

**MACROFAUNA DIVERSITY OF UNIQUE, FLUVIALLY-DEPENDENT
SOFT-SEDIMENT HABITATS IN THE UTHUKELA MARINE
PROTECTED AREA, SOUTH AFRICA**

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As the candidate's supervisor, I approve the submission of this dissertation for examination

A solid black rectangular box used to redact the signature of the supervisor.

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PREFACE

The research contained in this dissertation was completed by the candidate while based in the Discipline of Biological Sciences, School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville, South Africa. The research was financially supported by the Oceanographic Research Institute (ORI) and the National Research Foundation (NRF).

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.



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DECLARATION: PLAGIARISM

I, Stacey Badenhorst, declare that:

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(ii) this thesis has not been submitted in full or in part for any degree or examination to any other university;

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ABSTRACT

The uThukela shelf is a large section of the KwaZulu-Natal (KZN) Bight, and being situated adjacent to the largest river on South Africa's east coast and the fluvially-dominated uThukela Estuary, is an excellent example of a fluvially-dependent coastal ecosystem. Previous studies found that this shelf contains structurally and functionally unique macroinvertebrate communities that contributed to the promulgation of the uThukela Marine Protected Area (MPA), as part of the South African MPA network of 20 new or extended systems. This study expands on this evidence using recent samples collected prior to the protection of the uThukela shelf to provide a good baseline database for future monitoring within the MPA. The uThukela macrofauna distributions and the environmental parameters correlated with these patterns were investigated through replicated sediment grabs that were collected with corresponding abiotic parameters, along coast-perpendicular transects. Macrofauna were subsequently classified taxonomically and their functional attributes determined. One replicate collected on the inner-shelf was particularly noteworthy as the taxa composition was unique and unexpected for a mud depocenter as it was indicative of hard substrata, suggesting a nearby low-lying reef. This habitat anomaly should be further investigated as it may play an important role in biodiversity and ecosystem functioning within the uThukela benthic system that mostly consists of soft sediments. Overall, the uThukela shelf soft-sediment community represented a wide variety of taxa but in low abundance, and was dominated by burrowing polychaetes. These ubiquitous polychaetes exhibited diverse biological traits, and a finding of this study was that this group alone is a potential surrogate for future studies and monitoring of the entire uThukela shelf macroinvertebrate community. This community consisted of mostly facultative deposit feeders that shift to suspension-feeding and rely significantly on terrestrial particulate organic matter (POM) and mud deposited onto the shelf by the fluvially-dominated uThukela Estuary. The adaptive behaviour of these taxa allows intermittent shifts in food acquisition when conditions do not favour this optimal deposition (such as during reduced fluvial outflow), thereby enhancing ecosystem resilience to natural environmental fluxes. Natural fluctuations in the uThukela River flow results in reduced freshwater penetration onto the shelf during the dry (winter) season, and was observed during this study by the higher-than-expected salinity measurements further inshore and the resultant atypical salinity gradient across the uThukela shelf. Salinity, along with dissolved oxygen, were the measured near-bottom water parameters most correlated with macrobenthic distribution. Sediment composition also affected distribution patterns, forming fine-grained and medium-coarse-grained assemblages on the

inner and mid-shelf, and a muddy assemblage on the outer-shelf. The muddy outer-shelf is mostly old deposits that suggests the uThukela has functioned as a fluviially-dominated system for a long time. Overall, sediments contained a large amount of crushed-shell and high Foraminifera abundances, contributing to habitat complexity and increasing diversity. Maintaining macrofauna diversity by preserving benthic habitats is vital in the functional success of marine ecosystems; particularly so in the uThukela system that is classified as strongly benthic-driven. This study provides baseline information contributing to future monitoring of whether the uThukela MPA achieves the aim of protecting rare benthic habitats associated with the connection of the coast to the deep sea and whether macrofauna diversity and associated ecological processes are maintained. In addition, it will support future studies within the MPA that emphasise the importance of the critical role of freshwater to the marine system and that ensure areas important for life-history strategies of vertebrates and invertebrates with high conservation status are conserved.

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“For I know the plans I have for you,” declares the LORD, “plans to prosper you and not to harm you, plans to give you hope and a future.” – Jeremiah 29: 11

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CHAPTER 1. GENERAL INTRODUCTION

1.1. The uThukela Marine Protected Area

Conservation of marine processes and biodiversity is typically achieved through the establishment of Marine Protected Areas (MPAs) (Margules and Pressey 2000), which are formally protected by law and aim to preserve marine systems and taxa for sustainability and climate change adaptations (Skowno et al. 2019). The South African government recently launched Operation Phakisa, an initiative aimed at accelerating solutions to the country's key development issues, with one of the aims being the maximisation of the ocean economy whilst also adequately protecting the ocean resources through MPAs (Skowno et al. 2019). An MPA network of 20 new or extended regions was declared in October 2018, gazetted in May 2019, and implemented on 1 August 2019 (Republic of South Africa Government Gazette 2019). This network increased the protection of the South African marine territory to 5% (57 736 km²), with 87% of ecosystem types receiving at least some protection (Skowno et al. 2019). The uThukela MPA in KwaZulu-Natal (KZN) was incorporated into this new network and includes the coastal and offshore regions, as well as part of the uThukela Estuary (Republic of South Africa Government Gazette 2019). The purpose of declaring this MPA was to protect rare habitats connecting the coast to the deep sea, such as estuaries, sandy beaches, rocky shores, reefs, fluvial fans, unique mud beds, and the uThukela submarine canyon; to conserve ecologically sensitive biodiversity and the associated ecosystem processes; to preserve sensitive ecosystem types and the critical role of freshwater input; to protect areas important for life-history strategies; to provide refuge areas for threatened species; to contribute to nature-based tourism and environmental education (Republic of South Africa Government Gazette 2019). Indications that the uThukela shelf contained structurally and functionally unique macrobenthic communities (MacKay et al. 2016, Untiedt and MacKay 2016) contributed to the protection of the region, and this study expands on this preliminary evidence to provide a more fine-focussed baseline database. Baseline information of this region is crucial in the monitoring process as it assesses the original state of the shelf system to evaluate subsequent changes in the MPA (Hall 2002, Edgar et al. 2007).

1.2. The continental shelf

The continental shelf is generally defined as extending from the low-water mark to the shelf edge (± 200 m), where the seafloor gradient significantly steepens (Hall 2002). Although occupying only a small part of the ocean, these nearshore marine areas are among the most

productive habitats, combining pelagic and benthic carbon and nutrient cycles (Snelgrove et al. 2014, Scharler and Ayers 2019). Shelf productivity is often further enhanced by terrestrial inputs that are mostly delivered by river discharge that passes through an estuary and into the ocean (Cooper 2001, Scharler and Ayers 2019). An example of this type of fluvially-influenced shelf is the uThukela as it is situated off the large fluvially-dominated uThukela Estuary (van Niekerk et al. 2020).

1.2.1. Fluvially-influenced shelf ecosystems

Estuary plume fronts are highly productive zones (Karati et al. 2018) due to the direct supply of particulate organic matter (POM) by river flooding, and the indirect enhancement of *in situ* planktonic production as a result of increased terrigenous nutrient supply to the shelf (Salen-Picard et al. 2002). Freshwater outflow not only increases coastal productivity but is also a vital source of sediments to the coast and affects coastal circulation patterns and vertical stability (Drinkwater and Frank 1994, Snelgrove 1998, Hall 2002, Salen-Picard et al. 2002, McKee et al. 2004, Lutjeharms 2006c). Thus substantial fluvial input is crucial for the functioning of many shelf systems and associated biota (Snelgrove 1998, Hall 2002, Lutjeharms 2006c, Skowno et al. 2019). Although the influence of this outflow generally decreases with increasing distance from shore, global cycles still allow linkages with the deeper ocean (Snelgrove 1998) through a complex combination of factors controlling when and where particulate materials are distributed, deposited, and transformed and whether these are exported from or sequestered on the shelf (McKee et al. 2004).

1.2.2. Soft-sediment habitats

The establishment of benthic habitats for macrofauna occupation relies on sediment distribution and deposition mostly influenced by continental shelf bathymetry (Verfaillie et al. 2006). At local scales, however, the pattern of sediment grain size distribution depends on hydrographical processes such as currents, waves, river run-off, and fronts that impact the region's energy balance (Gray 1981, Hall 2002, Bale and Kenny 2005, Gray and Elliott 2009). Coarse, well-sorted, and mostly homogeneous sediments are usually characteristic of high-energy environments with large wave and current patterns (Gray 1981, Gray and Elliott 2009). Little deposition occurs during these conditions as only the heaviest particles settle to the bottom, and as such, coarse sediments contain little organic material (Pearson and Rosenberg 1978). Alternatively, fine muds and clays are generally found in low-energy environments with relatively stable wave and current patterns (Gray 1981, Gray and Elliott 2009, Akoumianaki et

al. 2013). These sediment particles remain suspended for variable periods, causing overlying turbid water (MacKay 2006), but once settled are usually packed tightly and are not easily resuspended (Sanders 1958, Gray 1981, Gray and Elliott 2009). The deposition site is generally poorly-sorted and heterogenous, with increased organic concentrations (Pearson and Rosenberg 1978, Gray 1981, Gray and Elliott 2009, Akoumianaki et al. 2013).

1.3. Macrobenthic invertebrate communities

Unconsolidated sediments provide three-dimensional habitats for invertebrates that reside in (infauna) and on (epifauna) the seafloor (McClurg 1988, Snelgrove 1999, Lohrer and Hancock 2004), including organisms retained on a 1000 µm or 500 µm sieve, referred to as macrobenthos (McClurg 1988, Gray 2002). Macrobenthos comprise a diverse array of organisms with the most common groups including polychaete worms, bivalve molluscs, and amphipod and decapod crustaceans (Gray and Elliott 2009). These invertebrates occur mostly within the top few centimetres of the sediment, where oxygen and organic contents are maximised (Snelgrove 1997), as macrofauna utilise organic detritus and microscopic algae as food (Lohrer and Hancock 2004). Most of these organisms are completely reliant on the settling of organic matter from the water column above, due to very limited mobility disabling them from actively searching for food (Snelgrove 1999). It is this relative immobility, the relatively long lifespans, and the spatial stability of macrobenthos that allows these organisms to be widely used in baseline and monitoring studies, where local environmental changes can be observed through the alteration of the macrobenthic community (Pearson and Rosenberg 1978, McClurg 1988, Clarke and Warwick 2001, Hyland et al. 2005, Udalov et al. 2021).

Macroinvertebrates play an important role in marine ecosystem functioning (Reise 2002, Lohrer and Hancock 2004, Hyland et al. 2005). They are integral in the marine food web, transferring nutrients to higher trophic-level species such as other benthic organisms, important fish species, and humans (Snelgrove 1997, Snelgrove 1999, Thrush and Dayton 2002, Gray and Elliott 2009, Grippo et al. 2011). They are also important habitat engineers and through their feeding and movement behaviours, as well as living habits, assist in the penetration of oxygen and nutrients into subsurface sediments and aid in carbon and nutrient cycling (Snelgrove 1997, Snelgrove 1999, Reise 2002, Dutertre et al. 2013). Some species also modify their habitats by acting as sedimentary “conveyor belts”, transporting sediment grains from subsurface to surface levels, and altering sediment cohesivity through mucus secretion (Snelgrove 1997, Reise 2002). Additionally, structure-forming benthos (e.g. constructors of tubes or burrows) contribute to

greater habitat dimensionality, increasing spatial availability for other taxa and altering processes such as water flow (Gray 1981, Gray 2002, Reise 2002, Thrush and Dayton 2002, McArthur et al. 2010).

The importance of macroinvertebrates in marine ecosystem functioning indicates that the evaluation of community traits is vital (Lohrer and Hancock 2004). Trait analysis offers further information on the ecology of the area (Gray and Elliott 2009) by assessing the traits of each species in a community and combining these to evaluate the entire ecosystem functioning (Norling et al. 2007). Functional consistency or redundancy implies that more than one species is fulfilling a specific role and indicates ecosystem stability and the relative ability of soft-bottom communities to resist habitat fluctuations (Snelgrove 1997, Snelgrove 1998, Jax 2005, Macdonald et al. 2012).

1.4. Environmental influences on macrobenthos distribution

Macroinvertebrate distributions are naturally patchy due to external influences and juvenile recruitment, as well as processes occurring within the already existing benthic assemblage (Underwood and Chapman 2005). Interactions between biotic and abiotic factors are complex (Khan et al. 2017) and natural perturbations greatly contribute to spatial variations in populations (Underwood and Chapman 2005). Species have different tolerances to each abiotic variable, hence as the environment fluctuates, so does the corresponding community according to the preferences of its taxa (Gray and Elliott 2009). Macrofauna distributions are usually affected by sediment grain size, organic content, and water depth (Snelgrove 1999, Ellingsen 2002), and the near-bottom water parameters temperature, salinity, and oxygen (Gray 1981). Shallow-water zonation usually occurs alongside altering depth (Clarke and Warwick 2001), however, depth is a possible proxy for other water quality or seafloor characteristics as macroinvertebrates lack an apparent mechanism for depth measurement (McArthur et al. 2010), and water depth affects hydrodynamic conditions and sedimentation patterns (Zalmon et al. 2013).

In shallow regions with a strong physical reworking of sediments, benthic communities usually contain fewer macrobenthic individuals, fewer taxa, and reduced faunal diversities (Rhoads et al. 1985, McKee et al. 2004, Lohrer et al. 2006, Dutertre et al. 2013). Alternatively, heterogenous sediments potentially contain higher benthic diversities and abundances due to the combinations of different sediment types likely providing more niche spaces (Gray 1981,

Zalmon et al. 2013, Carvalho et al. 2017). Bioclastic sediments (shell-gravel) are found in isolated pockets throughout the world and usually contain a very high species richness (Gray 2002). Coarse sediments usually contain low diversity (Gray 1981) and sediments with smaller mean particle sizes generally contain higher diversities (Zalmon et al. 2013), with medium and fine sands generally having high macrofauna abundances (Gray and Elliott 2009). Mud particles are usually packed tightly together, which results in poor water circulation and often low oxygen tension, reducing oxygen availability as the limited oxygen that diffuses into the sediments is rapidly consumed (Gray and Elliott 2009). Increased silt content also inhibits certain animal activities (Cocito et al. 1990), so fauna that are present in areas dominated by mud are expected to be more tolerant over short-term, small-scale changes to sediment grain size and water clarity (MacKay 2006). These communities are particularly prevalent adjacent to large rivers where high siltation rates can act as a stressor to benthic communities (Careddu et al. 2015).

Fine sediments and shallow areas usually have higher food availability in the form of organic content (Gray 1981, Snelgrove 1999, Gray and Elliott 2009), and the alteration in food availability is usually considered a primary cause of macrobenthic community change (Pearson and Rosenberg 1978). Continental shelf sediments usually comprise organic content that is a heterogenous mix of phytobenthos, settled phytoplankton and zooplankton, and detritus from marine and terrestrial sources (Gray 1981, Schumacher 2002, Grippo et al. 2011, Cresson et al. 2012, De Lecea et al. 2013). Detritus that settles at the sediment surface is largely degraded by bacteria (Gray 1981), affecting bottom water oxygen levels, recycling important nutrients, and determining the amount of organic materials eventually stored in sediments and used by macrobenthos (McKee et al. 2004). On a fluvially-influenced shelf, benthic primary consumers are inclined to shift their source of organic matter from phytoplankton to terrigenous detritus with decreasing distance from the estuary mouth, but this is dependent on topographic conditions and the hydrological regime (Careddu et al. 2015). The general response of benthic organisms to the introduction of organic matter is that as input to an area increases macrofauna abundance initially increases, then decreases to a community transition point, followed by another increase of a few small, short-lived, opportunistic species which disappear as well if enrichment continues to rise to an eventually uninhabitable condition (Pearson and Rosenberg 1978, Hyland et al. 2005). The number of species (richness) typically has a peak at low to slightly moderate levels of organic carbon and decreases as concentrations increase toward the high-end of the scale (Hyland et al. 2005). A significantly large input of organic matter

ultimately reduces the oxygen concentration and the sediment can become devoid of macrofauna unless there is substantial flushing of the system (Pearson and Rosenberg 1978, Hyland et al. 2005, Harmelin–Vivien et al. 2009). Relationships between benthic consumers and organic matter, therefore, do not follow a specific pattern, but rather a variety of scenarios exist in which energetic input of organic matter can act as a feeding or stress source depending on quantity and quality (Cocito et al. 1990).

1.5. Previous studies on the macrobenthic communities of the South African shelf

Limited sampling of South African benthic habitats and subsequent knowledge of marine macrobenthic communities are mostly due to the expense and time required during sample collection and processing as well as restricted taxonomic expertise in this field (Snelgrove 1998, Snelgrove 1999, Griffiths et al. 2010, Skowno et al. 2019). Knowledge of the uThukela shelf biota is further constrained due to many South African macrofauna still requiring formal descriptions (Griffiths et al. 2010). Due to the shift in focus to phylogenetic, biological, and ecological studies, studies on macrobenthic systematics have declined (Griffiths et al. 2010). Systematics and taxonomy are the foundation of all biology, so this information is vital in understanding the biodiversity and functioning of the benthic environment (Brown 1999).

The majority of benthic samples that have been collected on the South African shelf have origins along the west coast, with scientists virtually neglecting the benthos of KZN (Griffiths et al. 2010, MacKay et al. 2016). This regional focus has been mainly due to the west coast supporting large, commercially important fish-stocks as a result of intense coastal upwelling causing high productivity in the region (Griffiths et al. 2010). However, the west and east coasts of South Africa differ significantly in hydrological features and species compositions (Heydorn et al. 1978, Griffiths et al. 2010), so the information gathered on the west coast is of limited use to the east coast. Although the colder upwelling region of the west coast generally supports higher species biomass, the number of species in the subtropical east coast waters is greater, resulting in a more intricate ecology (Heydorn et al. 1978).

There were a few macrofauna studies that occurred along the KZN coastline between 1974 and the late 1980s and these indicated a general trend of Annelida (largely polychaete worms) numerically dominating the macrofaunal community, followed by Arthropoda (almost entirely crustaceans), and then a small but significant presence of Echinodermata and Mollusca (McClurg 1988). Additional information about these communities has been recorded more

recently through widespread studies of the KZN Bight (MacKay et al. 2016, Untiedt and MacKay 2016, Maduna 2017). Dominance patterns remained similar during the 2010 African Coelacanth Ecosystem Programme (ACEP) Natal Bight study with Annelida (Polychaeta) dominating richness and abundances, followed by Arthropoda (Crustacea), Mollusca, Sipuncula, and Echinodermata (MacKay et al. 2016, Untiedt and MacKay 2016). The subsequent ACEP Surrogacy project included samples from the KZN mid-shelf in 2010 and 2014 and showed that Arthropoda (mostly peracarid crustaceans) dominated abundances, followed by Annelida (Polychaeta), and Sipuncula (Maduna 2017). Richness was noted as still being dominated by Annelida (Polychaeta) and followed by Arthropoda (Crustacea) (Maduna 2017).

The uThukela shelf benthic research has mostly focussed on stocks and bycatch of the seasonal commercial trawl fishery that previously existed on the uThukela Banks that predominantly targeted the white prawn *Penaeus indicus* (Demetriades and Forbes 1993, Fennessy et al. 1994, Fennessy and Groeneveld 1997, De Lecea and Cooper 2016, De Lecea et al. 2016). Historical data on the uThukela shelf macrobenthic community is therefore limited, but a recent study by Untiedt and MacKay (2016) focussing on the entire KZN Bight has provided some information on the uThukela region and found it to be a significant component of the KZN shelf as it supports a richer and more abundant macrobenthic community than the shelf areas off Durban and Richards Bay. This study expands on this foundational study to further elucidate the uThukela shelf macrobenthic community structure and functioning and provide more baseline information using additional samples collected before uThukela MPA promulgation.

1.6. Study aims, objectives, and hypotheses

This study aims to focus an investigation on the uThukela shelf macroinvertebrate composition and biological traits and determine the potential influence of measured near-bottom water parameters, sediment habitats, and shelf position on fauna distributions. Through the analysis of biological traits, the study intends to reveal the role of macrofauna in the greater ecosystem functioning and the relative link between the uThukela Estuary and the adjacent shelf. In addition, further analysis of characteristic taxonomic groups identified during initial taxa analysis aims to propose potential ecological indicators that could be used in future monitoring.

These findings represent a baseline of the condition, diversity, and functioning of the uThukela system (without trawling) up until it was protected. This will provide important information,

knowledge, and data for the uThukela MPA, representing one of the first baseline studies of the macrofauna in the MPA.

Objectives:

1. To characterise the uThukela shelf environment according to measured physico-chemical near-bottom water parameters and sediment habitats.
2. To describe benthic assemblages based on taxonomic and functional (biological traits) characteristics.
3. To relate taxa assemblages to biological traits assemblages.
4. To determine the extent to which measured environmental conditions and sediment habitats influence benthic assemblages.
5. To reveal characteristic taxa and assemblages that can be targeted for future research into potential MPA indicators for ecosystem monitoring.

Hypotheses:

H₀₁: There are no significant differences in measured physico-chemical near-bottom environmental conditions on the uThukela shelf.

H₀₂: There are no significant differences in sediment measurements on the uThukela shelf.

H₀₃: There is no significant relationship between taxa assemblages and biological traits assemblages.

H₀₄: There is no significant relationship between measured near-bottom water parameters and macrobenthic taxa distributions.

H₀₅: There is no significant relationship between measured near-bottom water parameters and macrobenthic biological traits patterns.

H₀₆: There is no significant relationship between sediment habitats and macrobenthic taxa distributions.

H₀₇: There is no significant relationship between sediment habitats and macrobenthic biological traits patterns.

1.7. Dissertation structure

This dissertation is presented in six chapters, comprising a general introduction (Chapter 1), general material and methods (Chapter 2), chapters investigating uThukela macrobenthic community structure (Chapter 3) and functioning (Chapter 4), a chapter expanding on interesting community attributes revealed in the community analyses (Chapter 5), and a general discussion and conclusion (Chapter 6):

- Chapter 1 introduces the importance of macrobenthos and in the context of the positioning of the study site off the fluviially-dominated uThukela Estuary and within the newly promulgated uThukela MPA.
- Chapter 2 describes the uThukela shelf study area and the processes influencing the region and presents the methods used for field sampling, laboratory protocols, and generic statistical analyses of biotic and abiotic data. Detailed methodology and analyses pertinent to a specific component are provided in the respective chapters (Chapters 3-5).
- Chapter 3 investigates the taxonomic structure of the uThukela macrobenthic community, the uThukela shelf environment, and the link between these biotic and abiotic trends.
- Chapter 4 expands further on Chapter 3 by evaluating the functional attributes of the uThukela macrobenthic community through Biological Traits Analysis (BTA). The potential correlations between these traits and measured environmental variables, as well as shelf positions, were assessed.
- Chapter 5 highlights the findings from Chapters 3 and 4 (taxonomic composition and functional attributes) and investigates focal groups (selected because of dominance) as potential indicators. It focuses specifically on the important taxonomic groups Polychaeta, Decapoda, and Mollusca and investigates the large benthic Foraminifera community found in the uThukela shelf sediments.
- Chapter 6 integrates outcomes from preceding chapters to discuss the overall study findings and implications. This final chapter discusses whether the original study aims were achieved and provides recommendations for future research.

CHAPTER 2. GENERAL MATERIALS AND METHODS

2.1. Study site – The uThukela shelf

2.1.1. Study area location

This study is located in the tropical/subtropical Natal-Delagoa ecoregion of South Africa's east coast (Skowno et al. 2019). This region is microtidal (typically 0.6 – 2.0 m), has a high wave energy, and is swell-dominated (Cooper 2001, Skowno et al. 2019). Here, the continental shelf is narrow (3 – 12 km wide) with a steep shelf slope, except the area between Richards Bay (28° 48' 42.354" S, 32° 05' 53.988" E) and Durban (29° 51' 54.565" S, 31° 03' 43.801" E), known as the KwaZulu-Natal (KZN) Bight (Bosman et al. 2007, Engelbrecht et al. 2020). This coastal offset widens considerably along approximately 160 km of shoreline to a maximum of 50 km off the uThukela Estuary mouth (Lutjeharms et al. 2000). The study was undertaken on the uThukela shelf, that is positioned on the central KZN Bight, and was fully contained within the newly established uThukela Marine Protected Area (MPA) that extends between the uMlalazi (28° 55' 58.127" S, 31° 52' 6.625" E) and the uSetheni (29° 25' 58.152" S, 31° 18' 1.080" E) estuaries (Republic of South Africa Government Gazette 2019) (Figure 2.1).

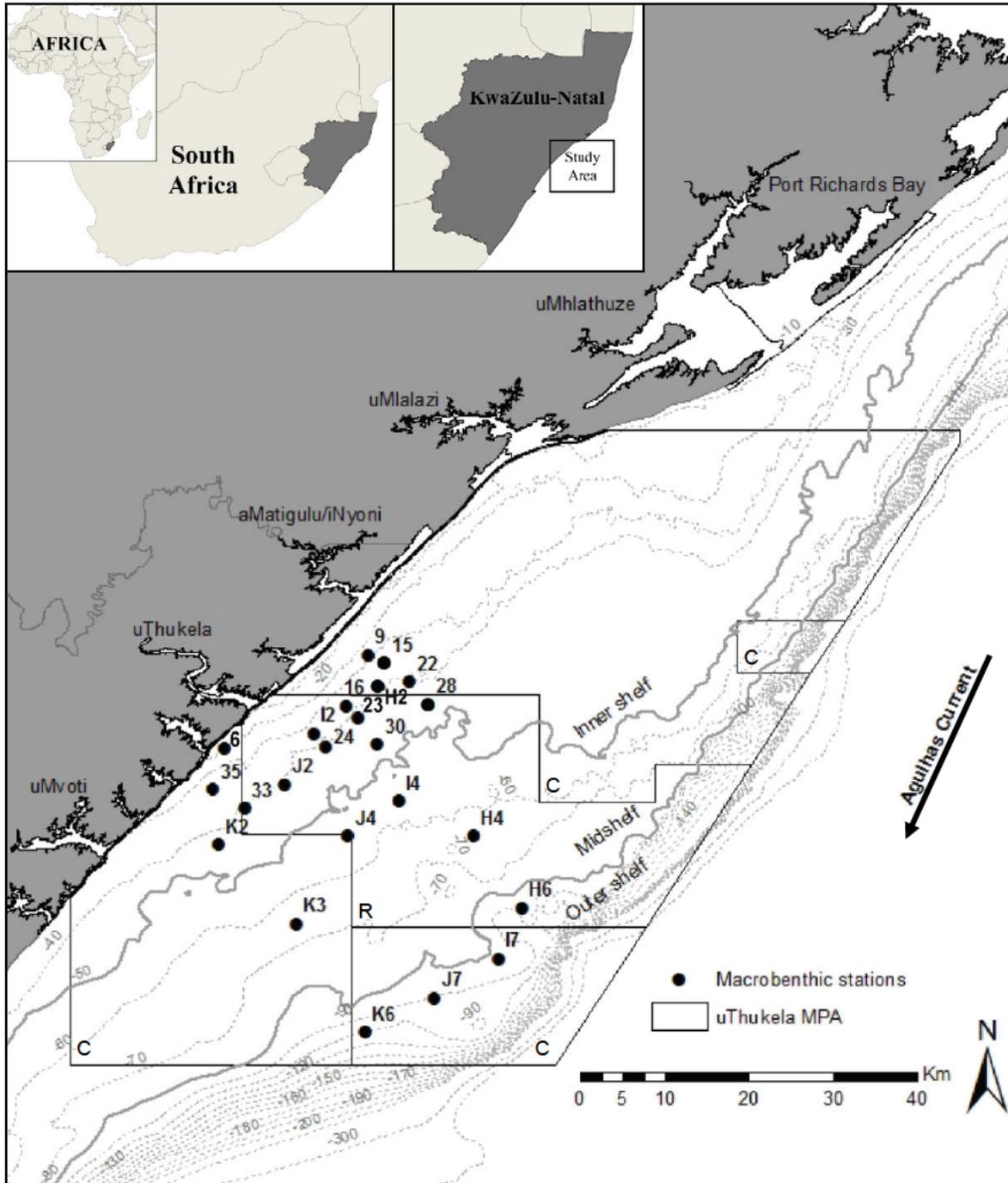


Figure 2.1. uThukela shelf study area with macrobenthic sampling stations, bathymetry, major estuaries, and the uThukela MPA depicted. C = Controlled zone, R = Restricted zone

2.1.2. Climate

The subtropical KZN coast is influenced by both tropical and temperate weather systems (Hunter 1988) and is significantly affected by the Agulhas Current. The summer rainfall

(Lutjeharms 2006a, b, De Lecea et al. 2016) peaks in January (mean monthly rainfall of 118 mm), with a dry winter peak in August (mean monthly rainfall of 39 mm) (Hunter 1988, Scharler et al. 2016b). Air temperatures have a relatively low seasonal range due to the damping effect of the adjacent Indian Ocean, and winds generally travel in a south-westerly or a north-easterly direction (Hunter 1988).

2.1.3. Oceanography

The uThukela shelf is a unique system dependent on complex offshore oceanographic processes and inshore coastal dynamics, including high freshwater and sediment input (Bosman et al. 2007).

2.1.3.1. The Agulhas Current

The KZN shelf edge is followed closely by the strong, well-defined, poleward-flowing western boundary Agulhas Current that virtually encloses the shelf (Pearce et al. 1978, Schumann 1988). This current is relatively narrow (only ± 100 km wide) and characteristic of a typical western boundary current, with depths extending below 1 000 m (Schumann 1987) and core speeds averaging $1.1 - 1.4 \text{ m}\cdot\text{s}^{-1}$ (occasionally recorded $> 2.5 \text{ m}\cdot\text{s}^{-1}$) (Pearce et al. 1978, Lutjeharms 2006a). The Agulhas Current temperatures are $1 - 6 \text{ }^\circ\text{C}$ higher than the surrounding waters and approximate $20 - 28 \text{ }^\circ\text{C}$ at the sea surface (Pearce et al. 1978, Lutjeharms 2006a, c). Seasonal variations cause temperature peaks in February and lows in August (Lutjeharms 2006a). The surface salinity of the Agulhas Current is also season-dependent and averages between $35.0 - 35.5$ PSU (Heydorn et al. 1978, Lutjeharms 2006c).

The South-West Indian Ocean subgyre is the main source of the Agulhas Current but mesoscale eddies from the Mozambique Channel and the East Madagascar Current (carrying waters from the east coast of Madagascar) also indirectly influence the current's behaviour (Lutjeharms 2006b). The Agulhas Current is fully formed along the shelf edge between Maputo and Durban (Lutjeharms 2006c), carrying warm tropical and subtropical water southward and influencing the ecosystems found along South Africa's east coast (Schumann 1987, Lutjeharms 2006a). The current's end-point is the Agulhas Current Retroflexion that occurs at the southern tip of Africa as the current refracts and sheds rings of warm Indian Ocean water that are frequently carried into the South Atlantic Ocean (Lutjeharms et al. 2000).

2.1.3.2. Inshore hydrodynamics

The widening of the shelf in the KZN Bight restricts the direct influence of the strong Agulhas Current on inshore ecosystems (Roberts et al. 2016), and ecosystems are instead affected by wind and wave energies (Schumann 1987, Roberts et al. 2016). Therefore this region has highly variable circulation patterns fluctuating from an alongshore current throughout, to almost no inshore currents, to an intermediate situation where northerly currents dominate south of the uThukela Estuary with very little circulation north of this point (Roberts et al. 2016). Offshore eddies significantly influence inshore currents, interrupting the general flow with non-permanent cyclonic water circulations (Roberts et al. 2016). Overall KZN Bight water moves northwards, carrying cooler water inshore of the counterflowing warm Agulhas Current (Heydorn et al. 1978). These shelf currents reach maximum speeds of approximately $0.5 \text{ m}\cdot\text{s}^{-1}$ (Roberts et al. 2016).

The numerous estuaries along the KZN coast largely influence the marine coastal waters, particularly the uThukela shelf (Heydorn et al. 1978, Schumann 1988, Scharler et al. 2016b). KwaZulu-Natal has 76 notable estuaries (CoastKZN 2019), with seasonal fluctuations in river flow resulting in maximum outflow around February and minimum outflow in August when many estuary mouths close (De Lecea et al. 2016). The uThukela Estuary ($29^{\circ} 13' 37.844'' \text{ S}$, $31^{\circ} 30' 10.724'' \text{ E}$) in northern KZN is classified as a large fluvially-dominated system (van Niekerk et al. 2020) and connects the largest river on South Africa's east coast (the uThukela River) to the ocean (Begg 1978, Cooper 2001, De Lecea and Cooper 2016). The uThukela River has a catchment area of $28\,000 - 29\,101 \text{ km}^2$ and a mean annual run-off of $3\,865 \times 10^6 - 5\,071 \times 10^6 \text{ m}^3$ (Begg 1978, Whitfield and Harrison 2003, Hutchings et al. 2010), and through the uThukela Estuary is responsible for approximately 35 – 40% of the freshwater entering the KZN Bight (Lamberth et al. 2009, De Lecea and Cooper 2016).

Offshore processes also indirectly affect inshore hydrodynamics as cool, nutrient-rich water of the deep ocean is transported onto the shelf by the Richards Bay upwelling cell in the north and the semi-permanent mesoscale Durban Eddy in the south (Lutjeharms 2006a, Guastella and Roberts 2016, Roberts et al. 2016). The uThukela shelf is typically influenced by these systems as the Richards Bay upwelling cell extends as far south as the uThukela Estuary, and the water within the sub-circular Durban Eddy is either expelled into the Agulhas Current or advected and transported northwards along the inner-shelf toward the uThukela Estuary (Guastella and Roberts 2016, Roberts et al. 2016). Under an initial strong south-westerly wind, the water from

the Durban Eddy can even extend beyond the uThukela shelf and connect the southern and northern KZN Bight regions within just 24 days (Roberts et al. 2016).

2.1.4. Temperature and salinity

The important properties used in characterising water type include temperature and salinity (Schumann 1988). There are slight seasonal variations in KZN sea temperatures and salinities as increased summer temperature causes warmer coastal waters, and increased summer rainfall causes less saline coastal waters due to greater estuarine outflow (Schumann 1988). Marginally lower salinity readings just north of the uThukela Estuary outflow indicate that freshwater exits this estuary and is transported in the north-flowing longshore current (Lutjeharms et al. 2000). Previous measurements indicate that the uThukela shelf has mid-winter sea temperatures of approximately 17.0 °C (100 m depth) to 22.0 °C (surface) and salinities of approximately 35.16 PSU (surface) to 35.34 PSU (100 m depth) (Lutjeharms et al. 2000).

2.1.5. Productivity

The KZN coast is typically oligotrophic as it is fed by the nutrient-poor Agulhas Current originating from the tropics (Lamberth et al. 2009, Griffiths et al. 2010, Bernard and Smith 2011). However, mesotrophic conditions are usually noted in the central KZN Bight (Meyer et al. 2002) due to terrigenous input of nutrients mostly via the uThukela Estuary (Lamberth et al. 2009, Scharler et al. 2016b). The trophic dynamics of the system are strongly benthic-driven (Scharler et al. 2016a), and high organic carbon concentrations measured in uThukela shelf sediments indicate major contributions from riverine outflow (De Lecea et al. 2013, MacKay et al. 2016). The freshwater plume (containing particulate material) is suggested to have vast effects on the shelf as it has been observed to protrude outward from the uThukela Estuary and extend to approximately 25 km offshore (Meyer et al. 2002, Lutjeharms 2006b), reaching this furthest point within eight days (Roberts et al. 2016).

2.1.6. Sediment characteristics

The KZN Bight mostly consists of sand, except for the region off the uThukela Estuary, where the shelf is almost completely devoid of large-grained sediments (such as gravel) and is rather dominated by mud (Lutjeharms 2006b, Green and MacKay 2016, MacKay et al. 2016). This mud mainly originates from the uThukela Estuary, through which the uThukela River delivers $6.79 \times 10^6 - 10.5 \times 10^6 \text{ m}^3$ of sediment to the shelf per year, with plumes extending up to 5 km offshore and 15 km alongshore during the wet season (Begg 1978, Whitfield and Harrison 2003,

Hutchings et al. 2010). Adequate river flow is therefore critical for sediment transportation, with these fluvial sediments deposited seaward or deflected into a north-flowing longshore current before being distributed over larger areas (Begg 1978, Heydorn et al. 1978, Lutjeharms et al. 2000, Cooper 2001, Green and MacKay 2016, Skowno et al. 2019).

The uThukela Estuary is fluvially-dominated and, therefore, relatively small, allowing large amounts of terrigenous particulates to pass straight through the typically open mouth and be deposited on the ocean floor, establishing the uThukela Banks (De Lecea and Cooper 2016, De Lecea et al. 2016). This mud depocenter is a rare phenomenon along the coast of southern Africa and can be compared to an estuarine system due to the constantly turbid environment, fluctuating salinities, good nutritional availability, and provision as a nursery area for juvenile fish and invertebrates (Demetriades and Forbes 1993, Fennessy et al. 1994). Soft inner-shelf mud is separated from older, compacted outer and mid-shelf mud by an intersecting paleo-dune of coarse sediments that stretches subparallel to the coastline between 55 m and 70 m depth (Flemming 1981, Flemming and Hay 1988, Green and MacKay 2016, MacKay et al. 2016). According to Green and MacKay (2016) these uThukela shelf mud deposits appear to have predominantly occupied the same position over the last 30 years.

2.2. Sampling procedure

Samples collected at 23 stations on the uThukela shelf (within the polygon 29° 10' 27.030" S – 29° 34' 50.819" S and 31° 27' 12.089" E – 31° 46' 59.160" E) during the dry (winter) season, were considered for this study. These consisted of two datasets from samples collected along coast-perpendicular transects during 18 – 21 August 2008 (numeric labels) and 11 – 15 August 2010 (alphanumeric labels). Macrobenthic samples were collected on the inner (0 – 50 m), mid (50 – 80 m), and outer (80 – 130 m) uThukela shelf in 2010 during the African Coelacanth Ecosystem Programme (ACEP) Natal Bight cruise on the research vessel F.R.S. Algoa. These were supplemented with 2008 samples collected on the inner uThukela shelf aboard the research vessel T.B. Davies.

2.2.1. Field sampling

On the initial arrival at a station, sea and weather conditions were noted in a field logbook, and the exact spatial reference points (latitude and longitude) were recorded, demarcating the locations of subsequent individual near-bottom water measurements and sediment grabs.

2.2.1.1. Physico-chemical readings

At each station, a single cast of a Conductivity-Temperature-Depth (CTD) multiparameter profiler (YSI6600 in 2008 and Sea-Bird: SBE 19 Plus V2 SEACAT in 2010) was undertaken to within 1 – 5 m of the seabed (1 m for the YSI and 5 m for the SEACAT). The depth (m), temperature (°C), salinity (PSU), and dissolved oxygen (DO) (mg.L^{-1}) of the near-bottom water were noted during this study. Turbidity (NTU) was also measured in 2008, but not in 2010.

2.2.1.2. Sediment and macrobenthic sampling

Sediment samples were collected during daylight hours and collected in triplicate (≤ 100 m apart) at each station using a 0.25 m^2 Day grab in 2008 and a 0.20 m^2 Van Veen grab in 2010. Unfortunately, due to difficulty in successfully sampling the bottom, station 9 (sampled in 2008) retrieved only two replicates. Grab retrieval was conducted by a mechanical winch and sediment depth in the grab was measured to ensure an adequate sample (≥ 50 mm) was collected. The sediment characteristics (depth, colour, and odour) were noted to further assess different habitats.

Two sub-samples (maximum 175 g) were “cored” from the sediment of one of the three successful replicate grabs collected at each station in 2008 and from all three successful grabs in 2010 and set aside for later sediment analysis. During this process, care was taken to avoid removing visible fauna from the sample. One sediment sub-sample, for analysis of total organic carbon (TOC), was fixed with 5 ml of 40% formaldehyde to ensure that further bacterial degradation did not alter the TOC content (Bale and Kenny 2005). The remaining sub-sample was retained without fixation to determine sediment grain size composition.

After removal of sub-samples, the grab was opened and the remainder of the sediment was released into a square stainless-steel sieve (mesh size $1000 \mu\text{m}$) and washed using deck hoses. Washing was gentle to prevent the loss of macrofauna out of the sieve and to ensure that organisms were not damaged. In addition to this, any visible fauna were handpicked before and during washing and placed gently in an appropriately sized sample container. Washing continued until no excess sediment remained and the water leaving the sieve was clear of fine sediments. Particles and fauna retained in the sieve post-washing were placed in the sample jar, labelled, and preserved with 4% formaldehyde solution, buffered with filtered seawater (1-part 40% formaldehyde solution to 9-parts seawater) (MacKay 2010).

2.2.2. *Laboratory protocol*

Sediment samples were sent to an external geological laboratory for analyses (Environmental Mapping and Survey (EMS)).

2.2.2.1. Sediment grain size analysis

Dry sediment sieving was employed during this study as it is simple, inexpensive, and produces comparable data, making it the most practical technique for describing sediments with a diameter greater than 0.063 mm (anything below this is considered mud and was grouped for the purposes of this study) (Bale and Kenny 2005). Sieve mesh sizes followed the universally adopted Wentworth scale (Wentworth 1922) and used seven grain-size categories ranging from large gravel (> 2.000 mm) to mud (< 0.063 mm that includes the silt and clay fraction) (Buchanan and Kain 1971, Bale and Kenny 2005) (Table 2.1). The sieves were stacked in decreasing geometric sizes and closed at the top and bottom during sieving (Bale and Kenny 2005). A pre-weighed sample of dried sand was placed in the top (2.000 mm) sieve and the stack was mechanically agitated for a fixed period (Bale and Kenny 2005). After agitation, the weight of the contents in each sieve (including the bottom tray) determined the quantity of sediment in each grain size category (Bale and Kenny 2005). A logarithmic transformation of the Wentworth categories produced Phi (Φ), which is a measure commonly used in sediment analyses that originated due to the need for graphical manipulation of data (Bale and Kenny 2005).

Table 2.1. Wentworth scale classification of sediment type based on grain size (mm), with the accompanying Phi (Φ) scale (where $\Phi = -\log_2$ (grain size)). Adapted from Wentworth (1922) and Gray (1981).

Sediment type	Grain size (mm)	Phi (Φ) scale
Gravel	> 2.000	< -1.0
Very coarse sand	1.000 – 2.000	-1.0 – 0.0
Coarse sand	0.500 – 1.000	0.0 – 1.0
Medium sand	0.250 – 0.500	1.0 – 2.0
Fine sand	0.125 – 0.250	2.0 – 3.0
Very fine sand	0.063 – 0.125	3.0 – 4.0
Mud	< 0.063	> 4.0

2.2.2.2. Sediment sorting and skewness

Sediment sorting was used to represent the spread of grain sizes around the central value (Blott and Pye 2001, Bale and Kenny 2005), with poorly sorted sediments (1.00 – 2.00 Φ) having many varying particle sizes (Gray and Elliott 2009) and well-sorted sediments (0.00 – 0.50 Φ) being relatively homogeneous with a small interquartile range in the grain size data (Buchanan and Kain 1971) (Table 2.2).

Table 2.2. Sediment sorting classification based on the Phi (Φ) scale. Adapted from Gray (1981) and Gray and Elliott (2009).

Sorting classes	Phi (Φ) scale
Very well sorted	< 0.35
Well sorted	0.35 – 0.50
Moderately well sorted	0.50 – 0.71
Moderately sorted	0.71 – 1.00
Poorly sorted	1.00 – 2.00

The sediment skewness measurement was an indication of the symmetry of the grain size data on either side of the central value (Blott and Pye 2001, Bale and Kenny 2005). Positive skewness indicated that coarse sediments dominated, while negative skewness indicated that sediments were mostly fine (Buchanan and Kain 1971).

2.2.2.3. Sediment total organic carbon (TOC) analysis

Total organic carbon is a chemical component of organic content and is commonly used as an indicator of organic matter present in sediments (Schumacher 2002). Techniques employed to determine sediment TOC require that organic matter be destroyed by chemical or heat energy (Schumacher 2002). This converts the organic material to carbon dioxide (CO_2) and the loss can then be measured directly or indirectly and converted to TOC (Schumacher 2002). The method used in this study was adopted from Schumacher (2002) and incorporated the semi-quantitative hydrogen peroxide (H_2O_2) digestion method to calculate rough estimates of sediment TOC through sample weight loss. This involved the continual addition of 6% H_2O_2 to a known weight of sediment sample until the frothing ceased. After digestion, the sample was oven-dried at 105 °C, cooled, and weighed. Organic matter was then calculated using the difference between sample weight before and after digestion.

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

Where OM is organic matter (%), W_i is the initial sample weight (g), and W_f is the final sample weight (g). Organic matter was converted to TOC by employing the appropriate factor. A conversion factor of 1.72 is traditionally used and was used during this study, based on the assumption that organic matter contains 58% organic carbon (Schumacher 2002).

2.2.2.4. Macrobenthic invertebrate identification and enumeration

In the macrobenthic laboratory, samples were emptied into sorting trays and organisms were manually separated from sediment and detritus under a magnifying lamp. These organisms were sorted into broad groups (e.g. polychaetes, crustaceans, echinoderms, molluscs) and placed in labelled glass polytop vials filled with 4% formaldehyde saline (formal saline) solution.

After sorting, organisms were counted and identified to the lowest taxon level possible (preferably species) using a stereomicroscope (Zeiss stemi-DV4) and appropriate taxonomic keys (e.g. Barnard 1950, Day 1967, Kensley 1972, Griffiths 1976, Kensley 1978, Kilburn and Rippey 1982, Steyn and Lussi 1998, Olbers et al. 2015). Taxonomic identifications were verified using the World Register of Marine Species (World Register of Marine Species Editorial Board 2021) online database and altered where needed to ensure that the most current classifications were employed at the time of publishing. Reference specimens for each taxon were placed in separate labelled glass polytop vials filled with 4% formalsaline solution and compiled into a collection for comparison against past and future studies. After analysis, these were transferred to 70% ethanol for long-term storage.

2.3. Generic statistical analyses

Statistical plots and analyses were performed using Microsoft Excel for Office 365, Paleontological Statistics (PAST) v3.25 (Hammer et al. 2001), and the Plymouth Routines in Multivariate Ecological Research (PRIMER) v7.0.13 (Clarke and Gorley 2015) packages. Environmental and taxa maps were constructed using Ocean Data View (ODV) and Quantum Geographic Information System (QGIS) 3.14.16 packages. Where means were calculated, the standard deviation was used as the measurement of error.

2.3.1. Abiotic data

A critical component of this study is the potential influence of environmental (abiotic) parameters on biotic distribution. However, before analysing these effects, the abiotic parameters were investigated on their own to determine local environmental conditions on the uThukela shelf (Clarke and Warwick 2001). A total of 17 environmental variables (five physico-chemical near-bottom water readings and twelve sediment measurements) were considered during this study (Table 2.3).

Table 2.3. Abiotic factors measured on the uThukela shelf in August 2008 and 2010.

Environmental variable		Unit	Sampling level
Physico-chemical	Depth	m	Station
	Temperature	°C	
	Salinity	PSU	
	Dissolved oxygen (DO)	mg.L ⁻¹	
	Turbidity*	NTU	
Sediment	Gravel	%	Sample (2010) Station (2008)
	Very coarse sand (vcs)		
	Coarse sand (cs)		
	Medium sand (ms)		
	Fine sand (fs)		
	Very fine sand (vfs)		
	Mud		
	Organics		
	Mean grain size	Φ	
	Median grain size		
Sorting			
Skewness			

*Only measured in 2008

An attempt was made to acquire turbidity data for 2010 (even through satellite remote sensing), but the KZN Bight has high optical variation due to the extreme ocean dynamics of the area and a lack of suitable *in situ* validation data limited the ability to use this method (Bernard and Smith 2011). Turbidity was excluded from further analyses as it only existed for August 2008 and during this dry winter month seemed to have a negligible effect (according to the BIO-ENV procedure) on the inner-shelf macrofauna community distribution.

A parametric analysis of variance (ANOVA) (F) test was employed to test for significant differences in environmental variables at different shelf positions when assumptions of normality and homogeneity of variance were met. When parametric assumptions were not satisfied, data transformations ranging from less to most severe (square root to log) were applied and assumptions re-tested after each. If assumptions were still not met, a non-parametric Kruskal-Wallis (H) test was conducted for non-normal data, while a Welch F test was carried out for unequal variances. The corresponding post-hoc pair-wise tests were subsequently used to determine the samples responsible for any significant differences identified during analyses.

Draftsman plots were used to identify highly correlated environmental variables and skewed data. Highly correlated variables ($\rho \geq 0.950$) indicate that as one variable increases so does the other, and these are reduced to a single chosen variable to avoid unnecessary noise during analyses (Clarke and Warwick 2001). Sediment data revealed that mean phi and median phi were highly correlated ($\rho = 0.979$), so only the median phi sediment variable was retained for subsequent analysis as this has shown to be the simplest descriptive measure of sediment grain size (Gray and Elliott 2009). This parameter is also the most widely utilised by a wide variety of scientists, so this data is highly valuable for comparison across studies (Verfaillie et al. 2006). Plots for the remaining 15 environmental variables revealed that data for sedimentary parameters %gravel, %vcs, %cs, and %vfs were right-skewed. Data for these variables were log-transformed as outliers dominate the analyses and often lead to poor-quality interpretation (Clarke and Gorley 2006). The variables were then normalised to allow the comparison of variables that contained different units (Clarke and Gorley 2006). Dissimilarity in environmental variables was computed using Euclidean distance that is an appropriate measure for abiotic data that produces a triangular distance matrix (Clarke and Gorley 2006). Spatial variations in these parameters were analysed by a principal components analysis (PCA) ordination that approximates the continuum of relationships between samples and portrays them in a two-dimensional (2D) plot while identifying the variables most responsible for the distances observed (Clarke and Warwick 2001, Dutertre et al. 2013).

2.3.2. Biotic data

Pelagic, larval, and unidentified organisms were removed from the dataset before statistical analyses. An abundance matrix was constructed for the remaining biological data and values were standardised to 1.0 m². Standardisation converted counts to densities (used interchangeably with abundances) and involved the multiplication of 2008 data by a factor of

four (as samples were collected using a 0.25 m² Day grab) and the multiplication of the 2010 data by a factor of five (as samples were collected using a 0.20 m² Van Veen grab). When considering data per station, the three replicates per station (except station 9) were combined and divided by 3 to calculate the mean.

2.3.2.1. Univariate analyses

The number of benthic species in a sample area is usually not accurately measurable, so an estimation of the extent that the values obtained from sampling represent the biological community is required (Ellingsen 2001). A species accumulation curve was used to determine this, as an area is considered well-sampled when this graph reaches an asymptote (McArthur et al. 2010). An estimation of the true species richness of the study area was determined by the non-parametric *Chao2* method, which is based on the total number of observed taxa in addition to the prevalence of community uniques (restricted to a single sample) and duplicates (present in only two samples) (Colwell and Coddington 1994, Ellingsen 2001).

Univariate tests collapse the full biotic dataset into a single coefficient (Clarke and Warwick 2001). The primary community variables of taxa abundance (N : ind.m⁻²) and number of taxa (S), as well as various diversity indices, were analysed using the DIVERSE function in PRIMER v7.0.13 software. Numerous indices have been utilised to measure macrobenthic community diversity, with three aspects being considered in the present study. Biodiversity measures use data on the abundance of individuals among taxa and how these abundances are spread between these taxa (Gray and Elliott 2009). The Shannon-Wiener diversity index (H') is the most commonly used measurement in macrobenthic community studies (Clarke and Warwick 2001) and is strongly affected by the taxa in the middle of the rank sequence (Gray and Elliott 2009).

$$H' = - \sum_{i=1}^S p_i \ln p_i \quad (2.2)$$

Where p_i is the proportion of individuals of the i th taxon (N_i/N).

The calculated diversity value encompasses both taxa richness and evenness (Gray 1981, Gray and Elliott 2009), and to discern which of these were responsible for the high or low diversity

values, two additional indices were calculated. Margalef's richness index (d) measures the number of taxa present for a specified number of individuals (Clarke and Warwick 2001). It differs from the primary species richness measurement as it is calculated as independent of sample size (Clarke and Warwick 2001).

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

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

Pielou's evenness index (J') explains the distribution of individuals per taxon in the community and is the opposite of dominance (Gray and Elliott 2009).

$$J' = \frac{H'}{\ln S} \quad (2.4)$$

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

In macrobenthic community studies, the Shannon-Wiener diversity index is usually more affected by evenness, so the addition of rare species to the assemblage will have less of an effect on the H' value than changing species dominance (Gray 1981, Gray and Elliott 2009).

ANOVA tests were employed to assess significant differences in these univariate outcomes at different shelf positions and were conducted identically to the significance testing of abiotic values (see section 2.3.1.).

2.3.2.2. Multivariate analyses

Community ecology does not usually exhibit linear responses as the community is complex and contains many taxa (Clarke and Warwick 2001). The data collected during ecological studies, therefore, require multivariate analyses. Normal Q-type analysis was used for this study, in which samples were grouped according to the similarity in taxa composition (Field et al. 1982). Community studies frequently reveal many rare taxa and only a few abundant ones, so the biotic

data are often highly skewed (Clarke and Warwick 2001). Although multivariate tests do not require the transformation of data to attain normality, data transformations are necessary to reduce the contribution of common taxa so that rare taxa may also contribute to the analyses (Clarke and Warwick 2001, Underwood and Chapman 2005). Square root ($\sqrt{}$), fourth root ($\sqrt[4]{}$), and log or log ($x + 1$) transformations downweigh data values, with more severe transformations reducing the influence of abundant taxa and increasing the influence of rare taxa in analyses outputs (Clarke and Warwick 2001). For this study, abundance data were fourth root (root-root) transformed to allow the mid-range and rarer species, as well as the common ones, to influence similarity calculations.

Marine surveys commonly result in numerous taxa being absent from sampled stations, but this does not imply that these stations are similar due to sharing joint absences (Field et al. 1982). The Bray-Curtis (B-C) similarity coefficient considers this information (Field et al. 1982) and for this reason, is most widely used in benthic studies. It was therefore employed in this study, with group-average linking, to calculate sample similarity of the transformed abundance data. Samples were considered similar if they had analogous biotic communities and dissimilar if they had very few or no taxa in common (Clarke and Warwick 2001, Underwood and Chapman 2005).

This similarity was diagrammatically summarised using hierarchal classification and ordination (Field et al. 1982). Hierarchical classification, otherwise known as cluster analysis (used in Chapters 3 and 5), was represented by a dendrogram where samples were grouped based on their similarity to one another in terms of taxa composition (Clarke and Warwick 2001). Similarity profile (SIMPROF) permutation routines identified the significance of the groups formed during cluster analysis, and significant groups ($p < 0.05$) were represented by black solid lines (Clarke and Gorley 2015). Non-metric multidimensional scaling (nMDS) ordination (used in Chapter 4) was another method used to visually represent the dissimilarity between samples (based on the rank orders calculated previously in the Bray-Curtis matrix) on a 2D plane (Clarke and Warwick 2001). The relative distance between samples represented their similarity to one another, with nearby points having the most similar macrobenthic communities (Clarke and Warwick 2001, Underwood and Chapman 2005). Points placed in a 2D configuration do not usually satisfy the exact similarity, resulting in a level of distortion (measured by the Kruskal stress value) (Field et al. 1982, Clarke and Warwick 2001). Low stress values (< 0.05) usually indicate that the sample relationships are extremely well

represented, values 0.05 – 0.10 indicate a good representation, 0.10 – 0.20 give potentially useful results, and > 0.30 are considered highly stressed with points regarded as randomly positioned (Clarke and Warwick 2001).

The significance of the *a priori* groups related to shelf position was tested using the permutational analysis of variance (PERMANOVA) with unrestricted permutation of raw data. The larger the resultant Pseudo-*F* value, the less likely the null hypothesis of no differences among groups was true (Anderson et al. 2008). The average contribution of each taxon to the separation or closeness between and within groups was calculated through the “similarity percentages” (SIMPER) routine (Clarke and Warwick 2001, Clarke and Gorley 2006). A taxon was characteristic of a group (contributed highly to the similarity of samples within the group) if there were consistent abundances and low associated standard deviations across samples within that group (Fennessy et al. 1994).

2.3.3. Linking biotic assemblages to environmental variables

The RELATE function, in PRIMER v7.0.13, was used to ascertain the strength of the relationship between biotic and abiotic similarity matrices. The resulting rank correlation coefficient (ρ) measures the agreement between the Bray-Curtis similarity matrix and Euclidean distance matrix, where a value of one indicates a perfect relationship (Clarke and Gorley 2006). The BIO-ENV procedure within the BEST function was employed to determine the combination of environmental variables that maximised rank correlation between biotic and abiotic matrices (Clarke and Warwick 2001, Clarke and Gorley 2006). The resultant Spearman Rank Correlation coefficient (ρ) ranges between -1 and 1, with extreme values signifying that the two sets of ranks are in complete opposition (-1) or complete agreement (1) and a value of zero implying no relationship (Clarke and Warwick 2001). This test provides evidence as to which suite of measured environmental variables appears to most affect the observed macrobenthic community structure but does not prove cause and effect (Clarke and Warwick 2001).

The relative importance of each environmental variable in contributing to the community variation was further analysed by a distance-based redundancy analysis (dbRDA) using the distance-based linear model (distLM) procedure in PRIMER v7.0.13 or a Canonical Correspondence Analysis (CCA) in PAST v3.25. The dbRDA routine is used for biological assemblage data (Chapter 3), providing a visual ordination using the model constructed from

the previous BEST test and with the distLM procedure using multiple regression analyses to test the relative importance of each environmental variable (independent of every other environmental parameter) in explaining the biotic community variations (Anderson et al. 2008). The test employed a stepwise routine for 9 999 permutations based on the second-order Akaike Information Criterion (AICc). The CCA is also a visual ordination that assumes a unimodal response and is used for traits data that are not on comparable ranges (Chapter 4), providing a direct gradient analysis of habitat preferences by inputting the *a priori* selected environmental variables identified using the BEST function (Hammer et al. 2001).

The methods presented in this chapter are general analyses, and subsequent Chapters 3 – 5 provide further in-depth analyses pertaining to the specific study hypotheses.

CHAPTER 3. A BASELINE MACROBENTHOS COMMUNITY AND THE ASSOCIATED POTENTIAL ABIOTIC DRIVERS IN THE NEW UTHUKELA MARINE PROTECTED AREA

3.1. Overview

The uThukela shelf is off the large fluvially-dominated uThukela Estuary on the east coast of South Africa and within the newly promulgated uThukela Marine Protected Area (MPA). Macroinvertebrates collected at 23 stations were identified and enumerated to characterise the uThukela community at various shelf positions (along a depth gradient and indicating distances from terrestrial influence and the influence of the uThukela Estuary). The macrofauna community was diverse and dominated by Polychaeta, Crustacea, and Mollusca in terms of taxa numbers and abundances. Abundance, number of taxa, and diversity did not differ significantly at different shelf positions, however, multivariate analyses identified five distinct macrobenthic assemblages with different taxa types. These distribution patterns were related to near-bottom water physico-chemistry and sediment habitats and appeared to be correlated mostly with the combination of depth, dissolved oxygen (DO), salinity, and sediment composition (mud, coarse sand, and medium sand). An atypical salinity gradient was observed during this analysis, with slightly more saline near-bottom waters near the shore and less saline bottom conditions near the shelf edge. This was unexpected but potentially due to the reduced penetration of freshwater from the uThukela Estuary onto the shelf during the dry season and the possible divergent upwelling at the shelf edge due to the widening of the uThukela shelf.

3.2. Introduction

The characteristically muddy uThukela is a relatively broad region of the KwaZulu-Natal (KZN) shelf, situated off the largest river on South Africa's east coast and the fluvially-dominated uThukela Estuary (van Niekerk et al. 2020) (see Chapter 2). This makes for a characteristic ecology as the uThukela shelf habitats are influenced by both oceanographic processes and estuarine inputs (including sediment and particulate organic matter) (Bosman et al. 2007). Indications that this environment contains structurally and functionally unique macrobenthic communities (Untiedt and MacKay 2016) (see Chapter 1) contributed to the protection of this region and the recent establishment of the uThukela MPA. The present study expands on this preliminary evidence and provides more fine-focussed investigation into the diversity of the uThukela shelf macrofauna communities. Biodiversity is an ecological property of the benthic community, with higher values generally indicating higher ecosystem

performance (Lohrer and Hancock 2004). It is traditionally studied through a taxonomic approach (Kaminsky et al. 2018), as used in this chapter, and provides information on community composition through enumeration and identification of taxa to the lowest classification level possible, ideally species (Gray and Elliott 2009). The information gathered through this process is foundational to understanding the biology of an environment and provides an essential taxonomic database for future comparison (Brown 1999, Maggiore and Keppel 2007). There are limited data available for South African macrofauna, especially on the east coast, as there have been limited studies focusing on this group due to restricted taxonomic expertise, as well as the expense and time required during sample collection and processing (Griffiths et al. 2010). Therefore, this study is an invaluable contribution to the baseline knowledge of the unconsolidated seafloor habitat off uThukela and is a biodiversity inventory for potentially interesting species that can be targeted for further study. Baseline datasets for MPAs are vital and provide essential knowledge on the reference conditions preceding protection to allow for a better understanding of community changes post-protection (Louzao et al. 2010).

Due to the study site being situated off a major river system, the “position on shelf” (which is a factor detailing distance from estuary and shore) appears an appropriate predictor for this type of study (MacKay et al. 2016). Freshwater is important in defining these fluvially-dependent shelf communities, and its influence typically decreases with increasing distance from the terrestrial source (Snelgrove 1998). The mid-shelf is expected to have the highest macrofauna diversities as the intermediate shelf section is typically exposed to minimum flow rates and wave disturbances (Zalmon et al. 2013). On the inner-shelf, fluctuating flow rates of a major river generally cause environmental and sediment instability (Drinkwater and Frank 1994, Zalmon et al. 2013), with an increase in suspended particle concentration and a greater amount of fine sediment during regular estuarine discharge (Akoumianaki and Nicolaidou 2007). The macrobenthic organisms occurring in this region are, therefore, at risk of burial and sediment instability which results in a typically poor community that is mostly characterised by small early colonisers and rare but persistent larger burrowing species (Akoumianaki and Nicolaidou 2007). The outer-shelf is also expected to contain lower standing stocks as although there is a decrease in sedimentation and resuspension of sediments, there is also a reduction in food supply (Akoumianaki and Nicolaidou 2007). Spatial factors, along with individual environmental variables, were therefore included during this investigation to determine if similar patterns existed on the uThukela shelf.

3.2.1. Aims, objectives, and hypotheses

This chapter aimed to examine the taxonomic composition of the uThukela shelf macroinvertebrate communities and determine the potential influence of environmental conditions on these benthic distributions. The effect of shelf position (shelf zone, most direct distance from shore, and distance from the uThukela Estuary mouth) was also investigated.

Objectives:

- 3.1. To characterise the uThukela shelf environments according to measured physico-chemical and sediment parameters and determine potential differences in shelf position.
- 3.2. To describe the uThukela shelf macroinvertebrate communities and determine whether there is a significant difference in communities occurring at different shelf positions.
- 3.3. To relate measured environmental parameters to benthic assemblages and to determine the extent to which these conditions and habitats influence community patterns.

Hypotheses:

H₀₁: There are no significant differences in environmental conditions at different uThukela shelf positions (shelf zones, distances from shore, and distances from the uThukela Estuary mouth).

H₀₂: There are no significant differences in macroinvertebrate communities at different uThukela shelf positions (shelf zones, distances from shore, and distances from the uThukela Estuary mouth).

H₀₂: There is no significant relationship between measured near-bottom physico-chemical parameters and macrobenthic community patterns.

H₀₃: There are no significant differences in macrofauna communities in the different sediment habitats.

3.3. Materials and methods

The study site description, general sampling and laboratory procedures, and general data analyses are presented in Chapter 2. Sampling was conducted during the dry (winter) season on the inner (IS: 0 – 50 m), mid (MS: 50 – 80 m), and outer (OS: 80 – 130 m) uThukela shelf in August 2010 and on the inner-shelf in August 2008 (Figure 3.1). Specific methods pertaining to this chapter are presented further.

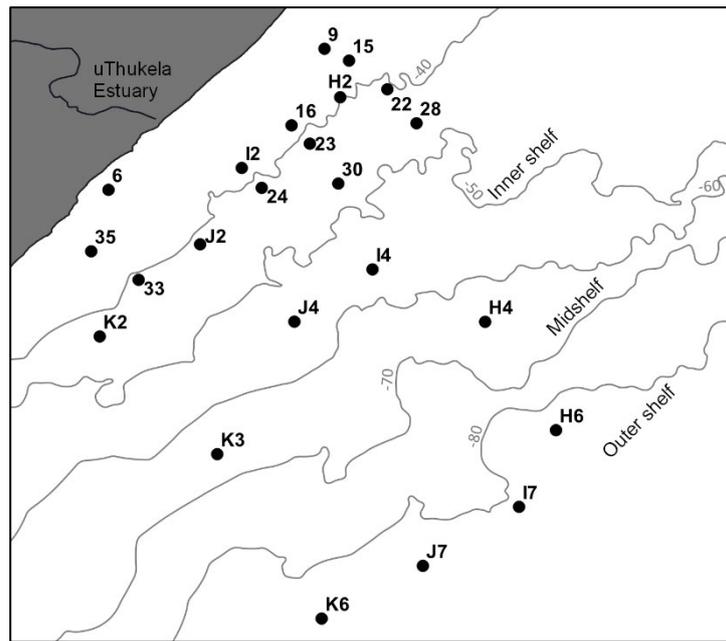


Figure 3.1. Study site depicting sampled stations on the inner (0 – 50 m), mid (50 – 80 m), and outer (80 – 130 m) uThukela shelf. Refer also to Figure 2.1 for regional context.

3.3.1. Data analyses

3.3.1.1. Abiotic data

Data from two closely associated but non-consecutive years were used during this study. Near-bottom water readings were significantly different (measured using a parametric *t*-statistic or non-parametric Mann-Whitney *U*) for the inner-shelf samples in 2008 and 2010, so data were separated into respective years for abiotic data analyses. Ocean Data View (ODV) was used to visualise these near-bottom water characteristics. Due to the difference in near-bottom water measurements between years, the analyses of differences between the *a priori* factor of shelf zone for physico-chemical data used only 2010 water measurements, while sediment analyses included data from both years (as no significant differences occurred between 2008 and 2010). One-way analysis of variances (ANOVAs) (*F*) were employed to test the significance of these potential differences (Chapter 2).

Near-bottom water parameters are commonly observed to fluctuate along with depth (McArthur et al. 2010) (Chapter 1). Depth was, therefore, linearly correlated (*r*) with temperature (°C), salinity (PSU), and dissolved oxygen (DO) ($\text{mg}\cdot\text{L}^{-1}$) to explore whether this

was true for this study. Additionally, the correlation between sediment grain size and sediment total organic carbon (TOC) was tested, as these variables are also typically related (Pearson and Rosenberg 1978) (Chapter 1). Data were then transformed, normalised, and similarities were presented in a principal components analysis (PCA) plot (Chapter 2).

3.3.1.2. Macroinvertebrate data

In this study, a single replicate grab from station 9 was an outlier as species observed in this sample were completely different from taxa found in other samples. After initial inclusion of 9B in the study of taxa and individuals present, it was subsequently removed, resulting in station 9 being left with only one replicate. Due to station 9 providing unique and interesting results, it was not entirely excluded from the study, and replicate 9A was included (along with other stations) in further statistical analyses.

Univariate analyses

The true species richness of the study area was approximated by the non-parametric *Chao2* estimate (Chapter 2). The primary community variables mean abundance (N) and mean number of taxa (S), as well as the Shannon-Wiener diversity (H'), Margalef's richness (d), and Pielou's evenness (J'), were computed for stations and the assemblages obtained in cluster analysis. One-way ANOVA (F) testing (or Kruskal-Wallis H testing for non-normal and Welch F for inequality of variances) was used to identify any significant differences in univariate measures (Chapter 2) between shelf zones (inner-shelf, mid-shelf, and outer-shelf), between distances from shore (1 – 5 km, 5 – 10 km, 10 – 15 km, 15 – 20 km, 20 – 30 km, 30 – 40 km), and between distances from the uThukela Estuary mouth (< 10 km, 10 – 15 km, 15 – 20 km, 20 – 30 km, 30 – 40 km, > 40 km).

Multivariate analyses

Macrobenthic abundance data of 67 uThukela shelf sample replicates (excluding 9B) were root-root transformed prior to the calculation of Bray-Curtis (B-C) similarities and subsequent cluster analysis (Chapter 2). The resultant clusters were verified statistically using the similarity profile (SIMPROF) routine, while the taxa responsible for sample groupings and dissimilarities were identified through similarity percentages (SIMPER) (Chapter 2). The potential effect of shelf position on macrobenthic composition was also tested using PERMANOVA (Pseudo- F) on *a priori* selected factors shelf zone, distance from shore, and distance from the uThukela Estuary mouth.

3.3.1.3. Relating macroinvertebrate distributions to abiotic variables

The relationship between the abiotic (Euclidean) and biotic (Bray-Curtis) similarity matrices was tested using the RELATE procedure (Chapter 2). The suite of environmental parameters best describing the multivariate community distribution was identified by the BIO-ENV algorithm in the BEST procedure, and these were input to the distance-based linear model (distLM) with the distance-based redundancy analysis (dbRDA) (Chapter 2). The distLM, through marginal and sequential testing, identified the relative importance of each environmental variable in explaining macrofauna distribution. Marginal tests investigated the importance of each variable in isolation, while sequential tests indicated the importance of each variable when added to the model in a particular sequence (“step-wise” in this study). These results contributed to the dbRDA, a constrained ordination plot that reflects multivariate community variations and the environmental variables responsible for these distributions (Anderson et al. 2008). The vector overlays on the dbRDA plot indicated the extent that each variable influenced benthic distribution, with longer vectors having a greater effect on the dbRDA axes. Another predictor variable, taxa, was also overlaid on the plot to indicate the relationship between these organisms and the environmental conditions identified as responsible for the multivariate variation.

3.4. Results

3.4.1. *Abiotic factors*

3.4.1.1. Depth

The bathymetry of stations sampled on the uThukela shelf ranged from 24 m (station 6) to 126 m (station K6) (Figure 3.2). The inner-shelf stations ranged between 24 – 48 m ($\bar{x} = 39.44 \pm 7.11$ m), mid-shelf between 51 – 69 m ($\bar{x} = 59.50 \pm 7.77$ m), and outer-shelf between 87 – 126 m ($\bar{x} = 107.50 \pm 16.01$ m).

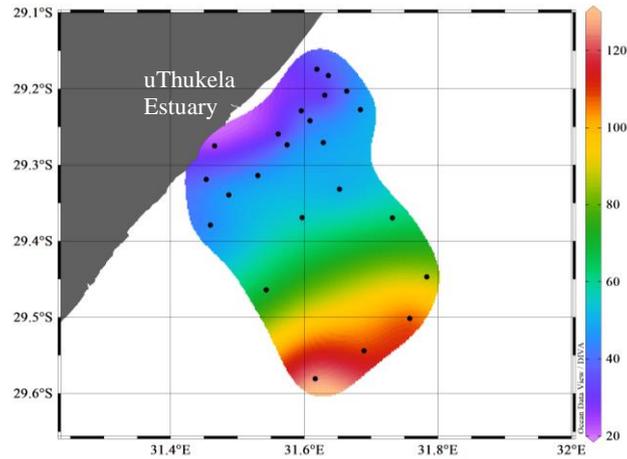


Figure 3.2. Depth (m) gradient of the uThukela shelf using interpolation between sampling stations.

3.4.1.2. Temperature

Near-bottom water temperatures for the inner uThukela shelf were significantly lower ($t = 12.869$, $p < 0.001$) during the 2008 cruise ($\bar{x} = 18.10 \pm 0.10$ °C) than the 2010 cruise ($\bar{x} = 19.86 \pm 0.45$ °C) (Figure 3.3). During the 2008 cruise, where only the inner-shelf was sampled, temperatures ranged from 17.98 °C (station 24 and 30) to 18.29 °C (station 35), and temperature readings did not have any relation to depth ($r = 0.110$, $p = 0.747$, $n = 11$). Rather, the pattern observed was that of cooler water offshore in the area of estuary outflow, with slightly warmer temperatures bordering either side of this (Figure 3.3a). Across all stations in 2010, near-bottom temperatures ranged between 14.47 °C (station K6) and 20.35 °C (station K3) (Figure 3.3b), declining significantly with increasing depth ($r = -0.792$, $p = 0.002$, $n = 12$). The outer uThukela shelf ($\bar{x} = 16.90 \pm 2.50$ °C) was significantly cooler (Welch $F = 2.891$, $df = 4.744$, $p = 0.151$), than the inner-shelf ($\bar{x} = 19.86 \pm 0.45$ °C, Tukey's $p = 0.046$) and mid-shelf ($\bar{x} = 20.04 \pm 0.22$ °C, Tukey's $p = 0.036$).

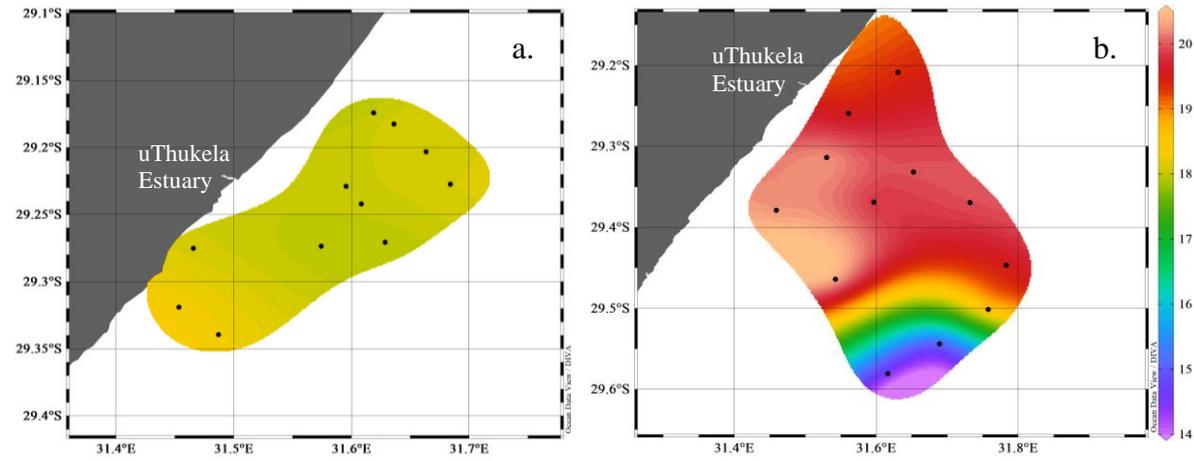


Figure 3.3. Near-bottom temperatures ($^{\circ}\text{C}$) for (a) the uThukela inner-shelf in 2008 and (b) the uThukela inner, mid, and outer-shelf in 2010, using interpolation between sampling stations.

3.4.1.3. Salinity

Near-bottom salinities for the inner uThukela shelf were significantly higher ($U = 0.000$, $p = 0.005$) for the 2008 cruise ($\bar{x} = 36.32 \pm 0.09$ PSU) than the 2010 cruise ($\bar{x} = 35.46 \pm 0.01$ PSU) (Figure 3.4). Inner-shelf salinities in 2008 ranged between 36.16 PSU (station 33) and 36.41 PSU (station 16) but did not show any relation to depth ($r = 0.014$, $p = 0.968$, $n = 11$) (Figure 3.4a). The pattern showed slightly more saline water just north of the estuary outflow region and less saline on either side of this (especially south of the estuary mouth) (Figure 3.4a). In 2010, salinities across all stations ranged from 35.32 PSU (station K6) to 35.47 PSU (station H2), showing a significant decrease with increasing depth ($r = -0.888$, $p < 0.001$, $n = 12$) and significant differences between the inner, mid, and outer-shelf ($F = 13.150$, $df = 11$, $p = 0.002$) (Figure 3.4b). This atypical salinity gradient showed that the outer-shelf had significantly lower salinities ($\bar{x} = 35.37 \pm 0.04$ PSU) than the inner-shelf ($\bar{x} = 35.46 \pm 0.01$ PSU, Tukey's $p = 0.003$) and mid-shelf ($\bar{x} = 35.45 \pm 0.01$ PSU, Tukey's $p = 0.006$).

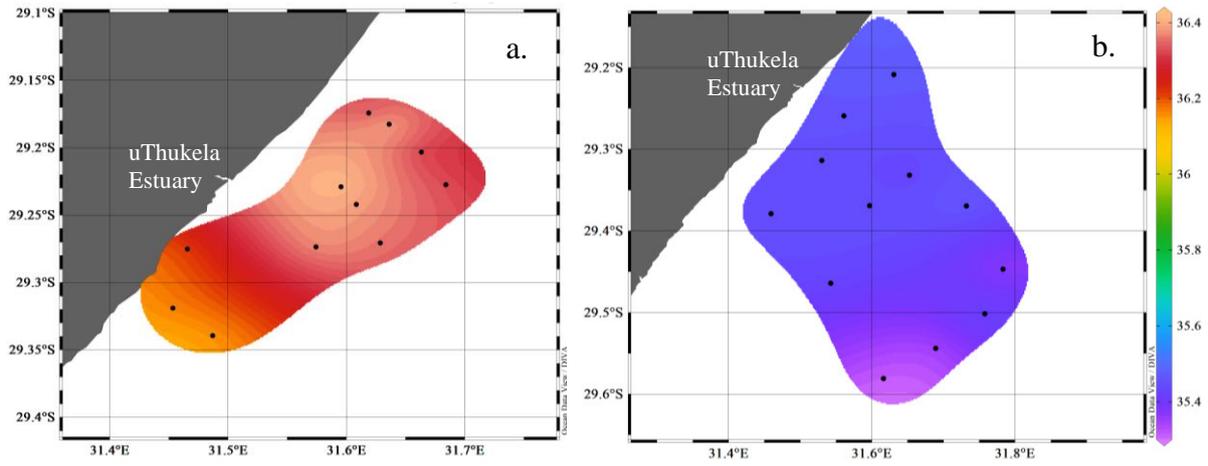


Figure 3.4. Near-bottom salinities (PSU) for (a) the uThukela inner-shelf in 2008 and (b) the uThukela inner, mid, and outer-shelf in 2010, using interpolation between sampling stations.

3.4.1.4. Dissolved oxygen (DO)

The near-bottom waters of the inner uThukela shelf were significantly less oxygenated ($U = 0.000$, $p = 0.005$) in 2010 ($\bar{x} = 6.52 \pm 0.13 \text{ mg.L}^{-1}$) than in 2008 ($\bar{x} = 7.29 \pm 0.10 \text{ mg.L}^{-1}$) (Figure 3.5). Depth and DO were negatively correlated during the 2008 inner-shelf cruise ($r = -0.768$, $p = 0.006$, $n = 11$), ranging from 7.18 mg.L^{-1} (station 30) to 7.54 mg.L^{-1} (station 6) (Figure 3.5a). In the 2010 cruise across the shelf, DO significantly declined with increasing depth ($r = -0.913$, $p < 0.001$, $n = 12$), with lowest readings (5.21 mg.L^{-1}) recorded at the deepest station (station H6) and highest readings (6.63 mg.L^{-1}) noted at two of the shallow stations (stations H2 and I2) (Figure 3.5b). Like temperature and salinity, significantly lower DO concentrations ($F = 145.300$, $df = 11$, $p < 0.001$) were measured on the outer-shelf ($\bar{x} = 5.31 \pm 0.11 \text{ mg.L}^{-1}$) than the inner-shelf ($\bar{x} = 6.52 \pm 0.13 \text{ mg.L}^{-1}$, Tukey's $p < 0.001$) and mid-shelf ($\bar{x} = 6.38 \pm 0.09 \text{ mg.L}^{-1}$, Tukey's $p < 0.001$).

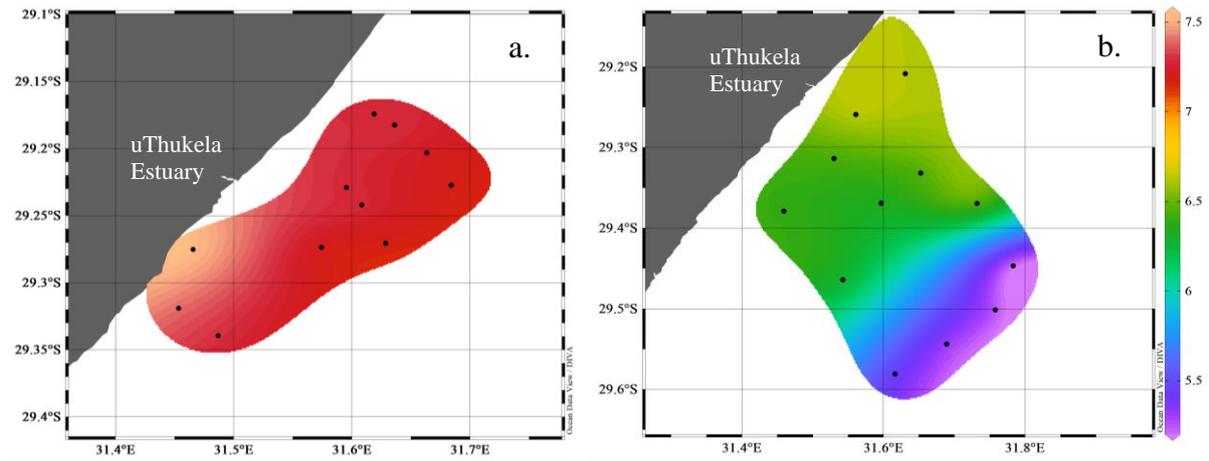


Figure 3.5. Near-bottom dissolved oxygen (DO) concentrations (mg.L^{-1}) for (a) the uThukela inner-shelf in 2008 and (b) the uThukela inner, mid, and outer-shelf in 2010, using interpolation between sampling stations.

3.4.1.5. Sediment grain size and total organic carbon (TOC)

When considering only uThukela inner-shelf sediment samples, there was no significant difference between the 2008 and 2010 cruises for either median grain size ($U = 55.500$, $p = 0.538$) or sediment TOC ($t = 0.840$, $p = 0.410$). Thus, all stations sampled on both cruises were combined for analysis. The uThukela shelf consisted mostly of mud (54.9%) with medium sand (14.8%) and fine sand (14.3%), and little coarse sand (7.9%), very fine sand (5.8%), very coarse sand (1.8%), and gravel (0.6%) (Table 3.1). Overall, sediments were dominated by fine grains (indicated by the mean negative skewness -0.78 ± 3.44), containing a modest TOC ($\bar{x} = 2.2 \pm 2.2\%$) (Table 3.1). Sediments were moderately sorted ($\bar{x} = 0.79 \pm 0.36 \Phi$), implying some heterogeneity of the bottom and that numerous sedimentary habitats existed on the uThukela shelf during this study. A significantly positive relationship ($r = 0.493$, $p < 0.001$) was observed between sediment TOC and median grain size (phi) during this study, with a higher correlation for the 2010 data ($r = 0.668$, $p < 0.001$) than the 2008 data ($r = 0.425$, $p = 0.015$).

Further analyses revealed significant differences for both TOC ($F = 10.260$, $df = 35$, $p < 0.001$) and median grain size (Welch $F = 12.170$, $df = 14.710$, $p < 0.001$) in different shelf zones. The outer-shelf (stations K6, J7, I7, and H6) was dominated by poorly sorted ($\bar{x} = 1.04 \pm 0.21 \Phi$) mud ($\bar{x} = 72.6 \pm 8.3\%$, Figure 3.6). When compared to the mid-shelf, the outer-shelf had significantly higher sediment TOC (Tukey's $p < 0.001$) and median grain size (Tukey's $p < 0.001$). The mid-shelf consisted of three stations characterised by little mud, with coarse-grained sands dominating (stations K3, J4, and I4), and one station that was almost exclusively

mud (station H4: 95.3%) (Figure 3.6). Overall, this shelf zone had a high dominance of coarse sediments (\bar{x} skewness = 1.97 ± 3.16) with a low percentage of TOC ($\bar{x} = 1.0 \pm 0.6\%$). The inner-shelf showed no significant differences from the mid-shelf and was only significantly different from the outer-shelf in terms of a lower TOC percentage (Tukey's $p = 0.005$). It was characterised as mostly muddy (\bar{x} mud% = $57.2 \pm 38.9\%$) with a medium TOC ($\bar{x} = 2.3 \pm 2.6\%$), and while some stations were dominated by mud (stations 24, 16, 23, 9, 15, 22, 28, I2, and H2), others were dominated by different sand types (stations 6, 35, 33, 30, K2, and J2) (Figure 3.6). The inner-shelf generally comprised the most well-sorted sediments overall ($\bar{x} = 0.69 \pm 0.34 \Phi$).

Table 3.1. Percentage distribution of sediment grain size categories and statistics of the uThukela shelf bottom habitat.

Variables	Mean	Std Dev	Min	Max
%Gravel	0.61	2.21	0.00	10.69
%Very coarse sand (vcs)	1.75	6.10	0.00	29.63
%Coarse sand (cs)	7.85	14.72	0.00	59.04
%Medium sand (ms)	14.81	17.04	0.08	48.75
%Fine sand (fs)	14.29	15.85	0.26	48.07
%Very fine sand (vfs)	5.79	6.18	0.45	27.49
%Mud	54.91	37.79	1.38	98.80
Median grain size (Φ)	3.33	1.38	0.37	4.49
Sorting (Φ)	0.79	0.36	0.31	1.58
Skewness	-0.78	3.44	-8.26	6.52
TOC (%)	2.22	2.23	0.22	10.01

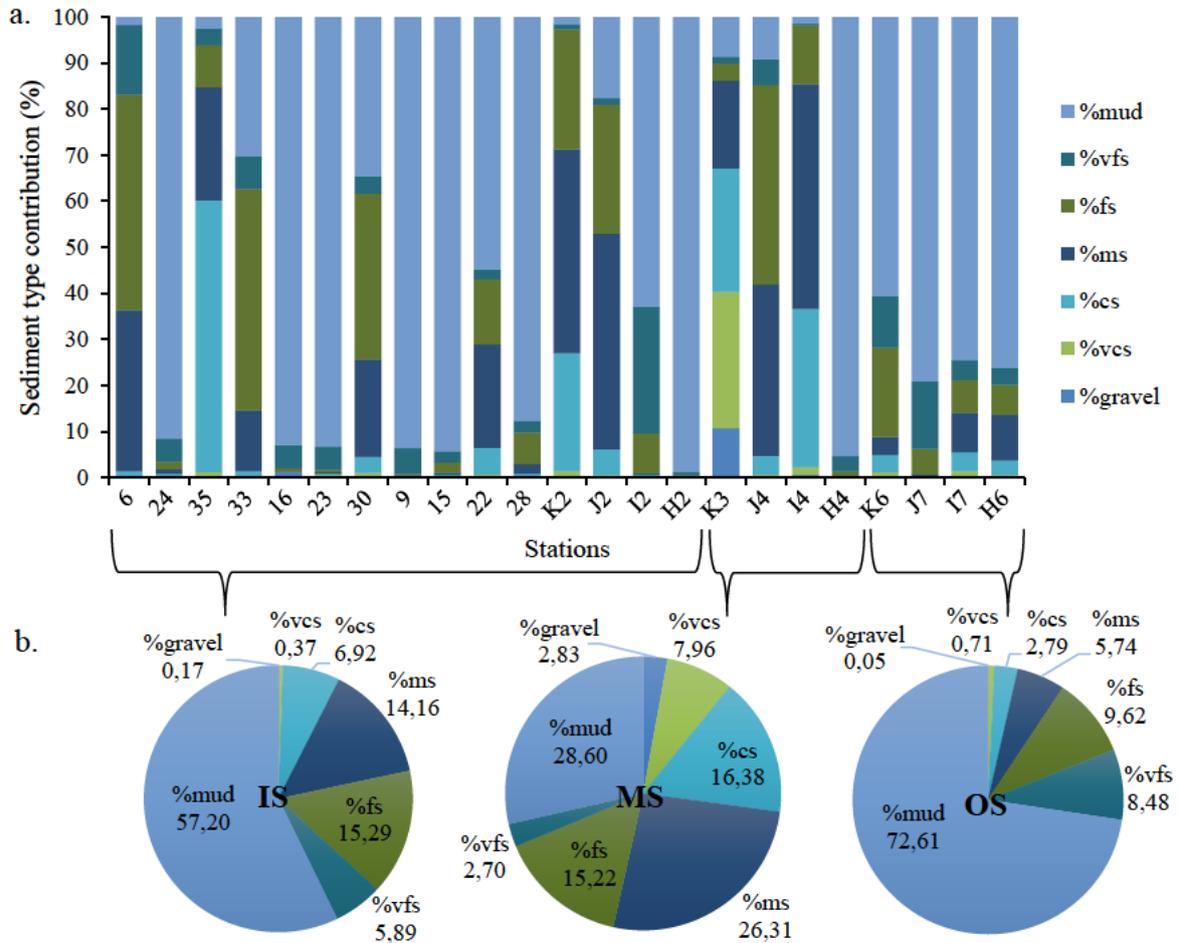


Figure 3.6. Soft-sediment habitats, (a) according to contributions (%) by sediment type at stations (b) on the inner (IS), mid (MS), and outer (OS) uThukela shelf.

3.4.1.6. Principal Components Analysis (PCA)

The PCA using 15 environmental predictor variables revealed that five axes explained 87% of the cumulative variation between stations, with PC1 and PC2 jointly explaining 58% of this (Figure 3.7). Axis PC1 (37%) separated stations according to grain size categories along a gradient of mud (affecting median grain size) to medium and very coarse sands. Axis PC2 (21%) was defined mostly by near-bottom water parameters and separated stations along a gradient of high DO and salinity to increased depth and sediment sorting. Outer-shelf stations (K6, J7, I7, and H6) were characterised by high mud content, poor sediment sorting (high sediment sorting coefficients), and increased depth. Inner and mid-shelf stations overlapped, being characterised by increased DO and salinity and varying sediment grain sizes from mud to coarser sands. An exception to this was station K3 that separated from all other stations,

being the most poorly-sorted (high sediment sorting coefficient) and with the most coarse sediments of all stations sampled.

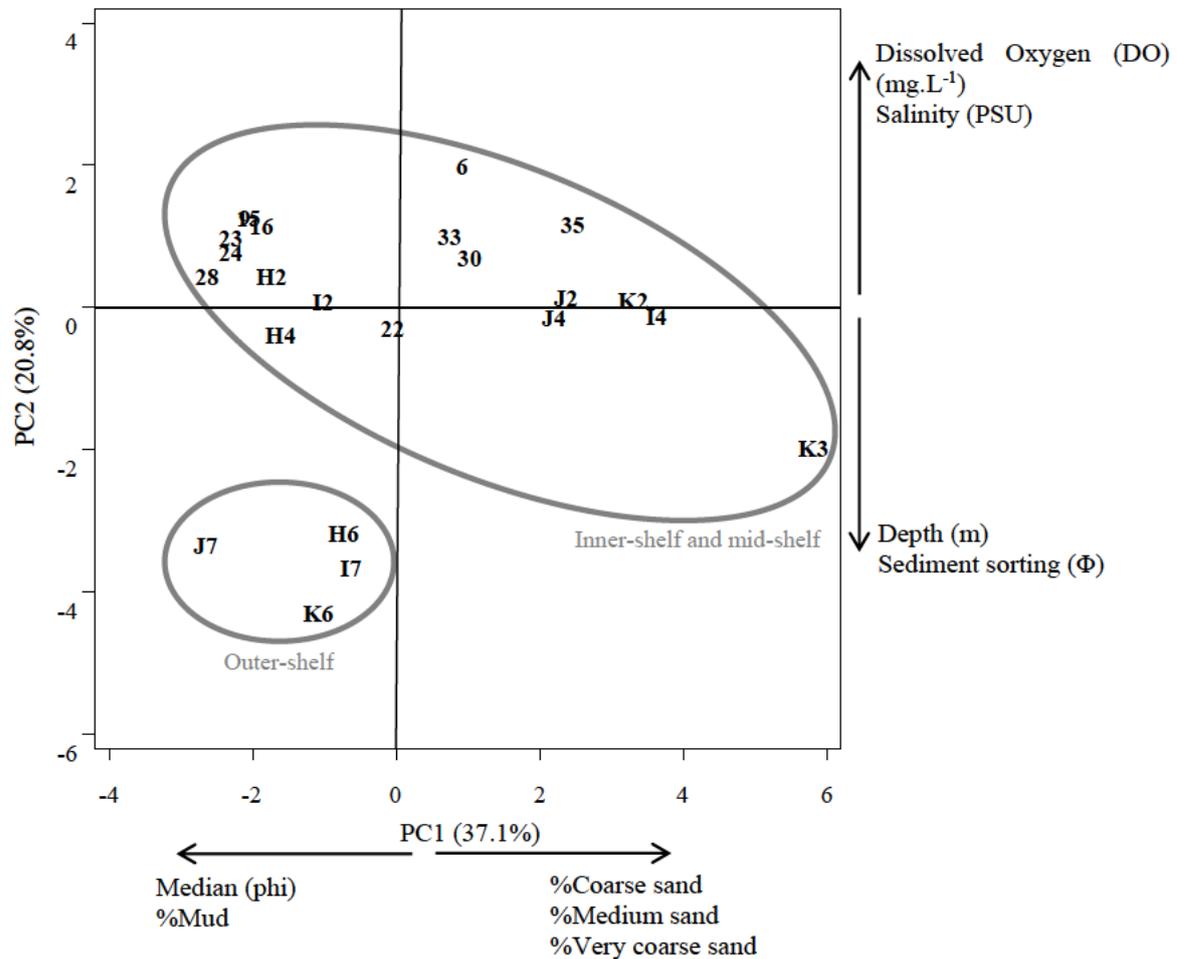


Figure 3.7. Two-dimensional Principal Components Analysis (PCA) plot visualising the abiotic environment of 23 stations on the uThukela shelf. Responsible vectors are indicated adjacent to axes PC1 and PC2.

3.4.2. Biota distributions

3.4.2.1. Macroinvertebrate community composition

With the conversion of counts to abundance/density (per m⁻²) for comparison between samples and different studies, the total abundance sampled for this study was 35 645 individuals over 68 m², with a mean of 512 ind.m⁻² across the study area. These individuals belonged to 455 taxa representing 12 phyla, 19 classes, 48 orders, 154 families, and 259 genera. Within this community, 190 taxa (42% of the total *S*) were unique (restricted to one sample), and 76 taxa

(17% of the total S) were duplicates (present in only two samples). Taxonomic resolution reached species level in 215 cases (47% of total taxa), genus level in 120 cases (26% of total taxa), family level in 38 cases (8% of total taxa), and only 82 taxa (18% of total taxa) were left at a higher classification. The Annelida and Arthropoda had the highest resolution of all the phyla, having 64% and 55% of their taxa identified to species level, respectively. The lowest resolution of species-level identification was for the Cnidaria (4%), Sipuncula (0%), and “other” phyla (0%). Phyla represented as “other” refer to those with minor individual contributions, thus not playing major roles in community indices (i.e. Bryozoa, Nemertea, Platyhelminthes, Phoronida, Ctenophora, and Hemichordata).

3.4.2.2. Taxa estimators

The species-accumulation and *Chao2* curves did not reach asymptotes (Figure 3.8), indicating that there is still sampling to be done before representative biodiversity is captured for the study area. The true taxa richness approximated by the *Chao2* non-parametric estimator was 751 taxa, but the number of taxa observed during the study ($S_{obs} = 455$ taxa) was 61% of this value (Figure 3.8).

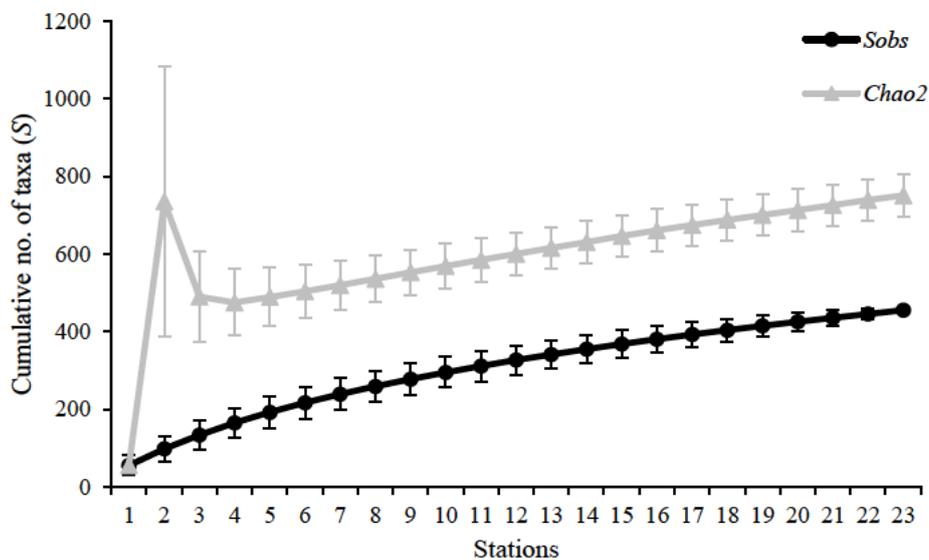


Figure 3.8. Observed species accumulation (S_{obs}) and *Chao2* curves (\pm SD) for macroinvertebrates of 23 uThukela shelf stations.

3.4.2.3. Taxa contributions

Annelida (almost entirely Polychaeta) was the dominant phylum for macroinvertebrate abundance (N : 50%) and number of taxa (S : 40%), while Arthropoda (almost exclusively

Crustacea and mostly from the order Decapoda) was the second-highest contributor to these indices (N : 23%, S : 26%). Mollusca (N : 10%, S : 17%), Sipuncula (N : 6%, S : 4%), Echinodermata (N : 4%, S : 4%), and Cnidaria (N : 1%, S : 5%) also contributed significantly to the uThukela community, and only 6% of abundance and 4% of taxa numbers were attributed to the “other” phyla (Figure 3.9).

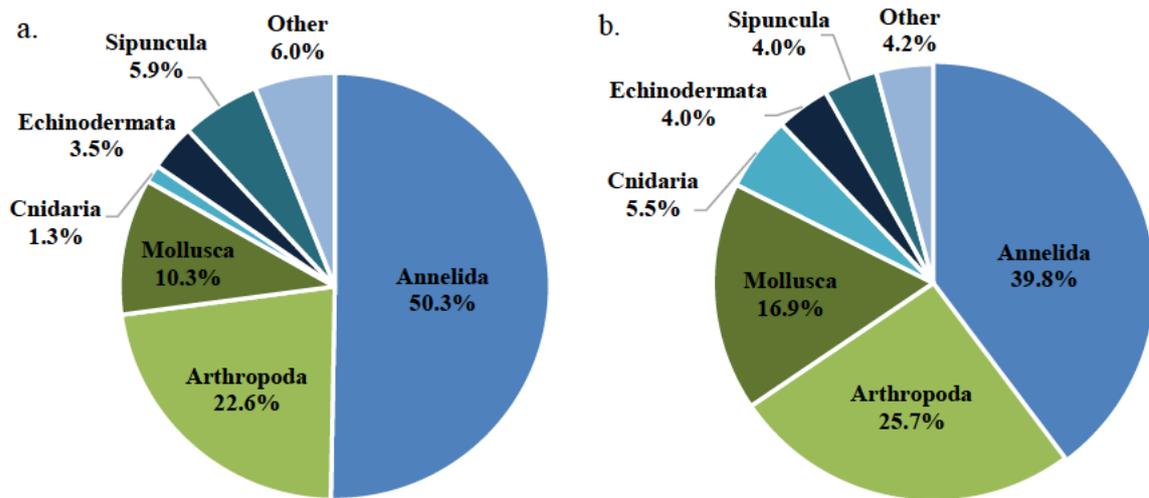


Figure 3.9. Contribution per phylum to (a) abundance (N : ind.m⁻²) and (b) number of taxa (S) in the macroinvertebrate community sampled on the uThukela shelf.

The most widely distributed (frequently encountered) taxa were the peanut worm Sipunculidae sp.2 (71% of samples), the polychaetes *Aglaophamus dibranchis* (59% of samples) and *Owenia fusiformis* (44% of samples), the crab *Xenophthalmodes cf. moebii* (47% of samples), and the bivalve *Macomopsis moluccensis* (41% of samples). The most abundant taxa in the study site were the sandprawn *Balsscallichirus gilchristi* (N : 6% dominance), the polychaetes *Cirratulus concinnus* (N : 5% dominance), *Aglaophamus dibranchis* (N : 5% dominance), and *Aonides oxycephala* (N : 5% dominance), the bryozoan *Cupuladria* sp.1 (N : 5% dominance), and the peanut worm Sipunculidae sp.2 (N : 5% dominance). The most wide-spread taxa were, therefore, not necessarily the most abundant, as seen by *B. gilchristi* and *C. concinnus* that were the most abundant taxa but only appeared in 10% and 29% respectively of all samples collected.

3.4.2.4. Sample 9B

Replicate sample 9B was considerably different from all other samples collected on the uThukela shelf and was, therefore, removed for analyses from this point onward. However, this replicate contained unique and interesting macrobenthos, so these findings are presented.

Sample 9B contained 2 864 ind.m⁻² from 88 macrobenthic taxa representing 9 phyla, 11 classes, 20 orders, 52 families, and 59 genera. Of these, 66 taxa were unique to the sample and not found in any of the other samples collected during the study. Although the macrofauna abundance of grab 9B was dominated by Annelida (N : 34%), there was a high contribution by Echinodermata (N : 26%). This was in contrast to the other samples collected, and was due to the high abundance of the brittle star *Ophiothela mirabilis* (N : 544 ind.m⁻²), which was the most abundant organism overall. Also noteworthy for this sample, was the relatively high Cnidarian abundance and number of taxa (N : 6%, S : 13%). All indications were of the habitat complexity presented because of a nearby reef.

3.4.2.5. Macrobenthic community and diversity indices

Number of taxa

After the removal of outlier replicate sample 9B, the number of taxa (S) collected during this study decreased to 389 macrobenthic taxa. Station 9 was overall the most taxa rich (S : 106 ± 49 taxa), but after exclusion of the replicate 9B, the mean number of taxa (S) at each station ranged between 10 ± 2 taxa (station H4) and 93 ± 6 taxa (station K2) (Figure 3.10). Most stations followed the overall trend of Annelida and Arthropoda being the most taxa-rich phyla, but some inner-shelf stations showed Mollusca to dominate local taxa numbers (stations 24, 16, 23, 9, 15, and 28) (Figure 3.10). The numbers of taxa were similar for the inner (S : 14 – 93 taxa), mid (S : 10 – 89 taxa), and outer-shelf (S : 42 – 78 taxa), and did not differ significantly between shelf zones ($H = 1.981$, $df = 22$, $p = 0.371$). There were no significant differences in number of taxa for stations sampled at variable distances from the shore ($F = 0.802$, $df = 22$, $p = 0.564$), and variable distances from the uThukela Estuary mouth ($F = 0.965$, $df = 22$, $p = 0.451$).

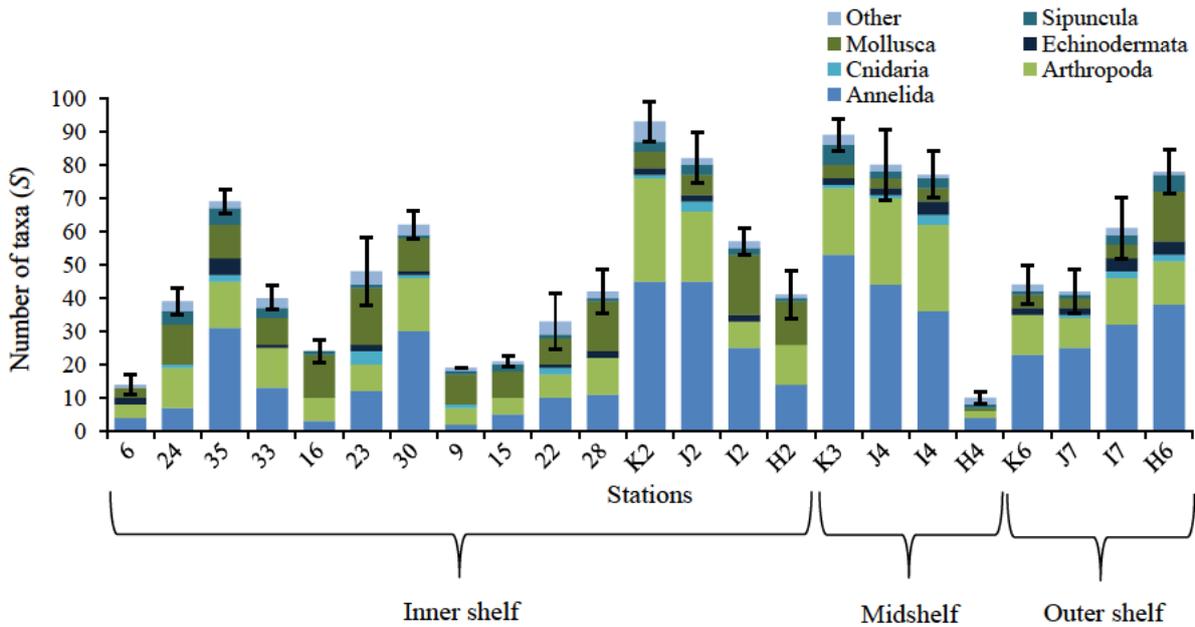


Figure 3.10. Spatial distribution of the mean number of macroinvertebrate taxa ($S \pm SD$) aggregated to major phyla for stations sampled on the inner, mid, and outer uThukela shelf.

Abundance

Prior to the removal of replicate 9B, station 9 was the most abundant station sampled on the uThukela shelf ($N: 1\ 552 \pm 1\ 855\ \text{ind.m}^{-2}$), but after exclusion of this sample, mean macroinvertebrate abundances (N) ranged from $28 \pm 12\ \text{ind.m}^{-2}$ (station 6) to $1\ 095 \pm 363\ \text{ind.m}^{-2}$ (station H6) (Figure 3.11). Most stations (except stations 33 and K2) followed the overall trend of Annelida being the most abundant (Figure 3.11). However, station 33 was Arthropoda-dominated with a very large variance due to a high abundance of *B. gilchristi* in one of the replicates ($N: 1\ 536\ \text{ind.m}^{-2}$), and station K2 also showed a dominance of Arthropoda due to a high proportion of Amphipoda. The mean abundance per station was not significantly different ($H = 1.229$, $df = 22$, $p = 0.541$) between the inner ($\bar{x} = 432 \pm 301\ \text{ind.m}^{-2}$), mid ($\bar{x} = 576 \pm 419\ \text{ind.m}^{-2}$), and outer-shelf ($\bar{x} = 578 \pm 359\ \text{ind.m}^{-2}$). There were also no significant differences between abundances of stations at different distances from shore (Welch $F = 0.917$, $df = 3.943$, $p = 0.550$), and at different distances from the uThukela Estuary mouth ($F = 0.538$, $df = 22$, $p = 0.710$).

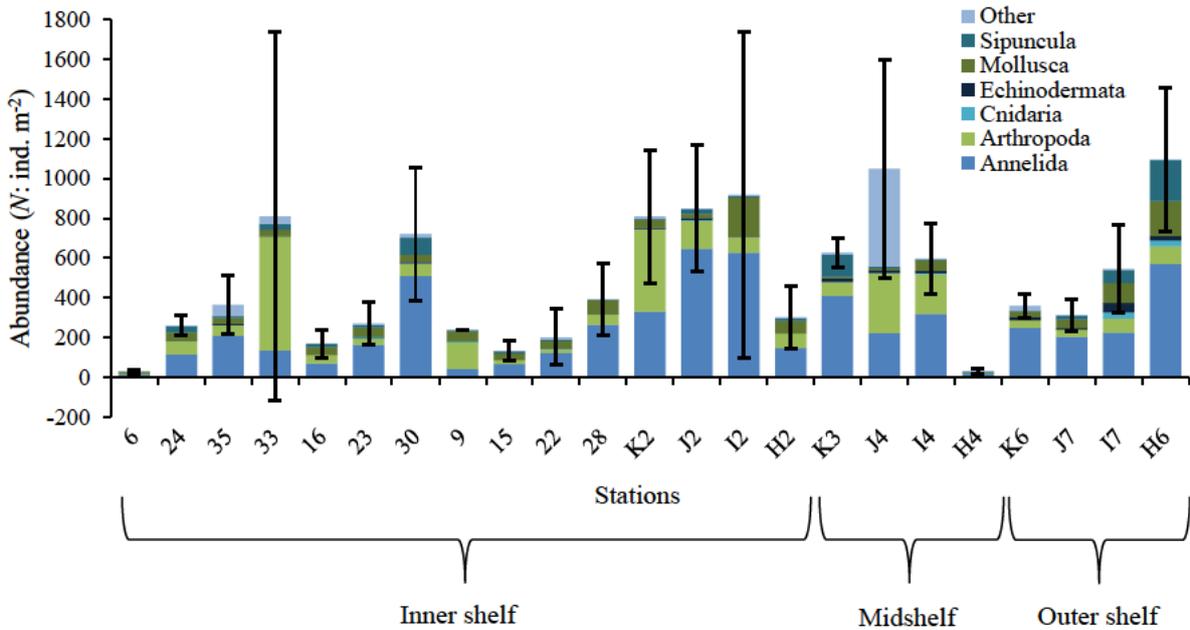


Figure 3.11. Spatial distribution of the mean macroinvertebrate abundance ($N \pm SD$: ind.m⁻²) aggregated to major phyla for stations sampled on the inner, mid, and outer uThukela shelf.

Diversity

The stations sampled on the uThukela shelf indicated that mean Shannon-Wiener diversity (H') varied between 1.68 ± 0.76 (station 33) and 3.85 ± 0.14 (station K3, with very heterogeneous and mostly coarse sediments) (Figure 3.12). Mean diversity was not significantly different (Welch $F = 3.694$, $df = 6.930$, $p = 0.081$) between the inner (H' : 2.72 ± 0.57), mid (H' : 2.99 ± 0.92), and outer-shelf (H' : 3.24 ± 0.20); between different distances from shore ($F = 0.680$, $df = 22$, $p = 0.645$); and between different distances from the uThukela Estuary mouth (Welch $F = 2.049$, $df = 5.121$, $p = 0.223$). When considering all sampled stations combined, the overall Shannon-Wiener diversity for the uThukela shelf was 2.90.

Mean Margalef's richness (d) ranged between 2.65 ± 0.42 (station H4, a very muddy habitat) and 13.74 ± 0.50 (station K2, with medium to coarse sediments) (Figure 3.12), with no significant differences between shelf zones ($F = 0.962$, $df = 22$, $p = 0.340$), distances from shore (Welch $F = 3.949$, $df = 4.123$, $p = 0.100$), and distances from the uThukela Estuary mouth (Welch $F = 1.237$, $df = 5.105$, $p = 0.400$).

The lowest mean Pielou's evenness (J') was recorded at station 33 (J' : 0.45 ± 0.26), due to the high abundance of the burrowing sandprawn *B. gilchristi* in one replicate grab, while the

highest evenness was recorded at station 6 (J' : 0.95 ± 0.02), which had the lowest abundance (Figure 3.12). There were no significant differences in mean evenness between the inner, mid, and outer-shelf ($H = 2.468$, $df = 22$, $p = 0.291$); between different distances from shore ($H = 7.393$, $df = 22$, $p = 0.193$); and between different distances from the uThukela Estuary mouth ($F = 1.417$, $df = 22$, $p = 0.269$).

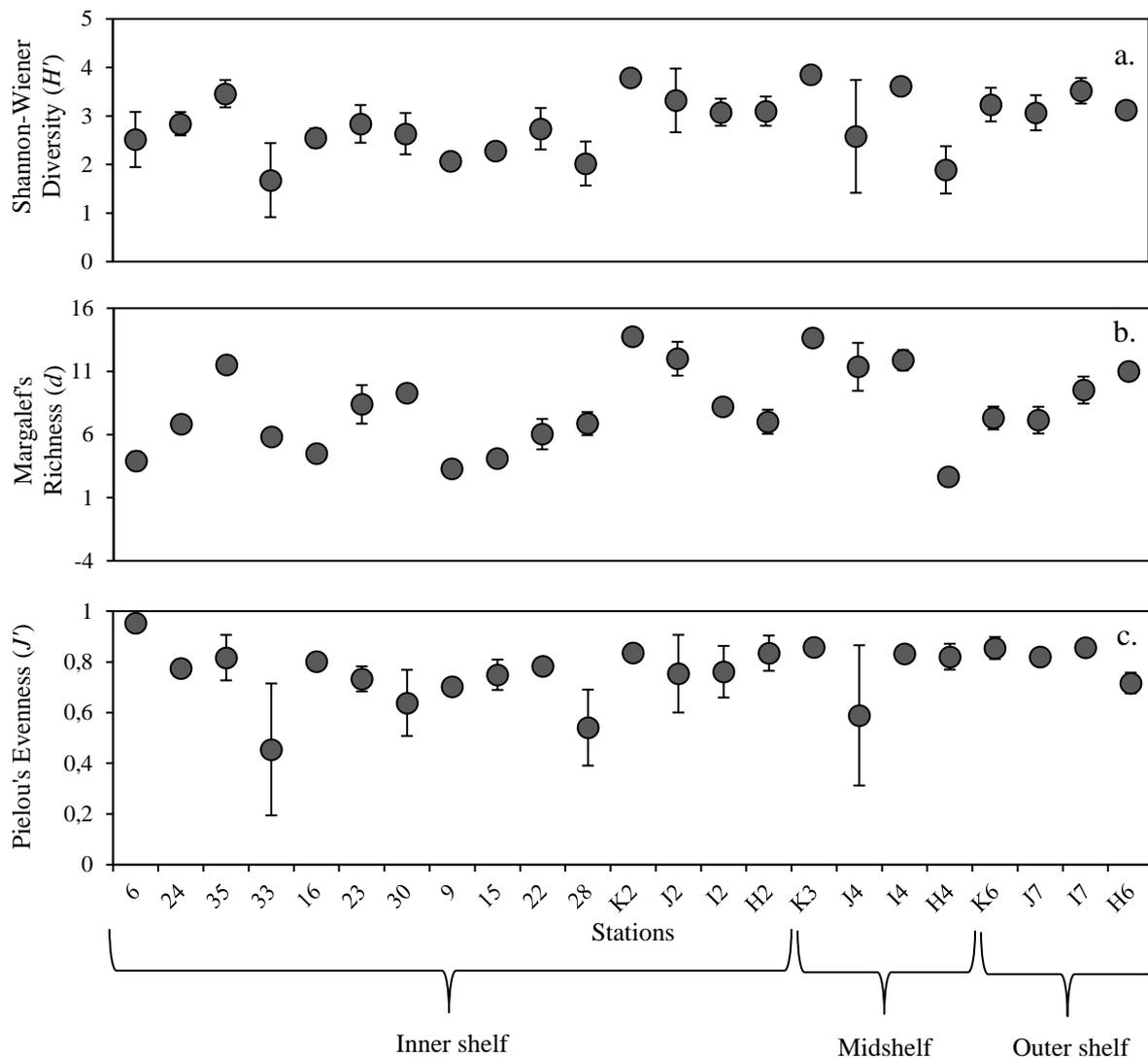


Figure 3.12. (a) Mean Shannon-Wiener diversity ($H' \pm SD$), (b) mean Margalef's richness ($d \pm SD$), and (c) mean Pielou's evenness ($J' \pm SD$) calculated from abundance data for macroinvertebrates sampled on the inner, mid, and outer uThukela shelf.

3.4.2.6. Characterisation of macrobenthic assemblages

Permutational ANOVA tests using taxa abundances for all 67 samples detected significant global differences for the *a priori* selected factors of shelf zone (Pseudo- $F = 7.814$, $df = 66$, p

< 0.001), distance from shore (Pseudo- $F = 4.949$, $df = 66$, $p < 0.001$), and distance from the uThukela Estuary mouth (Pseudo- $F = 4.169$, $df = 66$, $p < 0.001$). Pairwise comparisons indicated that these factors were almost entirely distinct in their taxa compositions, except for stations sampled “< 10 km” (stations 6, 16, 24, and I2) and “10 – 15 km” (stations 9, 15, 23, 30, 33, 35, H2, and J2) from the uThukela Estuary mouth, which were shown as similar ($p = 0.085$).

Hierarchical classification of the 67 uThukela shelf macrobenthic samples distinguished five distinct macrobenthic assemblages at a 16% similarity (Assemblages I – V, Figure 3.13). Clustering indicated that the overall resemblance of branches was low, indicating great variability between samples collected during this study.

Assemblage I

Cluster I separated from the other clusters at only 5% similarity and contained a single station on the inner-shelf, station 6 (the shallowest depth sampled), that was characterised by fine sand (Figure 3.13) with low TOC ($\bar{x} = 0.3 \pm 0.0\%$). The samples in this assemblage had an average similarity of 23%, and the assemblage was characterised by the polychaete worms *Aphelochaeta filibranchia* and *Armandia leptocirris* (Table 3.2). Taxa in this group had the lowest mean taxa abundance ($\bar{x} N: 28 \pm 12$; Figure 3.14b) and were the most evenly distributed ($J': 0.95 \pm 0.00$; Figure 3.15c).

Assemblage II

Cluster II comprised just a single mid-shelf station, the very well-sorted ($\bar{x} = 0.31 \pm 0.00 \Phi$) muddy station H4, which separated from other stations at 7% similarity (Figure 3.13). The samples in this assemblage had an average similarity of 28% that was represented entirely by the polychaete *A. dibranchis* (100% of the contribution) (Table 3.2). It had the lowest mean number of taxa ($\bar{x} S: 4 \pm 2$; Figure 3.14a), corresponding with the lowest mean Margalef's richness ($d: 2.00 \pm 0.62$) and mean diversity ($H': 1.89 \pm 0.53$) (Figure 3.15).

Assemblage III

Cluster III was the largest assemblage, characterised by mostly fine sediments and separated from the remaining stations at 10% similarity (Figure 3.13). This assemblage contained 12 of the 15 inner-shelf stations and had an average similarity of 31%, represented by a diverse array of taxa including polychaetes (*A. dibranchis* and *O. fusiformis*), peanut worms (Sipunculidae

sp.2), crabs (*X. cf. moebii*), and scaphopod molluscs (*Antalis longitrorsa*) (Table 3.2). Taxa of this assemblage were the least evenly distributed (J' : 0.69 ± 0.01 ; Figure 3.15c).

Assemblage IV

Cluster IV comprised mid and inner-shelf samples with heterogeneous medium-coarse sediments containing low TOC ($\bar{x} = 0.59 \pm 0.43$). It was split from cluster V at 11% similarity (Figure 3.13) and contained samples that were 27% similar, characterised by the amphipod crustaceans *Basuto stimpsoni* and *Byblis gaimardii*, as well as the polychaete worms *Lumbrineris aberrans*, *Onuphis eremita*, and *Prionospio nirripa* (Table 3.2). Assemblage IV had the largest mean abundance ($\bar{x} N$: 690 ± 351) and mean number of taxa ($\bar{x} S$: 42 ± 7) (Figure 3.14), corresponding with the highest mean Margalef's richness (d : 24.45 ± 1.28) and mean Shannon-Wiener diversity (H' : 4.24 ± 0.20) (Figure 3.15).

Assemblage V

Cluster V represented exclusively outer-shelf samples belonging to the deepest stations (87 – 126 m) and was characterised by poorly-sorted ($\bar{x} = 1.04 \pm 0.28 \Phi$), muddy substrates (Figure 3.13), with high TOC ($\bar{x} = 3.1 \pm 1.5\%$). This assemblage had an average similarity of 35%, with representation from various taxa groups including bivalve molluscs (*Tellina* sp.1), peanut worms (Sipunculidae sp.2), polychaete worms (*Notomastus latericeus* and *Linopherus microcephala*), and burrowing prawns (*Callinassa* sp.1) (Table 3.2).

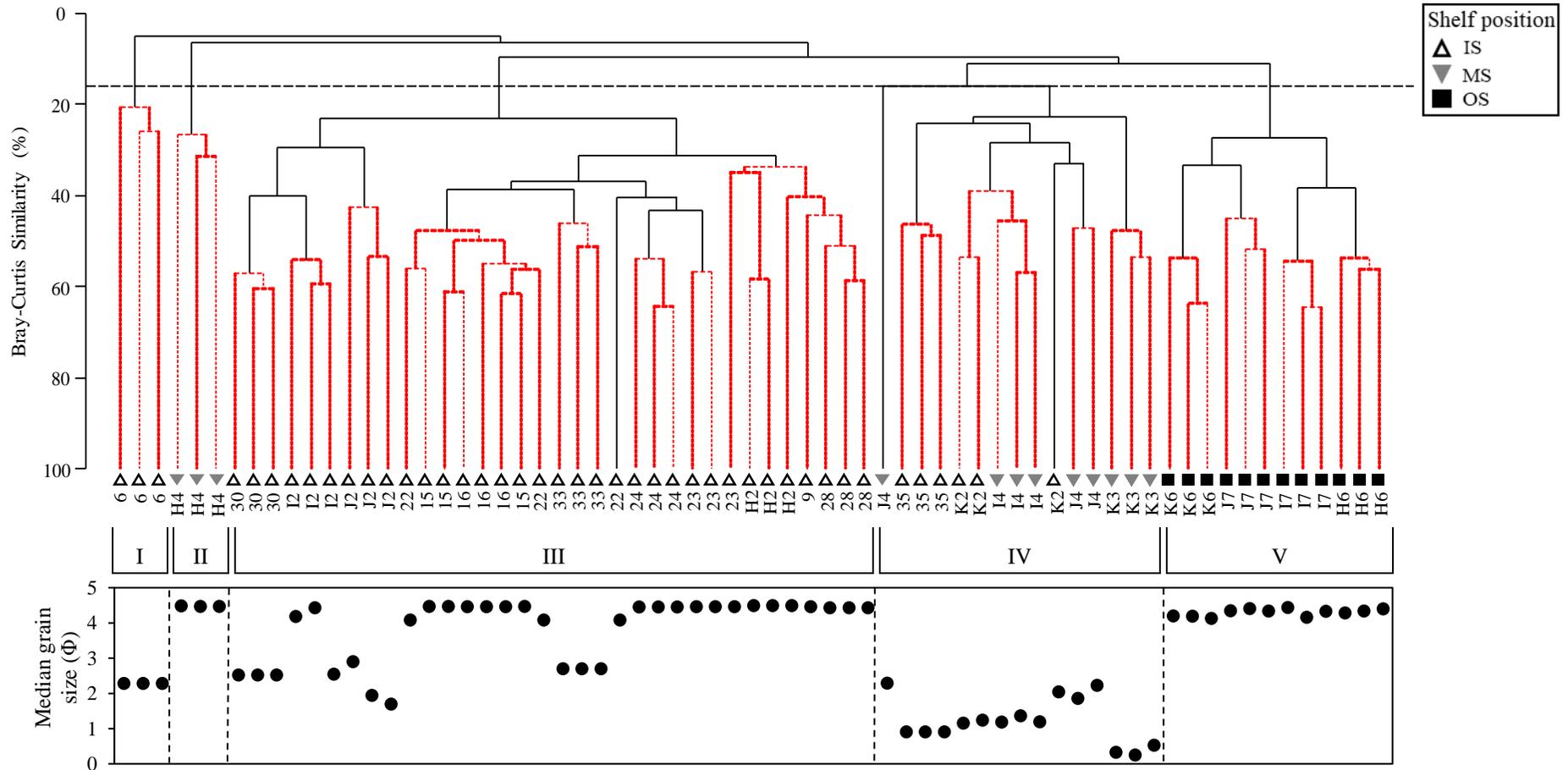


Figure 3.13. Hierarchical clustering (using group-average linkage) for 67 uThukela shelf macrobenthic samples. Analysis is based on Bray-Curtis similarities calculated from root-root transformed taxa abundances. Similarity profile (SIMPROF) routines representing genuine clusters at 5% significance are indicated by black solid lines. Samples within assemblages (I – V) defined at 16% (indicated by horizontal dotted line) are presented with corresponding median grain sizes (Φ) as an indication of bottom habitat type.

Table 3.2. Contribution (%) of representative taxa to assemblages I – V, defined by SIMPER analysis of root-root transformed abundance data. The top five taxa (where applicable) contributing to within-group similarity are presented.

Taxon	Average Abundance	Average Similarity	Sim/SD	Contribution (%)
Group I: Average Similarity = 22.51%				
<i>Aphelocheata filibranchia</i>	1.12	8.45	0.58	37.56
<i>Armandia leptocirris</i>	0.94	5.39	0.58	23.93
Clypeasteroida juvenile 1	0.94	4.34	0.58	19.26
<i>Owenia fusiformis</i>	0.94	4.34	0.58	19.26
Group II: Average Similarity = 28.25%				
<i>Aglaophamus dibranchis</i>	1.89	28.25	5.25	100.00
Group III: Average Similarity = 31.28%				
<i>Aglaophamus dibranchis</i>	2.27	4.97	1.33	15.90
Sipunculidae sp.2	1.79	3.82	1.62	12.22
<i>Xenophthalmodes cf. moebii</i>	1.48	2.84	1.37	9.07
<i>Antalis longitrorsa</i>	1.27	2.39	0.95	7.65
<i>Owenia fusiformis</i>	1.17	2.13	0.75	6.82
Group IV: Average Similarity = 26.89%				
<i>Basuto stimpsoni</i>	1.96	1.83	1.23	6.80
<i>Lumbrineris aberrans</i>	1.53	1.62	1.62	6.02
<i>Onuphis eremita</i>	1.68	1.58	1.22	5.89
<i>Byblis gaimardii</i>	1.63	1.46	1.22	5.43
<i>Prionospio nirripa</i>	1.43	1.11	0.84	4.14
Group V: Average Similarity = 34.62%				
<i>Tellina</i> sp.1	2.49	3.64	4.11	10.51
Sipunculidae sp.2	2.27	2.50	1.35	7.21
<i>Notomastus latericeus</i>	1.92	2.29	1.26	6.60
<i>Linopherus microcephala</i>	1.84	1.83	1.00	5.28
<i>Callianassa</i> sp.1	1.21	1.45	0.80	4.20

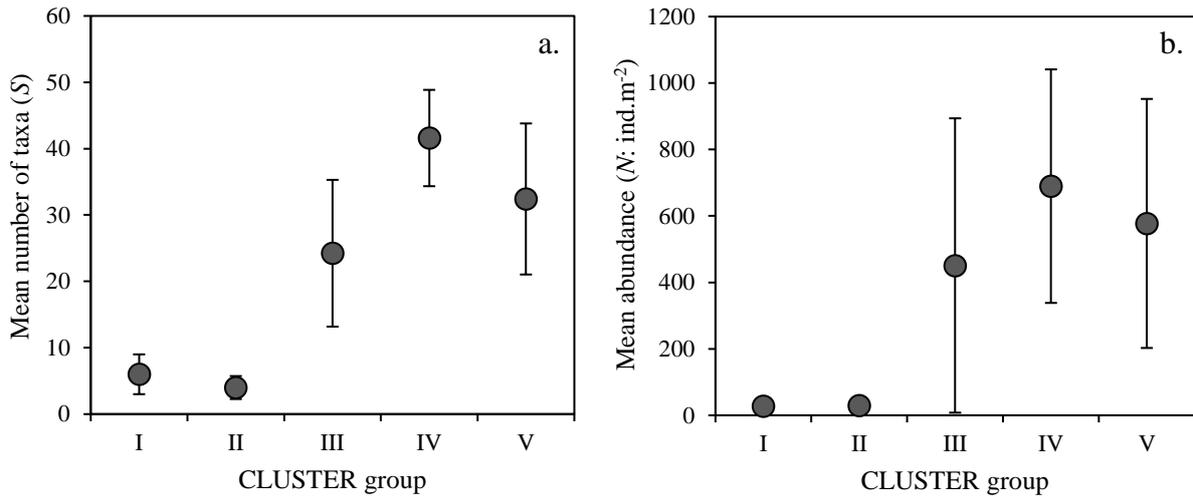


Figure 3.14. (a) Mean number of taxa ($S \pm SD$) and (b) mean abundance ($N \pm SD$: ind.m^{-2}) for assemblages I – V defined in cluster analysis.

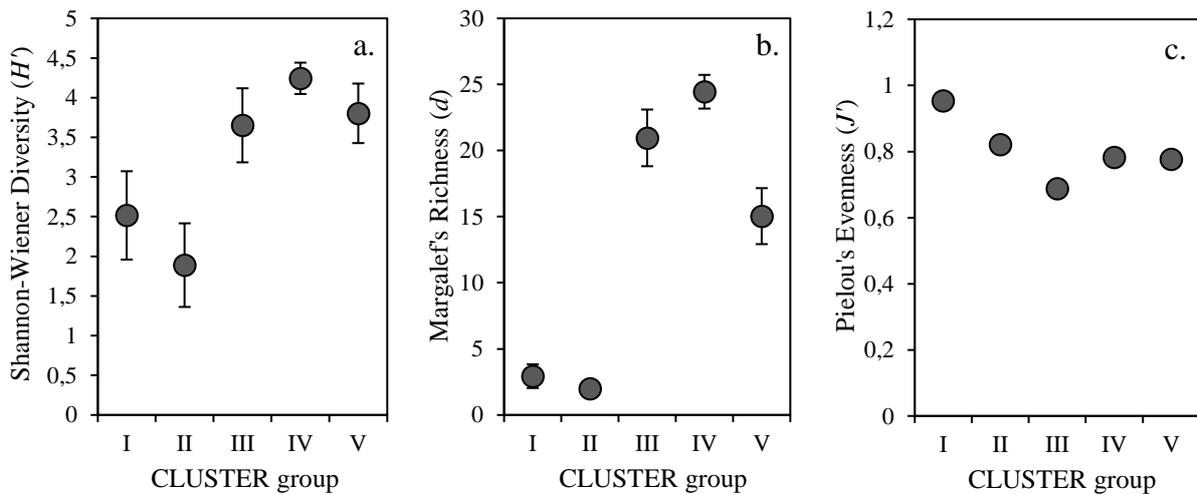


Figure 3.15. (a) Mean Shannon-Wiener diversity ($H' \pm SD$), (b) mean Margalef's richness ($d \pm SD$), and (c) mean Pielou's evenness ($J' \pm SD$) calculated from taxa abundances for assemblages I – V defined in cluster analysis.

Phyla contributions

Annelida contributed the highest number of taxa and the majority of the taxa abundance for all five assemblages (S : 29 – 49%; N : 43 – 67%; Figure 3.16). Arthropoda followed as the second largest contributor to taxa abundances for assemblages I – IV (located on the inner and mid uThukela shelf) and to numbers of taxa for assemblages I, II, IV, and V (Figure 3.16). The

number of taxa in assemblage III, associated with fine sediments, was represented by a relatively high proportion of Mollusca (S : 25%; Figure 3.16a). Assemblage V, located on the muddy outer-shelf, represented the most diverse phyla contributors to taxa abundances. Mollusca (N : 15%), Sipuncula (N : 13%), and Cnidaria (N : 3%) were relatively well represented in comparison to other assemblages, while Arthropoda was a relatively poor contributor to abundance (N : 10%) (Figure 3.16b). Assemblage IV, associated with medium to coarse sand, had the lowest proportion of abundance attributed to Annelida (N : 43%) but the highest proportion contributed by Arthropoda (N : 30%) and contained a comparatively high proportion of “other” Phyla (N : 17%) (Figure 3.16b).

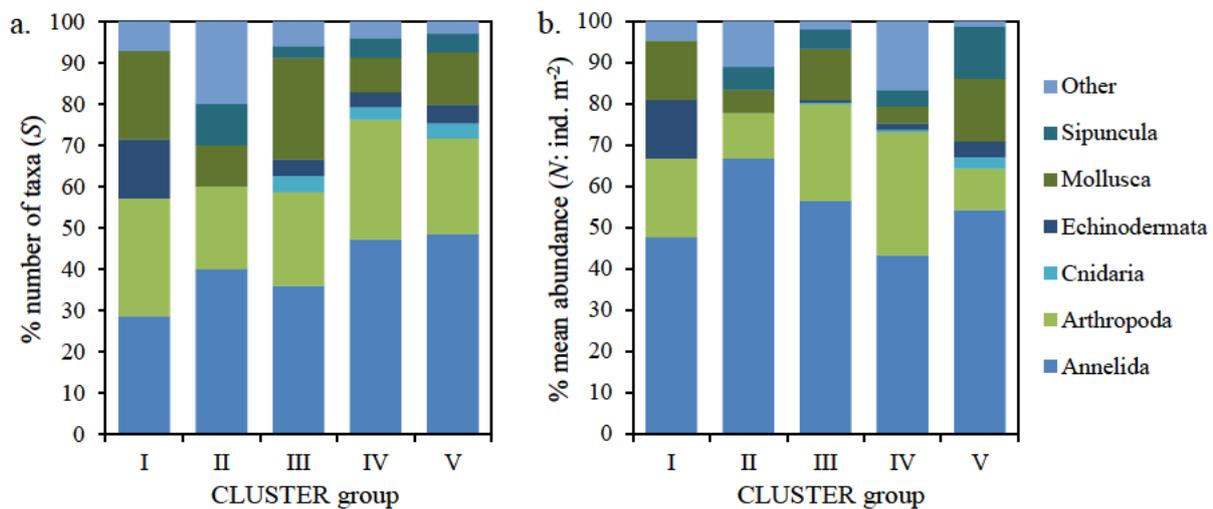


Figure 3.16. Contribution (%) of major phyla to the (a) mean number of taxa (S) and (b) mean abundance (N) of assemblages I – V defined in cluster analysis.

Discriminating taxa

The SIMPER analysis, whilst utilised previously to identify the taxa responsible for within-group similarity, was also used to assess which taxa contributed most to dissimilarities among assemblages I – V. Overall, differences in taxa compositions between assemblages was high (dissimilarities > 88%). In the pairwise comparisons between groups I and II (dissimilarity: 100%) and I and III (dissimilarity: 93%), the polychaete *A. dibranthis* was the highest contributor to between-group differences (Table 3.3), entirely absent in assemblage I but abundant in assemblages II and III. *Basuto stimpsoni* was abundant in assemblage IV, consistently being part of the top five taxa contributing to dissimilarities between this and all other assemblages (dissimilarities: 89 – 98%) (Table 3.3). Assemblage V contained a high abundance of *Tellina* sp.1, which was the top contributor in differentiating it from every other

assemblage (dissimilarities: 89 – 97%) (Table 3.3). Sipunculidae sp.2 was the main contributor to the dissimilarity between assemblages II and III (dissimilarity: 91%) (Table 3.3), and an important contributor to differences between assemblages I and III, being abundant in assemblage III but absent from assemblages II and I.

Table 3.3. Results from SIMPER analysis of root-root transformed taxa abundance data, listing the main discriminating taxa identified by pairwise comparisons between assemblages I – V. The contribution (%) of the top five discerning taxa to between-group dissimilarities are presented, with dissim/SD values in brackets.

Taxon	I vs. II	I vs. III	I vs. IV	I vs. V	II vs. III	II vs. IV	II vs. V	III vs. IV	III vs. V	IV vs. V
	100.00%	92.94%	97.43%	96.81%	90.85%	97.53%	96.17%	90.26%	89.96%	88.75%
<i>Aglaophamus dibranchis</i>	13.46 (3.07)	5.86 (1.72)					2.83 (1.88)	1.78 (1.68)	2.50 (1.66)	
<i>Aphelocheata filibranchia</i>	9.15 (1.20)	2.74 (1.05)								
<i>Armandia leptocirris</i>	6.97 (1.12)									
Clypeasteroidea juvenile 1	5.63 (1.26)									
<i>Owenia fusiformis</i>	5.63 (1.26)				3.61 (1.10)					
Sipunculidae sp.2		4.39 (1.92)		3.42 (1.89)	4.75 (1.89)		3.57 (1.88)			1.46 (1.52)
<i>Xenophthalmodes cf. moebii</i>		3.45 (1.70)			3.73 (1.68)					
<i>Antalis longitrorsa</i>		3.25 (1.29)			3.53 (1.27)					
<i>Basuto stimpsoni</i>			2.44 (1.81)			2.51 (1.81)		1.86 (1.67)		1.62 (1.71)
<i>Onuphis eremita</i>			2.09 (1.63)			2.15 (1.63)				1.45 (1.68)
<i>Byblis gaimardii</i>			2.06 (1.69)			2.11 (1.69)		1.57 (1.61)		
<i>Lumbrineris aberrans</i>			1.96 (2.17)			2.02 (2.17)		1.50 (1.99)		
<i>Cupuladria sp.1</i>			1.86 (0.63)			1.92 (0.63)		1.47 (0.72)		
<i>Tellina sp.1</i>				3.97 (3.71)			4.15 (3.64)		2.85 (3.46)	2.04 (3.33)
<i>Notomastus latericeus</i>				3.11 (1.42)			3.25 (1.39)		2.18 (1.52)	
<i>Linopherus microcephala</i>				2.89 (1.33)			2.60 (1.19)		2.03 (1.35)	1.51 (1.45)
<i>Sthenelais sp.1</i>				2.42 (1.04)					1.63 (1.04)	
<i>Diogenes costatus</i>					2.79 (0.98)					

3.4.3. Relationship between environmental variables and macrobenthic distribution

The RELATE function revealed that the relationship between the biotic and abiotic similarity matrices was average ($\rho = 0.538$). The variables responsible for this relationship were identified through a BIO-ENV procedure, with DO as the single variable best correlated with macrobenthic distribution ($\rho = 0.531$) (Table 3.4). Having removed covariates and correlates, the analysis of these 15 environmental parameters combined showed that the Spearman correlation coefficient was highest ($\rho = 0.664$) for a combination of the six variables salinity (PSU), depth (m), DO (mg.L^{-1}), %coarse sand, %medium sand, and %mud (Table 3.4). When %mud was substituted with median (ϕ), the coefficient remained comparable ($\rho = 0.655$), indicating a similar influence of these parameters on macrobenthic distribution due to the dominance of mud.

A distance-based linear model (distLM) provided further insight into the relationship between the measured abiotic variables and macroinvertebrate distribution. Marginal tests indicated DO as the most influential variable (agreeing with results from the BIO-ENV) and medium sand as the least influential out of the six variables identified in the BIO-ENV procedure as having the highest correlation with macrobenthos (Table 3.5). The sequential test revealed that the combination of DO and mud content best correlated with macrofauna distribution during this study (Table 3.5).

Table 3.4. Results of the BIO-ENV procedure indicating the measured environmental parameters best correlated to macrobenthic distribution on the uThukela shelf.

No. of variables	ρ	Variables
Best single variable		
1	0.531	DO
Best combination of variables		
6	0.664	Salinity, Depth, DO, %cs, %ms, %mud
7	0.661	Salinity, Depth, DO, %cs, %ms, %mud, median (ϕ)
6	0.655	Salinity, Depth, DO, %cs, %ms, median (ϕ)

Table 3.5. Distance-based linear model (distLM) results for the relationship between uThukela shelf macrobenthic assemblages and measured environmental parameters.

Variable	MARGINAL TESTS			
		Pseudo-F	p	Proportion
DO		10.613	0.0001	0.140
Salinity		10.369	0.0001	0.138
%cs		9.207	0.0001	0.124
%mud		8.960	0.0001	0.121
Depth		8.797	0.0001	0.119
%ms		8.368	0.0001	0.114
	SEQUENTIAL TESTS			
	AICc	Pseudo-F	p	Proportion
DO	541.59	10.613	0.0001	0.140
%mud	533.06	11.104	0.0001	0.127
Depth	531.55	3.649	0.0001	0.040
Salinity	530.50	3.219	0.0001	0.034
%cs	529.46	3.231	0.0001	0.033
%ms	529.28	2.448	0.0003	0.025

A distance-based redundancy analysis (dbRDA) aided in understanding the relative importance of each measured environmental variable in contributing to the uThukela macrofauna community variation and assisted in visualising this relationship. The first axis of the dbRDA (dbRDA1) explained 19% of the total variation, separating samples along a gradient from those containing a high percentage of coarse sand to those with increased DO, salinity, and mud content (Figure 3.17a). On the second axis (dbRDA2), samples were separated along a gradient of increased DO to increased salinity, explaining 10% of the total variation (Figure 3.17a). The deep outer-shelf samples (stations K6, J7, I7, H6) were separated from the other samples due to increased depth and reduced levels of DO. The taxa most correlated ($r > 0.65$) to these conditions were the bivalve *Tellina* sp.1, the brittle star *Amphelimna cribriformis*, and six polychaetes including *N. latericeus*, *Synelmis* sp.1, and *Euclymeninae* sp.1 (Figure 3.17b). The other two main groups in the dbRDA consisted of a mixture of inner and mid-shelf samples. One group (containing stations I4, J4, K3, K2, J2, and 35) was separated from the other as the samples in this group contained high percentages of medium to coarse sand that correlated with the amphipods *Byblis gaimardii* and *Basuto stimpsoni*, as well as the polychaetes *P. nirripa*, *L. aberrans*, and *Nephtys capensis* (Figure 3.17). The other group (containing all other inner-shelf stations and station H4) contained muddy samples with increased salinity and DO, correlating with the polychaete *A. dibranhis* and the scaphopod *A. longitrorsa* (Figure 3.17).

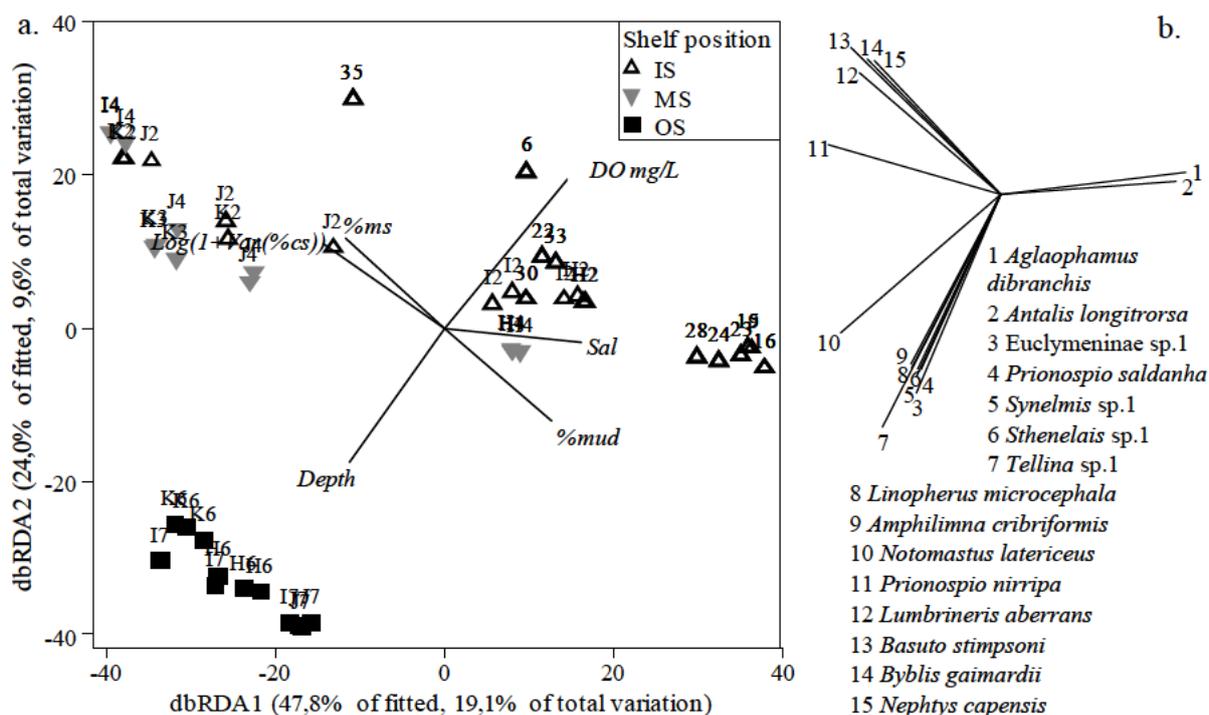


Figure 3.17. Distance-based redundancy analysis (dbRDA) of the uThukela shelf using a stepwise routine based on the AICc selection criterion showing the (a) six main environmental parameters influencing macrobenthic distribution and (b) the taxa best correlating ($r > 0.65$) to these conditions.

3.5. Discussion

This macrofauna study observed a mean of 512 ind.m⁻² from 24 – 126 m depth on the uThukela shelf, and had similar findings to the 2010 African Coelacanth Ecosystem Programme (ACEP) Natal Bight study where Untiedt (2013) found 809 ind.m⁻² on the uThukela shelf. Maduna (2017) also observed comparable abundances on the KZN mid-shelf during the ACEP Surrogacy project, where 587 ind.m⁻² were sampled. Studies from other regions of the world, using analogous sampling designs (i.e. samples collected using a benthic grab and sieved on a 1000 μ m mesh), revealed similar outcomes. A macrobenthic study on the Great Australian Bight (< 200 m depth) sampled an average of 352 ind.m⁻² (Currie et al. 2009), while a 1994 study on the east coast of the tropical Reunion Island (20 – 140 m depth) observed a mean 515 ind.m⁻² (Bigot et al. 2006).

3.5.1. *Species estimators*

Due to sampling limitations restricting the ability to detect the true richness of any given study site, several indices have been proposed to estimate this, including the non-parametric *Chao2* estimate (Colwell and Coddington 1994, Gotelli and Colwell 2011). For this study, both the species accumulation of observed taxa and *Chao2* estimation curves did not reach asymptotic values, indicating that the study did not collect all potential taxa in the area and further sampling is required for a complete census (Colwell and Coddington 1994, Mackie et al. 2005, Gotelli and Colwell 2011). This is common for benthic studies as the number of slightly different patches increases as the sampling area increases because of small-scale spatial variability that occurs in soft sediments (Ellingsen 2002). A complete census of marine macrofauna is difficult as it requires that all small-scale variability be covered and entails a large sampling effort (collection and processing) that is both time-consuming and expensive (Snelgrove 1998). The *Chao2* estimator is useful in finding a point at which no further sampling effort is needed for an area (as no additional undetected taxa are expected) due to a “stop rule” that states a census is complete if all taxa are observed at least twice and are no longer unique (Colwell and Coddington 1994, Chao et al. 2009, Gotelli and Colwell 2011). The census for the uThukela shelf was not completed during this study, and the observed taxa were 61% of the *Chao2* non-parametric estimator (Chao et al. 2009). The difference between the observed and estimated values represented a relatively large heterogeneity in the areas sampled and a high occurrence of rare taxa (Chao et al. 2009). During this study, restricted-range taxa (190 uniques and 76 duplicates) comprised a large proportion (58%) of the macrofauna collected, with one sample, grab 9B, individually comprising 15% of the uniques sampled. Rare species, although not important to abundance, can provide unique biological traits to an area and be an indication of a richer variety of food resources and habitats available through certain environmental conditions (Ellingsen et al. 2007). Therefore, when considering critical areas, the selection of only species-rich areas will not necessarily guarantee effective protection of these restricted-range taxa, so it is vital that rarity is also examined (Ellingsen 2002, Ellingsen et al. 2007).

3.5.2. *Macroinvertebrate community structure on the uThukela shelf*

Polychaeta-dominance is common for coastal macrobenthic studies worldwide (Karakassis and Eleftheriou 1997, Ellingsen 2002, Shin et al. 2004, Bigot et al. 2006, Ellingsen et al. 2007, Jayaraj et al. 2007, Currie et al. 2009, Raja et al. 2014), and is also observed in fluvially-dependent shelf ecosystems, such as on the south-east and west coasts of India (Jayaraj et al. 2008, Joydas and Damodaran 2009, Khan et al. 2017) and on the inner Brazilian shelf (Zalmon

et al. 2013). Jayaraj et al. (2008) noted that the fluviially-influenced west coast of India had a Polychaeta-dominated benthic community containing high abundances of Crustacea and Mollusca. Previous studies on the macroinvertebrates of the KZN Bight show this same Polychaeta-dominated community containing a large proportion of Crustacea and Mollusca (McClurg 1988, MacKay et al. 2016, Untiedt and MacKay 2016), while the present study found that these dominance patterns were also true of the muddy uThukela shelf. The prevalence of polychaetes during this study and other macrobenthic studies globally is attributed to their wide distribution in a variety of marine habitat types due to the diversity of the group, playing vital roles in food webs, sediment reworking, and bioturbation (Khan et al. 2017). Although dominance patterns of this study followed the global trend, it is important to note the relatively large abundance of Sipuncula, the fourth most abundant phylum on the uThukela shelf. Just one taxon of Sipunculidae was the most widely distributed and among the most abundant taxa sampled during this study. This high Sipuncula abundance on the uThukela shelf was also apparent during the 2010 Natal Bight dry season study that found Sipuncula and Polychaeta as typical of this region (MacKay et al. 2016).

Replicate 9B was distinct from every other sample and may have been more a reflection of a community associated with hard substrata than soft sediments, resulting in it being treated as an outlier and removed before data analyses as to not cause skewed results. This replicate was situated north of the uThukela Estuary and collected in 2008 from a shallow station on the uThukela inner-shelf. It had a unique composition, with a relatively high number of taxa and rare taxa, as well as a large abundance. Although dominated by Polychaeta, the comparatively high abundance of Echinodermata was noteworthy. This was due to the high densities of the brittle star *O. mirabilis*, found mostly wrapped around a branch of *Leptogorgia* coral. This habitat type is common for *O. mirabilis*, as it is typically seen wrapped around soft corals on shallow reefs (World Register of Marine Species Editorial Board 2021). This finding, along with the notable presence of Cnidaria in this sample, indicates the possibility of a nearby low-lying reef. Reefs are associated with high habitat heterogeneity and may have facilitated the proliferation of diverse macroinvertebrate taxa (Crame 2000) that was observed in sample 9B. Although, even with the removal of sample 9B, overall diversity on the uThukela shelf was relatively high ($H' = 2.90$), ranging between 1.68 – 3.85 at the sampled stations. This macrobenthic community was found to be more diverse than the communities on the east coast of the tropical Reunion Island (maximum $H' = 2.5 - 2.8$ at intermediate depths) (Bigot et al. 2006) and on the subtropical northwest coast of India ($H' = 0.04 - 2.27$) (Jayaraj et al. 2007),

but contained similar diversities to the benthic assemblages in subtropical Hong Kong that ranged between 1.36 – 3.07 (Shin et al. 2004).

3.5.2.1. The effect of shelf position

This study did not follow the typical patterns observed on most fluviially-dominated shelves of higher diversities at intermediate depths, as there was an increase in diversity values from the inner to outer-shelf but there were no significant differences between macrobenthic abundance, number of taxa, Shannon-Wiener diversity, Margalef's richness, or Pielou's evenness for different shelf positions (factors shelf zone, distance from shore, and distance from the uThukela Estuary mouth). Although univariate community indices were similar for all shelf positions, multivariate tests indicated that communities were significantly different, implying that specific taxa types were distributed according to varying local environments on the uThukela shelf. These were not distinctly according to shelf zones as there was an observed overlap of inner and mid-shelf stations during multivariate analyses. A reduction in marine penetration of the estuary plume, especially during the dry season when sampling occurred, could cause greater environmental stability (Zalmon et al. 2013) and is a possible reason for the similarity observed between stations at different shelf positions, especially on the inner and mid-shelf. Also, soft sediments and their associated community indices can be more affected on small rather than large scales (such as shelf zone) as many ecological processes operate at small scales, causing small-scale patchiness (Chapman et al. 2010).

3.5.2.2. Macrobenthic community assemblages

Cluster analysis identified groups of samples forming macrobenthic assemblages that were related according to community composition (Clarke and Gorley 2015). Assemblage I comprised fauna from the most shallow station (station 6) that was closest to terrestrial influence (shore and uThukela Estuary mouth). It was characterised by fine sand, with low TOC, containing the small deposit-feeding polychaetes *Aphelochaeta filibranchia* and *Armandia leptocirris*. This community had a small mean number of taxa and abundance, resulting in a low calculated richness and diversity but a high evenness. Assemblage III also consisted of inner-shelf samples from 12 of 15 inner-shelf stations sampled during this study. It was the largest (but least even) assemblage, containing mostly fine-grained sedimentary habitats that are characteristic of the inner uThukela shelf. This shelf section is influenced by longshore currents and much wave action, causing resuspension and redistribution of sediments with small grain sizes, resulting in fine-sediment dominance (Flemming 1981, Bosman et al.

2007). The absence of significant differences in both grain size and TOC between inner-shelf samples from 2008 and 2010 indicates a stable bottom habitat during this period. Notable of assemblage III was the inclusion of the least diverse station (station 33), which had a large abundance of the burrowing sandprawn *B. gilchristi*. Although the most abundant overall, *B. gilchristi* was not widespread and this finding resulted from an abundance of this organism collected at station 33. *Balsscallichirus gilchristi* inhabits subtidal sandy areas (Wooldridge and Coetzee 1988) and, unlike most uThukela shelf stations that are characteristically muddy, station 33 contained a high percentage of fine sand which could provide a suitable habitat for this species. Despite these high abundances, *B. gilchristi* was not among the main characterising taxa of assemblage III, and this group was distinguished by a variety of different organisms. These included the deposit-feeding Sipunculidae peanut worm, the scavenging crab *X. cf. moebii*, the carnivorous polychaete *A. dibranchis* and scaphopod *A. longitrorsa*, and the facultative deposit feeder *O. fusiformis* that shifts to suspension-feeding when food sources are altered.

Assemblage II consisted of a single mid-shelf station (H4) that was positioned within the paleo-channel that intersects the paleo-dune cordon on the uThukela mid-shelf (Green and MacKay 2016). It was considerably less diverse and was only represented by one species, the polychaete *A. dibranchis*, which was the polychaete encountered most frequently in this uThukela shelf study and also comprised a large portion of the overall shelf abundance. This species is usually common in sandy mud habitats (World Register of Marine Species Editorial Board 2021), which were usual for the overall study site. Station H4, however, was one of the muddiest stations sampled, with very well-sorted sediments creating a homogeneous environment. Homogeneous environments are limited in potential niche spaces (Gray 1981), and very fine sediments often inhibit certain macrobenthic activities, so these areas only contain fauna that are tolerant of these conditions (Cocito et al. 1990). Therefore, both these characteristics limit organisms and reduce community diversity, and could be an explanation for the low mean number of taxa, abundance, and diversity observed for assemblage II. Although station H4 was very muddy, this was not the case for the other uThukela mid-shelf samples as these contained mostly coarse substrates. Assemblage IV comprised these remaining mid-shelf samples, along with the last inner-shelf samples, and was distinguished by medium to coarse sediments. These sediments that are seen to dominate the mid-shelf stations K3, J4, and I4 included in this assemblage, correspond with the position of the sub-continuous paleo-dune cordon that stretches subparallel to the coastline at 55 – 70 m (Flemming 1981, Flemming and Hay 1988,

Bosman et al. 2007, Green and MacKay 2016, MacKay et al. 2016). Coarse sediments are reported to contain little TOC as these environments are usually indicative of high energy, allowing only heavy particles to settle on the bottom and thus not including organic particulates (Pearson and Rosenberg 1978). This was shown to be true of cluster IV, as the sediments in this group contained lower levels of TOC. The sedimentary environment also contained a combination of sediment types, comprising the highest mean macrobenthic abundance and diversity, as well as the greatest mean number of taxa and calculated richness. High richness and diversity were also observed in medium grain-sized, heterogeneous sediments on the west coast of India (Jayaraj et al. 2008), and is expected for this habitat-type as heterogeneous sediments provide many potential niche spaces for a diverse range of macrofauna (Huston 1979, Gray 1981, Zalmon et al. 2013, Carvalho et al. 2017). Characterising taxa of assemblage IV included the amphipods *Basuto stimpsoni* and *Byblis gaimardii*, as well as the carnivorous *L. aberrans*, omnivorous *O. eremita*, and facultative deposit-feeding (that switches to suspension-feeding) *P. nirripta* polychaetes. A relatively large proportion of the macrobenthic abundance for this group was attributed to Arthropoda, potentially due to the high abundance of Amphipoda observed at station K2.

Assemblage V contained exclusively deep, muddy, outer-shelf samples. The poorly-sorted mud typical of this outer-shelf assemblage agrees with the uThukela shelf sediment distribution described by Bosman et al. (2007). This is an unusual finding for the KZN shelf edge as the scouring of the offshore sediments by the Agulhas Current usually results in gravel patches (Lutjeharms 2006b), but the uThukela shelf edge mud appears to be consolidated enough to not be eroded (Green and MacKay 2016). This group of samples contained the highest concentration of sediment TOC, which is typical of poorly-sorted muddy environments (Gray 1981, Gray and Elliott 2009). It had the highest within-group similarity characterised by diverse taxa groups, including the deposit-feeding worms Sipunculidae and *N. latericeus*, the deposit-feeding burrowing prawn *Callianassa* sp., the facultative deposit-feeding (that switches to suspension-feeding) bivalve *Tellina* sp., and the carnivorous polychaete *L. microcephala* that can facultatively switch to deposit-feeding. Mollusca, Sipuncula, and Cnidaria were relatively well represented in this group, while Arthropoda had comparatively poor representation.

3.5.3. Relationship between macroinvertebrate variation and soft-sediment habitats

Ecological studies require that the potential drivers of macroinvertebrate distribution patterns are defined (Akoumianaki et al. 2013). Broad-scale community distribution is not influenced

by just a single abiotic factor, but rather by an interaction of sedimentary and hydrographic parameters (Snelgrove 1999). For example, the benthos on the fluvially-influenced west coast of India was shown to be driven by the environmental variables sediment texture, depth, and dissolved oxygen (DO) (Jayaraj et al. 2008). A similar combination of variables was observed in this study, with the BIO-ENV procedure identifying the physico-chemical parameters DO, depth, salinity, and the sediment composition (mud, coarse sand, and medium sand), as most correlated to macrobenthic patterns. However, the parameters mud and median grain size had a similar relationship with benthic distribution patterns due to the dominance of mud on the uThukela shelf.

Many studies show that macrofauna patterns are related to depth (Karakassis and Eleftheriou 1997, Ellingsen 2002, Zalmon et al. 2013) and shelf zonation patterns, and these changes seem characteristic of shallow-water benthic communities (Clarke and Warwick 2001, Raja et al. 2014). However, the environmental changes that occur with depth are likely the reason for this observed depth effect (McArthur et al. 2010), as seen by the decrease in DO with increasing depth in the study on the southeast coast of India (Raja et al. 2014), and the decrease in temperature and DO with increasing depth in the study on the fluvially-dependent western Indian shelf (Joydas and Damodaran 2009). The 2008 environmental measurements used during this study were only for the inshore uThukela Bank, and there was very little change in depth, so the finding that depth did not affect temperature and salinity was expected. However, in 2010 where measurements were taken for the inner, mid, and outer-shelf, the parameters temperature, salinity, and DO decreased with increasing depth, and values were significantly reduced on the outer-shelf. Dissolved oxygen was the most correlated variable during this study and the Raja et al. (2014) study, and the reduced measurements with increasing depth were expected due to the natural decrease in oxygen saturation with depth and less mixing of offshore waters by wind and wave energy (Dutertre et al. 2013). Alternatively, the findings of higher salinity measurements closer inshore and lower salinities further offshore were unexpected as there is usually a large freshwater input to the shelf from the uThukela Estuary (De Lecea and Cooper 2016). However, river flow is typically reduced during the dry season and could result in higher salinities on the shelf (MacKay et al. 2016), as was observed during this study. The lower salinities nearer the shelf edge could be due to the widening of the shelf in the uThukela region, causing the Agulhas Current to be displaced further offshore and resulting in divergent upwelling that transports cooler, less saline water from the depths of the Agulhas Current onto the shelf (Roberts et al. 2010).

Water movement also influences sediment composition that directly affects the movement and feeding behaviour of macrobenthos, and also indirectly affects fauna by impacting other environmental variables that are important for survival, such as oxygen and food supplies (Pearson and Rosenberg 1978, Gray and Elliott 2009). Sediment types appear among the key determinants of biotic distribution in multiple benthic studies worldwide, including those on fluvially-dependent shelves (Jayaraj et al. 2008, Zalmon et al. 2013). These shelves are typically muddy due to the fine-grained sediment that is transported by rivers to the coast (Lutjeharms 2006b), and the findings of this study agreed with this trend as the uThukela shelf contained mostly mud. Fine sediments, especially those on fluvially-influenced shelves, are expected to contain increased organic content (Salen-Picard et al. 2002, Gray and Elliott 2009). Only a medium sediment TOC concentration was measured for the study site, but increased with increasing depth, having the highest measurements recorded on the outer-shelf. This corresponds with the findings of the Indian west coast study, where shelf edge sediments contained more TOC than nearshore sediments (Joydas and Damodaran 2009). Although there was a positive (weak) relationship between median grain size and TOC in this uThukela shelf study, and median grain size influenced benthic distribution, TOC was not shown to be directly correlated to biota. Organic content is usually considered a primary cause of macrobenthic community change (Pearson and Rosenberg 1978), and the lack of correlation between biota and TOC could indicate that the interaction is not necessarily non-existent but merely more complicated (e.g. through feeding preferences, see Chapter 4).

3.5.4. *Habitat heterogeneity influences biotic assemblages*

Due to the relationship between biota and their environments, it is expected that changes in abiotic parameters within a marine environment will alter macrobenthic community compositions (Gray and Elliott 2009). Changes in environmental variables at various scales result in habitat heterogeneity, and this is the reason for the numerous benthic assemblages (with distinct fauna compositions) observed on a continental shelf (McClain and Barry 2010).

Communities occurring on the deep outer uThukela shelf were characterised by reduced levels of DO. These conditions were correlated to diverse taxa types, including the facultative deposit-feeding (that switches to suspension-feeding) brittle star *A. cribriformis* that has been previously recorded on the outer-shelf (86 – 200 m) in south-east Africa (Olbers et al. 2015), as well as the deposit-feeding polychaetes *Euclymeninae* sp. and *N. latericeus*. Maurer and Leathem (1980) also found that *N. latericeus* favoured this environment as they observed an

increase in densities of this polychaete with increasing depth and decreasing oxygen on Georges Bank, USA. This deep, less oxygenated environment was also preferred by a few carnivores (*Synelmis* sp., and *Sthenelais* sp.) and facultative carnivores (*L. microcephala*), as well as some facultative deposit feeders that shift to suspension-feeding when conditions do not allow for optimal organic deposition (*Tellina* sp. and *Prionospio saldanha*).

The two remaining groups consisted of the shallower stations with increased DO that correlated with more facultative-feeding organisms. One group containing mostly mid-shelf stations and a few inner-shelf stations (assemblage IV, as well as station J2) was characterised by high percentages of medium to coarse sand that favoured diverse taxa. Among these were the wide-ranging, tubicolous, facultative deposit-feeding amphipod *Byblis gaimardii*, and carnivorous amphipod *Basuto stimpsoni*, as well as the polychaetes that included carnivores (*L. aberrans*), facultative carnivores that switch to deposit-feeding (*N. capensis*), and facultative deposit feeders that switch to suspension-feeding (*P. nirripa*) when food sources change. The group containing the remaining inner-shelf stations and station H4 comprised muddy samples with increased salinity and DO, correlating with the carnivores *Aglaophamus dibranhis* and *Antalis longitrorsa*.

Other abiotic and biotic factors not considered for this study may also contribute to macrofauna distributions on the uThukela shelf. For example, ecosystem engineers that dig burrows (e.g. *Callichirus* prawns) and form biogenic structures (e.g. polychaete and amphipod tubes) can influence community composition by altering their local sedimentary and hydrodynamic environment to the benefit or detriment of other macrofauna (Reise 2002, Passarelli et al. 2012). Productivity, predation, and direct and indirect competition can also affect benthic diversity (Huston 1979), with the high frequency and abundance of carnivores among the uThukela shelf macrobenthos indicating that this may contribute to the biotic patterns observed. Biotic factors were not analysed in this study, but Chapter 4 does provide insight into the biotic functioning of the uThukela shelf.

3.6. Conclusion

This study section provided an understanding of the macrobenthic community composition on the uThukela shelf and some of the environmental factors responsible for this observed structure and distribution. The study site contained a high percentage of unique taxa, and Polychaeta dominated numbers of taxa and abundances due to their vast distribution in various habitat

types. Numbers of benthic taxa, abundances, diversity, richness, and evenness did not differ based on shelf position, but multivariate analyses revealed that there were differences attributed to actual taxa that showed correlations to specific environmental conditions.

Sediment composition varied across the shelf, resulting in heterogeneous habitat types. While the inner and outer-shelf corresponded mostly with the typically muddy environment expected off a fluvially-dominated estuary, the mid-shelf comprised coarser sediments, owing to the paleo-dune that is known to occur in this region. Near-bottom water parameters also varied on the shelf, with temperature, salinity, and DO declining with increasing depth. These variables, along with sediment TOC, were significantly different on the outer uThukela shelf. The variation in local environmental conditions resulted in five unique macrobenthic assemblages that were mostly correlated to the combination of depth, DO, salinity, mud, coarse sand, and medium sand. The significant difference observed for the outer-shelf environment was reflected in the macrofauna samples forming a distinct assemblage. However, the inner and mid-shelf samples did not separate into their respective shelf zones in terms of unique assemblages, possibly due to the greater environmental stability that potentially exists in the dry season with the reduction in river input to the coastal region. This was also seen by the atypical salinity gradient of more saline water on the shelf and less saline conditions at the shelf edge. The inner and mid-shelf macrofauna samples instead formed four assemblages: two contained just a single station, and the other two separated into a fine-grained assemblage and a medium-coarse-grained assemblage. Therefore, the *a priori* separation of samples into shelf zones appears artificial and is not advisable as a determinant of macrobenthic community composition for this area, as this does not appear to be the factor most influencing distribution. This factor was, however, still used in Chapter 4 and Chapter 5 of this dissertation for comparisons with other benthic studies.

This chapter provides further insight into the macrobenthic community structure and distribution on the uThukela shelf at finer spatial scales than the recent ACEP KZN Bight studies (MacKay et al. 2016, Untiedt and MacKay 2016, Maduna 2017). These findings confirm previous indications that the uThukela shelf has a structurally diverse and unique macrobenthic community and assists in filling the knowledge gaps that exist for the macrofauna in this region. Ultimately, this contributes towards building a record of baseline information for the uThukela MPA, that will assist in all aspects of conservation, protection, and management of the area.

CHAPTER 4. FUNCTIONAL DIVERSITY PATTERNS OF THE UTHUKELA SHELF MACROBENTHOS

4.1. Overview

This chapter follows on from the taxonomic analysis of the uThukela shelf macrofauna in Chapter 3, by exploring the community functions. Functional analysis is important as it explains how a shift in the taxonomic composition may affect the ecological processes that the macrofauna community provides. The newly promulgated uThukela Marine Protected Area (MPA) aims to protect the benthic ecological processes and this focussed study contributes to the baseline information by providing a better understanding of the macrofauna community traits. Biological Traits Analysis (BTA) revealed that the community of the uThukela shelf is functionally diverse and mostly represented by traits that imply community resilience. No spatial differences were observed for community traits, and the entire uThukela shelf community was found to have a high level of functional redundancy, implying that the macrofauna community is relatively stable and resilient during natural environmental fluctuations. Taxa have potentially adapted to the large inputs of sediment and detritus to the shelf and the high environmental variability off the fluvially-dominated uThukela Estuary. The reliance of the community functioning on terrestrial inputs emphasises the importance of the uThukela MPA in protecting the link between the estuary and the ocean. The similarity in traits across the shelf resulted in a weak relationship between traits and measured environmental parameters, but salinity and fine sand mostly correlated with the variance in community traits that did exist.

4.2. Introduction

The uThukela MPA aims to protect the ecological processes associated with the interconnecting coastal and offshore benthic ecosystems (Republic of South Africa Government Gazette 2019). However, the functioning of a system is not explained by taxa composition but by the traits of individuals, the distributions and abundances of these organisms, and their biological behaviours (Naeem and Wright 2003). Traits analysis identifies the ecological processes provided by particular taxa in the community (Miatta et al. 2021) and emphasises the need for adequate baseline information on both macrofauna composition and traits (Bremner 2008, Frid et al. 2008). The recent African Coelacanth Ecosystem Programme (ACEP) Natal Bight (Untiedt and MacKay 2016) and ACEP Surrogacy (Maduna 2017) projects supplied foundational information on the functioning of the uThukela shelf macrobenthic community.

This study expands on these findings and contributes toward a baseline database for the uThukela shelf before formal protection.

A trait refers to a specific biological characteristic of a species in a given system, that affects the performance of this organism in relation to ecosystem properties and processes (Naeem and Wright 2003, Jax 2005). Functional analysis uses the concept that only certain species will be able to prevail under a given set of environmental conditions, as they have evolved biological and behavioural characteristics that permit them to exploit the specific combination of resources present in their habitats (Legendre et al. 1997, Bremner 2008, Sigala et al. 2012, Beauchard et al. 2017). “Effect traits” contribute to the ecosystem function being measured (Naeem and Wright 2003), integrating the connection between how organisms utilise resources and modify trophic webs, as well as their habitat preferences and influence on environmental processes (Bremner et al. 2003, Petchey and Gaston 2006, Gray and Elliott 2009, Kaminsky et al. 2018). Macrofauna contribute to ecosystem processes by secondary production, carbon and nutrient cycling, habitat creation, bioturbation and irrigation, and sediment stability (Snelgrove 1997, Reise 2002, Sigala et al. 2012). This implies that a shift in benthic diversity could potentially impact the entire ecosystem (Pratt et al. 2014). The overlap of traits between different taxa (representing the potential for functional redundancy) predicts how a shift in diversity and potential species loss could affect system functioning, with a high functional redundancy expected to increase ecosystem stability and resilience (Hewitt et al. 2008).

Biological Traits Analysis is an analytical method that considers multiple variables to describe the ecological functioning of benthic assemblages, indicating links between fauna and their environments (Bremner et al. 2006, Pacheco et al. 2011, Miatta et al. 2021). Biological traits act as indicators of ecosystem functioning (Pacheco et al. 2011, Miatta et al. 2021), reflecting the morphology, life history, and behaviour characteristics of the taxa present in the system (Bremner et al. 2006, Paganelli et al. 2012, Kaminsky et al. 2018). Traits mask the taxonomic differences among communities to reveal their functional differences (Beauchard et al. 2017). Biological Traits Analysis has proven more useful than simply considering the relative taxon composition (which indirectly addresses functioning) or trophic group approaches, as although it includes information on the macrofauna trophic groups, it encompasses a wider range of trait information (Bremner et al. 2003). Traits are usually split into those that are biological (e.g. life history) and those that are ecological (e.g. mobility, skeleton, trophic group) (Costello et al. 2015). The use of multiple indicators results in a good guideline of overall system functioning

and how functioning may respond to environmental changes (Pacheco et al. 2011). It, therefore, has the potential to identify subtle differences between samples and provide information on the mechanisms structuring benthic communities (Paganelli et al. 2012).

4.2.1. Aims, objectives, and hypotheses

This chapter aimed to explore the biological traits characterising the uThukela shelf macrofauna, and determine the potential relationships that exist between these traits and the measured environmental parameters of the study area. The potential influence of shelf position (shelf zone, distance from shore, and distance from the uThukela Estuary mouth) was also considered.

Objectives:

- 4.1. To determine the biological traits and functional diversities of the uThukela shelf macrobenthic communities.
- 4.2. To determine if there is a significant difference in functional diversity and biological traits of the macrobenthic communities present at different shelf positions.
- 4.3. To relate measured abiotic variables to the uThukela shelf macrobenthic assemblage traits to determine the extent to which these environmental conditions affect trait patterns.
- 4.4. To relate taxonomic and functional assemblages.

Hypotheses:

- H₀₁: There are no significant differences between biological traits of macroinvertebrate communities at different uThukela shelf positions.
- H₀₂: There are no significant differences between functional diversities of macroinvertebrate communities at different uThukela shelf positions.
- H₀₃: There is no significant relationship between abiotic parameters measured during this study and the patterns in the biological traits of the uThukela shelf macroinvertebrate communities.
- H₀₄: There is no relationship between taxonomic and functional assemblages.

4.3. Materials and methods

The study site description (with associated map), general sampling and laboratory procedures, as well as general data analyses, were presented in Chapter 2 of this dissertation. Sampling occurred during the dry (winter) season on the inner (IS: 0 – 50 m), mid (MS: 50 – 80 m), and outer (OS: 80 – 130 m) uThukela shelf in August 2010 and on the inner-shelf in August 2008 (Figure 4.1). Specific methods relating to this chapter are presented further.

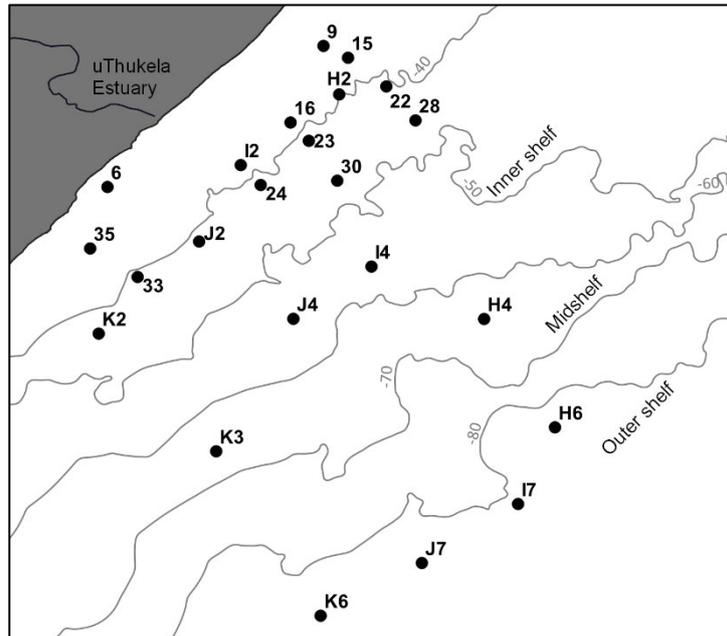


Figure 4.1. Study site depicting sampled stations on the inner (0 – 50 m), mid (50 – 80 m), and outer (80 – 130 m) uThukela shelf. Refer also to Figure 2.1 for regional context.

4.3.1. *Biological Traits Analysis (BTA)*

Macrobenthos were classified according to their functional groups using BTA. The initial step in BTA is to identify suitable traits for the ecosystem being studied (Bremner 2008). Ten biological traits were considered for the uThukela shelf system, reflecting morphology (support structure), adult behaviour (level of mobility, movement type, life habit, bioturbation), adult feeding ecology (diet, feeding mode), and life history (sexual differentiation, reproductive technique, larval development) (Table 4.1). The choice of biological traits, and subsequent divisions into relevant categories, was based on trait importance to ecosystem functioning and the availability of trait information for the taxa being studied (Veríssimo et al. 2012). This was determined using several marine studies and databases (Bremner et al. 2006, Tyler et al. 2012,

Costello et al. 2015, Beauchard et al. 2017, Dauvin et al. 2017, Maduna 2017, Degen and Faulwetter 2019). Each taxon was assigned to its corresponding trait category using information gathered from the available literature (e.g. Fauchald and Jumars 1979, Wilson 1991, Macdonald et al. 2010, Queirós et al. 2013, Jumars et al. 2015) and appropriate databases (Marine Life Information Network 2006, Encyclopedia of Life 2014, Degen and Faulwetter 2019, World Register of Marine Species Editorial Board 2021). When information on a taxon was unavailable, or the taxon was at a high classification level with multiple categories exhibited by different species, “trait unknown” was assigned to avoid the improper influence of that taxon.

Table 4.1. Traits table (based on Maduna 2017, Degen and Faulwetter 2019) with categories, category codes, explanation of categories, and the function of the chosen trait.

MORPHOLOGY		
Support structure (S)		
Categories	Hydrostatic (S1)	Hydrostatic skeleton; No endo-/exoskeleton
	Hard – Calcareous (S2)	Skeleton of calcite or aragonite
	Hard – Chitinous (S3)	Skeleton of chitin
	Cuticle (S4)	Thin, protective outer covering (e.g. in Sipuncula)
Function	Resistance to predation and vulnerability to ocean acidification (Amaral et al. 2012, Costello et al. 2015).	
BEHAVIOUR		
Level of mobility (Mob)		
Categories	None (Mob1)	No movement as an adult
	Low (Mob2)	Slow movement: including burrowers & tube-dwellers
	Medium (Mob3)	Medium movement (e.g. starfish, brittle stars)
	High (Mob4)	Fast movement: swimmer or fast crawler (e.g. crab)
Function	Indicates the dispersal potential of the adult form and the ability of the animal to escape pressure (e.g. predation) (Costello et al. 2015, Beauchard et al. 2017).	
Movement type (Mov)		
Categories	Sessile (Mov1)	Attached or in tube
	Burrow (Mov2)	Move in the sediment
	Crawl (Mov3)	Move on substratum using legs, appendages, or muscles
	Swim (Mov4)	Move above the sediment; actively swim in the water
Function	Indicative of the mode of dispersal, the ability of an organism to escape predation, the recolonization potential of organisms in response to changing environmental conditions, and carbon and nutrient cycling (Bremner 2008, Tyler et al. 2012, Beauchard et al. 2017).	

Table 4.1. (continued)

Living habit (H)		
Categories	Free-living (H1)	Able to move freely; not restricted to any structure
	Tubicolous (H2)	Live in a tube constructed by themselves
	Burrow-dweller (H3)	Live in permanent or temporary burrows constructed by themselves or other organisms
	Shell-dweller (H4)	Inhabiting shells made by molluscs
	Commensal (H5)	Living on or in other organisms or with them in their tubes/burrows
	Attached (H6)	Fixed to a substratum
Function	Indicates mode of dispersal and ecological role, and facilitates carbon transport and nutrient cycling (Bremner 2008, Costello et al. 2015).	
Bioturbation (B)		
Categories	None (B1)	No sediment displacement
	Biodiffusor (B2)	A constant and random local sediment biomixing over short distances
	Conveyor-belt transport (B3)	Translocation of particles from above to below or from below to above the sediment surface
	Surficial modifier (B4)	Bioturbator with activities restricted to the sediment layer immediately below the surface
Function	Impact on sediment biogeochemistry, organic matter redistribution, and habitat provision and maintenance (Beauchard et al. 2017).	
FEEDING ECOLOGY		
Diet (D)		
Categories	Carnivore (D1)	Feed on other living animals
	Herbivore (D2)	Feed on living plants
	Omnivore (D3)	Feed on living animals & plants
	Detritivore (D4)	Feed on detrital material: animal and plant
Function	Indicates the trophic level occupied by the organism, the food resource requirement, as well as the energy flow and nutrient cycling within the community (Tyler et al. 2012, Costello et al. 2015, Beauchard et al. 2017).	
Feeding mode (F)		
Categories	Suspension feeder (F1)	Removal of particulate matter from the overlying water column via passive use of tentacles or active pumping
	Surface deposit feeder (F2)	Removal of particulate matter from the sediment surface
	Subsurface deposit feeder (F3)	Burrow beneath the sediment surface to consume particulate matter from within the sediment
	Predator (F4)	Actively search for and prey on other animals
	Scavenger (F5)	Feed on dead material
	Parasite (F6)	Live on or in other animals, feeding on them
	Grazer (F7)	Consume benthic primary producers

Table 4.1. (continued)

Function	Expresses the food resource requirement and utilisation driven by environmental conditions. Food acquisition impacts interactions between taxa, nutrient and energy cycling within the environment, and can predict responses to disturbances (Bremner 2008, Tyler et al. 2012, Beauchard et al. 2017)	
LIFE HISTORY		
Sexual differentiation (SD)		
Categories	Gonochoristic (SD1)	Separate sexes; male and female
	Sequential hermaphrodite (SD2)	Change sex during lifespan
	Simultaneous hermaphrodite (SD3)	Possessing both male and female reproductive organs at the same time
Function	Relates to the persistence of individuals and populations (Costello et al. 2015).	
Reproductive technique (R)		
Categories	Asexual (R1)	Budding and fission
	Sexual (broadcast spawn) (R2)	Fertilisation external; eggs and sperm released into the water column
	Sexual (brood) (R3)	Fertilisation external; eggs brooded on the animal, in a gelatinous mass, or in a tube
	Sexual (internal) (R4)	Fertilisation internal
Function	Relates to the ability of a population to disperse, become invasive, and recover from reduced abundance (Costello et al. 2015).	
Larval development (L)		
Categories	Planktotrophic (L1)	Larvae feed and grow in the water column for fairly long periods
	Lecithotrophic (L2)	Non-feeding larvae, which depend on the egg's yolk reserve supplied by the mother; pelagic for short periods
	Benthic/direct (L3)	Larvae have benthic larvae or direct development (no pelagic larval stage)
Function	Indicates juvenile survival and dispersal potential (Beauchard et al. 2017).	

The fuzzy-coding procedure was used to indicate the extent to which taxa exhibited each trait category (Chevenet et al. 1994, Frid et al. 2008). Fuzzy coding permits the allocation of an individual taxon to multiple trait categories, allowing flexibility for intraspecific variances that may occur (Bremner 2008). This is done through a coding process, and while many coding schemes exist, the 0 – 3 scale was chosen for this study as it appears to be the most widely used in the observed literature. In the case of this scale, a zero indicates no affinity to a trait category, while a three specifies complete affinity (Table 4.2). If the affinity of a taxon for a specific trait was unknown, it was coded a zero for every category within that trait.

Table 4.2. The fuzzy-coding scale used to indicate the affinity of a taxon to a trait category (based on Degen and Faulwetter 2019).

Code	Affinity
0	None
1	Low
2	High, but other categories can occur with equal or lower affinity
3	High & complete

The frequency of each trait category expressed per taxon was multiplied by the pre-transformed taxa-by-stations abundance matrix used in Chapter 3 (community assessments) to calculate the abundance-weighted category scores per taxon per station. These abundance-weighted category scores were then summed across taxa to give one value per trait category in each sample, resulting in a traits-by-sample matrix. This matrix was used in the analyses of the traits composition and distribution in the uThukela shelf macrobenthic community.

4.3.2. Data analyses

4.3.2.1. Biological traits data

The number of categories, and the percentage of each trait expressed by associated categories, were calculated for each station to compare the distribution of traits expressed by macrobenthic communities on the uThukela shelf. Functional diversity, richness, and evenness were then determined for each station using the mean of station replicates. Functional diversity was measured using the Shannon-Wiener diversity index (H') to allow comparison with findings from taxonomic analyses. Functional richness, using Margalef's richness index (d), measured the niche space occupied by species, not weighted by species abundance (Schleuter et al. 2010). Functional evenness measured the degree to which the community was distributed in niche space to effectively utilise the range of resources available to it (Mason et al. 2005), with Pielou's evenness index (J') being used in this study to reflect this. Generalised linear models (GLMs) (G) were employed using PAST v3.25 to determine whether these diversity indices responded to spatial (i.e. shelf position) and environmental (i.e. measured variables) gradients. These models accommodate response variables with non-normal conditional data, and the Poisson distributions and log link functions were used as these are the most appropriate for count data (O'Hara and Kotze 2010).

The possible influence of shelf position (shelf zone, distance from the shore, and distance from the uThukela Estuary mouth) on BTA was investigated using PERMANOVA (Pseudo- F). A Bray-Curtis (B-C) similarity matrix, based on a square-root transformation of the abundance-weighted traits-by-sample matrix, was subsequently subjected to ordination by nMDS (method explained in Chapter 2). Distributions did not form distinct explanatory groups in terms of shelf position, so further distribution or distance-type analyses were not undertaken. However, the similarity percentages (SIMPER) analysis was performed to determine trait categories responsible for the functional assemblages identified by nMDS. This analysis was also used for the predefined taxonomic assemblages in Chapter 3 to provide better insight into the trait categories characterising assemblages that were based on shelf position.

4.3.2.2. Relationship between biological traits and environmental parameters

The RELATE procedure was used to investigate the relationship between BTA and environmental variables. The BIO-ENV analysis, using the BEST procedure, identified the environmental variables that best correlated with the distribution of traits on the uThukela shelf. This was also employed to test the main drivers of individual traits and trait groups (morphology, adult behaviour, adult feeding ecology, life history). The variables identified as best correlating with the entire community distribution were then included in a Canonical Correspondence Analysis (CCA) using PAST v3.25 (Chapter 2).

4.4. Results

4.4.1. *Macroinvertebrate community functioning*

4.4.1.1. Data overview

Although there were 575 gaps in the overall biological traits (BT) dataset, there was still 88% data completeness. Information on the “support structure” of species was the most available BT data (almost 100% of taxa), contrasting with the reproduction information which had the most gaps, as “larval development” and “reproductive technique” had 73% and 75% of BT data complete, respectively.

One taxon (Mollusca sp.1) had no information available for biological traits, and many others had information available for only one or two traits. Most of these taxa were classified to a high taxonomic level (above family), so it was expected that there would be limited information

available, as traits were not inferred if multiple categories were exhibited by individuals within these groups. A total of 249 taxa (55%) had complete traits datasets, with information available for every trait.

4.4.1.2. Distribution of community traits

Number of trait categories

There were 31 – 42 categories represented per station (Figure 4.2) out of a possible 43. No station represented all 43 categories, but stations 9, 35, 23, K3, and H6 represented over 40 categories each (Figure 4.2). Stations 6, 15, and H4 represented the least number of biological trait categories ($S_{bt} < 35$ categories; Figure 4.2), which corresponded to the lowest number of taxa observed during taxonomic analysis (Chapter 3).

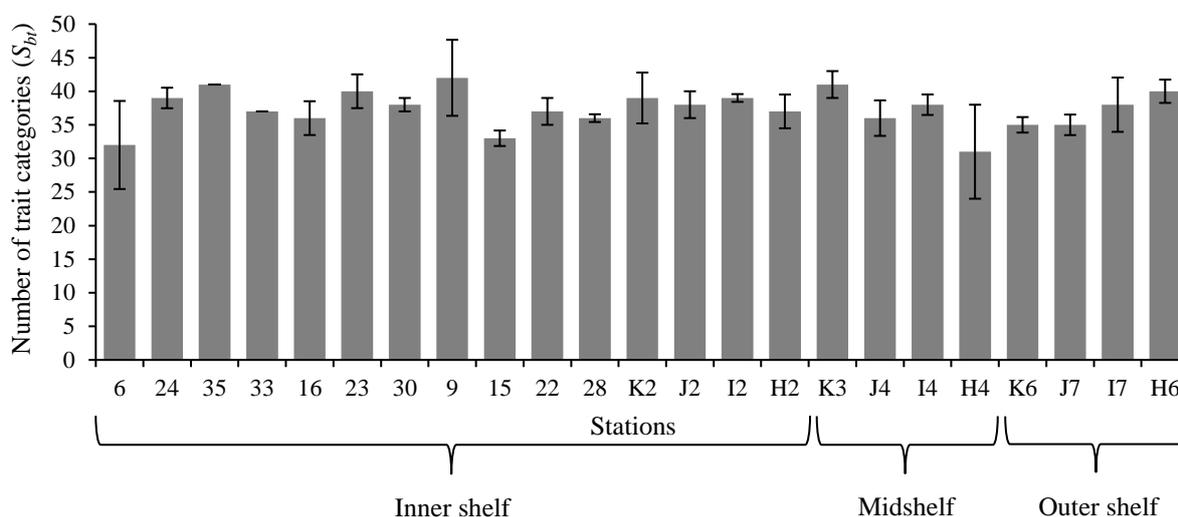


Figure 4.2. Mean number of macrobenthic trait categories ($S_{bt} \pm SD$) expressed at each station sampled on the uThukela shelf.

Dominant traits

The uThukela shelf communities were mostly dominated by soft-bodied macroinvertebrates (S1), although fauna with hard calcareous skeletons (S2) were also present in great abundances (Figure 4.3a). Macrofauna were generally free-living (H1), but tubicolous taxa (H2) were also abundant and mostly capable of leaving their tubes to relocate when disturbed. Taxa had low mobility (Mob2) and most moved by crawling over the sediment surface (Mov3), although burrowing through the sediment (Mov2) was also common (Figure 4.3b-d). Many organisms in this study exhibited more than one type of movement (e.g. could both crawl on and burrow

through the sediment). These activities resulted in the continuous movement of sediment mostly by biodiffusors (B2) and surficial modifiers (B4) (Figure 4.3e). The uThukela shelf macrofauna were predominantly gonochoristic (SD1), with sexual reproduction by broadcast spawning (R2) and brooding (eggs carried on animal or laid in gelatinous mass) (R3) (Figure 4.3h-i). Broadcast spawning with mostly planktotrophic larval development (L1) was dominant on the outer and inner-shelf (although brooding being largely dominant at stations 28, 33, and K2), and brooding with direct development (L3) dominated the mid-shelf (Figure 4.3i-j). The uThukela shelf macrobenthos showed a diverse range of feeding modes but were predominantly characterised as suspension (F1) and surface deposit-feeding (F2) detritivores (D4) (Figure 4.3f-g), with a dependence on particulate organic matter (POM). High abundances of predators (F4), but very few parasites (F6) and grazers (F7), were also observed in the region (Figure 4.3.f-g). Carnivores (D1) were found in the greatest proportions on the mid-shelf (due to dominance at stations J4 and H4), although this region was dominated by suspension-feeding detritivores (Figure 4.3f-g). Surface deposit-feeding was the main mode of food acquisition on the outer-shelf, while on the inner-shelf a combination of suspension and surface deposit-feeding predominated (Figure 4.3f-g). Although fuzzy coding revealed these feeding modes as dominant on the uThukela shelf, many of the taxa present exhibited more than one of these strictly-defined feeding modes and are known as facultative feeders, capable of shifting feeding behaviours depending on environmental conditions (Macdonald et al. 2012). These slight differences observed between community trait composition in the different shelf zones were not significant when considering the communities in their entirety (Pseudo- $F = 2.137$, $df = 67$, $p = 0.059$).

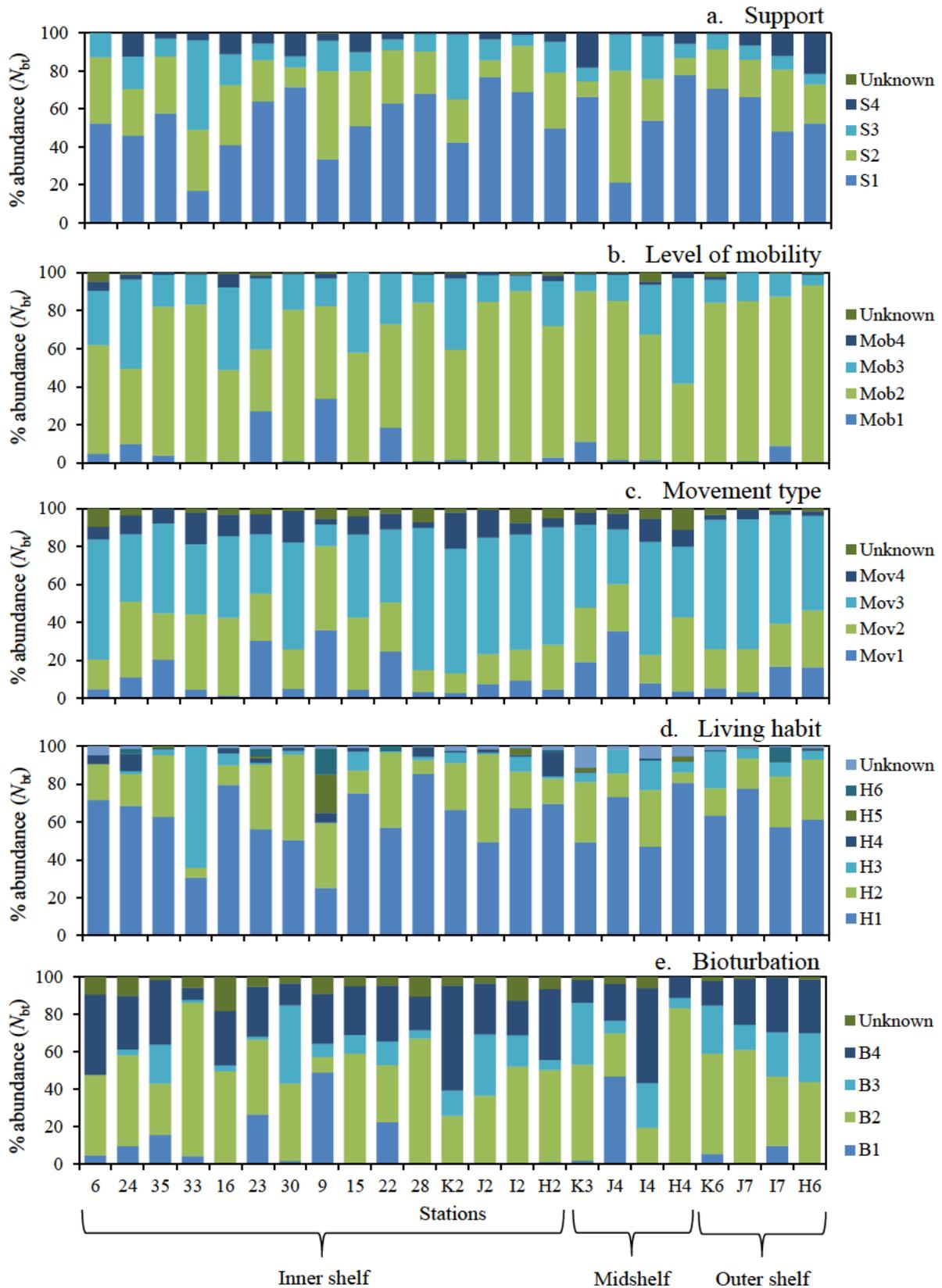


Figure 4.3. Contribution (%) of each category to the abundance-weighted traits of stations sampled on the inner, mid, and outer uThukela shelf. See Table 4.1 for trait category codes.

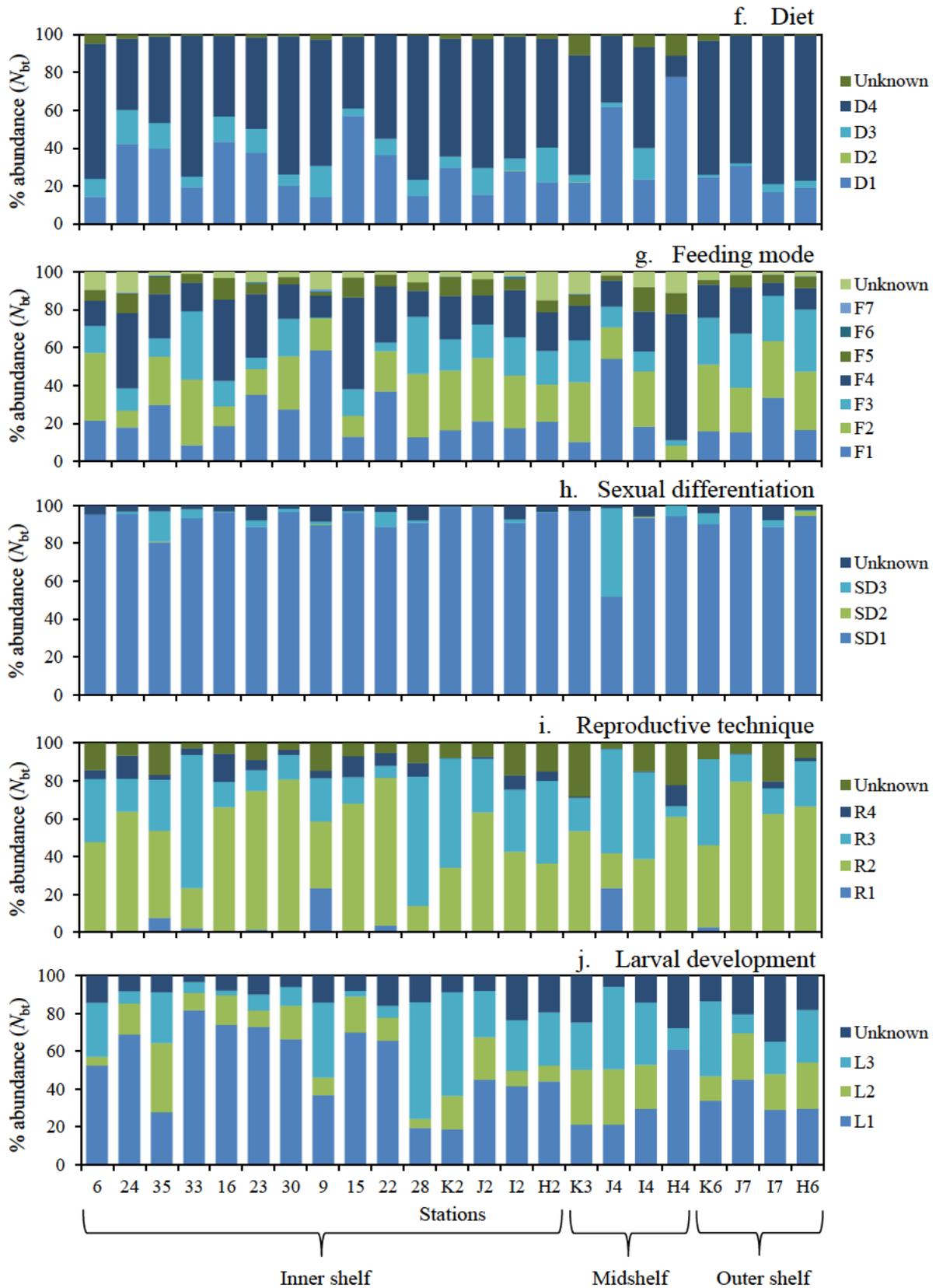


Figure 4.3. (continued) (Caption on previous page).

Functional diversity and redundancy

Mean Margalef's richness (d_{bt}) varied from 3.79 ± 0.17 (station J4) to 5.62 ± 0.90 (station 6) and there was no dominance of specific traits, with mean evenness (J'_{bt}) ranging between 0.84 ± 0.04 (station 28) and 0.91 ± 0.04 (station J4) (Figure 4.4b-c). Mean Shannon-Wiener diversity (H'_{bt}) was high across stations for the traits analysis, ranging between 2.92 ± 0.25 (station H4) and 3.32 ± 0.04 (station 35) (Figure 4.4a). Functional diversity did not respond to the distance gradients from the shore ($G = 0.006$, $p = 0.939$) or from the uThukela Estuary mouth ($G = 0.005$, $p = 0.943$), and neither functional richness or functional evenness were related to these distance gradients (FR shore: $G = 0.056$, $p = 0.813$; uThukela Estuary mouth: $G = 0.055$, $p = 0.814$. FE shore: $G = 0.001$, $p = 0.978$; uThukela Estuary mouth: $G = 0.001$, $p = 0.979$). Taxonomic and functional diversities had a significantly positive relationship ($r = 0.586$, $p = 0.003$).

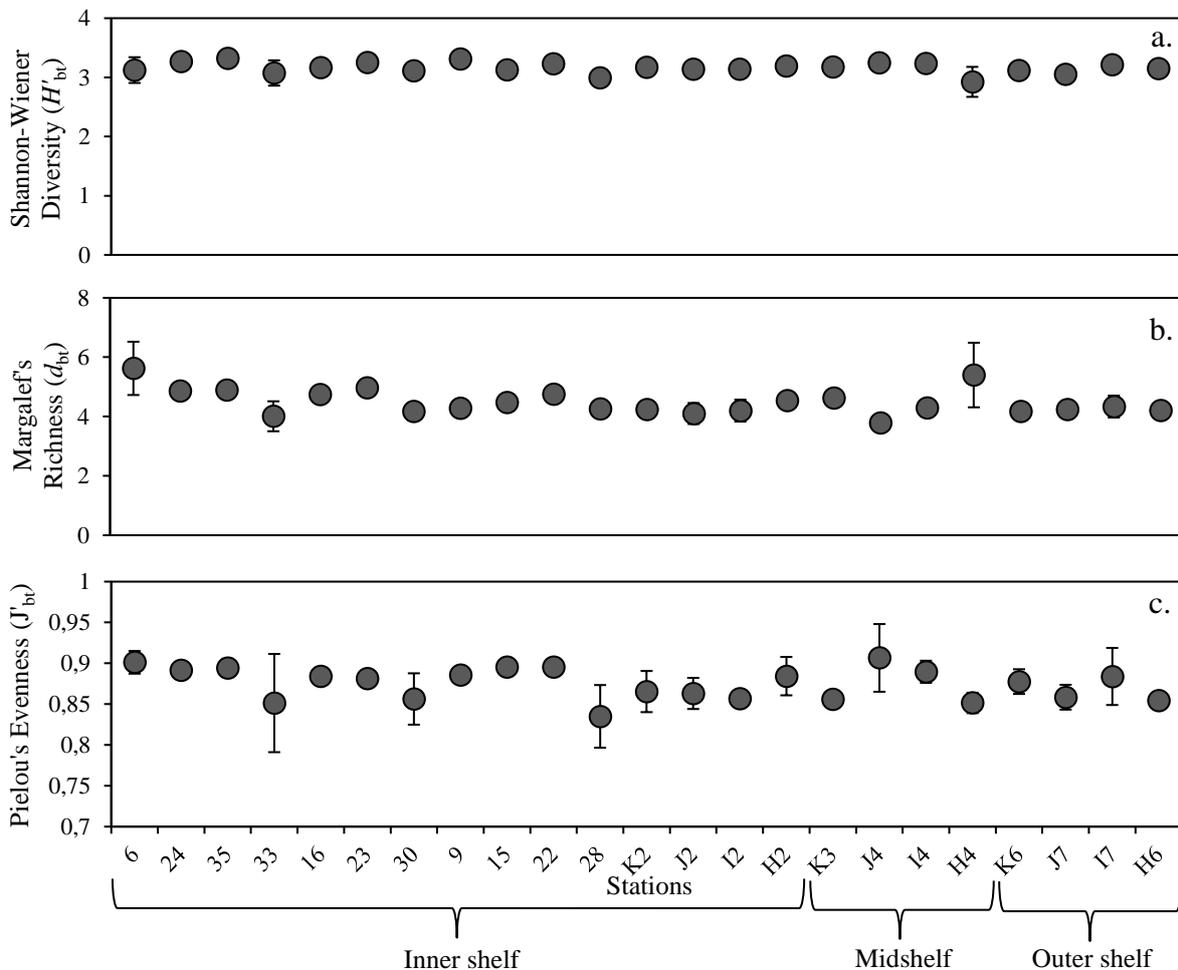


Figure 4.4. (a) Mean functional diversity ($H'_{bt} \pm SD$), (b) richness ($d_{bt} \pm SD$), and (c) evenness ($J'_{bt} \pm SD$) for stations on the inner, mid, and outer uThukela shelf.

4.4.1.3. Characterisation of macrobenthic assemblages based on biological traits

Ordination of all 68 replicate samples used in BTA resulted in two sample groups at 60% similarity (Figure 4.5). One group contained stations 6 and H4, whilst the other group comprised the remaining 21 stations. At 65% similarity, ordination resulted in four assemblages (Figure 4.5). There were no patterns observed for the distribution of samples in terms of shelf position, and replicates from the same station were often distributed among different groups. This implied similar traits expression across the uThukela shelf.

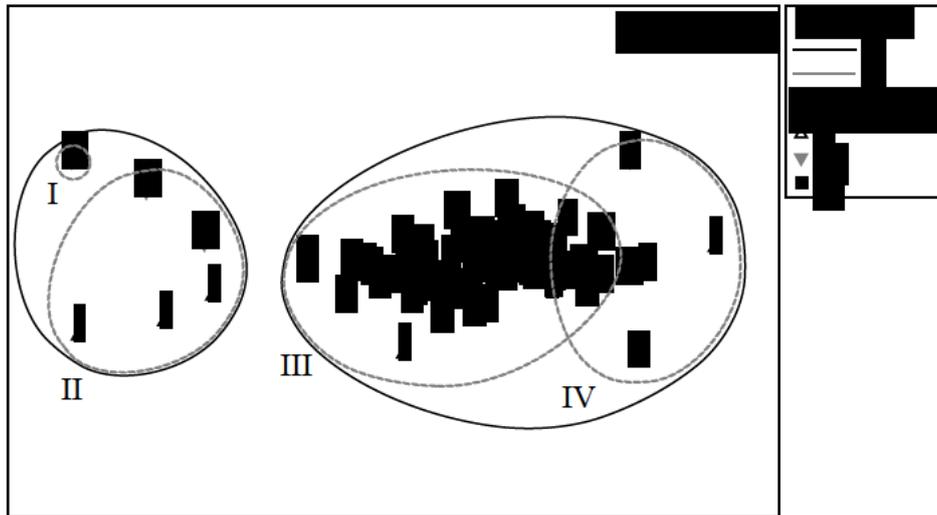


Figure 4.5. Ordination of samples from different stations by nMDS showing the distribution of trait assemblages with similarities at 60% and 65% (assemblages I – IV).

Assemblage I was excluded from SIMPER analysis using functional assemblages as it contained just a single sample. Analysis of assemblages II – IV revealed that the assemblages were all typified by similar trait categories (Table 4.3). The only major differences observed were that assemblage III was the only group that had a consistently large presence of carnivores (indicated by the relatively high sim/SD) and assemblage IV was the only group that had a consistently high occurrence of surface deposit feeders (Table 4.3).

Table 4.3. The percentage contribution (along with sim/SD) of the trait categories contributing to 50% within-group similarity of assemblages II – IV (excluding the single H4 replicate), with the top five categories indicated in bold.

Trait category	II	III	IV
	70.54%	75.24%	73.15%
Gonochoristic (SD1)	9.10 (8.81)	6.53 (6.49)	6.71 (4.30)
Free-living (H1)	8.09 (7.49)	5.54 (6.71)	4.69 (4.88)
Hydrostatic (S1)	7.19 (7.78)	4.92 (5.08)	4.33 (2.06)
Low mobility (Mob2)	7.02 (10.01)	5.25 (4.20)	7.32 (9.95)
Biodiffusor (B2)	6.74 (5.58)	4.37 (4.93)	4.08 (3.68)
Crawl (Mov3)	6.68 (6.64)	4.67 (4.58)	4.44 (2.83)
Detritivore (D4)	6.43 (7.14)	4.68 (3.70)	6.17 (4.51)
Broadcast spawn (R2)		4.89 (4.71)	4.12 (2.41)
Planktotrophic (L1)		4.47 (4.72)	4.93 (5.23)
Carnivore (D1)		3.79 (4.74)	
Predator (F4)		3.47 (4.37)	
Surface deposit feeder (F2)			4.06 (4.93)

The relationship between the functional assemblages (Figure 4.5) and taxonomic assemblages (formed in Chapter 3) was relatively weak (RELATE: $\rho = 0.488$), but the taxonomic assemblages formed distinct communities according to shelf position and were, therefore, used to spatially examine the functioning of the uThukela shelf macrofauna, resulting in Table 4.4. Gonochoristic differentiation characterised all five assemblages (Table 4.4). Assemblage I contained a single station (6) and was typified by soft-bodied, free-living detritivores (Table 4.4), due to the dominant polychaetes *Aphelochaeta filibranchia*, *Armandia leptocirris*, and *Owenia fusiformis*. Assemblage II also contained a single station (H4) that was characterised entirely by *Aglaophamus dibranchis*, a bio-diffusing carnivore with planktotrophic development (Table 4.4). Assemblage III (most inner-shelf samples) was characterised by free-living broadcast spawners with planktotrophic development and comprised a characteristic combination of detritivores (Sipunculidae and *O. fusiformis*) and carnivores (*Aglaophamus dibranchis* and *Antalis longitrorsa*), with predation as the main mode of feeding (Table 4.4). Assemblage IV (mostly mid-shelf samples) was also identified by carnivores and detritivores, due to the presence of the carnivorous *Basuto stimpsoni* and *Lumbrineris aberrans*, and the detritus-consuming *Prionospio nirripa* and *Byblis gaimardii*. The amphipod abundance in this assemblage resulted in tubicolous brooders with direct development/benthic larvae typifying this group (Table 4.4). Assemblage V (entirely outer-shelf samples) was characterised by

Tellina sp., Sipunculidae, and *Notomastus latericeus*, resulting in the dominance of free-living detritivores utilising mostly broadcast spawning (Table 4.4).

Table 4.4. Characteristics of assemblages revealed by taxonomic analysis of the uThukela shelf (excluding 9B) in Chapter 3. The percentage contribution (along with sim/SD) of the categories contributing to 50% similarity within groups are listed, with the top five indicated in bold. Refer to Chapter 3 for samples included in these groupings.

Trait category	I	II	III	IV	V
	75.53%	69.84%	72.44%	78.86%	78.42%
Gonochoristic (SD1)	7.78 (13.22)	9.30 (6.52)	6.46 (5.37)	6.30 (5.94)	6.57 (7.07)
Detritivore (D4)	7.36 (9.74)		4.30 (3.48)	4.84 (5.99)	5.76 (6.80)
Free-living (H1)	7.12 (6.60)	7.84 (5.17)	5.57 (5.24)	5.05 (7.74)	5.50 (6.69)
Crawl (Mov3)	7.07 (10.09)		4.42 (4.47)	4.66 (5.34)	5.42 (6.95)
Hydrostatic (S1)	6.44 (11.02)		4.73 (4.22)	4.62 (4.98)	5.22 (6.20)
Low mobility (Mob2)	6.44 (11.02)		4.87 (4.06)	5.72 (8.17)	6.14 (7.08)
Biodiffusor (B2)	6.17 (6.60)	8.75 (9.43)	4.50 (4.64)		4.88 (6.15)
Planktotrophic (L1)	5.36 (13.27)	8.44 (8.45)	5.06 (4.50)		3.92 (5.80)
Carnivore (D1)		8.75 (9.43)	4.01 (3.95)	3.61 (6.22)	
Predator (F4)		8.60 (9.31)	3.82 (4.01)		
Broadcast spawn (R2)			4.90 (3.91)	4.09 (5.40)	5.24 (5.65)
Benthic/direct (L3)				3.75 (5.20)	
Sexual (brood) (R3)				3.73 (3.95)	
Surface deposit feeder (F2)				3.48 (7.67)	3.61 (6.37)
Tubicolous (H2)				3.45 (4.36)	

4.4.2. Environmental associations with traits distribution

Functioning of the uThukela shelf macrofaunal community did not relate well to the environmental variables measured during the study (RELATE: $\rho = 0.021$), as was expected due to the similarity in traits across the study area. The BIO-ENV function revealed fine sand as the single parameter most correlated to community traits distribution ($\rho = 0.192$) (Table 4.5). The best combination of variables was salinity and fine sand ($\rho = 0.276$), however, the Spearman correlation coefficient remained comparable with the addition of mud as a third variable ($\rho = 0.272$), and sorting as a fourth variable ($\rho = 0.271$) (Table 4.5).

The CCA constructed using these four environmental parameters revealed that all four variables had analogous importance in the distributing communities according to functioning, as all vectors were similar lengths. Axis 1 explained 41% of the variation, splitting samples primarily

by the sedimentary parameters mud and fine sand, while the second axis separated samples according to the variables sorting and salinity, explaining 30% of the variation (Figure 4.6, Table 4.6). Samples were not widely spread, showing the high similarity that existed between them.

When considering trait groupings, the BEST test revealed similar results to the findings regarding the entire community. Morphology (support structure), adult behaviour (level of mobility, movement type, living habit, bioturbation), adult feeding ecology (diet, feeding mode), and life history (sexual differentiation, reproductive technique, larval development) were all mostly correlated to the same four environmental variables: salinity, fine sand, mud, and sorting (Table 4.5). The single variable most related to these trait groups was also fine sand. However, when individual traits were considered, it was found that there were a few exceptions to fine sand being the most correlated environmental variable as living habit, feeding mode, and adult mobility were mostly associated with salinity, diet was mostly affected by depth, and larval development by mud.

Table 4.5. The results of the BIO-ENV analysis showing the environmental variables most correlated with the entire macrobenthic community functioning and the trait group distribution on the uThukela shelf.

Trait	No. of variables	ρ	Variables
Best single variable			
All	1	0.192	%fine sand
Morphology	1	0.212	%fine sand
Adult behaviour	1	0.184	%fine sand
Adult feeding ecology	1	0.158	%fine sand
Life history	1	0.202	%fine sand
Best combination of variables			
All	2	0.276	Salinity, %fine sand
	3	0.272	Salinity, %fine sand, %mud
	4	0.271	Salinity, %fine sand, %mud, sorting
Morphology	2	0.232	Salinity, %fine sand
	3	0.231	Salinity, %fine sand, sorting
	2	0.230	%fine sand, sorting
Adult behaviour	4	0.280	Salinity, %fine sand, %mud, sorting
	2	0.275	Salinity, %fine sand
	3	0.274	Salinity, %fine sand, sorting
Adult feeding ecology	2	0.247	Salinity, %fine sand
	4	0.240	Salinity, DO, %fine sand, %mud
	3	0.236	Salinity, DO, %fine sand
Life history	3	0.282	Salinity, %fine sand, %mud
	2	0.272	Salinity, %fine sand
	4	0.262	Salinity, %fine sand, %mud, sorting

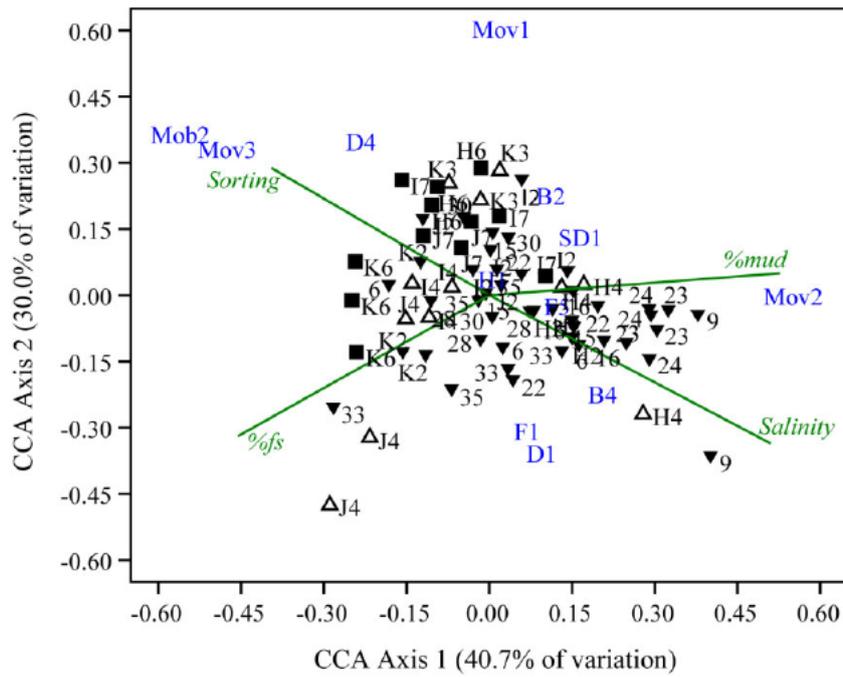


Figure 4.6. Canonical Correspondence Analysis (CCA) of the uThukela shelf samples showing the relationship between the four most correlated environmental variables (according to the PRIMER BEST procedure) and the macrofauna community, as well as the trait categories related to these conditions. Blue text denotes biological traits (BTs).

Table 4.6. Canonical coefficients from the CCA for the four environmental variables most related to community functioning of the uThukela shelf macrofauna community.

Variable	Axis 1	Axis 2
Salinity	0.511	-0.336
%Fine sand	-0.456	-0.319
%Mud	0.527	0.050
Sorting	-0.395	0.288

4.5. Discussion

The first step in understanding the functioning of a particular community is through taxonomic analysis and diversity (completed in Chapter 3), due to the importance of individual species traits in ecosystem regulation (Maggiore and Keppel 2007, Norling et al. 2007). Limited taxonomic information for South African macrofauna restricts functional analyses (Snelgrove 1997), however, this study managed to fill a large percentage (88%) of traits information for

the uThukela shelf taxa. This was an important attempt at contributing to the biological traits inventory and understanding of the benthic community functioning, yet only just over half (55%) of the taxa sampled during this study had complete datasets, which indicates that further focus is needed in this field.

4.5.1. *Functional diversity and community resilience*

High functional diversity and evenness were observed for the uThukela shelf macroinvertebrate community during this study. High diversity indicates that macrofauna in this region belong to a variety of functional groups (Akoumianaki et al. 2013), and there is great potential for interactions between functions, thus increasing ecosystem functionality (Hewitt et al. 2008). Functional diversity of the macrofauna communities did not change according to the spatial gradients of distance from the uThukela Estuary mouth and distance from the shore. This was in contrast to the macrobenthic study along the Emilia-Romagna coastline in the North-West Adriatic Sea, Italy, where functional diversity increased with distance from the Po River delta, suggesting that fluvial input had a detrimental effect on community functioning (Paganelli et al. 2012). The absence of functional differences between uThukela shelf positions during this study may be explained by the land-sea connection between the uThukela Estuary and the shelf edge (De Lecea et al. 2013, Scharler et al. 2016b). High functional evenness suggests that taxa have effectively utilised available resources across the shelf (Mason et al. 2005, Hewitt et al. 2008) or that the chosen traits are less sensitive to the inter-habitat differences in supporting different assemblages. The weak relationship between taxonomic and functional diversities implies that many of the species in this community exhibit similar traits (i.e. they are redundant) (Naeem and Wright 2003). Redundancy ensures the stability and resilience of the uThukela shelf community and may protect against the complete loss of a function where natural river flow may affect specific species (Hewitt et al. 2008, Miatta et al. 2021).

4.5.2. *Distribution in biological traits of the uThukela shelf macrobenthic communities*

Differences in biological traits between stations were most apparent for stations 6 and H4, while most of the other stations showed high similarity. These differences were driven by dissimilarities in the numbers and abundances of taxa, instead of the presence/absence of traits, indicating the significance of altering community numbers in influencing the traits composition of an area (Hewitt et al. 2008).

As expected by the abundance of Polychaeta on the uThukela shelf (Chapter 3), soft-bodied macroinvertebrates (with hydrostatic skeletons) were dominant during this study. Hard-bodied invertebrates have internal or external skeletons that are a better defence against predators, and also have more controlled and often quicker movements (Brusca and Brusca 2003). However, they form their support structures using biominerals, such as carbonates (Brusca and Brusca 2003), which may be affected by environmental shifts and disturbances (e.g. ocean acidification) (Costello et al. 2015). Organisms with hydrostatic skeletons are more resistant to these threats as they have flexible body shapes and movements, and have higher resilience to external impacts (Brusca and Brusca 2003).

Food composition is a limiting resource that creates competition among organisms, allowing the occupation of many non-overlapping niches (Levinton 1972). Various feeding modes were observed during this study and indicated diverse food sources on the uThukela shelf (Sigala et al. 2012), but the apparent dominance of detritivores indicated that the most important of these was POM that is mostly imported from the uThukela Estuary (Ayers and Scharler 2011, De Lecea et al. 2016, Scharler et al. 2016b). This dominance agreed with the general trend that suspension and deposit feeders are the most common among benthic communities (Rhoads and Young 1970, Snelgrove 1997, Snelgrove 1998, Macdonald et al. 2012), but this community also contained a noteworthy portion of carnivores. Suspension feeders in the Macdonald et al. (2012) study were found to also deposit feed, allowing greater distribution of suspension-feeding taxa. Most of the suspension and deposit-feeding detritivores encountered during this study were also able to alternate between the two major feeding modes, therefore agreeing with the findings by Untiedt and MacKay (2016) that interface feeding (utilising deposit and suspension-feeding interchangeably) and carnivory dominated the uThukela shelf. Facultative feeding during a shift in environmental conditions and food availability (Macdonald et al. 2012) is particularly beneficial on the uThukela shelf with fluctuating hydrodynamics and food supply (Jumars et al. 2015). This adjustment in feeding behaviour enhances community resilience, as macrofauna cannot relocate over large distances when resources are altered, so must be flexible to changes in food supply to survive these habitat changes (Levinton 1972, Pearson and Rosenberg 1978, Macdonald et al. 2012). The large abundance of detritivores does, however, indicate the reliance of the community on the uThukela River and even with the ability to shift behaviours with changing environmental conditions, there is a need for significant input of organic matter to the shelf. The primary consumers, i.e. herbivores and detritus feeders, also comprised the major portion of the benthic community in Buzzards Bay in the Sanders (1958)

study, with suspension feeders making up the majority of fauna in sandy sediments, while deposit-feeders dominated the community in finer sediments. Similar patterns were found for the uThukela shelf, with the sandy mid-shelf dominated by suspension feeders, the poorly-sorted outer-shelf mud dominated by deposit feeders, and the relatively well-sorted muddy-sand inner-shelf shared dominance of suspension and deposit feeders. Deposit feeders are known to thrive in muddy regions with an abundant supply of organic matter (Rhoads and Young 1970), and are relatively tolerant to different environments and environmental changes (Sigala et al. 2012). Through their feeding behaviours, deposit feeders affect the structure of the substratum (Levinton 1972) and play a vital ecological role in sediment turnover by removing organic matter from an area and preventing the subsequent depletion of oxygen by bacterial decomposition (Brusca and Brusca 2003). The particles of muddy bottoms, however, are frequently reworked and this is often detrimental to suspension-feeding fauna as their feeding structures are often clogged and feeding is inhibited (Rhoads and Young 1970, Brusca and Brusca 2003). It is due to this, and the need for attachment sites, that infaunal suspension feeders usually reach their maximum abundances in coarse sediments (Levinton 1972, Macdonald et al. 2012). This mid-shelf habitat also contained the highest proportion of carnivores due to sandy sediments providing a range of suitable accumulation sites for potential prey in the interstitial spaces between grains (Muniz and Pires 1999). The increase in this feeding mode further away from the shore suggests that these macrofauna benefit from food resources not directly linked to land inputs (Akoumianaki et al. 2013).

Although crawling was the dominant form of movement on the uThukela shelf, burrowing through the sediment was also common, with many organisms capable of both forms. Consequently, most organisms found in this study were involved in the bioturbation of the shelf sediments. Bioturbators assist in sediment oxygenation and increase the ventilation of produced compounds deeper into the sediment, potentially altering the rates and pathways of organic matter mineralisation and the overall recycling of materials between the benthic and pelagic realms (Norling et al. 2007, Manokaran et al. 2013, McGovern et al. 2020). Tube and burrow-builders are also involved in the modification of the bottom environment, affecting remineralisation processes, altering local hydrodynamics, and providing habitats to other organisms (Pacheco et al. 2011, Passarelli et al. 2012). While these were not the main habits expressed on the uThukela shelf (organisms were mostly free-living), tube-building was relatively common. These aforementioned traits that characterise macrofaunal behaviour in this region reflect the species' capability of habitat modification through their activities, providing

significant insights into the ecosystem functioning of the uThukela shelf (Pacheco et al. 2011). Due to complex interactions that exist in an ecosystem, by modifying sediment properties and altering resources available to other organisms, habitat engineers can influence functioning via other biological components of the system (Pratt et al. 2014).

Life-history traits influence community structure, determining long-term patterns of abundance (Giangrande et al. 1994). Sexual reproduction is energetically costly but is still the characteristic method utilised by multicellular organisms (Brusca and Brusca 2003), as observed in the uThukela shelf macrobenthic community. It is thought that the genetic variation that results from the sexual exchange between individuals is beneficial as it allows species to adapt to environmental fluctuations, such as shifts in the physical environment or changes in biological interactions with predators, prey, competitors, and parasites (Brusca and Brusca 2003). The macrofauna of the inner uThukela shelf mainly reproduced using free-spawning and had planktotrophic larval development. This reproductive strategy is the most widely distributed among macroinvertebrates in shallow tropical and temperate seas (Giangrande et al. 1994, Brusca and Brusca 2003) and is relatively simple and inexpensive, with the only reproductive energy required from the adult being in the production of gametes, as after this there is no parental care (Brusca and Brusca 2003). The larvae feed on material suspended in the water column and resultantly can survive extended periods as part of the plankton (Giangrande et al. 1994, Brusca and Brusca 2003). Many species can also prolong the larval period until suitable settlement conditions are encountered, which has obvious advantages for post-larval survival (Brusca and Brusca 2003) and wider regional and geographical distributions (Giangrande et al. 1994, Brusca and Brusca 2003). The elimination of local populations during a disturbance is therefore not likely to cause the extinction of the entire species, as these vast dispersal techniques indicate that larvae can recolonise from other populations (McHugh and Fong 2002). The dominance of taxa exhibiting planktotrophy, therefore, indicates that the uThukela inner-shelf is an area that consists of highly variable environments, whereby populations can be maintained during fluctuating conditions (McHugh and Fong 2002). However, the mid-shelf community (and subsequently assemblage IV from Chapter 3) contained mostly brooders with direct development/benthic larvae. The greater abundances of Arthropoda associated with the coarser sediments in this region (Chapter 3) were mostly responsible for this observed dominance. Brooding with direct development requires parental care and is more energy expensive than spawning, resulting in fewer embryos but with higher survival rates (Brusca and Brusca 2003). Taxa exhibiting these traits tend to have narrower area ranges than taxa with

planktotrophic development, and consequently, there is a greater risk of local extinctions threatening the entire population (McHugh and Fong 2002).

Although biological traits are discussed individually, the sensitivity of a single taxon, and the resulting community, should not be determined by a single trait, as traits are often coupled to determine resilience (e.g. sessile organisms are sensitive to disturbance but may have a pelagic larval stage that aids in dispersal and assists in recovery of the population) (Beauchard et al. 2017). Therefore, complex combinations should be considered in determining the species' ability to survive specific conditions: some species are adapted to physical stress and disturbance, while others from stable environments may be more adapted to biotic interactions (Beauchard et al. 2017). The uThukela shelf macrofauna are likely from the former species group, having adapted similar traits to survive the fluctuating river flow and thus POM and sediment supply off a fluvially-dominated estuary (van Niekerk et al. 2020). This functional redundancy and the lack of distinct assemblages according to shelf position resulted in a weak association between the taxa traits and environmental parameters measured during this study, but the combination of salinity and fine sand was mostly correlated to the community traits distribution. This relationship was even more weak than the correlation between the measured environmental parameters and taxa composition.

Traits analysis provides an understanding of the relationships between species and their environments and can predict changes in ecological processes that the community performs (Bremner 2008, Miatta et al. 2021). It is an important component in MPA studies as understanding this relationship allows the maintenance of important habitats required for certain trait types and functions (Bremner 2008, Frid et al. 2008) and can identify resilience in natural systems (Miatta et al. 2021). This study provided an insight into the interactions and functioning of the benthic system within the newly promulgated uThukela MPA. Although the findings presented here do not fully measure the entire gambit of uThukela ecosystem functioning as this is made up of many physical, chemical, and biological components, it does assist in identifying important ecological processes supplied by the macrobenthic community and contributes to the baseline macrofauna traits information for the region. The results indicated that the macrobenthic community functioning relies on the freshwater, POM, and sediment input from the uThukela Estuary and emphasises the importance of the uThukela MPA in protecting the riverine outflow that supplies these nutrients and sediments to the coast (Republic of South Africa Government Gazette 2019). These results can further be used in MPA

management and monitoring by providing macrobenthic system reference states to predict and analyse future changes and to evaluate the success of management actions (Bremner 2008, Veríssimo et al. 2012).

4.6. Conclusion

This section provided information on the functioning of the uThukela shelf macroinvertebrate community. The community was defined as mostly soft-bodied, free-living, facultative detritivores. These traits, along with high functional diversity, evenness, and redundancy on the shelf implies that the community is relatively stable and resilient to fluctuating environmental conditions. This is particularly important for the benthic community of the uThukela shelf due to the frequent variation in river hydrodynamics and thus food supply in this region. Although there were no significant differences between macrofauna communities at different shelf positions, the mid-shelf community was observed to be slightly different from the inner and outer-shelf communities, and the reproductive traits were particularly noteworthy. The inner and outer-shelf communities had mostly broadcast spawners with planktotrophic larval development, but the mid-shelf community was dominated by brooders with direct development. This difference could be attributed to the abundance of amphipods in the coarser sediments of the mid-shelf that coincided with the positioning of the uThukela paleo-dune. There were no distinct functional assemblages formed due to the high similarity in traits exhibited by the taxa, and consequently, the environmental parameters measured during this study did not strongly relate to the variance in biological traits expressed by the macrobenthic community.

The results presented in this chapter provide vital insights into the functioning of the uThukela shelf macrobenthic community, contributing to the biological traits database for this region and the baseline information of the uThukela MPA. The dominant traits indicated that the community is reliant on fluvial input from the uThukela Estuary and reiterates the importance of the uThukela MPA in protecting this unique shelf. This information further assists in guiding management decisions and monitoring MPA effectiveness by ensuring that these important habitats essential for the ecological processes performed by macrofauna are maintained.

CHAPTER 5. A CHARACTERISTIC MACROBENTHIC COMMUNITY OFF THE FLUVIALLY-DOMINATED UTHUKELA ESTUARY

5.1. Overview

This chapter builds on the findings of Chapters 3 and 4, by providing an in-depth analysis of the characteristic macrofauna typifying the uThukela shelf community, and identifies potential surrogates and biodiversity indicators for future monitoring. Polychaeta was the dominant group in terms of taxa numbers and abundances, followed by the Crustacea (dominated by Decapoda) and Mollusca (as revealed in Chapter 3), and these were selected as the focal groups for this chapter. Large benthic Foraminifera (LBFs), although not a component of the macrofauna community, were also studied as they were abundant in the uThukela shelf samples and are usually considered ideal bioindicators. The distribution patterns of each focal group related to the varying conditions at different shelf positions and depths. Polychaetes were identified as potential surrogates of the macrofauna community as their distribution patterns were similar to those of the entire community, implying that they can be used in future monitoring if resources are limited and the entire macrobenthic community cannot be examined.

5.2. Introduction

The analysis of macrofauna patterns is usually time-consuming and expensive (Snelgrove 1998), indicating the need to identify potential surrogates of community variability (Moreno et al. 2007, Lewandowski et al. 2010), especially for monitoring studies. Specific taxonomic groups can often be used as surrogates and indicators for the biodiversity of the entire community if the patterns of the focal group and macrofauna are correlated (Moreno et al. 2007). These focal groups, therefore, represent alternate routes to monitor diversity, ecological processes, and habitat quality and are often specific to particular environmental or biogeographical situations (Moreno et al. 2007). The dominant taxonomic groups, identified in Chapter 3, were used in this chapter to investigate potential benthic surrogates and biodiversity indicators for the uThukela shelf. These included Polychaeta, Decapoda, and Mollusca. Large benthic Foraminifera (that are generally larger than 1 mm) were also included as they were abundant in the uThukela shelf sediments, and although not representative of the entire Foraminifera community, can provide foundational data as potential surrogates that can be expanded through further study.

5.2.1. *Polychaeta*

Polychaeta are a characteristic group of macrofauna, widely distributed in marine sedimentary environments and often numerically dominating infaunal communities (Muniz and Pires 2000, Manokaran et al. 2013, Jumars et al. 2015). Polychaetes are well represented in every benthic habitat (Beesley et al. 2000) due to the development of different morphological, reproductive, and feeding traits allowing adaptation to various niches (Fauchald and Jumars 1979, Wilson 1991, Brusca and Brusca 2003). They are an integral part of the ecosystem by creating key trophic linkages in marine food webs (as they are common in the diet of many fish, crustaceans, and shorebirds), and through their respiration and feeding activities, irrigate sediments, greatly altering the sediment redox conditions and sediment-water fluxes of nutrients and material (Jumars et al. 2015, Khan et al. 2017). The ubiquitous and heterogenous nature of polychaetes signifies that they are very important as indicators of environmental quality and potentially can be used in monitoring studies (Pocklington and Wells 1992). Very little is known about the uThukela shelf polychaete community, but a previous African Coelacanth Ecosystem Programme (ACEP) Natal Bight macrobenthic study identified Spionidae and Onuphidae as the most abundant polychaete families in this region (Untiedt 2013).

5.2.2. *Decapoda*

Arthropoda was the second most abundant phylum on the uThukela shelf. Although dominated by Amphipoda in the KwaZulu-Natal (KZN) Bight, Decapoda dominated the Arthropoda in the uThukela region (Chapter 3). Decapods comprise a highly diverse group, including crabs, shrimps, and lobsters that have various feeding strategies and occur in all aquatic environments at all depths (Brusca and Brusca 2003). Previously, the larger uThukela shelf decapods were assessed during demersal fisheries assessments and reviews of the former uThukela Banks commercial trawl fishery that mostly targeted prawns (Demetriades and Forbes 1993, Fennessy et al. 1994, Fennessy and Groeneveld 1997). These studies provided insight into the range of uThukela shelf decapods through the analysis of bycatch, however, the results were limited to the larger-sized epifauna due to the use of a demersal trawl net. The ACEP Natal Bight study better analysed the infauna component and identified a large abundance of pagurids (hermit crabs) living in gastropod shells that were mostly on the inner uThukela shelf (Untiedt and MacKay 2016).

5.2.3. *Mollusca*

Gastropoda and Bivalvia are the main benthic Mollusca. Other minor classes include Scaphopoda, Caudofoveata, Monoplacophora, Polyplacophora, and Solenogastres that are less speciose but exclusively marine (Sigwart and Sumner-Rooney 2016). Most molluscs contain a shell (which forms part of the sediment when broken), with the calcified part of this shell consisting of aragonite or calcite, or a combination of these (Kennedy et al. 1969). Consequently, this group is sensitive to changing environmental conditions such as increasing temperature and acidification (Byrne and Przeslawski 2013). Early life stages are particularly sensitive to these changes, resultantly reducing growth and the chances of survival of individuals and the population (Byrne and Przeslawski 2013). Previous studies (MacKay et al. 2016, Hunter n.d.), as well as this study, noted a large amount of shell material in the uThukela shelf sediments. This observation indicated that the historic uThukela shelf macrobenthos potentially supported large abundances of this phylum and was possibly a Mollusca-dominated community with many different species of Gastropoda and Bivalvia (MacKay et al. 2016).

5.2.4. *Large benthic Foraminifera (LBFs)*

Foraminifera are not macroinvertebrates but are free-living protozoans that are widely distributed in the marine environment (Sen Gupta and Machain-Castillo 1993, Murray 2006). Benthic forms constitute a large portion of the benthic community (as also seen in this study), but despite this are usually not considered during biological studies investigating modern systems (Sen Gupta and Machain-Castillo 1993, Murray 2006). However, they are integral in the benthic food web as they consume a large amount of small epiphytes and bacteria and provide food for higher trophic levels, including macrofauna (Lipps and Valentine 1970). Foraminifera are also ubiquitous in all marine environments and are good at detecting ecosystem variations, so are usually considered useful indicators of habitat quality (Reymond et al. 2012). Many are opportunistic, surviving in small numbers during non-optimal conditions and rapidly increasing abundances when conditions are favourable (Murray 2001), and many larger forms can survive even during oligotrophic conditions (Murray 2006). Most have preservable (mostly calcareous) tests, meaning that once dead these organisms contribute to the fossil record and can provide details of past communities (Gustiantini et al. 2007). They can subsequently be used as proxies to paleoenvironmental conditions and can indicate sea level and climate fluctuations, signifying how a system has changed over time (Brusca and Brusca 2003, Murray 2006, Gustiantini et al. 2007). These Foraminifera tests, along with Mollusca shells, also greatly contribute to the bioclastic sediments of the uThukela shelf.

Carbonate sediments generally consist of bioclasts of Mollusca, Echinodermata, Bryozoa, Cirripedia, Foraminifera, and red calcareous algae in cool, temperate, and tropical regions (Murray 2006). These biogenic structures provide habitat complexity that usually increases benthic community diversity and related ecological processes (Passarelli et al. 2012) by modifying the structure and mixing properties of the benthic boundary layer (Moulin et al. 2007).

5.2.5. Aims, objectives, and hypotheses

This chapter further explored the structure and functioning of the characteristic taxonomic groups (Polychaeta, Decapoda, Mollusca, and LBFs) found on the uThukela shelf and determined the potential influence of shelf position (shelf zone, distance from shore, and distance from the uThukela Estuary mouth) and environmental parameters on the distribution of these communities. Through this, taxa were identified as potential surrogates and biodiversity indicators that may be targeted for future monitoring.

Objectives:

- 5.1. To describe the uThukela shelf characteristic Polychaeta, Decapoda, Mollusca, and LBF communities.
- 5.2. To determine whether the distributions of these characteristic groups are influenced by shelf position.
- 5.3. To relate measured environmental parameters to community distributions to investigate potential abiotic drivers of these groups.
- 5.4. To determine whether the Polychaeta community is an appropriate surrogate for the entire macrobenthos by comparing the distribution patterns of both groups.
- 5.5. To reveal specific taxa that can be targeted for research into Marine Protected Area (MPA) indicators, ecosystem health, function etc., and the conditions in which they need to thrive.

Hypotheses:

- H₀₁: Polychaeta, Decapoda, Mollusca, and LBF communities do not change with shelf position.
- H₀₂: Measured environmental parameters did not influence Polychaeta, Decapoda, Mollusca, and LBF communities.

H₀₃: Distribution patterns are different for the polychaete community and the entire macrobenthic community.

5.3. Materials and methods

The study site description and map, general sampling techniques, and general statistics are presented in Chapter 2 of this dissertation. Sampling was conducted during the dry (winter) season on the uThukela inner-shelf (0 – 50 m) in 2008 and the inner, mid (50 – 80 m), and outer-shelf (80 – 130 m) in 2010 (Figure 5.1).

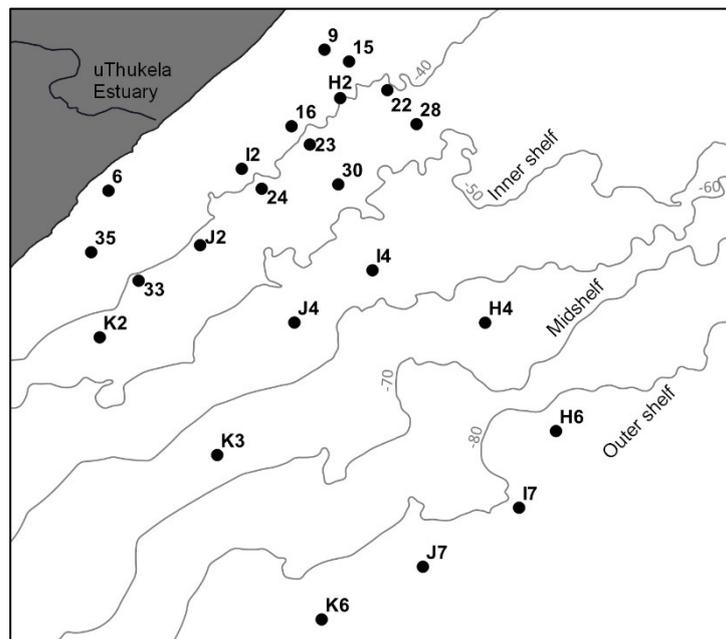


Figure 5.1. Study site depicting sampled stations on the inner (0 – 50 m), mid (50 – 80 m), and outer (80 – 130 m) uThukela shelf. Refer also to Figure 2.1 for regional context.

5.3.1. Data analyses

5.3.1.1. Biotic data

The characteristic taxonomic groups were discerned from the assemblages studied in Chapter 3 (using taxonomy) and Chapter 4 (using BTA). The taxa in these groups (Polychaeta, Decapoda, and Mollusca), as well as the LBFs, were identified to the lowest taxonomic level possible (Chapter 2), and each group was analysed as a separate matrix. During this study, the main Decapoda taxon *Callichirus gilchristi* was reclassified as *Balsscallichirus gilchristi* and moved from Callianassidae to Callichiridae. For analyses, these two families remained grouped

as Callianassidae as these sandprawns occupy a similar niche, and this allowed the comparison of different sandprawn taxa distributions across the shelf.

Sediment cores are usually used to sample Foraminifera (as they are a part of the meiofaunal component) but were not taken during this study as the focus was on the larger macroinvertebrates. Due to this, this study did not investigate the entire Foraminifera community but considered only the LBFs that were retained on the 1 mm sieve used to capture macrofauna. Consideration was also given to the empty Foraminifera tests of this size class to analyse if there was a difference between the distribution patterns in the “live” and dead communities.

During polychaete data analyses, a single replicate sample 9B was an outlier as it contained a considerably different polychaete community to the other replicate grabs. Although being included for the basic observation of taxa and individuals, it was removed for subsequent statistical analyses. One replicate remained as only two grabs were retrieved for station 9, but due to interesting results, this station was not excluded from the study, and replicate 9A was included (along with other stations) in further statistical analyses. The mean number of taxa (S) and abundances (N) of each group (separate groups signified by subscripts: e.g. N_p), as well as Shannon-Wiener diversity index (H'), Margalef's richness index (d), and Pielou's evenness index (J') for polychaete data, were calculated for each shelf zone. One-way ANOVA (F) testing (or Kruskal-Wallis H testing for non-normal and Welch F for inequality of variances) was used to identify any significant differences in these community indices. Generalised linear models (GLMs) (G), using Poisson distribution and a log link function, were carried out in PAST v3.25 (as in Chapter 4) for all focal groups to determine the relationships between the community indices and distances from the shore and the uThukela Estuary mouth. The most abundant taxa for each shelf zone were then identified for each biotic group.

In-depth multivariate analyses were only carried out for Polychaeta as the heterogenous nature and distributional patchiness of the other groups (e.g. abundances concentrated at certain sites and absent from many others) were not conducive to these analyses. Polychaete abundance data for 67 uThukela shelf samples (excluding sample 9B) were root-root transformed and the Bray-Curtis (B-C) similarity calculated. This matrix was subjected to group-average cluster analysis, and SIMPROF routines defined significant groups (Chapter 2). The polychaetes responsible for these sample groupings were identified through SIMPER. The RELATE

procedure was used to test the relationship between the polychaete and macrofauna similarity matrices (assemblages) (Chapter 2).

5.3.1.2. Link between environmental variables and biotic distributions

Measured environmental variables were correlated with the abundance of the main Polychaeta, Decapoda, Mollusca, and LBF families in PAST v3.25 to determine the potential univariate relationships between abiotic parameters and biotic groups. The most correlated environmental variables were identified using linear correlation (r) and used to plot group abundances/densities and environmental parameter distributions in Quantum Geographic Information System (QGIS) 3.14.16. When depth was the most highly correlated environmental variable, the second most highly correlated variable was used as sample depth is already indicated by shelf position. The environmental variables were plotted as heatmaps, where higher measurements were indicated by darker colours. Densities were overlaid as graduated markers, with the larger bubbles indicating higher densities.

The suite of measured environmental variables (log-transformed where needed to reduce right-skewness and then normalised) best associated with community distribution of each biotic group was determined by the BIO-ENV algorithm through the BEST procedure (Chapter 2). While no further analyses were conducted for Decapoda, Mollusca, and LBFs, the environmental variables most correlated to Polychaeta community distribution were used with the Polychaeta B-C resemblance matrix in a constrained linkage tree (LINKTREE) (Clarke and Gorley 2015). The program LINKTREE constructs a dendrogram where successive binary splits of biotic community samples are determined by thresholds on specific environmental variables that maximise the between-group variance (maximising the ANOSIM R-statistic) (Clarke and Gorley 2015). The environmental variables and accompanying thresholds essentially explain the splits and subsequent community branches. The R-statistic ranges from zero to one, with higher values indicating better rank separation where between-group dissimilarities are greater than within-group dissimilarities (Clarke and Gorley 2015). The B% was chosen for the y-axis scale as this uses the average original rank dissimilarities and does not re-rank at each division, allowing comparison between values across different parts of the tree (Clarke and Gorley 2015).

5.4. Results

5.4.1. Polychaeta

A mean of 256 polychaetes.m⁻² were collected during this study. Of the 180 polychaete taxa encountered, 91% were identified to family level or lower, representing 42 families and 123 genera. There has been a recent amalgamation of Echiura (spoon worms) into Polychaeta, but these contributed very little to taxa abundance or numbers. The analysis of the other subclasses resulted in sedentary polychaetes being dominant (N_p : 64%, S_p : 58%) over errant forms (N_p : 36%, S_p : 42%).

5.4.1.1. Dominance

The most abundant families were the sedentary Spionidae (N_p : 17%), Cirratulidae (N_p : 14%), and Capitellidae (N_p : 6%), and the errant Nephtyidae (N_p : 13%) and Onuphidae (N_p : 6%) (Figure 5.2a). The five most abundant taxa that characterised the uThukela shelf community and its functioning were *Cirratulus concinnus* (N_p : 11%), *Aglaophamus dibranchis* (N_p : 10%), *Aonides oxycephala* (N_p : 9%), *Onuphis eremita* (N_p : 4%), and *Linopherus microcephala* (N_p : 3%).

Spionidae was also the most speciose family (S_p : 12%), followed by Terebellidae (S_p : 6%), Onuphidae (S_p : 5%), Polynoidae (S_p : 5%), and Maldanidae (S_p : 4%) (Figure 5.2b). Rare taxa, restricted to one or two samples, made up 47% (33% uniques and 13% duplicates) of the polychaete population. Despite *Owenia fusiformis* being absent on the mid-shelf and *Onuphis eremita* being absent on the outer-shelf, these polychaetes were widespread (in 44% and 38% of samples respectively), along with *A. dibranchis* (59% of samples).

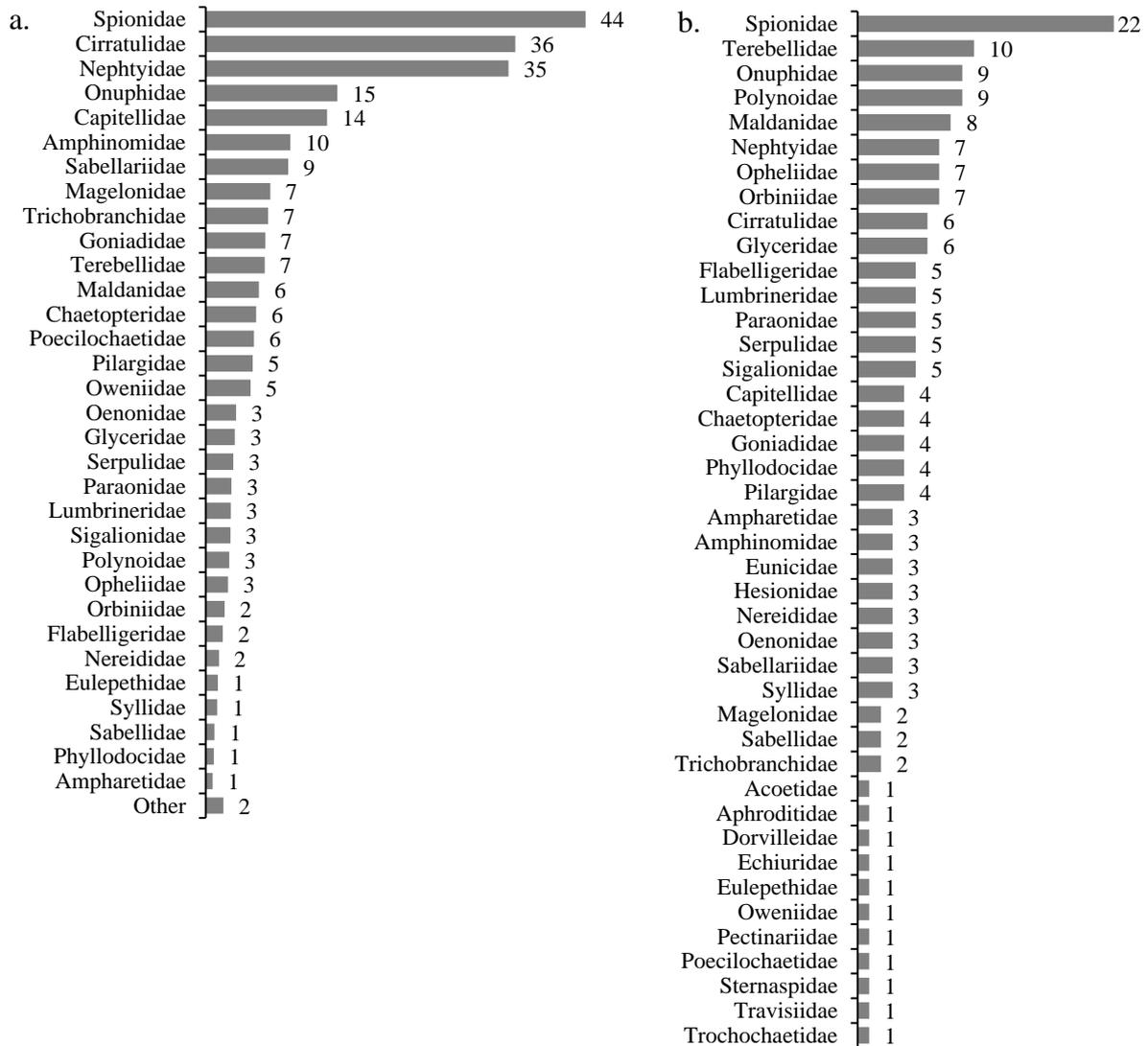


Figure 5.2. (a) Mean abundance (N_p : ind.m⁻²) and (b) number of taxa (S_p) of polychaete families on the uThukela shelf.

5.4.1.2. Sample 9B

Sample 9B was considerably different from other sample replicates and removed before further statistical analyses. This sample contained 960 polychaetes.m⁻² from 26 taxa, with 18 of these unique to this sample: *Sabellaria intoshi*, *Marphysa* sp.1, *Leocrates claparedii*, *Websterinereis punctata*, *Harmothoe* cf. *gilchristi*, *Lepidonotus tenuisetosus*, *Haplosyllis spongicola*, *Lamellisyllis comans*, *Pseudopotamilla reniformis*, *Ficopomatus* sp.1, *Hydroides* sp.1, *Hydroides* cf. *ralumiana*, *Serpulinae* sp.1, *Maldanella capensis*, *Phyllochaetopterus socialis*, *Ampharete octocirrata*, *Daylithos parmatus*, and *Thelepus* sp.1.

5.4.1.3. Spatial differences

Polychaete abundances correlated to the distance from shore ($G = 117.930$, $p < 0.001$) and the uThukela Estuary mouth ($G = 38.000$, $p < 0.001$), but the polychaete abundances were not significantly different ($F = 0.601$, $df = 22$, $p = 0.558$) in the different shelf zones (inner-shelf $\bar{x} N_p$: 240 ± 208 poly.m⁻², mid-shelf $\bar{x} N_p$: 243 ± 167 poly.m⁻², outer-shelf $\bar{x} N_p$: 313 ± 174 poly.m⁻²). However, polychaete composition differed significantly between these shelf zones (Pseudo- $F = 0.590$, $p < 0.001$; all pairwise-tests: $p < 0.001$).

In 2008 there was a dominance of the errant family Nephtyidae on the inner-shelf, but in 2010 there was a shift in dominance to the sedentary family Spionidae. While *C. concinnus* was the most abundant polychaete on the inner-shelf in 2010 (N_p : 95 ind.m⁻²), *A. dibranchis* had the highest abundances in 2008 (N_p : 50 ind.m⁻²). Overall, Spionidae dominated the inner-shelf, mostly represented by *A. oxycephala* (N_p : 38 ind.m⁻²), the third most abundant polychaete taxon in this shelf zone (Table 5.1). Spionids were abundant and among the top five polychaete families in all shelf zones but did not dominate communities on the mid-shelf and outer-shelf. Onuphidae were the dominant family on the mid-shelf, mostly represented by *Diopatra papillosa* (the second most abundant polychaete on the mid-shelf; N_p : 16 ind.m⁻²) and *O. eremita* (the fourth most abundant polychaete on the mid-shelf; N_p : 10 ind.m⁻²), despite *Poecilochaetus serpens* (N_p : 21 ind.m⁻²) being the dominant polychaete taxon for this zone (Table 5.1). Onuphids were also abundant on the inner-shelf but were greatly reduced on the outer-shelf. The outer-shelf contained mostly Amphinomidae, represented by *L. microcephala* (N_p : 47 ind.m⁻²), the typifying taxon of this shelf zone (Table 5.1).

The number of polychaete taxa also responded to distance gradients from the shore ($G = 27.398$, $p < 0.001$) and the uThukela Estuary mouth ($G = 25.742$, $p < 0.001$), but did not differ significantly between shelf zones ($H = 3.659$, $df = 22$, $p = 0.160$), ranging between 2 – 45 taxa (overall S_p : 98 taxa) on the inner-shelf, 4 – 53 (overall S_p : 90 taxa) on the mid-shelf, and 23 – 38 taxa (overall S_p : 64 taxa) on the outer-shelf. The inner-shelf was the least diverse ($\bar{x} H'_p$: 1.63 ± 0.85), had the lowest mean richness ($\bar{x} d_p$: 2.92 ± 2.31), and the lowest mean evenness ($\bar{x} J'_p$: 0.66 ± 0.17) of the shelf zones. The mid and outer-shelf were similarly diverse ($\bar{x} H'_p$: 2.66 ± 1.16 and 2.64 ± 0.24 respectively), but the mid-shelf was slightly richer ($\bar{x} d_p$: 6.01 ± 3.49) and had a higher mean evenness ($\bar{x} J'_p$: 0.81 ± 0.09) than the outer-shelf ($\bar{x} d_p$: 5.01 ± 0.87 , $\bar{x} J'_p$: 0.79 ± 0.09).

Table 5.1. The five most abundant polychaetes for each uThukela shelf zone.

Taxon	Family	Abundance (ind.m ⁻²)
Inner-shelf (43 samples)		
<i>Cirratulus concinnus</i>	Cirratulidae	45
<i>Aglaophamus dibranchis</i>	Nephtyidae	39
<i>Aonides oxycephala</i>	Spionidae	38
<i>Onuphis eremita</i>	Onuphidae	15
<i>Sabellaria</i> sp.1	Sabellariidae	8
Mid-shelf (12 samples)		
<i>Poecilochaetus serpens</i>	Poecilochaetidae	21
<i>Diopatra papillosa</i>	Onuphidae	16
<i>Spiochaetopterus costarum</i>	Chaetopteridae	12
<i>Onuphis eremita</i>	Onuphidae	10
<i>Pherusa</i> sp.1	Flabelligeridae	9
Outer-shelf (12 samples)		
<i>Linopherus microcephala</i>	Amphinomidae	47
<i>Terebellides stroemii</i>	Trichobranchidae	42
<i>Notomastus latericeus</i>	Capitellidae	30
<i>Kirkegaardia dorsobranchialis</i>	Cirratulidae	16
<i>Euclymeninae</i> sp.1	Maldanidae	16

5.4.1.4. Community patterns

Classification of the 67 uThukela shelf samples distinguished four significant polychaete assemblages at 18% similarity, showing high variability in polychaete communities (Figure 5.3). The RELATE procedure revealed a highly significant correlation ($\rho = 0.841$) between the similarity matrices constructed for the polychaete abundances and the macrofauna abundances (in Chapter 3) and is attributed to the overriding dominance of polychaetes on the uThukela shelf. There were only slight differences in macrofauna assemblages and polychaete assemblages: station H4 formed its own assemblage for macrofauna but was included in assemblage II for polychaetes, and although the entire station J4 was included in assemblage III for macrofauna, one of the replicates belonged to assemblage II for polychaetes (Figure 5.3 and Figure 3.13 in Chapter 3).

Assemblage I

Assemblage I contained station 6, the most shallow station characterised by mostly fine sand (Figure 5.3) and low total organic carbon (TOC). This assemblage had an average similarity of 43% and was represented entirely by the detritivores *Aphelochaeta filibranchia*, *O. fusiformis*, and *Armandia leptocirris* (Table 5.2).

Assemblage II

Assemblage II was the largest cluster, containing 12 of the inner-shelf stations, the mid-shelf station H4, as well as one sample from station J4 (replicate 3). These samples generally consisted of fine-grained sediments (Figure 5.3). The assemblage contained an abundance of Spionidae and high quantities (the highest in all assemblages) of Nephtyidae and Cirratulidae. It had an average similarity of 32% and was characterised by the carnivorous *A. dibranchis* and the facultative detritivores *O. fusiformis*, *C. concinnus*, and *Magelona capensis* (Table 5.2). This assemblage had the highest percentage of carnivores, with the abundances of surface deposit feeders and predators being almost equivalent. It contained the most mobile polychaetes (many with a medium level of mobility), with the highest abundance of those with swimming ability.

Assemblage III

Assemblage III was formed by the remaining mid-shelf and inner-shelf samples and typically had heterogenous medium-coarse sediments with low TOC (Figure 5.3). This assemblage also contained mostly Spionidae, but Onuphidae, Terebellidae, and Goniadidae were also abundant. The samples had an average similarity of 32% and were primarily characterised by the facultative omnivore *O. eremita*, carnivorous *Lumbineris aberrans*, and the facultative detritivore *Prionospio nirripa* (Table 5.2). Most polychaetes in this assemblage produce larvae that have planktotrophic and lecithotrophic development.

Assemblage IV

The outer-shelf (i.e. deepest stations) combined to form polychaete assemblage IV. These samples were generally poorly-sorted mud with high TOC concentrations and had an average similarity of 35% (Figure 5.3). This assemblage contained an abundance of Amphinomidae, Trichobranchidae, and Capitellidae, and was represented by the subsurface detritus-feeding *Notomastus latericeus*, the facultative carnivore *L. microcephala*, and the facultative detritivore *Spiophanes duplex* (Table 5.2). It contained the least abundance of predators and most subsurface deposit feeders of all the communities but was still dominated by surface deposit feeders. These polychaetes had mostly planktotrophic larval development, but many had benthic or direct development. Consequently, this assemblage contained the most brooders of all the polychaete assemblages.

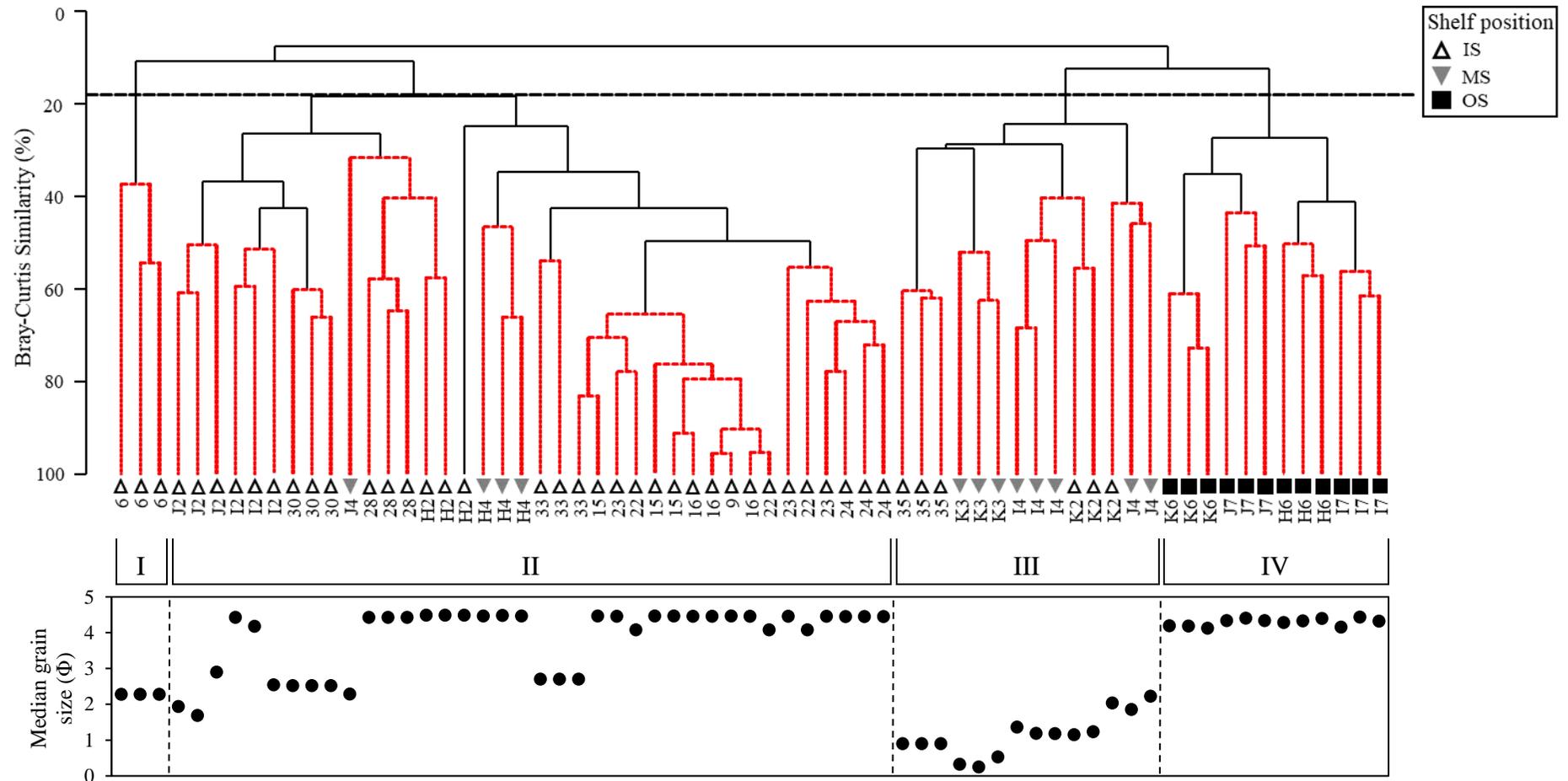


Figure 5.3. Hierarchical clustering (with group-average linkage) based on Bray-Curtis similarities of 67 root-root transformed uThukela shelf polychaete samples. Samples within assemblages (I – IV) defined at 18% similarity (indicated by horizontal dotted line) are presented with their corresponding median grain sizes (Φ) as an indication of bottom habitat type. SIMPROF results representing significant clusters ($p < 0.05$) are indicated by solid black lines.

Table 5.2. The top five polychaetes (where applicable) identified by SIMPER as contributing to the within-group similarity of assemblages formed during clustering of root-root transformed polychaete abundance data.

Taxon	Average Abundance	Average Similarity	Sim/SD	Contribution (%)
Group I: Average Similarity = 42.90%				
<i>Aphelochaeta filibranchia</i>	1.12	18.11	0.58	42.21
<i>Owenia fusiformis</i>	0.94	12.40	0.58	28.89
<i>Armandia leptocirris</i>	0.94	12.40	0.58	28.89
Group II: Average Similarity = 31.81%				
<i>Aglaophamus dibranchis</i>	2.24	17.08	1.16	53.70
<i>Owenia fusiformis</i>	1.05	5.77	0.61	18.14
<i>Cirratulus concinnus</i>	1.19	2.05	0.45	6.43
<i>Magelona capensis</i>	0.80	1.20	0.46	3.79
<i>Onuphis eremita</i>	0.82	0.94	0.36	2.96
Group III: Average Similarity = 31.57%				
<i>Onuphis eremita</i>	1.80	3.36	1.43	10.64
<i>Lumbrineris aberrans</i>	1.53	2.77	1.52	8.78
<i>Prionospio nirripa</i>	1.53	2.45	0.96	7.76
<i>Notomastus aberans</i>	1.41	1.95	0.95	6.19
<i>Nephtys capensis</i>	1.34	1.90	0.94	6.01
Group IV: Average Similarity = 35.33%				
<i>Notomastus latericeus</i>	1.92	4.36	1.27	12.34
<i>Linopherus microcephala</i>	1.84	3.50	1.00	9.91
<i>Spiophanes duplex</i>	1.34	2.63	1.06	7.44
<i>Sithenelais</i> sp.1	1.22	2.28	0.64	6.45
<i>Euclymeninae</i> sp.1	1.38	2.18	0.82	6.18

5.4.1.5. Associations between environmental variables and Polychaeta distributions

When considering the entire uThukela shelf polychaete population, the relationship between the biotic and environmental matrices was average (RELATE: $\rho = 0.527$). Salinity (PSU), depth (m), dissolved oxygen (DO) (mg.L^{-1}), %coarse sand, and %mud ($\rho = 0.673$) were mostly correlated to polychaete distribution, with DO as the most significant of these ($\rho = 0.593$) (Table 5.3).

Table 5.3. Correlations between environmental variables and the uThukela shelf polychaete distribution patterns (calculated through the BIO-ENV procedure).

No. of variables	ρ	Variables
Best single variable		
1	0.593	DO
Best combination of variables		
5	0.673	Salinity, depth, DO, %cs, %mud
5	0.663	Salinity, depth, DO, %ms, median (phi)
5	0.662	Salinity, depth, DO, %mud, median (phi)
5	0.662	Salinity, depth, DO, %cs, %ms

The six most abundant polychaete families (each contributing > 4% to polychaete abundance) were correlated with the measured environmental variables. Only the environmental variables with the highest correlations are presented as results. Spionidae abundances mostly correlated to medium sand (%ms) ($r = 0.472$, $p = 0.023$) and Onuphidae abundances greatly increased with the percentage of medium sand ($r = 0.696$, $p < 0.001$). The highest percentages of medium sand (and thus Onuphidae abundances) were observed on the mid-shelf and at some of the inner-shelf stations (Figure 5.4a-b). Cirratulidae were mostly related to sediment TOC ($r = 0.411$, $p = 0.051$) and very fine sand ($r = 0.409$, $p = 0.053$) (Figure 5.4c). Nephtyidae densities increased in the more saline regions of the inner-shelf ($r = 0.641$, $p < 0.001$) (Figure 5.4d) and Capitellidae showed the opposite pattern, with higher densities in deeper ($r = 0.623$, $p = 0.001$), less saline ($r = -0.671$, $p < 0.001$), and less oxygenated stations ($r = -0.756$, $p < 0.001$) on the outer-shelf (Figure 5.4e). Amphinomid densities also typically increased with depth ($r = 0.448$, $p = 0.032$) and decreased with higher concentrations of DO ($r = -0.575$, $p = 0.004$) (Figure 5.4f).

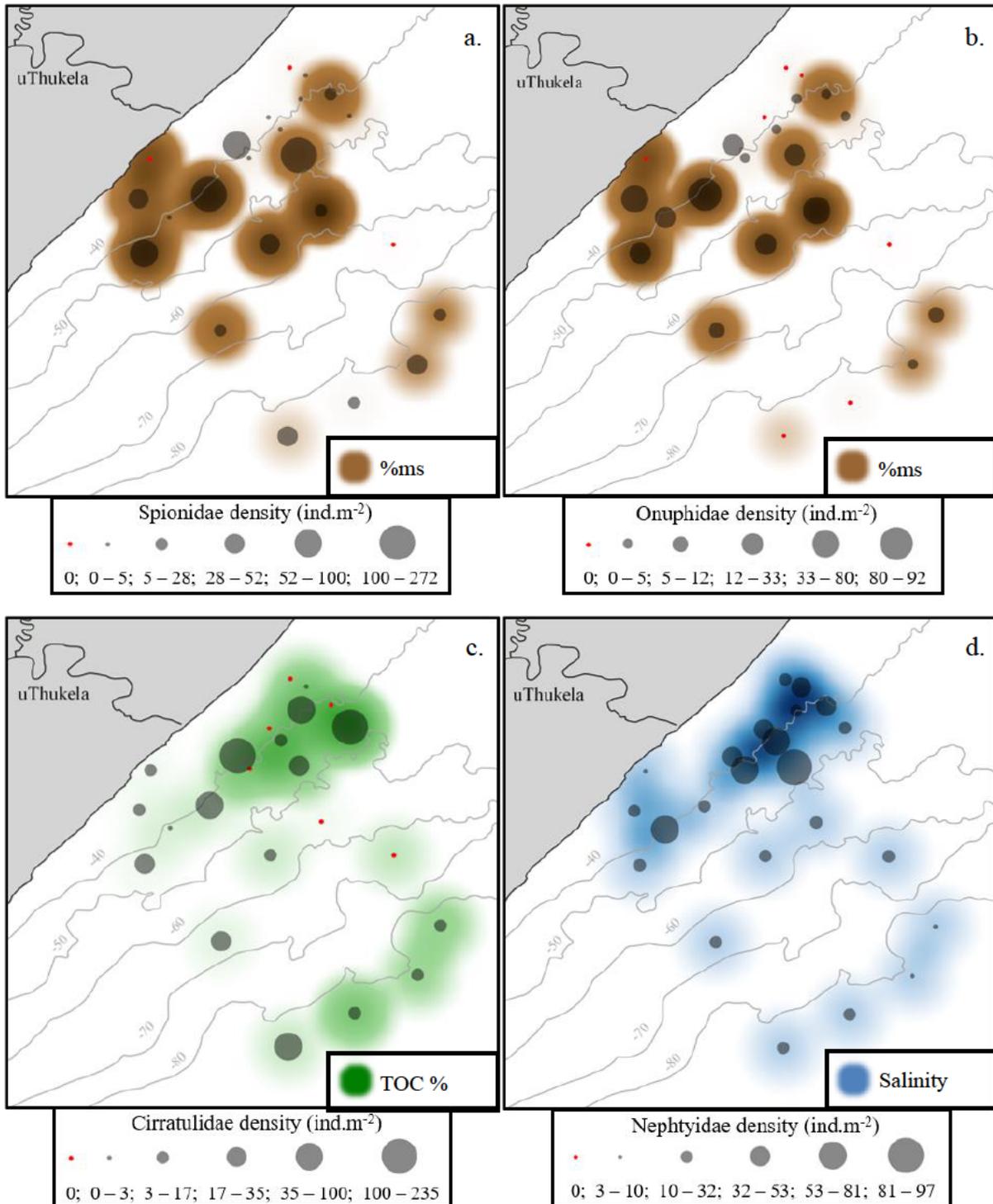


Figure 5.4. The density/abundance (N : ind.m⁻²) of major polychaete families on the uThukela shelf with their most highly correlated environmental variables (darker colours indicate higher measurements). (a) Spionidae and (b) Onuphidae correlated with %ms (maximum 49%); (c) Cirratulidae with sediment TOC (maximum 10%); (d) Nephtyidae with bottom salinity (maximum 36.41 PSU); and (e) Capitellidae and (f) Amphinomididae with bottom DO (maximum 7.54 mg.L⁻¹).

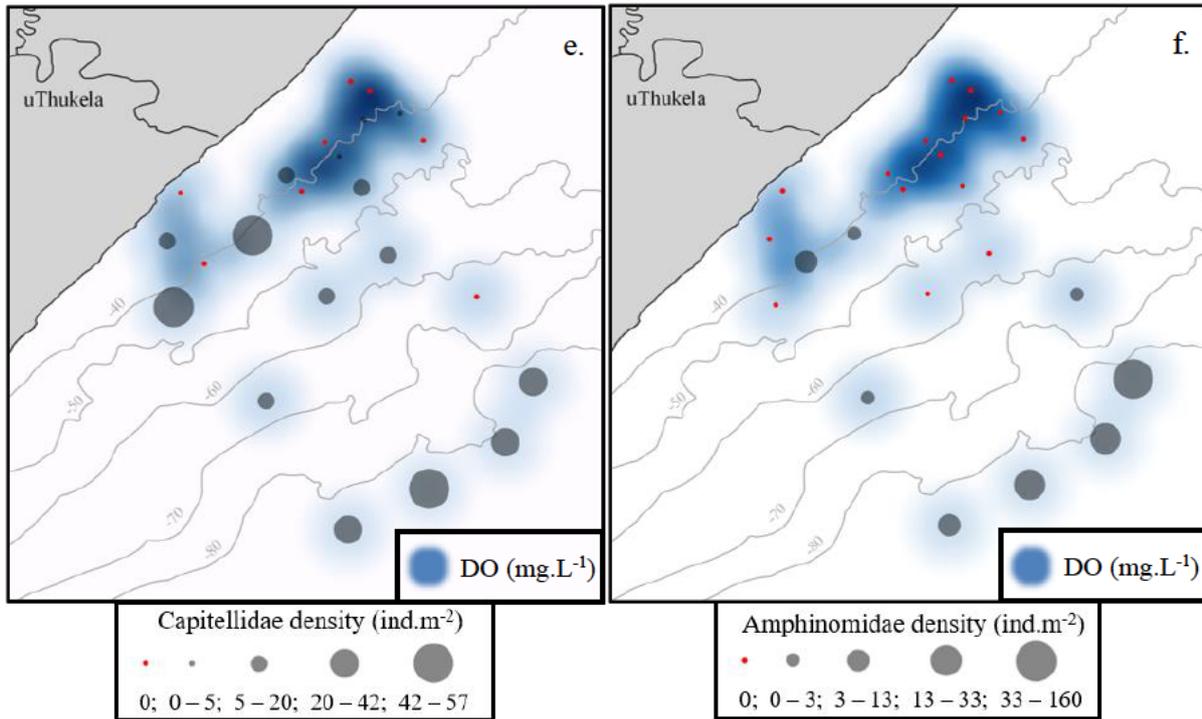


Figure 5.4 (continued). (Caption on previous page).

The combination of the five overall most correlated variables (salinity, depth, DO, coarse sand, and mud) was used to construct a linkage tree for the 67 uThukela shelf polychaete samples (Figure 5.5). Even though DO was selected as the best variable explaining polychaete distribution, mud content resulted in the most divisions of community samples (involved 21 times) in the LINKTREE analysis (Table 5.4). The first split (A) was explained by salinity (Table 5.4), separating the less saline (< 35.455 PSU) outer-shelf, most mid-shelf (stations K3, J4, I4), and some inner-shelf samples (stations K2 and J2), from the rest of the more saline, mostly inner-shelf samples (Figure 5.5). Although salinity was the primary descriptive variable, it was the least explanatory of the entire tree, being involved in only 11 of the divisions (Table 5.4). The second division (B: $R = 0.81$) suggested that the outer-shelf community (assemblage IV in Figure 5.3) is best defined by taxa associated with the least saline, less oxygenated, deep, muddy conditions (Table 5.4).

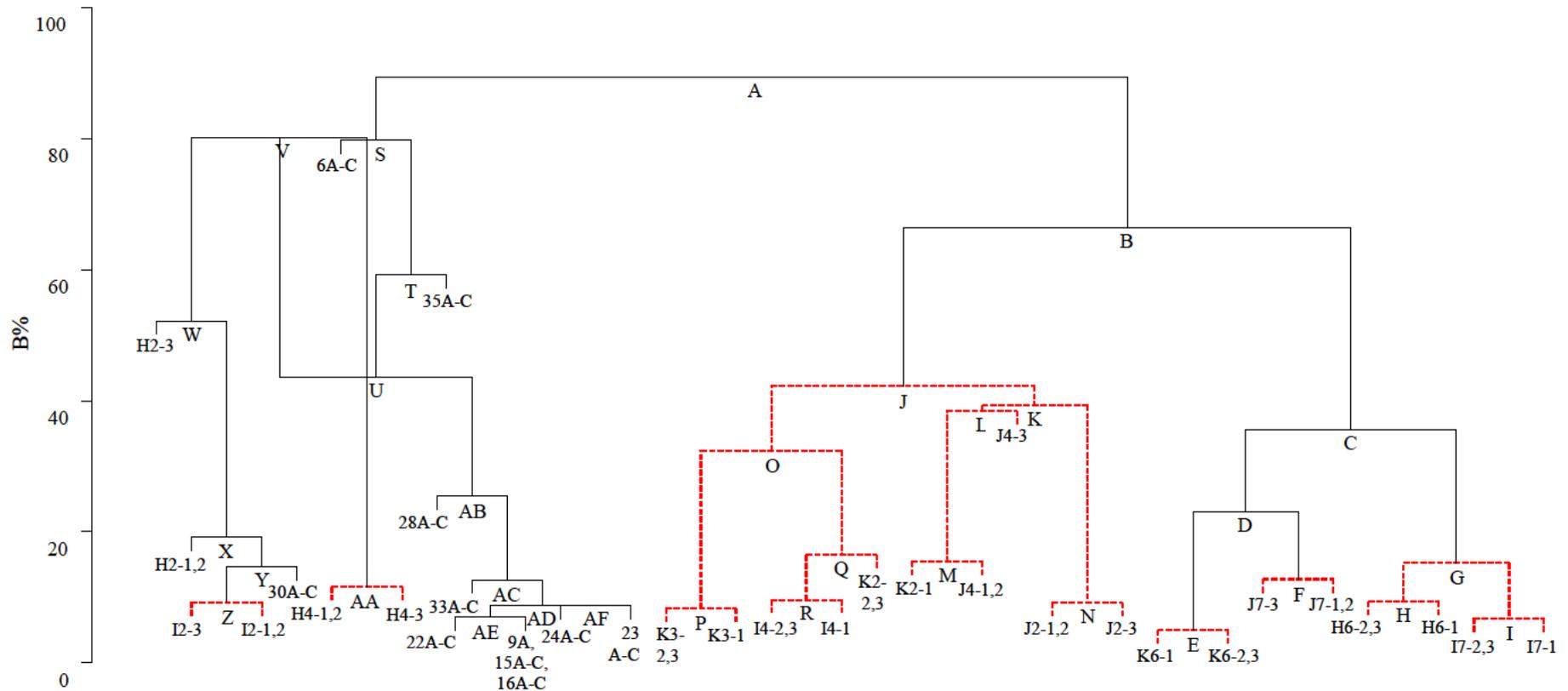


Figure 5.5. LINKTREE, constrained by the five variables best-describing polychaete patterns, showing the binary clustering of uThukela shelf replicate samples based on polychaete composition and indicating the environmental splits in sample groupings. SIMPROF results representing significant clusters ($p < 0.05$) are indicated by solid black lines. For each division A – AF, the optimal ANOSIM R-value, the dissimilarity %, and the range of environmental values explaining the split are given in the table below (Table 5.4).

Table 5.4. The optimal ANOSIM R-value, the dissimilarity %, and the range of environmental values explaining the splits A – AF in the LINKTREE above (Figure 5.5). For the threshold inequalities, the first value defines the group to the left and the second value (in brackets) explains the group on the right.

Split	R	B%	Variable and Threshold
A	0.69	89	Salinity > 35.456 (< 35.455)
B	0.81	66	DO > 6.26 (< 5.47) or depth < 69.01 (> 86.99) or %mud < 47.71 (> 57.48) or salinity > 35.426 (< 35.425)
C	0.72	36	Depth > 109.99 (< 107.01) or DO > 5.31 (< 5.27) or salinity < 35.36 (> 35.37)
D	0.85	23	%cs > 2.72 (< 0.15) or depth > 125.99 (< 110.01) or %mud < 62.23 (> 75.98) or DO > 5.45 (< 5.33) or salinity < 35.33 (> 35.34)
E	1.00	5	%cs < 2.74 (> 4.04) or %mud > 62.21 (< 61.94)
F	0.00	13	%cs < 0.09 (> 0.13) or %mud < 76.00 (> 76.14)
G	1.00	15	Depth < 87.01 (> 106.99) or salinity < 35.39 (> 35.41) or DO < 5.22 (> 5.25)
H	1.00	9	%cs < 3.02 (> 4.00) or %mud > 75.26 (< 70.17)
I	1.00	7	%mud > 74.39 (< 59.72) or %cs < 4.32 (> 6.68)
J	0.54	42	%cs > 23.78 (< 11.72)
K	0.65	39	DO < 6.40 (> 6.43)
L	1.00	38	%mud < 7.17 (> 17.17) or %cs < 4.07 (> 5.04)
M	1.00	15	Depth < 45.01 (> 55.99) or DO > 6.38 (< 6.34) or %mud < 1.95 (> 2.93)
N	1.00	9	%mud < 3.36 (> 47.69)
O	0.91	32	Depth > 68.99 (< 51.01) or DO < 6.28 (> 6.38) or %mud > 6.29 (< 2.25) or salinity < 35.435 (> 35.436)
P	1.00	8	%mud > 9.24 (< 6.31) or %cs < 27.44 (> 29.18)
Q	1.00	16	Depth > 50.99 (< 45.01) or DO > 6.45 (< 6.40) or salinity < 35.445 (> 35.446)
R	1.00	10	%cs < 36.82 (> 39.14) or %mud > 1.20 (< 0.71)
S	0.63	80	Depth < 23.95 (> 30.99) or DO > 7.53 (< 7.41) or %mud < 1.74 (> 2.49)
T	0.61	59	%cs < 5.75 (> 59.03) or %mud > 30.29 (< 2.51) or DO < 7.31 (> 7.39)
U	0.64	44	DO < 7.185 (> 7.186)
V	0.89	80	Depth < 47.56 (> 61.99) or DO > 6.62 (< 6.46)
W	1.00	52	%mud > 99.08 (< 98.77)
X	0.61	19	%mud > 98.55 (< 87.78)
Y	0.89	15	Salinity < 35.47 (> 36.35) or %cs < 0.41 (> 3.42) or DO < 6.64 (> 7.17) or depth < 31.01 (> 47.54) or %mud > 39.81 (< 34.53)
Z	1.00	9	%mud < 39.83 (> 61.14)
AA	1.00	12	%cs < 0.15 (> 0.17)
AB	0.77	25	DO < 7.195 (> 7.20)
AC	0.48	13	%mud < 30.31 (> 54.73) or salinity < 36.17 (> 36.32) or depth > 47.87 (< 41.87) or DO > 7.296 (< 7.295)
AD	0.46	9	Depth < 41.25 (> 41.33)
AE	0.35	7	%cs > 5.73 (< 0.33) or %mud < 54.75 (> 92.92) or depth > 41.23 (< 36.30) or DO < 7.24 (> 7.27) or salinity < 36.335 (> 36.34)
AF	0.41	9	%cs > 0.54 (< 0.33) or DO < 7.22 (> 7.27) or %mud < 91.60 (> 93.29) or salinity < 36.375 (> 36.38) or depth > 41.85 (< 41.35)

5.4.2. Decapoda

Arthropoda, the second most abundant phylum, was dominated by Decapoda (N_a : 47%; Figure 5.6a), with 58 decapods.m⁻² belonging to 41 taxa recorded on the uThukela shelf. Rare decapods, restricted to one or two samples, made up 61% (51% uniques and 10% duplicates) of the infauna decapod population, while the most widespread taxon was *Xenophthalmodes* cf. *moebii* (present in 47% of samples). This crab was abundant and widespread on the inner-shelf, with only two samples from the other shelf zones containing this taxon, and in very low abundances. Callianassidae (including Callichiridae) was the most abundant family, mainly represented by *Balsscallichirus gilchristi* (the most abundant decapod; N_d : 53%), followed by the hermit crab family Diogenidae that was dominated by *Diogenes costatus* (the second most abundant decapod; N_d : 10%) (Figure 5.6b).

5.4.2.1. Spatial differences

The number of decapod taxa corresponded with distance from the shore ($G = 5.431$, $p = 0.020$) and the uThukela Estuary mouth ($G = 5.568$, $p = 0.018$). The highest number of taxa occurred on the inner-shelf (S_d : 34 taxa) when compared to the mid (S_d : 10 taxa) and outer-shelf (S_d : 11 taxa), but these differences between shelf zones were not significant ($F = 2.065$ df = 22, $p = 0.153$). Decapod abundances also reflected distance from the shore ($G = 249.630$, $p < 0.001$) and the uThukela Estuary mouth ($G = 211.470$, $p < 0.001$), decreasing from the inner to the outer-shelf (inner-shelf \bar{x} N_d : 71 ± 136 deca.m⁻², mid-shelf \bar{x} N_d : 38 ± 55 deca.m⁻², outer-shelf \bar{x} N_d : 19 ± 7 deca.m⁻²), but with no significant differences between shelf zones ($F = 0.731$ df = 22, $p = 0.494$).

The facultative deposit-feeding, burrow-dwelling Callianassidae (including Callichiridae) dominated all shelf zones, with *B. gilchristi* as the most abundant taxon for both the inner and mid-shelf, and the outer-shelf containing a higher abundance of *Callianassa* sp.1 (Table 5.5). The second most abundant were the relatively active, omnivorous hermit crabs from the family Diogenidae. Although these were plentiful on the inner and outer-shelf, there were relatively few specimens on the mid-shelf. The hermit crabs on the inner-shelf were mainly *D. costatus* (Table 5.5), but this taxon was absent from both the mid and outer-shelf stations. The outer-shelf hermit crab community was dominated instead by *Paguristes* sp.1, which was also relatively abundant on the inner-shelf (Table 5.5) but rarely sampled on the mid-shelf.

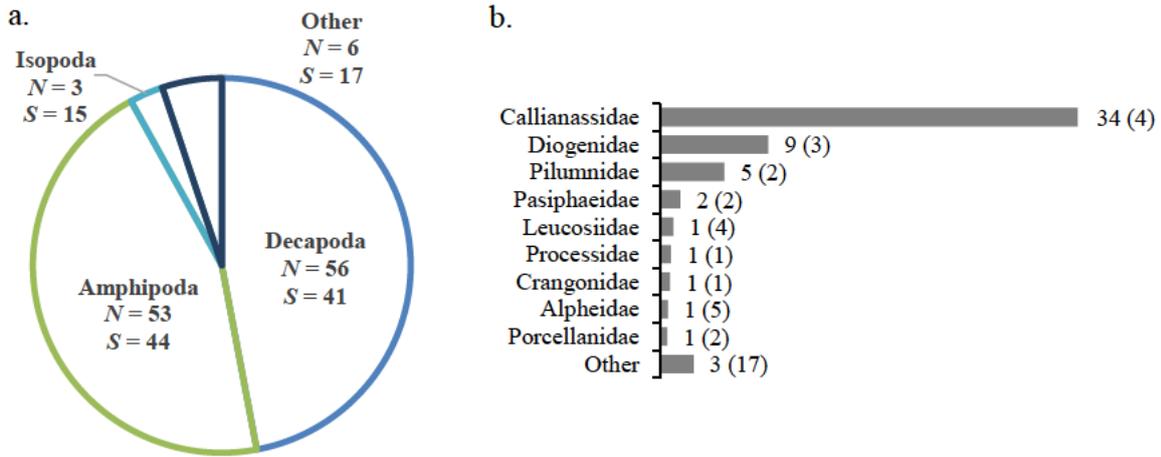


Figure 5.6. (a) Dominance of Arthropoda orders (b) with the mean abundance (N_d : ind.m⁻²) and number of taxa (S_d in brackets) of the families within the dominant order, Decapoda.

Table 5.5. The five most abundant decapods in each uThukela shelf zone.

Taxon	Family	Abundance (ind.m ⁻²)
Inner-shelf (44 samples)		
<i>Balsscallichirus gilchristi</i>	Callichiridae	38
<i>Diogenes costatus</i>	Diogenidae	8
<i>Xenophthalmodes cf. moebii</i>	Pilumnidae	7
<i>Paguristes</i> sp.1	Diogenidae	3
<i>Callianassa</i> sp.1	Callianassidae	3
Mid-shelf (12 samples)		
<i>Balsscallichirus gilchristi</i>	Callichiridae	27
<i>Processa austroafricana</i>	Processidae	3
<i>Callianassa</i> sp.3	Callianassidae	1
<i>Philocheras hendersoni</i>	Crangonidae	1
<i>Pilumnidae</i> sp.1	Pilumnidae	1
Outer-shelf (12 samples)		
<i>Callianassa</i> sp.1	Callianassidae	8
<i>Paguristes</i> sp.1	Diogenidae	3
<i>Processa austroafricana</i>	Processidae	2
<i>Callianassa</i> sp.3	Callianassidae	1
<i>Ommatocarcinus pulcher</i>	Goneplacidae	1

5.4.2.2. Associations between environmental variables and Decapoda distributions

The uThukela shelf decapod community distribution was mostly associated with the combination of depth (m), DO (mg.L^{-1}), and %very coarse sand ($\rho = 0.385$) during this study, with DO being the single most correlated variable ($\rho = 0.330$) (Table 5.6).

Table 5.6. Results of the BIO-ENV procedure displaying the measured environmental parameters most correlated with the decapod distribution on the uThukela shelf.

No. of variables	ρ	Variables
Best single variable		
1	0.330	DO
Best combination of variables		
3	0.385	Depth, DO, %vcs
4	0.369	Depth, DO, %vcs, median (ϕ)
2	0.369	DO, %vcs
4	0.368	Depth, DO, %vcs, %ms

The abundance of Callianassidae (including Callichiridae) was mostly associated with the distribution of fine sand ($r = 0.529$, $p = 0.010$), peaking at station 33 that contained the highest percentage of fine sand (48%) (Figure 5.7). Diogenidae (the second most abundant decapod family) abundance distributions were also related to sediment composition and mostly correlated (albeit a weaker relationship) to the percentage of mud at the site ($r = 0.404$, $p = 0.056$) (Figure 5.8). Diogenidae abundances were significantly correlated to Gastropoda abundances ($\rho = 0.648$, $p < 0.001$), possibly due to their reliance on empty shells.

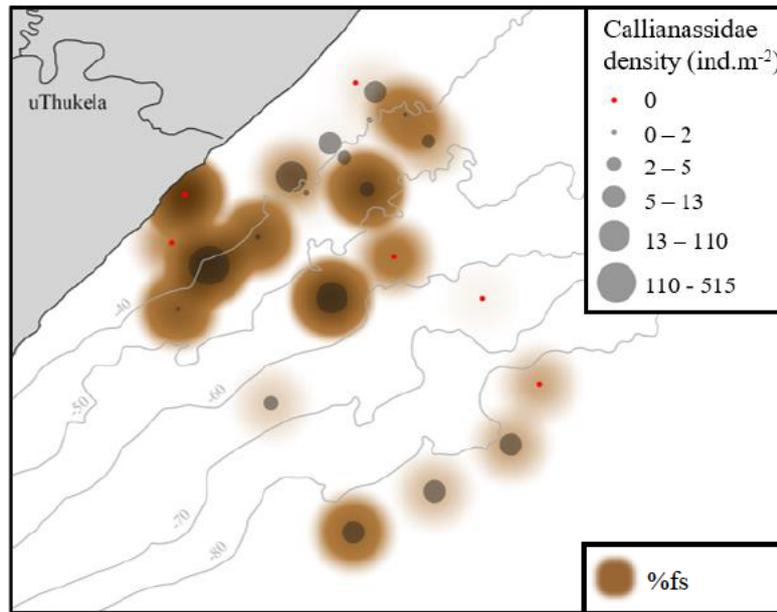


Figure 5.7. Callianassidae density/abundance (N : ind.m⁻²) in relation to the percentage of fine sand (maximum 48% indicated by the darkest shade of brown) on the uThukela shelf.

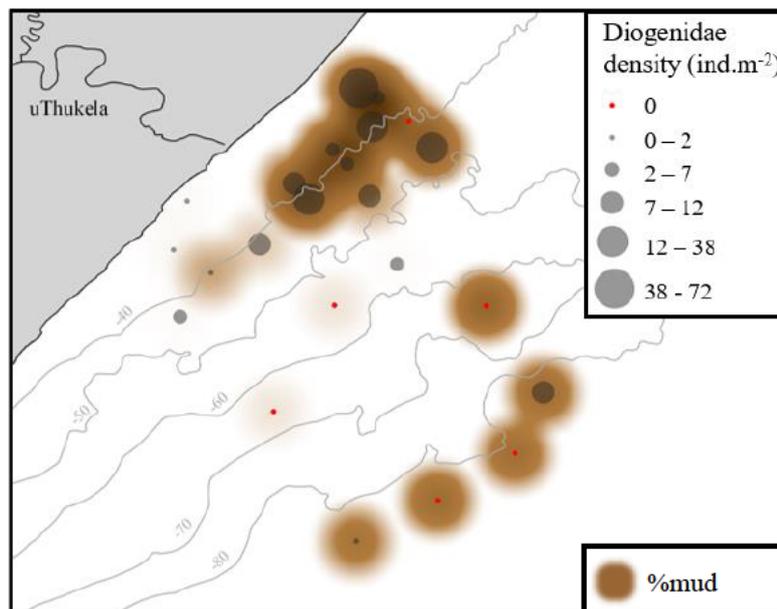


Figure 5.8. Diogenidae density/abundance (N : ind.m⁻²) in relation to the distribution of mud (maximum 99% indicated by the darkest shade of brown) on the uThukela shelf.

5.4.3. *Mollusca*

Mollusca was the third most abundant phylum (after Annelida and Arthropoda), with 53 molluscs.m⁻² belonging to 77 mollusc taxa sampled on the uThukela shelf. Molluscs restricted to one or two samples (rare taxa) made up 65% (45% uniques and 19% duplicates) of the population, while *Macomopsis moluccensis* was the most widespread taxon (in 41% of the samples). Bivalvia was the dominant class, with 41 bivalves.m⁻² belonging to 37 taxa encountered during sampling (Figure 5.9a). The burrowing, facultative deposit-feeding Tellinidae was the most abundant bivalve family (and also mollusc family) on the uThukela shelf (N_b : 19 ind.m⁻²; Figure 5.9b).

5.4.3.1. Spatial differences

The number of mollusc taxa corresponded to the distance from shore ($G = 13.822$, $p < 0.001$) and the distance from the uThukela Estuary mouth ($G = 15.898$, $p < 0.001$). The inner-shelf comprised the highest number of mollusc taxa (S_m : 63 taxa) and was significantly different ($F = 9.010$ df = 22, $p = 0.002$) to the mid-shelf that had the least number of taxa (S_m : 10 taxa). Mollusc abundances also responded to the spatial gradients (from shore: $G = 14.256$, $p < 0.001$; from the uThukela Estuary mouth: $G = 5.543$, $p = 0.019$). The outer-shelf had the highest abundance of molluscs ($\bar{x} N_m$: 88 ± 69 moll.m⁻²), while the mid-shelf had the lowest abundance of molluscs ($\bar{x} N_m$: 18 ± 23 moll.m⁻²), but the differences between shelf zones were not significant ($H = 4.191$ df = 22, $p = 0.123$).

The outer-shelf displayed the highest mollusc abundances due to the high abundance of the facultative detritivore *Tellina* sp.1 (Table 5.7). The abundance of Chaetodermatida sp.1 on the outer-shelf was noteworthy as it was among the top five in this shelf zone but was absent from the inner and mid-shelf. The mid-shelf had the highest abundance of the facultative-feeding small nut clam, *Nucula nucleus* (Table 5.7). Although dominated by bivalves, the inner-shelf had a large abundance of the carnivorous tusk shell *Antalis longitrorsa* that was found exclusively in this shelf zone (Table 5.7).

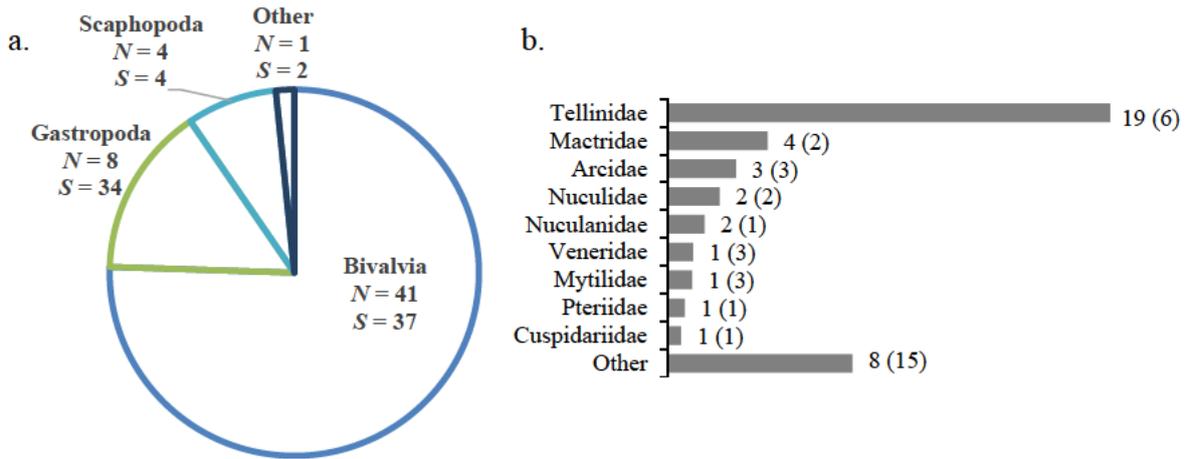


Figure 5.9. (a) Dominance of Mollusca classes (b) with the mean abundance (N_b : ind.m⁻²) and number of taxa (S_b in brackets) of the families in the dominant class, Bivalvia.

Table 5.7. The five most abundant molluscs in each uThukela shelf zone.

Taxon	Family	Abundance (ind.m ⁻²)
Inner-shelf (44 samples)		
Venerida juvenile sp.1		8
<i>Antalis longitrorsa</i>	Dentaliidae	6
<i>Moerella vidalensis</i>	Tellinidae	5
<i>Barbatia foliata</i>	Arcidae	4
<i>Macomopsis moluccensis</i>	Tellinidae	3
Mid-shelf (12 samples)		
Bivalvia sp.6		5
<i>Nucula nucleus</i>	Nuculidae	4
<i>Macomopsis moluccensis</i>	Tellinidae	3
<i>Lembulus gemmulatus</i>	Nuculanidae	3
<i>Moerella vidalensis</i>	Tellinidae	1
Outer-shelf (12 samples)		
<i>Tellina</i> sp.1	Tellinidae	53
<i>Tellina</i> sp.2	Tellinidae	11
Chaetodermatida sp.1		5
<i>Macomopsis moluccensis</i>	Tellinidae	4
<i>Mactra aequisulcata</i>	Mactridae	3

5.4.3.2. Associations between environmental variables and Mollusca distributions

Depth (m), DO (mg.L^{-1}), %coarse sand, and %medium sand were identified as most correlated to the uThukela shelf mollusc distributions ($\rho = 0.480$; Table 5.8). Dissolved oxygen was the single environmental parameter most associated with mollusc distribution ($\rho = 0.410$; Table 5.8) and the variable most correlated with the abundance of the characteristic family Tellinidae ($r = -0.679$, $p < 0.001$). However, this was an inverse relationship with generally higher tellinid densities in less oxygenated areas (Figure 5.10). Gastropoda distribution patterns were also investigated due to their relationship with hermit crabs, and these Mollusca were concentrated on the inner-shelf and mostly correlated to %very fine sand ($r = 0.634$, $p = 0.001$) (Figure 5.11).

Table 5.8. Results of the BIO-ENV procedure displaying the environmental parameters most correlated to mollusc distribution on the uThukela shelf.

No. of variables	ρ	Variables
Best single variable		
1	0.410	DO
Best combination of variables		
4	0.480	Depth, DO, %cs, %ms
4	0.476	Depth, DO, %ms, median (phi)
3	0.476	Depth, DO, median (phi)
3	0.472	Depth, DO, %ms

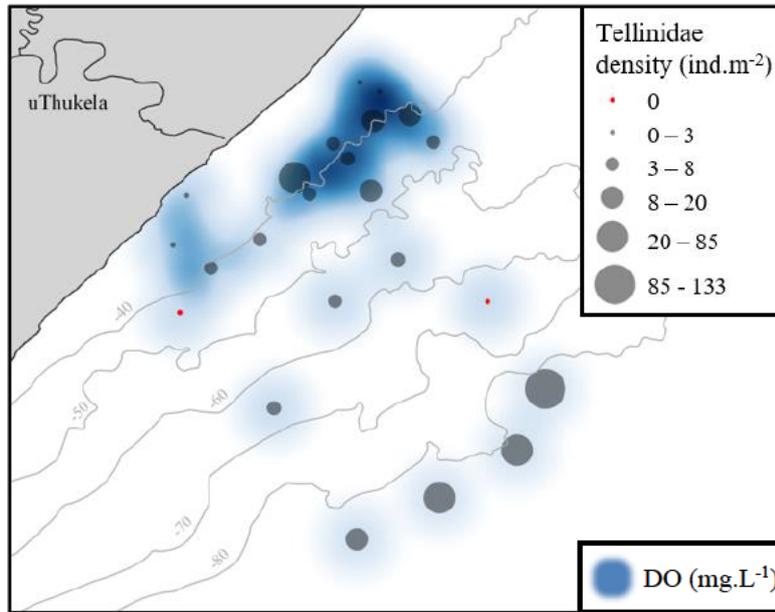


Figure 5.10. Tellinidae density/abundance (N : ind.m⁻²) in relation to bottom dissolved oxygen (DO) concentrations (maximum 7.54 mg.L⁻¹ indicated by the darkest shade of blue) on the uThukela shelf.

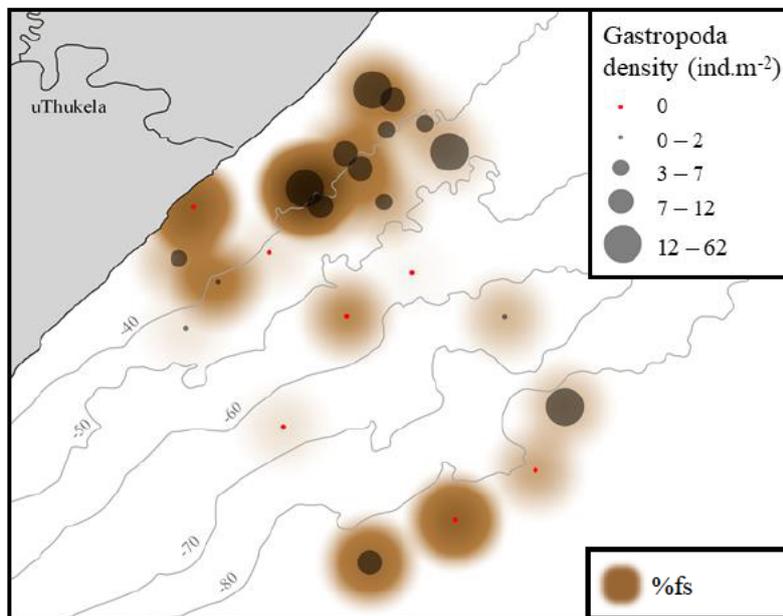


Figure 5.11. Gastropoda density/abundance (N : ind.m⁻²) in relation to the distribution of very fine sand (maximum 27% indicated by the darkest shade of brown) on the uThukela shelf.

5.4.4. Large benthic Foraminifera (LBFs)

A mean of 3 521 foram.m⁻², belonging to 22 Foraminifera taxa, were sampled on the uThukela shelf. Of these, 634 foram.m⁻² belonging to 18 taxa were likely alive when sampled. *Ammonia* sp.1 and *Rotalinoides* sp.1 (both from the family Ammoniidae) were the most abundant (N_f : 276 ind.m⁻² and 274 ind.m⁻² respectively) and among the most widely distributed (present in 25% and 24% of the samples respectively) “live” LBFs on the uThukela shelf (Figure 5.12).

5.4.4.1. Spatial differences

The number of LBF taxa corresponded with the distance of samples from the shore ($G = 87.911$, $p < 0.001$) and the uThukela Estuary mouth ($G = 88.187$, $p < 0.001$), with significantly less taxa ($H = 12.040$ df = 22, $p < 0.001$) on the inner-shelf (overall $S_f = 4$) than the mid-shelf (overall $S_f = 11$) and outer-shelf (overall $S_f = 17$). Large benthic Foraminifera abundances also responded to the distance gradients (shore $G = 31\,050.000$, $p = 0.000$; uThukela Estuary mouth: $G = 42\,366.000$, $p = 0.000$), increasing with distance offshore and indicating a significantly lower abundance ($H = 10.990$, df = 22, $p = 0.001$) for the inner-shelf compared to the mid and outer-shelf.

The inner-shelf supported very few LBFs (N_f : 5 ± 21 forams.m⁻²), with *Astrorhiza* sp.1 being the most abundant taxon in this region (Table 5.9). The mean abundance of LBFs increased further offshore, with the mid-shelf having $714 \pm 1\,119$ forams.m⁻² and the outer-shelf having $3\,285 \pm 5\,289$ forams.m⁻². *Ammonia* sp.1 and *Quinqueloculina* sp.1 were abundant in the mid-shelf community, while the outer-shelf community was dominated numerically by *Rotalinoides* sp.1 and *Ammonia* sp.1 (Table 5.9).



Figure 5.12. Mean abundance (N_f ind.m⁻²) and frequency of occurrence (%) of “live” LBFs on the uThukela shelf.

Table 5.9. Up to the top five most abundant “live” LBFs in each uThukela shelf zone.

Taxon	Abundance (ind.m ⁻²)
Inner-shelf (44 samples)	
<i>Astrorhiza</i> sp.1	2
<i>Rotalinoides</i> sp.1	1
<i>Ammonia</i> sp.1	1
Mid-shelf (12 samples)	
<i>Ammonia</i> sp.1	472
<i>Quinqueloculina</i> sp.1	122
<i>Rotalinoides</i> sp.1	49
<i>Lenticulina</i> sp.1	24
<i>Lenticulina</i> sp.2	18
Outer-shelf (12 samples)	
<i>Rotalinoides</i> sp.1	1 684
<i>Ammonia</i> sp.1	1 273
<i>Lenticulina</i> sp.1	155
<i>Cassidulina</i> sp.1	71
<i>Quinqueloculina</i> sp.1	35

5.4.4.2. Dead Foraminifera

The dead LBF community was comprised of similar taxa to the “live” community analysed above. Most of the empty tests belonged to *Ammonia* sp.1 and *Rotalinoides* sp.1 and there were only four LBFs encountered during the analysis of empty tests that did not appear in the live LBF community. These were *Vaginulinopsis* sp.1, *Dentalina* sp.1, *Dentalina* sp.2, and *Glandulina* sp.1, but only appeared in small numbers (125, 70, 30, 5 overall individuals sampled respectively).

5.4.4.3. Associations between environmental variables and Foraminifera distributions

A combination of salinity (PSU), DO (mg.L⁻¹), and %medium sand was identified as most correlated with the uThukela shelf LBF community ($\rho = 0.472$; Table 5.10). When considered individually, the variable best related to the LBF distribution was salinity ($\rho = 0.423$; Table 5.10).

Table 5.10. Results of the BIO-ENV procedure displaying the environmental parameters most correlated to the LBF distribution on the uThukela shelf.

No. of variables	ρ	Variables
Best single variable		
1	0.423	Salinity
Best combination of variables		
3	0.472	Salinity, DO, %ms
3	0.468	Salinity, DO, %cs
2	0.465	Salinity, DO
4	0.464	Salinity, DO, %cs, %ms

The density of the dominant family, Ammoniidae, was mostly related to depth ($r = 0.707$, $p < 0.001$), and inversely to temperature ($r = -0.537$, $p = 0.008$). This meant that higher Ammoniidae densities were usually found in deeper, cooler areas (Figure 5.13).

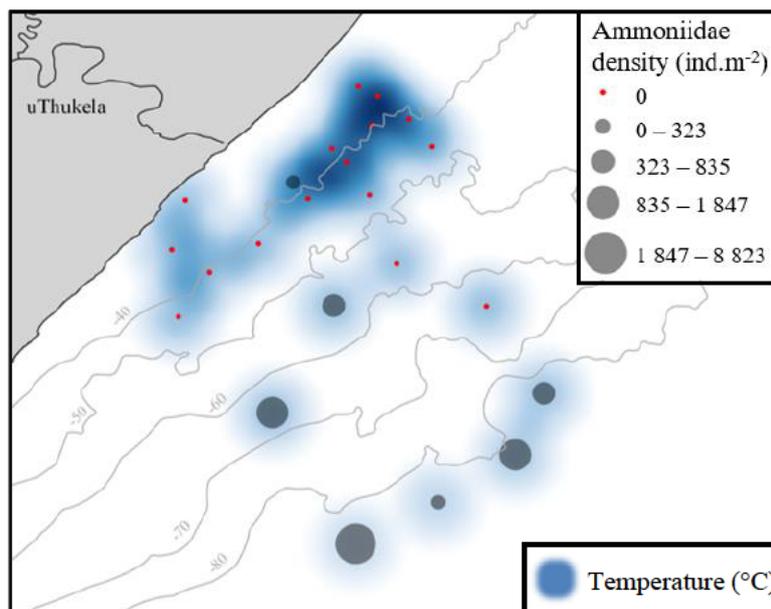


Figure 5.13. Ammoniidae density/abundance (N : ind.m⁻²) in relation to bottom temperature readings (maximum 20.35 °C indicated by the darkest shade of blue) on the uThukela shelf.

5.5. Discussion

5.5.1. *Polychaeta*

The uThukela shelf polychaetes were diverse, with 3 885 individuals belonging to 180 taxa from 42 families, collected during this study. This was comparable to the Venezuelan coast off the major Orinoco River where 2 452 individuals, representing 43 families, were sampled in 16.4 m² (Bone et al. 2011). The results were also comparable to other polychaete studies in areas with no major freshwater influences. The western Indian coast contained 165 taxa belonging to 32 families (Joydas and Damodaran 2009) and the São Sebastião Channel, Brazil, had 126 taxa from 34 families (Muniz and Pires 2000). Polychaete rarity was high on the uThukela shelf, with 47% of taxa being found in only one or two samples. This does not seem to be uncommon as rare polychaetes comprised 45% of the population for the study in the tropical/subtropical São Sebastião Channel, Brazil (Muniz and Pires 2000).

Spionids are typically known to be a major component of benthic communities (Abe et al. 2019), and previous studies on fluvially-influenced shelves around the world have found them to be the most abundant polychaete family (Probert et al. 2001, Bone et al. 2011, Manokaran et al. 2013). This study agreed with this trend and confirmed the finding by Untiedt (2013) that Spionidae is one of the most abundant families on the uThukela shelf. The success of spionids in a naturally disturbed environment, such as off the uThukela Estuary mouth, is potentially due to their ability to shift between suspension and deposit-feeding modes depending on food availability (Vijapure et al. 2019).

The polychaete assemblages were similar to those explored for the macrofauna community analyses (in Chapter 3) as the muddy outer-shelf samples formed a unique assemblage, and the fine to coarser-grained inner and mid-shelf samples formed multiple assemblages based on measured near-bottom water parameters and habitat type. The main sediment parameters correlating with these assemblages were coarse sand and mud, and Untiedt (2013) observed these same sediments as potential drivers of polychaete distribution on the KZN Bight. The deep, muddy, least saline, and least oxygenated samples from the outer-shelf were characterised by the subsurface deposit-feeding *N. latericeus*. The high abundance of Capitellidae showed a strong inverse relation to dissolved oxygen (DO) and shows the ability of this family to withstand adverse conditions, especially reduced oxygen concentrations (Jayaraj et al. 2007). The stations with the highest percentages of coarse sand belonged to assemblage III, containing

most of the mid-shelf samples and corresponding with the sub-continuous paleo-dune that exists on the mid-shelf (Flemming and Hay 1988, Green and MacKay 2016). Both this study and the study by Untiedt and MacKay (2016) found *D. papillosa* (family Onuphidae) dominated this coarse-grained uThukela mid-shelf environment, but this taxon was not characteristic of assemblage III, as it was spatially restricted and only found in large abundances at station I4. This coarse sediment characteristic of this shelf region could be the reason that *O. fusiformis*, although being the most widespread polychaete, was completely absent from the mid-shelf, as this taxon requires fine particles to build a tube and grow (Pinedo et al. 2000). Instead, *O. fusiformis* was one of the characterising taxa in the assemblage associated with fine sand (assemblage II), containing mostly inner-shelf samples. This species also numerically dominated shallow, fine sandy bottoms in the study by Dutertre et al. (2013) along the coastal fringe of South Brittany on the French Atlantic shelf. Assemblage II was mostly characterised by the same family (Spionidae) and taxa (*A. dibranchis* and *C. concinnus*) that characterised the polychaete community overall. The community on the inner-shelf is at risk of burial and environmental instability, which results in many small, opportunistic taxa (Akoumianaki and Nicolaidou 2007), such as from the family Spionidae. This environmental instability could also be the reason for the higher abundances of mobile taxa (capable of swimming when disturbed) that were found in this region (Pacheco et al. 2011).

The uThukela shelf polychaetes exhibited similar patterns in dominant traits that were observed for the entire macrobenthos (Chapter 4) due to the abundance of polychaetes in the community. The major differences were that polychaetes mostly burrowed through the sediment while other macrofauna mostly crawled on the sediment, and suspension feeders that were common among macrofauna were not common in the polychaete community. Surface deposit feeders and carnivores were dominant (taxa and abundance-wise) feeding modes in the uThukela shelf polychaete community. These were best represented by the three most abundant taxa, *C. concinnus* and *Aonides oxycephala* (facultative detritivores), and *Aglaophamus dibranchis* (carnivore). Other studies, such as on the oligotrophic Creten shelf (Karakassis and Eleftheriou 1997) and off the Amazon River (Alongi and Robertson 1995), also recorded this dominance of surface deposit feeders and carnivores. Although subsurface deposit feeders were not common in the uThukela shelf macrofauna community (Chapter 3), they were the third most abundant group in the polychaete community, with the highest concentrations on the outer-shelf. The top representative of the outer-shelf, *N. latericeus*, represented this feeding group. Subsurface deposit feeders appear to have a higher tolerance to extreme environmental

conditions (Macdonald et al. 2012). They may modify the habitat by transporting sediment particles vertically and altering the spectrum of sediment grain sizes by egesting larger faecal pellets than originally ingested (Manokaran et al. 2013).

It has been suggested that due to polychaete dominance, it is likely that this taxonomic group provides a good approximation of the entire infaunal community (Probert et al. 2001). This study found that the uThukela shelf polychaetes comprised 50% of the sampled macrofauna (Chapter 3) and their distribution patterns show a strong correlation to macrofauna patterns (analysed in Chapter 3). Polychaetes are, therefore, possible surrogates that can determine macrofauna responses to natural environmental changes, as the polychaete community variability influences the patterns of the entire macrofauna community. The identification of polychaetes as potential surrogates implies that the polychaete community patterns may allow an understanding of the entire macrofauna community in a more efficient and less costly manner if resources are limited and the entire community cannot be studied (Moreno et al. 2007). This is particularly beneficial in monitoring and when rapid decision-making may be needed (Moreno et al. 2007). However, information about the complete biodiversity is lost when using surrogates (Moreno et al. 2007), so it is advised that the entire macrofauna community is studied when possible.

5.5.2. *Decapoda*

The uThukela shelf decapod abundances decreased with the distance offshore, therefore decreasing with the increasing depth gradient. The study on the Creten shelf showed a similar trend with Crustacea as their abundances also decreased with increasing depth (Karakassis and Eleftheriou 1997).

The most abundant decapod family on the uThukela shelf was Callianassidae (including Callichiridae), and these sandprawns had the highest abundances at the shallower fine-grained stations. The shallow sand and mud habitats near the Amazon mouth were also found to contain many thalassinid shrimp (Alongi and Robertson 1995). This group of decapods often occur in high densities (Reise 2002) and characteristically build and inhabit burrows in sedimentary environments (Stamhuis et al. 1997). They are some of the most effective bioturbators, altering the sediment structure and nutrient processes, and although they have been known to exclude other organisms that rely on sediment stability, they accommodate burrow inhabitants and small

infauna similar to those that dwell in hydrodynamically-disturbed habitats, such as on the uThukela shelf (Reise 2002).

Diogenidae were the second most abundant decapod family on the uThukela shelf, with the highest abundances on the inner-shelf. Untiedt and MacKay (2016) also found that the abundance of hermit crabs was prominent on the uThukela inner-shelf during the dry (winter) season, and these scavengers have also been reported in other regions continuously subjected to high environmental stress (Dolbeth et al. 2009). Hermit crabs have soft abdomens and typically inhabit empty gastropod shells that are needed for protection and survival (Brusca and Brusca 2003, de la Haye et al. 2011). They require the availability of shells occupied by other conspecifics or that are empty, and relocate to larger shells as they grow (de la Haye et al. 2011, Laidre 2011). However, these shells are only accessible to the crabs for a short period between the disappearance of the previous animal and the burial of the shell (Laidre 2011). This may explain the similarity in distributions of the hermit crabs and live gastropods during this study.

5.5.3. *Mollusca*

Gastropods were concentrated on the inner uThukela shelf, but the analysis of the live molluscs during the present study and the remanent shell material during a previous study (Hunter n.d.) revealed that bivalves dominated both the non-recent and recent mollusc communities across the shelf. The observed remanent shell material was very fragmented and sub-angular, indicating that the dead mollusc shells undergo extensive reworking due to currents and waves (Hunter n.d.), and that the shell material has potentially been there for a long time.

The live bivalve community observed during this study had a relatively large abundance of Tellinidae. Tellinids are facultative detritivores that rapidly burrow in sediments and are common in tropical open seas (Simone and Wilkinson 2008). This study found that they were concentrated at stations on the outer uThukela shelf with low oxygen concentrations and thus agreeing with the findings of Untiedt (2013). This pattern was also found on the west coast of India during postmonsoon conditions, where *Tellina* were characteristic of the cooler, less oxygenated, deeper stations (Jayaraj et al. 2008). Although *Tellina* was the most abundant taxon on the outer-shelf, Chaetodermatida, belonging to the minor class Caudofoveata, also characterised this shelf region. This mollusc was not abundant but was exclusively found on the outer-shelf. Members of Caudofoveata commonly dwell in deep marine waters where they burrow through mud, mostly feeding on detritus (Todt et al. 2008). They are worm-shaped and

lack a shell but are covered by a coat of calcareous sclerites (Sigwart and Sumner-Rooney 2016) that potentially evolved to ward off predators (Todt et al. 2008).

5.5.4. Large benthic Foraminifera (LBFs)

The sampling design was not optimal for the full analysis of Foraminifera as there are many smaller forms that would have not been retained by the 1 mm sieve used during sampling. The results, however, allowed an analysis of the larger taxa and can be used as preliminary information for future studies. The LBFs were concentrated on the muddy outer-shelf, agreeing with a previous study focussing on the uThukela shelf sediments (Hunter n.d.), and this distribution was also observed on the eastern Great Australian Bight where Foraminifera were proportionally best represented in the silty sediments of the deep outer-shelf (Currie et al. 2009). The most abundant taxon was *Ammonia* sp.1, and members of this genus are usually common in marginal marine environments with high mud content (Bird et al. 2020). During the study in Chesapeake Bay, the historic abundance of *Ammonia* was shown to be related to periods of seasonal oxygen lows (Murray 2006). The highest abundance of *Ammonia* sp.1 was also recorded in the least oxygenated areas of the uThukela shelf, which were further offshore. Large benthic Foraminifera distribution overall was mostly related to reduced salinity, reduced DO, and the reduced percentage of medium sand. This does not imply that these LBFs are confined exclusively to these low oxygen areas, but rather that some species have very low critical thresholds and can survive in areas that other organisms may not be able to (Murray 2001). The dead LBF community of the uThukela shelf comprised similar taxa and is assumed to have been alive in the recent past and representative of current conditions due to only collecting surficial sediments and not sediment cores. Sediment cores provide details of historic communities (Gustiantini et al. 2007) and sample the entire size spectrum so can indicate how the uThukela system has changed over a relatively long period and it is, therefore, recommended that sediment cores are collected in future studies to analyse these changes. Additionally, by investigating the chemistry of these carbonate Foraminifera tests (usually through isotope analysis), the chemistry of the environment in which they calcified can be explained and can assist in understanding past climate changes (including temperature, sea-level, carbonate chemistry etc.) (Katz et al. 2010), so studies should also consider chemical analysis to understand the historical conditions of the uThukela shelf.

5.6. Conclusion

This chapter provides an in-depth assessment of the important uThukela shelf macrofauna groups at finer spatial scales than previous studies. Decapoda abundances decreased with depth, with the dominant sandprawns and hermit crabs concentrated on the fine-grained inner-shelf. Large benthic Foraminifera and Mollusca showed the opposite trend, with higher abundances of the dominant families (Ammoniidae and Tellinidae respectively) on the deep, muddy outer-shelf. This was due to their association with muddy habitats. However, gastropod abundances were concentrated on the inner-shelf and correlated with hermit crab abundances, possibly due to the use of empty gastropod shells by these crabs. Polychaeta abundances and traits were similar across the shelf, but multivariate analysis revealed that there was a distinct less saline, less oxygenated, muddy outer-shelf, deeper water community and that the inner and mid-shelf Polychaeta did not form distinct assemblages according to shelf zones but rather based on habitat conditions that overlapped between these zones. The polychaete distributions presented similar patterns to the entire macrofauna community analysed in Chapter 3 (signifying polychaete dominance) and indicated that this focal group may be a good surrogate for understanding the uThukela macrofauna community patterns. This may assist in more efficient and less costly monitoring and decision-making in a situation where resources are limited and the entire benthic community cannot be studied.

CHAPTER 6. GENERAL DISCUSSION AND CONCLUSIONS

This study expands on the findings of the African Coelacanth Ecosystem Programme (ACEP) Natal Bight and Surrogacy projects of the structural and functional uniqueness of the uThukela shelf macrofauna community, and that contributed to the recent promulgation of the uThukela Marine Protected Area (MPA). This study contributes to the uThukela macrofauna taxonomic and traits inventories, providing a good baseline database of the macrofauna and conditions off the large fluvially-dominated uThukela Estuary from collections prior to its protection. The macrobenthic communities were characterised by taxa composition and biological traits, and further related to measured near-bottom water and sediment parameters to determine the potential influence of local conditions on these distribution patterns. The key hypotheses investigated were that changes would occur in the uThukela shelf community composition and functioning with shelf position (indicating distances from terrestrial influence and the influence of the uThukela Estuary) and that macrofauna distribution patterns would relate to the changes in environmental conditions and sediment habitats at local spatial scales.

6.1. The uThukela shelf community composition

The initial step in environmental research and conservation studies involves taxonomic exploration of the community diversity, as this provides an essential dataset for future comparison (Maggiore and Keppel 2007). Many ecological studies exclude rare taxa (those only encountered once or twice during the study) during analysis due to them occurring infrequently and in low abundances. However, a large portion of the species diversity is usually composed of these rare species (sometimes containing rare traits) and they are often significant in determining differences in communities (Murray 2006). This study comprised many rare taxa too, and the exclusion of these taxa would potentially fail to accurately represent the full ecological structure and functioning of the uThukela shelf (Bremner 2008). Overall, this region supported a structurally diverse macrobenthic community, which the uThukela MPA aims to protect (Republic of South Africa Government Gazette 2019). There were no significant differences observed between shelf positions with regards to numbers of taxa, abundances, and diversity, and broad taxonomic groupings specified Polychaeta as the most abundant and speciose across the uThukela shelf. This agreed with the KwaZulu-Natal (KZN) dominance patterns (McClurg 1988, MacKay et al. 2016, Untiedt and MacKay 2016) and other global studies in fluvially-dependent shelf ecosystems (Jayaraj et al. 2008, Joydas and Damodaran 2009, Zalmon et al. 2013, Khan et al. 2017). Arthropoda (almost exclusively Crustacea) was

the second most dominant phylum, and although the ACEP Natal Bight and Surrogacy studies identified Amphipoda as the most abundant crustacean group in the KZN Bight (MacKay et al. 2016, Maduna 2017), this study found that the uThukela shelf was dominated by Decapoda. Mollusca was also important in the uThukela shelf community and was dominated by the order Bivalvia, agreeing with the patterns observed for the KZN shelf (MacKay et al. 2016, Maduna 2017). Dead mollusc shells, along with a large abundance of large benthic Foraminifera (LBFs), contributed greatly to the uThukela shelf bioclastic sediments that enhance bottom habitat complexity and thus increase benthic diversity (Passarelli et al. 2012). The live Foraminifera do not contribute to macrofauna diversity as they are free-living protists, but they are controlled by a wide range of environmental conditions and are usually considered useful bioindicators due to easily detecting ecosystem variations (Murray 2006). This study focussed on the larger macroinvertebrates of the uThukela shelf so only LBFs were collected on the sieve used to sample macrofauna. It is recommended that sediment cores or subsamples (like those for sediment analysis) are collected in future studies to better analyse the full community (including the smaller forms).

6.2. A unique single replicate indicates a potential low-lying reef

One replicate (9B) from the uThukela inner-shelf had a unique macrofauna composition, high diversity of taxa, and many species that were exclusive to the sample. These included numerous cnidarians and associated brittle stars (*Ophiothela mirabilis*) along with other taxa usually associated with hard substrata, that potentially indicate a nearby low-lying reef. This perhaps explained the high diversity of taxa as reefs generally contain high habitat heterogeneity that usually facilitates diverse communities (Crame 2000). The presence of a reef could also explain the difficulty that was encountered during sampling of station 9 and the reason for two out of three successful replicates being collected. The composition of replicate 9A collected at this station was completely different from 9B but was similar to the other samples collected on the inner-shelf. The replicates within station 9, therefore, do not appear to come from the same habitat type and this could be due to the small-scale variation that occurs in soft sediments (Ellingsen 2001, Chapman et al. 2010). To understand this habitat anomaly, going forward it would be beneficial to collect more sediment samples in this area to study the macrofauna community composition and traits, and map the bottom topography or collect images to identify the positioning of the potential reef. This reef habitat may play an important role in the uThukela benthic ecosystem as it may be an isolated habitat patch (an “ecological island”) containing

many unique species for this region, and it would then need to be closely monitored to ensure that this habitat is not lost (Cartwright 2019).

6.3. The uThukela shelf community functioning

Although informative, taxa composition does not explain ecosystem functioning which is an important component of biodiversity and conservation (Bremner 2008). To explain this connection between uThukela shelf benthos and their habitats, functional analysis was conducted through Biological Traits Analysis (BTA) (Chapter 4). The uThukela macrofauna community was functionally diverse, and shelf position did not affect community functioning as many of the taxa sampled during this study exhibited similar biological traits. The functional similarity of communities at different shelf positions is likely due to the land-sea connection between the uThukela Estuary and the shelf edge (De Lecea et al. 2013, Scharler et al. 2016b), and indicates that the relative stability and resilience of the community occurs across the shelf as multiple taxa fulfil the same functional roles and potentially have adapted similar traits to survive fluctuating river flow and corresponding environmental conditions (Hewitt et al. 2008, Miatta et al. 2021). The presence of various trophic groups including carnivores, surface deposit feeders, subsurface deposit feeders, and omnivores, indicated that there are numerous food sources available (Pacheco et al. 2011), but the apparent dominance of detritivores indicates that the most important of these is particulate organic matter (POM) mostly imported from the uThukela Estuary (Ayers and Scharler 2011, De Lecea et al. 2016). The estuary inputs fluctuate naturally according to river flow but most of the uThukela shelf macroinvertebrates are capable of facultative-feeding, whereby they can intermittently switch between feeding modes when conditions alter the type of food available and sediment deposited (Macdonald et al. 2012). This indicates that most uThukela shelf macrofauna are relatively resilient to these naturally fluctuating habitat conditions (Macdonald et al. 2012, Jumars et al. 2015), but that the shelf cannot be entirely separated from the estuary as it is still reliant on terrestrial inputs for the benthic habitats and food web. This emphasises the importance of the uThukela MPA in conserving the critical role of river input in supplying nutrients and sediments to the shelf and protecting the link between the estuary and the deep ocean in order to preserve the conditions required by the macrobenthic community for its ecological functioning (Republic of South Africa Government Gazette 2019).

6.4. Associations between measured environmental variables and uThukela shelf macrofauna communities

Although the uThukela shelf is mostly muddy due to the input of terrestrial sediment, a paleodune cordon bisects the shelf to separate the newly-deposited mud on the inner-shelf from the older mud deposits of the outer-shelf (Flemming and Hay 1988, Green and MacKay 2016). This provides for heterogenous habitats, thus sediment parameters were combined with near-bottom water parameters to distinguish environmental conditions influencing unique assemblages in this region. The combination of near-bottom water parameters dissolved oxygen (DO) ($\text{mg}\cdot\text{L}^{-1}$), salinity (PSU), and depth (m), along with sediment composition (specifically %coarse sand, %medium sand, and %mud), best explained the relationship that existed between the measured environmental variables and macrofauna community distribution. The correlation of depth with taxon assemblages may not have been along a depth gradient *per se*, but rather likely indicates the effects of changing environmental conditions (McArthur et al. 2010) that may be confounded due to the distance away from coastal influences (MacKay et al. 2016). Dissolved oxygen and salinity were environmental variables that decreased with increasing uThukela shelf depth. Dissolved oxygen may be reduced further offshore due to the natural decrease in oxygen saturation with depth and less mixing of offshore waters by wind and wave energy (Dutertre et al. 2013), but the salinity gradient was atypical for a shelf off a fluvially-dominated estuary as it is expected that the less saline water would be inshore due to the introduction of freshwater to the coastal region through the uThukela Estuary mouth (De Lecea and Cooper 2016). However, the uThukela River flow is usually reduced during the dry season, resulting in less freshwater input to the shelf, and is likely the reason for the elevated salinities closer to shore than usual (MacKay et al. 2016, van Niekerk et al. 2020). Alternatively, the lower salinities recorded further offshore could be the result of cooler, less saline deep water from the Agulhas Current being transported onto the shelf, as the Agulhas Current is displaced further from the coast by the widening of the shelf and this results in divergent upwelling (Roberts et al. 2010).

Macrofauna traits showed limited responses to the variability in measured environmental conditions, as although the environmental parameters varied across the uThukela shelf, the functioning did not change significantly with shelf position. This indicates that the community has potentially adapted to the large inputs of sediment and detritus to the shelf and is tolerant to the high environmental variability off the fluvially-dominated uThukela Estuary. The relationship between the biota and environment may also be more complex than the direct influence that was assumed during analyses. This is seen by the apparent lack of relationship

between the macrofauna community and total organic carbon (TOC) during this study, but the dominance of facultative deposit feeders on the uThukela shelf implying that there is a reliance on POM mostly supplied by the uThukela Estuary (Ayers and Scharler 2011). The TOC measurement during this study may be an indirect correlation of food use as although TOC is present in the uThukela shelf sediments, it may not be available for consumption by macrofauna (McArthur et al. 2010). Future studies may benefit from considering the reactive (labile) and unreactive (recalcitrant) components of TOC due to the importance of organic matter in the uThukela system. Biological interactions were not tested but may also explain much of the observed species distribution patterns observed during this study (Gray 1981, Ambrose 1991). For example, biogenic structures, such as the large amount of shell material observed, provide habitats for macrofauna (Pacheco et al. 2011). Although noted in the sediments, shell material was only observational and could not be assumed to have a direct relationship with macrofauna distribution. However, the importance of shell remnants in increasing habitat complexity was recognised during the analysis of samples, as cnidarians and tubicolous polychaetes were found attached to dead fragments and some tubicolous fauna incorporated these pieces into their tubes. This indicates that biogenic structures should possibly be considered in future studies investigating macrofauna and factors influencing their distributions. This possibly can be done *in situ* by using a specialised camera that captures the bottom environment and where subsequent observations can be made about the biogenic structures within the sediment. The inclusion of environmental measurements and corresponding benthic communities from different seasons and years would also be beneficial for future studies and during the integration of other baseline information. This would provide more robust evidence of the relationship between abiotic parameters and the uThukela shelf macrofauna while considering the environmental variability that exists off the uThukela Estuary.

6.5. Distinct assemblages according to local environmental conditions

Multivariate analyses of the remaining 67 samples (excluding replicate 9B) collected during this study identified five uThukela shelf assemblages, reflecting differences in shelf position in terms of taxa composition. Although the outer-shelf stations formed a distinct assemblage, the inner and mid-shelf samples did not form assemblages according to shelf zone but grouped according to bottom habitat type that overlapped between the two zones. Therefore, the separation of the uThukela shelf into inner, mid, and outer zones, although having worked for other shelf-wide studies, was artificial for the macrobenthic community in this shelf section during the dry (winter) season.

Two of the five distinct assemblages in this study did not form distinct zones as they each consisted of just a single station (one on the inner-shelf and one on the mid-shelf) that had the lowest numbers and abundances of taxa and represented the least number of trait categories. The first assemblage was formed by fine-sand samples at the most shallow station (station 6) and was typified by small deposit-feeding polychaetes. Deposit feeders are beneficial in areas exposed to high terrestrial inputs as they play a vital role in the removal of organic matter and are often involved in sediment turnover that assists in the oxygenation and nutrient cycling in the top sediment layers (Brusca and Brusca 2003). The other fine-grained inner-shelf assemblage comprised many facultative deposit feeders and was characterised by the most widely distributed taxa overall, the carnivorous polychaete *Aglaophamus dibranchis* and the deposit-feeding peanut worm from the family Sipunculidae. This assemblage had the highest numbers of *Balsscallichirus gilchristi*, the most abundant taxon overall. The abundance of these thalassid shrimp on the inner-shelf corresponds with the distribution observed by Barnard (1950) at 37 m depth along the Natal coast. Thalassids are among the most effective bioturbators and habitat engineers, and although they exclude fauna reliant on sediment stability, they accommodate small infauna similar to those occurring in hydrodynamically-disturbed habitats, such as the inner uThukela shelf (Reise 2002). These habitats were also rich in diogenid hermit crabs inhabiting dead gastropod shells. The success of these crabs relies on the availability of shells occupied by other conspecifics or that are empty (Laidre 2011), and these shells are only accessible to them for a narrow period between the disappearance of the previous organism and the burial of the shell (Laidre 2011). This time constraint may explain the similar distributions observed between the hermit crab and gastropod communities on the inner-shelf. The inner-shelf community can withstand environmental instability caused by naturally fluctuating estuarine inputs and this was evidenced in the analysis of the polychaetes that were represented by a higher abundance of mobile taxa (capable of swimming) (Pacheco et al. 2011) and resilient spionids. The success of these spionids is potentially due to their ability to effectively shift between suspension and deposit-feeding when food sources change (Vijapure et al. 2019). They are typically a major component of benthic communities due to their taxa diversity (Abe et al. 2019) and have also been observed to dominate other fluvially-influenced shelves around the world (Probert et al. 2001, Bone et al. 2011, Manokaran et al. 2013).

The second assemblage containing just a single station was formed by samples from the only muddy mid-shelf station sampled (station H4). The position of this station corresponded with a

paleo-channel that intersects the paleo-dune cordon on the uThukela mid-shelf (Engelbrecht et al. 2020) and was characterised by the carnivorous polychaete *A. dibranchis*. This station had a relatively homogenous habitat due to the high mud content, and only contained fauna that were tolerant of these conditions, resulting in a low diversity. The other mid-shelf stations sampled during this study corresponded with the paleo-dune cordon (Green and MacKay 2016) and these, along with two inner-shelf stations sampled south of the uThukela Estuary mouth, formed a medium-coarse-grained assemblage. Alternatively, this assemblage contained heterogenous sediments that provided many potential niches for a diverse community (Gray 1981, Carvalho et al. 2017) that was characterised by the amphipods *Basuto stimpsoni* and *Byblis gaimardii*, the carnivorous polychaete *Lumbrineris aberrans*, and the omnivorous polychaete *Onuphis eremita*. Carnivores and suspension feeders were abundant as sandy sediments allow the accumulation of potential prey of carnivores in the interstitial spaces between grains (Muniz and Pires 2000) and provide attachment sites for infaunal suspension feeders (Macdonald et al. 2012). There was also a large proportion of arthropods, and resultantly there was a dominance of brooders with direct (benthic) development. These life-history traits result in species generally having narrower area ranges, indicating that there is a greater risk of local disturbances and consequent extinction threatening the entire population (McHugh and Fong 2002), however, the establishment of the uThukela MPA protects these taxa with vulnerable life-history traits. The MPA aim of protecting vulnerable life-history traits of crustaceans mostly considered the penaeid prawns (that also brood but have pelagic larvae that rely on estuaries) important in the industrial trawl fishery that previously occurred inshore and offshore on the uThukela Banks (Fennessy et al. 2014).

The fifth macrofauna assemblage is on the outer uThukela shelf and just inshore of the previous offshore prawn fishery location. It was characterised by deep, muddy, less-oxygenated samples with distinguishable facultative-feeding tellinid bivalves, deposit-feeding peanut worms, and the subsurface deposit-feeding polychaete *Notomastus latericeus*. Consequently, surface deposit-feeding was the main form of food acquisition in this shelf zone, which is expected as this muddy, organically enriched habitat is suited to the dominance of deposit feeders (Rhoads and Young 1970). It is, therefore, probable that the facultative deposit feeders in this shelf zone would deposit feed as opposed to suspension feed. This muddy habitat on the outer-shelf was previously observed by other authors and indicates the transport of fine sediments across the shelf and over the shelf edge (Flemming and Hay 1988, Bosman et al. 2007, Green and MacKay 2016). It is an interesting environment as this shelf zone corresponds with the positioning of

the strong Agulhas Current that is expected to scour the bottom habitat (Lutjeharms 2006b). However, this outer-shelf mud appears to be consolidated, meaning that the sediment is not easily resuspended, thus creating a relatively consistent habitat (Sanders 1958, Gray and Elliott 2009, Green and MacKay 2016). Large benthic Foraminifera were concentrated in the sediments of the outer-shelf and these were mostly from the genus *Ammonia* that is common in marginal marine environments with high mud content and seemingly able to withstand broad ranges of oxygen, salinity, and temperature that other organisms may not be able to (Murray 2006).

6.6. Polychaetes as surrogates

The analysis of the uThukela shelf macrofauna revealed that polychaetes were the most ubiquitous and abundant in all assemblages. They are globally considered some of the most characteristic macrofauna (Jumars et al. 2015), exhibiting various behaviours, reproductive techniques, and feeding traits that allow them to inhabit a diverse range of habitats (Brusca and Brusca 2003). Due to their dominance and diversity, it has been suggested that the polychaete community provides a good approximation of the entire infaunal community (Probert et al. 2001). This was investigated by determining whether the assemblages defined during multivariate analyses of the uThukela macrofauna and the uThukela polychaetes would demonstrate similar patterns. The analysis revealed that polychaetes and macrobenthos did form very similar assemblages, implying that polychaetes could potentially be used as surrogates if there are limited resources available to investigate and monitor the entire macrofauna community.

6.7. Conserving and monitoring the unique uThukela shelf

These unique habitats and associated macrobenthic communities are within the uThukela MPA and protected from certain direct anthropogenic activities that sometimes occur on the continental shelf (e.g. trawling, mining, etc.) but are still indirectly affected by activities that occur in the uThukela catchment, moving into the river, and out of the estuary. Agriculture, land development, and deforestation cause high land runoff that potentially increases the coastal pollutants and excess sedimentation on the shelf, whereas freshwater abstraction and damming leads to a decline in river flow and consequently reduces the freshwater, sediment, and nutrient inputs to the shelf (Drinkwater and Frank 1994, Hall 2002, Skowno et al. 2019). There has already been a reduction in the uThukela freshwater outflow due to damming and abstraction, with nearly a third of the freshwater no longer reaching the coast (Skowno et al. 2019). South

Africa will likely experience additional water demands in the future as it is a water-stressed developing country with a growing population (De Lecea and Cooper 2016), and this will put further pressure on the uThukela River as it is a potential source of surplus water for the KZN grid, but decisions on water abstraction and utilisation of this area should be carefully considered (De Lecea and Cooper 2016). This study has shown that the uThukela shelf macrofauna community is reliant on the sediment and POM imports from the uThukela Estuary and indicates that if the river flow was considerably reduced (due to abstraction) that it no longer reached the coast even during the wet season, the macrofauna, and thus the entire food web, would be altered due to the system being strongly benthic-driven (Scharler et al. 2016b). Communities that thrive in these generally muddy, organically enriched environments will potentially shift to an alternate state as species from adjacent sandy habitats move into this area, and there is a risk of losing the unique uThukela shelf biodiversity and the ecosystem processes that originally contributed to declaring this MPA (Republic of South Africa Government Gazette 2019). Effective ecological conservation is, therefore, necessary and involves sufficient baseline information on the taxonomic composition and ecological functioning of a protected area (Bremner 2008, Vijasure et al. 2019). Due to the importance of benthic communities in the uThukela system, the preservation of community taxa and traits are vital in management efforts to sustain the functioning of this coastal environment (Villnäs et al. 2019). The success of management also involves understanding the factors influencing these complex biotic communities (Vijasure et al. 2019). It is important to monitor both the macrofauna taxa and traits as communities can show variability in their abundances and compositions that will affect taxonomic biodiversity, but if one taxon is replaced by another taxon with similar functional attributes, the impact of this change on the functioning of the system may not be noticed (Frid and Caswell 2015). This study showed that although taxa composition changed with shelf position, biological traits did not, suggesting that the shifts in the uThukela shelf community due to habitat variability may be more easily noticed in taxonomic analysis than traits analysis. This baseline information assists in assessing whether the aims of the uThukela MPA are being achieved as it helps to monitor whether the rare benthic habitats associated with the connection of the coast to the deep sea are being protected, whether the critical role of freshwater input is preserved, whether the macrofauna diversity is being maintained, and whether the areas important for life-history strategies are conserved (Republic of South Africa Government Gazette 2019). This evaluates the direction of response and status of the protected area and can only be investigated through consistent MPA research and monitoring going forward (Edgar et al. 2007).

REFERENCES

- Abe H, Takeuchi T, Taru M, Sato-Okoshi W, Okoshi K. 2019. Habitat availability determines distribution patterns of spionid polychaetes (Annelida: Spionidae) around Tokyo Bay. *Marine Biodiversity Records* 12.
- Akoumianaki I, Nicolaidou A. 2007. Spatial variability and dynamics of macrobenthos in a Mediterranean delta front area: the role of physical processes. *Journal of Sea Research* 57: 47-64.
- Akoumianaki I, Paspasyrou S, Kormas KA, Nicolaidou A. 2013. Environmental variation and macrofauna response in a coastal area influenced by land runoff. *Estuarine, Coastal and Shelf Science* 132: 34-44.
- Alongi DM, Robertson AI. 1995. Factors regulating benthic food chains in tropical river deltas and adjacent shelf areas. *Geo-Marine Letters* 15: 145-152.
- Amaral V, Cabral HN, Bishop MJ. 2012. Effects of estuarine acidification on predator-prey interactions. *Marine Ecology Progress Series* 445: 117-127.
- Ambrose WG. 1991. Are infaunal predators important in structuring marine soft-bottom communities? *American Zoologist* 31: 849-860.
- Anderson MJ, Gorley RN, Clarke KR. 2008. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. Plymouth: PRIMER-E.
- Ayers MJ, Scharler UM. 2011. Use of sensitivity and comparative analyses in constructing plausible trophic mass-balance models of a data-limited marine ecosystem — The KwaZulu-Natal Bight, South Africa. *Journal of Marine Systems* 88: 298-311.
- Bale AJ, Kenny AJ. 2005. Sediment analysis and seabed characterisation. In: Eleftheriou A, McIntyre A (eds). *Methods for the Study of Marine Benthos*. Oxford: Blackwell Science. pp. 43-86.
- Barnard KH. 1950. Descriptive catalogue of South African decapod Crustacea (crabs and shrimps). *Annals of the South African Museum* 38: 1-837.
- Beauchard O, Veríssimo H, Queirós AM, Herman PMJ. 2017. The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecological Indicators* 76: 81-96.
- Beesley PL, Ross GJB, Glasby CJ. 2000. *Polychaetes & Allies: The Southern Synthesis*. Fauna of Australia, Vol. 4A: Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. Melbourne: CSIRO Publishing.
- Begg G. 1978. *The Estuaries of Natal*. Natal Town and Regional Planning Report, Vol. 41. Natal.
- Bernard S, Smith M. 2011. *An investigation of the potential use of ocean colour remote sensing to assess the influence of variations in freshwater inputs to coastal ecosystems*:

- phytoplankton and sediment dynamics of the Natal Bight*. Water Research Commission Report No. 1852/1/10: Water Research Commission.
- Bigot L, Quod JP, Conand C. 2006. Bathymetric distribution of soft bottom tropical macrobenthos from the exposed east coast of Reunion Island (Southwest Indian Ocean). *Western Indian Ocean Journal of Marine Science* 5: 1-15.
- Bird C, Schweizer M, Roberts A, Austin WEN, Knudsen KL, Evans KM, Filipsson HL, Sayer MDJ, Geslin E, Darling KF. 2020. The genetic diversity, morphology, biogeography, and taxonomic designations of *Ammonia* (Foraminifera) in the Northeast Atlantic. *Marine Micropaleontology* 155: 101726.
- Blott SJ, Pye K. 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surface Processes and Landforms* 26: 1237-1248.
- Bone D, Rodriguez CT, Chollett I. 2011. Polychaeta diversity in the continental shelf off the Orinoco River Delta, Venezuela. In: Grillo O, Venora G (eds). *Changing Diversity in Changing Environment*. Croatia: InTech. pp. 87-98.
- Bosman C, Uken R, Leuci R, Smith AM, Sinclair D. 2007. Shelf sediments off the Thukela River mouth: complex interaction between fluvial and oceanographic processes. *South African Journal of Science* 103: 490-492.
- Bremner J. 2008. Species' traits and ecological functioning in marine conservation and management. *Journal of Experimental Marine Biology and Ecology* 366: 37-47.
- Bremner J, Rogers SI, Frid CLJ. 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series* 254: 11-25.
- Bremner J, Rogers SI, Frid CLJ. 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators* 6: 609-622.
- Brown AC. 1999. Marine invertebrate systematics and zoogeography in southern Africa: an historical overview. *Transactions of the Royal Society of South Africa* 54: 21-30.
- Brusca RC, Brusca GJ. 2003. *Invertebrates* (2nd edn). Massachusetts: Sinauer Associates, Inc.
- Buchanan JB, Kain JM. 1971. Measurement of the physical and chemical environment. In: Holme NA, McIntyre AD (eds). *Methods for the Study of Marine Benthos*. Oxford: Blackwell Scientific Publications. pp. 30-52.
- Byrne M, Przeslawski R. 2013. Multistressor impacts of warming and acidification of the ocean on marine invertebrates' life histories. *Integrative and Comparative Biology*. 53: 582-596.
- Careddu G, Costantini ML, Calizza E, Carlino P, Bentivoglio F, Orlandi L, Rossi L. 2015. Effects of terrestrial input on macrobenthic food webs of coastal sea are detected by stable isotope analysis in Gaeta Gulf. *Estuarine, Coastal and Shelf Science* 154: 158-168.
- Cartwright J. 2019. Ecological islands: conserving biodiversity hotspots in a changing climate. *Frontiers in Ecology and the Environment* 17: 331-340.

- Carvalho LRS, Loiola M, Barros F. 2017. Manipulating habitat complexity to understand its influence on benthic macrofauna. *Journal of Experimental Marine Biology and Ecology* 489: 48-57.
- Chao A, Colwell RK, Lin C-W, Gotelli NJ. 2009. Sufficient sampling for asymptotic minimum species richness estimators. *Ecology* 90: 1125-1133.
- Chapman MG, Tolhurst TJ, Murphy RJ, Underwood AJ. 2010. Complex and inconsistent patterns of variation in benthos, micro-algae and sediment over multiple spatial scales. *Marine Ecology Progress Series* 398: 33-47.
- Chevenet F, Dolédec S, Chessel D. 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* 31: 295-309.
- Clarke KR, Gorley RN. 2006. *PRIMER v6: User Manual/Tutorial*. Plymouth: PRIMER-E.
- Clarke KR, Gorley RN. 2015. *PRIMER v7: User Manual/Tutorial*. Plymouth: PRIMER-E.
- Clarke KR, Warwick RM. 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation* (2nd edn). Plymouth: PRIMER-E.
- CoastKZN. 2019. Available at <http://www.coastkzn.co.za/> [accessed 29 November 2019].
- Cocito S, Fanucci S, Niccolai I, Morri C, Bianchi CN. 1990. Relationships between trophic organization of benthic communities and organic matter content in Tyrrhenian Sea sediments. *Hydrobiologia* 207: 53-60.
- Colwell RK, Coddington JA. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B* 345: 101-118.
- Cooper JAG. 2001. Geomorphological variability among microtidal estuaries from the wave-dominated South African coast. *Geomorphology* 40: 99-122.
- Costello MJ, Claus S, Dekeyser S, Vandepitte L, Tuama ÉÓ, Lear D, Tyler-Walters H. 2015. Biological and ecological traits of marine species. *PeerJ* 3.
- Crame JA. 2000. Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of recent bivalve faunas. *Paleobiology* 26: 188-214.
- Cresson P, Ruitton S, Fontaine M-F, Harmelin-Vivien M. 2012. Spatio-temporal variation of suspended and sedimentary organic matter quality in the Bay of Marseilles (NW Mediterranean) assessed by biochemical and isotopic analyses. *Marine Pollution Bulletin* 64: 1112-1121.
- Currie DR, Sorokin SJ, Ward TM. 2009. Infaunal macroinvertebrate assemblages of the eastern Great Australian Bight: effectiveness of a marine protected area in representing the region's benthic biodiversity. *Marine and Freshwater Research* 60: 459-474.
- Dauvin J-C, Bakalem A, Baffreau A, Delecrin C, Bellan G, Lardicci C, Balestri E, Sarda R, Grimes S. 2017. The well sorted fine sand community from the western Mediterranean Sea: A resistant and resilient marine habitat under diverse human pressures. *Environmental Pollution* 224: 336-351.

- Day JH. 1967. *A Monograph on the Polychaeta of Southern Africa*. London: British Museum of Natural History.
- de la Haye KL, Spicer JI, Widdicombe S, Briffa M. 2011. Reduced sea water pH disrupts resource assessment and decision making in the hermit crab *Pagurus bernhardus*. *Animal Behaviour* 82: 495-501.
- De Lecea AM, Cooper R. 2016. The importance of the Thukela River Estuary, east coast of South Africa, for the biology of the near-shore environment and associated human aspects: a review. In: Diop S, Scheren P, Machiwa JF (eds). *Estuaries: A Lifeline of Ecosystem Services in the Western Indian Ocean*. Estuaries of the World. Switzerland: Springer. pp. 53-65.
- De Lecea AM, Fennessy ST, Smit AJ. 2013. Processes controlling the benthic food web of a mesotrophic bight (KwaZulu-Natal, South Africa) revealed by stable isotope analysis. *Marine Ecology Progress Series* 484: 97-114.
- De Lecea AM, Smit AJ, Fennessy ST. 2016. Riverine dominance of a nearshore marine demersal food web: evidence from stable isotope and C/N ratio analysis. *African Journal of Marine Science* 38(Supplement): S181-S192.
- Degen R, Faulwetter S. 2019. The Arctic Traits Database – a repository of Arctic benthic invertebrate traits, Earth System Science Data. Available at <https://www.univie.ac.at/arctictraits> [accessed July 2020].
- Demetriades NT, Forbes AT. 1993. Seasonal changes in the species composition of penaeid prawns on the Tugela Bank, Natal, South Africa. *South African Journal of Marine Science* 13: 317-322.
- Dolbeth M, Teixeira H, Marques JC, Pardal MÂ. 2009. Feeding guild composition of a macrobenthic subtidal community along a depth gradient. *Scientia Marina* 73: 225-237.
- Drinkwater KF, Frank KT. 1994. Effects of river regulation and diversion on marine fish and invertebrates. *Aquatic Conservation: Freshwater and Marine Ecosystems* 4: 135-151.
- Dutertre M, Hamon D, Chevalier C, Ehrhold A. 2013. The use of the relationships between environmental factors and benthic macrofaunal distribution in the establishment of a baseline for coastal management. *ICES Journal of Marine Science* 70: 294-308.
- Edgar GJ, Russ GR, Babcock RC. 2007. Marine protected areas. In: Connell SD, Gillanders BM (eds). *Marine Ecology*: Oxford University Press. pp. 534-565.
- Ellingsen KE. 2001. Biodiversity of a continental shelf soft-sediment macrobenthos community. *Marine Ecology Progress Series* 218: 1-15.
- Ellingsen KE. 2002. Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. *Marine Ecology Progress Series* 232: 15-27.
- Ellingsen KE, Hewitt JE, Thrush SF. 2007. Rare species, habitat diversity and functional redundancy in marine benthos. *Journal of Sea Research* 58: 291-301.
- Encyclopedia of Life. 2014. Available at <http://eol.org> [accessed July 2020].

- Engelbrecht L, Green AN, Cooper JAG, Hahn A, Zabel M, Mackay CF. 2020. Construction and evolution of submerged deltaic bodies on the high energy SE African coastline: The interplay between relative sea level and antecedent controls. *Marine Geology* 424: 106170.
- Fauchald K, Jumars PA. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* 17: 193-284.
- Fennessy S, Mann B, Steyn E, West W. 2014. Commercial Fisheries. *Ugu Lwethu – Our Coast. A profile of coastal KwaZulu-Natal*. Cedara: KwaZulu-Natal Department of Agriculture and Environmental Affairs and the Oceanographic Research Institute. pp. 124-127.
- Fennessy ST, Groeneveld JC. 1997. A review of the offshore trawl fishery for crustaceans on the east coast of South Africa. *Fisheries Management and Ecology* 4: 135-147.
- Fennessy ST, Villacastin C, Field JG. 1994. Distribution and seasonality of ichthyofauna associated with commercial prawn trawl catches on the Tugela Bank of Natal, South Africa. *Fisheries Research* 20: 263-282.
- Field JG, Clarke KR, Warwick RM. 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37-52.
- Flemming B, Hay R. 1988. Sediment distribution and dynamics on the Natal continental shelf. In: Schumann EH (ed). *Coastal Ocean Studies off Natal, South Africa*. Lecture Notes on Coastal and Estuarine Studies No. 26. Germany: Springer-Verlag. pp. 47-80.
- Flemming BW. 1981. Factors controlling shelf sediment dispersal along the southeast African continental margin. In: Nittrouer CA (ed). *Sedimentary Dynamics of Continental Shelves*. Developments in sedimentology No. 32. The Netherlands: Elsevier Scientific Publishing Company. pp. 259-277.
- Frid CLJ, Caswell BA. 2015. Is long-term ecological functioning stable: The case of the marine benthos? *Journal of Sea Research* 98: 15-23.
- Frid CLJ, Paramor OAL, Brockington S, Bremner J. 2008. Incorporating ecological functioning into the designation and management of marine protected areas. *Hydrobiologia* 606: 69-79.
- Giangrande A, Geraci S, Belmonte G. 1994. Life-cycle and life-history diversity in marine invertebrates and the implications in community dynamics. *Oceanography and Marine Biology: an Annual Review* 32: 305-333.
- Gotelli NJ, Colwell RK. 2011. Estimating species richness. In: Magurran AE, McGill BJ (eds). *Biological diversity: frontiers in measurement and assessment* Vol. 12. United States: Oxford University Press. pp. 39-54.
- Gray JS. 1981. *The Ecology of Marine Sediments: An Introduction to the Structure and Function of Benthic Communities*. Cambridge Studies in Modern Biology, Vol. 2. Cambridge: Cambridge University Press.
- Gray JS. 2002. Species richness of marine soft sediments. *Marine Ecology Progress Series* 244: 285-297.

- Gray JS, Elliott M. 2009. *Ecology of Marine Sediments: From Science to Management* (2nd edn). New York: Oxford University Press.
- Green AN, MacKay CF. 2016. Unconsolidated sediment distribution patterns in the KwaZulu-Natal Bight, South Africa: the role of wave ravinement in separating relict versus active sediment populations. *African Journal of Marine Science* 38: S65-S74.
- Griffiths CL. 1976. *Guide to the Benthic Marine Amphipods of Southern Africa*. Cape Town: Trustees of the South African Museum.
- Griffiths CL, Robinson TB, Lange L, Mead A. 2010. Marine biodiversity in South Africa: an evaluation of current states of knowledge. *PloS One* 5: e12008.
- Grippo MA, Fleeger JW, Dubois SF, Condrey R. 2011. Spatial variation in basal resources supporting benthic food webs revealed for the inner continental shelf. *Limnology and Oceanography* 56: 841-856.
- Guastella LA, Roberts MJ. 2016. Dynamics and role of the Durban cyclonic eddy in the KwaZulu-Natal Bight ecosystem. *African Journal of Marine Science* 38(Supplement): S23-S42.
- Gustiantini L, Dew KT, Müller A, Praptisih. 2007. Paleoenvironmental reconstruction from benthic foraminiferal assemblages of early Holocene, shallow marine deposits in Gombang, Central Java. *Bulletin of the Marine Geology* 22.
- Hall SJ. 2002. The continental shelf benthic ecosystem: current status, agents for change and future prospects. *Environmental Conservation* 29: 350-374.
- Hammer Ø, Harper DAT, Ryan PD 2001. PAST: Paleontological Statistics software package for education and data analysis. *Palaeontologia Electronica*.
- Harmelin-Vivien ML, Bănaru D, Dierking J, Hermand R, Letourneur Y, Salen-Picard C. 2009. Linking benthic biodiversity to the functioning of coastal ecosystems subjected to river runoff (NW Mediterranean). *Animal Biodiversity and Conservation* 32: 135-145.
- Hewitt JE, Thrush SF, Dayton PD. 2008. Habitat variation, species diversity and ecological functioning in a marine system. *Journal of Experimental Marine Biology and Ecology* 366: 116-122.
- Heydorn AEF, Bang ND, Pearce AF, Flemming BW, Carter RA, Schleyer MH, Berry PF, Hughes GR, Bass AJ, Wallace JH. 1978. Ecology of the Agulhas Current region: an assessment of biological responses to environmental parameters in the south-west Indian Ocean. *Transactions of the Royal Society of South Africa* 43: 151-190.
- Hunter CL. n.d. A sedimentological study of the Thukela Shelf, KwaZulu-Natal. MSc dissertation, University of KwaZulu-Natal, South Africa.
- Hunter IT. 1988. Climate and weather off Natal. In: Schumann EH (ed). *Coastal Ocean Studies off Natal, South Africa*. Lecture Notes on Coastal and Estuarine Studies No. 26. Germany: Springer-Verlag. pp. 81-100.

- Huston M. 1979. A general hypothesis of species diversity. *The American Naturalist* 113: 81-101.
- Hutchings L, Morris T, van der Lingen CD, Lamberth SJ, Connell AD, Taljaard S, van Niekerk L. 2010. Ecosystem considerations of the KwaZulu-Natal sardine run. *African Journal of Marine Science* 32: 413-421.
- Hyland J, Balthis L, Karakassis I, Magni P, Petrov A, Shine J, Vestergaard O, Warwick R. 2005. Organic carbon content of sediments as an indicator of stress in the marine benthos. *Marine Ecology Progress Series* 295: 91-103.
- Jax K. 2005. Function and “functioning” in ecology: what does it mean? *Oikos* 111: 641-648.
- Jayaraj KA, Jayalakshmi KV, Saraladevi K. 2007. Influence of environmental properties on macrobenthos in the northwest Indian shelf. *Environmental Monitoring and Assessment* 127: 459-475.
- Jayaraj KA, Josia J, Dinesh Kumar PK. 2008. Infaunal macrobenthic community of soft bottom sediment in a tropical shelf. *Journal of Coastal Research* 24: 708-718.
- Joydas TV, Damodaran R. 2009. Infaunal macrobenthos along the shelf waters of the west coast of India, Arabian Sea. *Indian Journal of Marine Sciences* 38: 191-204.
- Jumars PA, Dorgan KM, Lindsay SM. 2015. Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science*. 7: 497-520.
- Kaminsky J, Varisco M, Fernández M, Sahade R, Archambault P. 2018. Spatial analysis of benthic functional biodiversity in San Jorge Gulf, Argentina. *Oceanography* 31: 104-112.
- Karakassis I, Eleftheriou A. 1997. The continental shelf of Crete: structure of macrobenthic communities. *Marine Ecology Progress Series* 160: 185-196.
- Karati KK, Vineetha G, Raveendran TV, Muraleedharan KR, Habeebrehman H, Philson KP, Achuthankutty CT. 2018. River plume fronts and their implications for the biological production of the Bay of Bengal, Indian Ocean. *Marine Ecology Progress Series* 597: 79-98.
- Katz ME, Cramer BS, Franzese A, Hönisch B, Miller KG, Rosenthal Y, Wright JD. 2010. Traditional and emerging geochemical proxies in Foraminifera. *Journal of Foraminiferal Research* 40: 165-192.
- Kennedy WJ, Taylor JD, Hall A. 1969. Environmental and biological controls on bivalve shell mineralogy. *Biological Reviews* 44: 499-530.
- Kensley BF. 1972. *Shrimps and Prawns of Southern Africa*. Cape Town: Trustees of the South African Museum.
- Kensley BF. 1978. *Guide to the Marine Isopods of Southern Africa*. Cape Town: Trustees of the South African Museum.

- Khan A, Manokaran S, Lyla S. 2017. Changes in macrobenthic community structure from estuary to continental slope in the south-east coast of India. *Journal of the Marine Biological Association of the United Kingdom* 97: 161-180.
- Kilburn R, Rippey E. 1982. *Sea Shells of Southern Africa*. Johannesburg: Macmillan South Africa (Publishers) (Pty) Ltd.
- Laidre ME. 2011. Ecological relations between hermit crabs and their shell-supplying gastropods: Constrained consumers. *Journal of Experimental Marine Biology and Ecology* 397: 65-70.
- Lamberth SJ, Drapeau L, Branch GM. 2009. The effects of altered freshwater inflows on catch rates of non-estuarine-dependent fish in a multispecies nearshore linefishery. *Estuarine, Coastal and Shelf Science* 84: 527-538.
- Legendre P, Galzin R, Harmelin-Vivien ML. 1997. Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology* 78: 547-562.
- Levinton J. 1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. *The American Naturalist* 106: 472-486.
- Lewandowski AS, Noss RF, Parsons DR. 2010. The effectiveness of surrogate taxa for the representation of biodiversity. *Conservation Biology* 24: 1367-1377.
- Lipps JH, Valentine JW. 1970. The role of Foraminifera in the trophic structure of marine communities. *Lethaia* 3: 279-286.
- Lohrer AM, Thrush SF, Lundquist CJ, Vopel K, Hewitt JE, Nicholls PE. 2006. Deposition of terrigenous sediment on subtidal marine macrobenthos: response of two contrasting community types. *Marine Ecology Progress Series* 307: 115-125.
- Lohrer D, Hancock N. 2004. Marine soft sediments: more diversity than meets the eye. *Water & Atmosphere* 12: 26-27.
- Louzao M, Anadón N, Arrontes J, Álvarez-Claudio C, Fuente DM, Ocharan F, Anadón A, Acuña JL. 2010. Historical macrobenthic community assemblages in the Avilés Canyon, N Iberian Shelf: baseline biodiversity information for a marine protected area. *Journal of Marine Systems* 80: 47-56.
- Lutjeharms JRE. 2006a. *The Agulhas Current*. Germany: Springer.
- Lutjeharms JRE. 2006b. The coastal oceans of south-eastern Africa. In: Robinson AR, Brink KH (eds). *The Sea* Vol. 14B. The Global Coastal Ocean: Interdisciplinary Regional Studies and Syntheses. Cambridge: Harvard University Press. pp. 783-834.
- Lutjeharms JRE. 2006c. The ocean environment off southeastern Africa: a review *South African Journal of Science* 102: 419-426.
- Lutjeharms JRE, Valentine HR, Van Ballegooyen RC. 2000. The hydrography and water masses of the Natal Bight, South Africa. *Continental Shelf Research* 20: 1907-1939.

- Macdonald TA, Burd BJ, Macdonald VI, van Roodselaar A. 2010. *Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia*. Canadian Technical Report of Fisheries and Aquatic Sciences Report No. 2874. Canada.
- Macdonald TA, Burd BJ, van Roodselaar A. 2012. Facultative feeding and consistency of trophic structure in marine soft-bottom macrobenthic communities. *Marine Ecology Progress Series* 445: 129-140.
- MacKay CF. 2006. *Macrobenthic survey of the subtidal soft sediment communities of the Port of Richards Bay during dredging for Berth 306*. Oceanographic Research Institute. ORI Unpublished Report No. 239. Durban.
- MacKay CF 2010. ACEP macrobenthic sampling protocol R/V Algoa survey of Natal Bight, February 2010. Durban: Oceanographic Research Institute.
- MacKay CF, Untiedt CB, Hein L. 2016. Local habitat drivers of macrobenthos in the northern, central and southern KwaZulu-Natal Bight, South Africa. *African Journal of Marine Science* 38(Supplement): S105-S121.
- Mackie ASY, Oliver PG, Darbyshire T, Mortimer K. 2005. Shallow marine benthic invertebrates of the Seychelles Plateau: high diversity in a tropical oligotrophic environment. *Philosophical Transactions of the Royal Society A*. 363: 203-228.
- Maduna SM. 2017. Macrobenthos used to validate multi-criteria derived marine biodiversity spatial zones in KwaZulu-Natal, South Africa. MSc dissertation, University of KwaZulu-Natal, South Africa.
- Maggiore F, Keppel E. 2007. Biodiversity and distribution of polychaetes and molluscs along the Dese estuary (Lagoon of Venice, Italy). *Hydrobiologia* 588: 189-203.
- Manokaran S, Khan SA, Lyla S, Raja S, Ansari KGMT. 2013. Feeding guild composition of shelf macrobenthic polychaetes of southeast coast of India. *Tropical Zoology* 26: 120-139.
- Margules CR, Pressey RL. 2000. Systematic conservation planning. *Nature* 405: 243-253.
- Marine Life Information Network. 2006. BIOTIC - Biological Traits Information Catalogue. Available at www.marlin.ac.uk/biotic [accessed July 2020].
- Mason NWH, Mouillot D, Lee WG, Wilson JB. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111: 112-118.
- Maurer D, Leathem W. 1980. Dominant species of polychaetous annelids of Georges Bank. *Marine Ecology Progress Series* 3: 135-144.
- McArthur MA, Brooke BP, Przeslawski R, Ryan DA, Lucieer VL, Nichol S, McCallum AW, Mellin C, Cresswell ID, Radke LC. 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. *Estuarine, Coastal and Shelf Science* 88: 21-32.
- McClain CR, Barry JP. 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* 91: 964-976.

- McClurg TP. 1988. Benthos of the Natal continental shelf. In: Schumann EH (ed). *Coastal Ocean Studies off Natal, South Africa*. Lecture Notes on Coastal and Estuarine Studies No. 26. Germany: Springer-Verlag. pp. 178-208.
- McGovern M, Poste AE, Oug E, Renaud PE, Trannum HC. 2020. Riverine impacts on benthic biodiversity and functional traits: A comparison of two sub-Arctic fjords. *Estuarine, Coastal and Shelf Science* 240: 106774.
- McHugh D, Fong PP. 2002. Do life history traits account for diversity of polychaete annelids? *Invertebrate Biology* 121: 325-338.
- McKee BA, Aller RC, Allison MA, Bianchi TS, Kineke GC. 2004. Transport and transformation of dissolved and particulate materials on continental margins influenced by major rivers: benthic boundary layer and seabed processes. *Continental Shelf Research* 24: 899-926.
- Meyer AA, Lutjeharms JRE, de Villiers S. 2002. The nutrient characteristics of the Natal Bight, South Africa. *Journal of Marine Systems* 35: 11-37.
- Miatta M, Bates AE, Snelgrove PVR. 2021. Incorporating biological traits into conservation strategies. *Annual Review of Marine Science*. 13: 421-443.
- Moreno CE, Pineda E, Escobar F, Sánchez-Rojas G. 2007. Shortcuts for biodiversity evaluation: a review of terminology and recommendations about the use of target groups, bioindicators and surrogates. *International Journal of Environment and Health* 1: 71-86.
- Moulin FY, Guizien K, Thouzeau G, Chapalain G, Mülleners K, Bourg C. 2007. Impact of an invasive species, *Crepidula fornicata*, on the hydrodynamics and transport properties of the benthic boundary layer. *Aquatic Living Resources* 20: 15-31.
- Muniz P, Pires AMS. 1999. Trophic structure of polychaetes in the São Sebastião Channel (southeastern Brazil). *Marine Biology* 134: 517-528.
- Muniz P, Pires AMS. 2000. Polychaete associations in a subtropical environment (São Sebastião Channel, Brazil): a structural analysis. *Marine Ecology* 21: 145-160.
- Murray JW. 2001. The niche of benthic foraminifera, critical thresholds and proxies. *Marine Micropaleontology* 41: 1-7.
- Murray JW. 2006. *Ecology and Applications of Benthic Foraminifera*. New York: Cambridge University Press.
- Naeem S, Wright JP. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* 6: 567-579.
- Norling K, Rosenberg R, Hulth S, Grémare A, Bonsdorff E. 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology Progress Series* 332: 11-23.
- O'Hara RB, Kotze DJ. 2010. Do not log-transform count data. *Nature Precedings*.

- Olbers JM, Samyn Y, Griffiths CL. 2015. New or notable records of brittle stars (Echinodermata: Ophiuroidea) from South Africa. *African Natural History* 11: 83-116.
- Pacheco AS, González MT, Bremner J, Oliva M, Heilmayer O, Laudien J, Riascos JM. 2011. Functional diversity of marine macrobenthic communities from sublittoral soft-sediment habitats off northern Chile. *Helgoland Marine Research* 65: 413-424.
- Paganelli D, Marchini A, Occhipinti-Ambrogi A. 2012. Functional structure of marine benthic assemblages using Biological Traits Analysis (BTA): A study along the Emilia-Romagna coastline (Italy, North-West Adriatic Sea). *Estuarine, Coastal and Shelf Science* 96: 245-256.
- Passarelli C, Olivier F, Paterson DM, Hubas C. 2012. Impacts of biogenic structures on benthic assemblages: microbes, meiofauna, macrofauna and related ecosystem functions. *Marine Ecology Progress Series* 465: 85-97.
- Pearce AF, Schumann EH, Lundie GSH. 1978. Features of the shelf circulation off the Natal coast. *South African Journal of Science* 74: 328-331.
- Pearson TH, Rosenberg R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology Annual Review* 16: 229-311.
- Petchey OL, Gaston KJ. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9: 741-758.
- Pinedo S, Sardá R, Rey C, Bhaud M. 2000. Effect of sediment particle size on recruitment of *Owenia fusiformis* in the Bay of Blanes (NW Mediterranean Sea): an experimental approach to explain field distribution. *Marine Ecology Progress Series* 203: 205-213.
- Pocklington P, Wells PG. 1992. Polychaetes: key taxa for marine environmental quality monitoring. *Marine Pollution Bulletin* 24: 593-598.
- Pratt DR, Lohrer AM, Pilditch CA, Thrush SF. 2014. Changes in ecosystem function across sedimentary gradients in estuaries. *Ecosystems* 17: 182-194.
- Probert PK, Read GB, Grove SL, Rowden AA. 2001. Macrobenthic polychaete assemblages of the continental shelf and upper slope off the west coast of the South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 35: 971-984.
- Queirós AM, Birchenough SNR, Bremner J, Godbold JA, Parker RE, Romero-Ramirez A, Reiss H, Solan M, Somerfield PJ, Van Colen C, Van Hoey G, Widdicombe S. 2013. A bioturbation classification of European marine infaunal invertebrates. *Ecology and Evolution* 3: 3958-3985.
- Raja S, Khan SA, Lyla PS, Manokaran S. 2014. Diversity of macrofauna from continental shelf off Singarayakonda (southeast coast of India). *Pakistan Journal of Biological Sciences*.
- Reise K. 2002. Sediment mediated species interactions in coastal waters. *Journal of Sea Research* 48: 127-141.

- Republic of South Africa Government Gazette. 2019. *National Environmental Management: Protected Areas Act (57/2003) Government Gazette 42478*. Republic of South Africa.
- Reymond CE, Uthicke S, Pandolfi JM. 2012. Tropical Foraminifera as indicators of water quality and temperature, *Proceedings of the 12th International Coral Reef Symposium 2012, Cairns, Australia*.
- Rhoads DC, Boesch DF, Zhican T, Fengshan X, Liqiang H, Nilsen KJ. 1985. Macrobenthos and sedimentary facies on the Changjiang delta platform and adjacent continental shelf, East China Sea. *Continental Shelf Research* 4: 189-213.
- Rhoads DC, Young DK. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* 28: 150-178.
- Roberts MJ, Nieuwenhuys C, Guastella LA. 2016. Circulation of shelf waters in the KwaZulu-Natal Bight, South Africa. *African Journal of Marine Science* 38(Supplement): S7-S21.
- Roberts MJ, van der Lingen CD, Whittle C, van den Berg M. 2010. Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: their relevance to the KwaZulu-Natal sardine run. *African Journal of Marine Science* 32: 423-447.
- Salen-Picard C, Darnaude AM, Arlhac D, Harmelin-Vivien ML. 2002. Fluctuations of macrobenthic populations: a link between climate-driven river run-off and sole fishery yields in the Gulf of Lions. *Oecologia* 133: 380-388.
- Sanders HL. 1958. Benthic Studies in Buzzards Bay, I. Animal-Sediment Relationships. *Limnology and Oceanography* 3: 245-258.
- Scharler UM, Ayers MJ. 2019. Stoichiometric multitrophic networks reveal significance of land-sea interaction to ecosystem function in a subtropical nutrient-poor bight, South Africa. *Plos One* 14: e0210295.
- Scharler UM, Ayers MJ, de Lecea AM, Pretorius M, Fennessy ST, Huggett JA, MacKay CF, Muir D. 2016a. Riverine influence determines nearshore heterogeneity of nutrient (C, N, P) content and stoichiometry in the KwaZulu-Natal Bight, South Africa. *African Journal of Marine Science* 38(Supplement): S193-S203.
- Scharler UM, van Ballegooyen RC, Ayers MJ. 2016b. A system-level modelling perspective of the KwaZulu-Natal Bight ecosystem, eastern South Africa. *African Journal of Marine Science* 38(Supplement): S205-S216.
- Schleuter D, Daufresne M, Massol F, Argillier C. 2010. A user's guide to functional diversity indices. *Ecological Monographs* 80: 469-484.
- Schumacher BA. 2002. *Methods for the determination of total organic carbon (TOC) in soils and sediments*. United States Environmental Protection Agency. Las Vegas.
- Schumann EH. 1987. The coastal ocean off the east coast of South Africa. *Transactions of the Royal Society of South Africa* 46: 215-229.

- Schumann EH. 1988. Physical oceanography off Natal. In: Schumann EH (ed). *Coastal Ocean Studies off Natal, South Africa*. Lecture Notes on Coastal and Estuarine Studies No. 26. Germany: Springer-Verlag. pp. 101-130.
- Sen Gupta BK, Machain-Castillo ML. 1993. Benthic foraminifera in oxygen-poor habitats. *Marine Micropaleontology* 20: 183-201.
- Shin PKS, Huang ZG, Wu RSS. 2004. An updated baseline of subtropical macrobenthic communities in Hong Kong. *Marine Pollution Bulletin* 49: 119-141.
- Sigala K, Reizopoulou S, Basset A, Nicolaidou A. 2012. Functional diversity in three Mediterranean transitional water ecosystems. *Estuarine, Coastal and Shelf Science* 110: 202-209.
- Sigwart JD, Sumner-Rooney LH. 2016. Mollusca: Caudofoveata, Monoplacophora, Polyplacophora, Scaphopoda and Solenogastres. In: Schmidt-Rhaesa A, Harzsch S, Purschke G (eds). *Structure and Evolution of Invertebrate Nervous Systems*: Oxford University Press. pp. 172-189.
- Simone LRL, Wilkinson S. 2008. Comparative morphological study of some Tellinidae from Thailand (Bivalvia: Tellinoidea). *The Raffles Bulletin of Zoology* 18: 151-190.
- Skowno AL, Poole CJ, Raimondo DC, Sink KJ, Van Deventer H, Van Niekerk L, Harris LR, Smith-Adao LB, Tolley KA, Zengeya TA, Foden WB, Midgley GF, Driver A. 2019. *National Biodiversity Assessment 2018: The status of South Africa's ecosystems and biodiversity. Synthesis Report*. South African National Biodiversity Institute, an entity of the Department of Environment, Forestry and Fisheries Pretoria.
- Snelgrove PVR. 1997. The importance of marine sediment biodiversity in ecosystem processes. *Ambio* 26: 578-583.
- Snelgrove PVR. 1998. The biodiversity of macrofaunal organisms in marine sediments. *Biodiversity and Conservation* 7: 1123-1132.
- Snelgrove PVR. 1999. Getting to the bottom of marine biodiversity: sedimentary habitats: ocean bottoms are the most widespread habitat on Earth and support high biodiversity and key ecosystem services. *BioScience* 49: 129-138.
- Snelgrove PVR, Thrush SF, Wall DH, Norkko A. 2014. Real world biodiversity–ecosystem functioning: a seafloor perspective. *Trends in Ecology & Evolution* 29: 398-405.
- Stamhuis EJ, Schreurs CE, Videler JJ. 1997. Burrow architecture and turbative activity of the thalassinid shrimp *Callinassa subterranea* from the central North Sea. *Marine Ecology Progress Series* 151: 155-163.
- Steyn DG, Lussi M. 1998. *Marine Shells of South Africa: An illustrated collector's guide to beached shells*. Hartbeespoort: Ekogilde Publishers.
- Thrush SF, Dayton PK. 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annual Review of Ecology and Systematics* 33: 449-473.

- Todt C, Okusu A, Schander C, Schwabe E. 2008. Solenogastres, Caudofoveata, and Polyplacophora. In: Ponder WF, Lindberg DR (eds). *Phylogeny and Evolution of the Mollusca* Vol. 4: University of California Press. pp. 71-96.
- Tyler EHM, Somerfield PJ, Berghe EV, Bremner J, Jackson E, Langmead O, Palomares MLD, Webb TJ. 2012. Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. *Global Ecology and Biogeography* 21: 922-934.
- Udalov A, Chikina M, Azovsky A, Basin A, Galkin S, Garlitska L, Khusid T, Kondar D, Korsun S, Kremenetskiy V, Makkaveev P, Portnova D, Sapojnikov P, Simakov M, Vedenin A, Mokievsky V. 2021. Integrity of benthic assemblages along the arctic estuarine-coastal system. *Ecological Indicators* 121: 107115.
- Underwood AJ, Chapman MG. 2005. Design and analysis in benthic surveys. In: Eleftheriou A, McIntyre A (eds). *Methods for the Study of Marine Benthos*. Oxford: Blackwell Science. pp. 1-42.
- Untiedt CB. 2013. Community structure and function of macrobenthos in three feature areas of the Natal Bight, South Africa. MSc dissertation, University of KwaZulu-Natal, South Africa.
- Untiedt CB, MacKay CF. 2016. Distribution and feeding modes of macrobenthos within three oceanographic feature areas of the KwaZulu-Natal Bight, South Africa. *African Journal of Marine Science* 38(Supplement): S91-S104.
- van Niekerk L, Adams JB, James NC, Lamberth SJ, MacKay CF, Turpie JK, Rajkaran A, Weerts SP, Whitfield AK. 2020. An estuary ecosystem classification that encompasses biogeography and a high diversity of types in support of protection and management. *African Journal of Aquatic Science* 45: 199-216.
- Verfaillie E, Van Lancker V, Van Meirvenne M. 2006. Multivariate geostatistics for the predictive modelling of the surficial sand distribution in shelf seas. *Continental Shelf Research* 26: 2454-2468.
- Veríssimo H, Bremner J, Garcia C, Patrício J, van der Linden P, Marques JC. 2012. Assessment of the subtidal macrobenthic community functioning of a temperate estuary following environmental restoration. *Ecological Indicators* 23: 312-322.
- Vijapure T, Sukumaran S, Neetu S, Chandel K. 2019. Macrobenthos at marine hotspots along the Northwest Indian inner shelf: patterns and drivers. *Marine Environmental Research* 144: 111-124.
- Villnäs A, Janas U, Josefson AB, Kendzierska H, Nygård H, Norkko J, Norkko A. 2019. Changes in macrofaunal biological traits across estuarine gradients: implications for the coastal nutrient filter. *Marine Ecology Progress Series* 622: 31-48.
- Wentworth CK. 1922. A scale of grade and class terms for clastic sediments. *The Journal of Geology* 30: 377-392.

- Whitfield AK, Harrison TD. 2003. River flow and fish abundance in a South African estuary. *Journal of Fish Biology* 62: 1467-1472.
- Wilson WH. 1991. Sexual reproductive modes in polychaetes: classification and diversity. *Bulletin of Marine Science* 48: 500-516.
- Wooldridge TH, Coetzee PS. 1988. Marine invertebrates. In: Lubke R, Moor Id (eds). *Field Guide to the Eastern & Southern Cape Coasts*. Rondebosch: University of Cape Town Press.
- World Register of Marine Species Editorial Board. 2021. World Register of Marine Species. Available at <http://www.marinespecies.org> [accessed 01 February 2021].
- Zalmon IR, Macedo IM, Rezende CE, Falcão APC, Almeida TC. 2013. The distribution of macrofauna on the inner continental shelf of southeastern Brazil: The major influence of an estuarine system. *Estuarine, Coastal and Shelf Science* 130: 169-178.