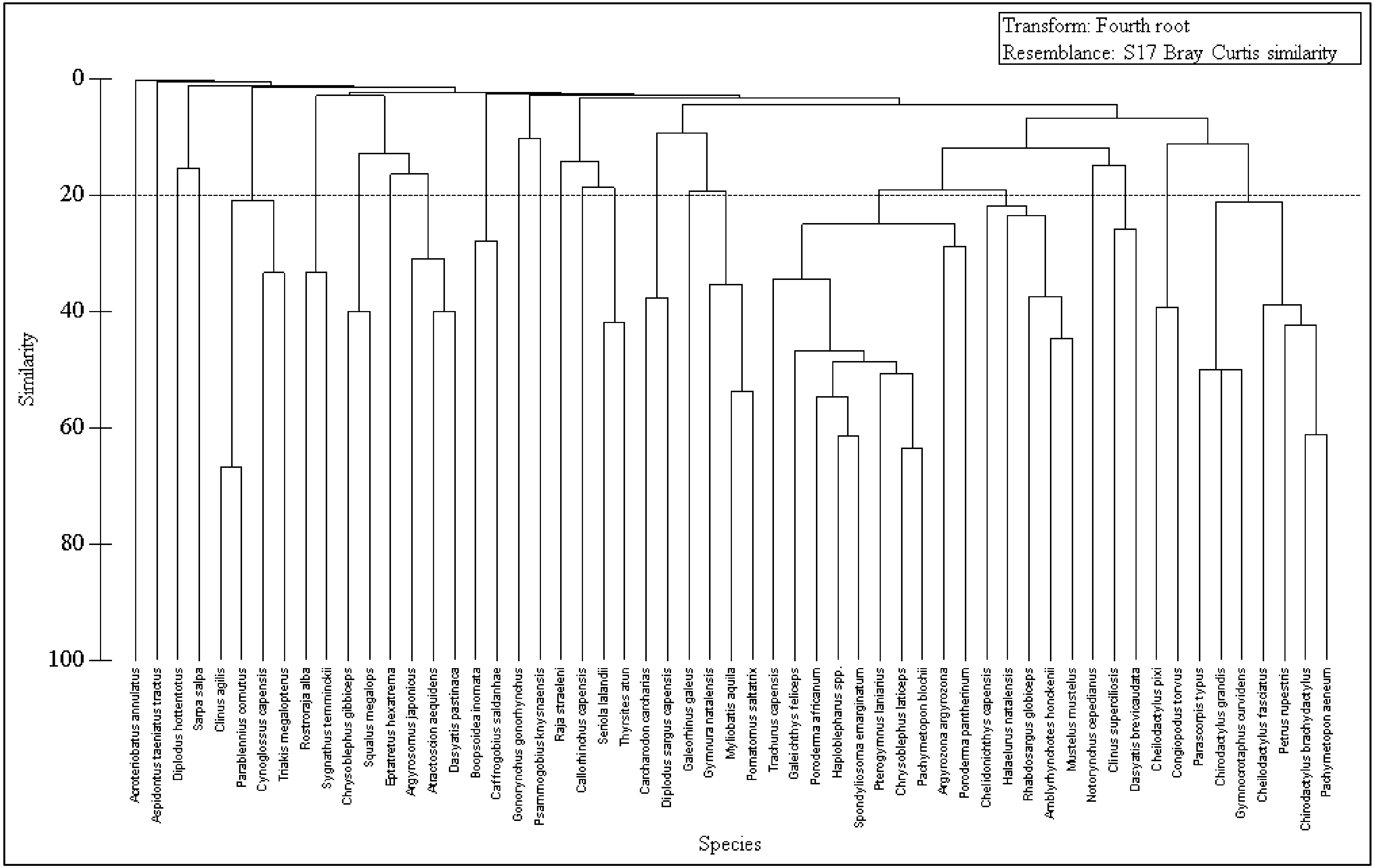

Figure 46. Species cluster analysis based on Bray-Curtis similarity among 209 sites where ichthyofauna were recorded across False Bay. A 20% Bray-Curtis cut-off was chosen to identify community types.

Several species formed groups that were higher in percentage similarity. *Clinus agilis* and *Parablennius cornutus* formed a group at 67% similarity, which was the highest similarity for all species (**Figure 46**). *Chrysoblephus laticeps* and *Pachymetopon blochii* formed a group at 64% similarity. These species were recorded on all three reef types (Malmesbury Group shale, Cape Granite Suite and Table Mountain Group sandstone). *Poroderma africanum*, *Haploblepharus spp.*, *Spondyliosoma emarginatum*, *Pterogymnus laniarius, C. laticeps* and *P. blochii* formed a group at 48% similarity. These species were recorded together in kelp, and in habitats that had mixed reef and sand.

Gymnocrotaphus curvidens, Parascorpis typus and *Chirodactylus grandis* formed a group at 50% similarity (**Figure 46**). *Chirodactylus brachydactylus*, *Petrus rupestris* and *Pachymetopon aeneum* formed a group at 42% similarity. *Chrysoblephus gibbiceps* and *Squalus megalops* formed a group at 40%.

4.4.12. Species that typify sites in each habitat type, depth category and region

A one-way SIMPER showed that the average similarity between sand sites was 31% and 41% between reef sites. *Haploblepharus spp.* were common on both reef and sand where their presence contributed 24% and 25%, respectively, to the average similarity among sites in each habitat. *Chelidonichthys capensis* (34% contribution to average similarity) and *Trachurus capensis* (16% contribution to average similarity) were typical of sand sites, and *P. blochii* (14% contribution to average similarity) and *C. laticeps* (14% contribution to average similarity) were typical of reef sites.

The average similarity was 32% between shallow sites, 35% between medium sites and 54% between deep sites. *Haploblepharus spp.* (32% contribution to average similarity), *T. capensis* (14% contribution to average similarity) and *Spondyliosoma emarginatum* (10% contribution to average similarity) were typical of shallow samples in depths between 0 – 30 m. *Chelidonichthys capensis* (48% contribution to average similarity), *T. capensis* (16% contribution to average similarity) and *Haploblepharus spp.* (16% contribution to average similarity) were typical of sites medium depths between 30 – 60 m. *Chelidonichthys capensis* (100% contribution to average similarity) typified sites between 60 – 90 m depth.

The average similarity between SUSF sites was 31%, the average similarity between SUSC sites was 35%, the average similarity between SCR sites was 41%, the average similarity between SUPG sites was 64% and the average similarity between SCC sites was 32%. *Haploblepharus spp.* were ubiquitous across all CATAMI habitat types. *Chelidonichthys capensis* (40% contribution to average similarity) and *T. capensis* (18% contribution to average similarity) typified fine sand (SUSF) sites. *Chelidonichthys capensis* (36% contribution to average similarity), *T. capensis* (13% contribution to average similarity) and *S. emarginatum* (9% contribution to average similarity) typified coarse sand (SUSC) sites. *Pachymetopon blochii* (16% contribution to average similarity), *C. laticeps* (15% contribution to average similarity) and *T. capensis* (10% contribution to average similarity) typified rock (SCR) sites. *Pachymetopon blochii* (18% contribution to average similarity), *S. emarginatum* (17% contribution to average similarity) and *C. laticeps* (15% contribution to average similarity) were abundant on boulder habitat (SCB). *Pterogymnus laniarius* (23% contribution to average similarity) typified gravel habitat (SUPG) and *C. capensis* (18% contribution to average similarity) typified cobble habitat (SCC).

Table 31. Species that typify nine regions in False Bay. These regions correspond to the nine zones allocated for the stereo-BRUVs survey. Zone i = North West, Zone ii = North Central, Zone iii = North East; Zone iv = Central West, Zone v = Central, Zone vi = Central East; Zone vii = South West, Zone viii = South Central, Zone ix = South East.. Species that contribute to a maximum of 75% cumulative similarity among sites in that region are listed, except where a species contributes to all similarity (100%).

Region	**Species**	**Contribution to site similarity (%)**
North West	*Haploblepharus spp.*	33.51
	Amblyrhynchotes honckenii	22.26
	Galeichthys feliceps	9.78
	Chelidonichthys capensis	7.26
North Central	*Trachurus capensis*	29.12
	Haploblepharus spp.	19.45
	Galeichthys feliceps	17.33
	Spondyliosoma emarginatum	8.57
North East	*Haploblepharus spp.*	25.13
	Trachurus capensis	17.15
	Spondyliosoma emarginatum	12.05
	Galeichthys feliceps	11.71
	Chrysoblephus laticeps	7.77
Central West	*Haploblepharus spp.*	44.43
	Chelidonichthys capensis	13.83
	Spondyliosoma emarginatum	13.42
Central	*Chelidonichthys capensis*	44.67
	Pterogymnus laniarius	9.83
	Poroderma africanum	9.05
	Pachymetopon blochii	8.27
Central East	*Trachurus capensis*	37.04
	Haploblepharus spp.	28.48
	Pterogymnus laniarius	10.78
	Chelidonichthys capensis	4.38
South West	*Haploblepharus spp.*	50.8
	Poroderma africanum	21.42
South Central	*Chelidonichthys capensis*	100
South East	*Haploblepharus spp.*	21.69
	Pachymetopon blochii	19.6
	Chelidonichthys capensis	11.57
	Trachurus capensis	10.03
	Pterogymnus laniarius	9.58

4.5. DISCUSSION

4.5.1. Comparison with previous surveys of ichthyofauna diversity in False Bay

This study recorded 57 fish species from 30 families across reef and sand habitats, from 4 – 84 m depth in False Bay. This is the first synthesis of the subtidal ichthyofauna at the full scale of False Bay using a single, standardised method. The application of BRUVs has largely been restricted to reefs elsewhere in South Africa (Bernard 2012; Bernard & Götz 2012; Sanguinetti 2013; De Vos et al. 2014; Parker 2015; Heyns-Veale 2016; Parker et al. 2016a). Forty-three of the species recorded in this study occurred on sand, 10 of which are of conservation concern and at least four of which are commercially important in False Bay. The extension of BRUVs surveys on the coastline to include significant coverage of soft sediments is important: these habitats were considered largely homogenous, but studies increasingly demonstrate that patterns in sand-associated fish distribution are detected using BRUVs, with implications for monitoring and MPA zoning (Moore et al. 2010; Schultz et al. 2015; Fetterplace 2017).

No single survey or method has previously surveyed subtidal fish communities across both reef and sand in False Bay, so comparisons with previous assessments are separated by these habitat types. Thirty-eight species from 18 actinopterygian families were recorded; 35 of these species were recorded at least once on reef habitat and 23 species of these species, such as *Chrysoblephus laticeps* (Kerwath et al. 2007) and *Pachymetopon blochii* (Lechanteur & Griffiths 2001), are typically reef-associated. This compares favourably with the 22 species recorded by underwater visual census (UVC) on reef in the TMNP MPA (Lechanteur 2000). Relative to UVC, BRUVs record higher species diversity; a finding that mirrors global results that show BRUVs outperform other biodiversity survey methods in terms of species richness (Colton & Swearer 2010; Harvey et al. 2012). In addition, this comparison highlights that the efficiency of at-sea logistics (a single vessel and crew can survey more sites in a single day) mean BRUVs are suitable for sampling across larger spatial scales (covering the western Cape Granite Suite reefs, the eastern Malmesbury Group shale reef habitat, and Whittle Rock, York and East Shoal in a single assessment) and encompass a higher variety of habitat-types (Cappo et al. 2003; White et al. 2013; Bernard et al. 2014). They gather several hours of data simultaneously to improve over-all sampling effort (Langlois et al 2010; Bernard & Götz 2012; White et al. 2013; De Vos et al. 2014; Bernard et al. 2014), which helped achieve the sample size in this study.

Eighteen chondrichthyan species from 11 families were recorded, whereas 37 chondrichthyan species were recorded from historical trawl and beach-seine scientific surveys, trawl, demersal shark longline, linefish and beach-seine commercial catch records and recreational shore-angling catch records in False Bay between 1897 and 2011 (Best et al. 2013). While the species count is lower in this study, when BRUVs are considered as a single survey method, they offer improvement relative to any other single survey method in False Bay, improving taxonomic resolution and fisheries-independent design (Brooks et al. 2011; Sherman et al. 2018). The five most frequently recorded species in this study were *Haploblepharus spp.*, *Poroderma africanum*, *Mustelus mustelus*, *P. pantherinum* and *Halaelurus natalensis*. The predominance of Scyliorhinidae in this study differs from the five most frequently recorded species across all catch records; namely, *Galeorhinus galeus*, *M. mustelus*, *Notorynchus cepedianus*, *Acroteriobatus annulatus* and *Callorhinchus capensis* (Best et al. 2013). This study recorded all these species, but only *M. mustelus* was in the five most frequently recorded species of both surveys.

A UVC in the Castle Rocks no-take zone of the TMNP MPA recorded six chondrichthyans (Lechanteur & Griffiths 2002), and a survey on artificial reefs in False Bay recorded three chondrichthyans (Lechanteur & Griffiths 2001). These surveys were reef-restricted but were conducted on a timescale more comparable to this study than the synthesis of a century of catch records by Best et al. (2013). The results of this study still compare favourably, with 13 chondrichthyan species specifically recorded on reef. This supports the finding that BRUVs are useful to detect chondrichthyans (Brooks et al. 2011; Devine et al. 2018; Jabado et al. 2018).

4.5.2. Actinopterygian species records

Trachurus capensis, *Spondyliosoma emarginatum*, *Galeichthys feliceps* and *Chelidonichthys capensis* were most frequently observed across all sites in this study.

This differs from the most frequently recorded species in the reef-specific surveys by Lechanteur (2000), where only *S. emarginatum* was common to both. Sampling across more habitat types and a greater depth range will change the ecosystem level picture of False Bay. Species will also differ in their detection using SCUBA or BRUVs, especially where certain species are deterred by divers (Emslie et al. 2018). In an assessment of reef samples only, *C. laticeps*, *P. blochii* and *S. emarginatum* were the most frequently recorded species in this study. In a survey of the artificial reefs, Lechanteur (2000) found *S. emarginatum*, *Cheilodactylus fasciatus* and *P. blochii* in higher numbers. The five most abundant species recorded across natural reefs were *P. blochii*, *Sarpa salpa*, *Boopsoidea inornata*, *C. laticeps* and *S. emarginatum* (Lechanteur 2000). There was a slight increase in the frequency of *C. laticeps*, accounting for 10.4% of samples in previous surveys (Lechanteur 2000) and 13% of reef samples in this study. Populations of *C. laticeps* respond positively to MPA protection (Kerwath et al. 2013) and the species shows some sign of recovery (SASSI 2018). Detection of this species remains important to monitor the efficacy of the TMNP MPA, and *C. laticeps* has been noted for potential medium-low impacts from climate change (Ortega-Cisneros et al. 2018).

Species from the family Sparidae were the most frequently recorded; of these, *S. emarginatum, C. laticeps*, *Pterogymnus laniarius* and *P. blochii* were most common in this study. This finding matches those of earlier surveys restricted to the reefs (Lechanteur & Griffiths 2002). There are two reasons why the abundance of species from this family is important to discuss.

Firstly, the high diversity that results from two oceanographic regimes converging around False Bay (Griffiths et al. 2010) is reflected in these results. Species typical of the Benguela upwelling regime such as *P. blochii* and species typical of the southern Cape coast and the Agulhas Current such as *B. inornata* were both recorded. This study also recorded Sparidae typical of various habitats and various economic importance; for instance, *Diplodus sargus capensis* and *D. hottentotus* are typical of shallow reefs (Mann & Buxton 1992), *Pachymetopon aeneum* of deep reefs (Götz 2006) and *Rhabdosargus globiceps* is typical of both reef and sand habitats (Heemstra & Heemstra 2004). *Chrysoblephus laticeps*, *P. laniarius* and *Argyrozona argyrozona* are all of fisheries importance along the South African coast (Mann 2013; DAFF 2016), and *R.*

globiceps and *P. blochii* have been important to the False Bay linefishery (Bennett 1991; Penney 1991). The detection of species that are indicative of regional diversity patterns, that reflect distribution across habitat types, and that are of economic importance, is important to corroborate whether this improves previous surveys. Patterns of species distribution and abundance are not fixed in space or time (Blamey et al. 2015): the detection of species across an ecosystem, at various levels of interest and for different monitoring concerns, is necessary for long-term monitoring in False Bay.

Secondly, these results corroborate findings that BRUVs are more likely to record species that are resident and attracted to bait (Harvey et al. 2007; Brooks et al. 2011; Bernard & Götz 2012). Both traits are typical of many seabreams (Sparidae) (Buxton & Smale 1989). The species recorded in this study are not limited to territorial, predatory species. A herbivore *S. salpa*, the parasitic *Aspidontus taeniatus tractus* (Smith & Heemstra 1991), and planktivores *T. capensis* and *Parascorpis typus* were also recorded, together with species such as *Chirodactylus brachydactylus* that do not directly approach the bait canister. The BRUVs recorded diversity across a range of feeding guilds and included species attracted by activity at the bait canister but may underrepresent their true diversity (Watson et al. 2010). A rotenone survey of the cryptic ichthyofauna of False Bay between 0 - 20 m recorded 39 species from 16 families (Prochazka 1998). While this study recorded opportunistic sightings of species such as *Sygnathus temminckii*, *Clinus agilis*, *Parablennius cornutus* and *P. typus*, BRUVs underrepresent cryptic and small species. No single method will capture the full complement of biodiversity, but there may be times when a full biodiversity assessment is required. In these instances, improvements in the configuration of BRUVs (Whitmarsh et al. 2018) and targeted survey design may improve these records.

However, the study objective was an assessment of biodiversity at the scale of the bay, and in this regard BRUVs improved on previous surveys. Many seabreams are important linefishery (Bennett 1991; Penney 1991) and spearfishery targets (Lechanteur 2000) in False Bay. At the same time, the life history traits of many seabreams make them vulnerable to overexploitation and several species are in decline (Mann 2013). Their strong representation in this study, which was not limited to the western reefs that fall under the current marine protected area (MPA) zonation, recommends BRUVs for their future monitoring in False Bay. Moreover, the capacity to assess species in the context of their wider ecosystem is an important improvement in this methodology (Bernard et al. 2014). The interactions of species within their communities are complex and changes are difficult to predict (Palumbi 2001). While the abundance of individual species will change over time, limiting assessments to tracking fishery target species will miss changes in the habitat and its associated biological communities. Baited remote underwater video systems (BRUVs) are more suitable for ecosystem level monitoring in False Bay than controlled angling surveys (CAS) or SCUBA.

4.5.3. Chondrichthyan species records

The predominance of Scyliorhinidae, especially Haploblepharus *spp.*, is notable. This may be a sampling artefact. The configuration of mono-BRUVs and stereo-BRUVs is now low, relative to the first BRUVs deployed in South Africa that stood higher above the seafloor (Bernard 2012; De Vos et al. 2014). This may better capture species such as scyliorhinids that swim near the seafloor (Ebert et al. 2013). *Haploblepharus edwardsii* is a generalist, found across a large depth range and on both sand and reef, which may account for some of its ubiquity (Ebert et al. 2013). Neither *H. edwardsii* nor *H. pictus* are targets of any fishery in False Bay. However, they are often caught and discarded by recreational fishermen and caught in lobster traps (Best et al. 2013). That they have never been intentional target species may also account somewhat for their abundance in this study. Best et al. (2013) noted that there has never been a market or intentional fishery for scyliorhinid species in South Africa, which in combination with their low trophic level and small size, may have sustained their numbers.

This result may also point to some form of mesopredator release, especially where other shark species in False Bay have shown significant declines (Best et al. 2013). However, the predominance of *P. africanum* in this study indicates that the threat of predation has not entirely disappeared for *Haploblepharus spp.* in the same habitats; the larger scyliorhinid is known to prey on other small sharks (Ebert et al. 2013). Larger sharks such as *G. galeus*, *Triakis megalopterus* and *N. cepedianus* were recorded on both reef and sand habitat, where *Haploblepharus spp.* were ubiquitous, but the frequency of the larger sharks was lower. Best et al. (2013) recorded declines in populations of *G. galeus* and *T. megalopterus* in False Bay, and cautioned that the high catch records of *N. cepedianus*, coupled with its low productivity, marks the species as one to monitor for future declines. All three species were highlighted as priorities for monitoring and management (Best et al. 2013).

It is unlikely that declines in piscivorous actinopterygians is linked to any mesopredator release, and little evidence exists to demonstrate that the removal of predatory fish directly affects prey and non-target species (Götz et al. 2009). *Petrus rupestris* has shown significant declines across its range (Mann et al. 2014c; Kerwath et al. 2019). Smale (1986) reported that the diet of large *P. rupestris* between 701 – 1300 mm size from East London, Algoa Bay, Tsitsikamma National Park (TNP) and Mossel Bay included *Haploblepharus fuscus*. While *H. fuscus* was not recorded in this study, it is conceivable that large *P. rupestris* were capable of preying on the other *Haploblepharus spp*. in False Bay. *Petrus rupestris* was only recorded nine times out of 213 samples, despite a concerted focus on the reef systems that represent its preferred habitat. This may be a first indication that the decline of this large, predatory fish in False Bay at the edge of its core distribution in False Bay has consequences for the wider ecosystem (Kerwath et al. 2019). Future studies should investigate the possibility of trophic cascades in False Bay. These ecological interactions in disturbed environments are difficult to interrogate; rather, this finding highlights the need to monitor species abundance and distribution on an ongoing basis at the full scale of the bay and across its different reef types, rather than remain limited to the western reefs. Indeed, Best et al. (2013) recommend improved monitoring and taxonomic resolution for species without clear population trends, and pointed specifically to *H. edwardsii, H. pictus, P. africanum* and *P. pantherinum*.

It seems more likely, then, that previous survey techniques have under-sampled small Scyliorhinidae in the region, and that the relative abundance of *Haploblepharus spp.* may historically have been high in the bay. *Haploblepharus edwardsii* is known to take fish offal in addition to its invertebrate diet and may benefit from the discards from fishing activity in False Bay. This study confirms that BRUVs are well-suited to monitor these populations. The study detected all the most commonly caught chondrichthyan species reported for False Bay (*G. galeus, M. mustelus, N. cepedianus, A. annulatus* and *C. capensis*) that were recommended for future management focus, as well as several species (*T. megalopterus*, *Raja spp.* and *G. galeus*) with declining populations that require conservation prioritisation (Best et al. 2013).

4.5.4. Species of conservation concern

Fifteen species recorded in this study were highlighted as of conservation concern. Of these, nine species were listed as either Vulnerable, Endangered or Critically Endangered on the IUCN Red List of Threatened Species™ and 14 were listed as red by the SASSI programme. *Raja straeleni* is data deficient (Smale 2009) but considered of conservation concern in False Bay by Best et al. (2013). Taxonomic resolution of skate species in fisheries catch data is often coarse, and species of concern are inadequately monitored (Best et al. 2013; Sherman et al. 2018). This study detected both *R. straeleni* and *Rostroraja alba*, the latter of which is Endangered (Dulvy et al. 2006). Skates and rays form a significant part of fisheries catch worldwide (Walker & Hislop 1998; Graham et al. 2001) and are considered of conservation concern (Ebert et al. 2007; Dulvy et al. 2014). Both *R. straeleni* and *R. alba* were recorded in the shallow northern central region of False Bay, where shore-angling effort has increasingly targeted chondrichthyans (Bennett 1991) and the beach-seine fishery is operational (Lamberth 1994). Improving the detection of batoids is important for monitoring (Best et al. 2013; Sherman et al. 2018), and BRUVs present a method to do so at an ecosystem level, such that both target and non-target species, as well as diver-shy species, are detected (White et al. 2013; Sherman et al. 2018).

More species of conservation concern were detected on sand than on reef in this study. Reef species are vulnerable to overexploitation (Buxton 1993; Griffiths 2000), respond positively to MPA protection (Buxton & Smale 1989; Bennett & Attwood 1991; Attwood & Bennett 1994; Götz et al. 2009; Kerwath et al. 2013) and undoubtedly merit the current focus on reef habitat for protection in False Bay (Sanguinetti 2013). However, this study highlights other vulnerable species that are associated with various habitat types that remain outside current protected areas zonation in the bay. Four threatened chondrichthyans; namely, *R. straeleni*, *G. galeus*, *M. mustelus* and *R. alba*, were primarily detected on sand. All species with conservation listings were most frequently recorded in shallow depths between 0 – 30 m, in direct contact with an increasingly urbanised coastline. Species declines of *R. globiceps*, *A. inodorus* and *A.*

aequidens have been linked to the recreational shore-angling fishery (Bennett 1991) and the commercial beach-seine fishery (Penney 1991; Lamberth et al. 1995a) which operate in shallow depths and on many sand habitats in False Bay (Penney 1991). An understanding of the preferred habitat and depth for species of conservation concern can guide future monitoring programmes so that surveys can be targeted and efficient, especially where specific species are a monitoring priority. Some shallow, sand habitats in False Bay present a challenge to BRUVs monitoring: where turbidity is high, visibility on sample videos is often low, and this will require further address. In these areas, complementary methods that are not reliant on good visibility, such as acoustic telemetry (Cowley et al. 2017), should supplement the bay-wide overview of the ichthyofauna of False Bay.

Poroderma africanum had the highest relative frequency of all species of conservation concern in this study, was the sixth most frequently recorded species across all sites and was recorded at 36% of all sites. However, *P. africanum* is on the SASSI red list and, together with *P. pantherinum*, the Threatened or Protected Species (TOPS) list (DEA 2017). Under section the National Environmental Management: Biodiversity Act (NEMBA) 57(2) regulations, *P. africanum* and *P. pantherinum* cannot be caught (NEMBA 2004), except where the fisher is in possession of a valid permit issued in accordance with the Marine Living Resources Act 18 of 1998. Their life history data present *P. africanum* and *P. pantherinum* as candidates for conservation prioritisation: endemic, with low productivity, (Compagno 2009; Human 2009), both species are protected. However, Best et al. (2013) noted that *Poroderma* species in False Bay show no clear population trends and were abundant in SCUBA surveys, making it difficult to interrogate their regional population status without empirical evidence. Both *Poroderma* species were among the most frequently recorded species in this survey. This finding is at odds with current conservation listings for both species: however, it illustrates an important point. Pre-emptive monitoring is desirable where species life histories suggest vulnerability to exploitation, and where there may already be evidence of declines at the edge of species' distributions. Ongoing regional monitoring at the core of species' distributions is also key to informing conservation assessments. Scyliorhinids may not be current fisheries targets, but a wider range of threats than simply overexploitation require consideration in shallow, coastal waters. Ecosystem level impacts are difficult to predict, and a method that detects species across a spectrum of conservation concern is necessary. Survey methods that adequately detect these species is a useful addition to assessments that have previously underrepresented Scyliorhinidae in the region.

Other species of conservation concern were not recorded with high frequency, which may indicate one of two things: either, species are not particularly well-suited to being sampled by this method, or they have declined in False Bay and would not be detected with any significant frequency by any method. The preferred habitats of *Carcharodon carcharias* in False Bay are difficult to monitor using BRUVs: poor visibility limits the use of BRUVs in the northern region where female *C. carcharias* move inshore in summer (Kock et al. 2013). Visibility was also generally poorer in summer than in winter in the bay and repeated algal blooms were more common in this season, compounding issues with detection. The area around Seal Island is preferred winter habitat (Kock et al. 2013), where BRUVs sampling in the clearer visibility of this season is recommended. The average depth here would require stereo-BRUVs (Bernard et al. 2014) or mono-BRUVs with lights. Findings from New South Wales, Australia, recommend stereo-BRUVs for the detection of *C. carcharias* (Harasti et al. 2017). Stereo-BRUVs recorded 34 incidences of 22 individual white sharks from 22 deployments of 5-hour duration each (Harasti et al. 2017). This survey recorded 3 individuals from 213 deployments of 1-hour duration each. This method is most likely not well suited to the detection of *C. carcharias*. However, tailoring a survey design to specifically target chondrichthyans of interest might yield different results (Sherman et al. 2018).

The problem of visibility in a preferred habitat also holds true for *Argyrosomus inodorus*, a species that would be of significant conservation concern for the region and a monitoring priority (Hutchings & Lamberth 2002), but its detection on fine sand in the very shallow reaches of northern False Bay is less suitable for BRUVs. *Argyrosomus inodorus* is considered heavily fished and severely depleted (DAFF 2012); its low relative frequency in this survey is difficult to link to evidence of rarity in False Bay, because its relative frequency is confounded by the low probability of detection in turbid waters using BRUVs.

Rhabdosargus globiceps was the twelfth most frequently recorded species in this survey. Penney (1991) demonstrated significant competition between the commercial beach-seine and linefisheries in False Bay as catch rates of species such as *Atractoscion aequidens*, *Pomatomus saltatrix* and *R. globiceps* declined. These species are Vulnerable on the IUCN Red List and red on the SASSI list; their populations were reported in high abundance by Biden (1930) prior to the significant fluctuations in catch rates for all three species throughout the 1960s – 1980s, which is discussed in Penney (1991). However, declines in these species were reported as early as the early 20th century, and *R. globiceps* was of particular concern (Penney 1991). The results of this survey suggest that *R. globiceps* may be well represented using BRUVs for ongoing assessments. A standardised, fishery-independent method to survey *R. globiceps*, *A. aequidens* and *A. inodorus* – species that are of both fisheries interest and conservation concern – may be important in False Bay.

The BRUVs detected many species in the Sparidae family with success and the method appears well suited to sampling fish in this family. It is likely then that the low detection rates of the sparids *Chrysoblephus gibbiceps* and *P. rupestris* in this study indicate that these species have declined significantly in False Bay, rather than the method under sampling their abundance. In particular, the predatory *P. rupestris* should be well suited to detection using BRUVs, which have been shown to be useful for recording large-bodied predators elsewhere (Brooks et al. 2011; Speed et al. 2018; Wellington et al. 2018). *Petrus rupestris* was recorded with higher frequency using BRUVs further east along the South African coast, in the MPA at Stilbaai (De Vos et al. 2014) and in the Tsitsikamma MPA (Bernard & Götz 2012), both sites that are closer to the core of the species' distribution (Smale 1988; Mann 2013). *C. gibbiceps* was recorded with slightly higher frequency using BRUVs in the Tsitsikamma MPA (Bernard & Götz 2012), but with much higher frequency at Stilbaai, which is closest to its core distribution (De Vos et al. 2014). This study may reflect declines of both species in False Bay (Kerwath et al. 2019).

4.5.5. Species of commercial interest

The only species of commercial interest in False Bay that were suitably detected using BRUVs in their current configuration are the Sparidae, and *C. capensis* and *T. capensis*.

These species were detected with consistent frequency across seasons and depths. *Chrysoblephus laticeps* is listed as Near Threatened by the IUCN (Mann et al. 2014a), but this study seems to corroborate findings that its populations are slowly recovering (Kerwath et al. 2013). The seasonal arrival of nomadic predators such as *S. lalandi* necessitates summer sampling if several species that remain important to the False Bay fisheries are to be monitored. These include *P. saltatrix*, *A. aequidens*, *Thyrsites atun* and *A. inodorus* (Penney 1991). There are several improvements that may better represent these species in future: pelagic or mid-water BRUVs would extend coverage to the water column (Santana-Garcon et al. 2014a; Bouchet et al. 2018) and a higher sampling frequency in summer with a larger sample size may increase the number of usable videos (although it is expected that the relative proportion will remain the same). Further investigation is required into modifying the methodology for consistently low visibility environments, such as near the mouths of rivers, or shallow waters where the seafloor is sand, and turbidity is high (Unsworth et al. 2014).

Declines in catch rates of several species are not only linked to their commercial importance, and to their popularity with the recreational fishery in False Bay (Bennett 1991). *Rhabdosargus globiceps*, *C. gibbiceps*, *C. laticeps* and *S. lalandi* were all important targets within the recreational fishery prior to 1960 and their abundance has since declined (Bennett 1991). All four species were detected in this survey, where the frequency and relative abundance of *C. laticeps* was highest. In another species grouping, *Lithognathus lithognathus* and *Umbrina canariensis* were not well represented in catches prior to 1960, increased in importance into the 1970s and suffered declines again after that (Bennett 1991). Neither of these species were detected in this survey. This may reflect the challenge of assessments in the surf zone and in turbid environments, particularly in the northern reaches of False Bay.

4.5.6. Species diversity indices

Shannon-Wiener diversity was highest between 20 – 30 m depth. Thereafter, diversity decreased with increasing depth. This finding mirrors those of epibenthic megafauna (Chapter 3; Heyns et al. 2016) and other fish surveys (Stefanescu et al. 1994; Brokovich et al. 2008). Teleosts exhibit a range of feeding habits: herbivorous species such as *S. salpa* and omnivores that prefer invertebrates, such as *D. capensis* and *B. inornata*, were typical of shallow sites. These findings mirror results from Lechanteur (2000) on the Cape Peninsula and Götz et al. (2009) further east in the Goukamma MPA. This is linked to food abundance, as well as shelter from predation, available at shallow reef sites (Buxton & Smale 1989). Shallow sites will have higher light availability (Götz 2006) and dietary studies on *D. hottentotus* and *D. capensis* showed that higher algal productivity at shallow sites facilitates diverse benthic invertebrate production, creating an important food source for juvenile fish, accommodating generalist and specialist feeders including species such as *S. salpa* and *D. capensis* with different dietary requirements at various life stages (Mann & Buxton 1992).

However, it is difficult to separate depth here from its relation to habitat distribution in False Bay. It is tempting to link the high diversity of ichthyofauna between 20 – 30 m to the high diversity of epibenthic megafauna in this same depth range, especially when coupled with the predominance of omnivores that prefer invertebrates in this survey. However, most reefs in the bay (where species diversity was highest) are shallow, and the prevalence of rocky seafloor decreases with increasing depth (Chapter 2; Simpson et al. 1970; Du Plessis & Glass 1991). Species diversity was lowest between 70 – 80 m depth, which is where the seafloor is largely homogenous sand (Chapter 2; Bowie et al. 1970).

At the level of the bay, diversity was similar between reef and sand. The gamma diversity was not markedly different between the two habitats; that is, the total diversity of the system represented by the sum of alpha and beta diversity in False Bay. The difference lay in the distribution of this diversity within each habitat type. It was expected that sand-associated species would be more evenly distributed across the False Bay than on the reefs, given that 83% of the bay is sand and it was expected that this seafloor type was more homogenous. Higher biological diversity is often linked to higher habitat heterogeneity (Gaston 2000). However, species diversity was more even on reefs than on sand. This is an important result for the consideration of planning and protection in the region: a much larger area of sand would be required to protect representative sand-associated fish diversity. Protected area design for soft sediments is complex, and studies in temperate Australian waters show that, while sand-associated species respond to MPA protection at various scales, the response is highly variable across species (Fetterplace 2017). Several reef fish are known to be resident and respond well to MPA protection (Kerwath et al. 2007; Kerwath et al. 2013), but there has been some suggestion that sand-associated species also show site attachment, as demonstrated for the blue-spotted flathead (*Platycephalus caeruleopunctatus*) in Australia (Fetterplace et al. 2016).

The alpha diversity and the Shannon-Wiener diversity index at the level of the site, however, were significantly higher on reef than on sand. This mirrors findings globally that biological diversity is higher on rocky reefs than on sand (Guidetti 2000), a result that is often related to the physical nature of the seafloor. That is, diversity increases where habitat complexity, seafloor rugosity and reef profile increase (Friedlander & Parrish 1998; Pittman et al. 2007). By implication, protecting a small area of reef would capture a wider diversity of reef-associated fish than what protecting the same sized area of sand would capture in terms of sand-associated fish diversity in False Bay.

In South Africa, higher diversity was recorded on reef and kelp beds than on sand in the Betty's Bay MPA using mono-BRUVs (Roberson et al. 2015). However, a direct comparison of reef versus sand habitat using a standardised method in a random, stratified design that balances the number of sites sampled in each habitat type has not previously been shown for temperate coastal waters in South Africa. Surveys elsewhere on the coast are generally limited to one habitat or the other, with a particular focus on reef systems (Buxton & Smale 1989; Götz et al. 2009; Kerwath et al. 2013; Bernard & Götz 2012; De Vos et al. 2014; Heyns-Veale et al. 2016). The increased habitat complexity represented by reefs in the form of refuge holes and rugose surfaces has a positive effect on increasing fish species diversity (Gratwicke & Speight 2005). Many reef fish common to False Bay, such as *C. laticeps*, are territorial (Kerwath et al. 2007), which limits their movement in a region and restricts them primarily to reef patches in the bay. However, several species of conservation concern in False Bay are sand associated, especially the chondrichthyans. Where monitoring is mandated to maximise biodiversity, the distinction between reef and sand at the broadest resolution may be a useful delineation to focus limited resources on regions of maximum per site reef diversity. However, the introduction of BRUVs to monitoring protocols offers a means of surveying diversity across both habitat types, which may capture a more representative picture of False Bay. This is important to consider where the relative abundance of individual species may be lower on sand, but the total diversity may still harbour species of interest and concern that are key to monitor (Fetterplace 2017).

Species richness did not differ significantly between winter and summer. However, the Shannon-Wiener diversity index was higher in winter than in summer. North-westerly winds associated with approaching cold fronts are typical in winter in False Bay (Atkins 1970a; Jury 1991). These winds are one part of the complex range of factors associated with colour fronts (Shannon et al. 1991) and plankton blooms (Grindley & Taylor 1970), but are anecdotally linked to improved water clarity and therefore provide the best conditions for camera observations in False Bay. In this survey, visibility recorded on the BRUVs was best in winter. The species that were observed in this survey only in winter, and not in summer, were typically cryptic or small; it is therefore most likely that the observed higher winter diversity is the result of clearer water conditions that improved observation capability. This is an important consideration for future monitoring using cameras in False Bay. Summer onshore winds and plankton blooms pose a serious challenge to visibility, which is essential for adequate species detection using videos and the feasibility of achieving a suitable sample size.

Importantly, evenness was greater in winter than in summer and while at the level of the site winter was more diverse than summer, the total diversity of the region reflects the presence of a similar number of species in False Bay all year round. This result may indicate that the arrival of shoaling species such as *T. capensis* influences evenness and the Shannon-Wiener diversity index in summer. The presence of a similar number of species all year round is useful for the design of any future monitoring protocol: given that BRUVs rely on suitable water clarity for optimal efficiency, monitoring in winter would likely yield a higher number of successful video deployments for the same effort applied across seasons. This study shows that a similar complement of ichthyofauna diversity could be monitored during the winter season when BRUVs deployments are optimal.

4.5.7. The influence of environmental factors

All environmental factors assessed in this survey; namely, depth, habitat (reef and sand), CATAMI habitat, seafloor profile, reef-type and season explained differences in community composition. The relative importance of these factors differed, and the consideration of one or two key factors may be more useful to direct monitoring and planning (Gilby et al. 2016). The question is: which factors, and at what resolution? Heyns-Veale et al. (2016) found that habitat and depth were suitable factors to explain differences in community composition, as did Götz (2006). Previous surveys in South Africa's temperate waters link the importance of each of these different factors to what each provides in terms of feeding opportunities, refuge from predators and optimal metabolism for mobility (Buxton & Smale 1989; Götz et al. 2009). This information can direct species-specific monitoring, tailor future survey design, and facilitate data interpretation (Colton & Swearer 2010; Chatfield et al. 2010). Most reef fish of the family Sparidae were present in both seasons, making them suitable representatives around which to design a monitoring protocol.

Habitat (reef and sand) explained most of the difference in community composition across sites. Fish are often associated with a particular habitat-type (Friedlander & Parrish 1998; Pittman et al. 2007; Knudby et al. 2010), a finding linked to feeding preferences, refugia and the availability of nurseries (Friedlander & Parrish 1998; Pittman et al. 2007). The PERMANOVA model showed that habitat explained more variation than season, but both were significant. Several species in False Bay are known seasonal migrants: *S. lalandi*, *A. inordorus*, *T. atun*, *A. aequidens*, *P. saltatrix* and *T. capensis* are more abundant in summer (Penney 1991; Lamberth et al. 1994). In the second model, habitat explained much more than depth, even though both were significant: however, habitat is not evenly distributed with depth around False Bay.

The distinction between reef and sand at a broad landscape resolution may be useful for monitoring, and national or regional planning and prioritisation. However, this study demonstrates that species-habitat associations are more nuanced and will vary according to the scale of analysis. Several habitat modifiers were included in this survey, but not analysed, since their distribution across samples was uneven. However, the identification of kelp beds, biogenic material and sand veneer over underlying bedrock undoubtedly demonstrate that there is no clear line between where reef and sand habitats start and end in False Bay. Species associated with rocky reefs such as *C. laticeps* appeared in samples with a sandy veneer, together with sand-associated species such as *Psammogobius knysnaensis*. Some species, such as *R. globiceps,* appeared consistently across both reef and sand habitats in equal abundance. These fine-scale associations could not be built into an *a priori* survey design at the scale of the bay with the existing bathymetry and geological information, but reiterate the importance of integrating a landscape ecology approach to understanding biodiversity patterns in marine systems (Moore et al. 2011; Gilby et al. 2016).

The use of region as an explanatory factor was a step towards integrating “seascape context” (Gilby et al. 2016) into understanding differences in community composition. Given that “region” incorporates different levels of factors, some of which were measured in this study as part of a landscape composition approach (e.g. habitat, depth, reef type, reef profile) and many that were not (e.g. localised circulation patterns), this helped delineate the bay into monitoring units. This is especially useful where whole regions have previously been excluded from surveys and where specific approaches may need to guide future BRUVs monitoring (visibility in the north central and north eastern regions, high diversity in the east, species of conservation concern such as *P. rupestris* in the south-east). This factor is used to describe patterns in species distribution and abundance at the full scale of the bay in the last section of this discussion.

The classification into finer-scale habitat units using CATAMI had the least explanatory power out of the factors tested in the PERMANOVA models. However, the classification of habitats at a finer scale is a useful first step to describe habitat heterogeneity across False Bay. Even where sand is considered homogenous, this study detected higher numbers of *C. capensis* on fine sand than on coarse sand, while the opposite was true for *Amblyrhynchotes honckenii*. While the delineation of species associations at the resolution of reef and sand habitat is more reasonable for bioregional descriptions, these fine scale details of habitat are important for long-term monitoring. This is particularly true when considering that it is not simply the individual species that will change over time in abundance and distribution, but that many habitats are not fixed in space and time. The eastward shift of kelp beds (Bolton et al. 2012) will have consequences for the species assemblage, as will the movement of sediment which has been shown to vary not only with wind and current patters, and freshwater influxes, but also with coastal development (De F Retief 1970).

This study demonstrated that these associations can be even more complex than simply an affiliation with either reef or sand but can be linked to specific underlying geology and consequent reef profile. The Cape Granite Suite reefs in the western half of False Bay tend to be most steep-sided whereas the Malmesbury Group shale of the eastern section is more eroded and comprises lower profile reef, with the Table Mountain Group sandstone representing an intermediate profile (Du Plessis & Glass 1991). The western reefs of the bay therefore represent high vertical habitat heterogeneity in the form of rugose rock surfaces, but the eastern reefs reflect horizontal heterogeneity and patchiness across the seafloor. These patterns are reflected in the distribution of ichthyofauna across False Bay.

4.5.8. Community composition

Haploblepharus spp. were ubiquitous and typified communities on both reef and sand habitat, in shallow (0 – 30 m) and medium (30 – 60 m) depths. The presence of *C. capensis* and *T. capensis* typified sand sites. The former is recorded on sand shelf habitat, in areas of low bottom water dissolved oxygen and relatively lower diversity, in the Benguela Upwelling region (Mas-Riera et al. 1990). In the upwelling region, *C. capensis* is associated with *Merluccius capensis* and *Nematogobius bibarbatus* between 50 – 250 m depth before an upwelling peak and between 50 – 360 m after an upwelling peak (Mas-Riera et al. 1990). In this study, *C. capensis* typified fine and coarse sand sites and medium (30 – 60 m) to deep (60 – 90 m) depths. Trawling was banned in False Bay in 1928 (Penney 1991), and so this species that is typically caught in the inshore and offshore demersal trawl elsewhere in South Africa escapes fishing pressure in the bay. The presence of *P. blochii* and *C. laticeps* typified reef sites. The latter are known resident reef fish, occupying home ranges between 1 – 3 km^2 (Kerwath et al. 2007).

Species associations give an overview of which other species may be found in similar habitats, depths, and regions in False Bay. This kind of information is key to direct monitoring of not only target species, but to consider potential bycatch species or knock-on effects across the ecosystem. This is also useful where the range of species extends outside False Bay, to help define bycatch lists for multispecies fisheries assessments (Winker et al. 2013). *Rhabdosargus globiceps*, *M. mustelus*, *Amblyrhynchotes honckenii*, *H. natalensis* and *C. capensis* were grouped at 20% similarity. All these species were strongly sand associated in this survey, except for *R. globiceps,* which occurred on reef and sand. It seems unlikely that fishers targeting *R. globiceps* would impact other species in this group: however, it is often the case that where there is incidental catch in the stead of a target species, the incidental catch is discarded (as is the case for *Haploblepharus spp*. at the harbour wall in Kalk Bay). Where a decline in teleost species has prompted a shift to chondrichthyan targets in the recreational fishery (Bennett 1991), both *R. globiceps* and *M. mustelus* are listed as Vulnerable on the IUCN Red List. Their association is interesting for two reasons: it is confirmation of *R. globiceps* in shallow depths on sand, which is where the other species were predominantly found, and it indicates which other species, such as *M. mustelus,* might merit monitoring in False Bay in future. Currently, the latter species has been the only chondrichthyan surveyed with an increasing population in False Bay (Best et al. 2013).

Pachymetopon blochii and *C. laticeps* were closely associated, forming a group at 64% similarity. Both species are strongly reef associated in False Bay and typified this habitat type in this survey. In a more fine-scale assessment of habitat, both species occurred on boulder rock habitat, which is some indication of the nature of the geology and the profile of the reef that these species prefer. High profile, Cape Granite Suite boulder reef is typical of the western margin of False Bay, a region that is protected by the four no-take zones of the Table Mountain National Park (TMNP) marine protected area (MPA). At 48% similarity, *P. blochii* and *C. laticeps* were grouped with *P. africanum*, *Haploblepharus spp.*, *S. emarginatum* and *P. laniarius*. *Spondyliosoma emarginatum* was typical of both coarse sand sites and boulder reef sites, and in shallow depths. It is possible to characterise the reefs of western False Bay according to this species grouping. These results confirm findings further east, at the Goukamma MPA and at Tsitsikamma MPA, where these species were recorded on high profile reefs (Götz 2006; Heyns-Veale et al. 2016). However, where species were typically found on deeper reefs in the Tsitsikamma MPA (Heyns-Veale et al. 2016), the lack of deeper reefs, coupled with cooler mean water temperatures deeper in False Bay (Atkins 1970b), means that reef-associated species are predominantly in shallow waters in this region.

Forty-three of the 58 total species were recorded in the western half of False Bay, which is currently the only region of designated protection in the bay, except for the small Helderberg MPA. This is interesting for two reasons: the BRUVs are suitable for monitoring a large proportion of species in the current MPA network, and there is good representation of the species detected in this survey in the current MPA zonation. *Haploblepharus spp*. and *P. africanum* were common in the south western margin, where Cape Granite Suite reefs predominate and where depth drops off sharply moving south east away from the cliffs near Smitswinkelbay and Paulsberg. Species typical of both reef and sand were found here: some notable records include *N. cepedianus* which was recorded in the south-west, south-east and central regions of False Bay. Typically recorded on rocky reef, *N. cepedianus* was also recorded on the biogenic screwshell habitat that was only recorded in the south-west near the Paulsberg no-take zone of the TMNP MPA.

Fifty of the 58 total species were recorded on the eastern half of False Bay. *Spondyliosoma emarginatum*, *G. feliceps*, *C. laticeps* and *T. capensis* were frequently recorded here, which is an indication of the diversity of reef habitat and its interspersion with sand patches in this half of the bay. Interestingly, most *P. rupestris* recorded in this survey were on the eastern reefs in shallow water (0 – 30 m). This is of consequence, given that the current protected area is in the west. The Helderberg MPA covers a small area of reef in the north-east, but *P. rupestris* was more commonly recorded in the unprotected south-east. *Petrus rupestris* prefer high profile reef and are typically abundant on deeper reefs (Buxton & Smale 1989). In this study, *P. rupestris* was recorded on various reef profiles, but most frequently on high profile. Malmesbury Group shale reef profile clearly also supports reef-associated species. If this is true, the east represents high benthic, macroinvertebrate diversity (Chapter 3), fish diversity and supports threatened species such as *P. rupestris* that would still be exposed to fishing pressure here. Sixteen chondrichthyans were recorded on this side of the bay, with frequency of *M. mustelus*, *G. galeus* and *H. natalensis* highest.

The northern, central reaches of False Bay were frequented by *M. mustelus*, with records of *Gymnura natalensis* and *R. straeleni*. The central bay between 30 – 60 m was characterised by *C. capensis*, *T. capensis* and *Haploblepharus spp*. *Chrysoblephus gibbiceps* was recorded in the central bay. This is interesting, because descriptions of this species' preferred habitat would indicate that the western margins of False Bay would be target areas to detect and monitor this species; however, it would appear that reefs such as Whittle Rock may be of importance, even though they fall outside the current protected area network.

4.5.9. Advantages and disadvantages of the BRUVs methods

Of the 200 species presented by Day et al. (1970) for False Bay, this study recorded 57 species using BRUVs. The disadvantages of BRUVs are evident in the lower detection of cryptic species on both reef (Morgans & Day 1956; Prochazka 1998; Lechanteur 2000) and on sand (Morgans 1962). This does not mean that cryptic species were entirely missed: species such as sand tonguefish (*Cynoglossus capensis*) and commafin goby (*Caffrogobius saldanhae*) were detected, but camouflaged sand-associated species in turbid environments would likely be under-sampled. The intertidal zone cannot be sampled using the current BRUVs configuration. Sampling of surf zone species with BRUVs is limited by the deployment capacity of the vessel and visibility; galjoen (*Dichistius capensis*) was not captured in this survey but has been recorded with BRUVs in the TMNP MPA (Sanguinetti 2013).

Larval stages and juvenile fishes will be limited by small size in their detection using BRUVs, but juvenile Cape knifejaw (*Oplegnathus conwayi*) can be seen on videos (Sanguinetti 2013) and many juvenile *C. laticeps* were detected in this study. The size distribution of key fisheries species will be important to survey using stereo-BRUVs that can concentrate sampling effort near the TMNP MPA, where visibility is frequently more suitable. The species most underrepresented by BRUVs were pelagic species such as the southern African anchovy (*Engraulis capensis*), sardine (*Sardinops sagax*) and the Scombridae. Those pelagic species important to False Bay's linefishery; namely, yellowtail (*Seriola lalandi*), geelbek (*Atratoscion aequidens*) and snoek (*Thyrsites atun*), were detected in this study. However, pelagic stereo-BRUVs (Santana-Garcon et al. 2014b) may better address specific questions about the diversity of pelagic species visiting False Bay.

The BRUVs were particularly useful for detecting species in the seabream family Sparidae. Of the 23 seabreams recorded in Day et al. (1970), 14 are captured in this study. *Pachymetopon blochii* is duplicated in records as *Pachymetopon canescens Norman* (Day et al. 1970), which is not accepted as a separate species (WoRMS 2019). The actual number of seabreams recorded in False Bay by Day et al. (1970) is therefore 22 species (199 total species). The absence of certain seabreams may not be a sampling artefact, but they are likely no longer found in False Bay. Dageraad (*Chrysoblephus cristiceps*) is largely absent from its former range in south-western South Africa and limited to select locations in the Eastern Cape province (Parker et al. 2016b). Black musselcracker (*Cymatoceps nasutus*) is recorded from Cape Town (Heemstra & Heemstra 2004) and on rocky reefs (Buxton & Clarke 1989), but is only listed as far west as Pearly Beach near Gansbaai on the IUCN Red List, where it is listed as Vulnerable (Mann et al. 2014d). The white musselcracker (*Sparodon durbanensis*) was still listed in False Bay on the IUCN Red List, where it is listed as Near Threatened (Mann et al. 2014b) but is considered depleted by many spearfishermen. Seventy-four (*Polysteganus undulosus*) disappeared from False Bay and the fishery for this species was closed; it is unlikely to be detected at this stage in the bay. However, having a method in place that has been shown to survey other seabreams, as this study shows the BRUVs do, is a useful basis for a monitoring programme in False Bay that can track any possible future recoveries.

Bronze bream (*Pachymetopon grande*) was not detected in this survey but has been recorded on BRUVs in the TMNP MPA (Sanguinetti 2013). White steenbras (*Lithognathus lithognathus*) are likely difficult to detect using BRUVs, given that they are more frequently captured in the beach-seine fishery (Clark et al. 1996b) in turbid waters inshore in northern False Bay, and are often estuarine-dependent and surf-zone associated (Bennett 1993). Visibility presents a major challenge to BRUVs sampling in False Bay, where the detection of species associated with turbid conditions, particularly in the northern regions of False Bay, will require either concerted sampling effort or improvements in the current configuration of both mono- and stereo-BRUVs. This is important where capacity will limit the ability to repeatedly re-sample areas of known poor visibility until sufficient samples are collected. Aside from increasing the sampling effort (number of samples) and sampling without lights, improving camera technology may increase the number of successful samples achieved in future surveys. Increasing the BRUVs soak-time is unlikely to improve species detection in poor visibility in False Bay. However, this has been shown to optimise sampling in estuarine systems (Gladstone et al. 2012) and this should be tested, especially where species of concern would be important to detect near freshwater inputs (Zandvlei, Zeekoevlei, Eerste river, Lourens river, Sir Lowry's river).

Using BRUVs as the primary, and standardised, survey method facilitated what this study could achieve: the first description of the ichthyofauna of False Bay across a range of depths, habitats, and seasons. The method improves on previous surveys in several ways: firstly, several hours of data can be gathered simultaneously, increasing the overall sampling effort and affording the first description of subtidal ichthyofauna on the reefs in the east of False Bay. This provided insights into the distribution of species of conservation concern that were more frequently recorded outside the current protected area network, such as *P. rupestris* on the south-eastern reefs and red stumpnose (*Chrysoblephus gibbiceps*) on scattered reefs in central False Bay. It is the only standardised method to have sampled both reef and sand habitats in a single assessment, providing the first description of ichthyofauna with comparative samples on both that can interrogate patterns of diversity across these habitat types. This study showed that BRUVs detected more species than comparable previous surveys on reef in False Bay (Lechanteur 2000; Lechanteur & Griffiths 2001; Lechanteur & Griffiths 2002), greatly improving the number of chondrichthyan species detected in this habitat type.

The use of the BRUVs method in this study gives archived visual record that increases the taxonomic resolution of data processed for chondrichthyans that were generally lumped into broad groups in previous surveys that depended on fishers' observations and catch records (Best et al. 2013). This is an important improvement: many of the chondrichthyans detected in this survey are of conservation concern and were either absent or underrepresented in all other non-extractive surveys in False Bay. The BRUVs also improved representation of the endemic Scyliorhinidae. The BRUVs provide a fisheries-independent monitoring method that improves on the non-random effort typical of fisheries-dependent surveys. This is particularly advantageous in providing information where catch data may not be available because an area is of low fishing interest, but the monitoring of species in regions where other threats (pollution, coastal development, desalination plants) exist will be important.

Mono-BRUVs outperformed the stereo-BRUVs for sampling efficiency in False Bay for several reasons. The lighter configuration facilitated faster sampling, increasing the overall effort per sampling day where the research team was small, and a single researcher was responsible for all sampling. A winch was not needed to lower and hoist the mono-BRUVs, so a variety of faster vessels that could cover a greater extent of False Bay could be used to repeat-sample challenging areas. This was important given the size of the survey region and the scale of the survey. The GoPro cameras in the mono-BRUVs recorded higher resolution footage than the Sony Handycams in the stereo-BRUVs. Continuous advances in camera technology (internal focus, internal light capacity) and the addition of GoPros to stereo-BRUVs calibration, coupled with new configurations to build lighter and smaller stereo-BRUVs frames, will help improve the efficiency of stereo-BRUVs sampling in False Bay where visibility is often poor. The introduction of stereo-BRUVs sampling to False Bay will be important to detect size differences inside and outside the MPAs (Sanguinetti 2013) and to interrogate the seasonal depth-related movement of several chondrichthyans (De Vos et al. 2015). It is therefore important to take the best elements of mono-BRUVs sampling and adapt these to stereo-BRUVs configurations wherever size data will be important to collect over time.

The BRUVs provide a comprehensive species list for a rapid biodiversity assessment method and will likely detect more species when employed as part of a long-term monitoring programme in False Bay. However, where there are specific monitoring objectives, BRUVs will need to be supplemented by other complementary methods. Given that the largest component of the False Bay ichthyofauna missing from this study were pelagic species, the development of pelagic stereo-BRUVs should be a focus for future research in the region. The species of the surf zone and in turbid water represent the component of the ecosystem missing from this survey that are, aside from the reef fish and chondrichthyans, are of most conservation concern. Targeted by shore anglers, and also at risk from significant land use changes, especially in the northern and north eastern bay, these species will need to be additionally monitored using beach-seine catch data and controlled angling surveys (CAS). There is also potential for additional focus in this area using acoustic telemetry as part of the existing Acoustic Tracking Array Platform (ATAP) that facilitates the monitoring of inshore fish and sharks across more than 100 data-logging acoustic receivers along the South African coastline

(Cowley et al. 2017). The focus on animals to tag should include data-deficient species such as the batoids to improve the resolution of information available on their inshore movement patterns (*sensu* Elston et al. 2019).

4.5.10. Conclusion

False Bay is a region of significant fish diversity that shows complex patterns of species distribution across its extent. The bay hosts species of conservation concern, of commercial importance and of recreational interest. These species' distributions are not limited to the current protected area network, or to the reefs where diversity was assumed to be highest. This is most true for the chondrichthyan species, which are assumed to be more mobile predators and less suited to spatial planning for protection. However, chondrichthyans did show patterns of distribution that could be linked to habitat and depth. Differences in community composition can be detected at several scales, from the broadest extent of the bay, to localised seafloor descriptions and specific habitat characteristics. The identification of these different scales can guide future efforts to plan and monitor at a resolution that is both logistically feasible and able to address key scientific and conservation aims.

Habitat and depth are key environmental factors that explain some of the variation in community composition across False Bay. This is useful where broad-scale patterns are required to inform regional spatial planning and ecosystem threat at the level of the South African coastline. However, reef profile, reef type, region in the bay (which incorporates various environmental parameters not measured in this survey), season and fine-scale habitat (CATAMI) were also significant. The CATAMI classification would be particularly useful where species are not strictly reef or sand associated, and in regions where seafloor heterogeneity is more complicated than a classical geological split between reef and sand. An improved understanding of the relative influence of these factors and their distribution across False Bay is useful to inform local monitoring and any protected area expansion or review at the scale of the bay. This is especially true where key species would be assessment targets, and their finer-scale associations can direct more effective monitoring with lower logistical investment.

Diversity at the level of the site was higher on reef, and in winter. The distinction between reef and sand in temperate waters confirms assumptions that increased habitat complexity has a positive effect on species diversity. However, while Shannon-Wiener diversity was higher on reef than on sand, the differences were nuanced and require concerted interrogation. What constitutes habitat complexity is more complicated than the vertical heterogeneity on high profile reefs that are classically predicted to host higher species diversity because they provide rugose surfaces, overhangs, caves, and a variety of niches. There is no significant difference in the total species richness across both reef and sand, and across seasons, in False Bay. It was originally anticipated that the sand habitat of False Bay was largely homogenous, and that this would be reflected in the evenness and richness of species diversity on sand. Where reefs have remained the focus of protected areas in the region, it is important to incorporate an understanding of how much more sand would require protection to address the uneven distribution of sand-associated species in False Bay.

More species were recorded in the eastern half of False Bay, where the seafloor is patchy and reflects the highest horizontal heterogeneity across its extent. In this region, low profile reef was interspersed with patches of sand, interrupted with biogenic reef, kelp beds, cobble, and boulder habitat. This is an important result, because the threats to ichthyofauna in False Bay are not limited to the western reefs. Indeed, the presence of several key species of conservation concern in this region of False Bay, together with high levels of both invertebrate and ichthyofauna diversity, mark this region for improved assessments. The assessment methods outlined in this chapter provide a standardised way to survey False Bay across the full extent of its depths and habitats, and offer the potential to extend surveys beyond their previous focus on the shallow, western reefs. Ultimately, monitoring programmes and future spatial planning efforts in the region cannot be limited to the assumption that the full, or even the highest, complement of biodiversity is captured in the western reefs of False Bay.

CHAPTER 5

SYNTHESIS OF BIODIVERSITY PATTERNS ACROSS FALSE BAY AND CONCLUSIONS

A Cape seabream (*Pachymetopon blochii*) secreted in the kelp. Photo: Joris van Alphen

5.1. Towards a new description of grounds in False Bay

Patterns in the nature of the seafloor and bathymetry are reflected in the distribution and composition of the epibenthic megafauna and fish in False Bay. The Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) habitat types and depth characteristics for nine regions across False Bay (**Figure 47**) sampled in this study were summarised in **Table 32** with a synthesis of the description of "grounds" first attempted by Morgans (1962) and extended by Field (1971). Location was a significant predictor of species assemblage for both epibenthic megafauna (transect) and fish (region), and the regions break False Bay into units that are easy to discuss and characterise. These units were the most useful and natural way to highlight previously under-represented areas of False Bay, compare the previous descriptions of "grounds" with relevant spatial overlap and create a framework to focus monitoring priorities.

This study improves the coverage of the east that was infrequently sampled in previous subtidal invertebrates studies (Morgans 1956, 1962; Field 1970, 1971) and absent in previous subtidal fish studies (Lechanteur 2000, Lechanteur & Griffiths 2001, Lechanteur & Griffiths 2002, Sanguinetti 2013). The greatest horizontal seafloor heterogeneity was here, characterised by encrusting sponges and the predominance of the featherstar *Comanthus wahlbergi*. The invertebrate diversity recorded here reflects the consolidated seafloor habitat heterogeneity. In the same region, the fish community comprised species typical of reef such as Cape seabream (*Pachymetopon blochii*) and roman (*Chrysoblephus laticeps*), species typical of sand such as Cape gurnard (*Chelidonichthys capensis*) and species such as white stumpnose (*Rhabdosargus globiceps*), panga (*Pterogymnus laniarius*) and steentjies (*Spondyliosoma emarginatum*) that move across both habitat types. The patterns in fish distribution indicate that the absolute distinction between reef and sand habitats in eastern False Bay is unclear, and finer-scale habitat descriptions of CATAMI classifications such as pebbles, cobbles, boulders, fine and coarse sand are useful to help describe this complexity. The reef habitats of south-eastern False Bay hosted the highest records of red steenbras (*Petrus rupestris*) recorded in this study, a seabream that has declined by 96% in south-western South Africa (Kerwath et al. 2019).

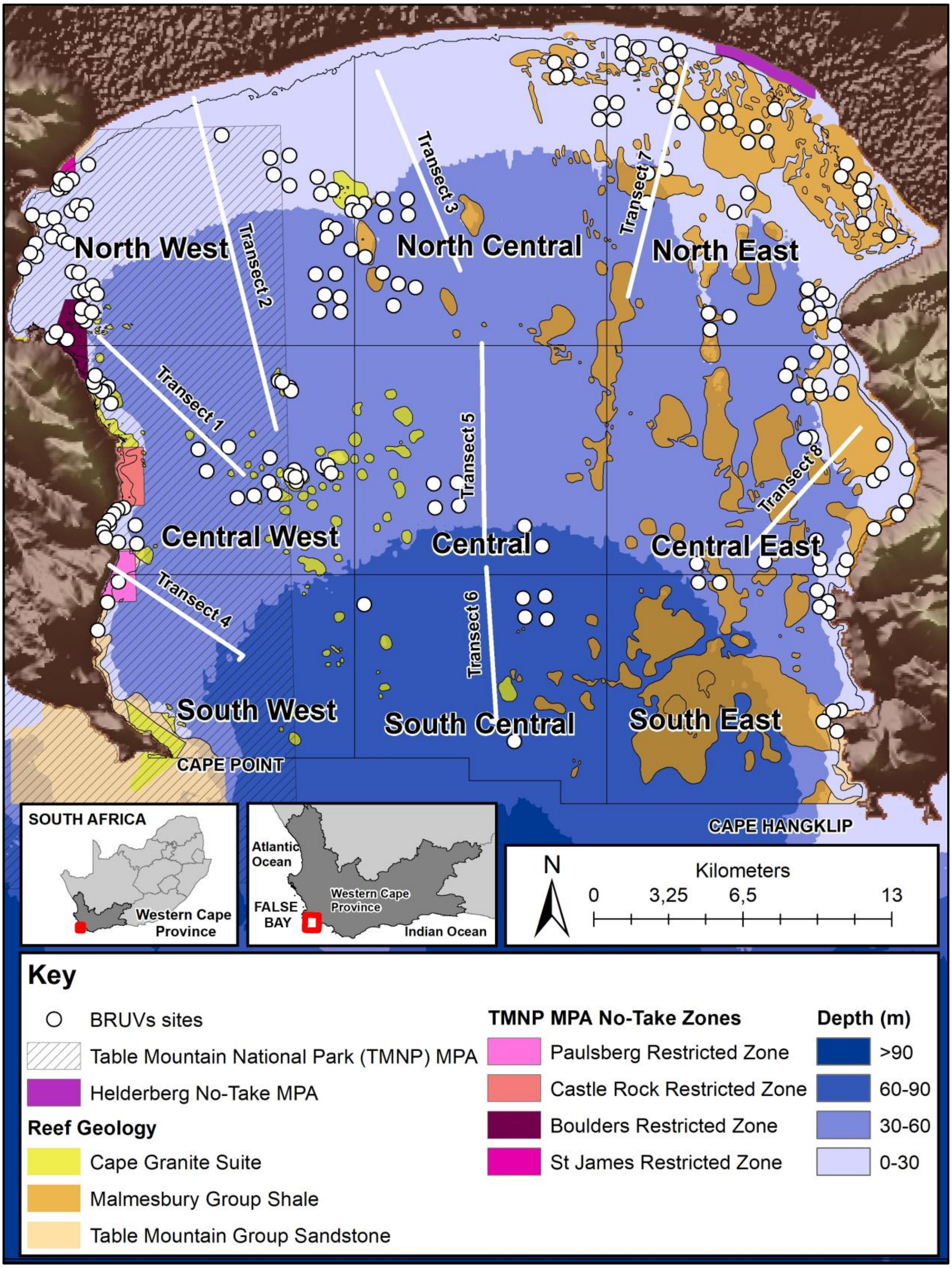

Figure 47. Nine functional regions across False Bay delineated in **Table 32**. The location of each transect where grab samples, jump camera photographs and multibeam sonar were collected, and the distribution of baited remote underwater video systems (BRUVs), is given in relation to the marine protected areas (MPAs) (DEA 2019a). The distribution of subtidal reef geology (Van Zyl 2011) and depth (m) range (Van Zyl 2011) are visualised in this figure and explained in **Table 32**.

Table 32. Synthesis of the 1) Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) (Althaus et al. 2015) seafloor description and multibeam depth range (m), 2) most frequently recorded epibenthic megafauna species and 3) the dominant taxonomic group (relative CATAMI cover) on each jump camera transect, and 4) fish species that typify nine regions across False Bay. Also included are the depth categories as defined in this study sampled in each region, where shallow = 0 -30 m, medium = 31 – 60 m and deep = 61- 90 m. The percentage of samples that were of each reef type (Table Mountain Group Shale, Cape Suite Granite, Malmesbury Group Shale) is also listed for each region. Ichthyofauna species of conservation concern appear in brackets. They are included based on a) conservation listing (IUCN or SASSI) and b) are noted as declining in False Bay specifically (Bennett 1991; Penney 1991; Best et al. 2013). Species that were "perfect indicators" for stations sampled by Field (1971) and the "grounds" described by Morgans (1962) are listed in relation to this study's nine sampling regions.

Region	**Transect**	**Depth Categories**	**Reef Type**	**Habitat**	**Epibenthic megafauna**	**Ichthyofauna**	**Morgans (1962)**	**Field (1971)**
North West	2	Shallow, Medium	Table Mountain Group shale (26%)	Fine sand (85%), coarse sand (8%) & shallow rocky reef (8%). Depth range: 0 - 50 m	*Ceriantheopsis nikitai*, sea cucumbers (ESCB)	*Haploblepharus spp., Amblyrhynchotes honckenii, Galeichthys feliceps* *[Rhabdosargus globiceps]*	*Diopatra neapolitana*, with *Ampelisca* ground offshore from Fish Hoek	Stations 1,2, 3: *Urothoe grimaldii, Tellina gichristi;* Stations 4 & 9: *Pontharpinia strompsoni, Bodotria* c.f. *australis, Spio filicornis;* Station 5: *Glycinde capensis*
North Central	3	Shallow, Medium	Malmesbury Group Shale (26%)	Fine sand (89%), cobble (8%) & coarse sand (3%). Depth range: 0 - 50 m	*Virgularia schultzei*, unstalked featherstars (EFU)	*Trachurus capensis, Haploblepharus spp., Galeichthys feliceps, Spondyliosoma emarginatum* *[Rhabdosargus globiceps, Raja straeleni, Petrus rupestris, Rostroraja alba]*	*Diopatra neapolitana*	Undescribed

North East	7	Shallow	Malmesbury Group Shale (65%)	Fine sand (30%), pebble (15%), coarse sand (12%) & cobbles (9%). Depth range: 0 - 30 m	*Clathria oudekraalensis*, encrusting sponges (SPCE)	*Haploblepharus spp., Trachurus capensis, Spondyliosoma emarginatum, Galeichthys feliceps, Chrysoblephus laticeps [Rhabdosargus globiceps, Argyrosomus japonicas]*	*Diopatra neapolitana*	Undescribed
Central West	1	Shallow, Medium	Cape Suite Granite (29%)	Fine sand (50%), coarse sand (48%), biogenic screwshell (2%). Depth range: 0 – 50 m	*Atrina squamifera, Comanthus wahlbergi;* unstalked featherstars (EFU)	*Haploblepharus spp., Chelidonichthys capensis, Spondyliosoma emarginatum [Raja straeleni]*	Extension of *Diopatra neapolitana*	Undescribed
Central	5	Shallow, Medium, Deep	Cape Suite Granite (44%)	Fine sand (87%), biogenic screwshell (7%) & pebbles, cobbles & coarse sand (2%). Depth range: 11 – 70 m	*Atrina squamifera*, bivalve molluscs (MOB)	*Chelidonichthys capensis, Pterogymnus laniarius, Poroderma africanum, Pachymetopon blochii, [Chrysoblephus gibbiceps, Petrus rupestris]*	Undescribed	Station 6: *Scoloplos uniramus*, *Lysianassa certatina*
Central East	8	Shallow, Medium	Malmesbury Group Shale (62%)	Fine sand (46%), coarse sand (16%), pebbles &	*Comanthus wahlbergi;* encrusting sponges (SPCE)	*Trachurus capensis, Haploblepharus spp., Pterogymnus laniarius,*	Undescribed	Undescribed

				cobbles (3%). Depth range = 11 – 60 m		*Chelidonichthys capensis*, *[Rhabdosargus globiceps]*		
South West	4	Shallow, Medium	Table Mountain Group shale (23%), Cape Granite Suite (31%)	Biogenic screwshell (48%), fine sand (34%), coarse sand (17%). Some shallow reef inshore. Depth range: 0 – 50 m	*Comanthus wahlbergi*, *Atrina squamifera;* sea cucumbers (ESCB)	*Haploblepharus spp.*, *Poroderma africanum*, *[Galeorhinus galeus]*	Extension of *Spatangus/Epizoanthus*	Undescribed
South Central	6	Medium, Deep		Fine sand (100%). Depth range: 50 – 90 m	*Jasus lalandii*	*Chelidonichthys capensis*, *[Galeorhinus galeus]*	*Spatangus/Epizoanthus*	Station 7: *Laonice cirrata*, *Prionospio pinnata*, *Leptanthura laevigata*, *Urothoe grimaldii*
South East	8 continued	Shallow, Medium	Table Mountain Group shale (22%), Malmesbury Group shale (28%)	Fine sand (46%), coarse sand (16%), pebbles & cobbles (3%). Depth range: 0 – 50 m	*Comanthus wahlbergi;* encrusting sponges (SPCE)	*Haploblepharus spp.*, *Pachymetopon blochii*, *Chelidonichthys capensis*, *Trachurus capensis*, *Pterogymnus laniarius*, *[Petrus rupestris]*	Green pellet mud	Undescribed

The nature of the seafloor reflects changes in the visible biota and adds to the existing descriptions of the infauna from Morgans (1962) and Field (1970, 1971). The datasets are complimentary, describing different components of the ecosystem. There are differences in sampling design and survey methods, with consequent differences in the habitats and species they best target, and the coverage they afford, that do not allow for direct comparisons. Rather, it is when they are combined that the clearest picture of False Bay is gained. Central False Bay is predominantly sand, which becomes more homogenous with depth. *Chelidonichthys capensis* characterised the deepest regions of False Bay where the seafloor was predominantly fine sand, where the epibenthic megafauna were mobile predatory species such as the west coast rock lobster (*Jasus lalandii*) and, from Field (1971), *Goneplex angulata*. *Jasus lalandii* was previously detected in surveys on shallow, reef habitat (Carr 2014) and the species had not previously been recorded on sand at depth, where sampling had been limited to dredge and grab samples (Morgans 1962; Field 1970; Field 1971). The soupfin shark (*Galeorhinus galeus*), a vulnerable species (IUCN listing) that has declined in False Bay (Best et al. 2013) was found here.

The shallow, northern regions of False Bay broadly described as the polychaete (*Diopatra neapolitana*) ground (Morgans 1962) reflect more heterogeneity in seafloor habitats and community composition than previously described along an east-west axis. Over 200 species, predominantly infauna, were described in this ground (Morgans 1962) that stretches over some shallow rock patches and onto the Malmesbury Group shale in the eastern bay. Although the northern, central region of False Bay was dominated by the ubiquitous presence of *Haploblepharus spp.*, several other threatened chondrichthyans were recorded here. The north-eastern reefs were dominated by encrusting sponges, predominantly the red encrusting sponge (*Clathria oudekraalensis*), and the diversity of fish species here once again reflects the patchy seafloor habitat, where broad descriptions of reef and sand fail to distinguish habitat-associations for species such as maasbanker (*Trachurus capensis*) and *R. globiceps*.

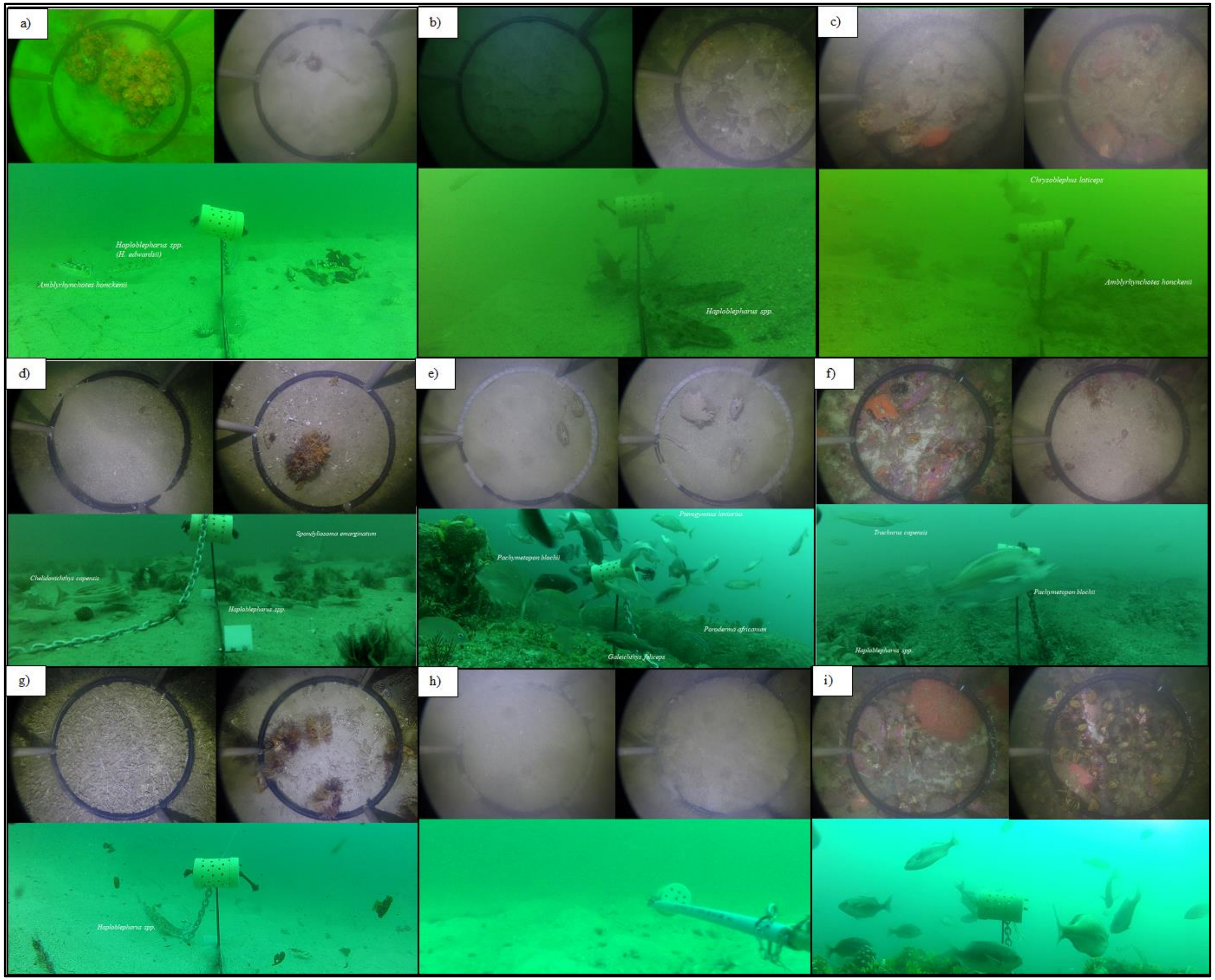

Figure 48. Representative jump camera photographs (the two topmost photos in each square from panel a – i) and mono- and stereo-BRUVs screengrabs (the bottom photograph in each square from panel a – i) from the nine regions where False Bay is delineated into a) North West, b) North Central, c) North East, d) Central West, e) Central and f) Central East, g) South West, h) South Central and i) South East.

5.2. Accounting for similarities in invertebrate and ichthyofauna distributions

Patterns in invertebrate and ichthyofauna distribution reflect patterns in depth and the nature of the seafloor but connecting these changes to associations between the invertebrate and fish communities is more difficult. The sampling design for this study did not allow for the direct comparison of invertebrate communities with ichthyofauna communities, except for the broad-scale description of patterns in feeding guild distributions. Broadly, more fish classified as omnivores that preferred invertebrate prey were recorded on reef than on sand. This may reflect the high diversity of the epibenthic megafauna on reefs. Certain records confirm known associations; for instance, blue hottentot (*Pachymetopon aeneum*); a species known to feed on sponges (Buxton & Smale 1986; Heemstra & Heemstra 2004) was recorded on the north-eastern reefs of False Bay where sponges characterised the invertebrate community. *Chelidonichthys capensis*, a species known to eat crustaceans, cephalopods, and other fish (Heemstra & Heemstra 2004), typified habitats where mobile crustaceans characterised the seafloor surface in this study and were abundant in the infauna (Field 1971).

Associations across the trophic system would be useful to detect regime shifts and test for evidence of trophic cascades. In future, the kind of data collected by jump camera and baited remote underwater video systems (BRUVs) would need to be combined to sample in the same location, and ideally, at the same time. The sampling design could target reef and sand habitats separately, and sample within each broad habitat type along a depth gradient (*sensu* Heyns et al. 2016; Heyns-Veale et al. 2016). It is also possible, but time-consuming and logistically tricky, to sample using multiple methods deployed from the same vessel. In shallow waters where a winch is not required, the jump camera can be deployed first, followed by the BRUVs. The effect of a jump camera scaring away species that do not return once the BRUVs are deployed would need to be tested. A modified jump camera could integrate a BRUVs configuration, such that a single rig could gather two datasets simultaneously. Alternatively, an improved sampling configuration that facilitates photographs and video both laterally and vertically would make a useful addition to the current remote imagery sampling capability in South Africa.

5.3. Integrating descriptions of the seafloor to provide an ecological view

A total of seven seafloor types were classified according to the CATAMI scheme (Althaus et al. 2015), where six were represented on the jump camera transects and seven in the BRUVs videos. This represents a first attempt to describe the physical seafloor through an ecological lens, capturing some of the ecosystem variation that may be relevant to describing biological communities in False Bay. Previous studies have all described False Bay according to its underlying geology and sediments (Flemming 1982; Simpson et al. 1970; Terhorst 1987; Bowie et al. 1970; Du Plessis & Glass 1991). This study added some habitat modifiers to the description of the seafloor, the most notable of which is kelp and the monitoring of which is important given its commercial value and ecological importance (Blamey & Bolton 2018). This enriches the information available to biologists and explains patterns in species distribution for both the epibenthic megafauna and ichthyofauna.

A broad delineation between consolidated and unconsolidated sediments in False Bay was useful for describing patterns at one scale: however, this study confirmed that the boundaries between biological assemblages do not divide quite as clearly as geological classifications, as more than one community type was found within a broader delineation (Kutser et al. 2006) and several species that did not strictly associate with either reef or sand. Biodiversity is generally considered higher on reef systems (Bolton et al. 2018). The assumption at the outset of this study was that, by contrast, species diversity on a more homogenous sand seafloor would be relatively lower, or at least, more evenly distributed across False Bay. This was true of the per site fish species richness and diversity, where a small patch of reef hosted a proportionally higher number of species than the same sized patch of sand. However, it was not true of the total species richness for each habitat type, which was in fact similar at the scale of the bay. Given that 83% of False Bay comprises sand, the classification of such a broad habitat-type into smaller planning and monitoring units is useful to disentangle the patchy distribution of sand-associated fish species.

CATAMI seafloor descriptions were significant predictors of species assemblage composition for both epibenthic megafauna and fish. Of these, CATAMI was of relatively higher importance for epibenthic megafauna than broad-scale habitat (unconsolidated and consolidated). This result illustrates the usefulness of CATAMI for capturing enough of the seafloor variation such that it can be used to explain variation in communities across False Bay, where sediment grain size and substrate type are broken into finer-scale units than the geological delineation of rock or sand. At the same time, it was more useful than ARA and classical geological descriptions of sediment particle size, because it abstracted fine-scale variation that was either difficult to interpret or unhelpful for planning at a regional scale into groupings that could be used to meaningfully interpret ecological data.

The eastern reefs harboured a higher diversity of CATAMI seafloor types, epibenthic megafauna communities and fish than had previously been described using other methods. The distribution of sand-associated fish is patchy across the extent of the bay, and it cannot be assumed that monitoring the western reef margins of the bay will encapsulate the full complement of biodiversity, especially for certain threatened species or sensitive habitat types. The CATAMI characterisation of the seafloor established an archived record of photographs and videos as a basis for ongoing monitoring and assessment: on land, biodiversity surveys are often paired with descriptions of the state of habitats (pristine, degraded) and a quantification of the percentage cover change over time (SANBI & UNEP-WCMC 2016).

An ecosystem level assessment of marine biodiversity that captures biological communities paired with a finer scale description of their associated CATAMI seafloor type is useful to keep track of vulnerable or changing habitat types: for instance, siltation at Gordon's Bay harbour (De F. Retief 1970), the eastward movement of kelp beds (Bolton et al. 2012) and potential sedimentation at freshwater inflow points. This kind of information informs the classification of habitat threats and ecosystem assessments (SANBI & UNEP-WCMC 2016).

5.4 Methods to sample pattern and process in False Bay

Monitoring of any one element of False Bay should be done alongside the other elements that need to be considered together. The jump camera and BRUVs provide *in situ* habitat information that is paired with the biological assemblage and is useful for ecosystem-level insights into patterns of distribution across False Bay. Both methods detected patterns of species distribution: habitat and depth were useful landscape indicators that explained variation in species assemblages, but where broad-scale reef and sand habitat explained fish community composition, the CATAMI seafloor descriptions were more important for epibenthic megafauna. This was important for two reasons: for fish, the BRUVs and CATAMI detected patterns of distribution that were more nuanced than a simple delineation of reef or sand, and for epibenthic megafauna, the jump camera and CATAMI grouped sediment variability at a scale more useful for regional monitoring than classical grain size analyses, but more adequately incorporated sediment variability than the broad designation of unconsolidated or consolidated seafloor habitat. The capacity to detect and refine patterns at several scales will be useful to answer different questions in False Bay in the future. The repeatability of the methods makes them useful to monitor processes over time. This study demonstrates that photographic and video sampling is suitable for understanding feeding guilds, habitat associations and species associations. This will be important where the introduction of alien species (Robinson et al. 2005), pollution (Day & Gardiner 1991; Sparks & Mullins 2017), land cover change and freshwater outflow (Chingombe 2012, Mwangi 2014), desalination plants and overfishing will require that the ecosystem be monitored over time, with a number of different key considerations.

5.5. Environmental drivers of community composition across False Bay

Habitat (reef and sand) explained most of the variation in ichthyofauna communities across False Bay. Habitat could be represented at various scales. CATAMI habitat classifications, reef type (Malmesbury Group shale, Cape Granite Suite or Table Mountain Group sandstone) and reef profile were all statistically significant predictors of community composition. Depth and season were also significant predictors of fish community composition. By contrast, depth explained most of the variation in the epibenthic megafauna communities. In both cases, habitat is confounded by depth: most reef habitat in False Bay is shallow (most is in water depths of less than 60 m), and this may explain in part why the results in this study do not entirely mirror those of Field (1971) where depth was considered a weak explanatory factor for the variation in infauna invertebrate communities.

At fine scales, the roughness and slope of the seafloor showed a weak correlation with patterns in invertebrate communities, and were only significant when considered separately, in combination with depth. It is therefore likely that some of the structuring of the invertebrate communities is determined by the nature of the seafloor at localised scales: the sediment grain size, its organic content, and the sediment type. At the scale of the bay, the CATAMI classification of habitat at a finer resolution than the geological delineation (reef and sand) is useful for the epibenthic megafauna communities and explains some of the variation. The influence of depth needs to be considered in conjunction with habitat, where different species were characteristic of reef and sand in the same depth category.

Habitat (reef and sand) and depth explain patterns of biodiversity across False Bay and are more stable in time, than biological communities that are exposed to shifts in water masses, recruitment, pollution and harvesting. CATAMI seafloor types also explain patterns of biodiversity, providing more insight into seafloor heterogeneity and providing a factor that can be monitored over time to assess habitat changes across False Bay.

5.6. The application of remote imagery techniques to monitor the Table Mountain National Park (TMNP) marine protected area (MPA)

The current zonation of the TMNP MPA incorporates no-take zones over the western reefs that require ongoing monitoring of the epibenthic megafauna and the ichthyofauna communities, as well as the condition of the ecosystem with which both are associated. The South African National Parks (SANParks) is the single conservation agency tasked with monitoring the TMNP MPA, and its mandate is biodiversity management (SANParks 2008). Funding and capacity constraints hinder both the enforcement of the MPA’s no-take zone boundaries, and the monitoring activities needed to inform whether the MPA is meeting its biodiversity conservation goals. Therefore, sustainable monitoring solutions must consider cost and effort. The minimised sea time that remote imagery rapid assessments offer is a first step in addressing these constraints. There is confusion and contestation over the designation of the MPA boundaries (Brill & Raemaekers 2013), with consequent illegal fishing in the no-take zones. Overfishing therefore remains a key threat to biodiversity in this MPA (Skowno et al. 2019) and its impacts should guide the indices that SANParks monitor over time. Several results from, and focus areas identified by, this study could be incorporated into a new survey design (*sensu* Foster et al. 2017) to track the condition of important ecosystems and enable strategic, area-based prioritisation of enforcement effort. This section discusses some key indices, and the sampling effort, intensity, and coverage, that may guide improved longevity and repeatability of monitoring in the MPA.

A jump camera survey design for monitoring epibenthic megafauna in the TMNP MPA should consider annual sampling that targets the shallow reefs and kelp forests identified in the National Biodiversity Assessment (NBA) (Skowno et al. 2019) as moderately protected ecosystem types and vulnerable functional ecosystem groups (Sink et al. 2019). The TMNP MPA's no-take zones in False Bay incorporate a narrow depth range (all less than 60 m, most less than 30 m depth) on reef (Table Mountain Group sandstone and Cape Suite Granite) and kelp habitat (**Figure 47**). These two habitat types also form the majority of what is protected within these no-take zones (**Figure 47**) (DEA 2019a, Skowno et al. 2019). At this local scale, MPA monitoring should therefore focus on incorporating the effect of protection into survey design for sampling on reefs and kelp beds in the 0 – 60 m depth range. This study's transect format at the extent of the bay should be replaced with a grid that structures random-stratified sampling across protection levels on reef and in kelp (which is where the jump camera performs best and the CPCe random points method is most usefully applied to gain relative abundance data). Focusing MPA monitoring using the jump camera on reef and in kelp will lower the overall sampling effort (which lowers the post-processing time) and reduce the required number of sea-going days. The effects of improved protection and climate change on species diversity and abundance are unlikely to be detected annually, but ecosystem condition can be subject to rapid, dramatic change, and declines may be detected within an annual cycle. Therefore, an annual record of species presence/absence would be a useful addition to track trophic shifts or significant habitat alteration. Management may consider moderating the significant post-processing time and expertise associated with annual image analysis by adopting the CATAMI classification of species presence/absence into broad taxonomic groups and functional feeding guilds.

The distance between samples used in this study (185 m) is practical to implement from a vessel at sea in a new grid design. The grid should designate samples on similar habitat and at similar depths inside the St James, Castle Rocks, Boulders and Paulsberg no-take zones and in the adjacent exploited zones. To monitor condition change on reefs and in kelp, and community composition of the epibenthic megafauna in both, it is important to develop ecosystem condition indicators (Keith et al. 2013, Rowland et al. 2018) and track species relative abundance and diversity. These indices can be integrated into the existing NBA (SANBI 2018, SANBI 2019) and pre-empt the requirements for a National Ecosystem Assessment (NEA) programme and the IUCN Red Listing of ecosystem threat status (IUCN 2012, Keith et al. 2013, Bland et al. 2017). The sampling frequency should therefore consider the timescale of both assessments (every five years). Given the low effort of sampling at sea, monitoring that results in analysis at a coarse taxonomic level to detect sudden changes should be annual. To balance the capacity and skills issues associated with processing photographic data (and given that the sampling effort would be the same), standardised data management and a centralised repository could support later expert analysis at a finer taxonomic resolution and provide an archived record against which change can be measured.

A BRUVs survey design for monitoring ichthyofauna in the TMNP MPA should consider annual sampling to target the resident IUCN Red Listed reef-associated sparids (Mann et al. 2014b and 2014c) and IUCN Red-listed chondrichthyans (Pollom et al. 2020) identified in the NBA as especially threatened (Skowno et al. 2019). Relative abundance, species diversity and species size frequencies are key indices required to guide effective management of fish in the TMNP MPA. Monitoring with BRUVs at the local scale of the MPA would be most usefully focused on the reefs, and should follow a Before-After Control-Impact (BACI) type (Stewart-Oaten et al. 1986) design to detect changes in community composition, and increases or decreases in species abundance and size (Sanguinetti 2013). All samples should be designated 500 m apart, and to monitor the effect of protection on fish abundance, diversity and size, a paired BACI design used to assign samples inside the current no-take zones and the adjacent exploited areas on similar reef habitat and at similar depths (Sanguinetti 2013).

It is beneficial for adaptive local management to conduct annual monitoring to detect changes as a result of management decisions (Pfaff et al. 2019), coastal development (i.e. the construction of the Strandfontein desalination plant in response to the drought), the introduction of aquaculture or alien species (Van Wilgen & Wilson 2018). Lightweight BRUVs frames that can be deployed from any patrol vessel without the use of a winch (i.e. the mono-BRUVs design in this study) would address the labour constraints at sea and facilitate minimal field time. The development of small, collapsible BRUVs that use GoPros regardless of a mono- or stereo-camera configuration would increase the variety of vessels from which BRUVs can be deployed; an important consideration for management that often employ patrol vessels and experience high turnover of skippers and sea-based staff. Visibility and oceanographic conditions are favourable for BRUVs sampling in winter in False Bay, and the residency of most species in the TMNP MPA detected in this study recommends a single sampling season where the quality of data collected will be highest. Consistent, reliable and high resolution footage generated within the MPA increases transparency and facilitates participation by MPA stakeholders, promoting an inclusive approach to monitoring that is essential to the current mistrust of monitoring institutions that is discussed by Brill and Raemaekers (2013) and Pfaff et al. (2019).

However, significant time is necessary for processing, analysing and interpreting BRUVs data. In particular, stereo-BRUVs require pre- and post-calibration, and incur significant cost to obtain the EventMeasure software (SeaGIS 2017) required to derive size data to compare with other surveys (Bernard et al. 2014) and international monitoring programmes (Cappo et al. 2003, Dorman et al. 2012, Langlois et al. 2018). The NBA for 2018 (Skowno et al. 2019) highlighted that human and financial capacity are lacking in the South African biodiversity sector. Monitoring agencies may therefore consider eliminating annual size data, and moderating annual winter (May – August) sampling to obtain relative abundance (MaxN) and diversity measures, and a record of ecosystem condition. In addition to sudden changes that need to be detected on an annual basis, the life histories of many resident, reef-associated fish mean that changes in the community are likely only recorded over longer timescales (Jennings 2001). The annual sampling effort should also aim to detect increases in threatened species such as *C. gibbiceps* and *P. rupestris* over long timescales, which recommends the adoption of a moderate sample size of 130 BRUVs annually to detect a recovery in both rare and commercially important reef fish (De Vos et al. 2014). Power analyses using data collected from this focused survey design should adjust the required sample size to detect increases or decreases tailored to the specific management question and species of concern.

Intensive stereo-BRUVs sampling over survey cycles at five-year intervals would be more appropriate to detect changes in size in slow-growing, long-lived species (Bernard et al. 2014, De Vos et al. 2014) and take into consideration the significant field logistics, cost and processing associated with stereo-BRUVs surveys that do not constrain similar monitoring programmes overseas (Langlois et al. 2018). This is especially true where the management authority tasked with long-term monitoring is dependent on government funding, rather than an academic institution. The longer interval would facilitate collaboration on the coastline, and therefore support management in the form of shared equipment and software (Bernard et al. 2014). Strategic Objective 5 in the National Biodiversity Strategy and Action Plan (NBSAP) and National Biodiversity Framework (NBF) is dedicated to addressing a skilled workforce in South African biodiversity conservation and management (DEA 2015, DEA 2019B). It is therefore important that management integrates their own moderated sampling effort with a more intensive survey cycle that is supported by scientific agencies and academic institutions. The former means that adaptive management can answer questions as they arise, and the latter means that the biodiversity skillset is expanded, and appropriate size data are added to a refined assessment of MPA performance. The SANParks marine programme is already implementing the findings from this study in their biodiversity monitoring design and skills-building programme (A Kock, South African National Parks (SANParks) Cape Town, personal communication; S. Mayekiso, South African National Parks (SANParks) Cape Town, personal communication).

5.7. The application of remote imagery techniques to monitor and manage False Bay

The management of False Bay involves multiple, often conflicting, stakeholders (Pfaff et al. 2019). The bay has been earmarked by several agencies as a priority for improved long-term monitoring and the regions outlined in this study can be used to guide annual prioritization of monitoring efforts. Repeat-sampling should be prioritized for the western reefs where the current TMNP MPA is zoned, and along the eastern reefs where seafloor heterogeneity, as well as epibenthic megafauna and ichthyofauna diversity, was highest. The survey design explained for both jump camera and BRUVs monitoring described for the TMNP MPA could equally apply to the eastern reefs of False Bay. The absence of a single agency tasked with monitoring outside formal MPAs in False Bay complicates achieving jump camera and BRUVs samples on the eastern reefs annually. However, this study has shown that the Department of Environment Forestry and Fisheries (DEFF), the City of Cape Town (CoCT) and SANParks should consider prioritising effort in the North East, Central East and South East regions of False Bay where Malmesbury Group shale reefs predominate. Signals of trophic shifts (Blamey et al. 2010, 2012 & 2015), ecosystem condition deterioration (Chingombe 2012, Mwangi 2014) and the recovery of species of conservation concern outside formal protection, are all evident in eastern False Bay. Achieving the same intensity and coverage of sampling across multiple methods as this study is costly, reliant on skilled labour and unsuited to an annual timeframe.

A bay-wide monitoring programme cannot be reliant on remote imagery techniques alone. This study shows that, while the current MPA zonation prioritizes reefs, and most monitoring focus assumes that biodiversity is higher in these systems, the total species richness at the scale of the bay was similar for reef and sand. However, achieving the sampling effort necessary to detect sand-associated species will be labour-intensive and costly if conducted annually. In the absence of a single, dedicated management authority, it may prove more useful to randomly rotate the assessment of the deeper and sand-dominated regions (North Central, Central and South Central) over the five year timescale that would coincide with a dedicated stereo-BRUVs sampling effort. Mimicking terrestrial models of rotational "paddocks" (Savory 1983) may help reduce the number of intensive surveys required each year, but ensure that each region is revisited over time such that a continuous database builds on each preceding survey (Foster et al. 2017). Concerted effort is needed to improve the holistic management of biodiversity monitoring in False Bay [something that is applicable to the rest of South Africa (Skowno et al. 2019)] such that monitoring programmes are complementary to one another. A good example of this is assessing the objectives for a long-term monitoring programme that cannot be met using imagery techniques outlined in this study alone (i.e. the detection of species in turbid waters in northern False Bay where there is high recreational fishing effort on chondrichthyans, and significant input of pollutants from land-based sources), and targeting species of particular concern using other methods (such as acoustic telemetry).

5.8. The application of remote imagery techniques in monitoring of South Africa's MPAs

South Africa's MPA network was expanded to add twenty new MPAs to the existing coverage, increasing protection of ocean spaces to 5% of the country's Exclusive Economic Zone (EEZ) (DEA 2019a). Most of these MPAs are located offshore (Sink 2016), which significantly increases the logistics required to monitor MPA performance and enforce protection measures. Sampling is therefore needed for the South African MPA network at large across a range of depth gradients and habitat types, and this study adds to a growing body of evidence that remote imagery surveys afford sampling at greater depths, in lower water visibility and over greater spatial scales (Bernard et al. 2014; Heyns-Veale et al. 2016). A national platform that standardises sampling protocols and data management for all remote imagery surveys across South Africa would be a useful addition to existing programmes such as the commercial fishery surveys or the Acoustic Tracking Array Platform (ATAP) that operate at the scale of the coast (Cowley et al. 2017) and, offering data to complement information on movement patterns of key species to include updated information on aggregation sites, essential habitats and ecosystem condition. This would be a step towards addressing the significant shortfalls identified in long-term biodiversity monitoring in South Africa in the 2018 NBA (Skowno et al. 2019). This study shows how existing methods and programmes elsewhere in the world (Langlois et al. 2018) can be adapted to meet the challenges of monitoring in South Africa.

This study emphasises the need for BRUVs surveys of ichthyofauna in South Africa to broaden from their focus on reef systems to include soft sediments. Indeed, the detection of many recently updated IUCN Red Listed chondrichthyans is reliant on this more equitable focus of monitoring effort (Kyne et al. 2020). Moreover, the application of these standardised methods using classification schemes that make data comparable at an ocean-basin scale is becoming increasingly important as global assessments of MPA designation and performance gain momentum (Dwyer et al. 2020, MacNeil et al. 2020). The absence of South African data in these large-scale assessments is notable and should be redressed. This study provides a range of options to inform remote imagery sampling at fine and coarse scales, using a range of indices by which to monitor changes in community composition. The contribution adds to scientific work that seldom balances the logistics of long-term monitoring in developing nations with the conservation imperative of keeping up with the technological development of surveys.

5.9. Conclusion

This study assessed patterns of diversity in the epibenthic megafauna and ichthyofauna of False Bay using remote, non-extractive techniques that are novel to the region. Insights have been provided that outline a monitoring programme at different scales: for the TMNP MPA, at the full extent of False Bay, and across the South African MPA network. The way that these novel methods were applied in this study extended biodiversity sampling across more depths and habitats than any single, previous survey of the bay. Importantly, this study not only provided the first quantitative account of the epibenthic megafauna and ichthyofauna at this scale, with an assessment of the landscape characteristics that describe their distribution, but presented new data on the eastern reefs where species diversity was highest. The two new classifications applied to describe the seafloor showed that horizontal seafloor heterogeneity was highest in the east, and reef was distributed along the eastern and western margins. These results were matched by those from Rényi diversity analyses that showed that epibenthic megafauna species diversity was also highest in the east. The BRUVs data showed that several threatened fish species were present on these same eastern reefs. These combined data show that the full complement of diversity across habitats, epibenthic megafauna and fish is not limited to western reefs in the current MPA, and there are communities of particular interest that may be threatened by land-cover change, freshwater outflow and coastal development in other regions of False Bay. The insights from this study therefore provide critical evidence to motivate for improved monitoring of eastern False Bay, and its consideration as a matter of priority for suitable conservation management. These results should form the basis, therefore, of a monitoring programme that can account for a much more representative coverage of biodiversity and its associated threats.

This study also provided a new characterisation of the seafloor that introduced an ecological perspective in a region that was largely geologically described. CATAMI classification represents a useful intermediary between ARA and classical grain size analyses at fine-scales and the delineation of reef and sand at broad scales that is significant for both epibenthic megafauna and fish. The classification system is an important, and now tested, foundation for a standardised, nationwide monitoring programme using remote imagery techniques. Cameras can sample the seafloor and its associated biodiversity concurrently, with good coverage and at low cost. These are important considerations for sustainable monitoring to inform conservation management in resource-limited regions. This study's delineation of nine regions can be used to guide the application of such a monitoring programme. Moreover, the synthesis of information for these regions in this study provides the first seafloor descriptions that are matched with the descriptions of epibenthic megafauna and ichthyofauna. This study updated the current state of knowledge in a bay that has undergone significant change. Given that this study covers a wider range of species and habitats than any other previous assessment of False Bay, and that the methods it employs to achieve this are what facilitated this at this scale, it should serve as a blueprint for future monitoring.

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Appendix 1

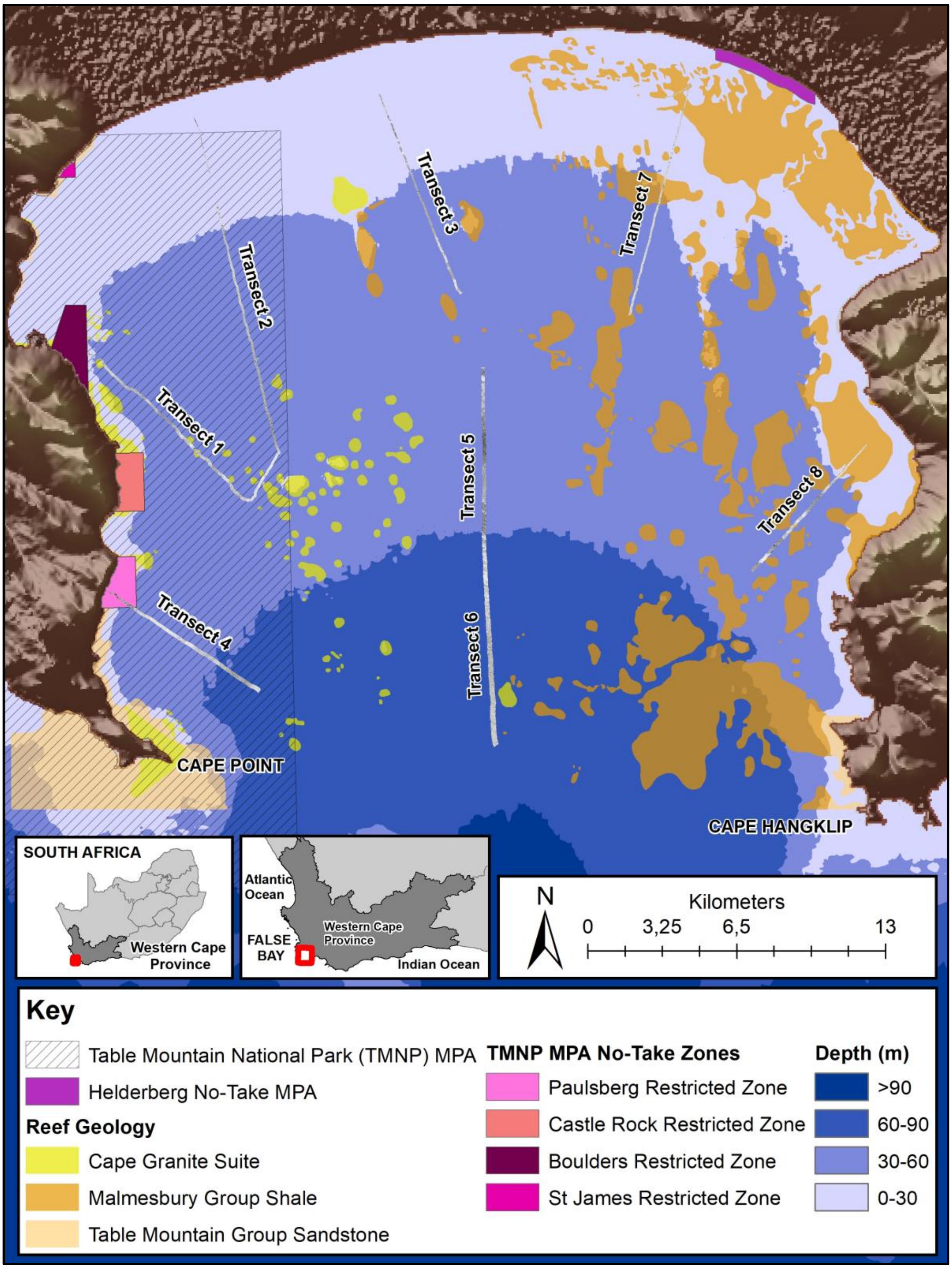

Figure 49. A view of the provisional beam time series (BTM) data (0.5 m grid size) collected along eight transects by multibeam sonar surveys in False Bay, South Africa in the context of: terrestrial topography (EKZNW 2015), river network (SANBI 2011), subtidal reef geology (Van Zyl 2011), ocean depth (m) (Van Zyl 2011) and marine protected areas (MPAs) (DEA 2019a).

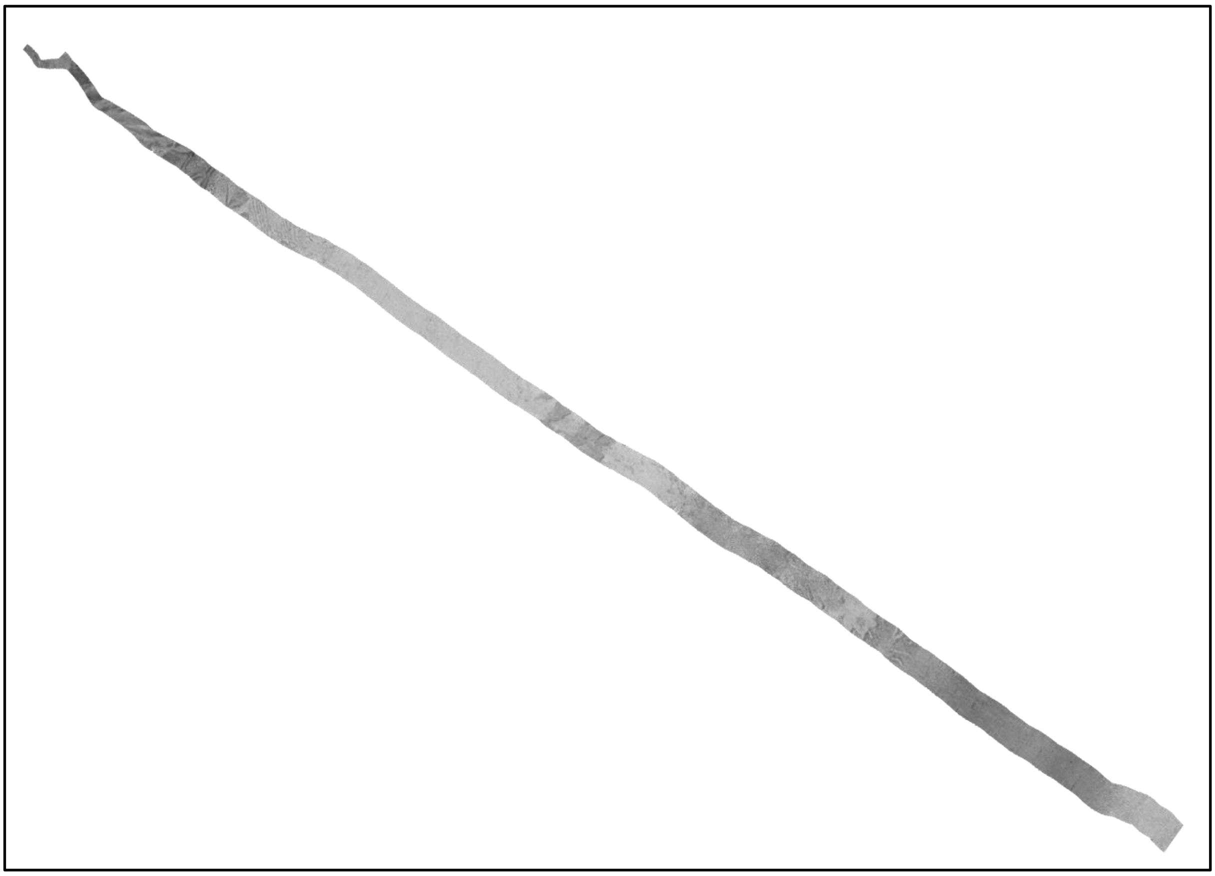

Figure 50. Provisional beam time series (0.5 m grid size) from a multibeam sonar survey of transect 1 (**Figure 49**) in False Bay, South Africa.

Figure 51. Provisional beam time series (0.5 m grid size) from a multibeam sonar survey of transect 2 (**Figure 49**) in False Bay, South Africa.

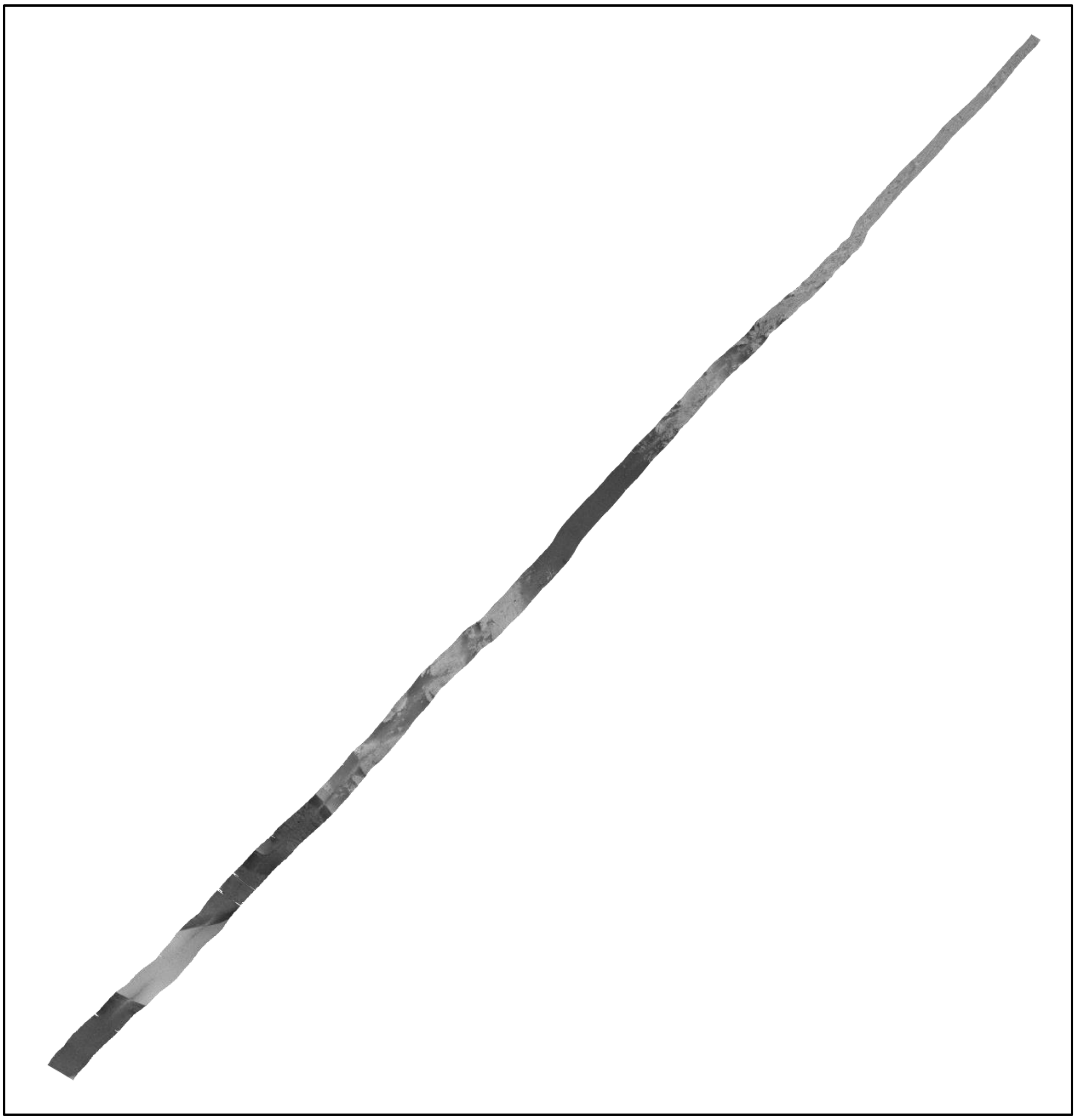

Figure 52. Provisional beam time series (0.5 m grid size) from a multibeam sonar survey of transect 3 (**Figure 49**) in False Bay, South Africa.

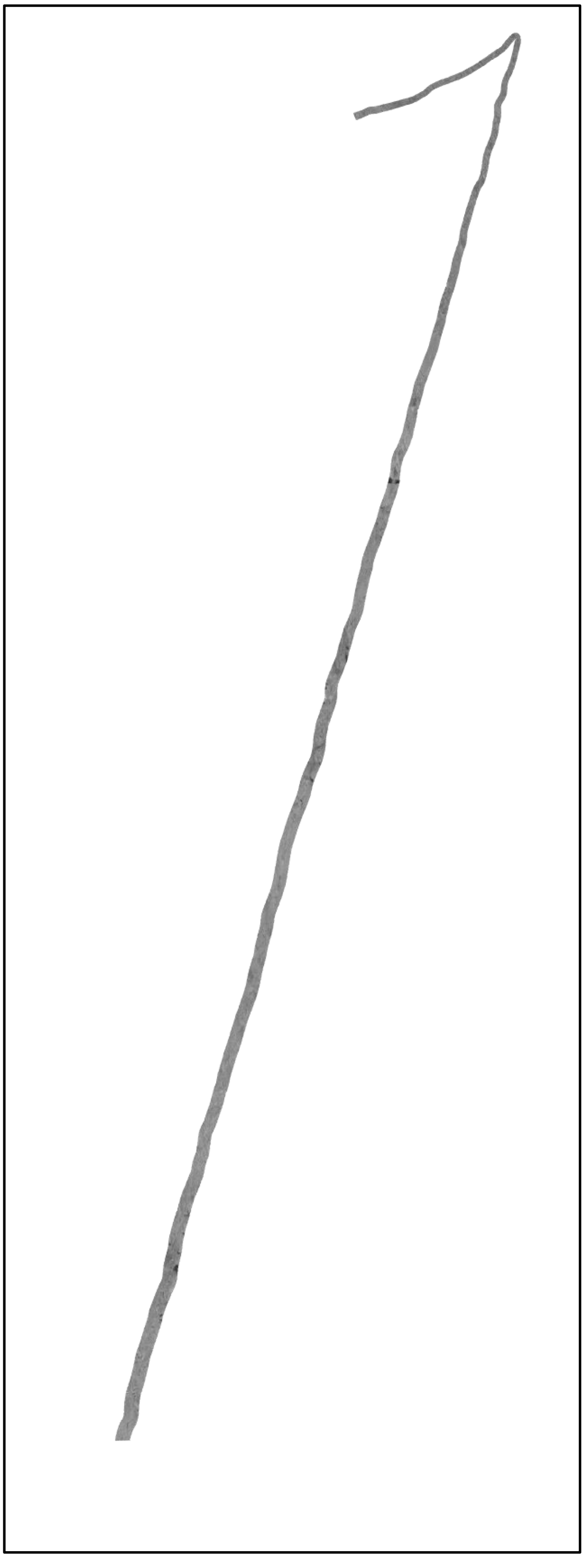

Figure 53. Provisional beam time series (0.5 m grid size) from a multibeam sonar survey of transect 4 (**Figure 49**) in False Bay, South Africa.

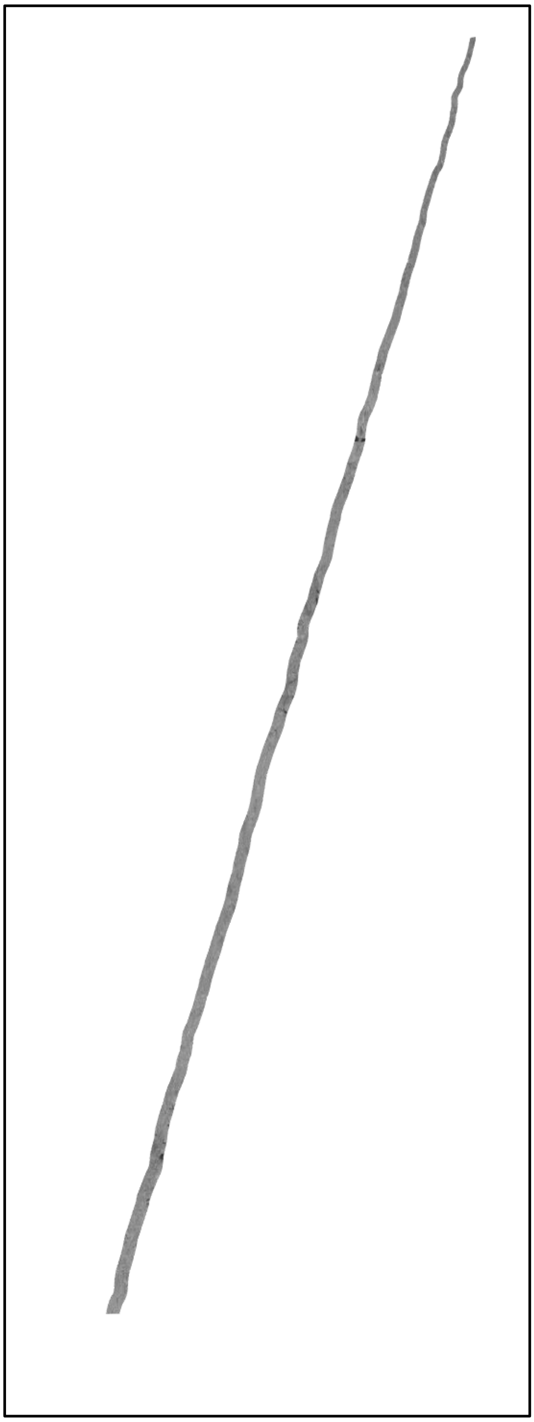

Figure 54. Provisional beam time series (0.5 m grid size) from a multibeam sonar survey of transect 5 (**Figure 49**) in False Bay, South Africa.

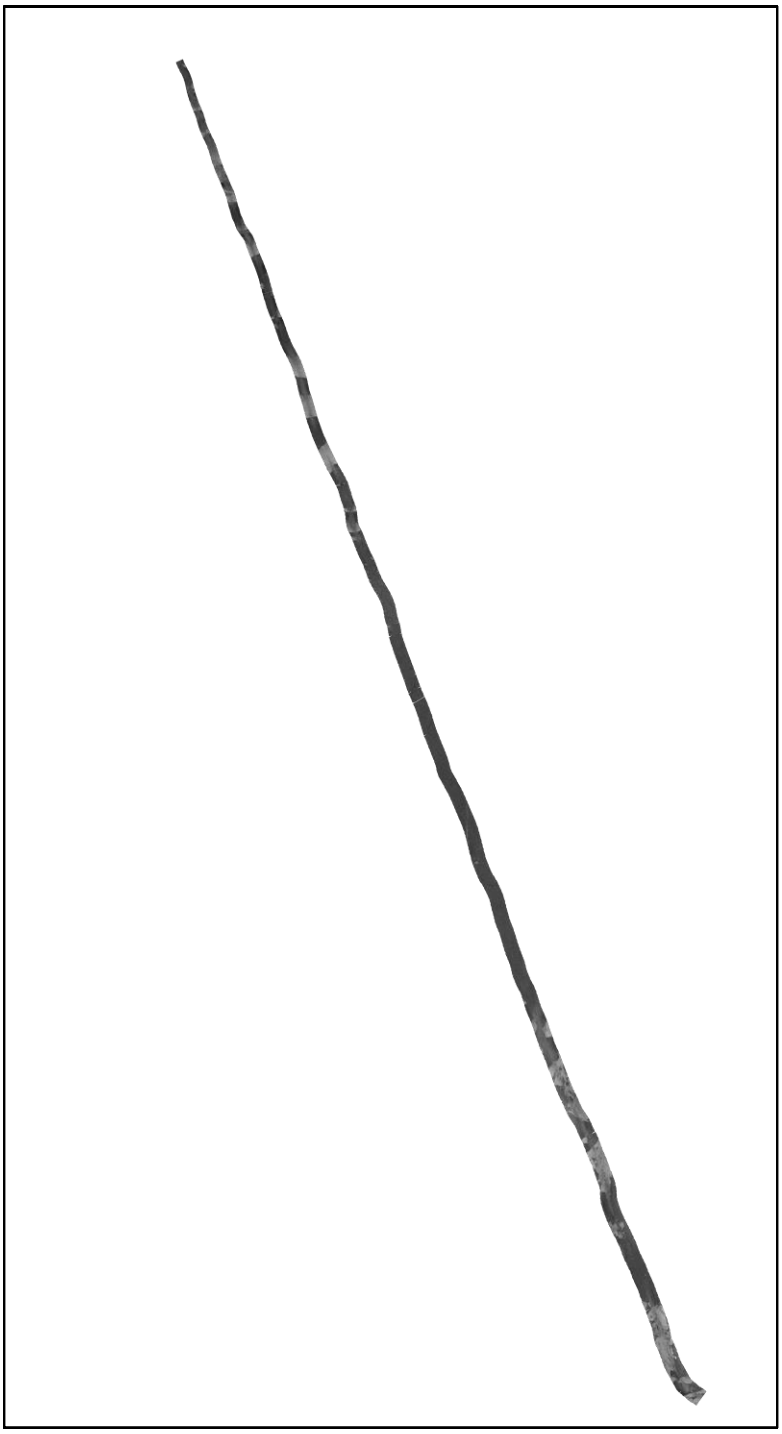

Figure 55. Provisional beam time series (0.5 m grid size) from a multibeam sonar survey of transect 6 (**Figure 49**) in False Bay, South Africa.

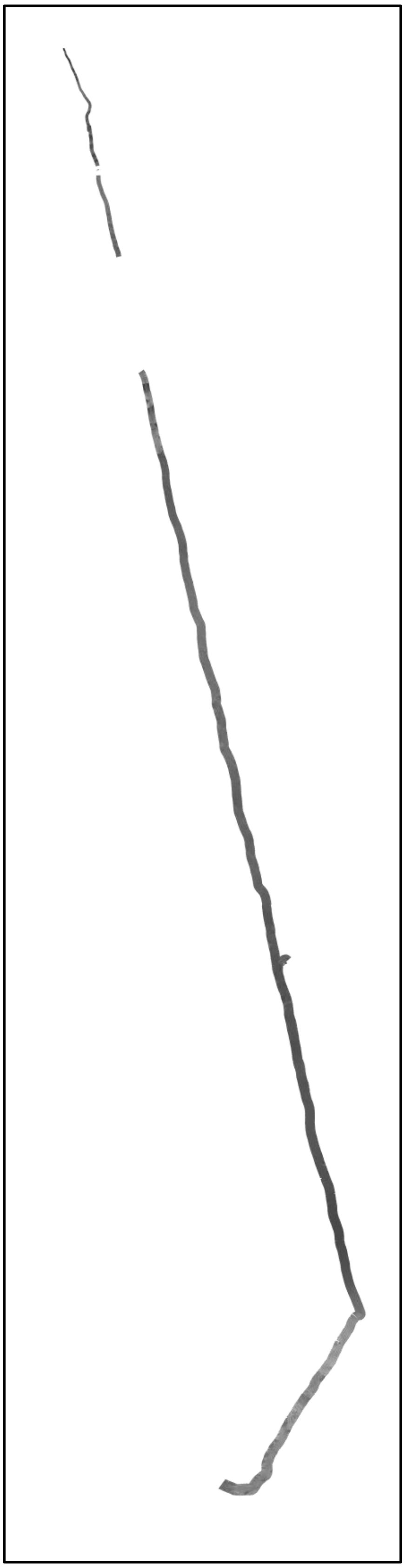

Figure 56. Provisional beam time series (0.5 m grid size) from a multibeam sonar survey of transect 7 (**Figure 49**) in False Bay, South Africa.

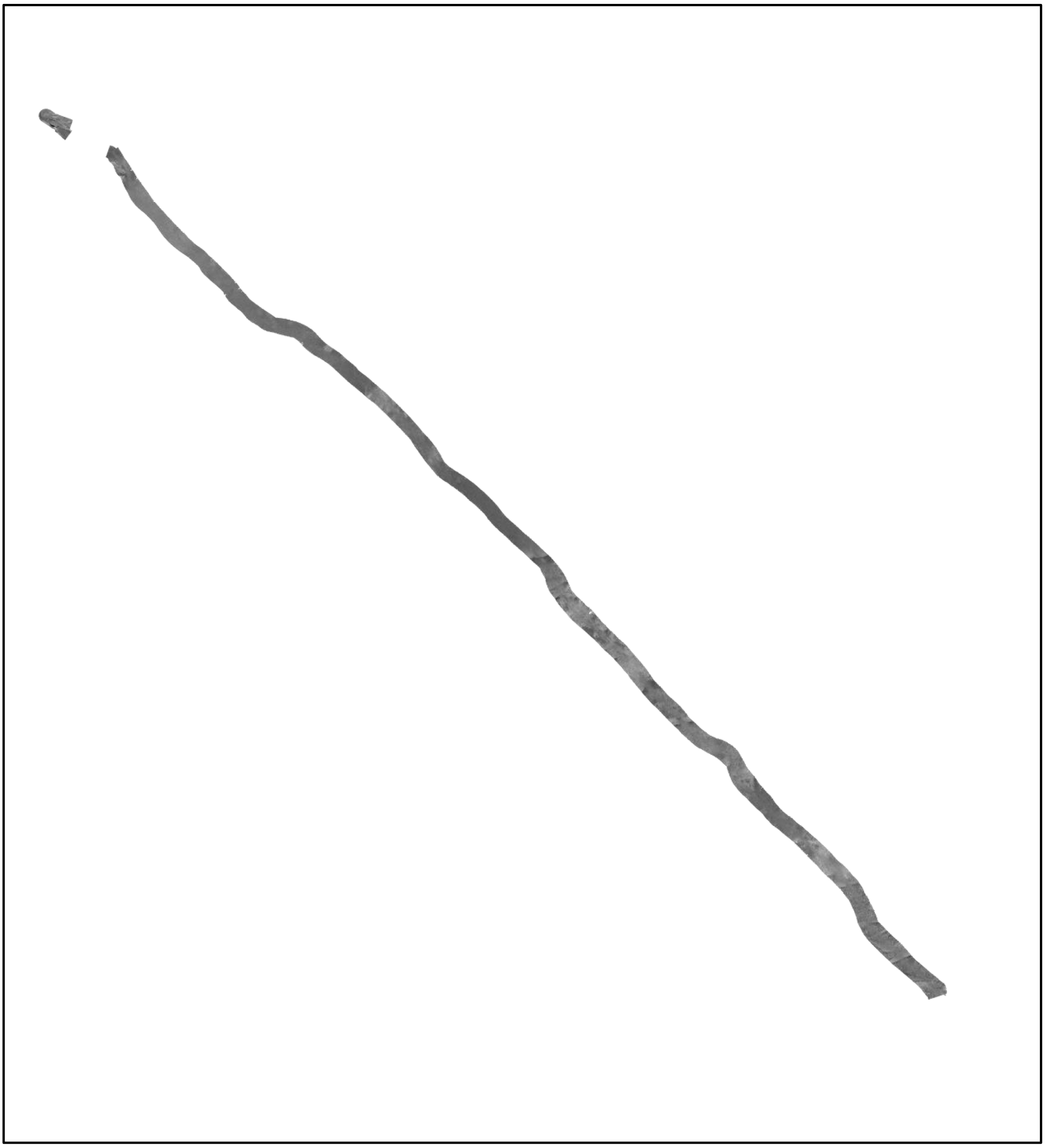

Figure 57. Provisional beam time series (0.5 m grid size) from a multibeam sonar survey of transect 8 (**Figure 49**) in False Bay, South Africa.

Appendix 2

Table A.1. List of species identified from 373 photographs across False Bay. Species are identified to species level wherever possible. Where a species name was not available, but a separate organism was distinguished, the organism was given a unique identified (spp.). Sponges are differentiated by growth form and CATAMI was used to characterise species that could not be given a name from reference guides, or expert consultation

Phylum	Scientific name	Common name	Feeding Guild	CATAMI
Chordata	*Ascidian spp. 1*	Ascidian 1	Filter feeder	AUS
Chordata	*Ascidian spp. 2*	Ascidian 2	Filter feeder	ASC
Porifera	*Ircinia arbuscula*	Black stink sponge	Filter feeder	SPCE
Porifera	*Sponge spp.1*	Blue encrusting sponge	Filter feeder	SPCE
Cnidaria	*Ceriantheopsis nikitai*	Burrowing anemone	Suspension feeder	CNTU
Cnidaria	*Isozoanthus capensis*	Cape zoanthid	Suspension feeder	CNCAZ
Cnidaria	*Capnella thyrsoidea*	Cauliflower soft coral	Filter feeder	CBBFM
Chordata	*Apletodon pellegrini*	Chubby clingfish	Predator	FB
Mollusca	*Marginella nebulosa*	Cloudy marginella	Predator	MOG
Echinodermata	*Comanthus wahlbergi*	Common feather star	Suspension feeder	EFU
Rhodophyta	*Coralline spp. 1*	Coralline algae	Autotroph	MAENRC
Mollusca	*Cypraeaovula fuscodentata*	Cowrie shell	Predator	MOG
Cnidaria	*Anthopleura michaelseni*	Crevice anemone	Suspension feeder	CNTR
Arthropoda	*Hymenosoma spp.*	Crown crab	Predator	CRCT
Porifera	*Hymeniacidon perlevis*	Crumb of bread sponge	Filter feeder	SPCE
Cnidaria	*Balanophyllia bonaspei*	Cup coral	Suspension feeder	CSSOA
Echinodermata	*Tropiometra carinata*	Elegant feather star	Suspension feeder	EFU
Chordata	*Ascidian spp. 3*	Encrusting colonial ascidian	Filter feeder	AUC
Echinodermata	*Amphiura capensis*	Equal-tailed brittle star	Suspension feeder	EOBSS
Bryozoa	*Bicellariella ciliata*	Eyelash moss animal	Filter feeder	BRYSF
Cnidaria	*Pseudactinia flagellifera*	False plum anemone	Suspension feeder	CNTR
Mollusca	*Bullia laevissima*	Fat plough shell	Scavenger	MOG
Cnidaria	*Virgularia schultzei*	Feathery sea pen	Filter feeder	CBQ
Ulvophyceae	*Chaetomorpha spp.*	Filamentous green algae	Autotroph	MAFG
Polychaeta	*Filograna impexia*	Filigreed coral worm	Suspension feeder	WPOT
Rhodophyta	*Jania adhaerens*	Finely forked coralline algae	Autotroph	MAAR
Cnidaria	*Eunicella albicans*	Flagellar sea fan	Filter feeder	CBBNA
Porifera	*Isodictya grandis*	Flat leaf sponge	Filter feeder	SPEL
Echinodermata	*Thyone aurea*	Golden sea cucumber	Suspension feeder	ESC
Echinodermata	*Austrofromia schultzei*	Granular sea star	Detritivore	ESS
Porifera	*Sponge spp. 2*	Grey sponge spp. 1	Filter feeder	SPMSI
Porifera	*Sponge spp. 3*	Grey sponge spp. 2	Filter feeder	SPMSI

Porifera	*Sponge spp. 4*	Grey sponge spp. 3	Filter feeder	SPMSI
Porifera	*Sponge spp. 5*	Grey sponge spp. 4	Filter feeder	SPM
Porifera	*Sponge spp. 6*	Grey sponge spp. 5	Filter feeder	SPMSI
Echinodermata	*Ophiothrix fragilis*	Hairy brittlestar	Filter feeder	EOBSS
Echinodermata	*Echinocardium cordatum*	Heart urchin	Detritivore	ESUI
Mollusca	*Atrina squamifera*	Horse mussel	Filter feeder	MOB
Cnidaria	*Hydrozoa spp. 1*	Hydroid 1	Suspension feeder	CNHYD
Cnidaria	*Hydroid spp. 2*	Hydroid 2	Suspension feeder	CNHYD
Cnidaria	*Bunodosoma capensis*	Knobbly anemone	Suspension feeder	CNTR
Chordata	*Didemnum spp*	Lattice ascidian	Filter feeder	AUC
Bryozoa	*Flustra spp.*	Leafy moss animal	Filter feeder	BRYS
Arthropoda	*Mursia cristiata*	Masked crab	Scavenger	CRCT
Porifera	*Sponge spp. 7*	Massive sponge spp. 1	Filter feeder	SPMSI
Echinodermata	*Pentacta doliolum*	Mauve sea cucumber	Suspension feeder	ESC
Chordata	*Botryllus maeandrius*	Meandering ascidian	Filter feeder	AUC
Chordata	*Aplidium circulatum*	Mushroom ascidian	Filter feeder	ASC
Cnidaria	*Eunicella papillosa*	Nippled sea fan	Filter feeder	CBFFS
Cnidaria	*Stylaster nobilis*	Noble coral	Suspension feeder	CNHYD
Porifera	*Sponge spp. 8*	Orange sponge	Filter feeder	SPM
Porifera	*Sponge spp. 9*	Orange variable sponge	Filter feeder	SPEL
Porifera	*Spirastrella spinispirulifera*	Orange wall sponge	Filter feeder	SPM
Cnidaria	*Leptogorgia palma*	Palmate sea fan	Filter feeder	CBBNA
Annelida	*Sabella pavonina*	Peacock fanworm	Filter feeder	WPOT
Porifera	*Sponge spp. 10*	Pink encrusting sponge	Filter feeder	SPCE
Porifera	*Sponge spp. 11*	Pink massive sponge	Filter feeder	SPM
Bryozoa	*Laminopora jellyae*	Pore-plated false coral	Filter feeder	BRYHM
Porifera	*Sponge spp. 12*	Purple encrusting sponge	Filter feeder	SPCE
Echinodermata	*Callopatiria formosa*	Purple sea star	Detritivore	ESS
Cnidaria	*Clathria oudekraalensis*	Purple soft coral	Suspension feeder	CBBFM
Ochrophyta	*Zeacarpa leiomorpha*	Ralfsia	Autotroph	MAENB
Porifera	*Sponge spp. 13*	Red encrusting sponge	Filter feeder	SPCE
Rhodophyta	*Grateloupia longifolia*	Red rubber weed	Autotroph	MASR
Echinodermata	*Callopatiria granifera*	Red sea star	Detritivore	ESS
Echinodermata	*Pseudocnella insolens*	Red-chested sea cucumber	Suspension feeder	ESC
Porifera	*Psammocinia arenosa*	Sand cup sponge	Filter feeder	SPCLCC
Echinodermata	*Astropecten irregularis pontoporaeus*	Sand sea star	Predator	ESS
Mollusca	*Nucella squamosa*	Scaly dogwhelk	Predator	MOG
Bryozoa	*Chaperia spp.*	Scrolled false coral	Filter feeder	BRYHM
Echinodermata	*Marthasterias africana*	Spiny sea star	Predator	ESS
Annelida	*Spirorbis spp.*	Spiral fan worm	Filter feeder	WPOT
Ochrophyta	*Laminaria pallida*	Split-fan kelp	Autotroph	MALCB
Porifera	*Sponge spp. 13*	Sponge spp. 1	Filter feeder	SPM
Porifera	*Sponge spp. 14*	Sponge spp. 2	Filter feeder	SPES
Porifera	*Sponge spp. 15*	Sponge spp. 3	Filter feeder	SPM
Porifera	*Sponge spp. 16*	Sponge spp. 4	Filter feeder	SPM
Echinodermata	*Roweia stephensoni*	Stephenson's sea cucumber	Suspension feeder	ESC

Cnidaria	*Anthothoe chilensis*	Striped anemone	Suspension feeder	CNTR
Cnidaria	*Malacacanthus capensis*	Sunburst soft coral	Suspension feeder	CBBFM
Annelida	*Thelepus spp.*	Tangleworm	Deposit feeder	WPOT
Rhodophyta	*Leptophytum foveatum*	Thin coralline crust	Autotroph	MAENRC
Porifera	*Sponge spp. 17*	Toothed sponge	Filter feeder	SPC
Porifera	*Haliclona anonyma*	Turret sponge	Filter feeder	SPC
Cnidaria	*Alcyonium valdiviae*	Valdivian soft coral	Suspension feeder	CBBFM
Arthropoda	*Jasus lalandii*	West Coast rock lobster	Predator	CRLR
Chordata	*Ascidian spp. 4*	White encrusting ascidian	Filter feeder	AUC
Porifera	*Sponge spp. 18*	White sponge	Filter feeder	SPM
Porifera	*Sponge spp. 19*	White encrusting sponge	Filter feeder	SPCE