Minor Dissertation

Distribution of epifauna in offshore benthic environments along the west and south coast of South Africa

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Abstract

Marine unconsolidated sediments, such as sand, gravel and muds, constitute the most extensive benthic ecosystems globally. Biological data for these ecosystems are frequently sparse which can hinder the success and implementation of marine management strategies for benthic ecosystems. There are limited studies in South Africa on benthic epifauna. This study investigates the composition and distribution of epibenthic invertebrate assemblages along the west and south coast of South Africa (sampled using depth-stratified demersal trawls) to inform marine environmental management. Sample depth varied from 36m to 899m. Multivariate tools (PRIMER and PERMANOVA+) were used to analyse spatial (west vs south coast) and temporal (2011 vs 2017) patterns in epifauna. This study also investigated an overlap region between the west and south coast. A group average linkage cluster analysis defined biotopes using significant branching ($p<0.05$). Biotopes were compared against the 2012 National Biodiversity Assessment (NBA) benthic habitat map to investigate whether epifaunal biotopes identified, align with the existing classification. A significant difference among epifauna between region and depth was found, where the west coast had a higher average number of individuals and species per station. *Sympagarus dimorphus* and *Pelagia noctiluca* were characteristic species for west and south coast respectively. Epifauna was found to be significantly different between 2011 and 2017, with a notable increase in the abundance of *Crossaster penicillatus* in 2017. The majority of the biotopes aligned with the current NBA classification, in particular the Agulhas Sandy Shelf Edge ecosystem type on the south coast and South Atlantic Upper Bathyal and Namaqua Muddy Inner Shelf ecosystem types on the west coast. This thesis contributes to the mapping and description of offshore ecosystem types to inform marine environmental impact assessments, marine spatial planning and marine protected area expansion.

KEY WORDS: Benthic, Epifauna, South Africa, Ecosystem, Biotopes, National Habitat Classification

1.Introduction

Benthic Ecosystem & Anthropogenic Pressures

The ocean covers 70% of the Earth and a large percentage of the seabed is made up of different types of sediments (Snelgrove, 1997). These marine unconsolidated sediments, such as sand, gravel and fine muds, comprise the most extensive of all benthic ecosystems (Snelgrove, 1997). Due to the vastness of unconsolidated marine sediment ecosystems, biological data from these systems are seldom comprehensive (Leslie et al., 2000). Different components of these ecosystems can be studied to provide insight and understanding of deep sea habitats. For example, benthic infauna can provide information about characterising soft-sediment habitats (Joydas & Damodaran, 2009; Yesson et al., 2015) and studies on epifauna can reveal information about individual abundance and taxon richness at regional and local scales (Yesson et al., 2015) caused by differences in sediment composition, currents and food input (Yesson et al., 2015). Various types of benthic sediments are also an important delimiting factor for the association of fish species in different communities. Diverse communities of fish can also provide information about the contrasting types of benthic sediments as there is a strong association between the two (Demestre et al., 2000; Laidig et al., 2009; Anderson et al., 2009).

Many benthic epifauna play vital roles in the deep sea environment and support a plethora of ecosystem services (Griffiths et al., 2010; Thurber et al., 2014; Murillo et al., 2016). They contribute significantly to benthic biomass and are key links between benthic and pelagic ecosystems (Murillo et al., 2016). These organisms play a role in benthic-pelagic coupling, which is the exchange of energy, mass or nutrients between benthic and pelagic habitats (Griffiths et al., 2017). Benthic invertebrates consume a large volume of benthic biomass and themselves become important prey items for fish and other upper trophic level organisms. Many epibenthic organisms also play a significant role in structuring the marine ecosystem with their three dimensional body forms (Lange & Griffiths, 2014; Yesson et al., 2015). Coral mounds and sea pens provide nursery areas for juvenile fish, some of which may be commercially utilised (De Clippele et al., 2015).

Ecological structuring can occur through various processes and interactions such as competition or predation, as well as exerting significant influences on bioturbation, sediment composition and oxygen consumption (Meyer et al., 2013; Lange & Griffiths, 2014). Yesson et al., (2015) conclude that epifauna also function as a substrate upon which and within which other organisms settle or live. Furthermore, they can also serve as food for other organisms and redistribute and remineralise carbon in the sediment (Buhl-Mortensen et al., 2010; Yesson et al., 2015). Benthic organisms directly benefit society in many ways, including as a possible source of biopharmaceuticals (McArthur et al., 2010). These ecological services result from healthy functioning of ocean ecosystems. Impact on these ecosystem services as a result of anthropogenic pressures, is likely to negatively impact the health and functioning of benthic ecosystems, ultimately having negative effects on human-well being.

Globally, continental shelves are highly disturbed by anthropogenic activities (de

Juan et al., 2012) and yet there is a lack of general information on the distribution of benthic species and habitats beyond coastal areas (Griffiths et al., 2010; de Juan et al., 2012). Furthermore, their vulnerability to human pressures is poorly understood (de Juan et al., 2012). Unconsolidated sediment ecosystems are subject to a diverse array of anthropogenic pressures including demersal fishing, mining, pollution and changing climate effects (Mead et al., 2011). By gaining insight into the community structure and drivers of benthic epifauna, we can assess which habitat types or species may be more vulnerable to indirect and direct impacts. For example, trawling is known to impact the seabed and benthic communities in several ways such as, destruction or damage to complex three dimensional habitats, reduction in bioturbation, death and damage to epifauna and a decline in abundance of larger, slow growing species (Jennings et al., 2001; McArthur et al, 2010). The selective removal of large epibenthic organisms in areas that have been heavily fished for long periods of time has been associated with declines in fish productivity (Murillo et al., 2016). Another threat to the seabed and continental shelf is seabed mining, where at the moment the most advanced in South Africa is that of phosphate mining which would be detrimental to benthic life (Currie, 2013).

Abiotic factors & potential surrogates

In cases where comprehensive information and data are lacking, biological surrogates are often used to define the distributions of ecosystems for the purpose of conservation and management (Sink et al., 2012). A surrogate is a simple estimator of its biological surroundings, and can be physical or biological (Howell, 2010; Mellin et al., 2011). Substrate type is frequently used as a physical surrogate for biodiversity pattern because it is known to significantly influence species assemblages and distributions (Howell, 2010). Substrate type can be a useful surrogate because specific species assemblages occur on, or in, certain substrates (Howell, 2010). The predictable and intimate linkages between biological assemblages and physical habitats has been extensively explored (McBreen et al., 2008). Species evolve within the physical and biological constraints of their niches, therefore their habitat residency reflects their morphological and behavioural traits. For instance, soft sediment burrowing species and hard ground species would be found in two distinctly different habitats. Ward et al. (1999) demonstrated the efficacy of biological assemblages as surrogates for biological diversity in marine protected area selection in shallow water environments. Fish and invertebrate assemblages were found to be good surrogates for species richness (Ward et al., 1999; Regina & Craig, 2006).

It is well established that abiotic factors such as substrate type, temperature and depth, influence the distribution of benthic epifauna (Mcbreen et al., 2008; Howell, 2010; McArthrur et al., 2010). Distribution of benthic epifauna is influenced by ambient water temperature, dissolved oxygen and availability of food (Gross, 2000; Lange & Griffiths, 2014). Depth, which affects light levels changes the distribution and community structure of benthic epifauna (Buhl-Mortensen et al., 2010; Ansari et al., 2011; Murillo et al., 2016), particularly beyond 100-200m (Lange & Griffiths, 2014). Substrate type helps in habitat classification and used in tandem with the application or analysis of biotic data assists in refining spatial boundaries to validate habitat classifications and support improved management.

At greater depths (> 200m), other environmental factors, such as temperature, carbon, oxygen and pH, have greater influence on the community composition (Snelgrove, 1997; Buhl-Mortensen et al., 2010; Howell, 2010). Epifauna which are relatively immobile (in comparison to fish) are less able to rapidly move away from an area experiencing unsuitable conditions (Birchenough et al., 2011). As a result, macrobenthic species (including epifauna) are considered sensitive indicators of change in the marine environment that may be caused by natural or anthropogenic disturbances (Reiss & Kroncke, 2005). In addition to this, benthic species rely on water above them to supply food due to their limited mobility (Snelgrove, 1999). Observational studies have shown that climate change has already impacted deep-sea environments as evidenced by fluctuations in deep-sea temperatures (Brierley & Kingsford, 2009; Sweetman et al., 2017). The longevity of the epifauna and their limited mobility means that community structure can demonstrate how climate change, over time, has affected them. (Birchenough et al., 2011; Sweetman et al., 2017). Benthic epifauna can provide good information for long-term monitoring that is likely to reflect the health of these deep-water ecosystems.

Habitat Mapping (Global) & Marine Classification Systems

Marine protected areas (MPAs) have been established worldwide for species, habitat and biodiversity conservation (Kenchington et al., 2003). The evaluation of benthic biodiversity has become crucial to support effective and representative conservation of marine offshore environments (Ward et al., 1999; Spalding et al., 2007; Douglass et al., 2014). Marine ecosystems are classified for a number of reasons, namely identifying meaningful areas of conservation and for appropriate management of these ecosystems (Kenchington et al., 2003; Costello, 2009). The process of marine conservation planning requires standardised classifications and terminology for ecosystems to ensure consistent mapping of the environment across all possible regions (Costello 2009; Spalding et al., 2007; Sink et al., 2012). Knowing what ecosystem types feature in a region, what biodiversity they support and their vulnerabilities is important for environmental management, including environmental impact assessment and marine spatial planning (MSP). Benthic habitat maps are an important and essential tool for providing marine resource assessments for coastal and offshore management and ecological analysis (Cogan et al., 2009).

A wide range of sea-bed mapping such as broad acoustic beam systems and multiple narrow-beam swath bathymetric systems are used to reveal geophysical characteristics of the sea bed (map the sea floor) (Kenny et al, 2003). Key drivers and tools for creating these classification maps draw on global and local information. For example, information about depth can be sourced from the GEBCO (general bathymetric chart of the oceans) database and from previous literature such as Howell, (2010) and Last et al., (2010). Global temperature readings can be found from NOAA (National Oceanic and Atmospheric Administration) world ocean atlas and locally from Roberts & Nieuwenhuys (2016).

The International Union for Conservation of Nature (IUCN) is an international organisation working in the field of conservation and sustainable use of resources. The IUCN has developed a marine ecosystem classification system that also provides accessible online data. Their classification schemes are divided into marine neritic, oceanic and deep ocean floor (benthic and demersal), intertidal and coastal.

In Europe, the broad habitat classification is called the European Nature Information System (EUNIS). It includes sediment habitats such as Sublittoral sediment and Littoral sediment. EUNIS has simplified substrates into four categories; rock, mixed, sand, muddy sand and mud (Howell, 2010). The habitat classification system includes pelagic water column and the deep-sea bed (include link for all habitats). To classify the deep-sea bed, the system uses geomorphology, depth zones, wave action and substrate types. Due to the nature of deeper water, the oceanographic characteristics can vary greatly on a geographic scale, and thus impact on communities more than would be expected in shallower locations within the photic zone (Fabri et al., 2006).
For this reason, substantial efforts have been made to include information on marine benthic habitats from different regions, aiming to provide a comprehensive geographical coverage of European seas. However, many concerns still remain on its applicability as only a small fraction of Europe's seas are fully mapped and increasing knowledge and application raise further issues to be resolved.

Several other habitat classification systems use substrate as a primary factor in classifying marine habitats such as the national Marine Habitat Classification for Britain and Ireland (McBreen et al., 2008), as well as a multitude of Acoustic Habitat Classification systems (Gleason et al., 2008; de Juan et al., 2013). Remote sensing techniques such as multi-beam echo-sounding and side-scan sonar combined with ground-truthing techniques such as sediment grabs and dredging can be used to create detailed habitat maps (JNCC, 2018). The current Marine Habitat Classification for Britain and Ireland (Connor *et al* 2004) describes seabed habitats from the intertidal zone down to depths of 200m.

Another global marine classification system is the Marine Ecoregions of the World (MEOW). MEOW is the first global biogeographic classification of the world’s coasts and shelves. It was developed by an international team of conservation organisations, academic institutes and intergovernmental organisations (Spalding et al., 2007). The current MEOW classification focuses on coast and shelf areas and does not include realms in pelagic or deep benthic environments below 200m. Their methods were based on existing global and regional literature. For example, an important systematic approach aimed mainly at pelagic systems, is the two-tier system devised by Longhurst (1998), which focuses on biomes and biogeochemical provinces. These subdivisions were based on a detailed array of oceanographic factors using a large global databased of chlorophyll profiles (biological samples) (Spalding et al., 2007).

These classifications are always in the process of adding new information and levels to their system hierarchies. The importance of biological data to test bioregionalisations based on surrogate variables is a good step to completing the picture on habitat mapping.

South African National Habitat Classification

At a national scale, South African ecosystem classification is conducted as part of the National Biodiversity Assessment (NBA) led by the South African National Biodiversity Institute (SANBI), every five years. South Africa's first national marine assessment, which included the first marine habitat classification, was conducted by Lombard et al. (2004).

Four distinct broad-scale biogeographic provinces are currently recognised for the South African marine environment. These are the (1) cold temperate Namaqua Province; (2) the warm temperate Agulhas Province; (3) the sub-tropical Natal Province; and (4) Delagoa Province (Bustamante and Branch, 1996; Lombard et al., 2004; Spalding et al., 2007).

Lombard et al. (2004) used biogeographic literature, expert knowledge and a bathymetric data set as part of the Marine National Spatial Biodiversity Assessment. In 2011, Sink et al. (2012) further developed the Lombard et al. (2004) assessment and classified 136 marine and coastal ecosystem types grouped into 14 broad ecoregions (Sink et al., 2012). The NBA 2011 marine habitat classification was developed using biogeographic literature and data-informed expert knowledge. Inshore and offshore benthic habitat types were mapped using existing data sets for wave exposure, geological features and grain size (Sink et al., 2012) with boundaries being developed from expert opinion informed by biodiversity pattern data. The marine classification also incorporates key drivers such as benthic-pelagic connectivity, substrate, depth and slope (Sink et al., 2012). Depth data were updated using the General Bathymetric Chart of the Oceans (GEBCO) global data set in 2009 (Sink et al., 2012).

Unconsolidated sediments in inshore and offshore regions were mapped using the Marine Geoscience (1986) texture map (Dingle et al., 1987). Ecosystem types were classified into three main groups based on the stability of substrate namely, consolidated (rocky, reefs and hard ground), unconsolidated (sandy, muddy, gravel and mixed sediments) and additional mixed categories. In both inshore and offshore regions maps of reefs, hard grounds and other consolidated features, such as seamounts, submarine canyons and banks were used to demarcate rocky habitat types (Sink et al., 2012).

Based on the above, Figure 1 shows the offshore NBA marine classification system (divided into ecoregions) and the study area for this project.

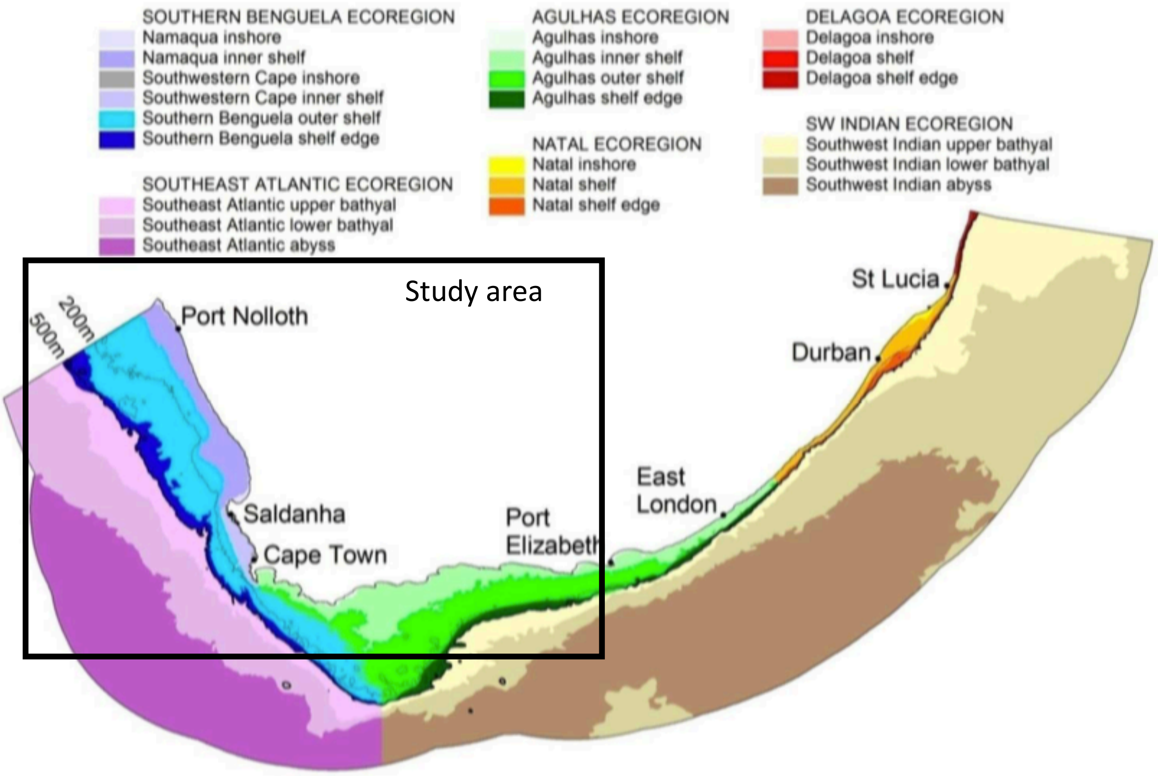


Figure 1: The South African coastal and marine offshore ecoregions derived through the National Biodiversity Assessment 2012 (Sink et al. 2012). The black box demarcates the survey area of relevance to this study

The NBA marine classification system aids in supporting management strategies, environmental impact assessments and MSP. MSP is the planning process that unites multiple users of the ocean (industries, government and recreation) to formulate informed and consistent decisions about how to use marine resources sustainably (Douvere, 2008; Baker et al., 2012). MSP uses maps to create a comprehensive picture of marine areas to identify what natural resources and habitats exist in the ocean (Harris et al., 2008; Baker et al., 2012). The NBA marine classification maps identify ecosystem types in the South African Exclusive Economic Zone (EEZ) and are used to support the implementation of MSP and MPAs*.*

In South Africa, information on the distribution of deep sea benthos is largely limited to taxa such as crustaceans and fish that are readily identified or play a significant role in macrofaunal communities (Griffiths et al., 2010). Similar to global findings, studies in South Africa also revealed demersal and benthic community types vary with depth. These studies have been conducted as follows: Roel (1987) found that species composition of demersal fish on the west coast of South Africa is predominantly influenced by depth with a significant change in species composition occurring at a depth of 385 ±45m (i.e. on the continental shelf slope). Depth was also found to influence a change in size structure of the fish community on the south coast (Yemane et al., 2007). The results of the study indicated that there had been a change in the size structure of fish community demonstrated by the existence of three distinct communities delineated by depth (<100 m, 100-200 m and >200 m).

Atkinson et al. (2010) and Steffani et al. (2015) studied infauna on the west coast. Steffani et al., found infauna were dominated by polychaetes and peracarid crustaceans. The fauna is dominated by species that enjoy a widespread regional and global distribution and is characterised by relatively low diversity,

A study conducted by Lange & Griffiths (2014) on the west coast of South Africa on epifauna from one demersal research survey found a coarse sampling resolution and overlap between biological communities. Foundational information to support accurate species identification was very limited during the 2007 survey reported on by Lange & Griffiths (2014). Since then, substantial investment in invertebrate collection and taxonomy during surveys has greatly improved species information (Atkinson & Sink, 2018). Their study used only three bioregions (Agulhas, Southern Benguela and Southeast Atlantic) because Lombard et al. (2004) assumed that marine biota become progressively more homogenous from the intertidal to the abyssal zones, based on decreasing water temperature. Samples from their study were not collected shallower than 80m or deeper than 700m, hence they did not cover all ecoregions identified by Sink et al. (2012) (Fig.1). Six epifaunal communities were identified using multivariate analyses, with depth being the major factor determining benthic distribution patterns. The results from the study found that epifauna were heterogeneous and diverse, with a slight overlap between communities. Other studies have typically surveyed isolated transects which specifically identified depth-delineated changes in a limited spatial context (Field, 1971; Christie, 1976).

Past studies have also detected a trend of increasing species richness along the coast from west to east (Awad et al., 2002; Griffiths et al., 2010). The South African coast is largely influenced by the Benguela upwelling system (west coast) and the south-flowing Agulhas current (east coast) (Lutjeharms et al., 2001; Lutjeharms, 2007). Endemicity is thought to be higher along the south coast compared to the west coast (Griffiths et al., 2010; Griffiths & Robinson, 2016). The Benguela upwelling system is amongst the most productive in the world where biomass is generally high and diversity is low (Steffani et al., 2015; Fréon et al., 2009) which could be a reason for low diversity at the west coast in comparison to the south coast. Further analysis between these two regions could be useful to highlight areas of species overlap and provide new information for protected areas (Awad et al., 2002).

Owing to a lack of biological data it is challenging to map fine-scale habitats such as fluvial and and deep sea sediments (Sink et al., 2012). To improve the resolution of the 2012 NBA marine habitat map, there needs to be fine-scale systemic mapping of offshore unconsolidated sediments in South Africa, specifically of muds and gravels. Given the current status of knowledge on the extent and distribution of benthic marine communities in South African waters (Griffiths et al., 2010), further surveys and assessment of the species composition in diverse offshore habitats would serve to improve delineation of future habitat classification (Shears et al., 2004; Buhl-Mortensen et al., 2015). Improved maps of benthic habitats could support towards representative offshore ecosystem protection.

The current study provides biodiversity information about some ecosystem types (unconsolidated, sandy and mixed mainly offshore) across the west and south coast of South Africa. The survey area for this study stretches from the Orange river mouth in the north-west to Port Alfred in the south-east and from 30 m to 800 m depth. The west coast is categorized mainly by Southern Benguela, Namaqua and Southeast Atlantic upper Bathyal ecoregions and the south coast mainly by Southwest Indian upper Bathyal and Agulhas ecoregions.

The aim of this study was to determine patterns in benthic epifaunal assemblages on the west and south coast offshore regions of South Africa. This study included a spatial (west vs south) and temporal (2011 vs 2017) scale to analyse how epibenthic communities may differ over time and space. The spatial component compared the west and south coast regions of South Africa. The temporal component analysed epifauna datasets from the year 2011 and the year 2017. In addition to this, an area of overlap was investigated to assess whether species distributions overlap between the west and south coast. Furthermore, this study investigated whether the benthic epifaunal biotopes detected, align with the existing national benthic habitat map (Sink et al. 2012). The results from this study will provide insight on the distribution of benthic epifauna in the western and southern offshore region of South Africa.

The key questions addressed in this study are:

1. What patterns are detected in benthic epifaunal assemblages and what are the characteristic and distinguishing species of defined epifaunal biotopes?
2. Do epifauna differ significantly between the west and south coast (spatial)?
3. Do epifauna differ significantly between 2011 and 2017 on the west coast (temporal)?
4. Do the identified benthic epifaunal biotopes align with the existing National classification for benthic ecosystem types?

Table 1 contains a list of specific terminology that is applied throughout this thesis.

Table 1. A list of key definitions that are used in this study (adapted from the lexicon of biodiversity of South Africa (SANBI, 2016))

Term	Definition
Epifauna	Organisms, mainly invertebrates that live on the bottom of the ocean or attached to other organisms or submerged rocks (Christian et al., 2010)
Community	Assemblage of two or more different species occupying the same geographical area

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 study are defined primarily on biodiversity pattern data (i.e. their biota) which are assumed to reflect abiotic or physical characteristics
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 e.g. Agulhas sandy outer shelf
Habitat Type	Refers to a physical environment occupied by species, assemblages and biotopes (a culmination of biotopes and ecosystem)

2. Methods and Materials

2.1 Study Area & Sampling

This study analyses epifaunal abundance data that was provided by the Department of Agriculture, Forestry and Fishery (DAFF) during the 2011 and 2017 annual research trawl surveys conducted on the research vessel, FRS *Africana*. The details of the surveys are highlighted in the following section.

The surveys were conducted on the west and south coast offshore regions of South Africa, spanning from the South African border with Namibia (29°12’ S, 15°91’ E) to Port Alfred (33°80’ S, 26°71’ E, Fig. 2). The DAFF surveys define their stations as being either west or south, with stations surveyed west of Cape Agulhas (20° east line of longitude) being classified as 'west' and those east of Cape Agulhas being classified as 'south’. Sampled stations were plotted to show spatial coverage using QGIS version 2.18.14 (QGIS, 2009).

A spatial analysis was conducted on stations surveyed on the west and south coasts in 2011 while stations surveyed on the west coast in 2011 and 2017 were analysed for temporal changes.

The west coast surveys (2011 and 2017) were conducted during summer months (January to February) whilst the south coast survey (2011) was conducted during autumn months (April to May). On the west coast, 120 stations were sampled in 2011 and 124 stations in 2017, while 103 stations were sampled on the south coast in 2011. The stations trawled were selected using a randomly stratified survey design that targets five depth zones, spanning from 36 m to 850 m, and aims to sample the same density of stations within each depth zone (i.e. homogenous sampling across the shelf, Atkinson et al., 2011). Trawl duration at each station was standardised to 30-minute bottom tows. The trawl gear used by the *Africana* was a four-panel 180 ft. German otter trawl, 9m sweeps and 1.5 t Morgere multipurpose otter boards. The door spread was 60-75 m, mouth opening 3-4 m vertical and 20-29 m horizontal (Atkinson et al., 2011).

Once the trawl net was retrieved on deck, all epibenthic fauna retained in the trawl net (including the wings of the net) were sorted to the lowest possible taxonomic level. The swept area for each trawl was calculated using the equation: *Swept area = (tow speed x duration/60) x (mouth width/1852)*. The calculated swept area (provided by DAFF) was used to standardise species per square nautical mile using the equation below.

$$\text{Standardised abundance} = \frac{\text{Abundance (number of individuals)} \times 1\ \text{nm}^2}{\text{Swept area (nm}^2\text{)}}$$

The trawl surveys do not target hard grounds due to such habitat being likely to damage the research trawl gear, however, species that are known to occur on hard grounds do occasionally feature in the catch and were recorded and included in this study.

Depth was recorded at each station using a conductivity, temperature and depth profiler (CTD). The relationship between depth and a plethora of benthic species is well documented (Buhl-Mortensen et al., 2010; Ansari et al., 2011; de Juan et al., 2013) and for the purposes of this study, stations were classified into 100 m depth intervals for the overall comparison. The depth categories start from 36 m because this was the shallowest station in the dataset (not zero).

Ecosystem types were noted for each of the stations as per the 2012 National Biodiversity Assessment marine benthic ecosystem classification (Fig.1) (Sink et al., 2012) for later validation analyses.

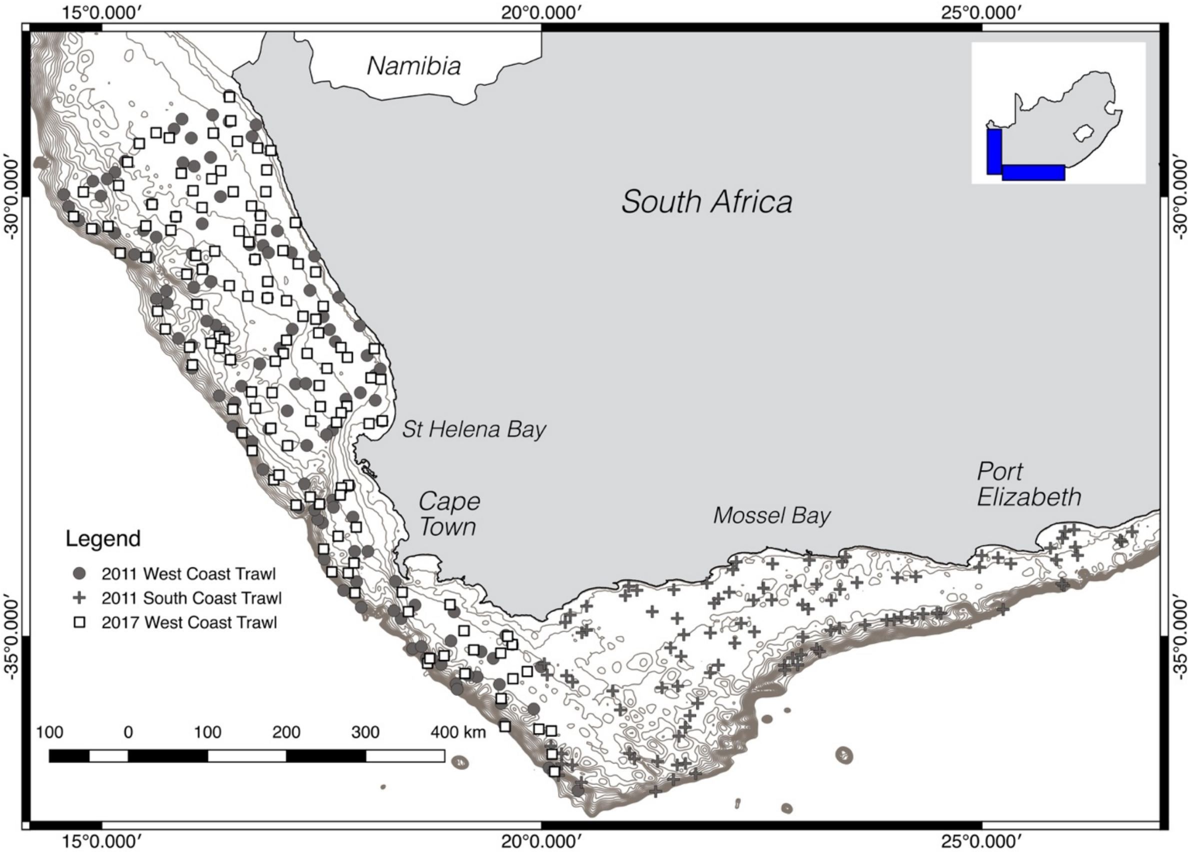


Figure 2: Stations surveyed along the west (•) and south (+) coast of South Africa during the demersal trawl research surveys of 2011 (n=223) and along the west coast (□) during the 2017 survey (n=124)

2.2 Data & Multivariate Statistical Analyses

2.2.1 Spatial Analysis

2.2.2 Overall Dataset

Spatial analysis was conducted using the 2011 epifaunal data provided by DAFF from the west and south coast research trawl surveys, initially combined to test for significant differences between west and south. Subsequent analyses were conducted

separately on west and south coast regions. Total abundance and biomass of each species were recorded for each station and standardised to numbers per square nautical mile (nm^2). The total number of species per phyla was summed and compared between the west and south coasts. Species accumulation plots were compiled to assess whether adequate numbers of stations (replicates) were sampled in each region using non-parametric species estimates. Three species estimators were used; Chao1 and Chao2 (richness estimator), Jackknife 1 (first-order richness estimator) and Bootstrap richness estimator (Ugland et al., 2003; Yurkov et al., 2011). Sobs curve was also included, which estimates observed richness (number of species in the sample). Chao1 is an incidence based estimator, where it relies on the number of unique individuals and duplicates (species found in only one and two samples) to estimate the number of missing species (Chao, 1984; Yurkov et al., 2011). The first-order Jackknife richness estimator additionally relies on the number of species only found once (Yurkov et al., 2011). Following Chao2 for the west coast and Chao1 for the south coast, asymptotes indicate adequate sampling (Ugland et al., 2003).
Univariate analyses, (total number of species (S), total number of individuals (N) and Shannon's diversity index (H')) were calculated for each region. This diversity index takes into account species diversity and evenness (how evenly species are distributed throughout stations) (Magurran, 2004). The index (H') increases as both species richness and evenness of a community increase, typically ranging from 0 to 4.

Multivariate analysis software PRIMER-E version 6 and PERMANOVA+ (Clarke & Gorley, 2006; Anderson et al., 2008) was used to analyse epifaunal abundance and biomass data. Biomass and abundance data were fourth-root transformed, to prevent highly abundant species masking the effect of less abundant species (Field et al., 1982). A Bray-Curtis resemblance measure was used to generate a resemblance matrix of epifaunal abundances between stations (this reduces the effect of dominant values). A non-metric multidimensional scaling (nMDS) plot was constructed to visually represent the spatial relationship among samples in a two-dimensional plane. A PERMANOVA (semi-parametric permutational multivariate analysis of variance) was used to test for significant differences between the west and south coast regions in 100m depth bins. This was performed using the permutation model parameters of residuals under a reduced model and a Type III sum of squares. A SIMPER (similarity percentage breakdown) analysis was performed on the transformed data to determine the similarity (or dissimilarity) in species occurring on the west and south coast and to identify the characteristic and distinguishing species from each region.

2.2.3 Separate West and South Coast analyses

Taking into account the significant regional results of the combined dataset analysis, further multivariate analyses were conducted separately on west and south coast data. From here the west coast data was analysed in 100m depth bins and 50m depth bins for the south coast. The corresponding National Biodiversity Assessment ecosystem type was assigned as a factor to each trawl station by overlaying the stations on the national habitat classification map in *Google Earth Pro* (Google Earth Pro, 2018).

A Bray-Curtis resemblance measure was used to generate a resemblance matrix of epifaunal abundances between stations from each region (this reduces the effect of dominant values). A non-metric multidimensional scaling (nMDS) plot was constructed to visually represent the depth relationship among samples in a two-dimensional plane.

A two-way PERMANOVA tested for significant differences among ecosystem types and each 100 m-depth category for west coast and 50 m-depth category for south coast. Pairwise PERMANOVA tests were then carried out among each depth and ecosystem type combination where feasible. The model parameters used were an unrestricted permutation of residuals under a reduced model and a Type III sum of squares. Monte Carlo permutation values were included in the pairwise tests to account for smaller sample sizes in the sparsely sampled deeper depth categories. A SIMPER analysis was also conducted for species characterising ecosystem types sampled as per reported in table nine and 15.

A group average linkage cluster analysis was conducted including a SIMPROF analysis to test for significant differences among the resulting clusters (associations were random). To explore the resulting west and south coast biotopes, only ecosystem types that had 10 or more replicate trawl stations were included. Ecosystem types that had fewer than 10 replicate trawls in that ecosystem type were considered too sparsely surveyed for inclusion. In this study communities derived from the SIMPROF analysis (significant branching at $p < 0.05$) will be referred to as biotopes. As per the definition (Table 1), a biotope required more than two stations in a cluster to be classified as such.

Biotopes identified from the cluster analysis for the west and south coast data were overlaid on the national biodiversity habitat classification (Sink et al., 2012) to spatially visualise location of stations grouped into the different biotopes. Habitat types classified from the national habitat classification (Sink et al., 2012) are to referred to as ecosystem types (Table 1).

Lastly, a SIMPER (similarity percentage breakdown) analysis was performed on the transformed data to identify the epifaunal species that characterise or distinguish the ecosystem types and spatially defined biotopes, as identified in the cluster (SIMPROF).

2.2.4 Overlap Area Analysis

For practical purposes, the DAFF demersal research surveys define the regions 'west' and 'south' as either side of the 20°E line of longitude however, biodiversity is unlikely to adhere to such definitive delineations. To test for natural breaks (differences) in the epifaunal communities as one moves from the west coast to the south coast, a subset of stations was selected from Cape Point to Mossel Bay irrespective of depth and whether they were labelled 'west' or 'south' in the data set. With this subset of data, a group average linkage cluster analysis was carried out with a SIMPROF (similar profile test) to test for biotopes arising from this 'overlap' area. The stations, classified into the biotopes were then overlaid on the national habitat classification map (Sink et al., 2012) and compared to biotopes from similar, separate west and south coast analyses (section 2.2.3).

2.2.5 Temporal Analysis

To assess for changes in epifauna over time, a temporal analysis was conducted analysing west coast epifauna data from 2011 and 2017. Total abundance of each species were recorded for each station and converted to abundance per nm^2. Univariate analyses were conducted for each year and species accumulation plots calculated to assess whether sufficient number of stations had been sampled in each year (following Chao1 curve).

Using multivariate analyses, an nMDS plot was constructed to display the spatial distribution of stations between the years and depth. A two-way PERMANOVA (semi-parametric permutation analysis of variance) was used to test for significant differences between depth and year. This was performed using a Bray-Curtis similarity matrix with permutation of residuals under a reduced model and a Type III sum of squares. Pairwise PERMANOVA tests were run for depth and year to determine where the depth categories were significant. The model parameters used were an unrestricted permutation of residuals under a reduced model and a Type III sum of squares. Monte Carlo permutation values were included in the pairwise tests to account for smaller sample sizes in the sparsely sampled deeper depth categories.
A SIMPER (similarity percentage breakdown) analysis was performed on the transformed data to determine which epifaunal species were key to differences observed between the two years. The SIMPER analysis was used to identify distinguishing and characteristic species for the identified epifaunal biotope types (Clarke, 1993). This was done for each depth category to determine which species were present or absent at different depth categories in the two years analysed.

3. Results

3.1 Spatial analysis

3.1.1 Overall Dataset

A total of 243 species (west and south coast) was recorded in the 2011 dataset. Epifauna species belonging to 11 phyla were obtained; Annelida, Arthropoda, Brachiopoda, Bryozoa, Chordata, Cnidaria, Echinodermata, Mollusca, Hemichordata, Porifera and Sipuncula. The four most diverse phyla were Arthropoda, Echinodermata, Mollusca and Cnidaria. Figure 3 illustrates the distribution of phyla across both regions.

A total of 241 836 epifauna individuals, weighing 9010 kg, was recorded for the west and south coast surveys in 2011. On average, the west coast yielded a greater number of epifaunal individuals than the south coast (n = 71 per west coast compared to n = 40 per south coast station, Fig.4). There were also a greater number of species occurring on the west coast (16) in comparison to the south coast (11), per station.

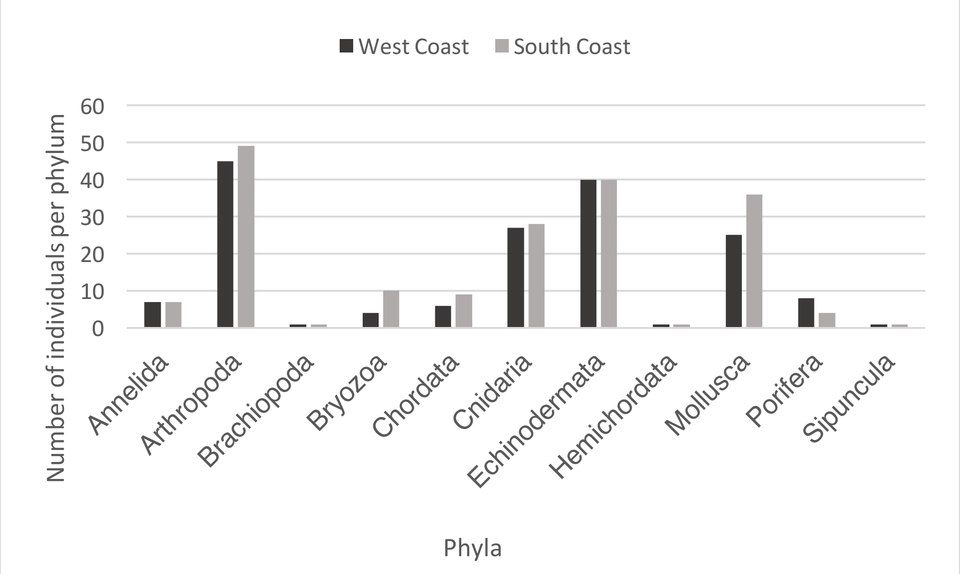


Figure 3: Bar graph displaying epifaunal abundance categorised per phylum on the west and south coast of South Africa during the demersal research trawl surveys conducted in 2011

Athropoda are the most abundant phyla, followed by Echinodermata and then Mollusca. Overall, Annelida and Echinodermata are equal across the two regions. The south coast yielded more species belonging to the Mollusca, Arthropoda, Bryozoan, Cnidaria and Chordata phyla than the west coast. However, the west coast yielded double the number of (eight species in comparison to four) Porifera compared to the south coast. Hemichordata, Brachiopoda and Sipuncula were the least common phyla in both regions.

Shannon's diversity index (H’) was marginally higher on the west coast (H’=2.56) in comparison to the south coast (H’=2.23).

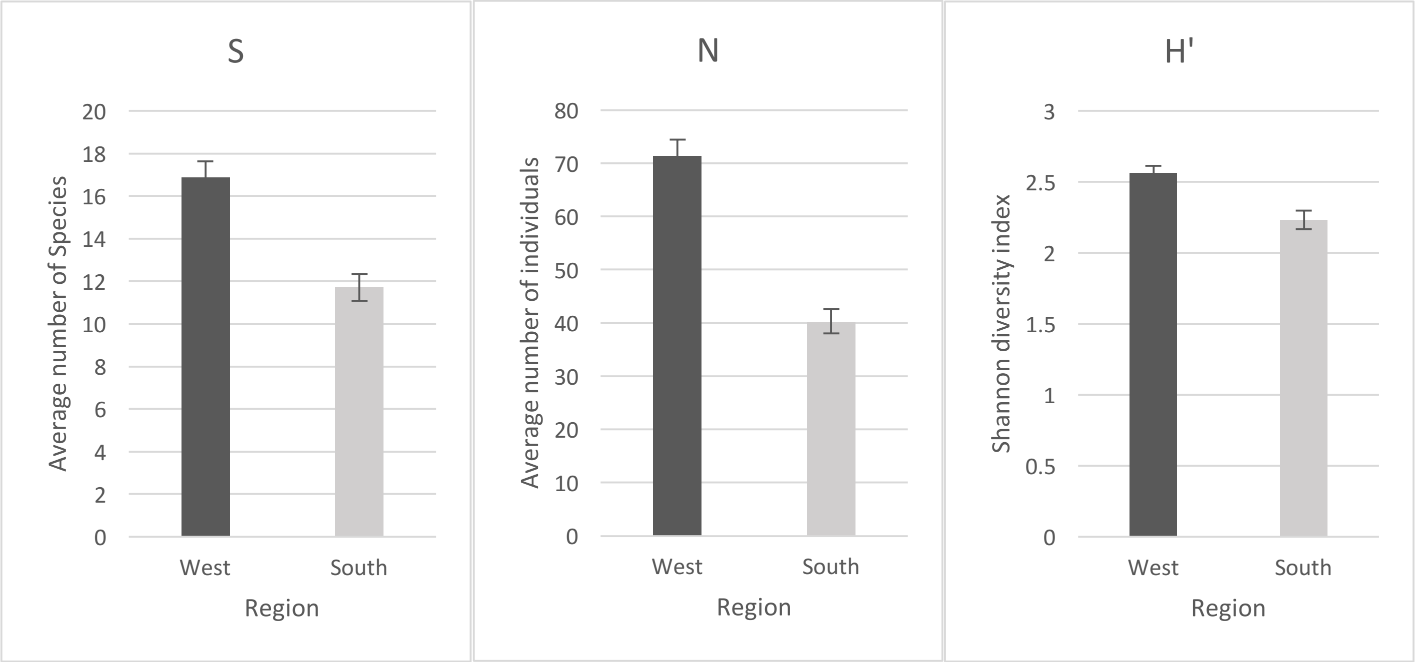
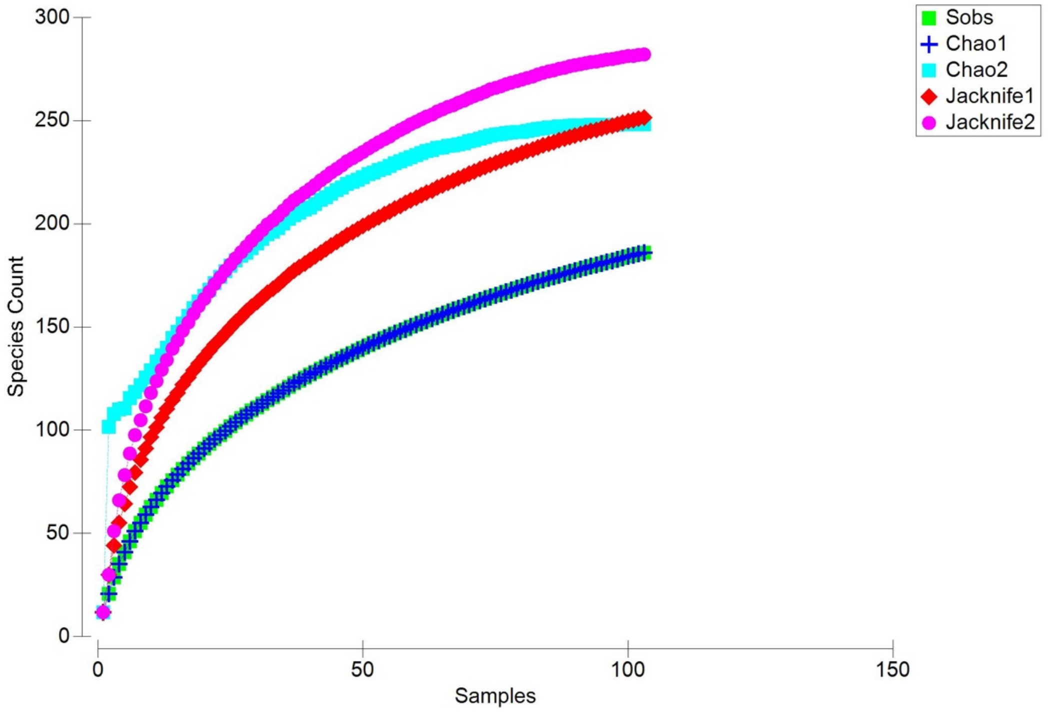


Figure 4: Number of species per station (S), number of individuals per station (N) and Shannon's diversity index (H') for west (n = 120) and south (n = 103) coast epifauna. H' = 1.5 can be used as an example of low diversity and H' =3.5 for high diversity

Species accumulation curves for the west coast (Fig.5a) reached asymptotes after approximately 100 samples indicating that epibenthic assemblages were well sampled in this region. The chao2 curve for the west coast (Fig.5a) reaches a distinct asymptote. Although the species accumulation curves required more samples to reach asymptotes on the south coast, they do nonetheless plateau after approximately 110 samples, indicating sufficient sampling in the region for epifaunal representation. The chao1 curve starts to gradually plateau for the south coast (Fig.5b).

(a)



(b)

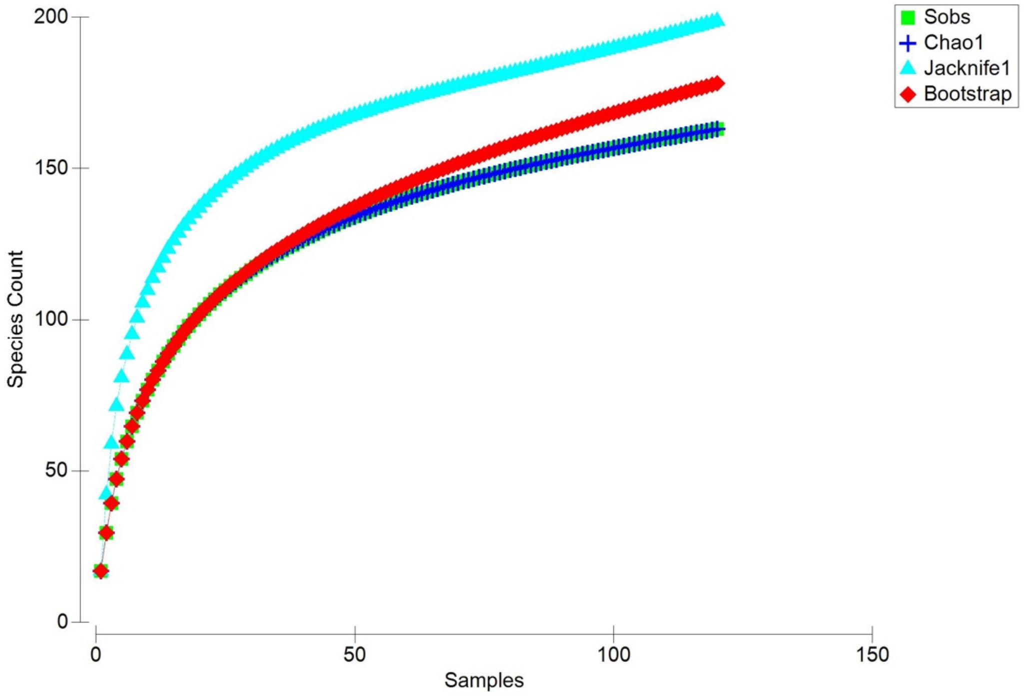
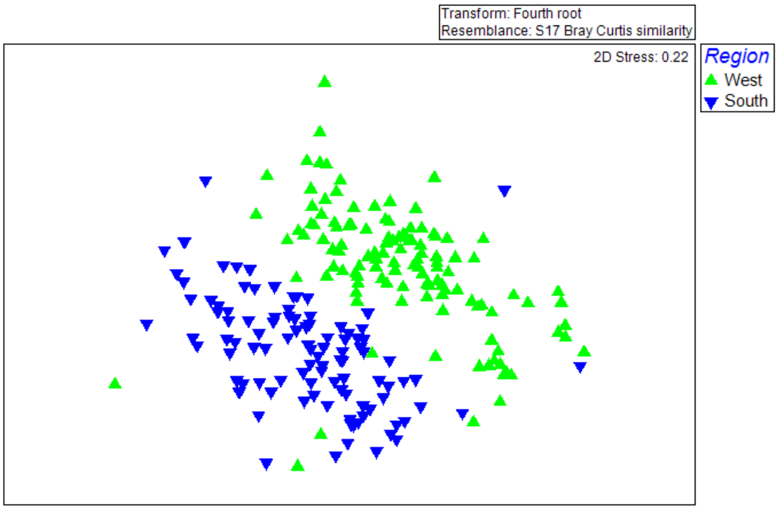


Figure 5(a & b): Species accumulation curves for a) the west coast epifauna (n = 120), and b) south coast epifauna (n = 103). Species estimators used are Sobs (estimates number of species in sample, i.e. observed richness), Chao1 (incidence based estimator), Jacknife1 (first *order richness estimator) and Bootstrap richness estimator. Refer to section 2.2.2 for detailed explanation*

Epifaunal biomass for the 2011 west and south coast surveys combined are shown on an nMDS plot (Fig.6a) illustrating a clear separation between west and south coast assemblages. In Figure 6(a), there was an area where stations from the two regions closely meet, indicating some potential overlap between epibenthic assemblages. The same plot is shown in Figure 6(b) with depth categories illustrated, showing a clear delineation by depth moving from left (shallow) to right (deep), again with a clear separation between regions. There was a change in species assemblages from shallow to deep on both the west and south coasts.

(a)



(b)

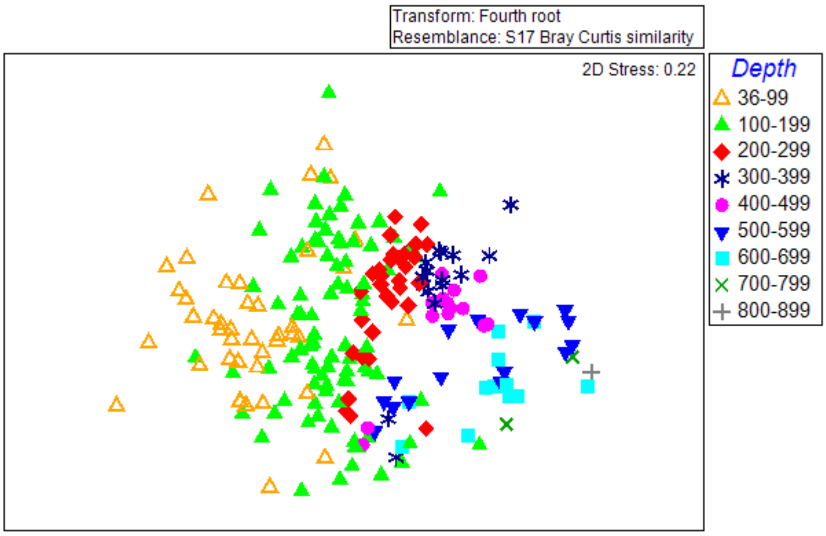


Figure 6(a): Non-metric multidimensional scaling (nMDS) ordination of epifaunal assemblages for west and south coasts at each station sampled. (b): Non-metric multidimensional scaling (nMDS) ordination of epifaunal assemblages for west and south coast regions demarcated in 100m depth intervals at each station sampled.

There was a defined separation between each of the depth categories (Fig.6b), however there was a point where 200-299 m and 100-199 m cluster together which could indicate overlap between communities around these depth zones. This potential overlap zone was investigated in section 3.1.4 to further explore any species overlap between these two regions.

The PERMANOVA analyses investigating the difference between depth and region (west vs. south) found a highly significant difference (Pseudo-F= 3.2616 P(perm)<0.001) between the two groups, (Table 2).

*Table 2. PERMANOVA analysis testing the effects of region and depth and their interaction on epifaunal abundance on west and south coast combined (De = depth and Re = region) * indicates a significant difference at p < 0.05. This shows that each region and depth has a statistically significant difference in epifaunal abundance.*

Source	**Df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Region	1	29437	294.37	11.42	0.0001*	9920
Depth	12	1.1766	9805.2	3.8041	0.0001*	9716
Re x De	6	50441	8406.8	3.2616	0.0001*	9790
Res	203	8406.8	2577.5			
Total	222	2577.5				

The results from Table 2 indicated that epifaunal communities were significantly different on the west and south coast, and differed among the depth categories.
The SIMPER results shown in Table 3 and 4 display the characteristic species for the west and south coast, respectively. A SIMPER analysis showed the most dominant species on the west coast was the dimorphic hermit crab, *Sympagurus dimorphus*, contributed 11% to the average abundance, followed by the pelagic jellyfish, *Pelagia noctiluca* (8.28 %) and the mantis shrimp *Pteryogosquilla capensis* (7.25 %, Table 3). *Pelagia noctiluca* was the most dominant species on the south coast, followed by two additional pelagic species, Salps and jellyfish *Chrysaora agulhensis,* contributing 49% to the average abundance (Table 3).

Table 3. SIMPER results for the top five characteristic species for the west coast with the average abundance and percentage contribution

Species	**Average Abundance (per nm^2)**	**Contribution (%)**
Sympagurus dimorphus	5.72	11.02
Pelagia noctiluca	2.59	8.28
Pterygosquilla capensis	3.18	7.25
Exodromidia spinosa	2.1	5.74
Pseudarchaster tessellatus	1.84	5.21

The characteristic species for the west coast were mostly made up of Arthropods, while Cnidarians (*Pelagia noctiluca, Chrysaora agulhensis* and *Hydrozoa spp.)* are characteristic on the south coast.

Table 4. SIMPER results for the top five characteristic species for the south coast providing the average abundance and contribution

Species	**Average Abundance (per nm^2)**	**Contribution (%)**
Pelagia noctiluca	2.76	20.82
Salpa spp.	2.62	18.91
Chrysaora agulhensis	1.69	9.3
Luidia sarsii africana	1.49	6.48
Hydrozoa spp.	1.25	5.64

A SIMPER analysis comparing the epifaunal species distinguishing the west and south coast revealed that the hermit crab, *S. dimorphus*, mantis shrimp *Pterygosquilla capensis*, urchin *Brissopsis lyrifera capensis*, crab *Exodromidia spinosa*, starfish *Pseudarchaster tessellatus*, crab *Chaecon chuni* and starfish *Psilaster acuminatus* all occurred in greater abundance on the west coast (Fig.7). Species that were distinguishing on the south coast were jellyfish *Pelagia noctiluca* and *Chrysaora agulhensis*, salps and the sea slug *Plurobranchia bubala*. The SIMPER results found an average dissimilarity between west and south coast of 90.65% (3.5% similarity). A summary for species that are absent on the West and South Coast can be found in the appendix section 8.1.

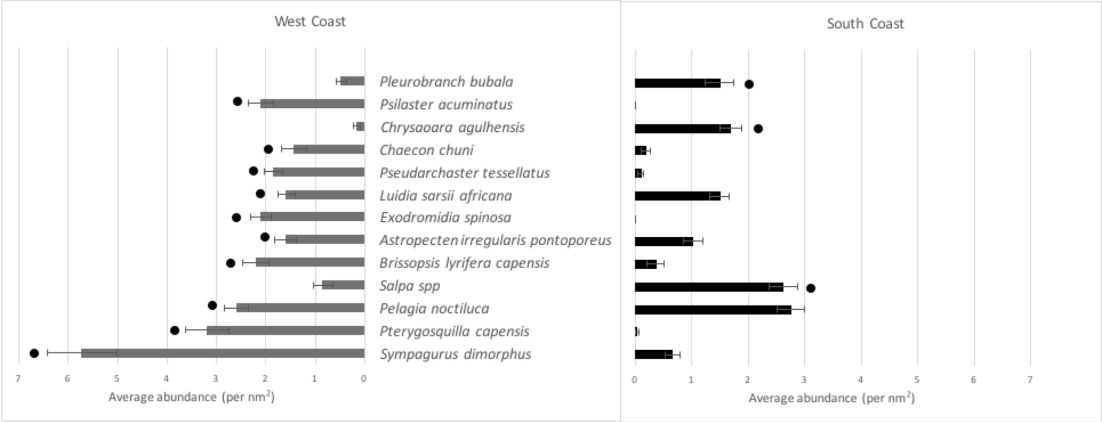


Figure 7: Histogram showing the average abundance of distinguishing species for West versus south coast based on SIMPER results. The average abundance of species that contribute up to 50% of the cumulative distribution (±SE)) of epifaunal data by square root transformation (x axis represents the average abundance (per nm^2) are shown. The black dots indicate the region where the species was more abundant.

As shown in Figure 7, *P. capensis, E. spinosa* and *P. acuminatus, S. dimorphus*, *B. lyrifera capensis* and *C. chuni* were all present on the west coast but were either absent or had a low average abundance (< 1) on the south coast.

The significant difference detected between epifaunal biomass on the west and south coasts ($p < 0.0001$, Pseudo-F = 3.2616, d.f =1, Table 2) supported further analyses of community patterns in each region independently.

3.1.2 West Coast

An nMDS plot of west coast epifauna clearly depicted a separation across the 100 m depth categories (Fig.8) with the most distinct separation appearing between 200-299 m and 300-399 m depth categories.

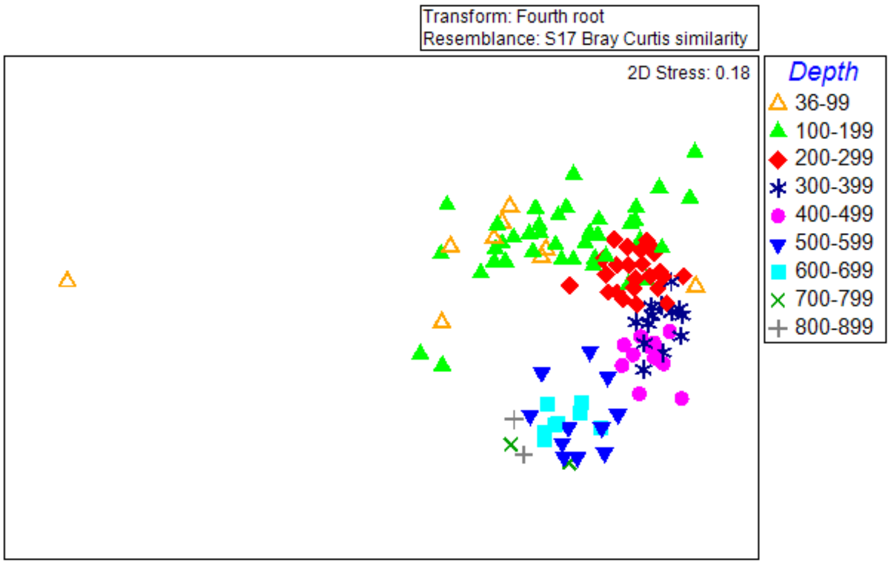


Figure 8: nMDS of epifaunal biomass on the west coast displaying depth categories in 100m intervals, based on Bray-Curtis resemblance after 4th root transformation

Results from the two-way PERMANOVA analysis for the west coast data with depth (De) and ecosystem type (Ec) as factors showed each factor to be significantly different, however there was no significant interaction effect between depth categories and ecosystem type (Table 5).

*Table 5. Two-way PERMANOVA for west coast data with factors depth and ecosystem type (De = depth and Ec = ecosystem type) *indicates significant difference at $p < 0.05$*

Source	**d.f**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Depth	8	50561	6320.1	3.6217	0.0001*	9839
Ec	12	49175	4097.9	2.3483	0.0001*	9832
DexEc	5	10810	2162.1	1.239	0.1227	9876
Res	94	1.64E+05	1745.1			
Total	119	3.72E+05				

Although the interaction effect between depth category and ecosystem type was not significant it was nonetheless deemed useful to further explore for any significant differences between specific depth categories and ecosystem types using a pairwise PERMANOVA. This analysis employed Monte Carlo permutation (P(MC)) p values, which take into account the low number of permutations (< 100) possible due to the relatively low sample size, specifically for the deeper categories.

- Depth category comparisons within South Atlantic Upper Bathyal

Results from pairwise depth category comparisons within the South Atlantic Upper Bathyal indicated significant differences in epifauna between six depth categories (Table 6). The only significant difference in consecutive depth category was detected between 400-499 m and 500-599 m (p=0.0192, Pseudo-t = 1.5756, permutations = 120). All remaining comparisons between consecutive depth categories were not significantly different (Table 6).

Table 6. Pairwise interactions for each depth category combination within the South Atlantic Upper Bathyal. Values highlighted in bold indicate a statistically significant difference at p < 0.05 between these groups. P(MC) indicates Monte Carlo p-values. Groups were only considered significant if the P(MC) < 0.05 to account for low permutations

Depth (m)	t	P(perm)	perms	P(MC)
500-599, 600-699	1.147	0.1965	5080	0.2461
500-599, 400-499*	**1.5756**	**0.0192**	**120**	**0.0452**
500-599, 800-899*	**1.6094**	**0.0263**	**36**	**0.0431**
500-599, 700-799	1.4471	0.0272	36	0.0964
500-599, 300-399	1.2217	0.2476	8	0.229
600-699, 400-499*	**2.1482**	**0.0063**	**165**	**0.0025**
600-699, 800-899	1.5573	0.022	45	0.0558
600-699, 700-799	1.1344	0.2944	45	0.2825
600-699, 300-399*	**1.7152**	**0.1171**	**9**	**0.0257**
400-499, 800-899*	**2.2658**	**0.1039**	**10**	**0.036**
400-499, 700-799*	**2.2383**	**0.0971**	**10**	**0.0369**
400-499, 300-399	0.85367	0.7544	4	0.5613
800-899, 700-799	1.0058	0.6749	3	0.4458
800-899, 300-399	2.2696	0.3318	3	0.187
700-799, 300-399	2.3082	0.3343	3	0.1895

As would be expected, depth categories that involved comparison between very deep with shallow have significantly different epifauna. For example, epifaunal communities were significantly different at 500-599 m compared with 800-899 m and at 400-499 m compared with 800-899 m. Comparisons that had less than 10 permutations were considered statistically weak tests.

- Depth category comparisons within Southern Benguela Sandy Outer Shelf

Within the Southern Benguela Sandy Outer Shelf, four out of six of the interactions were statistically significant. When comparing the depth group 300-399 m and 36-99 m the P(perm) value obtained is < 0.05 indicating a significant difference, however, the low permutations possible (35) suggest the non-significant Monte Carlo p-value to be more appropriate. The P(MC) value is 0.059, which is on the border of being non-significant and could indicate that there are nonetheless some differences between epifaunal communities between these two depth categories.

Table 7. A pairwise interaction between Southern Benguela Sandy Outer Shelf and interacting depth groups. Values highlighted in bold indicate a statistically significant difference at p < 0.05 between these groups. P(MC) indicates Monte Carlo p-values

Depth (m)	t	P(perm)	perms	P(MC)
100-199, 200-299	**2.2775**	**0.0001**	**9922**	**0.0001**
100-199, 300-399	**2.1135**	**0.0004**	**6432**	**0.0006**
100-199, 36-99	1.0538	0.3276	1763	0.3508
200-299, 300-399	**1.9481**	**0.0002**	**5964**	**0.0012**
200-299, 36-99	**1.495**	**0.0149**	**1536**	**0.0306**
300-399, 36-99	1.6457	0.0271	35	0.0593

In the Southern Benguela Sandy Outer Shelf there was no statistical difference between 100-199 m and 36-99 m (p = 0.3) indicating that similar epifauna species occur from inshore up to 199 m. The significant differences in epifaunal communities between the depth categories 100-199 m and 200-299 m (p = 0.0001) and between 200-299 m and 300-399 m, however, indicate significantly different epifauna occur in these different depth zones.

- Depth category comparisons within Southern Benguela Sandy Shelf Edge

Pairwise tests among depth categories in the Southern Benguela Sandy Shelf Edge indicated a significantly different epifaunal community in the 500-599 m depth category (Table 8). Epifauna among other depth categories of 200-299 m, 300-399 m and 400-499 m were not significantly different in this ecosystem type.

Table 8. A pairwise interaction between Southern Benguela Sandy Shelf Edge and interacting depth groups. Values highlighted in bold indicate a statistically significant difference at p < 0.05 between these groups for P(MC). P(MC) indicates Monte Carlo p-values

Depth (m)	t	P(perm)	perms	P(MC)
500-599, 200-299	**1.9204**	**0.07**	**15**	**0.0364**
500-599, 400-499	**2.1866**	**0.004**	**210**	**0.0036**
500-599, 300-399	**2.3327**	**0.005**	**209**	**0.0023**
200-299, 400-499	1.569	0.0363	28	0.0577
200-299, 300-399	1.1723	0.1105	28	0.2456
400-499, 300-399	1.1693	0.1494	462	0.2273

The Southern Benguela Sandy Shelf Edge was similar to South Atlantic Upper Bathyal, indicating a significant difference in epifaunal communities between the depth categories of 400-499 m and 500-599 m. For the remaining ecosystem types, namely; Southern Benguela Muddy Outer Shelf, Southern Benguela Hard Shelf Edge, Namaqua Muddy Inner Shelf, and Namaqua Sandy Inner Shelf there were insufficient number of replicates within depth categories to generate statistically meaningful pairwise analyses and these were not further tested.

The SIMPER results summarise the main characteristic species in each ecosystem type. Agulhas Sandy Outer Shelf was spatially classified as a 'south coast' ecosystem type but two stations sampled during a west coast survey lie within this ecosystem type. The mantis shrimp, *Pterygosquilla capensis,* and the sea slug, *Pleurobranch bubala*, have the highest average abundance in the Agulhas Sandy Outer Shelf, contributing 25% of the average abundance. *P. capensis* and *P. bubala* were distinguishing species for the west and south coast respectively which could indicate that this ecosystem type is a likely overlap zone. Other species that characterised the Agulhas Sandy Outer Shelf included a pelagic jellyfish and two starfish species.

The South Atlantic Upper Bathyal is a deep ecosystem type (The Upper Bathyal according to the NBA marine classification, extends from the deeper boundary of the shelf edge zone to the 1800 m depth contour) (Sink et al., 2012).
Species characteristic of this ecosystem include *Chaecon chuni* (crab) with the highest average abundance of 5.54 (Table 9), followed by the anemone, *Actinostola capensis*, and the quill worm *Hyalinoecia tubicola* that were also found in deeper ecosystem of the ocean (up to 1000m, Day, 1968).

Table 9. The average abundance and percentage contribution to similarity for the top five characteristic species per west coast marine ecosystem type. Ecosystem types are based on those mapped and reported in the 2012 National Biodiversity Assessment

Ecosystem type	**Species**	**Average Abundance (per nm^2)**	**Contribution%**
Agulhas Sandy Outer Shelf	*Pterygosquilla capensis*	5.06	25.25
	Pleurobranch bubala	4.91	25.25
	Pelagia noctiluca	3.48	18.46
	Mediaster bairdi capensis	3	15.52
	Toraster tuberculatus	3.23	15.52
South Atlantic Upper Bathyal	*Chaecon chuni*	5.54	21.16
	Actinostola capensis	3.37	11.71
	Hyalinoecia tubicola	4.15	10.4
	Pelagia noctiluca	3.08	7.6
	Plesionika martia	3.53	7.39
Southern Benguela Carbonate Mound	*Sympagurus dimorphus*	6.96	14.77
	Spatangus capensis	4.91	8.78
	Ophiura costata costata	7.97	8.39
	Pelagia noctiluca	3.76	8.17
	Bolocera kerguelensis	4.79	8.17
Southern Benguela Muddy Outer Shelf	*Sympagurus dimorphus*	15.46	33.09
	Brissopsis lyrifera capensis	6.46	16.64
	Pseudarchaster tessellatus	3.36	8.75

	Toraster tuberculatus	3.8	7.98
	Lamellaria/ Coriocella spp.	2.47	5.13
Southern Benguela Sandy Outer Shelf	*Sympagurus dimorphus*	9.98	17.69
	Exodromidia spinosa	3.29	9.06
	Brissopsis lyrifera capensis	3.21	7.9
	Pterygosquilla capensis	3.75	6.27
	Pseudarchaster tessellatus	2.54	6.09
Southern Benguela Sandy Shelf Edge	*Rochinia hertwigi*	4.17	7.01
	Doryhnchus thomsoni	2.89	6.85
	Psilaster acuminatus	3.3	6.29
	Sympagurus dimorphus	3.94	6.07
	Rochinia spp.	2.55	6.03
Southern Benguela Hard Shelf Edge	*Rochinia hertwigi*	7.48	17.31
	Merhippolyte agulhasensis	4.18	10.18
	Sympagurus dimorphus	6.48	7.99
	Actinostola capensis	4.42	7.01
	Mursia cristiata	3.1	6.61
Namaqua Muddy Inner Shelf	*Pterygosquilla capensis*	12.14	40.59
	Cavernularia spp.	7.83	13.09
	Polychaete tubes	3.11	9.44
	Astropecten irregularis pontoporeus	4.24	8.95
	Exodromidia spinosa	3.24	6
Namaqua Sandy Inner Shelf	*Pterygosquilla capensis*	7.3	27.61
	Athleta lutosa	3.48	16.8
	Salpa spp.	3.91	14.57
	Polychaete	3.04	10.23
	Pseudarchaster tessellatus	2.45	9.26

The dimorphic hermit crab, *S. dimorphus*, featured prominently in all five of the Southern Benguela ecosystems (Table 9). These ecosystems mostly support Crustaceans, Echinoderms and Cnidaria. The Southern Benguela Sandy Shelf Edge is characterised by Arthropods (Crustaceans) and an Echinoderm (*P. acuminatus).* The Southern Benguela Hard Shelf Edge and Sandy Shelf Edge both feature the crab *Rochinia hertwigi.*

The two Namaqua ecosystem types had one species in common; *P. capensis* (mantis shrimp) contributing the greatest average abundance in both these ecosystems (Table

9). In the Namaqua Muddy Inner Shelf this species contributes more than 40% of the average abundance and 27% on the Namaqua Sandy Inner Shelf.

- West coast Biotopes

The four west coast ecosystem types that had sufficient (> 10) replicate stations to consider further exploring biotopes were; Namaqua Muddy Inner Shelf, South Atlantic Upper Bathyal, Southern Benguela Sandy Outer Shelf and Southern Benguela Sandy Shelf Edge. A cluster analysis, with SIMPROF for the west coast stations revealed 14 significant biotopes, labelled A to N (Fig.9). A biotope was only considered if three or more stations formed a significant cluster (denoted by a solid black line) resulting in 15 stations not being included in any classified biotope.
The biotopes were spatially plotted on a map using the national habitat classification (NBA) (Sink et al., 2012), shown in Figure 10. The SIMPER analysis displays the top five species characteristic of each biotope identified in the cluster dendrogram with SIMPROF. In the case of biotope 'E' only four species featured in this biotope.

Biotopes A, B and C lay within the South Atlantic Upper Bathyal and all supported the species *C. chuni* (crab) and *Hyalinoecia tubicola* (quill worm). Many species were shared among biotopes A, B and C, however biotope A and C have a wider spatial range than B (Fig.10). Biotopes A, B and C all occur in deep waters (500-800 m). Biotope G also lied within the South Atlantic Upper Bathyal but had a different species composition to that of biotopes A, B and C. The only species in common was *Actinostola capensis* (sea anemone). Stations making up biotope G also lie within the Southern Benguela Sandy Outer Shelf (Fig.10), which could result in the difference in species composition.

Biotope N, consisting of 13 stations (Fig.9) had a wide spatial extent covering much of the west coast. Biotope M and N were located further from each other on the map (Fig.10). The majority of biotope M, with the exception of one station, lie within the inshore, northern portion of ecosystem Southern Benguela Sandy Outer Shelf, while stations making up biotope N are mostly offshore and lie within the same ecosystem and the Southern Benguela Sandy Shelf Edge.

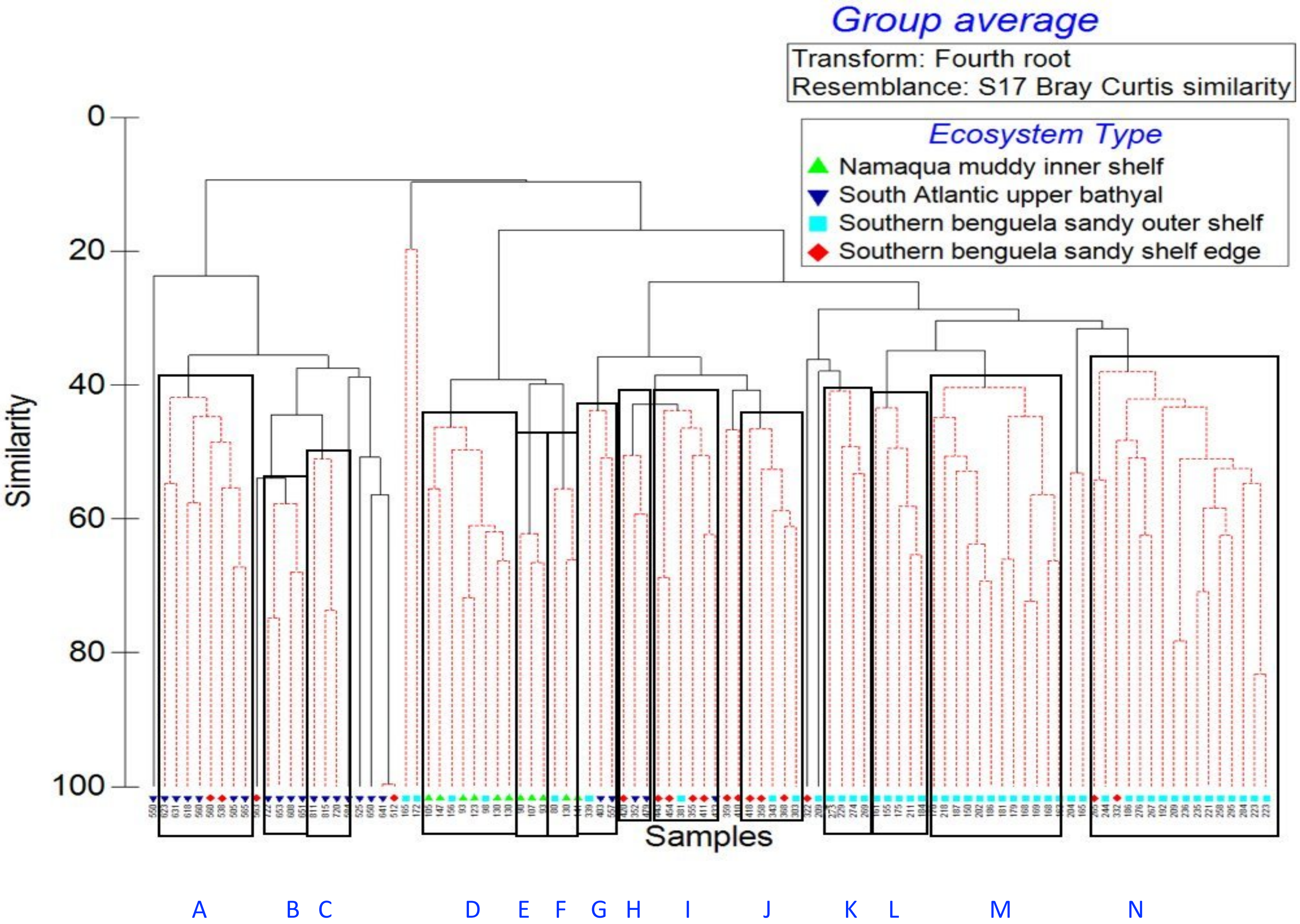


Figure 9: Cluster analysis using group-average linkage (SIMPROF) of ecosystem types that had more than 10 replicates. The x axis depicts symbols corresponding to ecosystem type and actual depth (m). Significant branching is indicated by the black line. Biotopes are labelled A – N

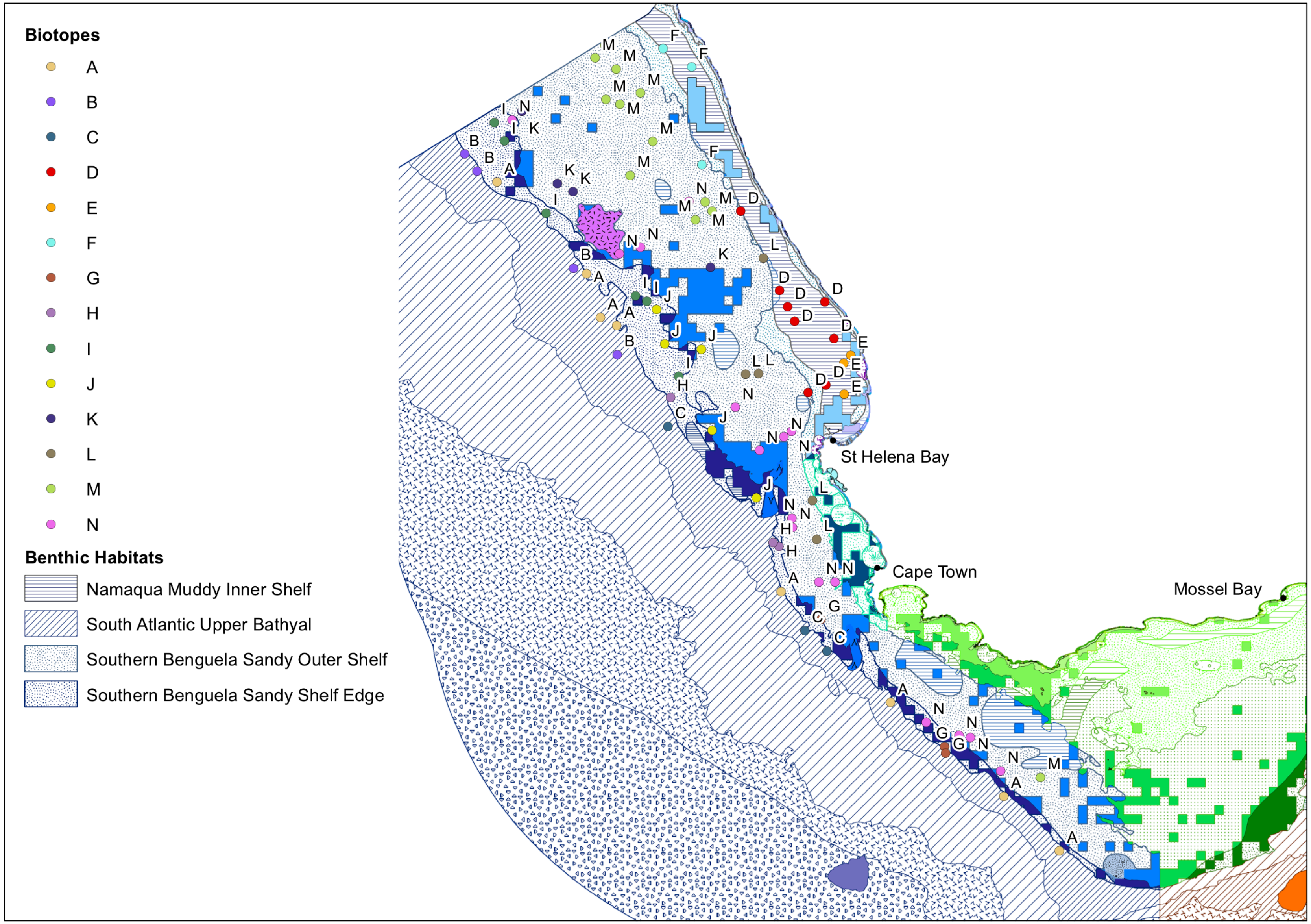


Figure 10: Map of ecosystem types from the National Biodiversity Assessment (Sink et al., 2012) of the west coast showing SIMPROF-derived biotopes A to N and ecosystem types that these biotopes lie within, legend of the map can be found in the page below

Table 10. Percentage species composition of the dominant benthic epifauna defined from the SIMPER analysis for the 14 different biotopes.

Biotope	**Species**	**Average Abundance (per nm^2)**	**Contribution (%)**
A	*Chaecon chuni*	6.91	31.38
	Plesionika martia	6.37	23.34
	Hyalinoecia tubicola	4.44	11.88
	Actinostola capensis	2.65	8.55
	Fusitriton murrayi	2.47	8.27
B	*Hyalinoecia tubicola*	6.84	15.38
	Chaecon chuni	6.78	15.02
	Funchalia woodwardi	5.94	13.84
	Sergia spp.	5.71	10.54
	Actinostola capensis	3.43	7.22
C	*Chaecon chuni*	8.78	23.78
	Aristeus varidens	7.7	20.41
	Pasiphaea spp.	4.47	9.94
	Sergia spp.	5.1	7.31
	Hyalinoecia tubicola	4.62	6.47
D	*Pterygosquilla capensis*	13.69	42.77
	Exodromidia spinosa	5.05	13.91
	Pseudarchaster tessellatus	4.82	13.57
	Astropecten irregularis pontoporeus	4.09	9.29
	Polychaete spp.	2.5	6.31
E	*Cavernularia spp.*	15.92	39.95
	Pterygosquilla capensis	9.58	29.25
	Polychaete spp.	4.73	14.11
	Aequorea spp.	4.85	13.21
F	*Cavernularia spp.*	13.84	23.42
	Pterygosquilla capensis	12.34	19.79
	Astropecten irregularis pontoporeus	7.09	11.73
	Salpa spp.	6.97	10.6
	Macropipus australis	5.21	9.13
G	*Crossaster penicillatus*	7.89	15.25
	Actinostola capensis	6.09	13.4
	Cheiraster hirsutus	3.93	9.89
	Pseudarchaster tessellatus	3.72	9.81

	Rochinia hertwigi	4.09	8.99
H	*Parapagurus bouvieri*	5.87	9.8
	Fusitriton murrayi	4.93	8.04
	Plesionika martia	6.55	7.94
	Rochinia hertwigi	4.47	7.6
	Sympagurus dimorphus	6.36	7.12
I	*Parapagurus bouvieri*	6.8	13.94
	Doryhnchus thomsoni	4.26	8.99
	Luidia sarsii africana	4.03	7.67
	Pelagia noctiluca	3.98	6.42
	Merhippolyte agulhasensis	3.92	6.22
J	*Parapagurus bouvieri*	7.45	8.04
	Sympagurus dimorphus	9.66	7.92
	Ophiura trimeni	5.31	7.24
	Mursia cristiata	4.37	5.35
	Ophiomyxa vivpara capensis	4.17	4.59
K	*Sympagurus dimorphus*	9.47	9.98
	Spatangus capensis	6.26	8.89
	Psilaster acuminatus	8.85	8.24
	Ophiothrix aristulata	4.2	5.51
	Paguridae spp.	3.51	5.15
L	*Pseudarchaster tessellatus*	4.95	12.7
	Exodromidia spinosa	4.94	12.23
	Brissopsis lyrifera capensis	3.51	9.88
	Astropecten irregularis pontoporeus	3.2	9.51
	Pterygosquilla capensis	8.39	9.17
M	*Astropecten irregularis pontoporeus*	5.51	18.24
	Brissopsis lyrifera capensis	5.27	14.32
	Luidia sarsii africana	3.99	11.53
	Pterygosquilla capensis	3.72	8.98
	Exodromidia spinosa	3.02	6.78
N	*Sympagurus dimorphus*	19.85	40.66
	Exodromidia spinosa	4.15	8
	Mursia cristiata	3.39	6.17
	Psilaster acuminatus	3.74	5.05
	Toraster tuberculatus	2.57	3.99

Biotope D spanned the Namaqua Muddy Inner Shelf and the Southern Benguela Sandy Outer Shelf ecosystems and was made up of species characteristic to both these ecosystems (4 out of the top 5 species from the Namaqua Muddy Inner Shelf ecosystem and 3 out of the top 5 species from the Southern Benguela Sandy Outer Shelf ecosystem, Table 10). There appeared to be high epifaunal species overlap between these two ecosystem types. Biotopes E and F both supported abundant populations of the seapens species *Cavernularia spp.* and mantis shrimp *P. capensis*. These two biotopes range from the Orange river mouth to St Helena Bay (Fig.10). Biotope E congregated around St Helena Bay, and could have arisen due to a bay effect. Furthermore, biotopes D, E and F were shallow inshore biotopes that lied within the Namaqua Muddy Inner Shelf and shared many of the same species.

Biotope H occurred within within the Southern Benguela Sandy Shelf Edge. Biotope I and J also consisted of stations mostly within the Southern Benguela Sandy Shelf Edge, (Fig.10) and these biotopes also spanned a wide area but supported similar species (*Parapagurus bouvieri* and *Rochinia hertwigi)* and lie within a similar depth stratum.

Biotopes K, L, M and N all lie within the same ecosystem type, the Southern Benguela Sandy Outer Shelf. Biotope K and L had different characteristic species with *S. dimorphus, Spatangus capensis (urchin) and Ophiothrix aristulata (*brittle star) being present in biotope K while *E. spinosa (crab), P. tessellatus (*starfish) and *B. lyrifera capensis* (urchin) occurred in biotope L.

3.1.3 South Coast

The nMDS plot of south coast epifaunal abundance data did not show a very clear pattern with respect to depth categories. The shallower stations (36-49 m, 50-99 m and 100-149 m) were mostly distributed on the right hand side of the plot (Fig.11), while stations deeper that 150 m clustered more on the left hand side of the plot. There were very few stations representing deeper depth categories (400-650 m) which limits the data interpretation. There were also no stations present in the 250-299 m depth category.

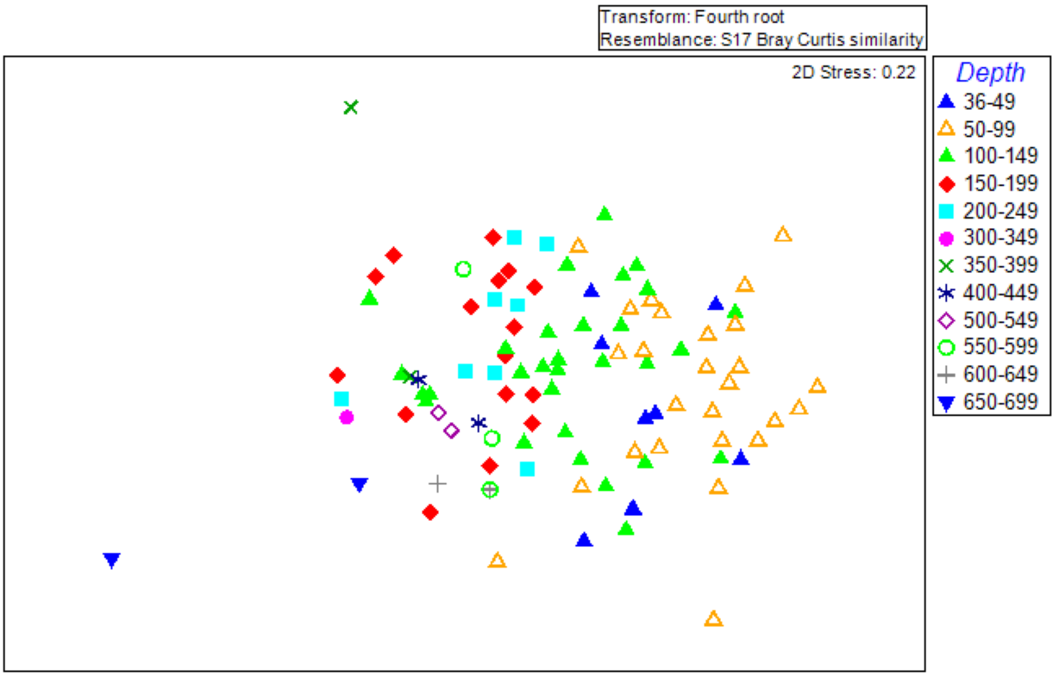


Figure 11: MDS plot of epifauna abundance displaying depth categories in 50 m-intervals on the south coast, based on Bray-Curtis resemblance after 4th root transformation

A two-way semi-parametric PERMANOVA analyses revealed a significant difference in both factors of depth and ecosystem type and a significant interaction effect between the two factors (Table 11). The p(perm) value was close to $p < 0.05$ and therefore could be interpreted as a weakly significant interaction effect.

Table 11. *A PERMANOVA analysis to determine the interaction between depth and ecosystem type (De = depth and Ec = ecosystem type) * indicates a significant interaction at $p < 0.05$*

Source	**Df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Depth	9	30598	3399.7	1.3259	0.0183	9828
Ec	11	41011	3728.2	1.454	0.0015	9768
DexEc**	8	26394	3299.2	1.2867	0.0415	9810
Res	72	1.85E+05	2564.2			
Total	102	3.47E+05				

A pairwise PERMANOVA was carried out to see which depth groups varied significantly in which ecosystem type.

- Depth category comparisons within Agulhas Sandy Outer Shelf

Four depth categories were significantly different in the Agulhas Sandy Outer Shelf (Table 12). Depth categories between 100-149m and 350-399m were classified as significant, which could indicate species variation at this level.

Table 12. *Pairwise interactions for each depth category combination within the Agulhas Sandy Outer Shelf ecosystem type. Values highlighted in bold indicate a statistically significant difference at p < 0.05 between these groups. P(MC) indicates Monte Carlo p-values*

Depth (m)	**t**	**P(perm)**	**Unique perms**	**P(MC)**
100-149, 200-249	1.3669	0.0334	6409	0.0596
100-149, 150-199	**1.6339**	**0.0056**	**9905**	**0.0108**
100-149, 350-399	**1.5868**	**0.0497**	**21**	**0.0175**
100-149, 50-99	1.2842	0.0476	21	0.1191
100-149, 36-49	0.96913	0.4893	231	0.4681
200-249, 150-199	1.1271	0.2174	495	0.2765
200-249, 350-399	1.4861	0.1973	5	0.1513
200-249, 50-99	1.2718	0.2069	5	0.2386
200-249, 36-49	1.3839	0.0672	15	0.1513
150-199, 350-399	1.6157	0.1087	9	0.0506
150-199, 50-99	**1.5045**	**0.1097**	**9**	**0.0748**
150-199, 36-49	**1.6196**	**0.0217**	**45**	**0.0375**
350-399, 36-49	1.9061	0.3344	2	0.2385
50-99, 36-49	1.6807	0.3369	3	0.271

- Depth category comparisons within Southern Benguela Sandy Outer Shelf

Table 13. *Pairwise interactions for each depth category combination within the Southern Benguela Sandy Outer Shelf ecosystem type. Values highlighted in bold indicate a statistically significant difference at p < 0.05 between these groups. P(MC) indicates Monte Carlo p-values*

Depth (m)	**t**	**P(perm)**	**Unique perms**	**P(MC)**
200-249, 150-199	0.85005	1	4	0.5401
150-199, 300-349	0.9238	1	4	0.4932

The Southern Benguela Sandy Outer Shelf is a typical west coast ecosystem, however the few stations sampled in this ecosystem (only four permutations possible), greatly limits any meaningful interpretation. Both categories displayed an insignificant interaction effect.

- Depth category comparisons within Agulhas Sandy Inner Shelf

Table 14. *Pairwise interactions for each depth (m) category combination within the Agulhas Sandy Inner Shelf ecosystem type. Values highlighted in bold indicate a statistically significant difference at p < 0.05 between these groups. P(MC) indicates Monte Carlo p-values*

Depth (m)	**t**	**P(perm)**	**Unique perms**	**P(MC)**
100-149, 50-99	**1.3978**	**0.0244**	**6874**	**0.0488**
100-149, 36-49	1.2564	0.1152	210	0.1679
50-99, 36-49	1.152	0.1723	9751	0.213

Only one depth category had a significant effect (100-149 m and 50-99 m) in the Agulhas Sandy Inner Shelf ecosystem (Table14).

There were not enough depth replicates for the other ecosystem types for further depth category analyses, namely; Agulhas Muddy Inner Shelf, Agulhas Sandy Shelf Edge, Agulhas Hard Shelf Edge, Agulhas hard outer shelf, South Atlantic Upper Bathyal and Southwest Indian Upper Bathyal.

The SIMPER results (Table 15) summarise the main characteristic species in each ecosystem type. The jellyfish species *C. agulhensis* occurred throughout the South Coast ecosystems except for those on the shelf edge (Agulhas Sandy Shelf Edge and Hard Shelf Edge) and in the South Atlantic Upper Bathyal (Table 15). This species contributed most to the average abundance on the Agulhas Sandy Inner Shelf and least in the Agulhas Sandy Outer Shelf. The Agulhas Hard Shelf Edge and Outer Shelf had only two species contributing to this ecosystem as a result of only three and two stations surveyed in these ecosystems, respectively. The Agulhas Inner Shelf (Sandy and Muddy) hosted similar species composition.

Table 15. The average abundance and percentage contribution to similarity for the top five characteristic species per south coast marine ecosystem type. Ecosystem types are based on those mapped and reported in the 2011 National Biodiversity Assessment

Ecosystem type	***Species***	**Average Abundance (per nm^2)**	**Contribution%**
Agulhas Sandy Inner Shelf	*Chrysaora agulhensis*	2.64	37.9
	Pleurobranch bubala	0.91	12.32
	Astropecten irregularis pontoporeus	0.61	7.71
	Astrocladus euryale	0.94	4.97
	Salpa Spp.	0.53	4.61
Agulhas Muddy Inner Shelf	*Chrysaora agulhensis*	2.88	41.07
	Pelagia noctiluca	2.33	53.99
	Nassarius vinctus	2.19	65.67
	Astrocladus euryale	1.49	75.49

	Astropecten irregularis pontoporeus	2.05	83.7
Agulhas Sandy Outer Shelf	*Pelagia noctiluca*	1.53	29.77
	Salpa spp.	0.94	18.54
	Luidia sarsii africana	0.68	7.82
	Jasus lalandii	0.9	6.6
	Chrysaora agulhensis	1.04	6.13
Agulhas Sandy Shelf Edge	*Salpa spp.*	3.67	13.65
	Sympagurus dimorphus	3.23	26.3
	Luida sarsii africana	3.17	38.44
	Cosmasteria felipes	2.49	47.15
	Pelagia noctiluca	2.91	55.2
Agulhas Hard Shelf Edge	*Salpa spp.*	5.3	53.04
	Pelagia noctiluca	3.84	46.96
Agulhas Hard Outer Shelf	*Pelagia noctiluca*	4.35	59.43
	Chrysaora agulhensis	3.41	40.57
South Atlantic Upper Bathyal	*Chaecon chuni*	3.24	48.55
	Plesionika martia	0.92	14.4
	Sergia spp.	1.19	14.4
	Pasiphaea spp.	0.74	12.11
	Acanthephyra pelagica	0.8	10.53
Southwest Indian Upper Bathyal	*Pelagia noctiluca*	4.49	23.3
	Rochinia spp.	4.5	46.13
	Salpa spp.	4.92	65.01
	Chrysaora agulhensis	1.9	69.76
	Mediaster bairdi capensis	1.84	74.51
Southern Benguela Sandy Outer Shelf * (not more than 3 species)	*Sympagurus dimorphus*	0.81	41.24
	Aequorea spp.	1.07	24.78
	Salpa spp.	1.06	24.5

The South Atlantic Upper Bathyal ecosystem was surveyed during both the west and south coast surveys. The crab, *Chaceon chuni* contributed the highest average

species abundance for this habitat. Both *Chaceon chuni* and *Plesionika martia* were present in both west and south coast. *Sergia spp.* and *Acanthephyra pelagica* are deep sea prawns which are characteristic for this ecosystem.
Southern Benguela Muddy Outer Shelf, Southwest Indian Lower Bathyal, Agulhas Hard Inner Shelf and Agulhas Gravel Inner Shelf all had less than 2 samples per group, preventing further SIMPER analyses for characteristic species in these ecosystem types.

- South Coast Biotopes

Only three ecosystem types on the south coast had sufficient (> 10) replicate stations sampled to consider further exploring biotopes, these being Agulhas Sandy Inner Shelf, Agulhas Sandy Outer Shelf and Agulhas Sandy Shelf Edge. The cluster analysis, with SIMPROF, of the south coast epifauna abundance revealed seven biotopes labelled T to Z (Fig.12). A biotope was considered only if three or more stations formed a significant cluster (denoted by a solid black line) resulting in 18 stations not being included in any classified biotope. Table 12 displays the five main species contributing to each biotope. Biotopes were overlaid on the NBA marine classification with respective ecosystem types shown in Figure 13.

Biotopes T, Y and Z consist of stations that predominantly lie within the Agulhas Sandy Outer Shelf. Biotope Y was only made up of only pelagic species whereas biotope T was more mixed consisting of a pelagic species, echinoderms and a mollusc (*Turitella declivis).* Biotope Y and Z are also clustered close together on Figure 14 and have the same species composition, (*Pelagic noctiluca* and *Salpa spp.)* in addition to other species only appearing in biotope Z (Table 16) which could indicate overlap between these two biotopes, potentially forming one larger biotope. In addition to this, biotope Y and T were the only biotopes clustered under the Agulhas Sandy Outer Shelf (Fig.13) whereas the rest of the biotopes were a mix of two ecosystem types.

Biotopes W and Z were the largest biotopes with the widest spatial range (Fig.13) made up of Agulhas Sandy Inner shelf and Agulhas Sandy Outer Shelf respectively. Biotope W was mainly an inshore inner shelf biotope with only two stations located on the outer shelf (Fig.13).

Biotope X consisted mostly of Agulhas Sandy Shelf Edge stations, which were fairly tightly clustered along the shelf edge region south-west of Port Elizabeth (Fig.13). It comprises of a notable west coast species (*Sympagarus dimorphus)* and echinoderms (*Luida sarsii africana* and *Cosmasteria felipes).*

According to Figure 13 Biotope U was mainly an inner shelf biotope with only one station on the outer shelf. The opposite was true for biotope V, where it was mainly an outer shelf biotope with one station on the inner shelf. Similar species between these two biotopes, *Toraster tuberculatus (*starfish) and *Pleurobranch bubala* (sea slug), could be species that lie on the boundary of the inner and outer shelf (Fig.13 and Table 16).

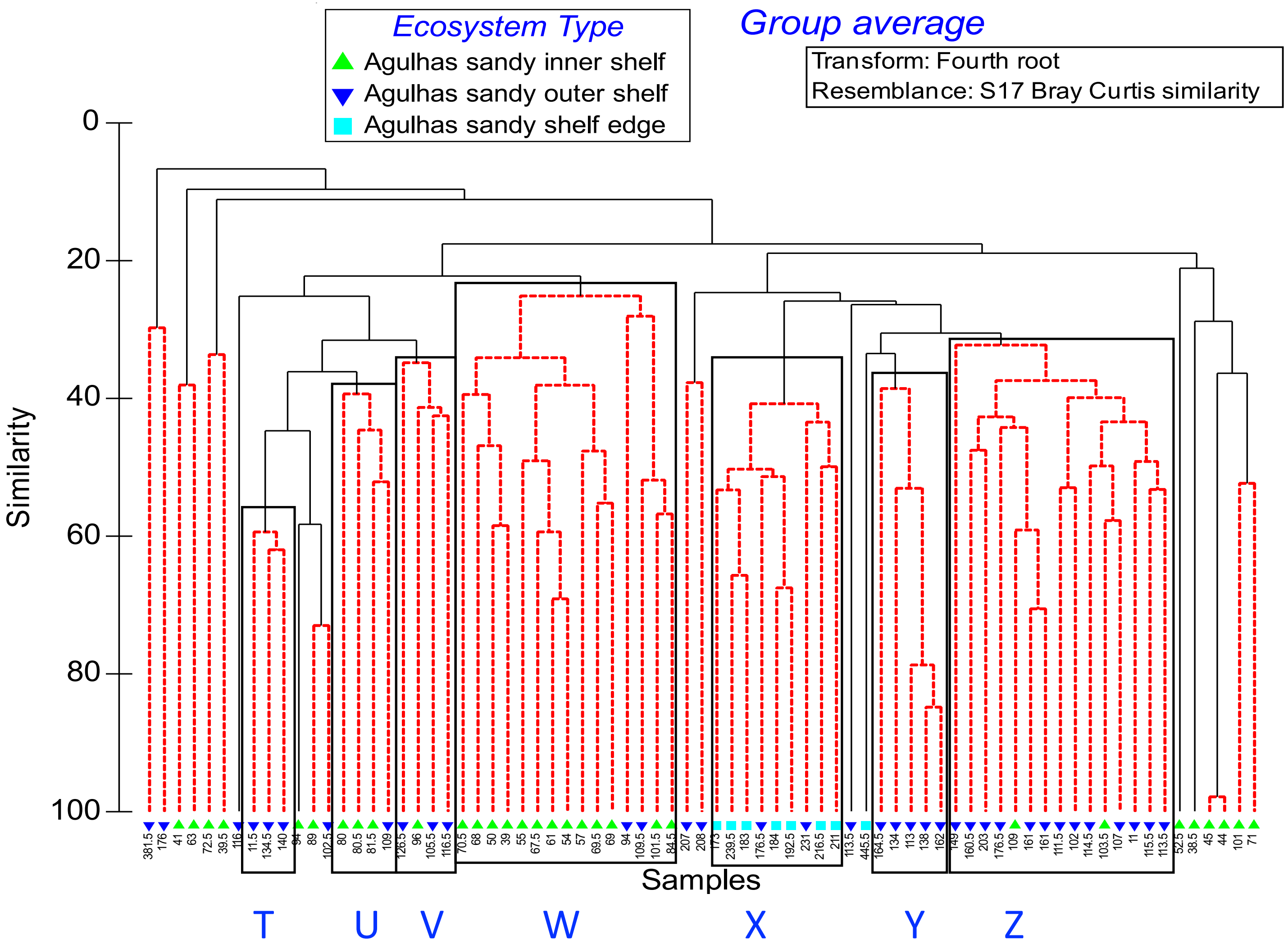


Figure 12: Biotopes (labelled T – Z) defined from epifaunal abundance on the south coast region, which lie within 3 ecosystem types; Agulhas Sandy Inner Shelf, Outer Shelf and Shelf Edge. Symbols indicate ecosystem type and are paired with actual depth (m)

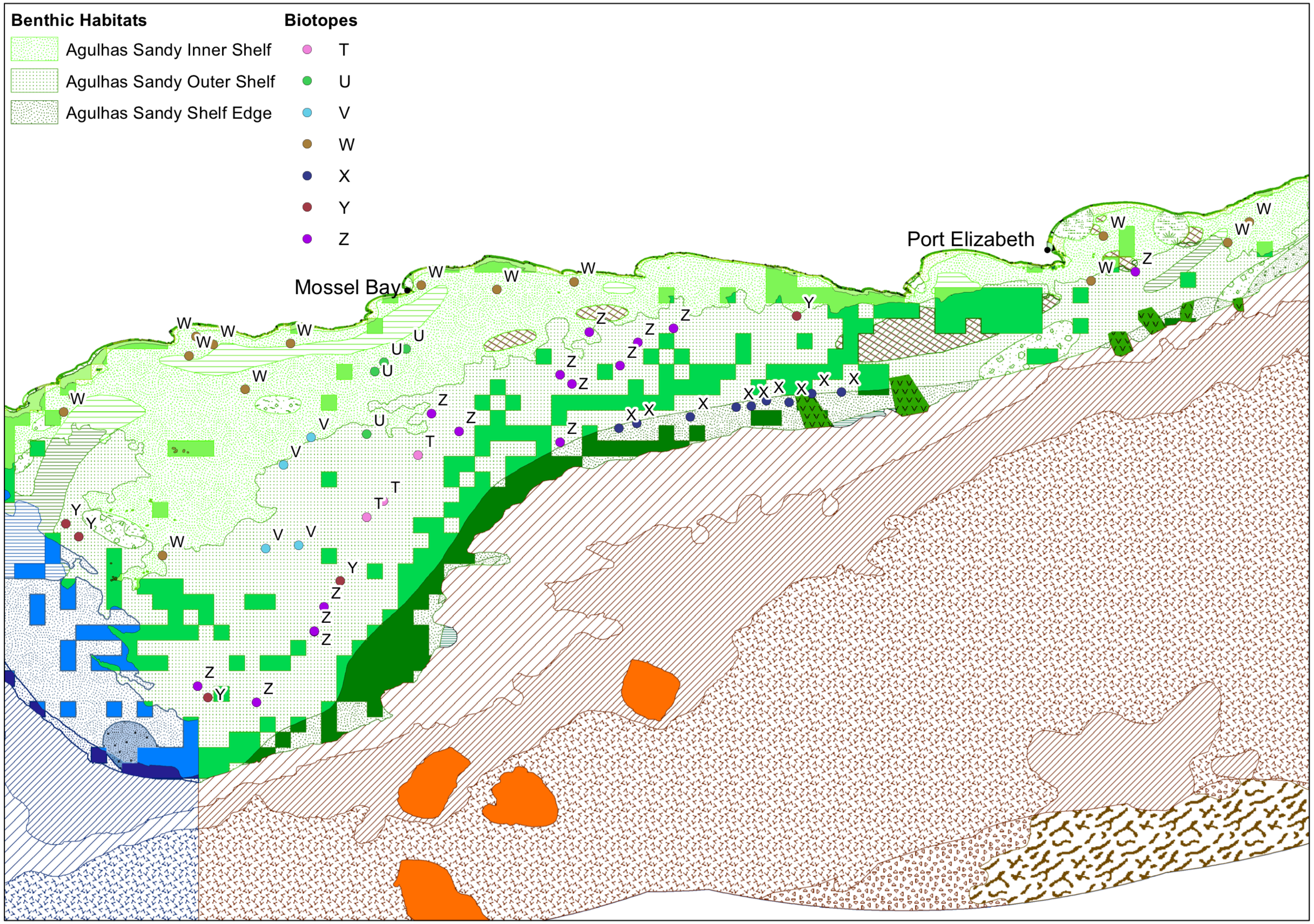


Figure 13: Map of ecosystem types from the National Biodiversity Assessment (Sink et al., 2012) of the south coast containing T to Z biotopes (3 or more stations) defined by SIMPROF and ecosystem types

Table 16. Percentage species composition of the dominant benthic epifauna defined from the SIMPER analysis for the seven different biotopes

Biotope	**Species**	**Average Abundance (per nm^2)**	**Contribution (%)**
T	*Echinus gilchristi*	5.97	13.27
	Spatangus capensis	5.2	9.69
	Turritella declivis	5.14	9.4
	Pelagia noctiluca	4.79	9.17
	Luidia sarsii africana	3.87	7.66
U	*Spatangus capensis*	4.2	12.74
	Pleurobranch bubala	5.27	12.65
	Nassarius speciosus	3.54	11.48
	Toraster tuberculatus	2.87	10.11
	Paguridae spp.	2.87	10.09
V	*Brissopsis lyrifera capensis*	6.34	16.84
	Luidia sarsii africana	3.69	11.88
	Chrysaora agulhensis	3.76	10.57
	Toraster tuberculatus	2.55	6.25
	Pleurobranch bubala	2.68	6.02
W	*Chrysaora agulhensis*	3.97	29.35
	Astropecten irregularis pontoporeus	3.13	16.5
	Pleurobranch bubala	2.25	9.72
	Nassarius speciosus	1.88	8.31
	Hydrozoa spp.	1.87	7.2
X	*Sympagurus dimorphus*	3.64	15.19
	Luidia sarsii africana	3.62	14.79
	Cosmasteria felipes	2.93	11.5
	Salpa spp.	3.13	8.5
	Pelagia noctiluca	2.67	7.19
Y	*Salpa spp.*	4.01	65.76
	Pelagia noctiluca	4.26	34.24
Z	*Salpa spp.*	5.28	32.1
	Pelagia noctiluca	4.44	21.99
	Luidia sarsii africana	2.37	11.1
	Hydrozoa spp.	1.96	8.14
	Chrysaora agulhensis	1.67	5.03

The biotopes defined from the south coast displayed species overlap within similar ecosystem types and could indicate the possible merging of biotopes such as Y and Z.

3.1.4 Overlap Area

The overlap area discussed in section 3.1.1 was investigated here. A subset of stations was selected from Cape Point to Mossel Bay to explore any potential species overlap between the west and south coast. A cluster analysis (using SIMPROF) was run and nine biotopes were identified. In this section the remainder of the stations that did not cluster with more than two stations were considered as potential biotopes. Both biotopes and potential biotopes were overlaid on the national habitat map (Fig.15) from the NBA (Sink et al., 2012). Potential biotope three consisted of ‘south coast’ stations as per the research survey during which it was sampled, but spatially it lies within the west coast ecosystem, South Atlantic Upper Bathyal. Biotope six was made up of three stations that were classified as the west coast but occurred within the south coast Agulhas Sandy Outer Shelf ecosystem type.

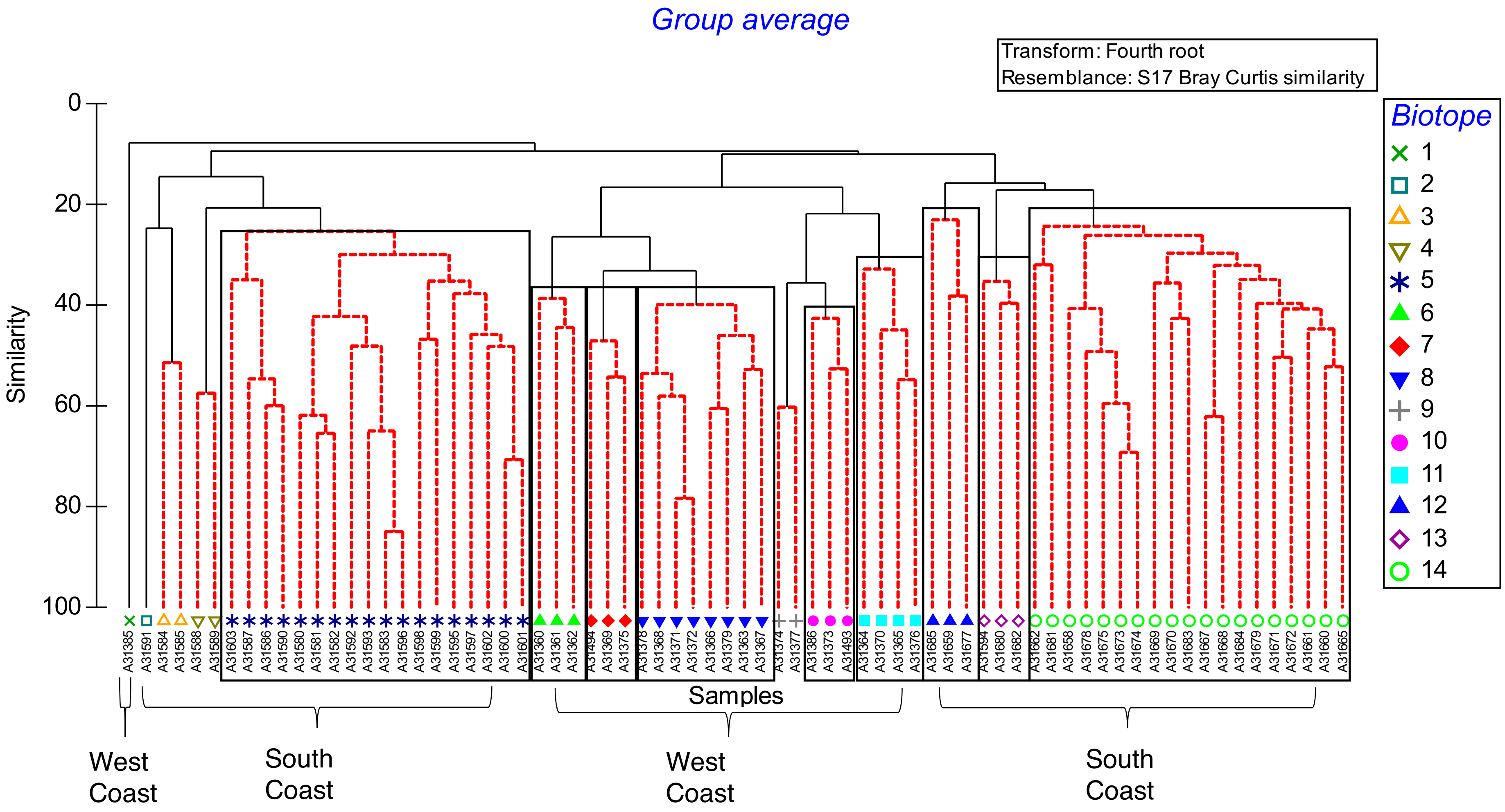


Figure 14: Cluster dendrogram of a subset of epifaunal abundance data which includes stations from Cape Point to Mossel Bay. Symbols indicate biotopes and potential biotopes and stations sampled. The boxes indicate the nine biotopes identified and potential biotopes were left unboxed. Clusters are labelled either west or south coast

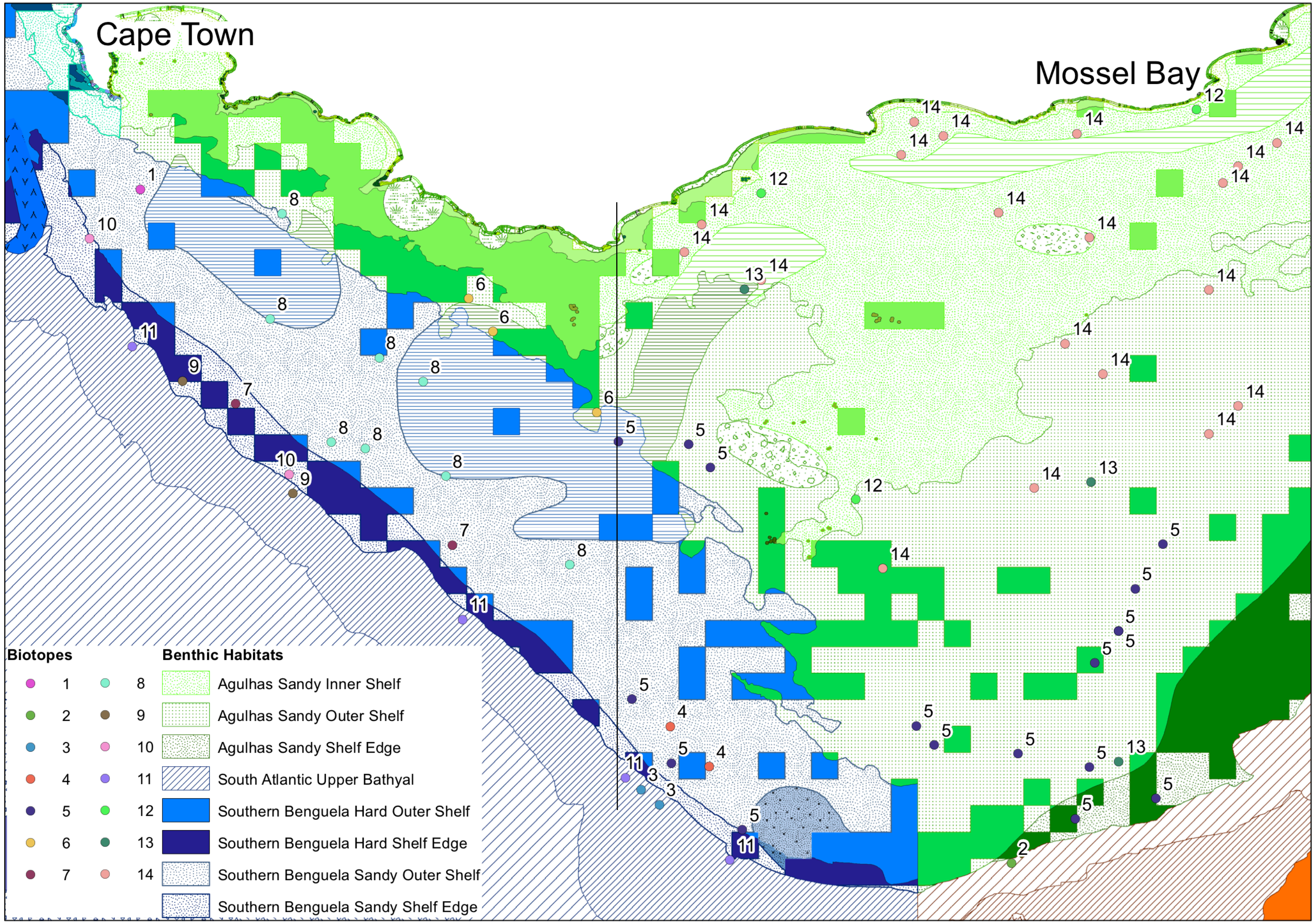


Figure 15: Map of ecosystem types from the NBA (Sink et al., 2012) of the subset stations containing biotopes and potential biotopes labelled 1-14 defined by SIMPROF

Biotope five (Fig.15) could be an extension of biotope Y (Fig.13) from the south coast biotope classification and could comprise of pelagic species that have more mobility than true benthic invertebrates. Biotope five mostly consisted of stations that occurred within south coast ecosystems but also had stations that were present on the west coast (Fig.15). Biotope six lies on the boundary between west and south coast ecosystem types, which is also the case for biotope eight (Fig.15)

3.2 Temporal Analysis

A temporal analysis was conducted to investigate for a change in composition and abundance of epifaunal assemblages on the west coast after a five-year period. Epifaunal abundance recorded during the west coast surveys during 2011 and 2017 were compared.

A total of 125 species was recorded from the 2017 dataset, in comparison to 165 species from the 2011 dataset. *Melithaea cf. spp.* (Colourful Seafan), *Tetilla capilosa* (furry sponge) and *Antho cf. prima* (orange sponge) were omitted from the abundance analysis because only biomass data were available for these species. The most abundant organism for 2017 was *Sympagarus dimorphus* (dimorphic hermit crab), which was the same for 2011. A total of 191 species were analysed for the temporal analysis with 127 species occurring in both years. Approximately 30% of those species were present in 2011 but absent in 2017 (38 species) while 25 species were present in 2017 but absent in 2011. A full list of species absent in both years can be found in appendix section 8.2. The phyla recorded for 2017 were similar to 2011 (Fig.16).

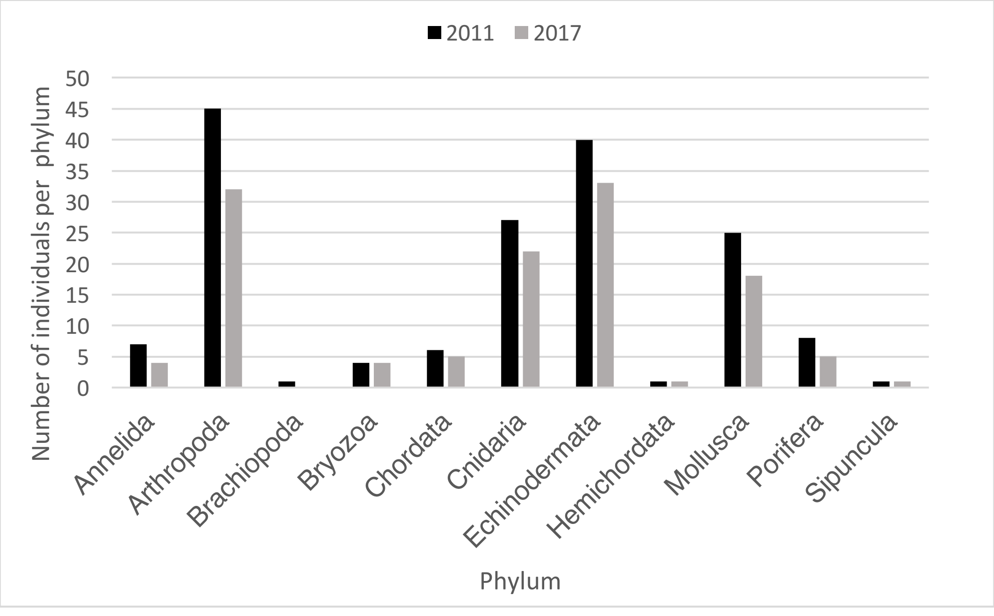


Figure 16: Bar graph displaying phyla distribution for the 2011 and 2017 west coast dataset (n=120 for 2011 and n=124 for 2017). Graph represents the number of individuals per phylum where Athropoda were the most frequent from the year 2011 and Echinodermata for 2017

On average the west coast in 2011 yielded a greater number of epifaunal individuals in comparison to 2017 (n = 71, σ = 3.00 for 2011 n = 50, σ = 1.95 for 2017). There was also a greater average number, of species occurring per station in 2011 (16) compared to 2017 (12), per station.

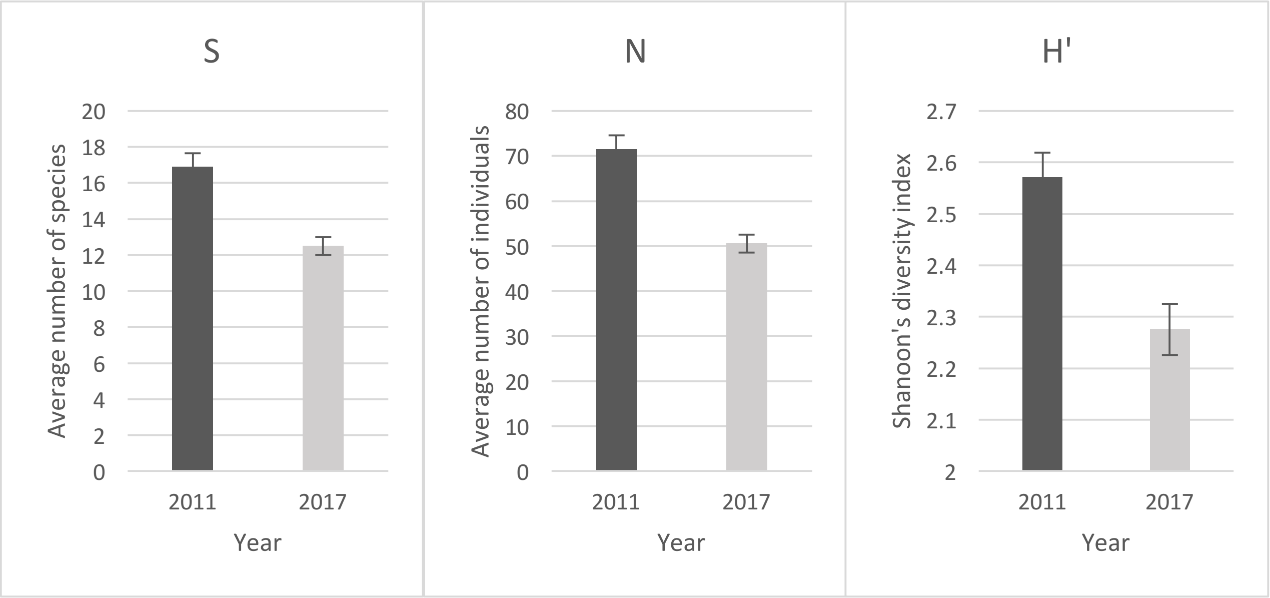


Figure 17: Comparing the average number of species per station (S), average number of individuals (N) and Shannon's diversity index (H') for 2011 and 2017(+- SE) (n=120 for 2011 and n=124 for 2017)

Species accumulation curves for the west coast can be seen on Figure 5(a). The accumulation curves for 2017 reached gradual asymptotes at approximately 75 samples, indicating epibenthic assemblages were adequately sampled in this region (Fig.18).

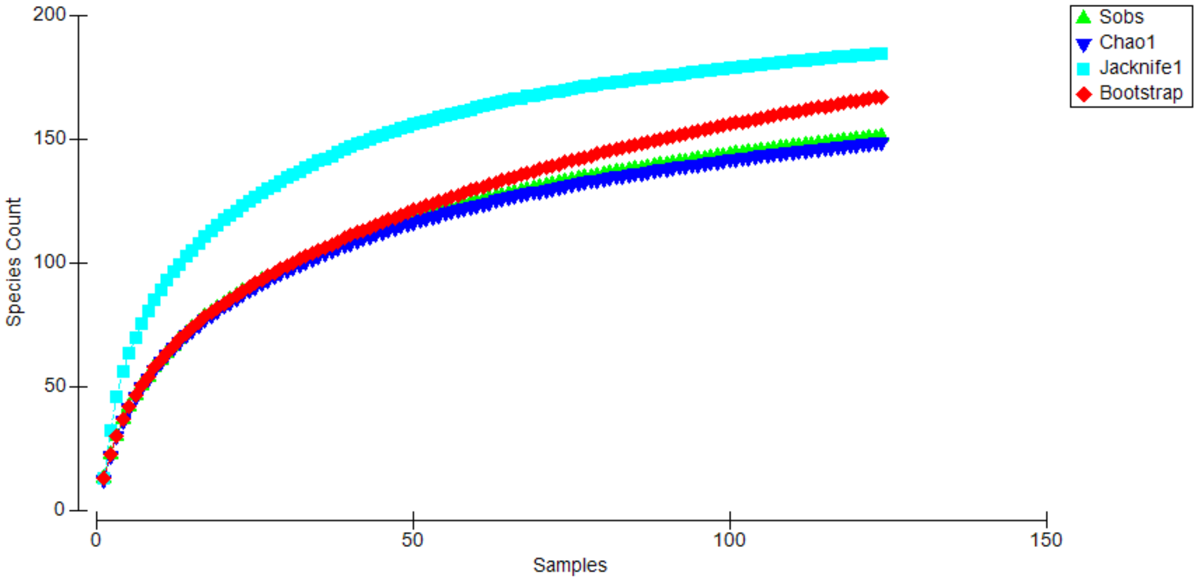
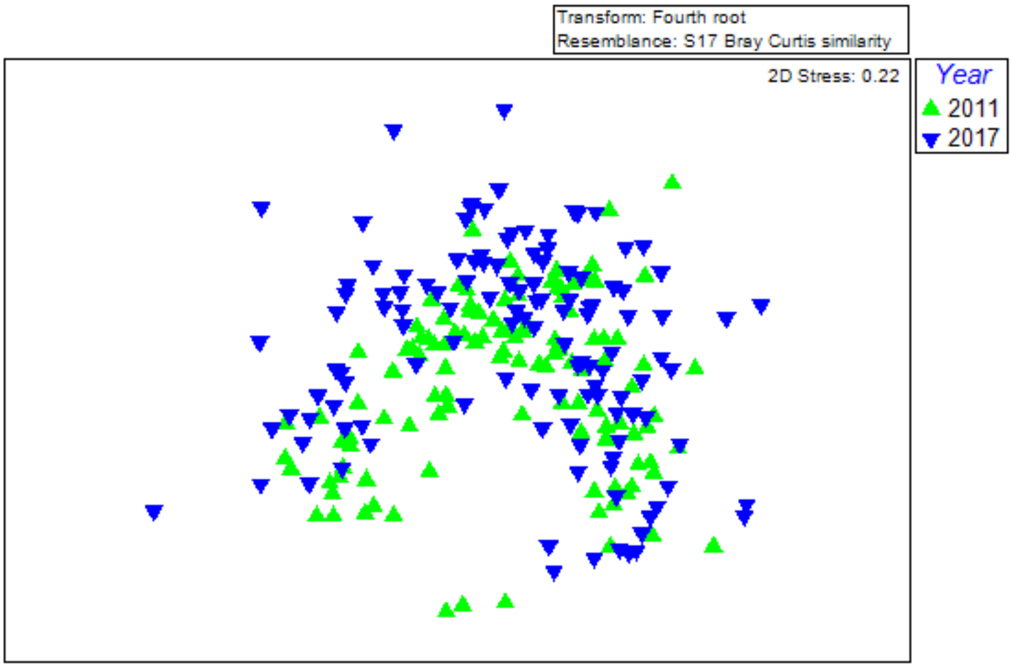


Figure 18: Species accumulation curves for the 2017 epifauna (n=124). Species estimators used are Sobs (estimates number of species in sample, i.e. observed richness), Chao1 (incidence based estimator), Jacknife1(first order richness estimator) and Bootstrap richness estimator. Refer to section 2.2.2 for detailed explanation

Species accumulation curves following chao2 (same as for the west coast 2011 epifauna Fig.5a) reached a clear asymptote.

A nMDS plot of epifaunal abundance in 2011 and 2017 illustrates the spatial variation among species assemblages and year (Fig.19a). A clear pattern of epifaunal distribution with depth categories was illustrated in the same nMDS in Figure 19(b).

(a)



(b)

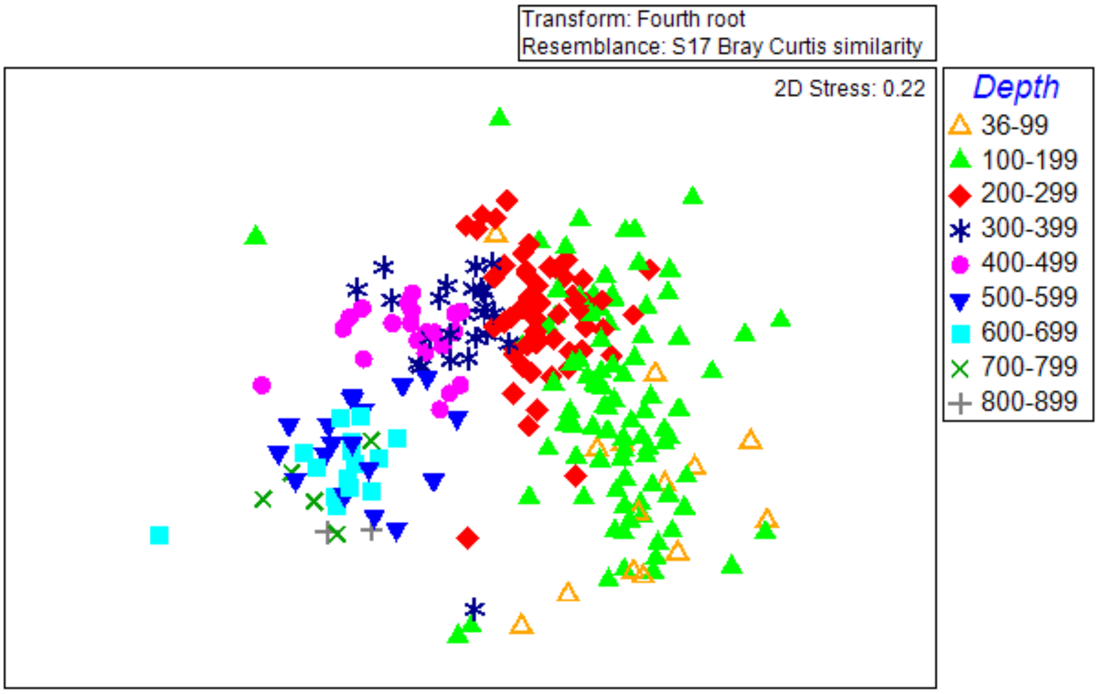


Figure 19(a): Non-metric multidimensional scaling (nMDS) ordination of Bray-Curtis epifaunal similarity for 2011 and 2017. (b) nMDS ordination of Bray-Curtis faunal similarity across 100m depth intervals for 2011 and 2017.

The nMDS plot did not illustrate any clear temporal separation in the epifaunal species assemblages, however, the clear separation among depth categories observed in 2011 west coast was further emphasised with the addition of the 2017 data. Stations sampled in each depth category in different years cluster close together, for example it was evident in the category 100-199 m from both years that similar epifauna occur at this depth over time. The shallow categories clustered close together (36-99 m, 100-199 m and 200-299 m).

Although there were fewer replicates from the deeper stations than the shallower, (Fig.19b) stations in the depth category 700-799 m and 800-899 m still cluster together indicating that epifaunal communities were similar in each year within respective depth categories. There also appeared to be a possible community break between shallow (36-200 m) and deeper (400-899 m) stations.

A two-way PERMANOVA analysis with year (2011 and 2017) and depth factors revealed significant differences between years and depths (Table 17). The significant difference between 2011 and 2017 resulting from the PERMANOVA analysis was not evident in the nMDS plot (Fig. 19a).

Table 17. Two-way PERMANOVA to comparing year (2011 and 2017) and depth (100m interval categories) ($p < 0.05$)

Source	Df	SS	MS	Pseudo-F	P(perm)	Unique perms
Year	1	15678	15678	6.3742	0.0001	9896
Depth	8	2.42E+05	30266	12.306	0.0001	9787
YexDe**	7	23016	3288.1	1.3369	0.0075	9786
Res	226	5.56E+05	2459.5			
Total	242	8.54E+05				

To further investigate the significant difference in epifaunal assemblages between years, a SIMPER analysis between the two years found that in 2017 there was more than double the amount of starfish, *Crossaster penicillatus (*Fig. 20*). T*here were no substantial differences in the abundance of *Chaceon chuni (*crab*), Brissopsis lyrifera capensis (*urchin*)* and *Exodromidia spinosa (*crab*)* (Fig.20). There was a substantial decrease (more than half) in the abundance of jellyfish *P. noctiluca* from 2011 to 2017. Overall, there was a greater average abundance of epifaunal species in 2011 compared to 2017.

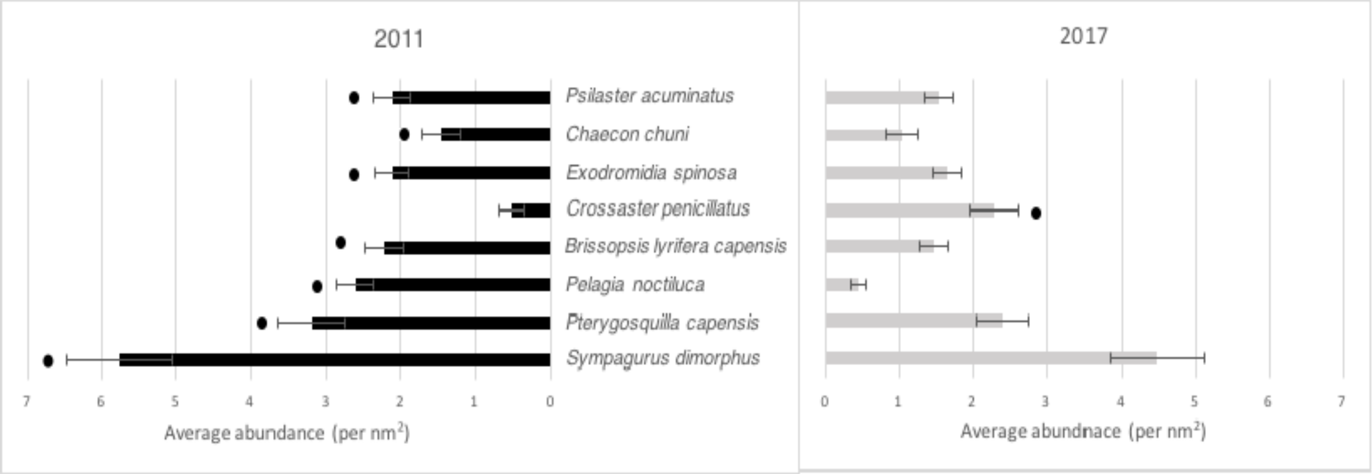


Figure 20: The average abundance for key distinguishing species between years (2011 versus 2017) based on SIMPER results. The average abundance of species that contributed up to 50% of the cumulative distribution (±SE)) of epifaunal data by square root transformation of average abundance per nm^2 are shown. The black dots indicate the year in which the species was more abundant

A significant interaction effect between year and depth category (P(perm) = 0.0075) warranted further pairwise analyses to explore this significant interaction (Table 18).

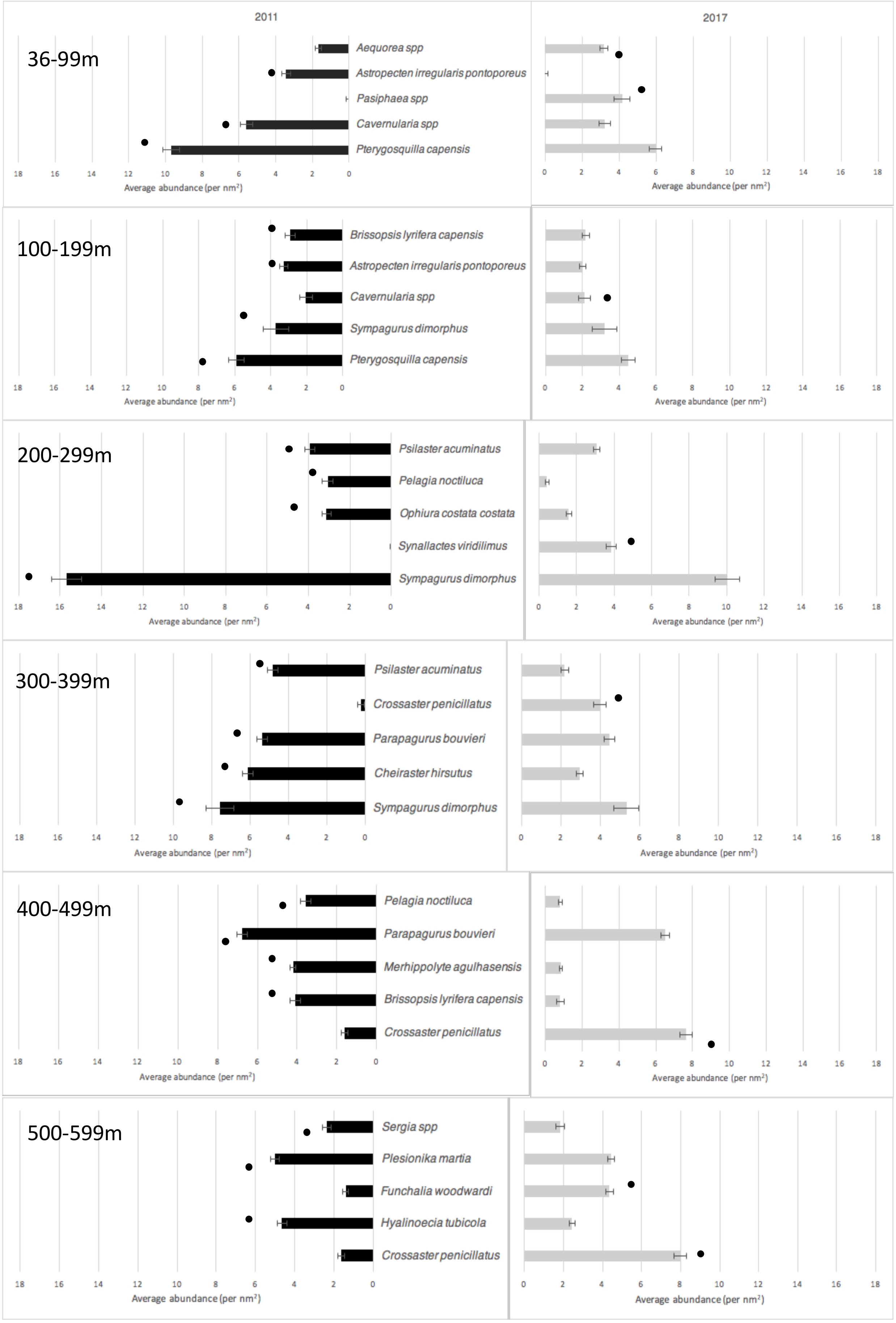
Table 18. Pairwise PERMANOVA comparing depth categories between years. The rows highlighted in bold refer to a significant difference (p < 0.05) between the years.

Depth (m)	**Years**	**t**	**P(perm)**	**Unique perms**	**P(MC)**
36-99	2011, 2017	1.3796	0.0368	2883	0.0845
100-199	**2011, 2017**	**1.7873**	**0.0008**	**9908**	**0.0015**
200-299	**2011, 2017**	**2.3123**	**0.0001**	**9923**	**0.0001**
300-399	**2011, 2017**	**1.8605**	**0.0001**	**9877**	**0.0014**
400-499	**2011, 2017**	**2.1593**	**0.0001**	**9771**	**0.0002**
500-599	**2011, 2017**	**1.611**	**0.0006**	**8533**	**0.0139**
600-699	2011, 2017	1.3215	0.0495	5047	0.1085

700-799	2011, 2017	1.0732	0.3072	10	0.3794

Epifaunal abundance in most of the depth categories differed significantly between the two years. Epifaunal species in the deeper categories (600-699 m and 700-799 m) did not differ significantly between years. The deepest category (800-899 m) could not be analysed due to insufficient samples from the 2017 dataset.

The results of SIMPER analyses identifying the average abundance of species contributing the most to differences between years are shown in Figure 21. Each depth category was analysed individually. In the shallowest depth category (36-99m) *Pterygosquilla capensis* (mantis shrimp) showed a substantial decline in 2017, reducing by an average abundance of approximately 4. The starfish *Astropecten irregularis pontoporeus* was absent from 2017, whereas the shrimp *Pasiphea spp.* was absent in 2011 in this depth category. Fewer *Cavernularia spp.* seapens were recorded in 2017 than in 2011, however the abundance of jellyfish species *Aequorea spp.* increased in 2017.


2011
2017
36-99m
Aequorea spp
Astropecten irregularis pontoporeus
Pasiphaea spp
Cavernularia spp
Pterygosquilla capensis
100-199m
Brissopsis lyrifera capensis
Astropecten irregularis pontoporeus
Cavernularia spp
Sympagurus dimorphus
Pterygosquilla capensis
200-299m
Psilaster acuminatus
Pelagia noctiluca
Ophiura costata costata
Synallactes viridilimus
Sympagurus dimorphus
300-399m
Psilaster acuminatus
Crossaster penicillatus
Parapagurus bouvieri
Cheiraster hirsutus
Sympagurus dimorphus
400-499m
Pelagia noctiluca
Parapagurus bouvieri
Merhippolyte agulhasensis
Brissopsis lyrifera capensis
Crossaster penicillatus
500-599m
Sergia spp
Plesionika martia
Funchalia woodwardi
Hyalinoecia tubicola
Crossaster penicillatus
18 16 14 12 10 8 6 4 2 0
0 2 4 6 8 10 12 14 16 18
Average abundance (per nm²)

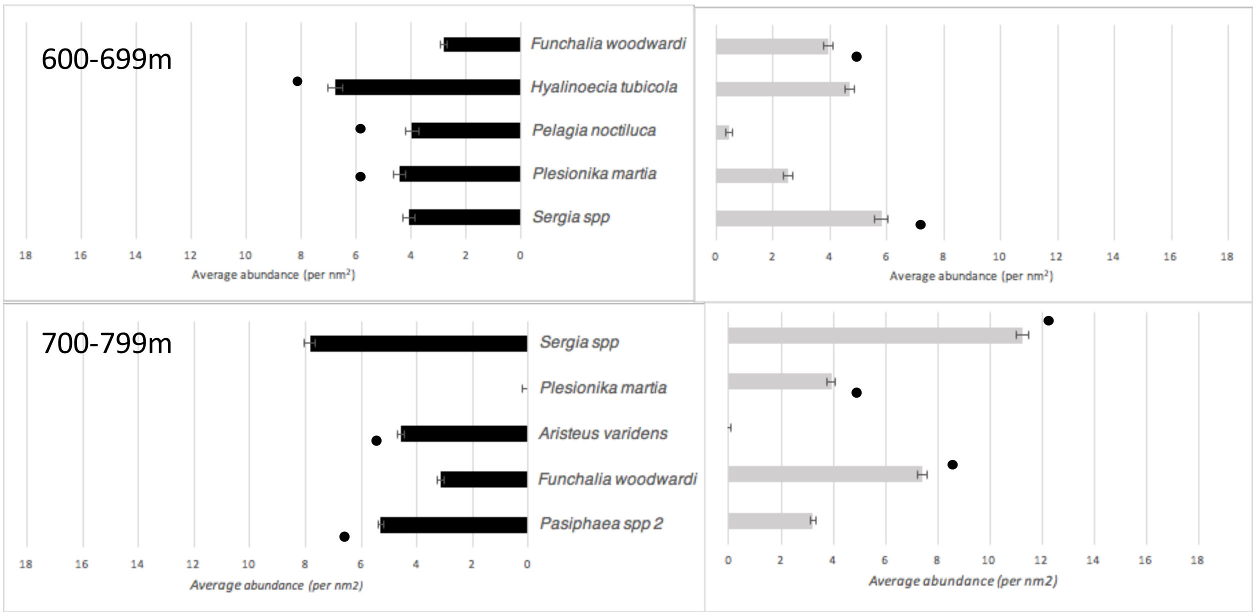


Figure 21: The average abundance for key distinguishing species between depth (2011 versus 2017) based on SIMPER results. The average abundance of species that contributed up to 50% of the cumulative distribution (±SE)) of epifaunal data by square root transformation of average abundance per nm^2 are shown. The black dots indicate the year in which the species was more abundant

Species composition between 2011 and 2017 in the 500-599 m depth category were fairly similar except for an increase in the average abundance for the starfish *Crossaster penicillatus* and prawn *Funchalia woodwardi*, in 2017. This increase in *C. penicillatus* was also evident in the 300-399 m depth category. *Pelagia noctiluca* was virtually absent in the deeper categories in 2017. The shrimp *Plesionika martia* was absent from 2011 while a different species of shrimp, *Aristeus varidens (*striped red shrimp) was absent from 2017 in the 700-799 m depth category. *F. woodwardi,* characterized as a deep-water prawn, occurs in each of the deeper depth categories with an increasing abundance in 2017.

4. Discussion

Epifauna showed a clear demarcation by depth and region where there was a trend of increasing species richness towards the south coast. The south coast epifauna were more diverse than the west coast (Fig.3) with more Molluscs, Arthropods, Chordata, Bryozoa and Cnidaria. On the other hand, the west coast epifauna were more abundant with a higher average number of individuals and species at each station (Fig.4). The characteristic species of the west coast were largely made up of crustaceans such as the dimorphic hermit crab (*Sympagarus dimorphus*) and mantis shrimp (*P. capensis)* and furry baboon crab (*Exodromidia spinosa*). These results also coincide with Lange and Griffiths (2014) where crustaceans were the dominant taxa. The characteristics species found for the south coast were mainly pelagic cnidarians namely; *Pelagia noctiluca,* and *Chrysaora agulhensis, Hydrozoa spp.* and the tunicate *Salpa spp.*

4.1 Spatial Analysis

Epifauna differed significantly between the west and south coast. *Pelagia noctiluca (*Pink stripe jellyfish) were found to be a characteristic species for both west and south coast regions. *P. noctiluca* is common pelagic species and more likely to tolerate a wide range of environmental conditions. This is possibly why it was found on both the west and south coast.

The hermit crab, *Sympagarus dimorphus* was found to be the characteristic and most abundant species on the west coast. This species also had the widest distribution range as it was featured in most ecosystem types – a uniform presence within all Southern Benguela ecosystems. Similarly, Lange and Griffiths, (2014) also identified this species as the most abundant in their study. This could mean that the feeding and ecosystem type preferences for this species has a wide range. Lemaitre (1990) found that species from the genus *Sympagarus* had a depth range of 80-2537m.

Pairwise interactions showed that there was a significant difference between the 400m and 500m depth in the South Atlantic Upper Bathyal and Southern Benguela Sandy Shelf Edge ecosystem types. This indicated that there was a difference in epifauna between these depth categories that lie adjacent to each other (Table 6 and Table 8). This difference displays a species break between 400m and 500m. In the Southern Benguela Sandy Outer Shelf there was also a significant difference between epifauna in depth categories that were adjacent to each other (Table 7). This is supported by Lange & Griffiths (2014) where a distinct community was found where the Southeast Atlantic and Southern Benguela ecosystem types meet. This is in agreement with other studies conducting research on the shelf edge (Cleary et al. 2005; De Léo & Pires-Vanin, 2006).

Interestingly, biotopes identified for the west coast (A to N) during this study support similar species compositions to the communities (or biotopes) identified by Lange and Griffiths (2014). Significantly different epifauna between regions and among depth categories show that epifauna differ between west and south coast and are influenced by depth gradient (Table 2). This was also found by Lange and Griffiths (2014) on the west coast. There is limited published literature on epifaunal communities in offshore habitats along the South African coast, with Lange and Griffiths (2014) being the only study to date. Other studies have examined coastal or shallow subtidal systems (Bustamante 1994, Bustamante & Branch 1996).

The biotopes determined for the west coast were clustered within four ecosystem types namely; Namaqua Muddy Inner shelf, South Atlantic Upper Bathyal, Southern Benguela Sandy Outer Shelf and Southern Benguela Sandy Shelf Edge. This study corroborates hypotheses of previous studies, that the distribution of benthic epifauna is dictated by depth and sediment type (Day, 1963; Basford et al., 1990; de Juan et al. 2013). An increase in depth influenced biotope species composition. Inner shelf biotopes such as D, E and F within the Namaqua Muddy Inner Shelf ecosystem have a similar species composition (Table 10). Species dominating this habitat include *Pterygosquilla capensis* (mantis shrimp), which are known to be shallow, soft substrata species (Abello & Macpherson, 1990) and would be expected to populate shallow, muddy ecosystems such as the Namaqua Muddy Inner Shelf. Deep offshore ecosystem types such as South Atlantic Upper Bathyal (< 500 m and < 400 m as the shelf narrows down near the cape) supports deep-water species such as *Chaecon chuni (red crab)* and *Hyalinoecia tubicola (*quill worm, polychaetes) which have a depth range reported to 1389m and 1035m respectively (Day, 1963; Ng & Davie, 2015). The Southern Benguela Sandy Outer shelf biotopes (K, L, M and N) ranging from 150m to 250m (Fig.9) all had a similar species composition made up of Arthropods and Echinoderms which indicated an even distribution of these two phyla across the outer shelf (and this depth range) as shown by the biotope distribution on the west coast map (Fig.10). The deepest station from this ecosystem type (340m) clustered with a South Atlantic Upper Bathyal biotope, G. This is a notably deep ecosystem type which indicates that there was species variation at different depths within the Southern Benguela Sandy Outer Shelf. This can also be seen in Table 7 where there was a significant difference in epifauna between 200-299m – 300-399m.

The Orange River mouth is located at the border between Namibia and South Africa, and discharges freshwater into the Atlantic Ocean on the west coast of South Africa (Matthews et al., 2012). Biotopes M and F occur at the border of these two regions and thus could be influenced by the input of freshwater in the region. Low salinity and high sediment load from the Orange River outflow was found to be a barrier to fish movement in the region of the mouth (Matthews et al., 2012) and these effects could similarly influence the benthic community.

Biotope A and B had the same wide distribution range as Lange and Griffiths (2014) 'community 1' with similar characteristic species namely; *Plesionika martia, Funchalia woodwardi,* and the same species from the *Chaceon* genus. Biotopes A, B, and C could potentially form one larger biotope as all of these biotopes lie within the South Atlantic Upper Bathyal ecosystem and within a similar depth range (538 – 815m). On the other hand, these biotopes also have different characteristic species contributing to the average abundance. *Plesionika martia* (common golden shrimp) contributes 23% average abundance (Table 10) to biotope A which could mean that this species is present on the shelf edge of the west coast (wide range) and could drive the differences between biotopes B and C.

The south coast epifauna did not display as clear depth demarcation when compared to the west coast, although fewer stations were sampled in the deeper categories (450 to 800m) on the south coast. The significant interaction effect between depth and ecosystem type on the south coast suggests epifauna differs within ecosystem type and depth. On the contrary, insignificant pairwise interaction effects were found for more than half of the depth groups. This result was opposite for the west coast which in comparison to the south coast has a much clearer depth gradient and pattern (Fig.8). Additional stations would need to be sampled on the south coast to provide more statistical power and could also provide information on whether a depth pattern would arise.

The biotopes determined on the south coast were clustered within three ecosystem types namely; Agulhas Sandy Outer Shelf, Inner Shelf and Sandy Shelf Edge. Biotope X is clearly identified as a shelf edge community (Fig.13) as stations making up this biotope lie predominantly within the Agulhas Sandy Shelf Edge ecosystem. This biotope largely hosted pelagic species (*Salpa spp. and Pelagic noctiluca*). The starfish species *Cosmasterias felipes* featured only in this biotope as the main characteristic species and contributes 11% to the average abundance. For this species to extend as far as the south-west of Port Elizabeth (Fig.13) indicates a wide range and not just an ecosystem overlap.

Biotope X is located south-west of Port Elizabeth, an area which is considered to be a transition zone for the Agulhas current dynamics as it flows from the northern narrow shelf area onto the wider south coast shelf (Lutjeharms & Van Ballegooyen, 1988, Yemane et al., 2015) where wind-driven upwelling and alongshore coastal current become more important. It is likely that these distinctive upwelling mechanisms have significant impact on nutrient inputs resulting in different ecosystem drivers and responses (Roberson et al., 2017). This could have an effect on species composition in this area, especially filter-feeding species that rely food supply from the water column. This may explain the abundant presence of two pelagic species (*Pelagia noctiluca* and *Salpa spp.*) in this biotope (Madin, 1995; Gordoa et al 2013).

Biotopes T, Y and Z all lie in the outer shelf area and are dispersed across the outer shelf in a band. Despite biotope T being spatially close to biotopes Y and Z, biotope T was dominated by different species, except for *Pelagic noctiluca* which was ubiquitous in most biotopes and was considered to be a characteristic species for the south coast region. Biotope Y appears to be a subset of biotope Z as the species composition is very similar and the stations forming these biotopes are spatially close together (Fig.13). For broader classification purposes, it is possible that biotope Y and Z could be merged. The burrowing heart urchin, *Spatangus capensis,* featured in both the Agulhas Sandy Inner and Outer Shelf ecosystems, which could mean that this is a common species on the south coast with a wide depth range.

Stations forming biotope W were located in the shallow inner shore area along the south coast (39-110m), mostly within the Agulhas Inner Shelf ecosystem. Species contributing to this ecosystem varied greatly to those that featured in the Agulhas Sandy Shelf Edge (biotope X). *Chrysaora agulhensis* (jellyfish), *Astropecten pontoporeus* (star) and the whelk *Nassarius speciosus* contributed to the Agulhas Inner Shelf whereas *Sympagarus dimorphus*, *Luida sarsii africana* and *Cosmasteria felipes* (star) contributed to the Agulhas Sandy Shelf Edge. This could be due to the change in depth range as the shelf edge is deeper than the inner shelf (173-240m).
There is some species overlap at the boundaries between the Agulhas Inner and Outer Shelf. Biotopes U, V, W and Z all had stations at the boundaries of these two

ecosystem types and shared species in common (*Chrysaora agulhensis, Pleurobranch bubala, Nassarius speciosus* and *Toraster tuberculatus).* The boundary of these two ecosystem types could host the same species composition. Further away from the boundary the epifauna composition changes distinctly, as seen by the composition of biotopes T and W (Table 16).

Pleurobranch bubala (sea slug) has previously been reported to have a depth range of 5-60m (Zsilavecz, 2007) but in this study it was found at 135m in the Agulhas Sandy Outer Shelf, which could represent an extension of it's known depth range. Taxonomic studies would be necessary to confirm the species identification before this can be confirmed as a depth range extension.

Three stations that were sampled during a west coast survey were located in the south coast ecosystem type Agulhas Sandy Outer Shelf. There was only one species in common (*Pelagia noctiluca)* between this ecosystem type at the west and south coast. Being on the edge of this boundary between defined west and south coast ecosystem types could have an impact on species composition. *Pterygosquilla capensis* (mantis shrimp) which is notably a west coast characteristic species is found in the Agulhas Sandy Outer Shelf (notable south coast ecosystem type) for the west coast (Table 9) which could indicate species overlap between these boundaries. This is also true for *Salpa spp.* appearing under the west coast ecosystem type (Southern Benguela Sandy Outer Shelf) in the south coast. The Agulhas Sandy Outer Shelf which borders the Southern Benguela Sandy Outer Shelf, could support this species overlap.

4.2 Overlap Area

The DAFF demersal research survey defines the sampling area for the west and the south coast either side of the 20° east line of longitude. Such a fixed line to divide research boundaries is practical for survey purposes however can potentially lead to an overlap in species composition surrounding the boundary area. The subset of stations selected from Cape Point to Mossel Bay identified nine biotopes from the cluster analysis and five potential biotopes.

In assessing whether the overlap area between the west and south coast at the 20°E longitude is sensible for epifaunal biodiversity, the results from this study found that biotope five reflects more of the south coast than the west. All the stations in this biotope lie eastward of the 20°E longitude line which is suited for the separation of the west and south coast (according to DAFF). This biotope could also be an extension of biotope Y from the south coast cluster (Fig.23 in appendix).

The potential biotope three was made up of two stations that were defined as the south coast by the DAFF research survey. This biotope falls within a west coast ecosystem; South Atlantic Upper Bathyal. In section 8.2 Figure 23, this potential biotope is located near biotope A (west coast cluster), which denotes sampling overlap by the DAFF research survey. This could indicate that stations located near each other are being defined as two different regions despite lying within the same ecosystem type.

Biotope 11 comprises of stations that spans both sides of the 20°E longitude line, but are labelled as west coast stations. This biotope also lies on the shelf edge and instead of representing typical western or southern ecosystems, it could instead represent general 'shelf edge' ecosystems.

Biotope six is classified under a south coast ecosystem (Agulhas Sandy Outer Shelf) despite being 'defined' as the west coast (located west of the 20°E longitude line). However, species characteristic of this biotope frequently occur on the west coast (*Pterygosquilla capensis* and *Pelagia noctiluca*). Despite being classified under a south coast ecosystem; it is likely to reflect more west coast species.

On the other hand, biotopes six, seven, eight and ten are spatially located on the west coast and lie west of the 20°E longitude. Stations making up 12, 13 and 14 are spatially located east of 20°E longitude. These results align with delineating the offshore ecosystems along the 20°E longitude line.

In summary, a majority of the biotopes mentioned above are supported by the DAFF longitudinal boundary with the exception of biotopes three and 11. Further research and testing of other components of the ecosystem such as fish and infauna should be tested in this region to create a holistic picture.

4.3 Temporal analysis

A temporal analysis was conducted to assess whether epifaunal assemblages change over a six-year period, specifically from 2011 to 2017 on the west coast. Epifauna are known to be stable and therefore it was expected that they would not have notable seasonal variability in composition (Birchenough et al., 2011, Sweetman et al., 2017).

There has also been no change in fish assemblages between summer and winter (Atkinson et al., 2011) and therefore it is unlikely that epifauna would differ since fish are much more mobile species (Roel, 1987). A greater number of species were detected in the 2011 (n = 16 species per station) survey when compared with 2017 (n = 12 species per station), which could indicate some extent of temporal changes in abundance of the benthos in the west coast over this five-year period. A significant difference was detected in epifaunal assemblage abundance between the years 2011 and 2017, despite the similar spatial pattern shown in the multi-dimensional scaling plot (Fig.19a). In the case of the 400-499 m depth category heart urchin (*B. lyrifera capensis)* and crustacean (*Merhippolyte agulhasensis*) were almost absent (abundance < 1) from 2017. If the abundance of benthic epifauna is decreasing, the pelagic realm can be negatively affected as benthic epifauna are important prey for upper trophic level organisms (Murillo et al., 2016; Griffiths et al., 2017).

Distinguishing species detected for 2017 and 2011 were similar, although there was a substantial decrease in the abundance of *P. noctiluca* in the 2017. In Namibia, overfishing in the pelagic industry has added to a bloom in jellyfish abundance in this region (Christopher et al., 2006) which could be the one of the reasons for such a high average abundance in 2011. Although, this species has a wide environmental range (Houghton, 2008) and has more mobility than benthic epifauna which could cause the decrease in abundance in 2017.

The abundance of the starfish *Crossaster penicillatus* more than doubled in 2017 between 300-599 m whereas in 2011 it had a low average abundance (< 2). This could be due to nutrient availability or abundance of prey for *C. penicillatus.* The deeper stations were characterized by the benthic shrimp *Sergia spp.* and the polychaete quill worm *Hyalinoecia tubicola* during both years, which indicates varying species composition between shallow and deeper stations.

In summary for the temporal analysis, the varying abundance in epifaunal species occurring in both years was driving the difference between 2011 and 2017 (Fig.21). The differences detected were not confined to a particular range of depths but rather a majority of the categories (Table 18). *P. noctiluca* was a species that was driving this difference. An analysis excluding the pelagic species may result in the years being the same.

This study only had data for comparing the west coast over a temporal scale and so in the future a component that includes a temporal change with the south coast would be ideal.

4.4 *Patterns Aligning with NBA marine classification*

This study assessed whether patterns detected in benthic epifaunal assemblages align with the existing national marine benthic habitat classification (Sink et al., 2012). The main ecosystems that were analysed for this study were the Agulhas Sandy Inner, Outer and Shelf Edge along the south coast and the Southern Benguela Outer Shelf and Shelf Edge and the Namaqua Muddy Inner Shelf on the west coast. The NBA ecosystems types were shown to host significantly different epifaunal communities (Table 5 and Table 11). The statistically different epifaunal biotopes derived from analyses conducted (Fig. 9, 12 and 14) also indicate that epifaunal communities differ between west and south coast regions. The biotopes derived from the benthic epifaunal communities correlate with the boundaries of some of the ecosystems depicted in the current NBA (Sink et al., 2012). This section highlights which biotopes from the study aligned with the ecosystem types from the NBA.

A number of biotopes derived from this study were found to align with the ecosystem types from the NBA. On the west coast several biotopes were found to align well with the NBA marine classification. Biotope M largely represents the inshore portion of the Southern Benguela Sandy Outer Shelf. Biotopes A, B and C align very well with the South Atlantic Upper Bathyal ecosystem type characterised by deep sea species (*Chaecon chuni, Hyalinoecia tubicola* and *Sergia spp.)*. Biotopes D, E and F are located within the Namaqua Muddy Inner Shelf and hosts similar species. These patterns align with this marine classification. On the south coast biotope X clearly represents the Agulhas Sandy Shelf Edge, biotopes Z and T (and to an extent Y) represent the Agulhas Sandy Outer Shelf. Biotope W clearly denotes the Agulhas Sandy Inner Shelf. Whilst many of the epifaunal biotopes identified in this study did align with the ecosystems of the NBA, there were several biotopes that did not match such as U and V on the south coast and H, I, J, K and L on the west coast. Species composition was also seen to overlap on boundary areas between the west and south coast as seen from the results investigated in section 3.1.4. This composition shows the gradient in community one would expect from sediment communities rather than hard boundaries.

5. Overall Limitations & Future studies

The primary limitations encountered in this study are the high level of species variability among stations, limited samples covering a large spatial area and inconsistent sample numbers in different depth categories. For example, Southern Benguela Sandy Shelf Edge did not have enough replicates for the medium depth groups (200-299 m and 300-399 m). Few stations were sampled in the 800-899 m range in either the west of south coast region limiting the extent of statistical analysis of epifauna in this depth category. There was an insufficient amount of depth categories in the Southern Benguela Muddy Outer Shelf, Southern Benguela Hard Shelf Edge, Namaqua Muddy Inner Shelf and Namaqua Sandy Inner Shelf to conduct a pairwise analyses, therefore, these habitats were not included in the pairwise analysis.

Upon comparing the 2011 and 2017 dataset many unknown species were found, for example, there were two unknown gastropods in each dataset. It is unclear whether they could be the same species or completely different species. Limited taxonomic knowledge and identification skills resulted in inconsistency in identifying species across different surveys. This highlights the need for a consistent identification system over time to enable direct comparisons between the epifaunal datasets in the future. The recent publication of an offshore invertebrate identification guide (Atkinson and Sink 2018) helps address this problem.

To improve assessment of temporal changes in epifauna, a sampling frequency of less than five years is desirable. The time span of six years in this study showed a significant difference in epifaunal communities, however, it was not possible to determine whether either of the two years tested were potentially anomalous years. Variations in epifauna could also be as a result of patchy sampling in one year due to the large area covered and limits on the number of stations surveyed each year. It is possible that species were present in the region/year but not caught in the sample collection. To provide a stronger analysis for changes in abundance of epifauna over a temporal scale, annual sampling for at least a period of four to five years would provide more concrete information of potential changes in epifaunal communities in offshore regions. Information from previous years are not currently available, but this preliminary analysis remains valuable and indicates that the annual differences in epifaunal surveys should be given attention. This study provides valuable information for future temporal studies.

The demersal trawl surveys are primarily focussed on conducting surveys of demersal fish abundance to inform stock assessment models and have been designed as such. Unfortunately, the design of the surveys is driven by depth stratification for their purpose and is unable to take into account the benthic ecosystem classification. In the future dedicated surveys of the seabed that are more aligned with assessing different benthic ecosystem types would be more suitable to investigate epifaunal communities.

Further studies could explore functional epifaunal groups (e.g. filter feeders, detritivores, burrowing species, emergent species etc.) to assess whether benthic ecosystem functions are changing or being altered. There are similar species that have the same functional role in an ecosystem (Fonseca et al., 2001; Norling et al., 2007). If a species disappears in one year, the functional role of that species may be adopted by an alternative species and the ecosystem will continue to function. If enough species disappear from an ecosystem and their functional role is not adopted by alternative species, the ecosystem functioning may not be maintained (Fonseca et al., 2001). Analysing the abundance of certain functional groups could provide information about potential ecosystem shifts that could occur. The five-year gap that was analysed would also need to be refined to detect small scale changes as well as a longer time frame to investigate long term changes.

6. Conclusion & Future Implications

Benthic epifauna should be closely monitored and incorporate more data to analyse temporal change as small shifts could be indicative of unfavorable conditions. This study highlighted the species composition in offshore regions across the west and south coast of South Africa. In summary the results of this study found 14 biotopes within four ecosystem types on the west coast and nine biotopes within three ecosystem types on the south coast. This study provided biodiversity information about mainly offshore ecosystem types which was found to align with the current NBA marine classification. The results of this study also contribute to general community ecology on the west and south coast of South Africa for benthic epifauna. This contributes to mapping and description of offshore ecosystem types as well as, aiding in biological verification of existing habitat classifications. This is essential to form the basis for marine ecosystem assessments, which in turn inform MSP and decision making for MPA extension in diverse offshore environments.

7. References

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8. Appendix

The list of species that are absent from the two regions (West and south coast) can be seen in Table 19 where there are more species absent from the west coast in comparison to the south.

Table 19. List of species that are absent from the west and south coasts of South Africa

Species	**West Coast**	**Species**	**South Coast**
Marthasterias africana	-	*Tethya cf.aurantium*	-
Comitas stolida	-	*Polyechinus agulhensis*	-
Conus gradatulus	-	*Diplopteraster multipes*	-
Lembulus belcheri	-	*Laetmonice benthaliana*	-
Maja cornuta	-	*Synallactes viridilimus*	-
Amphipoda spp.	-	*Thysanostoma spp.*	-
Glyphocrangon spp.	-	*Ceramaster patagonious euryplax*	-
Eguchipsammia cf.	-	*Fusinus africanae*	-
Astrocladus euryale	-	*Astrothorax waitei*	-
Mycale anisochela	-	*Synoicum spp.*	-
Stegnobrisinga splendens	-	*Isididae spp.*	-
Ophiothrix fragilis	-	*Comatas saldanhae*	-
Hornera erugata	-	*Chrysaora fulgida*	-
Pseudodromia spp.	-	*Coluzea radialis*	-
Ostrea antherstonei	-	*Phormosoma placenta africana*	-
Ophiomitrella hamata	-	*Bolocera kerguelensis*	-
Persephonaster spp.	-	*Filograna implexa*	-
Nucula nucleus	-	*Stereomastis sculpta*	-
Onchoporella buskii	-	*Odontaster australis*	-
Gynandrocarpa placenta	-	*Fusivoluta pyrrhostoma*	-
Lithodes ferox	-	*Ophiactis carnea*	-
Stylaster spp.	-	*Flabellum messum*	-
Monodaeus spp.	-	*Exodromidia spinosa*	-
Pseudamussium gilchristi	-	*Scaphander punctostriatus*	-
Hygrosoma petersii	-	*Neptuneopsis gilchrisi*	-
Fusinus hayesi	-	*Pasiphaea spp.*	-
Semicassis labiata	-	*Inflatella belli*	-
Phidoloporid spp.	-	*Flustramorpha marginata*	-
Pulsarella fultoni	-	*Exodromidia spinosissima*	-
Spoladaster veneris	-	*Polymastia bouryesnaultae*	-
Ovalipes iridescens	-	*Anthoptilum grandiflorum*	-
Glyphus marsupialis	-	*Actinoscyphia plebeia*	-

Marginella musica	-	*Latrunculia (Latrunculia) biformis*	-
Euspira napus	-	*Ophiura trimeni*	-
Turitella sanguinea	-	*Parapontophilus gracilis gracilis*	-
Thyone cf venusta	-	*Eleutherobia variable*	-
Ascidia incrassata	-	*Ostracod spp.*	-
Securiflustra spp.	-	*Macropipus australis*	-
Stereocidaris excavata	-	*Psilaster acuminatus*	-
Pennatulacea	-	*Chondsraster elattosis*	-
Homola barbata	-	*Athleta lutosa*	-
Aspidostoma spp.	-	*Crossaster penicillatus*	-
Callopatiria formosa	-	*Bathynectes piperitus*	-
Actinoptilum molle	-	*Neolithodes asperrimus*	-
Pyura stolonifera	-	*Isophellia algoaensis*	-
Errina spp.	-	*Pseudostichopus langeae*	-
Granulifusus rubrolineatus	-	*Cavernularia spp.*	-
Halcurias capensis	-	*Sclerasterias spp.*	-
Cladopsammia cf. spp.	-	*Africolaria rutila*	-
Pseudodromia rotunda	-	*Calocaris barnadi*	-
Aplidium spp.	-	*Pseudodistoma spp.*	-
Euphione alisabethae	-	*Poraniopsis echinaster*	-
Atrina squamifera	-	*Ophiomisidium pulchellum*	-
Philocheras sculptus	-	*Cheiraster hirsutus*	-
Aristaeopsis edwardsiana	-	*Munida benguela*	-
Astropecten cingulatus	-	*Tanaid spp.*	-
Nassarius speciosus	-	*Alcyoniidae spp.*	-
Scyllarides elisabethae	-	*Funchalia woodwardi*	-
Paradoris spp.	-		
Charybdis smithii	-		
Triviella spp.	-		
Synallactes mollis	-		
Turritella ferrugina	-		
Menipea marionesis	-		
Dromidia aegibotus	-		
Fusinus oceliferus	-		
Pteropurpura spp.	-		
Distaplia spp.	-		
Dardanus arosser	-		
Armina spp.	-		
Kaloplocamus ramosus	-		
Ovalipes iridescens	-		

Hippasteria phrygiana	-		
Crassiboughia clausicaudata	-		
Crustacea spp.	-		
Hydrozoa spp.	-		
Holothuroidea spp.	-		
Pectinidae spp.	-		

The NBA marine classification map containing all biotopes from west and south coast and the overlap area can be seen in Figure 22 and Figure 23. A detailed legend comprising of all the ecosystem types (offshore) from the NBA can be found in Figure 24.

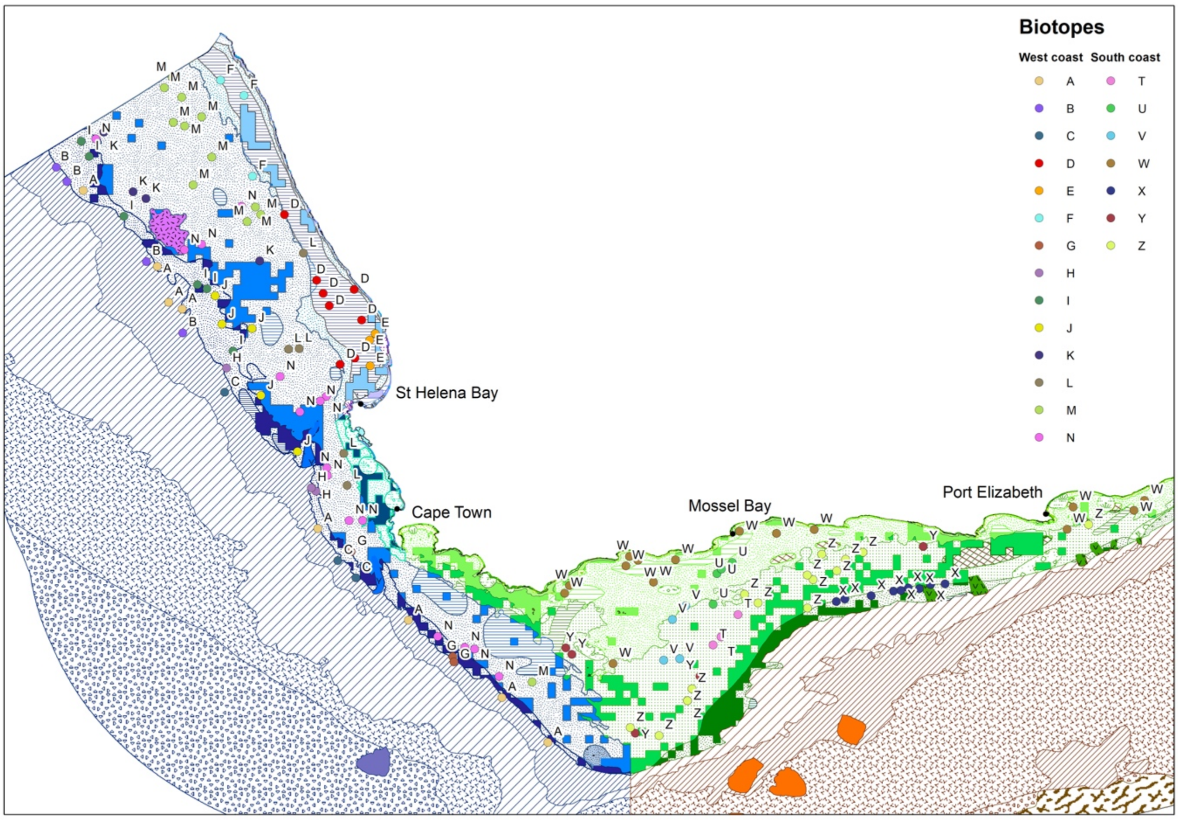

Figure 22: NBA habitat map containing biotopes from the west and south coast, biotopes from the west coast labelled (A-N) and the south coast (T-U)

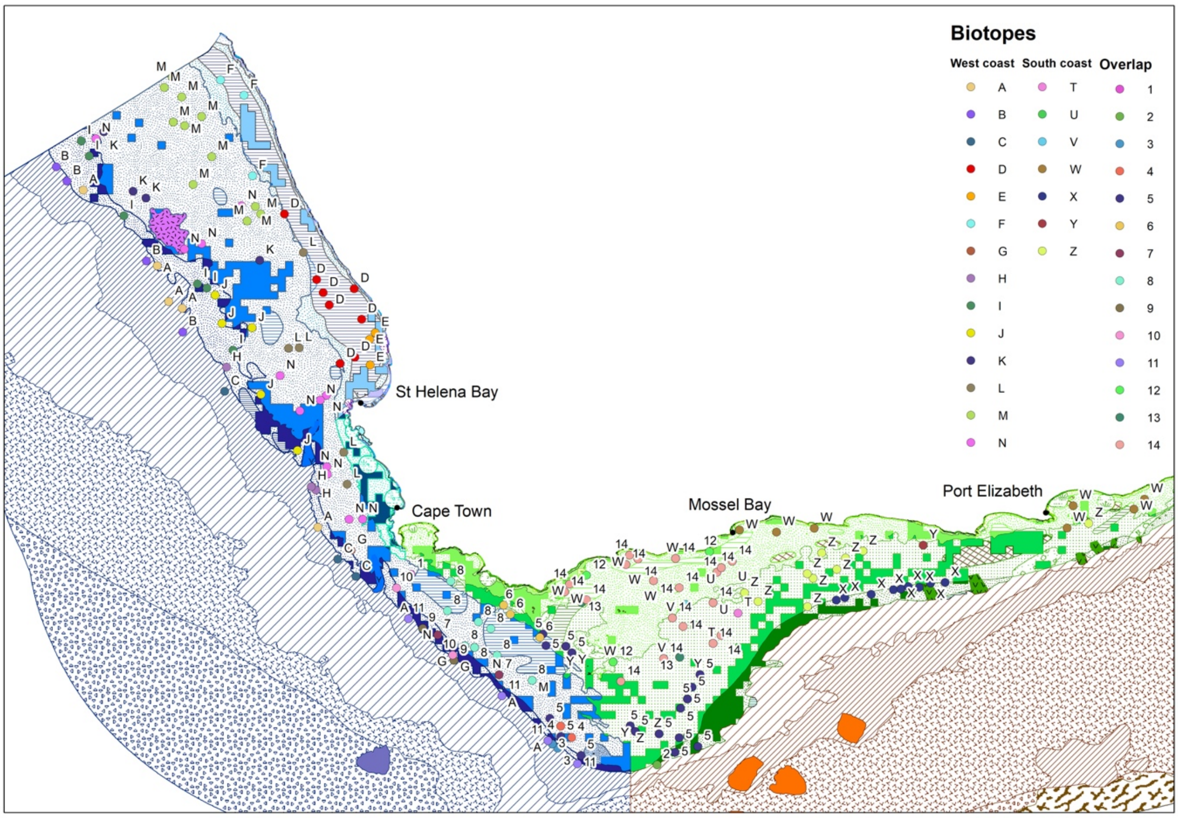

Figure 23: An overall habitat map that includes the biotopes form the west and south coast and the potential overlap region

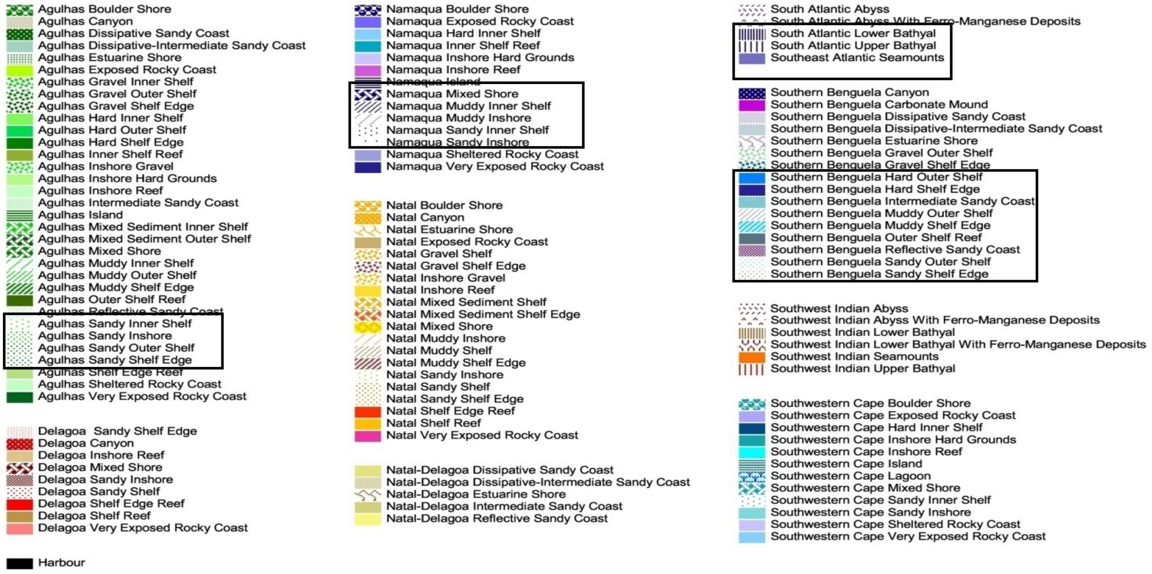

Figure 24: An overview of the complete extensive NBA habitat marine classification of all ecosystem types. Ecosystems that have been boxed indicate relevance for this study

An overview of species that are absent in the 2011 and 2017 dataset are found in Table 20. There were more species missing from 2017 than in 2011. A large proportion of the species are not identified to species level but only genus.

Table 20. Species that were absent from 2011 and 2017

Species	**2011**	**Species**	**2017**
Suberites dandelenae	-	*Fusinus africanae*	-
Bolocera kerguelensis	-	*Calliostoma perfragile*	-
Mycale anisochela	-	*Coluzea radialis*	-
Chloeia inermis	-	*Cerianthus spp.*	-
Gorgonocephalus pustulatum	-	*Macropodia falcifera*	-
Lucinoma capensis	-	*Comanthus wahlbergii*	-
Lithodes ferox	-	*Filograna implexa*	-
Stylaster spp.	-	*Leptochiton sykesi*	-
Pseudamussium gilchristi	-	*Odontaster australis*	-
Cypraeovula iutsui	-	*Fusivoluta pyrrhostoma*	-
Phidoloporid spp.	-	*Ophiactis carnea*	-
Nematocarcinus longirsotus	-	*Flustramorpha angusta*	-
Euspira napus	-	*Aristaeomorpha foliacea*	-
Chaceon maritae	-	*Fusinus bonaespei*	-
Tethya spp.	-	*Exodromidia spinosissima*	-
Aulacomya atra	-	*Astropecten exilis*	-
Halcurias capensis	-	*Latrunculia (Latrunculia) biformis*	-
Aplidium spp.	-	*Ascidia incrassata*	-
Aphrodita alta	-	*Ostracod spp.*	-
Dromida hirsutissima	-	*Philine aperta*	-
Anthosactis capensis	-	*Laetmonice benthaliana*	-
Holothuroidea spp.	-	*Anseropoda grandis*	-
Tetolla capillosa	-	*Securiflustra spp.*	-
Antho cf. prima	-	*Synallactes viridilimus*	-
		Bathynectes piperitus	-
		Pseudostichopus langeae	-
		Caryophylliidae spp.	-
		Palinurus gilchristi	-
		Pseudodistoma spp.	-
		Synallactes mollis	-
		Ophiomisidium pulchellum	-
		Dardanus arosser	-
		Actiniaria spp.	-
		Bryozoa spp.	-
		Caridea spp.	-
		Alcyoniidae spp.	-
		Afrocominella capensis simoniana	-
		Nassarius vinctus	-