

An Investigation of Benthic Epifauna to Support Classification and Mapping of Outer Shelf Ecosystems in KwaZulu-Natal

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DECLARATION

I, Mapula Salome Makwela, student number 3571978, declare that “*An Investigation of Benthic Epifauna to Support Classification and Mapping of Outer Shelf Ecosystems in KwaZulu-Natal*” is my own work. It has not been submitted for any degree or examination at any other university. All references and sources of information to my knowledge are accurately reported.

Signed this day 17th of December 2017 atUniversity of the Western Cape (Bellville).....

Signature.....

akwela

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An Investigation of Benthic Epifauna to Support Classification and Mapping of Outer Shelf Ecosystems in KwaZulu-Natal

ABSTRACT

Ecosystem classification and mapping are foundational steps for effective ecosystem-based marine spatial planning, marine ecosystem assessment and integrated ocean management. The aims of this study were to interrogate and refine existing ecosystem classification and maps using quantitative data for epifaunal communities and to investigate the potential physical drivers which may contribute most to the distribution patterns of these ecosystem types. A total of 27 sites between Pennington and Ballito on the east coast of South Africa, including unconsolidated sediment, mixed and reefs habitat types, in the 48 to 85m depth range, was examined. Epifauna data were quantified from seabed imagery collected by remotely-operated vehicle covering more than 13 130 epifaunal individuals counted representing over 170 morphospecies from five taxa. Multivariate analyses of data from 17 sites surveyed in southern KwaZulu-Natal (KZN) revealed that epifauna at unconsolidated sediment sites were significantly different to that occurring on either mixed or reef substrates and epifauna occurring on mixed substrates were also significantly different to those occurring on reefs. Epifauna at mixed sites were more similar to epifaunal assemblages at reef sites than epifauna at unconsolidated sediment sites. The significantly different epifaunal communities detected did not align with the existing national or provincial habitat classifications. To further investigate the patterns and potential drivers of epifaunal assemblages on deep reefs, epifauna data were analysed from 17 reef sites (including the eight reef sites from southern KZN i.e. south of Durban; and nine additional reefs from central KZN i.e. north of Durban). Multivariate analyses revealed a potential biogeographic break off Durban with reef assemblages north and south of this break differing by approximately 65%. Reefs located north of Durban were characterised by a mix of octocorals and porifera morphospecies while southern reefs hosted more porifera morphospecies. Potential environmental drivers of these patterns were investigated and distance from shelf edge, latitude, sea surface temperature, phosphate and bottom temperature were identified as key potential drivers. In all, four biotopes along with their characteristic and distinguishing species were classified and described with three additional potential biotopes requiring further sampling effort. One biotope was described from sandy outer shelf habitats, one mixed habitat biotope was recognised and two clear deep reef biotopes were determined. This

study advances classification, description and mapping of outer shelf ecosystem types for improved spatial biodiversity assessment and management in KZN.

Key words: Epifauna, Outer shelf, Ecosystems, KwaZulu-Natal, Classification and mapping, Marine Spatial Planning, Remotely Operated Vehicle, Biotopes, Epifaunal assemblages, Deep reef



1 Introduction and background to the study

1.1 Introduction

The South African Biodiversity Act (2004) defines ecosystems as “the dynamic complex of animal, plant and microorganism communities and their non-living environment, interacting as a functional unit” (Government Gazette, 2004). This definition allows for ecosystems to be recognised at multiple scales. For the purpose of this thesis the term ‘ecosystem’ has been used to represent habitats (defined by physical components such as depth and substrate) and ‘biotopes’ (defined as a distinct biological assemblage that characterises a specific habitat) (Diaz *et al.* 2004, Connor *et al.* 2004, SANBI 2016). South Africa’s marine environment supports high biodiversity (Costello *et al.* 2010) and the sponge, scleractinian and octocoral dominated ecosystems of the warm, north eastern coastal waters of KwaZulu-Natal (KZN) political province are no exception (Williams 1993).

The KZN political province has a rich diversity of marine ecosystems due to its tropical and subtropical nature (Palmer *et al.* 2011). There is limited knowledge of benthic invertebrate ecosystems in the outer continental shelf of KZN (deeper than 30 m) due to complexities and challenges of the environment (Lutjeharms *et al.* 2010) with knowledge decreasing with depth (Fennessy *et al.* 2016, Untiedt and MacKay 2016). Existing research below 30 m has focused on benthic infauna and fish assemblages and is sampled mostly by benthic grab and trawl. Few visual surveys and limited work on epifauna have been conducted in the region; as a result this study focuses on the epifauna of the KZN outer shelf.

1.1.1 Status of marine ecosystems

Ecosystem services provide fundamental benefits to human survival, well-being, health and livelihoods (Liquete *et al.* 2013, Costanza *et al.* 2014). Many studies have dealt with the assessment of food production (fisheries) services, but less research has been done on the other services that marine ecosystems provide (Liquete *et al.* 2013). The diverse array of South Africa’s marine ecosystems plays a vital role in the overall health of marine environments, such as transferring energy from primary production to higher trophic levels (Blanchard *et al.* 2013) and as food sources for resource species (Snelgrove 1998, Reiss *et al.* 2011). Studies have shown that many marine ecosystems are being damaged by anthropogenic factors such as pollution, overfishing, invasive species and climate change (Schleyer and Tomalin 2000, Diaz *et al.* 2004, Leslie 2005 Costello *et al.* 2010, Weeks *et al.* 2010). It has been reported that about 47% of South Africa’s marine and coastal habitats are

classified as ‘threatened’ (Sink *et al.* 2012). Opportunities exist to restore impacted habitats, secure remaining healthy habitats, prevent further damage and improve marine biodiversity management (Sink *et al.* 2012). Government initiatives such as Operation Phakisa aim to “implement an overarching integrated governance framework for sustainable growth of the ocean economy that maximises socio-economic benefits while ensuring adequate ocean environmental protection” (Marine Protection Services and Governance 2014). Globally, studies are underway to build marine biodiversity knowledge to support informed decision making and marine ecosystem conservation (Spalding *et al.* 2007, Howell 2010). It is important to support ecosystem sustainability through processes such as science-based Marine Spatial Planning (MSP) and systematic conservation planning (Ehler and Douvère 2009, Cogan *et al.* 2009, Holness and Biggs 2011, Roberson *et al.* 2017).

1.1.2 Marine conservation and spatial planning

Marine conservation planning, if undertaken with a systematic planning approach, requires priority setting in a geographically explicit manner, making efficient use of limited resources and promoting persistence of biodiversity (Leslie 2005, Weeks *et al.* 2010, Osmond *et al.* 2010). Marine conservation planning forms part of the suite of tools that can be implemented to improve biodiversity management. Conservation planning involves developing a planning framework and bringing together all major users of the ocean such as government, industry, conservation and recreation sectors, to make informed decisions about sustainable use of the marine environment and its resources (Leslie 2005, Osmond *et al.* 2010, Weeks *et al.* 2010, Knowlton *et al.* 2010). The process of marine conservation planning requires standardised classifications and terminology for habitats (in the form of policies or guidelines) to ensure consistent mapping of the environment across all possible regions (Costello 2009, Osmond *et al.* 2010, Sink *et al.* 2011). These policies will provide guidelines for the implementation and identification of areas which require protection for better understanding of biodiversity patterns and sensitive ecosystems. The current study provides biodiversity information about some habitats (unconsolidated sand, mixed and reefs) of the KZN outer shelf; supporting identification of areas for conservation with proper management strategies.

MSP is the planning process that enables integrated, visionary and consistent decision making on the human uses of the sea (Douvère 2008, Pomeroy and Douvère 2008). The process of MSP in South Africa is still in its infancy and the main purpose of South Africa’s recently developed MSP Bill (2017) is to provide a statutory basis for the implementation of marine protected area (MPA) networks for the country (Government Gazette, 2017).

Integrated ocean management (IOM) promotes the management of various ocean areas as one (Guenette and Alder 2007). IOM is implemented through the collaboration of all interested groups (stakeholders) based on sound science and ecosystem based management (Rutherford *et al.* 2005). Globally this integration is often achieved in collaboration with implementation of MPA networks. IOM often results in targeted social and economic development as well as conservation goals (Rutherford *et al.* 2005, Guenette and Alder 2007).

Approaches to MSP often emphasize the need for protecting a representative coverage of habitat types while aiming to minimize impacts on resource users (Edgar *et al.* 2008). Ball and Possingham (2000) developed a conservation planning tool called Marxan that covers the important basic steps in designing effective marine reserves. This tool provides users additional information about the proposed reserve such as costs, boundary length, fragmentation and representation requirements for conservation features. Naidoo *et al.* (2006) review the importance of costs associated with conservation and how costs can be estimated or modelled in a spatially explicit manner. Naidoo *et al.* (2006) also give empirical examples of how plans differ when costs are formally considered. Objectives of conservation planners include i) to achieve representation of all marine biological diversity ii) to achieve quantitative targets of biodiversity representation at a minimal cost iii) to develop solutions on how marine resources and services are utilised without compromising marine ecosystem health and biodiversity conservation and iv) to preserve spiritual and cultural values, sustain ecosystem services and provide places for research and education e.g. marine reserves and other types of MPAs (Leslie 2005, Weeks *et al.* 2010, Howell *et al.* 2010, Sink *et al.* 2011).

1.1.3 Marine ecosystem classifications and mapping

Marine ecosystems are classified for various reasons including identifying biologically meaningful areas for conservation (Gegr and Bodtke 2007) and for proper management of these ecosystems (Costello 2009). Many ecosystem classification systems have been developed by research, fishery, intergovernmental and conservation organisations (Allee *et al.* 2000, Fox *et al.* 2014). One approach to ecosystem classification requires knowledge of species distributions within an area of concern (Heiskanen *et al.* 2016), others include physical or environmental based approaches (McArthur *et al.* 2010). Studies have shown that marine species are sensitive towards their surroundings and distribution patterns are driven by the surrounding environmental factors (McArthur *et al.* 2010). There is no universal agreement on the method for conducting marine environmental classifications; however,

methods employed depend on the user's requirements and resources. Marine ecosystem classification systems allows natural resource managers to effectively identify representative or threatened biological communities, so that these ecosystems can be better managed or protected and conserved as deemed necessary (Allee *et al.* 2000). These classification systems are developed with the main aim of organizing and providing information in the form of maps and reports that can enable comparisons between areas and support unbiased decision making during processes such as MSP, marine ecosystem assessment and integrated ocean management (IOM) (Costello 2009).

Numerous marine ecosystem classifications exist and some provide accessible online data, such as the International Union for Conservation of Nature (IUCN) and Global Open Oceans and Deep Seas (GOODS) (Costello 2009). Organisations such as the Global Biodiversity Information Facility (GBIF) provide global databases of various species with tools to map species against environmental data (<http://data.gbif.org>). Spalding *et al.* (2007) reports on a biogeographic classification for global coastal and shelf areas, also known as Marine Ecoregions of the World (MEOW) that relies mainly on existing literature. Spalding *et al.* (2007) defines ecoregions as areas of relatively homogenous species composition, clearly distinct from adjacent systems. Ecoregions can also be defined based on the effect of temperature, geology and biological interactions on species' ranges and distributions (Heyns 2015).

1.1.4 South African National marine ecosystem classification

The South African National Biodiversity Institute (SANBI) provides ecosystem type maps of both terrestrial and aquatic ecosystems (<http://bgis.sanbi.org> retrieved on 2015/08/19) through their in-house platform the Biodiversity Geographic Information System (BGIS). This website also provides the results from the National Biodiversity Assessment (NBA), South Africa's national scientific assessment that reports on the status of marine and terrestrial biodiversity and ecosystems; most recently assessed in 2011 but is repeated every five to seven years using updated information (Driver *et al.* 2012). The NBA primarily aims to provide a high level summary of the state of South Africa's biodiversity with a strong focus on spatial assessment (Sink *et al.* 2012). Factors which have been used to classify national coastal and marine habitats include depth, slope, substrate type, geology, grain size, wave exposure, terrestrial and benthic-pelagic connectivity and biogeography. The resulting 2011 habitat map of marine ecosystems (Figure 1.1) incorporates the biogeographic and depth divisions in the South African marine environment, defining six ecoregions with 22

ecozones at the finest scale and 14 broad ecosystem types (Sink *et al.* 2012, Driver *et al.* 2012).

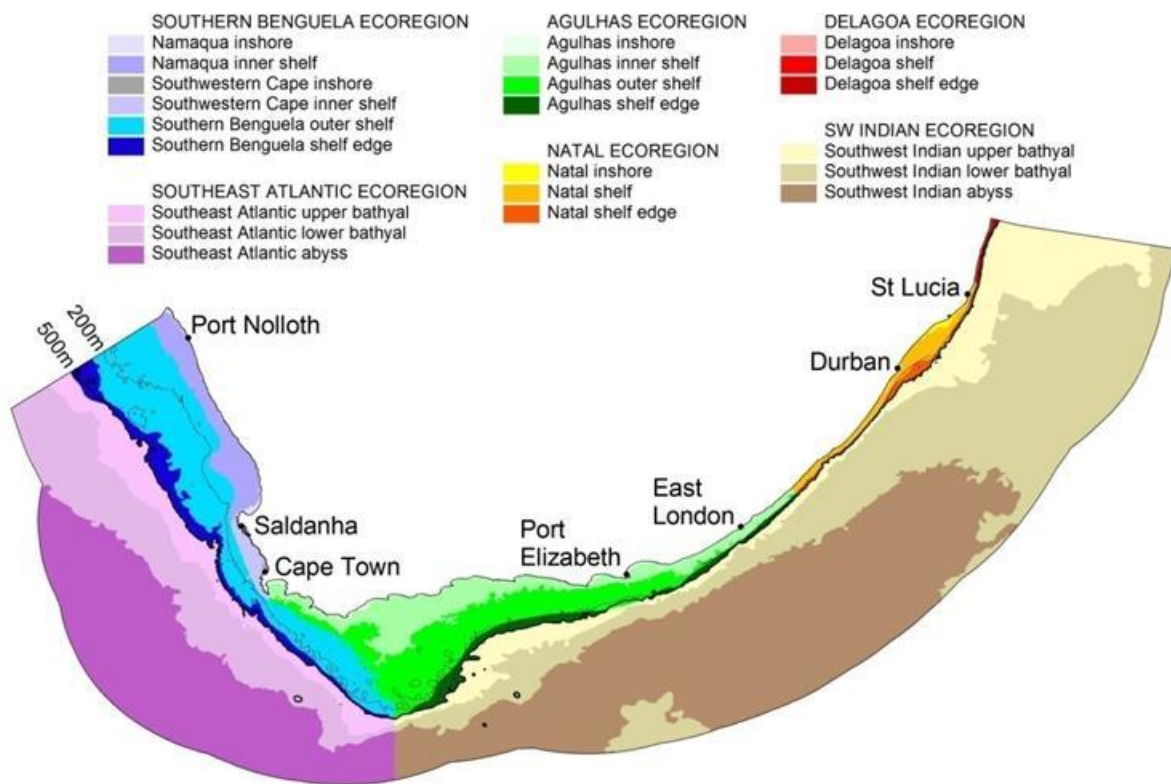


Figure 1.1: The South African coastal and marine inshore and offshore ecoregions and their ecozones (Sink *et al.* 2012).

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The 2011 NBA was produced by updating the 2004 National Spatial Biodiversity Assessment (NSBA). The NSBA dealt only with the spatial aspects of biodiversity, while the 2011 NBA included both the spatial and non-spatial aspects of biodiversity such as a summary of the state of invasive species and species of special concern (Driver *et al.* 2012). Changes incorporated in the 2011 NBA included a change of terms such as 'bioregions' and 'biozones' into 'ecoregions' and 'ecozones' respectively (Lombard *et al.* 2004, Sink *et al.* 2012). Many ecosystem assessments make use of ecoregions (Olson and Dinerstein 2002, Spalding *et al.* 2007, Costello 2009). Ecoregions were defined based on broad-scale biological variability and biogeography, also considering broad-scale habitat differences related to different ocean current systems with different temperatures and productivity. Ecozones incorporate distinct species assemblages in different depth strata and this needs to be considered in biodiversity assessments and planning for representative MPA networks (Lombard *et al.* 2004, Spalding *et al.* 2007, Sink *et al.* 2012). The South African 2011 NBA defined six ecoregions namely

Benguela, Agulhas, Natal, Delagoa, Southeast Atlantic and Southwest India (Figure 1.1). The current study focus lies within the Natal ecoregion which is further divided into three ecozones namely Natal inshore, Natal shelf and Natal shelf edge. There are several studies that have documented the coast and inshore of the KZN shelf; however there is less research beyond 30m i.e. beyond scuba diving depth (Schleyer and Tomalin 2000, Bolton *et al.* 2004, Celliers and Schleyer 2008, Porter *et al.* 2017) although recent studies on benthic macrofauna and deep demersal fish assemblages have been published (Fennessy 2016, MacKay *et al.* 2016, Untiedt and MacKay 2016). These studies were not able to employ visual techniques, relying mostly on grab sampling of benthic infauna and trawl sampling of demersal fish. Finally, a recent study by Roberson *et al.* (2017) used remote-sensing data to create a bioregional map of the upper-mixed layer of the South African continental marine realm.

At a provincial scale Ezemvelo KwaZulu-Natal Wildlife (EKZNW), a South African provincial conservation organisation, developed the KZN Coastal and Marine Biodiversity Plan through their fine-scale planning project, also known as SeaPLAN (Harris *et al.* 2011, Mills *et al.* 2015). SeaPLAN is a systematic conservation plan for the marine environment of the KZN province and includes collection and compilation of fine-scale spatial data on biodiversity features (species, habitats and processes). The SeaPLAN project also includes mapping of threats and resource use activities from the coastline out to the Economic Exclusive Zone (EEZ) of KZN (Harris *et al.* 2011). Factors which were used to classify habitats in SeaPLAN include nutrient availability (organic carbon and phosphate), depth, sediment type and temperature. Currently, the SeaPLAN classification delineates five biozones (or five benthic clusters) which are based on varying characteristics of the above-mentioned factors (Figure 1.2). Research conducted in the current study incorporates sites in biozones 1 and 2. Biozone 1 is described as a shallow sandy shelf with low organic carbon and phosphate levels and overlying warm but oxygen-depleted waters. Biozone 2 is described as a shallow gravel area with low organic carbon and phosphate and warm oxygenated bottom water (Livingstone 2016).

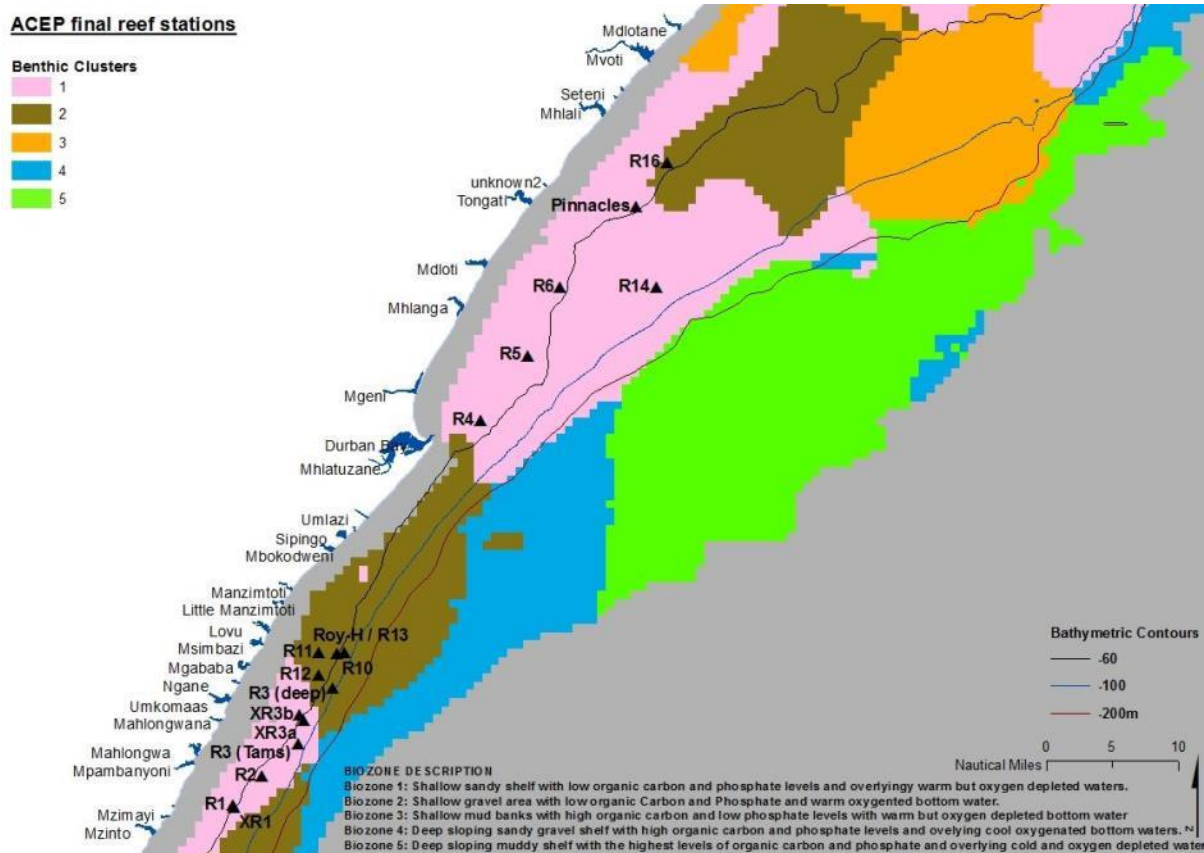


Figure 1.2: The Ezemvelo KwaZulu-Natal wildlife's SeaPLAN map, with the five described biozones also referred to as benthic clusters in this figure.

1.1.5 Use of benthic epifauna

Marine epifauna are defined as species that protrude from, live on, are anchored in or are attached to benthic substrates (Jennings and Kaiser 1998 as cited in Atkinson 2009). They are preferred organisms for biological monitoring studies, due to their limited mobility which prevents them rapidly moving away from unfavourable habitat changes (Türkmen and Kazanci 2010). Epifauna have longer life cycles than infauna, which help inform ecology and studies of potential impacts of long-term environmental change. The species composition of epifaunal communities is known to change in response to environmental changes (Türkmen and Kazanci 2010). Furthermore, epifauna provide useful indices to evaluate the status of marine ecosystems in monitoring long-term responses and site specific impacts (Atkinson 2009, Monk *et al.* 2016).

Maintenance of marine biodiversity is essential to sustain healthy marine ecosystems (Costanza *et al.* 2014, Heiskanen *et al.* 2016) and such diversity plays an important role in ecosystem processes such as nutrient cycling, pollutant metabolism, secondary production and dispersion (Snelgrove 1998, McArthur *et al.* 2010, Heiskanen *et al.* 2016). Benthic-

pelagic coupling processes such as nutrient, carbon and oxygen cycling are driven by marine epifaunal species (Dale *et al.* 2017). Appropriate consideration of these processes in regional modelling of species distribution is important. The two way exchange of matter between the benthos and the overlying water body is important for both benthic and pelagic components as these define the link between organisms on the seafloor to those at the surface (Raffaelli *et al.* 2003).

The current study aims to explore benthic ecosystem types off the KZN coast using epifaunal data quantified from seabed imagery and to investigate the potential environmental drivers that contribute to their species distribution patterns. This study incorporates epifauna data to refine the underlying maps of ecosystem types in this province on the east coast of South Africa. The results from this study will inform ecosystem type delineation for future conservation plans and assessments of the region.

The aim of this research is therefore to examine patterns and understand potential drivers of patterns in epifaunal assemblages, and to test and refine existing ecosystem classifications and maps for the outer shelf of KZN. Three specific objectives were set.

Objectives:

- To investigate patterns in benthic epifauna and describe benthic biotopes on the outer shelf (45–85m) of KwaZulu-Natal.
- To identify potential drivers of observed epifaunal biodiversity patterns.
- To test and refine existing ecosystem classifications in southern and central KwaZulu-Natal.

Research questions:

- What are the characteristic and distinguishing epifaunal species for the marine habitats defined in the study area?
- What are the potential key drivers of epifaunal biodiversity patterns in the study area?
- Do existing national and provincial habitat classifications reflect habitats as defined by the benthic epifaunal assemblages quantified in the study area?

Table 1.1: Definition of key terms used in this study.

Term	Definition
Biotope	A distinct biological assemblage that characterises a specific habitat. This represents the smallest geographical scale for defining ecosystem types in this study. Biotopes in this context are defined based on biodiversity pattern data (i.e. their biota) rather than abiotic or physical habitat characteristics. A biotope was only recognised in this study when represented by three or more sites. Single sites that did not cluster with any other sites were considered as outliers and when only two sites emerged as significantly different these were considered potential biotopes.
Deep reef	Reefs of the mesophotic zone (30-100m) (Linklater <i>et al.</i> 2016)
Ecosystem	A dynamic complex of animal, plant and micro-organisms communities and their non- living environment interacting as a functional unit. In this study ecosystems were defined using the definition from NEMBA (Government gazette, 2004)
Ecosystem type	An ecosystem unit or set of ecosystem units that has been identified and delineated as part of a hierarchical classification system, based on biotic and/or abiotic factors. Ecosystems of the same type are likely to share broadly similar ecological characteristics and functioning (SANBI 2016).
Epifaunal assemblage	Community of marine invertebrates living on the seafloor, reef or other benthic environment. In this study, sessile taxa greater than 1 cm in size were quantified to represent the epifaunal assemblages in reef, mixed substrata and unconsolidated sediment habitats.
Habitat	The physical environment occupied by species, assemblages and biotopes.
Morphospecies	A species distinguished from others only by its morphology (i.e. distinction from others is based solely on their particular form, shape or structure).

1.2 Study area

The KZN coastline extends approximately 570 km along the east coast of South Africa (Sink *et al.* 2005, Untiedt and MacKay 2016). The coast can be divided into three regions; the Northern (from Mozambique boarder to Richards Bay), Central (from Richards Bay to Durban) and the Southern (from Durban to the Mtamvuna Estuary) regions (Palmer *et al.* 2011). The Northern coastal region lies on a sandy plain, with very few rivers that drain across the wide coastal plain. The input of inland matter into the nearshore northern region, together with the warm temperature of the coast, allows tropical coral species to flourish in greater abundance on the Northern reefs than in other regions (Celliers and Schleyer 2008). Both the Central and Southern regions have numerous rivers draining to the sea, with more

than 60 rivers flowing into the sea from Thukela River southward. This results in major sea influx with high loads of discharged sediment washing down the rivers into the nearshore environment during summer (Anderson *et al.* 2009, de Lecea *et al.* 2016, Porter *et al.* 2017).

Within part of the Northern and Central regions lies the KZN Bight; a widened area of the continental shelf from Cape St Lucia to just below Durban (Lamont *et al.* 2016). The KZN Bight is characterised by increased turbidity and sediment load resulting from inflow from the Thukela, Umfolozi and other rivers (Green & MacKay 2016, Livingstone 2016). The topography of this area supports well-defined sand, mud and gravel sediments (Mackay *et al.* 2016) with predominately northward flowing currents (Lutjeharms *et al.* 2010, Roberts and Nieuwenhuys 2016). The KZN Bight has recently received much attention with various studies being conducted here as described by Fennessy *et al.* (2016). Sites surveyed in the current study are located in parts of the Central and Southern regions of KZN, with few sites within the KZN Bight.

The fast flowing Agulhas Current is regarded as one of the largest and swiftest currents on earth, it also plays an important role in weather patterns and influences the diversity of marine species along the KZN coast (Lutjeharms *et al.* 2010). The Agulhas Current plays an important oceanographic role along the KZN coast; flowing through the southern KZN region carrying warm water towards the Agulhas Bank where it meets with the cold Benguela Current (Meyer *et al.* 2002, Lamont *et al.* 2016); cooling slightly as it travels to the South. The Agulhas Current reaches a depth of 2000m and a maximum speed of 4 knots, carrying about $70 \times 10^6 \text{ m}^3/\text{s}$ of seawater past the eastern shores of South Africa (Lutjeharms *et al.* 2010). Moving to south of Durban, the Agulhas Current drives the Durban Eddy which is the lee-trapped, semi-permanent cold core cyclonic eddy that occurs off the east coast of South Africa (Roberts *et al.* 2010). The Durban eddy provides the nutrient source for primary production and therefore plays an important role in ecosystem functioning of the region (Guastella *et al.* 2012).

The reefs of the Southern KZN region host a rich diversity of marine communities, and provide popular diving locations such as Aliwal shoal and Protea Banks. The reef ecosystems of KZN are comprised of rocks heavily encrusted with marine life such as sponges, corals and seaweeds (Olbers *et al.* 2009). The Northern region supports more subtropical reefs that are covered with rich layers of hard and soft coral, many of which lie within the Isimangaliso

Wetland Park Marine Protected Area (Schleyer and Tomalin 2000, Palmer *et al.* 2011, Porter *et al.* 2017).

1.3 Survey Approach

The development of underwater video tools such as baited remote underwater video (BRUV), remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs) has enabled breakthroughs in marine research by providing access to previously inaccessible environments (Williams *et al.* 2012, Monk *et al.* 2016). These instruments allow surveys in remote, hazardous environments (often cold and dark) beyond normal scuba diving range (Heyns-Veale 2016). The SAAB Seaeye falcon 121777 ROV model (Figure 1.3) can operate to depths of up to 300m. It is controlled from aboard an anchored research vessel, and is tethered with an umbilical cord that connects the ROV to the surface unit controls. Two laser pointers installed on the ROV 6.42 cm apart are used to estimate the processed area coverage in images and the length of organisms in observations. The ROV provides data in the form of images, video recordings and depth. Other than stationary video recording, ROV video transects allow observations of the surrounding habitat. Furthermore estimates of density and/or percentage cover of non-motile benthic species can be extracted from images (Guinan *et al.* 2009, Dumas *et al.* 2009). Although research-focused ROV surveys have increased in recent years in South Africa (Sink *et al.* 2010, Franken 2015, Heyns 2015) little has been formally published about the work done to date (Heyns *et al.* 2016, Heyns-Veale *et al.* 2016, Makwela *et al.* 2016).



Figure 1.3: The SAIAB Seaeye falcon 121 777 remotely operated vehicle (ROV) during deployment.

Makwela *et al.* (2016) showed that the use of ROV footage to survey reef fish species provides similar results to methods such as BRUVs, based on fish species accumulation curves. ROV surveys however provided more additional information than stationary video sampling methods as they allowed wider observations of the surrounding seafloor. Limitations of using the ROV to survey habitats include identification of organisms to species level from images, as often organisms are not in focus and the colour can be misleading (Trenkel *et al.* 2014, Makwela *et al.* 2016). Dumas *et al.* (2009) reports that formal testing for the efficiency of video/photo studies is often difficult as it requires intensive, time consuming field work in contrasted habitats. An additional limitation of using the ROV in the KZN study area is the fast flowing Agulhas Current (average speed of 2.06 m/s) which often hinders sampling. Apart from the Franken (2015) study on the unconsolidated sediment sites of the KZN coast, this study is the first to use ROV imagery to quantify epifauna and unlike Franken (2015) which only covered soft sediment habitats, this study covers both consolidated and unconsolidated habitats of KZN.

1.4 Thesis Overview

This thesis has five chapters and the contents per chapter are outlined below.

Chapter 1: Introduction—This Chapter introduces the study, the rationale for this work and the aims and objectives of this research. It includes a literature review that covers marine ecosystem classifications, the study area and methods used.

Chapter 2: *Testing existing marine ecosystem classifications and establishing the effect of substrate in shaping epifaunal assemblages in southern KwaZulu-Natal outer shelf.*

This Chapter includes the analyses of imagery to quantify epifaunal communities from three different substrate types. Existing classifications are tested using epifaunal data, and the potential effect of substrate as a factor correlating with the observed epifaunal patterns is examined. The key characteristic and distinguishing species of epifauna from different substrate types are identified and biotopes from different substrate types were described.

Chapter 3: *Identification of the potential drivers of patterns in deep reef epifaunal assemblages in KwaZulu Natal.*

This Chapter incorporates additional reef sites and focuses on biodiversity assemblage patterns in reef epifauna. The potential key physical drivers of observed patterns in epifaunal assemblages of reef sites are investigated. Reef biotopes are described including characteristic and distinguishing epifaunal species.

Chapter 4: *Synthesis*

This Chapter summarises the overall key results from this thesis, discusses relevance and limitations of the study and draws conclusions with suggestions for future work.

Chapter 5: *References*

A full list of all used referenced material in this thesis.

2 Testing existing marine ecosystem classifications and assessing the effect of substrate in shaping epifaunal assemblages in southern KwaZulu-Natal outer shelf

2.1 Abstract

Despite their diverse temperate and subtropical fauna, marine ecosystems of the KwaZulu-Natal (KZN) outer shelf have received limited attention in terms of incorporating this diversity into existing ecosystem classifications. This Chapter aims to test two existing ecosystem classifications in the outer shelf using epifauna data. A total of 17 sites, including habitats comprised of reef, mixed and unconsolidated substrate types, were surveyed between depths of 48 and 85 m in southern KZN. Epifauna abundance data were quantified from seabed imagery collected by remotely-operated vehicle (ROV). Indices of diversity were calculated in order to estimate species composition and diversity across substrate types. Unconsolidated habitats yielded the lowest total number of species, followed by mixed substrates with reef habitats having the highest number of species per sample. For non-parametric species estimators, species accumulation curves were generated from the 17 sites to estimate the species richness of the biotope types. For both mixed substrates and reef habitats the curves reached an asymptote after 25 quadrats but for unconsolidated habitats the curves did not reach an asymptote, even after 60 quadrats. Cluster analysis and non-metric multi-dimensional scaling (nMDS) were used to visualize patterns in species assemblages across substrates. Epifauna at unconsolidated sediment sites were significantly different to that occurring on both mixed substrates or reef substrate and epifauna occurring on mixed substrates were also significantly different to those occurring on reefs. Epifaunal assemblages at sites with mixed substrates were more similar to those at reef sites than epifaunal assemblages at unconsolidated sediment sites. Simper analysis was used to characterise three distinct biotopes, at least one from each of the substrate types and characteristic and distinguishing taxa were identified. The significantly different epifaunal communities detected did not align with the existing national or provincial ecosystem classifications signaling the need for improvement in both classifications. The current study provides key insights that can be used to revise the existing ecosystem classifications and provides the first description of three distinct biotopes in southern KZN. Two potential biotopes were also tentatively recognized and further sampling, spanning a greater area and depth range, is recommended.

2.2 Introduction

Habitat can be defined as the chemical or physical environment which provides suitable conditions for the survival of a particular species or organism, an environment where a particular species lives or where a biotic community is normally found (Costello 2009, Gaillard *et al.* 2010). Marine ecosystems can be classified and distinguished in various ways and this includes methods based on characteristic species, substrate type, intertidal zonation and pelagic or benthic nature (Costello 2009). Environmental managers and conservation planners require standardised classifications and terminology to enable consistent mapping of the environment across all possible habitats (Brown *et al.* 2011). Ecosystem classification aids the understanding and ranking of biodiversity areas to support management actions, such as Marine Spatial Planning (MSP) and, the design and implementation of Marine Protected Areas (MPAs). Ecosystem classification also provides a language through which data and information regarding ecosystems can be communicated and managed (Mace *et al.* 2012).

Brown *et al.* (2011) define marine ecosystem mapping as the use of spatially continuous environmental data sets to represent and predict biological patterns on the seafloor in a continuous or discontinuous manner. Marine ecosystem mapping is an essential tool to support modelling and management of marine ecosystems (Cogan *et al.* 2009). Ecosystem mapping can encompass various maps such as geological maps that are produced from acoustic surveys of the seabed combined with maps that represent biological assemblages or biotopes e.g. coral reef, sea grass bed and mangroves (Kurland and Woodby 2008). Habitat mapping plays an important part in assessing the role of the ecosystem and how it changes over time. Various instruments and survey techniques have evolved to support habitat mapping. Appropriate techniques are selected depending on the objective(s) of a project, particularly with respect to the scale and distribution of the seafloor features of interest and the required resolution of the resulting maps (Diaz *et al.* 2004).

Costello (2009) explains the three general approaches used in habitat mapping, namely: *in situ* sampling, remote sensing and expert opinion. *In situ* sampling can provide both physical and biological data. This type of sampling includes the use of visual tools, grabs, cores, dredges, nets and traps. Remote sensing methods include satellite, aerial and acoustic sampling of the sea and seafloor (Kenny *et al.* 2003, Diaz *et al.* 2004). Data gathered using remote sensing provide different information at different spatial and temporal scales to *in situ* sampling. *In situ* sampling, however, provides a more accurate report of the species-habitat

relationship than remote sensing. Expert opinions are generally used when there is insufficient or no data available from a particular habitat (Costello 2009).

2.3 Biodiversity surrogates for ecosystem mapping

Habitat classification generally employs surrogate information as appropriate detailed levels of data are often not available at a national level (Przeslawski *et al.* 2011). There are two main types of biodiversity surrogates namely: taxonomic and environmental surrogates (Grantham *et al.* 2010). Taxonomic surrogates use well known groups of species (i.e. biological data), which are extrapolated geographically using statistical techniques (Setersdal and Gjerd 2011). Environmental surrogates are based on the use of both physical and biological data. These kinds of surrogates are further divided into those that are based on discrete classes (usually biological data) and those that use continuous data from selected areas. Classifications based on biological data as a surrogate are referred to as ecological classifications (also known as biotopes). Ecological classification surrogacy has been widely used in conservation planning, with the idea that they represent the larger number of the subsumed species (Grantham *et al.* 2010).

The use of biological data as biodiversity surrogates for ecosystem mapping beyond scuba diving depths is still in its infancy (Howell 2010) when compared to other methods used. Many studies use acoustic ground truthing methods and deploy oceanographic instruments such as echo sounders, while other studies use physical and abiotic marine measures to create ecosystem maps (Beaman and Harris 2005, McDougall *et al.* 2007, Dumas *et al.* 2009, Davies *et al.* 2014). Kobryn *et al.* (2013) demonstrated that, hyperspectral remote sensing techniques can offer an efficient and cost effective approach to mapping and monitoring reef habitats of remote and inaccessible areas. Brown and Collier (2008) classified and produced an ecosystem map from high resolution side scan sonar data and further verified their habitat map using biological data derived from underwater video footage. Their study reports that side scan sonar is able to predict biological communities to an acceptable level of accuracy.

2.3.1 The effect of substrate on biodiversity patterns

Benthic environments support a significant and vital component of the ocean's productivity and biodiversity. Substrate is used in ecosystem classifications globally (Howell *et al.* 2010, Sink *et al.* 2012), and it is regarded as the primary determinant of community structure and biodiversity (Kostylev *et al.* 2001, McArthur *et al.* 2010). Hard substrate hosts a large portion of sessile suspension feeders such as encrusting sponges and most corals, while soft substrate

hosts small, discretely motile invertebrates and some small corals that have adapted to survive here (McArthur *et al.* 2010).

2.3.2 *Photographic imagery derived data versus data from physical samples*

Photographic imagery data and data derived from physical samples provide realistic estimates on species abundance and richness, respectively (Costello 2009). The combination of physical sampling and imagery-based methods to describe benthic diversity yields a better understanding of the habitat and provides more informed results on benthic diversity (Williams *et al.* 2015). It is however not always possible to get physical samples from deep sea habitats in comparison to obtaining imagery from such habitats—this is due to technological limitations, frequent adverse conditions and high costs of working in depths beyond scuba diving.

The use of imagery provides a good platform to count abundance of epifaunal data (Solan *et al.* 2003), whereas physical samples provide richness and biomass data (Gotelli and Colwell 2001, Diaz *et al.* 2004). Furthermore data derived from imagery can be used to support ecosystem conservation and it is easier to conduct repeat studies using images (Lam *et al.* 2006, Williams *et al.* 2015). However, a downfall of imagery analysis is that it is often difficult to identify organisms to genus or species level without having physical samples to verify against (Deter *et al.* 2012, Davies *et al.* 2014).

2.3.3 *Habitat classification studies in South Africa*

Most recent habitat classification studies conducted in South Africa include that of Olbers *et al.* (2009), Heyns (2015), Franken (2015), Karenyi *et al.* (2016) and Roberson *et al.* (2017). Roberson *et al.* (2017) selected relevant variables and parameters (such as sea surface temperature, Chlorophyll-*a*, net primary productivity, sea slope and depth data) that best reflected key ecosystem properties at broad-, meso- and fine-scales to create a bioregional map of South Africa's pelagic realm. Karenyi *et al.* (2016) used physical variables such as sediment grain size, depth and upwelling-related variables (such as maximum chlorophyll *a* concentration, summer bottom oxygen concentration and sediment organic carbon content) to classify unconsolidated sediment seascapes of the South African west coast. Heyns (2015) incorporated the use of baseline data (collected by underwater video methods) to compare the classifications of community structure and functioning of the well-studied, shallow (< 25 m) and poorly studied, deep (45–75 m) reefs of the Agulhas Ecoregion.

Franken (2015) investigated the patterns and potential drivers of benthic communities in unconsolidated sediment habitats of KwaZulu-Natal (KZN), incorporating epifaunal communities into marine ecosystem classifications. Olbers *et al.* (2009) described and zoned the benthic communities of the subtropical Aliwal shoal, an MPA along the KZN region. Few studies have been conducted in the southern region of KZN that specifically examine the benthic biota with respect to proposed ecosystem maps. Studies conducted by Bolton and Stegenga (2002) and Schleyer *et al.* (2006), report that the region largely consists of subtropical reefs which host temperate and tropical fauna. Species dominating this region include sponge, algae, corals, echinoderms, ascidians and anemones, many of which colonise reef habitats. Sink *et al.* 2005 described the intertidal reef communities of the east coast of South Africa while Porter *et al.* 2013 described shallow subtidal reef communities of this area; however their studies extended further up to Mesali Island in northern Tanzania. Porter *et al.* 2017 identified depth, turbidity and suspended sediment as potential abiotic determinants of shallow reef community composition in the Natal region (i.e. central KZN). Benthic communities in the southern region of KZN appeared to be influenced by topography, sediment cover and wave energy (Olbers *et al.* 2009). The current study incorporates epifaunal data from unconsolidated sediments and findings presented in Franken (2015) and further investigate benthic communities occurring in mixed and reef habitats of the southern KZN shelf.

The South African national ecosystem classification as reported in the National Biodiversity Assessment (NBA), defined three main categories of ecosystem types, based on the stability of their substrate, as consolidated, unconsolidated and mixed ecosystem types (Sink *et al.* 2012, Karenzi *et al.* 2016); while the KZN regional classification developed by the SeaPLAN project, defined five biozones (or benthic clusters) in the region including shallow sandy shelf, shallow gravel area, shallow mud banks, deep sloping sandy gravel shelf and the deep sloping muddy shelf (Livingstone 2016). The main difference between the national habitat classification and regional biozone classification is the approach employed in classifying ecosystem types. The national classification drew from biodiversity pattern data and expert derived divisions in physical data. The regional classification was based purely on physical data sets and did not take expert knowledge or any biodiversity data into account. The regional classification did however incorporate additional physical variables which were not incorporated in the national classification (Sink *et al.* 2011). This Chapter tests the existing

ecosystem classifications (national and regional) for a shelf region in southern KZN, using epifauna data derived from seabed photographic imagery as biodiversity surrogates.

2.3.4 Aim and Objectives

The aim of the current study is to test and support the improvement of existing ecosystem classifications using epifaunal assemblages of outer shelf ecosystems in southern KZN.

Objectives:

- To examine the effect of substrate type on epifaunal assemblages on the outer shelf of KwaZulu-Natal
- To identify and define potential biotopes in the study area.
- To examine the validity of existing ecosystem types proposed by the National (NBA) and Provincial (SeaPLAN) ecosystem classifications and maps, using epifauna data.

Key Questions:

- Is there a significant difference between the epifaunal assemblages in deep reef, mixed substrate and unconsolidated habitats of the southern KwaZulu-Natal outer shelf?
- What are the biotopes and their characteristic and distinguishing taxa in the study area?
- Do existing national and provincial ecosystem classifications reflect habitats as defined by the benthic epifaunal assemblages?

Hypotheses:

- H0: There are no significant differences in epifaunal communities between substrate types (i.e. reef, mixed and unconsolidated habitats) on the outer shelf of southern KwaZulu-Natal.
- H0: The existing national and provincial ecosystem classifications reflect the same biodiversity pattern as those defined by benthic epifaunal assemblages.

2.4 Methods

2.4.1 Data collection

Data were collected as part of the Biodiversity Surrogacy Project, a collaboration enabled by the African Coelacanth Ecosystem Programme (ACEP). Surveys were conducted aboard *M.Y.*

Angra Pequena vessel during May to June 2014, and June 2015. Images of the seabed and epifauna were obtained using a SAAB Seaeye falcon 121 777 remotely-operated vehicle (ROV) at 17 sites along the KZN shelf (Figure 2.1) from depths between 48–85 m, in unconsolidated sediment (sand, mud and gravel), mixed (both sand sediment and reef) and deep reef habitats.

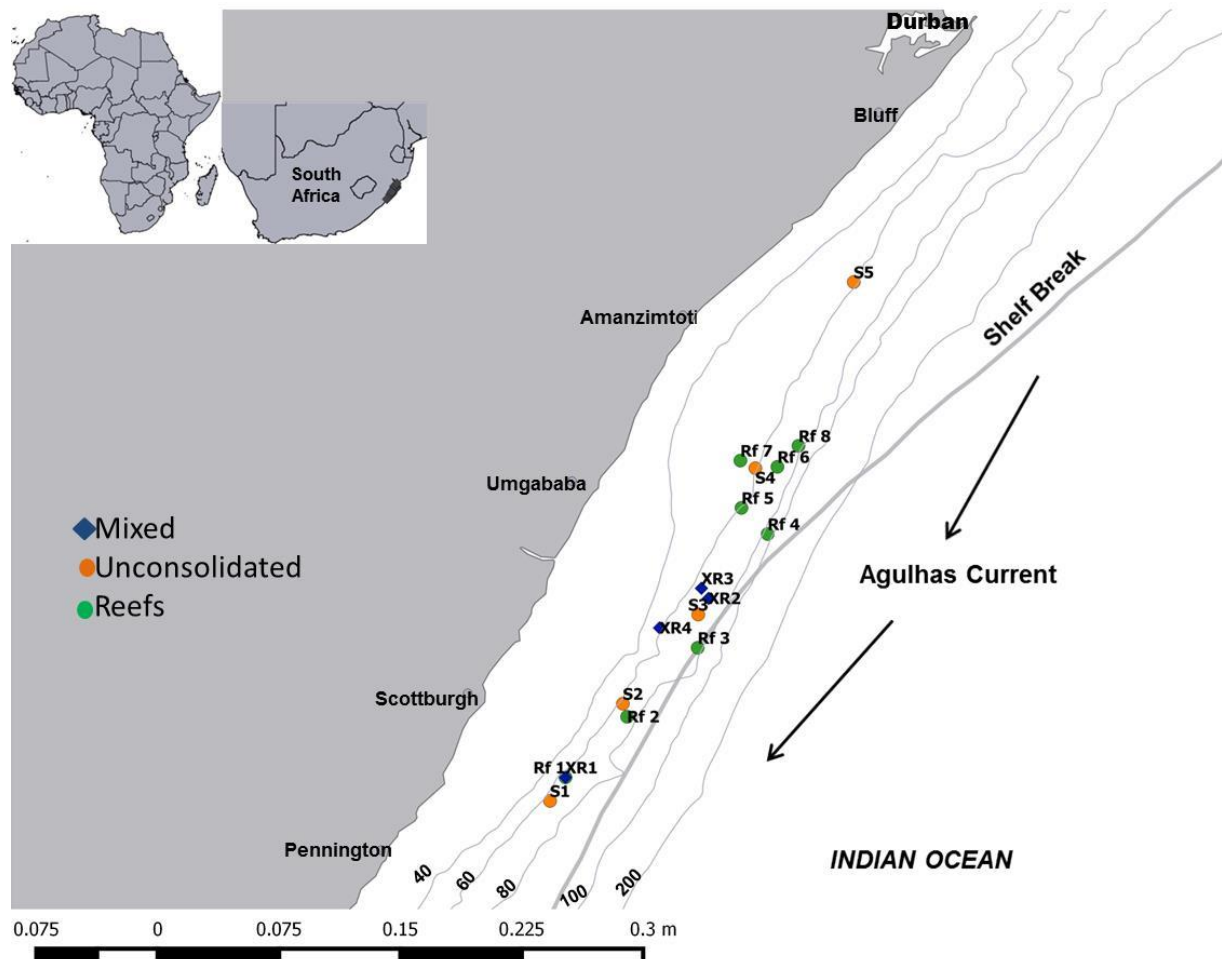


Figure 2.1: The southern KwaZulu-Natal shelf map showing the 17 study sites.

At each site, the ROV was deployed from the vessel but remained tethered by an umbilical at all times. Once the ROV had settled on the seafloor, images of the seafloor and biota were captured using a fixed 45 degree camera angle. A two-point laser measure, 6.42 cm apart, was displayed at all times to enable calibration of the seabed area. Complementary seabed videos were also captured at all sites, which were used to supplement still images to increase sample size when necessary. The ROV was kept on or as close to the seabed as possible. All survey sessions were conducted while the vessel remained on anchor during daylight hours (07h00 to 17h00), and each session took approximately 1 hour per site. For the purposes of this

Chapter, 17 sites were sampled off the southern KZN shelf: 8 reefs, 4 mixed and 5 unconsolidated ecosystem types with depth ranges between 48–85 m (Table 2.1).

Table 2.1: Unconsolidated sediment (S), mixed (XR) and reef (RF), sites sampled off the southern KwaZulu-Natal region for this study. The ecosystem types were categorised quantitatively based on visual observations during the current study: unconsolidated sediment (sand, mud and gravel), mixed (constitute both sand and reef) and deep reef habitat.

	Sampling Site	Latitude (South)	Latitude (East)	Depth (meters)	Regional Classification (SeaPLAN)	National Ecosystem Classification (NBA)
Unconsolidated sediments	S1	-30.34983	30.80083	69	Shallow Sandy Shelf	Natal Sandy Shelf
	S2	-30.28983	30.84583	65	Shallow Sandy Shelf	Natal Shelf Reef
	S3	-30.23478	30.8924	67	Shallow Sandy Shelf	Natal Sandy Shelf
	S4	-30.14445	30.92768	66	Shallow Gravel Area	Natal Sandy Shelf
	S5	-30.02950	30.98850	60	Shallow Gravel Area	Natal Sandy Shelf
Mixed	XR1	-30.33530	30.81038	66	Shallow Sandy Shelf	Natal Sandy Shelf
	XR2	-30.22483	30.89872	66	Shallow Sandy Shelf	Natal Sandy Shelf
	XR3	-30.21858	30.89437	65	Shallow Sandy Shelf	Natal Sandy Shelf
	XR4	-30.24305	30.86848	64	Shallow Sandy Shelf	Natal Sandy Shelf
Reef	RF1	-30.33530	30.81038	60	Shallow Sandy Shelf	Natal Sandy Shelf
	RF2	-30.29788	30.84845	72	Shallow Sandy Shelf	Natal Shelf Reef
	RF3	-30.25530	30.89207	75	Shallow Sandy Shelf	Natal Shelf Edge Reef
	RF4	-30.18508	30.93528	85	Shallow Sandy Shelf	Natal Sandy Shelf
	RF6	-30.14357	30.94132	69	Shallow Gravel Area	Natal Sandy Shelf
	RF7	-30.13972	30.91843	48	Shallow Gravel Area	Natal Shelf Reef
	RF5	-30.16893	30.91910	60	Shallow Gravel Area	Natal Shelf Reef
	RF8	-30.13065	30.95433	72	Shallow Gravel Area	Natal Sandy Shelf

2.4.2 Image analysis

Image manipulating software (Adobe Photoshop CC 2015) was used to merge each quadrat with a digital grid which was designed to estimate the constant area of all images processed. The digital grid (Figure 2.2) was designed using R Version 3.2.2 software package, with two solid middle lines, set at a distance of 6.42 cm apart, and replicating the distance between the laser pointers of the ROV (Franken 2015).

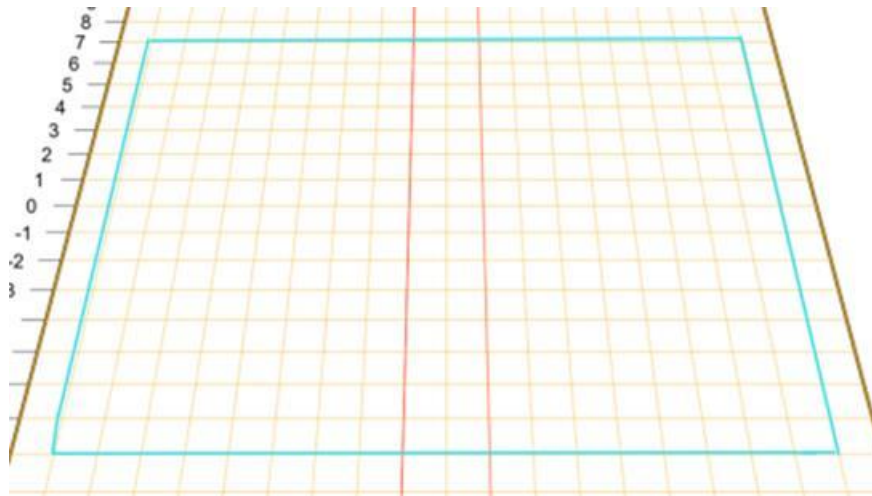


Figure 2.2: The designed 0.278 m² grid used to help define the processed area with the middle red solid lines being overlaid on laser points of the image being processed.

The grid was overlaid on all images (Figure 2.3), with the two red colour lines aligned over the laser point markers, therefore denoting a fixed distance and enabling a constant area of analysis on each image. The total area processed was calculated by using the standard area of the grid multiplied by the number of images processed. This study includes re-analysis of data from the unconsolidated sediment sites presented by Franken (2015), with Makwela and Franken working together to ensure consistency and a standard approach. Data from all reef and mixed sites were acquired by Makwela.

All biota greater than 1 cm² in size, visible within each standardized grid-defined area, were quantified (individual counts) and identified to the lowest possible taxon level. Taxonomic guides as well as taxonomic expert opinions were used for identification of taxa. A minimum of 25 images per study site were quantified in mixed and deep reef habitats, and 60 images per site in unconsolidated sediment habitat. The current study excluded identification of mobile epifauna, although they were observed in the footage.

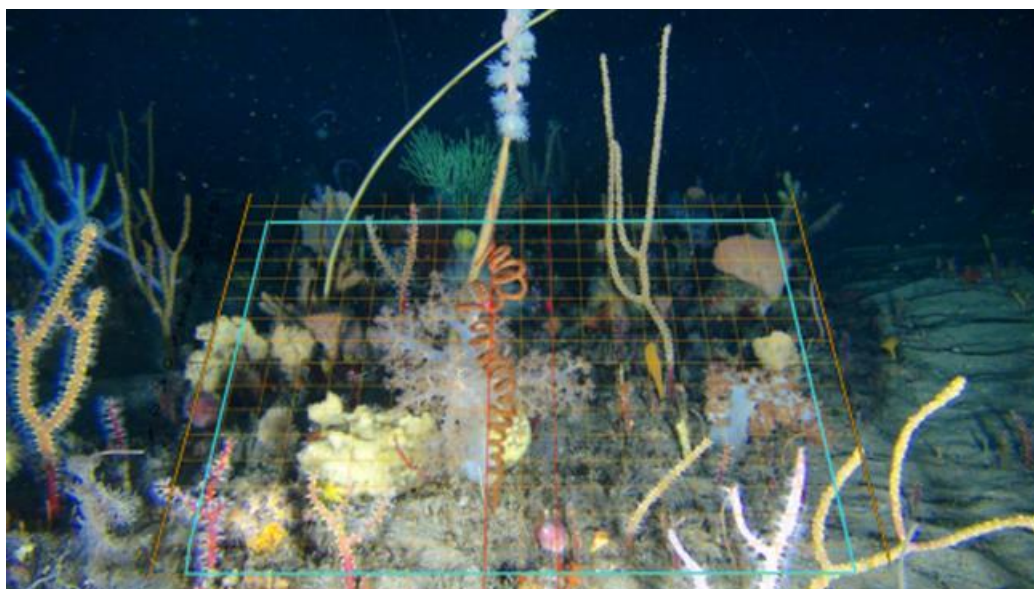


Figure 2.3: An exemplar image captured from a mixed ecosystem type with an overlaid grid. Only species within the blue square area (0.278 m²) were quantified.

2.4.3 Diversity Indices

The following indices of diversity were calculated in order to estimate species composition and diversity of the three different ecosystem types: Shannon Wiener ($H' (\log_e)$), Pielou's Evenness (J'), Species Richness (D), Total individuals (N) and Total species (S). Diversity indices were calculated using the DIVERSE function in PRIMER v6 (Clarke and Gorley 2006). The Shannon Wiener diversity index is a commonly used diversity index, which accounts for both abundance and evenness of the species present. Pielou's evenness index is derived from the Shannon Wiener index (Heip *et al.* 1998, Türkmen and Kazanci 2010) and represents a measure of how evenly the relative abundance of species diversity (richness) is distributed in an environment.

2.4.4 Non-parametric species estimator

Species accumulation curves were generated using PRIMER v6 and PERMANOVA software (Clarke and Gorley 2006, Anderson *et al.* 2008) from each of the 17 sites to assess the cumulative species estimation over the full sample size. Additionally, three species accumulation curves were generated to represent combined data from each ecosystem type. The following non-parametric species estimators, which use abundance data, were selected to generate the species accumulation curves: observed richness (Sobs) and species estimators (Chao1, Bootstrap and Jackknife1). Sobs determines the number of species in the sample by randomising the species collected. Chao1 calculates the estimated true species diversity of a sample. It uses the number of singletons (only one individual) and doubletons (two

individuals) i.e. the rare species, to estimate the number of missing species, whereas Jackknife1 uses only the number of singletons to estimate the number of missing species (Chao *et al.* 2009, Gotelli and Chao 2013). Bootstrap species estimator uses abundance data and was originally developed for quadrat sampling (Gotelli and Chao 2013). The Bootstrap estimator method was generated to obtain a variance estimator and confidence interval (Chao *et al.* 2008).

2.4.5 Statistical analysis

Two existing ecosystem classifications, SeaPLAN and the NBA, were assessed using quantified epifaunal data collected from 17 sites. PRIMER v6 and PERMANOVA software (Clarke and Gorley 2006, Anderson *et al.* 2008) was used to perform multivariate analyses of the epifauna abundance data and to identify characteristic and distinguishing taxa among the different, pre-defined ecosystem types.

The epifaunal abundance data were pre-treated with 4th root transformation and a Bray Curtis measure of resemblance. The 4th root transformation down-weights the dominance of over-abundant species and increases possible inclusion of all species without being over-shadowed by the dominant species (Field *et al.* 1982). Furthermore the 4th root transformation prevents unusually large-bodied species from influencing the Bray Curtis dissimilarity measures (Clarke and Gorley 2006).

Measures of (dis)similarity were explored with a cluster dendrogram (constructed with group average linkage), which defines species assemblages by grouping them according to their level of similarity. Similar samples were clustered within the same group while dissimilar samples were represented on a separate part of the dendrogram. A similarity profile analysis (SIMPROF) was run in conjunction with the cluster dendrogram to identify the significantly different groupings of sites as represented in the cluster dendrogram. SIMPROF results were superimposed on the dendrogram. A multi-Dimensional Scaling (nMDS) plot was generated to visualise sites with high similarity in epifauna community composition. The significantly different groups identified in the SIMPROF analysis were superimposed on the nMDS to reflect the proposed biotopes.

A three-way PERMANOVA analysis was performed to test for significant differences in community structure among the three defined ecosystem types based on epifauna abundance data. Fixed factors, substrate type, SeaPLAN biome type and NBA ecosystem type were

included in the analysis, with type III sum of squares. PERMANOVA pairwise tests were used to test the significant differences within the groups of the substrate type only.

Similarity percentage (SIMPER) analysis was conducted to detect which species characterise each ecosystem type and which species distinguish the ecosystem types, i.e. those species which contribute most to differences detected among groups. Furthermore SIMPER analysis was conducted to identify characteristic and distinguishing species of the proposed biotopes.

2.5 Results

2.5.1 Description of dataset

The total area processed ranged between 6.95 m² and 11.12 m² per site for reef and mixed ecosystems and between 13.90 m² and 16.69 m² for unconsolidated sediment ecosystem type. A total of 166 morphospecies was recorded, with most being octocorals, followed by Porifera, bryozoans, ascidians and anemones. The total number of quadrats processed was 623, resulting in a total of 13 128 individual fauna counted.

2.5.2 Diversity and evenness indices

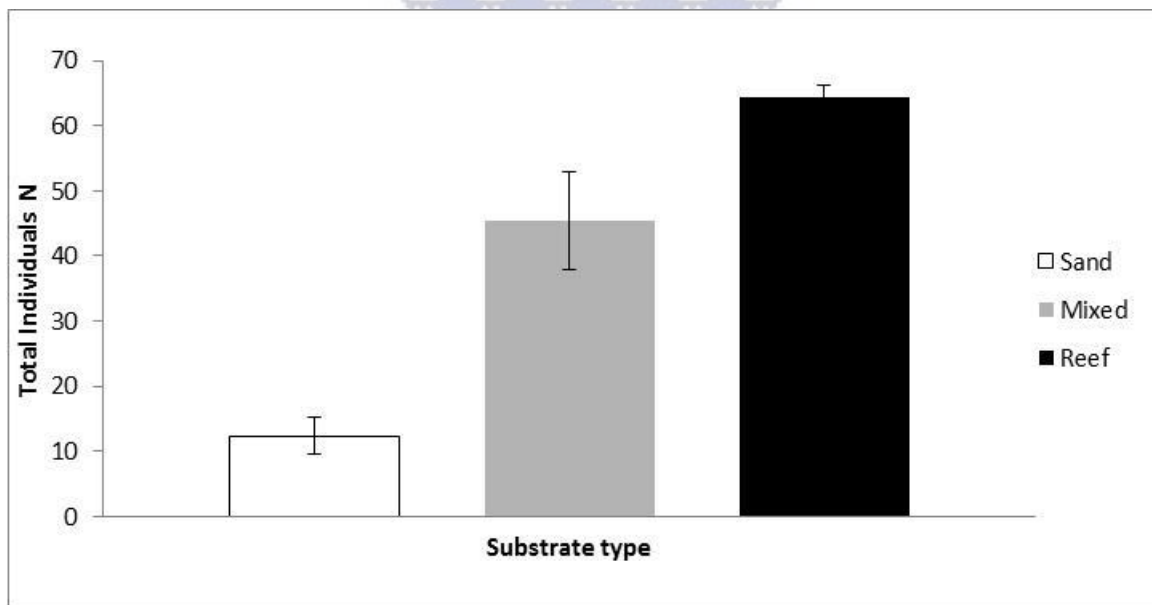


Figure 2.4: Average total number of individuals (N) recorded per ecosystem type with standard error bars (\pm SE).

As expected, results obtained for both average total number of individuals (N) and average total number of species (S) per ecosystem type (Figure 2.4 and 2.5) showed that reef ecosystem type had more species and more individuals than the other two ecosystem types. Unconsolidated sediment had the lowest total number of species.

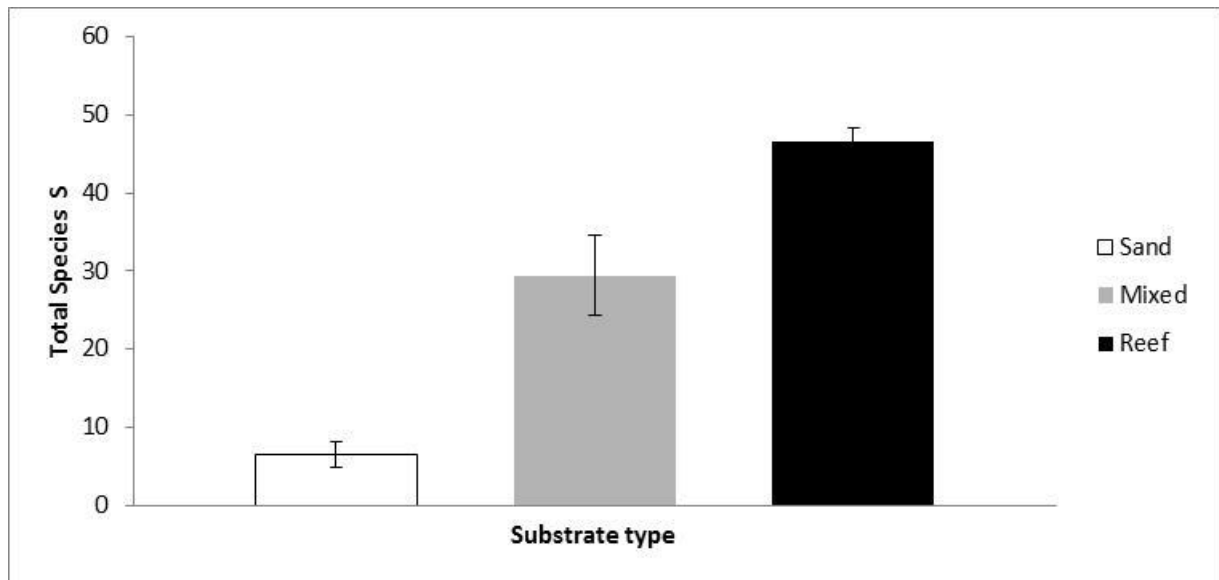


Figure 2.5: Average total number of species (S) per ecosystem type with standard error bars (\pm SE).

In terms of species richness (Figure 2.6), reef ecosystem type had a relatively high number of species per sample when compared to the other two ecosystem types, followed by mixed ecosystem type and unconsolidated sediment which had relatively low number of species.

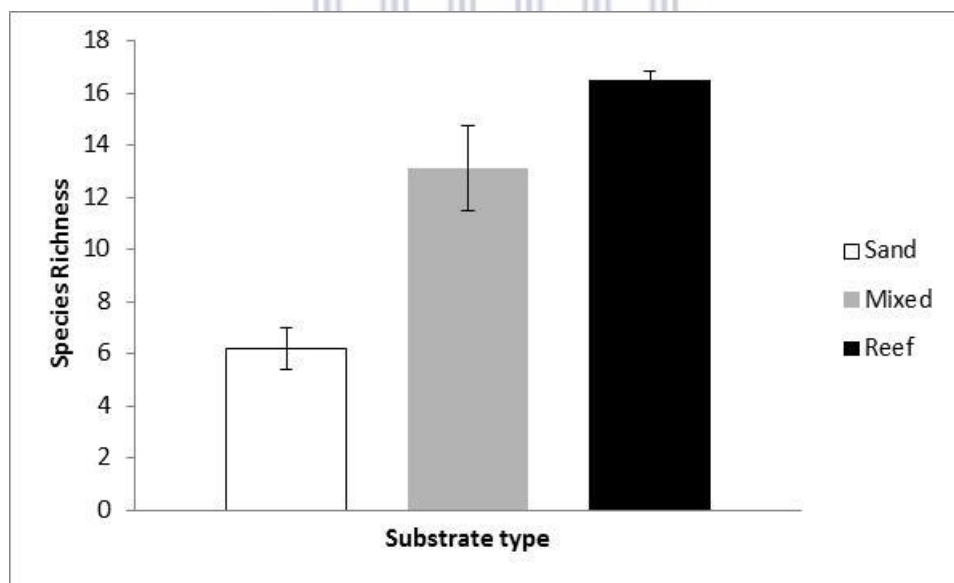


Figure 2.6: Average species richness of the three ecosystem types with standard error bars (\pm SE).

The Shannon Wiener index of diversity (Figure 2.7) indicated that both reef and mixed habitats had values above 3, indicating that these ecosystem types displayed greater diversity than unconsolidated sediment which had a value of around two. Pielou's Evenness index (Figure 2.8), showed that species distribution in all three ecosystem types had similar evenness

(between 0.974–0.987), however there was relatively high level of inconsistency (skewed distribution) in evenness among sites from unconsolidated sediment.

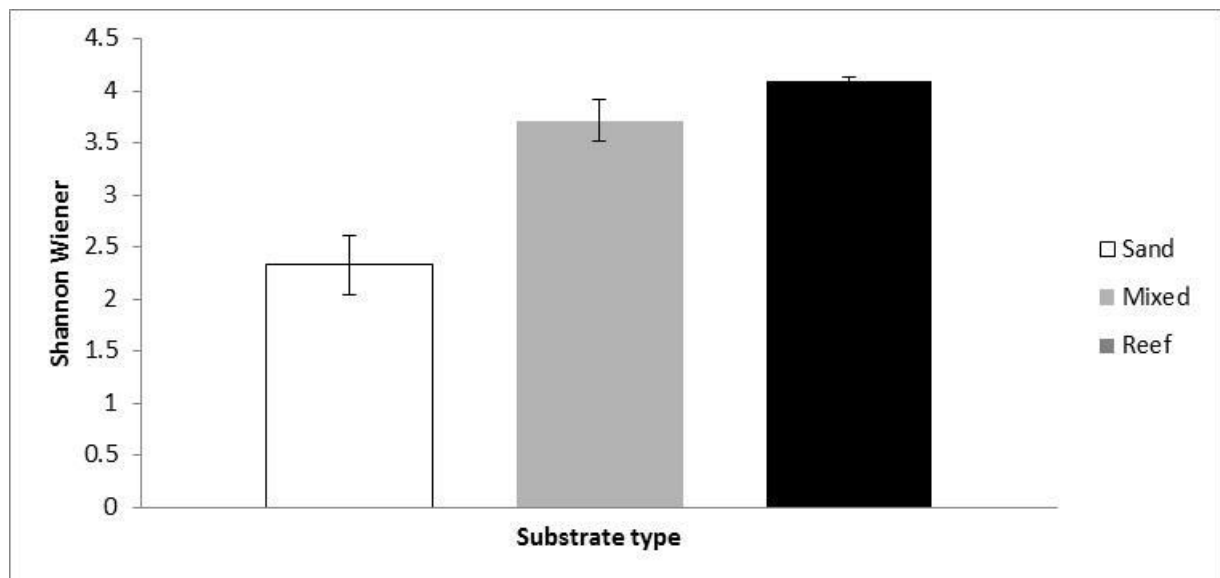


Figure 2.7: Shannon Wiener index diversity of the three ecosystem types with standard error bars (\pm SE).

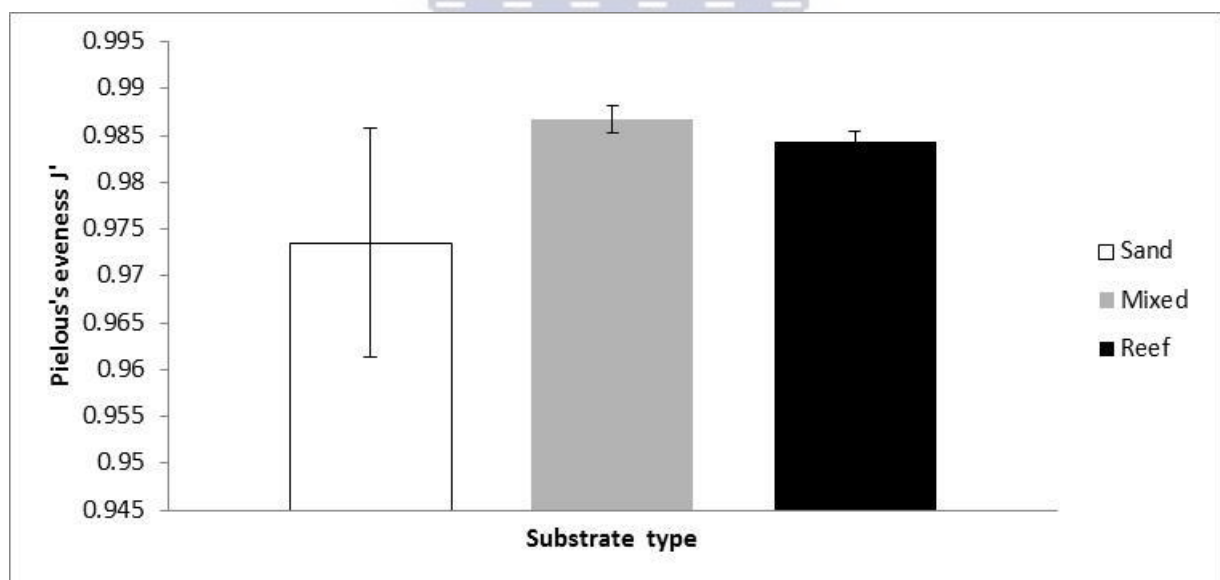
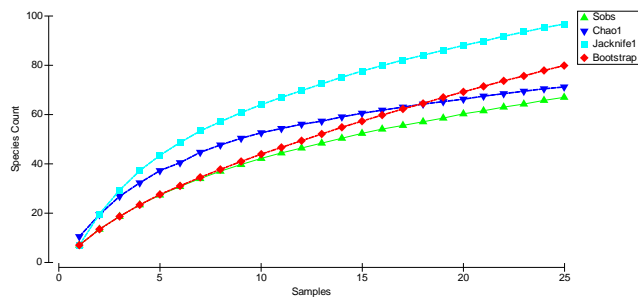


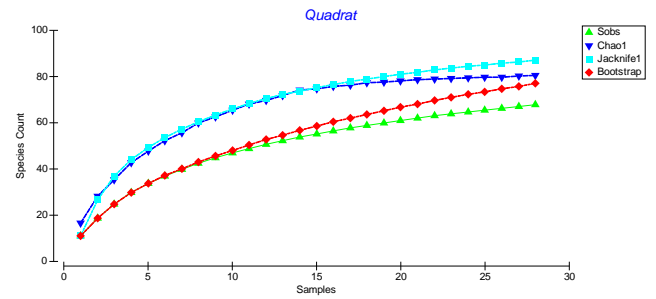
Figure 2.8: Pielou's evenness of the three ecosystem types with standard error bars (\pm SE).

2.5.3 Non-parametric species estimator

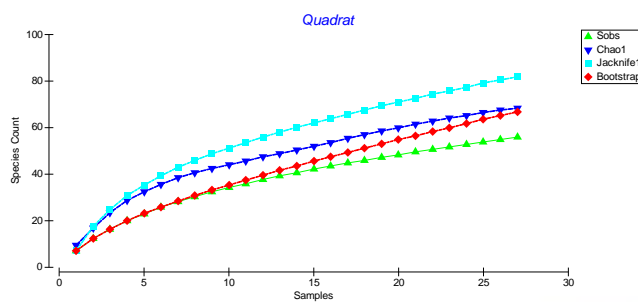
Species accumulation curves (Figure 2.9-11) were plotted to observe and estimate the species richness of the three ecosystem types.



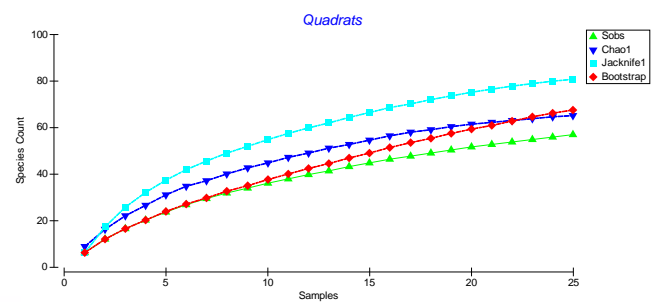
RF1



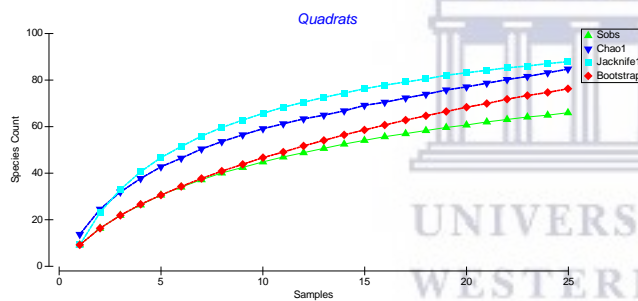
RF2



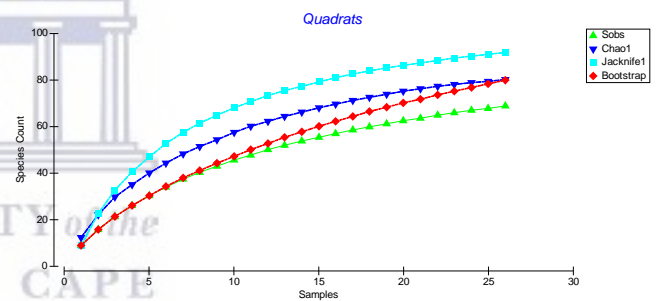
RF3



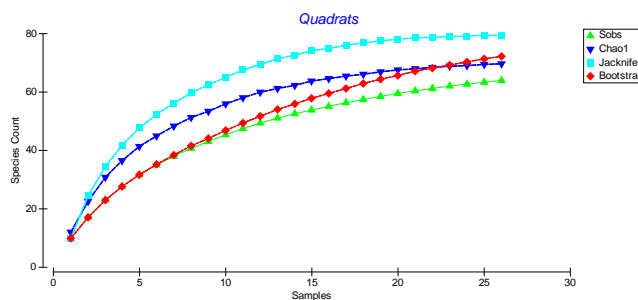
RF4



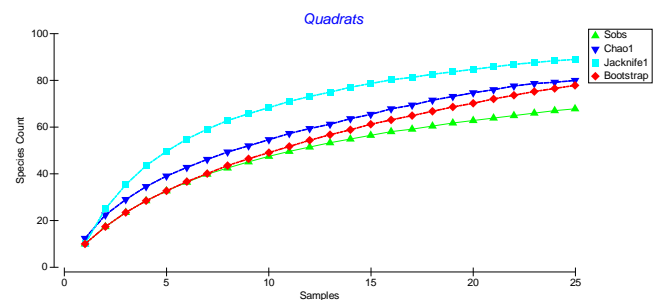
RF6



RF7



RF5



RF8

Figure 2.9: The species accumulation curves generated from eight reef sites through non-parametric approaches. Sobs determines number of species; Chao1 calculates the estimated true species diversity, Jackknife 1 uses only the number of singletons while bootstrap obtains variance estimator and confidence interval.

For both reef (Figure 2.9) and mixed ecosystem (Figure 2.10) types, most curves reached an asymptote after 25 quadrats, indicating that 25 samples were sufficient to identify most species present in those ecosystem types. The results, however, implied that more samples needed to be processed in order to reach an asymptote for curves of sites RF1, RF6, XR1 and XR3. At site XR4 (Figure 2.10) the Sobs, Jackknife1 and Bootstrap curves flatten out after approximately 25 samples, but the Chao1 curve showed some interesting results in which the curve flattened out initially but thereafter started to show an increase in species count with an increase in quadrats.

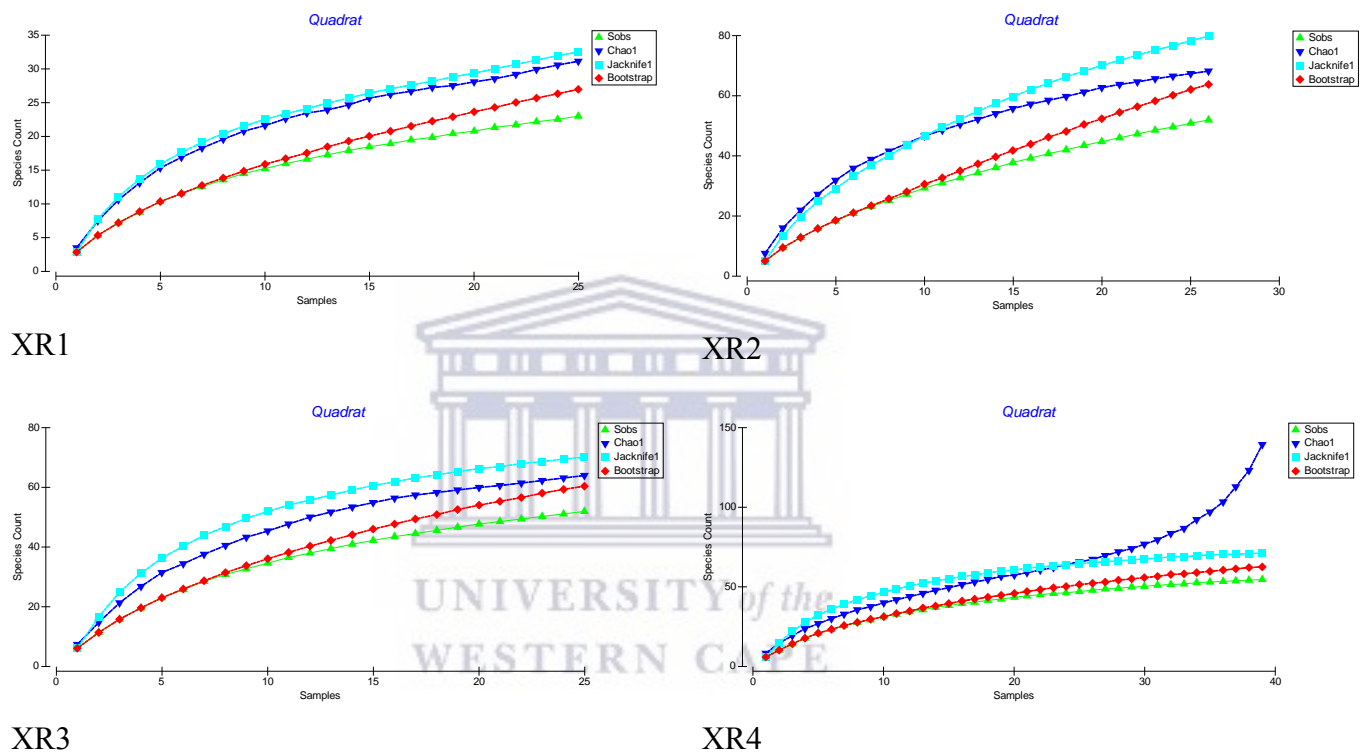


Figure 2.10: Species accumulation curves generated from four mixed ecosystem sites through non-parametric approaches.

The results for unconsolidated sediment sites (Figure 2.11) were different from the other two ecosystem types results, in that the species accumulation curves did not reach asymptotes (in particular Bootstrap and Sobs results at S1, S2, S3 and S4) even after processing a maximum of 60 quadrats (13.9m²) per site. It was only at Site S5 where the Sobs curve reached an asymptote and met with the Chao1 curve. This implied that after processing 60 samples from Site S5, both the observed richness and estimator agree that all species of this area are likely to be detected. The Jackknife estimator curve of S5 showed an overestimation of rare species.

More interesting results were observed with the Chao1 curves at sites S1, S3 and S4 showing an overestimation of rare species in these samples.

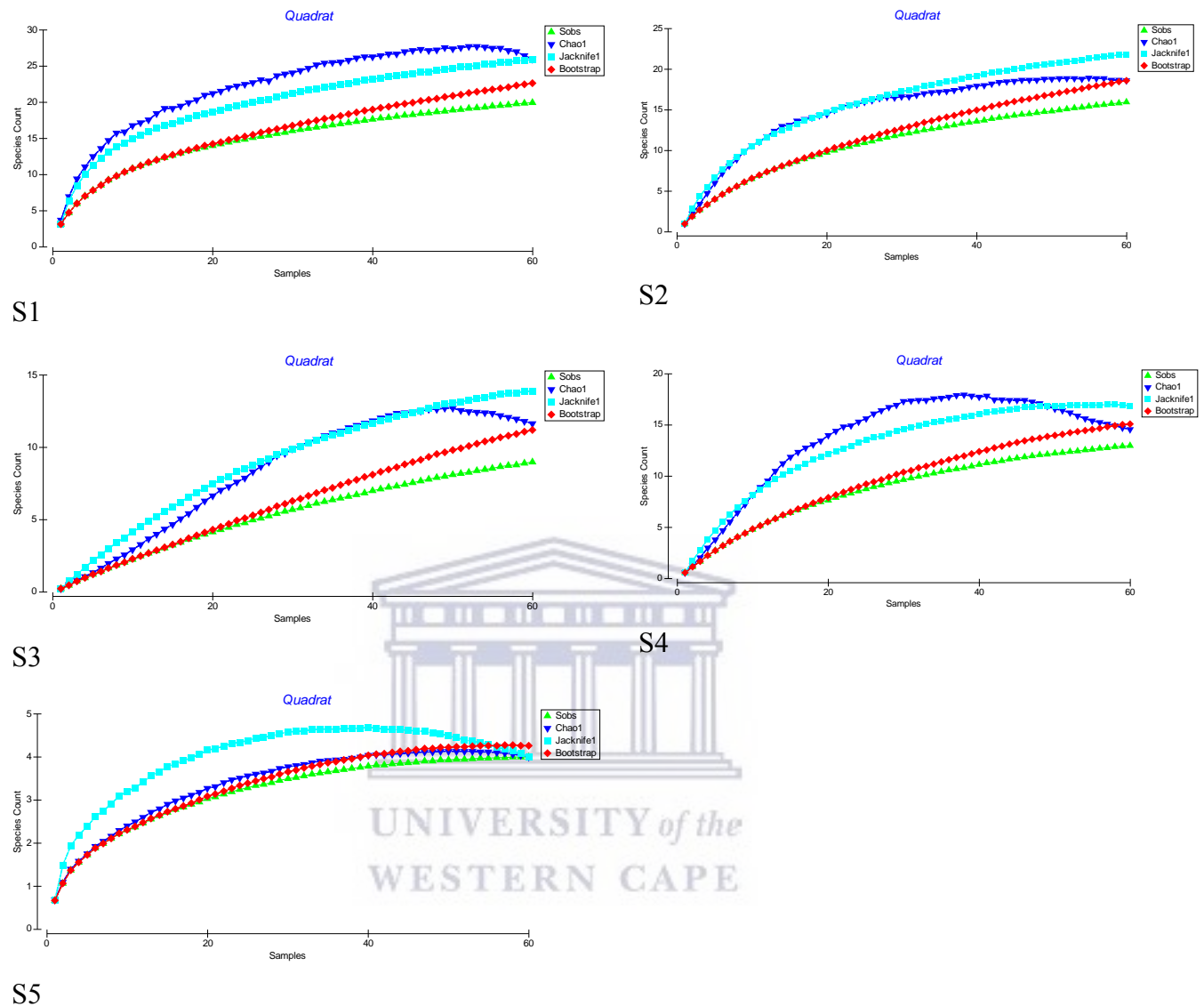


Figure 2.11: Species accumulation curves generated from five unconsolidated sediment sites through non-parametric approaches.

2.5.4 Benthic epifauna community types

The cluster dendrogram (Figure 2.12a) and nMDS plot (Figure 2.13) showed a clear separation between epifaunal assemblages from unconsolidated sediment and those from mixed and reef sites. The solid black lines in the dendrogram represented significant differences among groups defined by SIMPROF analysis while dotted red lines indicated no significant differences. All unconsolidated sediment sites namely S1, S2, S4 and S3, S5 clustered together and within this cluster there were further subgroups, with S1, S2 and S4 sites forming biotope 1 and a potential biotope A made up of sites S3 and S5. The second cluster of the mixed and reef ecosystem types consist of RF1, RF2, RF3, RF4, RF5, RF6, RF7, RF8, XR2, XR3 and XR4, with XR1 being an outlier. The sites were further divided into subgroups of sites RF1 and RF4 (forming a potential biotope B for mixed sites), grouping away from XR2, XR3 and XR4 (forming biotope 2 made up of mixed sites); and the second subgroup sites are RF6, RF7, RF5 and RF8 (forming biotope 3 made up of reef sites) grouping away from RF2 and RF3 which were outliers within the reef group.



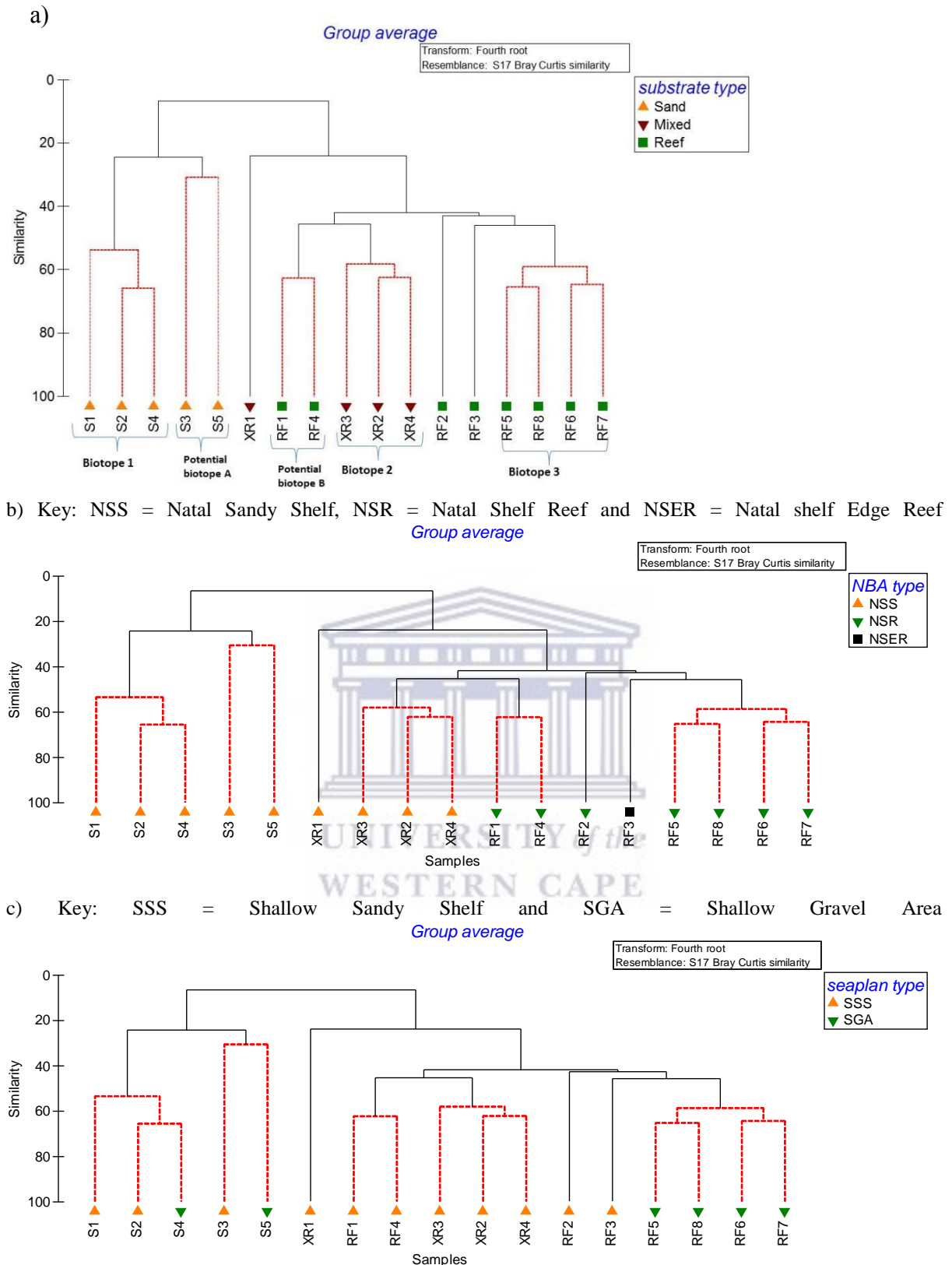


Figure 2.12: A dendrogram with SIMPROF showing two distinct groupings one from unconsolidated sediment sites and the other group from reef and mixed substrate sites combined. Figure 2.12 b and c show classification of sites according to the existing ecosystem classifications (NBA and SeaPLAN respectively). SIMPROF dashed lines implies that there is no significant difference within the groups.

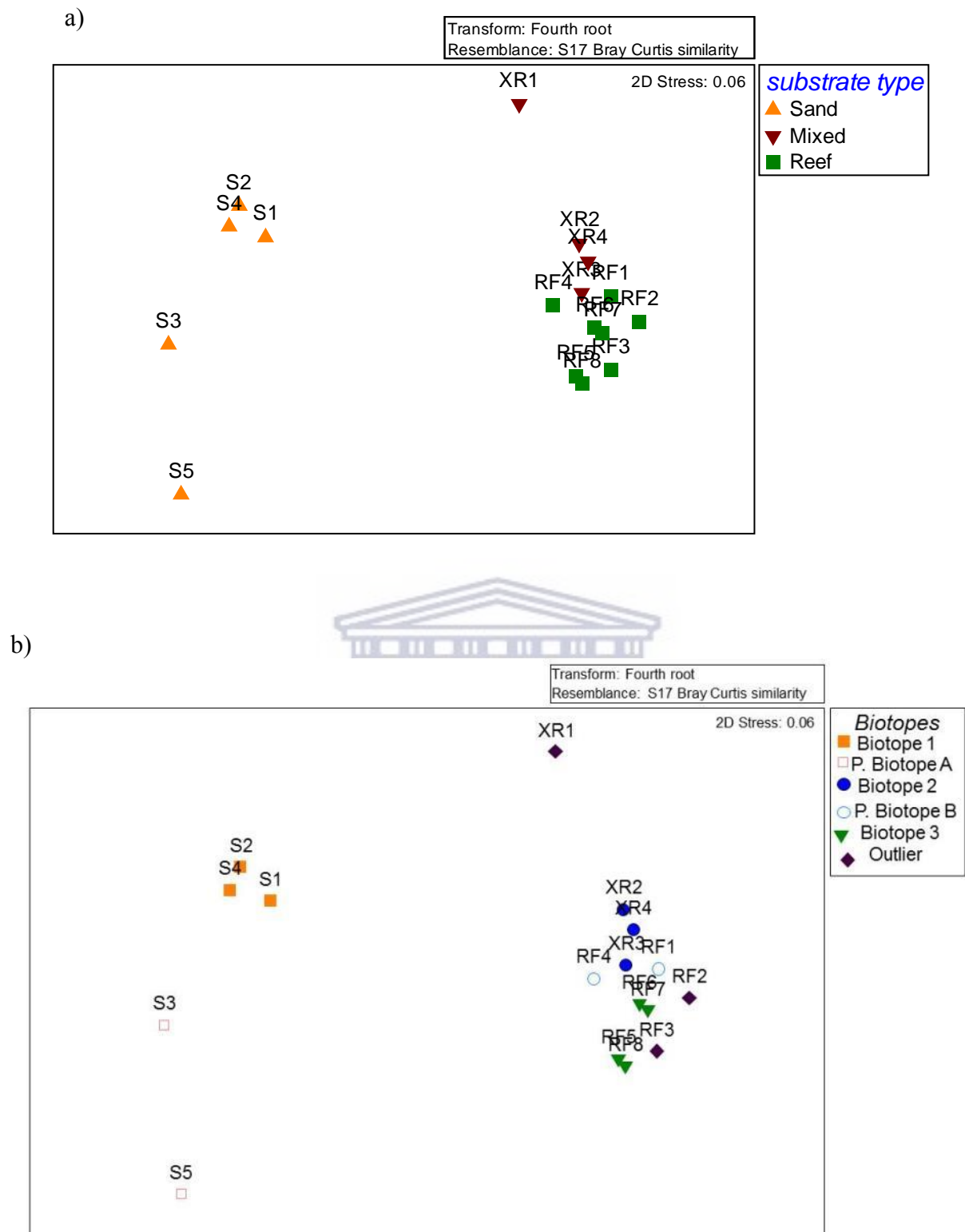


Figure 2.13: Multi-dimensional scaling plot (a) showing epifaunal assemblage separation between unconsolidated sediment sites and the mixed and reef sites. Reef and mixed sites grouped together except for one mixed site (XR1) which seemed to be an outlier. (b) The nMDS plot showing sites labelled with newly assigned three biotopes and two potential biotopes based on significantly different groupings from the SIMPROF analysis.

2.5.5 Testing existing ecosystem types with epifauna

Ecosystem types depicted by epifauna data in the current study contradicted both the NBA and SeaPLAN ecosystem classifications. The NBA (Figure 2.12b) grouped site S2 as Natal shelf reef while the current study grouped site S2 as unconsolidated sediments. Sites XR1, XR2, XR3 and RF1, RF8 and RF6, which were categorised as mixed and reef ecosystem types in this study, were all classified as Natal sandy shelf in the NBA. Some similarity was observed among sites S1, S3, S4 and S5 which were classified as unconsolidated sediment sites in both the NBA classification and the current study. SeaPLAN (Figure 2.12c) classified sites S4 and S5 as reef; however epifauna data from this study classified those reefs as unconsolidated sediment sites. All sites defined as mixed ecosystems in the current study were classified as shallow sandy shelf sites in SeaPLAN. The four sites classified as shallow gravel area in SeaPLAN clustered together in the current study as reef sites.

2.5.6 Testing the significance of epifauna for three factors (substrate type, NBA, and SeaPLAN)

The PERMANOVA analysis revealed a significant difference in substrate types defined in this study as unconsolidated sediment, mixed and reef ($p = 0.0001$, pseudo $F = 7.0368$, d.f. = 2; Table 2.2). Pairwise tests of the significantly different substrate types indicated that the epifaunal communities in all three substrates types were significantly different to each other (Table 2.2). Results from the PERMANOVA analysis showed no significant difference among the NBA ecosystem types depicted by the epifauna community ($p = 0.6457$, pseudo- $F = 0.78$, d.f. = 2; Table 2.2). Similarly, there was no significant difference among the SeaPLAN ecosystem types depicted by the epifauna community in this study ($p = 0.2164$, pseudo $F = 1.27$, d.f. = 1; Table 2.2).

Table 2.2: Three-way PERMANOVA results for the three factors namely substrate type, NBA type and SEAPlan with pairwise test performed for substrate type factor.

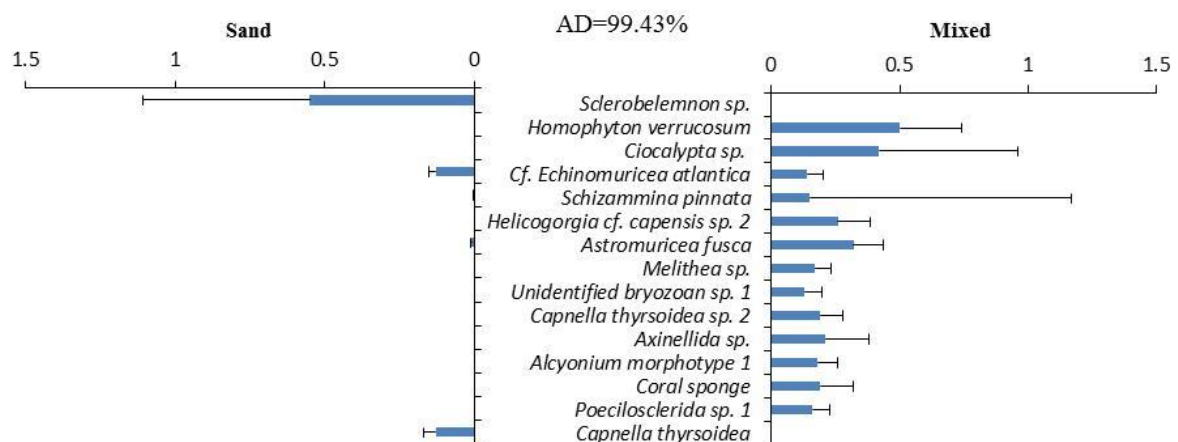
type and SEAF with pairwise test performed for substrate type factor.							
Main	Factors	Df	SS	MS	Pseudo- <i>f</i>	<i>P</i> (perm)	Unique perm
	Substrate type	2	23496	11748	7.03684	0.0001	9893
	NBA	2	3578.7	3578.7	0.78026	0.6457	6807
	SeaPLAN	1	4700.3	2350.2	1.24	0.2164	8515
Pairwise	Factors	Groups	<i>t</i> -value			<i>P</i> (perm)	Unique perm
	Substrate type						
		Sand, Mixed	2.4827			0.0064	126
		Sand, Reef	3.2748			0.0009	1286
		Mixed, Reef	1.785			0.0029	495

2.5.7 Distinguishing species between ecosystem types

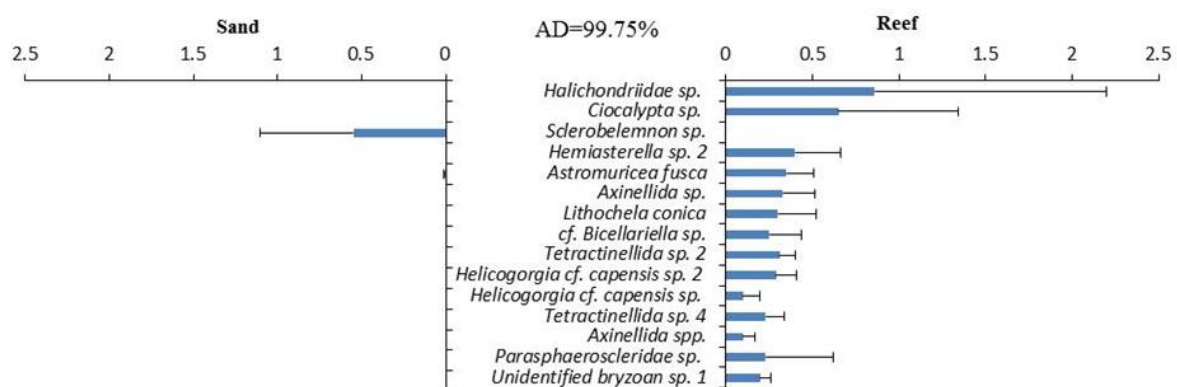
A SIMPER dissimilarity analysis showed high dissimilarity between epifauna from unconsolidated sediment and mixed habitats (average dissimilarity = 99.43%, Figure 2.14(a)) and between unconsolidated sediment and reef habitats (average dissimilarity = 99.75%, Figure 2.14(b)). The average dissimilarity between the mixed and reef epifauna was 93.83% (Figure 2.14(c)) indicating that epifaunal communities occurring in mixed and reef habitats were more similar than those occurring in unconsolidated sediment.

In Figure 2.14(a) *Sclerobelemnon* sp., *Homophyton verrucosum* and *Ciocalypta* sp. were the top three species which contributed most to the difference between epifaunal assemblages in unconsolidated sediment and mixed habitat. Species such as *Sclerobelemnon* sp. and *Capnella thyrsoidea* occurred in unconsolidated sediment ecosystems only. In Figure 2.14(b) the top three species which contributed most to the difference between unconsolidated sediment and reef ecosystem were *Halichondriidae* sp., *Ciocalypta* sp. and *Sclerobelemnon* sp. In Figure 2.14(c) *Halichondriidae* sp., *Ciocalypta* sp. and *Astromuricea fusca* were the top three species which contributed to the difference between epifauna at mixed and reef habitats. *Sclerobelemnon* sp. is a burrowing sea pen which occurred only on the sand habitat, whereas sponges *Ciocalypta* sp. and *Halichondriidae* sp. preferred reef and mixed habitat. The warty twig coral *Homophyton verrucosum* occurred in all ecosystem types, but with a greater abundance in mixed ecosystem than in the other two habitats.

a)



b)



c)

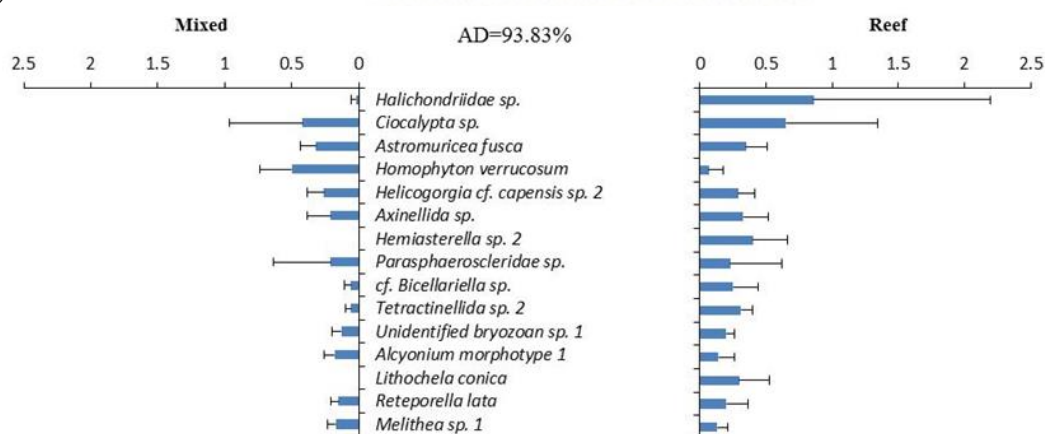


Figure 2.14: Graphical presentation of SIMPER results between the three ecosystem types, showing standard error bars with the average dissimilarity (AD). A to c shows the distinguishing species between (a) unconsolidated sediment and mixed, (b) between unconsolidated sediment and reef and between mixed and (c) reef ecosystem types respectively. The x-axis denotes average abundance of species.

2.5.8 The characteristic and distinguishing species of the observed biotopes and the potential biotopes as determined by SIMPER analysis

The average similarity within the biotopes 1, 2 and 3 were 53.60 %, 58.98 % and 60.51 % respectively; while the average similarity within potential biotopes A and B were 19.56 % and 64.22 % respectively. The average dissimilarity between biotope 1 and potential biotope A was 83.57 % while the average dissimilarity between biotope 2 and potential biotope B was 54.20 % (Table 2.3).

Table 2.3: SIMPER analyses of the three biotopes and two potential biotopes, black cells indicate average similarity (%) within each biotope or potential biotope while white cells indicate average dissimilarity (%) between any two biotopes or potential biotopes.

	Biotope 1 (3 sites)	Biotope 2 (3 sites)	Biotope 3 (5 sites)	Potential biotope A (2 sites)	Potential biotope B (2 sites)
Biotope 1 (3 sites)	53.60				
Biotope 2 (3 sites)	88.18	58.94			
Biotope 3 (5 sites)	92.25	58.57	60.51		
Potential biotope A (2 sites)	83.57	97.78	99.36	19.56	
Potential biotope B (2 sites)	91.52	54.20	54.29	96.66	64.22

The top five species characteristic to biotope 1 were all octocorals (sea pens and seafans), while in potential biotope A only one octocoral species served as a characteristic species. In both biotope 2 and potential biotope B the top five characteristic species were a mix of octocorals, sponge and bryozoan; while characteristic species of biotope 3 were all Porifera (sponge) morphospecies (Table 2.4).

An octocoral *Homophyton verrucosum* and sponge *Ciocalypa* sp. were the two top distinguishing species between biotope 1 and biotope 2, while Porifera morphospecies *Halichondriidae* sp. and *Ciocalypa* sp. were the two top distinguishing species between biotope 1 and biotope 3. The top two distinguishing species between biotope 2 and biotope 3 were two Porifera morphospecies *Halichondriidae* sp. and *Hemiasterella* sp. 2 (Table 2.5).

Table 2.4: Similarity percentages breakdown analysis (SIMPER analysis) of all biotopes and potential biotopes, presenting top five characteristic taxa and their average contribution (%) to the overall similarity of the biotopes.

Biotope Potential biotope	/ Sampling sites	Characteristic species	Contribution (%)	Common name
Biotope 1	S1, S2, S4	<i>Capnella thyrsoidea</i>	18.71	Cauliflower coral
		<i>Cf. Echinomuricea fusca</i>	13.90	Octocoral
		<i>Biemnidae sp.</i>	12.43	Sponge
		<i>Leptogorgia gilchristi</i>	12.07	Soft coral
		<i>Melithaea sp. 1</i>	11.33	Octocoral
Biotope 2	XR2, XR3, XR4	<i>Homophyton verrucosum</i>	5.62	Seafan Octocoral
		<i>Astromuricea fusca</i>	4.30	Seafan Octocoral
		<i>Ciocalypa sp.</i>	4.17	Sponge
		<i>Reteporella lata</i>	3.57	Bryozoan
		<i>Axinellida sp.</i>	3.51	Sponge
Biotope 3	RF3, RF5, Rf6, Rf7, RF8	<i>Ciocalypa sp.</i>	6.01	Sponge
		<i>Halichondriidae sp.</i>	4.60	Sponge
		<i>Axinellida sp.</i>	3.95	Sponge
		<i>Hemiasterella sp. 2</i>	3.78	Sponge
		<i>Tetractinellida sp. 2</i>	3.37	Sponge
Potential biotope A	S3, S5	<i>Sclerobelemnon sp.</i>	100	Seapen
Potential biotope B	RF1, RF4	<i>Cf. Bicellariella sp.</i>	4.53	Bryozoan
		<i>Ciocalypa sp.</i>	4.31	Sponge
		<i>Clavularia sp.</i>	3.79	Soft Coral
		<i>Flustramorpha sp.</i>	3.68	Bryozoan
		<i>Parasphaeroscleridae sp.</i>	3.65	Seapen

Table 2.5: Similarity percentages breakdown analyses (SIMPER analysis) of all biotopes (and or potential biotopes) with distinguishing taxa between any two biotopes (including potential biotopes). Average abundance = counts per unit area

Community types compared	Distinguishing species	Common name	Average abundance (in brackets) for each biotope	Contribution %
Biotope 1 & 2	<i>Homophyton verrucosum</i>		B 2(0.00), B 3(1.14)	3.25
	<i>Ciocalypa</i> sp.		B 2(0.00), B 3(1.13)	3.24
	<i>Parasphaeroscleridae</i> sp.		B 2(0.00), B 3(0.97)	2.75
	<i>Clathria</i> sp. 1		B 2(0.00), B 3(0.94)	2.64
	<i>Axinellida</i> sp.		B 2(0.00), B 3(0.86)	2.41
Biotope 1 & 3	<i>Halichondriidae</i> sp.		B 1(1.63), B 2(0.00)	3.32
	<i>Ciocalypa</i> sp.		B 1(1.53), B 2(0.00)	3.27
	<i>Hemiasterella</i> sp. 2		B 1(1.12), B 2(0.00)	2.38
	<i>Lithochela conica</i>		B 1(1.07), B 2(0.00)	2.27
	<i>Tetractinellida</i> sp. 1		B 1(0.93), B 2(0.00)	1.90
Biotope 3 & 2	<i>Halichondriidae</i> sp.		B 1(1.63), B 3(0.22)	3.18
	<i>Hemiasterella</i> sp. 2		B 1(1.12), B 3(0.00)	2.44
	<i>Lithochela conica</i>		B 1(0.93), B 3(0.00)	1.98
	<i>Parasphaeroscleridae</i> sp.		B 1(0.47), B 3(0.97)	1.60
	<i>Helicogorgia</i> cf. <i>capensis</i> sp.		B 1(0.00), B 3(0.73)	1.59

A seapen *Sclerobelemnon* sp. and seafan cf. *Echinomuricea atlantica* (contributing 12.91 and 8.32 % respectively) were the top two distinguishing species between potential biotope A and biotope 1, while bryozoan cf. *Bicellariella* sp. and sponge *Ciocalypa* sp. (contributing 2.92 and 2.85 % respectively) were the top two distinguishing species between potential biotope B and biotope 2 (Table 2.6).

Table 2.6: Similarity percentages breakdown analyses (SIMPER analysis) of all community types with distinguishing taxa between any two biotopes or potential biotopes. Average abundance = counts per unit area

Biotopes & / Potential Biotopes compared	Distinguishing species	Common name	Average abundance (in brackets) for each Biotope/Potential biotope	Contribution %
Potential biotope A & Biotope 1	<i>Sclerobelemnon</i> sp.	Sea pen	Pb B(0.77), B 2(0.72)	12.91
	<i>Cf. Echinomuricea atlantica</i>	Sea fan	Pb B(0.00), B 2(0.63)	8.32
	<i>Leptogorgia gilchristi</i>	Octocoral	Pb B(0.00), B 2(0.53)	7.04
	<i>Capnella thyrsoidea</i>	Cauliflower coral	Pb B(0.24), B 2(0.74)	6.89
	<i>Biemnidae</i> sp.	Sponge	Pb B(0.00), B 2(0.48)	6.76
Potential biotope B & Biotope 2	<i>Cf. Bicellariella</i> sp.	Bryozoan	Pb A(1.24), B 3(0.00)	3.05
	<i>Helicogorgia cf. capensis</i> sp.	Sea fan	Pb A(0.97), B 3(0.00)	2.39
	<i>Dendronephthya</i> sp.	Octocoral	Pb A(0.88), B 3(0.00)	2.17
	<i>Homophyton verrucosum</i>	Octocoral	Pb A(0.32), B 3(1.14)	2.07
	<i>Clavularia</i> sp.	Octocoral	Pb A(1.02), B 3(0.23)	1.95

2.6 Discussion

This Chapter presents the first set of results obtained from visually surveying epifauna from three different substrate types (unconsolidated sediment, reef and mixed habitat) on the outer shelf in the southern region of KZN. The current study tested the effectiveness of the South African national ecosystem classifications (NBA) and the KZN provincial biozone classification (SeaPLAN) in reflecting benthic epifaunal diversity.

2.6.1 Testing the existing classifications

The results obtained from the current study indicated a mismatch between epifaunal patterns and both existing classifications. When testing for significant difference in epifaunal assemblages between different ecosystem types as defined by existing ecosystem classifications, there was no significant difference between shallow sandy shelf (SSS) and the shallow gravel area (SGA) groups as defined by SeaPLAN. There were no significant differences among epifauna between Natal sandy shelf (NSS), Natal shelf reef (NSR) and Natal shelf edge reef (NSER) as defined by the national ecosystem classification (Sink *et al.* 2012). However, the *p*-values obtained (Table 2.2) show significant differences between the different substrate types (reef, mixed and unconsolidated sediment).

The first null hypothesis, which states that there is no significant difference among reef, mixed and unconsolidated sediment epifaunal communities of the study area, was rejected. The epifauna at unconsolidated sediment sites were significantly different to both mixed and reef substrates and epifauna occurring on mixed substrates were also significantly different to those occurring on reef. The significantly different epifaunal communities detected in sand, mixed and reef habitats are not reflected in the ecosystem types represented in either of the existing ecosystem classifications tested. The second null hypothesis, which states that existing national and provincial ecosystem classifications reflect the same habitats as those defined by benthic epifaunal assemblages, was also rejected by the study findings.

2.6.2 *SeaPLAN and NBA versus the current study classifications*

There was a mismatch in classifying sites using the SeaPLAN and the NBA ecosystem typologies. According to the NBA ecosystem classification, sites RF1, RF6 and RF8 are classified as NSS, which contradict this study finding as they are grouped within the Natal reefs. Site S2 is classified as a NSR on the NBA ecosystem classification however it was established as an unconsolidated site in this study. The SeaPLAN ecosystem classification classified RF1, RF2, RF3 and RF4 as SSS while this study classified them as reef sites. Sites S4 and S5 were classified as SGA in SeaPLAN, while in this study they were found to be unconsolidated sediment sites.

This mismatch shows some gaps which are produced by the methods used in developing the two existing ecosystem classifications using broad-scale (produced from available remote sensing data (SeaPLAN), physical data and expert opinion, Sink *et al.* 2012), versus the narrow-scale of using biodiversity surrogates as done in the current study through *in situ* sampling. Costello (2009) reports that *in situ* sampling provides a more accurate report on species-ecosystem relationships than remote sensed methods. Expert opinion provides low cost maps as the information relies on the knowledge of experts in the field. Combining these various methods will provide well informed classifications with better maps and fewer data gaps.

2.6.3 *Species composition and diversity*

Owing to their limited mobility and ability to integrate environmental conditions, benthic macro-invertebrates are widely used in biological monitoring studies (Türkmen and Kazanci 2010). The current study reports that of the three ecosystem types in KZN southern region, both reef and mixed habitats have more diverse species than unconsolidated habitats. These species require hard substrate to anchor and grow on, such as hard corals, soft corals and encrusting species (Porifera morphospecies). Non-parametric analyses showed that both reef and mixed ecosystems have greater diversity of epifaunal communities that are evenly and equally distributed. Furthermore, results obtained from non-parametric species estimators (species accumulation curves) for both reef and mixed sites reached asymptotes, indicating that sufficient samples were processed to capture most species present in these ecosystem types. It is however observed that results from site XR4 suggested that there was possibility of detecting more rare species with an increase in sampling effort.

On the contrary, unconsolidated sediments results for non-parametric species estimators implied that it was unlikely to capture all species occurring using random sampling due to the sparseness of species found in unconsolidated sand. The unconsolidated sediment ecosystem had sparse species distribution, mostly comprised of sea pens and some soft corals such as *Sclerebelemnion* sp. and *Capnella thyrsoidea*; these epifauna require soft substrate to grow on. Due to their physical nature, unconsolidated sediment habitats are easily disturbed and highly mobile, and they are therefore not able to support long-lived sedentary epifaunal species. The current study agrees with other international studies (Kostylev *et al.* 2001, Olenin and Ducrotoy 2006, Howell 2010) in that species composition and community patterns are strongly determined by the nature of the ecosystem (surrounding abiotic conditions) with a greater abundance of species found on hard substrate than on soft substrate.

The current study shows the strong relationship between the substrate type and its fauna, as also indicated by Howell (2010). Reef ecosystem sites were mostly composed of gorgonians and Porifera species, agreeing with literature, as these species are known to occur on hard substrates (Ofwegen and Schleyer 1997, Samaai *et al.* 2010, Mohammad *et al.* 2016). It is however noted that the results from this study need to be interpreted with caution as some of the species which are known to be found on hard substrate (reef) were observed on unconsolidated sediment — these include octocoral species such as *Melithaea* sp. 1, *cf. Echinomuricea atlantica* and *Menella* sp. We suspect that unconsolidated sediment sites

which have reef species are actually reefs covered by sand, and therefore should be classified as mixed habitat.

Furthermore, mixed ecosystem sites were composed of species which are generally associated with both hard (reef) and soft (unconsolidated sediment) substrates, with most species being from reef rather than unconsolidated sediment. An octocoral, *cf. Echinomuricea atlantica*, was observed in both mixed and reef habitat, but showed a greater abundance in mixed habitat. This implies that although this species anchors on hard substrate it does however tolerate sand very well. Mixed ecosystem types were observed to be reef/rock inundated by sand, hence the presence of hard ground species in mixed habitat, especially those which appeared to be sand sites. De Clerk *et al.* (2005) reported some low-lying flat reefs that experience sand burial in the study area. Periodic sand inundation might result from topography and the fast flowing Agulhas current which frequently flows at more than 4 knots through the study region (Lutjeharms *et al.* 2010, Porter *et al.* 2017). Thomson *et al.* (2014) reported that close coupling between sediments characteristics and reef communities are due to possible change in water flow that affect translocation on materials or organisms between reef and soft-sediments habitats. Their study further highlights the importance of sand as a physical surrogate, indicating that measures of habitat are good predictors of biodiversity when using predictive methods.

2.6.4 Other study findings from the current study area

The current study identified three biotopes (biotope 1, 2 and 3) and two potential biotopes (potential biotope A and B) from the three substrate types. The unconsolidated sediments sites which formed community type 1 were composed of pure sand and gravel sites as defined by Franken (2015), who investigated patterns of benthic epifaunal communities in unconsolidated sediments habitats of the KZN shelf. The current study findings revealed a clear separation within unconsolidated sediment sites, with pure sand sites forming biotope 1 and the gravel sites forming a potential biotope A. The current results from unconsolidated sites agreed with the results of Franken (2015) in which the two sites which form potential biotope A identified here were grouped with other gravel sites. Biotope 2 and potential biotope B were mixed sites (reefs with high sand cover) while biotope 3 consisted of high profile reefs that appear to be less vulnerable to sand inundation. We recommend further sampling in the study area in order to understand the current potential biotopes especially for mixed substrate types, as this substrate type appeared to be characterised by species originating from both unconsolidated sediments and reef ecosystems.

Findings from the current study conform with the earlier reports of Schleyer *et al.* (2006), and Bolton and Stegenga (2002), except that their findings include identification of algae and echinoderms because their study was much shallower than the current study. The current study excluded identification of mobile epifauna such as echinoderms, although they were observed in the footage. There were no record of algae in the current study; this is due to the different depth range of the current study compared to that used in earlier studies (light penetration is limited in the current study).

Results from this study should be interpreted with care, as they contradict the findings of Olbers *et al.* (2009), who reported that the Aliwal Shoal (which forms part of this study as sites RF1, RF2 and RF3) has three communities, while this study only recognised two different community types (Figure 2.7). The reason the results from these two studies are not comparable is most likely because of the different depth range. In their study (Olbers *et al.* 2009) collected data using underwater photography at a shallower depth than the current study and analysed the data by point intercept method.

A complementary project conducted by Franken (2015) visually surveyed epifauna of the unconsolidated sediment habitats on the KZN shelf. The results from the Franken (2015) study agree with the current study results, as both the national and provincial ecosystem classifications were found to poorly represent the epifaunal community distributions when tested against the benthic epifauna data. Franken (2015) further states that biological verification of the existing ecosystem classifications is important as they form the basis for marine ecosystem assessments.

2.6.5 Conclusion and future study suggestions

Despite assistance from experts and taxonomic guides, a limitation of this study lies in the identity and taxonomy of observed taxa (Deter *et al.* 2012, Davies *et al.* 2014). It was frequently difficult or impossible to accurately identify taxa to species level due to poor image resolution quality; and lack of specimens which required laboratory and microscopic work to accurately identify to species level. Due to limited field time for the current study, we were unable to collect specimens by specialist diving or using the ROV manipulator arm. Collection of specimens is strongly recommended when preparing future investigations similar to the current study. Further investigations of monitoring the KwaZulu-Natal seabed should be implemented to improve understanding of the constantly changing seabed which might be due to the extremely fast current speed in the area and other environmental factors.

The results from the investigations have improved the understanding of the seabed ecosystems and will contribute to updating relevant ecosystem maps. The next Chapter focuses on investigating key potential drivers of marine biodiversity patterns of KwaZulu-Natal reef ecosystems.



3 Identification of potential drivers of patterns in deep reef epifaunal assemblages in KwaZulu-Natal

3.1 Abstract

Benthic epifaunal assemblages are strongly influenced by their surrounding environment. The aim of this study was to identify the key potential environmental drivers of reef epifaunal assemblage patterns in the 48 to 85m depth range between Pennington and Ballito on the KwaZulu-Natal (KZN) outer shelf. Epifauna data were extracted from seabed imagery collected using a remotely-operated vehicle (ROV). Environmental data were collected during project cruises, supplemented with data collated from collaborative research and online resources such as ocean colour data. Multivariate analysis of epifaunal data showed a significant difference between the reefs north and south of Durban. This is interpreted as a possible biogeographic break off Durban with reef assemblages north and south of this break differing by approximately 65%. Reefs located north of Durban had higher abundance of octocorals such as *Leptogorgia gilchristi*, *Paraspaerasheridae* sp. and *cf. Echinomuricea atlantica*, while south of Durban, reefs hosted more Porifera morphospecies such as *Halichondriidae* sp., *Hemiasterella* sp. 2 and bryozoan *cf. Bicellariella* sp. The species *Ciocalypa* sp. was identified as characteristic of all deep reefs across the study area. SIMPER analysis revealed two biotopes and two potential biotopes each from North and South of Durban. DISTLM analysis was used to examine the relationship between observed patterns in epifauna and 12 potential environmental drivers. Distance from shelf edge, latitude, sea surface temperature, phosphate and distance from shore showed a significant relationship with patterns in epifauna, while bottom temperature, turbidity, light attenuation, bottom oxygen and depth did not emerge as significant potential drivers of epifaunal patterns. There were limitations to the study including the restricted sampling area, relatively narrow depth range and the challenges due to poor knowledge of reef distribution and high current in the area. This study is the first to provide quantitative descriptions of epifaunal assemblages on the deep reefs of KZN and contributes to the understanding of the relationship between epifaunal assemblages and their physical environment.

3.2 Introduction

Marine environments can be classified and mapped in various ways depending on the user requirements and resources (Kenny *et al.* 2003). Classification systems can be developed by defining habitats according to their physical environment and their associated fauna and flora. Benthic biodiversity is readily incorporated into classification systems and reflects physical components of ecosystems (e.g. benthic assemblages vary with depth, wave exposure and substrate) and serves as an appropriate ecosystem component to test ecosystem classification (Blanchard *et al.* 2013, Thomson *et al.* 2014, Porter *et al.* 2017). Approaches to classification have been driven by geophysical structure, oceanographic and biological processes, species-habitat relationships and their combinations (Costello 2009). There are various factors which contribute to the growth and productivity of an ecosystem, regardless of the environment being terrestrial or marine. Among others, physical factors play an important role in predicting the relationship between the environment and its living organisms; hence the role of physical factors cannot be overlooked in ecosystem classification processes (Bremner *et al.* 2006, Howell *et al.* 2010, Przeslawski *et al.* 2011). Studying these factors gives a better understanding of the habitat structure and the biodiversity of the area (McArthur *et al.* 2010, Richmond and Stevens 2014, Smit *et al.* 2017).

3.2.1 Definition of environmental drivers

Douglass *et al.* (2014) define environmental drivers as the physico-chemical processes and other factors that determine habitat conditions and influence the distribution and abundance of taxa, including their connectivity between similar habitats. The strength of environmental drivers depends on the scale of the sampling area. Some drivers are more influential at finer scales while others are more influential at broader scales (Bremner *et al.* 2006, Blanchard *et al.* 2013). For example, seabed morphology is important for structuring species assemblages at local scales while salinity can play an important determinant of broad scale species assemblages (Bremner *et al.* 2006).

3.2.2 Using environmental variables as surrogates

The use of environmental variables to define species distributions and the link between abiotic and biotic components of marine environments remains poorly defined (Post *et al.* 2006). Depth is one of the commonly used biodiversity surrogates, since many species have a predictable and restricted depth range (Howell 2010, Howell *et al.* 2010, Fennessy 2016). Across the globe studies have established the importance of depth and it is the most studied

factor in marine species distribution studies (Bergen *et al.* 2001, Lesser *et al.* 2009, Richmond and Stevens 2014, Heyns *et al.* 2016). Depth serves as one of the widely accepted surrogates for the combined influence of environmental parameters, such as topography, food supply, light, sediment type and slope, on benthic biological communities (Howell 2010). The influence of environmental variables on species distributions often depends on more than one environmental variable; for example sediment grain size is not the only determinant of species distribution and community structure, however currents may also play an important role in defining species distribution and community structure (Post *et al.* 2006). Spatial variables such as latitude, longitude, and depth are not direct drivers of biodiversity patterns but they often correspond with driving gradients and may assist with prediction of these patterns (McArthur *et al.* 2010, Anderson *et al.* 2011). On the contrary, variables such as temperature, salinity, oxygen concentration, light availability and sediment composition have been reported to have strong influence over benthic species distributions (Post *et al.* 2006, McArthur *et al.* 2010).

Variables such as temperature, salinity and pH often have a direct influence on presence and abundance of benthic species and differ over spatial and temporal scales. However studies have shown that there are no fixed primary factors for species distribution as they are unique to different study regions (Bergen *et al.* 2001, Bremner *et al.* 2006, Post *et al.* 2006). The shelf edge zone or continental margin including the shelf break has been reported to form a distinct habitat type due to the upwelling events and nutrient rich waters associated with this zone (Meyer *et al.* 2002, Sink *et al.* 2012, Richmond and Stevens 2014).

3.2.3 Global studies on physical drivers

Monk *et al.* (2016) quantified the diversity of morphotype classes occurring on the outcropping reef system in Southern Australia. They outlined the importance of outcropping reef features (drivers of biodiversity patterns) in representing epibenthic faunal diversity and the relevance of these habitats to conservation planning. Furthermore, their study demonstrated the difference in epibenthic morphotype assemblages between outcropping reef edge features and adjacent sediment inundated reefs. Post *et al.* (2006) investigated the link between physical and biological data sets for the Southern Gulf of Carpentaria (Australia). Their results revealed that the distribution of benthic macrofauna changed gradually across the Gulf and that fine scale species-environment relationships were long-term, consistent with the broader associations observed for some organisms within the Gulf. The study of Blanchard *et al.* (2013) investigated factors that drive macrofaunal distributions of the

northeast Chukchi Sea using benthic macrofauna and environmental characteristics. Their studies report that variations in study sites were correlated with depth and bottom temperature, whereas topographic control rather than circulation appeared to be a primary driver in structuring benthic communities of this region. Neumann *et al.* (2009) found that the cold winter temperature influenced shallow area epifauna whereas the increased sea surface temperature during the warming season influenced the entire epifauna through increased food supply. This suggests that there is a link between temperature and food supply.

The Ocean Colour Climate Change Initiative (OC-CCI), was launched in 2010 by the European Space Agency with the goal to create long term, consistent, stable, error-characterised merged ocean-colour products (MODIS-Aqua, SeaWiFS and MERIS), for use in climate change and other studies (Brewin *et al.* 2015, <https://www.oceancolour.org/>). The use of MODIS satellite data allows for investigation of ocean colour data which often are difficult to obtain due to limited resources. Miller *et al.* (2015) incorporated satellite imagery data of Chlorophyll and Sea Surface Temperature (SST) to identify zones of ecological importance in the process of defining marine protected areas. Álvarez-Romero *et al.* (2013) report that MODIS-Aqua true-colour satellite imagery data were useful to map river plumes and to qualitatively assess exposure to land-based pollutants across the Great Barrier Reef. Furthermore their results produced maps of exposure to suspended sediment and dissolved inorganic nitrogen. These studies present the importance of MODIS-Aqua data in monitoring the exposure of coastal and marine ecosystems to riverine flow and plumes (Constantin *et al.* 2016) and their ecological influences.

3.2.4 Studies on physical drivers in South Africa

Karenyi *et al.* (2016) conducted infauna studies in unconsolidated sediments of the west coast of South Africa, defining seascapes for shelf sediments in this eastern boundary upwelling region. They measured geophysical variables including depth, sediment grain size and sediment organic carbon; resulting in the recognition of depth and sediment type as key drivers of the marine benthic ecosystems. Franken (2015) described the community structure of the epifauna of unconsolidated sediment habitat types for KwaZulu-Natal (KZN); the following five factors emerged as their potential drivers: percentage gravel, chlorophyll-*a* levels in August, mean annual bottom temperature, distance from shore and percentage sediment organic carbon. Franken (2015) reported that the distribution of benthic macrofaunal communities was most frequently related to depth and sediment type; their results agreeing with Karenyi *et al.* (2016) findings. Porter *et al.* (2017) investigated the

abiotic determinants of community composition on shallow subtidal reefs along the East African coast including the Natal region. Depth, turbidity and suspended sediments were strongly associated with community composition within the Natal region. Heyns *et al.* (2016) established depth-related distribution patterns and drivers of macrobenthos between shallow (11-25 m) and deep (45-75 m) reef communities of the Tsitsikamma Marine Protected Area (MPA) (south coast of South Africa). Heyns *et al.* (2016) report the first survey of macrobenthos using a remotely-operated vehicle (ROV) in South Africa; however the study was conducted at a smaller area compared with the current study.

Various studies have been conducted on the KZN continental shelf (Sink *et al.* 2005, Samaai *et al.* 2010, Franken 2015, Fennessy *et al.* 2016, MacKay *et al.* 2016, Porter *et al.* 2017). Sink *et al.* (2005) investigated biogeographic patterns by characterising and identifying the differences in intertidal community structure at a broad scale along the KZN coast. Species characteristic of the Natal region were identified to be subtropical, differing from Maputaland species which were identified to have tropical affinities, forming a biogeographic break between these regions. Samaai *et al.* (2010) recorded a total of 96 sponge species surveyed within the iSimangaliso Wetland Park which is a MPA located in the northern part of KZN province. Sponges play an important ecological role in substrate modification, nutrient cycling and microbial associations; and they are increasingly used in biodiversity and impact assessments (Samaai *et al.* 2010, Van Soest *et al.* 2012, Przeslawski *et al.* 2015). They are regarded as one of the major ecosystem engineers of the sea floor that provide habitat for different types of species (Ilan *et al.* 1999, Przeslawski *et al.* 2015).

In addition to the studies mentioned above, various studies have focused on the KZN Bight as part of the African Coelacanth Ecosystem Programme (ACEP) (Fennessy *et al.* 2016). MacKay *et al.* (2016) investigated the local habitat drivers of macrobenthos in different parts of the KZN Bight, concluding that the variances of overall sediment type were the habitat drivers underlying the macrofaunal abundance distribution in the region. Green and MacKay (2016) examined distribution patterns of unconsolidated sediments in the KZN Bight; their results showed that sediment distribution reflected the partitioning between sediment populations that were influenced by current and associated with submerged shorelines. Fennessy (2016) reports on subtropical demersal fish communities on soft sediments in the KZN Bight, concluding that species composition was structured mainly by depth and proximity to the Thukela River.

Studies of marine ecosystem classification and mapping need to investigate the species distribution patterns in order to understand the diversity of the area and to gain insight into the ecological processes in marine ecosystems (Reiss *et al.* 2011). This is also important in decision making for MPA designs and marine spatial planning (MSP). As part of these investigations, it is important to know the driving factors of species distribution pattern; and to have a firm understanding of the principle factors that contribute to species distribution patterns of a particular area when developing classification systems for use in representing the biological diversity of the area (Cogan *et al.* 2009, Howell 2010, Lecours *et al.* 2015). This study is the first to examine patterns in epifaunal assemblages of the KZN deep reefs. In this Chapter we aim to identify the physical drivers of the benthic epifaunal reef communities of the KZN outer shelf.

3.2.5 Aim and objectives

This Chapter aims to investigate the potential environmental drivers of patterns in epifaunal assemblages of the KwaZulu-Natal deep reefs.

Objectives:

- To examine patterns in epifaunal assemblages on the deep reefs of KwaZulu-Natal.
- To define and describe deep reef biotopes with a focus on characteristic and distinguishing species.
- To identify potential environmental drivers of patterns in epifaunal assemblages of the study area.

Key Questions:

- What are the patterns of epifaunal assemblages in the deep reef communities of KwaZulu-Natal outer shelf?
- What are the environmental factors potentially driving patterns in epifaunal assemblages of the study area?

Hypotheses:

- H_0 : There are no significant differences in deep reef epifaunal assemblages between pre-defined regions (previous chapter) in KwaZulu-Natal.
- H_0 : There is no significant relationship between environmental variables and the epifaunal assemblages on deep reefs in KwaZulu-Natal

3.3 Methods

This Chapter focused on deep reef ecosystems across a portion of the KZN outer shelf (Figure 3.1). In total, 17 reef sites were surveyed by a ROV ranging from a depth of 48 to 85 metres in an area between Ballito and Scottburgh. The sites in this Chapter were categorised into four *a-priori* regions (on the basis of their geographic location) as north, central, south and far south reefs (Appendix Table 1). The detailed data collection method is explained in Chapters 1 and 2. In summary, seabed imagery were collected using a ROV at each site, with a 45 degree fixed-camera angle. Images were processed to quantify visible biota using a photo-grid overlay which allowed for easy measurement and standardisation of area (Figure 3.2). Between 25 and 30 images were processed per site, depending on suitability.

3.3.1 Abiotic variables

Environmental data used in this study were similar to that of Livingstone (2016) who collated information to characterise the marine environment of the east coast of South Africa as part of the ACEP Surrogacy project. Physical data were collected *in-situ* and supplemented with additional longer term abiotic data collated from the broader ACEP Surrogacy project and online sources (<http://www.esa-oceancolour-cci.org/>). Depth was recorded *in-situ* from the live feed of the ROV at all sites. The Global Positioning System (GPS) coordinates (longitude and latitude) were also recorded *in-situ* upon anchoring at each site. The physical variable 'distance from shore', defined as distance from sampled position to shore line for all sites, was measured manually in metres using Quantum Geographic Information System (QGIS version 2.10.1-Pisa) software. The physical variable 'distance from shelf break,' defined as the shortest distance from the sampled position to the shelf edge (for the purpose of this study, as defined by Sink *et al.* 2012.), was also measured manually in metres using QGIS. Sand inundation (SI %) was measured on individual images for each site by counting the number of squares (or parts thereof) of the grid overlay that were covered by sand. The total number of squares covered with sand was then converted to percentage of sand cover or inundation per image (Figure 3.2).

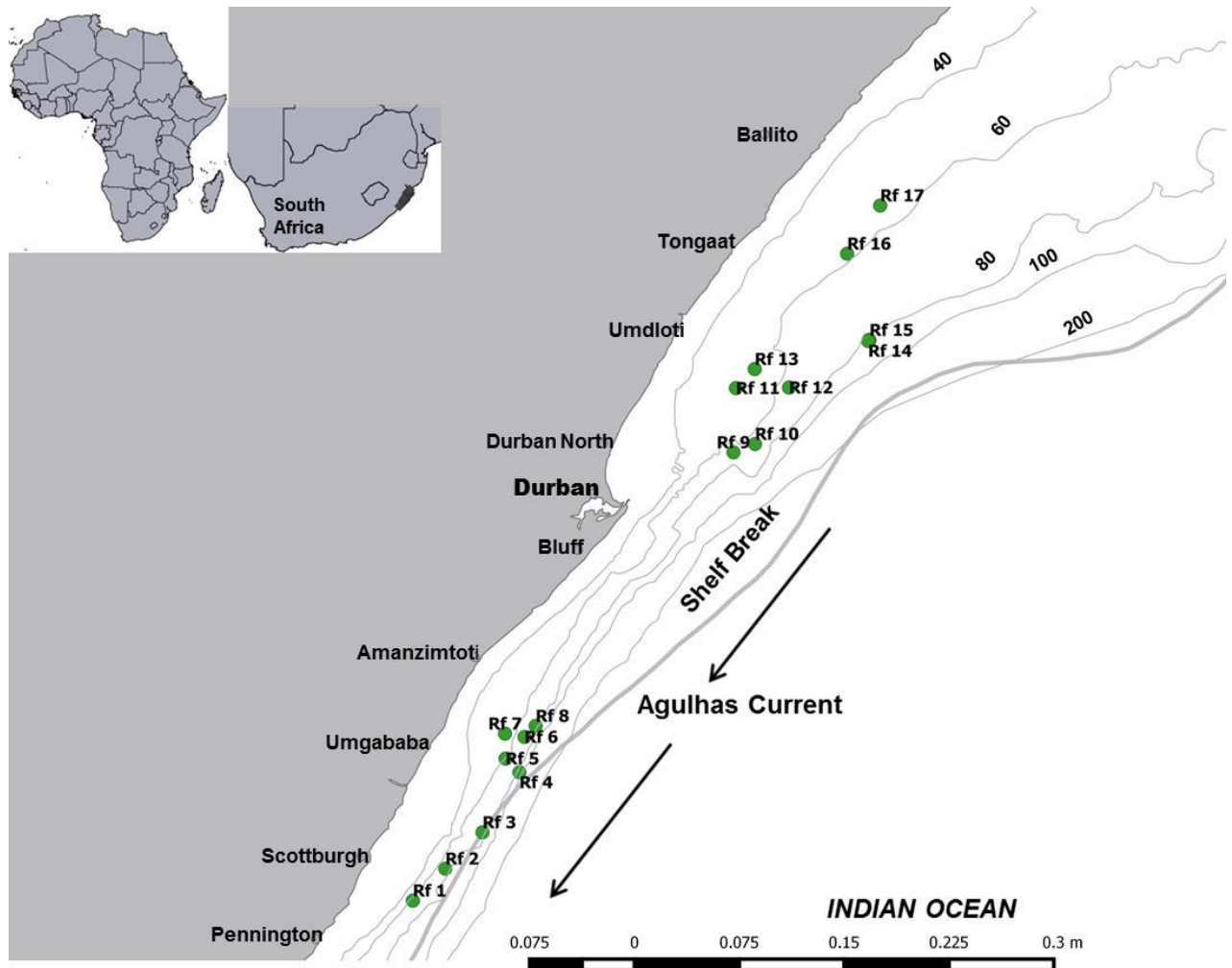


Figure 3.1: The study area located on the east coast of South Africa between Pennington and Ballito in the KwaZulu-Natal province. The shelf break as reflected in the national habitat classification (Sink et al. 2012) is shown.



Figure 3.2: An exemplar image of the photo grid used to calculate the sand inundation cover (SI %) and area standardisation for each site.

Chlorophyll *a* (mg/m^3) and the 'attenuation coefficient for down-welling irradiance (m^{-1})' (KD 490nm) seasonal data (which is used in this study to represent a measure of light attenuation) were extracted at a 4km resolution from the online Ocean Colour-Climate Change, Phase 2 version 3.0 standard Mapped Image (<http://www.esa-oceancolour-cci.org>). The mean chlorophyll *a* and KD 490nm (light attenuation) levels from the best single-day image per month over a period of 17 years (1999 to 2015) were calculated for each site. Data were accessed from <http://www.esa-oceancolour-cci.org/> retrieved on 14th, 16th and 17th March 2017 as NetCDF format files. NetCDF operators and MatLab were used to read and convert the obtained NetCDF files into text files which are compatible with PRIMER software.

Mean Sea Surface Temperature (SST) and mean turbidity were acquired from Livingstone (2016). Livingstone (2016) processed time series analysis of turbidity data downloaded from the NASA ocean colour website (<http://oceancolor.gsfc.nasa.gov/cgi/level3.pl>), from July 2001 up to December 2004. SST was obtained from NOAA website and processed by Oceanspace Institute (University of KwaZulu-Natal). The SST data resolution was 1.01km, and was supplied as text files representing the best single-day image per month over a four-year period from January 2001 to December 2004 (Livingstone 2016). Livingstone (2016) mapped phosphate distribution over the KZN continental shelf at 1.021km^2 resolution using ArcGIS from data provided in Birch (1996). Distribution of phosphate concentration was tested as a potential environmental driver of epifauna pattern.

Additional oceanographic data analysed in this study included the mean, maximum and minimum values for bottom oxygen and bottom temperature for each study site. These data were provided by Fiona Duff (University of Cape Town), who amalgamated data from the South African Data Centre for Oceanography (SADCO), Marine and Coastal Management (MCM) and the Bayworld Centre for Research and Education (BCRE) and provided this as a raster data set (Livingstone 2016). These data were based on a collection of hydrographic data over a time period from 1930 to 2005.

3.3.2 Statistical analysis

PRIMER V6 with PERMANOVA+ software was used to perform non-parametric, multivariate analysis (Anderson *et al.* 2008). Epifauna abundance data were 4th root transformed and a Bray Curtis (dis)similarity measure used to generate a resemblance matrix.

The 4th transformation down-weights excessive contributions of dominant species, (Field *et al.* 1982, Clarke and Gorley 2006).

To evaluate the spatial pattern of epifauna from the KZN deep reefs, a cluster analysis (dendrogram) with Similarity Profile permutation test (SIMPROF), was performed on averaged (standardised) epifauna abundance per site. A cluster analysis defines species assemblages by grouping them according to their level of similarity. SIMPROF identifies the significantly different groupings of sites represented by solid black lines in the cluster dendrogram.

A main effects permutational multivariate ANOVA (PERMANOVA, Anderson *et al.* 2008) was used to test the significance between the *a-priori* groups north, central, south and far south (9999 unrestricted permutations). PERMANOVA tests the dissimilarity values generated by the resemblance matrix on which permutations are based, generating a pseudo-*F* (or pseudo-*t* for pair-wise) test statistic. Due to the low number of unique permutations possible (less than 100), the Monte Carlo *P*-values (P (MC)) were included in the analysis and used for interpretation. Pair-wise PERMANOVA analyses were conducted for factors that were significantly different in the main effects test.

A non-metric multi-dimensional scaling (nMDS) plot was generated to visualise the multi-dimensional distribution among samples and/or groups. The significantly different groups identified in the SIMPROF analysis were superimposed on the nMDS to reflect proposed biotopes. Similarity of percentages (SIMPER) analysis was conducted to determine key distinguishing and characteristic species that contributed to the observed patterns in the north of Durban and south of Durban reefs, furthermore to identify the characteristic and distinguishing species of proposed biotopes.

Many abiotic factors are predicted to potentially impact patterns of species composition and distribution in the study area (Appendix Table 1). Abiotic factors further examined in this study were selected based on their potential relevance as suggested by literature reviews and data availability. Draftsman plots were examined to assess for correlated environmental variables. Where the correlation between two variables was greater than 0.85, only one variable was selected for further analyses. The environmental data were normalised and the resemblance matrix was compiled using the Euclidian distance measure. Normalizing data helps to assess variability among environmental variables which usually have different

measurement scales e.g. depth in meters, salinity in ‰ and temperature in °C (Clarke & Warwick 2001).

The relationship between epifaunal distribution patterns at each site and the measured environmental variables were investigated using a distance based linear model (DistLM). DistLM provides quantitative measures and tests the variation explained by the predictor variables. The 'Best' procedure which examines the value of selection criteria for all possible combinations of predictor variables, and R^2 criteria (the proportion of explained variation for the model) options (Anderson *et al.* 2008) were selected in this study. The environmental variables selected for the model were: distance from shelf-edge, distance from shore, turbidity (mean), bottom temperature, bottom oxygen, SST mean, phosphate, KD 490nm (light attenuation), latitude, sand inundation (SI %) and depth (Appendix Table 1).

3.4 Results

3.4.1 Description of dataset

This study surveyed 17 reef sites in a portion of KZN with the total area per reef site processed ranging between 6.95 m² and 11.12m². A total of 491 image quadrants were processed resulting in a total count of 15 310 epifaunal individuals. The most commonly occurring morphospecies at these sites were octocorals, followed by sponges, bryozoans, ascidians and anemones with an overall total of 164 morphospecies.

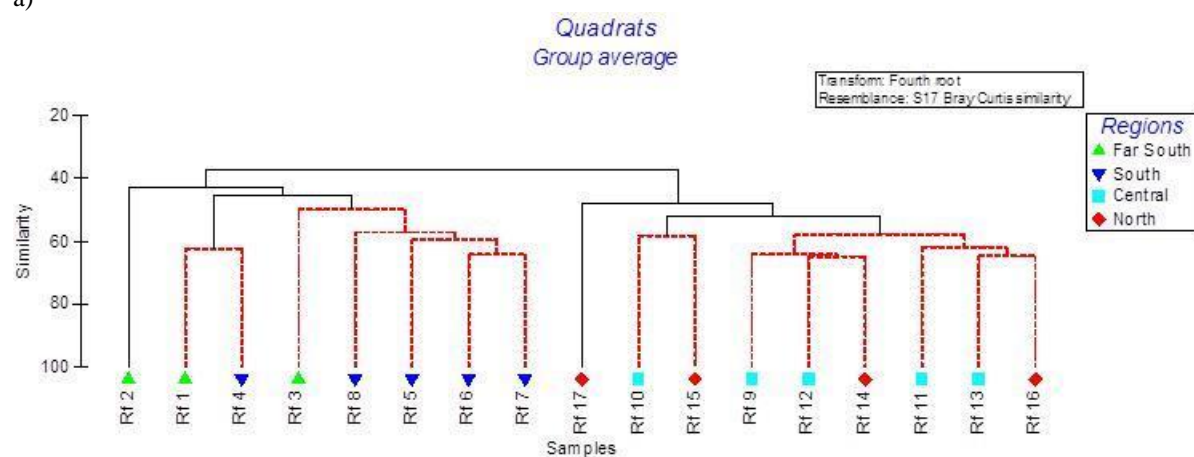
3.4.2 Testing community distribution

The cluster analyses with SIMPROF (Figure 3.3) of site-averaged epifauna abundance showed six significant groups with similarity cut off at 64.07%. Two of these groups were outliers consisting of single sites (RF2 and RF17). The sites south of Durban (RF1 to RF8) clustered separately from the sites north of Durban (RF9 to RF17). Sites RF1 and RF4 clustered together forming potential biotope B south of Durban, while sites RF3, RF5, RF6, RF7 and RF8 clustered together forming biotope 3 and RF2 was an outlier (Figure 3.3). In the area north of Durban, sites RF10 and RF15 clustered together forming potential biotope C, sites RF9, RF11, RF12, RF13, RF14 and RF16 cluster together forming biotope 4 and site RF17 was an outlier (Figure 3.3 a and b).

The one-way main effects PERMANOVA generated P (perm) = 0.0001, pseudo F = 23.137 for regions indicating that epifauna were significantly different among the four *a-priori* regions. A pair-wise PERMANOVA analysis among the *a-priori* regions showed that there

was no significant difference between the north and central regions (P (MC) = 0.632, Table 3.1) and between far south and south regions (P (MC) = 0.46, Table 3.1). There were significant differences between far south and central, south and central and between south and north regions (Table 3.1). There was no significant difference between far south and north regions (P (MC) = 0.0645, Table 3.1). The nMDS plot (Figure 3.4) also showed a clear separation of the reef sites north of Durban from reefs south of Durban, while sites RF2 and RF17 were outliers. The biotopes and potential biotopes identified within the clearly separated sites south of Durban and the sites north of Durban, were further shown in the map (Figure 3.5).

a)



b) Representing identified biotopes and potential biotopes

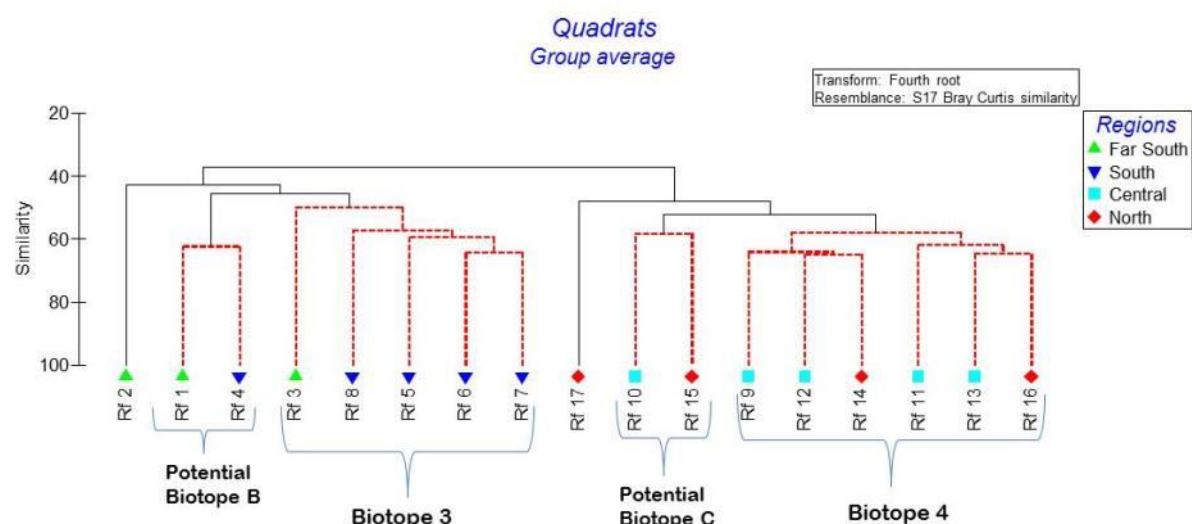


Figure 3.3: The cluster analysis with SIMPROF showing the significantly different (solid lines) groups of deep reef epifaunal communities in KwaZulu-Natal. SIMPROF dashed lines implies that there was no significant difference within groups.

Table 3.1: PERMANOVA pairwise test results for the four regions. P-values in bold indicate significantly different at 95% level.

Groups	pseudo t value	P - value	Unique perm	P (Monte-Carlo)
Far South, South	0.97946	0.5731	56	0.46
Far South, Central	1.6978	0.0177	56	0.0345
Far South, North	1.5624	0.0291	35	0.0645
South, Central	2.2636	0.0083	126	0.0023
South, North	2.0672	0.0074	126	0.0072
Central, North	0.83467	0.7772	126	0.632

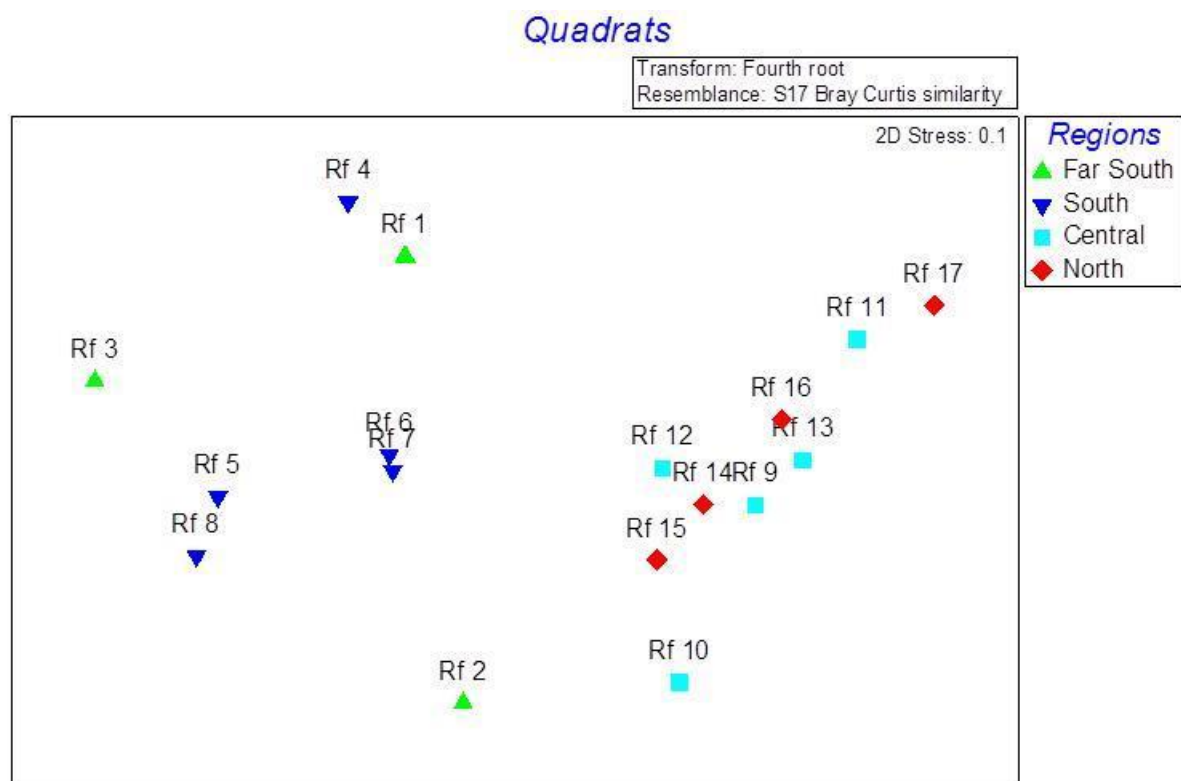


Figure 3.4: The multi-dimensional scaling plot (averaged epifauna abundance data) showing separation between sites north of Durban to sites south of Durban.

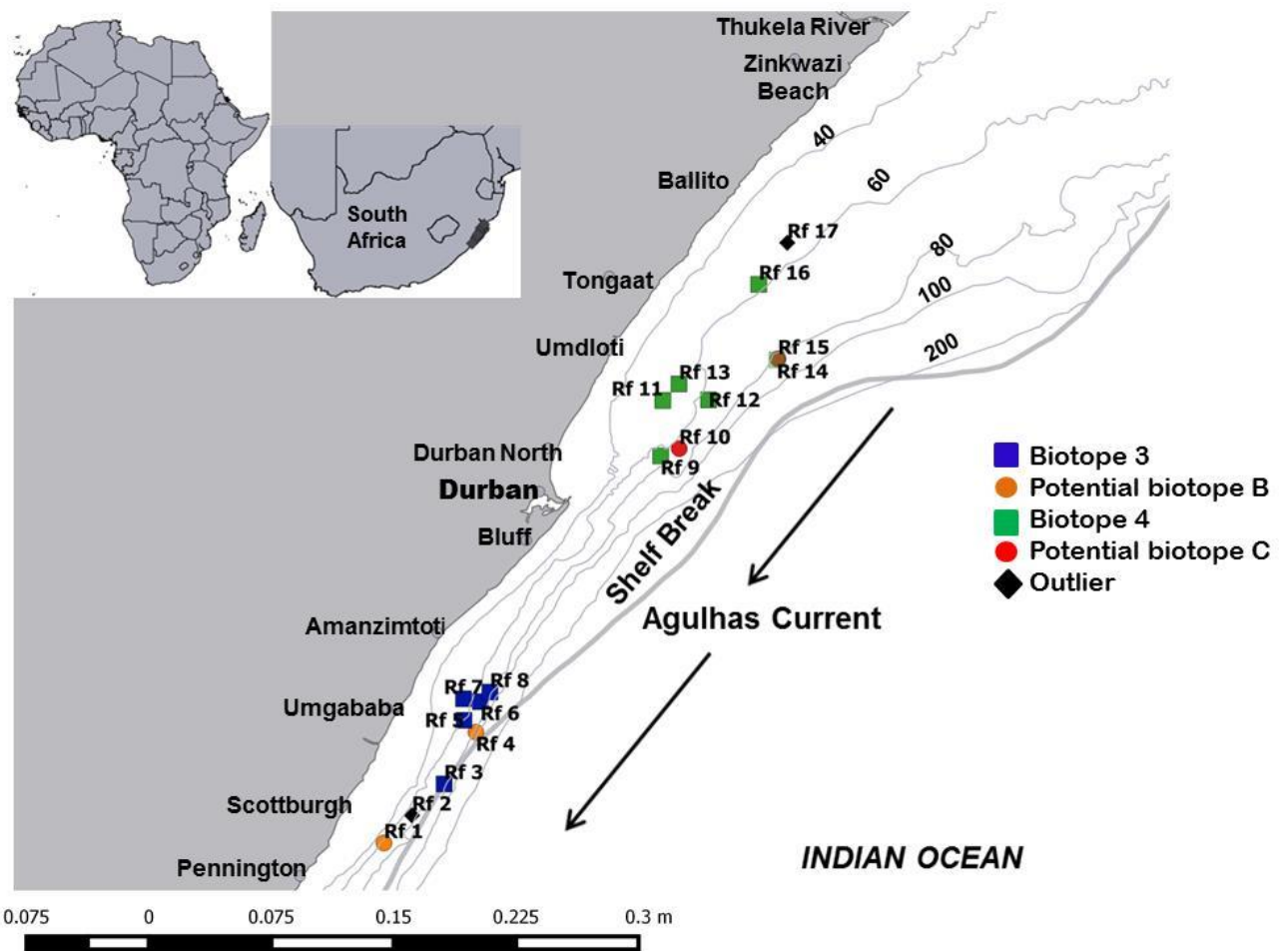


Figure 3.5: Map of the study area showing the distribution of two biotopes and the two potential biotopes of the south and north of Durban. Please note sites RF14 and RF15 overlay each other although they were classified as a biotope 4 and potential biotope C respectively.

3.4.3 Characteristic and distinguishing species of the two main groups, north and south of Durban.

SIMPER analysis showed that the three characteristic species that contributed the greatest average abundance at north of Durban sites were octocoral *Parasphaerascleridae* sp., sponge *Ciocalypta* sp. and seafan *cf. Echinomuricea atlantica* with their average abundance of 3.37, 2.97 and 2.83 respectively (Table 3.2). The sites south of Durban were characterised by the sponges *Ciocalypta* sp., *Halichondriidae* sp. and bryozoan *cf. Bicellariella* sp. with their average abundance of 3.32, 1.98 and 1.90 counts per unit area respectively (Table 3.2). The species *Ciocalypta* sp. occurred in both regions in high abundance throughout the study area.

The results for SIMPER analyses of distinguishing species (Figure 3.6) showed that most epifauna occurred in both regions however they occurred in different quantities. Some were

abundant north of Durban while others were more abundant south of Durban. For example octocorals such as *cf. Echinomuricea atlantica*, *cf. Menella* sp. and *Parasphaerascleridae* sp. were characteristic of sites north of Durban while species such as *cf. Bicellariella* sp. (bryozoan), sponge *Hemiasterella* sp. 2 and *Lithochela conica* were more abundant south of Durban. Species such as *Pteroides cf. isosceles* and *Helicogorgia cf. capensis* occurred only in the southern region (Figure 3.6). The top three species which contributed most to the dissimilarity between regions north and south of Durban are *cf. Echinomuricea atlantica*, *cf. Menella* sp., which were more abundant at northern sites, and *cf. Bicellariella* sp. which was more abundant at southern sites (Figure 3.6).

The results of further SIMPER analyses of the four community types are outlined in Table 3.3 and 3.4. The potential biotope B comprised of only two sites had 62.23% similarity in epifaunal assemblages with *cf. Bicellariella* sp., *Ciocalypa* sp. and *Clavularia* sp. being the top three characteristic species (Table 3.4). Biotope 3, consisting of 5 sites, had 55.27 % similarity in epifaunal assemblages with *Ciocalypa* sp., *Axinella* sp. and *Hemiasterella vasiformis* being the top three characteristic species. *Ciocalypa* sp., *Parasphaerascleridae* sp. and *Stellidae* sp. were the top three characteristic species in potential biotope C (two sites) while *Parasphaerascleridae* sp., *Leptogorgia gilchristi* and *Ciocalypa* sp. were the top three characteristic species of biotope 4 (six sites) with 58.14 % and 60.01 % similarity in epifaunal assemblage of the two biotopes respectively. The dissimilarity between south of Durban biotopes (potential biotope B and biotope 3) was 54.70 %; while the dissimilarity between north of Durban biotopes (potential biotope C and biotope 4) was 48.12 % (Table 3.3). Furthermore the average similarities within community types were highest in potential biotope B and lowest in biotope 3 (Table 3.3).

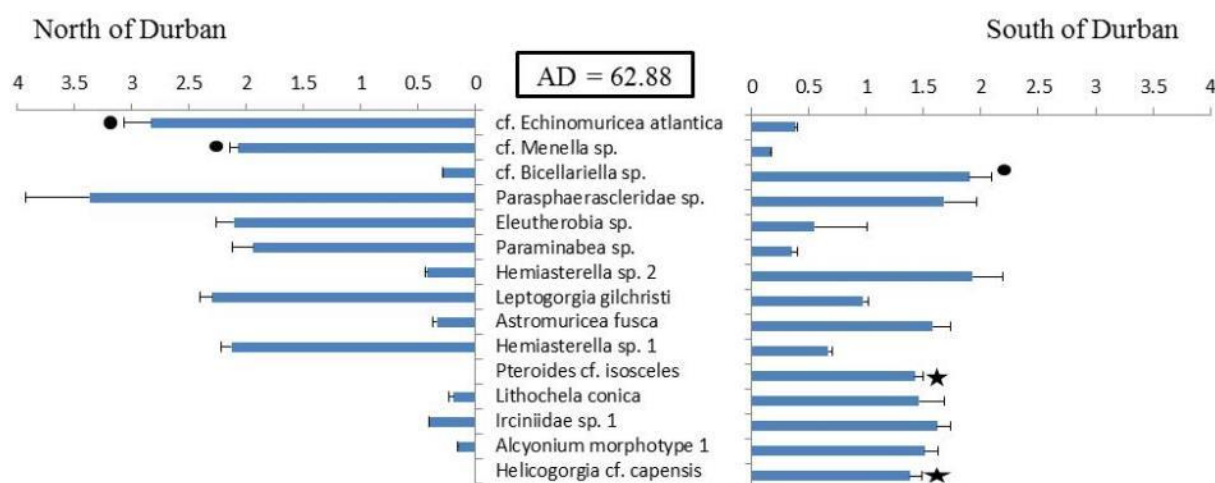


Figure 3.6: The SIMPER results for the two main groups showing species which contributed most to the dissimilarity between the two areas (north and south of Durban). The species are ordered from the most distinguishing species (top) to the least distinguishing species (bottom). Black circles highlight the top three species which contributed to the dissimilarity while the black stars highlight species which were only found south of Durban. The x-axis denotes average abundance of species.

Table 3.2: SIMPER analyses of the identified two biotopes and two potential biotopes. Black cells indicate average similarity (%) within each biotope / potential biotope while white cells indicate average dissimilarity (%) between any two biotopes / potential biotopes.

	Potential biotope B (three sites)	Biotope 3 (five sites)	Potential biotope C (two sites)	Biotope 4 (six sites)
Potential biotope B	62.23			
Biotope 3	54.70	55.27		
Potential biotope C	60.25	61.27	58.14	
Biotope 4	63.29	63.04	48.12	60.01

Table 3.3: The top 10 characteristic epifaunal species of the two main groups, sites north of Durban and sites south of Durban, as determined by SIMPER analyses with the average similarity of 54.57% and 48.83% respectively. Average abundance = Counts per unit area

North of Durban (Average similarity 54.57%)				South of Durban (Average similarity 48.83%)			
Species	Av. Abund	Av. Sim	Contrib (%)	Species	Av. Abund	Av. Sim	Contrib (%)
<i>Parasphaerascleridae</i> sp., Octocoral	3.37	4.10	7.52	<i>Ciocalypa</i> sp., Sponge	3.32	3.22	6.60
<i>Ciocalypa</i> sp., Sponge	2.97	3.31	6.07	<i>Halichondriidae</i> sp., Sponge	1.98	1.98	4.05
<i>cf. Echinomuricea atlantica</i> , Octocoral	2.83	3.23	5.93	<i>cf. Bicellariella</i> sp., Bryozoan	1.90	1.52	3.12
<i>Leptogorgia gilchristi</i> , Octocoral	2.43	2.84	5.20	<i>Hemiasterella</i> sp. 2, Sponge	1.93	1.40	2.86
<i>Halichondriidae</i> sp., Sponge	2.30	2.68	4.91	<i>Leptogorgia</i> sp. 3, Octocoral	1.44	1.34	2.74
<i>cf. Menella</i> sp., Octocoral	2.07	2.50	4.57	<i>Irciniidae</i> sp. 1, Sponge	1.62	1.23	2.52
<i>Hemiasterella</i> sp. 1, Sponge	2.13	2.44	4.47	<i>Clathria</i> sp. 1, Sponge	1.64	1.23	2.51
<i>Eleutherobia</i> sp., Octocoral	2.11	2.35	4.31	<i>Pteroides cf. isosceles</i> , Octocoral	1.42	1.17	2.41
<i>Irciniidae</i> sp. 2, Sponge	1.86	2.29	4.20	<i>Menella</i> sp., Octocoral	1.53	1.16	2.38
<i>Trichogorgia cf. flexilis</i> , Octocoral	1.91	2.10	3.84	<i>Reteporella lata</i> , Bryozoan	1.55	1.16	2.37

Table 3.4: SIMPER analysis of the identified biotopes, presenting top five characteristic taxa and their average contribution (%) to the overall similarity of the biotope / potential biotope. Average abundance = Counts per unit area

Potential biotope B				Biotope 3			
Species	Av. Abund	Av. Sim	Contrib (%)	Species	Av. Abund	Av. Sim	Contrib (%)
<i>cf. Bicellariella</i> sp., Bryozoan	2.77	3.08	4.94	<i>Ciocalypa</i> sp., Sponge	3.45	3.50	6.34
<i>Ciocalypa</i> sp., Sponge	2.70	2.92	4.70	<i>Axinella</i> sp., Sponge	2.41	2.30	4.17
<i>Clavularia</i> sp., Octocoral	2.28	2.57	4.14	<i>Hemiasterella</i> <i>vasiformis</i> , Sponge	2.53	2.19	3.96
<i>Flustramorpha</i> sp., Bryozoan	2.21	2.50	4.02	<i>Stellidae</i> sp., Sponge	1.96	1.96	3.55
<i>Parasphaerascleri</i> <i>dae</i> sp., Octocoral	2.61	2.47	3.97	<i>Helicogorgia cf.</i> <i>capensis</i> sp., Octocoral	1.91	1.76	3.19
Potential biotope C				Biotope 4			
Species	Av. Abund	Av. Sim	Contrib (%)	Species	Av. Abund	Av. Sim	Contrib (%)
<i>Ciocalypa</i> sp., Sponge	3.63	3.46	5.94	<i>Parasphaerascl</i> <i>eridae</i> sp., Octocoral	3.15	4.07	6.79
<i>Parasphaerascleri</i> <i>dae</i> sp., Octocoral	3.60	3.37	5.80	<i>Leptogorgia</i> <i>gilchristi</i> , Octocoral	2.60	3.57	5.95
<i>Stellidae</i> sp., Sponge	2.75	2.86	4.92	<i>Ciocalypa</i> sp., Sponge	2.88	3.35	5.58
<i>Paraminabea</i> sp., Octocoral	2.64	2.71	4.66	<i>cf.</i> <i>Echinomuricea</i> <i>atlantica</i> , Octocoral	2.77	3.23	5.39
<i>Helicogorgia cf.</i> <i>capensis</i> sp. 2, Octocoral	2.39	2.43	4.18	<i>Stellidae</i> sp., Sponge	2.49	3.17	5.28

3.4.4. Testing the potential drivers of the community distribution patterns

The draftsman plot indicated strong correlation between some environmental variables (Table 3.5). Only one of the two correlated variables with a correlation value above 0.85 was selected for further analyses as listed in Table 3.5.

Table 3.5: Results from draftsman plots of variables that showed correlations >0.85.

Environmental variables	Correlation	Variables selected for further analysis
Latitude + Longitude	0.98	Latitude
Latitude + Distance from shelf edge	0.87	Distance from shelf edge
Light attenuation + Chl <i>a</i>	0.98	Light attenuation

Table 3.6: Results from DISTLM marginal test, with the significant *P*-values in bold.

Environmental Variables	SS (trace)	Pseudo-F	P	Prop.
Latitude	6966.5	5.5428	0.0001	0.2698
Depth	1278.1	0.78119	0.6432	4.9501
Bottom Oxygen (ml/l)	2179.2	1.3827	0.1702	8.4400
Bottom temp (°C)	1765.6	1.101	0.3006	6.8381
SST (mean)	5878.8	4.4222	0.0003	0.2276
Phosphate	4762.6	3.3926	0.003	0.1844
Distance from shore (km)	3288.8	2.1896	0.0327	0.1273
Distance from shelf-edge (km)	6828	5.393	0.0001	0.2644
SI %	2035.3	1.2836	0.2054	7.8830
KD 490nm	1709.8	1.0638	0.3292	6.6221
Turbidity (mean)	1159.8	0.7055	0.7468	4.4921

The distance based linear model (DistLM) (Figure 3.7) explained 54.4% of the total fitted variation and 43.1% of the total variation in epifauna distribution. Distance from shelf edge, latitude, SST (mean), phosphate and distance from shore significantly contributed to the separation among sites ($P = 0.0001$, 0.0002, 0.0003, 0.003 and 0.0327, respectively, Table 3.6); however bottom O₂, sand inundation, bottom temperature, light attenuation (KD 490nm), depth and turbidity did not significantly influence site separation ($P = 0.1702$, 0.2054, 0.3006, 0.3292, 0.6432 and 0.7468 respectively, Table 3.6).

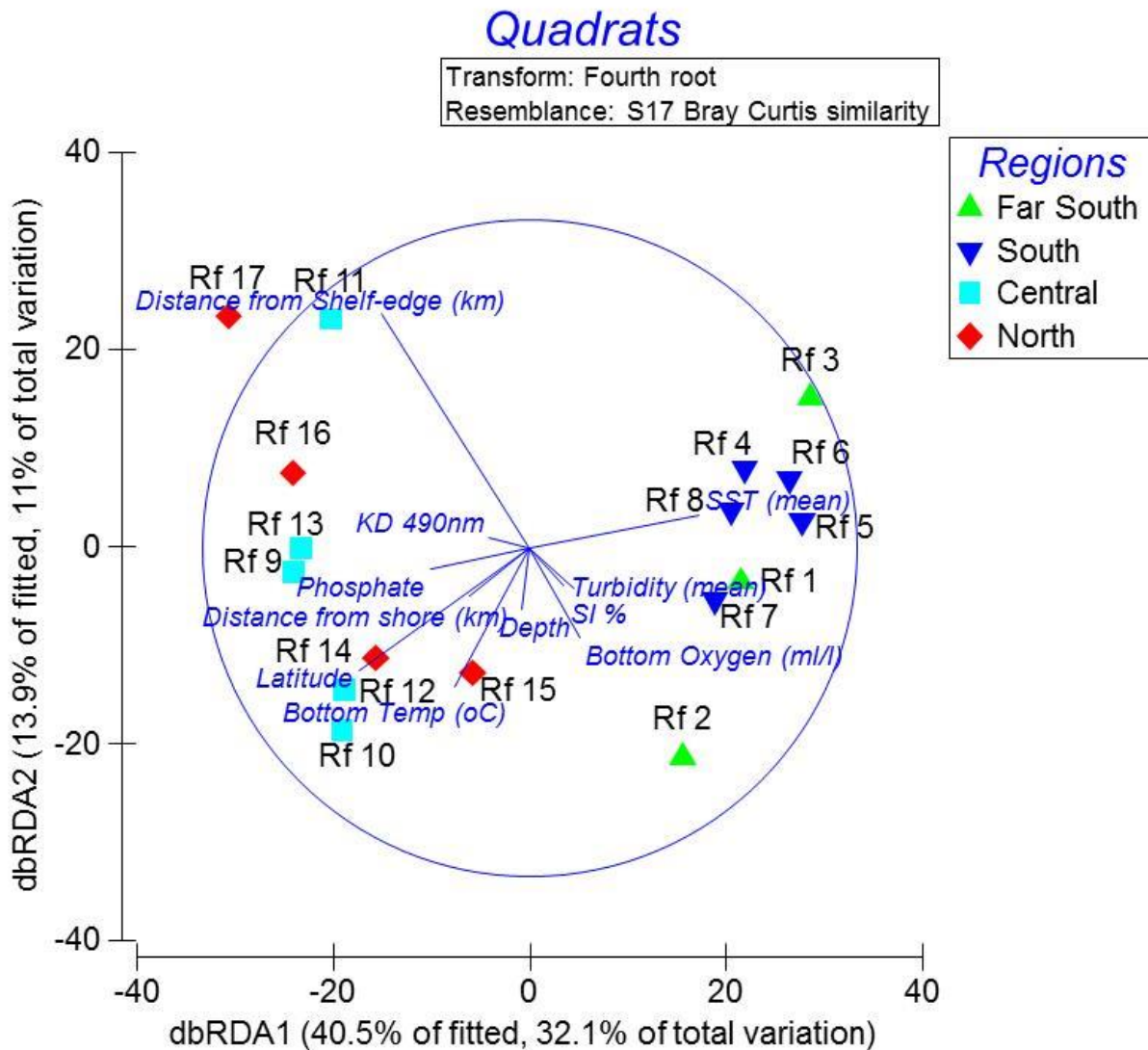


Figure 3.7: The distance-based redundancy analysis (dbRDA) plot of the DistLM analysis, based on the environmental parameters fitted to the variation of patterns in epifaunal assemblages of the 17 study sites.

‘Distance from shelf edge’ had the strongest influence on the distribution of two central sites (Rf11 and Rf17) and contributed most to the separation of these sites from other central region sites. ‘Distance from shore,’ ‘latitude,’ bottom temperature, ‘depth’ and phosphate influenced (but not necessarily significantly) the species assemblages of other ‘north of Durban’ sites (Rf14, Rf15, Rf10 and Rf12) while Rf9, Rf13 and Rf16 were influenced (but not significantly so) by down-welling irradiance (KD 490nm). SST (mean) influenced the species assemblages south of Durban (Far South and South), and influenced the separation between northern and southern region sites. Turbidity, sand inundation (SI %) and bottom O₂ also contributed to the separation (but not significantly so) of some south of Durban sites (Figure 3.7).

3.5 Discussion

The aim of the current study was to investigate physical drivers of epifaunal communities of the deep reefs in an area of KZN. One of the challenges in investigating the relationships between organisms and their environment is to select environmental parameters that have a direct, or at least a predictable, association to the organisms. The five measured environmental drivers that most influenced patterns in epifaunal assemblages of the KZN deep reefs were distance from shelf edge, latitude, sea surface temperature (SST mean), phosphate and distance from shore. Latitude, distance from shelf edge, phosphate and distance from shore strongly influenced epifaunal assemblages of many sites north of Durban whereas sea surface temperature had a greater influence on the reef epifauna assemblages south of Durban.

3.5.1 *Potential biogeographic break*

There was a distinct difference in epifauna north and south of Durban with 60% dissimilarity in community structure between these two regions. This may constitute a biogeographic break or transition, as these two regions are known to be more tropical (north of Durban) and subtropical (south of Durban; see Chapter 1, Sink *et al.* 2005, Porter *et al.* 2013). The current study identified two definitive biotopes, two potential biotopes (which had two sites each hence further sampling required in the study area) and two outliers from each region. The currently identified biotope 3, and the potential biotope B from south of Durban, is the same biotope 3 (with additional site, RF3) and potential biotope B identified for reefs in Chapter 2 of the current study. However in Chapter 2 the sites forming potential biotope B clustered with the mixed reef group. The current Chapter was based entirely on reefs and did not include mixed substrate sites; however, a preliminary analysis performed (results not shown) indicated that the addition of mixed sites to the analysis did not have a significant effect on the results. Biotope 4 and potential biotope C were identified from sites north of Durban.

Most species occurred across the entire study area; however, in different quantities, some species were more abundant to the north of Durban than the south of Durban and *vice versa*. While there were few species which were rare and appeared in low abundance in one region. Encrusting Porifera species dominated the reefs to the south of Durban, while upright seafans and other octocorals and Porifera were more prevalent north of Durban. Octocorals *Parasphaeroscleridae* sp., *cf. Echinomuricea atlantica* and *Leptogorgia gilchristi* were among the most abundant species in the northern region, while sponges *Halichondriidae* sp.,

Hemiasterella sp. 2 and bryozoan *cf. Bicellariella* sp. were more abundant in the southern reefs, with sponge *Ciocalypta* sp. being prevalent throughout the study region. Sink *et al.* (2005) identified a clear biogeographic break between Maputaland and Natal Provinces in the rocky intertidal shores along the KZN coast. Their study identified the Natal region to host different rocky intertidal species from Maputaland and the warm-temperate south coast Agulhas province. Porter *et al.* (2013) identified the subtidal reefs of the current study area to be subtropical Natal bioregion, with no difference in species composition between subtidal reefs north of Durban to those located to the south. The current study identified two biotopes from deep reefs north and south of Durban. No study has reported the biogeographic break around Durban for deep reefs; however Emanuel *et al.* (1992) described a break just north of Durban for rocky shores, and Bolton and Anderson (1997) identified an eastern overlap in community structure from around East London to Durban, and regarded the area north of Durban as part of the Tropical Indo-West Pacific Province. The difference in community composition between shallow subtidal reefs and deep reefs need to be accounted for when comparing the current study findings to other studies conducted in this region. The current study suggests a biogeographic break around Durban, and further sampling is required in the region.

3.5.2 Key characteristic species of the study area

Ciocalypta sp. was among the top three characteristic species in all biotopes and potential biotopes making it one of the most common epifaunal species of the current study area. It is a genus that has been described as characteristic of temperate and subtropical waters with a depth range reported from 12–49 m (Carballo 2001, Carvalho *et al.* 2003). The northern regions (north and central sites) are mostly dominated by octocorals such as *Parasphaerascleridae* sp., *Leptogorgia gilchristi* and *cf. Echinomuricea atlantica*. The subclass Octocorallia has received recent global attention due to the recognition of these taxa being important habitat forming species (Reed and Ross 2005, Berrue and Kerr 2008, Cairns and Bayer 2009, Cúrdia *et al.* 2012, Haverkort-Yet *et al.* 2013, Mohammad *et al.* 2016). In South Africa, the soft coral fauna of the KZN reefs have been the subject of numerous studies (Riegl 1996, Ofwegen and Schleyer 1997, Williams 2000) due to their ecological importance and abundance. Regardless of these studies, many species of octocorals have not yet been described and studies on Octocorallia taxonomic classifications for the KZN reefs are required.

The southern regions (south and far south sites) were dominated by Porifera morphospecies such as *Ciocalypa* sp., *Halichondriidae* sp., *Hemiasterella* sp. 2, and bryozoan cf. *Bicellariella* sp. The narrowing of the shelf edge in the southern part of KZN results in a faster Agulhas Current flow (Lutjeharms *et al.* 2010), which might be contributing to the different epifaunal species occurring north and south of Durban. The southern region is further influenced by the Durban Eddy which draws cold water upwards, facilitating biological production in the region (Guastella *et al.* 2012, Robertts *et al.* 2010). The most abundant, characteristic species of this region are encrusting Porifera species, which are well adapted to the harsh conditions caused by the fast flowing current and the effects of this eddy. Sponges have an important ecological role in marine habitats and are considered to be ecosystem engineers (Beazley *et al.* 2015, Przeslawski *et al.* 2015). Przeslawski *et al.* (2015) report that environmental factors that regulate sponge species distributions include wave exposure, temperature, light, sediment load and substrate type, while depth, slope and distance offshore relate to sponge assemblage structure and abundance. However, in the current study, only sea surface temperature emerged as a key driver of general species distributions of the southern regions. Samaai *et al.* (2010) observed a consistent decrease in sponge species richness with increasing depth linked to changes in environmental factors such as light attenuation, wave action, productivity, temperature or seasonality. Due to limited data availability and resources, factors such as wave exposure, current velocity, slope and sediment load were not readily available for the study area. Future investigation of the potential role of these variables in structuring species assemblage patterns is required.

3.5.3 Environmental drivers of species distribution patterns

It should be noted that for the purpose of this study (systematic conservation planning purposes), the following environmental variables: 'latitude, distance from shelf edge, distance from shore and depth'; were used as proxies for reef epifaunal assemblages patterns but they are not actual drivers of patterns. These environmental variables cannot explain biological patterns but they are often convenient descriptors of some other environmental variables which might not have been described or sampled.

As expected, latitude proved to be the best proxy which contributed significantly to the observed pattern in epifaunal reef assemblages; possibly signalling a potential biogeographic break around Durban along the KZN coast. Blanchard *et al.* (2013) reported that latitude and latitude were the significant predictors of bottom temperature of the northeastern Chukchi Sea. Similarly, in the current study latitude and bottom temperature were shown to have

strong link signalling patterns in epifaunal assemblages of some northern region sites. However the mean SST is mostly correlated with the species assemblages of the southern reefs. Long term mean SST has been reported to have an important role in determining species distributions in marine environments (Bremner *et al.* 2006, Blanchette *et al.* 2008, Neumann *et al.* 2009).

Distance from shelf edge served as a proxy for environmental variables that mostly influence central region epifaunal patterns. The shelf-edge is known to be an area of high diversity due to the steep change in slope and depth, and is often regarded as an enhanced region of upwelling (Buhl-Mortensen *et al.* 2012, Kämpf 2012, Richmond and Stevens 2014). In KZN, species distribution patterns along the shelf edge were reported to be influenced by the Agulhas Current (Untiedt and MacKay 2016). Untiedt and MacKay (2016) reported that shelf-edge upwelling along the KZN Bight, which was caused by the meeting of Thukela River inflow and Agulhas Current, provided ideal conditions for suspension feeding. Species dominating the reefs north of Durban were observed to be mostly emergent, upright species (e.g. cf. *Echinomuricea atlantica* and *Leptogorgia gilchristi*) while those to the south of Durban were mostly encrusting sponges. This may be due to the narrowing shelf edge south of Durban where the current speed is much greater than towards the northern reefs where the shelf region is wider. Furthermore the south of Durban region is affected by the Durban Eddy (Roberts *et al.* 2010).

Phosphate serves as a proxy of turbidity (Lannergård 2016). We suspect turbidity has a strong correlation on the epifaunal assemblages patterns of the northern sites, based on the current study findings (Figure 3.7). This partially agrees with the study of Porter *et al.* (2017) which revealed that turbidity and suspended sediments are strongly associated with shallow subtidal communities' composition of the Natal region. However in contrast, turbidity measured for the current study did not significantly influence the epifaunal species assemblages. Livingstone (2016) showed an increased phosphate content stretching northwards and eastwards of the KZN Bight off Durban, with poor phosphate and organic matter south of Durban. The high turbidity and suspended sediments present in the KZN Bight region might be due to high riverine inflow of the region (Meyer *et al.* 2002, Porter *et al.* 2014); in particular the flow of the Thukela River (De Lecea and Cooper 2016).

The water column at nearshore reef sites was expected to have higher sediment and nutrient content than offshore reef sites due to their exposure to high riverine inflow nearshore (Green

and MacKay 2016). The riverine inflow is known to influence the patterns of species distribution in this region (Mallela 2007, MacKay *et al.* 2016). Although the current study did not measure the direct influence of riverine inflow, incorporating variables such as distance from shore, phosphate and down-welling irradiance somewhat serves as proxies for riverine inflow. The current study identified that 'distance from shore' also served as a proxy for some environmental variable that had a significant influence on the species assemblages of the central region.

Many of the KZN reefs are subject to some degree of sand inundation due to their topography and sediment movement attributed to the fast-flowing Agulhas Current (Porter *et al.* 2017b). The influence of substrate on species assemblages was addressed in Chapter 2 of this thesis and Porter *et al.* (2017) examined the potential of a reef to be inundated by sand, based on topographic potential of the reef to trap sand. Sand inundation, as measured by sand cover in this Chapter, did not seem to have significant influence in the current study, and this is in contrast to the findings in Chapter 2 that there are certain epifaunal species which thrive on sand inundated or mixed substrate reefs e.g. *Homophyton verrucosum* and *Melithea* sp. 1. The current results might be due to the fact that in Chapter 2, mixed habitat types, which are likely to experience a far greater degree of sand inundation were included in the analyses, while the current study only examined medium to high profile reef habitats (excluding sites of mixed habitat type). It is hypothesized that there is a correlation between current speed and extent of sand inundation with less sand inundation expected the higher the current speed. Further investigations on the relationship between the extent of sand inundation, species assemblages and the influence of current speed are recommended. Furthermore topography might be a determinant of sand inundated reefs (Adjeroud 1997, Porter *et al.* 2017b) in that reefs with greater topographic complexity are prone to higher sand inundation (Beisiegel *et al.* 2017, Monk *et al.* 2016, Porter *et al.* 2017b).

Depth is widely included in conservation planning studies, it is inversely related to light penetration; light penetration is an important environmental variable that drives species distribution patterns as it has influence on primary production (Adjeroud 1997, Post *et al.* 2006, Przeslawski *et al.* 2008, Anderson *et al.* 2011, MacKay *et al.* 2016). The current study is conducted in a relatively narrow depth range (between 48 to 85 m) and depth did not significantly influence the species distribution patterns observed within this narrow depth range. Untiedt and MacKay (2016) demonstrated differences in macrobenthic communities, sampled between Durban and Richards Bay, KZN from 16–184 m depth. The highest

numbers of individuals were found at inner (16–27 m) and mid-shelf (31–85 m) positions with the lowest number of individuals occurring on the outer shelf region (41–184 m). Lesser *et al.* (2009) also reported change in species composition from shallow to deeper waters in mesophotic reef communities. Heyns *et al.* (2016) investigated diversity patterns of epifauna on shallow and deep reefs of the Tsitsikamma MPA (south coast South Africa), and revealed higher species diversity and richness in shallow reefs (11–25 m) than in deep reefs (45–75 m). Their study revealed that deep reefs in the south coast were characterised by epifaunal species having upright growth forms such as bryozoans, sponges, hydroids and seafans. This was also seen in the northern region of the current study where a greater abundance of upright octocorals and sponges were observed at similar depths to deep reefs of the Heyns *et al.* (2016) study.

3.5.4 Limitations to the current study

In the current study only 43.1% total variation was explained by the environmental drivers tested using the distance-based linear model (PERMANOVA, Anderson *et al.* 2008); from this analysis, it appears that there are additional, unmeasured abiotic/physical or other variables that contribute to the separation between north of Durban and south of Durban sites. However this total variation was relatively high compared to a similar study of Pitcher *et al.* (2012), in which they included 29 predictor variables and their total variation predicted was 35% of the variation in species abundance distributions. Furthermore, Porter *et al.* (2017) included 9 abiotic variables which explained up to 32% of the total variation in species abundance for shallow reefs. Further analysis is required with examination of other environmental variables. These include wave exposure, current velocity, slope and sediment loads; however the total variation explained is further influenced by other determinants of species/ community compositions aside from abiotic variables. The limited study area and depth range also confined the results and we recommend additional sampling with a more balanced study design, where feasible. The study demonstrated that our findings were affected by the area and depth range as some variables, such as depth, did not influence patterns in epifaunal assemblages, contradicting the expected results and literature. There is a need for additional sampling of reefs in the region including in between south and north of Durban to further test and validate the proposed biogeographic break. Furthermore additional sampling is required for sites to investigate the validity of the described potential biotopes.

3.5.5 Further studies and recommendations

There is a possibility that fish and other invertebrates prey on some epifauna (Dulvy *et al.* 2004). Changes in fish assemblages within regions can lead to altered predation pressure on the epifaunal species (Bremner *et al.* 2006). Cúrdia *et al.* (2012) report that in shallow waters, where there is similarity in abundance patterns of seafans, there is also low competition and high association among the seafans. de Juan *et al.* (2013) incorporated fishing effort as one of the important drivers of epifauna in soft sediments of Mediterranean continental shelves in depths between 32 to 82 m. Fennessy (2016) report diverse fish communities within the soft sediments of the KZN Bight which increased with depth from the inner shelf (28–71 m) to the upper slope (233–253 m) of the region. Further investigation of biological processes such as the influence of fish assemblages on epifauna in the region is required, and monitoring of the new MPAs might help develop this understanding as fish populations recover.

Marine epifauna play an important role in ecosystem processes such as carbon, oxygen and nutrient cycling, and their assemblages, abundance and distributions are known to affect benthic-pelagic coupling processes (Dale *et al.* 2017). Few studies have examined the benthic-pelagic coupling process in the KZN Bight; however, Muir *et al.* (2016) investigated the prokaryotic biomass and heterotrophic productivity in the KZN Bight. Their study highlights the importance of bacterial populations in the region, and this may be incorporated in further understanding the benthic-pelagic coupling processes of the region. Benthic-pelagic processes can define spatial variability in benthic communities, as seasonal productions constantly change their environments. Carbon cycling studies revealed linkages between primary production in the water column and the distributions of epifauna (Blanchard *et al.* 2013, Griffiths *et al.* 2017). It is therefore important that the benthic-pelagic coupling process be incorporated in future work to improve regional understanding. This can be done by building on the current study with investigations of phytoplankton and or ichthyofauna diversity present in the study area.

3.5.6 Conclusion

The current study provides the first visual survey and assessment of deep reef epifauna in the KZN outer shelf. This study was limited in spatial extent; however it revealed a clear separation of deep reef epifauna north and south of Durban. The potential environmental drivers and proxies that significantly influenced epifaunal assemblages were ‘distance from shelf edge’, ‘latitude’, sea surface temperature, phosphate and ‘distance from shore’. Further investigations are recommended to explore distributional differences resulting from an

increase in depth and distance from shore by expanding the research into the deeper offshore region and broadening the study area with increased sampling effort. The results from this study highlight limitations of using environmental variables for ecosystem classification at the local scale and the need for robust surveys to quantify patterns of biodiversity. Furthermore the study highlights patterns in epifaunal assemblages and diversity of the KZN outer shelf, with a dominance of Porifera and octocoral species, known to play an important ecological role (Cúrdia *et al.* 2012, Beazley *et al.* 2015, Beisiegel *et al.* 2017). The current study is the first to describe two deep reef biotopes; this will be useful for updating the South Africa's national ecosystem classification and mapping of the KZN outer shelf.

Acknowledgements

Ocean Colour Climate Change Initiative dataset, Version 3.0, European Space Agency, available online at <http://www.esa-oceancolour-cci.org/>



4 Synthesis

The current study investigated the use of benthic epifauna to support ecosystem classification and mapping in the KwaZulu-Natal (KZN) outer shelf. The study was twofold; in Chapter 2, existing marine ecosystem classifications were tested using epifaunal data quantified from seabed imagery and the effect of substrate in shaping epifaunal assemblages was established for the southern KZN outer shelf. In Chapter 3, potential drivers and the proxies for environmental drivers of patterns in deep reef epifaunal assemblages were investigated for the entire study area. The results from this study provide information on ecosystem types of the KZN shelf which can be incorporated in future conservation plans, marine spatial planning (MSP) and assessments of the region. This is the first study to quantify epifaunal assemblages of deep reef communities of the KZN outer shelf.

4.1 Key findings

The current study identified four biotopes and three potential biotopes. Three biotopes were made up of reef, mixed substrate and sand ecosystem types of southern KZN, and one biotope from reef sites of central KZN (north of Durban) (Figure 4.1). One potential biotope originated from north of Durban reef sites, while the two other potential biotopes consisted of unconsolidated sediments and reefs south of Durban. The two reef sites from south of Durban which constitute a potential biotope, were not significantly different to the mixed substrate types. It is likely that some form of sand inundation occurs on these reefs. The potential biotopes each comprised two sites, and further sampling is required to explore these potential biotopes.

Mixed ecosystems can be considered a subset of reef ecosystem types and they also host different biodiversity to unconsolidated sediments. We observed in Chapter 2 that most species occurring on reefs also occurred on mixed ecosystem types, although in different quantities. There were certain species which favoured mixed ecosystems more than reefs and vice versa. This may indicate that some species thrive on reefs with sand inundation while other species may not be adapted to cope with sand inundation. Furthermore, we learned in Chapter 2, that the existing ecosystem classifications for both national and regional classifications do not effectively represent the epifaunal assemblages of the study area. When testing the existing ecosystem classifications with epifaunal data, the results indicated a mismatch. Ecosystems which were classified as reefs were often found to be mixed or

unconsolidated sediments and vice versa. These observations highlight the importance of incorporating *in situ* sampling and epifauna in future ecosystem classifications and mapping.

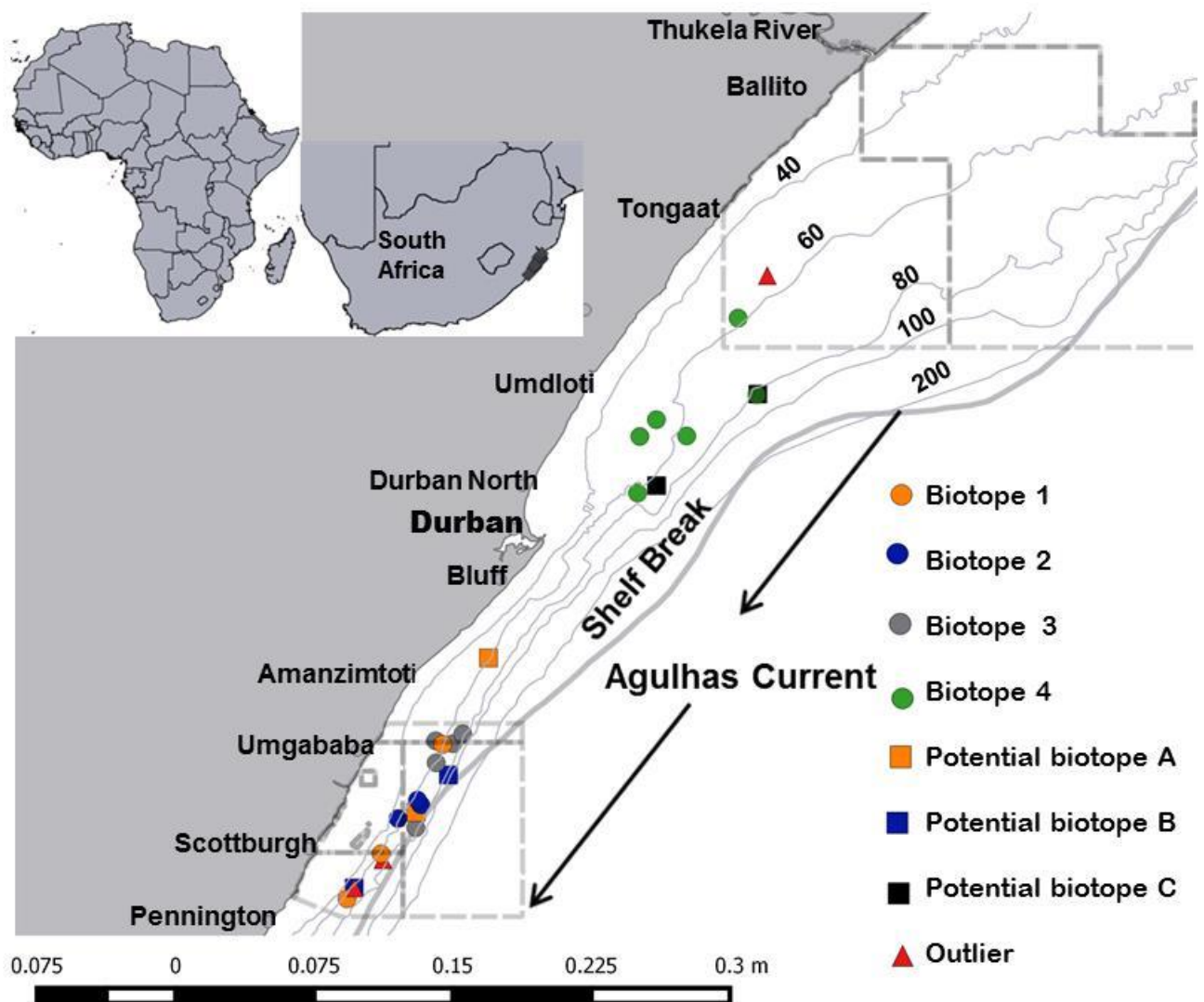


Figure 4.1: Most of the study sites are incorporated in the proposed KwaZulu-Natal MPA design. Proposed MPAs (uThukela Banks (north) and Aliwal Shoal (south)) in dashed squares, sites which form biotopes are represented by circles while sites which form potential biotopes are represented by square shapes. The outlier sites are represented by red triangles.

Analyses conducted in Chapter 3 showed that there is a significant difference in epifaunal assemblage distribution patterns between the reefs north of Durban and that south of Durban. These findings suggest a possible biogeographic break offshore of Durban with different deep reef epifaunal assemblages occurring north and south of Durban. Further sampling is required in this region to explore this proposed break.

Although most species occurred throughout the study area, some were abundant on the reefs north of Durban while other species were abundant on the reefs south of Durban. Only a few species were unique to any particular region. Distance from shelf edge, latitude and distance from shore were the major proxies of environmental variables which contributed to patterns in epifaunal assemblages patterns of the KZN deep reefs; whereas sea surface temperature and phosphate were identified as the major potential driving factors of patterns in epifaunal assemblages of these reefs.

4.2 Limitations

4.2.1 Unbalanced design

Time constraints, limited resources and the limited geographical location of the study resulted in the unbalanced design of Chapter 2. In this Chapter, images from 17 sites were processed; eight were reef sites, five were unconsolidated sediment sites while four were mixed sites. The data for the current study was collected as a subset of a collaborative research project in which planning was not designed to cater only for the current study but to cover requirements of different projects during the research expeditions. At some sites, sampling could not be completed as a result of adverse weather conditions which often hindered the remotely-operated vehicle (ROV) operations. Furthermore some reef sites which were initially planned to be surveyed were omitted as no reef could be found (due to the unavailability of multi-beam data). Despite several subsequent attempts to detect their reported positions in the area, they were not successful, limiting the number of sites that could be surveyed and data that could be collected. Other habitat classification studies have relied on multibeam data, both for sampling design and data interpretation (Kostylev *et al.* 2001, Kobryn *et al.* 2013). The lack of such data was a limitation to the current study. Time constraints and limited resources also influenced the design as it was not possible to revisit sites which were affected by the weather during the original sampling period. However the statistical tools used in this study helped in compensating in the analysis of the unbalanced project design. Future projects need to plan for these limitations.

4.2.2 Challenges working with epifaunal imagery data

Identifying epifauna from underwater images with limited knowledge and taxonomic resources proved to be challenging. In South Africa there are few taxonomic guides or experts in marine epifauna from deeper waters of the KZN subtropical region. Some experts, both local and international, were however consulted with identifications of the epifauna

from this study. The use of taxonomic guides and expertise to identify specimens from images is still limiting in that actual specimens and microscopic examination are required to accurately key out most species. Images can only be analysed to a coarse level of identification, with most species only being identified to genus level at best. Image processing is also likely to undersample obscure and camouflaged species and functional groups (Deter *et al.* 2012, Beisiegel *et al.* 2017). Some octocorals and encrusting sponges (e.g. *Mycale* sp.1) grew over other octocoral species in the study area. Przeslawski *et al.* (2015) reported that some sponge taxa were difficult to taxonomically identify even on well-studied ecosystems. Where possible we recommend supplementary collection of physical samples of the most dominant species with the use of an ROV arm or benthic sled for accurate identifications. Further taxonomic studies and collaborations with international experts are encouraged to improve knowledge of the South African benthic epifauna, especially in the KZN region where few trawl surveys take place and modern epifaunal samples from beyond 30 m are scarce. Support is needed to develop detailed taxonomic guides and online databases for the region. Intense taxonomic training and collaborations with taxonomic experts are recommended for similar future studies.

4.2.3 Environmental variables

The implementation and success of marine management strategies relies on the knowledge of species distributions and diversity. Analyses in Chapter 3 revealed significant patterns in epifaunal assemblages of the KZN reefs and identified potential drivers of these patterns. However limitations with the size of the study area, number of sites and narrow depth range were experienced in the current study. The study is located along a narrow continental shelf thus limiting the possible depth range to be surveyed. Wind, strong current and limited detailed bathymetric information is also a hindrance. Additional sampling within the study area and within sites should be conducted to allow further investigation and interpretation of the observed biological patterns. The abiotic variable of sand inundation may also require further investigation as this variable clearly impacted on epifaunal assemblages in Chapter 2 but in Chapter 3, this driver did not seem to contribute significantly to the observed pattern. Longer-term data to understand sand inundation at sites may be needed.

4.2.4 Competition and predation

Biological interactions, such as competition and predation, might further influence the epifaunal assemblages patterns observed in the current study (Chesson and Kuang 2008). Often competition for resources is proven to be a key interaction that limits diversity; and

predation of epifauna by subtropical fish and crown of thorns starfish has been reported elsewhere (Kayal *et al.* 2012, Strong *et al.* 2015). This study did not address such biological interactions despite their recognised importance in ecological studies.

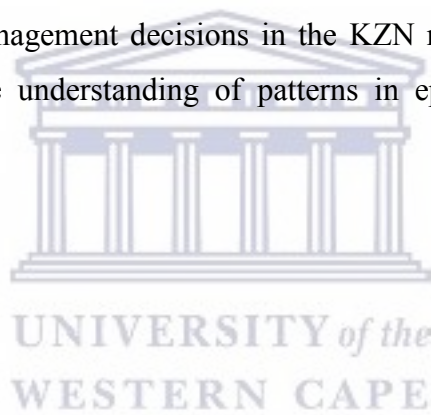
4.3 Management recommendations and future work

Elsewhere in the world, an increased use of geomorphometry (the science of quantitative terrain analysis which originated from terrestrial investigations) has been adopted in marine research. This has resulted in the production of continuous acoustic seabed imagery which is important in understanding changes in marine habitats and the distribution of sediments (Cogan *et al.* 2009, Lecours *et al.* 2015). Coupling these forms of research with our current biodiversity surrogacy can improve marine habitat mapping and classifications that provide more accurate predictions of biodiversity patterns (Anderson *et al.* 2011, Lecours *et al.* 2015). The current study demonstrates the importance of biodiversity surrogates in marine habitat classification. Incorporating benthic biodiversity into the verification processes of existing classifications is essential as these habitats play an important part in marine ecosystem assessments (Cogan *et al.* 2009, Heiskanen *et al.* 2016). A good combination between mapping of physical habitat distribution and the ecological knowledge of patterns in species assemblages is required (de Juan *et al.* 2013). The current study provides valuable information about patterns in epifaunal assemblages of the KZN outer shelf and findings will be useful to inform future MSP projects of the region.

The implementation of Operation Phakisa, which among other objectives, aims to unlock the potential of South Africa's ocean economy, has facilitated the fast tracking of research in the marine environment (Government gazette, 2016). Since the implementation of Operation Phakisa, 22 proposed Marine Protected Areas (MPAs) are under discussion, and will cover 5 % of South Africa's Exclusive Economic Zone (Livingstone 2016, Sink 2016). Of the 26 sites sampled in this study, 18 are incorporated in two of the proposed KZN MPAs (Figure 4.1). Hence we recommend further sampling north of Ballito so as to investigate more sites within the proposed MPA. The current study suggests future work to investigate the proposed biogeographic or regional break off Durban; no previous studies have reported this and more sampling in this area is needed (i.e the deep reefs between north and south of Durban (that is between Tongaat and Pennington) and further north of Ballito).

4.4 Conclusions

The primary aim of this study was to interrogate and refine existing national and provincial ecosystem classifications and maps using epifauna, and to identify the key potential drivers of observed epifaunal biodiversity patterns. Significantly different patterns in epifauna were detected among reef, mixed and sand habitats and this information needs to be incorporated into both regional and national classifications. The current study highlights the importance of ROV imagery data to contribute towards mapping community distribution patterns. Part of the study area is incorporated in two proposed MPAs which capture the diversity of epifauna occurring here (Figure 4.1). It is clear from the results obtained that additional sampling is required to further test the proposed biogeographic break off Durban and the three potential biotopes. The current study serves as a baseline for the implementation of MPA expansions and MSP; however we suggest further surveys in the region to better understand bioregional patterns and inform spatial management (the proposed MPA networks). The current study will support conservation management decisions in the KZN region and also represents an important contribution to the understanding of patterns in epifaunal assemblages of this region.



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Appendix

Table 1: All reef sites sampled in this study with environmental variables collated for the current study.

Regions	Sites	Longitude	Latitude	Depth (m)	Distance from shore (km)	Distance from Shelf-edge (km)	Bottom Oxygen (ml/l)	Bottom Temp (°C)	SST (mean) (°C)	Chlorophyll (Chl <i>a</i>) (mg/m ³)	Turbidity (mean) (m ⁻¹)	Phosphate (%)	Sand Inundation SI %	Light attenuation KD 490nm
Far South	Rf 1	30.81038	-30.3353	60	8.376	3.542	5.328	19.550	23.860	0.606	22908.140	0.123	21.348	0.094
Far South	Rf 2	30.84845	-30.2979	72	10.604	1.082	4.933	18.912	23.800	0.529	23403.830	0.124	30.533	0.085
Far South	Rf 3	30.89207	-30.2553	75	13.036	0.004	3.637	17.039	23.800	0.505	22940.730	0.122	60.311	0.082
South	Rf 4	30.93528	-30.1851	85	13.576	1.380	5.159	15.431	23.800	0.538	23003.030	0.129	17.926	0.085
South	Rf 5	30.9191	-30.1689	48	10.942	3.974	5.300	17.937	23.760	0.538	23494.600	0.132	14.341	0.085
South	Rf 6	30.94132	-30.1436	60	11.550	4.290	5.084	16.969	23.780	0.550	23280.297	0.130	24.756	0.086
South	Rf 7	30.91843	-30.1397	69	8.781	6.335	5.483	16.783	23.770	0.642	23311.210	0.132	14.696	0.096
South	Rf 8	30.95433	-30.1307	72	12.090	4.300	5.625	16.585	23.760	0.550	23391.380	0.132	15.768	0.086
Central	Rf 9	31.18623	-29.8102	68	16.278	11.738	4.327	18.269	23.595	0.583	22689.990	0.184	8.711	0.091
Central	Rf 10	31.21152	-29.8004	60	18.508	9.954	4.546	19.302	23.550	0.532	23331.960	0.168	29.067	0.086
Central	Rf 11	31.1892	-29.735	72	11.888	16.196	4.708	16.827	23.560	0.539	22219.660	0.247	3.911	0.086
Central	Rf 12	31.2514	-29.7343	74	18.710	10.576	4.640	16.988	23.570	0.519	22206.720	0.247	14.104	0.084
Central	Rf 13	31.2112	-29.7127	55	12.901	15.438	4.766	17.773	23.400	0.560	23528.610	0.154	34.163	0.088
North	Rf 14	31.3442	-29.6797	56	25.802	7.821	5.680	17.781	23.370	0.536	23802.910	0.122	32.430	0.086
North	Rf 15	31.34570	-29.6787	71	25.768	8.040	4.459	17.646	23.710	0.536	23458.850	0.193	8.815	0.086
North	Rf 16	31.31958	-29.5776	72	15.265	19.651	4.437	17.349	23.700	0.580	22908.170	0.204	18.815	0.091
North	Rf 17	31.35832	-29.5211	49	14.556	23.295	4.6092	19.5548	23.550	0.617	23653.310	0.1975	2.741	0.095



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