

# **COMMUNITY STRUCTURE AND FUNCTION OF MACROBENTHOS IN THREE FEATURE AREAS OF THE NATAL BIGHT, SOUTH AFRICA**

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

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This thesis is dedicated to Robert

## ABSTRACT

The Natal Bight off the east coast of South Africa is a unique shelf habitat, exhibiting high secondary productivity and supporting high diversity. Ecosystem attributes are influenced by local oceanographic features and outwelling via one of the largest rivers in the country. This study forms part of a larger, multi-institutional, multi-disciplinary study under the second phase of the African Coelacanth Ecosystem Programme (ACEP II) Natal Bight Project, investigating how material sources, posited to be derived from these features, shape the ecological structure and functioning of the region. Macrobenthic samples were collected along cross shelf transects off Richard's Bay, Durban and the Thukela River mouth during two cruises, corresponding with periods of variable rainfall. Macrobenthic communities were classified taxonomically, to the lowest level possible, and functionally. Community patterns were investigated within and between feature areas and related to measurable environmental factors in order to determine environmental drivers and assess the importance of identified oceanographic features. Environmental parameters measured included sedimentary characteristics as well as physico-chemical conditions in the surrounding pelagic milieu. A total of 38 215 individuals belonging to 826 taxa were recorded from the three feature areas, of which the majority were Polychaeta and Crustacea. An in-depth investigation of the polychaete component has shown that this group can be used as a proxy for the whole macrobenthic community which has important implications for future studies. Facultative feeding modes dominated the trophic functioning macrobenthic communities sampled on the Natal Bight. Primary community metrics of abundance and numbers of macrobenthic taxa were reduced from the high to low rainfall period but differences were not significant, probably due to the lack of temporal repetition. The Thukela feature area was found to support the most abundant and taxon rich macrobenthic community. Mid-shelf stations sampled along the Thukela and Durban transects were in close proximity to the coarse paleo-dune cordon, running along the 60 m isobath and supported a diverse assemblage. Despite the lack of temporal repetition in the present study, there were significant short-term changes in the structure and functioning of macrobenthic communities on the Thukela shelf. This suggests that Thukela River outflow has a significant effect on the functioning of the Natal Bight ecosystem. This was surprising given the importance which has previously been placed on the Cape St. Lucia upwelling cell in terms of contributing nutrients and sustaining biological productivity and diversity on the Natal Bight.

## **PREFACE**

The work described in this thesis was carried out at the Oceanographic Research Institute, an affiliate of the University of KwaZulu Natal, Durban, in the School Life Sciences, from April 2010 to November 2013, under the supervision of Fiona Mackay.

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

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## **DECLARATION**

### **PLAGIARISM**

I, ....., declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
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.....

Candice Bobby Untiedt

Date

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# TABLE OF CONTENTS

<b>ABSTRACT .....</b>	<b>iii</b>
<b>PREFACE.....</b>	<b>iv</b>
<b>DECLARATION .....</b>	<b>v</b>
<b>ACKNOWLEDGEMENTS.....</b>	<b>vi</b>
<b>TABLE OF CONTENTS.....</b>	<b>vii</b>
<b>CHAPTER 1. GENERAL INTRODUCTION .....</b>	<b>1</b>
<b>1.1 Context of study.....</b>	<b>1</b>
<b>1.2 Continental shelves.....</b>	<b>1</b>
1.2.1 Shelf Productivity .....	2
<b>1.3 Macrobenthic communities .....</b>	<b>3</b>
1.3.2 Classification of macrobenthic communities.....	4
<b>1.4 The influence of environmental factors .....</b>	<b>8</b>
1.4.1 Inter-relation of environmental factors .....	9
1.4.2 Relationship between macrobenthic communities and environmental factors .....	10
<b>1.5 Macrobenthos of South African shelf environments .....</b>	<b>10</b>
<b>1.6 Project Aims and Objectives.....</b>	<b>13</b>
<b>1.7 Thesis Outline .....</b>	<b>13</b>
<b>CHAPTER 2. GENERAL MATERIAL AND METHODS.....</b>	<b>15</b>
<b>2.1 Study Area – Natal Bight.....</b>	<b>15</b>
2.1.1 Location and characteristics .....	15
2.1.2 Oceanography.....	17
2.1.3 Physico-chemical characteristics .....	18
2.1.4 Sediment characteristics.....	21
2.1.5 Feature Areas.....	22
<b>2.2 Study design and sampling protocol.....</b>	<b>25</b>
2.2.1 Field sampling procedure .....	26
2.2.2 Laboratory procedure .....	29
2.2.3 Generic Statistical analysis .....	33
<b>CHAPTER 3. MACROBENTHIC COMMUNITIES AND FEEDING MODE PATTERNS WITHIN AND BETWEEN THREE OCEANOGRAPHIC FEATURE AREAS OF THE NATAL BIGHT .....</b>	<b>42</b>
<b>3.1 Introduction.....</b>	<b>42</b>
<b>3.2 Materials and Methods.....</b>	<b>44</b>
3.2.1 Study area and Sampling Design .....	44

3.2.2 Data handling and analysis.....	44
<b>3.3 Results .....</b>	<b>48</b>
3.3.1 Environmental parameters.....	48
3.3.2 Faunal distribution patterns.....	53
3.3.3 Relation of faunal patterns to environmental parameters .....	71
<b>3.4 Discussion.....</b>	<b>76</b>
<b>CHAPTER 4. THE INFLUENCE OF THE THUKELA RIVER FLOW REGIME ON MACROBENTHIC TAXONOMIC RELATIONSHIPS AND FEEDING MODES ..</b>	<b>87</b>
<b>4.1 Introduction .....</b>	<b>87</b>
<b>4.2 Materials and Methods .....</b>	<b>92</b>
4.2.1 Study area and Sampling Design .....	92
4.2.2 Data handling and analysis.....	92
<b>4.3 Results .....</b>	<b>96</b>
4.3.1 Environmental conditions .....	96
4.3.2 Macrobenthic community analysis: lowest identifiable taxa and major Phyla.....	99
The effect of cruise (variable periods of outflow) .....	99
The influence of shelf position during periods of variable outflow .....	101
Community patterns based on lowest identifiable taxa .....	107
4.3.3 Macrobenthic community analysis – feeding modes.....	110
The effect of cruise (variable periods of outflow) .....	110
The influence of shelf position during high and low outflow periods.....	113
Community patterns based on feeding mode.....	115
4.3.4 Macrobenthic-environment relationship .....	118
The relationship between lowest identifiable taxa and environmental variables .....	118
The relationship between feeding modes and environmental variables.....	121
<b>4.4 Discussion.....</b>	<b>123</b>
<b>CHAPTER 5. POLYCHAETES OF THE NATAL BIGHT: PATTERNS CONSIDERING FAMILIES AND FEEDING GUILDS .....</b>	<b>130</b>
<b>5.1 Introduction .....</b>	<b>130</b>
<b>5.2 Materials and Methods.....</b>	<b>133</b>
5.2.1 Study area .....	134
5.2.2 Laboratory procedure.....	134
5.2.3 Data analysis .....	136
<b>5.3 Results .....</b>	<b>138</b>
5.3.1 The effect of Cruise .....	138
5.3.2 The effect of feature area .....	144

5.3.3 The effect of shelf position .....	146
5.3.4 Polychaete Community patterns.....	149
<b>5.4 Discussion.....</b>	<b>158</b>
<b>CHAPTER 6. GENERAL DISCUSSION AND CONCLUSIONS.....</b>	<b>168</b>
<b>REFERENCES .....</b>	<b>177</b>

## LIST OF FIGURES

Figure 1.1.	General trophic structure of an ecosystem. Solid lines indicate the flow of energy and dashed lines the flow of nutrients (modified from Gray 1981).....	6
Figure 2.1.	The Natal Bight study area with feature areas, bathymetry and shelf circulation shown (modified from Schuman 1987).....	16
Figure 2.2.	Test model of factors considered in the present study and their interactions. <b>Cruise A</b> (High rainfall – February 2010), <b>Cruise B</b> (Low rainfall – August 2010), <b>RB</b> =Richards Bay, <b>TK</b> =Thukela, <b>DN</b> =Durban, <b>IS</b> =Inner shelf, <b>MS</b> =Mid-shelf, <b>OS</b> =Outer shelf.....	33
Figure 2.3.	Summary of the stages in multivariate Q-type analysis (modified from Field <i>et al.</i> 1982).....	38
Figure 3.1.	Map of the study area showing shelf position stations, nutrient and primary productivity stations sampled along cross-shelf transect in three feature areas during a high (February 2010) and low (August 2010) rainfall period.....	47
Figure 3.2.	Pearson Correlation ( $r$ ) between depth (m) and near bottom temperature ( $^{\circ}\text{C}$ ), salinity and dissolved Oxygen ( $\text{mg.L}^{-1}$ ) for feature area: Richard's Bay (RB), Thukela (TK) and Durban (DN), samples collected during cruises A and B.....	51
Figure 3.3.	Pearson Correlation ( $r$ ) between mean grain size ( $\phi$ ) and total organic contents (%TOC) of sediment sampled from each feature area: Richard's Bay (RB), Thukela (TK) and Durban (DN), during cruises A and B.....	53
Figure 3.4.	Chlorophyll $a$ (Chl- $a$ ) and nutrient characteristics (Nitrate: $\text{NO}_3$ , Silicate: Si and Phosphate: $\text{PO}_4$ ) of feature areas sampled on the Natal Bight during cruises A (black symbol) and B (grey symbol).....	54
Figure 3.5.	Boxplots of abundance ( $N$ : no of ind. $\text{m}^{-2}$ ) and no. of taxa ( $S$ ) for macrobenthos sampled during two cruises, pooled for three feature area cross-shelf transects. Black line within boxplot represents the median, white line represents the mean.....	56
Figure 3.6.	Mean abundance ( $N$ : no of ind. $\text{m}^{-2}$ ) and no. of taxa ( $S$ ) for macrobenthos sampled in three feature areas (RB, TK and DN) during cruises A and B. Bars = $\bar{x}$ $N$ and Circles = $\bar{x}$ $S$ .....	57

Figure 3.7. Mean abundance ( $N$ : no of ind.m<sup>-2</sup>) and no. of taxa ( $S$ ) for macrobenthos sampled in the inner (IS), mid (MS) and outer shelf (OS) positions during cruises A and B. Bars =  $\bar{x}$   $N$  and Circles =  $\bar{x}$   $S$ .....58

Figure 3.8. Dendrograms of hierarchical clustering (using group-average linkage) for samples collected within each feature area (RB, TK, DN) during cruises A and B. Plots are based on Bray-Curtis similarities calculated from square root transformed taxon and feeding mode abundance ( $N$ ) data.....60

Figure 3.9. Dendrogram of hierarchical clustering (using group-average linkage) for 54 samples collected during cruises A and B. The plot is based on Bray-Curtis similarities calculated from taxon abundance ( $N$ ) data that was pre-transformed by square root. The seven sample Groups (I-VII) defined at a similarity of 21% are presented with the corresponding depth (m) and mean grain size ( $\phi$ ).....63

Figure 3.10. Mean abundance ( $N$ : no of ind.m<sup>-2</sup>) and no. of taxa ( $S$ ) for sample Groups I-VII defined by cluster analysis. Circles =  $\bar{x}$   $N$  and Crosses =  $\bar{x}$   $S$ .....65

Figure 3.11. Contribution (%) of major Phyla to the abundance of Groups I-VII defined in cluster analysis.....66

Figure 3.12. Contribution (%) of feeding modes to the abundance of Groups I-VII defined in cluster analysis. IF=Interface feeder, C=Carnivore, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, SF=Suspension feeder, MM=Multi-modal, O=Omnivore, Par=Parasite, U=Unknown.....67

Figure 3.13. Canonical Correspondence Analysis showing the relation between environmental variables and macrobenthic communities of Groups I-VII as well as taxa contributing more than 3% to “within group” similarity and “between group” dissimilarity.....75

Figure 4.1. Map showing the location and bathymetry of shelf position, nutrient and primary productivity stations samples along a transect from the Thukela River mouth to shelf edge during cruises A and B.....94

Figure 4.2. Temperature (°C), Salinity and Dissolved Oxygen concentration (mg.L<sup>-1</sup>) of near-bottom waters plotted against depth (m) for stations sampled along the Thukela transect during cruises A and B. I1=Inner shelf, I2 and I3=Transition zone 1, I4=Mid-shelf, I5 and I6=Transition zone 2. Cruise A (High outflow: February 2010), Cruise B (Low outflow: August 2010).....98

Figure 4.3. Boxplots of abundance ( $N$ ) and no. of taxa ( $S$ ) for macrobenthos sampled during two cruises along a cross-shelf Thukela River transect. Black line within boxplot represents the median, white line represents the mean.....101

Figure 4.4. Contribution of major macrobenthic Phyla to total abundance (N) and total no. of taxa (S) sampled during two cruises along a cross-shelf Thukela River transect Cruise A (high outflow: February 2010), Cruise B (Low outflow: August 2010).....102

Figure 4.5. Mean abundance (N), mean no. of taxa (S) and indices of Richness (d), Diversity ( $H'$ ) and Evenness ( $J'$ ) calculated from abundance data at the level of lowest identifiable taxon for shelf position stations (mean  $\pm$  SD) sampled during cruise A and B....104

Figure 4.6. Abundance (N) of major macrobenthic Phyla sampled at three shelf position stations (mean  $\pm$  SD) during cruise A and B. IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf.....107

Figure 4.7. Dendrogram for hierarchical clustering (using group-average linkage) of 18 samples collected during cruise A and B, based on Bray-Curtis similarities calculated from square root transformed taxon abundance data. The five groups separated at a 40% similarity threshold are indicated.....110

Figure 4.8. Contribution (%) of feeding modes to total abundance (N: no. of ind.m<sup>-2</sup>) and numbers of taxa (S) sampled across the central Natal Bight during cruises A and B. C=Carnivore, SF=Suspension feeder, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, O=Omnivore, FC=Facultative carnivore, FD=Facultative detritivore, FO=Facultative omnivore, MM=Multi-modal, Par=Parasite, U=Unknown.....112

Figure 4.9. Contribution (%) of feeding modes to mean ( $\pm$ SD) abundance (N: no. of ind.m<sup>-2</sup>) and mean ( $\pm$ SD) numbers of taxa (S) for inner (I1), mid (I4) and outer shelf (I7) positions sampled during cruises A and B. C=Carnivore, SF=Suspension feeder, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, O=Omnivore, FC=Facultative carnivore, FD=Facultative detritivore, FO=Facultative omnivore, MM=Multi-modal, Par=Parasite, U=Unknown.....115

Figure 4.10. Indices of functional Richness (d), Diversity ( $H'$ ) and Evenness ( $J'$ ) calculated for feeding mode abundance data from shelf position stations (mean  $\pm$  SD) sampled during cruises A and B. IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf.....116

Figure 4.11. Dendrogram for hierarchical clustering (using group-average linkage) of 18 samples collected during cruise A and B, based on Bray-Curtis similarities calculated from square root transformed feeding mode abundance data. The three groups (I-III) separated at a 75% similarity threshold are indicated.....119

Figure 4.12. Distance-based redundancy analysis (db-RDA) triplot of taxon data fitted to significant explanatory variables identified using forward selection and the sum of total canonical eigenvalues as selection criteria. ¥ indicates the nominal variable shelf position.....121

Figure 4.13.	Distance-based redundancy analysis (db-RDA) triplot of feeding modes identified in SIMPER analysis, fitted to significant explanatory variables identified using forward selection and the sum of total canonical eigenvalues as selection criteria. ¥ indicates the nominal variable shelf position.....	122
Figure 5.1.	Frequency of occurrence ( <i>F</i> ) for polychaete families sampled on the Natal Bight during cruises A (high rainfall) and B (low rainfall).....	140
Figure 5.2.	Total numbers of taxa ( <i>S</i> ), abundance ( <i>N</i> ) and biomass ( <i>B</i> ) attributed to polychaete families sampled during high (Cruise A) and low rainfall periods (Cruise B).....	141
Figure 5.3.	Frequency of occurrence ( <i>F</i> ) for polychaete feeding guilds collected on the Natal Bight during cruises A and B.....	142
Figure 5.4.	Total numbers of taxa ( <i>S</i> ), abundance ( <i>N</i> ) and biomass ( <i>B</i> ) attributed to polychaete feeding guilds sampled during high (Cruise A) and low rainfall periods (Cruise B).....	145
Figure 5.5.	Comparison of <i>k</i> -dominance curves, for polychaete abundance ( <i>N</i> ) and biomass ( <i>B</i> ), between the Richard's Bay, Thukela and Durban feature areas during cruises A and B.....	147
Figure 5.6.	Comparison of <i>k</i> -dominance curves, for polychaete abundance ( <i>N</i> ) and biomass ( <i>B</i> ), between the inner (IS), mid (MS) and outer shelf (OS) positions sampled during cruises A and B.....	148
Figure 5.7.	MDS ordinations of square root transformed abundance data for all macrobenthic fauna and polychaete abundance ( <i>N</i> ) and biomass ( <i>B</i> ).....	150
Figure 5.8.	Comparison of MDS ordinations from square root transformed polychaetes abundance data analysed to levels of lowest identifiable taxon, family and feeding guild.....	152
Figure 5.9.	MDS plot of polychaete taxon abundance data at the level of lowest identifiable taxon for the 54 samples collected during cruises A and B. Bubbles are superimposed values of the most abundant polychaete Families .....	155
Figure 5.10.	MDS bubble plot of significant environmental parameters, identified by BIO-ENV, as best describing abundance patterns of polychaetes at the level of lowest identifiable taxon.....	157

## LIST OF TABLES

Table 2.1.	Details of the location and number of times nutrient and primary productivity stations were sampled in each feature area during cruises A and B.....	27
Table 2.2.	The Wentworth scale: characterisation of sediment types based on grain size (mm) of sedimentary particles, with the accompanying phi ( $\phi$ ) notation. (Where phi ( $\phi$ ) = $-\log_2$ (particle size) (modified from Gray 1981 and Bale and Kenny 2005).....	30
Table 2.3.	Sorting classes used to characterize sediments (modified from Gray 1981).....	30
Table 2.4.	Characterisation of the percentage total organic content (TOC) of sediment samples (modified from Mackay 2006).....	32
Table 2.5.	Physico-chemical and sedimentary variables measured in the present study.....	34
Table 3.1.	<i>R</i> and <i>p</i> -values of ANOSIM (1000 000 permutations) comparisons between the taxon and feeding mode assemblages sampled during cruises A and B at three shelf positions within each feature area. RB=Richard's Bay, TK=Thukela, DN=Durban, IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf. Values in bold are significant * <i>p</i> <0.05, ** <i>p</i> <0.01, *** <i>p</i> <0.001.....	61
Table 3.2.	<i>R</i> and <i>p</i> -values of ANOSIM (1 000 000 permutations) comparisons between the factors: cruise, feature area and shelf position. RB=Richard's Bay, TK=Thukela, DN=Durban, IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf. Values in bold are significant * <i>p</i> <0.05, ** <i>p</i> <0.01, *** <i>p</i> <0.001.....	62
Table 3.3.	Details of sample Groups I-VII obtained from cluster analysis of 54 samples collected on the Natal Bight during cruises A (February 2010) and B (August 2010). IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf, RB=Richard's Bay, TK=Thukela, DN=Durban.....	62
Table 3.4.	Shannon-Wiener Diversity ( <i>H'</i> ), Margalef's Richness ( <i>d</i> ) and Pielou's Evenness ( <i>J'</i> ) indices calculated from taxon abundance data for sample Groups I-VII defined in cluster analysis.....	65
Table 3.5.	Shannon-Wiener Diversity ( <i>H'</i> ), Margalef's Richness ( <i>d</i> ) and Pielou's Evenness ( <i>J'</i> ) indices calculated from feeding mode abundance data for sample Groups I-VII defined in cluster analysis.....	65

Table 3.6. Results from SIMPER analysis of taxon abundance data, listing the main characterising taxa within each sample Group (I-VII). Taxa contributing more than 2% to “within group” similarity are presented. **Amp=Amphipoda, Biv=Bivalvia, Cho=Chordata, Cru=Crustacea, Iso=Isopoda, Pol=Polychaeta, Sip=Sipuncula**, C=Carnivore, IF=Interface feeder, MM=Multi-modal, O=Omnivore, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, SF=Suspension feeder Grey shading indicates typifying taxa. ....69

Table 3.7. Results from SIMPER analysis of taxon abundance data, listing the main discriminating taxa identified from pairwise comparisons of Group I-VII. Taxa contributing more than 2% to “between group” dissimilarity are presented, with cumulative % values in brackets. Grey shading indicates discriminating taxa and the inter-group comparison in which these taxa were identified as being important is indicated in bold. **Amp=Amphipoda, Biv=Bivalvia, Cho=Chordata, Cru=Crustacea, Iso=Isopoda, Pol=Polychaeta, Sip=Sipuncula**, C=Carnivore, IF=Interface feeder, MM=Multi-modal, O=Omnivore, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, SF=Suspension feeder.....70

Table 3.8. Results from SIMPER analysis of feeding mode abundance data, listing the main characterising feeding modes within each sample Group I-VII. Feeding modes contributing more than 10% to “within group” dissimilarity are presented, with cumulative % values in brackets. Typifying feeding modes within each Group are indicated in bold. **C=Carnivore, IF=Interface feeder, MM=Multi-modal, O=Omnivore, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, SF=Suspension feeder**.....71

Table 3.9. Results from SIMPER analysis of feeding mode abundance data, listing the main discriminating feeding modes identified from pairwise comparisons of Group I-VII. Feeding modes contributing more than 5% to “between group” dissimilarity are presented and cumulative % values are enclosed with brackets. **C=Carnivore, IF=Interface feeder, MM=Multi-modal, O=Omnivore, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, SF=Suspension feeder**.....73

Table 3.10. Weighted Spearman correlation coefficient ( $\rho_w$ ) values between macrobenthic communities and environmental variables measured in three feature (RB, TK, DN) areas on the Natal Bight. Variable combinations in bold indicate those that were determined to be significant \*\*\* $p < 0.001$  .....74

Table 3.11. Weighted Spearman correlation coefficient ( $\rho_w$ ) values between macrobenthic communities and environmental variables measured in three feature areas (RB, TK, DN) on the Natal Bight. The variable combination presented in bold is significant \*\*\* $p < 0.001$  .....74

Table 3.12. Eigenvalues ( $\lambda$ ) of the axes and Total Inertia obtained from the CCA ordination of a subset of 32 taxa identified by SIMPER analysis as contributing more than 3% to “within group” similarity and “between group” dissimilarity of Groups I-VII and five

environmental variables identified by BIO-ENV as being significant descriptors of macrobenthic community structure in three feature areas of the Natal Bight.....75

Table 3.13. Canonical coefficients ( $\lambda$ ) for the five environmental variables obtained for each axis in the CCA ordination of a subset of 32 taxa identified by SIMPER analysis as contributing more than 3% to “within group” similarity and “between group” dissimilarity of Groups I-VII. Values in bold represent environmental variables primarily responsible for determining each axis.....76

Table 4.1. Morphometric and physico-chemical characteristics of the Thukela River system.....90

Table 4.2. Sedimentary characteristics and nutrient concentration of shelf position stations sampled along the Thukela River transect during Cruise A (High outflow: February 2010) and B (Low outflow: August 2010).....100

Table 4.3. Two-way Analysis of Variance (ANOVA) and post-hoc Student-Newman-Keuls (SNK) testing based on univariate measures of taxon abundance data collected during cruise A (February 2010) and B (August 2010). IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf,  $F$ =critical value of ANOVA,  $q$ =critical value of SNK test,  $df$ =degrees of freedom,  $p$ =level of significance ( $p=0.05$ ). Values in bold are significant \* $p<0.05$ , \*\* $p<0.01$ , \*\*\* $p<0.001$ .....105

Table 4.4. Taxa identified by SIMPER analysis as contributing more than 2% to average similarity within sample Groups I-V. Grey shading indicates typifying taxa. **Amp=Amphipoda, Biv=Bivalvia, Cru=Crustacea, Gas=Gastropoda, Pol=Polychaeta, Sip=Sipuncula.** *C=Carnivore, SF=Suspension feeder, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, FC=Facultative carnivore, FD=Facultative detritivore, FO=Facultative omnivore.*.....111

Table 4.5. Taxa identified by SIMPER analysis as contributing more than 2% to average dissimilarity between sample Groups I-V. Bold values indicate discriminating taxa. (Cumulative percentage), **Amp=Amphipoda, Biv=Bivalvia, Cru=Crustacea, Gas=Gastropoda, Pol=Polychaeta, Sip=Sipuncula.** *C=Carnivore, SDF=Surface deposit feeder, FD=Facultative detritivore, FO=Facultative omnivore.*.....112

Table 4.6. Two-way Analysis of Variance (ANOVA) and post-hoc Student-Newman-Keuls (SNK) testing based on univariate measures of feeding mode abundance data collected during cruises A (February 2010) and B (August 2010). IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf,  $F$ =critical value of ANOVA,  $q$ =critical value of SNK test,  $df$ =degrees of freedom,  $p$ =level of significance ( $p=0.05$ ). Values in bold are significant \* $p<0.05$ , \*\* $p<0.01$ , \*\*\* $p<0.001$ .....118

Table 4.7.	Feeding modes identified by SIMPER analysis as being responsible for the similarity within and dissimilarity between sample Groups I-III. Only those feeding modes with the five highest contributions are presented. C=Carnivore, SF=Suspension feeder, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, FC=Facultative carnivore, FD=Facultative detritivore, FO=Facultative omnivore.....	120
Table 5.1.	States used for <i>in-situ</i> gut contents analysis of Polychaeta sampled from the Richard's Bay, Thukela and Durban feature areas.....	135
Table 5.2.	Polychaete feeding guild classification scheme adopted in the present study, (modified from Fauchald and Jumars 1979).....	135
Table 5.3.	Pairwise comparisons of multivariate community structure using the RELATE procedure on polychaete abundance data analysed to the levels of lowest identifiable taxon, family and feeding guild. Spearmans rank ( $\rho$ ) correlations, $p<0.001$ (10 000 permutations).....	153
Table 5.4.	Summary of results from 2-way ANOSIM for comparisons among feature areas (RB, TK, DN) and shelf positions (IS, MS, OS) using polychaete abundance data analysed to the level of lowest identifiable taxon and aggregated to family and feeding guild. RB=Richard's Bay, TK=Thukela, DN=Durban, IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf. Bold values indicate significant differences, $p<0.001$ .....	153
Table 5.5.	Results of BIO-ENV analysis showing the weighted Spearman rank correlation ( $\rho_w$ ) between combinations of environmental variables and polychaete community structure. Bold type indicates the best variable combination which was significant $p<0.001$ (10 000 permutations).....	156

## CHAPTER I. GENERAL INTRODUCTION

### 1.1 Context of study

The Natal Bight off the east coast of South Africa is a highly productive shelf habitat (Burchall 1968), attributed to the influence of local oceanographic features and outwelling via the Thukela, one of the largest rivers in the country (Begg 1978). This study forms part of a larger, multi-institutional, multi-disciplinary programme under the auspices of the African Coelacanth Ecosystem Programme (ACEP) investigating how material sources of oceanic and terrestrial origin, posited to be derived from these features, shape the ecological structure and functioning of the Natal Bight. This study contributes by investigating the structural and functional dynamics of macrobenthic communities and relating these patterns to measured environmental parameters. The three oceanographic feature areas considered were Durban, Thukela and Richards Bay.

### 1.2 Continental shelves

The continental shelf occupies 7.5% of the total ocean area, and is defined as the region extending from the low water mark to shelf edge (<200 m) where the slope of the seafloor steepens dramatically (Harris 1978, Schumann 1987, Gray 1994, Hall 2002). Soft-sediments, ranging from large gravel (>2 mm) elements to fine muds (<0.063 mm), occupy over 70% of the seafloor and cover continental shelves (Thorson 1957, Snelgrove 1997, Lohrer *et al.* 2006, McArthur *et al.* 2010). The sediment type is determined by various factors e.g. currents and allochthonous loads from rivers (Jones 1950, Thorson 1957, Snelgrove 1998, Wijsman *et al.* 1999, Hall 2002, Covich *et al.* 2004, McArthur *et al.* 2010) and provides a three dimensional habitat, due in part to the unconsolidated nature in that biota are not confined to hard, impermeable substrates (Thorson 1957, Lohrer and Hancock 2004, McArthur *et al.* 2010).

Continental shelves fall within the productive coastal zone, a transitional area between the land and sea which is nutrient rich and supports a high richness and diversity of resources drawing more than half the human population to settle along coastlines around the world (Gray 1997, Marinelli *et al.* 1998, Ellis *et al.* 2000, Solan *et al.* 2004, Crossland *et al.* 2005, dre 2012).

### 1.2.1 Shelf Productivity

Continental shelves in tropical and subtropical regions are driven by intermittent injections of nutrient rich, upwelled water along the shelf break and by riverine outflow of sediments and detritus (Alongi 1989, Marinelli *et al.* 1998, Gray 2002, Meyer *et al.* 2002, Syvitski *et al.* 2005). Freshwater input has a major impact on the coastal environment by providing a conduit for nutrients and pollutants leading to conditions of oligotrophy, reduced salinity, anoxia, pollution and fine, suspended sediments (Hunt 1925, Sanders 1968, Alongi 1989, Snelgrove 1998, Hall 2002, Meyer *et al.* 2002, Salen-Picard *et al.* 2002, Crossland *et al.* 2005). Anoxic conditions arise due to large inputs of particulate organic matter fueling primary production in the water column, as phytoplankton, and in the sediment, as microphytobenthos (Alongi 1989, Snelgrove 1997). Approximately 30% of the continental shelf area receives sufficient light to support pelagic primary production, this being confined to shallow, (14-45 m) inner shelf waters (Hunt 1925, Marinelli *et al.* 1998, Krönke *et al.* 2004, Syvitski *et al.* 2005). Microphytobenthos, in contrast, are found at low light levels in waters as deep as 190 m and thus the potential for benthic primary production exists over much of the continental shelf (Grippo *et al.* 2011). Macrobenthic fauna are important secondary producers which utilise particulate organic matter (POM) of plant and animal origin that settles to the sea floor, as well as sedimentary algae and bacteria as a food source (Sanders *et al.* 1962, Grippo *et al.* 2011). It is estimated that 25-50% of the primary productivity in the pelagic zone reaches the bottom where biogeochemical reactions return nutrients to the overlying water (Marinelli *et al.* 1998, Sumida *et al.* 2005). Allochthonous detrital material brought into the coastal zone by rivers may first need to be broken down by sedimentary bacteria as it is too refractory to be utilised by macrobenthos (Thorson 1957, Levinton 1972, Snelgrove 1997, Nixon 1981, Clark *et al.* 1999, Levinton and Kelaher 2004, Wieking and Krönke 2005). The input of nutrients from external sources and sinking of particulate carbon is seasonally variable resulting in the episodic supply of organic material to the benthos (Sumida *et al.* 2005, Grippo *et al.* 2011).

Soft-sediment environments support high taxon diversity and because most of the shelf area lies below the photic zone, macrobenthic invertebrates are a dominant component of the biota (Thorson 1957, Alongi 1989, Snelgrove 1998, Hall 2002, Thrush and Dayton 2002, Hewitt *et al.* 2008, Gray and Elliott 2009). Marine fauna originated in benthic sediments and consequently marine diversity is concentrated in the benthic rather than the pelagic realm (Gray 1997). These environments tend to be patchy or heterogenous due to the combined effects of large scale factors such as regional and local hydrodynamics as well as physical and biological

features operating on a smaller scale. The latter include sediment types and feeding behaviour of macrobenthos (Ford 1923, Gray 1981, Muniz and Pires 2000, Covich *et al.* 2004, van Hoey *et al.* 2004, Zajac 2008a, Zajac 2008b, Akoumianaki *et al.* 2012). While marine continental shelves occupy a small percentage of the area covered by marine sediments, they are responsible for 52% of global organic matter mineralisation (Snelgrove 1998, Hall 2002). This reflects the importance of macrobenthic activity within marine bottom environments, with these fauna accounting for up to 30% of the total Oxygen uptake in shelf sediments (Nixon 1981, Snelgrove 1998, Thrush and Dayton 2002, Wheatcroft 2006). Macrobenthic organisms may also be commercially important or provide food for demersal taxa on which commercial fisheries rely (Hunt 1925, Thorson 1957, Marques and Bellan-Santini 1993, Snelgrove 1997, Salen-Picard *et al.* 2002, Elliot *et al.* 2007, Dubois *et al.* 2009, Christoffersen *et al.* 2011). Continental shelf environments support a major component of global fisheries production, with an estimated 90% of marine fish stocks coming from the coastal zone (Hall 2002, Crossland *et al.* 2005). Globally, fisheries provide more than 6% of protein consumed by humans and are especially important in developing economies. The viability of these populations is reliant on a healthy benthic environment (Alongi 1989, Snelgrove 1998, Hall 2002, Thrush & Dayton 2002, Lohrer *et al.* 2004, Crossland *et al.* 2005).

### **1.3 Macrobenthic communities**

Macrobenthic marine fauna are the suite of invertebrate animals associated with the seafloor and live directly on, or in sediments. They are defined as animals which are large enough to be retained by a 1000µm or 500µm sieve (Jones 1950, Gray 1981, McClurg 1988, Karakassis and Eleftheriou 1997, Snelgrove 1998, Eleftheriou and Moore 2005, Gray and Elliott 2009). Macrobenthos encompass a wide range of organisms that are small, influenced by conditions in the abiotic environment, have limited mobility and exhibit varied life history strategies (Gray 1981, Gray 2002, Shin *et al.* 2004, Bigot *et al.* 2006). It is the relative sessility of these small animals which makes them useful for marine monitoring programmes as they are unable to escape unfavourable environmental conditions. Natural or anthropogenic disturbances will eliminate some animals while others survive, aggregating in communities that reflect environmental conditions integrated over time (Gray 1981, Warwick 1988a, Gray and Elliott 2009). Macrobenthos have functional roles crucial to many important ecosystem processes such as altering chemical conditions at the sediment-water interface by irrigating sediments, promoting decomposition, contaminant sequestering and nutrient recycling as well as transferring energy to other food web components (Nixon 1981, Snelgrove 1998, Brown *et al.*

2000, Thrush and Dayton 2002, Hewitt *et al.* 2008, Gray and Elliott 2009, Reiss *et al.* 2009, Barrio-Froján *et al.* 2012).

### **1.3.2 Classification of macrobenthic communities**

#### ***Taxonomic classification***

The classification of macrobenthic communities is commonly based on taxonomic information separating fauna at the lowest level possible, which is usually species (Elliot *et al.* 2007, Gray and Elliot 2009). Species based analyses are important because they contribute to the knowledge of regional biodiversity and endemism, particularly relevant in the South African context as the biodiversity of the subtidal continental shelf environment has been scarcely studied (Griffiths *et al.* 2010).

#### ***Functional classification***

Measures of species based data such as diversity detail only which and how many taxa are present without providing any information regarding their functioning within the ecosystem (Ellingsen 2001, Cheung *et al.* 2008, Gray and Elliott 2009, Pacheco *et al.* 2011). An equally important and perhaps more useful description, is information regarding functional traits of the taxa involved. An example is feeding mode, as the ability of an ecosystem to function is linked to the functional roles of constituent taxa as opposed to the species themselves (Hooper *et al.* 2001, Lohrer and Hancock 2004). While loss and changes of taxa are a common characteristic of macrobenthic communities, the critical question is not if changes occur, but to what extent these affect the overall functioning of the system (Duarte 2000, Hewitt *et al.* 2008, Macdonald *et al.* 2012). Many macrobenthic species have redundant roles in ecosystem services so that their removal may not have an appreciable effect on functioning (Gray 1997, Snelgrove 1998, Gray 2001, Covich *et al.* 2004, Solan *et al.* 2004, Elliot *et al.* 2007).

Analysis of macrobenthic trophic structure groups large numbers of taxa based on similar feeding modes and resource requirements, in order to determine the role of macrobenthos and evaluate energy flow through the ecosystem (Roth and Wilson 1998, Bonsdorff and Pearson 1999, Pearson 2001, Arruda *et al.* 2003, Gray and Elliot 2009, Christoffersen *et al.* 2011, Pacheco *et al.* 2011). The way in which fauna feed and their food source, is related to the physical characteristics of the environment so that a functional analysis also provides indirect information about factors such as depth gradients, food supply, substrate type and the

hydrodynamic conditions that shape these factors (Sanders 1958, Levinton 1972, Probert 1984, Gaston 1987, Brown *et al.* 2000, Dolbeth *et al.* 2009, Christoffersen *et al.* 2011, Macdonald *et al.* 2012).

#### *Feeding modes of macrobenthos*

Here, feeding mode is used to describe the mechanism of food transport from the environment into the organism (Fauchald and Jumars 1979). In the trophic structure of benthic communities primary producers, such as benthic algae (microphytobenthos), comprise the first level. Macrobenthos may be detritivores, obtaining their energy from other fauna or plants, representing secondary producers or be predators falling into the third trophic level (Gray 1981, Christoffersen *et al.* 2011, Fig. 1.1). Detritivores can be broadly classified into deposit and suspension feeders, typically the dominant groups encountered in soft-sediment coastal ecosystems. These groups provide an important link between organic matter produced in the pelagic realm and higher trophic levels like demersal ichthyofauna (Hunt 1925, Thorson 1957, Sanders 1960, Young and Rhoads 1971, Gray 1981, Cacabelos *et al.* 2009).

Deposit feeders ingest sediment and tend to be associated with fine substrates indicating a deep, stable, depository environment with reduced current activities and increased sediment organic content such as habitats influenced by river outflow (Sanders 1958, Whitlatch 1981, Snelgrove and Butman 1994, Brown *et al.* 2000, Pinn and Robertson 2003, Simonini *et al.* 2004, Pagliosa 2005, Jayaraj *et al.* 2008a, Rodil *et al.* 2009, Macdonald *et al.* 2012). Further divisions of this trophic group categorise surface deposit feeders as ingesting newly settled organic matter and subsurface deposit feeders as burrowers utilising older organic matter colonised by micro-organisms, and incorporated into deeper layers of the substrate (Fauchald and Jumars 1979, Snelgrove 1998, Tait and Dipper 1998, Riisgård and Kamermans 2001, Wieking and Krönke 2005, Dolbeth *et al.* 2009). This feeding strategy allows for recovery and trophic transfer of organic matter falling to the ocean floor as dead animal matter, faecal material and plant detritus thus influencing particle and nutrient flux over the sediment-water interface (Levinton 1972, Karakassis and Eleftheriou 1997, Snelgrove 1998, Pearson 2001). Many polychaete worms such as those belonging to the families Terebellidae, Orbiniidae, Capitellidae and Spionidae are deposit feeders. Bivalves including the families Tellinidae and Nuculidae and numerous Crustacea such as Amphipoda, Taniadacea, Cumacea and brachyuran crabs are common deposit feeding macrobenthos (Hunt 1925, Sanders *et al.* 1962, Fauchald and Jumars 1979).

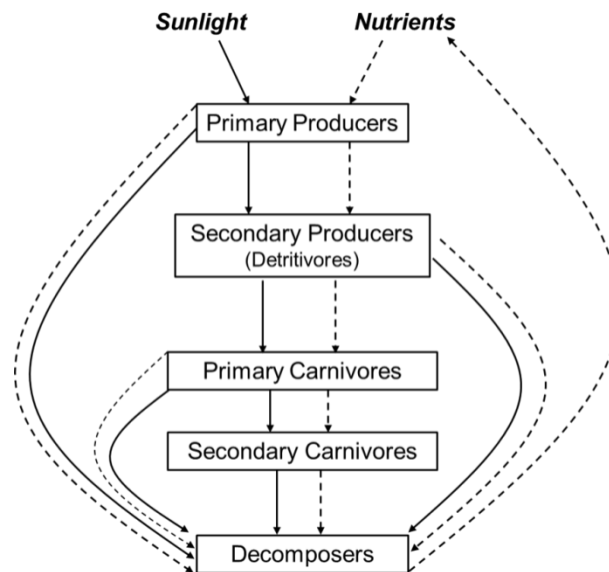


Figure 1.1. General trophic structure of an ecosystem. Solid lines indicate the flow of energy and dashed lines the flow of nutrients (modified from Gray 1981).

Suspension feeders are sedentary animals that obtain their food by actively or passively filtering particles from the water. This trophic group is generally abundant in shallower areas characterised by a pronounced hydrodynamic regime and coarser grades of sediment, low in organic carbon (Hunt 1925, Sanders *et al.* 1962, Pearson 1970, Tait and Dipper 1998, Riisgård and Kamermans 2001, Arruda *et al.* 2003, Dolbeth *et al.* 2009). Planktonic organisms and dissolved organic matter are strained from the water column but suspension feeders may also ingest a significant amount of sedimentary bacteria and detritus which is re-suspended in near bottom waters (Hunt 1925, Levinton 1972, Levinton and Kelaher 2004). These food sources are often seasonally variable leading to a relatively unpredictable food supply for suspension feeders. Porifera, Bryozoa and certain taxa belonging to Polychaeta and Crustacea are common suspension feeding macrobenthos (Jones 1950, Tait and Dipper 1998).

Other studies make reference to additional feeding modes such as carnivores and omnivores. Carnivorous macrobenthos are defined here as those that prey on other live fauna or carrion (Hunt 1925, Sanders *et al.* 1962, Fauchald and Jumars 1979, Wilson 1990, Tait and Dipper 1998, Cacabelos *et al.* 2009). Errant Polychaeta, Decapoda, Gastropoda, Asteroidea and Ophiuroidea are common carnivorous animals (Wilson 1990, Tait and Dipper 1998). Investigations of gut contents commonly attribute the consistent occurrence of an empty gut to a predatory life (Sanders *et al.* 1962, Fauchald and Jumars 1979, Gaston 1987). Carnivores increase the functional complexity of macrobenthic communities by mediating the effects of large epibenthic predators on infaunal communities (Quijón and Snelgrove 2008). Carnivores

are generally abundant on sandy sediments and generalist in their prey selection, which is attributed to the plethora of diverse food items supported within and on these sediments as opposed to the sandy bottoms themselves (Sanders 1958, Gaston 1987, Carrasco and Carbajal 1998, Pinn and Robertson 2003, Carvalho *et al.* 2005, Pagliosa 2005, Dolbeth *et al.* 2009, Rodil *et al.* 2009, Zaabi *et al.* 2010). In this study, parasitic fauna are distinguished from carnivores in that they do not kill their hosts and therefore are not considered as predators (Jaksić 1981). Parasites significantly increase the functional diversity of communities and their presence is thought to indicate healthy ecosystems (Christoffersen *et al.* 2011). Several macrobenthic fauna, particularly within the Polychaeta are reported to feed as herbivores and carnivores depending on environmental constraints, so here they are considered omnivores (Sanders *et al.* 1962, Cheung *et al.* 2008, Consentino and Giacobbe 2008). Omnivores utilise a wide range of food resources but are selective in doing so (Hunt 1925, Sanders *et al.* 1962, Wijsman *et al.* 1999, Pacheco *et al.* 2011). Since carnivores and omnivores are not reliant on a single food item whose abundance may fluctuate seasonally, these feeding modes are expected to exhibit greater ecological stability than suspension and deposit feeders (Sanders *et al.* 1962, Pagliosa 2005).

Although taxa may be assigned to a specific trophic group based on typical behaviour, numerous taxa possess the ability to change their feeding mode in response to environmental conditions (Thorson 1957, Probert 1984, Taghon 1992, Snelgrove 1997, Riisgård and Kamermans 2001, Salas *et al.* 2006, Consentino and Giacobbe 2008, Gray and Elliott 2009). Polychaeta, such as Spionidae and Oweniidae as well as some Amphipoda and Ophiuroidea are capable of switching their feeding mode. Dauer *et al.* (1981) used the term “interface” feeder to refer to taxa that are capable of switching between deposit and suspension feeding and it is this terminology that is applied in Chapter 3, which focuses on macrobenthic patterns of the three feature areas (Riisgård and Kamermans 2001). More recently Macdonald *et al.* (2012) extended this concept to include all facultative feeders which is the approach adopted in Chapter 4, focussing on the central Natal Bight. This trophic plasticity has been identified as an important characteristic of macrobenthic communities. Because these fauna are able to vary their method of food acquisition with food supply, they are thought to confer resilience to the community in response to a changing habitat (Macdonald *et al.* 2012). It is hypothesized that the functional composition of the community will change only under conditions of changes in organic matter (food) supply (Macdonald *et al.* 2012).

### *Feeding guilds*

Recently, the focus has been to take account of multiple biological traits, reflecting not only feeding mechanisms but also including information on life history, morphology, behaviour and reproduction of the constituent taxa because this provides a more comprehensive picture of the functional structure of communities and ecosystems (Bremner 2003, Cheung *et al.* 2008, Marchini *et al.* 2008, Pacheco *et al.* 2011, Oug *et al.* 2012, Paganelli *et al.* 2012).

A group of animals that utilises the same environmental resources in a similar way with no consideration of their taxonomic relationships is a feeding guild (Root 1967, Simberloff and Dayan 1991). Guilds simplify the analysis of complex biological communities and are useful for investigating specific functional relationships (Jaksić 1981, Adams 1985, Simberloff and Dayan 1991, Bonsdorff and Pearson 1999, Elliot *et al.* 2007). The concept of functional classification of macrobenthic taxa by incorporating information on feeding appendages and locomotion with the classical feeding mode approach is used to construct feeding guilds of polychaete taxa, for example (Fauchald and Jumars 1979, Gaston 1987).

### **1.4 The influence of environmental factors**

Because of the close association between macrobenthic organisms and the seafloor communities of macrobenthic taxa are structured and distributed in response to local environmental conditions (Petersen 1914, Jones 1950, Thorson 1957, Sanders 1968, Coleman *et al.* 1978, Fresi *et al.* 1983, Shackley and Collins 1984, Snelgrove 1998, Martin *et al.* 2000, Bergen *et al.* 2001). The activities of these fauna can also result in fundamental physical and chemical changes at the sediment-water interface (Pillay *et al.* 2007, Pacheco *et al.* 2011). Bottom fauna burrow and destabilise sediments by creating mounds and depositing faecal material at the sediment surface, thereby effectively conveying nutrients and regulating Oxygen penetration in sediments. Some macrobenthic fauna build tubes which influence the complexity of substrate, modify local bottom hydrodynamics, increase the vertical penetration and transfer of nutrients and Oxygen and destabilise or stabilise the substrate, thus influencing the establishment and survival success of other macrobenthic organisms (Levinton 1972, Rhoads and Young 1984, Wilson 1990, Griffis and Suchanek 1991, Lohrer and Hancock 2004, Consentino and Giacobbe 2006, Dubois *et al.* 2009, Passarelli *et al.* 2012).

Environmental factors such as depth, sediment granulometry and organic content are well established as important habitat drivers organising the structure, distribution, abundance and diversity of marine macrobenthic communities (Petersen 1914, Ford 1923, Jones 1950, Coleman *et al.* 1978, Fresi *et al.* 1983, Gray 1994, Wheatcroft 2006, Reiss *et al.* 2009, Pacheco *et al.* 2011). In addition, abiotic characteristics of the pelagic realm influence macrobenthic distribution, including temperature, salinity, dissolved Oxygen concentration and light penetration (Jones 1950, McArthur *et al.* 2010). Environmental factors are inter-related and are shaped by the surrounding hydrodynamic regime so that analysing environmental factors help investigators to make the connection between water column dynamics and benthic structure, providing key insights into the ecology of the benthos within their environmental milieu (Jones 1950, Duineveld *et al.* 1991, Snelgrove and Butman 1994, Bergen *et al.* 2001, Zajac 2008b, Hewitt *et al.* 2008, Dolbeth *et al.* 2009).

#### **1.4.1 Inter-relation of environmental factors**

Hydrographic processes are directly responsible for determining substrate characteristics in that the effect of physical energy acting on the bottom environment is diminished with distance offshore. Deeper areas are thus typically characterised by fine sediments, while coarser sediments generally dominate shallow depths subjected to increased hydrodynamic energy and fluctuations in temperature and salinity (Fresi *et al.* 1983, Karakassis and Eleftheriou 1997, Zajac *et al.* 2000, Dolbeth *et al.* 2009). Hydrodynamics also influence the supply of organic matter to the sea floor (Sanders *et al.* 1962, Zajac *et al.* 2000, Hall 2002, Sumida *et al.* 2005). Sediment particle size is correlated with organic contents in that fine sediments, such as mud have higher organic content due to smaller particles having greater surface area per unit volume when compared with sandy sediments (Levinton 1972, Weston 1988, Hyland *et al.* 1991, Tait and Dipper 1998, Sumida *et al.* 2005, McArthur *et al.* 2010). Macrobenthic communities are directly affected by hydrodynamics as currents and river outflow aid the transportation of pelagic larvae to suitable habitats for settlement (Thorson 1957, Tait and Dipper 1998, Zajac *et al.* 2000, Hall 2002, Covich *et al.* 2004).

When environmental patterns change as a result of natural or anthropogenic disturbance the structure and distribution of macrobenthic communities may also change (Jones 1950, Sanders 1968, Sanders *et al.* 1962, Gray 1981, Gray 2002, van Hoey *et al.* 2004, Wheatcroft 2006, Hewitt *et al.* 2008). Seasonal cycles can alter hydrodynamics which may be translated to the

bottom environment and reflect as changes in the macrobenthic community. The effect of seasonal variations in temperature, salinity and nutrient concentration are expected to be more notable in inner shelf environments, particularly those influenced by riverine outflow (Ford 1923, Thorson 1957, Gray 1981, Bonsdorff and Pearson 1999, Sumida *et al.* 2005, Consentino and Giacobbe 2006, Reiss *et al.* 2009).

#### **1.4.2 Relationship between macrobenthic communities and environmental factors**

The influence of environmental parameters on macrobenthic communities are features of most continental shelf systems studied and there are thus well established general patterns of macrobenthic community dynamics in response to measurable habitat drivers (Hall 2002). Abundance, biomass and diversity of soft-sediment macrobenthic communities tend to decrease with increasing depth, regardless of season or geographical location (Thorson 1957, Sanders 1968, Alongi 1989, Hyland *et al.* 1991, Snelgrove 1998, Tselepides *et al.* 2000, Jayaraj *et al.* 2008a, Barrio-Froján *et al.* 2012), as food typically becomes limited with increasing depth (Jayaraj *et al.* 2008a, Jayaraj *et al.* 2008b, Karakassis and Eleftheriou 1997). Although this trend is well documented, a study conducted on the continental shelf off California found that abundance and diversity values peaked at mid-shelf depths (60 m) (Bergen *et al.* 2001, Wheatcroft 2006). Mid-shelf depths (50-75 m) off the southwest coast of India were also found to support the highest diversity and richness of macrobenthos (Jayaraj *et al.* 2008b).

Macrobenthic communities are inherently connected to and influenced by substrate type, with communities of sandy habitats tending to support a high diversity but low abundance because of the greater amount of biogenics and variety of microhabitats that sandy substrata provide (Sanders 1968, Coleman *et al.* 1978, Fresi *et al.* 1983, Marques and Bellan-Santini 1993, Simonini *et al.* 2004, Mackie *et al.* 2005, Lourido *et al.* 2008, Barrio-Froján *et al.* 2012). In contrast, food rich fine deposits tend to support a community with high abundance and biomass but low species diversity (Mancinelli *et al.* 1998, Gray 2002, Simonini *et al.* 2004, van Hoey *et al.* 2004, Lourido *et al.* 2008, Rodil *et al.* 2009).

#### **1.5 Macrobenthos of South African shelf environments**

Published data on tropical and subtropical subtidal benthic invertebrate assemblages are limited (Alongi 1989, Ferraro and Cole 1990, Chang *et al.* 1992, Gray 1997, Karakassis and Eleftheriou 1997, Bergen *et al.* 2001, Ellingsen 2001, Gray 2001, van Hoey *et al.* 2004, Christoffersen *et al.*

2011). In general tropical and subtropical benthic habitats are characterised by smaller macrobenthos, higher taxon diversity and lower abundances than temperate systems (Christoffersen *et al.* 2011).

Exploration of the South African shelf commenced in the the 19<sup>th</sup> Century (Brown 1999; 2003). The appointment of Keppel K.H. Barnard to the South African Museum in 1911 was a major event in the history of South African marine invertebrate taxonomy and he remains the most prolific marine taxonomist South Africa has ever known (Brown 1999; 2003). Barnard's (1950) monograph of South African Decapoda provides descriptions and keys for the identification of some 800 taxa and remains the seminal work on this group (Brown 1999; 2003). After the Second World War investigations of South African shelf fauna were undertaken aboard the research vessel, *R.V. Meiring Naudé* (Brown 1999; 2003). Important taxonomic works emanating from these studies were provided for the Echinodermata through the work of Clark (1923) and Clark and Courtman-Stock (1976), Amphipoda were investigated by Griffiths (1976), while Kensley (1972) described shrimp and subsequently (Kensley 1978) described Isopoda and Day (1975-1980) contributed to knowledge on Cumacea. John Day devoted most of his career to the extensive study of polychaete worms culminating in the publication of a two volume monograph, *The Polychaeta of southern Africa* (Day 1967).

A review of available macrobenthic data collected along the entire KwaZulu-Natal (KZN) coastline from 1974 to the late 1980's showed that in terms of taxonomic trends, Polychaetes were the most abundant and speciose groups sampled (McClurg 1988). Generally, regardless of location, polychaetes tend to be the most commonly encountered animals inhabiting marine sediments followed by crustaceans, molluscs and echinoderms (Fauchald and Jumars 1979, Gray and Elliott 2009). Thirty seven polychaete families were recorded from the last widespread study of the Natal Bight (McClurg 1988), with Syllidae and Spionidae being the most abundant. Knowledge regarding offshore fauna is still lacking, but surveys conducted in the northern and southern regions of the Natal Bight have shown that this Phylum dominates in terms of number of taxa and abundance of organisms (McClurg 1988, McClurg *et al.* 2000, McClurg 2005, Weerts and Mackay 2008: cited in Fennessy *et al.* 2008, Mackay 2012: unpublished data off Zululand and Durban). When considering the Crustacea, the Natal Bight was found to support a high number and wide variety of Amphipoda, with recent surveys off Durban in 2004 recording 26 taxa, many of which are endemic to the region (McClurg 1988,

McClurg 2005). Of the 20 amphipod taxa recorded on the Natal Bight the families Haustoriidae, Ampeliscidae, Corophiidae and Phoxocephalidae were most numerous (McClurg 1988). To date, 48 subtidal Isopoda and 35 Cumacea have been recorded off KZN, with taxa belonging to the Caridea, Penaeida, Anomura and Brachyura being identified in more recent subtidal surveys off Durban and Richard's Bay (McClurg 1988, McClurg *et al.* 2000, McClurg 2005). In terms of the Mollusca, KZN waters support the highest diversity in South Africa (Kilburn 1999). McClurg (1988) noted a significant increase in the occurrence of tropical Indo-Pacific molluscs in KwaZulu-Natal waters, when compared with the southern and western coasts. At the Natal Museum specialists have continued to study and describe the mollusc fauna obtained from material collected during the Natal Museum Dredging Programme (1981-1996) (Herbert 1989, Herbert 1991, Kilburn 1992, Kilburn 1998, Kilburn 1999, etc). Compared with the Bivalvia, few Gastropoda have been identified in subtidal benthic samples collected off Durban and Richards Bay (McClurg *et al.* 2000, McClurg 2005). Considering the Echinodermata, a significant 40% of the 280 echinoderm taxa recorded in South Africa are found in this region (McClurg 1988). Recent investigations into echinoderms of this region include studies on the holothuroid fauna (Samyn 2003, Thandar and Rowe 2005, Thandar 2009) and a revision of the Ophiocoma (Ophiuroidea) taxa of South Africa (Olbers and Samyn 2012). In the only depth transect sampled during McClurg's (1988) comprehensive survey of macrobenthic communities on the Natal Bight, abundance and number of taxa was found to decrease both inshore and offshore of a station located in the mid-shelf region off Durban at a depth of 61m, with a number of physical factors, such as reduced wave turbulence being hypothesised as driving these changes (McClurg 1988).

By in large, extensive taxonomic and community work on macrobenthos have not been undertaken since the 1980's and those studies that have been conducted in South African waters, have concentrated mainly on the west coast (Griffiths *et al.* 2010). Long term benthic monitoring programmes have however been on going in localised areas of interest on the Natal Bight, namely Durban and Richards Bay where large amounts of effluent are being discharged through offshore pipeline systems (McClurg 1988, McClurg *et al.* 2000, McClurg 2005, Fennessy *et al.* 2008). Given what is known of the diversity and endemism of marine fauna becoming progressively more taxon rich towards the subtropical east coast this paucity of data hinders an accurate appreciation of the benthic biodiversity in South African waters (Heydorn *et al.* 1978, Field and Griffiths 1991, Griffiths *et al.* 2010).

## **1.6 Project Aims and Objectives**

This research aimed to investigate the structural and functional patterns and changes in macrobenthic communities within and between three feature areas of the Natal Bight sampled during a high (Cruise A) and low rainfall (Cruise B) period and to relate these patterns to measurable environmental parameters.

### **Objectives**

1. Enumerate, and identify macrobenthic fauna within each feature area to the lowest taxonomic level possible.
2. Assign each taxon to a trophic group based on available literature.
3. Delineate assemblages based on taxonomic and functional characteristics.
4. Characterise the habitat of each of the three feature areas and shelf positions based on measured environmental variables.
5. Determine spatial and short-term temporal differences in macrobenthic community structure and function.
6. Relate community structure to environmental variables (physico-chemical conditions and sediment composition).
7. Compare results obtained from a high (Cruise A) and low rainfall (Cruise B) period to determine if there are significant differences.

## **1.7 Thesis Outline**

This thesis is presented in six chapters. A general introduction (Chapter 1) general methodology (Chapter 2) followed by two chapters investigating macrobenthic community patterns (Chapter 3 and 4), a chapter investigating only Polychaeta patterns (Chapter 5) and a general discussion and conclusion (Chapter 6).

Chapter 1 provides background information, places the research in context and highlights its importance. Chapter 2 offers a general description of the Natal Bight and the physical characteristics of each feature area. A focussed description of the field sampling and lab protocols used throughout the current study are provided along with information regarding the generic treatment of biological and environmental data and analyses used. Methodology specific to each of the three main sections are presented in detail in the respective chapters.

Chapter 3 investigates the macrobenthic communities and feeding modes found in three oceanographic feature areas: Durban, Thukela and Richards Bay, sampled during two cruises corresponding with high and low rainfall periods. Stations in each feature area were orientated along a depth gradient from the shallow inner and mid shelf to the deeper outer shelf. Macrobenthic taxa were classified according to their dominant feeding mode and community patterns were investigated both within and between feature areas and related to measurable environmental factors. Following from findings of the preceding chapter, Chapter 4 takes an in-depth look at communities collected along a coast perpendicular transect sampled off the Thukela River. This study compares the communities sampled during periods of variable rainfall and hence river outflow, along a depth gradient, and links patterns with measured environmental factors. Although both Chapters 3 and 4 make use of taxon and functional level analyses, the classification of feeding modes differs in that taxa are assigned to dominant modes in Chapter 3 while facultative feeding was considered in Chapter 4. The content of Chapter 5 is focussed on the Polychaeta, using information on abundance, biomass (wet weight), gut contents and feeding guilds to elucidate trends within and between the three oceanographic feature areas sampled and compare them with results from analysis of the whole macrobenthic community. The final chapter integrates and discusses findings from preceding chapters, the implications of these findings and provides some recommendations for future research.

## CHAPTER 2. GENERAL MATERIAL AND METHODS

### 2.1 Study Area – Natal Bight

#### 2.1.1 Location and characteristics

The KwaZulu-Natal coastline extends for approximately 570 km and is influenced by the south-west Indian Ocean (Pearce 1977, Heydorn *et al.* 1978, Schumann 1988, Cooper *et al.* 1998). The principal hydrological feature in this region is the Agulhas Current (Burchall 1968, Pearce 1977, Schumann 1987, Lutjeharms *et al.* 2007, Roberts *et al.* 2010). There are approximately 75 named estuaries along this coastline, most of which have a connection with the ocean at some point during the year (Begg 1978, Cooper *et al.* 1998, Turpie *et al.* 2012).

Off the east coast the continental shelf is characterised as being narrow (3-12 km) with a sheer slope (Schumann 1987, Lutjeharms *et al.* 2000a, Meyer *et al.* 2002, Bosman *et al.* 2007, Roberts *et al.* 2010). An exception to this typical situation is an anomalously wide area between Richard's Bay (28° 58'S, 32° 38'E) and Durban (29° 91'S, 31° 05'E), known as the Natal Bight, stretching for 160 km, reaching 50 km at its broadest point off the Thukela River mouth (29° 25'S, 31° 54' E) (Heydorn *et al.* 1978, Pearce *et al.* 1978, Lutjeharms and Roberts 1988, Lutjeharms 2006, Roberts *et al.* 2010, Fig. 2.1).

The three oceanographic feature areas chosen for this study represent regions of the Natal Bight under the influence of specific hydrodynamic regimes, and as such are hypothesised, in the broader ACEP context, to be vital sources of nutrients driving the ecology of this region (Lutjeharms 2000a, Meyer *et al.* 2002, Barlow *et al.* 2008). The Durban (DN) area is under the influence of a cyclonic lee-eddy, the Thukela (TK) feature area is characterised by the influence of the third largest river system in South Africa, and Richards Bay (RB) is the site closest to an upwelling cell generated offshore of Cape St. Lucia (Heydorn *et al.* 1978, Lutjeharms 2000a, Lutjeharms 2000b, Meyer *et al.* 2002, Roberts *et al.* 2010).

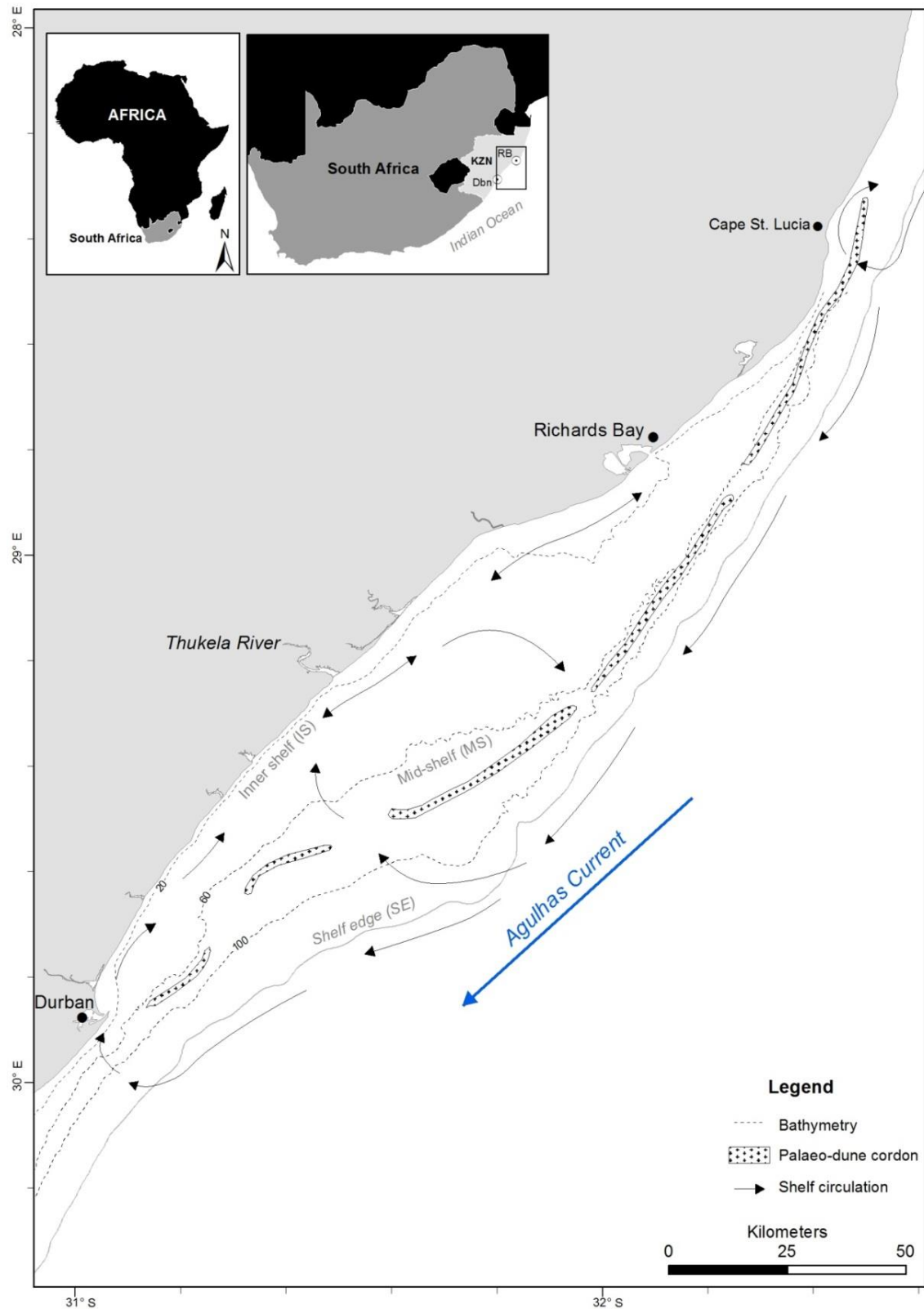


Figure 2.1. The Natal Bight study area with feature areas, bathymetry and shelf circulation shown (modified from Schumann 1987).

### 2.1.2 Oceanography

The east coast of South Africa is characterised by a high energy environment with strong current and wind conditions leading to a well mixed water column with little evidence of significant thermocline development (Burchall 1968, Schumann 1987, Field and Griffiths 1991, Green and Garlick 2011).

#### ***The Agulhas Current***

This western boundary current is fed from waters of the Mozambique Current and the East Madagascar Current. The flow extends below 1000 m, moving southwards along the east coast of South Africa, transporting warm water and larvae of subtropical and tropical regions, exerting a significant influence on the coastal environment and marine fauna of this region (Isaac 1937, Pearce 1977, Harris 1978, Schumann 1987, McClurg 1988, Gründlingh 1992, Beckley 1998, Lutjeharms 2007). Agulhas Current surface water is a mixture of low salinity (<35) Tropical Surface Water (TSW) from the South Equatorial Current and high salinity (>35) Subtropical Surface Water (STSW) originating from the south-west region of the south Indian gyre so that the surface salinity of the current is typically 35.2-35.4 (Pearce 1977, Heydorn *et al.* 1978, Lutjeharms *et al.* 2000a, Lutjeharms 2006). The mean width of the current is ~100 km and its core is generally 1-2°C warmer than surrounding waters with a mean flow rate of 1.4 m.s<sup>-1</sup> and a maximum value of 2.5 m.s<sup>-1</sup> being recorded (Burchall 1968, Heydorn *et al.* 1978, Pearce *et al.* 1978, Schumann 1988, Field and Griffiths 1991, Lutjeharms 2006, Roberts *et al.* 2010). In a recent survey core sea surface temperatures of the Agulhas Current varied from 24-26°C in May to 22.0-22.5°C in July, while shelf waters were up to 4°C cooler (Roberts *et al.* 2010). While the core of the Agulhas tends to follow the shelf break, bottom topography and shape of the continental shelf have a major influence on the structure and flow of this current (Isaac 1937, Anderson *et al.* 1988, Speich *et al.* 2006, Lutjeharms 2007). On narrow regions of the shelf, such as at the northern and southern reaches of the Natal Bight, the current is close inshore and shelf circulation is strongly influenced by the Agulhas Current, but in wider shelf regions the current tends to diverge from the coast (Harris 1978, Cooper *et al.* 1998, Roberts *et al.* 2010). The interaction between the Agulhas Current and continental shelf results in small eddies being found over the mid and outer shelf regions (Harris 1978, Lutjeharms *et al.* 1989, Lutjeharms 2007). There is also a persistent upwelling cell in the northern region of the Natal Bight and a recurrent lee-eddy system off Durban (Harris 1978, Lutjeharms *et al.* 1989, Lutjeharms 2007, Barlow *et al.* 2008). Upwelling along the continental slope at the edge of the Agulhas current is a persistent feature along the full length of the

current with water from depths of hundreds of meters being brought onto the shelf as a result of Ekman veering (Pearce 1977, Heydorn *et al.* 1978, Lutjeharms *et al.* 2000b). The Agulhas Current has a notable effect on the coastal ocean along the entire KwaZulu-Natal coast, and understanding the dynamics of this feature is essential to understand processes occurring on the shelf (Schumann 1987, Schumann 1988, Beckley 1998).

### ***Inshore currents***

Inshore currents on the Natal Bight are primarily wind driven and alternate between southerly and northerly directions, with velocities exceeding  $0.5 \text{ m.s}^{-1}$  (Burchall 1968, Harris 1978, Schumann 1989, Lutjeharms 2006, Roberts *et al.* 2010). There appears to be no major seasonal patterns in shelf circulation on the Natal Bight although the frequency of southerly inshore currents may increase during the winter months (Pearce 1977, Pearce *et al.* 1978, Lutjeharms 2006).

### **2.1.3 Physico-chemical characteristics**

Physico-chemical measurements began in coastal waters off KZN in the 1960's under the auspices of the Council for Scientific and Industrial Research (CSIR) and continued until the 1980's (Pearce 1977, Heydorn *et al.* 1978, Schumann 1987). Temperature and depth profiles were taken, with water samples being collected at certain depths for salinity and nutrient analyses. Recently there has been renewed interest in the oceanography of this region, with numerous surveys being undertaken since the early 2000's (Barlow *et al.* 2008, Lutjeharms *et al.* 2010, Roberts *et al.* 2010).

### ***Climate and Temperature***

The climate of the KwaZulu-Natal region is described as humid, subtropical with warm summer conditions (Pearce 1977, Schumann 1988a, Cooper 2001). Average sea surface temperatures off Durban reach a maximum of  $25^{\circ}\text{C}$  in February, during the summer, dropping to  $21^{\circ}\text{C}$  in the months of July and August (Heydorn *et al.* 1978). More recently surface waters of the Natal Bight were reported to range from  $20\text{--}22^{\circ}\text{C}$  in September 2005 (Barlow *et al.* 2008). Marine biota are not able to maintain body temperatures independent of their external environment, so temperature is a critical factor influencing biological processes and the distribution of fauna (Jones 1950, Clark *et al.* 1999, Barlow *et al.* 2008). The seasonal variability in temperature is due to prevailing weather patterns, with most rainfall occurring during the

summer months (November to March) in this region (Pearce 1977, Begg 1978, Cooper 2001, Hutchings *et al.* 2002, Barlow *et al.* 2008). During periods of high rainfall rivers, depending on the size of the system, flood and discharge various volumes of fresh water and large quantities of detritus and fine-grained sediment into the ocean (Pearce 1977, Martin and Flemming 1988, Schumann 1988, Clark *et al.* 1999). The east coast of South Africa is generally characterised as being oligotrophic, but this periodic supply of nutrients into coastal regions must boost local productivity (Cooper *et al.* 1998).

### **Salinity**

During the summer months when rainfall is maximum, outflow of freshwater onto the shelf may affect the salinity of coastal waters (Isaac 1937, Pearce 1977, Heydorn *et al.* 1978 Clark *et al.* 1999). Seasonal variation in salinity and temperature will be particularly notable in shallow waters where the effects of changes in these parameters are transferred down to the sea floor. In deeper, offshore areas seasonal variations are largely restricted to the upper 70 m of the water column (Pearce 1977). This stratification results from the fact that salinity increases the density of water (Vos 2011). Certain taxa may be intolerant of brackish waters and variations in salinity could therefore be a controlling factor governing the distribution and occurrence of macrobenthic fauna (Jones 1950).

### **Nutrients and Primary Productivity**

The three areas (Richards Bay, Thukela and Durban) under investigation are characterised by features which bring nutrients onto the shelf. The inclusion of nutrient and primary productivity measurements in the present study serves as an indication of whether these features are in fact conveying nutrients onto the shelf and our macrobenthic work helps us to infer whether this productivity (pelagic) is reflected biologically (secondary production in the case of macrobenthos). The nutrient and Primary Productivity measurements are also used in the exploration of potential habitat drivers for observed macrobenthic community patterns.

Carbon (C), Nitrogen (N) and Phosphorus (P) are essential nutrient elements used to build biological molecules such as proteins or carbohydrates and are thus required for life processes and the survival of all marine organisms (Odum 1969, Smith *et al.* 2005, Sunda 2010). These elements are brought into the ocean from a variety of sources such as groundwater, fluvial and atmospheric inputs (Marinelli *et al.* 1998, Smith *et al.* 1999, Vos 2011). Of the three nutrients,

C is the least limiting, with most carbon entering the ocean through the diffusion of carbon dioxide ( $\text{CO}_2$ ) into surface waters. Nitrogen and P are the two main nutrients limiting growth of photosynthetic algae (phytoplankton) and bacteria in marine waters and sediments (Smith *et al.* 1999, Sunda 2010, Vos 2011, Jurgensone and Aigars 2012). While primary productivity in the ocean is well known to be limited primarily by Nitrate ( $\text{NO}_3$ ), researchers have gained an appreciation for the vital role that other elements such as Iron (Fe) and Silica (Si) play in facilitating this process (Smith *et al.* 1999, Sunda 2010, Vos 2011, Jurgensone and Aigars 2012). Research suggests that Si may have become a limiting nutrient in freshwater systems, significantly affecting the diatom component and structure of the phytoplankton community on which higher trophic levels rely (Vos 2011, Jurgensone and Aigars 2012).

The photosynthetic production of organic matter by phytoplankton is made possible by the fixation of N and P taken up from the surrounding water (Smith *et al.* 1999). The determination of Chlorophyll *a* (Chl-*a*) concentration in coastal waters serves as a proxy for pelagic primary production and the amount of organic matter available to macrobenthos (Tselepidis *et al.* 2000, Krönke *et al.* 2004, Bale and Kenny 2005, Wieking and Krönke 2005). The major role of this compound (Chl-*a*) in phytoplankton is to absorb light for photosynthesis (Barlow *et al.* 2008). The global average Chlorophyll *a* value for the open ocean is approximately  $0.3 \text{ mg.m}^{-2}$  while continental shelf waters are more productive ( $2.5 \text{ mg.m}^{-2}$ ) (Sanders *et al.* 1962, Karakassis and Eleftheriou 1997). High macrobenthic abundance and biomass may be attributed to increased levels of primary production influencing higher trophic levels through bottom-up effects (Dubois *et al.* 2009).

Waters specifically associated with the Natal Bight have higher mean nutrient levels than waters of the narrower shelf region (Burchall 1968, Carter and d'Aubrey 1988). Values of primary production on the Natal Bight ranged from  $17 \text{ mg C.m}^{-2}.\text{day}^{-1}$  to  $942 \text{ mg C.m}^{-2}.\text{day}^{-1}$  during a survey conducted in the winter of 1965. The highest rates of primary production were obtained for the region south-east of the Thukela River mouth, possibly due to the enrichment of coastal waters by the outflow of nutrients (Burchall 1968, Grindley 1979). Based on a survey conducted in July 1989 three distinct provinces were identified, based on nutrient distributions namely: a northern, central and southern Natal Bight (Meyer *et al.* 2002). Measurements of Chl-*a* and other physical data also conformed to the pattern of distinct provinces, similar to those observed from nutrient data (Meyer *et al.* 2002). In a survey conducted on the Natal Bight in September of 2005, Chlorophyll *a* concentrations of 1.0-1.5

mg.m<sup>-3</sup> were associated with the northern region of the Natal Bight, while in the southern region near Durban, Chl-*a* levels were usually <0.5 mg.m<sup>-3</sup> (Barlow *et al.* 2008). These zones of enhanced productivity are most likely due to upwelling events which inject nutrients into shelf waters (Burchall 1968, Barlow *et al.* 2008).

#### **2.1.4 Sediment characteristics**

Hydrological patterns control sediment transport and distribution on the shelf which is a critical determinant of the structure and distribution of macrobenthic communities (Heydorn *et al.* 1978, Schumann 1987, Lutjeharms 2006, Chapter 1). Current speeds near the sea bottom are reported to be 30-40% lower than surface speeds with velocities <2 knots recorded on occasion (Pearce 1977, Heydorn *et al.* 1978). On the Natal Bight fluvial processes and biogenic products are considered the most significant sources of sediment (Flemming and Hay 1988). Substantial amounts of terrigenous sediments are carried to the shelf by rivers particularly during the high rainfall, summer months affecting the turbidity of inshore waters (Heydorn *et al.* 1978, Flemming and Hay 1988, Lutjeharms 2006). Biogenic material includes shell gravel, animal tubes, mounds, pits and faecal casts (Marinelli *et al.* 1998, Passarelli *et al.* 2012). The Natal Bight can be broadly divided into three zones based on sedimentary characteristics. The inner shelf is covered by terrigenous sediments which are thickest in front of major river mouths (Heydorn *et al.* 1978). This inshore terrigenous belt has accumulated in the years following the last glaciation (Heydorn *et al.* 1978, Hutchings *et al.* 2002, Green and Garlick 2011). Shallow areas between the Thukela River and Durban are dominated by medium sand (0.25–0.5 mm) whereas between Richard's Bay and the Thukela River, inner shelf sediments are characterised by fine sand (0.125–0.25 mm) (Flemming and Hay 1988, Bosman *et al.* 2007). The outer shelf, scoured by the inshore shoulder of the Agulhas Current, is dominated by gravels (>2 mm) composed predominantly of relict shell fragments, resulting in relatively high carbonate content of these bioclastic sediments (Heydorn *et al.* 1978, Flemming and Hay 1988, Lutjeharms 2006, Green and Garlick 2011). An exception to this general condition is encountered in the central Natal Bight, under the influence of the Thukela River, which results in muddy sediments being deposited and moved over the shelf edge onto the slope and into the Thukela Canyon (Heydorn *et al.* 1978, Flemming and Hay 1988, Lutjeharms 2006). The inner shelf terrigenous facies and the outer shelf relict carbonate facies are separated along the 60 m isobath by a belt of gravelly substrate (60%), characterised by aeolianites, that forms an almost continuous ridge (Flemming and Hay 1988, Green and Garlick 2011). This remnant paleo-dune cordon was formed during the last recorded lowstand 18 000 BP, when the sea

level was approximately 130 m below present (Heydorn *et al.* 1978, Hutchings *et al.* 2002, Green and Garlick 2011).

### 2.1.5 Feature Areas

#### ***The northern Bight – Richard’s Bay***

The narrow northern shelf (7 km) is shallow (50 m) and characterised by upwelling which occurs year round between Richard’s Bay and Cape St. Lucia, and results in colder, low salinity, nutrient rich water from depth (75 m) being brought up onto the shelf (Carter and d’Aubrey 1988, Lutjeharms *et al.* 1989, Gründlingh 1992, Lutjeharms 2007, Barlow *et al.* 2008, Roberts *et al.* 2010). Airborne radiation thermometry has revealed that waters of the upwelling plume are below 17.5°C, whereas the core of the Agulhas Current is warmer (21°C). Regular hydrographic investigations of the upwelling cell have shown that, on average, the difference in temperature between the Agulhas Current and the plume is 2-4.5°C (Lutjeharms *et al.* 1989). It is well established that the upwelling is not wind-driven but rather it is caused by the Agulhas Current passing from a narrow to a wider shelf in this region (Lutjeharms *et al.* 2000b, Lutjeharms 2006). This upwelling cell has been postulated as being the primary source of nutrients for the northern Bight (Lutjeharms *et al.* 2000a, Meyer *et al.* 2002) with satellite imagery indicating it is present for 80% of the time (Lutjeharms *et al.* 1989). Upwelling events drive bottom water onto the shelf to depths of 40 m or shallower and increase the concentration of nutrients in surficial waters, which create ideal conditions to support primary productivity and presumably have significant effects on ecosystem functioning in this region (Carter and d’Aubrey 1988, Meyer *et al.* 2002, Lutjeharms 2006). Concentrations of Nitrates in near bottom waters of the northern Bight (30 m) were 0.18-18.27  $\mu\text{mol.L}^{-1}$ , with Phosphate and Silicate values ranging from 0.37-1.39 and 2.40-12.22  $\mu\text{mol.L}^{-1}$ , respectively (Meyer *et al.* 2002). The Chl-*a* concentration of shelf waters sampled off Richard’s Bay were in excess of 1.5  $\text{mg.m}^{-3}$  and the uplift of deep water was also reflected in salinity (35.45) and temperature (19°C) values (Meyer *et al.* 2002). As this water is moved southwards the nutrient content is progressively diminished through the action of biological processes, by mixing with other water bodies, or a combination of these two mechanisms (Meyer *et al.* 2002). Coastal currents in the northern Natal Bight are wind-driven, exhibiting strong reversals and no seasonal patterns in shelf circulation (Lutjeharms *et al.* 1989).

### ***The central Bight – The Thukela River***

The shelf is widest in the central region of the Bight, extending approximately 50 km offshore of the Thukela River mouth (Fig. 2.1.), which means that the Agulhas Current, further offshore exerts less influence on coastal waters in this region (Burchall 1968, Schumann 1987, Schumann 1988, Lutjeharms *et al.* 2000a, Bosman *et al.* 2007). Currents on the central Bight appear to be driven by local wind patterns with eddy structures common features (Pearce *et al.* 1978, Schumann 1987).

The main hydrographic feature of this region is the Thukela River, the largest river system in KZN with a small estuarine area ( $0.6 \times 10^6 \text{ m}^2$ ) but a large catchment of ca. 29 100 km<sup>2</sup> and it therefore functions as a conduit for a significant amount of freshwater, dissolved nutrients, detritus and sediment to enter the marine environment (Begg 1978, Cooper 2001, Lutjeharms 2006, Wepener 2007). Research indicates that detrital input has a significant role in the trophic functioning of macrobenthic communities (Heydorn *et al.* 1978, Field and Griffiths 1991). Freshwater inflow is highest in the rainy, summer months (December-March) with runoff peaking from January to February and extending as far as 25 km offshore (Pearce 1977, Flemming and Hay 1988, Meyer *et al.* 2002, Whitfield and Harrison 2003, Hutchings *et al.* 2010). The water column over the central Bight is well mixed and of intermediate nutrient concentration, lying between the high nutrient concentrations of waters in the northern Bight and low concentration of waters in the southern Bight (Meyer *et al.* 2002). Near surface Nitrate concentration of waters over the central Bight range from 1.01–1.86  $\mu\text{mol.L}^{-1}$ , with Phosphate and Silicate concentrations ranging from 0.48–0.72 and 3.50–4.69  $\mu\text{mol.L}^{-1}$ , respectively (Meyer *et al.* 2002). The area near the Thukela River mouth and shelf edge have higher nutrient concentrations than the rest of the central Bight, with Phosphate values of 1.39  $\mu\text{mol.L}^{-1}$  and Silicate values of over 4.0  $\mu\text{mol.L}^{-1}$  recorded (Meyer *et al.* 2002). The Thukela system is thus a net source of dissolved inorganic nutrients (DIN: Dissolved inorganic Nitrogen; DIP: Dissolved inorganic Phosphorous) (Wepener 2007).

An estimated  $5.1 - 6.79 \times 10^6 \text{ m}^3$  (Nicholson 1983, Flemming and Hay 1988, Bosman *et al.* 2007) of fluvial sediment is transported to the ocean annually from the Thukela River, with this load being deposited in a matter of days during extreme flood conditions (Begg 1978, Flemming and Hay 1988, Bosman *et al.* 2007). The sedimentary regime of the central shelf is characterised by the presence of two large mud depocentres, one inshore (20-50 m) and the other located on the outer shelf (70-100 m) (Flemming and Hay 1988, Cooper 2001, Bosman

*et al.* 2007). Inshore muds are recently deposited, brown and soft, whereas offshore muds are older (50 000 years), grey and stiff (Flemming and Hay 1988). A belt of sand and gravel sized bioclastic debris separates these two muddy regions at the mid-shelf (65 m) with high gravel contents also encountered at the shelf break in this region (Flemming and Hay 1988, van der Elst and Fennessy 1990).

An economically important commercial trawl fishery operates on the muddy, inner shelf, known as the Thukela Banks (Demetriades and Forbes 1993, Groeneveld and Melville Smith 1995, Sauer *et al.* 2003, Turpie and Lamberth 2010). The importance of Thukela River outflow has been established through investigations of catch data, which show that the abundance of fauna increases during periods of high river flow and are reduced during low outflow periods (Groeneveld and Melville-Smith 1995, Whitfield and Bate 2007, Lamberth *et al.* 2009). Freshwater runoff is also likely to provide cues for the spawning and recruitment of juvenile fish and invertebrate taxa that utilise the Thukela Banks as a nursery area (Forbes and Demetriades 2005, Lamberth *et al.* 2009). Benthic fauna are thus important, contributing to the productivity and functioning of the central shelf (Forbes and Demetriades 2005, Whitfield and Bate 2007, Lamberth *et al.* 2009).

### ***The southern Bight – Durban***

Towards the southern extremity of the Bight the shelf narrows again (15 km) with the Agulhas Current exhibiting significant meandering in this region particularly in the mid-shelf characterised by mobile bedload and the exposed, current swept outer shelf (Harris 1978, Pearce *et al.* 1978, Lutjeharms and Roberts 1988, Lutjeharms *et al.* 1989, Meyer *et al.* 2002, Green and Garlick 2011). The most important oceanographic feature here is a persistent cyclonic lee-eddy. This feature is formed by current/shelf dynamics and results in the upwelling of cold, low salinity, nutrient-rich water at about 300 m, 30-50 km offshore of Durban, leading to enhanced primary productivity and facilitating the retention of larvae (Burchall 1968, Anderson *et al.* 1988, Lutjeharms *et al.* 2000a, Hutchings *et al.* 2002, Meyer *et al.* 2002, Roberts *et al.* 2010). Nitrate concentrations as high as 18.33  $\mu\text{mol.L}^{-1}$  and Phosphate concentrations of 1.59  $\mu\text{mol.L}^{-1}$  have been recorded for waters originating at the core of this eddy system (125 m) (Meyer *et al.* 2002). Nutrient concentrations of waters over the mid-shelf (75m) were in the range of 0.18-13.45  $\mu\text{mol.L}^{-1}$  for Nitrate, 0.46-5.43  $\mu\text{mol.L}^{-1}$  for Phosphate and 3.03-10.73  $\mu\text{mol.L}^{-1}$  for Silicate, while shallow waters were the most nutrient poor with Nitrate

concentrations of 0.18-1.89  $\mu\text{mol.L}^{-1}$ , Phosphate values ranging from 0.37 to 0.59 and Silicate concentrations of 2.83-4.05  $\mu\text{mol.L}^{-1}$  (Meyer *et al.* 2002).

Inshore currents in this area of the shelf are northward moving when the Agulhas Current is hard up against the shelf break but switch to a southerly direction when the current meanders further offshore, with local weather patterns and shelf topography postulated as being responsible for this meandering behaviour (Harris 1964, Pearce *et al.* 1978, Schumann 1987, Anderson *et al.* 1988, Gründlingh 1992, Lutjeharms 2007, Roberts *et al.* 2010). This warm, inshore counter current off Durban is actually oligotrophic Agulhas Current water spun onto the shelf from the offshore cyclonic eddy (Meyer *et al.* 2002). When these northerly moving coastal currents are present a positive nutrient gradient with distance offshore is created, with higher nutrient water found at the shelf edge (Meyer *et al.* 2002). These occasional offshore meanders of the Agulhas Current, known as “Natal Pulse” events are present for about 7% of the time (Lutjeharms and Roberts 1988) and are caused by the enlargement of a cyclonic eddy as it moves down the coast along a weak continental slope (Lutjeharms and Roberts 1988, Hutchings *et al.* 2002, Bryden *et al.* 2005, Speich *et al.* 2006, Lutjeharms 2007, Roberts *et al.* 2010). It appears that “Natal Pulse” events are responsible for generating warm Agulhas rings that facilitate the exchange of water between the Indian and Atlantic Oceans (Lutjeharms *et al.* 2000a).

## 2.2 Study design and sampling protocol

Two cruises (A and B) were conducted aboard the research vessel, *F.R.S. Algoa* with the first cruise (A) conducted from the 2<sup>nd</sup> to the 21<sup>st</sup> of February 2010, during the summer period of high rainfall and the second cruise (B) taking place in the same year from the 2<sup>nd</sup> to the 26<sup>th</sup> August.

In addition to macrobenthic samples, those forming part of other ACEP work packages were also collected during this time, detailed information of which is provided in Lamont *et al.* (2010). The sampling design for the proposed study was pre-established and forms part of a larger macrobenthic sampling protocol which will serve to fill “gaps” in areas of the KwaZulu-Natal Bight not presented in this study (Lamont *et al.* 2010, Mackay 2010). Prior to the first sampling cruise, the coarse spatial extent and underlying sediments of the central Bight were mapped. This model then formed the template for selecting macrobenthic sampling stations

presented here (Mackay 2010). Position of transect stations, in addition to being based on available sedimentary data for the region, were chosen to avoid reefs as far as possible (Mackay 2010, C.F Mackay, 2010, pers. comm.). Sampling stations were orientated along a depth gradient from the shallow inner shelf (~20 m) to the outer shelf (~200 m) in three oceanographic feature areas: Richard's Bay (RB) (28° 58'S, 32° 38'E), Thukela (TK) (29° 25'S, 31° 54'E) and Durban (DN) (29° 91'S, 31° 05'E) corresponding with the northern, central and southern Natal Bight, respectively (Mackay 2010, Fig. 3.1). Transects sampled in this study are therefore considered to be representative of the depth range, sediment facies and physico-chemical regime of the Natal Bight as well as the patchy distribution characteristic of macrobenthic assemblages (Mackay 2010, C.F Mackay, 2010, pers. comm.).

## **2.2.1 Field sampling procedure**

### ***Physico-chemical sampling***

At each of the thirteen stations sampled details such as the prevailing weather conditions were recorded in a field log book. A single Conductivity-Temperature-Depth (CTD) cast (Sea-Bird: SBE 19 Plus V2 SEACAT) was conducted to the maximum depth of each shelf position station in order to record physical habitat parameters of the undisturbed bottom environment (Mackay 2010). This instrument provides measures of depth (m), temperature (°C), dissolved Oxygen concentration (mg.L<sup>-1</sup>) and salinity (Mackay 2010). Once the CTD was received on deck, the grab sampling could proceed.

As part of a more focussed study on nutrients and Primary Productivity, Chlorophyll-*a* (Chl-*a*), Silicate (Si), Nitrate (NO<sub>3</sub>) and Phosphate (PO<sub>4</sub>) determinations were made at a single station in the narrow northern (Richards Bay) and southern Bight (Durban), corresponding with locations of potential nutrient input through the action of an upwelling cell and lee-eddy, respectively. Two stations were sampled on the central shelf, one close to the Thukela River mouth, a third potential site of nutrient input on the Natal Bight, and the other located close to the outer shelf region where a phytoplankton bloom was opportunistically encountered during cruise A (Fig. 3.1). Samples analysed for nutrient concentration and Primary Productivity (Chlorophyll *a* (Chl-*a*)) were collected at different depths through the water column and each station was sampled on a number of occasions during cruises A and B (Table 2.1). Due to the fact that different depth strata were sampled during each sampling bout, an accurate determination of near bottom conditions was not possible. Nutrient and Chl-*a* concentrations were therefore integrated throughout the sampled water column for each sampling time

(cruise), with mean ( $\pm$  SD) concentration values taken as representative of sampling location (feature area). Details of Chl-*a* determinations can be found in Barlow *et al.* (2008). These environmental data were used to characterise the physico-chemical habitat of the feature areas under investigation, assess whether there were changes between sampling cruises A and B and explain variation in biotic data.

Table 2.1. Details of the location and number of times nutrient and primary productivity stations were sampled in each feature area during cruises A and B.

Feature area	Location	Cruise	No. of times sampled
Richard's Bay (RB)	OS	A	7
	OS	B	10
Thukela (TK)	IS	A	6
	IS	B	6
	MS	A	6
	MS	B	2
Durban (DN)	OS	A	10
	OS	B	10

### **Macrobenthic and sediment sampling**

Sampling was conducted during daylight hours where possible (Mackay 2010). Three replicate grab samples were collected from each station with a 0.2 m<sup>2</sup> van Veen grab deployed over the side of the vessel by means of a mechanical winch (Mackay 2010). Samples of this size are considered appropriate for the determination of abundance and biomass of macrobenthic fauna (Eleftheriou and Moore 2005). Bucket grabs such as the van Veen provide reasonably accurate sampling of soft bottoms although the amount of sediment sampled is affected by the nature of the substrate, with muddy bottoms tending to fill grabs samples completely while those collected from sandy grounds will generally penetrate to lower depths (Pearson 1970, Blomqvist 1991, Marques and Bellan-Santini 1993, Eleftheriou and Moore 2005). During the collection of replicate grab samples drift of the vessel was limited to less than 200 m from the site of the initial collection to maintain the integrity of replicate samples. In cases where drift exceeded this distance, the vessel steamed back to the station location (Mackay 2010). Additional weights (4 x 10 kg lead blocks) were added to the arms of the grab to aid in the successful operation of the sampling gear (Mackay 2010).

Once a successfully collected sample was received on deck, the windows on the top of the grab were opened and the depth of sediment collected measured, to the nearest mm, with a ruler. Only collected samples with a sediment depth of at least 50 mm and no evidence of

sample disturbance were accepted for further processing (Bergen *et al.* 2001, Mackay 2010, C.F Mackay, 2010, pers. comm.).

The close association that macrobenthos have with the sediment necessitates characterisation of the bottom environment. Two small sub-samples (175 g) of sediment were collected from the top of each grab sample and used for granulometric and organic content analysis (TOC), the latter sediment sample requiring fixation by adding approximately 5ml of 40% formalin (Bale and Kenny 2005). The remaining sample was then released into a stainless steel sieve, with a square mesh size of 1000  $\mu\text{m}$  and washed through using deck hoses (Mackay 2010). Square mesh sieves are preferable as they provide a larger percentage of open area (Morgans 1956, Eleftheriou and Moore 2005). Washing was gentle in order to ensure that no sediment was displaced out of the sieve and that animals were not damaged with strong jets of water (Mackay 2010). Visible fauna were carefully handpicked out during the washing stage and placed in the appropriately labelled sample jar to avoid unnecessary damage (Shin *et al.* 2004, Mackay 2010). After sieving, all organisms and residual sediment were placed in the appropriate sample jar, labelled and preserved unstained with formalin (4%) for future examination (Eleftheriou and Moore 2005, Mackay 2010). Sufficient preservative was added to samples with a high detrital content and the preserving fluid was adequately mixed throughout the sample, especially in the case of coarser grades of sediment (Eleftheriou and Moore 2005, C.F Mackay, 2010, pers. comm.). Unbuffered formalin tends to become acidic with time so concentrated formalin was diluted with seawater in order to limit the erosion of calcium carbonate structures and dissolution of lipids and fatty acids (Eleftheriou and Moore 2005).

Occasionally grab samples collected large quantities (>10 L) of sandy sediment which were difficult and time consuming to wash through the sieve. In these cases the technique of elutriation was applied to separate out smaller animals and fine debris (Eleftheriou and Moore 2005). A standard amount of substrate from the large sample was put in a bucket, well agitated with a deck hose and the suspension poured through a fine screen to collect floating organisms. This washing and pouring process was repeated seven times or until the running water ran clear before sorting through the sediment for the recovery of heavy animals and characteristic sedimentary elements (Eleftheriou and Moore 2005, C.F Mackay, 2010, pers. comm.). The claimed efficiency of this process is 98-100% (Eleftheriou and Moore 2005).

### **2.2.2 Laboratory procedure**

#### ***Sedimentary analysis***

All sedimentary analysis was carried out at an external geology laboratory. Granulometric analysis characterises the sedimentary environment and provides an insight into local physical conditions (Gray 1981, Bale and Kenny 2005).

#### ***Grain size analysis***

The purpose of grain size analysis is to characterise the dimension of a population of sedimentary particles using a single measure (Morgans 1956, Buchanan and Kain 1971, Gray 1981, Bale and Kenny 2005). Grain size analysis may be achieved through a variety of methods. In this case sieving was employed as it is an inexpensive, easily reproducible, albeit time consuming, slow method, considered the most practical way of characterising particle sizes larger than 0.063 mm (Morgans 1956, Bale and Kenny, 2005).

Grade scales apply an arbitrary set of finite ranges to the continuous frequency distribution of particle sizes in order to generate rational classifications for the numerical divisions (Buchanan and Kain 1971, Gray 1981, Bale and Kenny 2005). The Wentworth scale is most commonly adopted by marine ecologists and geologists to characterise sediment particles (Morgans 1956, Gray 1981, Bale and Kenny 2005, Mackay 2006, Table 2.2). Applying a logarithmic transformation to the Wentworth scale produces the phi ( $\Phi$ ) notation which was initially employed to graphically manipulate data (Morgans 1956, Gray 1981 Bale and Kenny, 2005). Seven grain size categories, ranging from gravel to mud, were used in this study (Table 2.2).

Grain size analysis required the initial separation of the sand fraction from the mud fraction as particles of the latter are of a size that cannot be practically separated by sieving (Morgans 1956, Buchanan and Kain 1971, Gray 1981, Bale and Kenny 2005, Gray and Elliott 2009). The grain size distribution of the sand fraction was determined through using a set of Wentworth sieves ranging from 2–0.063 mm (Buchanan and Kain 1971, Bale and Kenny 2005). This stack of sieves was closed at both the top and bottom ends to prevent the loss of sample. An amount of sediment sample was weighed prior to placing it in the top (2 mm) sieve and the stack was then mechanically agitated for a fixed period, after which time the amount of sedimentary material retained by each sieve was determined by weighing (Bale and Kenny 2005).

Table 2.2. The Wentworth scale: characterisation of sediment types based on grain size (mm) of sedimentary particles, with the accompanying phi ( $\Phi$ ) notation. (Where phi ( $\Phi$ ) =  $-\log_2$  (particle size)) (modified from Gray 1981 and Bale and Kenny 2005).

Sediment type	Grain size (mm)	phi ( $\Phi$ ) scale
Gravel (gvl)	> 2	< -1.0
Very coarse sand (vcs)	1 – 2	-1.0 - 0.0
Coarse sand (cos)	0.5 – 1	0.0 - 1.0
Medium sand (mms)	0.25 - 0.5	1.0 - 2.0
Fine sand (fns)	0.125 - 0.25	2.0 - 3.0
Very fine sand (vfs)	0.0625 – 0.125	3.0 - 4.0
Mud (mud)	< 0.0625	> 4.0

### **Sorting and Skewness**

Sediments were also characterised according to their sorting classes and skewness (Table 2.3). Sorting is an indication of the range of particle sizes making up a particular sediment sample (Gray 1981). Well sorted sediments, typical of bottom areas subject to increased wave and current activity, are those in which the majority of the sample is comprised of particles with the same diameter (Gray 1981, Mackay 2006). On the other hand, poorly sorted sediments are comprised of a wide range of particle sizes, a situation typical of stable bottom areas that are subject to little hydrodynamic energy (Gray 1981, Mackay 2006).

Table 2.3. Sorting classes used to characterise sediments (modified from Gray 1981).

Sorting classes	phi ( $\Phi$ ) scale
Very well sorted	< 0.35 $\Phi$
Well sorted	0.35 - 0.50 $\Phi$
Moderately well sorted	0.50 - 0.71 $\Phi$
Moderately sorted	0.71 - 1.00 $\Phi$
Poorly sorted	< 1.00 $\Phi$

The skewness measure provides an indication of the symmetry of the spread of data on either side of the average (median particle diameter). If there is a tendency for the data to spread on one side more than the other this asymmetry is called skewness (Buchanan and Kain 1971). Skewness is positive if the coarse components dominate (positively/fine skewed, mode of coarse sed), otherwise it is negative (negatively/coarse skewed, fine sed dominate) (Gray 1981).

### **Organic content**

Organic matter in marine sediments is derived from the decomposition of plant and animal matter and its settlement and accumulation on the seafloor. In addition to these natural sources, pollutants and contaminants also contribute to sediment organic matter (Schumacher 2002). The Carbon content of marine sediments is comprised of inorganic and organic forms, the latter being an important food resource for macrobenthic communities (Cocito *et al.* 1990). Fine grained sediments provide a greater surface area for adsorption of organic matter and contaminants (Hyland *et al.* 2005). The higher abundances of deposit feeding infauna in muddy when compared with sandy sediments is often explained by the fact that there is more organic matter, and thus food, associated with finer particles (Cocito *et al.* 1990, Hyland *et al.* 2005). In general community variables (abundance, species richness and biomass) increase in relation to increased organic matter, expressed as total organic content (TOC), up to a certain point, beyond which they decline as the benthos is exposed to increasing levels of stress due to oxygen depletion and toxic by-products of the decomposition process (Hyland *et al.* 2005). In addition to the quantity of organic matter present, variations in the quality and bioavailability of this material have an appreciable effect on macrobenthic patterns (Hyland *et al.* 2005).

The suite of techniques used to determine organic content all rely on the principle of destroying the organic matter present in the sediment by chemical or heat energy and then measuring the loss directly or indirectly (Buchanan and Kain 1971, Schumacher 2002). The method of hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) digestion was employed to determine the total organic content (TOC) of sediment samples for the proposed study (Parker 1983, Schumacher 2002). The basic steps of this method are (Parker 1983, Schumacher 2002):

1. The inorganic carbonates are removed by the addition of 6% Hydrogen peroxide to a known weight of sediment, until the frothing reaction ceases.
2. The sample is oven dried at 105°C, cooled and weighed.
3. Organic matter present in the sediment sample is determined gravimetrically and calculated as:

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

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

4. Organic matter is converted to a value of TOC (Table 2.4) by using an appropriate factor. A conversion factor of 1.72 is commonly used based on the assumption that organic matter contains 58-60% Carbon (Schumacher 2002, Beasy and Ellison 2013).

Table 2.4. Characterisation of the percentage total organic Carbon (TOC) content of sediment samples (modified from Mackay 2006).

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

### **Macrobenthos**

In the laboratory, animals from each sample were picked out in order to separate benthic fauna from non-living, substrate and detrital particles. After this process, identification was carried out with the use of stereomicroscopes (Zeiss stemi-DV4, Zeiss Stereo V.12) to identify each animal to the lowest taxonomic level possible, with the use of appropriate taxonomic keys (e.g. Clark 1923, Kensley 1972, Day 1975, Clarke and Courtman-Stock 1976, Day 1976, Griffiths 1976, Kensley 1978, Kilburn and Rippey 1982, Steyn and Lussi 1998). For quality control purposes each sorted sample was checked by a second person to ensure that no animals were left behind, after which the sample was discarded. The identification of fauna was also checked by a specialist (C.F. Mackay). All taxonomic information was cross-checked against the World Register of Marine Species (WoRMS) database and taxonomic classifications presented here were up to date at the time of publishing this thesis.

The number of individuals of each species was counted after which every taxon was assigned to a feeding mode based on available literature (eg. Fauchald and Jumars 1979, Gaston 1987, Macdonald *et al.* 2010). Species that could not be confidently assigned to a feeding mode were designated as unknown (U). Specific details of feeding classification schemes applied in the present study are presented in the relevant chapters. Dominant feeding modes were

investigated in Chapter 3, while facultative feeding was considered in the classification of taxa used in Chapter 4, and feeding guilds corroborated by *in situ* gut contents analysis of polychaete taxa were considered in Chapter 5.

### 2.2.3 Generic Statistical analysis

We excluded from the analysis larval and pelagic fauna. From the remaining data macrobenthic taxa and feeding mode/guild by sample matrices were constructed. The abundance of each taxon was standardised to 1.0 m<sup>2</sup>. As a standard area of 0.2 m<sup>2</sup> was sampled with the van Veen grab, abundance values were multiplied by a factor of 5 in order to express values per m<sup>2</sup>. Three factors (cruise, feature area and shelf position), with associated levels, were investigated in this thesis (Fig. 2.2). A variety of software was utilised during data analyses including Excel 2010, Brodgar v.2.7.2 (an interface to R v.2.9.1), SigmaPlot v.11, and PRIMER v.6.

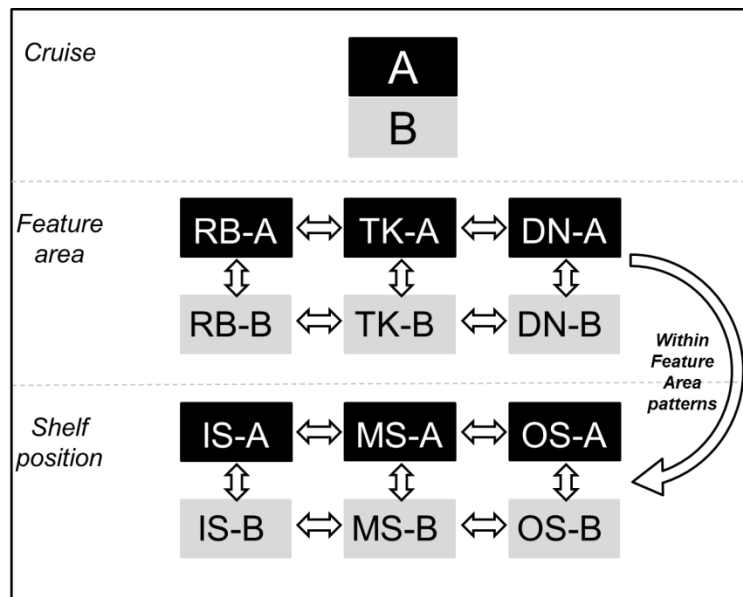


Figure 2.2. Test model of factors considered in the present study and their interactions. **Cruise A** (High rainfall – February 2010), **Cruise B** (Low rainfall – August 2010), **RB**=Richard's Bay, **TK**=Thukela, **DN**=Durban, **IS**=Inner shelf, **MS**=Mid-shelf, **OS**=Outer shelf.

#### Abiotic data

A total of 22 environmental variables were determined in the present study (Table 2.5). The relationships between environmental parameters measured were determined through parametric Pearson (product-moment) Correlation analysis, which measures the strength and significance of the linear relationship between two variables (Quinn and Keough 2002). The Pearson correlation coefficient ( $r$ ) varies in value from +1 to -1, the former indicates that both variables increase together, whereas the latter indicates that as one variable increases the

other decreases in value. A correlation of zero indicates that there is no relationship between the two variables (Quinn and Keough 2002).

### **Univariate analysis**

Univariate community measures were calculated from raw taxon and feeding mode abundance data using the DIVERSE procedure within the PRIMER v.6 statistical programme (Clarke and Warwick 1994). The primary community variables of abundance ( $N$ : no. of ind.m<sup>-2</sup>) and taxon/feeding mode richness ( $S$ : no. of taxa/feeding modes) were included in the present study. Biodiversity encompasses more than just information on how many different species are present in an area. A variety of diversity indices have been developed and used in the study of macrobenthic communities which combine both the taxon richness and how evenly individuals have been distributed amongst the species present (Sanders 1968, Gray 1981, Gray 1997, Gray 2000, Ellingsen 2001, Maurer and McGill 2011). In ecological studies a habitat is defined as a physical area and the biota it supports (Gray 1997). At this small scale there are biological interactions between species and the constituent taxa are also competing for resources. This is defined by ecologists as within-habitat ( $\alpha$ ) diversity which is the type of diversity considered in the present work (Gray 1997, Gray 2000).

Table 2.5. Physico-chemical and sedimentary variables measured in the present study.

Environmental variable			Sampling level
Physico-chemical	Chlorophyll a	µg.L <sup>-1</sup>	Feature Area
	Silicate		
	Phosphate	µmol.L <sup>-1</sup>	
	Nitrate		
	Depth	m	Station
	Temperature	°C	
	Salinity		
	Dissolved oxygen	mg.L <sup>-1</sup>	
Sediment	Gravel		Sample
	Very coarse sand		
	Coarse sand		
	Medium sand		
	Fine sand	%	
	Very fine sand		
	Mud		
	Organics		
	Mean phi		
	Median phi	Φ	
	Sorting		
	Mean grain size		
	Median grain size	mm	
	Skewness		

Three aspects of diversity were measured, the Shannon-Wiener diversity index ( $H'$ ) (Shannon and Weaver 1963) which is the most commonly used in macrobenthic community studies (Gray 1981, Bertrand *et al.* 2006, Gray and Elliott 2009, Maurer and McGill 2011). This index is most affected by taxa in the middle of the rank sequence (Gray 1997, Gray and Elliott 2009, Maurer and McGill 2011).

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

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

High values of diversity can be due to an increase in the number of species or because the number of members of each taxon becomes more constant (Sanders 1968, Gray 1981). Therefore to tease out the driving factor of high or low diversity values, two additional indices were calculated (Gray 1981). The Margalef's Richness ( $d$ ) index (Margalef 1961), was computed which is a measure of taxon richness.

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

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

Pielou's Evenness index ( $J'$ ) (Pielou 1966) was also calculated and considers how the number of individuals is apportioned among taxa making up the community.

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

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

This index assumes a value in the range (0, 1) where zero indicates dominance of a few taxa with high abundance, while values close to 1 indicate similar number of individuals across all taxa (Maurer and McGill 2011).

An unpaired *t*-test was used to test for differences ( $p < 0.05$ ) in abiotic and biotic parameters recorded during cruises A and B (Quinn and Keough 2002). One and two-way analysis of variance (ANOVA) testing, within the statistical software package SIGMAPLOT v. 11.0, was used to test for significant differences ( $p < 0.05$ ) in univariate measures between the factors cruise (A,B), feature area (RB, TK, DN) and shelf position (IS, MS, OS), as well as the interactions between these factors (Fig. 2.2). Where statistically significant differences were found, Student-Newman-Keuls (SNK) *post-hoc* tests were applied to detail the pair-wise interactions between the levels of these factors to reveal which were responsible for the observed changes. Both *t*-tests and ANOVA are parametric techniques, so prior to analyses, normality and homogeneity of variance were determined and if necessary, data transformations were applied in order to try satisfy these assumptions (Clarke and Green 1988, Quinn and Keough 2002). Transformations were applied along a continuum of increasing severity (squareroot to log) and after each transformation data were re-checked (Clarke and Green 1988, Quinn and Keough 2002). Where conditions of normality and equality of variance could not be satisfied, the alternative non-parametric tests (Mann-Whitney *U*-test, Kruskal-Wallis) were conducted on ranked data (Quinn and Keough 2002).

### **Multivariate analysis**

Integral to the aim of this study is the analysis of the biotic community, its attributes and the influence of local abiotic factors on the macrobenthos. The proposed study therefore also necessitated the use of multivariate statistical techniques to explore these non-linear relationships (Clarke and Warwick 1994, Underwood and Chapman 2005). These methods have been identified as being the most sensitive for detecting small changes in macrobenthic assemblages (Clarke and Warwick 1994, Roth and Wilson 1998, Ellingsen 2001, Gray 2002).

The multivariate analysis strategy adopted in this thesis was normal Q-type analysis, in which samples are compared and grouped together with respect to the extent to which they share taxa or feeding modes/guilds (Field *et al.* 1982, Clarke and Warwick 1994). The stages comprising normal Q-type analysis are summarised in Fig 2.3. In community analysis in which taxa have been identified and counted, there are often many rare species and only a few common, abundant ones so that the distributions of data are highly skewed (Clarke and Warwick 1994, Ter Braak and Verdonschot 1995, Legendre and Birks 2012).

Although few assumptions are made about the nature of the data when employing multivariate techniques and there is no need to transform data to attain normality it is still necessary to apply a transformation in order to balance the contributions from common and rare taxa (Field *et al.* 1982, Clarke and Ainsworth 1993, Legendre and Birks 2012). This can be accomplished through a number of means: square root ( $\sqrt{\phantom{x}}$ ), fourth root ( $\sqrt[4]{\phantom{x}}$ ), log or log ( $x + 1$ ) transformation (Clarke and Green 1988, Clarke and Warwick 1994). The more severe the transformation applied the greater the influence less abundant taxa will have on the output (Clarke and Green 1988, Clarke and Warwick 1994). Abundance (taxa and feeding mode) values were square root ( $\sqrt{\phantom{x}}$ ) transformed prior to further analysis in order to prevent a small number of abundant taxa from dominating the results (Field *et al.* 1982, Clarke and Green 1988, Clarke and Ainsworth 1993).

The commonly applied Bray-Curtis (B-C) similarity coefficient was then calculated from the transformed biotic data. This similarity coefficient is generally used in marine benthic studies as it is not affected by joint absences and it gives more weight to abundant taxa (Field *et al.* 1982). Joint absences are common in ecological data in that a taxon can be absent in two different samples but this does not mean that these samples are similar on the basis that neither contains this particular animal (Clarke and Green 1988, Clarke *et al.* 2006). Zero values are therefore important in ecological data and can't be treated as any other number (Clarke and Green 1988, Clarke *et al.* 2006).

The B-C coefficient expresses the similarity in abundance or biomass of each taxon or feeding mode/guild between two samples in a single value that indicates similarity in community structure. The similarity between samples was then further investigated by applying the multivariate methods of hierarchical classification or multidimensional scaling (Clarke and Warwick 1994, Underwood and Chapman 2005). Hierarchical classification or cluster analysis produces a dendrogram by linking samples in groups on the basis of their similarity in terms of taxon or feeding mode/guild composition (Clarke and Warwick 1994, Underwood and Chapman 2005, Gray and Elliot 2009). Clustering was by hierarchical agglomerative method using group-average linking, which combines pairs of samples based on the average level of similarity (Field *et al.* 1982, Clarke and Green 1988, Clarke and Warwick 1994). While this method is useful for simplifying sample relationships, there are a number of disadvantages, notably the fact that the order in which samples are arranged within a cluster group is random

so that it in no way reflects the relationships between samples within a group. It is therefore often advisable to employ the additional method of ordination (Field *et al.* 1982).

Ordination represents sample relationships in a specified number of dimensions (Field *et al.* 1982). Ordination was by non-metric multidimensional scaling (MDS) which finds the 2-dimensional representation that best depicts the patterns of hyper-dimensional multivariate data (Clarke and Warwick 1994). In this analysis the Bray-Curtis similarity between two samples is reflected as distance separating samples in the ordination space, so that samples lying close together are interpreted as being more similar in terms of macrobenthic taxon or feeding mode/guild abundance (Field *et al.* 1982, Clarke and Green 1988, Gray *et al.* 1988, Clarke and Warwick 1994). The final MDS ordination plot is produced through a number of iterations (typically ~25) which proceed with several alternate starting configurations (Field *et al.* 1982, Clarke and Warwick 1994). The extent to which this ordination map represents actual relationships between samples is expressed as a Kruskal stress value (Field *et al.* 1982, Clarke and Warwick 1994). Large stress values ( $0.5 > \text{Stress} > 0.25$ ) indicate that the ordination plot poorly represents observed sample relationships in 2D space while stress values between 0.1 and 0.25 indicate satisfactory results and values  $< 0.1$  indicate a good representation (Clarke 1993).

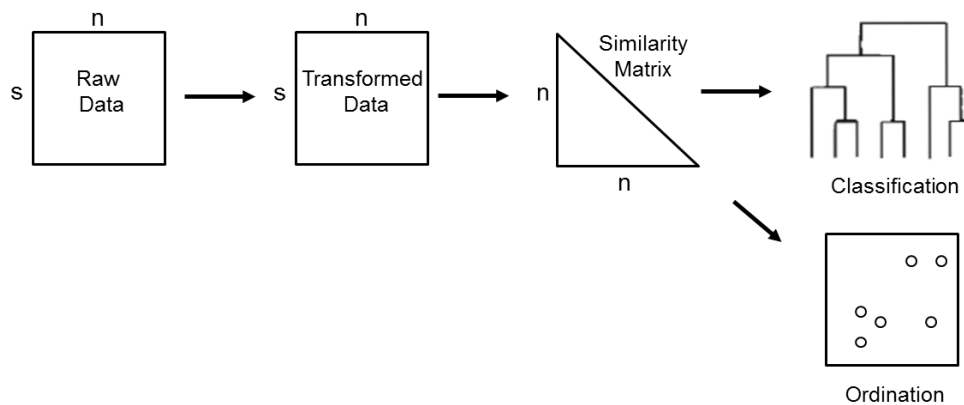


Figure 2.3. Summary of the stages in multivariate Q-type analysis (modified from Field *et al.* 1982).

The taxa and feeding modes/guilds responsible for the groupings observed in the cluster and ordination analyses were examined through the Similarity Percentage breakdown (SIMPER) procedure within the PRIMER package. This analysis uses pairwise comparisons of samples and finds the average contribution of each taxon or feeding mode/guild to the similarity between all pairs of samples within a group and to the dissimilarity of sample pairs between groups (Clarke and Warwick 1994). The average of these percentage contributions ( $\bar{\delta}_i$ ) with associated

standard deviation  $SD(\bar{\delta}_i)$  are then computed. The ratio of  $(\bar{\delta}_i)/SD(\bar{\delta}_i)$  is a measure of how consistently a taxon or feeding mode/guild contributes to the average similarity within groups or the average dissimilarity between groups. Large values of  $(\bar{\delta}_i)/SD(\bar{\delta}_i)$  indicate those taxa or feeding modes/guilds that typify sample groups and best discriminate between groups (Clarke and Warwick 1994).

Differences among the *a priori* selected factors: cruise, feature area and shelf position (Figure 2.2) were statistically tested using Analysis of Similarity (ANOSIM) permutation-based hypothesis testing, a counterpart to univariate ANOVA (Clarke and Green 1988). This test takes into account the similarities among samples within a cruise, feature area or shelf position and makes comparisons with replicates from different sampling sessions, areas or shelf positions. The null hypothesis being tested is that of no differences between the factors under consideration (Clarke and Green 1988). The test statistic produced is  $R$  which assumes a value between 1 and 0. If  $R=1$  all samples within a cruise, area or shelf position are more similar to each other than to samples from a different cruise, feature area or shelf position. An  $R$  value is approximately 0 when the null hypothesis is not rejected, that is similarities within and between sites are the same (Clarke and Green 1988, Clarke and Warwick 1994).

### ***Relating faunal and environmental patterns***

Crucial to the aim of this study is the question of whether the measured environmental variables had an effect on the distribution, structure and function of macrobenthic communities. Prior to environmental analysis used in Chapters 3 and 4, a Draftsman plot was constructed for all variables in order to identify skewed distributions (Ter Braak 1986, Clarke and Warwick 1994, Legendre and Birks 2012). The plot revealed that the sedimentary parameters of gravel (gvl), very coarse sand (vcs), coarse sand (cos) and total organic content (TOC) should be transformed. These four variables were square root ( $\sqrt{\phantom{x}}$ ) transformed and subsequently Pearson Correlation coefficient values ( $r$ ) were calculated between each pair of environmental variables to identify instances of multi-collinearity (Clarke and Ainsworth 1993, Clarke and Warwick 1994). In general, sets of environmental variables that are highly correlated ( $r=0.95$ ) should be reduced to a single representative (Clarke and Ainsworth 1993). The sediment descriptors mean phi and median phi were highly correlated ( $r=0.974$ ) as were median mm and mean mm ( $r=0.974$ ). Because each pair of the four variables depicts the same kind of information only mean phi was retained for subsequent analysis. The remaining

19 measured environmental variables were standardised to enable the comparison of variables with different sampling units (Clarke and Warwick 1994).

The BEST procedure, contained within PRIMER v.6, was then employed to identify the single variable or combination of variables which maximises the rank correlation between the abiotic and biotic (dis)similarity matrices (Clarke *et al.* 2008). In this analysis the weighted Spearman Rank Correlations ( $\rho_w$ ) between a similarity matrix derived from biotic data and matrices derived from various combinations of environmental parameters are calculated, thereby identifying the suite of variables best correlated with the observed biotic patterns (Clarke and Ainsworth 1993, Clarke and Warwick 1994). Values of  $\rho_w$  lie in the range (-1, 1), where extreme values correspond to a complete disagreement (-1) or agreement of ranks (+1). A value of  $\rho_w$  around 0 would indicate that there is no relationship between the two matrices (Clarke and Ainsworth 1993, Clarke and Warwick 1994). The similarity matrix computed for environmental data was based on Euclidean distance while that for biotic data were based on Bray-Curtis Similarity (Clarke and Ainsworth 1993, Clarke and Warwick 1994). More than 15 environmental variables were used, thus the BVSTEP algorithm was used to carry out a stepwise search of the 19 environmental variables using both forward selection and backward elimination techniques. Starting with the environmental variable that yields the maximum match (highest  $\rho_w$  value) between environmental and biotic matrices, variables are successively added, the combination tested and, at each stage, the variable contributing least is eliminated (Clarke and Warwick 1998). This stepwise procedure is repeated a number of times using environmental variables chosen at random until the combination of environmental variables with the largest  $\rho_w$  is found that provides the best match with macrobenthic community patterns (Clarke and Warwick 1998). The significance of the subset of environmental variables was determined through a “global BEST test” which tests the null hypothesis that there is no relationship between the biotic and abiotic information collected for the given set of samples (Clarke *et al.* 2008). The correlation between these two matrices describes how much of the variation in the biological data is accounted for by the measured abiotic factors (McArthur *et al.* 2010). The environmental variables identified through the BEST procedure can be superimposed as bubbles onto the ordination of biotic samples to provide a visual representation, which was the approach adopted in Chapter 5. Although this method is useful in visually depicting the effects of a single variable, a number of other ordination methods such as Canonical Correspondence Analysis (CCA) and Redundancy Analysis (RDA) applied in Chapters 3 and 4, respectively may be more suitable in terms of visualising the inter-sample

relationships (in terms of the taxon composition and functioning) and the relation of the taxa (or spatially distinct communities) to each other and measured environmental variables (Clarke and Green 1988, Clarke and Warwick 1994, Legendre and Anderson 1999, Legendre and Gallagher 2001, Legendre and Birks 2012).

## **CHAPTER 3. MACROBENTHIC COMMUNITIES AND FEEDING MODE PATTERNS WITHIN AND BETWEEN THREE OCEANOGRAPHIC FEATURE AREAS OF THE NATAL BIGHT**

### **Overview**

This chapter investigates the macrobenthic communities sampled, during a high and low rainfall period, along a depth gradient in three areas of the Natal Bight: Durban, Thukela and Richards Bay. These feature areas correspond with potential nutrient input features which are hypothesised, in the broader ACEP context, to drive the ecology of the Natal Bight. Macrobenthic communities were classified taxonomically, to the lowest level possible, and functionally by assigning each taxon to a dominant feeding mode. Community patterns were investigated within and between feature areas and related to measured environmental factors.

### **3.1 Introduction**

The three areas under consideration represent regions of the Natal Bight characterised by features which bring nutrients onto the shelf (Chapter 2). The narrow, northern region is characterised by a persistent upwelling cell offshore of Cape St. Lucia (Pearce *et al.* 1978, Carter and d'Aubrey 1988, Lutjeharms *et al.* 2000a, Lutjeharms *et al.* 2000b, Roberts *et al.* 2010). The warm Agulhas Current tends to follow the shelf break quite closely where it is narrow but the widening shelf causes perturbations in the current which is thought to drive this upwelling (Lutjeharms *et al.* 2000a, Lutjeharms *et al.* 2000b, Chapter 2). Numerous studies have found that enriched, upwelled waters are transported southwards, leading to the contention that this upwelling cell is the primary source of nutrients for the Natal Bight (Meyer *et al.* 2002, Lutjeharms 2007, Chapter 2). There has up until now though, been no indication of whether this nutrient input is bio-available, especially given that east coast waters are generally considered to contain little phytoplankton (Carter and d'Aubrey 1988). The widest part of the shelf is under the influence of the Thukela River, which carries large amounts of terrigenous sediment, dissolved nutrients and detrital material into the coastal zone, particularly during the rainy summer months when river outflow is high (Begg 1978, Schumann 1988, Lutjeharms *et al.* 2000a, Bosman *et al.* 2007, Wepener 2007, Chapter 2). Towards the southern limit of the Natal Bight the shelf narrows again with a large lee-eddy system offshore of Durban characterising this region and resulting in upwelling of nutrient rich waters onto the shelf

(Pearce 1977, Schumann 1987, Hutchings *et al.* 2002, Lutjeharms 2007, Roberts *et al.* 2010, Chapter 2).

Macrobenthic organisms respond to continental inputs by an increase in abundance and biomass which is presumably related to the increased input of nutrients and particulate organic matter (POM) (Pearson and Rosenberg 1978, Salen-Picard *et al.* 2002, Harmelin-Vivien *et al.* 2006). It is therefore expected that communities closest to sites of nutrient input will be distinct from sampling stations further away. Sampling within each of the three feature areas was stratified by depth zone as depth is well known to be a primary determinant of macrobenthic community structure (Sanders 1968, Gray 1981, Snelgrove 1998, Hall 2002). Environmental parameters measured included sedimentary characteristics as well as physico-chemical conditions in the surrounding pelagic milieu (Chapter 2). The species composition, distribution and feeding strategies of macrobenthic communities are well known to be driven by a number of environmental factors (Chapter 1). Thus information about the structure and functioning of this component provides an indication of conditions in the surrounding environment and the biological importance of identified nutrient input features.

### **Aims, Objectives and Hypotheses**

This chapter compares macrobenthic communities found within and between three feature areas of the Natal Bight to determine functional and spatial patterns and makes an attempt to look at short-term temporal change. These patterns are related to measured environmental parameters in order to determine the impact and importance of oceanographic features on the structure and function of macrobenthic communities.

### **Objectives**

1. Characterise the abiotic habitat of each feature area.
2. Determine whether the macrobenthic communities sampled during cruise A and cruise B were different.
3. Determine whether there were differences between the feature areas and shelf positions under consideration in terms of the macrobenthic communities sampled.
4. Consider each feature area separately and determine whether macrobenthic communities sampled from inner, mid and outer shelf depths were different.

5. Relate measured environmental variables to macrobenthic community patterns and determine the influence of nutrient sources.

### **Hypotheses**

H<sub>a1</sub>: There is a difference in environmental parameters or macrobenthic community structure between high (Cruise A) and low (Cruise B) rainfall periods.

H<sub>a2</sub>: There are differences in environmental parameters or macrobenthic communities found between the Richard's Bay, Thukela and Durban feature areas.

H<sub>a3</sub>: There are differences in environmental parameters or macrobenthic communities found at inner, mid and outer shelf positions sampled.

H<sub>a4</sub>: There are interactions between cruise, shelf position and feature area.

H<sub>a5</sub>: There is a significant relationship between macrobenthic community structure and environmental parameters measured in the present study.

## **3.2 Materials and Methods**

General field sampling, lab processing and data analysis information is presented in Chapter 2 of this thesis.

### **3.2.1 Study area and Sampling Design**

Three shelf position stations, orientated along a depth gradient from the shallow inner shelf to the outer shelf, were sampled in three feature areas: Richard's Bay (RB), Thukela (TK) and Durban (DN) during a high (Cruise A: February 2010) and low (Cruise B: August 2010) rainfall period (Fig. 3.1, Chapter 2).

### **3.2.2 Data handling and analysis**

#### ***Abiotic data***

Temperature, dissolved Oxygen (DO) and salinity have been correlated with depth to investigate how these environmental variables change across the sampled transects. Mean grain size ( $\phi$ ) is known to decrease with depth and be inversely related to sediment organic content (Chapter 1, Chapter 2). This was investigated through correlating total organic content of sediment with mean  $\phi$  values).

### ***Biotic data***

Each taxon was assigned to a feeding mode according to its dominant feeding mechanism. Eight trophic modes were defined namely: carnivore (C), interface feeder (IF), omnivore (O), multi-modal (MM), suspension feeder (SF), surface deposit feeder (SDF), subsurface deposit feeder (SSDF) and Parasite (Par). Interface feeding (IF) was assigned to those taxa which utilise both suspension and deposit feeding with no apparent dominance of either mode while Ostracoda were designated as MM due to these animals feeding using three different modes (C, SDF and SF). Two sets of data were considered in this study namely that of taxon abundance and feeding mode abundance for the 54 samples collected. Detailed information regarding the materials and methods applied in the present study are presented in Chapter 2 of this thesis.

### ***Univariate analysis***

The primary community variables of abundance ( $N$ : no. of ind.m<sup>-2</sup>) and number of taxa/feeding modes ( $S$ : no. of taxa/feeding modes) were calculated from raw data for the factors cruise, feature area and shelf position. These two community metrics were also computed for the sample groups obtained in cluster analysis considering all 54 samples. In addition the Shannon-Wiener Diversity ( $H'$ ), Margalef's Richness ( $d$ ) and Pielou's Evenness ( $J'$ ) indices were calculated for clusters obtained from taxon abundance data as well as for the feeding modes characterising these clusters (Chapter 2).

Two way analysis of variance (ANOVA) testing, within the statistical software package SIGMAPLOT v. 11.0, was used to test for significant differences in univariate measures between the factors cruise (A,B), feature area (RB, TK, DN) and shelf position (IS, MS, OS). Where statistically significant differences were found, the Student-Newman-Keuls (SNK) post-hoc test was applied to detail the pair-wise interactions between the levels of these factors and reveal which were responsible for the observed changes (Chapter 2).

### ***Multivariate analysis***

#### ***Macrobenthic community patterns***

Taxon abundance data were transformed prior to computation of Bray-Curtis similarity between each pair of samples and the resulting triangular similarity matrix subjected to cluster analysis (Chapter 2). Taxa and feeding modes characterising and discriminating clusters from one another were identified through the SIMPER procedure. Analysis of Similarity testing

(ANOSIM) was employed to test the null hypothesis of no significant differences in the taxon composition and distribution of macrobenthic communities. The *a*-priori factors tested both within and between feature areas were cruise (A, B), feature area (RB, TK, DN) and shelf position (IS, MS, OS) (Chapter 2).

*Relationship between macrobenthic communities and environmental factors*

The set of abiotic factors identified, through the BVSTEP algorithm contained within the BEST procedure (Chapter 2), as being the best descriptors of macrobenthic communities sampled in all three feature areas were used as input for Canonical Correspondence Analysis (CCA) using the BROD GAR v.2.7.2 statistical programme (Zuur *et al.* 2007). Canonical Correspondence Analysis is a multivariate ordination method commonly applied in ecology to investigate linkages between biotic assemblages and environmental parameters (Ter Braak and Verdonschot 1995, Legendre and Legendre 1998, Quinn and Keough 2002, Chapter 2). In contrast with Principal Co-ordinate Analysis (PCA), CCA is a direct gradient technique in which response (biotic) variables are directly linked to explanatory (environmental) variables (Ter Braak 1986, Palmer 1993, Quinn and Keough 2002, Zuur *et al.* 2007, Legendre and Birks 2012). The dissimilarity measure underlying CCA is the Chi-square distance function. One of the primary disadvantages of using this metric is that it is extremely sensitive to rare taxa (Oug 1998, Zuur *et al.* 2007, Legendre and Birks 2012). To account for this, auto down weighting was selected in the software and applied to rare taxa prior to CCA analysis (Zuur *et al.* 2007).

Canonical Correspondence Analysis is unique in that it provides an ordination of taxa, samples and environmental variables in a combined plot (Palmer 1993, Ter Braak and Verdonschot 1995, Oug 1998, Quinn and Keough 2002). Explanatory (environmental) variables are presented as vectors that extend from the origin of the CCA plot (Ter Braak 1986, Ter Braak and Verdonschot 1995). The length of the vector denotes the strength of influence which the environmental variable has in determining community structure, so that important variables are represented by longer vectors (Ter Braak 1986, Palmer 1993, Ter Braak and Verdonschot 1995). Vector length is also an indication of the maximum rate of change of the environmental variable so that variables presented by short arrows do not vary much (Ter Braak and Verdonschot 1995). The angle between vectors intimates the degree of correlation between environmental variables with obtuse angles indicating a negative correlation (Palmer 1993, Ter Braak and Verdonschot 1995). Samples are presented as points in the ordination space with

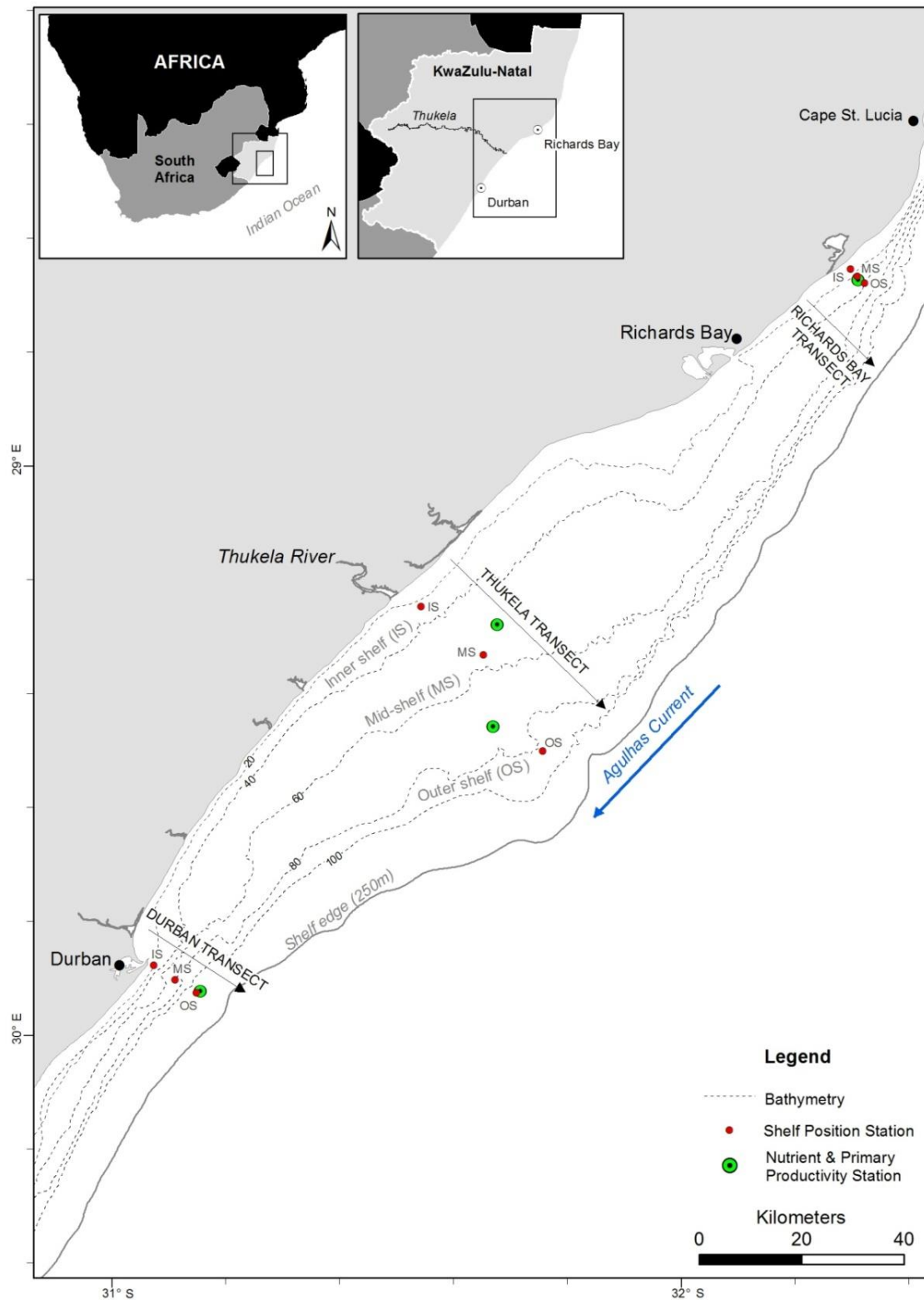


Figure 3.1. Map of the study area, showing shelf position stations, nutrient and primary productivity stations sampled along cross-shelf transects in three feature areas during a high (February 2010) and low (August 2010) rainfall period.

their position relative to environmental variables denoting the conditions of the habitat in which samples were collected. Species are also represented by points on the CCA plot, the position of which indicates their environmental preferences (Ter Braak 1986, Palmer 1993, Ter Braak and Verdonschot 1995, Oug 1998). Taxa that are located close to each other on the CCA triplot are similar to each other in terms of Chi-square distance and those positioned far away from the origin contribute more to variance than those lying close to the origin. In addition distant taxa tend to be rare while those positioned closer to the centre are more common (Ter Braak 1986).

The ordination axes of the CCA plot are linear combinations of environmental variables and are defined by canonical eigenvalues ( $\lambda$ ) calculated for each variable. The value and sign of these canonical eigenvalues gives an indication of how important a particular explanatory variable is in determining the community composition (Ter Braak 1986, Ter Braak and Verdonschot 1995). An eigenvalue close to 1 indicates a strong taxa-environment relationship while a value close to 0 represents very little correspondence (Palmer 1993). Total inertia is a measure of the lack of independence between taxa and environmental variables. The sum of all canonical eigenvalues as well as the first two axes can be expressed as a percentage of the total inertia (Oug 1998, Quinn and Keough 2002, Zuur *et al.* 2007). The overall significance of the CCA plot was determined by applying Monte-Carlo permutation tests to the final model (Legendre and Birks 2012).

### 3.3 Results

#### 3.3.1 Environmental parameters

##### **Depth**

Bathymetric data collected during cruises A and B showed that the Richard's Bay (RB) feature area, located on the narrow northern shelf was characterised by shallow depths ( $17.3 \text{ m} \pm 1.84\text{SD}$  to  $43.5 \text{ m} \pm 3.54\text{SD}$ ). Although the Natal Bight is widest in the central shelf, stations located along the Thukela (TK) transect were not the deepest sampled. While the depths at which inner shelf (IS) samples were collected in the TK ( $32 \text{ m} \pm 1.41\text{SD}$ ) and Durban (DN) ( $24.5 \text{ m} \pm 3.54\text{SD}$ ) feature areas were similar, both the mid (MS) and outer shelf (OS) position along the DN (MS:  $81 \text{ m} \pm 5.66\text{SD}$ ; OS:  $179.5 \text{ m} \pm 6.36\text{SD}$ ) transect were located in deeper water ( $p > 0.05$ ) than those of the TK (MS:  $54 \text{ m} \pm 2.83\text{SD}$ ; OS:  $110.5 \text{ m} \pm 2.12\text{SD}$ ) transect

(Fig. 3.2). This indicates that the profile of the shelf edge in the DN feature area is steep when compared with the gentle profile encountered at the shelf edge in TK.

### **Temperature**

No significant difference between near bottom temperatures were detected when comparing cruises A and B ( $t=0.328$ ,  $df=16$ ,  $p=0.747$ ). Near bottom temperatures were generally lower at sampling stations during cruise B with the exception of the TK transect MS (cruise A:  $16.99^{\circ}\text{C}$ ; cruise B:  $19.98^{\circ}\text{C}$ ) and OS (cruise A:  $14.77^{\circ}\text{C}$ ; cruise B:  $18.55^{\circ}\text{C}$ ) where temperatures were higher in cruise B when compared with cruise A ( $t=-1.363$ ,  $df=4$ ,  $p=0.244$ ) (Fig. 3.2). The three feature areas under consideration were characterised by waters with significantly different ( $F=7.160$ ,  $df=2$ ,  $p=0.007$ ) near bottom temperatures. The narrow, shallow northern shelf had the warmest waters (RB:  $23.09^{\circ}\text{C} \pm 1.92\text{SD}$ ), followed by waters of the central shelf (TK:  $18.40^{\circ}\text{C} \pm 2.15\text{SD}$ ), with the deepest transect sampled in the DN feature area having the coolest waters (DN:  $17.23^{\circ}\text{C} \pm 3.95\text{SD}$ ). For all samples, across all feature areas and shelf positions pooled there was a highly significant negative correlation between depth and temperature ( $r=-0.842$ ,  $p<0.001$ ,  $n=18$ ). When considering feature areas individually, there were no significant differences ( $F=2.523$ ,  $df=2$ ,  $p=0.114$ ) in temperature detected with increasing depth, although near bottom temperatures were lower at the deepest locations sampled (OS:  $17.28^{\circ}\text{C} \pm 4.20\text{SD}$ ) when compared with waters over the MS ( $19.79^{\circ}\text{C} \pm 3.62\text{SD}$ ) and IS ( $21.69^{\circ}\text{C} \pm 2.05\text{SD}$ ). Minimum near bottom temperature was recorded for the DN transect OS ( $179.5\text{m} \pm 6.36\text{SD}$ ) during both cruises A ( $13.33^{\circ}\text{C}$ ) and B ( $12.91^{\circ}\text{C}$ ) while maximum near bottom temperature was recorded for the Richard's Bay (RB) transect MS during cruise A ( $25.99^{\circ}\text{C}$ ) and for the OS during cruise B ( $22.01^{\circ}\text{C}$ ) (Fig. 3.2).

### **Dissolved Oxygen**

There were no significant overall variations between Dissolved Oxygen (DO) values obtained during cruises A and B (Mann-Whitney  $U=20$ ,  $p=0.077$ ,  $n=9$ ) (Fig. 3.2). When considering each feature area, DO values remained approximately the same at all shelf positions sampled along the DN transect during cruises A and B ( $t=0.103$ ,  $df=4$ ,  $p=0.923$ ) but were elevated along the TK transect at the IS and MS ( $t=-1.046$ ,  $df=4$ ,  $p=0.354$ ) as well as being significantly higher at all shelf position stations in the RB feature area ( $t=-3.103$ ,  $df=4$ ,  $p=0.036$ ) during cruise B. In terms of shelf position, lower values of DO were recorded during cruise A for the inner ( $t=-2.754$ ,  $df=4$ ,  $p=0.051$ ), mid ( $t=-1.155$ ,  $df=4$ ,  $p=0.312$ ) and outer shelf ( $t=-0.421$ ,  $df=4$ ,  $p=0.695$ ),

although these differences were not significant. There was no significant correlation between depth and DO ( $r=-0.347$ ,  $p=0.158$ ,  $n=18$ ) despite the highest values of DO being recorded for shallow depths during both cruises. Maximum values were recorded at the DN transect IS (27 m, 4.39 mg.L<sup>-1</sup>) station during cruise A and at the RB transect IS (16 m, 4.76 mg.L<sup>-1</sup>) position during cruise B. Near bottom water with the lowest DO concentration was sampled from the TK transect MS during cruise A (56 m, 3.53 mg.L<sup>-1</sup>) and the OS during cruise B (109 m, 3.68 mg.L<sup>-1</sup>) (Fig. 3.2).

### **Salinity**

When considering all samples there was no statistically significant difference ( $t=-0.875$ ,  $df=16$ ,  $p=0.395$ ) detected between both salinity values recorded during cruises A and B and between the salinity of waters in each feature area ( $F=2.543$ ,  $df=2$ ,  $p=0.112$ ). When considering shelf position, however there was a significant difference ( $F=4.128$ ,  $df=2$ ,  $p=0.037$ ) in salinity values recorded, with the inner ( $35.39 \pm 0.06SD$ ) and mid-shelf ( $35.40 \pm 0.04SD$ ) being characterised by higher ( $p<0.05$ ) salinity values than the outer shelf ( $35.30 \pm 0.09SD$ ). At shallow shelf positions in all feature areas, salinity values were higher ( $t=-1.910$ ,  $df=4$ ,  $p=0.129$ ) during cruise B. The salinity of mid-shelf waters remained approximately the same ( $t=0.138$ ,  $df=4$ ,  $p=0.897$ ) during both sampling cruises, whereas OS waters in the RB (cruise A: 35.29; cruise B: 35.34) and TK (cruise A: 35.34; cruise B: 35.42) feature area had higher values of salinity and those of the DN (cruise A: 35.22; cruise B: 35.19) outer shelf had slightly lower values of salinity in cruise B ( $t=-0.371$ ,  $df=4$ ,  $p=0.729$ ). The environmental parameters salinity and depth were significantly negatively correlated ( $r=-0.569$ ,  $p=0.014$ ,  $n=18$ ). During cruise A the most saline waters were found at the TK transect MS (35.44) while IS (35.47) waters had highest salinity values recorded in cruise B. The DN transect OS waters were the least saline sampled in both cruises A (35.22) and B (35.19) (Fig. 3.2).

### **Grain size distribution and total organic content of sediment (TOC)**

When considering all 54 samples there were no significant differences in either the mean phi (Mann-Whitney  $U=336$ ,  $p=0.628$ ,  $n=27$ ) or total organic content (TOC) (Mann-Whitney  $U=264$ ,  $p=0.084$ ,  $n=27$ ) of sediment sampled during cruises A and B. In terms of feature area and shelf position, mean phi was significantly different between feature areas (Kruskal-Wallis  $H=16.11$ ,  $df=2$ ,  $p<0.001$ ) while TOC differed significantly with shelf position (Kruskal-Wallis  $H=9.97$ ,  $df=2$ ,  $p=0.007$ ). During both cruises A and B there was a strong positive correlation

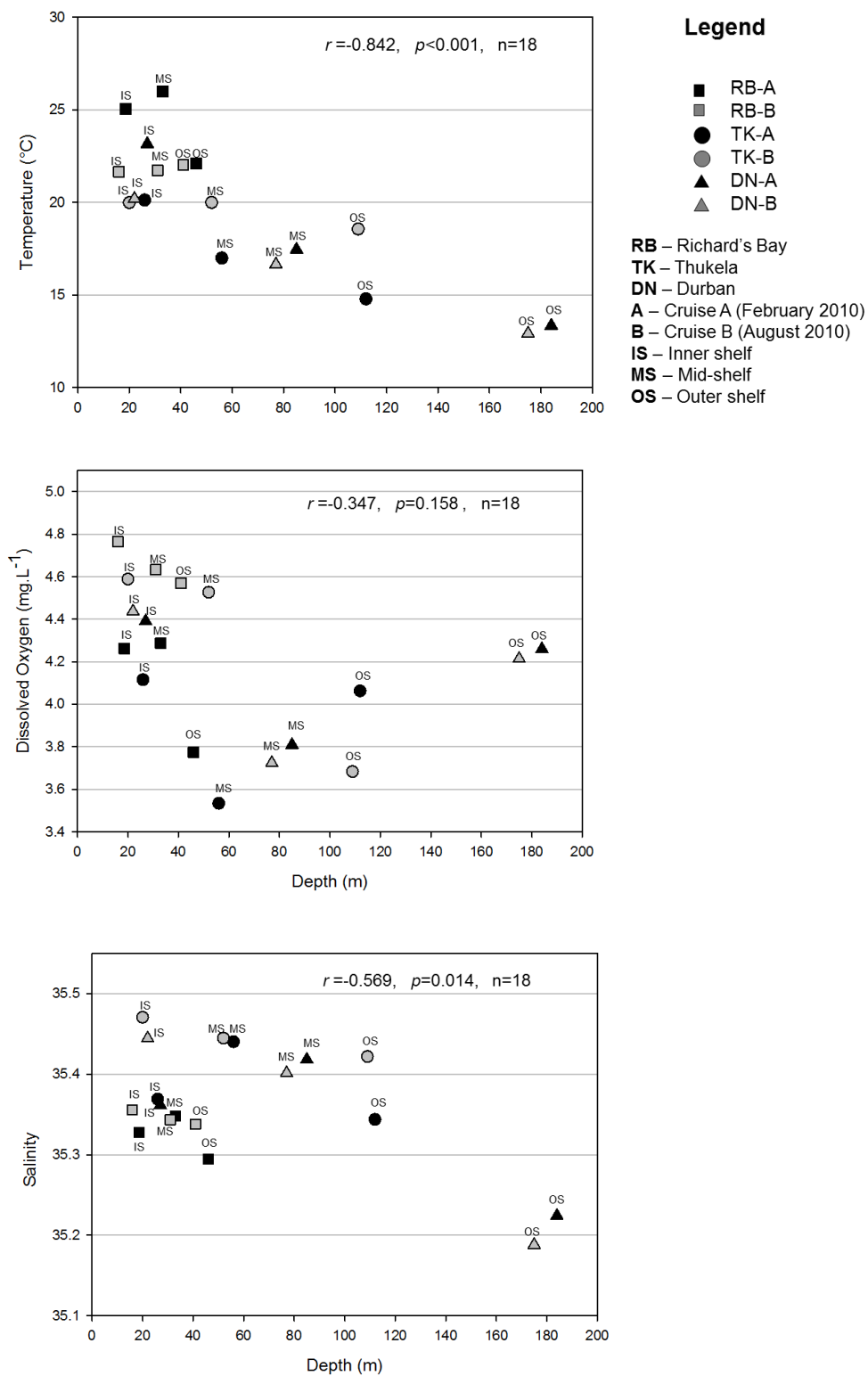


Figure 3.2. Pearson Correlation ( $r$ ) between depth (m) and near bottom temperature (°C), salinity and dissolved Oxygen (mg.L<sup>-1</sup>) for feature area: Richard's Bay (RB), Thukela (TK) and Durban (DN), samples collected during cruises A and B.

between mean grain size and organic contents of sediment (cruise A:  $r=0.724$ ,  $p<0.001$ ,  $n=27$ ; cruise B:  $r=0.820$ ,  $p<0.001$ ,  $n=27$ ) (Fig. 3.3). The shallow (16–46 m) sedimentary environment was characterised by a predominance of fine sand (fns), low in organic contents (0.11–1.03%) with mean phi values of 2–3 at all RB shelf positions and the TK and DN transect IS stations (Fig. 3.3). The MS and OS samples collected in the DN feature area and the TK transect MS station were characterised by medium sand (mms) (mean phi=1–2) with a coarser grade of material, slightly lower in organic content being found in the TK feature area (Fig. 3.4). In contrast, the sediment at the OS station along the TK transect was predominantly very fine sand (vfs) (mean phi=3–4) and mud (mean phi>4) high in organic content (1.88%–8.55%) (Fig. 3.3).

### ***Nutrients and Primary Productivity***

There were no significant differences ( $p>0.05$ ) between nutrient and Chl-*a* concentrations recorded during cruises A and B. The Chlorophyll *a* concentration of waters in the TK (Chl-*a*:  $1.28 \mu\text{g.L}^{-1} \pm 0.76\text{SD}$ ) feature area was the highest recorded in cruise A, with both the RB (Chl-*a*:  $0.67 \mu\text{g.L}^{-1} \pm 0.28\text{SD}$ ) and DN (Chl-*a*:  $0.53 \mu\text{g.L}^{-1} \pm 0.12\text{SD}$ ) feature areas being characterised by similar but lower Chl-*a* concentrations during this sampling cruise (Fig. 3.4). This contrasts with patterns found during cruise B where the RB (Chl-*a*:  $1.85 \mu\text{g.L}^{-1} \pm 0.53\text{SD}$ ) and DN (Chl-*a*:  $1.47 \mu\text{g.L}^{-1} \pm 0.80\text{SD}$ ) feature areas had the highest concentrations of Chl-*a*, while waters of the central shelf (Chl-*a*:  $0.60 \mu\text{g.L}^{-1} \pm 0.13\text{SD}$ ) contained little Chl *a* (Fig. 3.4). Nitrate ( $\text{NO}_3$ ) and Silicate (Si) concentrations were lowest for waters in the RB feature area ( $\text{NO}_3$ :  $0.95 \mu\text{mol.L}^{-1} \pm 0.50\text{SD}$ ; Si:  $1.52 \mu\text{mol.L}^{-1} \pm 0.34\text{SD}$ ), elevated in the TK feature area ( $\text{NO}_3$ :  $1.87 \mu\text{mol.L}^{-1} \pm 0.68\text{SD}$ ; Si:  $2.54 \mu\text{mol.L}^{-1} \pm 0.56\text{SD}$ ) and reached maximum values in DN ( $\text{NO}_3$ :  $2.54 \mu\text{mol.L}^{-1} \pm 0.50\text{SD}$ ; Si:  $2.75 \mu\text{mol.L}^{-1} \pm 0.24\text{SD}$ ) during cruise A (Fig. 3.4). In contrast, Phosphate ( $\text{PO}_4$ ) values were highest in the RB ( $\text{PO}_4$ :  $0.31 \mu\text{mol.L}^{-1} \pm 0.24\text{SD}$ ) feature area during cruise A with concentrations decreasing in TK ( $\text{PO}_4$ :  $0.27 \mu\text{mol.L}^{-1} \pm 0.04\text{SD}$ ) and reaching minimum values in DN ( $\text{PO}_4$ :  $0.24 \mu\text{mol.L}^{-1} \pm 0.07\text{SD}$ ). Patterns of  $\text{NO}_3$  and Si concentrations were the same during cruise B but the  $\text{PO}_4$  concentration of near bottom waters was highest in the DN ( $\text{PO}_4$ :  $0.41 \mu\text{mol.L}^{-1} \pm 0.25\text{SD}$ ) feature area with minimum values recorded for RB ( $\text{PO}_4$ :  $0.20 \mu\text{mol.L}^{-1} \pm 0.95\text{SD}$ ) during this cruise (Fig. 3.4).

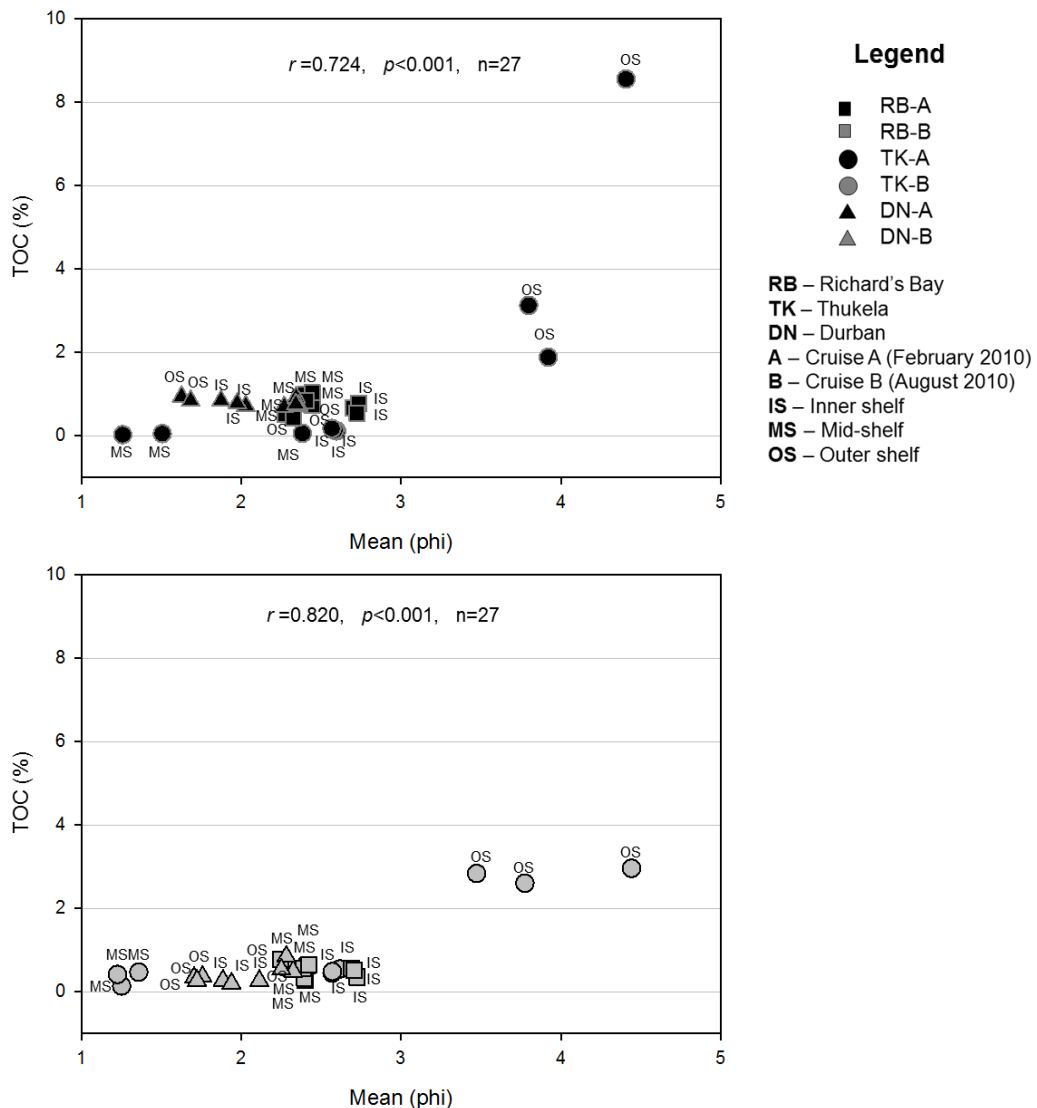


Figure 3.3. Pearson Correlation ( $r$ ) between mean grain size ( $\phi$ ) and total organic contents (% TOC) of sediment sampled from each feature area: Richards Bay (RB), Thukela (TK) and Durban (DN), during cruises A and B.

### 3.3.2 Faunal distribution patterns

#### **Patterns of Abundance (N) and No. of taxa (S)**

##### **Test model: The effect of cruise**

A total of 20 215 macrobenthic fauna belonging to 642 taxa were collected from the nine stations sampled during cruise A. Reduced numbers of individuals (18 000 ind.m<sup>-2</sup>) and taxa (503) were recorded during cruise B (Fig. 3.5) but these differences were not statistically significant (N: Mann-Whitney  $U=326.5$ ,  $p=0.516$ ,  $n=27$ ; S: Mann-Whitney  $U=301$ ,  $p=0.275$ ,  $n=27$ ).

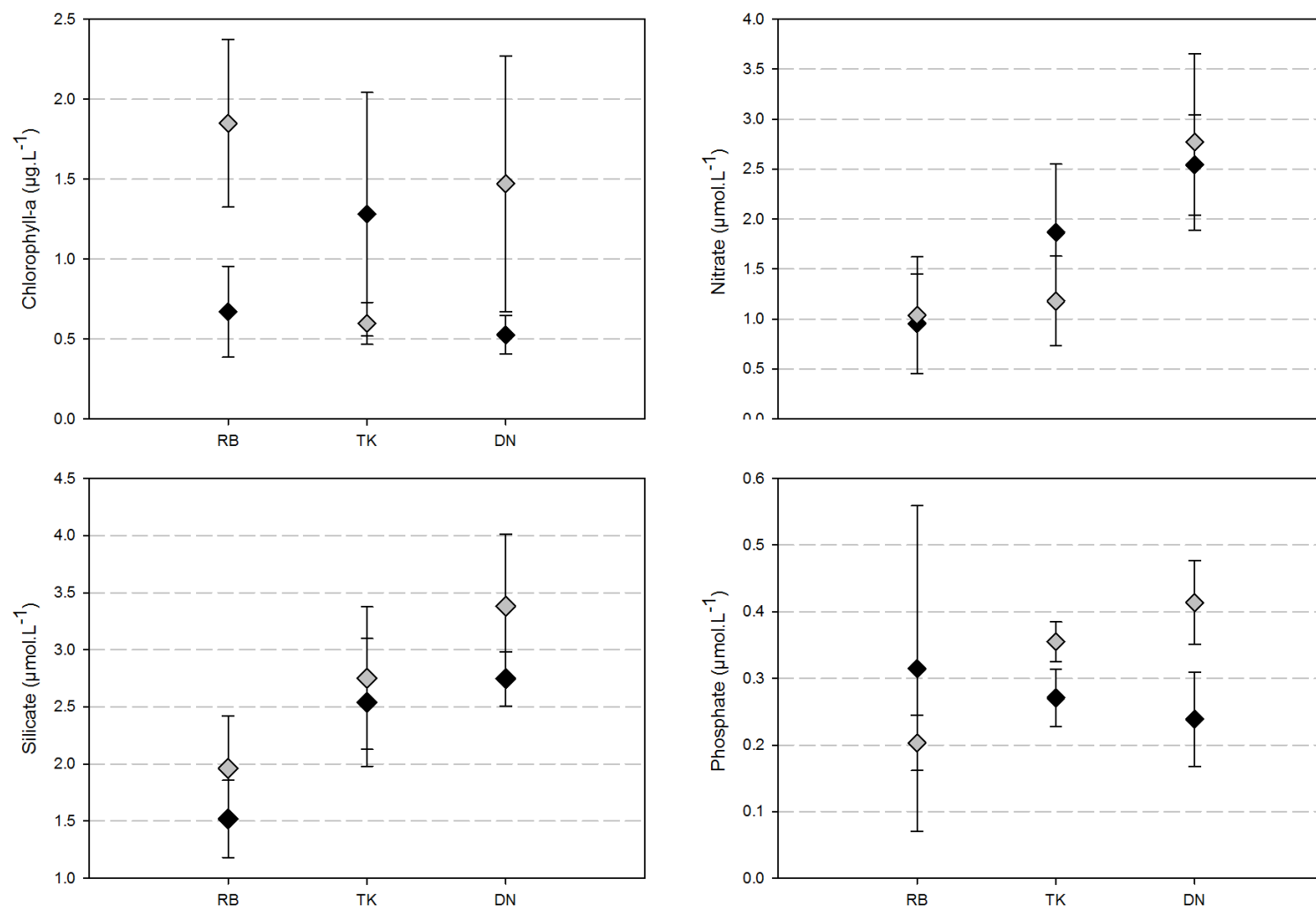


Figure 3.4. Chlorophyll *a* (Chl-*a*) and nutrient characteristics (Nitrate:  $\text{NO}_3$ , Silicate: Si and Phosphate:  $\text{PO}_4$ ) of feature areas sampled on the Natal Bight during cruises A (black symbol) and B (grey symbol).

Annelida were the dominant Phylum sampled from the three feature areas during cruise A in terms of both abundance (N: 38.36%) and numbers of taxa (S: 43.93%) with the vast majority belonging to the Class Polychaeta (N: 37.97%, S: 42.83%). Crustacea were similarly abundant during cruise A (N: 36.28%) with Mollusca (N: 12.14%), Sipuncula (N: 6.04%) and Echinodermata (N: 3.54%) also relatively well represented during this sampling cruise. In terms of feeding modes, interface feeding (IF) and carnivorous (C) macrobenthos dominated during cruise A in terms of both numbers of individuals (IF: 23.99%; C: 21.10%) and taxa (IF: 23.83%; C: 29.28%). Surface (N: 16.50%; S: 15.26%) and subsurface deposit feeders (N: 14.69%; S: 10.90%) were also well represented during this sampling cruise. During cruise B, Crustacea accounted for 40.86% of the total abundance of macrobenthic fauna collected followed by Annelida (N: 36.47%) of which 35.67% were Polychaeta. The percentage contribution of Mollusca decreased to 9.72% during cruise B but Sipuncula (N: 6.33%) and Echinodermata (N: 3.28%) comprised similar percentages of the total numbers of individuals sampled. Carnivores increased in abundance and were the dominant functional group sampled during cruise B in terms of both abundance (N: 32.89%) and numbers of taxa (S: 29.62%), followed by interface (N: 17.33%; S: 25.45%) and deposit feeding (SDF-N: 16.72%, S: 14.91%; SSDF-N: 13.78%; S: 10.14%) macrobenthos.

#### ***Test model: The effect of Feature Area***

There was no significant difference in the abundance of macrobenthos sampled during cruises A and B in any of the three feature areas (all data pooled-RB:  $t=-0.105$ ,  $p=0.917$ ; TK:  $t=1.124$ ,  $p=0.277$ ; DN:  $t=0.166$ ,  $p=0.870$ ;  $df=16$ ) (Fig 3.6). Considering each feature area separately, the number of taxa sampled were also not significantly different between cruises A and B in either Richard's Bay ( $t=-0.175$ ,  $df=16$ ,  $p=0.864$ ) or Durban ( $t=-0.270$ ,  $df=16$ ,  $p=0.791$ ), but there were significantly less taxa ( $t=3.814$ ,  $df=16$ ,  $p=0.002$ ) recorded from the Thukela feature area during cruise B when compared with cruise A (Fig. 3.6). When considering patterns of abundance (N) and taxon richness (S) between feature areas sampled during cruise A, significant differences in both community metrics (N:  $F=7.009$ ,  $df=2$ ,  $p=0.004$ ; S:  $F=6.015$ ,  $df=2$ ,  $p=0.008$ ) were detected through one-way ANOVA testing. Pairwise comparisons (Student-Newman-Keuls: SNK) revealed that values of S were significantly higher in the TK feature area when compared with DN ( $p=0.042$ ) and that both N and S were significantly different between TK and RB (N:  $p=0.003$ ; S:  $p=0.006$ ) during cruise A. There were no significant differences ( $p>0.05$ ) detected between the sampled feature areas for either N or S during cruise B. Mean abundance and number of taxa per feature area were lowest for RB during cruise A (N:  $476.11 \text{ ind.m}^{-2} \pm$

160.13SD;  $S: 40.22 \text{ taxa} \pm 12.42\text{SD}$ ) and B ( $N: 483.33 \text{ ind.m}^{-2} \pm 128.99 \text{ SD}; S: 41.11 \text{ taxa} \pm 9.25\text{SD}$ ) (Fig. 3.6). The highest mean abundance of macrobenthic fauna was recorded for the Thukela (TK) feature area during cruises A ( $N: 1037.22 \text{ ind.m}^{-2} \pm 366.50\text{SD}$ ) and B ( $N: 808.89 \text{ ind.m}^{-2} \pm 486.68\text{SD}$ ) with mean taxon richness peaking during cruise A ( $S: 68.67 \text{ taxa} \pm 17.66\text{SD}$ ) and attaining maximum values in DN during cruise B ( $S: 53.56 \text{ taxa} \pm 20.25\text{SD}$ ) (Fig. 3.6).

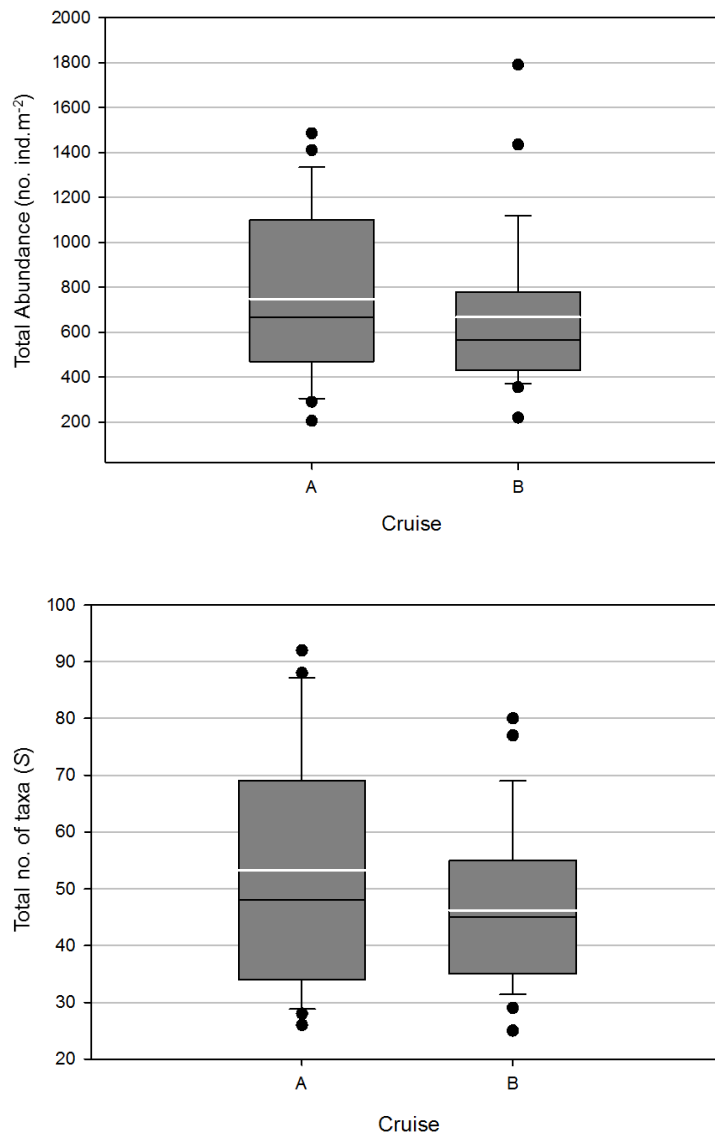


Figure 3.5. Boxplots of Abundance ( $N$ : no. of ind.m<sup>-2</sup>) and no. of taxa ( $S$ ) for macrobenthos sampled during two cruises pooled for three feature area, cross-shelf transects. Black line within boxplot represents the median, white line represents the mean.

**Test model: The effect of Shelf position**

Abundance (IS: Mann-Whitney  $U=35$ ,  $p=0.659$ ; MS: Mann-Whitney  $U=33.5$ ,  $p=0.566$ ; OS:  $t=0.180$ ,  $p=0.860$ ;  $df=16$ ) and numbers of taxa (IS:  $t=1.248$ ,  $p=0.230$ ; MS:  $t=1.036$ ,  $p=0.316$ ; OS:  $t=0.374$ ,  $p=0.714$ ;  $df=16$ ) did not differ significantly within any of the three shelf positions sampled when comparing cruises A and B (Fig. 3.7). When considering differences between shelf positions sampled within cruise A and B there were no also no significant differences in either  $N$  (Cruise A: Kruskal-Wallis  $H=3.284$ ,  $p=0.194$ ; Cruise B: Kruskal-Wallis  $H=2.401$ ,  $p=0.301$ ) or  $S$  (Cruise A:  $F=2.100$ ,  $p=0.144$ ; Cruise B:  $F=2.939$ ,  $p=0.072$ ). The mid-shelf (MS) supported the most individuals ( $N$ :  $896.11 \text{ ind.m}^{-2} \pm 487.09\text{SD}$ ) and taxa ( $S$ :  $64.11 \text{ taxa} \pm 26.63\text{SD}$ ) during cruise A (Fig. 3.7). Although the most taxa were again recorded at this shelf position ( $S$ :  $53 \text{ taxa} \pm 18.07\text{SD}$ ) during cruise B, the inner shelf (IS) supported the highest abundance ( $N$ :  $782.22 \text{ ind.m}^{-2} \pm 493.95\text{SD}$ ). During both sampling cruises the outer shelf (OS) was the least abundant (Cruise A:  $476.11 \text{ ind.m}^{-2} \pm 379.43\text{SD}$ ; Cruise B:  $483.33 \text{ ind.m}^{-2} \pm 246.31\text{SD}$ ) while the IS consistently supported the lowest taxon richness (Cruise A:  $45.89 \text{ taxa} \pm 17.52\text{SD}$ ; Cruise B:  $38 \text{ taxa} \pm 7.28\text{SD}$ ) (Fig. 3.7).

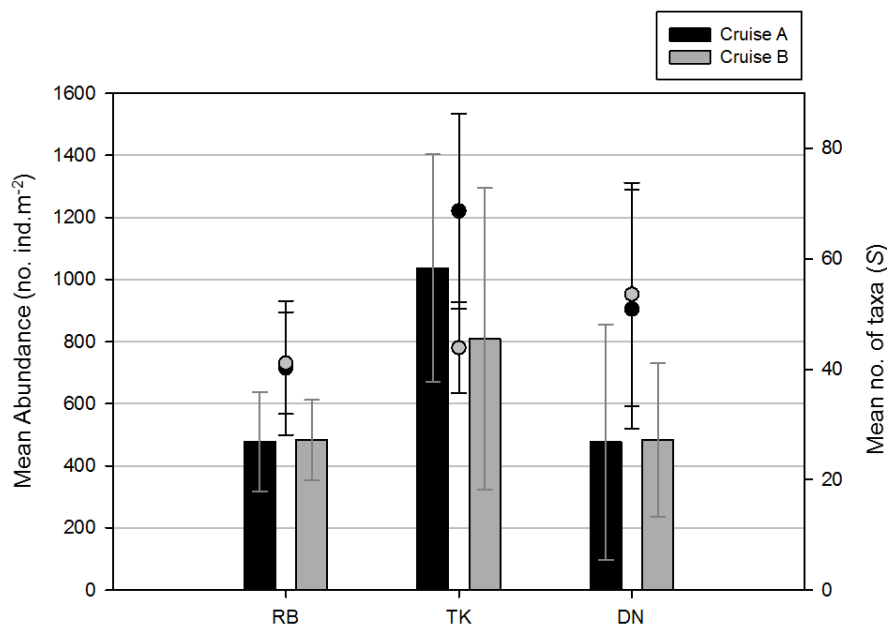


Figure 3.6. Mean abundance ( $N$ : no. of ind.m<sup>-2</sup>) and no. of taxa ( $S$ ) for macrobenthos sampled in three feature areas (RB, TK and DN) during cruises A and B. Bars =  $\bar{x}$   $N$  and Circles =  $\bar{x}$   $S$ .

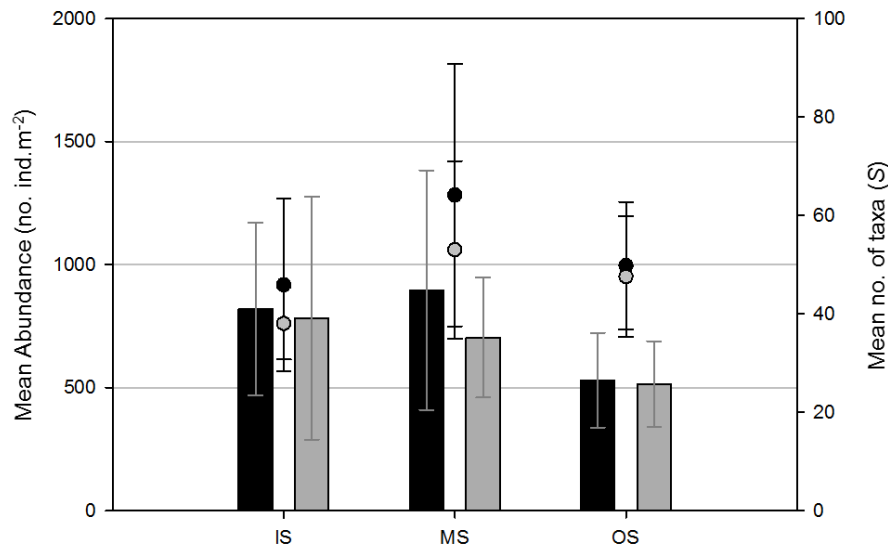


Figure 3.7. Mean abundance ( $N$ : no. of ind. $m^{-2}$ ) and no. of taxa ( $S$ ) for macrobenthos sampled at inner (IS), mid (MS) and outer shelf (OS) positions during cruises A and B. Bars =  $\bar{x}$   $N$ , Circles =  $\bar{x}$   $S$ .

### ***Taxon and feeding mode abundance data: elucidating patterns in community structure***

#### ***Within Feature Area patterns***

##### *Taxa*

Analysis of Similarity (ANOSIM) tests performed for taxon abundance data revealed that there were no significant differences ( $p > 0.05$ ) in macrobenthic communities sampled during cruises A and B in any of the three feature areas (Table 3.1). There were however highly significant global ( $p < 0.001$ ) and pairwise ( $p = 0.002$ ) differences detected with shelf position resulting in the clustering of samples from the same shelf position so that three main faunal groups (inner (IS), mid (MS) and outer shelf (OS)) were distinguished within RB, TK and DN (Table 3.1, Fig. 3.8).

##### *Feeding mode*

The results of ANOSIM tests conducted on feeding mode abundance data revealed that communities in the TK feature area during cruise A were significantly functionally different ( $p = 0.008$ ) from those sampled during cruise B, while this effect of sampling time was not apparent for the RB and DN feature areas ( $p > 0.05$ ) (Table 3.1). As with taxon abundance data, significant global differences ( $p < 0.05$ ) in feeding mode composition were detected between the factor shelf position in all feature areas, with shelf positions being well separated ( $R = 0.828$ ) in the DN area (Table 3.1). Pairwise testing established that in terms of feeding mode, IS and OS samples collected in RB were similar to each other ( $R = 0.180$ ;  $p = 0.074$ ), resulting in most of the

samples collected from these shelf positions grouping together, in the Bray-Curtis coefficient based dendrogram, separate from the MS ( $p=0.009$ ) samples (Fig. 3.8, Table 3.1). In TK there was almost no distinction between the feeding mode composition of communities sampled at the IS and MS ( $R=0.004$ ;  $p=0.370$ ) with samples from both these shelf positions clustering together according to cruise but being functionally distinct from the OS sample group in which there was no separation of samples collected in cruises A or B (Fig. 3.8). Despite this, MS and OS ( $R=0.380$ ;  $p=0.017$ ) communities were more similar in terms of feeding mode composition than IS and OS ( $R=0.465$ ;  $p=0.009$ ) communities (Table 3.1). The feeding mode composition of communities collected from the IS, MS and OS positions in the DN feature area were distinct ( $p<0.01$ ) with three main groups evident in the dendrogram, although the separation between MS and OS communities was less clear ( $R=0.619$ ) than for other pairwise combinations (Fig. 3.8, Table 3.1).

### ***Between Feature Area patterns***

#### *Classification of all samples*

ANOSIM tests using taxon abundance data for all 54 samples, detected significant global differences for the factors of feature area (FA:  $p<0.001$ ) and shelf position (SP:  $p<0.001$ ), but not for cruise (cruise:  $p=0.826$ ) (Table 3.2). Pairwise comparisons showed that although all feature areas and shelf positions were distinct in terms of taxon composition, there was considerable overlap of taxa found in TK and DN ( $R=0.29$ ,  $p<0.001$ ) as well as communities sampled from the MS and OS ( $R=0.196$ ,  $p=0.002$ ). This being reflected in the lower  $R$ -values associated with these comparisons (Table 3.2). Classification analysis of the 54 samples distinguished seven major sample groupings, at a B-C similarity of 21% reflecting differences in feature area and shelf position in terms of species composition (Table 3.3, Fig. 3.9). Group I consisted of six samples collected from the TK transect OS (109-112 m), characterised by very fine sand (vfs) (mean  $\phi=3-4$ ) and mud (mean  $\phi>4$ ). Group II (six samples) consisted of the deepest (175-184 m) locations sampled at the DN transect OS, characterised by medium sand (mms) (mean  $\phi=1-2$ ) (Fig. 3.9). Group III included six samples collected at the Thukela (TK) transect mid-shelf (MS) at depths of 52-56 m, predominated by a coarser grade of mms (mean  $\phi=1-1.5$ ). Group IV comprised all the samples collected at the DN transect MS (77-85 m) characterised by a finer sediment (mean  $\phi=2-3$ ) (Fig. 3.9).

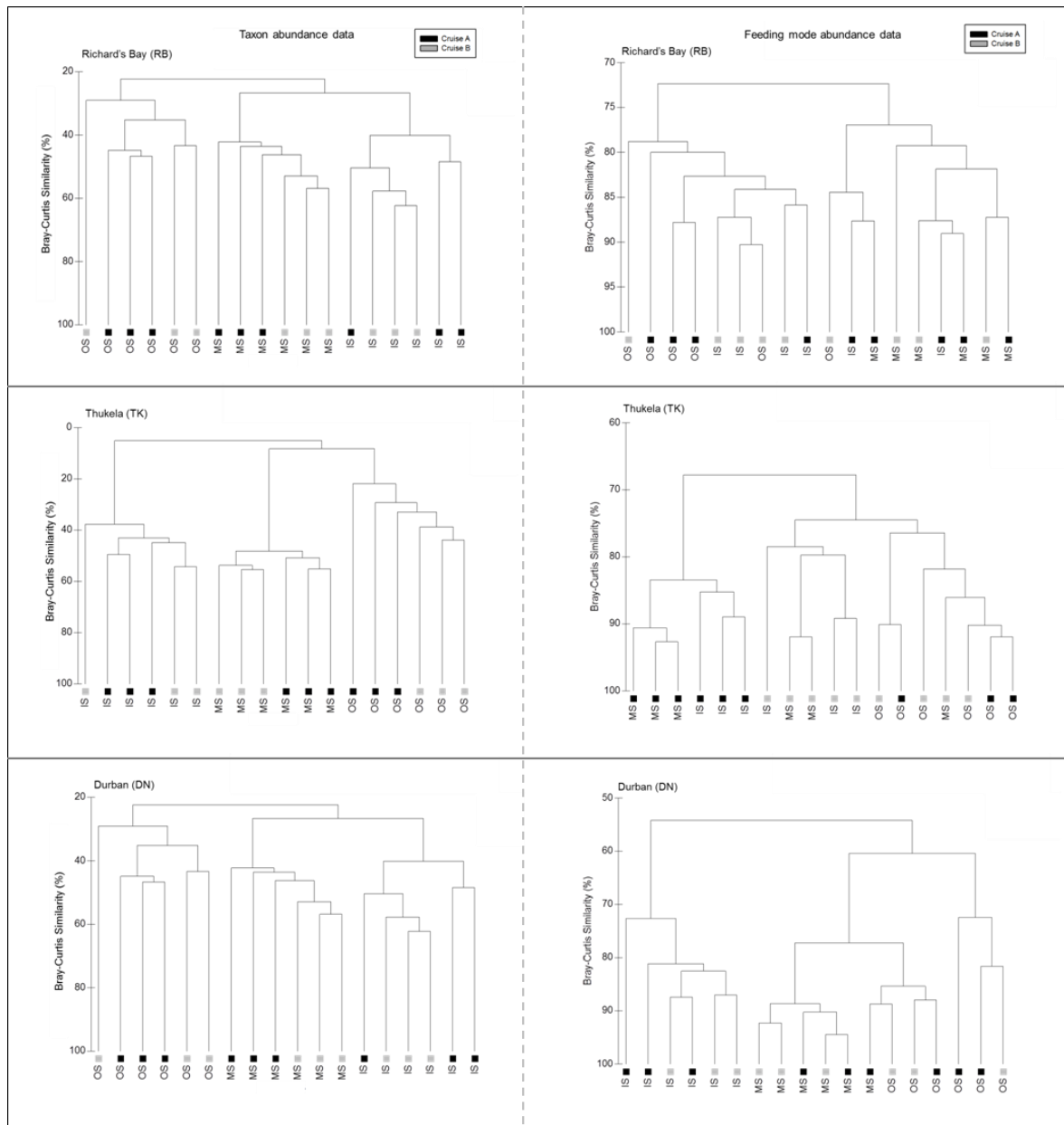


Figure 3.8. Dendrograms of hierarchical clustering (using group-average linkage) for samples collected within each feature area (RB, TK, DN) during cruises A and B. Plots are based on Bray-Curtis similarities calculated from square root transformed taxon and feeding mode abundance (*N*) data.

Group V comprised the most shallow locations (22-27 m) sampled along the DN transect with the sediment here being predominantly medium-fine sand (mean  $\phi$ =1.5-2.5). Fine sand (fns) (mean  $\phi$ =2-3) characterised Group VI which included the six samples collected from the Richard's Bay (RB) transect OS (41-46 m) (Fig. 3.9). The last sample grouping (Group VII)

Table 3.1. *R* and *p*-values of ANOSIM (1 000 000 permutations) comparisons between the taxon and feeding mode assemblages sampled during cruises A and B at three shelf positions within each feature area. RB=Richard's Bay, TK=Thukela, DN=Durban, IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf. Values in bold are significant \**p*<0.05, \*\**p*<0.01, \*\*\**p*<0.001.

TAXA						
Factor	RB		TK		DN	
	Global <i>R</i>	<i>p</i>	Global <i>R</i>	<i>p</i>	Global <i>R</i>	<i>p</i>
Cruise (A vs. B)	-0.085	0.880	0.014	0.334	-0.022	0.494
Shelf position	<b>0.956</b>	<b>&lt;0.001***</b>	<b>1</b>	<b>&lt;0.001***</b>	<b>1</b>	<b>&lt;0.001***</b>
<b>Pairwise testing</b>	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>
IS vs. MS	<b>1</b>	<b>0.002**</b>	<b>1</b>	<b>0.002**</b>	<b>1</b>	<b>0.002**</b>
IS vs. OS	<b>0.981</b>	<b>0.002**</b>	<b>1</b>	<b>0.002**</b>	<b>1</b>	<b>0.002**</b>
MS vs. OS	<b>0.935</b>	<b>0.002**</b>	<b>1</b>	<b>0.002**</b>	<b>1</b>	<b>0.002**</b>
FEEDING MODES						
Factor	RB		TK		DN	
	Global <i>R</i>	<i>p</i>	Global <i>R</i>	<i>p</i>	Global <i>R</i>	<i>p</i>
Cruise (A vs. B)	-0.086	0.893	<b>0.333</b>	<b>0.008**</b>	-0.049	0.683
Shelf position	<b>0.362</b>	<b>0.002**</b>	<b>0.281</b>	<b>0.014*</b>	<b>0.828</b>	<b>&lt;0.001***</b>
<b>Pairwise testing</b>	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>
IS vs. MS	<b>0.42</b>	<b>0.009**</b>	0.004	0.370	<b>1</b>	<b>0.002**</b>
IS vs. OS	0.18	0.074	<b>0.465</b>	<b>0.009**</b>	<b>0.907</b>	<b>0.002**</b>
MS vs. OS	<b>0.504</b>	<b>0.009**</b>	<b>0.38</b>	<b>0.017*</b>	<b>0.619</b>	<b>0.002**</b>

comprised samples collected from the IS located in the RB (16-18 m) and TK (20-26 m) feature areas as well as the RB transect MS (31-33 m). This large sample grouping was characterised by fns (mean phi=2-3) and consisted of samples collected from shallow (16-33 m) depths sampled on the shelf during both cruises A and B (Fig. 3.9). These sample groups therefore reflect differences in factors of feature area and shelf position and subsequent univariate and multivariate analysis will be based on this classification.

#### Univariate measures: Taxa

Macrobenthic abundance (*N*), numbers of taxa (*S*), Shannon-Wiener Diversity (*H'*) and Margalef's Richness (*d*) indices were highest for Group III (*N*: 1011.67 ind.m<sup>-2</sup> ± 443.54SD; *S*: 68.33 taxa ± 21.06SD; *H'*=3.60 ± 0.24SD; *d*=9.73 ± 2.42SD) and IV (*N*: 970 ind.m<sup>-2</sup> ± 117.68SD; *S*: 74.17 taxa ± 11.39SD; *H'*=3.92 ± 0.15SD; *d*=10.63 ± 1.40SD) located at intermediate shelf depths (52-85 m) sampled in the TK and DN feature areas, respectively (Fig. 3.10, Table 3.4). In contrast Groups I, II and VI (OS in each FA) supported the lowest numbers of individuals. Minimum values of abundance were recorded for samples comprising Group II (*N*: 455.83 ind.m<sup>-2</sup> ± 117.68SD) followed by Group VI (*N*: 521.67 ind.m<sup>-2</sup> ± 187.90SD) and I (*N*: 589.17 ind.m<sup>-2</sup> ± 161.23SD) which had similar values of mean abundance although Group VI displayed the highest levels of community Evenness (*J'*=0.92 ± 0.02SD) (Fig. 3.10, Table 3.4). Groups V and VII, comprised IS samples collected from all feature areas as well as MS samples from RB,

which supported intermediate numbers of individuals (N-Group V: 735 ind.m<sup>-2</sup> ± 318.32SD; Group VII: 695.78 ind.m<sup>-2</sup> ± 432.07SD) but the least taxa (S-Group V: 33.67 taxa ± 6.74SD; Group VII: 41.78 taxa ± 13.40SD). The community of Group V (DN transect IS) had the lowest values of Richness ( $d=4.99 \pm 0.80SD$ ), Diversity ( $H'=2.69 \pm 0.34SD$ ) and Evenness ( $J'=0.77 \pm 0.10SD$ ) of all sample groups (Fig. 3.10, Table 3.4).

Table 3.2. *R* and *p*-values of one-way ANOSIM (1 000 000 permutations) comparisons between the factors: cruise, feature area and shelf position. RB=Richard's Bay, TK=Thukela, DN=Durban, IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf. Values in bold are significant \**p*<0.05, \*\**p*<0.01, \*\*\**p*<0.001

TAXA		
Factor	Global <i>R</i>	<i>p</i>
Cruise (A vs. B)	-0.021	0.826
Feature area (FA)	<b>0.437</b>	<b>&lt;0.001***</b>
Shelf position (SP)	<b>0.298</b>	<b>&lt;0.001***</b>
<b>Pairwise testing (FA)</b>	<i>R</i>	<i>p</i>
RB vs. TK	<b>0.498</b>	<b>&lt;0.001***</b>
RB vs. DN	<b>0.552</b>	<b>&lt;0.001***</b>
TK vs. DN	<b>0.29</b>	<b>&lt;0.001***</b>
<b>Pairwise testing (SP)</b>	<i>R</i>	<i>p</i>
IS vs. MS	<b>0.306</b>	<b>&lt;0.001***</b>
IS vs. OS	<b>0.414</b>	<b>&lt;0.001***</b>
MS vs. OS	<b>0.196</b>	<b>0.002**</b>

Table 3.3. Details of sample Groups I-VII obtained from cluster analysis of 54 samples collected on the Natal Bight during cruises A (February 2010) and B (August 2010). IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf, RB=Richard's Bay, TK=Thukela, DN=Durban.

Group	Cruise	Feature Area	Shelf Position
I	A and B	TK	OS
II	A and B	DN	OS
III	A and B	TK	MS
IV	A and B	DN	MS
V	A and B	DN	IS
VI	A and B	RB	OS
VII	A and B	RB	IS, MS
		TK	IS



*Univariate measures: Feeding mode*

Values of Shannon-Wiener Diversity ( $H'$ ) calculated for feeding mode abundance data mirrored those for taxon abundance data in that values were highest for Groups III ( $H'$ :  $1.74 \pm 0.04SD$ ) and IV ( $H'$ :  $1.74 \pm 0.05SD$ ), whilst the lowest value of this index was recorded for samples comprising Group V ( $H'$ :  $1.43 \pm 0.22SD$ ) (Table 3.5). Margalef's Richness ( $d$ ) was highest for Group IV ( $d$ :  $1.00 \pm 0.04SD$ ) in accordance with results obtained from abundance data analysed to the level of lowest taxon ( $d$ :  $10.63 \pm 1.40SD$ ) but the value of this index was also high for Group V ( $d$ :  $1.00 \pm 0.11SD$ ), in contrast with the lowest values of this index calculated from taxon data ( $d$ :  $4.99 \pm 0.80SD$ ) (Table 3.5). When considering feeding modes, Group VII ( $d$ :  $0.84 \pm 0.14SD$ ) had the lowest Richness while the second lowest value of this index was calculated from taxon abundance data ( $d$ :  $6.32 \pm 1.72SD$ ). Feeding modes were most equitably distributed amongst the macrobenthic community of Group III ( $J'$ :  $0.87 \pm 0.05SD$ ), although Groups I ( $J'$ :  $0.85 \pm 0.05SD$ ), II ( $J'$ :  $0.83 \pm 0.05SD$ ), IV ( $J'$ :  $0.84 \pm 0.03SD$ ) and VI ( $J'$ :  $0.83 \pm 0.05SD$ ) had similarly high values of Evenness ( $J'$ ). In accordance with results obtained for taxon abundance data ( $J'$ :  $0.77 \pm 0.10SD$ ) values of Evenness calculated for feeding mode abundance data were lowest for Group V ( $J'$ :  $0.71 \pm 0.11SD$ ) (Table 3.5).

*Broad taxonomic groupings*

Annelida and Crustacea together accounted for most (58.8 - 89.9%) of the faunal abundance in the seven sample groups. Annelida (Ann) dominated the abundance of Groups I-III (46.7 - 55.4%) located at MS and OS depths (52-184 m) while Crustacea (Cru) was the most numerous (34.8 - 58.4%) Phylum recorded from Groups V-VII, located at shallower depths (16-46 m) (Fig. 3.12). Group IV was characterised by approximately equal (Ann: 39.4%; Cru: 35.9%) contributions by these two Phyla. In all cases, over 95% of the Annelida were represented by members of the Class Polychaeta (Pol). Groups I and VI, had the lowest combined percentage of Polychaeta and Crustacea (58.8% and 60.5%, respectively) with Mollusca (Group I: 16.8%; Group VI: 16.3%), Sipuncula (Group I: 11.2%; Group VI: 13.1%) and Echinodermata (Group I: 9.5%; Group VI: 6.2%) well represented in samples from these groups (Fig. 3.11). Echinodermata comprising primarily Ophiuroidea were best represented (9.5%) in samples collected from the muddy outer shelf in TK (Group I) (Fig. 3.11). Sipunculans were found in the greatest abundance (13.1%) in fine sands characterising the Richard's Bay OS (Group VI) while molluscs contributed approximately the same percentage (~16%) to abundance recorded for both these groups (Fig. 3.11). While contributing little to abundance, Cnidaria were best represented (~4%) in the fine sediment samples comprising Groups IV and VII. The remaining

Phyla ("Other"), namely Chordata and Nemertea contributed <3% to the mean abundance of any sample grouping (Fig. 3.11).

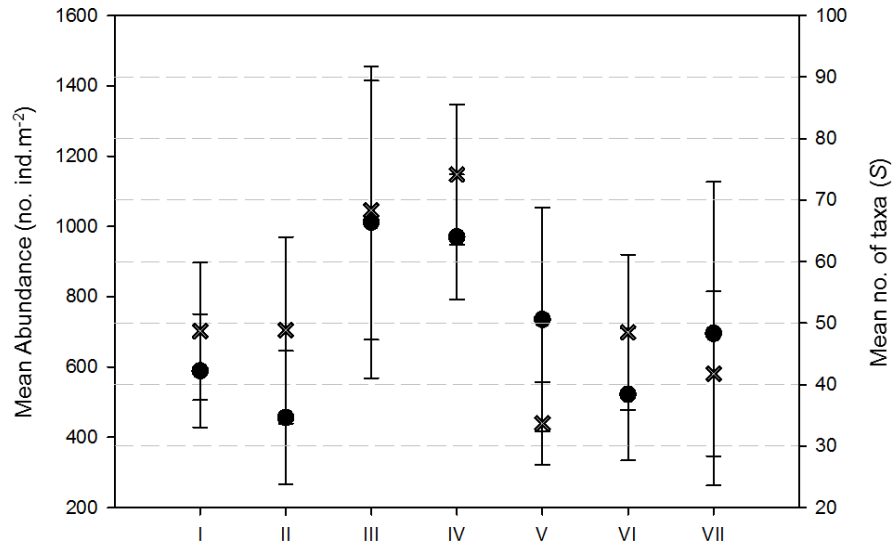


Figure 3.10. Mean abundance ( $\bar{N}$ ) and mean no. of taxa ( $\bar{S}$ ) for sample Groups I-VII defined in cluster analysis. Circles =  $\bar{N}$ , Crosses =  $\bar{S}$ .

Table 3.4. Shannon-Wiener Diversity ( $H'$ ), Margalef's Richness ( $d$ ) and Pielou's Evenness ( $J'$ ) indices calculated from taxon abundance data for sample Groups I-VII defined in cluster analysis.

Diversity Index (Taxon abundance)	Group						
	I	II	III	IV	V	VI	VII
Shannon-Wiener Diversity ( $H'$ )	3.49 ± 0.17	3.50 ± 0.32	3.60 ± 0.24	<b>3.92 ± 0.15</b>	<b>2.69 ± 0.34</b>	3.53 ± 0.31	3.02 ± 0.63
Margalef's Richness ( $d$ )	7.46 ± 1.45	7.81 ± 2.00	9.73 ± 2.42	<b>10.63 ± 1.40</b>	<b>4.99 ± 0.80</b>	7.58 ± 1.64	6.32 ± 1.72
Pielou's Evenness ( $J'$ )	0.90 ± 0.02	0.91 ± 0.03	0.86 ± 0.02	0.91 ± 0.02	<b>0.77 ± 0.10</b>	<b>0.92 ± 0.02</b>	0.82 ± 0.15

Table 3.5. Shannon-Wiener Diversity ( $H'$ ), Margalef's Richness ( $d$ ) and Pielou's Evenness ( $J'$ ) indices calculated from feeding mode abundance data for sample Groups I-VII defined in cluster analysis.

Diversity Index (Feeding Mode abundance)	Group						
	I	II	III	IV	V	VI	VII
Shannon-Wiener Diversity ( $H'$ )	1.59 ± 0.05	1.71 ± 0.10	<b>1.74 ± 0.04</b>	<b>1.74 ± 0.05</b>	<b>1.43 ± 0.22</b>	1.58 ± 0.10	1.44 ± 0.39
Margalef's Richness ( $d$ )	0.87 ± 0.09	1.14 ± 0.09	0.95 ± 0.11	<b>1.00 ± 0.04</b>	<b>1.00 ± 0.11</b>	0.92 ± 0.12	<b>0.84 ± 0.14</b>
Pielou's Evenness ( $J'$ )	0.85 ± 0.05	0.83 ± 0.05	<b>0.87 ± 0.05</b>	0.84 ± 0.03	<b>0.71 ± 0.11</b>	0.83 ± 0.05	0.75 ± 0.18

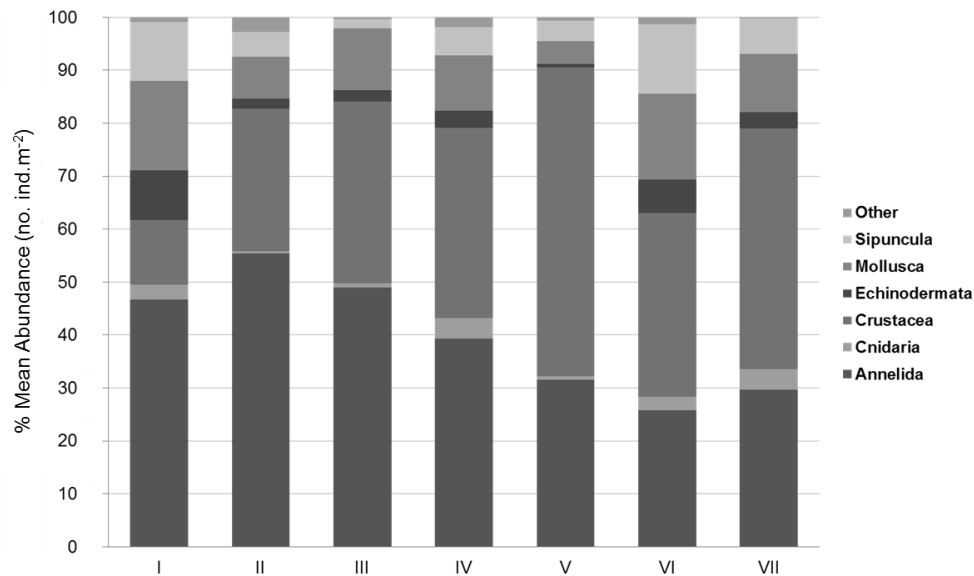


Figure 3.11. Contribution (%) of major Phyla to the abundance of Groups I-VII defined in cluster analysis.

#### Feeding mode

Interface feeding fauna (IF) dominated OS sample groups from TK (Group I: 33.2%) and DN (Group II: 28.7%) with surface deposit feeders (SDF) (Group I: 19.2%; Group II: 21.8%), carnivores (C) (Group I: 16.8%; Group II: 13.7%) and suspension feeders (SF) (Group I: 10.9%; Group II: 18.5%) also being well represented in these groups (Fig. 3.12). Parasitic fauna, while contributing very little to the number of individuals, were most abundant in the Durban feature area OS sample group (Group II: 15.8ind.m<sup>-2</sup> ± 29.05SD), with this mode being represented primarily by members of the isopod family Gnathiidae. Group III samples were characterised by equal contributions from IF (23.1%) and SDF (23.4%), with C (15.7%) and subsurface deposit feeders (SSDF) (12.3%) also being well represented (Fig. 3.12). This sample group also had the highest contribution of omnivorous (O) fauna (Group III: 18.7%). Mid-shelf samples collected from DN were dominated by suspension feeding fauna (SF) (Group IV: 30.2%) with IF (21.5%) and C (20.2%) also contributing significantly to the mean abundance of this group. The medium-fine sands of Group V were dominated by SSDF (43.7%) with C also being well represented (21.7%) (Fig. 3.12). Carnivores dominated shallow water (16-46 m) samples comprising Groups VI (30.2%) and VII (41.4%). Interface feeders (Group VI: 20.8 %; Group VII: 19.3%) and SDF (Group VI: 25.2%; Group VII: 17.3%) also contributed significantly to the abundance of these sample groups (Fig. 3.12).

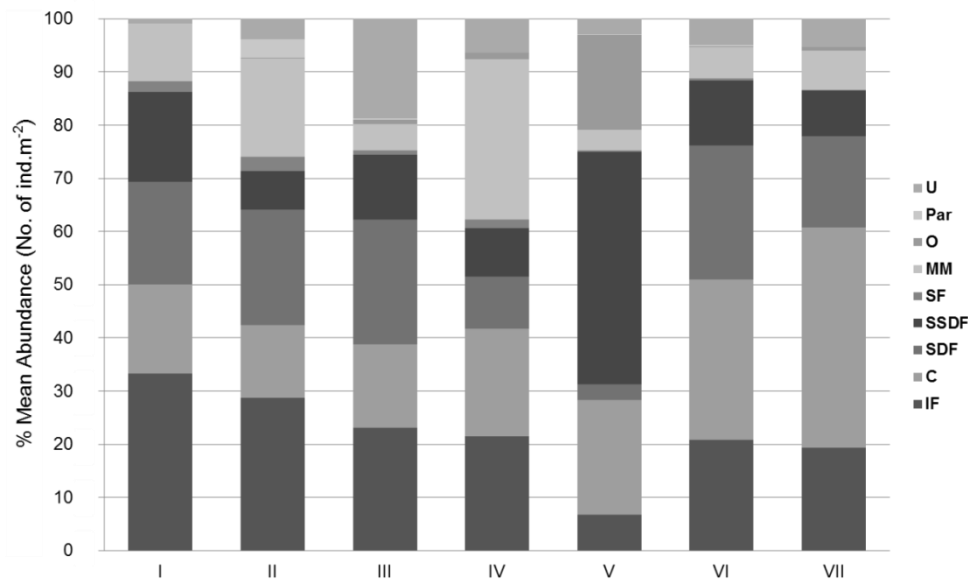


Figure 3.12. Contribution (%) of feeding modes to the abundance of Groups I-VII defined in cluster analysis. IF=Interface feeder, C=Carnivore, SDF=Surface deposit feeder, SSDF=subsurface deposit feeder, SF=Suspension feeder, MM=Multi-modal feeder, O=Omnivore, Par=Parasite, U=Unknown.

#### *Taxon and feeding mode contributions*

SIMPER analysis was undertaken to assess which taxa and feeding modes contributed most to similarities within, and dissimilarities between Groups I-VII. Results indicated that all sample groupings were characterised by small subsets of taxa with restricted distributions (Table 3.6).

Group I consisted of 134 taxa, with five taxa representing two Phyla typifying this group and an additional three taxa contributing more than 2% to within group similarity (48.40%). Typifying taxa included polychaetes from the families Spionidae: *Prionospio dubia* and *Spiophanes* cf. *soederstromi*, Capitellidae: *Rashgua* sp.1 and Chaetopteridae: *Spiochaetopterus* sp.12 as well as the sipunculan *Golfingiidae* sp.1 (Table 3.6). In pairwise comparisons between Groups I and II, VI and VII (Ave. Dissimilarity>95%) the SDF bivalve *Tellinidae* sp.5, found exclusively, and in the highest abundance in Group I samples, consistently contributed more than 2% to between group dissimilarity (Table 3.6). Group II comprised a total of 168 taxa with four taxa contributing more than 2% to within group similarity (29.68%), none of which were found in abundances greater than 4.55 ind.m<sup>-2</sup>. The primary discriminating taxon for this group (Group II) was the SDF bivalve, *Nuculana* sp.1 whilst the taxon contributing most to within group similarity was the IF spioinid, *Prionospio* sp.13 (Table 3.6). The TK transect MS sample group (Group III) comprised one of the richest collections of taxa (213), few of which were locally abundant and most of which were rarely present in abundances greater than 2 ind.m<sup>-2</sup>. One

exception was the omnivorous polychaete species, *Epidiopatra papillosa*, which occurred in the highest average abundance (10.61 ind.m<sup>-2</sup>) and was the primary discriminating taxon for this sample group. Three other taxa contributed >2% to similarity within Group III (39.62%) and were also identified as good discriminating taxa. These were the polychaete, *Poecilochaetus serpens* and the amphipods, cf. *Basuto* sp.2 and *Byblis gaimardii* (Table 3.6). Pairwise comparisons of Group III with all other sample groups (Ave. Dissimilarity>90%) identified the polychaete, *Epidiopatra papillosa*, occurring exclusively in this group, as the taxon consistently contributing >2% to between group dissimilarity (Table 3.7). Only three taxa of a total 171 recorded, contributed >2% to similarity within Group IV (50.18%). The spionid, *Dipolydora capensis* was the primary discriminating species for this group, found boring into dead *Astrorhizida* Foraminifera, while the barnacle *Lepadidae* sp.1 was found growing on chateopterid tubes (Table 3.6). The medium-fine sand, IS sample group in the DN feature area (Group V) contained 104 taxa, eight of which contributed >2% to within group similarity (42.58%). Four of these occurred in relatively high abundances (7.66-10.43 ind.m<sup>-2</sup>), with *Callichirus gilchristi* (SSDF) contributing the most to the similarity within this group, followed by the SSDF polychaetes *Notomastus latericeus* and *Ophelia* cf. *roscoffensis* and the ostracod *Myodocopida* sp.16 (Table 3.6). All of these taxa, found exclusively in Group V also contributed >2% to dissimilarity between this, and all other, sample groups (Ave. Dissimilarity>85%) (Table 3.7). Group VI consisted of 156 taxa with the gastropod inhabiting *Aspidosiphonidae* sp.5 contributing most to within group similarity (35.71%). Three amphipod taxa, *Ampelisca* cf. *brevicornis*, *Hippomedon* sp.5 and cf. *Basuto* sp.5, also characterised OS samples from RB (Group VI) and individually contributed >2% to within group similarity (Table 3.6). The largest sample group (Group VII) was typified by the Phoxocephalidae amphipod, cf. *Basuto* sp.1, which contributed the most to similarity within this shallow water, fns assemblage. The hermit crab, *Paguristes* sp.1 was the only other taxon contributing >2% to similarity within Group VII (30.01%) and dissimilarity between Group VII and II, IV and VI (Ave. Dissimilarity>75%) (Table 3.6, Table 3.7).

When considering feeding modes (FM) interface feeders (IF) were the FM contributing most to within group similarity in the deepest Groups I (IF =29.63%) and II (IF=22.69%), as well as being the FM that typified these groups (Table 3.8). Comparisons between the feeding modes of Group I and V-VII identified IF as the FM contributing the most to between group dissimilarity, occurring in higher abundance in Group I in all instances (IF-Group I: 48.82 ind.m<sup>-2</sup>, Group V: 16.7 ind.m<sup>-2</sup>, Group VI: 29.29 ind.m<sup>-2</sup>, Group VII: 31.59 ind.m<sup>-2</sup>) (Table 3.8).

Table 3.6. Results from SIMPER analysis of taxon abundance data, listing the main characterising taxa within each sample Group (I-VII). Taxa contributing more than 2% to “within group” similarity are presented. **Amp=Amphipoda, Biv=Bivalvia, Cho=Chordata, Cru=Crustacea, Iso=Isopoda, Pol=Polychaeta, Sip=Sipuncula**, C=Carnivore, IF=Interface feeder, MM=Multi-modal, O=Omnivore, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, SF=Suspension feeder. Grey shading indicates typifying taxa.

	Ave. Abundance	Ave. Similarity	( $\delta_i$ )/SD( $\delta_i$ )	Cumulative %
<b>Group I (Average similarity: 48.40%)</b>				
<i>Tellinidae</i> sp.5 (Biv, SSDF)	6.41	2.82	2.81	5.83
<i>Golfingiidae</i> sp.2 (Sip, IF)	5.86	2.8	1.3	11.63
<i>Spiochaetopterus</i> sp.12 (Pol, SF)	4.58	2.67	3.86	17.14
<i>Golfingiidae</i> sp.1 (Sip, IF)	4.06	2.56	7.13	22.42
<i>Rashgua</i> sp.1 (Pol, SSDF)	4.61	2.53	4.31	27.65
<i>Prionospio dubia</i> (Pol, IF)	4.47	2.43	4.43	32.68
<i>Spiophanes</i> cf. <i>soederstromi</i> (Pol, IF)	4.61	2.36	3.08	37.55
<i>Tellina gilchristi</i> (Biv, SSDF)	5.02	2.31	1.34	42.33
<b>Group II (Average similarity: 29.68%)</b>				
<i>Prionospio</i> sp.13 (Pol, IF)	4.16	2.7	3.09	9.11
<i>Magelona</i> sp.6 (Pol, SDF)	4.55	2.15	2.4	16.34
<i>Ascidacea</i> sp.1 (Cho, SF)	3.41	2.09	3.33	23.39
<i>Nuculana</i> sp.1 (Biv, SDF)	3.55	2.04	4.26	30.26
<b>Group III (Average similarity: 39.62%)</b>				
<i>Epidiopatra papillosa</i> (Pol, O)	10.61	3.85	5.5	9.72
cf. <i>Basuto</i> sp.2 (Amp, SDF)	6.19	2.31	2.44	15.56
<i>Poecilochaetus serpens</i> (Pol, SDF)	7.19	2.31	2.14	21.38
<i>Byblis gaimardii</i> (Amp, IF)	5.42	2.09	3.56	26.65
<b>Group IV (Average similarity: 50.18%)</b>				
<i>Spiochaetopterus</i> sp.13 (Pol, SF)	6.89	2.16	4.12	4.31
<i>Lepadidae</i> sp.1 (Cru, SF)	7.5	2.12	1.85	8.53
<i>Polydora capensis</i> (Pol, IF)	5.98	2.08	10.6	12.68
<b>Group V (Average similarity: 42.58%)</b>				
<i>Callichirus gilchristi</i> (Cru, SSDF)	10.43	6.09	2.81	14.3
<i>Notomastus latericeus</i> (Pol, SSDF)	9.1	5.61	3	27.48
<i>Ophelia</i> cf. <i>roscoffensis</i> (Pol, SSDF)	7.66	4.92	2.68	39.03
<i>Myodocopida</i> sp.16 (Cru, MM)	9.15	3.85	1.18	48.07
<i>Eusiridae</i> sp.6 (Amp, C)	4.93	2.97	3.28	55.05
<i>Hippomedon</i> sp.5 (Amp, C)	4.23	2.47	2.71	60.86
<i>Nucula</i> sp.1 (Biv, SSDF)	3.8	2.3	1.33	66.26
<i>Natatolana pilula</i> (Iso, C)	4.54	2.25	1.29	71.56
<b>Group VI (Average similarity: 35.71%)</b>				
<i>Aspidosiphonidae</i> sp.5 (Sip, SDF)	5.41	2.76	4.07	7.73
<i>Ampelisca</i> cf. <i>brevicornis</i> (Amp, IF)	5.65	2.58	2.86	14.96
<i>Hippomedon</i> sp.5 (Amp, C)	4.7	2.38	3.7	21.62
cf. <i>Basuto</i> sp.5 (Amp, SDF)	4.04	2.33	2.65	28.14
<b>Group VII (Average similarity: 30.01%)</b>				
cf. <i>Basuto</i> sp.1 (Amp, SDF)	5.28	2.95	2.24	9.82
<i>Paguristes</i> sp.1 (Cru, C)	8.11	2.3	0.63	17.47

Interfacing feeding macrobenthos also made the highest contribution to within group similarity in the MS assemblages in TK (Group III) (IF=20.08%) and DN (Group IV) (IF=21.44%) and while this FM typified the latter group, SSDF were the FM that characterised Group III samples (Table 3.8). Pairwise comparisons between trophic communities sampled in Group III and Group II, V-VII found that IF were the FM most responsible for distinguishing these groups from one another, with these fauna being found in the greatest abundance in Group III (IF-Group III: 61.36 ind.m<sup>-2</sup>, Group II: 38.07 ind.m<sup>-2</sup>, Group V: 16.7 ind.m<sup>-2</sup>, Group VI: 29.29

Table 3.7. Results from SIMPER analysis of taxon abundance data, listing the main discriminating taxa identified from pairwise comparisons of Group I-VII. Taxa contributing more than 2% to “between group” dissimilarity are presented, with cumulative % values in brackets. Grey shading indicates discriminating taxa and the inter-group comparison in which these taxa were identified as being important is indicated in bold. **Amp=Amphipoda, Biv=Bivalvia, Cru=Crustacea, Pol=Polychaeta, Sip=Sipuncula**, C=Carnivore, IF=Interface feeder, MM=Multi-modal, O=Omnivore, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, SF=Suspension feeder.

Taxon	I vs II 97.43%	I vs III 95.95%	I vs V 99.27%	I vs VI 98.46%	I vs VII 98.31%	II vs III 95.98%	II vs V 98.10%	II vs VII 99.10%	III vs IV 90.82%	III vs V 93.15%	III vs VI 93.02%	III vs VII 95.51%	IV vs V 92.04%	IV vs VII 90.49%	V vs VI 86.45%	V vs VII 89.57%	VI vs VII 79.70%
<i>Callichirus gilchristi</i> (Cru, SSDF)	-		3.75 (3.77%)	-	-	-	<b>4.05</b> (4.13%)	-	-	3.07 (3.29%)	-	-	2.82 (3.06%)	-	<b>3.89*</b> (4.5%)	<b>4.01*</b> (4.48%)	-
<i>Notomastus latericeus</i> (Pol, SSDF)	-	-	3.35 (7.15%)	-	-	-	<b>3.34*</b> (10.99%)	-	-	2.29 (11.75%)	-	-	2.14 (7.98%)	-	<b>3.49*</b> (8.53%)	<b>3.54*</b> (8.43%)	-
<i>Myodocopida</i> sp.16 (Cru, MM)	-	-	3.15 (10.32%)	-	-	-	3.39 (7.59%)	-	-	2.59 (9.29%)	-	-	2.39 (5.66%)	-	3.26 (12.31%)	<b>3.36*</b> (12.18%)	-
<i>Ophelia</i> cf. <i>roscoffensis</i> (Pol, SSDF)	-	-	2.79 (13.13%)	-	-	-	<b>3.02*</b> (14.07%)	-	-	<b>2.28*</b> (14.20%)	-	-	<b>2.09*</b> (10.26%)	-	<b>2.9*</b> (15.66%)	<b>2.99*</b> (18.91%)	-
cf. <i>Basuto</i> sp.1 (Amp, SDF)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<b>2.01*</b> (21.15%)	-
<i>Tellinidae</i> sp. 5 (Biv, SSDF)	2.18 (2.24%)	-	2.24 (15.39%)	2.1 (2.14%)	2.16 (5.09%)	-	-	-	-	-	-	-	-	-	-	-	-
<i>Golfingiidae</i> sp.2 (Sip, IF)	2.07 (4.36%)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Epidiopatra papillosa</i> (Pol, O)	-	<b>2.77*</b> (2.88%)	-	-	-	<b>2.81*</b> (2.92%)	-	-	<b>2.22*</b> (2.45%)	<b>3*</b> (6.51%)	<b>2.84*</b> (3.05%)	<b>2.9*</b> (3.04%)	-	-	-	-	-
<i>Paguristes</i> sp. 1 (Cru, C)	-	-	-	-	2.85 (2.90%)	-	-	3.08 (3.1%)	-	-	-	2.34 (5.49%)	-	2.15 (2.38%)	-	3.04 (15.57%)	2.8 (3.51%)
<i>Poecilochaetus serpens</i> (Pol, SDF)	-	-	-	-	-	2.1 (5.12%)	-	-	-	2.15 (16.51%)	2.04 (5.24%)	2.03 (7.61%)	-	-	-	-	-
<i>Lepadidae</i> sp.1 (Cru, SF)	-	-	-	-	-	-	-	-	-	-	-	-	2.01 (12.44%)	-	-	-	-

ind.m<sup>-2</sup>, Group VII: 31.59 ind.m<sup>-2</sup>) (Table 3.9). Suspension feeders contributed >10% to within group similarity in Groups II and IV only, with macrobenthic communities of the latter group being distinguished from those of Group I, III-VII based on this FM. Subsurface deposit feeders were most important in shallow water communities sampled from the DN feature area (Group V-SSDF: 27.49%) while C were the FM contributing most to average similarity within Groups VI (C=23.24%) and VII (C=27.21%) (Table 3.8, Table 3.9). Trophic functioning of the macrobenthic community sampled in Group V was distinguished from that of Group II and VII largely due to the higher abundance of SSDF in Group V samples (SSDF-Group V: 38.44 ind.m<sup>-2</sup>, Group II: 11.43 ind.m<sup>-2</sup>, Group VII: 16.75 ind.m<sup>-2</sup>). Carnivores typified the macrobenthic functioning of Group V and VII while SDF characterised the OS community in the RB feature area (Group VI) (Table 3.8, Table 3.9).

Table 3.8. Results from SIMPER analysis of feeding mode abundance data, listing the main characterising feeding modes within each sample Group (I-VII). Feeding modes contributing more than 10% to "within group" similarity are presented with cumulative % values in brackets. Typifying feeding modes within each Group are indicated in bold. **C=Carnivore, IF=Interface feeder, SDF=Surface deposit feeder, SSDF=Subsurface deposit feeder, SF=Suspension feeder.**

Feeding mode	Group I (82.32%)	Group II (74.56%)	Group III (74.82%)	Group IV (87.20%)	Group V (79.48%)	Group VI (74.75%)	Group VII (74.47%)
C	15.03 (74.63%)	13.19 (70.28%)	14.91 (67.84)	19.77 (47.52%)	<b>24.07</b> ( <b>64.87%</b> )	23.24 (31.08%)	<b>27.21</b> ( <b>36.54%</b> )
IF	<b>29.63</b> ( <b>36.00%</b> )	<b>22.69</b> ( <b>30.44%</b> )	20.08 (26.84%)	<b>21.44</b> ( <b>24.58%</b> )	10.53 (78.12%)	15.22 (77.75%)	15.02 (56.71%)
SDF	11.41 (88.50%)	16.52 (52.59%)	15.77 (47.92%)	11.39 (82.63%)	-	<b>19.66</b> ( <b>57.38%</b> )	14.61 (76.32%)
SSDF	16.77 (56.37%)	-	<b>10.6</b> ( <b>82%</b> )	-	27.49 (34.59)	-	-
SF	-	10.18 (83.94%)	-	19.46 (69.56%)	-	-	-

### 3.3.3 Relation of faunal patterns to environmental parameters

#### *Within Feature Area Patterns*

The weighted Spearman correlation coefficients ( $\rho_w$ ) for the relationship between benthic assemblages found within each of the three feature areas and abiotic variables are presented in Table 3.10. The single variable responsible for structuring macrobenthic communities in all three feature areas was depth, reflecting the known importance of this variable in influencing the distribution of benthic assemblages. In the RB feature area depth ( $\rho_w=0.738$ ) was determined as being most influential in the distribution and abundance of macrobenthos at the level of lowest identifiable taxon. A combination of 11 variables ( $\rho_w=0.820$ ) were determined as being the best descriptors of the macrobenthic community sampled from the Thukela feature area, but when analysing a combination of only 5 variables the Spearman correlation coefficient ( $\rho_w=0.819$ ) did not drop significantly so the combination of depth and Silicate concentration are considered the most important abiotic factors influencing macrobenthic

communities in this feature area (Table 3.10). In the Durban feature area, depth together with mean grain size ( $\phi$ ) and water column Nitrate ( $\text{NO}_3$ ) concentration were the environmental parameters primarily responsible for driving macrobenthic patterns. These results indicate that a combination of physico-chemical factors were responsible for structuring the macrobenthic communities within the DN and TK feature areas (Table 3.10).

### ***Between Feature Area patterns***

The weighted Spearman correlation coefficients ( $\rho_w$ ) for the correlation between the macrobenthic communities found in three feature areas on the Natal Bight and environmental factors are presented in Table 3.11. Depth was once again the single most important variable ( $\rho_w=0.724$ ) while the combination of depth, temperature and the sedimentary parameters: coarse sand (cos), medium sand (mms) and mud ( $\rho_w=0.848$ ) were determined to be the most influential determinants of macrobenthic distribution and abundance. Canonical Correspondence analysis (CCA) provided further insight into the relationship between benthic assemblages and measured environmental variables (Fig. 3.13). All five environmental variables considered seemed to have approximately the same importance in structuring the benthic communities on the Natal Bight as reflected by vector length. There was a positive correlation between depth and mud content of sediment with the highest mud contents characterising the Thukela OS (Group I). Coarse sand and mms were also positively correlated, with Groups II and III being characterised by high values of both these sediment grades. Depth was negatively correlated with temperature, with shallow water Groups VI and VII located in warm waters. The position of Group IV in the centre of the CCA plot indicated that this was a relatively average sample in terms of the five abiotic variables considered while it appears that the environmental factors important in structuring Group V communities were not included in the CCA ordination (Fig 3.13).

Canonical coefficients ( $\lambda$ ) of the environmental variables showed that the first axis was determined primarily by the sedimentary parameters mud ( $\lambda=-0.707$ ) and cos ( $\lambda=-0.380$ ) while the second axis was determined by mms ( $\lambda=-0.530$ ) and cos ( $\lambda=-0.352$ ) (Table 3.12, Table 3.13). The five environmental variables used together explained 53.97% of the total inertia while the first two axes of the CCA plot explained 86.51% of the total variation in the data. Thus 46.69% of the variation that can be explained by the environmental variables is captured in the first two axes (Table 3.12).

Table 3.9. Results from SIMPER analysis of feeding mode abundance data, listing the main discriminating feeding modes identified from pairwise comparisons of Group I-VII. Feeding modes contributing more than 5% to “between group” dissimilarity are presented and cumulative % values are enclosed with brackets. **C=Carnivore, IF=Interface feeder, SDF=Surface deposit feeder O=Omnivore, SSDF=Subsurface deposit feeder, SF=Suspension feeder.**

FM	I vs II 26.98%	I vs III 28.64%	I vs IV 27.78%	I vs V 37.41%	I vs VI 28.53%	I vs VII 29.98%	II vs III 33.33%	II vs IV 33.55%	II vs V 45.50%	II vs VI 28.45%	II vs VII 30.26%	III vs IV 27.39%	III vs V 93.15%	III vs VI 30.27%	III vs VII 32.79%	IV vs V 46.07%	IV vs VI 32.50%	IV vs VII 34.31%	V vs VI 86.45%	V vs VII 35.80%	VI vs VII 25.42%
C	5.06 (39.71%)		6.14 (56.27%)	5.58 (45.95%)	6.42 (46.85%)	5.88 (50.19%)	5.42 (55.67%)	7.95 (51.64%)	6.31 (72.14%)	7.92 (27.83%)	7.59 (25.07%)					5.73 (78.07%)			6.3 (63.27%)	5.63 (59.27%)	5.66 (45.97%)
IF		5.6 (62.34%)		11.61 (31.04%)	6.95 (24.36%)	9.17 (30.58%)	7.28 (21.84%)	5.40 (67.74%)	7.97 (41.26%)	5.25 (46.30%)	6.96 (48.07%)		11.97 (27.92%)	8.39 (27.72%)	9.62 (29.35%)	10.89 (52.49%)	7.28 (57.28%)	8.48 (57.74%)	5.51 (77.95%)	5.51 (74.65%)	6.03 (23.71%)
SDF		6.55 (22.87%)					5.86 (39.41%)		7.75 (58.28%)				10.71 (52.89%)		6.42 (48.94%)	6.06 (65.65%)			9.47 (25.23%)	6.75 (43.55%)	
O		5.7 (42.78%)					5.06 (70.85%)						5.08 (64.75%)								
SSDF	5.65 (20.95%)								10.81 (23.75%)										7.97 (46.47%)	8.84 (24.70%)	
SF			9.49 (34.16%)					9.37 (27.93%)	5.43 (84.07%)			8.52 (31.13%)				13.29 (28.85%)	11.34 (34.88%)	11.33 (33.03%)			

Table 3.10. Weighted Spearman correlation coefficient ( $\rho_W$ ) values between macrobenthic communities and environmental variables measured within three features (RB, TK, DN) areas on the Natal Bight. Variable combinations in bold indicate those that were determined to be significant. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

Richards Bay Feature Area (RB)		
No. of variables	$\rho_W$	Variables
<i>Single variable</i>		
1	<b>0.738</b>	<b>Depth***</b>
1	0.594	mms
1	0.549	Sorting
<i>Best combination of variables</i>		
2	0.734	Depth, mud
2	0.731	Depth, NO <sub>3</sub>
3	0.724	Depth, mud, NO <sub>3</sub>
4	0.720	Depth, cos, mud, NO <sub>3</sub>
Thukela Feature Area (TK)		
No. of variables	$\rho_W$	Variables
<i>Single variable</i>		
1	0.809	Depth
1	0.626	fns
1	0.618	Mean phi
<i>Best combination of variables (using 5 variables)</i>		
<b>2</b>	<b>0.819</b>	<b>Depth, Si***</b>
5	0.799	DO, cos, fns, mud, TOC
5	0.795	vcs, fns, mud, Si, PO <sub>4</sub>
4	0.794	vcs, cos, mud, Chl-a
<i>Best combination of variables (using 19 variables)</i>		
<b>11</b>	<b>0.820</b>	<b>Depth, salinity, DO, vcs, cos, fns, vfs, mud, TOC, Si, NO<sub>3</sub>***</b>
Durban Feature Area (DN)		
No. of variables	$\rho_W$	Variables
<i>Single variable</i>		
1	0.840	Depth
1	0.756	Temperature
1	0.618	Salinity
<i>Best combination of variables</i>		
<b>3</b>	<b>0.852</b>	<b>Depth, Mean phi, NO<sub>3</sub>***</b>
2	0.850	Depth, Mean phi
4	0.850	Depth, cos, Mean phi, NO <sub>3</sub>
5	0.850	Depth, cos, vfs, Mean phi, NO <sub>3</sub>

Table 3.11. Weighted Spearman correlation coefficient ( $\rho_W$ ) values between macrobenthic communities and environmental variables measured in three feature areas (RB, TK, DN) on the Natal Bight. The variable combinations presented in bold are significant. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

All Feature Areas (RB, TK, DN)		
No. of variables	$\rho_W$	Variables
<i>Single variable</i>		
1	0.724	Depth
1	0.655	Mean phi
1	0.533	Cos
<i>Best combination of variables</i>		
<b>5</b>	<b>0.848</b>	<b>Depth, Temperature, cos, mms, mud***</b>
3	0.846	Depth, cos, mud
3	0.846	Depth, mud, Mean phi
2	0.844	Depth, Mean phi

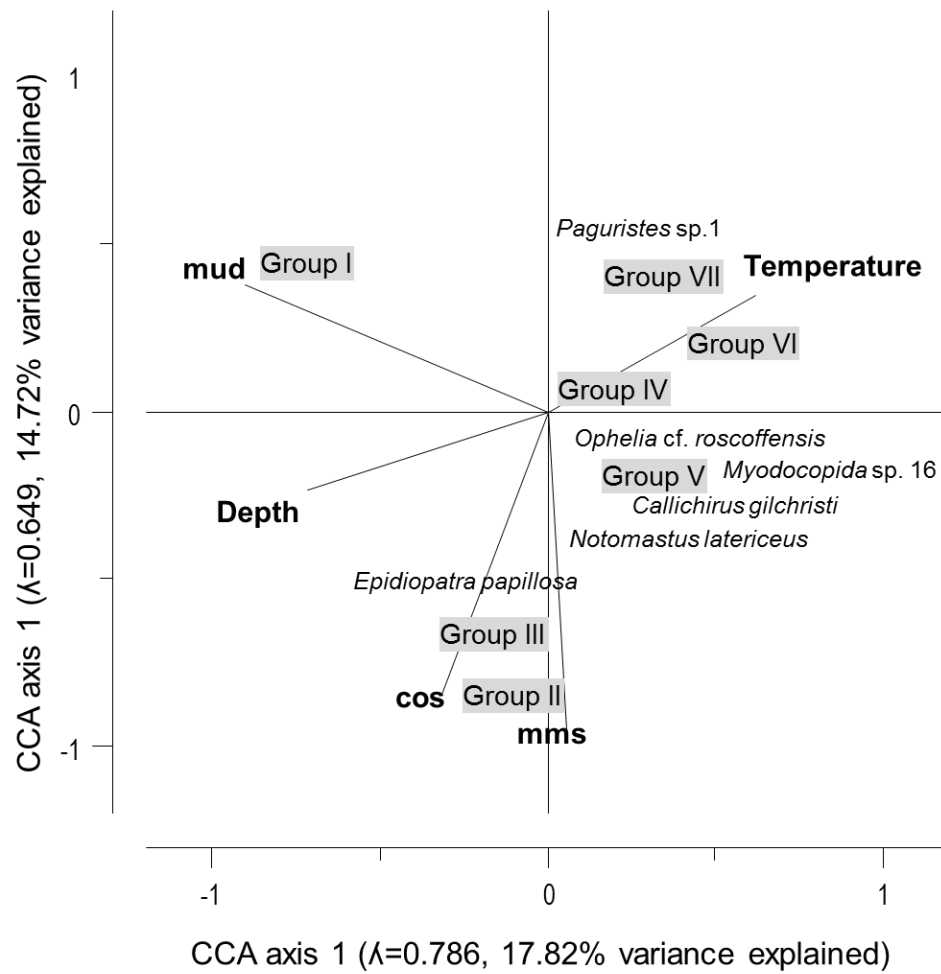


Figure 3.13. Canonical Correspondence Analysis (CCA) showing the relation between environmental variables and macrobenthic communities of Groups I-VII as well as taxa contributing more than 3% to “within group” similarity and “between group” dissimilarity.

Table 3.12. Eigenvalues ( $\lambda$ ) of the axes and Total Inertia obtained from the CCA ordination of a subset of 32 taxa identified by SIMPER analysis as contributing more than 3% to “within group” similarity and “between group” dissimilarity of Groups I-VII and five environmental variables identified by BIO-ENV as being significant descriptors of macrobenthic community structure in three feature areas of the Natal Bight.

Axis	$\lambda$	$\lambda$ as a % of Total Inertia	Cumulative % of Total Inertia	$\lambda$ as a % of canonical eigenvalues	Cumulative % of canonical eigenvalues
1	0.786	17.816	17.816	33.042	33.042
2	0.649	14.720	32.536	27.301	60.342
Total Inertia = 4.41, Sum of all canonical eigenvalues = 2.38					

Table 3.13. Canonical coefficients ( $\lambda$ ) for the five environmental variables obtained for each axis in the CCA ordination of a subset of 32 taxa identified by SIMPER analysis as contributing more than 3% to “within group” similarity and “between group” dissimilarity of Groups I-VII. Values in bold represent environmental variables primarily responsible for determining each axis.

Environmental variable	Axis 1	Axis 2
Depth	-0.285	-0.174
Temperature	0.047	0.119
cos	<b>-0.380</b>	<b>-0.352</b>
mms	0.148	<b>-0.530</b>
mud	<b>-0.707</b>	0.307

The purpose of this chapter was to compare macrobenthic communities found within and between three feature areas of the Natal Bight. Spatial and short-term temporal patterns in taxon and feeding mode abundance were investigated and related to measured physico-chemical factors in order to assess the importance of identified oceanographic features. Considering Bight-wide patterns there were no statistically significant differences between physico-chemical factors or the primary community metrics of macrobenthic taxon richness and abundance between high and low rainfall periods. In contrast to this, when considering the scale of feature area and shelf position significant differences were detected. Univariate results showed that the Thukela feature area and mid-shelf positions supported the most abundant and diverse communities sampled in the present study. No significant differences in the taxon or feeding mode composition of macrobenthic communities were detected with cruise. Multivariate results delineated seven sample groups reflecting significant differences in taxon composition of macrobenthic communities with feature area and shelf position. Results from CCA analysis showed that biotic data were significantly related to a set of five environmental variables measured in the water column and sediment.

### 3.4 Discussion

A total of 38 215 individuals belonging to 826 taxa were recorded in this study. Comparison of these values with those obtained from similar studies is complicated by variations in sampling methods and habitat type. It is therefore often more meaningful to express values of total abundance and no. of taxa in terms of the area sampled. The 54 samples collected from the three feature areas sampled on the Natal Bight covered a combined area of 10.8 m<sup>2</sup>. A study of macrobenthic communities on the Great Australian Bight found 240 taxa in a combined area of 6.5 m<sup>2</sup> along a similar depth range (40-200 m) (Currie *et al.* 2009), while a total of 18 858 individuals belonging to 547 taxa were found on the Cretan shelf in a combined area of 19.8 m<sup>2</sup>

sampled along a depth gradient of 40-190 m (Karakassis and Eleftheriou 1997). In a study of subtropical macrobenthos off Reunion Island a total of 7 885 individuals from 174 taxa were recorded in a sampled area of 7.2 m<sup>2</sup> (Bigot *et al.* 2006). A large scale study conducted in the subtropical waters off Hong Kong covering a sample area of 120 m<sup>2</sup>, recorded a total of 603 taxa and over 50 000 individuals (Shin *et al.* 2004). The three feature areas investigated on the Natal Bight therefore support a high abundance and number of macrobenthic taxa compared with results from other studies on continental shelves covering a similar sampling area and depth range.

In terms of Phyla, Polychaeta generally dominate soft-sediment shelf communities, followed by Crustacea, Mollusca and Echinodermata (Ellingsen *et al.* 2005, Bigot *et al.* 2006). Other taxa, such as Nemertea and Anthozoa tend to contribute little to numbers of individuals or taxa (Dubois *et al.* 2009). Our results agree well with these general patterns, with polychaetes contributing most to the numbers of individuals and taxa sampled during cruise A. However the high abundance and taxon richness of crustaceans recorded during this study was noteworthy. Crustaceans were almost as abundant as polychaetes during the high rainfall period and were even more abundant than polychaetes in the low rainfall period. Specific locations of interest with regards to crustaceans are elaborated upon in the sample group discussion.

#### ***The effect of sampling time: Was there a difference between Cruise A and B?***

The months in which cruises A and B were conducted correspond with periods of peak summer rainfall and reduced winter rainfall, respectively on the KwaZulu-Natal coast. While both numbers of individuals and taxon richness were lower during cruise B there were no significant differences in either metric when considering all 54 samples collected during this study. The lack of temporal replication in the present study precludes a discussion of seasonal patterns on the Natal Bight, but comparisons are made with studies conducted on other shelves where seasonal patterns were considered. In a study conducted off the tropical Cote-d'Ivoire numbers of individuals and taxa were highest for the rainy summer season (le Loeuff and Intes 1999). Seasonal patterns in macrobenthic taxon richness were apparent on the continental shelf off the United States, with a significant decrease in the number of taxa recorded from spring to autumn, whilst no seasonal variation was found for other community metrics (Dubois *et al.* 2009). On the Arabian Sea shelf macrobenthic abundance decreased from 2099 ind.m<sup>-2</sup> ± 2030SD during the premonsoon period to 1084 ind.m<sup>-2</sup> ± 1413SD

postmonsoon (Jayaraj *et al.* 2008b). A long term data series from the Wadden Sea showed variation in numbers of macrobenthic individuals and taxa between winter and summer although changes were not significant (Beukema and Dekker 2012).

***The effect of feature area: Were there differences between Richard's Bay, Thukela and Durban?***

The Thukela feature area appears to be an important region of the Natal Bight in that it supported the richest and most abundant community during both cruises A and B. Nutrients and detrital material carried into the marine realm by rivers affects the productivity of coastal regions and influences macrobenthic community patterns (Drinkwater and Frank 1994, Salen-Picard and Arlhac 2002). In a study off the coast of Japan investigators found that benthic communities utilised organic matter brought into the marine realm (leaf litter and POM) by rivers (Antonio *et al.* 2011). In addition, enhanced pelagic production can, after settling on the seafloor, influence the macrobenthic community as has been demonstrated for the shelf off the Amazon River where macrobenthic biomass was significantly related to planktonic productivity (Alongi and Robertson 1995). In the Mediterranean macrobenthic diversity was negatively influenced by riverine derived POM, while abundance increased (Harmelin-Vivien *et al.* 2009). Terrestrial material is refractory in nature and the role of bacteria in making this particulate organic matter (POM) available to the macrobenthos is integral for the transfer of energy in aquatic food webs (Alongi and Robertson 1995, Antonio *et al.* 2011). Unfortunately no data were available for sediment bacteria but water column bacteria were quantified from surface and near bottom waters (Kunnen 2012). Areas of higher bacterial numbers and biomass were identified in association with the Thukela River mouth and also over the Thukela Bank area (Kunnen 2012). During cruise A, when outflow from the Thukela was at a maximum, the highest bacterial activity recorded was associated with a transient phytoplankton bloom over the mid and outer shelf areas in this region (Kunnen 2012). It is reasonable to expect that the benthic bacterial numbers, biomass and production would be higher in areas of enhanced pelagic productivity (Kunnen 2012). This result is in contradiction to what was expected based on previous studies in which high water column nutrient concentrations have led researchers to hypothesize that the persistent upwelling cell offshore of Cape St. Lucia is the main oceanic source of nutrients for the Natal Bight (Lutjeharms *et al.* 1989, Lutjeharms *et al.* 2000a, Meyer *et al.* 2002). The Richards Bay feature area, closest to this upwelling cell, supported the lowest numbers of macrobenthic individuals and taxa during both high and low rainfall periods.

***The effect of shelf position: Was there a difference between inner, mid and outer shelf depths?***

Depth was the factor most strongly correlated with macrobenthic community structure between and within each of the feature areas under consideration. There was a clear separation between fauna of shallow depths, subjected to hydrodynamics acting on the bottom and those inhabiting deeper areas with significantly less physical impact on the bottom. A similar separation of macrobenthic communities along depth gradients on continental shelf environments has been observed in waters off Australia, California, India, Belgium and New Zealand, to name a few (Probert and Grove 1998, Bergen *et al.* 2001, van Hoey *et al.* 2004, Jayaraj *et al.* 2008b, Currie *et al.* 2009). Depth is however unlikely to be the causative factor because many other environmental factors, such as sediment type, that directly influence community composition are correlated with depth (Weston 1988, Oug 1998, Zajac *et al.* 2000, Currie *et al.* 2009, McArthur *et al.* 2010, Barrio Froján *et al.* 2012). The literature is rich with studies showing that macrobenthic community patterns are related to sediment grain size (Sanders 1958, Posey 1986, Gray 2002, Jayaraj 2008a). The findings of the present study, in which macrobenthic communities were defined largely on the basis of depth and sediment type is consistent with the notion that hydrodynamic patterns may actually be the driving factors shaping these parameters. The hydrodynamics of an environment are complex and difficult to measure and it is therefore the more easily quantified environmental parameters like depth and sediment grain size that used as surrogates for conditions in the surrounding milieu, integrating and reflecting effects over time (Hyland *et al.* 1991, Bergen *et al.* 2001).

When considering the scale of shelf position in the present study, numbers of individuals.m<sup>-2</sup> were highest for inner and mid-shelf communities during both cruises A and B. Mid-shelf communities were also the most diverse, while values of these community metrics were lowest for the outer shelf position. In agreement with these findings a large scale study conducted around the United Kingdom found that macrobenthic abundance was significantly negatively correlated with depth offshore (9-138 m) (Barrio-Froján *et al.* 2012). In a study conducted off the south-west coast of India investigators found that macrobenthic abundance and diversity was highest at mid-shelf depths (50m-75 m) and decreased further offshore (>75 m) (Jayaraj *et al.* 2008a). Similarly, the highest abundance and taxon richness was supported at mid-shelf depths (<32 m) on the continental shelf off California (Bergen *et al.* 2001).

***Shallow water communities of Richard's Bay and Thukela – The influence of terrigenous sediments and river outflow.***

Group VII comprised IS samples from TK and RB as well as MS samples collected from the latter feature area, with abundance values increasing at all these shelf positions in cruise B when compared with cruise A. This is probably due to the outwelling of turbid freshwater from the Thukela and other nearby river systems during peak rainfall periods. Outflow may be a natural disturbance agent and results in waters with reduced salinity and dissolved Oxygen (DO) concentration being found on the shallow northern and central shelf during cruise A. Some macrobenthic organisms will be negatively impacted by river outflow by for example, Oxygen deficiency which is known to cause mass mortality of benthic fauna although recovery is rapid (Heip *et al.* 1992). Canonical correspondence analysis identified temperature as an important environmental factor distinguishing this from other sample groups on the Natal Bight. Temperature is known to influence the amount of DO water contains, further emphasising the importance of riverine outflow in driving changes in these shallow water communities. Higher temperatures were recorded for Group VII stations, particularly those in the Richards Bay feature area, during cruise A, when compared with cruise B due to the outflow of warmer, freshwater during the high rainfall summer months. River systems also discharge a large amount of terrigenous sediment and detritus onto adjacent shelves which may have deleterious effects on the macrobenthic community. Studies investigating the experimental deposition of terrigenous sediments have found that as little as 3 mm of sediment led to a reduction of both numbers of individuals and taxa (Lohrer *et al.* 2004, Lohrer *et al.* 2006). Discharged particulate material can remain in suspension for variable periods of time, impacting light penetration, primary productivity and macrobenthic organisms living in the surficial sediment layer (Akoumianaki *et al.* 2012).

Suspension feeders contributed very little to the total abundance of Group VII (SF: 7.3%) which is consistent with the notion that fine particles carried into the marine realm by rivers may inhibit suspension feeders through, for example, clogging their filtering apparatus (Akoumianaki *et al.* 2012). The fossorial amphipod, cf. *Basuto* sp.1 and the hermit crab, *Paguristes* sp.1 characterised this sample grouping (Group VII) with abundance of the latter taxon increasing dramatically during Cruise B (cruise A:  $31.11 \text{ ind.m}^{-2} \pm 34.08 \text{ SD}$ ; cruise B:  $299.44 \text{ ind.m}^{-2} \pm 444.16 \text{ SD}$ ). These suprabenthic carnivores are important agents in nutrient regeneration and have been reported to dominate in areas following physical disturbances, such as the deposition of terrigenous sediment (Lohrer *et al.* 2004, Dolbeth *et al.* 2009). Shallow water environments are subjected to more physical disturbance of both a natural and

anthropogenic nature when compared with habitats located further offshore which make for a relatively unstable bottom habitat (Zajac *et al.* 2003). The abundance of the fossorial Phoxocephalidae, cf. *Basuto* sp.1 remained stable between cruises A and B, which is not surprising as these animals are able to burrow rapidly and maintain contact with the sediment using their enlarged, setose pereopods (Zajac *et al.* 2008). In terms of functioning these stations were dominated by carnivores (41.4%) due almost entirely to the presence of *Paguristes* sp.1. These hermit crabs are predominately scavengers, which may further explain their proliferation, following the period of high river outflow which would certainly have resulted in the mortality of sensitive macrofauna, providing an ample food resource. Surface deposit and interface feeders accounted for much of the remaining (36.6%) community, with these feeding groups being represented mainly by cf. *Basuto* sp.1 and Tellinidae bivalves, respectively. This group was characterised by fine and very fine sand with values of mean phi showing very little variation between cruises A and B. Deposit feeding macrobenthos are well known to prefer finer grades of substrate so their high abundance at this station is to be expected (Sanders 1958, Levinton 1972, Wijsman *et al.* 1999, Levinton and Kelaher 2007, Jayaraj *et al.* 2008b).

***The outer shelf community off Richard's Bay – upwelling of Natal Bight source nutrients***

Although the continental shelf was most narrow in the northern reaches of the Natal Bight, the OS position along the RB transect supported a distinct community (Group VI) characterised by a number of taxa, the most important of which was the gastropod inhabiting sipunculid, *Aspidosiphonidae* sp.5. Several fossorial amphipods including *Ampelisca* cf. *brevicornis*, cf. *Basuto* sp.5 and *Hippomedon* sp.5 were also abundant and characteristic taxa of this community. This shelf position was closest to the upwelling cell off Cape St. Lucia and it was expected that some evidence of this would be detected at this station. Persistent upwelling has been reported here as a result of the Agulhas Current moving from a narrow to a wider shelf with upwelling being identified by the presence of cool water, higher nutrient concentrations and enhanced Chlorophyll *a* concentrations, which spreads southwards over the KZN Bight at the surface and the bottom (Meyer *et al.* 2002, Hutchings *et al.* 2010). The current was hard up against the shelf edge during the first cruise in February which led to Ekman veering driving cold, nutrient-rich water from the bottom onto the shelf in this region (M Roberts, 2012, pers comm.). Near bottom temperatures recorded at this station were lower than inner and mid-shelf positions along the Richard's Bay transect, confirming the intrusion of colder, upwelled waters at the outer shelf. Near bottom water temperatures remained stable between cruises A and B emphasizing the persistence of upwelling in this region independent of rainfall

variations. The local upwelling event during cruise A may have caused the elevated  $\text{PO}_4$  values recorded off Richard's Bay during this time. It appears as though this nutrient increase was not transferred or available to the macrobenthic community in Richard's Bay as the number of macrobenthic individuals and taxa were lowest for this sample group during both high and low rainfall periods.

***The inner shelf community off Durban– Biotic Ecosystem engineers and indications of a polluted habitat***

Subsurface deposit feeders are often associated with stable bottoms and organic-rich sediments found in deep areas (Gaston 1987, Dolbeth *et al.* 2009). In contrast, results from the present study revealed that the shallow water station sampled off Durban (Group V) was dominated (17%) by high numbers of the SSDF sandprawn, *Callichirus gilchristi*. Callianassids are referred to as ecosystem engineers, taxa that increase the complexity of bottom habitats and influence local abundance and biodiversity (Griffis and Suchanek 1991, Coleman and Williams 2002). The burrow structures created by these organisms facilitate the recycling of deposited organic matter by increasing the surface area of sediment in contact with overlying water, thereby increasing Oxygen availability and the return of nutrients to the water column (Gaston 1987, Coleman and Williams 2002). In addition, the continual reworking of surficial sediments has profound and varied effects on the surrounding benthos (Posey 1986). An experimental study conducted in Durban Bay demonstrated that areas associated with high densities of the Callianassid, *C. kraussi* have low richness, diversity and abundance of macrobenthos (Pillay *et al.* 2007). In a study on the effects of *Callianassa californiensis*, investigators found a negative relationship between the abundance of sedentary fauna and dense communities of the sandprawn (Posey 1986). These results are in agreement with the present study in which minimum values of all diversity indices were recorded for sample Group V. The abundance of sandprawns also influences the trophic functioning of the surrounding macrobenthos in that communities associated with callianassids have statistically lower abundances of surface deposit and suspension feeders, while burrowing SSDF appear to be unaffected (Pillay *et al.* 2007). In the present study the lowest abundance of IF and SF feeders were recorded for Group V samples, probably due to the fact that suspension feeding is not viable here because the bioturbatory activity of *C. gilchristi* not only destabilises the sediment surface but may also lead to the clogging of filtering apparatus. Even if macrobenthos switch to a SDF mode they will encounter difficulty in terms of the negative influence that callianassids have on this source of food (Pillay *et al.* 2007). Burrowing macrobenthos are unaffected by the bioturbation activities of sandprawns because they do not rely on the sediment surface to feed (Pillay *et al.* 2007).

This sample group was characterised by a high abundance of *Ophelia* cf. *roscoffensis* and *Notomastus latericeus*, subsurface deposit feeding polychaetes. The proximity of this station to the Durban harbour complex infers that this is quite a polluted habitat which may serve to explain the high abundance of *Notomastus latericeus* as some taxa belonging to the family Capitellidae have become widely accepted as indicators of organic pollution (Tsutsumi 1987, Elias et al. 2001, Dean 2008).

#### ***Thukela mid-shelf – the influence of coarse substrate and river plumes***

The mid-shelf station group in the Thukela feature area (Group III) was the only location studied in which significant differences were found between cruises A and B. There was a significant decline in the number of individuals and taxa sampled during the low rainfall period, with analysis between the community of Group III and environmental parameters revealing that Chl-*a* in combination with other factors was significantly correlated with the macrobenthic fauna. This indicates a link between surface productivity and the abundance of bottom fauna at this location (Heip et al. 1992). During the high outflow period nutrients injected into shelf waters led to enhanced planktonic production which translated to the benthic community as increased numbers and taxa. The turbidity of inner shelf waters during high river outflow periods may impede light penetration and primary production despite adequate nutrient supplies, but in deeper waters (50 m) some distance away from the mouth, phytoplankton thrive in the enriched plume waters (Salen Picard et al. 2002). Benthic communities have been shown to be responsive to changes in phytoplanktonic production due to the implications that this has on food availability (Salen-Picard et al. 2002, Sumida et al. 2005). Group III was characterised by the coarsest grade of sediment sampled in this study consistent with the location of this group on the mid-shelf, paleo-dune cordon. The high, richness, abundance and diversity of this group is therefore also attributable to the increased proportion of coarse sediment which is thought to offer a greater number of microhabitats for interstitial taxa to exist as well as increasing sediment permeability and Oxygen concentrations (Hyland et al. 1991, Jayaraj et al. 2008a, Barrio-Froján et al. 2012).

#### ***The mid and outer shelf community in the Durban feature area – The importance of biogenics and hydrodynamics***

The MS position in the DN (Group IV) feature area supported the highest number of taxa recorded during the present study. This community was located at the origin of the CCA triplot, indicating that the conditions responsible for structuring the benthic community were

not adequately determined in this study. Suspension feeders were found to contribute significantly to the abundance of macrobenthic communities sampled at the outer (Group II) (SF: 18.5%) and mid-shelf (Group IV) (SF: 30.2%) positions in this feature area, which may be due to the effects of the eddy located offshore of Durban which has been reported to extend onto the shelf at times (Lutjeharms *et al.* 2000a). Suspension feeders are generally located in areas characterised by strong hydrodynamics acting on the seafloor which leads to sandy substrates with low organic matter content and indicates the reliance of these taxa on small re-suspended particles for feeding (Rosenburg 1995, Dolbeth *et al.* 2009). In terms of granulometry, Group II and Group IV were characterised by medium and fine sand, respectively. Characteristic taxa of the mid-shelf sample grouping (IV) include the suspension feeding polychaete, *Spiochaetopterus* sp.13 and the interface feeder, *Dipolydora capensis* with the suspension feeder, *Lepadidae* sp.1 also contributing to the similarity within this group. *Dipolydora capensis* specimens were found almost exclusively in empty *Astrorhizidae* Foraminifera, while *Lepadidae* sp.1 individuals were found inhabiting the external surface of these biogenic structures as well as being present on the outside of chaetopterid tubes. Habitat modifiers and structure forming animals such as the tube building *Spiochaetopterus* sp.13 and the dead Foraminifera increase the heterogeneity of the bottom environment facilitating the establishment of abundant and diverse communities (McArthur *et al.* 2010, Passarelli *et al.* 2012). Because the characterisation of substrates requires that sediments be separated from biogenic structures, the important role that these play in structuring benthic assemblages is not reflected in grain size analysis. It is therefore important to bear in mind that grain size parameters may not accurately reflect the physical nature of the sediment that macrobenthic fauna encounter in the natural environment (McArthur *et al.* 2010).

### ***The muddy Thukela outer shelf***

The outer shelf position sampled along the TK (Group I) transect was the only sample group characterised by a high percentage of mud. Fine sediments are cohesive in nature and therefore Oxygen is not able to penetrate deeply into muddy sediments (Weston 1988). Fine particles also play an important role in the trophic structure of benthic communities as they contain more organic matter than the same amount of sandy sediment (Weston 1988, Dauwe *et al.* 1998). Deposit feeders favour these food rich fines and tend to dominate muddy sediments (Weston 1988, Dauwe *et al.* 1998). In the present study deposit feeding taxa comprised over a third (36.2%) of the total abundance recorded for sample Group I, with IF contributing approximately the same (33.2%). The macrobenthic community supported at this shelf position was separated from other sample groups in the CCA based on the high

proportion of muddy sediments found here. Mud has been identified as an important sediment parameter in differentiating benthic communities in several studies conducted in areas of high mud content (50-90%) (Weston 1988).

### ***The importance of potential nutrient sources to macrobenthos***

Oceanic features such as upwelling and riverine outwelling represent regions of increased abundance and diversity of marine taxa due to the increased food ability, facilitating enhanced development and survival (Woodson *et al.* 2012). These features also represent natural disturbance agents that play a key role in determining community structure and distribution (McArthur *et al.* 2010). River outflow and localised upwelling promotes high primary productivity in the pelagic system which may be transferred to benthic assemblages (Sumida *et al.* 2005).

### ***Conclusion***

The present study has provided novel insights into the macrobenthic dynamics in three feature areas of the Natal Bight and some of the environmental factors governing structure and distribution. Macrobenthic community composition and distribution within and between three feature areas on the Natal Bight is determined by a combination of factors associated with depth, which alone explains 72% of the variation in taxon data. Depth has been identified as a critical factor controlling many physical processes as well as the distribution of biota. Several important habitat drivers vary with depth, with results from the present study showing that sample groupings can be interpreted largely by sediment parameters. The sediment variables significantly related to macrobenthic communities were coarse sand, medium sand and mud. Results from this study suggest that the Thukela feature area represents unique physical regime leading to a distinct sedimentary habitat on the Natal Bight with the inner and mid-shelf representing a transitional area between estuarine and marine conditions. Taxon composition analysis revealed differences between high and low rainfall periods emphasizing the significance of Thukela River flow regime in driving biotic changes. These findings prompted an in-depth analysis of macrobenthic structure and function on the Thukela shelf (Chapter 4).

The relative influence of environmental factors on the structure of communities depends on the spatial scale and the environmental gradients under consideration. Therefore the relationship we observed between environmental variables and faunal structure seems to be valid on a Bight-wide scale, but less so on a smaller spatial scale. Sedimentary characteristics

were the most important variables affecting community structure in the Thukela feature area but the influence of sedimentary characteristics was less pronounced for communities supported in the Richard's Bay and Durban areas where macrobenthic community structure seems to be influenced mainly by water column processes.

## CHAPTER 4. THE INFLUENCE OF THE THUKELA RIVER ON MACROBENTHIC TAXA AND FEEDING MODES

### Overview

This chapter follows on from Chapter 3 where results showed that of the three feature areas under investigation, Thukela supported the highest abundance and richness and was the only area in which significant changes were detected when comparing low and high rainfall periods. These findings warranted a detailed investigation of structural and functional patterns across the central shelf in relation to variations in rainfall and concomitant Thukela River outflow. The continental shelf adjacent to the Thukela River experiences high freshwater, detrital and sediment input during the rainy summer months which is expected to have a significant effect on macrobenthos. Sediments on the central Bight are characterised by rich mud deposits, a unique habitat which supports an economically important, commercial trawl fishery. Macrobenthic trophic studies commonly classify taxa according to their dominant feeding mode (Chapter 3) despite evidence that many taxa are capable of switching feeding modes under different environmental conditions. Facultative behaviour is a functional adaptation particularly important in areas of variable nutrient supply, such as the central shelf, so that the feeding mode classification scheme applied here differs to that presented in the preceding chapter. An in-depth investigation of macrobenthic community patterns in the Thukela feature area will contribute to the understanding of ecosystem functioning and biological productivity of the Natal Bight.

### 4.1 Introduction

Macrobenthic communities are usually classified in terms of the taxa they comprise. This taxon based level of analysis contributes to the knowledge of regional biodiversity which is particularly relevant as current knowledge of marine benthic invertebrate diversity in South Africa is based largely on surveys conducted between the 1940s and 1980s, with the fewest samples coming from the KwaZulu-Natal region (Griffiths *et al.* 2010, Chapter 1). No Bight-wide benthic invertebrate surveys have been undertaken in KwaZulu-Natal since that time which means that taxon level information is lacking for much of the continental shelf area in this region and the taxa that have been recorded and described are in urgent need of taxonomic revision (McClurg 1988, Griffiths *et al.* 2010, Chapter 1). An alternative method of classifying macrobenthic communities is by aggregating taxon level data to a coarser taxonomic resolution or according to some functional characteristic such as feeding mode. Aggregating

taxa into groups of feeding modes is beneficial because it incorporates information on community structure and the functioning of macrobenthos within the environment (Gaston *et al.* 1998, Bremner *et al.* 2003, Christoffersen *et al.* 2011, Chapter 1).

Feeding modes in the context of the present study are defined as groups of taxa that feed in the same way regardless of their taxonomic relationships (Gaston *et al.* 1998, Bremner *et al.* 2003, Hewitt *et al.* 2008, Christoffersen *et al.* 2011). Feeding modes are broadly classified as deposit feeders, suspension feeders, carnivores, herbivores and omnivores (Hunt 1925, Sanders 1960, Young and Rhoads 1971, Gray 1981, Pearson 2001, Macdonald *et al.* 2012, Chapter 1). Sanders (1958) and many after him (Young and Rhoads 1971, Probert 1984, Roth and Wilson 1998, Arruda *et al.* 2003, Macdonald *et al.* 2012) observed that suspension feeding organisms are typically found in shallow, high energy environments with coarse sediments, while deposit feeders are more abundant in deeper, low energy environments with a high percentage of fine particles. Suspension feeders extract particles from the surrounding water while deposit feeders utilise the living components of the sediment they ingest for nourishment (Sanders 1958, Riisgård and Kamermans 2001, Thrush and Dayton 2002, Dolbeth *et al.* 2009, Chapter 1). Deposit feeders can be further classified into those that feed on material at the sediment surface (surface deposit feeders) and those that burrow to seek nourishment below the surface (subsurface deposit feeders) (Gray 1981, Riisgård and Kamermans 2001, Dolbeth *et al.* 2009). The abundance and distribution of carnivorous fauna appears to be independent of flow or sediment characteristics, while the presence of predatory fauna may serve as a proxy for the hosts that they infest (Pearson 2001, Chapter 1).

Many taxa are capable of adopting more than one feeding mode under different environmental conditions (Probert 1984, Taghon and Greene 1992, Pearson 2001, Riisgård and Kamermans 2001, Consentino and Giacobbe 2008, Pacheco *et al.* 2011). For example, Polychaeta such as Spionidae, Tellinidae bivalves and certain Amphipoda (eg. Ampeliscidae) are known to switch from deposit to suspension feeding during periods of increased flow while others, routinely classified as carnivores (eg. Polychaeta: Glyceridae, Nephtyidae) are also reported to deposit feed (Fauchald and Jumars 1979, Taghon and Greene 1992, Riisgård and Kamermans 2001, Consentino and Giacobbe 2008, Chapter 1). Few trophic studies have considered this facultative feeding behaviour, but several assessments of macrobenthic feeding modes have shown that in hydrodynamically complex coastal environments the most ubiquitous and dominant taxa are facultative feeders (Wieking and Kröncke 2003, Macdonald *et al.* 2012). The

ability of these animals to change their method of food acquisition in response to local food availability is thought to confer ecosystem resilience in the face of habitat change (Macdonald *et al.* 2012). Facultative feeders are thus expected to be common in dynamic environments where the concentration of suspended food particles is variable.

Measures of diversity not only provide integrated information regarding which and how many macrobenthos, at the level of lowest identifiable taxon or aggregated to feeding modes, are present but also give insight into system attributes (Christoffersen *et al.* 2011). Functional diversity, calculated analogously to taxon diversity, is a measure of the range of feeding modes in a given community (Bremner *et al.* 2003, Hewitt *et al.* 2008). It is generally accepted that changes in taxon diversity will result in functional diversity changes but the nature of this relationship is system dependent and affected by the numbers of taxa and individuals in a feeding mode (Hewitt *et al.* 2008). If the loss of taxa leads to an increase in functional diversity the ecosystem is functionally redundant and thus more stable (Bremner *et al.* 2003, Hewitt *et al.* 2008, Christoffersen *et al.* 2011). The degree of evenness of feeding modes also provides fundamental information on community dynamics (Hewitt *et al.* 2008). High evenness suggests that many taxa share the same feeding mode and thus reflects the ability of an ecosystem to retain its function in the light of taxon loss (Hewitt *et al.* 2008).

Interacting abiotic and biotic factors are responsible for shaping macrobenthic communities. Abundance and numbers of marine macrobenthic taxa are well reported to vary along gradients of temperature, salinity, DO and substrate characteristics such as grain size and organic content (Gaston and Nasci 1988, Gaston *et al.* 1998, Bremner *et al.* 2003, Hewitt *et al.* 2008, Christoffersen *et al.* 2011, Chapter 1). Hydrodynamic agents are responsible for shaping abiotic factors so that studying macrobenthic community structure serves as a proxy for water column dynamics (Bremner *et al.* 2003). Many of these factors co-vary with depth so that this is the factor often identified as most critical in determining the distribution and structure of macrobenthic communities (Cosentino and Giancobbè 2008, Hermand *et al.* 2008, Chapter 3). Functional attributes of macrobenthic fauna are a good indicator of the physical environment in that physico-chemical characteristics influence how macrobenthos feed (Elliot *et al.* 2007, Cacabelos *et al.* 2009). The way in which macrobenthic fauna acquire their food also has an effect on the topography and chemistry of the bottom environment (Gray 1981, Probert 1984, Karakassis and Eleftheriou 1997, Roth and Wilson 1998, Bergen *et al.* 2001, Dolbeth *et al.* 2009, Chapter 1).

The Natal Bight is widest in its central region, and unique due to outwelling from the largest river system in KwaZulu-Natal, the Thukela (Table 4.1, Chapter 2). During periods of high outflow the freshwater plume emanating from the Thukela River mouth can extend for kilometres out to sea and influence the salinity, temperature, turbidity, nutrient and dissolved Oxygen content of coastal waters (Pearce 1977, Olivier 1998, Lutjeharms *et al.* 2000a, Meyer *et al.* 2002, Turpie 2004, Whitfield 2005, Chapter 2). In addition, rivers transport large amounts of detritus to the marine realm (Smith *et al.* 2005). These inputs are expected to have a marked effect on the marine fauna, particularly in light of the generally oligotrophic nature of Natal Bight waters (Pearce 1977, Schumann 1988, Lutjeharms *et al.* 2000a, Lamberth *et al.* 2009). Material inputs from riverine systems have been identified as the primary source of nutrients sustaining productive coastal ecosystems in Brazil (Han *et al.* 2012), Chesapeake Bay (Dauer *et al.* 2000), China (Han *et al.* 2012), Italy (Simonini *et al.* 2004) and other regions of the Mediterranean, (Hermand *et al.* 2008, de Juan and Cartes 2011) New Zealand (Probert and Grove 1998) and South Africa (Lamberth *et al.* 2009). Changes in the volume of material inputs carried into the coastal realm, be they naturally or anthropogenically induced can cause modifications of macrobenthic community structure (Sauer *et al.* 2003, Vorwerk 2006, Han *et al.* 2012, Sink *et al.* 2012).

Table 4.1. Morphometric and physico-chemical characteristics of the Thukela River system

Characteristic	Value	Source
Width (m)	50- 1000	Begg, 1978
Length (km)	290 – 520	Begg, 1978
Catchment Area (m <sup>2</sup> )	28 x 10 <sup>6</sup>	Begg, 1978
Estuarine Area (m <sup>2</sup> )	0.6 x 10 <sup>6</sup>	Begg, 1978
Flow (m <sup>3</sup> )	74 x 10 <sup>6</sup> (low) – 481 x 10 <sup>6</sup> (high)	Begg, 1978, Day 1981
Sediment load (m <sup>3</sup> )	5.1 - 6.3 x 10 <sup>6</sup>	Nicholson 1983, Goodlad 1986, Flemming and Hay 1983
Nitrate (μmol.L <sup>-1</sup> )	137	Dupra and Smith 2001, Wepener 2007
Phosphate (μmol.L <sup>-1</sup> )	5.5	Dupra and Smith 2001, Wepener 2007
Dissolved Oxygen (mg.L <sup>-1</sup> )	8.2	Begg, 1978
Salinity	12	Day, 1981
Temperature (°C)	24.2	Begg, 1978

Currents on the central shelf are largely wind driven moving in a northwards direction inshore and eddy structures are thought to be present here (Schumann 1987, Lutjeharms *et al.* 2000a,

Bosman *et al.* 2007). Two large mud depocentres, one inshore (0-50 m) and the other located on the outer shelf (70-100 m) characterise the sedimentary environment of the central shelf with a belt of coarse, medium sand and gravel sized bioclastic debris separates these two muddy regions at the mid-shelf (65 m) and the shelf edge, scoured by the action of the southward flowing Agulhas Current, is also characterised by high gravel contents (Felhaber 1985 cited in: Olivier 1998, Flemming 1981, Flemming and Hay 1988, van der Elst and Fennessy 1990, Meyer *et al.* 2002, Bosman *et al.* 2007, Chapter 2).

### **Aims, Objectives and Hypotheses**

The aim of this chapter is to describe short-term changes in the structure and function of macrofaunal communities sampled along a coast-perpendicular transect from the Thukela River to shelf edge, repeated during two cruises corresponding with high and low river outflow, and to test the relationship between these biotic patterns and measured physico-chemical variables.

### **Objectives**

1. Determine whether Thukela River flow regime has an effect on the habitat parameters measured on the central Bight.
2. Determine whether the structure and function, assigned according to a different feeding mode classification scheme, of macrobenthic communities across the central shelf changes between high and low outflow periods.
3. Determine the relationship between the biotic community and measured environmental parameters.

### **Hypotheses**

H<sub>a1</sub> – There is a difference between habitat parameters measured along the studied depth gradient during periods of high and low outflow from the Thukela River.

H<sub>a2</sub> – There is a difference in the taxon or facultative feeding mode composition of macrobenthic communities sampled across a depth gradient in the central Bight during periods of high (Cruise A) and low (Cruise B) outflow from the Thukela River.

H<sub>a3</sub> – There is a significant relationship between the macrobenthic community environmental variables measured across the central shelf.

## 4.2 Materials and Methods

General field sampling, lab processing and data analysis information is presented in Chapter 2 of this thesis.

### 4.2.1 Study area and Sampling Design

In total seven stations (I1-I7) were sampled along the Thukela transect during both sampling cruises, corresponding with relative shelf positions along the studied depth gradient. Despite the lack of temporal sample collection repetition some idea of potential differences and outflow influence can be gleaned. Stations were designated *a priori* as: Inner (I1), mid (I4), outer shelf (I7) and transition zone stations (TZ-1: I2, I3; TZ-2: I5, I6). All stations were processed for cruise A but due to project constraints only stations I1, I4 and I7 were analysed for the second cruise (Fig 4.1). Thus, although this presented an unbalanced study design transition zone samples were included in the analysis as they provided a fuller picture of macrobenthic community dynamics along the studied depth gradient during a period of high riverine outflow.

### 4.2.2 Data handling and analysis

#### **Biotic data**

Each taxon was assigned to a feeding mode according to reported feeding mechanism/s using available literature. Eleven feeding modes were defined namely: carnivore (C), omnivore (O), parasite (Par), suspension feeder (SF), surface deposit feeder (SDF), subsurface deposit feeder (SSDF), facultative carnivore (FC), which are predators or scavengers but are also able to deposit feed, facultative detritivore (FD) designated to fauna which are reported to be suspension and deposit feeders or are both surface and subsurface deposit feeders, facultative omnivores (FO) which feed on animal and plant matter but are also reported to deposit feed and multi-modal (MM) feeders which are facultative feeders that occupy more than two feeding modes designated to Ostracoda (Chapter 3).

A variety of univariate and multivariate statistical techniques were used to determine patterns in taxon and feeding mode community structure between shelf positions and sampling cruises (Chapter 2). Prior to analyses data were combined as: i) abundance data at the level of lowest identifiable taxon for all samples (I1-I7) collected during cruise A ii) taxon abundance data for the inner (I1), mid (I4) and outer shelf (I7) samples collected during both cruises and iii) abundance data at the level of feeding mode for these three shelf positions.

### **Multivariate analysis**

#### **Macrobenthic community structure and function**

Groups identified in cluster analysis (Chapter 2) contained very few samples due to the lack of temporal repetition and thus it was difficult to determine how accurate a representation they were. Therefore the Similarity Profile (SIMPROF) procedure was employed to test the statistical significance of sample groups, which involves a series of null hypothesis tests that sample groups presented in the dendrogram have no meaningful internal structure, inferring that the samples were drawn from different macrobenthic assemblages (Clarke *et al.* 2008).

The interpretation of a sample group is only permissible if the null hypothesis is rejected. Plots are constructed in which the Bray-Curtis (B-C) similarities calculated from abundance data at the level of lowest identifiable taxon and feeding mode are ordered from smallest to largest and plotted against their rank similarities (Clarke *et al.* 2008). The test statistic used in the SIMPROF procedure is  $\pi$  ( $\pi$ ), defined as the deviation of the real profile from the mean of the permuted profile. Starting at the top of a dendrogram and performing SIMPROF with all samples it is allowable to move onto successive sub-groups of samples only if the sample set is deemed to have internal structure (Clarke *et al.* 2008). This procedure is repeated until a non-significant result is obtained indicating that the samples in that group are homogenous and can therefore be further analysed (Clarke *et al.* 2008).

#### **Relationship between macrobenthic communities and environmental factors**

BROD GAR v. 2.7.2 (Zuur *et al.* 2007) (an interface to R v.2.9.1) was used to investigate relationships between measured environmental variables and community data. The relationship between explanatory (environmental) variables and response (biotic) variables was investigated using distance-based redundancy analysis (db-RDA) with a Chord distance transformation (Legendre and Gallagher 2001, Legendre and Birks 2012). Chord distance is recommended for the analysis of ecological data and is equal to the Euclidean distance calculated after scaling the site vectors to a length of 1 (Legendre and Anderson 1999, Legendre and Gallagher 2001, Zuur *et al.* 2007, Lee 2012). The application of this partial transformation on the biotic data, prior to the computation of Euclidean distances allows ecologists to use ordination methods, RDA in this case, which are Euclidean based, with community data that inherently contain many zeros (Legendre and Gallagher 2001, Zuur *et al.* 2007, Legendre and Birks 2012).

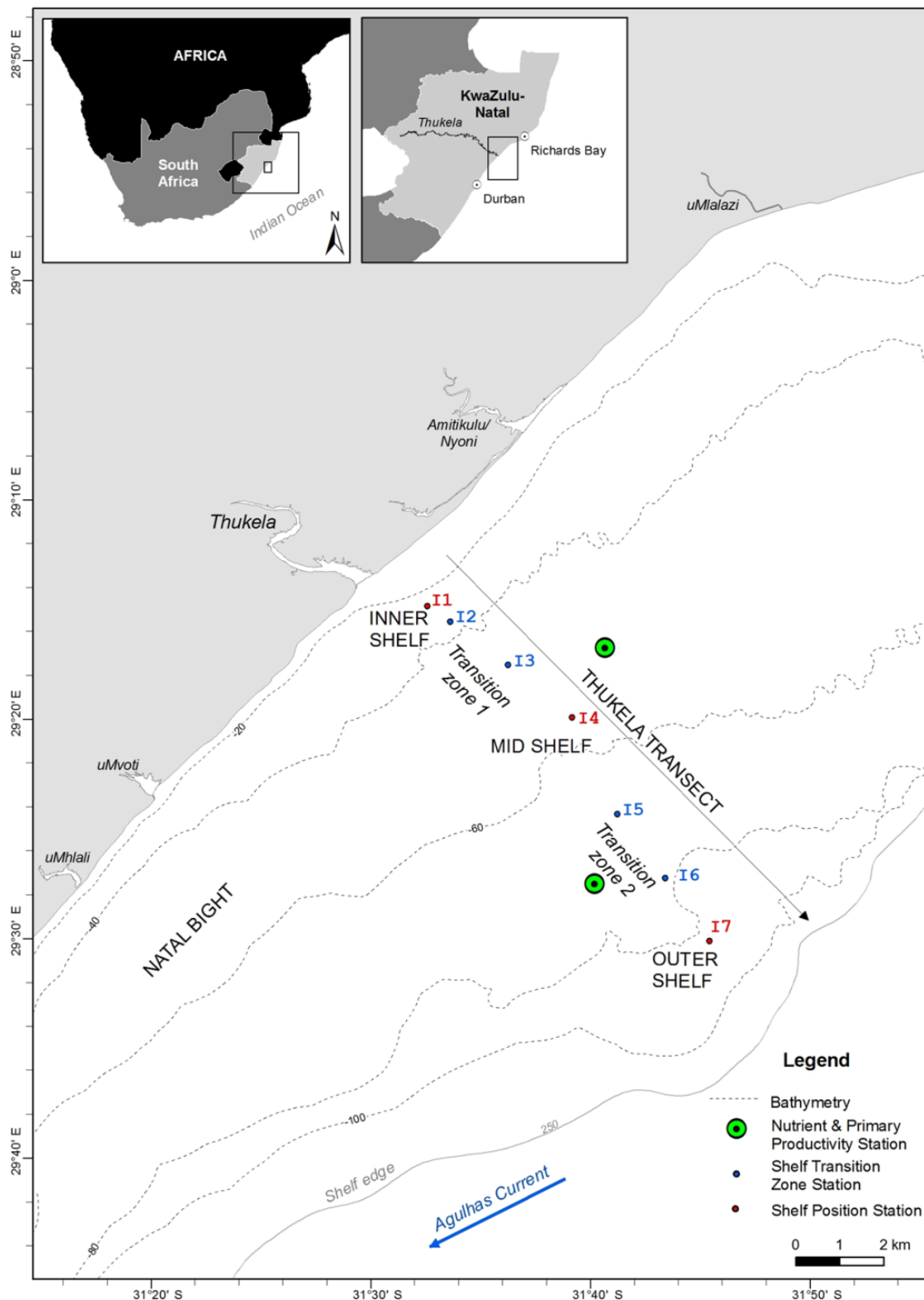


Figure 4.1. Map showing the location and bathymetry of shelf position, nutrient and primary productivity stations sampled along a transect from the Thukela River mouth to shelf edge during cruises A and B.

The sum of all canonical eigenvalues ( $\lambda$ ) produced in the db-RDA analysis is equal to the amount of variation in biotic data that is explained by the set of explanatory variables (Legendre and Anderson 1999, Legendre and Gallagher 2001). A distinct advantage of using this analysis is that the db-RDA model can be employed to perform statistical tests of multivariate hypotheses using a permutation test. The benefit of using a permutation test is that it does not rely on assumptions of multivariate normality (Legendre and Gallagher 2001). Although db-RDA is less commonly applied than the more popular method of Canonical Correspondence Analysis (CCA), the latter was not used in this case as the intention was not to give high weights to rare taxa and abundant sites (Legendre and Gallagher 2001, Zuur *et al.* 2007).

Twenty-two measured environmental variables were reduced to fifteen after removing those that were highly correlated with each other ( $r=0.95$ ) (Chapter 2). Also the number of explanatory variables must be fewer in number, by at least one, than samples in order to perform db-RDA analysis (Zuur *et al.* 2007). The nominal variables 'cruise' and 'shelf position' were added to the list of environmental variables and a total of seventeen explanatory variables were used as input. Before the RDA analysis is performed, the Variance Inflation Factor (VIF) values are determined to assess the co-linearity between environmental variables. If VIF values are too high ( $VIF > 150$ ) the analysis is terminated (Zuur *et al.* 2007). If this is true, the variable with the highest VIF value is removed and the analysis repeated until a successful model is produced (Zuur *et al.* 2007).

For both the taxon and feeding mode analysis ten explanatory variables were needed to produce a successful db-RDA model. To determine which of these variables were important and the order of their importance, a forward selection procedure was applied which uses explained variance (sum of all canonical eigenvalues) as a criteria to indicate which environmental variables should be included in the final model (Zuur *et al.* 2007). The conditional effects output from forward selection shows the increase in the total sum of eigenvalues after including a new variable. To test the null hypothesis that the explained variation in biotic data from these variables is larger than or equal to a random contribution, a Monte-Carlo permutation test was applied by including explanatory variables one by one starting with the best single explanatory variable presented in the conditional effects output (Zuur *et al.* 2007). Only those variables that were identified as being significant ( $p < 0.05$ ) were included in the final db-RDA model and the significance of the final model was tested with a

Monte-Carlo permutation test. The null hypothesis in this case was that the set of environmental variables does not explain a significant proportion of the variability in biotic data (Zuur *et al.* 2007).

## 4.3 Results

### 4.3.1 Environmental conditions

No statistically significant differences were detected between cruises A and B in temperature, salinity or dissolved Oxygen (DO) concentrations. Near bottom temperatures decreased from a maximum of 20.12°C at the inner shelf (IS) (26 m) to reach minimum values (14.77°C) at the outer shelf (OS) (112 m) during the period of high river outflow (Fig. 4.2). During the winter period of low freshwater outflow, near bottom temperature was slightly lower at the IS (19.98°C) and elevated at the mid-shelf (MS) (19.89°C) and OS (18.55°C) where the coolest waters were again found, although there was much less of a difference between maximum and minimum values recorded across the central shelf during cruise B (Fig. 4.2). During the summer period of high rainfall and outflow from the Thukela River salinity was lowest at the OS (35.34) and IS (35.37) while the salinity of waters at transition zone stations and MS were similar. Higher values of near bottom salinity were recorded for IS (35.47) and OS (35.42) waters during cruise B, while the salinity of MS waters remained unchanged (35.44) (Fig. 4.2). During the period of high outflow, dissolved Oxygen values exceeded 4 mg.L<sup>-1</sup> for both the IS (I1) and OS (I4), with lower, similar values recorded for stations falling within the first transition zone (I2: 3.47 mg.L<sup>-1</sup>; I3: 3.41 mg.L<sup>-1</sup>) and MS (I4: 3.53 mg.L<sup>-1</sup>) (Fig. 4.2). During the low outflow period higher DO concentrations were recorded for IS (I1: 4.59 mg.L<sup>-1</sup>) and MS (I4: 4.53 mg.L<sup>-1</sup>) waters while lower values were recorded at the OS (I7: 3.68 mg.L<sup>-1</sup>) (Fig. 4.2).

The IS was characterised by well sorted (cruise A: 0.36  $\Phi \pm 0.04$ SD; cruise B: 0.36  $\Phi \pm 0.05$ SD), sediment with fine skewed distribution, mean grain size of 0.17 mm  $\pm 0$ SD and a mean phi of approximately 2.6  $\Phi$  (Table 4.2). Fine (fns) and very fine sands (vfs) dominated the sedimentary grain size distribution at this shelf position during both sampling cruises A (fns: 68.81%  $\pm 2.97$ SD; vfs: 25.40%  $\pm 3.60$ SD) and B (fns: 68.69%  $\pm 1.58$ SD; vfs: 25.54%  $\pm 1.29$ SD) with very little difference in the percentage contribution of these two sediment grades between high and low rainfall periods (Table 4.2). The mud contents of sediment at the shallowest depths sampled (20-26 m) remained constant between sampling cruises and contributed little (cruise A: 4.48%  $\pm 0.44$ SD; cruise B: 4.67%  $\pm 0.92$ SD) to the total sediment

composition (Table 4.2). The organic content (TOC) of inner shelf sediments was very low during cruise A (TOC:  $0.14\% \pm 0.03\text{SD}$ ), with an increase recorded for samples collected from this shelf position during cruise B (TOC:  $0.49\% \pm 0.05\text{SD}$ ) (Table 4.2).

In contrast the substrate at TZ-1 stations (I2: 35 m and I3: 50 m) sampled during cruise A was negatively skewed with sediments here composed almost entirely of mud (I2: 94.45%, I3: 97.05%), rich in organic material (TOC-I2: 4.62%, I3: 9.09%) (Table 4.2).

The mid-shelf (MS) located at a depth of 52-56 m was characterised by a coarser grade of moderately sorted (Cruise A:  $0.94 \Phi \pm 0.47\text{SD}$ ; Cruise B:  $0.67 \Phi \pm 0.07\text{SD}$ ) sediment, low in organic content (Cruise A:  $0.04\% \pm 0.02\text{SD}$ ; Cruise B:  $0.33\% \pm 0.18\text{SD}$ ) with a mean grain size of  $0.32 \text{ mm} \pm 0.12\text{SD}$  recorded during cruise A and similar values recorded during cruise B ( $0.41 \text{ mm} \pm 0.02\text{SD}$ ) (Table 4.2). The percentage of medium sand (mms) remained relatively constant at this shelf position between sampling cruises (Cruise A:  $50.19\% \pm 4.93\text{SD}$ ; Cruise B:  $48.75\% \pm 5.65\text{SD}$ ) while the amount of coarse sand (cos) increased from  $23.13\% \pm 11.64\text{SD}$  in cruise A to  $34.49\% \pm 6.15\text{SD}$  in cruise B (Table 4.2). Although gravel (gvl) contributed very little to the overall composition of sediment on the central shelf, the highest proportion of this sediment grade was found at the MS position during both cruises (Cruise A:  $0.36\% \pm 0.21\text{SD}$ ; Cruise B:  $0.54\% \pm 0.66\text{SD}$ ) (Table 4.2). Mud contributed approximately 10% to the overall sediment composition at the MS during cruise A with a large reduction in the amount of this sediment grade during the period of low freshwater outflow (Cruise B) ( $1.38\% \pm 0.78\text{SD}$ ) (Table 4.2).

Mud, rich in organic carbon dominated the sedimentary grain size distribution at TZ-2 stations (I5: 74 m and I6: 76 m) during cruise A (mud:  $86.26\% \pm 5.20\text{SD}$ ) but this deposit was moderately well sorted (I5:  $0.48 \Phi$ , I6:  $0.69 \Phi$ ), compared to the well sorted deposit at TZ-1 (Table 4.2).

The OS (109-112 m) was characterised by poorly sorted (Cruise A:  $1.05 \Phi \pm 0.25\text{SD}$ ; Cruise B:  $1.11 \Phi \pm 0.45\text{SD}$ ) sediment with mean grain size ranging from  $0.06 \text{ mm} \pm 0.01\text{SD}$  in cruise A to  $0.07 \text{ mm} \pm 0.02\text{SD}$  in cruise B and mean phi values of  $3.9 \Phi \pm 0.50\text{SD}$  -  $4.04 \Phi \pm 0.32\text{SD}$  recorded during cruises A and B, respectively (Table 4.2). This shelf position had a strongly

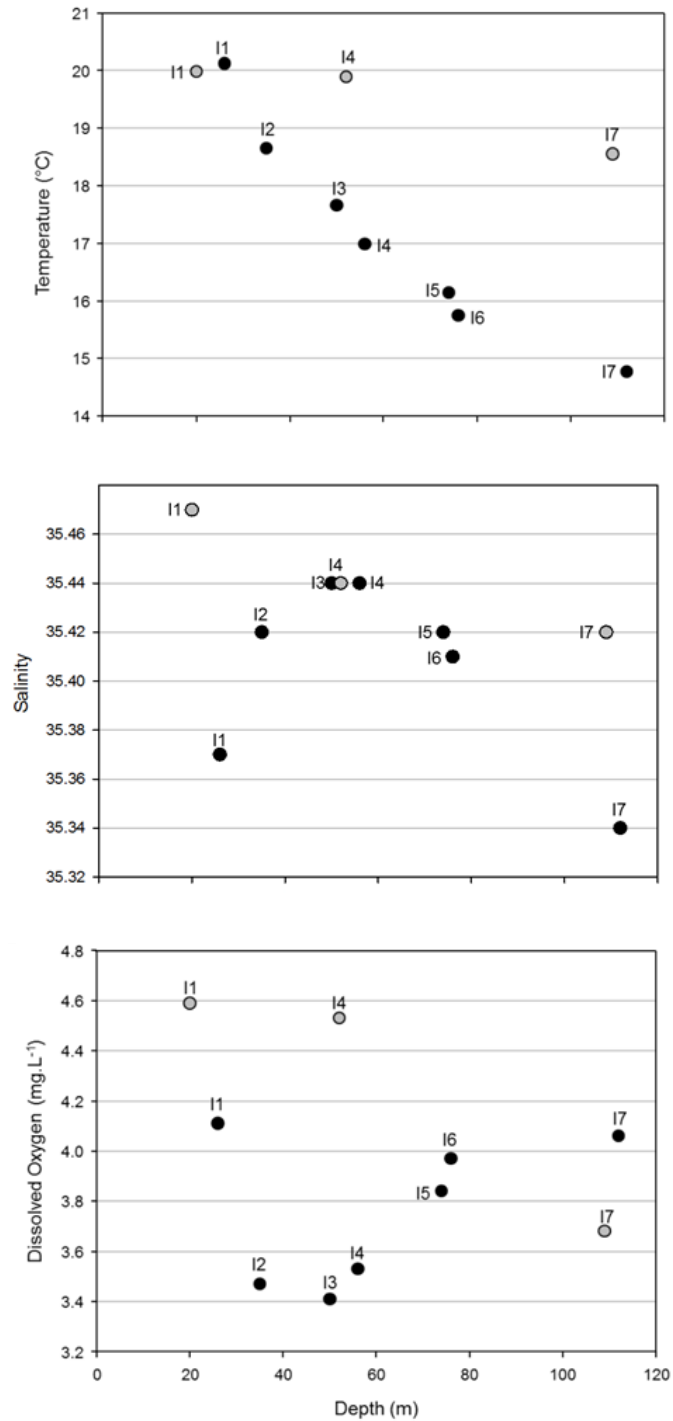


Figure 4.2. Temperature (°C), Salinity and Dissolved Oxygen concentration (mg.L<sup>-1</sup>) of near-bottom waters plotted against depth (m) for stations sampled along the Thukela transect during cruises A and B. I1=Inner shelf, I2 and I3=Transition zone 1, I4=Mid-shelf, I5 and I6=Transition zone 2. Cruise A (High outflow: February 2010), Cruise B (Low outflow: August 2010).

negatively skewed sediment distribution and was thus dominated by fine, mud deposits during both sampling cruises (Cruise A:  $81.73\% \pm 3.65\text{SD}$ ; Cruise B:  $74.60\% \pm 1.84\text{SD}$ ), although the percentage contribution was reduced during the low outflow period. Organic content of the

sediment at the OS followed the same pattern as mud with high values recorded for the first sampling period (Cruise A:  $4.52\% \pm 3.55SD$ ) and medium values recorded during the low rainfall period (Cruise B:  $2.79\% \pm 0.18SD$ ) (Table 4.2). Medium and fns made a significant contribution to the sediment composition at the OS during cruise A (mms:  $6.49\% \pm 1.45SD$ ; fns:  $5.10\% \pm 0.67SD$ ) with increased percentages of both these sediment grades found during cruise B (mms:  $8.64\% \pm 6.01SD$ ; fns:  $7.02\% \pm 3.91SD$ ) (Table 4.2).

Samples for nutrient concentration and primary productivity analysis were only collected at two stations on the shelf during cruises A and B, therefore statistical differences between nutrient concentrations for the factors of cruise and shelf position were not determined. Nitrate ( $NO_3$ ) and Chlorophyll *a* concentrations were highest some distance away from the river mouth during both cruises A ( $NO_3$ :  $2.21 \mu mol.L^{-1}$ , Chl-*a*:  $1.82 \mu g.L^{-1}$ ) and B ( $NO_3$ :  $1.75 \mu mol.L^{-1}$ , Chl-*a*:  $0.70 \mu g.L^{-1}$ ), despite dropping by more than half in the latter period of reduced freshwater outflow (Table 4.2). Phosphate ( $PO_4$ ) values remained relatively constant across the width of the central shelf during cruise A ( $PO_4$ :  $0.26-0.27 \mu mol.L^{-1}$ ) with higher but also constant values recorded during cruise B ( $PO_4$ :  $0.35-0.37 \mu mol.L^{-1}$ ) (Table 4.2). Concentrations of Silicate (Si) decreased slightly from the IS and MS ( $2.70 \mu mol.L^{-1}$ ) to  $2.34 \mu mol.L^{-1}$  at the OS when Thukela River outflow was high. This situation was reversed during cruise B when Si concentrations increased from the IS and MS ( $2.56 \mu mol.L^{-1}$ ) to the OS ( $3.33 \mu mol.L^{-1}$ ) where values were approximately  $1 \mu mol.L^{-1}$  higher than during cruise A (Table 4.2).

#### **4.3.2 Macrobenthic community analysis: lowest identifiable taxa and major Phyla**

##### ***The effect of cruise (variable periods of outflow)***

##### *Abundance (N) of individuals and lowest identifiable taxa (S)*

Abundance across the central shelf decreased ( $t=1.124$ ,  $df=16$ ,  $p=0.277$ ) from a total of 9335 individuals.m<sup>-2</sup> collected during the period of high freshwater outflow (Cruise A) to a total 7280 .m<sup>-2</sup> individuals recorded during cruise B. The spread of abundance data was greatest during cruise B (395-1790 ind.m<sup>-2</sup>), while the distribution was right skewed with the bulk of abundance data lying above the mean (Fig. 4.3). Cruise A had a slightly smaller range of abundance values (470-1485 ind.m<sup>-2</sup>) and the distribution was slightly left skewed, indicating

that most values lie below the mean (Fig. 4.3). The total number of taxa recorded during the time of reduced outflow (223 taxa) was significantly ( $t=3.814$ ,  $df=16$ ,  $p=0.002$ ) lower than

cruise A (361 taxa). The spread of taxon richness data was greatest during cruise A (42-92 taxa) and the distribution was symmetrical with the median and the mean having the same value and lying in the centre of the data (Fig. 4.3). Cruise B had a smaller range of values (33-56 taxa) with the bulk of data being slightly lower than the mean (Fig. 4.3).

Table 4.2. Sedimentary characteristics and nutrient concentration of shelf position stations sampled along the Thukela River transect during Cruise A (High outflow: February 2010) and B (Low outflow: August 2010).

Shelf position		Cruise	Inner shelf (IS)	Transition Zone 1 (TZ-1)		Mid-shelf (MS)	Transition Zone 2 (TZ-2)		Outer shelf (OS)
Station			I1	I2	I3	I4	I5	I6	I7
Sedimentary parameters	%Gravel (gvl)	A	0.01 ± 0.01 SD	0.00	0.00	0.36 ± 0.21 SD	0.00	0.04	0.34 ± 0.31 SD
		B	0.03 ± 0.04 SD	-	-	0.54 ± 0.66 SD	-	-	0.12 ± 0.13 SD
	%Very coarse sand (vcs)	A	0.01 ± 0.01 SD	0.00	0.00	0.98 ± 0.27 SD	0.14	0.02	1.21 ± 0.41 SD
		B	0.02 ± 0.04 SD	-	-	1.59 ± 1.41 SD	-	-	1.25 ± 0.98 SD
	%Coarse sand (cos)	A	0.03 ± 0.03 SD	0.00	0.12	23.13 ± 11.64 SD	0.75	0.07	3.04 ± 0.46 SD
		B	0.03 ± 0.00 SD	-	-	34.49 ± 6.15 SD	-	-	4.10 ± 2.70 SD
	%Medium sand (mms)	A	1.27 ± 0.48 SD	0.05	1.03	50.19 ± 4.93 SD	1.64	0.23	6.49 ± 1.45 SD
		B	1.01 ± 0.22 SD	-	-	48.75 ± 5.65 SD	-	-	8.64 ± 6.01 SD
	%Fine sand (fns)	A	68.81 ± 2.97 SD	1.02	1.37	15.01 ± 5.18 SD	2.41	5.39	5.10 ± 0.67 SD
		B	68.69 ± 1.58 SD	-	-	12.80 ± 1.49 SD	-	-	7.02 ± 3.91 SD
	%Very fine sand (vfs)	A	25.40 ± 3.60 SD	4.48	0.44	0.58 ± 0.30 SD	5.12	11.68	2.17 ± 0.54 SD
		B	25.54 ± 1.29 SD	-	-	0.45 ± 0.08 SD	-	-	4.26 ± 1.30 SD
	%Mud (mud)	A	4.48 ± 0.44 SD	94.45	97.05	9.74 ± 13.18 SD	89.94	82.58	81.73 ± 3.65 SD
		B	4.67 ± 0.92 SD	-	-	1.38 ± 0.78 SD	-	-	74.60 ± 14.99 SD
	%Total Organic Content (TOC)	A	0.14 ± 0.03 SD	4.62	9.09	0.04 ± 0.02 SD	1.66	7.57	4.52 ± 3.55 SD
		B	0.49 ± 0.05 SD	-	-	0.33 ± 0.18 SD	-	-	2.79 ± 0.18 SD
	Mean grain size (mm)	A	0.17 ± 0.00 SD	0.05	0.04	0.32 ± 0.12 SD	0.05	0.06	0.06 ± 0.01 SD
		B	0.17 ± 0.00 SD	-	-	0.41 ± 0.02 SD	-	-	0.07 ± 0.02 SD
	Mean phi (Φ)	A	2.58 ± 0.01 SD	4.47	4.48	1.72 ± 0.59 SD	4.44	4.16	4.04 ± 0.32 SD
		B	2.59 ± 0.03 SD	-	-	1.28 ± 0.07 SD	-	-	3.90 ± 0.50 SD
Sorting	A	0.36 ± 0.04 SD	0.39	0.32	0.94 ± 0.47 SD	0.48	0.69	1.05 ± 0.25 SD	
	B	0.36 ± 0.05 SD	-	-	0.67 ± 0.07 SD	-	-	1.11 ± 0.45 SD	
Skewness	A	0.20 ± 0.18 SD	-0.29	0.00	2.56 ± 3.89 SD	-0.93	-1.48	-6.54 ± 1.58 SD	
	B	0.26 ± 0.34 SD	-	-	0.29 ± 0.25 SD	-	-	-6.71 ± 3.77 SD	
Nutrients	Chlorophyll a (Chl-a) (µmol.L <sup>-1</sup> )	A	0.84				1.81		
		B	0.56				0.70		
	Silicate (Si) (µmol.L <sup>-1</sup> )	A	2.70				2.34		
		B	2.56				3.33		
	Phosphate (PO <sub>4</sub> ) (µmol.L <sup>-1</sup> )	A	0.28				0.26		
		B	0.35				0.37		
	Nitrate (NO <sub>3</sub> ) (µmol.L <sup>-1</sup> )	A	1.58				2.21		
		B	0.99				1.75		

#### Patterns (N, S) of major macrobenthic Phyla

Annelida contributed most to the abundance (N: 48.21%) and no. of taxa (S: 47.92%) sampled during cruise A, with the majority of this Phylum being represented by Polychaeta (Pol-N:

47.99%; S: 46.81%). Crustacea was the next most abundant (Cru-N: 20.32%) Phylum and contributed 25.76% to the total number of taxa (S) recorded during the period of high freshwater outflow (Fig. 4.4). Mollusca (Mol-N: 12.32%; S: 11.36%), Sipuncula (Sip-N: 5.20%; S: 4.99%) and Echinodermata (Ech-N: 3.16%; S: 7.48%) contributed most of the balance. Cnidaria, Chordata and Nemertea (Oth) contributed <1% to total abundance ( $\text{m}^{-2}$ ) and <3% to the total numbers of taxa collected during cruise A (Fig. 4.4). Although fewer taxa were recorded during the period of low outflow, the percentage contribution of each Phylum to total numbers of taxa remained approximately the same. During cruise B, Crustacea contributed most to total abundance (N: 46.15%), followed by Annelida (34.48%), of which the majority were Polychatea (33.93%), Mollusca (8.59%), Sipuncula (5.70%) and Echinodermata (3.16%) with other Phyla contributing <2% (Fig. 4.4).

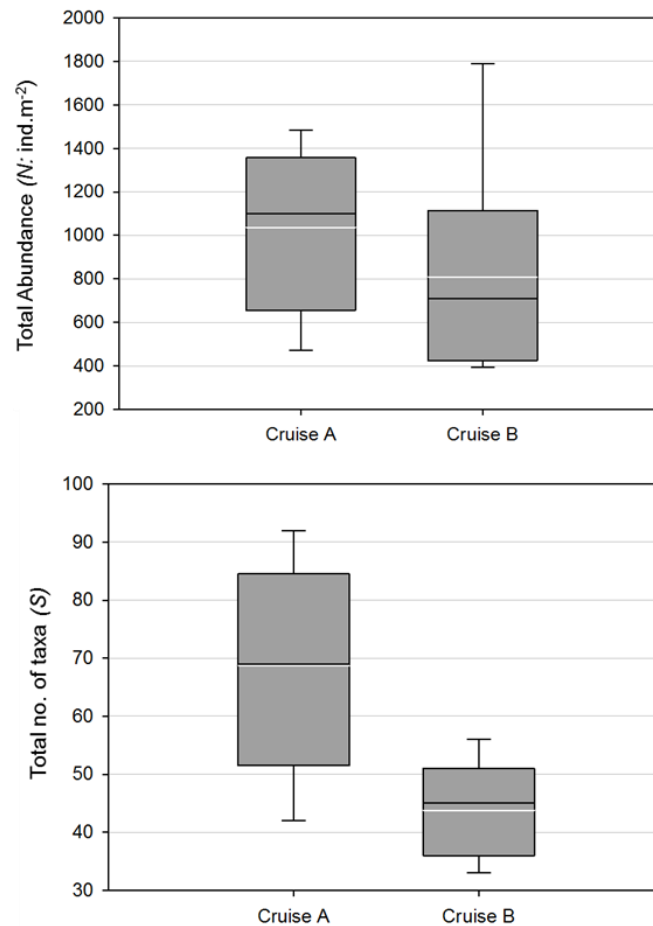


Figure 4.3. Boxplots of total abundance (N) and no. of taxa (S) for macrobenthos sampled during two cruises along a cross-shelf Thukela River transect. Black line within boxplot represents the median, white line represents the mean.

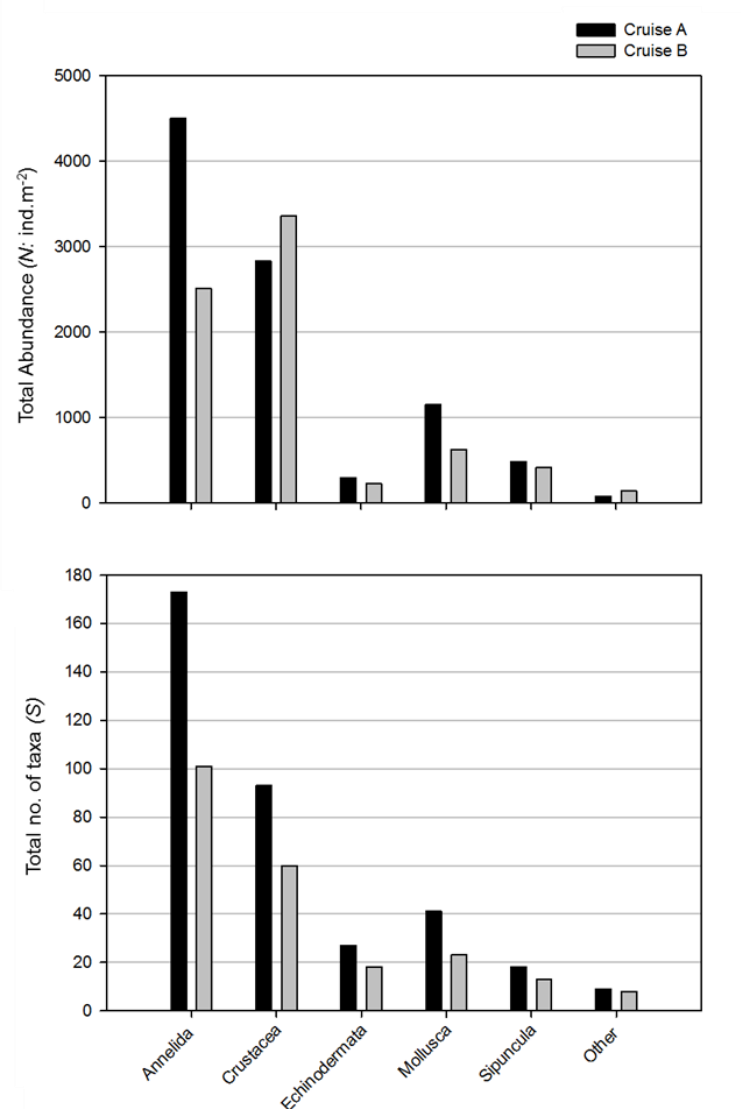


Figure 4.4. Contribution of major macrobenthic Phyla to total abundance (N) and total no. of taxa (S) sampled during two cruises along a cross-shelf Thukela River transect. Cruise A (High outflow: February 2010), Cruise B (Low outflow: August 2010).

### ***The influence of shelf position during periods of variable outflow***

#### ***Abundance (N) of individuals and lowest identifiable taxa (S)***

During the first sampling cruise (A), corresponding with high freshwater outflow from the Thukela River, abundance (N) and no. of taxa (S) increased from the inner shelf (N: 1118 ind.m<sup>-2</sup> ± 40.72SD; S: 67 taxa ± 7.78SD) to reach maximum values at the mid-shelf (N: 1400 ind.m<sup>-2</sup> ± 90.42 SD; S: 87 taxa ± 5.57SD) (Fig. 4.5). Values of Richness (d) and Diversity (H') followed the same trend with the highest values of both indices recorded for the MS (d: 11.87 ± 0.66SD; H': 3.80 ± 0.12SD) (Fig. 4.5). Transition zones (TZ-1, TZ-2) supported reduced

numbers of individuals and taxa when compared with the IS, MS and OS positions. The most depauperate (I5: 22 ind.m<sup>-2</sup>; 6 taxa) sample with the lowest recorded values for Diversity ( $H'=1.673$ ) and Richness ( $d=1.618$ ) was located in TZ-2, between the mid and outer shelf positions, while TZ-1 samples, interjecting the inner and mid-shelf positions had the highest ( $13-J'=0.9397$ ) and lowest ( $12-J'=0.7337$ ) levels of community Evenness.

Numbers of taxa ( $S$ ),  $d$ , and  $H'$  were significantly lower for the IS ( $p<0.001$ ) and MS ( $p<0.01$ ) during cruise B, when riverine outflow was reduced (Table 4.3). There was also a significant decline in  $N$  recorded at the MS ( $p=0.027$ ) during cruise B, while  $N$  at the IS increased slightly ( $p>0.05$ ) (Table 4.3, Fig. 4.5). During the period of low outflow, numbers of taxa ( $S$ : 36.33 taxa  $\pm$  4.16SD), Richness ( $d$ : 5.11  $\pm$  0.50SD), Diversity ( $H'$ : 2.20  $\pm$  0.83SD) and Evenness ( $J'$ : 0.62  $\pm$  0.25SD) were lowest at the IS, despite abundance being highest at this shelf position ( $N$ : 1218.33 ind.m<sup>-2</sup>  $\pm$  705.41SD). Numbers of taxa ( $S$ ) and  $d$ , as in cruise A, were highest at the MS ( $S$ : 49.67 taxa  $\pm$  5.69SD;  $d$ : 7.59  $\pm$  0.64SD) during cruise B while the outer shelf supported the most diverse ( $H'$ : 3.43  $\pm$  0.19SD) community (Fig. 4.5). The OS position was stable with no significant differences ( $p>0.05$ ) in any of the measured community metrics between cruises A and B (Table 4.3). This shelf position supported the lowest numbers of taxa during cruise A ( $S$ : 51.67 taxa  $\pm$  14.22SD) and the lowest numbers of individuals during both cruises A and B ( $N$ -Cruise A: 593.33 ind.m<sup>-2</sup>  $\pm$  156.95SD; Cruise B: 585 ind.m<sup>-2</sup>  $\pm$  200.75SD) (Fig. 4.5). Minimum values of  $d$  and  $H'$  were also recorded for the OS during cruise A ( $d$ : 7.91  $\pm$  1.88SD;  $H'$ : 3.55  $\pm$  0.15SD), while the macrobenthic community at this shelf position was the most equitably distributed during periods of high and low freshwater outflow from the Thukela River ( $J'$ -Cruise A: 0.91  $\pm$  0.02SD; Cruise B: 0.90  $\pm$  0.02SD) (Fig. 4.5). Comparing Evenness values obtained during cruises A and B, it was found that there were no significant differences ( $p>0.05$ ) within any of the shelf positions sampled (Table 4.3).

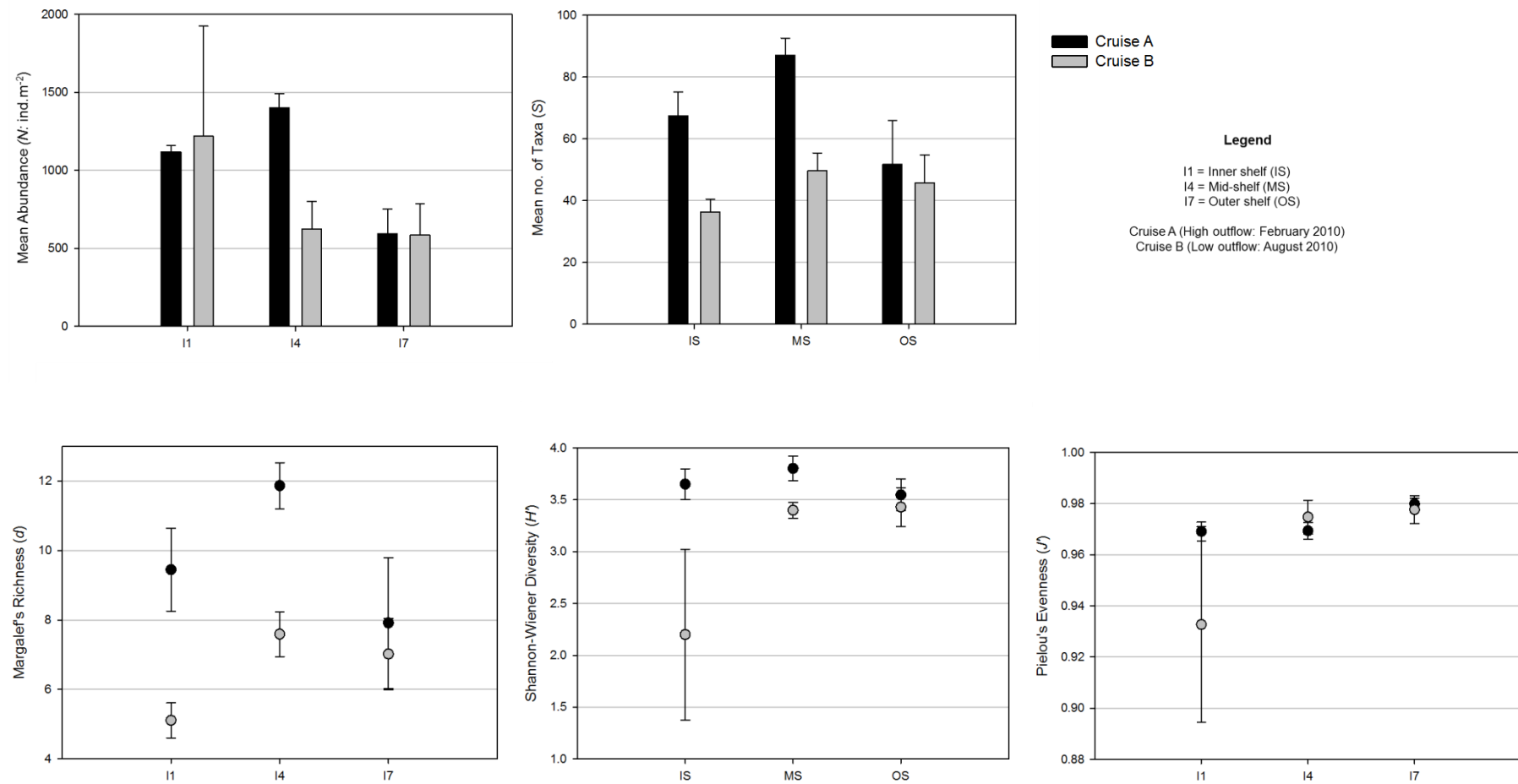


Figure 4.5. Mean abundance ( $N$ ), mean no. of taxa ( $S$ ) and indices of Richness ( $d$ ), Diversity ( $H'$ ) and Evenness ( $J'$ ) calculated from abundance data at the level of lowest identifiable taxon for shelf position stations (mean  $\pm$  SD) sampled during cruises A and B.

Table 4.3. Two way ANOVA and post-hoc Student-Newman-Kuels (SNK) testing based on univariate measures of taxon abundance data collected during cruises A and B. IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf,  $F$ =critical value of ANOVA,  $q$ =critical value of SNK test,  $df$ =degrees of freedom,  $p$ =level of significance ( $p=0.05$ ). Values in bold are significant \* $p<0.05$ , \*\* $p<0.01$ , \*\*\* $p<0.001$ .

Abundance ( <i>N</i> : no. ind. m <sup>-2</sup> )				Number of Taxa ( <i>S</i> )			Margalef's Richness ( <i>d</i> )			Shannon-Wiener Diversity ( <i>H'</i> )			Pielou's Evenness ( <i>J'</i> )		
<i>Main factors</i>															
Anova	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
Shelf position (SP)	2	5.018	<b>0.026*</b>	2	9.151	<b>0.004**</b>	2	9.378	<b>0.004**</b>	2	2.531	0.121	2	5.895	<b>0.016*</b>
Cruise (Cr)	1	2.798	0.120	1	37.788	<b>&lt;0.001***</b>	1	37.982	<b>&lt;0.001***</b>	1	39.396	<b>&lt;0.001***</b>	1	0.142	0.712
SP x Cr	2	2.754	0.104	2	5.631	<b>0.019*</b>	2	4.893	<b>0.028*</b>	2	3.110	0.082	2	0.709	0.511
<i>Pair-wise Comparisons</i>															
SNK Test	Difference of means	<i>q</i>	<i>p</i>	Difference of means	<i>q</i>	<i>p</i>	Difference of means	<i>q</i>	<i>p</i>	Difference of ranks	<i>q</i>	<i>p</i>	Difference of ranks	<i>q</i>	<i>p</i>
IS vs MS	2.448	1.117	0.445	16.500	4.727	<b>0.006**</b>	2.453	5.502	<b>0.006**</b>	3.583	3.159	0.106	0.333	0.187	0.897
MS vs OS	7.008	3.199	<b>0.043*</b>	19.667	5.634	<b>0.005**</b>	2.265	5.081	<b>0.005**</b>	2.167	1.910	0.202	7.667	4.296	<b>0.026*</b>
IS vs OS	9.456	4.316	<b>0.025*</b>	3.167	0.907	0.771	0.188	0.421	0.771	1.417	1.249	0.395	7.333	4.109	<b>0.013*</b>
A vs B	4.231	2.365	0.120	24.778	8.693	<b>&lt;0.001***</b>	3.172	8.716	<b>&lt;0.001**</b>	11.667	7.272	<b>&lt;0.001***</b>	0.778	0.534	0.713
IS-A vs IS-B	0.204	0.066	0.964	31.000	6.280	<b>&lt;0.001***</b>	4.341	6.886	<b>&lt;0.001***</b>	11.667	7.272	<b>&lt;0.001***</b>	3.667	1.453	0.325
MS-A vs MS-B	12.623	4.074	<b>0.014*</b>	37.333	7.563	<b>&lt;0.001***</b>	4.281	6.790	<b>&lt;0.001***</b>	9.167	5.713	<b>0.002**</b>	2.333	0.924	0.526
OS-A vs OS-B	0.275	0.089	0.951	6.000	1.215	0.407	0.895	1.420	0.335	3.833	2.389	0.117	1.000	0.396	0.784
IS-A vs MS-A	3.966	1.280	0.383	19.667	3.984	<b>0.016*</b>	2.423	3.843	<b>0.019*</b>	2.333	1.454	0.324	9.333	3.698	0.55
MS-A vs OS-A	13.181	4.254	<b>0.027*</b>	35.333	7.157	<b>&lt;0.001***</b>	3.958	6.278	<b>0.002**</b>	4.833	1.3013	0.125	6.000	2.377	0.119
IS-A vs OS-A	9.216	2.975	0.057	15.667	3.174	<b>0.045*</b>	1.535	2.435	0.111	2.500	1.558	0.292	3.333	1.321	0.369
IS-B vs MS-B	8.861	2.860	0.066	13.333	2.701	0.178	2.483	3.939	<b>0.041*</b>	4.833	3.013	0.055	8.667	3.434	0.076
MS-B vs OS-B	0.834	0.269	0.852	4.000	0.810	0.577	0.572	0.908	0.533	0.500	0.312	0.829	6.000	2.377	0.119
IS-B vs OS-B	9.695	3.129	0.109	9.333	1.891	0.206	1.911	3.031	0.053	5.333	3.324	0.087	2.667	1.057	0.470

*Patterns (N) of major macrobenthic Phyla*

During the period of high outflow numbers of Annelida ( $N: 558.33 \text{ ind.m}^{-2} \pm 105.65\text{SD}$ ) most of which were represented by Polychaeta ( $N: 556.67 \text{ ind.m}^{-2} \pm 102.75\text{SD}$ ), Crustacea ( $N: 380 \text{ ind.m}^{-2} \pm 83.22\text{SD}$ ) Mollusca ( $N: 91.67 \text{ ind.m}^{-2} \pm 83.22\text{SD}$ ) and other Phyla namely Chordata, Cnidaria and Nemerta (Oth- $N: 3.33 \text{ ind.m}^{-2} \pm 5.77\text{SD}$ ) increased from the IS to reach maximum values at the MS ( $N\text{-Ann: } 650 \text{ ind.m}^{-2} \pm 83.22\text{SD}$  of which Pol:  $646.67 \text{ ind.m}^{-2} \pm 81.45\text{SD}$ ; Cru:  $493.33 \text{ ind.m}^{-2} \pm 65.52\text{SD}$ ; Mol:  $183.33 \text{ ind.m}^{-2} \pm 20.21\text{SD}$ ; Oth:  $18.33 \text{ ind.m}^{-2} \pm 7.64\text{SD}$ ) (Fig 4.6). The outer shelf supported significantly fewer ( $p < 0.01$ ) annelids ( $N: 291.67 \text{ ind.m}^{-2} \pm 12.58\text{SD}$ ; Pol:  $290.00 \text{ ind.m}^{-2} \pm 13.23\text{SD}$ ) and crustaceans ( $N: 70 \text{ ind.m}^{-2} \pm 22.91\text{SD}$ ) during cruise A when compared with shallower shelf positions (Fig 4.6). During cruise B when freshwater outflow was low, significantly ( $p < 0.01$ ) fewer annelids ( $N: 340 \text{ ind.m}^{-2} \pm 112.58\text{SD}$ ; Pol- $N: 340.00 \text{ ind.m}^{-2} \pm 112.58\text{SD}$ ), crustaceans ( $N: 200.00 \text{ ind.m}^{-2} \pm 56.35\text{SD}$ ) and molluscs ( $N: 53.33 \text{ ind.m}^{-2} \pm 15.28\text{SD}$ ) were sampled from the MS (Fig. 4.6).

The abundance of Annelida supported at the shallow IS was significantly lower during cruise B ( $N: 283.33 \text{ ind.m}^{-2} \pm 92.51\text{SD}$ ; Pol:  $238.33 \text{ ind.m}^{-2} \pm 92.51\text{SD}$ ) when compared with cruise A, while numbers of Crustacea increased significantly at this shelf position during the period of reduced outflow ( $N: 846.67 \text{ ind.m}^{-2} \pm 598.78\text{SD}$ ). Molluscs ( $N: 90 \text{ ind.m}^{-2} \pm 52.92\text{SD}$ ) and other Phyla (Chordata, Cnidaria and Nemertea) ( $N: 40 \text{ ind.m}^{-2} \pm 52.20\text{SD}$ ) were most abundant at the OS during cruise B while numbers of Annelida and Crustacea remained approximately the same ( $p > 0.05$ ) at this shelf position when comparing cruises A and B (Fig 4.6). Numbers of echinoderms increased with depth to reach maximum values at the muddy OS during both sampling cruises A and B. During cruise B when riverine outflow was low there were fewer echinoderms sampled at IS ( $N: 6.67 \text{ ind.m}^{-2} \pm 2.89\text{SD}$ ) and MS ( $N: 11.67 \text{ ind.m}^{-2} \pm 10.41\text{SD}$ ) positions, while the abundance of this Phylum at the OS remained stable ( $N\text{-Cruise A: } 53.33 \text{ ind.m}^{-2} \pm 10.41\text{SD}$ ; Cruise B:  $58.33 \text{ ind.m}^{-2} \pm 17.56\text{SD}$ ) between sampling cruises (Fig 4.6). Significantly ( $p < 0.05$ ) fewer individuals belonging to the Phylum Sipuncula were recorded at the MS during both cruises A ( $N: 23.33 \text{ ind.m}^{-2} \pm 15.28\text{SD}$ ) and B ( $N: 11.67 \text{ ind.m}^{-2} \pm 2.89\text{SD}$ ) when compared with shelf positions both inshore and offshore of this shelf position. The abundance of Sipuncula was approximately the same for the IS ( $N: 71.67 \text{ ind.m}^{-2} \pm 15.28\text{SD}$ ) and OS ( $N: 66.67 \text{ ind.m}^{-2} \pm 27.54\text{SD}$ ) positions sampled during cruise A and despite lower values being recorded, the abundance of this group did not change significantly ( $p > 0.05$ ) during cruise B (IS- $N: 61.67 \text{ ind.m}^{-2} \pm 18.93\text{SD}$ ; OS- $N: 65 \text{ ind.m}^{-2} \pm 13.23\text{SD}$ ) (Fig 4.6).

THE INFLUENCE OF THE THUKELA RIVER ON MACROBENTHIC TAXA AND FEEDING MODES

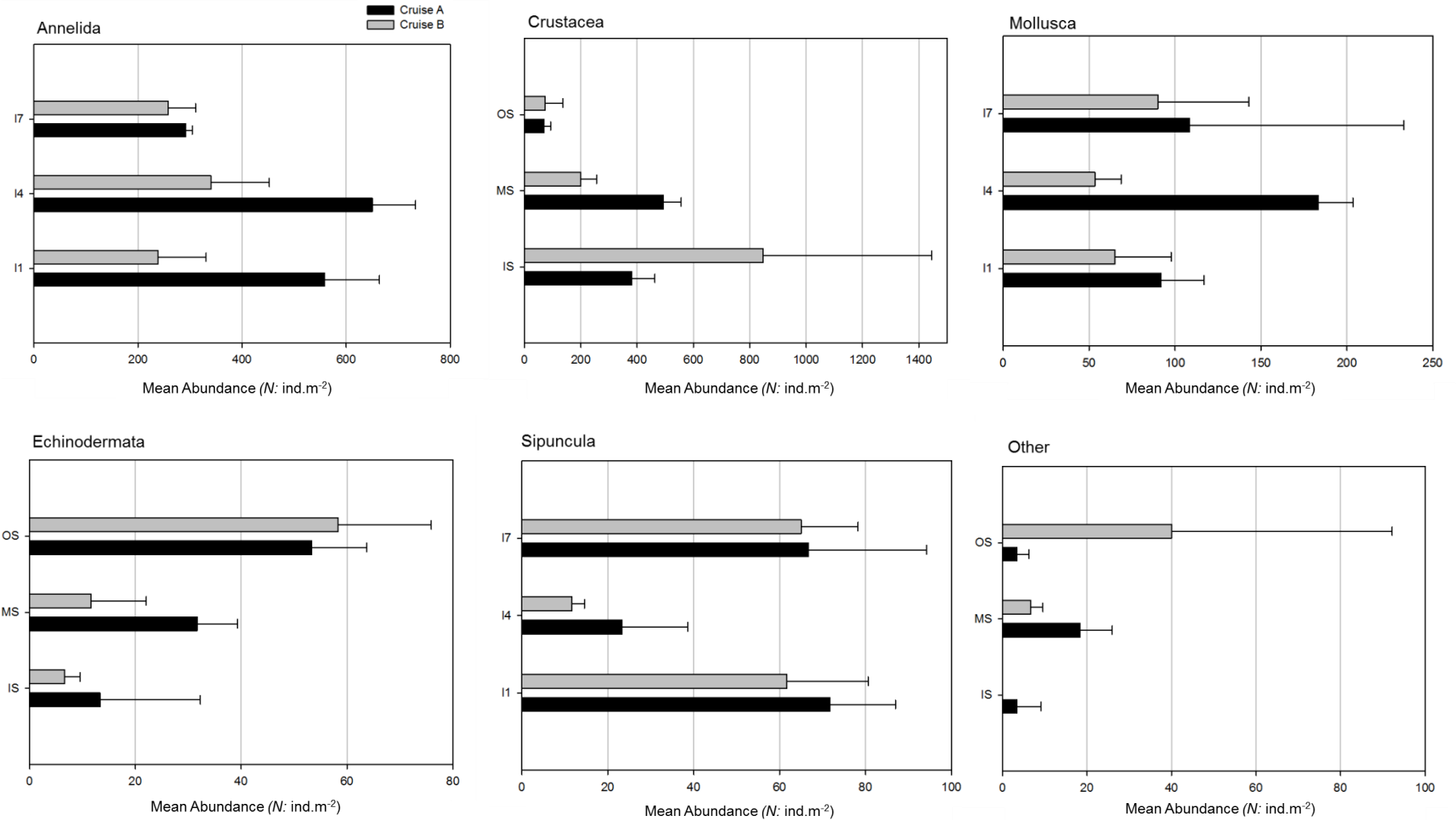


Figure 4.6. Abundance (N) of major macrobenthic Phyla sampled at three shelf position stations (mean ± SD) during cruise A and B. IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf.

### **Community patterns based on lowest identifiable taxa**

Cluster analysis based on Bray-Curtis (B-C) similarity identified five sample groups at a similarity percentage of 40% reflecting depth and cruise (outflow regime) related differences in macrobenthic communities (Fig. 4.7). Group I comprised the deepest, OS samples (109-112 m) collected during cruises A and B with sediment characterised by high mud content. Group II included the shallow, fine sand IS samples collected during the low outflow period (20 m) while samples collected from this shelf position during cruise A (26 m) formed Group III. Groups IV and V consisted of MS samples, characterised by medium sand collected, from intermediate depths during cruises A (56 m) and B (52 m), respectively (Fig. 4.7). Inner and mid-shelf samples therefore clustered together on the basis of shelf position and cruise, whereas OS samples were separated by shelf position only with no distinction between communities collected during cruises A or B.

Two-way Analysis of Similarity (ANOSIM) testing using the factors shelf position ( $R=1$ ,  $p<0.001$ ) and cruise ( $R=0.741$ ,  $p=0.001$ ) showed that both factors were globally significant. A series of Similarity Profile (SIMPROF) permutation tests confirmed the statistical significance ( $p<0.05$ ) of sample Groups I-III, V obtained from cluster analysis (Clarke *et al.* 2008). The main taxa responsible for characterising and discriminating between sample Groups I-V obtained from cluster analysis were determined by means of the SIMPER procedure (Table 4.4; 4.5). Group I, comprising the largest number of samples was dominated by the facultative detritivore (FD), *Tellinidae* sp.5 found exclusively in this group and contributing most to the average similarity within this outer shelf assemblage (Table 4.4). An additional seven taxa contributed more than 2% to within group similarity, five of which were identified as being characteristic of Group I. These typifying taxa included the FD, *Golfingiidae* sp. 1, the spionid polychaetes *Prionospio dubia* and *Spiophanes* cf. *soederstromi*, the subsurface deposit feeding capitellid, *Rashgua* sp. 1 and the suspension feeding *Spiochatopterus* sp. 12 (Table 4.4).

Cluster analysis elucidated a clear difference in assemblages supported at IS and MS stations sampled during cruises A and B (Fig. 4.7). During cruise A the IS (Group III) was dominated and typified by the tanaid, *Leptochela* sp.1 and the polychaetes *Owenia fusiformis* and *Spiophanes* sp.1, all of which are facultative detritivores. An additional three taxa contributed >2% to within group similarity during the period of high riverine outflow, with the surface deposit feeder, *Aspidosiphon* sp.1, and the carnivorous gastropod *Bullia similis* also being identified as

characteristic taxa of Group III (Table 4.4). During cruise B, corresponding with a period of reduced freshwater outflow from the Thukela River, this shallow water group (Group II) was dominated by a dense population of the carnivorous hermit crab, *Paguristes* sp. I, found almost exclusively inhabiting empty *Bullia similis* shells (personal observation). Three taxa were consistently sampled from the inner shelf, namely *Owenia fusiformis*, the sipunculan, *Aspidosiphon* sp. I and the fossorial amphipod, cf. *Basuto* sp. I. The polychaete and sipunculan were found in greater abundance during cruise A (Group III), while numbers of the amphipod remained approximately the same, although this taxon contributed more to within group similarity during cruise B (Group II). Despite being rarely sampled, *Thalassinidea* sp. I was identified as the most discriminating taxon for this sample group (Table 4.4)

The facultative omnivore, *Epidiopatra papillosa* dominated and typified MS assemblages during both cruises A and B with the highest abundance of this taxon recorded during the period of high outflow. The only other taxon common to MS assemblages was the amphipod *Ampelisca* sp. 9, a FD found in greater numbers at this shelf position during the period of high freshwater outflow from the Thukela River (Group IV) (Table 4.4). In addition to *Epidiopatra papillosa*, five taxa contributed >2% to similarity within Group IV with the bivalves, *Nucula* sp. I and *Nuculana* sp. I typifying this sample group during the high outflow period. During cruise B the MS was characterised by the amphipods cf. *Basuto* sp. 2, *Ampelisca* sp. 9 and the polychaetes, *Epidiopatra papillosa* and *Capitellidae* sp. 10 who along with two additional taxa contributed more than 2% to the similarity within Group V (Table 4.4).

Samples collected from the IS position during cruise A (Group III) differed from those at the outer shelf (Group I) due to the exclusive occurrence of *Leptochela* sp. I in shallow water sediments (Table 4.5). *Epidiopatra papillosa*, a taxon unique to the MS (Group IV) was responsible for the discrimination between the muddy, outer shelf assemblage and the community supported at mid-shelf depths during periods of high and low river outflow. During cruise B the IS assemblage (Group II) was differentiated from the OS (Group I) based mainly on the presence of *Paguristes* sp. I and cf. *Basuto* sp. I found exclusively in Group II (Table 4.5). When freshwater outflow from the Thukela River was high, inner and mid-shelf assemblages were distinguished based on the polychaete, *Epidiopatra papillosa* found to occur only at this station. The exclusive occurrence of *Paguristes* sp. I in Group II was the primary discriminating taxon between these Group II and Group IV during cruise B (Table 4.5). When comparing IS assemblages found during cruise A and B, the carnivore *Paguristes* sp. I present in high

abundance in Group II and the taniad, *Leptochela* sp.I, unique to Group III, were the primary discriminating taxa. SIMPER results showed that no taxa contributed >2% to the dissimilarity between Groups IV and V (Table 4.5).

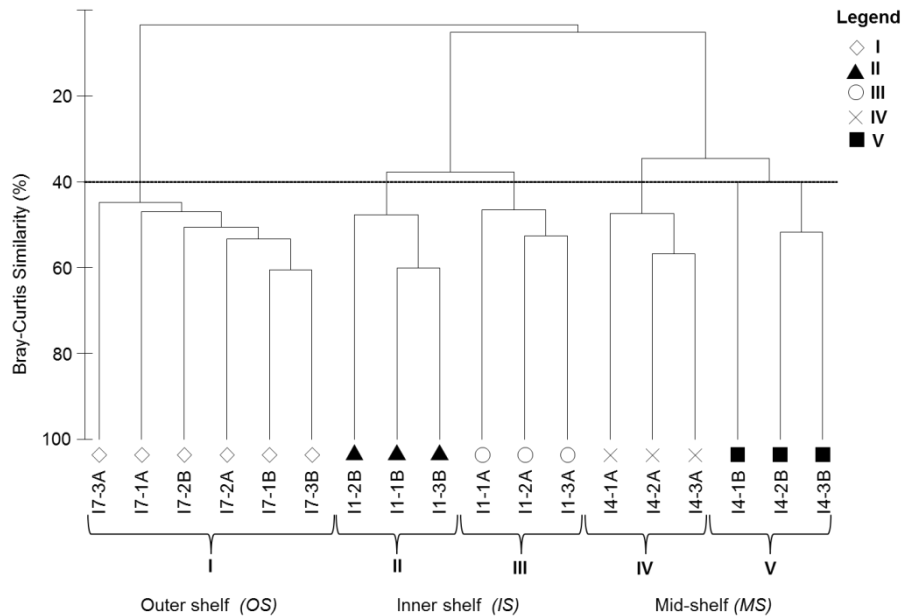


Figure 4.7. Dendrogram for hierarchical clustering (using group-average linkage) of 18 samples collected during cruise A and B, based on Bray-Curtis similarities calculated from square root transformed abundance data at the level of lowest identifiable taxon. The five groups separated at a 40% similarity threshold are indicated.

#### 4.3.3 Macrobenthic community analysis – feeding modes.

##### *The effect of cruise (variable periods of outflow)*

*Abundance (N) and number of taxa (S) attributed to feeding modes*

Facultative detritivores (FD) ( $N: 3800 \text{ ind.m}^{-2}$ ) dominated the feeding mode of macrobenthos collected along the central shelf during cruise A, accounting for approximately half ( $N: 41\%$ ) the total abundance (Fig 4.8). Facultative omnivores (FO) ( $N: 1175 \text{ ind. m}^{-2}$ ), surface deposit feeders (SDF) ( $N: 1170 \text{ ind. m}^{-2}$ ) and carnivores ( $N: 1140 \text{ ind. m}^{-2}$ ) all contributed a similar percentage ( $N: \sim 12\%$ ) of total abundance recorded during the period of high freshwater outflow from the Thukela River (Fig 4.8). During cruise B carnivores were the most abundant ( $N: 2950 \text{ ind. m}^{-2}$ ) feeding mode sampled. Numbers of FD ( $N: 1850 \text{ ind. m}^{-2}$ ) were reduced by approximately half during cruise B, while the abundance of FO was reduced to a third of that recorded during the high outflow period (Fig 4.8). The percentage contribution of the remaining feeding modes to total abundance remained relatively constant between sampling cruises. Despite the reduced number of taxa recorded during cruise B (Section 4.3.2.1), the

percentage contribution of each feeding mode to total numbers remained stable between cruises A and B (Fig 4.8). Most taxa belonged to the feeding mode, FD (S-Cruise A: 119 taxa; S-Cruise B: 82 taxa), followed by carnivores (S-Cruise A: 68 taxa; S-Cruise B: 44 taxa) and deposit-feeding (SDF, SSDF) taxa (S-Cruise A: 72 taxa; S-Cruise B: 46 taxa) (Fig 4.8).

Table 4.4. Taxa identified by SIMPER analysis as contributing >2% to average similarity within sample Groups I-V. Grey shading indicates typifying taxa. **Amp=Amphipoda, Biv=Bivalvia, Cru=Crustacea, Gas=Gastropoda, Pol=Polychaeta, Sip=Sipuncula, C=Carnivore, SF=Suspension feeder, SDF=Surface deposit feeder, SSDF Subsurface deposit feeder, FC=Facultative carnivore, FD=Facultative detritivore, FO=Facultative omnivore.**

	Ave. Abundance	Ave. Similarity	( $\delta_i$ )/SD( $\delta_i$ )	Cumulative %
<b>Group I (Average similarity: 48.66%)</b>				
<i>Tellinidae</i> sp.5 ( <b>Biv</b> , FD)	6.41	2.82	2.81	5.81
<i>Golfingiidae</i> sp.2 ( <b>Sip</b> , FD)	5.86	2.8	1.3	11.58
<i>Spiochaetopterus</i> sp.12 ( <b>Pol</b> , SF)	4.58	2.67	3.86	17.07
<i>Golfingiidae</i> sp.1 ( <b>Sip</b> , FD)	4.06	2.56	7.13	22.33
<i>Rashgua</i> sp.1 ( <b>Pol</b> , SSDF)	4.61	2.53	4.31	27.54
<i>Prionospio dubia</i> ( <b>Pol</b> , FD)	4.47	2.43	4.43	32.55
<i>Spiophanes</i> cf. <i>soederstromi</i> ( <b>Pol</b> , FD)	4.61	2.36	3.08	37.4
<i>Tellina gilchristi</i> ( <b>Biv</b> , FD)	5.02	2.31	1.34	42.15
<b>Group II (Average similarity: 51.74%)</b>				
<i>Paguristes</i> sp.1 ( <b>Cru</b> , C)	24.34	10.56	1.33	20.41
cf. <i>Basuto</i> sp.1 ( <b>Amp</b> , FC)	6.92	4.04	6.86	28.21
<i>Sipunculidae</i> sp.2 ( <b>Sip</b> , SSDF)	5.95	3.13	6.66	34.26
<i>Owenia fusiformis</i> ( <b>Pol</b> , FD)	5.22	3.09	3.96	40.24
<i>Aphroditidae</i> sp.1 ( <b>Pol</b> , C)	4.55	2.68	2.73	45.42
<i>Laonice</i> sp.1 ( <b>Pol</b> , FD)	4.04	2.54	3.38	50.33
<i>Thalassinidea</i> sp.1 ( <b>Cru</b> , SSDF)	3.84	2.36	32.76	54.89
<i>Aspidosiphon</i> sp.1 ( <b>Sip</b> , SDF)	3.6	2.21	9.76	59.17
<b>Group III (Average similarity: 48.49%)</b>				
<i>Leptochela</i> sp.1 ( <b>Cru</b> , FD)	8.89	3.24	24.88	6.68
<i>Owenia fusiformis</i> ( <b>Pol</b> , FD)	7.95	3.2	11.79	13.27
<i>Spiophanes</i> sp.1 ( <b>Pol</b> , FD)	7.74	2.79	17.58	19.03
<i>Aspidosiphon</i> sp.1 ( <b>Sip</b> , SDF)	5.46	2.16	47.77	23.48
<i>Bullia similis</i> ( <b>Gas</b> , C)	5.57	2.07	5.62	27.75
cf. <i>Basuto</i> sp.1 ( <b>Amp</b> , FC)	6.81	2.03	1.6	31.94
<b>Group IV (Average similarity: 50.41%)</b>				
<i>Epidiopatira papillosa</i> ( <b>Pol</b> , FO)	13.35	4.36	25.83	8.64
<i>Nucula</i> sp.1 ( <b>Biv</b> , FD)	8.16	2.62	21.31	13.85
<i>Nuculana</i> sp.1 ( <b>Biv</b> , SDF)	8.59	2.56	9.66	18.93
<i>Hippomedon</i> sp.1 ( <b>Amp</b> , C)	8.53	2.22	4.52	23.35
<i>Ampelisca</i> sp.9 ( <b>Amp</b> , FD)	6.76	2.01	6.19	27.33
<i>Urothoe</i> sp.1 ( <b>Amp</b> , FD)	7.16	2.01	6.19	31.32
<b>Group V (Average similarity: 43.92%)</b>				
<i>Epidiopatira papillosa</i> ( <b>Pol</b> , FO)	7.87	4.48	7.37	10.21
cf. <i>Basuto</i> sp.2 ( <b>Amp</b> , FC)	5.88	3.51	5.85	18.2
<i>Poecilochaetus serpens</i> ( <b>Pol</b> , SDF)	8.25	3.17	1.76	25.41
<i>Byblis giamardii</i> ( <b>Amp</b> , FD)	5.4	2.66	2.9	31.46
<i>Ampelisca</i> sp.9 ( <b>Amp</b> , FD)	3.84	2.19	6.5	36.45
<i>Capitellidae</i> sp.10 ( <b>Amp</b> , SSDF)	4.08	2.04	11.99	41.08

Table 4.5. Taxa identified by SIMPER analysis as contributing >2% to average dissimilarity within sample Groups I-V. Bold values indicate discriminating taxa. (Cumulative percentage), **Amp=Amphipoda**, **Biv=Bivalvia**, **Cru=Crustacea**, **Pol=Polychaeta**. **C=Carnivore**, **SDF=Surface deposit feeder**, **FD=Facultative detritivore**, **FO=Facultative omnivore**.

Taxon	I vs II 97.30%	I vs III 97.30%	I vs IV 95.22%	I vs V 96.67%	II vs III 62.27%	II vs IV 94.72%	II vs V 95.48%	III vs IV 92.99%	III vs V 96.36%
<i>Paguristes</i> sp.1 (Cru, C)	7.97 (8.19)	-	-	2.02 (4.75)	5.16 (8.29)	5.36 (5.66)	7.88 (8.25)	-	-
<i>cf. Basuto</i> sp.1 (Amp, FC)	<b>2.34</b> (10.6)	-	-	-	-	-	2.31 (16.02)	-	-
<i>Tellinidae</i> sp.5 (Biv, FD)	2.1 (12.76)	-	-	-	-	-	-	-	-
<i>Leptochela</i> sp.1 (Cru, FD)	-	2.27 (2.33)	-	-	<b>2.11</b> (11.68)	-	-	-	2.25 (2.33)
<i>Epidiopatra</i> <i>papillosa</i> (Pol, FO)	-	-	<b>2.96</b> (3.11)	2.58 (2.67)	-	<b>3.02</b> (8.85)	<b>2.66</b> (11.03)	<b>2.48</b> (2.67)	2 (6.51)
<i>Poecilochaetus</i> <i>serpens</i> (Pol, SDF)	-	-	-	-	-	-	2.45 (13.6)	-	-
<i>Owenia fusiformis</i> (Pol, FD)	-	-	-	-	-	-	-	-	<b>2.02</b> (4.43)

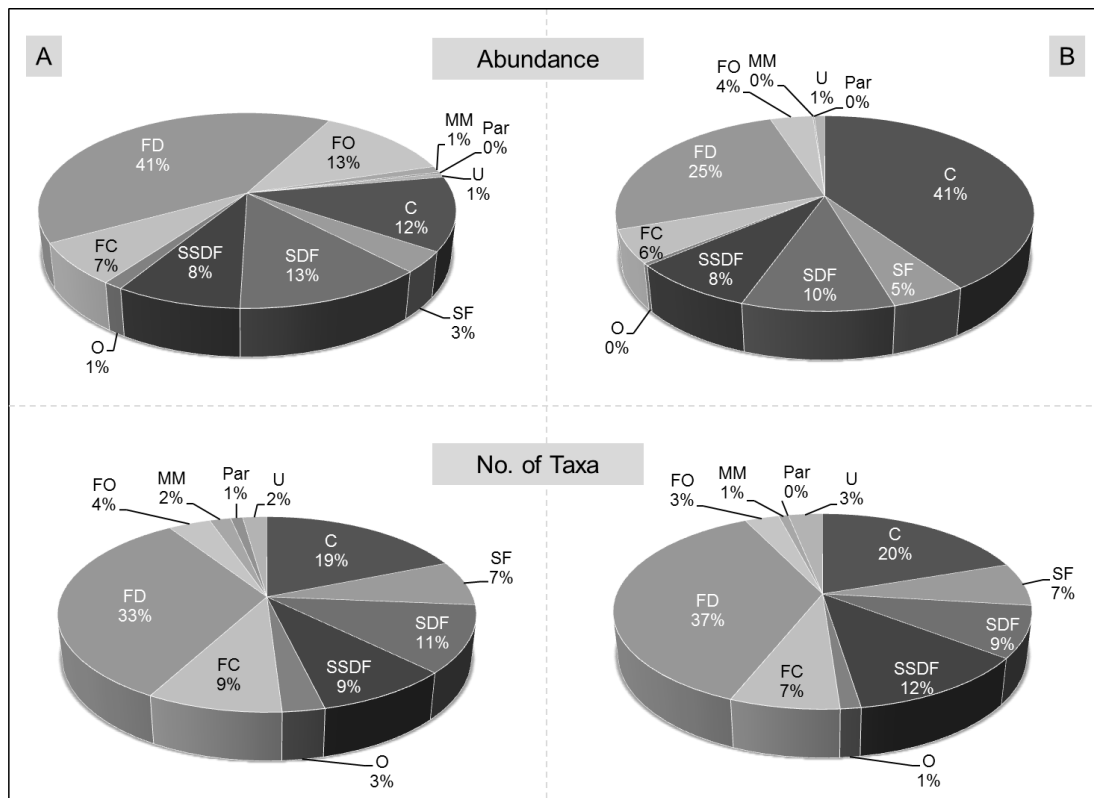


Figure 4.8. Contribution (%) of feeding modes to total abundance ( $N$ : ind.m<sup>-2</sup>) and no. of taxa ( $S$ ) sampled across the central Bight during cruises A and B. **C=Carnivore**, **SF=Suspension feeder**, **SDF=Surface deposit feeder**, **SSDF=Sub-surface deposit feeder**, **O=Omnivore**, **FC=Facultative carnivore**, **FD=Facultative detritivore**, **FO=Facultative omnivore**, **MM=Multi-Modal**, **Par=Parasite**, **U=Unknown**.

***The influence of shelf position during high and low outflow periods****Abundance (N) and number of taxa (S) attributed to feeding modes*

During cruise A the IS, MS and OS were dominated by facultative detritivores in terms of numbers of individuals (IS-N: 44.41%; MS-N: 31.43%; OS-N: 55.62%) and taxa (IS-S: 33.66%; MS-S: 33.33%; OS-S: 40.65%) (Fig. 4.9). Carnivores were the second most important feeding mode contributing to abundance and numbers of taxa sampled from the IS (N: 12.37%; S: 17.82%) and OS (N: 14.61%; S: 28.87%) during cruise A while at the MS, facultative omnivores (N: 19.52%) made the second highest contribution to abundance (Fig 4.9). Facultative carnivores and strictly omnivorous fauna were similarly abundant and taxon rich at the IS (FC-N: 8.94%; S: 10.89%; O-N: 1.64%; S: 3.47%) and MS (FC-N: 7.14%; S: 8.81%; O-N: 1.43%; S: 3.07%) with lower values of both metrics recorded at the OS (FC-N: 2.81%; S: 3.23%; O-N: 0.28%; S: 0.65%). The abundance and number of suspension feeding taxa increased with distance offshore, with the highest values recorded for OS (N: 5.90%; S: 7.74%) samples (Fig 4.9). Surface deposit feeders were most abundant and taxon rich at the MS (N: 17.02%; S: 16.48%), while the most SSDF individuals and taxa were recorded at the deepest shelf position (OS) (N: 11.52%; S: 10.97%) (Fig 4.9). Multi-modal feeders, represented by ostracods were most abundant and taxon rich at the shallowest IS (N: 1.94%; S: 3.47%), while parasites, represented by the isopod family Gnathidae, reached highest numbers of individuals and taxa at the MS (N: 0.48%; S: 1.53%). Both these feeding modes were absent from OS samples (Fig 4.9).

During cruise B, when outflow from the Thukela was low, most taxa sampled from all shelf positions were classified as facultative detritivores. This feeding mode dominated in terms of abundance (N:  $326.67 \text{ ind.m}^{-2} \pm 55.84\text{SD}$ ) and taxon richness (S:  $21.33 \text{ taxa} \pm 2.52\text{SD}$ ) at the OS, with C (N:  $85.00 \text{ ind.m}^{-2} \pm 14.53\text{SD}$ ; S:  $7.33 \text{ taxa} \pm 3.21\text{SD}$ ) also being well represented. Facultative detritivores (N:  $153.33 \text{ ind.m}^{-2} \pm 24.60\text{SD}$ ) and SDF (N:  $126.67 \text{ ind.m}^{-2} \pm 20.32\text{SD}$ ) were similarly abundant at the mid-shelf, with the majority of individuals sampled here belonging to these two feeding modes. The inner shelf position was characterised by a proliferation of carnivorous (N:  $810.00 \text{ ind.m}^{-2} \pm 66.48\text{SD}$ ) macrobenthos during the low outflow period, with FD (N:  $136.37 \text{ ind.m}^{-2} \pm 11.22\text{SD}$ ) making the second highest contribution to abundance recorded during cruise B (Fig. 4.9).

The abundance of SF more than doubled at the OS during cruise B (N-Cruise A:  $35 \text{ ind.m}^{-2} \pm 13.23\text{SD}$ ; Cruise B:  $73.33 \text{ ind.m}^{-2} \pm 12.54\text{SD}$ ) while numbers of deposit feeders were reduced by approximately a third (N-Cruise A-N:  $55.83 \text{ ind.m}^{-2} \pm 18.82\text{SD}$ ; Cruise B:  $35 \text{ ind.m}^{-2} \pm$

19.49SD) (Fig 4.14). Numbers of taxa followed the same trends as abundance with values increasing for SF during cruise B ( $S: 9.49\%$ ) and decreasing for SDF and SSDF ( $S$ -Cruise A:  $5.17 \text{ taxa} \pm 1.17\text{SD}$ ; Cruise B:  $3.67 \text{ taxa} \pm 1.03\text{SD}$ ). There was an increase in abundance and decrease in numbers of carnivorous taxa during cruise B, while the numbers of individuals and taxa of all other feeding modes were reduced (Fig 4.9).

During cruise A feeding mode diversity indices increased from the IS (Cruise A:  $H'=1.72 \pm 0.08\text{SD}$ ;  $d=1.28 \pm 0.01\text{SD}$ ;  $J'=0.75 \pm 0.04\text{SD}$ ) to reach maximum values in MS samples (Cruise A:  $H'=1.86 \pm 0.07\text{SD}$ ;  $d=1.29 \pm 0.07\text{SD}$ ;  $J'=0.80 \pm 0.04\text{SD}$ ) (Fig. 4.10). Minimum values of feeding mode diversity indices were recorded at the OS (Cruise A:  $H'=1.39 \pm 0.06\text{SD}$ ;  $d=0.99 \pm 0.05\text{SD}$ ;  $J'=0.7 \pm 0.05\text{SD}$ ) during cruise A (Fig. 4.10). There were no statistically significant differences ( $p>0.05$ ) between equitability values recorded for IS, MS and OS positions sampled during cruise A, but both measures of Richness ( $d$ ) ( $p=0.012$ ) and Diversity ( $H'$ ) ( $p=0.004$ ) calculated for feeding mode abundance were significantly ( $p<0.05$ ) lower for OS samples when compared with the mid-shelf (Table 4.6). Significant differences were also detected between the inner and outer shelf ( $p=0.016$ ) positions sampled during the high outflow period (Table 4.6).

During the low outflow period feeding mode diversity indices were reduced at the MS with significantly lower ( $p=0.02$ ) values of  $d$  calculated for this shelf position (Fig. 4.10, Table 4.6). The same trend of peak feeding mode Diversity ( $H'$ ), Richness ( $d$ ) and Evenness ( $J'$ ) values at the MS was observed during cruise B ( $H'=1.84 \pm 0.08\text{SD}$ ;  $d=1.04 \pm 0.15\text{SD}$ ;  $J'=0.91 \pm 0.04\text{SD}$ ). Diversity and Evenness indices of IS and OS feeding mode communities were significantly lower ( $p<0.05$ ) than those obtained for the MS during cruise B (Fig. 4.10, Table 4.6). Lowest values of all feeding mode diversity indices were recorded for the OS ( $H'=1.33 \pm 0.11\text{SD}$ ;  $d=1.00 \pm 0.10\text{SD}$ ;  $J'=0.67 \pm 0.06\text{SD}$ ) position during the period of reduced freshwater outflow, with values remaining stable ( $p>0.05$ ) between sampling cruises. Shallow water feeding mode communities had significantly lower values of Richness ( $p=0.004$ ) and Diversity ( $p=0.01$ ) during cruise B when compared with cruise A (Fig. 4.10, Table 4.6).

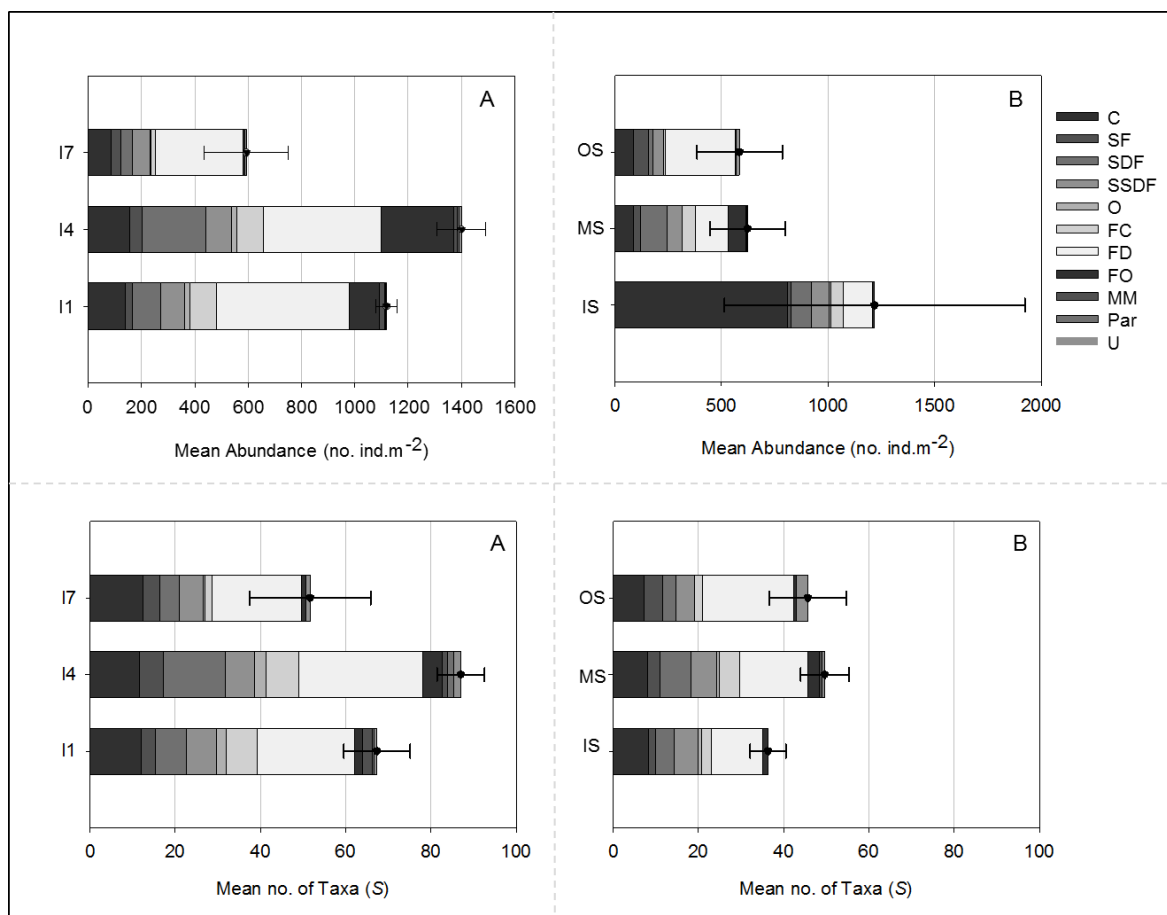


Figure 4.9. Contribution (%) of feeding modes to total abundance ( $N$ : ind.m<sup>-2</sup>  $\pm$  SD) and mean no. of taxa ( $S \pm$  SD) for inner (I1), mid (I4) and outer (I7) shelf stations sampled during cruises A and B. C=Carnivore, SF=Suspension feeder, SDF=Surface deposit feeder, SSDF=Sub-surface deposit feeder, O=Omnivore, FC=Facultative carnivore, FD=Facultative detritivore, FO=Facultative omnivore, MM=Multi-Modal, Par=Parasite, U=Unknown.

### Community patterns based on feeding mode

Cluster analysis using feeding mode abundance data identified three sample groupings at a 75% Bray-Curtis similarity that reflected cruise and shelf position related differences (Fig. 4.11). Group I comprised inner shelf and mid-shelf samples collected during the period of high freshwater outflow from the Thukela River. Shallow water samples collected from the IS and MS during cruise B formed Group II. Samples from the deepest, muddy outer shelf collected during cruises A and B comprised Group III (Fig. 4.11). Inner and mid-shelf samples therefore clustered together on the basis of cruise, while OS samples clustered together on the basis of shelf position without any distinction between feeding mode communities collected in cruises A and B. Two-way Analysis of Similarity (ANOSIM) permutation testing was employed to ascertain whether the feeding mode compositions of macrobenthic assemblages differed

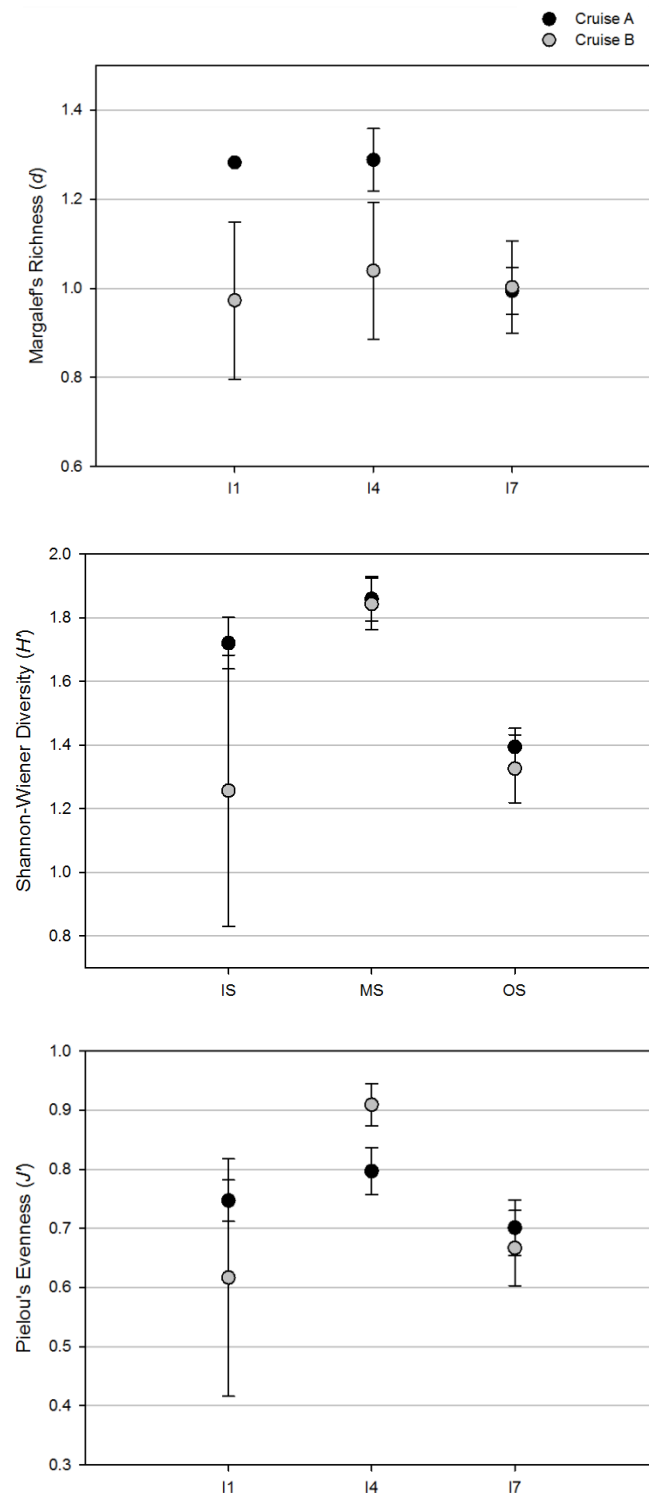


Figure 4.10. Indices of functional Richness ( $d$ ), Diversity ( $H'$ ) and Evenness ( $J'$ ) calculated for feeding mode abundance data from shelf position stations sampled during cruises A and B.

significantly among shelf positions and sampling cruises. Results showed that overall, the feeding mode compositions differed significantly among shelf positions and cruises. The global  $R$ -statistic was greater for cruise ( $R=0.728$ ) than for shelf position ( $R=0.679$ ). Similarity profile (SIMPROF) analysis confirmed the statistical significance of Groups I-III.

Results from SIMPER analysis showed that facultative detritivores and carnivores were the feeding modes contributing most to the similarity within sample groups, with the highest abundances of both these feeding modes occurring in Group I (Table 4.7). An additional five feeding modes contributed more than 2% to similarity within Group I, of which facultative omnivores were unique to this sample grouping. Surface and subsurface deposit feeders contributed to the similarity within Groups II and III, with both these feeding modes having a higher abundance in the muddy outer shelf sample group (Group II) (Table 4.7). Suspension feeders and facultative carnivores were the other feeding modes contributing >2% to similarity within Group II and III, respectively. SIMPER analysis indicated that the feeding mode responsible for most of the difference between the outer shelf sample group (Group III) and the shallow water inner (Group I) and mid-shelf samples (Group II) collected during cruises A and B was facultative detritivores which were least abundant in Group III and accounted for approximately a third of the average B-C dissimilarity (Table 4.7). Differences in feeding mode composition of macrobenthic assemblages in Group I and II were mainly due to SDF and FD, both of which were more numerous in inner and mid-shelf samples collected during the period of high outflow from the Thukela River (Table 4.7).

Table 4.6. Two way ANOVA and post-hoc Student-Newman-Kuels (SNK) testing based on univariate measures of feeding mode abundance data collected during cruises A and B. IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf, *F*=critical value of ANOVA, *q*=critical value of SNK test, *df*=degrees of freedom, *p*=level of significance (*p*=0.05). Values in bold are significant \**p*<0.05, \*\**p*<0.01, \*\*\**p*<0.001.

Margalef's Richness ( <i>d</i> )				Shannon-Wiener Diversity ( <i>H'</i> )			Pielou's Evenness ( <i>J'</i> )		
<i>Main factors</i>									
Anova	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
Shelf position (SP)	2	3.155	0.079	2	20.741	<0.001***	2	11.293	0.002**
Cruise (Cr)	1	12.108	0.005**	1	5.245	0.041*	1	0.111	0.745
SP x Cr	2	3.586	0.060	2	2.007	0.177	2	2.031	0.174
<i>Pair-wise Comparisons</i>									
SNK Test	Difference of ranks	<i>q</i>	<i>p</i>	Difference of ranks	<i>q</i>	<i>p</i>	Difference of ranks	<i>q</i>	<i>p</i>
IS vs MS	0.333	0.227	0.875	7.667	6.758	<0.001***	7.333	5.081	0.004**
MS vs OS	4.667	3.184	0.102	9.833	8.668	<0.001***	9.167	6.351	0.002**
IS vs OS	4.333	2.975	0.059	2.167	1.910	0.202	1.833	1.270	0.387
A vs B	5.889	4.921	0.005**	3.000	3.239	0.041*	0.556	1.960	0.745
IS-A vs IS-B	10.333	4.985	0.004**	6.667	4.155	0.013*	4.000	1.960	0.191
MS-A vs MS-B	7.667	3.699	0.023*	0.667	0.416	0.774	4.000	1.960	0.191
OS-A vs OS-B	0.333	0.161	0.911	1.667	1.039	0.477	1.667	0.816	0.575
IS-A vs MS-A	1.000	0.482	0.739	4.667	2.909	0.62	3.333	1.633	0.271
MS-A vs OS-A	8.667	4.181	0.012*	9.333	5.187	0.004**	6.333	3.103	0.113
IS-A vs OS-A	9.667	4.664	0.016*	4.667	2.909	0.62	3.000	1.470	0.319
IS-B vs MS-B	1.667	0.804	0.839	10.667	6.648	0.002**	11.333	5.552	0.002**
MS-B vs OS-B	0.667	0.322	0.824	10.333	6.441	<0.001***	12.000	5.879	0.004**
IS-B vs OS-B	1.000	0.482	0.739	0.333	0.208	0.886	0.667	0.327	0.821

#### 4.3.4 Macrobenthic-environment relationship

##### *The relationship between lowest identifiable taxa and environmental variables*

The first 2 db-RDA axes explained 70% of the variability in taxon abundance data and 99.60% of the relationship between taxon community metrics and the environmental variables (Fig. 4.12). The triplot shows that in terms of the explanatory variables the sediment grades gravel (gvl) and coarse sand (cos) are highly correlated while positive correlations between mud and organic content (TOC) as well as dissolved Oxygen and salinity were apparent. A negative correlation existed between DO and gravel or coarse sand while salinity was negatively correlated with organic content. In terms of the biotic data Shannon-Wiener Diversity (*H'*) was correlated with taxon richness (*S*) and both of these community metrics appear to be negatively correlated with abundance (*N*) (Fig. 4.12)

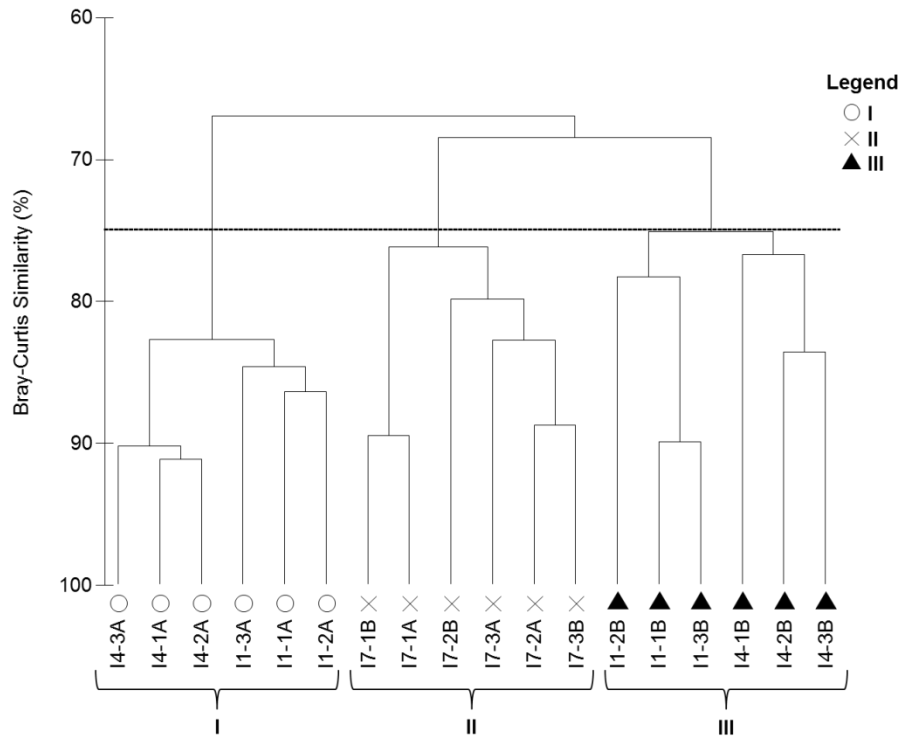


Figure 4.11. Dendrogram for hierarchical clustering (using group-average linkage) of 18 samples collected during cruise A and B, based on Bray-Curtis similarities calculated from square root transformed feeding mode abundance data. The three groups (I-III) separated at a 75% similarity threshold are indicated.

The separation in community structure between most OS samples and those from the shallower IS and MS was based on differences in the mud contents of the sediment, which increased towards the shelf edge (Fig. 4.12). Outer shelf samples were also associated with high Diversity ( $H'$ ) and there was no clear separation between communities collected during cruises A and B. Inner shelf samples from each sampling cruise are more homogenous than those from other shelf positions as they are orientated very close to each other in the triplot indicating similar environmental conditions and taxon composition. An evident separation between community structure at the IS during cruise A and B was observed, with samples from the latter, low outflow period, associated with high levels of dissolved Oxygen and salinity and the IS being characterised, during both sampling cruises, by a high abundance of macrobenthic fauna (Fig. 4.12). Comparable numbers of individuals were supported at the MS region during cruise A with community structure changing during cruise B along a gradient of decreasing abundance and increasing sediment organics and numbers of taxa. Mid-shelf samples were generally characterised by coarser sediment grades (Fig. 4.12).

Table 4.7. Feeding modes identified though SIMPER analysis as being responsible for the similarity within and dissimilarity between sample Groups I-III). Only those feeding modes with the five highest contributions are presented. *C=Carnivore, SF= Suspension feeder, SDF=Surface deposit feeder, SSDF Subsurface deposit feeder, FC=Facultative carnivore, FD=Facultative detritivore, FO=Facultative omnivore.*

Feeding Guild	Group I			Group II			Group III			Group I vs II				Group I vs III				Group II vs III			
	Ave. Sim = 84.79%			Ave. Sim = 79.53%			Ave. Sim = 77.30%			Ave. Dissim = 31.84%				Ave. Dissim = 34.28%				Ave. Dissim = 31.52%			
	Ave. Abun.	Ave. Sim.	Cum %	Ave. Abun.	Ave. Sim.	Cum %	Ave. Abun.	Ave. Sim.	Cum %	Ave. Abun.	Ave. Diss.	Ave. Cum %		Ave. Abun.	Ave. Diss.	Ave. Cum %		Ave. Abun.	Ave. Diss.	Ave. Cum %	
FD	96.69	34.63	40.84	74.91	42.74	53.74	41.99	24.43	31.61	96.69	74.91	5.58	37.89	96.69	41.99	13.17	38.41	74.91	41.99	10.71	33.97
C	36.99	12.54	55.63	27.32	12.99	70.07	35.86	16.66	53.16	36.99	27.32	2.96	75.4	36.99	35.86	3.76	62.96	27.32	35.86	5.7	52.05
SDF	38.58	10.69	68.24	10.51	5.07	95.61	20.75	10.63	83.34	38.58	10.51	6.48	20.35	38.58	20.75	4.66	52	10.51	20.75	3.52	63.22
SSDF	23.73	6.8	85.39	16.21	9.27	81.72	19.49	12.7	69.59	-	-	-	-	-	-	-	-	-	-	-	-
FC	23.82	7.75	77.37	-	-	-	12.91	6.9	92.27	23.82	4.53	4.63	52.44	23.82	12.91	2.74	80	4.53	12.91	2.84	72.24
SF	-	-	-	13.84	5.97	89.23	-	-	-	-	-	-	-	-	-	-	-	13.84	7.06	2.81	81.16
FO	-	-	-	-	-	-	-	-	-	20.7	1.86	4.35	66.1	20.7	8.36	3.1	72	-	-	-	-

### ***The relationship between feeding modes and environmental variables***

The first 2 db-RDA axes explained 80% of the variability in feeding mode abundance data and 76.39% of the relationship between the feeding modes and environmental variables (Fig. 4.13). Carnivores were ordered separately from all other feeding modes and distributed in high numbers in shallow, inner shelf samples collected during cruise B, where higher values of dissolved Oxygen and salinity were evident. During cruise A the inner shelf area supported feeding mode assemblages more similar to those found at the mid-shelf. This result was related to increasing gradients of gravel, coarse sand and skewness at these shelf positions (Fig. 4.13). The mid-shelf region was characterised by the presence of facultative carnivores and omnivores as well as SDF and there appears to be no distinction between feeding mode communities collected during cruise A and B. The presence of suspension feeders, subsurface deposit feeders and facultative detritivores characterised outer shelf samples from both sampling cruises where high levels of mud, sediment organic content, sorting and water column Silicate concentrations were evident (Fig. 4.13).

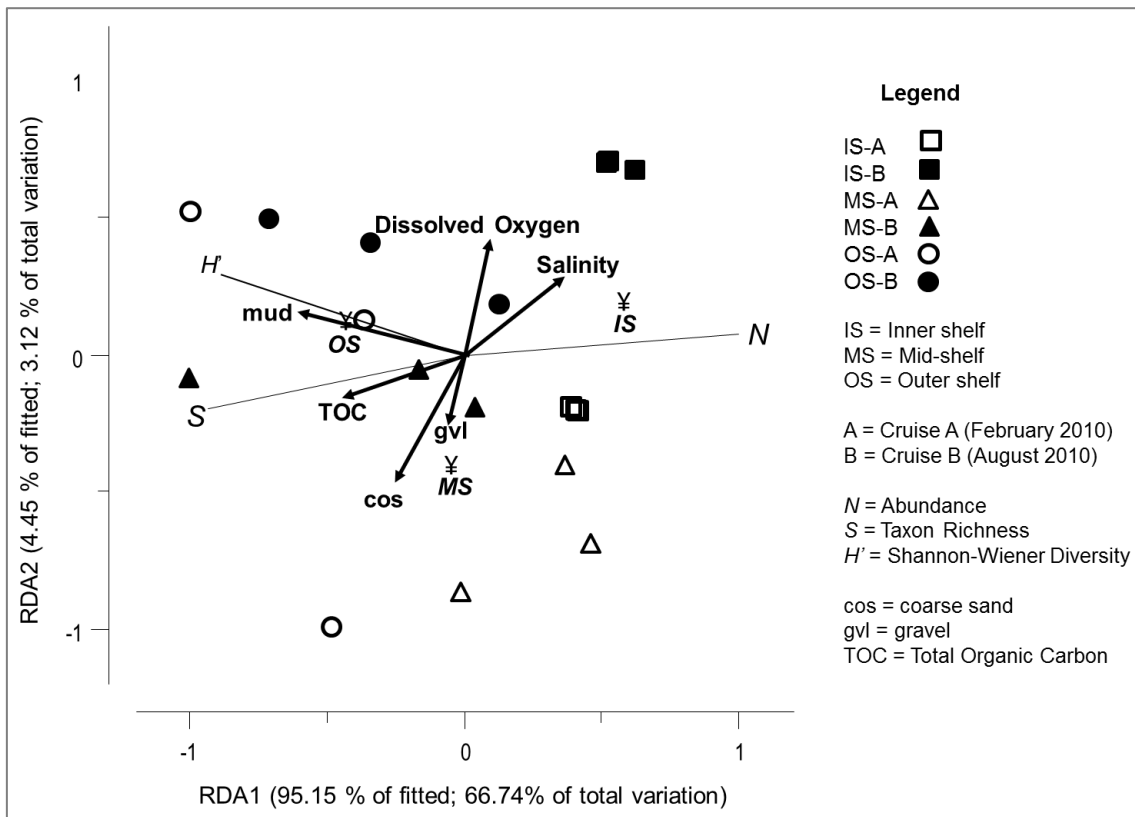


Figure 4.12. Distance-based redundancy analysis (db-RDA) triplot of taxon abundance data fitted to significant explanatory variables identified using forward selection and the sum of total canonical eigenvalues as selection criteria. ¥ indicates the nominal variable shelf position.

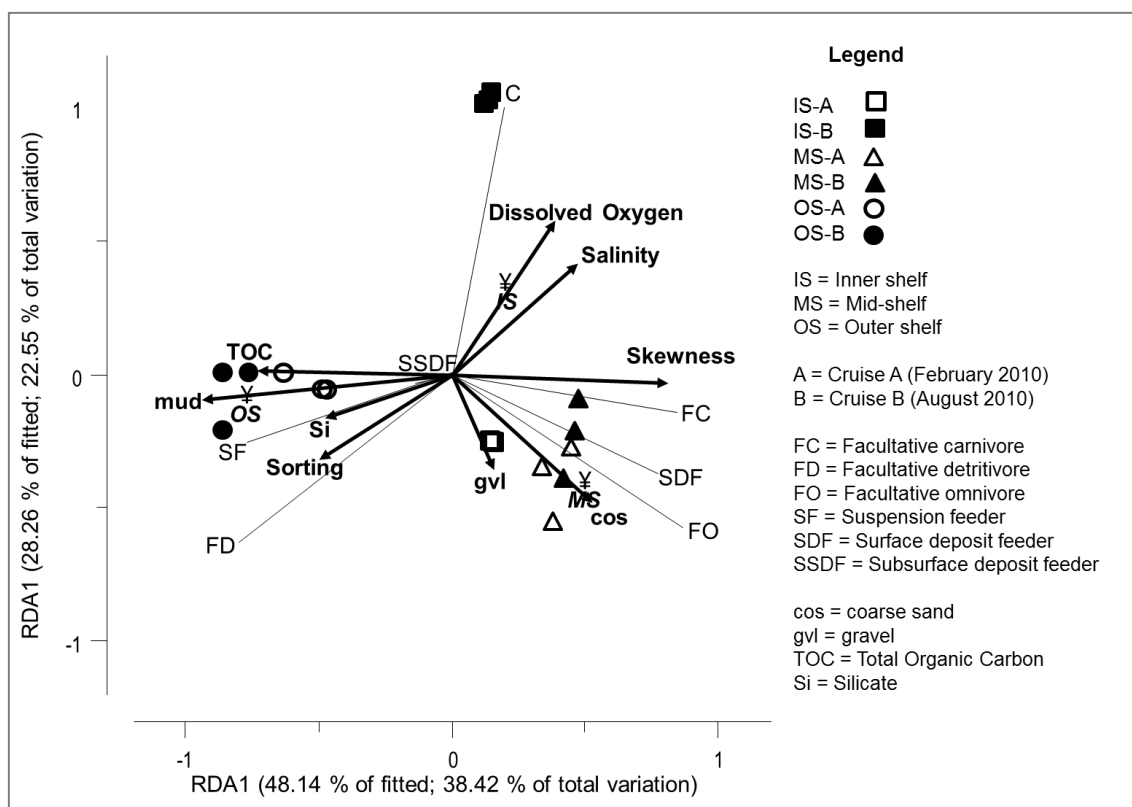


Figure 4.13. Distance-based redundancy analysis (db-RDA) triplot of feeding modes identified in SIMPER analysis, fitted to significant explanatory variables identified using forward selection and the sum of total canonical eigenvalues as selection criteria. ¥ indicates the nominal variable shelf position.

The present chapter undertook to investigate the Thukela feature area in detail in terms of the structure and function of macrobenthic communities sampled across the central shelf during a period of high and low outflow. Biotic patterns were related to measured environmental parameters in order to determine the influence of the Thukela River on macrobenthic structure and function, in terms of facultative feeding. There were no differences in the abiotic variables measured across the central shelf during high and low outflow periods although the influence of riverine outflow at the inner shelf station was reflected in physico-chemical variables measured. Facultative detritivores and carnivores were the dominant feeding modes sampled across the central shelf. Univariate results showed that while there were no differences in abundance, the number of macrobenthic taxa sampled was significantly lower during the low outflow period. The mid-shelf supported a diverse macrobenthic community characterised by the facultative omnivore, *Epidiopatra papillosa*. Results from db-RDA analysis showed the environmental variables coarse sand and gravel were primarily responsible for

driving biotic patterns at the mid-shelf. Numbers of taxa sampled at the inner shelf were significantly lower during cruise B, but abundance increased slightly due to a proliferation of the carnivorous hermit crab *Paguristes* sp.l. Community structure at the inner shelf was significantly related to dissolved Oxygen and Salinity confirming the influence of riverine outflow. The outer shelf was relatively stable, with no significant changes in univariate measures or macrobenthic community structure and function between high and low outflow periods. Macrobenthic community structure and function at the outer shelf were significantly related to high percentages of mud and sediment organic content. Multivariate results showed that when analysing patterns of macrobenthic taxon abundance across the central shelf, inner and mid shelf communities were significantly distinct from one another and in extension communities sampled from these shelf positions were significantly different during high and low outflow periods. When analysing patterns of feeding mode abundance, inner and mid shelf stations were not significantly different, but there were significant changes in the feeding mode composition of this community between high and low outflow periods.

#### **4.4 Discussion**

##### ***The influence of outflow from the Thukela River on environmental parameters***

Cruise A and B corresponded with different flow regimes of the Thukela River. The sampling cruise conducted in February 2010 (cruise A) corresponded with a period of peak precipitation and outflow from the Thukela River while the second sampling cruise (cruise B) was conducted in August 2010, during a time of low rainfall and reduced outflow. This variation in freshwater input was reflected in the salinity and dissolved Oxygen concentration of near bottom waters across the central Natal Bight which were lower during cruise A, when compared with the low outflow period. Nitrate and Chl-*a* concentration of central Bight waters were also higher during cruise A.

##### ***The influence of outflow from the Thukela River on the macrobenthic community***

###### ***Patterns across the central shelf***

In terms of the macrobenthic community, abundance and numbers of taxa were lower during cruise B across the central shelf. Total abundance of macrobenthos decreased by 22% between sampling periods whereas the total number of taxa decreased by a significant 38% (Fig. 4.6). Riverine outflow represents a natural disturbance agent for macrobenthic communities which may be positively or negatively impacted by low salinity, nutrient rich anoxic waters and by

smothering from allocthonous sediment (Kaiser *et al.* 2000, Simonini *et al.* 2004, Thrush *et al.* 2004, Wepener 2007, Jayaraj *et al.* 2008a, Jayaraj *et al.* 2008b).

Studies investigating the effects of experimental sediment deposition on macrobenthic communities which have found that community structure is altered and numbers of individuals and taxa are reduced by up to 50% following deposition of 3-7 mm of terrigenous sediment (Lohrer *et al.* 2004, Lohrer *et al.* 2006). In contrast with results from the present study an investigation of macrobenthic communities along a depth gradient on the Amazon shelf found higher numbers of individuals and taxa during the low outflow period of reduced physical stress (Alongi and Christoffersen 1992, Aller and Stupakoff 1996).

Polychaeta were the most abundant and taxon rich group sampled during the period of high riverine outflow, followed by Crustacea and Mollusca. The majority of polychaetes were facultative omnivores or facultative detritivores while approximately half of the crustaceans and molluscs were represented by the latter feeding mode. During cruise B when outflow from the Thukela River was reduced the dominance of abundance shifted to Crustacea, over 70% of which were carnivores. Polychaeta, comprising mostly facultative detritivores and surface deposit feeders and facultative detritivore Mollusca were the next most abundant groups during cruise B. Polychaeta and Crustacea are commonly reported to be the most abundant taxonomic groups in terms of numbers of individuals and taxa sampled from continental shelf environments (McClurg 1988, Aller and Stupakoff 1996, Karakassis and Eleftheriou 1997, Probert and Grove 1998, Ellingsen 2001, Ganesh and Raman 2007, Jayaraj *et al.* 2008a, Dolbeth *et al.* 2009, Harmelin-Vivien *et al.* 2009).

#### ***Patterns according to shelf position***

Macrobenthic communities reflect the spatial variability of the bottom environment generated by physical and biotic factors. The three shelf positions investigated in this study corresponded with varying sediment distribution regimes, with the inner shelf being characterised by fine sand, the mid-shelf by medium sand and the outer shelf by mud with high organic contents. Clear spatial differences in the macrobenthic community were thus linked with changes in depth and sediment related parameters. In a study investigating the by-catch of commercial prawn trawlers on the Thukela Bank, Fennessy (1994) found that flow regime and depth were the primary factors influencing the distribution of demersal ichthyofauna.

*The inner and mid-shelf*

When outflow from the Thukela River was high, the inner shelf was dominated by Polychaeta and Crustacea. Both these Phyla comprised mostly facultative detritivores of which members of the families Spionidae, the taniad *Leptochela* sp.1 and Ampeliscidae amphipods were the most abundant representatives. While numbers of individuals sampled at this shelf position remained high, despite variations in outflow, the Diversity was significantly lower during the period of reduced riverine discharge due to a proliferation of carnivorous hermit crabs (*Paguristes* sp.1) which comprised over half the abundance recorded for the inner shelf. Studies investigating macrobenthic communities of continental shelves under the influence of river systems have found changes in the abundance of crustaceans in shallow waters linked to riverine discharge and sediment organic matter content (Jayaraj *et al.* 2008a, Consentino and Giacobbe 2008, de Juan and Cortes 2011). There was a significant ( $p < 0.001$ ) increase in sediment organic content at the inner shelf during cruise B reflecting the deposition of terrigenous sediment by the Thukela River during the period of high outflow which settles on the seabed and may have provided favourable conditions for the establishment of the carnivorous hermit crab population.

The mid-shelf supported the most abundant and diverse community during the period of high freshwater outflow. Several studies have found a mid-shelf (~60 m) peak in macrobenthic abundance and Richness (Wheatcroft 2006, Jayaraj *et al.* 2008a). Coarse grades of sediment generally harbour rich and abundant communities due to the greater variety of microhabitats that these sediments provide (Sanders 1968, Snelgrove 1998, Simonini *et al.* 2004, Jayaraj *et al.* 2008a). Polychaeta and Crustacea dominated the MS community during cruise A. The former Phylum was comprised mainly of Onuphidae polychaetes which are facultative omnivores, whereas the latter Phylum was dominated by facultative detritivore amphipods belonging to the Families Ampeliscidae and Urothoidae. When outflow from the Thukela River was low, both abundance and numbers of taxa were dramatically reduced at the mid-shelf. Polychaetes comprised over half the numbers of individuals recorded at this shelf position during cruise B of which Spionidae polychaetes were the sole component. Crustacea were also abundant at the mid-shelf during cruise B with interface feeding Ampeliscidae and carnivorous Lysianassidae amphipods being the dominant representative of this Phylum. The db-RDA model produced from taxon data shows the separation between mid-shelf communities collected during cruise A and B based on gradients of decreasing abundance and increased dissolved Oxygen and salinity towards samples collected during the period of reduced outflow.

*Relation of inner and mid-shelf biotic patterns with environmental variables*

The change in dynamics of the macrobenthic community at the inner and mid-shelf position was most probably linked to the variation in outflow from the Thukela River. Freshwater outflow from rivers is known to increase the nutrient concentration of coastal waters near the mouth as well as at the boundaries of different water bodies some distance away, increasing primary productivity in coastal waters (Vorwerk 2006, Hermand *et al.* 2008, Vorwerk *et al.* 2008, Taljaard *et al.* 2009, de Juan and Cortes 2011). During periods of high outflow the Thukela River plume can extend for kilometers across the shelf resulting in the turbulent mixing of shallow waters and re-working of bottom sediments (Olivier 1998, Turpie 2004, Bosman *et al.* 2007).

The paleo-dune cordon characteristic of the mid-shelf in this study area appears to represent a front between the well mixed waters of the inner shelf and the stratified waters of the outer shelf (Lutjeharms *et al.* 2000a, Mann and Lazier 2006). Biological productivity is enhanced in frontal areas and this may provide an explanation for the abundant and diverse community sampled at mid-shelf depths during cruise A (Mann and Lazier 2006). Increased primary productivity in oligotrophic environments has been shown to sustain abundant and diverse macrobenthic communities adapted to exploit variable nutrient input (Consentino and Gaicobbe 2008). The reduced outflow and concomitant nutrient supply during cruise B, as evidenced by Chl-*a* and Nitrate concentrations, likely contributed to the lower abundances of macrobenthos recorded from the mid-shelf during this period (Gaston *et al.* 1998).

In contrast, the dominance of carnivorous hermit crabs at the inner shelf during the low outflow period indicates that the high abundance recorded at this shelf position during cruise B was independent of sediment or outflow conditions. Large numbers of scavengers are known to be drawn to areas by the odour of damaged biota and provide an indication of recent disturbance (Kaiser *et al.* 2000). It may be that the mortality of other taxa following the period of high outflow at this shelf position provided an ample food supply for *Paguristes* sp.1. This contention is supported by the observation that numbers of the plough snail, *Bullia similis*, were reduced by more than half during the period of low riverine outflow while individuals of *Paguristes* sp.1 were found occurring predominantly in empty plough snail shells during cruise B. The enrichment of inshore coastal waters due to high riverine inputs has been postulated as one of the factors facilitating the establishment of abundant and taxon rich communities in shallower shelf regions (Jayaraj *et al.* 2008a). Other studies have found that inshore benthic

communities under the influence of riverine flow are relatively impoverished when compared with communities of deeper shelf locations due to the intrusion of poorly oxygenated, low salinity water (Alongi 1990, Alongi and Christoffersen 1992, Aller and Stupakoff 1996).

*Macrobenthic community of the inner and mid-shelf elucidated at the level of lowest identifiable taxon and feeding mode*

Analysis of abundance data for inner and mid-shelf samples, at the level of lowest identifiable taxon, collected during periods of high and low outflow differentiated communities from these shelf positions based on the exclusive presence of the facultative omnivore, *Epidiopatra papillosa* in MS samples from cruise A and B and the exclusive presence of the carnivore *Paguristes* sp.1 at the IS during cruise B. Detrital material brought into the marine realm has been postulated to sustain high densities of omnivorous polychaetes during periods of high riverine outflow (Consentino and Giacobbe 2008). Despite differences in the taxon composition of inner and mid-shelf communities during cruise A and B this did not lead to changes in macrobenthic functioning. This result illustrates the concept of functional redundancy which involves the notion that taxon replacements do not always lead to changes in community functioning (Bremner *et al.* 2003). Increased taxon richness is thought to be linked with increased functional performance and the provision of more ecosystem services (Duarte 2000, Cardinale *et al.* 2006, Ieno *et al.* 2006). Assemblages containing many taxa are more likely to contain a greater functional diversity and therefore be less affected by a loss of taxa than those of taxon poor assemblages (Duarte 2000). Patterns of functional diversity computed for shelf positions in this study followed those found when computing diversity measures from taxon abundance data. Diversity ( $H'$ ) and Margalef's Richness ( $d$ ) of feeding modes was higher for inner and mid-shelf samples collected during cruise A when compared with the outer shelf, with the values of both these indices reaching maximum values at the mid-shelf. Trophic analysis revealed that inner and mid-shelf samples grouped together on the basis of sampling time with a higher abundance of facultative detritivores, surface deposit feeders and carnivores, recorded during cruise A, being primarily responsible for separating communities from varied flow regimes. The shift in trophic structure of inner and mid-shelf communities between sampling periods is evidence of altered community function and probably ecosystem function (Gaston *et al.* 1998).

Suspension feeding fauna are reliant on suspended particles and are therefore generally associated with areas where strong hydrodynamics are acting on the seafloor (Dolbeth *et al.*

2009). In the present study suspension feeders represented by bivalves, chaetopterid worms, ascidians and amphipods were more abundant at inner and mid-shelf positions during cruise A which is most likely due to the reduction in suspended particulate matter, nutrient and primary production during the period of low outflow from the Thukela River. While parasites contributed little to the abundance of macrobenthos sampled in this study, these fauna represented by Gnathiidae isopods were only recorded from the mid-shelf during cruise A. Gnathids are external parasites of a variety of fish and they have several non-feeding, benthic life cycle stages. During these non-feeding periods gnathids seek refuge in the crevices of rubble, sediment or sponges (Ferriera 2011). This may provide an explanation for the exclusive presence of these fauna in the mid-shelf sands adjacent to the paleo-dune cordon. The abundance of demersal fish fauna on the Thukela bank is reduced during low outflow periods and the absence of gnathids in samples from cruise B may be as a result of this (Whitfield 2005, Lamberth *et al.* 2009, Hutchings *et al.* 2010).

#### *The outer shelf*

The muddy outer shelf was a stable area of the central shelf with both taxon and functional analysis finding no differences between outer shelf communities sampled from cruises A and B. Organic rich sediments of deep, stable benthic habitats are known to support abundant and taxon rich communities (Duineveld *et al.* 1991, Gaston *et al.* 1998, Simonini *et al.* 2004). In contrast with this commonly held tenant, the lowest numbers of individuals and taxa were recorded for the outer shelf position in the present study while the highest values of these metrics were recorded for the inner and mid-shelf, which had lower organic contents. Numerous studies conducted on continental shelf regions off New Zealand, California, India and Crete found that macrobenthic abundance decreases with depth offshore (Karakassis and Eleftheriou 1997, Probert and Grove 1998, Bergen *et al.* 2001, Ganesh and Raman 2007, Jayaraj *et al.* 2008b).

Polychaeta and Mollusca were the dominant Phyla at the outer shelf, most of which were facultative detritivores. Spionidae polychaetes and Tellinidae bivalves were the most abundant representatives of these Phyla and this feeding mode. The organic content of outer shelf sediments was lower during the period of reduced outflow but this did not have an effect on the numbers of individuals or taxa supported here. There were however interesting changes in the feeding mode composition of outer shelf communities. When river outflow and sediment deposition was high the abundance of strictly surface and subsurface deposit feeders at the

outer shelf was greater than in cruise B. Near bottom temperatures were higher at the outer shelf when riverine outflow was low suggesting impingement of the Agulhas Current onto the central shelf during this time which is corroborated by temperature and concentrations of Silicate and Phosphate which were higher at the outer shelf during cruise B when compared with cruise A. Outer shelf sediments also had reduced mud contents and an increase in coarse sediment grades and gravel at this shelf position during cruise B which may be indicative of the scouring action of the current on the shelf edge. The action of the southward flowing Agulhas current is known to cause shelf edge upwelling and the movement of unconsolidated sediment over the shelf edge and into submarine canyons (Lutjeharms *et al.* 2000a, Bosman *et al.* 2007).

### **Conclusion**

The ability of macrobenthic taxa to shift their diet in response to environmental constraints has been identified as an important functional strategy in the Thukela feature area. In shelf habitats under the influence of riverine outflow the assignment of macrobenthic taxa to discrete feeding modes may be an oversimplification that has implications for ecosystem functioning. The majority of macrobenthic fauna inhabiting the central Natal Bight are deposit feeding taxa, most of which exhibit plastic feeding behaviour, having some reliance on suspension feeding and thus are intimately connected with and reliant on conditions at the sediment-water interface. Reduced outflow from the Thukela River and concomitant reduction in suspended particulate matter during cruise B may account for the dramatic reduction of facultative detritivores recorded during this sampling period. Variations in taxa and feeding mode composition of macrobenthic communities occurring along width of the central Natal Bight were related to environmental variables measured in the present study with depth and the sediment characteristics gravel, coarse sand and mud being primarily responsible for explaining biotic patterns. This link indicates that these environmental variables are among the principal drivers of spatial and temporal distribution of the macrobenthic taxa and feeding modes in this coastal environment.

## CHAPTER 5. POLYCHAETES OF THE NATAL BIGHT: PATTERNS CONSIDERING FAMILIES AND FEEDING GUILDS

### Overview

This chapter is focused on Polychaeta which were the dominant macrobenthic group sampled on the Natal Bight, in terms of abundance and taxon richness (Chapter 3). The polychaete fauna inhabiting three shelf positions in the northern, central and southern regions of the Natal Bight are investigated in this chapter, with biomass determinations added to the data compliment. Polychaetes are one of the most characteristic groups of soft-bottom macrobenthos, widely used by ecologists to evaluate spatial and temporal patterns of the macrobenthic community as a whole. Surrogacy was investigated in this chapter by comparing multivariate results obtained from the analysis of all macrobenthic groups with those obtained from using only polychaete data. Taxonomic sufficiency was investigated within the Polychaeta by aggregating lowest taxon abundance and biomass data to the levels of Family and feeding guild and comparing results. The functional component of the analysis presented in this chapter is an extension from schemes adopted in previous chapters in that the concept of feeding guilds, incorporating information on feeding mode, feeding apparatus and mobility is considered. *In situ* gut contents observations of all polychaete taxa were used to corroborate facultative feeding behaviour, which was found to be an important functional adaptation of macrobenthos in Chapter 4. This study represents the first detailed investigation of subtidal polychaetes inhabiting sediments of the Natal Bight.

### 5.1 Introduction

Polychaetes are generally the most abundant and taxon rich component contributing most to the biomass of macrobenthic communities (Day 1967, Warwick 1986, McRae *et al.* 1998, Muniz and Pires 1999, Tselepides *et al.* 2000, Arasaki *et al.* 2004, Barrio Froján *et al.* 2005, Martí *et al.* 2007, Cheung *et al.* 2008, Mandal and Harkantra 2013). They play an important role in macrobenthic ecosystem structure and functioning as they exhibit a wide range of feeding behaviours, lifestyles and are able to thrive in a variety of habitats from the seashore to abyssal depths (Day 1967, Fauchald and Jumars 1979, Gaston 1987), whilst contributing to the diet of many commercially important, demersal fauna (Muniz and Pires 1999, Salen-Picard *et al.* 2002, Anbuezhian *et al.* 2012).

### ***Polychaeta of South Africa***

John Day (1967) summarised the taxonomy and distribution of southern African polychaetes in a two-part monograph, which today still serves as the only comprehensive identification guide for the region. This work contains over 800 taxa, with high levels of endemism (~36%) and diversity characteristic of South African polychaetes (Day 1967). This seminal publication described specimens collected along the entire South African coast, but few data were obtained for the Natal Bight (Day 1967). Subsequent studies in local waters have confirmed high levels of endemism and diversity with the subtropical east coast having strong Indo-Pacific affinities (McClurg 1988, Gibbons *et al.* 1999). No dedicated polychaete studies have been conducted on the Natal Bight, although environmental monitoring is done on a regular basis offshore of Richards Bay and Durban to investigate for example, the effects of pollution, dredging and mining on the marine environment (McClurg 1999, McClurg 2005, Mackay 2008, Chapter 1). Despite its rich and varied polychaete fauna, South Africa has few full time taxonomists and ecologists working on this group (Gibbons 1999, Mead *et al.* 2011). The limited work being undertaken in the area of polychaete taxonomy is currently focused on shell-boring spionids, common pest organisms in the aquaculture industry (Simon *et al.* 2006, Simon and Booth 2007, Simon 2009, Simon *et al.* 2010, Simon 2011). This lack of local specialist expertise, particularly for offshore, soft-sediment taxa significantly impedes our understanding of marine biodiversity and the ability to appropriately manage and conserve these resources at a time when threats to these environments are greatest (Gibbons *et al.* 1999).

### ***Polychaete traits analysis***

Fauchald and Jumars (1979) introduced the “feeding guild” concept in studies of polychaete ecology. Their classification system incorporated aspects of functional morphology and mobility together with feeding mode (Fauchald and Jumars 1979, Dauer *et al.* 1981, Gaston 1987, Muniz and Pires 1999, Pagliosa 2005). Recently feeding guild concepts have expanded to include a range of morphological, behavioural and life-cycle characteristics in an approach known as biological traits analysis (BTA) (Paganelli *et al.* 2012, Chapter 1). The underlying tenant is that traits are related to the ecological functioning of the community and habitat (Paganelli *et al.* 2012). While the classification of macrobenthic organisms into trophic groups is a useful and widely applied approach there are several problems with this method, the most notable being the accurate assignment of taxa to feeding modes (Gaston 1987, Mancinelli *et al.* 1998, Maurer *et al.* 1999, Tselepidis *et al.* 2000, Pagliosa 2005). Examining gut contents is one of the best ways to confidently classify or verify the feeding mode of

macrobenthic fauna (Hunt 1925, Sanders *et al.* 1962, Fauchald and Jumars 1979, Gaston 1987, Salas *et al.* 2006). Sanders *et al.* (1962) investigated the gut contents of intertidal macrobenthos in Barnstable Harbour and Gaston (1987) analysed polychaete diets from the middle Atlantic Bight, comparing his results with the classification scheme provided in Fauchald and Jumars (1979). Many taxa (e.g. glycerids, lumbrinerids and nephtyids) were carnivorous but also adopted deposit feeding behaviour at times (Sanders *et al.* 1962, Gaston 1987), thus leading to changes in the classification proposed by Fauchald and Jumars (1979).

### ***Surrogacy and taxonomic sufficiency***

Due to the impracticality and cost of conducting large scale surveys of all macrobenthic fauna, surrogacy methods are commonly employed. These include analyzing a single faunal component or analyzing the entire assemblage to a coarser taxonomic level (Ellingsen *et al.* 2005, Bertrand *et al.* 2006). The Polychaeta have been shown to be good indicators of species richness and macrobenthic community patterns. This has implications on the amount of time and money required to analyse data (Warwick 1988a, Warwick 1988b, Pavia 1993, Tselepidis *et al.* 2000, Giangrande *et al.* 2005, Cheung *et al.* 2008).

Taxonomic sufficiency involves the notion that identification of macrobenthos to levels higher than species is sufficient to detect community patterns and may produce analogous results to those obtained from higher order taxon data (Warwick 1988a, Warwick 1988b, Ferraro and Cole 1990, Clarke and Warwick 1998, Mistri and Rossi 2001, Ellingsen *et al.* 2005, Joydas *et al.* 2009, Benedetti-Cecchi *et al.* 2010). The practical advantages of this approach again include saving time and money as species level analysis is a laborious enterprise requiring a high level of expertise (Warwick 1988a, Warwick 1988b, Ferraro and Cole 1990, Olsgard *et al.* 1997, Muniz and Pires-Vanin 2005, Bertrand *et al.* 2006, Benedetti-Cecchi *et al.* 2010). In addition, many macrobenthic groups are far from being taxonomically well known so that analysis to coarser taxonomic levels allows benthic studies to take place in poorly known habitats (Warwick 1988a, Warwick 1988b, Terlizzi *et al.* 2003, Joydas *et al.* 2009). It is generally accepted that Family level analysis is a sufficient surrogate for Species level analysis, particularly in the area of pollution impacts, although few studies have tested the credibility of this approach in tropical and subtropical habitats (Ferraro and Cole 1990, Olsgard *et al.* 1998, Mistri and Rossi 2001, Terlizzi *et al.* 2003, Muniz and Pires-Vanin 2005, Bertrand *et al.* 2006, Yeung *et al.* 2010). Data on individual biomass often produce the same results as individual counts (Mason *et al.* 1983) and are more relevant (Pagliosa 2005), thus precluding the need for species identification. The effects of aggregating data to different

levels are variable from one study to the next because the degree of taxonomic, functional redundancy and the relationships between abundance, taxon richness and biomass vary depending on habitat (Warwick 1988a, Ferraro and Cole 1990, Terlizzi *et al.* 2003, Bertrand *et al.* 2006). It is thus imperative to conduct baseline studies at the finest resolution of taxa before an appropriate taxonomic or functional surrogacy method is credibly identified and applied (Mistri and Rossi 2001, Gomez Gesteira *et al.* 2003, Terlizzi *et al.* 2003, Bertrand *et al.* 2006).

### **Aims, Objectives and Hypotheses**

This chapter examines the structure and functioning of the polychaete community inhabiting the Richard's Bay, Thukela and Durban feature areas along with ambient environmental parameters during high and low rainfall conditions in the KwaZulu-Natal province.

#### **Objectives**

1. Determine whether the results obtained from macrobenthic community analyses (Chapters 3 and 4) using only polychaetes are comparable to those using all Phyla.
2. Test whether the same spatio-temporal patterns are obtained from polychaetes data at the level of lowest identifiable taxon, Family and feeding guild.
3. Determine whether there are structural and functional differences in the polychaete community using discriminant factors of cruise, feature area and shelf position.
4. Relate measured environmental variables to polychaete community patterns.

#### **Hypotheses**

H<sub>a1</sub>: There are differences between community analyses using all macrobenthic Phyla and Polychaeta only.

H<sub>a2</sub>: There are differences between spatio-temporal patterns obtained from polychaete data at the lowest identifiable taxon when compared with patterns obtained when aggregating data to Family and feeding guild.

H<sub>a3</sub>: There are structural or functional differences in polychaete communities considering the factors of cruise, feature area and shelf position.

H<sub>a4</sub>: There is a relationship between polychaete community patterns and measured environmental variables.

### **5.2 Materials and Methods**

General field sampling, lab processing and data analysis information is presented in Chapter 2 of this thesis.

### 5.2.1 Study area

The study site was divided into three areas (Richard's Bay, Thukela, Durban) selected for their importance in terms of associated features (Chapter 2). Three shelf position stations (inner, mid and outer) were sampled from transects in each feature area during both cruises A and B along a depth gradient from the shallow sub-tidal to shelf edge (Fig. 3.1, Chapter 2).

### 5.2.2 Laboratory procedure

#### *Biotic analysis*

Biomass refers to the amount of substance in living organisms per unit surface area or volume and is an indication of the energy content of an animal or group of animals (van der Meer *et al.* 2005). Biomass was determined per individual for each polychaete taxon as wet weight (g ww) (Thorson 1957, Pearson 1970) and upscaled to area (m<sup>2</sup>). Biomass determinations were based on whole specimens where possible. For abundant taxa, up to five individuals of different sizes were weighed and the biomass expressed as a mean value (g ww.m<sup>-2</sup> ±SD) (Pearson 1970). Before weighing, excess moisture was removed by placing each specimen onto absorbant paper and rolling or blotting gently (Thorson 1957, Pearson 1970, Crisp 1971, Tselepides *et al.* 2000, Consentino and Giacobbe 2008). Biomass was presented in this study as wet weight due to the fact that non-destructive procedures needed to be adopted, because the biological material is integral for subsequent taxonomic work, which inherently requires that the integrity of morphological structures be maintained as far as possible (van der Meer *et al.* 2005). However, the problem with this measure (ww) is that it includes additional water inside the body or on the outer surfaces of animals as well as gut contents which may contain inorganic material (van der Meer *et al.* 2005). Ash free dry weight (AFDW) is actually a more useful measure of an animal's energy content and is defined as the heat energy liberated from combustion (Thorson 1957, van der Meer *et al.* 2005). Feeding modes were assigned as in Chapter 2 while the feeding apparatus and mobility characteristics were designated according to Fauchald and Jumars (1979). The assignment of feeding modes was corroborated through *in situ* gut contents observations which were made for each polychaete taxon with one of five states being recorded (Table 5.1). The purpose of these observations was to record the absence of gut contents or the presence of sediment and/or faecal pellets in guts, which indicated carnivorous and deposit feeding behaviour, respectively (Gaston 1987). These non-destructive procedures were adopted because fauna will be required for subsequent taxonomic work (Crisp 1971).

Table 5.1. States used for *in-situ* gut contents analysis of Polychaeta sampled from the Richard's Bay, Thukela and Durban feature areas.

State	<i>in-situ</i> gut contents observation
0	No gut contents, specimen damaged
1	No gut contents
2	Gut full of sand grains
3	Gut full of dark, fine material
4	Gut full of dark, fine material, faecal pellets visible

Polychaete taxa were classified into feeding guilds adopting the scheme proposed in Fauchald and Jumars (1979) and modified to include facultative forms confirmed with *in situ* gut contents observations. The system of feeding guild classification used in the present study included seven feeding modes (carnivores (C), facultative carnivores (FC), omnivores (O), facultative omnivores (FO), surface deposit feeders (S), subsurface deposit feeders (B) and interface feeders (I), 3 morphological subgroups (unarmed pharynx (X), jawed pharynx (J) and bearing tentacles or feeding palps (T)), and 3 mobility subgroups (mobile (M), discretely mobile (D), sessile (S)). The classification discretely mobile was applied to polychaetes that move around between feeding bouts but remain sessile while feeding (Fauchald and Jumars 1979, Gaston 1987). These three components were combined to form 15 feeding guilds (Table 5.2).

Table 5.2. Polychaete feeding guild classification scheme adopted in the present study (modified from Fauchald and Jumars 1979).

Feeding Guild	Feeding mode	Mobility	Functional Morphology
CMJ	Carnivore	Mobile	Pharynx with jaws
CMX	Carnivore	Mobile	Unarmed pharynx
FCMJ	Facultative carnivore	Mobile	Pharynx with jaws
FCMX	Facultative carnivore	Mobile	Unarmed pharynx
OMJ	Omnivore	Mobile	Pharynx with jaws
FOMJ	Facultative omnivore	Mobile	Pharynx with jaws
BMX	Subsurface deposit feeder	Mobile	Unarmed pharynx
BSX	Subsurface deposit feeder	Sessile	Unarmed pharynx
SMX	Surface deposit feeder	Mobile	Unarmed pharynx
SMT	Surface deposit feeder	Mobile	Bearing tentacles or feeding palps
SDT	Surface deposit feeder	Discretely mobile	Bearing tentacles or feeding palps
SST	Surface deposit feeder	Sessile	Bearing tentacles or feeding palps
IDT	Interface feeder	Discretely mobile	Bearing tentacles or feeding palps
IST	Interface feeder	Sessile	Bearing tentacles or feeding palps
FST	Suspension feeder	Sessile	Bearing tentacles or feeding palps

### 5.2.3 Data analysis

For analysis data were combined as: abundance of all macrobenthic fauna (Chapter 3), polychaete abundance and biomass data at the level of lowest identifiable taxon, polychaete abundance data aggregated to the levels of Family and feeding guild as well as environmental data for the shelf position stations sampled in each feature area.

#### *Univariate analysis*

Frequency of occurrence ( $F$ ) (Guille 1970) was calculated for Family and feeding guild data using the formula.

$$F = \left( \frac{m}{M} \right) \times 100 \quad (5.1.)$$

Where,  $m$  = the number of samples in which a Family or feeding guild was recorded and  $M$  = the total number of samples.

Based on these values polychaete families and feeding guilds were classified as constant ( $F > 50\%$ ), common ( $10\% \leq F \leq 50\%$ ) and rare ( $F < 10\%$ ) (Muniz and Pires 2000).

#### *Dominance curve analysis*

Distribution models visually depict the relationships between the number of taxa and the number of individuals and biomass comprising those taxa (Magurran 2004). The  $k$ -dominance curve method was applied in the present study. Taxa are ranked in order of decreasing importance in terms of abundance or biomass on the x-axis (logarithmic scale) and plotted against percentage dominance on the y-axis (cumulative scale) (Warwick 1986, Clarke 1990, Magurran 2004).  $K$ -dominance curves provide insight into the dominance pattern without reducing information to a single summary statistic, such as a diversity index and thus extract universal community features (Clarke 1990). The more elevated the  $k$ -dominance curves the less diverse the assemblages they represent (Magurran 2004). Testing of the  $H_a$  that  $k$ -dominance curves of abundance and biomass differ significantly among feature areas or shelf positions was conducted using the DOMDIS procedure within the PRIMER v6 package (Clarke and Warwick 2001). In this analysis the distance between  $k$ -dominance curves is computed and a triangular similarity matrix produced which is used as input for Analysis of Similarity ANOSIM (Chapter 2) testing of *a priori* selected factors (Clarke and Warwick 2001).

### **Multivariate analysis**

#### *Polychaete community patterns*

Analysis of a subset of macrobenthic taxa may give a similar result to that incorporating all macrobenthic fauna (Warwick 1988a, Warwick 1988b, Ferraro and Cole 1990, Clarke and Warwick 1998, Mistri and Rossi 2001, Ellingsen *et al.* 2005, Joydas *et al.* 2009, Benedetti-Cecchi *et al.* 2010). We investigated whether the Polychaeta can be used as a surrogate for the whole macrobenthic community by comparing MDS plots based on the abundance of all macrobenthic fauna (Chapter 3) with those constructed from polychaete abundance and biomass data analysed to the level of lowest identifiable taxon (Clarke and Warwick 1998).

Taxonomic sufficiency within the Polychaeta was investigated by comparing MDS ordination plots based on matrices derived from data aggregated to the levels of lowest identifiable taxon, Family and feeding guild. The ANOSIM procedure was used to statistically test the effects of data aggregation ( $H_{a2}$ ) (Clarke and Warwick 1994).

To investigate the comparability of multivariate structures based on all macrobenthic data with polychaete data only as well as polychaete data aggregated to different levels, the RELATE routine was used ( $H_{a1}$ ,  $H_{a2}$ ) (Clarke and Warwick 1994). The input for this analysis is the relevant resemblance matrix, calculated from Bray-Curtis similarity coefficients, which are compared by the Spearman rank correlation coefficient ( $\rho$ ) (Clarke and Warwick 1994, Thrush *et al.* 2001). The  $\rho$  statistic indicates the degree of correlation between the similarity matrices under consideration where  $\rho=1$  indicates a perfect match and  $\rho=0$  indicates that there is no correlation (Clarke and Warwick 1994, Tillin *et al.* 2006). The significance of the correlation was tested running 10 000 permutations of the datasets (Clarke and Warwick 1994).

The relationship between environmental parameters and the polychaete community was investigated through the BVSTEP algorithm (Chapter 2). The set of abiotic factors identified as being the best descriptors were superimposed as bubbles onto the MDS ordination to provide a visual representation (Chapter 2). In these plots the diameter of the bubble represents the magnitude of the variable being presented (Clarke and Warwick 1994).

### 5.3 Results

#### 5.3.1 The effect of Cruise

##### ***Polychaete abundance (N), richness (S) and biomass (B)***

A total number of 14 110 polychaetes weighing 281.56g ww.m<sup>-2</sup> and representing 342 lowest identifiable taxa from 40 families were recorded in the present study. Polychaete taxon richness (S) and abundance (N) decreased ( $p>0.05$ ) from a total of 7675 individuals belonging to 277 taxa collected from the three feature areas during cruise A to 6435 individuals from 199 taxa sampled during cruise B. The biomass of polychaete fauna also decreased ( $p>0.05$ ) from a total of 149.485 g ww obtained during the high rainfall period to 132.075 g ww during cruise B.

##### ***Polychaete Families: Frequency of occurrence (F), richness (S), abundance (N) and biomass (B)***

Of the 40 families recorded in the present study, 11 (27.4%) were classified as rare ( $F < 10\%$ ), 19 (45.7%) as common ( $10\% \leq F \leq 50\%$ ) and 10 (25%) as constant ( $F < 50\%$ ) (Fig. 5.1). The most abundant families sampled during cruises A and B were the Spionidae (N: Cruise A F: 81.48%, Cruise B F: 81.48 %) and Onuphidae (N: Cruise A F: 77.78%, Cruise B F: 88.89%) with the former Family being one of the most species rich sampled during both cruises A (S: 11.55%) and B (S: 15.58%) (Fig. 5.1; Fig. 5.2). Orbiniidae, Lumbrineridae, Cirratulidae, Capitellidae and Sigalionidae were also frequently recorded, occurring in more than 60% of samples collected during both high and low rainfall periods (Fig. 5.1). Cossuridae, Dorvilleidae and Pholoidae were the rarest families sampled, each of which were present in only one of the total 54 samples collected. Five families were unique to cruise A: Ctenodrilidae, Dorvilleidae, Nereididae, Sabelliidae and Scalibregmatidae while the families Cossuridae and Pholoidae were found exclusively in samples collected during cruise B (Fig. 5.1).

Nineteen families contributed  $>3\%$  to total numbers and biomass of polychaetes across the three feature areas sampled during cruises A and B. The remaining 21 families (grouped for analysis purposes as “other”) contributed most to the total number of polychaete species recorded during both cruises A (S: 61 taxa) and B (S: 37 taxa) despite a notable decrease (Mann-Whitney  $U=163$ ,  $p=0.14$ ) in the total numbers of taxa recorded for this group during the winter, low rainfall period (Fig. 5.2). Relatively high numbers of taxa belonging to the Family Spionidae (Cruise A-S: 32 taxa, Cruise B-S: 31 taxa) and Terebellidae (Cruise A-S: 20 taxa, Cruise B-S: 13 taxa) were also found, with a greater number of taxa recorded for most

families during cruise A when compared with cruise B ( $p>0.05$ ). Of the 19 families, a single taxon belonged to Oweniidae while the Poecilochaetidae were represented by just two taxa (Fig. 5.2). Numbers of onuphid polychaetes were reduced from a total of 1 465 individuals.m<sup>-2</sup> in cruise A to 615 individuals.m<sup>-2</sup> recorded during the low rainfall period (Mann-Whitney  $U=328.5$ ,  $p=0.54$ ). The abundance of Spionidae and “other” families were also lower during cruise B ( $p>0.05$ ) although their contribution to the total abundance recorded for this sampling period remained approximately the same at 12.35% and 10.88%, respectively (Fig. 5.2). Numbers of Chaetopteridae were relatively high during cruise B contributing over 10% to total abundance during the low rainfall period, while Capitellidae contributed 8-10% to total abundance recorded during cruises A and B. The Eunicidae, Glyceridae, Paraonidae and Phyllodocidae were among the least abundant families sampled, together accounting for less than 6% of the total numbers recorded during high and low rainfall periods (Fig. 5.2). A higher number of polychaete individuals belonging to the former two families (Eunicidae and Glyceridae) were recorded during cruise B while lower numbers of the latter two families (Paraonidae and Phyllodocidae) were recorded during this low rainfall sampling period. No universal pattern in abundance values were apparent when comparing cruises A and B, with numbers of individuals increasing for some families and decreasing for others (Fig. 5.2).

Biomass patterns differed from those of abundance with Capitellidae (Cruise A-B: 31.55 g ww.m<sup>-2</sup>), Maldanidae (Cruise A-B: 19.26 g ww.m<sup>-2</sup>) and Chaetopteridae (Cruise A-B: 15.24 g ww.m<sup>-2</sup>) contributing most to the weight of polychaetes recorded during the summer period of high rainfall (Fig. 5.2). During cruise B the highest biomass was again recorded for the Capitellidae (Cruise B-B: 30.19 g ww.m<sup>-2</sup>) and Chaetopteridae (Cruise B-B: 24.02 g ww.m<sup>-2</sup>) while the group of “other” (Cruise B-B: 10.92 g ww.m<sup>-2</sup>) families replaced Maldanidae (Fig. 5.2). The lowest biomass was recorded for the Paraonidae, Phyllodocidae and Poecilochaetidae during both cruises A (Paraonidae-B: 0.10 g ww.m<sup>-2</sup>; Phyllodocidae-B: 0.33 g ww.m<sup>-2</sup>; Poecilochaetidae-B: 0.20 g ww.m<sup>-2</sup>) and B (Paraonidae-B: 0.13 g ww.m<sup>-2</sup>; Phyllodocidae-B: 0.16 g ww.m<sup>-2</sup>; Poecilochaetidae-B: 0.37 g ww.m<sup>-2</sup>) (Fig. 5.2).

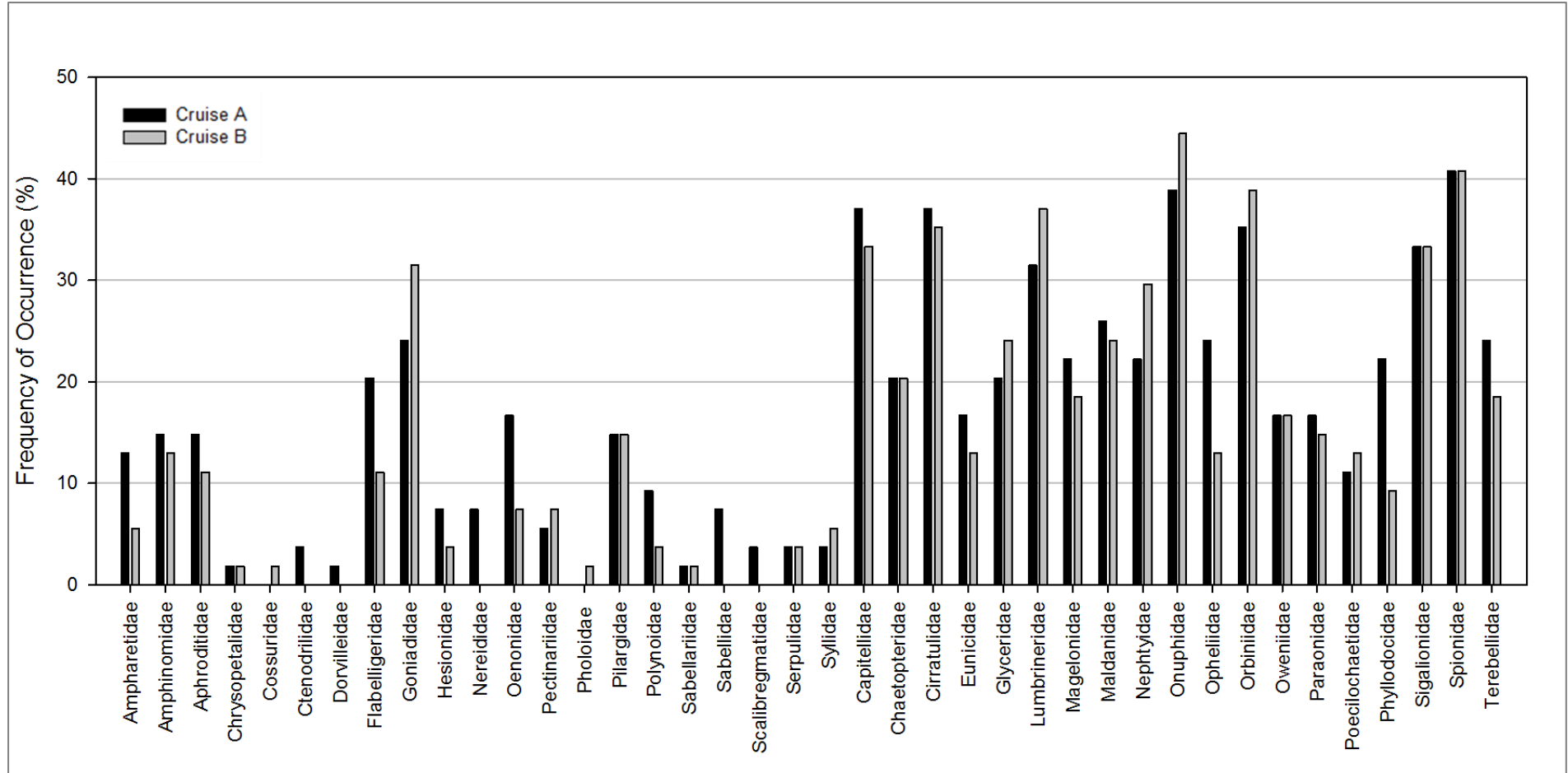


Figure 5.1. Frequency of occurrence ( $F$ ) for polychaete families sampled on the Natal Bight during cruises A (high rainfall) and B (low rainfall).

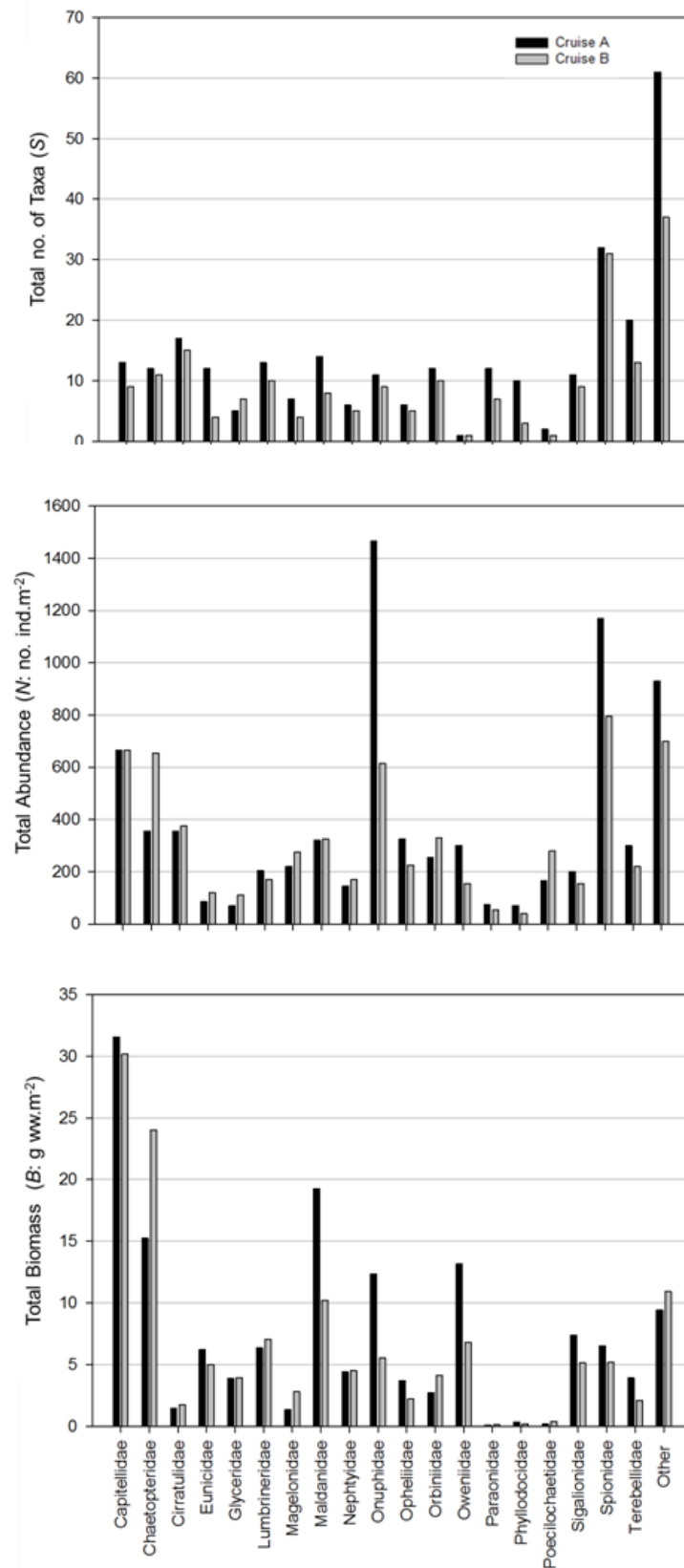


Figure 5.2. Total number of taxa (*S*), abundance (*N*) and biomass (*B*) attributed to polychaete families sampled during high (Cruise A) and low rainfall (Cruise B) periods.

**Polychaete Feeding Guilds: Frequency of occurrence (*F*), richness (*S*), abundance (*N*) and biomass (*B*)**

Fifteen polychaete feeding guilds were defined in the present study; one being classified as rare ( $F < 10\%$ ), and seven of which were classified as common ( $10\% \leq F \leq 50\%$ ) and constant ( $F > 50\%$ ) (Fig. 5.3). The most widespread feeding guild encountered during the high rainfall period were mobile, jawed carnivores (CMJ) which were found in 26 of the 27 ( $F=96.30\%$ ) samples. Mobile subsurface deposit feeders without jaws (BMX) were the most commonly encountered feeding guild during cruise B and occurred in all the samples collected (Fig. 5.3). Mobile (SMT) and discretely mobile surface deposit feeders (SDT), discretely mobile interface feeders (IDT), mobile facultative omnivores (FOMJ) and facultative carnivores with jaws (FCMJ) also demonstrated a high frequency of occurrence ( $F > 75\%$ ) in cruises A and B (Fig. 5.3). The rarest polychaete feeding guild found was mobile, surface deposit feeders lacking jaws (SMX) which were recorded in only two ( $F=7.41\%$ ) of the samples collected during cruise A and were not encountered at all during cruise B. Mobile, jawed omnivores (OMJ) and sessile suspension feeders (FST) also exhibited a low frequency of occurrence ( $10\% < F < 20\%$ ) during both cruises A and B (Fig. 5.3).

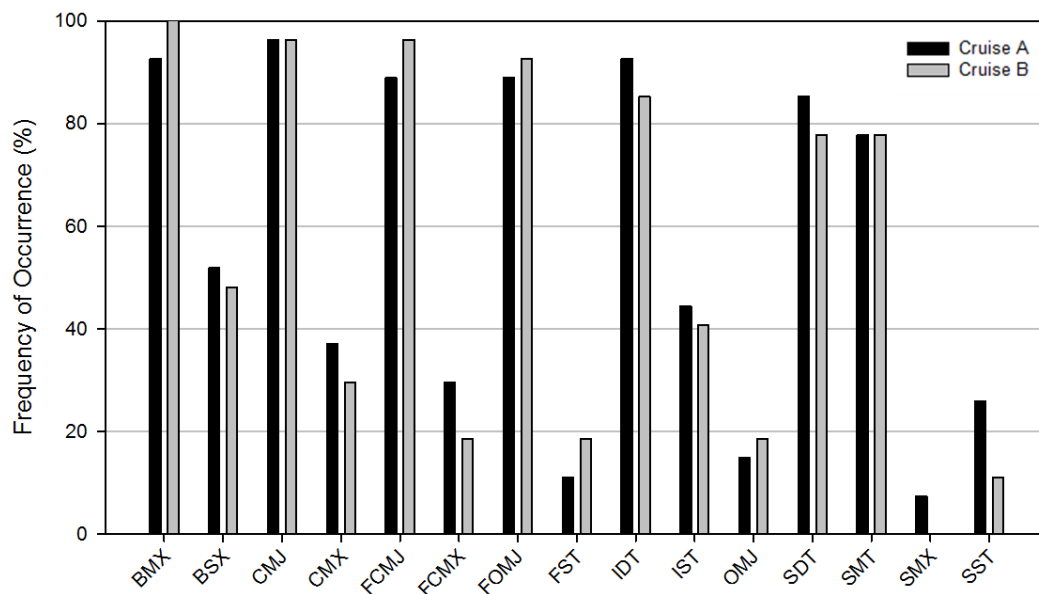


Figure 5.3. Frequency of occurrence (*F*) of polychaete feeding guilds collected on the Natal Bight during cruises A and B.

Mobile, subsurface deposit feeders without jaws (BMX) were the richest polychaete feeding guild sampled during cruise A (BMX-*S*: 45 taxa) followed by mobile carnivores with jaws (CMJ-*S*: 40 taxa), discretely mobile interface (IDT-*S*: 35 taxa) and surface deposit feeders

(SDT-S: 35 taxa) (Fig. 5.4). Despite lower values ( $p>0.05$ ) being recorded for these trophic groups they were again the most taxon rich feeding guilds sampled during cruise B (BMX-S: 33 taxa; CMJ-S: 31 taxa; IDT-S: 32 taxa; SDT-S: 21 taxa). Eight out of the 15 feeding guilds considered in this study were represented by less than 15 lowest identifiable taxa and contributed <5% to the total number recorded during cruises A and B (Fig. 5.4). During the latter sampling period mobile surface deposit feeders lacking jaws (SMX) were represented by only two taxa (0.72%) and were not recorded during cruise B. Most feeding guilds had reduced numbers of taxa during cruise B ( $p>0.05$ ) with the exception of sedentary, palpal suspension feeders (FST), represented by a total of three taxa (1.08%) during cruise A and five taxa (2.51%) during cruise B (Fig. 5.4).

Mobile facultative omnivores with jaws (FOMJ-N: 1515 ind.m<sup>-2</sup>) and IDT (N: 1480 ind.m<sup>-2</sup>) were the most abundant feeding guilds sampled during the high rainfall, summer period together contributing approximately 40% to total abundance (Fig. 5.4). The main facultative omnivores were *Onuphis eremita* and *Epidiopatra papillosa*, while the most abundant interface feeders were *Owenia fusiformis*, *Diploydora capensis* and *Spiophanes* sp.1. Despite fewer ( $p>0.05$ ) individuals from these feeding guilds being sampled during cruise B (FOMJ-N: 765 ind.m<sup>-2</sup>; IDT-N: 950 ind.m<sup>-2</sup>) they were still among the most abundant sampled, along with SDT (N: 825 ind.m<sup>-2</sup>) and BMX (N: 1310 ind.m<sup>-2</sup>) who dominated total number of individuals recorded during this low rainfall period (Fig. 5.4). The main discretely mobile surface deposit feeders (SDT) were *Magelona* sp.6 and *Poecilochaetus serpens*, while the main subsurface deposit feeding taxa (BMX) were the capitellids, *Notomastus latericeus*, *Rashgua* sp.1 and the ophelid, *Ophelia* cf. *roscoffensis*. In accordance with Family data, SMX represented by Ctenodrilidae were the least abundant feeding guild sampled during cruise A (SMX-N: 10 ind.m<sup>-2</sup>) followed by FST and mobile facultative (FCMX) and strictly carnivorous Polychaeta without jaws (CMX), which together accounted for < 5% of total abundance recorded for both sampling cruises A and B (Fig. 5.4). Strictly carnivorous polychaetes lacking jaws (CMX) were mainly *Phyllodoce* sp.2 and *Pareurythoe* sp.4 while facultative carnivores (FCMX) were mainly *Amphinomidae* sp.1 individuals. Most feeding guilds were represented by fewer individuals ( $p>0.05$ ) during cruise B with the exception of sessile, subsurface deposit (BSX), interface (IST) and filter feeders (FST) who were sampled in greater numbers ( $p>0.05$ ) during the low rainfall period (Fig. 5.4). Sessile subsurface deposit feeders (BSX) were mainly *Euclymeninae* sp.2 and other maldanids while the main sessile suspension and interface feeders (FST, IST) were *Mesochaetopterus* sp.1, *Chaetopteridae* sp.9, *Spiochaetopterus* sp.6 and *Spiochaetopterus* sp.12.

Biomass was dominated by BMX polychaetes during cruises A and B, accounting for approximately 40g ww.m<sup>-2</sup> during both periods and contributing 25.8-28.5% to total biomass (Fig. 5.4). Mobile, facultative carnivores armed with jaws (FCMJ-B: 15.54 g ww.m<sup>-2</sup>), FOMJ (B: 18.07 g ww.m<sup>-2</sup>), IDT (B: 19.71 g ww.m<sup>-2</sup>) and mobile surface deposit feeders (SMT-B: 15.74 g ww.m<sup>-2</sup>) also contributed significantly to the biomass of polychaetes recorded during the summer period of high rainfall (Fig. 5.4). A reduction in the biomass of this group of feeding guilds (FCMJ-B: 15.06 g ww.m<sup>-2</sup>; FOMJ-B: 10.52 g ww.m<sup>-2</sup>; IDT-B: 12.00 g ww.m<sup>-2</sup>; SMT-B: 9.21 g ww.m<sup>-2</sup>) was recorded during cruise B, but they still featured among the highest contributors to total biomass during this sampling period (Fig. 5.4). Considering feeding guilds that contributed the least to total biomass of Polychaeta, similar patterns emerged as with taxon and abundance data. Mobile, surface deposit feeders lacking jawed appendages (SMX) made the lowest contribution to total biomass during cruise A (SMX-B: 0.01 g ww.m<sup>-2</sup>) and together with mobile, jawed omnivores (OMJ), FST and CMX contributed <1% to the total polychaete biomass recorded for high and low rainfall periods (Fig. 5.4).

### 5.3.2 The effect of feature area

#### *Dominance curve analysis*

Dominance curves for abundance and biomass of the three feature areas under consideration are presented in Fig. 5.5. The *k*-dominance curves of abundance for the Richard's Bay, Thukela and Durban areas sampled during cruises A and B indicated a relatively even contribution of polychaetes to overall abundance (Fig. 5.5). Results from cruise B showed that the feature areas were better separated, with values increasing slightly from Richard's Bay to Durban (Fig. 5.5). Thukela supported the largest richness of polychaetes during cruise A, while Durban supported the highest polychaete richness during the low rainfall period. The narrow northern Bight was the least diverse region sampled with the lowest number of polychaete taxa recorded for both high and low rainfall sampling periods (Fig. 5.5). Considering biomass curves constructed for feature areas sampled during cruise A, assemblages in TK and RB region exhibited the highest dominance, with four polychaete taxa contributing over 50% to biomass compared with just over 30% in DN. Fewer polychaete taxa were required to reach 100% cumulative dominance in Richard's Bay and Durban (~40 taxa) during the high rainfall period, when compared with the Thukela feature area biomass curve which leveled off at approximately 100 polychaete taxa (Fig. 5.5). The TK area also exhibited high dominance during the low rainfall period, with four taxa contributing 60% to overall biomass. The DN and RB biomass *k*-dominance curves showed

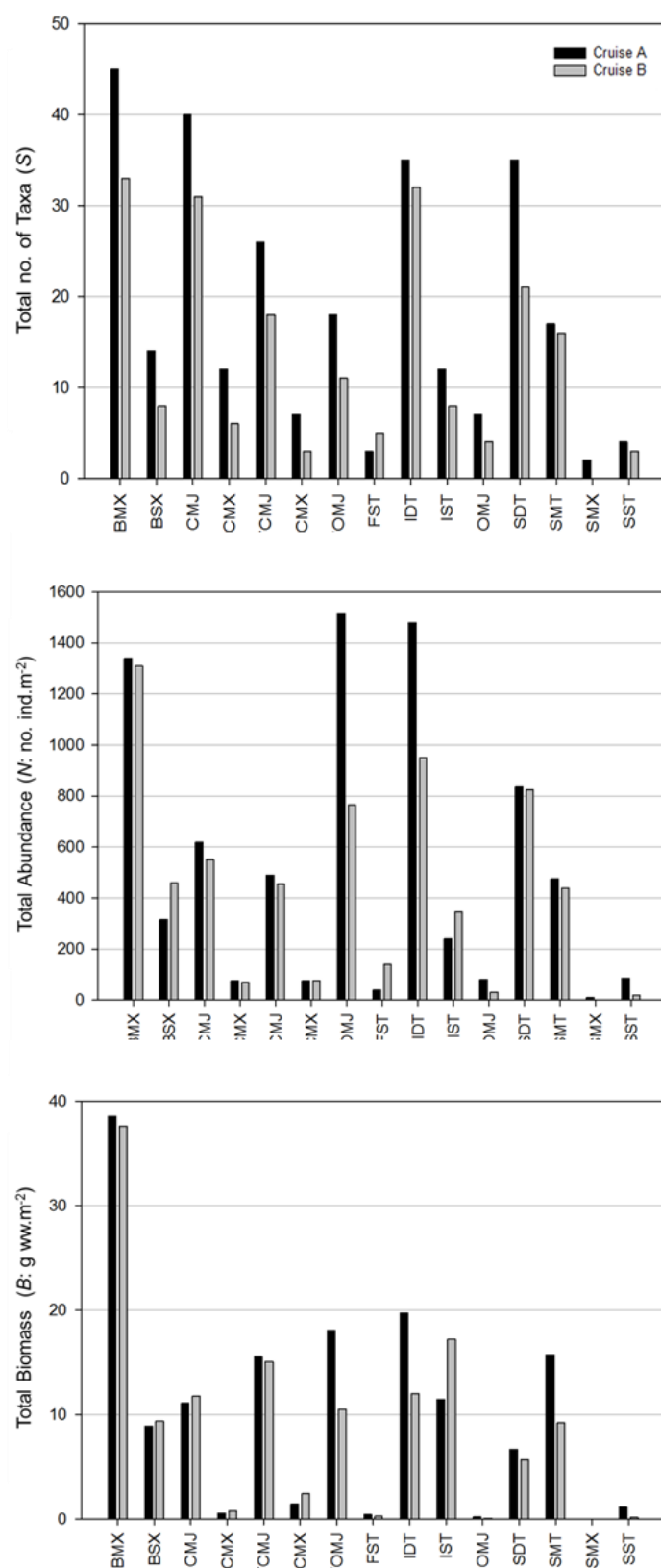


Figure 5.4. Total number of taxa (*S*), abundance (*N*) and biomass (*B*) attributed to polychaete feeding guilds sampled during high (Cruise A) and low rainfall (Cruise B) periods.

low dominance (<20%) and the shape indicated a relatively even contribution of polychaete taxa to overall biomass recorded for these feature areas during cruise B (Fig. 5.5). Results of DOMDIS analysis showed that there were no significant global differences in the distribution of abundance ( $R=0.389$ ,  $p=0.20$ ) and biomass ( $R=0.056$ ,  $p=0.47$ ) among polychaetes at the level of lowest identifiable taxon in the three feature areas under consideration.

### 5.3.3 The effect of shelf position

#### *Dominance curve analysis*

When considering distribution patterns of the inner (IS), mid (MS) and outer shelf (OS),  $k$ -dominance curves showed that the contribution of polychaetes, at the level of lowest identifiable taxa, to overall abundance was relatively evenly distributed during cruises A and B, with all three shelf positions displaying low dominance ( $\leq 20\%$ ) (Fig. 5.6). The OS supported the greatest variety of taxa and most diverse assemblages while shallow, IS assemblages had the lowest richness and diversity during both high and low rainfall periods. The MS displayed slightly higher dominance when compared with OS positions sampled during cruise A, while during the low rainfall period IS assemblages showed a higher dominance throughout the spectrum of polychaete taxa collected (Fig. 5.6). Comparison of biomass  $k$ -dominance curves for each of the three shelf positions sampled during cruises A and B showed higher dominance for common taxa at the inner and mid-shelf during the former period with five taxa contributing ~60-70% to overall biomass compared with ~40% dominance at the outer shelf (Fig. 5.14). During the low rainfall period OS assemblages showed a very high dominance with the two most common taxa contributing 60% to overall biomass while the MS curve showed the lowest dominance (<20%). As with the abundance curves the biomass curve for the IS showed the lowest diversity during cruise A and B although the OS biomass curve lies above that of the IS for most of its length during the latter period (Fig. 5.6). The outer shelf supported the most diverse assemblage during cruise A, in accordance with the abundance curves, but during cruise B the highest diversity was found at the mid-shelf with this biomass curve lying below the others for most of its length (Fig. 5.6). Comparisons of abundance and biomass curves show that fewer taxa were required to reach 100% cumulative dominance in the case of biomass, indicating that polychaete taxa were more dominant in weight than numbers (Fig. 5.6). Results of DOMDIS analysis showed that there were no significant global differences in the distribution of abundance ( $R=0.611$ ,  $p=0.67$ ) and biomass ( $R=0.611$ ,  $p=0.13$ ) among the three shelf positions under consideration.

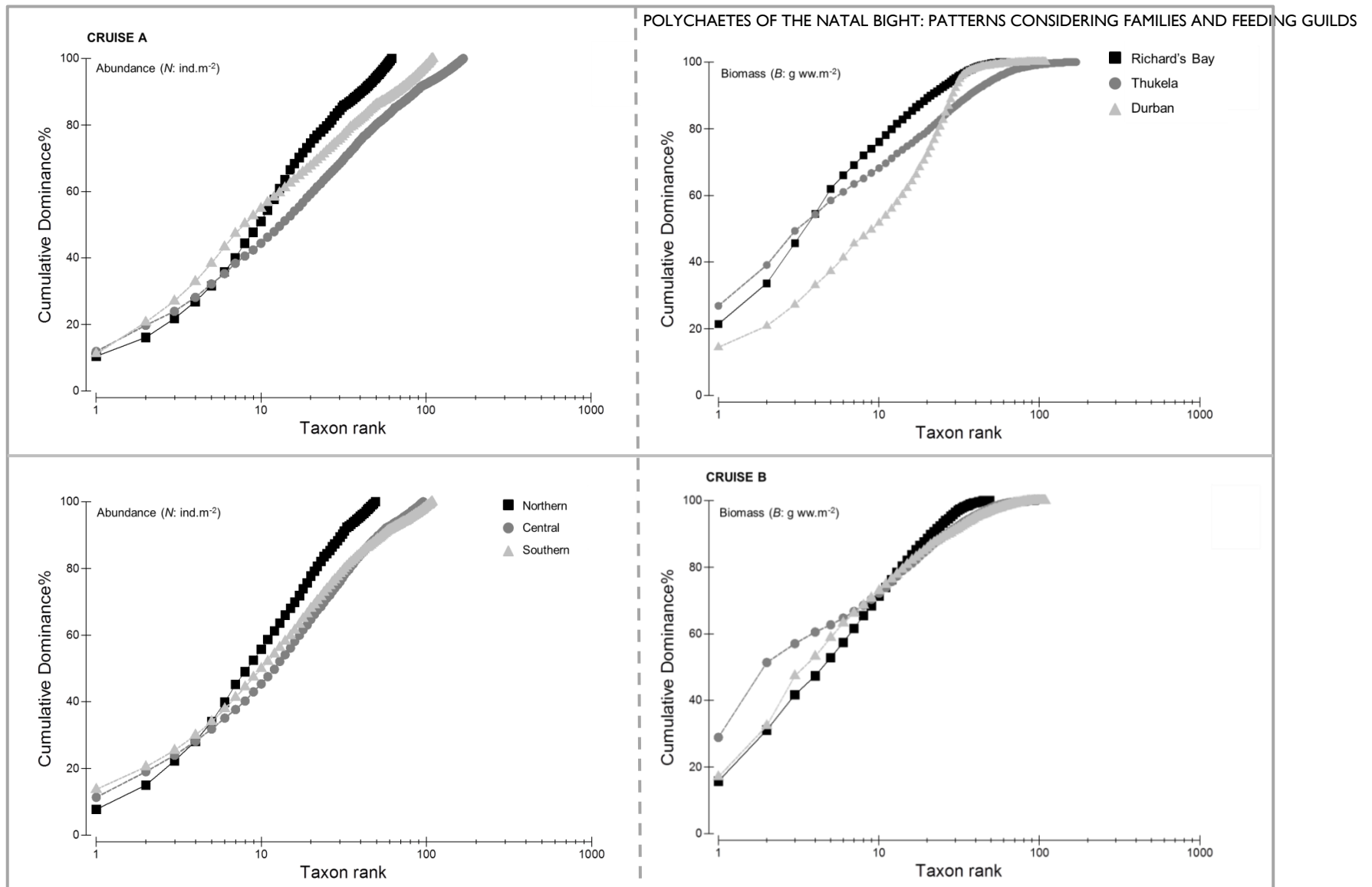


Figure 5.5. Comparison of  $k$ -dominance curves for polychaete abundance ( $N$ ) and biomass ( $B$ ) between the Richard's Bay, Thukela and Durban feature areas during cruises A and B.

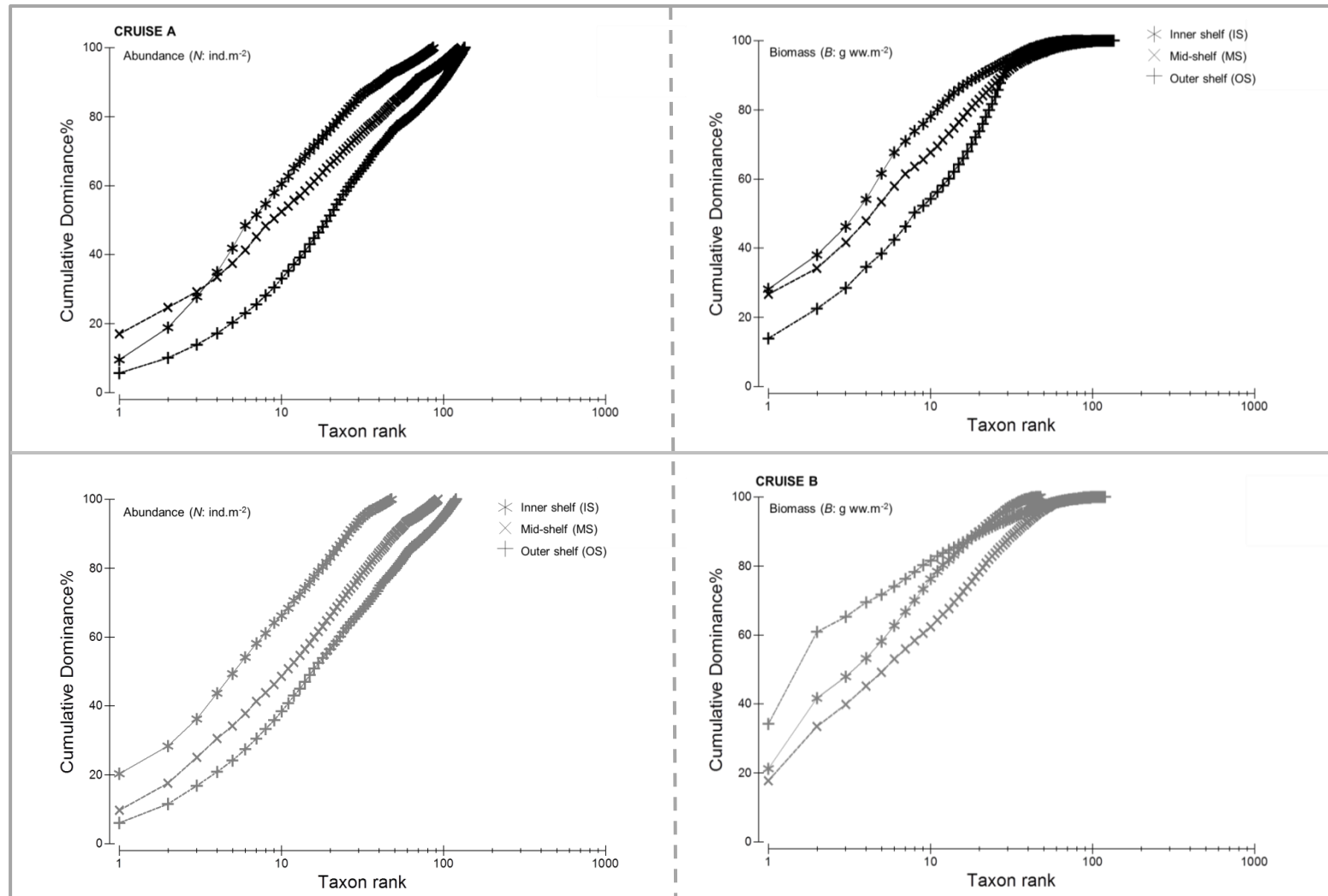


Figure 5.6. Comparison of  $k$ -dominance curves for polychaete abundance ( $N$ ) and biomass ( $B$ ) between the inner (IS), mid (MS) and outer shelf (OS) positions sampled during cruises A and B.

### 5.3.4 Polychaete Community patterns

#### ***Agreement between multivariate patterns based on abundance of Polychaeta and all macrobenthic taxa***

The ordination of samples constructed from abundance data of all macrobenthic fauna compared with those of polychaete abundance and biomass data at the lowest identifiable taxon showed similar results with samples aggregating into the same groups (Fig. 5.7). The plot constructed from abundance of all macrobenthic fauna showed a tighter clustering of samples within the six sample groups which were defined at a higher similarity level (All macrobenthos: 19%, Polychaeta Abundance: 15%) and resulted in a slightly lower stress (0.16) value being produced for this ordination when compared with that for polychaete abundance (0.17) data (Fig. 5.7). Ordination of taxon biomass data identified 1 outlying sample (07-3A) which was removed prior to the analysis being re-performed. The MDS ordination plot of polychaete biomass data at the level of lowest identifiable taxon revealed the same six sample groups as those in the ordination produced from abundance of all macrobenthic fauna, although in the former the groups were defined at a lower B-C similarity level (15%) (Fig. 5.7). Results from the RELATE procedure showed that there was a highly significant correlation between matrices constructed from abundance of all macrobenthos compared with polychaete abundance ( $\rho=0.902$ ,  $p<0.001$ ) and polychaete biomass ( $\rho=0.880$ ,  $p<0.001$ ) data at the level of lowest identifiable taxon. Thus polychaete abundance and biomass data are good surrogates for assessing macrobenthic community patterns. Due to the presence of an outlying sample in the polychaete biomass data and the fact that a higher correlation coefficient was obtained when relating abundance data with that of the whole macrobenthic community, polychaete abundance data were used to investigate taxonomic sufficiency within this group and the relationship of polychaete community patterns to environmental factors.

#### ***The effects of aggregating Polychaete abundance data to higher levels***

MDS ordinations of matrices derived from square root transformed polychaete abundance data at the level of lowest identifiable taxon and aggregated to Family and feeding guild were dissimilar (Fig. 5.8). At the level of lowest identifiable taxon, analysis delineated six sample groups. Group I was composed of inner shelf samples from Durban, while Groups II and III were comprised of outer shelf samples collected from this and the Thukela feature area, respectively. Mid-shelf samples collected from DN formed Group IV, while those collected from this shelf position in TK formed Group V. The largest sample grouping was composed of IS samples collected from RB and TK as well as mid and OS samples (B3) from the latter

feature area (Fig. 5.8). Ordination of Family level data identified two outlying samples (RB-MS-1A, DN-OS-1A) which were removed and the ordination re-performed.

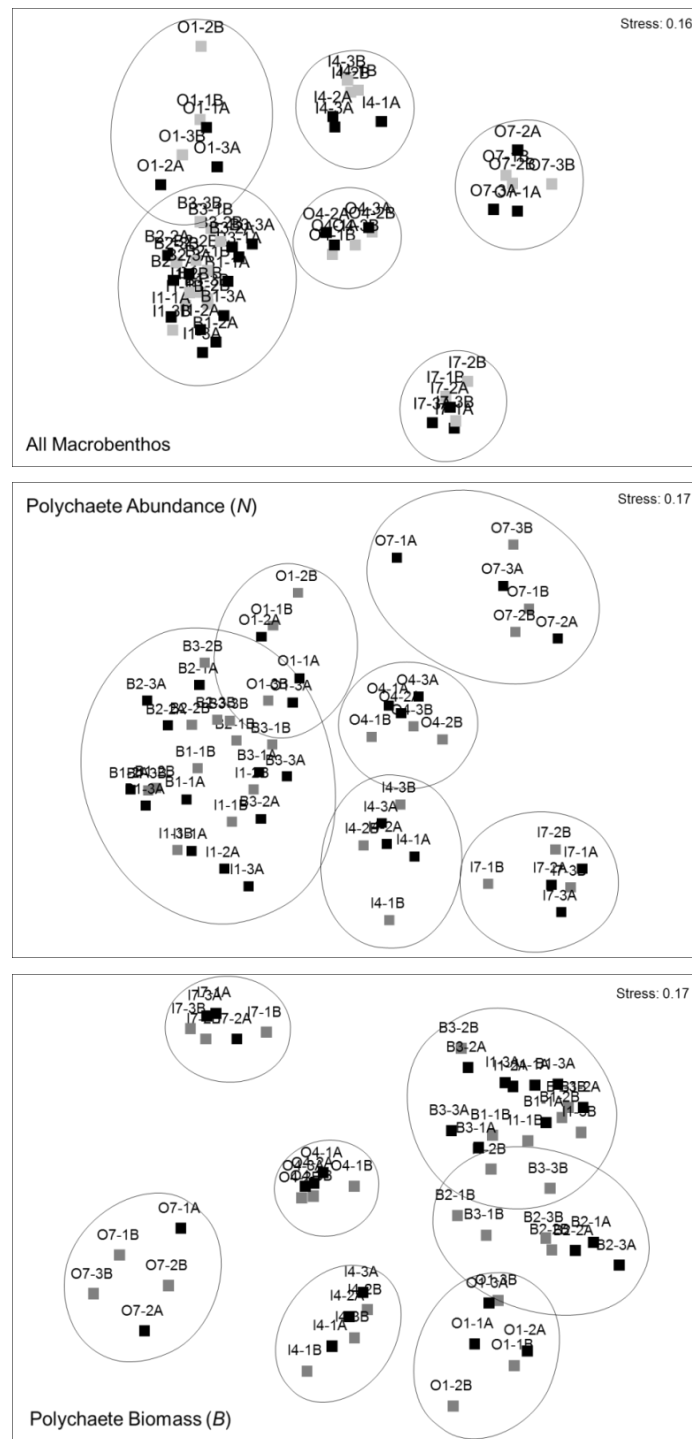


Figure 5.7. MDS ordinations of square root transformed abundance data for all macrobenthic fauna and polychaete abundance (*N*) and biomass (*B*) only.

The MDS plot of polychaete Family abundance data defined four sample groups at a B-C similarity of 40% (Fig. 5.8). Group I was comprised of IS and MS samples from DN and TK, respectively. The second sample group (Group II) was comprised of outer shelf samples collected from TK and DN as well as mid-shelf samples from the latter region. Inner shelf samples from Richard's Bay and Thukela as well as outer shelf samples collected during cruise A from the former region formed the third sample group (Fig. 5.8). The last sample Group (IV) was composed of MS and OS samples collected during cruise B from the RB feature area. Ordination analysis of polychaete feeding guild abundance identified one outlier (DN-OS-1A) which was removed and the analysis re-done. The MDS plot of polychaete feeding guild abundance data revealed the presence of four sample groups defined at a B-C similarity of 54% (Fig. 5.8). The aggregation of replicate samples from the same station were less clear in this ordination with samples from all station in RB and the MS in TK falling in several groups.

The correlation between matrices obtained from polychaete abundance data aggregated to different levels are used to infer the effect of such aggregations. The strength of the relationship, as measured by the Spearman correlation coefficient ( $\rho$ ) calculated between matrices, decreases as greater levels of aggregation are applied to polychaete abundance and biomass data reflecting the loss of information associated with aggregations to the Family and feeding guild levels (Table 5.3). The stress values associated with MDS ordination plots also increase as greater levels of aggregation are applied on the polychaete abundance and biomass data, reflecting the loss of ability to adequately represent sample relationships (Fig. 5.8).

The effects of aggregating polychaete abundance data were also examined by two-way ANOSIM testing for significant differences in polychaete community structure between Bight regions and shelf positions. Values of the ANOSIM *R*-statistic in global tests for differences between these factors decreased with aggregation to the Family and feeding guild level (Table 5.4). When considering the pairwise interactions, aggregating polychaete abundance data to higher levels affected the ability of ANOSIM to discriminate between feature areas and shelf positions. Despite this, differences in polychaete community structure among regions and shelf positions were highly significant ( $p < 0.001$ ) at each aggregation level (Table 5.4).

Lowest identifiable taxon

Stress: 0.17

Family

Stress: 0.18

Feeding guild

Stress: 0.18

Table 5.3. Pairwise comparisons of multivariate community structure using the RELATE procedure on polychaete abundance data analysed to the lowest identifiable taxon and aggregated to family and feeding guild. Bold values indicate significant Spearman's rank ( $\rho$ ) correlations,  $p < 0.001$  (10 000 permutations).

LEVEL	Family	Feeding guild
Lowest identifiable taxon	<b>0.540</b>	<b>0.327</b>
Feeding guild	<b>0.794</b>	

Table 5.4. Summary of results from two-way ANOSIM for comparisons among feature areas (RB, TK, DN) and shelf positions (IS, MS, OS) using polychaete abundance data analysed to the level of lowest identifiable taxon and aggregated to family and feeding guild. RB=Richard's Bay, TK=Thukela, DN=Durban, IS=Inner shelf, MS=Mid-shelf, OS=Outer shelf. Bold values indicate significant differences,  $p < 0.001$ .

LOWEST IDENTIFIABLE TAXON Region: $R=0.994$ , $p < 0.001$ Shelf position: $R=0.902$ , $p < 0.001$ <i>Pairwise R-statistic</i>				FAMILY Regions: $R=0.861$ , $p < 0.001$ Shelf positions: $R=0.793$ , $p < 0.001$ <i>Pairwise R-statistic</i>				FEEDING GUILD Regions: $R=0.767$ , $p < 0.001$ Shelf positions: $R=0.682$ , $p < 0.001$ <i>Pairwise R-statistic</i>			
Feature Area	RB	TK	DN	Feature Area	RB	TK	DN	Feature Area	RB	TK	DN
RB	0.000	<b>0.996</b>	<b>0.991</b>	RB	0.000	<b>0.870</b>	<b>0.883</b>	RB	0.000	<b>0.755</b>	<b>0.802</b>
TK		0.000	<b>0.999</b>	TK		0.000	<b>0.938</b>	TK		0.000	<b>0.848</b>
DN			0.000	DN			0.000	DN			0.000
Shelf position	IS	MS	OS	Shelf position	IS	MS	OS	Shelf position	IS	MS	OS
IS	0.000	<b>0.958</b>	<b>0.876</b>	IS	0.000	<b>0.897</b>	<b>0.857</b>	IS	0.000	<b>0.834</b>	<b>0.717</b>
MS		0.000	<b>0.878</b>	MS		0.000	<b>0.591</b>	MS		0.000	<b>0.465</b>
OS			0.000	OS			0.000	OS			0.000

### ***Polychaete community patterns related to families and feeding guilds***

Bubble plots of the most prolific Families superimposed on the MDS ordination of polychaete abundance data provided a visual interpretation for observed spatial differences in polychaete community composition between feature areas and shelf positions, while SIMPER analysis identified the polychaetes responsible for typifying sample groups and discriminating between them (Fig. 5.9).

The highest numbers of the most abundant Family, Onuphidae were recorded from inner and mid-shelf samples collected from TK during cruise A (Fig. 5.9). *Epidiopatra papillosa*, recorded exclusively in mid-shelf samples from the DN was identified by SIMPER as the primary taxon typifying sample Group V and separating this from the other sample groups defined in the ordination of polychaete abundance data. Fewer numbers of onuphid polychaetes were recorded across all depths sampled in RB and DN but were rarer in outer shelf samples from TK (Fig. 5.9). Gut contents analysis confirmed the presence of fine dark

material and faecal pellets in many onuphids resulting in their classification as mobile, jawed facultative omnivores (FOMJ).

Spionidae individuals were most abundant in the fine sands of the IS and muddy OS (Group III) positions sampled in TK during the high rainfall period. Spionid polychaetes were also found in high numbers in DN outer (Group II) and mid-shelf (Group IV) samples. All shelf positions sampled in Richard's Bay and shallow depths (IS) sampled in Durban supported the fewest numbers of these polychaetes. Results of SIMPER analysis identified *Prionospio* sp.13, *Prionospio dubia* and *Dipolydora capensis* as important typifying and discriminating taxa for Groups II, III and IV, respectively. Spionids are interface feeders (IDT), switching between suspension and surface deposit feeding under different environmental conditions (Fig. 5.9).

The bubble plot of Capitellidae abundance superimposed on the MDS ordination showed that this Family was most abundant at inner shelf depths sampled in the Durban feature area (Group I) (Fig. 5.9). These polychaetes were also recorded in relatively high numbers in mid (Group IV) and outer shelf (Group V) samples from TK. *Notomastus latericeus* was the primary typifying taxon for Group I samples as well as being an important discriminating taxon in the pairwise comparisons between this and other sample groups. *Capitellidae* sp.10 and *Rashgua* sp.1 were also identified by SIMPER analysis as being good typifying taxa for Groups IV and V, respectively, as well in the discrimination of these sample groups from others. Capitellids are mobile, subsurface deposit feeders with an eversible sac like pharynx (BMX) (Fig 5.9).

#### **Polychaete community patterns related to environmental variables**

The results of BIO-ENV analysis showed that a combination of physico-chemical variables provided the best match between environmental parameters measured in the present study and polychaete community patterns (Table 5.5). To aid visualisation, values of the environmental parameters identified in BIO-ENV analysis were also superimposed as bubbles on the MDS ordination plot, Bubble sizes corresponding to the magnitude of the presented variable. As in analysis of the whole macrobenthic community (Chapter 3) depth ( $\rho_w=0.696$ ) was the single most important variable describing polychaete community structure, with depths increasing from left to right on the MDS plot (Fig 5.10, Table 5.5).

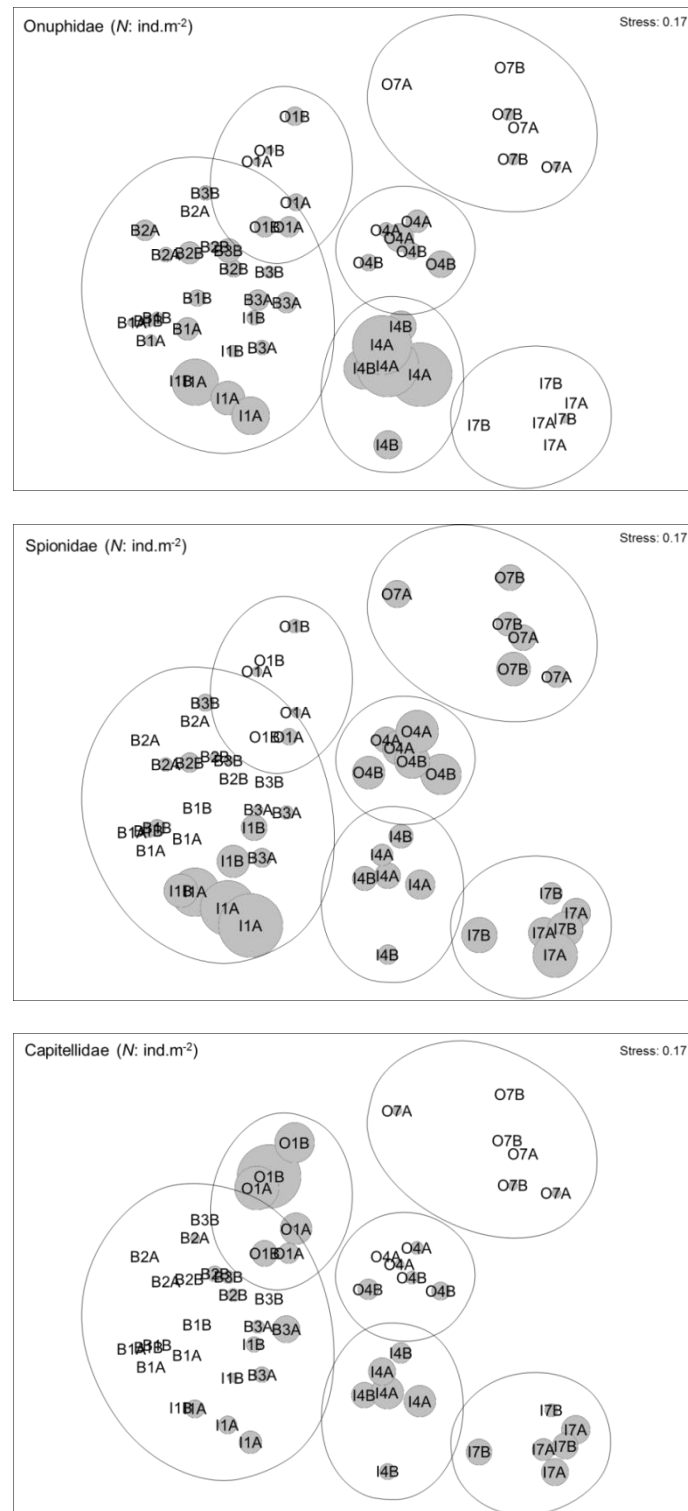


Figure 5.9. MDS plot of polychaete abundance data at the level of lowest identifiable taxon for the 54 samples collected during cruises A and B. Bubbles are superimposed values of the most abundant polychaete Families.

medium sand (mms) and mud ( $p_w=0.848$ ) were determined to be the most influential environmental factors (Chapter 3). The bubble plot of temperature values superimposed on the ordination of polychaete taxon abundance showed that near bottom temperatures were

The highest correlation coefficient ( $\rho_w=0.768$ ) was obtained for the combination of depth, temperature, coarse sand (cos), mud and Nitrate concentration ( $\text{NO}_3$ ) (Table 5.5). These results agree well with those obtained when considering all macrobenthic fauna, where the combination of depth, temperature and the sedimentary parameters: coarse sand (cos), highest across the narrow Richard's Bay area ( $23.09^\circ\text{C} \pm 1.92\text{SD}$ ) and wide, Thukela area ( $18.40^\circ\text{C} \pm 2.15\text{SD}$ ) (Fig. 5.10). Relatively high temperatures were also associated with inner ( $21.67^\circ\text{C} \pm 2.09\text{SD}$ ) and mid-shelf stations ( $17.04^\circ\text{C} \pm 0.57\text{SD}$ ) in Durban, while the lowest temperatures were recorded at the outer shelf ( $13.12^\circ\text{C} \pm 0.30\text{SD}$ ) in this area (Fig. 5.10).

The percentage of coarse sand (cos) and mud were identified as the most important sedimentary parameters influencing polychaete community patterns at the level of lowest identifiable taxon (Table 5.6). While the amount of cos was generally low in all samples, the highest percentages of this sediment grade were recorded in MS samples from the TK (cos:  $28.81\% \pm 10.39\text{SD}$ ) (Fig. 5.10). Inner (cos:  $5.75\% \pm 2.79\text{SD}$ ) and OS (cos:  $9.01\% \pm 2.45\text{SD}$ ) sediments from DN as well as outer shelf sediments from the TK (cos:  $3.57\% \pm 1.83\text{SD}$ ) also contained small amounts of cos. Muddy sediments were concentrated on the OS in the Thukela feature area (mud:  $78.16\% \pm 10.51\text{SD}$ ) (Fig. 5.10).

Concentrations of Nitrate were highest in waters of the DN ( $\text{NO}_3$ :  $2.66\mu\text{mol.L}^{-1} \pm 0.16\text{SD}$ ) and Thukela feature area ( $\text{NO}_3$ :  $1.52\mu\text{mol.L}^{-1} \pm 0.49\text{SD}$ ), with the lowest nutrient concentrations recorded for Richard's Bay ( $\text{NO}_3$ :  $0.10\mu\text{mol.L}^{-1} \pm 0.06\text{SD}$ ) waters (Fig. 5.10).

Table 5.5. BIO-ENV analysis showing the weighted Spearman rank correlation ( $\rho_w$ ) between combinations of environmental variables and polychaete community structure. Bold type indicates the best variable combination which was significant  $p<0.001$  (10 000 permutations).

No. of variables	$\rho_w$	Variables
1	0.696	Depth
2	0.761	Depth, Mean phi ( $\phi$ )
3	0.759	Depth, mud, Mean phi ( $\phi$ )
4	0.765	Depth, Temperature, cos, mud
5	<b>0.768</b>	<b>Depth, Temperature, cos, mud, <math>\text{NO}_3</math></b>

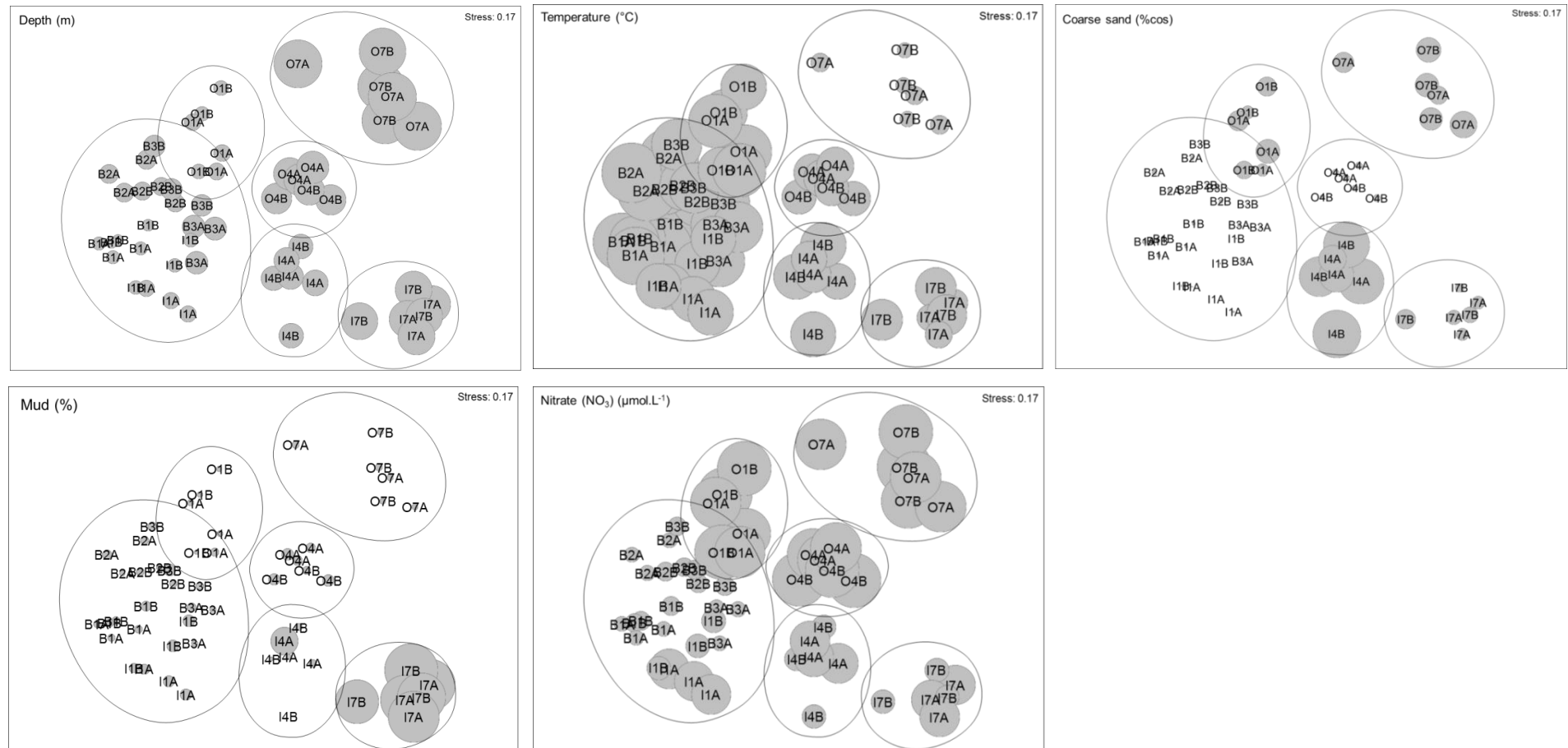


Figure 5.10. MDS bubble plots of significant environmental variables , identified through BIO-ENV analysis, as best describing abundance patterns of polychaetes at the level of lowest identifiable taxon.

## 5.4 Discussion

The Natal Bight supports a rich polychaete fauna with 40 families and over 300 taxa recorded in this study. Many taxa could not be assigned to Species or even Genus level, as taxonomic information pertaining to South African Polychaeta is outdated. It appears that there may be new distribution information here for taxa occurring elsewhere in the world and even that some specimens sampled may be new species. The number of families recorded is comparable to other studies. For example 36 polychaete families were recorded from the coast of Thailand, while the continental shelf off India, Brazil and New Zealand supported 32 and 34 families, respectively (Probert and Wilson 1984, Muniz and Pires 2000, Barrio-Froján *et al.* 2005, Joydas *et al.* 2009). At the level of lowest taxon, less than half the number of taxa recorded in the present study were sampled on the Indian shelf (165 taxa), while 150 taxa were recorded off the coast of Tunisia and 126 taxa were found off Brazil (Muniz and Pires 2000, Joydas *et al.* 2009, Zaâbi *et al.* 2010).

### *The effect of cruise*

In the present study samples were collected from the same stations during a high and low rainfall period in order to investigate what effect short-term seasonal patterns may have on polychaete community dynamics. The input of nutrients from rivers and estuaries to the coastal zone, the availability of these nutrients to water column processes and their incorporation within sediments changes seasonally together with the structure and function of the polychaete community. Although the temporal scale adopted in this study does not adequately represent seasonal variation, higher polychaete taxon richness, abundance and biomass was recorded during the summer period of high rainfall. In contrast with these results, studies conducted off Thailand and India found that numbers of polychaetes were higher during the low rainfall period (Barrio-Froján *et al.* 2005, Anbuezhian *et al.* 2012). The differences in univariate measures were not significant and no significant differences in polychaete community structure were detected between high and low rainfall periods in the present study. Despite this there were subtle and important changes in the composition and functioning of polychaete communities between cruises A and B, as was found for the entire community (Chapter 3), and it is probable that the small time scale adopted in the present study may not be sufficient to elucidate significant seasonal patterns.

### ***Polychaete Family patterns***

Onuphidae and Spionidae were the most abundant and taxon rich polychaete families sampled from the three feature areas under investigation. Members of the Onuphidae Family are commonly classified as omnivores, but analysis of gut contents revealed that the guts of many onuphids were full of sediment and they were thus classified as facultative omnivores in the present study. Some authors have indicated that since omnivores are not dependent on a single food source, whose abundance may vary markedly throughout the year, they achieve greater ecological stability by utilising a wider range of food than a specific niche feeder (Sanders *et al.* 1962, Pagliosa 2005). Numerous studies have found that Spionidae are among the most diverse families sampled on continental shelves (Probert and Wilson 1984, Muniz and Pires 2000, Dubois *et al.* 2009, Joydas *et al.* 2009) while Onuphidae were the most abundant Family sampled in a recent study conducted off the northeast coast of Tunisia (Zaâbi *et al.* 2010).. The high abundance and number of spionid taxa recorded for the Thukela area is not surprising as these polychaetes are known to be tolerant of high turbidity conditions associated with freshwater and sediment outflow from rivers, being able to colonise mobile sediments with ease (Dauer *et al.* 1981, Maurer and Leathem 1981, Paiva 1993).

### ***Feeding guild assignment***

The feeding guild assignments applied in this study were based on *in situ* gut contents observations, which led to changes in classification from those provided in Fauchald and Jumars (1979). Many of the taxa commonly accepted to be strict carnivores or omnivores had guts full of fine, dark sediment and were therefore classified as facultative feeders. While useful and commonly applied, this finding highlights that divisions of polychaetes into feeding modes or guilds is often misleading. In extension, results for the present study and others show that the same taxa may utilise alternative feeding modes in different geographic locations or under different environmental conditions (Gaston 1987, Taghon and Greene 1992, Salas *et al.* 2006, insert 2013 ref). Feeding guild classifications are often applied at the Family level which further emphasises the cautionary approach that should be applied when extending results from one closely related taxon to another. The criteria for assignment should be defined *a priori* and be as unambiguous as possible (Simberloff and Dayan 1991). While the analysis of gut contents in the present study enabled crude observations and inferences about feeding mode, there is a need to corroborate these observations through classical laboratory feeding studies and techniques like stable isotope analysis.

***Feeding guild patterns***

Biomass of BMX far outweighed the wet weight of other feeding guilds during both sampling periods, with the majority being supported in Thukela at the outer shelf position, characterised by high percentages of mud and TOC. This is not surprising given that deposit feeding polychaetes are well known to be abundant in fine sediments owing to their reliance on these fine grains and their associated organic matter for feeding (Maurer and Leathem 1981, Gaston 1987, Muniz and Pires 2000, Mandal and Harkantra 2013).

The abundance of surface deposit feeders generally decreases with depth (Gaston 1987-). Results from the present study are in agreement, with the lowest numbers of surface deposit feeding polychaetes recorded for the outer shelf position. Surface deposit feeders have also been reported to be negatively correlated with fine sand and high organic contents, dominating in areas of enhanced phytoplankton production (Gaston 1987). The greatest abundance and biomass of surface deposit feeding polychaetes sampled in the present study were supported in the Thukela area and mid-shelf station, characterised by the highest Chl-*a* concentrations and medium and coarse sand, low in organic contents. In contrast, numbers of subsurface deposit feeders tend to increase with depth across continental shelves and are positively correlated with mud, rich in organic carbon (Gaston 1987, Pagliosa 2005). In the present study the greatest abundance of subsurface deposit feeders was recorded for the inner shelf while mid-shelf depths supported the greatest biomass. Subsurface deposit feeders are generally considered to be less temporally variable than surface deposit feeders because they inhabit deeper sedimentary layers and are thus able to evade disturbance events which unsettle surficial layers (Levinton and Kelaher 2004). Results from the present study showed that numbers of both surface and subsurface deposit feeders were lower during the low rainfall period but individuals of the latter feeding mode were always more abundant than surficial feeders.

In this study suspension feeders and niche feeding omnivores contributed little to the total abundance of polychaetes in accordance with a study conducted off Brazil (Muniz and Pires 1999). Gaston (1987) found that suspension feeders were supported in the greatest abundance at intermediate depths on the mid-Atlantic Bight. In the present study the greatest number and wet weight of suspension feeders and sessile, interface feeders were recorded from outer shelf depths. The increase in this feeding mode at the shelf break may be due to a frontal system which is present here causing enrichment of bottom waters (Gaston 1987).

Mobile polychaetes, indicative of unstable habitats, dominated all Bight regions and shelf positions sampled in the present study, in agreement with results from the mid-Atlantic Bight, Cretan and Hong Kong shelves (Gaston 1987, Tselepides *et al.* 2000, Cheung *et al.* 2008). Sessile polychaetes were most abundant in the Durban feature area and outer shelf position with the abundance of most sessile feeding guilds increasing during the low rainfall period. A sessile life style is generally associated with deep areas characterised by organic-rich fines (Maurer and Leathem 1981, Gaston 1987, Muniz and Pires 2000). Gaston (1987) found that discretely mobile polychaetes were most abundant at inner and mid-shelf depths in accordance with results from the present study.

The abundance of carnivorous polychaetes has been reported to decrease with depth and be correlated with sandy substrates (Gaston 1987, Pagliosa 2005, Zaâbi *et al.* 2010). Other studies have found the abundance of carnivores to increase with depth which is thought to be related to the limited nutrients available in these environments (Tselepides *et al.* 2000). The vertical penetration of Oxygen as well as feeding and movement of carnivores depends on the size of interstitial spaces and has been reported to increase in sandy substrates which generally support an abundant macrobenthic community (Gaston 1987, Rodil *et al.* 2009). In the present study the highest numbers and biomass of niche feeding carnivores were sampled from mid-shelf depths characterised by a medium to fine sandy bottom supporting a diverse community. The greatest abundance and biomass of facultative carnivores (C) was supported in the fine and very fine sands of the outer shelf. This confirms general trends reported in the literature for carnivores and illustrates the reliance of facultative feeders on finer sediment grades. When comparing sampling periods, there was a general increase in a number of C, jawed polychaetes during cruise B namely: Glyceridae, Nephtyidae and Eunicidae. This is in agreement with numerous studies which have reported an increase in carnivorous benthic taxa following river outflow and sediment deposition (Consentino and Giacobbe 2006)

Deposit feeding polychaetes and interface feeders were thus among the most abundant feeding guilds recorded from the present study during both high and low rainfall periods. Numerous studies conducted in shelf, intertidal and estuarine habitats have found that deposit feeding polychaetes/macrobenthos dominate in all seasons (Sanders *et al.* 1962, Whitlatch 1981, Paiva 1993, Muniz and Pires 2000, Tselepides *et al.* 2000, Cheung *et al.* 2008, Rodil *et al.* 2009, Mandal and Harkantra 2013). Deposit and suspension feeding polychaetes have been shown to

be more tolerant to environmental changes and thus are able to occupy a wider range of habitats (Muniz and Pires 1999).

### ***Surrogacy and taxonomic sufficiency***

Analysing macrobenthic communities to various higher taxonomic and functional levels is important in terms of the potential this approach has for saving time and money required to process benthic samples (Warwick 1988a, Warwick 1988b, Ferraro and Cole 1990, Olsgard *et al.* 1997, Clarke and Warwick 1998, Mistri and Rossi 2001, Ellingsen *et al.* 2005, Joydas *et al.* 2009, Benedetti-Cecchi *et al.* 2010). Similarly, analyzing only one faunal component may produce the same results as for the whole macrobenthic community so that savings can be achieved in this way too (Warwick 1988a, Warwick 1988b). Results from the present study showed that the same community patterns were obtained from the analysis of polychaete abundance and biomass data at the level of lowest identifiable taxon when compared with the full complement of macrobenthic fauna. Other studies have confirmed the usefulness of polychaetes structure as a proxy for all macrobenthos (Pavia 1993, Tselepides *et al.* 2000, Cheung *et al.* 2008). This is an important finding in the context of future studies on the Natal Bight which could confidently rely on the polychaete component as a proxy for the macrobenthic community as a whole.

While Family level analysis has been identified, by numerous authors as a sufficient to elucidate patterns at the lowest taxon level, the effects of data aggregation are variable (Warwick 1988a, Warwick 1988b, Olsgard *et al.* 1997). Results from the present study showed that ordinations of polychaete abundance data at both the Family and feeding guild level produced sample configurations which varied considerably from lowest taxon level analysis. In contrast with this, Pagliosa (2005) found that analysis based on guilds produced similar results to those found using taxa. This suggests that for the polychaete fauna of the Natal Bight ecological information is lost when aggregating taxon data to higher taxonomic and functional levels. The results of the present study emphasize the fact that caution is necessary when using data analysed to higher taxonomic and functional levels and that baseline studies at the finest resolution of taxa need to be undertaken before an appropriate aggregation level is defined (Terlizzi *et al.* 2003).

***Polychaete community patterns***

The shallow water (28.95m  $\pm$  10.34SD) Richard's Bay and Thukela, inner shelf group was dominated by discretely mobile interface feeders such as, *Owenia fusiformis*, a tubiculous polychaete with a cosmopolitan distribution and commonly found inhabiting shallow coastal areas subjected to riverine input (Probert and Wilson 1984, Paiva 1993). Wieking and Krönke (2005) found that interface feeding macrobenthos dominated shallow stations on the Dogger Bank. The low organic contents of the sediments characterising this group infers that the large number of interface feeding polychaetes found here may have been reliant on the nutrients brought into the coastal zone by the Thukela River and therefore were most likely to suspension feed during the period of high rainfall, when freshwater outflow was at a maximum. Detritus and fine particulate organic material carried into the coastal realm by rivers provides a direct source of nutrition for interface feeders and it is expected that these generalists would dominate in such environments, particularly during periods of high rainfall (Dauer *et al.* 1981, Maurer and Leathem 1981, Pagliosa 2005, Consentino and Giacobbe 2006). This group also supported high numbers of mobile, jawed strict carnivores and facultative carnivores represented by *Nephtys* sp.4 and *Lumbrineridae* sp.1, respectively. Carnivores are typically associated with sandy substratum with low organic contents (Fauchald and Jumars 1979, Maurer and Leathem 1981, Gaston 1987, Gaston and Nasci 1988, Paiva 1993, Zaâbi *et al.* 2010, Mandal and Harkantra 2013). Sandy bottoms are thought to be preferred because of the proliferation of potential prey items in the interstitial spaces (Muniz and Pires 2000).

The shallow water assemblage in Durban was located near to the harbour entrance. Harbours are heavily impacted coastal marine areas subjected to a range of anthropogenic, industrial and maritime discharges (Mandal and Harkantra 2013). The polychaete community of this inner shelf, fine sand group was characterised by a high abundance and biomass of the capitellid, *Notomastus latericeus*, and the Ophelid, *Ophelia* cf. *roscoffensis*, both being mobile subsurface deposit feeders without jaws (BMX). High densities of capitellids and ophelids are characteristic of disturbed habitats (Tsutsumi 1987, Dean 2001, Dean 2008).

Mid-shelf stations, characterised by a mixture of fine, medium and coarse sand with gravel, supported a diverse community with the most polychaete taxa and individuals being recorded here during both high and low rainfall periods. In agreement with this, Zaâbi *et al.* (2010) found the greatest diversity of polychaetes at sites with heterogenous sediment composition, while

Joydas *et al.* (2009) recorded most polychaete taxa from 51-150m on the continental shelf off India.

The mid-shelf polychaete community in Thukela inhabited medium to coarse sands with low organic contents and was characterised by a high abundance and biomass of the facultative omnivore, *Epidiopatra papillosa*. The abundance of this taxon was dramatically reduced during the period of low rainfall. Mancinelli *et al.* (1998) reported that the availability of specific grain sizes seemed to be crucial to the survival of many tubiculous polychaetes. The presence of suitable sediment for tube building may therefore be a controlling factor affecting the permanence of tubiculous polychaetes at this station following periods of high rainfall. Another possibility for the reduction in numbers of *Epidiopatra papillosa* during cruise B may be that river waters, rich in detrital material have been implicated as contributing to sustaining large aggregations of omnivorous polychaetes (Consentino and Giacobbe 2008). Similarly, the high abundance and biomass of polychaetes supported at this shelf position may be attributed to the high levels of primary production recorded in this region during cruise A (Consentino and Giacobbe 2008). Changes in primary production have been documented to cause reductions in macrobenthic biomass and an alteration in community composition (Dubois *et al.* 2009). Surface deposit feeders, such as *Poecilochaetus serpens* and subsurface deposit feeders, typically represented by *Capitellidae* sp.10 were also supported in high abundance and biomass here.

The polychaete community supported in the fine sands of the mid-shelf in the central region was characterized by high numbers and biomass of the interface feeding *Dipolydora capensis* and *Spiochaetopterus* sp.13, the facultative omnivore, *Onuphis eremita* and the tubiculous, subsurface deposit feeder, *Maldanidae* sp.45. This shelf position was dominated by fine sands but there were biogenic elements present here which increased the complexity of the bottom environment and facilitated the establishment of a diverse polychaete community. The spionids, *Dipolydora capensis*, were found exclusively inhabiting dead Astrorhizida Foraminifera and other macrobenthic fauna such as Cnidaria and Cirripedia were supported by the structural integrity of chaetopterid tubes.

The outer shelf in the Richards Bay feature area supported the greatest biomass but low abundance of polychaetes, during cruises A and B. In contrast with these results, Tselepidis *et al.* (2000) found that dry weight macrofaunal biomass decreased with depth on the Cretan

shelf. This suggests that compared to the inner and mid-shelf, polychaetes inhabiting the outer shelf are of a larger body size. The fact that the biomass of polychaetes recorded from cruises A and B were not significantly different at this shelf position suggests that nutrient supply, which serves as a proxy for food supply in the present study, is relatively constant at this shelf position, potentially maintained by shelf edge upwelling in the Northern Natal Bight due to the persistent course of the Agulhas Current (Pearce 1977, Heydorn *et al.* 1978, Lutjeharms *et al.* 2000b).

The muddy outer shelf in Thukela was dominated by interface and subsurface deposit feeders which contributed most to the abundance and biomass of polychaetes sampled here. The relatively high organic content (~2-9%) of outer shelf sediments infers that these trophic groups derive their nutriment from the substrate, suggesting that interface feeders may preferentially adopt deposit feeding behaviour here. Taxa characterizing this group in terms of abundance and biomass included *Rashgua* sp.1, *Spiochaetopterus* sp.12 and *Prionospio dubia*. Organic-rich, fine grained sediments are well known to support a high density of deposit feeding polychaetes which ingest the sediment and associated organic matter when feeding (Pearson 1970, Fauchald and Jumars 1979, Field *et al.* 1982, Arasaki *et al.* 2004).

The medium to fine sands characterizing the outer shelf in Durban supported a high abundance and biomass of *Magelona* sp.6, *Prionospio* sp.13 and *Rhodine* sp.1. Functionally the polychaete community here was characterized by a high abundance and biomass of interface and surface deposit feeders. The greatest number of sessile, suspension feeding polychaetes were also supported here, particularly during the period of low rainfall. It is uncommon for suspension feeders to be abundant in deeper waters which are expected to be nutrient poor (Maurer and Leathem 1981). The abundance of sessile, suspension feeding polychaetes at this station, which are reliant on increased water movement and water column nutrient concentrations supports the known presence of an eddy system offshore of Durban.

### **Relating polychaetes patterns to environmental variables**

The multivariate analysis, based on polychaete taxon abundance, clearly separated communities based on Bight region and shelf position. Depth was identified as the single most important environmental variable driving polychaete community structure on the Natal Bight in accordance with results obtained when considering the full compliment of macrobenthos (Chapter 3). This environmental variable is well documented to be the most significant abiotic

determinant affecting benthic community structure on continental shelves (Maurer *et al.* 1999, Bergen *et al.* 2001).

Despite the well-known effect of depth, it is often the environmental factors that co-vary with depth, such as Primary Production, temperature, physical stress and grain size, which have the greatest influence on benthic communities (Maurer *et al.* 1999, Zaâbi *et al.* 2010, Mandal and Harkantra 2013). Current velocities were not measured directly in the present study, but hydrodynamics are responsible for shaping the sedimentary environment and are therefore important indirect habitat drivers of polychaete community patterns. Results from the present study indicate that the combination of depth with the water column variables, temperature and Nitrate concentration as well as the sedimentary parameters, mud and coarse sand were most strongly correlated with polychaete community patterns elucidated at the level of lowest identifiable taxon. In a study investigating polychaete community structure and function in a Bay off Chile, South America it was found that the combination of depth, mud, grain size and organic content explained over 90% of the observed patterns of polychaete abundance and distribution (Carrasco and Carbajal 1998).

Muddy sediments are known to support high numbers but low diversity while sandy habitats support fewer individuals but higher diversity (Sanders 1968, Field *et al.* 1982, Gray 2002, Barrio-Frojan *et al.* 2012). Results from the present study showed that the polychaete assemblage supported in the fine sand and mud at the outer shelf was the most diverse sampled during both cruises A and B. In contrast, the community with the lowest diversity was found at the inner shelf characterized by fine and very fine sand. The low diversity of inner shelf stations is most likely related to the physical disturbance experienced at these shallow depths. Inner shelf sediments also supported the lowest number of polychaete taxa and biomass. During the period of high rainfall, conditions in the pelagic realm indicated the influence of river and estuarine outflow, as warmer, low salinity waters are discharged into shallow shelf waters. Abundance, number of polychaete taxa and biomass were all reduced at this shelf position during the low rainfall period affirming the importance of river outflow in this region.

**Conclusion**

This study showed that the Natal Bight has a heterogeneous pattern of bottom sediment which is reflected in the structure of polychaete assemblages. Two sampling cruises were conducted to compare the community structure during high and low rainfall periods. There was little evidence of seasonality in the structure of polychaete communities on the Natal Bight, although the time period adopted in this study is not sufficient to elucidate temporal patterns. Results from this study have shown that changes in macrobenthic community structure can be elucidated by analyzing the polychaete community. The aggregation of polychaetes abundance data to higher taxonomic and functional levels resulted in a loss of ecological information and the ability to discriminate between feature areas and shelf positions. These results emphasize the importance of being cautious when using families and feeding guilds as surrogates for polychaete taxon data. The feeding guild classification scheme developed for this group by Fauchald and Jumars (1979) may be too general but at the same time the “fine tuning” of classification through *in situ* gut contents applied in the present study may have resulted in the guilds becoming too narrow. The present study has provided baseline information on polychaete community structure and functioning in three regions of the Natal Bight. This work remains a preliminary assessment and research must be expanded to reveal the full scale of polychaete biodiversity in the study area.

## CHAPTER 6. GENERAL DISCUSSION AND CONCLUSIONS

This study characterised the macrobenthic communities of inner, mid and outer shelf depths sampled in three oceanographic feature areas on the Natal Bight. Communities were compared and related to local water-column and sedimentary parameters measured during two cruises, correlated with a period of high and low rainfall aboard the *F.R.S Algoa*. The primary hypotheses under investigation were that there would be discontinuities in macrobenthic communities considering different sampling times, with depths and between feature areas. Communities were classified in terms of their taxon composition and the ecological function of constituent taxa. The last comprehensive benthic survey carried out on the Natal Bight was undertaken over 30 years ago, underlying the importance of the present study in providing baseline information for the region and in presenting the first attempt to relate structural and functional macrobenthic community patterns on the Natal Bight with local environmental parameters.

The present study formed part of a larger, multi-disciplinary programme under the auspices of the ACEP II, Natal Bight Ecosystem functioning project which aimed to investigate the influence of three potential nutrient sources driving the ecology of the Natal Bight. The oceanographic features identified as possible agents of nutrient input were located in each of the three areas under investigation namely Richard's Bay, Thukela and Durban.

Macrobenthic communities sampled off Richards Bay, Thukela and Durban were classified in terms of their dominant feeding mode, with interface feeding fauna defined as those which both suspension and deposit feed (Chapter 1, Chapter 3). The Natal Bight was found to support a diverse macrobenthic community, underlying the importance of biodiversity conservation and the sustainable management of coastal resources (Tselepedis *et al.* 2000). Comparison between the two sampling cruises revealed that there were no significant overall differences in measurable environmental parameters, macrobenthic community metrics or community composition. This is not surprising given that only one sampling period of each was included in the study. In terms of broad taxonomic groupings Polychaeta were the dominant macrobenthos accounting for 37.97% of the total abundance and 42.83% of the total numbers of taxa collected during the high rainfall period. Crustaceans were also an important faunal component accounting for a similar proportion of the macrobenthos (40.86%) collected during

the period of low rainfall. Crustaceans were predominantly Amphipoda followed by Decapoda including Brachyura, Penaeidea and Caridea, Ostracoda and Isopoda in decreasing order of abundance. Mollusca contributed an average of 11% to the total number of individuals sampled in the present study. Within the Mollusca, Bivalvia were dominant (76.58%), Gastropoda were less abundant (21.64%) and while dead Scaphopoda were abundant (personal observation), live specimens were rarely (1.78%) sampled. The remaining macrofaunal groups contributed little in number, with the most notable contribution from the Sipuncula (6.2%).

Comparisons within the three feature areas revealed no significant differences between high and low rainfall periods in the Richards Bay and Durban feature areas. Macrobenthic communities sampled in the central region of the Natal Bight during cruise A were significantly different, in terms of numbers of taxa, structure and functioning, from those sampled during the low rainfall period. This feature area is under the influence of the Thukela River, which discharges large amounts of nutrient-rich freshwater and fine sediments onto the shelf, particularly during the summer period of high rainfall. This finding warranted a more in depth analysis of the structure and functioning of macrobenthic assemblages in this feature area (Chapter 4).

Multivariate analyses of the 54 samples collected in the present study distinguished seven major sample groups, reflecting differences in feature area and shelf position in terms of taxon composition of macrobenthic communities. Inner and mid-shelf samples from the Richards Bay area clustered with inner shelf samples collected in the Thukela area to form a shallow (16-33 m), warm water (22.4°C), fine sand (mean  $\phi$  = 2.57) assemblage characterised by the surface deposit feeding amphipod, cf. *Basuto* sp. 2 and the carnivorous hermit crab, *Paguristes* sp. 1.

The shallow water samples collected off Durban were characterised by a coarser grade of fine sand (mean  $\phi$  = 2.02) and near bottom waters were slightly cooler (21.7°C) than found in the central and northern regions, probably reflecting the lack of significant freshwater and sediment outflow from estuarine systems in the Durban inshore area. During laboratory processing, it was noted that these samples contained a considerable amount of biogenic material in the form of mollusc shells, but the recovery of live specimens was low. The presence of empty limpet shells was noted exclusively from these samples indicating the presence of a subtidal rocky component in this area. The depths sampled on the inner shelf in

the southern Bight (22-27 m) were within the range sampled in the central and northern regions, but the community sampled here was notable and characterised by the presence of an abundant *Callichirus gilchristi* population. This taxon is presented in Barnard (1950) as *Callianassa gilchristi*, but has subsequently been moved to the genus *Callichirus* (Sakai 2011). Barnard (1950) found this taxon in Durban Bay and off the Natal coast at a depth of 36.6 m, which is in good agreement here, with inner shelf depths sampled off Durban. Specimens sampled from the second sampling cruise in the low rainfall period were of a larger body size, and numerous female specimens were gravid (personal observation) when compared with those collected during the high rainfall period, indicating that these animals reach sexual maturity and reproduce in the winter months close to August. Callinanassid shrimp are important ecosystem engineers in benthic communities (Cadée 2001, Reise 2002, Pillay and Branch 2011). They burrow beneath the sediment surface, transporting material to depth and expelling residual sediment and faecal material to the surface, creating mounds (Cadée 2001, Pillay and Branch 2011). These crustaceans are considered highly important bioturbators in macrobenthic habitats, reworking a vast amount of sediment, thereby significantly modifying physical and chemical conditions and the surrounding macrobenthic community (Griffis and Suchanek 1991, Cadée 2001, Reise 2002, Krönke *et al.* 2004). Numerous studies have reported enhanced organic content and phaeopigments within burrow structures and on burrow walls, which stimulates microbial activity (Reise 2002, Pillay and Branch 2011). The burrowing activity of callinanassid shrimp also increases the penetration of Oxygen into the sediment and the diffusion of solutes across the sediment-water interface (Reise 2002, Pillay and Branch 2011). Burrow openings, referred to as pits and sediment mounds at the other end of the burrow structure also have an effect on bottom flow dynamics and nutrient entrainment (Pillay and Branch 2011). Sand prawns occur in high numbers, excluding from the sediment suspension and surface deposit feeders but allowing the accommodation of mobile taxa, such as ostracods, other subsurface deposit feeding macrobenthos (Pillay *et al.* 2007, Reise 2002, Pillay and Branch 2011). The ostracod, *Myodocopida* sp.16 and the subsurface deposit feeding polychaetes, *Notomastus latericeus* and *Ophelia* cf. *roscoffensis* were abundant and were major contributors to the total polychaete biomass supported at this station. The ophelids were observed to have guts full of sand grains. While subsurface deposit feeding macrobenthos are generally considered more abundant at deeper locations, the occurrence of macroalgal fragments in these samples indicates that light penetration is sufficient to support photosynthesis and benthic primary production. Benthic phototrophs are a ubiquitous component of shallow water bottoms receiving sufficient light, where sediments and biogenic material in the form of mollusc shells, for example, provides suitable substrate for attachment

(Reise 2002, Grippo *et al.* 2011). Cyanobacteria excrete extracellular polymeric substances which bind them to sand grains, creating microbial mats that stabilise and enrich the sediment, allowing for the development of a rich microbial community, providing food for deposit feeders (Reise 2002, Grippo *et al.* 2011). In contrast, the turbid conditions associated with river outflow and northwards advection of river plume waters mean that light penetration and primary production will be significantly impeded in the shallow central and northern regions. In addition the deposition of fine sediments would cover biogenic elements limiting their role in the shallow sedimentary environment of the central Bight.

Mid-shelf communities of the central and southern regions were particularly diverse, supporting an abundant and taxon rich community. This is due to the heterogeneous sediments characterising these stations. Complex sediments are known to support diverse macrobenthic communities, in part due to the increased availability of microhabitats (Gray 1981, Probert and Wilson 1984, Hutchings *et al.* 2002). The mid-shelf community off the Thukela River was characterised by a dense population of the tubiculous polychaete, *Epidiopatra papillosa*, occurring exclusively at this station. This taxon was particularly abundant at this station during the summer period of high rainfall and along with the bivalves *Nucula* sp.1 and *Nuculana* sp.1 were typifying and abundant taxa. This facultative omnivore, *Epidiopatra papillosa* remained a characteristic inhabitant of this station during cruise B, but numbers of onuphids were dramatically reduced as fossorial amphipoda, cf. *Basuto* sp. 2, *Ampelisca* sp.9 and *Byblis giamardii* characterised the community sampled here. Onuphid polychaetes have been documented to rely on phytoplankton and macrodetrital material brought into the marine realm by rivers (Grippo *et al.* 2011). The faunal component sampled here indicated an exposed rocky component at this location due to the proximity of this shelf position to the coarse paleo-dune cordon which runs along the 60 m isobath. Adults of the parasitic isopod family Gnathiidae and the amphipod *Leucothoe spinicarpa* that inhabit sponges as well as the pelagic prawns, *Lucifer* spp. and caprellid amphipods that cling to algae, hydroids or bryozoa were sampled from this station. During the high rainfall period a surface phytoplankton bloom was found in the mid to outer shelf regions of the central Bight. The large volume of fines brought into the shallow coastal zone during periods of high river outflow increases the turbidity of inner shelf waters so that the nutrient rich plume waters are only available to primary producers some distance away from the river mouth in deeper waters. Boundaries between different water masses are characterised by high primary production (Mann and Lazier 1996, Sumida *et al.* 2005). The macrobenthic community at this station was significantly affected by nutrient input from the

Thukela, with significant alteration in community structure between high and low rainfall periods.

In contrast to our finding that there were no significant overall differences in macrobenthic community metrics or community composition between cruises A and B, an in depth analysis of the Thukela feature area revealed significant changes in macrobenthic community structure at the inner shelf between high and low rainfall periods. During the period of high rainfall the inner shelf was characterised by facultative detritivores typified by *Leptochela* sp.1, *Owenia fusiformis* and *Spiophanes* sp.1. These facultative feeders may initially benefit from the nutrient rich river waters discharged at the beginning of the rainy, summer season but prolonged outflow, deposition of fines and anoxic freshwater outflow deleteriously affects these tubiculous and nestling fauna, leading to the establishment of a different community here during the winter period of low rainfall.

While inner and mid-shelf stations sampled in the central region were structurally distinct, when considering feeding mode, communities were not different. Shallow areas are subjected to greater physical stress and consequently support a more variable macrobenthic community (Bonsdorff and Pearson 1999). Facultative detritivores, surface deposit feeders and carnivores dominated during the period of high rainfall. These feeding modes were still dominant during the second cruise but the abundance of the former two were reduced while carnivores were more numerous at these shelf positions during the period of low rainfall. Numerous authors have attributed the dominance of mobile carnivores to benthic recovery in habitats that have been subjected to disturbance and sediment deposition (Bonsdorff and Pearson 1999). These were the only stations sampled during the present study where significant short-term seasonal changes were detected, further underlying the likely importance of Thukela River outflow in driving macrobenthic community structure and function on the adjacent Natal Bight. This was surprising given the importance which has been placed on the Cape St. Lucia upwelling cell in terms of contributing nutrients and sustaining biological productivity and diversity on the Natal Bight (Meyer *et al.* 2002). Comparative analysis between coastal systems using network analysis has shown that the detritus based systems are characterised by a higher magnitude of nutrient recycling when compared with upwelling systems where phytoplankton dominate (Crossland *et al.* 2005). Ecosystem modelling of the Natal Bight has shown that this system is dominated by macrobenthos and reliant on detrital material transported from river systems (Ayers and Scharler 2011). Isotope analysis of demersal fish collected from similar shelf positions in these

feature areas indicate a significant reliance on terrestrial material brought into the marine realm by the Thukela River (De Lecea *et al.* 2013). The presence of an economically important, commercial demersal fishery in the central Bight and the crucial role that Thukela River outflow plays in maintaining the sedimentary environment on which demersal fauna are crucially dependant further emphasizes the importance of this area of the Natal Bight. Water abstraction schemes in the Thukela catchment area, deleterious agricultural practices and water pollution is expected to have a significant effect on the shelf community of the central Bight, affecting the capacity of this area to support crucial biotic resources (Gray 1997, Dauer *et al.* 2000, Gray 2001, Crossland *et al.* 2005).

The mid-shelf community in the southern region of the Bight was stable between sampling periods. The macrobenthic community here was typified by the presence of the spionid, *Dipolydora capensis*, which was found burrowing into tests of dead Astorhizida foraminifera. The accumulation of dead hardparts in marine sediments is well known to play a crucial role in structuring macrobenthic communities by changing the sediment structure and providing a habitat for internal and external fauna (Probert and Wilson 1984, Kidwell 1986, Gray 2001, Reise 2002). An abundant cnidarian component was supported at this station, these sessile animals attaching to chaetopterid tubes and Astorhizida with barnacles also found attached to these biogenic structures. Results from CCA analysis revealed that the environmental parameters measured and included in the present investigation did not account for the biological variation at this station. It is probable that the presence of biogenic elements in this area positively influence macrobenthic biodiversity and function by providing small patches of hard substrate for borers and the attachment of sessile epifauna, increasing the complexity of an otherwise soft-sediment environment (Kidwell 1986). The determination of grain size requires that these biogenic elements be removed from sediment which emphasizes the importance of noting the presence of biogenic elements when collecting and sorting sediment samples (Pearson 1970, Whitlatch 1981, Kidwell 1986). These dead biotic elements are also of particular interest to paleoecologists in terms of the information they provide regarding the biological and environmental history of the area (Kidwell 1986).

The process by which dead biotic material aids the establishment and survival of live biota is termed facilitative taphonomic feedback (Kidwell 1986). Further examples of facilitative taphonomic feedback on the Natal Bight are the aforementioned inner shelf of the Thukela feature area which, during the low rainfall period, was dominated by the hermit crab *Paguristes*

sp.1. This taxon appeared to preferentially inhabit *Bullia similis* shells, an abundant living component of the faunal assemblage sampled at this station during the high rainfall period. These dead gastropod shells provide refugia for these fauna which perhaps may otherwise not be able to inhabit this sedimentary environment. Sediments of the shallow water assemblage sampled in the central and northern Bight were characterised by a significant shell component, particularly in samples from inner and mid shelf depths sampled off Richard's Bay. These biogenic structures supported hydroids and gastropod egg capsules found attached to dead gastropods and shell fragments. The support of such a faunal component increases the reproductive success of surrounding fauna and represents an evolutionary pathway by which fauna reliant on hard substrate are accommodated in soft-sediments (Kidwell 1986).

The sedimentary environment at the outer shelf in the Thukela feature area was dominated by mud rich in organic carbon. This is consistent with sediment distribution patterns described by other investigators, indicating the transport of fine sediments from the Thukela River, onto the adjacent Natal Bight and over the shelf edge into the Thukela Canyon (Flemming and Hay 1988, Cooper 2001, Bosman *et al.* 2007). Deposit feeding macrobenthos are well known to dominate in fine, food-rich sediments. Results from the present study are in agreement with the outer shelf position in the Thukela feature area being characterised by a high abundance of the subsurface deposit feeding bivalve, *Tellinidae* sp.5, interface feeding Golfingiidae sipunculids, spionid polychaetes and *Spiochaetopterus* sp.12 as well as the subsurface deposit feeding capitellid *Rashgua* sp.1. Given the high mud and organic contents of sediments found here, in addition to the sediment reworking activities of deposit feeders (Levinton 1972), it is expected that interface feeding macrobenthos would deposit feed as opposed to suspension feed at this shelf position.

The fact that environmental parameters such as near bottom physico-chemical conditions and water column nutrient concentrations were only measured on two occasions during the present study, but still explained a significant proportion of the variation in the macrobenthic community is noteworthy. Shallow water assemblages were separated from deeper stations based largely on the temperature of near bottom waters which were higher at the shallow water shelf stations. Mid and outer shelf communities were most influenced by sediment grain size. The mid-shelf community in the Thukela feature area was significantly correlated with the proportion of medium and coarse sand in the sediments. The orientation of the mid-shelf macrobenthic community sampled from the Durban feature area in the centre of the CCA

plot (Chapter 3) suggests that the measured environmental parameters in the present study do not adequately account for the biotic variation at this station. The previous discussion concerning the important role of biogenic elements at this shelf position provides a possible explanation for this. The dominance of mud at the outer shelf in the Thukela feature area is the most important habitat driver influencing the macrobenthic community of this station.

Polychaetes are the most ubiquitous of all macrobenthic fauna and are found inhabiting a wide variety of habitats from rocky shores to estuaries and the deep sea (Day 1967, Fauchald and Jumars 1979, Gaston 1987, Pavia 1993, Tselepidis *et al.* 2000, Simon *et al.* 2010). These animals occupy a wide range of life styles, reproductive and feeding strategies and are well established as effective indicators of environmental condition (Day 1967, Warwick 1988a, Pavia 1993, Dean 2008, Cheung *et al.* 2008). In addition the taxonomy of this group is well studied with many international researchers working in the field of polychaete taxonomy. For these reasons, it was decided to investigate whether multivariate analyses would delineate the same communities based on all macrobenthos and polychaetes only. The results showed that analysing only the polychaete component yielded the same result as using all macrobenthos, but with the caveat that fauna need to be classified to the lowest level of taxon possible (preferably species). An in-depth look at the polychaete fauna supported on the Natal Bight yielded many new, possibly undescribed taxa and new distribution information highlighting the fact that the taxonomy of many groups presented in the seminal work of Day (1967) require revision. This taxonomic shortfall was not limited to the Polychaeta, with available, regional keys for many other taxonomic groups (eg. Sipuncula, Amphipoda, Brachyura, Cumacea, Ostracoda, Ophiuroidea and Mollusca) being insufficient during the present study. There is a clear need for updated, detailed taxonomic information for subtidal macrobenthos on the subtropical east coast.

Total organic carbon (TOC) content of the sediment was measured here, but is only a rough indication of food quantity and gives no information regarding the quality of food available to the benthos (Dauwe *et al.* 1998, Krönke *et al.* 2004). Values of TOC include the refractory component, which is of little nutritional value to macrobenthos (Wieking and Krönke 2005). The determination of water column Chl-*a* concentration suggested that pelagic primary production has a significant effect on the macrobenthic communities of the Thukela feature area. Benthic primary production is probably more important, given the general dominance of deposit feeding macrobenthos. While no data on benthic primary production were collected

during the present study, Wieking and Krönke (2003) inferred that benthic primary production comprised a major food source in communities dominated by sand licking, fossorial amphipods, such as Haustoriidae and Ampeliscidae, which browse directly on microphytobenthos and macroalgal cells (Krönke *et al.* 2004, Grippo *et al.* 2011). A number of ovigerous female macrobenthos as well as pelagic and benthic juveniles were sampled in the present study. The Natal Bight is therefore a locally important habitat for reproduction and recruitment, providing a suitable area for larval settlement and the development of a diverse macrobenthic community.

While useful in terms of reflecting ecosystem functioning, the designation of macrobenthic fauna into feeding modes or more comprehensive trophic guilds is largely a subjective enterprise relying on criteria developed decades previously (eg. Fauchald and Jumars 1979, Gaston 1987), with results varying depending on the investigator concerned and their particular area of interest (Adams 1985, Simberloff and Dayan 1991, Bonsdorff and Pearson 1999, Mancinelli *et al.* 1998, Elliot *et al.* 2007, Cheung *et al.* 2008, Macdonald *et al.* 2010). The *in situ* analysis of polychaete gut contents presented in Chapter 5 revealed that for many of the taxa, the feeding mode was found to be different to that presented in Fauchald and Jumars (1979). This emphasizes the need for future work in the area of macrobenthic functioning considering the same taxa from different geographical areas or depth zones. It is likely that the same fauna collected from the different Bight regions and shelf positions under investigation will adopt different feeding modes. This distinction was not considered in the present study but may be an important consideration in future studies which should include the study of stomach contents, laboratory feeding experiments and stable isotope analysis (Salas *et al.* 2006). Future functional studies should also consider extending the functional characteristics considered to include neglected biological traits such as behavioural and reproductive characteristics (Bonsdorff and Pearson 1999, Bremner *et al.* 2003, Cheung *et al.* 2008).

## REFERENCES

- Adams J (1985) The definition and interpretation of guild structure in ecological communities. *Journal of Animal Ecology* 54: 43-59.
- Akoumianaki I, Papaspyrou S, Kormas KA and Nicolaidou A (2012) Environmental variation and macrofauna response in a coastal area influenced by land runoff. *Estuarine, Coastal and Shelf Science*, *In Press*, *Corrected Proof*.
- Aller JY and Stupakoff I (1996) The distribution and seasonal characteristics of benthic communities on the Amazon shelf as indicators of physical processes. *Continental Shelf Research* 16: 717-751.
- Alongi DM (1989) Ecology of tropical soft-bottom benthos: a review with emphasis on emerging concepts. *Revista de Biología Tropical* 37: 85-100.
- Alongi DM (1990) The ecology of tropical soft-bottom benthic ecosystems. *Oceanography and Marine Biology Annual Review* 28: 381-496.
- Alongi DM and Christoffersen P (1992) Benthic infauna and organism-sediment relations in a shallow, tropical coastal area: influence of outwelled mangrove detritus and physical disturbance. *Marine Ecology Progress Series* 81: 229-245.
- Alongi DM and Robertson AI (1995) Factors regulating benthic food chains in tropical river deltas and adjacent shelf areas. *Geo-Marine Letters* 15: 145-152.
- Anderson FP, Gründlingh ML and Stavropoulos CC (1988) Kinematics of the southern Natal coastal circulation: some historic measurements 1962-63. *Suid-Afrikaanse Tydskrif vir Wetenskap* 84: 857-860.
- Anbuchezhian RM, Ravichandran S, Murugesan P and Sesh Serebiah J (2012) Assessment of soft bottom polychaete diversity in Thondi, Palk Bay, India. *Journal of Environmental Biology* 33: 917-921.
- Antonio ES, Kasai A, Ueno M, Ishihi Y, Yokoyama H and Yamashita Y (2012) Spatial-temporal feeding dynamics of benthic communities in an estuary-marine gradient. *Estuarine, Coastal and Shelf Science* 112: 86-97.
- Arasaki E, Muniz P and Pires-Vanin AS (2004) A functional analysis of the benthic macrofauna of the São Sebastião Channel (south-eastern Brazil). *Marine Ecology* 25: 249-263.
- Arruda EP, Domaneschi O and Amaral ACZ (2003) Mollusc feeding guilds on sandy beaches in São Paulo State, Brazil. *Marine Biology* 143: 691-701.
- Ayers MJ and 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 and Kenny AJ (2005) Sediment analysis and seabed characterisation. In: Eleftheriou A, McIntyre A (eds), *Methods for the study of marine benthos* (3<sup>rd</sup> Edition). Oxford: Blackwell Publishing. pp 43-86.
- Barlow R, Kyewalyanga M, Sessions H, van den Berg M and Morris T (2008) Phytoplankton pigments, functional types, and adsorption properties in the Delagoa and Natal Bights of the Agulhas ecosystem. *Estuarine, Coastal and Shelf Science* 80: 201-211.
- Barnard KH (1950) Descriptive catalogue of South African decapod Crustacea. *Annals of the South African Museum* 38: 1-837.

- Barrio-Froján CRS, Hawkins LE, Aryuthaka C, Nimsantijaroen S, Kendall MA and Paterson GLJ (2005) Patterns of polychaete communities in tropical sedimentary habitats: a case study in south-western Thailand. *The Raffles Bulletin of Zoology* 53: 1-11.
- Barrio-Froján CRS, Bolam SG, Eggleton JD and Mason C (2012) Large-scale faunal characterisation of marine benthic sedimentary habitats around the United Kingdom. *Journal of Sea Research* 69: 53-65.
- Beasy KM and Ellison JC (2013) Comparison of three methods for the quantification of sediment organic carbon in salt marshes of the Rubicon Estuary, Tasmania, Australia. *International Journal of Biology* 5: 1-13.
- Beckley LE (1998) The Agulhas Current ecosystem with particular reference to dispersal of fish larvae. In: Sherman K, Okemwa EN, Ntiba MJ (eds), *Large marine ecosystems of the Indian Ocean. Assessment, sustainability and management*. Oxford: Blackwell Publishing. pp 255-276.
- Begg GW (1978) The estuaries of Natal. Natal Town and Regional Planning Report 41: 1-657.
- Benedetti-Cecchi L, Iken K, Konar B, Cruz-Motta J, Knowlton A, Pohle G, Castelli A, Tamburello L, Mead A, Trott T, Miloslavich P, Wong M, Shirayama Y, Lardicci C, Palomo G and Maggi E (2010) Spatial relationships between polychaete assemblages and environmental variables over broad geographical scales. *PLoS ONE* 5: e12946. doi: 10.1371/journal.pone.0012946.
- Bergen M, Weisberg SB, Smith RB, Cadien DB, Dalkey A, Montagne DE, Stull JK, Velarde RG and Ananda Ranasinghe J (2001) Relationship between depth, sediment, latitude and the structure of benthic infaunal assemblages on the mainland shelf of southern California. *Marine Biology* 138: 637-647.
- Bertrand Y, Pleijel F and Rouse GW (2006) Taxonomic surrogacy in biodiversity assessments, and the meaning of Linnaean ranks. *Systematics and Biodiversity* 4: 149-159.
- Beukema JJ and Dekker R (2012) Estimating macrozoobenthic richness along an environmental gradient: sample size matters. *Estuarine, Coastal and Shelf Science* 111: 67-74.
- Bigot L, Conand C, Amouroux J-M, Frouin P, Bruggemann H and Grémare A (2006) Effects of industrial outfalls on tropical macrobenthic sediment communities in Reunion Island (Southwest Indian Ocean). *Marine Pollution Bulletin* 52: 865-880.
- Blomqvist S (1991) Quantitative sampling of soft-bottom sediments: problems and solutions. *Marine Ecology Progress Series* 72: 295-304.
- Bonsdorff E and Pearson TH (1999) Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: A functional-group approach. *Australian Journal of Ecology* 24: 312-326.
- Bosman C, Uken R, Leuci R, Smith AM and 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, Rogers SI and Frid CLJ (2003) Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series* 254: 11-25.
- Brown AC (1999) Marine invertebrate systematics and zoogeography in southern Africa: a historical overview. *Transactions of the Royal Society of South Africa* 54: 21-30.
- Brown AC (2003) Centennial history of the Zoology department, University of Cape Town, 1903-2003: A personal memoir. *Transactions of the Royal Society of South Africa* 58: 11-34.

- Brown SS, Gaston GR, Rakocinski CF and Heard RW (2000) Effects of sediment contaminants and environmental gradients on macrobenthic community trophic structure in Gulf of Mexico estuaries. *Estuaries* 23: 411-424.
- Bryden HL, Beal LM and Duncan LM (2005) Structure and transport of the Agulhas Current and its temporal variability. *Journal of Oceanography* 61: 479-492.
- Buchanan JB and Kain JM (1971) Measurement of the physical and chemical environment. In: Holme NA, McIntyre AD (eds), *Methods for the study of marine benthos* (1<sup>st</sup> Edition). Oxford: Blackwell Publishing. pp 30-59.
- Burchall J (1968) Primary production studies in the Agulhas Current Region of Natal – June, 1965. Investigational Report No. 20. Durban: Oceanographic Research Institute. pp 1-18.
- Cacabelos E, Domínguez M and Troncoso JS (2009) Trophic structure of soft-bottom macrobenthos in an inlet in north-western Spain. *Journal of the Marine Biological Association of the United Kingdom* 89: 439-447.
- Cadée GC (2001) Sediment dynamics by bioturbating organisms. In: Reise K (ed), *Ecological comparisons of sedimentary shores*. Germany: Springer-Verlag. pp 127-143.
- Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M and Jouseau C (2006) Effects of biodiversity on ecosystem functioning of trophic groups and ecosystems. *Nature* 443: 989-992.
- Carrasco FD and Carbajal W (1998) The distribution of polychaete feeding guilds in organic enriched sediments of San Vicente Bay, central Chile. *International Review of Hydrobiology* 83: 233-249.
- Carter RA and d'Aubrey J (1988) Inorganic nutrients in Natal continental shelf water's. In: Schumann EH (ed), *Lecture notes on coastal and estuarine studies Volume 26: Coastal ocean studies off Natal*. Germany: Springer-Verlag. pp 131-152.
- Carvalho S, Moura A, Gaspar MB, Pereira P, da Fonseca LC, Falcão M, Drago T, Leitão F and Regala J (2005) Spatial and inter-annual variability of the macrobenthic communities within a coastal lagoon (Óbidos lagoon) and its relationship with environmental parameters. *Acta Oecologica* 27: 143-159.
- Chang S, Steimle FW, Reid RN, Fromm SA, Zdanowicz VS and Pikanowski RA (1992) Association of benthic macrofauna with habitat types and quality in the New York Bight. *Marine Ecology Progress Series* 89: 237-251.
- Cheung SG, Lam NWY, Wu RSS and Shin PKS (2008) Spatio-temporal changes of marine macrobenthic community in sub-tropical waters upon recovery from eutrophication. II. Life-history traits and feeding guilds of polychaete community. *Marine Pollution Bulletin* 56: 297-307.
- Christoffersen ML, de Araújo ME and Branco JO (2011) An overview of studies on trophic ecology in the marine environment: achievements and perspectives. *Neotropical Biology and Conservation* 6: 143-155.
- Clark HL (1923) The echinoderm fauna of South Africa. *Annals of the South African Museum* 13: 221-435.
- Clark AM and Courtman-Stock J (1976) The echinoderms of southern Africa. Publication No. 776. London: British Museum of Natural History. pp 1-277.

- Clark BM, Steffani NC, Young S, Richardson AJ and Lombard AT (1999) The effects of climate change on marine biodiversity in South Africa. Cape Town: Anchor Environmental Consultants. pp 74-117.
- Clarke KR (1990) Comparison of dominance curves. *Journal of Experimental Marine Biology and Ecology* 138: 143-157.
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117-143.
- Clarke KR and Green RH (1988) Statistical design and analysis for an 'biological effects' study. *Marine Ecology Progress Series* 46: 213-226.
- Clarke KR and Ainsworth M (1993) a method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* 92: 205-219.
- Clarke KR and Warwick RM (1994) Change in marine communities: An approach to statistical analysis and interpretation. Plymouth: Natural Environment Research Council. pp 1-144.
- Clarke KR and Warwick RM (1998) Quantifying structural redundancy in ecological communities. *Oecologia* 113: 278-289.
- Clarke KR, Somerfield PJ and Chapman MG (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology* 330: 55-80.
- Clarke KR, Somerfield PJ and Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology* 366: 56-69.
- Cocito S, Fanucci S, Niccolai I, Morri C and Nike Bianchi C (1990) Relationships between trophic organisation of benthic communities and organic matter content in Tyrrhenian Sea sediments. *Hydrobiologia* 207: 53-60.
- Coleman FC and Williams SL (2002) Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology and Evolution* 17: 40-44.
- Coleman N, Cuff W, Drummond M and Kudenov JD (1978) A quantitative survey of the macrobenthos of Western Port, Victoria. *Australian Journal of Marine and Freshwater Research* 29: 445-466.
- Consentino A and Giacobbe S (2006) A case study of mollusc and polychaete soft-bottom assemblages submitted to sedimentary instability in the Mediterranean Sea. *Marine Ecology* 27: 170-183.
- Consentino A and Giacobbe S (2008) Distribution and functional response of sublittoral soft bottom assemblages to sedimentary constraints. *Estuarine, Coastal and Shelf Science* 79: 263-276.
- Cooper JAG (2001) Geomorphological variability among microtidal estuaries from the wave-dominated South African coast. *Geomorphology* 40: 99-122.
- Cooper JAG, Harrison T and Ramm A (1998) The role of estuaries in large marine ecosystems: examples from the Natal coast, South Africa. In: Sherman K, Okemwa EN, Ntiba MJ (eds), *Large marine ecosystems of the Indian Ocean. Assessment, sustainability and management*. Oxford: Blackwell Publishing. pp 237-246.

- Covich AP, Austen MC, Bärlocher F, Chauvet E, Cardinale BJ, Biles CL, Inchausti P, Dangles O, Solan M, Gessner MO, Statzner B and Moss B (2004) The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. *BioScience* 54: 767-775.
- Crisp DJ (1971) Energy flow measurements. In: Holme NA, McIntyre AD (eds), *Methods for the study of marine benthos* (1<sup>st</sup> Edition). Oxford: Blackwell Publishing. pp197-279.
- Crossland CJ, Baird D, Ducrotoy J-P and Lindeboom HJ (2005) The coastal zone – a domain of global interactions. In: Crossland CJ, Kremer HH, Lindeboom HJ, Marshall Crossland JI, Le Tissier MDA (eds), *Coastal Fluxes in the Anthropocene*. Germany: Springer-Verlag. pp 1-38.
- Currie D, Sorokin SJ and Ward TM (2009) Infaunal macroinvertebrate assemblages of the eastern Great Australian Bight: effectiveness of a marine protected area in representing the region's benthic diversity. *Marine and Freshwater Research* 60: 459-474.
- Dauer DM (1984) The use of polychaete feeding guilds as biological variables. *Marine Pollution Bulletin* 15: 301-305.
- Dauer DM, Maybury CA and Ewing RM (1981) Feeding behaviour and general ecology of several spionid polychaetes from the Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology* 54: 21-38.
- Dauer DM, Weisberg SB and Ranasinghe JA (2000) Relationships between benthic community condition, water quality, sediment quality, nutrient loads, and land use patterns in Chesapeake Bay. *Estuaries* 23: 80-96.
- Dauwe B, Herman PMJ and Heip CHR (1998) Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. *Marine Ecology Progress Series* 173: 67-83.
- Day JH (1967) A monograph on the Polychaeta of southern Africa. London: British Museum. pp1-878
- de Juan S and Cartes JE (2011) Influence of environmental factors on the dynamics of macrobenthic crustaceans on soft-bottoms of the Ebro Delta continental shelf (northwestern Mediterranean). *Scientia Marina* 75: 691-700.
- De Lecea AM, Fennessy SF and 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.
- Dean HK (2001) Capitellidae (Annelida: Polychaeta) from the Pacific coast of Costa Rica. *Revista de Biología Tropical* 49: 69-84.
- Dean HK (2008) The use of polychaetes (Annelida) as indicator species of marine pollution: a review. . *Revista de Biología Tropical* 56: 11-38.
- Demetriades NT and 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 and Pardal MA (2009) Feeding guild composition of a macrobenthic subtidal community along a depth gradient. *Scientia Marina* 73: 225-237.
- Duarte CM (2000) Marine biodiversity and ecosystem services: an elusive link. *Journal of Experimental Marine Biology and Ecology* 250: 117-131.

- Dubois S, Gelpi CG Jr, Condrey RE, Grippo MA, Fleeger JW (2009) Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf. *Biodiversity and Conservation* 18: 3759-3784.
- Duineveld GCA, Künitzer A, Niermann U, de Wilde PAWJ and Gray JS (1991) The macrobenthos of the North Sea. *Netherlands Journal of Sea Research* 28: 53-65.
- Eleftheriou A and Moore DC (2005) Macrofauna techniques. In: Eleftheriou A, McIntyre A (eds), *Methods for the study of marine benthos* (3<sup>rd</sup> Edition). Oxford: Blackwell Publishing. pp 160-228.
- Elias R, Bremec CS and Vallarino EA (2001) Polychaetes from a southwestern shallow shelf Atlantic area (Argentina, 38°S) affected by sewage discharge. *Revista Chilena de Historia Natural* 74: 523-531.
- Ellingsen KE (2001) Biodiversity of a continental shelf soft-sediment macrobenthos community. *Marine Ecology Progress Series* 218: 1-15.
- Ellingsen KE, Clarke KR, Somerfield PJ and Warwick RM (2005) Taxonomic distinctness as a measure of diversity applied over a large scale: the benthos of the Norwegian continental shelf. *Journal of Animal Ecology* 84: 1069-1079.
- Ellis JI, Norkko A and Thrush SF (2000) Broad-scale disturbance of intertidal and shallow sublittoral soft-sediment habitats; effects on the benthic macrofauna. *Journal of Aquatic Ecosystem Stress and Recovery* 7: 57-74.
- Fauchald K and Jumars P (1979) The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* 17: 193-284.
- Fennessy ST (1994) The impact of commercial prawn trawlers on linefish off the north coast of Natal, South Africa. *South African Journal of Marine Science* 14: 263-279.
- Fennessy ST, Mackay CF and Schleyer MH (2008) Specialist marine biodiversity and fisheries input for the EIA being undertaken for the proposed SEA Cable system of the KwaZulu-Natal North coast, South Africa. Unpublished Report No. 267. Durban: Oceanographic Research Institute. pp 1- 25.
- Ferraro S and Cole F (1990) Taxonomic level and sample size sufficient for assessing pollution impacts on the southern California Bight macrobenthos. *Marine Ecology Progress Series* 67: 251-262.
- Field JG, Clarke KR and Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37-52.
- Field JG and Griffiths CL (1991) Littoral and sublittoral ecosystems of southern Africa. In: Mathieson AC and Nienhuis PH (eds.), *Ecosystems of the world: Intertidal and littoral ecosystems*. Amsterdam: Elsevier. pp 323-346.
- Flemming BW (1981) Factors controlling shelf sediment dispersal along the southeast African continental margin. *Marine Geology* 42: 259-277.
- Flemming BW and Hay R (1988) Sediment distribution and dynamics of the Natal continental shelf. In: Schumann EH (ed), *Lecture notes on coastal and estuarine studies Volume 26: Coastal ocean studies off Natal*. Germany: Springer-Verlag. pp 47-80.
- Forbes AT and Demetriades NT (2005) A review of the commercial, shallow water penaeid prawn resource of South Africa: Status, fisheries, aquaculture and management. Durban: Marine and Estuarine Research. pp 1-68.

- Foster NM (1969) New species of spionids (Polychaeta) from the Gulf of Mexico and Caribbean Sea with a partial revision of the genus *Prionospio*. *Proceedings of the Biological Society of Washington* 82: 381-399.
- Fresi E, Gambi MC, Focardi S, Bargagli R, Baldi F and Falciai L (1983) Benthic community and sediment types: A structural analysis. *Marine Ecology* 4: 101-121.
- Ganesh T and Raman AV (2007) Macrobenthic community structure of the northeast Indian shelf, Bay of Bengal. *Marine Ecology Progress Series* 341: 59-73.
- Gaston GR (1987) Benthic Polychaeta of the Middle Atlantic Bight: feeding and distribution. *Marine Ecology Progress Series* 36: 251-262.
- Gaston GR and Nasci JC (1988) Trophic structure of macrobenthic communities in the Calcasieu Estuary, Louisiana. *Estuaries* 11: 201-211.
- Gaston GR, Rakocinski CF, Brown SS and Cleveland CM (1998) Trophic function in estuaries: response of macrobenthos to natural and contaminant gradients. *Marine and Freshwater Research* 49: 833-846.
- Giangrande A, Licciano M and Musco L (2005) Polychaetes as environmental indicators revisited. *Marine Pollution Bulletin* 50: 1153-1162.
- Gibbons MJ, Abiahy BB, Angel M, Assuncao CML, Bartsch I, Best P, Biseswar R, Bouillon J, Bradford-Grieve JM, Branch W, Burreson E, Casanova J-P, Channing A, Child CA, Compagno L, Cornelius PFS, Dadon JR, David JHM, Day J, Della Croce N, Emschermann P, Erseus C, Esnal G, Gibson R, Griffiths CL, Heard R, Heemstra PJB, Herbert D, Hessler R, Higgins R, Hiller N, Hirano YM, Kensley B, Kilburn R, Kornicker L, Lamshead J, Manning R, Marshall D, Mianzan H, Monniot C, Monniot F, Newman W, Nielsen C, Patterson G, Pugh P, Roeleveld M, Ross A, Ryan P, Rylans JS, Samaai T, Schleyer M, Schockaert E, Seapy R, Shiel R, Sluys R, Southward EC, Sulaiman A, Thandar A, van der Spoel S, van Soest R, Van der Land J, Vetter E, Vinogradov GAN, Williams G and Wooldridge T (1999) The taxonomic richness of South Africa's marine fauna: a crisis at hand. *South African Journal of Science* 95: 8-12.
- Gomez Gesteira JL, Dauvin JC and Salvande Fraga M (2003) Taxonomic level for assessing oil spill effects on soft-bottom sublittoral benthic communities. *Marine Pollution Bulletin* 46: 562-572.
- Gray JS (1974) Animal-sediment relationships. *Oceanography and Marine Biology Annual Review* 12: 223-261.
- Gray JS (1981) *The ecology of marine sediments: An introduction to the structure and function of benthic communities*. Cambridge: Cambridge University Press.
- Gray JS (1994) Is deep-sea diversity really so high? Species diversity of the Norwegian continental shelf. *Marine Ecology Progress Series* 112: 205-209.
- Gray JS (1997) Marine biodiversity: patterns, threats and conservation needs. *Biodiversity and Conservation* 6: 153-175.
- Gray JS (2000) The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *Journal of Experimental Marine Biology and Ecology* 250: 23-49.
- Gray JS (2001) Marine diversity: the paradigms in patterns of species richness examined. *Scientia Marina* 65: 41-56.
- Gray JS (2002) Species richness of marine soft sediments. *Marine Ecology Progress Series* 244: 285-297.

- Gray JS, Aschan M, Carr MR, Clarke KR, Green RH, Pearson TH, Rosenberg R and Warwick RM (1988) Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. *Marine Ecology Progress Series* 46: 151-165.
- Gray JS, Poore GCB, Ugland KI, Wilson RS, Olsfard F and Johannessen Ø (1997) Coastal and deep sea diversities compared. *Marine Ecology Progress Series* 159: 97-103.
- Gray JS and Elliott M (2009) *The ecology of marine sediments: from science to management*. Oxford: Oxford University Press.
- Green A and Garlick GL (2011) A sequence stratigraphic framework for a narrow, current-swept continental shelf: The Durban Bight, central KwaZulu-Natal, South Africa. *Journal of African Earth Sciences* 60: 303-314.
- Griffis RB and Suchanek TH (1991) A model of burrow architecture and trophic modes in thalassinidean shrimp (Decapoda: Thalassinidea) *Marine Ecology Progress Series* 79: 171-183.
- Griffiths CL (1976) *A guide to the benthic marine amphipods of southern Africa*. Cape Town: South African Museum.
- Griffiths CL, Robinson TB, Lange L and Mead A (2010) Marine biodiversity in South Africa: An evaluation of current states of knowledge. *PLoS ONE* 5: e12008. doi:10.1371/journal.pone.0012008
- Grindley JR (1979) Factors determining the productivity of South African coastal waters. In: Dunbar MJ (ed), *Marine Production Mechanisms*. Cambridge: Cambridge University Press. pp 89-132.
- Grippo MA, Fleeger JW, Dubois SF and Condrey R (2011) Spatial variation in basal resources supporting benthic food webs revealed for the inner continental shelf. *Limnology and Oceanography* 56: 841-856.
- Groeneveld JC and Melville-Smith R (1995) Spatial and temporal availability in the multispecies crustacean trawl fishery along the east coast of South Africa and southern Mocambique, 1988-1993. *South African Journal of Marine Science* 15: 123-137.
- Gründlingh ML (1992) Agulhas Current meanders: review and case study. *South African Geographical Journal* 74: 19-28.
- Hall SJ (2002) The continental shelf benthic ecosystem: current status, agents for change and future prospects. *Environmental Conservation* 29: 350-374.
- Han A, Dai M, Kao S-J, Gan J, Li Q, Wang L, Zhai W and Wang L (2012) Nutrient dynamics and biological consumption in a large continental shelf system under the influence of both a river plume and coastal upwelling. *Limnology and Oceanography* 57: 486-502.
- Harmelin-Vivien ML, Bănară D, Dierking J, Hermant R, Letoutneur Y and 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.
- Harris TFW (1964) Notes on Natal coastal waters. *South African Journal of Science* 60: 237-241.
- Harris TFW (1978) Review of coastal currents in South African waters. South African National Scientific Programme Report no. 30. Pretoria: CSIR. pp 1-103.
- Heip C, Basford D, Craeymeersch JA, Dewarumez J-M, Dörjes J, de Wilde P, Duineveld G, Eleftheriou A, Herman PMJ, Niermann U, Kingston P, Künitzer A, Rachor E, Rumohr

- H, Soetaert K and Soltwedel T (1992) Trends in biomass, density and diversity of North Sea macrofauna. *ICES Journal of Marine Science* 49: 13-22.
- Herbert DG (1989) A remarkable new species of *Diodora* Gray, 1821 (mollusca: Gastropoda) from south-east Africa. *Annals of the Natal Museum* 30: 173-176.
- Herbert DG (1991) New records of Mollusca from southern Africa and Mocambique. Part I. (Mollusca: Gastropoda). *Annals of the Natal Museum* 32: 305-318.
- Hermard R, Salen-Picard, C, Alliot E and Degiovanni C (2008) Macrofaunal density, biomass and composition of estuarine sediments and their relationship to the river plume of the Rhone River (NW Mediterranean). *Estuarine, Coastal and Shelf Science* 79: 367-376.
- Hewitt JE, Thrush SF and 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 PA, Hughes GR, Bass AJ, Wallace JH, van der Elst RP, Crawford RJM and Shelton PA (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.
- Hooper DU, Solan M, Symstad A, Díaz S, Gessner MO, Buchmann N, Degrange V, Grime P, Hulot F, Merillod-Blondin F, Roy J, Spehn E and van Peer L (2001) Species diversity, functional diversity, and ecosystem functioning. In: Loreau M, Naeem S, Inchausti P (eds,) *Biodiversity and Ecosystem Functioning: Synthesis and perspectives*. Oxford: Oxford University Press. pp 195-281.
- Hunt OD (1925) The food of the bottom fauna of the Plymouth fishing grounds. *Journal of the Marine Biological Association of the United Kingdom* 13: 560-599.
- Hutchings L, Beckley LE, Griffiths MH, Roberts MJ, Sundby S and van der Lingen C (2002) Spawning on the edge: spawning grounds and nursery areas around the South African coastline. *Marine and Freshwater Research* 53: 307-318.
- Hutchings L, Morris T, van der Lingen CD, Lamberth SJ, Connell AD, Taljaard S and van Niekerk L (2010) Ecosystem considerations of the KwaZulu-Natal sardine run. *African Journal of Marine Science* 32: 413-421.
- Hyland J, Baptiste E, Campbell J, Kennedy J, Kropp R and Williams S (1991) Macroinfaunal communities of the Santa Maria Basin on the California outer continental shelf and slope. *Marine Ecology Progress Series* 78: 147-161.
- Hyland J, Balthis L, Karakassis I, Magni P, Petrov A, Shine J, Vestergaard O and Warwick R (2005) Organic carbon content of sediments as an indicator of stress in the marine benthos. *Marine Ecology Progress Series* 295: 91-103.
- Ieno EN, Solan M, Batty P and Pierce GJ (2006) How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. *Marine Ecology Progress Series* 311: 263-271.
- Isaac WE (1937) South African coastal waters in relation to ocean currents. *Geographical Review* 27: 651-664.
- Jaksić FM (1981) Abuse and misuse of the term “guild” in ecological studies. *Oikos* 37: 397-400.

- Jayaraj KA, Jayalakshmi KV and Saraladevi K (2007) Influence of environmental properties on macrobenthos in the northwest Indian shelf. *Environmental Monitoring and Assessment* 127: 459-475.
- Jayaraj KA, Sheeba P, Jacob J, Revichandran C, Arun PK, Praseeda KS, Nisha PA and Rasheed KA (2008a) Response of infaunal macrobenthos to the sediment granulometry in a tropical continental margin-southwest coast of India. *Estuarine, Coastal and Shelf Science* 77: 743-754.
- Jayaraj KA, Josia J and Dinesh Kumar PK (2008b) Infaunal macrobenthic community of soft bottom sediment in a tropical shelf. *Journal of Coastal Research* 24: 708-718.
- Jones NS (1950) Marine bottom communities. *Biological Reviews* 25: 283-313.
- Joydas TV, Jayalakshmy KV and Damodaran R (2009) Polychaete community structure of Indian west coast shelf, Arabian Sea. *Current Science* 97: 634-636.
- Jumars PA and Nowell ARM (1984) Fluid and sediment dynamic effects on marine benthic community structure. *American Zoology* 24: 45-55.
- Jurgensone I and Aigars J (2012) Bioavailability of riverine dissolved organic matter to phytoplankton in the marine coastal waters. *Estuarine, Coastal and Shelf Science* 107: 97-104.
- Kaiser MJ, Ramsay K, Richardson CA, Spence FE and Brand AR (2000) Chronic fishing disturbance has changes shelf sea benthic community structure. *Journal of Animal Ecology* 69: 494-503.
- Karakassis I and Eleftheriou A (1997) The continental shelf of Crete: structure of macrobenthic communities. *Marine Ecology Progress Series* 160: 185-196.
- Kensley BF (1972) *Shrimps and prawns of southern Africa*. Cape Town: South African Museum. pp 1-65.
- Kensley BF (1978) *A guide to the marine isopods of southern Africa*. Cape Town: South African Museum. pp 1-173.
- Kidwell SM (1986) Taphonomic feedback in Miocene assemblages: testing the role of dead hardparts in benthic communities. *Palaos* 1: 239-255.
- Kilburn RN (1992) Turridae [s.l.] (Mollusca: Gastropoda) of southern Africa and Mocambique. Part 7. Subfamily Crassispirinae, section 2. *Annals of the Natal Museum* 33: 461-575.
- Kilburn RN (1998) The Limidae of South Africa and Mocambique (Mollusca: Bivalvia): genera *Limaria*, *Limatula*, *Divarilima*, *Ctenoides* and *Fukama*. *Annals of the Natal Museum* 39: 203-247.
- Kilburn RN (1999) The family Nuculidae (Bivalvia: Protobranchia) in South Africa and Mocambique. *Annals of the Natal Museum* 40: 245-268.
- Krönke I (2006) Structure and function of macrofaunal communities influenced by hydrodynamically controlled food availability in the Wadden Sea, the open North Sea, and the Deep-sea. A synopsis. *Senckenbergiana maritima* 36: 123-164.
- Krönke I, Stoeck T, Wieking G and Palojarvi A (2004) Relationship between structural and functional aspects of microbial and macrofaunal communities in different areas of the North Sea. *Marine Ecology Progress Series* 282: 13-31.
- Kunnen TH (2012) Marine nutrient dynamics of the KwaZulu-Natal Bight: Assessing bacterial numbers, biomass and productivity. MSc thesis, University of KwaZulu-Natal, South Africa.

- Lamberth SJ, Drapeau L and 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.
- Lamont T, Barlow R, Huggett J, Mackay CF, Smit AJ and Uken R (2010) Sailing orders for the F.R.S. Algoa voyage 175. January-April 2010. pp 1-28.
- Lee W-J (2012) Critical links among the sea, land and air: southeast Asia's coastal soft-sediment communities. *The Raffles Bulletin of Zoology Supplement* 25: 117-121.
- Legendre P and Legendre L (1998) *Numerical Ecology* (2<sup>nd</sup> Edition). Amsterdam: Elsevier Science.
- Legendre P and Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* 69: 1-24.
- Legendre P and Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271-280.
- Legendre P and Birks HJB (2012) From classical to canonical ordination. In: Birks HJB, Lotter AF, Juggins S, Smol JP (eds), *Tracking environmental change using lake sediments, Volume 5: Data handling and numerical techniques*. London: Springer. Pp 201-248.
- le Loeuff P and Intes A (1999) Macrobenthic communities on the continental shelf of Côte-d'Ivoire. Seasonal and diel cycles in relation to hydroclimate. *Oceanologica Acta* 22: 529-550.
- Levinton J (1972) Stability and trophic structure in deposit-feeding and suspension-feeding communities. *The American Naturalist* 106: 472-486.
- Levinton J (1995) Bioturbators as ecosystem engineers: control of the sediment fabric, inter-individual interactions and material fluxes. In: Jones CG, Lawton JH (eds) *Linking species and ecosystems*. USA: Chapman and Hall. pp 29-36.
- Levinton J and Kelaher B (2004) Opposing organizing forces of deposit-feeding marine communities. *Journal of Experimental Marine Biology and Ecology* 300: 65-82.
- Lohrer AM and Hancock N (2004) Marine soft sediments: more diversity than meets the eye. *Water and Atmosphere* 12: 26-27.
- Lohrer AM, Thrush SF, Hewitt JE, Berkenbesch K, Ahrens M and Cummings VJ (2004) Terrestrially derived sediment: response of marine macrobenthic communities to this terrigenous deposits. *Marine Ecology Progress Series* 273: 121-138.
- Lohrer AM, Thrush SF, Lundquist CJ, Vopel K, Hewitt JE and Nicholls PE (2006) Deposition of terrigenous sediment on subtidal marine macrobenthos: response of two contrasting community types. *Marine Ecology Progress Series* 307: 115-125.
- Lourido A, Cacabelos E and Troncoso JS (2008) Patterns of distribution of the polychaete fauna in subtidal soft sediments of the Ría de Aldán (north-western Spain). *Journal of the Marine Biological Association of the United Kingdom* 88: 263-275.
- Lutjeharms JRE (2006) The coastal oceans of south-eastern Africa. In: Robinson AR, Brink KH (eds), *The sea, Volume 14B: The global coastal ocean: Interdisciplinary regional studies and syntheses*. Cambridge: Harvard University Press. pp 783-834.
- Lutjeharms JRE (2007) Three decades of research on the greater Agulhas Current. *Ocean Science* 3: 129-147.
- Lutjeharms JRE and Roberts HR (1988) The Natal Pulse: an extreme transient on the Agulhas Current. *Journal of Geophysical Research* 93: 631-645.

- Lutjeharms JRE, Gründlingh ML and Carter RA (1989) Topographically induced upwelling in the Natal Bight. *South African Journal of Science* 85: 310-316.
- Lutjeharms JRE, Valentine HR and Van Ballegooyen RC (2000a) The hydrography and water masses of the Natal Bight, South Africa. *Continental shelf Research* 20: 1907-1939.
- Lutjeharms JRE, Cooper J, Roberts M (2000b) Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research* 20: 737-761.
- Lutjeharms JRE, Durgadoo JV, Schapira M and McQuaid CD (2010) First oceanographic survey of the entire continental shelf adjacent to the northern Agulhas Current. *South African Journal of Science* 9/10: 9-11.
- Macdonald TA, Burd BJ, Macdonald VI and 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* No. 2874. pp 1-69.
- Macdonald TA, Burd BJ and 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. Unpublished Report No. 239. Durban: Oceanographic Research Institute. pp 1-36.
- Mackay CF (2008) Responses of soft sediment invertebrates of the Port of Richards Bay and adjacent Mhlathuze Estuary to dredging and dredge spoil disposal for Berth 306. Unpublished Report No. 263. Durban: Oceanographic Research Institute. pp 1-134.
- Mackay CF (2010) ACEP macrobenthic sampling protocol. F.R.S. Algoa survey of the Natal Bight. Durban: Oceanographic Research Institute. pp 1-4.
- Mackie ASY, Oliver PG, Darbyshire T and Mortimer K (2005) Shallow marine benthic invertebrates of the Seychelles Plateau: high diversity in a tropical oligotrophic environment. *Philosophical transactions of the Royal Society* 363: 203-228.
- Magurran A (2004) *Measuring biological diversity*. Oxford: Blackwell Publishing pp 1-264.
- Mancinelli G, Fazi S and Rossi L (1998) Sediment structural properties mediating dominant feeding type patterns in soft-bottom macrobenthos of the northern Adriatic Sea. *Hydrobiologia* 367: 211-222.
- Mandal S and Harkantra SN (2013) Changes in the soft-bottom macrobenthic diversity and community structure from the ports of Mumbai, India. *Environmental Monitoring and Assessment* 185: 653-672.
- Mann KH and Lazier JRN (2006) *Dynamics of marine ecosystems: Biological-physical interactions in the oceans* (3<sup>rd</sup> edition). Oxford: Blackwell Publishing. pp 1-512.
- Marchini A, Munari C and Mistri M (2008) Functions and ecological status of eight Italian lagoons examined using biological traits analysis (BTA). *Marine Pollution Bulletin* 56: 1076-1085.
- Marinelli RL, Jahnke RA, Craven DB, Nelson JR and Eckman JE (1998) Sediment nutrient dynamics on the South Atlantic Bight continental shelf. *Limnology and Oceanography* 43: 1305-1320.
- Marques JC and Bellan-Santini D (1993) Biodiversity in the ecosystem of the Portuguese continental shelf: distributional ecology and the role of benthic amphipods. *Marine Biology* 115: 555-564.

- Martí E, Torres-Gavilá J, Tena J, Rodilla M, Sánchez-Arcilla A, Mestres M and Mössö C (2007) Temporal changes in mollusc and polychaete communities in the soft bottom of Cullera Bay (Western Mediterranean). *Journal of Coastal Research* 47: 76-83.
- Martin AK and Flemming BW (1988) Physiography, structure and geological evolution of the Natal continental shelf. In: Schumann EH (ed), *Lecture notes on coastal and estuarine studies Volume 26: Coastal ocean studies off Natal*. Germany: Springer-Verlag. pp 11-47.
- Martin D, Pinedo S and Sardá R (2000) Distribution patterns and trophic structure of soft bottom polychaeta assemblages in a north-western Mediterranean shallow-water bay. *Ophelia* 53: 1-17.
- Mason WT, Lewis PA and Weber CI (1983) An evaluation of benthic macroinvertebrate biomass methodology. *Environmental Monitoring and Assessment* 3: 29-44.
- Maurer BA and McGill BJ (2011) Measurement of species diversity. In: Magurran AE, McGill BJ (eds), *Biological Diversity: Frontiers in measurement and assessment*. Oxford: Oxford University Press. pp 55-65.
- Maurer D and Leathem W (1981) Polychaete feeding guilds from Georges Bank, USA. *Marine Biology* 62: 161-171.
- Maurer D, Nguyen H, Robertson G and Gerlinger T (1999) The Infaunal Trophic Index (ITI): its suitability for marine environmental monitoring. *Ecological Applications* 9: 699-713.
- McArthur MA, Brooke BP, Przeslawski R, Ryan DA, Lucieer, VL, Nichol S, McCallum AW, Mellin C, Cresswell ID and Radke LC (2010) On the use of abiotic surrogates to describe marine benthic biodiversity. *Estuarine, Coastal and Shelf Science* 88: 21-32.
- McClurg TM (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. Berlin: Springer-Verlag. pp 178-208.
- McClurg TP, Blair AG and Gumede SV (2000) Benthic fauna. In: Connell AD (ed), *Environmental studies in the Richards Bay offshore outfalls region*. Report no. 13. Durban: CSIR. pp 23-62.
- McClurg TP (2005) Benthic macrofauna. In: McClurg TP (ed), *Sea disposal of sewage: environmental surveys in the Durban outfalls region*. Report no. 23. Durban: CSIR. pp 39-69.
- McRae G, Camp DK, Lyons WG and Dix TL (1998) Relating benthic infaunal community structure to environmental variables in estuaries using nonmetric multidimensional scaling and similarity analysis. *Environmental Monitoring and Assessment* 51: 233-246.
- Meyer AA, Lutjeharms JRE and de Villiers S (2002) The nutrient characteristics of the Natal Bight, South Africa. *Journal of Marine Systems* 35: 11-37.
- Mistri M and Rossi R (2001) Taxonomic sufficiency in lagoonal ecosystems. *Journal of the Marine Biological Association of the United Kingdom* 81: 339-340.
- Morgans JFC (1956) Notes on the analysis of shallow-water soft substrata. *Journal of Animal Ecology* 25: 367-387.
- Muniz P and Pires AMS (1999) Trophic structure of polychaetes in the São Sebastião Channel (south-eastern Brazil). *Marine Biology* 134: 517-528.
- Muniz P and Pires AMS (2000) Polychaete associations in a subtropical environment (São Sebastião Channel, Brazil): A structural analysis. *Marine Ecology* 21: 145-160.

- Muniz P and Pires-Vanin AMS (2005) More about taxonomic sufficiency: a case study using polychaete communities in a subtropical bay moderately affected by urban sewage. *Ocean Science Journal* 40: 17-33.
- Nixon SW (1981) Remineralization and nutrient cycling in coastal marine ecosystems. In: Neilson BJ, Cronin LE (eds), *Estuaries and Nutrients*. New Jersey: Humana Press. pp 111-138.
- Odum EP (1969) The strategy of ecosystem development. *Science* 18: 262-270.
- Olbers J and Samyn Y (2012) The *Ophiocoma* species (Ophiurida: Ophiocomidae) of South Africa. *Western Indian Ocean Journal of Marine Science* 10: 137-154.
- Olivier MJ (1998) Foredune formation at the Tugela River mouth. MSc thesis, University of Natal, Durban, South Africa.
- Olsgard F, Somerfield PJ, Carr MR (1997) Relationships between taxonomic resolution and data transformations in analyses of a macrobenthic community along an established pollution gradient. *Marine Ecology Progress Series* 149: 173-181.
- Olsgard F, Somerfield PJ, Carr MR (1998) Relationships between taxonomic resolution, macrobenthic community patterns and disturbance. *Marine Ecology Progress Series* 172: 25-36.
- Oug E (1998) Relating species patterns and environmental variables by Canonical Ordination: An analysis of soft-bottom macrofauna in the region of Tromsø, northern Norway. *Marine Environmental Research* 45: 29-45.
- Oug E, Fleddum A, Rygg B and Olsgard F (2012) Biological traits analyses in the study of pollution gradients and ecological functioning of marine soft bottom species assemblages in a fjord ecosystem. *Journal of Experimental Marine Biology and Ecology* 432-433: 94-105.
- Pacheco AS, González MT, Bremner J, Oliva M, Heilmayer O, Laudien J and 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 and 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.
- Pagliosa PR (2005) Another diet of worms: the applicability of polychaete feeding guilds as a useful conceptual framework and biological variable. *Marine Ecology* 26: 246-254.
- Palmer MW (1993) Putting things in even better order: The advantages of Canonical Correspondence Analysis. *Ecology* 74: 2215-2230.
- Parker JG (1983) A comparison of methods used for the measurement of organic matter in marine sediment. *Chemistry in Ecology* 1: 201-210.
- Passarelli C, Olivier F, Paterson DM and Hubas C (2012) Impacts of biogenic structures on benthic assemblages: microbes, meiofauna, macrofauna and related ecosystem functions. *Marine Ecology Progress Series* 465: 85-97.
- Pavia PC (1993) Trophic structure of a shelf polychaete taxocoenosis in southern Brazil. *Cahiers de Biologie Marine* 35: 39-55.
- Pearce AF (1977) Some features of the upper 500 m of the Agulhas Current. *Journal of Marine Research* 35: 731-753.

- Pearce AF, Schumann EH and Lundie GSH (1978) Features of the shelf circulation off the Natal coast. *South African Journal of Science* 74: 328-331.
- Pearson TH (1970) The benthic ecology of Loch Linnhe and Loch Eil, a sea-loch system on the west coast of Scotland. I. The physical environment and distribution of the macrobenthic fauna. *Journal of Experimental Marine Biology and Ecology* 5: 1-34.
- Pearson TH (2001) Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanography and Marine Biology Annual Review* 39: 233-267.
- Petersen CGJ (1914) Valuation of the Sea II. The animal communities of the sea-bottom and their importance for marine zoogeography. Report of the Danish Biological Station 21: 1-44.
- Pillay D, Branch GM and Forbes AT (2007) Experimental evidence for the effects of the thalassinidean sandprawn *Callianassa kraussii* on macrobenthic communities. *Marine Biology* 152: 611-618.
- Pillay D and Branch GM (2011) Bioengineering effects of burrowing thalassinidean shrimps on marine soft-bottom ecosystems. *Oceanography and Marine Biology Annual Review* 49: 137-192.
- Pinn EH and Robertson MR (2003) Macro-infaunal biodiversity and analysis of associated feeding guilds in the Greater Minch area, Scottish west coast.
- Posey MH (1986) Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis*. *Marine Ecology Progress Series* 31: 15-22.
- Probert PK (1984) Disturbance, sediment stability, and trophic structure of soft-bottom communities. *Journal of Marine Research* 42: 893-921.
- Probert PK and Wilson JB (1984) Continental shelf Benthos off Otago Peninsula, New Zealand. *Estuarine, Coastal and Shelf Science* 19: 373-391.
- Probert PK and Grove SL (1998) Macrobenthic assemblages of the continental shelf and upper slope off the west coast of the South Island, New Zealand. *Journal of the Royal Society of New Zealand* 28: 259-280.
- Quijón PA and Snelgrove PVR (2008) Trophic complexity in marine sediments: new evidence from the Gulf of St. Lawrence. *Marine Ecology Progress Series* 371: 85-89.
- Quinn GP and Keough MJ (2002) *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.
- Reiss H, Degraer S, Duineveld GCA, Kröncke I, Aldridge J, Craeymeersch JA, Eggleton JD, Hillewaert H, Lavaleye MSS, Moll A, Pohlmann T, Rachor E, Robertson M, Vanden Berghe E, van Hoey G and Rees HL (2009) Spatial patterns of infauna, epifauna and demersal fish communities in the North Sea. *ICES Journal of Marine Science* 67: 278-293.
- Ricciardi A and Bourget E (1998) Weight-to-weight conversion factors for marine benthic macroinvertebrates. *Marine Ecology Progress Series* 163: 245-251.
- Riisgård HU and Kamermans P (2001) Switching between deposit and suspension feeding in coastal zoobenthos. In: Reise K (ed), *Ecological comparisons of sedimentary shores*. Germany: Springer-Verlag. pp73-104.
- Roberts MJ, van der Lingen CD, Whittle C and 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.

- Rodil IF, Lastra M, López J (2009) Spatial variability of benthic macrofauna in the Ria of Vigo (NW Spain): Effect of sediment type and food availability. *Marine Biology Research* 5: 572-584.
- Root RB (1967) The niche exploitation pattern of the Blue-gray Gnatcatcher. *Ecological Monographs* 37: 317-350.
- Roth S and Wilson JG (1998) Functional analysis by trophic guilds of macrobenthic community structure in Dublin Bay, Ireland. *Journal of Experimental Marine Biology and Ecology* 222: 195-217.
- Sakai K (2011) Axioidea of the world and a reconsideration of the Callianassoidea (Decapoda, Thalassinidea, Callianassida). *Crustacean Monographs* 13: 1-520.
- Salas F, Marcos C, Neto JM, Patrício J, Pérez-Ruzafa A and Marques JC (2006) User-friendly guide for using benthic ecological indicators in coastal and marine quality assessment. *Ocean and Coastal Management* 49: 308-331.
- Salen-Picard C, Darnaude AM, Arlhac D and 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.
- Samyn Y (2003) Towards an understanding of the shallow-water holothuroid fauna (Echinodermata: Holothuroidea) of the western Indian Ocean. PhD thesis, University of Brussels, Belgium.
- Sanders HL (1958) Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnology and Oceanography* 3: 245-258.
- Sanders HL (1960) Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. *Limnology and Oceanography* 5: 138-153.
- Sanders HL (1968) Marine benthic diversity: A comparative study. *The American Naturalist* 102: 243-282.
- Sanders HL, Goudsmit EM, Mills EL, Hampson GE (1962) A study of the intertidal fauna of Barnsdale Harbor, Massachusetts. *Limnology and Oceanography* 7: 63-79.
- Sauer WHH, Hecht T, Britz PJ and Mather D (2003) An economic and sectoral study of the South African fishing industry. Volume 2: Fishery profiles. Grahamstown, Rhodes University. pp 1-312.
- Schumacher BA (2002) Methods for the determination of total organic Carbon (TOC) in soils and sediments. Las Vegas: United States Environmental Protection Agency. pp 1-25.
- 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), *Lecture notes on coastal and estuarine studies Volume 26: Coastal ocean studies off Natal*. Germany: Springer-Verlag. pp 103-131.
- Schumann EH (1989) The propagation of air pressure and wind systems along the South African coast. *South African Journal of Science* 85: 382-385.
- Shackley SE and Collins M (1984) Variations in sublittoral sediments and their associated macro-infauna in response to inner-shelf processes; Swansea Bay, U.K. *Sedimentology* 31: 793-804.
- Shin PKS, Huang ZG and Wu RSS (2004) An updated baseline of subtropical macrobenthic communities in Hong Kong. *Baseline/Marine Pollution Bulletin* 49: 119-141.

- Simberloff D and Dayan T (1991) The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* 22: 115-143.
- Simon CA, Ludford A and Wynne S (2006) Spionid polychaetes infesting cultured abalone, *Haliotis midae*, in South Africa. *African Journal of Marine Science*. 28: 167-171.
- Simon CA and Booth A (2007) Population structure and growth of polydorid polychaetes that infest the cultured abalone, *Haliotis midae*. *African Journal of Marine Science* 29: 499-509.
- Simon CA (2009) *Pseudopolydora* species associated with mollusc shells on the south coast of South Africa, with the description of *Ps. dayii*, sp nov. *Journal of the Marine Biological Association of the United Kingdom*. 89: 681-687.
- Simon CA, Worsfold T, Lange L and Sterley J (2010) The genus *Boccardia* (Polychaeta: Spionidae) associated with mollusc shells on the south coast of South Africa. *Journal of the Marine Biological Association of the United Kingdom* 90: 585-598.
- Simon CA (2011) *Polydora* and *Dipolydora* (Polychaeta: Spionidae) associated with molluscs on the south coast of South Africa, with descriptions of two new species. *African Invertebrates* 52: 39-50.
- Simonini R, Ansaloni I, Bonvicini Pagliai AM and Prevedelli D (2004) Organic enrichment and structure of the macrozoobenthic community in the northern Adriatic Sea in an area facing Adige and Po mouths. *ICES Journal of Marine Science* 61: 871-881.
- Sink KJ, Holness S, Harris L, Majiedt P, Atkinson L, Robinson T, Kirkman S, Hutchings L, Leslie R, Lamberth S, Krewath S, von der Heyden S, Lombard A, Attwood C, Branch G, Fairweather T, Taljaard S, Weerts S, Cowley P, Awad A, Halpern B, Grantham H and Wolf T (2012) National Biodiversity Assessment 2011: Technical Report. Volume 4: Marine and Coastal component. Pretoria: South African National Biodiversity Institute. pp 1-325.
- Smith VH, Tilman GD and Nekola JC (1999) Eutrophication: impacts of excess nutrient inputs on freshwater, marine and terrestrial ecosystems. *Environmental Pollution* 100: 179-196.
- Smith SV, Buddemeier RW, Wulff F and Swaney DP (2005) C, N, P Fluxes in the coastal zone. In: Crossland CJ, Kremer HH, Lindeboom HJ, Marshall Crossland JI, Le Tissier MDA (eds), *Coastal Fluxes in the Anthropocene*. Germany: Springer-Verlag. pp 95-144.
- Snelgrove PVR (1997) The importance of marine sediment diversity 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 and Butman CA (1994) Animal-sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology Annual Review* 32: 111-177.
- Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL and Srivastava DS (2004) Extinction and ecosystem function in the marine benthos. *Science* 306: 1177-1180.
- Somerfield PJ and Clarke KR (1995) Taxonomic levels, in marine community studies, revisited. *Marine Ecology Progress Series* 127: 113-119.
- Speich S, Lutjeharms JRE, Penven P, Blanke B (2006) Role of bathymetry in Agulhas Current configuration and behaviour. *Geophysical Research Letters* 33: L23611.
- Sumida PYG, Yoshinaga MY, Ciotti ÁM and Gaeta SA (2005) Benthic response to upwelling events off the SE Brazilian coast. *Marine Ecology Progress Series* 291: 35-42.

- Sunda WG (2010) Iron and the Carbon pump. *Science* 327: 654-655.
- Syvitski JPM, Harvey N, Wolanski E, Burnett WC, Perillo GME, Gornitz V (2005) Dynamics of the coastal zone. In: Crossland CJ, Kremer HH, Lindeboom HJ, Marshall Crossland JJ, Le Tissier MDA (eds), *Coastal Fluxes in the Anthropocene*. Germany: Springer-Verlag. pp 39-94.
- Taghon GL (1992) Effects of animal density and supply of deposited and suspended food particles on feeding, growth and small-scale distributions of two spionid polychaetes. *Journal of Experimental Marine Biology and Ecology* 162: 77-95.
- Taghon GL and Greene RR (1992) Utilization of deposited and suspended particulate matter by benthic "interface" feeders. *Limnology and Oceanography* 37: 1370-1391.
- Tait RV and Dipper F (1998) *Elements of Marine Ecology*. Oxford: Butterworth-Heinemann. pp 1-462.
- Taljaard S, van Niekerk L and Joubert W (2009) Extension of a qualitative model on nutrient cycling and transformation to include microtidal estuaries on wave-dominated coasts: southern hemisphere perspective. *Estuarine, Coastal and Shelf Science* 85: 407-421.
- Ter Braak CJF (1986) Canonical Correspondence Analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
- Ter Braak CJF and Verdonschot PFM (1995) Canonical Correspondence Analysis and related multivariate methods in aquatic ecology. *Aquatic Ecology* 57: 255-289.
- Terlizzi A, Bevilacqua S, Fraschetti S and Boero F (2003) Taxonomic sufficiency and the increasing insufficiency of taxonomic expertise. *Marine Pollution Bulletin* 46: 556-561.
- Thandar AS (2009) A new species of the holothurian genus *Phyllophorus* from South Africa with a key to subgenus *Phyllophorella*. *Journal of Zoology* 234: 341-351.
- Thandar AS and Rowe FWE (2005) New species and new records of apodous holothurians (Echinodermata, Holothuroidea) from southern Africa.
- Thorson G (1957) Bottom communities (sublittoral or shallow shelf). *Geological Society of America Memoirs* 67: 461-534.
- Thrush SF, Hewitt JE, Funnell GA, Cummings VJ, Ellis J, Schultz D, Talley D and Norkko A (2001) Fishing disturbance and marine biodiversity: the role of habitat structure in simple soft-sediment systems. *Marine Ecology Progress Series* 223: 277-286.
- Thrush SF and 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.
- Thrush SF, Hewitt JE, Cummings VJ, Ellis JI, Hatton C, Lohrer A and Norkko A (2004) Muddy waters: Elevating sediment input to coastal and estuarine habitats. *Frontiers in Ecology and the Environment* 2: 299-306.
- Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series* 318: 31-45.
- Tselepides A, Papadopoulou KN, Podaras D, Plaiti W, Koutsoubas D (2000) Macrobenthic community structure over the continental margin of Crete (South Aegean Sea, NE Mediterranean). *Progress in Oceanography* 46: 401-428.
- Tsutsumi H (1987) Population dynamics of *Capitella capitata* (Polychaeta; Capitellidae) in an organically polluted cove. *Marine Ecology Progress Series* 36: 139-149.

- Turpie JK (2004) South African National Spatial Biodiversity Assessment Technical Report Volume 3: Estuary component. Cape Town: Anchor Environmental Consultants. pp 1-33.
- Turpie JK and Lamberth SJ (2010) Characteristics and value of the Thukela banks crustacean and linefish fisheries, and the potential impacts of changes in river flow. *African Journal of Marine Science* 32: 613-624.
- Turpie JK, Wilson G and Van Niekerk L (2012) National Biodiversity Assessment 2011: National Estuary Biodiversity Plan for South Africa. Anchor Environmental Consulting, Cape Town. Report produced for the Council for Scientific and Industrial Research and the South African National Biodiversity Institute.
- Underwood AJ and Chapman MG (2005) Design and analysis in benthic surveys. In: Eleftheriou A, McIntyre A (eds), *Methods for the study of marine benthos* (3<sup>rd</sup> Edition). Oxford: Blackwell Publishing. pp 1-42.
- van der Elst R and Fennessy ST (1990) An investigation into the discard catch of the Tugela Bank prawn trawlers: Unpublished Report No. 66. Durban: Oceanographic Research Institute. pp 1-13.
- van der Meer J, Heip CH, Herman PJM, Moens T, van Oevelen D (2005) Measuring the flow of energy in marine benthic animal populations. In: Eleftheriou A, McIntyre A (eds), *Methods for the study of marine benthos* (3<sup>rd</sup> Edition). Oxford: Blackwell Publishing. pp 326-353.
- van Hoey G, Degraer S and Vincx M (2004) Macrobenthic community structure of soft-bottom sediments at the Belgian continental shelf. *Estuarine, Coastal and Shelf* 59: 599-613.
- Vorwerk PD (2006) A preliminary examination of selected biological links between four eastern Cape estuaries and the inshore marine environment. PhD Thesis, Rhodes University, South Africa.
- Vorwerk PD, Froneman PW, Paterson AW, Strydom NA and Whitfield AK (2008) Biological responses to resumption in river flow in a freshwater-deprived, permanently open South African estuary. *Water SA* 34: 597-604.
- Voss M, Baker A, Bange HW, Conley D, Cornell S, Deutsch B, Engel A, Ganeshram R, Garnier J, Heiskanen A-S, Jickells T, Lancelot C, McQuatters-Gollop A, Middelburg J, Schiedek D, Slomp CP and Conley DP (2011) Nitrogen processes in coastal and marine ecosystems. In: Sutton MA, Howard CM, Willem Erisman J, Billen G, Bleeker A, Grennfelt P, van Grinsven H, Grizzetti B (eds), *The European Nitrogen Assessment*. Cambridge: Cambridge University Press. pp 147-176.
- Warwick RM (1986) A new method for detecting pollution effects on marine macrobenthic communities. *Marine Biology* 92: 557-562.
- Warwick RM (1988a) Analysis of community attributes of the macrobenthos of Frierfjord/Langesundfjord at taxonomic levels higher than species. *Marine Ecology Progress Series* 46: 167-170.
- Warwick RM (1988b) Effects on community structure of a pollutant gradient. *Marine Ecology Progress Series* 46: 207-211.
- Wepener V (2007) Carbon, Nitrogen and Phosphorus fluxes in four sub-tropical estuaries of northern KwaZulu-Natal: Case studies in the application of a mass balance approach. *Water SA* 33: 203-214.
- Weston DP (1988) Macrobenthos-sediment relationships on the continental shelf off Cape Hatteras, North Carolina. *Continental Shelf Research* 8: 267-286.

- Wheatcroft RA (2006) Time-series measurements of macrobenthos abundance and sediment bioturbation intensity on a flood-dominated shelf. *Progress in Oceanography* 71: 88-122.
- Whitfield AK (2005) Fishes and freshwater in southern African estuaries – A review. *Aquatic Living Resources* 18: 275-289.
- Whitfield AK and Harrison TD (2003) River flow and fish abundance in a South African estuary. *Journal of Fish Biology* 62: 1467-1472.
- Whitfield AK and Bate G (2007) A review of information on temporarily open/closed estuaries in the warm and cool temperate biogeographic regions of South Africa, with particular emphasis on the influence of river flow in these system. Report No. 1581/1/07. Pretoria: Water Research Commission. pp 1-232.
- Whitlatch RB (1981) Animal-sediment relationships in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. *Journal of Experimental Marine Biology and Ecology* 53: 31-45.
- Wieking G and Kröncke I (2003) Macrofauna communities of the Dogger Bank (central North Sea) in the late 1990's: spatial distribution, species composition and trophic structure. *Helgoland Marine Research* 57: 34-46.
- Wieking G and Kröncke I (2005) Is benthic trophic structure affected by food quality? The Dogger Bank example. *Marine Biology* 146: 387-400.
- Wijsman JWM, Herman PMJ and Gomoiu M-T (1999) Spatial distribution in sediment characteristics and benthic activity on the northwestern Black Sea shelf. *Marine Ecology Progress Series* 181: 25-39.
- Wilson RS (1990) *Prionospio* and *Paraprionospio* (Polychaeta: Spionidae) from southern Australia. *Memoirs of the Museum of Victoria* 50: 243-274.
- Woodson CB, McManus MA, Tyburczy JA, Barth JA, Washburn L, Caselle JE, Carr MH, Malone DP, Raimondi PT, Menge BA and Palumbi SR (2012) Coastal fronts set recruitment and connectivity patterns across multiple taxa. *Limnology and Oceanography* 57: 582-596.
- Yeung C, Yang M-S, McConnaughey RA (2010) Polychaete assemblages in the south-eastern Bering Sea: linkage with groundfish distribution and diet. *Journal of the Marine Biological Association of the United Kingdom* 90: 903-917.
- Young DK and Rhoads DC (1971) Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A transect study. *Marine Biology* 11: 242-254.
- Zaâbi S, Gillet P, Afli A and Boumaiza M (2010) Structure and diversity of polychaetous annelids population along the eastern coast of the Cap Bon Peninsula (north-east coast of Tunisia, western Mediterranean). *Marine Biodiversity records* 3: 1-11.
- Zajac RN, Lewis RS, Poppe LJ, Twichell DC, Vozarik J and DiGiacomo-Cohen ML (2000) Relationships among sea-floor structure and benthic communities in Long Island Sound at regional and benthoscape scales. *Journal of Coastal Research* 16: 627-640.
- Zajac RN, Lewis RS, Poppe LJ, Twichell DC, Vozarik J and DiGiacomo-Cohen ML (2003) Responses of infaunal populations to benthoscape structure and the potential importance of transition zones. *Limnology and Oceanography* 48: 829-842.
- Zajac RN (2008a) Macrobenthic diversity and sea floor landscape structure. *Journal of Experimental Marine Biology and Ecology* 366: 198-203.
- Zajac RN (2008b) Challenges in marine, soft-sediment benthoscape ecology. *Landscape Ecology* 23: 7-18.

- Zuur AF, Ieno EN and Smith GM (2007) Analysing Ecological Data. In: Gail M, Krickeberg K, Samet J, Tsiatis A, Wong W (eds), *Statistics for Biology and Health*. New York: Springer. pp 1-672.