Marine ecosystem classification and conservation targets within the Agulhas ecoregion, South Africa

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By

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Plagiarism declaration

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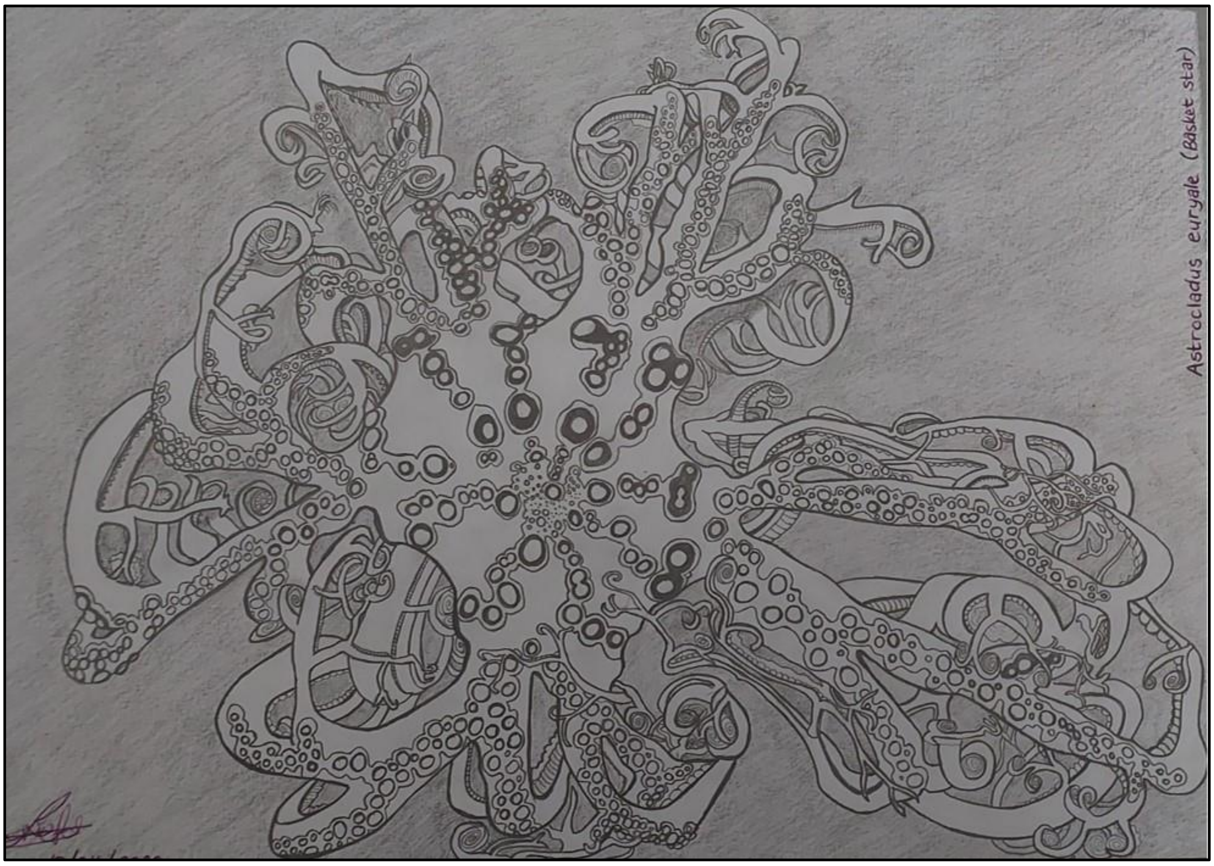

A sketch-drawing of a basket star, Astrocladus euryale, done by myself, during the hard lockdown of the COVID-19 pandemic, completed on the 10 April 2020.

I would like to dedicate this thesis in loving memory of my grandfather, Patrick Desmond Nefdt and his brother, Darryl Nefdt, who both sadly passed away during my studies. I would like to honour and thank them for always supporting my passion in studying marine life.

Abstract

Deep-sea benthic ecosystems remain poorly studied in South Africa, limiting understanding of community biodiversity patterns and their environmental drivers. This is one of the first studies to (i) visually investigate marine epifaunal community patterns and their environmental drivers along the Agulhas ecoregion outer shelf, shelf edge and upper slope to support marine ecosystem classification and mapping, and (ii) to determine the conservation targets for selected national marine ecosystem types to inform improved management of the marine environment, through Marine Spatial Planning processes.

Visual surveys of the seabed were conducted to quantify epifauna during the ACEP Deep Secrets Cruise in 2016, using a towed benthic camera system. Twenty-nine sites were sampled, ranging from 120-700 m in depth and spanning the shelf-slope transition from the western edge of the Agulhas Bank to offshore of the Kei River mouth. A total of 855 seabed images were processed, and 173 benthic taxa quantified. Corresponding environmental variables were used to determine potential drivers of observed biodiversity patterns. Data were analysed using multivariate analyses, including CLUSTER, MDS and DistLM, in PRIMER v6 with PERMANOVA.

Ten different epifaunal communities were classified and described with key characteristic taxa identified. Communities found in habitats that comprised mostly hard rocky substrata generally exhibited higher in species richness and were most commonly characterized by stalked crinoids, various corals and bryozoans, whereas communities found in habitats comprising unconsolidated sediment were lower in species richness and commonly characterized by polychaetes, cerianthids and brittle stars. Communities found in habitats comprising both hard and soft substrata had a mix of the above-mentioned epifauna. The distribution of these communities was mostly influenced by substratum type, longitude, trawling intensity, depth, and presence of visible particulate organic matter. The combined interactions of topography, substratum and the unique hydrodynamic conditions along the Agulhas ecoregion shelf-slope transition are likely responsible for the observed patterns. The observed community patterns were also compared to the existing classification of marine ecosystem types from the 2018 National Biodiversity Assessment. Fine-scale heterogeneity was revealed within the examined marine ecosystem types, particularly with substratum type and associated community variability and should be recognized and incorporated into future iterations of the national marine ecosystem classification and map.

Species-area curves were used to calculate conservation targets for three ecosystem types, defined by the 2018 National Biodiversity Assessment, namely the Agulhas Coarse Sediment Shelf Edge, South West Indian Upper Slope, and the Agulhas Rocky Shelf Edge. Considering the epifaunal species richness (using the bootstrap estimator) and area, per image and per ecosystem type, the rate of accumulation of species was calculated and used to estimate the percentage of species expected to be represented by any given percentage of protected ecosystem type area. Between 20 and 30% of the area within these ecosystem types will need to be protected to represent 80% of the species.

This study has shown that an integration of environmental parameters together with biodiversity measures to better understand and classify offshore benthic ecosystems has worked well. However, to improve the resolution of the national marine ecosystem classification and map, there needs to be greater input of fine-scale biological and environmental sampling and mapping of substratum types across the Agulhas ecoregion shelf-slope transition zone. This work is contributing to improvements in the national marine ecosystem classification and map and hence the spatial assessment and planning processes that rely on these products.

Keywords: benthic imagery, offshore biodiversity, epifaunal communities, ecosystem mapping, species-area relationship, systematic conservation planning

Chapter 1: General introduction and literature review

The deep-sea floor was previously believed to be homogenous, however, regional and fine-scale studies have shown that some of these areas comprise diverse terrains and geological features that create unique oceanographic conditions and hydrodynamics, influencing benthic fauna occupying these unique environments (Levin, Etter, et al. 2001, Levin and Sibuet 2012, Menot, Sibuet, et al. 2010, Ramírez-Llodra and Billett 2006). Comprising several substratum types, these environments can include muddy plains, unconsolidated sediments and/or hard rocky grounds (Buhl-Mortensen, Buhl-Mortensen, et al. 2012, Buhl-Mortensen, Vanreusel, et al. 2010, Snelgrove 1998). Within these deep-sea areas, many benthic ecosystems are found, including deep-water coral reefs, sponge and bryozoan gardens, microbial mats, polychaete- and mussel beds (Buhl-Mortensen, Vanreusel, et al. 2010, Cordes, Cunha, et al. 2010, Levin, Etter, et al. 2001, Menot, Sibuet, et al. 2010). The challenges of accessibility in these deep-sea benthic environments has limited exploration, but with recent advances in technology and sampling techniques, an improved understanding of the ecology and dynamic oceanographic processes of these areas has developed over the last two decades (Bicknell, Godley, et al. 2016, Ramírez-Llodra and Billett 2006, Sheehan, Stevens, et al. 2010), assisting in the conservation and management of these deep-sea environments (Howell 2010).

Marine benthic ecosystems deeper than 30 m are classified as offshore because of changes in physical conditions, such as reduced sunlight and wave exposure and weaker bentho-pelagic coupling, compared to inshore ecosystems (ranging between 5 - 30 m depths) (Kirkman, Holness, et al. 2019). Adjacent to shallow coral reef ecosystems (generally less than 30 m) lies a zone ranging from 30 – 150 m where very little light penetrates, called the mesophotic zone (Laverick, Piango, et al. 2018, Stefanoudis, Rivers, et al. 2019). Mesophotic coral ecosystems (MCEs) have recently been identified and assessed on a global scale, for example, in Japan (Sinniger, Harii, et al. 2019) and Western Australia (Abdul Wahab, Radford, et al. 2019), particularly by visual camera systems in Hawaii, Curaçao (Pyle and Copus 2019), in Bermuda (Stefanoudis, Rivers, et al. 2019) and locally in the Amathole region off the east coast of South Africa (Adams, Maneveldt, et al. 2020, Button, Parker, et al. 2021). Although these ecosystems are known to house some of the more common organisms found in shallow reefs, such as macroalgae, sponges and light-dependent corals, the environmental conditions there are more stable than in the shallower reefs (Pyle and Copus 2019, Stefanoudis, Rivers, et al. 2019). Extending beyond 150 m depth, another zone known as the rariphotic zone has also been discovered in various marine environments across the globe and reaches a depth of approximately 300 m (Stefanoudis, Rivers, et al. 2019). This particular zone was observed in Curaçao in the Caribbean Sea and was occupied by distinct fish communities, different to those in the shallower reefs and deeper depths (Baldwin, Tornabene, et al. 2018). Evidently, depth zonation exists within the marine environment, presenting different layers within the pelagic and benthic counterparts of the ocean, with each zone presenting a specific set of environmental conditions and with that a specific suite of marine species (Carney 2005, Gage and Tyler 1991).

Continental shelves are zones adjacent to a continent that extend from the low-water line to a depth that reaches a steep descent, termed the continental slope. Continental slopes are generally found at between 500 - 1000 m but can extend toward greater depths until they eventually connect with the abyssal plain (Greene, Yoklavich, et al. 1999, Ramírez-Llodra and Billett 2006). The continental shelf edge represents a marine ecotone, bridging the continental shelf and slope together as the area encompasses various components of the demersal, benthic and benthopelagic realms (Levin and Sibuet 2012). In most cases continental shelf edges are represented by specific “edge-effect” species (Longhurst 1998) and are characterized by high species richness (Carney 2005, Spalding, Fox, et al. 2007). Shelf-edge zones may exhibit unique environmental and ecological characteristics that vary from the adjacent outer shelf and slope ecosystems, and simultaneously represent an overlap in shallower and deeper species from adjacent ecosystems (Carney 2005) making them areas of great interest for marine research. These areas are associated with various pelagic (e.g., coccolithophore blooms of the North East Atlantic Ocean (Harlay, Borges, et al. 2010) and benthic phenomena, such as internal waves and shelf edge upwelling, which play a significant role, affecting biological and oceanographic processes (Levin and Sibuet 2012, Lorenzzetti and Dias 2013). Due to the limited knowledge of the deep sea, continental shelf edges and adjacent environments are ideal zones to explore benthic patterns and species assemblages.

Demersal surveys along continental shelves and slope environments have been more focused on investigating fish communities and megabenthos (Demestre, Sanchez, et al. 2000, Turpie, Beckley, et al. 2000, Williams, Althaus, et al. 2010), but very little attention has been directed toward epifaunal assemblages within these areas (Buhl-Mortensen, Buhl-Mortensen, et al. 2012, Griffiths, Robinson, et al. 2010, Lange and Griffiths 2014). Epibenthic species have a strict range of environmental tolerances, therefore limiting their distributions to a specific time and place (Gray, Clarke, et al. 1990) and they play a crucial role in the functioning of the deep-sea environment (Atkinson 2009, Monk, Barrett, et al. 2016). Due to the limited mobility and, generally, long lifespans of benthic epifauna (Türkmen and Kazanci 2010), they are recognized as ecosystem engineers, providing support for other organisms (Jones, Lawton et al., 1994, Wright and Jones, 2006) and regulating bentho-pelagic coupling processes (Bulman and Fulton 2015). They can improve understanding of hydrography and how benthic communities play a role in important ecological processes, such as nutrient cycling, changes in planktonic populations and the distribution of wide-ranging species (McArthur, Brooke, et al. 2010, Snelgrove 1998).

Temporally, the abundance and distribution of benthic communities are subject to natural variability and can also be influenced by seasonal variation, climate change (Danovaro, Dell'Anno, et al. 2004), and the interactions between species, such as competition and predation (Connor, Allen, et al. 2004). On a spatial scale, different communities occupy different niches on the seafloor (Gray, Clarke, et al. 1990), thus forming a mosaic of habitats that define the community niches. Considering the intricate nature of these marine benthic environments, it is important to integrate and apply both physical characteristics of the study area and its ecology and use them as potential surrogates to determine the drivers of marine benthic biodiversity.

Several biological and environmental factors may be used to explain why species diversity and abundance change along a gradient of interchanging seafloor topography at various scales. On a finer scale (10’s to 100’s of metres) some of these factors can include sediment grain size, substratum type, habitat heterogeneity (Hewitt, Thrush, et al. 2004), organic content, oxygen availability, temperature, current regime and catastrophic disturbances (Etter and Grassle 1992, Levin, Etter, et al. 2001). On a regional scale (100’s to 1000’s of metres), water masses, depth, substratum type and terrain properties, such as slope, all influence the distribution of marine faunal communities (Levin, Etter, et al. 2001, Howell 2010, Karenyi, Sink, et al. 2016, Sink, Holness, et al. 2012). The practicality of measuring the abundance of each species on a regional scale would be too costly and time consuming (Costello 2009). Applying the process of ecosystem classification, scientists identify environmental factors that represent the conditions that characterise a specific ecosystem type and designate them as potential "surrogates" to classify other similar marine ecosystems within the study area (Howell 2010, Sink, Holness, et al. 2012).

Pressures within the marine environment

Continental shelves, in particular, are disturbed by many anthropogenic pressures at a global scale (de Juan, Moranta, et al. 2012) and yet there remains limited knowledge about the distribution of benthic organisms and their respective assemblages in these regions (Griffiths 2005, Griffiths, Robinson, et al. 2010). Benthic ecosystems along the continental margin are poorly understood (Levin and Sibuet 2012), but there is evidence that pressures such as demersal fishing, marine mining (minerals, oil, and gas), pollution (Griffiths, Robinson, et al. 2010) and the intensification of climate change, have heavily transformed these ecosystems (de Juan, Moranta, et al. 2012, Mead, Griffiths, et al. 2013).

As a result of rapid growth in the human population, immense pressure is placed on the marine environment to supply resources and ecosystem services (Assessment 2005). There is a global drive towards a 'Blue Economy' which aims to increase the economic benefits derived from oceans, for example through increased tourism, mineral extraction, aquaculture, international trade, transportation, etc. (Bond 2019, Potgieter 2018). These increased activities in the ocean could, however, accelerate risk to these unknown deep-sea ecosystems, especially if they are not sustainably managed and monitored effectively (Potgieter 2018). The implementation of sustainable approaches towards marine spatial planning has become essential, given that the anthropogenic use of the ocean continues to grow steadily and is expanding further offshore (Davies, Roberts, et al. 2007). An increase in knowledge and understanding of these deep-sea systems will inform appropriate management actions to support improving the quality and maintenance of these marine ecosystems (Clark and Lombard 2007, Levin, Sibuet, et al. 2010).

Marine Spatial Planning

Marine Spatial Planning (MSP) is a coordinated process that proposes how and where human social and economic activities may take place in the ocean to ensure the sustainable use of marine space and resources (Ehler and Douvere 2009, Jones, Lieberknecht, et al. 2016). Through this process, it is important to consider and understand the distribution of marine organisms and ecological processes that occur within the marine environment. Systematic Conservation Planning (SCP) is a useful approach to support MSP, whereby multiple data sets are used by marine management and decision makers to identify priority areas in the ocean, also known as Critical Biodiversity Areas (CBAs) (Kirkman, Holness, et al. 2019). Systematic conservation planning is valuable for spatial biodiversity management (Kukkala and Moilanen 2013, Margules and Pressey 2000) and the conservation of representative species and ecosystems in the marine space through establishing a network of Marine Protected Areas (MPAs) (Kirkman, Holness, et al. 2019, Sink, van der Bank, et al. 2019). In South Africa, systematic conservation planning efforts are based on the national ecosystem classification and maps (Dayaram, Skowno, et al. 2021). Marine ecosystem mapping lags behind terrestrial efforts and it is important that the ecosystem map and the conservation targets used in systematic conservation planning are informed by science.

Identifying and quantifying ecosystem-based conservation targets has become a high priority for South Africa's marine environment, as it supports spatial assessment and planning processes (Sink, van der Bank, et al. 2019). These quantitative measures are used both to identify conservation priorities and to evaluate the success or impact of conservation actions through monitoring programmes. SANBI (2016) defines conservation or biodiversity targets as the "minimum proportion of each ecosystem type that needs to be kept in its natural state, or near-natural state, to conserve a viable representative sample of biodiversity of all ecosystem types over the long-term." Overall, these targets are typically conveyed as a proportion of the historical extent of each ecosystem type (SANBI 2016).

Current protection status in South Africa

South Africa has progressed in marine research capacity in recent decades, particularly focussing on the conservation of its coastline (Griffiths, Robinson, et al. 2010). In recent years, however, momentum has increased in establishing a network of Marine Protected Areas (MPAs) within the country's Exclusive Economic Zone (EEZ) (Sink, Holness, et al. 2012). In 2010, 23% of the coastline was formally protected (Griffiths, Robinson, et al. 2010), but deeper waters, including offshore marine communities, remained a neglected area of research and had very little formal protection (0.4%). In subsequent years, offshore MPAs were recognized as a national research priority under the government initiative, Operation Phakisa (Phakisa 2014). Amongst other research priorities, Operation Phakisa not only aimed to sustain the goals of ocean economy (Phakisa 2014), but also to protect marine and coastal ecosystems, therefore growing South Africa's MPA network (Sink, Holness, et al. 2012). As a result of this initiative, a Marine Spatial Planning Act (Act No. 16 of 2018) was established for South Africa to support improved management and the sustainable use of its ocean space (RSA 2019).

In early 2019, it was formally announced that the Department of Environmental Affairs (currently Department of Forestry, Fisheries and the Environment (DFFE)) had officially implemented and declared 20 new Marine Protected Areas in South Africa, with most of them located offshore, bringing the total percentage of protected ocean space up to 5.4% (including 41 MPAs in total, covering an area of 57 900 km^2) (Kirkman, Mann, et al. 2021, Sink, van der Bank, et al. 2019). This was a significant step forward for South Africa's marine conservation and protection expansion programmes. As marine scientific research progresses in South Africa, the ongoing collection of new data will continue to improve understanding of our coastal and offshore deep-sea marine ecosystems. Efforts to increase further protection are still required for South African waters and the next goal regarding the extension of South Africa's MPA network is to further increase protection of the surrounding marine environment to 10% (Sink, van der Bank, et al. 2019).

The importance of offshore processes and ecosystem services are increasingly being recognized as an incentive for offshore conservation. South Africa has prioritised establishing a representative network of offshore deep-sea Marine Protected Areas (Sink, van der Bank, et al. 2019), which will offer marine managers and decision-makers a way to address the conservation needs of the surrounding deep-sea environment. This plan of action will assist in safeguarding marine biodiversity and various resources found offshore within South Africa's Exclusive Economic Zone (EEZ).

1.1 Ecosystem classification and mapping

Marine ecosystems are classified for many reasons, including to provide foundational information and a map to assess their threat status and protection levels over time, to identify biologically important areas for conservation and to support appropriate management of these ecosystems (Costello 2009, Kenchington 2003, Sink, van der Bank, et al. 2019). Improved knowledge of the marine environment and which species live there, will inform improved management of human activities within the marine space, through Marine Spatial Planning processes (Sink, van der Bank, et al. 2019). Many countries opt to classify and map marine habitats which can be defined as “a space that is physically and biologically suitable for the habitation of a particular species” (Dayaram, Skowno, et al. 2021, page 56). Marine habitats are usually smaller in scale and cannot be defined without a target species in mind (Bogaart et al. 2019), whereas ecosystem types are broader spatial units based on “a complex of organisms and their associated physical environment that are united by similar ecological processes and exhibit substantial differences in their biotic structure and composition to that of other ecosystem types” (Dayaram, Skowno, et al. 2021, page 3). It is well-recognized that ecosystem types can be classified and mapped at multiple scales and approaches (Dayaram, Skowno, et al. 2021, Keith, Ferrer-Paris, et al. 2020). South Africa’s first national classification was termed a habitat classification (Lombard, Strauss, et al. 2004, Sink, Holness, et al. 2012) until ecosystem terminology was adopted in 2018 in line with consistent terminology across terrestrial, freshwater and marine realms (Dayaram, Skowno, et al. 2021, Sink, van der Bank, et al. 2019) and with international approaches (Keith, Ferrer-Paris, et al. 2020). Amongst many nations, marine habitats are mapped to assess their geographical distribution and monitored to track their status and changes over time (Day and Roff 2000, Connor, Allen, et al. 2004, Costello 2009).

Several marine ecosystem classifications are used around the world; some of these relevant at a national scale, whereas others accommodate a broader international scale. These classification systems provide a framework for environmental managers and enable them to effectively identify different marine ecosystems (Connor, Allen, et al. 2004, SANBI and UNEP-WCMC 2016) and to determine whether these ecosystems require protection (Allee, Dethier, et al. 2000, Sink and Atwood 2008, Kirkman, Holness et al. 2019) or more effective conservation management (Costello 2009, Bland, Keith et al. 2017, Kirkman, Holness et al. 2019). Once this information is organized, it can be mapped and reported on to provide decision-makers with the correct tools and knowledge to make informed decisions to facilitate the management and protection of natural resources within the necessary areas (Lange 2012).

The various ecosystem classification schemes rely on different approaches. Many were initially based only on environmental data or expert opinion (Costello 2009), or only on the knowledge of species distributions within a specific area (Heiskanen, Berg, et al. 2016). Since technology and sampling methods have advanced, ecosystem classification schemes should include ecological data where both the biological (including species interactions or associations) and environmental based approaches are considered (McArthur, Brooke, et al. 2010, O'Brien, Stanley, et al. 2021). The complexity of the ecological characteristics of marine ecosystems, environmental variables and topographic settings greatly influence the distribution of benthic species (Danovaro, Company, et al. 2010).

Some classifications provide accessible data online, such as the Global Open Oceans and Deep Sea (GOODS)(Agostini, Arico, et al. 2009) and the ecosystem typologies formed by the International Union for Conservation of Nature (IUCN) (Costello 2009**.** The IUCN specifically divides their scheme into hierarchical sections: intertidal and coastal, marine neritic, oceanic, and deep ocean floor (benthic). In other instances, global databases provide the necessary data to map lists of species against environmental data and are available through organisations such as the Global Biodiversity Information Facility (GBIF) [http://data.gbif.org] (Costello 2009).

Spalding, Fox, et al. (2007) describes the Marine Ecoregions of the World (MEOW) classification, which was one of the first global marine biogeographic classifications. This scheme excludes the pelagic and deep benthic environments beyond 200 m. MEOW’s approach was based on existing global and regional literature, expanding the Longhurst (1998) classification by integrating patterns of endemism and diversity across Large Marine Ecosystems (LMEs), countries’ Exclusive Economic Zones (EEZ) and ecoregions in coastal and shelf waters (Costello 2009, Spalding, Fox, et al. 2007).

The European Nature Information System (EUNIS) is a broad ecosystem classification scheme used in Europe (Davies, Moss, et al. 2004). EUNIS also provides an online application [http://eunis.eea.eu.int/index.jsp] that offers access to publicly available data in a consolidated database (Davies, Moss, et al. 2004). In terms of the marine component, this classification makes use of environmental factors, such as geomorphology, depth zones, substratum types and wave action, to classify the deep-sea ecosystems from several European regions (Davies, Moss, et al. 2004, Howell 2010).

The Marine Habitat Classification for Britain and Ireland scheme describes seabed habitats from the intertidal zone to depths of 200 m (Connor, Allen, et al. 2004) using various techniques to classify marine habitats. Data on benthic habitats are mostly collected by using acoustic mapping technologies (de Juan, Iacono, et al. 2013, Gleason, Reid, et al. 2008) and remote sensing techniques, combined with sediment grabs and dredging to effectively collect information. Sediment type is used as a primary factor in this classification scheme (McBreen, Wilson, et al. 2008), with wave exposure and depth contributing to produce detailed habitat maps within these regions (Connor, Allen, et al. 2004).

In Australia, the Integrated Marine and Coastal Regionalisation of Australia (IMCRA v4.0) (Commonwealth of Australia 2006) is used as a spatial framework for classifying marine bioregions covering the coast to the edge of Australia’s Exclusive Economic Zone, excluding Antarctica, and Heard and Macdonald Islands (Commonwealth of Australia 2005). With a combination of aerial photography and underwater video ground-truthing, the Australian classification scheme uses geomorphological (e.g., sediment type, topography, bathymetry, oceanographic data) and biological attributes to classify marine habitats (Butler et al 2001, Ball et al. 2006, Commonwealth of Australia 2006). In addition, Butler et al. (2017) describes the SeaMap Australia national benthic marine classification scheme for the Australian continental shelf, and a benthic habitat spatial layer that has been made available online through the Australian Ocean Data Network (AODN) [http://www.seamapaustralia.org]. Similarly, Canada makes use of a hierarchical classification comprising biological and geophysical (oceanographic and physiographic) features of the marine environment to classify marine habitat types (Zacharias et al. 1998, Day and Roff 2000, Roff and Taylor 2000) and the United States makes use of the Coastal and Marine Ecological Classification Standard

(CMECS) for identifying marine habitats and biotopes (FGDC 1996), whereas Madden et al. (2005, 2009) has produced a classification specifically for North America.

South African national classification

At a national scale, the South African National Biodiversity Institute (SANBI) leads the National Biodiversity Assessment (NBA) every five to seven years, which includes revising the South African marine ecosystem classification system (Driver, Sink, et al. 2012). The NBA incorporates both terrestrial and aquatic realms, providing ecosystem maps through an online platform called the Biodiversity Geographic Information System (BGIS) [https://www.sanbi.org/biodiversity/science-into-policy-action/biodiversity-information-management/biodiversitygis-bgis/]. The NBA informs various national strategies and frameworks across a range of sectors, such as the National Biodiversity Strategy and Action Plan (NBSAP), the National Biodiversity Framework (NBF) and the National Protected Area Expansion Strategy (NPAES) (Skowno, et al. 2019).

Lombard, Strauss, et al. (2004), conducted the first formal marine bioregion and biozone classification of southern Africa (originally called the National Spatial Biodiversity Assessment (NSBA)), which made use of both biogeographic literature and data-informed expert knowledge. The NSBA provides a comprehensive summary of the state of biodiversity in the country, spanning terrestrial, inland water, estuarine and marine realms (SANBI and UNEP-WCMC 2016). It also reports on the ecosystem threat status and protection levels of all ecosystem types. The area assessed within the marine classification scheme extended 500 m inshore of the coastline and 200 nautical miles offshore (i.e., to the edge of the South African Exclusive Economic Zone (EEZ)). The NSBA became a useful tool in helping users understand the concept and outputs of conservation plans. The first classification and map divided the South African marine environment into nine bioregions. These included five inshore and four offshore bioregions, namely the Namaqua, South-western Cape, Agulhas, Natal, Delagoa, South-west Indian Offshore, West Indian Offshore, Indo-Pacific Offshore and Atlantic Offshore (Lombard, Strauss, et al. 2004, Sink, Holness, et al. 2012).

Subsequently, the 2011 National Biodiversity Assessment (NBA) (Sink, Holness, et al. 2012), included an updated and refined ecosystem map and methodology of the assessment. It also included emphasis on the importance of conservation priorities in South Africa and a strategy for maintaining biodiversity within the country. To classify the national marine ecosystems, the team considered both biological distributions and environmental factors, including depth, substratum type, geology, sediment, wave exposure, terrestrial and benthic-pelagic connectivity and biogeography (Sink, Holness, et al. 2012). The 2011 NBA marine and coastal ecosystem map integrated six newly-defined ecoregions (replacing the previously known bioregions from the 2004 NSBA (Lombard, Strauss, et al. 2004) with their respective ecozones and at a finer scale, their 14 broad ecosystem types (Driver, Sink, et al. 2012, Sink, Holness, et al. 2012). Ecoregions were defined as "areas of relatively homogenous species composition, clearly distinct from adjacent systems" (Spalding, Fox, et al. 2007). The six ecoregions defined in the 2011 NBA were the Benguela, Agulhas, Natal, Delagoa, Southeast Atlantic and Southwest Indian ecoregions. Four of these ecoregions encompass the shore, continental shelves, and shelf edge, specifically the Benguela, Agulhas, Natal, and Delagoa, whereas the deep-sea Atlantic and Southwest Indian ecoregions encompass the upper and lower bathyal zones and the abyss (Sink, Holness, et al. 2012).

The 2011 NBA classified 136 ecosystem types in South African waters (Sink, Holness, et al. 2012). The national marine and coastal habitat classification identified and mapped 62 offshore (deeper than 30 m) benthic habitat types (Sink, Holness, et al. 2012). Many of these offshore habitat types have not yet been surveyed or sampled, preventing quantification of key ecosystem components. This poor knowledge and protection of offshore habitat types (Sink, Holness, et al. 2012) was and still is of great concern, especially as deeper waters of 2 000 - 5 700 m, are known to make up 65% the South African Exclusive Economic Zone (EEZ) (Griffiths, Robinson, et al. 2010).

The most recent National Biodiversity Assessment (NBA) compiled in 2018 by Sink, van der Bank, et al. (2019) further updated and refined the methodology of the assessment, classification, and mapping of the South African marine ecosystem types. The use of additional datasets from various studies ranging from the 1960's to 2018, have been used to improve the ecosystem classification and map. New datasets incorporated in the assessment included bathymetric (de Wet 2013), multi-beam and side-scan sonar data, remote sensing and historical seabed and dredge data, sediment, oceanographic and visual surveys, which further improved the fine-scale mapping and classification of offshore benthic and pelagic ecosystems (Sink, van der Bank, et al. 2019). The new marine ecosystem type map includes 150 marine ecosystem types and contains information on large-scale ecoregions to fine-scale regional patterns, depth, and seabed type (Sink, van der Bank, et al. 2019). A total of six ecoregions, namely the Southern Benguela, Agulhas, Delagoa, Natal, Southeast Atlantic Deep Ocean, and Southwest Indian Deep Ocean were assigned to southern Africa's marine realm (Fig. 1.1). Identifying key drivers of marine biodiversity patterns within these ecoregions was identified as a priority for the improvement of the classification and mapping of marine ecosystem types.

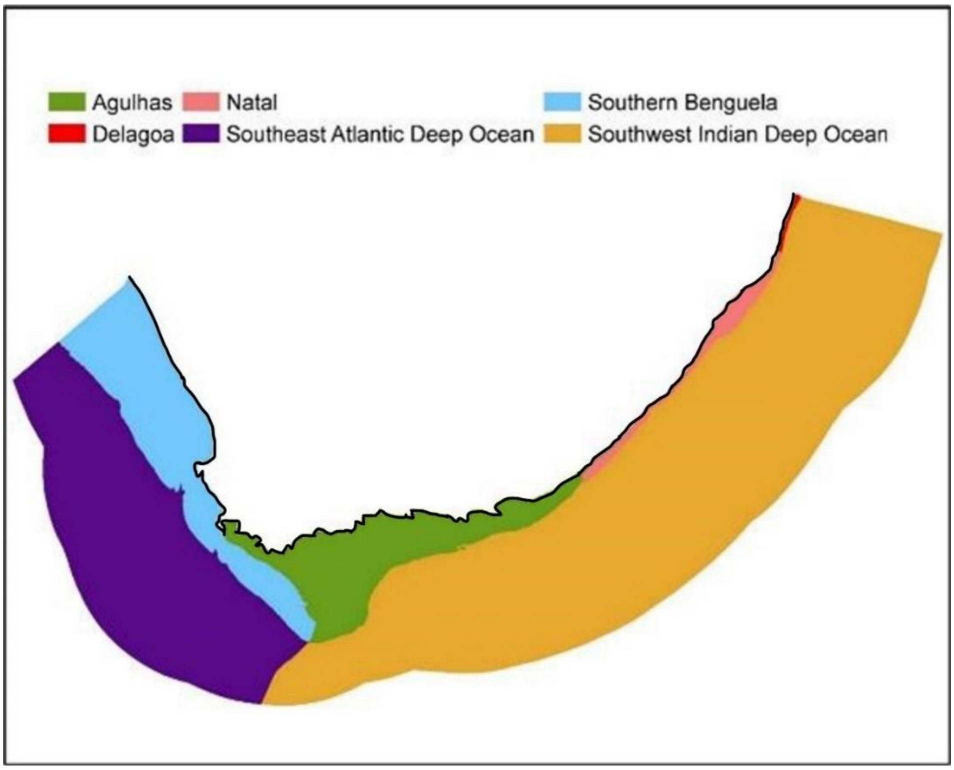

Figure 1.1. The marine ecoregions of South Africa, derived by the National Biodiversity Assessment 2018 (Sink, van der Bank, et al. 2019).

Challenges and solutions to collecting data

Deep-water research presents several challenges that limit the capacity to conduct research investigating deep-sea benthic ecology. It is understood that with increasing depths and distance from the coast, come greater challenges, specifically in biological sampling (Griffiths 2005, Griffiths, Robinson, et al. 2010). With limited taxonomic expertise, funding, and technical capacity (Anderson and Hulley 2000, Griffiths, Robinson, et al. 2010, Sink, van der Bank, et al. 2019) to sample in the deep sea, we are limited in assessing offshore biodiversity and measuring changes within deep-sea ecosystems on a long-term scale (Gage and Tyler 1991). With less sampling taking place in deeper waters, there is inadequate knowledge of deep-sea biodiversity (Griffiths 2005), particularly epifaunal communities along the deeper continental shelf and slope, especially in rocky areas. Restricted knowledge and understanding of these deep-sea ecosystems make it difficult to manage these areas.

With the intention of advancing our baseline knowledge of these deep-sea areas, there is a need to assess, classify and map marine ecosystems along the continental shelf and shelf-edge regions of South Africa and with that develop the technical capacity within offshore marine science and research (Sink, Holness, et al. 2012, Sink, van der Bank, et al. 2019). As research advances, representative biological and environmental data will be collected from these deep-sea areas and continue to inform the respective national and global classification systems. Not only will this information assist in spatially managing marine ecosystems, but also with designing a representative MPA network for these deep-sea environments (Trebilco, Halpern, et al. 2011) and enhancing offshore protection and conservation, to prevent further degradation of critically endangered and endangered marine ecosystem types (Armstrong, Foley, et al. 2012, Sink, Holness, et al. 2012).

Numerous approaches have traditionally been used to assess and survey offshore marine benthic communities along the seafloor, such as divers, still cameras, submersibles, benthic grabs, sediment cores, sleds, dredges, and bottom-trawling (Koslow, Gowlett-Holmes, et al. 2001, Ramírez-Llodra and Billett 2006). Many researchers use a combination of these methods to collect both physical and biological information from the environment being studied. Depending on conditions, deployment of these marine instruments is not always feasible at great depths, or in strong currents, and some equipment may require recovery ropes, which limits vessel manoeuvrability and seabed contact (Jamieson, Boorman, et al. 2013). Traditional methods of deep-sea sampling, such as dredges and trawls, are mostly not suitable for sampling complex deep-water coral reefs or hard-substrate communities, as the equipment is likely to damage these ecosystems or become damaged itself (Heyns, Bernard, et al. 2016).

Although some of these methods are advantageous in terms of collecting physical samples of benthic fauna, which facilitates taxonomy and genetic studies, they are not considered an environmentally-friendly and sustainable approach of sampling marine offshore areas and generally also provide limited spatial coverage (Davies, Roberts, et al. 2007). Advances in deep-sea technology and sampling equipment provide new options to apply and expand on traditional collection methods to allow observations of benthic fauna *in situ*. Through camera-based methods, visual surveys provide permanent records of *in situ* data that can be processed for different research questions over time and assist with mapping benthic ecosystems and habitats (Bicknell, Godley, et al. 2016, Howell 2010, Jones, Bett, et al. 2009, Ramírez-Llodra and Billett 2006). These methods also become quite costly compared to some of the traditional methods, as these *in situ* observations require research vessel time and expensive technologies to support these systems in extreme deep-sea depth and pressure conditions (Long, Blicher, et al. 2021) and to provide appropriate scaling of the footage (Bicknell, Godley, et al. 2016). Some of these new camera-based options include Remotely Operated Vehicles (ROV), Baited Remote Underwater Video (BRUV), Stereo-BRUVs and towed-camera surveys.

The application of underwater imagery to quantify *in-situ* benthic biodiversity has grown considerably over the past decade (Bernard, Götz, et al. 2014, Solan, Germano, et al. 2003) and is also less destructive to epifauna than, for example, trawling or dredging. The advantage of using camera tools is that they allow researchers to survey within isolated and difficult to access environments, that usually go well beyond the normal scuba diving range (Heyns, Bernard, et al. 2016). Additionally, these systems create more opportunities for researchers to study the behaviour of benthic organisms, as well as to examine species interactions and ecosystem functioning within these environments (Bicknell, Godley, et al. 2016). For example, an ROV is controlled from aboard an anchored vessel and has a tethered cord connecting itself to the surface unit controls. Some ROV's have manipulator arms that can be used to collect physical specimens, which other cameras do not usually have. This method is useful in providing supplementary information about the surrounding habitat, as this instrument allows a broader scope of seafloor observation (Ramírez-Llodra and Billett 2006). However, the identification of benthic organisms is usually constrained by the quality and clarity of the imagery collected by ROV, which can occasionally be reduced due to fluctuations in environmental conditions as the ROV moves around (Makwela, Kerwath, et al. 2016, Trenkel, Francis, et al. 2004).

Although these applications can enable access to formerly inaccessible environments (Monk, Barrett, et al. 2016, Williams, Pizarro, et al. 2012), some of them are not as time or cost efficient as others. For instance, ROVs and towed-camera surveys are both non-extractive, but towed-cameras are preferred to sample benthic biodiversity, as they are more cost-effective than ROVs (Sheehan, Stevens, et al. 2010, Williams, Althaus, et al. 2015). With a similar set up as the ROV, except for the camera technician not having complete control over the camera's movement and direction of movement, including the lack of manipulator arms to collect specimens, towed cameras still have control of when and where they want to capture images (either still photographs or video) along a transect. Like the ROV, the towed camera has an oblique view, making it possible to capture a large area of the seabed and the fauna living on the seafloor (Bowden and Jones 2016, Durden, Schoening, et al. 2016). This supports the description of seafloor attributes, the distribution of benthic epifaunal assemblages and essentially habitat and ecosystem classification across extensive transects along the seafloor (Jamieson, Boorman, et al. 2013).

1.2 Conservation targets

To conserve, manage and sustainably use marine biodiversity, the Convention on Biological Diversity (CBD) has recommended each of the signatories to protect at least 10% of their national coastal and marine areas by 2020 using conservation targets (CBD 2011, Metcalfe, Delavenne, et al. 2013). A conservation target is the proportion of a biodiversity feature that should be conserved (Rondinini and Chiozza 2010) within a particular marine environment. Different marine ecosystem types may require different conservation targets. Various stakeholders and experts utilise ecological marine datasets collected from consistent biodiversity assessments and monitoring initiatives to determine conservation targets (Rondinini and Chiozza 2010). Additionally, biodiversity surrogates, either based on known or predicted distributions of species and biologically-based ecosystem types, may be utilized for conservation planning (Porter, Sink, et al. 2011, Possingham, Grantham, et al. 2007).

Amongst several approaches for setting conservation targets, Rondinini and Chiozza (2010) state that the approach selection should be based on data availability, data quality and the type of biodiversity goal. Some of these approaches use fixed targets, heuristic targets, targets based on empirical models, or species-area relationships, and they each serve specific outcomes, whether for species representation, ecosystem function or species persistence

(Metcalfe, Delavenne, et al. 2013, Porter, Sink, et al. 2011, Rondinini and Chiozza 2010). A comparison of the advantages and disadvantages of these target-setting approaches is given by Porter, Sink, et al. (2011). However, for the sake of maximising the effectiveness of setting targets, a combination of these methods can be used simultaneously (Harris, Nel, et al. 2014, Porter, Sink, et al. 2011, Rondinini and Chiozza 2010).

When the appropriate data are available and sufficient sampling effort is achieved, the use of Species-Area Relationships (SAR) is considered one of the more reliable approaches for marine ecosystems (Porter, Sink, et al. 2011). Although this approach is sensitive to poor data and does not account for persistence, it does account for variability between different types of ecosystems and is usually a more defendable scientific approach (Porter, Sink, et al. 2011). Species-area relationships determine the percentage-area targets for the designated ecosystem types and demonstrate the number of species that rely on the area sampled (Connor and McCoy 2001, Metcalfe, Delavenne, et al. 2013).

Since many species are not constrained to a single habitat type, and may be distributed randomly within an ecosystem, it can be challenging to set ecosystem-specific conservation targets. In these cases, it would be best to secure a larger area to be conserved, as it would be unlikely that the position of every species in the area sampled would be known (Desmet and Cowling 2004). Furthermore, low sampling effort within the sampling area may strongly affect the outcome of setting targets using the SARs method (Desmet and Cowling 2004, Metcalfe, Delavenne, et al. 2013, Rondinini and Chiozza 2010).

Similar to Desmet and Cowling (2004) producing terrestrial targets using species-area curves to determine ecosystem representation targets, the United Kingdom (Rondinini 2011) and the United States of America (Heppell, Barth, et al. 2008) used the same method of setting conservation targets for marine habitats. Considering the assumptions of the species-area relationship approach (Rondinini 2011), you can only conserve 100% of the species present in a habitat or ecosystem type if the entire extent of the type has been protected. With the intention of representing 75 – 80% of the species within a marine ecosystem type, Rondinini (2011) states that, on average, 20 - 30% of a habitat would need to be protected. In terms of conserving deep-sea benthic habitats (EUNIS Level 3 deep-sea bed and deep-sea mixed substrata habitat types (A6 and A6.2)), using species area relationships, Rondinini (2011) shows that 11 - 20% of the habitat would be expected to represent 80% of its species.

The task of setting conservation targets is still in its developmental stages and currently, South Africa uses the standard 20% target for all marine ecosystem types (Sink, Holness, et al. 2012). These targets align with the current ecosystem threat status, which is mostly guided by the global benchmark for ecosystem risk assessment (Bland, Keith, et al. 2017), the IUCN Red List of Ecosystems (RLE), to influence government policy and decision-making (Botts, Skowno, et al. 2020), and the protection levels of these ecosystem types (Sink, Holness, et al. 2012). Once assessed, an effective plan can be executed to achieve the desired conservation outcomes of representation and persistence for these marine ecosystems (Sink, Holness, et al. 2012, Sink, van der Bank, et al. 2019). Developing ecosystem type-specific conservation targets is an improvement over the standard 20% target in South Africa's offshore marine environment, providing more refined information, particularly where the required data are available for specific habitat or ecosystem types (Metcalfe, Delavenne, et al. 2013).

1.3 Study area

Due to South Africa's geographical position, between latitudes 22° and 35°S, and longitudes 16° and 33°E, and bordered by the Atlantic, Southern, and Indian Oceans, the marine environment has a diverse range of oceanographic, topographical, and geological characteristics that influence marine species diversity and endemism (Sink, van der Bank, et al. 2019). South Africa's coastline extends 3 650 km from the Namibian border on the west coast to the Mozambique border on the east coast. The area within South Africa's Exclusive Economic Zone (EEZ) is 1.1 million km^2 (Sink, van der Bank, et al. 2019) and reaches a maximum depth of 5 700 m, with more than 65% of the EEZ occurring deeper than 2000 m (Griffiths, Robinson, et al. 2010). Although South Africa's coast and shallow waters have been relatively well sampled (Griffiths, Robinson, et al. 2010), the adjacent deep-sea environment, especially that beyond 1000 m, has been poorly explored (Griffiths, Robinson, et al. 2010).

The Agulhas ecoregion

On the south coast of South Africa, the Agulhas ecoregion extends along the continental shelf and shelf edge from Cape Point in the Western Cape to the Mbashe River in the Eastern Cape

(Fig.1.2) (Sink, van der Bank, et al. 2019). Its geographical position lies between the cooler Benguela and warmer Agulhas Currents, while being exposed to three different water masses, namely, the Atlantic, Indian and Southern Oceans. In southern Africa, offshore ecosystems are less well studied than their inshore counterparts and the Agulhas ecoregion has received less biodiversity research attention than the southern Benguela and Natal ecoregions (Sink, Holness, et al. 2012). Due to the influence of the Benguela and Agulhas Currents mixing in the Agulhas ecoregion, it is important to understand the ecological functioning of the diverse ecosystem types occurring here (Sink, Holness, et al. 2012), as they present unique conditions and topographic features compared to the Southern Benguela and Natal ecoregions (Fig. 1.1).

The diverse range of environmental conditions in this warm temperate Agulhas ecoregion hosts a vast array of marine benthic life and endemic species (Atkinson and Sink 2018, Awad, Griffiths, et al. 2002, Griffiths and Robinson 2016). Some of these species are of high economic value to commercial fisheries operating in this region, such as hake, sole, deep-water rock lobster, pilchard, anchovy, and squid (Sink, van der Bank, et al. 2019). The ecosystems of the Agulhas shelf and slope provide important spawning and nursery areas for some of these species (Atkinson and Sink 2018, Griffiths and Robinson 2016). Concern has risen with the recent intensification of fishing in these areas (Sink, van der Bank, et al. 2019), especially as some of the ecosystems located within this region are now known to host Vulnerable Marine Ecosystem (VME) indicator species, which include many hard and soft corals and habitat forming sponges and bryozoans (Samaai, Sink, et al. 2020, Sink, van der Bank, et al. 2019). An increased research focus within this ecoregion would provide valuable new knowledge and could guide implementation of long-term monitoring of both biodiversity and oceanographic patterns within this region.

Figure 1.2. The study area with relevant features within the Agulhas ecoregion, southern coast of South Africa (Image taken from Google Earth, 2021).

The Agulhas Current is a powerful, complex current originating from the Mozambique Channel (de Ruijter, Ridderinkhof, et al. 2002) with a major contribution from the East Madagascar Current and an even greater contribution from the recirculation in the southwest Indian Ocean sub-gyre (Lutjeharms 2006b, Stramma and Lutjeharms 1997). Flowing down the east coast of southern Africa from 27 - 40°S (Gordon 1986), the current collides with the very narrow continental shelf on the East coast of South Africa, resulting in extremely strong and rapidly changing gradients of ocean temperature, salinity and current speed (Malan, Backeberg, et al. 2018). Moving in a south-westerly direction, this warm western boundary current reaches a maximum speed of 200 $cm \cdot s^{-1}$ (Boebel, Duncombe Rae, et al. 1998), transporting large volumes of water. It flows past East London to Gqeberha (previously known as Port Elizabeth) along the eastern extremes of the Agulhas Bank, where the continental shelf starts to widen, thereby establishing the triangular shape of the Bank (Jackson, Rainville, et al. 2012, Lutjeharms 2006a, Lutjeharms, Valentine, et al. 2000). This portion of the Agulhas

Bank is the widest part of the continental shelf off southern Africa, reaching 250 km offshore (Jackson, Rainville, et al. 2012).

The Agulhas Bank is positioned in a very unique location where the oceanography of the south coast of South Africa is quite complex and is directly influenced by the combination of both the Indian and Atlantic Oceans (Jackson, Rainville, et al. 2012). Upwelled bottom waters of the Agulhas Current supply nutrients onto the shelf, therefore influencing the ecosystems located here and driving the patterns observed in biological assemblages (Malan, Backeberg, et al. 2018). The resulting productivity on the Agulhas Bank has been identified as an important economic commodity to the commercial fisheries mentioned earlier (Hutchings 1994). However, trawl fisheries that are active around the tip of the Agulhas Bank report that the eastern edge of the Agulhas shelf edge presents several patches of hard grounds that hamper their trawling activities (Sink, Wilkinson, et al. 2012).

Along the western part of the outer shelf and shelf edge, an offshore ground, called Browns Bank, extends from Cape Point to the southern tip of the Agulhas Bank. Since the 1930s, fishing became very popular within and around this area (Japp, Sims, et al. 1994). In the 1990s, this area became very important to the offshore trawl fishing fleets, as it was a productive area that managed to sustain more than half of the industry (Japp, Sims, et al. 1994). Fishing grounds were further expanded eastwards on the Agulhas Bank due to popular demand by the fisheries (Sink, Wilkinson, et al. 2012).

After the declaration of the Exclusive Economic Zone in 1978, restrictions were implemented for inshore trawling practises, where fishers were only allowed to fish in areas shallower than 110 m. The offshore trawlers were constrained to a region deeper than 110 m between Cape Agulhas and Knysna (Japp, Sims, et al. 1994). Sink, Wilkinson, et al. (2012) reports that these areas encompassed sandy shelf and hard grounds, hosting stylasterine corals, black corals, and gorgonians. In 1978 fishermen also reported that just offshore of Mossel Bay, reaching a depth of up to 130 m, there were areas characterised by sand and shale combined with occasional rocky outcrops (Sink, Wilkinson, et al. 2012). Between the 1970s and 1990s, it was reported that the so called 'Chalk-line region' offshore of Gqeberha was characterised by sandy, gravel and hard grounds along the outer shelf and shelf edge (Sink, Wilkinson, et al. 2012), comprised of coarse sand, coral rubble, and shell fragments.

Recent marine benthic surveys done in South Africa

Although offshore research in South Africa has increased in the last 10 years (Sink, can der Bank, et al. 2019), a review by Griffiths et al. (2010) revealed that 83% of benthic biological samples were taken in the 0 – 100 m depth zone and only 2% in water deeper than 1 000 m in South African waters spanning from the west to the east coast. Intertidal and shallow nearshore waters have been widely sampled, primarily by the University of Cape Town Ecological Survey, with a focus on coastal fish, algae and invertebrate distribution patterns (Griffiths, Robinson, et al. 2010). A bathymetric dataset produced by de Wet (2013) helped improve the bathymetry layers for South Africa's marine environment (de Wet and Compton 2021). From a research trawl survey conducted using the Norwegian research vessel Dr Fridtjof Nansen in 2007 between Cape Agulhas and the South African border with Namibia, Lange and Griffiths (2014) analysed offshore benthic epifaunal biodiversity patterns along the west coast of South Africa, from 85 - 700 m depth and identified six faunal communities which were mainly driven by depth and had their greatest abundance in the 200 – 299 m depth zone. Based on the 2011 and 2017 Department of Forestry, Fisheries and the Environment (DFFE) demersal research trawl survey data, Shah (2018) explored epifaunal abundance and biomass patterns between 36 - 899 m depth along the West and South Coast. From 2011 - 2018, the South African Environmental Observation Network (SAEON) invertebrate monitoring programme, in collaboration with DFFE and the South African National Biodiversity Institute (SANBI), identified 410 offshore invertebrate species and collated this information into the 'Field Guide to the Offshore Marine Invertebrates of South Africa' (Atkinson and Sink 2018). Using these data, along with geological and oceanographic data, the 2018 National Biodiversity Assessment (NBA) produced an ecosystem classification and map (Sink, van der Bank, et al. 2019).

Through ongoing research surveys of these offshore areas, we continue to build knowledge of the epifaunal community compositions and the main environmental drivers occurring along these regions on the South African continental shelf. Using this information, we can assess and classify the various ecosystem types and determine which benthic species may be more vulnerable to various human pressures, such as bottom trawling, climate change, etc. and set quantitative conservation targets with the aim of conserving these marine ecosystem types. This project forms part of a larger, multidisciplinary project that aims to develop offshore research capacity and knowledge to support improved marine management of the outer shelf, shelf edge and upper bathyal ecosystems of the Agulhas ecoregion.

1.4 Aims and objectives

The overarching aim of this study is to investigate epifaunal communities in the shelf-slope transition of the Agulhas ecoregion to support marine ecosystem classification, mapping and management. Using recently-collected *in-situ* biological data, in conjunction with data for physical variables, including substratum type, depth, temperature, salinity, conductivity, distance to shelf edge and shore, slope and current strength, biodiversity patterns will be explored (Table 1). Findings from this study will be compared with an existing ecosystem classification and map for the region (Sink, van der Bank, et al. 2019) to improve understanding of patterns observed. In addition, conservation targets for select outer shelf and slope ecosystems of the Agulhas ecoregion will be determined (Table 1).

Table 1.1. The main objectives and research questions for this study.

Objectives	Research Questions
1. Classify marine epifaunal communities within the outer shelf to slope of the Agulhas ecoregion	What are the patterns in benthic epifaunal communities across the Agulhas outer shelf and slope?
2. Identify the species composition of these epifaunal communities	What are the characterising and distinguishing species that define the communities within this region?
3. Identify potential physical drivers of the observed patterns in the epifaunal communities	What are the abiotic variables that may explain observed biodiversity patterns?
4. Determine conservation targets for outer shelf and slope ecosystem types of the Agulhas ecoregion	What are the range of plausible conservation targets for these ecosystem types?

1.5 Dissertation overview

This dissertation consists of four chapters, the contents of which are outlined below.

Chapter 1: General introduction and literature review

Chapter 2: Methods

This chapter details the sampling methods and equipment used in the field, data collection and image processing methods, and the analytical methods used to perform multivariate statistical analyses on the data.

Chapter 3: Results

3.1 Marine ecosystem classification along the Agulhas ecoregion

This component focuses on the analysis of the benthic imagery collected to quantify epifaunal communities across various substratum types, depth zones and oceanographic variables. The existing classification and map are tested using epifaunal abundance data in combination with various environmental variables (identified as potential drivers of these communities), such as depth, substratum type, temperature, longitude, salinity, conductivity, trawling intensity and current strength. Previously assigned offshore ecosystem types from the most recent national marine ecosystem map developed in 2018 (Sink *et al.* 2019) are assessed and compared with the new information collected. A description of the key characteristic and distinguishing epifaunal species per community identified are provided and proposed as "ecosystems" for the Agulhas ecoregion.

3.2 Setting conservation targets along the Agulhas ecoregion

This component determines the first quantitative conservation targets for three selected ecosystems identified in the Agulhas ecoregion. The proportion of each ecosystem type that should be preserved in order to represent 80% of the benthic epifaunal species within that ecosystem type are determined. These targets are used to assess ecosystem protection levels and form a baseline for future marine spatial planning processes within the Agulhas ecoregion.

Chapter 4: Discussion and recommendations for future work

The final chapter summarises the overall findings from the study and discusses the importance and limitations of the study. It concludes with suggestions and recommendations for future work.

Chapter 2: Methods

2.1 Study area

This study focusses on the Agulhas ecoregion, spanning the area along the continental shelf edge of southern Africa from the tip of the Agulhas Bank in the west to offshore of the Kei River mouth in the east (36°S, 19°E to 33°S, 28°E, Fig. 2.1). Seabed imagery from a total of 29 sites was analysed with depths ranging from 120 - 700 m. A total area of 1745.84 m^2 was surveyed (see site overview in Appendix, Table A1 and Figure A1) during September-October 2016, as part of the African Coelacanth Ecosystem Programme (ACEP) Deep Secrets Cruise.

2.2 Visual survey

A sampling method was required that would enable sampling heterogenous seabed terrains, simultaneously preserving species-substrate relationships. These terrains included cold-water coral mounds, sand, muds, gravel, hardgrounds and submarine canyons. For this component of the project, the most effective technique for deep-sea sampling was to use image analysis. Deep-water towed cameras (Howell 2010, Narayanaswamy, Hughes, et al. 2013) were used to collect the first benthic imagery from this region. Although video footage has some advantages, still imagery was favoured for data extraction, as the imagery provided a higher resolution than the video footage, making it easier to identify the benthic organisms accurately. Two identical SkiMonkey towed benthic camera systems (Fig. 2.2) were used to collect seabed imagery for this project up to a depth of 700 m.

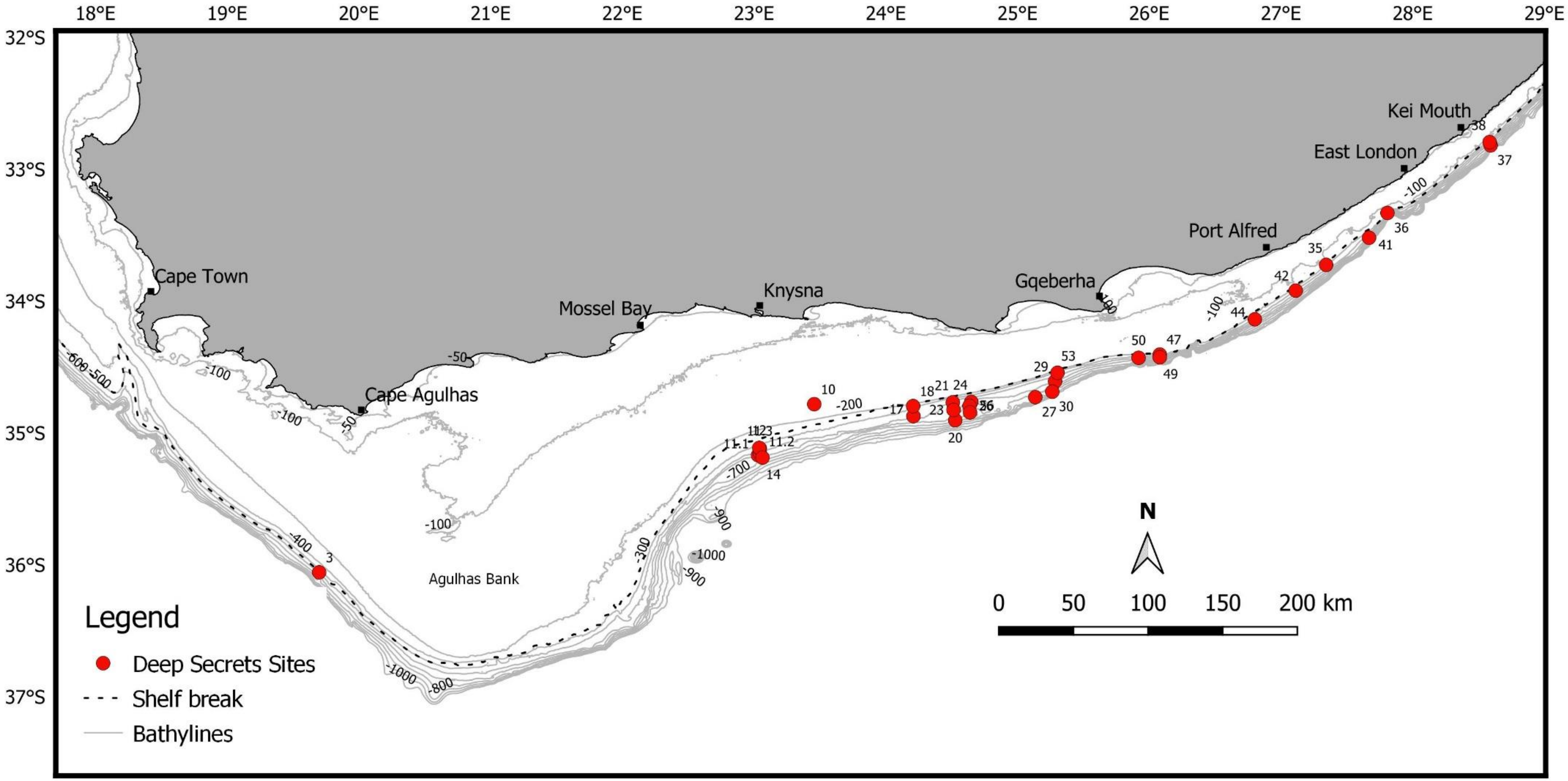

Figure 2.1. Location of the study area along the continental shelf edge of the southern coast of South Africa indicating the position of the 29 sites surveyed during the ACEP Deep Secrets cruise. The shelf break line was derived from the NBA 2018 (Sink, van der Bank, et al. 2019) and the bathylines were derived from de Wet (2013).

The SkiMonkey camera systems, designed and manufactured by Sea Technology Services Pty Ltd, are towed deep-sea camera systems intended for use in benthic environments. The camera used during the Deep Secrets Cruise was a Canon 550D DSLR with two lights, attached onto a heavy steel frame mounted on skis (Fig. 2). The SkiMonkey unit was also fitted with three lasers projecting onto the seabed to enable scaling of imagery. An SBE 37-SI MicroCAT C-T (conductivity and temperature) sensor was attached to the unit providing physical variable data for each transect. The SkiMonkey III camera was connected to the ship data core conducting copper cable, providing live view of the seabed to the scientists onboard.

Figure 2.2. The SkiMonkey towed benthic camera just before deployment.

At each benthic survey site, the camera system was towed from the aft winch of the vessel at speeds of 0.5-2 knots for 20 minutes. The first 10 minutes were allocated to capturing still images and the second 10 minutes were used for capturing video footage during each transect. Approximately 150 still images were captured along each transect, from which a minimum of 25 and a maximum of 30 suitable images (in focus and at an appropriate angle of 35°, for quantitative analysis) were randomly selected from the pool of suitable available images as replicate samples from each site. Where 30 suitable still images were not available, we limited sites utilised to those with a minimum of 25 suitable images resulting in the 29 sites in this current study. A study by Adams (2017), using the same towed-camera system, established that 25 – 30 good quality images with the seabed, lasers and benthic species being in focus, captured per site reached the peak of the curve for species accumulation, suggesting that this number of images per site are suitable for sampling heterogenous seabed habitats. On soft, level seabed, the camera was towed along the seabed, but a 'drop-hop approach' (where the camera was raised in the water column and lowered onto the seabed when safe to do so, similar to a drop camera) was used in rockier terrain and that of higher relief. Occasionally the camera was lifted to avoid rocky features, or the dive was terminated in cases of extreme high-profile topography.

2.3 Image processing

In preparation for the image analysis, an attribute table was collated, comprising all morphospecies observed across all images with their respective taxonomic attributes (Phylum, Class, etc.) listed. Identification of most of the benthic invertebrate taxa were confirmed using the Field Guide to the Offshore Marine Invertebrates of South Africa (Atkinson and Sink 2018), a comprehensive guide titled Soft Corals and Sea Fans (Fabricius and Alderslade 2001) and Two Oceans: A Guide to Marine Life of Southern Africa, Second Edition (Branch, Griffiths, et al. 2010) and Fourth Edition (Branch, Branch, et al. 2016). Several invertebrate taxonomists and experts were also consulted to assist with the identification of the remaining unidentified benthic taxa (see Acknowledgements).

The attribute table was imported into the image analysis software, TransectMeasure© (SeaGIS), providing the correct annotations to be assigned to species visible in each image. The digital images were imported according to the requirements of the software to provide 25 - 30 non-overlapping image frames per site. A customised version of TransectMeasure© enabled the area processed in each image to be quantified using the position of the three lasers. An in-water calibration file was generated prior to the survey by fitting a plane to the three measured laser points, which could then generate a virtual quadrat of known dimensions within the software. This calibration file was saved and loaded into the software to aid the calibration of each image analysed in this study (Fig. 2.3a). The three laser points projected from the benthic camera in each frame were used to quantify the area of seabed processed using the customised calibration formula in TransectMeasure©.

Once the digital images were imported into TransectMeasure© and calibrated using the laser scaling, an "Interest area" (shown as a pink line in Fig. 2.3a) was generated around the lasers. Following this, an “Area of Measurement” (shown as a blue line in Fig. 2.3b) was manually drawn on the image, capturing the area of the image that was in focus (ranging between 0.38 and 9.19 m^2 with an average of 2.04 m^2 per image quadrat), including as much species diversity as possible.

Prior to assigning a dot grid overlay on each image, species accumulation curves were generated using the statistical software PRIMER v6 (Clarke and Gorley 2006) to assess the cumulative species estimation. Species accumulation curves were generated using the epifaunal abundance data collected from two sites, one rocky site (site 27) and one finer sediment site (site 47) to represent the range of substratum types available. This information was used to inform selection of an appropriate number of dots in a grid overlay. Two scenarios were tested across different habitat types, one with 400 dots and another with 600 dots per image. The results showed that using 400 dots overlaid on an image captured sufficient species per image across the different habitat types and that adding the extra 200 dots did not improve the species accumulation substantially. Thus, a 20x20 dot grid (i.e., 400 dots) was overlaid on each image to process the abundance of epifaunal taxa in the collected imagery (Fig. 2.3b). Only organisms that fell under the dots of the grid were identified and counted. Organisms that covered multiple dots were only counted once, including colonial organisms. In total, 855 images were processed from 29 sites.

All of the species abundance values extracted from the Area of Measurement within each image were standardised to per m^2 values by using the formula below:

$$\frac{N}{y}$$

With N representing the abundance data per species per image, and y representing the area measured per quadrat image (m^2). The scaled species abundance data per image were used in the statistical analysis.

Collection and categorization of environmental variables

Fourteen environmental variables were collected and selected for the statistical analysis. Three variables were assigned at the quadrat-level. They were substratum type, Particulate Organic Matter (POM) presence and coral rubble presence. The remaining 11 variables were assigned at the site-level as the initial bottom measurement was extracted for each of the variables. These were start depth, bottom temperature, conductivity, salinity, longitude, latitude, distance to shore, distance to shelf break, slope, current strength, and trawling intensity (Swept Area Ratio). Although Bio-ORACLE datasets were considered, the scale of data were either too coarse or they were not verified for this region and in some cases, data were missing for the area of interest. Therefore, further variables were not available for this study.

I. Substratum types

Field constraints enabled sediment samples to be collected with a van Veen Grab (0.2 m^2) sampler from only 13 of the 29 sites. The winch cable was used to lift the grab system overboard and was lowered below the water surface to the seabed, at a speed that ensured no jerking or premature triggering. Once the grab was back onboard, one 250 g sample of sediment was collected from each of the sites and was frozen at -20°C. The remaining sediment was sieved using different sizes of mesh to separate infauna by size for other studies. The collected sediment samples were taken back to the lab and were processed by a student from South African Environmental Observation Network (SAEON) for sediment particle grain size (based on the Folk and Ward method; Folk 1954, Folk and Ward 1957) using a sediment shaker. Including the Wentworth Grading system (Wentworth 1922), the results were used as a guide while the substratum types of all 29 sites were visually categorised. The four different categories assigned to the substratum types were: a) fine to medium sand (0.0625 – 0.35 mm), b) medium to coarse sand (0.35 – 2 mm), c) pebbles and medium sand mixed (2 – 64 mm) and d) rock and sand mixed (> 64 mm), as shown in Figure 2.4.

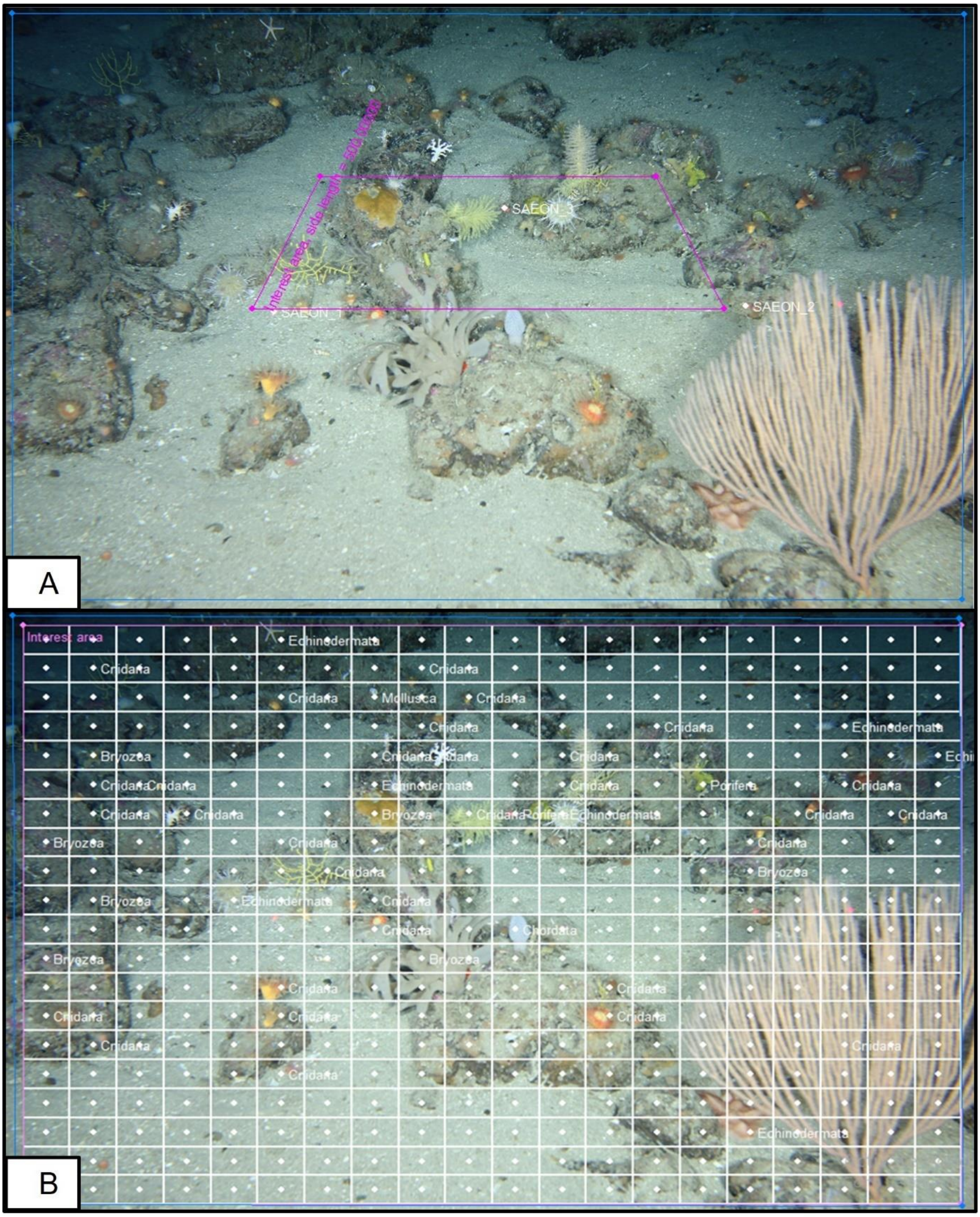

Figure 2.3. Example of an image captured by the SkiMonkey camera imported into TransectMeasure© software, A) laser points are used to calibrate the area producing the Interest Area (pink square) while the Area of Measurement (blue square) is defined by the user. B) Same image with 20x20 dot grid overlay. Only one species per grid cell under the dot was identified and quantified within the Area of Measurement (abundance per 1 m^2).

Figure 2.4. Photographs showing images classified into each of the four different substratum types recognised: (A) fine to medium sand, (B) medium to coarse sand, (C) pebbles and medium sand mixed and (D) rock and sand mixed.

II. Presence of Particulate Organic Matter and coral rubble

In this study, the presence or absence of Particulate Organic Matter (POM) refers to being with or without a layer of visible POM on the surface of the substratum. The presence or absence of POM and coral rubble were visually categorized per quadrat image and recorded using the following scoring system, POM: score of 0 = no POM, 1= presence of POM, and coral rubble: score of 0 = no coral rubble, 1= presence of coral rubble.

III. Temperature, conductivity and salinity

Measurements for temperature, conductivity and salinity were collected at each site and were taken from the SBE 37-SI MicroCAT C-T (conductivity and temperature) sensor which was attached to the SkiMonkey towed camera.

IV. Distance to shore and distance to shelf break

In QGIS, the distance to shore was measured between each site and the shoreline border. Additionally, distance to the shelf break was calculated using the Shelf break line layer shapefile, which was derived from the NBA 2018 (Sink, van der Bank, et al. 2019).

V. Slope and current speed

Actual measurements for slope and current speed were absent for the selected sites, and for this reason expert-based knowledge (Sink 2019) was used to categorize slope and current speed, based on what was evident within the footage and experienced on board the Deep Secrets cruise. Though global scale datasets are available online, investigations showed that these were too coarse a scale for the region of study. Slope was categorized into four types: Flat, Gentle, Steep and Very Steep. Current Speed was categorized into three grades: Low, Medium and High.

VI. Trawling intensity

Using commercial trawl log data from 2005 to 2018 (Currie, Atkinson, et al. 2021), trawling intensity values (as a Swept-Area Ratio) were derived for each site from the spatial layer within the Geographic Information System software, Quantum Geographic Information System (QGIS) version 3.16.6 (QGIS Development Team (2020), Open-Source Geospatial Foundation Project (http://qgis.osgeo.org). Where there was no value, it was assumed that no trawling had taken place in that area. The Swept Area Ratio is a metric of trawling intensity. Amoroso, Pitcher, et al. (2018) reports that Swept Area Ratio is defined as the total area swept by trawl gear over a defined time period (usually one year) divided by the total seabed area at a defined spatial scale (ranging from grid cell to region).

VII. Depth zones

Based on the National Biodiversity Assessment 2018 (Sink, van der Bank, et al. 2019), depth boundaries were assigned to differentiate the various depth zones along the continental shelf (Fig. 2.5). Using these boundaries, two of the four finer scale depth zones along the shelf were sampled in this study: the outer shelf (100 - 150 m) and the shelf edge (depth band usually varies along the south coast, but follows approximately the 200 - 500 m contour). One of the deeper ocean depth zones was also sampled in the current study, the Upper Slope (500 - 1000 m).

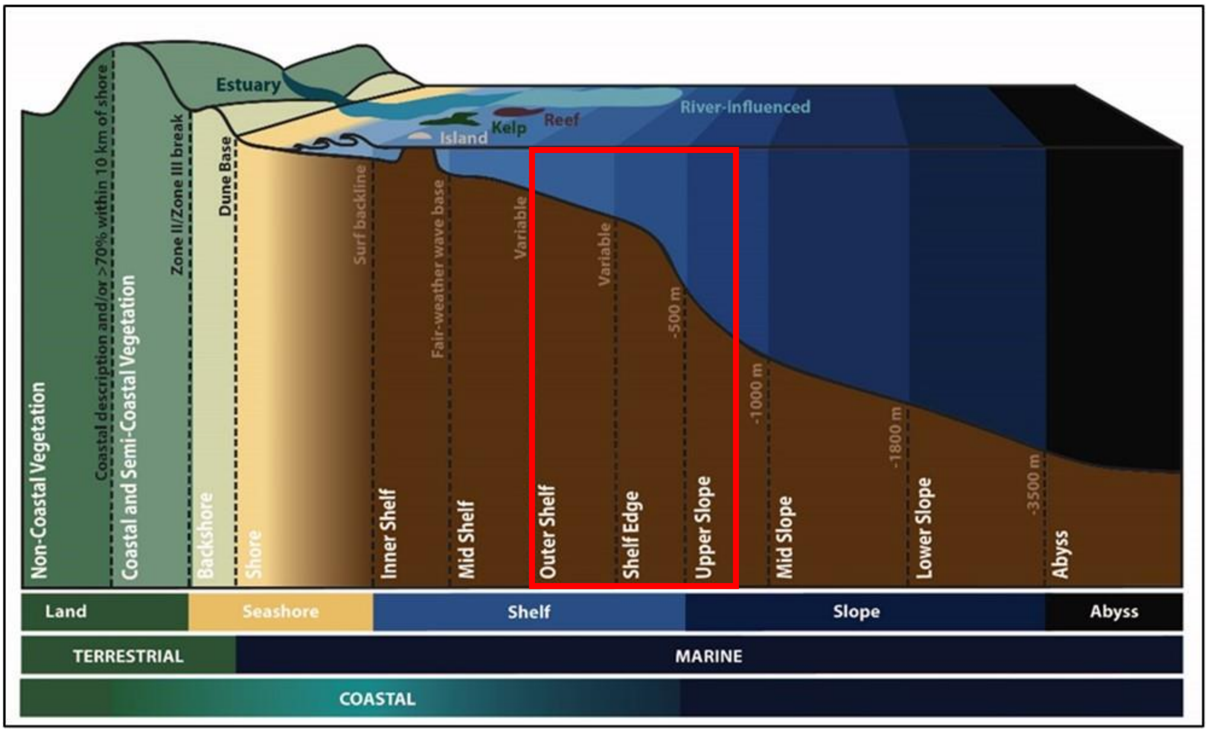

Figure 2.5. Depth zones sampled in this study are highlighted within the red rectangle. Adapted image used with permission from the National Biodiversity Assessment 2018 (Sink, van der Bank, et al. 2019).

VIII. Ecosystem types

Each site sampled within this study was classified into the NBA 2018 ecosystem types (Sink, van der Bank, et al. 2019). Of the 150 marine ecosystem types classified in the NBA 2018 ecosystem map, only 10 were surveyed within the study area, these being the Southern Benguela Rocky Shelf Edge Mosaic, Agulhas Outer Shelf Reef Coarse Sediment Mosaic, Agulhas Rocky Shelf Edge, Agulhas Coarse Sediment Shelf Edge, Kingklip Koppies, Kingklip Ridge, South Indian Mid Slope, South West Indian Upper Slope, Amathole Hard Shelf Edge, and Natal Deep Shelf Edge.

2.4 Data and statistical analysis: ecosystem classification

2.4.1 Defining biological communities

Multivariate analyses

The statistical software R (tidyr package) was used to manipulate the data into the format required for PRIMER statistical analyses. PRIMER v6 with the PERMANOVA+ add-on package was used to perform non-parametric multivariate analyses (Anderson, Gorley, et al. 2008, Clarke and Gorley 2006). The epifaunal abundance data were square root transformed to down-weight the high contribution of abundant species (Clarke and Gorley 2006, Field, Clarke, et al. 1982). A Bray-Curtis similarity measure was used to generate a resemblance matrix. Based on the resemblance matrix, a Cluster Analysis was performed to define the species assemblages by grouping the samples according to their level of similarity in a dendrogram plot. Major groups were defined at similarity levels between 10 and 20%. A Similarity Profile (SIMPROF) analysis was also performed, however the SIMPROF groups defined assemblages at the 100 m scale which contained too few samples and were too numerous as expected in a heterogenous environment. The aim of the study was to capture the broad scale biodiversity pattern at the 10 - 100 km scale, hence the SIMPROF results were not deemed appropriate for this scale.

To graphically represent the relationships (dis/similarities) between the samples, a non-metric multi-dimensional scaling (nMDS) plot was generated. In addition, the average epifaunal species richness per quadrate for each of the identified communities was calculated to compare the diversity across communities. To determine the characteristic and distinguishing species that contributed towards significantly different groups of samples to form communities, a Similarity of Percentages (SIMPER) analysis was conducted. A SIMPER analysis was also conducted to determine the characteristic and distinguishing species for the 10 NBA 2018 ecosystem types (Sink, van der Bank, et al. 2019), substratum types (four categories) and depth zones (three categories) covered in this study.

As a result of having an unbalanced design with an unequal number of quadrat replicates, a One-way Analysis of Similarities (ANOSIM) test was used instead of using a PERMANOVA test;

including pair-wise tests; 9999 permutations and was individually performed to test whether there were any significant differences between the substratum types (four categories) and depth zones (three categories) covered in this study. Thereafter, a Canonical Analysis of Principal coordinates (CAP) was performed to assess the differences between the four substratum types (fine to medium sand, medium to coarse sand, pebbles, and medium sand mixed and rock and sand mixed) identified within each sample. A CAP analysis based on the *a priori* assigned substratum types was used to detect separation in the data cloud along these constrained axes that were not readily detected from the unconstrained nMDS. The CAP analysis was used to cross-validate any misclassification errors (Anderson, Gorley, et al. 2008) based on the way that the software characterized the biota according to the grouping variable, substratum type.

The identified epifaunal communities were mapped using the start longitude and start latitude coordinates per site in QGIS software to display the distribution of the communities across the study area (QGIS Development Team (2021), QGIS Geographic Information System. Open-Source Geospatial Foundation Project. http://qgis.osgeo.org", Geometry CRS: “EPSG: 4326 – WGS84”).

2.4.2 Relating environmental variables to biological assemblages

To understand the potential environmental drivers of the benthic communities found along the outer shelf, shelf edge and slope of the Agulhas ecoregion, the influence of abiotic and biotic factors on epifaunal species composition were investigated. The following biotic factors were recorded and included in the analyses: start depth, bottom temperature, conductivity, salinity, longitude, latitude, distance to shelf-break, distance to shore, slope, current strength, trawling intensity (Swept-Area Ratio), substratum type, and biological variables including the presence of Particulate Organic Matter (POM, score of 0 = no POM, while 1= presence of POM) and coral rubble (score of 0 = no coral rubble, while 1= presence of coral rubble). These 14 environmental factors were used to test the relevance of observed patterns within benthic communities. Using PRIMER v6, a draftsman plot was generated to show the correlation between the abiotic variables. Where the correlation between two variables was greater than 0.8, only one variable was selected for further analyses.

Descriptive comparisons

To investigate the underlying environmental factors that may be driving the biological communities and their processes, epifaunal species richness data were analysed with 10 selected environmental factors recorded from the sampled region. These included depth, bottom temperature, longitude, distance to shelf-break, slope, current strength, trawling intensity (Swept-Area Ratio), substratum type, POM presence, coral rubble presence. Graphs were generated in the statistical software R version 3.6.2 (using ggplot2, vegan and tidyr packages) to test for relationships between the selected environmental variables and species richness per quadrat sample across the study area.

Univariate Analyses

Univariate analyses were performed in R-statistics (R Core Team 2022). Non-parametric, Kruskal Wallis tests were performed (using the Rstatix package; Kassambara 2021, unpublished [https://rpkgs.datanovia.com/rstatix/]) to test for significant differences in species richness per m^2 for categories of substratum type, longitude, current strength, depth and trawling intensity. This was followed by Dunn tests (in the FSA package; Ogle, Doll et al. 2022) for pairwise comparisons using the adjusted p-values with the Bonferroni method.

Multivariate analyses

Using the resemblance matrix from the species abundance data, in conjunction with the environmental data (10 selected factors), a Distance-based Linear Model (DistLM) was generated in the PERMANOVA add-on package of PRIMER v6 (Anderson, Gorley, et al. 2008). Using the ‘Best’ procedure with the Akaike selection criterion (AIC) to select the best model fit to examine the contribution of all variables to the model, the DistLM was generated to test which environmental variables significantly influenced the epifaunal communities recorded. A distance-based redundancy analysis (dbRDA) plot was included to graphically represent the relationship between epifaunal abundance and all the selected environmental variables for each sample. In addition, bubble plots were overlayed onto the same dbRDA ordination to show the total abundance of each of the main taxa groups found within this study.

Testing for differences in communities across recognised South African marine ecosystem types in the Agulhas ecoregion

As a result of having an unbalanced design with an unequal number of ecosystems and unequal quadrat replicates, a One-way Analysis of Similarities (ANOSIM) test was used instead of using a PERMANOVA test; including pair-wise tests; 9999 permutations and was performed to test whether there were any significant differences between the 10 NBA 2018 ecosystem types (Sink, van der Bank, et al. 2019) covered in this study. This was done using the epifaunal abundance data at the quadrat-level and site-level (the data was averaged per site).

Additionally, a Canonical Analysis of Principal coordinates (CAP) was used to detect separation amongst the data from the 10 surveyed ecosystem types that were previously classified by the NBA2018 (Sink, van der Bank, et al. 2019) and was used to cross-validate any misclassification errors (Anderson, Gorley, et al. 2008) based on the way that the software characterized the biota according to the grouping variable, ecosystem type (Table A9).

2.5 Data and statistical analysis: setting conservation targets for selected ecosystem types

Using the same benthic imagery as that for section 2.4, all epifaunal taxa present within the entire area of measurement from each image was also recorded (in contrast to taxa associated with the dot overlay as previously explained). This enabled a Presence-Absence data matrix (in comparison to an abundance data matrix used in section 2.4) to be compiled for all sites against all species. Only ecosystem types (as per NBA 2018, (Sink, van der Bank, et al. 2019) that had three or more sites surveyed in this study were selected for further conservation target analyses. Of the 10 ecosystem types surveyed, only three had sufficient site replication to enable meaningful conservation target analyses, these being Agulhas Rocky Shelf Edge, South West Indian Upper Slope and Agulhas Coarse Sediment Shelf Edge ecosystem types (Karenyi, Nel, et al. 2016).

Conservation targets were calculated using the Species-Area Relationship (SAR) approach developed by Desmet and Cowling (2004) in which the SAR is treated as a power function. To calculate the targets per ecosystem type, the requirements were the total number of species per ecosystem type, the average number of species per sample within the ecosystem type, the total area covered by the ecosystem type and the average area processed per sample within each ecosystem type.

Using PRIMER v6 (Clarke and Gorley 2006), the species richness for each NBA 2018 ecosystem type selected for analysis was calculated using the species accumulation plots function. From the results, the bootstrap estimator was selected rather than the ICE, Chao2, Jacknife1 and Jacknife2 estimators, as it is suggested to be a more conservative species richness estimator (Desmet and Cowling 2004, Metcalfe, Delavenne, et al. 2013). The average number of species per sample was obtained by calculating the mean of the total species per sample within the entire ecosystem type.

The total area for each ecosystem type was obtained from the attribute file of the NBA 2018 Integrated Marine Coastal Ecosystems (Sink, van der Bank, et al. 2019) shapefile through the Geographic Information System software QGIS version 3.16.6 (QGIS Development Team (2020), Open-Source Geospatial Foundation Project. http://qgis.osgeo.org”). The average area per sample was collected by calculating the mean of the area processed per image (measured within each image quadrat using TransectMeasure©) across the entire ecosystem type.

Following Desmet and Cowling (2004), the conservation targets per ecosystem type were calculated as follows:

(1) Calculate constant c per ecosystem type, using the equation:

$$S = cA^{z}$$

[S = number of species, A = area, z = rate of accumulation of species, c = constant]

Provided with the z and c values, the number of species observed in each ecosystem type was predicted if a given percentage of an ecosystem type was sampled.

$$LogA' = LogS'^{z}$$

(2) Thereafter the equation was reversed to predict the proportion of area sampled in each ecosystem type if a given percentage of species was observed.

$$A' = EXP\ (LN\ (S'/c)\ /\ z)$$

(3) Calculated the rate of accumulation of species (z) per ecosystem type, using the equation:

$$z\ =\ (y2 - y1)/(x2 - x1)$$

[where z is the slope of the straight line; y2 = log(total number of species in an ecosystem type); y1 = log(average number of species per survey sample; x2 = log(total area of ecosystem type); and x1 = log(average area of samples).

Once the data were derived, species-area curves for the three selected ecosystem types were developed based on the ecosystem-specific z values. Z values were used to estimate the percentage of species expected to be represented by any given percentage of ecosystem type protected (i.e., 10 equal intervals between 10 and 100%) and to estimate the percentage of area expected to be represented by any given percentage of species protected. The species-area curve graphs were compiled in Microsoft Excel and compared amongst the three ecosystem types selected. These results were compared to conservation targets reported by Rondinini (2011) using the bootstrap estimator with samples equal to 1 m^2. Conservation targets were then set for each ecosystem type selected for the analysis.

Chapter 3: Results

3.1 Description of dataset

A total of 173 invertebrate taxa were identified within the dataset. Cnidaria (24.8%, 47 taxa/morphotaxa, including octocorals, scleractinians and seapens), Annelida (24.6%, four taxa/morphotaxa, including various types of polychaetes and polychaete tubes) and Foraminifera (17%, including multiple taxa/morphotaxa considered as one species) contributed the largest proportions of the fauna detected in the images. Echinodermata (15.2%, 49 taxa/morphotaxa, including sea stars, brittle stars, sea urchins and sea cucumbers), Arthropoda (7.8%, 24 taxa/morphotaxa, including spider crabs, shrimp and hermit crabs) and several other species from different Phyla occurred in lower proportions and were grouped as 'Other' (10.6%, 48 taxa, including various sea squirts, salps, bryozoans, gastropods, sponges and a hemichordate) (Figure 3.1).

One site (DSC10) was positioned in the outer shelf at 135 – 137 m, 19 sites were sampled in the shelf edge covering a depth range 124 – 500 m, and nine sites were positioned in the upper slope of the Agulhas ecoregion covering a depth range 509 – 626 m (Appendix, Table A1). These 29 sites span ten different South African National Marine Ecosystem types according to the NBA2018 (Sink, van der Bank, et al. 2019), including the Southern Benguela Rocky Shelf Edge Mosaic, Agulhas Outer Shelf Reef Coarse Sediment Mosaic, Agulhas Rocky Shelf Edge, Agulhas Coarse Sediment Shelf Edge, Kingklip Koppies, Kingklip Ridge, South Indian Mid Slope, South West Indian Upper Slope, Amathole Hard Shelf Edge, and Natal Deep Shelf Edge (Fig. A2).

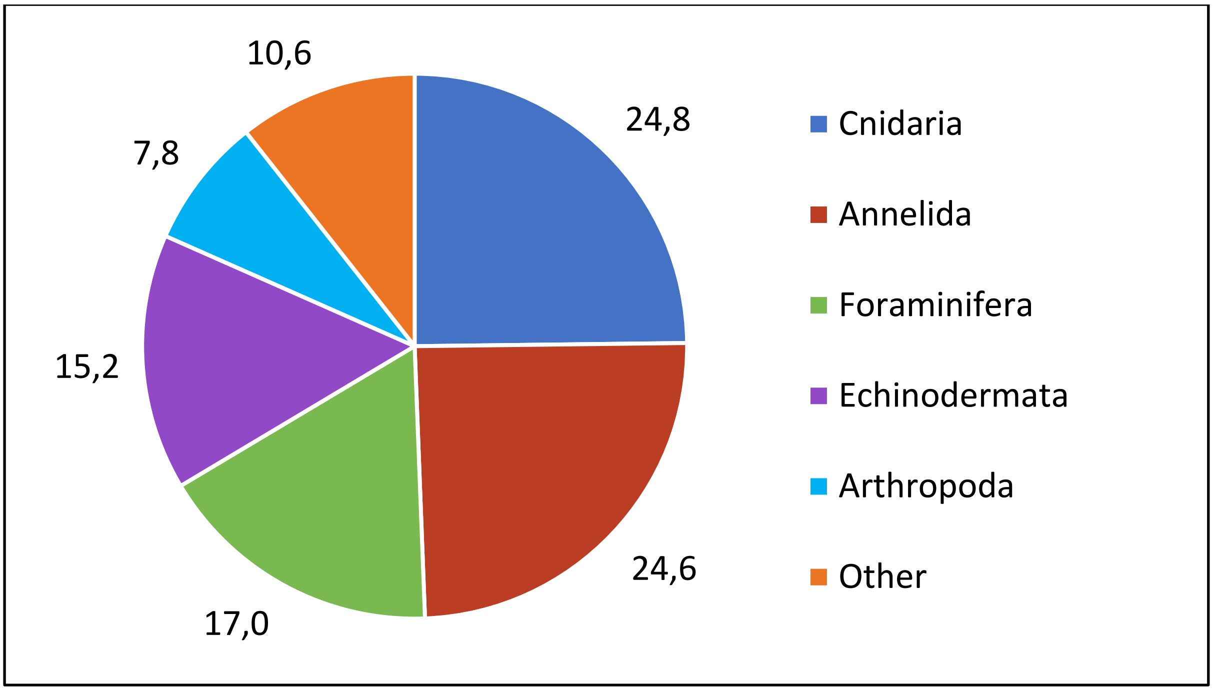

Figure 3.1. Taxonomic composition, as proportions of total taxa abundance (the number of individuals per taxa (%)), detected in 855 image quadrats from 29 sites along the outer shelf, shelf edge and upper slope of the Agulhas ecoregion. The "Other" category includes the taxa Chordata, Bryozoa, Porifera, Mollusca and Hemichordata.

3.2 Identifying biodiversity patterns and testing the distribution of benthic communities

Multivariate analyses

3.2.1 Identification of marine epifaunal communities and their distribution

Based on the epifaunal composition, ten communities (A – J) were distinguished from the cluster dendrogram (Fig. 3.2, clusters were grouped at different similarity percentage levels). For most of the sites surveyed, the majority of replicate samples co-occurred within a single community, however, there were a few replicate samples that were classified with other communities or were outliers. Three replicate samples from Site 10 were outliers, as they did not contain any species and were hence excluded from all subsequent community analyses. The ten communities (A-J) are not clearly distinguished on the Multi-Dimensional Scaling ordination plot (Fig. 3.3). Though there is separation between communities, they seem to have an overlap of common species from one community to the next. Community A was most clearly distinguished in consisting of samples entirely from site 37 (Fig. 3.2 – Fig. 3.5) and was situated off the Kei River mouth (Fig. 3.5). Similar to community A, community B is limited to a single site, that being site 10, on the outer shelf just offshore of Knysna, and the same for community J being limited to site 50 on the shelf edge offshore of Gqeberha, whereas the rest of the communities C – I are distributed across most of the longitudinal range (Fig. 3.5).

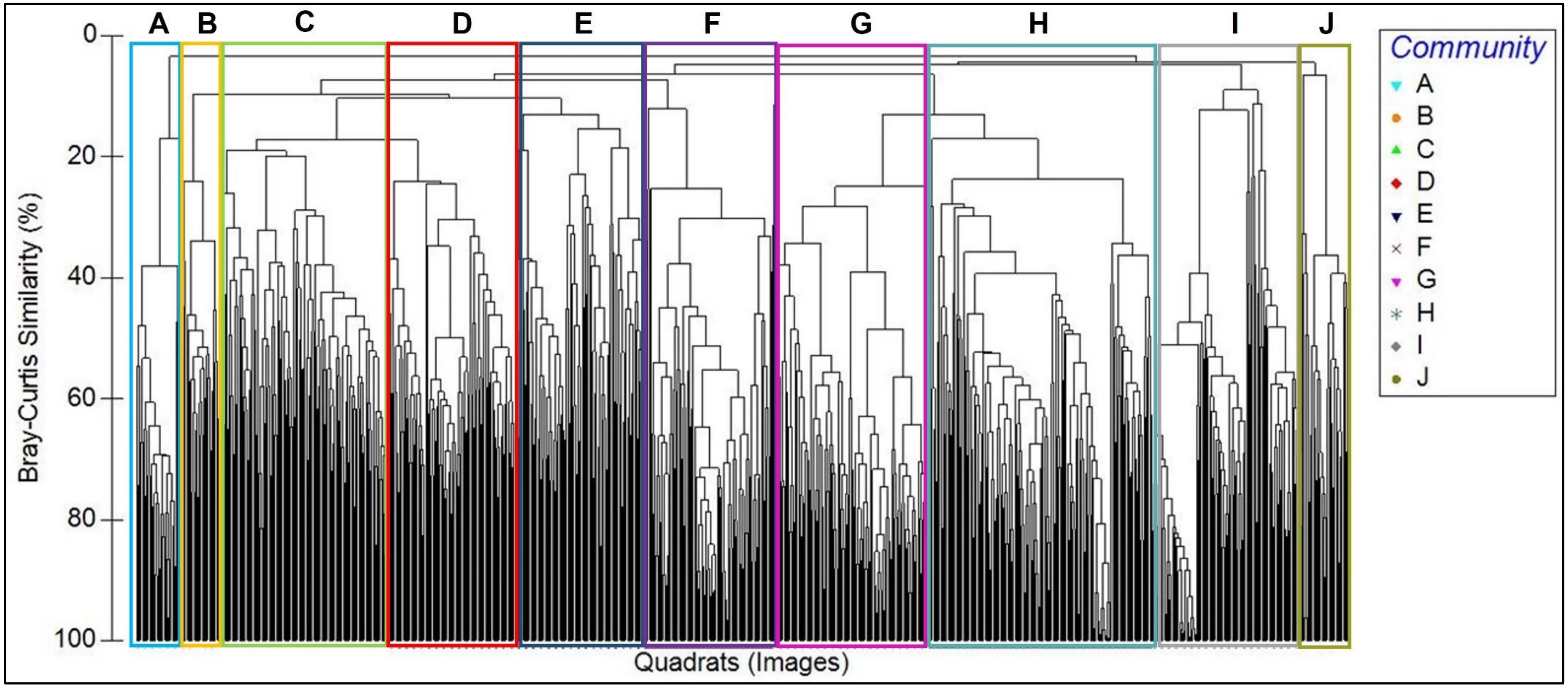

Figure 3.2. Dendrogram based on Cluster Analysis of Bray Curtis similarities (Square-root transformed) among 852 replicate samples collected (excluding the outliers), showing the ten different offshore benthic epifaunal communities (A – J) along the Agulhas ecoregion.

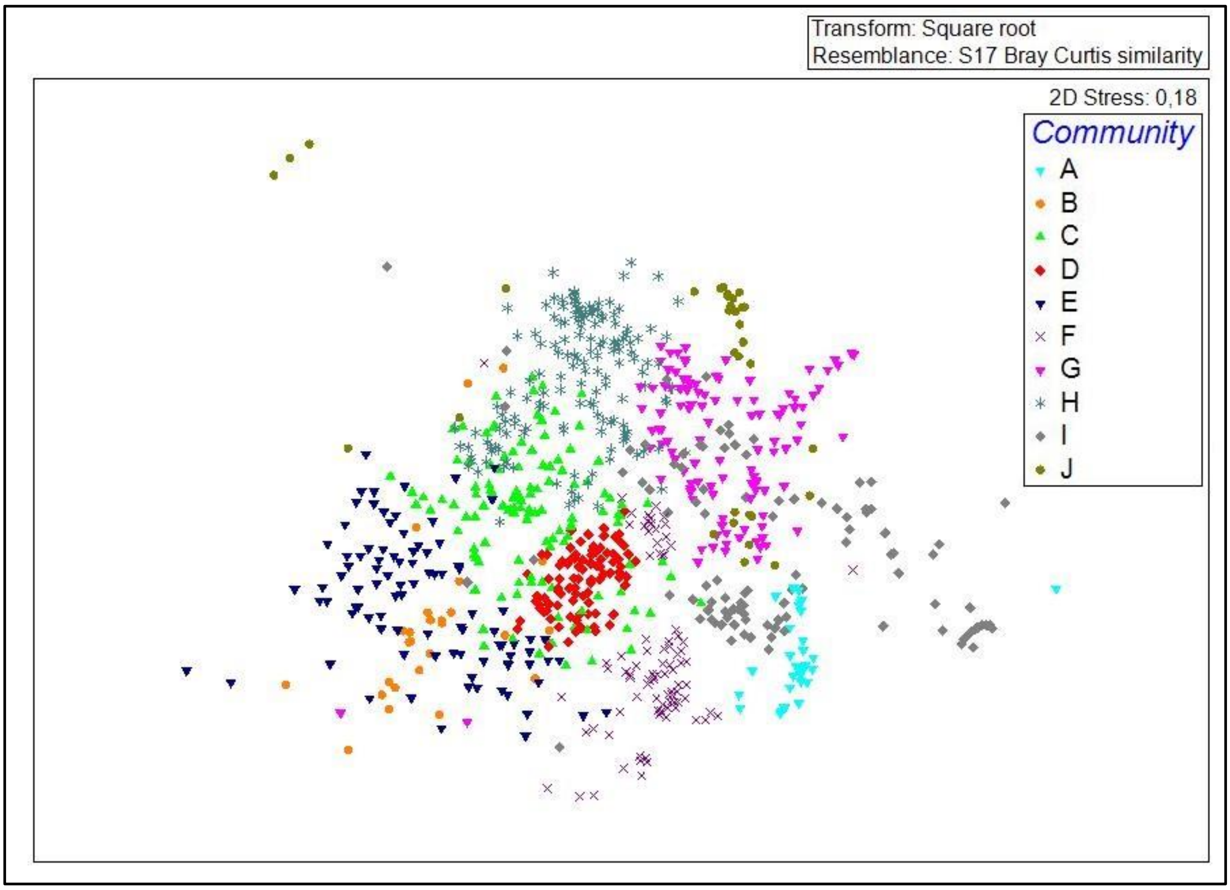

Figure 3.3. Multi-Dimensional Scaling Ordination of Bray-Curtis similarities among 852 replicate epifaunal samples collected (excluding the outliers) from 29 sites, showing the relationships among ten different offshore benthic epifaunal communities (A – J) along the Agulhas ecoregion based on species abundance data.

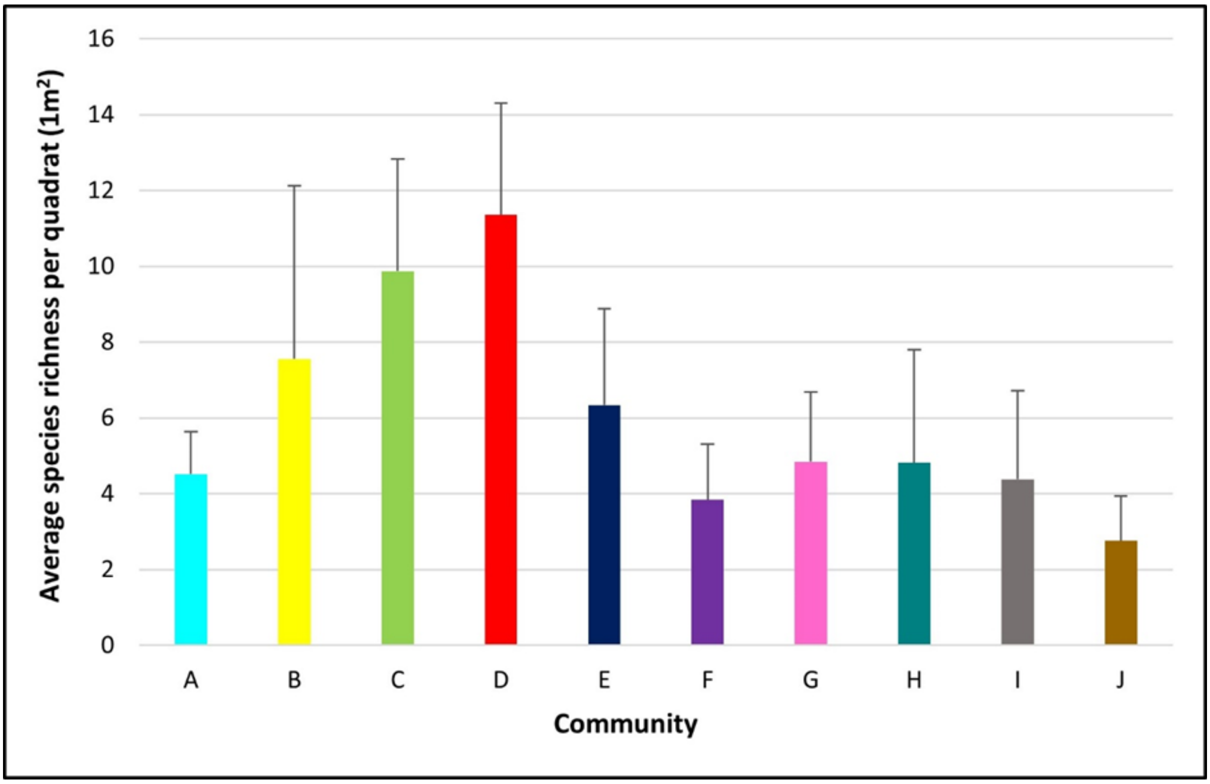

Figure 3.4. Average species richness per quadrat replicate (1 m^2) per identified epifaunal community (A – J) in the Agulhas ecoregion, with standard deviation error bars.

Communities D (mean = 11.4 spp. and stdev = 2.9 spp.), C (mean = 9.9 spp. and stdev = 3.0 spp.) and B (mean = 7.6 spp. and stdev = 4.6 spp.) are higher than the rest of the communities, presenting higher species richness (Fig. 3.4). Contrastingly, Communities F (mean = 3.8 spp. and stdev = 1.5 spp.) and J (mean = 2.8 spp. and stdev = 1.2 spp.) present the lowest species richness and are mostly different from the rest of the communities (Fig. 3.4).

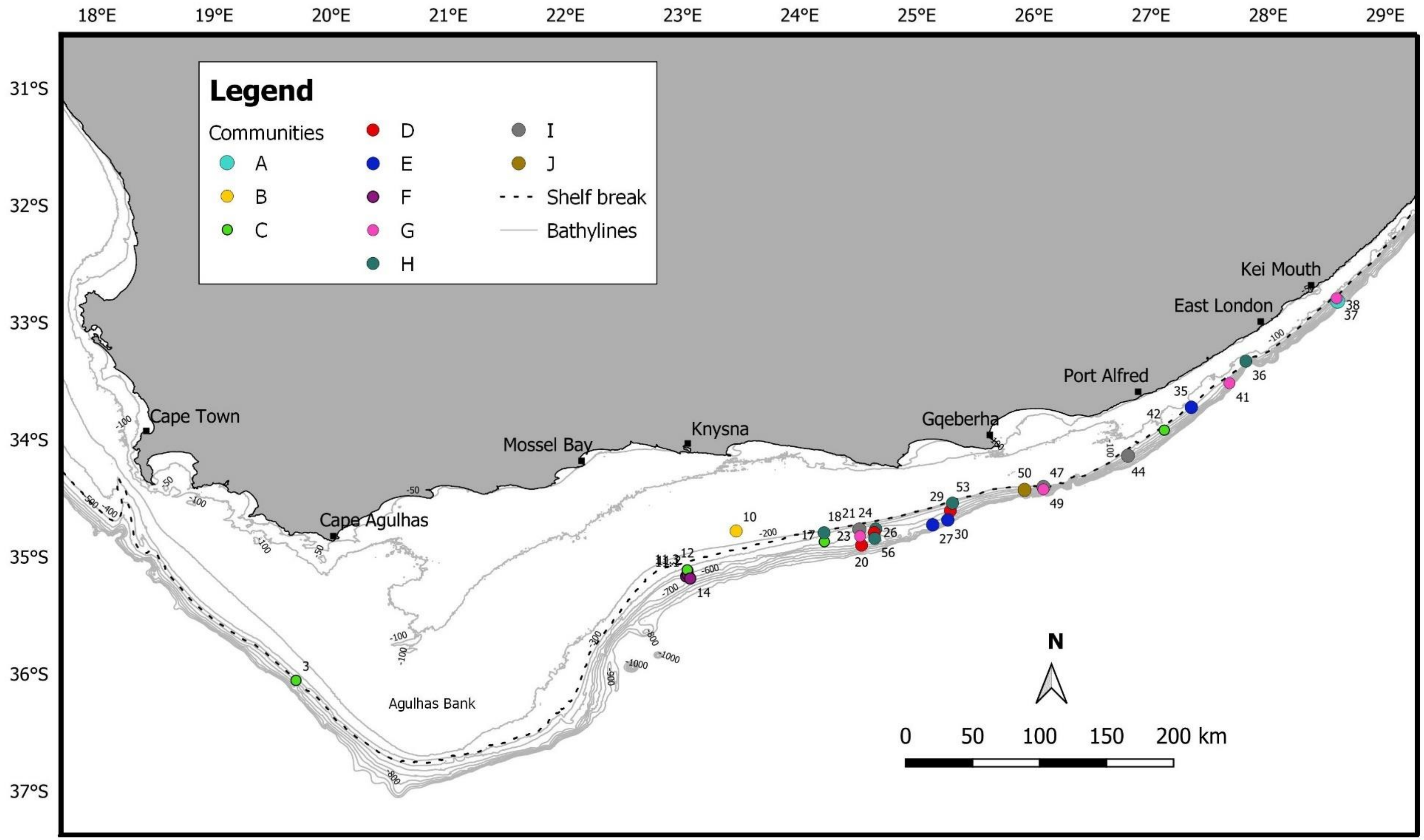

Figure 3.5. Map depicting the spatial distribution of the ten identified epifaunal communities (A-J) across the 29 sites (identified by the numbers in bold) surveyed along the outer shelf, shelf edge and upper slope of the Agulhas ecoregion. The shelf break line is derived from the NBA 2018 (Sink, van der Bank, et al. 2019) and the bathylines were derived from de Wet (2013).

3.2.2 Differentiating characteristic and distinguishing species amongst epifaunal communities

Community A was mostly made up of replicate samples from one deep site (37) off the Kei River mouth on the upper slope, at a depth of 539 m (Fig. 3.5). As defined by the Similarity of Percentages (SIMPER) analyses, the replicates of Community A were 56.30% similar. Of that 56.30% similarity, the characteristic species that contributed the most to the similarity in this community were stalked crinoid (36.86%), seapen *Virgularia* sp. (30.46%), unidentified transparent radial octocoral (16.22%) and sponge *Hyalonema* sp. (14.41%) (Table 3.1). Community B comprised most of the replicate samples from the shallowest site (10) which was located on the outer shelf off Knysna, at a depth of 135 m (Fig. 3.5). Cup coral (orange) (37.75%), unidentified Melithaeidae (27.74%) and bryozoan *Aspidostoma* spp. (17.05%) consistently characterized Community B, contributing most to the similarity within this community (39.97%, Table 3.1). The replicate samples clustered into Community C were mostly from five sites (03, 11.3, 12, 17, 42) along the shelf edge between the western end of the Agulhas Bank and Port Alfred, within a depth range of 314 – 463 m (Fig. 3.5). The replicate samples for Community C were 27,54% similar and were consistently characterized by *Stylaster* sp.1 (29.69%) and bryozoan *Adeonella* sp. (12.10%, Table 3.1). Community D comprised replicate samples from three sites (20, 26, 29) on the shelf edge and upper slope (480 – 525 m) of the continental shelf between Knysna and Gqeberha (Fig. 3.5). Stalked crinoids (28.85%) consistently characterized Community D, as they contributed most to the similarity within the community (33.51%, Table 3.1). Most of the replicate samples from three sites (27, 30, 35) clustered into Community E and spanned a depth range of 185 - 615 m across the shelf edge and upper slope between Knysna and Port Alfred (Fig. 3.5). These replicate samples were 20.64% similar and were mostly populated by Hydroid spp. (35.95%), soft coral *Anthomastus* sp. A (15.19%) and Shrimp sp. A (10.60%, Table 3.1). Community F comprised replicate samples mostly from three sites (11.1, 11.2, 14) that spanned a depth range of 445 - 535 m across the shelf edge and upper slope off Knysna (Fig. 3.5). A burrowing anemone, *Ceriantheopsis* sp. (43.41%), polychaete *Praxillura* sp. (32.02%) and crustacean *Rochinia hertwigi* (10.61%) consistently characterized Community F contributing most to the similarity within the community (41.47%, Table 3.1). The replicate samples making up Community G are mostly from four sites (23, 38, 41, 49) that spanned a depth range of 340 - 555 m across the shelf edge and upper slope between Knysna and the Kei River mouth (Fig. 3.5). The replicate samples of Community G were 37.18% similar and were consistently characterized by Polychaete tubes (76.77%) with foraminifera, a burrowing anemone, *Ceriantheopsis* sp. and stalked crinoids contributing small proportions to their similarity (Table 3.1). Community H comprised replicate samples mostly from five sites (18, 24, 36, 53, 56) that spanned a depth range of 120 - 555 m across the shelf edge and upper slope between Knysna and East London (Fig. 3.5). Foraminifera (88.01%) consistently characterized Community H contributing most to the similarity within the community (35.35%, Table 3.1). The replicate samples making up Community I were mostly from three sites (21, 44, 47) on the shelf edge (245 – 400 m) between Knysna and Port Alfred (Fig. 3.5). These replicate samples were 29.51% similar and were mostly populated by the brittle star *Ophiura trimeni* (68.58%) and Polychaete sp.A (12.28%, Table 3.1). Community J comprised most replicate samples from one site (50) on the shelf edge off Gqeberha, at a depth of 404 m (Fig. 3.5). Shrimp sp. B (75.30%) and hermit crab *Sympagurus dimorphus* (11.89%) consistently characterized Community J contributing most to the similarity within the community (32.57%, Table 3.1).

Stalked crinoids, a seapen *Virgularia* sp., unidentified transparent radial octocorals and a sponge, *Hyalonema* sp. consistently distinguished Community A from all other communities (Table 3.2). Cup coral (orange), unidentified Melithaeidae (sea fans) and a bryozoan, *Aspidostoma* spp. were all distinguishing taxa for Community B (Table 3.2). *Stylaster* sp.1 (hydrocoral) consistently distinguished Community C from all other communities (Table 3.2). Stalked crinoids and *Adeonella* sp. (bryozoan) were distinguishing taxa for Community D (Table 3.2). Hydroid spp. consistently distinguished Community E from all other communities (Table 3.2). *Ceriantheopsis* sp. (burrowing anemone) and *Praxillura* sp. (tube polychaete) were distinguishing taxa for Community F (Table 3.2). Polychaete tubes consistently distinguished Community G from all other communities (Table 3.2). Foraminifera were a distinguishing taxa for Community H (Table 3.2). *Ophiura trimeni* (brittle star) consistently distinguished Community I from all other communities while Shrimp sp. B was a distinguishing species for Community J (Table 3.2).

Table 3.1. Characteristic taxa of the 10 identified epifaunal communities occurring in their respective sites, number of quadrat replicates sampled and average similarity. The five epifaunal taxa contributing most to the similarity within each community, representing between 40-90 % of the similarity are listed under Contributing %. In the Similarity/Standard Deviation (Sim/SD) column, bold figures represent the taxa that consistently characterized their respective community. Site numbers highlighted in **bold** indicate that all the replicate samples within that site were present within their allocated community. Sites that are underlined indicate that nearly all the replicate samples for that site were present in the community.

Community	***Characteristic taxa***	***Ave. Abundance***	***Sim/SD***	***Contributing %***
A	Stalked crinoid	1.32	**1.59**	36.86
Sites: **37**	*Virgularia* sp.	1.01	**1.82**	30.46
31 replicate samples	Unidentified transparent radial octocoral	0.60	**1.11**	16.22
(Ave. Similarity = 56.30%)	*Hyalonema* sp.	0.61	**1.00**	14.41
B	Cup coral (orange)	1.27	**1.43**	37.75
Site: **10**	Unidentified Melithaeidae	1.03	**1.38**	27.74
27 replicate samples	*Aspidostoma* spp.	0.83	**1.08**	17.05
(Ave. Similarity = 39.97%)	*Thouarella* spp.	0.53	0.66	7.99
C	*Stylaster* sp.1	1.26	**1.70**	29.69
Sites: 03, 11.3, 12, 17, 42	*Adeonella* sp.	0.91	0.66	12.10
119 replicate samples	Ascidian unknown	0.70	0.63	8.31
(Ave. Similarity = 27.54%)	Foraminifera	0.64	0.43	7.21
	Stylaster cf. griseus	0.63	0.51	6.76
D	Stalked crinoid	1.62	**1.90**	28.85
Sites: **20, 26, 29**	*Adeonella* sp.	0.86	0.70	9.82
89 replicate samples	Hydroid spp.	0.77	0.77	9.74
(Ave. Similarity = 33.51%)	Primnoid sp.1	0.72	0.70	8.04
	Praxillura sp.	0.66	0.59	6.30

Table 3.1 cont.

Community	*Characteristic taxa*	*Ave. Abundance*	*Sim/SD*	*Contributing %*
E	Hydroid spp.	0.99	0.90	35.95
Sites: **27,** 30, 35	*Anthomastus* sp. A (white)	0.72	0.53	15.19
93 replicate samples	Shrimp sp. A (bright red rocky shrimp)	0.88	0.36	10.60
(Ave. Similarity = 20.64%)	*Thouarella* spp.	0.40	0.35	8.95
	Porifera unknown encrusting sponge	0.57	0.31	5.94
F	*Ceriantheopsis* sp.	1.65	**1.06**	43.41
Sites: 11.1, 11.2, 14	*Praxillura* sp.	1.07	**1.03**	32.02
88 replicate samples	*Rochinia hertwigi*	0.46	0.53	10.61
(Ave. Similarity = 41.47%)	Cup coral (pink)	0.42	0.55	9.20
G	Polychaete tubes	3.89	**2.03**	76.77
Sites: 23, 38, **41, 49**	Foraminifera	1.02	0.48	8.88
111 replicate samples	*Ceriantheopsis* sp.	0.26	0.32	2.46
(Ave. Similarity = 37.18%)	Stalked crinoid	0.34	0.24	2.37
H	Foraminifera	2.78	**1.91**	88.01
Sites: **18**, 24, 36, 53, 56	Hydroid spp.	0.34	0.25	2.20
156 replicate samples				
(Ave. Similarity = 35.35%)				
I	*Ophiura trimeni*	2.36	0.84	68.58
Site: **21, 44,** 47	Polychaete sp.A	0.81	0.41	12.28
105 replicate samples	*Ceriantheopsis* sp.	0.34	0.34	4.84
(Ave. Similarity = 29.51%)	*Ophiactis carnea*	0.33	0.24	2.91
	Cup coral (pink)	0.22	0.21	2.15
J	Shrimp sp. B (Euphausiid-like shrimp)	1.29	**1.22**	75.30
Sites: 50	*Sympagurus dimorphus*	0.43	0.36	11.89
33 replicate samples	*Ophiura costata costata*	0.29	0.21	5.68
(Ave. Similarity = 32.57%)				

Table 3.2. Average Bray-Curtis dissimilarities between all pairs of community groups across the Agulhas ecoregion. Light-grey blocks represent the average dissimilarity between respective paired community groups (paired in the first row and first column) and white blocks represent the top three distinguishing epifaunal taxa discriminating each pairing of community groups, contributing towards a 55% cut-off. Black blocks represent the average similarity percentage within the indicated community.

Communities	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**
A	56.3	99.54	98.92	86.58	98.51	98.92	92.04	99.17	97.85	99.67
B	Stalked crinoid, Cup coral (orange), Unknown *Virgularia* sp.	39.97	90.12	89.72	91.15	96.34	98.15	95	97.58	97.98
C	Stalked crinoid, *Stylaster* sp.1, Unknown *Virgularia* sp.	Cup coral (orange), *Stylaster* sp.1, Unidentified Melithaeidae	27.54	82.78	92.15	91.93	94.75	88.97	93.49	94.79
D	Unknown *Virgularia* sp., Stalked crinoid, *Adeonella* sp.	Stalked crinoid, Cup coral (orange), Unidentified Melithaeidae	Stalked crinoid, *Stylaster* sp.1, *Adeonella* sp.	33.51	86.37	89.65	92.49	94.2	96.27	92.71
E	Stalked crinoid, Unknown *Virgularia* sp., Hydroid spp.	Cup coral (orange), Unidentified Melithaeidae, Hydroid spp.	*Stylaster* sp.1, Hydroid spp., *Adeonella* sp.	Stalked crinoid, *Adeonella* sp., Hydroid spp.	20.64	95.78	98.6	95.33	98.29	99.43

Table 3.2 cont.

Communities	A	B	C	D	E	F	G	H	I	J
F	*Ceriantheopsis* sp., Stalked crinoid, *Praxillura* sp.	*Ceriantheopsis* sp., Cup coral (orange), *Praxillura* sp.	*Ceriantheopsis* sp., *Stylaster* sp.1, *Praxillura* sp.	Stalked crinoid, *Ceriantheopsis* sp., *Praxillura* sp.	*Ceriantheopsis* sp., *Praxillura* sp., Hydroid spp.	41.47	93.49	93.41	93.05	95.96
G	Polychaete tubes, Stalked crinoid, Unknown *Virgularia* sp.	Polychaete tubes, Cup coral (orange), Unidentified Melithaeidae	Polychaete tubes, *Stylaster* sp.1	Polychaete tubes, Stalked crinoid, *Adeonella* sp.	Polychaete tubes, Hydroid spp.	Polychaete tubes, *Ceriantheopsis* sp., *Praxillura* sp.	37.18	87.31	96.44	93.49
H	Foraminifera, Stalked crinoid, *Unknown Virgularia sp.*	Foraminifera, Cup coral (orange), Unidentified Melithaeidae	Foraminifera, *Stylaster sp.1, Adeonella sp.*	Foraminifera, Stalked crinoid, *Adeonella* sp.	Foraminifera, Hydroid spp.	Foraminifera, *Ceriantheopsis* sp., *Praxillura* sp.	Polychaete tubes, Foraminifera	35.35	94.65	96.23
I	*Ophiura trimeni*, Stalked crinoid, Unknown *Virgularia* sp.	*Ophiura trimeni*, Cup coral (orange), Unidentified Melithaeidae	*Ophiura trimeni*, *Stylaster* sp.1, *Adeonella* sp.	*Ophiura trimeni,* Stalked crinoid, *Adeonella sp.*	*Ophiura trimeni,* Hydroid spp.	*Ophiura trimeni*, *Ceriantheopsis* sp., *Praxillura* sp.	Polychaete tubes, *Ophiura trimeni*	Foraminifera*, Ophiura trimeni*	29.51	95.89
J	Stalked crinoid, Shrimp sp. B, Unknown *Virgularia* sp.	Shrimp sp. B, Cup coral (orange), Unidentified Melithaeidae	*Stylaster* sp.1, Shrimp sp. B, *Adeonella* sp.	Stalked crinoid, Shrimp sp. B, *Adeonella* sp.	Shrimp sp. B, Hydroid spp.	*Ceriantheopsis* sp., Shrimp sp. B, *Praxillura* sp.	Polychaete tubes, Shrimp sp. B	Foraminifera, Shrimp sp. B	*Ophiura trimeni,* Shrimp sp. B	32.57

3.2.3 Testing the significance of the distribution of epifaunal communities across different substratum types and depth zones using ANOSIM

The epifaunal assemblages found across the four defined substratum types (fine to medium sand, medium to coarse sand, pebbles and medium sand mixed, and rock and sand mixed) were significantly different from each other (ANOSIM, Global Test Sample statistic (Global R): 0.382, $p < 0.01\%$, 9999 permutations). Pairwise comparisons showed that all pairs of substratum types were significantly different from one another (Table A4), and this was supported by the Canonical analysis for principal coordinates (CAP) analysis below (Fig. 3.6). The epifaunal assemblages occurring in the three depth zones (outer shelf, shelf edge and upper slope) were significantly different from each other (ANOSIM, Global Test Sample statistic (Global R): 0.099, $p < 0.01\%$, 9999 permutations). In terms of the pairwise comparisons, all pairs of depth zones were significantly different from one another (Table A5).

3.2.4 Testing the distribution of epifaunal communities across different substratum types using CAP analysis

The taxonomic composition differed across the various substratum types, as seen in the Canonical analysis for principal coordinates (CAP) plot (Fig. 3.6). The four main substratum types that were present within the study area were fine to medium sand, medium to coarse sand, pebbles and medium sand mixed, and rock and sand mixed. The results from the CAP analysis showed that all four of these substratum types clustered separately from one another with 87.8% correctly classified as a measure of prediction.

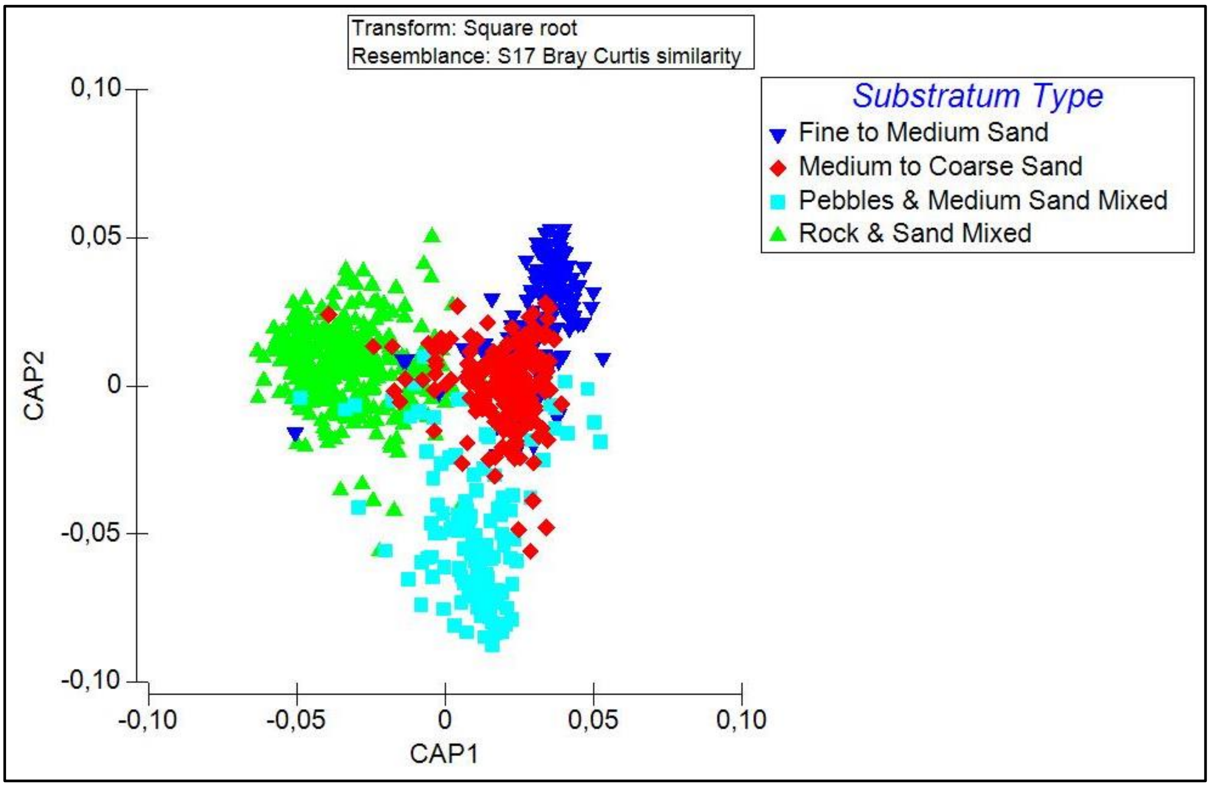

Figure 3.6. Visual representation of the distribution of the 852 replicate samples from 29 sites among the four different substratum types (fine to medium sand, medium to coarse sand, pebbles and medium sand mixed, and rock and sand mixed) in the Agulhas ecoregion, based on the Canonical analysis for principal coordinates (CAP).

3.3 Relating environmental variables to biological data

All 14 environmental variables were selected for the Draftsman plot analysis. The draftsman plots showed that conductivity was strongly correlated with bottom temperature ($r = 1$, Appendix Table A2). Salinity was also strongly correlated with bottom temperature ($r = 0.92$) and conductivity ($r = 0.93$). Latitude was strongly correlated with longitude ($r = 0.96$). Distance to shore had a strong correlation with longitude ($r = -0.9$) and latitude ($r = -0.95$). Conductivity, salinity, latitude, and distance to shore (indicated in bold) were excluded from further analyses due to them being strongly correlated with other variables. The remaining 10 variables selected for further analyses were depth, bottom temperature, distance to shelf break, slope, current strength, trawling intensity, substratum type, POM presence, coral rubble presence and longitude.

Descriptive comparisons and univariate analyses

Species richness (spp/m^2) was significantly different in **substratum type** (Kruskal Wallis, χ2 = 384.25, df = 3, $p < 0.05$). Rock and Sand samples were significantly different to Pebbles and Medium Sand mixed and sediment categories (Dunn Test, z values = 14.77 to -14.33, padj < 0.05). Where the pebbles and medium sand mixed and sediment categories comparisons were not significantly different from one another (Dunn Test, z values = 2.19 to -1,00, padj > 0.05). Rock and sand samples had higher species richness (median = 9 spp.) and a greater range (1 – 18 spp.) than all other substratum types (Fig. 3.7a).

Although no discernible patterns were observed in species richness with longitude (Fig. 3.7b), species richness (spp/m^2) was significantly different in **longitude** (Kruskal Wallis, $\chi^2 = 39.282$, df = 3, $p < 0.05$). All categories of longitude were significantly different (Dunn Test, z values = 5,8 – 3.37, $p_{adj} < 0.05$) except for the comparison between the categories 22 – 24 and 25 and 27 (Dunn Test, z value = -1,97, $p_{adj} > 0.05$).

Species richness (spp/m^2) was significantly different in **trawling intensity** (Kruskal Wallis, χ2 = 97.575, df = 3, $p < 0.05$). All trawling intensity categories, from 0 – 15, were significantly different from one another (Dunn Test, z values = 8.09 - -4.97, padj < 0.05). Areas with lower trawl intensity had greater species richness than those with higher trawl intensity (Fig. 3.7c).

Although no discernible patterns were observed in species richness with depth (Fig. 3.7d), species richness (spp/m^2) was significantly different in **depth** (Kruskal Wallis, χ2 = 44.43, df = 4, p < 0.05). Depths between 0 – 150 m were significantly different to 151 – 300 m and 301 – 450 m (Dunn Test, z values = 4.01 – 3.41, $p_{adj} < 0.05$); depths between 451 – 600 m were significantly different between 151 – 300 m and 301 – 450 m (Dunn Test, z values = 4.01 – 3.41, $p_{adj} < 0.05$), depths between 601 – 750 m were significantly different between 151 – 300 m and 301 – 450 m (Dunn Test, z values = -3.51 - -4.07, $p_{adj} < 0.05$). Depth categories between 0 – 150 m were not significantly different 451 – 600 m and 601 – 750 m (Dunn Test, z values = 0.99 – -0.85, $p_{adj} > 0.05$); depth categories between 151 – 300 m were not significantly different between 301 – 450 m (Dunn Test, z values = -1.58, $p_{adj} > 0.05$); depth categories between 451 – 600 m were not significantly different from 601 – 750 m (Dunn Test, z values = -1,73, $p_{adj} > 0.05$).

Samples with **particulate organic matter** had higher species richness (median = 10 spp.) and a greater range (3 – 18 spp.) than samples that lacked particulate organic matter (median = 5) (Fig. 3.7e). The medians for all four **slope** types were very similar at 5 – 6 species, however, samples collected in areas with a flatter gradient had a greater range of species richness (1 – 18 spp., Fig. 3.7f) than the other slope types.

Species richness (spp/m^2) was significantly different in **current strength** (Kruskal Wallis, χ2 = 28.848, df = 2, p < 0.05). All three current strength categories, Low, Medium, and High, were significantly different from one another (Dunn Test, z values = 4.78 to -3.54, $p_{adj} < 0.05$). Areas of low current speeds hosted greater species richness (median = 9 spp.) but had a slightly lower range (5 – 15 spp.) than the medium to high current-swept areas, where there was lower species richness (Fig. 3.7i).

Samples with **coral rubble** had higher species richness (median = 9 spp.) but had a slightly lower range (3 – 16 spp.) than those samples that lacked coral rubble (1 – 15 spp., Fig. 3.7j). No discernible patterns were observed in species richness with **distance to shelf break** (Fig. 3.7g) and **bottom temperature** (Fig. 3.7h).

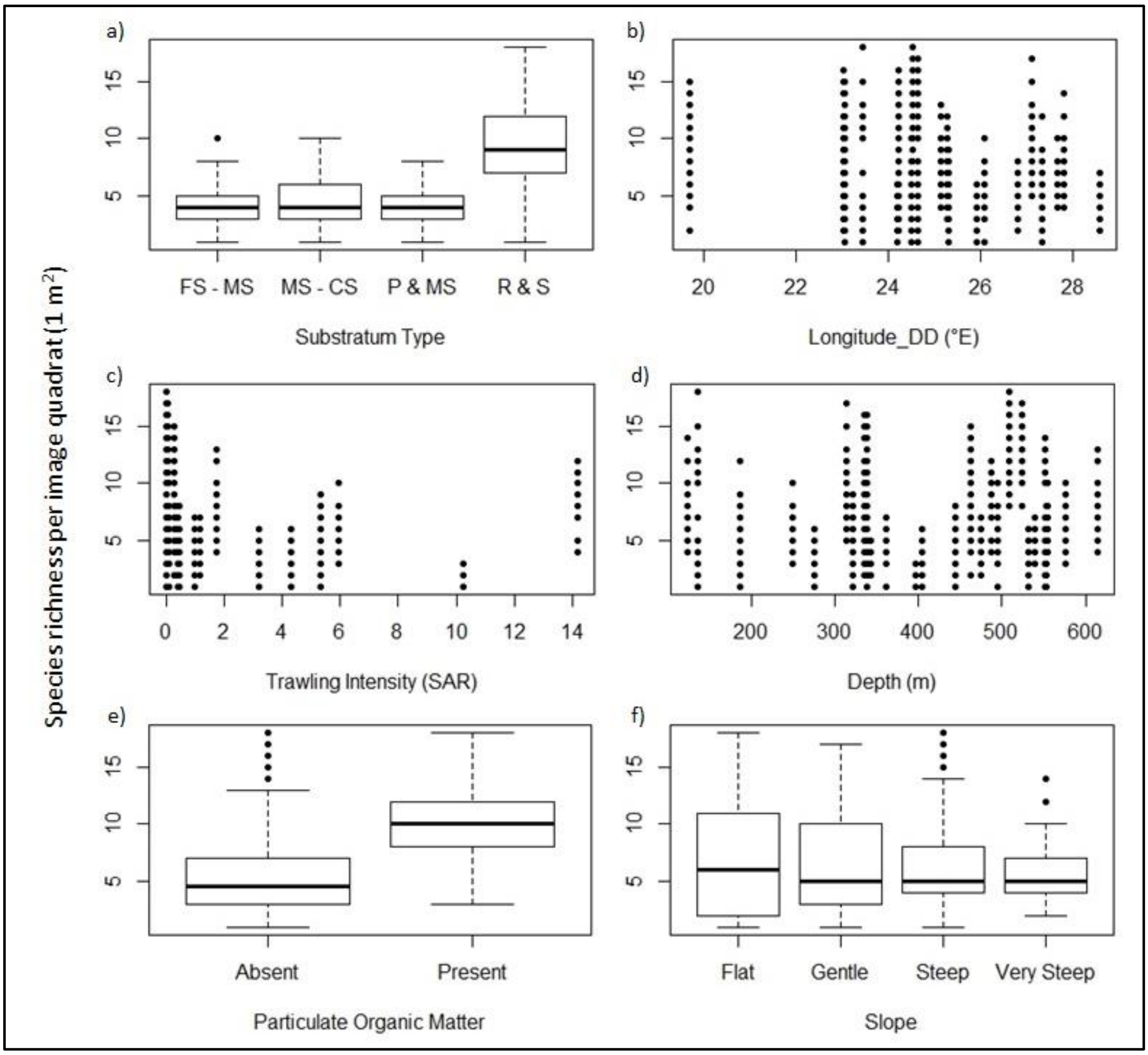

Figure 3.7. Scatterplots and Boxplots showing the relationships between species richness per image quadrat (1 m^2) and a range of selected environmental variables, (a) substratum type (FS-MS = Fine Sand to Medium Sand, MS-CS = Medium Sand to Coarse Sand, P & MS = Pebbles and Medium Sand, and R & S = Rock and Sand), b) longitude, c) trawling intensity as Swept-Area Ratio, d) start depth (m), e) presence of particulate organic matter, f) slope, g) distance to shelf break (km), h) bottom temperature (°C), i) current strength and j) presence of coral rubble) for 855 replicate samples collected along the Agulhas ecoregion. In the boxplots, the error bars represent the minimum and maximum of the range of values, the black line represents the median (midpoint) value.

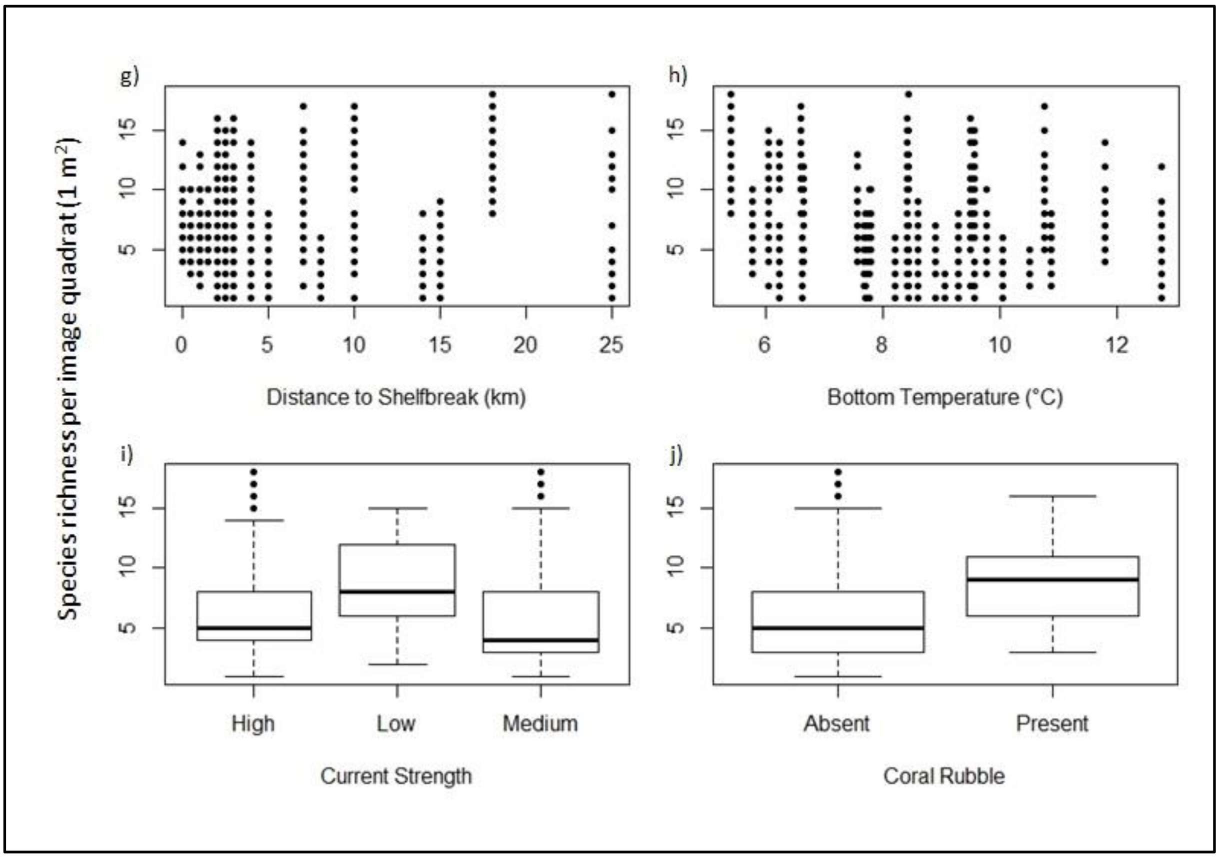

Figure 3.7 cont.

Multivariate analyses

Of the environmental variables measured, substratum type, Particulate Organic Matter (POM) presence, coral rubble presence, start depth, bottom temperature, longitude, distance to shelf break, slope, current strength, and trawling intensity, all 10 combined best explained 48.6% of the total fitted variation (Fig. 3.8 and Table A3b) in the epifaunal communities along the Agulhas ecoregion (AIC= 6857.3, R^2= 0.26704, RSS= 2.598E6). All variables significantly ($p < 0.01$) contributed to the total variation in the marginal tests (Table A3a). Although little variation was observed amongst the measured variables in the marginal tests (Table A3a), substratum type (7.38%), presence of POM (4.64%), longitude (3.40%), trawling intensity (3.21%) and depth (2.91%) had a greater influence on the distribution of these epifaunal communities. The total variation of the observed faunal patterns explained by the model was 26.7% with 12.98% explained by the first 2 axes and 21.7% explained by the first 5 axes related to the previously mentioned environmental variables (Table A3b). The distinction of the epifaunal assemblages among the different categories are shown for the derived communities A to J (Fig. 3.8a), substratum type (Fig. 3.8b) and depth zonation (Fig. 3.8c).

The first two dbRDA axes (Fig. 3.8) explained 48.62% of the fitted model variance, and 12.98% of the total variation. To reach a 75% cumulative fitted model variance, the variation would be explained by the first five dbRDA axes of the DistLM plot (Table A3b). The first dbRDA axis correlated most strongly with substratum categories (-0.848), dbRDA axis 2 correlated most strongly with longitude (0.710), dbRDA axis 3 correlated most strongly with depth (-0.464), dbRDA axis 4 correlated most strongly with trawling intensity (0.865) and dbRDA axis 5 correlated most strongly with current strength (0.544) (Table A3c).

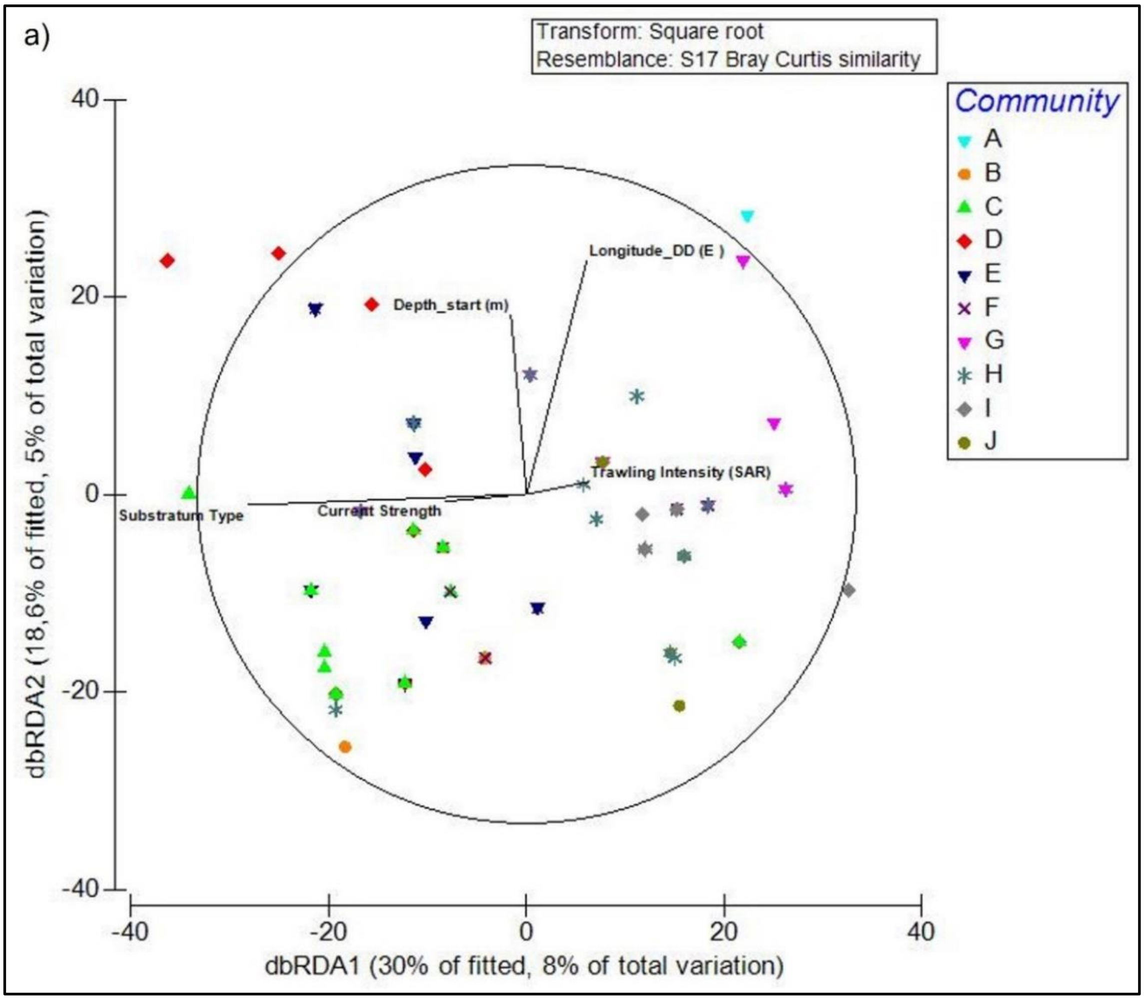

Figure 3.8. Distance-based redundancy analysis (dbRDA) on the resemblance matrix using species abundance data across the a) ten epifaunal communities (A – J), b) substratum categories and c) depth zones. Vectors of the top five environmental variables (longitude, depth, current strength, trawling intensity, and substratum type) are represented.

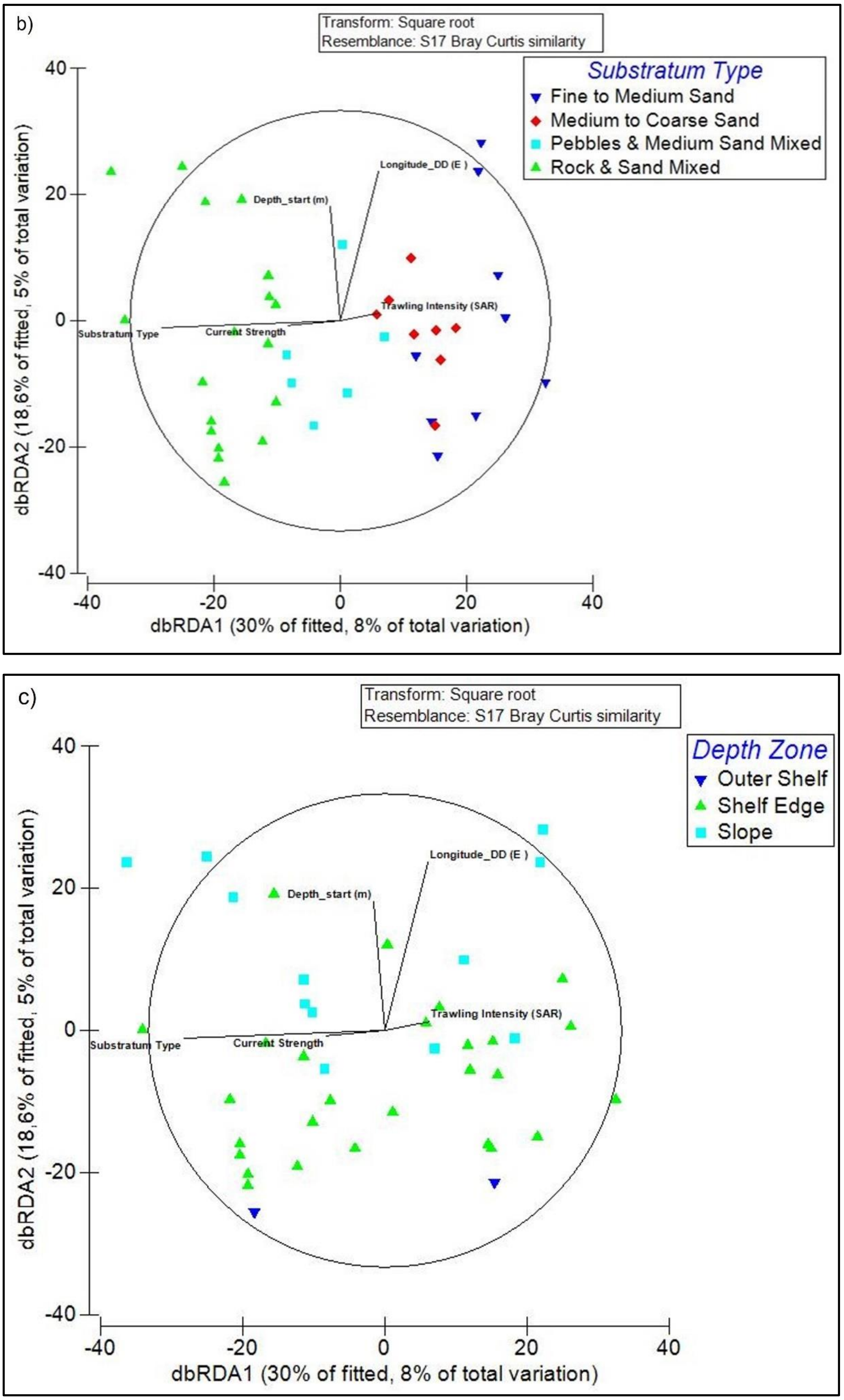

Figure 3.8 cont.

3.3.1 Testing the significance of the distribution of epifaunal communities across different ecosystem types using ANOSIM at the quadrat level in preparation for determining conservation targets

The classification of the replicate samples against the ten South African national marine ecosystem types represented in this study (Fig. A2) are shown in Fig. 3.9. Overall, the epifaunal assemblages found within the ten ecosystem types were significantly different from each other (ANOSIM, Global Test Sample statistic (Global R): 0.136, $p < 0.01\%$, 9999 permutations). Pairwise analyses showed that only three ecosystem pairs were not significantly different to each other (Table 3.3). Table 3.3 further illustrates overlap in species composition among several of the ecosystem types, namely i) Southern Benguela Rocky Shelf Edge Mosaic and Agulhas Coarse Sediment Shelf Edge (R statistic: -0.097, $p > 0.05$ or $p = 100\%$, 9997 permutations), ii) Kingklip Koppies and Agulhas Coarse Sediment Shelf Edge (R statistic: -0.086, $p > 0.05$ or $p = 100\%$, 9999 permutations), and iii) Agulhas Coarse Sediment Shelf Edge and Amathole Hard Shelf Edge (R statistic: -0.032, $p > 0.05$ or $p = 91.2\%$, 9111 permutations). The differences between the ecosystem types were confirmed by the recorded misclassifications (20.78%) according to the Canonical analysis for principal coordinates (CAP) and were reclassified into other ecosystem type groups (Table A8 and A9).

3.3.2 Testing the significance of the distribution of epifaunal communities across different ecosystem types using ANOSIM at the site level in preparation for determining conservation targets

Based on the averaged data per site, the ecosystem types were not significantly different between any of the sites (ANOSIM, Global Test Sample statistic (Global R): 0.02, $p > 0.05$ or $p = 40.1\%$, 9999 permutations), mainly because there were too few sites sampled in each of the different ecosystem types covered in the study area (refer to MDS, Fig. A3). For this reason, the conservation targets section will only use the image quadrats of the ecosystem types that possess three sites or more to ensure that a difference can be detected amongst the epifaunal data. The three ecosystem types meeting these criteria are Agulhas Coarse Sediment Shelf Edge, South West Indian Upper Slope and Agulhas Rocky Shelf Edge.

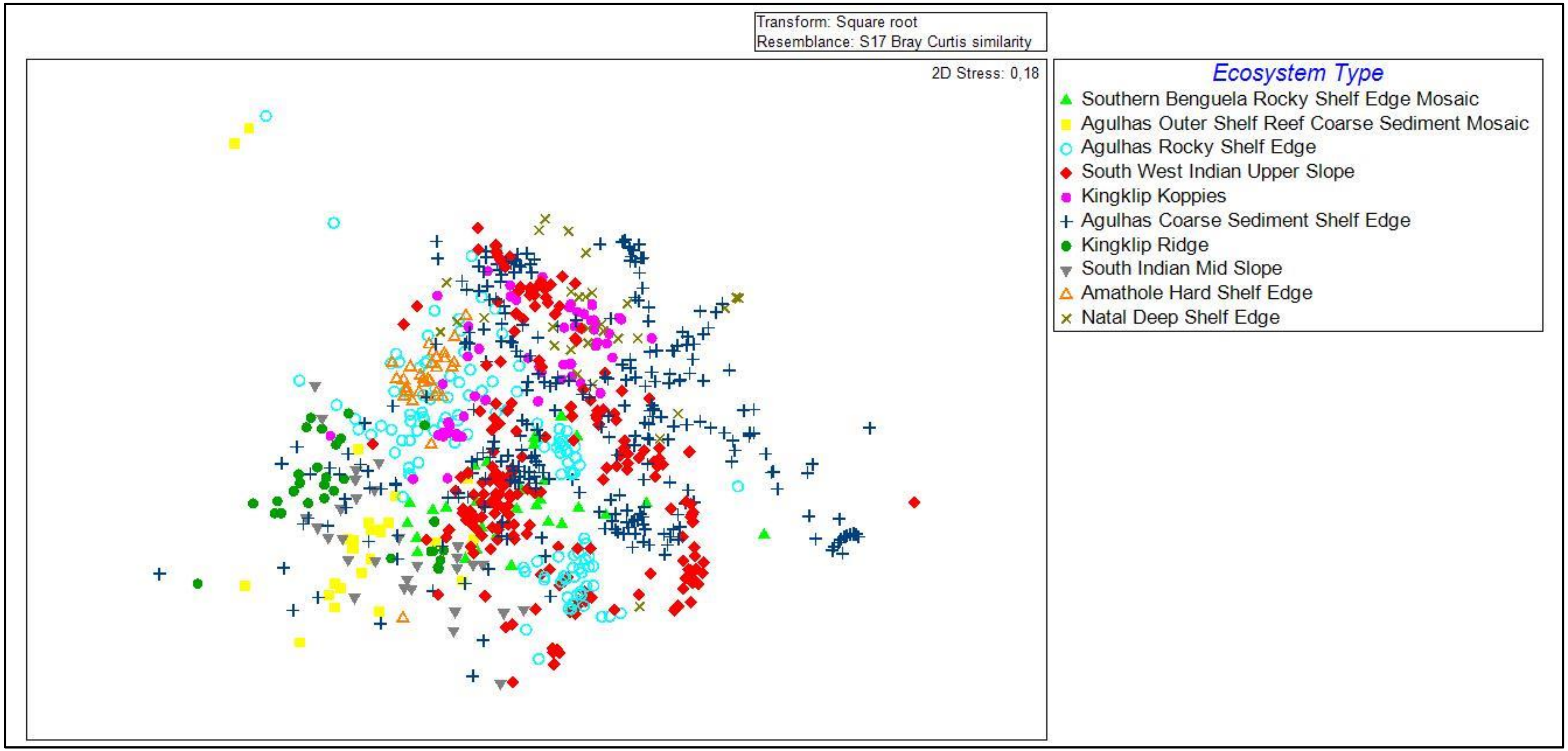

Figure 3.9. Multi-Dimensional Scaling Ordination plot depicting Bray-Curtis similarities among 852 replicate samples collected (excluding the outliers) from 29 sites, showing the relation among the ten NBA2018 ecosystem types (Sink, van der Bank, et al. 2019) along the Agulhas ecoregion based on species abundance data.

Table 3.3. One-way ANOSIM Pairwise comparisons between the benthic epifaunal communities of the 10 different ecosystem types covering 29 sites across the Agulhas ecoregion, based on the 2018 South African National Biodiversity Assessment (Sink, van der Bank, et al. 2019). The ecosystem pairs highlighted in bold font are not significantly different to each other

Ecosystem Type Pairings		**R Statistic**	**Sig. Level %**	**Actual Permutations**	**Number >= Observed**
Southern Benguela Rocky Shelf Edge Mosaic	Agulhas Outer Shelf Reef Coarse Sediment Mosaic	0.783	0.01	9999	0
Southern Benguela Rocky Shelf Edge Mosaic	Agulhas Rocky Shelf Edge	0.138	0.01	9999	0
Southern Benguela Rocky Shelf Edge Mosaic	South West Indian Upper Slope	0.169	0.01	9999	0
Southern Benguela Rocky Shelf Edge Mosaic	Kingklip Koppies	0.606	0.01	9999	0
Southern Benguela Rocky Shelf Edge Mosaic	**Agulhas Coarse Sediment Shelf Edge**	**-0.097**	**100**	**9999**	**9998**
Southern Benguela Rocky Shelf Edge Mosaic	Kingklip Ridge	0.951	0.01	9999	0
Southern Benguela Rocky Shelf Edge Mosaic	South Indian Mid Slope	0.803	0.01	9999	0
Southern Benguela Rocky Shelf Edge Mosaic	Amathole Hard Shelf Edge	0.847	0.01	9999	0
Southern Benguela Rocky Shelf Edge Mosaic	Natal Deep Shelf Edge	0.907	0.01	9999	0
Agulhas Outer Shelf Reef Coarse Sediment Mosaic	Agulhas Rocky Shelf Edge	0.409	0.01	9999	0
Agulhas Outer Shelf Reef Coarse Sediment Mosaic	South West Indian Upper Slope	0.421	0.01	9999	0

.

Table 3.3 cont.

Ecosystem Type Pairings		R Statistic	Sig. Level %	Actual Permutations	Number >= Observed
Agulhas Outer Shelf Reef Coarse Sediment Mosaic	Kingklip Koppies	0.79	0.01	9999	0
Agulhas Outer Shelf Reef Coarse Sediment Mosaic	Agulhas Coarse Sediment Shelf Edge	0.169	0.01	9999	0
Agulhas Outer Shelf Reef Coarse Sediment Mosaic	Kingklip Ridge	0.896	0.01	9999	0
Agulhas Outer Shelf Reef Coarse Sediment Mosaic	South Indian Mid Slope	0.745	0.01	9999	0
Agulhas Outer Shelf Reef Coarse Sediment Mosaic	Amathole Hard Shelf Edge	0.81	0.01	9999	0
Agulhas Outer Shelf Reef Coarse Sediment Mosaic	Natal Deep Shelf Edge	0.874	0.01	9999	0
Agulhas Rocky Shelf Edge	South West Indian Upper Slope	0.145	0.01	9999	0
Agulhas Rocky Shelf Edge	Kingklip Koppies	0.2	0.01	9999	0
Agulhas Rocky Shelf Edge	Agulhas Coarse Sediment Shelf Edge	0.077	0.01	9999	0
Agulhas Rocky Shelf Edge	Kingklip Ridge	0.448	0.01	9999	0
Agulhas Rocky Shelf Edge	South Indian Mid Slope	0.476	0.01	9999	0
Agulhas Rocky Shelf Edge	Amathole Hard Shelf Edge	0.281	0.01	9999	0
Agulhas Rocky Shelf Edge	Natal Deep Shelf Edge	0.394	0.01	9999	0
South West Indian Upper Slope	Kingklip Koppies	0.137	0.01	9999	0
South West Indian Upper Slope	Agulhas Coarse Sediment Shelf Edge	0.125	0.01	9999	0

Table 3.3 cont.

Ecosystem Type Pairings		R Statistic	Sig. Level %	Actual Permutations	Number >= Observed
South West Indian Upper Slope	Kingklip Ridge	0.426	0.01	9999	0
South West Indian Upper Slope	South Indian Mid Slope	0.279	0.01	9999	0
South West Indian Upper Slope	Amathole Hard Shelf Edge	0.123	0.02	9999	1
South West Indian Upper Slope	Natal Deep Shelf Edge	0.185	0.01	9999	0
Kingklip Koppies	**Agulhas Coarse Sediment Shelf Edge**	**-0.086**	**100**	**9999**	**9999**
Kingklip Koppies	Kingklip Ridge	0.825	0.01	9999	0
Kingklip Koppies	South Indian Mid Slope	0.843	0.01	9999	0
Kingklip Koppies	Amathole Hard Shelf Edge	0.386	0.01	9999	0
Kingklip Koppies	Natal Deep Shelf Edge	0.297	0.01	9999	0
Agulhas Coarse Sediment Shelf Edge	Kingklip Ridge	0.179	0.01	9999	0
Agulhas Coarse Sediment Shelf Edge	South Indian Mid Slope	0.178	0.01	9999	0
Agulhas Coarse Sediment Shelf Edge	**Amathole Hard Shelf Edge**	**-0.032**	**91.2**	**9999**	**9118**
Agulhas Coarse Sediment Shelf Edge	Natal Deep Shelf Edge	0.081	0.02	9999	1
Kingklip Ridge	South Indian Mid Slope	0.744	0.01	9999	0
Kingklip Ridge	Amathole Hard Shelf Edge	0.933	0.01	9999	0
Kingklip Ridge	Natal Deep Shelf Edge	0.951	0.01	9999	0
South Indian Mid Slope	Amathole Hard Shelf Edge	0.745	0.01	9999	0
South Indian Mid Slope	Natal Deep Shelf Edge	0.848	0.01	9999	0
Amathole Hard Shelf Edge	Natal Deep Shelf Edge	0.804	0.01	9999	0

3.4 Setting conservation targets for select ecosystem types

A total of 178 epifaunal taxa were identified across 615 quadrat samples within the three ecosystem types selected for the analysis to set conservation targets. The species-area curves representing the three ecosystem types were similar in terms of the steepness of the curve (Fig. 3.10). The Agulhas Coarse Sediment Shelf Edge has the greatest total number of species at 132 (Table 3.4). To reach a species target of at least 80% protection, 30% of the ecosystem type area would need to be protected (Table 3.5), with a z value of 0.15 (Table 3.3). The Southwest Indian Upper Slope had a z value of 0.12 and would require 20% representation of the ecosystem type area under protection to reach a species target of 80% (Table 3.4 and Table 3.5, Fig. 3.10). The Agulhas Rocky Shelf Edge has the lowest species richness recorded (94, Table 3.4) from the four sites surveyed within this ecosystem type. With a z value of 0.12, 20% of the ecosystem type area under protection would represent at least 80% of the species (Table 3.4 and Table 3.5, Fig. 3.10). If the species target is increased to 90%, then the target for the area under protection for all three ecosystem types becomes 50%, which would represent half of the area covered by each ecosystem type (Table 3.5).

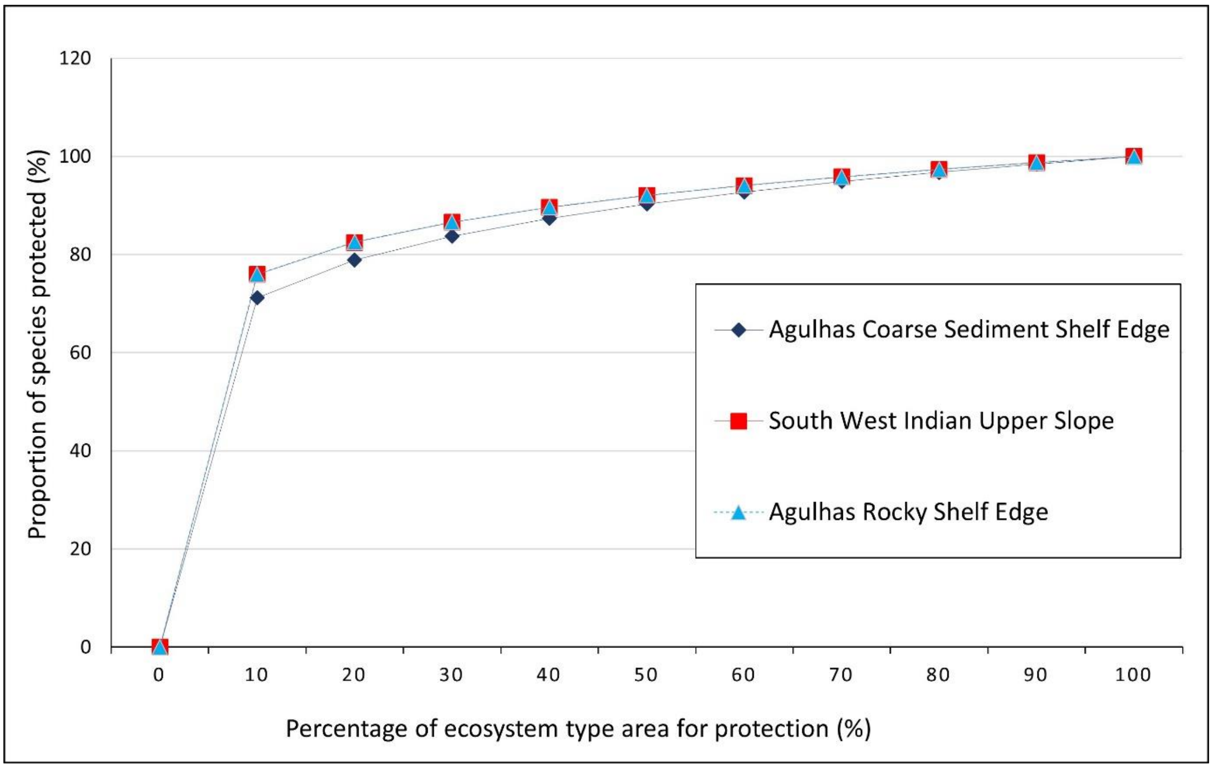

Figure 3.10. Proportion of species represented as a function of the proportion of original ecosystem type area for the Agulhas Coarse Sediment Shelf Edge, Southwest Indian Upper Slope and Agulhas Rocky Shelf Edge that is conserved.

Table 3.4. Associated number of sites, number of samples, total area (χ_2), area per sample (χ_1), total number of species (Bootstrap species richness estimator) (y_2), average number of species (y_1) per ecosystem type and z values (rate of accumulation of species) per ecosystem type utilized in species-area relationship-based conservation target calculations.

Ecosystem Type	**No. of sites**	**No. of quadrat samples**	χ_2	χ_1	y_2	y_1	**z**
			Total Area (km^2)	**Area per sample (m^2)**	**Total no. of species (bootstrap)**	**Ave. no. of species**	**Rate of accumulation of species**
Agulhas Coarse Sediment Shelf Edge	10	289	3990.51	1.74	132.54	5.52	0.15
Southwest Indian Upper Slope	7	206	17524.91	2.35	111.51	7.35	0.12
Agulhas Rocky Shelf Edge	4	120	5232.98	1.88	94.30	7.07	0.12

Table 3.5. Expected percentages of species represented in increasing percentages of the ecosystem type. Values calculated with the Bootstrap estimator of the total number of species and an estimated area of the sampling quadrats equal to 1m^2.

	Proportion of Species protected (Bootstrap)		
Percentage of ecosystem type area protected (10% incremental steps)	**Agulhas Coarse Sediment Shelf Edge**	**South West Indian Upper Slope**	**Agulhas Rocky Shelf Edge**
0	0	0	0
10	71.21	75.92	76.01
20	78.87	82.49	82.55
30	83.73	86.59	86.64
40	87.36	89.62	89.66
50	90.28	92.04	92.07
60	92.74	94.07	94.10
70	94.88	95.82	95.84
80	96.76	97.37	97.38
90	98.46	98.75	98.75
100	100	100	100

Chapter 4: Discussion

This study aimed to investigate epifaunal communities in the shelf-slope transition of the Agulhas ecoregion to support marine ecosystem classification, mapping, and management. Biodiversity patterns and potential drivers of offshore benthic biodiversity were examined using the data collected along the outer shelf and slope environment. A transition zone was recognized between the outer shelf and slope, namely, the shelf edge zone, which has been identified as a unique system, hosting an environmental envelope that is different from the shelf and slope in the Agulhas ecoregion. In this shelf-slope transition zone, substratum type appears to be a primary driver of the epifaunal assemblages. Conservation targets have also been quantified and form the basis for the first ecosystem-specific data-driven targets for offshore marine benthic ecosystems along the south coast of South Africa, to inform the expansion of South Africa's marine protected area network.

4.1 Epifaunal communities and their drivers within the Agulhas ecoregion

This study found that an interplay of various geological and oceanographic processes, including anthropogenic impacts, were most likely potential drivers of the biological patterns observed along the outer shelf and slope in the Agulhas ecoregion. Ten benthic epifaunal communities were identified in the Agulhas ecoregion shelf-slope transition (Fig. 3.2 and 3.3) and were mainly separated by substratum type, presence of particulate organic matter, longitude, trawling intensity and depth (Fig. 3.8). These communities were distributed across the entire longitudinal range of the study area (Fig. 3.5). However, no clear spatial boundaries separated these epifaunal communities, and an overlap in species composition for some of the communities was a common observation.

The species composition of each community was different, with most communities being represented by a specific suite of characteristic (Table 3.1) and distinguishing species (Table 3.2). These communities were mostly characterized by between one and four species (Table 3.1). Characteristic taxa of communities varied from species with very strong attachment, like stalked crinoids (communities A and D), various corals (communities B and C) and bryozoans (community B and C) to those that burrow, such as polychaetes (F, G and I) and cerianthid anemones (community F), to motile species such as brittle stars (community I), foraminifera (community H) and crustaceans (F and J) (Table 3.1).

Epifaunal species richness was lower in communities that occurred at one site (i.e., Community A, site 37, Fig.3.4 and Fig. 3.5), or sites that were in close proximity to one another (i.e., Community F, site 11_1, 11_2 and 14, Fig. 3.4 and Fig. 3.5), likely an artefact of sampling effort or if it was a single site, species turnover between samples were expected to be lower; while other communities were rich in epifaunal species and spanned a wide distributional range, which was mostly influenced by substratum type. Similarly, Makwela (2017) found that the distribution of epifaunal assemblages (biotopes) within the outer shelf of KwaZulu-Natal, along the east coast of South Africa, was mostly correlated with sediment type.

In this study, the distance-based linear model (DistLM) analysis identified substratum type as the highest contributing environmental variable, responsible for 7.38% variation in species composition across the study area (Table A3a). At a finer scale, substratum or sediment type is often reported to be a direct determinant of where a particular species occurs (Auster and Langton 1999). Evidently, substratum type plays a key role in shaping the community structure and influencing the composition of epifaunal biodiversity within the 10 identified epifaunal benthic communities (Fig. 3.8b) (Grinyó, Gori, et al. 2018, Howell 2010, McArthur, Brooke, et al. 2010).

Levin, Etter, et al. (2001) report that deep-sea sediments were once thought to be homogenous across the seafloor, however, following recent advancement in deep-sea sampling, these sediments are now recognized as a dynamic, heterogenous environment. An environment of this kind allows more epifaunal species to coexist by providing them with alternative sites to attach to or burrow into (Levin, Etter, et al. 2001). Similarly, the study area presented an array of substratum types that appeared to be a mosaic of habitat types which occur along a gradient of fine-coarse sediment to pebbles to rock (Fig. 3.6, Fig. 3.8b), thus forming patches across the study area. These patches may result from the impact of the Agulhas Current (Lutjeharms 2006b); more specifically through the process of sediment deposition and slumping within the area that stretches from the east of the Agulhas Bank to offshore of East London (de Wet and Compton 2021), thus increasing sediment heterogeneity along the outer shelf and slope of the Agulhas ecoregion.

Distinct differences in species composition were observed between habitats composed of unconsolidated sediments versus consolidated sediments. This pattern is similar to findings of Hemery and Henkel (2015) on the continental shelf of the Pacific Northwest, where habitats composed of a mix of sediment with rocks were greater in species richness than unconsolidated sediments (in this study, between 1 - 18 spp. per quadrat replicate, Fig.3.4, Fig. 3.7a), mostly comprising sessile and structure-forming invertebrates, such as hydroids, corals, bryozoans, and sponges. Rocky outcrops and boulders were frequently dispersed between sandy plains along the continental margin (Tissot, Yoklavich, et al. 2006), therefore offering a wide range of microhabitats for both attached and mobile epifaunal species, increasing habitat complexity and heterogeneity (Hemery and Henkel 2015).

Habitat heterogeneity was apparent in many of the rockier habitats of Communities B (outer shelf), D and E (on the shelf edge and upper slope), where hard and soft corals, sponges, sea fans, bryozoans and hydroids were among the more commonly-observed habitat-forming epibenthic fauna (Table 3.1 and Table A6). Grinyó, Gori, et al. (2018) documents a similar suite of epifauna in rockier habitats on the shelf edge of the Menorca Channel in the Mediterranean Sea. Due to the stability of their surrounding substrate and their individual complex structure and sessility, they were able to provide other epibenthic organisms with a unique, three-dimensional habitat to attach themselves to or settle on in the Agulhas ecoregion (Hemery and Henkel 2015, Lange and Griffiths 2014, Tissot, Yoklavich, et al. 2006, Yesson, Simon, et al. 2015). Smaller crustaceans, brittle and feather stars and shrimps were observed as common inhabitants of these larger habitat-forming species, potentially attempting to find shelter, food, or protection from predators (Hemery and Henkel 2015, Tissot, Yoklavich, et al. 2006).

Unconsolidated sediments along the shelf edge were alternatively characterized by the brittle star, *Ophiura trimeni*, polychaetes, and burrowing anemones, consequently forming Community I (Table 3.1 and Fig. 3.5). These unconsolidated sediments comprised fine to coarse sediment, creating a favourable environment for burrowing epifauna, such as the Polychaete sp. A, burrowing anemones, seapens and radial soft corals. In contrast, Communities F, G and H were comprised of unconsolidated sediment with a mix of pebbles along the shelf edge and slope (Table 3.1 and Table A6). Due to the more uniform nature of these habitats, they were mostly populated by burrowing species, such as polychaetes, burrowing anemones and seapens, or motile invertebrates, including brittle stars, foraminifera, shrimp and deep-water spider crabs. Smaller brittle stars and crustaceans were occasionally seen inhabiting some of the more complex “habitat-forming” burrowing invertebrates, such as seapens (Tissot, Yoklavich, et al. 2006). It may be that the interaction between these epibenthic fauna through various biological processes, such as competition and bioturbation, could also play a role in determining their geographic distribution in the Agulhas ecoregion (Levin, Etter, et al. 2001).

Although low species richness (between 1 – 10 spp. per quadrat replicate) was observed in these non-complex sediment environments (Fig.3.4, Fig. 3.7a), there were occasional sightings of high abundances of specific epifaunal species. Among certain transects along the shelf edge, large aggregations of brittle stars, specifically *Ophiura trimeni,* were observed embedded in sandy plains, particularly throughout site 21 (Fig. 3.5) within Community I. The same was seen for polychaete tubes, which were very abundant in Community G (site 49) and foraminifera in Community H (particularly, site 18 and 24) (Table 3.1 and Fig. 3.5). Gray and Elliott (2009) confirm that polychaetes, echinoderms, crustaceans, and molluscs tend to dominate the macrobenthos amongst unconsolidated sediments, which was evident in most of the sediment communities (Table 3.1). Although the reasons for these large aggregations are unclear, trawling activity may have contributed to the formation of these dense aggregations (site 21 was heavily trawled, whereas sites 18, 24 and 49 were lightly trawled, Table A1). This was specifically observed with an increase in ophiuroid brittle star aggregations along the outer continental shelf of the west coast of South Africa and Namibia (Atkinson, Field, et al. 2011) and polychaete aggregations in soft sediments of recovering transects of a benthic trawling study done along the central California continental shelf, in the United States of America (de Marignac, Hyland, et al. 2009).

Along the east coast, where the shelf is narrow and steep, ROV studies performed by Makwela (2017) along the KwaZulu-Natal outer shelf environment found that epifauna typically associated with harder substrata were also found occupying areas categorized as unconsolidated sediment (Makwela 2017). Similar patterns were seen in this study and these epifauna were mostly cnidarians, including cup corals, hydroids, and black corals. However, they were found in smaller numbers than were usually observed on hard rock substrata. Underlying rock may have been inundated by sand (Ryan, Brooke, et al. 2007) as a result of hydrodynamics related to the Agulhas Current in the area (Lutjeharms and Bornman 2010, Lutjeharms 2006a). This likely resulted in a mix of hard and soft sediment species present in areas observed as unconsolidated sediment (Makwela 2017) and could not easily be distinguished in the imagery.

Depth zonation was evident in the Agulhas ecoregion based on the distribution of benthic epifaunal species (Fig. 3.8c). Between the outer continental shelf and upper slope, an intermediate zone, namely the continental shelf edge, was identified and hosted a different array of benthic epifauna compared to the other two depth zones (Table A6). Though substratum types were similar across depth zones, the division of these zones might have been caused by differences in pressure, temperature and/or food availability (Carney 2005). Similarly, along the Gulf of Mexico, the shelf edge was identified as a distinct community (Sammarco, Nuttall, et al. 2016), whereas offshore of Namibia it was considered an intermediate zone between the outer shelf and slope zones (Eisenbarth and Zettler 2016). In this study, only one site represented the outer shelf (135 m, Table A6), which limits the interpretation for that specific depth zone (100 - 150 m). In contrast, the shelf edge and upper slope had more sites sampled within their zones, with 19 sites in the shelf edge (200 – 500 m depth) and nine in the upper slope (500 – 700 m) (Table A6).

Despite minor differences in species composition in the three depth zones of the Agulhas ecoregion (Table A6), they still proved to be significantly different from one another (Table A5). With each of these depth zones hosting a suite of characteristic epifaunal species (Table A6), there were communities limited to the outer shelf (community B), shelf edge (communities C, I and J) and upper slope (community A) (Table 3.2, Fig. 3.5, Table A6). Along the west coast of South Africa, similar studies have been carried out using epifauna data (Lange and Griffiths 2014, Shah 2018) confirming that depth plays a major role in the distribution of offshore epifaunal communities. Similarly, depth was identified as a significant variable driving biological patterns in the Australian margin (Przeslawski, Currie, et al. 2011) and Menorca Channel in the Western Mediterranean Sea (Grinyó, Gori, et al. 2018).

Shelf edge communities in the Agulhas ecoregion were characterized by a mix of substratum types and consequently the species differed along these gradients. Epifauna differentiating the shelf edge from the outer shelf and upper slope zones showed large abundances of foraminifera, *Ceriantheopsis* sp. *Ophiura trimeni*, polychaete tubes and shrimp sp. B (Table A6). This pattern most likely transpired from the combined effect of habitat heterogeneity, topography and the unique hydrodynamic conditions (including upwelling and internal waves) (Huthnance 1995, Jackson, Rainville, et al. 2012, Shillington, Reason, et al. 2006) along the shelf edge.

Coral gardens composed of hydrocorals, cup corals, the bryozoan, *Adeonella* sp., various ascidians and foraminifera formed Community C along the shelf edge and was consistently characterized by *Stylaster* sp.1 (Table 3.1). Occupying a wide distribution range, from offshore of Cape Agulhas to Port Alfred (Fig.3.5), the sites within Community C were a mix of rock and sand substrata, a favourable habitat for these kinds of species. Due to their position on the continental shelf, shelf edge habitats are most likely exposed to frequent currents, which provides a source of food, especially for passive suspension feeders (Grinyó, Gori, et al. 2018). Many of these reef-forming organisms, such as stylasterid hydrozoans and bryozoans, create large and complex structures that add to the multidimensional space and significantly increase habitat and biodiversity heterogeneity across the shelf edge (Buhl-Mortensen, Vanreusel, et al. 2010).

Continental slopes are usually considered to start at a depth of 200 m (da Costa, Mincarone, et al. 2015, Levin and Sibuet 2012), but along the south coast of South Africa the upper slope has been considered to span the depths 500 – 1000 m (Sink, van der Bank, et al. 2019). In this study, epifauna differentiating the upper slope from the outer shelf and shelf edge zones were large abundances of stalked crinoids, a polychaete, *Praxillura* sp., foraminifera, the burrowing anemone *Ceriantheopsis* sp. and various hydroids (Table A6). Unlike the outer shelf, epifauna living along the slopes usually experience extreme conditions that include reduced oxygen, cooler temperatures, lack of sunlight, high pressure and often low food availability (Carney 2005).

It was also noted that sites in close proximity did not necessarily have similar communities. Both site 37 (Community A) and site 38 (Community G) were located offshore of the Kei River mouth (Fig. 3.5), but their species composition and structure remained disparate (Table 3.1). With distinct differences in substratum type and having less than 200 m depth difference between these two sites, perhaps the steep topographic features and slope of this area (de Wet and Compton 2021, Lutjeharms 2006a) may be responsible for the differences observed within their community composition. Site 37 (Fig. 3.5) occupied the steep slopes, with fine to medium sand inhabited by stalked crinoids, seapens, octocorals, and a burrowing sponge, *Hyalonema* sp. (Table 3.1); whereas site 38 on the shelf edge, with a mix of pebbles and sand, was inhabited by a mix of motile, attached, and burrowing species, such as polychaete tubes, foraminifera, squat lobsters (*Munida benguela),* and soft corals (Table 3.1 and Fig. 3.5).

With a broad longitudinal range (between 19° and 29° E), this study presented an opportunity to assess biogeographic differences between the identified epifaunal communities found along the outer shelf and slope of southern Africa (Fig. 3.5). Although longitude was considered an influential environmental variable, there was no clear longitudinal distinction between communities, with many extending over the entire or most of the longitudinal range (Fig. 3.5). Perhaps the complication of longitude results from the influence of the Agulhas Current as it flows southwards along the south-east coast to the south coast of South Africa. Greater variation of epifaunal species richness was found between the longitudes of 23° and 27° E, which is between Knysna and Port Alfred (including, communities B, C, D, F, I, J and most of E,G, H, Fig. 3.7b and Fig. 3.5). Shah (2018) reports that epifaunal assemblages based on trawled data varied significantly between the west and south coast of South Africa, therefore showing that location is also important in determining epifaunal assemblages.

Demersal trawling can severely impact benthic biodiversity, by disturbing the habitat and biotic communities and hence affecting productivity, damaging species or removing larger species, therefore lowering species richness (Fig. 3.7c, (Buhl-Mortensen, Ellingsen, et al. 2016, Eigaard, Bastardie, et al. 2017, Kaiser, Ramsay, et al. 2000). This study showed that in areas of high trawl intensity, low epifaunal species richness was observed (Fig. 3.7c). Similarly, in unconsolidated sediments along the outer continental shelf of the west coast of South Africa and Namibia, epifaunal abundance, richness and diversity decreased with increasing trawling intensity (Atkinson, Field, et al. 2011). In this study, scour marks from deep-sea trawling were observed in a few of the fine-coarse sediment quadrat replicates within sites 11_1, 11_2, 14, 44 and 50, although these had swept-area ratio values lower than 5 (Table A1). Most of the epifauna found in these sites were burrowing anemones, polychaetes (*Praxillura* sp. and unknown Polychaete sp. A) and various crustaceans (*Rochinia hertwigi*, Shrimp sp. B and the hermit crab, *Sympagurus dimorphus*) (Table 3.1). Contrastingly, site 29 had mixed rock and sand substratum, but had the highest trawling footprint (swept-area ratio value of 14,2, Table A1) compared to the rest of the sites surveyed. This site was inhabited by a mix of epifaunal species, such as stalked crinoids, shrimp, hydroids, soft corals, and brittle stars. Perhaps the presence of rocky outcrops prevent trawling in the area and may explain the preservation of the observed high species richness within this transect (ranging between 4 - 12 species, with an average of nine species in site 29, Fig. 3.7c) (Grinyó, Gori, et al. 2018). Comparably, in European waters, deposit and suspension feeders were commonly found in areas impacted by heavy trawling along the continental shelf (Eigaard, Bastardie, et al. 2017).

Alternatively, the supply of food or POM flux in deep-sea communities can influence species richness (Levin, Etter, et al. 2001). In this study, a few of the sites surveyed (11_3, 12, 20, 26, 29, 30) along the shelf edge and upper slope between Knysna and Gqeberha, displayed a layer of particulate organic matter on the surface of various sediments across the transects (Table A1). In some cases, several of their quadrat replicates comprised a combination of coral rubble and particulate organic matter and had greater species richness than those that did not have either (Fig. 3.7e, Fig. 3.7j). Mostly hard substrata species, such as hydroids, soft corals and octocorals settled within these biogenic habitats (Taylor and Wilson 2003). Most of the quadrat replicates from these sites comprised hard bedrock or coarse biogenic coral reef habitat that were mostly fragments of dead coral rubble (site 30, i.e., which could either be part of a larger coral mound or represents an area damaged from trawling).

Benthic ecosystems within the southern and eastern coast of South Africa are greatly influenced by the movement of the Agulhas Current and its strong current speeds, together with the change in bathymetry moving southwards along the continental margin toward the Agulhas Bank (Lutjeharms 2006a). The bathymetry along the eastern shelf edge of the Agulhas Bank off Mossel Bay up to Gqeberha is quite different to that seen off the coast of the Eastern Cape (Fig. 3.5). More specifically, it is presented with a wide, double shelf break and narrows out toward the eastern margin of the continental shelf between Gqeberha and just offshore of the Kei River mouth, forming one shelf break that steeply descends into the slopes off the Eastern Cape (de Wet and Compton 2021, Sink, van der Bank, et al. 2019).

Moving further downstream, the waters between the outer shelf and continental slopes of the southern Agulhas Current become much cooler (Lutjeharms 2006a), therefore creating a shift in species assemblages off the southern coast of South Africa. In this study, a shift in temperature is evident moving from the outer shelf to the upper slopes, perhaps influencing the differences found within epifaunal assemblages spanning the three different depth zones. Off Knysna, the outer shelf experienced a temperature of 8,5°C (Table A1). The shelf edge probably encountered the most temperature variability, where it ranged from 6 – 10°C between Cape Agulhas and Port Alfred, and between 10 - 12°C north of Port Alfred to offshore of the Kei River mouth (Table A1), perhaps influencing the heterogeneity in species composition along the shelf edge. The upper slope environment across the Agulhas ecoregion endured cooler temperatures ranging between 5,4 – 7,8°C (Table A1). In other work, similar temperature gradients have been found on the west coast along the shelf to deep-sea areas off the coast of Namibia (Eisenbarth and Zettler 2016), with increasing depth accompanied by a decrease in temperature. However, overlapping temperatures may have been present between the three depth zones surveyed in the Agulhas ecoregion (Fig. 3.7h), as a result of the unique topography, bathymetry, and hydrodynamics of this ecoregion.

Considering the unique topography and hydrodynamics of the southern coast, the meandering Agulhas Current gives rise to a sporadic outflow of warmer Agulhas Current waters as a consequence of cyclonic eddy systems (Lutjeharms 2006a), particularly south of Gqeberha moving along the shelf toward the Agulhas Bank. Depending on the seasonal changes and wind strength, site 03, situated on the western margin of the Agulhas Bank (Fig. 3.5), may also be influenced by the Benguela upwelling system (Lutjeharms and Bornman 2010, Lutjeharms 2006a) which brings cooler, nutrient-rich waters on to the shelf, supporting benthic epifauna in that area. Although site 03 was found along the western margin of the Agulhas Bank (Fig.3.5), it also displayed a similar suite of species as the rest of the sites in community C (Table 3.1), which were mostly located on the north-eastern margin of the Agulhas Bank and stretched toward Port Alfred (Fig. 3.5). These habitats were mostly comprised of a mix of pebbles to mixed rock and sand (Table A1). The presence of an upwelling cell along the far-eastern margin of the Agulhas Bank on the wide shelf also brings in cool, nutrient-rich water onto the shelf, possibly increasing primary productivity within this area (Barlow, Lamont, et al. 2010, Lutjeharms 2006a, Russo, Lamont, et al. 2019). Thus, the mixing of cool and warmer waters presents unique conditions for epifauna inhabiting the southern margin of South Africa (Griffiths and Robinson 2016), therefore influencing the structure and composition of epifaunal assemblages in this part of the Agulhas ecoregion.

In addition to the five highest-contributing variables namely substratum type, presence of particulate organic matter, longitude, trawling intensity and depth, there were other variables that contributed to explaining 48.6% of the total fitted variation of epifaunal patterns within the Agulhas ecoregion (Fig. 3.8 and Table A3b). These variables included current strength, slope, distance to shelf-break, bottom temperature, and presence of coral rubble (Fig. 3.8, Table A3a and Table A3b). This value is greater than that of macro-infaunal variation explained by sediment particle sizes in the same area (18.71%, in a subset of the sites sampled in the Deep Secrets survey (Brandt 2019). It is also higher than the total fitted variation in studies on the west and east coasts of South Africa (± 40%, (Karenyi 2014, Makwela 2017)).

It can be concluded that there are key variables missing from the analysis, therefore limiting the explanatory power of environmental drivers of epifaunal communities within the Agulhas ecoregion. Some of these missing variables could potentially be relief, oxygen concentration, pressure, food availability and primary productivity, however, this information is not currently available, although it could potentially be investigated in future studies. These investigations could also look for better quantitative data to define variables such as slope and current velocity, or perhaps by measuring these two variables it would improve the total fitted variation of the DistLM model. Additionally, only one value was recorded per site for most of the environmental variables collected, therefore variation within each study site could not be considered. Also, epibenthic biodiversity assessments along the continental margin of the south coast of southern Africa have not been sufficiently assessed to date. The use of quantitative towed-camera data has revealed that the shelf-slope transition zone exhibits some unique environmental features, including a variety of benthic substrata and oceanographic features that influence epifaunal species composition and abundance at a local scale.

No single spatial scale should be used to examine biodiversity patterns observed within the Agulhas ecoregion, as the observed patterns may be a result of multiple spatial scales (Levin 1992, Silberberger, Renaud, et al. 2019). A combination of local, regional, and possibly global hydrodynamic systems and oceanographic parameters may potentially be influencing the environmental heterogeneity (Levin, Etter, et al. 2001) across South Africa's continental outer shelf and slopes (Sink, van der Bank, et al. 2019). This was seen by Williams, Althaus, et al. (2010), where ocean circulation, water mass structure, temperature, oxygen, and latitude would vary at large spatial scales, mostly at a regional scale along the Australian south-western continental margin, and seabed type was important for explaining variation of megabenthic biodiversity at a smaller megahabitat scale (~ 10 – 100 km) or mesohabitat scale

(10 m – 1 km). The data used in the present study were used to capture the fine-scale variation that results from the mosaic of substrata present within and across sites, but for management purposes, the site-level may be more appropriate when distinguishing ecosystem types. For monitoring purposes, it is important to consider various scales and biota types. As part of the Deep Secrets project, fish (Weston 2021), epifauna and macro-infauna (Brandt 2019) were collected. This provides an opportunity for comparisons with these other datasets in the future to develop a more holistic view of biodiversity within the Agulhas ecoregion. Marine benthic ecosystems within the Agulhas ecoregion can and probably should be defined at multiple (regional and local) scales, and the same goes for the management of these ecosystems.

The IUCN typology of marine ecosystems (Keith, Ferrer-Paris, et al. 2020) recognises the marine shelves and deep-sea floor as two distinct biomes and distinguishes between rocky and unconsolidated shelves in their ecosystem functional groups. The global system provides little guidance in classifying the shelf edge or transition between shelf and deep sea and does not recognize or accommodate mosaic habitats in ecosystem types for either the shelf or the deep-sea floor. More research is needed to explore and compare ecosystem functionality between these unconsolidated, consolidated and mosaic ecosystem types. The results of this study and future studies may be informative in guiding further iterations of global marine ecosystem classifications.

In South Africa, the marine ecosystem types surveyed within the current study tend to be heterogeneous, particularly since substratum type has previously been under sampled and not efficiently mapped in this area. This may be a result of the diverse and dynamic environmental conditions of the south coast, however, considering the national marine ecosystem classification and map (Sink, van der Bank, et al. 2019), the divisions between these ecosystems are not as clear as in other areas in South Africa. For example, Karenyi (2014) showed strong divisions between distinct biological assemblages of unconsolidated sediments along the continental shelf and shelf edge of the west coast, perhaps because more accurate information had been collected about the underlying substratum and physical processes within that region. The exploratory research done in the current study has revealed that the classification and mapping of the marine ecosystem types in the shelf to slope transition zone has not yet been resolved. Considering the results of this study, the main substratum type suggested by the ecosystem type classifications of the NBA2018 (Sink et al 2019) were inaccurate, particularly for the Agulhas Coarse Sediment Shelf Edge, which consisted of a mixture of fine to coarse sediments, including rock (Table A1). As seen in this study, all 10 of the ecosystem types examined were significantly different to one another, except three of them showed a contrast in terms of their classification using epifaunal abundance data from this study in comparison to the existing classification of ecosystem types (ANOSIM, Table 3.3, MDS Fig. 3.10, Fig. A2). Similarly, Makwela (2017) found that the ecosystem types depicted by the epifaunal data used in her study contradicted both the NBA 2011 (Sink, Holness, et al. 2012) ecosystem classification and the South African East Coast marine bioregion classification (Livingstone, Harris, et al. 2018) derived from the SeaPLAN project (Harris, Livingstone, et al. 2012). Evidently, further verification of the substratum type map and an update of the delineation of the ecosystem types within the Agulhas ecoregion is required. For management purposes, the best available information was used to update the map and in moving forward with the task of reaching the goal of expanding South Africa's MPA network, the boundaries of the existing map were therefore used to calculate conservation targets for the ecosystem types in the shelf-slope transition zone of the Agulhas ecoregion.

4.2 Determining conservation targets for selected marine ecosystem types in the Agulhas ecoregion

Using species-area relationships, ecosystem-specific conservation targets have been quantified for offshore national marine ecosystem types (unconsolidated and consolidated) in the Agulhas ecoregion. Most epifaunal species observed within this study area were not confined to a single ecosystem type, therefore 80% deemed appropriate for species representation in setting targets for the three selected marine ecosystem types (Karenyi, Nel, et al. 2016, Porter, Sink, et al. 2011, Rondinini 2011). The rapid achievement of species accumulation at 10% area (Fig. 3.10) could have been a result of the turnover of species between quadrats and sites and possibly the use of the bootstrap method, which is known to be more conservative. However, to ensure representation of benthic epifaunal diversity within the Agulhas ecoregion, 20% of the area of both the South West Indian Upper Slope and the Agulhas Rocky Shelf Edge ecosystem types would need to be protected to reach a target of representing 80% of the species present. However, 30% of the Agulhas Coarse Sediment Shelf Edge ecosystem type area would need to be protected to represent 80% of the species present (Table 3.5 and Fig. 3.10). These targets falls within the average range of 20 – 30% suggested by Rondinini (2011) to represent 75 – 80% of species within ecosystems. Contrastingly, 10 - 15% of the habitat area was considered sufficient to represent 80% of the species present within macrofaunal communities in unconsolidated sediment habitats along the continental shelf of the South African west coast (Karenyi, Nel, et al. 2016).

An increase in species richness can be expected with habitat heterogeneity, which therefore increases the ecosystem type target substantially (Desmet and Cowling 2004, Metcalfe, Delavenne, et al. 2013). The Agulhas Coarse Sediment Shelf Edge, which had the highest target (Table 3.5), covered a number of different substratum types, spanning a large expanse of the study area (Fig. A2) and is therefore seemingly more heterogenous than the other two ecosystem types selected. The sites sampled within the Agulhas Coarse Sediment Shelf Edge ecosystem type displayed a high species turnover across the sites (with a z value of 0.15, Table 3.4) which may have been a result of sediment type, habitat heterogeneity and patchiness. Hence, it has a higher target than the other two ecosystem types (Foster, Foggo, et al. 2013, Metcalfe, Delavenne, et al. 2013). Within the English Channel, Metcalfe, Delavenne, et al. (2013) observed that by increasing the sample size of the habitat type, in addition to using the Bootstrap species richness estimator, the habitat target can significantly increase. Meanwhile, Foster, Foggo, et al. (2013) used the Chao1 species richness estimator to determine targets for a depth band of 200 – 1100 m in the deep NE Atlantic and resulted in representing 69 – 82% species with a habitat target of 10 – 30%. They found that the proportion of the habitat area required to protect a given proportion of species was influenced by the substratum type and depth (Foster, Foggo, et al. 2013).

Not knowing the accurate extent of the boundaries of these marine ecosystem types is one of the major constraints for setting targets within the Agulhas ecoregion. Along with not having enough coverage and potential flaws in the delimitation of the ecosystem types, conservation targets have nonetheless been set for the three selected existing ecosystem types, as this is currently the best available information. In future, larger sample sizes and more accurate mapping of ecosystems will improve target estimates, however for now, based on the best available information, the calculated targets fall within the ranges found elsewhere (Harris, Nel, et al. 2014, Rondinini 2011).

Based on the latest National Biodiversity Assessment (Sink, van der Bank, et al. 2019), South Africa has shifted away from working with conservation targets in ecosystem assessment and instead has taken on the International Union for Conservation of Nature (IUCN) Red List of Ecosystems (RLE) criteria approach (Bland, Keith, et al. 2017) to determine ecosystem threat status. Despite the shift in focus for conservation targets, South Africa continues to set targets for species, however, this kind of research is still relevant in terms of international literature and to a certain extent, this information will aid systematic conservation planning processes within this region, particularly providing an estimate of the ecosystem type area required to protect a given proportion of epifaunal species. Considering the Agulhas ecoregion supports many important commercial fisheries, as well as provides essential nursery and spawning areas, including migratory routes for various megafauna (Lutjeharms 2006a), this information will help improve our understanding of these deep-sea ecosystems and decision-making for new priority areas within the Agulhas ecoregion. Therefore, integrating a more comprehensive description of the benthic component of South Africa's continental margin and slopes and having set conservation targets for these areas will serve as a starting point for South Africa's systematic conservation planning and management.

4.3 Overall limitations of the study

Several challenges were encountered during both the sampling phase and the data processing phase of this study. These challenges were attributed to various factors, including limited ship-time and limited sampling gear (the survey was limited to using a towed camera and did not have access to a deep Remotely Operated Vehicle (ROV)). Most of the samples were collected along a narrow depth band, perhaps due to infrastructure constraints. Limited environmental data were collected for most of the sites surveyed and many global data sets lack accurate data in this region. To better assess and determine the environmental drivers of the Agulhas epifaunal communities, a broader scope of environmental data is required. Future studies should include the data collection of dissolved oxygen, primary productivity, substratum type from multi-beam echosounders, current velocity, slope (topographic coverage) and sediment grain size/characteristics for analysis (preferably grab or cone dredge samples to be taken at the start and end of each transect) for each site surveyed.

Although the use of benthic camera footage is a cost-effective and eco-friendly sampling method (Sheehan, Stevens, et al. 2010, Williams, Althaus, et al. 2015), it is still unfortunately not free of difficulties. Taxonomic challenges presented themselves while working through the underwater imagery and not having a physical sample made it difficult to identify organisms to a species level, because many of these species are not known (Jamieson, Boorman, et al. 2013). This may have also been due to a lack of good quality images taken across some of the surveyed sites. In future studies, this kind of issue may be averted by collecting clearer, more “in-focus” benthic images using an ROV, or if possible, ROV collections of a few physical samples of ‘unidentifiable epifauna’ to make the identification process more efficient. Nonetheless, using towed-camera imagery provides highly repeatable sampling over broad temporal and spatial scales (Bicknell, Godley, et al. 2016). In terms of analysing benthic imagery, a more user-friendly, more easily accessible software could be used to analyse the imagery, such as BIIGLE (Langenkämper, Zurowietz, et al. 2017). In such cases, the use of morphospecies and controlled universal classifications like CATAMI (Althaus et al 2015) can make working in BIIGLE standardised and interoperable across studies.

Only a few sites were sampled within the ecosystem types that covered the study area, therefore the conservation target work was limited to utilizing and evaluating three out of 10 ecosystem types. Future studies should survey more (more than three) sites (transects) in each of the ecosystem types and depth zones for a more efficient and holistic evaluation of the study area. Although this was not in the scope of the current study, a recommendation for future work is to perform a comparison between the communities based on the quadrat level with that of the site level, to see how the community configurations of sites would change and how substratum type would influence the distribution of epifaunal assemblages at these different scales.

4.3 Conclusion

This study has provided new insights into South Africa's poorly-studied deep-sea ecosystems. It is the first study of its kind to focus on the outer shelf and slope of the Agulhas ecoregion, which are notoriously dynamic and challenging environments within which to work. The visual surveys have revealed a mosaic of habitat types within the Agulhas shelf-slope transition zone, with higher heterogeneity in epifaunal communities than anticipated. At a quadrat level, 10 epifaunal communities were classified and described for the first time. The abiotic factor that correlated most with patterns in epifaunal communities was substratum type, with high variability within sites.

Various other factors that may contribute to benthic epifaunal community structure were also identified. These included longitude, depth, current strength, and trawling intensity. The influence of longitude and depth is recognized in South Africa's ecoregions and bathomes and these elements are already included in the national marine ecosystem classification. However, South Africa's Marine Ecosystem Committee must recognise and accommodate fine-scale heterogeneity with substratum type and associated community variability within the national marine ecosystem classification. The introduction of mosaic ecosystem types in 2018 to describe ecosystems of repeating patterns of both consolidated and unconsolidated substratum was a key step forward in this context. The Agulhas Current, one of the strongest currents in the world, likely plays a key role in the observed heterogeneity. Current strength and variability may be influencing the heterogeneity of substratum across the study area, thus influencing faunal patterns. However, reliable bottom current data are not currently available and collection of this kind of data is a priority if the dynamics of the outer shelf and slope are to be better understood. This study also detected an influence of trawling in epifaunal patterns, but this was less than other environmental variables. However, further work is required to improve abiotic data and then explore the extent of influence of anthropogenic factors on the fauna within this study area.

Other recommendations for future work include exploring and comparing ecosystem functionality between these unconsolidated, consolidated and mosaic ecosystem types. To get a better understanding of the heterogeneity and its potential oceanographic drivers within this study area, there needs to be greater input of fine-scale biological and environmental sampling across the Agulhas ecoregion shelf-slope transition zone. It is essential that abiotic datasets are strengthened, more specifically depth, current and substratum type needs refinement and should also be incorporated into the national marine ecosystem classification.

Further exploration in these previously inaccessible areas, including in deeper water is required. This study has showed that the shelf edge presents a unique environment and is more heterogenous than previously thought. Further work in other parts of Africa and beyond has the potential to change the global understanding of this important area between shelf and slope. Research in South Africa together with other parts of Africa and other poorly sampled regions can inform and improve global ecosystem typologies. Furthermore, the findings from this study are contributing towards future iterations of the national marine ecosystem map which is the foundation of the National Biodiversity Assessment and marine spatial planning and decision-making processes in South Africa.

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Appendices

Table A1. Overview Site information for all 29 Deep Secret sites surveyed along the Agulhas ecoregion.

Site	**SM tow Equipment**	**Total Samples**	**Community**	**Start Depth**	**Depth Zone**	**Distance to Shelf Edge (km)**	**Substratum type**	**F-MS**	**M-CS**	**P + S**	**R + S**	**Ecotype** (assigned by NBA 2018)
DSC003	DEA	30	**C**	463	Shelf Edge	7	Rock & Sand	6			24	Southern Benguela Rocky Shelf Edge Mosaic
DSC010	DEA	30	**B**	135.9	Outer Shelf	25	Rock & Sand	7			23	Agulhas Outer Shelf Reef Coarse Sediment Mosaic
DSC011_1	DEA	30	**F**	475	Shelf Edge	2.5	Pebbles & Medium Sand			30		Agulhas Rocky Shelf Edge
DSC011_2	DEA	30	**F**	445	Shelf Edge	2.5	Pebbles & Medium Sand			30		Agulhas Rocky Shelf Edge
DSC011_3	DEA	30	**C**	339	Shelf Edge	2.5	Rock & Sand	5			25	Agulhas Rocky Shelf Edge
DSC012	DEA	30	**C**	336	Shelf Edge	3	Rock & Sand				30	Agulhas Rocky Shelf Edge
DSC014	DEA	30	**F**	531	Slope	5	Pebbles & Medium Sand			30		South West Indian Upper Slope
DSC017	DEA	30	**H**	338	Shelf Edge	2	Rock & Sand	10			20	Kingklip Koppies
DSC018	DEA	30	**H**	275	Shelf Edge	8	Medium to Coarse Sand		30			Agulhas Coarse Sediment Shelf Edge
DSC020	DEA	30	**D**	509	Slope	18	Rock & Sand				30	South West Indian Upper Slope
DSC021	DEA	30	**I**	397	Shelf Edge	2	Fine to Medium Sand	30				Agulhas Coarse Sediment Shelf Edge
DSC023	DEA	30	**G**	495	Shelf Edge	10	Fine to Medium Sand	30				Kingklip Koppies
DSC024	DEA	30	**H**	553	Slope	14	Medium to Coarse Sand		29	1		South West Indian Upper Slope
DSC026	SAEON	27	**D**	524	Slope	10	Rock & Sand				27	South West Indian Upper Slope
DSC027_1	SAEON	30	**E**	615	Slope	1	Rock & Sand				30	Kingklip Ridge
DSC029	SAEON	26	**D**	487	Shelf Edge	7	Rock & Sand				26	Agulhas Coarse Sediment Shelf Edge
DSC030	SAEON	30	**E**	576	Slope	1	Rock & Sand				30	South Indian Mid Slope
DSC035	SAEON	30	**E**	187	Shelf Edge	4	Rock & Sand			13	17	Agulhas Coarse Sediment Shelf Edge
DSC036	SAEON	30	**H**	124	Shelf Edge	0	Medium to Coarse Sand		20		10	Amathole Hard Shelf Edge
DSC037	DEA	30	**A**	539	Slope	4	Fine to Medium Sand	30				South West Indian Upper Slope
DSC038	DEA	30	**G**	343	Shelf Edge	1	Pebbles & Medium Sand			30		Natal Deep Shelf Edge
DSC041	DEA	29	**G**	555	Slope	1.5	Fine to Medium Sand	29				South West Indian Upper Slope
DSC042	DEA	27	**C**	314	Shelf Edge	7	Rock & Sand				27	Agulhas Coarse Sediment Shelf Edge
DSC044	DEA	30	**I**	335	Shelf Edge	5	Medium to Coarse Sand		30			Agulhas Coarse Sediment Shelf Edge
DSC047	SAEON	30	**I**	249	Shelf Edge	0.5	Medium to Coarse Sand		30			Agulhas Coarse Sediment Shelf Edge
DSC049	DEA	30	**G**	361	Shelf Edge	3	Fine to Medium Sand	30				Agulhas Coarse Sediment Shelf Edge
DSC050	DEA	30	**J**	404	Shelf Edge	2.5	Medium to Coarse Sand		30			Agulhas Coarse Sediment Shelf Edge
DSC053	SAEON	26	**H**	321	Shelf Edge	15	Medium to Coarse Sand		26			Agulhas Coarse Sediment Shelf Edge
DSC056	SAEON	30	**H**	552	Slope	4	Rock & Sand		12		18	South West Indian Upper Slope

Table A1 cont.

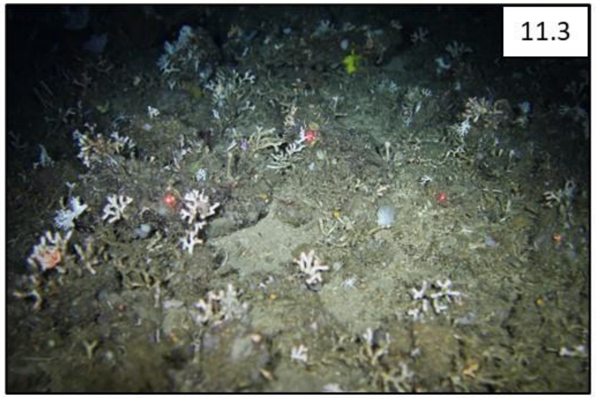
Site	Start_Latitude_DD (South)	Start_Longitude_DD	End_Latitude_DD (South)	End_Longitude_DD	Temperature (°C)	Conductivity	Salinity	Slope	Current Speed	Trawling Intensity (Swept Area Ratio)
DSC003	-36.05678	19.69937	-36.09389	18.12306	6.0382	3.4079	34.3977	Steep	Low	0.256951
DSC010	-34.78147	23.45763	-34.12611	23.78111	8.4484	3.63656	34.6519	Flat	Medium	0
DSC011_1	-35.16871	23.03090	-35.28972	23.04639	7.6891	3.57308	34.5605	Steep	High	1.136126
DSC011_2	-35.15409	23.04491	-35.25056	23.08806	9.2858	3.73516	34.7297	Steep	High	0.39119
DSC011_3	-35.11787	23.04498	-35.18417	23.06917	9.5634	3.75918	34.7512	Steep	High	0
DSC012	-35.11307	23.04035	-35.21500	23.04806	9.5015	3.7521	34.7423	Gentle	High	0
DSC014	-35.18683	23.06491	-35.34389	23.08556	6.6295	3.47701	34.5378	Steep	High	0.959912
DSC017	-34.87265	24.21069	-34.13556	24.33056	8.4204	3.64606	34.6874	Gentle	High	0
DSC018	-34.79611	24.20838	-34.11917	24.34833	10.0522	3.77978	34.5261	Gentle	Medium	3.190634
DSC020	-34.90333	24.52834	-34.15389	24.86861	5.4042	3.35858	34.4673	Steep	High	0.0152856
DSC021	-34.76780	24.50988	-34.15556	24.85250	9.0558	3.71096	34.7192	Gentle	Medium	**10.223205**
DSC023	-34.82541	24.51497	-34.14167	24.85500	7.762	3.58626	34.6209	Gentle	Medium	0.076242
DSC024	-34.76419	24.64995	-34.13278	24.11528	7.7041	3.58279	34.6152	Gentle	Medium	0.437514
DSC026	-34.79477	24.63616	-34.11917	24.11306	6.5956	3.47514	34.5543	Gentle	Medium	0.0252629
DSC027_1	-34.72852	25.13565	-34.12417	25.23583	7.561	3.5717	34.605	Steep	High	1.732137
DSC029	-34.60874	25.28593	-35.00194	25.48806	6.6388	3.47812	34.5655	Gentle	Medium	**14.203575**
DSC030	-34.68705	25.26498	-34.34389	25.45250	5.7763	3.40024	34.5275	Very Steep	High	0
DSC035	-33.72533	27.34366	-33.17833	27.56861	12.7712	4.08763	35.0468	Gentle	High	0
DSC036	-33.33158	27.80924	-33.55694	27.13944	11.8071	3.99038	35.0331	Very Steep	High	0
DSC037	-32.81881	28.59276	-32.18056	28.98500	7.6933	3.58218	34.6248	Very Steep	High	0
DSC038	-32.79430	28.58465	-32.38167	28.99722	10.518	3.8654	34.9172	Very Steep	High	0
DSC041	-33.51929	27.66944	-33.85750	27.10194	7.7851	3.58997	34.6104	Very Steep	High	0
DSC042	-33.92021	27.11293	-33.19444	27.20306	10.7509	3.88528	34.9098	Steep	High	0
DSC044	-34.13814	26.80278	-34.23889	26.14806	10.8732	3.8998	34.9268	Steep	High	0
DSC047	-34.40545	26.08128	-34.67222	26.13500	9.7654	3.77884	34.8026	Steep	Medium	5.929077
DSC049	-34.42613	26.08060	-34.74056	26.11889	8.8968	3.69443	34.7129	Steep	Medium	0.987677
DSC050	-34.43011	25.92009	-34.75389	25.15250	8.2202	3.62603	34.6568	Steep	High	4.2976604
DSC053	-34.54356	25.30461	-34.92278	25.49417	8.5966	3.66138	34.6827	Steep	Medium	5.2987175
DSC056	-34.84460	24.64018	-34.23889	24.11389	6.2404	3.44264	34.5409	Gentle	Medium	0


03


10


11.1


11.2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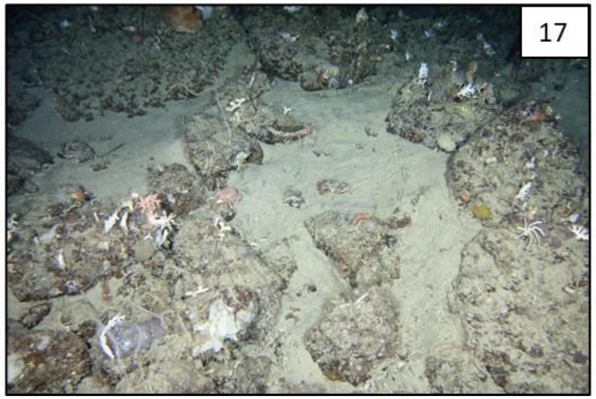
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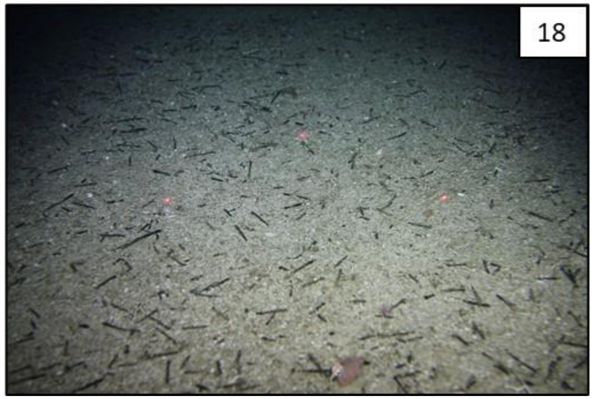
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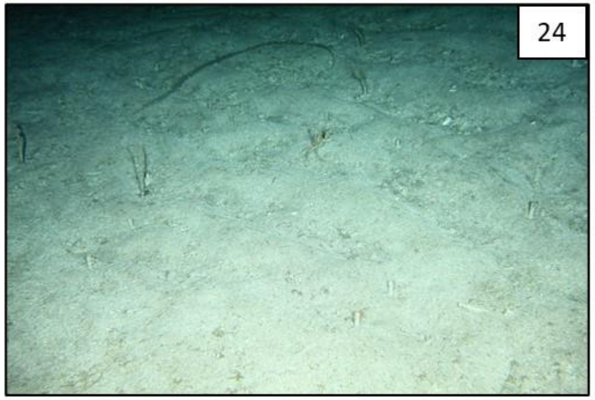
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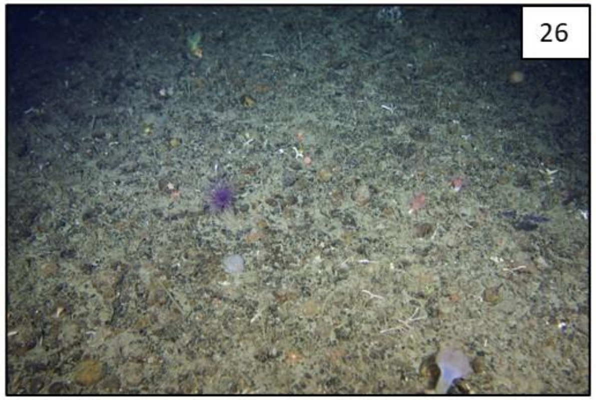
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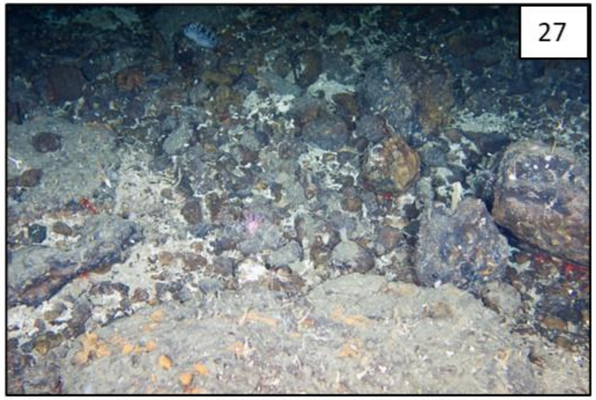
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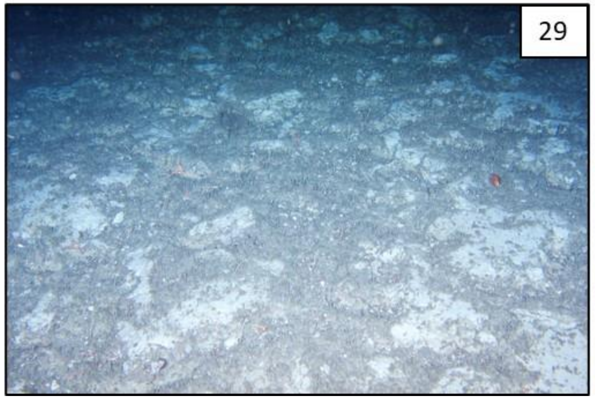
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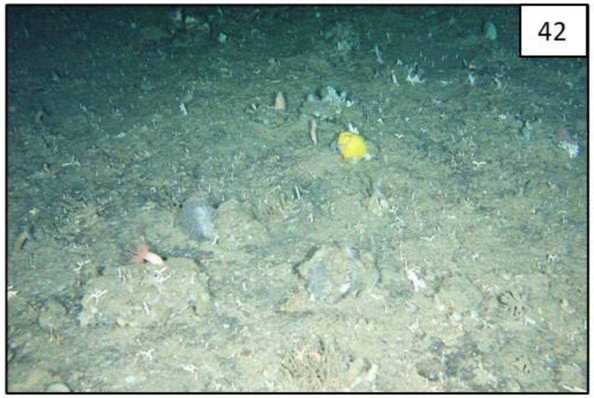
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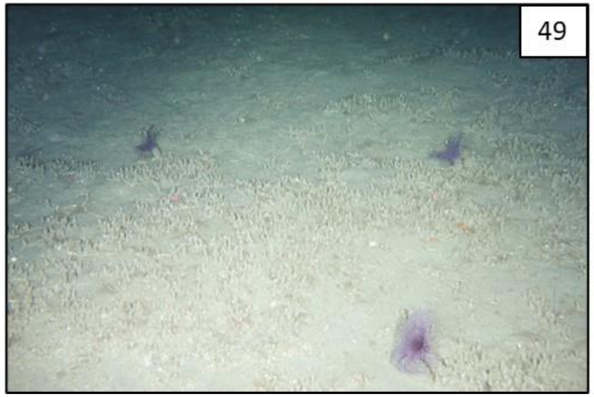
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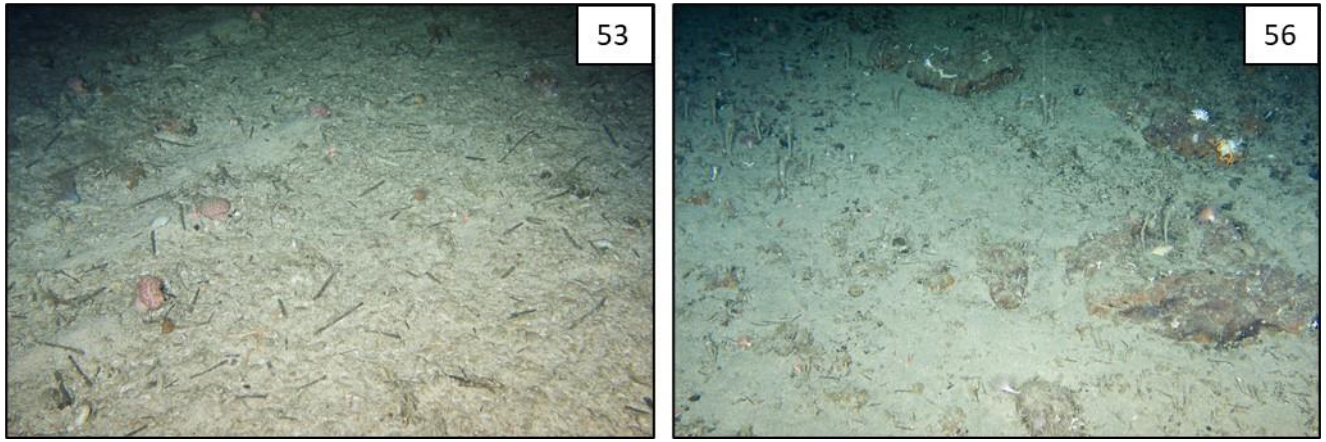

Figure A1. An overview of the representative images of each of the 29 sites sampled along the Agulhas ecoregion. Each site is identified by the label in the right top corner of each image.

Table A2. Draftmans plot resemblance matrix displaying the correlation between the environmental variables selected for analysis. Correlation values greater than 0.8 were highlighted in bold.

Variables	Depth (m)	Bottom temperature	Conductivity	Salinity	Shore to site distance	Distance to Shelfbreak	Slope	Current Strength	Trawling Intensity (SAR)	Substratum Type	POM/ Skuz	Coral Rubble	Latitude _DD (S)	Longitude _DD (E)
Depth (m)														
Bottom temperature (°C)	-0.79													
Conductivity	-0.77	**1.00**												
Salinity	-0.69	**0.92**	**0.93**											
Shore to site distance (km)	0.23	-0.42	-0.44	-0.54										
Distance to Shelfbreak (km)	-0.10	-0.27	-0.28	-0.31	0.08									
Slope	0.20	0.02	0.04	0.15	-0.27	-0.52								
Current Strength	0.01	0.28	0.30	0.40	-0.19	-0.39	0.46							
Trawling Intensity (SAR)	-0.02	-0.06	-0.07	-0.09	-0.07	-0.06	-0.21	-0.34						
Substratum Type	0.02	-0.14	-0.13	-0.06	0.30	0.09	-0.12	0.18	-0.13					
POM/Skuz	0.23	-0.37	-0.36	-0.26	0.21	0.12	-0.04	0.10	0.10	0.51				
Coral Rubble	0.06	-0.08	-0.08	-0.04	0.27	-0.20	0.12	0.24	-0.16	0.33	0.65			
Latitude_DD (S)	-0.23	0.49	0.51	0.60	**-0.90**	-0.24	0.49	0.42	-0.09	-0.28	-0.22	-0.18		
Longitude_DD (E)	-0.17	0.45	0.48	0.60	**-0.95**	-0.26	0.45	0.42	0.00	-0.28	-0.17	-0.18	**0.96**	

Table A3a. DistLM output: Marginal tests

Variable	**SS (trace)**	**Pseudo-F**	**P-value**	**Proportion (%)**
Depth_start (m)	1032400000	25.50	0.0001	2.91
Bottom temperature (°C)	93885	23.13	0.0001	2.64
Distance to shelf break (km)	59998	14.64	0.0001	1.69
Slope	81359	19.97	0.0001	2.29
Current strength	85423	20.99	0.0001	2.41
Trawling intensity	1140500000	28.26	0.0001	3.21
Substratum type	2616800000	67.75	0.0001	7.38
POM	1645200000	41.37	0.0001	4.64
Coral rubble	76027	18.63	0.0001	2.14
Longitude_DD (E)	1206400000	29.95	0.0001	3.40

Table A3b. DistLM output: Percentage of variation explained by individual axes.

	% explained variation out of fitted model		**% explained variation out of total variation**	
Axis	**Individual**	**Cumulative**	**Individual**	**Cumulative**
1	29.99	29.99	8.01	8.01
2	18.63	48.62	4.97	**12.98**
3	14.57	63.19	3.89	16.87
4	11.42	**74.61**	3.05	19.92
5	6.64	**81.25**	1.77	21.70
6	6.03	87.28	1.61	23.31
7	4.74	92.02	1.27	24.57
8	3.39	95.41	0.91	25.48
9	2.61	98.02	0.70	26.18
10	1.98	100	0.53	26.70

Table A3c. DistLM output: Relationships between dbRDA coordinate axes and the selected environmental variables (multiple partial correlations).

Variable	**dbRDA1**	**dbRDA2**	**dbRDA3**	**dbRDA4**	**dbRDA5**
Depth_start (m)	-0.048	0.543	**-0.464**	-0.165	0.129
Bottom temperature (°C)	0.227	-0.220	0.054	-0.213	0.090
Distance to shelf break (km)	-0.114	-0.025	0.237	-0.154	0.458
Slope	-0.006	0.164	-0.304	-0.098	-0.254
Current strength	-0.248	-0.022	-0.433	-0.260	**0.544**
Trawling intensity	0.189	0.037	-0.307	**0.865**	0.238
Substratum type	**-0.848**	-0.033	0.050	0.217	-0.286
POM	-0.288	0.323	0.317	0.097	0.365
Coral rubble	0.024	-0.131	0.331	0.144	0.350
Longitude_DD (E)	0.182	**0.710**	0.372	0.016	-0.106

Table A4. One-way ANOSIM Pairwise comparisons between the benthic epifaunal communities of the four different substratum types covering 29 sites across the Agulhas ecoregion.

Substratum Type Pairings	**R Statistic**	**Significance %**	**Permutations**
Rock & Sand Mixed, Fine to Medium Sand	0.504	0.01	9999
Rock & Sand Mixed, Pebbles & Medium Sand Mixed	0.418	0.01	9999
Rock & Sand Mixed, Medium to Coarse Sand	0.438	0.01	9999
Fine to Medium Sand, Pebbles & Medium Sand Mixed	0.262	0.01	9999
Fine to Medium Sand, Medium to Coarse Sand	0.213	0.01	9999
Pebbles & Medium Sand Mixed, Medium to Coarse Sand	0.263	0.01	9999

Table A5. One-way ANOSIM Pairwise comparisons between the benthic epifaunal communities of the three different depth zones covering 29 sites across the Agulhas ecoregion.

Depth Zone Pairings	**R Statistic**	**Significance %**	**Permutations**
Shelf Edge, Outer Shelf	0.203	0.01	9999
Shelf Edge, Slope	0.08	0.01	9999
Outer Shelf, Slope	0.29	0.01	9999

Table A6. Characteristic taxa of the three identified depth zones with their respective depth range, sites, number of quadrat replicates sampled and average similarity. The five epifaunal taxa contributing most to the similarity within each depth zone, representing between 40-90 % of the similarity are listed under Contributing %. In the Similarity/Standard Deviation (Sim/SD) column, bold figures represent the taxa that consistently characterized their respective depth zone.

Depth Zone (NBA2018)	***Characteristic taxa***	***Average Abundance***	***Sim/SD***	***Contributing %***
Outer Shelf	Cup coral (orange)	1.15	**1.09**	39.41
Depth Range: 100 - 150 m	Unidentified Melithaeidae	0.87	0.90	22.94
Site: 10	*Aspidostoma* spp.	0.74	0.88	17.80
30 quadrat replicates	*Thouarella* spp.	0.48	0.57	8.34
(Ave. Similarity = 30.89%)	Hydroid spp.	0.20	0.33	2.01
Shelf Edge	Foraminifera	0.90	0.39	30.79
Depth Range: 200 - 500 m	*Ceriantheopsis* sp.	0.38	0.24	9.97
Sites: 03, 11.1, 11.2, 11.3, 12, 17, 18, 21, 23, 29, 35, 36, 38, 42, 44, 47, 49, 50, 53	*Ophiura trimeni*	0.48	0.14	7.75
559 quadrat replicates	Polychaete tubes	0.68	0.14	6.73
(Ave. Similarity = 10.84%)	Shrimp sp. B (Euphausiid-like shrimp)	0.30	0.20	5.94
Upper Slope	Stalked crinoid	0.62	0.44	18.87
Depth Range: 500 - 700 m	*Praxillura* sp.	0.53	0.32	13.18
Sites: 14, 20, 24, 26, 27, 30, 37, 41, 56	Foraminifera	0.64	0.22	12.10
266 quadrat replicates	*Ceriantheopsis* sp.	0.33	0.30	7.46
(Ave. Similarity = 13.69%)	Hydroid spp.	0.42	0.30	6.37

Table A7. Characteristic taxa of the ten NBA 2018 national marine ecosystem types sampled in this study with their respective sites, number of quadrat replicates sampled and average similarity. The five epifaunal taxa contributing most to the similarity within each ecosystem type, representing between 40-90 % of the similarity are listed under Contributing %. In the Similarity/Standard Deviation (Sim/SD) column, bold figures represent the taxa that consistently characterized their respective ecosystem type.

Ecosystem type (NBA2018)	***Characteristic taxa***	***Average Abundance***	***Sim/SD***	***Contributing %***
Southern Benguela Rocky Shelf Edge Mosaic	**Cup coral (pink)**	**1.36**	**1.44**	**27.23**
Site: 03	***Stylaster* sp.1**	**0.95**	**1.34**	**19.14**
30 quadrat replicates	Cup coral (yellow)	0.65	0.80	10.18
(Ave. Similarity = 35.15%)	*Ophiura trimeni*	1.11	0.37	8.95
Community: C	Hydroid spp.	0.61	0.67	7.50
Agulhas Outer Shelf Reef Coarse Sediment Mosaic	**Cup coral (orange)**	**1.15**	**1.09**	**39.41**
Site: 10	Unidentified Melithaeidae	0.87	0.90	22.94
30 quadrat replicates	*Aspidostoma* spp.	0.74	0.88	17.80
(Ave. Similarity = 30.89%)	*Thouarella* spp.	0.48	0.57	8.34
Community: B	Hydroid spp.	0.20	0.33	2.01
Agulhas Rocky Shelf Edge	*Ceriantheopsis* sp.	1.00	0.45	26.07
Sites: 11.1, 11.2, 11.3, 12	Foraminifera	0.74	0.43	13.07
120 quadrat replicates	Cup coral (pink)	0.42	0.43	10.30
(Ave. Similarity = 21.72%)	*Praxillura* sp.	0.37	0.35	8.29
Communities: C, F	*Stylaster sp.1*	0.65	0.39	6.98
South West Indian Upper Slope	Stalked crinoid	0.75	0.55	22.58
Sites: 14, 20, 24, 26, 37, 41, 56	Foraminifera	0.83	0.29	16.40
206 quadrat replicates	*Praxillura* sp.	0.60	0.36	13.17
(Ave. Similarity = 16.87%)	*Ceriantheopsis* sp.	0.40	0.36	8.86
Communities: F, D, H, A, G	Polychaete tubes	0.40	0.23	5.56
Kingklip Koppies	**Foraminifera**	**2.22**	**1.17**	**44.88**
Sites: 17, 23	Polychaete tubes	3.06	0.49	27.33
60 quadrat replicates	Shrimp sp. B (Euphausiid-like shrimp)	0.80	0.64	9.47
(Ave. Similarity = 31.04%)	Unknown Polychaete sp.	0.32	0.36	3.42
Communities: C, G	*Stylaster* sp.1	0.40	0.29	2.86

Table A7 cont.

Ecosystem type (NBA2018)	*Characteristic taxa*	*Average Abundance*	*Sim/SD*	*Contributing %*
Agulhas Coarse Sediment Shelf Edge	*Ophiura trimeni*	0.81	0.24	23.58
Sites: 18, 21, 29, 35, 42, 44, 47, 49, 50, 53	Foraminifera	0.69	0.21	16.20
289 quadrat replicates	Shrimp sp. B (Euphausiid-like shrimp)	0.33	0.21	9.51
(Ave. Similarity = 10.68%)	*Ceriantheopsis sp.*	0.26	0.26	8.28
Communities: H, I, D, E, C, G, J	Polychaete tubes	0.55	0.11	5.19
Kingklip Ridge	**Shrimp sp. A (bright red rocky shrimp)**	**2.59**	**2.77**	**40.74**
Site: 27	**Porifera unknown encrusting sponge**	**1.61**	**1.52**	**21.72**
30 quadrat replicates	*Anthomastus* sp. A (white)	1.14	0.88	11.23
(Ave. Similarity = 44.96%)	Hydroid spp.	0.86	0.75	7.48
Community: E	*Anthomastus giganteus*	0.90	0.58	6.50
South Indian Mid Slope	*Anthomastus* sp. A (white)	1.01	0.97	23.85
Site: 30	Unidentified Primnoid octocoral	0.75	0.74	16.86
30 quadrat replicates	Hydroid spp.	0.86	0.70	15.95
(Ave. Similarity = 31.60%)	Primnoid sp.1	0.67	0.70	13.87
Community: E	*Praxillura* sp.	0.52	0.35	7.76
Amathole Hard Shelf Edge	**Foraminifera**	**1.39**	**1.98**	**31.50**
Site: 36	**Hydroid spp.**	**1.18**	**1.56**	**26.15**
30 quadrat replicates	*Stichopathes* sp. (black coral)	0.92	0.34	4.84
(Ave. Similarity = 43.66%)	*Desmophyllum spp.*	0.50	0.24	2.91
Community: H	Cup coral (orange)	0.40	0.21	2.15
Natal Deep Shelf Edge	Polychaete tubes	1.21	0.87	40.61
Site: 38	**Foraminifera**	**0.95**	**1.16**	**37.23**
30 quadrat replicates	*Munida benguela*	0.30	0.37	7.78
(Ave. Similarity = 37.98%)	Primnoid sp.1	*0.28*	*0.33*	*5.73*
Community: G				

Table A8. Cross validation of the distribution of the 852 replicate samples from 29 sites among the ten different national marine ecosystem types (NBA2018, (Sink, van der Bank, et al. 2019)) in the Agulhas ecoregion and allocation of observations to re-assigned groups, based on the Canonical analysis for principal coordinates (CAP).

Original group	**Re-assigned groups**										**Total**	**% correct**
	SBRSEM	AOSRCSM	ARSE	SWIUS	KKK	ACSSE	KKR	SIMS	AHSE	NDSE		
Southern Benguela Rocky Shelf Edge Mosaic (SBRSEM)	27	0	0	1	0	2	0	0	0	0	30	90.00
Agulhas Outer Shelf Reef Coarse Sediment Mosaic (AOSRCSM)	0	24	2	0	0	0	0	0	1	0	27	88.89
Agulhas Rocky Shelf Edge (ARSE)	3	3	101	4	3	6	0	0	0	0	120	84.17
South West Indian Upper Slope (SWIUS)	1	1	16	157	14	7	0	0	4	6	206	76.21
Kingklip Koppies (KKK)	0	0	7	4	46	2	0	0	1	0	60	76.67
Agulhas Coarse Sediment Shelf Edge (ACSSE)	10	3	5	17	31	210	1	5	0	7	289	72.66
Kingklip Ridge (KKR)	0	0	0	0	0	0	30	0	0	0	30	100.00
South Indian Mid Slope (SIMS)	0	0	0	5	0	0	0	25	0	0	30	83.33
Amathole Hard Shelf Edge (AHSE)	0	1	0	1	0	0	0	0	28	0	30	93.33
Natal Deep Shelf Edge (NDSE)	0	0	0	0	1	0	0	2	0	27	30	90.00
Total correct: 675/852 (79.225%)												
Mis-classification error: 20.775%												

Table A9. Individual quadrat replicates of the ten different national marine ecosystem types (NBA2018, (Sink, van der Bank, et al. 2019)) that were mis-classified according to the Canonical analysis for principal coordinates (CAP) and were reclassified into another ecosystem type group.

Quadrat replicate	Original group	Re-classified group
DSC003_.18..JPG	Southern Benguela Rocky Shelf Edge Mosaic	Agulhas Coarse Sediment Shelf Edge
DSC003_.187..JPG	Southern Benguela Rocky Shelf Edge Mosaic	Agulhas Coarse Sediment Shelf Edge
DSC003_.33..JPG	Southern Benguela Rocky Shelf Edge Mosaic	South West Indian Upper Slope
DSC010_.47..JPG	Agulhas Outer Shelf Reef Coarse Sediment Mosaic	Amathole Hard Shelf Edge
DSC010_.52..JPG	Agulhas Outer Shelf Reef Coarse Sediment Mosaic	Agulhas Rocky Shelf Edge
DSC010_.7..JPG	Agulhas Outer Shelf Reef Coarse Sediment Mosaic	Agulhas Rocky Shelf Edge
DSC011_.3._.149..JPG	Agulhas Rocky Shelf Edge	South West Indian Upper Slope
DSC011_.3._.150..JPG	Agulhas Rocky Shelf Edge	Agulhas Coarse Sediment Shelf Edge
DSC011_.3._.156..JPG	Agulhas Rocky Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC011_.3._.171..JPG	Agulhas Rocky Shelf Edge	Kingklip Koppies
DSC011_.3._.173..JPG	Agulhas Rocky Shelf Edge	Agulhas Coarse Sediment Shelf Edge
DSC011_.3._.178..JPG	Agulhas Rocky Shelf Edge	Agulhas Outer Shelf Reef Coarse Sediment Mosaic
DSC011_.3._.186..JPG	Agulhas Rocky Shelf Edge	Agulhas Outer Shelf Reef Coarse Sediment Mosaic
DSC011_.3._.191..JPG	Agulhas Rocky Shelf Edge	Agulhas Coarse Sediment Shelf Edge
DSC011_.3._.48..JPG	Agulhas Rocky Shelf Edge	Kingklip Koppies
DSC011_2_.113..JPG	Agulhas Rocky Shelf Edge	South West Indian Upper Slope
DSC011_2_.120..JPG	Agulhas Rocky Shelf Edge	South West Indian Upper Slope
DSC011_2_.160..JPG	Agulhas Rocky Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC011_2_.47..JPG	Agulhas Rocky Shelf Edge	Agulhas Outer Shelf Reef Coarse Sediment Mosaic
DSC011_2_.63..JPG	Agulhas Rocky Shelf Edge	Agulhas Coarse Sediment Shelf Edge
DSC011_2_.72..JPG	Agulhas Rocky Shelf Edge	South West Indian Upper Slope
DSC012_.109..JPG	Agulhas Rocky Shelf Edge	Agulhas Coarse Sediment Shelf Edge

Quadrat replicate	Original group	Re-classified group
DSC012_.47..JPG	Agulhas Rocky Shelf Edge	Kingklip Koppies
DSC012_.98..JPG	Agulhas Rocky Shelf Edge	Agulhas Coarse Sediment Shelf Edge
DSC11_1..36..JPG	Agulhas Rocky Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC014_.10..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC014_.12..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC014_.131..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC014_.169..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC014_.173..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC014_.34..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC014_.35..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC014_.41..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC014_.63..JPG	South West Indian Upper Slope	Agulhas Outer Shelf Reef Coarse Sediment Mosaic
DSC014_.66..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC014_.69..JPG	South West Indian Upper Slope	Southern Benguela Rocky Shelf Edge Mosaic
DSC014_.78..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC014_.99..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC020_.104..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC020_.105..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC020_.114..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC024_.10..JPG	South West Indian Upper Slope	Kingklip Koppies
DSC024_.20..JPG	South West Indian Upper Slope	Agulhas Coarse Sediment Shelf Edge
DSC024_.24..JPG	South West Indian Upper Slope	Kingklip Koppies
DSC024_.26..JPG	South West Indian Upper Slope	Agulhas Coarse Sediment Shelf Edge
DSC024_.44..JPG	South West Indian Upper Slope	Agulhas Coarse Sediment Shelf Edge
DSC024_.45..JPG	South West Indian Upper Slope	Kingklip Koppies
DSC024_.53..JPG	South West Indian Upper Slope	Kingklip Koppies
DSC024_.54..JPG	South West Indian Upper Slope	Kingklip Koppies

Quadrat replicate	**Original group**	**Re-classified group**
DSC024_.57..JPG	South West Indian Upper Slope	Agulhas Coarse Sediment Shelf Edge
DSC024_.60..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC024_.62..JPG	South West Indian Upper Slope	Agulhas Rocky Shelf Edge
DSC024_.64..JPG	South West Indian Upper Slope	Kingklip Koppies
DSC024_.67..JPG	South West Indian Upper Slope	Natal Deep Shelf Edge
DSC024_.8..JPG	South West Indian Upper Slope	Agulhas Coarse Sediment Shelf Edge
DSC024_56..JPG	South West Indian Upper Slope	Kingklip Koppies
DSC026_.84..jpg	South West Indian Upper Slope	Amathole Hard Shelf Edge
DSC041_.2065..jpg	South West Indian Upper Slope	Natal Deep Shelf Edge
DSC041_.2069..jpg	South West Indian Upper Slope	Natal Deep Shelf Edge
DSC041_.2097..jpg	South West Indian Upper Slope	Amathole Hard Shelf Edge
DSC056_.32..jpg	South West Indian Upper Slope	Amathole Hard Shelf Edge
DSC056_.34..jpg	South West Indian Upper Slope	Agulhas Coarse Sediment Shelf Edge
DSC056_.44..jpg	South West Indian Upper Slope	Agulhas Coarse Sediment Shelf Edge
DSC056_.48..jpg	South West Indian Upper Slope	Amathole Hard Shelf Edge
DSC056_.53..jpg	South West Indian Upper Slope	Kingklip Koppies
DSC056_.65..jpg	South West Indian Upper Slope	Kingklip Koppies
DSC056_.68..jpg	South West Indian Upper Slope	Kingklip Koppies
DSC056_.69..jpg	South West Indian Upper Slope	Natal Deep Shelf Edge
DSC056_.72..jpg	South West Indian Upper Slope	Natal Deep Shelf Edge
DSC056_.74..jpg	South West Indian Upper Slope	Kingklip Koppies
DSC056_.78..jpg	South West Indian Upper Slope	Kingklip Koppies
DSC056_.79..jpg	South West Indian Upper Slope	Kingklip Koppies
DSC056_.80..jpg	South West Indian Upper Slope	Natal Deep Shelf Edge
DSC056_.82..jpg	South West Indian Upper Slope	Kingklip Koppies
DSC017_.105..JPG	Kingklip Koppies	Agulhas Coarse Sediment Shelf Edge
DSC017_.125..JPG	Kingklip Koppies	Amathole Hard Shelf Edge

Quadrat replicate	Original group	Re-classified group
DSC017_.28..JPG	Kingklip Koppies	Agulhas Coarse Sediment Shelf Edge
DSC017_.41..JPG	Kingklip Koppies	Agulhas Rocky Shelf Edge
DSC017_.42..JPG	Kingklip Koppies	Agulhas Rocky Shelf Edge
DSC017_.51..JPG	Kingklip Koppies	Agulhas Rocky Shelf Edge
DSC017_.57..JPG	Kingklip Koppies	Agulhas Rocky Shelf Edge
DSC017_.58..JPG	Kingklip Koppies	Agulhas Rocky Shelf Edge
DSC017_.71..JPG	Kingklip Koppies	Agulhas Rocky Shelf Edge
DSC017_.9..JPG	Kingklip Koppies	Agulhas Rocky Shelf Edge
DSC023_.111..JPG	Kingklip Koppies	South West Indian Upper Slope
DSC023_.112..JPG	Kingklip Koppies	South West Indian Upper Slope
DSC023_.29..JPG	Kingklip Koppies	South West Indian Upper Slope
DSC023_.6..JPG	Kingklip Koppies	South West Indian Upper Slope
DSC018_.14..JPG	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC018_.18..JPG	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC018_.24..JPG	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC018_.25..JPG	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC018_.29..JPG	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC018_.50..JPG	Agulhas Coarse Sediment Shelf Edge	Agulhas Rocky Shelf Edge
DSC018_.59..JPG	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC018_.62..JPG	Agulhas Coarse Sediment Shelf Edge	Agulhas Rocky Shelf Edge
DSC018_.74..JPG	Agulhas Coarse Sediment Shelf Edge	Agulhas Rocky Shelf Edge
DSC018_.77..JPG	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC018_.78..JPG	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC029_.2162..jpg	Agulhas Coarse Sediment Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC029_.2166..jpg	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC029_.2168..jpg	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC029_.2173..jpg	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope

Quadrat replicate	Original group	Re-classified group
DSC029_.2174..jpg	Agulhas Coarse Sediment Shelf Edge	South Indian Mid Slope
DSC029_.2175..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC029_.2179..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Ridge
DSC029_.2181..jpg	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC035_.21..jpg	Agulhas Coarse Sediment Shelf Edge	Agulhas Outer Shelf Reef Coarse Sediment Mosaic
DSC035_.22..jpg	Agulhas Coarse Sediment Shelf Edge	Agulhas Outer Shelf Reef Coarse Sediment Mosaic
DSC035_.29..jpg	Agulhas Coarse Sediment Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC035_.32..jpg	Agulhas Coarse Sediment Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC035_.34..jpg	Agulhas Coarse Sediment Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC035_.36..jpg	Agulhas Coarse Sediment Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC035_.4..jpg	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC035_.44..jpg	Agulhas Coarse Sediment Shelf Edge	South Indian Mid Slope
DSC035_.49..jpg	Agulhas Coarse Sediment Shelf Edge	South Indian Mid Slope
DSC035_.50..jpg	Agulhas Coarse Sediment Shelf Edge	Agulhas Outer Shelf Reef Coarse Sediment Mosaic
DSC035_.52..jpg	Agulhas Coarse Sediment Shelf Edge	South Indian Mid Slope
DSC035_.6..jpg	Agulhas Coarse Sediment Shelf Edge	South Indian Mid Slope
DSC035_.64..jpg	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC042_.2104..jpg	Agulhas Coarse Sediment Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC042_.2121..jpg	Agulhas Coarse Sediment Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC042_.2137..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC042_.2141..jpg	Agulhas Coarse Sediment Shelf Edge	Agulhas Rocky Shelf Edge
DSC042_.2143..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC042_.2146..jpg	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC042_.2154..jpg	Agulhas Coarse Sediment Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC042_.2157..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.1965..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.1977..jpg	Agulhas Coarse Sediment Shelf Edge	Natal Deep Shelf Edge

Quadrat replicate	Original group	Re-classified group
DSC049_.1978..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.1983..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.1989..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.1991..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.1993..jpg	Agulhas Coarse Sediment Shelf Edge	Natal Deep Shelf Edge
DSC049_.1994..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.1995..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2002..jpg	Agulhas Coarse Sediment Shelf Edge	Natal Deep Shelf Edge
DSC049_.2016..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2021..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2023..jpg	Agulhas Coarse Sediment Shelf Edge	Natal Deep Shelf Edge
DSC049_.2027..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2028..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2029..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2030..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2035..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2039..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2040..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2042..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2046..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2047..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2057..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2058..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2060..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC049_.2061..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC050_.2131..jpg	Agulhas Coarse Sediment Shelf Edge	Natal Deep Shelf Edge
DSC050_.2132..jpg	Agulhas Coarse Sediment Shelf Edge	Natal Deep Shelf Edge

Quadrat replicate	Original group	Re-classified group
DSC050_.2133..jpg	Agulhas Coarse Sediment Shelf Edge	Natal Deep Shelf Edge
DSC053_.2..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC053_.28..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC053_.37..jpg	Agulhas Coarse Sediment Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC053_.52..jpg	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC053_.59..jpg	Agulhas Coarse Sediment Shelf Edge	Southern Benguela Rocky Shelf Edge Mosaic
DSC053_.64..jpg	Agulhas Coarse Sediment Shelf Edge	Kingklip Koppies
DSC053_.66..jpg	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC053_.67..jpg	Agulhas Coarse Sediment Shelf Edge	South West Indian Upper Slope
DSC053_.9..jpg	Agulhas Coarse Sediment Shelf Edge	Agulhas Rocky Shelf Edge
DSC030_.2536..jpg	South Indian Mid Slope	South West Indian Upper Slope
DSC030_.2550..jpg	South Indian Mid Slope	South West Indian Upper Slope
DSC030_.2579..jpg	South Indian Mid Slope	South West Indian Upper Slope
DSC030_.2586..jpg	South Indian Mid Slope	South West Indian Upper Slope
DSC030_.2592..jpg	South Indian Mid Slope	South West Indian Upper Slope
DSC036_.2212..jpg	Amathole Hard Shelf Edge	Agulhas Outer Shelf Reef Coarse Sediment Mosaic
DSC036_.2221..jpg	Amathole Hard Shelf Edge	South West Indian Upper Slope
DSC038_..68..JPG	Natal Deep Shelf Edge	South Indian Mid Slope
DSC038_.32..JPG	Natal Deep Shelf Edge	South Indian Mid Slope
DSC038_.35..JPG	Natal Deep Shelf Edge	Kingklip Koppies

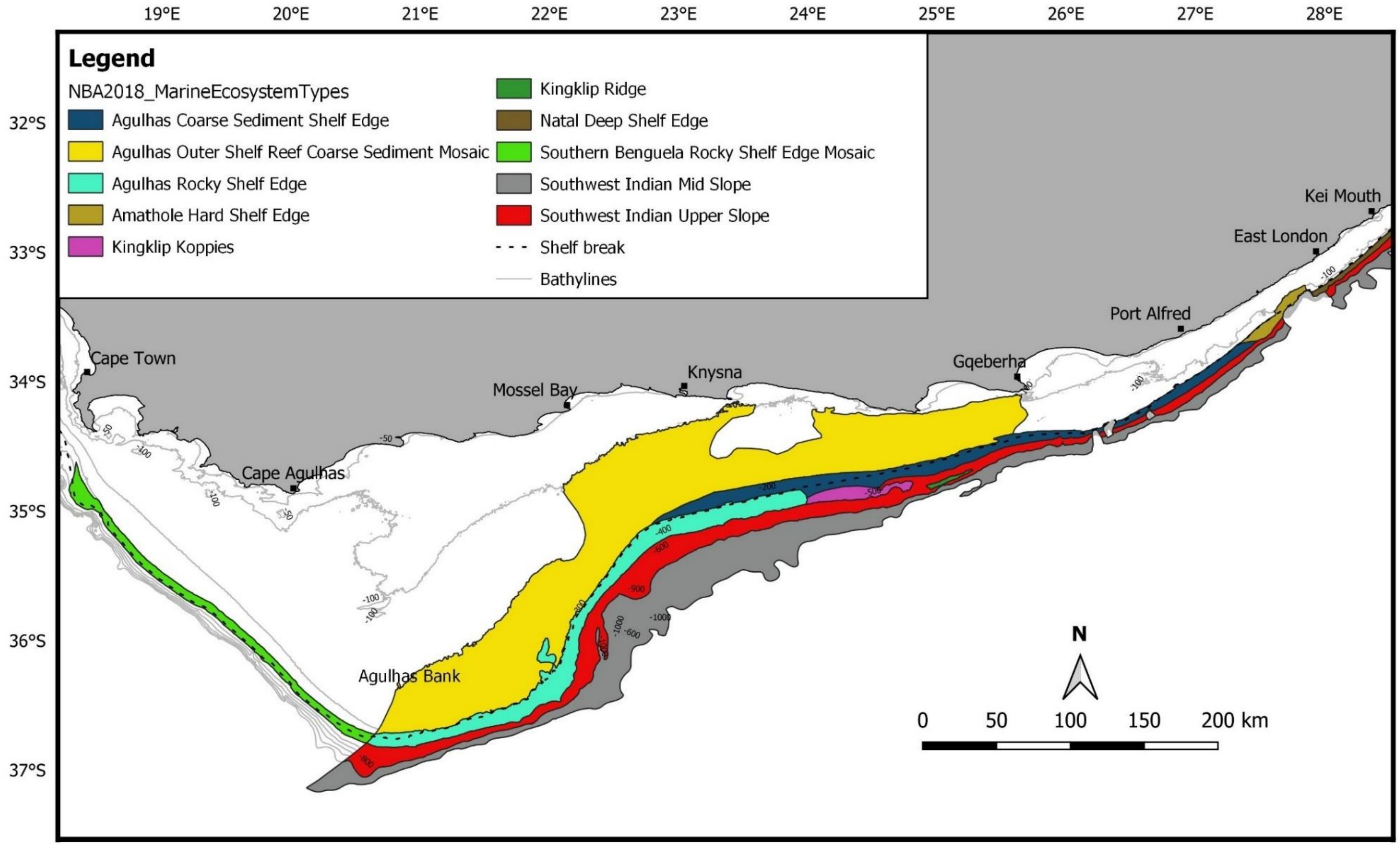

Figure A2. A map depicting the ten NBA2018 assigned marine ecosystem types (Sink, van der Bank, et al. 2019) sampled in the study area, Agulhas ecoregion.

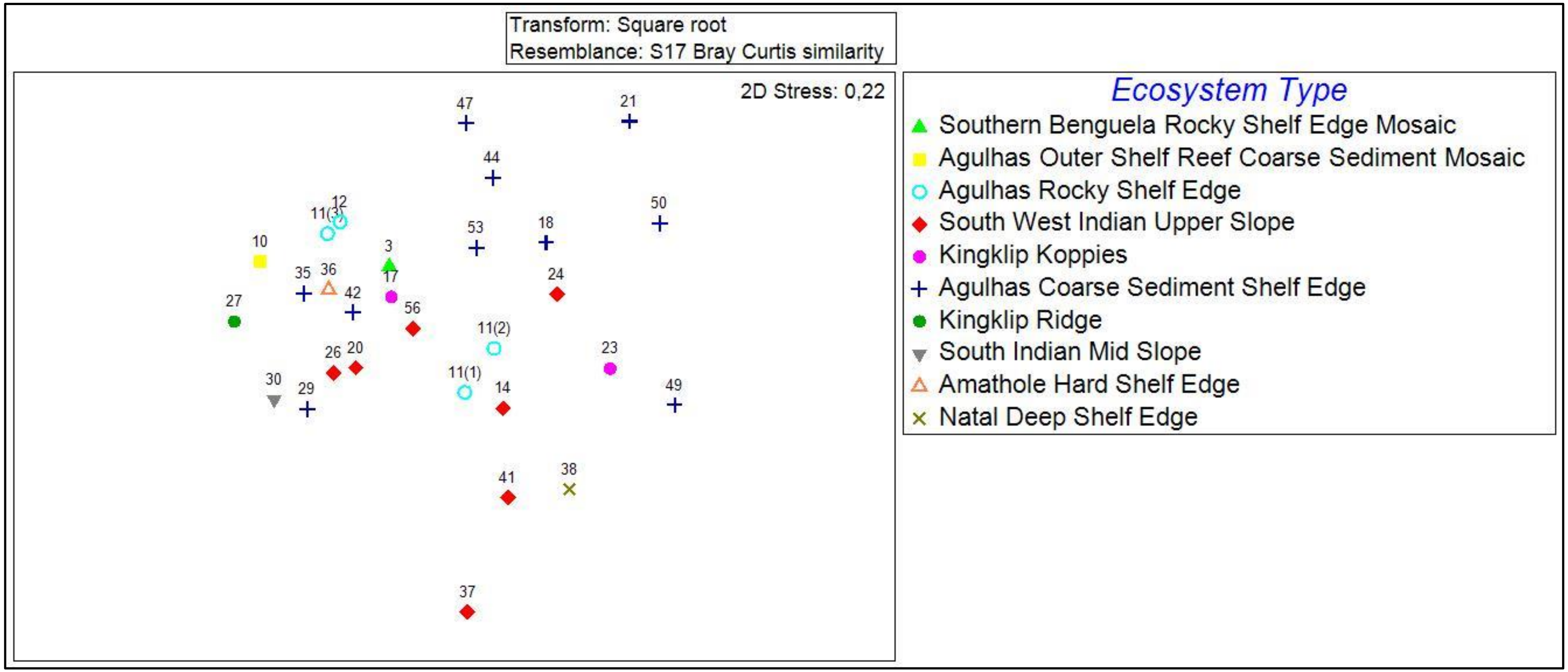

Figure A3. Multi-Dimensional Scaling Ordination plot depicting Bray-Curtis similarities among averaged species abundance data per site from 29 sites, showing the relation among the ten NBA2018 ecosystem types (Sink, van der Bank, et al. 2019) in the Agulhas ecoregion.