

**SPATIAL AND TEMPORAL VARIATIONS IN MACROZOOBENTHIC
COMMUNITIES IN KWAZULU-NATAL TEMPORARILY
OPEN/CLOSED ESTUARIES**

by

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*"But science is not about establishing certainty.
It's about understanding change. Certainty is a vestigial concept from the
time when constancy supposedly ruled life and the cosmos.
There is no constancy in nature - there is only constant change, and lots of it."*

TOM SIEGFRIED

Editor of Science News
For both universe and life, only constant is change
Science News, February 14, 2009

ABSTRACT

Estuaries are complex ecosystems, typified by remarkable fluctuations in environmental conditions. In addition to this natural variability, stochastic events and anthropogenic influences effect change at different spatial and temporal scales. Macrozoobenthic invertebrates are preferable biological indicators because of their sensitivity to variations in habitat quality. This thesis describes inherent changes in the macrozoobenthos of temporarily open/closed estuaries (TOCEs) in KwaZulu-Natal, 'change' as measured in spatial and temporal community differences using various community metrics, namely species composition, abundance and diversity. Standard and widely published quantitative sampling techniques were employed, with simultaneous measurements of ambient physico-chemical conditions, including sediment characteristics. The thesis is in three parts.

Regional distributions and long-term decadal-type changes in macrozoobenthic community structure were determined for 31 TOCEs using historical data (1998/9) compared with more recently collected data (2009/10). Results showed that, although of the same estuary type, the macrozoobenthic communities of these estuaries differed significantly. Furthermore, community composition did not reflect a north to south progression of predominantly tropical species to predominantly warm-temperate species. In the last decade, the macrozoobenthos of these systems had indeed changed (in composition, abundance and/or diversity), the scale of change within each estuary being estuary-dependent.

The recolonisation of two urban and non-urban estuaries by macrozoobenthos following a stochastic flood disturbance was investigated, describing the short-term community changes during the recovery process. Differential recolonisation patterns were attributed to inherent differences in community composition and not to the influence of urbanisation. Recolonisation was marked by distinct changes in community structure, with the recovery trajectory being interrupted by localised disturbances (e.g. change of mouth state).

Species indicative of the observed spatial and temporal community changes were examined for similarities in habitat association and trophic characteristics. The species that were

representative of these KwaZulu-Natal TOCEs were identified and included common and highly abundant generalists of varying trophic groups.

In conclusion, the present findings illustrated the effectiveness of using macrozoobenthic communities to depict 'change' over multiple temporal and spatial scales. This also supports their usefulness as a study group in environmental monitoring and detecting the loss of ecological functioning and biodiversity in estuaries in the long- and short-term.

FACULTY OF SCIENCE AND AGRICULTURE

PREFACE

The work described in this thesis was carried out at the Oceanographic Research Institute, an affiliate of the University of KwaZulu-Natal, Durban, under the School of Biological and Conservation Sciences. This work was undertaken from January 2008 to March 2011, under the supervision of Fiona Mackay.

DECLARATION - PLAGIARISM

I,, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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Signed

.....
Catherine Anne Stow

June 2011

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CHAPTER 1

GENERAL INTRODUCTION

Estuaries are dynamic aquatic ecosystems found at the interface between rivers, land and sea. They include a wide variety of shapes and sizes with varying degrees of connectivity with the marine environment (McLusky and Elliott 2004). Estuaries are inherently complex, typified by remarkable natural changes in environmental conditions over a range of spatial and temporal scales, and can thus be considered as being in a constant state of flux (Baird 1999, McLusky and Elliott 2004, Bemvenuti et al. 2005). Consequently, there are many definitions of an estuary. In the South African context, the accepted definition of an estuary, and the one which is used in the classification of South African estuaries (Whitfield 1992) and in the National Water Act (Act 36 of 1998), is that given by Day (1980) as *“a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with freshwater derived from land drainage”*.

Estuaries are internationally recognised as very important ecological habitats because they support exceedingly high levels of productivity and biological diversity (De Villiers et al. 1999, Hobbie 2000, McLusky and Elliott 2004). Considerable productivity is attributable to the cycling of large amounts of nutrients derived from the marine, riverine and terrestrial environments (McLusky and Elliott 2004). The protected, calm-water habitat afforded by estuaries, combined with high productivity, provides essential feeding, breeding and nursery areas for a variety of invertebrates, birds and commercially important marine fish species (Lamberth and Turpie 2003, McLusky and Elliott 2004). They also serve as migration corridors for diadromous crustacean and fish species, and roosting areas for migratory birds (McLusky and Elliott 2004). Accordingly, estuaries are significant areas of high biological diversity. In addition to nutrient cycling, estuaries also provide other critical ecological functions, including decomposition and remineralisation of organic and inorganic compounds, and serve as natural sinks of land-derived sediment, particulate matter, sewage effluent and other forms of pollution (Baird and Ulanowicz 1993, Dolbeth et al. 2007). To coastal human populations, they offer shoreline protection, commercial fisheries resources and are used as transportation routes, harbours and for recreational purposes (McLusky and Elliott 2004, Dolbeth et al. 2007). Despite the

wealth of goods and services that they provide, estuaries are among the most threatened habitats in the world due to anthropogenic activities, and the impacts of such activities will continue to increase unless effective management strategies are implemented (Morant and Quinn 1999, Dauer et al. 2000, Turpie et al. 2002, Kennish 2004, McLusky and Elliott 2004).

1.1 Types of Estuaries in South Africa

There are approximately 370 drainage outlets on the South African coastline however, only 258 of these systems function as estuaries according to Day's definition (Whitfield 2000). The total estuarine area of South Africa is approximately 600 km², of which 408 km² (68%) occurs in KwaZulu-Natal and 80% of this is attributed to the extensive area of Lake St Lucia (360 km²) (Begg 1978, Cooper et al. 1995, Gilavovic 2000). South African estuarine systems increase in density from west to east, and fall under three biogeographical zones according to their location along the coastline: the Subtropical Zone, which extends from Kosi Bay in KwaZulu-Natal to the Mbashe Estuary in the Eastern Cape, the Warm-Temperate Zone between the Mbashe Estuary and Cape Point, and the Cool-Temperate Zone on the west coast (Whitfield 2000, Turpie 2004).

There exists a variety of estuarine types owing to variations in climate and rainfall patterns, hinterland and coastal topography and geology, terrestrial runoff, fluvial discharge, rates of sediment input and types of sediment supplied by rivers, marine sediment availability and coastal dynamics (Cooper et al. 1999, Schumann et al. 1999, Whitfield and Bate 2007). The resulting forms are broadly classified into five estuarine types based on mouth characteristics, tidal prism, mixing processes and salinity features of each system (Whitfield 1992). These are: permanently open estuaries (POEs), temporary open/closed estuaries (TOCEs), estuarine lakes, estuarine bays and river mouths (Table 1.1) (Whitfield 1992). Individual systems may alternate between estuarine types or behave like other types over time depending on natural or anthropogenic influences that may alter river flow and the mouth dynamics, thus making strict classification difficult (Whitfield 1992, 2000). In addition, systems within each category often differ due to differences in catchment characteristics and the management of the catchment areas, including upstream land-use practises, impoundments and water abstraction, as well as artificial breaching of the mouth (Morant and Quinn 1999, Turpie 2004).

Table 1.1 Physical characteristics of the five estuarine types according to Whitfield's (1992) classification of South African estuaries

Type	Tidal Prism	Mixing Process	Average Salinity (g.kg ⁻¹)
Estuarine Bay	Large (>10 x 10 ⁶ m ³)	Tidal	20 - 35
Permanently Open	Moderate (1-10 x 10 ⁶ m ³)	Tidal/Riverine	10 - >35
River Mouth	Small (<1 x 10 ⁶ m ³)	Riverine	< 10
Estuarine Lake	Negligible (<0.1 x 10 ⁶ m ³)	Wind	1 - >35
Temporarily Closed	Absent	Wind	1 - >35

1.1.1 Characteristics of Temporarily Open/Closed Estuaries

Approximately 71% of South African estuaries are classified as temporarily open/closed estuaries (TOCEs) (Turpie 2004, Perissinotto et al. 2004, 2010). Estuaries of this type are characteristically isolated from the sea for varying periods of time by a sandbar that forms at the mouth during low river flow (Whitfield 1992, Whitfield and Bate 2007). Generally these systems have small river catchments (<500 km²), limited marine exchange when open (small tidal prisms <1 x 10⁶ m³), and normally low river flow often resulting in the formation of a terminal basin in the lower reaches during the prolonged closed phase (Begg 1978, Whitfield 1992). As such, these systems have also been termed 'lagoonal' estuaries (Begg 1978), 'blind' estuaries (Day 1981a) and intermittently open estuaries (James et al. 2007). In other regions of the world, TOCEs are referred to as 'intermittently closed and open lakes and lagoons' in Australia (Roy et al. 2001), and 'seasonally open tidal inlets/coastal lagoons' in India and Sri Lanka (Ranasinghe and Pattiaratchi 2003). Similar estuaries are also found on the southeastern coasts of Uruguay and Brazil, along the west and south coasts of the USA, and in parts of New Zealand and the Mediterranean (Perissinotto et al. 2010).

The open or closed state of the mouth is controlled by the marine processes of longshore transport and flood-tidal influx of sediment into the system, against the scouring potential of the river outflow and ebb-tidal currents, mediated by wave activity (Whitfield 1992, Cooper et al. 1999, Schumann et al. 1999, Whitfield and Bate 2007, Perissinotto et al. 2010). Depending on the interplay between these processes and the size of the estuary, beach profile and the level of mouth protection, TOCEs can exist in one of five hydrodynamic states, namely the outflow phase, tidal phase, semi-closed phase and closed phase (Whitfield et al. 2008). The marine overwash phase occurs during the closed mouth state (Whitfield et al. 2008). During both the outflow phase and the tidal phase, the estuary is effectively open and connected to

the sea. The former phase is dominated by freshwater conditions and strong river outflow commonly due to flooding, while during the latter, a tidal regime is established within the estuary after floodwaters have subsided (Whitfield et al. 2008). Salinity increases rapidly across most of the estuary due to saline intrusion, beginning in the lower reaches and penetrating as far as the upper reaches. In the 'semi-closed' phase, river inflow is low while marine input is limited to near peak high tide levels, and the ebb flow is prevented by the development of the sandbar, or berm (Whitfield et al. 2008). The shorter the duration of the closing phasing, the lesser the amount of saline intrusion that takes place, and thus the prevalence of lower salinity conditions at the start of the closed phase (Whitfield et al. 2008). In the 'closed' phase, there is no connection to the sea as the berm prevents both saline input and the outflow of estuary water, resulting in the accumulation of water within the system (Whitfield et al. 2008). This is the most common phase in South African TOCEs (Cooper et al. 1999, Harrison 2004, Whitfield et al. 2008, Perissinotto et al. 2010). Marine overwash occurs either during spring high tides, where the volume of saline water introduced is relatively small, or as a result of storm surges and high waves, where a greater amount of marine water overtops the sandbar (Whitfield et al. 2008). When the water level within the system exceeds that in the open sea, seepage of estuary water takes place through the sandbar (Whitfield et al. 2008).

Breaching occurs when increased wave action on the sea front, or overtopping by high water levels within the basin, results in the down-cutting and erosion of the sandbar (Gaston et al. 1996, Cooper et al. 1999, Perissinotto et al. 2010). The system soon becomes reconnected to the sea via the open mouth, followed by a reduction in water level within the basin (Gaston et al. 1996, Cooper et al. 1999, Whitfield and Bate 2007, Perissinotto et al. 2010). Many KwaZulu-Natal TOCEs systems are referred to as 'perched', that is, during the closed phase the water level is maintained above high tide level behind a characteristically high berm (Cooper 2001). This 'perched' condition is the product of the high sediment load carried by east coast rivers and subsequent siltation, and thus, such estuaries drain dramatically following the opening of the mouth (Allanson and Winter 1999, Cooper 2001, Harrison 2004, Perissinotto et al. 2004, 2010). The opening of TOCEs is often seasonal. In KwaZulu-Natal, these systems are generally open after high rainfall periods and increased river flow during the wet summer months (October-March), but during dry winter months, they are closed or close more frequently and for longer periods of time (Day 1981b, Begg 1984a, Schumann et al. 1999, Perissinotto et al.

2010). Flood events are often responsible for the breaching of closed estuary mouths causing the dramatic, and often complete, erosion of the terminal sandbar, deepening of the system and the scouring of large quantities of sediment from the lower reaches of the estuary (Whitfield 1992, Whitfield and Bate 2007, Perissinotto et al. 2010). Infilling and reclosure of a system occurs fairly rapidly depending on marine wave energy, marine- and fluvial-derived sediment availability, and river flow (Whitfield and Bate 2007). The state of the estuary mouth governs the mixing between fluvial and marine input within the estuary and thus influences the structure of the water column (Day 1981b, Harrison 2004, Whitfield and Bate 2007, Whitfield et al. 2008).

In terms of salinity, TOCEs are generally considered low salinity environments, however broad salinity fluctuations do occur. Such fluctuations are dependent on the state of the mouth and freshwater inputs from precipitation and land derived runoff (Day 1981b, Whitfield 1992, Harrison 2004). Uniform oligohaline (0-4.9) to mesohaline (5-17.9) conditions prevail during the closed and semi-closed phases with sporadic saline input via marine overwash (Whitfield 1992, Whitfield and Bate 2007, Whitfield et al. 2008, Perissinotto et al. 2010). During the open phase typical horizontal salinity gradients are often present (Whitfield and Bate 2007, Whitfield et al. 2008). In addition, strong vertical salinity stratification results from low freshwater input entering the estuary as surface water, thereby entrapping bottom saline water (Whitfield and Bate 2007, Perissinotto et al. 2010). Conversely, during flood conditions, TOCEs behave like river mouths where salinity gradients are absent and become largely freshwater environments (Branch and Branch 1985, Whitfield 1992, Perissinotto et al. 2010).

Similarly, dissolved oxygen levels within TOCEs are also determined by the state of the mouth. During the open phase, estuary water is relatively well oxygenated (Harrison 2004, Whitfield and Bate 2007). However, during the semi-closed state, increased water depth may result in reduced dissolved oxygen levels ($<3 \text{ mg.L}^{-1}$) in stratified bottom waters attributed to poor wind-induced mixing, poor water circulation, and decomposition of organic detritus (Harrison 2004, Whitfield and Bate 2007, Perissinotto et al. 2010). Oxygen-deficient bottom waters are replenished by oxygen-rich water during marine overwash (Whitfield and Bate 2007). Closed systems generally have uniform oxygen concentrations, however this is largely dependent on depth and water circulation (Day 1981b, Harrison 2004, Whitfield and Bate 2007, Perissinotto et al. 2010). Anoxic or hypoxic conditions are common in narrow and well-sheltered TOCEs of

KZN that have been closed for an extended period of time (Perissinotto et al. 2004, 2010). Such rapid and dramatic changes in the water quality of TOCEs impose extreme physiological constraints on the residing estuarine organisms.

In estuaries, species abundance and biomass is generally high but diversity is low because few species from either the freshwater or the marine realms can tolerate the dynamic nature of the estuarine environment (Day 1981c, Warwick 1983, De Villiers et al. 1999, McLusky and Elliott 2004). The fauna of TOCEs is dominated by estuarine-endemic and marine species, however freshwater species may become more abundant in the lower reaches of these systems during low salinity periods during the closed phase, or during and soon after, flood events (Day 1981c, Whitfield 1992).

1.2 Susceptibility of South African Estuaries to Change

It can be stated unequivocally, that human intervention has resulted in changes to the South African estuarine environment (Begg 1984a, Morant and Quinn 1999, Boyd et al. 2000, Perissinotto et al. 2004, Turpie et al. 2004). The ever-increasing demands of the burgeoning coastal population and rapid urban development continue to place increasing pressure on South African estuaries particularly through destructive activities such as artificial breaching, impoundments, water abstractions, discharges from waste water treatment works, poor catchment land use, floodplain encroachment, sand-winning operations and overexploitation of natural resources (Morant and Quinn 1999, Perissinotto et al. 2004). Such activities have brought about dramatic changes in the natural ecological condition of the country's estuaries, and as a result, many are functionally degraded (Begg 1978, 1984a, Morant and Quinn 1999, Whitfield 2000, Turpie 2004, Forbes and Demetriades 2008). In addition to anthropogenic impacts, coastal areas and estuaries are most at risk of ecosystem shifts attributed to global climate change, including altered climatic regimes, sea level rise, intensified weather events (storms and storm surges), increased freshwater inflow (or reductions) and increased water temperatures (Whitfield 1992, Clark 1999).

Fortunately, the global increase in environmental awareness, further escalated by the potential impacts of climate change, has led to intensified marine and estuarine research, regarding biological, physico-chemical and socio-economical elements, in an effort to better

understand coastal ecosystems and the effects of anthropogenic activities on them (Alongi 1998, Hobbie 2000). Such research is not only utilised in the development of more effective management strategies, but also in the formulation of policies and legal frameworks as a means to curtail destructive practises and offer protection to threatened ecosystems, including estuaries. In South Africa, the protection of estuaries is encapsulated under the Marine Living Resources Act (Act 18 of 1998), the National Environmental Act (Act 107 of 1998), the National Water Act (Act 36 of 1998) (Turpie et al. 2002) and the National Environmental Management: Integrated Coastal Management Act (Act 24 of 2008). The latter includes the Resource Directed Measures (RDM) process for the determination and preservation of the 'Ecological Reserve' (freshwater supply) of estuaries required to maintain ecosystem function (DWA 2010).

1.3 Estuarine Macrozoobenthos and the Response to Environmental Change

In South African systems, benthic invertebrates (also referred to as macrozoobenthos) are the largest and most numerically dominant group of aquatic fauna inhabiting estuarine environments (De Villiers et al. 1999). This group includes invertebrate taxa (greater than 0.5 mm in size) of both marine and freshwater origin, typically polychaetes, oligochaetes, amphipods, isopods, bivalves, gastropods, crabs, varieties of caridean shrimp and penaeid prawns, and insect larvae (Day 1981c, Perissinotto et al. 2004, 2010). Benthic invertebrates are relatively sedentary, long-lived organisms residing within the sediment or at the sediment-water interface and possess various physiological and/or behavioural adaptations to tolerate extreme fluctuations in the physical and chemical conditions of the estuarine environment, which in turn limit their distribution and the persistence of viable populations through the effects of environmental stress (Day 1981c, Dauer 1993, Kennish 1994, De Villiers et al. 1999, Clarke and Warwick 2001, McLusky and Elliott 2004). These organisms occupy a critical niche in estuarine foodwebs as the primary consumers of suspended and sediment organic carbon and as a food source for secondary consumers, such as birds and benthic feeding fish (Baird and Ulanowicz 1993, Clark 1999, McLusky and Elliott 2004). They contribute significantly to the biochemistry of the sediment, through activities such as feeding, bioturbation, and tube construction, leading to enhanced decomposition and remineralisation of detritus, aeration of anoxic sediments and release of nitrogen products for benthic and pelagic primary productivity (Alongi 1998, McLusky and Elliott 2004).

Macrozoobenthos also display different foraging strategies and morphological features to extract various forms of food material from the surrounding environment (Fauchald and Jumars 1979, Kennish 1994). Benthic invertebrates can be thus divided into several broad feeding groups, or trophic guilds, namely, detritivores (further separated into suspension feeders, surface deposit feeders, and subsurface deposit feeders), herbivores (grazers), carnivores (predators) and omnivores (Kennish 1994, De Villiers et al. 1999, Cardoso et al. 2008). Suspension and deposit feeders are the dominant constituents of macrozoobenthic communities (Probert 1984, Kennish 1994, Herman et al. 1999). Changes in the feeding guild structure of a benthic community are attributable to the differential responses of species to changes in food resources, which in turn are governed by changes in habitat characteristics, including sediment and water quality (Maurer and Leathem 1981, Maurer et al. 1999). Correlations have been drawn between feeding guilds and environmental variables, particularly sediment organic content, sediment type and turbidity as well as organic enrichment (Pearson and Rosenberg 1978, Maurer and Leathem 1981, Dauer 1984, Kennish 1994, Roth and Wilson 1998, De Villiers et al. 1999, Kotta et al. 2007a, 2007b, Cardoso et al. 2008). For example, in South Africa, the silt-laden subtropical estuaries generally host more deposit-feeding organisms than suspension-feeding organisms because the high concentration of suspended particulate matter causes clogging of the filtering organs of the latter (Fauchald and Jumars 1979, De Villiers et al. 1999, Norkko et al. 2002).

Because of their sensitivity to changes in water and sediment quality, macrozoobenthos exhibit complex spatial and temporal variations in community characteristics (including species composition, distribution, abundance, biomass and feeding guild structure) in response to both natural and human-induced environmental changes (Gray 1981, Day 1981c, Kennish 1994, De Villiers et al. 1999, Clarke and Warwick 2001, Bursey and Wooldridge 2003, McLusky and Elliott 2004, Dolbeth et al. 2007, Goodsell et al. 2007, Muxika et al. 2007, Cardoso et al. 2008). For these reasons, benthic invertebrates are effective indicators of environmental change, and are commonly used to assess the effects of pollution and anthropogenic activities on the health of marine and estuarine ecosystems (Pearson and Rosenberg 1978, Gray 1981, Weisberg et al. 1997, Borja et al. 2000, Clarke and Warwick 2001, Rosenberg et al. 2004, Muxika et al. 2007, Borja and Dauer 2008, Pinto et al. 2009, Neto et al. 2010). As such, many European-developed indices, or ecological indicators, draw on the structure and functioning of

macrozoobenthic communities to determine the ecological quality of marine and estuarine environments impacted by various forms of pollution, particularly organic enrichment. The common indices include AMBI (AZTI Marine Biotic Index, Borja et al. 2000), BENTIX (Benthic Quality Index, Simboura and Zenetos 2002), BOPA (Benthic Opportunistic Polychaetes Amphipods index, Dauvin and Ruellet 2007), ITI (Infaunal Trophic Index, Word 1980, Maurer et al. 1999), H' (the Shannon-Wiener diversity index), BQI (Benthic Quality Index, Rosenberg et al. 2004) and M-AMBI (Multivariate AMBI, Muxika et al. 2007).

1.4 Monitoring Change in South African Macrozoobenthos

Since the management of South African estuaries has moved toward a more ecosystem-based approach, a sound understanding of the structure and functioning of all the components of a particular estuarine system is required (Turpie et al. 2002). This includes information on both the biotic and abiotic components as well as the forcing factors that induce changes in these components. However, there is a paucity of empirical data for invertebrates, including macrozoobenthos, for the majority of South African estuaries. Such data is available for only 20% of South African estuaries, and only 7% of estuaries in KwaZulu-Natal (Turpie et al. 2004). Furthermore, much of the research has been haphazardly conducted by various workers through time on a selection of specific estuaries, using different sampling techniques and in different estuarine habitats (e.g. subtidal vs intertidal) leading to poor comparability of the data (Perissinotto et al. 2004, Turpie et al. 2004). Consequently, most of the macrozoobenthic data used in current estimations of biodiversity of individual estuaries are based on a predictive model of the communities of warm-temperate estuaries of the Eastern Cape (Turpie et al. 2004). Hence, the need exists for 1) sustained and systematic collection of high quality invertebrate data from 2) more South African estuaries, particularly KwaZulu-Natal estuaries, toward the improved determination of the biodiversity importance of estuaries. These are two important considerations of the current study.

In terms of understanding sources of estuarine ecosystem variability, changes in the different biological communities, such as macrozoobenthos, are a reflection of natural environmental fluctuations manipulated by a suite of anthropogenic impacts coupled with the growing effects of climate change. Therefore, changes in macrozoobenthic communities have value as predictive tools for detecting ecosystem change (Morant and Quinn 1999, McLusky and Elliott

2004, Muxika et al. 2007). However, the lack of community-type data for macrozoobenthos (baseline information, short-term and long-term dynamics) (De Villiers et al. 1999, Turpie et al. 2004), in combination with rapid changes in community composition and abundance over space and time (DWA 2010), impedes our ability to predict accurately the consequences of change on this particular group of organisms and their role in estuarine ecosystems. Thus, measuring, monitoring and predicting change through such biological communities, and developing methods to prevent undesirable change, are central to contemporary estuarine research particularly in the light of deteriorating estuarine condition and the unknown effects of global warming (Dauer 1993, De Villiers et al. 1999, Morant and Quinn 1999, Boyd et al. 2000, Hobbie 2000, Kennish 2004, Bortone 2005, Lotze et al. 2006, Dolbeth et al. 2007, Elliott and Quintino 2007, Ruellet and Dauvin 2007). The abovementioned issues are addressed in the current study, the objectives of which are outlined in the following section.

1.5 Project Aim and Objectives

The aim of the current study was to describe changes in the macrozoobenthos of temporarily open/closed estuaries of KwaZulu-Natal (change as measured by differences in species composition, abundance and diversity), relative to 1) local and regional spatial distributions and 2) short-term (1 year) and long-term (11 years) temporal distributions. This was achieved through completion of the following objectives:

- To determine species composition and abundance through taxonomic classification (to species level or as far as practically possible) and enumeration of individuals;
- To calculate and describe spatial and temporal patterns of species diversity;
- To relate changes in community structure to changes in environmental factors (physico-chemical variables and sediment composition);
- To describe the stages of macrozoobenthic recolonisation after short-term flood disturbance;
- To conduct the sampling of macrozoobenthos of 31 TOCEs in a manner comparable to historical collection conducted 11 years ago for both spatial and temporal comparisons;
- To determine changes to the macrozoobenthos of TOCEs after an 11 year period;
- To establish a broad classification scheme of subtropical TOCEs based on their macrozoobenthic communities; and

- To identify key species assemblages as proxies for community change at different spatial and temporal scales.

1.6 Thesis Outline

The thesis comprises five sections, namely, methodology (Chapter 2), two individual investigations with tested hypotheses regarding macrozoobenthos (Chapters 3 and 4), an exploratory chapter (Chapter 5) and a general discussion and conclusion (Chapter 6). Chapter 2 comprises firstly a general description of the KwaZulu-Natal coastline as a broad study area and features pertinent to the estuarine environment, and secondly, the description of the general field sampling and laboratory protocols used throughout the current study. Generic treatment of the biological and environmental data and types of analyses used are also described. Field methodology and data analyses specific to each topic under investigation are described in detail in the respective chapters. Chapter 3, a descriptive study, discusses the national assessments of the state of South African estuaries, and the value of macrozoobenthos in such assessments. It goes on to describe the spatial and temporal differences of macrozoobenthos among 31 TOCEs along the KwaZulu-Natal coast in comparison with a survey conducted in 1998/9. This chapter identifies estuaries that are similar based on the composition of their macrozoobenthic communities and provides insight into the long-term, decadal-type changes that may occur in these communities. Chapter 4, an experimental study, covers the short-term response of macrozoobenthos to a stochastic flood event. The study compares the recolonisation of macrozoobenthic communities of two urban and two non-urban TOCEs affected by flooding with the view that urbanisation of the estuarine environment affects the recovery response of the communities. The content of Chapter 5 is focussed at the species level, whereby species indicative of the temporal (short- and long-term) and spatial community changes observed in the preceding chapters, are examined for similarities in their habitat associations and feeding modes (trophic groups). Chapter 6 is the integration and general discussion of the different types of 'change' in macrozoobenthos elucidated during this study. This chapter also discusses briefly the implications of these findings and recommendations for future research.

CHAPTER 2

GENERAL MATERIALS AND METHODS

2.1 Study Area – The KwaZulu-Natal coastline

The number of estuaries in KwaZulu-Natal and their functioning is determined by the topography, climate and geology of the region, as well as the impact of the human population.

2.1.1 Location and Topography

The KwaZulu-Natal province is located on the east coast of South Africa, between the Mozambique border to the north and the provincial border of the Eastern Cape to the south (Figure 2.1). The steep hinterland of the Drakensberg Mountains (>3000 m amsl) gives rise to a greater number of rivers draining smaller catchments, therefore the vast majority of KwaZulu-Natal estuaries are found in the southern region (Begg 1984b, Cooper et al. 1995, 1999). In contrast, there are few estuaries north of the Thukela River as a result of the flat topography of the coastal plain, and these comprise mainly large estuarine lake systems such as Kosi Bay and Lake St Lucia (Cooper et al. 1995). In this region, estuaries were generally formed from drowned river valleys which have since been silted up resulting in shallow estuaries with large surface areas, the biggest being Lake St Lucia (360 km²) (Begg 1978, Cooper et al. 1999). The most southern part of the coastal plain bears few freshwater wetlands of any significance (Ngubane et al. 1997b). To the south of the province, there is virtually no coastal plain and estuaries follow bedrock-confined river valleys (Cooper et al. 1999).

2.1.2 Climate

Within the subtropical region, the climate of the KwaZulu-Natal coastline is typically warm and humid, governed largely by the warm Agulhas Current. The mean annual rainfall on the coast is higher than in most of the KwaZulu-Natal interior (Figure 2.2) and other coastal provinces, and generally exceeds 1000mm, which falls mainly during the summer months (October-March) (Day 1981b, Ngubane et al. 1997a, Harrison 2004).

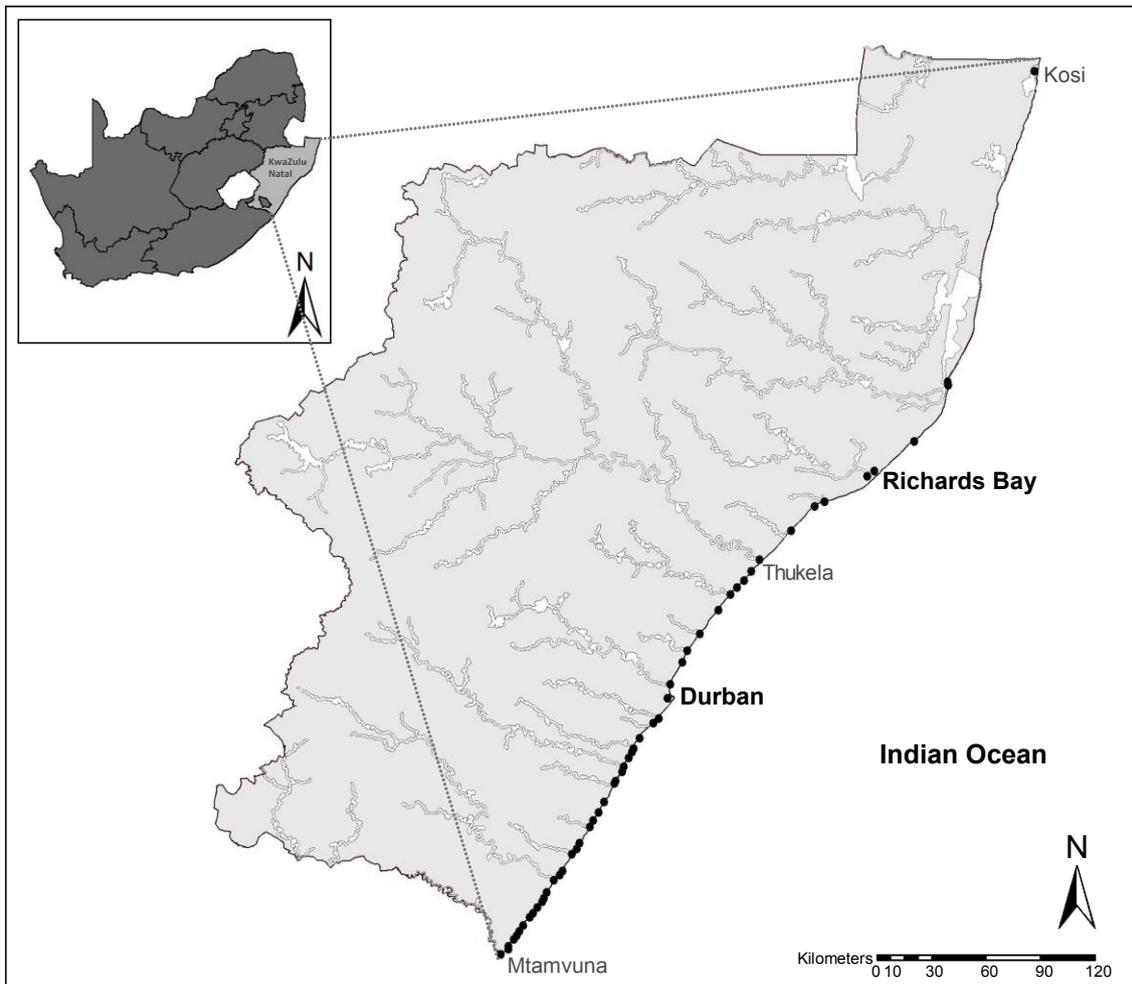


Figure 2.1 Map of the KwaZulu-Natal province showing selected rivers (lines) and estuaries (dots) along the coast.

Flooding of rivers and estuaries frequently occurs during the summer months as a result of peaks in seasonal rainfall in the catchment areas (Cooper et al. 1995, Harrison 2004). Maximum daily summer (air) temperatures are warm (~25 °C), with extremes ranging between 32-37 °C, while during the winter months temperatures are generally mild (~12 °C) (Ngubane et al. 1997a). Water temperatures along the KwaZulu-Natal coastline are largely influenced by the south flowing warm Agulhas Current, with average sea temperatures generally greater than 22 °C (Harrison 2004). Water temperatures in KwaZulu-Natal estuaries are generally within the range of 14-28 °C (Day 1981e, Harrison 2004). The prevailing wind direction is NE-SW, parallel with the coastline, and is stronger on the north coast of KwaZulu-Natal than the south coast (Ngubane et al. 1997a). Due to the bimodal nature of the coastal wind, together with predominant wave approach direction (parallel with the shore) and the headland-bay

morphology of the coastline, the volume of sediment transported by longshore drift in the littoral zone is relatively low (Day 1981d, Ngubane et al. 1997a).

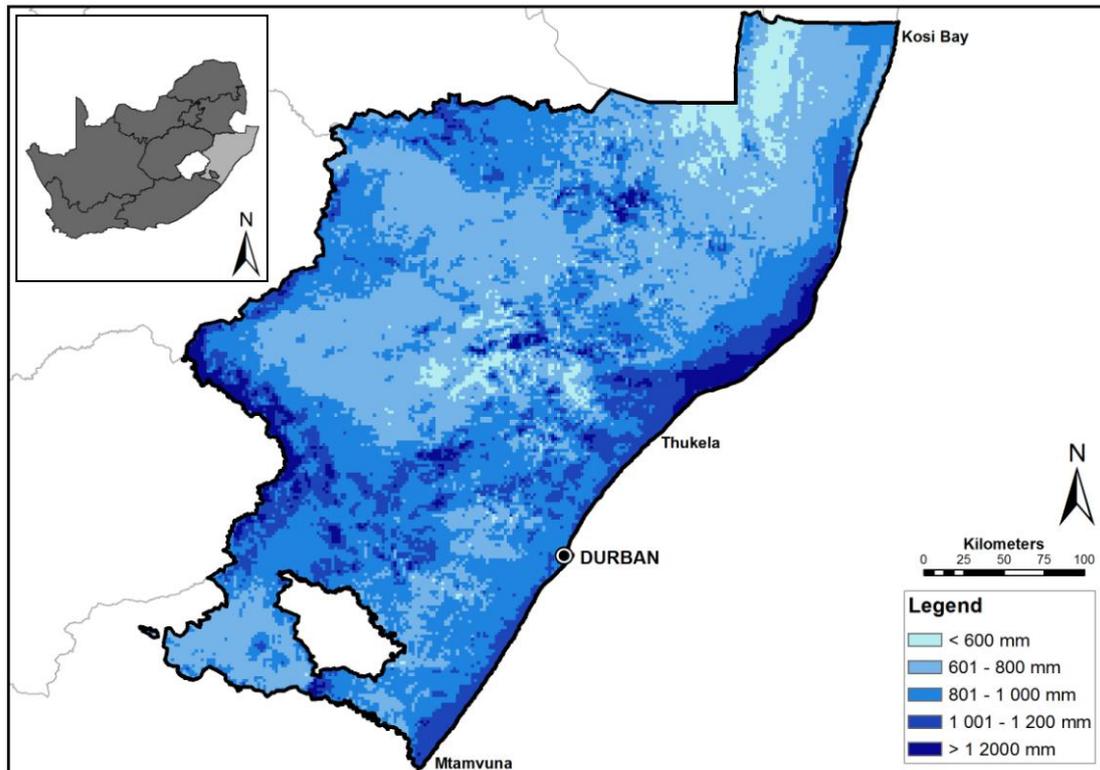


Figure 2.2 Map of KwaZulu-Natal showing distribution of mean annual precipitation throughout the province

2.1.3 Geology

The geological formations of the KwaZulu-Natal coastline is diverse, particularly south of Durban, and ranges in age from Archaean Basement Granite/Gneiss (~1100 million years) to Cenozoic (<100 million years) sedimentary deposits (King 1972). Frequent outcrops of Basement Granite/Gneiss/Quartzite, Dwyka tillite and Ecca shales intercept the coastline south of Durban, with isolated occurrences of the sandy Table Mountain Series (Arenite) in the most southern region (King 1972) (Figure 2.3). These rock types are visible at the mouth regions of the different estuarine systems. The seabed sandstones, mudstones and shelly limestones of the Cainozoic era and recent aeolianites dominate the KwaZulu-Natal coastline from around Durban to the Mozambique border (King 1972, Ngubane et al. 1997a).

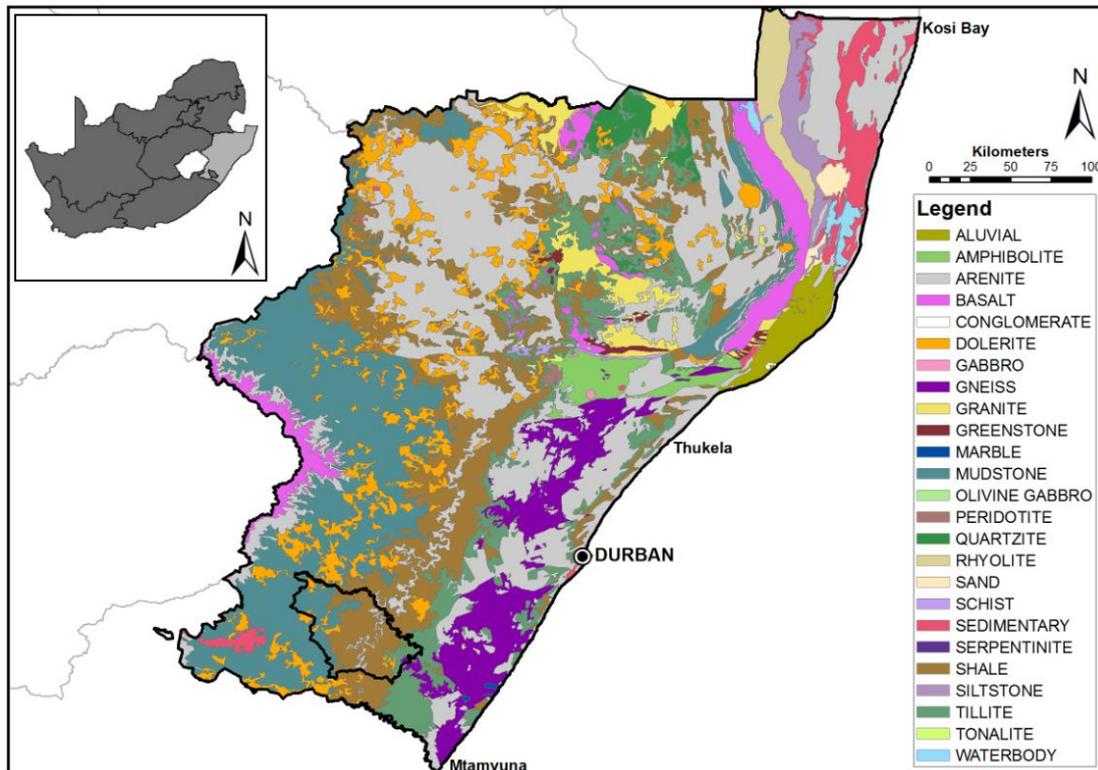


Figure 2.3 Map of KwaZulu-Natal showing the dominant geology throughout the province

2.1.4 Human Settlement

According to Statistics South Africa (StatsSA 2010), the KwaZulu-Natal province hosts the second highest proportion (21.3%) of the South African population after the Gauteng province (22.4%), with the estimated population of KwaZulu-Natal during 2010 in excess of 10.6 million people. The majority of South Africa's economy is based on industrial and commercial imports and exports from the Port of Durban and Port of Richards Bay located on the KwaZulu-Natal coast (Schumann 1988). As a result, they are places of intense residential, commercial and industrial development, for example the large industrial sector extending south of Durban (Ngubane et al. 1997a) (Figure 2.4). Approximately one third of the KwaZulu-Natal population lives along the coast, with an influx of holiday makers during vacation periods (Ngubane et al. 1997a). The appeal of the KwaZulu-Natal coastline as a holiday destination rests on the sandy beaches and estuaries and thus much of the economy of the coastal zone is derived from the tourist and holiday-based industries, which are particularly concentrated along the south coast (Ngubane et al. 1997a) (Figure 2.4). Estuaries are frequently used by holidaymakers for

consumptive and non-consumptive purposes including fishing, marine boat launching, swimming, wind-surfing and canoeing/paddling (Ngubane et al. 1997a).

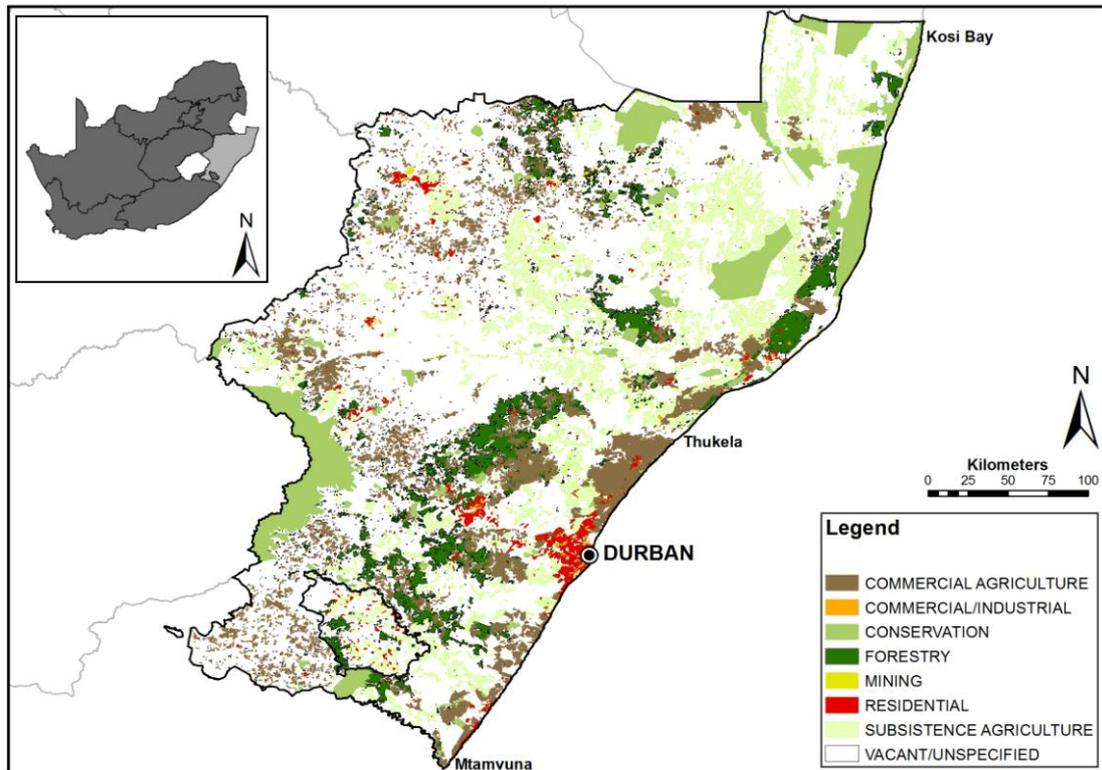


Figure 2.4 Map of KwaZulu-Natal showing the different types of land use throughout the province

2.1.5 Estuaries of KwaZulu-Natal

There are 73 estuaries along the KwaZulu-Natal coastline (Begg 1978) comprising representatives of each of the five estuarine types. The classification of some South African estuaries has changed with time as certain systems no longer function as their initial title described (Whitfield 2000, Turpie 2004). Currently, 62 systems are classified as temporarily open/closed estuaries (TOCEs, 85%), 4 are permanently open estuaries (POEs, 5%), 3 are estuarine bays (4%), 2 are estuarine lakes (3%), and 2 are river mouths (3%) (Whitfield 2000, Turpie 2004). These subtropical estuaries differ from those of the warm-temperate Eastern Cape and the tropical estuaries of Mozambique because of the differences between the climatic regimes, geomorphological features of the provinces and characteristics of the catchment areas (Begg 1984b). Furthermore, individual estuaries differ due to the size and location of the catchment area, the steepness of the coastal topography and the degree of

silting and turbidity (Day 1981e, Cooper et al. 1999). Despite these differences, the fringing vegetation of the majority of estuaries in KwaZulu-Natal, and typical of those sampled during the current study, is characterised by relatively few species, including *Hibiscus tiliaceus*, *Barringtonia racemosa* and *Phragmites* reed beds, with mangrove stands (*Avicennia marina*, *Bruguiera gymnorhiza*) being limited to estuaries that are not closed for prolonged periods (e.g. the Sipingo Estuary, a modified permanently open estuary, where tidal exchange, albeit limited, is enabled by means of pipes through the sandbar) (Begg 1984b, Ngubane et al. 1997a, Whitfield 2000, Forbes and Demetriades 2008).

Flooding is characteristic of many South African estuaries, particularly in the subtropical region, where they feature as frequent and cyclical disturbances that emanate from extreme storm and rainfall events or prolonged periods of rainfall within the catchment areas (Cooper et al. 1999). Flood events in TOCEs are usually short-lived and intense because of the small catchment sizes of these estuaries and can result in severe changes to the physical structure of such systems (Perry 1989, Whitfield 1992, Cooper et al. 1999, Schumann et al. 1999, Turpie 2004). KwaZulu-Natal estuaries are known to carry high silt loads and are frequently turbid because of the steep topography, subtropical climate, deep weathering profiles in soils and heavy summer rainfall (Begg 1978, Day 1981d, Cooper et al. 1994). This is further exacerbated by poor farming practices of agricultural plantations of sugar-cane and banana situated in the catchment areas of many of these estuaries (Begg 1978). These, together with uncontrolled urban development and other associated activities, have resulted in the degradation of most of KwaZulu-Natal estuaries and the loss of natural coastal habitat (Begg 1978, Ngubane et al. 1997b, Morant and Quinn 1999, Turpie 2004). Consequently, the KwaZulu-Natal coastline is internationally recognised as a region heavily impacted by human activities and elevated coastal degradation (Alongi 1998). Unfortunately, a limited number of KwaZulu-Natal estuaries (12 systems) fall within conservation areas (e.g. Lake St Lucia in the iSimangiliso Wetland Park), or are partially protected (e.g. Mbizana Estuary), and are thus subject to increased anthropogenic pressures over time (Turpie et al. 2002).

2.2 Estuary Sampling Procedure

In the current study, 31 TOCEs were sampled once-off in 2009/10 (Chapter 3), of which four systems were selected and repeatedly sampled over a period of one year (July 2008 to July

2009) to establish the effects of flood disturbance on the macrozoobenthos (Chapter 4). The sampling of macrozoobenthos and collection of environmental data followed standardised sampling protocols used in macrozoobenthic studies in various South African estuarine systems for the past ten years (Blaber et al. 1983, Schlacher and Wooldridge 1996d, Mackay and Cyrus 2001, Mackay et al. 2010, Ngqulana et al. 2010). These methods have been successfully implemented in biological investigations for the determination of the freshwater requirements for South African estuaries (DWA 2010). In this chapter, the general materials and methods concerning macrozoobenthic sampling and environmental data collection are described as well as the generic statistical analyses carried out in this study. Details specific to each investigation are presented in the respective chapters.

2.2.1 Macrozoobenthos

The subtidal macrozoobenthos of each estuary was sampled in three generalised regions representing the upper, middle and lower estuarine environments. For the investigation of long-term community change (Chapter 3), sampling was undertaken at the same sites used by Harrison et al. (2004) and the same number of replicate samples per site were collected (three replicates) for comparative purposes. To obtain stronger evidence of the community changes taking place during the post-flood recolonisation of macrozoobenthos (Chapter 4), five replicates (instead of three) were collected from each of the upper, middle and lower regions of the selected TOCEs. Samples were taken at each site using a Zabalocki-type Eckman sediment grab, which samples a uniform area of 0.0236 m² to a minimum depth of 4.5 cm (Blaber et al. 1983). The contents of each grab were emptied into individual buckets, thoroughly stirred and 40% formaldehyde added to induce the benthic invertebrates to release the sediment (Mackay 1996). The supernatant was then decanted through a 500 µm mesh. This pouring and sieving procedure was repeated five times to obtain the majority of the organisms present in the sample (Blaber et al. 1983). The remaining material was washed through a 1000 µm sieve to remove larger and heavier invertebrates, such as molluscs, from the sediment. The retained fauna and debris were preserved in 10% formaldehyde, combined with the vital dye Phloxine B, to facilitate sorting in the laboratory (Warwick 1983, Mackay 1996).

2.2.2 Physico-Chemical Environment

Prior to benthic sampling at each site, various physico-chemical parameters were measured at surface and bottom water levels using a YSI® 6600 Multiparameter Sonde designed specifically for *in situ* monitoring and profiling. These parameters included depth (m), temperature (°C), dissolved oxygen content (mg/L and % saturation), salinity (Practical Salinity Units, PSU), pH, total dissolved solids (mg/L), conductivity (mS/cm) and turbidity (NTU). An additional sediment sample was taken at each site using the Zabalocki-type Eckman grab for determination of the nature of the substratum. From this, two sub-samples were collected for sediment grain size and organic content analyses in the laboratory. Formaldehyde (10% concentration) was added to the sediment organic content sample to prevent organic decomposition and consumption of the organic material by benthic invertebrates (Mackay 1996).

2.3 Laboratory Processing

2.3.1 Macrozoobenthos

Laboratory processing of all preserved macrozoobenthic samples involved sorting, enumeration and identification to the lowest possible taxonomic level using a Zeiss StereoV12 stereo microscope and a Zeiss Axiolmager M1 compound microscope (and associated computer software). Published identification keys and species descriptions of various invertebrate groups were used to assist in species identification (Barnard 1950, Day 1967a, 1967b, Kensley 1972, Day 1974, Griffiths 1976, Kensley 1978, Kilburn and Rippey 1982, Branch et al. 1994, Steyn and Lussi 1998, Day et al. 2001, Epler 2001, Appleton 2002, Day and de Moor 2002a, 2002b, Day et al. 2003, de Moor et al. 2003, Wilson et al. 2003, Courtney and Merritt 2008). Male amphipods of the genus *Grandidierella* (*G. lutosa*, *G. lignorum* and *G. chelata*) were morphologically easily distinguishable, however females were practically insperable. They were therefore grouped together as a new multispecific taxon, *Grandidierella* spp. which was enumerated separately from the males to account for this uncertainty. The mean faunal abundance (density) for each site/time/estuary was expressed as individuals per square metre (ind.m⁻²).

2.3.2 Physico-Chemical Environment

2.3.2.1 Sediment Granulometry

The technique of wet sieving was used to determine the sediment grain size composition instead of dry sieving to overcome the difficulty of isolating and measuring the finer sediment fractions (Buller and McManus 1979). For wet sieving, a known weight of sediment was placed over a series of graded sieves, which decreased geometrically in mesh size from 2 mm (2000 μm , gravel fraction) to 0.063 mm (63 μm , mud fraction) and was gently washed through with water. The sieves used were graded according to the Wentworth Scale such that the sediment particle size retained by each sieve corresponded to a particular grade of sediment (Table 2.1) (Gray 1981, Bale and Kenny 2005). The proportion of the different grain size classes present (calculated as percentage) was then determined after drying and weighing the sediment retained by each sieve. The Wentworth Scale also corresponds with particle size measured in phi units (Φ) (Table 2.1). By plotting the cumulative percentage dry weight of sediment from each sieve against grain size (Φ), various statistical grain size parameters, including mean (M) and median particle size (Md), sorting and skewness can be determined. Thus, particle size measurements in millimetres (mm) were converted to phi units (Φ) prior to statistical analysis, using the following equation: $\text{phi } (\Phi) = -\log_2(\text{grain diameter in mm})$

(Buller and McManus 1979).

Table 2.1 Grain size characteristics.
Taken from Gray (1981).

Grain Size (mm)	Phi (Φ) scale	Type of sediment		
256	-8	GRAVEL	Cobble	
64	-6		Pebble	
16	-4			
4	-2	GRAVEL	Granule	
2	-1		SAND	Very coarse sand
1	0			Coarse sand
0.5	1	Medium sand		
0.25	2	Fine sand		
0.125	3	Very fine sand		
0.0625	4	MUD	Coarse silt	
0.031	5		Silt	
0.0039	8			
0.002	9		Clay	
0.00006	14			

2.3.2.2 Organic Content

The percentage organic content of the sediment at each site was determined using the Hydrogen Peroxide digestion method (Schumacher 2002). That is, concentrated hydrogen peroxide (H_2O_2) was added to a known weight of sediment and heated to increase peroxide digestion of the organic material. Once frothing had ceased and the digestion was complete, the sample was dried, and weighed. The amount of organic material removed by hydrogen peroxide digestion was calculated as the difference between the initial and final weight measurements of the sample (Schumacher 2002). This was expressed as a percentage of the total sample and the resulting content was classified according to the following ranges as suggested by DWA (2010) (Table 2.2).

Table 2.2 Classification of sediment organic content (%)

Class	Organic Content (%)
Very Low	< 0.5%
Low	0.5 - 1%
Moderately Low	1 - 2%
Medium	2 - 4%
High	> 4%

Processing of the sediment samples and calculation of statistical grain size parameters was undertaken by Environmental Mapping and Surveying¹, using the abovementioned laboratory methods, between two and three weeks after field collection.

2.4 Generic Statistical Analyses

The distribution and structure of the macrozoobenthos of the selected TOCEs were analysed using a community-based approach. Statistically, community data are inherently multivariate because of the presence of numerous species (Clarke and Warwick 2001). Benthic organisms are typically concentrated in specific habitats due to a variety of biotic and abiotic forcing factors that give rise to species distributions that are non-random and spatially heterogeneous (Clarke and Warwick 2001). Thus, community data are generally not amenable to parametric statistical tests because the criteria for normality are not satisfied, unless the data are condensed into a univariate measure or single co-efficient, such as diversity indices or average

¹Environmental Mapping and Surveying (EMS), P. O. Box 201155, Durban North, 4016, KwaZulu-Natal

species abundances (Clarke and Warwick 2001). These measures summarise large volumes of information into a single value for use as simplified descriptors of community structure and are also amenable to standard parametric statistical tests (Pearson and Rosenberg 1978, Clarke and Warwick 2001). Therefore, a combination of univariate and multivariate statistical methods was explored using the statistical software package PRIMER (Plymouth Routines in Multivariate Ecological Research, version 6; Clarke and Warwick 2001). This package incorporates analytical techniques most commonly used in marine benthic studies to establish the structure of macrozoobenthic communities and determine the possible linkages to environmental factors (Clarke and Warwick 2001). Data analysis followed the step-wise procedure suggested by Clarke and Warwick (2001) for univariate and multivariate data. A pure description of the community attributes for each site was first given. Various statistical techniques were then used to discriminate between samples and groups of samples. Lastly, the biological data were linked to the environmental data to examine possible causal relationships (Clarke and Warwick 2001). Microsoft Excel software was used for the initial data entry, basic data manipulation and diagrammatic presentation of the data.

2.4.1 Univariate Techniques

Several univariate measures were employed to describe the basic benthic community structure. Abundance data (ind.m^{-2}) were recorded for each species in each replicate sample in the form of a species-by-sample matrix, and the mean (3 replicates: Chapter 3, 5 replicates: Chapter 4) number of taxa and faunal abundance (ind.m^{-2}) (\pm standard deviation, SD) were calculated for every site in all estuaries for all sampling periods (2 sample periods: Chapter 3, 6 sample periods: Chapter 4). In addition, the percentage contribution of each taxon to the mean total abundance was also calculated to describe the numerical dominance of specific taxa within each community.

Another important univariate method used throughout all fields of community studies is the measure of biological diversity (Cao et al. 1996). Diversity indices are critical ecological tools used in environmental management strategies and conservation planning because of their effectiveness as summary statistics and their simple explanatory power (Clarke and Warwick 2001). The Shannon-Wiener Diversity Index (H'), is one of the most commonly used diversity

indices and incorporates both aspects of species richness and equitability into a single index (Pearson and Rosenberg 1978, Clarke and Warwick 2001), using the following equation:

$$H' = -\sum_i P_i (\log P_i)$$

where P_i is the proportion of individuals contributed by the i th species (N_i/N).

The Shannon-Wiener Diversity Index is further supported by two other community indices, namely, Margalef's Index (d) and Pielou's Evenness Index (J'). The Margalef's Index, used as a measure of species richness, incorporates both the total number of individuals and the total number of species, and is a "*measure of the number of species present for a given number of individuals*" (Clarke and Warwick 2001):

$$d = (S-1) / \log N$$

where S is the total number of species and N is the total number of individuals.

Pielou's Evenness Index is a measure of equitability, or evenness of spread of individuals among species. The greater the J' value, the more even the distribution of individuals among species (Pearson and Rosenberg 1978).

$$J' = H' (\text{observed}) / H'_{\max} (H'_{\max} = \log S)$$

"where H'_{\max} is the maximum possible diversity that would be achieved if all species were equally abundant" (Clarke and Warwick 2001).

These two indices were used in conjunction with the Shannon-Wiener Diversity Index because the measurement of diversity of a particular habitat may be biased toward either high organism abundances or large numbers of species (Gray 1981). Thus, measures of richness and evenness reflect community attributes responsible for increased or decreased diversity. The PRIMER sub-programme DIVERSE was employed to calculate the various community indices, which were presented as the mean (\pm SD) per site/time/estuary. The parametric T-test or the non-parametric Mann-Whitney U test (where appropriate), within the statistical software package SIGMAPLOT, were used to test for significant differences between pairs of data sets. Using the same software, Analysis of Variance (ANOVA) was used to test for significant differences in number of taxa, abundance and diversity between estuary, site and time, and the interactions between these factors.

2.4.2 Multivariate Techniques

Species abundance data were first entered into a species-by-sample matrix, and log-transformed ($\log [x+1]$), to dampen the overwhelming effect of the most abundant species over the less dominant and rare species in the calculation of sample similarities (Clarke and Warwick 2001). Triangular similarity matrices were computed where every pair of samples was compared for their similarities in their community attributes according to the Bray-Curtis Similarity co-efficient (Warwick 1983, Clarke and Warwick 2001). Bray-Curtis co-efficient was used because it has a proven record of robustness for benthic community data (Warwick 1983, Heino 2008), it takes into account the high prevalence of zero counts, and it ensures that even the rarest species contribute to sample similarity while maintaining the numerical importance of the commoner species (Clarke and Warwick 2001). This is appropriate to the current study because estuarine invertebrate fauna is generally dominated by common euryhaline marine and true estuarine species, with few or rare stenohaline marine species and stenohaline freshwater species (Day 1981c). The similarity matrices formed the basis to all subsequent multivariate analyses.

Discrete macrozoobenthic communities were identified using cluster (CLUSTER) and non-metric multidimensional scaling (NMDS) techniques within the PRIMER package. Hierarchical agglomerative clustering is a classification technique that is used to elicit the natural groupings of samples on the basis of their similarities, such that samples within a group share more community similarities than samples in different groups (Clarke and Warwick 2001). A hierarchical form, or dendrogram, was created from the similarity matrix, by the clustering of samples into broader groups (agglomerative) at consecutively lower similarities using the average level of similarity between the constituents of each group, known as group-average linking (Warwick 1983). Several dendrograms were produced and factored according to estuary, site and sampling period to identify discrete macrozoobenthic communities under these spatial and temporal criteria. However, cluster analysis is non-directional, and does not show the inter-relatedness of communities or the possible reasons for their separation (Clarke and Warwick 2001). This was achieved using sample ordination.

The ordination technique, non-metric multidimensional scaling (NMDS), was used in conjunction with cluster analysis to visually display the dissimilarity/similarity between groups

of samples in a simplified manner in either two-dimensional or three-dimensional space (Warwick 1983). Ordinations are performed on ranked data from the similarity matrices, and samples are then plotted in two- or three-dimensional space while best preserving their multidimensional relationships (Clarke and Warwick 2001). The adequacy of an NMDS plot at successfully preserving the sample similarities despite the reduction in dimensionality is given as a stress value (Clarke and Warwick 2001). The higher the stress value, the lower the reliability of the NMDS plot. A stress value less than 0.1, indicates a good representation of sample similarities and is the most desired level of representation, while stress values between 0.1 and 0.2 indicate a satisfactory representation that requires careful interpretation (Clarke and Warwick 2001). The physical distance between the mapped samples reflects their community similarities, such that samples that are located closer together are more similar to each other than samples spaced at a greater distance apart (Clarke and Warwick 2001). Generally, the clusters of samples produced in the ordination match the clusters generated by the dendrogram (Warwick 1983), and a gradient in their configuration is often discernable (Clarke and Warwick 2001).

Analysis of Similarity (ANOSIM) was used to test for significant differences between groups of samples defined *a priori* according to site, time period and estuary. It is a non-parametric permutation procedure, based on the ranked data from the similarity matrix, whose resultant Global R-statistic (with a level of significance) is a measure of separation between groups of samples and samples within groups (Clarke and Warwick 2001). The closer R is to 1, the more discrete the groups of samples, or the closer R is to 0, the lower the discrimination between samples across groups (Clarke and Warwick 2001). Furthermore, pair-wise tests were used to identify comparisons with the greatest degree of dissimilarity or similarity between samples. Two-way crossed ANOSIM was used to unmask the interacting effects of site and time on community variability between estuaries with more than one site (Chapter 4).

Taxonomic verification of the differences between groups of samples was carried out using the Similarity Percentages (SIMPER) sub-programme within PRIMER. This identifies the taxa responsible for the discriminations between groups based on their contribution to the average dissimilarity between groups and the average similarity to samples within groups. Taxa which contribute consistently to the similarity/dissimilarity between groups of samples are good discriminating species (dissimilarity) or typical species (similarity) of a discrete group (Clarke

and Warwick 2001). The level consistency of a species is indicated by the ratio between the average contribution of the species to dissimilarity (δ_i) (or similarity, S_i) and the standard deviation of dissimilarity ($SD(\delta_i)$) (or similarity, $SD(S_i)$) across all pairs of samples. Good discriminating taxa, those with comparably high ratios, were selected for species analyses described in detail in Chapter 5.

In order to establish a possible correlation between the faunal distribution patterns and environmental conditions, the environmental data were similarly entered into a sample-by-variable matrix. Draughtsman plots (Clarke and Warwick 2001) were used to search the abiotic data for high degrees of skewness or co-variation. Those variables that were highly skewed were root-transformed and where variables covaried, one was removed. Thereafter, the abiotic data were normalised to account for the different scales and units of measurement of the different environmental variables. Ordination of the environmental data was carried out using a triangular matrix based on the ranked dissimilarities between pairs of samples measured by Euclidean Distance (Clarke and Warwick 2001). The correlation between the biotic data and the abiotic data was then examined using the BIO-ENV sub-programme within PRIMER. The BIO-ENV procedure calculates a correlation co-efficient (non-parametric) between the ranked matrices of both the multivariate community data and the environmental data (Clarke and Warwick 2001). The Spearman Correlation (P_s) was selected over the Weighted Spearman Correlation (P_w), because it accounts for comparisons of tied ranks that might result from different variables with potential implications for community distribution (Clarke and Warwick 2001). The ordinations of the environmental variables were correlated with the biotic ordination at increasing levels of complexity until the 'best-fitting' subset of environmental variables was reached, indicated by the highest P_s value (Clarke and Warwick 2001). Clarke and Warwick (2001) emphasise that BIO-ENV is merely an exploratory tool used to examine plausible determinants of community distribution.

CHAPTER 3

LONG-TERM CHANGE AND INTER-ESTUARINE VARIABILITY

3.1 Rationale

The state of South African estuaries has been sporadically documented over the last ca. 40 years in response to the perceived escalating degradation of the estuarine environment (Begg 1978, Heydorn 1986, Whitfield 1995, 2000, Harrison et al. 2000). Various methods have been used to determine the ecological state of estuaries ranging from expert opinion to empirical methodologies. During a 'snapshot' survey of the state of South African estuaries conducted between 1994 and 1999 (Cooper et al. 1993, Harrison et al. 2000), the macrozoobenthos of most of the KwaZulu-Natal estuaries were uniformly sampled, but not analysed. Invertebrate data therefore were not available for inclusion in the Estuarine Health Index (EHI) formulated by Cooper et al. (1993), or recent assessments on the conservation priority and health status of South African estuaries conducted by Turpie (2002, 2004). Moreover, no attempt has been made to classify the country's estuaries using macrozoobenthic communities to the same extent as birds (Turpie et al. 2002) and fishes (Cooper et al. 1993, Whitfield 1996, Harrison et al. 2000). Resampling of the macrozoobenthos of 31 KwaZulu-Natal temporarily open/closed estuaries in 2009/10 provided the opportunity to describe spatial trends, as well as potential decadal-type shifts, in macrozoobenthic community composition and distribution between estuaries, which forms the basis of the current chapter.

3.2 Introduction

3.2.1 Assessment of the state of the South African estuarine environment

This history of nationwide assessments of the state of South African estuaries originated from the increasing concern about the perceived degradation of estuaries in KwaZulu-Natal in the early 1970s. The initial condition of these estuaries was determined from a synthesis of available information, research undertaken and expert opinion regarding each estuary (Begg 1978, 1984a). This was followed by the first broad overview of the condition of most of the South African systems as part of a nationwide investigation into the freshwater requirements of estuaries (Heydorn 1986). The impetus for this programme was the rising concern about the downstream effects of freshwater abstraction from rivers in catchment areas (Heydorn 1986).

The key objectives of these historical assessments remained unchanged for more recent appraisals conducted in the mid 1990's and 2000. The objectives were 1) to collect information regarding various aspects of the estuarine environment to improve the knowledge base of South African estuaries, 2) to use this information to facilitate the formulation of various regional and/or national management policies for estuaries and 3) to identify information gaps and subsequent research priorities (Begg 1978, Heydorn 1986, Harrison et al. 2000, Whitfield 2000).

An updated collation of the available scientific information on South African estuaries, including an assessment of estuarine condition, was produced by Whitfield (1995, 2000) to complement the advanced requirements of estuarine conservation and management programmes. The results regarding estuaries of KwaZulu-Natal illustrated that estuarine lakes (n=2) and estuarine bays (n=3) were in 'good' and 'fair' condition, respectively (Table 3.1). All river mouths (n=2) and half of the permanently open estuaries (n=4) were in less than 'good' condition. Approximately 25% of the temporarily open/closed estuaries (TOCEs, n=62) were in 'good' condition, 50% were considered as 'fair' and 25% considered as 'poor'. Based on the findings of this assessment, the vast majority of the KwaZulu-Natal estuarine environment in 2000 was thus in less than 'good' condition.

Table 3.1 Percentage of KwaZulu-Natal estuaries of each estuarine type in Excellent, Good, Fair and Poor condition (Whitfield, 2000)

Estuarine Type	Condition (%)			
	Excellent	Good	Fair	Poor
Permanently Open (n=4)	0	50	25	25
Temporary Open/Closed (n=62)	2	23	48	27
Estuarine Lakes (n=2)	0	100	0	0
Estuarine Bays (n=3)	0	0	100	0
River Mouths (n=2)	0	0	50	50

Up until this point, the designated condition of a particular estuary was dependent on the literature database and expert scientific opinion (Whitfield 2000). Comprehensive field sampling of South African estuaries using standardised sampling methods had not been undertaken. Between 1994 and 1999, the condition of 250 of South Africa's 373 estuaries was evaluated by members of the Council for Scientific and Industrial Research (CSIR), as part of a national programme commissioned by the Department of Environmental Affairs and Tourism (DEAT) to assess the state of South Africa's estuarine environment (Cooper et al. 1993,

Harrison et al. 2000). The study was the first of its kind to express the condition of an individual system according to different aspects of the estuarine environment, namely, estuary morphology, fish communities, water quality and aesthetic appeal (Cooper et al. 1993, Harrison et al. 2000). During this survey, benthic invertebrates were sampled only in the KwaZulu-Natal estuaries but were not analysed, and were thus not included in the evaluation of estuarine condition.

Based on the aspects of fish fauna and aesthetics only, the majority of KwaZulu-Natal estuaries were considered to be in 'good' to 'moderate' condition (Table 3.2). However, water quality assessments revealed that a substantial proportion of these estuaries were in 'poor' to 'very poor' condition, which was not apparent from the former two assessments. The authors concluded that in terms of biota, fish communities were not effective indicators of degraded estuarine systems (Harrison et al. 2000).

Table 3.2 Percentage of KwaZulu-Natal estuaries in each category of condition according to Ichthyofauna, Water Quality and Aesthetic assessments (Harrison et al, 2000)

Condition	Assessment (%)		
	Ichthyofauna	Water Quality	Aesthetics
Very Good	0	0	0
Good	37	23	26
Moderate/Fair	21	26	34
Poor	5	16	4
Very Poor	0	11	0
Not sampled	36	23	36
Not analysed	1	0	0

Nonetheless, the results of this particular nationwide study culminated in the formulation of a composite index, the Estuarine Health Index (EHI) (Cooper et al. 1993, 1994), which integrates the values of the physical (morphology), chemical (water quality), biological (fishes) and aesthetic components into a single rating for each estuary (Cooper et al. 1993, Morant and Quinn 1999). The EHI has been strongly criticised for the use of a single biotic component (fish communities), to define the biological integrity of South African estuaries (Morant and Quinn 1999). This highlights the gross under representation of the multitude of flora and fauna associated with estuaries, particularly those that maintain estuarine structure and function in a healthy ecological state. Harrison et al. (2000), did however acknowledge this limitation and alluded to the fact that the inclusion of surveys on other biological components, such as

vegetation, zooplankton, benthic invertebrates and birds, would have contributed to a more satisfactory and holistic assessment of the state of the South African estuarine environment (Harrison et al. 2000).

The overall health of South African estuaries was recently reviewed by Turpie (2004) using a combination of Whitfield's assessments (Whitfield 2000), validated by assessments of estuarine health of several estuaries using Resource Directed Measures methodology (Turpie 2004), and further substantiated by expert opinion. Collectively, 50% of all subtropical TOCEs were considered in 'good' and 'excellent' condition and the remaining 50%, in 'fair' and 'poor' condition (Table 3.3). All of the estuaries along the KwaZulu-Natal coast, except those of northern KwaZulu-Natal, were in 'fair' to 'poor health' because of the intense coastal development along this stretch of coastline (Turpie 2004). Furthermore, 50% of TOCEs were classified as 'endangered', that is, vulnerable to changes in ecosystem functioning that may result in a loss of biodiversity and decreased value (Turpie 2004).

Table 3.3 Percentage of subtropical estuaries of each estuarine type in Excellent, Good, Fair and Poor condition (Turpie, 2004)

Estuarine Type	Condition (%)			
	Excellent	Good	Fair	Poor
Permanently Open (n=15)	47	33	13	7
Temporary Open/Closed (n=98)	32	18	32	18
Estuarine Lakes (n=2)	0	50	50	0
Estuarine Bays (n=3)	0	0	100	0
River Mouths (n=3)	0	33	67	0

An assessment of the conservation priority status of South African estuaries was undertaken by Turpie (2002) as part of the investigation into the quantity and quality of freshwater input needed by individual systems to maintain their ecological function (known as the 'Ecological Reserve') (Turpie et al. 2002). Estuaries were prioritised according to their conservation importance, which in turn was based on aspects of estuary size, rarity of estuary type, habitat diversity, and biodiversity (Turpie et al. 2002). The latter incorporated four biotic groups including plants, invertebrates, fish and birds. The fish data collected by Harrison et al. (2000) were utilised in this assessment because of the comparability of the data between estuaries (Turpie et al. 2002). However, invertebrate data were assembled from several sources and reduced to distributional presence-absence. Furthermore, the overall importance of

invertebrates to biodiversity was down-weighted in comparison with the other components due to the coarseness of the available data and overestimation of species richness in many estuaries (Turpie et al. 2002). Thus, invertebrates might have had a greater contribution to the calculation of biodiversity importance had consistently collected data been available for most estuaries.

3.2.2 Factors affecting the distribution of macrozoobenthos in KwaZulu-Natal estuaries

Although many estuarine macrozoobenthic species exhibit broad geographical distributions, there are general differences in species composition between the three biogeographic zones along the coastline (Day 1981c, De Villiers et al. 1999). It may thus be possible to detect gradual changes in community structure with the southward progression of estuaries in KwaZulu-Natal from the tropical climate of Mozambique to the warm-temperate biogeographic zone of the Eastern Cape. Conversely, such a trend may not exist because the boundaries of the biogeographic zones are not distinct and because the fauna of South Africa estuaries is largely dependent on the physical characteristics of a system (e.g. depth, mouth persistence, salinity regime, nature of the sediment and turbidity) as opposed to the geographic position (Day 1964, De Villiers et al. 1999).

South African estuaries differ in their physico-chemical characteristics according to their location within one of the biogeographical zones (Harrison 2004). Subtropical TOCEs (and permanently open estuaries) are characterised by low salinities and high turbidities due to increased rainfall and terrestrial runoff, and large silt loads attributed to poor land-use practices in the catchments (Day 1981b, 1981e, De Villiers et al. 1999, Harrison 2004, Perissinotto et al. 2010). These factors contribute to the poor species diversity of subtropical estuaries in comparison with warm-temperate estuaries further south and the tropical estuaries to the north in Mozambique (De Villiers et al. 1999). While the number of species recorded varies from estuary to estuary, species diversity is generally low in estuaries that exhibit prolonged periods of mouth closure in comparison to permanently, or predominantly open, estuaries (De Villiers et al. 1999, Perissinotto et al. 2010). Large open estuaries provide a greater diversity of habitats and extensive mudflats, therefore generally support higher species diversity and larger populations of organisms (De Villiers et al. 1999, Turpie et al. 2002). The closed condition, however, is characteristic of most of KwaZulu-Natal's small TOCEs (Begg

1978, 1984a) and the low species diversity is presumably due to restricted recruitment of individuals from the marine environment (Day 1964). Furthermore, impacts of urban development and land-use patterns within the catchment areas of rivers have an important influence on the state of estuaries and are likely to influence the residing macrozoobenthic communities (Morant and Quinn 1999, Turpie 2004, Bilkovic et al. 2006). Estuaries within the same catchment area are assumed to have similar characteristics, with respect to health status and impacts (Turpie 2004), in comparison to other catchment areas. Macrozoobenthic communities in TOCEs within the same catchment area can therefore be expected to share similar species assemblages. Despite the large assortment of factors likely to influence the spatial distribution of macrozoobenthos among KwaZulu-Natal TOCEs, discernable latitudinal trends in species composition would have important implications for predicting the effects of increasing ocean temperatures and climate change on macrozoobenthos and the potential shifts in species distributions (Clark 1999).

The unprecedented increase in coastal development and human interference over the last decade has led to changes in the coastal environment, including estuaries (Morant and Quinn 1999, Turpie 2004). Estuaries of the KwaZulu-Natal coast are particularly prone to loss of biodiversity and ecosystem function because they are among the worst degraded estuaries in the country (Turpie 2004). It can be expected that estuarine macrozoobenthic communities within KwaZulu-Natal TOCEs have undergone a dramatic change in both structure and function during this time because of these influences. Such decadal-type comparisons are critical for environmental monitoring programmes in South Africa to enable the long-term prediction of possible changes to the estuarine environment.

3.2.3 Aim and Hypotheses

The purpose of this chapter was to compare the macrozoobenthos previously collected from several KwaZulu-Natal TOCEs (Cooper et al. 1993, Harrison et al. 2000) with macrozoobenthos recollected from the same estuaries 11 years later, and in so doing determine the spatial and temporal changes in community structure. This chapter is divided into two phases. The first phase aimed to determine the spatial distribution of macrozoobenthic communities among TOCEs in KwaZulu-Natal. The null hypotheses (H_0) that were tested are outlined as follows:

The combined macrozoobenthos of all estuaries in each time period (1998/9 and 2009/10) were first individually described to establish basic community characteristics. Estuaries of each time period were tested for similarities/dissimilarities in community structure to ascertain the level of spatial homogeneity, or heterogeneity, of estuarine macrozoobenthos across KwaZulu-Natal TOCEs (H_{01}).

H_{01}) In 1998/9 and 2009/10, respectively, there was no difference in macrozoobenthos between TOCEs in KwaZulu-Natal.

Intuitively, significant differences in macrozoobenthic communities would exist between some or all of the investigated estuaries, due to the diversity of environmental and anthropogenic factors affecting each individual system at variable rates and intensities.

The differences between estuarine macrozoobenthic communities (within each time period) were then tested in relation to the biogeographic location of each estuary to investigate the possible gradation of macrozoobenthos with more tropical affinities in the northern systems to more temperate affinities in southern systems (H_{02}).

H_{02}) In 1998/9 and 2009/10, there was no linear north-to-south gradation in macrozoobenthic communities of TOCEs along the KwaZulu-Natal coast.

The second phase of this study explored the possibility of discernable decadal-type shifts between these communities sampled once-off in 1998/9 and again in 2009/10. The macrozoobenthos of these two time periods were tested for significant differences in community structure (H_{03}). The correlation between community changes and environmental conditions was also investigated. It was expected that the macrozoobenthos of the estuaries sampled in 1998/9 would have changed over the 11-year period, such that significantly different macrozoobenthic communities would exist in the same estuaries resampled in 2009/10.

H_{03}) There was no difference between the macrozoobenthic communities of KwaZulu-Natal TOCEs sampled in 1998/9 and in 2009/10.

This study did not aim to determine the past and current health of KwaZulu-Natal TOCEs based on their macrozoobenthic communities but rather to increase our knowledge of these estuarine fauna and the ecological functioning of these systems.

3.3 Methods and Materials

A detailed description of the general procedures relating to the collection of macrozoobenthos, sediment samples, the measurement of *in situ* habitat characteristics, laboratory processing and background to statistical analyses, is provided in Chapter 2 (General Materials and Methods). Deviations from these procedures, used in this Chapter 3, are described below.

3.3.1 Study Area

Macrozoobenthic specimens were available for 35 TOCEs along the KwaZulu-Natal coast (Figure 3.1) that were sampled on a single occasion (once-off basis) between October 1998 and March 1999 by the CSIR (Harrison et al. 2000). However, sampling was repeated in only 31 of these estuaries between November 2009 and March 2010 due to logistical constraints and restricted access. The geographical location of these systems ranged from the Zinkwasi Estuary (29°16'45" S, 31°26'37" E) furthest north, approximately 100 km north east of Durban, to the Mtamvuna Estuary (31° 04'56" S, 30° 11'39" E), at the southern border of KwaZulu-Natal and the Eastern Cape province, approximately 200 km south west of Durban (Figure 3.1). Table 3.4 displays the characteristics of each estuary, including the abbreviated code used in analysis, the number of sites sampled, estuary category as assigned by Harrison et al. (2000), estuary morphometry (Begg 1978, 1984a), size of the catchment area and designated tertiary drainage region (Zietsman 2004), and EHI value as determined by Cooper et al. (1993).

The majority of the estuaries that were sampled (18 systems, 58%) persist as normally closed systems with a surface area between 0.02 and 1.5 km² (category B), six and five estuaries belong to the categories A and E, respectively, and two estuaries belong to the category F. Of the latter group, the Mtamvuna has the largest surface area and the largest catchment area. The Mkumbane Estuary is the smallest estuary, with a surface area of 0.003 km² (category A). According to the EHI, the Sipingo (EHI= 8.5) and Mbokodweni (EHI= 5.4) estuaries were described as the most unhealthy systems in the province, while the Zinkwasi (EHI= 23.2) and Mtamvuna (EHI= 25.5) estuaries were the healthiest systems (Cooper et al. 1993, Harrison et al. 2000). Most of the estuaries (11 systems, 35%), had an EHI value between 17.1 and 19.1. Seven of the 31 estuaries that were sampled lie within the eThekweni Municipal Area, namely the Mdloti, Mhlanga, Sipingo, Mbokodweni, Manzimtoti, Little Manzimtoti, and Lovu estuaries, and are heavily impacted by urban development and associated activities (Forbes and Demetriades 2008).

Table 3.4 List of the 31 KwaZulu-Natal TOCEs that were sampled and the characteristics of each system

Estuary No.*	Estuary Name	Code	No. of sites	Estuary Category**	Area (km ²)	Length (km)	Catchment Area (km ²)	Latitude Blocks (15' interval)	3° 4° Drainage Region		EHI
<i>North</i>								29° 16' S			
1	Zinkwasi	ZIN	4	B	0.252	7.5	73	LAT 1	U50	U500	23.2
2	Mdlotane	MDO	3	B	0.094	2.3	43	LAT 1	U50	U500	21.3
3	Mdloti	MDL	3	B	0.136	1.5	527	LAT 2	U30	U30B	22.0
4	Mhlanga	MG	3	B	0.114	2.2	118	LAT 2	U30	U30B	18.8
5	Sipingo	ISP	3	B	0.068	1.3	51	LAT 3	U60	U60E	8.5
6	Mbokodweni	MBO	3	E	0.072	0.7	283	LAT 3	U60	U60E	5.4
7	Manzimtoti	AT	3	B	0.067	2.0	39	LAT 4	U70	U70F	10.3
8	Little Manzimtoti	LAM	2	B	0.015	0.8	18	LAT 4	U70	U70F	10.3
9	Lovu	LOV	3	F	0.105	1.1	893	LAT 4	U70	U70D	21.2
10	Mpambanyoni	MY	3	B	0.023	0.3	562	LAT 5	U80	U80K	16.1
11	Mzimayi	MZ	1	A	0.009	0.3	31	LAT 5	U80	U80H	17.6
12	Mkumbane	MK	2	A	0.003	0.3	28	LAT 5	U80	U80H	15.5
13	Sezela	SZ	3	B	0.090	1.8	20	LAT 5	U80	U80H	18.4
14	Fafa	F	3	B	0.324	3.0	231	LAT 5	U80	U80G	17.7
15	Mhlabatshane	MAN	3	E	0.031	1.0	47	LAT 6	U80	U80D	19.4
16	Intshambili	INT	3	B	0.017	0.6	33	LAT 6	U80	U80A	19.9
17	Damba	D	2	A	0.017	0.5	25	LAT 6	U80	U80A	17.4
18	Mhlangankulu	MLK	2	B	0.039	0.9	11	LAT 6	U80	U80A	20.1
19	Zotsha	Z	3	E	0.073	2.3	57	LAT 7	T40	T40G	17.4
20	Mhlangeni	MH	3	B	0.040	1.0	38	LAT 7	T40	T40G	17.8
21	Kongweni	K	3	A	0.014	0.7	20	LAT 7	T40	T40G	15.1
22	Uvuzana	UV	1	A	0.006	0.2	8	LAT 7	T40	T40G	19.2
23	Bilanhlo	BI	3	B	0.026	0.5	21	LAT 7	T40	T40G	18.1
24	Mutshini	MSH	1	A	0.009	0.3	7	LAT 7	T40	T40G	19.7
25	Mbizana	MB	1	B	0.124	1.5	145	LAT 7	T40	T40F	21.7
26	Kaba	KAB	2	B	0.024	0.5	11	LAT 7	T40	T40F	18.0
27	Umhlangankulu	MLKB	3	B	0.058	0.9	9	LAT 7	T40	T40F	17.8
28	Kandandlovu	KA	2	B	0.018	0.6	9	LAT 7	T40	T40F	19.5
29	Tongazi	TG	1	E	0.008	0.4	17	LAT 7	T40	T40F	18.6
30	Sandlundu	SA	2	E	0.040	0.6	16	LAT 8	T40	T40F	19.3
31	Mtamvuna	MVA	4	F	0.527	5.3	1553	LAT 8	T40	T40E	25.5
<i>South</i>								31° 06' S			

* Estuary No. indicates the relative north to south geographical positioning of each estuary in KwaZulu-Natal. Latitudinal position increases with increasing estuary number.

**Estuary Category A = Normally closed, Surface area < 0.02 km²; B= Normally closed, Surface area 0.02-1.5 km²; E = Normally open, MAR < 15 x 10⁶m³; F= Normally open, MAR > 15 x 10⁶m³

3.3.2 Sampling Approach

The collection of biota and environmental data in 2009/10 was undertaken during the KwaZulu-Natal wet season (October-March), at the same sites in each estuary (Appendix 1.1) using the same sampling techniques employed by Harrison et al. (2000) to minimise variation introduced by differential sampling methods and to enable direct comparisons with the historical data. Three random replicate samples were collected at each site. The number of sites varied according to the axial length of each system with a maximum of four sites in large systems (e.g. Mtamvuna and Zinkwasi estuaries) and a minimum of one site in small systems (e.g. Uvuzana and Mzimayi estuaries) located in the lower reaches near the estuary mouth (Table 3.4) (Harrison et al. 2000). Replicates were then pooled for each site in accordance with Harrison's sampling method. Physico-chemical parameters at each site were measured prior to sampling, and two sediment samples were collected for sediment granulometry analyses and determination of sediment organic content, respectively.

3.3.3 Data Analyses

In certain cases where sites that were sampled in 1998/9 could not be reached in 2009/10, the 1998/9 dataset was reduced to those sites that were successfully resampled in 2009/10 in favour of a comparable statistical design. Biotic and abiotic data were collapsed into mean values (\pm SD) per estuary using site data as estuary replicates and entered into a species-by-estuary matrix in PRIMER. The similarities between estuaries in both the 1998/9 and 2009/10 sample periods were determined using CLUSTER analysis, based on the Bray-Curtis co-efficient. Estuaries were categorised according to various abiotic (Table 3.5) and biotic (Table 3.6) attributes to investigate the principal factor(s) governing the distribution of macrozoobenthos among KwaZulu-Natal TOCEs. Groups of similar estuaries were statistically verified by means of Analysis of Similarity (ANOSIM) using these attributes. The taxa responsible for the differences between the groups of estuaries were identified using Similarity Percentages (SIMPER). To ascertain which environmental variable(s) were likely responsible for the distribution of the macrozoobenthos between estuaries, the ordinations of the biota and abiotic samples were compared by means of the Spearman's Rank Correlation (P_s).

Table 3.5 Abiotic attributes used to categorise TOCEs sampled in 1998/9 and 2009/10

ESTUARY ID.	TIME PERIOD	GEOMORPHOLOGICAL CATEGORY		ESTUARY AREA (km ²)		ESTUARY LENGTH (km)		CATCHMENT AREA (km ²)		MOUTH STATE	LATITUDINAL BLOCK	DRAINAGE REGION		
				VS	S1	S2	M	L	VS			S1	S2	S3
TAG NO	1998/9	Categories as defined by Harrison et al. (2000)		VS	< 1x10 ⁻²	S1	< 0.5	VS	< 10	Open (O) Closed (C)	8 blocks at 15" S intervals Start: - 29° 16" S End : - 31° 06" S	U50; U20; U60; U70; U80; T40 U500; U20M; U60E; U70F; U70D; U80K; U80H; U80G; U80D; U80A; T40G; T40F; T40E		
	2009/10			S1	1x10 ⁻² - 5x10 ⁻²	S2	0.5 - 1.0	S1	10 - 30					
	A			Closed, Small Surface Area	S2	5x10 ⁻² - 1x10 ⁻¹	M	1.0 - 5	S2					30 - 50
	B			Closed, Moderate Surface Area	M	1x10 ⁻¹ - 2x10 ⁻¹	L	> 5	S3					50 - 100
	E			Open, Barred, low MAR	L	> 2x10 ⁻¹			M					100 - 300
F	Open, Barred, High MAR					L	300 - 1000							
								VL	>1000					

Key:

TAG= Label used as a code for each estuary

NO= Numerical order of estuaries from north to south

VS = Very Small

S2 = Small Category 2

M = Medium

VL = Very Large

S1 = Small Category 1

S3 = Small Category 3

L = Large

Table 3.6 Biotic attributes based on the number of taxa in each broad taxonomic group used to categorise TOCEs sampled in 1998/9 and 2009/10

Category	CRUSTACEA	POLYCHAETA	MOLLUSCA	INSECTA	OTHER	OLIGOCHAETA	PESTS
	Number of Taxa					Category	
A	0	0	0	0	0	Absent (A)	Absent (A)
1	1-3	1-2	1-2	1-2	1-2	Present (P)	Present (P)
2	4-6	3-4	3-4	3-4	3-4		
3	7-9	5-7	>4	5-6	>4		
4	10-12	>7		>6			
5	13-15						
6	>15						

Basic descriptive statistics for the macrozoobenthic community (mean faunal abundance, ind.m⁻², mean number of taxa) of each estuary and average environmental conditions were calculated. However, biotic and abiotic variation could not be determined for estuaries with a single sample site due to insufficient replication (i.e. the Mzimayi, Uvuzana, Mvutshini, Mbizana, and Tongazi estuaries). As an exception to the above treatment of environmental data, salinity was calculated as the difference between measurements taken at the lower and upper reaches of each system, as an expression of the *range* of salinity extremes experienced within each estuary. This was done to account for the possibility that macrozoobenthic communities subject to broader fluctuations in salinity may differ from those communities subject to narrower salinity fluctuations.

Diversity Indices, including Margalef's Species Richness (d), Pielou's Evenness Index (J) and Shannon-Wiener Diversity (H) were calculated based on the species-by-estuary matrix using the total mean faunal abundance and mean number of taxa for each estuary. These community indices together with the Estuarine Health Index (EHI) (Cooper et al. 1993), were also used as a means to categorise each estuary (Table 3.7). Tests for differences in univariate community metrics, namely faunal abundance, number of taxa, species richness, evenness and diversity, between sample periods were performed using T-tests for parametric data. Where criteria of normality and equal variance failed, the Mann-Whitney U test based on ranks of non-parametric data was employed.

Table 3.7 Various indices used to categorise TOCEs sampled in 1998/9 and 2009/10

Margalef Species Richness		Pielou's Evenness		Shannon Diversity		Estuarine Health Index	
Category	(d)	Category	(J')	Category	(H')	Category	(EHI)
VL	<0.5	VL	< 0.2	VL	<0.5	VP	<10
ML	0.5 - 1.0	L	0.2 - 0.4	L	0.5 - 1.0	P	10-17
L	1.0 - 1.5	M	0.4 - 0.6	M	1.0 - 1.5	F	17-20
M	1.5 - 2.0	H	0.6 - 0.8	H	1.5 - 2.0	G	20-25
H	2.0 - 2.5	VH	> 0.8	VH	>2.0	VG	>25
VH	> 2.5						

Key:
 VL = Very Low M = Moderate VP = Very Poor G = Good
 ML = Moderately Low H = High P = Poor VG = Very Good
 L = Low VH = Very Hgh F = Fair

3.4 Results

3.4.1 Macrozoobenthic Community Structure (1998/9)

3.4.1.1 Faunal abundance and number of taxa

The mean total macrozoobenthic abundance sampled per estuary per site in 1998/1999 was 14,246 ind.m⁻² ($\pm 13,875.97SD$) comprising 86 taxa from seven Phyla. An important feature of the macrozoobenthos was the high degree of variability within and between estuaries in terms of mean faunal abundance and the number of taxa (Figure 3.2A). The largest estuaries, the Zinkwasi (ZIN 9,257 ind.m⁻² $\pm 11,539.59SD$) and the Mtamvuna (24,710 ind.m⁻² $\pm 13,475.79SD$) exhibited low faunal abundance in comparison with several substantially smaller systems such as the Mkumbane (MK 60,431 ind.m⁻² $\pm 9.89SD$) and the Intshambili (INT 35,429 ind.m⁻² $\pm 16,185.09SD$) estuaries.

The Mkumbane Estuary supported the highest macrozoobenthic abundance of all the estuaries sampled in 1998/9. The minimum abundance was recorded from the Mdlotane Estuary (MDO 37 ind.m⁻² $\pm 35.23SD$). Approximately 50% of all the estuaries sampled supported invertebrate densities less than 10,000 ind.m⁻². There was a slight trend of increasing abundance from the systems sampled north to south. Similarly, there was a general trend of increasing mean number of taxa with increasing latitude (Figure 3.2B). The lowest number of taxa was recorded in the Mdlotane Estuary (MDL 2 taxa $\pm 1.53SD$) while the highest number of taxa was recorded in the Umhlangankulu Estuary (19 taxa $\pm 1.73SD$). Comparably high numbers of taxa were also collected from the Lovu (LOV 18 taxa $\pm 2.31SD$), Mkumbane (MK 17 taxa $\pm 1.41SD$) and Sandlundlu (SA 18 taxa $\pm 9.90SD$) estuaries. Approximately 60% of all the estuaries were host to macrozoobenthic communities comprising more than ten taxa.

3.4.1.2 Taxonomic composition

In 1998/9, the macrozoobenthos of the studied TOCEs was dominated by two faunal groups, Crustacea (Phylum Arthropoda) and Polychaeta (Phylum Annelida) (Table 3.8). In most estuaries, there was a high numerical dominance of one of these groups and few systems contained subequal proportions of Crustacea and Polychaeta. The numerical importance of the Crustacea component to the macrozoobenthos generally increased towards the south.

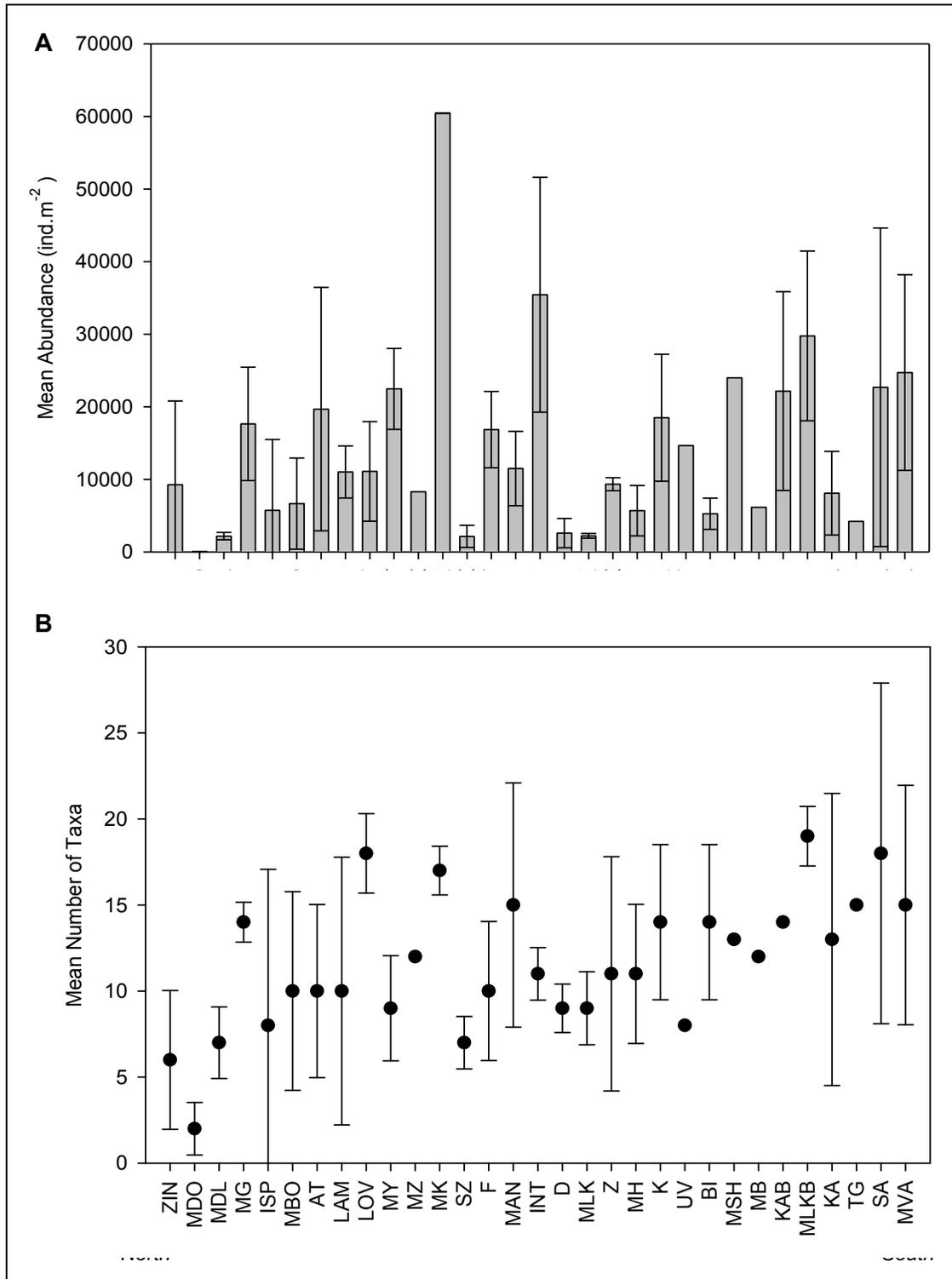


Figure 3.2 Mean abundance (\pm SD) (A) and mean number of taxa (\pm SD) (B) of macrozoobenthos collected from KwaZulu-Natal TOCEs in 1998/9

Crustacea contributed most to the macrozoobenthos in the Mpambanyoni Estuary (MY), comprising 92% of the community, followed by the Mbizana (MB 89%), the Intshambili (INT 85%) and the Fafa (F 80%) estuaries. Polychaeta were dominant in most estuaries, however their numerical importance was less in the southern estuaries in comparison with the northern estuaries. Their numbers contributed most to the macrozoobenthic community in the Manzimtoti Estuary (AT 87%), with similarly high occurrences in the Zinkwasi (ZIN 83%), Uvuzana (UV 82%) and Sipingo (ISP 81%) systems. In estuaries with low occurrences of both Crustacea and Polychaeta, either Oligochaeta (Mdlotane MDO 50%) or Insecta (Damba D 84%, Mdloti MDL 81%) dominated the macrozoobenthic communities. Mollusca and other fauna made minor contributions to the macrozoobenthos, of less than 5% and 20%, respectively.

Table 3.8 Proportions (%) of broad taxonomic invertebrate groups and the total mean abundance (ind.m⁻²) of organisms sampled in each estuary in 1998/9. Values in **bold** represent maximum values.

Estuary No.	Estuary Code	Crustacea	Polychaeta	Oligochaeta	Mollusca	Insecta	Other*	Abundance (ind.m ⁻²)
<i>North</i>								
12	ZIN	1	83	15			1	9,257
14	MDO		13	50		24	13	37
19	MDL	1	17	1		81		2,174
20	MG	35	62	3				17,640
23	ISP	8	81	10		1		5,735
24	MBO	46	54					6,645
25	AT	4	87	3		6		19,679
26	LAM	25	71	1	1	2		11,004
27	LOV	43	57					11,092
34	MY	92	7		1			22,465
35	MZ	30	63	6		1		8,288
37	MK	54	41	3		1	1	60,431
38	SZ	8	54	1		36	1	2,137
40	F	80	16			4		16,856
47	MAN	30	62	1	1	1	5	11,494
49	INT	85	13	2				35,429
51	D	1	7	8		84		2,590
52	MLK	26	19	20		35		2,219
57	Z	33	67					9,328
58	MH	56	40		3	1		5,684
60	K	57	16	2		25		18,484
61	UV	6	82			12		14,644
62	BI	47	25	5	3	3	17	5,259
63	MSH	32	63	1		4		23,982
64	MB	89	9		2			6,160
65	KAB	80	15	3		2		22,155
66	MLKB	74	17	6		3		29,759
68	KA	25	67	6	1		1	8,092
69	TG	53	47					4,214
71	SA	67	31		1		1	22,680
73	MVA	75	24	1				24,710
<i>South</i>								

* Other includes organisms from low contributing taxa: Hirudinea, Arachnida, Collembola, Cnidaria, Nematoda, Nemertea, Platyhelminthes, Sipunculida and Unidentified organisms.

Figure 3.3 illustrates the mean abundances of the broad taxonomic groups sampled within each estuary. Crustacea abundance was at a maximum in the Mkumbane Estuary (MK 32,375 ind.m⁻² ±12,265.47SD) while completely absent from the Mdlotane Estuary (MDO). The lowest recorded Crustacea density was 14 ind.m⁻² (±19.8SD) in the Damba Estuary (D). Similarly, Polychaeta were most abundant in the Mkumbane Estuary (MK 24,983 ind.m⁻² ±14,287.97SD) and scarce in the Mdlotane Estuary (MDO 4 ind.m⁻² ±8.08SD). Oligochaeta densities were particularly high in the Mkumbane (MK 2,051 ind.m⁻² ±1,395.83SD) and Umhlangankulu (MLKB 1,880 ind.m⁻² ±1,245.95SD) systems. Mollusca were absent from 42% of the investigated estuaries. Where Mollusca were present, the maximum recorded density was 196 ind.m⁻² (±277.19SD) in the Sandlundlu Estuary. The Kongweni Estuary hosted the greatest density of Insecta (4,648 ind.m⁻² ±4,494.22SD). Insecta were absent from the macrozoobenthos in four systems, the Zinkwasi (ZIN), Mbokodweni (MBO), Lovu (LOV) and Mbizana (MB) estuaries. Other low contributing taxa (including Hirudinea, Arachnida, Collembola, Cnidaria, Nematoda, Nemertea, Platyhelminthes, Sipunculida and several unidentified organisms) in combination, reached a maximum abundance in the Bilanhlolo Estuary (BI 910 ind.m⁻² ±1,252.12SD). These minor fauna were collectively absent from six systems, the Mpambanyoni (MY) Mzimayi (MZ), Damba (D), Mhlangamkulu (MLK), Mvutshini (MSH), and Tongazi (T) estuaries. A full list of taxa is given in Appendix 1.2.

3.4.1.3 Classification of 1998/9 estuaries

The estuaries sampled in 1998/9 were separated into two clusters and two individual systems ('outliers') based on 45% similarity between their macrozoobenthic communities (Figure 3.4). Cluster I included the following five estuaries: Mhlangamkulu (MLK), Damba (D), Mdloti (MDL), Uvuzana (UV) and Sezela (SZ). Cluster II comprised the majority of the estuaries, except the Mdlotane (MDL) and the Zinkwasi (ZIN), which separated out from the remaining estuaries at approximately 16% and 34% similarity, respectively.

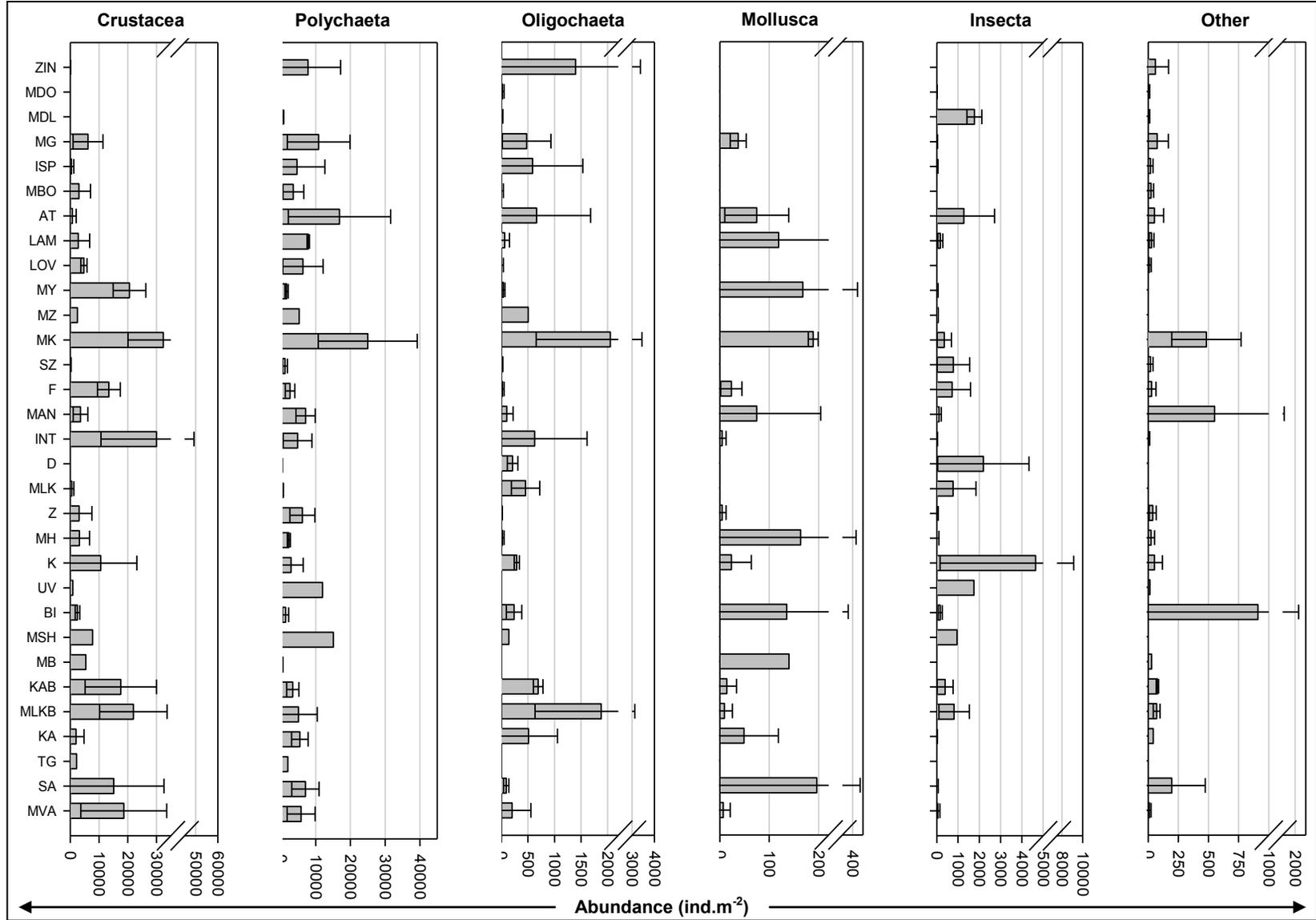


Figure 3.3 Mean abundances (\pm SD) of broad taxonomic invertebrate groups sampled per estuary sampled in 1998/9

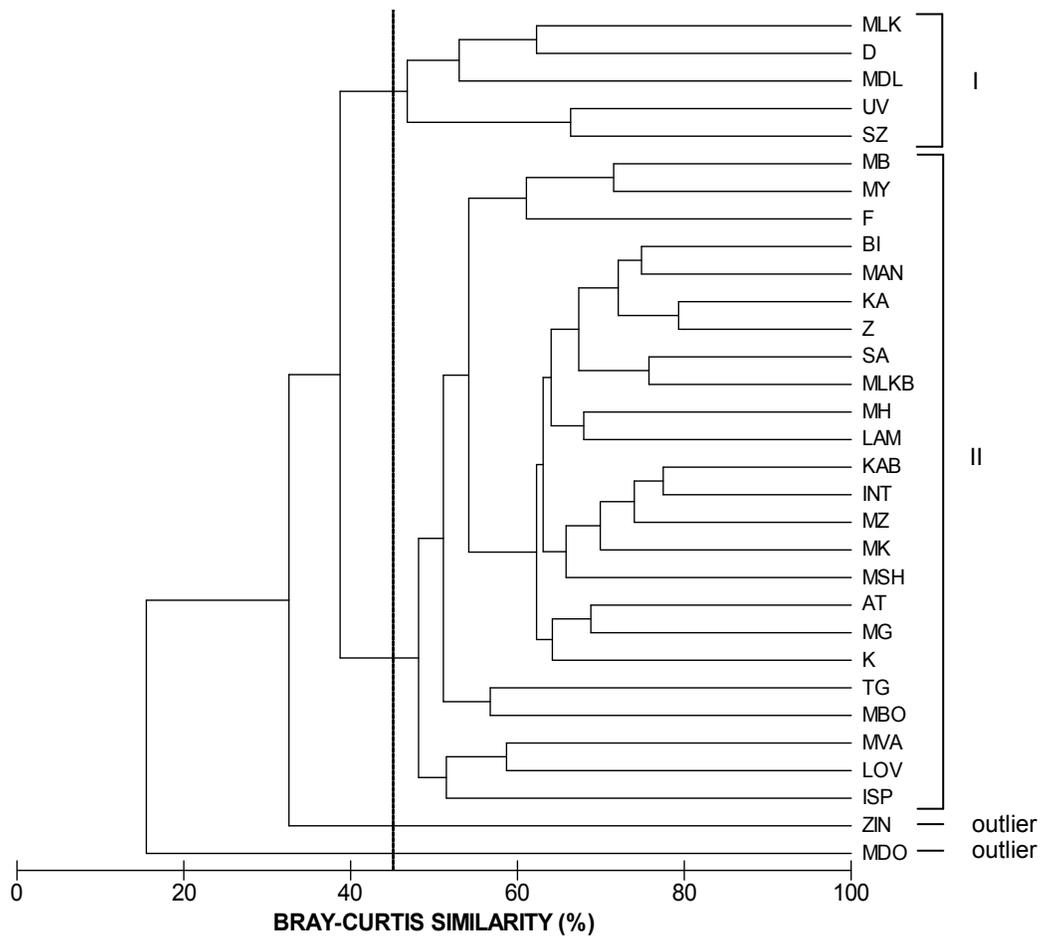


Figure 3.4 Hierarchical cluster diagram illustrating groups of estuaries in 1998/9 that share 45% similarity in macrozoobenthic community characteristics

Table 3.9 displays the essential taxonomic differences in the macrozoobenthic communities between the Cluster I and Cluster II estuaries based on the percentage contribution of each taxon to the average dissimilarity (61.3%) between the clusters (SIMPER analysis). The primary difference was the presence of a highly abundant Crustacean component in Cluster II estuaries, most importantly Amphipoda species of the Genera *Grandidierella* and *Corophium*. The Crustacea component in Cluster I estuaries was poorer, while Insecta larvae and pupae were more prominent. Polychaeta species, Oligochaeta spp., and Nematoda spp. were more abundant in Cluster II estuaries, which also possessed a greater number of rare species than Cluster I estuaries.

Table 3.9 Taxa responsible for the discrimination between Cluster I and II estuaries classified by hierarchical cluster analysis for 1998/9. Only species contributing greater than 2% to the total dissimilarity between groups are presented. Am= Amphipoda, Cu= Cumacea, Po= Polychaeta, In= Insecta, T= Tanaidacea.

Taxa	Cluster I	Cluster II	Ave. Dissim.	Contribution (%)	Cumulative (%)
	Ave. Abundance	Ave. Abundance			
<i>Grandidierella</i> spp. (Am)	1.52	7.66	4.73	7.72	7.72
<i>Grandidierella lutosa</i> (Am)	1.44	5.86	3.42	5.58	13.31
<i>Corophium triaenonyx</i> (Am)	1.14	4.62	3.17	5.17	18.48
<i>Grandidierella lignorum</i> (Am)	0.54	4.24	2.90	4.73	23.21
<i>Iphinoe truncata</i> (Cu)	.	3.64	2.81	4.59	27.80
Ostracoda spp.	2.82	3.49	2.50	4.08	31.87
<i>Desdemona ornata</i> (Po)	2.80	5.07	2.38	3.88	35.75
Chironomini larvae spp. (In)	6.99	4.13	2.36	3.85	39.59
<i>Ceratonereis keiskama</i> (Po)	3.49	6.00	2.35	3.83	43.42
Chironomini pupae spp. (In)	3.28	0.75	2.07	3.37	46.79
Tanypodinae larvae spp. (In)	2.72	0.16	2.02	3.29	50.08
<i>Prionospio multipinnulata</i> (Po)	6.16	7.28	2.00	3.27	53.35
Oligochaeta spp.	3.49	4.66	1.95	3.18	56.53
<i>Dendronereis arborifera</i> (Po)	.	2.45	1.80	2.93	59.47
<i>Apeudes digitalis</i> (T)	0.47	2.46	1.74	2.83	62.30
Nematoda spp.	1.01	2.06	1.33	2.16	64.46
Tanytarsini larvae spp. (In)	1.67	0.20	1.31	2.13	66.60
Average Dissimilarity = 61.30					

The isolation of the Mdlotane Estuary ('outlier') was attributed to the absence of both Crustacea and Polychaeta species (except Sabellidae juvenile T1) from the system that were common in estuaries of Cluster I and II. Furthermore, the macrozoobenthos of this estuary comprised only four taxa, namely Chironomini larvae spp., Oligochaeta spp., Sabellidae juvenile T1 and Nematoda spp. Consequently, this system showed high dissimilarities of 79% and 86% to Cluster I and II estuaries, respectively. In comparison, the Zinkwasi Estuary was more similar to Cluster I and Cluster II estuaries (Figure 3.4) than the Mdlotane Estuary, exhibiting 69% and 67% dissimilarity, respectively. The macrozoobenthos of the Zinkwasi Estuary was typified by, but not limited to, *Desdemona ornata* (Polychaeta), *Prionospio multipinnulata* (Polychaeta), Oligochaeta spp. and Sabellidae juvenile T1 (Polychaeta). These particular species were generally more abundant in the Zinkwasi Estuary in pair-wise comparisons with estuaries of Cluster I and Cluster II. This system was different from the remaining estuaries due to the absence of Chironomini larvae spp. (Insecta), *Ceratonereis keiskama* (Polychaeta) and the amphipod species, which were all numerically abundant in these systems. Furthermore, the macrozoobenthos of the Zinkwasi Estuary included species that were either absent or rare in Cluster I and II estuaries, including

Apseudes digitalis (Tanaidacea), *Cyathura estuaria* (Isopoda), *Dendronereis arborifera* (Polychaeta), *Mesopodopsis africana* (Mysidacea) and *Macrura* post-larvae T1 (Decapoda).

Estuaries were tested statistically for dissimilarities between their macrozoobenthic communities using Analysis of Similarity (ANOSIM). Results revealed that in 1998/9, the KwaZulu-Natal TOCEs contained significantly different communities ($R=0.458$, $p<0.0001$). In addition, ANOSIM was performed according to several abiotic and biotic attributes to statistically verify the groups of estuaries with similar macrozoobenthic communities outlined in the above Cluster analysis (Table 3.10). Of the 21 factors that were tested, only ten exhibited a significant relationship with the estuary groups. All Global R statistics were below 0.5, emphasising high levels of variability between estuaries grouped under each factor. The two abiotic attributes with the highest R statistics and most significant relationships with the macrozoobenthos were the Tertiary ($R=0.297$, $p<0.01$) and Quaternary ($R=0.305$, $p<0.01$) drainage zones.

The macrozoobenthos of estuaries belonging to the U50 tertiary drainage zone (Table 3.4) were significantly different from the macrozoobenthos of estuaries in the U80 ($R=0.889$, $p<0.05$) and T40 ($R=0.953$, $p<0.05$) drainage zones (Table 3.10). Estuaries of the U500 drainage zone were also most different from estuaries in the quaternary (Table 3.4) T40G ($R=0.927$, $p<0.05$) and T40F ($R=0.948$, $p<0.05$) drainage zones. In addition, estuaries of the U80A quaternary drainage zone were significantly different from estuaries of the T40F drainage zone ($R=0.525$, $p<0.05$). There were weak yet significant associations between macrozoobenthos distribution and estuary area ($R=0.194$, $p<0.05$), latitude ($R=0.288$, $p<0.05$) and EHI value ($R=0.271$, $p<0.05$). Estuaries with an area ranging between 0.01-0.05 km² (Small Size 1) supported macrozoobenthic communities that were markedly different from communities in estuaries with an area ranging between 0.1-0.2 km² (Medium Size) ($R=0.326$, $p<0.05$) and greater than 0.2 km² (Large Size) ($R=0.524$, $p<0.05$), respectively. The macrozoobenthic communities of the estuaries in the most northern latitude category, LAT 1 (29°16' – 29°31' S), were greatly different from those in LAT 7 (30°46' – 31°01' S) ($R=0.953$, $p<0.05$) and LAT 5 (30°16' – 30°31' S) ($R=0.836$, $p<0.05$). Interestingly, there was no discrimination between the macrozoobenthos of estuaries with Very Poor and Very Good EHI values therefore, unique 'healthy' or 'unhealthy' indicator communities in accordance with the EHI were not discernable. However, communities of estuaries with Poor EHI values differed

significantly from those with Very Poor EHI values ($R=0.818$, $p<0.05$), and estuaries with Fair EHI values were different from those with Very Good EHI values ($R=0.496$, $p<0.01$).

Table 3.10 Resultant R statistics from ANOSIM for different biotic and abiotic attributes tested against the biological sample similarity matrix for macrozoobenthos sampled in 1998/9

Factor	R Statistic	
Estuary Category	0.005	* $p<0.05$
Area	0.194 *	** $p<0.01$
Length	0.090	*** $p<0.001$
Catchment Area	0.093	
Tertiary Drainage Zone	0.297 **	
Quaternary Drainage Zone	0.305 **	
EHI value	0.271 *	
Mouth State	-0.009	
Latitude	0.288 *	
Crustacea	0.450 ***	
Polychaeta	0.257 **	
Oligochaeta	0.235	
Insecta	0.406 **	
Mollusca	0.297 ***	
Other	0.032	
Pests	0.154	
Richness	0.130	
Evenness	0.244 *	
Diversity	0.126	
Sediment Type	-0.027	
Salinity Category	-0.001	

Based on biotic composition, estuaries were separated according to the number of species of Crustacea ($R=0.450$, $p<0.001$), Insecta ($R=0.406$, $p<0.001$), Mollusca ($R=0.297$, $p<0.001$) and Polychaeta ($R=0.257$, $p<0.01$) (Table 3.10). Macrozoobenthic communities containing between 1-3 Crustacea species (Category 1) were significantly different from communities with between 4-6 (Category 2) ($R=0.755$, $p<0.001$) and between 7-9 (Category 3) ($R=0.581$, $p<0.01$) Crustacea species. Insecta and Mollusca species were important in discriminating between communities without an Insecta ($R=0.416$, $p<0.05$), and Mollusca ($R=0.376$, $p<0.001$) component, and those with between 1 and 2 species from these respective faunal groups. Macrozoobenthic communities containing between 5-7 Polychaeta species (Category 3) were significantly different from communities with between 1-2 (Category 1) ($R=0.725$, $p<0.001$) and greater than 7 (Category 4) ($R=0.506$, $p<0.05$) Polychaeta species. There was a poor, yet statistically significant, association

between macrozoobenthic distribution and community evenness, ($R=0.244$, $p<0.05$) such that communities with low evenness ($J'=0.2-0.4$) were markedly different from communities with moderate evenness ($J'=0.41-0.6$).

Overall, the discrimination between groups of estuaries investigated in 1998/9 was attributed to a suite of factors, rather than a single overriding attribute, of which the magnitude of influence was dependent on the factor. It appeared that the intrinsic community composition (number of Crustacea species and the presence or absence of Insecta) was a stronger determinant of estuary similarities than abiotic system characteristics.

3.4.2 Macrozoobenthic Community Structure (2009/10)

3.4.2.1 Faunal abundance and number of taxa

The mean total macrozoobenthic abundance sampled per estuary per site in 2009/10 was 7,819 ind.m⁻² ($\pm 10,582.94SD$), comprising 102 taxa from eight Phyla. Generally, the mean faunal abundance sampled per estuary in 2009/10 was somewhat lower than sampled in 1998/9. High inter-estuarine variability in mean faunal abundance and the mean number of taxa was strongly evident (Figure 3.5A). However, the degree of inter-site (within estuary) variability was relatively reduced in comparison with the 1998/9 dataset, with the main exception of the Sipingo Estuary. This was attributed to dramatic differences in abundance between the embayment (74,410 ind.m⁻²) and riverine environments (lower reaches 36,484 ind.m⁻², upper reaches 1,176 ind.m⁻²). Nonetheless, the maximum macrozoobenthic abundance was recorded in this system (ISP 37,356 ind.m⁻² $\pm 36,624.79SD$), principally due to the extremely high faunal abundance in the embayment area. Abundance was comparatively high in the Mvutshini Estuary for which there was only one sample site in the lower reaches (MSH 31,080 ind.m⁻²). The lowest invertebrate density was recorded in the Damba Estuary (D 126 ind.m⁻² $\pm 98.99SD$). Of all the estuaries that were sampled, 74% supported mean total macrozoobenthic abundances less than 10,000 ind.m⁻², including the two largest systems, the Mtamvuna (MVA 2,208 ind.m⁻² $\pm 1,499.30SD$) and the Zinkwasi (ZIN 8,820 ind.m⁻² $\pm 3,542.95SD$) estuaries.

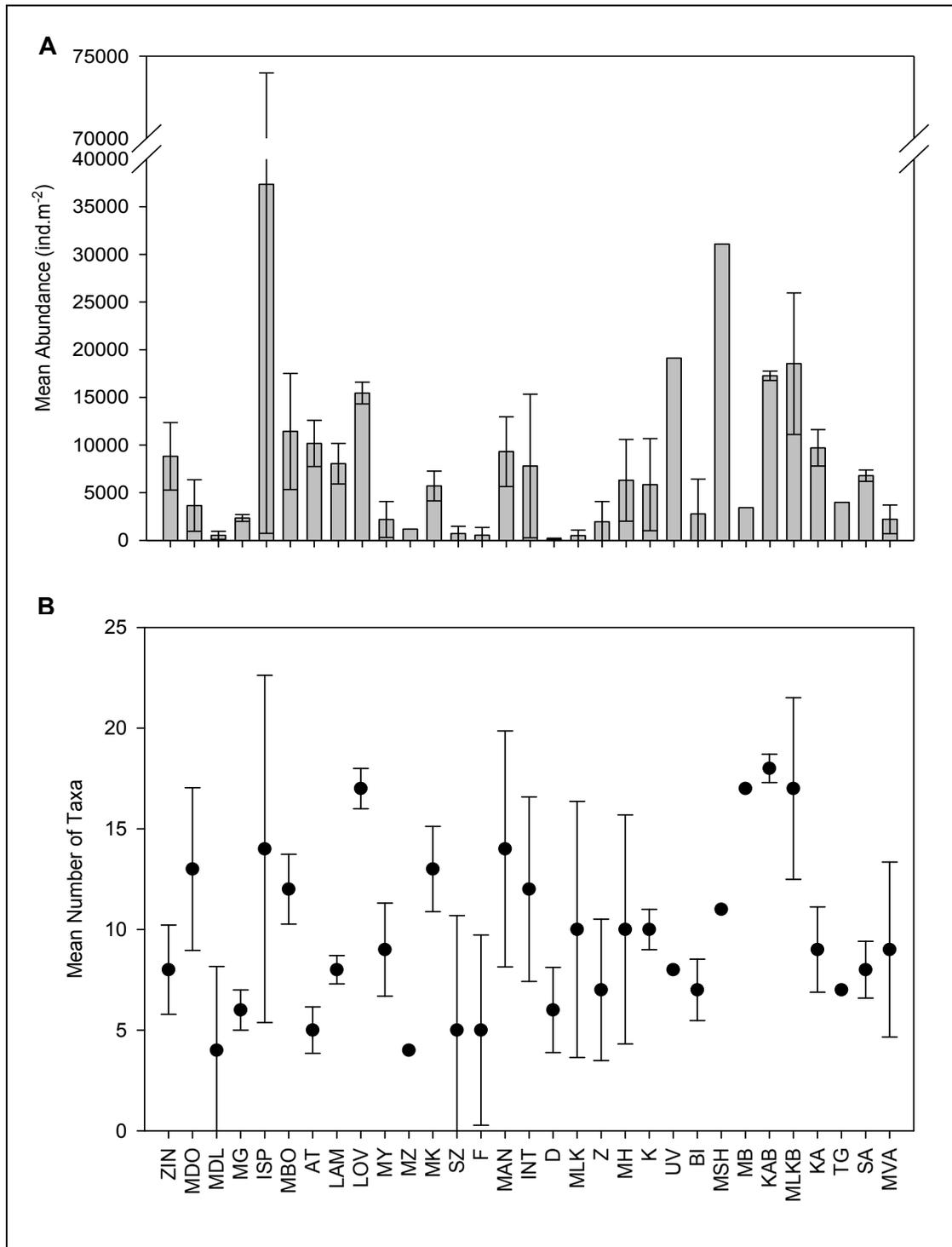


Figure 3.5 Mean abundance (\pm SD) (A) and mean number of taxa (\pm SD) (B) of macrozoobenthos collected from KwaZulu-Natal TOCEs in 2009/10

The number of taxa fluctuated markedly between estuaries (Figure 3.5B). There was a poorly defined trend of decreasing number of taxa with increasing latitude. The highest number of taxa was recorded in the Kaba Estuary (KAB 18 taxa ± 0.71 SD), followed by the Umhlangankulu (MLKB 17 taxa ± 4.51 SD), Lovu (LOV 17 taxa ± 1 SD) and Mbizana (MB 17 taxa, single site) systems. The estuary with the lowest number of taxa was the Mzimayi Estuary (MZ 4 taxa) collected from a single sample site. Approximately 58% of all the estuaries that were sampled supported macrozoobenthic communities comprising less than 10 taxa.

3.4.2.2 Taxonomic composition

As in 1998/9, Crustacea (Phylum Arthropoda) and Polychaeta (Phylum Annelida) were again the dominant invertebrate faunal groups in 2009/10 (Table 3.11). In contrast with the 1998/9 dataset, the contribution of Crustacea to the mean abundance per estuary gradually decreased with increasing latitude. Also, there was a general trend of increasing Polychaeta contribution with increasing latitude in 2009/10, where there was no apparent trend in 1998/9. Crustacea contributed most to the macrozoobenthos in the Lovu Estuary (LOV), comprising 85% of the macrozoobenthic community, followed by the Umhlangankulu Estuary (MLKB 78%). The macrozoobenthic communities in the Tongazi (TG) and Sandlundlu (SA) estuaries comprised the highest proportions of Polychaeta (99%) and Crustacea constituted the remainder (1%) of these communities. The macrozoobenthos of the Mdloti (MDL) and Manzimtoti (AT) estuaries was dominated by Oligochaeta (46%) and Mollusca (53%), respectively. Mollusca were also an important component in the Mdloti Estuary (MDL 24%). In the Damba Estuary (D), Insecta and other fauna were the dominant groups, contributing up to 56% and 28% to the mean total abundance, respectively. In this system, Crustacea made little contribution (10%) to overall abundance and Polychaeta were absent. Insecta were similarly an important component of the macrozoobenthos in the Fafa Estuary (F), comprising 32% of the faunal abundance.

The mean abundances of the broad taxonomic groups sampled within each estuary in 2009/10 are illustrated in Figure 3.6. Crustacea abundance was at a maximum in the Umhlangankulu Estuary (MLKB 14,406 ind.m⁻² $\pm 7,367.66$ SD), with comparably high abundances in the Sipingo (ISP 13,804 ind.m⁻² $\pm 23,848.63$ SD) and Lovu (LOV 13,094 ind.m⁻² $\pm 1,934.15$ SD) estuaries. Crustacea were most poorly represented in the Manzimtoti Estuary (AT 9 ind.m⁻² ± 8.08 SD). Polychaeta densities were

highest in the Mvutshini Estuary at a single sample site (MSH 23,772 ind.m⁻²) and completely absent from the Damba Estuary (D). The lowest Polychaeta density was 51 ind.m⁻² ($\pm 49.17SD$) sampled in the Fafa Estuary (F). Oligochaeta were most abundant in the Mvutshini Estuary (MSH 4102 ind.m⁻², single site). Mollusca were absent from 23% of the investigated estuaries. When present, abundances were low, except in the Sipingo and the Manzimtoti systems where extremely high abundances were recorded, 6,584 ind.m⁻² ($\pm 6,531.66SD$) and 5,385 ind.m⁻² ($\pm 5,656.37SD$), respectively. Similarly, Insecta were absent from 23% of the estuaries, but were better represented across most of the systems than in 1998/9. Insecta were at a maximum in the Intshambili Estuary (INT 499 ind.m⁻² $\pm 724.27SD$). Other low contributing taxa reached a combined maximum abundance in the Sipingo Estuary (ISP 410 ind.m⁻² $\pm 687.19SD$). These fauna were absent from 35% of the sampled estuaries. A full list of taxa is given in Appendix 1.3.

Table 3.11 Proportions (%) of broad taxonomic invertebrate groups and the total mean abundance (ind.m⁻²) of organisms sampled in each estuary in 2009/10. Values in **bold** represent maximum values.

Estuary No.	Estuary Code	Crustacea	Polychaeta	Oligochaeta	Mollusca	Insecta	Other*	Abundance (ind.m ⁻²)
<i>North</i>								
12	ZIN	65	10	24	1			8,820
14	MDO	60	31	4	2	3		3,654
19	MDL	3	16	46	24	11		536
20	MG	13	73	1	12	1		2,347
23	ISP	37	39	5	18		1	37,356
24	MBO	11	88				1	11,428
25	AT		46		53	1		10,168
26	LAM	25	72	1	1	1		8,043
27	LOV	85	11	2	2			15,456
34	MY	25	61	10		4		2,184
35	MZ	1	97			2		1,190
37	MK	24	64	9		3		5,705
38	SZ	13	79	1		7		723
40	F	56	9	1	2	32		546
47	MAN	47	46	6			1	9,305
49	INT	63	25	6		6		7,798
51	D	10			6	56	28	126
52	MLK	20	52	14	6	8		497
57	Z	17	70			13		1,946
58	MH	5	91	1	1	1	1	6,300
60	K	26	72	1			1	5,842
61	UV	19	79	2				19,124
62	BI	3	95	1			1	2,781
63	MSH	11	76	13				31,080
64	MB	5	94		1			3,430
65	KAB	40	47	10		2	1	17,262
66	MLKB	78	14	8				18,540
68	KA	1	98			1		9,709
69	TG	1	99					3,990
71	SA	1	99					6,790
73	MVA	24	54	6		16		2,208
<i>South</i>								

* Other includes organisms from low contributing taxa: Hirudinea, Arachnida, Collembola, Cnidaria, Nematoda, Nemertea, Platyhelminthes, Sipunculida and Unidentified organisms.

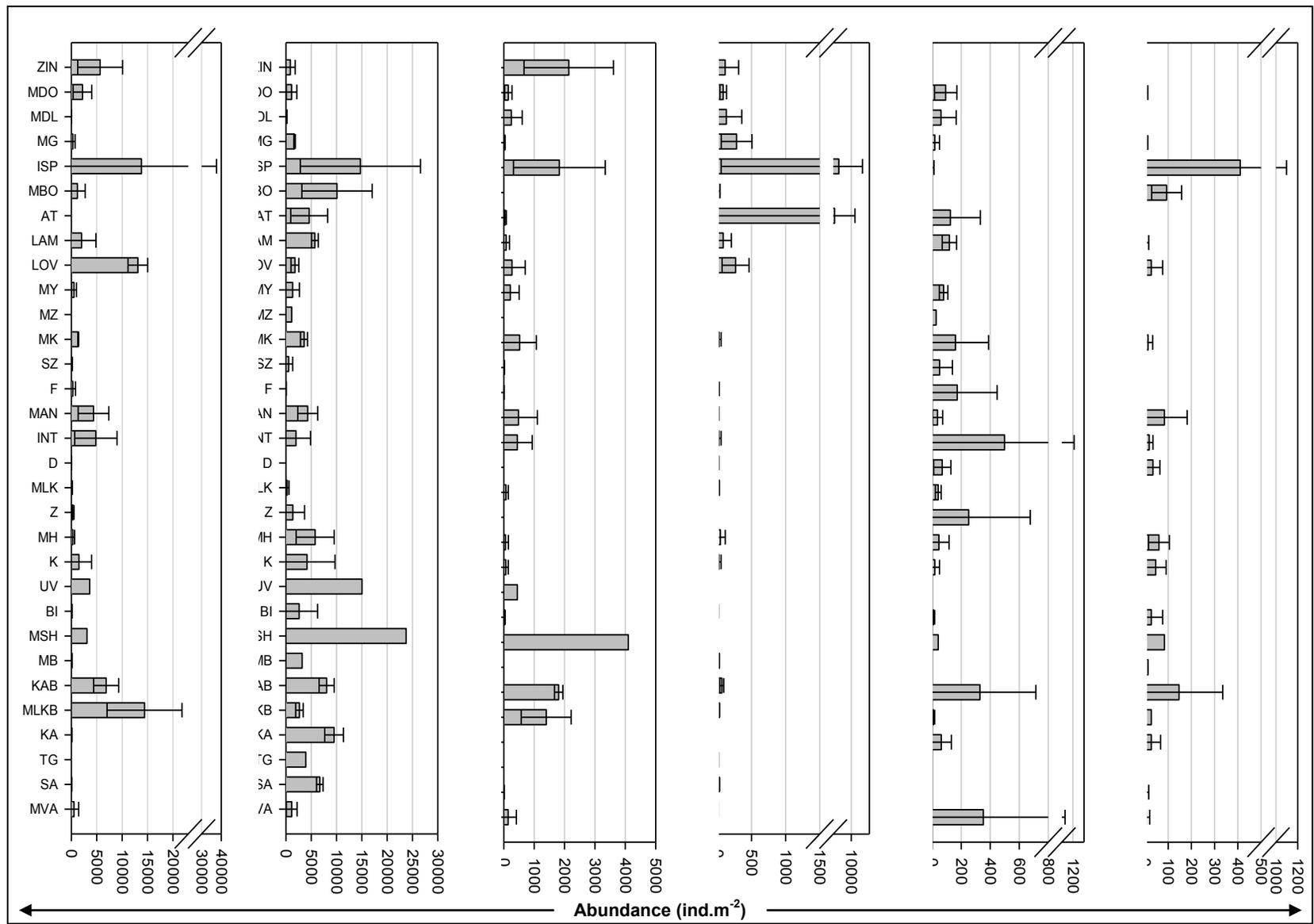


Figure 3.6 Mean abundances (\pm SD) of broad taxonomic invertebrate groups sampled per estuary sampled in 2009/10

3.4.2.3 Classification of 2009/10 estuaries

Cluster analysis of the macrozoobenthos sampled in 2009/10 identified three groups of estuaries and two individual systems ('outliers') based on 35% similarity between their macrozoobenthic communities (Figure 3.7). Cluster I comprised the Sandlundlu (SA), Tongazi (TG) and Mbizana (MB) estuaries. Cluster II included the Manzimtoti (AT) and Mdloti (MDL) estuaries. The two isolated systems were the Damba (D) and the Mzimayi (MZ), which separated out from the remaining estuaries at approximately 12% and 23% similarity, respectively. Cluster III comprised the remaining 24 TOCEs.

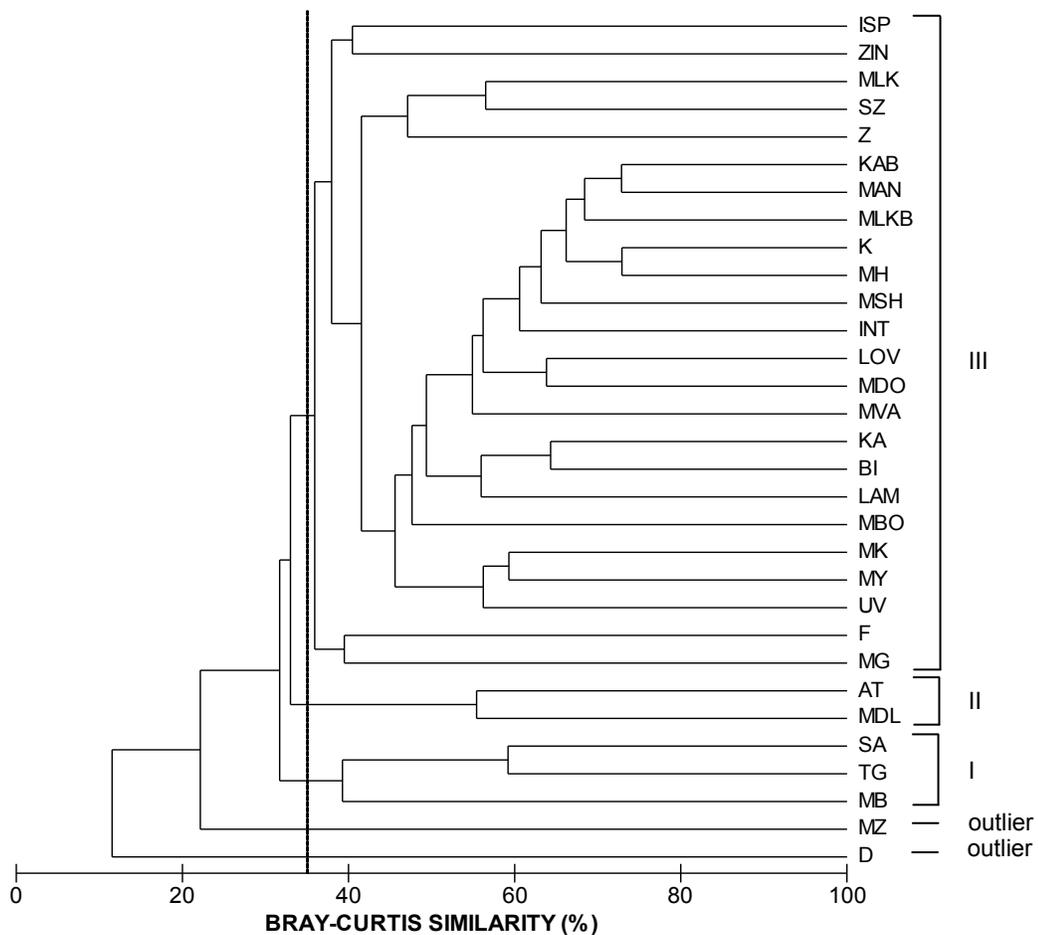


Figure 3.7 Hierarchical cluster diagram illustrating groups of estuaries in 2009/10 that shared 35% similarity in macrozoobenthic community characteristics.

The taxa responsible for the discrimination between these clusters, identified through SIMPER analysis, are displayed in Tables 3.12, 3.13 and 3.14. The separation of Cluster I estuaries from Cluster III estuaries (67.72% dissimilarity) (Table 3.12) was largely attributed to the higher average abundance of Polychaeta of the genus *Capitella* in the former. Abundance of species common to both groups was generally higher in Cluster III estuaries except *Prionospio multipinnulata* (Polychaeta). Three relatively important species were absent from Cluster I estuaries including *Grandidierella lutosa* (Amphipoda), *G. lignorum* (Amphipoda) and Chironomini larvae spp. (Insecta). The bivalve Tellinidae sp. 1 was exclusively present in this cluster.

Table 3.12 Taxa responsible for the discrimination between Cluster I and III estuaries classified by hierarchical cluster analysis for 2009/10. Only species contributing greater than 2% to the total dissimilarity between groups are presented. Po= Polychaeta, In= Insecta, Am= Amphipoda, T= Tanaidacea, Bv= Bivalvia

Taxa	Cluster III	Cluster I			
	Ave. Abundance	Ave. Abundance	Ave. Dissim.	Contribution (%)	Cumulative (%)
<i>Capitella</i> spp. (Po)	0.71	6.79	5.97	8.81	8.81
<i>Ceratonereis keiskama</i> (Po)	5.44	4.46	3.21	4.73	13.54
<i>Grandidierella lutosa</i> (Am)	3.69	.	3.16	4.66	18.20
Oligochaeta spp.	4.58	1.60	2.94	4.34	22.55
<i>Grandidierella</i> spp. (Am)	5.90	2.84	2.83	4.18	26.73
<i>Prionospio multipinnulata</i> (Po)	5.92	6.59	2.80	4.13	30.86
Chironomini larvae spp. (In)	2.93	.	2.65	3.92	34.78
<i>Desdemona ornata</i> (Po)	4.28	3.82	2.62	3.87	38.64
<i>Dendronereis arborifera</i> (Po)	2.76	1.60	2.46	3.63	42.27
<i>Corophium triaenonyx</i> (Am)	3.62	1.81	2.37	3.50	45.77
<i>Apeudes digitalis</i> (T)	2.31	1.60	2.26	3.33	49.10
<i>Grandidierella lignorum</i> (Am)	2.44	.	2.08	3.08	52.18
Tellinidae sp.1 (Bv)	.	1.81	1.76	2.59	54.77
Average Dissimilarity = 67.72					

It was evident from the comparison between Cluster II and Cluster III estuaries, that the gastropod species, *Tarebia granifera*, was most responsible for their separation (67.05% dissimilarity) (Table 3.13). In addition, the dominant presence of Sabellidae JuvT1 (Polychaeta) in Cluster II estuaries and *Ceratonereis keiskama* (Polychaeta) in Cluster III estuaries, also played an important role in cluster separation. Estuaries of Cluster II also lacked several important Amphipoda and one Tanaidacea crustacean species that were present in Cluster II. Similarly with Cluster I comparisons, Cluster III estuaries had higher abundances of the species common to both groups. However, Insecta larvae (Chironomini and Tanytarsini larvae spp.), Oligochaeta spp., Gastropoda and Bivalvia molluscs were more abundant in Cluster II.

Table 3.13 Taxa responsible for the discrimination between Cluster II and III estuaries classified by hierarchical cluster analysis for 2009/10. Only species contributing greater than 2% to the total dissimilarity between groups are presented. Po= Polychaeta, In= Insecta, Am= Amphipoda, T= Tanaidacea, Bv= Bivalvia, Ga= Gastropoda, JuvT1= Juvenile Type 1

Taxa	Cluster III	Cluster II			
	Ave. Abundance	Ave. Abundance	Ave. Dissim.	Contribution (%)	Cumulative (%)
<i>Tarebia granifera</i> (Ga)	1.07	6.52	5.31	7.92	7.92
<i>Ceratonereis keiskama</i> (Po)	5.44	0.87	4.45	6.63	14.55
Sabellidae JuvT1 (Po)	0.14	4.56	4.21	6.28	20.83
<i>Prionospio multipinnulata</i> (Po)	5.92	4.18	4.13	6.15	26.98
<i>Grandidierella</i> spp. (Am)	5.90	2.03	3.65	5.44	32.42
<i>Grandidierella lutosa</i> (Am)	3.69	.	3.32	4.95	37.37
<i>Corophium triaenonyx</i> (Am)	3.62	.	3.04	4.53	41.90
<i>Dendronereis arborifera</i> (Po)	2.76	0.87	2.34	3.49	45.39
<i>Grandidierella lignorum</i> (Am)	2.44	.	2.19	3.27	48.66
Oligochaeta spp.	4.58	4.64	2.07	3.09	51.75
<i>Apseudes digitalis</i> (T)	2.31	.	1.91	2.85	54.60
<i>Brachidontes virgiliae</i> (Bv)	1.31	1.76	1.89	2.82	57.43
Tanytarsini larvae spp. (In)	0.65	1.88	1.89	2.82	60.24
Chironomini larvae spp. (In)	2.93	3.91	1.79	2.66	62.91
<i>Desdemona ornata</i> (Po)	4.28	4.17	1.75	2.61	65.51
<i>Melanoides tuberculata</i> (Ga)	0.41	1.73	1.71	2.55	68.07
Average Dissimilarity = 67.05					

Similarly, the differentiation between Cluster I and Cluster II estuaries (75.92% dissimilarity) (Table 3.14) was based largely on the exclusive presence of *Capitella* spp. in Cluster I estuaries, and conversely, the exclusive presence of *Tarebia granifera* (Gastropoda), Sabellidae juvenile T1 (Polychaeta) in Cluster II estuaries. The absence of Chironomini and Tanytarsini larvae spp. (Insecta), *Brachidontes virgiliae* (Bivalvia) and *Melanoides tuberculata* (Gastropoda) from the former group of estuaries also contributed to the separation of the two clusters. Of the polychaete taxa that were common to both groups, only *Desdemona ornata* (Polychaeta) was more abundant in Cluster II estuaries.

In terms of the two isolated systems, the macrozoobenthos of the Damba Estuary comprised 11 taxa, of which the majority (7 taxa) was Insecta taxa. The taxa included Entomobryidae sp. 1 (Collembola), Hypogastruridae sp. 1 (Collembola), *Grandidierella* spp. (Amphipoda), *Macrura* post-larvae T1 (Decapoda), Chironomini larvae (Insecta) and pupae spp. (Insecta), Tanypodinae larvae spp. (Insecta), Tanytarsini larvae spp, Orthoclaadiinae larvae (Insecta), Ceratopogonidae larvae T3 (Insecta), *Caenis* spp. (Insecta) and *Burnupia* sp. 1 (Gastropoda). Most these taxa occurred

exclusively in the Damba Estuary in the pair-wise comparisons with Cluster I and Cluster II estuaries. Furthermore, the Damba community was devoid of all Polychaeta and Oligochaeta species, and most Crustacea species that were sampled from the other systems, except *Grandidierella* spp. and *Macrura* post-larvae. Thus, the macrozoobenthos of the Damba Estuary was markedly different from the remaining estuaries as indicated by the high level of dissimilarity between the Damba Estuary and estuaries of Cluster I (94%), Cluster II (88%) and Cluster III (88%).

Table 3.14 Taxa responsible for the discrimination between Clusters I and II estuaries classified by hierarchical cluster analysis for 2009/10. Only species contributing greater than 2% to the total dissimilarity between groups are presented. Po= Polychaeta, In= Insecta, Am= Amphipoda, T= Tanaidacea, Ga= Gastropoda, Bv= Bivalvia

Taxa	Cluster II	Cluster I			
	Ave. Abundance	Ave. Abundance	Ave. Dissim.	Contribution (%)	Cumulative (%)
<i>Capitella</i> spp. (Po)	.	6.79	8.15	10.73	10.73
<i>Tarebia granifera</i> (Ga)	6.52	.	7.57	9.98	20.70
Sabellidae JuvT1 (Po)	4.56	.	5.35	7.04	27.75
<i>Prionospio multipinnulata</i> (Po)	4.18	6.59	5.20	6.84	34.59
Chironomini larvae spp. (In)	3.91	.	4.56	6.01	40.60
<i>Ceratonereis keiskama</i> (Po)	0.87	4.46	4.45	5.86	46.47
Oligochaeta spp.	4.64	1.60	3.45	4.54	51.01
<i>Desdemona ornata</i> (Po)	4.17	3.82	3.07	4.04	55.05
Tanytarsini larvae spp. (In)	1.88	.	2.33	3.07	58.12
Tellinidae sp.1 (Bv)	.	1.81	2.32	3.05	61.17
<i>Brachidontes virgiliae</i> (Bv)	1.76	.	2.18	2.87	64.04
<i>Dendronereis arborifera</i> (Po)	0.87	1.60	2.14	2.82	66.87
<i>Apeudes digitalis</i> (T)	.	1.60	2.08	2.74	69.61
<i>Melanoides tuberculata</i> (Ga)	1.73	.	2.05	2.70	72.31
<i>Corophium triaenonyx</i> (Am)	.	1.81	1.89	2.49	74.80
Nemertea spp.	.	1.60	1.66	2.18	76.98
<i>Ancistrosyllis parva</i> (Po)	.	1.12	1.62	2.14	79.12
Average Dissimilarity = 75.92					

In comparison, the macrozoobenthos of the Mzimayi Estuary was characterised by only four species, namely, *Ceratonereis keiskama* (Polychaeta), *Grandidierella lutosa* (Amphipoda), Chironomini larvae spp. (Insecta) and Ceratopogonidae larvae T1 (Insecta). This estuary was also devoid of all other Polychaeta, Crustacea and Oligochaeta species common in the remaining estuaries, hence the high dissimilarities between the Mzimayi Estuary and Cluster I (88%), Cluster II (87%) and Cluster III (76%) estuaries. These values were somewhat lower than the values of the Damba Estuary. This suggests that the macrozoobenthic community of the Mzimayi Estuary was slightly more similar than that of the Damba Estuary to the majority of estuaries that were sampled.

As with the 1998/9 biological data, there was a significant difference between estuaries based on the dissimilarities in their macrozoobenthic communities (ANOSIM $R=0.442$, $p<0.0001$). The factor(s) responsible for the groups estuaries outlined during the Cluster analysis were identified (Table 3.15). Generally, results were similar to those computed for the 1998/9 dataset. That is, global R statistics were below 0.500, indicating high levels of variability between estuaries grouped under each factor. However, only five of the 21 factors tested exhibited a significant relationship with the estuary groups. Thus, several factors identified in 1998/9 as important attributes of similarity were not prominent in 2009/10.

Table 3.15 Resultant R statistics from ANOSIM for different biotic and abiotic attributes tested against the biological sample similarity matrix for macrozoobenthos sampled 2009/10

Factor	R Statistic	
Estuary Category	0.047	
Area	0.206 *	* $p<0.05$
Length	0.089	** $p<0.01$
Catchment Area	0.030	*** $p<0.001$
Tertiary Drainage Zone	0.186 *	
Quaternary Drainage Zone	0.178	
Mouth State	-0.010	
Latitude	0.130	
Crustacea	0.124	
Polychaeta	0.278 ***	
Oligochaeta	0.430 **	
Insecta	0.134	
Mollusca	0.105	
Other	0.033	
Pests	0.136	
Richness	-0.016	
Evenness	0.202	
Diversity	0.306 ***	
Sediment Type	0.136	
Salinity Category	-0.081	

Despite the low R statistics, the biotic attributes had a larger influence on the grouping of the macrozoobenthic communities than the abiotic attributes (Table 3.15). There was a relatively strong discrimination between estuary groups based on the presence or absence of Oligochaeta ($R=0.430$, $p<0.01$). Differentiation between estuaries according to the number of Polychaeta species was poor but significant ($R=0.278$, $p<0.001$). Macrozoobenthic communities comprising between 1-2 Polychaeta species (Category 1) (Table 3.6) were significantly different from those containing 3-4 (Category 2) ($R=0.348$, $p<0.001$) and 5-7 ($R=0.286$, $p<0.01$) species. Diversity was

also an important factor influencing the distribution of macrozoobenthos among KwaZulu-Natal TOCEs ($R=0.306$, $p<0.001$). Estuaries of high benthic diversity ($H'=1.5-2.0$) possessed faunal assemblages markedly different from those of low ($H'=0.5-1.0$; $R=0.443$, $p<0.01$), and very high ($H'>2$; $R=0.518$, $p<0.05$) diversity. Estuaries were poorly grouped according to estuary Area ($R=0.206$, $p<0.05$) and Tertiary drainage zone ($R=0.186$, $p<0.05$) (Table 3.15). Similar to 1998/9, the macrozoobenthic communities of estuaries with an area size ranging from 0.01-0.05 km² (Small Size 1) were markedly different from those in estuaries with an area ranging from 0.1-0.2 km² (Medium Size) ($R=0.396$, $p<0.05$). Pair-wise comparisons between the communities of estuaries in the T40 drainage zone with those of the U30 and U80 drainage zones yielded significant R statistics, 0.643 ($p<0.05$) and 0.155 ($p<0.05$), respectively.

Overall, the results of ANOSIM for the 2009/10 macrozoobenthic communities were relatively similar to those for the 1998/9 communities. Furthermore, the discrimination between the macrozoobenthos of different groups of TOCEs was similarly not attributed to a single factor, but rather a suite of factors, of which the number of Polychaeta species, the presence or absence of Oligochaeta and the diversity of each community played important roles in determining macrozoobenthic community similarities.

3.4.3 Environmental Characteristics in 1998/9 and 2009/10

3.4.3.1 Physico-Chemical Variables

Physico-chemical conditions varied substantially from estuary to estuary (Table 3.16), reflecting localised conditions (within each estuary) at the time of sampling. In 1998/9, Mdlotane Estuary was the deepest system with the greatest average depth of 2.93m ($\pm 1.95SD$), and the Mhlanga Estuary was the shallowest (0.45m $\pm 0.29SD$). In 2009/10 the deepest and shallowest estuaries that were sampled were the Tongazi (2.75m, single site) and Fafa estuaries (0.10m $\pm 0.02SD$), respectively. Estuary depth was often related to the open or closed state of the mouth. In addition, water depth was governed by the extent to which the mouth was open and the time elapsed after mouth closure, before measurements were made (pers. obs.).

Table 3.16 Mean water quality variables (\pm SD) measured in each estuary sampled in 1998/9 and 2009/10, including calculated salinity range and mouth state. Shaded areas represent maximum (black) and minimum (grey) values.

ESTUARY NAME		Depth (m)		pH		Turbidity (NTU)		Dissolved Oxygen (mg/L)		Temperature (°C)		Salinity (PSU)		Salinity Range (Lower-Upper)		Mouth State (Open/Closed)	
		1998/9	2009/10	1998/9	2009/10	1998/9	2009/10	1998/9	2009/10	1998/9	2009/10	1998/9	2009/10	1998/9	2009/10	1998/9	2009/10
ZINKWASI	Mean	1.30	1.65	7.80	7.29	69.25	52.75	3.21	3.83	27.90	26.84	12.75	9.89	3.20	4.77	C	C
	\pm SD	0.22	0.14	0.11	0.44	12.47	19.09	2.00	1.37	1.66	0.67	1.61	2.17				
MDLOTANE	Mean	2.93	1.95	6.95	6.60	12.00	39.10	0.02	1.58	26.33	23.58	0.27	18.45	0.10	6.74	C	C
	\pm SD	0.31	0.20	0.02	0.51	1.73	56.13	0.01	0.95	0.15	0.08	0.06	3.38				
MDLOTI	Mean	2.33	1.25	7.23	7.74	8.00	190.43	2.47	4.69	21.63	22.59	0.10	2.43	0.00	6.17	C	C
	\pm SD	0.81	0.69	0.27	0.39	2.65	277.12	2.90	3.48	0.38	0.35	0.00	3.53				
MHLANGA	Mean	0.45	0.29	7.63	7.69	36.67	145.87	4.22	3.61	20.67	22.16	9.57	1.12	24.10	2.01	O	O
	\pm SD	0.09	0.05	0.33	0.24	25.17	36.74	1.74	0.19	0.35	0.09	13.11	1.02				
SIPINGO	Mean	0.63	0.61	7.71	7.38	24.33	12.23	8.13	2.89	25.53	25.00	17.43	21.84	27.00	12.77	O	C
	\pm SD	0.15	0.38	0.46	0.36	9.07	9.30	1.64	4.02	2.55	1.75	14.97	7.37				
MBOKODWENI	Mean	0.88	1.83	7.24	6.84	17.00	16.33	2.08	4.56	24.50	24.01	19.97	23.62	9.10	6.04	O	C
	\pm SD	0.38	0.15	0.23	0.36	2.65	9.08	1.03	0.80	0.95	0.90	4.86	5.10				
MANZIMTOTI	Mean	1.05	1.27	7.30	8.08	45.00	10.10	2.66	11.01	21.97	22.72	2.57	1.02	1.40	1.31	O	C
	\pm SD	0.13	0.35	0.39	0.66	13.75	7.01	2.91	5.43	0.40	1.28	1.21	0.73				
LITTLE MANZIMTOTI	Mean	1.15	0.58	7.33	7.61	69.00	9.35	1.57	2.00	21.90	22.82	3.25	0.97	1.90	1.16	O	O
	\pm SD	0.07	0.17	0.24	0.01	5.66	1.48	0.78	0.55	0.14	0.71	1.34	0.82				
LOVU	Mean	0.60	0.44	7.86	7.86	27.33	29.10	6.79	7.03	21.63	28.82	20.17	3.06	24.50	2.70	O	O
	\pm SD	0.20	0.09	0.14	0.21	9.24	8.02	0.67	0.21	0.38	0.19	14.92	1.38				
MPAMBANYONI	Mean	0.68	0.31	8.02	8.70	20.33	10.23	7.59	9.35	24.80	32.63	4.10	0.42	5.20	0.54	C	O
	\pm SD	0.49	0.11	0.59	0.23	5.86	6.03	4.79	0.62	3.10	1.76	3.03	0.30				
MZIMAYI	Mean	0.60	0.13	7.35	7.54	94.00	70.60	5.08	7.99	20.80	21.72	0.60	0.13			C	O
	\pm SD																
MKUMBANE	Mean	1.15	0.67	7.45	7.84	34.00	11.00	2.79	7.17	23.50	27.11	5.75	18.05	0.30	35.67	C	O
	\pm SD	0.07	0.03	0.20	0.05	1.41	3.68	2.88	0.64	1.13	0.18	0.21	25.22				
SEZELA	Mean	1.80	1.83	7.57	7.95	18.67	6.50	2.82		25.70	27.23	4.30	19.40	0.30	16.59	C	C
	\pm SD	0.50	0.73	0.15	0.15	7.23	2.08	1.17	5.59	0.36	0.20	0.17	9.58				
FAFA	Mean	0.73	0.10	7.97	8.05	7.67	64.03	6.92	7.35	28.30	27.99	2.03	0.20	2.50	0.25	C	O
	\pm SD	0.59	0.02	0.12	0.15	3.21	34.71	0.64	0.14	0.89	1.65	1.42	0.14				
MHLABATSHANE	Mean	1.15	1.05	7.27	7.47	19.67	14.07	2.89	4.51	27.60	22.66	14.97	26.58	8.30	18.95	C	O
	\pm SD	0.43	0.57	0.16	0.28	16.50	3.73	2.13	0.38	0.72	1.69	4.25	10.05				

Table 3.16 continued.../

Table 3.16 continued.../

ESTUARY NAME		Depth (m)		pH		Turbidity (NTU)		Dissolved Oxygen (mg/L)		Temperature (°C)		Salinity (PSU)		Salinity Range (Lower-Upper)		Mouth State (Open/Closed)	
		1998/9	2009/10	1998/9	2009/10	1998/9	2009/10	1998/9	2009/10	1998/9	2009/10	1998/9	2009/10	1998/9	2009/10	1998/9	2009/10
INTSHAMBILI	Mean	1.15	1.71	7.30	7.11	7.67	14.83	4.12	1.55	24.93	22.13	3.17	16.22	0.30	4.18	C	O
	±SD	0.38	0.37	0.07	0.10	0.58	4.30	0.33	1.07	0.51	0.34	0.15	2.17				
DAMBA	Mean	0.90	0.29	7.15	7.91	20.00	65.40	4.74	8.12	24.60	21.88	0.35	0.14	0.10	0.01	C	O
	±SD	0.99	0.01	0.32	0.33	14.14	6.79	0.25	0.09	2.12	0.20	0.07	0.01				
MHLANGAMKULU	Mean	1.68	0.65	7.37	7.64	7.50	104.20	3.85	7.32	22.30	21.22	0.50	4.46	0.00	8.60	C	O
	±SD	0.25	0.52	0.18	0.05	3.54	40.73	2.40	0.99	0.57	1.03	0.00	6.08				
ZOTSHA	Mean	1.23	0.78	7.26	7.56	26.00	27.63	1.87	5.54	24.00	29.10	13.20	11.45	10.90	2.06	O	O
	±SD	0.32	0.90	0.38	0.54	12.17	36.87	1.48	4.79	0.72	1.69	5.65	17.91				
MHLANGENI	Mean	1.07	0.35	7.71	7.94	9.67	35.07	6.00	9.36	26.93	33.64	17.07	5.54	11.70	13.62	C	O
	±SD	0.25	0.26	0.26	0.21	8.50	14.27	3.67	2.08	1.65	1.58	6.41	7.52				
KONGWENI	Mean	0.78	1.34	7.64	7.53	15.33	10.03	6.36	6.63	22.70	28.63	0.23	12.03	0.30	14.74	C	C
	±SD	0.23	0.66	0.45	0.11	8.62	5.49	1.29	3.96	0.53	0.20	0.15	7.91				
UVUZANA	Mean	1.00	0.61	7.14	7.91	40.00	27.80	3.68	12.45	21.80	26.23	0.20	1.48	.	.	C	C
	±SD				
BILANHLOLO	Mean	1.37	1.73	7.05	6.62	7.00	34.23	4.61	0.84	26.77	26.00	18.67	11.50	7.10	3.35	C	C
	±SD	0.46	0.31	0.43	0.22	7.00	31.02	0.69	0.97	0.93	0.45	3.74	1.92				
MVUTSHINI	Mean	1.30	0.95	7.64	7.98	9.00	20.70	3.83	3.38	23.10	27.96	0.40	3.93	.	.	O	C
	±SD				
MBIZANA	Mean	1.80	0.78	7.78	6.93	3.00	1.50	6.23	6.71	23.30	22.07	3.10	35.92	.	.	C	O
	±SD				
KABA	Mean	0.85	1.18	7.51	7.50	19.50	14.45	7.26	4.03	27.20	30.28	13.00	5.33	0.20	0.05	C	C
	±SD	0.35	0.07	0.20	0.06	3.54	1.20	0.54	0.69	1.98	0.90	0.14	0.04				
UMHLANGANKULU	Mean	2.00	0.39	7.82	8.02	12.00	23.20	5.42	6.46	22.77	30.09	4.03	12.57	0.20	2.32	C	C
	±SD	0.50	0.39	0.07	0.31	1.73	13.18	0.47	2.35	0.51	2.48	0.12	1.16				
KANDANDLOVU	Mean	1.00	0.52	7.42	7.94	8.50	9.35	3.43	4.88	24.65	29.67	14.85	5.29	14.10	0.35	O	O
	±SD	0.42	0.17	0.50	0.11	7.78	0.35	0.17	0.67	1.77	1.05	9.97	0.25				
TONGAZI	Mean	2.30	2.75	8.14	7.23	4.00	23.10	6.88	0.87	22.50	25.14	23.30	26.39	.	.	O	O
	±SD				
SANDLUNDLU	Mean	1.95	0.83	7.65	7.56	9.50	6.35	3.49	4.26	22.00	32.26	13.30	11.83	8.20	6.81	C	C
	±SD	1.20	0.42	0.31	0.11	6.36	1.48	1.59	2.52	1.70	0.79	5.80	4.82				
MTAMVUNA	Mean	2.80	2.31	7.67	6.78	17.75	26.73	3.84	2.83	23.45	23.50	28.95	27.30	2.90	25.42	O	O
	±SD	0.77	0.92	0.23	0.53	9.60	20.88	2.55	3.11	1.52	0.69	1.89	12.65				

For example, the Tongazi Estuary was the deepest estuary sampled in 2009/10 and the mouth was recorded as open. However, the connection to the sea comprised an extremely shallow and narrow stream of accumulated water flowing out over the sandbar. In comparison, sampling of the Damba Estuary occurred soon after breaching. The mouth was similarly open and water depth within the basin was shallow (0.3m), but the channel was deeply incised across sandbar. Furthermore, estuaries that had closed relatively quickly after breaching (e.g. Umhlangankulu Estuary, $0.39\text{m} \pm 0.39\text{SD}$), were also shallow prior to the accumulation of freshwater input. Despite the variation in water depth between estuaries, there was a slightly higher frequency of deeper systems towards the south in 1998/9 while in 2009/10 there was no apparent trend (Table 3.16).

In 2009/10, the average estuary temperatures generally increased toward the south and in 1998/9, there was no trend. In 1998/9 and 2009/10, the highest recorded water temperatures were $28.30^{\circ}\text{C} (\pm 0.89\text{SD})$ and $33.64^{\circ}\text{C} (\pm 1.58\text{SD})$ in the Fafa and Mhlangeni estuaries, respectively. These peaks in temperature were likely related to the extremely shallow depth of these systems (Fafa $0.73\text{m} \pm 0.59\text{SD}$; Mhlangeni $0.35\text{m} \pm 0.26\text{SD}$) compounded by the high air temperature on the day of sampling (2009/10, pers. obs.). In contrast, the lowest recorded temperatures in 1998/9 and 2009/10 were $20.67^{\circ}\text{C} (\pm 0.35\text{SD})$ and $21.22^{\circ}\text{C} (\pm 1.03\text{SD})$ in the Mhlanga and Mhlangamkulu estuaries, respectively, which were also relatively shallow (Mhlanga $0.45\text{m} \pm 0.09\text{SD}$, Mhlangamkulu $0.65\text{m} \pm 0.52\text{SD}$).

Average estuary salinity generally increased towards the south in both sample periods, while turbidity seemed to decrease in the same direction. The highest salinities were recorded in the Mtamvuna ($28.95 \pm 1.89\text{SD}$) and in the Mbizana (35.92, single site) estuaries, in 1998/9 and 2009/10, respectively (Table 3.16). These systems, which are predominantly open, have broad mouth regions permitting strong marine exchange. The systems with the lowest salinities in each period, and thus least amount of marine exchange, were the Mdloti (1998/9, $0.10 \pm 0.00\text{SD}$) and Mzimayi (2009/10 0.13, single site) estuaries. In terms of salinity ranges, wider ranges were more prominent in the northern estuaries than in the southern systems in 1998/9, while in 2009/10 there was no apparent trend. The most turbid systems in 1998/9 and 2009/10 were the Mzimayi (94.00 NTU, single site) and Mdloti ($190.43\text{NTU} \pm 277.12\text{SD}$) estuaries, respectively. The decrease in turbidity towards the south was possibly attributed to the erosion-resistant geology of some of the southern estuaries (Whitfield and Bate 2007).

The maximum pH levels recorded in 1998/9 and 2009/10 were 8.14 (single site) in the Tongazi and (8.70 \pm 0.23SD) in the Mpambanyoni estuaries, respectively (Table 3.16). The Mdlotane Estuary maintained the lowest pH level recorded in both time periods (1998/9 6.95 \pm 0.02SD; 2009/10 6.60 \pm 0.51SD). In 1998/9, there was a gradual trend of increasing dissolved oxygen concentration with increasing latitude. However, in 2009/10 there was no apparent trend. In the former time period, the Sipingo Estuary was the most well-oxygenated system with the highest dissolved oxygen concentrations (8.13 mg/L \pm 1.64SD), while the Mdlotane Estuary was the most oxygen-poor system (0.02 mg/L \pm 0.01SD). In 2009/10, Uvuzana Estuary was the most well oxygenated system, where dissolved oxygen concentrations were at a maximum (12.45 mg/L, single site). Dissolved oxygen concentrations were lowest in the Bilanhlolo Estuary (0.84 mg/L \pm 0.97SD) (Table 3.16). Again, wide ranges of dissolved oxygen concentration indicated the existence of strong inter-site variability within estuaries.

3.4.3.2 Sediment Granulometry and Organic Content

Granulometry

The substrates of the studied estuaries were mostly composed of medium- and coarse-grained sands, with varying amounts of mud. In approximately 50% of these systems, sediment grain size composition remained relatively unchanged between 1998/9 and 2009/10 (Appendix 1.4). In estuaries where there was a noteworthy change, there was generally a shift from the dominance of coarse sand and gravel fractions in 1998/9 to a medium sand fraction in 2009/10, for example in the Mdloti, Mbokodweni, Mkumbane, Sezela, and Damba systems. In contrast, the sediment of the Mbizana Estuary had a higher percentage of coarser material in 2009/10 in comparison to that in 1998/9. In the Fafa and Mzimayi estuaries, the sediment was more evenly spread over several classes in 2009/10. In 1998/9, the sediment of the following systems comprised a high proportion of mud (>20%), the Zinkwasi, Mdlotane, Sipingo, Mtamvuna, Kaba, Umhlangankulu, and the Mvutshini estuaries. In addition to the first four systems, the sediment mud content of the Lovu, Sezela, Fafa, Mhlabatshane, Tongazi and Sandlundlu estuaries was markedly higher in 2009/10 than in 1998/9.

Organic Content

Estuaries that were identified as having sediment with high mud content similarly contained greater proportions of particulate organic matter, particularly those of 2009/10 (Figure 3.8). In 1998/9, the sediment of the Mvutshini Estuary had the highest percentage organic content

(MSH 2.32%, single site) coinciding with the highest mud content. During the same period (1998/9), the Mbokodweni Estuary had the lowest sediment organic content (MBO 0.19% \pm 0.05SD), and negligible mud fraction. It was evident that sediment organic content varied markedly between estuary sites. For example, in 1998/9, wide variations in sediment organic content was observed in the Mdlotane (MDO 1.95% \pm 1.59SD), Mhlanga (MG 1.46% \pm 1.54SD), Sezela (SZ 1.78% \pm 1.19SD), Kaba (KAB 1.24% \pm 1.11SD), Umhlangankulu (MLKB 1.58% \pm 1.35SD) and Mtamvuna (MVA 2.01% \pm 1.15SD) estuaries and in 2009/10, the Lovu Estuary (LOV 3.99% \pm 5.35SD) which had the highest percentage sediment organic content, the Mdlotane (MDO 3.09% \pm 4.03SD), Fafa (F 2.39% \pm 2.58SD), Mhlabatshane (MAN 3.55% \pm 5.57SD) and Sandlundlu (SA 3.25% \pm 3.88SD) estuaries. The organic content of the sediment in the Damba Estuary was the lowest recorded value of the estuaries in 2009/10 (D 0.03%, 0SD). Overall, these findings illustrated the extreme spatial heterogeneity of sediment organic content within estuaries in addition to observed differences between estuaries.

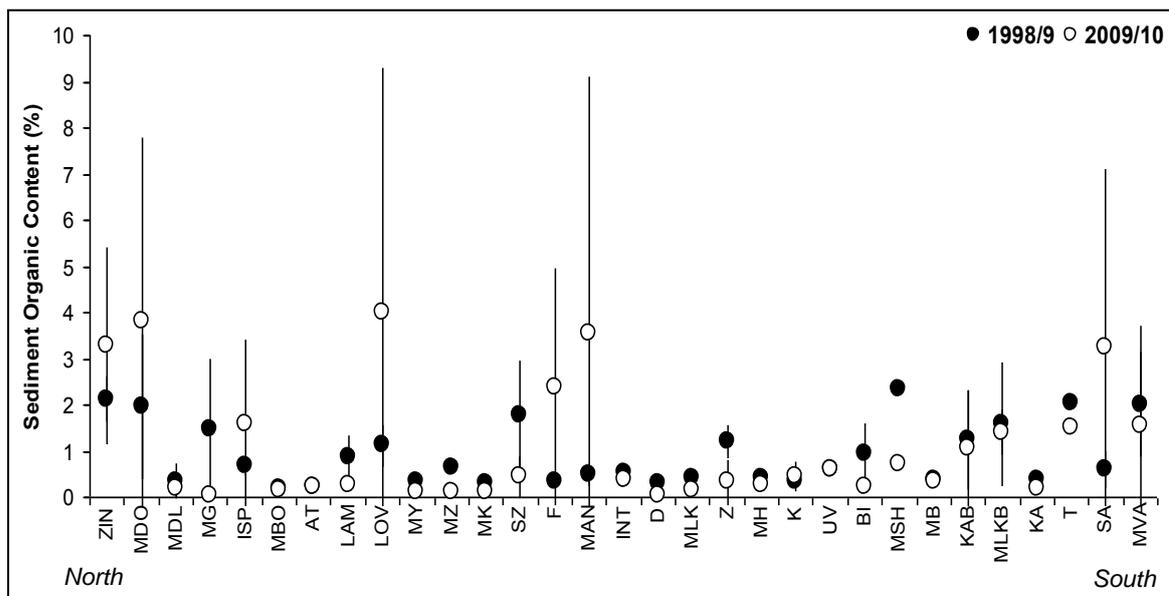


Figure 3.8 Mean sediment organic content (%) (\pm SD) for each TOCE sampled in 1998/9 and 2009/10

3.4.4 Long-term changes in KwaZulu-Natal macrozoobenthos

3.4.4.1 Comparisons between the 1998/9 and 2009/10 communities

In terms of basic community metrics, the overall macrozoobenthic abundance sampled in 2009/10 (7,819 ind.m⁻²) was significantly lower than that sampled in 1998/9 (14,246 ind.m⁻²) (Mann-Whitney U=2072, p <0.001). In contrast, there was no significant change in the overall

number of taxa (T-test $t=1.898$, $p=0.06$). Analysis of Similarity was performed on the full biotic dataset, containing estuary sites as replicates, to investigate spatial and temporal changes in the macrozoobenthic communities. Changes in community structure were manifested as differences in the types of species present, the abundance of organisms or a combination of both. Discrimination between the macrozoobenthos in 1998/9 and 2009/10 was significantly low ($R=0.062$, $p<0.001$). These results indicated that the overall macrozoobenthos of the two time periods was broadly similar. Nonetheless, the level of significance showed that certain estuaries had undergone significant changes. Two-way crossed ANOSIM revealed that the temporal differences in the macrozoobenthic communities were greater within individual estuaries of both periods than between the combined comparison of estuaries of 1998/9 and 2009/10 ($R=0.370$, $p<0.0001$).

Ordination revealed that, in terms of macrozoobenthic community structure, every estuary had undergone a degree of modification between 1998/9 (H) and 2009/10 (C) (Figure 3.9). Furthermore, the degree of change between time periods varied according to estuary. For example, the macrozoobenthos of the Damba (D), Mdlotane (MDO) and Mzimayi (MZ) estuaries underwent dramatic changes in community structure based on the placement of their historical (H) and current (C) faunal assemblages in the NMDS plot (Figure 3.9). In contrast, the macrozoobenthos of the Sezela Estuary (SZ), and to a lesser extent the Mhlangamkulu (MLK) and Mbokodweni (MBO) estuaries, remained relatively unchanged with time. Based on the degree of temporal change, the relative similarity of a particular system to other estuaries was altered, such that an estuary assigned to a specific cluster in 1998/9, for example the Mdloti and Sandlundlu estuaries (see Figure 3.4), became more similar to a different collection of estuaries in 2009/10 (see Figure 3.7).

3.4.4.2 Trends in community indices

In terms of general spatial trends across all the estuaries sampled in 1998/9, species richness and diversity increased slightly with estuaries sampled north to south, while there was no apparent trend in species evenness (Figure 3.10). During this period, species richness (Figure 3.10 A) was exceptionally high in the Lovu Estuary (LOV 32 taxa, $d=3.33$, *Very High*), and lowest in the Uvuzana (UV 4 taxa, $d=0.73$, *Very Low*).

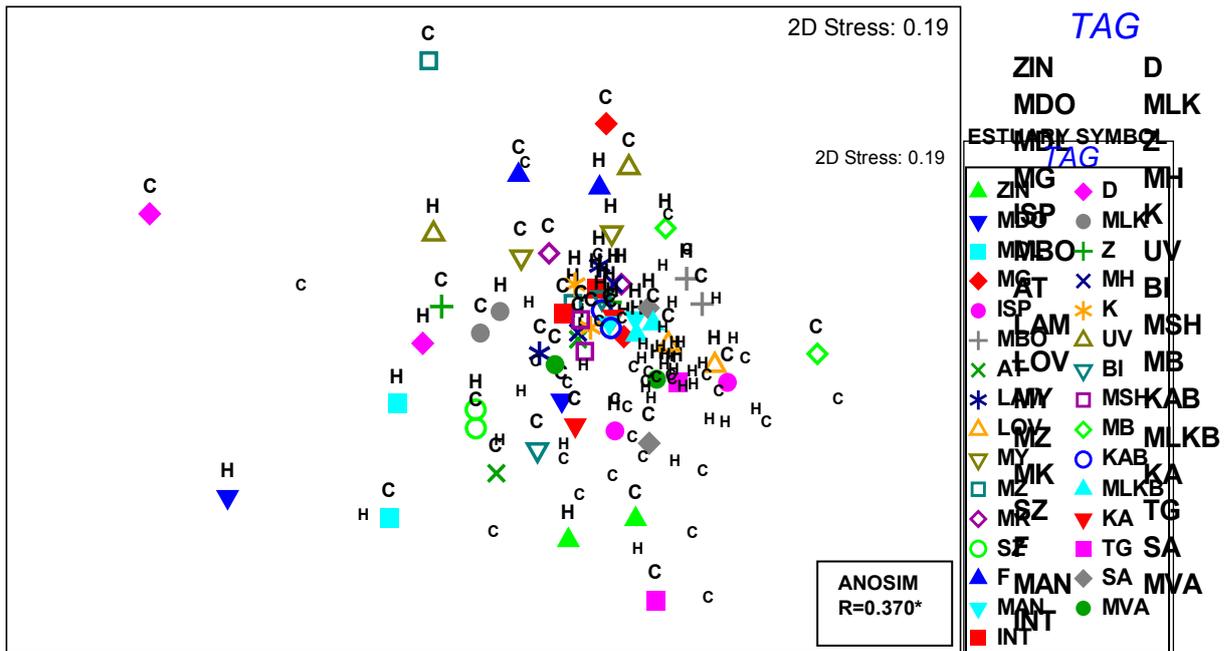


Figure 3.9 NMDS plot of macrozoobenthic communities from each estuary sampled in 1998/9 (H) and repeated in 2009/10 (C). (* $p < 0.0001$)

The macrozoobenthos of the Mlotane Estuary had the highest level of community evenness (MDO $J' = 0.88$, *Very High*) (Figure 3.10 B), while evenness was lowest in the Damba (D $J' = 0.34$, *Very Low*) and Mpambanyoni (MY $J' = 0.35$) estuaries. The Bilanhlolo Estuary supported the most diverse macrozoobenthic community (BI 20 taxa, $H' = 2.23$, *Very High*) (Figure 3.10 C), while the system immediately adjacent, the Uvuzana Estuary, supported the least diverse community (UV 8 taxa, $H' = 0.75$, *Very Low*). In 1998/9, 58% of the estuaries contained macrozoobenthic communities more diverse than the overall average diversity of communities across all estuaries ($H' = 1.5$, *Moderate-High*).

In 2009/10, diversity and evenness exhibited a general decrease with increasing latitude, while there was no apparent trend in species richness. Species richness (Figure 3.10 A) was highest in the Mtamvuna Estuary (MVA 23 taxa, $d = 2.86$, *Very High*) and lowest in the Mzimayi (MZ 4 taxa, $d = 0.42$, *Very Low*), followed closely by the Uvuzana (UV 8 taxa, $d = 0.71$, *Moderately Low*) and the Tongazi (TG 7 taxa, $d = 0.72$, *Moderately Low*) estuaries. The macrozoobenthos of the Damba Estuary had the highest level of community evenness (D $J' = 0.92$, *Very High*) (Figure 3.10 B) and the Mzimayi macrozoobenthos, the lowest (MZ $J' = 0.14$, *Very Low*). The most diverse macrozoobenthic community of 2009/10 occurred in the Sipingo Estuary (ISP 29 taxa, $H' = 2.23$, *Very High*) (Figure 3.10 C) with comparably high diversities in the Mhlangamkulu (MLK 17 taxa, $H' = 2.16$, *Very High*) and the Damba (D 10 taxa, $H' = 2.12$, *Very High*) estuaries.

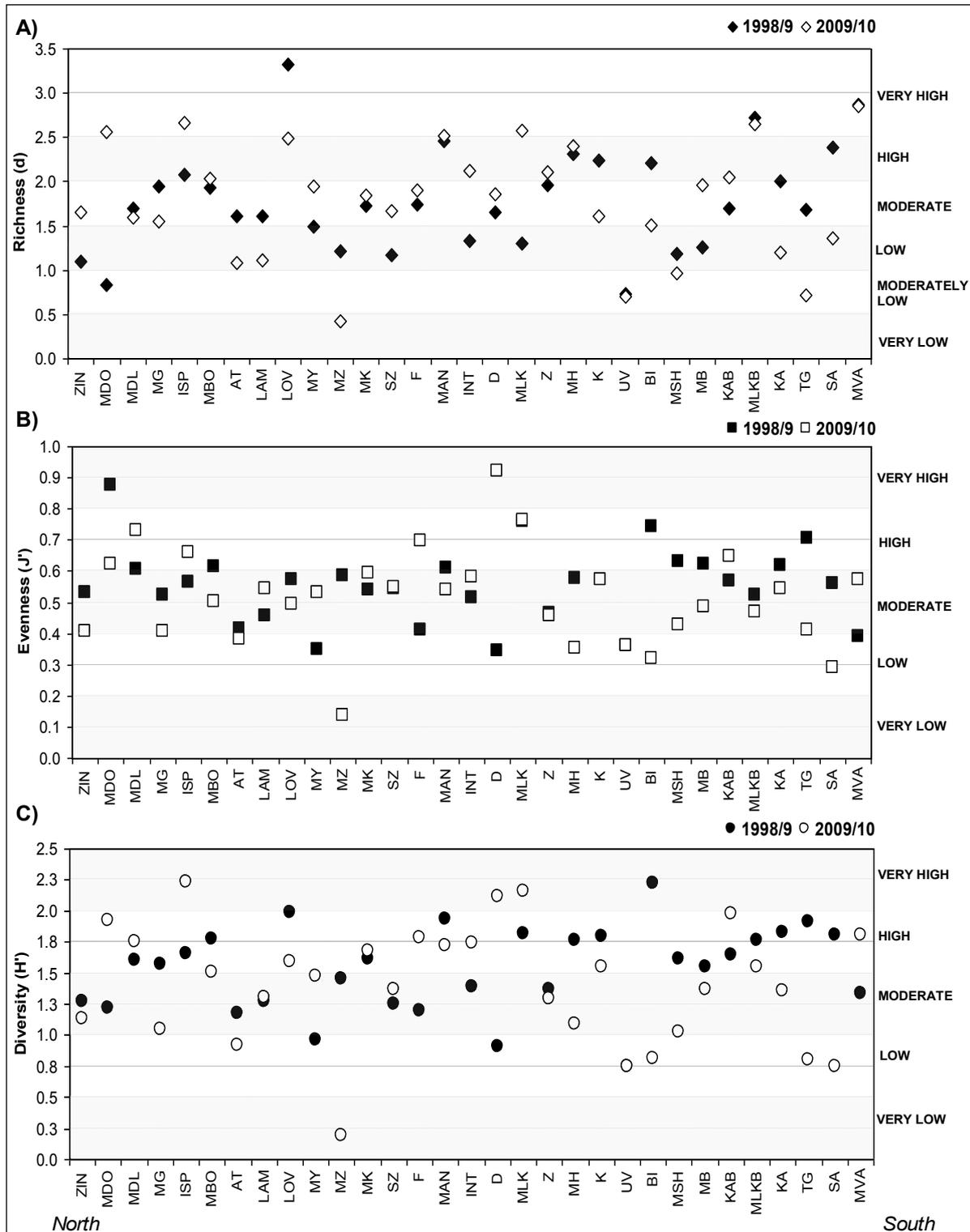


Figure 3.10 Indices of Species Richness (A), Evenness (B) and Diversity (C) calculated for each estuary in 1998/9 and 2009/10. Grades of each index are also given.

The peak in diversity in the Sipingo Estuary was attributed to the high species richness in this system, whereas high diversity in the latter estuaries was related to high community evenness. Community diversity was lowest in the Mzimayi Estuary (MZ 4 taxa, $H'=0.19$, *Very Low*).

In 2009/10, the overall average diversity across all macrozoobenthic communities was slightly lower ($H'=1.4$), however not significantly (Mann-Whitney $U=2670.5$, $p=0.189$), in comparison with 1998/9. The percentage of estuaries supporting macrozoobenthic communities more diverse than the average diversity ($H'= 1.4$, *Moderate*), across all communities had also decreased (52%). The Mhlanga and Bilanhlolo estuaries were the only estuaries that experienced significant changes in diversity over the 11-year period (Mhlanga T-test $t=3.291$, $p=0.03$; Bilanhlolo T-test $t=4.875$, $p=0.008$). The macrozoobenthos of the Bilanhlolo Estuary exhibited the greatest change in diversity from *Very High* status in 1998/9, to *Low* status in 2009/10 (BI, Figure 3.10 C). This was attributed to a decrease in both species richness and evenness, thus indicating a loss of species and the increased dominance of certain species within the community. In comparison, the decrease in diversity of the Mhlanga macrozoobenthic community was due to a decrease in evenness only (despite the increase in number of taxa), thus the decrease in diversity was less severe, from *High* in 1998/9 to *Moderate* 2009/10. This similarly indicated by the predominance of specific species that may, or may not, be new to the system. As with diversity, there was no change in overall species richness (T-test $t=0.951$, $p=0.343$), or evenness (Mann-Whitney $U=2825.0$, $p=0.443$) of the estuarine macrozoobenthos sampled in the two time periods. Changes within estuaries with a single sample site (e.g. Mzimayi, Uvuzana, Mvutshini, Tongazi and Mbizana estuaries), could not be tested for significance due to the lack of sample replication. However, it must be stated that the Mzimayi Estuary exhibited a dramatic decrease in community diversity in the 11-year period, while the community diversity in the Uvuzana Estuary remained the same.

3.4.4.3 Linking patterns in macrozoobenthos to environmental variables

The correlations between the environmental and biotic ordinations were relatively low ($P_s < 0.6$) for both the 1998/9 and 2009/10 datasets. This was expected based on the known dynamic nature of the estuarine environment and the observed high variability in macrozoobenthic communities and physico-chemical variables between estuaries. In 1998/9, the distribution of the macrozoobenthos was possibly attributed to two different combinations of environmental variables (Table 3.17). The configuration of four and seven variables both

yielded the best correlation ($P_s=0.392$) with the biological data of this time period. The best combination of four abiotic variables included depth (m), pH, fine sand (%) and sediment organic content (%). The best combination of seven abiotic variables included salinity range, dissolved oxygen (mg/L), depth(m), pH, very coarse sand (%), mud (%) and sediment organic content (%).

Table 3.17 Combinations of eight environmental variables measured in 1998/9, taken k at a time, yielding the highest correlations between the biotic and abiotic similarity matrices for each k, as measured by Spearman's Rank Correlation (P_s). **Bold** type indicates the best fitting combination.

k	P_s	Environmental Variables
1	0.267	Depth
2	0.361	Depth, pH
3	0.379	Depth, pH, %Org
4	0.392	Depth, pH, %fs, %Org
5	0.389	Depth, pH, %vcs, %fs, %Org
6	0.388	Sal R, Depth, pH, %vcs, %mud, %Org
7	0.392	Sal R, DO, Depth, pH, %vcs, %mud, %Org
8	0.387	Sal R, DO, Depth, pH, %vcs, %fs, %mud, %Org

Key:

fs = fine sand (%)

DO= Dissolved Oxygen (mg/L)

vcs = very coarse sand (%)

Sal R = Salinity Range (max-min)

Org = Organics content (%)

In 2009/10, the distribution of the macrozoobenthos was attributed to a different suite of environmental variables in comparison with the communities of 1998/9 (Table 3.18). Furthermore, the correlation between the macrozoobenthos and these particular factors was higher. The highest correlation ($P_s=0.547$) with the biotic data was shown by five variables: Turbidity (NTU), Depth (m), very coarse sand (%), medium sand (%) and fine sand (%). In addition to these variables, combinations including gravel (%) and coarse sand (%) yielded similarly high correlations ($P_s=0.546$).

Table 3.18 Combinations of eight environmental variables measured in 2009/10, taken k at a time, yielding the highest correlations between the biotic and abiotic similarity matrices for each k, as measured by Spearman's Rank Correlation (P_s). **Bold** type indicates the best fitting combination.

k	P_s	Environmental Variables
1	0.396	Turbidity
2	0.437	Turbidity, %vcs
3	0.516	Turbidity, %ms, %fs
4	0.540	Turbidity, %gvl, %ms, %fs
5	0.547	Turbidity, Depth, %vcs, %ms, %fs
6	0.546	Turbidity, Depth, %vcs, %cs, %ms, %fs
7	0.546	Turbidity, Depth, %gvl, %vcs, %cs, %ms, %fs
8	0.537	Turbidity, Depth, %gvl, %vcs, %cs, %ms, %fs, %vfs

Key:

vfs = very fine sand (%)

fs = fine sand (%)

ms = medium sand (%)

cs = coarse sand (%)

vcs = very coarse sand (%)

gvl = gravel (%)

3.5 Discussion

3.5.1 Spatial trends in macrozoobenthos in 1998/9 and 2009/10

A certain degree of spatial similarity between macrozoobenthic communities of the investigated estuaries was expected based on three assumptions: 1) that estuaries of the same type, that is TOCEs, would support similar macrozoobenthic communities; 2) that estuaries within the same biogeographic (subtropical) region would all host macrozoobenthic communities typical of the region; and 3) that climatic effects would be equally experienced across the investigated estuaries due to the localised nature of study area relative to the length of the South African coastline. In general, the macrozoobenthos was characterised by a set of persistent species found in the vast majority of the TOCEs in both study periods. These included polychaete, crustacean, molluscan and insect species typical of southern African estuaries (Day 1981c, Perissinotto et al. 2010). Common polychaete species included *Ceratonereis keiskama* (Family Nereidae), *Dendronereis arborifera* (Family Nereidae), *Desdemonia ornata* (Family Sabellidae) and *Capitella* spp. (Family Capitellidae). Although common in the current study, *Prionospio multipinnulata* (Family Spionidae) is not well known in South African estuarine waters. Common amphipod and tanaid crustacean taxa included *Grandidierella lignorum*, *G. lutosa*, *Grandidierella* spp. (Family Corophiidae), *Corophium triaenonyx* (Family Corophiidae), and the tanaid *Apseudes digitalis* (Family Apseudidae). Other less prominent species included two mollusc species, the invasive gastropod *Tarebia granifera* and the brackwater mussel *Brachidontes virgiliae*, Oligochaeta spp. and larvae of various chironomid fly species. These species are commonly found in other estuarine types along the KwaZulu-Natal coastline (Perissinotto et al. 2010), including river mouths (Forbes and Demetriades 2008, Ngqulana et al. 2010), permanently open estuaries (Forbes and Demetriades 2008) and the estuarine lakes of northern KwaZulu-Natal (Vivier and Cyrus 1999, Mackay and Cyrus 2001, Mackay et al. 2010, Miranda et al. 2010). Despite these commonalities, the key feature of the macrozoobenthos of the estuaries surveyed in both time periods was a high level of community variability between all estuaries.

In both 1998/9 and again in 2009/10, the KwaZulu-Natal TOCEs contained significantly different macrozoobenthic communities (1998/9 $R=0.458$, $p<0.0001$; 2009/10 $R=0.442$, $p<0.0001$). Thus, the null hypothesis (H_{01}), that 'in 1998/9 and 2009/10, there was no difference in macrozoobenthos between TOCEs in KwaZulu-Natal' was rejected. In addition,

the similarities between estuarine communities in each respective period were highly variable, such that certain estuaries were more similar to each other than others. Essentially, not all macrozoobenthic communities were unique in composition. Cluster analyses of 1998/9 samples revealed two main groups of estuaries and two isolated systems that were 45% similar in terms of their macrozoobenthic communities. The macrozoobenthos of the five estuaries contained in the smaller group (Cluster I) (Mhlangamkulu, Damba, Mdloti, Uvuzana and Sezela), could be classified as poor in crustacean taxa yet dominated by insect taxa (*Low Crustacea, High Insecta*). The macrozoobenthos of the 24 estuaries contained in Cluster II characteristically supported high abundances of amphipod crustaceans, particularly *Grandidierella* spp., *G. lutosa*, *G. lignorum* and *Corophium triaenonyx*, and low abundances of insects. All other invertebrate groups (Polychaeta, Oligochaeta, Mollusca, Other), which were generally common to both clusters of estuaries, were more abundant in Cluster II estuaries. Cluster II estuaries were ultimately classified as estuaries poor in insect taxa but dominated by crustacean taxa (*High Crustacea, Low Insecta*).

The Mdlotane and Zinkwasi estuaries were highly dissimilar to both Cluster I and Cluster II estuaries, because they contained markedly different macrozoobenthic communities. The Mdlotane Estuary was devoid of all Crustacea and most Polychaeta taxa (except Sabellidae juvenile T1) and the community was essentially composed of freshwater associated taxa (Chironomini larvae spp., Oligochaeta spp., Nematoda spp.). In the Zinkwasi Estuary, several species, which were common in the majority of estuaries, were absent namely Chironomini larvae spp. (Insecta), *Ceratonereis keiskama* (Polychaeta) and the amphipod species. Other species that were either absent or rare in Cluster I and II estuaries were present, including *Apeudes digitalis* (Tanaidacea), *Cyathura estuaria* (Isopoda), *Dendronereis arborifera* (Polychaeta), *Mesopodopsis africana* (Mysidacea) and *Macrura* post-larvae T1 (Decapoda). Thus, the macrozoobenthic community of the Zinkwasi Estuary was set apart from the communities of Cluster I and Cluster II estuaries.

In 2009/10, the macrozoobenthos of the investigated estuaries were less similar in comparison with 1998/9, indicated by the lower level of similarity (35%) between the three groups of estuaries, and again two individual systems. The separation of these clusters was largely attributed to specific taxa rather than broad taxonomic groups. The macrozoobenthos of the three estuaries of Cluster I (Sandlundlu, Tongazi and Mbizana estuaries) was typified by high

abundances of the polychaete taxa, *Capitella* spp. and *Prionospio multipinnulata*, and the negligible occurrence and absence of the normally highly abundant amphipod Crustacea species and Chironomini larvae spp., respectively. The communities were thus classified as *Capitella – Prionospio multipinnulata* communities. The macrozoobenthic communities of the Manzimtoti and Mdloti estuaries (Cluster II) were classified as *Tarebia granifera – Sabellidae* JuvT1 – Oligochaeta spp. communities because these three taxa were most abundant in these two estuaries in all pair-wise comparisons between clusters of estuaries. In addition, these communities similarly possessed a negligible Crustacea component but were rich in Insecta larvae. They were thus markedly different from other systems. The remaining 26 estuaries (Cluster III) characteristically supported high abundances of Crustacea, particularly the amphipod species *Grandidierella* spp., *G. lignorum*, *G. lutosa* and *Corophium triaenonyx* (which were rare/absent in estuaries of Cluster I and II), and Polychaeta, especially *Ceratonereis keiskama* and *Desdemona ornata*. Therefore, the estuaries of Cluster III were classified as *Grandidierella* species – *Corophium triaenonyx* – *Ceratonereis keiskama* – *Desdemona ornata* communities.

In contrast, the Mzimayi and Damba estuaries supported markedly different communities from all estuaries in 2009/10. The macrozoobenthos of the Damba Estuary was dominated by freshwater associated taxa, particularly insect fly larvae, and Polychaeta, Oligochaeta and Crustacea were essentially absent. Furthermore, most of the taxa present occurred exclusively in this system. In comparison, the community of the Mzimayi Estuary comprised three species that were common in most estuaries, *C. keiskama* (Polychaeta), *G. lutosa*, and Chironomini larvae. Thus, the Mzimayi Estuary was more similar than the Damba Estuary to all other estuaries. Nonetheless, all other common Polychaeta, Crustacea and Oligochaeta species were absent from the Mzimayi Estuary, therefore representing a unique macrozoobenthic community.

In 1998/9, there was a significant difference between the macrozoobenthos of the northern most estuaries and other more southern estuaries, while in 2009/10 there was no apparent relationship. The estuaries within this block (LAT 1) (the Zinkwasi and Mdlotane estuaries) each possessed communities different from several estuaries in two higher latitude blocks (LAT 5 and LAT 7) and they constituted the two isolated systems identified through cluster analyses. It was noted that these were the only two pair-wise comparisons relating to latitude that yielded

significant R statistics. More specifically, there were no significant differences in terms of community characteristics between the estuaries of other latitude blocks. These two estuaries also showed negligible similarity (92% dissimilar), suggesting that the correlation was attributed to their combined dissimilarity to other estuaries in different latitudinal blocks, rather than possessing macrozoobenthic communities characterising the northern (more tropical) extent of the study region. Thus, the correlation was considered spurious. Therefore, the null hypothesis (H_{02}), that 'there is no linear north-to-south gradation in macrozoobenthic communities of TOCEs along the KwaZulu-Natal coast', was rejected for both sample periods. There are two possible explanations for the absence of a southward change in macrozoobenthic community structure, namely, 1) that critical species from adjacent biogeographic regions (tropical/warm temperate) were poorly represented because of the central position of the study area away from the biogeographical extremes of the subtropical region, resulting in a specific suite of benthic invertebrates that was common to most TOCEs, or 2) the influence of intrinsic estuary characteristics, such as physico-chemical and sediment characteristics, depth, mouth state, was greater than the biogeographic position of the estuary as suggested by Day (1964).

The correlation between the macrozoobenthic communities and various other factors was significantly low for attributes of estuary size, shared drainage regions and the EHI (historical data only). The low R statistics produced during Analysis of Similarity (ANOSIM) suggested high levels of variability between estuaries within the categories of each attribute, such that the categories could not be used to describe the pattern of distribution of the macrozoobenthos. The most important deduction made from the results of ANOSIM was that the similarity between macrozoobenthic communities could not be assumed based on common estuary morphometric characteristics (estuary area, estuary length, catchment area) nor shared drainage regions. Furthermore, there was no difference in the macrozoobenthic communities between estuaries with Very Poor and Very Good EHI values, thus the characteristics of estuarine macrozoobenthos did not coincide with the composite health evaluation of the KwaZulu-Natal estuaries provided by Cooper et al. (1993) and Harrison et al. (2000).

In addition, the correlation between the macrozoobenthic communities and the environmental variables that were measured was relatively poor in both time periods (1998/9 $P_s = 0.392$, 2009/10 $P_s = 0.547$). It was thought that different environmental variables were

important for separating different groups of estuaries. In 1998/9, there were two sets of environmental parameters most likely responsible for the distribution of the macrozoobenthos among the TOCEs. Depth, pH, and percentage fine sand and organic content of the sediment were included in the first set. In the second set were salinity range, dissolved oxygen concentration, depth, pH, and percentage very coarse sand, mud and sediment organic content. Based on the natural high variability of TOCEs, it was expected that a greater number of environmental variables was likely to influence the macrozoobenthos. Overall, these eight variables encompass the natural functioning of a TOCE and hence the environmental conditions typically experienced by macrozoobenthic communities residing in this type of estuary. Salinity range, depth and dissolved oxygen concentrations are dependent on the state of the estuary mouth and the duration of closure (Day 1981b, Whitfield and Bate 2007, Whitfield et al. 2008, Perissinotto et al. 2010). Similarly, pH of the water column is influenced by the degree of mixing between freshwater (the pH of which is dependent on catchment characteristics) and seawater, which in turn is determined by the state of the mouth (McLusky and Elliott 2004, Whitfield and Bate 2007). The sediment at the head of an estuary is generally composed of soft mud or very coarse sand, depending on the gradient of fluvial inflow (Day 1981c). From the middle reaches into the lower reaches, the sediment comprises variable proportions of sand and mud depending on flow velocities, while the sediment at the mouth is generally composed of clean coarse beach/marine sand (Day 1981c, McLusky and Elliott 2004, Perissinotto et al. 2010). High sediment organic content is associated with fine-grained sediment, specifically mud, which is deposited in calm, slow flowing estuarine environments (McLusky and Elliott 2004). Low flow conditions contribute significantly to the closure of TOCEs (Whitfield and Bate 2007), allowing for the development of calm water environments, within which deposition and accumulation of particulate organic matter occurs, thus providing a rich food source for macrozoobenthic communities.

In 2009/10, the following five environmental parameters influenced the distribution of the macrozoobenthos, depth, turbidity, and percentage very coarse sand, medium sand and fine sand. This suite of variables was somewhat different from those in 1998/9 and the correlation with the biological data was higher. It could be argued that these variables were reflective of the predominantly open state of most of the estuaries (55%) sampled in 2009/10. In comparison, most of the estuaries (65%) in 1998/9 were closed. High flow velocities, such as those experienced during breached conditions and/or flood events, result in increased

turbidities from the turbulent mixing of resuspended particulate matter, particularly fine sediment (Day 1981d, Schumann et al. 1999, McLusky and Elliott 2004, Whitfield and Bate 2007). During these conditions, depth of a particular TOCE is shallower than during the closed state and sediment becomes coarser, because finer sediment, including particulate organic matter, is flushed from the system. As scouring velocities subside, fine-grained sediment is once again deposited.

Distribution of the macrozoobenthos was therefore associated with a multitude of environmental factors, which appeared reflective of the dynamic conditions determined by the state of the mouth. These findings are typical of estuarine macrozoobenthos (Day 1981c, De Villiers et al. 1999, Burse and Wooldridge 2003, McLusky and Elliott 2004) and are proof of the adaptability of these fauna to the highly variable nature of TOCEs. The relatively low correlations between the biological and environmental data suggest the possible influence of variables not recorded in this study, for example nutrient concentrations (phosphates and nitrates) and heavy metal contaminants. These factors would have an effect on the macrozoobenthic communities because many of these estuaries are likely impacted by the dense urban development along their shores and in the catchment areas (Cao et al. 1996, Ardisson and Bourget 1997, Austen and McEvoy 1997, Dauer et al. 2000, Inglis and Kross 2000, Savage et al. 2002, Bilkovic et al. 2006, Forbes and Demetriades 2008).

3.5.2 Temporal trends in macrozoobenthos between 1998/9 and 2009/10

Long-term temporal investigations revealed that there was an overall decrease in the abundance of organisms collected in 2009/10 in comparison with 1998/9, while there was no significant change in the overall number of taxa nor diversity. A change in the global macrozoobenthos between the two time periods, albeit minimal, was also evident ($R= 0.062$, $p<0.001$). Thus, the null hypothesis (H_{03}) that, 'there is no difference between the macrozoobenthic communities of KwaZulu-Natal TOCEs sampled in 1998/9 and in 2009/10' was rejected. The very low R value indicated that the similarity between estuaries within either time period was lower than the average similarity of all estuaries in both periods combined. This denoted a high degree of sample variability (Clarke and Warwick 2001). Close study at the individual estuary level revealed that temporal changes were more pronounced within an estuary than between the combined comparison of estuaries of 1998/9 and 2009/10. This was

indicated by higher R statistics produced from the interaction between 'estuary' and 'time' ($R=0.370$; $p<0.0001$) than that of 'time' alone ($R= 0.062$, $p<0.001$). It was observed that the magnitude of change that took place in the macrozoobenthos within each estuary was estuary-dependent. Several estuaries, such as the Damba, Mdlotane, and Mzimayi, underwent dramatic changes in community structure in contrast to others, such as the Sezela, Mhlangamkulu and Mbokodweni estuaries, which remained relatively unchanged. These changes did not alter the overall macrozoobenthic diversity of these systems. The only two estuaries that exhibited significant reductions in diversity between the two time periods were the Bilanhlolo and the Mhlanga estuaries. In 1998/9, the former system was dominated by crustacean amphipods, namely *Corophium triaenonyx* and *Grandidierella* spp., and Nematoda spp., which contributed 25%, 17% and 16% to the overall faunal abundance, respectively. However, in 2009/10 the polychaete worm, *Prionospio multipinnulata* was the dominant species, contributing 80% to the overall faunal abundance. The decrease in faunal abundance was not significant, thus, the lowered diversity in the Bilanhlolo Estuary was attributed to the increased dominance of a few species, specifically *P. multipinnulata*. In the Mhlanga Estuary in 1998/9, the macrozoobenthic community was characterised by high abundances of *P. multipinnulata* (48% of overall faunal abundance), *D. ornata* (12%) and *Grandidierella* spp. (25%). However, in 2009/10, the polychaete *Ceratonereis keiskama* was the dominant species, contributing 73% to the overall faunal abundance, followed by the next most abundant taxa, the amphipod *Grandidierella* spp. (10%) and gastropod *Tarebia granifera* (9%). As with the Bilanhlolo Estuary, there was no significant decrease in the overall faunal abundance between the years and therefore decreased diversity was also due to the overwhelming abundance of a few species, namely *C. keiskama*.

In conclusion, this study has shown that long-term changes in macrozoobenthos at this regional scale were less apparent when estuaries were collectively assessed. Thus, to ascertain whether macrozoobenthic communities have changed over a period of time, estuaries must be investigated at the individual system level. These findings are in agreement with those of Edgar and Barret (2002) and Hirst and Kilpatrick (2007) who found that overall variation among macrozoobenthic invertebrates was best explained according to spatial variation between estuaries, in comparison to temporal variation. In the current study, it was illustrated that, although many species present in the macrozoobenthos in 1998/9 were still present in 2009/10, the communities of all the selected TOCEs had undergone a degree of change (in

composition, abundance and/or diversity) in the last decade, such that no community remained in its former state of 1998/9. However, this was largely a function of the 'snapshot' nature of this investigation, compounded by sampling conducted during different mouth states. Once-off sampling strategies, and short-term monitoring programmes, do not cover the natural temporal variation of the temporarily open/closed estuarine environment, such as changes related to the open/closed state of the mouth, seasonal variations and fluctuations in available habitat (Jones 1990, Turpie et al. 2002). These factors are known to critically influence the structure of macrozoobenthic communities as well as other biota. More specifically, the mouth state (and duration of the state) is a key driver of physico-chemical conditions and ecological processes in TOCEs (De Villiers et al. 1999, Whitfield and Bate 2007, Whitfield et al. 2008, Perissinotto et al. 2010, de Juan and Hewitt 2011). In the current study, the sampling of the 31 selected estuaries did not provide for the replication of mouth state and the correlated environmental conditions. That is, in 1998/9, 65% of the estuaries were closed in comparison with 45% in 2009/10. It is likely that this factor contributed to the significant difference (in terms of abundance and composition) in the macrozoobenthos of estuaries collectively assessed, as well as within a single estuary, between the two surveys by virtue of the prevailing differential conditions. Therefore, the quantitative and qualitative future reassessment of the macrozoobenthos of South African estuaries should be performed 1) taking into account the state of the estuary mouth, in conjunction with seasonality; and 2) at intervals shorter than a decadal period because changes in the estuarine environment (for example aesthetics, water quality and function) are taking place at different rates and magnitudes in individual systems than all estuaries simultaneously.

It was also illustrated that the composition of the macrozoobenthos of (selected) KwaZulu-Natal TOCEs was not entirely uniform. That is to say, these estuaries supported distinguishable macrozoobenthic communities. Notwithstanding, there was a degree of similarity among most estuaries because they supported the same, highly abundant macrozoobenthic species, many of which are endemic to South Africa. However, certain estuaries having different macrozoobenthic communities were identified by means of unique species assemblages and/or the overwhelming dominance of specific species. The similarity of KwaZulu-Natal TOCEs based on their macrozoobenthic communities was not attributed to a single abiotic/biotic feature of the respective systems, particularly in respect to geographic location, estuary size, drainage region and the EHI. The absence of a relationship between the macrozoobenthos of

these estuaries and their calculated EHI value suggested that estuarine 'health' as measured from fish communities may be very different from estuarine 'health' measured by macrozoobenthic communities. Overall, the composition of the macrozoobenthos was attributed to the complex interplay between a multitude of factors, both biotic and abiotic, and possibly factors that were not measured, such as water nutrient levels and contaminants.

High intra-estuarine variability was evident in the number of taxa and faunal abundance. This was attributed to marked habitat heterogeneity, in terms of changes in physico-chemical and sediment characteristics that typically occur along the length of an estuary, leading to the patchy distribution of organisms (Day 1981c, McLusky and Elliott 2004). These findings illustrated the importance of habitat heterogeneity in determining macrozoobenthic community structure. Furthermore, community metrics were over/under-represented in estuaries with dramatically different habitat types through the calculation of average values per estuary. For example, the Sipingo Estuary with 'river' and 'embayment' habitats (pers. obs.). Thus, examination of spatial variation within estuaries exposes an important source of variability among macrozoobenthic communities, which may mask broad scale comparisons between estuaries (Morrisey et al. 1992a, Hirst and Kilpatrick 2007, de Juan and Hewitt 2011). Thus, for the purposes of monitoring medium to long-term changes in the macrozoobenthic communities that reside in KwaZulu-Natal TOCEs (and TOCEs throughout South Africa), surveys of these estuaries should be conducted at intervals shorter than a decade, possibly every two to three years with samples representative of the wet and dry seasons within the same year. For comprehensive ecological determinations, the ideal sampling frequency required for estuarine invertebrates is four times a year (i.e. seasonally) for two years (DWA 2010), however this would be exhaustive and extremely costly for national and provincial assessments. Key habitats for macrozoobenthic organisms as well as the open/closed state of the mouth should also be accounted for (DWA 2010). The knowledge gained through such surveys would further accentuate the position of macrozoobenthos as an integral component of the South African estuarine environment.

CHAPTER 4

SHORT-TERM RESPONSE OF COMMUNITIES TO ENVIRONMENTAL DISTURBANCE

4.1 Rationale

During June 2008, the KwaZulu-Natal south coast experienced an abnormally high rainfall event lasting two days that resulted in severe flooding of numerous estuaries. Within the first 24 hours, heavy falls in several south coast towns broke historical rainfall records, the greatest being Paddock, which received 382 mm of rain compared with the 44 year old (1964) record of 337 mm (WeatherSA 2008). Given the extensive damage to coastal infrastructure and the physical changes that occurred in several rivers and estuaries (Figure 4.1), this chapter tracks the recovery of four small, flood affected systems through the recolonisation of the macrozoobenthos. The macrozoobenthic communities of the Manzimtoti, Little Manzimtoti, Intshambili and Mhlabatshane estuaries were studied in terms of the differences in post-flood recolonisation patterns in their respective urban and non-urban environmental settings.

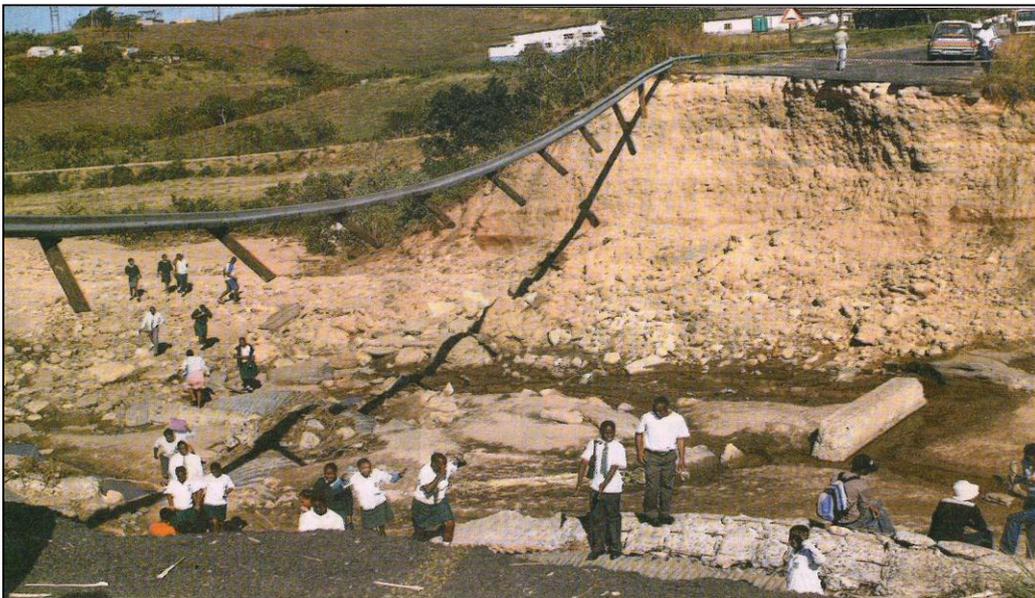


Figure 4.1 An example of the severe damage to coastal roads and bridges caused by swollen rivers and flooding on the KwaZulu-Natal South Coast in June 2008. (Taken from *The Mercury*, 27 June 2008. Photograph of the Umzinto River by Zanele Zulu)

4.2 Introduction

4.2.1 Flooding as an ecological disturbance in KwaZulu-Natal estuaries

Environmental perturbations (or disturbances) are important events that influence the spatial and temporal heterogeneity of estuarine macrozoobenthic communities (Zajac and Whitlatch 1982a, Sousa 1984, Ford et al. 1999, Van Colen et al. 2010). The definition of a disturbance used in this chapter is that given by (Zajac and Whitlatch 1982a) as “*any stochastic event initiating species populational change either from density-independent mortality and/or a change in the resources base of the community*”. Environmental disturbances may take the form of natural disasters, such as flooding (McLachlan and Grindley 1974, Stephenson et al. 1977, Moverley et al. 1986, Hanekom 1989, Salen-Picard et al. 2003, Eyre and Ferguson 2006, Cardoso et al. 2008, Rader et al. 2008) and drought periods (Jones 1990, Attrill et al. 1996, Hastie and Smith 2006), or be anthropogenically-induced, such as eutrophication and pollution (Pearson and Rosenberg 1978, Hall and Frid 1995, Schratzberger et al. 2003, Kotta et al. 2007), oxygen depletion (Santos and Simon 1980, Breitbart et al. 1997, Nilsson and Rosenberg 2000, Lardicci et al. 2001), habitat modifications (Goodsell et al. 2007, Neto et al. 2010), and dredging (Rosenberg 1977, Jones 1986, Bemvenuti et al. 2005). In the estuarine benthic environment, such events may create opportunities for the recolonisation of defaunated soft-sediment by various assemblages of invertebrate species (Thistle 1981, Ritter et al. 2005). It is both the nature of the disturbance, in terms of intensity, duration, extent, and frequency, and the compositions of the ambient and invading faunal populations, that determine the community response, patterns of recolonisation and ultimately the organisation of the resultant community (Zajac and Whitlatch 1982a, Sousa 1984, Thrush and Whitlatch 2001, Mistri 2002, Ritter et al. 2005, Cardoso et al. 2008). Disturbances are thus key drivers of community and ecosystem change (Pearson and Rosenberg 1978, Thistle 1981, Zajac and Whitlatch 1982a, 1982b, Sousa 1984, Thrush and Whitlatch 2001, Cardoso et al. 2008).

In South African estuaries, flooding is a major disturbance that influences the structure and functioning of macrozoobenthic communities (De Villiers et al. 1999). Flooding is particularly common in TOCEs on the eastern coast as a result of the rugged topography and the uneven distribution of precipitation across the country, which often occurs as intense episodic rainfall events (De Villiers et al. 1999, Harrison 2004). KwaZulu-Natal estuaries have had a history of extreme, large-scale flooding events (1:~25years, Perry 1989) during which, road and rail

bridges, buildings and holiday resorts on the adjacent floodplains were swept away and the morphology of many estuarine systems was modified as a result of changes to the configuration of the mouth (Begg 1978, Branch and Branch 1985, Perry 1989, Alexander 2002). The immediate and direct effect of floods on estuarine macrozoobenthos is particularly destructive because unconsolidated sediments and available food sources, together with resident benthic invertebrates, are scoured from the system by strong flood currents (Zajac and Whitlatch 1982a, Zajac et al. 1998). New populations must then be seeded from the few surviving organisms or from populations of neighbouring less-affected estuarine systems when favourable conditions are re-established (Thrush and Whitlatch 2001).

4.2.2 Effects of flooding on the benthic physico-chemical environment

Flooding in the estuarine environment affects principal environmental factors that influence both the abundance and distribution of benthic macroinvertebrates. Increased freshwater input and high flow rates alter the estuarine hydrodynamics, which in turn alters salinity regimes, sediment composition and organic content (food supply), turbidity, and dissolved oxygen (Gray 1981, Day 1981c, Zajac et al. 1998, De Villiers et al. 1999, Harrison 2004, McLusky and Elliott 2004). Salinity is one of the primary factors controlling the spatial heterogeneity of estuarine macrozoobenthos (Perkins 1974, Day 1981c, De Villiers et al. 1999, McLusky and Elliott 2004). Thus, drastic reductions in saline concentrations due to increased freshwater input during a flood event will have a critical effect on the emergent macrozoobenthic community (McLachlan and Grindley 1974, Stephenson et al. 1977, Moverley et al. 1986, Hanekom 1989, De Villiers et al. 1999, Ritter et al. 2005, Dolbeth et al. 2007). Furthermore, the predominance of freshwater conditions for extended periods of time after flooding may exceed the physiological capacity of several estuarine species, resulting in reduced populations (De Villiers et al. 1999), while conversely extending the ranges of freshwater species (Whitfield 1992). In contrast, previously closed estuaries (TOCEs) that have developed fresh or brackish water conditions may become reconnected to the sea and may remain open for some time, during which uncommonly high salinities may prevail. In extreme circumstances, large scale flood events have been shown to induce stratification of the water column as a result of strong density differences between saline water and freshwater masses (Boesch et al. 1976a). This in turn induced low oxygen conditions in bottom water, adversely affecting the survival of deep benthic communities (Boesch et al. 1976a). To a lesser degree, flooding may lower water

temperatures of warm, shallow estuarine systems, such as those along the subtropical KwaZulu-Natal coastline, because the temperature of the estuarine environment is influenced by both fluvial freshwater and marine inputs (De Villiers et al. 1999). Therefore, the ability of estuarine macrozoobenthic communities to withstand dramatic changes in environmental conditions generated by flood events is limited by the differential physiological and behavioural adaptations of the individual species (Forbes 1974, Day 1981c, De Villiers and Allanson 1989, Hanekom 1989, Webb et al. 1997, Owen and Forbes 2002).

The nature of the sediment is another factor contributing significantly to the distribution and abundance of benthic invertebrates in estuaries (Perkins 1974, De Villiers et al. 1999, Teske and Wooldridge 2003, McLusky and Elliott 2004, Perissinotto et al. 2010). Post-flood sediment composition has a direct effect on the re-establishment of benthic communities because different species exhibit specific habitat preferences with regards to sediment type and organic content (Gray 1981, Probert 1984, Moverley et al. 1986, Zajac et al. 1998, Herman et al. 1999). During flooding, high flow velocities scour away fine sediment particles leaving behind coarser material, while subsiding floodwater enables the settlement and accumulation of finer fractions including mud and particulate organic matter. Since sediment of high mud content is more stable and provides a greater source of food material (Gray 1981, Sakamaki and Nishimura 2009), highly turbid waters and excessive deposition of fine material are known to negatively impact benthic communities through the smothering of fauna, clogging of their feeding apparatus, induction of low oxygen conditions and generation of toxic by-products through decomposition of the organic matter (Pearson and Rosenberg 1978, Gray 1981, De Villiers et al. 1999, Norkko et al. 2002, Lohrer et al. 2004, Sakamaki and Nishimura 2009). Ultimately, flow-mediated patterns in substrate composition and food resources govern the spatial heterogeneity and structure of estuarine macrozoobenthic communities (Day 1981c, Moverley et al. 1986, Herman et al. 1999, Riisgard and Kamermans 2001, Connolly et al. 2005, Sakamaki and Nishimura 2009). The availability of food material is critical during the post-flood recolonisation process for the survival of both larval recruits and adult colonists (Grassle and Grassle 1974, Thistle 1981, Zajac and Whitlatch 1982a, 1982b, Moverley et al. 1986).

4.2.3 Post-flood response and recolonisation of macrozoobenthic communities

The potential for successful recolonisation of estuarine sediments following a flood event is dependent on the responses of the fauna to changes in biological factors relating to the species themselves, such as larval supply and interspecific competition, in addition to changes in the physico-chemical environment (Sousa 1984, Zajac et al. 1998, Thrush and Whitlatch 2001, McLusky and Elliott 2004). The post-flood recolonisation of macrozoobenthos is governed by the supply and species composition of potential colonists, and their life history traits (Zajac and Whitlatch 1982a). The composition of both larval and adult colonisers is generally a reflection of the ambient community and they are transported over varying distances by the prevailing hydrodynamic conditions until they reach an area suitable for re-establishment (Zajac et al. 1998, Thrush and Whitlatch 2001). Recruitment is typically prompted by various environmental cues, including biological, chemical and physical conditions (Woodin et al. 1995, Turner et al. 1997, Zajac et al. 1998, Thrush and Whitlatch 2001). Successful recruitment and post-settlement community dynamics are subsequently affected by various species interactions, which in turn will determine the structure of the emerging benthic community (Connell and Slatyer 1977, Pearson and Rosenberg 1978, Wilson 1991, Thrush and Whitlatch 2001, McLusky and Elliott 2004, Van Colen et al. 2010).

The recolonisation and successional changes of soft-sediment infaunal communities following environmental disturbance have been extensively studied (Grassle and Grassle 1974, Connell and Slatyer 1977, Pearson and Rosenberg 1978, Santos and Simon 1980, Arntz and Rumohr 1982, Moverley et al. 1986, Zajac et al. 1998, Lu and Wu 2000, Nilsson and Rosenberg 2000, Ritter et al. 2005). Several small-scale studies based on the recolonisation of (experimentally) defaunated sediment placed in the natural environment concluded that infaunal recovery was rapid (hours to ~2 months) and the experimental community matched the ambient community at the end of recovery (Grassle and Grassle 1974, McCall 1977, Thistle 1981, Zajac and Whitlatch 1982a, 1982b, Bell and Delvin 1983, Hall and Frid 1998, Ford et al. 1999). These studies investigated mechanisms of recolonisation, the seasonal and tidal effects on recolonisation, species-environmental relationships and/or successional stages during the recovery process.

Large-scale studies evaluating the effects of flood events on macrozoobenthos typically involved assessments of long-term community changes in relation to fluxes in environmental conditions (McLachlan and Grindley 1974, Boesch et al. 1976a, Stephenson et al. 1977, Moverley et al. 1986, Hanekom 1989, Owen and Forbes 1997, Salen-Picard and Arlhac 2002, Salen-Picard et al. 2003, Robinson et al. 2004, Chollett and Bone 2007, Cardoso et al. 2008, Rader et al. 2008, Grilo et al. 2011). In contrast to short-term studies, the dynamics of such interactions were spatially and temporally complex, the duration of recovery spanned months to several years, and the resultant benthic community was often markedly different in comparison with the pre-disturbance community. Nonetheless, all studies shared one key conclusion, that the response of macrozoobenthic communities to disturbance was both species- and habitat-dependent. This response was mediated by the scale and intensity of the disturbance, and this in turn governed the duration of the recovery period and the pattern of succession.

Recovery from one environmental disturbance may be disrupted by another, and the entire successional process may be either reset or held static at a specific stage (Sousa 1984, Ritter et al. 2005). Ritter et al. (2005) explain that environments with frequent disturbances, for example reoccurring sewage inputs or heavy rainfall events typical of KwaZulu-Natal estuaries, will support benthic invertebrate communities in an intermediate stage of succession. If the sediment is not completely defaunated by the disturbance, colonisation may continue via several mechanisms, including: 1) settlement of larvae, 2) bedload transport of non-planktonic larvae, post-larvae and adults, 3) burrowing, and 4) post larval swimming, and various combinations of these mechanisms (Shull 1997, Lundquist et al. 2004, Ritter et al. 2005). These mechanisms vary between species, within species between different life stages, and with environmental conditions (Shull 1997, Thrush and Whitlatch 2001). These factors, as determined by the nature of the disturbance (Probert 1984, Sousa 1984), further contribute to the complexity of recolonisation of estuarine sediments.

Another factor that is likely to affect the recolonisation and recovery of estuarine macrozoobenthos following flood disturbance, is the urbanisation of the estuarine environment (Dolbeth et al. 2007, Cardoso et al. 2008, Rader et al. 2008). Estuaries have been extensively modified by human interference as a result of escalating urbanisation. In South Africa, many estuaries particularly along the KwaZulu-Natal coastline, are highly degraded and

in poor ecological condition due to the unprecedented increase in urban development and associated activities along this stretch of coast (Begg 1978, Morant and Quinn 1999, Harrison 2004, Turpie 2004). Such disturbances include the destruction of riparian vegetation, land reclamation, hardening of natural surfaces, coastal development and infrastructure, disruption of the natural hydrological processes by upstream impoundments and water abstraction, and severe deterioration of sediment and water quality by urban contaminants (Day and Grindley 1981f, Schumann et al. 1999, Dauer et al. 2000, Inglis and Kross 2000, Lindegarth and Hoskin 2001, Turpie et al. 2002, Hale et al. 2004, McLusky and Elliott 2004, Findlay and Taylor 2006). For macrozoobenthos, such disturbances are manifested in extreme habitat changes and variations in food availability, which influence community distribution, species diversity and recovery patterns (Pedersen and Perkins 1986, Cardoso et al. 2008). Furthermore, the simultaneous exposure of benthic invertebrates to natural perturbations and the multitude of frequent urban disturbances is likely to lower their resilience and resistance to future perturbations, with consequences for ecosystem integrity and sustained functioning (Dolbeth et al. 2007, Cardoso et al. 2008). The abovementioned anthropogenic disturbances also contribute significantly to increased flood severity within urbanised areas and their adjacent rivers and estuaries (Paul and Meyer 2001, Findlay and Taylor 2006, Douglas et al. 2008, Kenwick et al. 2009). Therefore, macrozoobenthic communities of urban estuaries are likely to be more impacted by a variety of disturbances, which are different to those experienced by macrozoobenthic communities in non-urbanised estuaries (Pedersen and Perkins 1986, Morrisey et al. 2003, Pagliosa and Barbosa 2006). This ultimately affects the patterns of recolonisation and succession, and overall success of community re-establishment.

4.2.4 Aim and Hypotheses

The aim of this chapter was to determine the response of macrozoobenthic communities in two urban and two non-urban TOCEs to short-term flood disturbance. It was assumed that the climatic conditions that led to flooding were uniform over the short stretch of coastline, such that the effects of flooding were equally felt across the four selected estuaries. Furthermore, it was assumed that complete defaunation of the estuarine sediments by flood currents did not take place and that recolonisation was initiated by species that had survived within each system. Four null hypotheses (H_0) were tested, and are outlined as follows:

Under the premise that urban estuaries are theoretically more disturbed than non-urban estuaries and that the observed community response could be a product of this condition, adjacent systems within the same environmental setting (urban or non-urban) were first tested for similarities in community characteristics to determine whether the post-flood response was universal.

H₀₁) Within urban and non-urban environmental settings, there was no difference in the response of macrozoobenthic communities of adjacent TOCEs to short-term flood disturbance.

The testing of either of the following two null hypotheses was dependent on the outcome of H₀₁. If the macrozoobenthos of adjacent TOCEs were highly similar (H₀₁ accepted), the respective communities could be legitimately classed as 'urban' and 'non urban', and the difference between these could then be tested under the following null hypothesis,

H₀₂) There was no difference between the response of macrozoobenthos in urban TOCEs and the response of macrozoobenthos in non-urban TOCEs to short-term flood disturbance.

Conversely, if there was a marked difference between adjacent estuaries, and the urban/non-urban classification proved redundant, it was then hypothesised that the response of the macrozoobenthos of each of the four TOCEs would be significantly different despite belonging to the same estuarine type,

H₀₃) There was no difference between the responses of macrozoobenthos to flood disturbance in each of the four TOCEs.

Lastly, stages of recolonisation of estuarine macrozoobenthos after flood disturbance were investigated, in combination with environmental variables. Based on the rejection of either H₀₂ or H₀₃, the final null hypothesis tested the difference between the recolonisation patterns of macrozoobenthos in urban and non-urban estuaries (H₀₂), or within the individual TOCEs (H₀₃). This null hypothesis was formulated on the premise that the macrozoobenthic communities would not become static following flood disturbance and that recolonisation of the estuaries would take place, represented by significant positive changes in community characteristics

(including species richness, abundance and diversity) and shifts in species composition with time in relation to post-flood fluctuation in environmental factors.

H₀₄) There were no significant changes in macrozoobenthic community structure with increasing time after flood disturbance in the four TOCEs.

4.3 Methods and Materials

A detailed description of the general procedures relating to the collection of macrozoobenthos, sediment samples, the *in situ* measurement of habitat characteristics (environmental variables), laboratory processing and background to statistical analyses, is provided in Chapter 2 (General Materials and Methods).

4.3.1 Study Sites

Four TOCEs on the south coast of KwaZulu-Natal were selected from several flood-affected systems based on their similarities in estuary type (TOCEs), morphometries, catchment size and state of urbanisation (Table 4.1). The Manzimtoti and Little Manzimtoti systems were defined as ‘urban’ estuaries because of their close proximity to the urban centre of Manzimtoti, and the high level development within their catchments and along their immediate shorelines (Faku et al. 2009) (Figure 4.2). Consequently, the condition of these systems has been regarded as poor (Whitfield 2000). Urban development around the Mhlabatshane and Intshambili systems was substantially less in comparison with the ‘urban’ estuaries (Figure 4.3). Therefore, these two systems were defined as ‘non-urban’ estuaries. They were previously considered to be in fair and good condition, respectively, by Whitfield (2000).

Table 4.1 System characteristics for the Manzimtoti, Little Manzimtoti, Mhlabatshane and Intshambili estuaries collected from previous studies and personal observations (Begg 1978, 1984a, Whitfield 2000, Zietsman 2004)

Estuary Name	Code	Estuary Type	Area (km ²)	Length (km)	Catchment Area (km ²)	State of Urbanisation	Condition
Manzimtoti	AT	TOCE	0.067	2.0	39	Urban	Poor
Little Manzimtoti	LAM	TOCE	0.015	0.8	18	Urban	Poor
Mhlabatshane	MAN	TOCE	0.031	1.0	47	Non-Urban	Fair
Intshambili	INT	TOCE	0.017	0.6	33	Non-Urban	Good

4.3.2.1 Urban Estuaries: The Manzimtoti and Little Manzimtoti

The Manzimtoti (30°03'34"S, 30°53'00"E) and the Little Manzimtoti (30°04'38"S, 30°52'21"E) estuaries are situated approximately 30 km and 35 km south west of Durban, respectively, in the densely developed town of Manzimtoti (Figure 4.2). The South Coast railway line, the National Road and several arterial road bridges span the two systems. On the banks of both estuaries, particularly the Manzimtoti Estuary, there are high-rise residential and holiday flats, restaurants, pubs, shopping malls, municipal buildings, sports and recreational amenities. Because of this heavily urbanised coastal setting, these estuaries have been impacted upon by a various forms of pollution including sewage effluent, stormwater run-off and vast amounts of litter (Begg 1978, Durban-Metropolitan 1999, Dlamini et al. 2002, Forbes and Demetriades 2008).

According to Cooper et al (1994), the Manzimtoti and Little Manzimtoti estuaries ranked amongst the five estuaries with the poorest water quality in KwaZulu-Natal. These systems remain in a highly degraded state due to their persistent sewage contamination and eutrophic condition (Forbes and Demetriades 2008). Consequently, the middle and upper reaches are prone to periodic and severe smothering by aquatic invasive plants, predominantly water hyacinth (*Eichhornia crassipes*) (Manzimtoti) and water lettuce (*Pistia stratiotes*) (Little Manzimtoti) (pers. obs., Figure 4.4). Algal blooms also occur in these urban estuaries, indicated by red coloured water (Manzimtoti) and high levels of dissolved oxygen during daylight productivity (Little Manzimtoti), likely due to increased nutrient levels (Steven Weerts, *pers. comm.*, 2008¹).

¹Steven Weerts, CSIR, P. O. Box 17001, Congella, Durban, 4013, KwaZulu-Natal



Figure 4.2 Aerial imagery of the urban Manzimtoti (A) and Little Manzimtoti (B) estuaries showing the locations of macrozoobenthic sampling sites. Site 1 = lower reaches, Site 2 = middle reaches, Site 3 = upper reaches. Imagery supplied by the ORI GIS Unit.



Figure 4.3 Aerial imagery of the non-urban Mhlabatshane (A) and Intshambili (B) estuaries showing the location of sampling site 1 in the lower reaches. Imagery supplied by the ORI GIS Unit.



Figure 4.4 Prolific growth of water lettuce (*Pistia stratiotes*) in upper reaches of the Little Manzimtoti Estuary

The two urban estuaries differ in that the Manzimtoti Estuary is relatively larger (Table 4.1) and predominantly closed, while the Little Manzimtoti Estuary is smaller, and predominantly open. The regular outflow, albeit minimal, in the latter system is attributed to the perched position above mean sea level from the combination of historical siltation and frequent infilling of fine beach sand (Begg 1984a). As TOCEs, water depth within these systems is largely dependent on the open or closed state of the mouth and volume of freshwater input (Whitfield and Bate 2007, Perissinotto et al. 2010). Low-lying roads adjacent to the Manzimtoti Estuary are frequently flooded during the closed mouth phase and concomitant increase in water levels. Both systems become almost completely drained following dramatic breaching of the mouth that takes places mainly after heavy rains (Figures 4.5 A, B), thereby exposing bedrock and rubble, and in the Manzimtoti basin, soft thick brown-black mud. In addition to mouth condition and variable fluvial input, the shape and extent of the terminal basin of each system are also influenced by wind-swept beach sediment and overwashed marine sediment (pers. obs.). Periodically, the Little Manzimtoti system was depositional in nature, whereby large amounts of organic floc was visible on the estuary floor (pers. obs.).

The vegetation surrounding the Manzimtoti and Little Manzimtoti estuaries is largely disturbed with few remaining indigenous species as result of urban encroachment. Typical estuarine fringing vegetation includes *Phragmites* and *Typhus* reed beds and dense *Hibiscus tiliaceus* (Lagoon Hibiscus). A noteworthy stand of indigenous *Strelitzia nicolai* (Natal Wild Banana) is

present along the middle reaches of the Little Manzimtoti Estuary. Invasive species are prevalent in both systems, particularly in the Manzimtoti Estuary, namely *Schinus terebinthifolius* (Brazilian Red pepper), *Ipomea indica* (Morning Glory), *Solanum mauritianum* (Bugweed), *Chromolaena odorata* (Triffid weed) and *Ricinus communis* (Castor oil plant). Towards the upper reaches of Little Manzimtoti system, rank growth of encroaching grasses and excessive litter contribute to clogging of the waterway. Low-lying coastal riverine forest line the upper reaches of both estuaries.



Figure 4.5 Drained conditions in the Manzimtoti (A) and Little Manzimtoti (B) estuaries following breaching of the estuary mouth

In the current study, evidence of flooding in the two urban estuaries was observed mainly in the middle to upper reaches and included substantial amounts of plant debris and litter suspended high up in the fringing vegetation and caught around the bridge bastions, as well as large branches deposited in the river channels. In the Little Manzimtoti, several *S. nicolai* palms had collapsed into the estuary (Figure 4.6) probably due to destabilisation of the muddy

riverbank caused by the floodwaters. Damage to infrastructure and buildings on the water's edge was not apparent.



Figure 4.6 Collapse of *Strelitzia nicolai* palms into the middle reaches of the Little Manzimtoti Estuary following flooding

4.3.2.2 Non-Urban Estuaries: The Mhlabatshane and Intshambili

The Mhlabatshane (30°35'02"S, 30°34'19"E) and Intshambili (30°38'12"S, 30°32'13"E) estuaries are situated in the coastal holiday villages of Hibberdene and Pumula, 106 km and 111 km south west of Durban, respectively (Figure 4.3). The catchments of these two systems are largely undeveloped and that of the Intshambili is considered particularly well conserved (Whitfield 2000). However, historically both systems have suffered from siltation caused by erosion in the lower catchment areas likely due to sugar cane farming (Begg 1984a). In particular, the Intshambili has been affected by long-term siltation attributed to the high sediment yield of its main tributary (Begg 1978). Historical water quality assessments revealed that nutrient and faecal contamination in these non-urban systems was negligible in comparison with the urban estuaries (Begg 1978, 1984a). Nevertheless, present-day contamination is expected due to the increasing holiday industry of the surrounding areas and the presence of a stormwater outlet in the Intshambili Estuary. Furthermore, these systems are popular ski-boat launch sites and are thus valued for recreational purposes.

The Intshambili Estuary is predominantly closed and is open only after high rainfall events for brief periods (Begg 1984a, Zietsman 2004). While the Mhlabatshane Estuary was closed during

four of five sample periods during the current study, it functions as a predominantly open system (Zietsman 2004). As with the urban estuaries, water level is similarly maintained by the state of the mouth and river input. Reshaping and infilling of the terminal basins frequently occurs during the closed phase due to marine overwash during high tide (pers. obs.). During the open phase, the mouth forms alongside granitic outcrops on the southern bank in both estuaries and saline influence is measurable throughout the system into the upper reaches (pers. obs.).

The vegetation of the Mhlabatshane and Intshambili estuaries is somewhat different. The former system is characterised by a dense fringe of *H. tiliaceous* (Figure 4.7 A) while the latter is bordered by a well-established *Barringtonia racemosa* swamp forest (Figure 4.7 B). For this reason, the Intshambili Estuary is considered a system of high ecological and botanical importance (Begg 1978, Harrison et al. 2000, Whitfield 2000). The upper reaches of the Mhlabatshane Estuary are flanked by coastal riverine forest, while continued reed encroachment characterises the upper reaches of the Intshambili Estuary, as first described by Begg (1978). The Mhlabatshane Estuary was most severely affected by the June flood event. The most striking features of adverse flooding were 1) the overflow of flood waters across the vegetated southern bank in the middle reaches, bypassing the normal meander (Figure 4.8 A), 2) undercutting and collapse of the road bridge support bank on the southern riverbank (Figure 4.8 B), 3) destabilisation of river banks and collapse of marginal trees into the estuary in the upper reaches (Figure 4.8 C), and 4) vast amounts of plant debris caught in fringing vegetation and large tree trunks washed up on the adjacent beach (Figure 4.8 D). The road bridge required subsequent reconstruction and reinforcement with stone gabions on both north and south banks of the system. In contrast, evidence of flooding in the Intshambili system was less dramatic and included slumping of riverbanks, plant debris suspended in the surrounding vegetation as well as large amounts of debris flushed from the floodplain and deposited in the mouth region and on the beach slope.



Figure 4.7 (A) Dense *Hibiscus tiliaceos* lining the Mhlabatshane Estuary and (B) the well-established *Barringtonia racemosa* swamp forest of the Intshambili Estuary



Figure 4.8 A-D Observed effects of June 2008 flooding in the Mhlabatshane Estuary. Arrow in Figure 4.8A indicating point of entry of bypassed flow (Photos courtesy of Steven Weerts, CSIR)

4.3.2 Sampling Approach

In view of the fact that the 2008 flood event provided a spontaneous investigative opportunity, the sampling strategy employed was restricted by availability of time, and by financial and laboratory resource constraints. Sampling intervals were consequently stretched to remedy these constraints while making the most of the opportunity. Invariably, sampling was not conducted during the summer time period. The field sampling of the urban Manzimtoti and Little Manzimtoti estuaries commenced approximately one month after flooding and continued over increasing time intervals for one year covering six sampling trips (Table 4.2). In these two systems, samples were collected from three individual sites representing the lower, middle and upper reaches of the estuary, respectively. Due to logistical constraints, sampling of the non-urban Mhlabatshane and Intshambili systems began during time period two (Table 4.2), and was limited to the lower reaches only. During each fieldtrip, five random samples were collected at each site to ensure sufficient spatial and temporal replication of the bottom communities. The location of benthic sampling sites within each estuary in relation to the surrounding coastal setting and distance from the mouth, are shown in Figure 4.2 (Manzimtoti and Little Manzimtoti) and Figure 4.3 (Mhlabatshane and Intshambili). Macrozoobenthic samples were assigned to specific time periods according to the number of days after flooding when sampling took place, starting from 18/06/2008 when severe flooding of the coastal areas was recorded (Table 4.2).

Table 4.2 Sampling dates, number of days after flooding and associated time periods for macrozoobenthos collected from the Manzimtoti, Little Manzimtoti, Mhlabatshane and Intshambili estuaries from June 2008 to July 2009.

Number of Days	Time Period	Manzimtoti	Little Manzimtoti	Mhlabatshane	Intshambili
0	0	18/06/2008			
1-40	1	24/07/2008	25/07/2008	.	.
41-60	2	05/08/2008	07/08/2008	30/07/2008	30/07/2008
61-80	3	05/09/2008	04/09/2008	03/09/2008	03/09/2008
81-160	4	28/10/2008	27/10/2008	03/11/2008	03/11/2008
161-320	5	28/04/2009	28/04/2009	29/04/2009	29/04/2009
321-400	6	14/07/2009	13/07/2009	13/07/2009	13/07/2009

4.3.3 Data Analyses

The nature of the substratum and physico-chemical environment of each sample site were first described to obtain a clear understanding of the fluxes in benthic habitat with increasing time

after flooding. To examine spatial and temporal changes in sediment composition, sediment data were plotted as cumulative frequency curves, whereby the weight of the sediment retained by each sieve was calculated as a percentage and cumulatively plotted on an arithmetic scale against grain size (Φ) for each time period at each site. Analysis of the biological data was divided into four phases according to the outlined hypotheses. The first phase aimed to describe changes in the community characteristics of the macrozoobenthos in each of the two urban and non-urban estuaries, by discriminating between samples of each time period and/or site based on changes in the community composition with ongoing recovery. This served to explain trends in inherent community variability at both spatial and temporal scales. Phase two aimed to define 'urban' and 'non-urban' communities by investigating relationships between samples of adjacent systems and by searching for common community characteristics. Failure to isolate specific urban/non-urban characteristics, led to between-system analyses, Phase 3, to examine the degree of separation of the four estuaries based on the differences in their biotic composition and community structure. In the fourth and final phase, changes in diversity indices and indicator species assemblages were used to describe the stages in macrozoobenthic community recolonisation in each estuary. In this phase, environmental variables were linked to changes in community data to ascertain possible causes for shifts in faunal assemblages and progression in post-flood recovery of each community. Data analysis was carried out using several PRIMER procedures (Clarke and Warwick 2001). Various multivariate techniques were used to classify benthic communities according to groups of samples (CLUSTER and NMDS). Analysis of Similarity (ANOSIM) and SIMPER were used for statistical and taxonomical verification of the sample groups, respectively. Community indices were computed using DIVERSE procedures. The Student t-test and the non-parametric Mann-Whitney U test were used to test for differences between two subsets of data (for example abundance between urban estuaries), and Analysis of Variance (ANOVA) with a *post hoc* Tukey Test, were performed to test and identify differences between benthic diversities of the different sites and estuarine systems. The configuration of the macrozoobenthic communities were related to changes in physico-chemical variables (sediment and water quality characteristics) using BIOENV.

4.4 Results

4.4.1 Environmental Characteristics

4.4.1.1 Water Physico-Chemical Variables

In the Manzimtoti Estuary, a horizontal salinity gradient existed (Table 4.3) with salinities highest at site 1 (14.64 \pm 0.54SD) and lowest at site 3 in the upper reaches (6.25 \pm 7.90SD). Dissolved oxygen concentrations were lowest at site 1 (3.38 mg/L \pm 2.99SD) and comparably higher at both sites 2 (4.88 mg/L \pm 2.11SD) and 3 (4.95 mg/L \pm 2.63SD). Temperature and pH were relatively consistent throughout the system. Turbidity was highly variable at each site, particularly at site 1 (46.49 \pm 89.7SD), which was generally more turbid than sites 2 and 3. In terms of depth, site 1 was the deepest site (2.03m \pm 1.04SD) and the maximum depth sampled at this point was 2.7m. During the open phase, the system was exceedingly shallow where depth measurements were at a minimum of 0.2m at all sites. Temporal trends in water physico-chemical variables of the Manzimtoti Estuary are displayed in Figure 4.9A. Salinity generally decreased with increased time after flushing, but was substantially low during (3.3 \pm 4.14SD) and after (2.36 \pm 0.38SD) an open phase that occurred at time 5. During the open phase, elevated levels in bottom turbidity (107.68NTU \pm 105.48) were recorded. This was attributed to extremely shallow depth at site one, which resulted from almost complete drainage of the system. Dissolved oxygen levels were below 5 mg/L prior to opening of the mouth, and increased to 6.59 mg/L thereafter. Bottom water temperatures were slightly warmer during Spring and Autumn. pH levels remained relatively stable with time.

Table 4.3. Mean water physico-chemical variables collected from macrozoobenthic sampling sites in each estuary

Site no.	Region	Temperature (°C)	Dissolved Oxygen (mg/L)	pH	Salinity (PSU)	Turbidity (NTU)	Depth (m)
Manzimtoti							
1	Lower	20.13 (2.06)	3.38 (2.99)	7.37 (0.54)	14.64 (7.90)	46.49 (89.70)	2.03 (1.04)
2	Middle	20.29 (2.15)	4.88 (2.11)	7.28 (0.50)	8.84 (7.68)	13.74 (16.33)	1.45 (0.69)
3	Upper	19.69 (2.11)	4.95 (2.63)	7.26 (0.43)	6.25 (4.71)	16.86 (15.33)	1.29 (0.56)
Little Manzimtoti							
1	Lower	23.01 (1.60)	12.47 (8.45)	8.25 (0.53)	22.71 (7.51)	19.91 (20.54)	0.83 (0.31)
2	Middle	19.36 (2.23)	2.18 (0.99)	7.17 (0.29)	10.10 (11.70)	12.48 (4.78)	1.10 (0.38)
3	Upper	18.77 (2.56)	1.20 (1.99)	7.01 (0.43)	14.87 (16.32)	13.15 (4.39)	3.21 (0.13)
Mhlabatshane							
1	Lower	21.62 (1.02)	3.41 (3.09)	7.47 (0.36)	22.95 (12.16)	13.86 (5.93)	1.69 (0.61)
Intshambili							
1	Lower	19.34 (1.81)	3.64 (1.72)	7.07 (0.24)	8.96 (8.07)	10.16 (6.27)	1.80 (0.29)

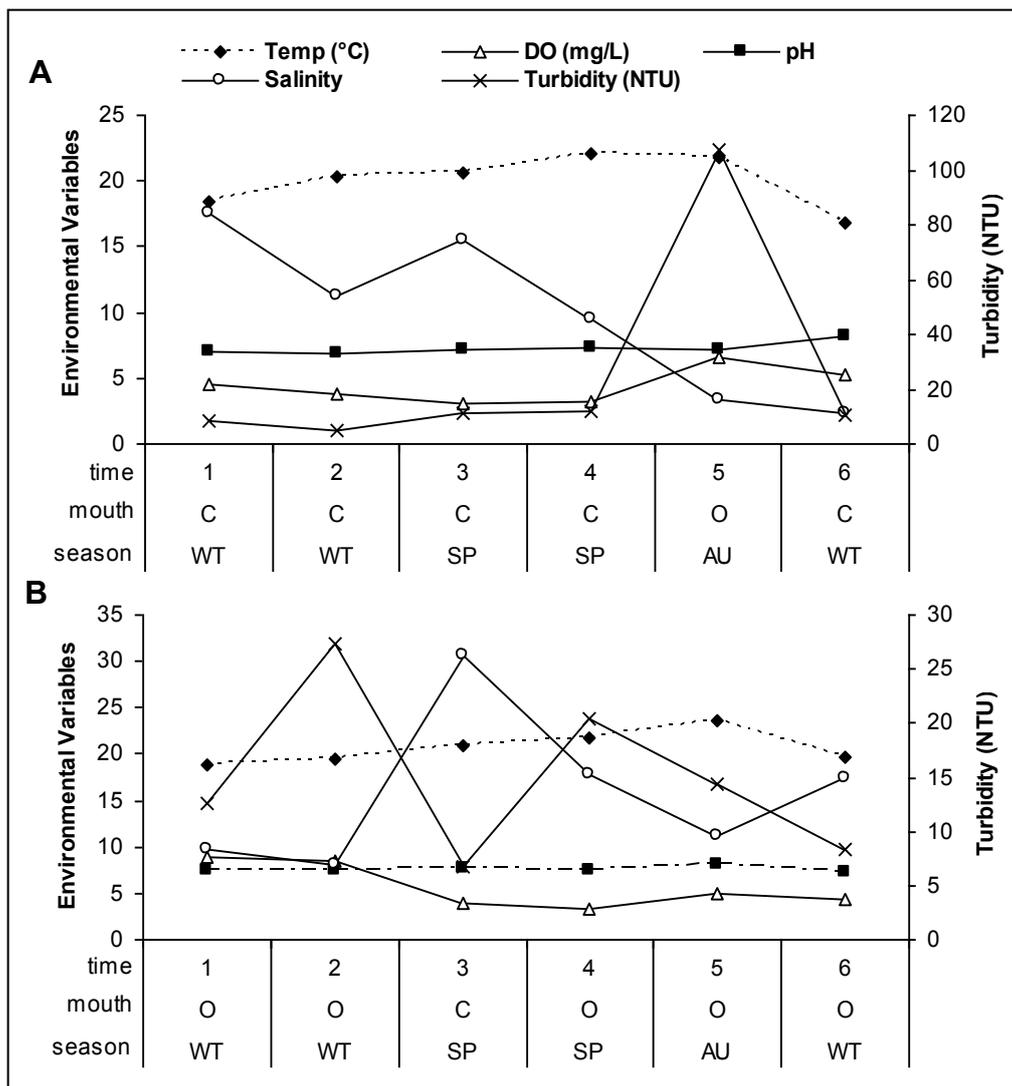


Figure 4.9 Mean water physico-chemical variables across 3 sites against time period, mouth condition and season measured in the Manzimtoti (A) and Little Manzimtoti (B). O = open phase, C= closed phase. WT= Winter, SP= Spring, AU= Autumn.

In the Little Manzimtoti Estuary, all physico-chemical parameters were highest at site 1 as a result of the normally open mouth condition and marine influence (Table 4.3). Consequently, the system was generally more saline than the Manzimtoti Estuary, However, a marked horizontal gradient in salinity was not apparent. While salinity was highest at site 1 ($22.71 \pm 7.51SD$), measurements at site 3 in the upper reaches were greater ($14.87 \pm 16.32SD$) than at site 2 ($10.10 \pm 11.70SD$). This was postulated to be a pocket of saline water, from salt water intrusion into the system, trapped at this deep water site ($3.21m \pm 0.13SD$). Concurrently, the maximum depth sampled was 3.4m at this site. Site 1 was generally the shallowest site ($0.83m \pm 0.31SD$). Turbidity was highest and markedly variable at site 1 ($19.91NTU \pm 20.54SD$).

Although the bottom water at site 1 was well oxygenated (12.47 mg/L \pm 8.45SD), sites 2 (2.18 mg/L \pm 0.99SD) and 3 (1.20 mg/L \pm 1.99) were generally hypoxic. Temporal examination of the water properties of the Little Manzimtoti Estuary revealed that, while fluctuations in pH and temperature were minimal, salinity, and turbidity were evidently influenced by the intermittent closure of the mouth (Figure 4.9 B). There was a peak in salinity during the closed phase (time 3) where measurements were near seawater at all three sites during this time (site 1= 29.71, site 2= 31.17; site 3= 31.33). This was attributed to marine overtopping of the sandbar (pers. obs.) and the likely upstream penetration of confined seawater in the absence of strong fluvial outflow. Concomitantly, turbidity was at a minimum (6.83 \pm 1.42SD) due to saline flocculation of suspended material. The system was well oxygenated prior to closure of the mouth, however during closure and subsequent re-opening, dissolved oxygen concentrations dropped below 5 mg/L.

The physico-chemical characteristics of the lower reaches of the Mhlabatshane Estuary were very similar to that of the lower reaches in the Manzimtoti and Little Manzimtoti estuaries (Table 4.3). Salinity was highly variable (22.95 \pm 12.16SD), and relatively similar to that at site 1 in the Little Manzimtoti. Turbidity at site 1 in the Mhlabatshane Estuary (13.86NTU \pm 5.93SD) was comparable to the turbidities in the middle and upper reaches of the two aforementioned systems. Over the duration of the study period, salinity and dissolved oxygen reached a maximum during the open phase at time 3 in early Spring (Salinity= 34.71; DO= 8.53 mg/L) (Figure 4.10 A). Essentially, the open mouth condition had a positive effect on dissolved oxygen concentrations which were very low before (1.87 mg/L) and after (0.76 mg/L) breaching. Salinity reached a minimum at time 5 (3.78), and increased thereafter. Temporal fluctuations in temperature and pH levels were negligible, while turbidity varied markedly between sampled periods and reached a maximum at time 6 (23.4NTU).

The Intshambili system exhibited physico-chemical characteristics generally similar to that of the Mhlabatshane Estuary (Table 4.3) however, it was substantially less saline (8.96 \pm 8.07SD), comparable to the middle reaches of the urban estuaries, and generally cooler in terms of bottom water temperature (19 °C \pm 1.81SD). Temporally, salinity was at a maximum (20.09) during the open mouth phase at the onset of sampling (Figure 4.10 B) and decreased steeply toward freshwater conditions (0.33) at time 5 after a period of prolonged mouth closure. While pH remained stable with increasing time, bottom water temperature was warmer by

3.5°C in mid-Spring. Initially, turbidity was low until time 4 (4.8 – 8.6NTU), and increased markedly thereafter to 20.2NTU at time 6.

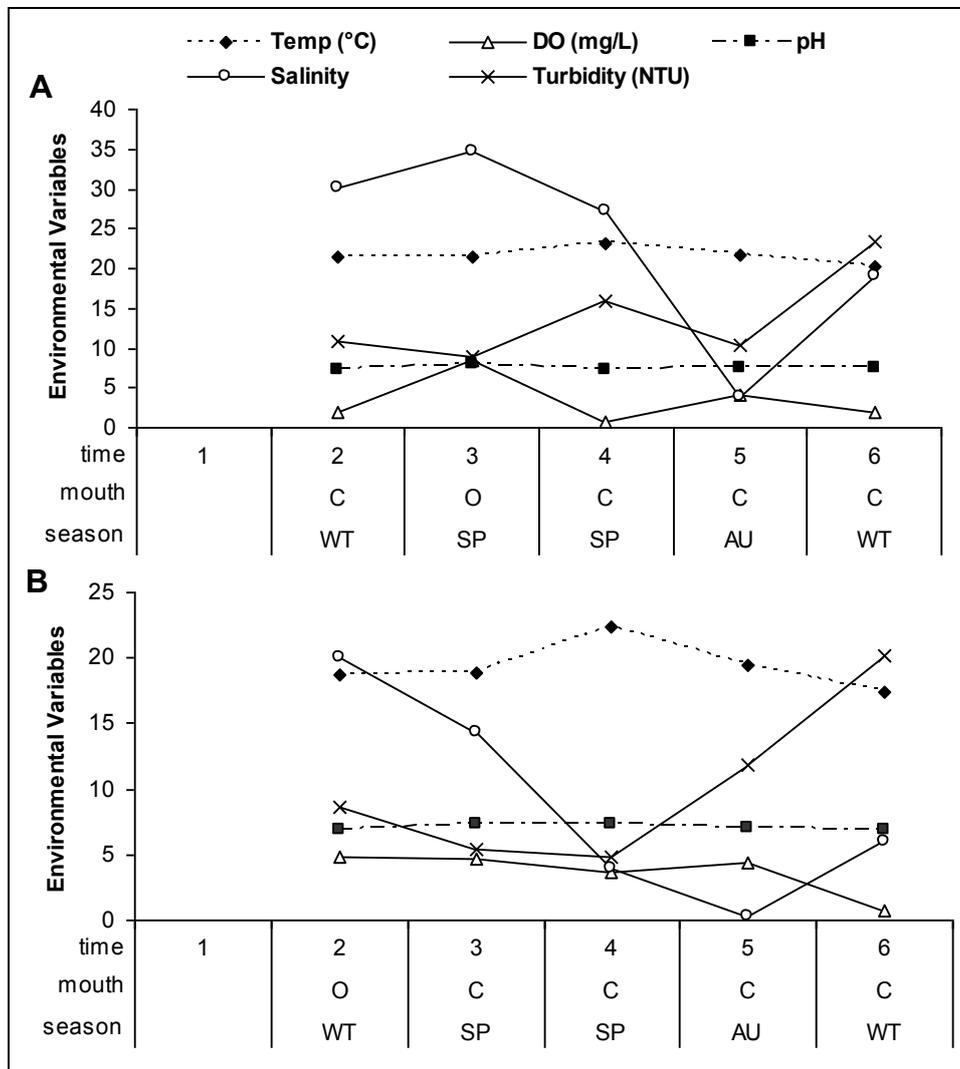


Figure 4.10 Water physico-chemical variables against time period, mouth condition and season measured in the Mhlabatshane (A), and Intshambili (B). O = open phase, C = closed phase. WT= Winter, SP= Spring, AU= Autumn.

4.4.1.2 Sediment Characteristics

Granulometry

The substrate of the Manzimtoti Estuary comprised moderately well sorted medium sand ($M=1.29 - 1.85\Phi$) with low organic content (0.25 – 0.67%), which decreased from site 1 near the mouth to the upper reaches (Table 4.4). The sediment of the Little Manzimtoti Estuary was predominantly moderately sorted medium sand, although the bottom material found at site 3

was substantially coarser ($M=0.60\Phi \pm 0.14SD$, $Md=0.56\Phi \pm 0.10SD$). In the Mhlabatshane, sediment grain size was similarly medium sand ($M=1.30\Phi \pm 0.74SD$), and moderately well sorted, while the substratum of the Intshambili Estuary was moderately sorted and coarser, with mean grain size at the boundary between coarse- and medium -grained sand ($M=1.02\Phi \pm 1.07SD$, $Md= 1.01\Phi \pm 1.08SD$).

Table 4.4. Mean grain-size parameters, organic content (%) ($\pm SD$) and sediment type computed from sediment samples collected from macrozoobenthic sampling sites in each estuary.

Site no.	Region	Grain Size (Φ)	Median Grain Size ($Md=\Phi_{50}$)	Sorting Co-efficient	Organic Content (%)	Sediment Type
Manzimtoti						
1	Lower	1.64 (0.60)	1.67 (0.58)	1.02 (0.47)	0.67 (0.90)	Medium sand
2	Middle	1.85 (0.48)	1.75 (0.28)	0.75 (0.34)	0.52 (0.62)	Medium sand
3	Upper	1.29 (0.28)	1.35 (0.24)	0.69 (0.17)	0.25 (0.10)	Medium sand
Little Manzimtoti						
1	Lower	1.11 (0.11)	1.11 (0.11)	0.68 (0.03)	0.27 (0.12)	Medium sand
2	Middle	1.41 (0.69)	1.73 (0.53)	1.08 (0.62)	0.42 (0.29)	Medium sand
3	Upper	0.60 (0.14)	0.56 (0.10)	1.03 (0.23)	0.31 (0.09)	Coarse sand
Mhlabatshane						
1	Lower	1.30 (0.74)	1.02 (0.38)	0.61 (0.36)	0.65 (0.51)	Medium sand
Intshambili						
1	Lower	1.02 (1.07)	1.01 (1.08)	0.85 (1.25)	1.24 (1.98)	Coarse sand

The sediment dynamics of each of the three sites in the Manzimtoti and Little Manzimtoti are presented in Figures 4.11 (A-C) and 4.12 (A-C), respectively. The substratum at all sites in the Manzimtoti Estuary comprised predominantly sand grains ranging in size between $1\Phi - 2\Phi$ (Figure 4.11 A-C). According to the Wentworth Scale (Bale and Kenny 2005) this is classified as medium sand. The substratum at site 1 (Figure 4.11 A) sampled at times 1 and 2 was typically medium to fine grained sand. At time 3, there was a greater proportion of coarse-grained material ($Md= 0.88\Phi$). At time 4, the substratum was finer due to an increased quantity of mud and a lower proportion of medium to fine sand ($Md= 2.61\Phi$). This is indicative of depositional environmental conditions possibly related to increased depth and slower water flow as site 1 was deepest at this time. The nature of the sediment at times 5 and 6 was slightly finer than at times 1 and time 2, possibly caused by post-breach abatement of water flow and concomitant deposition of the finer size fraction.

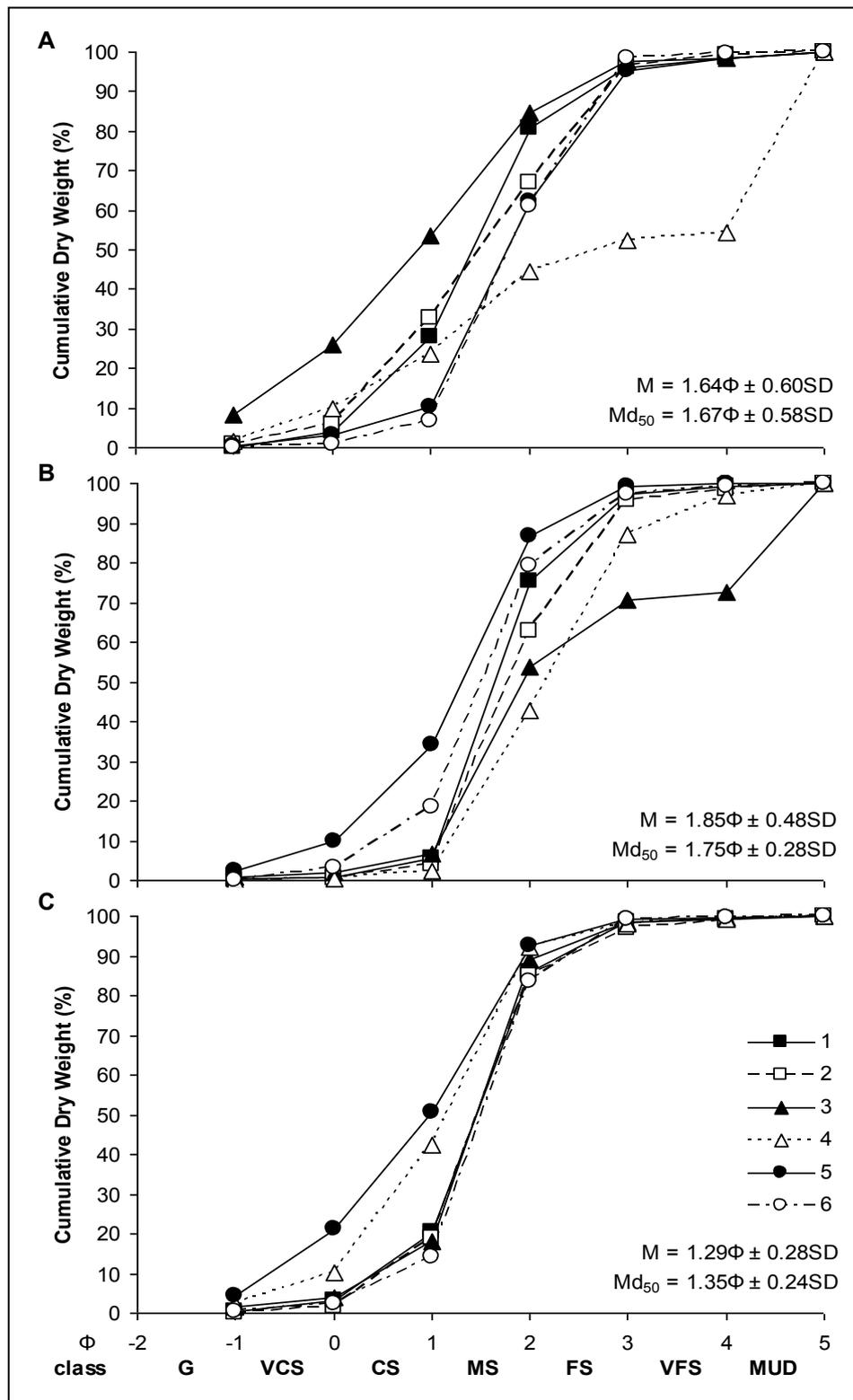


Figure 4.11 Cumulative percent dry-weight against grain size (Φ) of sediment sampled from the Manzimtoti Estuary at site 1 (A), site 2 (B), site 3 (C) during time periods 1-6.

At site 2 in the Manzimtoti Estuary (Figure 4.11 B), the proportion of medium-grained sediment decreased with time until time 4. Between times 2 and 3 a substantial amount of the mud was deposited ($Md= 1.94\Phi$), such that 28% of the sediment collected at site 3 comprised particles less than 4Φ (mud). This high volume of mud was no longer present at time 4. The sediment was coarsest at time 5 ($M= 1.20\Phi$). At site 3 sediment composition was relatively stable until times 4 and 5 (Figure 4.11 C), when the proportion of coarse material had increased and finer material decreased (Time 4 $Md=1.13\Phi$; Time 5 ($Md=0.98\Phi$). Thereafter, sediment composition at time 6 was similar to times 1-3. At both sites 2 and 3, the increased coarseness of the substrate at time 5 was most likely related to scouring flow velocities caused by the open mouth condition.

In the Little Manzimtoti Estuary, the sedimentary habitat at site 1 remained relatively uniform with time and was characterised by approximately 35-40% coarse- and 40-50% medium-grained sand, typical of beach type sedimentary environments (Figure 4.12 A). The substratum at time 5 was slightly coarser ($M=0.90\Phi$), and comprised up to 50% coarse- and 40% medium-grained sand ($Md=0.90\Phi$). The substratum at site 2 (Figure 4.12 B) had a higher percentage gravel to coarse-grained material than site 1, which varied considerably with time. There was no discernable temporal trend. This was possibly attributed to variable flow rates that in turn maintained the predominantly open state of the mouth. During times 5 and 6, the substratum comprised substantially less coarse-grained material, and up to 60% fine-grained sand ($Md=2.13-2.15\Phi$). This was possibly linked to changes in depth because the depth at site 2 during these times was shallower than in previous sample periods ($>1m$), 0.81m and 0.62m respectively. At site 3 (Figure 4.12 C), the sediment was predominantly coarse-grained sand. Fluctuations in the percentage of coarser fractions were evident yet low, 0.5-14% for gravel and 13-22% for very coarse sand. Differences in the percentage of the finer fractions were even less and negligible. There was no apparent relationship between the sediment dynamics at each site and the closure of the Little Manzimtoti Estuary mouth at time 3.

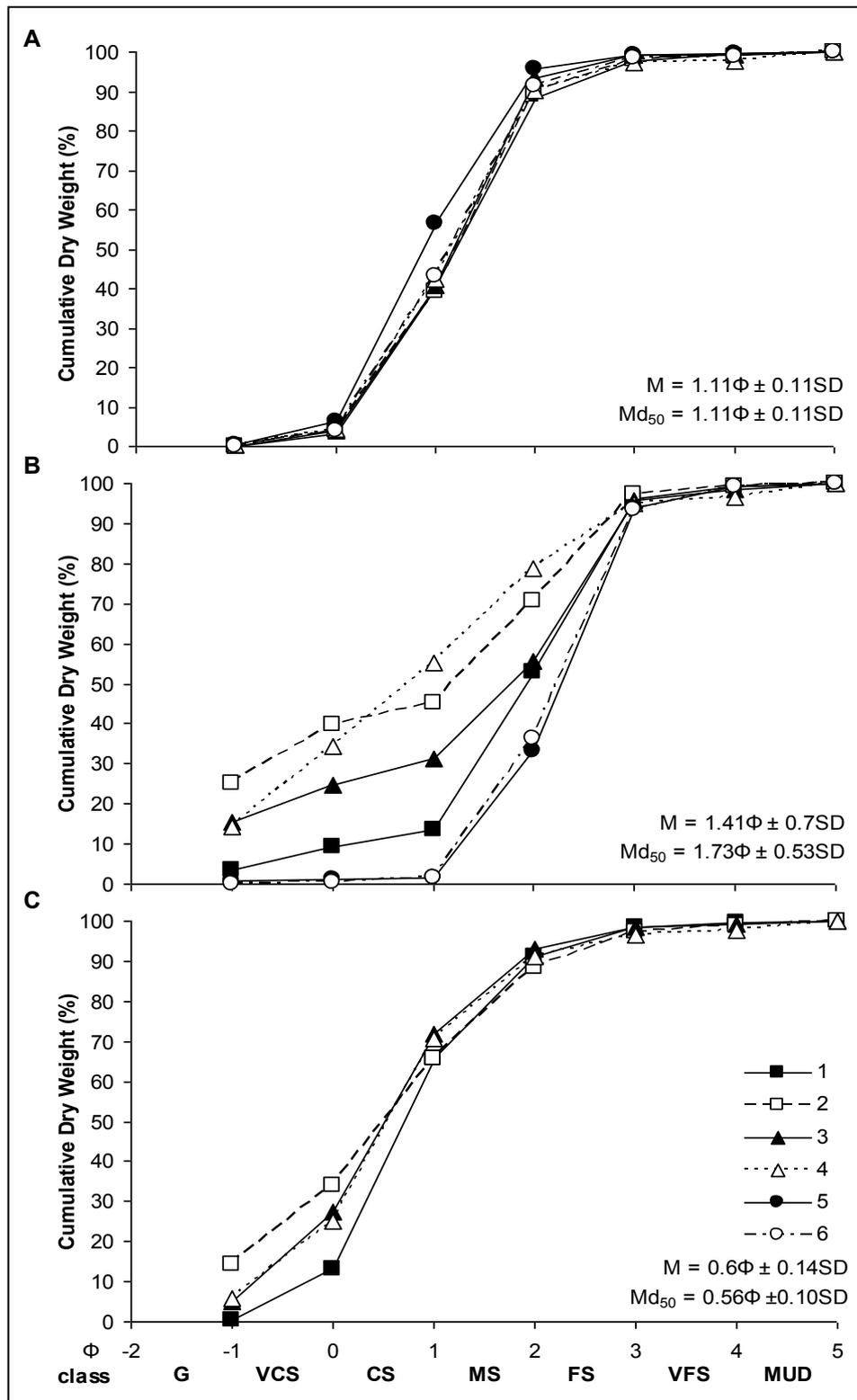


Figure 4.12 Cumulative percent dry-weight against grain size (Φ) of sediment sampled from the Little Manzimtoti Estuary at site 1 (A), site 2 (B), site 3 (C) during time periods 1-6.

In the Mhlabatshane Estuary, the sediment at the mouth comprised relatively similar proportions of coarse- and medium-grained sand across all sampling trips ($Md = 1.02\Phi \pm 0.38SD$) (Figure 4.13 A). The sediment composition at times 2 and 4 were very similar ($M = 0.64-0.66\Phi$), with a greater proportion of coarse material ($Md = 0.63-0.64\Phi$). The sediment at times 5 and 6 were also very similar, however, slightly finer in composition in comparison with other times ($M = 2.06-2.11\Phi$). This was due to a greater proportion of silt (20-21%), indicated by higher median phi values of 1.38Φ and 1.46Φ , respectively. The sediment composition at time 3 during the open state of the mouth was the intermediate ($Md = 0.95\Phi$) between times 2 and 4, and 5 and 6. A significant proportion of silt was not sampled as with times 5 and 6, but it did comprise lower percentages of gravel and very coarse-grained sand, and higher percentages of medium- to very fine-grained sand in comparison with times 2 and 4.

The predominant sediment type at site 1 in the Intshambili Estuary was coarse-grained sand (Figure 4.13 B). The substratum at times 2 to 4, during and following the open mouth phase, were extremely coarse ($M = 0.17-0.27\Phi$), and comprised between 58-63% coarse- and 29-37% very coarse-grained sand ($Md = 0.16-0.25\Phi$). The sediment at these times was representative of erosional flow velocities. At time 5, the sediment was substantially finer grained ($M = 2.27\Phi$), with less than 20% coarse-grained sand, greater proportions of medium, fine and very fine grained sand, and 35% silt. The sediment at time 6 comprised negligible amounts of gravel to coarse grained sand. The dominant size fractions at this time were medium- (39%) and fine-grained sand (38%) ($Md = 2.16\Phi$). The sediment during the last two time periods indicated increasing depositional environmental conditions, culminating at time 6 when the accumulation of medium to fine grained material was greatest.

Organic Content

The organic content of the sediment in the Manzimtoti Estuary decreased with increasing distance from the mouth (Table 4.4). That is, the area of greatest organic accumulation was site 1 ($0.67\% \pm 0.90SD$) in the lower reaches and the area that contained the least amount of organic matter was site 3 ($0.25\% \pm 0.10$). The higher levels of organic material at site 1 were likely due to the decomposing plant debris from the dense *Phragmites* reed bed immediately adjacent to the sample site. In the Little Manzimtoti system the proportion of sediment organic material was highest at site 2 ($0.42\% \pm 0.29$) and lowest at site 1 ($0.27\% \pm 0.12$).

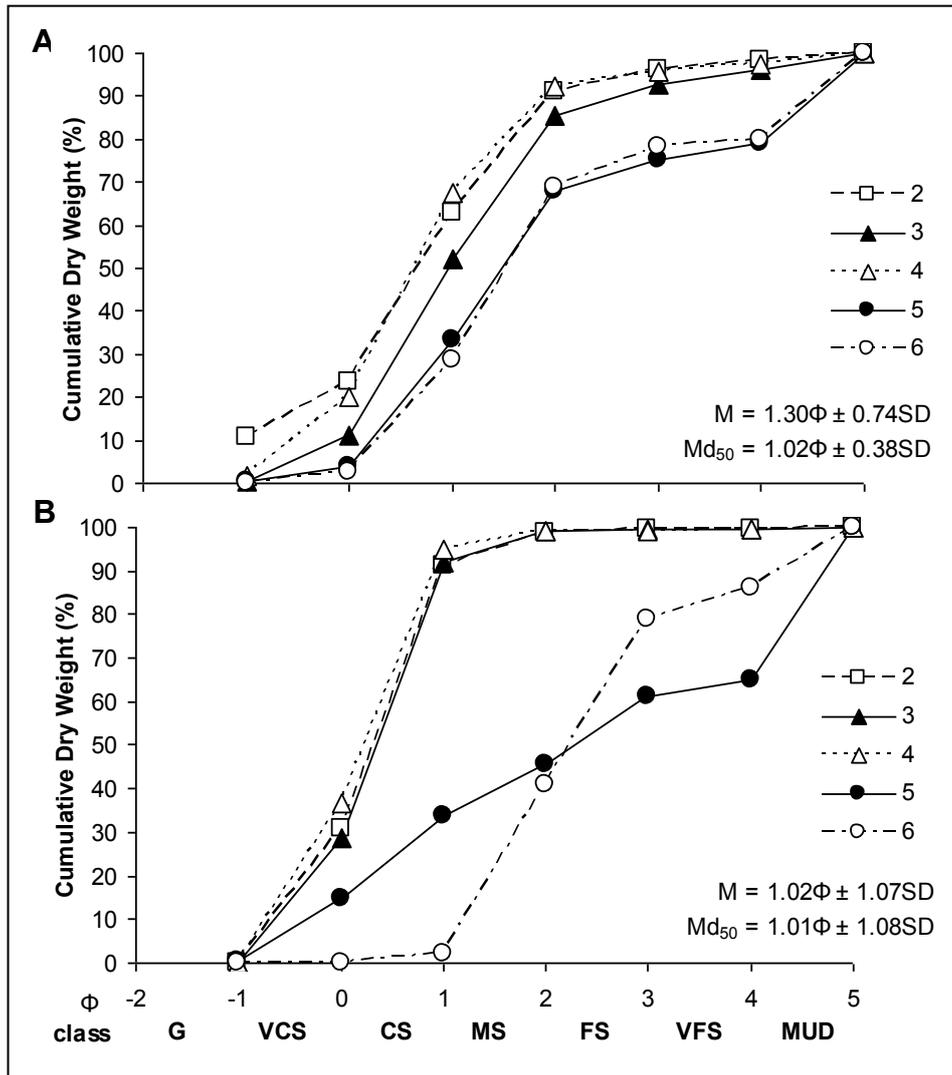


Figure 4.13 Cumulative percent dry-weight against grain size (Φ) of sediment sampled from the Mhlabatshane Estuary (A) and Intshambili Estuary (B) at site 1, during time periods 2-6.

Despite the slightly coarser nature of the sediment at site 3, the percentage organic material was comparable to sites 1 and 2. The sediment of the lower sites of both the Intshambili and Mhlabatshane estuaries had considerably greater percentages of organic content in comparison with the lower sites of the Manzimtoti and Little Manzimtoti. The site with the overall greatest amount of organic material was site 1 in the Intshambili Estuary ($1.24\% \pm 1.98SD$).

Figure 4.14 displays the fluctuations in mean sediment organic content with increasing time for each estuary and the association with the mud content. In all estuaries, percentage organic

content was low at the onset of sampling and at time 2 (0.13-0.31%). At times 3 and 4 (Spring) there was an increased amount of organic material, particularly in the Manzimtoti and Little Manzimtoti estuaries (0.76-1.21%). The Mhlabatshane and Intshambili estuaries experienced substantial accumulations of organic material at times 5 and 6 (1.02-4.71%) (Autumn-Winter), while sediment organic content of the two urban estuaries had decreased (0.20-0.31%). Close inspection of grain size analyses revealed that sediment organic content was strongly positively correlated to the proportion of mud present, such that increased organic content was associated with larger proportions of mud ($R^2 = 0.89-0.96$; $p < 0.05$). Sediment results revealed that although the bottom materials of three of the four systems were similar (medium sand), the relative proportion of grain sizes and organic content shifted with time, and varied between estuaries and between sites within estuaries, indicating the marked variability in the hydrodynamic processes of each system.

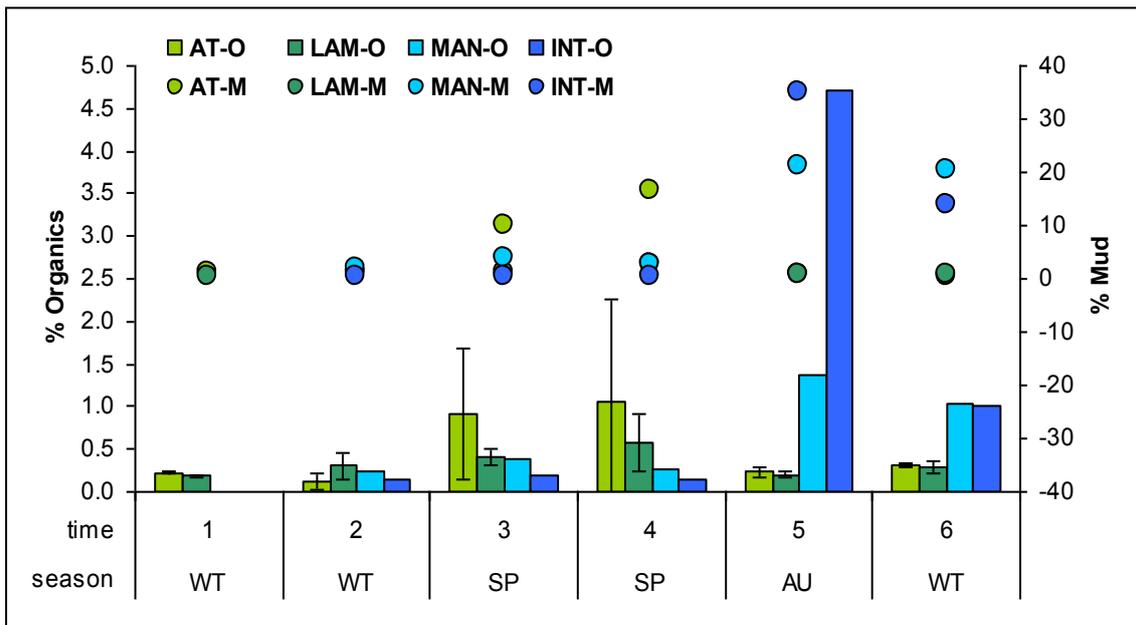


Figure 4.14 Mean sediment organic content (%) and mud content (%) per estuary per time. AT= Manzimtoti Estuary, LAM= Little Manzimtoti Estuary, MAN= Mhlabatshane Estuary and INT= Intshambili Estuary. O= Organics (bars), and M= Mud (circles). WT= Winter, SP= Spring, Au= Autumn.

4.4.2 Macrozoobenthic Communities

4.4.2.1 Community structure of adjacent estuaries

The following section aims to describe within-estuary, and between-estuary differences in macrozoobenthos of Manzimtoti, Little Manzimtoti, Intshambili and Mhlabatshane estuaries,

based on broad taxonomic composition, spatial and temporal changes in faunal abundance and number of taxa.

Taxonomic Composition

The mean total number of organisms per time period and the total number of taxa sampled from each of the four estuaries is as follows: Manzimtoti 67,249 (38 taxa), Little Manzimtoti 45,129 (53 taxa), Mhlabatshane 42,823 (32 taxa) and Intshambili 62,529 (34 taxa). A list of the identified taxa from each system is given in Table 4.5, together with their percentage contribution to the mean faunal abundance per time.

The macrozoobenthos of the Manzimtoti Estuary (Figure 4.15 A) was dominated by species from the Phyla Mollusca (56.9%) and Annelida (41.0%), with a minor contribution made by Arthropoda (2.1%). The mollusc component was dominated by a single gastropod species, *Tarebia granifera* (Table 4.5). Within the Phylum Annelida, Oligochaeta contributed 1% and Polychaeta 40% to the total number of organisms collected, similarly predominated by a single species, *Prionospio multipinnulata* (39.1%) (Table 4.5). In the Little Manzimtoti (Figure 4.15 B), Annelida comprised 92.1% of the community, of which 72.1% and 20% of the total abundance were contributed by Polychaeta and Oligochaeta, respectively. Again the most numerically abundant polychaete species was *P. multipinnulata*. (50.8%) (Table 4.5) Arthropoda comprised 5.6% of the total number of organisms, with minor contributions made by Mollusca (0.5%), Nematoda (1.0%) and Nemertea (0.8%).

Similarly, the benthic community of the Mhlabatshane Estuary (Figure 4.16 A) was dominated by Annelida (93.4%), of which Polychaeta comprised 92.6% (*P. multipinnulata* 70.2%). Arthropoda (5.5%) also occupied a minor proportion of the community, together with Mollusca (0.6%), Nematoda (0.3%), Unknown spp. (0.2%) and Oligochaeta (0.8%). In contrast to the three above-mentioned communities, the macrozoobenthos of the Intshambili Estuary (Figure 4.16 B) was dominated by Arthropoda (65.3%), of which 64.5% were Crustacea and 0.8% were Insecta. In this system, the amphipod taxa *Grandidierella* spp. and *Corophium triaenonyx* made important contributions to the faunal abundance, 40.2% and 15.5%, respectively. Annelida constituted 33.8% of the total number of organisms, comprising 31.9% Polychaeta and 1.9% Oligochaeta. Minor contributions were made by Cnidaria (0.1%) and Mollusca (0.8%).

Table 4.5 List of identified taxa, their percentage contribution to total faunal abundance and the total number of taxa for each estuary. Estuaries: AT= Manzimtoti, LAM= Little Manzimtoti, MAN= Mhlabatshane, INT= Intshambili. Species codes: sp= Species, Juv=Juvenile, L=Larvae, PL= Post-larvae, PreJuv= Pre-Juvenile, T=Type.

IDENTIFIED TAXA	URBAN		NON-URBAN	
	AT	LAM	MAN	INT
ANNELIDA:				
<u>Hirudinea</u>				
Hirudinea spp.		0.02	0.04	
<u>Oligochaeta</u>				
Oligochaeta spp	1.01	19.96	0.78	1.91
<u>Polychaeta</u>				
<i>Caulleriella</i> sp.1			0.04	
<i>Lumbrineris tetraura</i>		0.09	1.47	
<i>Magelona</i> sp.1		0.02		
<i>Scolaricia</i> sp.1		0.02		
<i>Brania</i> sp.1			0.27	
<i>Ceratonereis keiskama</i>	0.39	9.24	4.04	2.04
<i>Dendronereis arborifera</i>	0.10	9.74	8.38	0.01
<i>Exogone gemmifera</i>		0.02		
<i>Pisionidens indicus</i>		0.02		
<i>Desdemonia ornata</i>	0.34	2.19	8.10	15.46
<i>Ficopomatus enigmaticus</i>	0.04			0.01
<i>Ficopomatus</i> sp.1	0.01		0.02	
Sabellidae JuvT1				0.24
cf <i>Boccardi</i> sp.1				0.03
<i>Polydora kemp</i>		0.02		
<i>Prionospio multipinnulata</i>	39.17	50.78	70.24	14.07
ARTHROPODA:				
<u>Acarina</u>				
Trombidiformes sp.2	0.02			
<u>Pycnogonida</u>				
Pycnogonida sp.1		0.02		
<u>Collembola</u>				
Entomobryidae sp.1	0.01	0.03		
Entomobryidae sp.2	0.06	0.62		0.03
Hypogastruridae sp.1				0.01
<u>Crustacea</u>				
Amphipoda				
<i>Afrochiltonia capensis</i>	0.01			0.03
<i>Bolittsia minuta</i>				0.01
<i>Corophium triaenonyx</i>	0.01	0.02	0.14	15.46
<i>Grandidierella bonnieroides</i>			0.02	
<i>Grandidierella lignorum</i>		0.06	0.22	1.99
<i>Grandidierella lutosa</i>		0.11	0.59	6.49
<i>Grandidierella</i> spp.		0.51	3.16	40.21
Lysianassidae sp.1		0.02		
<i>Melita zeylanica</i>		0.02	0.06	0.01
<i>Orchestia rectipalma</i>				0.15
<i>Orchestia</i> sp.2	0.01			
<i>Talorchestia australis</i>	0.02	0.02		
Copepoda	0.04	0.47	0.02	
Cumacea		0.06	0.10	
Brachyura				
<i>Sesarma eulimene</i>	0.01			
<i>Varuna litterata</i>				0.01
Isopoda				
<i>Cirolana</i> sp.1			0.82	0.03
<i>Leptanthura</i> sp.1			0.02	
<i>Pseudosphaeroma barnadi</i>				0.03
Tanaidacea				
<i>Apseudes digitalis</i>			0.04	
<i>Sinelobus stanfordi</i>		0.06	0.02	0.11
Anomura	0.01	0.02	0.10	
Macrura	0.01			
Macrura PLT1				0.04

Table 4.5 continued...

Table 4.5 continued...

IDENTIFIED TAXA	URBAN		NON-URBAN	
	AT	LAM	MAN	INT
ARTHROPODA cont...				
<u>Insecta</u>				
Diptera				
	Ceratopogindae PT2	0.01		
	Ceratopogindae PT3	0.01	0.02	
	Ceratopogonidae LT3	0.01		
	Chironomini larvae spp.	1.55	2.67	0.16
	Chironomini pupae spp.	0.05	0.03	0.60
	Dolichopodidae PT1		0.02	
	Ephyridae LT1		0.02	
	Ephyridae LT3		0.03	
	Muscidae LT1		0.02	
	Muscidae PT1		0.02	
	Orthoclaadiinae larvae spp.	0.02	0.29	0.01
	Psychodidae PT1	0.01	0.09	
	Sciomyzidae LT2	0.01		
	Stratiomyidae LT1	0.01	0.02	
	Stratiomyidae PT1		0.02	
	Tanypodinae larvae spp.	0.01	0.26	
	Tanytarsini larvae spp.	0.10	0.02	0.02
	Tanytarsini pupae spp.	0.01		0.09
Ephemeroptera				
	Caenidae sp.1		0.02	
	Caenidae sp.3			0.01
	Caenis spp.		0.03	0.01
Odonata				
	Ictinogomphus sp.1		0.05	
	Onychogomphus sp.1	0.01	0.02	
Unidentified	Unidentified Insect T1	0.01		
MOLLUSCA:				
<u>Bivalvia</u>				
	Bivalvia sp1		0.02	
	<i>Brachidontes virgiliae</i>			0.19
<u>Gastropoda</u>				
	<i>Aplexa marmorata</i>	0.01		
	<i>Assimineia ovata</i>		0.23	0.04
	Assimineidae Juv spp			0.41
	Assimineidae sp.1	0.01		
	Assimineidae sp.2		0.02	0.06
	<i>Burnupia</i> sp.1			0.03
	Gastropoda PreJuv T1	0.02		
	<i>Melanoides tuberculata</i>	0.24		
	<i>Tarebia granifera</i>	56.55	0.06	
<u>Mollusca</u>	Mollusca PreJuv T1	0.05	0.19	0.06
			0.58	
CNIDARIA:				
<u>Hydrozoa</u>				
	Hydrozoa spp.		0.03	0.05
NEMATODA:				
	Nematoda spp.		0.87	0.33
NEMERTEA:				
	Nemertea sp.1		0.76	0.02
UNIDENTIFIED:				
	Unidentified sp.1		0.22	0.01
	Unidentified Worm T5		0.09	
	No. of sites (sample trips)	3 (6)	3 (6)	1 (5)
	Mean abundance per time	67249	45129	42823
	Total no. of taxa	38	53	32
			34	

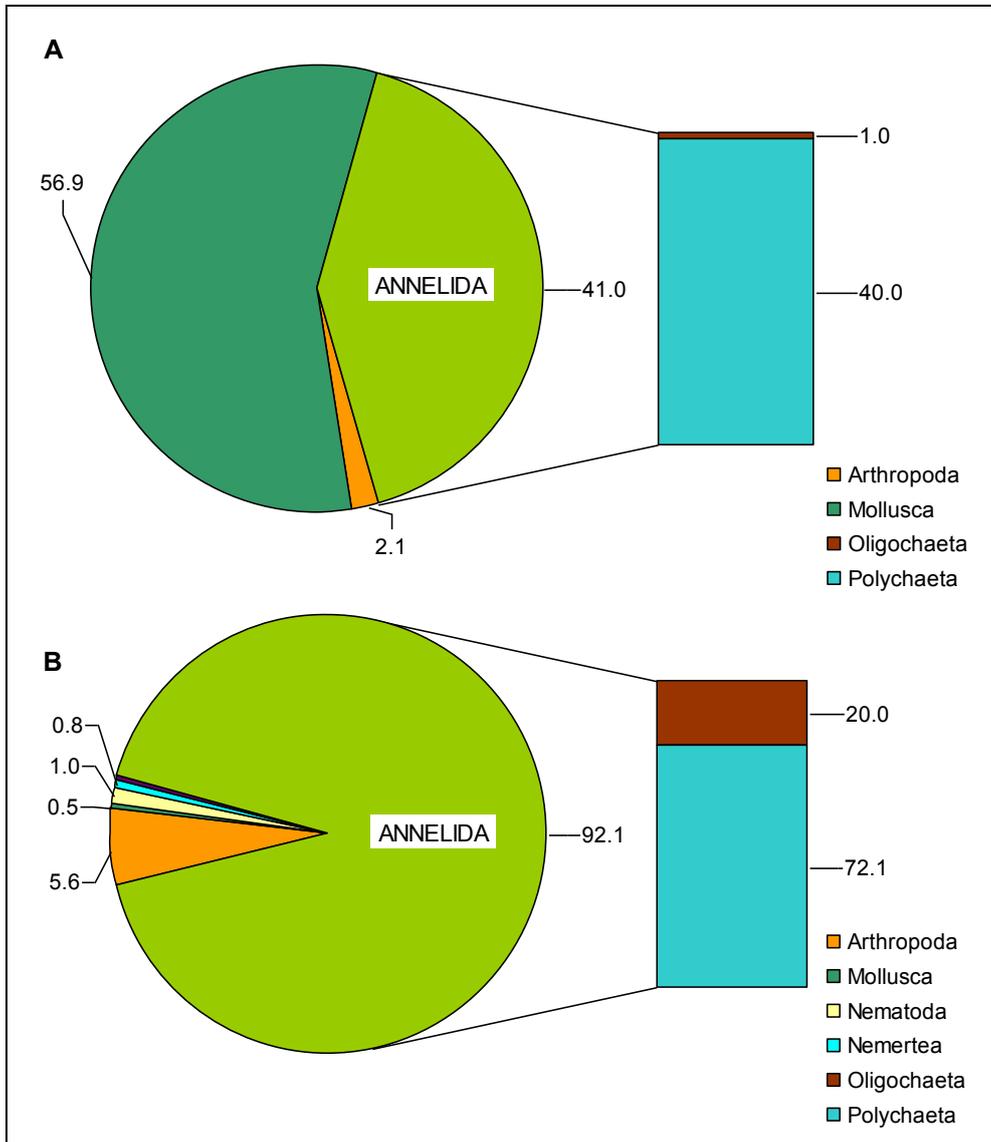


Figure 4.15 Macrozoobenthic community compositions for the Manzimtoti (A), and Little Manzimtoti (B), for the study period

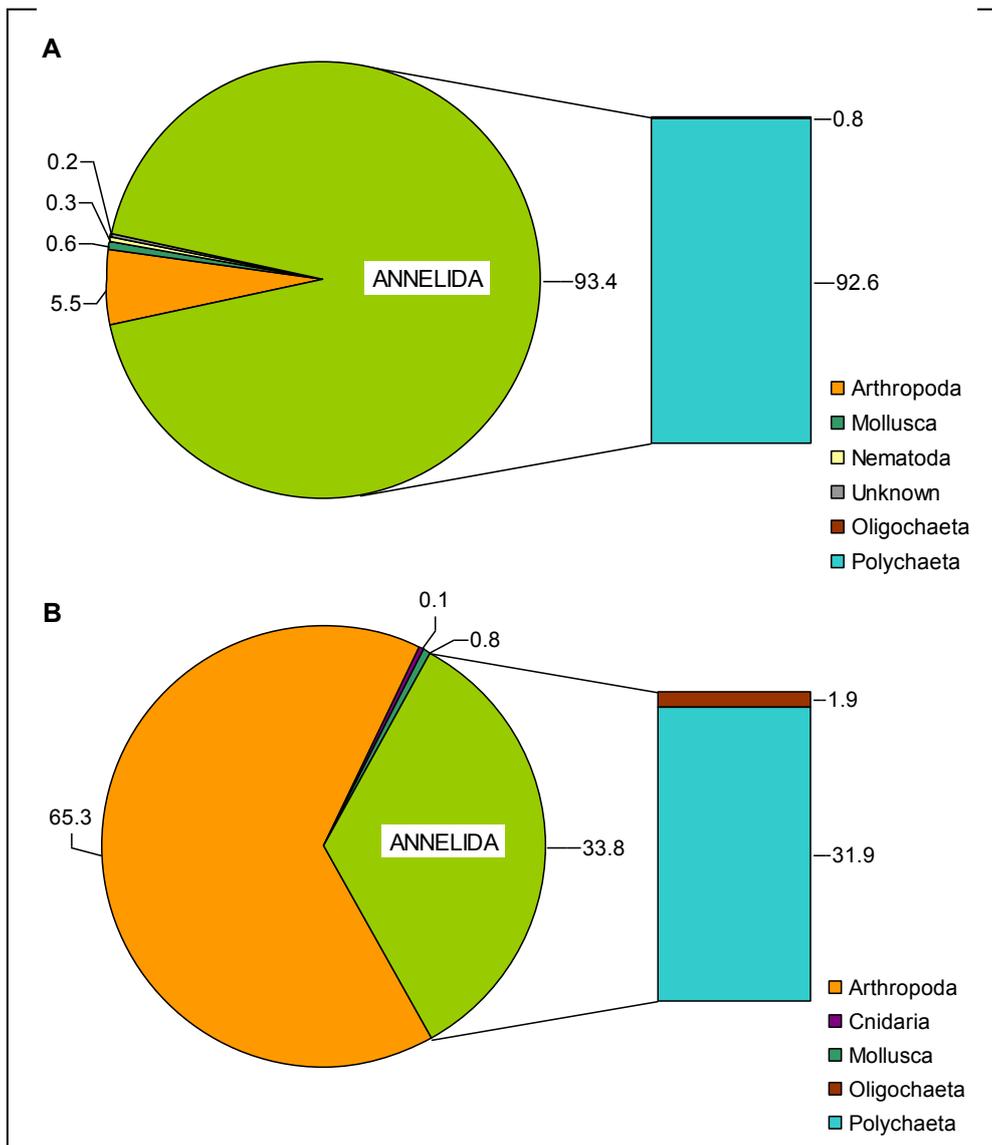


Figure 4.16 Macrozoobenthic community compositions for the Mhlabatshane (A), and Intshambili (B) for the study period

Changes in faunal abundance and number of taxa: Urban Estuaries

Figure 4.17 depicts the temporal and spatial distributions of community abundance and number of taxa in the Manzimtoti (A) and the Little Manzimtoti (B) estuaries. Each site was examined for trends in invertebrate abundance and number of taxa with increasing time after flooding.

In the Manzimtoti Estuary, there was a general trend of increasing total abundance from time 1 (1,722 ind.m⁻² ±2,294.02SD) to time 6 (7,691.6 ind.m⁻² ±8,055.07SD), except at time 5 when there was a decrease during the open mouth phase (3,189.2 ind.m⁻² ±3,539.43SD) (Figure 4.17 A). The high level of variability highlighted discrepancies in abundance due to inter-site differences. Faunal abundance was higher at site 1 than at other sites in the early stages of recolonisation during times 1 (4,519.2 ind.m⁻² ±1,915.17SD) and 2 (1,537.2 ind.m⁻² ±771.36SD). At both sites 2 and 3, macrobenthic abundance generally increased with time, except during the open phase, when there was marked decrease particularly at site 2. At this time abundance was lowest at site 2 (546 ind.m⁻² ±84.0SD). Maximum abundance at site 2 and site 3 was recorded at time 6 (14,624.4 ind.m⁻² ±10,340.98SD), and time 4 (10,172.4 ind.m⁻² ±2,214.56SD), respectively. The former was the greatest density of organisms recorded in this system over the entire study period. The number of taxa in the Manzimtoti Estuary was generally low. Nonetheless, there was an increase with increasing time after flooding from 1.7 (±0.59SD) to 4.3 (±0.82SD). The number of taxa similarly decreased at time 5 in agreement with abundance trends. Overall, the macrozoobenthic community of the Manzimtoti Estuary exhibited a relatively quick improvement following flood disturbance in terms of abundance and number of taxa. It appeared that breaching of the system had a negative influence on the community although, recovery was swift.

Faunal abundances of the two urban estuaries were not significantly different (Mann-Whitney U=2828.5; $p=0.205$). However, the systems differed in post-flood response such that the macrozoobenthic community of the Little Manzimtoti Estuary was dramatically influenced by the closed mouth phase (time 3) (Figure 4.17 B).

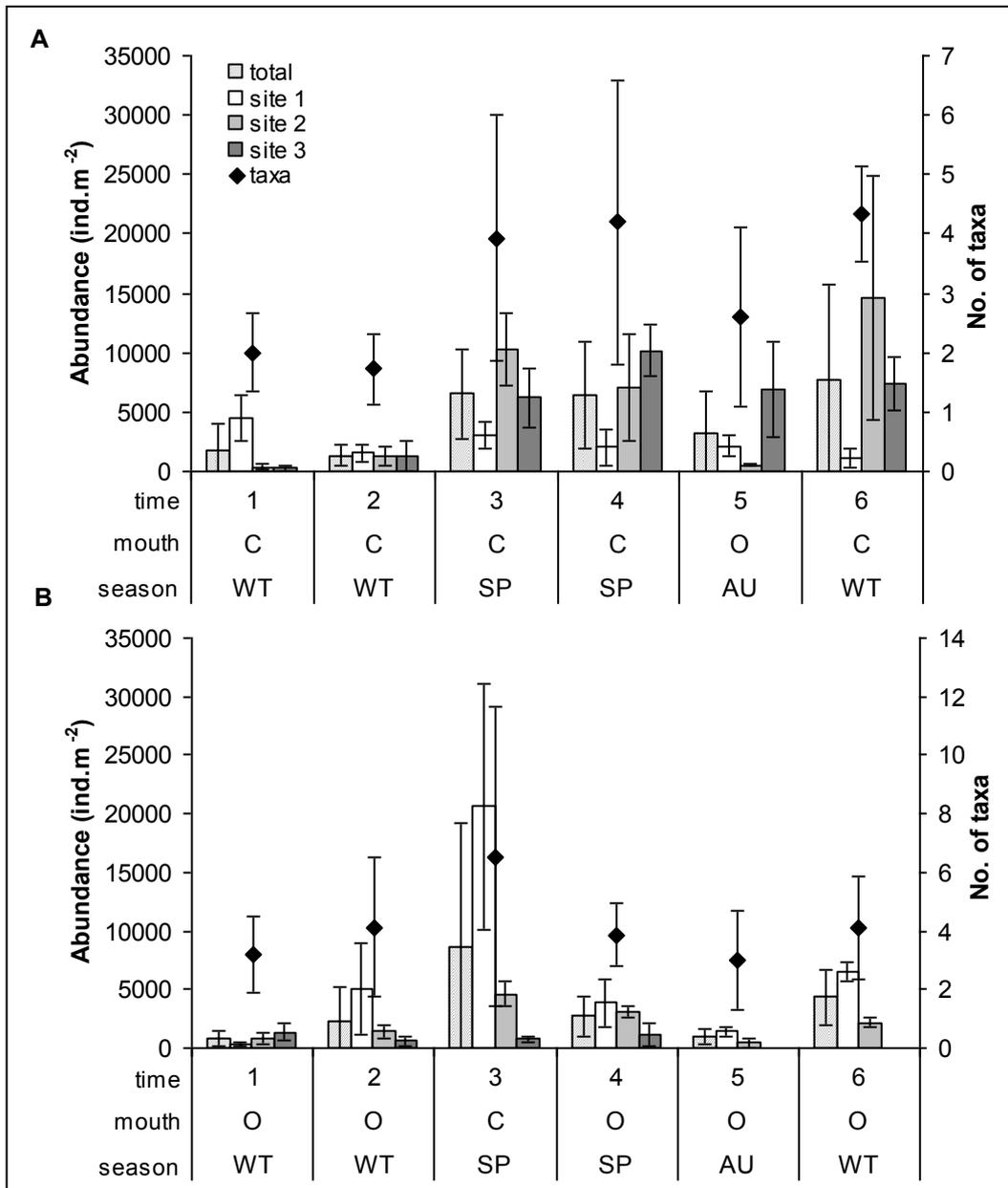


Figure 4.17 Mean abundance (bars) and number of taxa (points) (\pm SD) per time, mouth conditions and season, for macrozoobenthic communities sampled in the Manzimtoti (A) and Little Manzimtoti (B) estuaries. O = open phase, C= closed phase. WT= Winter, SP= Spring, AU= Autumn.

Total abundance increased from 820.48 ind.m⁻² (\pm 649.67SD) at time 1 to 8,671.6 ind.m⁻² (\pm 10,542.29SD) at time 3 and decreased thereafter to 945.0 ind.m⁻² (\pm 664.15SD) at time 5. At time 6, total abundance had increased to 4,342.8 ind.m⁻² (\pm 2,368.62SD). The peak in abundance during time 3 was attributed to an increase at site 1 which was significantly greater than that at sites 2 and 3 (Mann-Whitney U=0; p =0.008), and significantly greater than pre- and post-mouth closure abundances at the same site (time 2 t =3.121, p =0.014; time 4 Mann Whitney U=0; p =0.008). Site 3 was generally an area of poor abundance throughout the study period ranging between 280 - 2200 ind.m⁻². Site 2 was the area of intermediate abundance between site 1 and site 3. In terms of mean number of taxa, this was greatest at time 3 (6.5 \pm 5.1SD) coinciding with the peak in faunal abundance, both of which were associated with the intermittent closed state of the mouth. Apart from this anomaly, the mean number of taxa recorded from the Little Manzimtoti Estuary was generally uniform with time between 3 and 4 taxa. Overall, the recovery trajectory of the macrozoobenthic community of the Little Manzimtoti Estuary (in terms of abundance and number taxa) was interrupted by the closure of the mouth, which led to the rapid increase in abundance and number of taxa in the lower reaches. Subsequent re-opening caused a dramatic reduction in the community.

Changes in faunal abundance and number of taxa: Non-Urban Estuaries

In similarity with the urban estuaries, the Mhlabatshane and Intshambili non-urban estuaries were not significantly different in terms of faunal abundance (t =613.5; p =0.648). However, the lower reaches of the non-urban estuaries were generally richer in the number of taxa and faunal abundance than the lower reaches of the Manzimtoti and Little Manzimtoti estuaries. The temporal and spatial distributions of community abundance and number of taxa for the Mhlabatshane and the Intshambili estuaries are presented in Figure 4.18.

In the Mhlabatshane Estuary, abundance was lowest at the start of sampling at time 2 (2,167.2 ind.m⁻² \pm 826.02SD) (Figure 4.18 A). During the open mouth phase (time 3), abundance reached a maximum of 15,624.0 ind.m⁻² (\pm 4,393.27SD), but gradually decreased with increasing time to 2,545.2 ind.m⁻² (\pm 885.29SD) at time 6. There was a general decrease in the number of taxa with time from 10.4 (\pm 2.30SD) at time 2 to 7.6 (\pm 1.52) at time 6. However, at time 4 and time 5, the lowest (4.2 \pm 0.84SD) and highest (11.6 \pm 3.05SD) number of taxa were recorded, respectively.

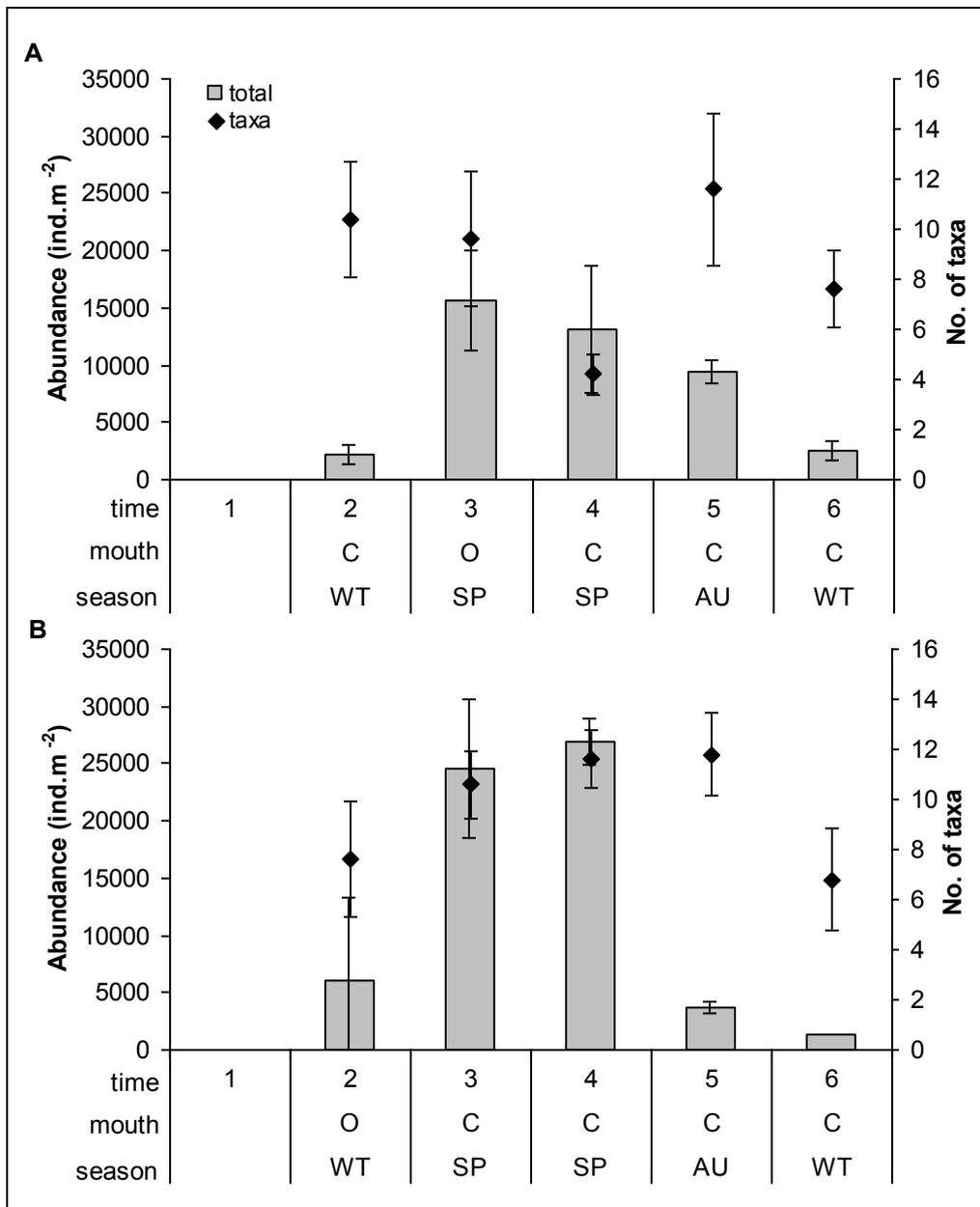


Figure 4.18 Mean abundance (bars) and number of taxa (points) (\pm SD) per time, mouth condition and season, for macrozoobenthic communities sampled in the Mhlabatshane (A) and Intshambili (B) estuaries. O = open phase, C= closed phase. WT= Winter, SP= Spring, AU= Autumn.

In the Intshambili Estuary (Figure 4.18 B), there was a trend of increasing faunal abundance with increasing time until time 5. This trend was seemingly related to the state of the estuary mouth and seasonality, because abundance was greatest during mouth closure at times 3 and 4, which coincided with Spring. Between time 4 and time 5 there was a significant decline in abundance from 26,846.4 ind.m⁻² ($\pm 6,067.39SD$) to 3,712.8 ind.m⁻² ($\pm 2,019.41SD$) ($t=8.09$, $p<0.001$). The minimum faunal abundance was sampled thereafter at time 6 (1,285.2 ind.m⁻² $\pm 502.77SD$). The number of taxa increased with increasing time after flooding and reached a peak at time 5 (11.8 $\pm 1.64SD$). However, at time 6 the number of taxa had decreased significantly (6.8 ± 2.05) ($t=4.26$, $p=0.003$).

Overall, the benthic communities of the Mhlabatshane and Intshambili estuaries exhibited relatively similar patterns in abundance following flooding such that abundance was low at the start and at the end of the sampling period, and highest at times 3 and 4. It appeared that changes in abundance were possibly linked to the state of the mouth and season. Trends in the number of taxa were markedly different between the two systems, and did not always follow the fluctuations in abundance.

Community-level changes following flood disturbance

Non-metric multidimensional scaling was used to examine the serial similarities/dissimilarities in the macrozoobenthic samples of each of the four estuaries. In the Manzimtoti Estuary, the samples from each time were not distinct such that they formed representative groups and samples were also not clearly separated based on site (Figure 4.19). Instead samples were divided at 50% similarity into 5 groups that comprised samples from various times and different sites. Group I was exclusively composed of samples from the middle region from times 3 and 4. Group II comprised the majority of samples from the lower reaches (site 1) from times 3 and 4. The majority of the Manzimtoti samples were combined into Group III, comprising a mixture of samples from each time and site. Group IV was mainly composed of samples from the upper region (site 3) from times 2 and 5, and small portion from time 1. A pair of samples from the upper reaches from times 3 and 4 defined Group V. Groups I and II indicated particular benthic communities that existed during times 3 and 4 in the middle and lower reaches, respectively. In Groups III and IV, all time 5 samples approximated to time 1 and 2 samples. This was likely related to the breached state of the Manzimtoti Estuary at time 5. Samples from the end of the study period (time 6) were also located within Group III indicating

similarity with samples at various stages of recolonisation. It was postulated that samples from this time were reflective of post-breach recolonisation.

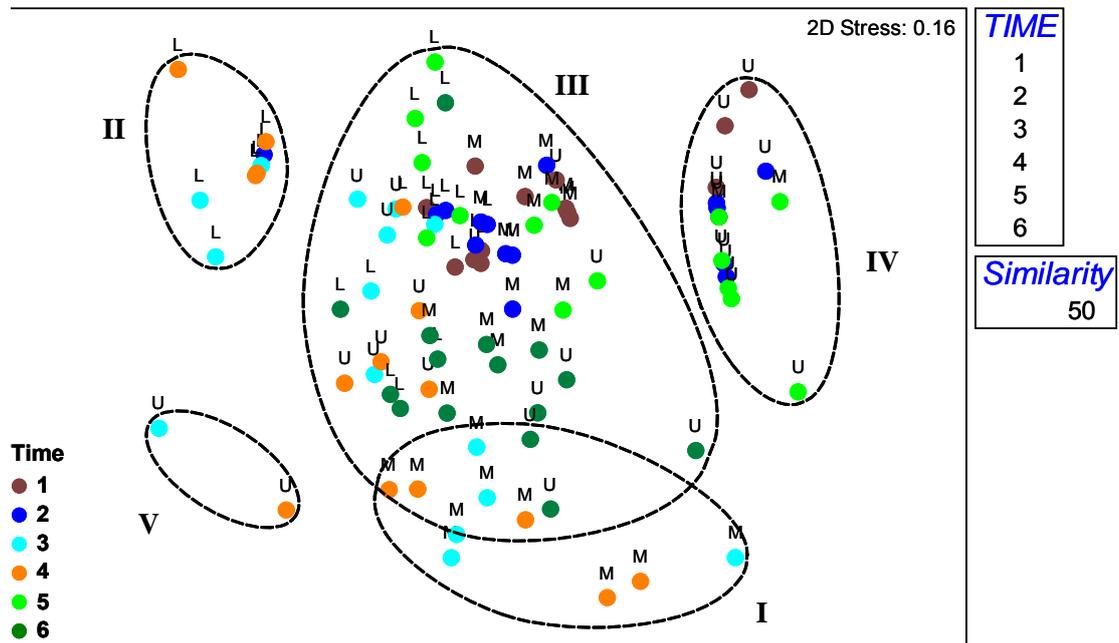


Figure 4.19 NMDS plot of Manzimtoti samples according to time and site, illustrating groups of samples that shared 50% similarity in benthic community characteristics. L= Lower reaches (site 1) M= Middle reaches (site 2), U= Upper reaches (site 3).

In contrast to the Manzimtoti Estuary, macrozoobenthic samples from the Little Manzimtoti Estuary (Figure 4.20) were better separated according to time (30% similarity). Five groups of samples were identified. Group I comprised the majority of samples from time 1 and time 2. Group II comprised predominantly samples from time 3 and time 4, and several lower reaches samples from time 2. Group III was exclusively comprised of all time 5 and time 6 samples. Group IV was a small group comprising samples from the upper reaches (time 4 and time 2). A pair of samples from the upper reaches during times 1 and 2 defined Group V. A single outlier from time 4 was identified. The configuration of the major groups (I, II, III) suggested three stages in macrozoobenthic recolonisation of the Little Manzimtoti Estuary. Within Group II, time 3 samples from the lower reaches formed a discrete cluster. It can be argued that closure of the mouth at time 3 enabled the development of a distinct community. Group IV samples presented a unique set of community characteristics only found in upper samples of time 4, and one upper sample of time 2.

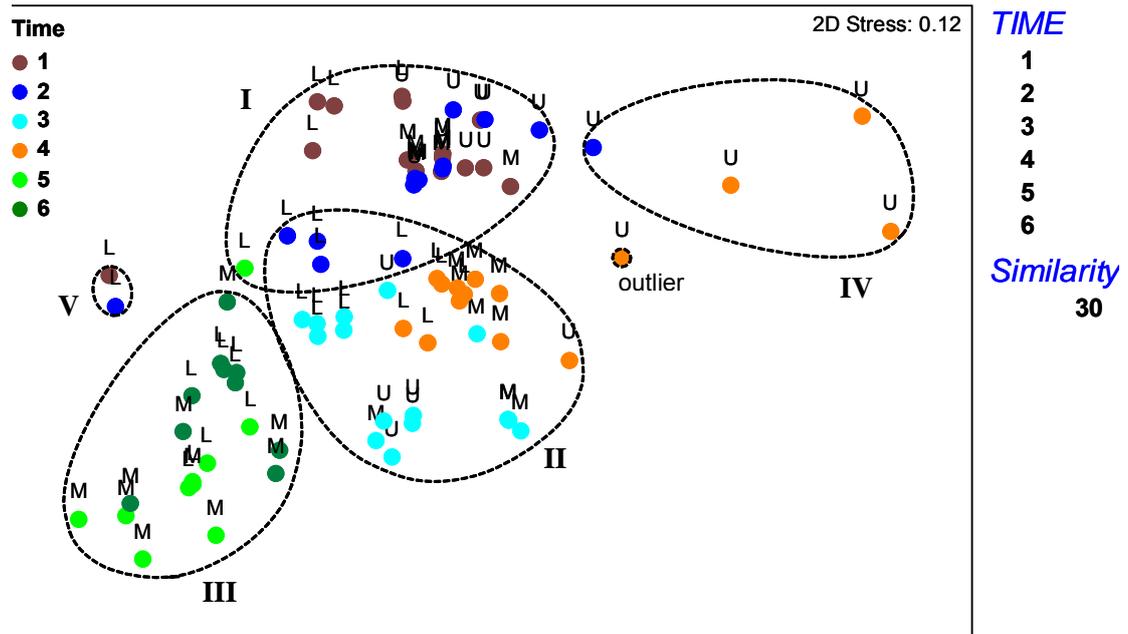


Figure 4.20 NMDS plot of Little Manzimtoti samples according to time and site, illustrating groups of samples that shared 30% similarity in benthic community characteristics. L= Lower reaches (site 1) M= Middle reaches (site 2), U= Upper reaches (site 3).

Ordination of the macrozoobenthos of the Mhlabatshane Estuary revealed four groups of samples (60% similarity) that were separated based on differences in time (Figure 4.21). Group I consisted of samples from times 2 and 3, and Groups II, III and IV exclusively comprised samples times, 4, 5 and 6, respectively. A single sample from time 2 constituted the outlier. It was thus established that during the initial stages of recolonisation, the macrozoobenthic community of the Mhlabatshane Estuary remained relatively uniform (times 2 and 3). Thereafter, distinct communities existed with increasing time after flooding (times 4 to 6). The offset of Group II (time 4) from the almost cyclic configuration of the remaining groups, suggested the occurrence of a unique community at this time.

Groups of samples from the Intshambili Estuary were less well defined as illustrated by NMDS (Figure 4.22). At 55% similarity, 3 groups of samples were evident. Group II comprised the majority samples, including all those from times 3 and 4, and several from times 2 and 5. Groups I and III, comprised a mixture of samples from time 2 and time 6, and time 5 and 6, respectively. A single time 6 outlier was present. In general, the changes that occurred during the recolonisation of the Intshambili Estuary were minor, indicated by the similarity between the majority of samples and by the absence of groups separated according to time. Similarities

between samples from the first and last time periods suggest a cyclical progression in recolonisation. This pattern was also reflected in the trends in faunal abundance and number of taxa.

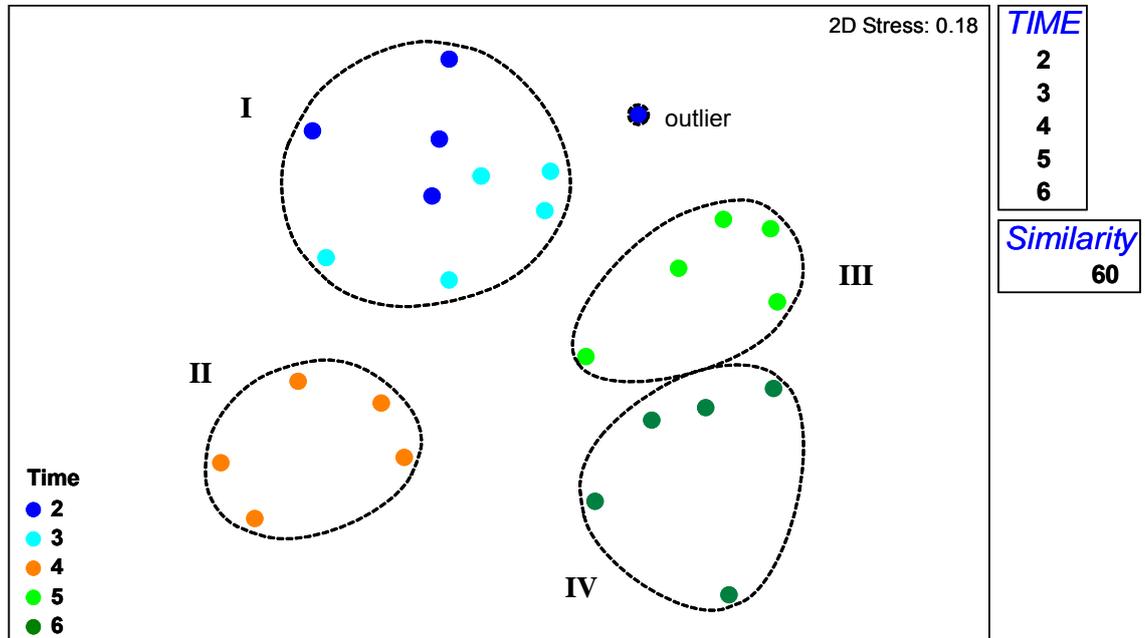


Figure 4.21 NMDS plot of Mhlabatshane samples according to time, illustrating groups of samples that shared 60% similarity in benthic community characteristics

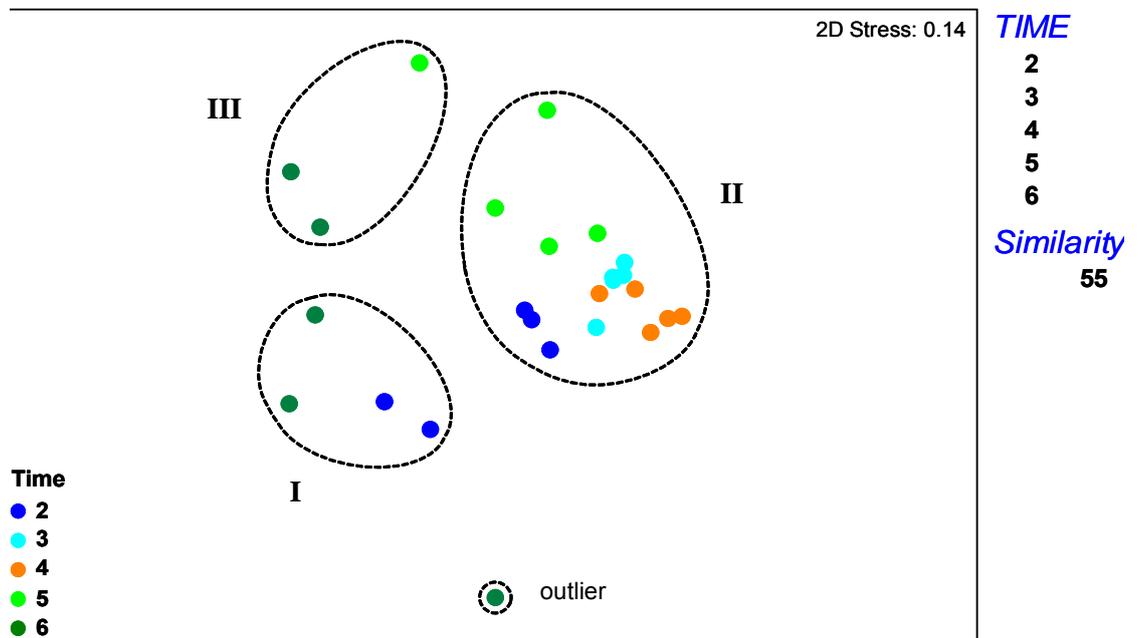


Figure 4.22 NMDS plot of Intshambili samples according to time, illustrating groups of samples that shared 55% similarity in benthic community characteristics

4.4.2.2 Differing responses of urban and non-urban communities

The macrozoobenthos of the adjacent estuaries was compared using the above information to determine whether the urban and non-urban environmental settings were reflected in the communities of the respective estuaries. In this section, the similarities between the macrozoobenthos of the adjacent systems are graphically represented in NMDS ordination plots, and statistically and taxonomically verified using Analysis of Similarity (ANOSIM) and Similarity Percentage (SIMPER) procedures, respectively.

Ordination of the urban samples (not illustrated) revealed less than 35% similarity between the macrozoobenthos of the Manzimtoti and Little Manzimtoti estuaries. Thus, despite the common urban setting, these two systems contained markedly different faunal communities. The macrozoobenthos of the Mhlabatshane and Intshambili estuaries was more similar. Samples from both estuaries were divided into two major groups at 50% similarity (Figure 4.23). Group I comprised several samples from the Intshambili Estuary from the beginning and end of the study period that were similar to most of the Mhlabatshane samples (times 2 to 4). Conversely, Group II comprised the remaining Mhlabatshane samples (time 5 to 6) and the majority of the Intshambili samples (times 2 to 5). However, within these groups, differentiation between the two systems was still evident. These findings were supported by Analysis of Similarity, in which intermediate R-values and significant *p*-values confirmed the differences in the macrozoobenthic communities between the Manzimtoti and Little Manzimtoti estuaries ($R=0.519$, $p<0.0001$), and the Mhlabatshane and Intshambili estuaries ($R=0.418$, $p<0.0001$). Thus, the benthic communities of each system remained discrete, notwithstanding the greater degree of similarity between the Mhlabatshane and Intshambili estuaries in comparison with the two urbanised estuaries.

In terms of species composition and their contributions to the sample similarities (SIMPER), the distinction between the Manzimtoti and Little Manzimtoti macrozoobenthic communities was based on the differences in the average abundance of four prominent taxa (Table 4.6), namely *Tarebia granifera* (Gastropoda), *Prionospio multipinnulata* (Polychaeta), Oligochaeta spp. and Chironomini larvae spp. (Insecta). Together, they were accountable for approximately 56% of the dissimilarity between the two estuaries. The most important attribute was the high abundance of *T. granifera* in the Manzimtoti Estuary and its virtual absence from the Little Manzimtoti Estuary. This discrepancy accounted for 20% of the dissimilarity between the

urban estuaries. *P. multipinnulata* was most abundant in the Manzimtoti, while *Oligochaeta* spp. and Chironomini larvae spp. were more abundant in the Little Manzimtoti system.

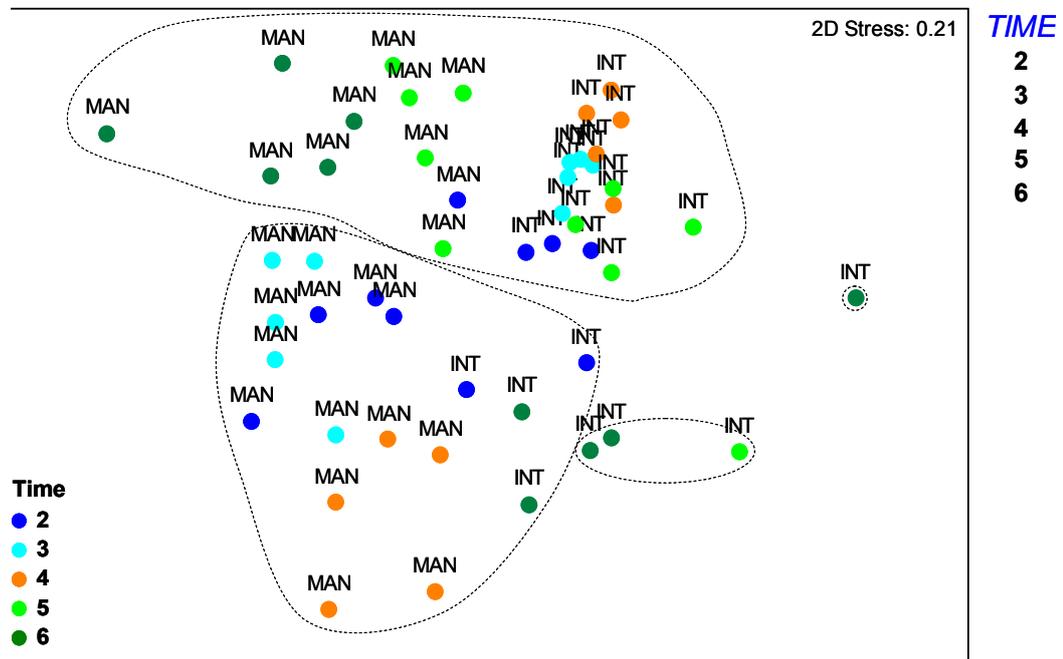


Figure 4.23 NMSD plot of non-urban samples according to estuary and time showing groups of samples that shared 50% similarity in benthic community characteristics. MAN = Mhlabatshane and INT = Intshambili

Table 4.6 Percentage contribution of invertebrate taxa to the dissimilarity between the benthic communities of Manzimtoti (AT) and Little Manzimtoti (LAM). Only species contributing up to 50% dissimilarity are presented.

Species	AT	LAM	Av. Dissimilarity	Contribution (%)	Cumulative (%)
	Av. Abundance	Av. Abundance			
<i>Tarebia granifera</i>	5.92	0.19	16.69	20.04	20.04
<i>Prionospio multipinnulata</i>	5.37	2.90	13.30	15.97	36.01
<i>Oligochaeta</i> spp.	0.88	3.56	10.01	12.02	48.04
Chironomini larvae spp.	1.48	2.16	6.32	7.59	55.62
Average Dissimilarity = 83.25					

Eight species were accountable for approximately 51% of the difference between the Mhlabatshane and Intshambili benthic communities (Table 4.7). The high abundance of *Corophium triaenonyx* (Crustacea) in the Intshambili Estuary and its negligible occurrence in the Mhlabatshane contributed most to the dissimilarity between the two systems (9.83%), followed by contributions made by other crustacean taxa, including *Grandidierella lutosa* (6.38%), *Grandidierella* spp. (5.91%) and *Grandidierella lignorum* (5.89%). Discrepancies in the

abundance of two polychaete species, *Dendronereis arborifera* and *Ceratonereis keiskama* between the two estuaries also made important contributions to the overall dissimilarity, 6.66% and 6.21% respectively. Oligochaeta spp. and Chironomini larvae spp. were more abundant in the Intshambili, adding 5.33% and 4.56% to the overall dissimilarity, respectively.

Table 4.7 Percentage contribution of invertebrate taxa to the dissimilarity between Mhlabatshane (MAN) and Intshambili (INT) benthic communities. Only species contributing up to 50% dissimilarity are presented.

Species	MAN	INT			
	Av. Abundance	Av. Abundance	Av. Dissimilarity	Contribution (%)	Cumulative (%)
<i>Corophium triaenonyx</i>	0.81	5.90	5.29	9.83	9.83
<i>Dendronereis arborifera</i>	3.70	0.15	3.59	6.66	16.49
<i>Grandidierella lutosa</i>	2.51	4.74	3.44	6.38	22.87
<i>Ceratonereis keiskama</i>	2.41	3.57	3.34	6.21	29.08
<i>Grandidierella</i> spp.	4.76	7.49	3.19	5.91	34.99
<i>Grandidierella lignorum</i>	1.29	3.57	3.17	5.89	40.88
Oligochaeta spp.	3.00	3.41	2.87	5.33	46.21
Chironomini larvae spp.	0.68	2.52	2.45	4.56	50.77
Average Dissimilarity = 53.86					

It was concluded that adjacent estuaries within specific urban and non-urban environments do not possess shared benthic community characteristics indicative of their common environmental setting. Each system hosted a unique benthic community based on differences in species composition and relative species abundance. Therefore, the classification of adjacent estuaries (in terms of macrozoobenthos) as 'urban' and 'non-urban' was invalid, further suggesting that the observed response to flood disturbance was not governed by the urbanised state of each estuary.

4.4.2.3 Distinction between temporarily open/closed estuaries

Differences in communities

The large disparities between the macrozoobenthos in estuaries within the same environmental setting warranted an investigation into the overall similarity between the macrozoobenthos of the selected TOCEs. The accepted classification of South African estuaries into five estuarine types was based on characteristic physical and chemical features, and key environmental processes shared by several systems (Whitfield 1992). Under the premise that the four TOCEs are similar in estuarine characteristics, the macrozoobenthos in the lower reaches (Site 1) of the Manzimtoti, Little Manzimtoti, Mhlabatshane and Intshambili estuaries

were simultaneously evaluated for inherent differences in community structure, using community classification and ordination techniques, and Analysis of Similarity (ANOSIM) and Similarity Percentage (SIMPER) procedures. Only the lower reaches could be compared because sampling was not conducted in the middle and upper reaches of the Mhlabatshane and Intshambili estuaries.

Ordination (NMDS) revealed the isolation of Manzimtoti samples from those of the Little Manzimtoti, Mhlabatshane and Intshambili because these two groups shared less than 40% similarity (Figure 4.24). At 40% similarity, three distinctive groups, and one outlier were evident. One group was solely composed of Manzimtoti samples, another only Little Manzimtoti samples, and the third group comprised both Mhlabatshane and Intshambili samples. Overall, there was a low level of similarity between the four systems (<50%).

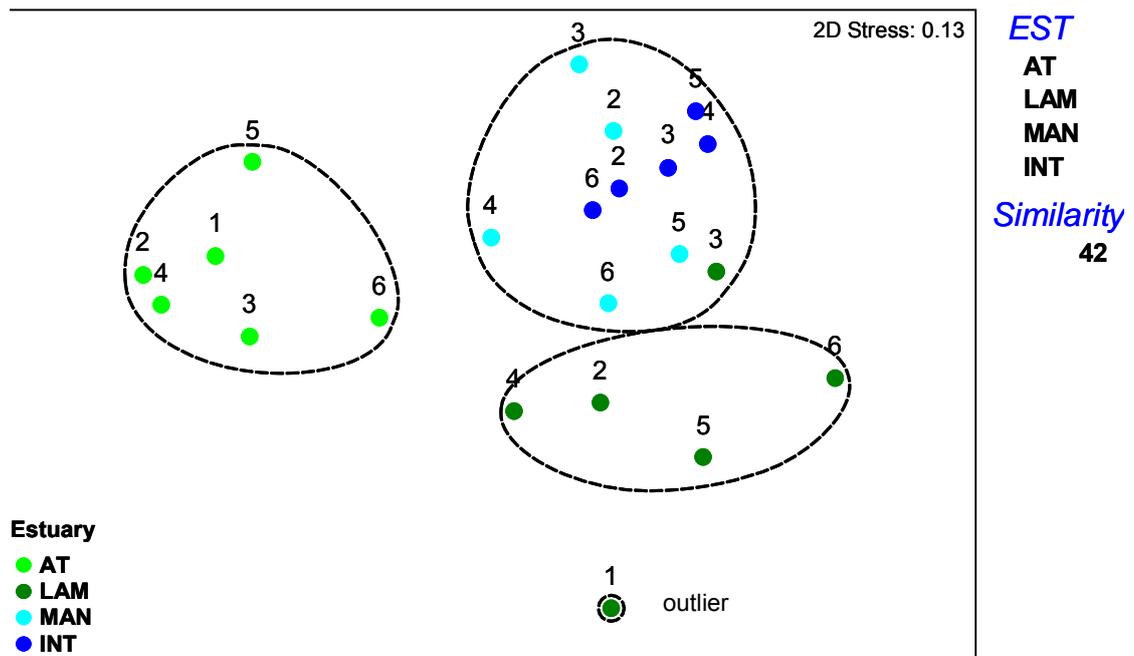


Figure 4.24 NMDS plot of site 1 (lower reaches) samples according to estuary and time, showing groups that shared 40% similarity in community characteristics. AT = Manzimtoti, LAM = Little Manzimtoti, MAN = Mhlabatshane and INT = Intshambili.

Analysis of Similarity confirmed that there were significant differences in the macrozoobenthic communities of all four estuaries (Global $R=0.726$, $p<0.0001$). The high Global R statistic indicated high levels of estuary exclusivity between samples. This was particularly evident in the pair-wise comparisons involving the Manzimtoti Estuary, which yielded high R-values and

significant p -values (Table 4.8). The greatest community differences occurred between the Manzimtoti and Mhlabatshane estuaries ($R=0.973$, $p=0.002$) and the Manzimtoti and Intshambili estuaries ($R=0.984$, $p=0.002$). The Little Manzimtoti and Mhlabatshane communities were most similar, however their communities remained significantly distinct ($R=0.309$, $p=0.03$). In addition, R-values of the comparisons between the adjacent systems were large and highly significant: Manzimtoti and Little Manzimtoti ($R=0.861$, $p=0.002$), and Mhlabatshane and Intshambili ($R=0.628$, $p=0.008$) (Table 4.8).

Table 4.8 Results from Analysis of Similarity between the Manzimtoti (AT), Little Manzimtoti (LAM), Mhlabatshane (MAN) and Intshambili (INT) estuaries ($p=0.05$)

Pair-wise Tests	R Statistic	Significance Level
AT vs LAM	0.861	0.002
AT vs MAN	0.973	0.002
AT vs INT	0.984	0.002
LAM vs MAN	0.309	0.030
LAM vs INT	0.629	0.004
MAN vs INT	0.628	0.008

The pair-wise comparisons that yielded the highest (AT vs. INT, AT vs. MAN) and lowest (LAM vs. MAN) R-statistic values were further examined to investigate the species responsible for their degree of separation. These species are presented in Tables 4.9-4.11. The most important discriminating feature of the comparisons involving the Manzimtoti and either the Mhlabatshane or the Intshambili estuaries, was the complete absence of certain invertebrate species from the Manzimtoti system. Crustacean amphipods of the genus *Grandidierella* were prominent species in both the Intshambili and Mhlabatshane estuaries. Their absence from the Manzimtoti system constituted 6.56-11.04% (Table 4.9) and 4.57-8.58% (Table 4.10) of the dissimilarities between them, respectively. In both cases, *Tarebia granifera* was present only in the Manzimtoti Estuary, which contributed 6.92% to dissimilarity in the AT-INT comparison and 8.31% to dissimilarity in the AT-MAN comparison. The differences between these estuaries were further emphasised by greater abundances of the amphipod *Corophium triaenonyx* and polychaete species, *Desdemonia ornata* and *Ceratonereis keiskama*, in the Intshambili Estuary (Table 4.9), and higher of abundances of *D. ornata*, *C. keiskama*, *Dendronereis arborifera* and *Oligochaeta* spp. in the Mhlabatshane Estuary (Table 4.10). The latter system was further

separated from the Manzimtoti Estuary by the exclusive presence of Nematoda spp. and Unidentified spp.

Table 4.9 Percentage contribution of invertebrate taxa to the dissimilarity between Manzimtoti (AT) and Intshambili (INT) benthic communities. Only species contributing up to 50% dissimilarity are presented.

Species	AT	INT	Av. Dissimilarity	Contribution (%)	Cumulative (%)
	Av. Abundance	Av. Abundance			
<i>Grandidierella</i> spp.	0.00	7.78	8.36	11.04	11.04
<i>Corophium triaenonyx</i>	0.37	6.41	6.33	8.36	19.41
<i>Desdemona ornata</i>	1.96	7.10	5.76	7.61	27.02
<i>Grandidierella lutosa</i>	0.00	5.46	5.70	7.53	34.55
<i>Tarebia granifera</i>	4.83	0.00	5.24	6.92	41.48
<i>Grandidierella lignorum</i>	0.00	4.69	4.96	6.56	48.04
<i>Ceratonereis keiskama</i>	0.37	4.55	4.42	5.85	53.88
Average Dissimilarity = 75.68					

Table 4.10 Percentage contribution of invertebrate taxa to the dissimilarity between Manzimtoti (AT) and Mhlabatshane (MAN) benthic communities. Only species contributing up to 50% dissimilarity are presented.

Species	AT	MAN	Av. Dissimilarity	Contribution (%)	Cumulative (%)
	Av. Abundance	Av. Abundance			
<i>Grandidierella</i> spp.	0.00	5.15	6.20	8.58	8.58
<i>Tarebia granifera</i>	4.83	0.00	6.00	8.31	16.88
<i>Desdemona ornata</i>	1.96	5.93	5.44	7.53	24.41
<i>Dendronereis arborifera</i>	0.92	3.90	4.28	5.92	30.33
<i>Ceratonereis keiskama</i>	0.37	3.45	3.88	5.37	35.70
Oligochaeta spp.	0.75	3.87	3.81	5.27	40.97
<i>Grandidierella lutosa</i>	0.00	2.99	3.30	4.57	45.54
Unidentified spp	0.00	2.46	3.20	4.43	49.97
Nematoda spp	0.00	2.29	2.86	3.96	53.93
Average Dissimilarity = 72.24					

In contrast to the abovementioned cases, the lowest degree of dissimilarity occurred between the Little Manzimtoti and Mhlabatshane estuaries (Table 4.8). These two systems had several species in common and the dissimilarity between them was based on differences in the average abundance of a few prominent species (Table 4.11). Three polychaete species, *Prionospio multipinnulata*, *D. arborifera*, and *D. ornata*, the amphipod species *G. lutosa* and *Grandidierella* spp., Nematoda spp. and Unidentified spp. were more abundant in the Mhlabatshane Estuary, while Nemertea sp. 1, Oligochaeta spp. and *Ceratonereis keiskama* were more abundant in the Little Manzimtoti Estuary.

Table 4.11 Percentage contribution of invertebrate taxa to the dissimilarity between Little Manzimtoti (LAM) and Mhlabatshane (MAN) benthic communities. Only species contributing up to 50% dissimilarity are presented.

Species	LAM	MAN	Av. Dissimilarity	Contribution (%)	Cumulative (%)
	Av. Abundance	Av. Abundance			
<i>Prionospio multipinnulata</i>	4.07	8.18	4.95	8.47	8.47
<i>Dendronereis arborifera</i>	3.28	3.90	3.52	6.03	14.50
Nemertea sp.1	3.21	0.45	2.84	4.86	19.37
<i>Desdemona ornata</i>	3.84	5.93	2.82	4.83	24.20
Oligochaeta spp.	5.49	3.87	2.79	4.77	28.97
<i>Grandidierella</i> spp.	2.70	5.15	2.64	4.52	33.48
<i>Ceratonereis keiskama</i>	4.78	3.45	2.62	4.49	37.97
<i>Grandidierella lutosa</i>	0.68	2.99	2.53	4.33	42.30
Unidentified spp.	0.00	2.46	2.50	4.27	46.58
Nematoda spp.	2.18	2.29	2.31	3.96	50.54
Average Dissimilarity = 58.41					

Differences in community diversity

Analysis of Variance (Table 4.12) exposed a highly significant difference in diversity between mouth samples largely due to inter-estuary variability (ANOVA $F= 90.186$, $p<0.001$). The effect of time, and interaction between estuary and time were also significant ($p<0.001$). Furthermore, the greatest differences in diversity occurred in comparisons involving the Intshambili Estuary (Table 4.12). The diversity of the Intshambili macrozoobenthic community was significantly greater than both the Manzimtoti (Tukey Test, $q=9.14$; $p<0.001$) and the Little Manzimtoti (Tukey Test, $q=6.22$; $p<0.001$) estuaries. Similarly, the diversity of the Mhlabatshane macrozoobenthos was significantly greater than the Manzimtoti ($q=5.88$; $p<0.001$), however not different from the Little Manzimtoti system (Tukey Test, $q=2.96$, $p<0.001$). There was no significant difference between the diversity of the Intshambili and the Mhlabatshane macrozoobenthic communities, nor the communities at site 1 in Manzimtoti and the Little Manzimtoti estuaries.

In the Manzimtoti and Little Manzimtoti estuaries, diversity was analysed for across-site differences (Table 4.13). Two-way ANOVA revealed a highly significant relationship between estuary and site ($F= 22.970$, $p<0.001$), indicating that diversity not only differed according to each estuary but also according to site. The relationships between time and site ($F= 3.531$, $p=0.003$), and estuary, time and site ($F= 4.165$, $p<0.001$) were also significant.

Table 4.12. Results of Analysis of Variance and Tukey Test for differences in diversity of macrozoobenthos between the lower sites (only) of the four estuaries. DF= Degrees of Freedom, F= critical value of ANOVA, and q= critical value of Tukey Test, P= level of significance ($p=0.05$). AT= Manzimtoti, LAM= Little Manzimtoti. MAN= Mhlabatshane. and INT= Intshambili.

ANOVA	DF	F	P
<i>Main Factors</i>			
Estuary (E)	3	90.196	<0.001
Time (T)	4	21.859	<0.001
<i>2-way Interactions</i>			
E x T	12	9.881	<0.001
Difference			
TUKEY TEST	of Ranks	q	P
<i>Pair-wise Comparisons</i>			
AT vs INT	1325.5	9.14	<0.001
LAM vs INT	902.0	6.22	<0.001
AT vs MAN	853.0	5.88	<0.001
INT vs MAN	472.5	3.26	>0.05
LAM vs MAN	429.5	2.96	>0.05
AT vs LAM	423.5	2.92	>0.05

Table 4.13. Results of Analysis of Variance for differences in diversity of macrozoobenthos between the Manzimtoti and Little Manzimtoti estuaries. DF= Degrees of Freedom, F= critical value of ANOVA, P= level of significance ($p=0.05$).

ANOVA	DF	F	P
<i>Main Factors</i>			
Estuary (E)	1	23.293	<0.001
Time (T)	3	0.074	0.974
Site (S)	2	0.044	0.957
<i>2-way Interactions</i>			
E x T	3	1.874	0.139
E x S	2	22.970	<0.001
T x S	6	3.531	0.003
<i>3-way Interactions</i>			
E x T x S	6	4.165	<0.001

4.4.2.4 Recolonisation sequence of macrozoobenthic communities

Trends in community indices

The recolonisation of the four estuaries by macrozoobenthos in response to flood disturbance was analysed using changes in abundance, indices of diversity and evenness, and shifts in prominent faunal assemblages and numerical dominance. Non-metric multidimensional scaling was used to plot the trajectory of the emergent communities at each time period. These groups were statistically verified through ANOSIM. SIMPER analyses identified definitive species assemblages for each time according to their percentage contribution to the similarity between samples within each time. The relative abundances of the top five most numerically abundant species per time period within each estuary were presented as percentage contributions to the total faunal abundance to illustrate changes in species dominance.

Figure 4.25 displays the trends in community diversity with increasing time after flooding, together with species richness and evenness, in the Manzimtoti Estuary. Overall, there was a small increase in the diversity of the Manzimtoti macrobenthic community with time (Figure 4.25 A) from 0.42 at time 1 to 0.58 at time 6. This was related to both increased species richness and faunal abundance. Species evenness was low at times 3 and 4 (when faunal abundance was high), suggesting the increased dominance of certain species at these times. Fluctuations in these indices varied between sites within the Manzimtoti Estuary.

At site 1 (Figure 4.25 B), diversity was relatively high ($H' = 0.54$) at the start of the sampling period (time 1). It was lowest ($H' = 0.09$) at time 3, but increased steadily thereafter to a maximum at time 6 ($H' = 0.94$). Species richness was low from times 1-4 ($J' = 0.1-0.17$), and only increased to 0.5 at time 6. Increases in all indices between time 4 and time 6 were possibly related to an influx of additional species after opening of the mouth at time 5. Trends in community indices at site 2 were variable in comparison with those at site 1 (Figure 4.25 C). At time 2 (Winter), evenness reached a maximum ($J' = 0.82$) while richness was at a minimum ($d = 0.18$). Inversely, evenness had decreased and richness had increased at time 3 ($d = 0.56$; $J' = 0.32$), and remained relatively unchanged at time 4. Although fluctuations in diversity were small, there was marked decline from a maximum at time 4 ($H' = 0.7$) to a minimum at time 5 ($H' = 0.41$), mirrored by a decrease in species richness ($d = 0.6$ to 0.19), and particularly in abundance.

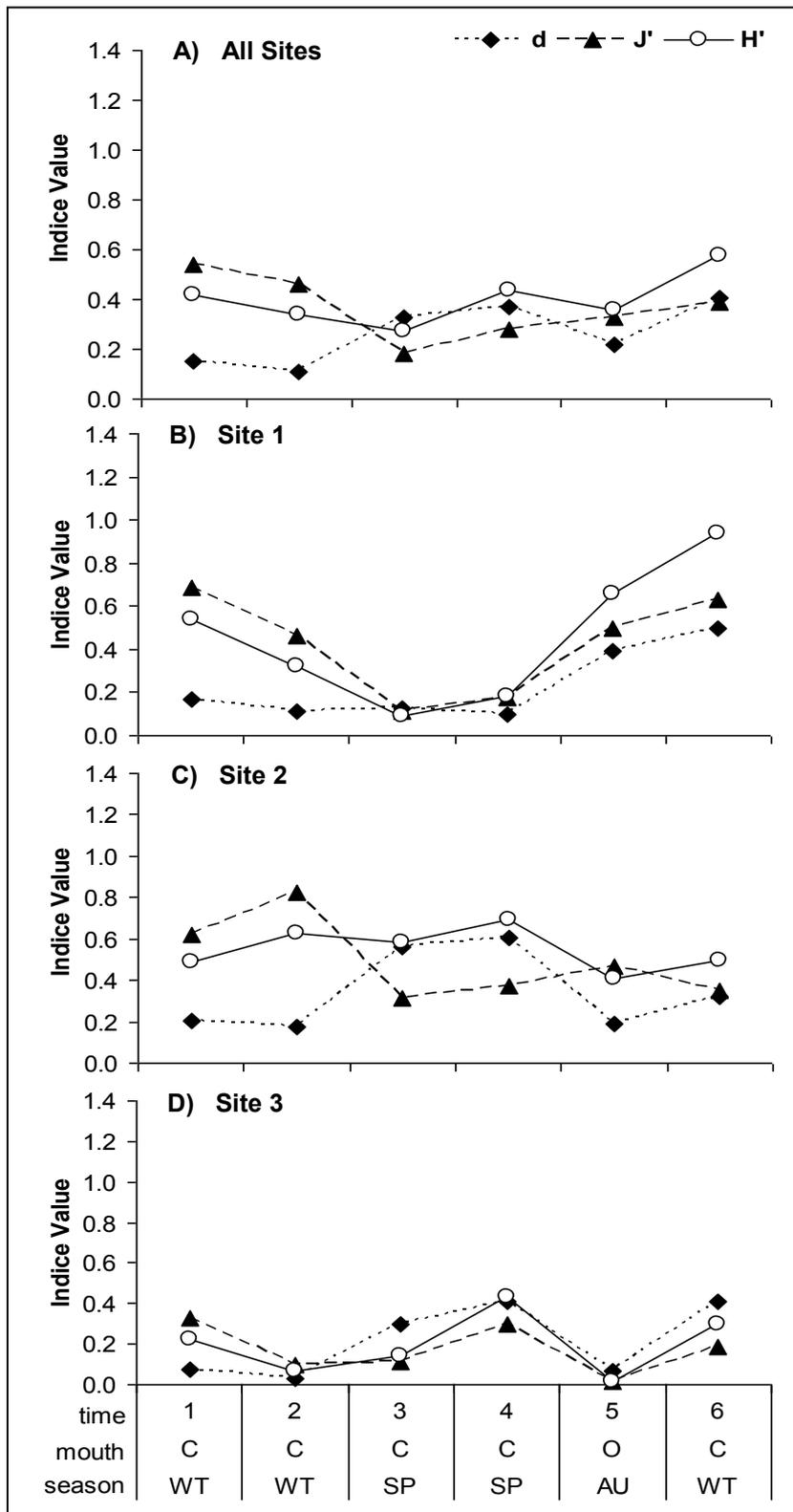


Figure 4.25 Community indices against time, month condition and season, calculated for the macrozoobenthic community of the Manzimtoti Estuary across all sites (A), and at site 1 (B), site 2 (C), site 3 (D) O = open phase, C= closed phase. WT= Winter, SP= Spring, AU= Autumn.

At site 3, all community indices were generally lower in comparison with site 2, and exhibited similar fluctuations with increasing time (Figure 4.25 D). All indices were low at time 2 during late Winter, and peaked at time 4 during Spring. The lowest values were calculated for time 5 during the open phase (Autumn). Diversity and species richness at the end of the study period were slightly higher than at the start (time 1), whereas evenness was lower at time 6.

General trends in community indices in the Little Manzimtoti Estuary showed no similarity with those of the Manzimtoti Estuary, however, index values were comparably low (Figure 4.26). Diversity across the Little Manzimtoti Estuary was relatively consistent with time (Figure 4.26 A), except at time 3 where there was a slight increase, coinciding with closure of the mouth and increased faunal abundance. Similarly, species richness peaked at time 3. In contrast, species evenness decreased at this time, and peaked at time 5. At site 1, species richness and diversity were positively influenced by the closure of the mouth at time 3 (Figure 4.26 B). In the early stages of recolonisation at time 1, species richness and diversity values were 0.31 and 0.64, respectively, which increased steadily until time 3 during mouth closure, where they were at a maximum ($d = 1.21$, $H' = 0.97$). Subsequently, these indices were lowest at time 4 ($d = 0.30$; $H' = 0.46$) during the reopening of the mouth, and continued to increase until time 6. Fluctuations in evenness were generally low, however peaks were recorded at times 1 ($J' = 0.59$) and 5 ($J' = 0.61$). At site 2, all community indices were negatively affected by the closure of the mouth and were at a minimum at this time (Figure 4.26 C). The changes in diversity were mirrored by changes in richness and evenness. Diversity was highest at the start of the study period ($H' = 0.68$) and this value was never again recorded for the duration of the study period. Diversity markedly to 0.05 at time 3, but gradually recovered to 0.49 by time 5. The final record of diversity was once again low ($H' = 0.28$) at time 6. Despite the decline at time 3, species richness and evenness were once again high at time 4 ($d = 0.35$) and time 5 ($J' = 0.59$), respectively. In the upper reaches of the Little Manzimtoti at site 3, species richness, evenness and diversity all reached a maximum at the time of mouth closure (Figure 4.26 D), and subsequently declined at time 4 during reopening. Diversity increased markedly between time 1 ($H' = 0.40$) and time 3 ($H' = 1.10$), however, the increases in evenness and species richness were less pronounced. Data was not available for times 5 and 6 in the Little Manzimtoti Estuary due to sampling difficulty at site 3.

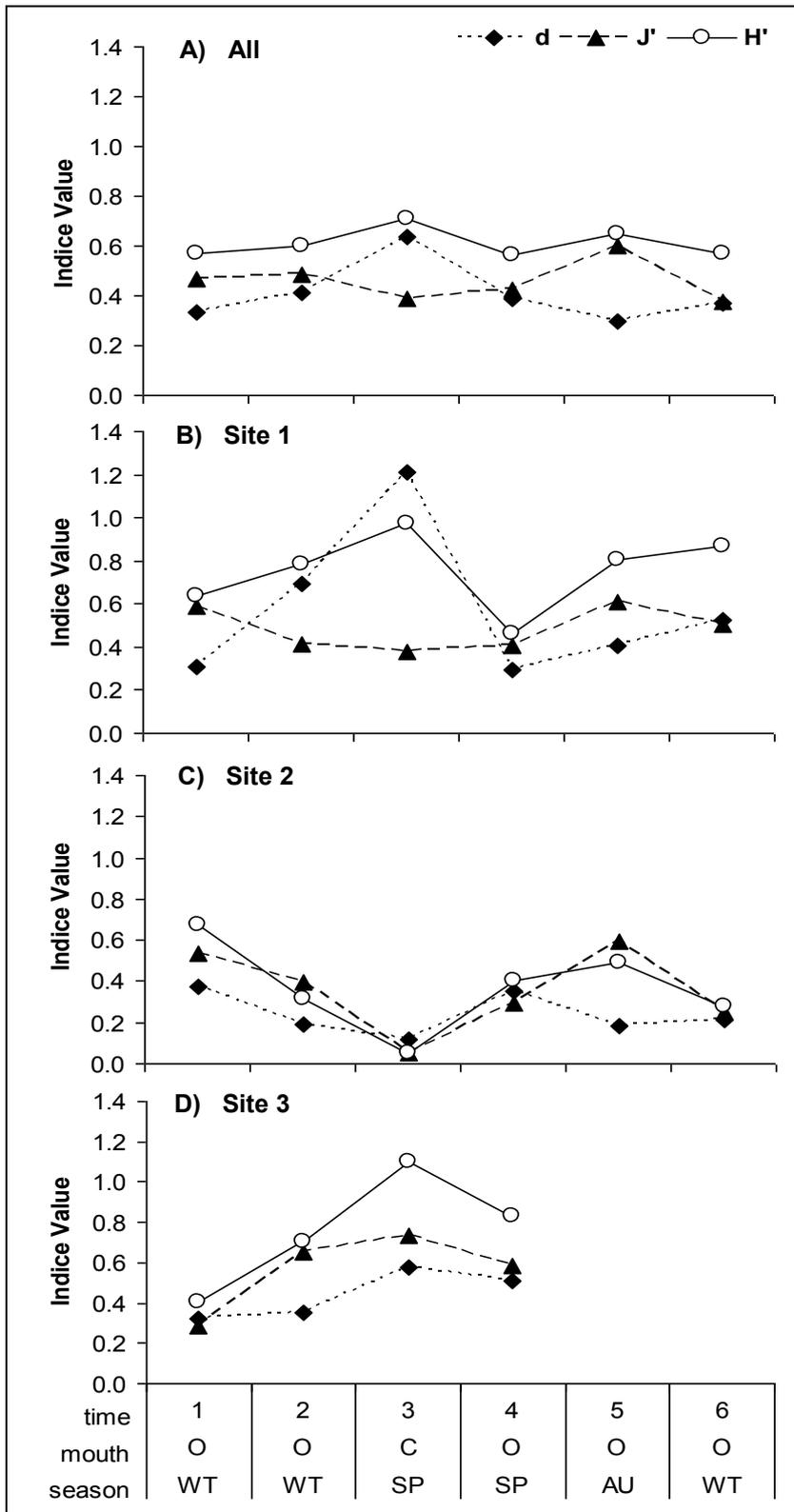


Figure 4.26 Community indices against time, mouth condition and season, calculated for the macrozoobenthic community of the Little Manzimtoti Estuary across all sites (A) and at site 1 (B), site 2 (C), site 3 (D) O = open phase, C= closed phase. WT= Winter, SP= Spring, AU= Autumn.

Diversity was significantly higher in the lower region sites of the Mhlabatshane and Intshambili estuaries, in comparison with the same sites of the Manzimtoti and Little Manzimtoti estuaries (Mann-Whitney $U= 13.0, p=0.003$). Sampling of the Mhlabatshane and Intshambili estuaries commenced at time 2, thus data was not available for time 1 at the start of the current study. In the Mhlabatshane Estuary, the trend in diversity was similarly evident in species richness and evenness (Figure 4.27 A). All indices were high at time 2 ($H'=1.60, d= 1.23, J'= 0.69$), and decreased sharply to time 3 at the opening of the mouth ($H'= 0.59, d= 0.89, J'= 0.26$). Minimum values were recorded at time 4 following mouth closure ($H'= 0.36, d= 0.34, J'= 0.25$). There was a peak in all indices at time 5 ($H'= 1.74, d= 1.16, J'= 0.72$) but these were subsequently lower at time 6.

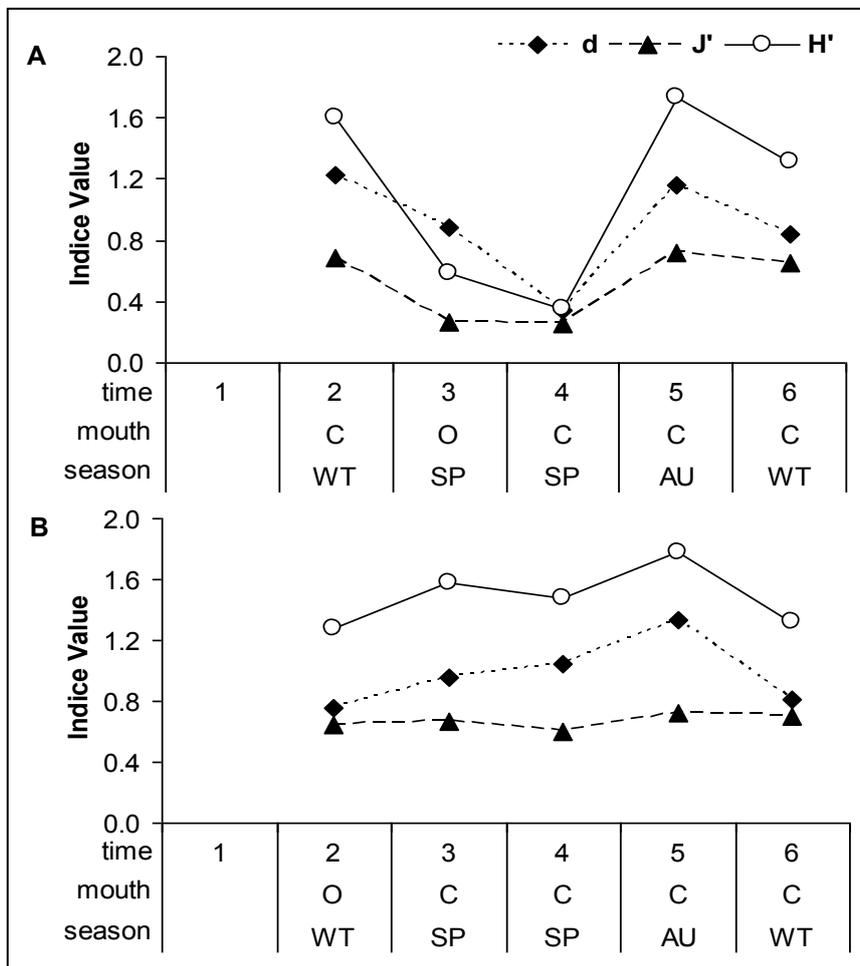


Figure 4.27 Community indices against time, mouth condition and season calculated for the macrozoobenthic communities in the Mhlabatshane (A), and Intshambili (B). O = open phase, C= closed phase. WT= Winter, SP= Spring, AU= Autumn.

In the Intshambili Estuary (Figure 4.27 B), non-normal, open mouth conditions prevailed at the start of sampling at time 2. From time 3 to time 6 only closed mouth conditions were sampled. Over the entire study period, fluctuations in diversity, species richness and evenness were relatively minor. Diversity gradually increased with time after flooding and reached a maximum at time 5 ($H' = 1.78$) and declined thereafter. This trend corresponded with the peak in species richness, which after a period of steady increase, was highest at time 5 ($d = 1.33$), but decreased sharply to time 6 ($d = 0.81$). Species evenness remained relatively constant over time. In summary, univariate analyses on community indices highlighted both inter- and intra-estuarine variability in diversity, accompanied by changes in species richness and evenness. These fluctuations appeared closely associated with changes in the open/closed state of the estuary mouth. Overall, diversity was significantly higher in the Mhlabatshane and Intshambili estuaries in comparison with the Manzimtoti and Little Manzimtoti estuaries. Diversity also varied according to position within a particular system. This highlighted the possibility that the macrozoobenthos that existed at the different sites within these estuaries differed in their response to the flood disturbance.

Stages of recolonisation: community trajectories

To explore the different stages of recolonisation, trajectories of the benthic communities at each site per estuary were first plotted using NMDS. The erratic array of samples in Manzimtoti (Figure 4.28) and the Little Manzimtoti (Figure 4.29) community trajectories illustrated the incongruence in the recolonisation sequence between sites. It was noted that 1) each site had a different starting point (and hence community characteristics) at the onset of sampling at time 1; 2) no two paths were alike; and 3) the end points of each recovery path were very different from the starting points. The high degree of overlap in the Manzimtoti system indicated extreme variability between samples over time and site. Analysis of Similarity revealed significant, yet poorly defined groups of samples according to time ($R=0.240$, $p<0.001$). However at each site, significant and clearly defined time groups were evident ($R=0.519$, $p<0.001$). Similarly in the Little Manzimtoti, the discrimination between samples according to time was less pronounced ($R= 0.545$, $p<0.001$) than samples grouped according to site and time ($R= 0.772$, $p<0.001$). Therefore, inter-site community variability obscured estuary-wide community changes with time. The 3D plots illustrate the overall changes that took place in the macrozoobenthos across each estuary in relation to the state of the mouth. In the Manzimtoti Estuary (Figure 4.28), recolonisation appeared cyclical and was reset by the

opening of the estuary mouth, such that time 5 samples were most similar to site 1 samples. Recolonisation in the Little Manzimtoti appeared to be almost linear except for time 3 where it was briefly interrupted by the non-normal closure of the estuary mouth (Figure 4.29). Thereafter, recolonisation continued from a community very similar to that prior to closure. That is, closure of the mouth had little effect on the macrozoobenthos.

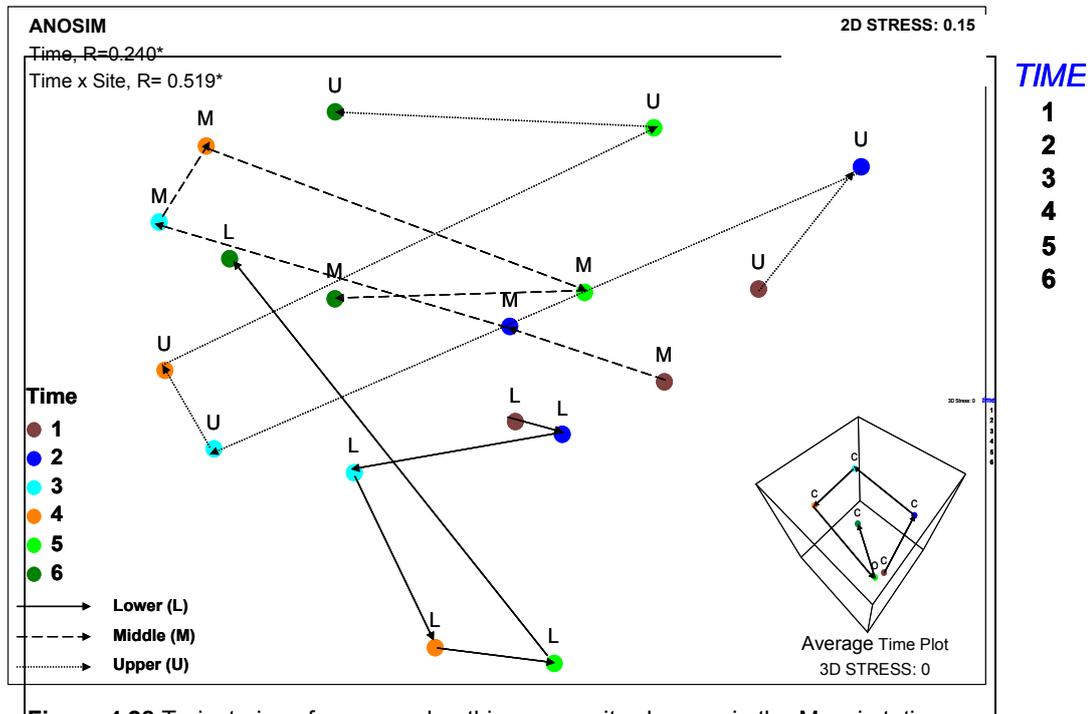


Figure 4.28 Trajectories of macrozoobenthic community changes in the Manzimtoti according to time (circles) for each site (arrows). R-values of ANOSIM indicate statistical validity of sample groups (* $p < 0.001$). 3D plot represents the average trajectory for all three sites according to time and mouth condition.

In the absence of inter-site comparisons, the trajectories of the Mhlabatshane (Figure 4.30) and Intshambili (Figure 4.31) estuaries were compared with the open/closed state of the mouth. Similar to the previous two urban estuaries, the end point of recolonisation (time 6) in both systems was different from the starting point (time 1). In the Mhlabatshane Estuary (Figure 4.30), the recolonisation process was offset by opening of the mouth and by an extraordinary event (M) or change in environmental conditions that resulted in a dramatic shift in community composition. In the Intshambili Estuary (Figure 4.31), a sub-cyclical, progressive change in community composition was evident. This was represented by an arc in the recolonisation trajectory, ending with a community relatively similar to the starting community. For both the Mhlabatshane and Intshambili estuaries, the communities at each time were well defined, indicated by significantly high R-values of 0.89 ($p < 0.001$) and 0.524 ($p < 0.001$), respectively.

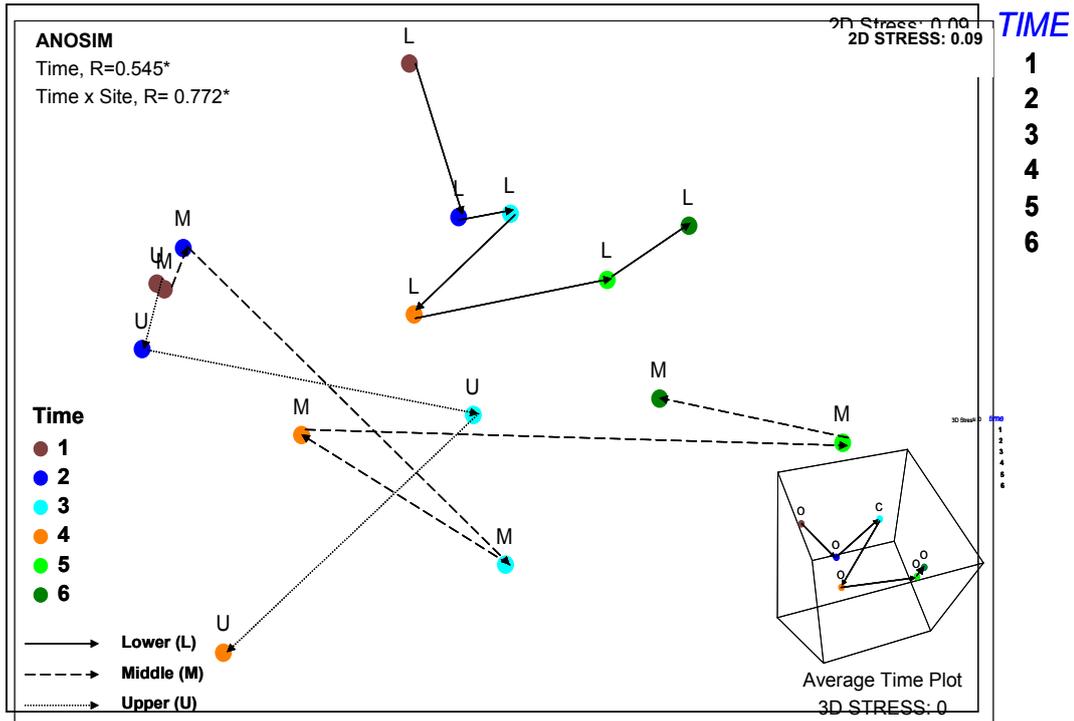


Figure 4.29 Trajectories of macrozoobenthic community changes in the Little Manzimtoti according to time (circles). R-values of ANOSIM indicate statistical validity of sample groups ($*p<0.001$). 3D plot represents the average trajectory for all three sites according to time and mouth condition.

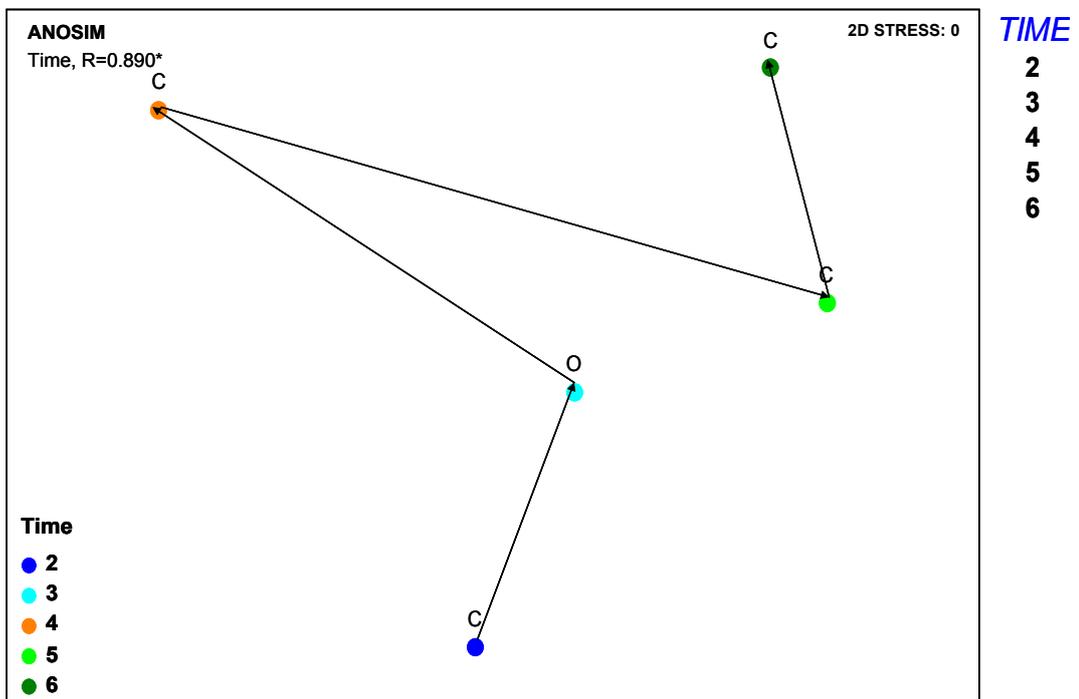


Figure 4.30 Trajectory (arrows) of macrozoobenthic community changes in the Mhlabatshane Estuary according to time (circles) in relation to mouth condition (C= closed, O= open). R-values of ANOSIM indicate statistical validity of sample groups ($*p<0.001$).

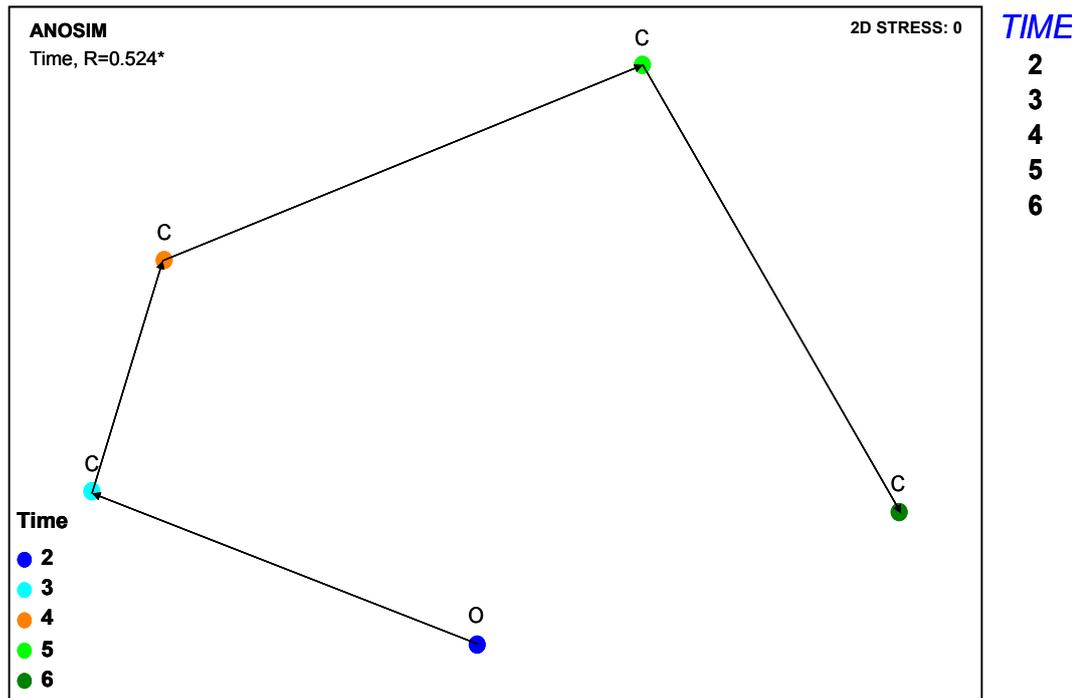


Figure 4.31 Trajectory (arrows) of macrozoobenthic community changes in the Intshambili Estuary according to time (circles) in relation to mouth condition (C= closed, O= open). R-values of ANOSIM indicate statistical validity of sample groups (* $p < 0.001$).

Stages of recolonisation: describing community changes

Using the above trajectories, temporal changes in the prominent species that typified the community at each time (identified using SIMPER) were described for each estuary. These prominent species were consistently present throughout the samples of the particular time period but were not necessarily the most abundant. Thus, the top five most numerically abundant species per time and their percentage contributions to overall community abundance were also described to identify shifts in species composition and dominance.

Manzimtoti Estuary

The macrozoobenthos of the Manzimtoti Estuary was typified by the gastropod mollusc, *Tarebia granifera* and spionid polychaete, *Prionospio multipinnulata* (Table 4.14, Figure 4.32). These two species were numerically dominant throughout the study period and together contributed between 94% and 99% to the total faunal abundance at each time. It could be argued that their overwhelming dominance prevented the colonisation of the estuary by additional species, as reflected by low evenness and species diversity.

Table 4.14. Mean values (\pm SD) for number of taxa, abundance, diversity and evenness, and defining species for each time period in the Manzimtoti Estuary. Only species responsible for 80% of the similarity between samples are presented.

Time Period	1	2	3	4	5	6
Number of Days	1-40	41-60	61-80	81-160	161-320	321-400
Season	Winter	Winter	Spring	Spring	Autumn	Winter
Mouth State	Closed	Closed	Closed	Closed	Open	Closed
Number of Taxa	2.00 (0.65)	1.73 (0.59)	3.93 (2.09)	4.20 (2.40)	2.60 (1.50)	4.33 (0.82)
Abundance (ind.m⁻²)	1,722.00 (2,294.02)	1,363.60 (881.55)	6,504.40 (3,783.69)	6,428.80 (4,461.54)	3,189.20 (3,539.43)	7,691.60 (8,055.07)
Diversity (H')	0.42 (0.25)	0.34 (0.29)	0.27 (0.26)	0.44 (0.37)	0.36 (0.33)	0.58 (0.36)
Evenness (J')	0.54 (0.33)	0.46 (0.38)	0.18 (0.12)	0.28 (0.23)	0.33 (0.28)	0.39 (0.23)
Sample Similarity (%)	68.32	66.49	52.62	47.44	56.93	59.63
Defining Species	<i>T. granifera</i> <i>P. multipinnulata</i>	<i>T. granifera</i> <i>P. multipinnulata</i>	<i>T. granifera</i> <i>P. multipinnulata</i>	<i>T. granifera</i> <i>P. multipinnulata</i> Chironomini larvae spp.	<i>T. granifera</i>	<i>T. granifera</i> <i>P. multipinnulata</i>

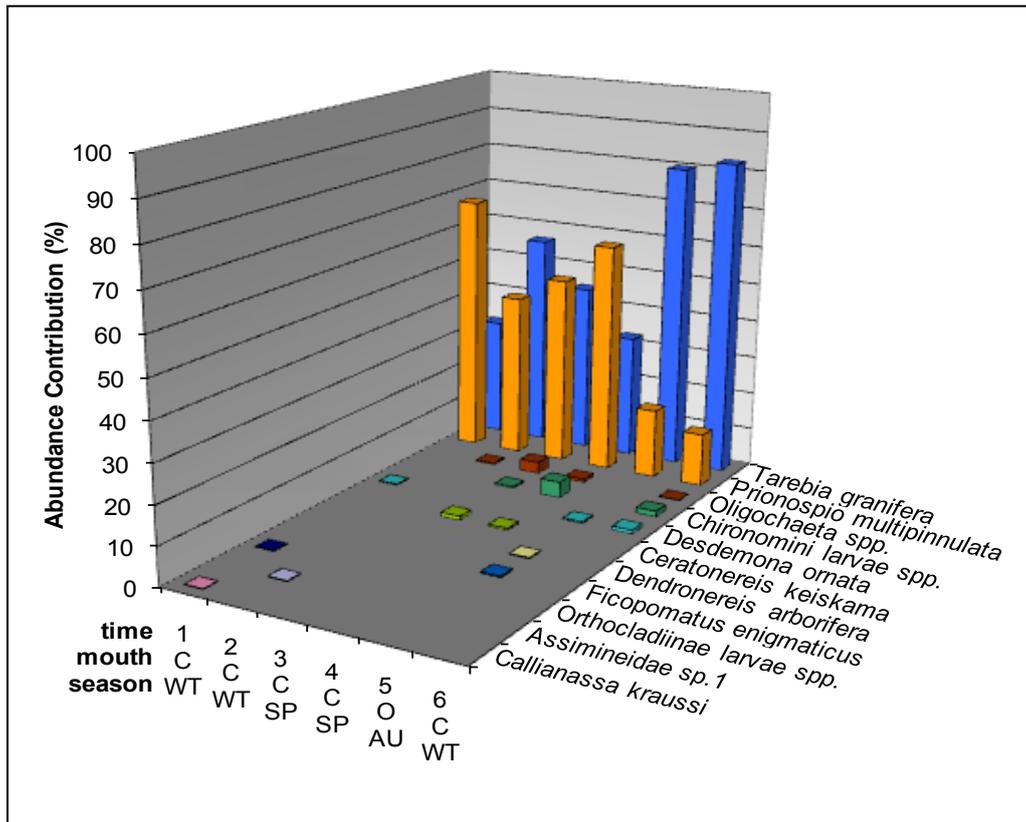


Figure 4.32 Top five most abundant species and their percentage contributions to the overall community abundance in the Manzimtoti Estuary per time, mouth condition and season. O= Open, C= Closed. WT= Winter, SP= Spring, AU=Autumn.

Evenness was particularly low during times 3 and 4 ($J'=0.18$ and $J'= 0.28$), when the faunal abundance was high ($6,504 \text{ ind.m}^{-2}$ and $6,428 \text{ ind.m}^{-2}$) (Table 4.14). This was largely due to a four-fold increase in population numbers of these two species and therefore increased dominance within the community. Between times 2 and 3, *Oligochaeta* spp., *Chironomini* larvae (Insecta), and *Ceratonereis keiskama* (Polychaeta) appeared in the benthos but were poorly abundant in comparison with *T. granifera* and *P. multipinnulata* (Figure 4.32). The increase in diversity at time 4 (Table 4.14) was likely due to the combination of increased number of taxa (3.93 to 4.20) and the greater contribution of *Chironomini* larvae to abundance (0.5% to 4.2%). At time 5 during the open mouth phase, overall abundance within the Manzimtoti Estuary decreased to approximately half the abundance at time 3 or 4 ($3,189.2 \text{ ind.m}^{-2}$). At this time, *T. granifera* completely dominated the benthic community, comprising 80% of the total abundance. The abundance of *P. multipinnulata* had decreased from $2,097.2 \text{ ind.m}^{-2}$ at time 4, to 579.6 ind.m^{-2} at time 5, and therefore, contributed <20% to overall benthic community abundance. In the final sample period (time 6), community abundance was at a maximum ($7,691.6 \text{ ind.m}^{-2}$). Similarly, number of taxa and diversity were at their maximum

(4.33 taxa; $H' = 0.58$). *Tarebia granifera* was still the most dominant species (83%), with small contributions made by *P. multipinnulata* (14%) and Chironomini larvae (1%).

Little Manzimtoti Estuary

In the Little Manzimtoti system, the community changes that took place during the process of recolonisation were markedly different to those that occurred in the Manzimtoti Estuary (Table 4.15, Figure 4.33). In the early stages of recolonisation during times 1 and 2, the benthos was characterised by Oligochaeta spp. and Chironomini larvae spp. Oligochaeta spp. were numerically dominant and comprised 81% and 79% of the total faunal abundance during these times, respectively. At time 2, overall community abundance had almost tripled (2,434.6 ind.m⁻²) and was accompanied by an increase in the number of taxa (4.13 taxa), diversity ($H' = 0.60$) and evenness ($J' = 0.49$). The dominance of Oligochaeta spp. (79%) and prevalence of Chironomini larvae (3%) remained unchanged. Other additional species, including Nemertea spp. (4%), Nematoda spp. (5%) and the polychaete *Desdemona ornata* (3%), made minor contributions to the overall community abundance. During closure of the mouth at time 3, community abundance was then 10 times greater than starting numbers (8,671.6 ind.m⁻²), and there were further increases in number of taxa (6.53 taxa) and diversity ($H' = 0.71$). At this time, Oligochaeta spp. was no longer the dominant species (9.2%), while the *P. multipinnulata* population had escalated to 80% of the community abundance within 28 days. The minor appearance of *C. keiskama* (1.4%) was also noted. The contribution made by Chironomini larvae (5%) was consistent. Reopening of the Little Manzimtoti Estuary mouth at time 4, saw a marked decrease in overall faunal abundance (2,690.8 ind.m⁻²), with concomitant drops in the number of taxa (3.87 taxa) and diversity ($H' = 0.57$), and a slight increase in evenness ($J' = 0.43$) (Table 4.15). The ratio between *P. multipinnulata* and Oligochaeta spp. remained unchanged, but the occurrence of *C. keiskama* was short-lived (Figure 4.33). At this time, Chironomini larvae comprised only 1.2% of the benthic community, and the two taxa Harpacticoida sp. 1 (Benthic Copepoda) (3.1%) and Entomobryidae sp. 1 (Collembola) (4%) similarly contributed minimally to overall abundance.

Table 4.15. Mean values (\pm SD) for number of taxa, abundance, diversity and evenness, and defining species for each time period in the Little Manzimtoti Estuary. Only species responsible for 80% of the similarity between samples are presented.

Time Period	1	2	3	4	5	6
Number of Days	1-40	41-60	61-80	81-160	161-320	321-400
Season	Winter	Winter	Spring	Spring	Autumn	Winter
Mouth State	Open	Open	Closed	Open	Open	Open
Number of Taxa	3.20 (1.32)	4.13 (2.36)	6.53 (5.13)	3.87 (1.06)	3.00 (1.70)	4.10 (1.73)
Abundance (ind.m⁻²)	820.40 (49.67)	2,343.60 (2,893.22)	8,671.60 (10,542.29)	2,690.80 (1,737.04)	945.00 (664.15)	4,342.80 (2,368.62)
Diversity (H')	0.57 (0.40)	0.60 (0.38)	0.71 (0.54)	0.57 (0.33)	0.65 (0.39)	0.57 (0.36)
Evenness (J')	0.47 (0.29)	0.49 (0.24)	0.39 (0.30)	0.43 (0.23)	0.60 (0.26)	0.38 (0.20)
Sample Similarity (%)	46.9	44.02	42.65	37.67	53.52	59.40
Defining Species	Oligochaeta spp. Chironomini larvae spp.	Oligochaeta spp. Chironomini larvae spp.	<i>P. multipinnulata</i> <i>C. keiskama</i> Chironomini larvae spp.	<i>P. multipinnulata</i> Oligochaeta spp Chironomini larvae spp.	<i>D. arborifera</i> <i>C. keiskama</i>	<i>D. arborifera</i> <i>D. ornata</i> <i>C. keiskama</i>

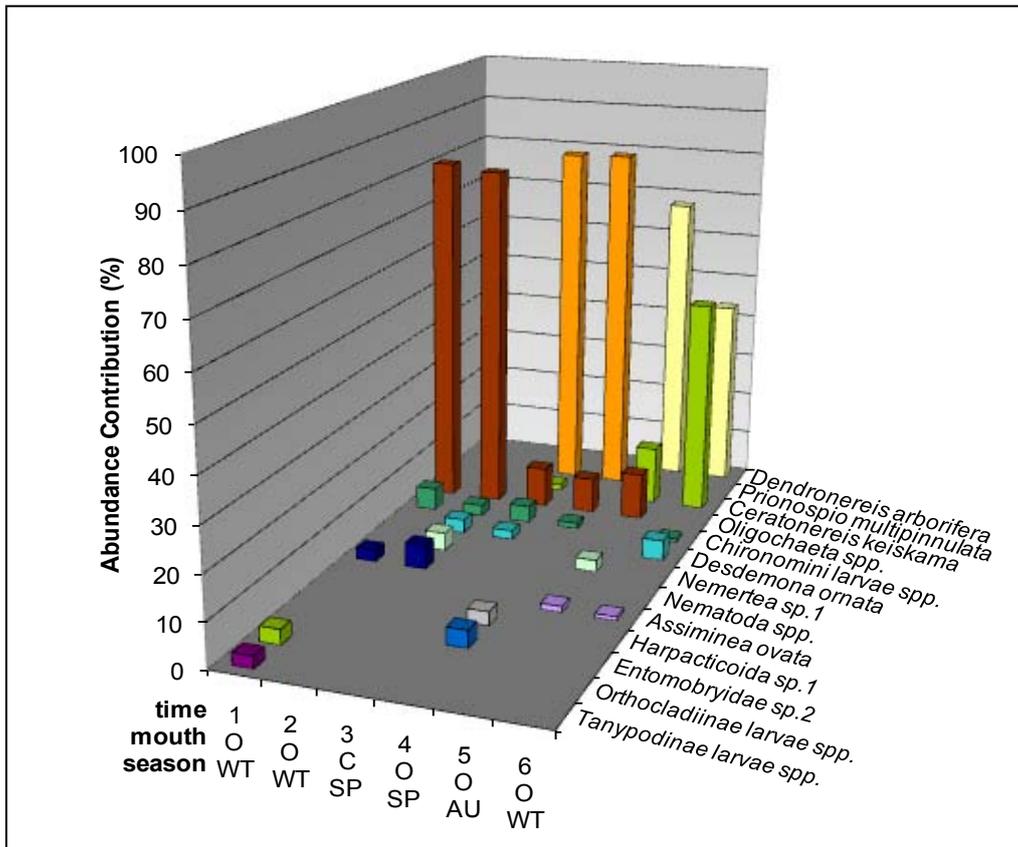


Figure 4.33 Top five most abundant species and their percentage contributions to the overall community abundance in the Little Manzimtoti Estuary per time, mouth condition and season. O= Open, C= Closed. WT= Winter, SP= Spring, AU=Autumn.

During time 5, faunal abundance and number of taxa had decreased further to near early-recolonisation numbers. Diversity was comparable to that at time 2 ($H' = 0.65$), and evenness was at a maximum ($J' = 0.60$). The return of *C. keiskama* and the appearance of *Dendronereis arborifera* in considerable numbers was a key feature of this time period. The benthic community was dominated by *D. arborifera* (68%), followed by *C. keiskama* (13.3%) and *Oligochaeta* spp. (10.7%). *Prionospio multipinnulata* and Chironomini larvae were absent from the community. In the final sampling period, time 6, faunal abundance and the number of taxa had recovered (4,343.8 ind.m⁻² and 4.1 taxa). The dominant species were *C. keiskama* and *D. arborifera*, comprising 49% and 43% of the overall community abundance, respectively, with Chironomini larvae contributing 1%. Although not a numerically dominant species, the presence of the polychaete, *Desdemona ornata*, was a noteworthy feature of the benthos at time 6.

In summary, the shifts in species assemblages during recolonisation of the Little Manzimtoti occurred in the 3 broad stages as illustrated by the NMDS plot (Figure 4.20). Times 1 and 2

were characterised by *Oligochaeta* spp. and Chironomini larvae spp. Both times 3 and 4 were characterised by *P. multipinnulata* and Chironomini larvae spp. in the same proportions, despite the dramatic reduction in overall abundance and decrease in diversity between these times. The benthos at times 5 and 6 were typified by *D. arborifera* and *C. keiskama*.

Mhlabatshane Estuary

In early stages of recolonisation of the Mhlabatshane Estuary (time 2), the benthos was characterised by a broader assemblage of organisms in comparison with the Manzimtoti and Little Manzimtoti (Table 4.16), namely, *P. multipinnulata*, *Grandidierella* spp. (Amphipoda), *D. ornata*, *Oligochaeta* spp., *Grandidierella lignorum* (Amphipoda), *Grandidierella lutosa* (Amphipoda), and *Lumbrineris tetraura* (Polychaeta). Although overall faunal abundance was relatively low at this time, the number of taxa, diversity, and evenness were comparatively high. *Prionospio multipinnulata* was the dominant species, contributing 52% to the total community abundance, followed by *D. ornata* (13%) and *Grandidierella* spp. (11%) (Figure 4.34). *Lumbrineris tetraura* (3.4%) and *Oligochaeta* spp. (4.3%) made minor contributions to the community. During the open mouth phase (time 3), community abundance increased dramatically to 15,624.0 ind.m⁻². However, this was accompanied by a sharp decrease in evenness ($J' = 0.26$) and particularly in diversity ($H' = 0.59$), indicating the overwhelming dominance of a few species. This was solely attributed to the proliferation of *P. multipinnulata* from 1,125.6 ind.m⁻² at time 1 to 13,507.2 ind.m⁻² at time 2, where it then constituted 86% of the benthic community. Concomitantly, the proportions of *D. ornata* (4%) and *Grandidierella* spp. (2%) were reduced.

During time 4, when the mouth was once again closed, faunal abundance remained relatively high (13,062.0 ind.m⁻²), however, the number of taxa, diversity and evenness had decreased (Table 4.16). *P. multipinnulata* (88%) remained the dominant species followed by *D. ornata* (11%) (Figure 4.34). Other minor species appeared in the benthos in very low abundance (<0.1%), including *Corophium triaenonyx* (Amphipoda), *Brania* sp. 1 (Polychaeta), Nematoda spp., *Oligochaeta* spp. and *C. keiskama*. Community abundance continued to decrease through times 4 to 6 (13,062.0 ind.m⁻² – 2,545.2 ind.m⁻²). In contrast, the number of taxa, diversity, and evenness all peaked at time 5 (11.6 taxa; $H' = 1.74$; $J' = 0.72$).

Table 4.16. Mean values (\pm SD) for number of taxa, abundance, diversity and evenness, and defining species for each time period in the Mhlabatshane Estuary. Only species responsible for 80% of the similarity between samples are presented.

Time Period	1	2	3	4	5	6
Number of Days	1-40	41-60	61-80	81-160	161-320	321-400
Season		Winter	Spring	Spring	Autumn	Autumn
Mouth State		Closed	Open	Closed	Closed	Closed
Number of Taxa		10.40 (2.30)	9.60 (2.70)	4.20 (0.84)	11.60 (3.05)	7.60 (1.52)
Abundance (ind.m⁻²)		2,167.20 (826.02)	15,624.00 (4,393.27)	13,062.00 (5,535.48)	9,424.80 (1,087.39)	2,545.20 (885.29)
Diversity (H')		1.60 (0.23)	0.59 (0.18)	0.36 (0.12)	1.74 (0.15)	1.31 (0.21)
Evenness (J')		0.69 (0.10)	0.26 (0.06)	0.25 (0.07)	0.72 (0.04)	0.66 (0.11)
Sample Similarity (%)		68.43	71.68	68.26	75.56	67.90
Defining Species		<i>P. multipinnulata</i> <i>Grandidierella</i> spp. <i>D. ornata</i> Oligochaeta spp. <i>G. lignorum</i> <i>G. lutosa</i> <i>L. tetraura</i>	<i>P. multipinnulata</i> <i>D. ornata</i> <i>L. tetraura</i> <i>Grandidierella</i> spp. <i>G. lutosa</i>	<i>P. multipinnulata</i> <i>D. ornata</i>	<i>D. arborifera</i> <i>P. multipinnulata</i> <i>C. keiskama</i> <i>D. ornata</i> <i>Grandidierella</i> spp. <i>G. lutosa</i>	<i>P. multipinnulata</i> <i>D. arborifera</i> Oligochaeta spp. <i>Grandidierella</i> spp.

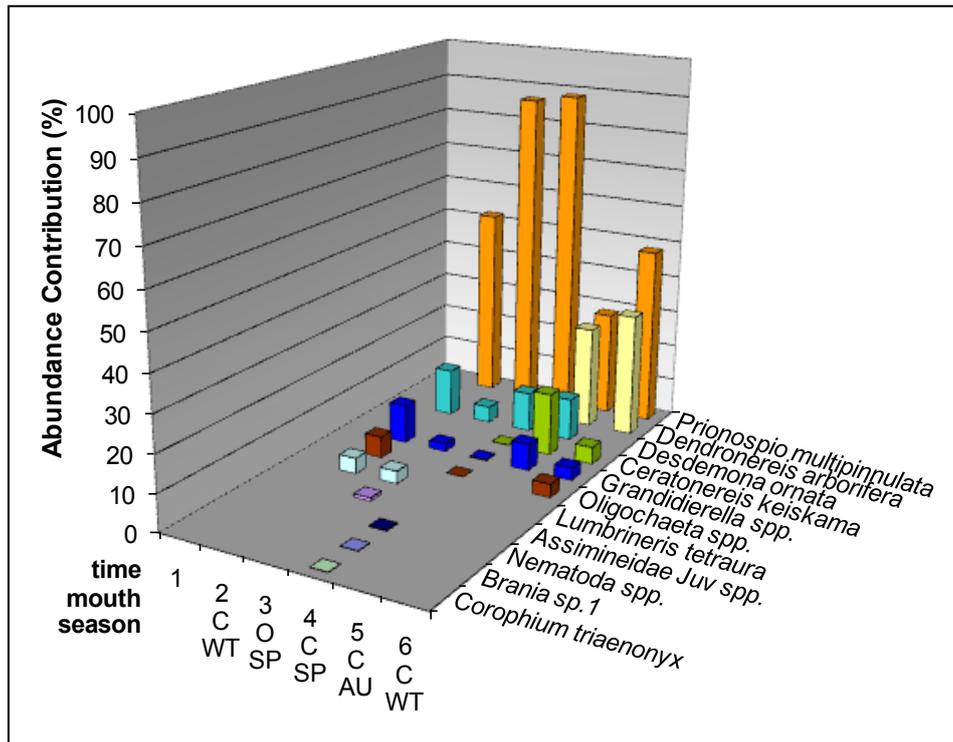


Figure 4.34 Top five most abundant species and their percentage contributions to the overall community abundance in the Mhlabatshane Estuary per time, mouth condition and season. O= Open, C= Closed. WT= Winter, SP= Spring, AU=Autumn.

At this time, the benthic community was not dominated by one or two overwhelmingly abundant species (Figure 4.34), instead the number of individuals was relatively evenly spread across the top five most abundant species. The overall community abundance was divided as follows: *P. multipinnulata* (28%), *D. arborifera* (28%), *C. keiskama* (17%), *D. ornata* (11%) and *Grandidierella spp.* (7%). *Ceratonereis keiskama* had successfully colonised the benthos from time 4. After time 5, all community measures decreased, and *P. multipinnulata* was again the most dominant species, comprising 48% of the overall faunal abundance, followed closely by *D. arborifera* (33%). *C. keiskama*, *Oligochaeta spp.* and *Grandidierella spp.* contributed 4.6%, 3.6% and 3.3% to the overall community abundance, respectively (Figure 4.34).

In summary, recolonisation of the Mhlabatshane Estuary was dominated by a single species, *P. multipinnulata*, despite the diverse species composition of the community. Fluctuations in community abundance were reflective of fluctuations in the population of *P. multipinnulata* particularly during the Spring season. In addition, it appeared unaffected by the opening of the mouth. It was postulated that the overwhelming dominance of this species precluded the successful recolonisation of other benthic species that appeared in the community following

the opening of the mouth. During the later stages of recolonisation (times 5 and 6), typical estuarine taxa, *C. keiskama*, *D. arborifera* and *Grandidierella* spp., occupied prominent positions in the benthic community.

Intshambili Estuary

In the Intshambili Estuary, the mouth was abnormally open in the early stages of recolonisation (time 2) and remained closed thereafter for the remainder of the study period (Table 4.17). At time 2, faunal abundance, diversity and number of taxa were relatively low. The macrozoobenthos was characterised by predominantly crustacean amphipod species, namely, *Grandidierella* spp., *Grandidierella lutosa* (Amphipoda), *C. triaenonyx* and the polychaete species, *P. multipinnulata* and *D. ornata* (Table 4.17, Figure 4.35). The benthic community was dominated by *Grandidierella* spp. which accounted for almost 50% of the overall faunal abundance, and likely responsible for the relatively low level of diversity. Important contributions were made by *P. multipinnulata* (22%) and *D. ornata* (15%), followed by *C. triaenonyx* (6%), and *G. lutosa* (3%). *Ceratonereis keiskama* was present in the benthos but was not among the most abundant species (<0.5%).

During time 3 and re-closure of the mouth (Spring), overall community abundance increased sharply to four times greater than at time 2 (24,553.2 ind.m⁻²). Similarly, diversity and evenness had also increased because of the increased number of taxa and the lowered dominance of *Grandidierella* spp. (35%). The community was characterised by the same five species as time 2 as well as *Grandidierella lignorum* (Amphipoda) and Oligochaeta spp. (Table 4.17). Community abundance remained high at time 4 (Spring), however, diversity and evenness had slightly decreased, suggesting an increased numerical dominance of a few species. Despite the increased importance of *C. triaenonyx* (21%), this was attributed to *Grandidierella* spp., which once again comprised a large proportion of the fauna abundance (46%), and the absence of *D. ornata* from the five most abundant species (3%)(Figure 4.35). Additional species in the defining assemblage were *C. keiskama* and Mollusca pre-juvenile T1.

Table 4.17. Mean values (\pm SD) for number of taxa, abundance, diversity and evenness, and defining species for each time period in the Intshambili Estuary. Only species responsible for 80% of the similarity between samples are presented.

Time Period	1	2	3	4	5	6
Number of Days	1-40	41-60	61-80	81-160	161-320	321-400
Season		Winter	Spring	Spring	Autmumn	Winter
Mouth State		Open	Closed	Closed	Closed	Closed
Number of Taxa		7.60 (2.30)	10.60 (1.34)	11.60 (1.14)	11.80 (1.64)	6.80 (2.05)
Abundance (ind.m⁻²)		6,132.00 (2,762.60)	24,553.20 (7,078.34)	26,846.40 (6,067.40)	3,712.80 (2,019.41)	1,285.20 (502.77)
Diversity (H')		1.28 (0.21)	1.57 (0.09)	1.47 (0.14)	1.78 (0.17)	1.33 (0.27)
Evenness (J')		0.65 (0.09)	0.67 (0.02)	0.60 (0.08)	0.72 (0.06)	0.70 (0.05)
Sample Similarity (%)		70.75	85.49	83.55	66.09	53.67
Defining Species		<i>Grandidierella</i> spp. <i>P. multipinnulata</i> <i>D. ornata</i> <i>G. lutosa</i> <i>C. triaenonyx</i>	<i>D. ornata</i> <i>Grandidierella</i> spp. <i>C. triaenonyx</i> <i>P. multipinnulata</i> <i>G. lutosa</i> Oligochaeta spp. <i>G. lignorum</i>	<i>Grandidierella</i> spp. <i>C. triaenonyx</i> <i>G. lutosa</i> <i>P. multipinnulata</i> <i>C. keiskama</i> <i>G. lignorum</i> <i>D. ornata</i> Mollusca PreJuv T1	<i>C. triaenonyx</i> <i>D. ornata</i> <i>Grandidierella</i> spp. <i>P. multipinnulata</i> Chironomini larvae spp. <i>C. keiskama</i> <i>G. lutosa</i>	<i>Grandidierella</i> spp. <i>P. multipinnulata</i> <i>D. ornata</i> <i>B. virgiliae</i>

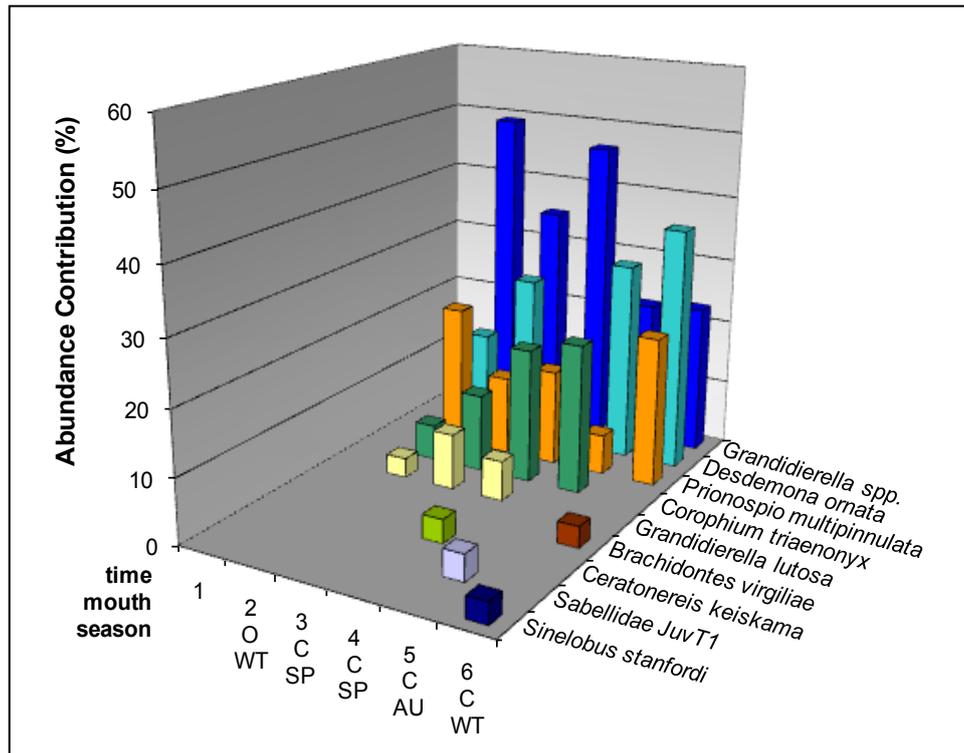


Figure 4.35 Top five most abundant species and their percentage contributions to the overall community abundance in the Intshambili Estuary per time, mouth condition and season. O= Open, C= Closed. WT= Winter, SP= Spring, AU=Autumn.

At time 5 (Autumn), the overall community abundance had declined markedly (3,712.8 ind.m⁻²) in comparison with time 4. The number of taxa, diversity and evenness were however at a maximum, because the majority of the community abundance was spread over three taxa, namely, *Grandidierella* spp. (22%), *D. ornata* (31%) and *C. triaenonyx* (23%). Important contributions were made by *P. multipinnulata* (6%), Sabellidae juvenile T1 (4%) and minor contributions by *G. lutosa* (3%) and *C. keiskama* (2%). This time period was characterised by the above-mentioned balance between the three species and the occurrence of Chironomini larvae (Table 4.17). At time 6 (Winter), community abundance was at a minimum, accompanied by a low number of taxa and species diversity that were near to early recolonisation values. Evenness however remained high. The benthic community of time 6 was characterised by four taxa, *Grandidierella* spp., *P. multipinnulata*, *D. ornata*, and the occurrence of the bivalve mollusc, *Brachidontes virgiliae*. The majority of the overall faunal abundance was distributed between *Grandidierella* spp. (23%), and *D. ornata* (37%), and included *P. multipinnulata* (23%) in place of *C. triaenonyx* (time 5). *Brachidontes virgiliae* and *Sinelobus stanfordi* (Tanaidacea) were equally lowly abundant (3.3%).

In summary, recolonisation of the Intshambili Estuary appeared influenced by seasonality in the absence of variable mouth conditions. During Winter, both at the beginning and at the final stage of sampling, abundance and number of taxa were lowest. These attributes were greatest during Spring, and the community was characterised by a broad species assemblage. At the onset of Autumn, abundance had declined but species composition remained stable.

4.4.2.5 Linking post-flood macrozoobenthic communities to environmental variables

Because soft-sediment invertebrates are intimately associated with the nature of the substrate and conditions of the water column (Boesch et al. 1976b, Gray 1981, Herman et al. 1999), the environmental conditions of the four estuaries were assessed in terms of their relationship to the macrozoobenthic communities. In the absence of biological interactions of competition and predation, the environmental variables most likely responsible for the distribution of the biotic samples in each estuary are presented in Table 4.18. In the Manzimtoti Estuary, the single environmental factor best correlated with the distribution of macrozoobenthos was the percentage organic content of the sediment ($P_s = 0.270$). However, the highly variable nature of the estuarine environment dictates that the distribution of fauna is not related to a single abiotic factor but rather several compounding variables (Day 1981c, Bursey and Wooldridge 2003). Thus, the highest correlation of five abiotic variables to the biotic data was met by dissolved oxygen, pH, turbidity, sediment skewness and percentage organic content ($P_s = 0.337$). This correlation was nonetheless low, and indicated complex faunal-environmental relationships. Close study of these particular variables revealed consistently greatest values at site 1 over time. Therefore, inter-site variability (spatial) of these environmental variables, not post-flood fluctuations (temporal), was most likely responsible for distribution of macrozoobenthos in the Manzimtoti Estuary.

Table 4.18 Combinations of five environmental variables, taken k at a time yielding the highest correlations between the biotic and abiotic similarity matrices for each estuary for each k, as measured by Spearman's Rank Correlation (*Ps*). **Bold** type indicates the overall optimum.

k	<i>Ps</i>	Environmental Variables
<u>Manzimtoti</u>		
1	0.270	% Organics
2	0.264	Turbidity, % Organics
3	0.334	pH, Turbidity, % Organics
4	0.333	pH, Turbidity, Skewness, % Organics
5	0.337	DO, pH, Turbidity, Skewness, % Organics
<u>Little Manzimtoti</u>		
1	0.295	% VCS
2	0.357	pH, % VFS
3	0.399	DO, Salinity, % FS
4	0.435	Depth, Salinity, % FS, Sorting
5	0.476	Depth, Salinity, % FS, Sorting
<u>Mhlabatshane</u>		
1	0.830	% VCS
2	0.891	Temperature, % VCS
3	0.903	Depth, % VCS, Median Φ
4	0.915	Depth, % VCS, % CS, MdΦ
5	0.915	Depth, Turbidity, % Gravel, % VCS, Sorting
<u>Intshambili</u>		
1	0.745	% Mud
2	0.903	Depth, Turbidity
3	0.903	Depth, Turbidity, % Gravel
4	0.891	% CS, % MS, % Mud, Md Φ
5	0.939	Depth, Turbidity, % MS, % FS, % Mud

The macrozoobenthos of the Little Manzimtoti system was governed by a suite of environmental variables different from the Manzimtoti Estuary (Table 4.18), namely depth, dissolved oxygen, salinity, percentage fine sand content and the degree of sorting of the sediment ($P_s = 0.476$). Throughout the study period, site 1 was the shallowest site, while dissolved oxygen was consistently highest at this same site. Salinity varied across sites but was abnormally high at all sites during the closed phase. Site 2 was the area with the greatest accumulation of fine sand. Furthermore, the sediment at site 1 was moderately well-sorted, while the sediment at sites 2 and 3 were only moderately sorted. These results suggest strong inter-site differences in environmental conditions, while changes in community structure associated with increased salinity took place during the closed phase of the system. In similarity with the Manzimtoti Estuary, spatial differences in environmental conditions, and changes related to the state of the mouth were more important for the distribution of the macrozoobenthos of the Little Manzimtoti Estuary than changes with time after flood disturbance.

There was a very high correlation between the benthic invertebrate community of the Mhlabatshane Estuary and percentage very coarse sand content of the sediment ($P_s = 0.830$) (Table 4.18). However, the best correlation occurred with a combination of depth, percentage very coarse sand and coarse sand content, and median grain size ($Md\Phi$) of the sediment ($P_s = 0.915$). Depth was shallowest during the open phase and was deepest in the subsequent closed phase, followed by decreasing depth with time. This process is typical of TOCEs whereby sediment is scoured out during the breached state of the mouth, and subsequent closure and backflooding results in increased depth (Whitfield and Bate 2007). Shallowing of the Mhlabatshane Estuary was attributed to siltation and accumulation of finer sand material with time as reflected by the sediment analyses (Figure 4.13 A). Therefore, the macrozoobenthos of this estuary was most affected by changes in sediment and depth related to breaching of the estuary mouth and prevailing changes thereafter.

In the Intshambili, the correlations between environmental variables and the faunal samples were also high (Table 4.18). Percentage mud content of the sediment was the single most influential abiotic factor ($P_s = 0.745$), as this constituted a large proportion of the sediment in the Intshambili Estuary (Figure 4.14). Interestingly, organic content which was correlated with mud content was not an important factor. However, the distribution of the macrozoobenthos was best explained by a combination of depth, turbidity, and the percentage composition of medium sand, fine sand and mud within the sediment ($P_s = 0.939$). The depth of the Intshambili Estuary increased with time after flooding, and was deepest at time 5. Up until this time, the grain size composition of the sediment had remained relatively unchanged (Figure 4.13 B). At time 5, the sediment was markedly finer, with much less coarse sand, and a greater proportion of mud. At time 6, coarser fractions were negligible and sediment was largely composed of medium and fine sand. These findings were possibly attributed to increased fluvial input from precipitation within the catchment, leading to increased depth at time 5 and the deposition of finer material. This was further confirmed by increased deposition of sediment and subsequent shallowing of the system at time 6 and higher than normal turbidities during these two periods. In the absence of variable mouth conditions, the post-flood changes in macrozoobenthos of the Intshambili Estuary were initially governed by increasing depth after mouth closure, since the sediment composition remained relatively unchanged with time until time 4. Thereafter, the distribution of the benthic community was

most influenced by changes in sediment composition due to pulses in sediment input and deposition.

4.5 Discussion

By monitoring the changes in the macrozoobenthic communities of four flood affected TOCEs over a period of one year, it was possible to determine the pattern of recolonisation by these communities in response to short-term flood disturbance. In addition, the response of estuarine macrozoobenthos to this disturbance in different urban and non-urban environments was also established. It was predicted that the urban Manzimtoti and Little Manzimtoti estuaries, situated in close proximity to dense urban development and visibly subject to anthropogenic interference, would comprise macrozoobenthic communities similar in structure and response to flood disturbance. Conversely, results of the current study revealed that the macrozoobenthos of these two estuaries were less than 35% similar and significantly different from one another ($R=0.519$, $p<0.0001$). In the Manzimtoti Estuary, the community was dominated by two species, *Tarebia granifera* (Mollusca) and *Prionospio multipinnulata* (Annelida Polychaeta) which constituted approximately 57% and 40% of the community, respectively. In the Little Manzimtoti Estuary, the predominance of the annelid component was far greater (92%), of which *P. multipinnulata* comprised 51%, Oligochaeta spp. 20% and other polychaete species 21%. Overall, the separation of these two communities was attributed to differences in the relative abundances of four common species, most importantly the large abundance of *T. granifera*, followed by *P. multipinnulata* in the former estuary and higher abundances of Oligochaeta and Chironomini larvae in the latter. The predominance of *T. granifera* in the Manzimtoti Estuary was likely due to its preference for freshwater/brackish conditions (Appleton et al. 2009) in comparison with the marine-dominated Little Manzimtoti system. The Manzimtoti community was significantly poorer in diversity (ANOVA, $F=23.29$, $p<0.001$), however the two estuaries did not differ in terms of faunal abundance (Mann Whitney $U= 2828.5$, $p=0.205$).

It was similarly predicted that the Mhlabatshane and Intshambili estuaries, with substantially less urban encroachment and fewer anthropogenic pressures, would share similar benthic communities with similar responses to flood disturbance. The macrozoobenthic communities of these non-urban estuaries were more similar to each other (50%) in comparison with

communities of the urban estuaries. Ordination showed that samples from each of these estuaries were more similar at specific times. That is, during the early and middle stages of recolonisation in the Mhlabatshane Estuary (time 2, 3 and 4), samples were similar to the earliest and latest stages of recolonisation of the Intshambili Estuary (time 1 and 6). Conversely, during the later stages of recolonisation (time 5 and 6), samples from the former system were more similar to the middle and near-end samples (times 3, 4 and 5) of the latter. These results suggest that the rate of change during community recolonisation was not uniform across both systems.

Despite their higher level of similarity, the benthic communities of these two estuaries remained distinct ($R=0.418$, $p<0.0001$). The macrozoobenthos of the Mhlabatshane Estuary was dominated by annelid polychaetes (~93%), particularly *P. multipinnulata* which comprised 70% of the community. An outstanding feature of the benthos of the Intshambili Estuary was the prevalence of a crustacean component, which constituted approximately 64%, of the community, of which the dominant taxa were corophid amphipods, *Corophium triaenonyx* and *Grandidierella* spp., *G. lutosa*, and *G. lignorum*. The two non-urban communities were differentiated by higher abundances of these taxa, together with *Ceratonereis keiskama* (Annelida Polychaeta), Oligochaeta spp. and Chironomini larvae, in the Intshambili Estuary and higher abundances of *Dendronereis arborifera* (Annelida Polychaeta) and *P. multipinnulata* in the Mhlabatshane Estuary. Nonetheless, there was no difference between these two systems in terms of abundance (T-Test $t=613.5$; $p=0.648$) or diversity (Tukey Test, $q=3.26$, $p>0.05$). In summary, the responses of the macrozoobenthic communities to flood disturbance within adjacent TOCEs of urban and non-urban environments were markedly different. The null hypotheses (H_{01}) was thus rejected as adjacent estuaries were proven poor reflections of each other and the sampled macrozoobenthos communities could not be strictly classified as 'urban' and 'non-urban', despite the perceived condition of the respective estuaries. These results are in contrast to those reported by Morrisey et al. (2003) who found that urbanised estuaries in the vicinity of Auckland, New Zealand, were in fact similar in terms of benthic community composition, yet these communities were different from those in rural estuaries, which in turn were different from each other. The dissimilarity between the urban and non-urban communities was attributed to contamination caused by urban run-off (Morrisey et al. 2003). It was possible during the current study, that the level and type of contamination differed between the Manzimtoti and Little Manzimtoti estuaries, giving rise to separate soft-

sediment communities. Nonetheless, it could therefore be stated with reasonable confidence that the observed differences in response of the macrozoobenthos in each of the four estuaries to flooding was not primarily attributed to differences in the degree of urbanisation.

The outcome of the first hypothesis implied that the response of macrozoobenthos of the four TOCES to flood disturbance was system-dependent. This was investigated by comparing the similarities of the macrozoobenthos sampled in the lower reaches of each estuary over the study period. The species compositions of the four estuaries were broadly similar, and this was expected based on the common location of the estuaries within the same subtropical biogeographic region, common estuarine type (TOCEs), narrow strip of coastline and the fact that relatively few taxa can survive the dynamics of the estuarine environment (Day 1981c). Despite these similarities, the benthic communities were significantly different from one another ($R=0.726$, $p<0.0001$). The community of the Manzimtoti Estuary was markedly different from the remaining three systems, particularly the non-urban estuaries which shared less than 30% similarity with the Manzimtoti community (AT vs MAN, 0.973 , $p<0.002$; AT vs INT, $R=0.984$, $p<0.002$). This was largely attributed to the prolific occurrence of *Tarebia granifera* and the complete absence of an amphipod component, comprising *Grandidierella* species and *C. triaenonyx*, from the Manzimtoti Estuary. Interestingly, the Little Manzimtoti system was least dissimilar (most similar) in benthic community characteristics to the Mhlabatshane Estuary despite the difference in urban setting. This was based on differential abundances of similar species, especially prominent polychaete and amphipod species and Oligochaeta. Therefore, the null hypothesis (H_{03}) was rejected because significant differences between the post-flood responses of the macrozoobenthos of the four selected TOCEs were evident, and the response to flood disturbance was system-dependent.

These results are corroborated by other studies on post-disturbance recovery of benthic communities which similarly illustrated that site-specific environmental conditions, as well as the scale and type of the disturbance, governed the rate and pattern of recovery (Owen and Forbes 1997, Zajac et al. 1998, Thrush et al. 2003, Chollett and Bone 2007, Cardoso et al. 2008, Norkko et al. 2010, Grilo et al. 2011). In the context of this study, site-specific differences in environmental conditions were considered to include both intra- (between sites) and inter- (between systems) estuarine spatial scales. It was probable that the intensity of the June 2008 flood event was not equally felt across all systems due to their inherent differences, therefore

resulting in differing community responses. For example, the four systems differed in the level of urban development along their margins and activities in their catchments, their recreational uses, the type and extent of their fringing vegetation that forms a natural buffer to flooding (Stephen 1999, Kenwick et al. 2009), and possible occurrence of pollution that was not measured in the current study. In addition, the response of infaunal communities to changes in disturbance has been shown to vary according to habitat type, species, taxon and functional group, and this is largely due to the diversity of morphological, physiological and behavioural characteristics of benthic invertebrates (Eggleston et al. 1999, Lindegarth and Hoskin 2001, Whomersley et al. 2010). Recovery time is also dependent on the prevalence of flow refugia and habitat type because flow refugia provide shelter to vulnerable organisms that may be otherwise scoured from the system during flooding (Robinson et al. 2004), and certain habitats are perceived as more favourable for re-establishment and will be colonised faster (Eggleston et al. 1999, Grilo et al. 2011). Therefore, not only were the communities different in composition but they were possibly at different stages of recolonisation at different times during the study period. These factors present sources of variation leading to the observed differences in community response between the four estuaries.

Within each of the four TOCEs, the trajectory of recolonisation by benthic macrozoobenthos in response to flood disturbance was described with respect to temporal changes in the number of taxa, overall community abundance, evenness, diversity, variations in species assemblages and numerical dominance. The final hypothesis (H_{04}) was rejected because comprehensive results showed that in each estuary, the post-flood response was marked by significant community changes with increasing time after flooding. In the urban Manzimtoti and Little Manzimtoti estuaries, the inter-site responses to flood disturbance were more pronounced than the estuary-wide differences in community characteristics. Broad analysis of the recolonisation trajectory of each site illustrated that the response differed according to the position within the estuary (Site x Time AT $R=0.519$, $p<0.001$; LAM $R=0.772$, $p<0.001$) as similarly determined by Zajac and Whitlatch (1982a, 1982b). The community configuration at each site at the start of the study period was different to that at the end of the study period, and from other sites, and no two trajectories were alike. Diversity was also shown to vary significantly according to site and time (Two way ANOVA, $F= 3.53$, $p=0.003$). These results indicated that different macrozoobenthic communities existed at each site, which underwent different post-flood changes with increasing time. Therefore, recolonisation in response to

(flood) disturbance is not uniform across the disturbed area (the four TOCEs). These site-specific responses to disturbance are common in both marine (Norkko et al. 2010) and estuarine soft-sediment communities, and are related to the physical and chemical characteristics of each site, which change along the estuarine gradient (Zajac and Whitlatch 1982a, 1982b).

Some important observations on the recolonisation in the four-flood affected estuaries were made. Firstly, these estuaries were recolonised relatively quickly by generally the same species (and in relatively the same proportions) that were present in these systems more than 10 years ago (1998 data, Chapter 3), with the exception of *T. granifera*. These results illustrate the persistence and resilience of the macrozoobenthic communities to various environmental disturbances that were expected to have occurred in these systems over time. The Manzimtoti community had however changed. Historical records (1998 data) showed that species have been lost from the Manzimtoti Estuary and others were new to the system. *Grandidierella lignorum*, *G. lutosa* and *Grandidierella* spp. were once present in the lower reaches of the system, however they were not recorded in this estuary throughout the current study nor by Forbes and Demetriades (2008) in 2007 and 2008. In addition, *Tarebia granifera* is a relatively new species that has invaded the Manzimtoti Estuary in very large numbers. This species was present in the system prior to the June 2008 flood event (Forbes and Demetriades 2008) and was therefore not new to the macrozoobenthos as a result of the disturbance. The invasion of the Manzimtoti Estuary by *T. granifera* was most likely triggered by low diversity and the highly degraded condition of the system. These two factors lower the resistance of macrozoobenthic communities to biological invasions (Herkul et al. 2006).

Secondly, dramatic peaks in overall community abundance were typically recorded during Spring in all systems, followed by a decrease in Autumn. This increase during Spring is common in estuarine macrozoobenthos of TOCEs and probably aligned with the breeding period of many species (Mackay and Cyrus 2001). In the current study, this was not always associated with maximum diversity, except in the Little Manzimtoti Estuary, thus also suggesting an opportunistic response of certain species. In three of the four estuaries (Manzimtoti, Little Manzimtoti and Mhlabatshane) this was attributed to the proliferation of *Prionospio multipinnulata*, a polychaete species belonging to the Family Spionidae, which are known to exhibit opportunistic behaviour (Chollett and Bone 2007). Opportunists (r-selected species) are

the first species to respond to the sudden environmental changes following a disturbance. Characteristically, these species respond rapidly by initiating recolonisation of denuded sediment and dominating the early stages of succession in high numbers (Grassle and Grassle 1974, Pearson and Rosenberg 1978, Whitlatch and Zajac 1985). They possess specialised life history traits that enable them to take advantage of disturbed conditions and maintain very high population densities, including high reproductive rates, year round breeding, wide dispersal ability (as larvae, juveniles or adults), short maturation period, as well as broad tolerance to disturbed conditions (Grassle and Grassle 1974, Pearson and Rosenberg 1978, Santos and Simon 1980, Whitlatch and Zajac 1985). It could be argued that the subsequent decrease in overall community abundance in Autumn, represented the second stage in typical community succession, known as the 'ecotone point', where abundance is low due to the replacement of opportunistic species by later immigrants and colonisers; and both evenness and diversity reach a maximum (Pearson and Rosenberg 1978). The decrease in abundance was evident in all estuaries however, only in the Mhlabatshane and Intshambili estuaries were evenness and diversity at maximum. In the Intshambili Estuary, population increases in several species contributed to the increase in overall community abundance. The brooding behaviour of the prominent amphipod species and their ability to disperse as late-stage pelagic larvae and as adults (Santos and Simon 1980, Day 1981c) were most likely responsible for their success in this system. It was postulated that the occurrences of these species in appreciable numbers and the construction of their burrows near or on the sediment surface reduced the prevalence of the similarly tubicolous *P. multipinnulata*.

Thirdly, in all four estuaries that were investigated, changes in the state of the estuary mouth did occur over the study period. Thus, the observed recolonisation patterns were likely a product of post-flood re-establishment in combination with community adjustment in response to fluctuating physico-chemical conditions related to mouth breaching or closure. In the Manzimtoti Estuary, breaching in Autumn resulted in a community relatively similar to that in the early stages of recolonisation. Thereafter, the community recovered quickly in composition and abundance to the community that existed during the middle stages of recolonisation, but the number of species, abundance and diversity were the highest recorded throughout the study period. Similarly, in the Little Manzimtoti Estuary, reopening of the mouth caused a dramatic decrease in number of taxa, abundance, evenness and diversity, such that the community was reverted to early recolonisation configuration. However, there

was a marked change in dominance from *Oligochaeta* spp. to *P. multipinnulata*, which coincided with the closure of the mouth. Prior to closure, the community comprised mainly *Oligochaeta*, and minor proportions of Chironomini larvae and small-bodied worm species, that is, taxa that are indicative of oxygen-poor, disturbed environments (Day and Grindley 1981g, Mackay and Cyrus 2000, McLusky and Elliott 2004). The community that prevailed in the subsequent period of open mouth conditions was initially dominated by *P. multipinnulata* while *Oligochaeta* spp. were reduced. This was likely related to the opportunistic increase of *P. multipinnulata* and the acclimatisation of the various species, including *Oligochaeta* spp., to the sharp increase in salinity and other factors of the physico-chemical environment (Pearson and Rosenberg 1978). In the later stages of recolonisation, the community was similar in number of taxa, diversity and evenness to pre-close characteristics and dominated by larger, typical estuarine polychaete species (*D. arborifera*, *C. keiskama*) together with low proportions of *Oligochaeta* spp. and other species. Overall, the impact of breaching on macrozoobenthos in the Manzimtoti and Little Manzimtoti estuaries was comparable to the effect of flooding which reset the process of recolonisation. ‘Severe’ effects of breaching have been documented in other South African estuaries (De Villiers et al. 1999).

In contrast, despite the switch to the open mouth phase, faunal abundance in the Mhlabatshane Estuary increased dramatically instead of decreasing due to flushing as in the Little Manzimtoti Estuary. The increase was due to the proliferation in the number of individuals at the time and not the influx of new species because the number of taxa had in fact declined and diversity was low. Thereafter, faunal abundance remained high following mouth closure and several new species increased in abundance but did not progress to dominant positions within the community. Thus alternating mouth conditions caused prominent adjustments in benthic community structure of these three systems which interrupted any linear progression in post-flood recolonisation. In comparison, the Intshambili Estuary was closed for most of the sample period, except at the start of sampling (time 2). Thus, changes that took place during recolonisation from time 3 to time 6 were not influenced by the state of the mouth. Interestingly, although the species composition of the Intshambili community was markedly different from the other systems, trends in abundance were similar from time 2 to 3, and from time 4 to 5, and trends in evenness and diversity were similar from time 4 to 5. Sediment deposition occurred in the Intshambili between time 4 and time 6, particularly of finer sand and mud. However, this was not an important factor for the

distribution of the fauna in terms of food availability, as the correlation with organic content was not significant. This was more likely related to the smothering of the benthic community by the extensive deposition of terrigenous sediment that contributed to the dramatic decline in abundance and species richness at time 6. Such smothering events have been shown to have deleterious consequences for estuarine benthic communities (Norkko et al. 2002).

In the current study, several environmental factors were most likely responsible for the distribution of the macrozoobenthic communities and the combinations of these factors differed between the four estuaries. The post-flood responses of the macrozoobenthic communities were mostly associated with depth and the nature of the sediment than with changes in water quality variables, such as salinity or temperature. Changes in depth were generally related to changes from open to closed mouth state, or vice versa, whereby breached conditions resulted in shallow depth while prolonged closure resulted in increased depth. Sediment composition varied between sites in the urban estuaries, but also varied with time in all four TOCEs, often in parallel with the state of the mouth, with finer sediment in the Mhlabatshane Estuary with increasing time after the breached period. Despite the closed mouth condition in the Intshambili Estuary for much of the study period, sedimentation was dramatic in the later stages of the study period, likely attributed to increased runoff and sediment input in the catchment area. Fluctuations in salinity were however important for the macrozoobenthos of the Little Manzimtoti Estuary when the entire system experienced increased salinity during the irregular closed phase. The correlations between the biological communities and environmental variables in the Manzimtoti and Little Manzimtoti estuaries were poor in comparison to the Mhlabatshane and Intshambili estuaries, indicating that the biological pattern could not be fully explained by the environmental variables that were measured. By virtue of the urbanised environment, the macrozoobenthic communities of these two estuaries are likely exposed to increased concentrations of contaminants including nutrients, pesticides, hydrocarbons, organochlorines and heavy metals from urban runoff (Inglis and Kross 2000, Lindegarth and Hoskin 2001, Paul and Meyer 2001, Morrisey et al. 2003, Douglas et al. 2008, Kenwick et al. 2009). The accumulation of these compounds to harmful concentrations has noticeable, long-term and often deleterious effects on soft-sediment communities (Inglis and Kross 2000, Morrisey et al. 2003). It was therefore postulated that these pollutants, which were not measured during the current study, were present in these

urban estuaries and possibly contributed to the distribution and changes observed in the communities during the post-flood response.

In conclusion, the response of macrozoobenthos to flooding in June 2008 differed between estuaries of the same type (TOCEs) with similar morphometries, and within similar urbanised settings. The differences between the four communities were based on the exclusive presence of specific species and differences in relative abundances of common species between estuaries. Recolonisation took place relatively quickly and within one year, typical stages of community adjustment and succession were observed (Pearson and Rosenberg 1978). Patterns in recolonisation were found to differ between sites within an estuary, attributed to the likelihood of different starting communities, which were possibly related to the patchiness of flood disturbance, shelter provided by flow refugia and different physico-chemical conditions at each site. Characteristics of the sediment were the most common factors in determining the distribution of the biological communities with increasing time after flooding in each of the four estuaries. It could be argued that macrozoobenthos of TOCEs are well-adapted to fluctuations in salinity, and their distribution therefore is independent of salinity variations and most affected by changes in sediment type (Teske and Wooldridge 2003, 2004, Perissinotto et al. 2010). The state of the mouth was observed to have an important impact on recolonisation, such that breaching reset the progression of the developing community to early post-flood characteristics. This is mostly beneficial to estuarine organisms as prolonged closure of the mouth may hinder recolonisation due to the development of anoxic conditions (Begg 1978, Whitfield and Bate 2007, Becker et al. 2009) and in some estuaries, hypersalinities (Froneman and Henninger 2009). In the current study, seasonal trends were not well represented due to 1) the short duration of the study period and the concomitant lack of seasonal replication, and 2) restricted experimental design resulting in the absence of summer community samples. Seasonality is likely to have an important effect on recolonisation of TOCEs because faunal activity, metabolic rate, breeding behaviour and supply of colonists are affected by changes in temperature, which coincide with season (Hall and Frid 1998, De Villiers et al. 1999). Summer abundances in all four estuaries may have been greater than during spring as this is also a highly productive season for many organisms in TOCEs (Mackay 1996, Perissinotto et al. 2010), thus affecting the observed trajectories of recolonisation and recovery, which may have been further influenced by frequent open mouth conditions typical of the KwaZulu-Natal wet season.

Overall, the macrozoobenthic communities in each system were highly persistent with time, as the emergent communities comprised the same fauna that were present a decade ago. In addition, the macrozoobenthos exhibited strong resilience to flood disturbance. This is not uncommon of macroinvertebrate communities, especially those residing in estuaries, because these fauna are naturally resilient to the extreme variability of the estuarine environment (McLusky and Elliott 2004, Robinson et al. 2004, Elliott and Quintino 2007). Their ability to survive flood events is dependent on their morphological, physiological and behavioural adaptations and the existence of flow refugia (Robinson et al. 2004). With interruptions in recolonisation caused by other disturbances, including breaching of the mouth and sediment deposition events, it is likely that the macrozoobenthic communities of the estuaries are in a constant state of flux as a result of the compounding perturbations and may never progress to stable climax communities (Warwick and Clarke 1995, Ritter et al. 2005). However, the duration of the current study period was short (~1 year) and full recovery of the macrozoobenthos from flood disturbance in these TOCEs might exceed this time frame. Further investigations and long-term monitoring are required to determine accurately the response of estuarine communities to various disturbances and the effects of seasonality and state of the mouth on their recovery.

The impetus for long-term monitoring studies and investigations into the health of estuaries in KwaZulu-Natal is strong because the functioning of many estuaries, particularly around urban centres, has been severely affected by anthropogenic activities (Begg 1978, Cooper et al. 1995, Durban-Metropolitan 1999, Harrison et al. 2000, Whitfield 2000). Coastal towns and holiday resorts are clustered around most estuaries on the KwaZulu-Natal coast and they serve an important function as popular areas of recreation, and it is therefore critical that the health of these systems be monitored and maintained above public nuisance levels. However, the discrimination between benthic community changes caused by natural and anthropogenic disturbance is difficult because these forces act synergistically and are not mutually exclusive (Frouin 2000, Dolbeth et al. 2007, Elliott and Quintino 2007, Cardoso et al. 2008). Studies on the effects of both natural and human-induced disturbances on macrozoobenthos (Dolbeth et al. 2007, Cardoso et al. 2008, Neto et al. 2010, Grilo et al. 2011) emphasise the fact that the recovery potential of the benthic assemblages, and ultimately community stability and resilience to future perturbations, is compromised by the history of disturbance and simultaneous occurrences of different types of disturbance. With repeated disturbance, the

composition of benthic communities may become altered with time as different species occupy new roles as community dominants and other species are eliminated or are unsuccessful in recolonisation (Santos and Simon 1980, Salen-Picard et al. 2003). In urbanised estuaries that are subject to frequent disturbance, communities may therefore undergo dramatic changes and be altered completely such that they bear no similarity to the original community of the once undisturbed estuary. This in turn may lead to loss of biodiversity with consequences for ecosystem functioning (Chapin III et al. 2000).

Furthermore, the frequency and intensity of extreme weather events, such as floods, are predicted to increase with the progression of climate change (Douglas et al. 2008, Chagutah 2009, Grilo et al. 2011). Investigations on the effects of such stochastic environmental disturbances are generally scarce, or conducted on a snapshot basis, because of their unpredictable nature and therefore cannot be repeated, leading to under-representation of natural ecological change (Santos and Simon 1980, Jones 1990). Although of relatively short duration, the current study not only presented a species record for biodiversity assessments and for future investigations, but also provided an estimation of the extent of spatial and temporal variation associated with a relatively small, short-term natural disturbance. In addition, insight into the recovery and resilience of estuarine communities to environmental disturbance was revealed. Thus, the findings of this study are vitally important for our understanding of the effects of natural perturbations on estuarine macrozoobenthos in the light of climate change. However, they do not provide a simple solution for the regional management of estuaries. As duly noted by Whitfield and Bate (2007), *“each estuary is unique because of the various factors that influence its structure and sensitivity to flow, and two similar sized estuaries adjacent to one another can be quite different”*. Therefore, based on the differential response of estuarine macrozoobenthos to natural disturbance in different estuaries, investigations at the individual system level are recommended for the effective management of estuarine ecosystems.

CHAPTER 5

IDENTIFYING CHANGE IN ESTUARINE COMMUNITIES: THE ROLE OF MACROZOOBENTHIC SPECIES ASSEMBLAGES

5.1 Introduction

To understand better the nature of change in estuarine macrozoobenthos, and to examine the potential causes of change, it is necessary to investigate communities at the species level, incorporating aspects of species ecology. As previously discussed in Chapter 1, it is the particular attributes of the constituent species that render macrozoobenthic communities effective indicators of environmental change in estuarine and marine ecosystems (Dauer 1993, Weisberg et al. 1997, McLusky and Elliott 2004, Heino 2008). The overall structure of these communities (Figure 5.1) is dependent on the differential physical and/or physiological tolerances of the different species to environmental conditions, their ecological requirements, and the complexity of their biological interactions (Baldó et al. 1999, Pinnegar et al. 2000, Lenihan et al. 2003). Changes in macrozoobenthic community structure, particularly in response to stress, or disturbance, are manifested through shifts in species composition, abundance, dominance, biomass, diversity and the strength and direction of species interactions (Pearson and Rosenberg 1978, Dauer 1993, Baldó et al. 1999, Wolanski 2007, Cardoso et al. 2008, Norkko et al. 2010). Furthermore, according to the 'hierarchical-response-to-stress' theory (Pearson and Rosenberg 1978), the response to stress is initiated at the species level (Figure 5.2), and dependent on the adaptability of the first individuals, which subsequently spreads to higher levels of organisation as the adaptability of each level is exceeded (Pearson and Rosenberg 1978, Ferraro and Cole 1990, Baldó et al. 1999). Therefore, species (and/or species assemblages) play an important role in determining the observed changes in macrozoobenthic communities over space and time.

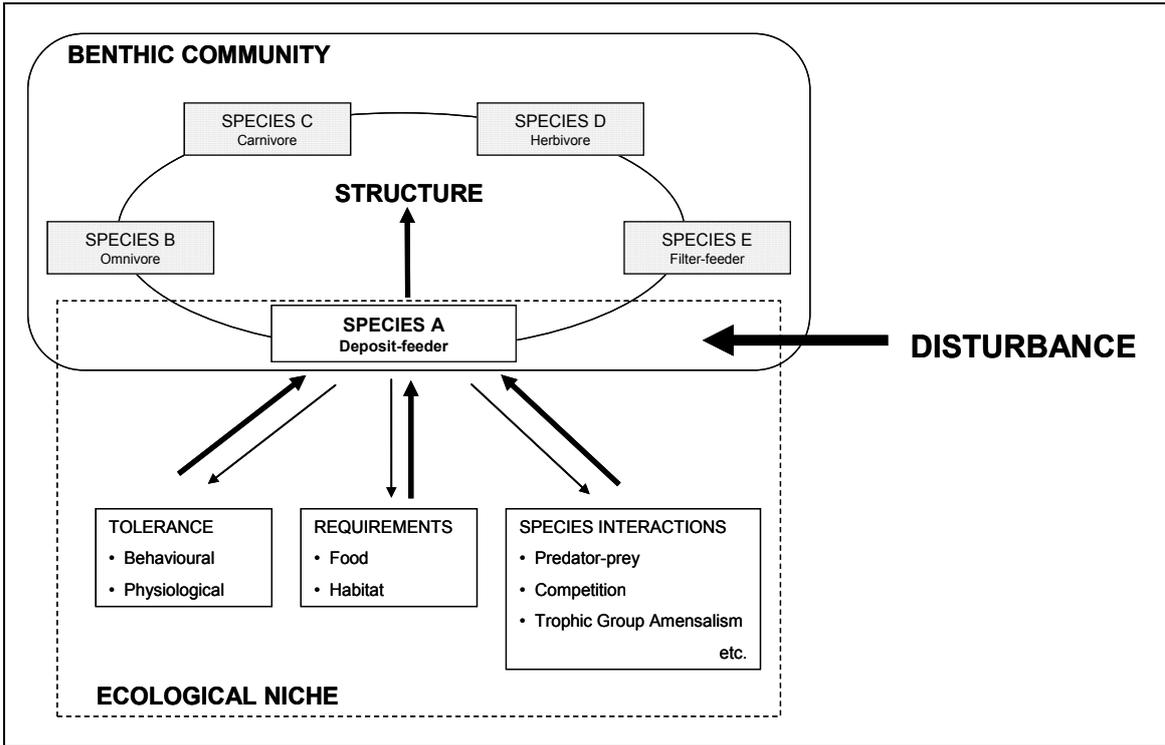


Figure 5.1 Schematic diagram of how perceived species-related factors influence the structure of macrozoobenthic communities in TOCEs in KwaZulu-Natal. Dark arrows indicate changes in response to disturbance that result in altered community structure. Species A-E represent hypothetical examples.

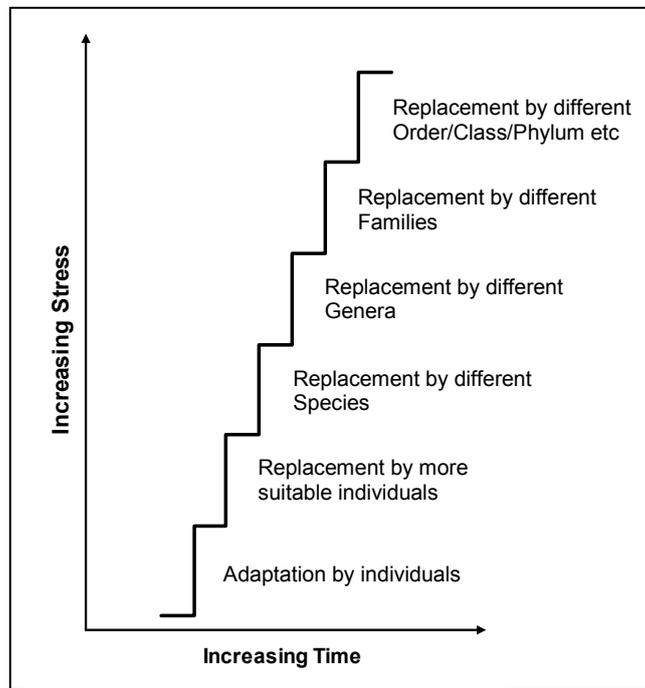


Figure 5.2 Schematic diagram of the relationship between environmental stress and taxonomic variability (Taken from Pearson and Rosenberg, 1978)

The ecological niche of a particular species (Figure 5.1) encompasses the physical habitat in which it lives, its functional role in the community (e.g. trophic role) and its position along multiple environmental gradients (e.g. salinity, temperature etc.) (Odum 1971). In order for species to co-exist in a particular habitat, they must occupy a unique ecological niche, most often separated by the utilisation of different resources (e.g. different food resources) (Odum 1971, Flint and Kalke 1986a). The role of a particular species within the community is defined by its effect on the distribution and abundance of other species (Piraino et al. 2002). However, the effect of each species on the community structure is not equal. The dominant species are the most abundant species which support the general community and have a large effect on other species (Piraino et al. 2002, Smee 2010). Non-abundant species contribute to the functioning of the community by maintaining species diversity (Piraino et al. 2002). The original concept of the 'Keystone Species' refers to those species which have a major impact on communities far out of proportion to their abundance (Piraino et al. 2002, Davic 2003, Smee 2010). They are the species, which through strong species interactions, maintain the structure and functioning of communities (and ecosystems) in a particular state (Piraino et al. 2002, Davic 2003) and the loss of these species causes dramatic changes in community dynamics and ecosystem processes (Golubiewski and McGinley 2010). Defining such important species has conservational significance, whereby keystone species, or groups of keystone species, may be afforded protection in order to maintain essential ecosystems processes (Payton et al. 2002, Davic 2003).

Several prominent species interactions occur in benthic communities including trophic group amensalism, competition and predation. Although these interactions were not directly observed or measured during the current study, they provide insight into the dynamics that occur within macrozoobenthic communities and the impact of species on community structure. Trophic group amensalism typically involves the interaction between infaunal deposit feeders and suspension feeders, whereby deposit feeders destabilise the sediment by their bioturbation during feeding, consequently excluding suspension feeders from muddy sediment (Rhoads and Young 1970, Gray 1981, Probert 1984). Resuspension of fine particulate material clogs the feeding and respiratory apparatus of suspension feeders, and prevents the settlement of their larvae (Rhoads and Young 1970). Thus, suspension feeders tend to occupy sediment with a greater proportion of sand and deposit feeders muddier substrates, respectively. However, soft sediment communities most often comprise a mixture of both

trophic groups (Gray 1981, Probert 1984, Herman et al. 1999). The sandprawn, *Callinassa kraussi*, a burrowing suspension feeder, exerts a similar form of amensalism on benthic fauna of subtropical sandflats, where bioturbation caused by *C. kraussi* during burrow construction reduces community diversity (Pillay et al. 2007). In its absence, a rich community comprising surface grazers, suspension feeders and surface deposit feeders exists (Pillay et al. 2007). In contrast, Dittman (1996) found that although burrowing sandprawns may exclude certain species, they also have a promotive effect on infauna communities, possibly related to the rich microbial and microalgal food sources and refuges provided by their burrows.

Competition between closely related species for resources, such as space and food, is also a major force driving the structure of benthic communities (Wilson 1991). Direct interactions, where two species actively inhibit each other ('Interference Competition') (Odum 1971), may lead to restricted foraging patterns, habitat restrictions or zonations, and population declines in the inferior species (Wilson 1991, Hosack et al. 2006, Holomuzki et al. 2010). Similarly, indirect interactions, where two species negatively influence each other in the struggle for a limited resource ('Exploitive Competition') (Odum 1971) may result in stunted growth, reduced growth rate and reproductive effort, and population migration of the disadvantaged species due to density-dependent effects (Wilson 1991, Holomuzki et al. 2010). Wilson (1991) stated that competitive exclusion is not common in soft sediment communities because of the multidimensionality of the sedimentary environment.

In soft sediment communities, predator-prey interactions occur both at the surface of the substratum, by epi-benthic decapods, gastropods, birds and fish, and within the sediment, primarily by nemertean and polychaete worms (Ambrose 1991, Wilson 1991). Essentially, predators contribute significantly to the structure of benthic communities by directly influencing the abundance, distribution and diversity of species at lower trophic levels, known as top-down effects (Commito 1982, Ambrose 1991, Wilson 1991, Pinnegar et al. 2000). Direct predation on specific size classes (Wilson 1991, Piraino et al. 2002) or gender (Schlacher and Wooldridge 1996a) can alter the structure of individual species populations. Through trophic cascades, predators indirectly regulate species at several trophic levels (Pinnegar et al. 2000, Heck and Valentine 2007). Removal of the key predator often results in reduced diversity of the ecosystem through competitive exclusion caused by unchecked prey species (Putman and Wratten 1984).

In contrast to top down control, changes in benthic community structure and species interactions in response to environmental change may result in shifts in the species composition of higher trophic levels (Pillay et al. 2008). For example, a shift in the nature of the substratum on a subtropical intertidal sandflat provided suitable habitat for the burrowing sandprawn, *C. kraussi* where it was previously absent. Pillay et al. (2008) maintain that, in addition to the effect of changes in sediment particle size, the change in the composition of the benthic community was largely attributed to the increased presence and extensive bioturbation of this species, effectively excluding several previously dominant filter-feeding bivalves. Concomitantly, the once benthic-feeding fish community, feeding primarily on bivalve siphons, was replaced by zooplanktivorous fish species following the reduction of the bivalves and non-burrowing benthic species. From their results, Pillay et al. (2008) identified *C. kraussi* as a potential keystone species in estuarine macrozoobenthic communities. This is an example of how higher (or lower) trophic levels and benthic community organisation may be affected by the response of a particular species to changes in benthic environmental conditions.

5.2 Aim and Questions

The above information highlights the underlying importance of species in determining overall macrozoobenthic community structure. The aim of this chapter was to identify and describe, by means of SIMPER and inverse analyses, the species assemblages that were indicative of the different types of community variation, or 'change', investigated in the preceding chapters. In Chapters 3 and 4, testable hypotheses were formulated regarding temporal and spatial differences between macrozoobenthic communities. In contrast, the current chapter is essentially exploratory with no testable hypotheses. Instead, a series of questions were addressed relating to 1) discriminatory species, and 2) similarity between species. Firstly, which species were important discriminators in each type of community change? Moreover, were there any species common to all three types? Secondly, did these species show a degree of similarity? If so, how were they similar in terms of their basic ecology (general habitat and trophic group)? These questions were to be answered using information gathered from the previous chapters in combination with multivariate analytical procedures as described in the following section.

5.3 Methods of Data Analysis

In the previous two chapters, SIMPER analyses were used to identify species assemblages that both typified and/or discriminated between groups of samples based on their average contribution to similarity or dissimilarity. Using this community data, the five best discriminatory taxa, that is species with the highest $\delta_i/SD(\delta_i)$ ratio (see Chapter 2 Methods and Materials) were selected as species indicative of each type of community change that was studied (Short-Term (ST), Long-Term (LT) and Spatial (SP)). Essentially, these species were predominantly responsible for the separation of samples into the groups depicted in the ordinations in the respective chapters. From these SIMPER analyses, a composite species list was compiled and abundance data for these taxa were entered into a species-by-sample matrix. Included in this was, 1) the time series data for each of the flood-damaged estuaries (the Manzimtoti, Little Manzimtoti, Mhlabatshane and Intshambili systems) for which abundance data were calculated as mean abundance per estuary per time and 2) inter-estuarine data for each of the 31 TOCEs sampled in 1998/9 and 2009/10, given as the mean abundance per estuary for each sample period. Inverse analysis was performed to determine the similarities between species. Species are considered similar if their numbers fluctuate in parallel across samples or sites (Clarke and Warwick 2001). Species abundances were first log-transformed ($\log [x + 1]$) and row standardised such that the abundance of a species at a particular estuary was a percentage of the total abundance of that species across all estuaries. A species similarity matrix was then computed using the Bray-Curtis Similarity co-efficient.

Using NMDS procedures, groups of similar species were identified and the possible sources of similarity were explored by factorising each species according to their dominant habitat association (marine, estuarine, freshwater) following Griffiths (1976), Day (1981c), and Mackay (1996), dominant trophic group (the mostly commonly documented), and the type of community variation represented (ST/LT/SP). Macrozoobenthic species were categorised into various trophic groups based on the mode of feeding gathered from pertinent literature. Certain species possess several modes of feeding (e.g. spionid polychaetes) and in such cases, the dominant feeding mode, as determined from the literature, was considered. The trophic groups that were used in the current study were based on those used by Cardoso et al. (2008). The authors separate detritivores into three sub-categories, namely subsurface deposit feeders, surface deposit feeders and suspension feeders. However, it was found that the terms

detrivore and deposit feeder are often used inexplicitly in the literature and detailed information regarding the feeding mode of some species is lacking. Therefore, species broadly termed as detritivores were grouped together with deposit feeders as fauna feeding on non-suspended detrital particles, in comparison with suspension feeders which extract detrital particles from the water column. The trophic groups thus used were detritivore/deposit feeders (D), detritivorous suspension feeders (S), herbivores (H) (grazers and scrapers of plant material), carnivores (C), omnivores/scavengers (O/Sc) and uncertain (U), as similarly used by Cardoso et al. (2008).

5.4 Results

5.4.1 Species Composition

A total of 34 discriminatory taxa were extracted from the previous SIMPER analyses, conducted in Chapters 3 and 4, that were used to assess the spatial and temporal differences in macrozoobenthos of the selected TOCEs (Table 5.1). Twenty taxa were isolated from the combined short-term (up to 12 months) recolonisation sequences of the four flood-damaged estuaries. There were 27 taxa that were consistently responsible for the spatial discriminations between groups of estuaries sampled in 1998/9 and 2009/10. Within this were the top six species responsible for the overall decadal difference in the benthos sampled in 1998/9 and in 2009/10. Thirteen taxa were common to both short-term and spatial differentiations, and the following six taxa were implicated in all three sources of community variation: Chironomini larvae spp., *Corophium triaenonyx*, *Grandidierella lignorum*, *Grandidierella lutosa*, *Grandidierella* spp. and Oligochaeta spp. Of the 34 taxa, the majority were typically estuarine-associated species, together with several freshwater species (mainly dipteran insects) and few marine taxa, or species with the affinity for more saline environments. In terms of trophic groups, detritivores/deposit feeders were most dominant.

Table 5.1 Full list of 34 taxa responsible for short-term temporal (ST), long-term temporal (LT) and spatial (SP) differentiations between macrozoobenthic samples, their habitat association and trophic group. Abbreviations: L= Larvae, T= Type, PL=Post-Larvae, Juv= Juvenile, PreJuv= Pre-juvenile

Faunal Group	Species	No.	Habitat Association*	Feeding Group**	ST	LT	SP
Gastropoda	<i>Assimineia ovata</i>	1	E	D/H	X		
Bivalvia	<i>Brachidontes virgiliae</i>	2	E	S	X		
Polychaeta	<i>Brania</i> sp.1	3	M	D	X		
Gastropoda	<i>Burnupia</i> sp.1	4	F	H			X
Insecta	<i>Caenis</i> spp.	5	F	D			X
Polychaeta	<i>Capitella</i> spp.	6	E	D			X
Polychaeta	<i>Ceratonereis keiskama</i>	7	E	O/Sc	X		X
Insecta	Ceratopogonidae LT1	8	F	C			X
Insecta	Ceratopogonidae LT3	9	F	C			X
Insecta	Chironomini larvae spp.	10	F	O/Sc	X	X	X
Insecta	Chironomini pupae spp.	11	F	U			X
Isopoda	<i>Cirolana</i> sp.1	12	E	O/Sc	X		
Amphipoda	<i>Corophium triaenonyx</i>	13	E	S	X	X	X
Isopoda	<i>Cyathura estuaria</i>	14	E	D			X
Polychaeta	<i>Dendronereis arborifera</i>	15	E	D	X		X
Polychaeta	<i>Desdemona ornata</i>	16	E	S	X		X
Amphipoda	<i>Grandidierella lignorum</i>	17	E	D	X	X	X
Amphipoda	<i>Grandidierella lutosa</i>	18	E	D	X	X	X
Amphipoda	<i>Grandidierella</i> spp.	19	E	D	X	X	X
Collembola	Hypogastruridae sp.1	20	F	O/Sc			X
Polychaeta	<i>Lumbrineris tetraura</i>	21	M	D	X		
Decapoda	Macrura PLT1	22	U	U			X
Gastropoda	<i>Melanooides tuberculata</i>	23	E	D/H			X
Mysidacea	<i>Mesopodopsis africana</i>	24	E	O/Sc			X
Mollusca	Mollusca PreJuv T1	25	U	U	X		
Nematoda	Nematoda spp.	26	F	U	X		X
Nemertea	Nemertea sp.1	27	M	C	X		
Oligochaeta	Oligochaeta spp.	28	F	D	X	X	X
Insecta	Orthoclaadiinae larvae spp.	29	F	O/Sc			X
Polychaeta	<i>Prionospio multipinnulata</i>	30	E	D	X		X
Polychaeta	Sabellidae JuvT1	31	E	U			X
Insecta	Tanypodinae larvae spp.	32	F	C	X		X
Gastropoda	<i>Tarebia granifera</i>	33	E	D/H	X		X
Acarina	Trombidiformes spp.	34	F	U			X

* F= Freshwater, E= Estuarine, M= marine, U=Uncertain

** D= Detritivore/Deposit feeder, S= Suspension feeder, H= Herbivore, O/Sc= Omnivore/Scavenger, U= Uncertain

5.4.2 Species Ordinations

Figure 5.3 presents the species ordination by inverse analysis of all 34 taxa. Six groups of similar taxa were distinguishable at 25% similarity and six taxa occurred in isolation. These taxa and their corresponding numbers are given in Table 5.2. Group I comprised four taxa, *Burnupia* sp. 1 (Gastropoda), *Caenis* spp. (Insecta) Ceratopogonidae LT3 (Insecta) and Hypogastruridae sp. 1 (Collembola).

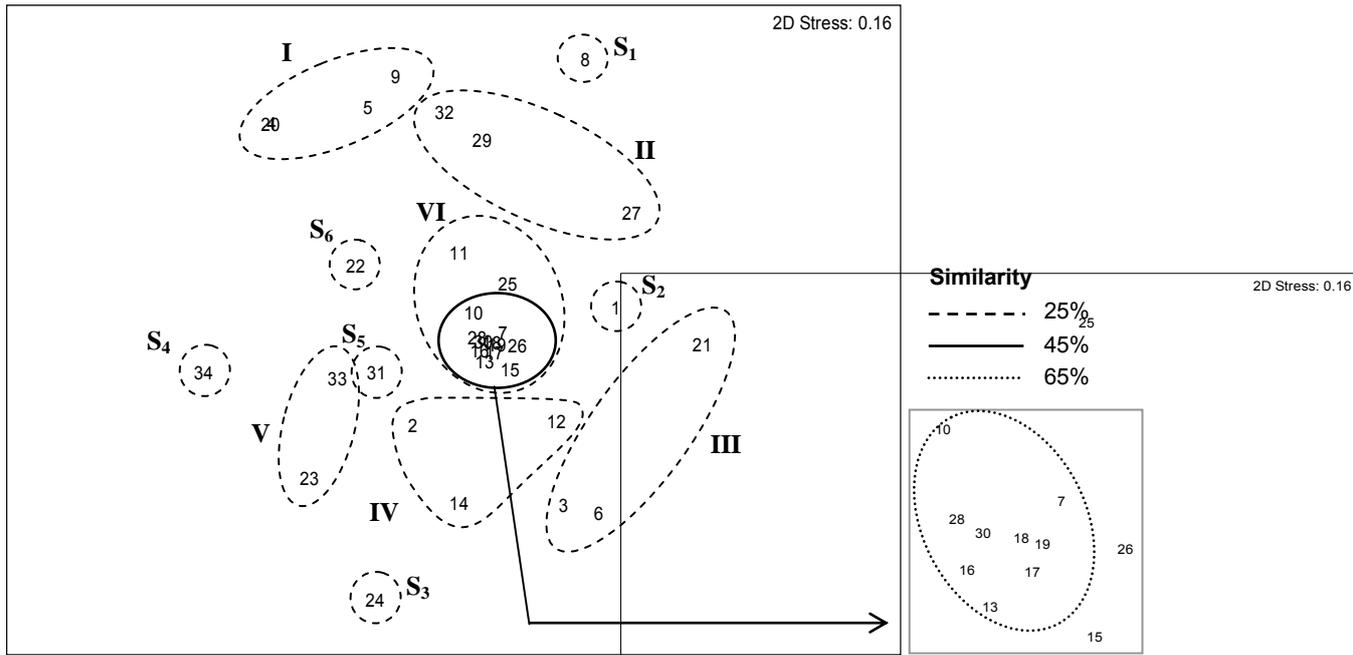


Figure 5.3 Ordination by inverse analysis comparing 34 macrozoobenthic species of KwaZulu-Natal TOCEs according to species number as given in Table 5.1. Species groups identified at 25%, 45% and 65% similarity. Densely clustered species grouped at 45% similarity are displayed alongside for better clarity.

Table 5.2 Species groups distinguished by inverse analysis. Groups based on the NMDS in Figure 5.1A at 25% similarity. Species numbers refer to those given in Table 5.1. Asterisk indicates species with >65% similarity.

<p>Group I</p> <p>4 <i>Burnupia</i> sp.1 5 <i>Caenis</i> spp. 9 Ceratopogonidae LT3 20 Hypogastruridae sp.1</p> <p>Group II</p> <p>27 Nemertea sp.1 29 Orthocladiinae larvae spp. 32 Tanypodinae larvae spp.</p> <p>Group III</p> <p>3 <i>Brania</i> sp.1 6 <i>Capitella</i> spp. 21 <i>Lumbrineris tetraura</i></p> <p>Group IV</p> <p>2 <i>Brachidontes virgiliae</i> 12 <i>Cirolana</i> sp.1 14 <i>Cyathura estuaria</i></p> <p>Group V</p> <p>23 <i>Melanoides tuberculata</i> 33 <i>Tarebia granifera</i></p>	<p>Group VI</p> <p>7 <i>Ceratonereis keiskama</i>* 10 Chironomini larvae spp.* 11 Chironomini pupae spp. 13 <i>Corophium triaenonyx</i>* 15 <i>Dendronereis arborifera</i> 16 <i>Desdemona ornata</i>* 17 <i>Grandidierella lignorum</i>* 18 <i>Grandidierella lutosa</i>* 19 <i>Grandidierella</i> spp.* 25 Mollusca PreJuv T1 26 Nematoda spp. 28 Oligochaeta spp.* 30 <i>Prionospio multipinnulata</i>*</p> <p>Single Taxa</p> <p>8 Ceratopogonidae LT1 S₁ 1 <i>Assiminea ovata</i> S₂ 24 <i>Mesopodopsis africana</i> S₃ 34 Trombidiformes spp. S₄ 31 Sabellidae JuvT1 S₅ 22 <i>Macrura</i> PLT1 S₆</p>
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Groups II to IV each contained three taxa. Group II contained Nemertea sp. 1 (Nemertea), and Orthocladinae and Tanypodinae fly larvae (Insecta). Group III was exclusively composed of Polychaeta, namely, *Brania* sp. 1, *Capitella* spp. and *Lumbrinereis tetraura*. *Brachidontes virgiliae* (Bivalvia) and the isopod species *Cirolana* sp. 1 and *Cyathura estuaria* were contained in Group IV. In Group V, were two mollusc species of the same family (Thiaridae), *Melanoides tuberculata* and *Tarebia granifera*. Group VI comprised 13 of the 34 taxa, of which 11 species were densely clustered together (Figure 5.3). The 11 concentrated taxa shared a high degree of similarity (45%) because they occurred simultaneously in 35% of the samples and constituted the species most common in the investigated TOCEs. Individually, species occurred in 50 – 84% of all samples. The taxa were the crustacean amphipods *Grandidierella lignorum*, *G. lutosa*, *Grandidierella* spp. and *Corophium triaenonyx*, the polychaetes species *Ceratonereis keiskama*, *Desdemona ornata*, *Dendronereis arborifera*, and *Prionospio multipinnulata*, insect fly larvae Chironomini larvae, Oligochaeta spp. and Nematoda spp. Furthermore, within this nucleus, nine taxa shared >65% similarity (indicated by an asterisk in Table 5.2). These species were the most numerically abundant of all species collected and co-occurred in 87% of the samples. The remaining two taxa in Group V were Chironomini pupae spp. (Insecta) and Mollusca PreJuv T1 (Mollusca). The six solitary taxa included Ceratpogonidae LT1 (Insecta, S₁), *Assimineia ovata* (Mollusca, S₂), *Mesopodopsis africana* (Mysidacea, S₃), Trombidiformes spp. (Acarina, S₄), Sabellidae JuvT1 (Polychaeta, S₅) and Macrura PLT1 (Decapoda, S₆).

Figure 5.4 A shows the same configuration of the 34 taxa with the species numbers replaced by the type of community variation characterised by each species. This ordination revealed that, apart from Group 1, each group contained species that represented a combination of the three types of community 'change'. Group I comprised taxa that were indicative only of spatial differences in benthic community structure. The species contained in Groups III and IV were mostly indicative of short-term temporal community changes. Groups II and V comprised taxa indicative of short-term temporal and spatial community differences, and a combination of both. In Group VI, there were five species that were indicative of both these types of change and six species that were important discriminators in all three types of community change. In addition, there were two species that individually represented spatial and short-term temporal change, respectively.

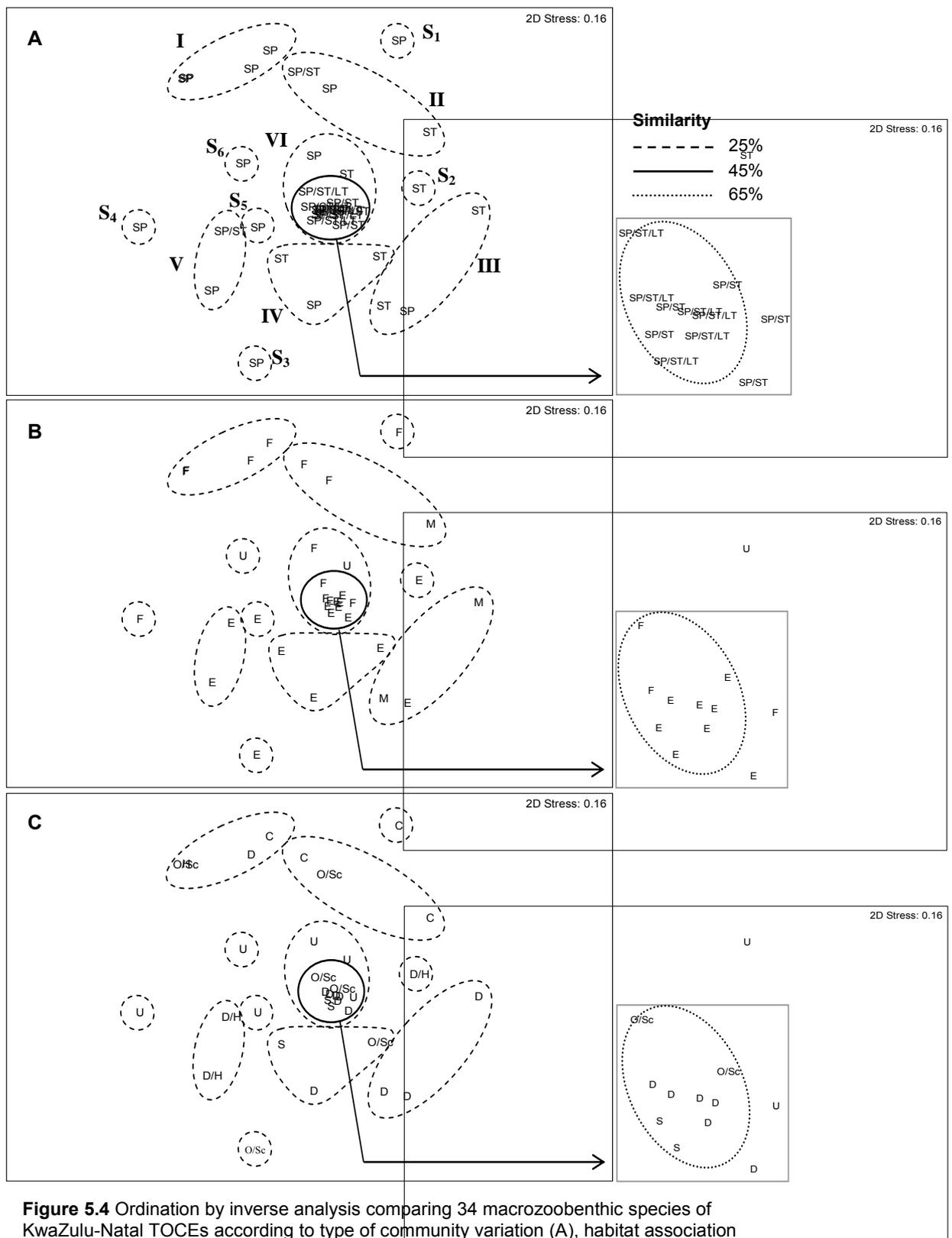


Figure 5.4 Ordination by inverse analysis comparing 34 macrozoobenthic species of KwaZulu-Natal TOCEs according to type of community variation (A), habitat association (B) and trophic group (C) as given in Table 5.1. Species groups identified at 25%, 45% and 65% similarity. Densely clustered species grouped at 45% similarity are displayed alongside for better clarity.

In terms of habitat associations (Figure 5.4 B), Group I, and Groups IV and V, exclusively comprised freshwater and estuarine-associated species, respectively. Groups VI contained predominantly estuarine-associates. Group III species were a combination of estuarine and marine fauna, and Group II species were a combination of freshwater and marine fauna. The solitary species were mostly estuarine and freshwater forms. The similarity of species contained in these groups was not clearly correlated with feeding mode (Figure 5.4 C). Groups III and IV were the only groups to contain mutually exclusive trophic groups, Detritivore/Deposit feeder and Detritivore/Herbivore, respectively. The remaining groups contained a mixture of trophic groups represented by the various species.

5.5 Discussion

After isolation of the best discriminatory species for each aspect of community change, it was apparent that the suite of species reflective of temporal changes were not completely unique from those that represented spatial differences between estuaries. Six taxa were important indicators in every type. These were *Corophium triaenonyx*, *Grandidierella lignorum*, *Grandidierella lutosa*, *Grandidierella* spp., Chironomini larvae spp. and Oligochaeta spp. These were also the taxa most responsible for the long-term differentiation between the benthos of the KwaZulu-Natal TOCEs sampled in 1998/9 and 2009/10. An additional seven species were common to the separation of sample groups in both short-term temporal and spatial SIMPER pair-wise comparisons. These included *Ceratonereis keiskama*, *Dendronereis arborifera*, *Desdemonia ornata*, *Prionospio multipinnulata*, Tanypodinae larvae spp., Nematoda spp. and *Tarebia granifera*. The remaining species were exclusively important to each aspect of either short-term or spatial change. However, the remaining species reflective of short-term change differed between estuaries, that is, they were also responsible for spatial differences in the macrozoobenthic communities between the four flood-affected estuaries (Chapter 4). Thus, in agreement with the findings of Chapter 4, short-term changes in macrozoobenthic communities, such as those that take place during the recolonisation of an estuary following a disturbance, are estuary-specific. That is, the response of macrozoobenthic communities of different estuaries to the same stress is not the same across all afflicted systems due to inherent differences in community structure.

Through inverse analyses, the similarity between these various species was assessed according to aspects of their basic ecology including general habitat type and trophic group.

GROUP VI (13 taxa)

Group VI was the largest group of taxa. Individually, these species occurred in most of the estuaries that were sampled (Mollusca PreJuvT1 30% – *Grandidierella* spp. 89% of all samples) and varying combinations occurred simultaneously. This was expected because 1) the majority of these species are known inhabitants of warm-temperate and subtropical South African estuarine systems, including freshwater relict estuarine lakes, and permanently open and temporarily open/closed estuaries (Day 1981c, Blaber et al. 1983, Blaber et al. 1984, Reavell and Cyrus 1989, Schlacher and Wooldridge 1996a, Mackay and Cyrus 2000, 2001, Teske and Wooldridge 2001, Forbes and Demetriades 2008, Mackay et al. 2010, Ngqulana et al. 2010, Perissinotto et al. 2010), and 2) these important species comprised euryhaline marine and freshwater forms, and typical estuarine species all capable of tolerating dramatic fluctuations in salinity (Day 1981c). Thus, as the species best adapted to the environmental conditions, many of these taxa were numerically dominant where they occurred (Golubiewski and McGinley 2010). Furthermore, six taxa, *C. keiskama*, *D. ornata*, *C. estuaria* and the species of *Grandidierella*, are endemic to South Africa (Griffiths 1976, Day 1981c) and were expected to occur in most of these estuaries.

These common species are likely generalists. That is, species that have broad ecological niches and which are tolerant of large fluctuations in environmental conditions (Kassen 2002), thus enabling them to survive in many South African estuaries. Their ability to co-exist could be explained by their preference for specific environmental conditions within the variable estuarine environment (Gray 1981). Research by Flint (1986a) on niche characterisation of estuarine macrozoobenthos, illustrated that dominant species living in the same habitat minimized niche overlap (thereby reducing severe competition) by occupying separate microhabitats. He found that species were subtly separated, according to 1) sediment type and organic content, 2) distribution of phytoplankton productivity, 3) temporal occurrences based on seasonal differences in water temperatures, and 4) specific sediment depths (Flint and Kalke 1986a). These different aspects represent the different niche dimensions along which closely related species may be separated (Gray 1981).

For example, the tubicolous amphipods *Corophium triaenonyx* and *Grandidierella lignorum* were numerically dominant in the benthos of many of the sampled TOCEs. In the Mpambanyoni (1998/9) and Intshambili (2009/10) they collectively accounted for up to 90% (22,465.33 ind.m⁻²) and 62% (7798 ind.m⁻²) of the total faunal abundance, respectively. These species share very similar ecological niches. Both are truly estuarine species with broad salinity tolerances from 2 to 60, they are tube dwellers, and brood their offspring which enables them to maintain station within an estuary (Day 1981c, Blaber et al. 1983, Read and Whitfield 1989). However, they require different sediment types for the construction of their tubes (Barnard et al. 1988, Cyrus and Martin 1988). While they have been sampled at various depths and from various substrates ranging from sandy sediment to glutinous mud to under stones (Reavell and Cyrus 1989), *G. lignorum* shows a preference for predominantly sandy substrata (Cyrus and Martin 1988). This species requires sand-sized particles (0.15 mm – 1.0 mm grain size diameter) for the construction of its burrows within the sediment, whereas *C. triaenonyx* constructs tubes above the sediment surface by cementing silt particles together using protein (or 'amphipod silk') (Barnard et al. 1988, Cyrus and Martin 1988). *Corophium triaenonyx* is thus considered more adaptable to shifts in sediment composition than *G. lignorum* because it is not as restricted by sediment type and can exploit a greater variety of habitats, such as decaying tree trunks, floating root masses (Cyrus and Martin 1988) and empty gastropod shells (pers. obs.) because the tubes can be attached to different surfaces.

Although typically benthic, *G. lignorum* and *C. triaenonyx* are not uncommon in estuarine planktonic (Grindley 1981) and hyperbenthic (Heyns and Froneman 2010) samples. The method of feeding is thus debated amongst authors, and includes errant surface deposit-feeding (emerging to collect detritus on the sediment) (McLusky and Elliott 2004), benthic filter-feeding (creating burrows through which water and particulate matter is pumped and filtered) (Reavell and Cyrus 1989, Schlacher and Wooldridge 1996b) and nektonic filter-feeding (Read and Whitfield 1989). Furthermore, their diet may include detrital aggregates (predominant item), filamentous algae and unicellular algae (Whitfield 1989). *Grandidierella lignorum* has also been shown to switch to a pelagic lifestyle, obtaining food material via filter-feeding, in estuaries experiencing increased freshwater input and reduced salinities during flooding (Read and Whitfield 1989). Presumably, this change in behaviour enables these organisms to capitalise on the peak in suspended food material in the water column due to increased river discharge (Read and Whitfield 1989). Adults have also been known to enter the

plankton at night in the calm water environments of estuarine lakes (Reavell and Cyrus 1989). Thus, through tube construction at different depths in the sediment, within different sediment types and different flexibility in their method of feeding, these amphipod species may limit severe interspecific competition for space and food resources, and can co-exist in the same habitat. These factors most likely contribute to their ability to outcompete other benthic species.

Similar to amphipods, polychaete worms were one of the most abundant faunal groups encountered that exhibit a variety of physiological and morphological adaptations to survive a range of salinities and in different estuarine habitats. *Ceratonereis keiskama* (Nereidae) is a truly estuarine, endemic species capable of surviving in low salinities of the upper reaches of estuaries, and commonly found burrowing in muddy sediment (Day 1967a, 1981c). This species is predominantly omnivorous (Day 1981c) and it has been suggested by Schlacher and Wooldridge (1996a) that epibenthic foraging takes place at night. Kalejta and Hockey (1991) found that *C. keiskama* was restricted to medium to fine sand in the Berg River, however, in the KwaZulu-Natal estuaries, it was most abundant in estuaries with medium to coarse grained sediment. *Dendronereis arborifera* (Nereidae) is a tropical, euryhaline, surface deposit-feeding species well adapted to surviving in thick soft mud where oxygen levels are low through the development of filamentous gills on the anterior parapodia (Day 1967a, Fauchald and Jumars 1979). It was recorded in the Siyaya and Nhlabane estuaries where salinities ranged between 1.4 and 5.6 (Mackay and Cyrus 2001), but also occurred in near marine water of St Lucia (Mackay et al. 2010) and hypersaline conditions in the estuaries of the Eastern Cape (Teske and Wooldridge 2001, 2003). *Desdemona ornata* (Sabellidae) is an endemic estuarine suspension feeder which may switch to deposit-feeding in favourable conditions (Rossi et al. 2001), which might explain its association with fine muddy, organic-rich sediments in the Gamtoos Estuary (Schlacher and Wooldridge 1996d). It can be argued that the trophic flexibility of *D. ornata* enables it to colonise different substrate types, as found in the current study, where it was sampled from sediment with high mud, low coarse-grained content, as well as low mud, high coarse grained content. Furthermore, Rossi et al. (2001) showed that the abundance of *D. ornata*, as a secondarily selective deposit feeder, can be influenced by the nutritive quality of the sediment in terms of protein content, and that seasonal fluctuations in this food source has an effect on its population dynamics.

Prionospio multipinnulata (Wilson 1990) was ubiquitous throughout the TOCEs that were investigated, occurring in 94% and 74% of the estuaries sampled in 1998/9 and 2009/10, respectively. Furthermore, it was the most numerically abundant species of all those that were recorded. Despite the prevalence of this particular species in this study, it has not been recorded in some of the earliest documentaries (Day 1981c, 1981e) and taxonomic literature (Day 1967b) relating to the benthic fauna of South Africa, suggesting its arrival in more recent years. In terms of global distribution, *P. multipinnulata* has been recorded primarily along the south-east coast of Australia and around Tasmania (Dorsey 1982, Wilson 1990, Wilson et al. 2003). In this region, it has been found only in inshore waters, including estuarine bays, and is particularly common in shallow muddy sediment (Dorsey 1982, Wilson 1990). As *P. multipinnulata* has not been recorded from South African waters, it is likely an exotic species, possibly historically introduced by means of ship ballast water, similar to the introduction of *Ficopomatus enigmaticus* (Polychaeta, Family Serpulidae) (Day 1967b), and has since become acclimatised to the environmental conditions of KwaZulu-Natal subtropical TOCEs where it forms a dominant component of the benthos.

Various *Prionospio* species have been documented in several estuaries in KwaZulu-Natal and the Eastern Cape, including records of an unidentified *Prionospio* sp. (Blaber et al. 1984, Mackay 1996, Schlacher and Wooldridge 1996d, Vivier and Cyrus 1999, Mackay and Cyrus 2001, Teske and Wooldridge 2001, 2004, Turpie et al. 2004, Forbes and Demetriades 2008) and *Prionospio* cf. *multipinnulata* in the St Lucia estuarine lake system (Mackay et al. 2010). Blaber et al. (1984) found *Prionospio* sp. to be the most dominant benthic organism in the polluted Tongati Estuary sampled in 1981. Teske and Wooldridge (2001) recorded the taxon *Prionospio* sp. from predominantly muddy sand in 11 of the 13 warm-temperate estuaries that were investigated, of which seven were temporarily open/closed systems. They suggested that this species is likely to be a 'true estuarine' species, a low salinity form of *Prionospio sexoculata*, which is typically found at salinities near seawater and above (Teske and Wooldridge 2004, Mackay et al. 2010). In the current study, *P. multipinnulata* was similarly found in fine muddy sediment and muddy sand, recorded in salinities ranging from fresh to seawater and tolerable of low oxygen levels (<2 mg/L). Based on these findings and overall prevalence of *P. multipinnulata*, it could be argued that previous records of *Prionospio* sp. may have reflected the occurrence of the former species. However, this cannot be stated with

confidence as the specimens of other authors were not compared with the specimens of this study.

Spionid polychaetes are generally sedentary surface deposit feeders (Fauchald and Jumars 1979) but may switch to suspension-feeding when concentrations of suspended particulate organic matter are high (Taghon et al. 1980, Dauer 1985, Riisgard and Kamermans 2001). This trophic flexibility allows *P. multipinnulata* to colonise a variety of estuarine habitats and survive variable environmental conditions that would otherwise limit particular food resources (e.g. changes in flow dynamics would influence the availability of suspended food material). Furthermore, this species exhibited opportunistic behaviour. It became highly abundant in the third sample period (61-80 days) during the recolonisation of each of the flood-affected estuaries, and decreased thereafter. This trend is characteristic of opportunistic species, or r-selected species, during the recolonisation of disturbed soft sediment environments (Grassle and Grassle 1974, Pearson and Rosenberg 1978, Norkko et al. 2006). This species thus shows affinities to *Paraprionsio pinnata*, which is a known indicator of environmental disturbance (Pearson and Rosenberg 1978, Dauer 1985).

Oligochaete worms are generally described as part of the freshwater component of estuarine benthos. Estuarine forms are tolerable of variable salinities, but prefer the low salinity environment of the upper reaches of estuaries (Teske and Wooldridge 2003). They are non-selective, subsurface deposit feeders found burrowing in mud and thrive in low oxygen and polluted environments (Dye and Furstenburg 1981, Mackay and Cyrus 2000, van Hoven and Day 2002, McLusky and Elliott 2004, Mackay et al. 2010). Nematode worms constitute a large portion of the permanent meiobenthos found in estuarine and marine sediments (Dye and Furstenburg 1981) and were likely under represented in the current samples based on the mesh size used (Gray 1981, Schlacher and Wooldridge 1996c). Nonetheless, Nematoda spp. ranked among the species of >45% similarity found clustered in Group V because they occurred with other members in 13% of the samples. Nematoda are typically extremely abundant in estuarine sediments (Coull 1999) and live in the interstices between the sediment grains (Gray 1981). Their distribution is dependent on the nature of the sediment and they cover an array of trophic groups ranging from selective deposit feeders to predators (Dye and Furstenburg 1981).

Although insects constitute a minor portion of the benthos in comparison with other faunal groups, the aquatic larvae of Chironomidae (Chironomini, Tanypodinae and Orthoclaadiinae) and Ceratopogonidae, are known to inhabit coastal marine and estuarine environments (Epler 2001, Courtney and Merritt 2008, Ferrington et al. 2008). They are also able to colonise deep-water habitats (such as those typically found in closed estuaries) because they do not require contact with the surface for respiration (Courtney and Merritt 2008). Chironomini larvae spp. (Family Chironomidae) was an important taxon in the short-term, long-term and spatial benthic community discriminations. These larvae were the most numerically abundant aquatic insect found in all the investigated TOCEs, in habitats ranging from glutinous mud to coarse marine sediment near the estuary mouth. In addition, Chironomini pupae were also common in the estuaries that were sampled, but were only collected in those systems where Chironomini larvae were recorded. Overall these findings are not uncommon because Chironomidae is the most widespread (globally) and diverse aquatic dipteran family, typically highly abundant in most habitats (Epler 2001, Courtney and Merritt 2008, Ferrington et al. 2008). Larval members of this family exhibit an assortment of morphological, physiological and behavioural adaptations that enable them to colonise a diversity of aquatic habitats and withstand a range of environmental conditions (Ferrington et al. 2008). Furthermore, these larvae feed on a variety of organic substrates ranging from coarse detritus, to fine particulate matter and benthic algae, and to a lesser degree, suspended particulate matter, as well as other organisms (Tanypodinae are active predators) (Ferrington et al. 2008), hence their ability to survive the dynamic nature of the estuarine environment.

GROUP I (4 taxa)

The species of Group I were grouped together due to their co-occurrence in the Damba Estuary in 2009/10. The benthos of this system was dominated by freshwater insect taxa, which contributed 56% to the overall abundance, in particular dipteran fly larvae (Ceratopogonidae and Chironomidae: Orthoclaadiinae and Chironomini), followed by Hypogastrurid collembolids (22%). The mollusc species, *Burnupia* sp. 1 constituted approximately 6% of the community abundance. The virtual absence of typical benthic fauna (polychaetes, oligochaetes and crustaceans) from the Damba benthos in 2009/10, as well as the low total mean abundance ($126 \text{ ind.m}^{-1} \pm 99.0\text{SD}$) was possibly attributable to the strong outward-flowing sampling conditions that prevailed due to recent breaching of the mouth. The high community diversity, attributed to high species evenness (Chapter 3, Figure 3.10B), and

the insect-dominated species composition resulted in the isolation of the Damba from all other estuaries in the cluster analysis (Chapter 3, Figure 3.7). Furthermore, it was postulated that the predominance of insect taxa was correlated with the extensive and well-preserved *Barringtonia racemosa* swamp forest, a rare feature among KwaZulu-Natal TOCEs (Begg 1978, 1984a). The occurrence of these freshwater taxa in a system where salinities range between freshwater and mesohaline conditions (Begg 1984a) (current study) was not unexpected because larvae of Ceratopogonidae and Chironomidae are tolerable of saline environments (Epler 2001, Courtney and Merritt 2008). Ceratopogonidae are primarily carnivorous, feeding on the aquatic larvae of other insects and oligochaetes (Courtney and Merritt 2008). Hypogastruridae are omnivorous and/or scavenging collembolids, certain species are common in intertidal mangrove habitats (Christiansen and Snider 2008). Aquatic ephemeropteran nymphs of the Genus *Caenis* are typically found in low flow environments in silty sediments where they feed on fine particulate organic matter and bacteria from various benthic surfaces (de Moor et al. 2003). The swamp forest likely provided suitable habitat and food resources for this species.

GROUP II (3 taxa)

The taxa contained within Group II were grouped together because they were present simultaneously in the Little Manzimtoti Estuary during three different time periods during post-flood recolonisation. They were most abundant during the early stages at times 1 and 2. In terms of their importance as discriminators of community change, Nemertea sp. 1 was important only in short-term changes in the Little Manzimtoti benthic community, Orthocladiinae larvae were important in the (spatial) isolation of the Damba Estuary from the remaining estuaries in 2009/10 (and almost as important as Nemertea sp. 1 in short-term differences) and Tanypodinae larvae were important in both cases. Orthocladiinae larvae and Tanypodinae larvae formed part of the predominantly freshwater insect benthic community of the Damba Estuary together with the taxa of Group I. In addition, Orthocladiinae larvae were almost as equally important in short-term community changes in the Little Manzimtoti Estuary as Nemertea sp. 1. In this estuary, Tanypodinae larvae were most abundant in the middle and upper reaches of the system where bottom salinities were essentially fresh (0.35-0.85) The decrease in their abundance between times 1 and 2 coincided with a marked decrease in oxygen levels and the increase in Oligochaete spp. abundance in these areas. This highlights the ability of oligochaetes to withstand low oxygen levels and therefore exist where conditions

are intolerable to other species (Mackay and Cyrus 2000, McLusky and Elliott 2004). The increased abundance of *Nemertea* sp. 1 between the same time periods in the lower reaches coincided with the general increase in abundance of most species (and potential prey items). Nemertean worms are marine predators (Branch et al. 1994), and the affinity of this taxon to the marine environment was evident in its restricted position in the lower reaches of the Little Manzimtoti Estuary where bottom salinities ranged between 23.3 and 29.7. The system was predominantly open due to its perched position above mean sea level and it is likely that marine fauna were seeded into the terminal basin via barrier overwash. Orthocladinae larvae are generally omnivorous, and/or scavengers, that feed on a variety of food items including fine particulate organic matter, microalgae and micro-organisms trapped in the sediment (Ferrington et al. 2008). Tanypodinae larvae are carnivorous and likely prey on oligochaetes and other benthic species found in both the Little Manzimtoti and Damba estuaries.

GROUP III (3 taxa)

The simultaneous occurrence of the polychaete species *Brania* sp. 1, *Lumbrineris tetraura* and *Capitella* spp. in the Tongazi (1998/9) and Mbokodweni (1998/9 and 2009/10) estuaries led to their association as similar species in Group III. This species combination did set the Mbokodweni and the Tongazi estuaries apart from the majority of the estuaries contained in Group II in the 1998/9 sample cluster (Chapter 3, Figure 3.4). For comparison, in the sample cluster analysis of 2009/10, *Capitella* spp. was the most important taxon from this species assemblage to characterise the estuaries of Group I (Sandlundlu, Tongazi and Mbizana estuaries)(Chapter 3, Figure 3.7). All three species are detritivores/deposit feeders (Fauchald and Jumars 1979) (*L. tetraura* is considered predatory by Day 1981c) and were expected to be found in organic-rich sediment, however the organic content of the substratum of the Mbokodweni and Tongazi estuaries was very low (0.14-0.19%) and moderately low (2.0%), respectively. *Capitella capitata* is a cosmopolitan species, common in marine and estuarine polluted muds and is frequently employed as an indicator of disturbed environments (Grassle and Grassle 1974, Pearson and Rosenberg 1978, Day 1981c). This is most certainly the case for the Mbokodweni and Sipingo estuaries, which are located in the industrial sector south of Durban. Both systems have a history of major habitat modifications (for example, infilling of the 'southern arm' of the Mbokodweni Estuary for the development of a golf course along its banks; diversion of the Mlazi and Sipingo Rivers that feed the Sipingo Estuary) and being heavily impacted upon by various sources of pollution, including faecal contamination (Begg

1984a), which still persists causing both systems to be currently considered as 'highly degraded' (Forbes and Demetriades 2008). In the Mbokodweni system, *Capitella* spp. were the second most numerically dominant group of species, where they contributed 28% and 40% to the total faunal abundance in 1998/9 and 2009/10, respectively. *Capitella* spp. were also extremely abundant in the Sipingo Estuary, and exceedingly so, during 2009/10. The densities recorded in the lower reaches during the current study were seven times greater than those recorded by Forbes and Demetriades (2008) in January 2008. *Lumbrineris tetraura* and *Brania* sp. 1 were present in comparatively very low numbers in the Mbokodweni in both sample periods. It is plausible that these species are less tolerable of high pollution levels reported by other workers (Forbes and Demetriades 2008). The historical occurrence of these three species in the Tongazi Estuary was unclear.

GROUP IV (3 taxa)

The brackwater bivalve *Brachidontes virgiliae*, and the isopod species *Cyathura estuaria* and *Cirolana* sp. 1 occurred together in the Mhlabatshane Estuary in 1998/9 (lower reaches) and in the Sipingo Estuary ('embayment' region) in 2009/10. *Brachidontes virgiliae* and *Cirolana* sp. 1 were indicative of short-term community changes in the recolonisation of the Intshambili and Mhlabatshane estuaries, respectively. Noteworthy changes in the benthic community of Intshambili Estuary between sample periods 3 and 4, and 4 and 5, were indicated by the appearance of *B. virgiliae* in the community at time 4 (67.2 ind.m⁻²) and its reduced abundance at time 5 (8.4 ind.m⁻²). The appearance of this species coincided with decreasing salinity with the system, and the decline at time 5 was likely related to increased turbidity and sediment deposition at this time as highly turbid conditions are not favoured by suspension-feeding organisms (De Villiers et al. 1999, Norkko et al. 2002). During the current study, *B. virgiliae* was recorded across a range of salinities from 1.55 in the Lovu Estuary to 26.1 in the Sipingo Lagoon in 2009/10, even though it is better known to occur in low salinities (Day 1981c, Kilburn and Rippey 1982, Branch et al. 1994). In the Sipingo Lagoon, it occurred as much larger individuals than found elsewhere and in the highest densities recorded during this study on rocks and rubble, mangrove roots and stems, and any hard surfaces (tyres and trash) found in the system. The exceptional water clarity observed in the lagoon region was possibly attributed to the combination of saline flocculation of suspended particulate matter and the high densities of this filter-feeding bivalve. Large bivalve populations are able to clear the water column of suspended particulate matter, dissolved nutrients and algae, and as such, are

regarded as a natural solution for eutrophication control (Officer et al. 1982, Soto and Mena 1999). Differences in the macrozoobenthic community of the Mhlabatshane Estuary at times 5 and 6 were characterised by the peak (319.2 ind.m⁻²) and subsequent decrease (25.2 ind.m⁻²) in abundance of *Cirolana* sp. 1, respectively. This was the highest recorded density of *Cirolana* sp. 1 from all sites (and time periods) where it occurred throughout the current study. During this time (time 5) salinity was at a minimum (3.78) and sediment composition was more fine grained (M=2.06Φ) than in previous sample periods, possibly as a result of rainfall in the catchment area and subsequent sediment deposition within the system. A study on the ecology of the estuarine isopod *Cirolana fluviatilis* has shown that this particular species preferentially selects fine-grained sediments based on mud content (Newman et al. 2007). This provides a plausible explanation for the increase in *Cirolana* sp. 1 during such conditions (and its occurrence in the Sipingo Estuary in 2009/10). As an omnivore or scavenger, *Cirolana* sp. 1 was likely to thrive on newly deposited decaying plant and animal material brought into the system during time 5.

Cyathura estuaria was one of the species most responsible for the isolation of the Zinkwasi Estuary from the estuaries in Group I in 1998/9 (Chapter 3, Figure 3.4). It was absent from the estuaries of this group. This species was most abundant in the Mtamvuna Estuary (1998/9) (332.0 ind.m⁻²). It also occurred in noteworthy densities in Sipingo (116.7 ind.m⁻²), Zinkwasi (63.0 ind.m⁻²) and Lovu (42.0 ind.m⁻²) estuaries in 2009/10. A common characteristic of the sediment of these four TOCEs was high mud content, ranging from 30% in the Sipingo Estuary to 60% in the Zinkwasi Estuary. Furthermore, within these estuaries, *C. estuaria* was more abundant at sites with higher mud content. These results are confirmed by several authors (Day 1981c, Reavell and Cyrus 1989, Day et al. 2001, Mackay et al. 2010), particularly Teske and Wooldridge (2003, 2004) who described *C. estuaria* as common in the mud zones of TOCEs and POEs of the Eastern Cape, where it featured prominently in sediment with a high mud content (20-95%).

GROUP V (2 taxa)

Tarebia granifera and *Melanoides tuberculata* were part of the same species group (Group V). They were only present in the benthos in 2009/10 and occurred most often simultaneously. *Tarebia granifera* was always more abundant than *M. tuberculata*, except in the Sipingo Estuary where *M. tuberculata* was the dominant species. Together, these two species were

indicative of the Manzimtoti and the Mdloti estuaries contained in Group II of the samples cluster analysis (Chapter 3, Figure 3.7). In these systems, *T. granifera* was the dominant gastropod species, and *M. tuberculata* maintained sub-equal abundances in both systems, hence the similarity of the two estuaries. Forbes and Demetriades (2008) recorded *Tarebia granifera* in the Manzimtoti Estuary, but not in the Mdloti Estuary, during a survey of the estuaries of the eThekweni Municipal Area in August 2007 and January 2008. Between 2007 and 2008, densities of *T. granifera* in the Manzimtoti Estuary had increased at each of the lower, middle and upper sample sites. During the current study, this species reached large densities between 5,863 and 12,062 ind.m⁻², which were markedly greater than the highest density recorded by Forbes and Demetriades (2008) (2,725 ind.m⁻²). These recent results indicate the proliferation of *T. granifera* in the Manzimtoti Estuary within the 6 months prior to the commencement of current study.

Both *T. granifera* and *M. tuberculata* are known as invasive species in many countries worldwide. They display typical invasive reproductive traits, specifically parthenogenetic and ovoviviparous females (Appleton 2002, Appleton et al. 2009). However, *M. tuberculata* is endemic to South Africa, and is at risk of being replaced by *T. granifera* as it continues to spread rapidly throughout the country (Appleton et al. 2009). These species inhabit the same habitats including rivers, lakes and estuaries, where they are found in high densities on shallow muddy bottoms, on moist exposed mud flats or on hard surfaces (rocks, concrete surfaces) (Appleton et al. 2009), typically feeding on detritus and/or benthic algae (Swaileh et al. 1994, Miranda et al. 2011). With regard to the benthic community of the Manzimtoti Estuary, species diversity was critically low ($H' = 0.40-0.49$). It can therefore be argued that the resistance of the system to biological invasion was lowered by its highly degraded state combined with poor diversity (Herkul et al. 2006), thus allowing the proliferation of *T. granifera*. This species has been recorded in several KwaZulu-Natal estuaries, and while it favours freshwater/brackish conditions, it is tolerable of variable salinities (this study and by other authors, Appleton et al. 2009, Miranda et al. 2010). It is therefore possible that these systems will suffer similar future invasions should their ecological state decline.

SINGLE TAXA

The estuarine mud snail, *Assiminea ovata*, was the only species of the six isolated taxa that was indicative of short-term community changes. During the investigation of the post-flood

recolonisation of estuarine macrozoobenthos, *A. ovata* was sampled only in the mouth region of the Little Manzimtoti system where it normally occurred in low numbers (8.4-25.2 ind.m⁻²). However, the increase in abundance of *A. ovata* (75.6 ind.m⁻²) at time 6 contributed to the change in community structure, together with other important discriminating species. At this time, the water depth was shallowest and the increase in *A. ovata* may have been related to the extensive microphytobenthos observed on the sediment surface (pers. obs.), which forms an important part of the diet of *Assiminea* species (Day 1981c, Kilburn and Rippey 1982, Whitfield 1989). Species of this genus are typically benthic algal/detritus feeders that forms large colonies on the surface of firm mud and muddy sand in many South African subtropical estuaries (Day 1981c, Kilburn and Rippey 1982). The remaining five taxa, Ceratopogonidae LT1, *Mesopodopsis africana*, Trombidiformes spp., Macrura PLT1 and Sabellidae JuvT1 were important in spatial discriminations between groups of estuaries. They occurred in several estuaries in comparatively low abundances. Ceratopogonidae LT1 contributed to the isolation of the Mzimayi Estuary from the remaining estuaries in 2009/10, where it constituted approximately 1% (14 ind.m⁻²) of the total faunal abundance. However, it was most abundant (140 ind.m⁻²) in the upper reaches of the Zotsha Estuary in the same sample, contributing 16% to the total faunal abundance. The Mzimayi Estuary and the upper reaches of the Zotsha Estuary were similarly well-oxygenated, extremely shallow (<0.2m), freshwater environments characterised by gravel-very coarse sand and coarse sand respectively, with very low (<0.2%) organic content. As a carnivorous species, Ceratopogonidae LT1 was likely preying on other aquatic insect larvae in these systems.

The last two taxa were thought to represent different life stages of the fauna that were collected and were generally associated with similar habitats. Sabellidae juvenile T1 was closely associated with *D. ornata*, and even in the premature state, displayed morphological characteristics (e.g. types of setae, number of body segments) similar to mature *D. ornata* specimens, and was thus considered to be developing offspring of this species. The taxon, Macrura PLT1, was an important spatial discriminator only in 1998/9, contributing to the separation of the Zinkwasi Estuary from all other estuaries sampled in this time period together with Trombidiformes spp. (Uncertain trophic group) and *M. africana* (Omnivore). Adult macruran (decapod) crustacea formed part of the very active epi-benthos of the estuary (pers. obs.) and large swarms of swimming prawns were observed in the system during 2009/10. They were however not present in the benthos. *Mesopodopsis africana* was present

with *Macrura* PLT1 in both 1998/9 and 2009/10, and it could be argued that *Macrura* PLT1 were the larvae of the former mysid species. Furthermore, it was unlikely that this taxon was macruran as shallow-water prawn populations spawn in offshore oceanic environments along the KwaZulu-Natal coast, and enter the estuaries as post-larvae much larger than the size of *Macrura* PLT1 (Dr. Sean Fennessey, *pers. comm.*, 2011¹). This taxon occurred in several estuaries in 2009/10 of variable sediment types and in salinities ranging between 0.14 (Damba) and 19.4 (Sezela). The habitat association and trophic group of this taxon were unknown. Although *M. africana* was an important spatial discriminator in 1998/9, it was most abundant in the Zinkwasi Estuary in 2009/10 where it reached maximum abundance of 299.0 ind.m⁻² in the lower reaches.

In conclusion, it can be stated that the species of Group VI are representative of the macrobenthic fauna of KwaZulu-Natal TOCEs, and most South African estuaries of this type. Population fluctuations of these important species determined the major changes in estuarine benthic communities over space and time. They were most the persistent species in this regard because they possess broad salinity tolerances, and occupy broad ecological niches which allow for the development of large populations in a variety of habitats. These attributes render macrozoobenthos as effective biological indicators for environmental monitoring. Polychaetes (Pearson and Rosenberg 1978, Cardell et al. 1999, Cardoso et al. 2007, Dauvin and Ruellet 2007), Amphipods (Dauvin and Ruellet 2007), Chironomidae (Epler 2001, Ferrington et al. 2008), Oligochaetes (van Hoven and Day 2002) and Nematodes (Coull 1999) have been previously used as indicators of environmental quality and pollution. Cyrus and Martin (1988) suggested that *G. lignorum* and *C. triaenonyx* might be useful biological indicators for South African estuaries because of their numerical dominance within the benthos. Furthermore, based on the high abundances of this group of species (Group VI), they may be potential keystone species depending on their different functional roles. Davic (2003) suggested that keystone species can be identified within the different functional groups that regulate various community processes, such as foodweb interactions, nutrient dynamics, niche partitioning and habitat modifications. He prescribes a new operational definition of the keystone species concept, whereby any dominant species (in terms of abundance/biomass) within a particular functional group has the *potential* to be a keystone species, therefore allowing for the *a priori* prediction of critical species (Davic 2003). Autecological studies on these particular species will provide valuable information regarding key components of estuarine macrozoobenthos and

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their response to different stressors, toward the preservation of important species (and key interactions) that maintain critical ecological processes.

Empirical investigations support the notion that community patterns are still evident at higher taxonomic levels such as genus, family or order and thus more favourable for rapid biodiversity surveys and pollution impact studies (Ferraro and Cole 1990, Olsgard et al. 1998, Baldó et al. 1999, Urkiaga-Alberdi et al. 1999, De Biasi et al. 2003, Heino 2008). Although changes in community structure may be distinguishable at these levels, the nature of the response remains unclear (Sommerfield and Clarke 1995) such that intrinsic mechanisms that bring about change in species compositions and distributions are overlooked. In order to determine the causes of change, it is necessary to investigate communities at the species level, as it is at this level where responses to environmental conditions are initiated (Pearson and Rosenberg 1978, Gray 1981, Heino 2008). Species level investigations are thus imperative for assessments of estuarine health and biodiversity, estuarine rehabilitation programmes and pollution impact studies, where changes in macrozoobenthic communities are anticipated.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

Ecosystem stress (natural or anthropogenic) is expressed through marked changes in the structure of biological communities (Dauer 1993, Baldó et al. 1999, McLusky and Elliott 2004, Wolanski 2007). The main objective of ecologists is to detect and characterise community change, as well as determine the possible causes of such change, to better understand essential ecological processes and the knock-on effects of human activities on ecosystem function (Pinnegar et al. 2000, Clarke and Warwick 2001). In the current study, long-term changes in macrozoobenthic communities between TOCEs in KwaZulu-Natal were investigated (Chapter 3). The inherent short-term changes in community structure in response to stochastic environmental disturbance were also documented (Chapter 4). Lastly, some ecological characteristics of the species representing these spatial and temporal variations were examined (Chapter 5). The aim of this chapter is to integrate the different findings relating to changes in macrozoobenthic communities and to evaluate these results according to the project objectives. The implications of this study for the general management for TOCEs and some recommendations for future research and collection of estuarine macrozoobenthos are also provided.

For the investigation of long-term changes in macrozoobenthos, 31 TOCEs were sampled in 2009/10 using the same field methodology previously used during a survey of the state of South Africa estuaries in 1998/9 (Harrison et al. 2000). The comparison between these two time periods revealed that the macrozoobenthic communities of these estuaries had indeed changed over the last decade. When collectively assessed at the regional scale, the degree of change was perceived as low. However, investigations at the independent estuary level indicated that the macrozoobenthos of certain estuaries had changed dramatically between periods while others had remained relatively unaltered. The degree of change was thus system-dependent. This particular finding highlighted the importance of unique system characteristics, including the state of the mouth, in determining the structure of macrozoobenthic communities and ultimately the observed high level of variability between

the TOCEs. This is largely a function of the sensitivity of benthic invertebrates to changes in environmental conditions and their preference for specific habitats.

Consequently, different macrozoobenthic species are found in different environments, therefore enabling the classification of the studied TOCEs based on the species composition of the communities. Although the structure of the macrozoobenthos differed markedly between estuaries, it was determined that several estuaries shared more similarities than others. The majority of the estuaries in both periods supported relatively similar communities that comprised predominantly Crustacea and Polychaeta fauna, of which the numerically dominant species were the same in most systems. In 1998/9, the differences between estuaries were based largely on the differences in abundance of Insecta and Crustacea taxa, particularly dipteran fly larvae and amphipods, respectively. In 2009/10, a greater number of estuaries were differentiated by virtue of their unique *Capitella*- or *Tarebia*-dominated species assemblages, in addition to the differential abundances of amphipod crustaceans. The similarities between macrozoobenthic communities did not correspond with the geographical position of the estuaries from north to south along the KwaZulu-Natal coast, estuary size, drainage region or the EHI value. In the absence of biological factors (such as predation and competition) and abiotic factors related to contamination, the distribution of the macrozoobenthos in either time period was mostly influenced by the grain-size composition of the estuary sediment, followed by patterns in water quality parameters related to the predominantly closed (1998/9) or open (2009/10) state of the estuary mouth at the time of sampling. Habitat heterogeneity also played an important role in determining the structure of these communities as high intra-estuarine variability was evident in the number of taxa and faunal abundance in many systems with more than one sample site.

In the short-term study of the response of macrozoobenthos to flood disturbance, the pattern of recolonisation in two urban and non-urban TOCEs was examined. It was found that the response of macrozoobenthos differed between the pairs of estuaries despite the relative similarity in terms of urbanised setting. That is to say, estuaries perceived to be subjected to the same levels of anthropogenic pressure did not elicit the same response (in terms of their biotic communities) to natural environmental disturbance. It was shown that the response to flooding was system-dependent such that the pattern of recolonisation differed markedly between the four estuaries. The changes in community structure over time were the product

of within-system changes in environmental conditions, particularly sediment composition, and the unique species composition of each estuary. This was also apparent at the level of sample site, whereby patterns in recolonisation differed between regions (upper, middle, lower) within an estuary. This was similarly attributed to differences in the species assemblages that initiated community re-establishment mediated by spatial differences in environmental conditions.

Overall, community changes that took place during post-flood recolonisation were characteristic of soft-sediment communities recovering from anthropogenic disturbance (Pearson and Rosenberg 1978, Dolbeth et al. 2007). In addition, changes in the state of the estuary mouth and localised disturbances, such as sediment deposition, were shown to influence the trajectory of recovery, generally negatively affecting faunal abundance and occasionally resulting in the reversion of macrozoobenthos to early post-flood community structure. This finding suggested that natural breaching has a similar effect on the macrozoobenthos of an estuary to that of flooding. Nonetheless, recovery of the community from breaching was rapid, as revealed in the Manzimtoti Estuary. In this urban system, where predominantly freshwater/brackish conditions prevailed and species diversity was particularly low, the invasive gastropod snail, *Tarebia granifera*, was the dominant species throughout recolonisation. This highlighted the vulnerability of urbanised estuaries to invasion because of their highly degraded condition. Moreover, preliminary results also suggested that the timing of the disturbance in relation to season is likely to influence the dynamics of community recolonisation.

Through the analysis of the macrozoobenthic communities at the species level, it was possible to isolate the taxa that reflected the fundamental spatial and temporal variations in community structure. Furthermore, the taxa that characterised the macrozoobenthos of the selected subtropical TOCEs were also identified. These taxa included the crustacean amphipod species *Grandidierella lignorum*, *G. lutosa*, *Grandidierella* spp. and *Corophium triaenonyx*, polychaetes species *Ceratonereis keiskama*, *Desdemona ornata*, *Dendronereis arborifera*, and *Prionospio multipinnulata*, insect fly larvae Chironomini larvae, Oligochaeta spp. and Nematoda spp. Of these species, five are endemic to South Africa's estuaries (Griffiths 1976, Day 1981c) and were common in the majority of estuaries studied. It was determined that the observed changes in macrozoobenthos at different temporal and spatial scales were

principally attributed to variations in abundance of these eleven taxa. These taxa were found in a variety of estuarine habitats, spanning wide salinity ranges and were numerically dominant over all other taxa. These are characteristics of ecological generalists and species best adapted to the variability of the estuarine environment. These taxa are likely to occupy critical functional roles in macrozoobenthic communities and affect key ecological processes, thereby representing potential keystone species. They also represent reliable indicators of environmental quality and pollution. Species level investigations therefore remain important for determining the nature of change in macrozoobenthic communities, and therefore our ability to identify and describe species.

It has been stated that communities residing in stressful environments, such as estuaries, are characterised by low species diversity (Lardicci et al. 2001, Mackay and Cyrus 2001) and are consequently relatively unstable (McCann 2000). The stability of a natural community can be described in terms of persistence, variability, resilience and resistance (Turner et al. 1995, Rader et al. 2008).

1. Persistence refers to the constancy in some community variable (e.g. abundance, species composition, number of taxa);
2. The degree to which a community variable fluctuates over time is termed variability;
3. Resilience is described as the ability of a community to recover to predisturbance conditions and regain functionality; and
4. Resistance is defined as the ability of a community to resist disturbance and remain unchanged.

(After Turner et al. 1995, Rader et al. 2008)

However, from the current study, the short-term and long-term species analyses indicated that the macrozoobenthic communities exhibited a degree of stability within the highly variable estuarine environment. Over the decadal study period, it was illustrated that communities containing the abovementioned common taxa were highly persistent with time, such that these taxa were present generally in the same estuaries in both time periods and retained similar numerical dominance. During the short-term study period, their persistence and resilience to flood disturbance was evident in the comparison between the similar community

compositions of 1998/9 and those which prevailed following flooding. In addition, changes in the state of the mouth often resulted in changes in species abundance, while taxonomic composition remained relatively the same. Thus, these communities exhibited variability and resilience in this regard (community resistance was not observed in this study). Overall, key attributes of estuarine macrozoobenthos were confirmed and it was shown that these fauna exhibit aspects of stable biological communities.

IMPLICATIONS FOR FUTURE ESTUARINE RESEARCH AND MANAGEMENT

In terms of the ecosystem-based approach to managing estuaries, macrozoobenthos constitutes an important faunal component that requires repeated sampling at appropriate time scales in order to capture the full extent of temporal variability. When the main objective of an ecological survey is to determine long-term changes in biological communities, consideration must be given to the spatial scale at which the data is to be analysed as this influences the nature of the result. For example, in the present study, it was revealed that spatial variation in macrozoobenthic communities between estuaries was greater than temporal variation over a decadal period. Temporal changes were most apparent within *individual* systems than between comparisons of estuaries combined. Furthermore, the scale of temporal change was dependent on the individual estuary. Thus, for future regional assessments of the state of South African estuaries using biological communities, and which include long-term comparisons, inter-estuarine variability must be addressed.

A key finding of this study was the level of variability between estuaries of the same type (ie TOCEs), and within this, between estuaries of the same size and those belonging to the same drainage region. This suggests that standardised management protocols for all estuaries of a specific type, size or catchment area may not be appropriate. Given the differences in the scale of changes that have taken place in the macrozoobenthos of KwaZulu-Natal TOCEs in the last decade, and the uncertainty regarding the causes of such change (due to insufficient surveying), it is highly probable that the benefit of broad estuarine management regulations to macrozoobenthic communities would differ between systems. Fortunately, the determination of the Ecological Reserve for estuaries as part of the Resource Directed Methods process, is conducted at the individual system level and the unique abiotic and biotic components of a particular estuary are taken into account. Furthermore, it was illustrated that spatial variations

of macrozoobenthos within individual estuaries may mask broad scale comparisons between estuaries. It is therefore critical to include representative samples of the different habitats along the estuarine gradient when conducting macrozoobenthic surveys for use in RDM studies or biodiversity assessments.

From the present study, it was deduced that the differences in the macrozoobenthic communities between estuaries were not effectively associated with the 'state' of the estuaries as expressed by the EHI. This indicated that the EHI does not provide a good reflection of macrozoobenthos, which further suggested that different faunal communities (fish, macrozoobenthos, zooplankton, birds) may give different impressions of the 'health' of South African estuaries. Fittingly, the calculation of the *biodiversity importance rating* of estuaries incorporates data of several biological groups including plants, fish, birds, and invertebrates which is further divided into zooplankton, nektonic invertebrates, benthic meiofauna and benthic invertebrates (macrozoobenthos)(Turpie et al. 2002, Turpie et al. 2004, Turpie and Clark 2007). This composite measure contributes toward the holistic determination of biodiversity and estuarine health as well as the formulation of effective conservation plans for the country's estuaries (Turpie and Clark 2007).

Alternatively, indices that use specific faunal groups as ecological indicators could be used to evaluate estuarine health in South Africa. For example, Whitfield and Harrison (2004) developed the Estuarine Fish Community Index (EFCI) using several metrics of fish communities, including species diversity, composition, abundance, nursery function and trophic integrity, to assess the environmental condition of South African estuaries. Macrozoobenthic organisms possess several characteristics that make them effective biological indicators:

1. they are generally unable to evade deteriorating environmental conditions because of their relatively sedentary lifestyle and thus reflect immediate environmental (sediment and water quality) conditions (Pearson and Rosenberg 1978, Dauer 1993, Weisberg et al. 1997, Borja et al. 2000, Clarke and Warwick 2001, Muxika et al. 2007, Pinto et al. 2009);

2. they exhibit relatively long life spans and therefore accumulate responses to changes in water/sediment quality conditions with time (Dauer 1993, Weisberg et al. 1997, Clarke and Warwick 2001); and
3. the different species possess different degrees of tolerance to stress which allows their classification into different functional groups (Pearson and Rosenberg 1978, Dauer 1993).

Since environmental stress can be detected through both quantitative and qualitative changes in macrozoobenthic community composition, these fauna have had a history of successful implementation as biological indicators in many European marine and estuarine ecological monitoring programmes, pollution impact studies, and ecosystem health assessments (Pearson and Rosenberg 1978, Dauer 1993, Hall and Frid 1995, Cao et al. 1996, Cardell et al. 1999, Clarke and Warwick 2001, Lenihan et al. 2003, Rosenberg et al. 2004, Bae et al. 2005, Bilkovic et al. 2006, Cardoso et al. 2007, Flaten et al. 2007, Kotta et al. 2007a, Neto et al. 2010, Norkko et al. 2010). Many biotic indices have been developed, each with different principles and merits, to summarise the ecological quality of macrozoobenthic communities (Word 1979, Weisberg et al. 1997, Borja et al. 2000, Simbhora and Zenetos 2002, Rosenberg et al. 2004, Dauvin and Ruellet 2007, Muxika et al. 2007, Ruellet and Dauvin 2007, Pinto et al. 2009). In the South African context, the use of these fauna as biological indicators of estuarine health has not yet been explored and 'benthic' indices have not been implemented to any known measure. Based on the variety of indices available, their success in international ecological assessments and their capacity to summarise large volumes of data, it is suggested that South African estuarine health be evaluated using benthic indices in similarity to the EFCI, which could possibly be incorporated into the *biodiversity importance rating* (Turpie et al. 2004, Turpie and Clark 2007) and in national assessment of the state of South African estuaries.

It was previously stated that the cause of the decadal change in the macrozoobenthos could not be determined due to insufficient sampling. Long-term data series on macrozoobenthos are lacking for the majority of South African estuarine systems, particularly in KwaZulu-Natal (Turpie et al. 2004). The once-off collection conducted by the CSIR in 1998/9 is the only quantitative baseline data of macrozoobenthos for most of the TOCEs in this province. Although sampling was repeated 11 years later in this study (Chapter 3), it does not possess the full benefits of a continuous long-term data series. Snapshot surveys provide a poor representation of the natural (high)temporal variability of estuarine communities and the data

therefore are not sufficient for accurate RDM evaluations. Investigations conducted over a period of one year to determine the post-flood recolonisation of macrozoobenthos (Chapter 4) illustrated that the duration of the study period, compounded by the intermittent sampling regime, was not sufficient to replicate community dynamics related to seasonal variations and the effects of mouth state, or to ascertain whether full recovery from disturbance was ever achieved in this time frame. In comparison, long-term monitoring studies provide valuable information regarding the internal mechanisms that regulate macrozoobenthic communities that would otherwise be under-represented by short-term surveys (Jones 1990), including population irruptions, temporary extinctions, seasonal community variations, longer term declines of common species and large changes in composition of the macrozoobenthos (Boesch et al. 1976b). Long-term investigations would be particularly important for monitoring the health or recovery of estuaries adversely affected by anthropogenic disturbances, such as those surrounding urban centres, and assessing the recovery potential of estuarine biota following large-scale (natural) environmental disturbance in the light of global climate change. Furthermore, long-term studies would enable the discrimination between the effects of natural environmental disturbance and human-induced changes on macrozoobenthic communities as these often have similar results (Dauvin 2007, Dolbeth et al. 2007). It is thus recommended that long-term monitoring studies of macrozoobenthos are included in future research needs of South African estuaries. During these studies, sampling should be carried out regularly, at intervals less than a decade and inclusive of seasonal variations, in order to capture the different magnitudes and rates of community change taking place in individual systems. Furthermore, water quality (nutrients) and contamination levels (heavy metal, faecal) need to be monitored in conjunction with macrozoobenthos as these factors are likely to influence community structure, particularly in urban estuaries. This information would contribute significantly to our knowledge of macrozoobenthic ecology.

In addition to long-term studies, surveys need to be conducted immediately after a stochastic natural event (such as flooding) has taken place as these events occur unpredictably and cannot be replicated. This would increase our ability to predict the effects of more frequent environmental disturbances due to climate change. In terms of flooding in KwaZulu-Natal estuaries, it was shown that the macrozoobenthos that recolonised the four flood-affected estuaries had been recorded from each system prior to flooding (1998/9) and that the pattern of recolonisation differed between sites within an estuary. This suggested that species survived

other previous disturbances that likely occurred over the years (1998/9 – 2008) and that different species assemblages survived the flooding in different regions of each estuary to initiate recolonisation, respectively. Their survival was likely attributed to the occurrence of flow refugia in the form of fringing vegetation and marginal habitats. Thus in terms of disaster management for estuarine ecosystems, removal of these vegetation flood buffers through urban development would negatively influence the survivorship of estuarine macrozoobenthos and therefore their ability to recover from flood disturbance. This again highlights the importance of estuarine habitats for macrozoobenthic communities. In addition, the present study illustrated that, although the spatial extent of a natural ‘disaster’ may be large, spanning several estuarine systems, these are not equally affected (e.g. flooding in the Mhlabatshane Estuary was more severe in comparison with the other three estuaries judging by the extent of physical damage). This is largely a function of differences in catchment characteristics, which in turn govern estuary physico-chemical conditions. Therefore, the recovery of estuarine communities in flood damaged systems cannot be assumed to be universal. Again, the inherent variability of TOCEs must be borne in mind when addressing the rehabilitation of estuaries damaged by natural events.

In conclusion, the present findings demonstrated

- the inherent variability between the macrozoobenthos of estuaries of a single estuary type;
- the potential for further changes to the macrozoobenthos of these estuaries within the next decade due to natural and anthropogenic influences or a combination of both;
- the persistence of estuarine communities which stems from the resilience of prominent species;
- that estuarine communities will respond differently to the same disturbance based on intrinsic differences in community composition and estuary system characteristics; and
- that managing change, as reflected in the macrozoobenthos, would require intervention at the individual estuary-level.

Moreover, this study illustrated the effectiveness of using macrozoobenthic communities to depict ‘change’ over multiple temporal and spatial scales. This also supports their usefulness as a study group in environmental monitoring and detecting undesirable change, importantly the loss of biodiversity and ecological functioning of estuaries, in the long- and short-term.

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APPENDICES

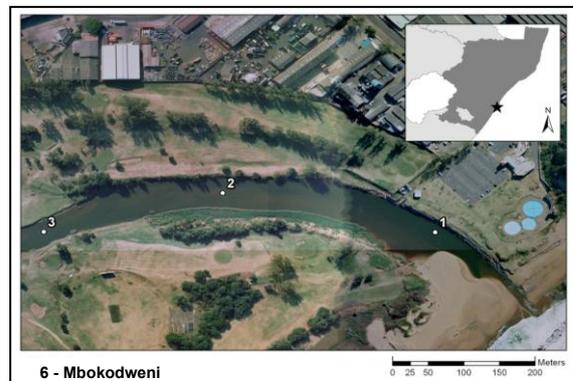
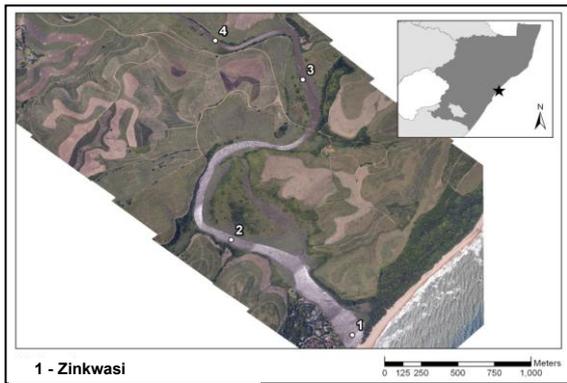
Appendix 1.1

Appendix 1.2

Appendix 1.3

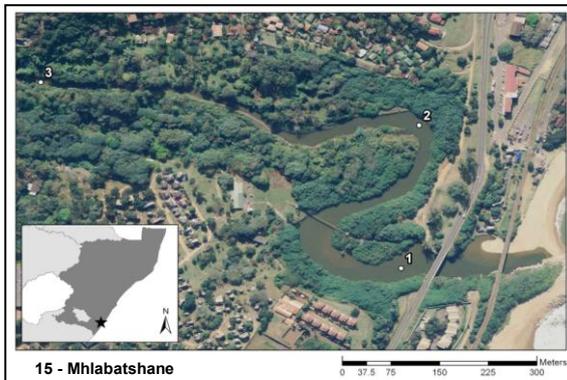
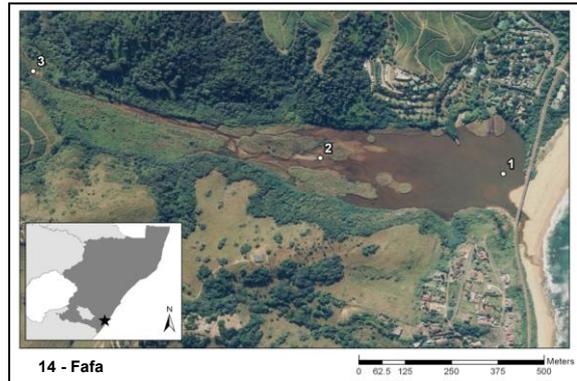
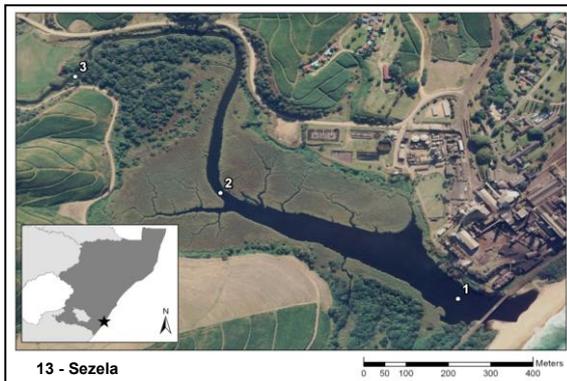
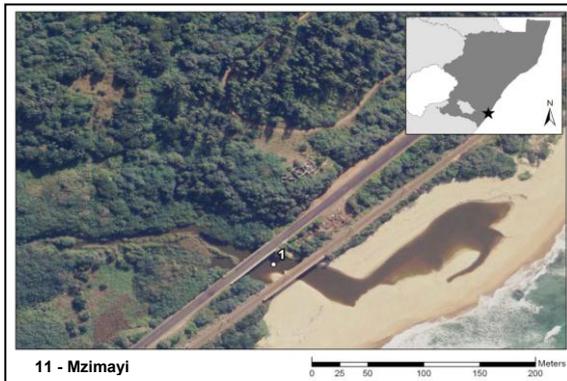
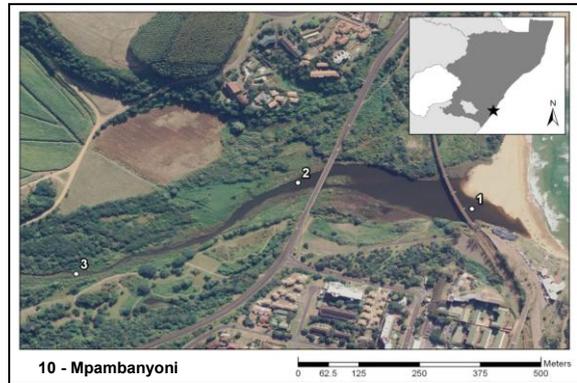
Appendix 1.4

Appendix 1.1 Aerial imagery of the 31 KwaZulu-Natal TOCEs that were investigated from north to south, illustrating the locations of the macrozoobenthic sites resampled in 2009/10. Star symbol indicates 1998/9 sample sites not sampled in 2009/10. Imagery supplied by the ORI GIS Unit.



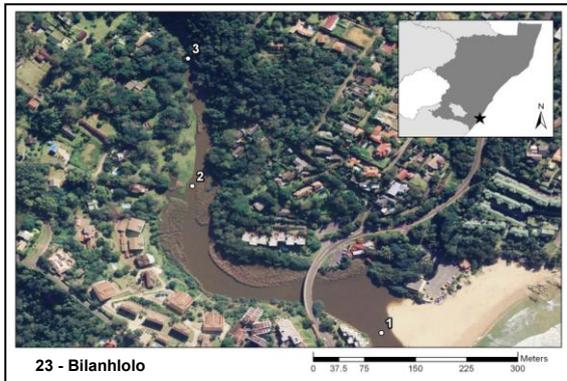
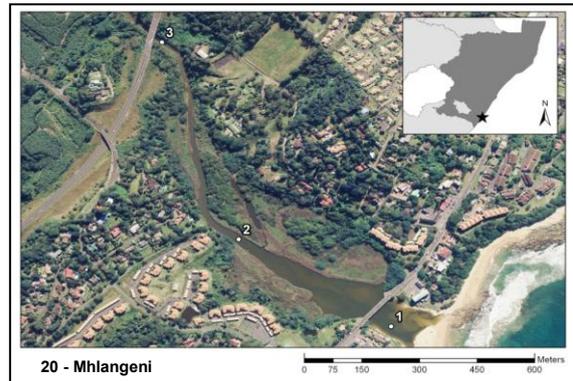
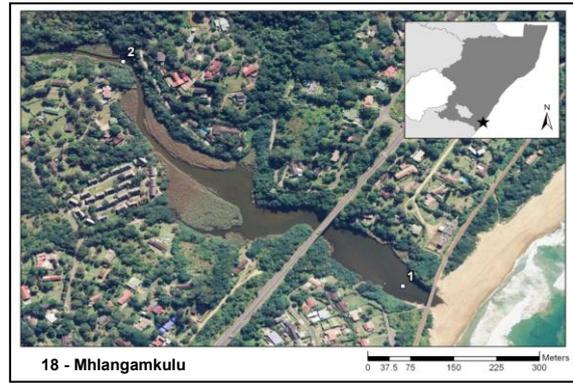
Appendix 1.1 continued... /

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Appendix 1.1 continued... /

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25 - Mbizana



Kaba



27 - Umhlangankulu



28 - Kandandlovu



29 - Tongazi



30 - Sandlundu



31 - Mtamvuna

Appendix 1.2 List of macrozoobenthic taxa collected from each TOCE in 1998/9 showing total mean abundance (ind.m⁻²) for the given number of sites per estuary and the total number of taxa. Abbreviations: T= Type, Juv= Juvenile, PreJuv= Pre-Juvenile, PL= Post-Larvae, L= Larvae, P= Pupae

Estuary No. (N-S)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31			
CLASS TAXA	ZIN	MDO	MDL	MG	ISP	MBO	AT	LAM	LOV	MY	MZ	MK	SZ	F	MAN	INT	D	MLK	Z	MH	K	UV	BI	MSH	MB	KAB	MLKB	KA	TG	SA	MVA			
Hirudinea spp.								X							X								X											
Oligochaeta: <i>Branchiura sowerbyi</i>																	X																	
Oligochaeta spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
Polychaeta: <i>Capitella</i> sp.3					X				X																									
<i>Capitella</i> spp.					X				X																									
cf. <i>Paracapitella</i> sp.1					X																													
<i>Mediomastus capensis</i>									X																									
<i>Mediomastus</i> sp.1																																		
<i>Notomastus fauveli</i>																																		
<i>Caulerielia</i> sp.2																																		
<i>Lumbrineris tetraura</i>						X																												
<i>Marphysa sanguinea</i>					X																													
<i>Ancistrosyllis parva</i>																																		
<i>Brania</i> sp.1						X			X																									
<i>Ceratonereis keiskama</i>			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
<i>Dendronereis arborifera</i>	X			X	X		X	X	X						X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Nereis</i> sp.1																																		
<i>Glycera alba</i>																																		
<i>Glycera</i> cf. <i>natalensis</i>									X						X																			
<i>Glycera convoluta</i>																																		
<i>Gyptis capensis</i>									X																									
cf. <i>Amphicomia</i> sp.1																																		
<i>Desdemona ornata</i>	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Sabellidae JuvT1	X	X		X	X		X		X						X	X	X			X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Ficopomatus enigmaticus</i>					X																													
<i>Ficopomatus</i> sp.1																																		
cf. <i>Boccardi</i> sp.1																																		
<i>Dipolydora</i> sp.1					X																													
<i>Polydora kempii</i>									X																									
<i>Polydora</i> sp.2					X																													
<i>Polydora</i> sp.3																																		
<i>Polydorella</i> sp.1									X																									
<i>Prionospio multipinnulata</i>	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
<i>Prionospio sexoculata</i>									X																									
<i>Rhynchospio</i> sp.1																																		
Arachnida: Trombidiformes spp.	X		X																															
Pycnogonida spp.					X																													
Collembola: Entomobryidae sp.1								X				X								X		X												
Entomobryidae sp.2																																		
Hypogastruridae sp.1																																		
Crustacea: <i>Afrochiltonia capensis</i>											X										X	X				X	X							
<i>Bolittsia minuta</i>									X			X														X	X							
<i>Caprella penantis</i>																																		
<i>Corophium triaenonyx</i>					X		X		X	X	X	X			X	X							X	X	X	X	X	X	X	X	X	X	X	
Dexaminidae sp.1									X																									
<i>Grandidierella bonnieroides</i>					X	X			X																									
<i>Grandidierella chelata</i>																																		
<i>Grandidierella lignorum</i>					X	X	X	X	X	X	X	X		X	X	X				X	X	X			X	X	X	X	X	X	X	X	X	
<i>Grandidierella lutosa</i>			X	X	X	X	X	X	X	X	X	X		X	X	X				X	X	X			X	X	X	X	X	X	X	X	X	
<i>Grandidierella</i> spp.				X	X	X	X	X	X	X	X	X		X	X	X				X	X	X			X	X	X	X	X	X	X	X	X	
Lysianassidae sp.2																																		
<i>Melita zeylanica</i>																											X							
<i>Orchestia</i> cf. <i>rectipalma</i>																																		
<i>Orchestia rectipalma</i>																																		
<i>Talorchestia australis</i>																																		
<i>Urothoe</i> cf. <i>serrulidactylus</i>																																		
Harpacticoida sp.1																																		
cf. <i>Dicoides</i> sp.1					X	X	X	X	X	X	X	X		X	X											X	X	X	X	X	X	X	X	
<i>Iphinoe truncata</i>					X																													
Grapsidae sp.1					X																													
<i>Hymenosoma orbiculare</i>																																		

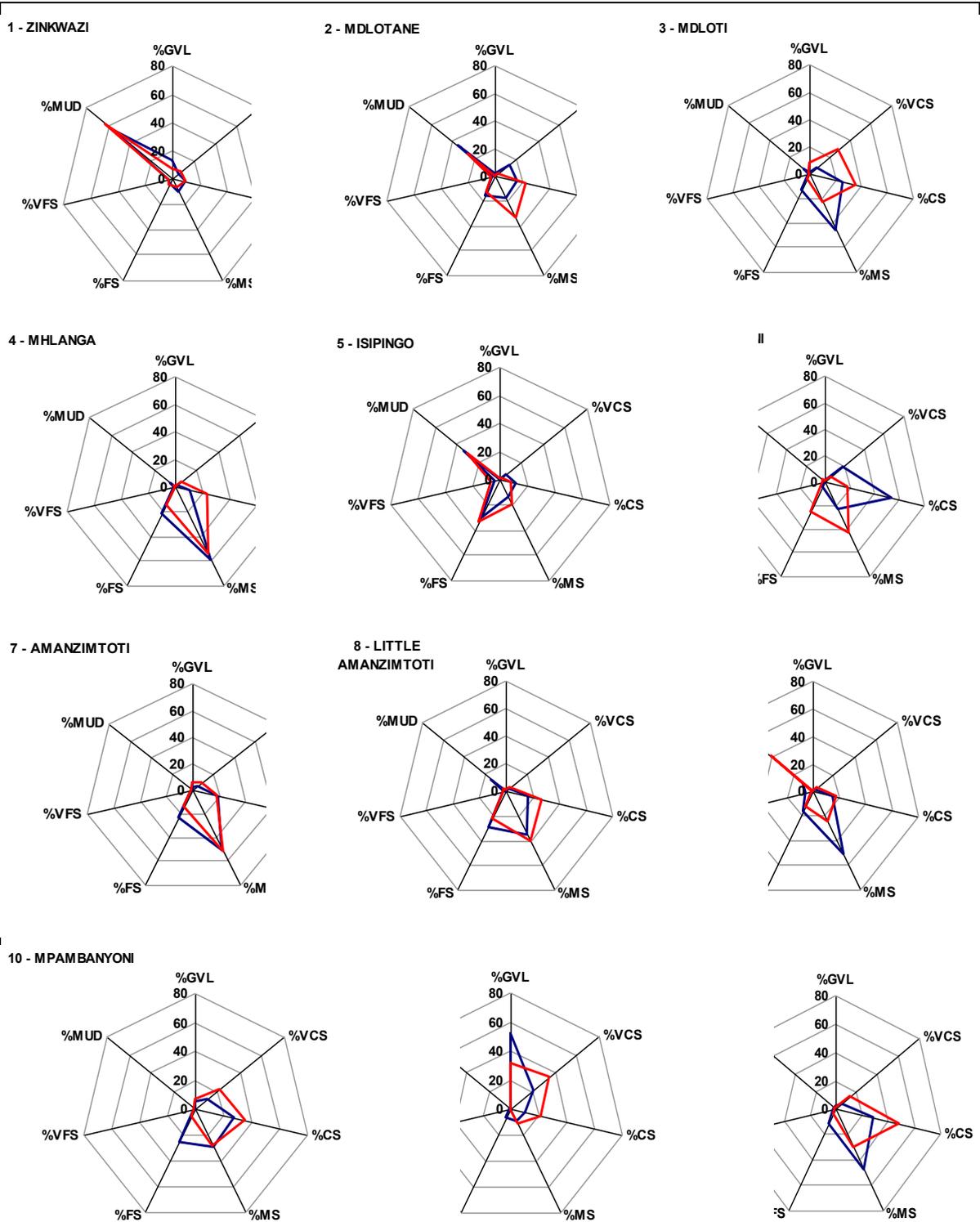
Appendix 1.2 continued.../

Estuary No. (N-S)		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31			
CLASS	TAXA	ZIN	MDO	MDL	MG	ISP	MBO	AT	LAM	LOV	MY	MZ	MK	SZ	F	MAN	INT	D	MLK	Z	MH	K	UV	BI	MSH	MB	KAB	MLKB	KA	TG	SA	MVA			
Crustacea:	<i>Caridina nitidica</i>																																		
	Palaemonidae sp.1																																		
	Macrura PLT1	X																																	
	<i>Metapenaeus stebbingi</i>										X																								
	Penaeidae sp.1										X																								
	Penaeidae sp.2																																		
	<i>Penaeus japonicus</i>																																		
	<i>Callinassa kraussi</i>											X																							
	<i>Upogebia capensis</i>																																		
	<i>Cirolana</i> sp.1																																		
	<i>Cyathura estuaria</i>	X									X					X	X																		
	<i>Leptanthura</i> sp.1										X					X																			
	<i>Pontogeloides latipes</i>															X								X											
	<i>Uromunna sheltoni</i>																																		
	<i>Dies monodi</i>																X								X										
	<i>Pseudosphaeroma barnadi</i>																																		
	<i>Mesopodopsis africanus</i>	X									X																								
	Ostracoda spp.			X					X	X							X	X						X	X	X	X								
<i>Apeudes digitalis</i>	X		X			X				X						X							X												
<i>Sinelobus stanfordi</i>						X		X		X													X												
Insecta:	Brachycera LT1																																		
	Ceratopogonidae LT1																																		
	Ceratopogonidae LT2																																		
	Ceratopogonidae LT3																																		
	Chironominae larvae spp.		X	X	X	X			X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
	Chironominae pupae spp.			X					X																										
	Orthocladinae larvae spp.																																		
	Tanypodinae larvae spp.			X																															
	Tanypodinae PT1			X																															
	Tanytarsini larvae spp.			X																															
	Tanytarsini pupae spp.			X																															
	<i>Erioptera conspicua</i>																																		
	Tabanidae LT1																																		
	Diptera LT5																																		
	<i>Caenis</i> spp																																		
	Leptoceridae LT1																																		
	Leptoceridae PT1																																		
	<i>Triaenodes</i> sp.1																																		
Anthozoa:	Actinaria sp.1																																		
	Hydrozoa spp.				X			X					X		X								X		X		X								
Bivalvia:	<i>Brachidontes virgillae</i>																																		
	<i>Corbicula fluminalis</i>																X	X																	
	<i>Dosinia hepatica</i>																																		
	<i>Macoma littoralis</i>																																		
	Tellinidae sp.1																																		
Gastropoda:	Semelidae sp.1																																		
	<i>Diodora</i> sp.1																																		
	<i>Melanoides tuberculata</i>																																		
	<i>Tarebia granifera</i>																																		
	<i>Thiara amarula</i>																																		
	<i>Assiminea ovata</i>									X																									
	Assimineidae Juv spp.					X						X															X								
	Assimineidae sp.2																																		
	<i>Natica gualteriana</i>																																		
	<i>Burmupia</i> sp.1																																		
Gastropoda PreJuv T1																																			
Mollusca:	Mollusca PreJuv T1				X			X	X		X				X	X																			
	Nematoda spp.	X	X		X	X	X	X		X					X	X	X						X	X			X	X	X	X	X	X	X		
Nemertea:	Nemertea spp.																																		
	Rhabdocoela sp.1					X										X																			
Sipunculida:	Golfingiidae sp.1						X																												
	Phascolomatidae sp.1							X																											
Unidentified:	Sipunculidae sp.1																																		
	Unidentified Organisms T1				X										X	X																			
Number of Sites		4	3	3	3	3	3	3	2	3	3	1	2	3	3	3	3	2	2	3	3	3	1	3	1	1	2	3	2	1	2	4			
Mean Total Abundance		9,257	37	2,174	17,640	5,735	6,645	19,679	11,004	11,092	22,465	8,288	60,431	2,137	16,856	11,494	35,429	2,590	2,219	9,328	5,684	18,484	14,644	5,259	23,982	6,160	22,155	29,759	8,092	4,214	22,680	24,710			
Total Number of Taxa		11	4	14	20	19	18	17	16	32	16	12	20	10	18	24	15	14	11	19	21	23	8	20	13	12	18	29	19	15	25	30			

Appendix 1.3 continued.../

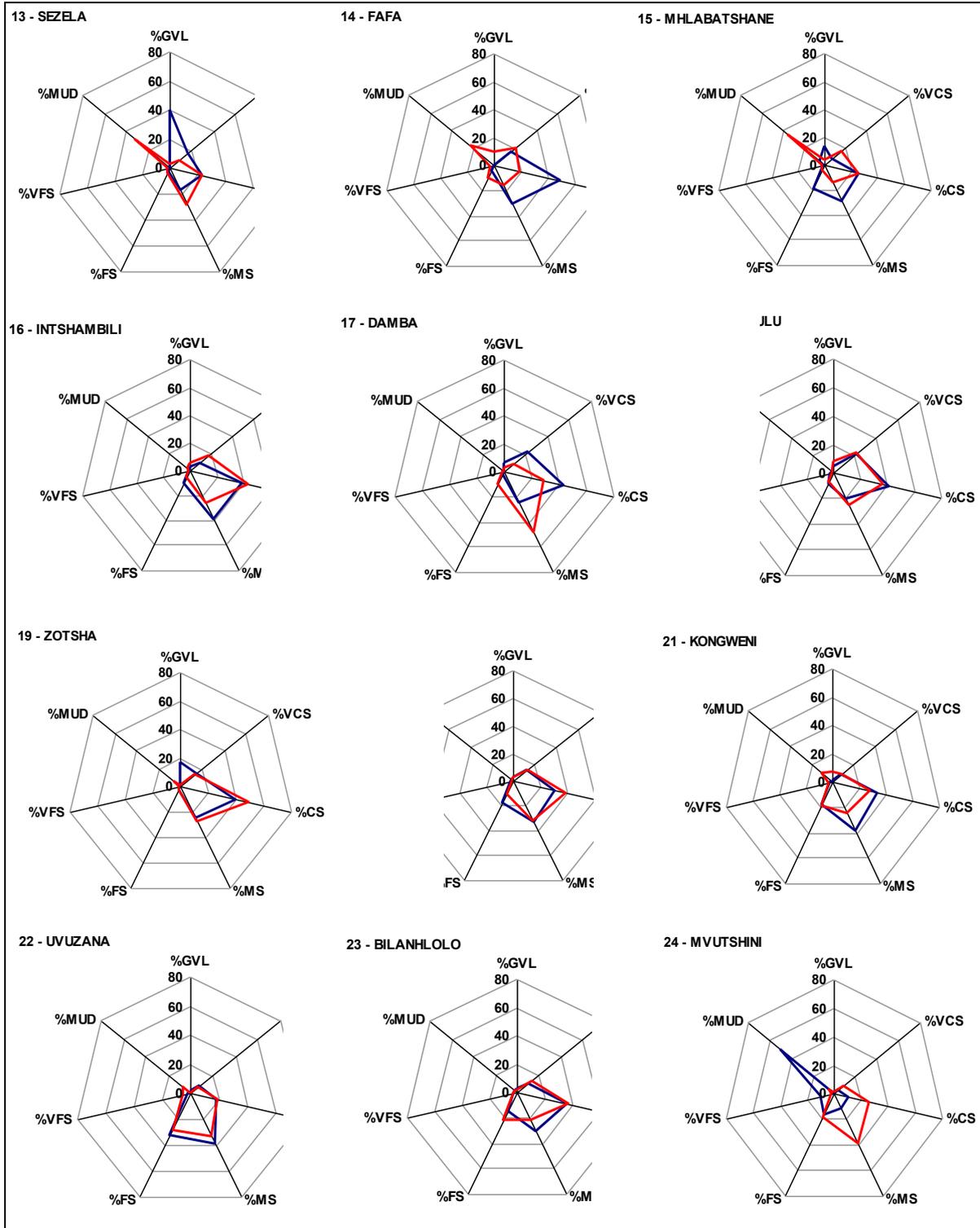
Estuary No. (N-S)		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31				
CLASS	TAXA	ZIN	MDO	MDL	MG	ISP	MBO	AT	LAM	LOV	MY	MZ	MK	SZ	F	MAN	INT	D	MLK	Z	MH	K	UV	BI	MSH	MB	KAB	MLKB	KA	TG	SA	MVA				
Crustacea:	<i>Candina nitotica</i>		X																	X																
	Palaemonidae sp.1																			X																
	Macrura PLT1	X	X												X						X						X	X	X							
	<i>Metapenaeus stebbingi</i>																																			
	Penaeidae sp.1				X																															
	Penaeidae sp.2																																			
	<i>Penaeus japonicus</i>																																			
	<i>Callinassa kraussi</i>						X			X	X												X				X	X	X	X						
	<i>Upogebia capensis</i>															X	X							X												
	<i>Cirolana</i> sp.1																																			
	<i>Cyathura estuaria</i>	X				X				X						X	X									X	X	X	X	X				X		
	<i>Leptanthura</i> sp.1									X																									X	
	<i>Pontogeloides latipes</i>									X																									X	
	<i>Uromunna sheltoni</i>									X																									X	
	<i>Dies monodi</i>		X							X																										
	<i>Pseudosphaeroma barnadi</i>												X																						X	
	<i>Mesopodopsis africanus</i>	X																																	X	
	Ostracoda spp.					X											X																			
	<i>Apseudes digitalis</i>	X	X			X				X	X					X	X											X	X		X	X	X	X		
	<i>Sinelobus stanfordi</i>					X			X	X												X														
Insecta:	Brachycera LT1																			X																
	Ceratopogonidae LT1									X	X										X					X										
	Ceratopogonidae LT2																				X															
	Ceratopogonidae LT3																				X															
	Chironominae larvae spp.		X	X		X		X	X	X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
	Chironominae pupae spp.		X							X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
	Orthoclaadiinae larvae spp.		X							X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
	Tanypodinae larvae spp.																				X															
	Tanypodinae PT1																				X															
	Tanytarsini larvae spp.				X					X	X				X	X					X	X	X													
	Tanytarsini pupae spp.									X	X				X	X					X	X	X													
	<i>Erioptera conspicua</i>																																			
	Tabanidae LT1																				X															
	Diptera LT5																																			
	<i>Caenis</i> spp.				X																															
	Leptoceridae LT1																																			
	Leptoceridae PT1																																			
	<i>Trienodes</i> sp.1																																			
Anthozoa:	Actinaria sp.1					X																														
Hydrozoa:	Hydrozoa spp.																																			
Bivalvia:	<i>Brachidontes virgiliae</i>	X	X	X		X				X																										
	<i>Corbicula fluminalis</i>			X																																
	<i>Dosinia hepatica</i>						X																													
	<i>Macoma littoralis</i>	X				X				X																										
	<i>Tellinida</i> sp.1																																			
Gastropoda:	<i>Semelida</i> sp.1	X																																		
	<i>Diodora</i> sp.1																																			
	<i>Melanoides tuberculata</i>	X		X		X		X																												
	<i>Tarebia granifera</i>	X	X	X	X	X		X		X						X	X																			
	<i>Thiara amarula</i>																			X																
	<i>Assimineia ovata</i>				X	X				X																			X							
	Assimineidae Juv spp.						X									X																				
	Assimineidae sp.2				X					X																										
	<i>Natica gualteriana</i>					X																														
	<i>Burnupia</i> sp.1																																			
	Gastropoda PreJuv T1																																			
	Mollusca PreJuv T1				X																															
Nematoda:	Nematoda spp.					X			X	X						X	X					X	X				X	X	X	X	X	X	X	X	X	
Nemertea:	Nemertea spp.						X																													
Turbellaria:	Rhabdocoela sp.1				X																															
Sipunculida:	Golfingiidae sp.1						X																													
	Phascolomatidae sp.1																																			
	Sipunculidae sp.1																																			
Unidentified:	Unidentified Organisms T1						X																													
	Number of Sites	4	3	3	3	3	3	3	2	3	3	1	2	3	3	3	3	2	2	3	3	3	1	3	1	1	2	3	2	1	2	4				
	Mean Total Abundance	8,820	3,654	536	2,347	37,356	11,428	10,168	8,043	15,456	2,184	1,190	5,705	723	546	9,305	7,798	126	497	1,946	6,300	5,842	19,124	2,781	31,080	3,430	17,262	18,540	9,709	3,990	6,790	2,208				
	Total number of Taxa	16	22	11	13	29	20	11	11	25	16	4	17	12	13	24	20	10	17	17	22	15	8	13	11	17	21	27	12	7	13	23				

Appendix 1.4 Mean percentage grain size contributions for sediment collected at macrozoobenthic sample sites in 31 TOCEs in KwaZulu-Natal in 1998/9 (blue) and 2009/10 (red). GVL= Gravel, VCS= Very Coarse Sand, CS= Coarse Sand, MS= Medium Sand, FS= Fine Sand, VFS= Very Fine Sand.



Appendix 1.4 continued... /

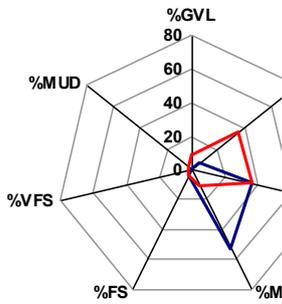
Appendix 1.4 continued Mean percentage grain size contributions for sediment collected at macrozoobenthic sample sites in 31 TOCEs in KwaZulu-Natal in 1998/9 (blue) and 2009/10 (red). GVL= Gravel, VCS= Very Coarse Sand, CS= Coarse Sand, MS= Medium Sand, FS= Fine Sand, VFS= Very Fine Sand.



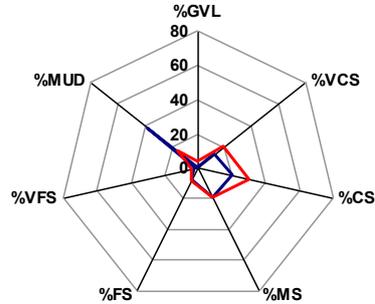
Appendix 1.4 continued... /

Appendix 1.4 continued Mean percentage grain size contributions for sediment collected at macrozoobenthic sample sites in 31 TOCEs in KwaZulu-Natal in 1998/9 (blue) and 2009/10 (red). GVL= Gravel, VCS= Very Coarse Sand, CS= Coarse Sand, MS= Medium Sand, FS= Fine Sand, VFS= Verv Fine Sand.

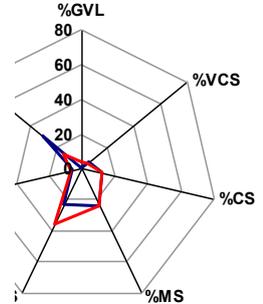
25 - MBIZANA



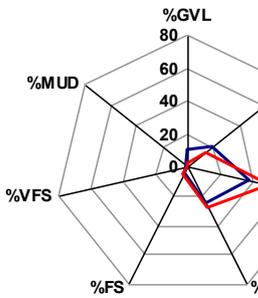
26 - KABA



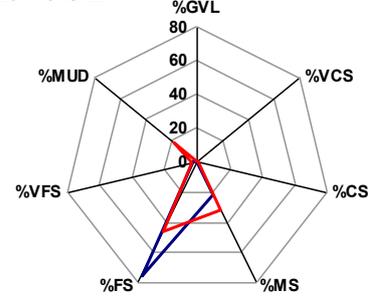
KULU



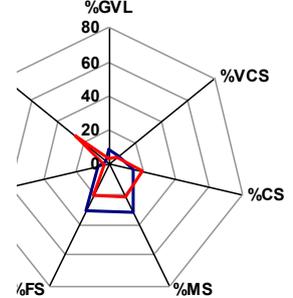
28 - KANDANDLOVU



29 - TONGAZI



I



31 - MTAMVUNA

