

**BIODIVERSITY OF SOFT SEDIMENT MACROBENTHIC
FAUNA OF THE KWAZULU-NATAL BIGHT
MIDSHELF**

by

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As the candidate's supervisor I have/have not approved this thesis/dissertation for
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ABSTRACT

The KwaZulu-Natal Bight is influenced by various nutrient inputs from the Thukela River and particular oceanographic features of the shelf such as the St Lucia upwelling cell and the Durban lee eddy that are in turn associated with Agulhas Current behaviour. Little is known about KZN Bight community dynamics of most faunal groups and so knowledge about the ecological functioning of this system as a whole is lacking. To address this, a large multidisciplinary project on the Bight was conducted through the African Coelacanth Ecosystem Programme. One aim of the programme was to establish whether nutrient inputs have significant impacts on this oligotrophic shelf and if so, how? This study looked at the macrobenthic compartment to examine variations in diversity across the KZN Bight in the midshelf habitat only. Changes in diversity were explained in relation to important habitat and/or process drivers. Replicated biological and sediment samples were collected in and between the three focus areas of high nutrient input along the Bight spanning an area from Durban to just south of the St Lucia Estuary mouth. Samples were collected twice at the same stations, once during a wet period (February 2010) and once during a dry period (August 2010). These periods were selected to represent high and low outflow and thus potentially higher and lower nutrient inputs to the Bight, respectively. Macrobenthos collected by 0.2m² Van Veen grab were identified to the lowest possible taxonomic level and resulting data were analysed using combinations of univariate and multivariate statistical procedures. Diversity was described using well-published techniques that related to community Alpha (α) and Beta (β) diversity and including several newer methods such as Taxonomic Diversity indices (Taxonomic Distinctness (Δ^*), Average Taxonomic Distinctness (Δ^+), Variation in Taxonomic Distinctness (Δ^{++})) to determine the taxonomic relatedness of macrobenthic communities within the study area. Midshelf macrobenthic community α and β diversity was highly variable across the shelf with no distinct patterns related to focus area. Diversity values were however similar to values obtained in what are considered highly diverse tropical and high latitude shelves.

Diversity was then related to hydrographic parameters measured on the Bight to understand the possible indirect or direct roles the Agulhas Current and Thukela River have in maintaining the macrobenthos. Findings were that diversity was only weakly related to measured environmental variables suggesting far more complex interactions in the biophysical environment of the Bight. This was highlighted by the finding that alpha and beta diversity measures had complimentary relationships as an inverse trend was found between these measures along the KZN Bight. Thus, more detailed systematic studies on the Bight are needed to fully understand the role and supply of nutrients on specific communities and how these pertain to the ecological function of the whole shelf ecosystem.

PREFACE

The experimental work described in this dissertation for the MSc was carried out in the School of Life Sciences, University of KwaZulu-Natal, Westville Campus, Durban, from January 2010 to December 2013, under the supervision of Mrs C.F. MacKay.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

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I, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
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LIST OF SYMBOLS

d (Margalef species richness)

J' (Pielou evenness)

H_{log_e} (Shannon-Wiener diversity index)

$1-\text{Lambda}'$ (Simpson diversity index)

$N_1 = \text{Exp}(H')$ (Hill's diversity index)

$N_2 = 1/\text{SI}$ (Hill's diversity index)

β_w (Whittaker's beta diversity)

α (Alpha diversity)

β (Beta diversity)

% BC (Percentage Bray-Curtis similarity)

σ^ϕ (Sediment sorting)

sk^ϕ (Sediment skewness)

Δ^* (Taxonomic diversity indices such as taxonomic distinctness)

Δ^+ (Average taxonomic distinctness)

Λ^+ (Variation in taxonomic distinctness)

LIST OF EQUATIONS

$\beta_w = (\gamma/\bar{a})-1$ (Pairwise Whittaker's beta diversity - where γ is the total number of species in the two combined sites and \bar{a} is the average number of species per site)

CHAPTER 1

GENERAL INTRODUCTION

1.1 THE KZN BIGHT AND THE AGULHAS CURRENT

Along the east coast of South Africa, exceptional biologically interesting habitats can be found, related to the great variety of environmental conditions as a result of the passing Agulhas Current circulation and wind systems (Heydorn et al. 1978). The Agulhas Current contributes to important oceanographic features that are key to the ecology of the Bight (Schumann 1988, Meyer et al. 2002). Compared with other western boundary currents, the Agulhas Current is relatively narrow at approximately 100 km wide (Lutjeharms 2006b), forming the western part of the South-West Indian Ocean anti-cyclonic circulation system that consists of tropical and subtropical water moving in a southerly direction (Lutjeharms 2006b).

The continental slope adjacent to the Agulhas Current can be divided into two sections according to topographical and current characteristics. The first is a narrow southern part approximately 15 km wide just upstream of Port Elizabeth to just downstream of Durban (Lutjeharms 2006b). Here all circulation is parallel with the narrow shelf slope (Lutjeharms 2006b). The KwaZulu-Natal Bight (KZN Bight) is the northern part of the shelf and constitutes the remaining section of the Agulhas Current, where the shelf is much wider (about 50 km wide) (McClurg 1988, Lutjeharms 2006b). Here circulation has a cyclonic upper current, with an opposing undercurrent (Lutjeharms 2006b). The KZN Bight shelf water has a clear seasonal variability in temperature and salinity (Schumann 1988). The Agulhas Current has a seasonally dependent surface temperature range of 20° C to 28°C, usually differing approximately 6 °C from its surrounding marine environment (Lutjeharms 2006b, Griffiths et al. 2010). Topography of the adjacent shelf and its interaction with the Agulhas Current seems to be the main driver of the characteristic oceanographic features along the KZN Bight (Pearce 1977, Gill and Schumann 1979, Lutjeharms et al. 1989, Meyer et al. 2002, Speich et al. 2006).

Four prominent circulation features are found in the KZN Bight, namely the St Lucia upwelling cell, Durban lee-eddy, a general cyclonic circulation in the KZN Bight (lateral circulation) and the shear edge features (Gründlingh 1986, Lutjeharms et al. 2000, Lutjeharms

2006b). The northern KZN Bight section of the current exhibits great stability with very low seasonal variability in surface speeds as well as high pathway stability (Gründlingh 1986).

It is suspected that these circulation features play an important role in the nutrient replenishment of shelf communities, along with affecting the composition and distribution of endemic species over space and time (Lutjeharms 2006b, Cawthra et al. 2012). The passing Agulhas Current with its high temperatures combined with the shelf topography of the KZN Bight, drives the upwelling of cold, nutrient rich water from the depths onto the shelf, enhancing primary productivity and chlorophyll-*a* production in and around these circulation features, distributing along a gradient, and decreasing with distance from the centre of origin along the shelf (Lutjeharms et al. 2000, Lutjeharms 2006b).

The most persistent features of the KZN Bight include an eddy off Durban and a upwelling cell between Richards Bay and St. Lucia (Gründlingh (1974), Schumann 1988, Lutjeharms et al. 1989, Lutjeharms 2006b). These two features, together with the largest KZN River, the Thukela River, were defined as the locations on the shelf for three main focus areas of oceanographic influence within this study. In the north, the persistent St Lucia upwelling cell brings cool nutrient-rich South Indian Subtropical water from a depth of ± 100 m onto the shelf bottom where it spreads southwards (Meyer et al. 2002). It consists of cooler water and lower salinities than elsewhere on the Bight (Lutjeharms et al. 2000, Lutjeharms 2006b). As the current moves south, chlorophyll-*a* values decrease on the shelf, reaching lowest levels just before reaching the Thukela River mouth (Meyer et al. 2002). Biological assimilation and lateral mixing within the shelf and ocean waters cause a patchy high nutrient pattern along this southward path of the upwelled nutrients (Meyer et al. 2002). In the Richards Bay area there exist distinctive vertical and horizontal nutrient gradients, such as a high near-shore to low off-shore nutrient gradient (Meyer et al. 2002).

Sedimentary processes of the south-eastern African outer shelf are also dominated by the Agulhas Current, which facilitates large-scale sediment movement along the coast (Lutjeharms 2006b). The northern part of the current has a characteristic high mean kinetic energy value ($500\text{cm}^2/\text{s}^2$), resulting in high speeds (Lutjeharms 2006b). The highest flow velocity of the current lies close to the continental shelf edge and can sometimes lie above the outer part of the shelf (Lutjeharms 2006b). Consequently, the sediment bed forms found on the shelf are characterised by dune fields at depths of > 50 m with heights up to 8 m, extending over a surface area of up to 20 km, while slowly migrating southwards (Lutjeharms 2006b). These dune fields are the primary source of sand for sediment fans along the continental slope (Lutjeharms 2006b).

In the southern part of the Bight, south-west off Durban a semi-permanent cyclonic eddy forms a dome of cold, less saline, nutrient rich water from shelf slope depths of 250 m up onto the bottom of the shelf table at depths of sometimes up to 30 m (Churchill et al. 1986, Carter and Schleyer 1988, Schumann 1988, Meyer et al. 2002, Lutjeharms 2006b). Strong coastal counter currents are present here, as seen by the presence of sand dunes in the bottom sediments (Lutjeharms 2006b, Cawthra et al. 2012). In the upper water column, warm Indian Tropical nutrient poor water intrudes onto the shelf moving along the coast in a north-western direction (Meyer et al. 2002). Thus in the upper water column off Durban there exists a gradient of low nutrients found near shore to higher nutrients found offshore (Meyer et al. 2002). However this part of the shelf water column is well mixed in lower layers, where weak horizontal and vertical gradients are found (Meyer et al. 2002). The southern section of the Bight allows for more intrusion of adjacent oceanic water, and the trapping of nutrients flowing along the bottom of the shelf because of its depth (Meyer et al. 2002). Closer to Durban due to “conveyer-belt” circulation caused by the current, the water is swept away off the shelf (Heydorn 1976, Meyer et al. 2002). It is in the southern shelf region that the Agulhas Current can intrude distances of up to 25 km from the coast (Meyer et al. 2002).

The Thukela River, has an annual sediment output of about $6.79 \times 10^3 \text{ m}^3$ and runoff of $3865 \times 10^6 \text{ m}^3$ (Birch 1996, Hutchings et al. 2010). In the central shelf region, most of the Thukela outflow occurs at a 30 m depth (Meyer et al. 2002). This is also an area with well mixed water as this outflow creates a turbid area in the central Bight region (Fennessy and Groeneveld 1997, Meyer et al. 2002). The shelf water closest to the Thukela River mouth has the highest nutrient concentrations of the central shelf, and this decreases gradually towards the shelf edge (Meyer et al. 2002). If nutrients transported from St. Lucia in a southerly direction, reach the Thukela River mouth region, movement will certainly be halted, as from there, the nutrients will be reflected off the shelf into deeper waters (Heydorn 1976). The Thukela River contributes a lot of detritus and inorganic nutrients towards the continental shelf system (Fromme 1970). However no detailed study on the effects that these riverine nutrients on the larger ecosystem has been undertaken (Cooper et al. 1995, Griffiths et al. 2010).

These three sources (also known as focus areas) provide large amounts of nutrient input and detritus via rivers or from lower depths via upwelling (Lutjeharms 2006b). How big a role each plays still needs to be understood. Macrobenthic studies did not in the past receive attention, as studies tended to be more biased toward more economically important demersal species, thus still much is left to be learnt, more so from benthos in continental shelf and deep sea regions of the ocean (Roberts 1997, Grassle and Stocks 1999). A dynamic variety of

pelagic-benthic interactions are formed on the KZN Bight, as the pelagic and benthic is influenced by many oceanographic processes across the shelf (McClurg 1988, Lutjeharms 2006b). These interactions are important for ecosystem functioning.

Many short-term smaller scale oceanographic features occur on the KZN Bight as the current follows its path along the shelf, leading to the formation of localised eddies, upwelling, and wind-induced currents inshore (Schumann 1988, Lutjeharms et al. 1989). In the more shallow depths of the shelf, many of these smaller short term features in the water column are often controlled by climatic factors such as the regular alteration of the north-easterly and south-westerly winds (Heydorn et al. 1978, Schumann 1988). From the structural and morphological information of the continental shelf, it is clear this system along with its complexities should not be considered as one entity, but as several separate smaller systems (Heydorn 1976).

1.2 MACROBENTHIC BIODIVERSITY

Marine diversity research has not been given sufficient weight in the past. Wright et al (1993) reviewed 53 studies done on the important factors structuring diversity (Williamson 1997). Of these, only three were marine-based (Williamson 1997). Global marine biodiversity is being threatened by a variety of factors, including overexploitation that alters food webs, physical alterations that have direct homogenising effects on habitats, and indirect effects including for example the effects of re-suspension of sediments and toxins and change in trophic dominance (Norse 1993). Due to the perceived fast changes in community structure and abundances of the most common and well known species, certain urgency has arisen to put more importance on the measurement of the present composition and limits of all marine life (Grassle and Stocks 1999). Many studies have been done on the influence of other factors on biodiversity but not enough has been done on the influence of biodiversity on other factors (Snelgrove 1998), although this has started to receive much deserved attention (Chapin et al. 1997, Loreau et al. 2001). Biological diversity as the modulator to ecosystem processes has been the basis of many ecosystem functioning studies (Loreau et al. 2001), but the focus has been on the use of species richness exclusively (Chapin et al. 1997, Bengtsson 1998).

Diversity can be divided into genetic diversity, species diversity and ecosystem diversity, as well as further separate categories found in genetic and ecological diversity (Norse et al 1986, Soulé 1991, Norse 1993, Williamson 1997). Bengtsson (1998) emphasised that there is a need to move away from the singular view of diversity as a term encompassing all in the

importance of diversity in the ecosystem, to a greater focus on understanding the mechanistic workings of the most significant facets of diversity. Most work on macrobenthic marine diversity has been done on near-shore, hard substrate communities and less on the soft-sediment macrobenthic biodiversity. Considering that soft-sediment macrobenthos are important for amongst other reasons, the survival of commercially important fish and other sediment-living organisms, much more effort has to be focused here (Pinnegar et al. 2000, Gillanders et al. 2003, Hoey et al. 2004). Recent technology involving breakthrough pharmaceutical and medical advances has been because of the biochemical diversity of animals (Norse 1993).

Most phyla in the marine environment are thought to inhabit the bottom sediments (Snelgrove 1998). Considering that the ocean takes up around ~ 70% of the earth's surface and sediment covers the entire bottom, it is logical to assume that macrobenthic fauna would have a significant impact on the world's marine ecosystems (Snelgrove 1998). Estimates are that only 1% of all macrobenthos have been described, making these biodiversity studies crucial in future understanding of our world's oceans (Snelgrove 1998).

Macrobenthos are invertebrates that spend most of their lives in close association with the ocean floor (McClurg 1988). The marine benthic fauna can be categorised into microfauna, meiofauna and macrofauna (McClurg 1988). Although they are categorised separately for convenience of study techniques, they are a continuum (McClurg 1988). Due to their size, differences in environmental pressures even within the same location may still be experienced because of different small-scale niches (McClurg 1996, Levin et al. 2010). Still they occur in the same habitat and interact with each other, forming largely discrete and sedentary communities (McClurg 1996). Macrofauna are those organisms that are larger and can be retained in a 1mm mesh sieve (McClurg 1996). Because of the large diversity of these animals, with an estimated 10^7 species believed to exist, they are able to inhabit almost every single inch of the sediment habitat of the ocean bottom (Snelgrove et al. 1997, Snelgrove 1998, Ormond et al. 2005, Appeltans et al. 2012a).

Macrobenthos in marine sediments are known to play an important role in biological material cycles, making them an important component in marine food webs and structural diversity, but little is known about their role in shelf ecosystems (Gray 1981, Steimle 1985, Melake 1993, Thrush et al. 2002, Stal et al. 2007, Chandrasekar et al. 2012). Nutrient cycles are influenced as macrobenthic fauna influence microbial activity and survival, which in turn influences the nitrogen, sulphate and carbon cycle and indirectly influences primary production (Snelgrove 1998, Darnis et al. 2012). Macrobenthos play a role in decreasing the

amount of pollutants in the water and sediments, in the distribution and re-suspension or burial of nutrients thus changing geology and nutrient availability through their feeding behaviours (Snelgrove 1998). They serve as prey for other higher trophic levels such as fish and through their activities they provide higher trophic levels with more digestible secondary produced nutrients (Snelgrove 1998). Lastly macrobenthos can influence sediment stability and water flow over sediments, in return influencing oxygen supply and other nutrient reactions (Snelgrove 1998).

1.3 MEASUREMENT OF BIODIVERSITY

Diversity studies have been mostly focused on species counts, but because of the new emphasis on the different definitions and components of diversity, there is no single and easy way of measuring diversity (Williamson 1997, Magurran 2010). The measurements used to determine biodiversity can have great effects on results as each uses certain components that carry different scales of weight (Magurran 2010). It is now realised how important it is to consider diversity patterns in terms of ambient environmental factors (Williamson 1997). Also, biodiversity patterns and bio-geographical patterns stem from complex interactions between regionally unique and interchanging ecological factors that maintain certain origination and extinction rates (Williamson 1997). Thus taxonomic diversity, ecological diversity and morphological diversity may be of higher importance than the species count. General factors influencing diversity are not always globally relevant, as groups of fauna do not all necessarily conform to general patterns in diversity, for example, north to south or east to west patterns in diversity can be different for different groups (Williamson 1997, Magurran 2010)

1.4 AGHULAS CURRENT AND KZN BIGHT MACROBENTHIC DIVERSITY

The Agulhas Current can have considerable influence on the benthic ecology of the shelf (Lutjeharms 2006b). The current transports tropical and subtropical species southwards, being important in the distribution of, and potential settlement and survival of larvae (Kensley 1981, McClurg 1988). Thus the KZN fauna's basic character originates from the tropical Indo-West Pacific (Kensley 1981, McClurg 1988). Some studies indicate that periodic hydrodynamic forces such as the kinetic energy of eddies in basin areas, would be very important ecological indicators for the understanding of macrobenthic community diversity and evenness (Gage 1997). This is because bed flow is important for the transportation of food and larvae and for sediment disturbance (Gage 1997). Even small consistent changes in current energy caused by

something like biogenic activities, can affect macrobenthic communities abundance and composition if persistent (Gage 1997). Still little is known about the life cycles of the animals that live in these circumstances and the effect the Agulhas Current has on the ecology of the KZN Bight (Lutjeharms 2006b). There is a need to fill the knowledge gap of benthic communities over a wide range of habitats and geographic ranges, to recognise possible patterns and gradients related to for example sediment, depth, organic content, temperature, salinity, current speeds, nutrients across the entire Indian Ocean (Mackie et al. 2005),

Along the KZN coast, the distributions of intertidal fauna in relation to physical and hydrographical factors have been well documented over many years (McClurg 1988, Bustamante et al. 1997, Hutchings et al. 2002). In contrast, little has been done on the effects of the Agulhas Current on the coastal and deep water ecology and the distributions of shelf fauna (Lutjeharms 2006b, McClurg 1988). Although Heydorn et al. (1978) highlighted this knowledge gap many years ago little has been done since to address this since then.

An idea of the composition of the marine macrobenthos of the KZN Bight was gained from baseline information from pollution monitoring surveys (McClurg 1988). Here it was noted that the macrofauna was dominated mostly by Annelida (mainly Polychaeta) and Arthropoda (mainly Crustacea), while Echinodermata and Mollusca were among the minority (McClurg 1988). Most of the data collected on macrobenthic groups are limited, and out-dated. Due to this lack of knowledge, few inferences can be made on species zoogeography and macrobenthic ecology (McClurg 1988). Examples of earlier studies done on the taxonomy of some soft sediment benthic groups along the east coast of South Africa include a focus on the Amphipoda (Barnard 1940, Griffiths 1976, 1977), Branchiopoda (Hiller 1986), Brachyura (Barnard 1950, Kensley 1977, 1981), Echiurida (Wesenberg-Lund 1963, Biseswar 1985), Hydroid (Millard 1958, 1977, 1980), Macrura (Barnard 1950), Mollusca (Kilburn and Rippey 1982), nemertean (Wheeler 1940), Polychaeta (Day 1967), Sipuncula (Stephen 1942, Wesenberg-Lund 1963), Tanaidacea (Brown 1956, 1957), Decapoda (Kensley 1977, 1981), Isopoda (Kensley 1978b, 1984), Echinodermata (Clarke 1977), Bryozoa (Hayward and Cook 1979, 1983). More recent examples from the Annals of the Natal Museum include – Pectindae (Bivalvia) (Dijkstra and Kilburn 2001), Limidae (Kilburn 1998), *Burnupena* (Gastropoda) (Dempster and Branch 1999), and South Africa Mollusca (Herbert and Warén 1999).

The information on marine life of especially the deeper waters of the east coast has been scarce, possibly because of the geographic isolation and lack of a large commercial fishery (McClurg 1988, Fennessy and Groeneveld 1997, Olbers and Fennessy 2007). Aside from the

biological surveys of the South African Museum most other shelf work was focussed on physical aspects of KwaZulu-Natal, including physical structure and geology (Martin and Flemming 1988), sediment dynamics (Flemming and Hay 1988), physical oceanography (Shumann 1988), inorganic nutrients (Carter and d'Aubrey 1988) and plankton (Carter and Schleyer 1988) and the Agulhas Current (Lutjeharms 2006a). Until the ACEP Natal Bight study, data on biotic and abiotic components of the KZN Bight have been sparse (Ayers and Scharler 2011), in particular inter- and multidisciplinary studies to better understand ecosystem functioning (Ayers and Scharler 2011).

Most of the macrobenthic collections on the South African marine environment were focused in the Cape region, except for a few collectors like Krauss, Wahlberg, Delegorgue who travelled towards the north-eastern coast (McClurg 1988). From 1980 the KwaZulu-Natal museum has been taking annual cruises collecting biological samples, still with the emphasis on Mollusca (McClurg 1988).

1.5 ENVIRONMENTAL INFLUENCES ON MACROBENTHIC BIODIVERSITY

The biological entities found within an ecosystem cannot be considered separate from the physical environment in which they occur. As diversity is measured on different levels and scales, it does not just consist of the biological aspect, but also diversity of environmental factors. One of the most important factors governing macrobenthos structure, function and diversity is the concentration of nutrients in the surrounding environment. The diversity of nutrients affects the composition of communities over space and changes that may occur over time, as different macrobenthic fauna are adapted for survival in different ways and thus utilise these nutrients (detritus) differently (Chapin and Shaver 1985, Gooday et al. 1990, Chapin et al. 1996, 1997, Smith et al. 1999, Tselepidis et al. 2000, Levin et al. 2001, Mittlebach et al. 2001, Diaz et al. 2003, Worm et al. 2006). Thus nutrient diversity has played its role in the regulation and resulting changes of different aspects of macrobenthic community diversity in marine ecosystems (such as food webs) (Chapin and Shaver 1985, Mittlebach et al. 2001, Worm et al. 2002, 2006, Diaz et al. 2003, Moore et al. 2004, Hooper et al. 2005, De Juan and Cartes 2011).

The east African coastal surface waters are characterised as oligotrophic, making any large amount of nutrient input and circulation a very important driving force behind the structure and function of the biological marine food webs (Fennessy et al. 2007). In oligotrophic environments, although increased phytoplankton production is possible in areas of upwelling

and terrestrial input, and communities there are characterised by organisms that tend to be slow-growing, have low rates of population turnover, have predictable food sources and have specialist diets (Taylor 1997). Taylor (1997) suggested the basis of oligotrophic food webs to be benthic algae and detritus, and food webs of eutrophic environments to be based on phytoplankton.

The waters of upwelling cells are usually characterised by lower temperatures and salinity than the surrounding ocean (Lutjeharms et al. 2000). Nutrient concentrations decrease from the centre to the outer edges of an upwelled cell (Lutjeharms 2006b). For example it has been found that temperature/nutrient (silicate and nitrate) concentrations have highest values close to the far north-eastern Agulhas Bank upwelling cell core, of the Port Alfred region, and are lowest further away from the core (Lutjeharms et al. 2000). Measurements of chlorophyll-*a* content over the KZN Bight upwelling regions show higher values as compared with other areas of the Bight that are not upwelled (Lutjeharms 2006b), supporting the fact that these upwelling's contribute a considerable nutrient load to a large area of the shelf.

The Agulhas Current and the many rivers entering the sea are important factors contributing to the survival and distribution of the benthic organisms across the KZN Bight (McClurg 1988, Carter and Scheyer 1988, Sumida et al. 2005, Dos Reis Melo et al. 2013). Each year there is a nutrient influx and large quantities of sediment discharged into the ocean from the rivers containing mainly silt and clay (Heydorn et al. 1978, McClurg 1988). The seasonal variation of sediment input is derived from natural and agricultural activities, which increases annually due to the fast growth of the human population (McClurg 1988, Lehohla 2011). These large inputs can potentially affect primary productivity and increase the amount of suspended solid particles off the shore of KZN, affecting benthic communities in different ways (Carter and Schleyer 1988, McClurg 1988, Boon et al. 1998, Sumida et al. 2005, Sivadas et al. 2013).

The Thukela River supplies large amounts of nutrient and detritus to the continental shelf (Bosman et al. 2007, Lamberth et al. 2009, Ayers and Scharler 2011, De Lecea et al. 2013). The large amounts of suspended particles and silt may inhibit primary production (Carter and Schleyer 1988), thus making nutrients derived from upwelling relatively more important for local community dynamics especially in certain sections and around certain times on the Bight. For example, the seasonal upwelling on the South Brazilian Bight governs biological productivity, via the sinking of particular organic carbon (Sumida et al. 2005).

It is certain that the mean input of nutrients would not be the only factor that plays a role in the variability experienced by the macrobenthic communities, other factors also need consideration. In this light, it is postulated that the KZN Bight might largely be detritus driven (dissolved and particulate), as the area has a small primary production potential (Carter and Schleyer 1988), and thus the Thukela River could also contribute considerably along with local upwelling in maintaining biodiversity. In turn, the river mediated turbidity could influence (lower) the amount of zooplankton available as food by reducing potential primary production. The detritus and nutrients derived from the Thukela River could play a vital role as a food source for macrobenthic invertebrates such as deposit feeders, suspension feeders, and other trophic groups, each in a different way, as was demonstrated in along the west coast of India by Sivadas et al. (2013).

A study done on the diversity of the marine molluscs and polychaetes of the Seychelles Plateau, where shallow coastal sediments were predominantly calcareous and the waters oligotrophic, still found higher diversity and species richness values for assemblages as compared to mesotrophic waters of the Irish Sea and the eutrophic waters of Hong Kong (Mackie et al. 2005). In fact, the oligotrophic waters of the Seychelles plateau support a benthic fauna as diverse as other nutrient rich tropical areas studied (Mackie et al. 2005). Another example is southern Moreton Bay in east Australia which also has a diverse macrobenthic community adapted to an oligotrophic environment, and influenced by riverine organic inputs (Eyre et al. 2011). Thus terrestrial input can play an important determining role on macrobenthic community diversity and survival; however there may be a limit to the amount of terrestrial influence in promoting diversity.

Sediment characteristics (grain size, level of sorting) and depth are also important in determining the structure and distribution of benthic assemblages found (Melake 1993, McClurg 1988, Teske and Wooldridge 2003, Otani et al. 2008). McClurg (1988) recognised an interesting relationship between the benthos distribution and the three sediment zones described by Flemming and Hay (1988) of the continental shelf of the KZN Bight. There is a question as to how the role of sediment will change with the influx of nutrients by recirculation, upwelling and outwelling over non-uniform substrates across different depths (Pearson and Rosenberg 1978, Fennessy et al. 2007). Benthic communities are ecological units separated by physical and biological interactions (Jones 1950). Small-scale variation of sediment grain sizes, organic matter content, and sorting, are among others important determinants of the non-random distributions of benthic macrofauna (Parsons et al. 1977). Sediment substrates that appear homogeneous may in reality include various microhabitats of varying sizes making it heterogeneous (Parsons et al. 1977). Consequently, environmental

gradients can occur within a few cm, each with different effects on different organisms (Parsons et al. 1977).

1.6 AIMS, OBJECTIVES AND HYPOTHESES OF THE STUDY

The KZN Bight programme, of the African Coelacanth Ecosystem Programme (ACEP) set about to understand the ecological functioning of the KZN Bight through a multidisciplinary project investigating physical oceanographic and geological processes and the relative importance of fluvial versus oceanic inputs on biodiversity patterns and ecosystem functioning. This particular study focussed on the subject of biodiversity patterns and components of macrobenthic community structure relative to the surrounding physical oceanographic processes of the KwaZulu-Natal Bight (KZN Bight) across one depth zone on the midshelf. Nutrients were not directly measured, but were addressed indirectly. However total organic content (TOC) was measured as a particulate form of nutrients. The defined three focus areas of the study (Durban focus area, Thukela focus area and St. Lucia focus area) were used as a proxy for nutrients. The study addressed the following aims:

- 1) To produce baseline data on which future studies can build
- 2) To describe and better understand the nature and biodiversity of the soft-sediment macrobenthic communities along the KZN Bight midshelf depth range
- 3) To investigate how this biodiversity is related to, and driven by, measurable and indirect habitat processes derived from the characteristics of the Agulhas Current

The objective was to enumerate and identify patterns of macrobenthic biodiversity across the KZN Bight within and between focus areas of oceanographic interest, through the use of replicated samples of biotic and abiotic features, laboratory work and statistical analysis.

The overall ACEP Program assumption was that the nutrient influx from the Thukela River, the St. Lucia upwelling and the Durban lee eddy change together with factors such as local circulations patterns and nature of the substrate as determined by the Agulhas Current, and may have driven patterns in macrobenthic fauna communities. In accordance, the following null hypotheses were posed:

H_{01} was: There is no difference in biodiversity of soft sediment macrobenthic communities across the KZN Bight, including between the three study focus areas of Durban eddy, Thukela River and St. Lucia upwelling.

The H_{02} was: There was no difference in macrobenthic community taxonomic diversity across the KZN Bight, including between the three focus areas and stations studied.

H_{03} was: There is no relationship between the biodiversity across the KZN Bight and the local measurable, indirect habitat process drivers in the three study focus areas.

The thesis is laid out in seven chapters commencing with a general introduction (Chapter 1) followed by the general methods and materials followed in this present study (Chapter 2). The third chapter focuses on the diversity measures used to describe the macrobenthos of the Bight along the midshelf. Chapter 4 explores the relationship between these diversity measures and the measured environmental variables as proxies of habitat process drivers. An in depth exploration of some less commonly used diversity measures is presented in Chapter 5 and how these are influenced by environmental drivers. The final chapters (6 and 7) include a general discussion of each of the chapter foci (3-5) and general conclusions of the study and all literature cited.

CHAPTER 2

GENERAL METHODS AND MATERIALS

2.1. THE KWAZULU-NATAL PROVINCE

South Africa's east coast forms the southern part of the South Western Indian Ocean (SWIO). It extends 3650 km (Heydorn et al. 1978, Griffiths et al. 2010). A quarter of the seafloor extends to depths of <1000 m (Griffiths et al. 2010). KwaZulu-Natal province is characterised by its dense sub-tropical vegetation, warm coastal temperatures (due to the influence of the warm Agulhas current) and has the highest mean annual rainfall (\pm 845mm per year) of all of South Africa's provinces (Breedlove and Fraser 2000). The highest rainfall occurs in the summer months of January until March (Heydorn 1976, Bolstad 2013).

The province has a complex topography ranging from the lowland subtropical coast, further inland to the undulating hilly plateau of the Natal Midlands and towards the west lay the basaltic Drakensberg mountains (3000m above sea level) and on the north, the granite Lebombo Mountains (Anon 2006). Due to its topography KwaZulu-Natal experiences large amounts of terrestrial erosion each year, because within this small space (the province being 130-200 km wide) the topography is steeply tilted and terrace-like, to an altitude of up to 3000m above sea level thus providing a large catchment area and contributing to high levels of runoff (Heydorn 1976, Alcock 1999, Anon 1999, Lynchs 2001, Wilson 2001). From the west to the east through KwaZulu-Natal, runs the Thukela River (Anon 2006). The Thukela contributes the largest amount of runoff to the adjacent continental shelf (KZN Bight) each year and thus is an important provider of detritus and nutrients for the marine ecosystem (Forbes and Cyrus 1991, Cooper et al. 1995, Groeneveld and Mellville-Smith 1995, Fennessy and Groeneveld 1997, Alcock 1999, Anon 1999, Meyer et al. 2002, Cawthra et al. 2012, De Lecea et al. 2013).

KwaZulu-Natal's coastline is relatively smooth and straight, stretching 570 km south-southwest (Heydorn et al. 1978, Cooper et al. 1995, Griffiths et al. 2010). Along the KwaZulu-Natal coast there are 75 estuaries (mainly temporarily open/closed) (Heydorn et al. 1978, Cooper et al. 1995, Anon 2013). Most of these estuaries (62) are found south of the Thukela River (representing 1.6% of Natal estuarine surface area), while the rest, including the largest of the estuaries found in KwaZulu-Natal, namely the Greater St. Lucia estuary (largest of the estuaries

in Natal, covering 80% of estuarine surface area) is found north of the Thukela River (Begg 1978, Begg 1984, Cooper et al. 1995). The coastline is characterised as having high wave energy and turbidity (Cooper et al. 1995), with turbidity being further intensified by varying input of silt, mud and agricultural erosion from rivers, especially during the summer months of high rainfall (Heydorn et al. 1978). North of St. Lucia, coastal waters are clear, with fewer rivers along that stretch of coast (Wallace 1975, Cooper et al. 1995).

2.2. KZN BIGHT WATERS AND THE AGULHAS CURRENT

The Agulhas current has a seasonally dependent surface temperature and the KZN Bight water temperature has been known to reach 25°C in February and for the upper layers of the offshore region > 26°C (Schumann 1988). Summer water temperatures tend to be high due to summer insolation, and salinities are lowered by the seasonal inflow of freshwater from rivers (Schumann 1988). According to Pearce (1978), the annual temperature range of the coastal water is 4.8°C, with a mean seasonal variation of 5°C. However variations of up to 8°- 9°C have been found, as short term (day to day) variations in the Bight can be much greater, and sometimes overshadow patterns of seasonal current behavioural variation (Pearce 1977, Schumann 1988).

Water surface temperatures are approximately 1.4 °C cooler and salinity values (ranges of 35.0 – 35.5) lower inshore than offshore (Heydorn 1976, Pearce 1978, Schumann 1988). This is partially the result of a permanent inshore counter-recirculation current moving northeast along the coast (Schumann 1988). However water of a lower salinity may appear in the surface layers offshore during late summer as a far reaching effect of the Thukela River as silt laden flood water penetrates several kilometres into the sea as visible plumes/fans (Schumann 1988). Thus generally in terms of surface temperature and salinity there exists a increasing gradient in temperature and salinity as one move more offshore (Pearce 1978, Schumann 1988). The inshore region (\pm 50 m depth) has a well-mixed vertical system and thus has no defined vertical thermocline, whereas offshore has a more layered structure (Schumann 1988). However the offshore, deeper water layers (> 100 m) seem to show no significant seasonal variation as indicated by the lack of a definite thermocline (Schumann 1988).

The salinity of the Agulhas current surface water ranges from 35.2 to 35.4 ‰ (Heydorn 1976). This is because the surface water is a mixture of Tropical Surface Water (TSW) (salinity = 35.0 ‰) and Subtropical Surface Water (STSW) (salinity = 35.5 ‰) (Heydorn 1976, Schumann

1988). The high salinity can partially be attributed to the intense rate of evaporation (mean annual evaporation range of < 1200 – 1400 mm) in the area (Heydorn 1976, Schumann 1988, DWAF 2013). Subsurface water salinity and temperature gradually decreases with depth (Heydorn 1976).

2.3. SEDIMENT HABITAT OF THE KZN BIGHT

The continental shelf off KwaZulu-Natal, has many complex structural features and displays a unique regional sediment pattern (Flemming 1981). The sediment system is mostly current and wave dominated (Flemming 1981), with the Agulhas Current steering the dynamic sediment distribution and pattern formations of the KZN Bight. In turn the faunal patterns and distribution are influenced (Heydorn 1976, Schumann 1988). Mass sediment transport of the entire Agulhas Current was estimated by Duncan (1970) to be at 80 M tons/s in summer and 100 M tons/s in winter relative to a distance of 2500m in the year 1970 and this amount has most certainly increased since then (Heydorn 1976). These waters have low productivity compared to that of the very high biologically productive waters of South Africa's west coast associated with intense upwelling and the cold Benguela Current (Griffiths et al. 2010).

During heavy rains, silt and mud enter the continental shelf from large rivers (annual sediment yield of the east coast catchment area as calculated by Flemming (1981)), involved the suspended load: $94.850 \times 10^6 \text{ m}^3$ and the bed load: $4.951 \times 10^6 \text{ m}^3$ (see Figure 9 from Flemming 1981). The inshore sediment system is wave dominated and is characterised as having reached a state of balance with the reigning current regime and consists mostly of a fine filament of terrestrial sediment (veins of terrigenous quartz sediments) (Heydorn 1976). According to Heydorn (1976) little shell material is usually found in the inshore section and sediment is thickened in areas in front of river mouths, like the Thukela. The inshore zone is separated from the central shelf current by a seaward sediment-bank boundary (Flemming 1981). An inshore wedge boundary of five km thickness is found off Durban and is one km thick on the Northern Bight narrow shelf region (Flemming 1981).

The central shelf sediment regime is current-dominated and allows for the suspension and transport of modern sediment along the shelf (Flemming 1981). Sediment deposition from the central shelf onto the shelf slope only occurs in a few locations along the shelf break (Flemming 1981). Areas of sediment deposition on the shelf break are associated with bedload partings, indicating the occurrence of a southerly current and the formation of a northerly return-flow

eddy (Gründlingh 1974, Flemming 1981). These bedload partings zones are not stationary and move in accordance to the long term behaviour of the Agulhas Current, as indicated by the occurrence of crest reversals (Flemming 1981). There are only a few other structural offsets like submarine canyons in which sediment can also be deposited (Flemming 1981).

The Thukela River runoff enters the KZN Bight, creating the broad Tugela Delta (Heydorn 1976). This part of the shelf has a generally smooth seabed, poorly defined shelf break, low gradient shelf slope and a rise and fall topography of broad and shallow ridges, oriented in a north-south direction (Heydorn 1976). And it is here, east of Durban, that the sediment differs from the normal trend of inshore terrigenous and outer shelf gravel in that there is a terrigenous streak stretching all across the whole shelf up to the shelf break (Heydorn 1976, Bosman et al. 2007). In the center of this deposit is a meandering section of mud that also stretches across the shelf from the Tugela mouth up to the Tugela canyon (Heydorn 1976). Likewise the sediments found on the continental shelf slope are mostly muddy foraminifera types (Heydorn 1976).

2.4. COLLECTION, PREPERATION AND ENUMERATION

2.4.1. IN THE FIELD

2.4.1.1. General Field Work Layout

Sampling was done during two ACEP cruises on the F.R.S. Algoa (a research vessel owned by DEA). Sampling took place during a “wet” and a “dry” season (wet = 2nd to 21st February 2010, dry = 1st to 27th August 2010), in association with three main focus regions (Durban eddy, Thukela mouth, St. Lucia upwelling) between the area just south of Durban (-29.86998, 31.13833) to south of St. Lucia (-28.67963, 32.32222). The sampling area consisted of a single transect that contained a number of sampling stations (Fig. 2.1). These stations were distributed across the shelf within and between these three focus areas.

Spatial reference (latitude and longitude) data and weather conditions were recorded on site and a Conductivity, Temperature and Depth sensor (CTD) was deployed with the use of a hydrographical winch, at each station, to a depth of five meters from the bottom, to obtain information on depth [m], temperature [°C], salinity [PSU] and dissolved oxygen [ml/L], prior to sediment grab samples being taken. Sediment samples were obtained at every station.

Sample sites represented a subsample of a greater set covering the whole KZN Bight from in- to offshore. In this study, samples and data were collected from nine stations, namely A, B, C, D,

E, F, G, H and I for each of the wet and dry seasons for along shelf biodiversity study. Study scales were defined according to relative distance from three main focus areas (nutrient sources) (Fig. 2.1 and 2.2).

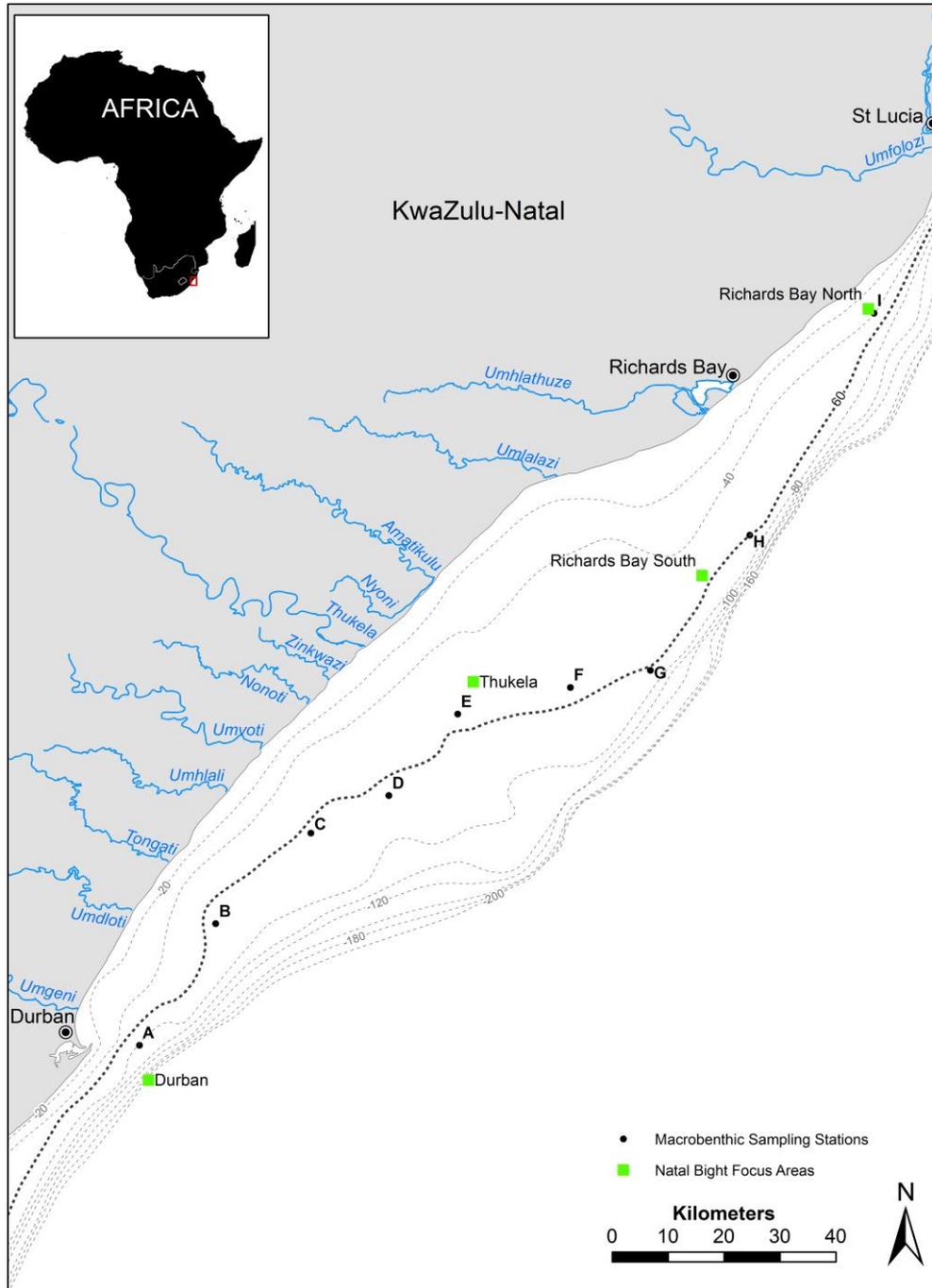


Figure 2.1: KZN Bight macrobenthos biodiversity study area and stations from a single transect along the midshelf. The study area stretched from off Durban in the south up to just south of St. Lucia in the north. Stations were numbered stations A (south) to I (north). (Map by Denis Rouillard, Oceanographic Research Institute (ORI), Durban, South Africa)

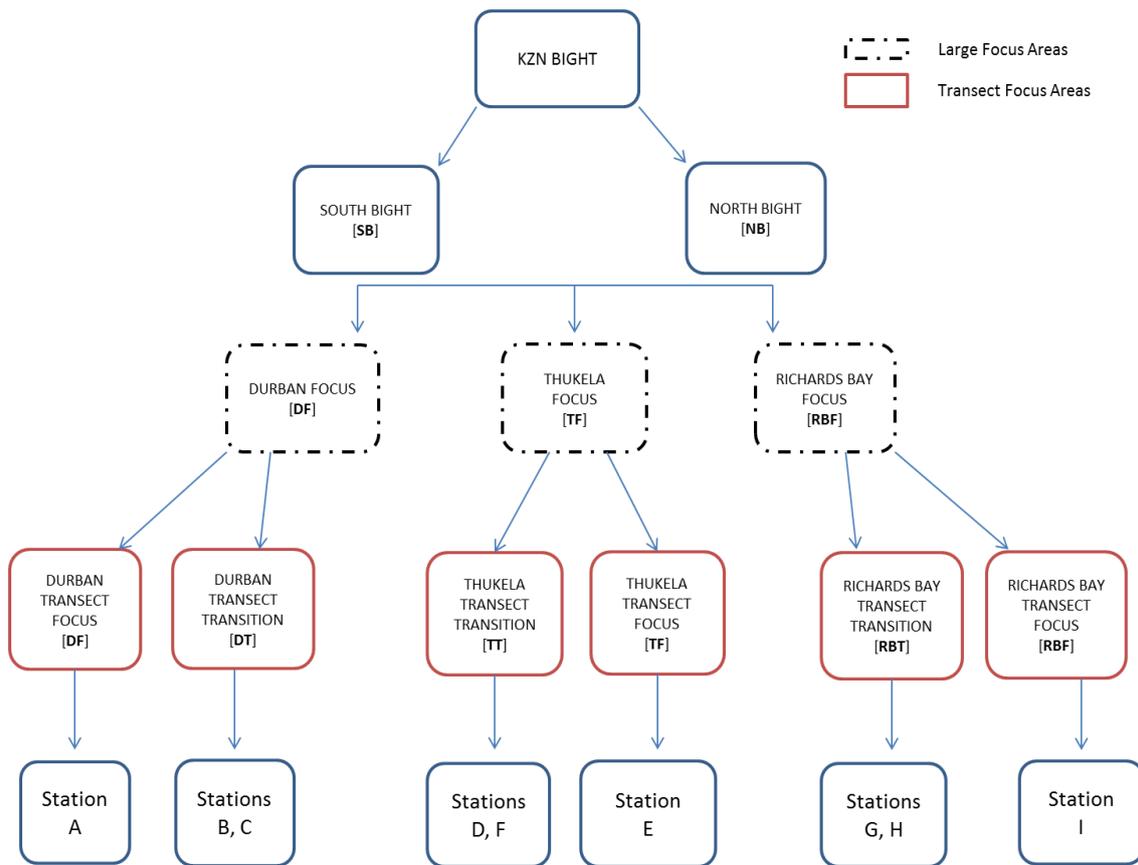


Figure 2.2: Diagram illustrating acronyms and the method in which stations were categorised and factorised for further analysis.

2.4.1.2. Sediment Sampling Methods

Three replicate samples were taken at each station at a minimum depth of 41 m, a maximum depth of 81 m, by using a 2000 cm³ Van Veen grab. These kinds of sample sizes are considered adequate for the quantification of more common species, abundance and biomass (Eleftheriou and Moore 2005).

Each grab sample was taken as close as possible to the pre-determined spatial location (GPS location) of each station. If the ship drifted > 10 m from this location between grabs, the ship was returned to its original location before another grab sample was attempted. The sediment depth of each successful sample in the grab was measured to the nearest mm before proceeding with sieving, for volume calculation purposes. Each grab sample was required to have a minimum sediment depth of 5 cm to be an adequate representation of the station.

From each successful replicate grab sample an additional two sub-samples (75g each) were collected before release into washing sieves. These sediment samples were obtained at every station for each of three replicates per station. One sediment sub-sample was fixed in a 4% formaldehyde saline solution (5ml per 175g sample jar) for later analysis of total combustible organic content (TOC) and the other subsample was kept to determine sediment distribution characteristics.

Sediment particles are generally classified according to size as: gravel (> 2 mm), sand (0.063 - 2.0 mm), mud/silts (< 0.063 mm). Sands can be further categorised as coarse to very coarse (0.5 - 2.0 mm), medium sand (0.25 - 0.5 mm), fine sand (0.125 - 0.25 mm) and very fine sand (0.063 - 0.125 mm) (Buchanan 1971, Flemming and Hay 1988).

The remainder of the samples sediments were released into a 1000 µm mesh sieve for washing and separation of fauna from sediment using deck hoses.

2.4.1.3. Fauna Preparation

From successful grab samples, any visible fauna were handpicked from the sieves and placed in appropriately labelled jars containing 4% formaldehyde saline solution. The rest of the sample remaining on the sieve was carefully washed until all fine sediments were rinsed through the 1000 µm. Retained fauna were carefully transferred into the jars for sorting in the laboratory.

Sediment samples > 50L and thus too large to be processed adequately in the field, were elutriated on deck (Aasen 2008). This was done using the whole grab sample and dividing it into portions no greater than 1/10th of a 20L bucket. The rest of the bucket volume was filled, with sea water, agitated for a minute and the suspended fauna decanted into a 1000µm sieve. The coarse material was sorted by hand to remove any larger fauna (such as Mollusca) that would not have been in the elutriate. This process was repeated seven times per portion. After an audit check the remaining sediment was discarded (Aasen 2008).

Thus each station comprised the following samples: 3x sediment samples, 3x TOC samples and 3x macrobenthic faunal samples.

2.4.2. LABORATORY

2.4.2.1 Sediment Grain and Organic Matter Analysis

Sediment and organic content samples were analysed by Environmental Mapping and Surveying (EMS) located in Durban. The methods employed are those of Gray (1981):

In determining grain size and sorting of sediment, usually the silt and clay are firstly separated from the rest of the sediment using a 0.062 mm screen. Different methods are applied to the measurement of silt and clay (< 0.062 mm sieve) and coarse sediment (> 0.062 mm). After this, sediments are dried through a range of screens, according to the Wentworth Scale, arranged in decreasing geometric scale. Particle size determined by each screen size is expressed on a phi (ϕ) scale. Phi is equal to $-\log^2$ of the particle size in mm and can range from phi = -8 (cobble size) to phi = 14 (clay size). Percentage dry weight of each screen is determined and expressed as cumulative percentage opposite the phi scale on plots. From the S-shaped plot (if the data follows a normal distribution) median particle size was determined from the 50% point.

To determine sorting coefficients, the curve was transformed to a straight line by plotting on a probability scale. After which the phi values for the 84% and 16% points were determined. After this either the Graphic Standard Deviation (σ_g) expressed as $\phi_{84} - \phi_{16}/2$; or the Inclusive Graphic Standard Deviation (σ_I) expressed as $\{((\phi_{84} - \phi_{16})/4) + ((\phi_{95} - \phi_5)/6.6)\}$ was used to determine the sorting coefficient. Sorting coefficients classes range from < 0.35 (very well sorted) up to > 4.00 (extremely poorly sorted).

Organic content was determined using the Hydrogen Peroxide digestion method (Schumacher 2002). This method uses a known weight of sediment, to which hydrogen peroxide (HO) was added and heated, as to increase the digestion of the organic matter by the peroxide. After digestion was complete, the sample was dried and weighed and the amount of organic matter removed calculated from the difference between the initial and the final sediment weight. Expressed as the percentage of the entire sample weight, the samples were then also classified according to ranges suggested by DWA (2010). These ranges were as follow: <0.5% as very low; 0.5-2% as low; 1-2% as moderately low; 2-4% as medium and >4% as high (DWA 2010).

2.4.2.2 Macrobenthic Fauna Preparation

Samples were rinsed to remove any excess sediment using a stainless steel soil analysis 1000 μ m sieve and the remaining fauna washed into large dishes filled with tap water. Separation of

fauna from sediment was done manually by picking out individuals and parts thereof. All whole and parts of fauna were sorted into groups, namely: Annelida, Crustacea, Mollusca, Echinodermata, Cnidaria and miscellaneous phyla in urine jars and polytops, then labelled and fixed in a 4% formaldehyde/seawater solution until further processing. Any interesting articles of observations were noted to support later analysis. After samples sorting, a Zeiss Stemi DV4 Stereo microscope was used for identification of only the individuals (unstained) that were judged to have been alive. Identification was done to the lowest possible taxonomic level and species enumerations as well as allocated names were recorded in a working log sheet along with descriptive notes of each specimen identified.

2.4.2.3 Macrobenthic Fauna Identification and Enumeration

During identification, an extensive reference material collection was made of the species found in each sample and a separate log sheet used for noting names and enumeration (counts as number of individuals per species per sample) of species in the reference collection. Various identification keys were used and photos taken of specimens for later reference (Barnard 1950, Barnard 1961, 1970, 1971, Day 1967, 1974, Imbach 1967, Kensley 1972, 1978a, Griffiths 1976, Day 1978, 1980, Barnard and Drummond 1979, Lincoln 1979, Mauchline 1980, Kilbum and Rippey 1982, Richards 1984, Uebelacker and Johnson 1984, Barnard and Karaman 1991a, 1991b, Branch 1994, Branch et al. 1994, Warren et al. 1994, Steyn and Lussi 1998, 2005, Gibbons 1999, Lowry 1999, Beesley et al. 2000, Dean 2001, LeCroy 2002, Heard et al. 2003, Beadman et al. 2004, Poore 2004, Petrescu 2006, Chapman 2007, Galil 2009, Lowry and Myers 2009, Ng et al. 2009, Aiken et al. 2010, Shalla 2011, Appeltans et al. 2012b, Cohen 2012, Markhaseva et al. 2012, Poppe and Poppe 2012). All names were verified afterwards using the World Register of Marine Species as up to date reference. For analysis purposes all Bryozoa and Foraminifera were not included as it was unsure if individuals were alive or dead. Also because of a lack of expertise and resources, all Sipunculids were aggregated to Family and most Asterozoa could only be identified to Order level.

2.5. STATISTICAL ANALYSIS

Combinations of parametric, non-parametric, univariate and multivariate statistical analysis were used. Abundance data per sample (station) were expressed as number of individuals per taxon per m⁻² by multiplying observed abundances by a factor of five. All non-parametric multivariate techniques used in the statistical analysis of this present study have been shown to

be effective in outlining and recognising central tendencies within fine scale community differences (McRae et al. 1998). More detailed accounts of specific statistical analysis which elucidated macrobenthic diversity and which explored relationships with the ambient environmental parameters have been included in the chapters to follow.

CHAPTER 3

BIODIVERSITY OF SOFT SEDIMENT MACROBENTHIC COMMUNITIES ALONG THE KZN BIGHT MIDSHELF

3.1. INTRODUCTION

3.1.1. Biodiversity of continental shelf substrates

Continental shelves only cover a small area of the world's surface, yet they play a large role in carbon fixation for their relative size (Karakassis and Eleftheriou 1997) and can be up to five times more productive than the open ocean (Walsh and Dieterle 1988, Bauer and Druffel 1998). The continental shelf, being regulated by benthic and pelagic components, creates a productive transition for essential ecological services, from the benthic-dominated coast to the predominantly pelagic-regulated deep sea off the shelf (Steimle 1985, Ott 1992, Levin and Dayton 2009). Spatial and temporal variability in the marine environment mean that patterns of diversity are considered to be different; in terms of community dynamics adapted to varying and continually changing environmental situations; on continental shelves compared to those of the deep sea benthos (Clarke and Crame 1997). Differences have been found to exist across continental shelves (Flach and De Bruin 1999), with highest diversities generally being found midshelf (Gray 2001, Ellingsen et al. 2005) and lowest diversity values occurring closest to the coast and shelf edge (Gray 2001, Ellingsen et al. 2005, Cusson et al. 2007, Levin and Dayton 2009).

Diversity and functional diversity are important focus points for ecosystem studies (Covich et al. 2004, Stachowicz et al. 2007). Each species plays a role, big or small, in maintaining ecosystem functioning, with different species being affected by different processes and indeed functional groups may too fit a different pattern, with the ecology affecting processes (Tilman et al. 1997). Any factor causing a change in the composition of a community would have a dramatic effect on ecosystem functioning and those indirectly affected (Elmgren and Hill 1997, Tilman et al. 1997). Not many studies have tested the relationship between ecosystem functioning and biodiversity, but marine benthic biodiversity is known to play a significant role in maintaining soft sediment ecosystem functioning. For example, in a replacement series experiment assessing the effects of benthic invertebrates on the flux of nutrients between the

sediment and the water column it was found that declining functional diversity results in a net loss of ecosystem function (Emmerson and Raffaelli 2000).

Macrozoobenthos play direct and indirect roles (Emmerson and Raffaelli 2000) in ecosystem functioning, thus making the description of benthic habitat and the species that occupy these habitats very important (Karakassis and Eleftheriou 1997). Unfortunately many macrobenthic species are yet to be described or discovered making our current knowledge of marine benthic diversity somewhat deficient (Snelgrove 1999, Terlizzi et al. 2003, Guzmán-Alvis and Carrasco 2005, Azrina et al. 2006, Butler et al. 2010, Kelly et al. 2010, Radziejewska et al. 2010, Griffiths et al. 2011, Koperski 2011, Nanajkar et al. 2011, Riehl and Kaiser 2012, Arman et al. 2013, Boets et al. 2013). Although more than a million species have been described, this is thought to only represent approximately a tenth of what is still to be discovered (Clarke and Crame 1997, Williamson 1997, Snelgrove 1999, Butler et al. 2010).

Although the role of diversity in ecology is understood, there is still some discussion as how exactly to estimate the true biodiversity of an area (Ellingsen 2001). Until now, the study of biodiversity was focused more on terrestrial habitats (Ellingsen 2001), and when in marine/coastal ecosystems, mostly on rocky shores and coral reefs of temperate, nutrient-rich areas (Melake 1993, Arango and Solano 1999, Flach and De Bruin 1999). The studies of Mackie et al. (2005) and Shin and Ellingsen (2004) are examples of some of the more comprehensive studies done on subtropical/tropical soft sediment macrobenthic ecology. Even basic studies of diversity still need a satisfactory methodology to be developed (Williamson 1997, Ellingsen 2001). Studies use different sampling methods, measures of diversity and different taxonomic resolutions, making it hard to draw comparisons (Clarke 1992, Gee and Warwick 1996, Clarke and Crame 1997, Shin and Ellingsen 2004).

Diversity studies results also vary tremendously for example depth gradients. Results vary according to taxa studied and the area of study (Clarke 1992, Kendall and Aschan 1993, Roy et al. 1994, Flach and De Bruin 1999, Gaston 2000, Shin and Ellingsen 2004, Munari and Mistri 2008). Due to the lack of biodiversity and distribution studies on especially soft sediment infauna (Gray 1997b), the need for biodiversity studies of macrobenthos in shelf habitats is great.

3.1.2. Measuring biodiversity

It is suggested that there is no single definition of biodiversity (Norse 1993, Maclaurin and Sterelny 2008) as the definition depends entirely on the purpose of study. Loreau (2000) proposes further that each differing level of biodiversity is its own entity with its own complexities and variables to consider. At present hierarchical levels of defining biodiversity are adopted globally (Norse 1993, Magurran 2009) and include, species diversity, genetic diversity, ecosystem diversity, phenotype diversity, phylogenetic diversity, developmental and life history diversity, functional diversity and diversity at different taxonomic levels, depending on resolution of the study and the question asked (Norse 1993, Shin and Ellingsen 2004, Reiss and Kröncke 2005, Maclaurin and Sterelny 2008).

Measures used for species diversity should ideally be non-parametric and statistically accurate, with small bias towards sampling variance and must be relevant for any community (Lande 1996). Also, a good diversity measure has the property that the total diversity in a combined set of communities, must either equal or exceed the mean diversity of the pooled communities diversity value (Lewontin 1972). Different diversity measures, put different emphasis on certain components of a community, and measurements that are applicable to one ecosystem may not be as effective or relevant for another (Loreau 2000, Magurran 2009). Thus a combination of different measurements and indices are needed to make up as much as possible for what is lacking in the other to get a more comprehensive view of true diversity values (Gray et al. 1990, Downes 2002, Cusson et al. 2007, Magurran 2009). Many diversity indices combine the properties of species richness and evenness to varying degrees (Clarke and Warwick 1994, Magurran 2004).

3.1.2.1. Measures of Species Richness

Species richness (the total number of species present) is the simplest way of measuring diversity (Lande 1996). As it makes no distinction between species that are very abundant or very rare (Magurran 2009), and a disproportionate contribution to community abundance is not considered (Maclaurin and Sterelny 2008). Generally, Margalef's Species Richness (Clifford and Stephenson 1975) (D), which is the distribution of individuals among species, is used together with a measure of evenness of distribution such as Pielou's index (Pielou 1969, 1975) (J) (Clarke and Warwick 1994, Warwick and Clarke 1995, Maclaurin and Sterelny 2008). Both indices are highly dependent on sample size and again, should not be the only measures

considered (Warwick and Clarke 1995). The Shannon-Wiener (Peet 1974, Magurran 2009) measure (H') of diversity, considered a Type I heterogeneity index, which is most sensitive to changes in the importance of rare species, also affected by sample size (Lande 1996). Sample size influences biodiversity since dominance values are affected (Gage and May 1993, Magurran 2009). The Simpson Diversity (Simpson 1949, Peet 1974) ($1-\lambda$) measure, is defined as: the probability that two randomly chosen individuals within a community are different species (Lande 1996). It is considered a Type II heterogeneity index, which is the most sensitive to changes that occur for the most common species (Peet 1974). The Shannon-Wiener index determines the mean degree of uncertainty as to which species a randomly chosen individual, from a group, belong to (Ludwig and Reynolds 1988). Simpsons index determines the probability that two individuals drawn from a population, are from the same species (Ludwig and Reynolds 1988). The heterogeneity indices like Shannon-Weiner and Simpsons are not diversities themselves and transformation of these values to effective number of species greatly increases unity, assessment and interpretation between diversity measures of different communities (Jost 2006). Such diversity indices result in what is termed by Hill (1973) as the “effective number of species” measured in units of number of species (Ludwig and Reynolds 1988, Jost 2006).

Many ecologists prefer the use of Hill's diversity numbers, because they are easily interpretable and comparable (Peet 1974, Ludwig and Reynolds 1988). Hills diversity numbers series have the same units (species) allowing results to be compared in the form of ratios, the ratios are independent of samples and varying ratio values carry the contributions made by rare and common species to the heterogeneity (Peet 1974). Thus it is a measure of the number of species in a sample and the degree of spread of the proportional abundances among species, as each species is weighed by its abundance (Ludwig and Reynolds 1988).

In this present study only $N1$ and $N2$ of Hill's diversity numbers were considered. $N1$ is related to the Shannon diversity index and $N2$ equals the reciprocal of the Simpsons index (Ludwig and Reynolds 1988). The latter is preferred above the usual form by many ecologists as it is a more unbiased measure for sampling from countless populations (Ludwig and Reynolds 1988). If abundance was equally distributed among species, $N1$ expresses Shannon diversity in units of the number of species present that would produce a given H' value (Ludwig and Reynolds 1988). It is also low in bias when estimating diversity in samples whose species accumulation curve has reached a asymptote or not (Beck and Schwanghart 2010). Thus, Hill's ratios indicate the shape of the underlying diversity-dominance relationship and the relative contribution of

richness and equitability to the community heterogeneity that can easily be compared (Peet 1974). By also including Hill's diversity numbers, it is possible to understand the index-independent macrobenthic community diversity, that has mathematical properties that more accurately capture the diversity concept (Jost 2006). By only measuring species richness, even for large sample sizes, the estimation of expected similarity of random samples from the same community will be low, because the different samples will represent parts of a community and not ever fully represent the entire community (Lande 1996).

3.1.2.2. Spatial Scales of Diversity Measures

Spatial scale is critical to consider when making comparisons and drawing conclusions around the relationships between diversity and the biotic and abiotic influencing factors (Loreau 2000, Ellingsen and Gray 2002). Many marine macrobenthic diversity studies have been done on small spatial scale and a few have focused on large community spatial scales in the marine environment (Shin and Ellingsen 2004). Faunal patterns and variability can change with scale in marine ecosystems despite uniform habitats (Gaston 2000, Loreau 2000, Ellingsen 2001). Traditional comparison of a few sites between areas is generally insufficient for diversity studies (Ellingsen 2001, Shin and Ellingsen 2004).

Measuring biodiversity at different scales can deliver very different results (Levin 1992, Ward et al. 1998). For example, it may be better to determine the community diversity and variability within a single habitat before comparisons can be made between habitats (Ellingsen 2001). The choice of the smallest and largest scale in the diversity measurement is important for the interpretation of results and making comparisons (Loreau 2000, Shine and Ellingsen 2004). Correlations of local and regional diversity and the insufficient merging of communities from similar habitats in many studies up to now have indicated that community patterns cannot only be explained by local processes and local scale alone (Crame and Clarke 1997, Gaston 2000). Community patterns, even within the same habitat and site can never really be explained by a single mechanism (Gaston 2000). Within different spatial scales, regional processes influence local patterns, however various possible relative combinations of processes and mechanisms at all scales will always be responsible for some kind of variation in patterns observed (Gaston 2000). In the long term there is a need for interpretation combined with a historical, regional, geological, and ecological point of views, and what their relationships are with local processes (Crame and Clarke 1997).

3.1.2.2.1 Alpha (α), Beta (β) and Gamma (γ) diversity

When measuring biodiversity of macrobenthic animals occurring within the same habitat (sample) and location, where they are presumably competing for all the same limiting resources, diversity is called within-habitat or Alpha Diversity (α) (Fisher et al. 1943, Whittaker 1960). A larger scale that measures diversity among different habitats and different communities is Beta Diversity (β) also known as turnover diversity or between-habitat diversity (Whittaker 1960) and the largest scale of measuring biodiversity within a whole region is called Gamma Diversity (γ). It is at the latter scale that evolutionary processes may carry more weight than ecological processes per se (Whittaker 1960).

Alpha Diversity (α) is maintained by an influence of a combination of complex local and regional factors (Munari and Mistri 2008, Magurran 2009). There is a dependence/relationship between local and regional diversity. According to Loreau (2000) the diversity at any scale is dependent on the diversity of the lower scale, like for Gamma diversity that would include the alpha and the beta (inter-scale) diversity, which is maintained by the heterogeneity and niche differences within the habitat at that specific scale (Flach and De Bruin 1999, Loreau 2000, Munari and Mistri 2008, Levin and Dayton 2009). Cornell and Lawton (1992) assert that there are two relationships between local and regional diversity. The first is a linear increase of local species' richness with the increase of the regional species' pool. The second is that local species richness reaches a limit in the number of species the environment can maintain, while the regional species' diversity species pool continues to increase (Cornell and Lawton 1992, Loreau 2000).

It is important look at the same study site on different scales, to understand the correlation and relationship between the alpha, beta and gamma diversity values of that area, which can give further information of types of processes that play a role in maintaining these diversity values (Shin and Ellingsen 2004, Munari and Mistri 2008). The proportion and distribution of rare species, and also conclusions drawn concerning influential processes, are influenced by different sampling intensities and the scales of the study area and the geographic location of the study area (Shin and Ellingsen 2004). In nine transitional waters sites of the Italian temperate coast studied, even those communities that were closely located to each other and has similar environmental unpredictability, had few species in common and many sites were characterised by having rare species only associated with that particular site (Munari and Mistri 2008). These sites were so different that classification to only Family or Order level was needed to detect rare

taxa in their analysis (Munari and Mistri 2008). This could be because of sampling intensity and scale of the study (Shin and Ellingsen 2004). Species that appear to have a restricted distribution, might in fact be more widely distributed if the scale of the study is increased (Shin and Ellingsen 2004). Thus this study of Shin and Ellingsen (2004) could have been further interpreted and insight gained through the study of the relationships that existed between the alpha, beta and gamma diversity of the region.

Many diversity studies have been based on alpha diversity (point diversity or sample species richness) and less have been based on the distribution of species and communities composition on other spatial scales (Ellingsen and Gray 2002, Shin and Ellingsen 2004). Few studies have looked at the relationships between alpha, beta and gamma diversity at both small and very large spatial scales (Shin and Ellingsen 2004). The relationships between alpha, beta and gamma diversity are not always set and constant (Loreau 2000, Ellingsen and Gray 2002, Munari and Mistri 2008), which encourages the use of a combination of measurements to come to comprehensive conclusions (Gaston 2000). Previous studies have concluded that local diversity is generally dependent on regional diversity (alpha diversity being correlated with gamma diversity) (Cornell and Lawton 1992, Griffiths 1997, Loreau 2000). Gamma and beta diversity seem often to be correlated, and an increase in beta diversity would lead to an increase in gamma diversity regardless of whether alpha diversity increases or not (Ellingsen and Gray 2002).

Munari and Mistri (2008) highlighted in their study that there exists a latitudinal variation in the extent to which regional factors play a role in local species diversity. And by considering alpha, beta and gamma diversity together, the proportionate role of each of local and regional factor may be determined. In their study, local species composition depended on the regional supply (Munari and Mistri 2008). Beta diversity, which is a component of the mutual dependence between local and regional diversity, and its position in this relationship within a study area as a whole, gives important insight into the internal structure and processes maintaining the study areas diversity (Cornell and Lawton 1992, Munari and Mistri 2008).

The relationship between alpha and beta diversity is scale dependent (Loreau 2000, Magurran 2009). The expected similarity of samples from the same community will tend to decrease as the number of samples increases, because more distinct communities are being included, increasing resemblance to the actual larger community (Lande 1996).

The study of beta diversity has been lacking compared to alpha diversity studies (Gray 2000). While alpha diversity is measured by species richness in a sample, beta diversity can be measured using combinations of univariate and multivariate statistics and the most frequently used statistic is Whittaker's (1960, 1972) β_w (Wilson and Shmida 1984). However the use of multivariate statistics, for example, Bray-Curtis similarity between sites, has shown to be much more sensitive to small changes in the faunal composition of communities and robust for the detection of transformations in species dynamics (Gray et al. 1990, Warwick and Clarke 1991, Ellingsen and Gray 2002, Shin and Ellingsen 2004, Cusson et al. 2007). Beta diversity has been found to be highest in taxonomic groups that have species with a restricted range (Ellingsen 2001, Shin and Ellingsen 2004).

Even within the same study area, diversity measures like alpha diversity (α) or beta diversity (β), and their relationship to various environmental variables can differ significantly among taxonomic groups (Harrison et al. 1992, Flach and De Bruin 1999, Bianchi and Morri 2000, Ellingsen 2001, Munari and Mistri 2008). Little success has been achieved in trying to use one taxon as a surrogate for another for extrapolation of diversity in different areas (Ricketts et al. 2002). Thus it is very important to study more than one taxonomic group per area (Ellingsen 2001, Ellingsen et al. 2005).

Even though there are generally acknowledged important factors to consider when measuring biodiversity, other unknown/hidden factors may play a relatively stronger role in maintaining diversity (Shin and Ellingsen 2004). The combination of diversity indices at different spatial scales helps in identifying underlying hidden processes that are important. With the range of biodiversity measures now available a combination of techniques were employed in this study to describe the macrobenthic infaunal diversity of the KwaZulu-Natal Bight midshelf. The principal aims were to use a combination of univariate statistics, diversity indices and multivariate statistics to calculate diversity values, similarities/dissimilarities and other community variables of the macrobenthic communities. Thus describing current macrobenthic communities through alpha and beta diversity measures such as species richness, heterogeneity indices, Whittaker's beta diversity and similarity indices and matrixes, along the midshelf of the KZN Bight, at different scales, namely within stations (alpha), and between stations and focus areas (beta). The main hypothesis tested was that soft sediment macrobenthic biodiversity changed along the KZN Bight midshelf and also with different measurements of different scales.

3.2. METHODS AND MATERIALS

3.2.1. DATA ANALYSIS

Macrobenthic community data were abundance (number of individuals per m^{-2}) per species per replicate at each site. Original factors of analysis ranged from smallest, station (nine in total), to transect focus area (FA – six in total) and large focus area (LFA – three in total) (Refer to Chapter 2, Figure 2.2, for acronyms). Factors for analysis as mentioned in the general methods and materials section, was further extended from just stations and focus areas to include pairs of adjacent stations as (AB,BC,CD,DE,EF,GH,HI), paired transect focus areas as (DF/DT, DT/TT, TT/TF, TF/RT, RT/RBF) and paired large focus areas as (DF/TF,TF/RBF) for use in Whittaker's (β_w) beta diversity analysis.

3.2.1.1. General Community Analysis

The distribution of abundance data and number of species sampled were tested for normality using the Anderson-Darling test and were visually evaluated by normal probability plots with 95% confidence intervals (Beadman et al. 2004). The Anderson-Darling test is deemed more sensitive than the Kolmogorov-Smirnov test, as it's critical values are based on the specific distribution in question and it is seen as one of the more powerful empirical distribution tests (NIST/SEMATECH 2012).

No overall significant difference in abundance and number of species per sample was found between data collected in the two different periods (February 2010 and August 2010) (p values > 0.05). Consequently data were pooled from both periods and each sampling station (A-I) presented as six replicates (3x2) (Refer to Chapter 2, Figure 2.1). Abundance data (indiv.m^{-2}) did not meet the assumptions required for further parametric testing and were accordingly transformed using an overall $\log(x+1)$ transformation to reduce the influence of very dominant taxonomic groups. Data on the counts of different individual species per station were normally distributed and therefore no transformation of the data was required.

To test for differences among the total number of species per station, transect focus area and large focus area, a ANOSIM with pairwise comparisons based on Bray-Curtis similarity in PRIMER v.6 (Clarke 1993, Clarke and Gorley 2006) was used, as well as a one-way ANOVA test, with *post hoc* Tukey pairwise comparison. Tukey was chosen for pairwise comparisons, because it has an intermediate power as it is not as conservative as Scheffé test but more

conservative than Fisher's LSD test (Anon 2012). When abundance data were transformed, and a Kruskal-Wallis test and a General Linear Model ANOVA test used (95% confidence interval).

Non-parametric multivariate community analysis was performed using the PRIMER v.6 software package (Clarke 1993). All $\log(x+1)$ transformed abundance (m^{-2}) data were used to produce a Bray-Curtis similarity matrix for replicates, stations, transect focus areas and large focus areas, on which a hierarchical group mean cluster analysis and non-metric multidimensional scaling ordination (MDS) with a minimal stress of 0.01, was performed. A species accumulation curve with 10 000 random sampling was produced using Chao 1 (abundance based and sensitive to the frequencies of rare species), Chao 2 (presence-absence based) and second order Jackknife non-parametric estimates of asymptotic true species richness, along with the observed number of species, to determine the adequacy of the study sampling effort to measure all occurring species in the area, (Witman et al. 2004, Chao et al. 2009). The second order Jackknife estimator is considered a good estimator for sparse collections and is less affected by sample bias (Chazdon et al. 1998, Hortal et al. 2006, Vavrek 2011).

The Chao 1 estimate is most dependent upon the distribution of individuals among species and Chao 2 is most dependent upon the distribution of species among samples (Colwell and Coddington 1994) as it is based on presence-absence data. As the species accumulation curve is strongly negatively bias and underestimates species richness, these estimators aim to reduce such bias, in different degrees, to give a more accurate estimate of true species richness of a study area (Colwell and Coddington 1994). According to Colwell and Coddington (1994) Chao 2 and second order Jackknife estimates are good estimators that provided the least biased estimate of true species richness in small samples, and have been found to be very accurate. The Chao 1 is a good estimator to consider as it does very well in databases that consist of many rare species and species with a small frequency range (Chao 1984, Colwell and Coddington 1994). The use of a combination of estimators is deemed useful for comparison (Vavrek 2011).

3.2.1.2. Alpha Diversity

Analysis of alpha diversity used untransformed abundance data (per m^{-2}) of all replicates to calculate the following diversity indices: Margalef species richness (d); Pielou evenness (J'); Shannon-Wiener diversity index (H'_{log_e}); Simpson diversity index ($1-\lambda'$) and Hill's diversity indices ($N_1 = \text{Exp}(H')$ and $N_2 = 1/SI$). The indices do not require conditions of

normality therefore untransformed data could be used, thus all comparisons of variance could be made using parametric techniques. Where results of indices met normality assumptions, a one-way ANOVA followed by a *post hoc* Tukey pairwise comparison test (95% confidence interval) was conducted.

3.2.1.3. Beta Diversity

Abundances (per m⁻²) were pooled to factors of individual stations; transect focus areas and large focus area scales respectively, for beta diversity analysis of paired adjacent stations arranged in a south to north direction. Beta diversity is the extent of species compositional change from one sample to the next or along a gradient and is not based on a spatial scale of measurement of diversity like that of alpha diversity (Whittaker 1975, Ellingsen 2001, Ellingsen and Gray 2002). According to Whittaker (1960, 1972) and Legendre et al. (2005) beta diversity (turnover) can be measured with the use of either presence-absence data or quantitative species abundance data. Wilson and Shmida (1984), Ellingsen (2001), Vellend (2001), Ellingsen and Gray (2002), Legendre et al. (2005) argued that variation in community composition among sites or turnover can be calculated using raw quantitative abundance data and expressed through Whittaker's beta diversity (β_w), a single number such as total sum of squares, percentage complementarity and also by the pairwise permutations from a similarity matrix among sites. The Bray-Curtis coefficient of similarity, used for this purpose, was deemed adequate for the description of community composition relationships between studied sites (Legendre et al. 2005). In contrast to β_w , this similarity measure takes the identities of the species into account as well (Shin and Ellingsen 2004).

Pairwise Whittaker's beta diversity of adjacent sites arranged in a south to north KZN Bight direction was measured using the equation $\beta_w = (\gamma/\bar{a}) - 1$, where γ is the total number of species in the two combined sites and \bar{a} is the mean number of species per site (Whittaker 1972, Ellingsen 2001, Vellend 2001). For this purpose pooled replicate presence-absence data from each station was used.

Complementarity, also known as biotic distinctness, varies from zero (identical) to a 100 per cent (completely dissimilar) (Colwell and Coddington 1994, Ellingsen 2001). EstimateS software assisted in the calculation of percentage complementarity. Log ($x+1$) transformed abundance (m⁻²) data was used for the calculation of Bray-Curtis pairwise similarity comparisons between adjacent sites as an additional estimate of Beta Diversity as it has been

found that multivariate analysis are much more sensitive than univariate analysis in detecting small changes in macrobenthic communities (Warwick and Clarke 1991, Vellend 2001, Ellingsen and Gray 2002).

3.2.1.4. Taxonomic Composition

Untransformed abundance (m^{-2}) data were used to investigate taxonomic composition except in SIMPER analysis where $\log(x+1)$ transformed abundance (m^{-2}) data was used. Replicates were pooled to taxonomic levels for the three large focus areas studied and the number of groups representing each taxonomic level per replicate within each large focus area was determined. Pooled replicate abundance (m^{-2}) data were also used to determine the dominant phyla, Classes and Orders present in the entire study area, using pooled replicates to phylum level and then averaged over the entire study area. Pie charts were used as a visual aid indicating the proportional abundance (m^{-2}) of the four most abundant phyla present in the entire study area, using pooled replicates and averaged over stations; the six defined transect focus areas; and focus areas. The distribution of the identified phyla along the KZN Bight midshelf was represented as the number of replicates occupied by each phylum using bar charts.

To evaluate which species most consistently contributed to and were possibly responsible for resulting significant differences between studied sites tested, a similarity percentage analysis (SIMPER) on transformed ($\log(x+1)$) abundance (m^{-2}) data was conducted. Only species contributing up to sixty per cent to differences were considered in the analysis.

Beta diversity of each of the four dominant phyla was calculated and compared between the six defined transect focus areas along the KZN Bight midshelf. Mean beta diversity between the four dominant taxonomic groups was compared to determine which was the most diverse in terms of turnover.

All analysis was done using a combination of the following statistical software: EstimateSWin752 (Cowell 2006), Microsoft Excel 2010, Minitab 16, PRIMER v6 (Clarke 1993, Clarke and Gorley 2006) and Sigmaplot11.0.

3.3. RESULTS

3.3.1 DESCRIPTIVE DISTRIBUTION STATISTICS

From both periods a total of 1177 taxa (mean per replicate \pm SD, 51 ± 31) and total abundance of 37165 (per m^2) (total mean \pm SD, 688 ± 573 , range: 5 - 3150) were found in the entire KZN Bight midshelf sampled area. In order of highest to lowest, mean abundance (per m^2) across stations was distributed as follows: stations B (1126 ± 909), C (1117 ± 401), I (1044 ± 498), E (1017 ± 442), A (737 ± 518), D (613 ± 297), F (211 ± 128), G (165 ± 61) and H (165 ± 70). Data variability (taken as standard deviation) was highest at stations A, B, E and I, while stations G and H had the lowest standard deviation values. Confidence levels were the highest for stations A, B and I, while stations F, G and H had the lowest confidence levels.

Transect focus areas such as DT (1121 ± 670), RBF (1044 ± 498) and TF (1017 ± 442) had the highest total mean abundance (per m^2) values of all the transect focus areas studied along the KZN Bight midshelf. DF (737 ± 518) and TT (412 ± 303) had the second highest total mean abundances and RT (165 ± 62) had the lowest total mean abundance of all the transect focus areas studied. However, of the large focus areas considered DF (993 ± 636) had the highest total mean abundance and RBF (458 ± 507) the lowest in total mean abundance. Degree of change represented between large focus areas was $R^2 = 0.9448$ (DF to TF), $R^2 = 0.9674$ (TF to DF).

3.3.2. COMMUNITY ANALYSIS

The hierarchical group mean cluster analysis using all replicates sampled, indicates that the KZN Bight midshelf macrobenthic fauna were divided into ten different compositional groups at a low Bray-Curtis similarity (12%) (Fig. 3.1). Analysis of similarity (ANOSIM) resulted in a high global R 0.783, also showing that all stations were highly dissimilar (Table. 3.1). High dissimilarity between station was found and most adjacent stations had high dissimilarity, for example station E and F (R 0.985), and stations B and C (R 0.961). Stations north and south of Thukela tended to cluster together (Fig. 3.1). Stations G and H were found to be the least dissimilar (ANOSIM, R 0.254, P : 0.043) and of all the stations these were considered as a single cluster at four per cent similarity, although 4 % was still extremely low in similarity (Table. 3.1, Fig. 3.1). Thus six different macrobenthic communities were identified along the KZN Bight midshelf as some stations were aggregated into groups (G and H; A and B, C and D) (Fig. 3.1) and other stations (F, I and E) remained distinct. This is also supported in the analysis of similarity as station E and I (R 1.00), B and I (R 1.00) and B and E (R 1.00) were 100%

dissimilar from each other while station F had an mean dissimilarity of R 0.893 to all other stations, except for station D that was slightly more similar to station F with an R of 0.661.

ANOSIM indicated high dissimilarity between most factors. Similarity was highest between stations G and H (R 0.254) followed by C and D (R 0.335), A and D (R 0.446) and A and B (R 0.544). Commonly grouped stations included A with B, C with D, G with H and I with E. This was supported by group mean cluster analysis. The ANOSIM of transect focus areas (Global R 0.611) contrasted with ANOSIM results for stations, as defined transect focus areas RBF (containing station I) and TF (containing station E) were 100% dissimilar (R 1.00), while DF (containing station A) and TF (R 0.794), and DF and RBF (R 0.822) were also highly dissimilar. There were very high dissimilarities between transect focus areas DF and RT (R 0.875), DT and RT (R 0.887), DT and RBF (R 0.829), as well as RT and RBF (R 0.748). Dissimilarity was lowest between DF and DT (R 0.216), DF and TT (R 0.375), DT and TT (R 0.404) and TF and TT (R 0.458).

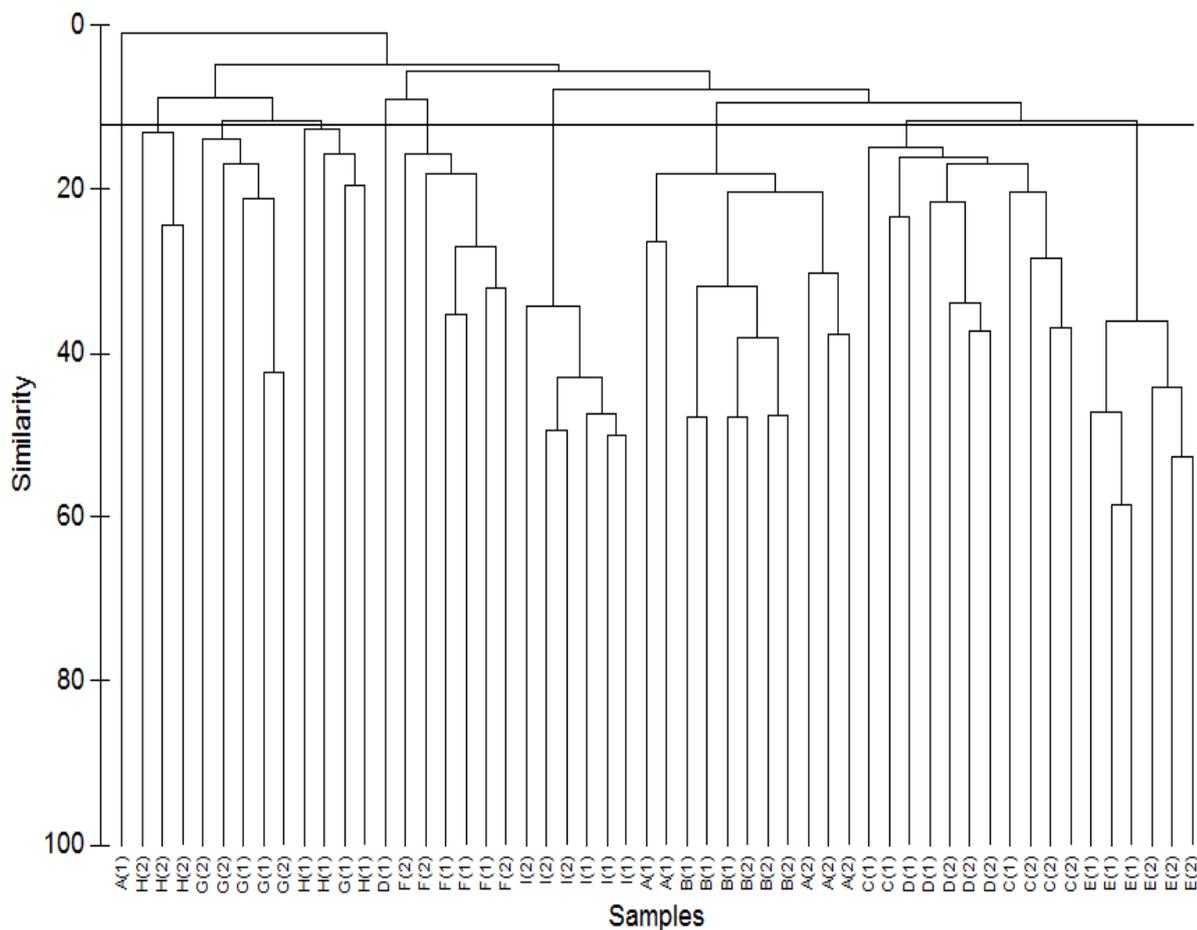


Figure 3.1: Hierarchical group average cluster analysis of $\log(x+1)$ transformed macrobenthos abundance (m^{-2}) data from the KZN Bight midshelf, based on Bray-Curtis similarity. Stations arranged from North, (St. Lucia, left) to South (Durban, right). (1) refers to February 2010 sampling period and (2) to August 2010 sampling period.

However, ANOSIM results of defined large focus areas (Global R 0.433, Table. 3.1), indicates that DF and RBF were now the most dissimilar of all the large focus areas (R 0.645) and TF and RBF now the least dissimilar (R 0.312). Species composition and/or abundance (m^{-2}) changed with increasing spatial scale of factors used in this present study followed by similarity with increasing scale (Table. 3.1).

Table 3.1: ANOSIM results, comparing the similarity of macrobenthic community composition and abundance (m^{-2}) within stations, transect focus areas and large focus areas.

Study region	Global R	Significance level of sample statistic	Number of Permutations
Stations	0.783	0.01%	10000
Focus Areas	0.611	0.00%	1400000
Large Focus Areas	0.433	0.00%	2000000

The 3D non-metric multidimensional scaling ordination at a stress of 0.15 was chosen to represent multivariate analysis of similarity in space, as this was a more detailed representation of community assemblages (Fig. 3.2). Here it was also evident that from all stations at twelve per cent similarity, ten macrobenthic communities were identified. Station F was the most dissimilar and distinct station and most similar to station I. Station I seemed to be characterised as having some similarity with most of the other stations. Demonstrated by a decrease in similarity from stations in the South (from station A) to stations in the North (to station I), forming a similarity/dissimilarity gradient of AB, CD, E to GH. Stations F and I did not fit into this gradient based on spatial location, but the gradient from left to right followed as A/B to C/D, E, I, G, H, with station F not fitting into the overall pattern.

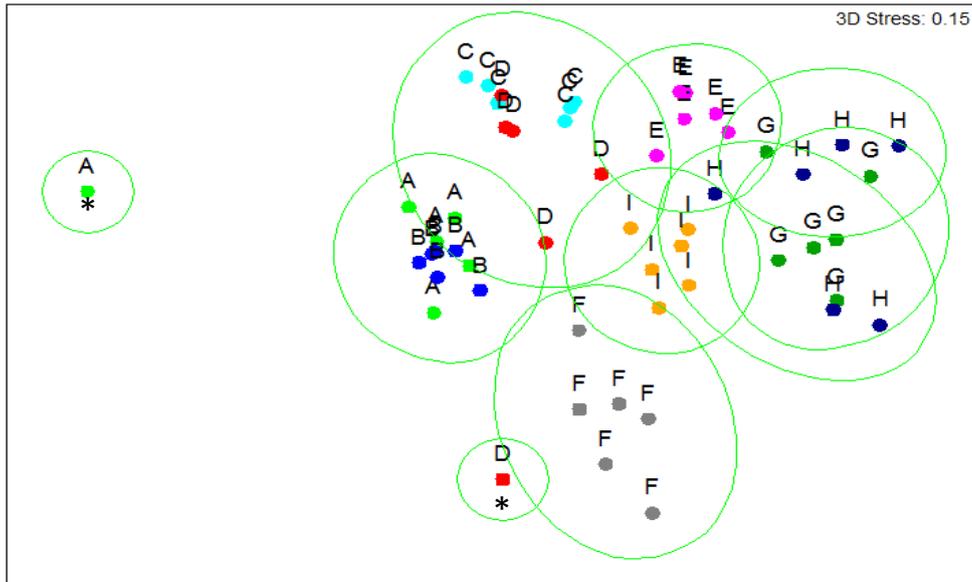


Figure 3.2: Multi-dimensional scaling (MDS) ordination of stations based on Bray-Curtis similarity. Boundaries represent 12 per cent similarity. 3D Stress (0.15). (*) outliers.

Similarity between stations south of the Thukela River mouth seemed to have had a more gradual decrease in similarity from Durban up to the Thukela River. Dissimilarity steeply increased in stations south of the Thukela to that north of the Thukela, with station I as the exception. All stations north of the Thukela River were highly dissimilar to each other. Defined stations, transect focus areas, and large focus areas all had significantly different macrobenthic communities at a Bray-Curtis similarity level of thirty-one per cent. Thus the KZN Bight midshelf, accommodated highly diverse and distinct macrobenthic communities within relative short distances along its length, from south to north. A gradient of similarity exists from a north to south and/or south to north direction. All three major regions of oceanographic influence had unique macrobenthic communities.

The species accumulation curve did not reach its asymptote which indicates that the number of samples analysed fell short of being fully representative of the entire macrobenthic community of the KZN Bight midshelf (Fig. 3.3). The Chao 1 projection of the estimated species richness of the entire KZN Bight followed the same trend as species observed (Sobs) (Fig. 3.3). However according to Chao 2 estimates species richness for the KZN Bight was projected to be much higher and the minimum started at a much higher level than Chao 1 and species observed (Fig. 3.3). Since the Chao 1 and Sobs converged from an early stage, it was concluded that all species did consist at least of two or more individuals in abundance (Colwell and Coddington 1994). However as the Chao 2 estimate and the Sobs did not converge, it was concluded that not all

species were represented in a minimum of two sites, and that species estimation was still largely dependent on sample size (Colwell and Coddington 1994). The second order Jackknife estimate did also not reach an asymptote, nor did it converge with observed number of species, but did however have a more gradual increase in species richness than the Chao 2 estimator. Chao2 and second order Jackknife estimates did however converge between 2000 and 2500 species counts and approximately 57 samples, supporting that an asymptote had not been reached and that each was in agreement with the other.

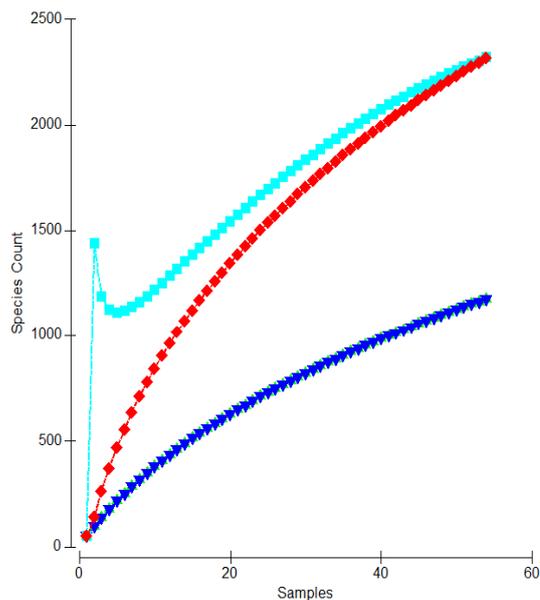


Figure 3.3: Species-accumulation curve representing observed number of species and estimated number of total species present in the entire study area. Chao 2 estimator (blue squares), Chao 1 estimator (blue triangles), Second order Jackknife estimator (red squares), Sobs (Bottom line converging with blue triangles).

3.3.3. ALPHA DIVERSITY (SAMPLE DIVERSITY)

As different diversity indices and measurement techniques measure different components of diversity to different degrees, it was necessary to include other means of diversity and similarity measurement as to achieve coherence of patterns and conclusions made about the macrobenthic communities of the KZN Bight midshelf (Clarke and Lidgard 2000, Ellingsen 2001, Willig et al. 2003, Magurran 2004, Shin and Ellingsen 2004).

Macrobenthic alpha diversity results show that the mean number of observed species found was highest for stations A, B, C, D (South Bight) and E (middle Bight region) (Table. 3.2). Stations

F, G H and I had a fewer mean number of species (Table. 3.2). The same trend was followed in mean abundance (m^{-2}) and mean species richness measures. Mean evenness for all stations was very high and close to a value of one, except for station I, which had the lowest evenness of all the stations (Table. 3.2). Similar results were found for Simpson's diversity index as for Pielou's evenness, as stations D and I had the lowest mean diversity (highest dominance) values (Table. 3.2).

Mean Shannon diversity was highest at stations A, B, C and E, with station D being more similar to station F, and stations G, H and I, having the lowest mean Shannon diversity values (Table. 3.2). Mean Hill (N1) diversity shows a similar trend to that of Shannon diversity, as stations from the South Bight region tended to have higher alpha diversity than those of the North Bight. Station C had the highest N1 diversity and D had the lowest N1 diversity values of the South Bight and stations F and I had the lowest N1 diversity values of the North Bight (Table. 3.2). Hill's (N2) diversity values were quite different from the Simpson's diversity values obtained, yet similar to the N1 diversity patterns across the KZN Bight midshelf. The difference between the mean N1 and N2 diversities was that N1 was always higher than N2.

Table 3.2: Macrobenthic alpha diversity results of replicates pooled to stations levels, along the KZN Bight midshelf. Top values are single station total diversity index values, bottom values are index mean \pm standard deviation values. (S) number of species observed, (N) untransformed abundance (m^{-2}), (d) Margalef species richness, (J') Pielou evenness, (H'_{log_e}) Shannon-Wiener diversity index, (1-Lambda') Simpson diversity index, (N1) Hill's diversity number, (N2) Hill's diversity number.

Station	S		N		d		J'		H'(log _e)		1-Lambda'		N1		N2	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
A	259		4420		30.74		0.878		4.879		0.9843		131.5		62.96	
	62.500	±36.833	736.667	±518.369	9.167	±4.771	0.924	±0.036	3.522	±0.917	0.947	±0.053	43.005	±23.835	28.609	±15.802
B	227		6755		25.63		0.841		4.563		0.9808		95.82		51.6	
	73.000	±30.640	1125.833	±909.365	10.340	±3.194	0.908	±0.042	3.821	±0.194	0.970	±0.003	46.353	±9.255	31.957	±3.352
C	374		6700		42.34		0.8632		5.114		0.9851		166.3		66.56	
	89.667	±27.833	1116.667	±400.583	12.612	±3.319	0.898	±0.025	4.007	±0.301	0.970	±0.011	57.188	±18.476	35.547	±12.853
D	225		3680		27.28		0.8371		4.534		0.9636		93.1		27.26	
	53.333	±26.942	613.333	±296.929	7.989	±3.868	0.867	±0.033	3.200	±1.033	0.892	±0.130	32.253	±17.007	17.825	±10.913
E	204		6100		23.29		0.7918		4.211		0.9667		67.42		29.85	
	67.667	±19.387	1016.667	±441.811	9.637	±2.182	0.863	±0.023	3.606	±0.222	0.952	±0.011	37.568	±8.313	21.353	±4.536
F	77		1265		10.64		0.8451		3.671		0.9541		39.3		21.44	
	19.833	±9.020	210.833	±128.196	3.509	±1.323	0.907	±0.068	2.603	±0.439	0.903	±0.040	14.621	±6.336	11.296	±4.913
G	118		990		16.96		0.9412		4.49		0.9849		89.13		62.03	
	26.500	±7.232	165.000	±60.828	4.996	±1.149	0.974	±0.025	3.161	±0.275	0.957	±0.014	24.345	±6.584	22.042	±6.891
H	112		990		16.09		0.9276		4.377		0.9787		79.59		44.86	
	23.667	±8.383	165.000	±69.785	4.423	±1.322	0.945	±0.055	2.944	±0.424	0.931	±0.048	20.338	±7.721	17.154	±8.327
I	142		6265		16.13		0.5683		2.816		0.741		16.72		3.859	
	47.000	±12.946	1044.167	±498.211	6.656	±1.418	0.670	±0.144	2.517	±0.361	0.757	±0.120	13.025	±4.177	5.471	±3.949

The general alpha diversity trend in large focus areas was a decrease from the South towards the North (Fig. 3.4 a-f, Table. 3.3).

Table 3.3: Macrobenthic alpha diversity measures of replicates pooled in large focus area levels, occurring along the KZN Bight midshelf. Top values are single large focus area diversity index values, bottom values are index mean \pm standard deviation values. (S) number of species observed, (N) untransformed abundance (m^{-2}), (d) Margalef species richness, (J') Pielou evenness, (Hloge) Shannon-Wiener diversity index, (1-Lambda') Simpson diversity index, (N1) Hill's diversity number, (N2) Hill's diversity number. (Acronyms

Large Focus area	S		N		d		J'		H'(loge)		1-Lambda'		N1		N2	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
DF	699		17875		71.29		0.8536		5.591		0.9917		268		119.7	
	75.056 \pm 32.179		993.056 \pm 635.816		10.706 \pm 3.886		0.910 \pm 0.035		3.783 \pm 0.572		0.962 \pm 0.031		48.849 \pm 18.207		32.037 \pm 11.569	
TF	443		11045		47.48		0.8168		4.977		0.9818		145		54.71	
	46.944 \pm 27.809		613.611 \pm 450.300		7.045 \pm 3.662		0.879 \pm 0.047		3.136 \pm 0.751		0.916 \pm 0.079		28.148 \pm 14.800		16.825 \pm 8.158	
RBF	325		8245		35.93		0.6568		3.799		0.8491		44.65		6.623	
	32.389 \pm 14.134		458.056 \pm 507.338		5.358 \pm 1.563		0.863 \pm 0.164		2.874 \pm 0.435		0.882 \pm 0.115		19.236 \pm 7.660		14.889 \pm 9.493	

Diversity indices were highly significantly different between stations, transect focus areas and large focus areas with the exception of evenness within the latter (Table. 3.4). One-way ANOVA and Tukey pairwise comparison tests of stations indicates that there were significant differences between the means of all diversity indices of certain stations along the KZN Bight midshelf ($P < 0.001$). In terms of Pielou's evenness (J'), (two groups recognised), station I (0.6698 ± 0.1435) was the only significantly different station ($P = 0.001$) from all the other South stations, had a uniform spread of individuals among species. As an indicator of dominance, Simpsons diversity (1-Lambda') (two groups recognised), followed the same trend, with station I (0.7572 ± 0.1197) being the only significantly different station in terms of dominance/diversity from other stations sampled.

In terms of the number of species (S) (five groups recognised) found within stations; station A (62.50 ± 36.83) was only significantly different from station F (19.83 ± 9.02); station B (73 ± 30.64) was significantly different from stations F (19.83 ± 9.02), G (26.50 ± 7.23) and H (23.67 ± 7.23); station C (89.67 ± 27.83) was different from stations F, G, H and I (47 ± 12.95); station E (67.67 ± 19.39) was different from stations F and H; whereas station D (53.33 ± 26.94) was not different from any of the other stations and stations F, G, H and I were not significantly different from one another. Station I as the northern-most station was not significantly different from most of the South Bight stations except for station C.

One-way analysis of variance to compare communities between transect focus areas, followed by a *post hoc* Tukey pairwise comparison test concluded that there was a significant difference between the means of all diversity indices of certain defined transect focus areas (Table. 3.4, $P < 0.001$).

One-way ANOVA and a *post hoc* Tukey pairwise comparison of diversity indices from large focus areas were significantly different (Table. 3.4, $P < 0.001$). However Pielou's evenness (J') was not significantly different between large focus areas (Table. 3.4, $P > 0.05$). Between the three large focus areas recognised, most diversity indices results indicates that DF was significantly different from TF and RBF, while TF and RBF were not significantly different from each other. Change in scale from station to transect focus area, did not result in a drastic change in similarity between stations, however when large focus area was considered, DF was generally the most dissimilar from TF and RBF.

Table 3.4: Results of comparison of variance of macrobenthos alpha diversity indices, using One-way ANOVA, the Kruskal-Wallis tests of medians and General Linear ANOVA between stations, transect focus areas and large focus areas. (*) Kruskal-Wallis rank test; (**) General linear model ANOVA.

Diversity indices	Stations	Focus Areas	Large Focus Areas
N (log (x+1) transformed)	H= 31.37; df= 8; P = 0.001*	$F_{(5,48)} = 9.07$; P = 0.001**	H= 15.81; df= 2; P = 0.001*
S	$F_{(8,45)} = 7.02$; P = 0.001	$F_{(5,48)} = 8.60$; P = 0.001	$F_{(2,51)} = 12.65$; P = 0.001
d	$F_{(8,45)} = 7.06$; P = 0.001	$F_{(5,48)} = 8.19$; P = 0.001	$F_{(2,51)} = 13.04$; P = 0.001
J'	$F_{(8,45)} = 12.13$; P = 0.001	$F_{(5,48)} = 19.37$; P = 0.001	$F_{(2,51)} = 1.02$; P = 0.369
H(log _e)	$F_{(8,45)} = 5.47$; P = 0.001	$F_{(5,48)} = 7.63$; P = 0.001	$F_{(2,51)} = 10.94$; P = 0.001
1-Lambda	$F_{(8,45)} = 6.27$; P = 0.001	$F_{(5,48)} = 10.44$; P = 0.001	$F_{(2,51)} = 4.26$; P = 0.019
N1	$F_{(8,45)} = 8.24$; P = 0.001	$F_{(5,48)} = 10.53$; P = 0.001	$F_{(2,51)} = 20.46$; P = 0.001
N2	$F_{(8,45)} = 7.01$; P = 0.001	$F_{(5,48)} = 10.63$; P = 0.001	$F_{(2,51)} = 16.40$; P = 0.001

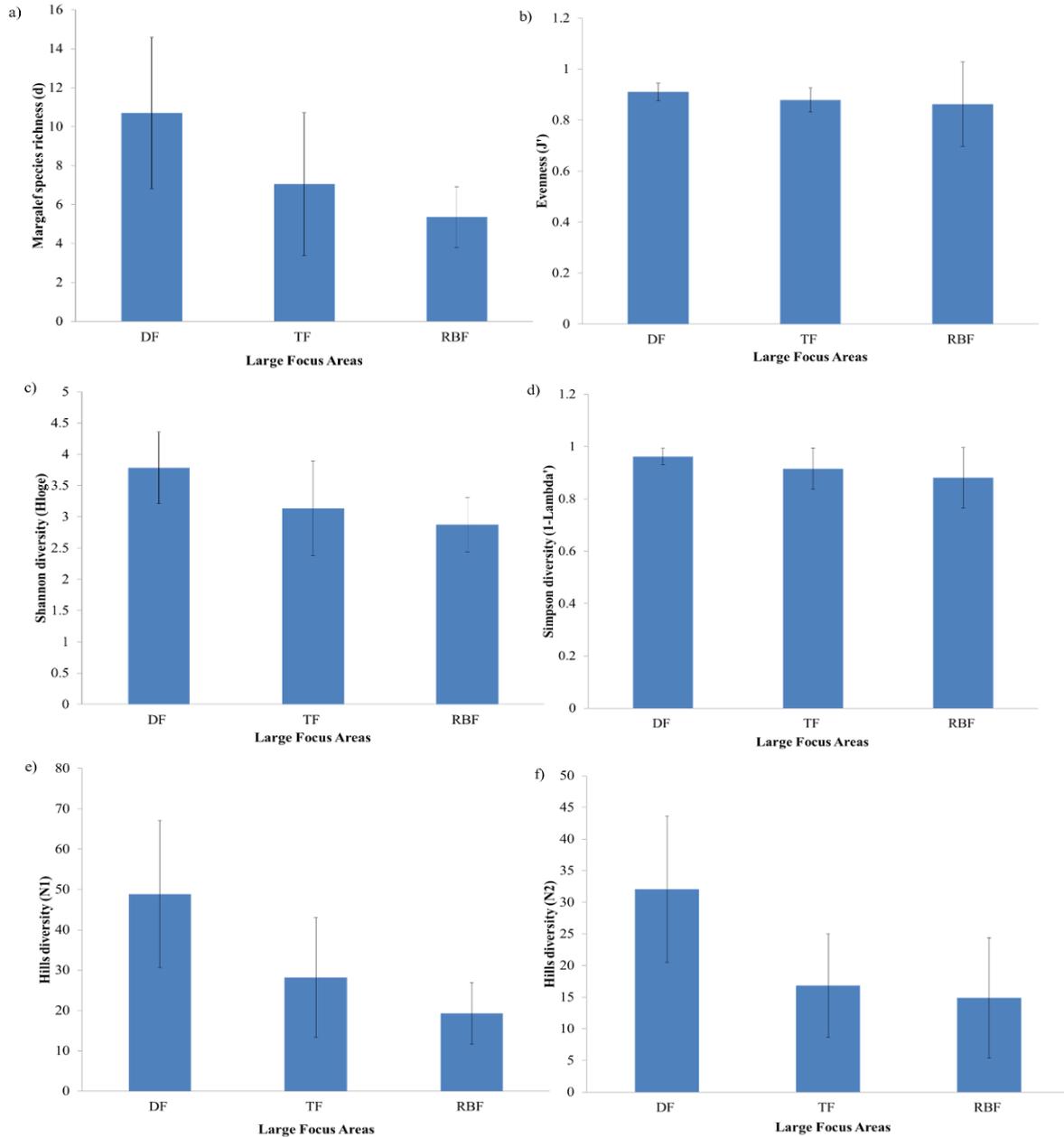


Figure 3.4: Community diversity attributes of a) species richness, b) evenness, c) Shannon diversity, d) Simpson diversity, e) Hill's diversity N1 and f) Hill's diversity N2, along the KZN Bight midshelf, representing change along the Bight from a South (DF) towards a North (RBF) direction. DF (Durban Focus area), TF (Thukela Focus area), RBF (Richards Bay Focus area); Error bars represent standard deviations.

3.3.4. BETA DIVERSITY (BETWEEN HABITAT DIVERSITY)

Stations F/G and H/I had the highest beta diversity (turnover diversity), percentage complementarity and the lowest percentage Bray Curtis (% BC) similarity (Fig. 3.5a and b).

Stations B/C, D/E and E/F also had very high beta diversity values, high percentage complementary and low percentage Bray-Curtis similarity (Fig. 3.5a and b). The smallest changes in turnover and the lowest values of percentage complementarity and high similarity, was found between stations A/B, C/D and G/H (Fig. 3.5a and b). Even though these pairs of stations had the highest similarity, they still had very high biotic distinctness. The largest change in diversity/turnover was found in the central and the North KZN Bight midshelf (Fig. 3.5). The degree of change between stations was $\beta_w R^2 = 0.3144$, of Bray-Curtis similarity was $R^2 = 0.2945$ and of % Complementarity was $R^2 = 0.3077$.

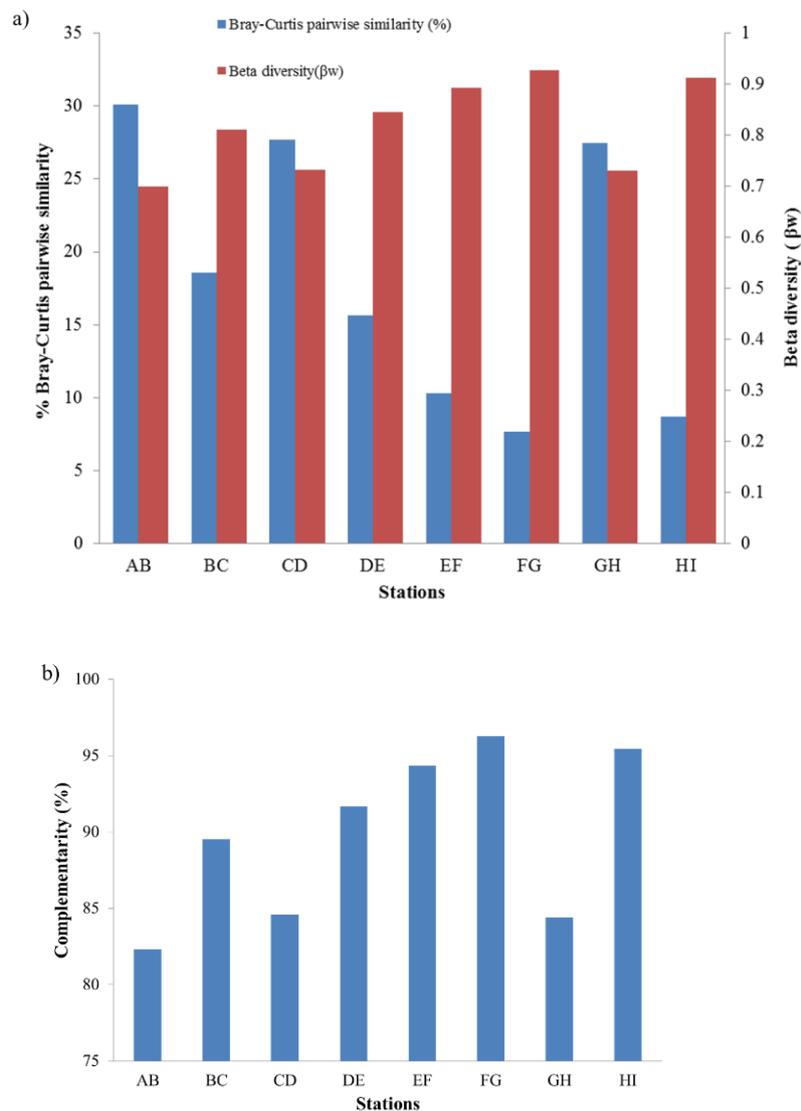


Figure 3.5: a) Whittaker's beta diversity and percentage Bray-Curtis percentage similarity between adjacent stations along the KZN Bight midshelf, b) Percentage Complementarity between adjacent stations along the KZN Bight midshelf.

When beta diversity, percentage complementarity and similarity were compared between transect focus areas there was much more of a clear trend of increased beta diversity and complementarity and decreasing similarity when samples were considered from the South to North midshelf on the KZN Bight (Fig. 3.6a and b).

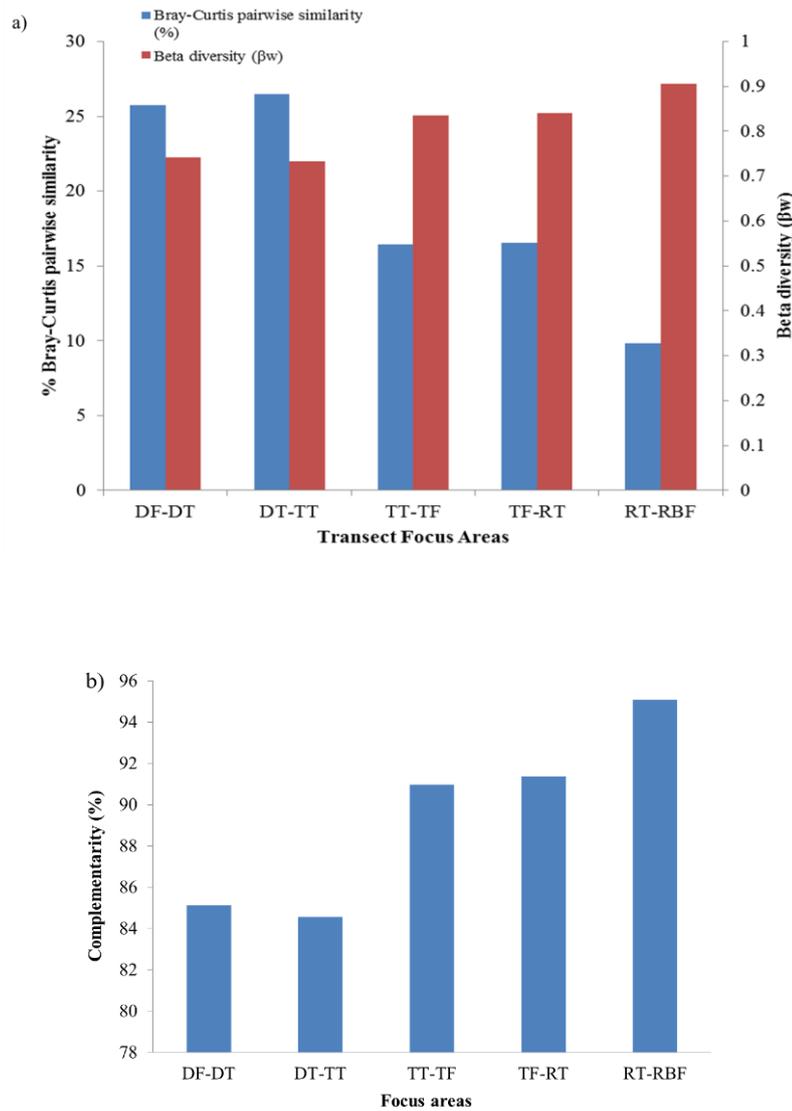
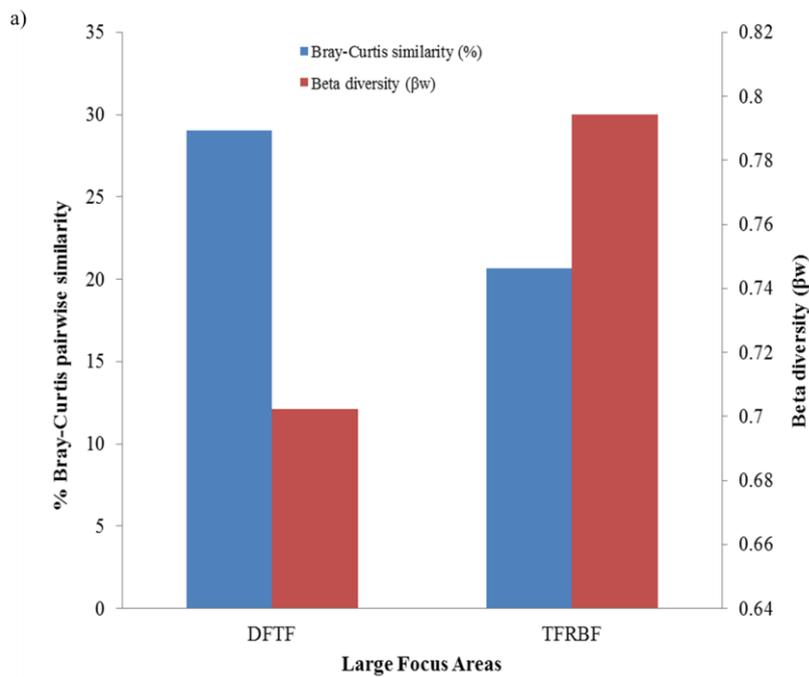


Figure 3.6: a) Whittaker’s beta diversity and percentage Bray-Curtis similarity between adjacent transect focus areas along the KZN Bight midshelf. b) Percentage Complementarity between adjacent transect focus areas along the KZN Bight midshelf.

When adjacent large focus area pairs were considered, there was a clear divide in the KZN Bight, between the lower turnover, higher similarity South Bight region and the higher turnover, lower similarity North Bight region (Fig. 3.7a and b). The strength of the result is increased by this high R^2 values (for stations $R^2 = 0.3144$, for transect focus areas $R^2 = 0.8938$, for large focus areas $R^2 = 1$). The degree of change between large focus areas was $R^2 = 1$, for β_w , Bray-Curtis similarity and % complementarity.

From results it was clear that although the alpha diversity indices used indicates a general pattern of decline in diversity from the South Bight towards the North Bight, beta diversity (turnover), Bray-Curtis similarity and complementarity indicate the opposite (Fig. 3.5, Fig. 3.6 and Fig. 3.7). Thus at all scales measured, beta diversity reflected the same pattern along the KZN Bight midshelf.



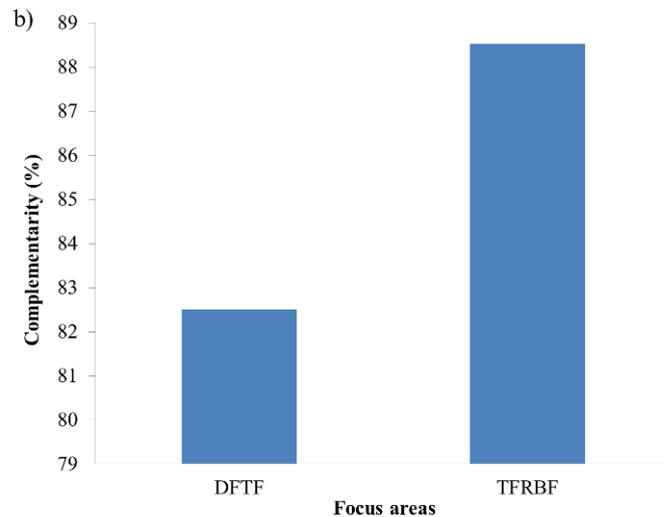


Figure 3.7: a) Whittaker's beta diversity and percentage Bray-Curtis similarity between adjacent large focus areas along the KZN Bight midshelf. b) Percentage Complementarity between adjacent large focus areas along the KZN Bight midshelf.

This made the North Bight potentially more diverse than the South Bight in terms of turnover in contrast to that initially indicated by the more commonly used alpha diversity indices (eg. Shannon-Wiener and Simpson's index) that incorporate species richness and abundance (Fig. 3.4, Fig. 3.5, Fig. 3.6 and Fig. 3.7). This could have been because alpha diversity indices are based on the relative importance of species richness and abundance, whereas beta diversity involves the change in species composition from one region to another.

3.3.5. TAXONOMIC COMPOSITION

Figure 3.8 shows the mean number of different taxonomic groups found within large focus areas per replicate (considering that it was not possible to identify all individuals to lowest taxonomic levels), which followed the same general trend as the results found from alpha diversity index values along the KZN Bight midshelf (Table. 3.3, Fig. 3.4). That is, highest diversity was found in the South region at DF and steadily decreased to the north (Fig. 3.8).

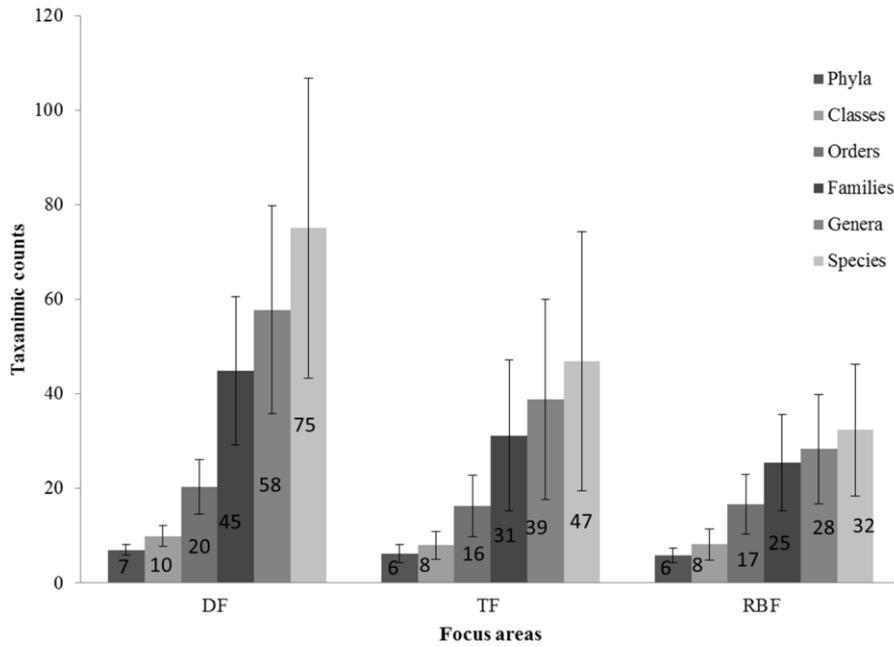


Figure 3.8: Mean number of taxonomic groups per replicate found in each large focus area along the KZN Bight midshelf.

The four most abundant taxonomic groups present in the KZN Bight midshelf were; in order of decreasing dominance Annelida, Arthropoda, Cnidaria and Mollusca (Fig. 3.9).

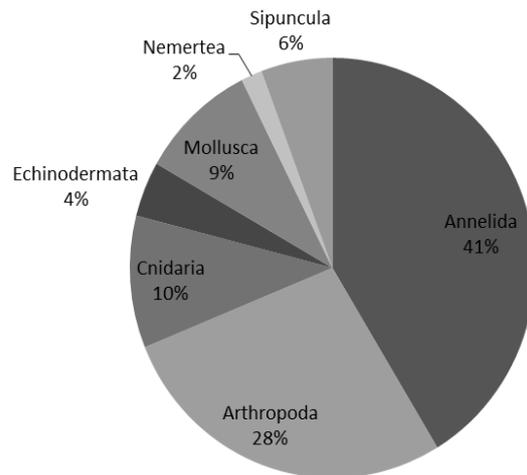


Figure 3.9: Graph showing the overall taxonomic composition along the entire KZN Bight midshelf study area. Percentages based on abundance (m²) per taxonomic group.

The most distinct differences in compositions of the transect focus areas, was that in DF, DT and TT, relative abundance (m^{-2}) was the highest, particularly in TT (Fig. 3.10a-f). For Arthropoda there was a sharp decrease in relative abundance in focus areas TT and RBF where Sipuncula and Cnidaria were at their most abundant (Fig. 3.10c and f). In focus area RT, the relative abundance of Mollusca was sharply decreased, while the relative abundance of Echinodermata was greatly increased and RT was thus the focus area where Echinodermata were most prevalent (Fig. 3.10e). Transect focus area RBF stands out as the focus area with the highest Cnidarian abundance and lowest Annelida abundance (Fig. 3.10f). Mollusca seem to maintain a relative constant abundance across all transect focus areas (Fig. 3.10a-f).

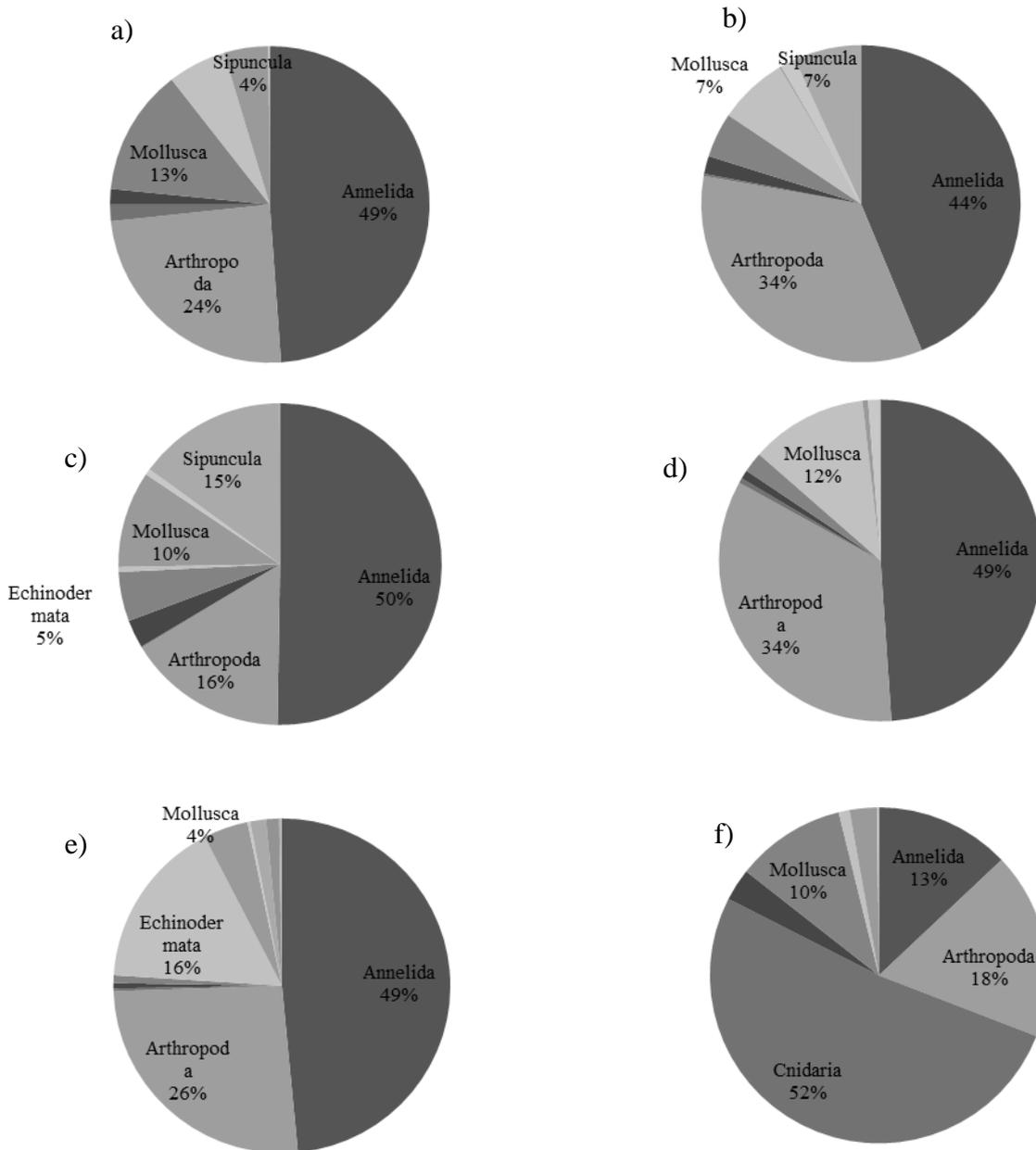


Figure 3.10: Taxonomic composition per transect focus area along the KZN Bight midshelf. a) Durban focus area, b) Durban transition focus area (stations B and C), c) Thukela transition focus area (stations D and F), d) Thukela focus area, e) Richards Bay transition focus area (stations G and H), f) Richards Bay focus area.

Taxonomic groups were distributed along most of the KZN Bight midshelf study area. Of the 54 replicates, most were occupied by Annelida, Arthropoda, Mollusca and Echinodermata (Fig. 3.11). Of the four most abundant taxa, Cnidaria occupied the smallest spatial range (Fig. 3.11) and although of higher abundance than Mollusca, they had a significantly smaller range of species than Mollusca (Fig. 3.14). But this could have been affected by the lack of expertise in

taxonomic identification. Nemertea and Cnidaria both occupied a total of 37 replicates each (Fig. 3.11). Taxonomic groups that occupied the least number of replicates were, Chordata, Echiura, Nematoda and Brachiopoda (Fig. 3.11).

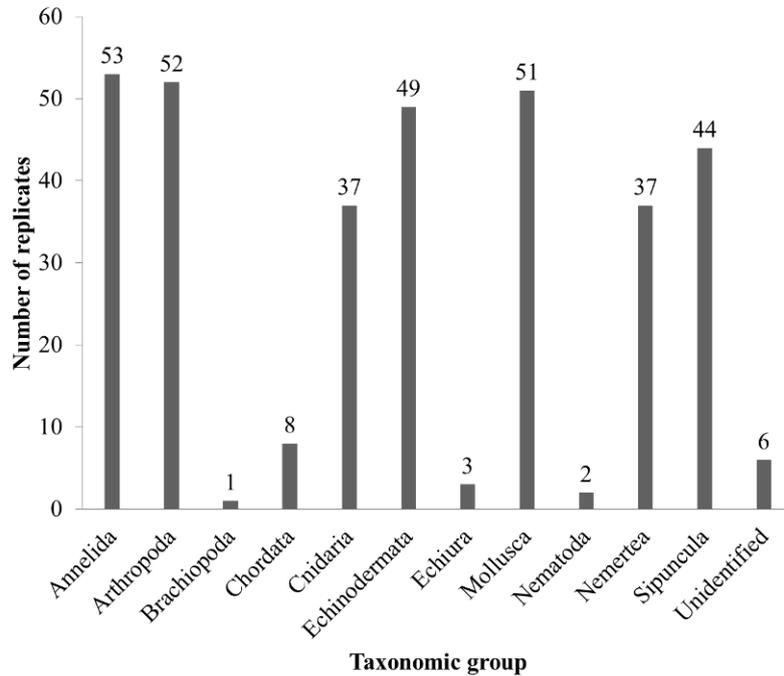


Figure 3.11: Number of replicates occupied by each taxonomic group found along the KZN Bight midshelf.

Figures 3.12 and 3.13 show which of the taxonomic Classes or Orders were dominant. The phylum Annelida (three Classes) consisted almost completely of the Class Polychaeta (mean abundance per replicate of 283 individuals). The second most dominant phyla, namely Arthropoda (14 Orders), consisted predominantly, in order of highest abundance to less abundant, of the Order Amphipoda, Decapoda and also Isopoda (Fig. 3.12).

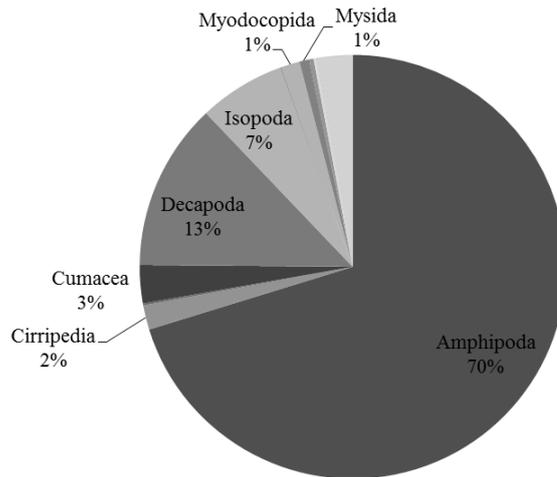


Figure 3.12: Dominant taxonomic Orders found in the phylum Arthropoda along the KZN Bight midshelf.

Mollusca (three classes) as the fourth most dominant phyla, consisted mostly of the Class, Bivalvia, secondly of Gastropoda and least of Scaphopoda (Fig. 3.13).

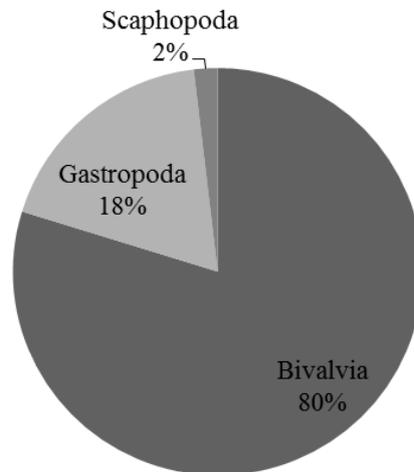


Figure 3.13: Dominant taxonomic Classes found in the phylum Mollusca along the KZN Bight midshelf.

Phylum Cnidaria had to be retained at this level due to difficulties in identification and the lack of taxonomic resources.

From SIMPER results (Table. 3.5), 60 % of dissimilarity between DF and TF was contributed by 218 species, between DF and RBF 217 species contributed and between TF and RBF 165 species accounted for 60 % dissimilarity. Large focus areas DF and RBF had the highest

dissimilarity (95.31 %) between them and DF and TF (91.84 %) had the lowest dissimilarity of the three defined large focus areas studied (Table. 3.5). The commonly and consistently contributing species to the mean dissimilarity among all three large focus areas was, *Notomastus aberans*, having had the strongest contribution between DF and RBF (Diss/SD: 1.66) and the second strongest and consistent contribution between DF and TF (Diss/SD: 1.1) (Table. 3.5).

The species that commonly and consistently contributed the most to the mean dissimilarity between DF from TF and RBF, but at different strengths, were, *Nemertea sp.*, *Euclymene cf. luderitziana*, *Arcturinoidea cf. sexpes*, *Ophiuroidea sp. 22* and *Mediomastus sp. 1* between DF from TF and RBF (Table. 3.5). Similarly *Golfingiidae sp.*, *Onuphis eremita* and *Amphiuridae sp. 9* were the species that commonly and consistently contributed the most to the mean dissimilarity between RBF and DF and TF respectively (Table. 3.5). *Notomastus aberans* was the only species in TF that consistently contributed to its dissimilarity from DF and RBF (Table. 3.5). Unique species, that consistently contributed to the mean dissimilarity between only two of the three defined large focus areas were, *Poecilochaetus serpens* between DF and TF (Diss/SD: 1.1), *Heterospionidae sp.1* between DF and RBF (Diss/SD: 1.08), and *Nuculana sp.1* between TF and RBF (Diss/SD: 1.06) (Table. 3.5).

Table 3.5: Species predominantly responsible for contributing to the dissimilarity between defined large focus areas along the KZN Bight midshelf. Species arranged in order of high to lower importance of contribution towards dissimilarity. Second row percentage dissimilarity represents total mean dissimilarity between samples.

DF/TF			DF/RBF			TF/RBF		
(91.84% dissimilarity)			(95.31% dissimilarity)			(93.73 % dissimilarity)		
Species contributing to dissimilarity	Diss/SD	Contribution %	Species contributing to dissimilarity	Diss/SD	Contribution %	Species contributing to dissimilarity	Diss/SD	Contribution %
<i>Nemertea sp.</i>	1.18	0.91	<i>Notomastus aberans</i>	1.66	0.99	<i>Golfingiidae sp.</i>	1.22	1.74
<i>Notomastus aberans</i>	1.1	0.77	<i>Golfingiidae sp.</i>	1.36	1.07	<i>Onuphis eremita</i>	1.06	1.27
<i>Poecilochaetus serpens</i>	1.1	0.76	<i>Nemertea sp.</i>	1.23	0.95	<i>Nucula sp. 1</i>	1.06	0.94
<i>Euclymene cf. luderitziana</i>	1.09	0.73	<i>Euclymene cf. luderitziana</i>	1.2	0.8	<i>Notomastus aberans</i>	1.04	0.85
<i>Arcturinoidea cf. sexpes</i>	1.05	0.64	<i>Arcturinoidea cf. sexpes</i>	1.11	0.69	<i>Amphiuridae sp. 9</i>	1.02	1.26
<i>Ophiuroidea sp. 22</i>	1.02	0.79	<i>Amphiuridae sp. 9</i>	1.09	0.92			
<i>Mediomastus sp. 1</i>	1	0.57	<i>Heterospionidae sp. 1</i>	1.08	1.04			
			<i>Onuphis eremita</i>	1.06	0.81			
			<i>Ophiuroidea sp. 22</i>	1.03	0.85			
			<i>Mediomastus sp. 1</i>	1.01	0.63			

For the four most abundant phyla found, beta diversity changed between adjacent transect focus areas across the KZN Bight, with an increase in turnover from the South DF focus area to the North RBF focus area. Of the four phyla, Cnidaria had the steepest increase of turnover across the KZN Bight from the South DF to the North RBF. Arthropoda had the most even and less drastic change in degree of turnover across the KZN Bight midshelf. These two phyla did however show the highest level of mean turnover among the four dominant groups as well (Fig. 3.14). Annelida and Mollusca had the lowest level of turnover among the dominant groups, yet also increased from DF to RBF.

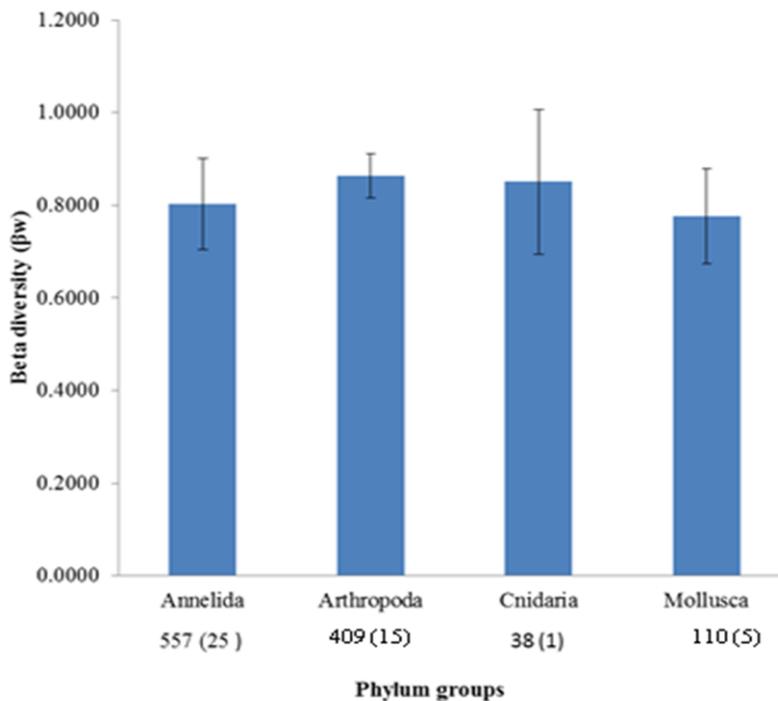


Figure 3.14: Mean Whittaker's beta diversity of dominant taxonomic groups between transect focus areas along the KZN Bight midshelf. Bottom numbers indicate total number of species found in each phylum; () mean number of species in each phylum.

3.4. DISCUSSION

3.4.1. KZN BIGHT DIVERSITY

It is possible that the KZN Bight ecosystem, in spite of its oligotrophic nature, has high macrobenthic diversity comparable to some tropical high diversity ecosystems. A similar contrast was found in a study by Poore and Wilson (1993) on benthos of the Australian coastal soft sediment in temperate Bass Strait, where 800 species were counted in an area of 10 m².

This is in line with some of the highest benthos soft sediment species richness found (Gray 1997a).

Similar to other large areas in the Indo-Pacific, which are oligotrophic and low in productivity, the KZN Bight midshelf macrobenthic biodiversity was high (Brewer et al. 2007, Sanciangco et al. 2013), with a total of 1177 species counted (mean of 51 species per 1 m^{-2}) and 37165 individuals (mean of 688 individuals per 1 m^{-2}) distributed highly evenly among species (mean evenness of 0.884 per m^{-2}). For individual replicates, Shannon diversity ranged from 1.154 – 4.47 and N1 from 3 - 87, Simpson diversity from 0.6303 – 0.9822 and N2 from 2 - 54, Pielou evenness from 0.8322 – 0.9098, number of species observed from 4 – 136, and abundance from 35 -1635 individuals per m^{-2} . According to the mean estimates of Hill's N1 and N2 diversity the effective number of species/diversity per 1 m^{-2} found on the KZN Bight midshelf was actually much lower at values of 32 species for N1 and a lower 21 for N2.

This was however not comparable to the diversity of Polychaetes and Mollusc of the soft sediment continental shelf of the oligotrophic tropical, river-influenced waters of the Seychelles (Mahé), as much higher diversity was uncovered, that rivalled equivalent data from the temperate Irish Sea by Mackie et al. (2005). Tropical Seychelles macrobenthic diversity is very high for an oligotrophic environment, since the Irish Sea gravel is known as one of the richest shelf habitats, with an mean count of 145 species per 0.2 m^{-2} and a high Shannon diversity value of 5.8 (Mackie et al. 2005).

The KZN Bight midshelf macrobenthic community shows much higher mean species density per m^{-2} than found by Gray (2002), who in his comparison of undisturbed areas found a much lower constant species density overall within coastal habitats of between 7.9 to 16 species. For an oligotrophic environment, this present study, though not an extreme exception seemed to have exceptionally high species richness. Longhurst and Pauly (1989) and Longhurst (2007) found that some tropical benthic diversities were found to be lower in diversity than this present study and those studies were more comparable to temperate continental shelves (Shin and Ellingsen 2004). The lower species richness of our study compared to off the Seychelles for example (Mackie et al. 2005), could be the influence of anthropogenic activities such as coastal pollution, trawling and dredging that occurs along the coast of KZN (Morton 1996, Griffiths et al. 2010).

Compared to the continental shelf of Crete located within oligotrophic Mediterranean waters, which is according to some not heavily affected by large rivers or major anthropogenic activities

(Karakassis and Eleftheriou 1997), our study had a higher species richness and abundance. Karakassis and Eleftheriou (1997) found a total of 547 species and 18858 individuals in a total of 99 quantitative macrobenthic samples at depth between 40 and 190m. However the total KZN mean abundance (m^{-2}) was equal to the lowest mean abundance (663 individuals per m^{-2}) in the deepest stations of the Crete continental shelf. The KZN Bight was however much more diverse than Crete; as more species and a higher abundance were found within a smaller depth range.

In this present study no species were represented by only one or two individuals. However, 72 % of the species were found in at least one site and 18 % were found in only two sites, showing that high diversity in terms of species counts could be very localised. Within the sampling area of Shin and Ellingsen (2004), 38 % of species were represented by one or two individuals and 45 % of species were only found in one or two sites. Rare species are either species that have low abundances and/or have small range sizes (Gaston 1994). This is typical of marine benthic data as species richness is mostly influenced by rare species (Gray 2002, Shin and Ellingsen 2004, Fontana et al. 2008). Ecological data generally have many species represented by few individuals, or many individuals represented by a few species, as most of the species having restricted ranges (Gaston 1994, Shin and Ellingsen 2004). Caution should be taken as the number of rare species present in a study could be the result of sampling effort that is also linked to the scale and geographical areas measured, as some species whose range may seem restricted may in actual fact be more widespread if the total area sampled was increased and also because of different methodology in studies, of which not many are easily comparable (Gaston and Blackburn 2000, Ellingsen 2001, Shin and Ellingsen 2004, Fontana et al. 2008).

The species accumulation curves of the KZN Bight did not reach an asymptote. This is because large areas are generally always sampled in small fractions and as the area of sampling increases, so does the number of species found, thus where assemblages are not fully sampled, an asymptote is never reached (Gray 2002). The slopes of the species accumulation curves are likely related to levels of environmental heterogeneity over space and time (Gray 2002, Shin and Ellingsen 2004). Subtidal habitats within the marine environment grade into each other gradually, thus as the species accumulation estimates attempt to estimate the species within a large area, new patches of habitat are continuously added and the species accumulation curve does not reach an asymptote (Ellingsen 2001). Even though Chao 2 is a very reliable estimate to some, estimates are generally underestimates (Ellingsen and Gray 2002).

3.4.2. SPATIAL HETEROGENEITY

The analysis of similarity, cluster analysis and analysis of variance, indicates that all pairwise stations, transect focus areas and large focus areas were significantly different and had significant low levels of similarity ranges ($P < 0.005$). Karakassis and Eleftheriou (1997) found similar results, and concluded that this is most likely a reflection that varying environmental attributes, other than depth, are important. Low but highly variable species richness found between samples in past studies and by Shin and Ellingsen (2004) in subtropical Hong Kong, concluded that although there seemed to be an exceptional number of species present in the tropics and subtropics, there was considerable variation over large scales within these regions.

According to Mistri (2002), and Munari and Mistri (2008) change and inter-site differences in diversity cannot only be attribute to one single factor, but there are always combinations of local and regional factors varying in their degree of influence between scales and locations. Processes such as confinement, demographic unpredictability, biological interactions and habitat heterogeneity are some of the factors important on local scales (Munari and Mistri 2008). Confinement is dependent upon biotic and hydrodynamic determinants, which in turn directly determine changes in oxygen, temperature, grain size and organic contents of a habitat (Munari and Mistri 2008). The relative importance of certain local and regional aspects of an environment vary across the globe, depending on the varying types of complex habitats that species inhabit, making different diversities among localities within the same geographical regions possible and it may not be the same for all localities that have very similar environmental circumstances (Kiflawi et al. 2003, Cole and McQuaid 2010).

High variability in species richness and diversity is possible within small spatial scales and is a general occurrence within marine environments, making more extensive sampling important (Shin and Ellingsen 2004). Patchy distribution of species is a general feature in nature, as most habitat features are patchy in distribution on different scales and over time (Levin 1992, Ellingsen 2001). Macrobenthic communities generally have very patchy distributions and this is regularly determined by environmental factors like sediment grain size and sorting, depth, food sources and temperature (Rabalais 1990, Glover et al. 2002, Hewitt et al. 2005, Guzmán-Alvis et al. 2006). The number of species found within replicates from the KZN Bight midshelf macrofauna sampled varied greatly and ranged from 4 to 136. These values are similar to these of Ellingsen and Gray (2002) who found sample species richness were varied between 32 to 148 species. Species richness in the study by Shin and Ellingsen (2004) varied between 10 and 78

species per sample and alpha diversity from the macrobenthos of Italian transitional waters varied between 5 to 87 species per sample (Munari and Mistri 2008).

The high species diversity of the KZN Bight could be further enhanced by microhabitats generated by other species, which are able to provide good quality regenerated nutrient and further structural heterogeneity within an oligotrophic habitat (Karakassis and Eleftheriou 1997, Williams et al. 2010). This then promotes the creation of a mosaic of different assemblages formed according to the degree of complementarity between each species tolerances and abilities, and prevailing determining factors such as temperature, oxygen, depth, sediment characteristics, hydrodynamics (Nowell et al. 1981, Brown 1984, Hutchings 1998, Levin et al. 2000, Clarke et al. 2004). Because fauna differ in their degree of tolerance, adaptation and needs to confounding factors, this likely plays a more important role in determining spatial distribution and association within and between assemblages (Brown 1984).

The dissimilarity between sites could in part have been because of the distance between stations/transect focus areas sampled. Although Ellingsen (2001) found no correlation between species richness and distance between adjacent sites, it was found that significant differences and similarities between communities do not necessarily have to always be inversely related to the distance between adjacent sites. In our study of the KZN Bight, many macrobenthic communities in stations closely located were significantly different in various aspects of diversity, while there were stations with large distances between them and yet they were more similar than those closely located to each other. Similar result were found by Ellingsen (2001) on the Norwegian continental shelf, with their northern sites, that had large distances between them, had more similar communities than southern sites, that were much more closely located to each other, but had the most dissimilar communities according to ordination analysis.

3.4.3. SCALE AND THE GENERAL SHELF DIVERSITY TREND

3.4.3.1. Alpha Diversity

On the KZN Bight, spatial scale considered did have an effect on similarities (ANOSIM, hierarchical cluster analysis, pairwise comparisons) and dissimilarities between factors considered, however not all different tests corresponded. As ecological processes differ between scales, so will the patterns and variability of faunal assemblages also differ on local and regional scales across a region (Gray 2000). Whittaker (1960) stated that the richness and diversity of any region is dependent on the richness of the smaller areas within it and the turnover in species composition among them. In this present study faunal patterns did change with spatial scale, as

similarity of macrobenthic assemblages of large focus areas was higher than that of smaller scales, and according to the cluster analysis of the mean abundance (m^{-2}) per large focus area, TF and DF was grouped together, while RBF was separate from them. However, on the transect focus area scale the mean TF assemblage was more similar to RBF than to DF.

There was a constant pattern of decrease in diversity and abundance, along the KZN Bight midshelf from the South stations to the North stations. This was the consistent pattern observed among the scales of transect focus area to large focus areas as well. Although this pattern was present at station scale, it was less strongly apparent on larger scale. The stronger directional trend of species richness patterns along the KZN Bight at a station scale could have a variety of explanations, including the energy hypothesis by Wright (1983) and Levin et al. (2001). In this present study, alpha diversity, especially at the transect focus area and large focus area scale maintained a trend of decrease from the South of the KZN Bight towards the North region. Food supply may be the most important determinant on the KZN Bight on all scales due to the carrying capacity of an area, but it is the spatial and temporal heterogeneity of sediment environments that determine variability and differences in diversity and species richness between habitats (Glover et al. 2002, Gray 2002, Longhurst 2007). These sediment habitat heterogeneities are caused by a combination of biological activities, hydrodynamics and geomorphological attributes, each varying in importance within different scales (Snelgrove 1997, Hutchings 1998, Gray 2002, Hewitt et al. 2005, Longhurst 2007).

3.4.3.2. Beta Diversity

Numbers of shared species and complementarity (biotic distinctness) is not necessarily linked to distance between all stations (Ellingsen 2001). This agrees with the findings of this present study as adjacent station and transect focus areas exhibited different levels of shared species and complementarity. The Bray-Curtis similarity is spatially dependent and is a very sensitive measure of beta diversity between sites (Ellingsen 2001). Thus sites closest to each other should on mean have higher similarity than those further away. Multivariate measures of diversity, such as Bray-Curtis similarity, are much more sensitive to small changes in faunal composition than simple species richness or other diversity indices (Warwick and Clarke 1991, Ellingsen et al. 2005). Partially in contrast to what Ellingsen (2001) found, Bray-Curtis similarity between adjacent sites of the KZN Bight were more similar to each other in the sites south of the Thukela, than the adjacent sites north of the Thukela. However it could be said that similarity did decrease from a high between sites in the South to a low between sites in the North.

In the KZN Bight, there was a clear general gradient of increase in beta diversity between adjacent transect focus areas to large focus areas from a South to a North Bight direction, and this was accompanied by complementarity that followed the inverse pattern. Beta diversity studies have been utilised to determine faunal compositional change along an environmental gradient (Wilson and Shmida 1984, Ellingsen 2001). These diversity measures could indicate that there are a few, but very influential environmental gradients playing a large role in community composition of the KZN Bight in varying ways. This is because alpha diversity indices and beta diversity measurements have inverse relationships (Karakassis and Eleftheriou 1997, Ellingsen 2001). There also exist gradients in beta diversity between adjacent sampled areas on a latitudinal scale, for example, on the Norwegian continental shelf, beta diversity decreased between sites from a south to a northern direction (Ellingsen 2001). The distance between stations may not be the actual main contributing factor to the difference between stations of North and South Bight regions in KZN, but the potential change and variation in habitat may confound the interpretation of the distance effect (Harrison et al. 1992). Other studies have also found low similarity between pairwise sites that did not correlate with distance (Schlacher et al. 1998).

Here, beta diversity was a very strong component on a station and regional scale, but followed the opposite trend to alpha diversity. Thus the study areas south of the Thukela and that north of the Thukela are both highly diverse, albeit on different levels. This could be attributed to the difference in properties measured by alpha diversity indices and beta diversity. Diversity indices combine the attributes of species richness with evenness of a community and related to spatial scale, whilst beta diversity, based on ratios and differences, refers to the extent of change of species composition of communities among samples or along a gradient and is not related to scale (Whittaker 1975, Ellingsen 2001, Shin and Ellingsen 2004). Whittaker beta diversity was also found to contrast (be higher than) alpha and gamma diversity results on the subtropical Hong Kong continental shelf, as supported by Bray-Curtis similarity results (Shin and Ellingsen 2004).

Even with a much lower alpha diversity (species richness) than the larger sampled area of temperate Norwegian continental shelf, the subtropical Hong Kong shelf benthos had a higher beta diversity than exhibited by the former shelf (Ellingsen and Gray 2002, Shin and Ellingsen 2004). Shin and Ellingsen (2004) concluded that other hidden factors/gradients, other than habitat heterogeneity in terms of depth, sediment grain size and sorting and spatial scale could have played a role in this contrasting pattern between alpha and beta diversity trends along some subtropical continental shelves. Beta diversity measures can be used to test the degree of faunal

heterogeneity between sites when a unknown gradient is in play and when it is hard to compare environmental gradient between sites (Vellend 2001). Beta diversity is thus an important means to compare faunal heterogeneity and thus environmental heterogeneity between sites that would not have been necessarily noticed by conventional measures (Vellend 2001).

Beta diversity also changes with spatial scale and considering only a single scale is not enough to accurately understand the entire ecological aspects of biodiversity (Shin and Ellingsen 2004). Beta faunal diversity was high at all scales within the subtropical Hong Kong macrobenthic communities (Shin and Ellingsen 2004). Similar results were found by Munari and Mistri (2008) from the soft sediment macrobenthos of Italian transitional waters, Mediterranean Sea. In that study beta diversity increased with spatial scale and potential habitat heterogeneity (Munari and Mistri 2008). In the KZN Bight study, beta diversity was highest between stations and transect focus areas, but then decreased and was lowest between large focus areas.

The pattern of beta diversity found could have been a reflection of the different relative contributions of local and regional species contributions. According to Loreau (2000) local diversity determines regional diversity and that local diversity is in turn determined by habitat heterogeneity. The change in local diversity with habitat diversity increases beta diversity, which then increases regional diversity (Loreau 2000, Munari and Mistri 2008). Regional enrichment of local diversity is, however, to varying degrees increased from high to low latitudes (Willig et al. 2003, Munari and Mistri 2008). Thus beta diversity is not a measure of scale, but indirectly forms the intermediate median in the relationship dynamics between alpha and gamma diversity on varying scales (Cornell and Lawton 1992, Munari and Mistri 2008).

3.4.4. TAXONOMIC GROUP COMPOSITION

The top four most dominant phyla present in terms of abundance (m^{-2}), were Annelida Arthropoda, Cnidaria and Mollusca. This is a general phenomenon amongst many similar studies (Ansari et al. 2012, Martins et al. 2013a). Annelida and in particular Polychaetes, found on the continental shelf of Crete, made up a similar proportion of the total abundance to this present study (48% of macrobenthic abundance in Crete and 41% for the KZN Bight midshelf; Karakassis and Eleftheriou 1997).

Polychaeta, Mollusca and Crustacea comprised 98 % of individuals and species collected from the East Gippsland continental shelf, Australia (Coleman et al. 1997, Munari and Mistri 2008). Ellingsen (2001) found similar results as Polychaeta, Crustacea, Mollusca and Echinodermata

were the most abundant phyla found on the Norwegian continental shelf. In this present study common species were the most widely distributed and those that were less common had more restricted distributions, also agreeing with results found by Ellingsen (2001) on the Norwegian continental shelf. Only 10 % of species found were distributed across the entire sampling region of the Norwegian continental shelf. These widespread species were among the most common species found (Ellingsen 2001).

Whittaker's beta diversity (extent of change in species composition among sites) differed between dominant taxa, with Crustaceans having the highest mean turnover along the KZN Bight and Cnidaria the second highest mean turnover. The measure of beta diversity needs to be focused on different phyla, as beta diversity is not the same for all phyla and varies considerably as environmental factors would have different effects on different phyla (Harrison et al. 1992, Ellingsen 2001, Ellingsen et al. 2005). Mollusca in our study exhibited the lowest mean beta diversity among dominant phyla, but beta diversity was highest for Mollusca followed by Crustacea and Annelida (Polychaeta) in studies by Ellingsen (2001), Shin and Ellingsen (2004), Munari and Mistri (2008).

Such high beta diversity patterns seemed to be strongly associated with communities with many species that were highly restricted in distributions. However Harrison et al. (1992) found no correlation between beta diversity and species range, as they found that habitat heterogeneity and overall spread of species over a larger scale was more important, and that on a smaller scale the beta diversity was overwhelmed by results of alpha diversity. According to Gibbons et al. (2010), life cycle could be an important determinant in beta turnover rate between different taxa, and this can have important implications for the dispersal and diversity of assemblages over time and space.

3.5 CONCLUSION

The biodiversity of the macrobenthic community from all study sites along the KZN Bight midshelf was very high, changing along the length of the KZN Bight midshelf. The KZN Bight had a higher alpha diversity than some tropical eutrophic and subtropical oligotrophic continental shelves across the world. KZN Bight alpha diversity was equal to many tropical areas and temperate regions that were equal and even higher than some deep sea benthic diversities found. However the KZN Bight did not have as high species density and low species/abundance per species ratio as some of the most diverse tropical continental shelves. All

sites measured on different scales, had very high dissimilarities in composition, variability and alpha diversity on all different scales. No distinguishable pattern could be found on small scale along the Bight. Bight macrobenthic communities were constantly changing along the midshelf, forming clearly divided dissimilar patches of diverse macrobenthic communities. On all scales, even in the comparison of large focus areas, there remained high levels of dissimilarity, even though there was all together a decrease in dissimilarity from small to large scale. On large scale the Bight macrobenthic communities could essentially be divided into a South region including the Thukela study area, and the North region, stretching north from the Thukela River, as these environments seem to possibly provide complementary habitats for communities.

Between the North and South Bight, composition, species richness and evenness had different strengths of influence. There was a general decreased alpha diversity from the South towards the North Bight region. This acted as a complimentary measure to the inverse relationship of beta diversity observed as it increased from South to North between adjacent sites. Thus taxonomical diversity may be higher in macrobenthic communities located north of the Thukela River. The macrobenthic communities phyletic composition and each phylum's life history found in the different sections of the Bight, could have contributed to the inverse pattern of alpha and beta diversity found. This inverse trend of alpha and Whittaker's beta diversity will be further explored in chapter 5, using taxonomic distinctness as a measure of beta diversity to further assess, support and possibly confirm results found in chapter 3.

Most of the species found could only effectively be identified to family level and some are probably new to science. A similar study by Williams et al. (2010) on the south-east continental margin of Australia, found that 57% of the macrobenthic fauna found were possible new species. Although the KZN Bight had a highly abundant macrobenthic stock, there was no minority species dominance and evenness was very equal along the Bight. However Polychaeta and Amphipoda were the dominant taxa present. Diversity could have increased further if better and effective taxonomical identification of other major phyla such as Cnidaria, Nemertea and Sipuncula was possible. There is a lack of recent and complete taxonomic description of macrobenthic fauna within the Indo-Pacific and many scientists working in this field and area have had to rely on old monographs from other regions (Hutchings 1998, Kendall et al. 2000). Much more work is needed to understand what environmental factors (anthropogenic, biotic and abiotic) play a role in the formation of these community patterns and which combinations have the strongest influence. These environmental influences on diversity findings are investigated in

the next chapter concerning environmental factors that could play a role in the observed diversity patterns along the KZN Bight midshelf.

CHAPTER 4

MACROBENTHIC DIVERSITY AND THE PHYSICAL ENVIRONMENT OF THE KZN BIGHT MIDSHELF

4.1. INTRODUCTION

4.1.1 CONTINENTAL SHELF ENVIRONMENT

It has been suggested that because the continental shelf is a heterogeneous environment, macrobenthic fauna that live there have a more complicated environment to adapt to than those located in regions in the deeper part of the ocean (Gray et al. 1997, Levin et al. 2010). The reason for such heterogeneity is due to influences from environmental processes from a variety of sources elsewhere, and a mosaic of localised processes occurring on the surface and/or bottom and influencing the entire shelf community. These influences could be from a pelagic open ocean origin, shallow benthic, shallow pelagic or terrestrial origins. It is at continental shelves that all these forces work in concert creating an unique environment for community adaptations that sets each continental shelf ecosystem apart from the other (Graf 1992, Karakassis and Eleftheriou 1997, Mann and Lazier 2006, Quintana et al. 2010, Akoumianaki et al. 2012).

On the continental shelf horizontal and vertical water movement facilitates the spread of temperature, salinity, nutrients and oxygen across the shelf (Mann and Lazier 2006). Rivers have a significant spatial and temporal impact on the macrobenthic community composition of continental shelves (Akoumianaki et al. 2012). Freshwater run-off, in addition to temperature, salinity and oxygen, promotes the formation of a pycnocline that intensifies stratification that may negatively or positively affect production and sedimentation to the bottom (Mann and Lazier 2006). While tidal and wind driven currents are responsible for turbidity, they also mix nutrients through the entire water column from the surface to the bottom and back (Jenness and Duineveld 1985, Mann and Lazier 2006).

Every continental shelf is a different and unique habitat, from the distinct environmental influences associated with that habitat. For example, macrobenthic community diversity and structure was found to be significantly controlled by the seasonal discharge of the Paraiba do Sul River in Brazil (Zalmon et al. 2013) and likewise on the Indian continental shelf of the

Arabian Sea a unique suite of environmental influences the diversity of that macrobenthic community (Jayaraj et al. 2007). The Arabian Sea as a low latitude sea is landlocked in the north and thus has significant influences from the land, such as strong land-ocean thermal gradients with seasonal reversals causing the upper pelagic layers to exhibit different oceanographic characteristics each season (Bhattathiri et al. 1996, Jayaraj et al. 2007). The continental shelf of Crete in the eastern Mediterranean basin is a highly oligotrophic region and is a shelf not influenced by large rivers or major anthropogenic perturbations (Karakassis and Eleftheriou 1997). The south-west Australian continental margin is an environment where sedimentation does not play a strong influence, yet the complex geology and continental rifting contributes to its varying forms and it is the prevailing water masses and current characteristics together with the seabed that play a large role in the macrobenthic community structuring (Williams et al. 2010). The oligotrophic waters of the Seychelles relatively similar to the North KZN Bight, has high temperatures, salinities and sediment carbonate content and in spite of its oligotrophic nature has a relatively higher macrobenthic diversity (Mackie et al. 2005).

4.1.2 MACROBENTHIC BIODIVERSITY AND THE CONTINENTAL SHELF ENVIRONMENT

Interactions between the environment and macrobenthic biodiversity and the resulting effects on the rest of the ecosystem are of great importance. The shallow water fauna of the Indo-Pacific are characterised by high species diversity and broad geographical ranges of species (Taylor 1997). The Indo-Pacific shows a longitudinal gradient in marine species diversity (Mackie et al. 2005) and within this large bioregion, there are considerable environmental difference between the continental margins. The most defining and important variation found within this region is that of nutrient supply on local and regional scales (Taylor 1997). Nutrients apply important controlling powers on the distribution, structure and organisation of benthic communities (Vermeij 1987, Taylor 1997) . The open ocean of the Indo-Pacific is generally nutrient poor and nutrition is usually provided in localised locations from river and upwelling (Taylor 1997). There have been large differences found between the macrobenthic diversity on the continental margins in this region and according to (Birkeland 1987), many of the regional differences in macrobenthic species diversity are due to nutrient supply rate differences.

Many environmental elements are important for the continued existence of macrobenthic fauna and the distribution and relative importance of these elements are paralleled by the distribution of macrobenthos that are reliant on many different elements (Vizakat et al. 1991, Gooday et al. 2001, Iriarte et al. 2012, Zalmon et al. 2013). On the continental shelf, these elements are very

variable over space and time because of the relatively more unstable environmental conditions of these habitats on the continental shelf (Gooday et al. 1990). Coastal systems, including upwelling systems and estuarine systems, display large changes in hydrographical regimes on varying temporal scales, and these changes may lead to equally drastic changes in the distribution and composition of phytoplankton communities, and as a result possibly macrobenthic communities (Iriarte et al. 2012).

The temporal and spatial availability of nutrients have significant effects on the distribution and diversity of macrobenthic fauna, as has been highlighted by studies of the continental slope, and abyssal zones (Copeland 1970, Boesch 1972). Tropical continental margins are of particular interest because they receive most of the global river sediment inputs (Jennerjahn et al. 2010, Zalmon et al. 2013). Continental margins receive significant inputs from rivers as floodwater, macrophytic detritus, suspended organic matter and all sort of debris (Levin et al. 2010). Rivers are an important source of nutrient and sedimentation to continental shelf ecosystems, and are in return associated with high productivity and variability of communities inhabiting these areas (Darnaude et al. 2004, De Juan and Cartes 2011, Jurgensone and Aigars 2012). Due to the combined input of nutrients from rivers and upwelling cells, the shallow nature of the shelf and the general potential availability of necessary light penetration for phytoplankton growth, river-influenced continental shelves have been found to be generally more productive than the surrounding waters (Wollast 1998, Snelgrove 1999, Tang and Kristensen 2007, Quintana et al. 2010). Even though factors like salinity, temperature and oxygen are important factors for the completion of important osmotic and metabolic processes, these elements do not mean much unless nutrients are supplied

(Boesch 1972, Gooday et al. 1990, Karakassis and Eleftheriou 1997, Taylor 1997, Hagberg and Tunberg 2000, Akoumianaki et al. 2012). Due to the current regimes, topography, terrestrial influences and sediment characteristics across continental shelves, there is great variety in the distribution and the availability of nutrients.

According to Witman and Smith (2003) there have not been many published studies on the influence of upwelling on macrobenthic diversity. The value of upwelled nutrients to macrobenthos is also determined by their source, quality and quantity, as different macrobenthic fauna are adapted to different types of nutrient sources (Gooday et al. 1990, Cowie and Hedges 1994, Levin et al. 2001, Moore et al. 2004, Quintana et al. 2010). According to Gooday et al. (1990) and Quintana et al. (2010), quality and abundance of organic matter deposited on the

seabed is the primary factor regulating macrobenthic communities diversity. The impact of organic matter on macrobenthic community structure has been found to be more complex because the interactions between micro-, meio- and macrobenthic fauna are more complex (Quintana et al. 2010). Although organic matter supply is abundant in especially the near shore marine sediments, the relationship with macrobenthic fauna is more complex, and it is organic forms like labile phytodetritus that are preferentially consumed, while more refractory forms are accumulated and over time mineralized by microorganisms increasing nutrient potential for higher trophic levels (Jumars and Nowell 1984, Graf 1987, Mann 1988, Gooday et al. 1990, Fernanda et al. 1999). Varying species distribution and structure on continental shelves over space and time are due to the adaptation to an ever changing heterogeneous environment (Mistri et al. 2000, Guzman-Alvis et al. 2006).

Macrobenthic fauna have limited mobility and thus are forced to deal with and adapt to sedimentary environments that form many patchy microhabitats. These habitats are constantly modified temporally by other large scale and small scale influences and from adjacent environments changing the sediment-water boundary layer (Graf 1992). Macrobenthic fauna are such a diverse group and have such a diverse variety of strategies to utilise and take advantage of these prevailing and changing circumstances that they form mosaics of diverse communities mirroring the prevailing physical and biological interacting environmental circumstances of different regions on many scales (Dauvin et al. 1994). Polychaetes have been found to be the most common macrobenthic phylum found on shelf sediments, and are adapted through a wide variety of feeding strategies to utilise a wide range of forms of organic matter from different sources, as well as a great variety of reproductive strategies including sexual and asexual reproduction (Wilson 1991, Dauvin et al. 1994, Hutchings 1998).

The combined effect of different life history strategies and organic supplies is thought to reflect the different macrobenthic diversity patterns and community structures along a depth gradient (Flach and de Bruin 1999). Thus different groups of marine organisms are affected differently by different environmental processes (Snelgrove 1999, Jayaraj et al. 2007). The response of macrobenthic fauna to environmental gradients, including the direct response to organic matter inputs, is of high importance since macrobenthos play important roles in ecosystem processes such as the nutrient cycle and ultimately secondary production on continental shelves (Costello 1998, Snelgrove 1998, Van Hoey et al. 2004, De Juan and Cartes 2011, Sivadas et al. 2013). Many macrobenthic species are important bio-engineers that promote the survival, expanding

niches and diversity of other species and provide important ecological maintenance and structural heterogeneity of a habitat (Gray 1981, Rabaut et al. 2007).

Different phyla have different distributions on different scales (Williams et al. 2010), thus it is important to measure diversity from different spatial and temporal scales as different species and processes function on different scales (Jumars and Nowell 1984, Levin 1992, Williams et al. 2010). Williams et al. (2010) importantly found that the provincial scale of macrobenthic distribution was in alignment with the distribution of economically important marine fish from the western Australian continental shelf margin. This has important implications in terms of the management of diversity and economically important resources. According to Mann (1988) bottom feeding fish that are dependent upon the detritus food web, constitute 30 - 50% of commercially important species. Thus understanding the benthic environment and processes governing them is highly important for economical consideration too (Ayers and Scharler 2011).

Orders such as Cumacea have a close relationship with substrata and reflect changes in the bottom environment in addition to playing an important role as frequent food source for many fish species (Melake 1993, Fennessy and Groeneveld 1997, Fernanda et al. 1999). Before the greater ecological web of an ecosystem can be understood and conserved, the mechanisms maintaining and setting the foundations need to be understood. Snelgrove (1999) stated that for an understanding of how the patterns of individual species are maintained, the mechanisms were firstly important in order to describe and understand biodiversity patterns. Central to the understanding of evolutionary processes and ecological processes that influence the development and persistence of a community, is firstly the understanding and description of patterns, their causes and consequences Levin (1992).

The principal aim of this chapter was to provide a baseline understanding of the physical environmental factors characterising the different sections of the KZN Bight midshelf, and their possible effects on macrobenthic biodiversity.

We hypothesised that macrobenthic community biodiversity patterns of the KZN Bight midshelf were related to the main environmental parameters measured in the study. Also, that these environmental influences were scale-dependent, at the highest factor level of 'focus area'.

4.2. METHODS AND MATERIALS

The following environmental variables were measured in the study and used further within these analysis: depth (m), temperature (°C), salinity (PSU), dissolved oxygen (ml/l), % gravel, % very coarse sand (%vcs), % coarse sand (%cs), % medium sand (%ms), % fine sand (%fs), % very fine sand (%vfs), % mud, % sediment organic matter and sediment statistic parameters of mean grain size (mm) and sediment sorting (See Chapter 2 for more in depth explanation of sediment distribution characteristics – Section 2.4). Although nutrients of the shelf were important, it was not looked at them *per se*, but rather used total particulate organic content (TOC) as an indicator of bottom enrichment, given that we were looking at macrozoobenthos, with the theory that many more were theoretically deposit feeders.

The focus areas represented different nutrient inputs thus we addressed nutrients indirectly by factorising data according to focus area. Biological variables used in this present study were, abundance (m^{-2}), observed number of taxa, Margalef species richness (d), Shannon diversity index ($H\log_e$), Simpson diversity index (1-Lambda'), Hill's diversity number (N1), and Hill's diversity number (N2). Diversity measure of evenness, Pielou's evenness (J) was not included in this analysis as it was similar to the results of Simpson's diversity/dominance index. Further analyses were done only on abundance (m^{-2}), observed number of species and diversities of the four most dominant taxonomic groups found (based on abundance (m^{-2})). All less abundant phyla found were classified as "other".

All measured environmental characteristics were described for each station (for station numbers and locations refer to Chapter 2, Figure 2.1 and 2.2). Abundance (m^{-2}) and most environmental variables did not meet the assumption of normality according to the Shapiro-Wilk test. Exceptions were number of taxa (S), depth and sediment sorting. To address this, $\log(x+1)$ transformation was used on all abundance (m^{-2}) and environmental data. Environmental variables were in addition, normalised to account for different sampling units. Using a One-way design for Analysis of Variance testing (ANOVA), seasonal differences between environmental variables were tested. A Kruskal-Wallis test determined which stations showed a temporal difference in environmental variables. All tests were done with an alpha value of 0.05.

Principal Component Analysis (PCA) was used as an ordination method on transformed, normalised environmental data, to visually determine the associations and similarities between stations sampled and thus the environmental components that best describe each study site. A

minimum of three principle components were used. Comparisons between multidimensional scaling ordination (MDS) of macrobenthic communities and PCA were visually assessed. Hierarchical group average cluster analysis based on Euclidean distance was used on environmental variables of stations. Biological clusters were based on Bray-Curtis similarity measures and identified by the group average cluster method. Analysis of similarity (ANOSIM) determined the degree of dissimilarity and/or similarity between environmental parameters of stations, transect focus areas and large focus areas (See model design in Chapter 2, Figure 2.2), as well as grouped environmental clusters identified by group average cluster analysis.

Multivariate correlation and similarity analyses were used to determine if environmental variables were related to macrobenthic community attributes. Draftsman plots were used to identify any collinearity between environmental variables. Variables used for further analysis were thus reduced to include only non-collinear variables. Spearman rank correlation analysis was used to test for the associations between biological characteristics (whole community and separate phylum group community abundance and diversity) and environmental variables and amongst environmental variables themselves. Pearson product moment correlation was applied between Whittaker's beta diversity and % complementarity (Refer to Chapter 3) and environmental variables from adjacent pairs of stations along the KZN Bight midshelf study area. A regression trend line was applied to beta diversity found across the KZN Bight midshelf between adjacent stations; transect focus areas and large focus area, to determine the degree of increase along the KZN Bight.

CONPLOT analysis found in the statistical software program Primer version 6 (Clarke and Warwick 2001) was used to visually assess differences between environmental characteristic of stations and to determine which environmental variables of biological communities were associated with designated stations.

Using a weighted Spearman rank correlation in the RELATE program of the PRIMER v6 package (Clarke and Warwick 2001), a resemblance matrix based on Bray-Curtis similarity measures of biological data and a resemblance matrix based on Euclidean distance of environmental data were combined to relate the degree of association between macrobenthic communities and the environment. The same correlation method was used again in the biological/environmental 'matching' program BIOENV, on transformed, normalised environmental data and $\log(x+1)$ transformed abundance (m^{-2}) data using a Bray-Curtis similarity matrix, and untransformed diversity data using the Bray-Curtis similarity index, from

which the combination of variables best explaining the complexities of the macrobenthic communities overall and amongst phylum groups were identified overall, at all different scales and locations of measurement.

Quadratic non-linear regression on ranks was applied to significantly correlated variables to determine the degree of the relationship between them. Regression graphs were created to determine how much biotic variation every individual significant BIOENV-identified environmental variable described for each of the community indices.

Assessments of the change in biological properties with environmental properties along biologically identified station clusters were attempted using basic plots of line and column charts. All analyses were done with the aid of Microsoft Excel 2010, Minitab 16, Sigmaplot 11, EstimateSWin752 (Cowell 2006) and PRIMER package version 6 (Clarke and Gorley 2006).

4.3. RESULTS

4.3.1 PHYSICAL ENVIRONMENT

The KZN Bight midshelf study area had a mean depth of 63 m, ranging between 41 m and 84 m (Table 4.1). Mean water temperature was 19°C, and reached a maximum of 22°C and a minimum of 17°C. The physical environment of the KZN Bight midshelf sediment was dominated by a mean percentage of 29% fine sand, 24% medium sand, 15% coarse sand and 12% mud content. In comparison, there was a low mean percentage of very coarse sand, gravel and very fine sand. Overall sediments were moderately sorted (σ^{\dagger} 0.988), and positively coarse-skewed (sk^{\dagger} 0.200) (Anderson 2013). In comparison to the USEPA (United States Environmental Protection Agency) standard value measurements of temperature and DO, the KZN Bight midshelf had a very low maximum dissolved oxygen concentration (4.57 ml/l at 22°C, compared to 8.72 ml/l at 22°C) (Agency USEP 2012). Salinity across the Bight was very constant throughout and fitted within the range of mean ocean salinity (33 - 37 PSU) (Team 2010). Organic matter was low at a mean percentage of 0.751, but showed large variation between locations (SD 0.839, range 4.988).

Table 4.1: Physical environment characteristics of the KZN Bight midshelf, % very coarse sand (% vcs), % coarse sand (% cs), % medium sand (% ms), % fine sand (% fs), % very fine sand (% vfs).

Environmental variable	Mean	SD	Range	Max	Min
Depth (m)	62.8	10.8	43.0	84.0	41.0
Temperature [°C]	19.407	1.841	5.634	22.190	16.557
Salinity [PSU]	35.408	0.042	0.155	35.449	35.294
Dissolved Oxygen [ml/l]	3.961	0.358	1.073	4.570	3.497
%Gravel	5.110	7.410	30.442	30.442	0.000
%vcs	9.303	10.847	34.121	34.121	0.000
%cs	15.371	13.323	39.056	39.148	0.092
%ms	24.022	16.084	54.128	55.420	1.292
%fs	28.695	28.896	80.745	84.009	3.264
%vfs	5.291	6.013	21.286	21.286	0.000
%mud	12.208	19.124	69.326	70.021	0.695
Mean(phi)	1.710	1.177	4.052	4.013	-0.039
Mean(mm)	0.405	0.273	0.965	1.027	0.062
Median(phi)	1.744	1.199	4.308	4.286	-0.023
Median(mm)	0.395	0.265	0.964	1.016	0.051
Sorting	0.988	0.370	1.312	1.667	0.355
Skewness	0.200	2.734	12.978	7.905	-5.074
%Organics	0.751	0.839	4.988	5.006	0.018

The three main focus areas around identified oceanographic features, determined by the ACEP program and around which this entire study was built, did have very distinct environmental and biological properties. Stations A, B, F and I represent the locations where there were substantial contrasts to the adjacent stations, which divided the KZN Bight midshelf environmentally. Station clusters A, B, F and I represented stations that had the most extreme amount of fine sand, organic content, mud and sediments having a higher degree of sorting.

ANOSIM analysis indicates that there was no overall significant difference in environmental variables between trips ($P > 0.05$). However, a simple sign rank test confirmed that there was a significant difference in salinity and measured dissolved oxygen between trips. Using ANOVA on ranks, no significant difference was found between variables at sampled stations from the two trips, however, on transect focus area scale, salinity differed significantly between trips within RT ($P < 0.05$) and dissolved oxygen within DT ($P < 0.05$) and TT ($P < 0.05$). On the scale of large focus areas there was a significant difference in salinity between trips within RBF ($P < 0.01$) and of dissolved oxygen within DF ($P < 0.01$) and TF ($P < 0.01$). Thus on a small spatial scale, environmental variables seemed to have been more stable over time than within

PC 1, PC 2 and PC 3 combined explained 80% of the variance found within environmental variables characterising stations (Table. 4.2). PC1 indicates the high importance of sediments for distinguishing habitats, and PC2 the importance of depth and temperature (Fig. 4.2). The top three eigenvalues suggests that PC1 represents median grain size (positive value), proportion of very fine sand (negative value), and proportions of coarse sand (positive value) together explained the highest variance (48%), while for PC2 the three highest eigenvalues were represented by depth (positive value), temperature (negative value) and salinity (positive value). The top PC3 eigenvalues represented the proportion of organic matter (negative value), proportion of fine sand (positive value) and proportion of mud (negative value) as the variables explaining the highest variance. Principal Component scores confirmed many of the previously mentioned physical habitat results. According to top PC scores, stations C, F and I were most affected by the environmental variables represented by PC1. Station I was also significantly affected by variables represented by PC2 (Fig. 4.2). Stations A and F were most affected by variables represented by PC3.

There was a clear division of stations into two main groups, with stations A, B, F and I located to the left of the PCA ordination plot and stations C, D, E, G and H located to the right of the PCA plot (Fig. 4.2). Stations C, D, G and H especially lay outside the circle of explained variance (Fig. 4.2) and thus were highly different from all other stations, indicating that the source of their variance may have been caused by some other unmeasured factor.

Table 4.2: Variance explained by principle components identified by Principle Component Analysis of environmental data.

PC	% Variance explained	% Cum. variance explained
1	48.2	48.2
2	17.2	65.4
3	14.7	80.1

reflection of biological similarity and dissimilarities found, as macrobenthic community similarities could be associated with most environmental similarities. However, the habitat variables of all stations do not successfully explain the full extent of the biological community's differences and relatedness across the KZN Bight midshelf. It was clear that most stations represented very different habitats and likewise all stations represented very different macrobenthic communities. There were different environmental and biological dynamics at work. Thus indicating that there were different macrobenthic communities established in similar habitats and that other influential unmeasured variables may have played an important role in determining the differences. From this it could have been inferred that different small-scale environmental differences play a larger role in determining the structure of communities. Even though environmental variables clearly had an important role to play, biological interactions within communities and unmeasured variables could play an additionally important role in shaping the macrobenthic communities.

Environmentally and biologically, sites in close proximity were not necessarily the most similar to each other, similarly transect focus areas RT and RBF differed biologically with an R^2 of 0.784 ($P < 0.05$) and environmentally with an R^2 of 1 ($P < 0.05$). Furthermore sites further from each other were not necessarily more dissimilar, nor for example, were transect focus areas DF and TT with a biological R^2 of 0.375 ($P < 0.05$) and an environmental R^2 of 0.138 ($P < 0.05$). This implied significant changes in habitat over short distances across the Bight. The distance between sites could not have played a significant role in causing similarities or dissimilarities between communities as ANOSIM results had very high R -values between all sites, whether close or far from each other, and many stations far from each other had higher biological and environmental similarity than those closely located.

In spite of the lack of distinctness in habitat at these large scales, biologically there was still higher significant differences between communities within small and large scales, than environmentally on similar scales. Overall macrobenthic KZN Bight midshelf community abundance (m^{-2}) was significantly related to environmental variables measured (Rho 0.355, $P < 0.05$) and overall variability in abundance (m^{-2}) was best explained by measured environmental variables, while variation in diversity was explained to a much lesser extent (Table. 4.3). Sediment characteristics seemed to have been the dominating factor controlling community abundances (m^{-2}) and diversity across the entire study area on the KZN Bight. Single linear regression based on ranks of variables indicates that the environmental variables who overall,

explained the highest amount of variance within the whole macrobenthic community diversity, was temperature, followed by coarse sediments (tables not included).

A combination of five environmental variables, namely temperature, salinity, organic matter, % fine sand and % very fine sand effectively explained 40 % of variability in whole macrobenthic community abundance (m^{-2}) (Table. 4.3). These combinations of variables explained the highest amount of variance in abundance, while any other combinations of variables could only explain similar levels of variability, having had significant R^2 values ranging between 0.397 - 0.401. Even though the Bight had a low value of organic matter available, this variable could have been very important as within an oligotrophic environment all sources of possible nutrition are important (Darnaude et al. 2004). The amount of variability explaining diversity was, always much lower than that explaining abundances (Table. 4.3). Skewness, depth, temperature, salinity, mud and organic matter were the only environmental variables that seemed to explain diversity in the macrobenthic communities. Whole community diversity was significantly best explained by sediment skewness (degree of asymmetry), which was also related to the sediment grain size and sorting. Much of the variance in individual diversity indices (observed number of species, species richness and Simpson's diversity) were significantly explained by skewness (Table. 4.3).

Table 4.3: BIOENV and quadratic regression results for macrobenthic community's abundances and diversities association with measured environmental variables. Variables in bold significantly explained a proportion of variation. (*) no variables, (ns) not significant.

Biological Groups	Global R and R-sqr	P	Variables	Individual dependent variables (R-sqr; P-value)
Abundance				
Macrobenthic community	0.40	<0.05	Temperature [°C] Salinity [PSU] % Organic matter %fs %vfs	N (0.17; <0.01) N (0.30; <0.001) N (0.36; <0.001)
Annelida	0.43	<0.05	Temperature [°C] Salinity [PSU] %fs %vfs Skewness	N (0.34; <0.001) N (0.32; <0.001) N (0.24; <0.01) N (0.35; <0.001)
Arthropoda	0.46	<0.05	Depth (m) Temperature [°C] %vfs %mud Skewness	N (0.27; <0.001) N (0.11; <0.05) N (0.33; <0.001)
Cnidaria	0.44	<0.05	Depth Temperature [°C] Salinity [PSU] % Organics matter % Mud	N (0.26; <0.001)
Mollusca	0.27	<0.05	Temperature [°C] %ms %vfs Skewness	N (0.13; <0.05) N (0.25; <0.001) N (0.30; <0.001)
Other	0.19	<0.05	Dissolved Oxygen [ml/l] %ms %vfs Skewness % Organic matter	N (0.21; <0.01) N (0.31; <0.001) N (0.23; <0.01) N (0.15; <0.05)
Diversity				
Macrobenthic community	0.15	<0.05	Skewness	S (0.36; <0.001); d (0.18; <0.01); 1-Lambda' (0.18; <0.01)
Annelida	0.21	<0.05	Temperature [°C] Salinity [PSU] % mud Skewness	S (0.34; <0.001); d (0.32; <0.001); Hloge (0.28; <0.001); 1-Lambda' (0.19; <0.01); N1 (0.28; <0.001); N2 (0.21; <0.01) S (0.35; <0.001); d (0.35; <0.001); Hloge (0.33; <0.001); 1-Lambda' (0.28; <0.001); N1 (0.33; <0.001); N2 (0.29; <0.001) d (0.12; <0.05); Hloge (0.19; <0.01); 1-Lambda' (0.23; <0.01); N1 (0.19; <0.01); N2 (0.24; <0.01) S (0.32; <0.001); d (0.31; <0.001); Hloge (0.28; <0.001); 1-Lambda' (0.16; <0.05); N1 (0.28; <0.001); N2 (0.18; <0.01)
Arthropoda	ns	ns	ns	
Cnidaria	0.23	<0.05	Depth (m) Salinity [PSU] %fs	S(0.13; <0.05) S (0.14; <0.05); d (0.13; <0.05); Hloge (0.12; <0.05); 1-Lambda' (0.12; <0.05); N1 (0.12; <0.05); N2 (0.14; <0.05)
Mollusca	ns	ns	ns	
Other	0.13	<0.05	Skewness % Organic matter	S (0.20; <0.01); d (0.14; <0.05); Hloge (0.13; <0.05); N1 (0.13; <0.05) S (0.19; <0.01); d (0.21; <0.01); Hloge (0.19; <0.01); 1-Lambda' (0.16; <0.05); N1 (0.19; <0.01); N2 (0.16; <0.05)

Averages of community diversity attributes per site, at scales of stations, transect focus areas and large focus areas, were not as a whole, significantly related to mean environmental variables values at certain scales of measurement. However, of the scales used, stations were the only scale at which any mean environmental variable significantly explained mean whole community and phyla abundance (Table.4.4).

Some environmental variables best explained community attributes only within specific locations (eg. Station E, transect areas DT and TT). Thus community variability was not so much effectively explained by environmental variables based on different scales, but was rather dependent on location, which decreased the importance of scale (Table. 4.4).

All the environmental variables measured played varying significant roles on large scales within different locations in shaping the macrobenthic community. Within individual sites, on scales larger than station, measured environmental variables could explain more community variability (abundance and diversity) than those within individual stations. Thus there was an intricate relationship between environmental variables functioning on certain scale of study and location within the Bight, determining biological attributes of the macrobenthic communities. The environmental variables used in this present study were more successful in explaining variability of macrobenthic communities on a larger scale, while within small scales (individual stations) that contained the most biological variation, these variables were unsuccessful and other factors could be in play. However on small scale, variability that was explained was much higher than an individual site on a larger scale (Table. 4.4).

Table 4.4: BIOENV and quadratic regression results of the association between environmental variables and biological abundance and diversity in individual study sites on stations, transect focus area and large focus area scale. Variables in bold individually significantly explain variability. (*) no variables, (ns) not significant. (For factors refer to Chapter 2, Figure 2.2)

Stations							
Site	Abundance			Diversity			
	Rho	Variables	Individual dependent variable (R-sqr; P-value)	Rho	Variables	Individual dependent variable (R-sqr; P-value)	
Station E	ns	*		0.97	Dissolved Oxygen % coarse sand Skewness % Organic matter	S(0.91;<0.05) Hloge(0.95;<0.01); 1-Lambda'(0.95;<0.05); N1(0.95;<0.01); N2(0.98;<0.01)	
All other stations	ns	*		*	*		
Transect Focus areas							
	Abundance			Diversity			
	Rho	Variables	Individual dependent variable (R-sqr; P-value)	Rho	Variables	Individual dependent variable (R-sqr; P-value)	
DF	ns	*		ns	*		
DT	0.80	Temperature [°C] Dissolved Oxygen [ml/l] %fs %vfs mean (mm)		ns	*		
TT	0.65	Temperature [°C] Salinity [PSU] Dissolved Oxygen [ml/l] mean (mm) Sorting	N (0.51; <0.05)	ns	*		
TF	ns	*		ns	*		
RT	ns	*		ns	*		
RBF	ns	*		ns	*		
Large Focus Areas							
	Abundance			Diversity			
	Rho	Variables	Individual dependent variable (R-sqr; P-value)	Rho	Variables	Individual dependent variable (R-sqr; P-value)	
DF	0.60	Depth (m) Temperature [°C] % fs mean (mm)		ns	*		
TF	0.63	Depth (m) Temperature [°C] %ms %vfs % Organic matter	N (0.37; <0.05) N (0.50; <0.01) N (0.52; <0.01) N (0.57; <0.01)	0.54	Salinity [PSU] % cs	S (0.44; <0.05); d (0.45; <0.05); Hloge (0.39; <0.05); N1 (0.39; <0.05) S (0.58; <0.01); d (0.59; <0.01); Hloge (0.48; <0.01); N1 (0.48; <0.01); N2 (0.34; <0.05)	
RBF	0.67	%cs mean (mm)	N (0.58; <0.01) N (0.62; <0.001)	0.60	Depth (m) Temperature [°C] Dissolved Oxygen [ml/l] %cs %vfs	S (0.57; <0.01); d (0.44; <0.05); Hloge (0.40; <0.05); 1-Lambda' (0.49; <0.01); N1 (0.40; <0.05); N2 (0.49; <0.01); Hloge (0.37; <0.05), N1 (0.37; <0.05); N2 (0.34; <0.05) S (0.45; <0.05); d (0.36; <0.05); Hloge (0.34; <0.05); 1-Lambda' (0.45; <0.05); N1 (0.34; <0.05); N2 (0.45; <0.05) S (0.61; <0.01); d (0.53; <0.01); 1-Lambda' (0.46; <0.05); N2 (0.46; <0.05)	

South Bight (Rho 0.448, $P < 0.05$, stations A to E) and North Bight (Rho 0.571, $P < 0.05$, stations F to I) macrobenthic communities were significantly related to environmental variables measured within these separate locations (Table. 4.5). Within the South Bight stations, abundance (m^{-2}) was significantly explained (Rho 0.54, $P < 0.05$) by depth, temperature, % coarse sand, % medium sand and % very fine sand, while none of the diversity within this region could be explained by environmental variables. In the North Bight, abundance (m^{-2}) was significantly (Rho 0.64, $P < 0.05$) explained by % fine sand, % mud, mean grain size and skewness. Macrobenthic community abundances (m^{-2}) within these two regions were maintained by very different environmental variable combinations. The North region was more dependent on sediment characteristics, particularly fine, and the South region on a combination of coarse and fine sediment characteristics as well as water column characteristics. Community diversity was not significantly explained for the South Bight region, although for the North Bight region, depth explained 55 % of variability. This was of particular interest as Whittaker's beta diversity was very strongly negatively correlated with depth.

Table 4.5: BIOENV and quadratic regression results of the association between environmental variables and biological abundance and diversity in stations A to E (South Bight) and stations F-I (North Bight). Variables in bold individually significantly explain variability. (*) no variables, (ns) not significant. (For factors refer to Chapter 2, Figure 2.2)

Macrobenthic communities	Global R/R-sqr	Variables	Individual dependent variables (R-sqr; P-value)
Community Abundance			
From stations A to E	0.54	Depth (m) Temperature [°C] %cs %ms %vfs	
From stations F to I	0.64	%fs %mud Mean (mm) Skewness	N (0.33; <0.05) N (0.40; <0.01) N (0.42; <0.01)
Community Diversity			
From stations A to E	ns	*	
From stations F to I	0.55	Depth	S (0.52; <0.001); d (0.39; <0.01); 1-Lambda* (0.43; <0.01); N2 (0.41; <0.01)

Different combinations of environmental variables explaining abundance (m^{-2}) and diversity were found to be important at different locations and scales.

Whole community diversity changed with the important environmental variables identified by BIOENV analysis, and it was clear that all diversity variables of the entire KZN Bight midshelf macrobenthic community were influenced similarly by sediment skewness. The quadratic regression line indicates that within the whole macrobenthic community, with a decrease in skewness, there was a general decrease in diversity (observed number of species, species richness, Shannon diversity, Simpson diversity, Hill's N1 and Hill's N2 diversity). This was not a linear relationship and there was an initial slight increase in diversity with the decrease in skewness, then a faster decrease in diversity with a further decrease in skewness.

Certain separate phylum groups were slightly more effectively explained by combinations of measured environmental variables within certain locations. A higher amount of variation within abundance (m^{-2}) and diversity could be explained for some individual phyla than from the combined community as a whole within certain locations. Within large focus areas, abundance (m^{-2}) of individual phylum groups was more effectively explained by measured environmental variables than was diversity (Table. 4.6). Overall abundance (m^{-2}) and diversity were explained within all scales and within certain locations along the KZN Bight by measured environmental variables. Annelida was the phylum group whose variance was most regularly explained and for which the highest proportion of variance could be explained. None of Annelida diversity was explained within transect focus areas, but Cnidaria diversity in transect TF and RT areas was explained. The lowest proportion of abundance (m^{-2}) and diversity was overall explained for other phyla groups.

Table 4.6: BIOENV results of the association between environmental variables and biological abundance and diversity of separate phylum communities located within individual study sites on stations, transect focus area and large focus area scale. (*) no variables, (ns) not significant. (For factors refer to Chapter 2, Figure 2)

Stations							
Abundance				Diversity			
Site	Phyla	Rho	Variables	Site	Phyla	Rho	Variables
All	All	ns	*	Station E	Annelida	0.92	Temperature [°C] % medium sand Sorting Skewness
Transect Focus areas							
Abundance				Diversity			
DF	All	ns	*	DF	All	ns	*
DT	Annelida	0.82	Temperature [°C] Dissolved Oxygen [ml/l] % fine sand Mean grain size (mm)	DT	Annelida	ns	*
	Arthropoda	0.70	Depth (m) Dissolved Oxygen [ml/l]		Arthropoda	ns	*
	Cnidaria	ns	*		Cnidaria	0.54	Temperature [°C] Dissolved Oxygen [ml/l] Skewness
	Mollusca	0.68	Temperature [°C] % fine sand		Mollusca	ns	*
	Other phyla	0.59	Temperature [°C] % very fine sand		Other phyla	ns	*
TT	Annelida	0.63	Temperature [°C] Salinity [PSU] % coarse sand % fine sand Skewness	TT	All	ns	*
TF	All	ns	*	TF	All	ns	*
RT	All	ns	*	RT	Cnidaria	0.70	% coarse sand % medium sand Mean grain size (mm) Sorting % Organic matter
RBF	All	ns	*	RBF	All	ns	*
Large Focus Areas							
Abundance				Diversity			
DF	Annelida	0.59	Depth (m) Temperature [°C] % medium sand % fine sand Mean grain size (mm)	DF	All	ns	*
	Arthropoda	0.54	Dissolved Oxygen [ml/l]				
	Cnidaria	0.51	Temperature [°C]				
	Mollusca	0.50	Temperature [°C] % fine sand % very fine sand Sorting Skewness				
	Other phyla	ns	*				
TF	Annelida	0.63	Depth (m) Temperature [°C] Salinity [PSU] % very fine sand Mean grain size (mm)	TF	Annelida	0.58	Salinity [PSU] % coarse sand % fine sand
	Arthropoda	0.55	Depth (m) Temperature [°C] % medium sand % very fine sand		Arthropoda	ns	*
	Cnidaria	ns	*		Cnidaria	ns	*
	Mollusca	0.50	% medium sand % very fine sand		Mollusca	ns	*
	Other phyla	0.31	Depth (m) Temperature [°C] % mud Sorting % Organic matter		Other phyla	ns	*
RBF	Annelida	0.57	% coarse sand Mean grain size (mm)	RBF	Annelida	ns	*
	Arthropoda	0.60	% fine sand Skewness % Organic matter		Arthropoda	0.57	Depth (m) Temperature [°C] Dissolved Oxygen [ml/l] % coarse sand % very fine sand
	Cnidaria	0.60	Depth (m) Temperature [°C] % coarse sand Mean grain size (mm) % Organic matter		Cnidaria	0.77	Depth (m) % very fine sand % mud Skewness % Organic matter
	Mollusca	ns	*		Mollusca	0.49	Depth (m) % Organic matter
	Other phyla	0.34	Temperature [°C] Salinity [PSU] Mean grain size (mm)		Other phyla	ns	*

Depth and temperature seemed to play an important role in explaining abundance (m^{-2}) over all the phyla groups. For Annelida and Arthropoda, additional sediment variables like % coarse sand, % medium sand, % very fine sand, and % fine sand played a further important role.

In the North Bight, mean grain size played a role in determining abundance (m^{-2}) in all phyla groups, while skewness was also a prominent environmental factor for all phyla, except Cnidaria. Here Annelida variance in abundance (m^{-2}) was not the most effectively explained among the phyla groups found, such as in the South region. A much higher proportion of the other phyla group variance of abundance (m^{-2}) was explained within the North Bight, while 36% of abundance variance of Mollusca was explained here as well (Table. 4.7).

Diversity of phyla groups was not significantly explained by any measured environmental variables of the South Bight, however, in the North Bight the variance in diversity was best explained for Cnidaria (R^2 : 0.61, $P < 0.05$), followed by Arthropoda (R^2 : 0.44, $P < 0.05$) and Mollusca (R^2 : 0.4, $P < 0.05$) (Table. 4.12). Variation in diversity explained was lowest for Annelida (R^2 : 0.27, $P < 0.05$) within the North Bight and none of the other phyla groups diversity could be explained by measured environmental variables from this region (Table. 4.7).

Table 4.7: BIOENV results of the association between environmental variables and biological abundance and diversity of separate phylum communities located within North and South Bight regions. (*) no variables, (ns) not significant. (South Bight from stations A to E; North Bight from stations F to I). (For factors refer to Chapter 2, Figure 2.2)

Macrobenthic communities	Phyla	Global R/R-sqr	Variables
Abundance			
From stations A to E	Annelida	0.52	Depth (m) Temperature [°C] % medium sand % fine sand % very fine sand
	Arthropoda	0.43	Depth (m) Temperature [°C] Salinity [PSU] % coarse sand % very fine sand
	Cnidaria	0.42	Depth (m) Temperature [°C]
	Mollusca	ns	*
	Other phyla	0.26	Depth (m) Temperature [°C]
From stations F to I	Annelida	0.5	Depth (m) Temperature [°C] % fine sand Mean grain size (mm) Skewness
	Arthropoda	0.62	% medium sand % fine sand % mud Mean grain size (mm) Skewness
	Cnidaria	0.53	Temperature [°C] Mean grain size (mm) % Organic matter
	Mollusca	0.36	% mud Skewness
	Other phyla	0.43	Temperature [°C] Mean grain size (mm) Skewness % Organic matter
Diversity			
From stations A to E	All	ns	*
From stations F to I	Annelida	0.27	Depth (m) Temperature [°C] % very fine sand % mud
	Arthropoda	0.44	Depth (m) % mud % Organic matter
	Cnidaria	0.61	Depth (m) Skewness
	Mollusca	0.41	% coarse sand
	Other phyla	ns	*

CONPLOT from the PRIMER v6 package was used to overlay the most important environmental variables identified by the BIOENV analysis, to determine with what type of habitats the communities in each station were associated with (Fig. 4.3 and 4.4).

Stations such as A, B, C, D and E macrobenthic communities that had the highest abundances (m^{-2}), species richness, Shannon diversity, Simpson diversity, and Hill's N1 and N2 diversity, were associated with lower temperatures, high relative salinity, and low percentages of organic matter, fine sand and very fine sand in sediment, except for stations A and B, that were among the stations with the higher levels of organic matter, fine sand and very fine sand (Fig. 4.3 and 4.4). Communities from G and H were among those that had low abundance (m^{-2}) and species richness, though high Shannon and Simpson diversity and relatively high Hill's N1 and N2 diversities, were associated with relatively high temperatures and salinities, and a low percentages of organic matter, fine sand and very fine sand in sediments.

Station F that had the lowest abundances (m^{-2}), species richness, high Shannon and Simpson diversity, and low Hill's N1 and N2 diversity, was associated with high temperatures, salinities, high levels of fine sand and the highest levels of organic matter and very fine sand. Station I macrobenthic communities had high abundance (m^{-2}), Shannon and Simpson diversity, and were similar in species richness to stations G and H, while having had low Hill's N1 and N2 diversities. Station I was associated with high temperatures, low salinities, similarly high organic matter levels, fine sand and very fine sand levels in sediment as stations A and B. Stations A, B and I had higher levels of fine sand than any of the other stations. Most community variability seemed to derive from sediment properties (Fig. 4.4).

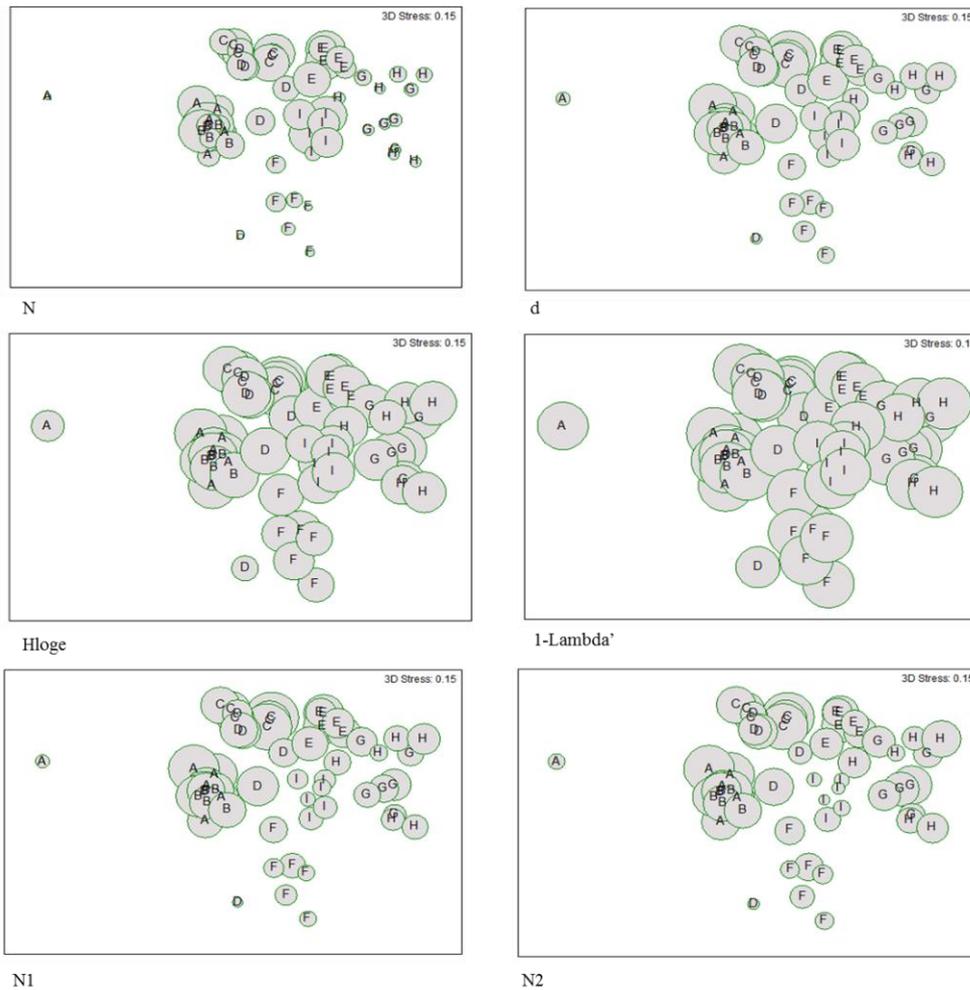


Figure 4.3: CONPLOT results of whole macrobenthic community diversity values from stations along the KZN Bight midshelf. (Definition of diversity symbols found in Chapter 3, Section 3.2.2.2)

As was seen before, temperature and salinity stayed at a fairly constant level throughout the length of the KZN Bight. Communities in stations F and I were associated with the highest temperatures and station A, B, C and E were occupied by communities associated with lowest temperatures measured (Fig. 4.4). Communities in station I were associated with the lowest measured salinity and communities in stations A, B, C, D, E, F, G and H, the highest salinities. The most variability seemed to have linked to sediment properties. Macrobenthic communities in stations A, B, F and I were associated with high proportions of very fine sand and fine sand, with station F having the lowest amount of fine sand out of the three stations.

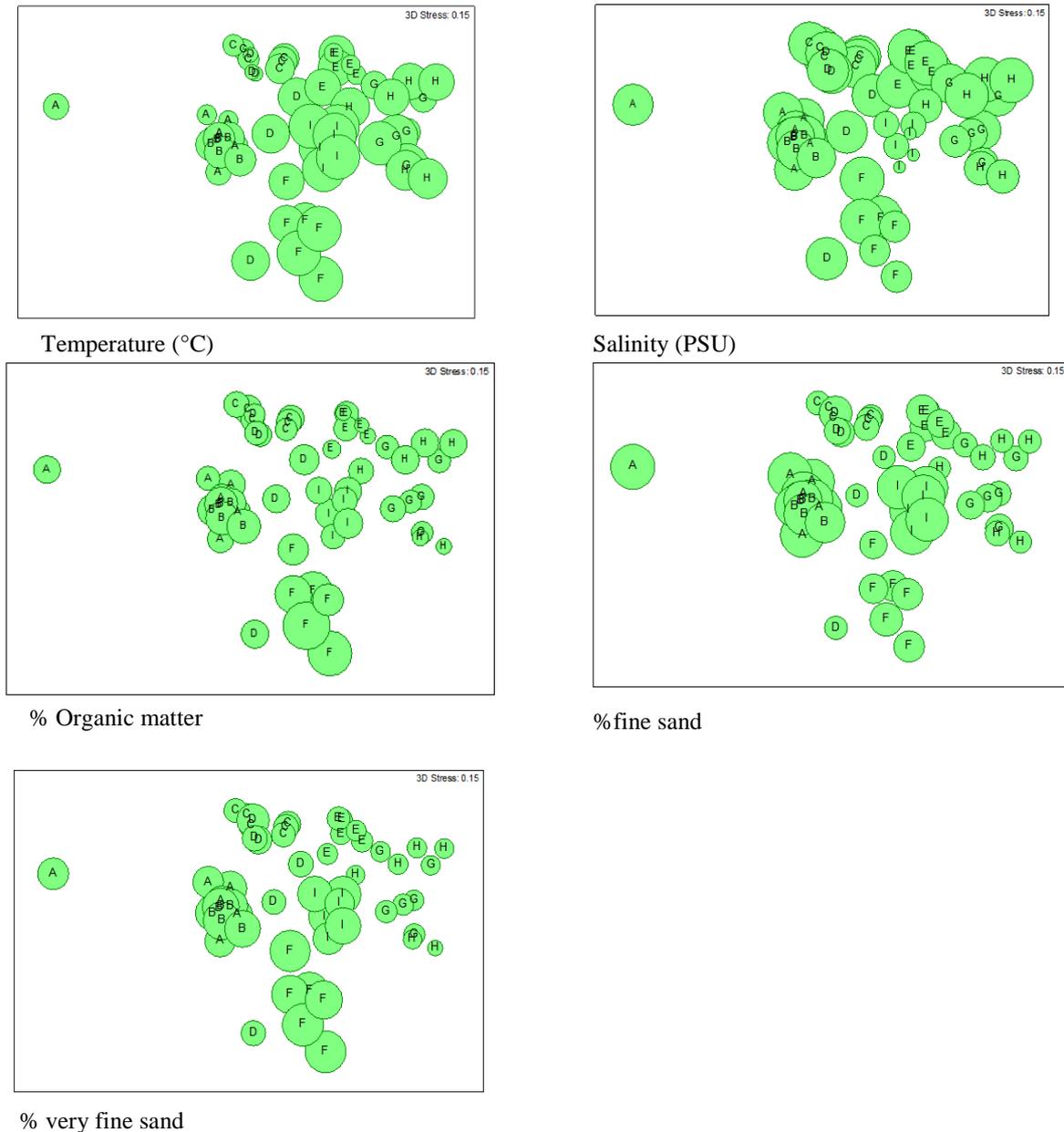


Figure 4.4: CONPLOT results for BIO-ENV important identified environmental variable values that macrobenthic community’s abundance were associated with from stations along the KZN Bight midshelf.

The community distributions in terms of sediment skewness, as the main environmental variable affecting diversity of the community, indicates that macrobenthic communities within stations A, B, C, D, E and I were associated with environments of coarse positively skewed sediments and communities in stations F, G and H were associated with environments of fine negatively skewed sediment (Fig. 4.5, refer to Boggs 1995 for the definitions of negative and positively skewed). Proportion of coarse sand within sediments seemed to have been important in terms of

the diversity of the macrobenthic community, and this could have been linked to the degree of sorting of the sediment.

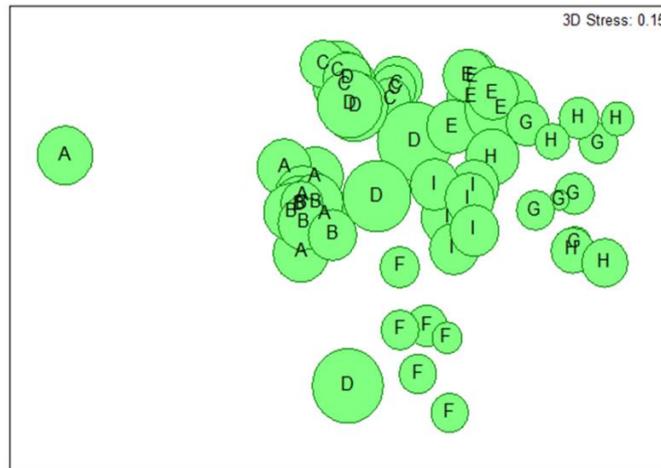


Figure 4.5: BIO-ENV identified sediment skewness values of stations along the KZN Bight midshelf as an important factor in explaining community diversity.

4.3.3 BETA DIVERSITY AND THE ENVIRONMENT

There was no real trend apparent between depth, salinity, temperature, sediment variables and beta diversity along the KZN Bight midshelf. The North KZN Bight midshelf (from station F to D), even though predicted to be low in diversity suggested by commonly used alpha diversity indices and abundance (m^{-2}), was in fact not, because of possible greater turnover (taxonomic diversity) in this section of the Bight compared to the section south of station E.

Pearson product moment correlations between Whittaker's beta diversity and % complementarity between adjacent stations and their associated environmental characteristics indicates that neither beta diversity and % complementarity had a significant correlation with any other environmental variables, except for a high negative relationship with depth, and bordered on significance with dissolved oxygen (Table. 4.8).

Whittaker's beta diversity had a very strong negative correlation with depth ($R -0.849$, $P < 0.01$) and depth explained a very large proportion of variation within beta diversity measured ($R^2 72\%$, $P < 0.01$) (Table. 4.8). The same results were observed for % complementarity as this was a complement measure of beta diversity (Table. 4.8). A quadratic regression analysis indicates that depth explained 72% ($R^2 0.72$, $P < 0.05$) of variance in beta diversity across the entire

study area, and 100% of the variance between stations F to I. Although the correlation and regression of beta diversity and % complementarity with dissolved oxygen was not significant, it was included as it was bordering on significant and still had a high R^2 value (Table. 4.8). There was a strong positive correlation (R 0.707, $P < 0.05$; R 0.703, $P = 0.052$) between beta diversity, % complementarity and dissolved oxygen respectively (Table. 4.13). Likewise a large proportion of variability present in beta diversity and % complementarity was explained by dissolved oxygen (R^2 50%, $P = 0.05$ and R^2 49%, $P = 0.052$).

Table 4.8: The relationship (R and R^2) between Whittaker's beta diversity and % complementarity to depth and dissolved oxygen concentration.

Dependent variables	Pearson Correlation		Linear Regression	
	Independent variables		Independent variables	
	Depth	Dissolved Oxygen	Depth	Dissolved Oxygen
Beta diversity	-0.849**	0.707*	72; 15.438**	50; 6.010"
% Complementarity	-0.849**	0.703'	72; 15.434**	49; 5.859'
*	P<0.05			
**	P<0.01			
"	P = 0.05			
'	P = 0.052			

What was interesting was that beta diversity and complementarity was strongly correlated with, and a high proportion of their variance explained by, the narrow range of depths (depth range of 41m to 84m). With increasing scale observed, the degree of turnover rate increased (Fig. 4.6).

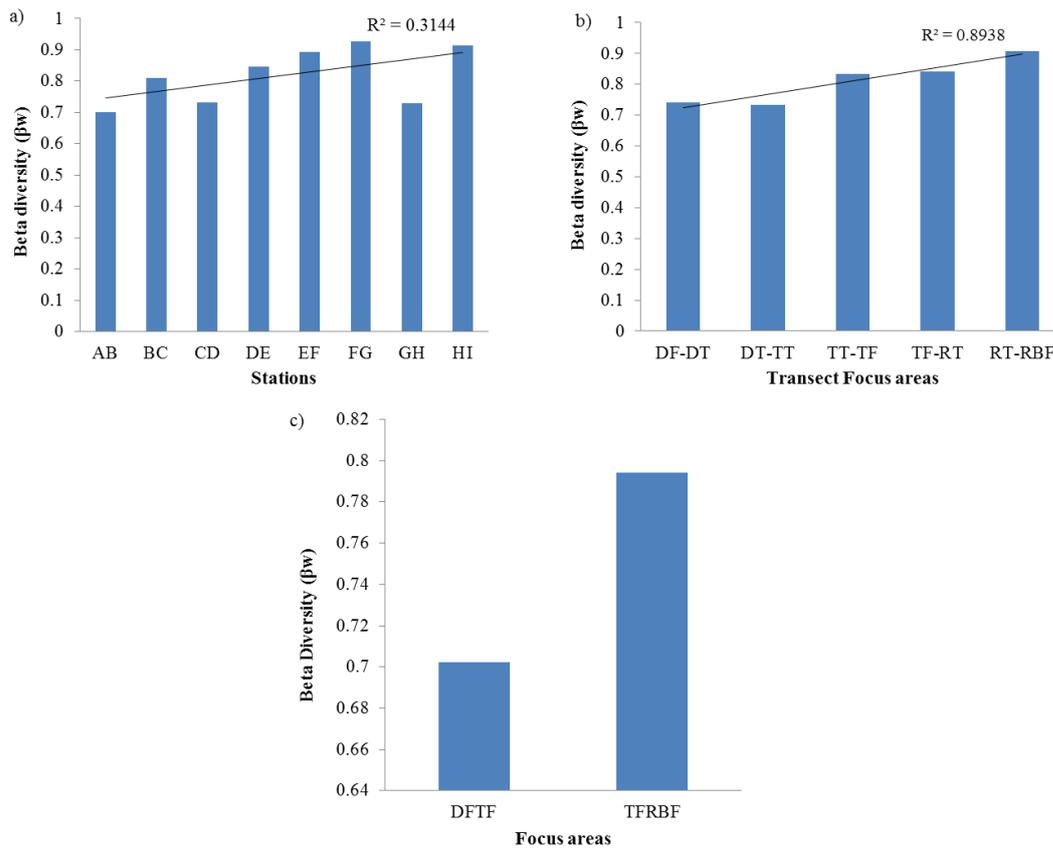


Figure 4.6: Percentage degree of increase in beta diversity along the KZN Bight midshelf from between adjacent stations, to between adjacent transect focus areas, and large focus areas. (For factors refer to Chapter 2, Figure 2.2, and Chapter 3, Section 3.2.1.3)

Figure 4.6 again highlighted the large differences between study area environments and macrobenthic communities. Biological diversity was maintained and even increased, possibly taxonomically, along the KZN Bight midshelf. The dissimilarities between macrobenthic communities of large focus areas was lower than between stations, and this was supported by the decrease in beta diversity from stations to large focus areas. Close proximity between stations did not increase their biological similarity. The environment was very different between all adjacent stations, though stations in the South Bight had a tendency to have closer biological similarity with each other than with and between stations located in the North Bight.

There was a large degree of change in turnover between larger focus areas, in spite of the general decrease in beta diversity with increasing scale. Even though according to the alpha diversity indices there was a decline in alpha diversity from Durban to Richards Bay, a possible high level of taxonomic dissimilarity was maintained between stations, transect focus areas and

large focus areas which indicated increased beta diversity between adjacent sites from Durban towards Richards Bay. Higher habitat heterogeneity in stations north of station E, compared to stations south of station E could not have been the reason, as ANOSIM indicated that the South and North Bight environments were not highly dissimilar (R^2 0.248, $P < 0.001$). Other important unmeasured factors causing great differences in survival needed to be considered.

4.4 DISCUSSION

4.4.1 THE ENVIRONMENT OF THE KZN BIGHT AND MACROBENTHIC COMMUNITY DIVERSITY

Combinations of the measured environmental variables only partly effectively explained macrobenthic diversity across the KZN Bight according to BIOENV analysis using Weighted Spearman's Correlation Analyses. Overall it was found that there were different habitats along the midshelf, despite a constant depth range, as different combinations of environmental variables were important and sections were occupied by different macrobenthic communities. However, at the individual station level, although the abiotic elements of the habitats were comparable some stations were characterised by a community incomparable to elsewhere along the midshelf. Further, stations which had similar habitats or biological communities were not necessarily located close to each other on the Bight. This has recently been found elsewhere in a northern temperate community where Dutertre et al. (2013) also noted that stations, near or far from each other, in the South Brittany continental shelf with similar environmental characteristics overall, had very dissimilar macrobenthic assemblages. Within a constant depth range in this study, sediment type was the most important determining factor of diversity. Principal components analysis divided stations according to their communities on the basis of differing sediment grain sizes. In particular, those ranging from medium to very fine size sediments.

A small degree of community variation explained by measured environmental variables was not an uncommon situation as, only 39% of the macrobenthic communities variation on the southern part of the Norwegian continental shelf were related to the measured environmental variables (Ellingsen 2001). Jayaraj et al. (2007) also found that no single environmental factor that they measured could efficiently explain variation in the macrobenthic communities or was even significantly correlated to macrobenthic attributes of the northwest Indian shelf, and only combinations of large numbers of environmental variables were successful drivers of macrobenthic distribution. Also, this was found too on a global scale in a study on the regional

and local relationship between species diversity, where site diversities differed significantly within regions, but specific physical and biological determinant of these high inter-site differences could not be adequately determined Witman et al. (2004).

Of the 18 variables considered in this study, variation in taxa and abundance of bottom communities was best explained by five, although this was attributable only at a low level of 40%. Temperature (°C), salinity (PSU), organic matter (%TOC) and fine to very fine sand were important in determining the abundance of the macrobenthic community on the Bight. Overall the macrobenthic community abundance (whole community and phyla groups) of the KZN Bight midshelf was more efficiently explained by measured environmental variables than metrics of diversity. Different environmental variables were important for abundance and diversity of the same community. Only 15 % of the entire midshelf community diversity could be explained by sediment skewness. In addition, many of the measured environmental variables did not have linear relationships with the measured macrobenthic community attributes. Different environmental variables were important in explaining abundance and diversity between the South and North parts of the KZN Bight.

4.4.2 ALPHA DIVERSITY AND INDIVIDUAL EFFECTS OF IDENTIFIED ENVIRONMENTAL VARIABLES OF THE KZN BIGHT

4.4.2.1 Sediment characteristics

The KZN Bight midshelf community diversity was only tenuously explained, according to BIOENV analysis, by sediment skewness (15% explanation of the variability in community diversity). More important was the fine to very fine sand gradient along the midshelf.

Sediment characteristics of the immediate environment play an important role in most of the distribution and composition of macrobenthic communities (Ellingsen 2002, Gray 2002, Otani et al. 2008). Macrobenthic species distributions has been found to be significantly correlated with the spatial arrangement of sediment characteristics (Otani et al. 2008). In this present study PCA (PC1) was most indicative of sediment attributes that explained 48% of variability in all stations, with characteristics like median grain size, fine sand and coarse sand being the most important environmental factors distinguishing stations along the KZN Bight midshelf.

Animal sediment relationships are complex, but a single variable like sediment grain size alone cannot determine the distribution of species (Snelgrove and Butman 1994). The importance of understanding environmental interrelationships such as between sediment and hydrodynamic

characteristics are realised (Snelgrove and Butman 1994). Boundary layer flow influences sediment sorting, distribution and grain size, that in turn is also correlated with organic matter content, microbial activity, sediment chemistry, trophic interactions, larval supply and food supply (Snelgrove and Butman 1994). Hydrography and sedimentation, among others, influence resulting food availability and the physiochemical characteristics of the sediment and water column (salinity, temperature, oxygen) that play determining roles in macrobenthic community characteristics (Gray 1981, Sellanes et al. 2007, Zalmon et al. 2013). Hydrodynamics play a very determining role in the distribution, composition and change in sediment characteristics and the physical-chemical attributes of the water column, while hydrodynamics are in turn influenced by topography of the sea bed (Dutertre et al. 2013).

High KZN Bight midshelf macrobenthic diversity was to a greater extent associated with medium sand, moderately sorted, with a fair amount of organic matter and low percentage mud content. Ingole et al. (2002) reported that medium grain-sized sediment supported larger amounts of benthos. These coarser grained sediment stations were more often situated in between the three oceanographically defined focus areas off Durban, Thukela River and St. Lucia, which had more fine sediment in contrast. The amount of coarse sand increased and the proportion of fine sand decreased from Durban towards St. Lucia. Similarly Jayaraj et al. (2007) found that macrobenthic communities preferred medium grain-sized textures with a medium/low organic matter content and some clay, as a too high level of organic matter negatively affected especially filter feeders (Harkantra et al. 1982, Jayaraj et al. 2007).

According to Snelgrove (1999), fine sediment affects macrobenthic fauna feeding capacity as this type of sediment is very easily re-suspended and organic content tends to increase with the fineness of sediment. Generally this was supposed to enhance food supply and increase carrying capacity of macrobenthic communities (Fernanda et al. 1999). However, on the KZN Bight midshelf lowest diversity and abundance was found in station F, associated with the highest mud content and very fine sand content. Similarly in the study by Dutertre et al. (2013), homogenous habitats consisting mostly of fine sediment were found to have very low species richness. A very high level of very fine sand and/or silt/clay can cause a state of hypoxia, and only fauna adapted to such anaerobic condition can thrive (Weston 1988).

High Annelida abundance was associated with low (< 3%) organic matter content in sediments of the northwest Indian shelf and low abundance in those locations with high organic matter content, fine sand and mud (Jayaraj et al. 2007). Thus it could be said that observed diversity

(alpha and beta respectively), determined by the adaptive abilities of the macrobenthic community, depended on what kind of organic matter was found where and the latter was also partly dependent on sediment characteristics, and what effects it had on potential oxygen concentrations and other vital elements.

In the northern Rio de Janeiro continental shelf, higher diversity was found in sediments of a smaller mean particle size, together with a low level of sorting, as a greater diversity of granulometric composition of sediment would support a greater diversity and richness of communities, because of an increase in potential niches, promoted further by the interactions of physical and biological factors (Gray 1981, Levinton 1995, Zalmon et al. 2013). Similarly crustacean community structure on the Ebro Delta continental shelf, associated with high river run-off, was found to be largely determined by the sediment characteristic indirectly facilitating the organic matter content available to the macrobenthic fauna (De Juan and Cartes 2011). These communities were also strongly correlated with sediment characteristics, however correlation between crustacean abundance and organic matter was lacking (De Juan and Cartes 2011). This did not mean that organic matter was not potentially vital in the structuring of this community as hydrography did also have a significant part to play (Cartes et al. 2007).

Albeit that sediment type is the most important factor in affecting variance, Seiderer and Newell (1999) found that sediments had very little correlation with the benthic community structures in coastal deposits off the south-east England, suggesting that factors other than sediment played an important role in the macrobenthic community structure of the seabed, through a complicated interaction between various physical and biological factors at the sediment-water interface. A combination of sediment, bathymetry and hydrodynamic characteristics of the South Brittany continental shelf contributed to explaining 26% of the variation found in the overall macrobenthic community on this shelf (Dutertre et al. 2013). Dutertre et al. (2013) found that even though much of the community variation was explained by these physical environmental factors, others could not be excluded, as the physical-chemical explained 25% of variance and thus was essential in the explanation of environmental and community dynamics. In our study the separation of stations in the PCA, according to the environmental variables best describing them, followed a similar sequence as the environmental variables that best described the macrobenthic community of South Brittany. Physical sediment characteristics were firstly responsible for most of the variation between environments of stations, followed by physical-chemical water column attributes and then the association with mud, organic matter and very fine sand.

According to Otani et al. (2008), chemical characteristics of sediment like the amount of organic matter and sulphide content are very qualitatively changeable, hence physical sedimentary characteristics are a more steady indicator of macrofauna distribution. Thus sediments could indirectly play the most stable role in variation between study sites as the sediment characteristics of a station lay down the foundation from which the rest of the environmental variables associated within that location can interact and build up from, creating sections of different habitats with different associated macrobenthic communities.

4.4.2.2 Sediment Organic Content

Macrobenthic abundance and biomass reflect the rate of nutrient inputs into the system (Levin et al. 2001) and from the identified important environmental variables such as temperature, salinity, organic matter, fine sand and very fine sand (Martins et al. 2013b), it could be concluded that the community variability was highly dependent on dynamics providing different nutrients (Levin and Gage 1998, Ayers and Scharler 2011, De Lecea et al. 2013). Environmental variables identified as important for the entire macrobenthic community of the KZN Bight midshelf, could be seen as closely linked to the reigning circulation dynamics of the KZN Bight, largely brought on by the Agulhas Current. In many cases, the role of, for example, sediment in maintaining diversity is masked by depth-related variables (Weston 1988). Gooday et al. (1990) stated that the persistence of life on the ocean floor could be viewed as a response to organic inputs, and the existence of communities are directly related to the presence and distribution of food that reaches the sediment surface and how this is utilised (Dayton and Hessler 1972, Tseytlin 1987). The understanding of the distribution and abundance of species in a community can only be achieved when detrital and phytoplankton pathways are both considered and integrated (Moore et al. 2004). Tselepidis et al. (2000) also concluded that food availability was the limiting factor in a habitat such as the oligotrophic continental shelf of Crete and that the macrobenthic community reflects prevailing environmental conditions.

According to Taylor (1997) the major regional and local differences of Indo-Pacific marine provinces macrobenthic community composition and structure, was due to the differences in nutrient availability. He said that there was evidence that rates of evolutionary diversification were related to nutrient regimes, as this could then be contributing to differential rates of speciation and evolution in different nutrient regimes (Taylor 1997). Because primary consumers and prey differ between different nutrient regimes, the predators associated with them are also different, thus different communities with different life histories and adaptations

occupy eutrophic (South Bight) and oligotrophic (North Bight) habitats, as these two sections of the Bight were expected to be associated with different hydrographic regimes and complementary habitats (Taylor 1997). The Bight has a low primary production level, where nitrate concentrations can range between 1 to 2 $\mu\text{mol l}^{-1}$ in the south and central bight to 9 $\mu\text{mol l}^{-1}$ in the north where there is an upwelling cell (Schleyer 1981, Meyer et al. 2002). These speciation and extinction rates are believed to be environmentally controlled and how high the diversity will be varies between different fauna, that do not react similarly to the different nutrient pressures (Vrba 1987, Taylor 1997).

Many studies have contradicting results when it comes to productivity as in some studies diversity increases, and in others decreases with productivity, while others have a unimodal relationship with productivity (Levin et al. 2001). Similarly in our study as productivity was not measured, diversity did not have a direct relationship with productivity; however the positive correlation with sediment skewness could have indirectly been attributed to productivity and oxygen consumption of the region. According to Akoumianaki et al. (2012) the high explanatory power of skewness and sorting of sediments indicated that macrofauna community structure was significantly influenced by sediment re-suspension and the current driven transport of species, differentially resulting in the increase of the number of species, promoted by the terrigenous and phytodetrital food input also interacting with other environmental variables, that supports higher diversity. Nutrient supply would not have been exclusively determined by the supply of detrital runoff, but also dependent on other associated environmental factors that macrobenthos were adapted to. According to Levin et al. (2001) diversity and sediment relationships are related to a hypothesis that more species coexist in sediments that vary more in size as species partition sediment with respect to size.

Macrobenthic fauna are able to utilize any form of available food on the seabed (Steimle 1985, Melake 1993). According to Mann (1988), more energy, materials and phytoplankton carbon of primary production of a system was transferred through the food chain from dead decomposing detrital plant tissue pathways than by grazers pathways. Graf (1992) found that benthic metabolism was split according to the origin of food supply and that old, decomposing stored material use, follows the annual temperature cycle and oxygen supply. Detritus, through its influence on food webs, can increase a system's community and individual species stability, persistence and resilience, having a significant effect on macrobenthic community biodiversity spatially (Moore et al. 2004). A slow steady input of energy has a significant effect on an ecosystem in spite of the presence of a large temporary variable input of energy from another

source (Moore et al. 2004). Thus detritus potentially sets the stage for the spatial variation in macrobenthic community diversity and abundance.

Detritus is not homogenous and as a result of its ontogeny, variability in quality, quantity, form and distribution, it has an interdependent relationship with diversity and abundance of macrobenthic communities (Graf 1992, Moore et al. 2004, Ayers and Scharler 2011, De Lecea et al. 2013). As the ontogeny of detritus progresses and because it has many system entry points, there are changes in the composition and functioning of communities as a result (Graf 1992, Moore et al. 2004, Ayers and Scharler 2011, De Lecea et al. 2013). Available organic matter occurs in the form of a dissolved organic matter or particulate organic matter (Mann 1988). According to Graf (1992) detritus with a higher supply of nitrogen is of higher quality. Detritus promotes a complexity within habitats as it changes the moisture, light penetration, temperature and flow velocity at locations (Moore et al. 2004). Some of these combined effects causes alteration of the thermocline depth that can have changing effects on the habitats sedimentation rate, oxygen and temperatures and thus on community diversities and structure (Williamson et al. 1999, Moore et al. 2004).

According to Hairston and Hairston (1993) on an immediate time scale, detritus can support a greater species diversity or abundance in a community than would be possible for communities that were solely dependent on autotrophs. The diversity of decomposers and detritivores in turn affect the efficiency of energy conversion that feed back to accentuate producer and consumer diversity (Cardinale and Palmer 2002, Moore et al. 2003, Moore et al. 2004). Lohrenz et al. (1997) found that as the primary production resources induced by the riverine input to the shelf decline, there is an increase in the relative importance of other nutrient sources, while the remaining phytodetritus provide nutrients on longer term to the system, through the biological and chemical regeneration of river detritus and phytodetritus (De Lecea et al. 2013).

Macrobenthos adapt feeding behaviour within environments of changing food availability, for example in a amphipod *Corophium volutator*, studied by Stuart et al. (1985), there was a change of diet from benthic diatoms in spring-summer to *Spartina* detritus in fall-winter. This also indicated that as algal cells are the more easily utilised and a rich nutrient source, detritus remains an important source of nutrition in the times when as usual algal cells are seasonally not available, to carry them through (Mann 1988). Within shallow waters, diatoms can still reach the seabed as intact cells that are of a high quality food source that can directly be utilised by benthic organisms (Graf 1992, Tang and Kristensen 2007). This hints to possible

mechanisms/adaptations possibly utilised by communities of the KZN Bight, especially perhaps the North Bight communities, where beta diversity can be promoted through the efficient utilisation of variable and/or scarce food sources..

Ayers and Scharler (2011) theoretically concluded that the ecosystem of the KZN Bight was detritus-based, and that there could have occurred a high degree of cycling and in particular detritus recycling, which has been associated with increased resilience of the ecosystem (Vasconcellos et al. 1997). According to Gooday et al. (1990) the types of organic material often associated with terrestrial runoff, such as twigs, branches, fruits, provide additionally food, substrate for attachment or shelter for benthic organisms. This terrestrial debris in combination with local disturbance creates a mosaic of patched microhabitats that helps to maintain diversity and habitat heterogeneity on a high level on the seabed over long term (Gooday et al. 1990).

Microbial populations play a central role in detrital and phytoplankton nutrient cycles, through components of the energy and carbon flow within the soft bottom ecosystems (Jumars and Nowell 1984). Microbes make otherwise unusable detrital material available to other fauna by renewing and increasing nutrient value (Jumars and Nowell 1984, Fernanda et al. 1999). Graf (1987, 1992) found that bacteria had a 50 – 60 % conversion efficiency of refractory and phytodetrital sources, and a large amount of nutrition could thus be transferred to higher trophic levels. Bacterial colonies have also been found to influence habitat selection of faunal recruits of soft substrata (Kirchman et al. 1982). In oligotrophic habitats plant detrital matter are important and an extensive amount of time of reworking is necessary for microbacteria to condition these sources, to make the nutrients more easily available, nutritious and usable for higher trophic levels (Mann 1988). Goldman (1984) with the aggregate spinning-wheel concept and Azam and Ammerman (1984) with the cluster hypothesis, suggested that rapid nutrient cycles occur in discrete communities attached to a detritus particle (Mann 1988). In the South and North Bight, these microbial activities could have played different roles to various degrees through similar and different nutrient sources provided. The mineralised nutrients produced from detritus are the sources reused in primary production of the euphotic zone (Graf 1992). The spatial and temporal difference in phytoplankton, as well as their use and re-use, is determined by the changes in the relative importance of river and upwelling nutrient supply, over small spatial scales and in the process its sustains and/or enhance the microbial food web over the shelf (Iriarte et al. 2012).

These types of relationships with sediments may be expressing rather other important proximal factors (Levin et al. 2001). Marine benthic communities are controlled by basic mechanisms like energy availability, biological interactions, disturbance and heterogeneity (Levin et al. 2001). The size, shape and type of organic matter entering the system determines the type of phyla present, the way they respond; and through these responses to the pulsed nature of phytodetritus input; regulate also the reproductive cycles and population dynamics of these phyla across areas (Gooday et al. 1990). There are for example a wide range of ecological strategies and trophic requirements displayed by benthic Metazoans and thus a variety of responses (Gooday et al. 1990). The interaction between benthic organism and incoming fresh organic material is highly modified by physical stress, coupled with ecological interactions like competition in highly hydrodynamic areas (Quintana et al. 2010).

In shallow water communities, species have been found to interspecifically differ in particle size preferences (Whitlatch 1980, Levin et al. 2001). Quintana et al. (2010) found that the benthic response to organic matter input on the Brazilian coast depended on the interaction between micro-, meio- and macrofauna as within this area there was no lack in TOC, but the competition for the labile available content was important. On large scale they found that resource driven aggregation and distribution was density-dependent and influenced by bottom currents and local upwelling, as they are responsible for the distribution of the heterogeneous deposition of particulate organic matter as well as the re-suspension and redistribution of food and fauna, creating additional microhabitats promoting diversity (Cosson et al. 1997).

4.4.2.3 Salinity and Temperature

In this study, lower alpha diversity and abundance was associated with marginally lower salinity and higher temperatures (see Section 4.3.1), Vizakat et al. (1991), also found a positive relationship between benthic production and salinity, and Jayaraj et al. (2007) found a decrease in the commonly used measure of macrobenthic species richness with lower salinities (Dos Reis Melo et al. 2013). Brown and Jarman (1978) suggested that temperature greatly influences the distribution of biota, that is in turn dependent upon prevailing currents, along the southern African coastline. Boesch (1972) also observed that macrobenthic diversity was highest in the polyhaline zone of the Virginia continental shelf and that the diversity decreased further at meso – to oligohaline zones. A similar trend found on the KZN Bight midshelf in terms of alpha diversity.

In the Baltic sea, macrobenthic communities were significantly affected by salinity these waters were highly saline-stratified, which affected the oxygen conditions at sediment level, by preconditioning hypoxic conditions and thus the breakdown of organic matter content, by slowing down mineralisation as oxygen decreased (Laine 2003, Witman et al. 2004). On the northwest Indian continental shelf, macrobenthic communities were similarly influenced by a combination of temperature, salinity, dissolved oxygen, sand and organic matter (Jayaraj et al. 2007). Cusson et al. (2007) found that the change in temperature and salinity caused by the inflow from local rivers significantly attributed to the difference in macrobenthic communities and similar findings were also found in other studies (Danisenko et al. 2003, Dutertre et al. 2013, Dos Reis Melo et al. 2013).

A multicellular organisms somatic growth is slower at lower temperatures, but this does not mean that they do not receive significant nutrition from the sedimentation of nutrient sources (Graf 1992). Graf (1992) indicated that temperature influence metabolic activity of microbial fauna (particularly also influencing oxygen and nutrient availability and use), and that on the Kiel Bight there were good correlations between seasonal oxygen consumption and annual temperature. However the food supply dominates temperature effects on metabolism (Graf 1992). Jayaraj et al. (2007) explained that the decrease in community production in the southern region of the northwest Indian shelf study areas was due to lower temperatures and low salinity. Similarly, in the KZN Bight a trend of decrease was also found within the whole community abundance with decreasing in salinity. However as temperature did not play the role in this study as it did in the southern region of northwest Indian shelf (Jayaraj et al. 2007), intricate dynamics with nutrient availability, use, as well as hydrodynamics could have been more important.

4.4.3 BETA DIVERSITY AND INDIVIDUAL EFFECTS OF IDENTIFIED ENVIRONMENTAL VARIABLES OF THE KZN BIGHT

4.4.3.1 Depth

According to Gage (1997), Levin and Gage (1998) and Levin et al. (2001) there are many unsuspected oceanographic conditions arising along changing depths that are important in interrupting and modifying patterns of bathymetric horizontal and vertical macrobenthic diversity. Depth is generally correlated with other important environmental factors, and the change in beta diversity from the South to the North could thus be associated with the difference in the temperature, salinity, dissolved oxygen and organic matter resources between the two

regions (Ayers and Schaler 2011, De Lecea et al. 2013). Beta diversity has previously been found to be correlated with differences in depth and not distance (Rex and Etter 2010). On the south Texas continental shelf, macrobenthic community distribution was best explained by depth and depth-related factors, such as chlorophyll-*a* content, hydrodynamics, sediments, temperature, salinity (Rabalais 1990, Mutlu and Ergev 2013). Species richness can change over small spatial scales and small changes in depth (Gray 2002). Species relatedness in communities may possibly have the same ability to change over small depth ranges. Dauvin et al. (1994) found that Polychaete community alpha diversity in warmer latitudes, increased with depth.

Depth is an especially important factor creating gradients, which are especially important within oligotrophic habitats, as they could have strong impacts in an area with limited food supply (Karakassis and Eleftheriou 1997, Sivadas et al. 2013). These gradients could be associated with an increase in habitat heterogeneity and beta diversity changes and increases with increasing habitat variability (Clarke and Lidgard 2000). Beta diversity has also been found to be high on the very deep to middle deep depths of continental slopes, highlighting the importance of strong environmental gradients and great habitat heterogeneity that may occur across depths (Rex and Etter 2010, Leduc et al. 2012). According to Gray (2002), gradients in species richness of soft sediment fauna were primarily related to depth and latitude.

Jayaraj et al. (2007) found a similar trend of inverse patterns of diversity on the northwest Indian shelf, as community alpha diversity decreased from deeper to shallower depths, but Polychaete diversity and richness increased from deeper to shallower depths. Thus composition of a community is important to consider. They attributed the lower richness (beta diversity) of Polychaetes at deeper depths to lower temperatures and dissolved oxygen, and the higher richness in the shallower depths to lower amounts of organic matter, more coarse sand and higher temperatures (Jayaraj et al. 2007). In Hong Kong subtropical waters, macrobenthic alpha diversity was found to be relatively low even at the large spatial scale of study, however, similar to our study, beta diversity was high (Shin and Ellingsen 2004).

The depth of the water column usually has a large influence on the sedimentation and reigning water dynamics of the region (Zalmon et al. 2013). Depth is in general a strong determinant of community structure and has strong correlations with most environmental and biological parameters, however in shallow regions, factors like sediment and biological interactions, may play a stronger role than depth *per se* (Gray 1981, Tsutsumi et al. 1990, Tselepides et al. 2000, Mutlu and Ergev 2013). On a continental slope off Scotland, Gage et al. (2000) found that depth related factors are important in maintaining macrobenthic diversity, for in shallow shelf regions,

a low abundance, biomass and diversity was found, and this was related to coarser sediments and a high level of hydrological phenomena found there (Mutlu and Ergev 2013). On the south-east Australian continental shelf, species richness and diversity also increased with depth and with lower levels of sediment sorting (Coleman et al. 1997).

Quintana et al. (2010) found that organic matter quality and quantity were the main determinants of benthic assemblage structures on the Brazilian coast and that hydrodynamics played a limited role in determining diversity through available labile organic matter. Here benthic diversity increased with increasing organic matter load in spite of physical exposure, and it was found that biological interrelationships can play a prevailing role in structuring benthic community diversity, as similar diversities and communities were found in different habitats (Quintana et al. 2010). Thus gradients formed along depths provided for high beta or alpha diversity through the provision of various environmental pressures and fauna differentially adapted to them. Similarly, depth limits determined the settlement and species composition of different communities (Arango and Solano 1999). Factors like temperature, salinity, depth and pressure are easily understood because of the physiological constraints on species within ranges to complete certain enzymatic and osmotic functions (Snelgrove 1999).

4.4.4 SCALE AND LOCATION NOMINAL EFFECTS

The effectiveness of explaining variance in the abundance and diversity of the KZN Bight midshelf macrobenthic community changed with scale of measurement and location. Variation was more effectively explained when larger scales were considered. Studies show that macrobenthic community diversities vary over varying spatial scales because of physical environmental covariates acting over various spatial and temporal scales (Williams et al. 2010). Van Hoey et al. (2004) found a strong correlation between the physical environmental characteristics of the Belgian continental shelf, such as sediment mud and median grain size, and concluded that it was these small scale factors that explained the largest proportion of variation seen in the macrobenthic communities and that on the large scale, communities were determined largely by currents.

Regional-scale diversity gradients are governed by regional ecological processes governing rates of local processes, and these regional processes are determined by global oceanographic and climatic processes (Levin et al. 2001). Regional environmental phenomena create gradients of ecological opportunity on local scales that affect population dynamics on a small scale and

thus community diversity (Levin et al. 2001, Sivadas et al. 2013). Local and regional processes work together to maintain species coexistence in a community (Witman et al. 2004). The composition of local coexisting species is regulated by the regional processes, such as larval dispersal, meta population dynamics, landscape ecology and evolution of the species pool interacting with smaller scale biological and non-biological processes (Witman et al. 2004). The question is can local diversity be explained by local processes alone without considering the impact of a matrix of other processes on larger scales? (Ricklefs 1987, Witman et al. 2004).

Environmental variables will have different importance depending on scale and location as well as the entities studied. Although temperature, fine sand and very fine sand content were shown to contribute individually to community dynamics, it was the combined direct and indirect influences they had on salinity and the available organic content that played an important role. Temperature and salinity may have more influence on a large scale than currents for example, that influence these physical attributes, that also occur on a large scale (Ysebaert and Herman 2002, Williams et al. 2010, Dutertre et al. 2013)

Combinations of environmental variables best explaining community abundance and diversity changed more significantly from one location to the next than one scale to another. As larger scales were considered, the explained proportion of community diversity and abundance decreased, but variability in locations was increasingly explained. Thus there is a trade-off between variability explained on small scale and on large scale or from one location to the next. Overall the South Bight communities were less efficiently explained than those of the North Bight. Thus the localised importance of measured environmental parameters could have been the result of the differential dependence/adaptability of local communities on differentially important environmental parameters at different locations. Species and individuals respond individually to variability, and these responses are different for different scales and from one location to the next, and no description of the environment makes sense unless a variety of scales are considered and those scales are relevant for the individuals and processes being examined (Levin 1992). Depending on the units that are studied, some species may only have evolutionary responses to a narrow and/or broad range of environmental influences and evolutionary forces may also act on different scales (Levin 1992).

4.4.5 INTERACTION OF VARIABLE COMBINATIONS AND EFFECTS ON ALPHA AND BETA DIVERSITY GRADIENTS ON THE KZN BIGHT

Fernanda et al. (1999) also stated that many factors simultaneously affect species richness and distribution, reflecting environmental complexity, as the marine environment consists of many integrated gradients (Seiderer and Newell 1999). Combinations of other external or internal pressures most certainly played more important roles in the KZN Bight. It has not been possible to single out mechanisms responsible for the influence of productivity on diversity (Waide et al. 1999, Levin et al. 2001). The way in which temperature, salinity, organic matter and sediments determine diversity depends on the aspect of the community being measured (Jayaraj et al. 2007). Different groups react to different environmental factors differently (Levin et al. 2001).

Life in the ocean is to a varying and large extents dependent on the complex benthic-pelagic coupling process (Graf 1992, Gooday 2002). Levin et al. (2001) concluded, in a study on the environmental influences on regional species diversity, that diversity was related to environmental gradients and habitat shifts that are brought on by multiple forces that are very interdependent. On large scales species diversity is determined by a combination of sediment characteristics, nutrient input, productivity, oxygen concentrations, and hydrology, while processes such as disturbance and facilitation acts as mediating factors between environmental forcing and diversity (Levin et al. 2001). In many previous studies, sedimentation, determines grain size, organic matter content and carbonate content; which in turn are determined by a wider set of environmental conditions from prevailing local and regional hydrographical influences, like bottom currents (Sternberg 1984, Chavez and Brusca 1991, Snelgrove and Butman 1994, Zalmon et al. 2013). Sedimentation rate, re-suspension and distribution within shallow regions; have been found to be highly influential in determining benthic communities composition and distributional characteristics (Sternberg 1984, Chavez and Brusca 1991, Snelgrove and Butman 1994, Zalmon et al. 2013).

The difference in environmental variables that play important roles in determining alpha and beta macrobenthic community diversity on the KZN Bight midshelf was as Leduc et al. (2012), found, that because alpha and beta diversity measure different things, they are influenced by different environmental factors. Leduc et al. (2012) concluded that there is a unimodal relationship between nutrient supply and alpha diversity in contrast to the relationship with beta diversity found on the New Zealand continental slope.

The environmental variables identified on the Bight as the most important influencing the distribution and overall composition and diversity of the macrobenthic community, highlight the presence of a community that was highly dependent upon available food resources (Dauvin et al. 1994, Ayers and Scharler 2011, De Lecea et al. 2013). This was because these variables work in concert providing and determining variation in food availability and type (Weston 1988). Of the macrobenthic communities from oligotrophic seas of Crete, Tselepidis et al. (2000) concluded that except for depth, the correlation between the macrobenthic fauna and sediment parameters, suggested that food availability was the main regulatory factor in such a system. On the continental shelf off Cape Hatteras, North Carolina, it was concluded that the environmental factors best controlling the macrobenthic community structure were those that inferred an area-related control on the type and amount of food resources (Weston 1988). These included sorting, that indicates sediment mobility, very fine sand and proportion silt/clay (Weston 1988).

Pearson and Rosenberg (1978) and Wieking and Kroncke (2005) indicated that infaunal communities are distributed and structured according to gradients of resource availability, for example the food particle distribution determined by current distribution and re-suspension of sediments, that are in turn modified by interactions with other environmental factors, like sediment stability, hardness, temperature, oxygen, and salinity (Warwick and Clarke 1993, Guzman-Alvis et al. 2006). Not forgetting other factors like predation and other biological interactions that also influence community structuring (Pearson and Rosenberg 1978, Karakassis and Eleftheriou 1997, Guzman-Alvis et al. 2006).

Gray et al. (1997) said that species richness on large scale using small scale ecological known determinants of diversity was untestable, as factors responsible for creating assemblages of species were different from those maintaining diversity and thus many combinations of variables needs to be considered relative to questions asked. Cosson et al. (1997) explained the patchy aggregated distribution of deep sea macrobenthic communities and the heterogeneity of the habitat is the result of a combination of physical and biological interactions that work on different scales. Cole and McQuaid (2010) found that, regional biogeography factors such as temperature and salinity, and upwelling, differentially were important influences in determining Mussels abundance and their associated fauna abundance and diversity.

4.5. CONCLUSION

The KZN Bight midshelf macrobenthic community was a diverse community adapted to the physical and chemical changes brought on by the Thukela River and the Agulhas Current. Oceanographic features divided and created different habitats along the KZN Bight, which were characterised by environmental processes that are differentially important for community dynamics in different locations along the Bight, contributing to the highly dissimilar and diverse habitats and macrobenthic diversity. Some measured environmental variables weakly explained variability in alpha (temperature, salinity, fine sand and very fine sand) and beta diversity (depth). Because of the oligotrophic nature of the waters; food type, distribution and availability was inferred to indirectly be the main drivers that maintains the macrobenthic community patterns and diversities. According to results from Ayers and Scharler (2011) and De Lecea et al. (2013), the KZN Bight was indeed largely detritus driven, while phytodetritus potentially had a role; possibly especially in the North Bight region; even though low levels of primary production has been found. In spite of the above, the measured environmental variables did not explain most of the community variability observed and thus other important unmeasured environmental, abiotic and biotic variables are responsible for the observed and unobserved macrobenthic community diversity patterns of the KZN Bight midshelf. This was also highlighted by the fact that none could effectively explain overall diversity and variability in abundance at any specific spatial scale measured as well as at most of the locations. Also depending on the question being asked, the units and variables measured; the relative importance of environmental variables differs.

This present study forms a valuable baseline study on which should be built on in future, although there is still much variability that we did not include, that remains unexplained and unaccounted for, thus taking a structured step by step approach in the study of ecosystems like the KZN Bight is important for a complete overall idea of the inner ecosystem workings.

CHAPTER 5

A COMPARISON OF MACROBENTHIC COMMUNITY TAXONOMIC DISTINCTNESS AND SPECIES RICHNESS GRADIENTS ALONG THE KZN BIGHT MIDSHELF

5.1 INTRODUCTION

Biodiversity changes found along environmental gradients have been described in many marine ecosystem studies (Zintzen et al. 2011, Sivadas et al. 2013). Patterns of diversity found along gradients depend on the aspect of diversity measured (Clarke and Lidgard 2000, Shin and Ellingsen 2004). Many studies have focused mainly on the use of commonly used species richness and other alpha diversity heterogeneity indices and have mainly been concerned with species identity and relative abundances; to assess community changes driven by environmental impact (Gray 2000, Arvanitidis et al. 2002). According to the number of species found within an area, the number of individuals, habitats and or biogeographic provinces per unit area present can be predicted (Rosenzweig 1995, Gray et al. 1997). However, criticisms are that commonly used diversity indices (e.g. Shannon-Wiener, Species richness indices) are insensitive to detecting community change compared to multivariate statistics (Gray 2000).

Species richness only measures the numbers of different units within a habitat, while indices that add additional information on species relatedness and functional position can add value for instance in conservation planning (Heino et al. 2005). Biodiversity measures need to incorporate the total of taxonomic or numerical, ecological, genetic, historical and phylogenetic diversity, and a measure of 'taxonomic distinctness' as a diversity index incorporating more of these attributes than commonly used species richness measures, has greater relevance (Van der Spoel 1994, Warwick and Clarke 1995, Clarke and Warwick 1999). Simply, average taxonomic distinctness is the mean number of steps along a hierarchy that must be taken to reach a taxonomic rank common to two species, using combinations of all possible pairs (Clarke and Warwick 1994, 1998, 1999, Mouillot et al. 2005). No real generalisation in patterns of biodiversity and processes influencing biodiversity has been made (Harrison et al. 1992). It has been highlighted that beta diversity is important to understand the extent to which habitats have been partitioned by species and, combined, beta and alpha diversity contribute to understanding

habitat diversity and an entire region's biotic heterogeneity (Wilson and Shmida 1984, Izsak and Price 2001). MacArthur (1967) recognised that alpha and beta diversity results together indicated species habitat and niche diversification, which are biologically more interesting than just species richness or heterogeneity diversity results alone (Gray 2000).

In comparison with alpha diversity, beta diversity has been applied much less especially in the marine context (Gaston and Williams 1996, Gray 2000, Merckx et al. 2009, Bevilacqua et al. 2012, Leduc et al. 2012). The continental shelf consists of habitats influenced by benthic and pelagic processes simultaneously (Karakassis and Eleftherious 1997) and benthic habitats area function of the integration of environmental conditions and the processes occurring in the water column above (Cusson et al. 2007). The important role beta diversity can play in understanding population connectivity, resilience, and conservation planning has been recognised (Thrush et al. 2009, Thrush et al. 2010). The consideration of a sites relative taxonomic diversity to the expected regional taxonomic diversity is useful for determining the environmental state and state of degradation (Warwick and Clarke 1998, Heino et al. 2005). Taxonomic distinctness as a measure of beta diversity can generally be seen as the mean taxonomic relatedness between species in a community (Heino et al. 2005).

Taxonomic distinctness is more ecologically relevant than alpha diversity measures of species richness, since it is related to changes in functional diversity (Warwick and Clarke 1998). Conventional diversity indices use only the relative abundance of species present and do not describe the taxonomic relatedness within communities. Thus communities with the same species richness could be completely different in terms of relatedness (Warwick and Clarke 1995, Rogers et al. 1999). Taxonomic distinctness indices are beneficial as they are robust, independent of sampling size and effort, and not significantly affected by habitats (Warwick and Clarke 1995, Rogers et al. 1999, Heino et al. 2005). A further index based on this is the variation in taxonomic distinctness, which represents the complexity of the hierarchy by the variance of the pairwise path lengths (Mouillot et al. 2005).

Knowledge of the mechanisms of environmental drivers of beta diversity has been limited primarily to that gained from terrestrial and freshwater studies (Rex and Etter 2010). The relationship between taxonomic distinctness and environmental variables such as depth and sediment characteristics have rarely been tested (Ellingsen et al. 2005) and even less frequently in the marine environment. Alpha or beta biodiversity dynamics are linked to environmental surroundings and the types and strength of pressures exerted on species adaptation and

evolutionary rates (KieSSLing and Aberhan 2007). A combination of processes can play a role in facilitating biodiversity. Some include habitat heterogeneity (Levin et al. 2010), and stable or unstable habitats that “produce” more specialized fauna that don’t need to compete for resources (Gray 1997a). A clear example of biogeographical differences related to alpha or beta diversity measures comes from the avian world. Avian alpha diversity in tropical and temperate regions was not different, but beta diversity was much higher in the tropics, because beta diversity highlighted that evolution in the tropical regions tended to increase habitat diversification and niche specialisation and utility (Macarthur 1967).

Taking into consideration this relatively underused method of determining beta diversity, the aim of this chapter was to determine the taxonomic diversity index values for stations along the KZN Bight, in order to determine if there were any differences between stations and larger regions (North and South Bight); and if, through a comparison of alpha (observed number of species) and taxonomic relatedness (taxonomic distinctness (Δ^*), average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Δ^+)) as an alternative/supplementary measure of beta diversity, support and confirmation could be gained for the general alpha and Whittaker’s beta diversity patterns results found in chapter 3. Further aims included to determine which stations differed from expected values of taxonomic diversity; as well as determining the environmental variables that explained the observed taxonomic diversity in the different regions of the Bight and if these could have been related to results of the alpha and beta diversity and environmental variables in chapter 3 and 4 respectively.

Here one hypothesis is expanded from Chapter 3 which focused on Whittaker’s beta diversity, in that it was postulated that the taxonomic diversity along the KZN Bight midshelf was not equally distributed. In particular, the taxonomic distinctness in the North section of the Bight (stations F to I) would show higher diversity than the South section (stations A to E).

The second hypothesis was that these taxonomic distinctness patterns were been related to environmental variables different from those determining alpha diversity and in particular that the taxonomic diversity of the North and South section of the Bight was explained by different sets of measured environmental variables than those that described alpha diversity.

5.2 METHODS AND MATERIALS

Whittaker's beta diversity is a measure of the variation of species identities from one location to the next and thus the compositional change of a community over a landscape and environmental gradients (Whittaker 1960). Whittaker's beta diversity is divided into turnover diversity (between two communities) and variation diversity (within communities) (Bevilacqua et al. 2012). Taxonomic diversity indices such as taxonomic distinctness (Δ^*), average taxonomic distinctness (Delta+ or Δ^+) and variation in taxonomic distinctness (Lambda+ or Λ^+) index values were measured using the PRIMER v6 package, to determine the taxonomic relatedness of macrobenthic communities as an supporting measure of beta diversity within the entire study area, within stations, as well as within the North (stations F to I) and South (stations A to E) sections of the KZN Bight midshelf (refer to Chapter 2, Figure 2.1 and 2.2 and indices definitions in Section 5.1). The combination of Δ^+ and Λ^+ is thought to be a robust statistical summary of a community's taxonomic relatedness and will thus be the two taxonomic distinctness indices focused on (Clarke and Warwick 2001).

Taxonomic levels used included Species, Genus, Family, Order, Class and phylum and weights of these taxonomic levels were determined and standardized by taxonomic richness so that the distinctness of two species connected at the highest taxonomic level was equal to 100, based on the master species richness list for the KZN Bight midshelf (Clarke and Warwick 1999). Taxonomic diversity indices were tested for normality using the Shapiro-Wilk test of normality and the relationships between average taxonomic distinctness, variation in taxonomic distinctness and species richness were determined by using a Spearman rank correlation (ρ). Average taxonomic distinctness and variation in taxonomic distinctness are independent from each other and each can provide important different information concerning community diversity and the factors that influence it (Arvanitidis et al. 2002).

One possible problem with measures using taxonomic path lengths is that different phyla groups have received different degrees of attention and thus taxonomy is not always complete and consistent (Ellingsen et al. 2005). However this does not pose a problem for average taxonomic distinctness, as it is always relative as long as it has been treated consistently (Clarke and Warwick 1994,1999). Also, assuming species misidentification is random across the species pool, this problem is considered irrelevant to the calculation of average taxonomic distinctness and is a thus further motivation for using this robust measure of beta diversity (Clarke and Warwick 1998).

Taxonomic diversity was compared with alpha diversity observed number of species results from the South and North Bight, found in chapter 3. To determine any differences between taxonomic distinctness and species richness values, a One-way ANOVA ($\alpha = 0.05$) was performed using Tukey pairwise comparisons test between stations and a two-sample t-test ($\alpha = 0.05$) was done on index values and observed number of species between the South and North Bight sections.

To determine if communities along the Bight were significantly different from the expected taxonomic distinctness found in the KZN Bight midshelf, funnel and ellipse graphs (average taxonomic distinctness and variation in taxonomic distinctness pairs) were produced based on summed macrobenthic abundances (m^{-2}) per station, with 1000 maximum numbers of randomly chosen Species/phyla selections (sublists) for each M value (number of phyla) drawn from the master list of 1177 species when calculating statistics. This indicated the expected average taxonomic distinctness and variation in taxonomic distinctness at 95% confidence intervals, by superimposing the observed values relative to confidence intervals and expected values.

Boxplots, column charts and line charts using averages, standard deviations and standard errors of the generated taxonomic diversity indices and observed species richness factored as 'station' and 'section' (South and North) were used to explore data pertaining to the macrobenthos of the KZN Bight midshelf.

A Bray-Curtis resemblance matrix (Clarke 1993) was created from untransformed taxonomic diversity index data for the entire Bight and the North and South Bight sections for use in the BIOENV analysis found in the PRIMER v6 software package. By using a Draftsman plot it was determined which environmental variables were collinear and these were removed before further analysis. By using the procedure BIOENV (see Chapter 4, Section 4.2), environmental variables were correlated with the taxonomic diversity of the entire KZN Bight midshelf and North and South sections separately, by using Euclidean distance on $\log(x+1)$ transformed normalized non-collinear environmental variables in a weighted Spearman rank correlation (ρ). These were compared to environmental variables (see Tables. 4.3–4.7) identified as important to alpha and Whittaker's beta diversity from chapter 4. The strength and description of the relationship between important environmental variables and taxonomic diversity indices were ranked and used in polynomial quadratic, cubic and linear regressions analysis depending on

best fit. All analysis was done with the use of PRIMER-E version 6 (Clarke and Gorley 2006), Brodgar version 2.7.1, Sigmaplot 11.0, Excel 2010 and Minitab 16.

5.3 RESULTS

5.3.1 TAXONOMIC DISTINCTNESS ALONG SECTIONS OF THE KZN BIGHT

The KZN Bight midshelf macrobenthic community had taxonomic distinctness (Δ^*) value that averaged at 86.76 ± 5.02 (Table. 5.1). An average taxonomic distinctness (Δ^+) of 85.10 ± 4.67 was found, with the variation in taxonomic distinctness (Λ^+) of 447.27 ± 126.26 (Table. 5.1). Taxonomic distinctness and average taxonomic distinctness averages were much higher than the diversity measured by species richness alone for the entire KZN Bight midshelf (S 51.46 ± 31.05).

Table 5.1: Descriptive averages \pm standard deviations of the macrobenthic communities taxonomic distinctness (Δ^*), average taxonomic distinctness (Δ^+), variation in taxonomic distinctness (Λ^+) and observed number of species (S) of the KZN Bight midshelf.

Diversity indices	KZN Bight
Δ^*	86.76 ± 5.02
Δ^+	85.10 ± 4.67
Λ^+	447.27 ± 126.26
S	51.46 ± 31.05

In terms of taxonomic distinctness at the level of 'station', the mean values were highest for station I, followed by stations F and A. In terms of the average taxonomic distinctness, average values of the macrobenthic communities found in stations, station I had the highest value, followed by stations F and H, E and G. Mean values for the variation in taxonomic distinctness were highest in stations D and C. Mean species richness was highest in station C, B, E and A (Table. 5.2).

Averages and standard deviation values for taxonomic distinctness and average taxonomic distinctness was higher within the North section of the KZN Bight midshelf than the South section, while for the mean and standard deviation values of variation in taxonomic distinctness and species richness, the highest values were found within the South section of the KZN Bight (Table. 5.3).

Table 5.2: Descriptive averages \pm standard deviations of the macrobenthic communities taxonomic distinctness (Δ^*), average taxonomic distinctness (Δ^+), variation in taxonomic distinctness (Λ^+), and observed number of species (S) of stations along the KZN Bight midshelf. (For locations of stations refer to Chapter 2, Figure 2.1.)

Diversity indices	Stations								
	A	B	C	D	E	F	G	H	I
Δ^*	87.89 \pm 3.05	83.30 \pm 4.03	84.77 \pm 2.26	85.72 \pm 5.35	84.70 \pm 1.22	87.94 \pm 8.37	85.14 \pm 3.40	86.75 \pm 1.63	94.64 \pm 4.00
Δ^+	85.07 \pm 2.58	83.03 \pm 3.58	83.66 \pm 1.51	79.53 \pm 6.31	85.47 \pm 0.60	86.76 \pm 8.14	85.17 \pm 3.52	86.64 \pm 1.87	90.55 \pm 0.83
Λ^+	437.20 \pm 59.44	475.19 \pm 39.15	508.45 \pm 41.91	588.11 \pm 271.01	445.61 \pm 17.68	344.75 \pm 140.19	444.77 \pm 60.01	455.47 \pm 68.68	325.90 \pm 26.17
S	63 \pm 36.83	73 \pm 30.64	90 \pm 27.83	53 \pm 26.94	68 \pm 19.39	20 \pm 9.02	27 \pm 7.23	24 \pm 8.38	47 \pm 12.95

Table 5.3: Descriptive averages \pm standard deviations of the macrobenthic communities taxonomic distinctness (Δ^*), average taxonomic distinctness (Δ^+), variation in taxonomic distinctness (Λ^+), and observed number of species of the South and North section of the KZN Bight midshelf. (Refer to Chapter 2, Figure 2.2)

Diversity indices	KZN Bight section	
	South	North
Δ^*	85.27 \pm 3.59	88.62 \pm 5.95
Δ^+	83.35 \pm 3.91	87.28 \pm 4.70
Λ^+	490.91 \pm 130.33	392.72 \pm 98.63
S	69 \pm 30	29 \pm 14

One-way ANOVA with pairwise Tukey’s comparison tests indicates significant differences (< 0.01) between stations values of taxonomic distinctness, average taxonomic distinctness and variation in taxonomic distinctness means (Tables. 5.4 and 5.5). (For significant differences between observed numbers of species (S) refer to Chapter 3).

Table 5.4: Results of One-way ANOVA testing for significant differences between macrobenthic taxonomic distinctness, average taxonomic distinctness and variation in taxonomic distinctness of station (A-I) along the KZN Bight midshelf. (95% CI, Alpha = 0.05).

	Stations	
	F-value	P-value
Δ^*	3.71	< 0.01
Δ^+	3.38	< 0.01
Λ^+	3.08	< 0.01

Significant difference testing of taxonomic distinctness of stations with a pooled standard deviation of 4.230 indicates a significant difference between the means of stations B, D, E and G from station I (Table. 5.5). For average taxonomic distinctness of stations, with a pooled standard deviation of 4.009, the only significant difference was found between stations D and I (Table. 5.5).

One-way ANOVA significance test with Tukey’s pairwise comparison test of variation in taxonomic distinctness with a pooled standard deviation of 110.2, indicates that station D was significantly different from station F and I (Table. 5.5).

Table 5.5: Results of One-way ANOVA and Tukey 95% simultaneous confidence interval results of stations that significantly differ from each other, according to their taxonomic distinctness, average taxonomic distinctness and variation in taxonomic distinctness values. (95% CI, Alpha = 0.05)

Taxonomic Distinctness indices	Significantly different stations
Δ^*	B, D, E, G from I
Δ^+	D from I
Λ^+	D from F and I

According to a two sample t-test there was a significant difference between the South and North means of taxonomic distinctness, average taxonomic distinctness and variation in taxonomic distinctness (Table. 5.6). These tests supported results displayed in Figures 5.4, 5.5, 5.6, 5.7 and 5.8.

Table 5.6: Two sample t-test results for significant differences in macrobenthic taxonomic distinctness, average taxonomic distinctness and variation in taxonomic distinctness between the South and North sections of the KZN Bight midshelf. (95% CI, Alpha = 0.05).

North and South Bight			
	T-value	DF	P-value
Δ^*	2.42	35	< 0.05
Δ^+	3.28	44	< 0.01
Λ^+	-3.15	51	< 0.01

Figure 5.1 displays the expected variation of overall average taxonomic distinctness around the mean, and if station values of distinctness indices fell within those limits. The expected average

taxonomic distinctness of the KZN Bight midshelf was high, constant and the variation around it was generally very small, with the highest variation found at small numbers of species (Table. 5.7, Fig. 5.1). The average taxonomic distinctness of macrobenthic communities from stations fell mostly within the expected range of average taxonomic distinctness found within the entire Bight studied. However station I average taxonomic distinctness was significantly higher, and stations A and C average taxonomic distinctness were significantly lower than the expected range. All other stations remained within the expected average taxonomic distinctness range found within the KZN Bight midshelf study area (Fig. 5.1).

Table 5.7: Taxonomic path weights determined by taxonomic richness from the master taxonomy list of the entire KZN Bight midshelf macrobenthos.

Taxon	Richness	Weight
Species name	1177	15.762
Genus	453	28.603
Family	226	45.271
Order	79	61.489
Class	29	76.511
Phylum	12	100

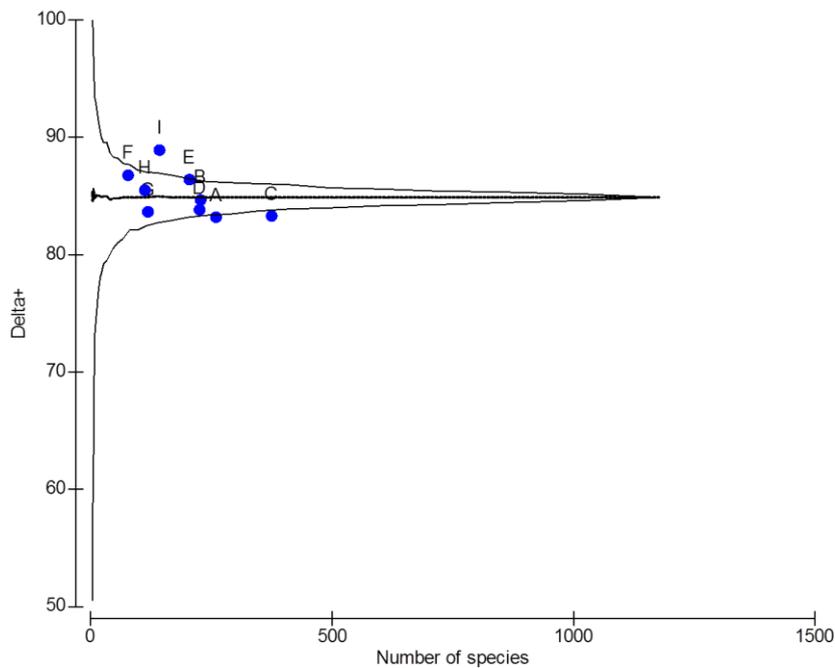


Figure 5.1: The 95% probability funnel for the macrobenthic average taxonomic distinctness values of stations along the KZN Bight midshelf. Expected mean indicated by the straight line in the middle of the funnel.

Figure 5.2 displays the expected variation of variation in taxonomic distinctness around the mean, and if station values fell within those limits. The expected theoretical mean of the variation in taxonomic distinctness was not constant as there was a steep decline with very small values of number of species (Fig. 5.2). The expected mean variation in taxonomic distinctness increased up to a certain level with the increase in the number of species present. Also, the variation around the mean was generally small especially at higher numbers of species. Again, stations I, A and C were significantly different from the expected range of variation in taxonomic distinctness found within the KZN Bight midshelf. In contrast to average taxonomic distinctness, station I was significantly lower and stations A and C were now significantly higher than the expected range (Fig. 5.2).

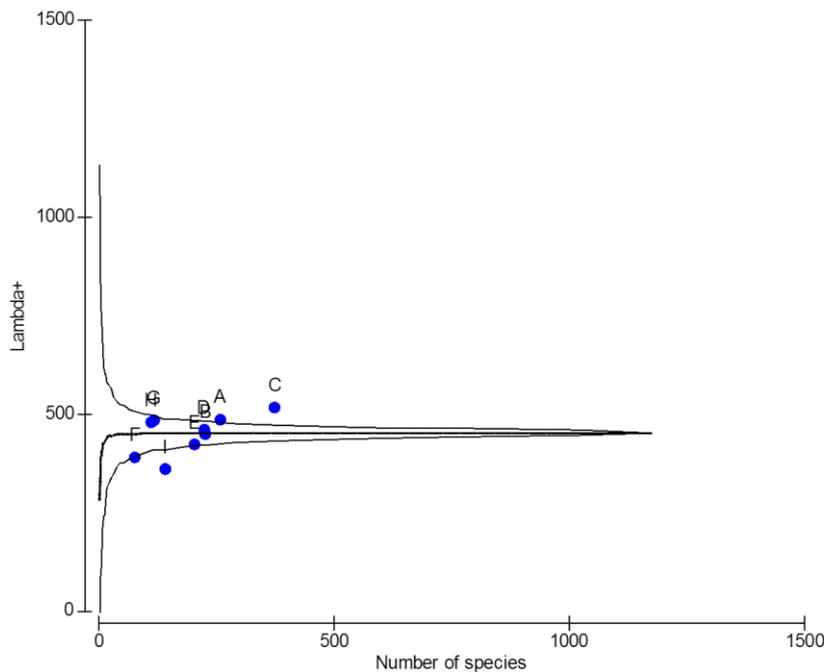


Figure 5.2: The 95% probability funnel for the macrobenthic variation in taxonomic distinctness values for stations along the KZN Bight midshelf. Expected mean indicated by the straight line in the middle of the funnel.

Combined expected average taxonomic distinctness and variation in distinctness indicates that all stations fell well within these ranges, close to the theoretical mean and none were significantly separated from expected ranges of the entire KZN Bight population (Fig. 5.3).

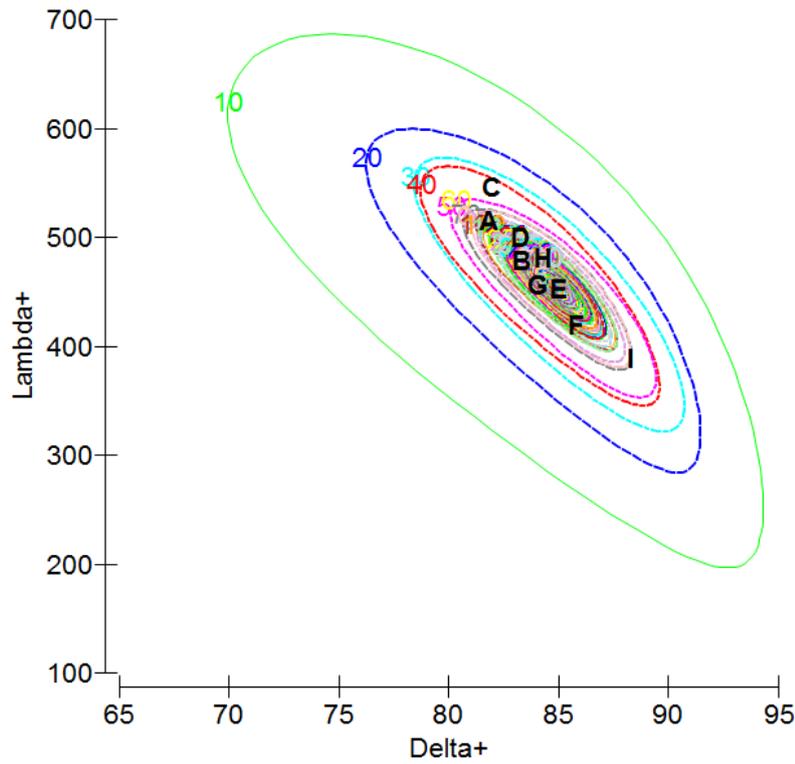


Figure 5.3: The 95% probability ellipse scatter plot indicating the region of expected average taxonomic distinctness and variation in taxonomic distinctness pairs from random selections of ($m = 1000$) species from the master list of the entire KZN Bight and the observed average taxonomic distinctness combined with variation in taxonomic distinctness of stations along the KZN Bight midshelf. Average taxonomic distinctness (Delta+), Variation in taxonomic distinctness (Lambda+)

From Figure 5.4 (refer to Chapter 3, Section 3.3.4, Figures 3.5, 3.6 and 3.7), it is apparent that taxonomic distinctness (Δ^*) and average taxonomic distinctness (Δ^+) were significantly higher within the North section of the KZN Bight than in the South section. Taxonomic distinctness and average taxonomic distinctness had a larger standard deviation within the North Bight than in the South Bight sections.

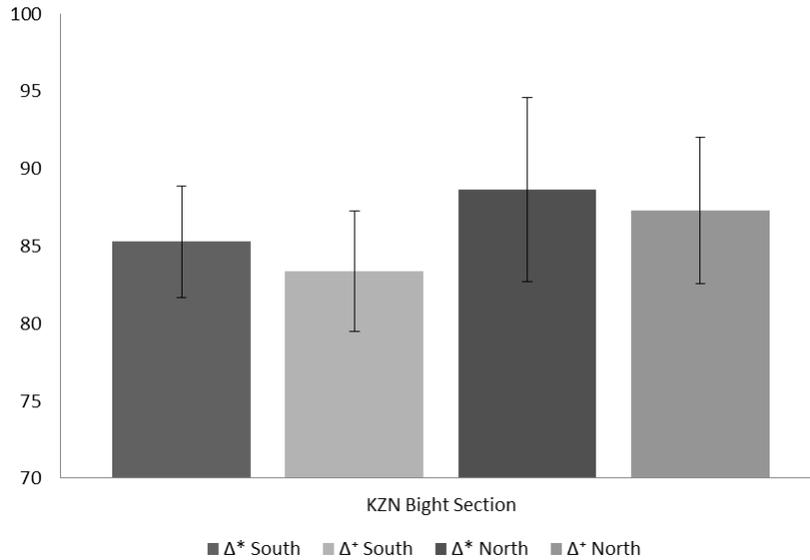


Figure 5.4: Averages and standard deviations of the South and North KZN Bight midshelf sections macrobenthic taxonomic distinctness (Δ^*) and average taxonomic distinctness (Δ^+) indices.

The variation in taxonomic distinctness (Λ^+) was significantly higher within the South Bight section (see Table 5.6 and Fig. 5.5, also refer to Chapter 3, Section 3.3.4, Figures 3.5, 3.6 and 3.7), however variability was comparable

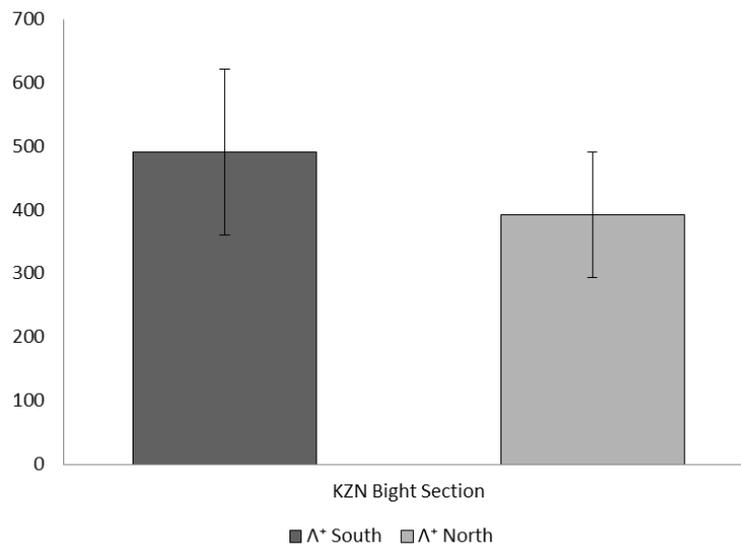


Figure 5.5: Averages and standard deviations of the variation in macrobenthic taxonomic distinctness in the South and North sections of the KZN Bight midshelf (Λ^+).

There existed significant correlations between average taxonomic distinctness and species richness ($R -0.344$, $P < 0.05$), between average taxonomic distinctness and variation in taxonomic distinctness ($R -0.879$, $P < 0.0001$) and between species richness and variation in taxonomic distinctness ($R 0.330$, $P < 0.05$), according to Spearman rank correlation testing (ρ). Where there was high species richness there were lower values of taxonomic distinctness and vice versa (Fig. 5.6, also refer to Chapter 3, Section 3.3.3 and 3.3.4, Figures 3.3, 3.5, 3.6 and 3.7). These areas of high species richness and low taxonomic distinctness were approximately located from stations A to E. Species richness was low but taxonomic distinctness was high especially from stations F to I. At station A, taxonomic distinctness and species richness were comparable at ~88.

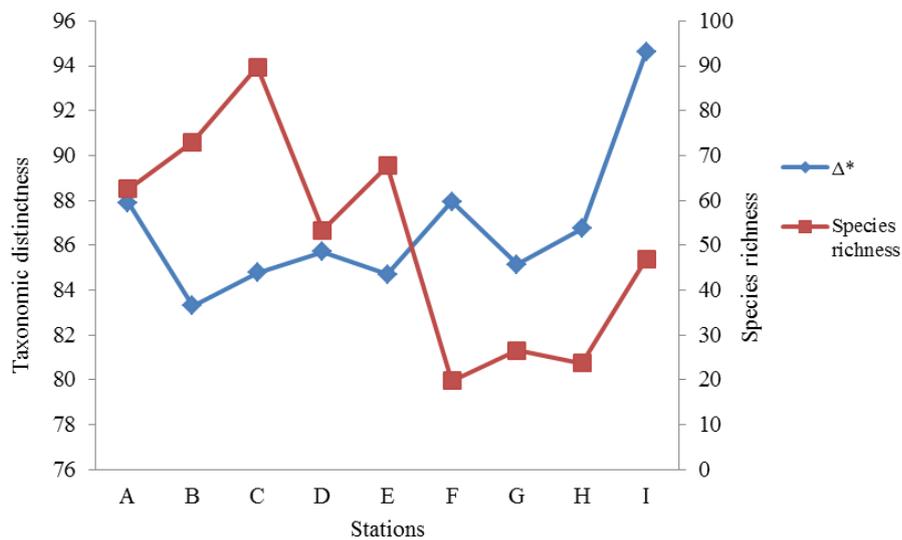


Figure 5.6: Change in macrobenthic fauna taxonomic distinctness and species richness along the KZN Bight midshelf. Taxonomic Distinctness (Δ^*)

Compared to taxonomic distinctness, average taxonomic distinctness along the KZN Bight midshelf study area, followed the same trend (Fig. 5.7, also refer to Chapter 3, Section 3.3.3 and 3.3.4, Figures 3.3, 3.5, 3.6 and 3.7). In stations A and I average taxonomic distinctness and species richness were also comparable to the trend found in Figure 5.6. Average taxonomic distinctness was highest in station I. Generally there was a lower average taxonomic distinctness in areas (south of the Thukela) with higher species richness, and a higher average taxonomic distinctness than species richness in areas north of the Thukela river mouth.

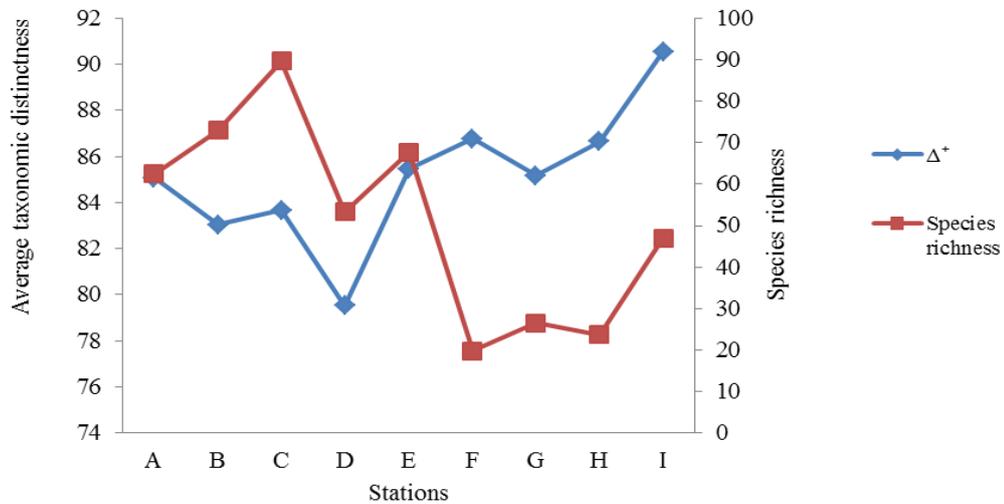


Figure 5.7: Change in macrobenthic fauna average taxonomic distinctness and species richness along the KZN Bight midshelf. Average Taxonomic Distinctness (Δ^+).

Variation in taxonomic distinctness along the KZN Bight followed the same general pattern as that of species richness, decreasing from stations A to I (Fig. 5.8, also refer to Chapter 3, Section 3.3.3 and 3.3.4, Figures 3.3, 3.5, 3.6 and 3.7). Stations in the South region of the KZN Bight midshelf had a significantly (see Table. 5.6) higher variation in taxonomic distinctness than the stations located in the North section of the Bight. Variation in taxonomic distinctness in the South Bight was approximately comparable in trend with species richness until station D. Here variation in taxonomic distinctness was higher than the species richness. From station F to H variation in taxonomic distinctness was higher than species richness, with comparative values being found at stations E and I, but lower than that found within the South section of the KZN Bight midshelf. Thus in spite of the higher species richness found in the South Bight, the high level of variation in taxonomic distinctness in this region supports other results, that this region is less taxonomically diverse. The converse was true of the North Bight. Also, in support of previous results on beta diversity in Chapter 3, this section of the KZN Bight supported communities that were taxonomically more rich and unrelated to the South section of the Bight.

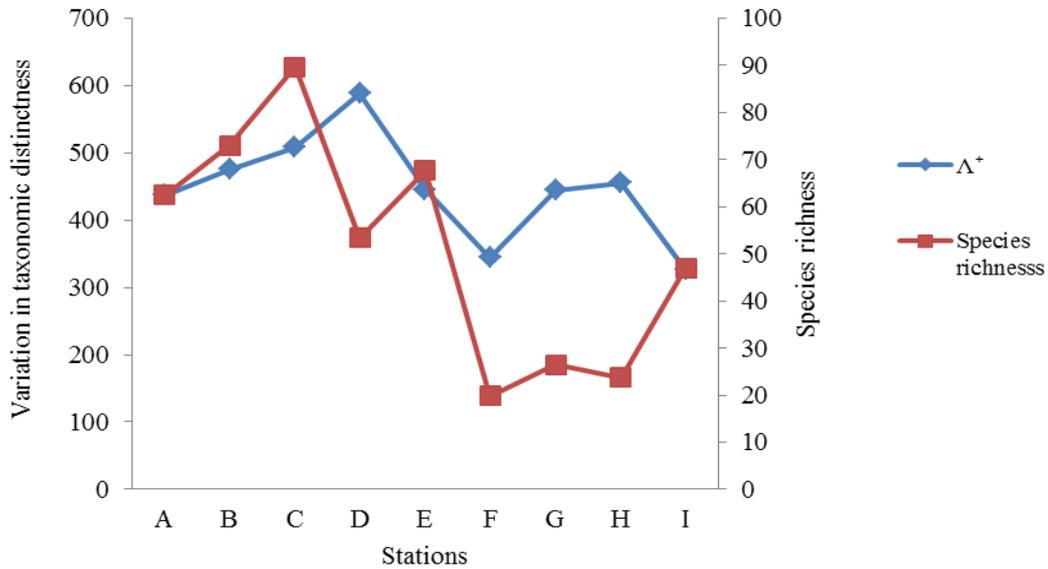


Figure 5.8: Change in macrobenthic fauna variation in taxonomic distinctness and species richness along the KZN Bight midshelf. Variation in Taxonomic Distinctness (Λ^+)

5.3.2 TAXONOMIC DISTINCTNESS AND ENVIRONMENTAL PARAMETERS

The KZN Bight midshelf macrobenthic community taxonomic distinctness indices were most significantly explained ($Rho = 0.281$, $P < 0.05$) by temperature [$^{\circ}C$], salinity [PSU] and % coarse sediment content (Table 5.8, also refer to Chapter 4, Section 4.3.2, Tables 4.3 and 4.5). These important environmental variables were similar to those that best explained patterns of abundance (m^{-2}) namely temperature [$^{\circ}C$], salinity [PSU], % organic matter, % fine sand and % very fine sand (see Chapter 4, Section 4.3.2). However % coarse sand was more important than fine sand in explaining beta diversity (taxonomic diversity) than for abundance (m^{-2}) of the Bight. These sediment attributes are related to sediment skewness. Sediment skewness played the most important role in explaining alpha diversity of the KZN Bight midshelf macrobenthic communities (see Chapter 4, Section 4.3.2). Alpha diversity of the North section of the Bight was best explained by depth (m) differences, despite trying to account for this confounding effect by sampling along a relatively constant depth gradient. Depth (m) showed the highest correlation with Whittaker's beta diversity ($R = -0.849$, $P < 0.01$). Here taxonomic distinctness indices calculated from the North section of the Bight were best explained by % fine sediment content ($Rho = 0.306$, $P < 0.05$). Comparable to results of correlations with alpha diversity measurements (Chapter 4), no measured environmental variables could explain the patterns of taxonomic diversity found within the South Bight.

Table 5.8: BIOENV identified environmental variables correlated to taxonomic distinctness measures of the KZN Bight midshelf and sections thereof.

KZN Bight Taxonomic distinctness and important environmental variables			
	Rho	P-value	Environmental variables
KZN Bight	0.281	< 0.05	Temperature, Salinity, Coarse sediment
North Bight	0.306	< 0.05	Fine sediment
South Bight	0.023	> 0.05	None

The strength of the relationships between significant environmental variables and taxonomic diversity indices was confirmed by regression analysis of ranked values (Fig. 5.9). Even with regression models that best fit these relationships, the strength with which these environmental variables explained observed taxonomic diversity was low, though significant. Water temperature [°C] significantly explained 27% of the variation in taxonomic distinctness, generally having a positive relationship that is as temperature increased so too did taxonomic distinctness. The relationship taxonomic distinctness had with salinity was a little more complex and less linear. Salinity significantly explained 27% of variability in taxonomic distinctness. Percentage coarse sediment distribution best explained taxonomic distinctness of the Bight (R^2 0.342, F-value: 8.472, $P < 0.001$). Taxonomic distinctness generally followed a negative relationship with coarse sand as there was a decrease in taxonomic distinctness with an increase in the amount of coarse sand present.

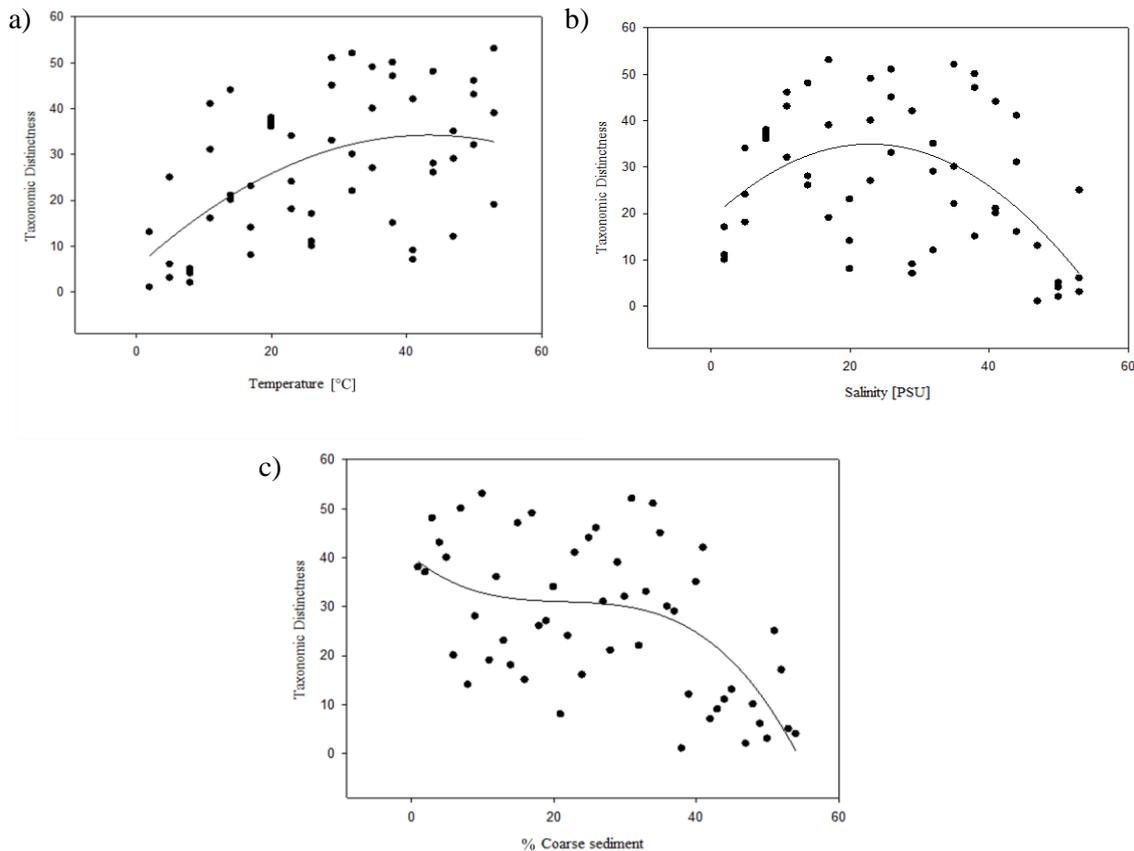


Figure 5.9: Regressions of a ranked taxonomic distinctness index and ranked important environmental variables. a) Quadratic regression with temperature (R^2 0.269, F-value: 9.206, $P < 0.001$), b) Quadratic regression with salinity (R^2 0.272, F-value: 9.321, $P < 0.001$), c) Cubic regression with coarse sediment (R^2 0.342, F-value: 8.472, $P < 0.001$).

As for average taxonomic distinctness, salinity [PSU] (59%) followed by temperature [°C] (41%) significantly explained most of the variation found within the Bight (Fig. 5.10). Ranked average taxonomic distinctness seemed to have a simple linear positive relationship with ranked temperature [°C] (Fig. 5.10). Ranked average taxonomic distinctness had a combination of positive and negative relationships with changing salinity values, as there was an initial decrease in average taxonomic distinctness with the decrease in salinity followed by an increase with the further decrease in salinity levels (starting at approximately 35.446 PSU). Ranked percentage coarse sediment values explained 30% of variation found in the average taxonomic distinctness. Similar to the relationship seen with taxonomic distinctness, there was a general negative relationship of average taxonomic distinctness to the proportion of percentage coarse sand present, with a decrease in average taxonomic distinctness with the decrease in the amount of coarse sand, and then increasing as the amount of coarse sand decreased further.

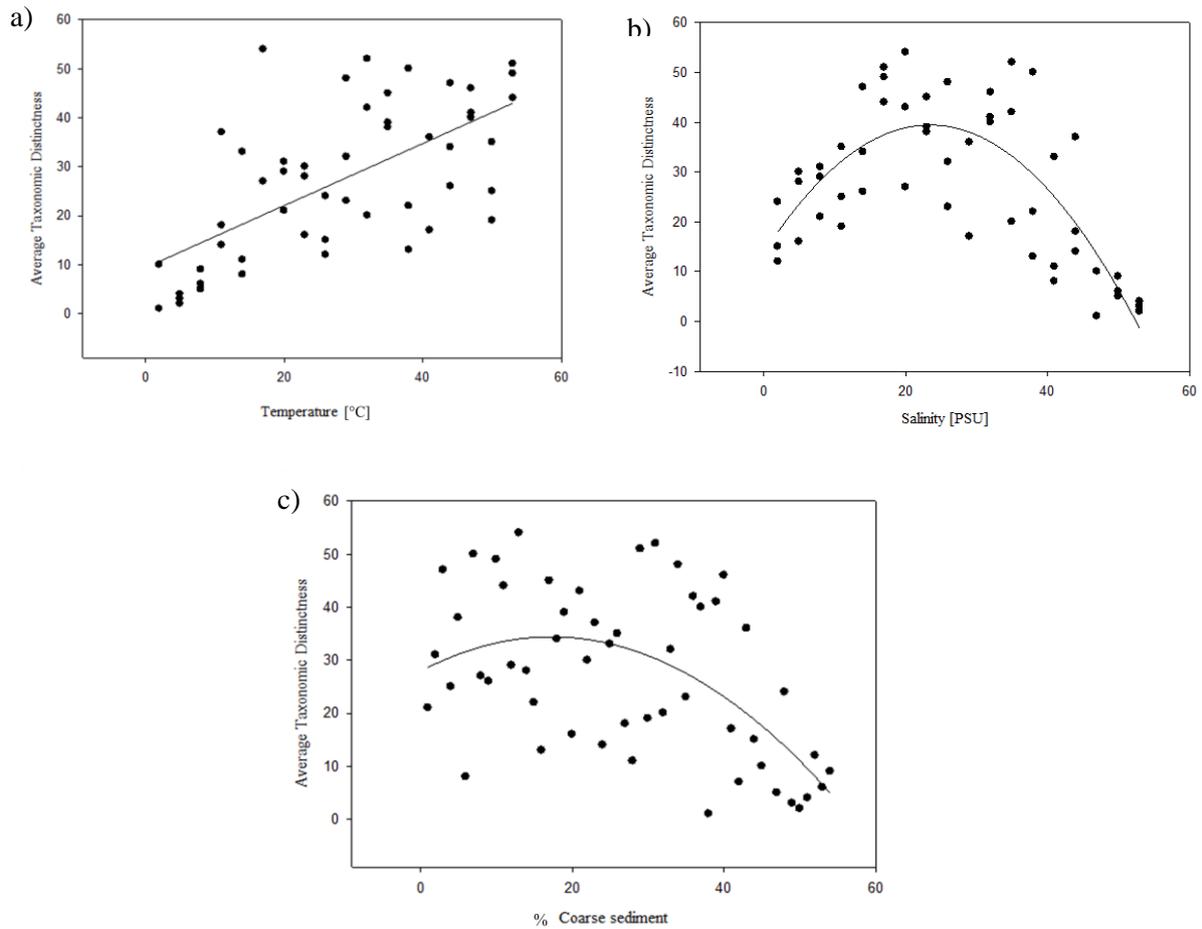


Figure 5.10: Regressions of ranked average taxonomic distinctness index and ranked important environmental variables. a) Linear regression with temperature (R^2 0.413, F-value: 34.529, $P < 0.001$), b) Quadratic regression with salinity (R^2 0.589, F-value: 35.151, $P < 0.001$), c) Quadratic regression with coarse sediment (R^2 0.299, F-value: 10.676, $P < 0.001$).

In contrast to both taxonomic distinctness and average taxonomic distinctness, ranked variation in taxonomic distinctness followed opposite relationships to ranked important environmental variables found (Fig. 5.11). Here salinity explained most of the variation found (46%). Ranked variation in taxonomic distinctness followed a negative relationship with temperature [°C]. Variation in taxonomic distinctness initially increased with the decrease in salinity. The highest level of variation in taxonomic distinctness was found at a salinity of around 35.446 PSU. Variation in taxonomic distinctness generally had a positive relationship with the percentage coarse sand. Variation in taxonomic distinctness seemed to be constant at certain higher levels of coarse sand and decreased with further decreases in the percentage coarse sediment present.

These results agree with the general environmental patterns found within the KZN Bight midshelf as areas of higher temperatures, fine sand with greater proportion coarse sediment, lower organic content, and lower salinity tended to have higher taxonomic distinctness, average taxonomic distinctness values and low variation in taxonomic distinctness values.

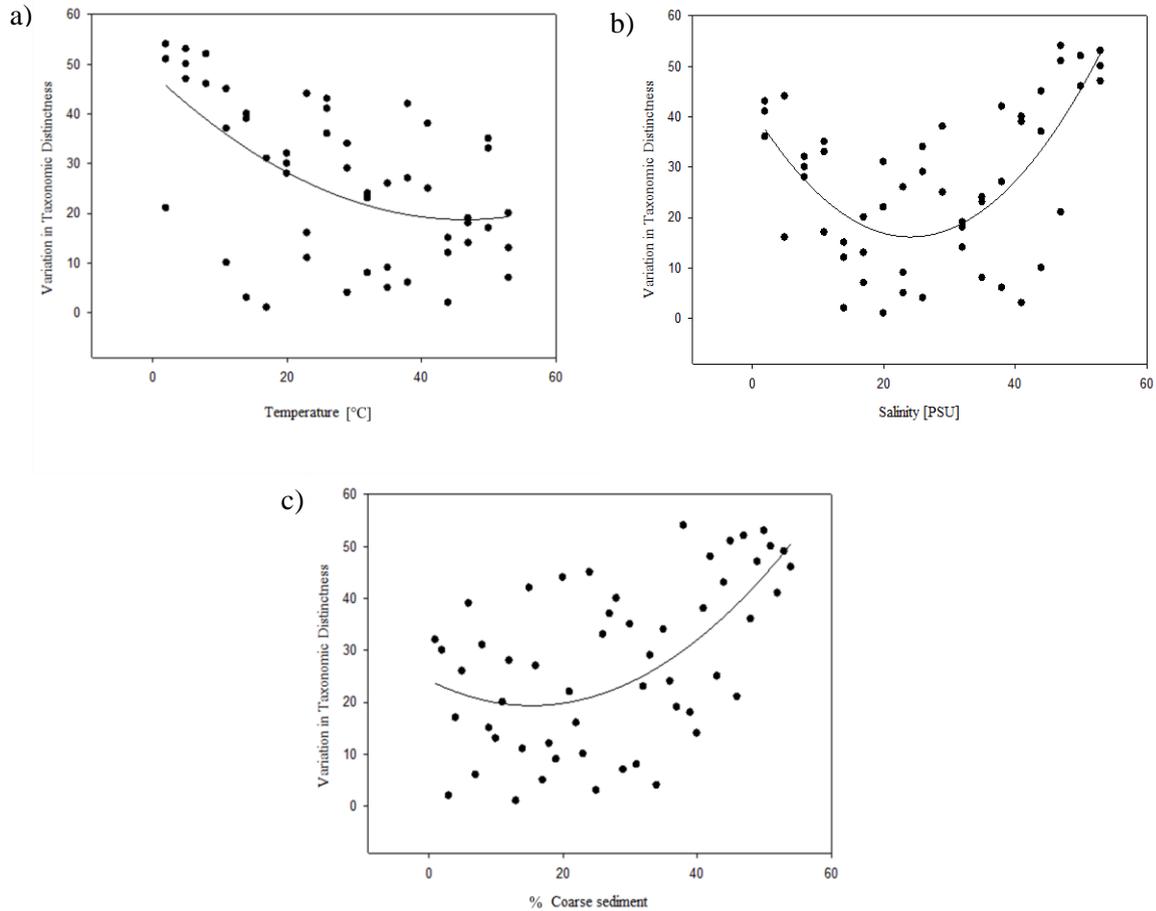


Figure 5.11: Regressions of ranked variation in taxonomic distinctness index values and ranked important environmental variables. a) Quadratic regression with temperature (R^2 : 0.308, F-value: 10.667, $P < 0.001$), b) Quadratic regression with salinity (R^2 : 0.461, F-value: 20.493, $P < 0.001$), c) Quadratic regression with coarse sediment (R^2 : 0.342, F-value: 13.230, $P < 0.001$).

Regarding the findings that taxonomic distinctness and average taxonomic distinctness increase with the decreasing amount of coarse sand and that the variation in taxonomic distinctness increased with increasing amounts of coarse sand, the higher taxonomic diversity in the North Bight is best explained with the proportions of fine and coarse sand present (Fig. 5.12). Ranked taxonomic distinctness had inconstant and a varying relationship with ranked percentage fine sand values, in some instances increasing with the decrease in fine sand and in others decreasing

with the decrease in fine sand. Ranked average taxonomic distinctness and variation in taxonomic distinctness shows approximately linear and constant relationships with ranked percentage fine sand content. Average taxonomic distinctness had a positive relationship with percentage fine sand, while variation in taxonomic distinctness had a negative relationship with fine sand.

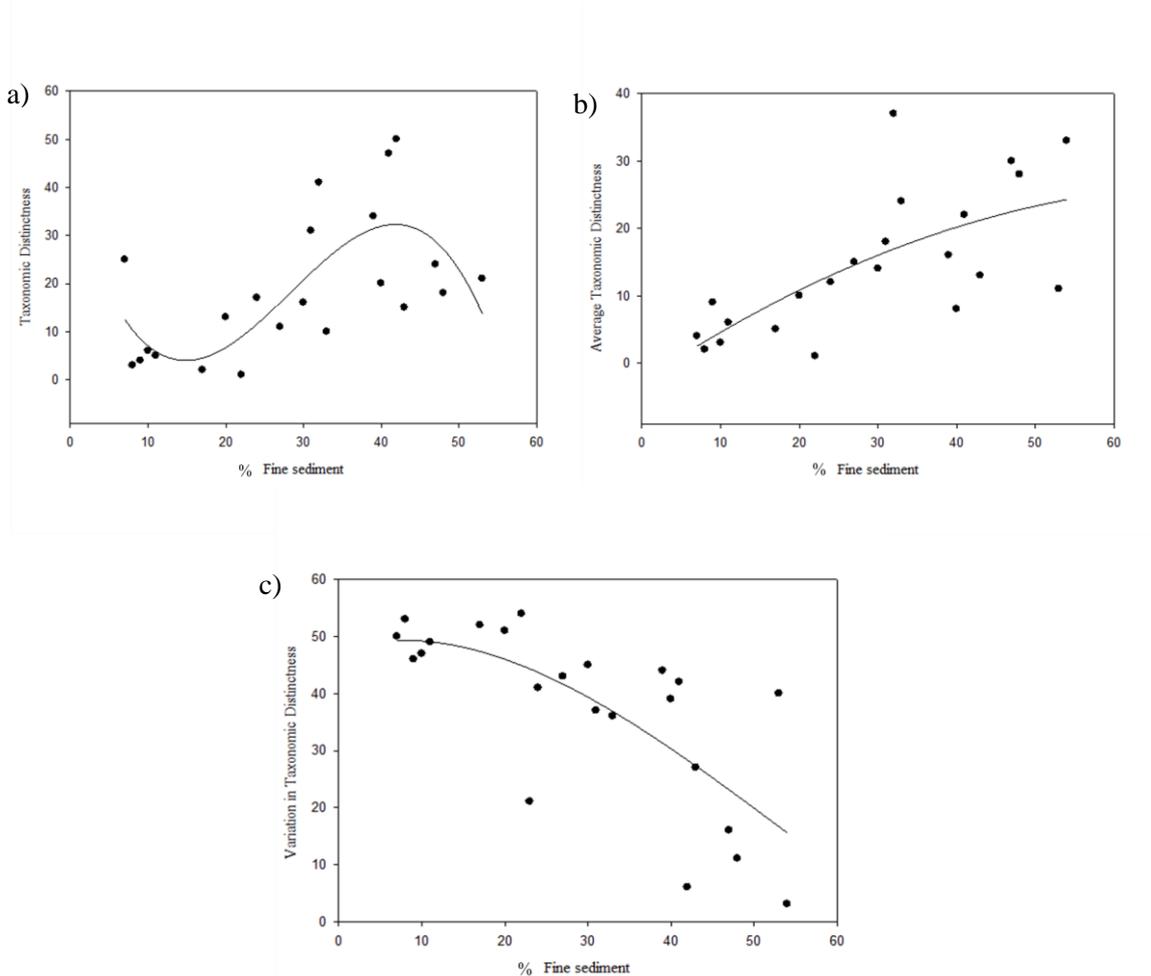


Figure 5.12: Regressions of ranked taxonomic distinctness indices with ranked important environmental variables found in the North Bight. a) Cubic regression of taxonomic distinctness with fine sediment (R^2 0.502, F-value: 6.059, $P < 0.01$), b) Quadratic regression of average taxonomic distinctness with fine sediment (R^2 0.482, F-value: 8.825, $P < 0.01$), c) Cubic regression of variation in taxonomic distinctness (R^2 0.521, F-value: 6.8854, $P < 0.01$).

5.4 DISCUSSION

5.4.1 TAXONOMIC RELATEDNESS VS. SPECIES RICHNESS

Shallow water habitats support rich and diverse communities (Clarke et al. 2004) and within these habitats, the relative role that local factors and regional diversity play vary greatly and this is why one may find considerable varying habitats and communities within the same geographic region (Kiflawi et al. 2003). Diversity values will depend on the element of diversity measured within different regions (Ellingsen and Gray 2002). As species richness and taxonomic distinctness are not related to the same environmental gradients, they describe diversity differently, as both are context-dependent as well (Heino et al. 2005). Along the KZN Bight, alpha diversity (as species richness) and beta diversity (as taxonomic distinctness (average and variation) and Whittaker's diversity (β_w)) followed opposite trends from south (from Durban) to north (to St. Lucia). These opposite and directional gradients results were not at all unique as many other studies have found similar patterns. Rogers et al. (1999), Ellingsen et al. (2005) suggested that it is not clear if all communities with a small number of species necessarily would have lower taxonomic distinctness values compared to communities with large numbers of species present, and this has apparently not been tested at a range of spatial scales.

Some studies however did not find these relationships between alpha and beta diversity, highlighting the unknown complexity of important role players, differing from location to location and between different phyla. In Britain it was found that community turnover was a small component of the regional community patterns as it was predominated by a strong gradient in alpha diversity (Harrison et al. 1992). Rogers et al. (1999) on the other hand found that there could also be positive correlations between taxonomic distinctness and species richness, such as for bottom-dwelling fish communities from the North-east Atlantic. However these results seem to be related to the spatial scale used in the study, because at local scale the same trend was not followed (Rogers et al. 1999).

The relationship between habitat heterogeneity and beta diversity is dependent on the spatial scale observed, and beta diversity seems to be higher at small spatial scales than at large scales (Izsak and Price 2001, Ellingsen 2002, Hewitt et al. 2005). For Ellingsen (2002), location rather than scale was the more important factor for the observation of beta diversity of macrobenthic fauna communities. In a study on the relationship between species richness and taxonomic distinctness of macrobenthic invertebrates from Finland's freshwater streams and lakes, Heino et al. (2005) found that there was much variation in the relationship between these diversity

measures, which at times ranged from significantly negative, positive or non-significant relationships. The increase of species richness with the decrease in average taxonomic distinctness is usually a scenario associated with the increase in highly related species and not species from highly different taxonomic levels (Heino et al. 2005).

According to Heino et al. (2005) a positive relationship between average taxonomic distinctness and species richness could also be associated with high ecological and habitat heterogeneity as this promotes taxonomic diversity as fauna were adapted to different conditions and thus species richness would increase, however with a negative relationship between these indices, habitat heterogeneity also can play a significant role, as species richness increases as a result of largely similar congeneric species either adapting to slightly different niches or avoid direct competition in heterogeneous conditions (Heino et al. 2005). On the other hand, within the North Bight region, higher taxonomic diversity could have been promoted because of the relatively lower amount, higher quality, and different type of, sporadic nutrient supply, and greater habitat heterogeneity compared to the South Bight.

As was found in Thayer (1986), and Kiessling and Aberhan (2007), Brachiopods that generally had a higher rate of speciation than Bivalves were commonly located within nutrient-deficient, low-turbidity, carbonate environments, as they are more resistant to starvation. Also, Hoffmann and Hercus (2000) and Nevo (2001) found that stressed environments with small temporal scale environmental disturbances and heterogeneity support greater speciation rates by creating and maintaining genetic diversity variability while also decreasing gene flow. Within environments that have many fluctuations, species richness tends to be lower as fewer species are adapted to these conditions especially over a short evolutionary time (Gray 2002). As communities from disturbed and undisturbed regions could have the same species diversity and yet different taxonomic distinctness values, it is speculated that any biome may have consistent genetic complements while there are differences in the division of species among hierarchical taxonomic units, that are related to the age of succession (Warwick and Clarke 1995). So the answer remains unclear if there was a difference between the environmental stability between the South and North KZN Bight regions and if this played an important role in the taxonomic distinctness and alpha diversity values observed.

However our study result could not exactly fall within any one of the categories described by Warwick and Clarke (1995). In future, it is important to determine the types (anthropogenic or natural) and strengths of disturbance found within the South and North KZN Bight midshelf.

Could it possibly happen that a more stable environment would have more related phyla with highly diversified species and in more unstable environments more unrelated phyla with fewer diversified species?

Beta diversity index values are strongly influenced by the relative values of common and rare species present, and were found to be higher in areas with more rare species that have restricted ranges (Clarke and Lidgard 2000, Ellingsen 2001, Munari and Mistri 2008). Hong Kong waters had high beta diversity in contrast to the low alpha diversity of macrobenthic fauna observed (Shin and Ellingsen 2004). Also here, the high proportion of rare species found with limited distribution had contributed to the high beta diversity and low local alpha diversity (Shin and Ellingsen 2004). This may have also played a role in the differences observed between the South and North Bight.

According to Shmida and Wilson (1985) beta diversity has two components namely habitat differentiation and ecological equivalency. These are related to the variety within habitats and species that are similar enough to functionally replace each other within the specific habitat (Shmida and Wilson 1985). The diversity of a macrobenthic community at any scale is maintained by the diversity at a lower level determined by habitat heterogeneity and niche differences (Loreau 2000). Beta diversity reflects different habitats found and the degree to which the species utilise it (Wilson and Shmida 1984). The trend in taxonomic distinctness could be related to a positive correlation with trophic diversity, independent of species richness of the area, as Warwick and Clarke (1998) found in their study on marine Nematodes, where a reduction in trophic diversity led to a reduction in taxonomic distinctness and not necessarily species richness. Thus in the North section of the KZN Bight with a higher average taxonomic distinctness a more diverse trophic structure could in theory be found and this indicates a highly variable specialised community adapted to a variety of niches and conditions. This can support the notion that there was a higher taxonomic distinctness within the North area of the KZN Bight as there was more variable environmental factors present, contributing to more specialised species and resilient communities, within this section of the Bight.

If taxonomic diversity equals ecological diversity, supporting more non-related species through for example mutualistic relationships, then the relative macrobenthic taxonomic range and specialisation may be important in maintaining the stability of the ecosystem during natural or anthropogenic disturbances (Tilman 1996, Rogers et al. 1999). Warwick and Clarke (1998) postulated that taxonomic distinctness and taxonomic composition reflect the pressures imposed

by ecological and evolutionary mechanisms and thus a limited amount of species would be capable of tolerating a physiologically stressful environment.

Generally habitat type seemed to be the major role player in the establishment of taxonomic distinctness and trophic group diversity (Ellingsen et al. 2005). Ellingsen and Gray (2002), Munari and Mistri (2008), found that on the Norwegian continental shelf habitat heterogeneity was a more prominent driver in macrobenthic fauna beta diversity than distance between sites. It was argued that with distance, there was an increase in habitat dissimilarity, and beta diversity is expected to increase with increasing habitat heterogeneity, while this was not necessarily the case with alpha diversity (Harrison et al 1992, Ellingsen and Gray 2002). Ellingsen and Gray (2002) speculated that the mean alpha diversity could be similar in heterogeneous and homogenous environments. Diversity can have a large rate of species turnover even within apparent homogenous habitats (Ellingsen 2001, Levin et al. 2010). According to Clarke and Lidgard (2000), the similar alpha diversity of Bryozoan fauna across all latitudes in the North Atlantic and the contrasting increase of beta diversity towards the lower latitudes was an indication of greater habitat heterogeneity contributing to greater beta diversity and greater habitat heterogeneity found in the warmer water environments.

Communities with high beta diversity have species with narrow and not highly overlapping niche tolerance for immediate factors such as temperature, rainfall, salinity and the associated large scale habitat changes (Harrison et al. 1992). The relative relatedness of habitat heterogeneity to diversity could be very context determined; as it depends on what part of the environment diversity is measured against. According to Heino et al. (2005), because of the great varieties of possible environmental variables that are important in determining biodiversity patterns, and the different relationship of these biodiversity patterns with environmental gradients, it is important to consider that communities will consist of fauna well adapted to that specific environment, such as was found in the lakes and streams in Finland. Contingency and context dependence hinders the generation and understanding of generalised and set patterns in biodiversity (Heino et al. 2005).

Much shell debris was found along the North part of the KZN Bight. Hewitt et al. (2005) highlighted the importance of especially small scale habitat heterogeneity in maintaining and creating a fruitful habitat for high species alpha and beta diversity. It is emphasised that temporary or persistent biogenic features, such as shell patches, even though small in scale, can contribute and drive an appreciable amount to the structural, functional and biological

heterogeneity (turnover rate) within the shelf environment (Hewitt et al. 2005). The influence of these biogenic shell patches depended on the patch size, density and debris particle size (Hewitt et al. 2005).

5.4.2 ENVIRONMENTAL INFLUENCES

As depth was the only significant environmental variable negatively correlated with the KZN Bight Whittaker's beta diversity and also explained most variability in alpha diversity in the North, depth associated variables like high temperature and lower salinity seemed to favour higher Whittaker's beta diversity and taxonomic distinctness. While coarse sand was one of the variables best explaining the overall macrobenthic taxonomic distinctness, and fine sand best explained taxonomic distinctness in the North Bight section, it could be inferred that coarse sand actually affected taxonomic distinctness negatively, but the association with small amounts of fine sand increased taxonomic distinctness. The absence of an excessively large amount of fine sand could have promoted taxonomic distinctness in the North Bight. Thus different macrobenthic assemblages were found within the South and North KZN Bight midshelf sections, and these assemblages differed in taxonomic distinctness because of internal taxonomic hierarchy and different responses to the environment between phyla.

The correlation between the macrobenthic community structure and the physical environmental variables was weak. Cusson et al. (2007) attributes this to community structure being better influence by the complex interaction between these abiotic variables and the macrobenthic communities. According to Leduc et. al. (2012), it is a combination of different environmental factors such as organic matter, terrestrial detritus, currents, temperature, oxygen concentrations and macro-habitat heterogeneity that determine beta diversity of a community within habitats. According to Gray (2002), evidence suggested that temperature, sediment grain size and production were the main determinants responsible for species turnover over local and regional scales. The patterns of species richness and taxonomic relatedness measures found along the midshelf of the KZN Bight were thought to be the result of two different ecological systems functioning in the South and North half of the Bight. This could have been due to potentially different nutrient regimes found in the two sections (see also Ayers and Scharler 2011, De Lecea et al. 2013). Low available food resources support smaller populations and according to Levin et al. (2001), larger food resource supply would support larger communities, however species richness and/or taxonomic diversity would fall (Gray 2002). This is because of a greater increase in competition for available resources or because of a more homogenous habitat (Gray

2002). Thus communities could be dominated by a few species or phyla (Gray 2002), such as was speculated to be the situation in the South Bight and the opposite in the North Bight section. Bremner et al. (2006) concluded that dominating functional traits in macrobenthic assemblages were associated with the complexities and changes in physic-chemical factors such as temperature, salinity and shell content, biotic factors such as fish species richness, and anthropogenic factors such as fishing effort, within the Irish Sea and the eastern Channel regions. Diversity of macrobenthic fauna communities depends on a combination of local and regional abiotic habitat heterogeneity, biological interactions and demographic uncertainties (Munari and Mistri 2008).

In line with this it was found that in the entire macrobenthic community sampled from the Norwegian shelf overall taxonomic distinctness of the macrobenthic community, also had a negative relationship with depth (Ellingsen et al. 2005), similar to our results found for Whittaker's beta diversity overall. Because phyla are differently influenced, Polychaetes and Crustacean groups alpha diversity and beta diversity on the Norwegian continental shelf had a positive relationship with depth, and depth also explained the highest amount of variance for these groups, while latitude explained the highest amount of variance in the entire macrobenthic community taxonomic distinctness (Ellingsen et al. 2005).

Also in our study, factors associated with depth and location, like temperature, salinity and coarse sand best explained beta diversity and taxonomic distinctness of the entire macrobenthic community. The environmental factors most significantly explaining our KZN Bight midshelf macrobenthic community best were variables associated with the change in depth and thus correlated with results previously mentioned. According to Gray et al. (1997), macro-invertebrate and fish communities species richness increase with moderate increases in moderate depth, and thereafter decrease again with further increases in depth. This was seen in our study as species richness increased with increasing depth in the South region. Sanders (1968) found that in tropical regions, shallow areas had the highest species diversity; however Grassle and Maciolek (1992) found results that indicated that in shallow regions outside the tropics marine communities tended to have a much lower species richness compared to deeper regions. The number of species found per unit area in the deep seas has been found to be higher than in shallow regions (Gray 2002).

The Norwegian shelf total community variability was best explained by latitude, however this has been shown not to be latitude directly but also environmental variables that change with

latitude like temperature, salinity, organic matter and so forth (Rohde 1992, Ellingsen et al. 2005). Heip et al. (1992) also found that longitude and depth had an effect on diversity on the North Sea macrofauna. In the KZN Bight, salinity was marginally higher in the South than in the North. This could have been the contribution of the close inshore north flowing current reversals. Thus possibly in the North Bight, sudden and periodic increase in low salinity could be responsible for decreased species richness as not many species are adapted to sudden changes in environments (Gray 2002, Warwick et al. 2002, Munari and Mistri 2008).

The relationship between sediment physical and chemical characteristics and their gradual change in space and time, and macrobenthic species composition, is well known for shallow habitats (Fonseca and Soltwedel 2009, Vanaverbeke et al. 2011, Leduc et al 2012). Sediment grain size at the Bay of Biscay decrease from the coast towards the slope of the continental shelf, thus from shallow to deep (Louzao et al. 2010). On the slope of the continental shelf of Spain, Louzao et al. (2010) found that this area represented unique key habitats , where reef-forming phyla were found maintaining a high level of diversity. This could have been possible in the North section of the KZN Bight as evidence of reef building fauna (Cnidaria and Polychaetes: Serpulidae) was found. Although sediment characteristics, as well as water mass characteristics, strength of pelagic-benthic coupling, and organic content, are important and significantly correlated to community composition, it is a fact that sediment characteristics are proxies for the underlying physical forces driving sediment and fauna characteristics, such as physical dynamics of currents, sources of disturbance, and the delivery of food (Thistle 1981, Snelgrove and Butman 1994, Grebmeier et al. 2006).

Chandrasekar et al. (2012) found that benthic macrofauna diversity was highly inter-correlated with coarse sand and this was also correlated with the supply of organic matter as a source for the food webs found along the Indian coast between Poompukar and Nagoor. In essence sediment conditions providing optimal niche heterogeneity and amounts and types of nutrients played a significant role in determining alpha and beta diversity along the Bight. Many other paleo studies have found a strong link between macrobenthic biodiversity and lithological (substrate) affinities (Miller and Connolly 2001, Foote 2006). According to Parry et al. (1999), which did a study on macrobenthic assemblages in and around Plymouth Sound, the type of species present and turnover in composition will change according to sediment granulometry, however these patterns may not have been caused by sediment granulometry directly but by factors associated with the granulometry, such as long term hydrography effects, short term disturbances, suspension, and organic flux variability (Buller and McManus 1979, Snelgrove

and Butman 1994). Therefore a measure of sorting variability as a measure of habitat heterogeneity, rather than just coarseness or fineness, may be a better measure to use when trying to link the environment to the macrobenthic community biodiversity (Parry et al. 1999). Gray (1981) said that wave action and current velocity are the two most important factors determining grain size distribution and sorting of sediment. In the subtropical Hong Kong water, Shin and Ellingsen (2004) found that the environmental variables best explaining beta diversity were, among others, depth, longitude and median grain size. It was speculated that other factors, in a biological or non-biological form, to have contributed to the level of beta diversity found (Shin and Ellingsen 2004).

According to Jayaraj et al. (2007), and Long and Lewis (1987), increased richness and alpha diversity of macrobenthic communities were attributed to the increased proportion of coarse sediment (and sand), even independent of bathymetry, and the increase in temperature. Coarse sediment has been found in other studies to harbour higher diversity than fine sediment, possibly mainly due to the very high organic content associated with the fine sediment, however medium sediment with moderate sorting have been known to have the highest diversity of macrobenthos (Rodrigues et al. 1982, Ingole et al. 2002). For example around the Plymouth Sound area, macrobenthic assemblage's beta diversity and species richness was found to be significantly positively determined by coarser more heterogeneous sediment and thus habitat complexity, than found in the finer more homogenous sediment of the study areas (Parry et al. 1999). The increased habitat complexity produced by the coarser sediment increases living space, providing for the occurrence of species with different life histories and life styles, as well as protection from predators (Morse et al. 1985, Gibbons 1988, Parry et al. 1999).

As the sediment characteristic have been found to be highly correlated with the taxonomic distinctness and thus diversity of possible trophic levels present (Warwick and Clarke 1998), a higher taxonomic distinctness and trophic diversity in the North part of the Bight and a lower value in the South may indicate a change in taxonomic distinctness along a possible nutrition gradient from South to North facilitated by the presence of different proportions of coarse and fine sediment. River discharge combined with currents could have had an effect on the type of nutrients reaching different parts of the KZN Bight. Heip et al. (1992) highlighted the possible importance current flow plays in the structuring of benthic communities with changing longitudes. Rabalais et al. (1996) found that changes in the Mississippi River discharge chemistry led to a phytoplankton species shift in the adjacent continental shelf and a further increase in primary production in an already hypoxic region. Thus a possible difference in the

water column characteristics expected in the river-impacted regions, could result in a difference in phytoplankton species composition between the North and South region that might also have had an impact of the difference in taxonomic diversity found. Species richness can be determined by the differing sediment structures maintained by hydrodynamic and geomorphological factors, depending on the amount and type of available food resources present (Gray 2002). Fenchel (2002) found that the small scale distribution of certain species of bacteria was linked to the distribution of certain species of macrobenthic fauna.

Overall the taxonomic distinctness of the entire community of macrobenthic fauna along the KZN Bight midshelf was accounted for by coarse sediment, however the taxonomic distinctness in communities located within the North Bight was best explained by fine sand, and none of the variance found in the South section could be explained by measured environmental variables. As alpha diversity and taxonomic distinctness were related to different environmental gradients, the important environmental variables that played a role could thus have differed even between data sets and fauna within the same data sets (Heino et al. 2005, Sivadas et al. 2013). A high amount of fine sediment has been known to have a negative influence, especially on certain macrobenthic fauna like filter feeders, by affecting their feeding and respiratory success, by causing increased drift due to re-suspension, by decreasing oxygen supply in sediment and so on (Rodrigues et al. 1982, Wood and Armitage 1997, Ingole et al. 2002). Thus the type of fine sediment regime determines and favours or disfavors the type of organisms found there, as only certain species are adapted and able to thrive within the type of environment that fine sand creates (Richards and Bacon 1994). Wood and Armitage (1997) emphasised the need to better understand fauna habitat requirements and responses to fine sand deposition.

Fine sand seemed to have a positive influence on the North Bight macrobenthic community's taxonomic distinctness. This could be due to the possible difference in community assemblage types associated with the different environment of this section (Ellingsen et al. 2005). Also because of the reigning nutrient system in this part of the Bight, the presence of small amounts of fine sand could be advantageous as, in the shallow shelf environments near the coast, organic content of the sediment increases with the amount of fine sand present (Gray 1981). Off the southern Bay of Biscay, NE Atlantic, Spain, sediment characteristics were very important in playing a role in the diversity of the macrobenthic communities (Louzao et al. 2010).

It is thought that communities containing a few species that fulfil key functional roles could be most sensitive to environmental changes and thus taxonomic distinctness indices play a valuable

role in helping to determine which communities will be able to withstand changes (Jennings and Kaiser 1998, Rogers et al. 1999). There are no real general guidelines to follow when it comes to the understanding variability of measures of diversity along environmental gradients as there are many contingencies and context-dependencies (Heino et al. 2005). The most important factor in changes and the maintenance of high macrobenthic heterogeneity, is the variability and heterogeneity of the habitat structure (Hewitt et al. 2005, Veech and Crist 2007, Bevilacqua et al. 2012). Also the same phyla can have drastically different patterns of heterogeneity in different habitats and within the same habitat different phyla can exhibit completely different patterns of beta diversity, even while displaying the same patterns of assemblage variation along an environmental gradients in an ecosystem (Bevilacqua et al. 2012). Thus the processes involved in the creation of heterogeneity for each phylum needs to be considered in conservation planning (Bevilacqua et al. 2012).

5.5 CONCLUSION

Macrobenthic communities found along the KZN Bight midshelf consisted of many patches of differentially taxonomically diverse communities, and thus taxonomic diversity along the KZN Bight was very variable. However most of the stations remained within the limits of the entire Bight communities average taxonomic distinctness and variation in taxonomic distinctness found. Average taxonomic distinctness and variation in taxonomic distinctness values along the KZN Bight midshelf concurred with the previous patterns in the results of Whittaker's beta diversity and alpha diversity found along the Bight midshelf (see Chapter 3). Similar patterns have been observed in previous studies of macrobenthic and other fauna in varying settings.

Species richness was highest in the South section of the Bight, while decreasing towards the North section, however because variation in taxonomic distinctness values follow the same trend as species richness, and average taxonomic distinctness and beta diversity followed the opposite trend, the North section of the Bight had a greater diversity level than previously thought. This was because the high values of variation in taxonomic distinctness and low average taxonomic distinctness in the South indicated that there was a community of many closely-related diverse species divided among a few higher phyla, with the opposite situation in the North section. The possible mechanisms for this involved the possible division of the environmental by interdependent complex interactions between different hydrodynamic, topographic, geological, nutrient diversity, and macrobenthic community's biological

characteristics and even possibly evolutionary history found in the different sections across the Bight.

Community taxonomic distinctness was significantly related to measured environmental variables, though weakly, thus other unmeasured important variables played more significant roles. Macrobenthic taxonomic diversity and Whittaker's beta diversity were explained by different measured environmental variables to those that explained alpha diversity. This was expected as these indices measure different aspects of diversity. The variation found in the taxonomic diversity of macrobenthic communities in the South and North Bight sections were not explained by the same measured environmental variables. No environmental variables could explain taxonomic diversity variation in the South Bight section and percentage fine sand was the only variable explaining taxonomic diversity; this included depth, which explained beta diversity in the North Bight section. All taxonomic diversity indices followed very non-linear relationships with identified important environmental variables.

Since more in-depth investigations need to be done on the state of the physical environment between these two regions, as well as on the biological dynamics (including larval, migration, assemblage types, genetics, trophic groups) involved, it can only be hypothesised that the KZN Bight midshelf could be divided in to two section, according to macrobenthic biological and taxonomical diversity, assemblage type attributes, nutrient regimes (see also Ayers and Scharler 2011, De Lecea et al. 2013), sediment combination type and chemistry, stability, type and intensity of disturbances, and water column characteristics; and all of which could be governed by regional reigning hydrodynamic systems. Hochard et al. (2012) using a modelling approach, found that through enhanced physical forcing, the release of nutrients and organic matter is increased and this stimulated the bacterio-plankton and phytoplankton sections of sediment and water column interactions, and possibly through such mechanisms, spares nutrient availability could have supported high taxonomic diversity in the North Bight.

There are still many unknowns surrounding the KZN Bight ecosystem, (see also Ayers and Scharler 2011), however this present study provides important baseline information in understanding the complex KZN Bight ecosystem for future conservation and it is hoped that this will be further built on in future.

CHAPTER 6

CONCLUDING DISCUSSION

6.1 MAIN FINDINGS

In chapter three, it was found that the macrobenthic communities were more diverse than expected for an oligotrophic environment. The biodiversity of the macrobenthic community from the KZN Bight midshelf, was very high, and this diversity varied along the length of the KZN Bight midshelf. The KZN Bight had a higher alpha diversity than many tropical eutrophic and subtropical oligotrophic continental shelves elsewhere. Its alpha diversity was equal to many tropical areas and temperate regions that had a diversity equal to and even higher than some deep sea benthic diversities, however, it did not have as high a species density per m⁻² and species/abundance ratio as some of the most diverse tropical continental shelves, for example from Australia. All sites measured at different spatial scales, had very high dissimilarities in composition, variability and alpha diversity. Along the KZN Bight, macrobenthic communities were constantly changing from section to section, forming clearly divided dissimilar patches of diverse macrobenthic communities.

On all scales, even in the comparison of large focus areas, there remained high levels of dissimilarity, even though there was an overall decrease in dissimilarity from small to large scale. On large scale the Bight could essentially have been divided into a South region including the Thukela focus area, and the North Bight, stretching north from the Thukela River, as these environments possibly provide complementary habitats for communities; community attributes (alpha, beta diversity and taxonomic diversity) started to change drastically from north of the Thukela River. Between the North and South Bight, composition, species richness and evenness were different. There was a general decreased alpha diversity from the South towards the North. This diversity measure however acted in a complimentary measure to the inverse relationship of Whittaker's beta diversity observed as it increased from south to north between adjacent sites. These gradients in diversity were maintained on all scales of study along the Bight. Annelida and Arthropoda were the most abundant and species rich phyla found on the KZN Bight midshelf. Cnidaria and Arthropoda had the highest mean beta diversity across the KZN Bight. The macrobenthic communities phyletic composition and each phylums life history found in the

different sections of the Bight, could have contributed to the inverse pattern of alpha and beta diversity found.

In chapter four, the KZN Bight midshelf macrobenthic community was found to be a diverse community adapted to physical and chemical changes in habitat brought on by the three focus areas (Thukela River, St. Lucia upwelling cell and Durban eddy). These oceanographic features divided and created different habitats along the KZN Bight. Because of the oligotrophic nature of the waters, food type, distribution and availability were speculated to be the main indirect driver that maintained the macrobenthic community abundance patterns and diversities (see also Ayers and Scharler 2011, De Lecea et al. 2013). Depth-related factors including the generally poor sorting and variety of sediment environments found on the Bight may have contributed to its high macrobenthic diversity.

The presence of these hydrological regimes, that differ spatially as they occupied different sections along the Bight, must have certainly contributed to the maintenance of distinct communities, adapted to different types of nutrients associated within deeper stable or shallower unstable environments, which provided for unique environments for the development of high alpha and low beta diversity communities in the South, and low alpha and high beta diversity communities in the North, maintained by different environmental dynamics. The measured environmental variables did not explain a large percentage of the community variability observed and thus other important unmeasured gradients of inter-correlated environmental, abiotic and biotic variables could have had a greater contribution to the observed and unobserved macrobenthic community diversity patterns of the KZN Bight midshelf. This was also highlighted by the fact that none of the environmental variables could effectively explain overall diversity and variability of abundance at any spatial scale or even at most locations. Also, the relative importance of environmental variables differed from one location to the next.

In chapter five, average taxonomic distinctness and variation in taxonomic distinctness values along the KZN Bight midshelf concurred with the previous results of Whittaker's beta diversity found along the Bight midshelf. Similar patterns have been observed in previous studies of macrobenthic and other fauna in varying settings. Species richness was highest in the South Bight, and decreased towards the North, however, because variation in taxonomic distinctness values follow the same trend as species richness and average taxonomic distinctness and beta diversity followed the opposite trend, the North Bight had a greater taxonomic diversity than the South section. This was because the high values of variation in taxonomic

distinctness and low average taxonomic distinctness in the South indicated that there were many closely related species divided among a few higher phyla, with the opposite situation in the North section. The possible mechanisms for this involved the environmental division by interdependent complex interactions between different hydrodynamic, topographic, geologic, nutrient diversity and biological characteristics found across the Bight. Macrobenthic taxonomic diversity was explained by different measured environmental variables from those that explained alpha diversity. The variation found in the taxonomic diversity of macrobenthic communities found in the South and North Bight sections were not explained by the same measured environmental variables.

It was further speculated that the KZN Bight midshelf could have been cautiously overall divided into two section, according to macrobenthic biological diversity, assemblage type attributes, nutrient regimes, sediment combination type and chemistry, environmental stability, type and intensity of disturbances, and water column characteristics, all of which were postulated to be governed by different reigning hydrodynamic systems. It was speculated that the South Bight consisted of assemblages adapted to a more stable harsh environment with a high consistent source of detrital nutrients that supported a large population density.

This could possibly be linked to the homogenising effect large quantities of river runoff had on communities on continental shelves. The North section macrobenthic assemblages could have been adapted to more unstable, constraining, heterogeneous habitats, characterised by possible periodic pulses of fresh pelagic nutrient inputs, high temperatures, low salinity and a variety of sediment organisation and structure characteristics. Thus possibly, the communities in the South Bight region were characterised by communities adapted to and coming from a eutrophic environment, while the North Bight community was characterised as communities specialised and adapted to and living in an oligotrophic habitat. Overall the ecosystem was detritus-based (Ayers and Scharler 2011, De Lecea et al. 2013).

6.2 THE WAY FORWARD

This present study has left more questions than answers, although these questions were more directional and hopefully will lead in the right direction. Diversity could never be encapsulated with a single number (Mouillot et al. 2005). Therefore in future it would be wise to include and use improved ways of measuring beta diversity and to continue with the contributions of interdisciplinary studies with the KZN Bight ecosystem in mind. According to Vellend (2001),

beta diversity and species turnover should not be used interchangeably and that different measures of beta diversity measure different properties of beta diversity. Vellend (2001) recommends that β_w be used not as a measure of species turnover but to be used when underlying gradients are unknown, to test for the degree that species composition heterogeneity differs between different functional groups and regions, as well as to test for the relationship between environmental and compositional heterogeneity between regions, as beta diversity is more of an abstract concept.

According to Vellend (2001), and Anderson et al. (2011), for the measure of species turnover along a gradient, the use of a similarity-distance curve is recommended as a visual and quantitative measure of the magnitude and rate of changing species composition per unit distance. In future it would be useful to also incorporate the use of non-directional beta diversity as variation, along with the directional measure of beta diversity as turnover, since in the past it has been noted that this measure was able to show the significant effects of sources of variability, even when there is no seeming effect on alpha diversity (Bevilacqua et al. 2012). A problem with beta diversity is that it is not able to let the researcher know to what extent it reflects the ongoing population processes (Soininen et al. 2007). Thus additional analysis accompanying beta and alpha diversity needs to be done. These include determining genetic, phylogenetic and functional diversity of the macrobenthic communities, as well as determining the trends in beta diversity in the opposite direction, namely from Richards Bay to Durban (Mouillot et al. 2005, Bevilacqua et al. 2011).

Patterns of taxonomic distinctness were suspected to be found due to the combined influence of natural and anthropogenic factors and it is hard to separate which plays the most important role in some regions (Ellingsen et al. 2005). Because the environment has a great influence on taxonomic relatedness and these reactions have great variation, it has been found that taxonomic distinctness indices are not successfully able to discriminate between natural or anthropogenic disturbances (Bevilacqua et al. 2011). As this study's measured environmental variables were not able to explain most of the macrobenthic communities variability, it was concluded that other unknown environmental variables and interactions played more important roles. Many more measurements detailing characteristics of the different aspects of the environment need to be undertaken, including the types and strength of pressures experienced within the different sections of the KZN Bight. These include studies on the littoral chemistry of the different section of the Bight, such as the carbonate and siliciclastic content. Also as upwelling cells and river sourced nutrient could have different effects on communities, the types, quality and

abundance of these and other nutrient sources need to be determined and how these separate nutrient sources influence community alpha and beta diversity. There should be determined if there might be other types and sources of nutrients available to the macrobenthic community in the different sections of the Bight. There needs to be a greater interest in what the role of microorganisms such as bacteria play in the sustainability of these ecosystem communities (De Lecea et al. 2013). It would also be interesting to see how the species taxonomic distinctness differs within similar habitats, and from this identify which of the differences in environmental variability within these habitats have an impact and how big a role they play (Bevilacqua et al. 2011).

Measured diversity indices did characterise macrobenthic biodiversity within the KZN Bight midshelf well. Through this, a general alpha and beta diversity pattern was recognised across the Bight, as well as changes in similarity and dissimilarity across scales. In order to measure macrobenthic diversity on the KZN Bight, a combination of older, well-established, diversity methods and modern improved methods needs to be used. More focused studies on separate entities, systems or habitats of the KZN Bight should be undertaken and their relationships established. Identifying habitat diversity would be important in this regard. Much needs to be done in terms of more detailed biotic and abiotic community studies, for example on the existence of the type of functional groups, specific species and individual families present, the number of endemics present, biomass and body size characteristics, species/abundance ratios and predator top-down regulation, that are characterised within/from sections of the Bight. It is also recommended that alpha and beta diversity be measured for all different groups separately along the Bight (Marquet et al. 2004).

The correlation between possible changing reproductive- and life history diversity to the temporal and spatially changing nutrient conditions would also contribute to a better understanding of the ecosystem. The exchange and distribution of different taxonomic groups, either via an understanding of their larval or suspension movement, within and between the Bight regions or from outside (supported by genetic analysis), would serve a useful purpose to understanding the apparent division of the Bight into two separate taxonomically different sections. As the subtropical waters of Hong Kong have also been found to be low in alpha but high in beta diversity, it would be interesting to know how the environmental pressures from that region differs to those found on the KZN Bight in determining alpha and beta diversity and how these habitats are unique (Shin and Ellingsen 2004).

Also important is to be able to determine the types and extent of human-induced changes and impacts on the environment and thus on the macrobenthic fauna of the KZN Bight. Human impacts on rivers change the chemistry and suspended particle content of water that play a significant role in changes found in macrobenthic communities (Wood and Armitage 1997, Lamberth et al. 2009, Ayers and Scharler 2011). Thus the construction of a barrier within a river would definitely cause changes in the macrobenthic communities in the river and the adjacent continental shelf, as shown in a study by Warwick and Somerfield (2010). Many continental shelf ecosystems and estuaries are dependent on the natural flow of rivers for healthy functioning and fauna that occupy them are adapted to the natural provisions and changes brought about by rivers (Norse 1993).

Disruption of the natural flow of rivers has significant effects, as rivers within a natural spatial-temporal rhythm, bring familiar changes to current flows, temperatures, input of sediments and freshwater to the adjacent shelves (Norse 1993). It is not only the amount but also the timing of river input that could have significant effects on the continental shelf ecology (Norse 1993). Examples of some of the effects caused by disturbance of the natural flow of river could be seen in the Murry River (Rozenfurt 1991) and the Nile River (Norse 1993). After the completion of the Aswan dam in the Nile River, fisheries from the adjacent continental shelf dropped by 80%, and erosion of the continental shelf increased due to a substantial decrease in sediment provision to the shelf from the river after the building of the dam (Norse 1993). According to Ayers and Scharler (2011), the impoundment of the Thukela River discharge could lead to the decrease of primary and secondary detritus feeders that are commercially important for the region.

This study provided useful and important initial insight into the macrobenthic community diversity of the KZN Bight marine ecosystem. Some questions concerning the importance of measured environmental variables and their relative influence on macrobenthos were addressed. However, the study also revealed yet more questions around how this complex ecosystem functions. The answers to which are still unknown. The study will provide a good platform to base more in-depth study of the shelf and its contribution to the diversity of South African and even regional shallow marine diversity.

CHAPTER 7

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