MACROBENTHOS USED TO VALIDATE MULTI-CRITERIA DERIVED MARINE BIODIVERSITY SPATIAL ZONES IN KWAZULU-NATAL, SOUTH AFRICA

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Submitted in fulfilment of the academic requirements for the degree of

Master of Science

in the School of Life Sciences,

University of KwaZulu-Natal, Durban, through the Oceanographic Research Institute

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ABSTRACT

Compared to terrestrial ecosystems, the characteristics of marine ecosystems remain largely under-explored. Marine and coastal ecosystems provide a number of ecological services and societal benefits (resources for commercial opportunity, food, recreation, and transport) which, in turn, has developed a strong reliance on these ecosystems. However, the increasing direct extraction of living and non-living resources and effects of urbanisation of adjacent coasts has placed a significant loss of habitats and associated essential diversity. To conserve biodiversity and retain specific goods and services provided by these ecosystems, marine conservation plans aim to protect spatial areas that are critical in the support of these benefits. Due to the paucity of adequate biological data and the prohibitive cost of directly sampling benthic biota over large areas, the most effective means of developing benthic habitat maps, used as biodiversity surrogates, is to use commonly available marine abiotic attributes.

In KwaZulu-Natal (KZN), through marine spatial planning (MSP) the derivation of a marine conservation plan is well underway. The next step is to expedite the plan by investigating whether surrogates for biodiversity exist at different ecosystem levels, one being the infauna of unconsolidated sediments, mid-shelf 50-80 m. This work presents an outcome of the ACEP 'Surrogacy Project' that assessed whether predefined biodiversity zones (biozones) represent the taxonomic/functional attributes of macrobenthic communities. Biozones were subdivided into various subclusters from Richards Bay to uMkhomazi with 19 (57 replicates) stations sampled during the winter of 2014 across the biozones to represent replicate 'treatments'. Macrobenthic communities were classified taxonomically, to the lowest level possible, and then on biological traits. Community patterns were investigated along the mid-shelf, and related to measurable biophysical factors. Environmental parameters measured included sedimentary characteristics as well as the bottom 5 m of water column characteristics per station. A total 33 215 individuals belonging to 634 taxa were recorded along the mid-shelf, of which the majority were Polychaeta and Crustacea, with the latter being highly abundant. Cluster analysis resolved into seven taxonomic groups distributed according to different habitats that are characteristic to the KZN shelf.

The use of coarser taxonomic resolution (Phylum-Genus) or indicator taxa (Polychaeta and Amphipoda) as surrogates for total community richness were independently investigated using the same macrofaunal abundance data. Results showed similar clustering of samples to total

fauna (Species-level) when data were analysed at Family-Genus taxonomic level and at Polychaeta indicator taxa, suggesting that the same amount of information was being gained using data based on these taxonomic level and indicator taxa. The results of the BIOENV analyses were also broadly similar for both taxonomic levels of analyses, in terms of both the proportion of the variation in assemblage structure explained by the selected environmental variables and the choice of selected variables. These results suggested that the information gathered at Family-Genus level and Polychaeta indicator can be used as a proxy for the whole macrobenthic community. This has important implications for future studies and for MSP. Using nine traits, across 51 categories, four main functional groups were found off Thukela, Zinkwazi to Durban, and Durban to uMkhomazi. The groups were characterised as being free-living carnivores, hard-skeleton direct-developing omnivores, and soft-bodied or hard-shelled omnivores with planktotrophic larvae. These patterns were explained by the KZN shelf habitat complexity, including level of different sediment grains, TOC, carbonates, water column turbidity, salinity, dissolved oxygen and temperature.

Thus far, distribution patterns and functional attributes of the macrobenthos do not fully agree with modelled biozone separations (KZN MSP biozone model). Because they are an important component of marine ecosystem functioning, biozone model derivations require the addition of a macrobenthic component, in particular information about diversity patterns, to identify areas for conservation. Suggested, is a refinement of the current benthic habitat layer by incorporating biological data. Further, by using validated sediment distribution, taxonomic and functional attributes that determine soft-bottom macrofaunal distribution at a variety of spatial scales, an alternative biozone model to the current MSP predefined biozones was proposed. This multi-approach resolved into a simplified model with four biozones. These are likely better predictors of spatial variation in ecosystem processes and biodiversity as domains that are biologically informed, and are a key requirement for effective marine management. This study demonstrates the critical importance of testing assumptions about surrogacy and an approach for refining surrogates. Further studies are required to establish whether the proposed model adequately represents other ecological components (e.g. epifauna).

The findings of this study contribute significantly to existing local knowledge, including augmenting and refining taxonomic information of the KZN shelf. In addition, this study subsidises poor information for large spatial areas in local and national marine conservation plans. The proposed biozone model may facilitate an understating of ecosystem process in the region and contributes to integrated marine management.

FACULTY OF SCIENCE AND AGRICULTURE

DECLARATION

PLAGIARISM

I **Sikhumbuzo M. Maduna** declare that:

1. The research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work.

2. This dissertation has not been submitted in full or in part for any degree or examination to any other university.

3. This dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

4. This dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

    i) Their words have been re-written but the general information attributed to them has been referenced.

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5. Where I have used material for which publications followed, I have indicated in detail my role in the work.

6. This dissertation is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included.

7. This dissertation does not contain text, graphics or tables copied and pasted from the internet, unless specifically acknowledged, and the source being detailed in the dissertation and in the References sections.

Signed S.M. Maduna.

Sikhumbuzo Maduna

Date: 10.12.2017

ACKNOWLEDGEMENTS

I would like to express my deepest gratitude to my supervisor Fiona MacKay for invaluable support, advice, patience, understanding, sacrifices made and the long hours worked. She is also responsible for nurturing my development, teaching me fundamental principles of Marine Ecology and always pointing me in the right direction.

I owe a great deal of thanks to my family for love, sincere support and encouragement throughout this study, especially, my mom Mmakasteng Anna Maduna, Sphesihle Maduna and Sizakele Ngcobo. To my old-time friends, Jabulile Nhleko, Sibusiso Majola, Sandile Ngwenya and Siyakudumisa Fodo, I am glad you were by my side on this long and eventful journey.

I would also like to extend thanks to the African Coelacanth Ecosystem Programme (ACEP), the National Research Foundation (NRF) and Oceanographic Research Institute (ORI) for funding and support throughout this study.

I am truly grateful to all the crew-members of *Angra Pequena* for hosting our team and assisting with sampling.

Special thank goes to Tamsyn Livingstone for providing me with the test model and the list of data layers used to derive marine spatial planning predefined biozones (the test model). My acknowledgement also goes to Jennifer Olbers for helping with echinoderm taxonomic identification.

Thanks are also due to Jill Langley and Desmond Hayes for their assistance in the field activities and for support and encouragement during this study, words cannot express how grateful I am.

I thank the following people Mike Dyer, Gareth Jordaan and Stacey Badenhorst for their support, lengthy discussions, advice, and for being special friends.

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CHAPTER 1. INTRODUCTION

1.1 Context of study

The continental shelf on the east coast of South Africa is recognised as a biologically important and productive environment (Heydorn et al. 1978, Hutchings et al. 2002, Meyer et al. 2002) owing to diverse environmental conditions arising from the Agulhas western boundary current (Lutjeharms 2006a, Roberts et al. 2010b). Furthermore, this shelf is characterised by unique benthic habitats that are central to the ecology of the region (Green and MacKay 2016, MacKay et al. 2016, Untiedt and MacKay 2016). As a consequence of the lack of protection and management, this offshore marine environment was among the main concerns identified in the recent National Spatial Biodiversity Assessment, with KwaZulu-Natal (KZN) recognised as a priority area for the establishment of offshore marine protected areas (MPAs) (Sink et al. 2011). The aim of Marine Protected Areas (MPAs) is to conserve biodiversity and maintain ecological integrity (Claudet 2011). The establishment of a representative system of protected areas is widely regarded as one of the most effective mechanisms for protecting biodiversity while permitting the sustainable use of natural resources (Lombard et al. 2004, Driver et al. 2012). South Africa, as a signatory to national and international conventions and agreements, has a mandatory task to develop and implement strategies for the conservation, sustainable use and equitable sharing of its unique marine and coastal environments and associated resources and biodiversity benefits. However, KZN shelf biodiversity has been poorly studied and therefore conservation plans primarily rely on abiotic information. Biophysical-based habitat classification schemes are often used as biodiversity surrogates in the absence or lack of biodiversity information to support conservation planning (Ward et al. 1999, McArthur et al. 2010a, McArthur et al. 2010b, Malcolm et al. 2012, McHenry et al. 2017). Such a plan for the KZN shelf has been a joint effort between the conservation authority Ezemvelo KZN Wildlife and the South African National Biodiversity Institute to define biodiversity zones (biozones) using multiple data layers. These include remotely sensed and seafloor characteristics as biodiversity surrogates for the KZN shelf (Harris et al. 2011a). The efficiency of abiotic-based habitat classification schemes as biodiversity surrogates in conservation planning is poorly understood (Ward et al. 1999, Mumby et al. 2008). The objective of this study is to test the efficiency of predefined abiotic-derived habitat classification schemes as surrogates for biodiversity conservation on the KZN continental shelf. In this case, to test marine macrobenthic distribution as a surrogate for overall biodiversity, through marine spatial planning biozones.

1.2 Coastal marine environments

The ocean is the largest ecosystem, covering approximately 70% of the earth's surface (Snelgrove 1997, Ellingsen 2002) and supports millions of diverse species, some as yet undiscovered (Snelgrove 1999). The ocean floor, of which 80% is unconsolidated sediments, encompasses a number of geological and biological structures, such as canyons, reefs, paleo-coastal lagoons and biogenic structures, which promote biodiversity wealth (Ellingsen 2002, Brooks et al. 2006, Lange 2013). Continental shelves are a relatively small portion of the ocean floor (7.5%) but are important for sediments transported from the coast to the deep ocean basins. Coastal shelves are also important for social, economic and ecological benefits, including supporting commercial and recreational fishery industries. This is due to their high biological productivity as they mineralise over 52% of the global organic content, being a significant hydrocarbon reservoir and carbon fixation area, among others (Karakassis and Eleftheriou 1997, Middelburg et al. 1997, Bauer and Druffel 1998, Weaver et al. 2000, Martín et al. 2006, Liu 2014, Snelgrove et al. 2014).

The Western Indian Ocean (WIO) shelves are generally wide and defined by a smooth relief owing to their tectonic inactivity, and are characterised by a thick accumulation of soft sediments where fluvial sediments supply is in excess (Falvey and Middleton 1981, Scrutton 1982, Griffiths et al. 2010). The South African east coast continental margin typifies the above and is characterised by deep basins filled with thick soft sediments and sedimentary rocks (Uenzelmann-Neben and Huhn 2009). On the east coast of South Africa, the KwaZulu-Natal continental margin exhibits a typical passive margin morphology formed by rifting with subsequent modification by sea-level rise and sedimentary processes (Moir 1974, Flemming 1978, 1981). This margin is notable for its narrow shelf and steep slope for the greater part, except for the shelf area off the uThukela Estuary, where the shelf widens considerably owing to the uThukela River sediments extending to the shelf break offshore (Flemming 1978, 1981, Martin and Flemming 1988, Bosman 2012). This shelf is separated from the continental slope by the shelf break or edge sharply defined at 200 m isobaths (Moir 1974, Flemming 1978). Sometimes, the shelf edge is incised by underwater canyons running perpendicular to it, and stretching to deeper waters (Flemming 1981, Ramsey and Miller 2002, Green 2009). These canyons may act as a sediment sink offering shelter and protection from the overlying Agulhas Current (Ramsay and Miller 2002, Green 2009). Furthermore, they may affect the biocoenosis of the region in the manner in which it deflects the flow of bottom water. This topographical configuration is said to be responsible for the behaviour of the Agulhas Current, sediment

distribution and oceanographic features on the shelf (Lutjeharms 2006a) and will be further explained in later sections.

1.3 Oceanography

1.3.1 Agulhas Current

On the east coast, long-term circulation patterns are established by the action of strong synoptic winds driven by earth's vorticity (Schumann 1987). These strong, local winds are not only instrumental in the formation of the Agulhas Current (AC), but also drive this highly dynamic coastal environment, contributing to a properly mixed water column with limited evidence of significant thermocline development (Davies and Clayton 1977, Field and Griffiths 1991, Green and Garlick 2011). The AC originates off the coast of northern KwaZulu-Natal at approximately 27º S flowing in a south-westerly direction and veering off the coast of Port Elizabeth at approximately 17º E (Lutjeharms 1981, Lutjeharms and Roberts 1988, Schumann 1988, Lutjeharms 2006a). This is a relatively narrow current, with a mean width of ~100 km, flowing close inshore near the 200-m isobath with mean speeds of about 1.4 $m.s^{-1}$ to about 1.6 $m.s^{-1}$ (Heydorn et al. 1978, Schumann 1987, Lutjeharms 2006b, Lutjeharms et al. 2010). The AC follows a stable path along this shelf, steered by a joint effect of a narrow continental shelf and steep slope (de Ruijter et al. 1999, Lutjeharms 2006a, 2007, Lutjeharms et al. 2010) and the core of which tends to follow the shelf break tightly (40-60 km offshore of the shelf break). The exception is the wider Natal Bight where it does not hold its path (Schumann 1988, Lutjeharms 2006a, Lutjeharms 2006c, Lutjeharms 2007, Louw 2014) and can meander 15 km to either side of the 200 m isobath resulting in mesoscale eddies and Durban sheared eddies (Roberts et al. 2010b, Louw 2014). Downstream propagation of this meander causes a current reversal along the shelf and may contribute to the upstream dispersal of biota (Heileman et al. 2008). Agulhas Current core waters are generally 1-2 ºC warmer than the surrounding waters (Heydorn et al. 1978, Pearson and Rosenberg 1978, Schumann 1988, Lutjeharms 2006a). In a recent survey the core AC sea surface temperature varied from 24-26 °C in May to 22.0-22.5 °C in July, while shelf waters were up to 4 °C cooler than the AC core (Roberts et al. 2010b). The surface waters at the edge of the AC originate inshore and are generally cooler with a slightly lower salinity than that of the Agulhas Current. The minimum and maximum average temperature varies between 22 ºC in winter and 27 ºC during summer, respectively. Salinity decreases even more during the summer months owing to high rainfall and increased river input (Heydorn et al. 1978). Neighbouring water masses of different salinity and temperature are known to form boundaries, and thus the formation of zoogeographical boundaries (Longhurst 1958). Occasional landward movement of the AC results in water from the current (including fauna)

being transferred to the inshore water contributing to the tropical and subtropical characteristics (Pearce 1977, Lutjeharms 2006b). This exerts an effect and impact on the coastal environment, biogeography of marine organisms and patterns of energy flow and nutrient recycling (Pearce 1977, Harris 1978, Schumann 1987, Beckley 1995, Heileman et al. 2008, Lutjeharms et al. 2010).

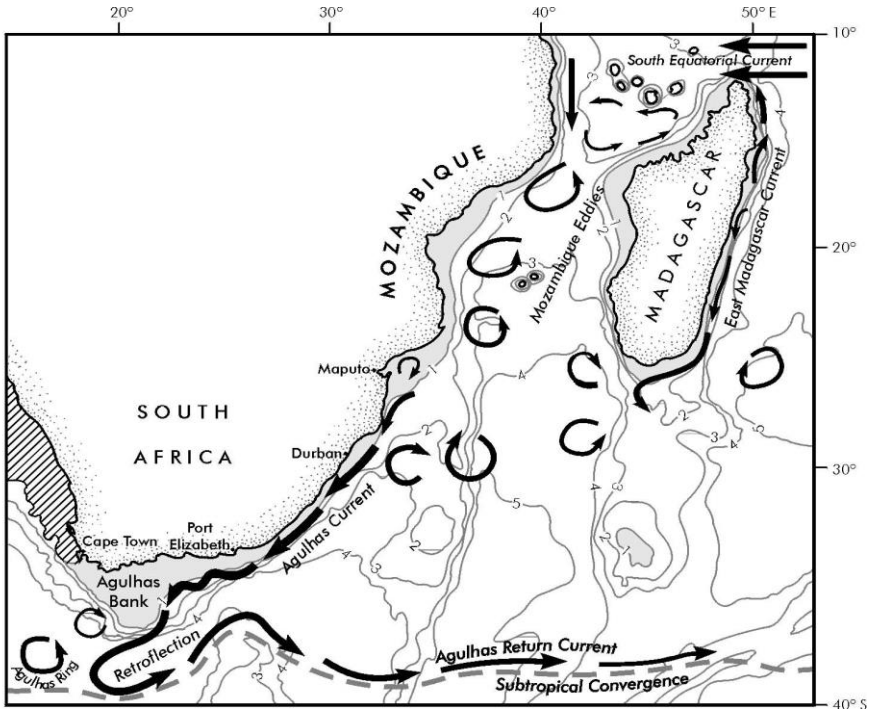

Figure 1.1. Bathymetry of the South West Indian Ocean and the major circulation features. Thick solid arrows indicate the direction of the Agulhas Current and circular arrows indicates mesoscale eddies (after from Lutjeharms 2006).

1.3.2 Local oceanographic features and circulation

The northern shelf between Richards Bay and St Lucia has a topographically induced upwelling cell (Lutjeharms et al. 1989, Lutjeharms 2006a, Barlow et al. 2008, Heileman et al. 2008, Lutjeharms et al. 2010), bringing nutrient-rich waters onto the shelf though Ekman transport which may determine the ecology of the region (Pearce 1977, Heydorn et al. 1978, Meyer et al. 2002, Merino and Monreal 2004, Lutjeharms 2006a).

The uThukela River outflow, discharges various volumes of freshwater and large quantities of detritus and fine-grained sediment (Begg 1978, Heydorn et al. 1978), and has been reported by several authors as a source of sediments and detritus along the shelf (Flemming and Hay 1988, de Lecea et al. 2013). Mud, from this feature migrates outwards in suspension, resulting in a turbid environment, and settles on offshore mud banks, creating a dynamic mud depocentre in the subtidal zone (Flemming and Hay 1988), which in turn influences local ecology (MacKay et

al. 2016, Untiedt and MacKay 2016). The Durban cyclonic eddy is formed as the AC overshoots the narrowing shelf offshore of Durban (Schumann 1988, Lutjeharms and Ansorge 2001, Lutjeharms 2006a, Lutjeharms et al. 2010, Louw 2014), bringing nutrient rich waters onto the shelf waters (Meyer et al. 2002, Lutjeharms 2006a). The pronounced effect of the AC on the coastal ocean along the entire KZN coastal stretch is remarkable and understanding the dynamics of this phenomenon is fundamental to understanding the ecosystem of this shelf (Schumann 1987, Schumann 1988, Beckley 1995, Lutjeharms 2006a, Heileman et al. 2008, Vousden et al. 2008, Lutjeharms et al. 2010, Louw 2014).

The nearshore northern regions of the KZN Bight are strongly influenced by synoptic coastal winds (Schumann 1988) and the northerly flow and frequent current reversals are consistent with the wind direction (Pearce 1977, Roberts et al. 2016). The trapped water on the KZN Bight causes a general cyclonic circulation in the northern Bight, triggering formation of small eddies on the mid and outer shelf areas (Schumann 1988). Their intensities of which rely on the distance and stability of the AC offshore (Pearce 1977, Harris 1978, Flemming and Hay 1988). The inshore currents south of the uThukela River flow in a northerly direction and form a general cyclonic circulation in the southern part of the Bight (Roberts et al. 2016), which is reflected in the long-shore drift patterns and bedload parting (Flemming and Hay 1988). The semi-permanent Durban eddy is associated with strong north-eastward counter currents (Guastella and Roberts 2016) transporting water southwards down the KwaZulu-Natal coastline as well as northwards onto the shelf and inner regions of the KwaZulu-Natal Bight. This eddy is also associated with increased primary productivity due to the upwelling of cooler nutrient rich water in the water column (Untiedt and MacKay 2016), which supports high numbers of suspension feeders in the macrobenthos on the mid-shelf area off Durban (Untiedt and MacKay 2016). The combined influence of the aforementioned conditions make for what are apparently unique benthic habitats along this shelf area (MacKay et al. 2016).

1.4 Physico-chemical characteristics

1.4.1 Temperature

The sea-surface temperature (SST) of the KZN shelf waters is linked to Southern African seasonal rainfall variability (Landman and Mason 1999a, b, Mason and Tyson 2000). Warmer SST of the AC system, for instance, has been correlated with the wetter summer season of the region, similarly, cooler SST has been associated dry winter season (Jury et al. 1993). The average maximum SST off Durban is 25 °C in February during the summer season, and the minimum is 21 °C in the months of July and August during the winter season (Heydorn et al.

1978). Recent records of SST indicate a range between 20-22 °C in the KZN Bight during the month of September 2005 (Barlow et al. 2008). Temperature is among the environmental gradients that define species' fundamental niches by affecting physiological processes and thus playing a critical role in the occurrence and distribution of fauna (Meynard and Quinn 2007, McArthur et al. 2010a). Temperature gradients are most apparent during summer months, which is also peak rainfall season.

1.4.2 Salinity

A large number of estuaries are on the KZN coastline (Begg 1978), discharging large quantities of freshwater onto the shelf during the peak rainfall of the summer months. This has a substantial effect on salinity and temperature gradients of coastal waters (Pearce 1977, Heydorn et al. 1978, Clark et al. 2000), with shallow waters being more likely to be affected because variation in these parameters are transferred down to the seafloor. Nevertheless, discharges of freshwater are sporadic and localised, therefore their overall effect on the vertical density structures and currents is negligible (Schumann 1988). In rare events, after heavy summer rains, silt-laden floodwaters extend several kilometres offshore, but are of short duration (Schumann 1988). KZNs shelf water is a composite of tropical and subtropical warm and saline waters, brought onto the shelf by the AC (Schumann 1988). On average, surface salinity varies between 35.3 and 35.5 psu (Schumann 1988), with high salinity values associated with sub-tropical water from the mid-latitude Indian Ocean and lower values attributed to tropical water. Certain taxa are sensitive to salinity gradients, consequently, variation in salinity could be a limiting factor exerting a direct influence on the benthic organism occurrence and distributions (Jones 1950). Nevertheless, an increase in vertical gradients may be very advantageous in the pelagic system by keeping planktonic organisms in the upper layers and concentrating food supply for larger organisms (Heileman et al. 2008, Lutjeharms et al. 2010).

1.4.3 Nutrients

Mesotrophic and eutrophic coastal waters are associated with high primary production (Bosman and Hockey 1986) and are dominated by few taxa able to monopolise these resources under ambient conditions (Huston 1979, Bertness et al. 2001) and therefore, support low species richness (Snelgrove and Butman 1994) and high species evenness (Hillebrand et al. 2007). This is in contrast to the oligotrophic waters, which support low biomass communities with high species richness, but have high levels of endemism (Poore et al. 2008). The meso-oligotrophic waters of KZN derives nutrients from the topographically induced upwelling cell south of Cape

St Lucia, phytoplankton primary productivity and detritus brought along by floods and freshwater discharge during the high rainfall season (Pearce 1977, Begg 1978, Heydorn et al. 1978, Schumann 1988, Lutjeharms and Ansorge 2001, Kunnen 2013, Scharler et al. 2016).

Lutjeharms et al. (1989) and Meyer et al. (2002) proposed that the upwelling cell off Richards Bay is the main source of nutrients for the greater part of the shelf environment. However, recent studies have indicated that the uThukela River outwelling is an important nutrient source compared with Richards Bay and Durban (Scharler et al. 2016, Untiedt and MacKay 2016). This area derives its nutrients from the fluvial input brought onto the shelf by the uThukela River. This affects the turbidity of inshore waters (Heydorn et al. 1978, Flemming and Hay 1988), preventing light penetration and therefore primary productivity. This is evident in the deposit-feeding macrobenthos found in the area (Untiedt and MacKay 2016). Several other upwelling cells occur and inject nutrients but at lower levels relative to the Richards Bay upwelling cell. For example, Gründlingh and Pearce (1990) indicated an upwelling that could be caused by an eddy in the large cyclonic rings (deeper than 100 m) propagating downstream from north of the KwaZulu-Natal Bight. Schumann (1988) and Carter and d'Aubrey (1988) identified an upwelling cell that could result from the Durban eddy. Although such upwelling cells last for a short period of time (2-3 days), their effects as fortuitous nutrient source often last longer.

1.4.4 Sediment characteristics

Sediment dispersal and distribution on the KwaZulu-Natal shelf are controlled by a complex interplay of the AC and associated oceanographic processes, shelf configuration, and sediment supply (Flemming 1981, Schumann 1987, Lutjeharms 2006a) and these are a vital determinant of the structure and distribution of macrobenthic assemblages (Sanders 1958, Heydorn et al. 1978, Gray 1981). Sediment input onto the KwaZulu-Natal shelf and margin is mainly of fluvial origin and from biogenic products (Flemming and Hay 1988). Fluvial entry is mainly from the uThukela, uMvoti, uMngeni and uMkhomazi estuaries (Birch 1996, Green and MacKay 2016). Shell gravel, animal tubes, mounds, pits and faecal casts constitute biogenic materials of this shelf environment (Walling 2006, Passarelli et al. 2012). The uThukela Estuary is by far the main source and when outflow is high, acts as an offshore estuary depositing organic matter in the sediments and plays an important role in the demersal food web by supporting the majority of organisms and communities which occur along the shelf (de Lecea et al. 2016, Untiedt and MacKay 2016). Sediments brought onto the shelf by these coastal systems are kept in suspension by wave action, wind regimes and ocean currents until they are transported out from

the shelf or trapped within closed eddies where they settle out (Flemming and Hay 1988). This is reflected by a fine and very fine, well sorted sediments cordon (0.125-0.25 mm) between Richards Bay and south of uThukela (Untiedt and MacKay 2016), running perpendicular to the shelf from uThukela Estuary to the shelf edge (Green and MacKay 2016). Course grade sediments (Green and MacKay 2016) dominate the sediments on the far north KwaZulu-Natal shelf, while south of the uThukela there is widespread mixing of the different sand grain sizes (Flemming 1978, Flemming and Hay 1988). The shelf area south of Durban is characterised by a thick accumulation of sediments and is the second largest sediment deposit on the eastern margin located between Amanzimtoti and Hibberdene, known as the uMkhomazi sediment deposit (Birch 1996). However, due to the presence of a sub-parallel ridge between Green Point and Scottburgh (forming a barrier against sediment movement) the mid-outer shelf area is devoid of fine sand. It is mostly characterised by gravels, while small quantities of fine sediment (mud, silt and clay) are found on the inner shelf with some mud off the uMkhomazi Estuary (Birch 1996).

On the shelf, the sedimentary characteristics are broadly described based on the inner and outer shelf zones. Flemming (1981) defined the inner shelf as a dynamic zone of terrigenous deposition and transport from the major river mouths forming an inshore terrigenous prism of fine sediments accumulated after the last glaciation (Heydorn et al. 1978). A frontier of the inner shelf finer terrigenous sediments from the outer shelf coarser biogenic sediments is evident between 50-60 m isobaths, defined by a band of gravel substrate of aeolianites associated with a consolidated paleo-dune feature (Flemming 1978, Flemming and Hay 1988, Green and MacKay 2016). Finer terrigenous sediments of this region are composed of terrigenous mud, which due to the increased levels of organic matter provide a suitable habitat for benthic communities, and is where unique communities of macrobenthos occur (MacKay et al. 2016). The outer shelf is vulnerable to winnowing and scouring by the AC and is therefore dominated by carbonate-rich current induced size-sorted gravel (>2 mm) mainly composed of relict shell fragments (Heydorn et al. 1978, Flemming 1981, Flemming and Hay 1988, Lutjeharms 2006a). Furthermore, the AC is responsible for the south-westerly facing large-scale subaqueous dunes in the unconsolidated sediment of the outer continental shelf (Flemming 1978, 1980, 1981, Flemming and Hay 1988, Ramsay 1994, Ramsay et al. 1996, Green 2009). Sediment composition and distribution is not only useful in determining geological history along the sea seafloor but is also an important predictor in species (Roland et al. 2012) abundance and community assemblages (MacKay et al. 2016) and is thus a useful biological proxy (Snelgrove and Butman 1994, Beaman 2005, McArthur et al. 2010a, Roland et al. 2012, MacKay et al. 2016).

1.5 Macrobenthic communities

Marine macrobenthic fauna are the suite of invertebrate animals with a close association with the seafloor, inhabiting the sediment, or living on, or in other available bottom substrates of the marine ecosystem (Sanders 1958, Gray 1974a, Gray 1981, Karakassis and Eleftheriou 1997, Somerfield et al. 2005, Gray and Elliott 2009). Macrobenthos encompasses a wide range of taxonomic and functional entities confined to relatively small areas due to their limited mobility, therefore unable to avoid unfavourable conditions and effectively integrate historical environmental conditions (Warwick 1993, Salas et al. 2006). As such, any disturbance, either natural or anthropogenic-induced will eliminate some organisms and the remaining community structure reflects species with traits optimised for the altered environment and prevailing conditions integrated over time (Townsend and Hildrew 1994). They have a long generation time (years rather than months), occur in a wide variety of forms (varied life history strategies) and habitats and respond to many types of environmental pressures, e.g. pollution, habitat degradation and disturbance (Pearson and Rosenberg 1978, Gray 1981, Warwick 1987, Snelgrove and Butman 1994, Snelgrove 1997). Therefore, macrobenthos offer more advantages in assessing local effect (Warwick 1993), and for assessing ecosystem quality and environmental changes (Gray 1981, Gray et al. 1990, Warwick et al. 1990, Warwick 1993, Stewart et al. 2000, Gray and Elliott 2009). Macrobenthic infaunal communities form a vital component of marine ecosystems, providing a number of ecosystem functions. These include altering chemical conditions between sediment and overlying water column through bioturbation activities, enhance nutrient cycling, pollutant metabolism, burial and dispersal and promote decomposition (Snelgrove and Butman 1994, Hansen and Kristensen 1997, Tweedley and Valesini 2008). Furthermore, macrobenthic fauna play an important component in the food web, not only by consuming detrital material and primary food sources (Riisgard 1991), but also providing a major food source to fish, thus transfering organic carbon to other food web components (Petti et al. 1996, Snelgrove 1999).

1.5.1 Classification of macrobenthic communities

1.5.1.1 Taxonomic classification

In marine benthic ecology, macrofauna community classification is normally based on biotic composition separating fauna at the lowest level possible, mostly species (Jones 1950, Boesch 1973, Gray and Elliott 2009). Analyses based on species taxonomic level are vital as they also augment knowledge of regional biodiversity and endemicity. In South Africa, the biodiversity

of the continental shelf soft-bottom habitats still remain poorly studied (Griffiths et al. 2010). Thus, focusing on the taxonomic approach is adopted in Chapter 3 of this study.

1.5.2 Functional classification

Using species based measures such a species richness and diversity provides only taxonomic relationships without information regarding their functioning (Ellingsen 2001, Hooper et al. 2005, Gray and Elliott 2009, Pacheco et al. 2011). Yet ecosystem level processes are influenced by species-specific traits rather than their identities (Giller et al. 2004, Hooper et al. 2005). An equivalent and perhaps more insightful description is of functional traits of the taxa involved, taking into account the limitation of taxon-based classification (e.g. Blondin et al. 2003, Mouillot et al. 2006). This approach groups species based on ecological equivalency, e.g. energy sources. Several methods are proposed to address different aspects of community or ecosystem structure.

1.5.2.1 Macrobenthos feeding modes

Derivation of trophic groups involves clustering of taxa based on similar feeding modes and resource requirements, to depict linkages between the taxa and the resources they potentially regulate (Gray et al. 1988, Roth and Wilson 1998, Bonsdorff and Pearson 1999, Hulot et al. 2000, Gray and Elliott 2009, Pacheco et al. 2011, Untiedt and MacKay 2016). This functional classification distinguishes between autotrophic and heterotrophic groups. Macrobenthos comprise detritivores, secondary producers (acquiring their energy from plants or other fauna) and predators (Pearson and Rosenberg 1978, Gray 1981, Gibson et al. 2001b). In this context, feeding mode refers to the mechanism of food transport from the environment into the organism (Fauchald and Jumars 1979), with food acquisition manner and food sources related to the physical characteristics of the environment. In this manner, feeding mode analysis also provides indirect information about hydrographic conditions and sedimentary characteristics (Sanders 1958, Probert and Grove 1998, Sanders et al. 2007, Dolbeth et al. 2009). This method focuses only on feeding method and neglects other important functions.

1.5.2.2 Macrobenthos feeding guilds

Feeding guilds (Fauchald and Jumars 1979, Morin et al. 1985, Mouillot et al. 2006, Dolbeth et al. 2009), take into account a few biological traits. These include feeding type, reproductive strategy, locomotion type and habitat preference of the constituent taxa, and provides a broader perspective of the functional structure of communities and ecosystems (Usseglio-Polatera et al. 2000a, Bremner et al. 2003b, Siefert 2012, Untiedt 2013). This classification offers stronger

links between species and ecosystem functioning, by focusing on a limited set of species traits. However, with this some important ecological information and interactions may be overlooked or lost (Charvet et al. 1998, Mancinelli et al. 1998).

All these efforts of classification are useful schemes that have been followed to simplify and extract information from the patterns and events shown by the collection of multi-species populations or to understand complicated ecological systems (Blondin et al. 2003). Despite their usefulness, these approaches can only offer limited information on ecosystem functions in view of a small number of traits selected and difficulty in making spatial comparisons (Elliott and Quintino 2007, Pacheco et al. 2011, Włodarska-Kowalczuk et al. 2012, Leung 2015a).

1.5.2.3 Macrobenthos biological traits

Both functional classification approaches described above simplify communities through partitioning of species into homogenous functional units. These units group species based on ecological equivalency, such as those based on energy sources (Persson et al. 1992, MacNeil et al. 1997, Pace et al. 1999). However, marine benthic organisms are involved in a number of ecosystem-level processes, often described as 'ecosystem functions', which refer to any transformation process that occurs in an ecosystem (Rosenburg 2001, Cooper et al. 2008). Fauna can therefore be classified according to their functional role, represented by a set of functional traits assigned to behavioural, reproductive and morphological characteristics displayed by the observed taxa (Paganelli et al. 2012) (Fig 1.2). In this way, a multifaceted nature of the ecosystem is recognised. Therefore, biological traits provide a holistic overview of the functional structure of communities and ecosystems (Bremner 2005, Bremner et al. 2006c, Beche and Resh 2007, Bremner 2008, Frid et al. 2008, Marchini et al. 2008, Pacheco et al. 2011, Macdonald et al. 2012, Paganelli et al. 2012, Törnroos and Bonsdorff 2012, Pacheco et al. 2013, Alves et al. 2014, Snelgrove et al. 2014, Berthelsen et al. 2015). Biological trait analysis (BTA) combine quantitative structural data (abundance) with a wider array of biological attributes of the taxa (Shettleworth 2012) to functionally characterise community assemblages (Bremner et al. 2006c) and is suitable for analysing assemblage responses to environmental gradients (Paganelli et al. 2012, Shettleworth 2012). Therefore, BTA offers mechanistic links between benthic communities, environment and ecosystem processes (Pacheco et al. 2011, Shojaei et al. 2015). This is the approach adopted in Chapter 4. This classification is based on sound ecological theory (Townsend and Hildrew 1994), where there are strong correlations between functional traits and ecosystem processes.

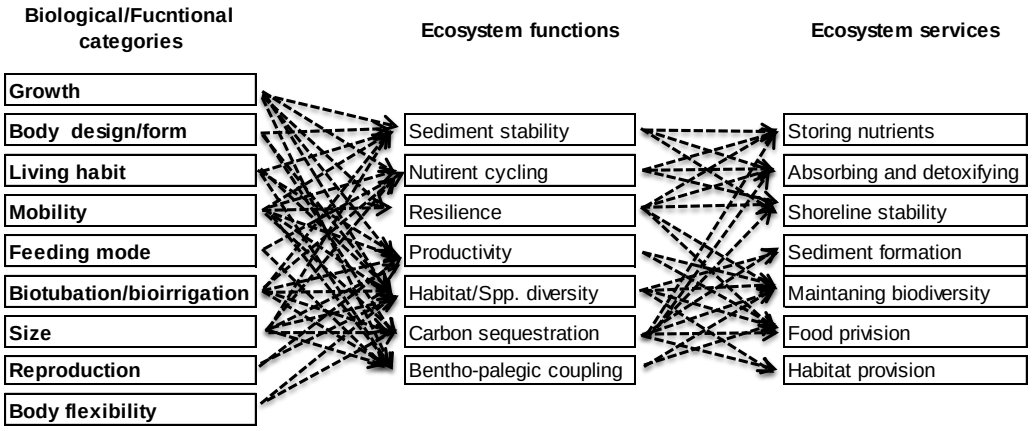

Figure 1.2. Examples of biological/functional traits linked with important ecosystem functions and services

1.6 The effect of environmental factors

Macrobenthos are directly linked to the substrate in which they reside (Alexander et al. 1981), such that the assemblage present at any given time is governed by the prevailing environmental conditions (Jones 1950, Thorson 1957, Sanders 1958, Browder 1983, Snelgrove 1999, McArthur et al. 2010a, Martins et al. 2013). These interactions play an imperative role in physical and chemical changes at the sediment-water interface (Eckman 1983, Pacheco et al. 2011). Tube-building and burrow construction activities on an otherwise smooth seafloor, result in an important architecture of biogenic material. The resultant structural complexity, provides refuge for other species (resident and migratory organisms), including juveniles of economically and ecologically important fish species (Van Hoey et al. 2004, Rabaut et al. 2007, Van Hoey et al. 2008). Furthermore, these structures are known to stabilise sediments by altering the character of the near-bed flow (Eckman et al. 1981, Eckman 1983). In contrast to the sediment-stabilisation effect, burrowing activities destabilise sediments creating mounds and depositing faecal material at the sediment surface, thus enhancing nutrient exchange and oxygen penetration into the sediments. Biological alteration of the sediment is extremely important; shells, animal tubes of a variety of shapes, sizes and durability, faecal piles, holes and pits are all key elements of the structure and functioning of these habitats (Eckman 1983, Probert and Wilson 1984, Kaiser et al. 1999, Wilson 2005, Levin et al. 2010, Kaiser et al. 2011, Passarelli et al. 2012).

Shelf macrobenthos in relation to environmental variables are widely studied and the best correlative habitat drivers shaping the structure, distribution, abundance and diversity of these fauna, include sediment granulometry, organic content and turbidity (Gray 1974b, Snelgrove and Butman 1994, Ellingsen 2001, Van Hoey et al. 2004, Jayaraj et al. 2007, Steffani et al.

2015, MacKay et al. 2016). Additionally, abiotic characteristics of the pelagic system influence macrobenthic community assemblages, including bottom water temperature, salinity, dissolved oxygen concentration and light penetration (Gray 1981, McArthur et al. 2010a). Therefore, knowledge of environmental variables can help to establish a mechanistic understanding of diversity patterns. In particular, where important links are establish between the bottom water dynamics and macrobenthic structure, providing insights into benthic ecology (Snelgrove and Butman 1994, Bergen et al. 2001, Gotelli et al. 2009, Dou et al. 2016, Herkül et al. 2016, Lee et al. 2016, Tittensor and Worm 2016, Veiga et al. 2016, Defeo et al. 2017).

1.6.1 Macrobenthic infauna in relation to environmental variables

The distribution of organisms relative to habitat environmental conditions is vital in ecology. A number of studies have highlighted that benthic assemblages are distributed according to their capability to cope with physico-chemical, hydrodynamic factors and biological forces (Labrune et al. 2008, Carvalho et al. 2011, Soto et al. 2017). In coastal ecosystems environmental factors are controlled by natural processes (e.g. water masses movement, sediment deposition) and factors related to coastal land use management (Akoumianaki et al. 2012, Veiga et al. 2016). Other than habitat types, important abiotic factors structuring coastal benthic communities include characteristics of the sedimentary environment (Gray 1974a, Snelgrove and Butman 1994, Martins et al. 2012, Soto et al. 2016, Ellis et al. 2017), sedimentary organic matter lability (Pearson and Rosenberg 1978, Rosenberg 1995, Soto et al. 2016), depth (Karakassis and Eleftheriou 1997, Hughes et al. 2009, Joydas et al. 2012) and hydrological gradients (e.g. turbidity, salinity) (McLusky 1993, Hughes et al. 2009, Anthony et al. 2010, Gogina and Zettler 2010, Veiga et al. 2017). However, the importance of certain environmental variables in shaping macrobenthic communities are related to a wider set of other environmental conditions, e.g. sediment configuration is related to current speed and depth (Gray 1974a, Probert et al. 2001, Dolbeth et al. 2007, Martins et al. 2012, Sampaio et al. 2016). By the same token, the importance of sediment may in the case of muds, play a role in the sediment organic content (e.g. a nutrient source) (Weston 1988, Santos and Pires-Vanin 2004). In addition, sediment discharge may adversely affect infauna by smothering immobile forms or forcing mobile animals to migrate and by altering grain size distribution, thus influencing colonisation during recovery (Gray 1997b). Fine sediments in areas with high river runoff are vulnerable to water agitation and in combination with discharged terrigenous material can remain in suspension for variable periods, affecting light penetration, primary production and in particular, filter feeders (Akoumianaki et al. 2012). Sediment texture is also linked to habitat provision where heterogeneous sediments, with more potential niches, support higher diversity, but low

abundance. This is in contrast to homogeneous nutrient rich sediments tending to support low diversity and high abundance (Gray 1974a, Burone et al. 2003).

Water depth is commonly identified as the most important environmental correlate of marine infaunal community structure (Carney 2005). However, depth co-varies with other important variables such as temperature, pressure and the downward flux of organic matter that fuels benthic organisms (Sanders 1968, Rhoads and Young 1970, Gray 1974b, Snelgrove and Butman 1994, Ellingsen 2002, Veiga et al. 2016). In this context, increased depth is therefore correlated with a decline in the abundance and richness of benthic organisms (Hyland et al. 1991, Karakassis and Eleftheriou 1997, Manokaran et al. 2015). Furthermore, with increasing depth, substrate variability decreases as do structures as a source of habitat heterogeneity (Sanders 1968, Levin et al. 2001, Carney 2005, Currie et al. 2009, Williams et al. 2010). Yet an inverse relationship between depth and organic content and community variables (# of taxa and abundance) has been widely cited for many continental shelf environments. This paradigm does not hold for all shelf environments and the opposite (highest abundance) was verified in the mid-shelf environments off California (Bergen et al. 2001) and central Chile (Soto et al. 2016).

1.7 Marine macrofauna of South Africa

Exploratory expeditions of the South African shelf benthic habitat began at the turn of the 19th century (Brown 1999, 2003). Most collection was limited to the seashore, only extending offshore in the second half of the 19th century (Brown 1999). The nomination of Keppel K.H. Barnard to the South African Museum in 1911 was a major event, having important implications for South African marine invertebrate taxonomy and he still is the most prolific marine taxonomist South Africa has known (Brown 1999, 2003). Barnard monographed some 800 South African Decapoda taxa (Barnard 1950) and provided descriptions and keys for their identification. This remains the formative work on this group (Brown 1999, 2003). During the first half of the 20th century, a series of oceanographic expeditions on the South African shelf were undertaken aboard the research vessel, *R.V. Meiring Naudé* (Brown 1999, 2003). Important taxonomic compendia emerged from these studies providing the descriptions of Echinodermata through the work of Clark (1923) and Clark and Courtman-Stock (1976), Amphipoda were studied by Griffiths (1976), while Kensley (1972) described shrimps and later Isopoda of the area (Kensley 1978). John Day dedicated most of his career to the extensive study of polychaete worms and compiled a comprehensive synopsis in two-parts (Errantia and Sedentaria); *The Polychaeta of southern Africa* (Day 1967). Day (1975-1980) also contributed to our little knowledge of Cumacea.

A composite taxonomic databank of marine benthic invertebrates collected for South Africa is still lacking, despite the taxonomic history of the shelf dating back to the 19th century. This is, in part, because the initial work was completed by well-known international taxonomists with most records deposited in the international museums, e.g. Europe (Brown 1999, Brown 2003). However, locally collections are archived at the Iziko Museum in Cape Town, formerly the South African Museum and by other collections such as the Mollusca at the Natal Museum. Considering the available taxonomic data collected along the entire KwaZulu-Natal (KZN) coast from 1974 to the late 1980s, Polychaeta were the most abundant and speciose group sampled (McClurg 1988). Generally, irrespective of location, polychaetes tend to be the most commonly encountered animals inhabiting marine sediments, followed by crustaceans, molluscs and echinoderms (Fauchald and Jumars 1979, Gray and Elliott 2009). McClurg (1988) reported 37 polychaete families in the last extensive study of the Natal Bight, with Syllidae and Spionidae being the most prolific. Subsequent studies also reported the dominance of polychaetes in terms of species and abundances (McClurg et al. 2000, McClurg 2004, McClurg et al. 2006, MacKay et al. 2016, Untiedt and MacKay 2016). Crustacea of the KZN shelf are in great abundance (per m^2), particularly the Amphipoda, as highlighted by McClurg (1998) and subsequent surveys off Durban in 2004 recording 26 taxa, many of which are endemic to this shelf (McClurg 2004). Of the 20 Amphipoda taxa recorded on the Natal Bight, the families Haustoriidae, Ampeliscidae, Corophiidae and Phoxocephalidae were the most abundant (McClurg 1988). The importance of Ampeliscidae in characterising KZN fauna was also confirmed by Arabi (2010). However, additional species and records have been made recently in widespread studies of the KZN Bight (MacKay et al. 2016, Untiedt and MacKay 2016), with the families Ampeliscidae, Corophiidae, Aoridae, Lysianassidae and Urothoidae recorded in high numbers. Until now, 48 subtidal Isopoda and 35 Cumacea are known along the KZN shelf, with other Crustacea belonging to Caridea, Penaeida, Anomura and Brachyura being identified in subtidal surveys off Durban and Richards Bay (McClurg 1988, McClurg et al. 2000, McClurg 2005). Recently, KZN Bight studies (MacKay et al. 2016, Untiedt and MacKay 2016), recorded Isopoda taxa belonging to the families Anthuridae, Arcturidae and Cirolanidae in excess of 10-20 individuals per family. Of the Mollusca, the KZN shelf supports the highest richness in South Africa (Kilburn 1999). McClurg (1988) recognised a significant increase in the occurrence of tropical Indo-Pacific molluscs in KwaZulu-Natal waters, when compared with the southern and western coasts. Many descriptions of mollusc fauna (mostly Bivalvia) were obtained from material collected during the Natal Museum Dredging Programme (1981-1996) (Herbert 1989, 1991, Kilburn 1992, 1998, Kilburn 1999). Few Gastropoda have been identified in KZN shelf benthic samples (McClurg et al. 2000, McClurg 2005, MacKay et al. 2016,

Untiedt and MacKay 2016). In terms of Echinodermata, McClurg (1988) recorded 40% of the 240 taxa known in South African on the KZN shelf. A recent examination of the regional echinoderms include the studies on holothuroid (Samyn 2003, Thandar and Rowe 2005, Thandar 2009) and a revision of the Ophiocoma (Ophiuroidea) taxa of South Africa (Olbers and Samyn 2012).

Comprehensive taxonomic and community studies on the KZN shelf are generally limited and far less definitive, with most of the studies undertaken in South African waters, focused mainly on the west coast (Mead 2007, Griffiths et al. 2010). Long-term benthic monitoring programmes have however been ongoing at specific sites of interest along the shelf, namely Richards Bay, Durban and Amanzimtoti, designed to assess the cumulative impacts of pipeline effluents (McClurg 1988, McClurg et al. 2000, McClurg 2004, Arabi 2010). These give limited information on the ecological aspects of the communities and on the distribution of other taxonomic groups. There are, however, recent studies on the region but limited to environments associated with coral reef habitat (Harmer 2014). Considering what is known of the diversity and endemism of marine fauna, such as becoming increasingly more taxon rich towards the subtropical east coast, this dearth of information hinders the ability to accurately appreciate, manage and conserve benthic biodiversity of South African waters (Heydorn et al. 1978, Emanuel et al. 1992, Mead 2007, Griffiths et al. 2010).

The first phase of the African Coelacanth Ecosystem Programme (ACEP) was carried out to understand the processes that support marine life. This was achieved by implementing a number of projects for biodiversity, genetics, environmental education and conservation planning including a KZN Bight wide survey for gathering biological, chemical and geological data. During the second phase of ACEP (ACEP II), the KZN Bight was surveyed in depth to determine and understand the dynamics (physical, geological and biological) of the ecosystem functioning within the Bight area. The work of MacKay et al. 2016 and Untiedt and MacKay (2016) which emerged from ACEP II publications, succeeds the generalised review of earlier mentioned studies based on limited sampling, and these appear to be the only studies focused macrobenthic community of the region, and for which results are available.

1.8 KZN marine spatial planning surrogacy approach

Marine ecosystems are suffering the synergistic effects of multiple extractive and non-extractive pressures from various human uses (e.g. fishing and mining) (Claudet 2011). Our understanding of the effects of these uncontrolled stressors on marine resources remains speculative, despite the severity of their accumulated impact (Peterson and Bishop 2005). Better recognition of the role of biodiversity and marine ecosystems to the health of the planet and the increasing human dependency on ocean resources is vital (Culotta 1996, Bengtsson et al. 1997, Aarts 1999, Snelgrove et al. 2014). In response, some pro-active governments have acknowledged the need for more ecosystem-based conservation measures in the marine environment (Douvere and Ehler 2009, Lester et al. 2013). The use of Marine Protected Areas (MPAs) is becoming widely adopted to protect ecosystems and their biodiversity (Halpern et al. 2010, Gleason et al. 2013, Edgar et al. 2014). Marine Protected Area (MPA) network design principles traditionally include objectives of protecting an exhaustive network of representative habitats and ecosystems; those which are rare, distinctive or inter/nationally important (Roberts et al. 2003). One major consideration when designing a network of MPAs, is the representation of habitat and the ability to capture the diversity and heterogeneity of habitat features that support biodiversity (Roberts et al. 2003, Stevens and Connolly 2005, Foley et al. 2010, Halpern et al. 2010). However, the scarcity of ecological data frequently limits understanding of spatial patterns of biodiversity features (both habitats and individual species) that underpin the design of biodiversity protection (Snelgrove et al. 2014, Lecours et al. 2015, Dunstan et al. 2016). The classification and mapping of ecosystems are foundational steps for biodiversity assessment and forms part of the marine spatial planning (MSP) process (McHenry et al. 2017). Marine Spatial Planning is an essential tool that provides a spatially explicit framework for assessing the spatial distributions of biological and physical patterns and processes that sustain marine biodiversity (Douvere 2008, Agardy et al. 2011). A clear understanding of the information derived through MSP (spatial distribution of the offshore environment and its biodiversity) is thus a precursor to informed decisions regarding spatial management.

Due to the lack of data for the offshore environment, different surrogate estimates and proxies, in which environmental variables are used to predict the patterns of marine biodiversity, provide a promising alternative to biological sampling (McArthur et al. 2010a, McArthur et al. 2010b). An increasingly-used proxy for biodiversity in the marine environment is some form of predefined or categorised seascape or habitat since they are distinguishable or separable in nature most often based on abiotic data (Törnroos et al. 2013). This is because abiotic factors determine the broad distributional patterns of marine biodiversity at a larger scale (Ellingsen

2002, Dutertre et al. 2013, McHenry et al. 2017). Therefore, relationships between fauna and environmental conditions can thus characterise seafloor habitats, defined as the physical and chemical environment in which assemblages are recognised.

The technological innovation of remote sensing, geographical information system (GIS), and mapping helped gather abiotic data layers which are more widely available (McArthur et al. 2010b, Brown et al. 2011). These have facilitated development of the relevant ecosystem classifications required for MSP-related biodiversity assessments (Ferrier and Watson 1997, Roberts et al. 2003, Lombard et al. 2004, Sink and Attwood 2008, Roberts et al. 2010a, Brown et al. 2011, Sink et al. 2011, Lecours et al. 2015, Shumchenia et al. 2015). Several studies have focused on characterising assemblages through classification of continuous abiotic variables into discrete zones of similar abiotic conditions (McArthur et al. 2010b, Brown et al. 2011). While abiotic proxies can prove valuable, their usefulness is still unknown as often ignored are complex underlying abiotic-biotic relationships, and confinement of continuous ecological patterns into discrete classifications, producing maps with assumed, and/or simplified values (Przeslawski et al. 2011). When surrogates are proposed, sufficient data to model relationships between biophysical and biotic measurements should be available to confirm whether surrogacy relationships are appropriate, before these surrogates are used to define MPA networks for biodiversity conservation (Roland et al. 2012, Dixon-Bridges et al. 2014). Often biological patterns are used to ground-truth and improve abiotic classifications (Greene et al. 2010, Kerrigan et al. 2010, Monteiro et al. 2015).

South Africa, and in particular the KwaZulu-Natal shelf, was identified as a priority area for the expansion of the MPA network in the last national marine spatial biodiversity assessment (Sink et al. 2011). This is due to this shelf being recognised as biologically important and productive (Heydorn et al. 1978, Meyer et al. 2002, Lutjeharms 2006a), and ascribed to environmental conditions emerging from the Agulhas Current (Lutjeharms 2006a, Roberts et al. 2010b). As a precursor to the MPAs, declaration information from the MSP sector is required. One such plan for KZN province was a joint development by Ezemvelo KZN Wildlife (EKZNW) and the South African National Biodiversity Institute (SANBI), through the KZN marine biodiversity plan, referred to as SeaPLAN (Harris et al. 2012). In this exercise, environmental data (Appendix 1) were digitally mapped and interpolated over the continental shelf and were used in systematic conservation planning software, Marxan, to define provincial benthic biozones that are potentially different and irreplaceable (Fig 2.2) (Livingstone 2016). This model was developed as a basis for conservation and protection of provincial and national biodiversity. The

usefulness of the biodiversity surrogate for representing marine benthic biodiversity remains poorly understood for marine conservation planning.

As part of the third phase of ACEP (ACEP Surrogacy) -a multidisciplinary and multi-institutional investigation- the KZN mid-shelf between Port Durnford and Scottburgh was surveyed to examine the validity of defining biozones using physical characteristics as proxies for biodiversity pattern in marine conservation planning. The main aims of this project were to test the robustness of the use of environmental surrogates for classification of offshore biodiversity and to investigate the validity of coupling spatial distribution patterns of benthic communities and their overlying pelagic systems in recently identified continental shelf Biozones as conservation planning units. Within this framework, the current study investigates one ecological component (macrobenthos) as a surrogate for the KZN provincial biozone template, where predefined biodiversity zones were established for MSP purposes and the establishment of MPAs.

1.9 Study Aims, Objectives and Hypotheses

This study investigates the validity of biophysical habitat surrogacy approaches for biodiversity pattern mapping by examining and describing soft-bottom macrobenthos taxonomic and biological trait community patterns and their relationships with measured environmental parameters. Observed patterns were tested relative to the KwaZulu-Natal marine spatial planning predefined biozones.

Objectives

1. To enumerate and identify macrobenthic fauna along KZN mid-shelf to the lowest practical taxonomic unit possible.
2. To assign each taxon to a biological trait based on available literature.
3. To characterise habitats based on measured sedimentary and hydrographic variables.
4. To describe assemblages based on macrobenthos taxonomic and biological trait characteristics.
5. To determine spatial differences in macrobenthic community structure and traitscape.
6. To relate macrobenthic community structure and traitscape to measured biophysical characteristics (sediment composition and hydrographic conditions).
7. To determine whether macrobenthos taxonomic and biological trait structural patterns agree with marine spatial planning predefined biozones.

Hypotheses

H_1: There is a significant relationship between macrobenthic community structure and biophysical variables measured.

H_2: There is a significant relationship between macrobenthic community traitscape and biophysical variables measured.

H_3: There are structural and/or functional differences in community patterns relative to marine spatial planning predefined biozones.

1.10 Thesis Outline

Despite previous and recent work, there remain many gaps in the knowledge of macrofauna of the KwaZulu-Natal shelf environment. This thesis aims to address some of the taxonomic and macrobenthic biodiversity gaps. It is presented as a general introduction (Chapter 1), general methods and materials (Chapter 2), followed by two chapters investigating taxonomic and trait community patterns, and test the efficiency of predefined spatial planning biozones in reflecting observed community patterns (Chapters 3 and 4). Chapter 5 integrates results from Chapters 3 and 4 to refine the existing biozone model, used by conservation planning and protection agencies. Lastly, a general discussion and conclusions are presented in Chapter 6. In more detail:

Chapter 1 provides a general description of the KZN shelf environment, its physical characteristics and macrofaunal communities, contextualising and highlighting the importance of this study.

Chapter 2 offers a focussed description of the field sampling and laboratory protocols adopted during the course of study, along with the information regarding the generic data treatment and analyses used for biological and environmental data. Methods and analysis specific to each component of the study (each hypothesis) are presented in detail in the subsequent chapters.

Chapter 3 investigates the general macrobenthic community patterns along the KwaZulu-Natal mid-shelf. Here macrobenthic fauna are classified based on taxonomic differences only. Community composition and distribution patterns are investigated and related to the measured environmental parameters and tested against the predefined biozones.

Building on the findings of the previous chapter, Chapter 4 takes two steps, firstly to investigate whether information aggregated to coarser taxonomic resolution or indicator group reflects

multivariate patterns abundance at species level? Secondly, the chapter examines KZN mid-shelf functional attributes of macrobenthic fauna classified according to biological traits. Each taxon and its traits structure were investigated and related to specific environmental parameters. In addition, this approach is used as an alternative to find agreement with the predefined biozones.

Chapter 5 uses the findings of Chapters 3 and 4 (taxonomic and trait structure) to refine the existing biozone model and to offer an alternative model based on taxonomic, traits and sediment characteristics. Further, species and trait assemblages along with sedimentary characteristic for the proposed model are provided.

Chapter 6 integrates and discusses findings from previous chapters, the implications of these findings and suggests future lines of investigation.

CHAPTER 2. GENERAL MATERIAL AND METHODS

2.1 Study area

The study area extends approximately 210 km south from Port Durnford (28° 58' 2" S 32° 10' 30" E) to Scottburgh (30° 21' 38" S 30° 47' 26" E) along the KZN continental shelf (Fig 2.1). The shoreward boundary was the 50 m isobath and the seaward boundary at the 80 m isobath, the area is considered the mid-shelf since the shelf break is sharply defined at 200 m (Moir 1974, Flemming 1978). The seaward boundary is subjected to southwest Indian Ocean influence (Pearce 1977, Heydorn et al. 1978, Schumann 1988, Cooper et al. 1995) with the Agulhas Current (AC) being the main hydrographic feature of the region that controls physical and biological processes, while being influenced by terrigenous inputs on its shoreward boundary (Lutjeharms 2006a, Chapter 1). The study area constitutes more than one third of the 570 km of KZN coast, including many of the 76 notable estuaries, most of which are intermittently connected to the sea during the year (Begg 1978, Turpie et al. 2012), bringing into it nutrient and sediment-laden freshwater (Cooper et al. 1995). Based on the Köppen classification (Boucher 1975), this coastal-shelf region has a humid sub-tropical climate with southern sub-tropical high-pressure systems being the main prevailing weather patterns of the region (Tyson and Preston-Whyte 2000).

The study area has been classified as oligotrophic (southern region) to mesotrophic (northern region) (Meyer et al. 2002), with intermittent eutrophic conditions in the northern region associated with the St. Lucia upwelling cell (Pearce 1977, Lutjeharms et al. 1989, Meyer et al. 2002). To the south, eutrophic conditions are associated with uThukela terrigenous organic input (Scharler et al. 2016, Untiedt and MacKay 2016), and a nutrient upwelling associated with the AC and its interaction with the shelf edge (Durban eddy) (Meyer et al. 2002, Barlow et al. 2008).

The study was limited to the mid-shelf depth (50-80 m isobaths) to limit issues related to community changes with depth and included a large part of the wider shelf - the KZN Bight (Port Durnford to Durban) and south of Durban to Scottburgh (Fig 2.1).

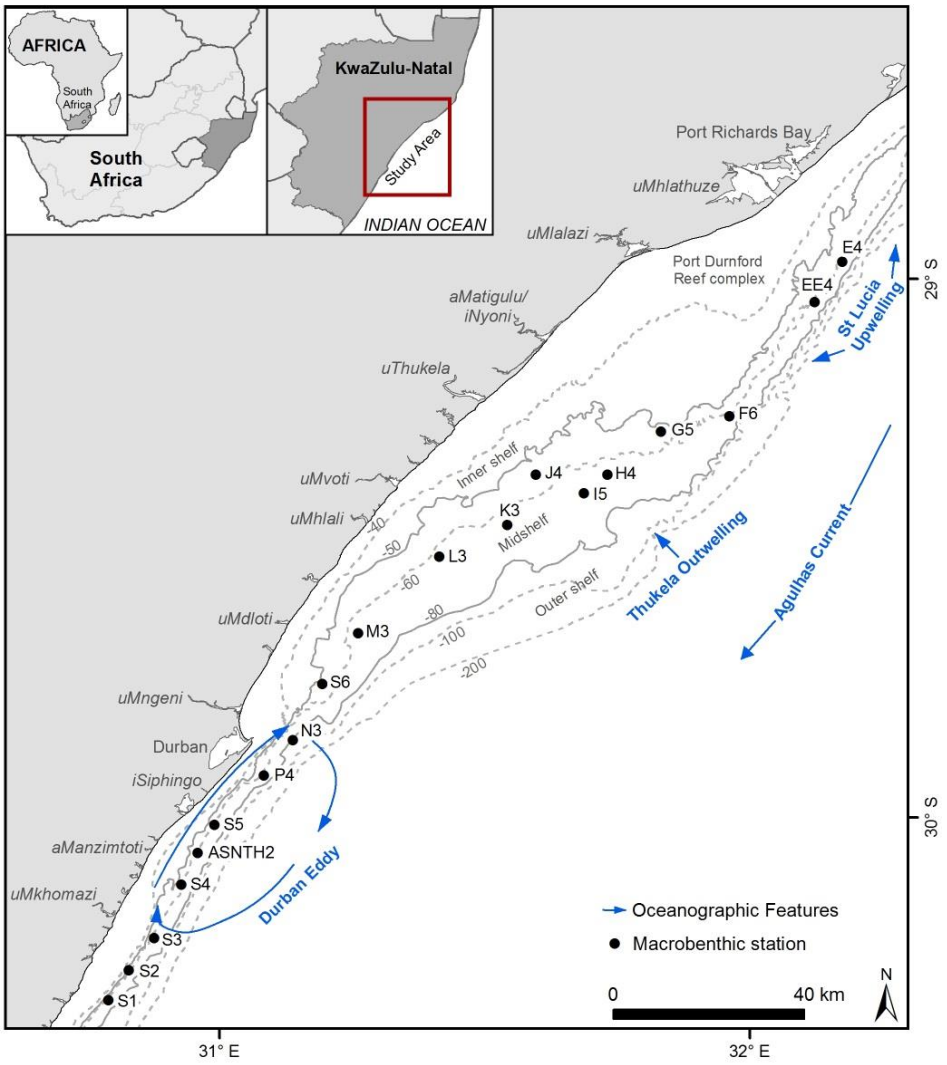

Figure 2.1. Study area with macrobenthic stations, bathymetry, main oceanographic features and main estuaries depicted.

2.2 Study design and sampling protocol

Two data sets were used; macrobenthic samples collected during the African Coelacanth Ecosystem Program (ACEP) KwaZulu-Natal Bight ecosystem functioning project in Winter 2010 and augmented with additional stations sampled in Winter of 2014 aboard the *Angra Pequena* during this ACEP Surrogacy project.

The SeaPLAN biozone model (see Chapter 1) resolved into three main biozones with respective biozone subclusters that were not adjacent (1A-1C: 2A-2B; 3A; Fig 2.2). With this model serving as a template, 19 stations were set on known (ACEP Natal Bight Project) and suspected unconsolidated sediment habitats to avoid reefs (MacKay 2014). Each subcluster hosted three stations, with exception of subcluster 2A where an additional station was included and was identified as an interesting habitat by video material from a remotely operated vehicle (ROV).

Sampling stations were set between the 50-80 m depth, representing mid-shelf sediment facies, physico-chemical parameters, and macrobenthic assemblages (MacKay et al. 2016, Untiedt and MacKay 2016).

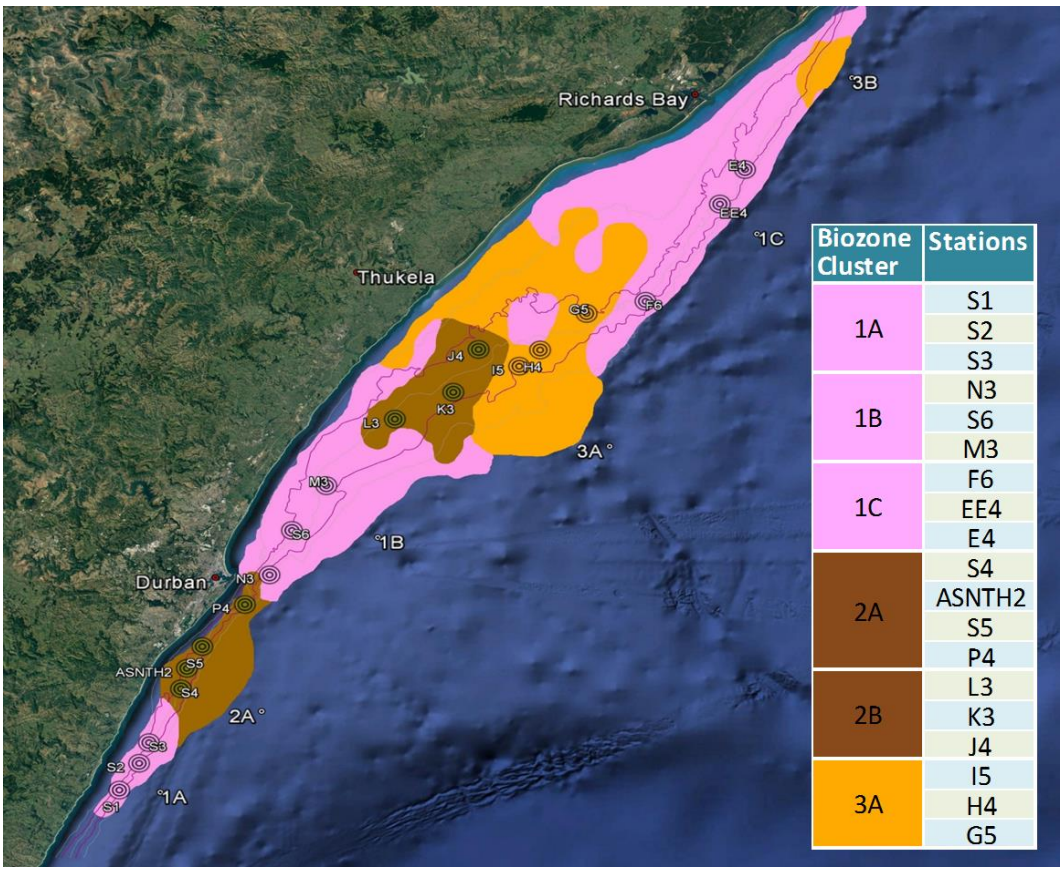

Figure 2.2. KZN biodiversity planning Biozones and the associated sampling stations. These are depicted relative to bathymetry (50-80 m depth shown as red lines) and sampling stations.

2.3 Field sampling procedure

2.3.1 Physico-chemical sampling

Prior to biophysical sampling at each station, spatial reference (latitude and longitude) along with prevailing weather conditions were recorded in a field logbook. The near-bottom environmental variables (conductivity (mS/cm), temperature (°C) and depth (m)) were recorded by means of a single multi-parameter profiler CTD (Sea-Bird: SBE 19 Plus v.2) deployed to just above the seafloor (deployment speed 1 m s^{-1}), equipped with auxiliary sensors to measure additional parameters. These included concentration of dissolved oxygen ($mg.l^{-1}$), pH, turbidity (NTU) and fluorescence content ($mg.l^{-1}$) (McArthur et al. 2010a, MacKay 2014). Only the bottom 5 m hydrographic characteristics measured at each station were used for further analysis. Grab sampling commenced once the CTD was retrieved on deck.

2.3.2 Macrobenthic and sediment sampling

Sample collection was limited to daytime hours (MacKay 2014), when many mobile species can be expected to be relatively inactive. Prior to grab deployment, a drop video was cast to the seafloor to validate the extent of unconsolidated sediments to avoid sampling reef (MacKay 2014). Triplicate biological samples were collected from each station, using a long armed 0.2 m^2 van Veen grab and extra weights to 40 kg. A minimum of three replicates were collected to increase the probability of sampling rare taxa (in this context refer to individuals with low abundance or small range size (Ellingsen 2001)) and are considered appropriate for statistical comparison (Gray and Elliott 2009). The grab was deployed through a mechanical winch over the side of the vessel (MacKay 2014).

Bucket type grabs such as the van Veen are appropriate in soft-bottoms, although the volumes of sediment sampled are mostly affected by the type of substrate, with samples collected from muddy bottoms often filling the grab completely, while samples collected in sand to gravel substrates often penetrate to minimum depth (Somerfield et al. 2005, Tagliapietra and Sigovini 2010). Care was taken to ensure all replicates were within 100 m of each other. Once a grabbed sample was retrieved, sediment depth was measured to the nearest mm through a top opening window on the grab. A sample was acceptable and considered a successful grab, only if vertical sediment depth was at least 50 mm or more with no indication of disturbance (MacKay 2014).

The interrelation between macrobenthos and sediments requires characterisation of the bottom environment. Therefore, a sub-sample (175 g) was taken from the upper 5 cm from each grabbed sample for bicarbonate content, sand grain size and organic content analysis. The latter required fixation by addition of 40% formalin (MacKay 2014). The remaining biological sample was washed through a square stainless steel sieve with 1000 µm mesh size. Square mesh sieves are advisable as they provide a larger percentage of open area (Somerfield et al. 2005).

Sediment colour and the odour were noted in a field trip logbook before washing. Any visible fauna were carefully handpicked and bottled in the suitably labelled sample jar. Sieving was gentle to minimise sediment being displaced out of the sieve and the impact of strong water pressure on delicate animals (MacKay 2014). Material remaining on the mesh sieve after washing, consisting of benthic animals, tubes, shells, shell hash, and coarse sediments, were bottled in a suitable biological sample jar and preserved unstained with buffered forma-saline (4%) allowing for subsequent analysis ashore (MacKay 2014).

In certain cases samples (e.g. at stations S1 and S3) were dominated by coarse sediments (sand and gravel >10 kg) that were retained on the sieve and precluded the sorting of infauna in a reasonable timeframe. In these cases, elutriation was conducted to separate light material and small animals from sediments (Wilson 2005, MacKay 2014). The process: 2 litres of unsorted sediments from the larger sample was put into a 20 L bucket three-quarter filled with seawater and well agitated to suspend light material and small animals. Floating animals and materials were collected by pouring the agitated volume of water through a 1000 µm sieve before resettlement. This was repeated at least five times or until the water ran clear before sorting for large and heavy fauna such as molluscs and characteristic sedimentary elements (Somerfield et al. 2005, Wilson 2005, MacKay 2014).

2.3.3 Laboratory procedure

Sedimentary analysis

The sedimentary analysis was performed at a sedimentological analysis laboratory (Environmental Mapping and Survey (EMS)) on samples collected from every grab. The granulometric analysis was used to characterise the sedimentary environment and provides an insight into local physical conditions.

Grain size analysis

The aim of grain size analysis is to define relative proportions of different grain sizes which make up a given sediment population (Gray 1981, Bale and Kenny 2005). A number of techniques have been defined for grain size analysis (Gray and Elliott 2009). In this regard, a sieving technique was employed as a result of the advantages associated with it, such as being less expensive, an easily reproducible method and deemed the most practical way of characterising particle size larger than 0.063 mm (Bale and Kenny 2005).

Grade scales apply random set of finite ranges to the continuous frequency distribution of particle sizes in order to produce logical classifications for the numerical divisions (Gray 1981, Bale and Kenny 2005). The Wentworth (1922) ordination scale is most commonly used by marine ecologists and geologists to characterise sediment particles (Bale and Kenny 2005, Gray and Elliott 2009). By applying a logarithmic scale transformation (millimetres into whole integers) to the Wentworth scale produces the phi (Φ) notation which was initially employed to graphically manipulate data (Gray 1981, Hayes et al. 1992, Bale and Kenny 2005), based on the following definition: phi units (F) = $-\log_2$ (diameter in mm). This was done to graphically manipulate data (Gray 1981, Bale and Kenny 2005). Three general categories (gravel, sand, and mud), classified according to the dominant size of the individual clasts are recognised. For data

analysis in this study, the substratum was retrospectively subdivided into seven categories (Table 2.1).

Table 2.1. Wentworth scale of sediment particle size (mm) classification with the accompanying phi (ϕ) notation. (Adopted from Wentworth 1922 and Gray 1981).

Sediment type	Grain size (mm)	Phi (ϕ) scale
Gravel	> 2	< -1.0
Very coarse sand	-3	-1
Coarse sand	0.5 - 1	0.0 - 1.0
Medium sand	0.25 - 0.5	1.0 - 2.0
Fine sand	0.125 - 0.25	2.0 - 3.0
Very fine sand	0.0625 - 0.125	3.0 - 4.0
Silt and clay fraction	< 0.0625	> 4.0

Sorting

Grain size alone does not account for particle size variation or the particle shape, therefore applicability of this measure is limited in describing a highly unimodal sediment grain size distributions (Lewis and McConchie 1994). Sorting is another measure used to characterise grain size according to sorting classes (Table 2.2). Sorting, or grain-size variation reflects the amount of interstitial space available within sediment as a habitat for biota (Gray 1974b). Well-sorted sediments are generally associated with a high energy or dynamic environment and the majority of the sample comprised of particles with the same diameter (Mackay 2006, Gray and Elliott 2009). In contrast, poorly-sorted sediments mostly comprise various grain sizes and are mostly associated with a stable environment, less frequently affected by hydrodynamics (Gray and Elliott 2009, McArthur et al. 2010a).

Table 2.2. Sediment sorting classes used to classify sediments (modified from Gray 1981).

Sorting classes	phi (ϕ) scale
Very well sorted	< 0.35 ϕ
Well sorted	0.35 - 0.50 ϕ
Moderately well sorted	0.50 - 0.71 ϕ
Moderately sorted	0.71 - 1.00 ϕ
Poorly sorted	> 1.00 ϕ

Skewness

This descriptive measure indicates symmetry, which is a preferential distribution to one side of the mean (Gray and Elliott 2009). Symmetrical sediments will have a value of 0.00, whereas those with more courser grain-size are positively skewed (- phi values). Negative skewed (+ phi values) sediments are dominated by finer grained size (Table 2.3) (Gray 1981).

Organic content

Features of organic matter include their ability to form water-soluble and insoluble complexes, interact with clay minerals, bind particles together, to absorb and release organic compounds

and plant nutrients and retain water in the sediment (Schumacher 2002). Therefore, examination of total organic carbon is critical, since organic materials present in sediments can be expressed as carbon, and carbon is available in inorganic and organic form, the latter being an important food resource for macrobenthic communities (Sverdrup et al. 1942, Cocito et al. 1990, Méndez and Green 1998)

Table 2.3. Skewness categories used to indicate a proportion of sediments grain-size (adopted from Folk 1974).

Values from	to	symmetry	Verbal classification Graphically skewed to
1	0.3	Strongly + skewed	Very – phi values (coarse sand)
0.3	0.1	+ skewed	- phi values
0.1	-0.1	Nearly symmetrical	symmetrical
-0.1	-0.3	- Skewed	+ phi value
-0.3	-1	Strongly - skewed	Very + phi values (fine sand)

A suite of techniques have been developed to determine organic content, all relying on the principle of destroying organic matter present in a given set of sediments through chemical or heat energy and then measuring the loss directly (Schumacher 2002). This study used a chemically-based digestion technique to determine total organic content (TOC) of sediments. This was adopted from Schumacher (2002) and the basic steps for this technique are:

1. Inorganic carbonates are eliminated by adding 6% Hydrogen peroxide (H_2O_2) to a known weight of sediment until the frothing reaction ceases.
2. The sample is incinerated at 105°C, cooled and weighed.
3. Organic matter present in the sediment sample is determined gravimetrically and calculated as:

$$OM = \frac{W_i - W_f}{W_i} \times 100\% \quad (2.1)$$

Where OM is organic matter (%), W_i is the initial sample weight (g) and W_f the final sample weight (g).

4. Organic matter is converted to a value of TOC (Table 2.4) by using an appropriate factor. A conversion factor of 1.72 is commonly used, based on the assumption that organic matter contains 58-60% Carbon (Schumacher 2002).

Table 2.4. Percentage total organic content of the sediments (adopted from Mackay 2006)

Verbal classification	Total Organic Contents (%)
High	> 4 %
Medium	2 - 4 %
Moderately low	1 - 2 %
Low	0.5 - 1 %
Very low	< 0.5 %

Macrobenthos

In the laboratory, prior to sorting, samples were rinsed with seawater through a 1000 µm sieve to remove all traces of formaldehyde. Animals from each sample were separated from non-biogenic material under a magnifying lamp/microscope and sorted according to major taxonomic groups (polychaetes, bivalves, decapods, amphipods and isopods) to aid taxonomic identification. To reduce the risk of human error, sorted samples were cross-checked between sorters to ensure that no animals were left. Sorted fauna were then identified to coarse operational taxonomic units (OTUs) by a single researcher to minimise observer bias. Stereomicroscopes (Zeiss stemi-DV4, Zeiss Stereo v.12) and appropriate taxonomic keys (Clark 1923, Barnard 1950, Day 1967, Kensley 1972, Griffiths 1976, Kensley 1978, Kilburn and Rippey 1982) and online keys (e.g. Crustacea.net (Lowry 1999)) were used for taxonomic identification. The species level (lower taxonomic resolution) is the level at which animals interact with their habitat (Bertrand et al. 2006), and quantification of biodiversity and the utility of potential surrogates therefore are often affected by the taxonomic resolution (Bertrand et al. 2006); coarse taxonomic resolution providing rudimentary spatial variation (Anderson et al. 2005).

In the case of a damaged specimen or when some of the diagnostic morphological features were not observable, a staining procedure (Methyl blue) was used (Winsnes 1985). Taxonomic identification was checked and verified by a macrobenthic scientist (C.F. MacKay at Oceanographic Research Institute). To confirm a species name, taxonomic information was checked against the World Registry of Marine Species (WoRMS Editorial Board n.d.) database and the nomenclature herein was based on the latest available taxonomic information during the drafting of this thesis. The number of individuals of species was counted and recorded together with sample details (e.g. date and sample location). Larval and pelagic fauna were excluded and only benthic fauna were considered for further analysis.

2.4 Generic statistical analyses

The abundance of each taxon was standardised to 1.0 m^2. As a standard area of 0.2 m^2 was sampled with the van Veen grab, abundance values were multiplied by a factor of 5 in order to

express values per m^2 (ind. m^{-2}). Abundance data was pooled over three replicates (divided by 3 to account for area sampled) from each station to even out variability and to give a holistic picture of the general community patterns (Ellingsen 2002). Community patterns were analysed at a station level and surrogacy testing was based on the biozones explained previously (Fig 2.2). Software packages Excel 2010, PAST v.3.15 (Hammer et al. 2001) and PRIMER v.6 (Clarke and Gorley 2006) were used for analysis.

2.4.1 Abiotic data

Nineteen environmental variables were measured for this study (Table 2.5). Occurrences of multi-collinearity were examined using parametric Pearson (product-moment) correlation analysis, which quantifies the strength and significance of the linear relationship between two data sets (Clarke and Warwick 2001). Pearson correlation analysis evaluates linear relationships and multi-collinearity between two or more sets of variables and report as correlation coefficients (r) varying between +1 and -1. The former indicates that a change in one variable is associated with a proportional change in the other variable, whereas the latter indicates an inverse relationship between variables. A value of zero indicates no relationship between variables (Quinn and Keough 2002). For highly correlated variables ($r=0.95$, sig. <0.05), only one variable was retained for subsequent analysis. As such, mean phi and median phi were highly correlated ($r=0.988$), as were mean mm and median mm ($r=0.966$). Since each pair of the four sets of variables represent similar information only one (Median phi) was retained for subsequent analysis. Verfaillie et al. (2006) highlighted the importance of median as the best descriptor that characterises sedimentary environments and being critical in describing and projecting soft-sediment benthic assemblages. All environmental data were presented as mean values (with SD) over the study area and in the case of stations, measured values were used.

To test for normality and homoscedasticity, Shapiro-Wilks tests (Shapiro and Wilk 1965) were used and data was further visually inspected using Draftsman's plots (Clarke and Warwick 1994). Variables including total organic carbon, carbonate, sediment grain particles (mud to fine sand), dissolved oxygen, fluorescence and turbidity were corrected by a square-root transformation. Due to outliers noted in other parameters, all parameters except for median phi and skewness were square root ($\sqrt{}$) transformed to reduce the influence of outliers as recommended by Anderson et al. (2008). Since environmental variables are expressed in different units of measure, the remaining set of variables were standardised to enable comparison (Clarke and Warwick 1994). A Q-type analysis was applied to evaluate whether environmental variables had similar patterns as biotic data, however, the environmental matrix was based on Euclidean distance as opposed to Bray-Curtis (B-C) similarity.

Assemblage distributions are presumably affected by various environmental factors related to the habitat type characteristics, analysis of PERMANOVA (9999 permutations) was performed to test for the significance of spatial differences.

Table 2.5. Environmental variables measured during this study.

Environmental variables			Units	Sampling level
Physico-chemical (water column)		Temperature Depth Salinity Dissolved oxygen Turbidity Fluorescence pH	ºC m PSU $mg.L^{-1}$ NTU $mg.L^{-1}$	Station
Sediment	Grain size	Gravel Very coarse Coarse sand Medium sand Fine sand Very fine sand Mud Organics Carbonate	%	Sample x3 per station
	Statistics	Mean grain size Median grain	mm	
		Skewness Sorting		

2.4.2 Biotic data

2.4.2.1 Univariate analysis

The raw taxon abundance data was used to calculate univariate community measures using the DIVERSE function within the PRIMER v.6 statistical programme (Clarke and Warwick 2001). Two primary community measures of abundance (N: no. of $ind.m^{-2}$) and number of species (S: no. of taxa) were used in this study. Univariate measures were computed to reduce the specific composition of a community to a single value or few single values that can easily be interpreted and manipulated (for subsequent analysis) and to further allow comparability of factors. A number of diversity indices have been established and used in the study of macrobenthic communities that integrate species richness and the equitability of species within a community (Gray 1981, Gray 2000, Gray and Elliott 2009). The diversity discussed here concerns samples and even at such small scale, there are biological interactions between species (competing for food and space). This is defined as within-habitat (α) diversity (Gray 2000).

Three main components of diversity were computed, the Shannon-Wiener index (H') (Shannon and Weaver 1963), which is widely employed in macrobenthic community studies (Gray 1981, 2000, Gray and Elliott 2009). This function gives a measure of species diversity with respect to number of species (S) and equitability of each species present. This index is greatly influenced by the taxa in the middle of the rank sequence (Magurran 2004, Gray and Elliott 2009).

$$H' = -\sum_{i=1}^{s} p_i \ln p_i \tag{2.2}$$

Where p_i is the proportion of individuals found in species *i*th (N_i/N)

Since this is a proportionality-based index, high values are recorded when a large number of taxa occur in similar numbers and a low value if a small number of species dominate a sample (Magurran 2004). To account for the factor contributing to low and high index values, two additional indexes were calculated (Gray 1981). The Margalef's Richness (*d*) index (Margalef 1961), was determined.

$$d = \frac{(S-1)}{\ln N} \tag{2.3}$$

Where S is the number of species and N is the number of individuals.

Pielou's Evenness index (*J'*) (Pielou 1966)determines how evenly distributed individuals are within a community, being high when all taxa have similar abundances and being low when certain taxa are numerically dominant.

$$J' = \frac{H'}{\ln S} \tag{2.4}$$

Where H' is Shannon-Wiener diversity index and S is the number of taxa.

This index assumes a value in a range (0, 1) where the dominance of few taxa with high abundance is indicated by 0, whereby values close to 1 indicate a similar number of individuals across taxa (Magurran 2004). One-way analysis of variance (ANOVA) within the PAST statistical software package v. 2.18 was used to test for significant differences ($p<0.05$) in the univariate measures between sample groups.

2.4.2.2 Multivariate analysis

The normal Q-type analysis was adopted as the multivariate analysis approach. This involves comparing and grouping samples in relation to the extent to which they share similar taxa (Clarke and Warwick 1994, 2001). Although few assumptions are made about the nature of the data when employing multivariate techniques and there is no need to transform data to attain normality, it is still necessary to apply a transformation in order to balance the contributions from common and rare taxa (Field et al. 1982). This can be accomplished through a number of means: square root (√), fourth root (√√), log or log (x + 1) transformation (Clarke and Green 1988, Clarke and Warwick 1994). The more severe the transformation applied the greater the influence less abundant taxa will have on the output (Clarke and Warwick 1994).

In community analysis in which taxa have been identified and counted, similar to this study, there are often many rare species and a few common, abundant ones so that the distributions of data are highly skewed (Clarke and Warwick 1994). Therefore, abundance data were square-root transformed prior to subsequent analysis to avoid undue influence of the dominant taxa on the overall results (Clarke and Warwick 1994). Square-root transformation has been widely used and recommended for count data (McDonald 2014) since it a mild transformation and has minor bias compared to other transformations (O'hara and Kotze 2010).

To examine patterns in the ecological structure of the macrobenthos assemblages, the first step was to determine ecologically meaningful distance (dissimilarity) between each pair of station. The commonly applied Bray-Curtis (BC) similarity coefficient was used (Bray and Curtis 1957), with a measure range of zero (identical assemblages) to one (no species in common). This similarity coefficient was chosen because it is considered one of the most vigorous and reliable measure of ecological dissimilarity (Faith et al. 1987), and has been widely used in marine benthic studies (Gauch 1982, Gray and Elliott 2009). Additionally, it has two properties that are appropriate for these data. Firstly, it is not affected by joint absences and secondly it gives more weight to abundant taxa (Clarke and Warwick 1994, Legendre and Legendre 1998). However, here data were square-root transformed to avoid undue influence of highly abundant taxa. Joint absences are common in ecological data in that a taxon can be absent in two different samples but this does not mean that these samples are similar on the basis that neither contains this particular animal (Clarke and Warwick 1988). Zero values are therefore important in ecological data and can't be treated as any other number (Clarke and Warwick 1988). The (dis)similarity between samples was further interrogated by applying multivariate methods of hierarchical classification which successively pools together samples into discrete groups

starting with samples sharing the highest similarity in a community composition, gradually lowering to the most trivial similarity level (Clarke and Warwick 1994, Gray and Elliott 2009). A hierarchical agglomerative clustering method was used, which pools samples together based on their average level of similarity (Clarke and Warwick 1994). The disadvantages of the method were noted, such as random sequencing of samples (unrelated samples can be placed close to one other), irreversible hierarchy (sample lose its identity once place in a group) and the fact that the dendrogram only shows inter-group relationships based on the average similarity. Thus, with cluster analysis, Similarity Profile (SIMPROF) analysis was used (9999 permutations) to ascertain statistical significance (α= 0.01) of recognised groupings, with the assumption of no *a priori* groups. The significance level was set more stringent given the multiple testing inherent in this hierarchical approach as suggested by Clarke et al. (2008).

Ordination allows a visual assessment of the similarity of assemblages among sites and represent sample relationships in a specified number of dimensions (Gray et al. 1988). Here, non-metric multidimensional scaling ordination (nMDS), which finds the 2-dimensions representation to accurately depict patterns of multidimensional multivariable data (Clarke and Warwick 1994), was used. Multidimensional scaling ordination was recommended as the most robust technique for the examination of ecological gradients for community data, using the B-C measure, in a simulation study comparing methods of ordination (Minchin 1987). This method represents the B-C similarity between two samples as Euclidean space separating the samples, such that proximity of samples reflects similarity in terms of macrobenthic taxon abundance (Clarke and Warwick 1994). The final nMDS ordination map is produced through a number of iterations, (~25) which proceed with several alternate configurations (Clarke and Warwick 1994). The extent to which this ordination map represents realistic relationships between samples is indicated by Kruskall stress value(Clarke and Warwick 1994). Large stress values (0.5> Stress <0.25) indicate that the ordination plot poorly represents observed sample relationships in 2D space while stress values between 0.1 and 0.25 indicate satisfactory results and values <0.1 indicate a good representation (Clarke 1993). Sample(s) with very low or very high abundance values compared to the rest of the data set are often encountered since normal distribution of abundance data is never approached in a natural condition. These samples are referred to as outliers and result in an condensed nMDS ordination plot (Clarke and Warwick 1994, Anderson et al. 2008b). Condensed display is corrected by omitting the outlier and repeats the ordination (Clarke and Warwick 1994). When the results drawn from ordination complement results from cluster analysis, interpretation of data is said to be intuitive and straightforward with less risk of misinterpretation (Clarke and Warwick 2001). Cluster analysis

was used in Chapter 3 and ordination used in Chapter 4 as each method best-suited the respective data types.

The resultant sample groups (clusters) from cluster analysis was further characterised in terms of number of taxa (S), abundance (N), species richness (d), Pielou's evenness (J'), and Shannon Wiener diversity (H'). Significant differences in these univariate parameters between sample groups were tested through one-way PERMutational ANalysis Of VAriance (PERMANOVA) analyses with unrestricted permutation of raw data and through pair wise tests (Anderson et al. 2008a). PERMANOVA produces a pseudo-F rather than classical Fisher's F ratio. Pseudo-F is a test statistic used to examine the extent to which a particular design of interest has explanatory power over community variation. Pseudo-F value tends to be higher when the model(s) have been fitted to the data using least squares. This is based on the ratio of explained to residual variation in the data. P-values indicate the significant difference (p<0.05) between the factors obtained using necessary permutations based on the design (Anderson 2001, 2006).

Taxa and trait modality characterising similarity and differences between groupings observed from cluster and ordination analyses were evaluated through the Similarity Percentage breakdown (SIMPER) function (cut-off 90%) in the PRIMER v.6 statistical package. This function uses a pairwise comparison of samples and finds the mean contribution (δ_i) of each taxon or trait modality to the (dis-)similarity computed from B-C similarity among all pairs of samples within a sample group (Clarke and Warwick 1994). In conjunction with the associated standard deviation (SD) δ_i are calculated. Deductions on whether taxon or trait modality characterise similarity or dissimilarity are based on the resultant ratio ((δ_i)/SD (δ_i)), which measures how consistent a taxon or trait modality contributes to the mean (dis-)similarity between the groups. An adequate discriminating taxon or trait modality contributes more often to dissimilarity/similarity and consequently has a low SD and accompanied by a high ((δ_i)/SD (δ_i)) ratio ($\geq$1) (Clarke and Warwick 1994). Therefore, large values of the ratio indicate those taxa or trait modalities that typify sample groups (Clarke and Warwick 1994). The more abundant a taxon or trait modality is within a group, the more it contributes to the intra-group similarity, while a taxon or trait modality with a consistently high contribution to the dissimilarity between groups is a good discriminating species (Clarke & Warwick 2001). SIMPER results were tabulated for all identified sample groups, focussing only on species contributing >2% of the abundance to the individual groups (Field et al. 1982).

Relating faunal and environmental patterns

A one-way fixed analysis was used (within PRIMER v.6) to test the assumption of homogeneity of variance between stations on square-root transformed abundance data. The RELATE function then computed a rank correlation coefficient (Spearman's (ρ)) between samples from the biological and environmental dataset. When ρ=1 or close to 1, it indicates that data correlate perfectly (Anderson 2006). The RELATE procedure was employed to ascertain whether the arrangement of rank orders of similarity among stations in the BC faunal matrix was significantly correlated with that in the complementary Euclidean distance matrix constructed from the environmental variables.

The Biota Environment Matching (BIO-ENV) procedure within the BEST function in PRIMER v.6 (Clarke and Ainsworth 1993) was used to determine the single or combination of variables that maximised the degree of correlation between biotic and abiotic matrices. In this analysis, the biota similarity matrix and a parallel environmental variables matrix (generated from various sets of environmental data) were compared to determine which variable best explained community patterns observed using the Spearman's Rank Correlation (ρ). Spearman Rank Correlation varies between (-1, +1), where negative values indicate inverse correlation and the latter indicating a perfect monotone of ranks. Where there is no relationship between matrices ρ will be indicated by 0 (Clarke and Warwick 1994). The BVSTEP algorithm was used on all environmental variables, with stepwise forward and backward techniques for selecting and eliminating variables. A stepwise forward selection technique selects a subset of variables by starting with no variables, trying iteratively each variable and progresses successively until environmental variables contributing least are eliminated and those accounting for macrobenthic assemblage structure are found (highest ρ values) (Clarke and Warwick 1994, Clarke 2005, Clarke et al. 2008). The global BEST test was used to determine significance of the subset of environmental parameters, testing the null hypothesis of a negative relationship between biotic and abiotic dataset collected for the chosen set of samples (Clarke et al. 2008).

A distance-based Redundancy Analysis (dbRDA) was further performed using a distance based Linear Model (distLM) routine from PRIMER v.6 (Clarke and Gorley 2006) and the PERMANOVA + add-on (Anderson et al. 2008a). This ordination technique operates on species abundances and corresponding environmental variables and extracts synthetic gradients from combinations of the measured environmental variables (ordination axes) that maximize the niche separation among species. Within distLM, marginal tests determine the relative importance of each environmental variable in explaining community variation and the

proportion of variance explained irrespective of other variables using a stepwise routine that employed 9999 permutations based on Akaike's AICc selection criterion (Clarke and Warwick 1988, Anderson et al. 2008a). In further chapters, specific analyses pertaining to testing individual aims and hypotheses are presented in more detail.

CHAPTER 3. SPATIAL PATTERNS OF SOFT-BOTTOM MACROBENTHIC COMMUNITIES ON THE KWAZULU-NATAL MID-SHELF, RELATIVE TO MARINE SPATIAL PLANNING BIOZONES

3.1 Overview

Macrobenthic species and communities were investigated on the KZN mid-shelf, to examine the influence of different environmental variables on the spatial distribution of the macrobenthos assemblages. These patterns were further examined (as biodiversity surrogates for macrobenthic communities) relative to predefined Marine Spatial Planning (MSP) biozones in KZN. Knowledge gained from these types of ecological assessments is critical for the effective management and conservation of marine ecosystems. Macrobenthic samples were collected using a 0.2 m^2 Van Veen grab from 19 stations. Total abundance, number of taxa and various diversity indices were computed and used for spatial comparison. Polychaetes, crustaceans, molluscs and sipunculids were the four dominant taxonomic groups with crustaceans being most abundant. Cluster analyses resolved into seven habitat specific benthic assemblages that differed significantly in terms of species composition and diversity. Spatial distribution as univariate measures were best explained by sediment grain size (mud to medium and coarse sand), sediment organic content and carbonates, and water column turbidity. In contrast, multivariate analyses identified median grain size, mud content and water column turbidity as the major variables influencing the faunal patterns. Results showed that macrobenthic communities (or community patterns) did not fully agree with the KZN spatial planning classification model. Disagreement between macrobenthic structure and predefined biozones unit does not suggest that traditional community structure-based measures are inappropriate rather a potential to illustrate variability on several scales. Furthermore, this suggests the need to refine the existing biozone classification model for effective representation of benthic biodiversity.

3.2 Introduction

Due to the synergistic effects of multiple stressors on shelf ecosystems that alter ecosystem structure and function (Worm et al. 2006), proper management measures are required to assure sustainable use of natural resources and to maintain ecosystem services (Barbier et al. 2011). To develop operational conservation plans, basic knowledge of the structure and functioning of the target ecosystem is critical (Reiss et al. 2010, Reiss et al. 2015). Regardless of soft-bottom

marine habitats being the largest ecosystem on Earth in terms of spatial coverage, only a small percentage of the macrobenthos has been studied there, and most of the species are still undescribed (Snelgrove 1997). Moreover, macrobenthic community studies have for many years been conducted to study species composition and community structuring for environmental monitoring, pollution assessment and anthropogenic impact, with little attention given to describing biodiversity patterns (Warwick 1987, Olsgard and Somerfield 2000); through a combination of species identification, characterisation and habitat mapping (Ellingsen 2002, Veiga et al. 2016).

Macrobenthos forms a substantial component of soft-bottom habitat biodiversity, and are important contributors to myriad of ecological functions (Schwinghamer 1981, Ganesh and Raman 2007, Sokołowski et al. 2012), as well as in local ecological processes including the food resources for higher trophic levels such as commercially important fish species (Joydas and Damodaran 2009). Also, community spatial configuration and heterogeneity have important implications for the distribution and relative abundance of marine organisms (Thrush et al. 2001, Anderson et al. 2009) and may be important predictors of biodiversity and ecosystem function (Reise 2002, Solan et al. 2004, Anderson et al. 2013, Dutertre et al. 2013). As such, studies of macrobenthic communities are relevant to assess biodiversity and establish the baseline knowledge required to detect future potential changes in species distribution which are useful for depicting or monitoring management issues (Desroy et al. 2002, Dutertre et al. 2013). Lastly, macrobenthos species distribution is used to assess benthic habitat status and to identify priority areas for marine protection, conservation and management (Snelgrove 1998, Koulouri et al. 2006, Cacabelos et al. 2008, Gogina and Zettler 2010, Claudet 2011, Dixon-Bridges et al. 2014, McHenry et al. 2017).

Some studies have detailed the distributional patterns of macrobenthic communities and identified factors and processes that are important in determining spatial patterns (Thrush 1991, Thrush et al. 1998, Moulaert et al. 2008). In several, sediment features (e.g. grain size, organic matter content and food availability) are identified as important factors responsible for macrofaunal distribution (Gray 1974a, Hily 1987, Snelgrove and Butman 1994, Ellingsen 2002, Van Hoey et al. 2004, Hily et al. 2008, MacKay et al. 2016, Veiga et al. 2017). However, on large spatial scales, other natural environmental factors such as the hydrodynamic conditions and physicochemical properties of the water column directly or indirectly affect the presence and distribution of macrobenthos by influencing food availability, bottom-water oxygenation and larval dispersion (Pearson and Rosenberg 1987, Rosenberg 1995, Dutertre et al. 2013, Blanchard and Feder 2014), making distribution heterogeneous (Hewitt et al. 2005, McClain and Barry 2010, Mann and Lazier 2013).

The KwaZulu-Natal (KZN) shelf is a region of unusual environmental conditions characterised by a complex current system, arising from the Agulhas western boundary current (Lutjeharms 2006a, Roberts et al. 2010b). The macrobenthos of KZN shelf environment is not well studied (Mead 2007, Griffiths et al. 2010, Milne 2012), despite transitional coastal habitats such as estuaries (MacKay et al. 2010, Ngqulana et al. 2010, Turpie et al. 2012), intertidal rocky shores (Bustamante et al. 1995, Bustamante and Branch 1996, Branch et al. 2005, Sink et al. 2005) and sandy beaches (Harris et al. 2011b) having been afforded attention. As proof of this, new macrobenthos species have been recently described from the intertidal and shallow reef habitat (Milne and Griffiths 2013), from a very limited set of samples in one area off the KZN north coast. Dedicated studies on the shelf communities were last carried out in the 1980s. Unpublished environmental impact and monitoring reports giving basic macrobenthic data exist (McClurg 1988, McClurg et al. 2000, McClurg et al. 2006), but these are area-specific and give limited information on ecological aspects of the communities and on the distribution of other taxonomic groups. There are, however, recent studies on the region but limited to environments associated with coral reef habitat (Harmer 2014). The only recent comprehensive studies on the unconsolidated KZN shelf habitats are those of MacKay et al. (2016), Untiedt and MacKay (2016). By using identical collection and analytical methods and applying similar taxonomic rigour to those of the aforementioned studies, this study offers a good opportunity to study the patterns of distribution and composition of benthic assemblages. Findings of this study will not only improve the regional knowledge by adding to the small number of studies describing infaunal community structure, but will also assist to develop proper strategies for management and conservation of soft-bottom benthic habitats.

3.3 Aims, Objectives and Hypotheses

The aim of this chapter is to identify and describe patterns of macrobenthic composition and distribution along the KwaZulu-Natal mid-shelf environment. Furthermore, to evaluate the relationship between physical seafloor conditions and macrobenthic faunal distribution to identify the key abiotic factors responsible for observed community patterns. Results obtained will not only complement our insights into the regional biodiversity but will further be used to test the efficiency of the KwaZulu-Natal marine spatial planning predefined biozones as a potential biodiversity surrogate (reflecting macrobenthic communities patterns).

Objectives

1. To characterise the KwaZulu-Natal mid-shelf abiotic habitat.
2. To characterise macrobenthic community assemblages.

3. To determine if there are spatial differences in macrobenthic communities along the KwaZulu-Natal mid-shelf.
4. To determine the possible relation between measured environmental variables and distributional patterns of the benthic fauna.
5. To determine if patterns observed in macrobenthic communities agree with provincial marine spatial planning predefined biozones.

Hypotheses

H_1: There are structural differences in macrobenthic communities observed along KZN mid-shelf.

H_2 There is a significant coupling between macrobenthic community structure and biophysical variables measured.

H_3: There are differences in macrobenthic community patterns relative to KZN marine spatial planning predefined biozones.

3.4 Materials and Methods

The general materials and methods including sections on the study area, the field-sampling protocol, laboratory processing and data analyses are presented in Chapter 2. The following are protocols relevant only to this chapter.

3.4.1 Study area and sampling design

Sampling stations were set along the shelf using the existing biozone model as a template of known and suspected unconsolidated sediment habitats. The stations were approximately evenly replicated between biozone subclusters.

3.4.2 Data treatment and analysis

3.4.2.1 Biotic data

Taxon abundance for the 57 samples collected was considered in this study. Frequently encountered taxa (F= occurred in more 50% of the sampled stations) were expressed as percentages of the number of stations where the taxon was recorded. Taxa restricted to a single station were regarded as ‘unique or rare’, while taxa represented by a single individual at a station as a ‘singleton’ and taxa represented by two individuals at a station as ‘doubleton’ adopting a terminology of Colwell and Coddington (1994). These classifications were used to refine data for statistical testing.

3.4.3 Univariate measures

The number of taxa (S) and Species abundance (N) were computed from raw data for each station and sample groups obtained from cluster analysis considering all 57 replicates. The 'DIVERSE' programme within PRIMER v.6 was used to compute univariate indices (d, J', and H') for each sampled station and for sample groups obtained from cluster analysis and the associated standard deviation (±SD). Non-parametric Chao 1 (abundance based and sensitive to the frequencies of rare species) and Chao 2 (presence-absence based) were used to estimate the true Species Richness of this study (Chao 1984, Colwell and Coddington 1994, Chao et al. 2009, Gotelli et al. 2009). The Chao 1 true richness estimator was considered due to its high performance in the case of many rare species and species with a small frequency range, whereas, Chao 2 provides a least biased estimate of true species richness in small samples, and have been found to be very accurate (Chao 1984, Colwell and Coddington 1994). Here Chao1= $S_{obs} + (Q_1^2/2Q_2)$, where S_{obs} is the number of species in the sample, Q1 is the number of singletons and Q2 is the number of doubletons and Chao2 = $S_{obs} + (Q_1^2/2Q_2)$, where S_{obs} is as above and Q1 and Q2 are the frequency of unique and duplicates, respectively. Curves were plotted in PRIMER v.6, which through permutation generates standard deviation values for the curve.

3.4.4 Community patterns

In order to characterise spatial patterns in macrobenthos, a Bray-Curtis (B-C) resemblance matrix was computed on square-root transformed abundance data and the subsequent triangular resemblance matrix was subjected to cluster analysis (Chapter 2). A series of Similarity Profiles (SIMPROF) (p=0.05) was used to test the validity of the clusters. Taxa with the greatest contribution to the division of stations into clusters (species assemblage) were determined using the similarity percentages procedure SIMPER (Chapter 2). Resultant clusters were subjected to non-parametric multivariate analysis of variance (PERMANOVA) (Anderson 2001) for testing the hypothesis that macrobenthic communities differed between clusters.

3.4.5 Relating faunal and environmental patterns

The correlation between the B-C similarity matrix and Euclidean distance matrix was evaluated through the RELATE procedure (Chapter 2). Patterns in sedimentary characteristics were investigated using Principal Component Analysis (PCA) and stations were ordinated based on the dissimilarity matrices. The BVSTEP algorithm contained within the BEST procedure in PRIMER v.6 was used to identify a suite of variables that best maximises the degree of correlation (highest ρ_w values) between biotic and abiotic matrices (Chapter 2). The Global

BEST test was used to determine the significance of the subset of environmental parameters. The relative importance of each environmental variable in accounting for univariate and community variation was analysed using nonparametric multivariate multiple regression. Environmental variables were subjected to a step-wise procedure with Akaike's Information Criterion (AICc) used as the selection criterion to develop a response model of the macrobenthos community attributes (i.e. S, N, d, H´ and the multivariate structure of assemblage). P-values were ascertained after 9999 permutations of residuals under the reduced model (Anderson 2001) using the Distance Based Linear Models (distLM) (Clarke and Warwick 1988, Anderson et al. 2008a) procedure. The distance-based Redundancy Analysis (dbRDA was used to visualise the relationship between the best correlative variables and the macrobenthic assemblages.

A non-parametric multivariate linkage tree test (LINKTREE) was used to determine what ranges of values of the explanatory variables were responsible for discriminating different sample groupings together with the associated SIMPROF test to determine statistically significant (p=0.05) groupings within the tree (Anderson et al. 2008a). In this procedure environmental parameters were placed into a single group, successively subdivided, in binary partitions, in a way as to minimise the within-group variance (Anderson et al. 2008a). Only the ranks of the resemblances are utilised to maximise the ANOSIM R statistic between the two groups formed at each division. The R measure depicts the degree of separation of two groups in the high-dimensional space represented by the resemblance matrix for those samples, with R=1 when dissimilarities between the two groups exceed any dissimilarity within either group (Anderson et al. 2008a). Ocean Data Viewer 4.7.10 was used to plot hydrographic variables of each station and interpolated between stations and biozones.

3.4.6 Biozones as surrogates for macrobenthic community structure

The number of species (S) and species abundance (N), Shannon-Wiener Diversity (H'), and Margalef's Richness (d) were computed for each biozone subcluster and subjected to two-factor nested non-parametric multivariate analysis of variance (PERMANOVA) (Anderson 2001) for hypothesis testing that these univariate indices differed among biozone subclusters but not among sites within each biozone subcluster. PERMANOVA was used over ANOVA, as it does not assume normal distribution (Anderson, 2001). When PERMANOVA showed significant differences ($p<0.05$), a pair-wise comparison (9999 permutations) was done to explore differences among all pairs of biozone subclusters. Homogeneity of richness and diversity was tested prior to PERMANOVA by Levene's test. Unequal-variance ANOVA (Welch test) was considered since it is more robust for data where assumption of constant variance is not met

(Hammer et al. 2001). Two-factor PERMANOVA (Anderson et al. 2008a) was used to compare and test if macrobenthic assemblages were significantly different or not, based on a Bray–Curtis similarity matrix of the square-root transformed abundance data. Spatial structuring of macrobenthic assemblages within biozone subclusters was visualized by nMDS (2-dimensional). In order to test whether differences in the structure of assemblages between biozones were due to varying multivariate dispersion, the permutational test of multivariate dispersion (PERMDISP) (Anderson 2004) procedure was used to test homogeneity in average dispersion of samples from their group centroids. Taxa characterising and discriminating the structure of the subcluster were analysed through the SIMPER procedure. PERMDISP was used to test the hypothesis of homogeneity in average dispersion of samples based on environmental variables. Average Euclidean distance to centroid (±SD) was used to visualise differences between biozone subclusters.

3.5 Results

3.5.1 Sedimentary Characteristics

3.5.1.1 Sediment grain size distribution, total organic carbon (TOC) and carbonates

Detailed results of grain-size analysis and the spatial distribution of superficial sediments on the KwaZulu-Natal (KZN) Bight are given in MacKay et al. (2016) and Green and MacKay et al (2016). However, for this study, the distributions of sediment classes along the KZN mid-shelf are illustrated in Fig 3.1. There were significant differences in sediment distribution (PERMANOVA, df=18, Pseudo-F=56.991, p-perm<0.001) across grain-size classes and associated statistics of sorting and skewness (Table 3.1, Fig 3.1). Medium sand (24.5%), fine sand (21.7%), mud (17.1%), coarse sand (16.4%) and comparable proportions of very coarse grains and gravel dominated the sediment grain-size classes (Table 3.1) along the study area. The seafloor is highly heterogeneous along the mid-shelf with distinct sediment habitat features such as coarse-grained sands ranging between 0.79-1.03 ϕ (15.0-48.0%) low in TOC (0.32-0.68%) with moderate percentage carbonates (22.9-36.4%) off Port Durnford (Fig 3.1), indicative of a habitat subjected to strong current activities coupled with minimal sediment supply. A mud deposition (>4 ϕ, >70.0%) area off the uThukela Estuary with moderate TOC (1.61-2.72%) and low in percentage carbonates (10.0-15.0%) was another distinct habitat (Fig 3.1). The area between Zinkwazi and uMdloti varied with stations J4 to M3 dominated by fine-grain sands, while coarse-grained sand characterised stations L3 and K3 off Zinkwazi (Fig 3.1). Medium-fine grain sand (-0.06-2.32 ϕ, >45.0%), low in organic content (0.18-0.64%) with moderate high ranges of carbonates (15.7-67.3%) predominated sampling stations between Durban and uMkhomazi (S1-S6).

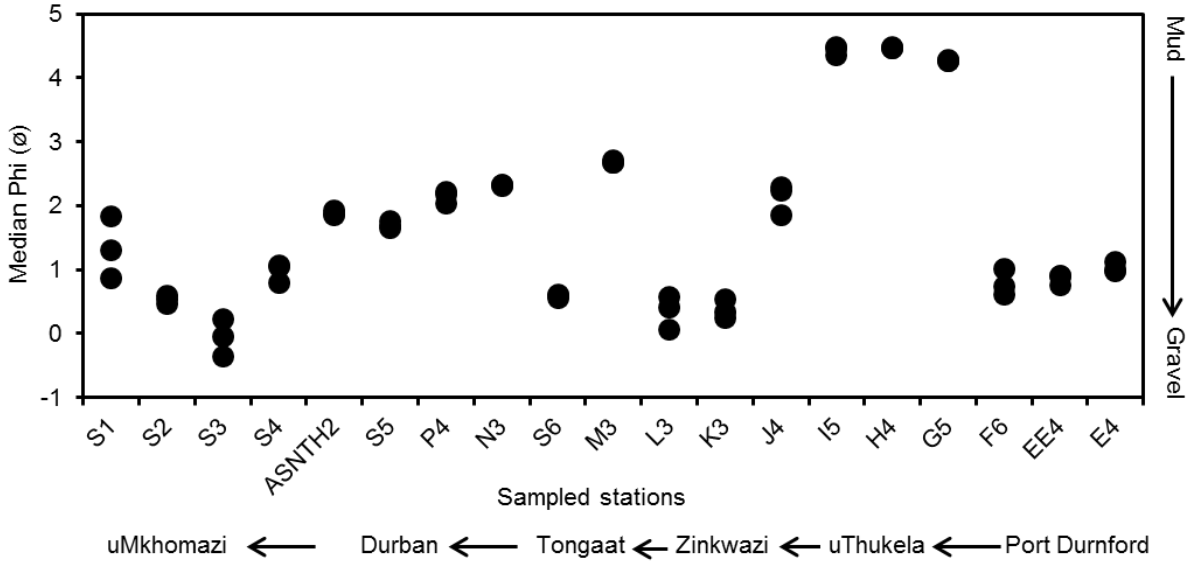

Figure 3.1. Sediment distribution along the KwaZulu-Natal mid-shelf from south (left) to north (right). Sediment classification is according to seven classes described by Wentworth (1922) and Gray (1981) expressed as median phi (ϕ). Main cities and coastal systems from north to south (Port Durnford-uMkhomazi).

Overall, the sediment grain along the KZN mid-shelf ranged from poorly sorted to moderately well sorted ($\bar{x}$: 1.02 ϕ ±0.39SD), indicating the presence of several textural types. The sediment gran size distribution was coarse skewed (negatively skewed) ($\bar{x}$: -0.50 ϕ ±2.71SD), suggestive of fine-grain sands dominance (Table 3.1). A positive correlation (r=0.771, p-perm<0.001, n=19) was obtained between the sediment TOC and median grain sizes, while an inversely (r=-0.674, p-perm=0.001, n=19) relationship was observed between carbonates and sediment organic content.

Table 3.1. Overview of the sedimentary characteristics along the KZN mid-shelf (mean, SD and range)

Variables	Mean	SD	Min	Max
%Gravel	7.43	8.70	0.00	28.44
%Very coarse sand	9.80	10.77	0.14	36.03
%Coarse sand	16.41	14.09	0.14	42.38
%Medium sand	24.54	15.96	0.17	54.18
%Fine sand	21.70	23.73	0.96	78.90
%Very fine sand	3.03	4.09	0.14	16.66
%Mud	17.10	30.62	1.19	95.32
Median phi (ϕ)	1.73	1.40	-0.06	4.48
Sorting	1.02	0.39	0.38	1.62
Skewness	-0.50	2.71	-5.95	6.52
%TOC	0.73	0.66	0.18	2.72
%Carbonates	30.40	14.55	10.00	67.25

3.5.1.2 PCA analysis

Classification analysis identified five groups (I-V) based on different sedimentary characteristics visualised in a Principal Component Analysis (PCA) ordination plot (Fig 3.2). PCA revealed that stations were distinguished mainly according to the dominant sediment grain size. The first two PC axes were retained as together they explained 75.4% of the total variance. The eigenvalues of the first two PC axes (displayed in Fig 3.2) were 7.09 and 1.95, respectively. The PCA plot shows that axis 1 (PC1-59.1%), mainly separated data along a gradient between coarse and very fine substrates and associated carbonate content, with approximately moderately sorted sediments. High mud content, sediment organics, fine-to- medium sand with highest eigenvector coefficient defines PC2, which accounted for 16.3% of the variation (Fig 3.3). Group (I) comprised of stations off the uThukela Estuary dominated by mud (68.0-95.0%) and high total organic content. Group II was mainly characterised by samples with an important contribution of medium-fine sand (10.0-78.0%), deficient in TOC.

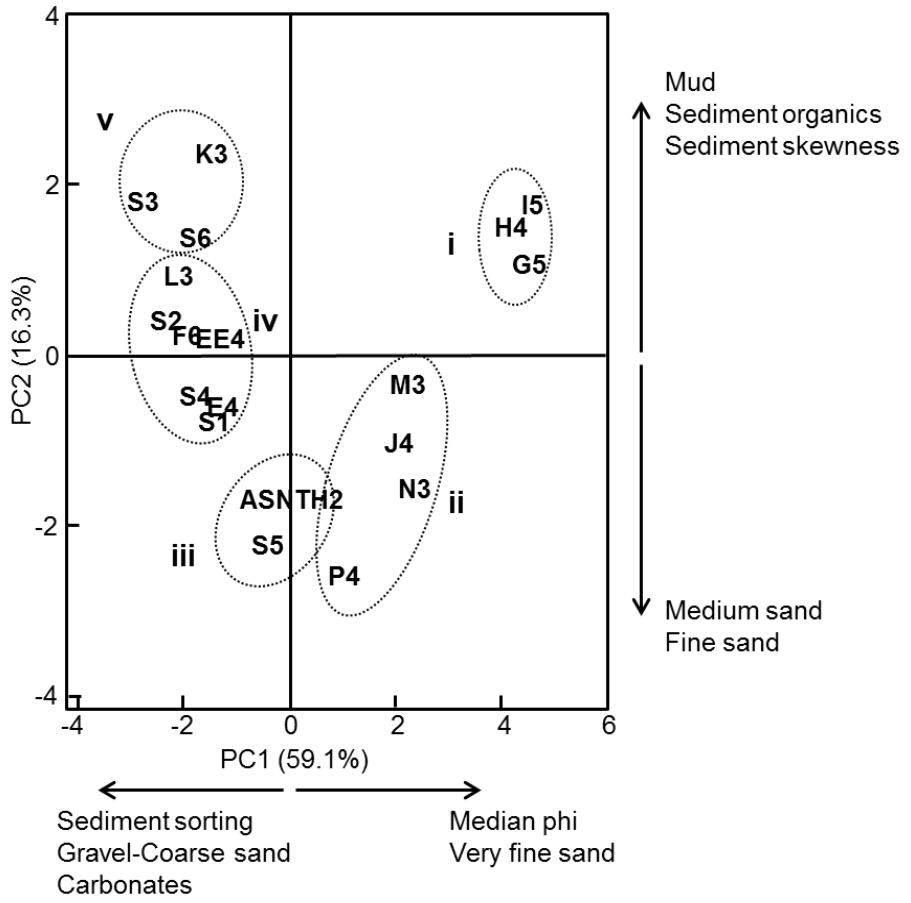

Figure 3.2. PCA plot. Two-dimensional visualisation of the sedimentary environment displaying the distribution of five sample groupings (Group I-V) of 19 samples collected along the KwaZulu-Natal mid-shelf. Responsible eigenvectors are indicated adjacent to axes PC1 and PC2.

The third (III) group comprised of stations dominated with coarser sand (10-35%), also low in TOC, but high in percentage carbonates. Group IV consisted of stations with coarse-to-fine sediments low in TOC with average values of carbonates. The remaining stations with low to moderate values of TOC, and showing heterogeneous sediment grain composition ranging from fine sand to gravel formed Group V.

3.5.2 Water column characteristics

3.5.2.1 Bottom-water temperature and salinity

Temperatures >20°C were consistently measured between Port Durnford and Zinkwazi. An exception was F6 where cooler water was measured, perhaps indicative of Agulhas Current cooler water on the shelf (Fig 3.3 a). An area of cooler water was also noted off Durban corresponding to the Durban Eddy. Overall, the study area exhibited a fairly large temperature range 16.31 and 21.65°C (Table 3.2). In general, a saline homogeneity was observed (range: 35.4 to 35.5, $\bar{x}$: 35.4 ± 0.03SD), despite some indication of hydrographically induced variability in other variables (Table 3.2 and Fig 3.3 b).

3.5.2.2 Dissolved Oxygen (O_2)

The bottom water along the KZN mid-shelf was consistently low in dissolved oxygen ($\bar{x}$: 4.06 $mg.l^{-1}$ ±0.45SD, range: 3.27 (S2) - 4.56 (S6), exhibiting a near-constant trend between Port Durnford and uThukela (Fig 3.3). An exception was F6 with the lowest O_2 concentration in the vicinity, suggestive of the offshore oxygen minimum zone commonly transported onto the shelf-edge by the Agulhas Current (Roberts et al. 2006). The area of low O_2 concentration between the sampling stations L3 and M3 could be associated with primary production as reflected by Chlorophyll-a coupled with high nutrient levels from the uThukela outflow (Scharler et al. 2016) (Fig 3.3 c). The low O_2 concentration was also noted off Durban between N3 and P4, suggestive of the hydrological conditions more typical of deeper water settings and this could be associated to the Durban Eddy, occasionally linked with the Natal pulse (Lutjeharms and Ansorge 2001, Bryden et al. 2005, Roberts et al. 2016).

3.5.2.3 Chlorophyll-a (Chl-a)

Chl-a was generally low and fairly uniform (0.41 $\mu g.l^{-1}$ ± 0.31SD) (Fig 3.3 d, Table 3.2). The highest Chl-a was found at sampling station K3 just south of Thukela River mouth (1.35 $\mu g.l^{-1}$). Elevated values were also recorded at station S6 corresponding to the Durban Eddy, S5 and ASNTH2 both located off iSiphingo Estuary and adjacent to the Amanzimtoti southern outfall

(Fig 3.3 d). The lowest Chl-a values were found between Port Durnford and uThukela, including where the lowest recorded value (0.17 µg.l^{-1}) during the study was found (off uMdloti Estuary) (Fig 3.3 d).

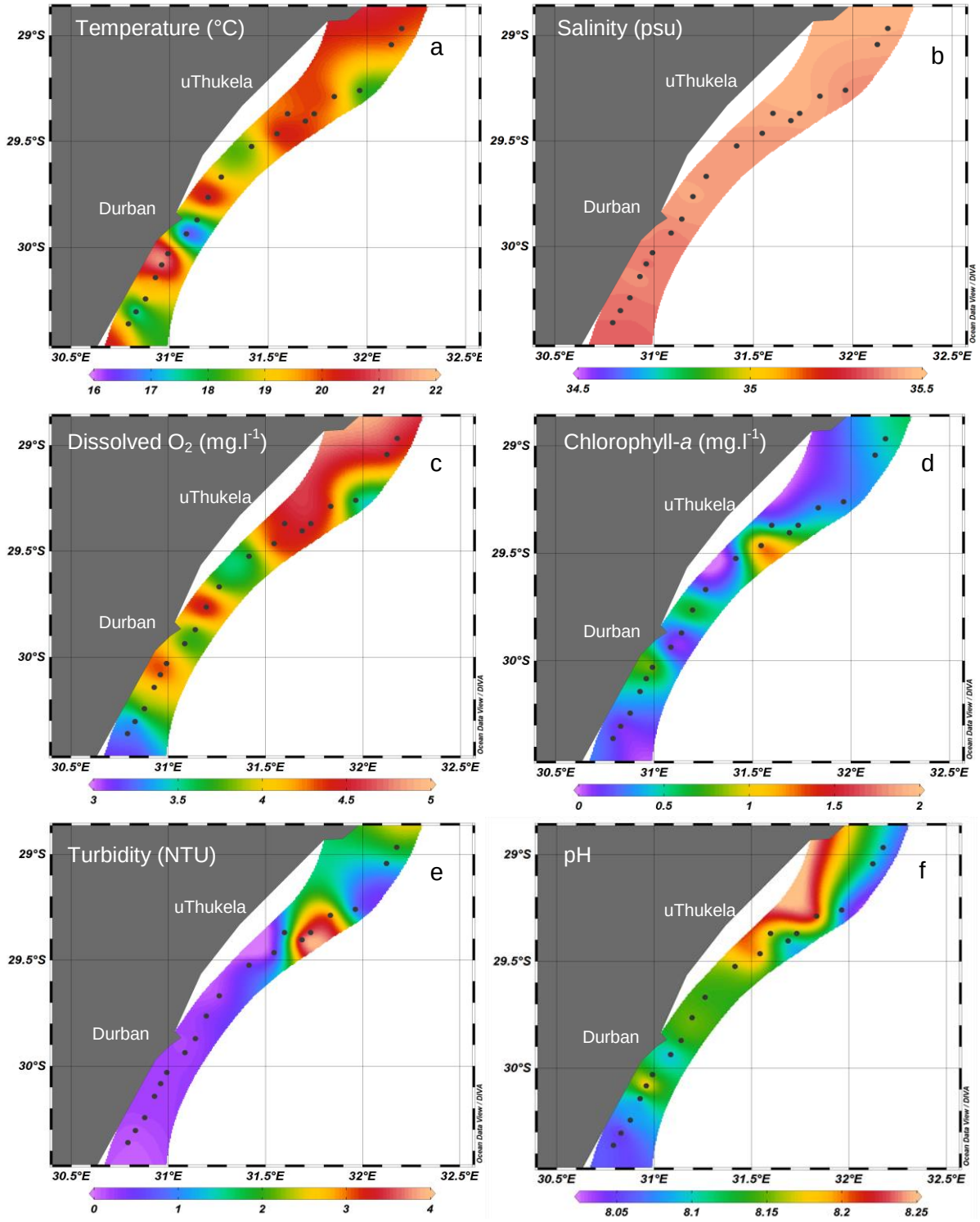

Figure 3.3. Near bottom environmental variables measured along the KwaZulu-Natal mid-shelf environment. Temperature (a), Salinity (b), Chlorophyll-a (c), Dissolved Oxygen (d), Turbidity (e), and pH (f).

3.5.2.4 Turbidity and pH

The turbidity showed a uniform trend of lower values ($\bar{x}$:0.58 NTU ±0.05SD). Turbidity values >1.5 NTU were generally recorded at stations between Port Durnford and uThukela, while values <1 NTU were consistently recorded south of uThukela to uMkhomazi (Fig 3.3 e). The highest turbidity (3.98 NTU) was recorded at sampling stations off the uThukela corresponding to uThukela outflow and dominated by high mud content. During the sampling period, pH values remained approximately constant along the study area, on average being $\bar{x}$:8.12±0.05 and reflected a narrow range between 8.04 and 8.20 (Table 3.2). Stations with lower pH were recorded off Port Durnford and uMkhomazi (Fig 3.3 f).

Table 3.2. Overview of the bottom-water environmental variables measured along the KZN mid- shelf.

Variables	Mean	SD	Min	Max
Temperature (°C)	19.26	1.36	16.31	21.17
Salinity (psu)	35.42	0.03	35.36	35.46
Dissolve Oxygen ($mg.l^{-1}$)	4.06	0.45	3.27	4.56
Chlorophyll-a ($\mu g.l^{-1}$)	0.41	0.31	0.05	1.35
Turbidity (NTU)	0.58	1.24	0.11	3.98
pH	8.12	0.05	8.04	8.20

3.5.3 Macrobenthos composition

From 57 grabs, a total of 33 272 macrobenthic organisms distributed across 634 taxa were sampled from approximately 11.4 m^2 of seafloor. Macrobenthic community was from seven Phyla representing 18 Classes, 149 Families, and 281 Genera. These are presented in Table 3.3 based on their percentage contribution to the number of taxa (*S*) and abundance (*N*). These included Annelida, Arthropoda, Mollusca, Echinodermata, Cnidaria, and Sipuncula. The remaining species summarised as 'others' played a minor role in diversity and were only important at specific stations (Platyhelminthes, nemerteans, nematodes, and echiurids) (Table 3.3). Annelida (almost exclusively Polychaeta) was the most diverse phylum constituting 45% of the total fauna (*S*), but only represented 27% of faunal abundance (*N*) (Table 3.3). Arthropoda (peracarid crustaceans) was the second most species rich phylum, represented 33% of the total fauna, but contributed 60% to the total abundance (Table 3.3), with Amphipods being the main representative. Mollusca (*S*: 7%, *N*: 3%), Echinodermata (*S*: 3%, *N*: 4%) and (*S*: 4%, *N*: 1%), and Sipuncula (*S*: 3%, *N*: 4%) were also an important part of KZN mid-shelf macrobenthos. Faunal groups summarised as 'others' contributed only 4% to total *S* and 1% to *N*. In total, unique (restricted to a single station) taxa were represented by 189 organisms and corresponded to 30% of the total *S* and 154 of the rare occurances were singletons (24% of the total community) and 21 were doubletons (3% of the total community).

Table 3.3. Contribution of the major Phyla to the total number of taxa (S), abundance (N), and their respective percentage contribution (%).

Phyla	S	% contribution	N	% contribution
Annelida	288	45	9019	27
Arthropoda	213	34	20035	60
Mollusca	45	7	1034	3
Echinodermata	20	3	468	4
Cnidaria	22	4	1173	1
Sipuncula	18	3	1283	4
Others	28	4	259	1

3.5.3.1 Species estimator

Estimates of the total number of taxa are presented in Fig 3.4. S_{obs} (634 taxa) was smaller than Chao 1 (1061 taxa) and Chao 2 (941 taxa) non-parametric estimators which gave almost identical results taking into account the variability associated with each estimator for all assemblages. The KwaZulu-Natal mid-shelf macroinvertebrate fauna were reasonably well sampled as the observed contributed >60 of the predicted total Richness (Fig 3.4).

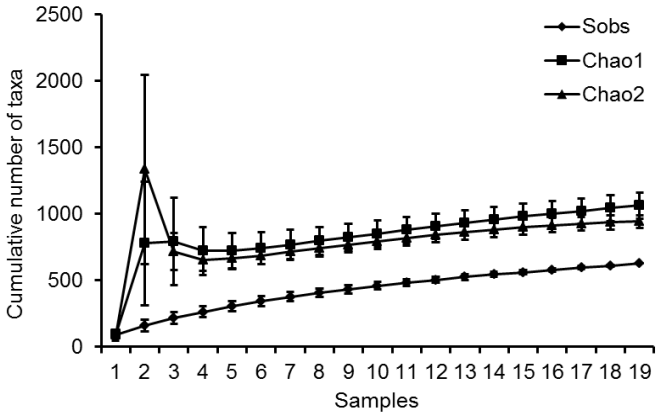

Figure 3.4. Species accumulation curve for macroinvertebrates of the KwaZulu-Natal mid-shelf (±SD).

3.5.4 Diversity (*S*) and abundance (*N*) gradients per major Phyla

The number of taxa (*S*) varied between sampled stations with highest values (84-163 taxa m^{-2}) recorded at the transition region of the uThukela River and Durban (stations J4-N3), however this was highly variable between replicates. Stations off uThukela River and Port Durnford supported lower number of taxa (13-53 taxa m^{-2}) (Fig 3.5). Overall, the mean ($\overline{x}$) number of taxa was 88 taxa m^{-2} (±41SD) with approximately 70% of the sampled stations each containing >85 taxa (Fig. 3.5). Species composition exhibited differences among stations, with Annelida and Crustacea together contributing the most to the number of taxa per station. Approximately equal numbers of different Species of Polychaeta and Crustacea occurred between south of Durban and uMkhomazi (stations P4-S1) (Fig. 3.6). However, this pattern did not hold between Durban

and uThukela (N3-J4) where Polychaeta showed high local richness. Stations between uThukela and Port Durnford (I5-E4) had lowest number of taxa recorded, yet diverse in that these stations contained most taxonomic groups.

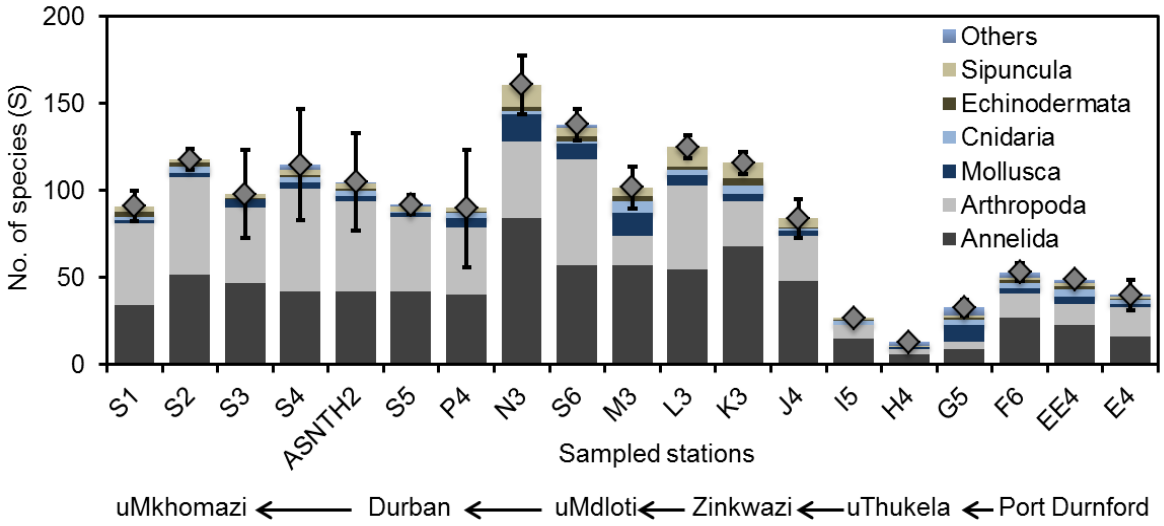

Figure 3.5. Spatial representation of number of taxa (S±SD) aggregated to main Phyla for macrobenthic fauna sampled along the KwaZulu-Natal mid-shelf stations. Arrows indicate the direction of the current.

The highest macrobenthos abundance (*N*) value was recorded at iSiphingo (S5-2096 ind. m^{-2}, ±451SD) and coincided with high abundances of specific faunal components (*Unciolella spinosa* (880 ind. m^{-2}) and *Byblis giamardii* (240 ind. m^{-2})). Relative intermediate values were recorded at the habitat between uThukela and Durban (K3-631 ind. m^{-2}, ±577SD; L3-769 ind. m^{-2}, ±208SD; S6-1305 ind. m^{-2}, ±1112SD), being comparable to S4 (609 ind. m^{-2}, ±147SD), S3 (679 ind. m^{-2}, ±283SD) and S2 (1132 ind. m^{-2}, ±465SD) south of iSiphingo to uMkhomazi. Lowest abundances (85-133 ind. m^{-2}) were recorded off uThukela Estuary (H4-36 ind. m^{-2}, ±31SD; G5-91 ind. m^{-2}, ±42SD) and off Port Durnford (E4-87 ind. m^{-2}, ±34SD). Overall, the mean abundance was $\bar{x}$:587 ind. m^{-2} (±512 SD) (Fig 3.6). In terms of taxa relative contribution, polychaetes worms were important from the uThukela to Durban (N3-J4), whereas crustaceans were ubiquitous between Durban and uMkhomazi (stations S1-S6) (Fig. 3.6). When considering the distribution range for each Phylum, only Annelida, Arthropoda, Mollusca, and Sipuncula featured similar spatial pattern (high in *N* at specific stations) (Fig. 3.6). This pattern was less clear for other Phyla due to a lower number of taxa. There were significant differences in *S* (pseudo-F=8.539, df=18, p=0.0004) and *N* (pseudo-*F*=10.650, df=18, *p*=0.0007) between stations (*n*=19).

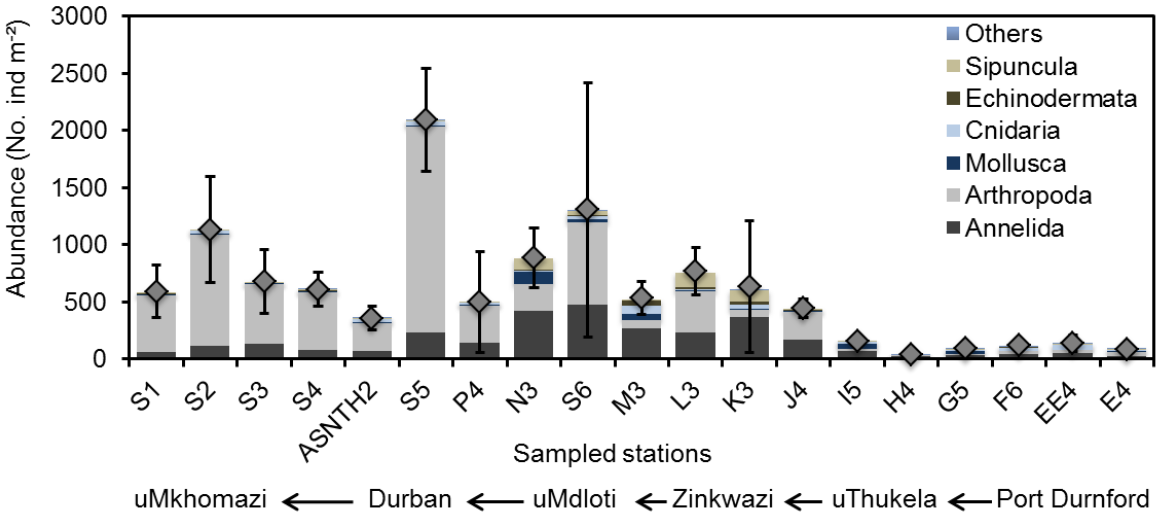

Figure 3.6. Spatial representation of mean abundance (No. ind. m^{-2} ±SD) aggregated to main Phyla for macrobenthos sampled along the KwaZulu-Natal mid-shelf stations. Arrows indicate the direction of the current.

3.5.5 Taxonomic composition

3.5.5.1 Polychaeta

Polychaeta was the most diverse group with a total number of 288 different taxa identified to lowest practical taxa (Species level) possible across 42 Families and 140 Genera representing 45% of the total community (Table 3.3). Within sampled polychaetes, both errant (51%) and sedentary forms (49%) were comparable, but sedentary forms were more diverse (representatives of different families and genus) over the errant members. In increasing order, Cirratulidae (5.5%), Maldanidae (6%), Syllidae (8%), Terebellidae (10%) and Spionidae (11%) presented the highest number of indivduals, each represented by >15 taxa (Fig 3.7). Terebellidae, Spionidae, Nephtyidae and Capitellidae were the most abundant Families, each represented by >500 individuals (Fig 3.7). Among the sampled Families, thirteen were rare (4.5% of the polychaete fauna, and 4% of polycheata N), only significant at specific stations and classified as 'others' (Fig 3.7). The families Nephtyidae, Glyceridae and Capitellidae were present at most sampled stations. Frequently encountered taxa (F) included *Lumbrineris aberrans* (F=52%), *Tharyx filibranchia* (F=57%), *Spiochaetopterus vitrarius* (F=57%), *Aglaophamus dibranchis* (F=57%), *Notomastus latericeus* (F=68%) and *Nephtys capensis* (F=74%). Of the thirteen taxa classified as 'others', seven were identified as rare. These included *Caulleriella acicula, Macroclymene cf monilis, Caulleriella bioculata, Haplosyllis spongicola, Oxydromus spinosus, Prionospio cirrifera* and *Sphaerosyllis cf semiverrucosa.* The remaining fauna were not classified because they were identified either to genus or to higher taxonomic level and represented existing taxa (e.g. *Scolelepis* and Syllidae). The most abundant

species included the terebellid, *Lanice conchilega* with 480 ind. m^{-2} (based on the individual abundance per total polychaete abundance (A_p)=5.3%) which was restricted to medium coarse substrates, followed by the spionid, *Prionospio nirripa,* with 338 ind. m^{-2}, accounting for A_P=3.8%. The spiochaetopterid, S*piochaetopterus vitrarius* was a distinct resident at several locations and textural types, being the third most abundant species (323 ind. m^{-2}), accounting for A_P=3.6% of polychaeta total abundance. *Nephtys capensis* with 288 ind. m^{-2} accounted for A_P=3.2% was also an important component in most of the stations.

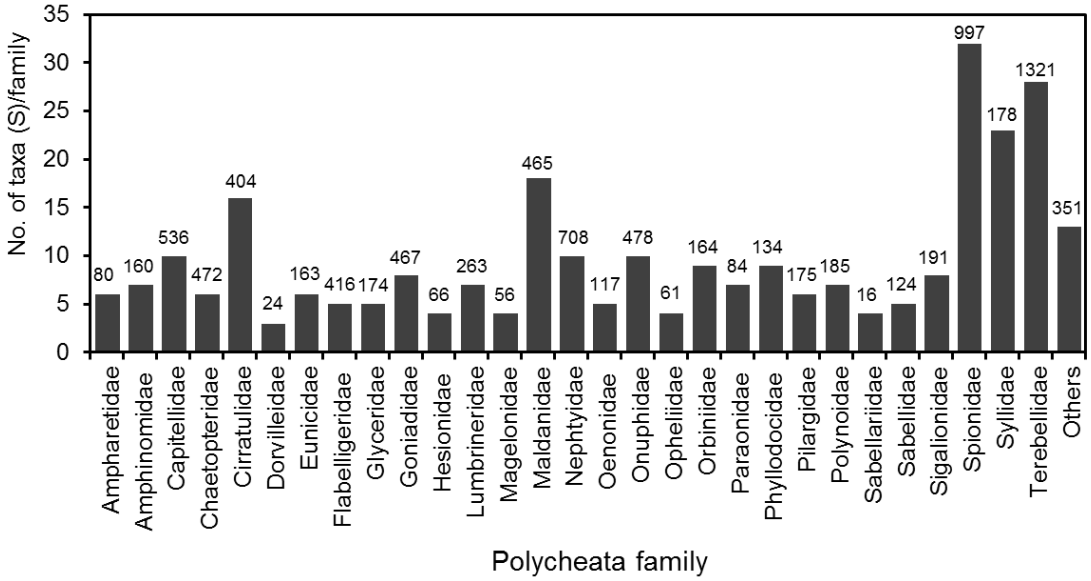

Figure 3.7. Number of taxa per polychaete Family and the associated abundance (number above each bar).

3.5.5.2 Crustacea

Within the peracarid Crustacea group, Amphipoda was the most dominant order represented by 25 Families, 43 Genera and 89 taxa and accounted for 42% of the total crustacean fauna (C_F) and 85% of the crustacean abundance (C_A) and overall contributing ~14% of the total fauna (T_F) (Fig 3.8). In decreasing order, Ampeliscidae with two Genera and seventeen Species (amphipod fauna: A_F=20% and C_F=8%), Photidae with 3 Genera and 12 Species (A_F=14% and C_F=6%), Mearidae comprising of six Genera and eight Species (A_F=9% and C_F=4%) and Lysianassidae with three Genera and seven Species (A_F=8% and C_F=3%) were the most species diverse Families. The most frequently encountered taxa included, *Mandibulophoxus stimpsoni* (F=47%), *Hippomedon onconotus* (F=47%), *Ampelisca diadema* (F=52%), *Urothoe pulchella* (F=52%), *Unciolella spinosa* (F=52%), *A. palmata* (F=68%), and *Byblis gaimardii* (F=68%). W The most abundant species based on the amphipod total abundance (A_A) were *A. insignus* (757 ind. m^{-2} (A_A=4%)), *U. pulchella* (1003 ind. m^{-2} (A_A=5%)), *A. diadema* (1632 ind. m^{-2} (A_A=8%)), *Byblis gaimardii* (2596 ind. m^{-2} (A_A=13%)), and *Unciolella spinosa* (3904 ind. m^{-2} (A_A=19%)).

Singletons represented 27% of the amphipods fauna (24 taxa) and 11% of the total Crustacea. Besides amphipods, Decapoda represented by 21 Families, 12 Genera and 49 species (C_F=23%, C_A=6% and T_F=8%) was the next dominant taxa (Fig 3.8). *Callichirus sp.1* (260 ind. m^{-2}) and Hippolytidae sp.1 (168 ind. m^{-2}) were the most abundant taxa, but restricted to muddy habitats (F>50). Singletons contributed 49% to the decapod fauna. Isopoda comprised nine Families, 16 Genera and 31 Species (C_F=15%, C_A=5% and T_F=5%) were also important (Fig 3.8). Specious families included Anthuridae (five Genera and seven Species) and Cirolanidae (one Genus and seven Species). *Leptanthura cf laevigata* and *Arcturinoides sexpes* were the most common species (F=50%) and dominant taxa included *L. laevigata* (110 ind. m^{-2}), *L. cf laevigata* (126 ind. m^{-2}), and *Amakusanthura africana* (185 ind. m^{-2}).

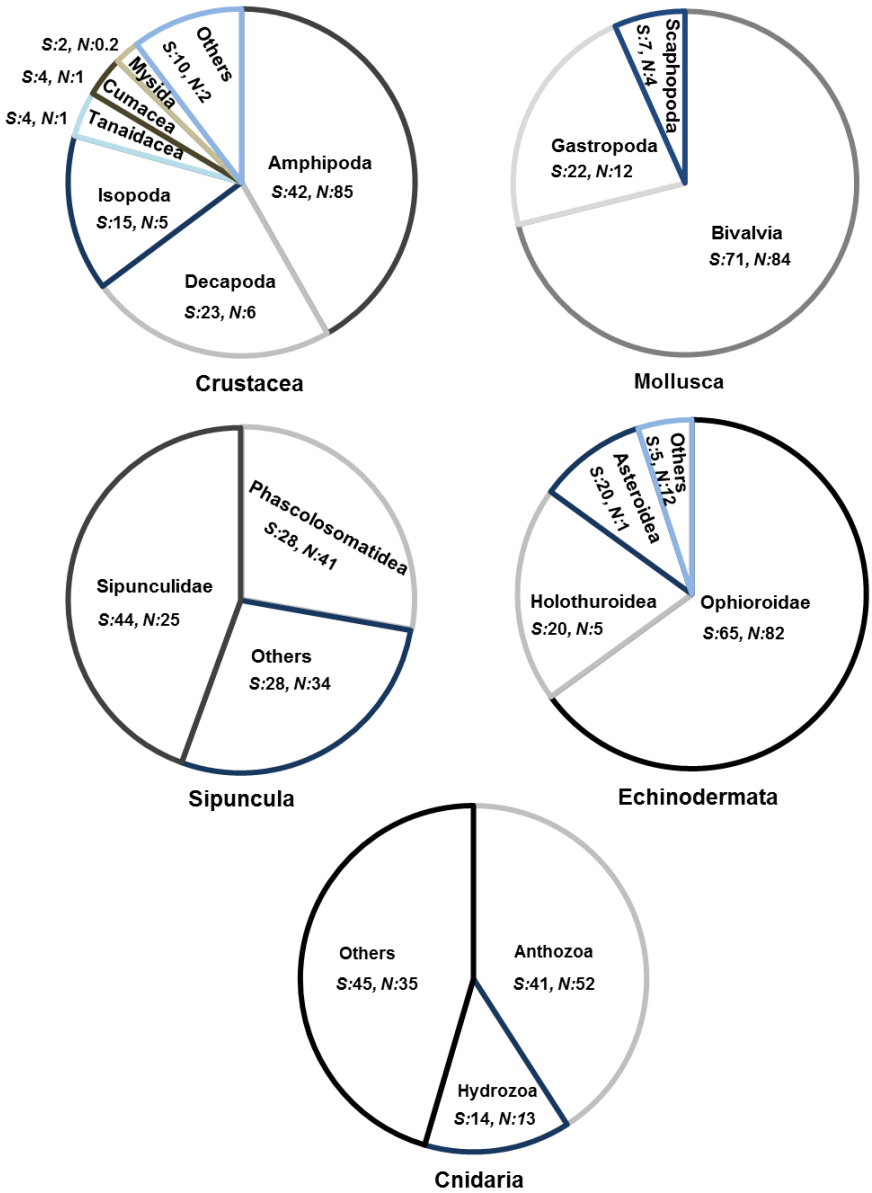

Figure 3.8. Composition represented as percentage contribution of the number of taxa (S) per Class (various colours in each chart) in Phyla and the associated abundance (N).

3.5.5.3 Mollusca

Altogether, 45 taxa were identified belonging to Bivalvia, Gastropoda, and Scaphopoda. Bivalvia was the most diverse group with 32 taxa spread across 14 Families (mollusc fauna: M_F=71%, mollusc abundance: M_A=84% and T_F=5%) (Fig 3.8). In sequential order, Veneridae, Tellinidae, and Nuculidae were the most species rich families, each represented by more than three taxa, common in muddy sediments. From 45 Mollusca taxa, seventeen were singletons and accounted for 38% of the total molluscan fauna. Taxa recorded in high abundances were restricted spatially (F=28%) and included *Pallidea palliderosea* (204 ind. m^{-2}), *Nucula sp.1* (164 ind. m^{-2}), *Diplodonta sp.1* (61 ind. m^{-2}) and *Donax burnupi* (60 ind. m^{-2}). Gastropods were present in markedly lower abundances (ten individuals in eight families). The scarce Scaphopoda belonged to two Families (three Species). Together, Gastropoda and Scaphopoda, constituted 29% of the remaining molluscan fauna (Fig 3.8).

3.5.5.4 Echinodermata and Sipuncula

Echinodermata, with 20 different taxa, spread across five Families and four Orders contributed 3% to the total community. The Order Ophioroidae was by far the most dominant (65%), whereas Holothuroidea and Asteroidae each contributed 20% to the Echinodermata fauna (Fig 3.8). Although restricted spatially (F=30%), *Amphiuridae sp.1* (152 ind. m^{-2}) and *Ophiopsila seminuda* (119 ind. m^{-2}) were the most abundant taxa. Of the 20 taxa recorded, 50% (10 Species) represented singletons. Sipuncula were represented by 18 taxa across two Orders (T_F=3%). Phascolionidea and Sipunculidae were equally important, each contribute 28% to Sipuncula fauna and the 'others' contributing the major fraction (44%) (Fig 3.8). Dominant taxa included *Aspidosiphon sp.1* (403 ind. m^{-2}), Phascolionidae sp.1 (199 ind. m^{-2}) and Sipuncula sp.3 (176 ind. m^{-2}).

3.5.5.5 Cnidaria and 'Others'

Cnidaria (22 taxa) and the 'others' group consisting of minor Phyla, such as Nemertea (three taxa), Echuira (three taxa), Nematode (two taxa), Platyhelminthes (four taxa), picnogonids (one taxon), worms (three taxa), and unidentified (four taxa) contributed a minor part (4% to the total fauna and 1% to the number of individuals) to the KZN mid-shelf macrobenthic community.

3.5.6 Macrofaunal diversity gradients

Margalef's Richness (d) ranged between 5.29 (off the uThukela (H4), a habitat characterised by high percentage mud) and 23.7 (north of Durban (N3), a habitat associated with fine-grained

sand) with a mean of $\bar{x}$:13.9±3.4 SD (Fig 3.9). The Pielou's evenness measure (J') showed a monotonic spatial trend with a lowest value recorded at a station off iSiphingo (S5) where there was a high abundance of specific faunal elements (e.g. *Unciolella spinosa* and *Byblis giamardii*) (Fig 3.9). The Shannon-Weiner diversity (*H'*) component varied in conformity with *J'* (mean 3.5±2.3 SD, range: 0.58 and 4.5) with an exception to H4 where low values of H' were recorded (Fig 3.9). In this study, averagely high diversity (H') and evenness (*J'*) values coincided with stations where abundance had the lowest values. The sampling station P4 reflected a highly variable fauna in terms of evenness and diversity component. This is attributable to one replicate where no live organisms were recorded. The distribution test performed for all diversity descriptors indicated significant differences between stations (n=19) (p<0.001).

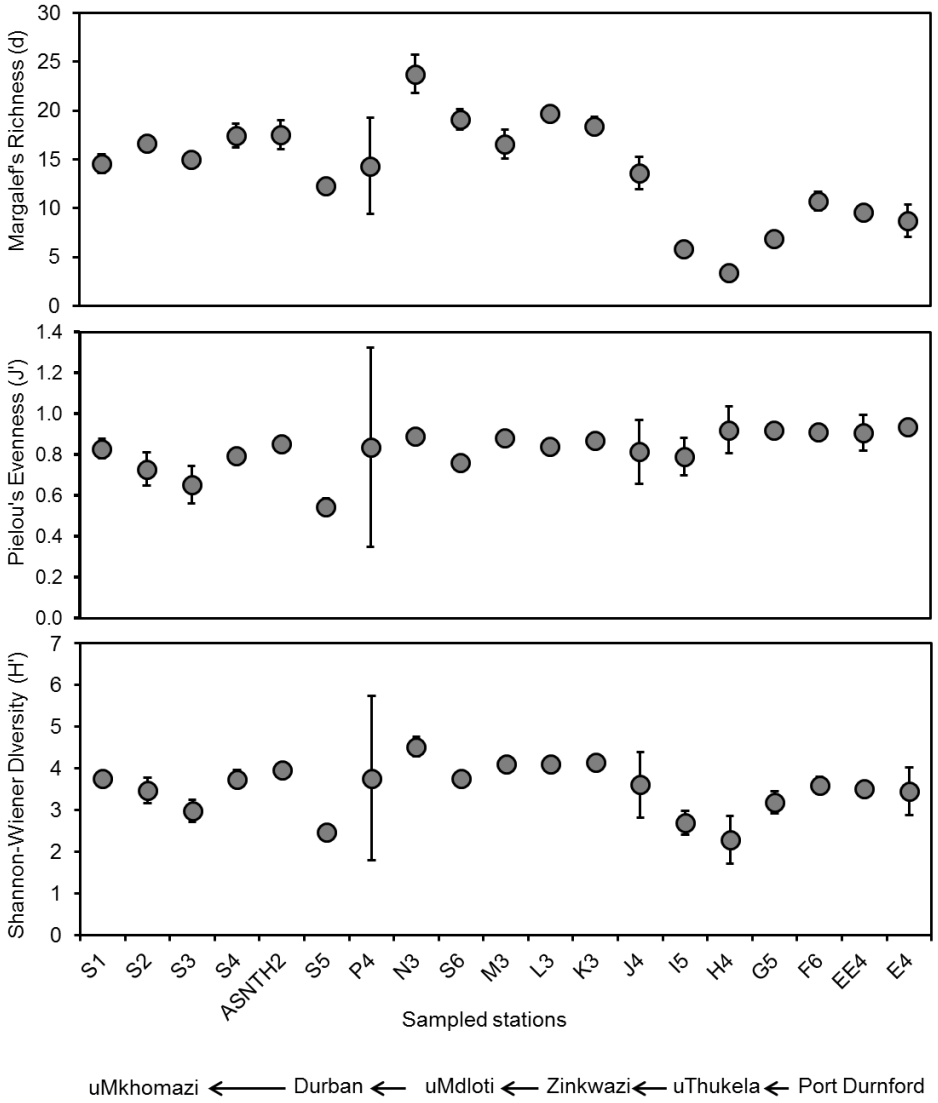

Figure 3.9. Richness (d±SD), Evenness (J'±SD), and Diversity (H'±SD) calculated from abundance data of macrobenthic species sampled along the KwaZulu-Natal mid-shelf stations. Arrows between the main cities or/and river indicate the direction of the current.

3.5.7 Univariate descriptors relationship with environmental parameters

Results of distLM showed that nine environmental variables were important in explaining variation in diversity indices (Table 3.4). The single variable that explained the greatest amount of variation in S was turbidity (72.10%) followed by mud content (44.40%), median phi (36.40%), and TOC (35.60%) (Table 3.4). However, after model fitting, the p-values associated with the conditional test to add other variables and the subsequently fitted terms in the model were not statistically significant ($p>0.05$) (Table 3.4). In this way, the best model to explain S included only turbidity and medium sand that together explained 78.91% of the variation (Table 3.4). Results further showed that seven variables were important in explaining variation in N, while nine variables were important for d and three explained variation in H'(Table 3.4). The fitted model showed turbidity to be important in explaining variation in S as alone it explained 52.73%, while medium sand, turbidity and salinity explained 83.40% of the variation in d and turbidity and salinity together accounted for 46.30% of the variation in H' (Table 3.4). Macrobenthic richness and abundance was highest in sandy sediment and minimum in mud. Grain size distribution may have played an important role in the distribution of macrobenthos.

Table 3.4. DistLM results for the number of taxa (S), abundance (N), Margalef's Richness (d) and Shannon-Weiner diversity (H'). M-tests=marginal tests and S-tests=Sequential tests. Prop=Proportion of variance in species data explained by that variable, Pse-F= Critical values of PERMANOVA, P=Level of statistical difference. Two variables together explaining most of the variance in the indices indicated in bold.

Variable	S			N			d			H'		
	M-TESTS			M-TESTS			M-TESTS			M-TESTS		
	Prop.	Pse-F	P	Prop.	Pse-F	P	Prop.	Pse-F	P	Prop.	Pse-F	P
Sediment												
%Medium sand (1.0-2.0 ϕ)	0.211	4.541	0.030	-	-	-	0.230	5.065	0.026	-	-	-
%Fine sand (2.0-3.0 ϕ)	0.215	4.665	0.025	0.171	3.515	0.046	0.221	4.820	0.028	0.206	4.406	0.047
%Mud (>4.0 ϕ)	**0.440**	**13.379**	**0.002**	**0.212**	**4.567**	**0.020**	**0.511**	**17.747**	**0.002**	**0.294**	**7.077**	**0.019**
Median phi	0.364	9.714	0.003	0.189	3.957	0.030	0.426	12.620	0.002	-	-	-
Sorting	0.215	4.659	0.030	-	-	-	0.245	5.510	0.023	-	-	-
%Total organics carbon (TOC)	0.356	9.395	0.003	0.202	4.298	0.022	0.392	10.940	0.003	-	-	-
%Carbonates	0.265	6.134	0.013	0.189	3.970	0.030	0.275	6.451	0.013	-	-	-
Water column												
Salinity	0.253	5.743	0.012	0.211	4.538	0.023	0.230	5.070	0.025	-	-	-
Dissolved Oxygen ($mg.l^{-1}$)	-	-	-	-	-	-	0.186	3.886	0.047	-	-	-
Turbidity (NTU)	**0.721**	**44.007**	**0.000**	**0.527**	**18.969**	**0.000**	**0.740**	**48.418**	**0.000**	**0.339**	**8.707**	**0.009**
	S-TESTS			S-TESTS			S-TESTS			S-TESTS		
	Prop.	Pse-F	P	Prop.	Pse-F	P	Prop.	Pse-F	P	Prop.	Pse-F	P
+%Medium sand (1.0-2.0 ϕ)	0.068	5.141	0.006	-	-	-	0.054	4.245	0.016	-	-	-
+Turbidity (NTU)	0.721	44.007	0.000	0.527	18.969	0.000	0.740	48.418	0.000	0.339	8.707	0.009
+Salinity	-	-	-	-	-	-	0.039	3.567	0.038	0.124	3.706	0.070
	Cum(%) = 78.91			**Cum(%) = 52.73**			**Cum(%) = 83.40**			**Cum(%) = 46.30**		

3.5.8 Faunal community analyses and spatial patterns

Cluster analysis, taking into account 634 studied species, distinguished two sets of sample groupings at 10% (dotted line and brackets), and at 20% (black line and brackets) B-C similarity, and several sub-groups that grouped at a wider range (15-50%) of similarities (Fig 3.10). The overall B-C similarity percentage was low and no sample groups shared >50% of resemblance (Fig 3.10). This indicated an important inter-sample variability. Group A (10% B-C similarity threshold) encompassed three stations off the uThukela at 15.25%, with H4 and I5 grouped tightly at a higher similarity (~30%) level than G5 (Fig 3.10). Sample Group B grouped the remaining stations, which shared 11.77% similarity (Fig 3.10).

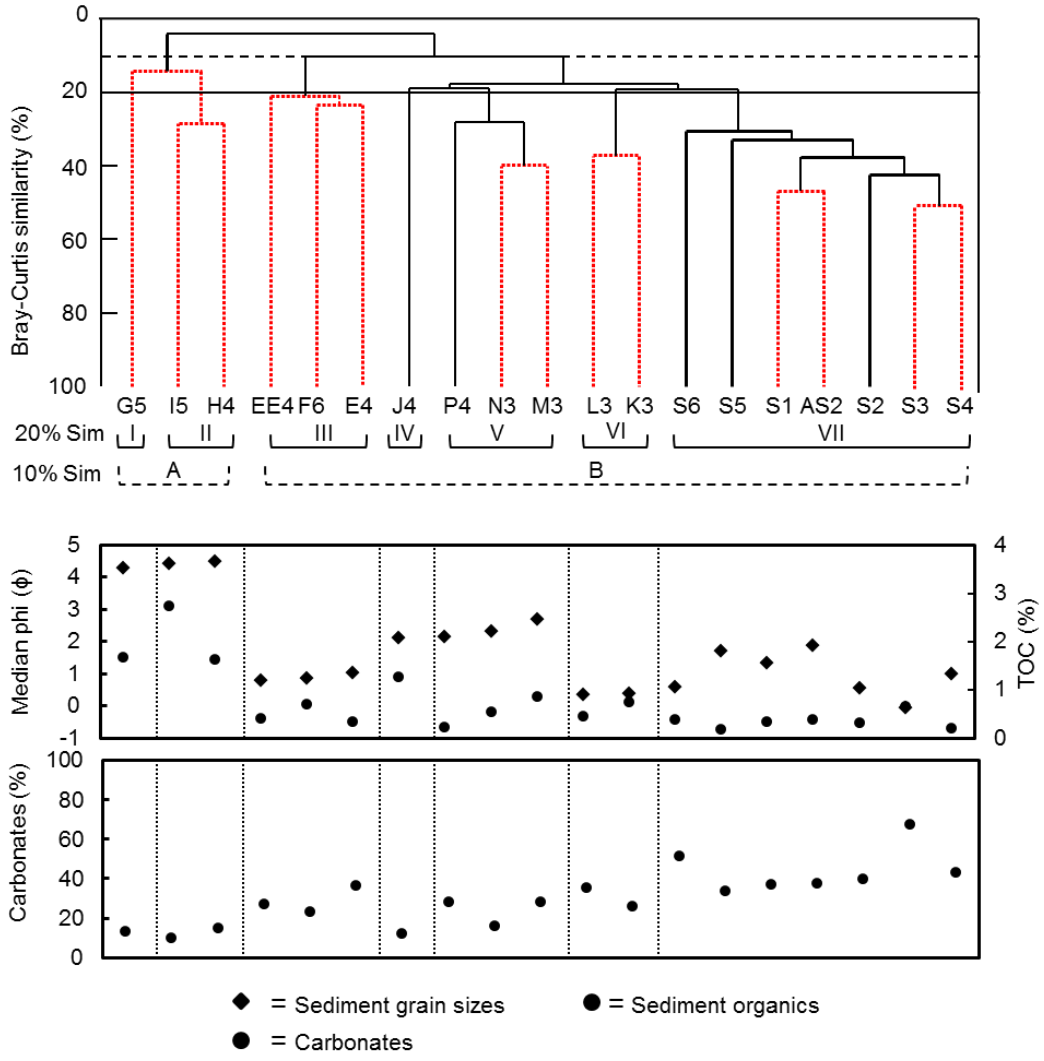

Figure 3.10. Dendrogram of hierarchical clustering (based on group-average linkage) of 19 KZN mid-shelf stations, based on Bray-Curtis similarities calculated from square root transformed abundance (N) data. Dotted line and respective bracket designate two groups (A and B) at 10% similarity level, while solid black line and respective bracket designate seven groups (I-VII) at 20% similarity level with corresponding median grain size (phi), sediment organics (%) and carbonates (%). Sim=similarity

The 20% B-C similarity based on macrofaunal abundance clearly demarcated seven main sample groups (communities) represented by numerals I-VII. A series of Similarity Profile (SIMPROF) permutation tests confirmed that assemblages were genuinely different at 5% significance (red dotted lines in Fig 3.10). Five species assemblages (I-IV, VI) showed confined geographical distribution, whereas the others (V and VII) were more widely distributed (Fig 2.2 and 3.10). Group I comprised of a single station collected off uThukela, separated from other stations at 19.96% similarity (Fig 3.10). H4 and I5 off the uThukela supported similar fauna and clustered at 15.75% similarity, forming group II. Group III samples off Port Durnford (E4-F6), characterised by coarser grains of sand, supported similar macrobenthic communities and clustered at 15.27% similarity. Group IV (J4) supported a unique community, representing a transition between macrobenthic communities in muddy substrate off the uThukela and those in coarse grain size south of the uThukela. Group V at 17.34% comprised of three stations that were widely separated geographically and included M3 off Umhlanga, supporting communities similar to N3 and P4 south of Durban. Stations off Zinkwazi (L3 and K3) formed group VI at 31.12% similarity level supported a distinct community (Fig 3.10). Group VII comprised the largest number of samples (seven) and two subgroups at approximately 50% similarity. Samples comprising Group VII were collected south of Durban to uMkhomazi.

3.5.8.1 Univariate measures: Taxa

Significant differences were observed between sample groups assemblages for macrobenthic abundance (Kruskal-Wallis ANOVA, N: df=6, Pseudo-F=5.627, p-perm=0.0007), numbers of taxa (S: df=6, Pseudo-F=13.764, p-perm=0.0004), Margalef's Richness (d: df=6, Pseudo-F=14.218, p-perm=0.0001) and Shannon-Weiner diversity index (H': df=6, Pseudo-F=3.784, p-perm=0.0297).

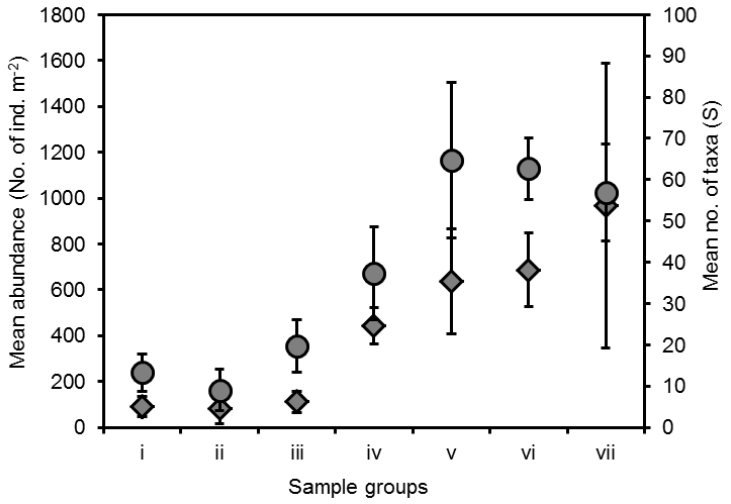

Figure 3.11. Mean abundance (N±SD) and mean taxa (S±SD) for sample groups I-VII defined in cluster analysis. Circles=mean S, Diamonds=mean N.

Abundance (N), numbers of taxa (S), and Margalef's Richness (d) index were highest in Group VII (N: 967 ind. m^{-2} ±620SD, S: 359 taxa ±12SD, d: 52.08 ± 1.54SD), while Shannon-Weiner diversity was highest in Group V (H': 4.83±0.09SD) and Group VI (H': 4.47 ± 0.37SD), respectively (Fig 3.11, Table 3.5). Lowest number of taxa and Margalef's Richness values were recorded for samples comprising Group I, II, and IV as well as abundance and Shannon-Weiner diversity index for samples comprising Group I, II, and III (Fig 3.11, Table 3.5). Lowest Pielou's Evenness values were recorded for sample Group VII (J': 0.67±0.10SD), while the maximum was recorded in sample Group I (J': 0.91±0.02SD) and group II (J': 0.91±0.04SD) (Table 3.5).

Table 3.5. Mean univariate measures (±SD) calculated from taxon abundance data for sample groups I-VII defined in cluster analysis.

Indices (Taxon abundance)	Sample Groups						
	i	ii	iii	iv	v	vi	vii
Margalef's Richness (d)	6.87±0.71	7.67±0.87	23.29±1.15	13.62±1.68	38.10±0.89	31.08±0.89	52.08±1.54
Pielou's Evenness (J')	0.91±0.02	0.8.±0.10	0.91±0.04	0.81±0.15	0.87±0.04	0.84±0.02	0.67±0.10
Shannon-Weiner Diversity (H')	3.1±0.26	2.85±0.56	4.28±0.37	3.60±0.78	4.83±0.35	4.47±0.09	3.96±0.42

3.5.8.2 Groupings of major macrobenthic Phyla

Annelida and Crustacea together accounted for most of the number of taxa (*S*: 46.43-88.73%) and faunal abundance (*N*: 40.00-95.22%) in the seven sample groups. Annelida dominated *S* (46.81-57.14%) of Groups II, III, IV, V, and IV and *N* (35.89-54.64%) of Groups II, III, V, and IV, while Arthropoda (Crustacea) was the most species rich (47.31%) Phylum for Group VII and numerically dominant (54.05-77.82%) Phylum recorded from Groups IV and VII (Fig 3.12). Group VII (Annelida 41.1%, Crustacea 38.68%) had approximately comparable contributions by these two Phyla in *S* and also Group V (Annelida 43.88%, Crustacea 38.68%) in *N*. In all cases, members of the Class Polychaeta represented over 95% of the Annelida, while within Crustacea, members of the Order Amphipoda represent at least 40%. The lowest combined percentage contribution of Polychaeta (*S*: 30.67%, *N*: 32.14%) and Crustacea (*S*: 9.33%, *N*: 14.29%) was observed in Group I, where Mollusca (*S*: 33.33%, *N*: 35.71) and Cnidaria (*S*: 10.71%, *N*: 5.33%) were well represented in the samples of this group (Fig 3.12). Mollusca was well represented in Group I in terms of S and Group I and II (23.12%) in terms of N comprising of muddy stations (Fig 3.12). Echinodermata was characteristic in Group I and III, whereas Sipuncula characterised V and VI, comprising of coarser grains of medium sand (Fig 3.12). Minor Phyla classified, as 'others' were numerous in Group I (Fig 3.12).

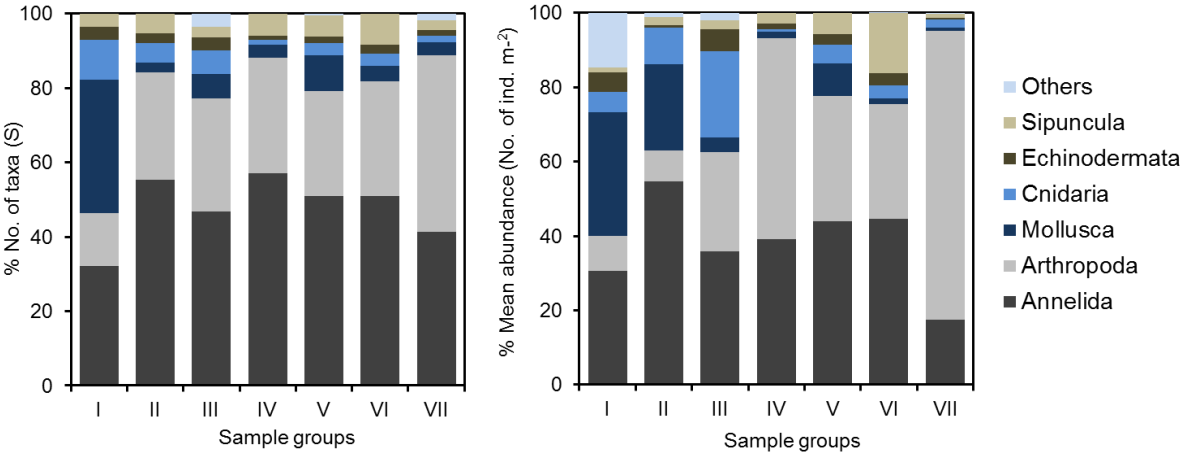

Figure 3.12. Contributions (%) of the seven major taxonomic groups to the relative number of taxa and abundance within the seven main sample groups identified on the basis of total macrofauna composition.

3.5.8.3 Taxon contribution

SIMPER results indicated that sample groupings were characterised by a small subset of taxa with distributions indicating a continuous change rather than a sharp discontinuity between the groups (Table 3.6, Table 3.7). Overall, 134 taxa were identified as being responsible for (dis)similarities between sample Groups I-VII. Collectively, these taxa contributed more than 90% to the total (dis)similarity, although only the contribution by seventeen of them was ≥2% (Table 3.6 and Table 3.7). Group I comprised six taxa representing four Phyla, three of which each contributed >2% to within group similarity (19.96%). The main discriminating taxon was a free-living carnivorous polychaete, *Aglaophamus sp 1* recorded in greater abundances on this group. The least discerning taxon was a tube-dwelling filter-feeding polychaete, *Spiochaetopterus cf vitrarius* (Table 3.6). In pairwise comparison between sample Groups I and II, I and III ($\bar{x}$. Dissimilarity >92%) the carnivorous Scaphopoda, Aglaophamus *sp 1* and *Antalis longitrorsa*, found in high abundance exclusively in Group I, contributed >2% to between group dissimilarity (Table 3.7). Group II comprised six taxa, three of which represented a single Phylum and contributed >2% to within group similarity (15.75%). *Pallidea palliderosea* and *Linopherus microcephala* contributed the most to the average abundance (Table 3.6). The latter also contributed >2% to dissimilarity ($\bar{x}$. Dissimilarity >96%) between Group II and III (Table 3.7). Anthozoa sp.5 dominated the community in Group III and contributed >2% to similarity (15.27%). Together with *Ophioroidae sp.2*, Anthozoa sp.5 was identified as the main discriminating taxa (Table 3.6). By comparison, the contribution of most taxa to similarity was generally low (<2%), reflecting their low abundance and irregular occurrence (Table 3.6).

Table 3.6. Characterization of the seven (I-VII) species assemblages defined by cluster analysis, showing species contributing >2% to average 'within group' similarity and abundance defined by sim/SD ratio based on one-way SIMPER analysis of square-root transformed abundance data. Species accounting for 90% cumulative contribution of the 'within group' similarity are listed along with their contribution (Contr.%). Text in grey shading indicates taxa typifying sample group. Text in bold indicates taxa contributing >2% mean similarity. Sim=similarity, SD=Standard deviation.

Species	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	x̄ abun.	x̄ sim.	Sim/SD	Contr.%
	Mean Sim GI = 19.96%				Mean Sim GII = 15.75%				Mean Sim GIII = 15.27%				Mean Sim GIV = 22.23%				Mean Sim GV = 17.34%				Mean Sim GVI = 31.12%				Mean Sim GVII = 25.65%			
Aglaophamus sp.1	**14.67**	**9.44**	**1.24**	**47.29**	**4.00**	**3.50**	**0.37**	**22.25**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ophiocentrus sp.2	**5.33**	**2.84**	**0.58**	**14.21**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Antalis longitrorsa	**5.33**	**2.42**	**0.58**	**12.14**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Callianassa australis	4.00	1.42	0.58	7.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dosinia sp.2	4.00	1.42	0.58	7.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spiochaetopterus cf vitrarius	2.67	1.21	0.58	6.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Linopherus microcephala	-	-	-	-	**12.67**	**3.17**	**0.76**	**20.12**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Opisthobranchia sp.1	-	-	-	-	4.00	1.50	0.74	9.52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aglaophamus dibranchis	-	-	-	-	**9.33**	**4.80**	**0.66**	**30.48**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.50	0.20	0.76	0.77
Pallidea palliderosea	-	-	-	-	16.67	1.10	0.26	6.96	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ommatocarcinus pulcher	-	-	-	-	1.33	0.36	0.26	2.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ophioroidae sp.2	-	-	-	-	-	-	-	-	3.11	1.94	1.12	12.70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anthozoa sp.5	-	-	-	-	-	-	-	-	**11.56**	**6.15**	**1.11**	**40.31**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quantanthura serenasinus	-	-	-	-	-	-	-	-	1.78	0.64	0.44	4.22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nephtys capensis	-	-	-	-	-	-	-	-	2.22	0.60	0.44	3.90	-	-	-	-	-	-	-	-	6.00	0.42	1.28	1.35	10.65	0.48	0.76	1.86
Ampelisca sp. 3	-	-	-	-	-	-	-	-	2.22	0.37	0.30	2.45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Onuphis eremita	-	-	-	-	-	-	-	-	2.22	0.31	0.30	2.02	-	-	-	-	14.22	0.94	0.92	5.42	-	-	-	-	-	-	-	-
Ampelisca palmata	-	-	-	-	-	-	-	-	1.33	0.31	0.30	2.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Streblosoma persica	-	-	-	-	-	-	-	-	1.33	0.29	0.30	1.89	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phascolionidae sp.1	-	-	-	-	-	-	-	-	-	-	-	-	4.00	0.91	11.16	4.06	-	-	-	-	**26.67**	**2.61**	**1.70**	**8.39**	-	-	-	-
Spiophanes duplex	-	-	-	-	-	-	-	-	-	-	-	-	5.33	0.91	11.16	4.06	-	-	-	-	-	-	-	-	-	-	-	-
Sigalion capensis	-	-	-	-	-	-	-	-	-	-	-	-	4.00	0.91	11.16	4.06	-	-	-	-	-	-	-	-	-	-	-	-
Lumbrineris aberrans	-	-	-	-	-	-	-	-	-	-	-	-	13.33	1.45	1.65	6.52	-	-	-	-	10.67	1.11	1.35	3.56	-	-	-	-
Byblis gaimardii	-	-	-	-	-	-	-	-	-	-	-	-	**25.33**	**2.83**	**0.87**	**12.66**	-	-	-	-	-	-	-	-	115.05	4.97	1.01	19.36
Callichirus sp.1	-	-	-	-	-	-	-	-	-	-	-	-	**86.67**	**4.60**	**0.58**	**20.60**	-	-	-	-	-	-	-	-	-	-	-	-
Mandibulophoxus stimpsoni	-	-	-	-	-	-	-	-	-	-	-	-	**40.00**	**3.84**	**0.58**	**17.21**	-	-	-	-	-	-	-	-	-	-	-	-
Onuphis holobranchiata	-	-	-	-	-	-	-	-	-	-	-	-	13.33	1.10	0.58	4.92	-	-	-	-	-	-	-	-	-	-	-	-
Ampelisca diadema	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	16.44	1.12	1.22	6.47	-	-	-	-	**70.69**	**2.61**	**0.85**	**10.18**
Arcturinoides sexpes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.78	0.48	1.02	2.79	-	-	-	-	-	-	-	-
Amakusanthura africana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	16.44	0.93	1.01	5.37	-	-	-	-	-	-	-	-
Phyllodoce longipes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.67	0.50	0.90	2.90	-	-	-	-	-	-	-	-
Scolaricia dubia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.56	0.23	0.80	1.32	-	-	-	-	-	-	-	-
Sipuncula sp. 5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.56	0.58	0.79	3.34	-	-	-	-	-	-	-	-
Spiochaetopterus vitrarius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23.56	1.23	0.78	7.12	-	-	-	-	-	-	-	-
Ophiurida sp.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.67	1.31	4.13	4.20	-	-	-	-
Aspiodosiphon sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**57.33**	**5.57**	**2.60**	**17.90**	-	-	-	-
Goniadella gracilis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**17.33**	**2.09**	**2.14**	**6.73**	-	-	-	-
Notomastus aberans	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.33	1.10	1.57	3.55	-	-	-	-
Pherusa sp.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	31.33	2.55	1.11	8.18	-	-	-	-
Hippolytidae sp.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**6.11**	**0.36**	**1.07**	**1.40**
Latigammaropsis atlantica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19.71	1.23	0.99	4.81
Cheiriphotis megacheles	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21.23	1.46	0.88	5.71
Unciolella spinosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**177.71**	**4.12**	**0.78**	**16.05**

Table 3.7. Results from SIMPER analysis of taxon abundance data, listing the main discerning taxa revealed by pairwise comparison to contribute >2% to 'between group' dissimilarity (I-VII), with Sim/SD ratio in parentheses. Sim=similarity, SD=Standard deviation, G=group, DS=Dissimilarity percentage.

Species	Gp	GI vs GII	GI GIII	GI GIV	GI GV	GI GVI	GI GVII	GII GIII	GII GIV	GII GV	GII GVI	GII GVII	GIII GIV	GIII GV	GIII GVI	GIII GVII	GIV GV	GIV GVI	GIV GVII	GV GVI	GV GVII	GVI GVII
	DM	92.9	98.47	96.23	98.26	98.5	99.77	98.34	97.21	97.43	98.09	96.06	97.53	96.36	96.39	97.14	93.84	92.53	92.94	91.87	92.75	90.62
Aglaophamus sp.1		7.34 (1.8)	7.15 (1.92)	- -	- -	1.91 (1.84)	1.83 (1.31)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Antalis longitrorsa		3.14 (1.15)	2.52 (1.33)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Spiochaetopterus cf vitrarius		1.57 (1.15)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Siphonodentalium booceras		1.57 (1.15)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Opisthobranchia sp.1		4.28 (1.05)	- -	- -	- -	- -	- -	1.86 (1.01)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Ophioroidae sp.2		- -	1.53 (1.65)	- -	- -	- -	- -	1.69 (1.47)	- -	- -	- -	- -	0.56 (1.76)	- -	0.39 (1.76)	0.37 (1.25)	- -	- -	- -	- -	- -	- -
Anthozoa sp.5		- -	6.05 (1.44)	- -	1.35 (1.06)	- -	- -	6.81 (1.34)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Siphonodentalium booceras		- -	1.26 (1.30)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Phascolionidae sp.1		- -	- -	0.76 (6.51)	- -	- -	- -	- -	- -	- -	- -	- -	0.65 (2.55)	- -	- -	- -	0.39 (1.62)	- -	0.32 (2.51)	2.15 (1.35)	- -	- -
Sigalion capensis		- -	- -	0.76 (6.51)	- -	- -	- -	- -	0.78 (5.40)	- -	- -	- -	0.73 (6.80)	- -	- -	- -	0.55 (1.84)	0.31 (2.14)	0.30 (2.24)	- -	- -	- -
Spiophanes duplex		- -	- -	1.01 (2.67)	- -	- -	- -	- -	1.03 (2.67)	- -	- -	- -	0.97 (2.79)	- -	- -	- -	0.56 (1.69)	0.48 (2.65)	0.37 (1.54)	- -	- -	- -
Lumbrineris aberrans		- -	- -	2.35 (1.76)	- -	1.48 (1.70)	- -	- -	2.40 (1.80)	- -	- -	- -	2.18 (1.71)	- -	1.38 (1.64)	- -	- -	- -	0.99 (1.32)	- -	- -	- -
Byblis gaimardii		- -	- -	4.52 (1.56)	- -	- -	9.53 (1.30)	- -	4.61 (1.59)	- -	- -	9.63 (1.30)	- -	- -	- -	9.33 (1.30)	- -	- -	- -	- -	6.31 (1.14)	6.31 (1.14)
Spiochaetopterus vitrarius		- -	- -	- -	2.84 (1.26)	- -	- -	- -	- -	2.82 (1.20)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Hippomedon onconotus		- -	- -	- -	0.92 (1.16)	- -	- -	- -	- -	- -	- -	- -	- -	2.68 (1.17)	- -	- -	- -	- -	- -	- -	- -	- -
Urothoe pulchella		- -	- -	- -	2.11 (1.08)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Ophiurida sp.2		- -	- -	- -	- -	1.42 (2.97)	- -	- -	- -	- -	- -	- -	- -	- -	1.38 (3.02)	- -	- -	- -	- -	0.95 (1.63)	- -	- -
Goniadella gracilis		- -	- -	- -	- -	2.35 (2.44)	- -	- -	- -	- -	- -	- -	- -	- -	2.24 (2.38)	- -	- -	1.59 (2.58)	- -	1.45 (1.92)	- -	- -
Aspiodosiphon sp. 1		- -	- -	- -	- -	6.98 (2.43)	- -	- -	- -	- -	1.36 (2.52)	- -	- -	- -	6.97 (2.23)	- -	- -	4.82 (2.25)	- -	4.42 (1.81)	- -	- -
Ampelisca diadema		- -	- -	- -	- -	- -	5.57 (1.30)	- -	- -	- -	- -	5.63 (1.30)	- -	- -	- -	5.45 (1.30)	- -	- -	- -	- -	3.61 (1.21)	3.61 (1.21)
Latigammaropsis atlantica		- -	- -	- -	- -	- -	2.20 (1.24)	- -	- -	- -	- -	2.24 (1.21)	- -	2.05 (1.10)	- -	2.13 (1.26)	- -	- -	1.46 (1.38)	- -	1.31 (1.11)	1.31 (1.11)
Hippolytidae sp.1		- -	- -	- -	- -	- -	0.64 (1.24)	- -	- -	- -	- -	0.65 (1.23)	- -	- -	- -	0.60 (1.23)	- -	- -	- -	- -	- -	- -
Aglaophamus dibranchis		- -	- -	- -	- -	- -	- -	4.79 (0.97)	- -	2.15 (1.09)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Linopherus microcephala		- -	- -	- -	- -	- -	- -	5.25 (0.89)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Phascolionidae sp.1		- -	- -	- -	- -	- -	- -	- -	0.78 (5.40)	- -	1.50 (1.70)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Onuphis eremita		- -	- -	- -	- -	- -	- -	- -	- -	1.65 (1.51)	- -	- -	- -	- -	- -	- -	1.15 (1.40)	- -	- -	0.86 (1.48)	0.89 (1.26)	0.89 (1.26)
Arcturinoides sexpes		- -	- -	- -	- -	- -	- -	- -	- -	0.77 (1.29)	- -	- -	- -	0.74 (1.32)	- -	- -	0.51 (1.38)	0.51 (1.38)	- -	- -	0.37 (1.23)	0.37 (1.23)
Phyllodoce longipes		- -	- -	- -	- -	- -	- -	- -	- -	0.94 (1.16)	- -	- -	- -	0.89 (1.17)	- -	- -	- -	- -	- -	- -	- -	- -
Pherusa sp.1		- -	- -	- -	- -	- -	- -	- -	- -	- -	7.16 (2.46)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Aorcho sp.2		- -	- -	- -	- -	- -	- -	- -	- -	- -	2.39 (2.43)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Unciolella spinosa		- -	- -	- -	- -	- -	- -	- -	- -	- -	1.56 (1.60)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Nephtys capensis		- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	1.07 (1.08)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Sipuncula sp. 5		- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	1.32 (1.07)	- -	- -	- -	- -	- -	- -	- -	- -

Only three taxa of 15 recorded, contributed >2% to similarity within Group IV (22.23%). *Phascolionidae sp.1*, *Spiophanes duplex* and *Sigalion capensis* were the primary discriminating species for this group (Table 3.6). Most of the taxa occurred in relatively high abundances (13.33-86.67 ind. m^{-2}). Pairwise comparison ($\bar{x}$. Dissimilarity >92%) revealed *Aspiodosiphon sp.1* as the only taxon that contributed >2% to between groups IV and VI dissimilarity (Table 3.7). Group V formed intermediate collection (in terms of no. of taxa per sample group) with 55 taxa, seven of which represented two Phyla characterising this group. *Spiochaetopterus vitrarius* dominated communities in this group (Table 3.6). Pairwise comparison ($\bar{x}$. Dissimilarity >91%) between Group V and VI indicated *Aspiodosiphon sp.1* to contribute >2% to dissimilarity. Two samples off Zinkwazi (Group VI) contained 104 taxa, eight of which characterised this group and four contributed >2% to within group similarity (31.12%) (Table 3.6). The siphonculid *Aspiodosiphon sp.1* and *Phascolionidae sp.1* dominated communities here. *Byblis gaimardii* and *Ampelisca diadema* contributed >2% to dissimilarity between group VI and VII ($\bar{x}$. Dissimilarity>90%). Group VII was the largest group, characterised by high abundances of *Byblis gaimardii* and *Unciolella spinosa* (115 ind. m^{-2} and 178 ind. m^{-2}). The latter together, with Hippolytidae *sp.1*, were the main taxa typifying this group (Table 3.6).

3.5.9 Linking faunal patterns to environmental parameters

Biological-environmental matching (BIOENV) analysis indicated that %mud and turbidity contributed to community structuring (rho=0.707, $p < 0.05$), showing a good match between biota and variables. In addition, when analysing a combination of five parameters the coefficient remained comparable rho=0.662 (Table 3.8), therefore, mud and turbidity remained the most structuring parameters.

Table 3.8. Summary of BIOENV results. Correlations (ρ) are presented relative to KZN mid-shelf macrobenthos patterns considering lowest taxon. fs=fine sand, vfs very fine sand

No of variables	ρ	Variables
Best combination (2 variables)		
2	0.707	%Mud Turbidity
Best combination (5 variables)		
5	0.662	%Mud,vfs, fs TOC,Turbidity

Marginal tests in distance-based redundancy analysis (dbRDA) showed most variables apart from very coarse sand, chlorophyll-a, pH and temperature explained a proportion of variation observed in the macrobenthos (Table 3.9). Environmental parameters depicted as significant by the marginal tests, each explained >10% of variation, except for sorting. Turbidity was the most important variable (16.4%) followed by %mud (15.6%) and TOC (15.4%) (Table 3.9).

Table 3.9. Distance Linear model results (Marginal and sequential tests) for the relationship between KZN mid-shelf macrobenthos and environmental variables. Asterisks denote statistical significance (*<0.05, ** <0.01, ***<0.001).

Variable	MARGINAL TESTS		
	Prop.	Pseudo-F	P
	Sediment		
%Gravel (<-1.0 ϕ)	0.113	2.171	0.003**
%Very coarse sand (-1.0-0.0 ϕ)	0.107	2.037	0.005**
%Coarse sand (0.0-1.0 ϕ)	0.116	2.232	0.003**
%Medium sand (1.0-2.0 ϕ)	0.121	2.348	0.001**
%Fine sand (2.0-3.0 ϕ)	0.101	1.906	0.009*
%Very fine sand (3.0-4.0 ϕ)	0.119	2.304	0.002**
%Mud (>4.0 ϕ)	0.155	3.109	0.000***
Median phi	0.141	2.784	0.000***
Sorting	0.088	1.640	0.030*
% Total organic carbon (TOC)	0.153	3.067	0.000***
%Carbonates	0.148	2.955	0.000***
	Water column		
Salinity	0.133	2.602	0.001**
Turbidity (NTU)	0.164	3.344	0.000***

	SEQUENTIAL TESTS			
	AICC	Prop.	Pseudo-F	P
+Turbidity (NTU)	156.22	0.16438	3.344	0.0001
	AICC=156.22		Cum(%)=16.43	

A dbRDA plot (Fig 3.13) indicated how different macrobenthic assemblages were distributed relative to environmental conditions. The first axis showed a gradient of conditions from the uThukela to uMkhomazi, underpinned by fine and coarse substratum, explaining 19.4% of the total variation of (Fig 3.13). On db-RDA2, Port Durnford reef complex stations were separated based on salinity and coarser grains of sediments. Indeed, the rest of the stations were separated from those in the Port Durnford reef complex by the factors turbidity, carbonates and levels of nutrient concentrations (TOC), explaining a total variation of 11.1% (Fig 3.13). The reduced model (not shown) explained 37.8% of the total variation.

The most correlated species suggestive of the aforementioned conditions, were *Ommatocarcinus pulcher, Aglaophamus sp.1* and Opisthobranchia sp.1 which showed high preference to very fine sand and mud nutrient enriched sediments as found off uThukela. Port Durnford reef complex stations presents the coexistence of coarser grains of sand and reef rubble low in TOC, and the presence of Anthozoa sp. 1, *Cyclaspis scissa*, *Pareurythoe chilensis* (Fig 3.13). Stations further south (uMdloti-uMkhomazi), presents heterogeneous grains (coarse-medium-fine sand) with higher sedimentary $CaCO_3$ content and separated a diverse community comprising species of capitellid terebellid and ampeliscid among others (Fig 3.13). The primary abiotic variables responsible for discriminating communities (assemblages) along KZN mid-shelf were %mud and turbidity.

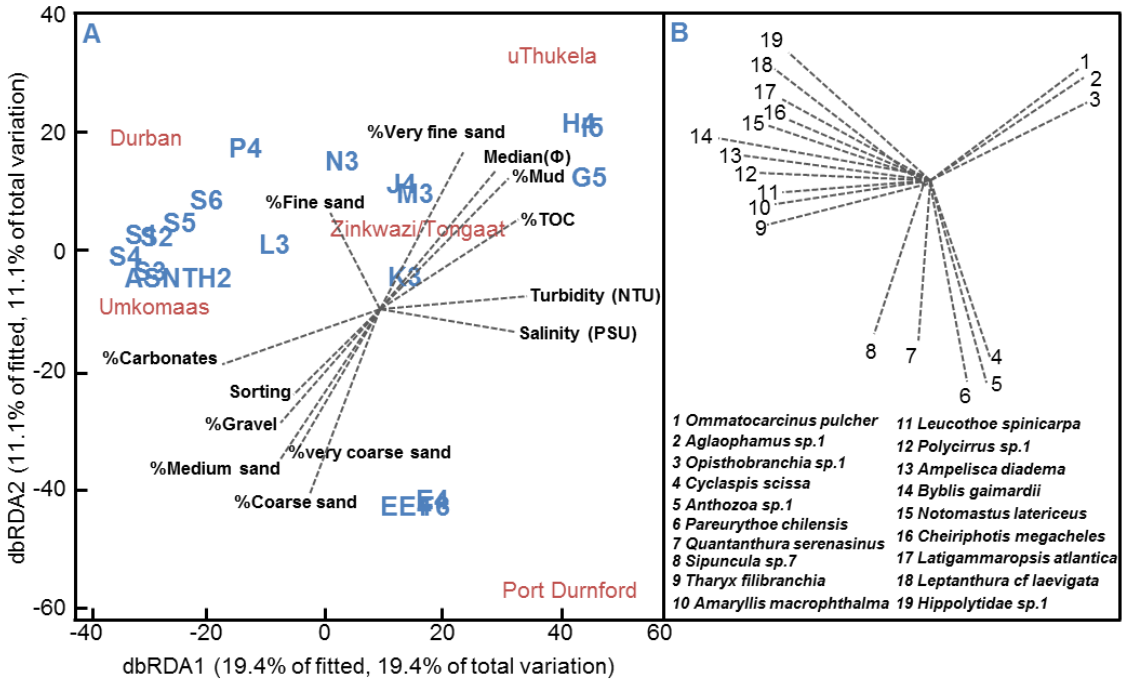

Figure 3.13. Distance-based redundancy analysis (db-RDA) of KZN mid-shelf macrobenthic data using a stepwise selection and AICc selection criterion: (A) db-RDA-axes with main habitat/area and (B) vector overlay of Spearman rank correlations of environmental variables (r>0.5) and vectors of the most correlated species (r>0.5) are provided.

However, different environmental parameters of the samples within each assemblage were also variable (Fig 3.3) and these might be responsible for the variance found in abundance, number of taxa and diversity. Macrobenthos at stations off uThukela was distributed based on high mud content (>68.7%) and turbidity (>3.1 NTU) (group A, R=0.93) (Fig 3.14) suggestive of the influence of the uThukela outflow. Conversely, on the right side of the division, Port Durnford reef complex stations split (group B, R=0.89) based on low mud content (<1.72%) (Fig 3.14). While mud and turbidity were the main factors explaining faunal structuring and distribution, other factors are more important at specific stations. Granulometry had an influence on macrobenthos distribution and diversity: medium sand (>37.0%) influenced macrobenthic distribution and abundance at a transitional station south of uThukela Estuary (group H, R=0.56), whereby well-sorted fine sediment (>64.1%) with low bottom water temperature (<16.3°C) was more important in explaining macrobenthos at P4 (Durban region: group D, R=0.80) (Fig 3.14). Group F (R=0.80) on the left (S5 and S6) split based on chlorophyll-a (as surrogate for primary productivity) >0.74 mg.l^{-1} and very fine sand >1.06%, driving macrobenthos abundance and distribution south of Durban (Fig 3.14). Group G (R=0.83) separated S1 and ASNTH2 on the left according to fine sand >25.9% with carbonate >37.3%, while on the right of the division, macrobenthos at S2-4 was distributed according to coarser grains (>35.4%) high in carbonates (>39.9%) (Fig 3.14).

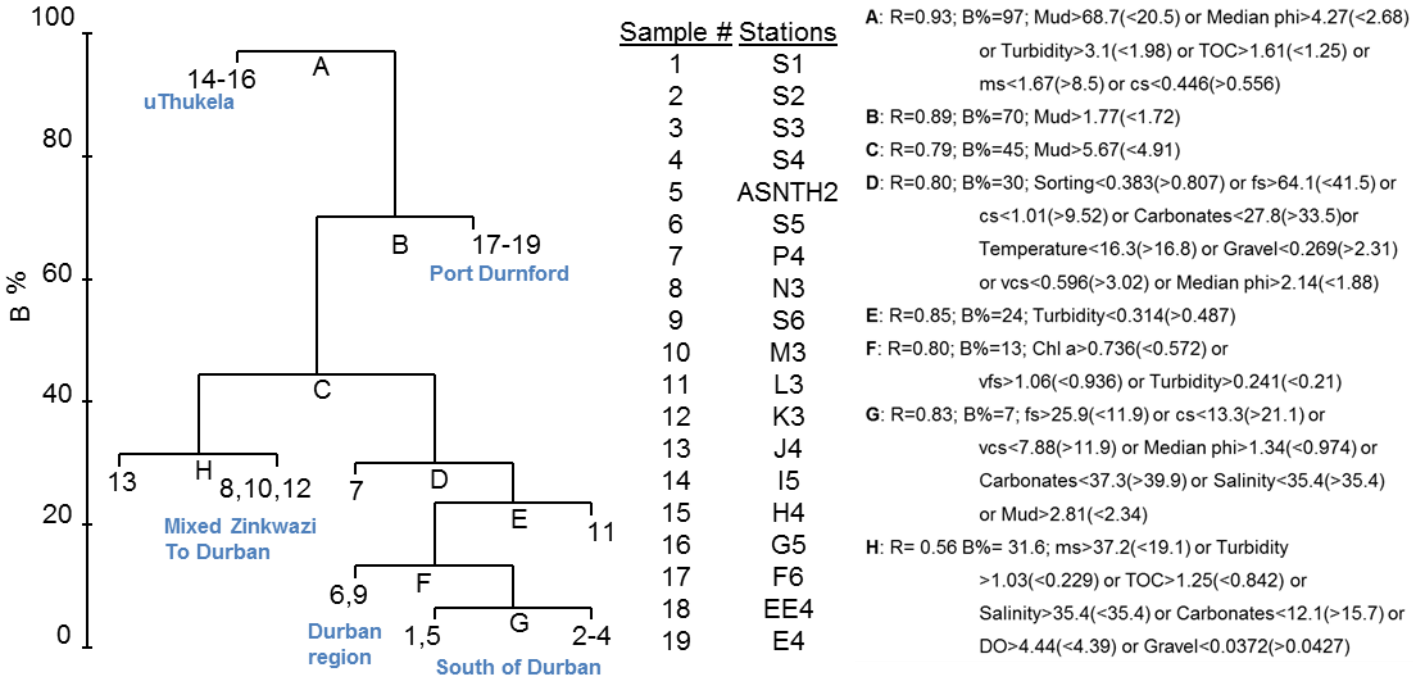

Figure 3.14. LINKTREE showing divisive clustering of sites from abundance data (left), constrained by inequalities on one or more abiotic variables (right). Given for each split is the optimal ANOSIM R value (relative subgroup separation) and B% (absolute subgroup separation, scaled to maximum for first division). For each binary partition (A-G), first inequality defines group to left, second inequality (in brackets) group to right.

3.6 Predefined biozones as surrogacy for KZN biodiversity

3.6.1 Diversity (S) and Abundance (N) within biozone subclusters

Univariate measures of macrobenthic community structure detected significant differences between the six biozone subclusters (BS). Both the mean number of taxa (S±SD) and abundance (N±SD) differed between BS (Table 3.14, Fig 3.17). The mean (S±SD) number of taxa recorded for each BS varied between 25±11.02 in BS 3A to 135±28.62 number of taxa in BS 1B, whereas abundance ranged between 86±58.79 in BS 3A to 1021±939.58 ind. m^{-2} in BS 2A (Fig 3.15). The significant variation amongst BS can be attributed to lower number of taxa recorded within stations of biozone subcluster 3A and 1C.

Table 3.10. PERMANOVA results of mean number of taxa (*S*) and mean abundance (*N*) differences among biozones (and respective subclusters). df=degree of freedom, MS=Mean square, F=critical values of PERMANOVA and *p*=level of statistical difference. Asterisks denote statistical significance *<0.05, **<0.01, ***<0.001. Var=square root of the components of variation.

PERMANOVA	No of Species (S)			Abundance (N)		
Factors (nested design)						
	df	F	p-perm	df	F	p-perm
Biozone	2	2.443	0.1593	2	1.309	0.3498
Biozone subclusters	5	6.314	0.001**	5	5.735	0.001**
Residual	38			38		
1A-C	2	19.720	0.01*	2	19.444	0.031
2A-B	1	0.568	0.718	1	0.649	0.594

3.6.2 Richness (d) and Diversity (H') within biozones

Margalef's Richness (d) differed significantly between BS (Fig 3.16, Table 3.11). Variation was due to lower values recorded within stations of BS 3A and 1C coupled with variation observed within stations of BS 2A, 1B and 2B (Fig 3.16). Significant differences in richness were also observed between BS 1 (A-C) (Table 3.11). Species diversity also differed significantly between BC and in particular between the subcomponents of BC 1 (A-C) (Table 3.11, Fig 3.16).

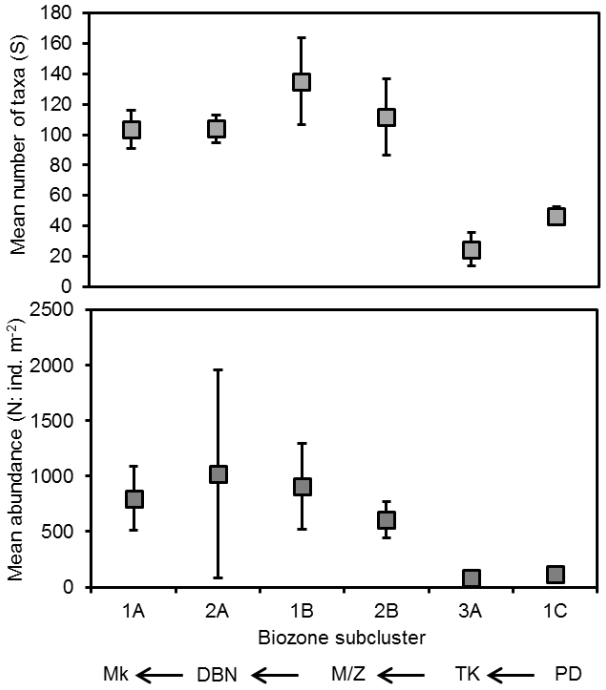

Figure 3.15. Mean number of taxa (S±SD) and abundance (N: of ind. m^{-2} ±SD) for square-root transformed macrobenthic taxa sampled between subclusters. PD=Port Durnford, TK=uThukela, M/Z=uMdloti/Zinkwazi, DBN=Durban, Mk=uMkhomazi.

Table 3.11. Two-factor nested PERMANOVA test on univariate measures of taxon abundance data. df=degree of freedom, F=critical values of PERMANOVA and *p*=level of statistical significant difference calculated from permutation of residuals under a reduced model (n=9999 permutations). Asterisks denote statistical significance *<0.05, **<0.01,***<0.001 .

PERMANOVA	Richness (d)			Diversity (H')		
Factors (nested design)						
	df	F	p-perm	df	F	p-perm
Biozones	2	3.100	0.106	2	1.119	0.035*
Biozone subclusters	5	4.611	0.007**	5	5.076	0.357
Residual	38			38		
1A-C	2	31.245	0.000***	2	15.566	0.000***
2A-B	1	320.630	0.980	1	0.711	0.709

3.6.3 Macrobenthic community patterns within biozones

Patterns in biozone subclusters (BS) as potential surrogates for KZN mid-shelf macrobenthic communities reflected a distinct community structure (nested PERMANOVA: p-perm <0.001, Table 3.12). Pairwise comparison revealed significant differences between pairs of BS 2A and 2B (p-perm=0.029), 2A and 3A (p-perm=0.028), 2A and 1C (p-perm=0.029). Visually, there was a limited structuring of species based on biozone classification, since grouping of stations from the same BS was only limited to BS 1C and 3A (Figure 3.10).

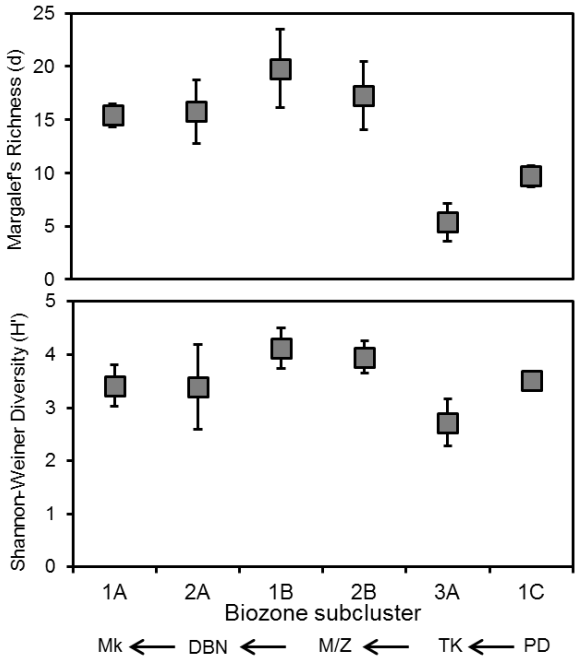

Figure 3.16. Mean Margalef's Richness (d±SD), and Shannon-Wiener Diversity (H'±SD) based on square-root transformed taxon abundance data for macrobenthos sampled between subclusters. PD=Port Durnford, TK=uThukela, M/Z=uMdloti/Zinkwazi, DBN=Durban, Mk=uMkhomazi.

Biozone subcluster 1A and 2A and 1B and 2B grouped closely (Fig 3.17), and pairwise comparison revealed no significant difference (p-perm=0.399, p-perm=0.104) respectively, nor were any clear differences detected by the univariate measures (Fig 3.15, 3.16). This suggested that biozone subclusters were not biologically distinct. Community assemblages in biozone subcluster 1C differed from both biozone subclusters 1A and 1B (Table 3.12) and stations grouping paralleled those of Group III (Fig 3.10) which clustered at 20% similarity, while BS 3A sample grouping was in agreement with those of group A (Fig 3.10) clustered at 10% similarity.

Table 3.12. PERMANOVA based on taxon abundance calculated between biozone subclusters. df=degree of freedom, pseudo-F=critical values of PERMANOVA and *p*=level of statistical difference. Asterisks denote statistical significance *<0.05, **<0.01, ***<0.001.

PERMANOVA	df	Pseudo-F	p-perm
Factors (nested design)			
Biozones	2	1.104	0.368
Biozone subclusters	5	2.172	0.000***
Residual	1		
Biozone 1 subclusters			
1A, 1B and 1C	2	2.326	0.004**
Residual	6		
Biozone 2 subclusters			
2A and 2B	1	2.125	0.029*
Residual	5		
components of variation			
Source		**Estimate**	**X^2**
Biozones		106.42	10.316
Biozone subclusters		1011.10	31.799
Residual		2711.60	52.073

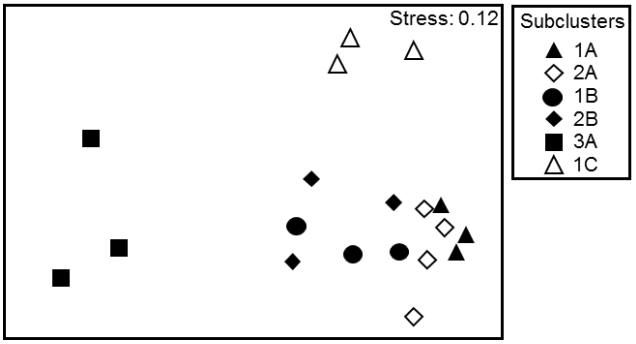

Figure 3.17. N-MDS of macrobenthic community structure, with biozone subcluster as a factor. Each point represents the community structure at a given station. The distance between points indicates the similarity among communities within and between biozone subclusters, with closer points denoting more-similar communities than distant points.

Differences were also detected in macrobenthic communities between BS of cluster 2 (A-B) (Tables 3.12). PERMDISP analyses results are summarised by *P*-values (>0.05) (Table 3.13) and showed that the dispersion of samples to be homogenous between and within BS. However, BC represented the smallest component of variation, while BS (X^2=31.799) represent the greatest component of variation (square root of estimated component of variation), therefore considering these results and those outlined above, the between BS differences was assumed valid (Table 3.13). Therefore, these results did not support MSP predefined biozones.

Table 3.13. PERMDISP test based on taxon abundance calculated between biozone subclusters. df=degree of freedom, F=critical values of ANOVA and *p*=level of statistical difference. Asterisks denote statistical significance *<0.05, **<0.01, ***<0.001.

PERMDISP	df	F	p-perm
Deviation from centroids			
Subclusters	5	1.697	0.534
Biozone 1 Subclusters			
1A, 1B and 1C	2	3.286	0.186
Biozone 2 Subclusters			
2A and 2B	1	8.223	0.717

3.6.4 Taxon contribution to biozone subclusters

SIMPER analyses identified 127 taxa contributing to (dis)similarities between biozone subclusters (BS) 1A-1C. Collectively, they contributed more than 90% to the total (dis)similarity; although only the contribution by ten was ≥ 2% similarity (Table 3.14 and Table 3.15). SIMPER analyses revealed that the dissimilarity among biozone subclusters was driven primarily by the abundances in polychaetes, sipunculids and amphipods species. The latter occurred in high abundances and contributed >2% to between BS similarity (Table 3.14). By comparison, the contribution of most of the other taxa to similarity among BS was generally low (<2% individually), reflecting their low abundance and irregular occurrence.

Biozone subcluster 1A stations comprised 28 taxa and were characterised by high abundances of Amphipods, with *Unciolella spinosa* and *Byblis gaimardii* contributing >2% to the within sample similarity (27.18%) (Table 3.14). The latter including *Latigammaropsis atlantica*, *Cheiriphotis megacheles* and *B. gaimardii* contributed to within BS 1A and 2A similarity (Table 3.14). Hippolytidae sp.1, *Ampelisca brevicornis* and *L. atlantica* distinguished this BS from all others (Table 3.14). Pairwise comparisons ($\overline{x}$. Dissimilarity >78%) revealed that the tube dwelling suspension feeder *A diadema* consistently contributed >2% dissimilarity between BS 1A and all others except for BS 2B and 1C (Table 3.15). Biozone subcluster 2A with four stations comprised 35 taxa, eight of which represented two Phyla characterising this biozone subcluster. The Amphipods, *B. gaimardii, A. diadema* and *Urothoe pulchella* were recorded in high abundances here and contributed >2% to within BS similarity (19.95%) except for the latter (Table 3.14) which consistently contributed >2% dissimilarity ($\overline{x}$. Dissimilarity>78%) between BS 2A and 1A-C and 3A (Table 3.15). The primary discriminating taxon for BS 1B was a facultative feeding polychaete, *Notomastus latericeus* and a filter suspension feeder *Spiochaetopterus vitrarius*. Most of the taxa here were recorded in excess of 4 ind. m^{-2} with *A diadema* contributing most to the abundance (Table 3.14). Pairwise comparisons ($\overline{x}$. Dissimilarity>95%) identified the polychaete, *S. vitrarius*, occurring exclusively here, as the taxon contributing >2% to between BS 1B and 1C dissimilarity (Table 3.15). Only one taxon (*Aspiodosiphon* sp.1) of 43 recorded, contributed >2% to similarity within BS 2B (18.56%). *Ophiurida sp.2*, *Lumbrineris aberrans* and Phascolionidae sp.1 were the main discerning taxa for this BS, with *Aspiodosiphon sp.1* contributing the most to the average abundances (Table 3.14). The latter, together with Phascolionidae sp.1 were unique here and contributed >2% to between biozone subcluster 2B and 3A and 2B and 1C dissimilarity ($\overline{x}$. Dissimilarity >95%) (Table 3.15). Biozone subcluster 3A comprised ten taxa, with two polychaete species (*Aglaophamus dibrachis* and *Aglaophamus sp.1*) contributing >2% similarity (11.77), while the bivalve, *Pallidea palliderosea* contributed the most to mean abundance here (Table 3.14). Faunal components here were similar to those of group I and II (see section 3.7.8). Pairwise comparison ($\overline{x}$. Dissimilarity >97%) identified Anthozoa sp.5, *Aglaophamus sp.1* and *Opisthobranchia sp.1* as taxa contributing >2% dissimilarity between BS 3A and 1C (Table 3.15). Biozone subcluster 1C communities mirrored those found in sample Group III including taxa typifying communities (section 3.7.8). Generally, BS 1C gathered 21 taxa with Ophioroidae sp.2 and Anthozoa sp.5 characterising communities here. The latter, also was the only taxon contributing >2% to within BS similarity (15.27%) (Table 3.14).

Table 3.14. Characterization of the biozone subclusters as per marine spatial planning model, showing species contributing >2% to average 'within group' similarity and abundance defined by sim/SD ratio based on one-way SIMPER analysis of square-root transformed abundance data. Species accounting for 90% cumulative contribution of the 'within group' similarity are listed along with their contribution (Contr.%). Grey shading indicates taxa typifying biozone subclusters. Text in bold indicate taxa contributing >2% to biozone subclusters mean similarity. Sim=similarity, SD=Standard deviation.

Species	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	x̄ abun	x̄ sim.	Sim/SD	Contr.%	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	x̄ abun.	x̄ sim.	Sim/SD	Contr.%
	Mean Sim 1A = 27.18%				Mean Sim 2A = 19.59%				Mean Sim 1B = 19.97%				Mean Sim 2B = 18.56%				Mean Sim 3A = 11.77%				Mean Sim 1C = 15.27%			
Hippolytidae sp.1	6.83	0.65	2.08	2.41	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ampelisca brevicornis	19.97	1.79	1.69	6.60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Latigammaropsis atlantica	15.88	0.85	1.33	3.11	21.25	1.38	0.86	7.06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cheiriphotis megacheles	27.57	1.56	0.93	5.76	14.81	1.07	0.67	5.47	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unciolella spinosa	**83.83**	**4.53**	**0.91**	**16.66**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Byblis gaimardii	**95.70**	**4.19**	**0.84**	**15.42**	**80.57**	**2.19**	**0.77**	**11.17**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aglaophamus dibranchis	2.23	0.14	0.79	0.53	-	-	-	-	-	-	-	-	-	-	-	-	**6.22**	**2.00**	**0.39**	**17.00**	-	-	-	-
Gammaropsis sp.4	19.43	0.80	0.77	2.94	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ampelisca diadema	-	-	-	-	**56.06**	**2.02**	**0.83**	**10.30**	42.67	1.29	0.84	6.44	-	-	-	-	-	-	-	-	-	-	-	-
Nephtys capensis	-	-	-	-	12.5	0.52	0.79	2.66	-	-	-	-	4.44	0.27	0.81	1.44	-	-	-	-	2.22	0.60	0.44	3.90
Notomastus latericeus	-	-	-	-	2.79	0.16	0.74	0.82	19.11	1.47	1.77	7.37	7.56	0.46	0.65	2.48	-	-	-	-	-	-	-	-
Leptanthura cf laevigata	-	-	-	-	5.03	0.28	0.71	1.40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Urothoe pulchella	-	-	-	-	52.38	1.37	0.69	6.98	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spiochaetopterus vitrarius	-	-	-	-	-	-	-	-	25.33	1.50	1.07	7.52	-	-	-	-	-	-	-	-	-	-	-	-
Sipuncula sp. 5	-	-	-	-	-	-	-	-	12.44	0.65	0.94	3.28	-	-	-	-	-	-	-	-	-	-	-	-
Diplodonta sp.1	-	-	-	-	-	-	-	-	6.22	0.30	0.88	1.51	-	-	-	-	-	-	-	-	-	-	-	-
Arcturinoides sexpes	-	-	-	-	-	-	-	-	4.00	0.27	0.74	1.34	-	-	-	-	-	-	-	-	-	-	-	-
Aphelochaeta marioni	-	-	-	-	-	-	-	-	5.33	0.27	0.71	1.37	-	-	-	-	-	-	-	-	-	-	-	-
Onuphis eremita	-	-	-	-	-	-	-	-	11.11	0.60	0.70	3.01	-	-	-	-	-	-	-	-	2.22	0.31	0.30	2.02
Ophiurida sp.2	-	-	-	-	-	-	-	-	-	-	-	-	9.33	1.16	1.59	6.26	-	-	-	-	-	-	-	-
Lumbrineris aberrans	-	-	-	-	-	-	-	-	-	-	-	-	11.56	1.28	1.52	6.92	-	-	-	-	-	-	-	-
Phascolionidae sp.1	-	-	-	-	-	-	-	-	-	-	-	-	19.11	1.52	1.13	8.21	-	-	-	-	-	-	-	-
Aspiodosiphon sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	**38.67**	**2.43**	**0.81**	**13.10**	0.89	0.26	0.17	2.25	-	-	-	-
Sipuncula sp.3	-	-	-	-	-	-	-	-	-	-	-	-	8.44	0.32	0.73	1.73	-	-	-	-	-	-	-	-
Goniadella gracilis	-	-	-	-	-	-	-	-	-	-	-	-	11.56	0.87	0.72	4.70	-	-	-	-	-	-	-	-
Aglaophamus sp.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**7.56**	**4.68**	**0.61**	**39.78**	-	-	-	-
Opisthobranchia sp.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.89	1.16	0.54	9.87	-	-	-	-
Linopherus microcephala	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.44	1.32	0.43	11.22	-	-	-	-
Pallidea palliderosea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.11	0.46	0.17	3.88	-	-	-	-
Ophiocentrus sp.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.78	0.24	0.17	2.01	-	-	-	-
Antalis longitrorsa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.78	0.20	0.17	1.72	-	-	-	-
Ophioroidae sp.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.11	1.94	1.12	12.70
Anthozoa sp.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**11.56**	**6.15**	**1.11**	**40.31**
Quantanthura serenasinus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.78	0.64	0.44	4.22
Ampelisca sp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.22	0.37	0.30	2.45
Ampelisca palmata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.33	0.31	0.30	2.02
Streblosoma persica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.33	0.29	0.30	1.89

Table 3.15. Results from SIMPER analysis listing the main distinguishing taxa revealed by pairwise comparisons as contributing >2% to the average dissimilarity between biozone subclusters (1A-1C), with Sim/SD ration in parentheses. DS=Bray-Curtis dissimilarity percentage. Sim=similarity, SD=Standard deviation.

Species	1A 2A	1A 1B	1A 2B	1A 3A	1A 1C	2A 1B	2A 2B	2A 3A	2A 1C	1B 2B	1B 3A	1B 1C	2B 3A	2B 1C	3A 1C
	DS=78.25%	DS=88.89%	DS=96.23%	DS=99.40%	DS=97.39%	DS=89.42%	DS=92.93%	DS=99.43%	DS=97.23%	DS=90.07%	DS=97.43%	DS=96.00%	DS=96.36%	DS=96.77%	DS=97.14
Latigammaropsis atlantica	1.21 (1.46)	- -	- -	1.69 (1.28)	1.63 (1.28)	1.13 (1.32)	1.41 (1.39)	2.54 (1.20)	2.54 (1.20)	- -	1.69 (1.28)	- -	- -	- -	- -
Ampelisca brevicornis	1.67 (1.37)	1.16 (1.59)	1.31 (1.55)	2.49 (1.68)	2.39 (1.72)	- -	- -	- -	- -	- -	2.49 (1.68)	- -	- -	- -	- -
Nephtys capensis	0.72 (1.32)	- -	- -	- -	- -	0.61 (1.17)	0.7 (1.26)	1.21 (1.16)	1.21 (1.16)	- -	- -	- -	- -	- -	- -
Ampelisca diadema	4.00 (1.29)	3.64 (1.18)	- -	5.51 (1.12)	- -	3.21 (1.27)	2.96 (1.30)	4.59 (1.39)	4.59 (1.39)	- -	5.51 (1.12)	- -	- -	- -	- -
Urothoe pulchella	2.94 (1.09)	- -	- -	- -	- -	2.49 (1.13)	- -	5.38 0.00	3.91 (1.05)	- -	- -	- -	- -	- -	- -
Notomastus aberans	- -	1.21 (1.53)	- -	- -	- -	1.28 (1.17)	3.93 (1.20)	- -	- -	- -	- -	2.13 (1.36)	- -	- -	- -
Hippolytidae sp.1	- -	0.39 (1.33)	0.47 (1.58)	0.89 (1.62)	0.80 (1.52)	- -	- -	- -	- -	- -	0.89 (1.62)	- -	- -	- -	- -
Notomastus latericeus	- -	0.29 (1.22)	- -	- -	- -	- -	- -	- -	- -	0.32 (1.21)	- -	- -	- -	- -	- -
Ophiurida sp.2	- -	- -	0.71 (1.83)	- -	- -	- -	0.79 (1.40)	- -	- -	- -	- -	- -	1.38 (1.80)	1.37 (1.90)	- -
Lumbrineris aberrans	- -	- -	0.8 (1.41)	- -	- -	- -	- -	- -	- -	0.62 (1.24)	- -	- -	1.79 (1.61)	1.65 (1.54)	- -
Nototropis granulosus	- -	- -	0.28 (1.23)	0.47 (1.27)	0.46 (1.27)	- -	- -	- -	- -	- -	0.47 (1.27)	- -	- -	- -	- -
Ophioroidae sp.2	- -	- -	- -	- -	0.39 (1.47)	- -	- -	- -	- -	0.8 (1.21)	- -	- -	- -	0.45 (1.68)	1.64 (1.51)
Byblis gaimardii	- -	- -	- -	- -	- -	- -	- -	- -	5.81 (1.25)	- -	- -	- -	- -	- -	- -
Goniadella gracilis	- -	- -	- -	- -	- -	- -	- -	- -	- -	0.99 (1.24)	- -	- -	1.58 (1.15)	- -	- -
Spiochaetopterus vitrarius	- -	- -	- -	- -	- -	- -	- -	- -	- -	1.73 (1.21)	- -	2.80 (1.30)	- -	- -	- -
Anthozoa sp.5	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	1.19 (1.28)	- -	1.66 (1.30)	6.56 (1.37)
Onuphis eremita	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	1.18 (1.22)	- -	- -	- -
Euclymene cf oerstedi	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	0.55 (1.13)	- -	- -	- -
Aspiodosiphon sp. 1	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	4.84 (1.21)	4.72 (1.20)	- -
Phascolionidae sp.1	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	2.62 (1.16)	- -	- -
Sipuncula sp. 5	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
Aglaophamus sp.1	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	4.15 (1.05)
Opisthobranchia sp.1	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	2.21 (0.82)
Quantanthura serenasinus	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	1.03 (0.81)

3.7 Discussion

The main objective of this chapter was to give an overview of the spatial variation of the macrobenthos at species and community level and to investigate the relation with the spatial variation of environmental variables. Observed patterns were further related to the predefined biozone model to test the surrogacy approach. To address the most relevant results from the analysis of KZN mid-shelf macrobenthic fauna, discussion of the findings is structured according to the research questions initially posed.

3.7.1 General characteristics of the macrobenthos of the KZN mid-shelf

This study, in the oligotrophic-to-mesotrophic KZN mid-shelf waters (Lutjeharms et al. 2000, Meyer et al. 2002), revealed a diverse soft-bottom benthic macrofauna in line with other tropical and subtropical shelves environments, e.g. the Seychelles (Taylor et al. 1997, Mackie et al. 2005). Nonetheless, this is contrary to Valiela's (1984) hypothesis that faunal diversities will be low under low food resource conditions due to limiting resources. A total of 32 215 individuals belonging to 634 different taxa were identified in sediments ranging from very coarse sand to mud. Direct comparison of values obtained from this study with those obtained from similar studies can be complicated by the heterogeneity in sampling strategies, gears, sampling effort, habitat type, and taxonomic knowledge. It is therefore often more meaningful to express diversity values (total number of taxa and abundance) in terms of the depth range and area sampled. The 57 samples collected from the KZN mid-shelf (50-80 m) covered a combined area of 11.4 m^2. Values presented here are in line with those of the previous studies in the region where Untiedt and MacKay (2016) found a total of 38 215 individuals belonging to 826 different taxa in a combined area of 10.8 m^2, while MacKay et al. (2016) recorded 33 630 individuals belonging to >1 000 taxa in a combined area of 9.6 m^2. A study of macrobenthic communities on the Great Australian Bight found 240 taxa in a combined area of 6.5 m^2 along 40-200 m depth range (Currie et al. 2009), while a total of 18 858 individuals belonging to 547 taxa were recorded on the Cretan shelf in a 19.8 m^2 area along 40-190 m depth gradient (Karakassis and Eleftheriou 1997). A widespread study conducted in the subtropical waters off Hong Kong, covering a sample area of 120 m^2, recorded a total of 603 taxa and over 50 000 individuals (Shin et al. 2004). Gray (1997a), on the Norwegian continental shelf, found 39 582 individuals belonging to 620 taxa along 70-300 m depth gradient in a combined area of 50 m^2. Considering that, this study area was limited to the mid-shelf, therefore this shelf supports a highly diverse community (in terms of abundance and number of taxa). Recent KZN Bight studies (MacKay et al. 2016, Untiedt and MacKay 2016) also reported a diverse community along the same depth gradient. These results are also in agreement with the earlier reports from

the Southern Californian Bight (45-100 m) (Bergen et al. 2001), Indian waters (50-75 m) (Ganesh and Raman 2007, Jayaraj et al. 2007, Jayaraj et al. 2008, Ansari et al. 2012).

Macrobenthos recorded here, included species expected within the area and others with no previous reference for KZN shelf and were possible new location records and corresponded to species previously known elsewhere in the West Indian Ocean region (e.g. Seychelles and Australian waters) (Pearson 1970). The polychaete *Litocorsa sp.1*. and the amphipod *Siphonoecetes (Orientoecetes) erythraeus* are known to occur in Red Sea (Ruffo 1959) and Madagascar (Ledoyer 1982), among others. In addition, some of the dominant taxa here are also conspicuous at middle shelf depths elsewhere, e.g. *Byblis, Ampelisca, Nephyts, Nucula* and *Corophiidae* (Mills 1971, Probert and Wilson 1984, Lange et al. 2014).

3.7.2 Macrobenthic taxonomic composition

Qualitative characterisation of macrobenthic community assemblages are based on large dominant groups (Manokaran et al. 2015). In terms of Phyla, Polychaeta generally dominate, followed by Crustacea, Mollusca and Echinodermata (Gray and Elliott 2009, Ansari et al. 2012, Manokaran et al. 2015, MacKay et al. 2016, Untiedt and MacKay 2016). Other taxa, such as Nemertea and Anthozoa tend to contribute little to numbers of taxa or individuals (Dubois et al. 2009). Results presented in this study agree with these general patterns, with polychaetes contributing most to the numbers of taxa. However, the high abundance of peracarid crustaceans, in particular amphipods, was noteworthy. Specific locations of interest concerning crustaceans are discussed further.

Polychaeta

The mid-shelf region of the KZN continental shelf showed polychaetes to support species richness with approximately equal numbers of sedentary and errant forms, which constituted the second most abundant group in terms of abundances. Such dominance of polychaetes on this shelf were previously reported by McClurg (1988), and recently by KZN Bight studies (MacKay et al. 2016, Untiedt and MacKay 2016). Various regions of Southern African waters (Lange and Griffiths 2014, Steffani et al. 2015) and other parts of the world, such as the Indian (Ganesh and Raman 2007, Jayaraj et al. 2007, Jayaraj et al. 2008, Joydas and Damodaran 2009, Manokaran et al. 2015), Belgian (Van Hoey et al. 2004), Portuguese (Martins et al. 2013), and Norwegian continental shelves (Ellingsen 2002) have also reported dominance of polychaetes. In this study, Spionidae, Terebellidae, Syllidae, Maldanidae and Cirratulidae presented the highest number of species, in agreement with previous regional study by McClurg (1988). The large number of species from these families, in this work, reflects the high heterogeneity of the

sediments along the shelf. Recent studies (MacKay 2010, MacKay et al. 2016, Untiedt and MacKay 2016) along the KZN Bight also reported the dominance of Spionidae, Terebellidae and Cirratulidae and associated these taxa with outwelling and the mud depocentre off the uThukela Estuary. In addition, the percentage of rare species found here was also comparable to these studies. Other studies, in tropics and subtropical regions (Lourido et al. 2008, Hernández-Alcántara and Solís-Weiss 2011, Montiel et al. 2011, Martins et al. 2013) have also reported >15 spionid and syllid species in fine sand-to-mud substrate. Polychaetes constituting the most dominant (in terms of number of taxa) group, with spionid species represented in high numbers have been reported off the west coast of South Island, New Zealand, Tasman Bay, (Probert et al. 2001), the North Queensland coast, Australia (Alongi and Christoffersen 1992), the Norwegian continental shelf (Ellingsen 2002) and the Bay of Bengal (Ganesh and Raman 2007). In contrast, studies elsewhere have generally reported lower number of polychaete taxa such as one undertaken in the North Sea, English Channel, Irish Sea and Outer Bristol Channel (Quiroz-Martinez et al. 2011). Differing habitat types and hydrodynamics may be a reason for the variability observed among the mentioned studies (De Grave et al. 2001). The dominance of polychaetes among the macrobenthic components is attributed to this group's high morpho-functional diversity resulting in a multi-faceted response to environmental gradients (Fauchald and Jumars 1979, Wilson 1991, Jumars et al. 2015b), whereby different species occupy different gradients and almost all substrate types (Day 1967, Fauchald and Jumars 1979). Moreover, polychaetes often constitute over one-third of the total number of species (Fauchald and Jumars 1979), with their dominance and wide distributional ranges linked to their quick reproduction (Hutchings 1998). The large number of species recorded from these families reflected the high variability of the sedimentary characteristics along the KwaZulu-Natal mid-shelf. High dominance of polychaetes is important for the functioning of the ecosystem as they play have roles in the food chain, bioturbation and sediment reworking (Snelgrove 1997, Rosenburg 2001, Snelgrove et al. 2014).

Crustaceans

In this study crustaceans were the second most taxon-rich group, as found in previous studies by McClurg (1988) and recently in MacKay et al. (2016). Such observations have been reported in other subtropical/tropical shelf environments (Levin et al. 2001, Jayaraj et al. 2007, Jayaraj et al. 2008, Joydas and Damodaran 2009). However, faunal composition was different among various crustacean groups in this study; amphipods were the most taxon rich and supported high abundances (>60% of the total fauna). Results from the tropical and subtropical continental shelves are uncommon, however, Joydas and Damodaran (2009) on the west coast of India

highlight the importance of crustaceans although precise details of species composition was not provided. Similar dominance of the crustacean fauna by amphipod species have also been recorded by Martínez et al. (2010) on the Bay of Biscay and by Mamouridis et al. (2011) on the Catalonia coast despite crustaceans being the third most important taxa in these studies.

In this study, amphipod families such as Ampeliscidae, Photidae, Mearidae, Gammaridae, Corophiidae, and Lysianassidae were speciose, with species *Byblis giamardii*, *Ampelisca palmata, Urothoe palmata*, and *Unciolella spinosa* being the main species recorded. Dominance of similar faunal components were previously cited by Griffiths (1974a), McClurg (1988) and recently by MacKay et al. (2016) at similar depths. Arabi (2010) recorded high abundance of species belonging to the Genus *Ampelisca* and advocated that these species are typical of the region. Other parts of the world also share similar faunal components as reported by Velerio-Berado et al. (2000), Sampaio et al. (2016), Khan et al. (2017). Amphipods owe their high abundance to a high degree of niche specificity and demonstrate a high tolerance to varying physico-chemical characteristics in sediment and water, allowing large distributional range in various biotopes (Thomas 1993, Thomas et al. 2000, Dauvin and Ruellet 2007). In general, crustaceans are more ambulatory than most of other macrofauna, which is an advantage in exporting local deadfall or other patchy nutrient sources (Martins et al. 2013). Moreover, amphipod dominance in tropical and subtropical areas is often linked to the fact that they breed almost continuously (Dauvin et al. 1994).

Mollusca

Mollusca were the third most species rich group. Bivalves overwhelmingly dominated the molluscan fauna and benthic biocoenosis dominated by bivalves has been cited in fine well-sorted sediments (Péres 1967, Michel et al. 2011, Martins et al. 2014). This was also true for the bivalves species recorded in this study, which were restricted to the shelf between uThukela and uMdloti in fine-mud sediments. *Donax burnupi*, which is known and diagnostic of the upwelling regions of Africa (Branch et al. 2002, Michel et al. 2011), was among the abundant molluscan taxa in this study. *Nucula nucleus* and *Papillicardium turtoni* and *Diplodonta sp.1* represent a clear tropical affinity (Michel et al. 2011, Huber 2015), which could have been transported as larvae by the Agulhas Current. Overall, the number of molluscs was low in comparison to other studies, e.g. Zettler et al. (2009) on the northern continental shelf of Namibia, Lange et al. (2014) on the Angolan shelf and Michel et al. (2011) on the Mauritania shelf. Visually, molluscs formed a large portion of bioclastic sediments and biogenic structures

as abraded shell fragments (noted during sorting), particularly in the fine-coarse sand between uThukela and uMkhomazi; however, live specimens were particularly rare.

In South Africa, 12 915 marine species are known (9 632 invertebrates) from which 2331 are crustaceans, 787 are annelids, 3154 are molluscs and 410 are echinoderms (Griffiths et al. 2010). Therefore, this study includes approximately 5% of the total animal species known in South Africa, and up to 37% of the polychaetes, 9% of the crustaceans, 1.4% of the molluscs, and 11% of the echinoderms. Given that, not all taxa from the samples were identifiable to species level, partly because of the lack of characteristic appendages that are required for identification, especially in case of immature or physically damaged individuals, being small and not more a few millimetres. It can be assumed that diversity was underestimated at certain stations. Furthermore, coarser level of taxonomic resolution in this study places limits on the ability to detect fine scale overview of the spatial variations in community patterns. However, while species level data would have potentially revealed additional spatial patterns, coarser taxonomic resolution can often provide similar results (Wlodarska-Kowalczuk and Kedra 2007, Tataranni et al. 2009), as shown in Chapter 4.

Considering the heterogeneity in sedimentary characteristics, complexity of the shelf morphology and hydrodynamics, studied area (11.4 m^2), the depth zone (50-80 m), narrowness of the shelf and marine species in South African (Griffiths et al. 2010), it is reasonable to conclude that the Polychaeta species richness found in this study was high, while Crustacea and Mollusca were a poor reflection.

Species estimators

The total number of species in a given sampled area often cannot be directly computed as the total number of identified species because of sampling limitations. Several indices have been proposed to infer true species richness (Chao 1984, Chao et al. 2009). Results from the extrapolation of singleton and doubleton ratios (Colwell and Coddington 1994, Chao et al. 2009) indicated the likelihood of recording high Richness with intense sampling using Chao 1 and 2 true richness estimators. The difference between observed and true Richness estimators was high (>40%), reflecting the higher heterogeneity of the sampled areas, resulting in differences in the scale of variation of species richness (Thrush et al. 2006). This was further shown by the occurrence of rare species by almost 30% of the total fauna and suggests that a more intense sampling effort should lead to the inclusion of the missing species. The true percent of uniques may be higher, considering that the number of uniques was likely deflated by the grouping of taxa to high taxonomic levels (where diagnostic features were damaged or

obscured). An attempt to identifying all taxa to species level is likely to substantially increase the current number of macrofaunal taxa recorded supporting the overall high biodiversity and endemism previously reported by Scott et al. (2012) for this region. However, the collection of realistic (true) richness is always confronted with the effort required to sample and process macrobenthos.

In macrobenthic communities with patchy distribution, the number of patches with minor differences increases with increasing sampling effort because of microscale habitat variation, therefore, even in well-sampled environment extrapolation curves are unlikely to assume asymptotes (Ellingsen 2001, 2002). Moreover, taxa with low local abundance, irrespective of the number of stations at which they were encountered, have a low probality of being recorded. Sampling effort of marine biological data generally has a relatively low spatial resolution and is often biased towards shallow sites close to the coast driven by politically, socially, and economically interesting areas (e.g. important fishing grounds, MPAs) (Phillips et al. 2009, Robinson et al. 2011) and toward regions close to research facilities (Milne 2012) and such has been the case for this coastal shelf environment recent KZN Bight studies.

3.7.3 Macrofaunal diversity and distribution

It is widely accepted that sediment heterogeneity is generated by hydrodynamic features such as terrigenous inputs, biological components, such as macrofauna bioturbation and engineering (Gooday et al. 2010). These features further cause habitat fragmentation and thus creation of macro-habitats. Such habitat heterogeneity creates high variability in species composition, distribution and diversity (Zalmon et al. 2013). Habitat heterogeneity or complexity is not further discussed, but conditions arising from it are noteworthy. On the other hand, abiotic factors determine the broad distributional patterns of benthic organisms (Ellingsen 2002). To characterise the mid-shelf habitat, hydrographic and sediment variables, which attempt to describe broad environmental conditions, were considered. Also considered was that some of the factors that affect macrobenthos distribution may be indirect, such as particulate organic matter (POM) (de Lecea et al. 2013), but these were not specifically considered further. In terms of species composition, abundance and number of taxa, the macrobenthic communities studied were typical of muddy and sandy KZN mid-shelf habitats. Composition variables *S* and *N* varied in relation to the nature of sediments (texture and organic content) and hydrographic features (turbidity gradient), which are related to known oceanographic features and coastal influences brought about by the uThukela Estuary. Weston (1988) studying macrobenthic fauna of the continental shelf off Cape Hatteras, North Carolina, corroborated that sediment texture

was the most important factor influencing faunal composition. The study assumed the importance of the sediment is, in part, a result of its role in determining the type and abundance of food resources available for different species. The loose and nutrient deficient sediment off Port Durnford and the mud nutrient richer sediment off the uThukela harboured a relatively impoverished macrobenthos. These differences were expected based on the different hydrodynamic regimes characterising these habitats (McClurg 1988, MacKay et al. 2016). Medium-to-fine sand with moderate nutrients in the transition area between Zinkwazi and Durban (Stations K3, L3, S6, and N3) and south of Durban to uMkhomazi (Stations N3 and S5) sheltered rich life. For the same stations (K3, L3, and N3), MacKay et al. (2016) recently reported high values of *S* and *N* and attributed this to the relatively stable nature of sediment in the area (Green and MacKay 2016) resulting from the current induced sorting (adjacent semi-tenacious Durban Eddy and the Southern Bight swirl (Roberts et al. 2016)). These finding are also in agreement with those reported by Ganesh and Raman (2007) on the mid-shelf (51-75 m) of the northeast Indian shelf, Bay of Bengal, where heterogeneous substrates (mixture of medium-fine sand) supported high species richness and abundance. The role of food resources in regulating abundance of macrobenthic communities was reported by Karakassis and Eleftheriou (1997) and has also been demonstrated by several manipulative laboratory and field experiments (Snelgrove et al. 2001, Currie and Small 2005). In this study, elevated chl-a recorded at S6 corresponding to the Durban Eddy, and at S5 corresponding to Amanzimtoti outfall, coupled with the heterogeneous nature of the sediment, were important in explaining high abundances at these stations.

The spatial diversity patterns were different to those observed for abundance and number of taxa. This may be an artefact of high abundance of crustaceans at specific stations. Species Richness varied with sediment structure along this shelf, i.e. low values were recorded in homogenous substrate (off uThukela River), intermediate values in habitat with much sand and the highest values were recorded in area with mixed coarse, medium and fine sands (transitional area between Zinkwazi and Durban). This gradient is largely explicable in terms of increasing grain heterogeneity, providing a range of potential niches for different fauna (Santos and Pires-Vanin 2004). This supports Gray's (1974a) view, who concluded that the faunal diversity of coarse and heterogeneous sediment tends to be higher than that of the homogenous sediment. Evenness values (in excess of 0.8) were very high and showed scarce variation between stations as species: abundance values were relatively high due to the community being characterised by a high number of low-abundance taxa.

Since Evenness (J') incorporates both Richness and Shannon-Weiner diversity (H') properties of the sample, the overall distribution trend assumed the pattern displayed by both indices. H' exhibited highest values at stations where polychaetes and peracarid crustacean were the important constituents and in a same way as data provided by Richness. Evenness was highest at station with low number of polychaetes and peracarid crustaceans. Therefore, the higher diversity values recorded in this study appeared to be characterised by the higher number of polychaetes and peracarid crustacean species.

3.7.4 KZN mid-shelf macrobenthos faunal communities

Univariate indices and multivariate community structure of macrobenthic assemblages differed spatially supporting the theory that the spatial composition of macrobenthic communities differs along the shelf. The term community usually indicates a group of species co-occurring in a particular place or physical habitat (Mills 1969). Based on Mackie et al. (1997) definition to define biological communities and the statistical analyses performed on taxa abundance, a clear faunal assemblage (Sample group III) on the medium-to-very coarse sand off Port Durnford could be discerned. This assemblage presented low values of composition variables S and N, but high in J' and H'. Conspicuous features of this assemblage include free-living carnivorous predators such as *Quantanthura serenasinus, Nephtys capensis* and *Onuphis eremita,* capable of switching to deposit feeding opportunities with a changing food supply (Riisgård and Kamermans 2001, Untiedt and MacKay 2016). The carnivorous species can facilitate the transport of nutrients retained in the detritivores and deposit feeders tissues back in to the mobile pool (Ngai and Srivastava 2006) and hence renew the nutrients for primary producers. Moreover, this assemblage was also characterised by interstitial species (*Protodorvillea biarticulata*, *Syllis amica* and *Podarkeopsis capensis*) and had no correspondence with the known shelf communities elsewhere.

Assemblage (sample group) I comprising a single station had a low number of exclusive species, suggesting that this station is a transition zone between Port Durnford and uThukela communities. A notable feature of this assemblage was the suspension feeding mollusc species, *Antalis longitrorsa* and *Dosinia sp.2* with tropical-subtropical affinities (Michel et al. 2011, Huber 2015). The uThukela mud assemblage (sample group II) characterised by muddy sediments and the highest content of organic matter, presented lowest values of diversity indices. The important features of this assemblage were free-living carnivorous polychaetes *Aglaophamus dibranchis* and *Linopherus microcephala,* the bivalve *Pallidea palliderosea* and the decapod *Ommatocarcinus pulcher.* The latter, also capable of switching between the feeding

methods. This assemblage has faunal affinities with the Nephtyid assemblage from the northeast Indian shelf, Bay of Bengal (Ganesh and Raman 2007) and was also closer to other terrigenous mud-shelf assemblages found elsewhere (Peres 1967). The continual resuspension of sediment either by current or actions of feeding animals and the subsequent burial of juveniles may be a limiting factor, with few species that can cope with such conditions. Moreover, shelves under severe riverine influences show reduced faunal populations (Aller and Aller 2004).

Van Hoey et al. (2004) showed that as a result of the unimodal distribution of species along environmental gradients, biological and physical boundaries of benthic communities are not strict and gradual shifts between communities exist. As such, the transition assemblage can be seen as a 'hybrid' assemblage, representing the shift between adjacent communities. The transition assemblage (sample group IV) characterised with medium-fine sand with TOC comparable to uThukela, hosted a mix of species and trophic groups of secondary importance in both assemblages. This could be related to the presence of the medium-fine sand, which is the sharp boundary separating assemblages (uThukela and Zinkwazi), but also provided a suitable habitat to allow for the colonisation and successful establishment of surface deposit-feeding polychaetes (e.g. *Spiophanes duplex*) characteristic of clean, fine to medium shelf sand (Dauer et al. 1981, Probert and Wilson 1984) despite their relatively low abundances.

Further South (Durban area), environmental conditions were more stable as a result of a semi-persistent eddy (Guastella and Roberts 2016, Roberts et al. 2016) and more beneficial for other benthic organisms, resulting in a completely different species assemblage. The Durban Eddy fine sand assemblage (sample group V) presented the highest number of taxa, diversity (H') and intermediate abundances. Adjacent to the Durban fine sand also, some differences could be noted southward, both in environmental parameters and macrobenthic communities. Sample group VII was characterized by lower sediment TOC in the sediment, carbonate rich coarse sediments with elevated chlorophyll-a. These conditions had a positive influence on the macrobenthic abundance (N) and richness (d). Noteworthy was the high dominance of suspension feeding and habitat engineering species *Byblis gaimardii*, *Unciolella spinosa* and *Lanice conchilega*, despite the latter being at relatively low abundances.

Overall, communities presented here have a relatively lower similarity and high species replacement suggesting that patterns may result from environmental filtering, which has been suggested as a major driver in areas influenced more by abiotic factors (Sommer et al. 2014). Most of the communities had limited correspondence with several shelf communities described elsewhere. This lack of correspondence can be due to the limited number of studies in the region

from which further conclusions can be drawn. However, one notable way in which KZN mid-shelf macrobenthos bears an affinity to shelf fauna in comparable habitats elsewhere (e.g. Amazon shelf (Nittrouer and DeMaster 1996) and Ebro Delta continental shelf (de Juan et al. 2007)), is in the abundance of certain tubicolous polychaetes and amphipods that are widely distributed or cosmopolitan (e.g. *Lanice conchilega, Nothria conchilega*, and *Ampelisca brevicornis*) (Probert and Wilson 1984, Alongi 1990, Darbyshire and Mackie 2003).

3.7.5 Macrobenthic faunal distribution and relationships with the habitat variables

Among the main goals of many subtidal soft-bottom benthic ecology studies was to define the spatial variation of the macrobenthos and identify the driving forces structuring spatial faunal patterns (Ellis and Schneider 2008, Moulaert et al. 2008, Veiga et al. 2017). The complex interaction between biological communities and biophysical factors act at different spatial scales and depends on a location (Moulaert et al. 2008). At a larger scale, biophysical factors determine the broad distributional patterns, while biotic factors take a leading stand at a local scale (Ellingsen 2002, Gogina and Zettler 2010). Benthic ecosystems are also naturally variable. This complicates the process of identifying the main variables that shape spatial patterns of benthic fauna (Rubal et al. 2014) and because they differ among areas (Lu 2005). In this way, studies that provides description of their assemblages and associated habitats are useful in establishing a baseline for detection of ecological changes (Schückel et al. 2015).

Many studies have investigated spatial distribution patterns of macrobenthic communities and have concluded that no single factor or mechanism alone has explained faunal patterns (Snelgrove and Butman 1994, Levin et al. 2000, Jayaraj et al. 2007). It has been recognised that at any given location, a variety of interacting hydrographic and sedimentary parameters driven by local processes and conditions are involved in explaining faunal patterns (Snelgrove and Butman 1994, Mackie et al. 1997, Zalmon et al. 2013, Veiga et al. 2017) as shown by BIOENV and distLM results here. The mid-shelf depth range was considered here to counteract confounding issues of depth and stations selection was based on maximising differences in other environmental factors, of which mud and turbidity were identified as best correlated with macrofaunal communities. These are a reflection of physical dynamics, which in turn indirectly influence macrobenthos through habitat disturbance (Blanchard and Feder 2014). As natural disturbance agents, physical dynamics also play a key role in determining community structure and distribution (McArthur et al. 2010b).

Mud predominantly originates from the uThukela Estuary, which provides large flux of suspended matter into the ocean each year (Begg 1978). From the river mouth, mud migrates

both in suspension resulting in a turbid environment and in the form of mudbanks creating a dynamic mud depocentre in the subtidal zone (Flemming and Hay 1988). These factors individually or in synergy seem to play a vital role in shaping the ecology of the soft sediment macrobenthic communities off uThukela Estuary.

Distance linear models showed that macrobenthos could be differentiated into distinct communities separated by a subset of medium sand, mud, TOC, carbonates, salinity and turbidity. When variables were analysed by sets (e.g. sediment and water column) results showed a significant synergistic contribution, although sedimentary variables explained a higher percentage of variation. Relationships between the distribution of soft-bottom macrofauna and sediment characteristics, in general, have been studied for decades, and historically, sediment type has often been emphasized as key a factor to determine the composition and structure of benthic systems (Pearson and Rosenberg 1978, Snelgrove and Butman 1994, Snelgrove 1997). This has been described in terms of the optimal sediment particle size range tolerated by each species (Hily 1987, Van Hoey et al. 2004, Hily et al. 2008). Based on their lifestyle, macrobenthic communities require particular sediment properties for tube building and burrowing capabilities, as mechanically it is difficult to burrow in certain grain sizes and thus choice of habitats is governed by sediment type (Probert and Wilson 1984). Likewise, in the KZN mid-shelf, variations in the community structure are directly linked to sediment types, since the sandy bottoms are populated by a more abundant and diversified fauna than the muddy habitat. Also considered is the influence of the Agulhas Current as the main driver of sediment distribution along this region (Flemming 1980, 1981, Flemming and Hay 1988), in the process of transporting sediment particles could also carry invertebrate larvae and therefore influence the spatial structure of the macrobenthos assemblages.

The relationship between animals and sediment can include other complex interactions; sediment types can influence other variables such as microbial content and food supply (Weston 1988, Snelgrove and Butman 1994, Barros et al. 2008). The retention of organic matter in sediment is influenced by the particle size (Milliman 1994) which in turn is largely governed by the hydrodynamic of the region. The sediment in the study area was mainly composed of fine-to-coarse sand, which has lower holding capacity than mud found predominantly off uThukela and as expected, a relatively high sediment organic content. Although there is a logical functional link between macrobenthic organisms and sediment organic matter as a food source, in this study low macrofaunal abundance were found off uThukela Estuary (high TOC concentrations).

In addition to substrate type, sediment carbonate and sorting were shown to be important factors associated with the distribution of the benthic taxa. Substrates with high sedimentary carbonate ($CaCO_3$) content contribute to grain/sedimentary heterogeneity and are associated with accumulation of the superficial sediment providing a wide range of potential ecological niches. This promote high variation in stochastic species occupancy patterns (Barton et al. 2013), and shell fragments could also help to protect the organisms against predation (Santos and Pires-Vanin 2004, Carvalho et al. 2011). In this study, sediment with high carbonate content supported a high number of taxa and abundance. Sediment sorting was also identified as an important variable contributing to the faunal distribution, although their precise role in controlling species number and abundance is harder to interpret. In this study, high number of taxa was found at stations (e.g. S5) with poorly sorted sediments. These results support Gray's (1974a) hypothesis that poorly sorted sediment support higher species richness because of the presence of a wide variety of grain size for benthic fauna to use.

Salinity is often regarded among the major factors affecting species richness and composition of macrobenthos (Moulaert et al. 2008). Results presented here showed salinity to be an important factor in explaining composition variables d and H'. Despite salinity being statistical important in explaining composition variables, it has a less definable role in explaining community patterns, and showed monotonic trend along the study area. Glockzin and Zettler (2008) and Veiga et al. (2017) also reported similar results.

Pelagic food supply plays an important role in the structure and abundance and biodiversity of macrofaunal communities especially in the oligotrophic area (Grebmeier et al. 1989, Albertelli et al. 1999). The quality and quantity nutrient that sinks to the bottom depend on the intensity of the primary production of the water column (Danovaro and Fabiano 1997). In this study, elevated values of chlorophyll-a ((Chl-a) surrogate for primary production) corresponded with stations (e.g. K3) where diversity and richness was high and stations where selective detritus/suspension-feeding amphipods (e.g. ampeliscid and unciolid) dominate both in abundance and number of taxa (e.g. S5). Therefore, it can be assumed that high resource availability and allochthonous inorganic nutrients via Zinkwazi and iSiphingo Estuary acted synergistically and positively influenced diversity and abundance. Moreover, the lack of predators at S5 could explain high abundance of filter/suspension feeders recorded there. Despite chl-a being less definitive statistically here, the relationship between macrofaunal abundance, diversity and chl-a was confirmed by a significant correlations found between chl-a and macrofaunal abundance and diversity. The importance of chl-a in driving macrofaunal patterns was also highlighted by MacKay et al. (2016) and Untiedt and MacKay (2016) in the

recent KZN Bight studies. On the other hand, stations where high carbonates and heterogeneous sediments occur had higher diversity (e.g. S6 and N3). This suggests that carbonate and sediment structure were more influential on macrobenthos abundance and species number. Sediment heterogeneity as a major factor affecting benthic diversity was also reported by Grebmeier et al. (1989). The relationship between macrofaunal diversity and sediment heterogeneity was confirmed by the significant correlations found between diversity and carbonates.

Aside from abiotic factors, engineering species can cause modifications of the environmental conditions, which are not usually accounted for in the output from statistical models (Reise 2002). For example, high densities of *Lanice congilega* tube-dweller can significantly increase the oxygen flux in the sediment by ventilating their burrows (Rhoads and Young 1970, Vopel et al. 2003, Rabaut et al. 2007). Changes in the structure of benthic communities may also be associated with the increased intensity of biotic factors such as competition and predation (Rhoads and Young 1970). These are important regulators of the abundance and exercise an influence on the distribution of species. For instance, *Thalamita spinifera, Lissocarcinus sp.1, Ommatocarcinus pulcher* and *carcinus sp.1* are active predators and may exert appreciable influence on macrobenthic organisms. Other biotic factors such as availability and abundance of benthic larvae may also be more important than sediment in determining benthic settlement and recruitment (Wu and Shin 1997). These were not considered in this study but may throw light in understading macrobenthos patterns and distribution.

Overall, the geomorphological complexity, the intricate patterns of sediment distribution and the oceanographic conditions of the KZN shelf lead to a rich habitat diversity, which in turn supports a higher variability of faunal assemblages. The high species richness of the assemblages associated with medium-to-coarse grained sediments draped with shell fragments, supports the hypothesis that enhanced sediment heterogeneity along shelf habitats promote beta diversity.

3.7.6 Habitat heterogeneity attributes and biodiversity patterns

Habitat heterogeneity is well recognised as a major driver of variability in ecological patterns and processes, affecting species distributions, community composition and diversity (Ellingsen and Gray 2002), supporting global species diversity by increasing niche availability and community complexity and thus facilitating the formation of distinct species assemblages (McClain and Barry 2010), as such, is among the key considerations for marine spatial planning (Foley et al. 2010). The importance of fine-scale habitat heterogeneity in enhancing diversity

has been established in several shelf settings (Hewitt et al. 2005, Thrush et al. 2010). In the case of the KwaZulu-Natal shelf, different sedimentary settings (e.g. ratio of sand, mud), proximity to river inflows (affecting sediment deposition) and local hydrographical conditions (e.g. primary production, mesoscale circulation) appeared important (e.g. Alongi 1990, Ganesh and Raman 2007) as a consequent of the known oceanographic features in the Port Durnford area, off uThukela and Durban. These, with Agulhas Current functioning as a driving force contribute to a variety of unique/rare habitats and each with a set of characterising variable ranges.

In tropical/subtropical latitudes, the coexistence of unconsolidated sediment with reef rubble is frequent (Alsaffar et al. 2017, Ellis et al. 2017). Seafloor heterogeneity associated with such mosaic of habitats and the resulting variability in the hydrographic factors, even within small spatial scales, provide a wide range of potential ecological niches for many species of different trophic groups (Barton et al. 2013), thus are expected to support a greater diversity (Santos and Pires-Vanin 2004, Oliveira et al. 2007). In the Port Durnford area, a comparable habitat type exists and the effects of stronger hydrodynamic regimes result in a gradation of sediment grain size, which translates into a presence of assemblages typical of coarse sediment. In this study, free-living carnivorous predators such as *Quantanthura serenasinus*, *Nephtys capensis* and *Onuphis eremita* dominated this habitat. The preference of carnivores for coarser sediments is well-established (Tena et al. 1993, Muniz and Pires 1999, Santos and Pires-Vanin 2004) due to large interstices among grains creating space enough to favour the mobility and feeding of carnivores, proliferation of potential prey organisms and the oxygenation of the sediments (Fenchel 1970, Gaston 1987, Muniz and Pires 1999). High abundance of filter/suspension feeders such as Anthozoa sp.5, *Ampelisca sp. 3,* and *Ampelisca palmata* could be related to the accumulation of particulate matter due to topographically induced upwelling in the vicinity (Lutjeharms et al. 1989). Sub/surface deposit feeding fauna were present in low abundances in this habitat, e.g. Ophioroidae sp.2. This might be a consequence of the effect of reef rubble and shell fragments in hampering the feeding of the species that ingest sediment and digest only organic matter and micro-organisms associated with the substrate (Santos and Pires-Vanin 2004).

A distinct situation occurs just south of the aforementioned habitat, where the uThukela Estuary faces the open sea and an effective transport of less saline waters to the adjacent shelf occurs (Begg 1978). Here, the potential effect of the riverine outwelling could be a function of the interaction between physical processes (e.g. sediment supply and advection causing muddy coasts), biological processes (e.g. losses due to low-salinity intolerance) and chemical processes (e.g. nutrient enhancement and increased primary production) resulting in productive shelf

waters (Keith et al. 2002, Rabalais et al. 2004) relative to the surrounding oligotrophic AC waters (Snelgrove 1998), which in turn influence macrobenthos composition and distribution. The environmental stress in tropical shelves under severe riverine-influence is naturally high: deposition and resuspension of fine sediments and turbid water due to extensive river runoff (Nittrouer and DeMaster 1996). Only few infauna and other taxa can thrive under these habitat conditions (Huston 1979), as a result support low infaunal populations (Aller and Aller 2004). Such deposition areas with negligible hydrodynamic movement allows fine particle to settle, so that only a small amount of organic content in suspension is available as food for filter/suspension, which in turn restrict filter/suspension feeding fauna from inhabiting such habitat. Species assemblage here were dominated by carnivorous fauna, capable of using deposit feeding opportunities with a changing food supply (Untiedt and MacKay 2016). The possibility exists that the newly settled larvae are eaten at the surface by carnivores (Thorson 1966), or may also be a consequence of considerable hydrodynamic movement exerting a negative effect on larval recruitment and settlement (Eckman 1983, Butman 1987).

Rosenberg (1995) discussed the importance of grain-size characteristics as predictors of benthic faunal assemblages and assumed that the importance of the sediment is, in part, a consequence of its role in determining the type and abundance of food available to fauna that flourish in specific sediment types. Therefore, differing feeding modes among habitat types reflects the covariance of hydrodynamics with ecological adaptation: stronger currents result in coarser sediments, reduced organic content deposition in sediments, and more suspension-feeding organisms due to the greater volume of particulate organic matter (POM) passing by in the water column. The alternate is that weaker currents result in greater deposition of POM and thus, greater proportions of deposit-feeding organisms (Milliman 1994, Sivadas et al. 2013, Blanchard and Feder 2014, Pilditch et al. 2015). However, the bioturbation activities of macrofauna ensure that the organic matter is transported and stored in deeper sediment for the subsurface deposit feeders. In this study, the bioturbation potential has been inferred from the functional traits, which are further discussed in Chapter 4.

Biogenic features are known to structure and modify benthic habitats and have a major influence on the macrobenthos distributional patterns (Passarelli et al. 2012). These include mollusc shells, polychaete and amphipod tubes, which increase habitat complexity and environmental heterogeneity, providing a large variety of ecological niches across a small spatial scale, thus promoting diversity and co-existance through non-equilibrium mechanisms (Pearson and Rosenberg 1978, Hewitt et al. 2008, Passarelli et al. 2012). However, high densities of biogenic features (e.g. *Calichirus* burrows (Pillay et al. 2007) and *L. congilega*

tubes (Rabaut et al. 2007)) can also reduce water flow at the sediment surface. This improves the settlement of both inert and living particles and ultimately result in the increase in organic content. Increased organic matter with increasing meshwork of tubes has also been highlighted by Godet et al. (2010). These organic enriched stable habitats may result in a colonisation of other species, thus increased diversity (Gooday et al. 2010, Leung 2015b). These may also provide refuge against predation such a *Bulia* gastropod shells occupied by *Paguristes sp.* (Thrush et al. 2001, Thrush et al. 2006, MacKay et al. 2016).

3.7.7 Spatial planning biozone as surrogates of benthic biodiversity

Abiotic based habitat classification as surrogates for marine biodiversity management and conservation involves the partition of the seafloor into spatial units (Kirkpatrick and Brown 1994, Stevens and Connolly 2005, Carmel and Stoller-Cavari 2006). In this approach, environmental data are interpolated and combined to form discrete seafloor habitats, each of which is assumed to correspond to a marine benthic habitat, that are relatively homogeneous in composition, community and functional characteristics with similar environmental characteristics and different from other seascapes (Harris et al. 2008, Heap et al. 2011). These biophysical factors are known to affect communities (McArthur et al. 2010b) and when used to define habitat should reflect the organismal diversity and result in protecting all biodiversity associated with each habitat class (Faith and Walker 1996). As such, high congruence is expected between abiotic based habitat and the actual distribution of many species that make up biodiversity. However, the efficacy of biophysical habitat surrogates for representing marine benthic biodiversity remains poorly understood (Przeslawski et al. 2011) and has been strongly criticised because of low overlap between habitat classes and actual species distributions (Faith et al. 2003, Brooks et al. 2004, Jackson and Lundquist 2016). Indeed, results from this study also showed limited overlap between marine spatial planning (MSP), predefined biozones and macrobenthic community patterns. Therefore biozones currently set for the province were not a useful predictor of spatial variation in macrobenthic biodiversity.

Biodiversity indices (S, N, d, and H') showed that biozones were not a consistently useful surrogate at all biozone subclusters, the strength and significance of relationships with macrobenthos varying. That is, some biozone subclusters differentiated communities and others showed no biological differences. The inference is that these animals are not distributed discretely rather in a continuum and vary relative to environmental gradient and habitat complexity (Mills 1969, Stephenson 1973, Gray 1976). The observed significant relationship

between some pairs of biozones could be attributed to differences in the individual stations within each subcluster, e.g. high abundance of a specific group in one station.

Biozone subcluster (BS) 3A corresponded well with the sedimentary patterns (grouping of samples) and macrobenthic community structure. This indicates that mapped surrogate (BS 3A) successfully captured patterns of both aforementioned attributes in the unique habitat off uThukela Estuary. Similarly, BS 1C (off Port Durnford) represented patterns in macrobenthic communities. These BS's were also significantly different from all other BS's in terms of composition variables and community patterns, indicating that biological communities at these BS's are likely to be consistently different from other assemblages in the region. Both BS's (3A and 1C) captured biological patterns at different similarity thresholds, as reflected by samples of BS 3A clustering at a very low similarity level, with G5 least similar to I5 and H4. This was attributed to the presence of moderately sorted fine sediment (>10%) at station G5, which allowed fauna with a preference for fine sand to establish and thus contributed to a shift in the community composition. Result presented here, highlighted the importance of the interrelation between sedimentary characteristics and biological community when selecting/classifying habitats. Biozone subclusters 1A and 2A and 1B and 2B grouped closely and there were no significant differences detected in the community structures. Likewise, no obvious differences were detected by the univariate measures. Therefore, these BS's were not biologically distinct, rather indicative of over-classification (Przeslawski et al. 2011).

Recent studies on classification systems have shown that biological communities respond to physiographic variables that are used to define ecological units. These are defined as the physical and chemical environment in which a species or a community lives (Bolam et al. 2008, McArthur et al. 2010b, Dutertre et al. 2013). Indeed, this study provided evidence that abiotic variables were responsible for spatial patterns in the KZN mid-shelf macrobenthic communities. However, here variables only explained 30.5% of the total variation and therefore does not serve as effective abiotic proxies for creating high-resolution maps of important ecological attributes. The inability of biozone classification to capture macrobenthic spatial patterns could have been driven by the microscale variation in environmental variables not included during biozone classification, overriding the effects of environmental factors incorporated in biozone derivations. Overall, the heterogeneous nature of KZN mid-shelf soft-sediment benthic habitat was overlooked in the MSP predefined biozone classification. Despite analytical techniques being sufficiently sophisticated to detect multiple gradients in ecosystems (Dolédec and Chessel 1991, Clarke and Warwick 2001, Clarke and Gorley 2006, Anderson et al. 2008a), correlations between species distributions and habitat characteristics have limited potential for a mechanistic

understanding of ecological patterns. This is because analyses based on taxonomic grounds alone do not provide confirmation of assembly rules independent of species biology (Fleishman et al. 2006).

Biophysical habitats are usually derived using a small subset of variables, yet habitat is defined by a collection of biotic and abiotic factors associated with it. Habitat features used to define abiotic habitat should include all abiotic factors that influence the distribution and abundance of species across a region. For a surrogate to be efficient, distribution of oceanographic and geomorphological characteristics that collectively define an ecosystem should be incorporated during biophysical habitat derivation (Young and Carr 2015). Abiotic habitat surrogates can assist in conservation planning, with substantial improvements in performance achieved when they are biologically informed (Young and Carr 2015, Jackson and Lundquist 2016). Despite the lack of correlation between the current biozone classifications for KZN, the use of macrobenthos is still advocated to be incorporated in such plans. Macrobenthos forms a substantial component of shelf biodiversity and are important contributors to ecological functions, and thus ecosystem functioning (Schwinghamer 1981, Ganesh and Raman 2007, Sokołowski et al. 2012). Also, their spatial configuration and heterogeneity have important implications for the distribution and relative abundance of marine organisms (Thrush et al. 2001, Anderson et al. 2009). Accordingly may be effective predictors of biodiversity and ecosystem functions (Reise 2002, Solan et al. 2004, Anderson et al. 2013, Dutertre et al. 2013). In addition, their sedentary lifestyle reflects habitat history (Dauvin and Ruellet 2007). Therefore, including macrobenthos into conservation planning will ensure representation and protection of biodiversity. Likewise, the ecological processes that sustain biodiversity and ecosystem services as a goal of marine conservation planning (Roberts et al. 2003).

Conclusion

This study provides an overall view of the spatial distribution of KZN (Port Durnford-uMkhomazi) mid-shelf soft-bottom macrobenthic communities. This study further showed the ecological importance of this study area due to its rich macrofauna community with high abundance and diversity. Polychaetes were the most common taxonomic group and had the highest proportion of widespread species, whereas crustaceans, bivalves and echinoderms were more confined with crustaceans being highly abundant. Quantitative characterisation of fauna distinguished seven species assemblages distributed according to different habitats characteristic along KZN mid-shelf, but overall structured by spatial differences in seafloor and water column characteristics such as the proportion of medium sand, fine sand, mud, TOC, associated statistic

of sorting and turbidity. Depending on the habitat type and the number of explanatory variables that were taken into account, different parameters were more important in influencing spatial variation, e.g. Northern mid-shelf (Port Durnford) macrobenthos is influenced more by coarse grades of sediment deficient in sediment organic content, while cohesive nutrient richer mud coupled with near bottom turbidity were important variables for macrobenthos off uThukela. The transition area between uThukela and Zinkwazi is influenced by poorly sorted coarse sand, while Zinkwazi to Durban is more influenced by fine sand as a consequent of current induced sorting owing to the semi-persistent Durban Eddy. Carbonate rich coarse sediment influenced the mid-shelf macrobenthos between Durban and uMkhomazi. Zinkwazi to Durban habitat support a highly taxon-rich community, while highly abundant macrobenthos was found south of Durban.

Overall, this study demonstrates a clear link between macrobenthic community structure and habitat heterogeneity. Stations with greater grain size heterogeneity supported high diversity. Environmental variables depicted as important in explaining community variation only accounted for a small percentage of variation, therefore it is probably that factor(s) other than those measured have influence on macrobenthic community structure. The results presented here provide a much more detailed account of biological communities of KZN mid-shelf and their distribution on much finer (station level-assemblages-biozones) spatial scales, which can be useful to inform conservation planning. Furthermore, this study addresses knowledge gap (macrobenthic biodiversity patterns) in the “Northern” east coast benthic communities, which are poorly studied.

The selection and use of biodiversity surrogates is part of marine conservation planning, yet there is no consensus regarding the criteria for the selection of appropriate surrogates (Lovell et al. 2007). This is in part due to marine conservation lagging significantly behind its terrestrial counterpart, with serious attempt at marine habitat not being undertaken until the 1990s (Zacharias and Roff 2000). Identification and testing of suitable surrogates for biodiversity will increase the likelihood that the selection or/and zoning of individual MPAs results in effective representation and protection of biodiversity or/and target habitats (Malcolm et al. 2012). Results from this chapter showed limited overlap between biophysical habitat surrogates (predefined biozone classification) and KZN mid-shelf macrobenthic community patterns, suggesting that the existing biozone model is not a good surrogate for KZN benthic communities. Refining of the existing model is recommended by optimising it against real, sampled biological data.

CHAPTER 4. TAXONOMIC AND FUNCTIONAL ATTRIBUTES OF KWAZULU-NATAL MID-SHELF MACROBENTHIC FAUNAL COMMUNITIES

4.1 Overview

This chapter uses the concept of taxonomic sufficiency (TS) and organism functional attributes to describe the KZN mid-shelf macrobenthic community. It focusses on this group in finer scale from those presented in Chapter 3 by considering different taxonomic levels (Species to Phylum), indicator groups (Polychaeta or Amphipoda) and biological traits to distinguish surrogates and establish traits responsible for patterns in community assemblages. Based on taxonomic levels and indicator taxa, minor information was lost when aggregating data from Species to Family level and to the Polychaeta indicator group considering Weighted-Spearman correlations and non-metric Multidimensional Scaling (NMDS). The biological trait analysis added new insight (confirmation of assembly rules) regarding the association of diverse biological traits as contributing to ecosystem functioning. Three main functional/taxonomic groups were found using nine traits, across 51 categories from 634 taxa; off uThukela, between Zinkwazi and Durban, and Durban to uMkhomazi. The groups were characterised as being free-living carnivores, hard-skeleton direct-developing omnivores and soft-bodied or hard-shelled omnivores with planktotrophic larvae. These patterns were explained by the KZN shelf habitat complexity, including sediment organic, carbonate content, water column turbidity, and dissolved oxygen. Results of nMDS, PERMANOVA and PERMDISP analyses showed that functional structure did not agree with current KZN spatial planning biozones classification.

4.2 Introduction

Growing awareness of biodiversity issues has brought the need for comparable and meaningful measures of diversity at many scales into sharp focus (Gray 1997, Snelgrove et al 2014). In particular, factors controlling the biodiversity of an area, and thus ecosystem function, are central to biodiversity research (Tilman, 2000). The typical methods for macrobenthic community analysis by aggregation of species data to higher taxonomic groups (such as Family, Genus, etc) show similar results (Wlodarska-Kowalczuk and Kedra 2007). However, traditional taxonomic-based macrobenthic community analysis may not fully account for the group diverse roles in ecosystem functioning. It has been recognised that protection of the habitat and its related functional processes is a key element ensuring ecological sustainability (Frid et al. 2008, Snelgrove et al. 2014).

4.2.1 Taxonomic resolution

Soft-bottom benthic communities are perhaps the most extensively used indicators of natural and human-induced environmental changes (Warwick 1993, Wlodarska-Kowalczuk and Kedra 2007, Alves et al. 2014). The commonly used responsive variables include taxon composition and distribution, examined with univariate and multivariate biodiversity measures (Clarke and Warwick 1994). Traditionally, analysis of distribution and diversity patterns has been based on the identification to the lowest possible taxonomic level, usually species-level. Biodiversity and its conservation are important and fundamental concepts in community ecology and its assessment requires data on species inventories (Yekta et al. 2017). However, this level is not always practical due to the taxonomic expertise required, budgetary constraints associated with it, and the presence of sibling or cryptic species (Knowlton 1993, Bickford et al. 2007). These major drawbacks limit mapping of biodiversity over a large spatial area using species level analyses (Olsgard et al. 2003), especially when dealing with large-scale data in a limited time span (Bertasi et al. 2009). As a consequence, selection of reserves or marine protected areas (MPAs) has largely relied on the use of rapid biodiversity assessments (Gladstone and Davis 2003) such as physical and habitat surrogates (McArthur et al. 2010b, McHenry et al. 2017), lower taxonomic resolution (Bowman and Bailey 1997, Olsgard and Somerfield 2000, Heino and Soininen 2007, Wlodarska-Kowalczuk and Kedra 2007, Shokri and Gladstone 2008, Mueller et al. 2013) or identification of indicator groups or/and taxonomically coherent subsets (Ward et al. 1999, Olsgard et al. 2003, Giangrande et al. 2005, Shokri et al. 2009). Few studies have evaluated the efficacy of biodiversity surrogates for marine reserve selection or to facilitate marine spatial planning. The KwaZulu-Natal shelf environment is no exception to these drawbacks. In order to address this and to find a time and cost-effective methods for more rapid description and cataloguing of biodiversity to expedite provincial marine spatial planning for conservation and management of biodiversity, the search for a surrogate in an ecological investigation is being explored. Surrogates are defined as quantities that reflect Species level community patterns but can be more easily determined than traditional analyses (Olsgard and Somerfield 2000).

The aforementioned approaches have been used extensively in the quest for a perfect surrogate in marine benthic studies and have proven useful in some applications, but has failed to accurately predict patterns of biodiversity elsewhere (Maurer 2000, Giangrande 2003, Drew 2011). Taxonomic Sufficiency (TS), involves identifying taxa to the highest taxonomic level when loss of information has no significant effect on the ability to assess community patterns (Ellis 1985). This approach to assessing biodiversity patterns, and the potential dis/advantages

alternatives, has for the past decades remained controversial (Bowman and Bailey 1997, Gaston 2000), but recent studies show the effectiveness of coarser taxonomic resolution in detecting spatial patterns (Bevilacqua et al. 2012, Mueller et al. 2013, Yekta et al. 2017).

The use of a single lower-order taxonomic group whose responses to a natural gradient may produce analogous responses to those obtained from a fine taxonomic resolution has been advocated by Olsgard and Somerfield (2000) and Olsgard et al. (2003) as a biodiversity indicator. Several groups are proposed, among others, assemblages of amphipods, polychaetes and molluscs are recognised as valid surrogates for total macrofaunal assemblages (Olsgard et al. 2003, Giangrande et al. 2005, Smith 2005, Mendes et al. 2007, Wlodarska-Kowalczuk and Kedra 2007, Shokri et al. 2009, Lindenmayer and Likens 2011). The use of selected taxa in conservation and management programmes is however limited to the few regions where ongoing comprehensive taxonomic and natural history investigations have also been undertaken. Potential for subset taxa as biodiversity indicators exist across a wide variety of environments, especially in the tropics. However, their incorporation as indicator species has remained debated because of the subjectivity of selection criteria and the ambiguity in the use of terminology (Morrison 2009, Lindenmayer and Likens 2011, Borrett et al. 2014, Siddig et al. 2016).

Most surrogacy studies consider coarse taxonomic resolution or selected taxa performance, with only a few that simultaneously examines the adequacy of both surrogacy methods (Wlodarska-Kowalczuk and Kedra 2007). To date, few studies of marine macroinvertebrates have considered the capability of detecting community patterns using coarser taxonomic levels in South Africa (Clarke 2005, Untiedt 2013). These also focused mainly on polychaetes.

4.2.1.1 South African Polychaeta

Polychaetes play a critical role in the functioning of benthic communities (Hutchings 1998). This is not solely driven by their richness (Fauchald and Jumars 1979) and abundances (Day 1967, Chambers and Muir 1997, Giangrande et al. 2005), but also because of the high morpho-functional diversity resulting in a multi-faceted response to environmental gradients (Wilson 1991, Jumars et al. 2015b), whereby different species occupy different gradients and almost all substrate types. A comprehensive synopsis of the South African polychaetes was given by Day (1967) in two separate volumes, which still serve as the only identification guide for the regional fauna to date. This work described more than 800 taxa high in endemism and diversity (Day 1967).

4.2.1.2 South African Amphipoda

Amphipoda are a highly abundant, taxonomically rich and ecologically important component of soft-bottom marine benthic communities (Thomas 1993, Smith 1995, Basset et al. 2004). These attributes, suggest that amphipods are frequently among the most dominant groups in the biocoenosis (Conlan 1994, De-la-Ossa-Carretero et al. 2012), and play a crucial role in the ecology of soft-bottom habitats through nutrient cycling and secondary production (Thomas et al. 2000, Jennings et al. 2002). Amphipods comprised of individuals with a high degree of niche specificity and those that demonstrate high tolerance to varying physico-chemical characteristics in sediment and water, allowing large distributional range in various biotopes (Thomas 1993, Thomas et al. 2000, Dauvin and Ruellet 2009, Arabi 2010). In consequence, they show a high diversity of feeding habits (Díaz and Cabido 2001, Navarro-Barranco et al. 2013). Benthic amphipods conform to several criteria that render them highly recommendable for inclusion in ecotoxicological studies and marine monitoring programmes (Marchini et al. 2008, Villéger et al. 2010, Navarro-Barranco et al. 2013). In addition, amphipods are an invaluable food source for numerous economically valuable fishes (Nair et al. 1973) and therefore their abundance and distribution have important implications for the distribution of fishery resources (Thrush et al. 2001, Anderson et al. 2009). Barnard (1950) provided a synopsis of all known South African representatives of the order Amphipoda. Subsequently, there have been some revisions of the taxonomy, and these have resulted in some additional records and changes in the nomenclature of South African species (Griffiths 1973, Griffiths 1974b). These have contributed to the listing of the benthic marine Amphipoda of Southern Africa by Griffiths (1976), however, additional species and records have been recognised since then, mainly by Griffiths (1976, 1977, 1979) and recently by Milne and Griffiths (2013).

4.3 Functional diversity

While many studies in soft-bottom benthic ecosystems have examined taxonomic diversity (and associated indices) of macrobenthic invertebrates and appreciated the advantages offered, this method provides a unimodal property of the ecosystem while omitting other biodiversity-related key functions (Pacheco et al. 2011). Therefore, does not fully account for taxon diverse roles in the ecosystem functioning (Schratzberger et al. 2007, Pavoine and Bonsall 2011, Leung 2015a). Knowledge of both taxonomic and functional diversity across different habitats is essential for understanding potential future change in provision of ecosystem services and to inform conservation objectives and management practices (Wong and Dowd 2015). Given that when attempting to evaluate biodiversity for conservation and management purposes, the inclusion of functional properties has been recommended (De Jonge et al. 2006, Snelgrove et al. 2014), an

alternative approach that incorporates species function is required. Few studies have examined functional trait diversity and how it relates to soft-bottom benthic habitats structures.

Functional diversity refers to a variety of roles performed by benthic species in a community (Tillin et al. 2006). These roles/functions are important in regulating ecosystem processes and can be portrayed by the biological traits organisms exhibit (Snelgrove, 1998). A biological trait is a measurable characteristic of an organism that reflects its adaptation to environmental conditions (Violle et al. 2007). As such, the range and contribution of the biological traits of species in a community will determine its ecosystem functional diversity (Tillin et al. 2006), which is considered a key indicator for conservation and management (Cadotte et al. 2011).

4.3.1 Biological Trait Analysis

Biological trait analysis (BTA) is increasingly used to examine the ecological functions of macrobenthic communities and patterns in response to environmental gradients (Pacheco et al. 2011, Paganelli et al. 2012, Fleddum et al. 2013, Berthelsen et al. 2015, Shojaei et al. 2015). This approach provides greater mechanistic understanding on how communities may respond to environmental change and as traits are known to influence the rate and relative importance of particular ecosystem processes, they are expected to further improve understanding of ecosystem functioning (Vandewalle et al. 2010, Snelgrove et al. 2014, Berthelsen et al. 2015). The BTA uses a series of life history, morphological and behavioural characteristics of the species present in assemblages to indicate key aspects of their ecological functioning over a multidimensional niche space (Chevene et al. 1994, Bremner et al. 2006c, Norling et al. 2007, Paganelli et al. 2012), where niche-processes are more likely to explain the patterns (Petchey and Gaston 2002). This approach differs from previous unidimensional trait-based approaches, such as trophic or functional groups (Pearson and Rosenberg 1987, Snelgrove and Butman 1994)) as it uses a wider range of trait information. Ecosystem functioning cannot be provided by a single parameter; simultaneous consideration of multiple variables is considered most effective, thus, this approach allows for synchronised assessments of several functions (Bremner 2008, Frid et al. 2008). The BTA incorporates information on the relative abundance of species and a wide variety of biological characteristics (trait information). Changes in the abundance of taxa resulting in changes in the patterns of trait expression within assemblages, may be indicative of the effects of impacts on ecological functioning (Bremner et al. 2006a) and are often reflected by an increase in those species able to withstand the impacts. Unlike the taxonomic based approach, biological trait analysis uses biological characteristics which can be shared by different species (Usseglio-Polatera et al. 2000b, Mah and Blake 2012). Therefore, BTA can be applied to different taxonomic groups of organisms and also over a wide spatial

coverage where there are gradients in species composition (Bremner 2005, Hewitt et al. 2008). In this context, trait-based approaches are robust with decreased taxonomic resolution (Menezes et al. 2010), and problems associated with misidentification are less critical since macrobenthic species with high morphological similarity will most probably share the same trait category (Alves et al. 2014).

Traits are usually divided into two categories (Costello et al. 2015): biological traits (e.g. life cycle, physiology and behavioural characteristics, and reproductive) and ecological traits (e.g. mobility, body design, diet and trophic level). Traits are measured at an individual level and used comprehensively across increasing taxonomic level. Moreover, traits can be compared among individuals within and between communities (Boersma et al. 2016), therefore may highlight patterns within and across ecosystems that are not apparent in taxonomic-based approaches (Boersma et al. 2016, Weigel et al. 2016, van der Linden et al. 2017). Each trait has several sub-categories, or modalities (e.g. the 'trait movement method' contains the modalities crawler, burrower and swimmer). Modalities allow for functional characterisation of the state of the membership of each taxon. This study is the first of its kind for invertabrates on the KZN shelf. Fleddum et al. (2013) used BTA on the west coast to examine impacts of demersal trawling on marine benthic habitat.

Aims, Objectives, and Hypotheses

This chapter examines if higher taxonomic levels (Genus-Phylum) or potential indicator groups (Polychaeta and Amphipoda) are surrogates for community patterns shown by whole microbenthic assemblages. The aims are to improve the poor state of knowledge of east coast macrobenthic species, between Richards Bay and Mkomaas by describing the biological trait structure of macrobenthos, and to test relationships between trait structure and measured environmental parameters relative to provincial marine spatial planning predefined biozones.

Objectives

1. To determine if data aggregated to lower taxonomic resolution or to potential indicator groups are comparable to those at Species level.
2. To characterise macrobenthic trait composition
3. To define KZN mid-shelf macrobenthic community traitscape and test if there are spatial differences between them.
4. To determine the relationship between the macrobenthic community traitscape and measured environmental parameters.

5. To determine whether functional structures of KZN macrobenthic communities agree with a predefined biozone classification.

Hypotheses

H_1: Species richness and diversity decrease with data aggregation to lowest taxonomic resolution, and is lowest when considering a potential indicator group.

H_2: The ability to detect abiotic factors responsible for spatial patterns decrease with data aggregation to lowest taxonomic resolution, and is lowest when considering a potential indicator group.

H_3: There is congruence in the spatial structure of macrobenthic fauna when the data are aggregated to lower taxonomic groups (Genus to Phylum), potential indicator groups and functional traits.

H_3: There are differences in macrobenthic trait composition between the stations and community traitscapes along the KZN mid-shelf.

H_4: There is a significant relationship between the macrobenthic community traitscape and biophysical variables measured.

H_5: There are functional differences in community patterns relative to the predefined biozones classification.

4.4 Materials and Methods

General materials and methods including a section on the study area, field-sampling protocol, laboratory processing and data analysis are given in Chapter 2. The following are protocols relevant to this chapter.

4.5 Data Treatment and analysis

Hypotheses were tested using two datasets; species abundance data (as per chapter 3) and weighted-abundance data (methods to follow).

4.5.1 Taxonomic resolution information

Fine resolution taxonomy data sets are required to study the fitness of different taxonomic resolution data for ecological analyses. The resolution of these data sets can be modified by aggregation to coarser levels. Taxonomic aggregation was applied by successively aggregating species abundance data (used in Chapter 3) to Genus, Family, Order, Class and Phylum (coarse-taxonomic resolution) to produce six test data sets.

From the abundance data, two additional data sets were extracted (Polychaeta and Amphipoda). The indicator group ‘Polychaeta’ (multiple species per group) was used, because it contributed

more than 60% to all taxa recorded (Chapter 3), and the 'Amphipoda' indicator group (multiple species per group) was used because it contributed approximately 70% to total abundance (Chapter 3). Furthermore, Amphipoda are a recognised, dominant component of the KZN macrobenthic communities (Arabi 2010). Polychaetes (Olsgard and Somerfield 2000, Olsgard et al. 2003) in particular has been suggested as possible surrogates of marine macrofauna communities in soft sediment because they are both abundant and ecologically important group.

4.5.2 Biological trait definition and information

For this study, eight biological traits (respective modalities) were considered (Table 4.1). Biological traits were chosen to represent processes, properties and activities that are either directly linked to these traits or are indirect indicators of important biological, chemical and structural properties of the ecosystem and its functioning (Fig 1.2 and Table 4.1). Trait and modality names as well as the general classification structure were kept standard as per other functional/biological trait studies cited herein (e.g. Bremner et al. 2003a, Frid et al. 2008 and Shojaei et al. 2015) to ensure comparability. Importantly, the traits used herein were selected because of their importance for the structure and key ecological functions of the benthic system. Furthermore, because they aid in designation and management of MPA's (Frid et al. 2008, Paganelli et al. 2012), thus addresses the main aims of this study.

Information for assigning taxa to biological traits were obtained from peer-reviewed articles, books and taxonomic keys (monographs), mostly collected at a lowest taxonomic level. Trait information included primary sources from the region (e.g. Day 1967), but when regional information was not available, species characteristics information from equivalent environment were used, e.g. Australia waters (Beesley et al. 2000). Benthic species have the potential to show plasticity in certain trait categories, such that congeneric species can respond differently within the same habitat (Törnroos and Bonsdorff 2012). Frequently, information for individual genera or species was not available and information from congeneric species were used, since phylogenetically related species might have evolved similar adaptations (Usseglio-Polatera et al. 2000a). The methodology of assigning traits follows the categorical approach where a trait (e.g. movement method) is divided into modalities (e.g. sessile, semi-sessile, or mobile). Individual taxa were then scored to the extent they exhibit trait modalities using a "Fuzzy coding" procedure (Chevene et al. 1994). This procedure expresses each category on a scale of ' 0' and ' 3' ,with ' 0 ' indicating no affinity of a species to a trait category, and '3 'indicating a high affinity to the trait category. This coding system allows for species traits to be dispersed over a number of modalities (code classes) to reflect its biology. For example, a tube-dwelling polychaete *Lanice conchilega* is a 'deposit feeder', but may feed as a 'suspension feeder'.

Table 4.1. Biological trait variables (including modalities), categories, function and processes used to describe functional diversity in the KZN mid-shelf macrobenthic communities. (Functions and processes, see also Tyler et al. (2012), van der Linden et al. (2017) and (Beauchard et al. 2017))

Traits	Modalities (or category)	Function and process
Body design (BD)	1 Soft (S) 2 Hard – exoskeleton (HE) 3 Hard – shell (HS)	Survival against abiotic damages and biotic aggressions.
Movement method (MM)	1 Sessile (Se) 2 Semi-mobile (SM) 3 Burrow (Bu) 4 Bore (Bo) 5 Crawl/creep/ (C/C) 6 Jump (J) 7 Swim (S) 8 Unknown (U)	Foraging mode, ability to escape predation, migratory requirements and dispersal, influences bioturbation processes and pumping or irrigation features for oxygenation. (Reise 2002)
Reproductive technique (RT)	1 Asexual (budding) (A) 2 Sexual (broadcast spawner) (SBS) 3 Sexual (egg layer/brooder–planktotrophic larvae) (SB-PL) 4 Sexual (egg layer/brooder-mini adult) (SB-MA) 5 Unknown (U)	Juvenile survival, dispersal potential, resource to higher trophic levels, recruitment success. (Christiansen and Fenchel 1979)
Sexual differentiation (SD)	1 Gonochoric (G) 2 Synchronous hermaphrodite (SYH) 3 Sequential hermaphrodite (SEH) 4 Unknown (U)	Larvae and juvenile survival, dispersal potential (Ghiselin 1969)
Larval development (LD)	1 Direct developer (DP) 2 Lecithotrophic (L) 3 Planktotrophic (P) 4 Unknown (U)	Juvenile survival, dispersal potential. (Jablonski and Lutz 1983, Jablonski 1986, McHugh and Fong 2002)
FD Feeding method (FD)	1 Filter/suspension feeder (F/SF) 2 Surface deposit feeder (SFD) 3 Subsurface deposit feeder (SSFD) 4 Interface feeder (IF) 5 Predator (P) 6 Scavenger (Sc) 7 Chemosymbiotic (Ch) 8 Grazer (G) 9 Unknown (U)	Food acquisition, growth requirements, demographic control (predation), influences energy flow and nutrient cycling. (Pearson and Rosenberg 1978, Fauchald and Jumars 1979, Watling 1993, Jumars et al. 2015a)
Diet preference (DP)	1 Carnivore (C) 2 Herbivore (H) 3 Omnivore (O) 4 Detritivore (D) 5 Unknown (U)	
Living habit (LH)	1 Tube dweller (TB) 2 Permanent burrower/gallery dweller (PB) 3 Crevice dweller (CD) 4 Shell dweller (SD) 5 Encrusting (E) 6 Attach (A) 7 Free-living (FL) 8 Unknown (U)	Foraging mode, protection against epibenthic and ben-thopelagic predators, biogeochemical impacts. (Ullberg and Ólafsson 2003)
Habitat engineering (HE)	1 None (N) 2 Forms settlement/attachment sites (FS/A) 3 Forms shelters (FS) 4 Sediment accretion/removal (S-A/R) 5 Unknown (U)	Biogeochemical requirements, niche creation, refuge, nursery, sediment oxygenation, Food acquisition, organic matter re-distribution.

Accordingly, this species was coded '1' for the suspension-feeding trait, '3' for deposit feeding, and '0' for scavenging, predatory, or interface feeding. This approach allows for a much more genuine representation of functional biology of assemblage (Frid et al. 2008). Where no information was available, 'trait unknown' was assigned to avoid undue influence on the overall results (Bremner et al. 2003b). Columns of the matrix were trait modalities and rows were trait score for each taxon. The BTA matrices computation followed the procedure described by Bremner et al. (2003b), where three different numerical matrices were computed using the 'taxa by station' abundance matrix used for analysis in Chapter 3, (1) 'taxa by traits' abundance matrix (biological trait for each taxon), (2) 'traits by station' (biological traits in each sampling station) and (3) abundance-weighted trait by multiplying trait categories for each taxon at a station by the taxon abundance. Finally, summation of trait over all taxa present at each station to obtain a single value for each trait category (trait score) (Bremner et al. 2006c).

4.6 Statistical Analysis

4.6.1 Taxonomic resolution

The reduction (H_1) in the information for each taxonomic level and potential indicator group was taken as a statistically significant drop in (1) diversity indices (indicating a change in taxon richness (Weighted-Spearman correlation coefficients)). Good surrogate taxa will have high ρ_w-values, reflecting a less noisy, and thus more predictable, relationship with richness and diversity. The reduction in r^2-values (2) (indicating a change in capability to detect environmental gradient; (BEST analysis)) and (3) ρ-values (indicating a change in multivariate community pattern; (2^{nd} stage)), from species level (fine resolution) to the next most coarse taxonomic level. This method was proposed by Demšar (2006) and recommended for comparison across datasets. Higher-level taxa likely to prove suitable surrogates are those that are proportionally rich and diverse. In this study, the 'Diverse' procedure (Clarke and Gorley 2006) was used to compute taxon richness (Pielou 1969) and diversity (Shannon and Weaver 1949) for each taxonomic level and potential indicator group.

Taxon richness and diversity values (1) were pooled over all data sets (Species-Phyla and indicator taxa) and tested for normality using Shapiro-Wilk test (Shapiro and Wilk 1965) being the most robust of the proposed normality tests (Hammer et al. 2001). Homogeneity of variance was tested using the Levine's test (Zar 1999). Unequal-variance (Welch) ANOVA was considered since it is more robust on non-normal distributions (Hammer et al. 2001). All univariate statistical analyses were carried out in the PAleontological STatistics (PAST) software program (Version 3.14) (Hammer et al. 2001). The BEST procedure (2) within

PRIMER (Clarke and Warwick 2001) that uses stepwise search procedure and Spearman rank correlation to find the best single or combination of environmental variable(s) that maximises correlation coefficient between environmental parameters and faunal abundance data aggregated to lower taxonomic resolution (r^2) was used to depict the best variables that explains community patterns (Olsgard et al. 1998).

A total of eight Bray–Curtis (B-C) similarity matrices (square root transformed abundance data) were incorporated into the 2nd-Stage MDS routine (3) (PRIMER v.6, Clarke and Gorley 2006) to examine the efficiency of data aggregated to higher taxonomic resolution in preserving the multivariate pattern (H_3) defined at species level. Independency constraints are maximised in 2nd-stage MDS. Weighted Spearman rank correlation (ρ_w), a nonparametric analog to the Mantel test, was used to compare B-C similarity matrices because it weights the distance between two ranks using a linear function of those ranks, giving more importance to higher ranks than lower ones (Somerfield and Clarke 1995, Olsgard et al. 1998, Olsgard and Somerfield 2000).

Results of the second stage analysis can be presented using a nonmetric multidimensional scaling (NMDS) plot to display patterns in the degree of correlation (Somerfield and Clarke 1995, Olsgard and Somerfield 2000). However, since an NMDS plot is only a two-dimensional estimation of all relationships (including those between surrogates), weighted-Spearman correlation coefficients between each surrogate set and the complete suite of fauna was computed. A statistical significant correlation (r=close to 1, sig. <0.05) suggest a high degree of concordance between pairs of similar matrices and therefore there are negligible changes between data analysed at different taxonomic levels. Non-metric multidimensional scaling (nMDS) was run on each B-C matrix from different taxonomic levels and indicator groups (ρ as similarity measure) to represent the relatedness of samples. Kruskal's stress (Kruskal 1964) values associated with each MDS plot reflect the accuracy of the plot represented (Chapter 2).

4.6.2 Biological trait analysis

Abundance–weighted data of nine traits subdivided into 51 categories were used to test if there are differences in trait composition and relative to environmental parameters driving each different traitscape. Here, the DIVERSE programme was used to compute Shannon-Wiener Diversity (H_t') (Shannon and Weaver 1949), Margalef's Richness (d_t) and Pielou's Evenness (J_t') (Pielou 1969) at each sample site. One-way analysis of variance (ANOVA) was used to test for significant difference in univariate measures within sampled stations (H_4).

The Bray-Curtis (B-C) similarity matrix for abundance-weighted biological trait was subjected to cluster analysis and visualised through nMDS. Similarity profiles (SIMPROF, p=0.05) was

used to test statistical significance of separate cluster. Each significant traitscape, resulting from the multivariate analyses, was characterised by the associated values of univariate indices (S_t, N_t, d_t, J_t' and H_t'). The SIMPER procedure was used to determine trait characterising assemblages and those that contribute to the average (dis)similarity between the samples (Chapter 2 and 3). One-way fixed PERMANOVA (9999 permutations) analysis was used to test the hypothesis of no significant differences in the trait composition and distribution of macrobenthic communities (Chapter 2 and 3).

4.6.3 Environmental-biological trait relationships

The BVSTEP algorithm was used to identify a suite of variables that best explains the patterns (H_4) observed in the traitscape, and Global BEST test was used to determine the significance of the subset of environmental parameters (Chapter 2 and 3). The relative importance of each environmental variable in accounting for the community variation was further investigated by distLM with Akaike's AIC as the selection criterion (Chapters 2 and 3). The dbRDA routine was used to visualise the relationship between the best correlative variables and the trait assemblages (Chapter 2 and 3). Biological trait distributions are presumably affected by various environmental factors related to the habitat type characteristics, PERMANOVA (9999 permutations) analysis was performed to test for the significance of environmental factors on trait distribution (Chapters 2 and 3).

4.6.4 Biozones as surrogates for functional structure

Trait modality abundance weighted scores (N_t: no. of ind. m^{-2}) and number of trait modalities (S_t: no. of trait modalities) were computed for biozone subclusters (BS), with the DIVERSE programme used to calculate Shannon-Wiener Diversity (H_t'), Margalef's Richness (d_t), and Pielou's Evenness (J_t'). Two-factor nested, non-parametric multivariate analysis of variance was used to test the hypothesis that the univariate indices differed among BS (H_5) and did not differ among sites within each BS. Two-factor PERMANOVA was used to test for the same hypothesis in the trait assemblages. Biological trait structure in BS was visualized through a principal component analysis (PCA) ordination. Permutational tests of multivariate dispersion (PERMDISP) were used with PERMANOVA analyses to test for homogeneity in average dispersion of samples from their group centroids. Taxa typifying the structure of the cluster were analysed through the SIMPER procedure. PERMDISP was used to test the hypothesis of homogeneity in average dispersion of samples based on environmental variables. Average Euclidean distance to centroid (±SD) was used to visualise differences between BS. This indicates whether samples on each BS group based on measured parameters or not.

4.7 Results

4.7.1 Taxonomic resolution

4.7.1.1 Effects of taxonomic resolution on biodiversity

Univariate comparisons of richness (d) and diversity (H') indices from different taxonomic levels (Species-Phylum) and indicator taxa are presented in Fig 4.1, and resulted in both d and H' values decreasing with increasing aggregation from Species-to-Phylum and to indicator taxon. The observed decrease with coarser taxonomic level was most strong for d and moderate for H' (Fig 4.1). Pairwise comparison showed significant drop in Order-to-Phylum taxonomic levels for both richness ($p<0.001$) and Shannon-Weiner index ($p<0.001$). Analyses of congruence in richness and diversity exhibited significant correlations between Species-to-Family taxonomic levels and indicator taxon (Polychaeta). Spearman rank correlation showed a strong correlation in richness between Species-to-Family taxonomic level ($r>0.85$, $p=0.001$) and between Genus level and the Polychaeta group ($r=0.98$, $p=0.001$). Similarly, there were strong correlation in Shannon-Weiner index between Species-to-Family and Polychaeta group ($r=0.88$, $p=0.001$).

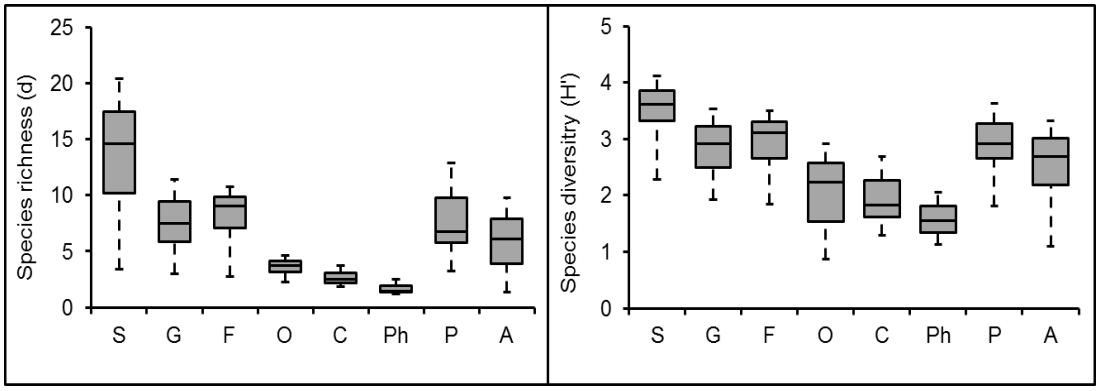

Figure 4.1. Box-and-whisker plots showing diversity indices (d and H') at various taxonomic levels and indicator taxon. Black lines within boxes represent the median, box ends show quartiles and whiskers show range. S=Species, G=Genus, F=Family, O=Order, C=Class, Ph=Phylum. Indicator taxon, P=Polychaeta A=Amphipoda at Species level.

4.7.1.2 Effects of taxonomic resolution on multivariate community patterns

Macrofaunal assemblages aggregated to higher taxonomic levels resulted in similar ordination plots, however, when taxa were aggregated to Order, Class or Phylum, the separation of stations was less apparent (Fig 4.2). High correlation was observed Genus and Family and comparable to Species, thus indicated congruence with species level. The indicator taxon 'Polychaeta' was comparable to Species assemblages, whereas 'Amphipoda' showed some differences when compared with Species-level assemblages.

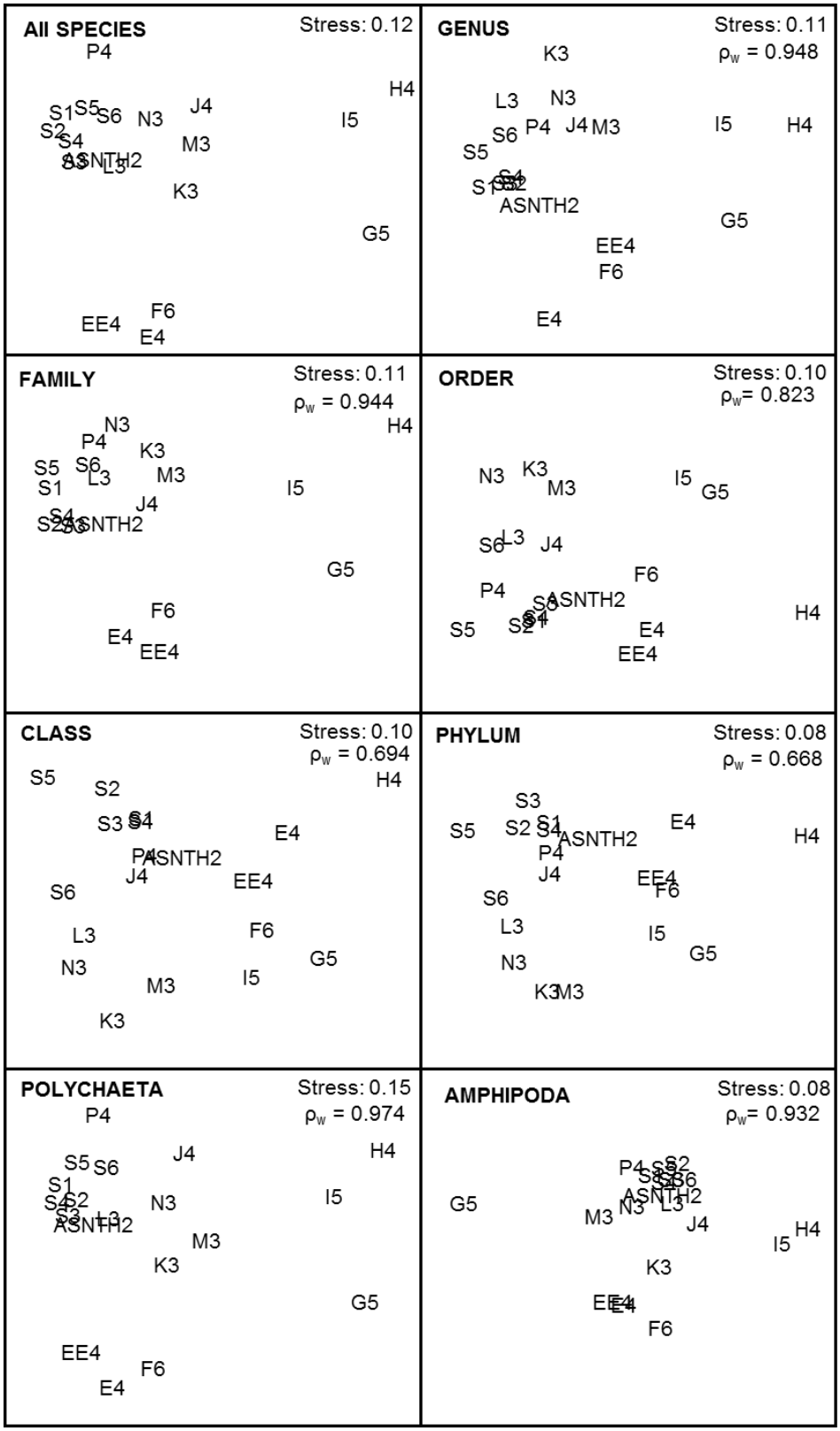

Figure 4.2. NMDS ordination plots at various taxonomic levels (Species-Order) and selected indicator groups (Polychaeta and Amphipoda) showing the efficiency of decreasing taxonomic resolution (relative to Species) at maintaining community spatial distribution across stations. Efficiency is measured by similarity of Weighted-Spearman rank correlation coefficients (ρ_w) of the coarser taxonomic levels compared with Species level.

However, a comparison of ρ_w-values indicated that a correlation between Species-level and 'Amphipoda' taxon was high (Fig 4.2). The highest correlation was observed between Species and the Polychaeta taxon (Fig 4.2). Stress values were relatively low (0.08-0.15=indicated satisfactory results) and almost constant along different taxonomic levels. Taxonomic aggregations showed a clear spatial segregation of the stations (e.g. uThukela stations (G5, H4 and I5), Port Durnford (E4, EE4 and F6)) irrespective of the taxonomic level and indicator taxon, and this reflects specific macrofaunal assemblages typical of these unique habitats.

4.7.1.3 Relationship of taxonomic level and environmental variables

Biological-Environmental matching (BIOENV) analysis indicated a combination of %mud, %medium sand on the sediment and turbidity as the variables best explaining community structuring at Species-to-Phylum taxonomic levels and selected indicator groups (Table 4.2). A significant lower correlation was observed at Order-to-Phylum taxonomic levels (Table 4.2). BEST analysis revealed the highest correlation at Species and Family levels.

Table 4.2. Spearman rank correlation coefficients (ρ) for macrobenthos and environmental variables. Macrobenthos aggregated to various taxonomic levels and selected indicator group. Asterisks denote taxonomic levels that were significantly correlated with environmental variables (p<0.001).

Resolution	ρ	Variables
Species*	0.859	Mud, Turbidity
Genus*	0.829	Mud, Turbidity
Family*	0.837	Mud, Turbidity
Order	0.751	MS, Mud, Turbidity
Class	0.633	MS, Mud, Turbidity
Phylum	0.634	MS, Mud, Turbidity
Polychaeta*	0.827	Mud, Turbidity
Amphipoda*	0.833	Mud, Turbidity

4.7.2 Biological trait analysis

4.7.2.1 Number of trait modalities (S_t) and trait abundance-weighted scores (N_t)

No significant difference was detected in abundance weighted scores amongst the stations (t=0.281, df=18, p>0.782). The mean (±SD) N_t was 18469 ± 16286 and spread amongst 883-65843 trait modalities per station, while the distribution was left skewed with the bulk of N_t lying below the median (Fig 4.3). In total, 51 trait modalities were considered, with most represented at all stations $\bar{x}$: 41±3, ranging between 33-48 trait modalities per station. Overall, no single station hosted all trait modalities.

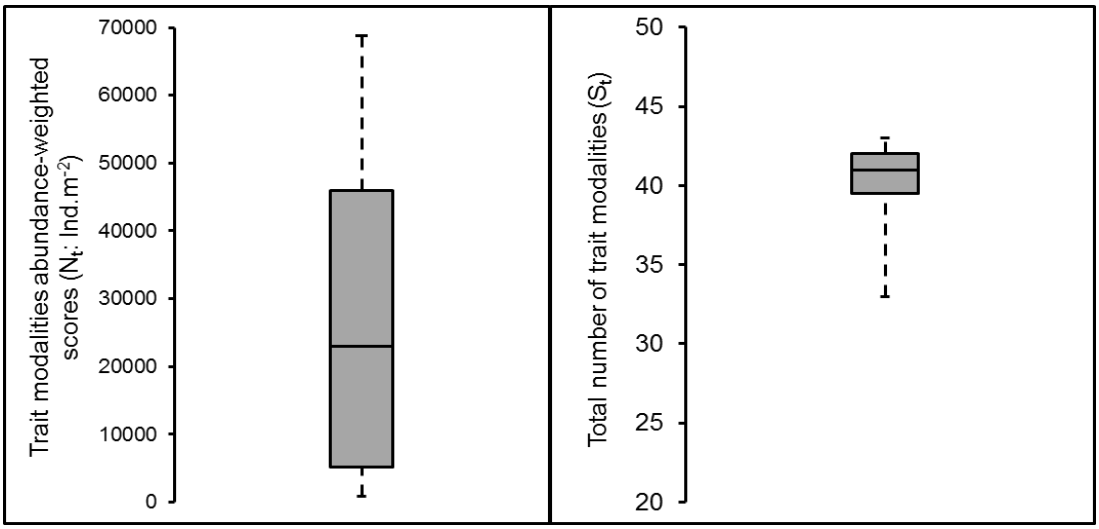

Figure 4.3. Boxplots of trait modalities abundance-weighted scores (N_t) and number of trait modalities (S_t) for macrobenthos sampled along the KwaZulu-Natal mid-shelf. Black lines within boxes represent the median.

4.7.3 Biological trait modality distribution

Trait modalities differed between the sampled stations and in their spatial distribution (Fig 4.4 a-e; 4.5 a-d). Overall, hard exoskeleton fauna (BDHE) dominated at most sampled stations and were recorded in high numbers at S2 and S5, while soft-bodied (BDS) fauna formed the second dominant group with hard shell (BDHS) fauna being rare in most stations (Fig 4.4 a). These fauna were generally moderately mobile (MMSM) to sessile (MMSe) with burrowing (MMBu) behaviours (Fig 4.4 b). There was a dominance of brooders (RTSB-MA) with direct larval development compared with broadcast spawners with forms producing early stage larvae (RTSB-PL) (Fig 4.4 c, e). The reproductive mode was mainly gonochoric (separate sexes-SDG) (Fig 4.4 d). Surface deposit (FDSDF) and filter/suspension (FDF/SD) feeding methods were generally the dominant feeding types, while predation (FDP) and scavenging (FDSc) feeding methods were also common at most sample stations.Overall, feeding types were more heterogeneous amongst stations (Fig 4.5 b). The diet preference trait was dominated by omnivores (DPO), which constituted the highest proportion within the individual stations, while carnivores (DPC) contributed the second dominant modality within stations. Herbivorous (DPH) and detrital (DPD) diets were rare in most sampled stations (Fig 4.5 a). However, it should be noted that where detrital diets were present, corresponded to the stations where facultative feeders (capable of switching between feeding methods with changing food resources) were also present. Living habitats were mainly tube dwelling (LHTD) and burrowing (LHPB) forms, which consequently contributed to bioturbation activities (HES-A/R) and habitat provision for other species (HEFS and HEFS/A) (Fig 4.5 c-d).

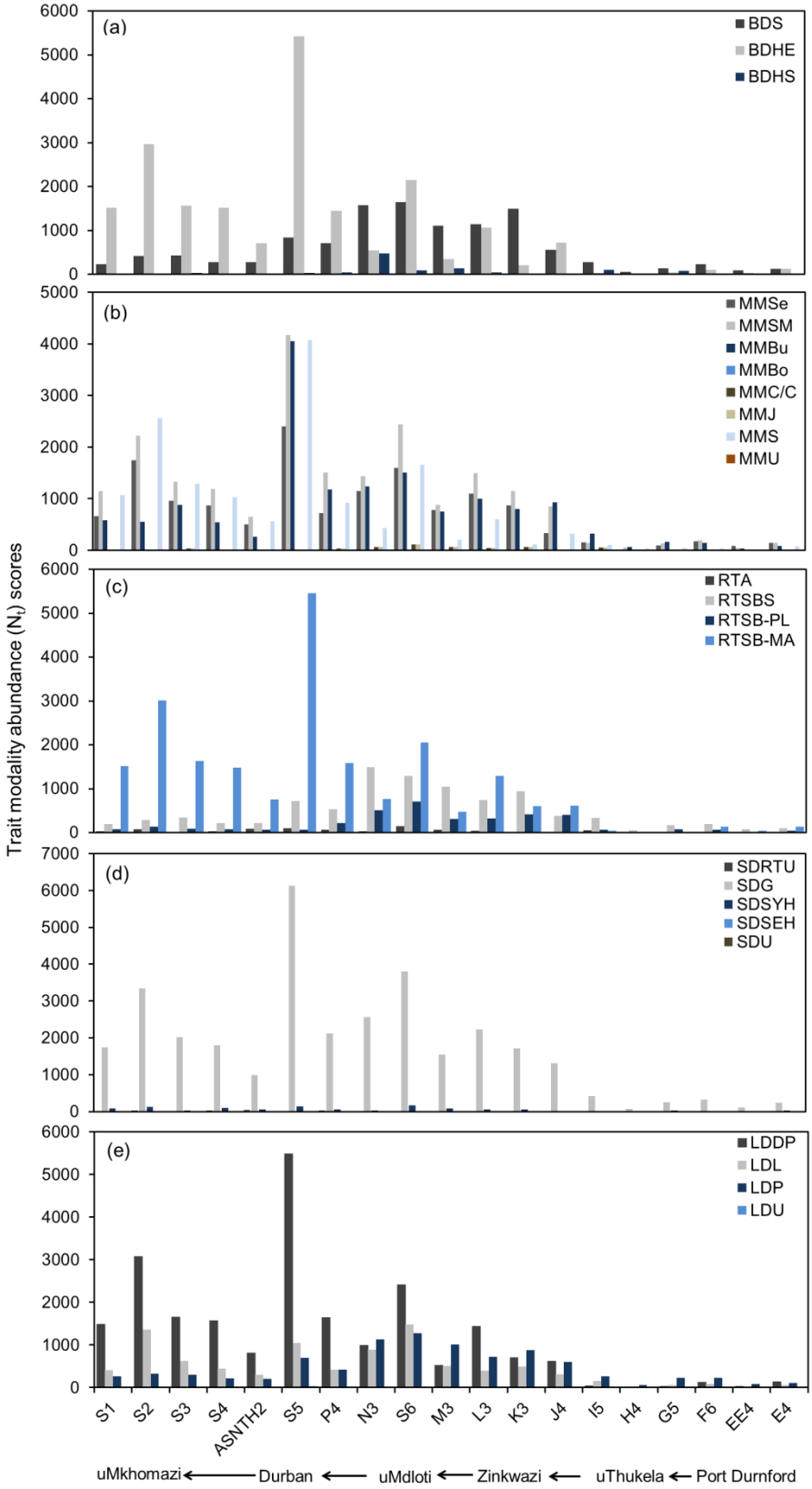

Figure 4.4. Distribution of abundance-weighted modality scores of benthic faunal assemblages across sampling station in KZN mid-shelf: (a) body design, (b) movement method, (c) reproduction technique, (d) sexual differentiation, and (e) larval development. Main cities and coastal systems from north to south (Port Durnford-uMkhomazi). For explanation of modality codes refer to Table 4.1.

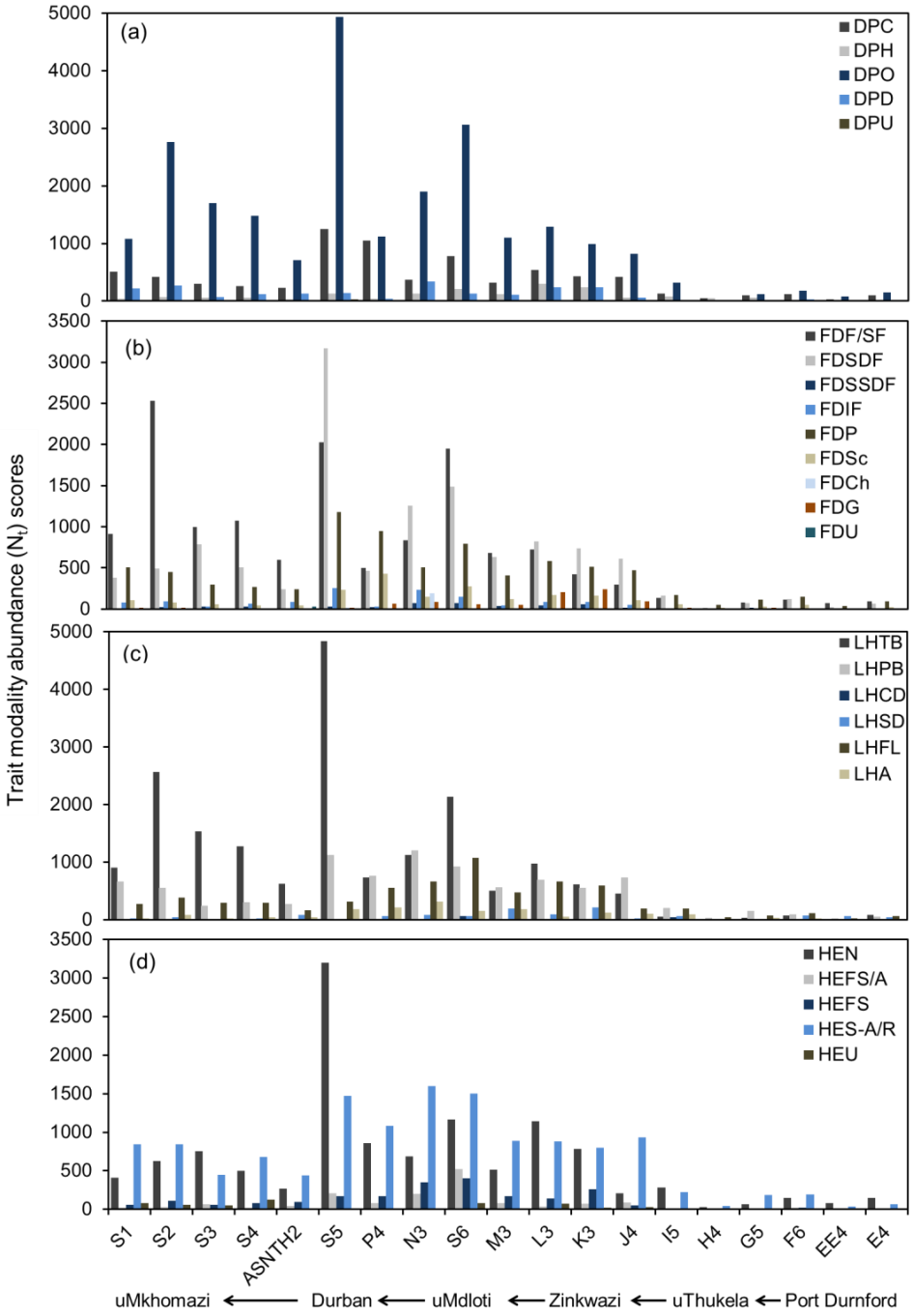

Figure 4.5. Distribution of abundance-weighted modality scores of benthic faunal assemblages across sampling station in the KwaZulu-Natal mid-shelf environment: (a) diet preference, (b) feeding mode, (c) living habit, (d) habitat engineering. Main cities and coastal systems from north to south (Port Durnford-uMkhomazi). For explanation of modality codes refer to Table 4.1.

4.7.4 Community patterns based on biological trait along KZN mid-shelf

Non-metric MSD ordination based on Bray-Curtis (B-C) similarity using biological traits identified four sample groups at 70% percentage reflecting geographical differences in traitscapes (Fig 4.6). The similarity amongst stations within sample groups ranged between 78-94%. Overall similarity percentage was high, and sample groups shared >70% of similarity resemblance (Fig 4.6). Group I comprised two stations (H4 off the uThukela and EE4 off Port

Durnford) represented habitat that hosted the lowest number of trait modalities and abundance-weighted scores. Group II comprised other samples off the uThukela and Port Durnford that also represented low number of trait modalities and abundance-weighted scores. Group III comprised of larger number of samples and together with Group IV consisted of stations from Zinkwazi to uMkhomazi, and represented high number of trait modalities and abundance-weighted scores. A series of Similarity Profile (SIMPROF) permutation tests confirmed the statistical significance (p=0.05) of sample Groups I-IV, obtained from cluster analysis (Clarke et al. 2008).

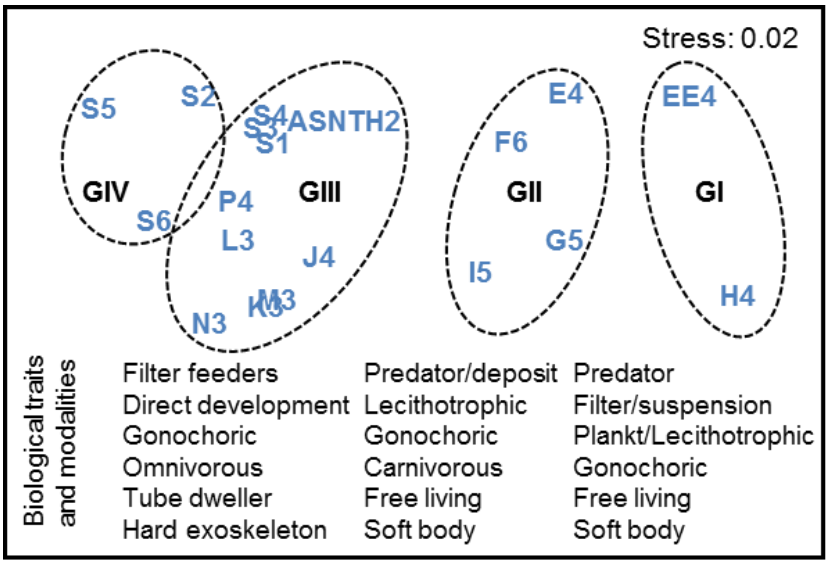

Figure 4.6. NMDS ordination plots of biological trait assemblages of macrobenthos per station. Dashed line indicates samples grouped at 70% Bray-Curtis similarity. GI-IV=Sample groups. For explanation of modality codes refer to Table 4.1.

4.7.5 Components of diversity

Univariate measures differed between sample groups (p-perm<0.001). Macrobenthic trait weighted abundance (N_t) and the number of traits (S_t) were highest in Group IV (N_t: 47424±16314, St: 43±1.15), while Margalef's Richness (d_t) was highest in Group I (d_t: 4.82±0.14) (Table 4.3). Pielou's Evenness (J'_t) was high in Group I and II (J'_t: 0.89±0.02, 0.89±0.01) and Shannon-Weiner diversity (H'_t) was high in Group II (H'_t: 3.26±0.02). Lowest number of traits and weighted abundance values were recorded for samples comprising Group I (EE4 and H4) as well as Margalef's Richness, Pielou's Evenness, and Shannon-Weiner diversity index for samples comprising Group IV (E4, F6, G5 and I4) (Table 4.3).

Table 4.3. Univariate measures of diversity (±SD) calculated from trait weighted abundance for sample groups I-IV defined in cluster analysis.

Indices	Sample groups			
(Trait-weighted abundance)	i	ii	iii	iv
No. of traits (S_t)	35±2.12	39±1.50	42±2.24	43±1.15
Abundance (N_t)	1052±239	3462±1025	19267±4827	47424±16314
Margalef's Richness (d_t)	4.82±0.15	4.18±0.26	4.18±0.31	3.88±0.03
Pielou's Evenness (J'_t)	0.89±0.02	0.89±0.01	0.85±0.02	0.81±0.04
Shannon-Weiner Diversity (H'_t)	3.18±0.01	3.26±0.02	3.19±0.09	3.06±0.16

4.7.6 Trait characterising sample groups

The main trait modalities responsible for characterising and discriminating between sample Groups I-IV obtained from cluster analysis were determined by SIMPER (Table 4.4; 4.5). Sample groups were dominated and characterised by gonochoristic differentiation (separate sexes: SDG), which further contributed to the (dis)similarity between the sample groups (Table 4.4).

Group I, comprising the smallest number of samples was also dominated by soft-bodied (BDS) broadcast spawners (RTSBS) with planktotrophic larvae (RTSB, LDP). The latter was found exclusively in this group and together with semi-mobile movement method (MMSM) and predatory feeding method contributed >4% to within group similarity (85.23%) and were identified as being characteristic of Group I (Table 4.4). Soft bodied (BDS) omnivores (DPO) dominated group II and contributed >4% to within group similarity (73.39%). Surface dwellers (LHFL) found exclusively here, together with additional six-trait modalities typified group II (Table 4.4). Pairwise comparison (Ave. Dissimilarity >65%) revealed semi-motile (MMSM) omnivores (DPO) to contribute >4% dissimilarity between group II, and III-IV (Table 4.5). Group III, comprising the largest number of samples was dominated by semi-motile (MMSM) omnivores (DPO). These further contributed >4% to within group III similarity (73.62%) and together with seven other trait modalities were identified as characteristic of this group (Table 4.4). Hard exoskeleton (BDHE) omnivorous (DPO) filter/suspension feeders (FDF/SF) were found in greater abundances in group IV. These tube dwelling (LHTB) brooders (RTSB-MA) with direct larval development (LDDP) resulted in the formation of shelter (HEFS) for other species as reflected by the presence of semi-mobile fauna (MMSM) and altogether contributed >4% to within group similarity (71.23%). These, including permanent burrowers, typified this group (Table 4.4). SIMPER results showed that no trait modality contributed >4% to the dissimilarity between groups III and IV (Table 4.5).

Table 4.4. Characterization of the four (I-IV) traitscapes defined by cluster analysis, showing trait modality contributing to average 'within group' abundance defined by sim/SD ratio based on one-way SIMPER analysis of square-root transformed trait weighted abundance data. Trait modalities accounting for 90% cumulative contribution of the 'within group' similarity are listed along with their contribution (Contr.%). Text in bold indicates trait modalities contributing >4% mean similarity. Text in grey shading indicates trait modalities typifying sample group. Sim=Similarity, SD=Standard deviation, Mean Sim=Similarity percentage and G=group. For explanation of modality codes refer to Table 4.1.

Traits	x̄ abun.	x̄ sim.	Sim/SD	Contr.	x̄ abun.	x̄ sim.	Sim/SD	Contr.	x̄ abun.	x̄ sim.	Sim/SD	Contr.	x̄ abun.	x̄ sim.	Sim/SD	Contr.
Modalities	**Mean Sim GI = 76.26%**				**Mean Sim GII = 73.39%**				**Mean Sim GIII =73.62%**				**Mean Sim GIV = 71.23%**			
RTSB-PL	16.67	1.46	23.78	1.91	-	-	-	-	-	-	-	-	-	-	-	-
BDS	**74.00**	**6.14**	**15.08**	**8.05**	**194.00**	**4.20**	**5.47**	**5.73**	-	-	-	-	-	-	-	-
RTSBS	**64.67**	**5.34**	**14.24**	**7.00**	-	-	-	-	-	-	-	-	-	-	-	-
FDSDF	18.67	1.52	12.23	1.99	104.75	2.17	5.42	2.95	644.69	2.48	3.28	3.37	-	-	-	-
LDP	**72.00**	**5.82**	**11.49**	**7.63**	-	-	-	-	-	-	-	-	-	-	-	-
SDG	**92.00**	**7.28**	**9.61**	**9.55**	**307.75**	**7.54**	**8.15**	**10.28**	**1802.94**	**7.91**	**7.60**	**10.74**	**4427.11**	**7.50**	**6.71**	**10.53**
BDHE	22.00	1.70	8.05	2.23	-	-	-	-	-	-	-	-	-	-	-	-
MMSM	**46.67**	**4.21**	**7.63**	**5.52**	150.42	3.98	6.45	5.42	**1162.20**	**5.09**	**6.82**	**6.91**	**2945.78**	**4.92**	**6.41**	**6.91**
HES-A/R	41.33	3.62	6.25	4.75	-	-	-	-	859.74	3.53	3.66	4.80	-	-	-	-
FDP	**47.33**	**4.07**	**5.61**	**5.34**	132.58	3.24	8.02	4.42	475.24	1.89	3.66	2.57	-	-	-	-
DPC	-	-	-	-	112.67	2.98	8.28	4.06	442.50	1.69	4.15	2.30	-	-	-	-
LDL	-	-	-	-	90.83	1.94	8.12	2.64	481.29	2.03	7.02	2.76	-	-	-	-
FDF/SF	-	-	-	-	105.25	2.57	7.64	3.50	-	-	-	-	**2168.00**	**4.25**	**5.56**	**5.97**
DPO	-	-	-	-	**193.00**	**4.13**	**7.32**	**5.62**	**1220.12**	**5.17**	**6.86**	**7.02**	**3588.00**	**6.14**	**6.48**	**8.62**
LHFL	-	-	-	-	112.08	2.15	5.54	2.92	-	-	-	-	-	-	-	-
MMSe	-	-	-	-	-	-	-	-	793.06	3.30	4.09	4.48	1912.00	3.53	5.86	4.96
LHTB	-	-	-	-	-	-	-	-	873.08	3.44	3.95	4.67	**3176.00**	**4.88**	**5.91**	**6.85**
LDDP	-	-	-	-	-	-	-	-	-	-	-	-	**3660.44**	**5.64**	**5.63**	**7.92**
BDHE	-	-	-	-	-	-	-	-	-	-	-	-	**3511.56**	**5.17**	**5.03**	**7.26**
RTSB-MA	-	-	-	-	-	-	-	-	-	-	-	-	**3506.22**	**5.05**	**4.53**	**7.10**
LHPB	-	-	-	-	-	-	-	-	-	-	-	-	862.22	1.41	4.51	1.98

Table 4.5. Results from SIMPER analysis of trait weighted abundance data, listing the main discerning trait modalities revealed by pairwise comparison to contribute to 'between group' dissimilarity (I-IV). Text in bold indicates trait modalities contributing >3% mean dissimilarity. Dis=Dissimilarity, SD=Standard deviation. Mean Dissim=Dissimilarity percentage, G=group. For explanation of modality codes refer to Table 4.1.

Traits	x̄ abun.I	x̄ abun. II	x̄ dis.	Dis/SD	Contr.	x̄ abun.I	x̄ abun. III	x̄ dis.	Dis/SD	Contr.	x̄ abun.I	x̄ abun. IV	x̄ dis.	Dis/SD	Contr.
Modalities	**Mean Dissim G I-II = 53.08%**					**Mean Dissim G I-III = 89.18%**					**Mean Dissim G I-IV =95.41%**				
DPC	38.00	112.67	1.65	10.26	3.11	-	-	-	-	-	-	-	-	-	-
SDG	**92.00**	**307.75**	**4.69**	**5.49**	**8.83**	**92.00**	**1802.94**	**8.36**	**20.72**	**9.37**	**92.00**	**4427.11**	**8.94**	**44.55**	**9.37**
FDP	47.33	132.58	1.84	5.42	3.47	-	-	-	-	-	-	-	-	-	-
MMSM	46.67	150.42	2.35	4.09	4.43	**46.67**	**1162.20**	**5.46**	**11.29**	**6.13**	**46.67**	**2945.78**	**5.95**	**23.58**	**6.23**
FDSDF	18.67	104.75	1.81	3.23	3.41	-	-	-	-	-	-	-	-	-	-
DPO	-	-	-	-	-	**48.67**	**1220.12**	**5.74**	**5.75**	**6.43**	**48.67**	**3588.00**	**7.32**	**31.69**	**7.67**
LDL	-	-	-	-	-	17.33	481.29	2.27	4.90	2.55	-	-	-	-	-
MMSe	-	-	-	-	-	52.67	793.06	3.60	4.75	4.03	52.67	1912.00	3.95	6.61	4.14
LHPB	-	-	-	-	-	-	-	-	-	-	23.33	862.22	1.73	6.09	1.82
Traits	x̄ abun.II	x̄ abun. III	x̄ dis.	Dis/SD	Contr.	x̄ abun.II	x̄ abun. IV	x̄ dis.	Dis/SD	Contr.	x̄ abun.III	x̄ abun. IV	x̄ dis.	Dis/SD	Contr.
Modalities	**Mean Dissim G II-III = 69.40%**					**Mean Dissim G II-IV = 85.86%**					**Mean Dissim G III-IV =45.44%**				
SDG	**307.75**	**1802.94**	**6.47**	**7.04**	**9.32**	**307.75**	**4427.11**	**8.04**	**19.12**	**9.36**	1802.94	4427.11	3.81	2.79	8.39
MMSM	**150.42**	**1162.20**	**4.39**	**7.30**	**6.33**	**150.42**	**2945.78**	**5.43**	**16.37**	**6.33**	1162.20	2945.78	2.58	2.70	5.67
DPO	**193.00**	**1220.12**	**4.46**	**4.08**	**6.43**	**193.00**	**3588.00**	**6.65**	**18.62**	**7.74**	1220.12	3588.00	3.47	3.36	7.63
LDL	90.83	481.29	1.69	3.38	2.44	-	-	-	-	-	-	-	-	-	-
MMSe	141.00	793.06	2.80	3.74	4.04	141.00	1912.00	3.56	7.22	4.15	793.06	1912.00	1.69	3.00	3.71
LHTB	-	-	-	-	-	**60.00**	**3176.00**	**6.01**	**5.66**	**7.00**	873.08	3176.00	3.32	2.58	7.30

4.7.7 Biological trait structure-environmental relationship

Biological-Environmental matching (BIOENV) analysis showed that turbidity and temperature contributed to trait structuring (rho=0.646). Marginal tests from distLM showed an additional five variables that were important in explaining variation in the biological trait structure as evidenced by the p-values <0.05 (Table 4.6). The most noteworthy variable (49.0% variation) was turbidity followed by TOC (32.2%) and dissolved oxygen (30.0%) (Table 4.6). The fitted model showed that gravel and very coarse sand added significantly to explain variation in trait structure and together with turbidity explained 64.6% of the total variation (Table 4.6).

Table 4.6. DistLM results (marginal and sequential tests) describing the relationship between KZN mid-shelf trait structures and environmental variables. AIC=Akaike's Information Criterion: a measure of the relative quality of model for a given set of environmental variables. Asterisks denote statistical significance *<0.05, **<0.01, ***<0.001.

Variables	MARGINAL TESTS		
	Prop.	Pseu-F	P-Perm
	Sediment		
%Mud (>4.0 ϕ)	0.222	4.853	0.020*
Median(phi)	0.182	3.786	0.044*
%Total organic carbon (TOC)	0.322	8.083	0.003**
% Sediment Carbonates	0.204	4.355	0.031*
	Water column		
Dissolved Oxygen (mg.l^{-1})	0.300	7.287	0.004**
Chlorophyll-a (mg.m^{-3})	0.229	5.060	0.021*
Turbidity (NTU)	0.490	16.304	0.0001***
	SEQUENTIAL TESTS		
	AICC	Prop.	Pseu-F	P-Perm
+Turbidity (NTU)	117.30	0.489	16.304	0.000***
+%Very coarse sand (-0.1-0.0 ϕ)	116.90	0.080	2.976	0.047*
+%Gravel (<-0.1 ϕ)	116.47	0.076	3.213	0.034*
	AICC=116.47		Cum=0.645	

The full model was visualised on the dbRDA plot (Figure 4.7) and indicated traitscape relative to environmental conditions along the KZN mid-shelf. The first two axes together explained >85% of the variability in trait structure. The first RDA axis separated stations in the shelf area between Durban and Mkomaas by higher percentage of positively skewed fine sand and carbonates and hosted a diverse traitscape. Conversely, the remaining Port Durnford and the uThukela stations were separated on higher bottom water chlorophyll-a (µg.l^{-1}), DO (ml l^{-1}), turbidity (NTU) and TOC (%) (Fig 4.7a). On RDA2, stations of groups I and IV were separated from groups II and III based on the distribution of mud and gravel, respectively (Fig 4.7a). In terms of trait modality suggestive of these conditions, tube dwelling omnivorous filter/suspension feeders with a hard exoskeleton prefer coarse substrates as found in Durban and uMkhomazi. In contrast, soft-bodied carnivores prefer fine sediment, whereas sessile, attached and surface dwelling forms prefer habitats high in mud, TOC and turbidity (Fig 4.7b).

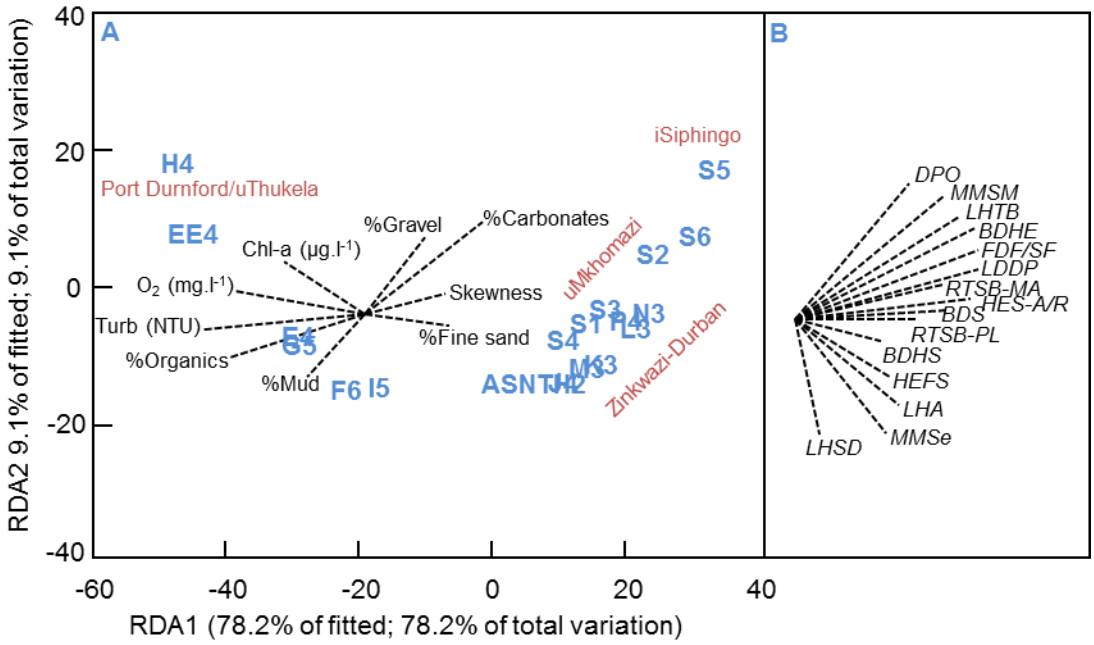

Figure 4.7. Distance-Based redundancy analysis (db-RDA) of KZN mid-shelf biological trait data using a stepwise selection and AICc selection criterion. (A) db-RDA-axes with main habitat/area and (B) vector overlay of Spearman rank correlations of environmental variables (r>0.5) and vectors of the most correlated species (r>0.5) are provided. Chl-a=chlorophyll-a, DO= dissolved oxygen and Turb=turbidity. Main cities and coastal systems from north to south (Port Durnford-uMkhomazi) highlighted in brown. For explanation of modality codes refer to Table 4.1.

4.8 Biozones units as surrogates – basic differences in trait structures

4.8.1 Traits (S_t) and Abundance-weighted (N_t) within biozone subclusters

The univariate measures of biological trait structure detected significant differences between all biozone cluster. The trait modality abundance-weighted scores also differed between biozone subclusters (BS) (df=5, Pseudo-F=8.97, p-perm=0.01). The mean (N_t±SD) trait modality abundance-weighted scores recorded for each BS varied from 2 490±1 223 in BS 1C to 31 829±29 709 trait modalities per station in BS 2A (Fig 4.8). Significant differences were also observed between BS 1 (A-C: df=1, Pseudo-F=15.1, p-perm=0.001) and BS 2 (A-B: df=1, Pseudo-F=12.9, p-perm=0.004). Subcluster 2A was characterised by a high variability in trait modality (Fig 4.8).The number of trait modalities across subclusters were also significantly different (df=5, Pseudo-F=4.81, p-perm=0.01). A significant relationship was also observed between SC in BS 1 (A-C: df=1, Pseudo-F=2 691, p-perm=<0.001) and in subcluster 2 (A-B: df=1, Pseudo-F=1457, p-perm=<0.001). The mean number of trait modalities (S_t±SD) ranged between 36±2.64 in SC 3A to 44±1.15 trait modalities in SC 2A (Fig 4.8). In total, 51 trait modalities were used in the present study, and no subcluster hosted all trait modalities.

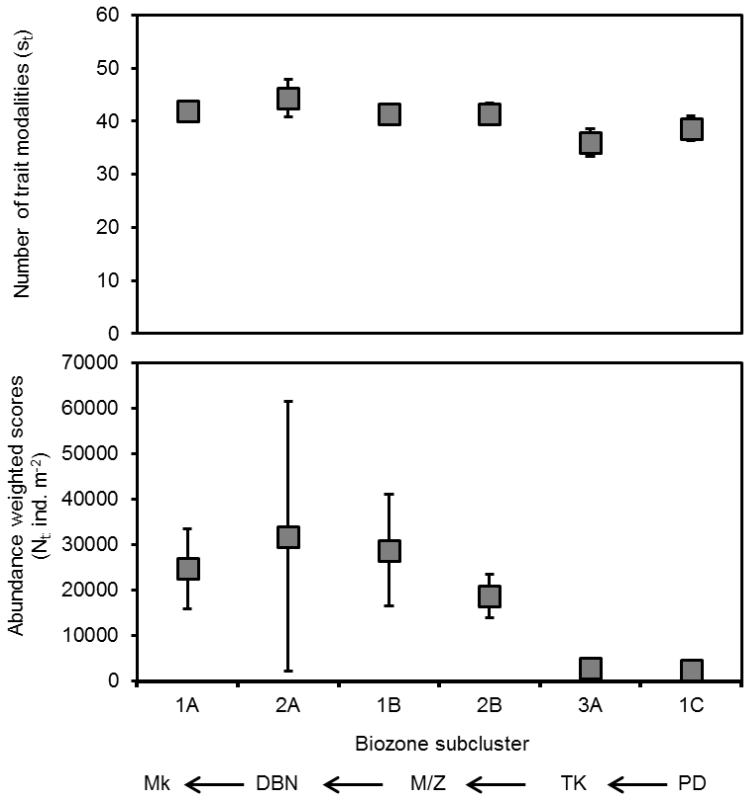

Figure 4.8. Mean biological trait abundance-weighted scores (N_t: ind.m^{-2} ± SD) and mean number of trait modalities (S_t±SD) per biozone subcluster. PD=Port Durnford, TK=uThukela, T/Z= uMdloti/Zinkwazi, DBN=Durban, Mk=uMkhomazi.

4.8.2 Biological trait Richness (d_t) and Diversity (H'_t) within biozones

Trait modality richness (d_t) was comparable between BS (Table 4.7, Fig 4.9), as most trait modalities were expressed in all BS and significant differences were only detected between BS 1 (A-C) and 2 (A-B) (Table 4.7). Trait diversity also exhibited a monotonic trend between BS (Figure 4.10). However, significant differences were detected between BS ($p<0.05$, Table 4.7) and within BS 1 (A-C) and 2 (A-B) (Table 4.7).

Table 4.7. Two-way PERMANOVA test on univariate measures of biological traits. Df= Degree of freedom, Pseudo-F=critical values of PERMANOVA, and *p*=level of statistical difference. Asterisks denote statistical significance *<0.05, **<0.01, ***<0.001.

PERMANOVA	Richness (d)			Diversity (H')		
Factors (nested design)						
	df	Pseudo-F	P-Perm	df	Pseudo-F	P-Perm
Subclusters	5	4.519	0.010	5	5.603	0.005**
Cluster	2	1.923	0.199	2	0.307	0.739
Residual	38			38		
1A-C	2	50.050	0.001***	2	16.480	0.001***
2A-B	1	122.900	0.001***	1	71.950	0.001***

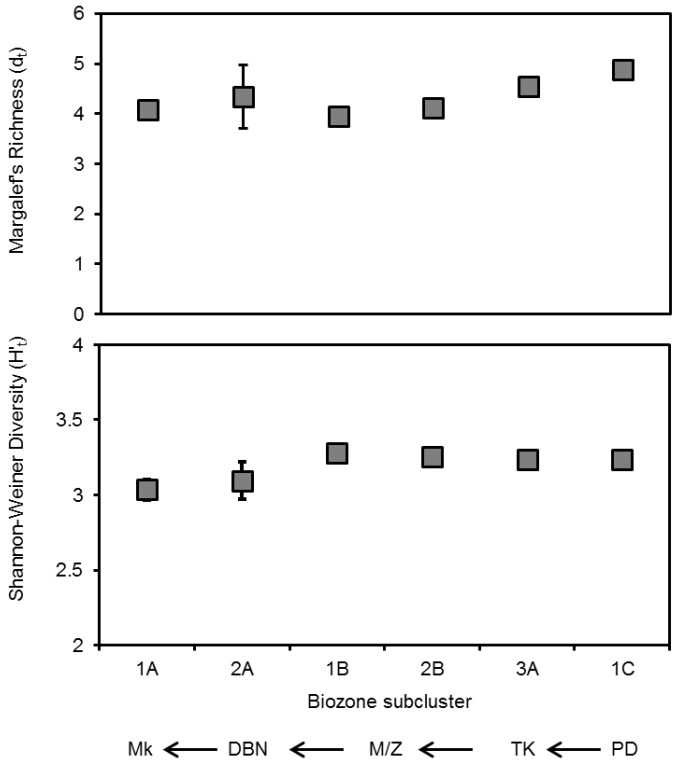

Figure 4.9. Mean biological trait Richness (d_t±SD) and Diversity (H'_t±SD) per biozone subcluster. PD=Port Durnford, TK=uThukela, M/Z=uMdloti/Zinkwazi, DBN=Durban, Mk=uMkhomazi.

4.8.3 Biological traits patterns within biozones

In agreement with the univariate analyses, biozone subclusters (BS) as surrogates for macrobenthic traits reflected a different trait structure (Table 4.8). Pairwise comparisons revealed that differences were between pairs of BS 2A and 3A (t=3.146, p-perm=0.026) and 2A and 1C (t=3.659, p-perm =0.028). Visually, there was no structuring of traits based on biozone classification, since there was no distinct grouping of stations from the same BS (Fig 4.10). Biozone subcluster 1A and 2A as well as 1B and 2B were similar (Fig 4.10), and pairwise comparisons revealed no significant differences (t=0.542, p-perm=0.800; t=1.280, p-perm=0.303). Trait assemblages in BS 1C were significantly different from assemblages in both BS 1A and 1B, but was most similar to BS 3A (Table 4.8, Fig 4.10).

PERMDISP analyses results are presented by *P*-values (>0.05) in Table 4.9. The dispersion of samples was homogenous between and within biozone subclusters. Despite this, the different outcomes of the PERMANOVA analysis regarding the fit of predefined biozones justified a more thorough examination of the role of within-subcluster variability for defining biozones as surrogates. Therefore, these results did not support KZN marine spatial planning, as trait structure did not group according to the predefined biozones and variability was among BS. Sample grouping did not match predefined biozone model.

Table 4.8. PERMANOVA results for functional measures of biozone subclusters differences. F=critical values of PERMANOVA, and *p*=level of statistical difference. Asterisks denote statistical significance *<0.05, **<0.01, ***<0.001.

PERMANOVA	df	Pseudo-F	p-perm
Factors (nested design)			
Subclusters	5	8.011	0.001***
Biozones	2	1.194	0.388
Residual	13		
Biozone 1 subclusters			
1A, 1B and 1C	2	17.056	0.002**
Residual	6		
Biozone 2 subclusters			
2A and 2B	1	1.276	0.279
Residual	5		
Components of variation			
Source		Estimates	X^2
Biozones		66	8.140
Subclusters		551	23.471

The similarity level on which any grouping in the functional structure could reflect predefined biozones was a Bray-Curtis similarity level of 50-65 % (e.g. Table 4.10). At this level, two subclusters can be distinguished (1C and 3A). At a lower similarity level, the functional structure was sufficiently homogenous and could not identify any subcluster as a separate unit.

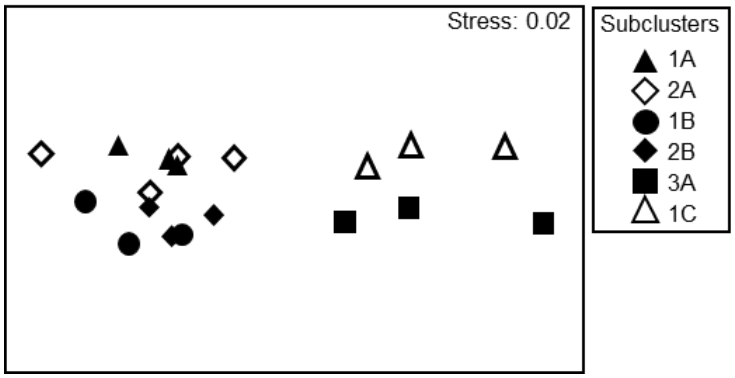

Figure 4.10. NMDS of macrobenthic trait structure, with biozone subcluster as a factor. Each point represents the trait structure at a given station.

4.8.4 Traits characterising biozones

SIMPER analysis based on biozone groups revealed trait modalities that contributed to dis(similarity) between and within biozone subclusters. Trait modalities that drove similarity were predominantly associated with reproduction, feeding and movement methods. These included gonochoristic differentiation (separate sexes), the highest abundances of which were found in BS 1A and 2A. This trait modality consistently contributed >4% to within BS 1A, 2A, 2B and 1C similarity (Table 4.10). Sessile movement method (MMSe) comperable found in 1A, 2A and 1B contributed to the similarity between these BS (Table 4.10). Filter/suspension

feeders (FDF/SF) recorded the highest abundances in BS 1 (A and B), also contributed to the similarity between BS 1 (A, B and C) and 2B (Table 4.10). A carnivorous (DPC) and herbivorous (DPH) diet preference and scavenging (FDSc) feeding method unique to BS 3A, as well as shell dwellers (LHSH) and burrowers (MMBu) unique to BS 1C distinguished these BS (Table 4.10). The between BS differences observed in PERMANOVA results were further confirmed by the high average dissimilarity observed between BS in post hoc tests (Tables 4.10). Differences within clusters were further supported by the high Bray-Curtis dissimilarities between the subclusters belonging to a particular biozones (e.g. biozone 1 (A-C)) (Table 4.10).

Table 4.9. PERMDISP results between biozone subclusters. Df=degree of freedom, F=critical values of ANOVA, and *p*=level of statistical difference. Asterisks denote statistical significance *<0.05, **<0.01, ***<0.001.

PERMDISP	df	Pseudo-F	p-perm
Deviation from centroids			
Subclusters	5	1.582	0.722
Subcluster (Cluster 1)			
1A, 1B and 1C	2	1.107	0.677
Subcluster (Cluster 2)			
2A and 2B	1	2.622	0.259

4.9 Discussion

Aspects of this study contribute to an improved understanding of the KZN mid-shelf macrobenthic community and therefore the contribution to ecosystem functioning. By describing the taxonomic and biological trait structure of shallow marine macrobenthic assemblages, and comparing the results obtained using these different approaches, this study has highlighted the importance of KZN shelf spatial gradients in driving the distribution of taxonomic and functional attributes. Surrogate studies have focused mainly on the efficient conservation of taxonomic diversity (e.g. Heap et al. 2011, Przeslawski et al. 2011, Dixon-Bridges et al. 2014), with only a few that have considered functional attributes (e.g. Törnroos et al. 2013). The main aim of this chapter was to broaden this knowledge and assess to what extent KZN marine spatial planning predefined biozones could efficiently capture functional structures (through biological traits) of macrobenthic communities. To address the most relevant results from the analysis of KZN mid-shelf macrobenthic fauna, discussion of the findings is structured according to this chapter's hypotheses and the main research questions initially posed (Chapter 2).

Table 4.10. Traits identified by SIMPER analysis as contributing to the average (dis)similarity within biozone clusters. Text in bold indicates trait modalities contributing >4% to within subclusters similarity. Text in grey shading indicates characteristic trait modality. Mean dissimilarities from pairwise comparison presented below.

Traits Modalities	x̄ abun.	x̄ sim.	Sim/SD	Contr.	x̄ abun.	x̄ sim.	Sim/SD	Contr.	x̄ abun.	x̄ sim.	Sim/SD	Contr.	x̄ abun.	x̄ sim.	Sim/SD	Contr.	x̄ abun.	x̄ sim.	Sim/SD	Contr.	x̄ abun.	x̄ sim.	Sim/SD	Contr.
	Mean Sim SB 1A = 74.66%				**Mean Sim SB 2A = 55.94%**				**Mean Sim SB 1B = 69.29%**				**Mean Sim SB 2B = 77.51%**				**Mean Sim SB 3A = 50.28%**				**Mean Sim SB 1C = 65.05%**			
FDSDF	553.16	1.71	6.71	2.29	-	-	-	-	-	-	-	-	725.78	3.51	14.63	4.53	-	-	-	-	-	-	-	-
MMS	**1639.81**	**4.70**	**6.61**	**6.29**	1644.63	2.90	2.61	5.19	-	-	-	-	-	-	-	-	59.11	1.35	3.24	2.68	-	-	-	-
SDG	**2372.93**	**7.56**	**6.42**	**10.13**	**2756.98**	**5.46**	**2.61**	**9.76**	-	-	-	-	**1751.56**	**7.74**	**12.71**	**9.99**	-	-	-	-	**227.56**	**6.15**	**4.05**	**9.60**
MMSM	**1561.92**	**4.96**	**6.35**	**6.65**	1881.07	3.64	2.65	6.51	-	-	-	-	**1164.00**	**5.06**	**11.03**	**6.53**	106.78	2.66	3.18	5.30	-	-	-	-
LDDP	**2073.49**	**6.36**	**6.09**	**8.52**	-	-	-	-	-	-	-	-	918.67	3.47	13.30	4.48	30.89	0.76	4.38	1.51	-	-	-	-
MMSe	1122.52	3.10	5.99	4.15	1119.10	2.45	2.66	4.39	1172.89	3.15	7.16	4.54	-	-	-	-	-	-	-	-	**135.56**	**4.28**	**6.70**	**6.68**
FDF/SF	1479.39	3.89	5.82	5.21	-	-	-	-	1155.56	2.59	6.61	3.73	481.33	1.81	9.06	2.33	-	-	-	-	92.00	3.13	7.01	4.88
RTSB-MA	**2052.49**	**6.43**	**5.72**	**8.61**	-	-	-	-	1096.89	1.98	6.15	2.86	-	-	-	-	-	-	-	-	-	-	-	-
LDL	795.51	1.94	5.17	2.6	-	-	-	-	-	-	-	-	402.22	1.84	14.07	2.37	-	-	-	-	-	-	-	-
BDHE	**2016.51**	**6.35**	**5.33**	**8.50**	-	-	-	-	1013.33	1.43	6.36	2.06	-	-	-	-	33.00	0.82	3.45	1.63	-	-	-	-
HES-A/R	-	-	-	-	918.96	2.34	2.88	4.19	-	-	-	-	-	-	-	-	-	-	-	-	96.00	1.79	6.40	2.80
DPO	-	-	-	-	2061.49	3.71	2.75	6.63	-	-	-	-	1034.22	4.72	14.62	6.09	-	-	-	-	136.44	3.96	4.75	6.18
LHTB	-	-	-	-	1865.00	2.94	2.73	5.25	892	2.36	6.02	3.4	679.11	2.69	10.50	3.48	-	-	-	-	-	-	-	-
RTSBS	-	-	-	-	421.45	1.01	2.60	1.80	1274.22	3.99	6.64	5.75	-	-	-	-	-	-	-	-	124.00	3.46	6.67	5.41
LHFL	-	-	-	-	-	-	-	-	736.44	1.88	7.43	2.72	-	-	-	-	105.89	2.02	4.52	4.02	-	-	-	-
BDS	-	-	-	-	-	-	-	-	**1446.67**	**4.44**	**7.40**	**6.40**	-	-	-	-	160.00	2.99	3.82	5.94	**148.00**	**4.06**	**7.88**	**6.35**
FDP	-	-	-	-	-	-	-	-	569.33	1.56	6.69	2.26	525.33	2.63	10.90	3.39	113.67	2.67	4.09	5.30	-	-	-	-
RTSB-PL	-	-	-	-	-	-	-	-	513.33	1.32	6.03	1.91	-	-	-	-	-	-	-	-	-	-	-	-
LDP	-	-	-	-	-	-	-	-	-	-	-	-	735.56	3.44	14.50	4.44	-	-	-	-	138.22	3.84	5.50	5.99
DPC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	95.11	2.35	4.04	4.67	-	-	-	-
FDSc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	34.11	0.72	4.58	1.44	-	-	-	-
DPH	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	59.00	1.86	3.44	3.70	-	-	-	-
LHSD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	62.22	2.19	3.60	3.42
MMBu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	89.33	2.09	3.30	3.26

Groups	1A 2A	1A 1B	2A 1B	1A 2B	2A 2B	1B 2B	1A 3A	2A 3A	1B 3A	2B 3A	1A 1C	2A 1C	1B 1C	2B 1C	3A 1C
x̄ Dis.	31.39	34.23	39.43	38.82	21.23	27.54	79.79	78.05	80.80	74.85	81.12	78.79	82.53	76.38	40.51

4.9.1 Taxonomic resolution

Biodiversity assessment studies provide the basis for conservation evaluation and planning across sets of sites. Large-scale assessment have practical limitations, such as being very costly to conduct in terms of money, human effort, expertise and time, especially when analyses have to be conducted at a lower (Species-level) taxonomic resolution (Villasenor et al. 2005). Thus, it would be highly desirable if taxonomic resolution could be used as surrogates for Species-level assemblage patterns. However, despite the advantages of a coarser resolution, in biodiversity assessment studies a finer resolution can be necessary to reveal differences in the community structure (Trigal-Domínguez et al. 2010).

Biodiversity is often presented as the total species richness at a site or time (Fleishman et al. 2004). Since total richness can be difficult to measure, researchers have suggested the use of surrogates based on the richness of particular higher taxa. In this chapter, significant pairwise correlations was identified between Species Richness (d) and Diversity (H') and that for Genera, Families the Polychaeta indicator taxon, indicating that even after aggregation of the data to the higher taxa, overall spatial pattern was retained. Therefore, spatial patterns obtained from higher taxonomic resolutions and/or subset indicator taxon could be used for predicting the overall pattern for Species Richness and Diversity in rapid biodiversity surveys where the objective is to use biodiversity patterns to rank sites according to their conservation priority. However, it should be noted that, mapping of rare occurrences that plays a vital role in ecosystem functioning is not practical when using this higher taxon approach. These observations raise the possibility that the variety of ecological and/or functional roles, rather than the number of individuals or taxa within a taxon, may be a better determinant of the suitability of a surrogate set. These results are in accordance with findings of Olsgard et al. (2003), Doerries and Van Dover (2003), Heino and Soininen (2007), Shokri and Gladstone (2008) and Yekta et al. (2017), who similarly found significant pairwise correlations between assemblages constructed based on species richness and those constructed by higher taxonomic resolutions. The magnitude of richness in each taxonomic level, as it decreases with taxa aggregated to courser taxonomic resolution, may violate the effectiveness of species richness for higher taxonomic resolutions. For instance, in this chapter, 634 taxa represented by 281 Genera, 149 Families 18 Classes and 7 Phyla were only correlated with richness at Genus and Family levels.

Since there are robust arguments to advocate use of multivariate similarity measures, such as Bray-Curtis to compare biodiversity among sites rather than total species richness or Shannon-Wiener diversity (Su et al. 2004), robustness of surrogates of multivariate patterns in community structure to spatial variation in community structure was tested. The spatial pattern

obtained from NMDS analyses based on Bray–Curtis similarity matrices in assemblage composition mirrored that of richness and diversity. Results of nMDS did not depict a similar grouping pattern at Order-to-Phylum taxonomic levels or the Amphipoda indicator taxon compared with species level. These results suggest that Genus and Family have potential applicability for conservation studies. Polychaeta as an indicator taxon provided the closest match to the overall dataset. This may be argued as a numerical artefact as polychaetes contributed more than 60% of all species found (Chapter 3). Many other species from other Phyla were relatively rare and occur in small abundances, their influence is negligible such that by analysing number of taxa and abundance may in essence provide similar patterns as the overall data set. The contrasting results between indicator taxa (Polycheata and Amphipoda) probably reflect differences in the ecological roles of these taxa in different habitat types and highlight the importance of validating a surrogacy technique for the specific community being examined. The spatial analysis of macrobenthic data at different taxonomic levels or indicator taxa revealed a clear spatial segregation of the communities, reflecting specific macrofaunal assemblages typical of unique habitats in the KZN mid-shelf.

However, the use of higher taxa may not prove useful in biogeography studies, since higher taxa are not very sensitive to the regional changes. As a result, some of the major geographical boundaries are not well demarcated by higher taxa data (Roy et al. 1996). Other studies have highlighted the relative importance of taxonomic distinctness as a reason for using the lower taxonomic resolution to assess the conservation priority of areas. Vane-Wright et al. (1991) suggested that taxonomically distinct groups (taxon diversity) should receive greater priority rather than species in terms of conservation (Vanderklift et al. 1998) which may cause the selection of areas for conservation differently than those on the basis of species-level diversity (May 1990). In addition, when communities are compared, differences in natural environmental variables may lead to enormous variability in species composition from place to place. At higher taxonomic levels the taxonomic composition of these communities becomes increasingly similar though (Warwick 1993).

Results from this chapter further showed that data aggregated to Genus and Family or/and Polychaeta and Amphipoda indicator taxa responded to similar environmental variables. In turn, it was asserted that these taxonomic resolutions and indicator taxa were efficient in detecting environmental gradients. Marchant et al. (1995) and Alves et al. (2014) reported similar results and concluded that Genus and Family taxonomic levels respond similarly to the same key environmental gradients. This suggests that higher taxonomic resolution may provide an alternative when examining environmental impacts or pollution in marine systems. Nonetheless,

many studies suggest the lower taxonomic resolution appropriate for environmental impact studies, mostly pollution in marine systems (Warwick 1988, James et al. 1995 , Yekta et al. 2017). Overall, results from this study show that temporally robust surrogates can be identified; however, the nature of these surrogates will depend on how biodiversity is defined (Noss 1990).

4.9.2 Biological traits

Biological trait-based studies conducted in marine benthic habitats are often confronted by the need to find available, detailed and accurate trait information for macroinvertebrates (Tyler et al. 2012). Gaps of knowledge and restricted availability of literature were a common problem in this chapter, especially with regard to the molluscs, crustaceans and small Phyla that are not well studied. The traits of many of these groups were neither described in scientific literature, nor on electronic trait databases, which mostly include trait information of macroinvertebrates from well-studied higher latitude waters (van der Linden et al. 2017). The trait information of these groups in this study was therefore based on available information for closely related species or the same species in the analogous biogeography elsewhere. Trait data are not yet readily being shared by research communities, and even if they are, a lack of trait data repositories and standards for data formats leads to the publication of trait information in forms which are not user-friendly (Faulwetter et al. 2014). Despite the challenges, a large number of traits than those with presumed important are recommended in order to accurately describe functioning over the assemblage (Bremner et al. 2006c, Snelgrove et al. 2014).

Some traits (e.g. body size) were excluded from this study because they are less informative than other biological traits (Bremner et al. 2006c, Paganelli et al. 2012). Other biological traits are generally neglected in benthic studies despite their importance when defining community structure (Costello et al. 2015). Auto-ecological knowledge is scarce and most often incomplete in the literature, if available, often contradictory (Paganelli et al. 2012) and thus were also excluded. This is more so for less used traits such as ‘reproductive technique’ and ‘life span’ and for rare species as mentioned by Bremner et al. (2003b) and Paganelli et al. (2012). Traits that affect resource use, feeding mechanism and habitat availability are regarded as fundamentally important for ecosystem functioning (Bremner 2005), thus were considered in this study as they relate to bentho-pelagic coupling (Grebmeier et al. 1989, Covazzi-Harriague et al. 2007).

Choosing optimal number of traits is not recipe-driven. A potential problem with using large numbers of biological traits in BTA relates to the time and data required for carrying out the analysis. Limiting the number of biological traits involved in BTA could mitigate the potential

time and effort in preparing databases for a large number of species, especially in an environment with high species richness such as KZN shelf environment. A number of methods have been proposed on the biological traits selection criteria. Mérigoux et al. (2001) suggested the removal of traits that behave the same. These traits were assessed through a correlation analysis and co-variates removed. Indeed, the set of traits and respective modalities used in this study synthesis ecological relevance, verified by a number of previous BTA studies (Bremner et al. 2003b, Bremner 2005, Bremner et al. 2006c, Pacheco et al. 2011, Paganelli et al. 2012, Shojaei et al. 2015). Here, traits contributed to the variability of the KZN mid-shelf macrobenthic communities varied spatially, thus suggesting differences in the ecosystem properties and functioning.

Communities were more governed by traits related to lifestyle and behaviour of species (body design, movement method, feeding method, diet preference, living habit and habitat engineering). Similar results were also obtained by Bremner et al. (2006b) off the British Atlantic coasts, Marchini et al. (2008) in Northern Adriatic lagoons and Paganelli et al. (2012) along the North-West Adriatic Sea. Traits related to life cycle properties (reproductive techniques, and larval development) were found to be poorly correlated with both RDA axes. This could be attributed to the dominance of individual trait modalities; for instance, species with hard exoskeletons largely dominates over species with a soft body or shell in most samples. Different organisms produce different forms of larvae, reflecting adaptation to environmental variability. An organism with direct development displays no dispersive potential and higher extinction risk than an organism with pelagic larval development (McHuhg and Fong 2002). Moreover, fauna with limited dispersal potential may result in an isolated community, at times characterising regional fauna. In the case of the present study, *Callianassa* and *Ampelisc*a populations typify the aforementioned. The dominance of species with a direct development larval type was not expected since this larval development type is associated with more stable environments, whereas this region is characterised by a fast flowing western boundary current. There were, however, habitats that displayed distinct and very different sediment character, indicative of stable environment but dearth of fauna with direct development larval type. Some studies have, however, highlighted dispersal potential in some immobile post-larvae inhabiting soft-sediment (Olafsson et al. 1995, Pacheco and Stotz 2006). Dispersal potential has also been documented in organisms with direct developing larval type (Levin 1984, Johnson et al. 2001, Pacheco et al. 2013), this might potentially account for their dominance. Life-cycle traits are related to the reproductive techniques of a species and to its habit. In a dynamic environment, such as the KZN shelf, marked differences between life cycle traits were expected. Instead,

minor differences were found and brooders that produce miniature adults (crustaceans) prevailed in most parts of the study area.

4.9.3 Shelf functional diversity

The extent to which a species loss can translate to a trait loss and threaten basic ecosystem processes depends on the functional richness (e.g. the number of trait and modalities) and evenness (e.g. the distribution of trait and modalities across functional structures) in an ecosystem (Mouillot et al. 2006, Faulwetter et al. 2014). Evenness is of vital importance to community dynamics as it is used as an argument for the competing theories of species composition being driven by environmental filters rather than competition (Zobel 1997). High functional evenness suggest that species have been environmental filtered and most of the niche space has been filled thus species share many traits, while low evenness indicates that some part of niche space, whilst occupied, may be under-utilized, which can lead to a decrease in system's productivity and an increased opportunity for invasion (Mason et al. 2005). Therefore, the high evenness between trait structures in this study reflects the potential for the maintenance of function with the loss or replacement of individual species. Lower functional evenness in this study was observed in the trait structure comprising stations in Durban to uMkhomazi. This likely resulted from the dominance of specific trait modalities conforming to the high dominance of amphipods. Functional richness measure the amount of niche space filled by species in the community. The presence of low richness indicated that some of the resources potentially available to the community are under-utilised and may thus reduce system primary productivity (Petchey and Gaston 2002).

Similar representation of traits across two habitat types (Port Durnford and uThukela) was observed despite these habitat characterized by taxonomically distinct assemblages (Chapter 3). Several reasons could be attributed to different habitats with homogenous functional structure: among them, strong connectivity and metacommunity dynamics between habitats and movements of nutrients between habitats (Törnroos et al. 2013). Homogeneity in functional structure suggests that the regional species pool is not a major constraint to trait assemblages (Bremner et al. 2006b, Hewitt et al. 2008) and that ecological functioning can be shared amongst assemblages that are taxonomically different (Veríssimo et al. 2012, Berthelsen et al. 2015). The ability of assemblages differing in taxonomic composition to be functionally similar allows BTA to be used across different groups of organisms (Bremner et al. 2006b), and also across large geographical scales where different species contribute to the overall make-up of an assemblage (Hewitt et al. 2008). Moreover, this functional consistency has consequences for

ecosystem management and conservation where geographical gradients in taxonomic composition make these difficult on a larger scale. Nonetheless, due to environmental filtering, differences were observed between Durban and uMkhomazi (elevated chlorophyll-a contributing to bentho-pelagic coupling), indicating differences in the ecosystem attributes and functioning. Habitat filters or deletes individual taxa from a regional pool because they own a set of traits suitable for a given habitats) (Southwood 1977, Townsend and Hildrew 1994, Maire et al. 2012). This further shows that life history assembly theories for ecological communities are important in defining distribution of trait values in an assemblage.

4.9.4 Biological trait composition

The benthic assemblages along the KZN mid-shelf are characterised by a few dominant taxa, combined with a large pool of rare taxa (Chapter 3). Accordingly, traits displayed the same pattern of dominance. For instance, higher frequencies of trait expression between Durban to uMkhomazi corresponding to high abundances of amphipods (Chapter 3), highlighted the importance of abundance shifts in driving the functional attributes of habitats (Hewitt et al. 2008, Paganelli et al. 2012, Berthelsen et al. 2015). This suggests that, depending on the relative abundance of trait expression, some ecosystem functions derived from macrobenthic invertebrates may differ across habitats. Body design, sexual differentiation, feeding method, diet preference, living habitat and habitat engineering strongly contributed to the overall trait structure. Surprisingly, two traits that were assumed to be important, such as 'movement method' that relates to locomotion, predation avoidance and life cycle attributes (e.g. reproductive techniques) contributed poorly to the biological typology of macroinvertebrates and were weakly correlated to environmental condition.

Ordination showed a clear spatial gradient of trait modalities reflecting geographical position. Such a gradient can be linked to a gradient in habitat characteristics (Evin and Talley 2002, Leung 2015a) such as sediment distribution (abundance of different grain sizes), sediment organic contents, near bottom turbidity, dissolved oxygen and chlorophyll-a and the presence of biogenic features. In this sense, biological trait analysis succeeded in showing the response of infauna to the existing sediment composition. The results of this study support the hypotheses that trait structure differed spatially and was related to habitat features.

Rather than describing elements of the food web the trait feeding method is one of the most important traits as it relates to energy pathway flows and nutrient recycling. The heterogeneous nature of KZN shelf feeding types suggest diverse pathways of energy and matter cycling (Pacheco et al. 2011). In shelf soft-bottom communities, several feeding groups are known to coexist in different proportions, relative to sediment characteristics (Sanders 1958, Snelgrove

and Butman 1994). In shelly-coarse sand, suspension feeders usually prevail, whereas detritus feeders dominate in muddy environment. This is because of the clogging effect of re-suspended particles on filter/suspension feeding apparatus (Rhoads and Young 1970, Paganelli et al. 2012). Trait composition relating to feeding method recorded in this study fitted this depiction. The presence of immobile surface deposit-feeders off uThukela and utilising organic matter may have attracted carnivores, while the presence of carrion that might have been left by predating carnivores could also attract scavengers (Navarro-Barranco et al. 2013). Dominance of carnivorous fauna in mudflats has been reported elsewhere suggesting a mechanism by which nutrients in deposit feeders and detritivore tissues could be transferred to the mobile pool (Ngai and Srivastava 2006), therefore together with bacteria renew the nutrients for primary producers. The high dominance of the omnivorous trait reflects an ability to utilise a variety of food sources, and could suggest they occupy relatively wide niches and thus multiple pathways (Thrush et al. 2011). This is important for functional maintenance.

Traits reflecting the species' capability of habitat modification were important in determining differences between trait structures. Biogenic structures such as shell litter and biogenic architecture (meshwork of tubes) provides an important secondary substrate/habitat that can be used as shelter or attachment sites or refuge by other species, therefore potentially enhancing the bottom structural complexity, and thus having implications for biodiversity and ecological functioning (Rabaut et al. 2007, Van Hoey et al. 2008, Pacheco et al. 2011). Habitat engineering fauna presented another interesting insight into the KZN shelf ecosystem functioning. For instance, fauna with temporary burrows that were semi-mobile and able to displace themselves contributed to sediment reworking. This influences the exchange of materials between the sediment and the overlying water column (Eckman 1983, Snelgrove and Butman 1994, Hansen and Kristensen 1997, Tweedley and Valesini 2008). Also, sessile species with permanent burrows or tube-constructing fauna influence nutrient cycling by increasing the area of the oxic-anoxic interface and the transport of ions through the sediment (Snelgrove 1999). This suggests that there is a possibility of water penetrating to lower sediment layers, which may serve to transport organic matter for decomposition, and concurrently providing oxygen (e.g. fluid pumping by *Lanice conchilega* (Forster and Graf 1995). Well-oxygenated environments through bioturbation actions of the dominant tube builders may have contributed to the establishment of species that would not be able to live in the low oxygenated sediment (Gomez-Gesteira and Dauvin 2000), therefore promoting biodiversity.

Tube-dwelling surface defecators are considered to have low bioturbation activity, while subsurface depositors and motile forms are good bioturbators (Gutiérrez et al. 2000). It may also be concluded that bioturbation activity could be high since the community was dominated

by subsurface deposit feeders, free living, burrowing, and mobile forms (mobile and discreetly mobile). The activity of these macrofaunal species possibly helps in the exchange of material not only between the water column and sediment but also to deeper sediment layers.

Analysis of traits related to reproduction and propagule dispersal, to some extent infer information about transport of matter within and between systems (Pacheco et al. 2011). For example, pelagic dispersal was represented in many stations but in order of magnitude lower than non-dispersal form, suggesting that the supply of propagules in the water column is an important form of matter export that contributes to bentho-pelagic coupling in both systems. It worth noting that most stations supported traits that indicate input of nutrients.

Larval development mechanisms influence macrobenthic communities through dispersal and offer recovery patterns (Jablonski and Lutz 1983, Jablonski 1986, Boström et al. 2010). In general, two types of larval development have planktonic phases (planktotrophic and lecithotrophic). Planktotrophic larvae have a longer planktonic stage and hence higher dispersal potential than lecithotrophic larvae and direct developers. The higher relative frequency of direct developers south of Durban to uMkhomazi area suggested limited dispersal potential as described by Pacheco et al. (2013). Limited dispersal potential suggests that the persistence of population relies on immigration of adults from the neighbouring pool and/or the recruitment of juvenile from within the habitat. Furthermore, limited dispersal potential is indicative of stable habitats (uThukela) (Paganelli et al. 2012), surpassing on this shelf with its multitudes of oceanographic features such as outwelling.

Biological traits relating to body design, depending on the environmental conditions, are often responsible for distinguishing trait structures (Paganelli et al. 2012). For instance, a soft body design associated with fine sand, (e.g. uThukela) may be an advantage for mobility in this habitat, while hard exoskeleton associated with medium-to- coarse sand may be an advantage for the coarse sediment habitats (e.g. uMkhomazi). Body design trait can further be used to infer potential linkages between traits and taxonomic relationships (Munari 2013). For instance, the frequent occurrence of the hard exoskeleton trait in this study reflected the numerical dominance of arthropod crustaceans.

Maintaining functional diversity in an ecosystem can provide a barrier against large environmental shifts caused by either natural effects or anthropogenic activities (Folke et al. 2004, Frid et al. 2008, Fleddum et al. 2013). Functional diversity is increasingly used to understand the ecological functions of a community following disturbance or management measures (Hulot et al. 2000, Usseglio-Polatera et al. 2000, Bady et al. 2005, Cadotte et al. 2011, Michel 2011). Normally, higher functional diversity indicates better performance, higher

productivity and higher utilisation of resources of a community in view of higher niche complementarity (Petchey and Gaston 2002). A number of studies have also underlined the functional diversity-environmental gradient relationship and its influence in ecosystem processes (Harmelin–Vivien et al. 2009, Karlson et al. 2010). Paganelli et al. (2012) observed that macrofaunal functional diversity increased away from sites with riverine input along the Po River delta and attributed excessive terrigenous input to contribute to low functional diversity. Similar results were obtained from this study, the uThukela outwelling as a natural disturbance agent, may have a deleterious effect on the fauna and associated traits, and thus contribute to low functional diversity. However, overall efficiency is heavily influenced by the choice and definition of traits, which are in turn reliant on the availability of detailed and accurate data (Usseglio-Polatera et al. 2000b). This is generally rare for many marine communities (Borja et al. 2011, Munari 2013), including here.

4.9.5 Biozone as surrogates for trait structure

This study showed that marine spatial planning predefined biozones do not agree with trait patterns, either considering univariate community measures or macrobenthic trait patterns. Therefore, biozones were not a useful predictor of spatial variation in macrobenthic functional structure. There were no significant relationships between biozone subclusters when considering trait richness and diversity. This was surprising given that the study area hosted unique habitats (e.g. Port Durnford reef complex and uThukela mud bank) with different suite of fauna. Chapter 3 of this study indicated under sampled species richness. This is particular so for rare occurrences and consequently rare trait modalities. This might therefore confront significant relationships between habitats and warrant further investigation. Predefined marine spatial planning biozones also did not reflect macrobenthic trait patterns, suggesting that variation in trait patterns was poorly correlated with biozones. The use of functional analysis to measure effectiveness of surrogates in this study, is in line with other studies that have assessed the validity of predefined habitats as biodiversity surrogates (Törnroos et al. 2013). Törnroos et al. (2013) found inconsistence in macrobenthic functional structure and predefined habitat.

The importance of using abundance-based measures for testing the efficiency of biophysical habitat as surrogates was clear from this study. Previous studies have also highlighted the role of abundance-weighted data rather than specific traits for understanding the functional structure (Hewitt et al. 2008, Przeslawski et al. 2011, Törnroos et al. 2013). In this chapter, the abundance-weighted functional analysis showed a similar community trait structure (e.g. station south of uThukela, Durban and uMkhomazi). In this context, trait structure refers to the distribution and composition of biological traits in a habitat (since functional analysis is habitat

specific). Here this corresponds to the clustering together of stations from Port Durnford and uThukela to form one functional unit. Several mechanisms could possible explain why different habitats seemed to function homogenously (e.g. strong connectivity and metacommunity dynamics between habitats).

The terrestrial surrogacy literature states that the selected set of surrogates must ultimately ensure the full representation of biodiversity more so than spatial correlation and agreements (Sarkar et al. 2005). Accordingly, the predefined biozones in this study could not be said to effectively represent functional structure, since biozone subclusters did not match the functional variability. Particularly noteworthy is the lack of biozone subclusters to capture functional variability due to the generally high functional similarity. Disagreement between traits patterns and predefined biozones does not suggest that the functional measure is inaccurate or unrelevant, rather that there is potential to illustrate variability on several scales. Such low functional beta-diversity has recently been emphasised for better understanding community assembly and processes structuring communities over different scales (Villéger et al. 2012). Despite that, there were no significant differences between biozone subclusters in terms of trait richness, the fact that no biozone subcluster hosted all trait modalities indicated a poor representation of functionality. In this context, it reasonable to combine subclusters identified by SIMPER to share similar trait modalities such that unique trait modalities within combined subclusters increase functional representation. Trait patterns in biozone subclusters 1A were similar to those of 2A, similarly for biozone subclusters 1B and 2B, while biozone subclusters 3A and 1C were different.

However, this spatial disagreement between biozone classification and trait structure is probably an effect of the openness of marine systems. This is a reason why surrogacy work in marine benthic systems should specifically attend to and address this issue (McArthur et al. 2010a, Mellin et al. 2011). Consequently, planners relying on biophysical habitat may cautiously proceed to do so under the assumption that it captures functional variability. These types of inherent species-related community differences in the habitats are contemporary to some extent incorporated as secondary parameters on lower levels in e.g. the EUNIS habitat classification system (Davies et al. 2004). However, including functional attributes more comprehensively in habitat classification and in the way habitat maps are derived is essential for more diverse and targeted future spatial planning (McGill et al. 2006). Especially since incorporating a broader knowledge of species traits such as feeding, reproductive, mobility and behavioural ones, apart from the most often used body size, is relevant for understanding spatial patterns of benthic functional diversity and for measuring human impacts on benthic communities (e.g. trawling impacts) (Frid et al. 2008, Fleddum et al. 2013).

Conclusion

The general conclusion that arise from the results of this chapter is that, in the examination of the macrobenthic fauna of the KZN mid-shelf, little information is lost about the inter-sample relationship when analyses are based on intermediate taxonomic levels such as Genus and Family level or/and the use of Polychaeta as potential indicator taxon. The structure of the macrobenthos at the Family, Genus and Species-level and Polychaeta indicator taxa was accounted for by mud distribution and water column turbidity and in each case explained >80% of the total variability. This indicates that spatial structuring of the macrobenthic community in KZN shelf can be reliably approximated when community data are aggregated to Genus of Family or restricted to one group of benthic organisms.

The BTA applied to macrobenthic fauna of KZN mid-shelf showed that biological traits of the communities respond to spatial gradient across habitats. This corresponds to differences in sediment composition and the influence of the river inputs from the uThukela. Functional composition analysis showed that changes in benthic assemblages are not necessarily linked with changes in ecological functions played by organisms as reflected by benthic assemblages off Port Durnford and uThukela. Biological traits analysis (BTA) is a sensitive method in identifying differences among benthic assemblages and thus, can provide additional information of community distribution patterns (Alves et al. 2014). Furthermore, BTA is less affected by the large-scale geographic influence. The gradients in environmental parameters filters species with particular functional traits in which this attribute was consequently reflected in the ecosystem functioning of the KZN mid-shelf. Therefore, it can be inferred that bioturbation activities of macrofauna transported organic matter to deeper sediment for subsurface deposit feeders. The presence of carnivorous species further helped to transfer the nutrients retained in the deposit feeders back into the mobile fauna. Thus, the functional diverse macrobenthic community rapidly consumed the organic matter and converted it to benthic biomass, which forms the food for organism at the higher trophic level such as the demersal fish.

One important product of this study is the production of a macrobenthos functional database, which will serve as a starting point for further functional analysis of attributes of the KwaZulu-Natal shelf. Results from this study highlighted significant discrepancies between coarse taxon and species level, and between biological communities relative to marine spatial planning biozones. Abiotic based habitat classifications often are unrepresentative of underlying biological assemblages, which frequently exhibit considerable spatial variability amongst areas. There is a clear need for improved surrogate and methods used for gathering and classifying marine biodiversity data in conservation planning. Future mapping of marine biodiversity

should not only emphasize biophysical characteristics, but also aim towards assessing distributions of functionally different units on the KwaZulu-Natal shelf. Moreover, knowledge of specific processes would benefit from comparisons among measures of community structure. Community analyses in this study have identified a number of significantly different communities associated with unique habitats. However, there were no correlations between benthic habitat distributions abiotic variables abiotic variables. Combined biotic and abiotic variables may provide the best representation of biodiversity in conservation planning. Using detailed KZN mid-shelf microbenthic characteristics, Chapter 5 refines the current biozone classification model.

CHAPTER 5. PROPOSED MARINE SPATIAL PLANNING MACROBENTHIC LAYER AS BIODIVERSITY SURROGATE

5.1 Overview

Effective marine spatial planning, which must be representative of ecological conditions, services and habitats, require spatial knowledge of biotic patterns, seafloor habitats and habitat-biotic relationships at a relevant scale. However, such information is mostly not available. Surrogates to any of these components often compensate for this constrain in marine conservation planning. However, habitat classification schemes are a potentially useful surrogate with prior confirmation of their relationship to spatial variation in biodiversity. This chapter builds on the findings of Chapters 3 and 4, which showed contrasting results in sediment, taxonomic and functional structure across the shelf and further showed that the predefined biozone scheme only partly depicted the true spatial variation in the KwaZulu-Natal mid-shelf macrobenthic biodiversity. Using habitat characteristics (validated sediment distribution and hydrographic variables that were significant in explaining patterns), and infauna taxonomic and functional attributes, this chapter aimed to refine and improve on the existing predefined biozone model and to propose an alternative biozone classification as an input into KwaZulu-Natal marine spatial planning efforts. An alternative biozone classification resolved into four biozones using a cluster analysis. This chapter demonstrates the importance of testing assumptions about surrogacy and introduce a proposed approach for refining the use of surrogates in the information poor environment. Further validation of the proposed biozone classification using other components of ecology (e.g. epifauna) is however still required.

5.2 Introduction

Recently, a major challenge faced by conservation efforts is how to incorporate the many aspects of biodiversity and ecosystem functioning (potentially unique, representative, or vulnerable habitats and species) when planning and establishing protected areas and reserves (Ward et al. 1999, Currie et al. 2009, Przeslawski et al. 2011). A key principle underpinning planning is efficient representation of biodiversity (Stevens and Connolly 2005). This involves habitat heterogeneity and microhabitats, as they are key considerations for marine spatial planning (Foley et al. 2010). Planning that aims to fulfil this principle requires spatial knowledge of biota, at scales relevant to marine spatial planning (MSP) (Brown et al. 2011). However, such information is often not available for most marine species and habitats,

particularly at a relevant spatial scale (Douvere 2008, Douvere and Ehler 2009, Ehler and Douvere 2009, Collie et al. 2013, Snelgrove et al. 2014, Dunstan et al. 2016, McHenry et al. 2017). If some information is available, it is often highly fragmented (Robinson et al. 2011). Furthermore, knowledge of the processes that sustain biodiversity is rudimentary for most regions (Grantham et al. 2010).

Macrobenthic patterns have been shown to relate to environmental variables, such as seafloor complexity, at a range of scales (McArthur et al. 2010b, Dixon-Bridges et al. 2014). Where strong relationships occur, biophysical variables can be applied as surrogates for biodiversity, especially where macrobenthic data is scarce (McArthur et al. 2010b). This involves classification of continuous abiotic variables into discrete zones of similar conditions (McArthur et al. 2010b, Brown et al. 2011). This approach assumes that biodiversity differs among habitat types and that faunal assemblages have strong associations (Heap et al. 2011). This approach can ignore complex underlying abiotic-biotic relationships and also confines inherently continuous ecological patterns into discrete classifications (e.g. patchy distributions of species within and between habitat types, especially for rare, locally endemic, and threatened taxa); (McHenry et al. 2017, Chapter 3 and 4), thereby producing maps with unknown, assumed, and/or simplified values (Mac Nally et al. 2002, Dangerfield et al. 2003).

Testing the effectiveness of the biophysical-based maps as biodiversity surrogates can improve methods for developing new surrogates and help to understand their unavoidable limitations (listed above) (Grantham et al. 2010). Studies that have tested this, have focused mainly on effectively safeguarding taxonomic diversity (Dalleau et al. 2010, Przeslawski et al. 2011, Dixon-Bridges et al. 2014, McHenry et al. 2017), with the functional component rarely considered (Törnroos et al. 2013), yet this aspect of biodiversity and ecosystem functioning contributes an important level of complexity which is acknowledged as a vital criterion for implementing sound and holistic ecosystem-based management (Arkema et al. 2006).

The focus of this thesis has been to test the effectiveness of predefined biozones as surrogates for marine macrobenthos taxonomic (Chapter 3) and functional structures (Chapter 4). Results showed that the predefined biozone model did not represent the existing variability in sedimentary, taxonomic and trait patterns (see results Chapter 3 and 4). The regional specificity and low level of agreement between macrobenthic patterns and the predefined biozones using taxonomic and functional structure reinforce the need to refine this biozone model for more effective and representative MSP. Integrating macrobenthic assemblage patterns (taxonomic and functional attributes) and seafloor characteristics, as a composite biodiversity surrogate, can improve spatial planning for KZN shelf (Dixon-Bridges et al. 2014) and may fortuitously

represent other groups with similar patterns in the benthic layer (Bridge et al. 2016). The aim of this chapter is to synthesise macrobenthic community patterns and sediment characteristics to refine the existing KZN biozones as identified by KZN MSP (Livingstone 2016). The results from this chapter should facilitate future methodological improvement, including the identification of additional environmental data layers for deriving the biozones.

Aim

The aim of this chapter is to combine habitat characteristics (hydrographic and sedimentary variables), macrobenthic taxonomic and functional characteristic attributes to refine a predefined biozone model for marine spatial planning.

Objectives

1. To improve and refine the existing MPS model by integrating habitat features and taxonomic and biological trait assemblage patterns.
2. To identify taxa and traits characterising a new, proposed model that best reflects the benthos.
3. To identify environmental factors driving biological patterns in the proposed benthic model.

5.3 Materials and methods

This chapter builds on the results of Chapters 3 and 4. The general materials and methods, the study area, field-sampling protocol, laboratory processing and data analyses are presented in Chapter 2 and the following present only protocols relevant to this chapter.

5.3.1 Data treatment

Taxon abundance (Chapter 3) and trait-weighted abundance (Chapter 4) data were square root transformed to allow rarer taxa and trait modalities to influence discrimination between groups without discarding abundance information. Rare fauna contributed 30% of the total macrobenthic community (Chapter 3). Here, the strong links between habitat and biota (Chapters 3 and 4) suggested incorporation of the habitat features, in order to capture the heterogeneity that shapes species diversity, distribution patterns and ecological functioning. Environmental (sediment and hydrographic) variables found to be responsible for spatial variation in macrobenthic taxonomic and functional patterns (Chapter 3 and 4) using the BIOENV procedure and distLM routines were incorporated to refine and define categories. The three datasets were combined to be analysed as a single dataset.

5.3.2 Integrating sediment, taxonomic and biological traits patterns

A similarity matrix was constructed using a modified Gower dissimilarity measure (Anderson et al. 2006) which derives similarity from conjoint absences and is more robust to variables with different measurement scales (Legendre and Legendre 1998, Clarke and Warwick 2001, Anderson et al. 2006). Moreover, although this is not a unitless measure, it has the advantage of being directly interpretable as the average change in orders of magnitude per species between two sampling units (Anderson et al. 2006). To define biozone clusters and distinguish between separate groups, a complete linkage hierarchical clustering was applied. That is, stations were allocated into groups of relative similarity, based on consistently occurring groups of stations. This was supplemented with SIMPROF analysis to test the validity of resultant biozone clusters. PERMANOVA was used to test for differences between subgroups within a biozone cluster and between biozone clusters (Chapter 2). Resultant biozone clusters were subsequently subjected to inter-group similarity using the SIMPER (similarity percentage breakdowns) module in the PRIMER package (Clarke 1993, Chapter 2). Additionally, for all new biozone clusters identified, univariate indices for taxonomic (S, N, d and H') and biological traits (S_t, N_t, d_t and H_t') were calculated from non-transformed data. Associated sediment characteristics were also to distinguish if biozone clusters were distinct community in different habitats (e.g. grain size, TOC and carbonate content)

5.4 Results

5.4.1 Biozone cluster analysis to propose a new MSP benthic layer for KZN mid-shelf

Hierarchical agglomerative clustering distinguished five sample groups (SIMPROF at 5% significance) (Fig 5.1). Sample groups 1, 2 and 4 (hereafter referred to as BZ1, BZ2, and BZ4) were clearly defined habitats on the shelf while sample group 3 (BZ3) resolved into subgroups corresponding, in part, to subclusters 1B and 2B of the existing MSP biozone model (Fig 5.1 and 5.2A). Visually (nMDS, not shown), subclusters grouped together and pairwise comparison (PERMANOVA) showed that subclusters 1B and 2B supported similar taxonomic assemblages ($t=1.135$, p-perm=0.199) and biological traits ($t=1.280$, p-perm=0.302), which were subsequently merged to form BZ3. PERMANOVA analysis verified that the proposed biozones (BZ1-4) were significantly different from each other (Table 5.1) (p-perm <0.05). This alternate scheme on benthic MSP proposed divides the KZN mid-shelf into four biozones (Fig 5.1 and 5.2b). Macrobenthos and functional traits compositions found on these biozones strongly separate from each other and are highly different. These strong biotic patterns have a clearly defined (pattern-based) surrogate model for MSP of soft sediments benthos.

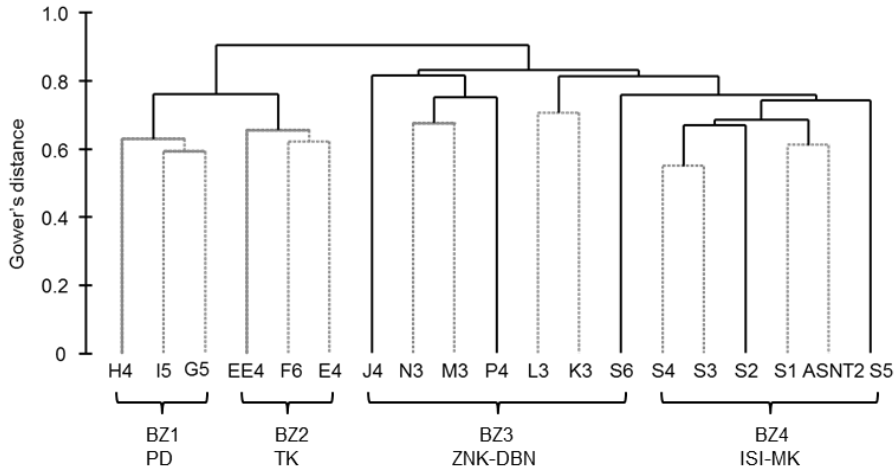

Figure 5.1. Proposed marine spatial planning biozone classification based on macrobenthic attributes. BZ=Biozone, PD=Port Durnford, TK=uThukela, ZNK=Zinkwazi, DBN=Durban, ISI=iSiphingo, MK=uMkhomazi. (SIMPROF 5% significance=grey dotted line.

Table 5.1. PERMANOVA results for biozone clusters differences. Df=degree of freedom, MS= Mean square, F=critical values of PERMANOVA and p=level of statistical difference. Asterisks denote statistical significance *<0.05, **<0.01, ***<0.001.

PERMANOVA	df	Pseudo-F	p-perm
Factor			
Biozone clusters	3	3.469	0.000***
Residual	15		
Components of variation			
Source		**Estimate**	**X^2**
BZ Clusters		0.197	0.444
Residual		0.361	0.601

5.4.2 Species, ecological traits and sedimentary attributes characterising biozones

The biological and sediment characteristics of the four biozones are summarised in Table 5.2. Inter-biozone similarity for taxa results was low (18.93 -38.23%) indicating an overall high level of variation in faunal composition (Table 5.2). Between-biozone dissimilarity was high (80.47-96.04%) (Table 5.3) driven primarily by the abundance of different species of polychaetes and amphipods. By comparison, the contribution of most of the other taxa to dissimilarity among biozones was generally low (<2%), reflecting their low abundance and irregular occurrence. In terms of traits, similarity was moderate, ranging between 50.28 to 73.22% (Table 5.2). In pairwise comparison, dissimilarity ranged between 36.58 and 79.64% (Table 5.3), indicating that identified biozones were potentially discrete in terms of taxa and traits.

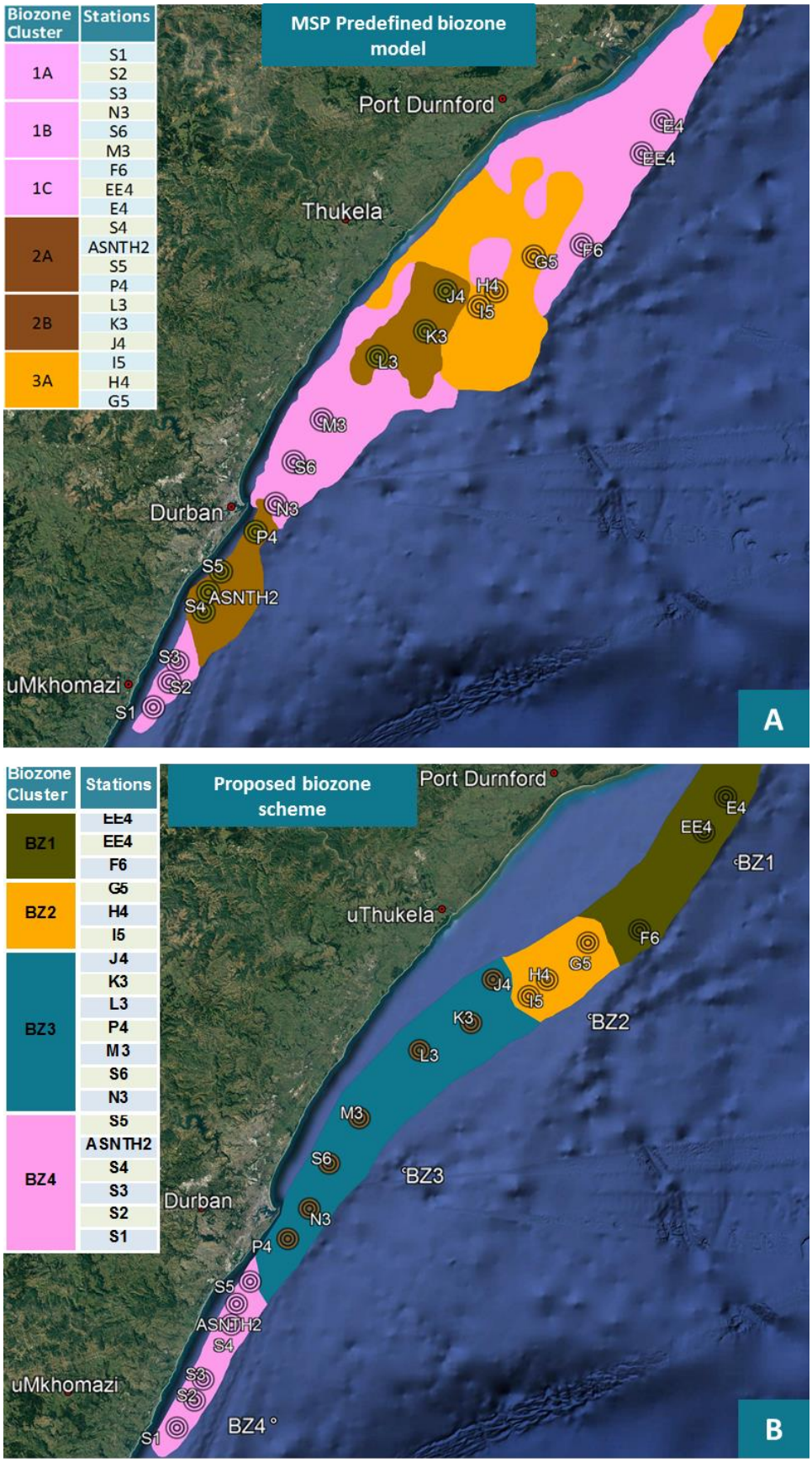

Figure 5.2. Maps illustrating (A) the KwaZulu-Natal marine spatial planning pre-defined biozone model and (B) proposed macrobenthic scheme.

Table 5.2. Species and biological traits from SIMPER analysis that characterise proposed biozones. Included are sediment characteristics for each biozone. Abun=Abundance, Sim=similarity, SD=Standard deviation. For explanation of modality codes refer to Table 4.1. A-D=results for BZ1-4.

BZ	Species	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	Traits	x̄ abun.	x̄ sim.	Sim/SD	Contr.%	Sediments
		Biozone cluster 1 = 21.88%					**Biozone cluster 1 = 64.05%**				**Biozone cluster 1**
A	*Nephtys capensis*	1.44	1.72	13.84	7.85	BDS	148.00	4.06	7.88	6.35	
	Mandibulophoxus stimpsoni	1.44	1.72	13.84	7.85	FDF/SF	92.00	3.13	7.01	4.88	
	Quantanthura serenasinus	1.31	1.72	13.84	7.85	MMSe	135.56	4.28	6.70	6.68	
	Ophioroidae sp.2	1.72	2.10	3.87	9.60	RTSBS	124.00	3.46	6.67	5.41	
	Anthozoa sp.5	3.19	3.38	1.92	15.45	HES-A/R	96.00	1.79	6.40	2.80	
	Ampelisca sp. 3	1.21	0.84	0.58	3.82	HEN	125.33	4.07	5.51	6.36	
	Poecilochaetus serpens	0.77	0.60	0.58	2.75	LDP	138.22	3.84	5.50	5.99	MCS
	Scoloplos uniramus	0.93	0.60	0.58	2.75	DPO	136.44	3.96	4.75	6.18	Median phi: 0.89ϕ
	Monticellina dorsobranchialis	0.77	0.60	0.58	2.75	SDG	227.56	6.15	4.05	9.60	TOC : 0.47%
	Pista macrolobata	0.93	0.60	0.58	2.75	LHSD	62.22	2.19	3.60	3.42	Carbonates: 28.77%
	Cyclaspis scissa	1.05	0.60	0.58	2.75	MMBu	89.33	2.09	3.30	3.26	
	Leptanthura urospinosa	0.77	0.60	0.58	2.75	FDP	94.67	2.27	3.10	3.54	
	Notomastus latericeus	0.93	0.59	0.58	2.70	LDL	58.22	1.49	2.73	2.32	
	Paratanaidae sp.1	0.93	0.59	0.58	2.70	FDSDF	68.44	1.37	2.45	2.15	
	Pareurythoe chilensis	0.77	0.59	0.58	2.70	LHFL	65.78	1.30	2.38	2.04	
		S	**N**	**d**	**H'**		**S_t**	**N_t**	**d_t**	**H'_t**	
		111	68	26.12	4.65		42	2490	5.24	3.28	
		Biozone cluster 2 = 18.93%					**Biozone cluster 2 = 50.28%**				**Biozone cluster 2**
B	Opisthobranchia sp.1	2.11	3.85	4.24	20.36	FDSc	34.11	0.72	4.58	1.44	
	Aglaophamus sp.1	2.59	4.85	2.53	25.61	LHFL	105.89	2.02	4.52	4.02	
	Aglaophamus dibranchis	1.99	2.15	0.58	11.35	LDDP	30.89	0.76	4.38	1.51	
	Linopherus microcephala	2.13	1.52	0.58	8.02	FDP	113.67	2.67	4.09	5.30	
	Aspiodosiphon sp. 1	0.77	1.15	0.58	6.07	DPC	95.11	2.35	4.04	4.67	
	Ommatocarcinus pulcher	0.77	1.07	0.58	5.67	BDS	160.00	2.99	3.82	5.94	
	Caprellidae sp. 1	0.77	1.07	0.58	5.67	HEN	125.33	1.43	3.47	2.85	VFS-Mud
	Carcinus sp.1	0.77	1.07	0.58	5.67	BDHE	33.00	0.82	3.45	1.63	Median phi: 4.39ϕ
	Platyhelminthes sp.1	0.77	0.73	0.58	3.86	DPH	59.00	1.86	3.44	3.70	TOC : 2.00%
	-	-	-	-	-	MMS	59.11	1.35	3.24	2.68	Carbonates: 12.67%
	-	-	-	-	-	MMSM	106.78	2.66	3.18	5.30	
	-	-	-	-	-	MMBu	183.56	3.31	2.91	6.58	
	-	-	-	-	-	RTSBS	185.33	3.09	2.20	6.14	
	-	-	-	-	-	SDG	244.11	4.26	2.02	8.48	
	-	-	-	-	-	HES-A/R	150.78	3.00	1.84	5.96	
		S	**N**	**d**	**H'**		**S_t**	**N_t**	**d_t**	**H'_t**	
		61	41	16.19	3.92		38	2827	4.66	3.29	
		Biozone cluster 3 = 22.26%					**Biozone cluster 3 = 73.22%**				**Biozone cluster 3**
C	Sipuncula sp.3	2.40	0.64	3.08	2.88	SDG	2182.57	7.35	6.30	10.04	
	Byblis gaimardii	4.47	0.90	1.82	4.05	DPO	1470.57	4.55	5.95	6.22	
	Notomastus latericeus	1.73	0.45	1.46	2.02	MMSM	1394.19	4.68	5.40	6.40	
	Lumbrineris aberrans	2.39	0.69	1.27	3.09	MMBu	1057.33	3.91	5.32	5.34	
	Notomastus aberans	2.97	0.73	1.24	3.27	FDP	604.86	2.16	5.28	2.95	
	Arcturinoides sexpes	1.64	0.45	1.22	2.04	LHTB	934.19	2.63	5.10	3.59	
	Hippomedon onconotus	2.53	0.47	1.00	2.13	HES-A/R	1098.19	4.01	5.06	5.47	FCS
	Spiochaetopterus vitrarius	3.00	0.60	0.97	2.69	LHPB	771.05	2.81	4.88	3.84	Median phi: 1.51ϕ
	Ophiurida sp.2	2.23	0.59	0.92	2.66	LDL	644.10	1.84	4.54	2.51	TOC : 0.63%
	Ampelisca palmata	1.27	0.34	0.91	1.53	DPC	559.33	1.79	4.18	2.45	Carbonates: 27.94%
	Aglaophamus sp.2	1.23	0.26	0.91	1.18	FDSDF	860.76	2.80	4.05	3.83	
	Lanice conchilega	2.43	0.22	0.91	1.00	FDF/SF	772.95	2.07	3.68	2.82	
	Onuphis eremita	2.31	0.54	0.90	2.43	LDDP	1189.05	3.32	3.29	4.53	
	Sipuncula sp. 5	1.77	0.30	0.90	1.33	RTSB-MA	1055.43	2.99	3.16	4.09	
	Monticellina dorsobranchialis	1.51	0.31	0.89	1.40	MMSe	934.10	2.95	3.16	4.02	
		S	**N**	**d**	**H'**		**S_t**	**N_t**	**d_t**	**H'_t**	
		439	242	79.82	5.72		46	23626	4.47	3.31	
		Biozone cluster 4 = 38.23%					**Biozone cluster 4 = 64.14%**				**Biozone cluster 4**
D	*Eunice vittata*	1.57	0.63	7.59	1.66	LDL	697.15	1.71	3.45	2.66	
	Ampelisca diadema	7.54	2.67	5.55	6.99	MMSe	1187.99	2.88	3.36	4.49	
	Nephtys capensis	3.27	1.23	5.50	3.21	FDF/SF	1354.98	3.51	3.32	5.48	
	Leptanthura cf laevigata	2.16	0.84	5.21	2.19	DPC	493.62	1.16	3.22	1.80	
	Latigammaropsis atlantica	4.56	1.81	4.04	4.74	HEN	958.87	1.65	3.20	2.57	
	Tharyx filibranchia	1.50	0.59	3.70	1.55	SDG	2672.12	6.28	3.18	9.79	
	Hippolytidae sp.1	2.11	0.77	3.26	2.02	MMSM	1783.34	4.13	3.16	6.44	FS-to- GvI
	Ampelisca brevicornis	4.58	1.39	2.74	3.65	FDP	489.73	1.20	3.16	1.86	Median phi: 1.06ϕ
	Unciolella spinosa	11.06	2.69	2.27	7.03	DPO	2111.86	4.61	3.12	7.18	TOC : 0.33%
	Cheiriphotis megacheles	4.56	1.62	2.27	4.25	LHTB	1953.24	3.99	3.09	6.22	Carbonates: 41.27%
	Ampelisca palmata	3.24	1.09	2.14	2.86	LDDP	2348.24	5.33	3.08	8.30	
	Byblis gaimardii	8.95	2.72	2.01	7.12	MMS	1763.32	3.78	3.02	5.89	
	Urothoe pulchella	4.73	1.15	1.72	3.00	FDSDF	928.92	1.53	3.02	2.38	
	Sipuncula sp.3	0.86	0.32	1.35	0.84	RTSB-MA	2308.92	5.16	2.97	8.05	
	Cirriformia cf filigera	0.92	0.34	1.34	0.88	HES-A/R	787.23	2.25	2.90	3.50	
		S	**N**	**d**	**H'**		**S_t**	**N_t**	**d_t**	**H'_t**	
		311	212	57.85	5.08		50	28261	4.78	3.05	

Table 5.3. Average dissimilarity in taxa and biological traits between biozone clusters. Dissim=Dissimilarity percentage

Biozone	1 & 2	1 & 3	1 & 4	2 & 3	2 & 4	3 & 4
Taxa $\bar{x}$ dissim (%)	96.04	90.17	88.97	94.11	97.68	80.47
Traits $\bar{x}$ dissim (%)	40.51	79.64	79.63	78.04	78.8	36.58

Overall, 171 taxa and 34 trait modalities were identified as being responsible for dissimilarities between BZ 1-4. BZ1 was characterised by clean coarse sand (median phi=0.89 ϕ, mud content <1%) (Table 5.1). Faunal components characterising BZ1 represented four Phyla (Annelida, Arthropoda, Echinodermata and Cnidaria). Annelid polychaetes were the most abundant taxon (7 taxa), whereas different Classes (Isopoda, Amphipoda and Tanaidacea) within Crustacea hosted equal number of taxa (2 taxa). Complex substrate, with spaces between broken branched forms and hard calcareous surfaces supported sessile fauna (MMSe), mainly represented by soft-bodied (BDS) omnivorous (DPO) filter/suspension feeders (FDF/SF) such as Anthozoa sp.5, free-living (LHFL) surface deposit feeders (Ophioroidae sp.2) and carnivorous predators (DPC: *Nephtys capensis, Mandibulophoxus stimpsoni* and *Quantanthura serenasinus*). These together distinguished BZ1 from all other biozones, with most trait modalities well represented despite low species richness. The presence of burrower (MMBu) and sediment accretion and removal (HES-A/R) suggest enhanced sediment oxygenation and nutrient cycling from the activities of macrobenthos (Table 5.2). BZ2 off uThukela Estuary, was supported by mud (median phi 4.39 ϕ, mud content >80%) high in TOC (Table 5.2). Such homogeneous sediments hosted five Phyla, low in species richness mainly comprising soft-bodied (BDS) predatory/scavenging (DPC/FDSc) surface dwellers (LHFL) (*Aglaophamus sp.1, Aglaophamus dibranchis* and *Linopherus microcephala*). These together with Opisthobranchia sp.1 distinguished BZ2. Low abundances in hard exoskeleton (BDHE) and direct developing larval type LDDP trait modality reaffirm the low number of crustaceans characterising this biozone. Bioturbation by actions of borrowers (MMBu) and habitat engineering fauna (HES-A/R) suggest enhanced oxygenation of the sediment. BZ3 was characterised by fine to coarse sediments (median phi >1.5 ϕ, mud content >7%) and supported a diverse community with high species richness (Table 5.2). In this BZ, Polychaeta and Crustacea represented most of taxa and were numerically dominated by Amphipoda, which have a direct developing larval type (LDDP). BZ 3 supported semi-motile (MMSM) tube dwelling (LHTD) filter/suspension feeders (FDF/SF) (e.g. *Byblis gaimardii, Spiochaetopterus vitrarius, Ampelisca palmata* and *Lanice conchilega*) and surfaced deposit feeders (FDSDF) (e.g. *Notomastus latericeus* and *N. aberans)* (Table 5.2). Overall, this BZ represented most of the trait modalities and appeared as a transitional region. High abundance of HES-A/R, MMBu and LHTD suggest enhanced sediment oxygenation and nutrient cycling from the activities of macrobenthos (Table 5.2). BZ4

was characterised by heterogeneous sediment showing a median phi varying between -0.36 to 1.93 ϕ. Amphipoda, direct developing (LDDP) tubicolous (LHTB) filter/suspension feeders (FDF/SF) presented most of the taxa in high abundances with least equitability (e.g. *Unciolella spinosa and B. gaimardii*). Overall, most traits were represented in this biozone (Table 5.1).

5.4.3 Environmental variables driving biological patterns

Biological-environmental matching (BIOENV) analysis indicated that mud and turbidity were the main variables driving biological patterns (rho=0.707, p <0.05), showing a good match between biota and variables. In addition, when analysing a combination of four parameters the coefficient remained comparable (rho=0.680) (Table 3.8), therefore, mud and turbidity remained the most structuring parameters.

Table 5.4. Summary of BIOENV results. Correlations (ρ) are presented relative to proposed macrobenthic scheme biological patterns. fs=fine sand

No of varibles	ρ	Variables
Best combination (2 variables)		
2	0.714	Mud Turbidity
Best combination (4 variables)		
4	0.680	Mud, fs, Turbidity Carbonates

Marginal tests in distance-based redundancy analysis (dbRDA) showed that most variables apart from sediment skewness, dissolved oxygen, chlorophyll-a, pH and temperature explained a proportion of the variation (mostly >10%) observed in biological patterns (Table 5.5). Turbidity was the only significant variable depicted by the marginal tests and explained 22% of the variation (Table 5.5).

5.5 Discussion

5.5.1 Proposed biozone characteristics

In terms of taxa, inter-biozone similarity was low and inter-biozone dissimilarity was high, suggesting that the newly identified biozones are distinct and variable in terms of spatial distribution. Indeed, there was a limited overlap in the characterising taxa for each identified biozone as determined by SIMPER, with very few taxa common between biozones. The presence of specialist taxa restricted over a narrow range of environmental conditions may also increase between-biozone dissimilarity (Brown et al. 2012).

Table 5.5. Distance linear model results (Marginal and sequential tests) for the relationship between KZN mid-shelf macrobenthos and environmental variables. Asterisks denote statistical significance (*<0.05, ** <0.01, ***<0.001).

Variable	MARGINAL TESTS		
	Prop.	Pseudo-F	P
	Sediment		
%Gravel (<-1.0 ϕ)	0.115	2.198	0.012*
%Very coarse sand (-1.0-0.0 ϕ)	0.103	1.961	0.021*
%Coarse sand (0.0-1.0 ϕ)	0.109	2.083	0.017*
%Medium sand (1.0-2.0 ϕ)	0.113	2.164	0.012*
%Fine sand (2.0-3.0 ϕ)	0.122	2.369	0.008**
%Very fine sand (3.0-4.0 ϕ)	0.100	1.884	0.023*
%Mud (>4.0 ϕ)	0.158	3.193	0.001**
Median phi	0.148	2.954	0.002**
Sorting	0.098	1.846	0.034*
% Total organic carbon (TOC)	0.160	3.245	0.000***
%Carbonates	0.152	3.058	0.000***
	Water column		
Salinity	0.139	2.7404	0.002**
Turbidity (NTU)	0.221	4.821	0.000***
	SEQUENTIAL TESTS		
	AICC	Prop.	Pseudo-F	P
+Turbidity (NTU)	-13.795	0.221	4.821	0.000***
	AICC=-13.795		Cum(%)=0.221	

Research suggests that benthic community distribution in offshore habitats is often characterised by faunal gradients rather than sharp discontinuities due to the lack of strong environmental changes (Brown el at. 2011, Chapter 3). This may explain the presence of the few taxa overlapping between the newly identified biozones. On the other hand, intra-biozone trait similarity was moderate and inter-biozone dissimilarity ranged between low and high, indicating high variability in the trait structure. This suggests that trait, as surrogates, were only, in part, important. Results obtained from SIMPER showed considerable trait overlap between biozones indicating that functionality was maintained between biozones. This is particularly the case for biozone 1, 3 and 4, which share movement methods and feeding traits, among others.

5.5.2 Biozone identification

Preservation of overall ecosystem function is implicit to the concept of marine spatial planning. This is not guaranteed in practice especially when multipurpose interests are involved. This chapter integrated sediment, taxonomic and biological trait data and proposed new biozone clusters for inclusion into marine spatial planning. Data not originally intended for defining biozones were repurposed. This led to challenges, particularly during the biozone identification stage. Cluster analysis and nMDS were used to identify biozones. Different types of association measure and cluster analysis produce different sample groupings, as would be expected. Due to

the low number of samples, minor changes in sample groupings had large impacts on biozone characteristics and boundaries.

Results illustrate consistently occurring associations of stations belonging to BZ1 BZ2 and BZ4, and sub-groups. For instance, J4-P4, L3-K3 and S6 were interpreted at a level where between-group difference might seem greatest. Since there is no reliable objective means of determining the optimal association measure, cluster analysis method, or number of groups, it was necessary to rely on comparisons of classifications with PERMANOVA. Results showed that the between-group difference is negligible. Therefore, subgroups were merged to form BZ3. The proposed biozone model divides KZN mid-shelf into four biozones with boundaries determined by gradients in the biophysical variables shown to be important in determining species and traits distribution patterns (Fig 5.2A). This is in contrast to the existing predefined model (Fig 5.2B) dividing the shelf into a complex mix of sediment and physico-chemical categories with sub-category biozone compartment spatially far-removed. The use of Gower's similarity (robust with heterogeneous data) was an important consideration in this study, as it suggests that the identified biozones can be optimised with any reliable benthic data.

5.5.3 Representability of proposed biozones

The revised model is likely a better predictor of spatial variation in biodiversity patterns, as well as ecosystem processes, as it was based on directly measured biological patterns (Stevens and Connolly 2005). Each biozone cluster in the revised model supported a statistically unique suite of biota (species and trait assemblages), associated with specific habitats and therefore also the environmental variables characterising these habitats (e.g. Port Durnford reef complex=BZ 1, uThukela mudbanks=BZ 2, among others), reflecting their ecological relevance.

These strong patterns in macrobenthos assemblage composition in relation to specific habitat characteristics provided the basis for a refined biozone model. Proposed biozone categories have unique biodiversity values in terms of representing individual species and traits, abundance of both species and trait modalities, species assemblages and functional structure. The importance of macrobenthic fauna in ecological processes is well documented (Hutchings 1998, Rosenburg 2001, Harmelin–Vivien et al. 2009) and representation and protection of both biodiversity and the ecological processes that sustain biodiversity and ecosystem services is a goal of marine conservation planning (Roberts et al. 2003, Frid et al. 2008). Overall, the refined biozone model is a tested surrogate for benthic biodiversity patterns, which can usefully inform marine spatial planning in KwaZulu-Natal.

5.5.4 Potential key drivers

Understanding the environmental variables that determine the biodiversity pattern will help in the effective conservation plans of coastal habitat. The distribution and composition of soft-bottom macrobenthic communities are potentially influenced by numerous environmental variables comprising characteristics of both the underlying seafloor and the overlying water column (Gray 1981, Gray and Elliott 2009, Brown et al. 2011). Depending on the spatial extent considered, certain variables may prove to have the strongest effects on biological features (Gogina and Zettler 2010). BIO-ENV results identified two potential key drivers of macrobenthic patterns within the proposed model. These indicated the importance of the uThukela outwelling. Oceanic features such as this is known to positively influence abundance and diversity of marine taxa by improving food availability, biological development and survival (Olafsson et al. 1995, Cowen and Sponaugle 2009, Dou et al. 2016). In contrast, as a natural disturbance agent, this feature may also have deleterious effects on the marine taxa, thus determining community structure and distribution (McArthur et al. 2010b). The large volume of fine sediments brought into the shelf during periods of high river flow results into a highly turbid water. This can reduce light transmission, thereby influencing the relative importance of primary production (Thrush et al. 2004). Nonetheless, high-resolution remote sensing data might throw the on the role and influence of terrigenous input (Lück-Vogel et al. 2016). Therefore, synchronisation of high-resolution multispectral imagery and ground truthing turbidity, primary productivity and sediment data can thus improve the classification accuracy of the proposed biozone model. Variables relating to sediment characteristics (e.g. grain size) are regarded as particularly important drivers of community composition in many studies (Gray 2002). Sediment characteristics and salinity were also considered as major influences in this study.

5.5.5 Implications for revised biozone model

The key to understanding and managing the biodiversity of soft-bottom benthic systems is an appreciation of the contributory functions of different organisms, communities, and habitats (Thrush et al. 2004, Snelgrove et al. 2014). The proposed model provides a useful tool that allows identification of important ecological attributes, defining foundational ecological principles for the study region, and developing planning priorities to guide effective MSP for conservation and management of biodiversity. This revised model resulted in ecological meaningful representatives of habitats and functional trait and taxa utilising and residing in these habitats. This allows a MSP exercise with clear expectations about what uses might be best suited across different areas. As an example, the proposed model reaffirms the widely

acknowledged importance of the uThukela mudbanks not only as a unique benthic habitat (MacKay et al. 2016), but also an important location on the KZN Bight for larvae of non-planktonic species as well as purely planktonic species (Beckley et al. 2002), fisheries (Fennessy and Groeneveld 1997, Lamberth et al. 2009) and more importantly a Phakisa proposed MPA. By incorporating these foundational principles early in the MSP process, this will likely result in suitable protection of important ecological processes and even create a spatial refuge from natural and anthropogenic disturbances, and perhaps to better stabilise food-web dynamics in these biologically productive and important areas (e.g. uThukela) (Foley et al. 2010). In addition, the proposed model provided insight regarding how ecological principles might be applied through ecological trait analysis. The fact that boundaries were defined by environmental variables found to be important in biotic patterns, improved the model to describe important ecological attributes of assemblages at a relevant scale, thereby allowing planning to begin to prioritise the most valuable habitats on the KZN mid-shelf. Eventually, the planning process will need to be informed by other ecological dimensions such as epifauna (Lester et al. 2013), however, studies that integrate biotic pattern and physical characteristics provide a useful starting point for advancing MSP.

Bio-physical based habitat surrogates are a potentially cost-effective, time efficient method for initial identification of priority areas to manage diversity of shelf and coastal marine ecosystems (Ward et al. 1999, Yekta et al. 2017). However, there is limited understanding of the variables that determine occurrence and patterns of most marine organisms (Hutchings et al. 2002). Use of bio-physical based habitat surrogates that protect particular habitat types will lead to the protection of a larger suite of species whose conservation needs, distribution and abundance remains unknown (Dixon-Bridges et al. 2014). Throughout the marine planning process it has been recognized that testing of effectiveness of surrogates is required to better define ecosystems and habitats at the scale relevant to MSP (Ehler and Douvere 2009, Collie et al. 2013, Snelgrove et al. 2014, McHenry et al. 2017). Studies such as this are crucial to ensure the success of MPA's in achieving representation and conservation of biodiversity in a system established.

The selection and use of biodiversity surrogates is part of conservation planning, yet there is no coherence in the selection procedure (Pressey 2004). Recognising and testing of suitable biodiversity surrogates will increase the likelihood that the selection of individual marine protected areas (MPAs) results in successful representation and protection of biodiversity and the associated ecosystem processes and services (Malcolm et al. 2012) (e.g. the proposed uThukela MPA through operation Phakisa). Benthic macrofauna plays a key role in marine

ecosystem, being involved in cycling of nutrients and detrital decomposition and constituting a food source for higher trophic levels (Constable 1999, Reiss et al. 2010). Macrobenthos are known to have low dispersal rates and relatively long life cycles, comprising diverse species with different tolerances to stress (Constable 1999, Borja et al. 2000). Due to these characteristics, macrobenthic species are ecological indicators of disturbances occurring in their habitat, either from natural or anthropogenic factors, being therefore widely used in marine monitoring and management programs (Borja et al. 2011, Schiele et al. 2014). Moreover, macrobenthos spatial configuration and heterogeneity have important implications for the distribution and relative abundance of other marine organisms (Thrush et al. 2001, Anderson et al. 2009). Therefore, macrobenthic based biodiversity surrogates similar to the revised biozone model developed in this chapter is likely to represent spatial variation of other taxa (Reise 2002, Solan et al. 2004, Anderson et al. 2013, Dutertre et al. 2013) as well as fortuitously represent other groups with similar patterns or groups that co-vary with macrobenthos spatio-temporal patterns (Bridge et al. 2016). As such, a network of MPAs selected to represent macrobenthic communities ultimately include species of other taxa and groups at a rate significantly greater than MPAs selected at random or MPAs selected using biophysical habitat with assumed value (Shokri et al. 2009, Yekta et al. 2017). The proposed model recommended in this chapter is a more accurate representation of variation in macrobenthic patterns and ecological functions. This suggests that future MSP planning should incorporate macrobenthic patterns in the classification process to improve accuracy of a proposed surrogate for capturing biodiversity patterns and to minimise discrepancies associated with biophysical based design. The proposed model has potential for wider application to other shelf and coastal marine environments, however, warrants further testing using other ecological components (e.g. epifauna and fish data).

5.6 Conclusion

This chapter integrated habitat characteristics, taxonomic and functional attributes to refine the predefined biozone model as used by various South African agencies responsible for conservation and management. Four benthic biozone clusters were identified using multivariate analysis. Each biozone cluster in the revised model supported unique species and trait assemblages distributed according to specific habitats and therefore the environmental variables characterising these habitats. The refined model resolved into a simple model, with boundaries determined by gradients in the biophysical variables shown to be important in determining species and traits distribution patterns. More importantly proposed model corresponds to the known habitats along the region. Overall, the proposed model is likely a better predictor of

spatial variation in ecosystem processes and biodiversity as it is based on a known surrogacy value of biological patterns (taxonomic and biological trait patterns), however, reliability can be affected most notably by trait used. The integration of sediment characteristics, taxonomic and functional patterns in other habitat classification systems can likewise improve the surrogate value and thus the capacity for effective spatial planning of MPAs.

CHAPTER 6. GENERAL DISCUSSION AND CONCLUSION

This study formed part of a larger, multi-disciplinary, multi-institutional programme under the auspices of the African Coelacanth Ecosystem Programme (ACEP) Surrogacy project, which investigated the validity, and robustness of habitat surrogacy approaches for biodiversity patterns mapping. Macrobenthos community characteristics and functional attributes tested whether infauna distribution is a proxy for overall biodiversity patterns within identified offshore biodiversity zones on the KwaZulu-Natal (KZN) shelf, between Port Durnford and uMkhomazi.

Chapters 3 and 4 answer the main study questions by addressing hypotheses posed in the introduction. The outcomes of the study provide a substantial new body of data about benthic habitats and are valuable contributions to the poorly studied KZN shelf environment. Furthermore, it was identified that existing MSP predefined biozones did not adequately capture spatial variation in both macrobenthic community and trait structure. The findings of Chapter 5 contribute to the refinement of the predefined marine spatial planning biozones and will improve conservation initiative for this ecosystem.

This study described macrobenthic communities and functional trait structure of the KwaZulu-Natal mid-shelf. Macrobenthos taxonomic and trait structure were compared and related to sediment and water-column habitat characteristics. Patterns observed were further related to the predefined marine spatial planning (MSP) biozones to test the validity of this as an overall ecosystem surrogate. The principal hypotheses under investigation were that there are discontinuities in taxonomic and trait composition along the shelf and these differ relative to the predefined MSP biozones. Communities were classified in terms of their taxon composition and the ecological function based on biological traits of constituent taxa.

6.1 Study contribution to understanding of subtidal east coast ecosystem

The KwaZulu-Natal mid-shelf sheltered a diverse macrobenthic community, this in itself making biodiversity conservation a priority for the area. Based on broad taxonomic groupings, Polychaeta were the most speciose group accounting for 45% of the total fauna collected and the second most numerous group accounting for 27% of the total abundance. Peracarid crustaceans were also an important faunal component accounting for 34% of the total fauna, while being the most abundant taxa accounting for 60% of the total abundance. Crustaceans, in decreasing order of number of taxa, were mainly Amphipoda followed by Decapoda including

Brachyura, Penaeidea and Caridea, Isopoda, Tanaidacea and Cumacea and Mysida sharing equal numbers. Mollusca contributed an average of 7% to the total fauna sampled and 3% to the total number of individuals. Bivalves overwhelmingly dominated molluscan fauna, accounting for 71% of the number of mollusc fauna, Gastropoda were less diverse (22%), and Scaphopoda were rarely sampled (7%). The remaining macrofaunal groups contributed the least to the number of taxa and abundance. The patterns of species diversity documented in this study conformed to the often-described general pattern of shelf environment under riverine influence. This pattern has been reported from a number of mid-shelf habitats in different geographical regions and differing in the nature of basic environmental gradients driving the biotic patterns and processes. Low species richness and species diversity on the muddy habitat off the major estuarine system has been recorded in other tropical and subtropical regions (e.g. off Amazon Estuary in Brazil (Willems et al, 2015)) and in temperate regions (e.g. off Vilaine and Loire estuaries in South Brittany (Dutertre et al, 2013)). Overall, the higher diversity values recorded in this study appeared to be influenced by the higher number of polychaetes and peracarid crustacean species. The high diversity of macrobenthos in this region, in part, may be related to the fact that the studied area is at the biotic transition between two biogeographical regions (tropical and subtropical bioregions) (Teske et al. 2011). Macrobenthos, for example, include possible endemic species and representatives from tropical regions north of Western Indian Ocean (Huber 2015) brought onto the shelf as larvae by the Agulhas Current (Lutjeharms 2006b). Despite this high richness and diversity, this is, however an under-representation of the true richness based on Chao 1 and 2 richness estimator. The difference between the results derived from these two estimators and observed is high.

Multivariate analyses of the 57 samples collected in this study identified seven major sample groups, reflecting differences in shelf habitats in terms of sediment and taxon composition of macrobenthic communities. Five assemblages showed limited geographical distribution, whereas two were more widely distributed. These assemblages provided a baseline against which the surrogate habitat classifications could be measured.

KZN mid-shelf communities are particularly diverse, supporting an abundant and taxon rich community. This is due to the heterogeneous sediments characterising habitats here. Grain size heterogeneity is known to influence richness (St Pierre and Kovalenko 2014) and support diverse macrobenthic communities (Ellingsen 2002, Santos and Pires-Vanin 2004). This is, in part, due to the increased availability of potential niches for many species (Probert and Wilson 1984, Hutchings et al. 2002). In tropical and subtropical regions, the coexistence of unconsolidated sediment (including coral rubble) and reef biotopes is frequent (Alsaffar et al.

2017). Such was exemplified by Port Durnford reef complex stations characterised by medium-coarse sand (median phi=0.89 ϕ) and warm bottom water (20.38°C). High level of complexity associated with this mosaic of habitats provided a wide range of potential ecological niches, across a small spatial scale, promoting high variation in stochastic species occupancy patterns (Barton et al. 2013). Furthermore, these habitats provide hard attachment and an elevated position off the sea floor, enhancing the food supply for sessile filter/suspension feeders (Starmans et al. 1999). In this case, this was exemplified by the high dominance of filter feeding anthozoa occurring exclusively at these stations and by the occurrence of fossorial amphipods, *Ampelisca sp. 3* and *A. diadema*. Dominance of filter/suspension feeders may also be related to the irregular pulses of organic matter fluxes from the upwelling cell in the vicinity (Lutjeharms et al. 1989), which also benefit opportunistic species (Soto et al. 2016). Naturally, the species that feed on surface detritus are better adapted to those conditions (López-Jamar et al. 1992), as reflected by the presence of *Ophioroidae sp.2.* Interestingly, the polychaetes of the family Capitellidae (*Notomastus laterice*us and Capitellidae sp) and Spionidae (*Prionospio nirripa*), considered as opportunistic organisms were also recorded in low abundance. Seemingly, the organic matter accumulating in the interstitial spaces of sediment was sufficient to allow for the colonisation and successful establishment of a community of such opportunistic taxa. The faunal component here was also characterised by the presence of tubicolous and free-living carnivorous fauna (*Onuphis eremita, Nephtys capensis* and *Mandibulophoxus stimpsoni*). The preference of carnivores to coarser sediments with low levels of mud is well-established (Tena et al. 1993, Muniz and Pires 1999, Santos and Pires-Vanin 2004). In these habitats, the large interstices among grains can create space enough to favour the mobility and feeding of carnivores, proliferation of potential prey organisms and oxygenation of the sediments (Fenchel 1970, Gaston 1987, Muniz and Pires 1999). Hydrodynamic conditions have been reported to influence sediment characteristics and physico-chemical properties of the water column (Dutertre et al. 2013). Strong hydrodynamic conditions induce high environmental selectivity, which in turn results in relatively low species richness (Dutertre et al. 2013, Willems et al. 2015, Veiga et al. 2017). Therefore, hydrodynamic conditions here may explain the low richness and composition recorded.

The uThukela mudbanks area revealed a unique community, low in number of taxa and abundances. Free-living carnivorous nephytids (*Aglaophamus sp.1* and *A. dibranchis)* dominated communities at these stations. Other abundant carnivores recorded here were *Pallidae palliderosa and Linopherus microcephala.* The scaphopod *Antalis longitrosa* and the bivalve *Dosinia sp.2* formed the intermediate faunal components of this community. Rare

faunal components of this community include, a parasitic isopod family Gnathiidae and the amphipod *Leucothoe spinicarpa* that inhabit sponges as well as the pelagic prawns, *Lucifer* sp.1 and caprellid amphipods that cling to algae, hydroids or bryozoan, indicated the presence of an exposed rocky component as a result of the coarse paleo-dune cordon which runs along the 60 m isobaths here. The large volume of fines brought onto the shelf during periods of high river outflow here increases the turbidity and nutrient input. The deleterious effect of these can alter benthic faunal composition. Numerical dominance of few species can be indicative of a stressed ecosystem (Méndez 2002). Therefore, the dominance of mobile carnivores here can be indicative of the stability and recovery potential of the benthic ecosystem when facing environmental change and mobile fauna may contribute to juvenile dispersal (disturbance and sediment deposition) (Bonsdorff and Pearson 1999, Foley et al. 2010, Pilditch et al. 2015). From a benthic ecosystem function perspective, dispersal, recolonization and connectivity are essential for maintaining biodiversity and the resilience of the ecosystem (Pilditch et al. 2015).

A station between habitats (J4) characterised by medium-fine sand (median phi=2.13 ϕ) with relatively warm near-bottom water presented species with contrasting mobility and feeding habit: burrowers, tube-dwellers and free-surface dwellers and may enhance predator–prey interactions, which determines food web stability and the existence of inter-specific relationships (Pires-Vanin et al. 2011). The community sampled here was characterised by a fossorial carnivorous amphipod (*Mandibulophoxus stimpsoni*). Notable feature of this assemblage was an abundant *Callichirus* population. This genus is presented in Barnard (1950) as *Callianassa* but has recently been moved to the genus *Callichirus* (Sakai 2011). Barnard (1950) reported this taxon to occur on the inner shelf (depth 36.6 m) off the KZN coast (Durban). Recently no further mention occured in local literature until it was also reported by Untiedt (2013) around the same depth range (22-27 m). This study reaffirms the importance of this population at this location, and also at the mid-shelf depth.

Samples collected between uThukela and uMhlali were characterised by a coarser grade of fine to sandy-gravel sediment (median phi 0.97 ϕ) with relatively cooler near bottom water (19.36°C). The assemblage here was characterised by the presence of interstitial fauna such as sipunculids (*Phascolionidae sp.1* and *Aspiodosiphon sp. 1*) and the carnivorous polychaete (*Goniadella gracilis*). Samples collected between uMdloti and Durban were characterised by a coarser grade of fine sand (mean phi=2.38 ϕ) with cooler near bottom waters (17.78°C) which hosted a filter feeding amphipod *Ampelisca diadema* and the isopod *Amakusanthura africana.* Among other taxa recorded here, notable was *Lanice conchilega* presented at relatively high abundances. Sand masons (*L. conchilega*), which lives in a tube of sand or shell breccia

attached to an inner thin organic layer are considered highly important bioturbators in macrobenthic habitats (Rabaut et al. 2007, Van Hoey et al. 2008). The tube itself is crowned with a sand-fringe, which protrudes 1–4 cm above the sediment surface (Rabaut et al. 2007). Specifically, benthic fauna type of tube construction and reworking mode are essential traits that regulate biological sediment mixing, which enhance sediment oxygenation and redox gradients and ultimately the benthic respiration and denitrification (Hansen and Kristensen 1997, Solan et al. 2004, Norling et al. 2007). This increases the hospitability for other organisms that are sensitive to low dissolved oxygen levels. Such benthic fauna through irrigation of burrows and tubes can also offer refugia for other species and increases sediment stability (Eckman et al. 1981). Tube aggregation further improves the settlement of passively transported particles (Passarelli et al. 2012) enhancing food availability for deposit feeding fauna. This was indicated by the presence of the facultative omnivores *Onuphis eremita* in this community.

Samples collected south of Durban to uMkhomazi (surrogacy samples) clustered together and were typified by an assemblage with a preference for cooler water (19.13°C), fine-coarse sand (median phi=0.99 ϕ) with relatively higher sediment carbonates (>40%). Noteworthy was the large amount of biogenic material in the form of mollusc shells (personal observation in sediment), but the recovery of these as live specimens was relatively low. Fauna collected here were characterised by a wide range of amphipod and polychaete species with a distinct dominance by the families Ampeliscidae and Unciolidae. *Byblis gaimardii, Ampelisca diadema* and *Unciolella spinosa* were found to contribute the most in terms of abundance. These fossorial crustaceans are presented in Griffiths (1974a): *U. spinosa* at 54 m depth off Umzimkhulu and *B. gaimardii* at 94 m depth. These are in good agreement with the depth range considered here (50-80 m isobath), besides being recorded further south of the study area. McClurg (2004) considered these as important constituents of the marine benthos along the KwaZulu-Natal continental shelf. Both of these Families comprise mostly of detritus-feeding species, with Ampeliscidae being the most diversified amphipod Family in the ocean (Griffiths 1976, Dauvin and Bellan-Santini 1996). They gather organic materials from the sediment surface and filter feed from the water column, but overall show preference for fine sands and mud. Faunal components of this community, through tube construction also contribute to the habitat engineering.

6.1.1 Higher taxa and indicator groups as community surrogates

The results presented in this study identified significant pairwise correlations between the spatial patterns of species richness and that for Genera, Families and the potential indicator

taxon: Polychaeta indicator taxa indicated that even after data aggregation to the higher taxonomic levels, the species richness found in this study was retained. The spatial structuring of the macrobenthic community of the KwaZulu-Natal mid-shelf can be reliably approximated when community data are aggregated to high taxonomic resolution (Genus, Family) and/or when restricted to one group of benthic organisms (Polychaeta). Further, spatial ecological patterns obtained from higher taxonomic resolution could be used for predicting the pattern for the species richness in rapid biodiversity surveys, where the objective is to examine overall biodiversity patterns or for spatial patterns estimated by multiple groups (Tyler and Kowalewski 2017, Yekta et al. 2017).

These results are in accordance with findings of Heino and Soininen (2007) who found significant correlations between assemblages based on species richness and those constructed by aggregating data to Genus and Family taxonomic level. Mackie et al. (1997) and Olsgard et al. (2003) showed that polychaetes are good surrogates for whole macrobenthic assemblages. The implication is that the limited association between assemblages based on species richness and those higher taxonomic levels may have be violated by the magnitude of richness in each taxonomic level or indicator taxa and, thus this limits the ability to infer richness since members of other taxa may maintain species diversity (Joydas and Damodaran 2009). Moreover, when species of a community are taxonomically distinct at higher taxonomic levels (e.g. Phylum, Class), then the community is more likely to show a correlation between species richness and richness for higher taxa in comparison to a community in which the species are distinct in lower taxonomic resolutions such as genus (Yekta et al. 2017). The decline in the correlation coefficient values from finer to coarser resolutions may occur, in part, due to the difficulties in assigning organism to a specific taxonomic level. This leaves an organism as unknown and therefore the richness of that taxonomic level would be reduced (Shokri and Gladstone 2008).

Although the outcomes of this study are consistent with previous studies demonstrating that coarser taxonomic resolution and subset-taxa surrogates perform well in capturing spatial ecological patterns (Mellin et al. 2011), further work is needed to assess the effect of the magnitude of richness. Especially in biogeography studies, where higher taxa are poor in detecting regional changes. As a result, some of the major geographical boundaries are not well demarcated by higher taxa data (Roy et al. 1997).

The spatial pattern obtained from nMDS analyses based on Bray–Curtis similarity matrices on assemblage composition for Genus and Family levels and indicator Polychaeta taxon were similar to the pattern obtained at Species level. The second stage non-metric MDS plots of

similarity matrices of different taxonomic levels, verified that resemblance of Genus and Family levels to species level. Results of nMDS did not depict similar grouping patterns based on Amphipoda indicator taxon with that obtained from species level. However, a relatively strong correlation was observed in their matrices. This could be an artefact of high abundance of this group and the presence of monotypic Families and Genera causing a reduction in similarity. Matching biota and environmental parameters using BIOENV analysis showed turbidity and mud as important explanatory variables. These discriminations were also reflected in Genus and Family taxonomic levels and by Polychaeta and Amphipoda indicator taxa, suggesting potential applicability in detecting environmental variables responsible for overall macrobenthic patterns. Thus, this study suggests that spatial structuring of macrobenthic community and factors influencing patterns can be reliably detected when community data are aggregated to Genus and Family taxonomic level or restricted to Polychaeta and Amphipoda indicator taxa for KZN mid-shelf macrobenthos.

Coarse taxonomic levels or subset surrogates may reduce time and costs associated with identification to the species level. Consequently, more resources can be allocated to further spatial and temporal sampling (Dauvin et al. 2003). However, coarser taxonomic levels are ideally used after a close relationship between species level and coarser levels has been established (Olsgard et al. 2003), which requires the species to be identified in the first place. Unfortunately, this has not been carried out for most of the marine macroinvertebrates on the KZN shelf. For instance, there are limited comprehensive macrobenthic studies and up-to-date taxonomic guides. Those available (e.g. Barnard 1950, Day 1967) are outdated (Clarke 2005). This is particularly true as taxonomy continues to be a low priority for both researchers and funding bodies and is conducted in relative isolation from the other disciplines in the life sciences (Magierowski and Johnson 2006). Therefore, yet coarser taxonomic levels may be used as effective surrogates for diversity patterns, species level studies are still critical when assessing biodiversity to understand the structure and function of macrobenthic assemblages (Naser 2010). Because any taxonomic rank higher than species can behave as a random group of species not providing ecologically meaningful information (Bevilacqua et al. 2012) and the outcomes of taxonomic groupings may vary between habitats and trophic levels.

Although diversity patterns vary among ecosystems and organisms (Heino and Soininen 2007), the outcomes of this study are consistent with previous studies demonstrating that data aggregated to higher taxa or subset-taxa surrogates perform well (Mellin et al. 2011) and provide congruent representations of macrobenthic spatial patterns. These results tentatively

indicate that spatial ecological analyses restricted to one group of marine benthic organisms may produce meaningful proxies for assessing spatial patterns estimated by multiple groups, a potentially powerful tool in conservation planning (Ward et al. 1999). For this shelf environment, where biodiversity information is poor, comprehensive studies on which surrogacy can be based on, are still required. Especially to assess the effect of richness magnitude in testing the surrogacy value of different taxonomic resolutions. Furthermore, to determine how morphological characteristics associated with the identification of families and genus can be aligned with functional properties of an organism as this has potentially important implications for the understanding of how biodiversity is linked to ecosystem properties and function.

6.1.2 Macrobenthos functional structure and characteristics on the KZN mid-shelf

One of the main aims of this study was to determine the trait structure of soft-bottom invertebrate assemblages, to study their spatial variation and to investigate the factors that may be responsible for these variations. As the data used to describe trait composition relate to a number of benthic habitats along the KZN mid-shelf, which together comprise most of the shelf sedimentary regions, results presented provide valuable information that could be used to inform effective provincial marine spatial planning. This is because habitat heterogeneity and multiple habitats are a key consideration for marine spatial planning (Foley et al. 2010).

In biological trait analysis studies, the choice of traits is generally of particular importance (Kokarev et al. 2017). Nonetheless, there is no theoretical limitation to the number of traits to use, at least if a procedure justifies the selection of a subset of traits significantly associated to habitats (Kleyer et al. 2012). Different numbers of traits and trait categories produce, different views of relationships between functional diversity/ecosystem functioning and species richness, with fewer traits producing an ambiguous view of assemblage functioning (Beauchard et al. 2017). In general, the inclusion of many traits as possible has been suggested, in order to obtain more perfect description of ecological functioning (Bremner et al. 2006a). This approach was adopted in this study since different body morphologies can result in different biological characteristics. Traits relating to behaviour, morphology and life history were considered for their potential ability to reflect patterns in community assembly, thereby addressing spatial variation. Overall, most traits used here were found useful to describe the observed patterns. Nine traits subdivided into 51 modalities were considered and overall, trait modalities were well represented at all stations, but no single station hosted all trait modalities.

Total abundances had a strong influence on biological trait representation (i.e. specific traits were present in higher abundances in stations where crustaceans were also recorded in high abundances), highlighting the ability of changes in macrobenthos abundance to drive trait frequency (Hewitt et al. 2008, Paganelli et al. 2012). On the other hand, benthic communities along the mid-shelf were characterised by the dominance of a few taxa, combined with a large pool of rare taxa accounting for 30% of total fauna (Chapter 3). Rare species often have traits that are distinct from those of common species (Mouillot et al. 2013). These 'rare' traits may be a reflection of a richer variety of available food resources and microhabitats that provide shelter from predation created by the environmental conditions (Ellingsen et al. 2007). For example, the grazing amphipod, Caprellidae sp.1 that clings to algae, only appeared off uThukela, despite being relatively unimportant in terms of abundance, it added traits (grazing) otherwise unrepresented, implying enhanced primary production and organic-matter flux as these relies on the grazing rate of planktonic heterotrophs (Wong and Dowd 2015, Alsaffar et al. 2017). This suggests that while faunal abundance may exert strong influences on biological trait frequencies, functional diversity could increase with species loss if functionally unique species are higher in abundance relative to less unique species (Petchey and Gaston 2006). In this study, two habitats Port Durnford and uThukela exemplifies this, where the constituent taxa were low in abundances and represented rare fauna that contributed to the maintenance of habitat functionality.

Examination of functional trait composition provided information on the range and distribution of traits and how they relate to environmental variables. Differences in the relative proportion of biological traits between habitats are in line with the habitat templet and environmental filtering concept, which state that the environment dictates community assembly through selection of specific species traits (Townsend and Hildrew 1994). In this study, the differences in trait are the reflection of the gradient in the community structure influenced by environmental parameter such as sedimentary characteristics (%mud and very coarse sand, TOC, carbonates) and hydrological gradient (turbidity, chlorophyll-a and DO). Results showed a clear difference in functional profiles across stations (i.e. the community weighted mean values for each single trait-category). Movement in sediments (surface dweller), living in burrows (burrower) and tubes (tube dweller) were mostly prevalent in this study and have important implication in the chemistry, nutrient cycling and composition of sediment. For example, burrow dwelling could augment the oxygen level in the bottom, thus increase the hospitable environment for other organisms that cannot obtain dissolved oxygen directly from the sediment or could influence the concentration of organic matter (Rhoads and Boyer 1982). Ventilation of burrow structures and

sediment by feeding (deposit feeding) and bioturbation (sediment accretion and removal) activities increases the processes of nitrification (Aller 1982) and facilitate biogeochemical reactions that include re-oxidation of reduced compounds (Norling et al. 2007). These, including respiration activities, directly affect the quality of the organic material that is mineralised (Norling et al. 2007). Patchwork of tubes (tube dweller) can also have a significant effect on sediment stability (Eckman et al. 1981).

In marine benthic communities, several feeding groups are known to co-occur in different proportions, according to sediment characteristics. In coarse sediments, suspension feeders usually dominate the community, whereas in fine to muddy sediments deposit feeders dominates (Snelgrove and Butman 1995). Suspension feeders are obviously disadvantaged in muddy sediments due to the clogging effect of re-suspended particles and the destabilising effect by the actions of deposit feeding organisms (Rhoads and Young 1970, Moore 1977). Results presented here are in agreement with this model. A further analogy is that the relationship between sediment characteristics and feeding method may be used as an indicator of hydrographic flow (Pisareva et al. 2015). In that study, it was concluded that, generally benthic filter/suspension feeders are associated with regions of stronger flow and deposit feeders with regions of calm hydrodynamic conditions. High current velocities tend to contain high loads of suspended particles that serve as food for filter feeders. In this study, high proportions of detritus/suspension feeders, some with pelagic dispersion dominated the coarse sediment on the narrow shelf area off Port Durnford and south of Durban. These fauna gather particulate organic material from the surrounding water, thereby coupling the pelagic and benthic environment Covazzi-Harriague et al. (2007). Furthermore, analysis of traits related reproduction and larval dispersal permit, to some degree, inferences about the transport of matter within and between systems. For example, pelagic dispersion, suggested that the supply of propagules via the water column is a vital form of matter export that contributes to benthic-pelagic coupling, while asexual trait may also perform this function (Pacheco et al. 2013).

Multivariate analyses distinguished four functional trait compositions that reflect geographical position. These compositions were more governed by traits related to lifestyle and behaviour of the species (movement method, feeding method, diet preference, living habit and habitat engineering). Similar results were also obtained by van der Linden et al. (2017) in tropical estuaries, Bremner et al. (2003a), (2006b) off the British Atlantic coasts, Marchini et al. (2008) in Northern Adriatic lagoons and by Paganelli et al. (2012) in North-West Adriatic Sea. Poor representation (variability) of trait modalities related to life history may be related to the homogeneous dominance of single modalities: For example, those traits representing

reproduction modes, sexual differentiation and larval development showed little to no variation. This high dominance may be suggestive that these traits are less influenced by oceanographic features, water mass properties and sediment composition than those mentioned earlier.

Several biological traits distinguished KZN mid-shelf associated faunal assemblages by being consistently more common than others. This suggests that, depending on the relative abundance of trait modality, ecosystem functions may differ across habitats. Potential linkages between expressed functional traits and subsequent ecosystem functions can be inferred from knowledge of the weighted functional trait values within each habitat (Wong and Dowd 2015). Patterns in functional diversity across Port Durford and uThukela were similar. Low species richness and the low abundance of trait modalities contributed to these results. Functional evenness indicated that, despite low diversity, niche space were generally utilised suggesting niche complementarity and thus buffer ecosystem processes (maintenance of ecosystem functioning) (Mason et al. 2005). The fact that there was no biological trait exclusive to either habitat suggest that they were functionally similar, which is surprising given the differences in taxonomy and environmental variables between them. This result supports the idea that species turnover can occur within the constraints imposed upon biological traits (Bremner et al. 2006b) and that ecological functioning can be shared amongst assemblages that are taxonomically distinct (Hewitt et al. 2008).

Port Durnford and uThukela, characterised by coarse sand and muddy bottom, respectively, favoured species that concentrate their activity on the surface of the sediment. Mud sediment off uThukela supported detritus/deposit feeding, while this trait off Port Durnford is likely explained by the complex substratum, which offers only small spaces for fauna to dwell and also trap detritus/fine sediment within spaces (Cowles et al. 2009). The thriving mobile carnivores and scavengers of uThukela might be suggestive of recovering macrobenthic community in habitats that are frequently subjected to disturbance and sediment deposition (Bonsdorff and Pearson 1999). While some traits (e.g. soft body design and surface dweller) displayed the same pattern of dominant modalities in both habitats, other traits (e.g. clinging and attachment) off uThukela allowed identification of differences and abundance patterns of single modalities.

Trait composition south of Zinkwazi to Durban displayed high functional heterogeneity. For example, most of the modalities of the biological traits (movement method and diet preference) were almost equally represented. These findings confirm those after the application of taxonomic-based methods (Chapter 3). The high level of omnivory exhibited by KZN mid-shelf

fauna reflects an ability to utilise a variety of food sources, and could suggest that they occupy relatively wide niches (Thrush et al. 2011).

In this study, dominance of direct developing larvae was largely driven by the high number of brooding peracarid crustaceans and egg-laying gastropods with direct larval development. The type of larva an organism produces reflects its adaptation to environmental variability: species with a direct developing larval type display limited dispersive potential and greater extinction risk (McHugh and Fong 2002). On the other hand, low dispersal suggests that the persistence of populations in KZN mid-shelf relies on the immigration of adults from adjacent habitats or brought about by the Agulhas Current (Lutjeharms 2006a) and/or the recruitment of juveniles from within the habitats. Asexuality (e.g. fragmentation in annelids, fissiparity in sea stars and brittle stars) shared further insight into the persistence of populations since it control recruitment and habitat colonisation (Mladenov and Emson 1984).Overall, low larval mobility indicated that the habitats along KZN mid-shelf were relatively stable (Verberk et al. 2008). Whether the prominence of taxa with direct larval development was driven by environmental conditions (e.g. adaptation strategy to avoid being swept by the current) or whether these differences are driven by competitive interactions within the community, is difficult to determine. Nonetheless, life-cycle traits are linked to the reproductive technique of a species and to its habit (Verberk et al. 2008) and these are especially complex processes with multiple trade-offs and often induce confounding effects (Verberk et al. 2008).

6.1.3 Taxonomic vs functional approach

In this study, Genus and Family taxonomic levels and Polychaeta indicator taxon showed similar findings regarding univariate descriptors of the faunal communities. This was also true in the multivariate analysis. However, the contrasting results between Species-level and taxonomic resolution higher than Family and Amphipoda indicator taxa probably reflect differences in the ecological roles of these higher taxa and indicator taxa in different habitat types. This suggests the possibility that the variety of ecological and/or functional roles, rather than the number of individuals or taxa within a taxon, may be a better determinant of the suitability of a surrogate set.

Ecosystem functioning is governed more by functional assemblages than by taxonomic assemblages (Walker 1992). Changes in functional diversity are thus more likely to affect the stability, resistance and resilience of species assemblages than changes in taxonomic diversity (Bellwood et al. 2002, Guillemot et al. 2011). For these reasons, conservation planning should incorporate functional criteria in the analysis to complement taxonomic data and improve

efficiency (Guillemot et al. 2011, Heap et al. 2011, Jackson and Lundquist 2016). In this study, MSP biozones were generally weak surrogates for both taxonomic and functional fish data. For both, results were highly variable but it was noted that for taxonomic data there were some agreement at specific habitats. Since both types of data did not provide the same general pattern suggests that conservation plans built on taxonomic criteria could not be transposed to functional criteria, and *vice versa*. Therefore, integration of both data types is deemed a viable option for effective conservation.

The taxonomic approach showed that KZN mid-shelf is not homogenous in terms of faunal assemblages, rather different faunal assemblages are characteristic to specific habitats along the mid-shelf. Trait categories were expected to tie with the taxonomic approach since the trait structure reflected the functional characteristics of the dominant species within assemblages. However, this was not the case here, since changes in phylogenetic diversity of species assemblages are not explicitly linked to change in functional diversity (Gibson et al. 2001a). Instead, traits analysis advanced the knowledge of community of organisms as a complement to a taxonomic composition analysis of abundance and distribution. Nonetheless, biological trait analysis proved to be a sensitive method of distinguishing differences between benthic communities and as outlined above provided complementary information and essential features of macrobenthic faunal communities on the KZN mid-shelf (Alves et al. 2014, Shojaei et al. 2015). Although multivariate patterns obtained through the taxonomic approach were not overlaid on that obtained through BTA analysis, community distributions related to a similar set of environmental parameters. Important to biodiversity protection, yet uncertain, is the issue of building a sound indicator system of biodiversity that could be standardised across organisms and disciplines. In this context, the combination of taxonomic and functional attributes has the potential to lead to improved biodiversity assessment tools (Díaz and Cabido 2001, Villéger et al. 2010).

Study of community composition and diversity in terms of functional traits can provide mechanistic insight into ecosystem functioning. Thus, the inclusion of both taxonomic and functional trait diversity can be useful when developing comprehensive management approaches for ecosystems (Lavorel et al. 2011).

6.1.4 Relation of KZN mid-shelf macrobenthic fauna with habitat features

Considerable number of studies has been carried out to understand the role of environmental factors in structuring the macrobenthic community in tropical coastal habitats (Alongi 1990,

Sivadas et al. 2013). However, the majority of the studies were based on species diversity, and very few studies have focused on the functional diversity, especially in the tropical/subtropical developing countries (Mertz et al. 2007). This study provides an opportunity to understand the biodiversity-environment relation of the KZN mid-shelf, and the knowledge of such natural variation in biodiversity patterns will be helpful for effective conservation plans of these ecologically important habitats. The first step to identify and understand the drivers that shape the structure of natural assemblages is to define their distribution patterns, based on which explanatory models of structuring processes can be proposed (Underwood et al. 2000).

The macrofaunal community patterns showed that turbidity and mud best explained overall patterns in taxonomic and functional composition. This congruence between taxonomical and functional dimensions of community organisation suggests that the functional groups and species composition seem to be modulated by the same environmental factors and possible processes acting at the same spatial scales. Overall, the taxonomic composition of faunal assemblages along the KZN mid-shelf showed a higher level of variation between stations along an overall environmental gradient than did the biological traits composition.

The large volume of terrigenous fines brought onto the shelf by the uThukela Estuary outflow increases the turbidity of the shelf waters so that the nutrient rich plume waters are also available to primary producers in mid-shelf waters. Boundaries between different water masses are characterised by high primary production (Mann and Lazier 1996). The macrobenthic community at this station was significantly affected by nutrient input coupled with mud from the Thukela. It was no surprise that sedimentary characteristics were the important ecological drivers underpinning biodiversity patterns. Because infaunal species inhabit spaces between sediment grains, as such their feeding, mobility and reproduction behaviours are regulated by sediment characteristics (Hirst 2004). This, therefore, reinforces the animal-sediment interrelations. Huang et al. (2014) in their study of predictive mapping of soft-bottom benthic biodiversity using a surrogacy approach in Carnarvon shelf, Western Australia, arrived into at this important conclusion.

Based on the patterns of db-RDA plot, it can be concluded that the communities and traits in Port Durnford and the Durban Eddy region were mostly influenced by sediment grain size. The Port Durnford community was significantly correlated with the proportion of medium and coarse sand, while the Durban Eddy area was significantly correlated with the proportion fine sand in the sediments. The orientation of the macrobenthic community and associated traits sampled from south of Durban to the uMkhomazi area are in the centre of the db-RDA plots

(Chapters 3 and 4), suggesting that the measured environmental parameters in this study do not adequately account for the biotic variation at these areas. The presence of biogenic elements in this area positively influences macrobenthic biodiversity and function. Sediments in these stations were characterised by a significant shell component as shown by high carbonate content recorded in these stations (Chapter 3). Biogenic structures (polychaetes tubes, gastropods shells) provided refuge areas and supported gastropod egg capsules that were found attached to dead gastropods and shell fragments. The presence of high polychaete tubes densities (network) reduces water flow at the sediment surface (Passarelli et al. 2012). This improves the settlement of both inert and living particles (Friedrichs et al. 2000), and enhances the accumulation of passively transported sediment and organic particles. Foraminifera tests (shell) provide an additional biogenic structure (Peachey and Bell 1997). In this study dead foraminifera were used by *Dipolydora capensis* as burrows (Untiedt 2013), which in turn contributed to the habitat heterogeneity (McArthur et al. 2010a).

The value of total organic carbon (TOC) content to macrobenthos as food source is well established (Alongi and Christoffersen 1992, Snelgrove and Butman 1995, Soto et al. 2016). However, in this study impoverished fauna in both number of taxa and abundance were recorded in stations with high TOC. This is not indicative of the absence of any direct relationship with TOC, but, suggest that the values of TOC include the refractory component, which is of little nutritional value to macrobenthos (Pilditch et al. 2015). Measured TOC does not accurately reflect the amount of labile organic carbon (Nodder et al. 2003). The values of water column Chl-*a* concentration suggested that pelagic primary production has a significant effect on the macrobenthic communities of the uThukela habitat as well as Durban Eddy area. Benthic primary production is probably more important, given the general dominance of deposit feeding macrobenthos. While no attempts were made to quantify benthic primary production in this study, Lange et al. (2014) found a high number of taxa in fine and medium grain sand, associated with diatoms and shell fragments and inferred that diatoms provide a good food source for benthic organisms with shell detritus providing protection. On the same token, Wieking and Kröncke (2003) inferred that benthic primary production comprised a major food source in communities dominated by sand licking, fossorial amphipods, such as Haustoriidae and Ampeliscidae, which browse directly on microphytobenthos and macroalgal cells (Grippo et al. 2011). A number of gravid female macrobenthos, especially peracarid crustaceans, were sampled here. This corresponds to the recruitment as both pelagic and benthic juveniles dominated the population. There is strong evidence that availability of high quality food is critical for the survival of juveniles and population dynamics of benthic species (stations with

high chlorophyll-a corresponded with high abundance of filter feeding *Ampelisca* and *Unciolella* species) (Covazzi-Harriague et al. 2007). On the other hand, this may be explained by the fact that crustaceans, in particular amphipods, breed almost continuously in tropical and subtropical areas (Rodrigues and Pires-Vanin 2012). This indicates that, the KZN shelf is a locally important habitat for reproduction and recruitment, providing a suitable area for larval settlement and the development of a diverse macrobenthic community.

6.1.5 Contribution to improved conservation planning (biodiversity surrogates)

The use of MPAs as a management strategy is increasing around the world (Stevens and Connolly 2005). Effective conservation planning for protection of biodiversity requires either detailed information on species distributions, or, where information on the ecology and biology of much of the marine fauna are not available, reliable surrogates for species distributions. Where surrogates are used in planning, these need to be representatives of biodiversity (habitat types, species and functioning) (Foley et al. 2010, Rees et al. 2010). The use of habitats in MPA planning is generally regarded as a useful strategy (Harris et al. 2008). The underlying principle of using broad habitat types for the creation and subdivision of MPAs into conservation zones is based on the absence of methodically surveyed biological data resulting in a considerable proportion of marine species yet to be described or even known (Gladstone and Davis 2003). Advances in remote sensing technology have enabled the production of high-resolution maps of biophysical factors that can be used to create habitat maps that are often used as surrogates for benthic biodiversity. Habitat maps as surrogates for marine biodiversity management and conservation involves the partition of the seafloor into spatial zones (Kirkpatrick and Brown 1994, Stevens and Connolly 2005, Carmel and Stoller-Cavari 2006). Each of which corresponded to a marine benthic habitat, that are relatively homogeneous in composition, community and functional attributes with similar habitat attributes and different from other habitats (Harris et al. 2008, Heap et al. 2011). These biophysical factors are known to affect communities (McArthur et al. 2010b) and when used to define habitat maps should reflect organismal diversity and result in the protection of all biodiversity associated with habitat class (Faith and Walker 1996). As such, high congruence is expected between abiotic based habitats and biodiversity. Nonetheless, efficacy of biophysical habitat surrogates for representing marine benthic biodiversity remains poorly understood (Przeslawski et al. 2011), as studies have produced inconsistent results (Faith et al. 2003, Brooks et al. 2004, Jackson and Lundquist 2016). Therefore, the use of a biodiversity surrogate, such as habitats and in the case of KZN MSP predefined biozones, for marine conservation planning should be preceded by tests, so that the surrogate actually represents variation in biodiversity at scales relevant to planning (Ward et

al. 1999, Mumby et al. 2008, Shokri and Gladstone 2013). Ideally, the classification of biozones Should be tailored to the scale of management (Stevens and Connolly 2005). In this study, KwaZulu-Natal MSP predefined biozones were tested for their effectiveness in reflecting spatial variability in macrobenthic communities (Chapter 3) and functional attributes (Chapter 4).

Although there was a relationship between abiotic variables and macrobenthic assemblages, results indicated limited overlap between marine spatial planning (MSP) predefined biozones and sediment distribution and macrobenthic community patterns, while functional characteristics showed no coherence with MSP predefined biozones. Therefore, biozones currently set for the province were not a useful predictor of spatial variation in macrobenthic biodiversity. The hypotheses set in Chapters 3 and 4 were accepted as predefined biozone classifications were found to not be representative of the macrobenthic community distributions when tested against benthic infauna data. Franken (2015) also reported limited overlap of benthic epifaunal patterns with KZN marine spatial planning predefined biozones. This non-generality of the relationship between macrobenthic community patterns and predefined biozone classifications is also found at high latitudes as demonstrated by Törnroos et al. (2013), who further concluded that predefined habitats did not meet the variation in functional structure. Studies along the subtropical regions have also found varying results in terms of bio-physically derived habitat as surrogates for distinguishing variation in soft-bottom communities (Heap et al. 2011, Mellin et al. 2011, Przeslawski et al. 2011). Over-classification and under-classification tend to occur when biophysical derived habitats are used as surrogates for biological communities (Stevens and Connolly, 2005). To test the Australian benthic seascape classification, Przeslawski et al. (2011) used epibenthic invertebrate community structures and found a limited overlap between abiotic surrogates and the benthic community structure. Results from Przeslawski et al. (2011) indicated that biophysical-derived surrogates were not biologically distinct, an example of over-classification. Seascapes defined in a heterogeneous habitat such as the Great Barrier Reef, were found to encompass more than one biological assemblage and were thus under-classified (Heap et al. 2011, Przeslawski et al. 2011). The utility of bio-physically derived habitat classifications as biodiversity surrogates is still to be fully established as studies have produced both negative (Stevens and Connolly 2005) and positive (Przeslawski et al. 2011) results.

Knowledge on the macrobenthos spatial distribution in relation to the environment is crucial to understand the functioning of the coastal ecosystem, and forms the ecological basis for sustainable management (Reiss et al. 2010). Of the suite of abiotic environmental attributes tested, macrobenthic assemblage structure (taxonomic and functional) was optimally explained

by a combination of turbidity and mud. These reflect the importance of uThukela outwelling in structuring marine benthic assemblages (Pilditch et al. 2015). Spatial variation in macrobenthic assemblages was also associated with variation in sediment particle size. Substrate type has a strong role in structuring marine benthic assemblages (Mair et al. 2009), and has been shown to act as an effective surrogate for macroinvertebrate assemblages (McArthur et al. 2010a, Dixon-Bridges et al. 2014). Using some of the biological dataset from which this study draws, MacKay et al. (2016) also found abundance of different sediment particle sizes to be a significant driver of macrobenthic biodiversity in the KZN Bight. From the biophysical variables used to define biozone model, mud and turbidity were the main variables that significantly correlated with macrobenthic invertebrate communities. Other strong relationships included fine sand and sediment carbonate. Therefore, turbidity and sediment distribution characteristics (%mud, fine sand and sediment carbonates) were the key drivers of community structure. However, for habitat classification systems such as the biozone approach to reach their full potential, basic surrogacy research quantifying the relationships between sediment grain size and turbidity and benthic community structure across a range of habitats, regions, and spatial scales is crucial (McArthur et al. 2010b).

Although MSP predefined biozones were not consistent surrogates here, the measure of biodiversity and data used should be considered in the evaluation. Biodiversity here is defined as community structure based on numerical abundance, which is driven by small animals. Future studies investigating other measures of biodiversity (e.g. biomass) may yield improved differentiation of communities among biozones. Nonetheless, the importance of using abundance-based measures for identifying community differences and efficiency of habitat as surrogates has been demonstrated by previous studies (Hewitt et al. 2008, Przeslawski et al. 2011, Törnroos et al. 2013). On the other hand, the type and the resolution of data used during habitat derivation may contribute to poor fit. One obvious explanation for KZN is that in such heterogeneous region, the sediment layer used was based on interpolated maps created from Birch (1996) coarse sediment data. This may have resulted in a poor representation of fine sand and muddy habitats and thus had an overriding effect on the other environmental factors incorporated during biozone classification. Future refinements to biozone derivations may improve their performance and utility to predict macrobenthic biodiversity across a range of spatial scales by incorporating additional abiotic layers relevant to seabed characterisation (e.g. suspended particulate organic matter, freshwater input) and updated layers of existing biophysical data (e.g. sediment data from Green and MacKay 2016).

Results here identified sediment properties as one of the ecological factors driving macrobenthos biodiversity. As such, marine spatial activities on the KZN shelf may be better focussed on the shelf unique benthic habitats (Green and MacKay 2016, MacKay et al. 2016). These complement each other (e.g. uThukela mudbank and Port Durnford reef complex) and correspond to the sediment distribution patterns on the KZN Bight (Green and MacKay 2016).

Existing MSP predefined biozones are not consistently useful surrogates because the strength and significance of their relationships with taxonomic and functional structure were incapacitated. Nonetheless, existing biozone classification (Livingstone 2016) can be effective when a biological data layer is incorporated into biozones at a relevant scale (Heap et al. 2011). The regional specificity and low level of agreement between macrobenthic patterns and predefined biozones reinforced the need to refine the biozone model for more effective and representative marine spatial planning. Therefore, biozones were weighted with macrobenthic taxonomic and functional attributes. The resultant model resolved into four biozones, with each supporting a distinct community, associated with specific habitat under the influence of well-known oceanographic features (e.g. uThukela outwelling=BZ 2, Durban Eddy=BZ 3, among others). The revised biozone classification scheme is, in part, supported by recent KZN Bight studies (MacKay et al. 2016, Untiedt and MacKay 2016), which identified distinct communities at these unique habitats. Furthermore, a study undertaken between the Phakisa proposed uThukela MPA and expanded Aliwal Shoal MPA investigating the efficiency of the existing biozone also found distinct benthic epifaunal assemblages between Zinkwazi and Durban (BZ 3) and the South of Durban to Umkhomazi (BZ 4), supporting the potential of dividing the shelf into zones (Franken 2015). Overall, these results indicated that habitat-classification (biozones and seascapes) methods based on environmental variables are useful in providing a broad-scale indication of habitat diversity at various scales (Freitas et al. 2011, Huang et al. 2011, Kostylev 2012), but they cannot entirely replace the need for biological sampling.

The proposed model is likely a better predictor of spatial variation in biodiversity patterns, as well as ecosystem processes, as it was based on directly measured biological patterns (Stevens and Connolly 2005), and therefore is considered a more accurate representation of variation in macrobenthic communities and ecological functions of the KZN mid-shelf. Each proposed biozone contains differing faunal communities with different functional characteristics. The importance of macrobenthos in benthic ecological processes is well-documented (Hutchings 1998, Pillay et al. 2007, Hewitt et al. 2008, Passarelli et al. 2012) and representation and protection of both biodiversity and the ecological processes that sustain biodiversity and ecosystem services is a goal of marine conservation planning (Roberts et al. 2003). Spatio-

temporal patterns in measures of macrobenthos biodiversity co-vary with other taxa (Anderson et al. 2009), therefore, macrobenthic pattern based biodiversity surrogate is likely to represent spatial variation of other co-varying marine fauna (Bridge et al. 2016). For instance, Gladstone (2002) suggested that marine reserves established to conserve mollusc diversity would also adequately protect total biodiversity (of noncryptic organism .5 mm maximum dimension) on rocky shores in New South Wales, Australia. This study has shown that the proposed biozone model for KZN MSP is adequate in capturing the variation in macrobenthos biodiversity represented by the revised biozone classification model and, based on the known surrogacy value of biological patterns.

Results obtained from Chapter 3 showed that fauna recorded in this study represent 60% of the KZN mid-shelf fauna. Therefore, multiple samples of macrobenthic assemblages from a range of locations subject to differing environmental influences are required to adequately conserve representative samples of biodiversity within KZN shelf. In such a case, each individual site would have a lower contribution to the overall diversity sampled and thus reduce the patchy distribution common in macrobenthic studies. The presence of transitional communities represented by a single station clearly reinforced the notion that macrobenthos is patchy distributed and vary at a very fine scale. In order to advance this knowledge, more studies documenting a great small-scale spatial variability under wide environmental domains are required. Furthermore, studies evaluating the sources of variation in macrofaunal biodiversity can share useful insight and improve the suitability of biozone classification schemes so they can act as a surrogate for biodiversity for the range of assemblages found along the shelf. However, the pressing factor to further advance the knowledge and conservation of this shelf is the need to update macrobenthic identification guides.

A beneficial extension to this thesis would be to incorporate several additional datasets not utilised for this research and relevant to biozone classification (e.g. synchronisation of high-resolution remote sensed and ground truthing data (including sea floor slope, freshwater input and suspended solutes) can improve classification accuracy of the proposed biozone model). In addition, future refined biozones should include updated layer of existing biophysical data. For instance, an updated sediment data (Green and MacKay 2016) and remote sensed turbidity data (Lück-Vogel et al. 2016). Macrobenthic distributions are only one of the several possible biotic datasets that could be used to improve classification efficiency. The inclusion of other ecological components (e.g. epifaunal communities) is likely to highlight additional important information and can help to establish whether the proposed model adequately represents overall biodiversity. It is also worthy to examine what additional conservation benefits can be provided

by the proposed biozone model. Notwithstanding the above, the use of macrobenthos to optimise the performance of biodiversity surrogates is justifiable for several reasons. Firstly, macrobenthos spatial configuration and heterogeneity have important implications for the distribution and relative abundance of other marine organisms (Gotelli et al. 2009). Furthermore, macrobenthos is one of the few groups for which such an extensive array of data are available on this shelf.

This thesis assessed the effectiveness of MSP biozone classification model as surrogates for biodiversity conservation in KZN, and found that the biozone model is not a suitable surrogate for biodiversity of macrobenthos. Subsequent analyses were constructed to support KZN MSP processes currently undertaken. Proposed biozone model will be used to inform pathways to protecting and enhancing the ecological value (being recognised as a biological productive area, presence of unique benthic habitats) of this shelf environment. While most MSP exercises are challenged by the lack of consistent, spatially comprehensive datasets, understanding the limitation of the current biozone model in representing KZN biodiversity can assist in future classification exercises (Ward et al. 1999). Further studies are required to effectively understand what additional information needs to be incorporated into MSP biozone classification to achieve high classification accuracy so that biozones can act as a surrogate for biodiversity for the range of assemblages that will be conserved within the MPA.

REFERENCES

Aarts BG. 1999. Ecological sustainability and biodiversity. *The International Journal of Sustainable Development & World Ecology* 6: 89-102.

Agardy T, Di Sciara GN, Christie P. 2011. Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Marine policy* 35: 226-232.

Akoumianaki I, Papaspyrou S, Kormas K, Nicolaidou A. 2012. Environmental variation and macrofauna responce in a coastal area influenced by land runoff. *Estuarine Coastal and Shelf Science* 3: 1-11.

Albertelli G, Covazzi-Harriague A, Danovaro R, Fabiano M, Fraschetti S, Pusceddu A. 1999. Differential responses of bacteria, meiofauna and macrofauna in a shelf area (Ligurian Sea, NW Mediterranean): role of food availability. *Journal of Sea Research* 42: 11-26.

Alexander S, Boothe P, Flint R, Giam C, Holland J, Neff G, Pequegnat W, Powell P, Rabalais N, Schwarz J. 1981. Benthic biota. In: Flint R, Rabalais N editors. *Environmental studies of a marine ecosystem, South Texas outer continental shelf.* Austin: University of Texas Press. p. 83-136.

Aller JY, Aller RC. 2004. Physical disturbance creates bacterial dominance of benthic biological communities in tropical deltaic environments of the Gulf of Papua. *Continental Shelf Research* 24: 2395-2416.

Aller RC. 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall PL, Tevesz MJS editors. *Animal-sediment relations. Topics in Geobiology* No. 100. Boston: Springer. p. 53-102.

Alongi D, Christoffersen P. 1992. Benthic infauna and organism-sediment relations in a shallow, tropical coastal area: influence of outwelled mangrove detritus and physical disturbance. *Marine Ecology Progress Series* 81: 229-245.

Alongi DM. 1990. The ecology of tropical soft-bottom benthic ecosystems. *Oceanography and Marine Biology - An Annual Review* 28: 381-496.

Alsaffar Z, Cúrdia J, Borja A, Irigoien X, Carvalho S. 2017. Consistent variability in beta-diversity patterns contrasts with changes in alpha-diversity along an onshore to offshore environmental gradient: the case of Red Sea soft-bottom macrobenthos. *Marine Biodiversity* 47: 1-16.

Alves A, Veríssimo H, Costa M, Marques J. 2014. Taxonomic resolution and Biological Traits Analysis (BTA) approaches in estuarine free-living nematodes. *Estuarine, Coastal and Shelf Science* 138: 69-78.

Anderson M. 2004. *PERMDISP: a FORTRAN computer program for permutational analysis of multivariate dispersions (for any two-factor ANOVA design) using permutation tests*. Department of Statistics, University of Auckland: New Zealand.

Anderson M, Gorley R, Clarke KP. 2008a. *PERMANOVA+ for PRIMER: guide to software and statistical methods*. Plymouth: PRIMER-E.

Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. *Austral ecology* 26: 32-46.

Anderson MJ. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62: 245-253.

Anderson MJ, Diebel CE, Blom WM, Landers TJ. 2005. Consistency and variation in kelp holdfast assemblages: spatial patterns of biodiversity for the major phyla at different taxonomic resolutions. *Journal of Experimental Marine Biology and Ecology* 320: 35-56.

Anderson MJ, Ellingsen KE, McArdle BH. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9: 683-693.

Anderson T, McArthur M, Syms C, Nichol S, Brooke B. 2013. Infaunal biodiversity and ecological function on a remote oceanic island: The role of biogeography and bio-physical surrogates. *Estuarine, Coastal and Shelf Science* 117: 227-237.

Anderson TJ, Syms C, Roberts DA, Howard DF. 2009. Multi-scale fish-habitat associations and the use of habitat surrogates to predict the organisation and abundance of deep-water fish assemblages. *Journal of Experimental Marine Biology and Ecology* 379: 34-42.

Ansari Z, Furtado R, Badesab S, Mehta P, Thwin S. 2012. Benthic macroinvertebrate community structure and distribution in the Ayeyarwady continental shelf, Andaman Sea. *Indian Journal of Geo-Marine Sciences* 41: 272-278.

Anthony JE, Gardel A, Gratiot N, Proisy C, Allison MA, Dolique F, Fromard F. 2010. The Amazon-influenced muddy coast of South America: A review of mud-bank–shoreline interactions. *Earth-Science Reviews* 103: 99-121.

Arabi S. 2010. Relationship between sediment structure and infaunal amphipod communities along the Durban outfalls region on the east coast of South Africa. MSc, University of KwaZulu-Natal, Westville.

Arkema KK, Abramson SC, Dewsbury BM. 2006. Marine ecosystem-based management: from characterization to implementation. *Frontiers in Ecology and the Environment* 4: 525-532.

Bady P, Doledec S, Fesl C, Gayraud S, Bacchi M, Schöll F. 2005. Use of invertebrate traits for the biomonitoring of European large rivers: the effects of sampling effort on genus richness and functional diversity. *Freshwater Biology* 50: 159-173.

Bale A, Kenny A. 2005. Sediment analysis and seabed characterization. In: Eleftheriou A, McIntyre A editors. *Methods for the study of marine benthos (3rd edition).* Oxford, UK.: Blackwell Science Publishing. p. 43-86.

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR. 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81: 169-193.

Barlow R, Kyewalyanga M, Sessions H, Van den Berg M, Morris T. 2008. Phytoplankton pigments, functional types, and absorption properties in the Delagoa and Natal Bights of the Agulhas ecosystem. *Estuarine, Coastal and Shelf Science* 80: 201-211.

Barnard KH. 1950. Descriptive catalogue of South African decapod crustacea. *Annals of the South African Museum* 38: 1-837.

Barros F, Hatje V, Figueiredo MB, Magalhaes WF, Dorea HS, Emídio ES. 2008. The structure of the benthic macrofaunal assemblages and sediments characteristics of the Paraguaçu estuarine system, NE, Brazil. *Estuarine, Coastal and Shelf Science* 78: 753-762.

Barton PS, Cunningham SA, Manning AD, Gibb H, Lindenmayer DB, Didham RK. 2013. The spatial scaling of beta diversity. *Global Ecology and Biogeography* 22: 639-647.

Basset A, Sangiorgio F, Pinna M. 2004. Monitoring with benthic macroinvertebrates: advantages and disadvantages of body size descriptors. *Aquatic conservation: marine and freshwater ecosystems* 14: S43-S58.

Bauer JE, Druffel ER. 1998. Ocean margins as a significant source of organic matter to the deep open ocean. *Nature* 392: 482-485.

Beaman RJ. 2005. A GIS Study of Australia's Marine Benthic Habitats. PhD, University of Tasmania, Australia.

Beauchard O, Veríssimo H, Queirós A, Herman P. 2017. The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecological Indicators* 76: 81-96.

Beche LA, Resh VH. 2007. Biological traits of benthic macroinvertebrates in California mediterranean-climate streams: long-term annual variability and trait diversity patterns. *Fundamental and Applied Limnology/Archiv für Hydrobiologie* 169: 1-23.

Beckley LE 1995. The Agulhas Current ecosystem with particular reference to dispersal of fish larvae. In: Okemwe K, Ntiba M, Sherman K editors. Status and future of large marine ecosystems of the Indian Ocean. A report of an international symposium and workshop. IUCN, Gland, Switzerland p. X + 201

Beckley LE, Hulley PA, Skelton PH. 2002. Synoptic overview of marine ichthyology in South Africa. *Marine and Freshwater Research* 53: 99-105.

Beesley P, Ross G, Glasby C 2000. Polychaetes and allies: the southern synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing: Melbourne xii.

Begg G. 1978. *The estuaries of Natal*. NTRPC Report No. 41. Pietermaritzburg: Natal Town and Regional Planning Commission.

Bellwood D, Wainwright P, Fulton C, Hoey A. 2002. Assembly rules and functional groups at global biogeographical scales. *Functional Ecology* 16: 557-562.

Bengtsson J, Jones H, Setälä H. 1997. The value of biodiversity. *Trends in Ecology & Evolution* 12: 334-336.

Bergen M, Weisberg SB, Smith RW, Cadien DB, Dalkey A, Montagne DE, Stull JK, Velarde RG, Ranasinghe JA. 2001. Relationship between depth, sediment, latitude, and the structure of benthic infaunal assemblages on the mainland shelf of southern California. *Marine Biology* 138: 637-647.

Bertasi F, Colangelo MA, Colosio F, Gregorio G, Abbiati M, Ceccherelli VU. 2009. Comparing efficacy of different taxonomic resolutions and surrogates in detecting changes in soft bottom assemblages due to coastal defence structures. *Marine Pollution Bulletin* 58: 686-694.

Berthelsen AK, Hewitt JE, Taylor RB. 2015. Biological traits and taxonomic composition of invertebrate assemblages associated with coralline turf along an environmental gradient. *Marine Ecology Progress Series* 530: 15-27.

Bertness MD, Gaines SD, Hay ME. 2001. *Marine community ecology*. vol. 550. Sinauer Associates Sunderland, Massachusetts, USA.

Bertrand Y, Pleijel F, Rouse GW. 2006. Taxonomic surrogacy in biodiversity assessments, and the meaning of Linnaean ranks. *Systematics and Biodiversity* 4: 149-159.

Bevilacqua S, Terlizzi A, Claudet J, Fraschetti S, Boero F. 2012. Taxonomic relatedness does not matter for species surrogacy in the assessment of community responses to environmental drivers. *Journal of applied ecology* 49: 357-366.

Bickford D, Lohman DJ, Sodhi NS, Ng PK, Meier R, Winker K, Ingram KK, Das I. 2007. Cryptic species as a window on diversity and conservation. *Trends in ecology and evolution* 22: 148-155.

Birch G. 1996. Quaternary sedimentation off the east coast of Southern Africa (Cape Padrone to Cape Vidal). *Oceanographic Literature Review* 6: 589.

Blanchard AL, Feder HM. 2014. Interactions of habitat complexity and environmental characteristics with macrobenthic community structure at multiple spatial scales in the northeastern Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 102: 132-143.

Blondin Á, Desrosiers G, Vervier P. 2003. Macroinvertebrates functional groups in freshwater and marine sediments: a common mechanistic classification. *Vie et Millieu* 53: 221-231.

Boersma KS, Dee LE, Miller SJ, Bogan MT, Lytle DA, Gitelman AI. 2016. Linking multidimensional functional diversity to quantitative methods: a graphical hypothesis-evaluation framework. *Ecology* 97: 583-593.

Boesch DF. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. *Marine Biology* 21: 226-244.

Bolam S, Eggleton J, Smith R, Mason C, Vanstaen K, Rees H. 2008. Spatial distribution of macrofaunal assemblages along the English Channel. *Journal of the Marine Biological Association of the United Kingdom* 88: 675-687.

Bonsdorff E, Pearson TH. 1999. Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: A functional-group approach. *Australian Journal of Ecology* 24: 312-326.

Borja A, Basset A, Bricker S, Dauvin JC, Elliott M, Harrison T, Marques JC, Weisberg SB, West R. 2011. Classifying ecological quality and integrity of estuaries. In: Wolanski E, McLusky D editors. *Treatise on Estuarine and Coastal Science*. Waltham: Academic Press. p. 125-162.

Borja A, Franco J, Pérez V. 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Marine Pollution Bulletin* 40: 1100-1114.

Borrett SR, Moody J, Edelmann A. 2014. The rise of network ecology: maps of the topic diversity and scientific collaboration. *Ecological modelling* 293: 111-127.

Bosman A, Hockey P. 1986. Seabird guano as a determinant of rocky intertidal community structure. *Marine Ecology Progress Series* 32: 247-257.

Bosman C. 2012. The marine geology of the Aliwal Shoal, Scottburgh, South Africa. PhD, University of KwaZulu-Natal. , Westville.

Boström C, Törnroos A, Bonsdorff E. 2010. Invertebrate dispersal and habitat heterogeneity: expression of biological traits in a seagrass landscape. *Journal of Experimental Marine Biology and Ecology* 390: 106-117.

Boucher K. 1975. *Global climate*. London: English Universities Press Ltd.

Bowman MF, Bailey RC. 1997. Does taxonomic resolution affect the multivariate description of the structure of freshwater benthic macroinvertebrate communities? *Canadian Journal of Fisheries and Aquatic Sciences* 54: 1802-1807.

Branch G, Griffiths C, Branch M, Beckley L. 2002. *Two Oceans. A Guide Book to the Marine Life of Southern Africa*. ABC Press, Cape Town.

Branch G, Sink K, Harris J. 2005. Biogeographic patterns in rocky intertidal communities in KwaZulu-Natal, South Africa.

Bray JR, Curtis JT. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325-349.

Bremner J. 2008. Species traits and ecological functioning in marine conservation and management *Journal of Experimental Marine Biology and Ecology* 366: 37-47.

Bremner J, Frid CLJ, Rogers SI. 2003a. Assessing marine ecosystem health: The long-term effects of fishing on functional biodiversity in North Sea benthos. *Aquatic ecosystem health & management* 6: 131-137.

Bremner J, Paramor O, Frid C (eds). 2006a. *Developing a methodology for incorporating ecological structure and functioning into designation of Special Areas of Conservation (SAC) in the 0-12 nautical mile zone*. University of Liverpool: Liverpool

Bremner J, Rogers S, Frid C. 2003b. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series* 254: 11-25.

Bremner J, Rogers S, Frid C. 2006b. Matching biological traits to environmental conditions in marine benthic ecosystems. *Journal of Marine Systems* 60: 302-316.

Bremner J, Rogers SI, Frid CLJ. 2006c. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators* 6: 609-622.

Bridge TC, Grech AM, Pressey RL. 2016. Factors influencing incidental representation of previously unknown conservation features in marine protected areas. *Conservation biology* 30: 154-165.

Brooks RA, Purdy CN, Bell SS, Sulak KJ. 2006. The benthic community of the eastern US continental shelf: A literature synopsis of benthic faunal resources. *Continental Shelf Research* 26: 804-818.

Brooks TM, Da Fonseca GA, Rodrigues AS. 2004. Protected areas and species. *Conservation biology*: 616-618.

Browder J. 1983. Environmental Studies of a Marine Ecosystem. *Bulletin of Marine Science* 33: 192-193.

Brown A. 1999. Marine invertebrate systematics and zoogeography in southern Africa: an historical overview. *Transactions of the Royal Society of South Africa* 54: 21-30.

Brown AC. 2003. Centennial history of the Zoology Department, University of Cape Town, 1903–2003: A personal memoir. *Transactions of the Royal Society of South Africa* 58: 11-34.

Brown CJ, Smith SJ, Lawton P, Anderson JT. 2011. Benthic habitat mapping: a review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuarine, Coastal and Shelf Science* 92: 502-520.

Bryden HL, Beal LM, Duncan LM. 2005. Structure and transport of the Agulhas Current and its temporal variability. *Journal of Oceanography* 61: 479-492.

Burone L, Muniz P, Pires-vanin A, Maria S, Rodrigues M. 2003. Spatial distribution of organic matter in the surface sediments of Ubatuba Bay (Southeastern-Brazil). *Anais da Academia Brasileira de Ciências* 75: 77-80.

Bustamante R, Branch G. 1996. Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. *Journal of biogeography* 23: 339-351.

Bustamante RH, Branch GM, Eekhout S, Robertson B, Zoutendyk P, Schleyer M, Dye A, Hanekom N, Keats D, Jurd M. 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* 102: 189-201.

Butman C. 1987. Larval settlement of soft-sediment invertebrates—the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanograpgy and Marine Biology* 25: 113-165.

Cacabelos E, Quintas P, Troncoso JS. 2008. Spatial distribution of soft-bottom molluscs in the Ensenada de San Simón (NW Spain). *American Malacological Bulletin* 25: 9-19.

Cadotte MW, Carscadden K, Mirotchnick N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of applied ecology* 48: 1079-1087.

Carmel Y, Stoller-Cavari L. 2006. Comparing environmental and biological surrogates for biodiversity at a local scale. *Israel Journal of Ecology & Evolution* 52: 11-27.

Carney R. 2005. Zonation of deep biota on continental margins. *Oceanography and Marine Biology: An Annual Review* 43: 211-278.

Carter R, d'Aubrey J. 1988. Inorganic nutrients in Natal continental shelf waters. In: Schumann EH editor. *Lecture Notes on Coastal and Estuarine Studies Volume 26. Coastal ocean studies off Natal, South Africa*. Germany: Springer-Verlag. p. 131-151.

Carvalho S, Cunha MR, Pereira F, Pousão-Ferreira P, Santos M, Gaspar M. 2011. The effect of depth and sediment type on the spatial distribution of shallow soft-bottom amphipods along the southern Portuguese coast. *Helgoland Marine Research* 66: 489.

Chambers SJ, Muir AI. 1997. *Polychaetes: British Chrysopetaloidea, Pisionoidea, and Aphroditoidea: keys and notes for identification of the species*. Published for the Linnean Society of London and the Estuarine and Coastal Sciences Association by Field Studies Council.

Chao A. 1984. Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of statistics*: 265-270.

Chao A, Colwell RK, Lin C-W, Gotelli NJ. 2009. Sufficient sampling for asymptotic minimum species richness estimators. *Ecology* 90: 1125-1133.

Charvet S, Kosmala A, Statzner B. 1998. Biomonitoring through biological traits of benthic macroinvertebrates: perspectives for a general tool in stream management. *Archiv für Hydrobiologie* 142: 415-432.

Chevene F, Doleadec S, Chessel D. 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* 31: 295-309.

Christiansen F, Fenchel T. 1979. Evolution of marine invertebrate reproductive patterns. *Theoretical population biology* 16: 267-282.

Clark AM, Courtman-Stock J. 1976. *The echinoderms of southern Africa*. British Museum Press.

Clark B, Steffani N, Young S, Richardson A, Lombard A (eds). 2000. *The effects of climate change on marine biodiversity in South Africa*. Anchor Environmental Consultants. Pretoria.

Clark HL. 1923. *The echinoderm fauna of South Africa*. Trustees of the South African Museums.

Clarke DT. 2005. The relationship between sediment composition and infaunal polychaete communities along the southern coast of Namibia. MSc, University of the Western Cape, Cape Town

Clarke K, Ainsworth M. 1993. A method of linking multivariate community. *Marine Ecology Progress Series* 92: 205-219.

Clarke K, Warwick R. 1988. Quantifying structural redundancy in ecological communities. *Oecologia* 113: 278-289.

Clarke K, Warwick R. 1994. Change in marine communities: an approach to statistical analysis and interpretation. *National Environment Research Council, Plymouth*.

Clarke K, Warwick R. 2001. An approach to statistical analysis and interpretation. *Change in Marine Communities* 2.

Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117-117.

Clarke KR, Gorley RN. 2006. *PRIMER V6: user manual-tutorial*. Plymouth Marine Laboratory.

Clarke KR, Somerfield PJ, Gorley RN. 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology* 366: 56-69.

Claudet J. 2011. *Marine protected areas: a multidisciplinary approach*. Cambridge University Press.

Cocito S, Fanucci S, Niccolai I, Morri C, Bianchi CN. 1990. Relationships between trophic organization of benthic communities and organic matter content in Tyrrhenian Sea sediments. *Hydrobiologia* 207: 53-60.

Collie JS, Beck MW, Craig B, Essington TE, Fluharty D, Rice J, Sanchirico JN. 2013. Marine spatial planning in practice. *Estuarine, Coastal and Shelf Science* 117: 1-11.

Colwell RK, Coddington JA. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 345: 101-118.

Conlan K. 1994. Amphipod crustaceans and environmental disturbance: a review. *Journal of Natural History* 28: 519-554.

Constable A. 1999. Ecology of benthic macro-invertebrates in soft-sediment environments: a review of progress towards quantitative models and predictions. *Australian Journal of Ecology* 24: 452-476.

Cooper J, Harrison T, Ramm A. The role of estuaries in large marine ecosystems: Examples from the Natal coast, South Africa*1995*: IUCN.

Cooper KM, Froján CRB, Defew E, Curtis M, Fleddum A, Brooks L, Paterson DM. 2008. Assessment of ecosystem function following marine aggregate dredging. *Journal of Experimental Marine Biology and Ecology* 366: 82-91.

Costello MJ, Claus S, Dekeyzer S, Vandepitte L, Tuama EO, Lear D, Tyler-Walters H. 2015. Biological and ecological traits of marine species. *PeerJ* 3: e1201.

Covazzi-Harriague A, Albertelli G, Bonomi A, Fabiano M, Zunini-Sertorio T. 2007. Pelagic–benthic coupling in a subtidal system of the North-Western Mediterranean. *Chemistry and Ecology* 23: 263-277.

Cowen RK, Sponaugle S. 2009. Larval dispersal and marine population connectivity. *Annual review of marine science* 1: 443-466.

Cowles A, Hewitt JE, Taylor RB. 2009. Density, biomass and productivity of small mobile invertebrates in a wide range of coastal habitats. *Marine Ecology Progress Series* 384: 175-185.

Culotta E. 1996. Exploring biodiversity's benefits. *Science* 273: 1045-1047.

Currie DR, Small KJ. 2005. Macrobenthic community responses to long-term environmental change in an east Australian sub-tropical estuary. *Estuarine, Coastal and Shelf Science* 63: 315-331.

Currie DR, Sorokin SJ, Ward TM. 2009. Infaunal macroinvertebrate assemblages of the eastern Great Australian Bight: effectiveness of a marine protected area in representing the region's benthic biodiversity. *Marine and Freshwater Research* 60: 459-474.

Dalleau M, Andréfouët S, Wabnitz CC, Payri C, Wantiez L, Pichon M, Friedman K, Vigliola L, Benzoni F. 2010. Use of habitats as surrogates of biodiversity for efficient coral reef conservation planning in Pacific Ocean islands. *Conservation biology* 24: 541-552.

Dangerfield J, Pik AJ, Britton D, Holmes A, Gillings M, Oliver I, Briscoe D, Beattie AJ. 2003. Patterns of invertebrate biodiversity across a natural edge. *Austral ecology* 28: 227-236.

Danovaro R, Fabiano M. 1997. Seasonal changes in quality and quantity of food available for benthic suspension-feeders in the Golfo Marconi (North-western Mediterranean). *Estuarine, Coastal and Shelf Science* 44: 723-736.

Darbyshire T, Mackie AY. 2003. Species of Litocorsa (Polychaeta: Pilargidae) from the Indian Ocean and South China Sea. *Hydrobiologia* 496: 63-73.

Dauer DM, Maybury CA, Ewing RM. 1981. Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology* 54: 21-38.

Dauvin J-C, Bellan-Santini D. 1996. Ampeliscidae (Amphipoda) from the bay of Biscay. *Journal of Crustacean Biology* 16: 149-168.

Dauvin J-C, Ruellet T. 2009. The estuarine quality paradox: is it possible to define an ecological quality status for specific modified and naturally stressed estuarine ecosystems? *Marine Pollution Bulletin* 59: 38-47.

Dauvin J, Gesteira JG, Fraga MS. 2003. Taxonomic sufficiency: an overview of its use in the monitoring of sublittoral benthic communities after oil spills. *Marine Pollution Bulletin* 46: 552-555.

Dauvin J, Iglesias A, Lorgeré J. 1994. Circalittoral suprabenthic coarse sand community from the western English Channel. *Journal of the Marine Biological Association of the United Kingdom* 74: 543-562.

Dauvin J, Ruellet T. 2007. Polychaete/amphipod ratio revisited. *Marine Pollution Bulletin* 55: 215-224.

Davies CE, Moss D, Hill MO. 2004. EUNIS habitat classification revised 2004. *Report to: European Environment Agency-European Topic Centre on Nature Protection and Biodiversity*: 127-143.

Davies JL, Clayton KM. 1977. *Geographical variation in coastal development*. Longman London.

Day J. 1967. A monograph on the Polychaeta of southern Africa, Part I (Errantia) & Part II (Sedentaria). London: Trustees of the British Museum. *London: British Museum*: 1-878.

De-la-Ossa-Carretero J, Del-Pilar-Ruso Y, Giménez-Casalduero F, Sánchez-Lizaso J, Dauvin J-C. 2012. Sensitivity of amphipods to sewage pollution. *Estuarine, Coastal and Shelf Science* 96: 129-138.

De Grave S, Casey D, Whitaker A. 2001. The accuracy of density standardization of infaunal benthos. *Journal of the Marine Biological Association of the United Kingdom* 81: 541-542.

De Jonge V, Elliott M, Brauer V. 2006. Marine monitoring: its shortcomings and mismatch with the EU Water Framework Directive's objectives. *Marine Pollution Bulletin* 53: 5-19.

de Juan S, Thrush S, Demestre M. 2007. Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). *Marine Ecology Progress Series* 334: 117-129.

de Lecea A, Smit A, Fennessy S. 2016. Riverine dominance of a nearshore marine demersal food web: evidence from stable isotope and C/N ratio analysis. *African Journal of Marine Science* 38: S181-S192.

de Lecea MA, Fennessy S, Smit A. 2013. Processes controlling the benthic food web of a mesotrophic bight (KwaZulu-Natal, South Africa) revealed by stable isotope analysis. *Marine Ecology Progress Series* 484: 97-114.

de Ruijter WP, van Leeuwen PJ, Lutjeharms JR. 1999. Generation and evolution of Natal Pulses: solitary meanders in the Agulhas Current. *Journal of physical oceanography* 29: 3043-3055.

Defeo O, Barboza CA, Barboza FR, Aeberhard WH, Cabrini T, Cardoso RS, Ortega L, Skinner V, Worm B. 2017. Aggregate patterns of macrofaunal diversity: An interocean comparison. *Global Ecology and Biogeography* 26: 823–834.

Demšar J. 2006. Statistical comparisons of classifiers over multiple data sets. *Journal of Machine learning research* 7: 1-30.

Desroy N, Warembourg C, Dewarumez J, Dauvin J. 2002. Macrobenthic resources of the shallow soft-bottom sediments in the eastern English Channel and southern North Sea. *ICES Journal of Marine Science: Journal du Conseil* 60: 120-131.

Díaz S, Cabido M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16: 646-655.

Dixon-Bridges K, Hutchings P, Gladstone W. 2014. Effectiveness of habitat classes as surrogates for biodiversity in marine reserve planning. *Aquatic conservation: marine and freshwater ecosystems* 24: 463-477.

Doerries M, Van Dover C. 2003. Higher-taxon richness as a surrogate for species richness in chemosynthetic communities. *Deep Sea Research Part I: Oceanographic Research Papers* 50: 749-755.

Dolbeth M, Ferreira O, Teixeira H, Marques J, Dias J, Pardal M. 2007. Beach morphodynamic impact on a macrobenthic community along a subtidal depth gradient. *Marine Ecology-Progress Series* 352: 113.

Dolbeth M, Teixeira H, Marques JC, Pardal MÂ. 2009. Feeding guild composition of a macrobenthic subtidal community along a depth gradient. *Scientia Marina* 73: 225-237.

Dolédec S, Chessel D. 1991. Recent developments in linear ordination methods for environmental sciences. *Advances in Ecology* 1: 133-155.

Dou P, Cui B, Xie T, Dong D, Gu B. 2016. Macrobenthos diversity response to hydrological connectivity gradient. *Wetlands* 36: 45-55.

Douvere F. 2008. The importance of marine spatial planning in advancing ecosystem-based sea use management. *Marine policy* 32: 762-771.

Douvere F, Ehler C. 2009. Ecosystem-based marine spatial management: An evolving paradigm for the management of coastal and marine places. *Management* 44: 563-566.

Drew LW. 2011. Are We Losing the Science of Taxonomy? As need grows, numbers and training are failing to keep up. *BioScience* 61: 942-946.

Driver A, Sink K, Nel J, Holness S, Van Niekerk L, Daniels F, Jonas Z, Majiedt P, Harris L, Maze K. 2012. National Biodiversity Assessment 2011: An assessment of South Africa's biodiversity and ecosystems. *Synthesis Report. South African National Biodiversity Institute and Department of Environmental Affairs, Pretoria*.

Dubois S, Gelpi CG, Condrey RE, Grippo MA, Fleeger JW. 2009. Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf. *Biodiversity and Conservation* 18: 3759-3784.

Dunstan PK, Bax NJ, Dambacher JM, Hayes KR, Hedge PT, Smith DC, Smith AD. 2016. Using ecologically or biologically significant marine areas (EBSAs) to implement marine spatial planning. *Ocean & Coastal Management* 121: 116-127.

Dutertre M, Hamon D, Chevalier C, Ehrhold A. 2013. The use of the relationships between environmental factors and benthic macrofaunal distribution in the establishment of a baseline for coastal management. *ICES Journal of Marine Science* 70: 294-308.

Eckman J. 1983. Hydrodynamic processes affecting benthic recruitment. *Limnology and Oceanography* 28: 241-257.

Eckman JE, Nowell AR, Jumars PA. 1981. Sediment destabilization by animal tubes. *Journal of Marine Research* 39: 361-373.

Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S, Baker SC, Banks S, Barrett NS, Becerro MA, Bernard AT, Berkhout J. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506: 216-220.

Ehler C, Douvere F (eds). 2009. *Marine spatial planning, a step-by-step approach towards ecosystem-based management*. Intergovernmental Oceanographic Commission Manuals and Guides Report No. 53. Paris, France: UNESCO.

Ellingsen K, Gray JS. 2002. Spatial patterns of benthic diversity: is there a latitudinal gradient along the Norwegian continental shelf? *Journal of Animal Ecology* 71: 373-389.

Ellingsen KE. 2001. Biodiversity of a continental shelf soft-sediment macrobenthos community. *Marine Ecology Progress Series* 218: 15.

Ellingsen KE. 2002. Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. *Marine Ecology Progress Series* 232: 15-27.

Ellingsen KE, Hewitt JE, Thrush SF. 2007. Rare species, habitat diversity and functional redundancy in marine benthos. *Journal of Sea Research* 58: 291-301.

Elliott M, Quintino V. 2007. The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin* 54: 640-645.

Ellis D. 1985. Taxonomic sufficiency in pollution assessment. *Marine Pollution Bulletin* 16: 459.

Ellis J, Anlauf H, Kürten S, Lozano-Cortés D, Alsaffar Z, Cúrdia J, Jones B, Carvalho S. 2017. Cross shelf benthic biodiversity patterns in the Southern Red Sea. *Scientific Reports* 7.

Ellis J, Schneider D. 2008. Spatial and temporal scaling in benthic ecology. *Journal of Experimental Marine Biology and Ecology* 366: 92-98.

Emanuel B, Bustamante R, Branch G, Eekhout S, Odendaal F. 1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *South African Journal of Marine Science* 12: 341-354.

Evin LA, Talley TS. 2002. Influences of vegetation and abiotic environmental factors on salt marsh invertebrates. *Concepts and controversies in tidal marsh ecology*: Springer. p. 661-707.

Faith D, Carter G, Cassis G, Ferrier S, Wilkie L. 2003. Complementarity, biodiversity viability analysis, and policy-based algorithms for conservation. *Environmental Science & Policy* 6: 311-328.

Faith DP, Minchin PR, Belbin L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69: 57-68.

Faith DP, Walker P. 1996. Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiversity and Conservation* 5: 399-415.

Falvey D, Middleton M. 1981. Passive continental margins: evidence for a prebreakup deep crustal metamorphic subsidence mechanism. Paper presented at the Geology of continental margins symposium, Paris.

Fauchald K, Jumars PA. 1979. The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* 17: 193-284.

Faulwetter MS, Markantonatou MV, Pavloudi MC, Papageorgiou N, Keklikoglou MK, Chatzinikolaou E, Pafilis E, Chatzigeorgiou MG, Vasileiadou MK, Dailianis T. 2014. Polytraits: A database on biological traits of marine polychaetes. *Biodiversity data journal*.

Fenchel T. 1970. Studies on the decomposition of organic detritus derived from the turtle grass Thalassia testudinum. *Limnology and Oceanography* 15: 14-20.

Fennessy S, Groeneveld J. 1997. A review of the offshore trawl fishery for crustaceans on the east coast of South Africa. *Fisheries Management and Ecology* 4: 135-147.

Ferrier S, Watson G. 1997. *An evaluation of the effectiveness of environmental surrogates and modelling techniques in predicting the distribution of biological diversity*. Environment Australia.

Field J, Clarke K, Warwick R. 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37-52.

Field J, Griffiths C. 1991. Littoral and sublittoral ecosystems of southern Africa. *Ecosystems of the World*.

Fleddum A, Atkinson LJ, Field JG, Shin P. 2013. Changes in biological traits of macro-benthic communities subjected to different intensities of demersal trawling along the west coast of southern Africa. *Journal of the Marine Biological Association of the United Kingdom* 93: 2027-2038.

Fleishman E, Noss RF, Noon BR. 2006. Utility and limitations of species richness metrics for conservation planning. *Ecological Indicators* 6: 543-553.

Flemming B. 1978. Underwater sand dunes along the southeast African continental margin—observations and implications. *Marine Geology* 26: 177-198.

Flemming B. 1980. Sand transport and bedform patterns on the continental shelf between Durban and Port Elizabeth (southeast African continental margin). *Sedimentary Geology* 26: 179-205.

Flemming B. 1981. Factors controlling shelf sediment dispersal along the southeast African continental margin. *Developments in Sedimentology* 32: 259-277.

Flemming B, Hay R. 1988. Sediment distribution and dynamics on the Natal continental shelf. In: Schumann EH editor. *Lecture notes on coastal and estuarine studies*. *Coastal ocean studies off Natal, South Africa* No. 26. Germany: Springer-Verlag. p. 47-80.

Foley MM, Halpern BS, Micheli F, Armsby MH, Caldwell MR, Crain CM, Prahler E, Rohr N, Sivas D, Beck MW. 2010. Guiding ecological principles for marine spatial planning. *Marine policy* 34: 955-966.

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35.

Franken M-L. 2015. Investigating patterns and potential drivers of benthic epifaunal communities in unconsolidated sediment habitats of the KwaZulu-Natal shelf. BSc Hons, University of the Western Cape, Cape Town.

Freitas R, Ricardo F, Pereira F, Sampaio L, Carvalho S, Gaspar M, Quintino V, Rodrigues AM. 2011. Benthic habitat mapping: concerns using a combined approach (acoustic, sediment and biological data). *Estuarine, Coastal and Shelf Science* 92: 598-606.

Frid C, Paramor O, Brockington S, Bremner J. 2008. Incorporating ecological functioning into the designation and management of marine protected areas. *Hydrobiologia* 606: 69-79.

Friedrichs M, Graf G, Springer B. 2000. Skimming flow induced over a simulated polychaete tube lawn at low population densities. *Marine Ecology Progress Series* 192: 219-228.

Ganesh T, Raman A. 2007. Macrobenthic community structure of the northeast Indian shelf, Bay of Bengal. *Marine Ecology Progress Series* 341: 59-73.

Gaston GR. 1987. Benthic polychaeta of the Middle Atlantic Bight: feeding and distribution. *Marine Ecology Progress Series* 36: 251-262.

Gaston KJ. 2000. Biodiversity: higher taxon richness. *Progress in Physical Geography* 24: 117-127.

Gauch HG. 1982. *Multivariate analysis in community ecology*. Cambridge University Press.

Ghiselin MT. 1969. The evolution of hermaphroditism among animals. *The Quarterly review of biology* 44: 189-208.

Giangrande A. 2003. Biodiversity, conservation, and the 'Taxonomic impediment'. *Aquatic conservation: marine and freshwater ecosystems* 13: 451-459.

Giangrande A, Licciano M, Musco L. 2005. Polychaetes as environmental indicators revisited. *Marine Pollution Bulletin* 50: 1153-1162.

Gibson R, Barnes M, Atkinson R. 2001a. Practical measures of marine biodiversity based on relatedness of species. *Oceanography and Marine Biology* 39: 207-231.

Gibson R, Barnes M, Atkison R. 2001b. Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanography marine biology annual review* 39: 233-267.

Giller P, Hillebrand H, Berninger UG, O Gessner M, Hawkins S, Inchausti P, Inglis C, Leslie H, Malmqvist B, T Monaghan M. 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos* 104: 423-436.

Gladstone W, Davis J. 2003. Reduced survey intensity and its consequences for marine reserve selection. *Biodiversity and Conservation* 12: 1525-1536.

Gleason M, Fox E, Ashcraft S, Vasques J, Whiteman E, Serpa P, Saarman E, Caldwell M, Frimodig A, Miller-Henson M. 2013. Designing a network of marine protected areas in California: achievements, costs, lessons learned, and challenges ahead. *Ocean & Coastal Management* 74: 90-101.

Glockzin M, Zettler M. 2008. Spatial macrozoobenthic distribution patterns in relation to major environmental factors-A case study from the Pomeranian Bay (southern Baltic Sea). *Journal of Sea Research* 59: 144-161.

Godet L, Le Mao P, Grant C, Olivier F. 2010. Marine invertebrate fauna of the Chausey archipelago: an annotated checklist of historical data from 1828 to 2008. *Cahiers de Biologie Marine* 51: 147-165.

Gogina M, Zettler ML. 2010. Diversity and distribution of benthic macrofauna in the Baltic Sea: data inventory and its use for species distribution modelling and prediction. *Journal of Sea Research* 64: 313-321.

Gomez-Gesteira JL, Dauvin JC. 2000. Amphipods are good bioindicators of the impact of oil spills on sof t-bottom macrobenthic communities. *Marine Pollution Bulletin* 40: 1017-1027.

Gooday AJ, Bett BJ, Escobar E, Ingole B, Levin LA, Neira C, Raman AV, Sellanes J. 2010. Habitat heterogeneity and its influence on benthic biodiversity in oxygen minimum zones. *Marine Ecology* 31: 125-147.

Gotelli NJ, Anderson MJ, Arita HT, Chao A, Colwell RK, Connolly SR, Currie DJ, Dunn RR, Graves GR, Green JL. 2009. Patterns and causes of species richness: a general simulation model for macroecology. *Ecology Letters* 12: 873-886.

Grantham HS, Pressey RL, Wells JA, Beattie AJ. 2010. Effectiveness of biodiversity surrogates for conservation planning: different measures of effectiveness generate a kaleidoscope of variation. *PLoS One* 5: e11430.

Gray J. 1974a. Animal-sediment relationships. *Oceanography and Marine Biology: An Annual Review* 12: 223-261.

Gray J. 1976. Are marine base-line surveys worthwhile. *New Scientist* 70: 219-221.

Gray J. 1997a. Gradients in marine biodiversity. *Marine Biodiversity: Patterns and Processes. Cambridge: Cambridge University Press. p 18Á/34*.

Gray J, Aschan M, Carr M, Clarke K, Green R, Pearson T, Rosenberg R, Warwick R. 1988. Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. *Marine Ecology Progress Series* 46: 151-165.

Gray JS. 1974b. Animal-sediment relationships. *Oceanography and Marine Biology: An Annual Review* 12: 223-261.

Gray JS. 1981. *The ecology of marine sediments: an introduction to the structure and function of benthic communities*. CUP Archive.

Gray JS. 1997b. Marine biodiversity: patterns, threats and conservation needs. *Biodiversity & Conservation* 6: 153-175.

Gray JS. 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *Journal of Experimental Marine Biology and Ecology* 250: 23-49.

Gray JS. 2002. Species richness of marine soft sediments. *Marine Ecology Progress Series* 244: 285-297.

Gray JS, Clarke K, Warwick R, Hobbs G. 1990. Detection of initial effects of pollution on marine benthos: an example from the Ekofisk and Eldfisk oilfields, North Sea. *Marine Ecology Progress Series* 66: 285-1990.

Gray JS, Elliott M. 2009. *Ecology of marine sediments: from science to management*. Oxford University Press.

Grebmeier JM, Feder HM, McRoy CP. 1989. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. 111. Benthic food supply and carbon cycling. *Mar Ecol Prog Ser* 53: 79-91.

Green A. 2009. Sediment dynamics on the narrow, canyon-incised and current-swept shelf of the northern KwaZulu-Natal continental shelf, South Africa. *Geo-Marine Letters* 29: 201-219.

Green A, Garlick GL. 2011. A sequence stratigraphic framework for a narrow, current-swept continental shelf: The Durban Bight, central KwaZulu-Natal, South Africa. *Journal of African Earth Sciences* 60: 303-314.

Green A, MacKay C. 2016. Unconsolidated sediment distribution patterns in the KwaZulu-Natal Bight, South Africa: the role of wave ravinement in separating relict versus active sediment populations. *African Journal of Marine Science* 38: S65-S74.

Greene J, Anderson M, Odell J, Steinberg N. 2010. The Northwest Atlantic marine ecoregional assessment: species, habitats and ecosystems. *Phase One. The Nature Conservancy, Eastern US Division, Boston, MA.*

Griffiths C. 1973. The Amphipoda of Southern Africa: 1. The Gammaridea and Caprellidea of southern Moçambique. *Annals of the South African Museum*.

Griffiths C. 1974a. The Amphipoda of Southern Africa: 3. The Gammaridea and Caprellidea of Natal. *Annals of the South African Museum*.

Griffiths C. 1974b. The Amphipoda of Southern Africa: 4. The Gammaridea and Caprellidea of Cape Province east of Cape Agulhas. *Annals of the South African Museum*.

Griffiths CL. 1976. *Guide to the benthic marine amphipods of Southern Africa*. Trustees of the South African Museum.

Griffiths CL, Robinson TB, Lange L, Mead A. 2010. Marine biodiversity in South Africa: an evaluation of current states of knowledge. *PLoS One* 5: e12008.

Grippo MA, Fleeger JW, Dubois SF, Condrey R. 2011. Spatial variation in basal resources supporting benthic food webs revealed for the inner continental shelf. *Limnology and Oceanography* 56: 841-856.

Gründlingh ML, Pearce AF. 1990. Frontal features of the Agulhas Current in the Natal Bight. *South African geographical journal* 72: 11-14.

Guastella L, Roberts M. 2016. Dynamics and role of the Durban cyclonic eddy in the KwaZulu-Natal Bight ecosystem. *African Journal of Marine Science* 38: S23-S42.

Guillemot N, Kulbicki M, Chabanet P, Vigliola L. 2011. Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage. *PLoS One* 6: e26735.

Gutiérrez D, Gallardo VA, Mayor S, Neira C, Vásquez C, Sellanes J, Rivas M, Soto A, Carrasco F, Baltazar M. 2000. Effects of dissolved oxygen and fresh organic matter on the bioturbation potential of macrofauna in sublittoral sediments off Central Chile during the 1997/1998 El Niño. *Marine Ecology Progress Series* 202: 81-99.

Halpern BS, Lester SE, McLeod KL. 2010. Placing marine protected areas onto the ecosystem-based management seascape. *Proceedings of the National Academy of Sciences* 107: 18312-18317.

Hammer Ø, Harper D, Ryan P. 2001. Paleontological Statistics Software: Package for Education and Data Analysis. *Palaeontologia Electronica*.

Hansen K, Kristensen E. 1997. Impact of macrofaunal recolonization on benthic metabolism and nutrient fluxes in a shallow marine sediment previously overgrown with macroalgal mats. *Estuarine, Coastal and Shelf Science* 45: 613-628.

Harmelin–Vivien M, Banaru D, Dierking J, Hermand R, Letourneur Y, Salen-Picard C. 2009. Linking benthic biodiversity to the functioning of coastal ecosystems subjected to river runoff (NW Mediterranean). *Animal Biodiversity and Conservation* 32: 135-145.

Harmer RW. 2014. Diversity and distribution of subtidal soft-bottom macrofauna of the iSimangaliso Wetland Park, South Africa. MSc, University of KwaZulu-Natal, Westville.

Harris J, Livingstone T, Lombard A, Lagabrielle E, Haupt P, Sink K, Mann B, Schleyer M. 2011a. Marine Systematic Conservation Assessment and Plan for KwaZulu-Natal-Spatial priorities for conservation of marine and coastal biodiversity in KwaZulu-Natal. *Ezemvelo KZN Wildlife*.

Harris J, Livingstone T, Lombard A, Lagabrielle E, Haupt P, Sink K, Schleyer M, Mann B. 2012. Coastal and Marine Biodiversity Plan for KwaZulu-Natal. Spatial Priorities for the Conservation of Coastal and Marine Biodiversity in KwaZulu-Natal.(Scientific Services Technical Report).

Harris L, Nel R, Smale M, Schoeman D. 2011b. Swashed away: Storm impacts on sandy beach macrofaunal communities. *Estuarine, Coastal and Shelf Science* 94: 210-221.

Harris PT, Heap AD, Whiteway T, Post A. 2008. Application of biophysical information to support Australia's representative marine protected area program. *Ocean & Coastal Management* 51: 701-711.

Harris TFW (ed). 1978. *Review of coastal currents in Southern African waters*. National Scientific Programmes Unit: CSIR.

Hayes MO, Hoff R, Michel J, Scholz D, Shigenaka G (eds). 1992. *Introduction to coastal habitats and biological resources for oil-spill response*. National Oceanic and Atmospheric Administration, Seattle, WA (United States). Coastal Monitoring and Bioeffects Assessment Div.

Heap AD, Anderson T, Falkner I, Przeslawski R, Whiteway T, Harris PT. 2011. Seascapes for the Australian margin and adjacent seabed. *Geoscience Australia, Record, Canberra*.

Heileman S, Lutjerharmsk J, Scott L. 2008. II-4 Agulhas Current: LME# 30. *Sherman, K. and Hempel, G.(Editors)*.

Heino J, Soininen J. 2007. Are higher taxa adequate surrogates for species-level assemblage patterns and species richness in stream organisms. *Biological Conservation* 137: 78-89.

Herbert D. 1989. A remarkable new species of Diodora Gray, 1821 from south-east Africa (Mollusca: Gastropoda: Fissurellidae). *Annals of the Natal Museum* 30: 173-176.

Herbert D. 1991. New records of Mollusca (Gastropoda) from southern Africa and Mozambique. Part 1. *Annals of the Natal Museum* 32: 305-318.

Herkül K, Torn K, Suursaar Ü, Alari V, Peterson A. 2016. Variability of Benthic Communities in Relation to Hydrodynamic Conditions in the North-Eastern Baltic Sea. *Journal of Coastal Research* 75: 867-871.

Hernández-Alcántara P, Solís-Weiss V. 2011. Distribution of the Polychaete assemblages on the continental shelf of the Northern Gulf of California, Eastern Pacific. *Italian Journal of Zoology* 78: 280-289.

Hewitt J, Thrush S, Dayton P. 2008. Habitat variation, species diversity and ecological functioning in a marine system. *Journal of Experimental Marine Biology and Ecology* 366: 116-122.

Hewitt JE, Thrush SF, Halliday J, Duffy C. 2005. The importance of small-scale habitat structure for maintaining beta diversity. *Ecology* 86: 1619-1626.

Heydorn A, Bang N, Pearce A, Flemming B, Carter R, Schleyer M, Berry P, Hughes G, Bass A, Wallace J. 1978. Ecology of the Agulhas Current region: an assessment of biological responses to environmental parameters in the south-west Indian Ocean. *Transactions of the Royal Society of South Africa* 43: 151-190.

Hillebrand H, Gruner DS, Borer ET, Bracken ME, Cleland EE, Elser JJ, Harpole WS, Ngai JT, Seabloom EW, Shurin JB. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences* 104: 10904-10909.

Hily C. 1987. Spatio-temporal variability of Chaetozone setosa (Malmgren) populations on an organic gradient in the Bay of Brest, France. *Journal of Experimental Marine Biology and Ecology* 112: 201-216.

Hily C, Le Loc'h F, Grall J, Glémarec M. 2008. Soft bottom macrobenthic communities of North Biscay revisited: Long-term evolution under fisheries-climate forcing. *Estuarine, Coastal and Shelf Science* 78: 413-425.

Hirst AJ. 2004. Broad-scale environmental gradients among estuarine benthic macrofaunal assemblages of south-eastern Australia: implications for monitoring estuaries. *Marine and Freshwater Research* 55: 79-92.

Hooper DU, Chapin F, Ewel J, Hector A, Inchausti P, Lavorel S, Lawton J, Lodge D, Loreau M, Naeem S. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75: 3-35.

Huang Z, Brooke BP, Harris PT. 2011. A new approach to mapping marine benthic habitats using physical environmental data. *Continental Shelf Research* 31: S4-S16.

Huang Z, McArthur M, Przeslawski R, Siwabessy J, Nichol S, Brooke B. 2014. Predictive mapping of soft-bottom benthic biodiversity using a surrogacy approach. *Marine and Freshwater Research* 65: 409-424.

Huber M. 2015. *Compendium of bivalves 2*. Germany: Conchbooks.

Hughes DJ, Lamont PA, Levin LA, Packer M, Feeley K, Gage JD. 2009. Macrofaunal communities and sediment structure across the Pakistan Margin oxygen minimum zone, North-East Arabian Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 56: 434-448.

Hulot FD, Lacroix G, Lescher-Moutoue F, Loreau M. 2000. Functional diversity governs ecosystem response to nutrient enrichment. *Nature* 405: 340-344.

Huston M. 1979. A general hypothesis of species diversity. *American naturalist*: 81-101.

Hutchings L, Beckley L, Griffiths M, Roberts M, Sundby S, Van der Lingen C. 2002. Spawning on the edge: spawning grounds and nursery areas around the southern African coastline. *Marine and Freshwater Research* 53: 307-318.

Hutchings P. 1998. Biodiversity and functioning of polychaetes in benthic sediments. *Biodiversity & Conservation* 7: 1133-1145.

Hyland J, Baptiste E, Campbell J, Kennedy J, Kropp R, Williams S. 1991. Macroinfaunal communities of the Santa-maria basin on the California outer continental-shelf and slope. *Marine Ecology Progress Series* 78: 147-161.

Jablonski D. 1986. Larval ecology and macroevolution in marine invertebrates. *Bulletin of Marine Science* 39: 565-587.

Jablonski D, Lutz RA. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews* 58: 21-89.

Jackson SE, Lundquist CJ. 2016. Limitations of biophysical habitats as biodiversity surrogates in the Hauraki Gulf Marine Park. *Pacific Conservation Biology* 22: 159-172.

James R, Lincoln Smith M, Fairweather P. 1995 Sieve mesh-size and taxonomic resolution needed to describe natural spatial variation in marine macrofauna. *Mar Ecol Prog Ser* 118: 187-198.

Jayaraj K, Jayalakshmi K, Saraladevi K. 2007. Influence of environmental properties on macrobenthos in the Northwest Indian shelf. *Environmental monitoring and assessment* 127: 459-475.

Jayaraj K, Sheeba P, Jacob J, Revichandran C, Arun P, Praseeda K, Nisha P, Rasheed K. 2008. Response of infaunal macrobenthos to the sediment granulometry in a tropical continental margin–southwest coast of India. *Estuarine, Coastal and Shelf Science* 77: 743-754.

Jennings S, Pinnegar JK, Polunin NV, Warr KJ. 2002. Linking size-based and trophic analyses of benthic community structure. *Marine Ecology Progress Series* 226: 77-85.

Johnson MP, Allcock AL, Pye SE, Chambers S, Fitton D. 2001. The effects of dispersal mode on the spatial distribution patterns of intertidal molluscs. *Journal of Animal Ecology* 70: 641-649.

Jones N. 1950. Marine bottom communities. *Biological Reviews* 25: 283-313.

Joydas T, Damodaran R. 2009. Infaunal macrobenthos along the shelf waters of the west coast of India, Arabian Sea. *Indian Journal of Marine Sciences* 38: 191-204.

Joydas TV, Qurban MA, Al-Suwailem A, Krishnakumar P, Nazeer Z, Cali N. 2012. Macrobenthic community structure in the northern Saudi waters of the Gulf, 14years after the 1991 oil spill. *Marine Pollution Bulletin* 64: 325-335.

Jumars P, Dorgan K, SM. L. 2015a. The diet of the worms emended: an update of polychaete feeding guilds. *Annual review of marine science* 7: 497-520.

Jumars PA, Dorgan KM, Lindsay SM. 2015b. Diet of worms emended: an update of polychaete feeding guilds. *Annual review of marine science* 7: 497-520.

Jury MR, Valentine HR, Lutjeharms JR. 1993. Influence of the Agulhas Current on summer rainfall along the southeast coast of South Africa. *Journal of applied meteorology* 32: 1282-1287.

Kaiser MJ, Cheney K, Spence FE, Edwards DB, Radford K. 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure VII. The effects of trawling disturbance on the fauna associated with the tubeheads of serpulid worms. *Fisheries Research* 40: 195-205.

Kaiser S, Griffiths HJ, Barnes DKA, Brandão SN, Brandt A, O'Brien PE. 2011. Is there a distinct continental slope fauna in the Antarctic? *Deep Sea Research Part II: Tropical Studies in Oceanography* 58: 91-104.

Karakassis I, Eleftheriou A. 1997. The continental shelf of Crete: structure of macrobenthic communities. *Marine Ecology Progress Series* 160: 185-196.

Keith D, Yoder J, Freeman S. 2002. Spatial and temporal distribution of coloured dissolved organic matter (CDOM) in Narragansett Bay, Rhode Island: implications for phytoplankton in coastal waters. *Estuarine, Coastal and Shelf Science* 55: 705-717.

Kensley B. 1978. *Guide to the marine isopods of southern Africa*. Cape Town: Trestees of the South Africa Museum.

Kensley BF. 1972. Shrimps and prawns of southern Africa.

Kerrigan B, Breen D, De'ath G, Day J, Fernandes L, Tobin R, Dobbs K. 2010. Classifying the biodiversity of the Great Barrier Reef World Heritage Area for the classification phase of the representative areas program.

Khan A, Manokaran S, Lyla S. 2017. Changes in macrobenthic community structure from estuary to continental slope in the south-east coast of India. *Journal of the Marine Biological Association of the United Kingdom* 97: 161-180.

Kilburn R. 1992. Turridae (Mollusca: Gastropoda) of southern Africa and Mozambique. Part 7. Subfamily Crassispirinae, section 2. *Annals of the Natal Museum* 35: 177-228.

Kilburn R. 1998. The Limidae of South Africa and Mozambique (Mollusca: Bivalvia): genera Limaria, Limatula, Divarilima, Ctenoides and Fukama. *Annals of the Natal Museum* 39: 203-247.

Kilburn R, Rippey E. 1982. Sea shells of southern Africa.

Kilburn RN. 1999. The family Nuculidae (Bivalvia: Protobranchia) in South Africa and Mozambique. *Annals of the Natal Museum* 40: 245-268.

Kirkpatrick J, Brown M. 1994. A comparison of direct and environmental domain approaches to planning reservation of forest higher plant communities and species in Tasmania. *Conservation biology* 8: 217-224.

Kleyer M, Dray S, Bello F, Lepš J, Pakeman RJ, Strauss B, Thuiller W, Lavorel S. 2012. Assessing species and community functional responses to environmental gradients: which multivariate methods? *Journal of Vegetation Science* 23: 805-821.

Knowlton N. 1993. Sibling species in the sea. *Annual Review of Ecology and Systematics* 24: 189-216.

Kokarev VN, Vedenin AA, Basin AB, Azovsky AI. 2017. Taxonomic and functional patterns of macrobenthic communities on a high-Arctic shelf: A case study from the Laptev Sea. *Journal of Sea Research* 129: 61-69.

Kostylev VE. 2012. Benthic habitat mapping from seabed acoustic surveys: do implicit assumptions hold? *Int. Assoc. Sedimentol. Spec. Publ* 44: 405-416.

Koulouri P, Dounas C, Arvanitidis C, Koutsoubas D, Eleftheriou A. 2006. Molluscan diversity along a Mediterranean soft bottom sublittoral ecotone. *Scientia Marina* 70: 573-583.

Kruskal JB. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29: 1-27.

Kunnen TH. 2013. Marine Nutrient Dynamics of the KwaZulu-Natal Bight: Assessing Bacterial Numbers, Biomass and Productivity. PhD, University of KwaZulu-Natal, Westville.

Labrune C, Grémare A, Amouroux J-M, Sardá R, Gil J, Taboada S. 2008. Structure and diversity of shallow soft-bottom benthic macrofauna in the Gulf of Lions (NW Mediterranean). *Helgoland Marine Research* 62: 201.

Lamberth SJ, Drapeau L, Branch GM. 2009. The effects of altered freshwater inflows on catch rates of non-estuarine-dependent fish in a multispecies nearshore linefishery. *Estuarine, Coastal and Shelf Science* 84: 527-538.

Landman WA, Mason SJ. 1999a. Change in the association between Indian Ocean sea-surface temperatures and summer rainfall over South Africa and Namibia. *International Journal of Climatology* 19: 1477-1492.

Landman WA, Mason SJ. 1999b. Operational long-lead prediction of South African rainfall using canonical correlation analysis. *International Journal of Climatology* 19: 1073-1090.

Lange G. 2013. Benthic Communities in Waters off Angola. MSc Marine Biology., University of Rostock, Angola.

Lange G, Darr A, Zettler M. 2014. Macrozoobenthic communities in waters off Angola. *African Journal of Marine Science* 36: 313-321.

Lange L, Griffiths C. 2014. Large-scale spatial patterns within soft-bottom epibenthic invertebrate assemblages along the west coast of South Africa, based on the Nansen trawl survey. *African Journal of Marine Science* 36: 111-124.

Lavorel S, Grigulis K, Lamarque P, Colace MP, Garden D, Girel J, Pellet G, Douzet R. 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology* 99: 135-147.

Lecours V, Devillers R, Schneider DC, Lucieer VL, Brown CJ, Edinger EN. 2015. Spatial scale and geographic context in benthic habitat mapping: review and future directions. *Marine Ecology Progress Series* 535: 259-284.

Ledoyer M. 1982. *Crustaceans: Amphipod, gammaridae*. CNRS.

Lee H-G, Yoon K-T, Park H-S, Hong J-S, Lee J-H. 2016. The Influence of Environmental Variables on Distribution of Macrobenthic Community in Salt Marsh Vegetation in Donggeomdo, Ganghwa on the West Coast of Korea. *Ocean and Polar Research* 38: 115-128.

Legendre P, Legendre L 1998. Numerical Ecology (second English edition) Elsevier Science BV. Elsevier Science BV. Amsterdam.

Lester SE, Costello C, Halpern BS, Gaines SD, White C, Barth JA. 2013. Evaluating tradeoffs among ecosystem services to inform marine spatial planning. *Marine policy* 38: 80-89.

Leung JY. 2015a. Habitat heterogeneity affects ecological functions of macrobenthic communities in a mangrove: Implication for the impact of restoration and afforestation. *Global Ecology and Conservation* 4: 423-433.

Leung JY. 2015b. Habitat Heterogeneity Determining the Macrobenthic Infaunal Community in a Mangrove Swamp in South China: Implication for Plantation and Plant Invasion. *Journal of Coastal Research* 31: 624-633.

Levin LA. 1984. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology* 65: 1185-1200.

Levin LA, Etter RJ, Rex MA, Gooday AJ, Smith CR, Pineda J, Stuart CT, Hessler RR, Pawson D. 2001. Environmental influences on regional deep-sea species diversity. *Annual Review of Ecology and Systematics* 32: 51-93.

Levin LA, Gage JD, Martin C, Lamont PA. 2000. Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. *Deep Sea Research Part II: Tropical Studies in Oceanography* 47: 189-226.

Levin LA, Sibuet M, Gooday AJ, Smith CR, Vanreusel A. 2010. The roles of habitat heterogeneity in generating and maintaining biodiversity on continental margins: an introduction. *Marine Ecology* 31: 1-5.

Lewis DW, McConchie D. 1994. *Analytical sedimentology*. Springer Science & Business Media.

Lindenmayer DB, Likens GE. 2011. Direct measurement versus surrogate indicator species for evaluating environmental change and biodiversity loss. *Ecosystems* 14: 47-59.

Liu X. 2014. Sediment Dynamics Off the East African Continental Margin During the Last Deglaciation and the Holocene: Constrained by Changes in Climate and Sea Level, Bremen, Universität Bremen, Diss., 2014.

Livingstone T-C. 2016. Identification of priority areas for protection of the offshore marine environment on the east coast of South Africa. MSc, University of KwaZulu-Natal, Westville.

Lombard A, Strauss T, Harris J, Sink K, Attwood C, Hutchings L. 2004. South African National Spatial Biodiversity Assessment: Marine Component. *South African National Biodiversity Institute Technical Report* 4: 96pp.

Longhurst AR. 1958. *An ecological survey of the West African marine benthos*. HM Stationery Office.

López-Jamar E, Cal R, González G, Hanson R, Rey J, Santiago G, Tenore K. 1992. Upwelling and outwelling effects on the benthic regime of the continental shelf off Galicia, NW Spain. *Journal of Marine Research* 50: 465-488.

Lourido A, Cacabelos E, Troncoso JS. 2008. Patterns of distribution of the polychaete fauna in subtidal soft sediments of the Ría de Aldán (north-western Spain). *Journal of the Marine Biological Association of the United Kingdom* 88: 263-275.

Louw GS. 2014. Monitoring the dynamics of the Agulhas Current System off Port Edward, Kwazulu-Natal, Cape Peninsula University of Technology.

Lovell S, Hamer M, Slotow R, Herbert D. 2007. Assessment of congruency across invertebrate taxa and taxonomic levels to identify potential surrogates. *Biological Conservation* 139: 113-125.

Lowry J. 1999. Crustacea.net. Available at http://crustacea.net/ [accessed 10-04-2015.

Lu L. 2005. The relationship between soft-bottom macrobenthic communities and environmental variables in Singaporean waters. *Marine Pollution Bulletin* 51: 1034-1040.

Lück-Vogel M, Mbolambi C, Rautenbach K, Adams J, Van Niekerk L. 2016. Vegetation mapping in the St Lucia estuary using very high-resolution multispectral imagery and LiDAR. *South African Journal of Botany* 107: 188-199.

Lutjeharms J. 1981. Features of the southern Agulhas Current circulation from satellite remote-sensing. *South African Journal of Science* 77: 231-236.

Lutjeharms J. 2006a. The Agulhas Current Springer-Verlag. *Berlin, Germany*.

Lutjeharms J. 2006b. Three decades of research on the greater Agulhas Current. *Ocean Science* 3: 129-147.

Lutjeharms J. 2007. Three decades of research on the greater Agulhas Current. *Ocean Science* 3: 129-147.

Lutjeharms J, Ansorge I. 2001. The Agulhas return current. *Journal of Marine Systems* 30: 115-138.

Lutjeharms J, Grundlingh M, Carter R. 1989. Topographically induced upwelling in the Natal Bight. *South African Journal of Science* 85: 310-316.

Lutjeharms J, Roberts H. 1988. The Natal pulse: An extreme transient on the Agulhas Current. *Journal of Geophysical Research: Oceans (1978–2012)* 93: 631-645.

Lutjeharms J, Valentine H, Van Ballegooyen R. 2000. The hydrography and water masses of the Natal Bight, South Africa. *Continental Shelf Research* 20: 1907-1939.

Lutjeharms JR. 2006c. The coastal oceans of south-eastern Africa (15, W). *The sea* 14: 783-834.

Lutjeharms JR, Durgadoo JV, Schapira M, McQuaid CD. 2010. First oceanographic survey of the entire continental shelf adjacent to the northern Agulhas Current: news & views. *South African Journal of Science* 106: 1-3.

Mac Nally R, Bennett AF, Brown GW, Lumsden LF, Yen A, Hinkley S, Lillywhite P, Ward D. 2002. How well do ecosystem-based planning units represent different components of biodiversity? *Ecological Applications* 12: 900-912.

Macdonald TA, Burd BJ, van Roodselaar A. 2012. Size structure of marine soft-bottom macrobenthic communities across natural habitat gradients: implications for productivity and ecosystem function. *PLoS One* 7: e40071.

MacKay. 2010. ACEP macrobenthic sampling protocol. F.R.S. Algoa survey of the Natal Bight. Oceanographic Research Institute: 1-4.

Mackay C. 2006. Macrobenthic survey of the subtidal soft sediment communities of the Port of Richards Bay during dredging for Berth 306. Unpublished Report No. 239. Durban:Oceanographic Research Institute: 1-36.

MacKay C, F. 2014. ACEP Surrogacy Macrobenthic Sampling Protocol: Angra Pequena Survey of Natal Bight. Durban: Oceanographic Research Institute: 1-7.

MacKay C, Untiedt C, Hein L. 2016. Local habitat drivers of macrobenthos in the northern, central and southern KwaZulu-Natal Bight, South Africa. *African Journal of Marine Science* 38: S105-S121.

MacKay F, Cyrus D, Russell K-L. 2010. Macrobenthic invertebrate responses to prolonged drought in South Africa's largest estuarine lake complex. *Estuarine, Coastal and Shelf Science* 86: 553-567.

Mackie AS, Oliver PG, Darbyshire T, Mortimer K. 2005. Shallow marine benthic invertebrates of the Seychelles Plateau: high diversity in a tropical oligotrophic environment. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences* 363: 203-228.

Mackie AS, Parmiter C, Tong LK. 1997. Distribution and diversity of Polychaeta in the southern Irish Sea. *Bulletin of Marine Science* 60: 467-481.

MacNeil C, Dick JT, Elwood RW. 1997. The trophic ecology of freshwater Gammarus spp.(Crustacea: Amphipoda): problems and perspectives concerning the functional feeding group concept. *Biological Reviews* 72: 349-364.

Magierowski RH, Johnson CR. 2006. Robustness of surrogates of biodiversity in marine benthic communities. *Ecological Applications* 16: 2264-2275.

Magurran AE. 2004. Measuring biological diversity. *African Journal of Aquatic Science* 29: 285-286.

Mah CL, Blake DB. 2012. Global diversity and phylogeny of the Asteroidea (Echinodermata). *PLoS One* 7: e35644.

Mair JM, Cunningham SL, Sibaja-Cordero JA, Guzman HM, Arroyo MF, Merino D, Vargas R. 2009. Mapping benthic faunal communities in the shallow and deep sediments of Las Perlas Archipelago, Pacific Panama. *Marine Pollution Bulletin* 58: 375-383.

Maire V, Gross N, Börger L, Proulx R, Wirth C, Pontes LdS, Soussana JF, Louault F. 2012. Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist* 196: 497-509.

Malcolm H, Foulsham E, Pressey R, Jordan A, Davies P, Ingleton T, Johnstone N, Hessey S, Smith SD. 2012. Selecting zones in a marine park: early systematic planning improves cost-efficiency; combining habitat and biotic data improves effectiveness. *Ocean & Coastal Management* 59: 1-12.

Mamouridis V, Cartes J, Parra S, Fanelli E, Salinas JS. 2011. A temporal analysis on the dynamics of deep-sea macrofauna: Influence of environmental variability off Catalonia coasts (western Mediterranean). *Deep Sea Research Part I: Oceanographic Research Papers* 58: 323-337.

Mancinelli G, Fazi S, Rossi L. 1998. Sediment structural properties mediating dominant feeding types patterns in soft-bottom macrobenthos of the Northern Adriatic Sea. *Hydrobiologia* 367: 211-222.

Mann KH, Lazier JR. 2013. *Dynamics of marine ecosystems: biological-physical interactions in the oceans*. John Wiley & Sons.

Manokaran S, Khan SA, Lyla PS. 2015. Macrobenthic composition of the southeast continental shelf of India. *Marine Ecology* 36: 1-15.

Marchant R, Barmuta L, Chessman B. 1995. Influence of sample quantification and taxonomic resolution on the ordination of macroinvertebrate communities from running waters in Victoria, Australia. *Marine and Freshwater Research* 46: 501-506.

Marchini A, Munari C, Mistri M. 2008. Functions and ecological status of eight Italian lagoons examined using biological traits analysis (BTA). *Marine Pollution Bulletin* 56: 1076-1085.

Martin A, Flemming B. 1988. Physiography, Structure Add Geological Evolution of The Natal Continental Shelf. In: Schumann EH editor. *Lecture Notes on Coastal and Estuarine Studies Volume 26. Coastal ocean studies off Natal, South Africa*. Germany: Springer-Verlag. p. 11-46.

Martín J, Palanques A, Puig P. 2006. Composition and variability of downward particulate matter fluxes in the Palamós submarine canyon (NW Mediterranean). *Journal of Marine Systems* 60: 75-97.

Martínez J, Adarraga I, Ruiz JM. 2010. Typification of benthic populations of the soft bottoms of the continental shelf of Guipúzcoa (southeast of the Bay of Biscay). *Boletín. Instituto Español de Oceanografía* 23: 85-110.

Martins R, Azevedo M, Mamede R, Sousa B, Freitas R, Rocha F, Quintino V, Rodrigues A. 2012. Sedimentary and geochemical characterization and provenance of the Portuguese continental shelf soft-bottom sediments. *Journal of Marine Systems* 91: 41-52.

Martins R, Quintino V, Rodrigues A. 2013. Diversity and spatial distribution patterns of the soft-bottom macrofauna communities on the Portuguese continental shelf. *Journal of Sea Research* 83: 173-186.

Martins R, Sampaio L, Quintino V, Rodrigues A. 2014. Diversity, distribution and ecology of benthic molluscan communities on the Portuguese continental shelf. *Journal of Sea Research* 93: 75-89.

Mason NW, Mouillot D, Lee WG, Wilson JB. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111: 112-118.

Mason S, Tyson P. 2000. The occurrence and predictability of droughts over southern Africa. *Drought: a global assessment*: 113-134.

Maurer D. 2000. The dark side of taxonomic sufficiency (TS). *Marine Pollution Bulletin* 40: 98-101.

May R. 1990. Taxonomy as destiny. *Nature* 347: 129-130.

McArthur M, Brooke B, Przeslawaki R, Ryan D, Lucieer V, Nicol S, McCallum A, Mellin C, Cresswell I, Radke L. 2010a. A review of surrogates for marine benthic biodiversity. *GeoScience Australia* 42: unknown.

McArthur M, Brooke B, Przeslawski R, Ryan D, Lucieer V, Nichol S, McCallum A, Mellin C, Cresswell I, Radke LC. 2010b. On the use of abiotic surrogates to describe marine benthic biodiversity. *Estuarine, Coastal and Shelf Science* 88: 21-32.

McClain CR, Barry JP. 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* 91: 964-976.

McClurg T. 1988. Benthos of the Natal continental shelf. In: Schumann EH editor. *Coastal ocean studies off Natal, South Africa*. *Lecture Notes on Coastal and Estuarine Studies Volume 26.* Germany: Springer-Verlag. p. 178-208.

McClurg T (ed). 2004. *Introduction, In: Sea disposal of sewage: environmental surveys in the Durban outfalls region.* CSIR Environmentel Report No. 23.

McClurg T, Blair AG, Gumede SV. 2000. Benthic fauna. In: Connell A editor. *Environmental studies in Richards Bay offshore outfalls region*: Report no. 13. Durban: CSIR. p. 23-62.

McClurg T, Parsons G, Pillay S, Newman B. 2006. Benthic macrofauna. . In: McClurg T editor. *Sea disposal of sewage: Environmental surveys in the Durban outfalls region-surveys made in 2006.* Report no. 23. Durban: CSIR. p. 39-69.

McDonald J. 2014. Handbook of Biological Statistics. 3rd edn.(Sparky House Publishing: Baltimore, MD.).

McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21: 178-185.

McHenry J, Steneck RS, Brady DC. 2017. Abiotic proxies for predictive mapping of nearshore benthic assemblages: implications for marine spatial planning. *Ecological Applications* 27: 603-618.

McHugh D, Fong PP. 2002. Do life history traits account for diversity of polychaete annelids? *Invertebrate Biology* 121: 325-338.

McHuhg D, Fong PP. 2002. Do life history traits account for diversity of polichaeta Annelids? *Invertebrate Biology* 121: 325-338.

McLusky D. 1993. Marine and estuarine gradients - an overview. . *Aquatic ecology* 27: 489-493.

Mead HB. 2007. Predicting South Africa's true marine biodiversity: a comparison of methods. MSc, University of Cape Town.

Mellin C, Delean S, Caley J, Edgar G, Meekan M, Pitcher R, Przeslawski R, Williams A, Bradshaw C. 2011. Effectiveness of biological surrogates for predicting patterns of marine biodiversity: a global meta-analysis. *PLoS One* 6: e20141.

Mendes CLT, Tavares M, Soares-Gomes A. 2007. Taxonomic sufficiency for soft-bottom sublittoral mollusks assemblages in a tropical estuary, Guanabara Bay, Southeast Brazil. *Marine Pollution Bulletin* 54: 377-384.

Méndez N. 2002. Annelid assemblages in soft bottoms subjected to human impact in the Urías estuary (Sinaloa, Mexico). *Oceanologica acta* 25: 139-147.

Méndez N, Green M. 1998. Superficial sediments and their relation to polychaete families in a subtropical embayment, Mexico. *Revista de Biología tropical* 46: 237-248.

Menezes S, Baird DJ, Soares AM. 2010. Beyond taxonomy: a review of macroinvertebrate trait-based community descriptors as tools for freshwater biomonitoring. *Journal of applied ecology* 47: 711-719.

Mérigoux S, Dolédec S, Statzner B. 2001. Species traits in relation to habitat variability and state: neotropical juvenile fish in floodplain creeks. *Freshwater Biology* 46: 1251-1267.

Merino M, Monreal A. 2004. Ocean currents and their impact on marine life. *Marine Ecology, CM Duarte, ed., in Encyclopedia of Life Support Systems (EOLSS), developed under the auspices of UNESCO, Eolss Publishers, Oxford, UK*: 1À22.

Mertz O, Ravnborg HM, Lövei GL, Nielsen I, Konijnendijk CC. 2007. Ecosystem services and biodiversity in developing countries. *Biodiversity and Conservation* 16: 2729-2737.

Meyer A, Lutjeharms J, De Villiers S. 2002. The nutrient characteristics of the Natal Bight, South Africa. *Journal of Marine Systems* 35: 11-37.

Meynard CN, Quinn JF. 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. *Journal of biogeography* 34: 1455-1469.

Michel J, Westphal H, Von Cosel R. 2011. The mollusk fauna of soft sediments from the tropical, upwelling-influenced shelf of Mauritania (northwestern Africa). *Palaios* 26: 447-460.

Michel L. 2011. Multidisciplinary study of trophic diversity and functional role of amphipod crustaceans associated to Posidonia oceanica meadows.

Middelburg JJ, Soetaert K, Herman PM. 1997. Empirical relationships for use in global diagenetic models. *Deep Sea Research Part I: Oceanographic Research Papers* 44: 327-344.

Milliman JD. 1994. Organic matter content in US Atlantic continental slope sediments: decoupling the grain-size factor. *Deep Sea Research Part II: Topical Studies in Oceanography* 41: 797-808.

Mills EL. 1969. The community concept in marine zoology, with comments on continua and instability in some marine communities: a review. *Journal of the Fisheries Board of Canada* 26: 1415-1428.

Mills EL. 1971. Deep-sea Amphipoda from the western north Atlantic Ocean. the family Ampeliscidae. *Limnology and Oceanography* 16: 357-386.

Milne R. 2012. Macroinvertebrates associated with macrophytes in Sodwana Bay: with further consideration of amphipod taxonomy. MSc, University of Cape Town.

Milne R, Griffiths CL. 2013. Additions to and revisions of the amphipod (Crustacea: Amphipoda) fauna of South Africa, with a list of currently known species from the region. *African Natural History* 9: 61-90.

Minchin PR. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Theory and models in vegetation science*: Springer. p. 89-107.

Mladenov P, Emson R. 1984. Divide and broadcast: sexual reproduction in the West Indian brittle star Ophiocomella ophiactoides and its relationship to fissiparity. *Marine Biology* 81: 273-282.

Moir G. 1974. *Bathymetry of the upper continental margin between Cape Recife (34° S) and Ponta do Ouro (27° S)*. Joint Geological Survey/University of Cape Town. Technical report No. 7.

Monteiro P, Bentes L, Oliveira F, Afonso CM, Rangel MO, Gonçalves JM. 2015. EUNIS habitat's thresholds for the Western coast of the Iberian Peninsula—A Portuguese case study. *Journal of Sea Research* 100: 22-31.

Montiel A, Quiroga E, Gerdes D. 2011. Diversity and spatial distribution patterns of polychaete assemblages in the Paso Ancho, Straits of Magellan Chile. *Continental Shelf Research* 31: 304-314.

Moore P. 1977. Inorganic particulate suspensions in the sea and their effects on marine animals. *Oceanogr Mar Biol Annu Rev* 15: 225-363.

Morin J, Kastendiek J, Harrington A, Davis N. 1985. Organization and patterns of interactions in a subtidal sand community on an exposed coast. *Marine Ecology Progress Series*: 163-185.

Morrison ML. 2009. *Restoring wildlife: ecological concepts and practical applications*. Island Press.

Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, Kulbicki M, Lavergne S, Lavorel S, Mouquet N. 2013. Rare species support vulnerable functions in high-diversity ecosystems. *PLoS biology* 11: e1001569.

Mouillot D, Spatharis S, Reizopoulou S, Laugier T, Sabetta L, Basset A, Do Chi T. 2006. Alternatives to taxonomic-based approaches to assess changes in transitional water communities. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16: 469-482.

Moulaert I, Hostens K, Hillewaert H, Wittoeck J. 2008. Spatial variation of the macrobenthos species and communities of the Belgian Continental Shelf and the relation to environmental variation.

Mueller M, Pander J, Geist J. 2013. Taxonomic sufficiency in freshwater ecosystems: effects of taxonomic resolution, functional traits, and data transformation. *Freshwater Science* 32: 762-778.

Mumby PJ, Broad K, Brumbaugh DR, Dahlgren C, Harborne AR, Hastings A, Holmes KE, Kappel CV, Micheli F, Sanchirico JN. 2008. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. *Conservation biology* 22: 941-951.

Munari C. 2013. Benthic community and biological trait composition in respect to artificial coastal defence structures: a study case in the northern Adriatic Sea. *Marine Environmental Research* 90: 47-54.

Muniz P, Pires A. 1999. Trophic structure of polychaetes in the São Sebastião Channel (southeastern Brazil). *Marine Biology* 134: 517-528.

Nair K, Jacob P, Kumaran S. 1973. Distribution and abundance of planktonic amphipods in the Indian Ocean. *The biology of the Indian Ocean*: Springer. p. 349-356.

Naser HA. 2010. Testing taxonomic resolution levels for detecting environmental impacts using macrobenthic assemblages in tropical waters. *Environmental monitoring and assessment* 170: 435-444.

Navarro-Barranco C, Tierno-de-Figueroa JM, Guerra-García JM, Sánchez-Tocino L, García-Gómez JC. 2013. Feeding habits of amphipods (Crustacea: Malacostraca) from shallow soft bottom communities: Comparison between marine caves and open habitats. *Journal of Sea Research* 78: 1-7.

Ngai JT, Srivastava DS. 2006. Predators accelerate nutrient cycling in a bromeliad ecosystem. *Science* 314: 963-963.

Ngqulana S, Owen R, Vivier L, Cyrus D. 2010. Benthic faunal distribution and abundance in the Mfolozi–Msunduzi estuarine system, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* 35: 123-133.

Nittrouer CA, DeMaster DJ. 1996. The Amazon shelf setting: tropical, energetic, and influenced by a large river. *Continental Shelf Research* 16: 553-573.

Nodder SD, Pilditch CA, Probert PK, Hall JA. 2003. Variability in benthic biomass and activity beneath the Subtropical Front, Chatham Rise, SW Pacific Ocean. *Deep Sea Research Part I: Oceanographic Research Papers* 50: 959-985.

Norling K, Rosenberg R, Hulth S, Grémare A, Bonsdorff E. 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology Progress Series* 332: 11-23.

O'hara RB, Kotze DJ. 2010. Do not log-transform count data. *Methods in Ecology and Evolution* 1: 118-122.

Olafsson E, Peterson C, Ambrose W. 1995. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanographic Literature Review* 8: 667.

Olbers J, Samyn Y. 2012. The Ophiocoma species (Ophiurida: Ophiocomidae) of South Africa. *Western Indian Ocean Journal of Marine Science* 10: 137-154.

Oliveira A, Santos A, Rodrigues A, Vitorino J. 2007. Sedimentary particle distribution and dynamics on the Nazaré canyon system and adjacent shelf (Portugal). *Marine Geology* 246: 105-122.

Olsgard F, Brattegard T, Holthe T. 2003. Polychaetes as surrogates for marine biodiversity: lower taxonomic resolution and indicator groups. *Biodiversity & Conservation* 12: 1033-1049.

Olsgard F, Somerfield PJ. 2000. Surrogates in marine benthic investigations-which taxonomic unit to target? *Journal of Aquatic Ecosystem Stress and Recovery* 7: 25-42.

Olsgard F, Somerfield PJ, Carr MR. 1998. Relationships between taxonomic resolution, macrobenthic community patterns and disturbance. *Marine Ecology Progress Series* 172: 25-36.

Pace ML, Cole JJ, Carpenter SR, Kitchell JF. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* 14: 483-488.

Pacheco A, Stotz WB. 2006. Will providing a filamentous substratum in the water column and shell litter on the bottom increase settlement and post-larval survival of the scallop Argopecten purpuratus? *Journal of Experimental Marine Biology and Ecology* 333: 27-39.

Pacheco AS, González MT, Bremner J, Oliva M, Heilmayer O, Laudien J, Riascos JM. 2011. Functional diversity of marine macrobenthic communities from sublittoral soft-sediment habitats off northern Chile. *Helgoland Marine Research* 65: 413-424.

Pacheco AS, Uribe RA, Thiel M, Oliva ME, Riascos JM. 2013. Dispersal of post-larval macrobenthos in subtidal sedimentary habitats: Roles of vertical diel migration, water column, bedload transport and biological traits' expression. *Journal of Sea Research* 77: 79-92.

Paganelli D, Marchini A, Occhipinti-Ambrogi A. 2012. Functional structure of marine benthic assemblages using Biological Traits Analysis (BTA): a study along the Emilia-Romagna coastline (Italy, North-West Adriatic Sea). *Estuarine, Coastal and Shelf Science* 96: 245-256.

Passarelli C, Olivier F, Paterson DM, Hubas C. 2012. Impacts of biogenic structures on benthic assemblages: microbes, meiofauna, macrofauna and related ecosystem functions. *Marine Ecology Progress Series* 465: 85-97.

Pavoine S, Bonsall M. 2011. Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews* 86: 792-812.

Peachey RL, Bell SS. 1997. The effects of mucous tubes on the distribution, behavior and recruitment of seagrass meiofauna. *Journal of Experimental Marine Biology and Ecology* 209: 279-291.

Pearce A. 1977. Some features of the upper 500 m of the Agulhas Current. *Journal of Marine Research* 35: 731-753.

Pearson T. 1970. Litocorsa stremma a new genus and species of pilargid (Polychaeta: Annelida) from the west coast of Scotland, with notes on two other pilargid species. *Journal of Natural History* 4: 69-77.

Pearson T, Rosenberg R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography marine biology annual review* 16: 229-311.

Pearson T, Rosenberg R. 1987. Feast and famine: structuring factors in marine benthic communities *Organization of communities: past and present (Blackwell Science, Oxford)*: 373-395.

Péres J-M. 1967. The mediterranean benthos. *Oceanography and Marine Biology: An Annual Review*.

Persson L, Diehl S, Johansson L, Andersson G, Hamrin SF. 1992. Trophic interactions in temperate lake ecosystems: a test of food chain theory. *The American Naturalist* 140: 59-84.

Petchey OL, Gaston KJ. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5: 402-411.

Petchey OL, Gaston KJ. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9: 741-758.

Peterson CH, Bishop MJ. 2005. Assessing the environmental impacts of beach nourishment. *BioScience* 55: 887-896.

Petti MAV, Nonato EF, Paiva PCd. 1996. Trophic relationships between polychaetes and brachyuran crabs on the southeastern Brazilian coast. *Revista Brasileira de Oceanografia* 44: 61-67.

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19: 181-197.

Pielou E. The use of information theory in the study of the diversity of biological populations*1966*. pp. 163-177.

Pielou EC. 1969. An introduction to mathematical ecology. *An introduction to mathematical ecology.*

Pilditch C, Leduc D, Nodder S, Probert P, Bowden D. 2015. Spatial patterns and environmental drivers of benthic infaunal community structure and ecosystem function on the New Zealand continental margin. *New Zealand journal of marine and freshwater research* 49: 224-246.

Pillay D, Branch G, Forbes A. 2007. Effects of Callianassa kraussi on microbial biofilms and recruitment of macrofauna: a novel hypothesis for adult–juvenile interactions. *Marine Ecology Progress Series* 347: 1-14.

Pires-Vanin AMS, Muniz P, Léo D, Cabrera F. 2011. Benthic macrofauna structure in the northeast area of Todos os Santos Bay, Bahia State, Brazil: patterns of spatial and seasonal distribution. *Brazilian Journal of Oceanography* 59: 27-42.

Pisareva MN, Pickart RS, Iken K, Ershova EA, Grebmeier JM, Cooper LW, Bluhm BA, Nobre C, Hopcroft RR, Hu H. 2015. The relationship between patterns of benthic fauna and zooplankton in the Chukchi Sea and physical forcing. *Oceanography* 28: 68-83.

Poore G, McCallum A, Taylor J. 2008. Decapod Crustacea of the continental margin of southwestern and central Western Australia: preliminary identifications of 524 species from FRV Southern Surveyor voyage SS10-2005. *Museum Victoria Science Reports* 11: 1-106.

Pressey R. 2004. Conservation planning and biodiversity: assembling the best data for the job. *Conservation biology* 18: 1677-1681.

Probert P, Read G, Grove S, Rowden A. 2001. Macrobenthic polychaete assemblages of the continental shelf and upper slope off the west coast of the South Island, New Zealand. *New Zealand journal of marine and freshwater research* 35: 971-984.

Probert PK, Grove SL. 1998. Macrobenthic assemblages of the continental shelf and upper slope off the west coast of South Island, New Zealand. *Journal of the Royal Society of New Zealand* 28: 259-280.

Probert PK, Wilson JB. 1984. Continental shelf benthos off Otago Peninsula, New Zealand. *Estuarine, Coastal and Shelf Science* 19: 373-391.

Przeslawski R, Currie DR, Sorokin SJ, Ward TM, Althaus F, Williams A. 2011. Utility of a spatial habitat classification system as a surrogate of marine benthic community structure for the Australian margin. *ICES Journal of Marine Science: Journal du Conseil* 68: 1954-1962.

Quinn GP, Keough MJ. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press.

Quiroz-Martinez B, Schmitt F, Dauvin J-C, Dewarumez J-M, Foveau A, Garcia C. 2011. Regional patterns of continental shelf polychaete diversity: examples for the North Sea, English Channel, Irish Sea and Outer Bristol Channel areas. *Italian Journal of Zoology* 78: 324-332.

Rabalais NN, Atilla N, Normandeau C, Turner RE. 2004. Ecosystem history of Mississippi River-influenced continental shelf revealed through preserved phytoplankton pigments. *Marine Pollution Bulletin* 49: 537-547.

Rabaut M, Guilini K, Van Hoey G, Vincx M, Degraer S. 2007. A bio-engineered soft-bottom environment: The impact of Lanice conchilega on the benthic species-specific densities and community structure. *Estuarine, Coastal and Shelf Science* 75: 525-536.

Ramsay P. 1994. Marine geology of the Sodwana Bay shelf, southeast Africa. *Marine Geology* 120: 225-247.

Ramsay PJ, Smith AM, Mason TR. 1996. Geostrophic sand ridge, dune fields and associated bedforms from the Northern KwaZulu-Natal shelf, south-east Africa. *Sedimentology* 43: 407-419.

Ramsey P, Miller W. 2002. Multibeam bathymetric survey defines coelacanth habitat. *Hydro International* 6: 57-59.

Rees SE, Rodwell LD, Attrill MJ, Austen MC, Mangi SC. 2010. The value of marine biodiversity to the leisure and recreation industry and its application to marine spatial planning. *Marine policy* 34: 868-875.

Reise K. 2002. Sediment mediated species interactions in coastal waters. *Journal of Sea Research* 48: 127-141.

Reiss H, Birchenough S, Borja A, Buhl-Mortensen L, Craeymeersch J, Dannheim J, Darr A, Galparsoro I, Gogina M, Neumann H. 2015. Benthos distribution modelling and its relevance for marine ecosystem management. *ICES Journal of Marine Science* 72: 297-315.

Reiss H, Degraer S, Duineveld GC, Kröncke I, Aldridge J, Craeymeersch JA, Eggleton JD, Hillewaert H, Lavaleye MS, Moll A. 2010. Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES Journal of Marine Science* 67: 278-293.

Rhoads DC, Boyer LF. 1982. The effects of marine benthos on physical properties of sediments. *Animal-sediment relations*: Springer. p. 3-52.

Rhoads DC, Young DK. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure.

Riisgard H. 1991. Suspension feeding in the polychaete Nereis diversicolor. *Marine Ecology Progress Series* 70: 29-37.

Riisgård HU, Kamermans P. 2001. Switching between deposit and suspension feeding in coastal zoobenthos. *Ecological comparisons of sedimentary shores*: Springer. p. 73-101.

Roberts CM, Andelman S, Branch G, Bustamante RH, Castilla JC, Dugan J, Halpern BS, Lafferty KD, Leslie H, Lubchenco J. 2003. Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications* 13: S199-S214.

Roberts JJ, Best BD, Dunn DC, Treml EA, Halpin PN. 2010a. Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. *Environmental Modelling & Software* 25: 1197-1207.

Roberts M, Nieuwenhuys C, Guastella L. 2016. Circulation of shelf waters in the KwaZulu-Natal Bight, South Africa. *African Journal of Marine Science* 38: S7-S21.

Roberts M, Ribbink A, Morris T, Van den Berg M, Engelbrecht D, Harding R. 2006. Oceanographic environment of the Sodwana Bay coelacanths (Latimeria chalumnae), South Africa: coelacanth research. *South African Journal of Science* 102: 435-443.

Roberts M, Van der Lingen C, Whittle C, Van den Berg M. 2010b. Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: their relevance to the KwaZulu-Natal sardine run. *African Journal of Marine Science* 32: 423-447.

Robinson L, Elith J, Hobday A, Pearson R, Kendall B, Possingham H, Richardson A. 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography* 20: 789-802.

Rodrigues CW, Pires-Vanin AMS. 2012. Spatio-temporal and functional structure of the amphipod communities off Santos, Southwestern Atlantic. *Brazilian Journal of Oceanography* 60: 421-439.

Roland PC, Lawton P, Ellis N, Smith SJ, Incze LS, Wei CL, Greenlaw ME, Wolff NH, Sameoto JA, Snelgrove PV. 2012. Exploring the role of environmental variables in shaping patterns of seabed biodiversity composition in regional-scale ecosystems. *Journal of applied ecology* 49: 670-679.

Rosenberg R. 1995. Benthic marine fauna structured by hydrodynamic processes and food availability. *Netherlands Journal of Sea Research* 34: 303-317.

Rosenburg R. 2001. Marine benthic faunal successional stages and related sedimentary activities *Scientia Marina* 65: 107-119.

Roth S, Wilson JG. 1998. Functional analysis by trophic guilds of macrobenthic community structure in Dublin Bay, Ireland. *Journal of Experimental Marine Biology and Ecology* 222: 195-217.

Roy K, Jablonski D, Valentine J. 1996. Higher taxa in biodiversity studies: patterns from eastern Pacific marine molluscs. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 351: 1605-1613.

Roy K, Jablonski D, Valentine J. 1997. Higher taxa in biodiversity studies: patterns from eastern Pacific marine molluses. *Oceanographic Literature Review* 6: 601.

Rubal M, Veiga P, Reis PA, Bertocci I, Sousa-Pinto I. 2014. Effects of subtle pollution at different levels of biological organisation on species-rich assemblages. *Environmental Pollution* 191: 101-110.

Ruffo S. 1959. Contributo alia conoscenza degli anfipodi del Mar Rosso (1.) Materiali raccolti a Ghardaqa e nel Golfo di Aqaba. *Sea FisheriesResearch Station Haifa Bulletin* 20.

Sakai K. 2011. Axioidea of the world and a reconsideration of the Callianassoidea (Decapoda, Thalassinidea, Callianassida). *Crustacean Monographs* 13: 1-520

Salas F, Patrício J, Marcos C, Pardal MA, Pérez-Ruzafa A, Marques JC. 2006. Are taxonomic distinctness measures compliant to other ecological indicators in assessing ecological status? *Marine Pollution Bulletin* 52: 162-174.

Sampaio L, Mamede R, Ricardo F, Magalhães L, Rocha H, Martins R, Dauvin J-C, Rodrigues AM, Quintino V. 2016. Soft-sediment crustacean diversity and distribution along the Portuguese continental shelf. *Journal of Marine Systems* 163: 43-60.

Samyn Y. 2003. Towards an understanding of the shallow-water holothuroid fauna (Echinodermata: Holothuroidea) of the western Indian Ocean.

Sanders HL. 1958. Benthic Studies in Buzzards Bay. I. Animal-Sediment Relationships1. *Limnology and Oceanography* 3: 245-258.

Sanders HL. 1968. Marine benthic diversity: a comparative study. *The American Naturalist* 102: 243-282.

Sanders JL, Kendall MA, Hawkins AJ, Spicer JI. 2007. Can functional groups be used to indicate estuarine ecological status? *Hydrobiologia* 588: 45-58.

Santos MFLd, Pires-Vanin AMS. 2004. Structure and dynamics of the macrobenthic communities of Ubatuba Bay, southeastern Brazilian coast. *Brazilian Journal of Oceanography* 52: 59-73.

Sarkar S, Justus J, Fuller T, Kelley C, Garson J, Mayfield M. 2005. Effectiveness of environmental surrogates for the selection of conservation area networks. *Conservation biology* 19: 815-825.

Scharler U, Ayers M, de Lecea A, Pretorius M, Fennessy S, Huggett J, MacKay C, Muir D. 2016. Riverine influence determines nearshore heterogeneity of nutrient (C, N, P) content and stoichiometry in the KwaZulu-Natal Bight, South Africa. *African Journal of Marine Science* 38: S193-S203.

Schiele K, Darr A, Zettler M. 2014. Verifying a biotope classification using benthic communities - an analysis towards the implementation of the European Marine Strategy Framework Directive. *Mararine pollution bulletin* 78: 181-189.

Schratzberger M, Warr K, Rogers S. 2007. Functional diversity of nematode communities in the southwestern North Sea. *Marine Environmental Research* 63: 368-389.

Schückel U, Beck M, Kröncke I. 2015. Macrofauna communities of tidal channels in Jade Bay (German Wadden Sea): spatial patterns, relationships with environmental characteristics, and comparative aspects. *Marine Biodiversity* 45: 841-855.

Schumacher BA. 2002. Methods for the determination of total organic carbon (TOC) in soils and sediments. *Ecological Risk Assessment Support Center* 2002: 1-23.

Schumann E. 1987. The coastal ocean off the east coast of South Africa. *Transactions of the Royal Society of South Africa* 46: 215-229.

Schumann EH. 1988. Physical Oceanography Off Natal. In: Schumann EH editor. *Lecture Notes on Coastal and Estuarine Studies Volume 26. Coastal ocean studies off Natal, South Africa* No. 31. Germany: Springer-Verlag. p. 101-130.

Schwinghamer P. 1981. Characteristic size distributions of integral benthic communities. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1255-1263.

Scott R, Griffiths C, Robinson T. 2012. Patterns of endemicity and range restriction among southern African coastal marine invertebrates. *African Journal of Marine Science* 34: 341-347.

Scrutton RA. 1982. *Crustal structure and development of sheared passive continental margins*. Wiley Online Library.

Shannon CE, Weaver W. 1949. *The mathematical theory of communication*. University of Illinois press.

Shannon CE, Weaver W. 1963. The mathematical theory of communication. *Urbana: University of Illinois Press*.

Shapiro SS, Wilk MB. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52: 591-611.

Shettleworth SJ. 2012. Do animals have insight, and what is insight anyway? *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale* 66: 217.

Shin P, Huang Z, Wu R. 2004. An updated baseline of subtropical macrobenthic communities in Hong Kong. *Marine Pollution Bulletin* 49: 128-135.

Shojaei MG, Gutow L, Dannheim J, Pehlke H, Brey T. 2015. Functional Diversity and Traits Assembly Patterns of Benthic Macrofaunal Communities in the Southern North Sea. *Towards an Interdisciplinary Approach in Earth System Science*: Springer. p. 183-195.

Shokri MR, Gladstone W. 2008. Higher taxa are effective surrogates for species in the selection of conservation reserves in estuaries. *Aquatic conservation: marine and freshwater ecosystems* 19: 626-636.

Shokri MR, Gladstone W. 2013. Limitations of habitats as biodiversity surrogates for conservation planning in estuaries. *Environmental monitoring and assessment* 185: 3477-3492.

Shokri MR, Gladstone W, Kepert A. 2009. Annelids, arthropods or molluscs are suitable as surrogate taxa for selecting conservation reserves in estuaries. *Biodiversity and Conservation* 18: 1117-1130.

Shumchenia EJ, Guarinello ML, Carey DA, Lipsky A, Greene J, Mayer L, Nixon ME, Weber J. 2015. Inventory and comparative evaluation of seabed mapping, classification and modeling activities in the Northwest Atlantic, USA to support regional ocean planning. *Journal of Sea Research* 100: 133-140.

Siddig AA, Ellison AM, Ochs A, Villar-Leeman C, Lau MK. 2016. How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. *Ecological Indicators* 60: 223-230.

Siefert A. 2012. Incorporating intraspecific variation in tests of trait-based community assembly. *Oecologia* 170: 767-775.

Sink K, Attwood C. 2008. *Guidelines for offshore marine protected areas in South Africa*. South African National Biodiversity Institute.

Sink K, Branch G, Harris J. 2005. Biogeographic patterns in rocky intertidal communities in KwaZulu-Natal, South Africa. *African Journal of Marine Science* 27: 81-96.

Sink K, Holness S, Harris L, Majiedt P, Atkinson L, Robinson T, Kirkman S, Hutchings L, Leslie R, Lamberth S. 2011. National biodiversity assessment 2011: Technical report 4: 325.

Sivadas S, Ingole B, Fernandes C. 2013. Environmental gradient favours functionally diverse macrobenthic community in a placer rich tropical bay. *The Scientific World Journal* 2013.

Smith L. 1995. Sieve mesh-size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. *Marine Ecology Progress Series* 118: 187-198.

Smith SD. 2005. Rapid assessment of invertebrate biodiversity on rocky shores: where there'sa whelk there'sa way. *Biodiversity and Conservation* 14: 3565-3576.

Snelgrove P, Butman C. 1994. Animal-sediment relationships revisited: cause versus effect. *Oceanographic Literature Review* 8: 668.

Snelgrove P, Butman C. 1995. Animal-sediment relationships revisited: cause versus effect. *Oceanographic Literature Review* 8: 668.

Snelgrove PV. 1997. The importance of marine sediment biodiversity in ecosystem processes. *Ambio*: 578-583.

Snelgrove PV. 1998. The biodiversity of macrofaunal organisms in marine sediments. *Biodiversity and Conservation* 7: 1123-1132.

Snelgrove PV, Grassle JF, Grassle JP, Petrecca RF, Stocks KI. 2001. The role of colonization in establishing patterns of community composition and diversity in shallow-water sedimentary communities. *Journal of Marine Research* 59: 813-830.

Snelgrove PV, Thrush SF, Wall DH, Norkko A. 2014. Real world biodiversity–ecosystem functioning: a seafloor perspective. *Trends in Ecology & Evolution* 29: 398-405.

Snelgrove PVR. 1999. Getting to the Bottom of Marine Biodiversity: Sedimentary Habitats: Ocean bottoms are the most widespread habitat on Earth and support high biodiversity and key ecosystem services. *BioScience* 49: 129-138.

Sokołowski A, Wołowicz M, Asmus H, Asmus R, Carlier A, Gasiunaite Z, Grémare A, Hummel H, Lesutiené J, Razinkovas A. 2012. Is benthic food web structure related to diversity of marine macrobenthic communities? *Estuarine, Coastal and Shelf Science* 108: 76-86.

Solan M, Cardinale BJ, Downing AL, Engelhardt KA, Ruesink JL, Srivastava DS. 2004. Extinction and ecosystem function in the marine benthos. *Science* 306: 1177-1180.

Somerfield P, Clarke K. 1995. Taxonomic levels, in marine community studies, revisited. *Marine Ecology Progress Series* 127: 113-119.

Somerfield P, Warwick R, Moens T, Eleftheriou A, Mcintyre A. 2005. Methods for the study of marine benthos. *Meiofauna techniques. Blackwell Science*: 229-272.

Sommer B, Harrison PL, Beger M, Pandolfi JM. 2014. Trait-mediated environmental filtering drives assembly at biogeographic transition zones. *Ecology* 95: 1000-1009.

Soto E, Quiroga E, Ganga B, Alarcón G. 2016. Influence of organic matter inputs and grain size on soft-bottom macrobenthic biodiversity in the upwelling ecosystem of central Chile. *Marine Biodiversity*: 1-18.

Soto E, Quiroga E, Ganga B, Alarcón G. 2017. Influence of organic matter inputs and grain size on soft-bottom macrobenthic biodiversity in the upwelling ecosystem of central Chile. *Marine Biodiversity* 47: 433-450.

Southwood T. 1977. Habitat, the templet for ecological strategies. *The Journal of Animal Ecology*: 337-365.

St Pierre JI, Kovalenko KE. 2014. Effect of habitat complexity attributes on species richness. *Ecosphere* 5: 1-10.

Starmans A, Gutt J, Arntz W. 1999. Mega-epibenthic communities in Arctic and Antarctic shelf areas. *Marine Biology* 135: 269-280.

Steffani N, Sedick S, Rogers J, Gibbons MJ. 2015. Infaunal Benthic Communities from the Inner Shelf off Southwestern Africa Are Characterised by Generalist Species. *PLoS One* 10: e0143637.

Stephenson W. The validity of the community concept in marine biology*1973*. pp. 73-86.

Stevens T, Connolly RM. 2005. Local-scale mapping of benthic habitats to assess representation in a marine protected area. *Marine and Freshwater Research* 56: 111-123.

Stewart P, Butcher J, Swinford T. 2000. Land use, habitat, and water quality effects on macroinvertebrate communities in three watersheds of a Lake Michigan associated marsh system. *Aquatic ecosystem health & management* 3: 179-189.

Su JC, Debinski DM, Jakubauskas ME, Kindscher K. 2004. Beyond species richness: Community similarity as a measure of cross-taxon congruence for coarse-filter conservation. *Conservation biology* 18: 167-173.

Sverdrup HU, Johnson MW, Fleming RH. 1942. *The Oceans: Their physics, chemistry, and general biology*. vol. 7. Prentice-Hall New York.

Tagliapietra D, Sigovini M. 2010. Benthic fauna: collection and identification of macrobenthic invertebrates. *NEAR curriculum in natural environmental sciences. Terre et Environ* 88: 253-261.

Tataranni M, Maltagliati F, Floris A, Castelli A, Lardicci C. 2009. Variance estimate and taxonomic resolution: an analysis of macrobenthic spatial patterns at different scales in a Western Mediterranean coastal lagoon. *Marine Environmental Research* 67: 219-229.

Taylor J, Ormond R, Gage J, Angel M. 1997. Diversity and structure of tropical Indo-Pacific benthic communities: relation to regimes of nutrient input. *Marine biodiversity: patterns and processes. Cambridge University Press, Cambridge*.

Tena J, Capaccioni-Azzati R, Torres-Gavila F, Porras R. 1993. Anélidos poliquetos del antepuerto de Valencia: distribución y categorías tróficas. *Publicacao Especial do Instituto Oceanografico* 11: 15-20.

Teske PR, Von der Heyden S, McQuaid CD, Barker NP. 2011. A review of marine phylogeography in southern Africa. *South African Journal of Science* 107: 43-53.

Thandar A. 2009. A new species of the holothurian genus Pkyllophorus from South Africa with a key to subgenus Phyllophorella. *Journal of Zoology* 234: 341-351.

Thandar A, Rowe F. 2005. New species and new records of apodous holothurians (Echinodermata, Holothuroidea) from southern Africa. *Zoologica scripta* 18: 145-155.

Thomas JD. 1993. Biological monitoring and tropical biodiversity in marine environments: a critique with recommendations, and comments on the use of amphipods as bioindicators. *Journal of Natural History* 27: 795-806.

Thomas KV, Blake SJ, Waldock MJ. 2000. Antifouling paint booster biocide contamination in UK marine sediments. *Marine Pollution Bulletin* 40: 739-745.

Thorson G. 1957. Bottom communities (sublittoral or shallow shelf). *Geological Society of America Memoirs* 67: 461-534.

Thorson G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. *Netherlands Journal of Sea Research* 3: 267-293.

Thrush S, Hewitt J, Cummings V, Dayton P, Cryer M, Turner S, Funnell G, Budd R, Milburn C, Wilkinson M. 1998. Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. *Ecological Applications* 8: 866-879.

Thrush S, Hewitt J, Cummings V, Ellis J, Hatton C, Lohrer A, Norkko A. 2004. Muddy waters: elevating sediment input to coastal and estuarine habitats. *Frontiers in Ecology and the Environment* 2: 299-306.

Thrush SF. 1991. Spatial patterns in soft-bottom communities. *Trends in Ecology & Evolution* 6: 75-79.

Thrush SF, Chiantore M, Asnaghi V, Hewitt J, Fiorentino D, Cattaneo-Vietti R. 2011. Habitat–diversity relationships in rocky shore algal turf infaunal communities. *Marine Ecology Progress Series* 424: 119-132.

Thrush SF, Gray JS, Hewitt JE, Ugland KI. 2006. Predicting the effects of habitat homogenization on marine biodiversity. *Ecological Applications* 16: 1636-1642.

Thrush SF, Hewitt JE, Cummings VJ, Norkko A, Chiantore M. 2010. β-diversity and species accumulation in Antarctic coastal benthos: influence of habitat, distance and productivity on ecological connectivity. *PLoS One* 5: e11899.

Thrush SF, Hewitt JE, Funnell GA, Cummings VJ, Ellis J, Schultz D, Talley D, Norkko A. 2001. Fishing disturbance and marine biodiversity: the role of habitat structure in simple soft-sediment systems. *Marine Ecology Progress Series* 223: 277-286.

Tillin H, Hiddink J, Jennings S, Kaiser M. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series* 318: 31-45.

Tittensor DP, Worm B. 2016. A neutral-metabolic theory of latitudinal biodiversity. *Global Ecology and Biogeography* 25: 630-641.

Törnroos A, Bonsdorff E. 2012. Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. *Ecological Applications* 22: 2221-2236.

Törnroos A, Nordström MC, Bonsdorff E. 2013. Coastal habitats as surrogates for taxonomic, functional and trophic structures of benthic faunal communities. *PLoS One* 8: e78910.

Townsend CR, Hildrew AG. 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology* 31: 265-275.

Trigal-Domínguez C, Fernández-Aláez C, García-Criado F. 2010. Ecological assessment of highly heterogeneous systems: The importance of taxonomic sufficiency. *Limnologica-Ecology and Management of Inland Waters* 40: 208-214.

Turpie J, Wilson G, Van Niekerk L. 2012. National Biodiversity Assessment 2011: National Estuary Biodiversity Plan for South Africa. *Anchor Environmental Consulting, Cape Town. Report*

produced for the Council for Scientific and Industrial Research and the South African National Biodiversity Institute.

Tweedley J, Valesini F. 2008. Inter-relationships between benthic macroinvertebrates and habitat types in Broke Inlet, south-western Australia. Report to the Ernest Hodgkin Trust for Estuary Education and Research, September 2008.

Tyler CL, Kowalewski M. Surrogate taxa and fossils as reliable proxies of spatial biodiversity patterns in marine benthic communities*2017*: The Royal Society. pp. 20162839.

Tyler EH, Somerfield PJ, Berghe EV, Bremner J, Jackson E, Langmead O, Palomares MLD, Webb TJ. 2012. Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. *Global Ecology and Biogeography* 21: 922-934.

Tyson PD, Preston-Whyte RA. 2000. *weather and climate of southern Africa*. Oxford University Press.

Uenzelmann-Neben G, Huhn K. 2009. Sedimentary deposits on the southern South African continental margin: Slumping versus non-deposition or erosion by oceanic currents. *Marine Geology* 266: 65-79.

Ullberg J, Ólafsson E. 2003. Free-living marine nematodes actively choose habitat when descending from the water column. *Marine Ecology Progress Series* 260: 141-149.

Underwood A, Chapman M, Connell S. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* 250: 97-115.

Untiedt C, MacKay C. 2016. Distribution and feeding modes of macrobenthos within three oceanographic feature areas of the KwaZulu-Natal Bight, South Africa. *African Journal of Marine Science* 38: S91-S104.

Untiedt CB. 2013. Community Structure and Function of Macrobenthos in Three Feature Areas of the Natal Bight, South Africa. Msc, University of KwaZulu Natal, Westville.

Usseglio-Polatera P, Bournaud M, Richoux P. 2000a. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology* 43: 175-205.

Usseglio-Polatera P, Bournaud M, Richoux P, Tachet H. 2000b. *Biomonitoring through biological traits of benthic macroinvertebrates: how to use species trait databases?* : Springer.

Usseglio-Polatera P, Bournaud M, Richoux P, Tachet H. 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology* 43: 175-205.

Valiela's I. 1984. *Marine ecological processes*. Springer Science & Business Media.

van der Linden P, Marchini A, Smith CJ, Dolbeth M, Simone LRL, Marques JC, Molozzi J, Medeiros CR, Patrício J. 2017. Functional changes in polychaete and mollusc communities in two tropical estuaries. *Estuarine, Coastal and Shelf Science* 187: 62-73.

Van Hoey G, Degraer S, Vincx M. 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuarine, Coastal and Shelf Science* 59: 599-613.

Van Hoey G, Guilini K, Rabaut M, Vincx M, Degraer S. 2008. Ecological implications of the presence of the tube-building polychaete Lanice conchilega on soft-bottom benthic ecosystems. *Marine Biology* 154: 1009-1019.

Vanderklift M, Ward T, Phillips J. 1998. Use of assemblages derived from different taxonomic levels to select areas for conserving marine biodiversity. *Biological Conservation* 86: 307-315.

Vandewalle M, De Bello F, Berg MP, Bolger T, Dolédec S, Dubs F, Feld CK, Harrington R, Harrison PA, Lavorel S. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation* 19: 2921-2947.

Vane-Wright R, Humphries C, PH W. 1991. What to protect? Systematics and the agony of choice. *Biological Conservation* 55: 235–254.

Veiga P, Redondo W, Sousa-Pinto I, Rubal M. 2017. Relationship between structure of macrobenthic assemblages and environmental variables in shallow sublittoral soft bottoms. *Marine Environmental Research*.

Veiga P, Torres AC, Aneiros F, Sousa-Pinto I, Troncoso JS, Rubal M. 2016. Consistent patterns of variation in macrobenthic assemblages and environmental variables over multiple spatial scales using taxonomic and functional approaches. *Marine Environmental Research* 120: 191-201.

Velerio-Berado MT, Flynn MN, Wakabara Y. 2000. Density and diversity patterns of a shelf amphipods taxocoenosis in Ubatuba, Southeastern Brazil *Oceanides* 15: 117-127

Verberk WC, Siepel H, Esselink H. 2008. Life-history strategies in freshwater macroinvertebrates. *Freshwater Biology* 53: 1722-1738.

Verfaillie E, Van Lancker V, Van Meirvenne M. 2006. Multivariate geostatistics for the predictive modelling of the surficial sand distribution in shelf seas. *Continental Shelf Research* 26: 2454-2468.

Veríssimo H, Neto JM, Teixeira H, Franco JN, Fath BD, Marques JC, Patrício J. 2012. Ability of benthic indicators to assess ecological quality in estuaries following management. *Ecological Indicators* 19: 130-143.

Villasenor JL, IBARRA-MANRÍQUEZ G, Meave JA, Ortiz E. 2005. Higher taxa as surrogates of plant biodiversity in a megadiverse country. *Conservation biology* 19: 232-238.

Villéger S, Miranda JR, Hernandez DF, Mouillot D. 2012. Low functional β-diversity despite high taxonomic β-diversity among tropical estuarine fish communities. *PLoS One* 7: 1-10.

Villéger S, Miranda JR, Hernández DF, Mouillot D. 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications* 20: 1512-1522.

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional. *Oikos* 116: 882-892.

Vopel K, Thistle D, Rosenberg R. 2003. Effect of the brittle star Amphiura filiformis (Amphiuridae, Echinodermata) on oxygen flux into the sediment. *Limnology and Oceanography* 48: 2034-2045.

Vousden D, Scott LEP, Sauer W, Bornman T, Ngoile M, Stapley J, Lutjeharms J. 2008. Establishing a basis for ecosystem management in the western Indian Ocean. *South African Journal of Science* 104: 417-420.

Walker BH. 1992. Biodiversity and ecological redundancy. *Conservation biology* 6: 18-23.

Walling D. 2006. Human impact on land–ocean sediment transfer by the world's rivers. *Geomorphology* 79: 192-216.

Ward T, Vanderklift M, Nicholls A, Kenchington R. 1999. Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecological Applications* 9: 691-698.

Warwick R. 1987. Comparative study of the structure of some tropical and temperate marine soft-bottom macrobenthic communities. *Marine Biology* 95: 641-649.

Warwick R. 1988. Analysis of community attributes of the macrobenthos of Frierfjord/Langesundfjord at taxonomic levels higher than species. *Marine Ecology Progress Series* 46: 167-170.

Warwick RM. 1993. Environmental impact studies on marine communities: pragmatical considerations. *Australian Journal of Ecology* 18: 63-80.

Warwick RM, Platt HM, Clarke KR, Agard J, Gobin J. 1990. Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. *Journal of Experimental Marine Biology and Ecology* 138: 119-142.

Watling L. 1993. Functional morphology of the amphipod mandible. *Journal of Natural History* 27: 837-849.

Weaver PP, Wynn RB, Kenyon NH, Evans J. 2000. Continental margin sedimentation, with special reference to the north-east Atlantic margin. *Sedimentology* 47: 239-256.

Weigel B, Blenckner T, Bonsdorff E. 2016. Maintained functional diversity in benthic communities in spite of diverging functional identities. *Oikos* 125: 1421-1433.

Wentworth CK. 1922. A scale of grade and class terms for clastic sediments. *The Journal of Geology* 30: 377-392.

Weston DP. 1988. Macrobenthos-sediment relationships on the continental shelf off Cape Hatteras, North Carolina. *Continental Shelf Research* 8: 267-286.

Wieking G, Kröncke I. 2003. Macrofauna communities of the Dogger Bank (central North Sea) in the late 1990s: spatial distribution, species composition and trophic structure. *Helgoland Marine Research* 57: 34.

Willems T, De Backer A, You KWT, Vincx M, Hostens K. 2015. Spatio-temporal distribution patterns of the epibenthic community in the coastal waters of Suriname. *Continental Shelf Research* 108: 25-40.

Wilson R 2005. Marine invertebrate sample processing procedures. Museum Victoria, September.

Wilson WH. 1991. Sexual reproductive modes in polychaetes: classification and diversity. *Bulletin of Marine Science* 48: 500-516.

Winsnes IM. 1985. The use of methyl green as an aid in species discrimination in Onuphidae (Annelida, Polychaeta). *Zoologica scripta* 14: 19-23.

Wlodarska-Kowalczuk M, Kedra M. 2007. Surrogacy in natural patterns of benthic distribution and diversity: selected taxa versus lower taxonomic resolution. *Marine Ecology Progress Series* 351: 53-63.

Włodarska-Kowalczuk M, Renaud PE, Węsławski JM, Cochrane SK, Denisenko SG. 2012. Species diversity, functional complexity and rarity in Arctic fjordic versus open shelf benthic systems. *Marine Ecology Progress Series* 463: 73-87.

Wong MC, Dowd M. 2015. Patterns in Taxonomic and Functional Diversity of Macrobenthic Invertebrates Across Seagrass Habitats: a Case Study in Atlantic Canada. *Estuaries and Coasts* 38: 2323-2336.

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JB, Lotze HK, Micheli F, Palumbi SR. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314: 787-790.

WoRMS Editorial Board n.d. World Register of Marine Species (WoRMS). Available at www.marinespecies.org [accessed 16 August 2017].

Wu R, Shin P. 1997. Sediment characteristics and colonization of soft-bottom benthos: a field manipulation experiment. *Marine Biology* 128: 475-487.

Yekta FA, Izadi S, Asgari M, Aghajan-Pour F, Shokri M-R. 2017. Higher taxa as surrogates for species richness in intertidal habitats of Qeshm Island in the Persian Gulf. *Marine Biodiversity* 47: 1-8.

Young M, Carr M. 2015. Assessment of Habitat Representation across a Network of Marine Protected Areas with Implications for the Spatial Design of Monitoring. *PLoS One* 10: 1-23.

Zacharias MA, Roff JC. 2000. A hierarchical ecological approach to conserving marine biodiversity. *Conservation biology* 14: 1327-1334.

Zalmon I, Macedo I, Rezende C, Falcão A, Almeida T. 2013. The distribution of macrofauna on the inner continental shelf of southeastern Brazil: the major influence of an estuarine system. *Estuarine Coastal and Shelf Science* 130: 169-178.

Zar JH. 1999. *Biostatistical analysis*. Pearson Education India.

Zettler ML, Bochert R, Pollehne F. 2009. Macrozoobenthos diversity in an oxygen minimum zone off northern Namibia. *Marine Biology* 156: 1949-1961.

Zobel M. 1997. The relative of species pools in determining plant species richness: an alternative explanation of species coexistence. *Trends in Ecology & Evolution* 12: 266-269.

Appendix 1. Biophysical layers used to define marine spatial planning biodiversity zones (biozones).

Data	Type	Period	Source
SeaSea surface temperature (SST)	Advanced High Resolution Radiometer (AVHRR)	2001-2004	Oceanspace institute, University of Cape Town
Chlorophyll-a	Sea-viewing Wide Field-of-view Sensor (SeaWiFS)	2001-2004	Oceanspace institute, University of Cape Town
Photosynthetically Available Radiation (PAR), as a surrogate for turbidity	K 490 data	2004	Level 3 browser, Oceancolor (http://oceancolor.gsfc.nasa.gov/cg/ilevel3.pl
Bottom oxygen	raster dataset	2006	Fiona Duff, University of Cape Town
Bottom temperature	SADCO	1930-2005	Fiona Duff, University of Cape Town
Bathymetric data	Grids and digitised contour maps 32 Datasets	2009	Paul Young
Slope data	Vector slopes along the X and Y gradients		Interpolated from bathymetric data
Sediment data	ArcGIS and maps (Mud-gravel, Organic carbon and phosphate)	1996	Birch manuscript (single source)