

Community dynamics of meiofauna during a wet phase in the St Lucia estuarine system, South Africa

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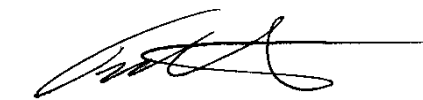
South Africa

December 2015

PREFACE

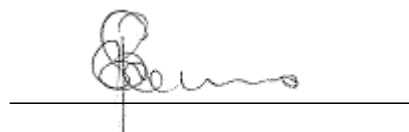
The research contained in this dissertation was completed by the candidate while based in the Discipline of Marine Biology, School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville Campus, South Africa. The research was financially supported by The National Research Foundation and the University of KwaZulu-Natal.

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate. As the candidate's supervisor and co-supervisor, we have approved this thesis for submission

A handwritten signature in black ink, appearing to read 'Renzo Perissinotto', written over a horizontal line.

Signed: Prof. Renzo Perissinotto

Date: 9 Dec 2015

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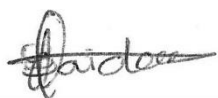
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DECLARATION 1 - PLAGIARISM

I, Bryaleen Leesa Naidoo, declare that

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ABSTRACT

Meiofauna are an important component within the benthic environment of any aquatic habitat. Despite their significance and ubiquitous nature, these organisms are relatively poorly studied in Africa. Following a decade long drought period, the St Lucia Estuary experienced higher than average amounts of rainfall at the end of 2010. These heavy rainfall events replenished the freshwater capacity of the system, raising the water level and subsequently reducing salinity throughout the estuarine lake, thus marking the start of a two year long wet phase. Meiofauna community dynamics were assessed to determine their response to a wet phase and to the disturbance brought on by intense rainfall. Diversity indices and a host of multivariate analyses were used to gain an understanding of the meiofaunal communities of the system during this wet phase. Meiofaunal density and richness tended to be higher during the first year of the wet phase. Meiofauna communities within each site became more homogenous in the second year of the wet phase, indicating a more established community adjusted to wet conditions. Following a flood disturbance in early January 2011, meiofaunal communities at each site differed in terms of primary and secondary colonisers. Over time, communities increased in dissimilarity, suggesting succession at some level. A successional pattern was observed as the taxonomic composition of the communities shifted over time. The lack of a climax community in St Lucia in the medium term was likely due to the uneven impact that the lake experienced with the onset of the disturbance, with the northern reaches experiencing a greater degree of impact than the southern reaches. The continuity in disturbance occurrences also caused the system to move back to a previous successional state. The meiofauna of St Lucia are therefore able to recover after disturbances related to a wet phase and maintain some form of resilience. In the long term, meiofaunal communities may require a longer time period, than the one considered in this study, to reach the levels of abundance previously recorded.

Dedicated to my biggest fans:

Maggie Govender (1919 – 2015) and Henry Naidoo (1940 – 2015)



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CHAPTER 1: INTRODUCTION

1.1 Context

Estuaries are among the most dynamic ecosystems that occur in nature (Kennish 2002, MacLusky & Elliott 2004), and provide a vast amount of ecological goods and services (Costanza et al. 1998). These include habitat provision (França et al. 2009), breeding and nursery grounds (Able 2005), nutrient cycling (Corbett 2010) and sediment trapping (Geyer et al. 2001). Estuaries are characterised by substantial variability in physico-chemical factors (Cyrus et al. 2011, Alves et al. 2013) such as temperature, salinity, dissolved oxygen, nutrient levels, turbidity and pH. These variations result in the resident biota being characterised by strong spatial and temporal variability (Carrasco & Perissinotto 2011). Spatial variability is caused by an estuarine gradient that usually shifts from freshwater at the source to more saline water at the mouth, the extent of which is dependent on the state of the mouth and its tidal prism (Whitfield 1992). For systems of this nature, climatic variability may cause further extreme fluctuations in salinity, as a result of freshwater shortages or floods (Pollack et al. 2011), while prolonged wet or dry cycles may cause these systems to move toward freshwater or hypersaline states, respectively. Freshwater flow into an estuary is an important aspect of estuarine health and function (Milliman & Farnsworth 2011). These include moderation of hypersalinity (Elexander & Dunton 2002), habitat provision (Kimmerer 2002) and the downstream transport of sediment and nutrients (Findlay et al. 1991, Longley et al. 1994).

1.2 Freshwater inflow: Environmental alterations and biological responses

Salinity plays a fundamental role in the chemical, physical and biological dynamics of estuaries (Gibson & Najjar 2000) and is primarily influenced by freshwater pulses (Pollack et al. 2011). With increased rainfall, these freshwater pulses become more frequent and with

sufficient intensity, the degree of freshening within an estuary increases (Valiela et al. 2012). Ecological features that characterise freshwater systems are reflected in many of the changes to estuarine functioning that arise from changing flow regimes. For example, the low salinity that defines freshwater systems creates a hypotonic environment for aquatic biota. These features are relevant to species that have acquired life strategies that are adapted to natural flow regimes. As proposed by Elliott and Whitfield (2011), estuarine biota are well adapted to the fluctuating nature of these systems; however estuarine functioning is greatly dependent on ecosystem connectivity from freshwater, marine and terrestrial systems. All biota within estuaries possess some form of salinity tolerance threshold, beyond which they are unable to maintain bodily functions and can no longer thrive in such environments. When the tolerance to low salinity becomes overwhelmed, mass mortalities are likely to follow, as seen with estuarine oysters on the Pacific coast of Panama (Valiela et al. 2012).

In the case of a prolonged wet phase with increased freshwater inflow, the drop in salinity would have multiple effects on the entire estuarine system. Physically, salinity impacts density as the less dense freshwater tends to float above more saline water, and hence determines circulation and stratification (Simpson et al. 1990). In a case of reduced salinity, there may be prevention of nutrient enrichment via upwelling in deeper waters or a countering effect, where there is enrichment of surface layers. With regards to chemical impacts, a decrease in salinity can cause a decrease in pH (thus increasing acidity), while the solubility of organic matter increases (Cai et al. 1998), leading to further biological implications in terms of oxygen deficits, for example. Modified salinity patterns, and the downstream transport of nutrients and sediments caused by altered freshwater regimes, are largely responsible for changes in the composition and abundance of estuarine biota.

Benthic organisms are useful for studying the ramifications of freshwater flow alterations on estuaries because of their rapid response to environmental changes and their sedimentary

lifestyle that impedes the ability of escape during episodes of increased flow. They are also easily sampled and are found in high densities in estuarine sediments (Coull 1999). Meiofauna are commonly used as a proxy for the assessment of variation in aquatic species diversity in response to environmental change (Montagna & Kalke 1992, Mees et al. 1993, Soetaert et al. 1995, Yamamuro 2000, Adão et al. 2009). Additionally, they have been apt models for disturbance studies, characterising the impact of floods and pollutants in estuaries over time (Zajac & Whitlatch 1982b, Montagna & Kalke 1992, Schratzberger & Warwick 1998, Neira et al. 2001, Austen & Widdicombe 2006, Moreno et al. 2008, Anderson 2015)

1.3 Benthic biota: Meiofauna

Meiofauna are benthic invertebrates that pass through a 500 µm mesh while being retained on a 40 - 63 µm mesh (Coull 1999). For the purpose of this study, two groups of larger protozoans that were found amongst the meiofauna (ciliates and foraminiferans) will be included in the study (see Giere 2008). Their size range allows for an interstitial lifestyle between sand grains while their vermiform body facilitates easy movement through the sediment. Within sediment these organisms have indirect involvement in the process of bioturbation and the stimulation of bacterial metabolism (Reichelt 1991, Vincx 1996). They are also vital constituents within food webs, as a food source for higher level organisms (Schlacher & Wooldridge 1996) and as consumers of benthic algae, detritus and bacteria. Meiofauna also participate in the mineralisation of organic matter (Gerlach 1978) and are used for environmental health monitoring, as their specific life history strategies give rise to their use as bioindicators (Kennedy & Jacoby 1999).

With regard to the vertical zonation of meiofauna in estuaries, the majority inhabit the upper 2 – 3 cm of muddy sediment. Their vertical distribution is largely limited by the redox potential discontinuity (RPD), below which sediments become anoxic and oxygen-sensitive

meiofauna, such as harpacticoid copepods, drastically decrease in abundance (Grego et al. 2014). Coull and Bell (1979) found meiofauna to be restricted to the upper layers of mud when oxidised sediments were laden with detritus. Another factor controlling the vertical zonation of meiofauna is desiccation. Pore water content is pivotal as meiofauna are sensitive to desiccation stress in intertidal sediments, regardless of sedimentary oxygen content (Jansson 1968).

The most important abiotic factors that control meiofaunal distribution are salinity, grain size and temperature (Coull 1999). The general trend in typical estuaries that have freshwater in the upper reaches and shift to more marine salinities at the mouth is for abundance and diversity to increase toward the lower reaches. Of greater importance to meiofaunal distribution, is periodic salinity change. As previously mentioned, sudden changes have multiple cascading effects on other physical aspects and can affect meiofaunal survivorship. Sediment grain size is a highly influential factor for meiofauna, as these burrowing organisms are more abundant in sediments that have a mean particle size of $>125\mu\text{m}$ as it provides the optimum interstitial space required for movement (Higgins & Thiel 1988, Carvalho & Santos 2013). With regards to temperature, meiofaunal community observations have revealed seasonal changes in diversity and abundance (Dye 1983, Santos et al. 1996, Meurer & Netto 2007). As proposed by Coull (1999), this is likely a direct cause of temperature trends or temperature-dependent factors such as food quantity or anoxic sediment depth. Within the St Lucia system, the meiofauna component has been the least studied (Bownes & Perissinotto 2012) despite their significance within sediments.

1.4 The St Lucia estuarine lake

The St Lucia estuarine lake system is the largest of its type in Africa and forms part of the iSimangaliso Wetland Park, on the north-east coast of South Africa (Begg 1978). The lake

has been recognised both as a Ramsar Wetland of International Importance (1989) and is a crucial part of South Africa's first UNESCO World Heritage Site (1999), due to its rich diversity of habitats and ecosystems that comprise a multitude of rare, endemic and threatened species (Porter & Blackmore 1998).

In the past, the Mfolozi River and the St Lucia Estuary used to flow into the St Lucia Bay before exiting to the sea via a common mouth (Cyrus et al. 2010). St Lucia received approximately 30% of its input from the neighbouring Mfolozi River, which drained through the vast Mfolozi swamps to the sea (Vivier & Cyrus 2009). In 1952, the Mfolozi River was deliberately separated from the St Lucia system, due to its swamp areas being drained and canalized as a result of sugarcane farming (Begg 1978, Whitfield & Taylor 2009), while the subsequent freshwater diversion from the St Lucia Estuary avoided the threat of siltation. This reduced freshwater inflow to the system eventually interfered with its natural mouth dynamics (Carrasco et al. 2009). These factors, combined with below average rainfall conditions during the 2001 – 2010 period, led to the closure of the St Lucia Estuary mouth for the greater part of the last decade. Without the Mfolozi linkage, St Lucia lacked its main source of freshwater during periods of drought (Whitfield & Taylor 2009).

The large size and shallowness of the lakes cause it to be vulnerable to the influence of climatic conditions as well as large-scale fluctuations in physico-chemical conditions, which are a characteristic feature of this system (Owen & Forbes 1997). The St Lucia estuarine lake experiences alternating dry and wet phases, which may each persist for a period of 4 to 10 years (Begg 1978). During the previous dry phase (2001 – 2010), St Lucia experienced low freshwater input and below average rainfall, which resulted in the formation of a persistent inverse salinity gradient, with significantly higher salinities (40 – 200) in the upper reaches than in the lower reaches and mouth (10 – 15) (Taylor 2006, Cyrus et al. 2010). The lack of freshwater also caused a 90 % desiccation of the lake (Stretch et al. 2013), which resulted in

the system being compartmentalised during the drought (Pillay & Perissinotto 2009). From the end of 2010 to early 2011, heavy rainfall was experienced in the St Lucia region due to the commencement of the latest La Niña event, marking the end of the dry phase. The higher than average rainfall that the catchment received in this period resulted in an influx of freshwater into the lake (Taylor et al. 2013). Consequently, salinity was drastically reduced, shifting the system out of the extreme hypersaline state that had persisted during the drought. Additionally, water levels in the lake increased and the different basins of the system became connected once again. Furthermore, the Mfolozi River and the St Lucia Estuary were recently linked via an artificial canal (beach spillway) in July 2012. Despite this provision of freshwater and inconsistent marine inflow when the Mfolozi mouth is open, to date the St Lucia Estuary maintains closure from the Indian Ocean (Taylor et al. 2013).

From 2011 to 2013, the amount of annual rainfall experienced in the St Lucia area increased drastically to well above average levels, resulting in a wet phase. These heavy rains and flood periods were not seasonal occurrences, but rather a climatic phase that St Lucia was experiencing at that stage. Currently the situation has reversed back to drought and the lake has been rapidly desiccating since 2014. With this shift in climatic conditions from a long-term dry phase to a wet phase and back to a drought, the system underwent drastic changes in physico-chemical conditions which are likely to have caused significant changes in the meiofauna community structure. The Mfolozi-St Lucia reconnection was partly responsible for the recent freshwater dominance in the St Lucia Estuary. The effects of the reconnection were evident in the lower reaches, where inflow from the Mfolozi aided in the dispersal of organisms into St Lucia (van Elden et al. 2014). The additional intermittent connection with the sea has led to marine organisms moving into the mouth region. This provides an additional factor of significance for the meiofauna community of the St Lucia estuarine lake system. Despite the system moving back into a drought phase since 2014, experiencing

desiccation and fragmentation, the wet phase meiofauna communities have remained unstudied. Chapter 1 of this thesis will therefore focus on the meiofaunal communities of the St Lucia Estuary during the first two years of the wet phase, by analysing seasonal differences in the community structure and composition at five representative sites along the estuary. It is hypothesised firstly, that there are spatial and seasonal differences in meiofauna community structure and composition between sites along the St Lucia Estuary following the increase in freshwater flow. Secondly, that meiofaunal community differences between sites varied between seasons and years during the wet phase.

Pickett and White (1985) defined disturbance as “*a discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment*”. These events are key structuring forces for ecological systems and their various communities (Cristoni et al. 2004) that alter environmental conditions, making new areas available for colonisation, thus starting a successional process (Ritter et al. 2005). Succession, as defined by Trueblood et al. (1994), is a “*directional change in the species composition of a community over time*”. Succession is also the manner in which a community recovers after disturbance. This recovery is based on both direct and indirect factors. Direct factors include recruitment based on life history traits and migration into the disturbed area, while competition may act as an indirect factor in community structuring (Widdicombe & Austen 2005). The community recovery model suggested by Pearson and Rosenberg (1978) uses the concept of *r*- and *K*-selected species, where primary colonisers would typically be classified as *r*-selected species and have life history traits that involve a short life span, rapid development and reproduction and some form of pelagic dispersal. These organisms would colonise a disturbed area once conditions became more favourable. Over time the *r*-selected species would be succeeded by *K*-selected species, which have a longer life span and slower growth; thus creating a successional pattern.

Patterns of succession may not necessarily be predictable but they are ultimately driven by external environmental fluctuations (Platt & Connell 2003). This type of succession is known as allogenic succession (Tansley 1920). Environmental perturbations in the form of floods are a characteristic example of an allogenic change. The intense rainfall event that occurred in the St Lucia system at the beginning of 2011 provided an apt example of a disturbance-causing event, as floods cause drastic salinity changes and these reductions are highly influential for benthic communities (Montagna et al. 2002). Organisms such as meiofauna have a relatively short generation time, are excellent monitoring communities and are able to rapidly reflect environmental changes; they therefore provide suitable models for succession. By following the community changes before and after the disturbance, the effect of a flood can be examined. Additionally, by analysing the short term changes in benthic community structure, the meiofaunal succession pattern can be established. Chapter 2 therefore examines the short to medium term successional patterns of the meiofauna of the St Lucia Estuary, at three representative sites with varying salinity ranges, following a flood disturbance. It is hypothesised firstly, that there would be differences in meiofaunal community structure and composition between sites and climatic phases (drought and flood) and secondly that there would be differences in meiofauna community structure and composition at each site over time following the flood disturbance.

1.5 Relevance and study aims

With climate change and further anthropogenic activities altering coastal habitats, estuarine systems have become heavily influenced and vulnerable to disturbance. It is predicted that global temperatures will increase by 1.4 to 3 °C by the year 2050 (Rowlands et al. 2012). Information regarding the structure and composition of meiofaunal communities, as well as their recovery potential from climatic-related stress, is important as climate change is

expected to bring about more frequent incidents of stress on these communities, such as droughts and floods. Additionally, knowledge of the meiofauna diversity in the St Lucia Estuary will also be of great value since very little is known about this functional group in South Africa (Griffiths et al. 2010, Barnes et al. 2011), and there is very limited literature on the meiofauna of this region. The information and knowledge gained from this study can be added to current data sets and be utilized as support for future management strategies which can be implemented towards the long-term sustainability of the St Lucia system.

The main aims of this study were as follows:

1. To analyse the meiofauna community structure and composition within the St Lucia Estuary during the wet phase of 2011 – 2012.
2. To determine the effect of a flood disturbance and the short-term succession patterns in its aftermath on the meiofauna community of St Lucia following a heavy rainfall event.

1.6 Study Site

The St Lucia estuarine lake is located on the eastern coast of South Africa, in the KwaZulu-Natal province. This region typically experiences summer rainfall, with inter-annual variability experienced in the form of droughts/floods caused by southward shifts of the Intertropic Convergence Zone and El Niño Southern Oscillation (Rautenbach & Smith 2001). Mean annual precipitation from the systems 45 subcatchments is 787 mm (Perissinotto et al. 2013). St Lucia has an estimated area of between 300 and 350 km², depending on water levels (Begg 1978). The estuarine lake system is subdivided into five regions, including three large, shallow interconnected lake basins in the upper reaches, namely False Bay, North Lake and South Lake. These lakes connect with the Mouth via a narrow channel, known as the Narrows, which then leads to the Indian Ocean (Figure 1.1). For the first chapter of this study, five representative sites were sampled in the St Lucia Estuary, namely Lister's Point, Charter's Creek, Catalina Bay, Esengeni and the Mouth, forming a gradient from head to mouth. With regards to salinity however, St Lucia has an inverse salinity gradient. Lister's Point is located in the northern lake and is predominantly hypersaline, Charter's Creek and Catalina Bay are located in the southern lake which has typical estuarine salinities and Esengeni is permanently freshwater and located in the Narrows. For the second chapter, three representative sites were chosen, namely Lister's Point, Charter's Creek and the Mouth.

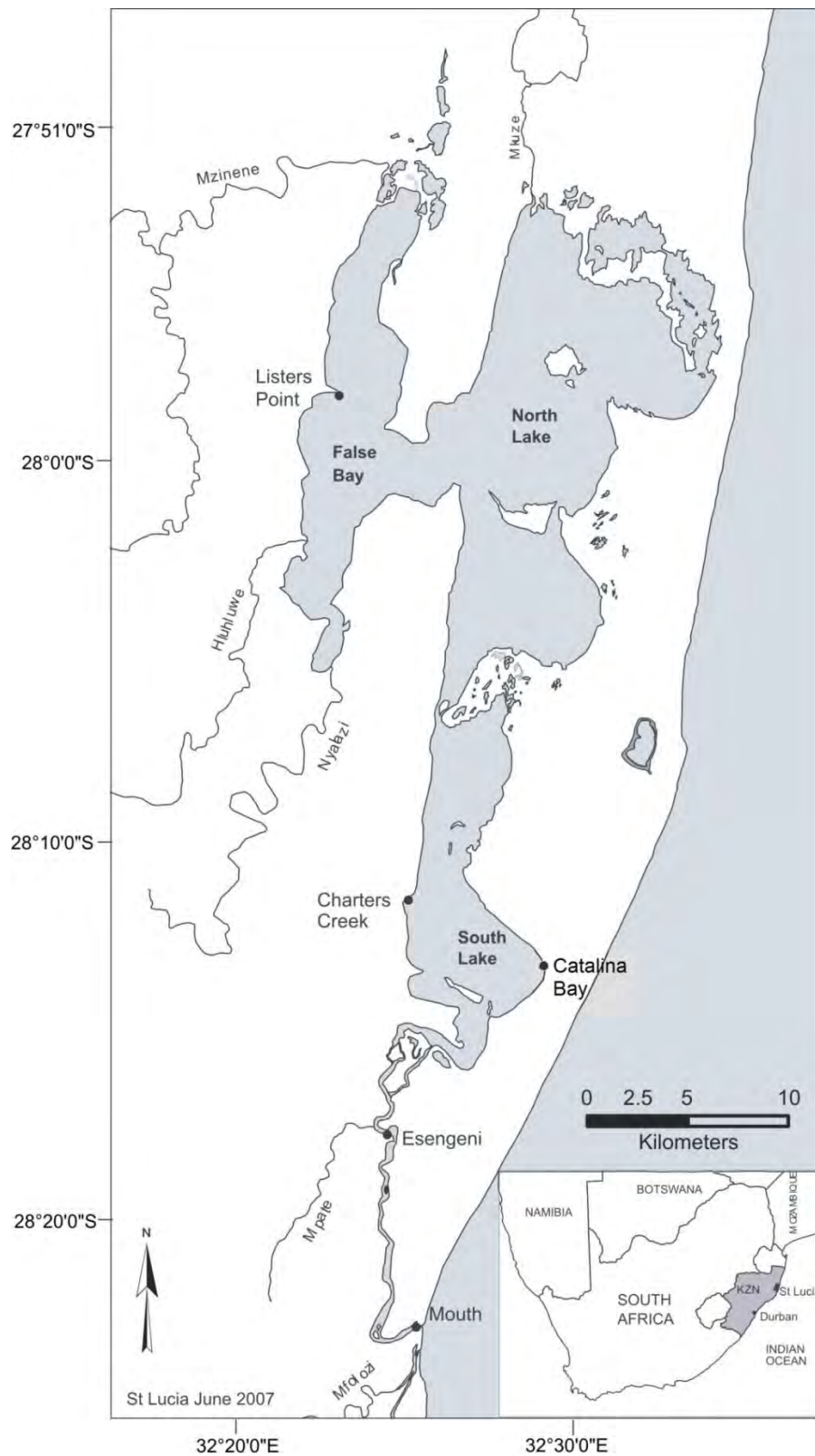


Figure 1.1: Map of the St Lucia estuarine system indicating the sampling stations chosen for this study (•), with the geographic position within South Africa.

CHAPTER 2: MEIOFAUNAL COMMUNITY CHARACTERISTICS DURING A CLIMATICALLY-INDUCED WET PHASE IN THE ST LUCIA ESTUARY, SOUTH AFRICA

2.1 Abstract

Following a decade long drought with hypersaline conditions, at the end of 2010 the St Lucia Estuary moved into a two year wet phase. The wet phase began with higher than average rainfall that lowered salinities throughout the system. Environmental data and meiofauna samples were collected from five representative sites along the estuary during quarterly surveys conducted in each season. Diversity indices suggest that 2011 experienced a generally greater meiofaunal density and taxon richness when compared to 2012. Community analyses revealed that meiofaunal communities differed between sites and seasons as a result of the estuarine gradient and seasonal variation in environmental parameters. The initial meiofaunal communities showed no distinction based on spatial or temporal differences. However, the increase in similarity of site specific communities in 2012 is indicative of a distinction between sites that was generally absent in 2011. The increase in site specific similarities, lower levels of variation and a greater level of homogeneity in 2012, suggest that communities had become more established within this phase. The two year transitional state in which these communities were studied suggests the possibility of a lag time for any change to become evident and may be the result of the drastic change that the system experienced, as the lake filled and the basins were once again connected. The overall meiofaunal dynamics during the two year wet phase were variable, but appeared to show potential for long term improvement in terms of increased overall diversity.

2.2 Introduction

Marine and coastal environments provide a vast amount of ecosystem goods and services and are important at ecological, social and economic levels. In addition to anthropogenic influences that disrupt coastal ecosystems, these environments are threatened by global climate change, which has the ability to disrupt their composition, diversity and function (Cardoso et al. 2008). Changes in sea-level, temperature and rainfall can drastically alter the functioning of these ecosystems. Globally, average temperatures are expected to increase by 1.4 to 3 °C by 2050 (Rowlands et al. 2012), while precipitation extremes may intensify conditions in particular areas (Trenberth 2011). Floods and droughts are the typical definition of hydrologically extreme events. The increasing climate variability leading to precipitation extremes and the climatic shifts between these hydrological extremes have been a focus of interest in the past two decades (Katz & Brown 1992, Trenberth & Hoar 1996, Meehl et al. 2000, Pollack et al. 2011). These changes will inevitably impact coastal ecosystems, such as estuaries, deltas and wetlands (Kjerfve et al. 1994).

The St Lucia Estuary is the largest estuarine lake in Africa, a Ramsar Wetland of International Importance since 1989 and forms part of the iSimangaliso Wetland Park, a UNESCO World Heritage Site since 1999. The St Lucia system is regulated by wet and dry cyclical periods, each lasting between 4 and 10 years (Begg 1978). From 2001 until 2010, the lake system experienced below average rainfall (Cyrus et al. 2011). These drought conditions were further intensified by the freshwater diversion of the Mfolozi River away from the St Lucia Estuary, as a measure of prevention against the threat of siltation (Whitfield & Taylor 2009). During this time, the system exhibited extremely low water levels, or near desiccation in the northern basins (Pillay & Perissinotto 2009), causing a disconnection between the upper and lower reaches. As a result, a persistent reversed salinity gradient

developed, where the upper reaches of the lake exhibited higher salinity levels than the lower reaches and the mouth area (Taylor 2006).

From the start of the rainfall season in October 2010 to January 2011, the St Lucia Estuary received 925 mm of rainfall (Taylor 2011). This vast increase in freshwater input raised the water levels in the lake by more than 0.5 m by the end of January 2011. The various compartments of the lake were re-connected as water levels throughout the system rose. The increase in rainfall and subsequent dilution of salinities throughout the system signalled the beginning of a new wet phase.

Within the St Lucia system, most communities have been studied extensively, however the meiofauna group remains relatively poorly studied (Pillay & Perissinotto 2009, Bownes & Perissinotto 2012). These organisms are essential within sediment; they are involved in processes such as bacterial metabolism stimulation and bioturbation (Bonaglia et al. 2014), and play a crucial role within benthic trophic interactions, as both consumers and prey (Schmid-Araya & Schmid 2000, Pusceddu et al. 2014). Their ecological characteristics, namely small size, high abundance, benthic lifestyle and rapid regeneration time, enable these communities to be more advantageous monitoring communities than macrofauna (Schratzberger et al. 2000, Austen & Widdicombe 2006, Alves et al. 2013).

As a result of climate change, the region of the St Lucia estuarine lake is expected to become warmer and wetter towards 2100 (Vaeret & Sokolic 2008). Having an understanding of the effects of a climatically induced wet phase on the meiofauna community could prove important in predicting responses of the system to natural perturbations in the future. This study therefore aimed to determine the meiofauna community structure as a result of environmental forcing from a new climatic state, and how it varied between sites along the estuary over time.

To achieve this, a temporal (seasonal) and spatial comparison was conducted between the meiofauna communities of the St Lucia system, in terms of their density, taxonomic structure and composition during the two year wet phase that followed the decade long drought. The following hypotheses were tested: 1) There are spatial and seasonal differences in meiofauna community structure and composition between sites along the St Lucia Estuary following the increase in freshwater flow. 2) Meiofaunal community differences between sites varied between seasons and years during the wet phase.

2.3 Methods

2.3.1 Environmental variables

All samples were taken from the nearshore water's edge, with the exception of Esengeni where samples were collected by boat from the channel. A YSI 6600 multiprobe was used to measure temperature (°C), depth (m), salinity, dissolved oxygen (mg l^{-1}), pH and turbidity (nephelometric turbidity units, NTUs). At shallow depths, the probe was placed horizontally, ensuring that all sensors were submerged. In deeper sites where measurements were taken from both top and bottom waters only the latter was used. For the measurement of total suspended solids (TSS), three replicate 250 ml water samples were collected. Each TSS sample was filtered through pre-weighed, combusted GF/F filters using a Millipore filtration system. Filters were dried and weighed to measure TSS (mg/L). Cumulative rainfall data for the month prior to each quarterly sampling was obtained from 3 stations closest to the study sites (South African Sugarcane Research Institute (SASRI) weather website) as per Bownes and Perissinotto (2012). For microphytobenthos (MPB) sampling, three replicates of the first 1 cm of sediment were collected using a Perspex corer (internal diameter 20 mm). Cores were added to 30 ml 90% acetone and incubated for 48 to 72 hours for the extraction of chlorophyll-a. Microphytobenthic samples were measured fluorometrically with a Turner

Designs 10-AU fluorometer, to establish the chlorophyll-a biomass in units of mg chl-a eq m⁻². For sediment organic matter (SOM), samples were collected by combining two cores of the upper 1 cm per sample, with 3 replicates per site per sampling occasion. Sediment was dried at 40 °C in a drying oven, weighed, combusted at 500°C for 6 hours and re-weighed to determine the percentage organic matter. Grain size composition for each site and season was measured from triplicate 100 ml sediment samples. Sediment was dried at 40 °C in a drying oven and analysed with a dry sieving method using analytical sieves with pore sizes ranging from 2000 µm to < 180 µm (c/o Environmental Mapping and Surveying).

2.3.2 *Meiofauna*

A perspex twin-corer (internal diameter: 20 mm) was used to collect 3 replicates of the upper 1 cm of sediment. Samples were fixed using 10 % formalin with Phloxin-B. In the laboratory, each sample was washed through a 500 and 63 µm mesh sieve, in order to separate the meiofauna fraction from the sample. Meiofauna were extracted by centrifugation with Ludox HS-40, following the procedure of Bownes and Perissinotto (2012). Sediment checks were conducted to ensure extraction efficiency by examining a portion of the sediment in search of any organisms that were not extracted. Samples were sorted under a dissecting microscope and all meiofauna were identified to the lowest possible taxonomic level.

2.3.3 *Statistical analysis*

Univariate statistics were conducted using IBM SPSS vs. 21 and Statistica 12. Community indices of meiofauna density and taxon richness were obtained for each sample with the use of Primer v6. A three-way factorial analysis of variance (ANOVA) was used to test for differences in density and richness between years, sites and seasons. Bonferroni post-hoc tests were conducted for comparisons between all pairs. The ANOVA assumptions of homogeneity of variances (Levene's test; density: $p = 0.138$ and richness: $p = 0.562$) and normality (One-sample Kolmogorov-Smirnov test, $p = 0.532$ for density and $p = 0.698$ for

richness) were satisfied in all cases. Spearman's Rank correlations were performed to examine the relationships between environmental variables and univariate indices for each year. A principal component analysis (PCA) was conducted on normalised environmental data.

Multivariate statistics were conducted using Primer v6 software. All data were square-root transformed to weight the contributions of common and rare species in the multivariate representation (Clarke & Warwick 2001). Comparisons of meiofauna community structure among samples were examined using a permutation-based hypothesis testing Analysis of Similarities (ANOSIM), based on Bray-Curtis similarity (Clarke & Warwick 2001, Clarke & Gorley 2006). Two-way ANOSIMs were conducted to analyze meiofauna community composition between sites and season for each year separately. The generated R statistic ranged from 0 (identical assemblages) to 1 (dissimilar assemblages) and indicated the probability (p) that the various assemblages came from the same distribution, based on a significance value of 5% ($\alpha = 0.05$).

Non-metric multidimensional scaling (MDS) was used to display the relationships among meiofauna assemblages between sites and seasons, with a superimposed cluster analysis showing 50 % similarity. This was done for each year separately, to accurately depict any changes that occurred between years. To determine which taxa were most important in distinguishing significant spatio-temporal patterns in community structure for each year, data were analysed using similarity percentage (SIMPER) analysis. The BIOENV procedure was applied to meiofauna data to determine whether the measured environmental variables correlated with community structure. Environmental data were normalised prior to analysis.

2.4 Results

2.4.1 Environmental variables

The temperature observed during the study period showed seasonal trends that were consistent in both years (Figure 2.1a). Salinity varied between sites, with mean salinity at Lister's Point of 53.9 ± 6.62 and 59.6 ± 26.9 , in 2011 and 2012 respectively. These levels were higher than those of all other sites, where salinities ranged from 1.14 to 16.83 in 2011 and 1.26 to 14.42 in 2012. Rainfall generally peaked in summer and spring for all sites, with lower rainfall being recorded in autumn and winter (Figure 2.1b). Turbidity was greatest at Lister's Point, Charter's Creek and the Mouth, peaking in spring 2011 (Table 2.1). Lowest turbidities were observed at Catalina Bay and Esengeni. TSS was much higher at Lister's Point throughout the study period ($302 - 1116 \text{ mg.L}^{-1}$); while at all other sites it remained lower than 400 mg.L^{-1} .

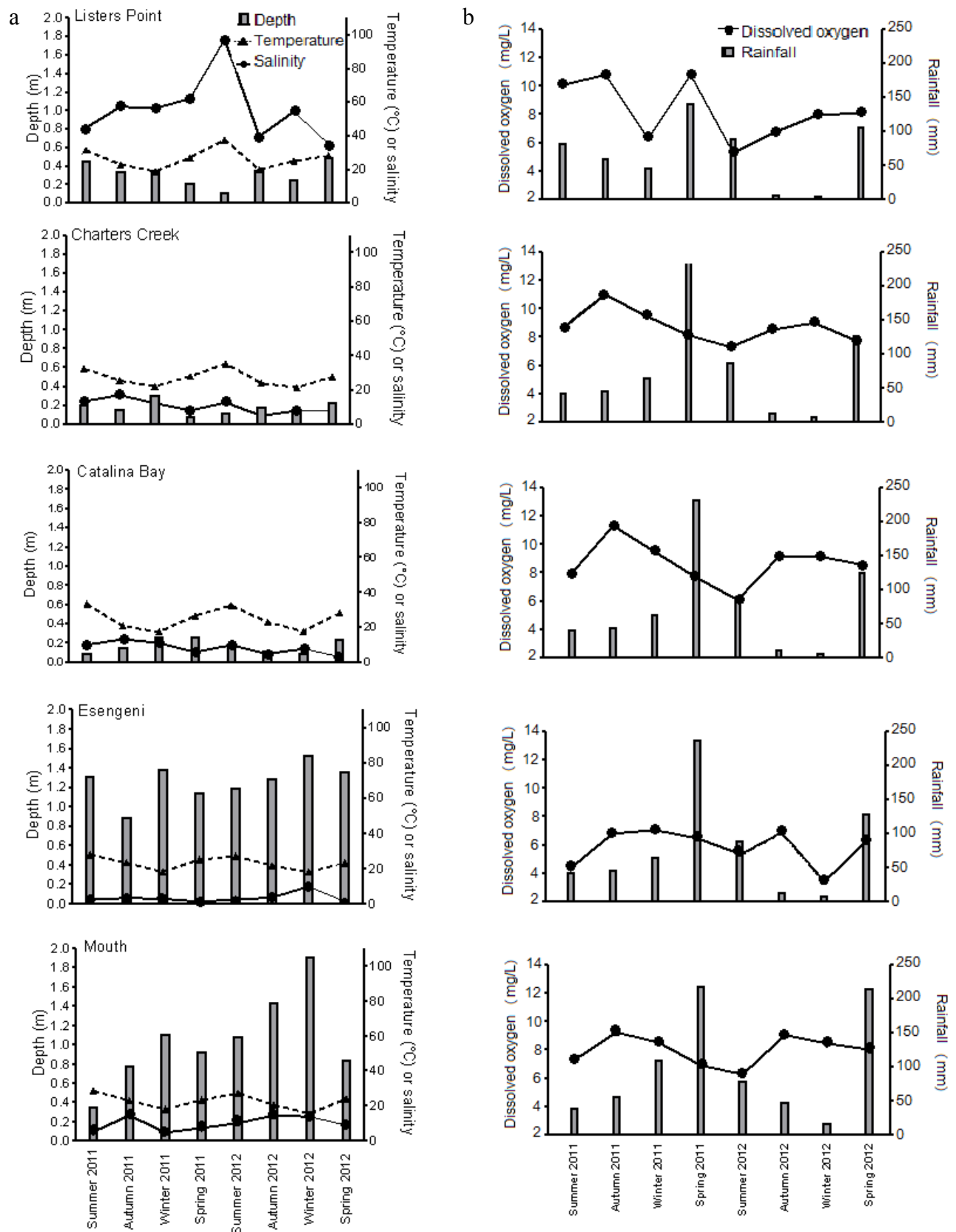


Figure 2.1: Variations in a) sampling depth, temperature and salinity; and b) dissolved oxygen and rainfall from quarterly samples collected between February 2011 and November 2012 at the 5 study sites in St Lucia Estuary (Listers Point, Charters Creek, Catalina Bay, Esengeni, Mouth).

Table 2.1: Mean \pm SD of combined environmental variables from 2011 and 2012 for summer, autumn, winter and spring, at each site. Minimum and maximum values across all phases (Range) are provided. Variables include turbidity (NTU: nephelometric turbidity units) and total suspended solids (TSS). Where no SD is present, only a single reading was obtained.

Site	Season	Turbidity (NTU)		TSS (mg.L ⁻¹)	
		2011	2012	2011	2012
Listers Point	Summer	21.4 \pm 5.9	144.6 \pm 23.2	302.0 \pm 25.9	1116.5 \pm 484.4
	Autumn	234.1	270.4 \pm 171.6	716.7 \pm 67.5	342.6 \pm 19.8
	Winter	180.0 \pm 9.9	257.5 \pm 17.7	554.7 \pm 179.3	93.5 \pm 7.8
	Spring	590.8	220.0	532.2 \pm 77.0	453.2 \pm 111.7
	Range	17.2 - 590.8	128.2 - 391.8	283.7 - 764.5	88.0 - 1459.1
Charters Creek	Summer	98.8 \pm 4.2	191.9 \pm 1.6	309.4 \pm 12.6	185.7 \pm 42.2
	Autumn	106.0	308.6 \pm 10.5	192.3 \pm 11.5	376.6 \pm 17.2
	Winter	125.5 \pm 36.0	129.6 \pm 16.9	93.6 \pm 24.0	243.9 \pm 32.9
	Spring	315.3 \pm 25.3	133.1 \pm 0.3	191.0 \pm 30.7	249.8 \pm 0.5
	Range	95.9 - 333.2	117.7 - 316.0	76.6 - 318.3	155.8 - 388.8
Catalina Bay	Summer	9.0 \pm 0.0	119.0 \pm 165.2	89.8 \pm 30.0	174.2 \pm 2.5
	Autumn	41.3	2.9 \pm 1.5	129.5 \pm 3.9	10.6 \pm 0.8
	Winter	13.3 \pm 6.7	124.3 \pm 5.3	23.7 \pm 2.0	154.7 \pm 8.2
	Spring	26.0 \pm 6.5	0.7	31.3 \pm 1.4	9.6 \pm 0.8
	Range	8.6 - 41.3	0.7 - 235.9	22.2 - 132.3	9.0 - 175.9
Esengeni	Summer	101.5	112.3	78.4 \pm 25.2	88.1 \pm 15.4
	Autumn	221.5	64.8	133.1 \pm 1.5	67.9 \pm 5.5
	Winter	86.6	164.5	40.4 \pm 4.2	108.8 \pm 55.2
	Spring	409.5	106.6 \pm 29.7	69.9 \pm 4.1	137.4 \pm 108.7
	Range	86.6 - 409.5	64.8 - 164.5	37.4 - 134.2	60.5 - 214.3
Mouth	Summer	23.3	18.7	86.2 \pm 23.7	39.5 \pm 4.3
	Autumn	8.8	26.0	122.0 \pm 7.8	33.9 \pm 0.5
	Winter	10.3	26.0	12.6 \pm 2.2	23.8 \pm 0.8
	Spring	21.1	202.0 \pm 52.3	30.8 \pm 1.3	54.8 \pm 34.0
	Range	8.8 - 23.3	18.7 - 239.0	11.1 - 127.6	23.3 - 78.9

Sediments at Lister's Point and Esengeni consisted largely of silt and mud (63 and 85 %, respectively), with a median particle size of $49 \pm 5 \mu\text{m}$ in 2011 and $131 \pm 81 \mu\text{m}$ in 2012 at Lister's Point and $48 \mu\text{m}$ at Esengeni (Figure 2.2) over the two year period. Charter's Creek and Catalina Bay were predominantly composed of fine and medium sands (median particle size of $230 \pm 50 \mu\text{m}$ and $245 \pm 13 \mu\text{m}$, respectively). The Mouth was composed mainly of medium sands (median particle size of $305 \pm 22 \mu\text{m}$) and very low silt content, compared to all other sites. Microphytobenthos was generally greater in 2011 than 2012 and varied seasonally between sites in both years with summer and spring having the highest chlorophyll a biomass levels (Table 2.2). Average organic content was low at Charter's Creek, Catalina Bay and the Mouth (between 0.1 and 0.8%) and higher at Lister's Point (3.26 – 12.25 %) and Esengeni (4.29 – 8.69 %).

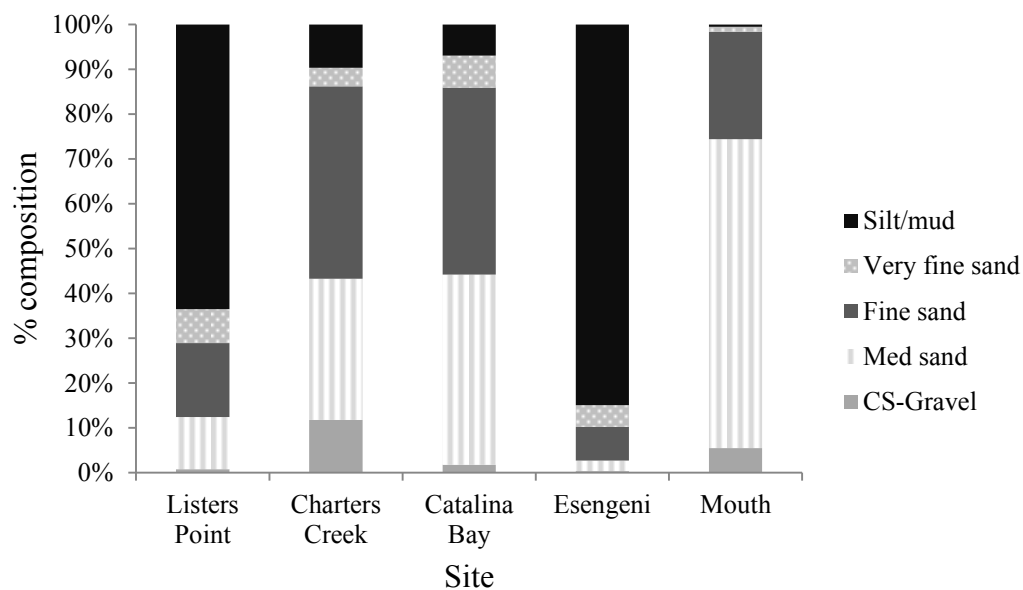


Figure 2.2: Mean percentage composition of grain size classes at 5 sites in St Lucia Estuary (Listers Point, Charters Creek, Catalina Bay, Esengeni, Mouth). 'cs-gravel' includes 3 size classes: coarse sand, very coarse sand and gravel.

Table 2.2: Sediment characteristics at 5 sites in St Lucia Estuary (Listers Point, Charters Creek, Catalina Bay, Esengeni, Mouth), including mean (\pm SD) microphytobenthos (MPB) and percentage sediment organic matter (SOM).

Site	Season	MPB (mg chl-a eq m ⁻²)		SOM (%)	
		2011	2012	2011	2012
Listers Point	Summer	83.0 \pm 24.0	52.7 \pm 4.9	7.00 \pm 1.7	8.76 \pm 3.2
	Autumn	80.5 \pm 15.6	7.8 \pm 1.9	9.28 \pm 2.8	9.185
	Winter	25.2 \pm 4.8	7.3 \pm 0.6	12.25 \pm 2.6	6.83 \pm 0.5
	Spring	33.3 \pm 12.9	2.0 \pm 0.2	3.26 \pm 1.7	4.32 \pm 2.6
Charters Creek	Summer	5.3 \pm 1.6	40.4 \pm 3.9	0.76 \pm 0.3	0.31 \pm 0.2
	Autumn	12.0 \pm 1.9	9.3 \pm 1.0	0.68 \pm 0.2	0.295
	Winter	18.2 \pm 5.9	10.5 \pm 1.3	0.81 \pm 0.1	0.66 \pm 0.3
	Spring	63.9 \pm 37.2	0.8 \pm 0.8	0.50 \pm 0.6	0.25 \pm 0.1
Catalina Bay	Summer	40.1 \pm 7.8	29.0 \pm 8.3	0.53 \pm 0.1	0.27 \pm 0.1
	Autumn	7.0 \pm 4.5	8.0 \pm 1.2	0.57 \pm 0.1	0.23
	Winter	20.1 \pm 3.5	8.4 \pm 1.0	0.65 \pm 0.1	0.29 \pm 0.0
	Spring	24.2 \pm 10.7	3.0 \pm 0.7	0.26 \pm 0.0	0.24 \pm 0.0
Esengeni	Summer	7.7 \pm 2.5	6.1 \pm 0.9	8.69 \pm 0.1	5.92 \pm 0.6
	Autumn	4.9 \pm 1.2	1.9 \pm 0.1	6.14 \pm 0.6	5.935
	Winter	7.3 \pm 1.5	1.4 \pm 0.3	6.25 \pm 0.3	6.56 \pm 0.3
	Spring	8.5 \pm 1.1	1.3 \pm 0.1	6.11 \pm 0.3	4.29 \pm 0.5
Mouth	Summer	54.7 \pm 30.8	4.4 \pm 0.8	0.33 \pm 0.0	0.27 \pm 0.0
	Autumn	7.3 \pm 4.8	1.7 \pm 0.0	0.26 \pm 0.0	0.205
	Winter	22.8 \pm 5.5	3.5 \pm 2.7	0.50 \pm 0.1	0.19 \pm 0.1
	Spring	14.1 \pm 1.0	0.6 \pm 0.4	0.12 \pm 0.0	0.21 \pm 0.0

Correlations between environmental variables can be seen in Table 2.3. Significant correlations pertaining to meiofauna include meiofauna taxon richness, which was positively correlated with MPS in both years (Table 2.3) and negatively correlated with SOM in 2012. Density was only positively correlated with MPS and negatively correlated with SOM in 2012

Table 2.3: Spearman's Rank correlation coefficients of the relationship between environmental variables and mean meiofaunal density (N) and taxon richness (d), including temperature (°C), salinity, pH, mean total suspended solids (TSS), median particle size (MPS), % sediment organic matter (SOM), microphytobenthos biomass (MPB) and rainfall (mm). Significant correlations are highlighted in bold ($\alpha = 0.05$).

Year	Variable	Temperature	Salinity	pH	TSS	MPS	SOM	MPB	Rainfall
2011	N	0.30	0.14	0.02	0.03	0.50	-0.10	0.41	-0.02
	d	0.02	0.25	0.09	0.04	0.58	-0.40	0.37	0.42
	Temperature	1.00	0.04	0.34	0.28	-0.16	-0.14	0.28	-0.04
	Salinity		1.00	-0.09	0.75	0.02	0.18	0.34	-0.21
	pH			1.00	-0.09	-0.06	-0.24	-0.01	0.46
	TSS				1.00	-0.52	0.51	0.20	-0.34
	MPS					1.00	-0.77	-0.01	0.11
	SOM						1.00	0.01	-0.37
	MPB							1.00	0.44
	Rainfall								1.00
2012	N	-0.01	-0.30	0.27	-0.06	0.44	-0.60	0.24	0.12
	d	-0.22	-0.30	-0.07	-0.30	0.72	-0.81	-0.25	0.27
	Temperature	1.00	0.10	0.46	0.28	0.03	0.15	0.25	0.61
	Salinity		1.00	0.10	0.32	0.13	0.27	0.21	-0.22
	pH			1.00	0.23	0.18	-0.03	0.58	0.15
	TSS				1.00	-0.38	0.46	0.38	-0.05
	MPS					1.00	-0.90	-0.12	0.33
	SOM						1.00	0.35	-0.41
	MPB							1.00	-0.38
	Rainfall								1.00

Principal component analysis showed slight separation of sites according to their location along the lake where four groups were observed in 2011: Lister's Point, Esengeni, the remaining three sites, and samples collected during spring (Figure 2.3a). The first two PCs accounted for 51.5% of the variance of the environmental data among the 20 sampling occasions and grouped these along spatial and seasonal divisions. The exceptions were Lister's Point and spring that did not group together and were not grouped with each site. PC 1 was a measure of differences in turbidity, SOM, and grain size (Eigenvalue = 3.54). Samples that loaded high on PC 1 (Catalina Bay and the Mouth) had lower SOM and turbidity, and larger grain size than samples that loaded low on PC 1 (Lister's Point and Esengeni), while samples with intermediate loadings on PC 1 (Charter's Creek) had low SOM, high turbidity and large grain size. PC 2 was a measure of differences in dissolved oxygen and rainfall (Eigenvalue = 2.53) and samples that loaded high on PC 2 (summer, autumn and winter samples from Lister's Point) had lower rainfall and higher dissolved oxygen content than samples that loaded low on PC 2 (spring samples and Esengeni samples).

The PCA for 2012 produced three different groups, similar to those based on site in 2011 (Figure 2.3b). The first 2 PCs accounted for 54.8 % of the environmental data variability. The only exception was the sampling occasion during summer at Lister's Point, which did not group with any other samples. PC 1 was a measure for differences in salinity and TSS (Eigenvalue = 3.93), and samples that loaded high on PC 1 (southern lake sites, Esengeni and Mouth) had lower salinities and TSS than those with lower loadings. PC 2 measured differences in SOM (Eigenvalue = 2.63) and sites that loaded high on this PC (southern lake sites) had lower SOM. Although pH was found to be an important environmental factor (PCA), the variation between sites and seasons was minor.

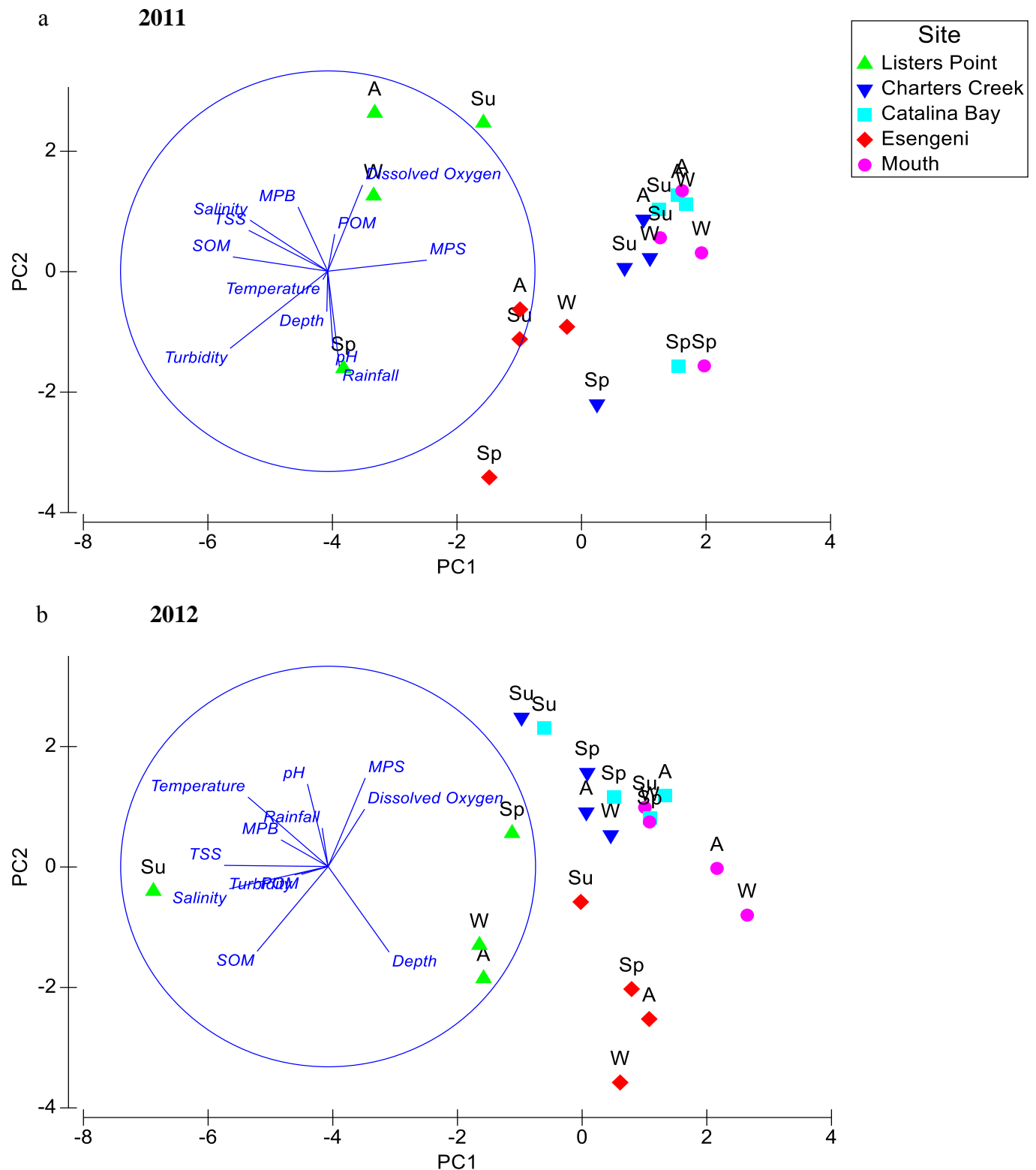


Figure 2.3: Principal Component Analysis (PCA) plot based on the environmental variables measured in summer (Su), autumn (A), winter (W) and spring (Sp) at each of the 5 sites in 2011 (a) and 2012 (b).

2.4.2 *Meiofaunal density and richness*

Average densities for all seasons varied among sites, and were 562 ± 639 and 103 ± 152 ind. 10 cm^{-2} at Lister's Point, 449 ± 216 and 198 ± 37 ind. 10 cm^{-2} at Charter's Creek, 346 ± 344 and 932 ± 583 ind. 10 cm^{-2} at Catalina Bay, 154 ± 205 and 59 ± 45 ind. 10 cm^{-2} at Esengeni, and 324 ± 210 and 163 ± 127 ind. 10 cm^{-2} at the Mouth, with an overall average of 367 and 291 ind. 10 cm^{-2} , for 2011 and 2012 respectively. Meiofaunal density was generally higher in 2011 than in 2012, with the exception of Catalina Bay (Figure 2.4). There were no general trends in density observed between sites and seasons for 2011. However, there appears to be clear site differences for both years, with the lowest overall density at Esengeni in both 2011 and 2012, and the highest at Lister's point and Catalina Bay in 2011 and 2012, respectively.

Meiofaunal density showed significant differences for the main effects of year and site ($p < 0.05$; ANOVA), with a significant interaction between year, site and season (Table 2.4). Mean meiofauna density at Lister's Point, Charter's Creek and Catalina Bay, were significantly higher than those found at Esengeni (107 ± 153 ind. 10 cm^{-2}) and the Mouth (243 ± 188 ind. 10 cm^{-2}) (Figure 2.4). Meiofauna densities were significantly higher in 2011 than 2012 at all sites except Catalina Bay. The three-way interaction suggests that the interaction between year and site varied across seasons. Seasonal variation between years was observed in all seasons at particular sites. At Lister's Point, density varied significantly between summer 2011 and 2012 and autumn 2011 and 2012. Catalina Bay experienced significant differences in density between years during autumn, winter and spring.

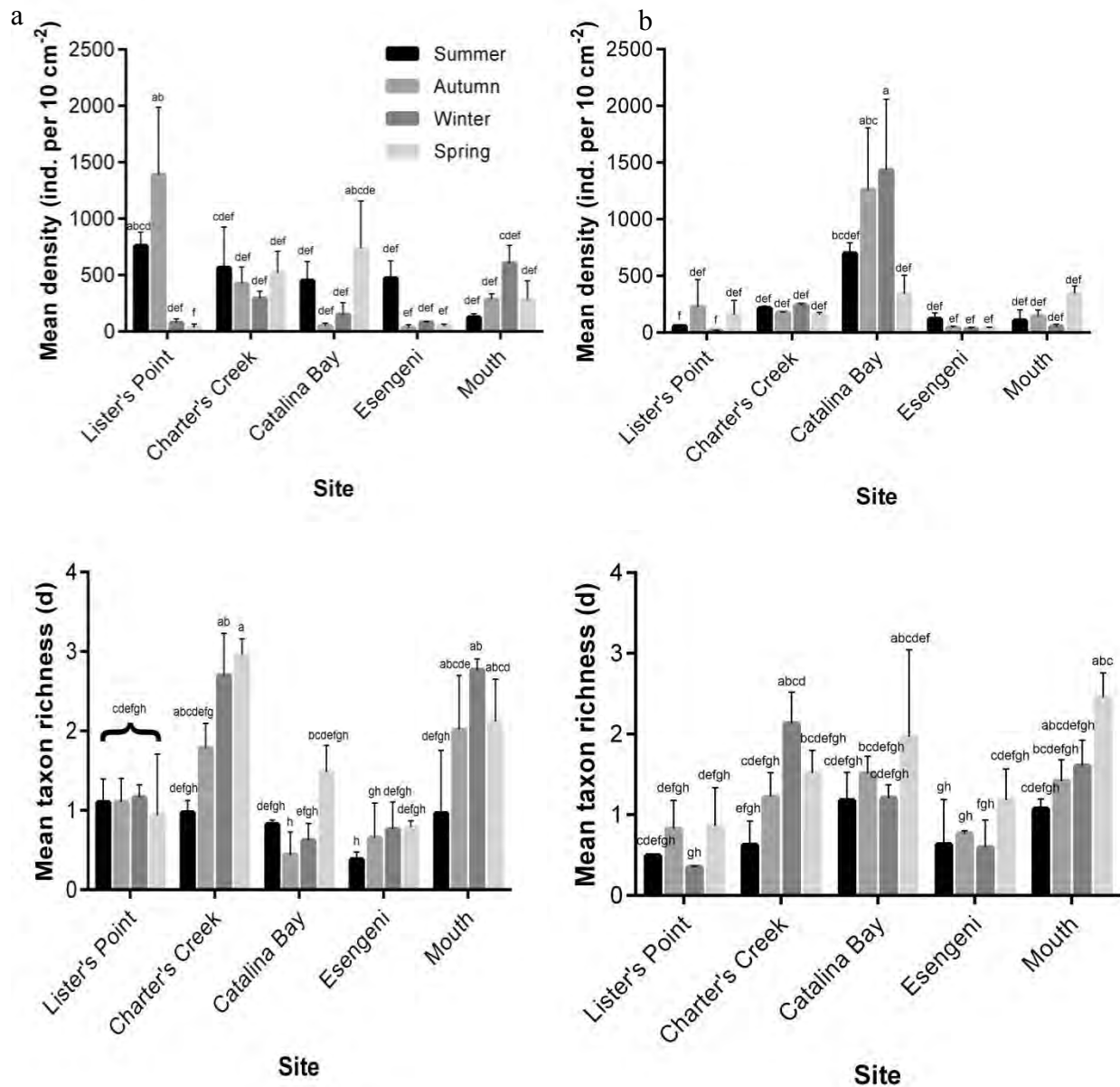


Figure 2.4: Spatial and temporal variation in mean (\pm SD) density (N) and taxon richness (Margalef's index, d) from 4 seasons (summer, autumn, winter, spring) at the 5 study sites (Listers Point, Charters Creek, Catalina Bay, Esengeni, Mouth) for a) 2011 and b) 2012. Bars that share common letters indicate homogenous grouping (Bonferroni post-hoc tests).

Table 2.4: Results of ANOVAs examining the effects of year (2011, 2012), site (Listers Point, Charters Creek, Catalina Bay, Esengeni, Mouth) and season (summer, autumn, winter, spring) on density and taxon richness (*d*) of meiofauna in the St Lucia Estuary. Significant results are marked with an asterisk ($\alpha = 0.05$).

Factors	SS	df	MS	<i>F</i>	<i>p</i>
Density					
Intercept	12991845	1	12991845	305,7440	< 0.001
Year	171659	1	171659	4,0398	0.048*
Site	3679514	4	919878	21,6480	< 0.001*
Season	341706	3	113902	2,6805	0.052
Year x Site	3744916	4	936229	22,0328	< 0.001*
Year x Season	486711	3	162237	3,8180	0.013*
Site x Season	2621551	12	218463	5,1412	< 0.001*
Year x Site x Season	4616406	12	384701	9,0534	< 0.001*
Error	3399404	80	42493		
Taxon Richness (d)					
Intercept	167,6129	1	167,6129	1023,990	< 0.001
Year	0,6314	1	0,6314	3,857	0.053
Site	24,5916	4	6,1479	37,559	< 0.001*
Season	9,9425	3	3,3142	20,247	< 0.001*
Year x Site	6,8067	4	1,7017	10,396	< 0.001*
Year x Season	0,7224	3	0,2408	1,471	0.229
Site x Season	8,0034	12	0,6669	4,075	< 0.001*
Year x Site x Season	3,7011	12	0,3084	1,884	0.049*
Error	12,2765	75	0,1637		

Patterns of taxon richness were less variable between years. Sites that differed between years were Lister's Point and Catalina Bay, which decreased and increased respectively. In 2011, taxon richness was generally highest at Charter's Creek and the Mouth compared to other sites (Figure 2.4). In 2012, taxon richness was higher at the Mouth than at all other sites. Esengeni possessed the lowest taxon richness for 2011 and Lister's Point for 2012. Seasonally, the highest taxon richness was observed in spring and the lowest in summer (Figure 2.4).

Taxon richness showed significant differences for the main effects of site and season ($p < 0.001$), with a significant interaction between year, site and season, as determined by ANOVA (Table 2.4). The three-way interaction suggests that the interaction between year

and site varied across seasons. Seasonal variation between years was observed at all sites during autumn, winter or spring. At Lister's Point and Esengeni, richness varied significantly between winter 2011 and 2012. Charter's Creek experienced differences in richness between years in autumn and spring, while Catalina Bay experienced significant differences in richness between years during autumn, winter and spring. Richness at the Mouth varied between years during autumn and winter.

2.4.3 Meiofaunal taxa

A total of 63 taxa were identified at various taxonomic levels (Table 2.5). The SIMPER analysis identified the important groups for distinguishing sites. In both 2011 and 2012, communities at all sites exhibited high dissimilarity to one another (60 - 92%). In 2011, Catalina Bay was the most similar to all other sites and Charter's Creek and Esengeni showed more dissimilarity between each other than any other sites. In 2012, the degree of dissimilarity increased (61 – 80 % in 2011 to 60 – 91 % in 2012) with slight similarity only evident between the southern lake sites, Charter's Creek and Catalina Bay. The important taxa at Lister's Point in 2011 were nematodes, harpacticoid copepods (*Cletocamptus confluens*) and soft walled foraminiferans (Allogromidae). In 2012, the important taxa were ostracods, hard walled foraminiferans (*Ammonia* spp.) and bivalve larvae. During 2011, nematodes, harpacticoid copepods (*Nitocra taylori* and Ectinosomatidae) and naupliar larvae were the important discriminatory taxa at Charter's Creek, while Catalina Bay was characterised by nematodes. In 2012, these two southern lake sites were both distinguished by nematodes and gastropod larvae, which were either lower in abundance or not found at other sites. Nematodes were the pivotal group at Esengeni throughout, whereas the communities of the Mouth were mainly influenced by nematodes and turbellarians (Macrostomida and Proseriata). Euryhaline taxa, such as particular nematodes and harpacticoid copepods, were found at all sites. The communities from 2012 tended to

converge and showed greater distinction of sites when compared to 2011 (Figure 2.5). This increase in similarity within sites is primarily caused by the greater similarity in the relative abundance of dominant taxa between seasons within each site in 2012 (Table 2.5), e.g. gastropod larvae, ostracods and nematodes (SIMPER).

Table 2.5: Mean density (ind.10 cm⁻²) of identified meiofauna taxa in the St Lucia estuarine lake system between 2011(a) and 2012 (b) for summer (Su), autumn (A), winter (W) and spring (Sp). * indicates where taxonomic identification were tentative. Unid.: unidentified (specimens could not be identified taxonomically e.g. if damaged or unknown).

Major groups and taxa		Lister's Point				Charter's Creek				Catalina Bay				Esengeni				Mouth			
a) 2011		Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp
1. Foraminifera																					
Calcareous forams																					
Miliolidae	Ammonia group	-	2	27	-	7	2	13	49	-	1	-	2	-	7	-	-	-	-	-	-
Bolivinitidae	Bolivina spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Monothalamous forams																					
Allogromiidae		98	83	16	1	-	5	6	6	-	-	-	-	213	1	-	3	1	3	1	-
Saccamminidae		-	-	2	-	-	-	2	2	-	-	-	1	-	-	-	-	-	8	-	-
2. Ciliophora																					
Tracheliidae		101	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	-
Frontonidae*		-	331	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Ciliate C		-	196	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Unid. Ciliates	Unid. ciliates	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platyhelminthes																					
3. Turbellaria																					
Macrostomida	Macrostomida A	-	-	-	-	-	-	10	5	-	-	4	17	-	-	-	-	-	16	61	67
	Macrostomida E	1	-	-	-	-	19	4	2	-	-	-	5	-	-	-	-	-	12	29	
Proseriata sp.	Proseriata	-	-	-	-	-	-	2	1	-	-	-	17	-	-	-	-	-	4	51	22
Rhabdocoela	Rhabdocoela	-	-	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-	-	5	2
Unid.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Turbellarians	Turbellarian type D	-	-	-	-	-	3	1	1	-	-	-	-	-	-	-	-	-	6	-	-
Unid.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Turbellarians	Turbellarian type H	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	3	1	
Unid.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Turbellarians	Unid. Turbellarians	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	15	6	2
4. Nemertea																					
Nemertea	Nemertea	-	-	-	-	-	-	1	-	-	-	2	4	-	-	-	-	-	4	4	4
5. Nematoda																					
Unid. Nematodes	Unid. Nematodes	124	720	8	5	91	174	115	123	84	47	133	480	252	20	59	17	84	135	38	80
6. Kinorhyncha																					
Echinoderidae	<i>Echinoderes maxwelli</i>	-	-	-	-	-	3	11	46	-	-	-	1	-	-	-	-	-	-	-	2
7. Rotifera																					
Lecanidae	Lecane cf. grandis	3	-	-	-	-	-	-	-	111	-	-	-	-	-	-	-	5	-	-	-
Annelida																					
8. Oligochaeta																					
Naididae*	Naididae sp. 1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
	Naididae sp. 2	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-
	Naididae sp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Lumbriculidae	Lumbriculidae sp.	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Aelosomatidae	Aelosomatidae sp.	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	1	-	2	2
Unid. Larvae	Oligochaete larvae	-	-	-	-	-	-	-	-	12	-	-	-	-	-	-	-	5	-	62	19
Unid.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oligochaetes	Unid. Oligochaetes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
9. Polychaeta																					
Capitellidae	<i>Capitella capitata</i>	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	2	-	-
	Mediomastus spp.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
	Unid. Capitellids	-	-	-	-	-	4	1	3	-	-	-	1	-	-	-	-	-	-	-	-
Nereidae	Nereidae spp.	-	-	-	-	-	-	2	2	-	-	-	-	-	-	-	-	-	5	1	-
Protodrilidae*	Protodrilidae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sabellidae	<i>Desdomona ornata</i>	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-

Table 2.5 cont.

		Lister's Point				Charter's Creek				Catalina Bay				Esengeni				Mouth			
		Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp
Spionidae	Polydora group	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Prionospio spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
	Unid. Spionids.	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1
	Polychaete postlarvae	-	-	-	-	7	4	-	2	-	-	-	-	-	-	-	-	5	-	-	-
Arthropoda																					
Crustacea																					
10. Amphipoda	Amphipods	-	-	-	-	5	-	2	-	-	-	-	-	-	-	-	-	2	8	11	1
11. Cumacea																					
Pseudocumatidae	Pseudocumatids	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	2	-
12. Copepoda																					
Harpacticoida	<i>Cletocampus confluens</i>	26	36	-	2	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	5
	Ectinosomatidae sp 1	-	-	-	-	-	-	12	2	-	-	-	-	-	-	-	-	-	-	4	-
	Ectinosomatidae sp 2	42	-	11	-	120	-	7	14	27	-	-	-	-	-	-	-	-	-	154	-
	<i>Nitocra taylori</i>	5	-	-	1	-	-	17	12	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Mesochra cf. wolskii</i>	-	-	-	-	38	-	21	-	-	-	-	-	-	-	-	-	-	-	32	-
	Copepodites	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
	Unid. harpacticoids	201	1	8	11	138	21	37	14	135	2	2	1	-	1	4	-	2	11	87	13
Cyclopoida	Cyclopoids	-	-	-	-	-	3	-	2	-	-	-	-	5	-	-	-	-	1	-	-
	<i>Pseudodiaptomus stuhlmanni</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5
Calanoida	Unid. Calanoids	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	3	6	-
13. Ostracoda		1	-	-	1	-	49	-	62	-	-	-	86	-	-	4	5	-	11	25	2
14. Tanaidacea																					
Apseudidae	<i>Apseudes digitalis</i>	-	-	-	-	-	-	1	-	-	-	-	-	1	1	10	6	-	-	-	-
Unid. Tanaid	Tanaid sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
15. Naupliar larvae		157	6	-	-	99	57	14	20	12	-	1	7	-	-	-	-	-	3	19	5
Hexapoda																					
16. Diptera																					
Ceratopogonidae	Ceratopogonid larvae	-	-	-	-	55	-	-	-	-	-	5	-	-	-	-	-	-	12	2	1
Chironomidae	Chironomid larvae	-	5	4	-	4	1	-	1	71	-	-	-	-	-	-	-	1	-	1	-
Unid. Diptera	Unid. Dipteran larvae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
17. Chelicerata																					
Acaridae	<i>Tyrophagus putrescentiae</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Uropodidae	Urobovella sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Halacaridae	Copidognathus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Mites	Unid. mites	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Mollusca																					
18. Bivalvia	Bivalve postlarvae	-	-	-	2	-	-	4	8	-	-	-	-	1	-	-	-	4	3	5	15
19. Gastropoda																					
Assiminidae	Assiminia spp.	-	-	-	-	-	2	-	10	-	-	-	-	-	-	-	-	-	-	-	-
	Gastropod larvae	-	-	-	-	-	62	8	113	-	-	-	99	-	-	-	-	1	33	-	-
Other		-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	2	-	2	-
Total meiofauna		759	1388	76	23	566	421	299	518	451	50	149	735	472	31	80	32	125	282	608	280

Table 2.5 cont.

Major groups and taxa		Lister's Point				Charter's Creek				Catalina Bay				Esengeni				Mouth			
b) 2012		Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp
1. Foraminifera																					
Calcareous forams																					
Miliolidae	Ammonia group	1	1	5	3	-	1	3	-	22	6	2	-	-	-	-	-	-	-	-	-
Bolivinitidae	Bolivina spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Monothalamous forams																					
Allogromiidae		-	3	-	36	1	-	4	-	1	5	-	1	2	-	-	-	-	-	-	5
Saccamminidae		-	-	-	-	-	-	-	-	-	-	-	1	5	-	-	-	31	-	-	1
2. Ciliophora																					
Tracheliidae		-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-
Frontonidae*		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ciliate C		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Ciliates	Unid. ciliates	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platyhelminthes																					
3. Turbellaria																					
Macrostomida	Macrostomida A	-	-	-	-	-	-	5	11	5	14	11	3	-	-	-	-	2	15	4	7
	Macrostomida E	-	-	-	-	1	3	2	2	-	7	11	15	-	5	-	-	7	10	-	50
Proseriata sp.	Proseriata	-	-	-	-	1	-	5	1	-	-	23	-	-	-	-	-	14	16	8	5
Rhabdocoela sp.	Rhabdocoela	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	2
Unid. Turbellarian type D		-	-	-	-	-	-	6	2	1	-	-	-	-	-	-	-	1	3	-	4
Turbellarians Unid. Turbellarian type H		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Turbellarians	Unid. Turbellarians	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4. Nemertea																					
Nemertea	Nemertea	-	-	-	8	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	3
5. Nematoda																					
Unid. Nematodes	Unid. Nematodes	-	2	-	4	86	46	81	38	97	1149	939	111	103	32	14	2	34	62	21	84
6. Kinorhyncha																					
Echinoderidae	<i>Echinoderes maxwelli</i>	-	-	-	-	10	10	18	13	-	-	1	2	-	-	-	-	-	-	-	-
7. Rotifera																					
Lecanidae	Lecane cf. grandis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Annelida																					
8. Oligochaeta																					
Naididae*	Naididae sp. 1	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	1
	Naididae sp. 2	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
	Naididae sp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lumbriculidae	Lumbriculidae sp.	-	-	-	-	-	-	-	-	-	1	-	5	-	-	-	-	-	-	-	-
Aeolosomatidae	Aeolosomatidae sp.	-	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	3	-
Unid. Larvae	Oligochaete larvae	-	-	-	-	-	1	-	1	-	7	-	3	-	-	-	-	-	-	-	-
Unid. Oligochaetes	Unid. Oligochaetes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
9. Polychaeta																					
Capitellidae	<i>Capitella capitata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Mediomastus spp.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Unid. Capitellids	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nereidae	Nereidae spp.	-	-	-	-	-	-	-	-	3	2	1	4	-	-	-	-	-	-	-	-
Protodrilidae*	Protodrilidae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Sabellidae	<i>Desdomona ornata</i>	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-

Table 2.5 cont.

		Lister's Point				Charter's Creek				Catalina Bay				Esengeni				Mouth			
		Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp
Spionidae	Polydora group	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Prionospio spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. postlarvae	Unid. Spionids.	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
	Polychaete postlarvae	-	-	-	-	-	-	-	2	-	1	-	5	-	-	-	1	-	-	-	4
Arthropoda																					
Crustacea																					
10. Amphipoda	Amphipods	-	-	-	-	-	4	1	2	3	-	-	-	-	-	-	1	-	-	-	-
11. Cumacea																					
Pseudocumatidae	Pseudocumatids	-	-	-	-	-	-	3	2	-	-	-	-	-	-	-	-	-	-	1	-
12. Copepoda																					
Harpacticoida	<i>Cletocampus confluens</i>	-	-	-	-	-	-	6	-	-	-	-	1	2	-	-	5	-	-	-	4
	Ectinosomatidae sp 1	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	12	14	1	5
	Ectinosomatidae sp 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Nitocra taylori</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Mesochra cf. wolskii</i>	-	-	-	-	-	-	-	2	-	-	-	3	-	-	-	1	-	-	3	32
	Copepodites	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. harpacticoids	Unid. harpacticoids	2	5	-	-	-	20	4	-	2	2	2	6	3	3	-	4	-	8	2	40
	Cyclopoids	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2
Cyclopoida	<i>Pseudodiaptomus stuhlmanni</i>	-	-	-	-	-	-	-	4	2	-	-	2	-	-	-	-	1	-	2	3
Calanoida	Unid. Calanoids	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13. Ostracoda		16	188	6	74	-	4	10	7	-	44	388	42	-	1	11	3	-	4	-	2
14. Tanaidacea																					
Apseudidae	<i>Apseudes digitalis</i>	-	-	-	-	1	1	-	-	-	-	-	1	5	1	7	15	-	-	-	-
	Unid. Tanaid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15. Naupliar larvae		-	-	-	-	-	2	3	3	-	-	41	4	-	1	-	-	-	-	4	76
Hexapoda																					
16. Diptera																					
Ceratopogonidae	Ceratopogonid larvae	-	-	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	4	-	-
	Chironomid larvae	-	-	-	-	-	-	-	-	-	4	-	21	-	-	1	-	-	-	-	2
Unid. Diptera	Unid. Dipteran larvae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17. Chelicerata																					
Acaridae	<i>Tyrophagus putrescentiae</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
	Uropodidae	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
Halacaridae	Copidognathus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Unid. Mites	Unid. mites	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mollusca																					
18. Bivalvia	Bivalve postlarvae	-	25	-	-	-	1	3	-	131	1	3	2	-	-	-	1	6	6	1	5
19. Gastropoda																					
Assiminidae	Assiminia spp.	-	-	-	3	1	-	-	-	17	-	-	-	-	-	-	-	-	-	1	-
	Gastropod larvae	-	-	-	22	115	84	82	66	409	-	4	100	-	-	-	-	-	-	-	-
Other		-	-	-	-	-	-	3	-	1	-	1	4	-	-	-	2	-	1	-	-
Total meiofauna		19	225	12	155	216	178	242	157	699	1259	1432	342	122	44	33	39	108	144	54	344

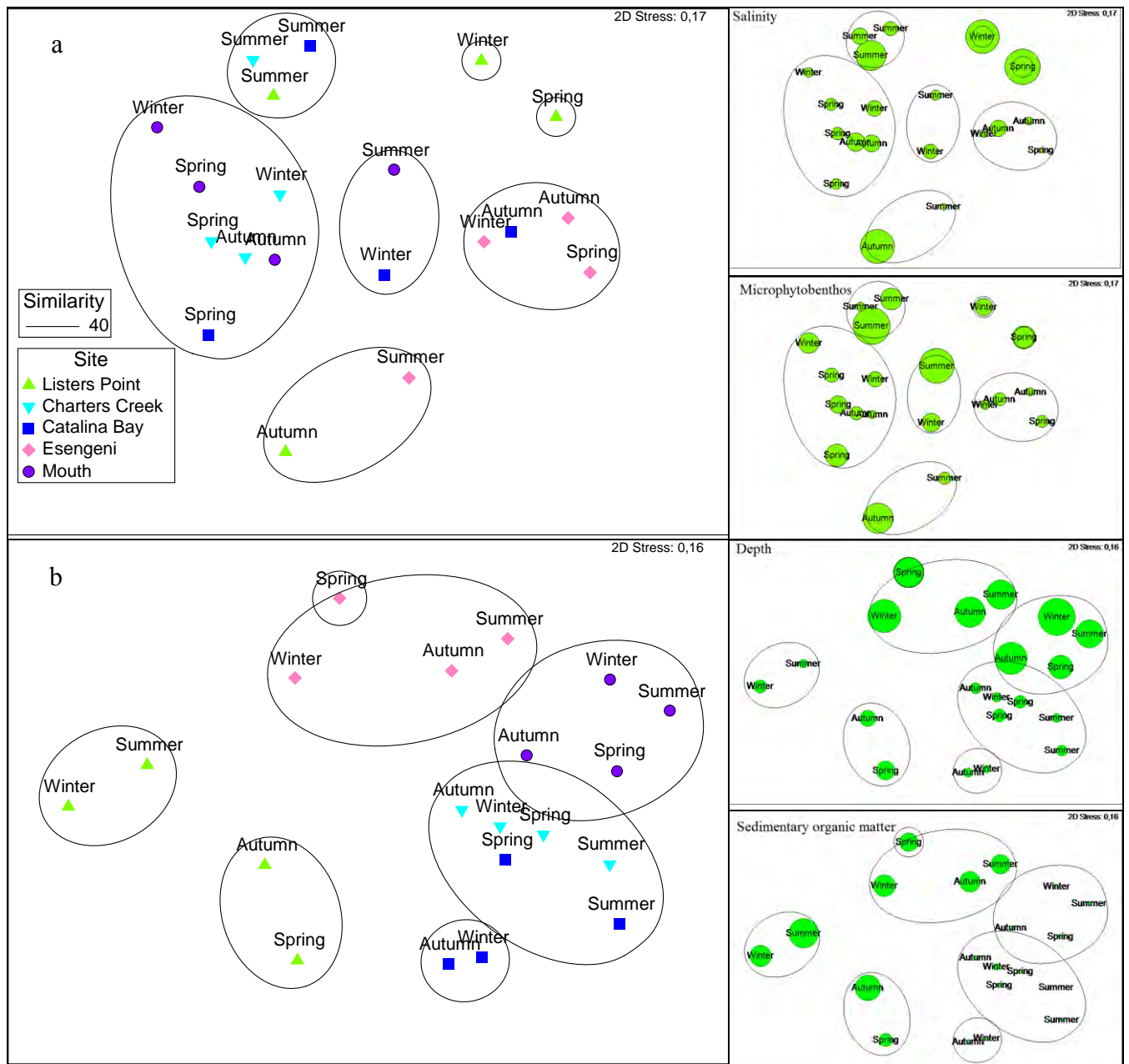


Figure 2.5: Non-metric multidimensional scaling (MDS) ordination of meiofauna communities in 2011 (a) and 2012 (b) and primary environmental variables (right) based on BIOENV, showing the distribution and grouping of samples in summer, autumn, winter and spring at each site (left). Results from the cluster analysis are superimposed to show groups defined at 40 % similarity.

2.4.4 Community structure

Two-way ANOSIM of the effects of site and season on meiofauna community structure within each year showed that both factors had a significant effect. In both 2011 and 2012, a highly significant difference was observed between sites ($R = 0.789$, $p = 0.001$; $R = 0.769$, $p = 0.001$, respectively) and between seasons ($R = 0.767$, $p = 0.001$; $R = 0.543$, $p = 0.001$, respectively) (Table 2.6). Pairwise comparisons revealed that communities at each site were distinct and differed significantly from each other (Table 2.6). Similarly, the communities of each season were all significantly different from each other.

Table 2.6: Results of multivariate analysis of similarity (ANOSIM) on community structure and composition of meiofauna in the St Lucia Estuary, examining the effects of site and season (2-way ANOSIM). The ANOSIM test statistic (R) significance level of 5% corresponds to $\alpha = 0.05$, Clarke & Warwick 2001).

Two-way ANOSIM (site and season)				
	2011		2012	
Site	<i>R</i>	Sig. (%)	<i>R</i>	Sig. (%)
Global test	0.789	0.1	0.769	0.1
Pairwise tests				
Listers Point, Charters Creek	0.75	0.1	0.743	0.1
Listers Point, Catalina Bay	0.843	0.1	0.691	0.1
Listers Point, Esengeni	0.703	0.1	0.704	0.1
Listers Point, Mouth	0.852	0.1	0.807	0.1
Charters Creek, Catalina Bay	0.926	0.1	0.907	0.1
Charters Creek, Esengeni	0.861	0.1	0.917	0.1
Charters Creek, Mouth	0.981	0.2	0.935	0.1
Catalina Bay, Esengeni	0.537	0.1	0.944	0.1
Catalina Bay, Mouth	0.917	0.3	0.972	0.1
Esengeni, Mouth	0.722	0.1	0.843	0.1
Season				
Global test	0.767	0.1	0.543	0.1
Pairwise tests				
Summer, Autumn	0.919	0.1	0.345	1.2
Summer, Winter	0.978	0.1	0.646	0.2
Summer, Spring	0.756	0.1	0.674	0.1
Autumn, Winter	0.763	0.1	0.563	0.1
Autumn, Spring	0.704	0.1	0.615	0.1
Winter, Spring	0.652	0.1	0.593	0.1

There were slight differences observed in 2011 between sites for each season (Figure 2.5a), with the Mouth and Charter's Creek generally being most similar to each other (autumn, winter and spring), and the lake sites (Lister's Point, Charter's Creek and Catalina Bay) being similar to each other during summer. Apart from this, there was no distinct separation between seasons. In 2012 (Figure 2.5b), there was distinct separation of communities by site, with season not influencing the clusters significantly. For 2011 and 2012, environmental variables correlated with spatial variability in meiofaunal communities (BIOENV, $R = 0.903$, $p = 0.01$ and $R = 0.897$, $p = 0.01$, respectively). Salinity, turbidity, MPB, SOM and rainfall were most important in collectively explaining the variability in 2011. Based on overlays of environmental variables, salinity and MPB were found to best explain the communities of 2011 (Figure 2.5a). Communities at Charter's Creek, Catalina Bay and the Mouth which experienced intermediate salinities were more closely clustered, while communities that experienced salinity extremes during summer and at Lister's Point and Esengeni were grouped amongst each other. Similar trends were observed with MPB. Temperature, depth, SOM and grain size were most important in collectively explaining the variability in 2012. Environmental variable overlays found depth and SOM to be important in separating the communities of 2012 (Figure 2.5b). Meiofaunal communities at the deeper sites (Esengeni and the Mouth) were separate from those of the shallower sites (Lister's Point, Charter's Creek and Catalina Bay). Communities at Lister's Point and Esengeni experienced higher SOM than Charter's Creek, Catalina Bay and the Mouth which experienced vastly lower SOM in comparison. The results of the BIOENV procedure were generally consistent with that of the PCA ordination.

2.5 Discussion

The wet phase that began in 2011, when salinity was drastically reduced following above average rainfall, led to a substantial alteration of the physical environment and the meiofauna communities of the system. The varying degrees of meiofaunal community changes between sites along the estuary are an indication of the inverse estuarine gradient and associated environmental variables, with site-specific community structure and composition creating spatial distinctions. Further differences between site specific communities may be attributed to seasonal effects.

Low salinities were noted in all sites (below 20 in the lower reaches), except Lister's Point, where levels remained hypersaline (40-97), regardless of the higher amount of rainfall experienced in the weeks leading up to each sampling occasion (with the exception of autumn and winter 2012) (Figure 2.2b). This is possibly due to the significant amount of salt that had been bound up in the sediments of the lake-bed, causing salinity to remain high despite the increase in freshwater inflow (Taylor 2011), with this inflow also being balanced by evaporative loss. Different ecological salinity states (as per Venice system (1958)), were dominant in different parts of the system during this study. An oligohaline state occurred predominantly at Esengeni where nematodes dominated, and was also the only site where *Apseudes digitalis* was found. The presence of this mud-dwelling tanaid was also observed in Eastern Cape estuaries of South Africa during similar states (Teske & Wooldridge 2004). Catalina Bay was hyposaline for the majority of the study and was characterised by nematodes, gastropod larvae and ostracods. Charter's Creek and the Mouth were predominantly low hyposaline and were characterised by nematodes, gastropod larvae, turbellarians, and copepods. Lister's Point varied between hyperhaline and extreme hypersaline states. During these states the site was characterised by ciliates, ostracods,

nematodes, foraminiferans, naupliar larvae, bivalve larvae and copepods (*Cletocamptus confluens*). It is important to note the presence of a vital core group of euryhaline organisms, mainly certain nematodes and harpacticoid copepods (Gilles & Pequeux 2014), in the varying salinity states experienced during the two years of this study, with at least one taxon being numerically significant at each site. Certain taxa possessed high salinity tolerances, namely gastropods (up to 40), chironomid larvae and mites (up to 60), *Cletocamptus confluens* (above 60) and ostracods (above 95), while others, such as kinorhynchs and turbellarians, required more favourable conditions before becoming successful. Four of the five important taxa in this study (nematodes, foraminiferans, ostracods and copepods) are also key taxonomic groups for predicting global climate change (Zeppilli et al. 2015).

Equally important environmental factors in the structuring of meiofauna communities are sediment characteristics, namely grain size and organic matter. Generally, meiofauna burrow in sediment with MPS of $> 125 \mu\text{m}$, as finer sediments have very small interstitial spaces that are not conducive for meiofauna to inhabit (Coull 1999). As a result, sediment characteristics have the ability to determine what organisms are likely to be present at a site (Fenchel 1978), and may therefore be a contributing factor to the differences in community structure and composition between sites. MPS had strong positive correlations with taxonomic richness during both years, suggesting that larger grain sizes are associated with higher levels of taxonomic richness. Similar findings were observed by Fonseca et al. (2010). Taxa such as turbellarians, nemerteans, kinorhynchs, oligochaetes and gastropods were more prevalent at sites with larger grain size. SOM was found to be negatively correlated with meiofaunal density and taxonomic richness, suggesting that high SOM reduces density and taxon richness. Gambi et al. (2003) also found that high levels of organic matter had a negative influence on meiofauna assemblages. In sediments of optimum grain size for meiofauna, SOM may limit the available space for meiofauna to inhabit or smother these

organisms, while decaying organic matter may lead to hypoxic conditions (Gray et al. 2002). According to Dell'Anno et al. (2002), large amounts of SOM are typically low in nutritional value and are therefore not an optimal food source for meiofauna. The negative correlation between SOM and MPS is indicative of larger grain sizes having a smaller surface area for organic adsorption (Alves et al. 2009, Parsons et al. 2013).

An additional environmental factor of great importance during this study is microphytobenthos. Estuarine microphytobenthos is usually dominated by benthic diatoms (Sanilkumar et al. 2009), which meiofauna are known to feed on (Daudi et al. 2013). The positive correlation between microphytobenthos (MPB) and meiofaunal density observed in 2012 suggests that a decrease in MPB biomass will have a negative impact on meiofauna due to reduced food availability. Organisms that were found to fluctuate with MPB include nemertean, ostracods and tanaids.

Meiofaunal density and taxonomic richness were found to be significantly different between sites and seasons in both years. The general trend for estuaries is for meiofaunal density and richness to increase towards the mouth, as a result of the salinity gradient ranging from freshwater at the head to marine at the mouth (Alves et al. 2009). At St Lucia however, where a reverse salinity gradient prevailed during the study, the highest density and richness were observed at Lister's Point and Catalina Bay in 2011 and 2012, respectively. These sites also had the shallowest depths. During summer 2012, Lister's Point exhibited extremely high temperature, with a peak in salinity and a drop in dissolved oxygen which resulted in very low meiofaunal density and taxonomic richness. Lister's Point appeared to be the most vulnerable site, as any change in environmental conditions had deleterious effects on meiofaunal density and richness. Esengeni remained in a near freshwater state throughout the drought and wet phase. This may be a potential factor accounting for the continuously

reduced density and richness observed at this site (Alves et al. 2009, Bownes & Perissinotto 2012).

Average densities found in this study were lower than those observed following a sea-induced breaching event during the previous drought, which exhibited an overall average of 457 ind. 10 cm^{-2} (Bownes & Perissinotto 2012). In other estuaries that have received freshwater inflow, such as the Upper Rincon Bayou in Texas, USA, meiofauna densities averaged 1200 ind. cm^{-2} (Montagna et al. 2002). Southern European estuaries such as the Mira and Mondego in Portugal, have meiofaunal densities of 583 and 441 ind. 10 cm^{-2} , respectively (Alves et al. 2009). Thus, compared to other estuaries around the globe, the densities recorded at St Lucia during the wet phase are relatively low. Although no marine meiofauna were identified during this study, van Elden et al. (2014) recorded the occurrence of marine zooplankton that were previously absent from the system since the late 1970s. This suggests that recruitment into St Lucia from both the sea and the Mfolozi River via the beach spillway is possible and may be observed in the meiofauna communities beyond 2012. Of the various possibilities that may account for low meiofaunal densities there are three that are most applicable to this system. Firstly, meiofauna density decreases may be the result of vertical migration as a response mechanism to unfavourable conditions (Steyaert et al. 2001). Secondly, increased water levels that reconnected the various compartments of St Lucia may have allowed for the migration of juvenile fish through the system, thereby increasing the predation pressure on meiofauna. Lastly and most importantly for this study, flooding had washed away surface sediment and resident biota (Grilo et al. 2011). Although these explanations may seem to be more applicable to sudden perturbations, the drastic changes that the physical environment had been subjected to ensured that these organisms would be predisposed to instability as the system adjusted. Salinity throughout the study was consistently low (< 20), in the greater part of the system in 2012 and the consistently low

density observed at this time may be a consequence of this. Furthermore, low densities may be indicative of the drastic change from the dry phase and the relatively short wet phase studied, and a potential lag time for meiofaunal community response (Palmer et al. 2002).

Since the initial changes in environmental variables in 2011, meiofaunal communities have shown no distinction based on site or season between the major parts of the system, with Lister's Point and the Mouth being the only sites that exhibited some level of similarity. Season played a more significant role in the clustering of communities during summer, winter and spring. As suggested by Storey and Williams (2004), physico-chemical parameters may have a greater impact during seasons when they shift towards their extremes. The area of sampling at each site also plays a pivotal role in the determination of variables such as temperature and depth. For all sites, except Esengeni, sampling was conducted at the water's edge, where it is shallow and water temperature may be warmer. Nonetheless, seasonal trends for temperature were consistent in both 2011 and 2012. During the second year of the wet phase, meiofauna communities showed a higher degree of stability as suggested by the clustering based on site. Although there was slight variation within sites, between seasons, meiofaunal communities within each site were generally similar throughout the year. This convergence may indicate the increased stability of the meiofauna community due to an established wet phase community being present as well as the formation of microhabitats within the system. Convergence of benthic communities have been observed following a dredging disturbance (Bolam et al. 2006), and in a drought phase (Stubbington et al. 2015), where communities within each site became more similar over time and eventually resembled undisturbed/unaffected sites. In this case, communities resemble each other over time as an indication of increased stability rather than suggesting that they represent the same community.

The drastic salinity change in 2011 was the primary indicator of a wet phase following the increased amount of rainfall. The most likely connection between climate variability and the changing nature of benthic communities is caused by a strong association between global climate signals, precipitation and local salinity patterns (Pollack et al. 2011). Although salinity was not correlated with univariate indices, such as meiofauna density or taxonomic richness, it was highly influential in defining the wet phase and its communities. As proposed by Pillay and Perissinotto (2009), the lack of correlation between indices and salinity could be a result of the extremely variable nature of the physical environment, and the meiofaunal assemblages. This is mainly due to the large area of Lake St Lucia, which has wide variation in salinity between the upper, middle and lower reaches. Additionally, identifications at higher taxonomic levels does not allow for changes in species specific abundance to be seen, thereby ignoring the potential correlations of these species with environmental variables (Nozais et al. 2005). Reduced salinity, which was especially drastic in the northern regions of the system (as observed at Lister's Point between summer and autumn 2012), would have caused an elimination of species that were hypersaline or stenohaline, thus selecting for organisms capable of survival at lower salinities.

It is anticipated that global mean temperatures will rise over the next century, with future increases in greenhouse gases potentially increasing the intensity of global precipitation. If the frequency of stochastic events, such as El Niño/La Niña periods, increase, the incidence and severity of droughts and floods are also likely to increase (Timmermann et al. 1999). With these climatic extremes and alternations between cyclical wet and dry phases, estuaries are subject to vast changes in environmental parameters. All biota will be influenced by the onset of such extremes; it is important to have an understanding of their responses and community dynamics. It is evident that an increasingly unstable climate will contest the resilience and resistance of ecosystems and may have potentially detrimental effects on these

environments and their biological communities (Pollack et al. 2011). The interconnected nature of estuaries and pelagic zones suggests that this environmental variability is not likely to be isolated to any particular area or species (Richmond et al. 2007).

In conclusion, this study found that the meiofauna communities differed between sites and seasons, suggesting that the wet phase and its resulting environmental parameters have played a role in the structuring of the meiofauna communities found in this study. The fundamental differences between sites can be explained by the variation in factors such as salinity, grain size, organic matter and depth. Given the significant role of estuaries and the St Lucia Estuary in particular, continuous monitoring of these benthic communities is imperative. These communities are understudied, yet are able to provide insight on the health of a system. The results of this investigation have provided important information regarding the influence of wet phase conditions on estuarine meiofauna and the underlying driving factors. Since this area is of great national and global significance, forming part of South Africa's first World Heritage Site, the iSimangaliso Wetland Park, it is imperative that the characteristic biota of the St Lucia system be understood and well documented. This knowledge will allow for management strategies to be implemented towards the sustainability and rehabilitation of this system.

CHAPTER 3: RESPONSE OF MEIOFAUNA TO A FLOOD DISTURBANCE IN THE ST LUCIA ESTUARY, ISIMANGALISO WETLAND PARK

3.1 Abstract

Disturbances are pivotal in the restructuring of biological communities, as they have the ability to initiate successional processes. Lake St Lucia is the largest estuarine lake in Africa and a crucial component of the iSimangaliso Wetland Park, South Africa's first World Heritage Site. Following a decade long drought (ending in 2010) characterised by low lake levels, hypersalinity and reduced biodiversity, the St Lucia system experienced a flood event that drastically reduced salinity levels and increased water depths, submerging previously dry areas. Due to the rapid regeneration time of meiofauna, these organisms were used to assess the effect of the flood event on benthic communities and succession in the estuary following this disturbance. Meiofauna samples were collected prior to and after the disturbance, from three representative sites along the estuary that exhibited various salinity ranges. Meiofaunal communities prior to the disturbance revealed no significant differences over time; however significant spatial and temporal differences in meiofaunal communities were present following the disturbance event. A distinct pattern of succession was evident throughout the system and each site displayed its own species composition changes over time that inferred site specific succession was also evident. The multiple peaks and declines in density over time are likely indicative of an intermediate frequency of disturbances (each displacing and eradicating organisms) that are at play and shape estuarine communities over time. Although the meiofauna of the St Lucia Estuary are in constant flux, they appear to maintain some level of resilience to flood disturbances.

3.2 Introduction

Disturbances are important structuring drivers of ecological systems and the communities therein (Cristoni et al. 2004). Such events cause interruptions both indirectly and directly, by altering environmental conditions and resource abundance, and through eradication or displacement of organisms (Snyder & Johnson 2006), thereby creating new areas available for colonisation, initiating a successional process (Ritter et al. 2005).

Succession can be defined as the apparent directional change in the species composition of a community over time (Trueblood et al. 1994). Margalef (1968) explained succession to be *“the occupation of an area by organisms involved in an incessant process of action and reaction which in time results in changes in both the environment and the community, both undergoing continuous reciprocal influence and adjustment”*. Succession is ideally characterised by an increase in abundance, diversity, and biomass; this occurs as the community shifts into different states (see Rosenberg et al. 2002), and reaches a climax community (Widdicombe & Austen 2005, Thompson & Lake 2010). Additionally, successional communities shift from opportunistic, *r*-selected species with rapidly growing populations to rarer, slower-growing *K*-selected species (Zajac & Whitlatch 1982a, Widdicombe & Austen 2005). However, succession isn't necessarily directional, therefore the replacement of species may not follow in a specific sequence (Platt & Connell 2003) that is characteristic of any successional pattern. Non-directional replacement is likely to be observed in areas of non-catastrophic disturbance, where residents are not completely removed after disturbance (Platt & Connell 2003). Other key aspects that relate to succession are that of resistance (ability to resist change caused by disturbance) and resilience (ability to rapidly recover after disturbance) (Grimm 1994). For example, environmental patchiness has the ability to affect community structure in a manner that can reduce or strengthen the

community's resistance and to modify the rate and pattern of recovery after a disturbance (Peterson & Stevenson 1992).

The St Lucia Estuary (northern KwaZulu-Natal, South Africa), Africa's largest estuarine lake is a Ramsar Wetland of International Importance and forms a crucial part of a UNESCO World Heritage Site, the iSimangaliso Wetland Park. This system characteristically experiences cyclical wet and dry phases that may last up to a decade (Begg 1978). However, droughts in recent years have been more severe as a result of a range of anthropogenic activities that have taken place in the system's catchment (Lawrie & Stretch 2011). During the most recent drought (2001 – 2010), the system became hypersaline and developed a persistent reverse salinity gradient with levels in the northern reaches exceeding 200 at times in 2010. An intense flood event (250 - 350 mm of rain over a few days) that occurred at the beginning of 2011 in the St Lucia region substantially decreased salinity levels and increased water depths throughout the lake system. This flood event signalled the onset of a new wet phase and provided a unique opportunity to determine the effects of this climatic shift on the meiofaunal communities.

Drastic changes in salinity are a source of disturbance in estuaries, as they have the potential to cause decreases in species abundance, richness and overall diversity (Montagna et al. 2002, Harkantra & Rodrigues 2003, Ritter et al. 2005). When measuring disturbance effects over a short time period, meiofauna are useful models for succession studies as they have a relatively short generation time (Danovaro 2000). Meiofauna are also key constituents within aquatic sediments, as they play vital roles with regards to trophic interactions, bacterial metabolism and bioturbation (Bonaglia et al. 2014).

This study aims to compare the meiofaunal communities of the St Lucia estuarine lake during the drought and start of the flood phase and to determine the short to medium term

successional patterns of the meiofauna in this estuary. This was done by following the changes in meiofaunal community structure and composition during the final stages of the drought, and after the flood disturbance at two week or monthly intervals. This was extended over a longer time period during 2011, in the attempt to follow successional/community patterns in the medium term. It is hypothesised firstly, that there would be differences in meiofaunal community structure and composition between sites and climatic phase (drought and flood phase) and secondly that there would be differences in meiofauna community structure and composition at each site over time following the flood disturbance.

3.3 Methods

Sampling was conducted on the following dates prior to the disturbance: 07 October 2010, 20 October 2010, 02 November 2010, 23 November 2010 and 13 December 2010, and on the following dates after the disturbance: 24 January 2011, 08 February 2011, 20 February 2011 and 07 May 2011, where possible. Three representative sites were chosen. Each site exhibits varying sensitivity to environmental change: Lister's Point, which experiences extreme salinity changes; Charter's Creek, which exhibits considerable changes in salinity; and the Mouth, which maintains a fairly stable and minor change in salinity (Figure 3.1).

3.3.1 Environmental characteristics

A YSI 6600 multi-probe was used to measure physico-chemical variables such as salinity, temperature ($^{\circ}\text{C}$), turbidity (NTU), dissolved oxygen (mg l^{-1}), pH and depth (m). On occasions where the YSI was unavailable, salinity, temperature and depth were measured individually with the use of a refractometer, a mercury thermometer and a ruler, respectively.

3.3.2 Field sampling and laboratory processing

For the sampling of microphytobenthos (MPB), three replicates of the first 1 cm of sediment were collected at each site using a Perspex, twin corer (internal diameter: 2 cm). Cores were

added to 30 ml 90% acetone and were incubated for 48 to 72 hours for the extraction of chl a. Chl a concentrations for MPB were measured fluorometrically with a Turner Designs 10-AU fluorometer. Sedimentary organic matter (SOM) samples were made up from 2 cores of the upper 1 cm of sediment. These were dried, weighted, combusted and reweighed to determine the organic matter content.

Triplicate meiofauna samples were collected at Lister's Point, Charter's Creek and the Mouth, whereby the upper 1 cm of sediment was extracted using a perspex twin-corer (internal diameter: 2 cm). Samples were fixed and stained with 10 % formalin and Phloxin-B, respectively. In the laboratory, the meiofauna fraction was separated from the sample by washing it through a 500 µm and 63 µm mesh sieve. Centrifugation with Ludox HS-40 was conducted following the procedure of Bownes and Perissinotto (2012) for the extraction of meiofauna. Extraction efficiency was ensured with sediment checks from each sample. Samples were sorted under a dissecting microscope (x 40) and all meiofaunal taxa were identified to the lowest possible taxonomic classification.

3.3.3 Statistical analysis

Primer 6 & Permanova + software were used to conduct all multivariate analyses to investigate the relationships between environmental variables and temporal distribution of meiofauna. Mean temperature, salinity, depth, turbidity and microphytobenthic biomass were used in the analysis due to missing data from other variables.

3.3.3.1 Environmental changes and diversity responses

Principal Components Analysis (PCA) was utilized on normalised data as an unconstrained method of ordination to visualise multivariate patterns in environmental data (Clarke & Warwick 2001). This was then superimposed with abundance and taxon richness, obtained using the DIVERSE function, to visualise any superficial linkage between environmental data

and abundance and taxon richness. Statistica 12 was used to conduct two-way analysis of variance (ANOVA) to compare differences in abundance and taxon richness between sites and climatic phases (drought and flood). This was done using averages of 3 replicates and using each date as a replicate within each climatic phase due to uneven sampling intervals and inconsistency between sites. Tukey post-hoc comparisons were used to examine significant results. SIMPER analysis was used to distinguish the important taxa that contributed to temporal changes in community structure.

3.3.3.2 Succession

A permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was used to test for differences over time between sites. Analyses were based on 999 permutation of residuals under a reduced model (Anderson 2001). A canonical analysis of principal coordinates (CAP) (Anderson & Willis 2003) was utilised as a constrained arrangement to visualise and highlight any meiofaunal patterns over time. Significantly correlated taxa (> 0.4) from Pearson correlation were superimposed on the CAP ordination to highlight any taxa that were responsible for temporal separation. The PERMANOVA and CAP analyses were performed using Bray-Curtis similarity matrixes based on square-root transformations, to weight the contribution of common and rare species in the multivariate representation (Clarke & Warwick 2001). MDS was also used to display harpacticoid copepod communities during the flood phase as a visualisation of successional changes within primary coloniser communities.

3.4 Results

3.4.1 Environmental changes and diversity responses

Based on the physico-chemical data, it is apparent that during the course of the study the state of the system had shifted from a hypersaline state to a diluted state. High rainfall in January

2011 (Figure 3.1a) resulted in a drastic reduction in salinity throughout the lake system (Figure 3.1b). This reduction was most significant in the northern reaches of the lakes. Lister's Point exhibited the highest salinities during the drought phase. Although salinities were lower during the flood, Lister's Point remained hypersaline with salinities similar to those experienced at Charter's Creek during the drought.

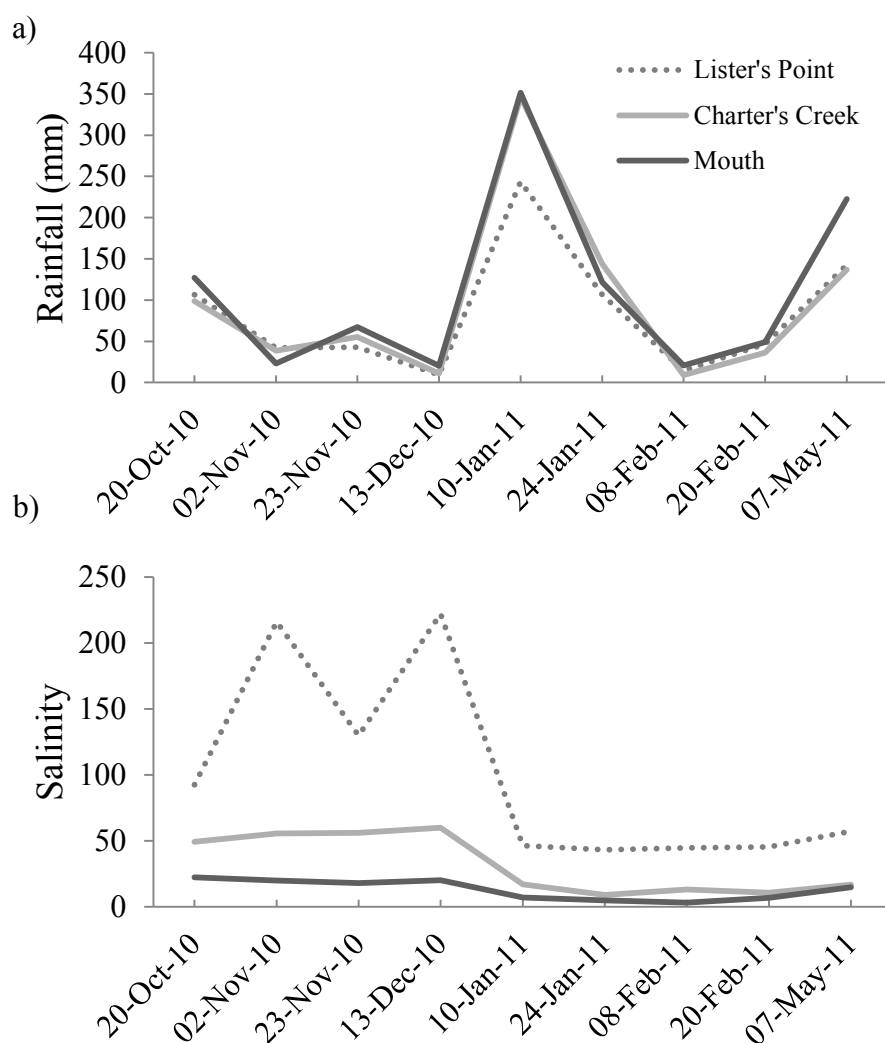


Figure 3.1: Rainfall (a) and salinity (b) measured in the St Lucia region at two week intervals for the three sites sampled (Lister's Point, Charter's Creek, Mouth) from October 2010 to May 2011.

Sedimentary organic matter (SOM) was greatest at Lister's Point during the drought (9.63 %, Table 3.1), and was generally lower at all sites during the flood phase. Lister's Point and Charter's Creek both exhibited high turbidity (25 – 591 and 26 – 951 NTU, respectively),

regardless of phase. As seen in table 3.1, MPB biomass was highest at Lister's Point (18 – 222 mg.m⁻²) regardless of phase, with Charter's Creek and the Mouth showing intermediate levels (19 – 76 mg.m⁻²) during the drought. MPB was lower at Charter's Creek and the Mouth during the flood (5 – 54 mg.m⁻²).

Table 3.1: Environmental parameters measured at the St Lucia Estuary from the three representative sites from the end of the drought and beginning of the flood phase. Values in bold are averages from data sampled around that time. * denotes missing data. Arrows denote the onset of the flood phase.

Site	Date	Temperature (°C)	Turbidity (NTU)	Depth (m)	SOM (%)	MPB (mg m ⁻²)
Lister's Point	20-Oct-10	34.76	55.7	0.1	*	220.38
	02-Nov-10	26.6	590.8	0.04	9.63	182.17
	13-Dec-10	32.38	243.85	0.06	9.12	56.78
	24-Jan-11	24.96	25	0.43	2.01	109.72
	08-Feb-11	31.28	25.6	0.45	7.00	81.20
	20-Feb-11	30.27	67.7	0.45	1.75	18.46
	↓ 07-May-11	22.77	234.1	0.33	9.28	79.01
	07-Oct-10	21.83	125.9	0.14	*	46.59
	20-Oct-10	31.17	25.9	0.11	*	66.27
	02-Nov-10	27.44	951	0.05	*	45.99
Charter's Creek	23-Nov-10	28	315.3	0.06	2.46	42.07
	13-Dec-10	30.3	170.8	0.12	2.31	19.36
	24-Jan-11	26.62	84.6	0.2	0.42	5.59
	08-Feb-11	32.25	101.8	0.2	0.76	5.34
	20-Feb-11	31.57	42.5	0.15	1.19	5.42
	↓ 07-May-11	25.29	106	0.15	0.68	11.72
	02-Nov-10	24.31	12.7	0.6	*	9.97
	23-Nov-10	26.5	21.1	0.92	0.46	75.86
	14-Dec-10	26.5	10.6	0.945	0.59	75.86
	24-Jan-11	26.81	31.7	0.05	0.05	11.72
Mouth	08-Feb-11	28.7	24	0.35	0.33	54.18
	20-Feb-11	26.62	10	1.02	0.04	19.32
	↓ 07-May-11	22.8	8.81	0.78	0.26	7.23

According to Principal Component Analysis (PCA), the first two principal components (PCs) accounted for 66.3% of the total variance of the abiotic data among the 23 samples, and grouped samples along spatial and temporal group divisions (Figure 3.2a). The only exceptions were the drought samples from the Mouth that grouped with the flood samples.

These patterns were interpreted as follows. Firstly, PC1 (Eigenvalue = 2.26) was a measure of differences in salinity and depth and samples that loaded high on PC1 (e.g. drought communities of Lister's Point and Charter's Creek) had higher salinities and shallower depths than samples that loaded low on PC1 (e.g. flood communities from the Mouth). Secondly, PC2 (Eigenvalue = 1.06) was a measure of differences in temperature, and samples that loaded high on PC2 had warmer temperatures (e.g. Lister's Point – 20 October 2010) than samples that loaded low on PC2.

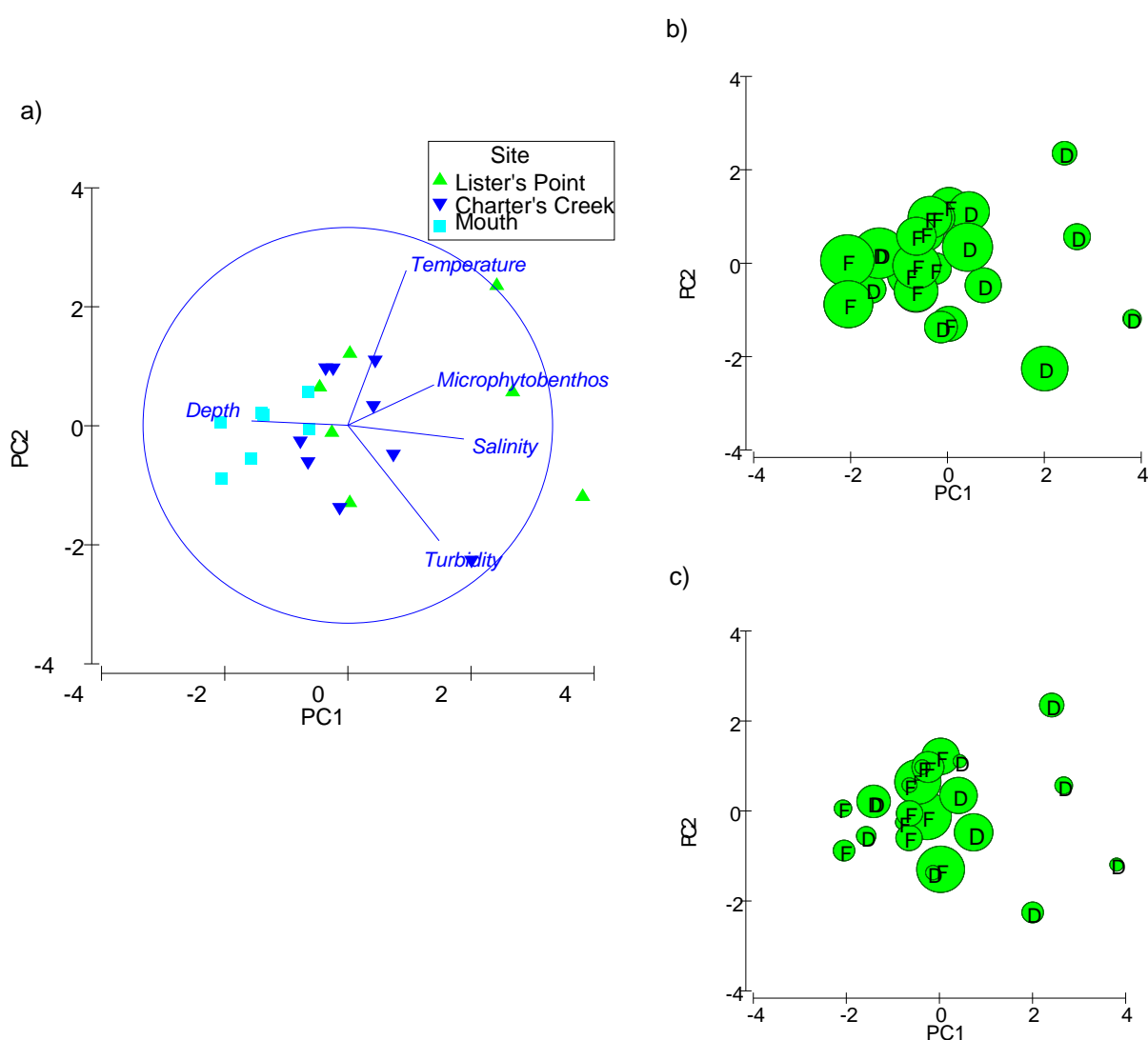


Figure 3.2: Principal Components Analysis (PCA) plots of environmental characteristics in 3 sites of the St Lucia estuarine lake: (a) over time; (b) with mean taxon richness; and (c) with mean abundance superimposed for each climatic state (where: D = drought and F = flood).

Significant differences were observed in taxon richness for the main effects of site and season (ANOVA, Table 3.2). Richness at Lister's Point was significantly lower (8 ± 3) than the other two sites (ANOVA, $p = 0.003$). Taxon richness was significantly lower at Lister's Point during the drought (5 ± 2) compared to the flood. Charter's Creek had similar richness during both drought (14 ± 5) and flood (15 ± 2), and the Mouth had generally higher taxon richness during the flood (19 ± 5) than the drought (16 ± 10). Superficial representations of these differences in richness can be seen in Figure 3.2b. There was a statistically significant interaction between the effects of site and state on abundance, ($F_{2,17} = 12.32$, $p < 0.001$, Table 3.2). Sites had significant differences, with Lister's Point having higher abundances than the other two sites (804 ± 580 ind. 10 cm^{-2}) (ANOVA, $p = 0.045$). Lister's Point also experienced greater numbers during the flood (1242 ± 259 ind. 10 cm^{-2}), Charter's Creek varied in abundance regardless of phase (454 ± 389 and 331 ± 233 ind. 10 cm^{-2}), while the Mouth experienced higher abundances during the drought (576 ± 148 ind. 10 cm^{-2}). Superficial differences in abundance are depicted in Figure 3.2c. Post-hoc comparisons between site and state for meiofaunal abundance suggest that climatic phase only significantly influenced abundance at the Mouth during the drought and at Lister's Point during the flood, with a significant difference observed at Lister's Point between states (Table 3.3).

Table 3.2: Two-way factorial ANOVA results between site and phase for abundance (N) and taxon richness (S). Significant differences are indicated with an asterisk (*).

	Source	df	SS	F	P
N	Intercept	1	5435358	80.348	< 0.001
	Site	2	602317	4.452	0.028*
	Phase	1	298080	4.406	0.051
	Site x phase	2	1667118	12.322	< 0.001*
	Error	17	1150018		
S	Intercept	1	3740.817	187.39	< 0.001
	Site	2	268.523	6.726	0.007*
	Phase	1	108.322	5.426	0.032*
	Site x phase	2	63.206	1.082	0.361
	Error	17	339.367		

Table 3.3: Tukey post-hoc test results for the interaction effect between site and phase on abundance where * denotes subsets in which a particular group falls under; common asterisks within a subset indicate homogenous groupings.

Site	Phase	1	2
Lister's Point	Drought	*	
Mouth	Flood	*	
Charter's Creek	Flood	*	
Charter's Creek	Drought	*	
Mouth	Drought	*	*
Lister's Point	Flood		*

3.4.2 Community composition

As seen in Figure 3.3, nematodes dominated at Lister's Point while all other organisms at this site had minor contributions in abundance prior to the disturbance. Charter's Creek was dominated by foraminiferans and nematodes during the drought period. Species composition varied widely at the Mouth and no specific trends were observed between phases. After the disturbance, ciliates, soft-walled foraminiferans and copepods became more prevalent at Lister's Point, while the dominance of nematodes was greatly reduced. Larvae (crustaceans, dipterans, gastropods and bivalves) contributed largely to the post-flood communities at Charter's Creek, and the greatest dominance of copepods was recorded 2 and 4 weeks after the disturbance (24/01/2010 and 08/02/2011, respectively) (Figure 3.3). Turbellarians and oligochaetes also contributed largely to the communities of the Mouth.

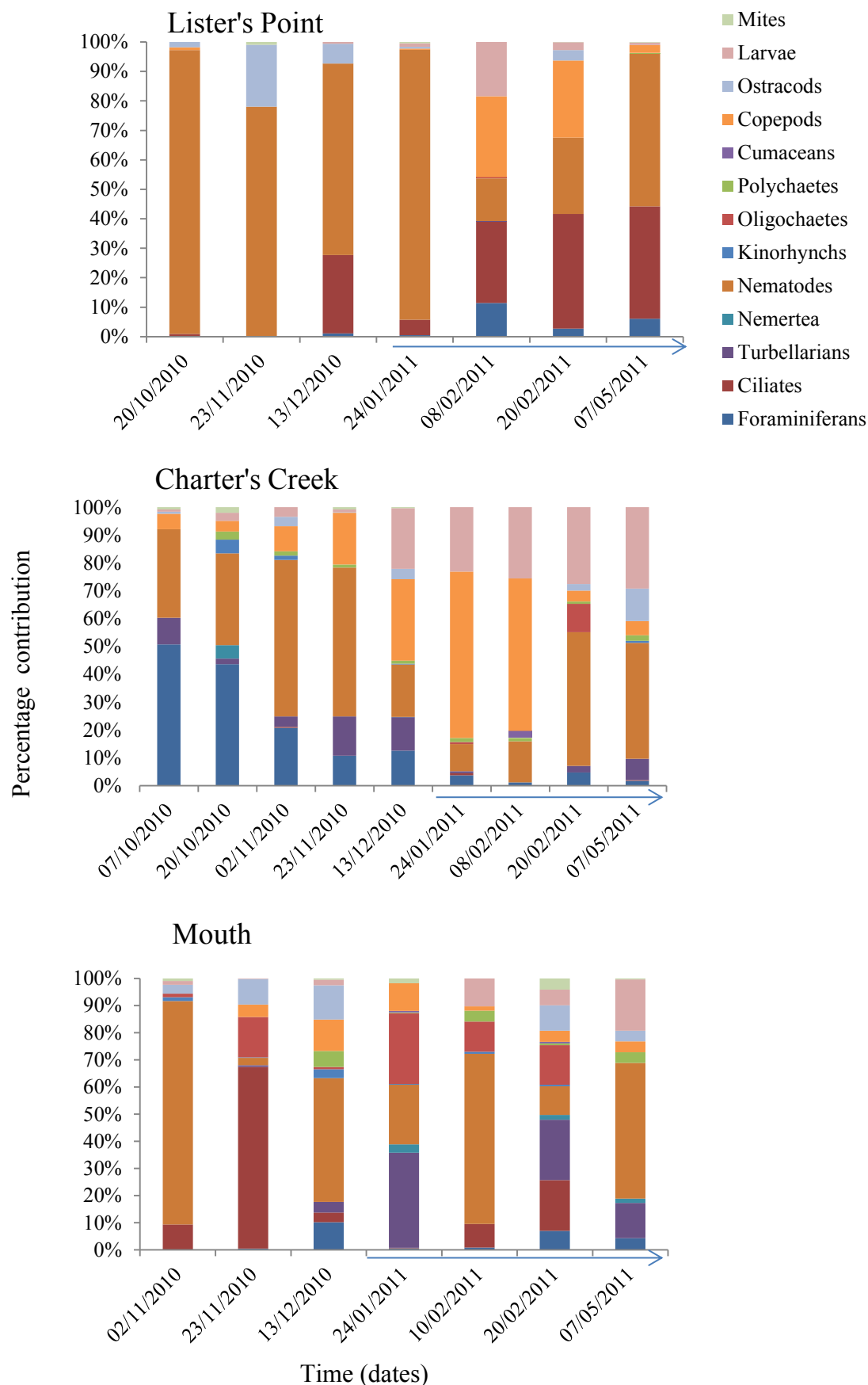


Figure 3.3: Percentage contribution of major taxa at Lister's Point, Charter's Creek and the Mouth, leading up to and following the flood disturbance. Arrows indicate the flood phase.

The important organisms highlighted in the SIMPER analysis were plotted separately over time (Figure 3.4). Nematode abundance at Charter's Creek and the Mouth were relatively low for the major part of the study, with Charter's Creek showing higher abundances during the drought. Copepods only entered the system in November at Charter's Creek then the Mouth but were absent from drought communities of Lister's Point. Ostracod abundances peaked in December (3 weeks prior to the disturbance) throughout the system. Foraminiferans were prevalent during the drought at Charter's Creek and the Mouth. Ciliates were most important in structuring the communities of Lister's Point and Charter's Creek. These two sites exhibited opposing trends, as ciliate abundance increased at the former while decreasing at the latter station from the end of November onwards.

3.4.3 Successional patterns

Meiofauna communities were affected by changes over time at all three sites. The composition of assemblages between site and over time were significantly different ($F = 14.019$; $df = 2$; $p = 0.01$, and $F = 5.389$; $df = 8$; $p = 0.001$; PERMANOVA, Table 3.4).

Table 3.4: Results of permutational multivariate analysis of variance (PERMANOVA) on meiofauna in the St Lucia Estuary, examining the relationship between temporal distribution and site.

Source	df	SS	MS	F	P
Site	2	28705	14352	16.251	0.001
Time	3	15299	5099.7	5.7741	0.001
Site x time	6	25278	4212.9	4.7701	0.001
Residual	24	21197	883.2		
Total	35	90478			

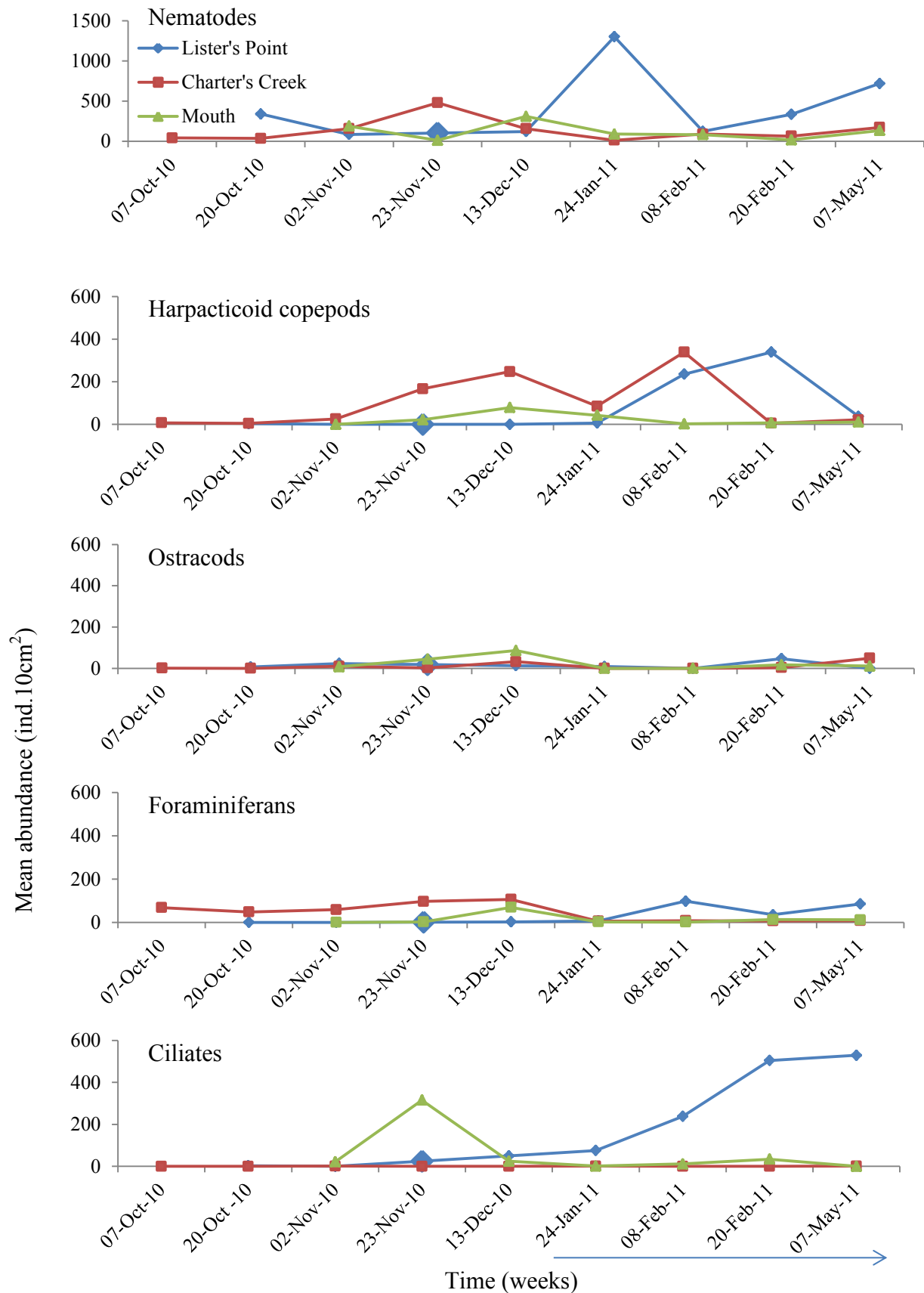


Figure 3.4: Temporal variations in mean abundance of the five most important taxa, as per SIMPER analysis, in the St Lucia Estuary (Lister's Point, Charter's Creek, Mouth) based on samples collected during the drought and flood. Arrow indicates the onset of the flood phase.

As seen in the species table (Table 3.5), at 2 weeks Allogromidae foraminiferans and naupliar larvae entered meiofauna communities at Lister's Point; these were previously not observed during the drought. Rotifers, oligochaetes, harpacticoid copepods and dipteran larvae were introduced at 4 weeks. Other species of harpacticoid copepods became part of the community at 6 weeks and polychaetes and *Ammonia* foraminiferans were the last settlers of this community at 20 weeks. Charter's Creek was occupied by soft-walled foraminiferans and oligochaetes at 2 weeks. Chironomid larvae and cumaceans entered after 4 weeks and cnidarian larvae, macrostomid turbellarians, Aelosomatidae and ostracods were found after 6 weeks. Kinorhynchs and Capitellid polychaetes joined these communities at 20 weeks. At the Mouth, nemerteans, rotifers, oligochaetes and cumaceans were present at 2 weeks. After 4 weeks amphipods, naupliar larvae, chironomid larvae, bivalve larvae and gastropod larvae had established themselves in the community. Rhabdocoel turbellarians, lumbriculid oligochaetes, ostracods, ceratopogonid larvae and *Tyrophagus putrescentiae* became present in the community at 6 weeks. Macrostomid turbellarians, Prionospio and Capitellid polychaetes were found in Mouth communities after 20 weeks. Despite the differences in settlement times between taxa at each site, the vital taxa that denoted the presence of succession were observed at all sites.

Meiofaunal community succession following the freshwater input into the St Lucia Estuary was illustrated with the use of CAP ordinations (Figure 3.5). Of the 35 potential principal coordinates, a choice of 12 best principal axes was obtained, correctly assigning 67 % of the samples and explaining 97 % of the total variance. Directional change was observed, as there was a propensity for samples to cluster together based on time. Distinct temporal distribution groupings can be seen after the disturbance. CAP 1 shows 3 distinct groupings. Communities at 6 weeks had the lowest loading, communities at 2 and 20 weeks had intermediate loadings and communities at 4 weeks had the highest loadings. CAP 2 also shows 3 groupings.

Communities at 2 weeks had the lowest loading, those at 4 and 6 weeks had intermediate loadings and communities at 20 weeks had the highest loadings. Pearson correlation distinguished 12 taxa that separated out primarily by sharing similarities in occurrence across all sites, and secondly by having a greater abundance than other taxa. Naididae occurrences were most similar between sites 2 weeks after the disturbance, while mites also contributed to these communities. Naupliar larvae, *Mesochra*, Ectinosomatidae sp. 2 and unidentified polychaetes, harpacticoids and oligochaetes, were found to occur 4 weeks after disturbance. These taxa were measures for CAP 1. Mites once again became influential after 6 week. The last communities observed were influenced by Macrostromida, Capitellidae, gastropod larvae and ostracods, which became prevalent 20 weeks after the disturbance. These taxa, along with Naididae and mites were measures of CAP 2.

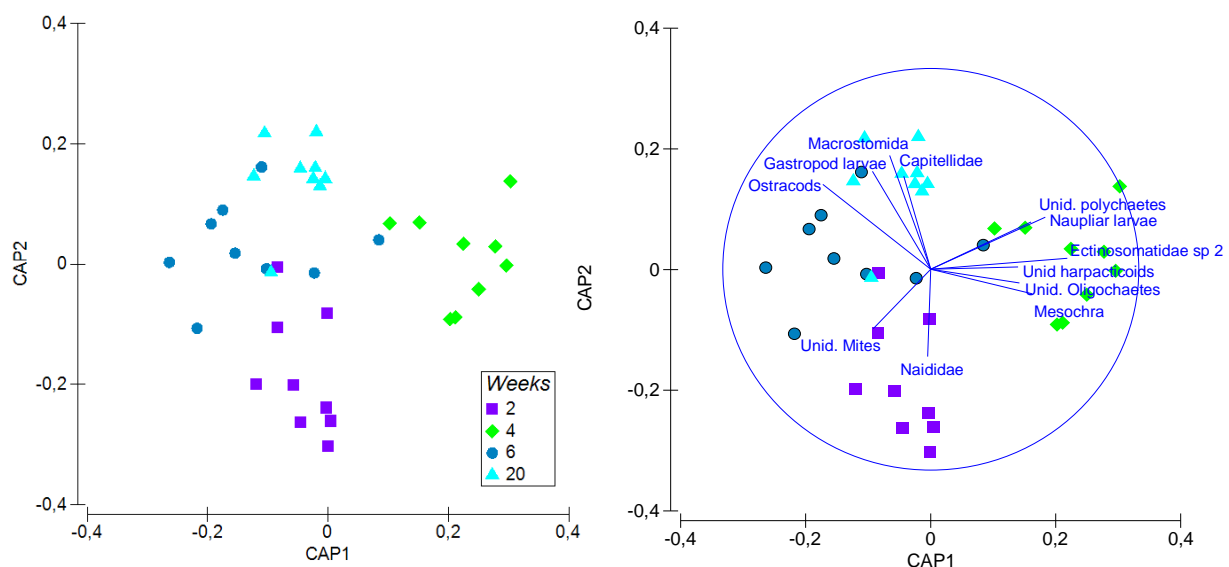


Figure 3.5: Canonical analysis of principal coordinates (CAP) ordinations for meiofauna communities over time (weeks), from all three sites, showing the distribution of samples following the disturbance. Based on Pearson correlation analysis, taxa deemed as important within these communities (> 0.4) are superimposed.

The ordination of similarities between copepod samples from all 4 sampling periods following the disturbance showed that there were clear differences over time (Figure 3.6). Copepod communities were distinctly different at all three sites, indicating that the relative

abundances of these primary colonisers did vary over time (Table 3.5). Lister's Point appears to have a lag in community response time, as copepods only become more diverse after 4 weeks; sharing similarities with the communities from 6 weeks. These communities appear to become "reset" after 20 weeks, with fewer species and lower abundance being recorded. Charter's Creek had a much more immediate response as copepods were already established here after 2 weeks and increased in abundance after 4 weeks. These communities were reset after 6 weeks, with low richness and abundance still evident after 20 weeks. At the Mouth, copepods were most diverse and abundant after 2 weeks, thereafter they became scarce, with a single species being found after 4 and 6 weeks, and another after 20 weeks. *Cletocamptus confluens* was important at Lister's Point, *Nitocra taylori* and *Mesochra cf. wolskii* were important at Charter's Creek, while Ectinosomatidae and *Mesochra cf. wolskii* were important at the Mouth. All communities differed over time, with the exception of those found at Lister's Point and the Mouth 4 and 6 weeks after disturbance.

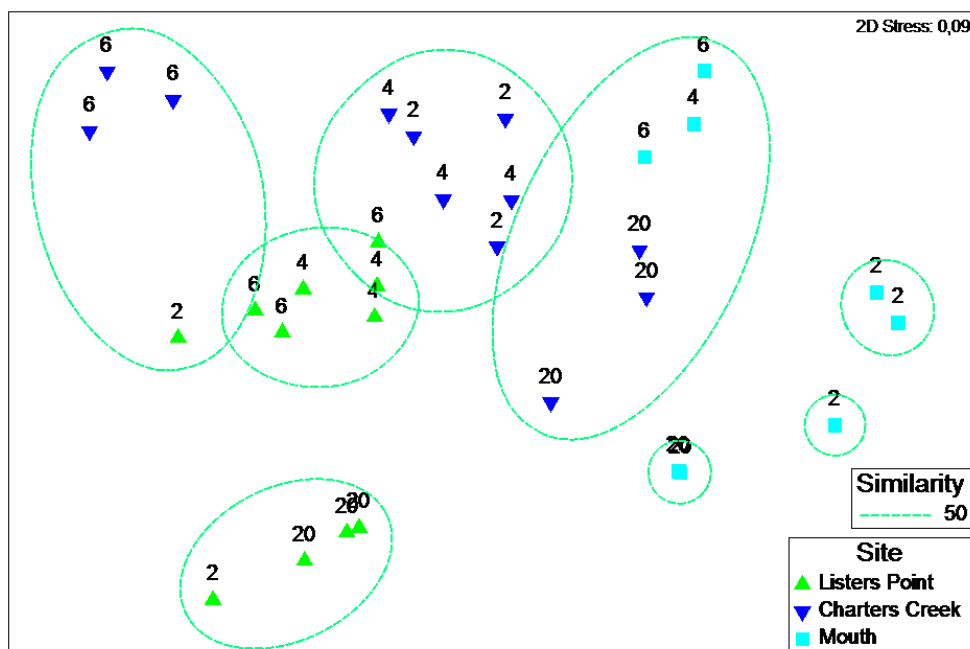


Figure 3.6: Non-metric multidimensional scaling (MDS) ordinations for copepod communities at all three sites, showing the distribution and grouping of samples from 2, 4, 6 and 20 weeks after the disturbance. Results from cluster analysis are superimposed to show groups defined at 50% similarity.

Table 3.5: Mean density (ind.10 cm⁻²) of identified meiofauna taxa in the St Lucia estuarine lake system between the drought and flood phase.

State		Drought - 2010							Flood - 2011							Drought - 2010							Flood - 2011									
		Lister's Point							Charter's Creek							Mouth																
		20/ 10	02/ 11	13/ 12	24/ 01	08/ 02	20/ 02	07/0 5	07/ 10	20/ 10	02/ 11	23/ 11	13/ 12	24/ 01	08/ 02	20/ 02	07/ 05	02/ 11	23/ 11	13/ 12	24/ 01	08/ 02	20/ 02	07/ 05								
Foraminiferans	Dates																															
	Ammonia group	-	-	2	-	-	-	2	33	34	47	2	75	-	7	1	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	
	Allogromiidae	-	-	-	6	98	35	83	35	14	12	94	31	1	-	5	5	-	2	66	1	1	12	3								
	Saccamminidae	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	2	1	-	1	8								
Ciliates		3	-	50	75	238	504	529	-	-	1	-	-	1	-	-	1	21	315	24	1	12	34	-								
Cnidarians		-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-								
Turbellarians	Macrostomida	-	-	-	-	1	-	-	7	1	2	-	29	-	-	2	19	-	-	-	-	-	-	16								
	Proseriata	-	-	-	-	-	-	-	-	1	7	-	15	-	-	-	-	-	-	1	16	-	1	4								
	Rhabdocoela Unid.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	14	-								
	Turbellarians	-	-	-	-	-	-	-	5	-	1	126	58	1	-	1	13	-	3	15	130	-	25	15								
Nemerteans		-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	13	-	3	4								
Nematodes		341	87	122	1301	124	335	720	42	36	158	480	159	14	91	65	174	132	13	310	91	84	19	135								
Kinorhynchs	<i>Echinoderes cf. maxwellii</i>	-	-	-	-	-	-	-	-	5	4	-	2	-	-	-	3	3	1	22	1	1	1	-								
	<i>Brachionus rotundiformis</i>	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-								
Rotifers	<i>Lecane cf. grandis</i>	-	-	-	-	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-								
	<i>Testudinella obscura</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-								
		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-								
Oligochaetes	Naididae	-	-	-	-	3	-	-	-	-	-	-	-	-	-	1	-	-	-	-	98	-	2	-								
	Lumbriculidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	16	-								
	Aelosomatidae Unid.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13	-	-	-	-	11	-	8	-								
	Oligochaetes	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	3	70	1	-	15	-	-								
Polychaetes	Capitellidae	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	4	-	-	5	-	-	-	4								
	Nereidae spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1	-	1	5								
	Unid. Sabellids	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21	-	-	-	-								
	Polydora group	-	-	-	-	-	-	3	-	1	-	-	2	2	-	-	-	-	-	-	-	-	-	-								
	Prionospio spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1								
	Unid. Spionids.	-	-	-	-	-	-	-	-	2	3	-	7	-	-	-	-	-	-	1	-	-	-	-								

Table 3.5 cont.

		Lister's Point							Charter's Creek							Mouth								
		20/ 10	02/ 11	13/ 12	24/ 01	08/ 02	20/ 02	07/ 05	07/ 10	20/ 10	02/ 11	23/ 11	13/ 12	24/ 01	08/0 2	20/ 02	07/ 05	02/ 11	23/ 11	13/ 12	24/ 01	08/ 02	20/ 02	07/ 05
Cumaceans	Unid. polychaetes	-	-	-	-	-	-	-	-	-	-	10	-	-	7	-	4	-	-	12	-	5	-	-
		-	-	-	-	-	-	-	-	-	-	-	-	-	16	-	-	-	-	2	-	1	-	
Harpacticoids	Ectinosomatidae sp 1	-	-	-	-	-	-	-	-	-	3	-	153	1	38	-	-	-	-	71	3	-	-	11
	Ectinosomatidae sp 2	-	-	-	-	45	6	-	-	-	-	18	-	71	-	-	-	-	-	-	-	-	-	
	Mesochra sp/p.	-	-	-	-	10	29	-	-	1	18	-	23	36	139	-	-	-	-	5	-	2	7	-
	<i>Nitocra taylori</i>	-	-	-	-	10	114	-	7	3	3	-	17	5	4	4	-	-	-	-	-	-	-	-
	Cylindropsyllidae sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	32	-	-	-	
	Cop 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	
	<i>Cletocamptus confluens</i>	3	-	-	5	52	105	36	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	
	Unid harpacticoids	-	-	-	1	120	85	1	-	-	-	167	36	42	86	1	21	-	21	2	-	-	-	-
Cyclopoids		-	-	2	1	-	-	-	-	-	-	-	1	2	-	-	3	-	-	-	-	-	-	1
Calanoids		-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2	-	2	3	
Ostracods		6	23	13	8	-	47	-	1	-	10	2	32	-	-	3	49	7	45	86	-	-	17	11
Nauiliar larvae		-	-	-	18	157	34	6	1	-	3	-	173	22	99	11	57	-	1	14	-	5	-	3
Dipteran larvae	Ceratopogonid larvae	-	-	-	-	-	-	-	-	-	-	-	-	-	55	-	-	-	-	-	-	5	12	
	Chironomid larvae	-	-	-	-	1	-	5	-	-	1	-	-	-	4	-	1	-	-	-	1	2	-	
	Unid. Dipteran larvae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	
Mites	<i>Tyrophagus putrescentiae</i>	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	
	<i>Uroobovella</i> sp.	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	
	<i>Copidognathis africanus</i>	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	
	Unid. Mites	-	1	-	5	-	1	1	-	-	-	6	-	-	-	-	-	2	-	3	7	-	6	1
Bivalve larvae		-	-	1	-	-	-	-	-	2	-	-	-	-	-	-	-	3	-	-	-	4	2	3
Gastropods	Assiminia spp.	-	-	-	-	-	-	-	-	1	5	8	11	8	-	1	2	-	-	-	-	1	-	-
	postlarvae	-	-	-	-	-	-	-	-	-	-	-	-	2	-	25	62	-	-	-	-	-	-	33
Total		361	111	190	1422	861	1297	1388	133	109	281	898	847	147	619	138	421	172	471	681	420	136	186	282

3.5 Discussion

The climatic phase shift, brought on by the intense rainfall event that occurred in January 2011 in the St Lucia catchments, caused major changes in meiofaunal communities, both temporally and spatially. The three sites sampled along the estuary exhibited successional changes following the disturbance. Species composition varied between sites during most sampling occasions, with significant differences in abundance between phases. Abundance generally increased during the flood phase in the upper reaches of the system and for specific taxa.

3.5.1 Phase comparisons

Lister's Point was generally characterised by nematodes, ciliates and the dominant harpacticoid copepod, *Cletocamptus confluens*, which became prevalent after the disturbance. This species is commonly found in brackish waters and can also endure hypersaline conditions (Mielke 2000). Charter's Creek communities were largely defined by nematodes and foraminiferans during the drought, and harpacticoid copepods, nematodes, naupliar larvae and gastropod larvae during the flood. The main groups observed at the Mouth were turbellarians, oligochaetes, nematodes and harpacticoid copepods (Figure 3.3). Meiofaunal communities showed significant spatial and temporal differences, with each site generally exhibiting dissimilarity with time for the 5 most important taxa, namely nematodes, harpacticoid copepods, foraminiferans, ciliates and ostracods (Figure 3.4). Charter's Creek and the Mouth appeared to share common responses in abundances over time, with Lister's Point occasionally having commonalities with Charter's Creek.

Lister's Point experienced the most extreme fluctuations in salinity. As a result, abundances of the few taxa recorded also fluctuated. Nematodes, ciliates and ostracods were the only abundant taxa, while a few mites and bivalves were also recorded. The three main taxa

showed alternating peaks and lows in abundance, reflecting the effect of extreme salinity fluctuations. The presence of ostracods at such extreme salinities is quite interesting, however these organisms have been observed in hypersaline conditions (De Deckker 1981). The longest monitoring time for drought communities was observed at Charter's Creek. At this site, foraminiferans, turbellarians, nematodes, kinorhynchs, polychaetes, harpacticoid copepods, ostracods, naupliar larvae, mites and gastropods were most abundant. Single observations of dipteran larvae and ciliates were also recorded. Abundance was also found to fluctuate with these more moderate changes in salinity. The most dominant taxa were the foraminiferans and nematodes. Hard-walled *Ammonia* sp. and soft-walled Allogromidae foraminiferans appeared to show opposing trends. The former increased from early October to early November, then decreased dramatically at the end of November and recovered in number in December, while the latter did the opposite. Foraminiferans belonging to the Allogromidae family are more successful in fresher water (Saraswat 2015), thus explaining their increases in times of lowered salinity. Nematodes decreased in October, increased in November and decreased in December. The Mouth possessed a wider variety of taxa and the general trend was for taxa to increase in abundance over time. According to Attrill (2002), salinity itself is not the main driver of organism distribution, but rather salinity fluctuations that add stress and inhibit organisms from capitalising on their distribution potential. For this reason, systems with great seasonal variability in flow (and salinity as a consequence) may alternate between salinity states and prevent communities from moving beyond early successional states (Teixeira et al. 2008).

3.5.2 Succession

Salinity was the primary driver of change as the increase in rainfall led to a climatic phase shift, lowering salinity throughout the system. Despite floods being part of a natural disturbance regime that these organisms may have adapted to, the observed patterns may also

be due to a host of physical and biological factors such as sedimentation or food resources. Substratum movement is a form of disturbance for benthic communities during floods (Snyder & Johnson 2006). The sudden change in sediment movement caused by the disturbance, and subsequent sedimentation, are likely to account for reduced MPB biomass (Duggan et al. 2014). It has been noted that meiofauna recruitment may be linked to food availability (Pasotti et al. 2014). MPB biomass levels were much lower in the flood phase, suggesting that food resources may have been limiting, possibly accounting for any higher abundances observed during the drought. The increase in turbidity at the Mouth following the disturbance may account for short term flood-induced mortality, however habitat alteration is relatively short lived and followed by rapid biological recovery (Resh et al. 1988).

No specific successional stages were observed in this study, however the progression of communities over time denoted the presence of succession. Although each site displayed its own characteristic successional pattern with different taxa becoming established at varying times, an overall supreme successional trend for the entire system was still evident (Figure 3.5). Following a disturbance, the primary meiofaunal succession community is usually characterised by nematodes and harpacticoid copepods, which are known to be early colonisers (Palmer 1988, da Fonse^{ca}-Genevois et al. 2006) and possess the character traits of opportunistic *r*-selected species (MacArthur 1962), namely rapid colonisation and reproduction as well as a high fecundity (Calabretta & Oviatt 2008). These groups were present throughout the study at all sites (Figure 3.3). Most meiofaunal taxa are characterised by direct development and lack a planktonic larval stage (Montagna et al. 2002). Harpacticoid copepods, however, do possess pelagic larval stages. Their dispersal is therefore facilitated by water movement (Gonçalves et al. 2010), allowing for these organisms to establish themselves in disturbed sediments. Boeckner et al. (2009) also observed passive meiofaunal dispersal via currents, sediment suspension and active dispersal into the water

column. Certain taxa may also have resting stages (Ricci & Balsamo 2000, Sabatino et al. 2000), which cater for rapid emergence once conditions become more favourable.

The successional harpacticoid communities showed spatial distinctions while temporal patterns were most interesting, exhibiting increases in taxonomic richness and abundance and dramatic decreases indicating small scale disturbances. Due to the wide host of factors that may affect succession, no specific climax community was observed during the present study. Meiofaunal colonisation patterns do not fit into the classical models of succession (Connell & Slatyer 1977), however there does appear to be an indication of species replacement. There is prompt establishment of opportunistic species and shifts between important taxa resulting in different succession endpoints. These end points are seen where a new organism becomes more important in structuring a community; several organisms were found to denote certain endpoints. Meiofauna are known to have great recovery potential (Lee et al. 2001). The post-flood increases in abundance are supported by a combination of resistance and resilience. All major taxonomic groups persisted throughout the duration of this study (possibly with use of micro refugia) and were able to recover (rapid reproduction) after dramatic decreases. These decreases in abundance may be indicative of the meiofauna community being in a constant state of disturbance, as a result of sediment resuspension and variations in salinity, as proposed by Ritter (1999). It is evident that population dynamics and the physical environment exert the greatest influence on successional processes (Zajac et al. 1998). Stochastic events related to climate extremes therefore hinder the predictability of these community responses (Kreyling et al. 2011).

The intermediate disturbance hypothesis suggests that the frequency and intensity of disturbances are key components in the establishment of community diversity (Widdicombe & Austen 2005). It is proposed that maximum species diversity is associated with an

intermediate level of disturbance, where competitive exclusion is lessened and co-existence of potentially competing species is increased (Connell 1978). This allows for the community to be maintained at non-equilibrium. A study conducted by Ritter et al. (2005) over an 8 week period, found that Rincon Bayou (Texas, U.S.A) was in a perpetual intermediate state of succession due to the ever-changing environmental characteristics of the system, with no specific climax community being reached and intermediate communities acting as successional end points. An important aspect to consider in the St Lucia estuarine lake (that separates it from the previously mentioned Rincon Bayou) is that the system had shifted from one climatic state to another; thereby creating a novel environment for colonisation. During this study period, the observed environmental fluctuations may have accounted for the lack of a specific climax community as proposed by Ritter et al. (2005), with equilibrium species not being able to establish themselves, particularly at Lister's Point. This theory of intermediate succession end points is supported by Zajac and Whitlatch (1982a), who state that end point communities that exhibit stability and resilience can still be heavily populated by opportunistic species in soft bottom habitats. Opportunistic species, such as nematodes and harpacticoid copepods, were prevalent in all communities found during this study. Copepods reach maturity rapidly, and have generation times of a few weeks. They are able to bear dozens of eggs in a clutch, while nematodes generally mature later, and produce fewer eggs per clutch (Giere 2008), possibly accounting for a delay in nematode abundance increases. These life history traits allow these opportunistic organisms to thrive. Although these communities experience an intermediate frequency of disturbance, the entire system is subjected to these intermediate disturbances uniformly. For this reason, the community will not be maintained at maximum diversity, as each disturbance may reset the diversity to some previous succession state and cause the recovery process to begin again (Widdicombe & Austen 2005). Meiofauna are sensitive to impacts over short temporal scales and small spatial

scales due to their direct benthic development and generation times that can be as brief as a month (Montagna et al. 2002). In this study, with sampling being conducted at two week intervals, changes may have occurred within these communities without being detected, thus hindering the analysis of succession. Due to the response differences observed in this system, it is important to be careful when relating general aquatic ecosystem principles and models (Milner et al. 2013).

If ecosystems are to thrive and maintain their functionality they need to possess the inherent capacity of adaptation and resilience. Resistance (stability) and resilience (recovery) from disturbances and disruptions of vital ecosystem functions are provided by biological diversity. The complex linkages between organisms often results in resistance. This may also be considered as functional redundancy (Folke et al. 2004), whereby multiple species hold similar capabilities, however it ensures optimal functioning by means of providing ecosystem stability. With regards to resilience, the diversity of functional groups in a dynamic, changing ecosystem, the diversity within populations and species, as well as the diversity of species within functional groups are all essential (Chapin et al. 1997, Luck et al. 2003).

In conclusion, it has been shown that meiofauna in the St Lucia Estuary exhibits some degree of resistance and resilience, as they have the ability to recover despite the prevailing conditions. During drought conditions these benthic organisms were generally lower in taxonomic richness and exposed to harsher conditions, including lower water levels. The current study revealed that there is some variability, with meiofauna becoming more diverse and abundant during the less saline period. The main reason for this change is that it is likely that salinity dropped to more tolerable levels during the less saline conditions. The canonical analysis also indicated a variation in the temporal positioning of different communities, where there are specific taxa accounting for successional changes. The analysis of meiofaunal communities also revealed that salinity changes from freshwater inflow is the driving factor

responsible for the successional changes of these communities in the system, either directly by influencing the meiofauna themselves, or indirectly by affecting the physical environment (e.g. water level increases, food resources, sedimentation). The hypotheses that there would be successional changes following the flood and community variation between the drought and flood phase are therefore supported. Overall, the success of these organisms and their subsequent resistance in the estuarine system can be attributed not only to their remarkable tolerance of salinity variations, but also in their ability to recover accordingly.

FINAL CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE WORK

As predicted by climate experts, global temperatures, and more specifically the temperatures experienced in the St Lucia region, are expected to rise by 2100, causing increased precipitation as a result (Vaeret & Sokolic 2008, Lumsden et al. 2009). Higher than average rainfall will result in an increased inflow of freshwater into the St Lucia system. It is also predicted that there will be an increase in the frequency of hydrologically extreme events, which will inevitably alter the St Lucia system. During extreme drought conditions Whitfield & Taylor (2009) and Cyrus et al. (2010) observed great alterations to the physical environments in St Lucia, with vast habitat loss due of low water levels.

Therefore, taxa which are able to adapt to these changing conditions, such as nematodes and harpacticoid copepods, are likely to succeed in the system and become dominant. Less environmentally tolerant taxa, such as polychaetes, kinorhynchs and turbellarians, rely on favourable environmental conditions to succeed and become dominant. When conditions become unfavourable, their distribution is limited to refuge areas in the Mouth region, where conditions are more stable. Meiofauna community responses to changing environmental conditions have been well documented (Santos et al. 1996, Ingole & Parulekar 1998, Montagna et al. 2002, Storey & Williams 2004, Nozais et al. 2005, Pillay & Perissinotto 2009). There have been no studies conducted on the meiofauna of South Africa that incorporate community dynamics during a wet phase. Understanding how these organisms respond to climatic phase shifts within the St Lucia Estuary is crucial to our understanding of South Africa's meiofaunal communities and the underlying driving mechanisms of their dynamics.

During the hypersaline drought period and a sea-induced breaching event, Pillay & Perissinotto (2009) and Bownes and Perissinotto (2012) documented the changes to

meiofauna communities in the St Lucia Estuary and assessed the effect of these conditions on meiofauna dynamics. During the drought period, meiofaunal communities in the St Lucia areas that were less severely impacted exhibited higher taxonomic richness and diversity, compared to areas that were highly impacted (Pillay & Perissinotto 2009). During a sea-induced breaching event (March-August 2007) that occurred in the middle of the drought period, the inflow of marine water into the system led to an increase in water levels. The density and diversity of meiofauna increased after the breach, thus indicating a partial and temporary recovery. However, conditions deteriorated once again as the drought continued (Bownes & Perissinotto 2012). After entering a wet phase, meiofauna communities of the St Lucia Estuary showed no initial distinctions in either spatial or temporal configuration; however abundance and richness did vary in both regards. Abundance was greater in the first year of the wet phase; this may be a reflection of a higher number of *r*-selected species that are able to proliferate under these conditions. After a year, site specific communities had been formed; suggesting a more established wet phase community being present where each site consisted of a characteristic taxonomic composition regardless of seasonal changes. In this time, the observed abundances were relatively low, therefore it is highly possible that the two year wet phase that was studied was not long enough for a true reflection of an established wet phase community to be presented in terms of abundance and diversity. Meiofauna communities were found to be most dependent on salinity, microphytobenthos chlorophyll-a biomass, depth and sedimentary organic matter. The hypothesis that there would be structural and compositional meiofaunal variation between sites and seasons was therefore supported, as well as showing that the wet phase communities show potential long-term improvement.

Following the isolated flood event that occurred in January 2011, causing the system to begin a successional process, meiofauna community structure and composition were drastically altered from that of the decade long drought phase. The concluding weeks of the drought

exhibited lower richness in the upper reaches of the system, in comparison to the Mouth. Drought communities consisted mainly of nematodes and harpacticoid copepods; these being the most tolerant taxa and were previously observed by Pillay and Perissinotto (2009). Each site exhibited its own characteristic community during this time; likely due to the extreme differences in salinity. While the flood communities showed a greater diversity and an increase in homogeneity, with taxon specific changes over time indicating a successional pattern. Meiofaunal communities persisted in an intermediate stage and no characteristic climax community was observed. This is indicative of continuous intermediate disturbances that reset these communities to some previous successional state. Salinity was identified as the most influential underlying driver of the successional pattern and resultant communities. The hypothesis that succession would take place following the flood disturbance was accepted. Additionally, changes were evident between the drought and flood communities, supporting this hypothesis.

According to both studies it is evident that from a spatial and temporal perspective, meiofauna communities are able to adapt to extreme and sudden environmental changes. Wet phase communities were shown to possess greater abundance in the first year and then become more established into site specific wet phase communities, facilitating changes in their composition according to the environment in which they inhabit. In contrast, communities after the disturbance were able to adjust in a shorter time period and other taxa had become established over the 20 week successional period. The success of meiofauna in the St Lucia system can therefore be attributed to their strong levels of resistance and resilience. Under extreme environmental conditions, such as hypersalinity, certain taxa have the added advantage of a wide tolerance of different environmental conditions, thus allowing them to proliferate in the St Lucia system. With the shift to a freshwater-dominated system,

meiofauna are predicted to flourish, as a result of environmental conditions becoming more favourable.

Recommendations for future research

The meiofauna community structure and composition was studied during the hypersaline/drought phase (Pillay & Perissinotto 2008) and under the influence of a sea-induced breaching event (Bownes & Perissinotto 2012). However, no work has been done on the intermediate phase between the drought and wet phase (2010). These samples need to be analysed so that a more comprehensive understanding of the various meiofauna communities can be gained. With respect to successional studies on the meiofauna of St Lucia, sampling should be conducted over a longer period of time while maintaining consistency in sampling intervals so that a more accurate picture of any successional trends can be identified.

This study has provided reference conditions and baseline data for the various regions of the St Lucia estuarine lake; describing the meiofaunal communities prior to a flood disturbance, following the disturbance with successional data and over a medium term wet phase. This information can ultimately be used to identify any future changes within these benthic communities and aid the description of changes that occur in the St Lucia estuarine lake system.

With the shift to a more freshwater state, the St Lucia community is more likely to be dominated by freshwater tolerant organisms. The recovery of these organisms to abundances that are similar to those observed in other estuaries will require a longer time frame. As previously discussed, the system is prone to great fluctuations in environmental variables; thereby acting as intermediate levels of ongoing disturbance. Over time stochastic events occur, with the ability to push these communities to a state of reduced abundance and diversity, further hindering the St Lucia meiofauna community from reaching such

abundances. It is therefore imperative that we gain as much information as possible to understand the community dynamics of these key benthic organisms. With ongoing environmental fluctuations, will the meiofauna of St Lucia be able to reach the abundances observed in other systems? If not, will the functionality of this vital component be limited in terms of benthic processes?

References

- Able KW (2005) A re-examination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. *Estuarine, Coastal and Shelf Science* 64:5-17
- Adão H, Alves AS, Patrício J, Neto JM, Costa MJ, Marques JC (2009) Spatial distribution of subtidal Nematoda communities along the salinity gradient in southern European estuaries. *acta oecologica* 35:287-300
- Alves AS, Adão H, Ferrero T, Marques J, Costa MJ, Patrício J (2013) Benthic meiofauna as indicator of ecological changes in estuarine ecosystems: The use of nematodes in ecological quality assessment. *Ecological Indicators* 24:462-475
- Alves AS, Adao H, Patrício J, Neto JM, Costa MJ, Marques JC (2009) Spatial distribution of subtidal meiobenthos along estuarine gradients in two southern European estuaries (Portugal). *Journal of the Marine Biological Association of the United Kingdom* 89:1529-1540
- Anderson KE (2015) Do hydrocarbon and salinity disturbance affect marine meiofauna diversity and community structure? Masters Thesis, University of Louisville
- Anderson MJ (2001) Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian journal of fisheries and aquatic sciences* 58:626-639
- Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84:511-525
- Attrill MJ (2002) A testable linear model for diversity trends in estuaries. *Journal of Animal Ecology* 71:262-269
- Austen MC, Widdicombe S (2006) Comparison of the response of meio- and macrobenthos to disturbance and organic enrichment. *Journal of Experimental Marine Biology and Ecology* 330:96-104

- Barnes N, Bamber RN, Bennell G, Cornelius N, Glassom D, Henderson SC-D, Jiddawi N, Lee CN, Macia A, Msangameno DJ (2011) Assessment of regional and local biodiversity in tropical and subtropical coastal habitats in the East African Marine Ecoregion. *Biodiversity and Conservation* 20:2075-2109
- Begg G (1978) The estuaries of Natal. Natal Town and Regional Planning Report 41
- Boeckner MJ, Sharma J, Proctor H (2009) Revisiting the meiofauna paradox: dispersal and colonization of nematodes and other meiofaunal organisms in low-and high-energy environments. *Hydrobiologia* 624:91-106
- Bolam S, Schratzberger M, Whomersley P (2006) Macro-and meiofaunal recolonisation of dredged material used for habitat enhancement: Temporal patterns in community development. *Marine Pollution Bulletin* 52:1746-1755
- Bonaglia S, Nascimento FA, Bartoli M, Klawonn I, Brüchert V (2014) Meiofauna increases bacterial denitrification in marine sediments. *Nature communications* 5:5133 DOI: 5110.1038/ncomms6133
- Bownes S, Perissinotto R (2012) Community structure and composition of meiofauna over a sea-induced mouth-breaching event in St Lucia Estuary, South Africa. *Marine Ecology Progress Series* 463:105-126
- Cai W-J, Wang Y, Hodson RE (1998) Acid-base properties of dissolved organic matter in the estuarine waters of Georgia, USA. *Geochimica et Cosmochimica Acta* 62:473-483
- Calabretta CJ, Oviatt CA (2008) The response of benthic macrofauna to anthropogenic stress in Narragansett Bay, Rhode Island: a review of human stressors and assessment of community conditions. *Marine pollution bulletin* 56:1680-1695

- Cardoso P, Raffaelli D, Lillebø A, Verdelhos T, Pardal M (2008) The impact of extreme flooding events and anthropogenic stressors on the macrobenthic communities' dynamics. *Estuarine, Coastal and Shelf Science* 76:553-565
- Carrasco NK, Perissinotto R (2011) The comparative diet of the dominant zooplankton species in the St Lucia Estuary, South Africa. *Journal of Plankton Research* 33:479 - 490
- Carrasco NK, Perissinotto R, Pillay D (2009) Zooplankton of the St. Lucia Estuary during the current drought cycle: a comparison between open-and closed-mouth conditions. *Marine Ecology Progress Series* 399:157
- Carvalho A, Santos P (2013) Factors affecting the distribution of epibenthic biodiversity in the Cávado estuary (NW Portugal). *Revista da Gestão Costeira Integrada* 13:101-111
- Chapin FS, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala OE, Tilman D (1997) Biotic control over the functioning of ecosystems. *Science* 277:500-504
- Clarke K, Gorley R (2006) PRIMER V6: User manual/tutorial. Primer-E Ltd Plymouth–2006
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation.
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310
- Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American naturalist*:1119-1144
- Corbett D (2010) Resuspension and estuarine nutrient cycling: insights from the Neuse River Estuary. *Biogeosciences* 7:3289-3300
- Costanza R, d'Arge R, De Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J (1998) The value of the world's ecosystem services and natural capital. *Ecological economics* 1:3-15

- Coull BC (1999) Role of meiofauna in estuarine soft-bottom habitats. *Australian Journal of Ecology* 24:327-343
- Coull BC, Bell SS (1979) Perspectives of marine meiofaunal ecology. *Ecological processes in coastal and marine systems*. Springer
- Cristoni C, Colangelo MA, Ceccherelli VU (2004) Spatial scale and meiobenthic copepod recolonisation: testing the effect of disturbance size in a seagrass habitat. *Journal of experimental marine biology and ecology* 298:49-70
- Cyrus D, Jerling H, MacKay F, Vivier L (2011) Lake St Lucia, Africa's largest estuarine lake in crisis: combined effects of mouth closure, low levels and hypersalinity. *South African Journal of Science* 107:01-13
- Cyrus D, Vivier L, Jerling H (2010) Effect of hypersaline and low lake conditions on ecological functioning of St Lucia estuarine system, South Africa: An overview 2002–2008. *Estuarine, Coastal and Shelf Science* 86:535-542
- da Fonseca-Genevois Vn, Somerfield PJ, Neves MHB, Coutinho R, Moens T (2006) Colonization and early succession on artificial hard substrata by meiofauna. *Marine Biology* 148:1039-1050
- Danovaro R (2000) Benthic microbial loop and meiofaunal response to oil-induced disturbance in coastal sediments: a review. *International Journal of Environment and Pollution* 13:380-391
- Daudi LN, Uku JN, De Troch M (2013) Role of the source community for the recovery of seagrass associated meiofauna: a field colonisation experiment with seagrass mimics in Diani Beach, Kenya. *African Journal of Marine Science* 35:1-8
- De Deckker P (1981) Ostracods of athalassic saline lakes. *Salt Lakes*. Springer
- Dell'Anno A, Mei M, Pusceddu A, Danovaro R (2002) Assessing the trophic state and eutrophication of coastal marine systems: a new approach based

- on the biochemical composition of sediment organic matter. *Marine Pollution Bulletin* 44:611-622
- Duggan M, Connolly R, Whittle M, Curwen G, Burford M (2014) Effects of freshwater flow extremes on intertidal biota of a wet-dry tropical estuary. *Marine Ecology Progress Series* 502:11-23
- Dye A (1983) Composition and seasonal fluctuations of meiofauna in a southern African mangrove estuary. *Marine Biology* 73:165-170
- Elexander HD, Dunton KH (2002) Freshwater inundation effects on emergent vegetation of a hypersaline salt marsh. *Estuaries* 25:1426-1435
- Elliott M, Whitfield A (2011) Challenging paradigms in estuarine ecology and management. *Estuarine, Coastal and Shelf Science* 94:306-314
- Fenchel TM (1978) The ecology of micro-and meiobenthos. *Annual Review of Ecology and Systematics* 9:99-121
- Findlay S, Pace M, Lints D (1991) Variability and transport of suspended sediment, particulate and dissolved organic carbon in the tidal freshwater Hudson River. *Biogeochemistry* 12:149-169
- Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling C (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557-581
- Fonseca VG, Carvalho GR, Sung W, Johnson HF, Power DM, Neill SP, Packer M, Blaxter ML, Lamshead PJD, Thomas WK (2010) Second-generation environmental sequencing unmasks marine metazoan biodiversity. *Nature communications* 1:98
- França S, Costa MJ, Cabral HN (2009) Assessing habitat specific fish assemblages in estuaries along the Portuguese coast. *Estuarine, Coastal and Shelf Science* 83:1-12

- Gambi C, Totti C, Manini E (2003) Impact of organic loads and environmental gradients on microphytobenthos and meiofaunal distribution in a coastal lagoon. *Chemistry and Ecology* 19:207-223
- Gerlach SA (1978) Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. *Oecologia* 33:55-69
- Geyer WR, Woodruff JD, Traykovski P (2001) Sediment transport and trapping in the Hudson River estuary. *Estuaries* 24:670-679
- Gibson JR, Najjar RG (2000) The response of Chesapeake Bay salinity to climate-induced changes in streamflow. *Limnology and Oceanography* 45:1764-1772
- Giere O (2008) *Meiobenthology: the microscopic motile fauna of aquatic sediments*. Springer Science & Business Media
- Gilles R, Pequeux A (2014) Interactions of Chemical and Osmotic Regulation with the Environment. In: Vernberg FJV, Winona B (ed) *Environmental Adaptations*, Book 8. Elsevier
- Gonçalves A, De Troch M, Marques S, Pardal M, Azeiteiro U (2010) Spatial and temporal distribution of harpacticoid copepods in Mondego estuary. *Journal of the Marine Biological Association of the United Kingdom* 90:1279-1290
- Gray JS, Wu RS-s, Or YY (2002) Effects of hypoxia and organic enrichment on the coastal marine environment. *Marine Ecology Progress Series* 238:249-279
- Grego M, Riedel B, Stachowitsch M, De Troch M (2014) Meiofauna winners and losers of coastal hypoxia: case study harpacticoid copepods. *Biogeosciences* 11:281-292
- Griffiths CL, Robinson TB, Lange L, Mead A (2010) Marine biodiversity in South Africa: an evaluation of current states of knowledge. *PLoS One* 5:e12008

- Grilo T, Cardoso P, Dolbeth M, Bordalo M, Pardal M (2011) Effects of extreme climate events on the macrobenthic communities' structure and functioning of a temperate estuary. *Marine Pollution Bulletin* 62:303-311
- Grimm NB (1994) Disturbance, succession and ecosystem processes in streams: a case study from the desert. In: Giller P, Hildrew A, Raffaelli D (eds) *Aquatic ecology: scale, pattern and process*: 93 - 112. Blackwell Scientific Publications, Oxford, England
- Harkantra SN, Rodrigues NR (2003) Pattern of species succession of soft-bottom macrofauna in the estuaries of Goa, west coast of India. *Current Science* 85:1458-1474
- Higgins RP, Thiel H (1988) *Introduction to the study of meiofauna*. Smithsonian Institution Press
- Ingole B, Parulekar A (1998) Role of salinity in structuring the intertidal meiofauna of a tropical estuarine beach: Field evidence. *Indian Journal of Marine Sciences* 27:356-361
- Jansson B-O (1968) Quantitative and experimental studies of the interstitial fauna in four Swedish sandy beaches. *Ophelia* 5:1-71
- Katz RW, Brown BG (1992) Extreme events in a changing climate: variability is more important than averages. *Climatic change* 21:289-302
- Kennedy AD, Jacoby CA (1999) Biological indicators of marine environmental health: meiofauna—a neglected benthic component? *Environmental Monitoring and Assessment* 54:47-68
- Kennish MJ (2002) Environmental threats and environmental future of estuaries. *Environmental conservation* 29:78-107
- Kimmerer W (2002) Physical, biological, and management responses to variable freshwater flow into the San Francisco Estuary. *Estuaries* 25:1275-1290

- Kjerfve B, Michener W, Gardner L (1994) Impacts of climate change in estuary and delta environments. *Impacts of Climate Change on Ecosystems and Species: Marine and Coastal Ecosystems*
- Kreyling J, Jentsch A, Beierkuhnlein C (2011) Stochastic trajectories of succession initiated by extreme climatic events. *Ecology letters* 14:758-764
- Lawrie RA, Stretch DD (2011) Anthropogenic impacts on the water and salt budgets of St Lucia estuarine lake in South Africa. *Estuarine, Coastal and Shelf Science* 93:58-67
- Lee H, Vanhove S, Peck LS, Vincx M (2001) Recolonisation of meiofauna after catastrophic iceberg scouring in shallow Antarctic sediments. *Polar Biology* 24:918-925
- Longley WL, Powell GL, Green A (1994) Freshwater inflows to Texas bays and estuaries: ecological relationships and methods for determination of needs. Texas Water Development Board Austin, Texas
- Luck GW, Daily GC, Ehrlich PR (2003) Population diversity and ecosystem services. *Trends in Ecology & Evolution* 18:331-336
- Lumsden T, Schulze R, Hewitson B (2009) Evaluation of potential changes in hydrologically relevant statistics of rainfall in Southern Africa under conditions of climate change. *Water SA* 35:649-656
- MacArthur RH (1962) Some generalized theorems of natural selection. *Proceedings of the National Academy of Sciences of the United States of America* 48:1893
- MacLusky DS, Elliott M (2004) *The estuarine ecosystem: Ecology, threats, and management*. Oxford University Press
- Margalef R (1968) *Perspectives in ecological theory*. University of Chicago Press, Chicago, Illinois, 111
- Meehl GA, Zwiers F, Evans J, Knutson T, Mearns L, Whetton P (2000) Trends in extreme weather and climate events: Issues related to modeling

- extremes in projections of future climate change. *Bulletin of the American Meteorological Society* 81:427-436
- Mees J, Dewicke A, Hamerlynck O (1993) Seasonal composition and spatial distribution of hyperbenthic communities along estuarine gradients in the Westerschelde. *Netherland Journal of Aquatic Ecology* 27:359-376
- Meurer AZ, Netto SA (2007) Seasonal dynamics of benthic communities in a shallow sublittoral site of Laguna Estuarine System (South, Brazil). *Brazilian Journal of Aquatic Science and Technology* 11:53-62
- Mielke W (2000) A new record of *Cletocamptus confluens* (Schmeil 1894)(Copepoda Harpacticoida) from a small pond in north-west Namibia. *Tropical Zoology* 13:129-140
- Milliman JD, Farnsworth KL (2011) River discharge to the coastal ocean: a global synthesis. Cambridge University Press
- Milner AM, Robertson AL, McDermott MJ, Klaar MJ, Brown LE (2013) Major flood disturbance alters river ecosystem evolution. *Nature Climate Change* 3:137-141
- Montagna PA, Kalke RD (1992) The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces estuaries, Texas. *Estuaries* 15:307-326
- Montagna PA, Kalke RD, Ritter C (2002) Effect of restored freshwater inflow on macrofauna and meiofauna in upper Rincon Bayou, Texas, USA. *Estuaries* 25:1436-1447
- Moreno M, Ferrero T, Gallizia I, Vezzulli L, Albertelli G, Fabiano M (2008) An assessment of the spatial heterogeneity of environmental disturbance within an enclosed harbour through the analysis of meiofauna and nematode assemblages. *Estuarine, Coastal and Shelf Science* 77:565-576
- Neira C, Sellanes J, Soto A, Gutiérrez D, Gallardo VA (2001) Meiofauna and sedimentary organic matter off Central Chile: response to changes caused by the 1997–1998 El Niño. *Oceanologica Acta* 24:313-328

- Nozais C, Perissinotto R, Tita G (2005) Seasonal dynamics of meiofauna in a South African temporarily open/closed estuary (Mdloti Estuary, Indian Ocean). *Estuarine, Coastal and Shelf Science* 62:325-338
- Owen R, Forbes A (1997) Salinity, floods and the infaunal macrobenthic community of the St Lucia estuary, KwaZulu-Natal, South Africa. *Southern African Journal of Aquatic Science* 23:14-30
- Palmer MA (1988) Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Marine ecology progress series* Oldendorf 48:81-91
- Palmer TA, Montagna PA, Kalke RD (2002) Downstream effects of restored freshwater inflow to Rincon Bayou, Nueces Delta, Texas, USA. *Estuaries* 25:1448-1456
- Parsons TR, Takahashi M, Hargrave B (2013) Biological oceanographic processes. Elsevier
- Pasotti F, Convey P, Vanreusel A (2014) Potter Cove, west Antarctic Peninsula, shallow water meiofauna: a seasonal snapshot. *Antarctic Science* 26:554-562
- Pearson T, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol Ann Rev* 16:229-311
- Perissinotto R, Stretch DD, Taylor RH (2013) Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model. Cambridge University Press
- Peterson CG, Stevenson RJ (1992) Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology*:1445-1461
- Pickett S, White P (1985) The ecology of natural disturbance and patch dynamics

- Pillay D, Perissinotto R (2008) The benthic macrofauna of the St. Lucia Estuary during the 2005 drought year. *Estuarine, Coastal and Shelf Science* 77:35-46
- Pillay D, Perissinotto R (2009) Community structure of epibenthic meiofauna in the St. Lucia Estuarine Lake (South Africa) during a drought phase. *Estuarine, Coastal and Shelf Science* 81:94-104
- Platt WJ, Connell JH (2003) Natural disturbances and directional replacement of species. *Ecological monographs* 73:507-522
- Pollack JB, Palmer TA, Montagna PA (2011) Long-term trends in the response of benthic macrofauna to climate variability in the Lavaca-Colorado Estuary, Texas. *Marine Ecology Progress Series* 436:67-80
- Porter R, Blackmore A (1998) St Lucia System South Africa. South African Wetlands Conservation Programme
- Pusceddu A, Gambi C, Corinaldesi C, Scopa M, Danovaro R (2014) Relationships between Meiofaunal Biodiversity and Prokaryotic Heterotrophic Production in Different Tropical Habitats and Oceanic Regions. *PloS one* 9:e91056
- Rautenbach CJd, Smith IN (2001) Teleconnections between global sea-surface temperatures and the interannual variability of observed and model simulated rainfall over southern Africa. *Journal of Hydrology* 254:1-15
- Reichelt A (1991) Environmental effects of meiofaunal burrowing. *The Environmental Impact of Burrowing Animals and Animal Burrows*, PS Meadows and A Meadows, eds, A Zoological Society of London Symposia 63:33-52
- Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, Wissmar RC (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society*:433-455

- Ricci C, Balsamo M (2000) The biology and ecology of lotic rotifers and gastrotrichs. *Freshwater Biology* 44:15-28
- Richmond CE, Wetthey DS, Woodin SA (2007) Climate change and increased environmental variability: demographic responses in an estuarine harpacticoid copepod. *ecological modelling* 209:189-202
- Ritter C, Montagna PA, Applebaum S (2005) Short-term succession dynamics of macrobenthos in a salinity-stressed estuary. *Journal of Experimental Marine Biology and Ecology* 323:57-69
- Rosenberg R, Agrenius S, Hellman B, Nilsson HC, Norling K (2002) Recovery of marine benthic habitats and fauna in a Swedish fjord following improved oxygen conditions. *Marine Ecology Progress Series* 234:43-53
- Rowlands DJ, Frame DJ, Ackerley D, Aina T, Booth BB, Christensen C, Collins M, Faull N, Forest CE, Grandey BS (2012) Broad range of 2050 warming from an observationally constrained large climate model ensemble. *Nature Geoscience* 5:256-260
- Sabatino Ad, Gerecke R, Martin P (2000) The biology and ecology of lotic water mites (Hydrachnidia). *Freshwater Biology* 44:47-62
- Sanilkumar M, Saramma A, Joseph K (2009) Vertical distribution of microphytobenthos in Cochin estuary. *Journal of the Marine Biological Association of India* 51:61-68
- Santos P, Castel J, Souza-Santos L (1996) Seasonal variability of meiofaunal abundance in the oligo-mesohaline area of the Gironde Estuary, France. *Estuarine, Coastal and Shelf Science* 43:549-563
- Saraswat R (2015) Non-Destructive Foraminiferal Paleoclimatic Proxies: A Brief Insight. *Proceedings of the Indian National Science Academy* 81:381-395
- Schlacher TA, Wooldridge TH (1996) Origin and trophic importance of detritus-evidence from stable isotopes in the benthos of a small, temperate estuary. *Oecologia* 106:382-388

- Schmid-Araya J, Schmid P (2000) Trophic relationships: integrating meiofauna into a realistic benthic food web. *Freshwater Biology* 44:149-163
- Schratzberger M, Gee J, Rees H, Boyd S, Wall C (2000) The structure and taxonomic composition of sublittoral meiofauna assemblages as an indicator of the status of marine environments. *Journal of the Marine Biological Association of the UK* 80:969-980
- Schratzberger M, Warwick R (1998) Effects of physical disturbance on nematode communities in sand and mud: a microcosm experiment. *Marine Biology* 130:643-650
- Simpson JH, Brown J, Matthews J, Allen G (1990) Tidal straining, density currents, and stirring in the control of estuarine stratification. *Estuaries* 13:125-132
- Snyder C, Johnson Z (2006) Macroinvertebrate assemblage recovery following a catastrophic flood and debris flows in an Appalachian mountain stream. *Journal of the North American Benthological Society* 25:825-840
- Soetaert K, Vincx M, Wittoeck J, Tulkens M (1995) Meiobenthic distribution and nematode community structure in five European estuaries. *Hydrobiologia* 311:185-206
- Steyaert M, Herman P, Moens T, Widdows T, Vincx M (2001) Tidal migration of nematodes on an estuarine tidal flat (the Molenplaat, Schelde Estuary, SW Netherlands). *Marine Ecology Progress Series* 224
- Storey RG, Williams D (2004) Spatial responses of hyporheic invertebrates to seasonal changes in environmental parameters. *Freshwater Biology* 49:1468-1486
- Stretch D, Chrystal C, Chrystal R, Maine C, Pringle J (2013) Estuary and lake hydrodynamics. In: Perissinotto R, Stretch DD, Taylor RH (eds) *Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. Cambridge University Press

- Stubbington R, Boulton AJ, Little S, Wood PJ (2015) Changes in invertebrate assemblage composition in benthic and hyporheic zones during a severe suprasedasonal drought. *Freshwater Science* 34:344-354
- Tansley AG (1920) The classification of vegetation and the concept of development. *The Journal of ecology*:118-149
- Taylor R (2011) The State of St Lucia. Unpublished Ezemvelo KZN Wildlife report
- Taylor R, Fox C, Mfeka S (2013) Monitoring the St Lucia Estuarine System: A synthesis and interpretation of the monitoring data for January-February 2013. Ezemvelo KZN Wildlife Unpublished report
- Taylor RH (2006) Ecological Responses to Changes in the Physical Environment of the St Lucia Estuary. Norwegian University of Life Sciences, Department of Plant and Environmental Sciences
- Teixeira H, Salas F, Borja A, Neto J, Marques J (2008) A benthic perspective in assessing the ecological status of estuaries: the case of the Mondego estuary (Portugal). *Ecological Indicators* 8:404-416
- Teske PR, Wooldridge TH (2004) Affinities of some common estuarine macroinvertebrates to salinity and sediment type: empirical data from Eastern Cape estuaries, South Africa. *African Zoology* 39:183-192
- Thompson RM, Lake PS (2010) Reconciling theory and practise: the role of stream ecology. *River research and applications* 26:5-14
- Timmermann A, Oberhuber J, Bacher A, Esch M, Latif M, Roeckner E (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398:694-697
- Trenberth KE (2011) Changes in precipitation with climate change. *Climate Research* 47:123
- Trenberth KE, Hoar TJ (1996) The 1990–1995 El Niño-Southern Oscillation event: Longest on record. *Geophysical Research Letters* 23:57-60

- Trueblood DD, Gallagher ED, Gould DM (1994) Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. *Limnology and Oceanography* 39:1440-1454
- Vaeret L, Sokolic F (2008) Methods for studying the distribution of groundwater-dependent wetlands: a case study from Eastern Shores, St Lucia, South Africa. PhD Thesis, Norwegian University of Life Sciences, Norway.,
- Valiela I, Camilli L, Stone T, Giblin A, Crusius J, Fox S, Barth-Jensen C, Monteiro RO, Tucker J, Martinetto P (2012) Increased rainfall remarkably freshens estuarine and coastal waters on the Pacific coast of Panama: Magnitude and likely effects on upwelling and nutrient supply. *Global and Planetary Change* 92:130-137
- van Elden S, Dyer MJ, Carrasco NK, Perissinotto R (2014) Meso-zooplankton movement through the newly constructed Mfolozi channel into and out of the St Lucia Estuary, South Africa: short communication. *African Zoology* 49:317-325
- Venice (1958) The Venice System for the Classification of Marine Waters According to Salinity. *Limnology and Oceanography* 3:346-347
- Vincx M (1996) Meiofauna in marine and freshwater sediments. In: Hall GS (ed) *Methods for the examination of organismal diversity in soils and sediments*, 187 - 195. CAB International IUBS UNESCO, New York
- Vivier L, Cyrus DP (2009) Alternative nursery habitat for estuarine associated marine fish during prolonged closure of the St Lucia estuary, South Africa. *Estuarine, Coastal and Shelf Science* 85:118-125
- Whitfield A (1992) A characterization of southern African estuarine systems. *Southern African Journal of Aquatic Science* 18:89-103
- Whitfield A, Taylor R (2009) A review of the importance of freshwater inflow to the future conservation of Lake St Lucia. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19:838-848

- Widdicombe S, Austen M (2005) Setting diversity and community structure in subtidal sediments: The importance of biological disturbance. *Interactions between macro-and microorganisms in marine sediments*:217-231
- Yamamuro M (2000) Abundance and size distribution of sublittoral meiobenthos along estuarine salinity gradients. *Journal of Marine Systems* 26:135-143
- Zajac RN, Whitlatch RB (1982a) Responses of estuarine infauna to disturbance. 11. Spatial and temporal variation of succession. *Marine Ecology Progress Series* 10:15-27
- Zajac RN, Whitlatch RB (1982b) Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonization. *Marine Ecology Progress Series* 10:1-14
- Zajac RN, Whitlatch RB, Thrush SF (1998) Recolonization and succession in soft-sediment infaunal communities: the spatial scale of controlling factors. *Recruitment, Colonization and Physical-Chemical Forcing in Marine Biological Systems*, 227 - 240. Springer, Netherlands
- Zeppilli D, Sarrazin J, Leduc D, Arbizu PM, Fontaneto D, Fontanier C, Gooday AJ, Kristensen RM, Ivanenko VN, Sørensen MV (2015) Is the meiofauna a good indicator for climate change and anthropogenic impacts? *Marine Biodiversity* 45:505-535