

Zooplankton dynamics during a regime shift in the St Lucia Estuary, South Africa

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Preface

The research contained and lab analyses reported in this dissertation was completed by the candidate while based in the Discipline of Marine Biology, College of Agriculture, Engineering and Science, School of Life Sciences, University of KwaZulu-Natal, Westville Campus, South Africa under the supervision of Dr Nicola K. Carrasco. The collection of samples in this study was carried out in the iSimangaliso Wetland Park, St Lucia Estuary, KwaZulu-Natal, South Africa under an iSimangaliso Wetland Park Authority Research Agreement together with the Environmental and Fisheries Research Permits (RES 2015/70, RES 2016/85, RES 2017/71 and RES 2018/101) issued by the South African Department of Agriculture, Forestry and Fisheries. The study was funded by The National Research Foundation (unique grant numbers: 109523 and 99441).

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.



Signed: Dr Nicola Kim Carrasco

Date: 15 March 2021

Plagiarism declaration- College of Agriculture, Engineering and Science

I, Merusha Govender declare that:

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

The St Lucia Estuary is the largest estuarine lake in Africa and forms part of the iSimangaliso World Heritage Site however historical anthropogenic changes, including the separation of the Mfolozi River from the St Lucia system, have exacerbated periodic drought conditions. A Global Environment Facilitated (GEF) funded project was carried out (June 2016 to July 2017) to relink the Mfolozi River and St Lucia Estuary to allow unimpeded flow of freshwater into the St Lucia Estuary that would alleviate drought conditions and ideally restore natural mouth functioning. This reconnection, combined with increased precipitation from 2017 onwards, initiated a transition to a new wet phase in the estuary. Zooplankton form an essential link between primary producers and higher trophic levels, and they are important indicators of change in aquatic ecosystems. This study aimed to firstly record the changes in the zooplankton community before, during and after the restoration project in the mouth region from February 2015 to November 2018. The zooplankton community structure at the mouth differed significantly before and after the restoration project. Estuarine resident taxa including the mysid *Mesopodopsis africana*, the copepods *Acartiella natalensis* and *Oithona brevicornis* were absent post project completion as mainly freshwater taxa dominated. Both total suspended solids and salinity were identified as major determinants of the zooplankton community structure at the mouth region. Secondly, the study aimed to investigate the system-wide impacts by monitoring the zooplankton community at 5 representative sites within the system as it transitioned from a hypersaline state to a freshwater state from February 2015 to November 2017. Following the reconnection, water levels increased, and salinity levels decreased throughout the lake system, however the reversed salinity gradient persisted with a mean salinity of 23 recorded in the upper reaches of the lake system in 2017. There was a clear shift in the zooplankton community to freshwater taxa such as cyclopoids, rotifers and cladocerans. Resident taxa declined in abundance, as *Oithona brevicornis* and *Acartiella natalensis* were virtually absent in 2017, possibly due to low salinity, or increased competition from freshwater taxa. The calanoid copepod *Pseudodiaptomus stuhlmanni* was still present throughout the lake system (in lower abundance) and the mysid *Mesopodopsis africana* was restricted to the upper reaches which served as refuge from the low salinity areas. While the increased freshwater input is positive, it has not yet been substantial enough to initiate a mouth breaching event that would flush the system of the excessive silt build-up. Furthermore, continuation of this already extended wet phase could force the exclusion of the estuarine resident zooplankton.

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Chapter 1: General introduction

Study context

An estuary is generally defined as a partially enclosed water body along the coastline where freshwater from rivers mixes with oceanic waters (Lyell 1833, Glamore et al. 2016, Tweedley et al. 2019). Whitfield (1992) identified five categories of estuaries, including: (1) Estuarine bays, (2) Permanently Open Estuaries (POE's), (3) River Mouth Estuaries, (4) Temporarily Open/Closed Estuaries (TOCE's), and (5) Estuarine Lakes. The categorisation of Whitfield (1992) has since been expanded to include nine estuarine types and three microsystem types (Van Niekerk et al. 2020). Estuaries are highly productive and perform a vital role in habitat and food provision for a high diversity of flora, and fauna (Tirok and Scharler 2014, Wetz and Yoskowitz 2013). They have also been recognised as vital nursery sites and breeding grounds for fish that are both economically and ecologically important (Whitfield and Bate 2007, Wetz and Yoskowitz 2013), and are essential for biogeochemical cycling (Bauer et al. 2013). Estuaries additionally provide aesthetic value as well as a wide variety of recreational activities (Thrush et al. 2004).

Estuaries are dynamic ecosystems both temporally and spatially (Wetz and Yoskowitz 2013, Carrasco and Perissinotto 2015, Jones et al. 2016), experiencing extreme variation in physico-chemical parameters (Carrasco et al. 2010). These ecosystems and their invaluable services are however, threatened by both natural and extreme climatic changes, and from anthropogenic activities (Thrush et al. 2004, Wetz and Yoskowitz 2013, Masson-Delmotte et al. 2018). A major determinant of estuarine health is the quantity as well as the quality of freshwater input as changes in freshwater inflow can affect the availability of habitat, geomorphology and inhabitants of the estuary (Coops et al. 2003, Adams et al. 2016). Estuaries are vulnerable to climatic changes and anthropogenic activities (Skowno et al. 2019). It is therefore essential for estuarine management to conserve estuarine ecosystem goods and services, and to restore ecosystems from past degradations (Elliot et al. 2016, Skowno et al. 2019).

Estuaries and wetlands are among the most threatened and least protected ecosystems in South Africa (Skowno et al. 2019). It has been estimated that 99 % of South Africa's total estuarine and 88 % of wetland areas are threatened (Skowno et al. 2019). Estuaries have the highest percentage of ecosystem types threatened (86 %), followed by inland wetlands (79 %) and rivers (64 %) (Skowno et al. 2019). The state/condition of an estuary is determined by the level of impact from anthropogenic activities (Whitfield and Baliwe 2013). In South Africa, 28 % of estuaries are in excellent condition, 31 % in good condition, 25 % in a fair condition and 15 % are regarded to be in poor condition (Turpie 2004). Estuarine systems are difficult to protect as they face numerous

pressures that impact them both directly and indirectly (Skowno et al. 2019). In South Africa there are at least 18 % of estuarine ecosystem types that are well protected, 36 % are moderately protected, 31 % are poorly protected and 13 % are not protected (Skowno et al. 2019).

Climate change: Future impacts

Climate, specifically rising air/sea temperatures and precipitation are major determinants of the environmental parameters of an estuary (Cronin et al. 2000, Hopkinson et al. 2008, Paerl et al. 2011, Masson-Delmotte et al. 2018). Given the current rate of anthropogenic activities, global warming is expected to increase temperatures by 1.5 °C in the years to come (2030-2052) (Glamore et al. 2016, Masson-Delmotte et al. 2018). Coastal systems, including estuaries, globally are vulnerable to floods, sea-level rise, droughts and coastal storms (Kimmel et al. 2009, Orton et al. 2015). Climate models have predicted that within the next 100 years, there will be high variability in terms of rainfall patterns (Chiu and Kuo 2012, Stocker et al. 2013, Breaux et al. 2019). As temperatures rise, precipitation is expected to increase unevenly globally (Masson-Delmotte et al. 2018, Breaux et al. 2019). In areas such as the southwest of the United States, rainfall events are predicted to be less frequent but more intense (Chiu and Kuo 2012, Stocker et al. 2013, Pachauri et al. 2015, Breaux et al. 2019). In Africa, some areas are predicted to have increased precipitation events such as the eastern parts and other areas are expected to have longer dry periods as a result of less rainfall (Hendrix and Salehyan 2012). Also, it is predicted there will be increased drought intensity and frequencies over the next century which will severely affect coastal ecosystems in areas such as, Southeast Asia, Southern Africa, eastern Australia, and America (Humphries et al. 2016).

Climatic changes are likely to alter the hydrodynamics and catchment sediments of estuarine ecosystems (Flemer and Champ 2006, Wetz and Yoskowitz 2013, Glamore et al. 2016). Climatic variability plays a role in the delivery of fresh water, nutrients and organic matter to estuaries (Paerl 2006). Severe climatic events such as droughts or floods bring about fluctuations in salinity which is a major driving factor of estuarine systems (Gibson et al. 2005, Wetz and Yoskowitz 2013). The imbalance between evaporative loss due to high temperatures and annual rainfall can lead to extreme climatic shifts (Eyre and Ferguson 2006, Glamore et al. 2016).

The consequences of an increase in temperature in estuarine systems include an increase in evaporation rates which could lead to hypersaline conditions in periodically closed estuaries that receive low quantities of freshwater (Glamore et al. 2016). In addition, increased temperatures could lead to intensified stratification, hypoxia and the reduction of habitats for estuarine organisms (Attrill and Power 2000, Wetz and Yoskowitz 2013, Glamore et al. 2016). Furthermore, increased

temperatures could affect ectothermic biota as their metabolic rates would increase, affecting their physiological functioning and could potentially exceed the temperature tolerance of organisms (Attrill and Power 2000, Madeira et al. 2012, Wetz and Yoskowitz 2013, Tagliarolo et al. 2018). Extreme climatic events, such as intense rainfall events, can change nutrient loads which in turn may impact the ecology of an estuarine system, alter sediment loads, influence freshwater input and increase flood frequencies (Eyre et al. 2006, Cook et al. 2010, Wetz and Yoskowitz 2013, Glamore et al. 2016).

Sea-level rise and ocean acidification are other processes likely to affect estuaries (Glamore et al. 2016, Wetz and Yoskowitz 2013). An increase in acidity would impact biota sensitive to pH levels (Glamore et al. 2016). Furthermore, climate change can increase storm events such as cyclones which elevates turbulence/wind (Eyre and Ferguson 2006, Elsner et al. 2008). Elevated turbulence could increase resuspension of sediments, increase coastal erosion and can influence flooding events (Eyre et al. 2006, Elsner et al. 2008, Wetz and Paerl 2008). Anthropogenic activities such as irrigation, dredging, water abstractions and agricultural activities can act in synergy with climate change to cause serious alterations in the biodiversity and the ecological state of estuarine systems (Glamore et al. 2016). The resilience of estuarine systems is tested when experiencing changes or disturbances which can cause the ecosystem to go through a regime shift (Glamore et al. 2016, Wetz and Yoskowitz 2013, Cooper et al. 2020).

Regime shifts

A general term used for intense changes in aquatic ecosystems is a ‘regime shift’ which refers to a transition from one state to an alternate stable state where the ecosystem can withstand the changed environmental conditions (Beisner et al. 2003, Scheffer and Jeppesen 2007). Regime shifts are expected to increase as a result of climate change and anthropogenic activities (Cooper et al. 2020). Regime or state shifts occur as a result of changing environmental variables or “disturbances”, where the ecosystem gets pushed past a threshold or tipping point (Scheffer and Carpenter 2003, Lindenmayer et al. 2011, Capon et al. 2015). Four characteristics which define regime shifts have been identified according to Lees et al. (2006): (1) regime shifts can be abrupt or sudden, (2) there are changes in the physical as well as the biological components of the system, (3) regime shifts can embody changes across trophic levels and (4) regime shifts can occur with high amplitude and low frequency in a system (Lees et al. 2006, Capon et al. 2015). Shifts in shallow lakes have become of interest as these ecosystems are highly sensitive to changing conditions which could be due to multiple causes including extreme weather conditions (Hamilton and Mitchell 1988), changes in

water level fluctuations (Wallsten and Forsgren 1989, Coops et al. 2003), and natural alterations (Scheffer and Jeppeson 2007).

Freshwater: Influence on an estuary and its biota

Freshwater is an essential and often limited resource in estuarine systems (Schlacher and Wooldridge 1996, Dix et al. 2008). Freshwater inflow into estuaries is accompanied by both detritus and dissolved nutrients that are vital in supporting the basis of estuarine life (Wetzel 1992, Nixon et al. 2004, Emmerton et al. 2008, McClelland et al. 2014, Atkinson et al. 2019). Water entering estuaries could, however, also contain plastic, industrial effluents and pesticides as runoff, which can have detrimental effects on biota (Naidoo et al. 2015, Bakir et al. 2014, Aminot et al. 2016).

Freshwater has a vital role in influencing salinity in an estuarine system (Tweedley et al. 2019). Salinity maintains the gradient along the estuary and influences both the physico-chemical parameters and the biological aspect of estuaries (Carrasco and Perrisinotto 2015). When there is an insufficient supply of freshwater in a closed mouth estuary and evaporation rates exceed freshwater input, an estuary is referred to as inverse or negative (Wooldridge et al. 2016). There are usually higher salinity levels in the lower reaches of estuaries, however, a reversed salinity gradient can exist in inverse estuarine systems (Potter et al. 2010). The osmotic physiology of organisms is dependent on the interactive effects of both temperature and salinity (Lasserre 1976, Perrisinotto et al. 2013). Biota in estuaries have an upper/lower threshold for salinity tolerance, below/above which they would not be able to function (Elliott and Whitfield 2011). Estuaries are therefore usually characterised by biota that are capable of surviving and proliferating in a variable environment (Elliott and Whitfield 2011).

Sedimentation: Impacts and catchment management

Sediments entering estuaries can carry both nutrients and harmful pollutants (Thrush et al. 2004). Sediment deposition is a natural process influenced by tidal currents, waves and precipitation, and may differ seasonally in different areas of an estuary (Henley et al. 2000). Sedimentation in estuaries has increased over the years due to human activities through land use, forestry, urban activities, mining and the development of structures within estuaries (Brooke 2003, Henley et al. 2000, Gao et al. 2013).

Humans have easy access to rivers due to their locality inland thereby making rivers vulnerable to human perturbations (Eyre et al. 1998, Jones 2015). Dams tend to trap sediment, limiting the amount of sediment transferred to both oceans and estuaries, and agricultural activities have

increased soil erosion rates which has increased the amount of sediment entering estuaries (Jones 2015, Glamore et al. 2016). Sedimentation is regarded as one of the most detrimental pollutants in aquatic environments as it can lead to the shallowing of an affected area and can alter biota abundance and communities (Lemly 1982, Henley et al. 2000, Thrush et al. 2004). Siltation affects an important water parameter which is turbidity and high levels of turbidity have been found to reduce invertebrate densities (Wagener and LaPerriere 1985, Henley et al. 2000). The particulates of sediment flowing from rivers are silt, different sized gravel particulates and sand (Henley et al. 2000). When the particulates are in suspension in the water, this is referred to as resuspension of sediments and once the sediment settles this is known as sedimentation (Henley et al. 2000). Turbidity is determined by how much sediment or particles are suspended in the water column and this in turn affects the transparency of the water (Henley et al. 2000).

The impact of turbidity and suspended sediment on the aquatic environment is dependent on the amount of time it persists and what levels it occurs at (Cairns 1990). When the levels are high and persistent, this has a negative consequence for the flora and fauna in aquatic habitats (Cairns 1990) as there could be the alteration of species diversity, abundance, mortality and reproduction rates (Henley et al. 2000). Sedimentation can affect primary producers (Henley et al. 2000, Thrush et al. 2004), as elevated turbidity levels reduce sunlight entering the water column, leading to decreased energy available for phytoplankton to photosynthesize, thereby bringing about a reduction in phytoplankton biomass (Henley et al. 2000). This in turn could decrease food availability for zooplankton and reduce energy transfer along the food chain (Henley et al. 2000). Siltation can be beneficial for zooplankton through reducing predation by obscuring the vision of zoo-planktivorous fish (McCabe and O'Brien 1983, Jones et al. 2016) and ingestion of silt particles containing dissolved organic matter (DOM) (Cuker and Hudson 1992). However, elevated siltation levels could lead to increased mortality rates and bring about reduced feeding rates in certain zooplankton taxa (Koenings et al. 1990, Carrasco et al. 2013, Jones et al. 2020). Additionally, microphytobenthic algal growth could be affected through increased sedimentation, as sediment settles at the bottom and reduces light penetration for primary production (Thrush et al. 2004).

Organisms such as macrobenthic invertebrates are also affected by sedimentation (Henley et al. 2000) as their diversity and abundance are dependent on the substrata in which they live in (Gore 1985, 1987, Gore et al. 2001). Silt affects the living space of macrobenthic invertebrates by clogging interstitial spaces between sediment particles leading to a reduction of water circulation and oxygen (Lenat et al. 1981, Gordon et al. 1992, Henley et al. 2000). Filter feeding bivalves are also impacted as exposure to silt could reduce filtration rates and decrease survival rates (Aldridge et al. 1987). Sedimentation could reduce both food availability and substrate suitability for

gastropods leading to a possible decline in snail populations (Henley et al. 2000). Local fish populations decline when there is an increase in turbidity and silt, however fish can migrate to less turbid waters (Barton 1977). Increased siltation could lead to the mortality of fish larvae and reduce spawning habitat (Barton 1977, Henley et al. 2000). Aquatic biota are also prone to lacerations (Henley et al. 2000, Jones 2015).

The rate of sedimentation affects the growth of mangroves and macrophytes (Lovelock et al. 2007, Lawniczak-Malinska et al. 2018). Moderate rates of sedimentation have been shown to favour growth of mangroves due to their associated nutrients, however high rates of sedimentation may have severe impacts on mangroves, bringing about an increase in mortality (Lovelock et al. 2007). Sediment deposition can also lead to eutrophication over time and cause the shallowing of lakes (Thrush et al. 2004). The shallowing as well as the increased nutrients would favour the growth of macrophytes but can also reduce habitat for many other biota (Lawniczak-Malinska et al. 2018). High levels of nutrients can cause a decline in growth rates of macrophytes (Lawniczak-Malinska et al. 2018).

High sediment input can negatively impact estuarine ecology. Catchment management therefore needs to address both the mobilisation and delivery of sediment into estuaries (Rollason et al. 2018). Measures can be put in place to both decrease erosion rates and to reduce the input of sediment into rivers (Henley et al. 2000). To control river sediment input, there has to be the control of sediment at the various source points (Brooke 2003). Some ways include traps to prevent sediment input, the diversion of water, more careful road construction and silt barriers (Waters 1995). The main source of silt input entering estuaries is from agricultural activities (Waters 1995). Ways of reducing sediment input are through the fencing of livestock referred to as riparian buffers (Lowrance et al. 1984, Henley et al. 2000). Riparian regions are areas along streams and rivers that are considered as agricultural areas for crop and livestock production (Lowrance et al. 1985, Henley et al. 2000).

Knowledge of the effects of sedimentation on ecosystems and organisms is essential for catchment management in decision making (Thrush et al. 2004). Catchment management needs to take into consideration the sustainability of essential ecological goods and services, human rights, taking into consideration global conventions and the protection of ecosystem resilience (Falkenmark and Folke 2002). Furthermore, there should be the consideration of environmental ethics as the freshwater environment and the provision of goods and services to humans are tightly interlinked (Daily 1997, Falkenmark and Folke 2002). The challenges faced by catchment management have intensified due to the extent of changes in land use (Rouillard and Spray 2017). There has been a shift to more adaptive approaches involving integrated catchment management (ICM) (Rouillard

and Spray 2017, Rollason et al. 2018). The ICM can be generally defined as the integration of management which considers land use, water use as well as human activities (Lerner and Zheng 2011). The integration of research has attracted scientists from different fields ranging from social sciences (Jeffrey 2003) to sustainability science (Jerneck et al. 2011) and many other disciplinary fields (Wallis et al. 2013). There are numerous ways that one can understand integrated management, but the most favoured way is by considering it as a knowledge production and a learning process (Rollason et al. 2018). Integration includes transdisciplinary fields which involves the combining of academic knowledge to solve the real-life problems of the world (Klein 2012, Rollason et al. 2018).

According to Kilvington et al. (2011) and Varis and Enckell (2014), there are two important perspectives of the ICM approach. Firstly, there is the horizontal integration that looks at management organisations both across as well as between the different disciplinary fields, for example agriculture, spatial planning, etc. (Rollason et al. 2018). The other integration is the vertical component between the public, experts and policymakers (Rollason et al. 2018). The traditional approach does not involve the participation of the public whereas the ICM approach has participation by the public and there is local decision making combined with scientific input (Rollason et al. 2018). The research thus far tracking ICM, in terms of implementation of policies has been successful at the catchment level but locally there needs to be further research conducted within catchments (Rollason et al. 2018). Due to the degradation of estuarine ecosystems, estuarine management has the role of protecting and restoring the natural functioning of estuarine ecosystems (Elliott et al. 2016).

Estuarine management, mouth manipulation and restoration projects

The main purpose of estuarine management is to ensure the enhancement and protection of the natural functioning of estuarine systems while also making sure important ecosystem goods and services are still obtained by society (Elliot et al. 2007, Elliot 2014, Elliot et al. 2016). Estuarine management is a very intensive and dynamic process as estuaries are influenced by riverine, marine and terrestrial habitats (Elliot et al. 2007, Elliot 2014, Elliot et al. 2016). More intensive planning and implementation has to be undertaken by management authorities (Higgs 2005, Weinstein 2008). Estuarine management and restoration scientists have the challenge of figuring out how to reverse past changes through restoration /rehabilitation initiatives, while also taking societal needs into account (McDonnell and Pickett 1993, Higgs 2005, Weinstein 2008).

Ecological restoration/ecoengineering is a process that involves rehabilitation of an estuarine system that has been damaged or degraded (Halme et al. 2013, Elliott 2014). The purpose of

ecoengineering is to restore the ecosystem from past deterioration or to enhance the natural functioning of the system to improve ecosystem goods and services (Elliott et al. 2016). Ecohydrology (Wolanski and Elliot 2015, Elliot et al. 2016) is the main focus that affects physico-chemical variables, water quantity as well as quality (Elliot et al. 2016). The modification of a system physically to restore natural processes is successfully done through the application of ecohydrology (Wolanski et al. 2009, Wolanski and Elliott 2015). Soft ecoengineering involves temporary features such as dredging by the beach, modification of substratum, manipulation of the mouth area, etc. (Elliott et al. 2016). Other types of ecoengineering involve constructing permanent features within the estuary (Elliott et al. 2016).

In South Africa, mouth manipulation has been a major hydrological management issue in temporarily closed estuaries (TCE's) (Taylor 2006, Whitfield et al. 2012, Van Niekerk et al. 2020). Mouth manipulation can occur when excess nutrients/ pollutants need to be flushed out to avoid hyper eutrophication, or to restore the ocean link and nursery function of estuaries (Anandraj et al. 2008, Perissinotto et al. 2010, Whitfield et al. 2012). Furthermore, mouth manipulation can occur during high water levels to avoid the flooding of human infrastructure or alternatively when high evaporation rates and low freshwater input threaten the integrity of the system (Anandraj et al. 2008, Whitfield et al. 2012, Perissinotto et al. 2013, Adams et al. 2016). The state of the mouth is a critical factor that influences the physical as well as chemical environment of an estuary and in turn determines the biological components of the system (Perissinotto et al. 2013). Restoration projects can also be used to adjust nutrient availability which affects the trophic state of estuarine ecosystems and most importantly the water levels, as this is a decisive factor of shallow lakes (Coops et al. 2003).

Water level fluctuations (WLFs) also affect the functioning as well as the ecology of shallow lakes (Coops et al. 2003). Changes in water levels can bring about regime shifts within ecosystems (Coops et al. 2003). Therefore, it is essential to allow for management to monitor shallow lakes and the adjustment of water levels can be used as a form of restoration (Coops et al. 2003). The pelagic environment in estuarine systems is not always stable, especially during changing water level fluctuations which alters physico-chemical variables (Carrasco et al. 2010). Planktonic organisms such as zooplankton have been identified as important indicators of changes in aquatic ecosystems as they form an essential link in the food web and respond quickly to perturbations. (Gibbons 1997, Wooldridge 1999, Buthelezi 2002, Hays et al. 2005, Pace et al. 2013).

Zooplankton

Planktonic organisms include both plants and animals that are found in the water column (Gibbons 1997, Wooldridge 1999). The plant component is referred to as phytoplankton and the animal component zooplankton (Gibbons 1997, Wooldridge 1999). Zooplankton either float or weakly swim in the water column and their dispersal is reliant on both the tides, and currents (Meadows and Campbell 1988, Gibbons 1997, Buthelezi 2002, Wooldridge 1999). Zooplankton can be divided into two groups called holoplankton (eg. copepods) and meroplankton (eg. crabs, prawns) (Gibbons 1997, Wooldridge 1999). Holoplankton remain as plankton for their entire life cycle and meroplankton spends the earlier part of their lives as larvae and thereafter settle on the floor of the ecosystem's substratum (Gibbons 1997, Buthelezi 2002). There are numerous estuarine as well as marine benthic invertebrates which have larvae that are planktonic (Eckman 1996, Buthelezi 2002, Wooldridge 1999) and the larvae use estuaries as nursery places for utilisation of food and as a place of protection (Cyrus and Forbes 1996, Buthelezi 2002, Wooldridge 1999). Zooplankton are further divided into 4 size classes which includes firstly microzooplankton (2 to 200 μm), secondly mesozooplankton (200 μm to 2mm), thirdly macrozooplankton (2 mm to 20 mm) and lastly megazooplankton (>20 mm) (Gibbons 1997, Wooldridge 1999).

Zooplankton play an essential role in linking primary producers (phytoplankton) to higher trophic levels (Hays et al 2005, Carrasco et al. 2011, Rice et al. 2013). They also aid in the transfer of energy between benthic and pelagic environments (Wooldridge 1999, Van Elden et al. 2014, Taylor 2006, Perissinotto et al. 2013) through diel-vertical migration (Gibbons 1997, Perissinotto et al. 2013) which is common in most zooplankton species (Gibbons 1997). Diel vertical migration occurs when zooplankton migrate to the surface waters during the night to feed and return to the bottom during the day in an effort to escape visual predators (Gibbons 1997, Wooldridge 1999).

Apart from their importance in the food web, zooplankton have short generation times allowing for a rapid response to stresses within aquatic ecosystems (Wooldridge and Deyzel 2009, Carrasco et al. 2010) and they can be used as early warning indicators (EWI) of regime shifts within a system (Pace et al. 2013). The pelagic environment of estuaries has varying environmental conditions which bring about change to the physico-chemical parameters such as salinity, turbidity, nutrients, dissolved oxygen and temperature which can cause spatial, and temporal variations in zooplankton communities (Perissinotto et al. 2013). Salinity is a major determinant of zooplankton abundance and community structure along an estuary as different species have different tolerance levels (Jeppesen et al. 2007).

Study site: The St Lucia estuarine lake

The St Lucia estuarine lake is located on the east coast of South Africa (Figure 1.1) (Begg 1978, Carrasco et al. 2010, Jones 2015). The estuarine system occupies around 80 % of the estuarine area in KwaZulu-Natal (Cyrus et al. 2010, Cyrus et al. 2020) and is regarded as the oldest estuary that has been protected worldwide (Whitfield et al. 2006). Out of the 250 estuarine systems in South Africa, the St Lucia Estuary was ranked fifth in terms of conservation priority (Turpie et al. 2002). The estuarine system is a Ramsar Site of International importance, and it forms part of the UNESCO World Heritage Site (Perissinotto et al. 2013, Tweedley et al. 2019). When the system has a full coverage of water, it has a surface area of 350 km² and has a mean depth of 0.9 m (Tweedley et al. 2019, Whitfield et al. 2013). The estuary contains a variety of habitats, accommodating a diverse range of fauna as well as flora that include endemic, rare and threatened taxa (Begg 1978, Naidoo 2015). When open to the sea, the estuarine system is an important nursery site for both juveniles of marine fish and penaeid prawns (Cyrus et al. 2010, Whitfield et al. 2013). The system also provides a wide range of ecosystem and economic services (eg. tourism, harvesting of raw materials as well as subsistence fishing) (Nunes et al. 2018).

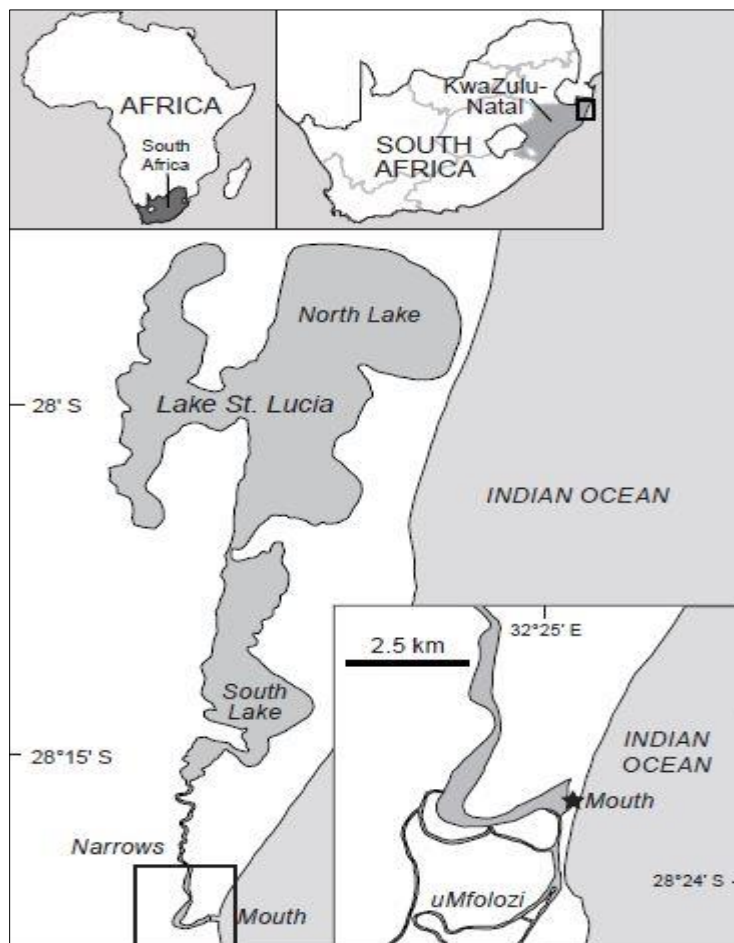


Figure 1.1: A map of the St Lucia estuarine lake in South Africa

There are 6 rivers that feed into Lake St Lucia which are the Mpate, Hluhluwe, Mzinene, Mkuze, Nyalazi and the main freshwater source the Mfolozi River (Begg 1978, Whitfield and Taylor 2009). In the past, the Mfolozi River and St Lucia shared a common mouth connection that allowed for freshwater input into the St Lucia Estuary and seawater input during open mouth conditions at the Mfolozi River (Cyrus et al. 2011). The Mfolozi River input into the shallow St Lucia estuarine system is essential for the alleviation of droughts as high evaporation rates can further lower the depth of the estuarine system (Cyrus et al. 2011). The St Lucia Estuary experiences cyclical shifts of wet and dry phases that can last up to 10 years (Begg 1978, Carrasco et al. 2010, Whitfield et al. 2013). Droughts in the system have been exacerbated since 1952 due to the artificial closure of the St Lucia-Mfolozi link as a result of increased sediment deposition into the estuary (Whitfield et al. 2013). The increased siltation into the St Lucia Estuary was due to the Mfolozi Swamplands being canalized for sugarcane farming (Whitfield and Taylor 2009, Whitfield et al. 2013). The decision of diverting the Mfolozi River away from St Lucia was done without taking into account future implications on the estuary and estuarine ecology (Bate and Taylor 2008, Whitfield et al. 2013).

Following the diversion, drought periods were severe due to the lack of freshwater input that led to prolonged periods of mouth closures (Carrasco et al. 2010, Whitfield et al. 2013). The reduced freshwater input during drought conditions in combination with less than average rainfall led to a detrimental drought period from 2001 to 2010 (Whitfield et al. 2013, Tweedley et al. 2019). Drought periods resulted in evaporative loss exceeding freshwater input thus leading to habitat fragmentation, hypersaline conditions and a strong reversed salinity gradient within the estuary (Cyrus et al. 2011, Carrasco and Perissinotto 2011, Whitfield et al. 2013). These uninhabitable conditions brought about a decline in diversity and abundance of zooplankton, benthic invertebrates and fish during periodic droughts (Pillay and Perissinotto 2008, Carrasco et al. 2010, Jerling et al. 2010, Cyrus et al. 2011). This isolation of the estuary from the sea and the Mfolozi River led to reduced biodiversity, a loss in a nursery site for marine breeding fish and penaeid prawns for completion of their life cycles, which severely affected the catches in the adjacent waters (Whitfield et al. 2013).

Earlier attempts to alleviate drought conditions included the excavation of a back channel into the Narrows from the Mfolozi River during the 1960s (Taylor 2013, Jones 2015) and a link canal in the early 1980s (Whitfield and Taylor 2009). Additionally, a beach spillway was created in 2012 to link the Mfolozi River to St Lucia at the mouth to allow for freshwater input and sea water input when the Mfolozi mouth was open to the sea (Whitfield et al. 2013, Tweedley et al. 2019). The beach spillway was successful in the recruitment of marine, estuarine and freshwater species; however, the channel would close during periods of low rainfall (Van Elden et al. 2014, Tweedley

et al. 2019). The Mfolozi River has one of the highest silt loads in comparison to other estuaries in South Africa (Carrasco et al. 2007, Nhleko et al. 2012, Jones 2015). Siltation is the major concern with regards to fully relinking the St Lucia-Mfolozi River connection (Tweedley et al. 2019). Siltation can bring about a decline in diversity and abundance of organisms (Thrush et al. 2004). However, due to the dire effects of severe drought conditions, scientists and environmental management decided to relink the Mfolozi River to St Lucia by restoring the full link at the mouth region (Tweedley et al. 2019).

A Global Environment Facility (GEF) funded project was initiated in June 2016 by iSimangaliso Wetland Park Authority to restore the connection by dredging spoil slurry out separating the two systems and removing the vegetation on the eastern island of the St Lucia mouth (Tweedley et al. 2019). The project was completed In July 2017. Prior to the rehabilitation project, the estuary experienced a short periodic drought phase which resulted in desiccation of up to 80 % of the lake surface area and disconnected the lake basins. Drought conditions were alleviated through the combination of increased freshwater input from the onset of restoration activities and increased precipitation. Increased freshwater input brought about the transition of the estuary to a freshwater state. The relinkage has been successful in increasing water levels within the estuarine system but there has been an increase in siltation at the mouth region (Jones et al. 2020). Increased siltation has elevated turbidity levels and the increased water input has not yet been sufficient for the initiation of a mouth breaching event to occur (Jones et al. 2020, Cyrus et al. 2020). A mouth breaching event would allow for excess sediment to be flushed out (Van Niekerk et al. 2020) and allow for marine input (Whitfield et al. 2013).

These changes occurring in the pelagic environment especially in terms of fluctuating temperature and salinity levels influence the zooplankton community structure as zooplankton have a short generation time and have been regarded as important indicators of changes in aquatic environments (Wooldridge 1999, Hays et al. 2005). The spatial structure of zooplankton has a strong link to the salinity gradients of estuaries (Wooldridge 1999, Mbandzi et al. 2018). It is therefore essential to record changes within the zooplankton community (Carrasco et al. 2010). Chapter one of this thesis focuses on the impact of the restoration project on the zooplankton community in the mouth region. Chapter two will aid in understanding the system-wide impacts of shifting states on zooplankton dynamics as a short periodic drought is alleviated through increased freshwater input from the onset of the restoration project and with increased precipitation. The dominant zooplankton community in the St Lucia Estuary consists of the resident estuarine calanoid copepods *Pseudodiaptomus stuhlmanni*, *Acartiella natalensis*, the resident cyclopoid *Oithona brevicornis* and the mysid *Mesopodopsis africana* (Grindley 1982, Carrasco et al. 2010, Carrasco and Perissinotto 2015).

There have been numerous studies which have documented the effects of dry conditions (Taylor 2006, Pillay and Perissinotto 2008, Carrasco et al. 2010, Cyrus et al. 2010, Cyrus et al. 2011) on the estuarine system but the current study reports on functioning during a transition to a wet phase, and also records changes associated with the restoration project.

Relevance of study

Estuaries are situated along the coastline, making them more susceptible to climatic changes and anthropogenic activities (Glamore et al. 2016, Masson-Delmotte et al. 2018, Tweedley et al. 2019). Globally, coastal systems will be affected by climate change as the regularity and extremity of droughts, and precipitation events is expected to increase within the next century (Humphries et al. 2016, Masson-Delmotte et al. 2018, Breaux et al. 2019). The resilience of estuarine systems is tested when experiencing changes or disturbances which can cause the ecosystem to experience a regime shift (Glamore et al. 2016, Wets and Yoskowitz 2013, Cooper et al. 2020). A determining factor for estuaries is the quantity and quality of freshwater (Coops et al. 2003). A GEF funded restoration project has fully relinked the St Lucia estuarine system to its historic main freshwater source (Mfolozi River) at the mouth region to have a common mouth connection and to allow for unimpeded freshwater into the St Lucia Estuary to alleviate drought conditions (Whitfield et al. 2013). However, increased siltation from the Mfolozi River is still of concern as it can cause a decline in species diversity and abundance and may facilitate further shallowing of the ecosystem (Thrush et al. 2004). The increased freshwater input has decreased salinities throughout the system, bringing about a prolonged freshwater phase and this spatial variability can be reflected in the changes in the zooplankton community structure. The information obtained from this study would aid in understanding the impacts of this newly prolonged wet phase in the St Lucia Estuary and help management on further decision making with regards to the St Lucia-Mfolozi link.

Aims of study

Overall, this study aims: (1) to determine whether the restoration project had an impact on the zooplankton community structure of the St Lucia mouth region before, during and after the rehabilitation project (February 2015- November 2018) and (2) to determine the spatial and temporal variations in the St Lucia zooplankton community structure from February 2015- November 2017 as the system transitioned to a wet phase.

Objectives:

1. To record the effects of the GEF-funded rehabilitation project on the zooplankton of the mouth area of the St Lucia Estuary by comparing the community structure before, during, and after the restoration project.
2. To investigate the system-wide impacts of a regime shift by monitoring the zooplankton community at 5 representative sites during quarterly surveys as the St Lucia system transitioned from a hypersaline state to a freshwater state.

Chapter 2: Monitoring zooplankton dynamics during hydrological changes in the mouth region of the St Lucia Estuary.

ABSTRACT

Despite the importance of the St Lucia Estuary as a World Heritage Site, it has been subjected to a long history of mouth manipulation. The expansion of agricultural activities in the Mfolozi swamplands resulted in the canalisation of the Mfolozi River and its eventual separation from the St Lucia Estuary in 1952. Periodic droughts are not uncommon to the area, however, freshwater deprivation during drought conditions following this artificial diversion threatened the integrity of this important lake system. A GEF-funded project was initiated in June 2016 to reconnect the Mfolozi River to the St Lucia Estuary, with the aim of increasing freshwater flow and restoring natural mouth functioning, although no mechanisms were in place to deal with the high silt load accompanying Mfolozi waters. Zooplankton constitute a vital link in food webs and respond rapidly to changes in aquatic ecosystems. This study therefore aimed to determine the effects of the rehabilitation project on the zooplankton of the mouth area of the St Lucia Estuary by comparing the community structure before, during, and after the project. Duplicate zooplankton samples and physico-chemical data were collected from the mouth region of the estuary during quarterly monitoring surveys from February 2015 to November 2018. Zooplankton community structure differed significantly before and after the restoration project. There was a clear shift from resident taxa including the mysid *Mesopodopsis africana*, the calanoid copepod *Acartiella natalensis* and the cyclopoid copepod *Oithona brevicornis* to freshwater taxa such as rotifers, cyclopoid copepods, and cladocerans. BIOENV identified salinity and total suspended solids as the critical environmental variables structuring the community. Increased freshwater input has alleviated drought conditions, but siltation is still of concern as a ~1 m layer of mud has persisted in the mouth region, and turbidity levels >1000 NTU were common after heavy rainfall or during windy conditions. Increased siltation will not only lead to the gradual shallowing of the affected region, but high turbidity may negatively affect certain primary and secondary producers, with cascading effects on higher trophic levels.

Keywords: Silt, restoration, mouth, zooplankton, freshwater

2.1. INTRODUCTION

Estuaries are highly dynamic and productive ecosystems, but their positioning along the coastline makes them susceptible to numerous anthropogenic activities such as water abstraction, effluents from waste treatment, etc. (Schlacher and Wooldridge 1996, Thrush et al. 2004, Perissinotto et al.

2013). The catchments of estuaries in highly populated regions are also susceptible to degradation through either agricultural and/or urban developments (Slinger and Breen 1995, Thrush et al. 2004, Perissinotto et al. 2010). Estuarine management and restoration scientists have the critical challenge of figuring out how to reverse past changes through restoration/rehabilitation initiatives, taking societal needs into account as well (Higgs 2005, Weinstein 2008, Elliot et al. 2016).

The St Lucia Estuary is located along the eastern coast of South Africa in KwaZulu-Natal and forms part of the iSimangaliso World Heritage Site (Begg 1978, Carrasco et al. 2010, Jones 2015). It is recognized as a Ramsar Site of International Importance that fosters a high biodiversity (Whitfield et al. 2013, Nunes et al. 2018). Lake St Lucia experiences periodic dry and wet phases that can last up to ten years (Begg 1978, Carrasco et al. 2010, Nunes et al. 2018). The Mfolozi River was historically the main freshwater supply for the St Lucia Estuary (Begg 1978, Taylor 2013, Naidoo 2015), however, the canalisation of the Mfolozi swamplands for agricultural activities during the 1930's (Taylor 2013, Tweedley et al. 2019) led to high silt loads accumulating in the mouth area of the St Lucia Estuary (Begg 1978, Carrasco et al. 2010, Taylor 2013, Tweedley et al. 2019). Increased siltation in the estuary resulted in the smothering of fauna and flora (Thrush et al. 2004), and elevated turbidity levels (Tweedley et al. 2019). The management decision was then taken to artificially separate the two systems in 1952 to prevent further siltation in the St Lucia Estuary (Taylor 2013, Tweedley et al. 2019). Without the important freshwater contribution from the Mfolozi River, drought periods were characterised by prolonged periods of mouth closure, desiccation, habitat fragmentation (Pillay and Perissinotto 2008, Naidoo 2015), hypersaline conditions in the upper reaches and an overall loss of biodiversity (Taylor 2006, Carrasco et al. 2010, Jerling et al. 2010, Carrasco and Perissinotto 2015, Cyrus et al. 2010, Cyrus et al. 2020, Whitfield et al. 2013). Furthermore, prolonged mouth closures have had ecological consequences for the nearshore meta-system (Cyrus et al. 2010) as the estuarine system loses its role as a nursery site for juveniles of marine breeding fish to complete their life cycles (Mann and Pradervand 2007, Cyrus et al. 2010, Cyrus et al. 2020). Socio-economic services obtained from the estuarine system were also affected, as there was a decline in recreational fishing and tourism in the St Lucia Estuary (Taylor 2013, Whitfield et al. 2013, Carrasco and Perissinotto 2015).

Earlier attempts at alleviating drought conditions included the excavation of a back channel into the Narrows from the Mfolozi River during the 1960s (Taylor 2013, Jones et al. 2015), a link canal in the early 1980s (Whitfield and Taylor 2009); and a beach spillway in 2012 (Jones et al. 2016). These past efforts have only partially alleviated drought conditions, mainly in the lower reaches of the system, but were not sufficient enough to restore mouth functioning and prevent further ecosystem degradation from freshwater deprivation (Whitfield et al. 2013). After a scientific

workshop was held in 2010 to discuss the different impacts of the full connection between the two systems, management decided to relink the Mfolozi River and the St Lucia Estuary (Whitfield et al. 2013, Tweedley et al. 2019). The relinkage was to allow for natural mouth functioning and to increase water levels in the system (Whitfield et al. 2013). Additionally, the relinkage would allow for biotic connectivity between the Mfolozi River and the St Lucia Estuary, and with the Indian Ocean during open mouth conditions (Bate et al. 2011, Whitfield et al. 2013, Jones et al. 2020). A Global Environment Facility (GEF) funded project started in June 2016 (Figure 2.1 a) by removing a part of the island in the mouth of the estuary, that was initially placed to artificially separate the two systems (Jones et al. 2020). Additionally, in November 2016 vegetation was cleared from the eastern tip of St Lucia Island (Tweedley et al. 2019). The rehabilitation project was completed in July 2017 (Figure 2.1 b) and has been successful so far in increasing water levels and decreasing salinities throughout the estuarine system (Tweedley et al. 2019, Cyrus et al. 2020), but silt accompanied with freshwater from the Mfolozi River is still a concern.

Sediment deposition may bring about an increase in turbidity that can lead to the decline of aquatic flora and fauna (Richter et al. 1997, Henley et al. 2000). Excessive and prolonged exposure to elevated levels of suspended sediment can perpetually bring about alterations in abundance, diversity and growth of certain biota (Cairns 1990, Henley et al. 2000). Suspended silt can be beneficial for zooplankton as the silt particles allow for adsorption of dissolved organic matter (DOM) that is ingested by the filter feeding zooplankton (Marzolf 1965, Hart 1988, Cuker and Hudson 1992) and increased turbidity can decrease predation of zooplankton by obscuring the vision of zoo-planktivorous fish (McCabe and O'Brien 1983, Jones et al. 2016). Though there can be advantages from siltation for zooplankton, there are more disadvantages. Siltation may result in bottom-up alterations in the food web by limiting primary production due to reduced sunlight penetration (Wulff et al. 1997, Zikhali et al. 2015). High levels of suspended silt could reduce energy transfer along the food chain, decrease zooplankton feeding rates which in turn can potentially reduce the productivity of zooplankton (McCabe and O'Brien 1983, Jones et al. 2016). Additionally, increased siltation can bring about the shallowing of regions in estuaries thereby reducing habitat for biota (Thrush et al. 2004, Whitfield et al. 2012). Catchment management therefore needs to provide strategies to control both the mobilisation of sediment as well as the delivery (Henley et al. 2000, Rollason et al. 2018).

Zooplankton form a vital component of food webs, linking primary producers to higher trophic levels (Deale et al. 2013, Jerling and Weerts 2018). Zooplankton have short generation times allowing for a rapid response to stresses within aquatic ecosystems (Moore and Folt 1993, Dam 2013, Rice et al. 2014). Generally, the variation within the zooplankton community indicates the

changes in water quality of an ecosystem (Inaotombi and Gupta 2019). The dominant zooplankton in the St Lucia Estuary include the estuarine calanoid copepods *Acartiella natalensis*, *Pseudodipatomus stuhlmanni*, the resident cyclopoid copepod *Oithona brevicornis* and the mysid *Mesopodopsis africana*. With the estuary fully linked to the Mfolozi River, the zooplankton community composition will likely change (Hays et al. 2005) as the estuary transitions to an almost fully freshwater state (Jones et al. 2020). It was hypothesized that there would be a difference in the zooplankton community composition before and after the restoration project. The current study aimed to record the changes in the zooplankton community structure in the St Lucia mouth region before, during, and after the GEF funded restoration project took place.

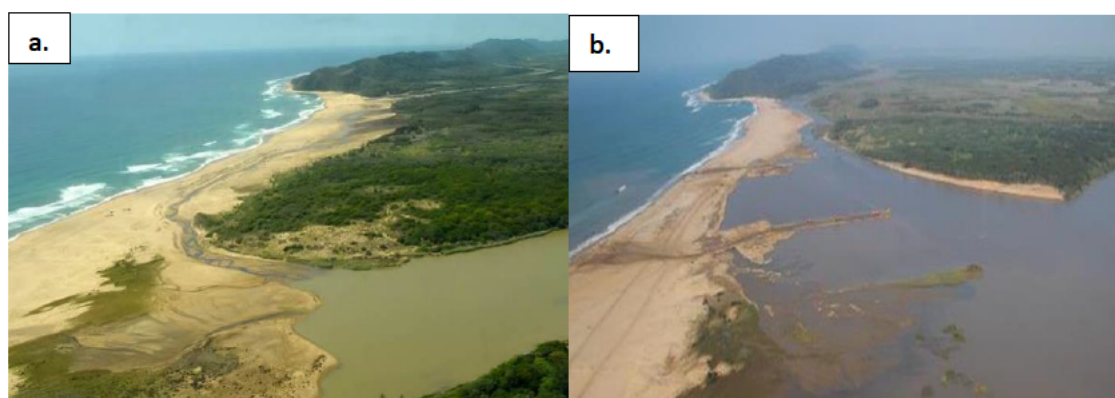


Figure 2.1: a. An aerial view of the mouth region before the restoration project began (Photo by D. King) and b. Shortly after the restoration project was completed with the mouth fully linked to the Mfolozi River (Photo by R. Taylor).

2.2. MATERIALS AND METHODS

2.2.1. Study site and sample collection

The St Lucia estuarine lake is a shallow water ecosystem located in Northern Kwa-Zulu Natal, South Africa. The St Lucia Estuary comprises of three shallow lakes that include the South Lake, North Lake and False Bay, which are interconnected to a 21 km long channel (The Narrows) leading to the estuarine mouth (Perissinotto et al. 2010, Figure 2.2). The estuarine mouth empties out into the Indian Ocean when there is no sand barrier separating the estuary from the ocean (Perissinotto et al. 2010). Quarterly surveys were carried out at the mouth (Figure 2.2) from February 2015 to November 2018 to record the changes that occurred before (February 2015- May 2016), during (August 2016- April 2017) and after (August 2017- November 2018) the completion of the restoration project. Samples of zooplankton, sediment grain size, and microphytobenthic biomass and phytoplankton biomass were collected together with physico-chemical data.

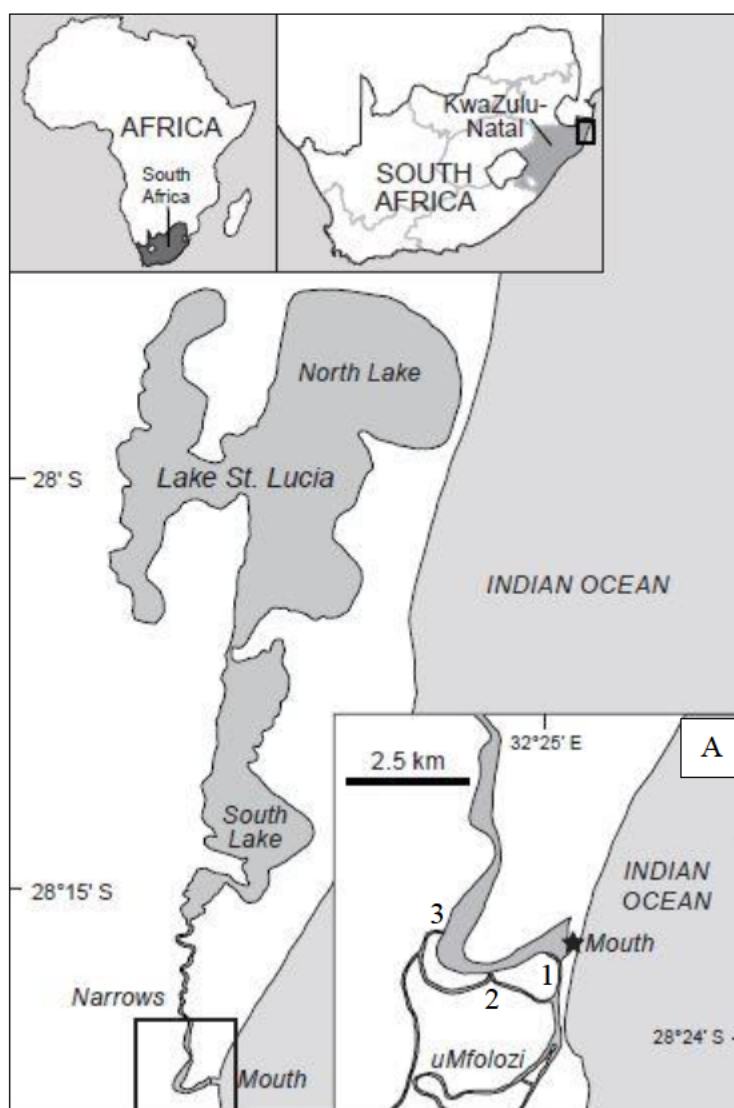


Figure 2.2: The St Lucia estuarine lake map showing the sampling station at the Mouth (A) and the three links to the Mfolozi River through the beach spillway (1), back channel (2) and the link canal (3) (Figure adapted from Jones et al. 2020).

2.2.2. Environmental variables

A YSI 6600-V2 probe was used to measure the temperature ($^{\circ}\text{C}$), pH, salinity, dissolved oxygen concentration (mg l^{-1}), and turbidity (Nephelometric turbidity units, NTU) of the water. When the water depth was very shallow the probe was either laid horizontally to ensure that all the sensors were submerged, or a bucket of water was collected to ensure the probe was submerged in the water. On some occasions, a hand-held refractometer (ATAGO S/Mill-E) was used for salinity determination and a turbidity meter instrument (HACH2100Qis) was used to obtain turbidity readings. During sampling occasions, subsurface water samples ($n=2$) were collected to determine dissolved inorganic nitrogen (DIN) and phosphorous (DIP), which were processed at Nelson

Mandela University (NMU). Rainfall data for St Lucia was supplied by Ezemvelo KZN Wildlife authority.

2.2.3. Phytoplankton and microphytobenthic biomass

To determine phytoplankton biomass, duplicate subsurface water samples were collected. Between 150 ml and 250 ml of estuarine water was vacuum (1.5 BAR) filtered through RGF Econofilt filters (1 μm) with the use of a Millipore filtration system. After filtration, the filters were placed in 8 ml of 90 % acetone and kept in the freezer for extraction of phaeopigments and chlorophyll *a* in the dark for 48 hours (Nozais et al. 2001). Triplicate microphytobenthic biomass (MPB) samples were collected with the use of a Perspex twin corer (2 cm internal diameter). The upper 1 cm of surface sediment was collected and placed in 100 ml polyethylene bottles containing 30 ml of 90 % acetone (Nozais et al. 2001). The bottles were kept in the freezer after collection for 48 hours. Both the MPB and phytoplankton biomasses were determined using a fluorometer (Turner Designs 10-AU non-Acidification system).

2.2.4. Total suspended solids, particulate organic matter and sediment organic matter

Duplicate subsurface water samples were collected to measure total suspended solids (mg l^{-1}) and particulate organic matter (%). The estuarine water (150-250 ml) was vacuum filtered through pre-combusted (420 °C, 6 hours) RGF Econofilt filters and dried in an air-circulating oven (48 hours, 60 °C). Once dry, the filters were weighed using a Shimadzu AUW220D Uni bloc balance and combusted again (420 °C, 6 hours) in a muffle furnace, thereafter the filters were re-weighed for the calculation of both total suspended solids (TSS) and particulate organic matter (POM) (Carrasco et al. 2007, Jones et al. 2016). Total suspended solids were calculated by finding the difference between the dry and pre-combusted weights which were then divided by the volume of water filtered and the TSS measurements were used to calculate POM as a percentage (Carrasco et al. 2007, Jones et al. 2016). Sediment organic matter (SOM) was analysed by firstly collecting triplicate sediment samples with the use of a Perspex twin corer (2 cm internal diameter). Each replicate was obtained through combining 2 cores of the upper 1 cm of sediment in pre-weighed crucibles. The sediment was dried in an air-circulating oven (60 °C, 48 hours), re-weighed, and combusted (420 °C, 6 hours) once again to calculate SOM as a percentage.

2.2.5. Zooplankton

Duplicate samples of zooplankton were collected during daytime with the use of an epibenthic sled which was fitted with a 100 μm mesh. The net mouth had a radius of 18.5 cm and was towed 27 m. To determine the volume filtered, the distance towed was multiplied by the mouth area (≈ 1.43

m³) (Carrasco et al. 2010). On sampling trips where the water was too shallow, water (30 L - 100 L, depending on water availability) was filtered through a handheld 100 µm sieve. In both cases, the zooplankton in the net was gently transferred into 500 ml polyethylene bottles containing 5 % phloxine stained formalin. In the laboratory, each zooplankton sample was diluted to 0.6 - 5 L, depending on the density. Triplicate subsamples were taken from mid-depth using either a 10 ml or 20 ml plastic vial attached to a metal rod, after stirring the sample to ensure a homogenous solution (Carrasco et al. 2010). A dissecting microscope (Zeiss Stemi 508) was used to count (magnification: 40×) and identify the zooplankton to the lowest possible taxonomic level with the use of identification guides (Day 1969, Griffiths 1976, Fernando 2002, Conway et al. 2003). Smaller zooplankton was identified with the use of a compound microscope (Nikon Eclipse E100) (Magnification: 100×). The use of a 100 µm mesh would have underestimated the abundance of smaller zooplankton taxa. Also, as a result of the hyperbenthic sampling method, benthic taxa were included which would have overestimated species richness and abundance. The counts from subsamples were converted to abundance (ind. m⁻³) and the coefficient of variation was consistently <10 %.

2.2.6. Statistics analyses

The univariate statistical analyses were run using STATISTICA version 13. 4 for Windows. The data were ranked as they violated the assumptions for parametric testing (Conover and Iman 1981). The One-Way Analysis of Variance (ANOVA) test was used to determine if there was a significant difference in zooplankton abundance, taxonomic richness, and the environmental variables before, during and after the restoration project. A Shannon-Wiener diversity index (H') was calculated to determine the evenness in taxonomic richness before, during, and post restoration project. Spearman's Rank correlation determined whether there was any relationship between the community parameters (abundance and taxonomic richness) and environmental variables.

Multivariate analyses were run using the PRIMER package (version 6.0) (Clarke and Warwick 2001). A square root transformation was used on the data to reduce the weighting of highly abundant taxa. A cluster diagram was obtained from a Bray Curtis similarity resemblance to observe differences in the zooplankton community structure before, during, and after the restoration project. PERMANOVA uses the ANOVA experimental design to test the response variables to one or more factors based on the similarity resemblance (Anderson et al. 2008). According to the experimental design, the total sum of squares is partitioned according to the factors (Anderson et al. 2008). Both a pseudo-F statistic and a *p* value are computed based on permutations (Anderson et al. 2008). The PERMANOVA main test was run to determine whether there was a significant

difference between the phases of the study and a pairwise comparisons was done to identify where the differences occurred. SIMPER was run to identify species that contributed to the differences between the phases. BIOENV (Harmonic spearman Correlation) was used to correlate the zooplankton community structure to the environmental variables and find out which environmental variables shaped the community structure.

2.3. RESULTS

2.3.1. Environmental variables

Over the course of the four-year study period (February 2015 to November 2018), temperatures were seasonal with the lowest water temperature of 18.3 °C recorded in winter (July 2015) and the highest water temperature of 34.6 °C recorded in summer (February 2018) (Figure 2.3). Salinity was higher before the commencement of the restoration project and it was lower during as well as after the project was completed (Figure 2.3). Salinity differed significantly ($F_{2,13} = 5.17, p < 0.05$) among the three periods, with salinity levels in the before period being significantly higher than during the restoration project (Tukey post hoc test $p < 0.05$). The highest salinity was recorded in May 2015 before the restoration project with a value of 35 due to the intrusion of seawater as the mouth of the Mfolozi River was open to the sea (Figure 2.3). The lowest salinity (0.13) was observed in November 2016 during the rehabilitation project. Aside from salinity, none of the other environmental variables showed significant differences before, during and after the rehabilitation project (One-Way ANOVA, $p > 0.05$). Overall total rainfall during 2015 was lower in comparison to the rest of the years (Figure 2.3). There were peaks that occurred during May 2016 (159.9 mm), November 2016 (163.4 mm), January 2017 (182.6 mm), and May 2018 (232.4 mm) (Figure 2.3). The increase in rainfall during November 2016 coincided with the lowest salinity level recorded in the study (Figure 2.3) and during the same time, there were equinox tides (Fox and Mfeka 2016).

Turbidity was lower before the restoration project and peaked in November 2016 (1246 NTU) during the dredging activities (Figure 2.3). Turbidity was generally higher after the restoration project was completed (Figure 2.3). Dissolved oxygen concentration varied throughout the years with the highest values occurring in August 2016 (9.78 mg l⁻¹), November 2017 (9.93 mg l⁻¹), and November 2018 (9.92 mg l⁻¹). The lowest DO concentration was recorded after the completion of the restoration project in February 2018 (3.45 mg l⁻¹) (Figure 2.3). The pH levels were fairly constant (≈ 8) throughout the years with the highest pH observed in November 2017 (9.13).

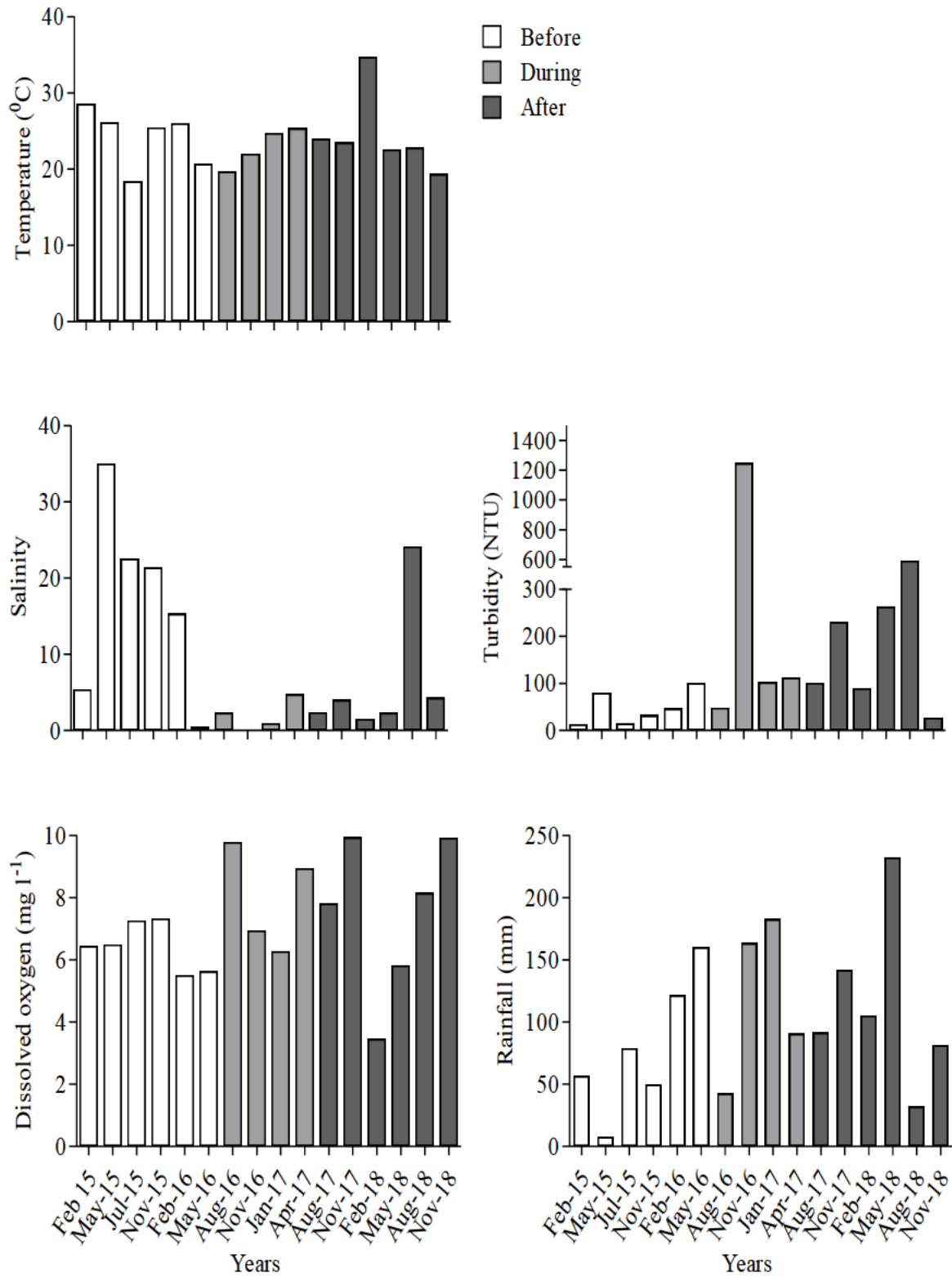


Figure 2.3: Environmental variables before, during and after the restoration project at the mouth region of the St Lucia Estuary over the four-year study period.

2.3.2. Phytoplankton and microphytobenthic biomass

Phytoplankton biomass varied during the study period but was generally higher after the rehabilitation project had been completed compared to before the project (Figure 2.4). Phytoplankton biomass did not differ before, during and post restoration project ($F_{2,13} = 2.55, p > 0.05$). The highest phytoplankton biomass was observed in February 2018 (437.24 mg m^{-3}) post restoration project completion and the lowest was in November 2016 (0.94 mg m^{-3}) during the restoration project (Figure 2.4). Similarly, to the phytoplankton biomass, microphytobenthic biomass had a high variability (Figure 2.4). Although microphytobenthic biomass was generally lower during the project activities, there were no significant differences found in between the three periods ($F_{2,13} = 1.35, p > 0.05$) (Figure 2.4).

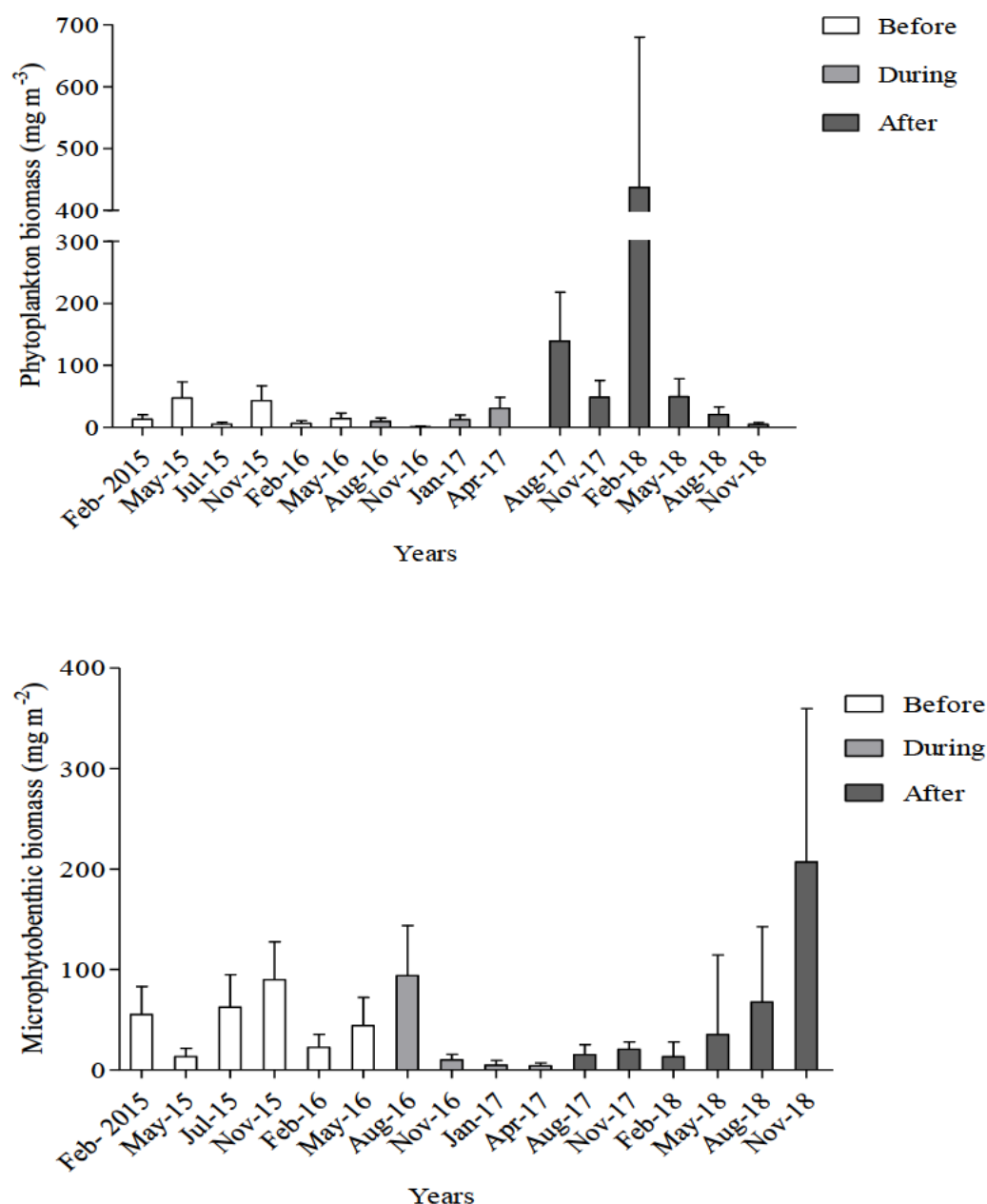


Figure 2.4: Phytoplankton and microphytobenthic biomass before, during and after the rehabilitation project at the mouth region during the study period (mean \pm SD).

2.3.3. Total suspended solids, particulate organic matter and sediment organic matter

Total suspended solids (TSS) varied, ranging from 31.45 mg l⁻¹ (February 2015) before the restoration project to 714.1 mg l⁻¹ (May 2018) post-project completion (Figure 2.5). The second highest TSS value was recorded during restoration project activities in November 2016 (645.65 mg l⁻¹) (Figure 2.5). There were no significant differences ($F_{2,13} = 0.09$, $p > 0.05$) found in TSS among the three periods of the study. Particulate organic matter (POM) forms a part of TSS

which also varied throughout ranging from 12.06 % (February 2016) during the restoration project to 29.59 % (August 2018) post project completion with no significant differences occurring ($F_{2,13} = 0.11$, $p > 0.05$) (Figure 2.6). Overall, sediment organic matter (SOM) was lower before the project started, with the lowest being 0.39 % (May 2015) (Figure 2.6). The highest SOM % was recorded during the rehabilitation project in November 2016 (7.67 %) (Figure 2.6). Although SOM was generally higher post project completion, there were no significant differences ($F_{2,13} = 1.42$, $p > 0.05$) found before, during and after the restoration project.

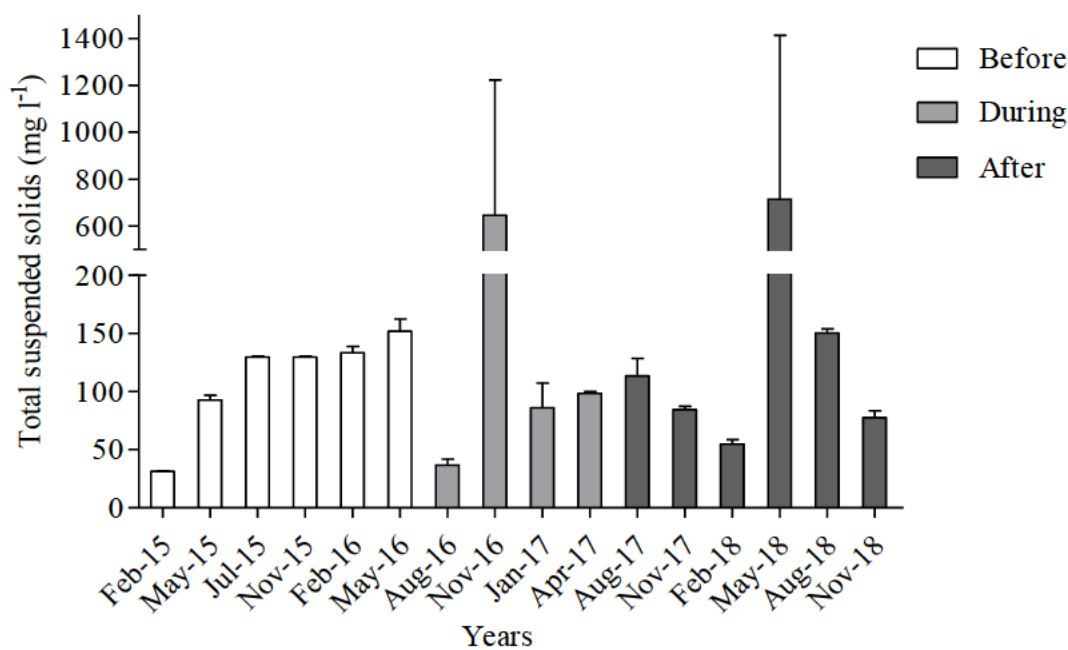


Figure 2.5: The amount of total suspended solids found in the mouth region before, during and after the rehabilitation project over the course of the study period (mean \pm SD).

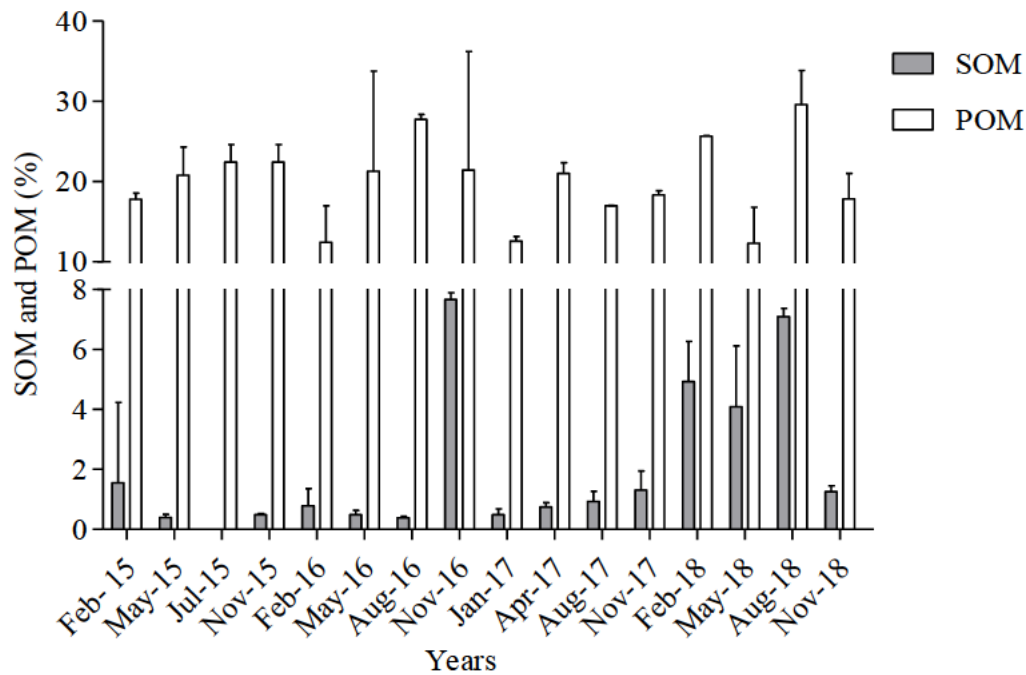


Figure 2.6: Particulate organic matter and sediment organic matter percentages over time (mean \pm SD). No bars indicate missing data.

2.3.4. Zooplankton abundance and taxonomic richness

Total zooplankton abundance ranged from 1.2×10^3 ind. m^{-3} to 8.79×10^5 ind. m^{-3} during the course of the study period (February 2015 - November 2018). Although abundance during the dredging period was generally lower than before and after the project (Figure 2.7 & 2.8), there was no significant difference in zooplankton abundance before, during and after the restoration project ($F_{2,13} = 0.24$, $p > 0.05$). Zooplankton abundance during the three periods were as follows (mean \pm SD): before = $2.03 \times 10^5 \pm 3.43 \times 10^5$ ind. m^{-3} , during = $3.6 \times 10^4 \pm 2.1 \times 10^4$ ind. m^{-3} , after = $6.2 \times 10^4 \pm 4.2 \times 10^4$ ind. m^{-3} .

Taxonomic richness was higher before the restoration project with the highest occurring in May 2015 (46 species, Figure 2.9). The lowest taxonomic richness occurred in August 2016 during the restoration project (11 species, Figure 2.9). There were no significant differences found in taxonomic richness before, during, and after the restoration project ($F_{2,13} = 0.17$, $p > 0.05$). Taxonomic richness for the three periods were as follows (mean \pm SD): before = 20.5 ± 12.7 , during = 20.8 ± 13.7 , after = 16.8 ± 8.03 . The Shannon-Weiner diversity index (Figure 2.9 & 2.10) shows there were no differences in between the three periods, which is in concurrence with no significant differences in taxonomic richness. The three periods (before, during and after restoration

project) had peaks in taxa richness, with May 2015 having the highest diversity index (Figure 2.9). The lowest diversity index occurred during May 2016, when the highest abundance was recorded with a low diversity (Figure 2.7 & 2.9). Shannon-Weiner diversity index values pre-restoration project ranged from 1.14 to 3.33, during restoration activities were from 1.5 to 3.13 and post restoration activities ranged from 1.82 to 3.06 (Figure 2.9).

There were no significant relationships between zooplankton abundance and the environmental parameters ($p > 0.05$), but there was a significant positive correlation between taxonomic richness and temperature ($R = 0.50$, $p < 0.05$) and a significant negative correlation between taxonomic richness and MPB ($R = -0.57$, $p < 0.05$).

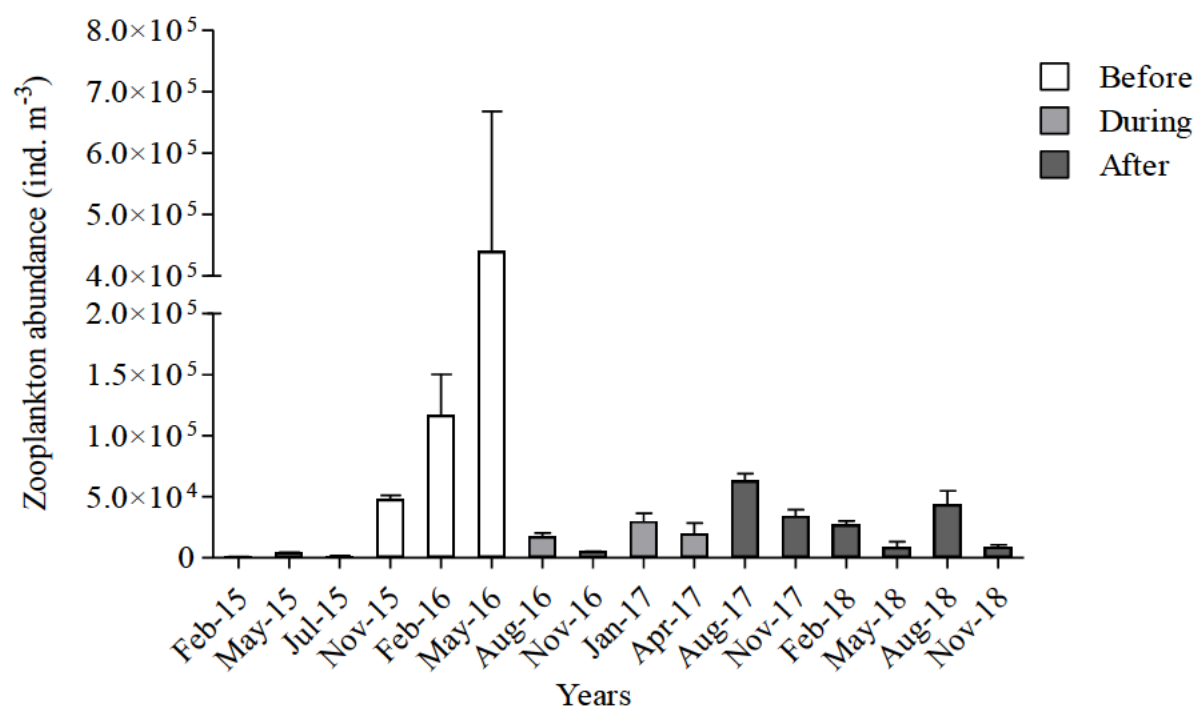


Figure 2.7: Average zooplankton abundance over time during the study period (mean ± SD).

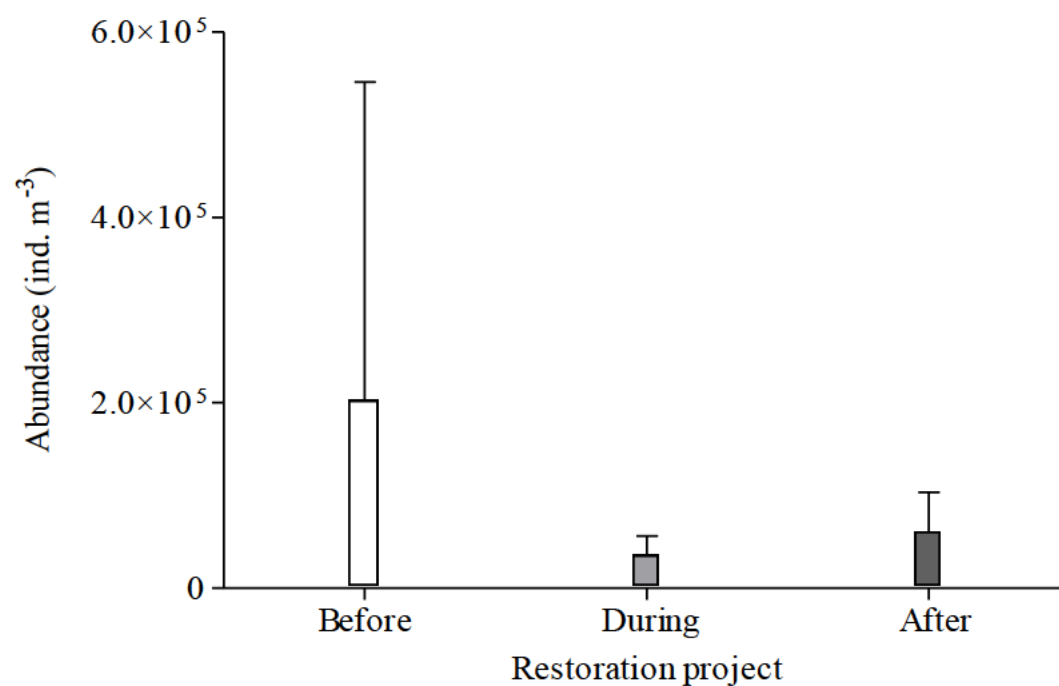


Figure 2.8: Zooplankton abundance before, during and after the restoration project (mean ± SD).

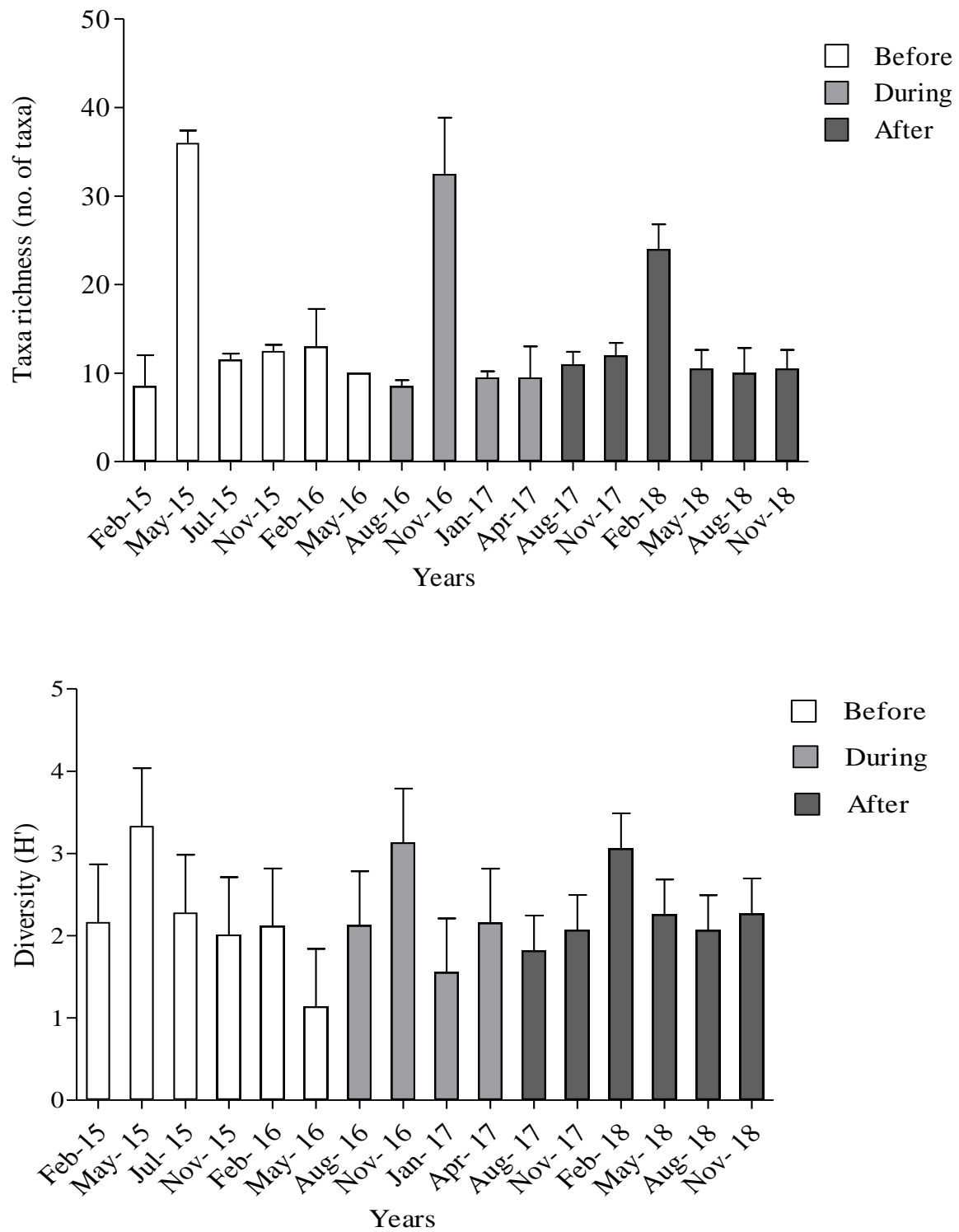


Figure 2.9: Taxonomic richness and a Shannon-Weiner diversity index over time during the study period (mean \pm SD).

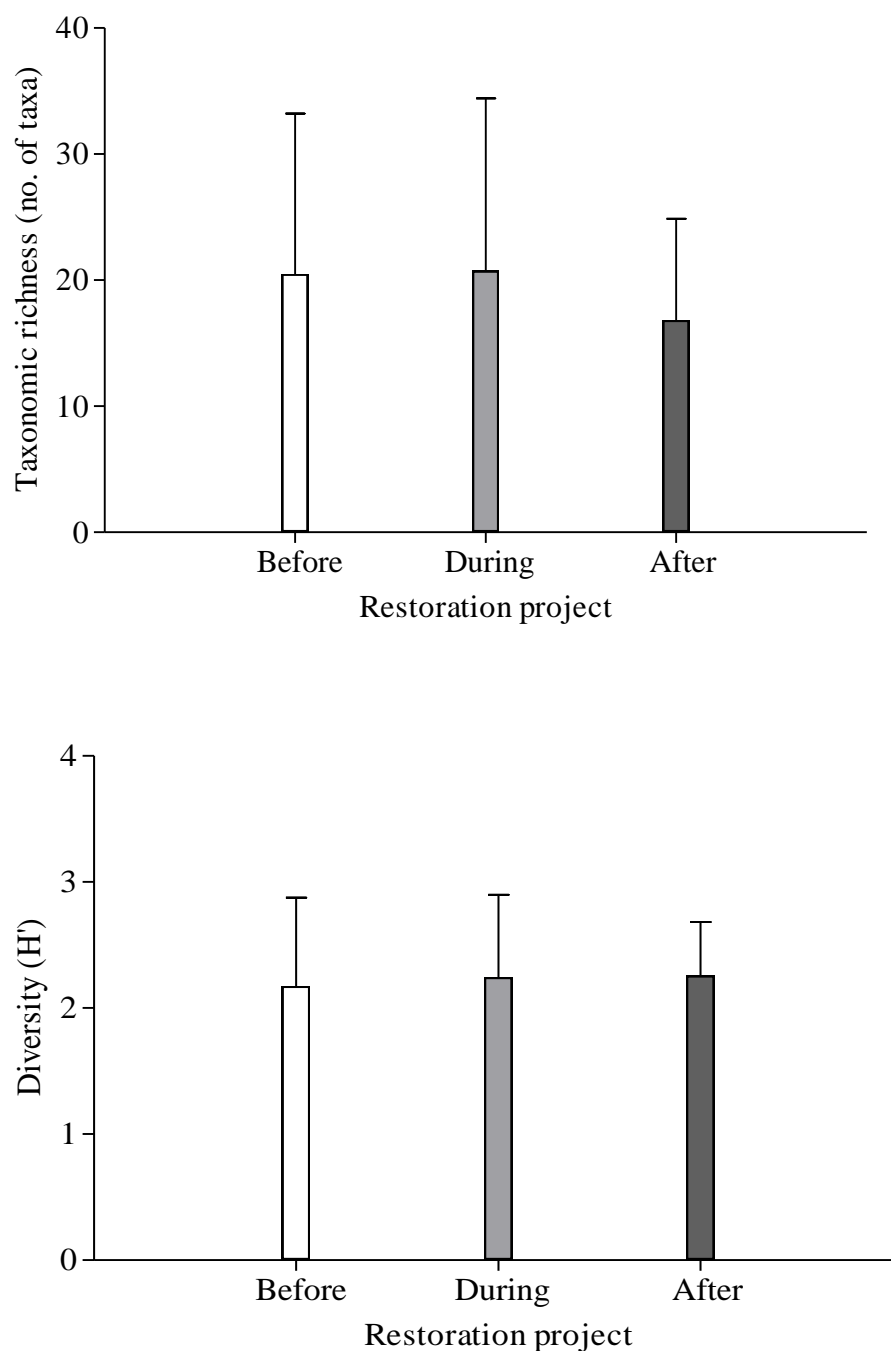


Figure 2.10: Taxonomic richness and Shannon-Weiner diversity index before, during and after the rehabilitation project (mean \pm SD).

2.3.5. Zooplankton community structure

A total of 96 taxa were recorded during the four-year study period at the mouth region of the St Lucia Estuary. This number also included some benthic taxa due to the hyperbenthic sampling

method. PERMANOVA revealed there was a significant difference in community structure between the phases (Pseudo- $F = 1.81$, $p < 0.01$). A pairwise PERMANOVA revealed that the community structure present before the restoration project, was significantly different from that after project completion (pairwise comparison, $p < 0.01$).

The resident cyclopoid copepod *Oithona brevicornis* and typical estuarine species including the calanoid copepods *Pseudodiaptomus stuhlmanni*, *Acartiella natalensis*, and the mysid *Mesopodopsis africana* dominated the zooplankton community in the mouth region before the project began (Figure 2.11). Thereafter there was a transition to freshwater/brackish zooplankton such as rotifers, cladocerans, and cyclopoid copepods (Figure 2.11). Post rehabilitation project, there was a decline in the estuarine resident species, except for *P. stuhlmanni*, which persisted in low densities after the restoration project (Table 2.1).

The cluster diagram revealed that the communities from both February and July 2015 (before the restoration project) had less than 20 % similarity to the rest of the samples (Figure 2.12). The pre-restoration community was mainly dominated by estuarine taxa. The zooplankton communities from November 2015 and February 2016 (before the restoration project) grouped with 55 % similarity (Figure 2.12). There were two outliers which were May 2015 and May 2016 having 25 % similarity (Figure 2.12). There was marine input in May 2015 and May 2016 had an unusually high abundance of nauplii and the rotifer *Brachionus plicatilis* (Table 2.1). The remaining samples had > 40 % similarity in community structure. The highest similarity (62 %) occurred between the January and November 2017 communities (Figure 2.12). The during and post-restoration project communities had mainly freshwater species as the resident species declined.

SIMPER analysis revealed that the highest average dissimilarity (84.75 %) in the community structure occurred in samples collected before and after the restoration project. The main taxa contributing to the dissimilarity were copepod nauplii (16.48 %), cyclopoids (13.53 %), rotifers (13.35 %), the calanoid copepod *Acartiella natalensis* (7.64 %), cladocerans (4.39 %), the mysid *Mesopodopsis africana* (3.34 %) and the cyclopoid copepod *Oithona brevicornis* (1.53 %). BIOENV identified salinity and TSS as the main environmental variables correlating with the zooplankton community ($R = 0.212$).

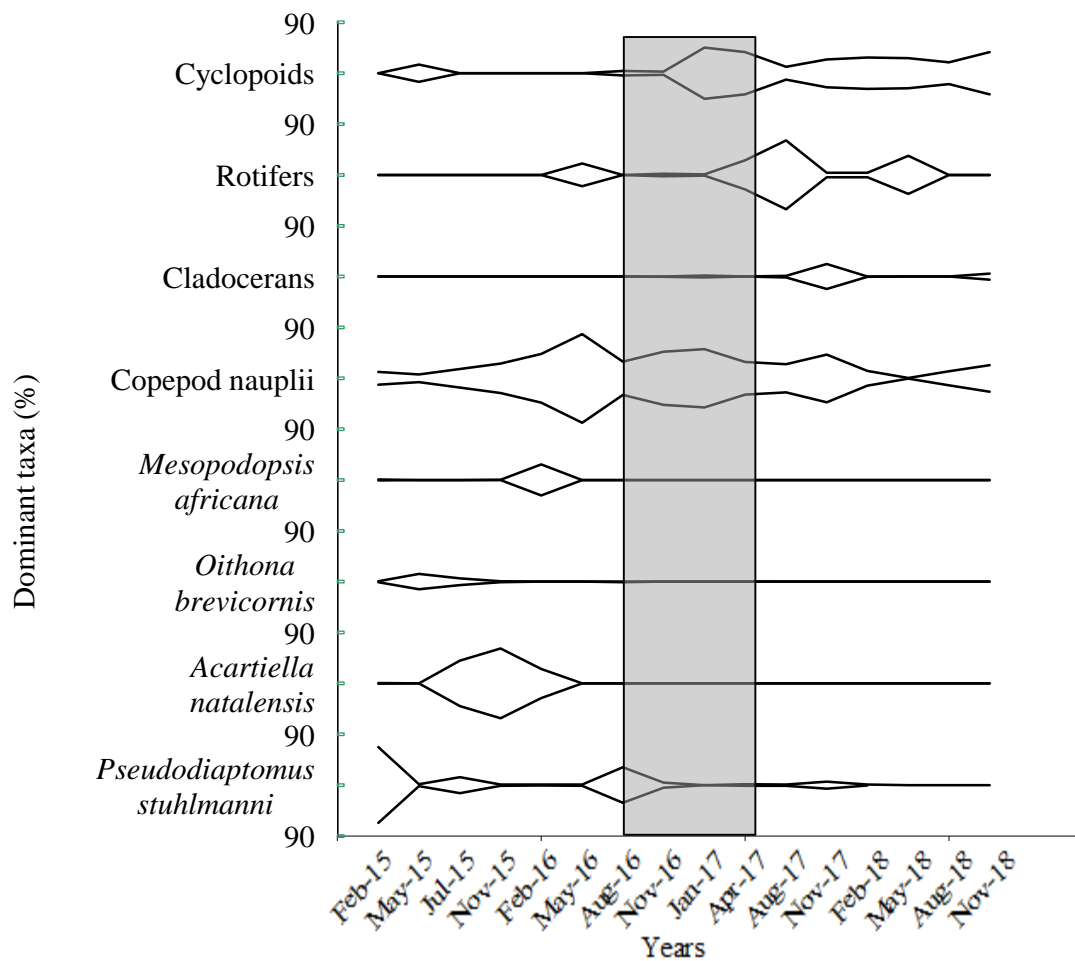


Figure 2.11: Total percentage composition of the dominant zooplankton taxa (>90 %) recorded during the study period. The shaded area indicates the time of rehabilitation project activities.

Table 2.1: Zooplankton abundance (mean ind. m⁻³ ± SD) in the mouth region before, during and after the restoration project. Unid: Unidentified.

	Before	During	After
FORAMINIFERA			
Foraminifera	1.914 ± 4.470	-	8.333 ± 28.87
Allogromids (Unid.)	28.73 ± 95.98	12.40 ± 35.08	16.67 ± 57.74
<i>Fabrea cf. salina</i>	-	1.550 ± 4.384	-
CNIDARIA			
Jelly polyp	0.057 ± 0.199	-	-
Hydromedusae juveniles	0.689 ± 1.992	-	-
<i>Obelia</i> sp.	6.086 ± 15.03	-	-
ROTIFERA			
<i>Brachionus</i> spp.	-	1 334 ± 2 463	158.4 ± 337.5
<i>Brachionus calyciflorus</i>	-	25.84 ± 73.07	6 709 ± 14 924
<i>Brachionus patulus</i>	-	18.60 ± 36.91	-

Table 2.1 cont.

	Before	During	After
<i>Brachionus cf. plicatilis</i>	14 774 ± 44 011	-	-
<i>Brachionus quadridentatus</i>	-	17.22 ± 48.72	-
<i>Brachionus rotundiformis</i>	-	-	1 250 ± 3 381
<i>Lecane grandis</i>	27.78 ± 96.23	1.550 ± 4.384	150.0 ± 350.3
ANNELIDA			
Polychaete larvae	50.09 ± 110.8	108.3 ± 236.2	191.7 ± 571.2
Nereidae	0.57 ± 1.99	-	258.3 ± 621.5
Oligochaeta (unid.)	1.148 ± 3.988	37.20 ± 69.21	3 867 ± 9 035
Nematoda (Unid.)	16.46 ± 35.10	247.1 ± 368.1	542.1 ± 743.3
PLATYHELMINTHES			
Turbellaria	9.569 ± 33.15	60.27 ± 116.1	-
Anura	-	0.155 ± 0.438	-
ARTHROPODA			
Branchiopoda			
<i>Diaphanosoma cf. excisum</i>	-	27.39 ± 72.58	40.18 ± 103.7
<i>Moina cf. micrura</i>	-	103.3 ± 194.9	461.9 ± 1 058
<i>Moina cf. oryzae</i>	-	-	51.67 ± 128.5
<i>Moina</i> spp.	-	3.100 ± 8.769	919.6 ± 1862
Malacostraca			
Decapoda			
<i>Caridina</i> sp.	-	0.078 ± 0.219	-
<i>Caridina africana</i>	-	0.403 ± 0.595	-
<i>Palaemon concinnus</i>	-	0.078 ± 0.219	-
<i>Palaemon debilis</i>	-	0.086 ± 0.244	-
Decapod juvenile (Unid.)	0.057 ± 0.199	-	-
Caridean larvae	5.193 ± 10.90	3.671 ± 6.997	9.683 ± 28.59
Megalopa	15.60 ± 41.64	-	-
Zoeae	-	15.66 ± 35.34	-
Mysida			
<i>Mesopodopsis africana</i>	5 352 ± 12 506	0.086 ± 0.244	-
Cumacea (Unid.)	0.976 ± 3.381	-	-
Tanaidacea			
<i>Halmyrapseudes cooperi</i>	55.73 ± 192.4	-	1 083 ± 1 815
Amphipoda			
<i>Afrochiltonia capensis</i>	5.670 ± 19.21	-	71.67 ± 167.4
Corophidae	2.835 ± 9.606	-	-
<i>Grandidierella</i> sp.	92.64 ± 227.5	-	-
<i>Grandidierella bonnieroides</i>	2.835 ± 9.606	-	-
<i>Orchestia</i> sp.	-	0.078 ± 0.219	-
Talitridae (Unid.)	-	0.698 ± 1.302	-
Stenothoidae	0.172 ± 0.597	-	-
Maxillopoda			
Cirripedia nauplii	12.44 ± 29.15	-	-
Copepoda			
Copepod nauplii	68 113 ± 137 717	7 135 ± 5 782	6 899 ± 6 753
<i>Acartia danae</i>	0.957 ± 3.315	-	-
<i>Acartiella natalensis</i>	9 980 ± 15 536	-	-
<i>Paracalanus</i> spp.	80.38 ± 188.1	-	-
<i>Pseudodiaptomus stuhlmanni</i>	1 238 ± 2 246	1 463 ± 2 399.	537.3 ± 940.2
<i>Temora</i> sp.	0.957 ± 3.315	-	-
Calanoid copepodites (Unid.)	441.1 ± 1 072	-	-
Cyclopoida			
Cyclopidae	143.5 ± 251.5	2 026 ± 3 616	3 292 ± 2 942
<i>Oithona brevicornis</i>	164.4 ± 300.1	41.67 ± 117.9	-
<i>Paracyclops</i> sp.	-	-	33.33 ± 88.76
<i>Mesocyclops</i> sp.	-	-	8.333 ± 28.87
<i>Thermocyclops</i> sp.	-	-	58.33 ± 137.9

Table 2.1 cont.

	Before	During	After
Cyclopoid copepodites (Unid.)	10.53 ± 21.60	3 427 ± 6 320	2 735 ± 3 276
<i>Corycaeus</i> sp.	4.402 ± 10.15	1.550 ± 4.384	-
<i>Farranula</i> sp.	0.957 ± 3.315	-	-
Harpacticoida			
<i>Clytemnestra</i> sp.	1.914 ± 6.629	-	-
Canthocamptidae	2.871 ± 9.944	-	-
Cletodidae	-	-	25.00 ± 45.23
Darcythompsoniidae	-	18.60 ± 52.61	8.33 ± 28.87
<i>Euterpina acutifrons</i>	2.926 ± 9.928	-	-
Ectinosomatidae	30.65 ± 95.83	6.201 ± 11.48	-
<i>Microsetella norvegica</i>	0.957 ± 3.315	-	-
<i>Microsetella</i> sp.	20.09 ± 49.96	-	-
Miraciidae	1.914 ± 6.629	7.826 ± 14.90	-
<i>Nitocra taylori</i>	-	62.40 ± 138.9	289.1 ± 660.7
<i>Porcellidium</i> sp.	0.057 ± 0.199	-	-
Tegastidae	27.78 ± 96.23	-	-
Harpacticoids (Unid.)	68.76 ± 188.9	48.35 ± 74.40	525.0 ± 954.5
Insecta			
Hymenoptera	8.493 ± 19.78	-	2.500 ± 6.216
Hemiptera	-	984.1 ± 1 700	55.00 ± 91.80
Corixidae	-	191.6 ± 370.7	-
Diptera fly	-	41.67 ± 117.9	-
Ephemoptera	-	123.3 ± 272.5	70.00 ± 103.9
Chironomid larvae	0.057 ± 0.199	15.61 ± 29.37	43.53 ± 77.85
Chironomid egg	-	4.650 ± 9.227	-
Arachnida	2.778 ± 9.623	4.253 ± 11.75	-
<i>Annurida</i> sp.	83.33 ± 207.2	-	0.833 ± 2.887
Hydrachnidia	-	-	9.167 ± 28.75
Trichopteran larvae	-	-	2.500 ± 8.660
Coleoptera	6.742 ± 19.19	2.578 ± 7.043	17.50 ± 57.54
Orthopteran	-	-	0.833 ± 2.887
Coleoptera pupa (different stages)	-	0.078 ± 0.219	16.67 ± 57.74
Damselfly larvae	1.914 ± 6.629	25.00 ± 70.711	-
Culicidae	-	-	1.67 ± 5.77
Insect larvae (Unid.)	-	-	33.33 ± 65.13
Ostracoda (Unid.)	38.88 ± 93.96	301.0 ± 408.4	318.5 ± 715.4
Gastropoda			
Gastropod larvae	200.2 ± 441.7	3.100 ± 8.769	-
Bivalvia			
Bivalve larvae	18.18 ± 47.84	-	-
Cyphonautes larvae	123.7 ± 288.0	-	-
Chaetognatha (Unid.)	0.115 ± 0.268	0.078 ± 0.219	-
Fish egg	16.97 ± 25.62	4.978 ± 11.37	10.89 ± 29.35
Fish larvae	64.91 ± 66.74	1.550 ± 4.384	1.781 ± 5.743
<i>Ambassis ambassis</i>	0.057 ± 0.199	0.405 ± 0.599	-
<i>Oreochromis mossambicus</i>	-	0.930 ± 2.173	-
<i>Clarias garipinus</i>	-	0.388 ± 0.736	-

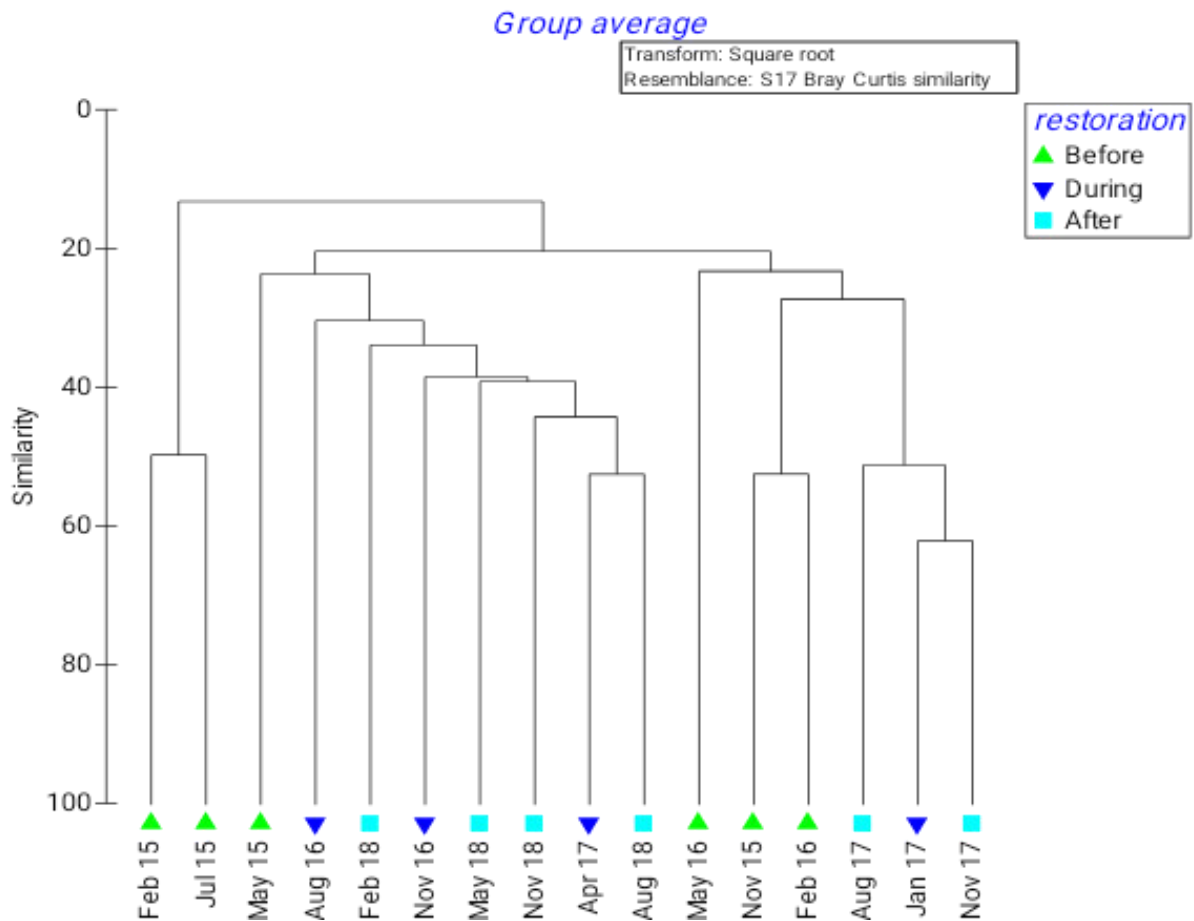


Figure 2.12: A Bray-Curtis similarity dendrogram showing the similarity of the zooplankton community structure from samples collected before, during and after the restoration project.

2.4. DISCUSSION

Estuarine systems are increasingly being subjected to extreme climatic events and anthropogenic impacts such as agricultural activities, hydrodynamic alterations and urban developments, to name a few (Perissinotto et al. 2010, Glamore et al. 2016, Elliot et al. 2016, Nunes et al. 2018). The degradation of estuarine ecosystems has led to the decline of ecosystem goods and services provided, including recreational activities as well as tourism, spawning sites, nursery habitat provision, filtration, and detoxification services (Elliot et al. 2016, Barbier 2016, Glamore et al. 2016). The St Lucia estuarine lake has undergone historic alterations, bringing about extreme changes in the mouth functioning (Whitfield et al. 2013) which has ultimately threatened the integrity of the system (Taylor 2006, Cyrus et al. 2010). The GEF-funded rehabilitation project (June 2016 to August 2017) was implemented to restore the St Lucia-Mfolozi mouth to allow increased freshwater input and natural mouth functioning (Whitfield et al. 2013, Cyrus et al. 2020,

Jones et al. 2020). This recent rehabilitation project has been successful with regards to increasing freshwater input into the system, but the silt-laden water accompanied by the Mfolozi River is still of concern.

Although the estuarine system experienced a short periodic drought from November 2015 to May 2016, the mouth region was partially alleviated from drought conditions due to freshwater input via the link canal, beach spillway and the Mpate River. Salinity varied throughout the study period (Feb 2015- Nov 2018) from predominantly fresh to oligo/mesohaline, aside from a couple instances where an oceanic link allowed for marine intrusion. Peaks in TSS and turbidity levels during and post rehabilitation activities coincided with heavy rainfall events. Overall, turbidity and TSS concentration was higher post project completion, and sediment grain size shifted as silt (<63 μm) was recorded as the dominant grain size post rehabilitation (Jones et al. 2020).

Total zooplankton abundance ranged from $1.2 \times 10^3 \pm 54.47 \text{ ind. m}^{-3}$ (February 2015) to $8.79 \times 10^5 \pm 3.7 \times 10^4 \text{ ind. m}^{-3}$ (May 2016) during the course of the study period (February 2015- November 2018). Lower abundance of zooplankton was generally recorded during the restoration project activities which coincided with lower salinity and higher turbidity levels. Jones et al. (2016) also recorded lower zooplankton abundance in the Narrows region of the St Lucia Estuary, following a small flood in the Mfolozi River that resulted in high turbidity (962 NTU) and markedly lower salinity levels (Jones et al. 2016). Similar findings were also recorded in an experimental study that was used to compare natural turbidity levels at the shallow Lake Taihu (China) where there was a decline in abundance of certain zooplankton taxa during high turbidity levels ($741.6 \pm 105.2 \text{ NTU}$) (Zhou et al. 2018).

During the study period at the mouth, 96 taxa were recorded, ranging from 11 taxa during restoration activities (August 2016) to 46 taxa before the restoration project (May 2015). The highest taxonomic richness occurred when there had been marine input from the beach spillway as the Mfolozi mouth was open to the sea. The flow of the Mfolozi River into St Lucia has importance for biotic connectivity for the recruitment of marine taxa and for caridean prawns which breed in the Mfolozi River and enter the St Lucia Estuary (Whitfield et al. 2013, Tweddle et al. 2016). During May 2015, there were numerous marine zooplankton taxa introduced such as the copepods *Paracalanus* spp., *Corycaeus* sp., *Microsetella* sp., cirripede nauplii and the jellyfish *Obelia* sp. Similar taxa were also recorded during open mouth conditions in 2007 (Carrasco et al. 2010) as well as in the beach spillway in 2012 (Van Elden et al. 2014). The second-highest taxa richness (41 species) occurred in November 2016. Although a low salinity was documented on this occasion due to high rainfall, there was seawater intrusion into St Lucia as a result of equinox tides (Fox and

Mfeka 2016) which allowed for the introduction of marine taxa such as chaetognaths and the copepod *Corycaeus* sp. The decapods *Caridina africana* and *Palaemon* sp. were also recorded, indicating biotic connectivity between the Mfolozi River and the St Lucia Estuary. *Caridina africana* are freshwater shrimp which in the past were recorded in the St Lucia system during open (Millard and Broekhuysen 1970, Grindley 1982) and closed mouth conditions (Tweddle et al. 2016) through freshwater inflow from the Mpate and Mfolozi River (Collocott et al. 2014). The decapod *Palaemon* sp. is a euryhaline shrimp, which in the past has been recorded during closed mouth conditions in the St Lucia Estuary (Collocott et al. 2014). *Palaemon concinnus* is regarded as a brackish water prawn (Hart et al. 2001), but mainly occurs in regions of low salinities which have been recorded (1964-1965) during open mouth conditions (Millard and Broekhuysen 1970) in the St Lucia estuarine system (Tweddle et al. 2016).

Juvenile fish, including the freshwater Mozambique tilapia (*Oreochromis mossambicus*), the North African catfish (*Clarias gariepinus*) and the glassy (*Ambassis ambassis*) were also incidentally collected within the zooplankton samples. *Oreochromis mossambicus* is euryhaline and occurs under closed mouth and drought conditions (Vrdoljak 2004). On the other hand, *Clarias gariepinus* has a narrow salinity tolerance (0 to 10) (Whitfield et al. 2006, Cyrus et al. 2020) and can be found during low salinity and high-water levels (Whitfield et al. 2006). The estuarine species *Ambassis ambassis* has been recorded in the St Lucia estuarine system mainly during low salinity levels (<10) (Martin 1988, Whitfield et al. 2006). Both *Oreochromis mossambicus* and *Ambassis ambassis* dominated the fish community pre and post-formation of the beach spillway in 2012 (Cyrus et al. 2020) and are known to expand their distribution in the St Lucia system during lower salinity regimes (Dyer et al. 2015, Carrasco and Perissinotto 2015). In the current study, the juvenile fish were most likely able to tolerate the lowest salinity levels at the Mouth region during November 2016 (Whitfield et al. 2006, Cyrus et al. 2020).

Zooplankton taxonomic richness exhibited a significant positive correlation with temperature and a negative correlation with microphytobenthic biomass (MPB). The correlation with temperature and taxonomic richness could be attributed to marine intrusion of taxa which occurred during the warmer months (Marques et al. 2006, Deale et al. 2013). In numerous studies (Mouny and Dauvin 2002, David et al. 2005, Gutierrez et al. 2018), including a similar shallow water system (Mondego Estuary, Portugal), temperature, as well as salinity, were important variables that influenced the abundance, composition and distribution of zooplankton taxa (Marques et al. 2006). The negative correlation between taxonomic richness and MPB could be due to the lower water levels reducing depths as MPB biomass proliferates during low water levels when there is sufficient nutrients and light available (Nunes et al. 2017).

There was a clear shift from estuarine species to freshwater taxa before and after the restoration project. The pre-restoration community structure consisted of the dominant estuarine zooplankton, including the calanoid copepods *Pseudodiaptomus stuhlmanni*, *Acartiella natalensis*, the mysid *Mesopodopsis africana*, and the resident cyclopoid copepod *Oithona brevicornis* (Grindley 1982, Carrasco and Perissinotto 2015). Post-restoration resulted in the absence of the dominant resident taxa, except for the estuarine calanoid *Pseudodiaptomus stuhlmanni* which persisted in lower abundance. From the onset of the rehabilitation project, freshwater taxa, including cyclopoids, rotifers, and cladocerans, dominated.

Both salinity and total suspended solids (TSS) were identified as major determinants of the zooplankton community structure in this study. Increased siltation affects zooplankton species differently as it can lead to increased mortality rates, can bring about reduced feeding rates in some taxa and can cause body lacerations (Carrasco et al. 2013, Koenings et al. 1990, Jones et al. 2020). Turbidity levels in this study increased during the onset of the restoration project. The impacts of turbidity differ amongst taxa and depending on the amount of time it lasts as well as at what levels it occurs at (Hart 1988, Kirk 1991, Henley et al. 2000, Jones 2015). Turbidity peaked during the restoration project (November 2016, 1246 NTU) and this coincided with the disappearance of both the mysid *M. africana* and the calanoid copepod *A. natalensis*. *Pseudodiaptomus stuhlmanni* remained present after November 2016 but their abundance declined substantially during restoration activities and remained low as turbidity was persistently high post restoration activities. Past experimental studies have been conducted to determine the impact of silt loading on the ecophysiology of the dominant St Lucia zooplankton, including *M. africana* (Carrasco et al. 2007), *A. natalensis* (Carrasco et al. 2013) and *P. stuhlmanni* (Jones et al. 2016). These experimental studies have revealed that high levels of turbidity (>1000 NTU) decreased the survivorship of both *A. natalensis* (Carrasco et al. 2007) and *M. africana* (Carrasco et al. 2013), and the increased silt hindered their feeding ability (Carrasco et al. 2007, Carrasco et al. 2013). The dominant estuarine resident *P. stuhlmanni* was more tolerant of high turbidity levels than *M. africana* and *A. natalensis* but was severely impacted when turbidity levels were between 1500-2500 NTU (Jones et al. 2016).

The absence of the mysid *M. africana* and the calanoid copepod *A. natalensis* could have also been due to the persistent lower salinity levels (Jones et al. 2016), less stable conditions (Carrasco and Perissinotto 2011) and increased competition from freshwater zooplankton (Carrasco and Perissinotto 2015, Jones 2015). During 2007 when the St Lucia estuarine system breached, tidal exchange led to less stable conditions in the mouth area and *M. africana* was subsequently only found in the lake regions (Carrasco et al. 2010). *Mesopodopsis africana* is euryhaline and tolerant of salinities ranging from 2.55 to 60 (Carrasco and Perissinotto 2011). In the past, *M. africana* has

been restricted to the Mouth and the Narrows during drought conditions (Carrasco et al. 2010, Carrasco and Perissinotto 2011) as these sites are in closer proximity to the Mphahlele and Mfolozi Rivers. In the current study, *M. africana* may have been absent from the mouth due to the persistent inflow of fresh silt-laden water. According to Grindley (1982), *A. natalensis* is tolerant of salinities ranging from fresh to 60 and have also been found to survive above 70 (Grindley 1982). Even though Grindley (1982) stated that *A. natalensis* is tolerant of lower salinity conditions, the opposite was recorded for the calanoid copepod in the Kromme Estuary (South Africa) where there had been a drastic decline in abundance that was recorded due to the lower salinity levels (Wooldridge and Callahan 2000).

Pseudodiaptomus stuhlmanni is also euryhaline, being able to withstand salinities from fresh to 70 (Grindley 1982). *Pseudodiaptomus stuhlmanni* densities decreased drastically from November 2016 onwards when it was exposed to lower salinity levels and silt laden water. Similarly, in a study looking at the impact of a flood event on the zooplankton community in the St Lucia Estuary along the Narrows, *A. natalensis* was absent from the community instantly while the population of *P. stuhlmanni* declined a month thereafter (Jones et al. 2016, Jones et al. 2020). Zooplankton during a wet and dry period were analysed in the Msunduzi-Mfolozi system and the study revealed that *A. natalensis* disappeared from the community structure as soon as the wet period began and *P. stuhlmanni* only declined a few months thereafter (Jerling and Cyrus 2016). *Pseudodiaptomus stuhlmanni* is more resilient to varying environmental variables compared to the other estuarine resident taxa. The last resident taxon which declined was *Oithona brevicornis* that occupies both estuarine and marine waters, tolerating salinities of 5 to 30 (Arfi et al. 1987, Etilé et al. 2012, Jones et al. 2016). In the Grand-Lahu lagoon in the southern Cote d'Ivoire, *O. brevicornis* abundance declined when salinities decreased to below 5 as a result of increased freshwater input (Etilé et al. 2012). Also, in the Grand-Lahu lagoon, females declined with an increase in turbidity as reproduction rates were affected (Etilé et al. 2012).

The post restoration community was dominated by taxa such as rotifers, cladocerans and cyclopoids. Jenson and Verschoor (2004) stated that rotifers can dominate short periods of time depending on environmental conditions, namely nutrient levels, as they are fast growing species and utilize niches that are less crowded (Elser et al. 2000). During sampling occasions post-restoration project, rotifers dominated the community structure. *Brachionus calyciflorus* dominated the assemblage (60 %) in August 2017. Their dominance could have been due to the favourable lower salinity levels, increased niche availability (Elser et al. 2000), their short development time (Branco et al. 2018) or it suggests they were continuously brought into the system through the Mfolozi input (Jones et al. 2020). In a shallow estuarine lake, the Nhlabane estuarine system,

rotifers were persistent in the community and were associated with lower salinities (Jerling and Cyrus 1998). In the current study, cladocerans were the least abundant of the freshwater taxa but they were markedly high from August 2017 to February 2018, possibly as a result of increased phytoplankton biomass, as phytoplankton has been identified as seasonally altering the succession of cladoceran communities (Jerling and Cyrus 1998, Abrantes et al. 2006) and possibly due to increased availability of suitable niches (Jerling and Cyrus 1998, Jones et al. 2016). Cladocerans are susceptible to high turbidity levels (Koenings et al. 1990, Jones et al. 2016) which could be the reason for their decline from May 2018 onwards as there were peaks in turbidity recorded.

Cyclopoids were abundant throughout the post-restoration project period once there was a full link between the St Lucia Estuary and the Mfolozi River. Cyclopoids are generally associated with freshwater conditions (Chambord et al. 2016). Their persistence throughout the sampling periods post restoration project can be mainly attributed to lower salinities, increased niche availability (Jones 2015) or due to the increased Mfolozi freshwater input (Jones et al. 2020).

Freshwater input from the Mfolozi River has been identified as a critical component in restoring the St Lucia estuarine system (Whitfield and Taylor 2009, Whitfield et al. 2013, Tweedley et al. 2019, Cyrus et al. 2020). Restoration activities in combination with increased rainfall have resulted in a peak in turbidity levels of 1246 NTU (November 2016), 263 NTU (May 2018) and 591 NTU (August 2018) in the mouth area. The restoration project has been successful in increasing freshwater input at the mouth thus far, but siltation may cause the gradual shallowing of the mouth area leading to a loss of habitat for biota (Whitfield et al. 2012). The siltation in the mouth region poses a serious threat to biota, with a 1m layer of mud persisting at the mouth during 2019 (Jones et al. 2020). Management needs to counteract the high silt load that is accompanied by the Mfolozi River (Whitfield et al. 2013). Some recommendations for reducing siltation included forming a sink in the Mfolozi floodplain for excess sediment deposition or the restoration of the Mfolozi swamplands to filter sediments before they enter the St Lucia Estuary (Whitfield et al. 2013, Tweedley et al. 2019).

In conclusion, the zooplankton community at the mouth region was restructured with freshwater taxa replacing resident taxa, except for the estuarine copepod *P. stuhlmanni* which persisted post-restoration, although in lower abundance. The hypothesis stating that there would be a difference in the zooplankton community composition before and after the restoration project was supported. The resultant zooplankton assemblage can be mainly attributed to the increased freshwater input from the Mfolozi River. To understand the full impact of the reconnection of the St Lucia-Mfolozi link, zooplankton from the rest of the estuarine lake needs to be analysed. So far, there have been

no measures put in place to reduce siltation and freshwater input has not been sufficient enough for a mouth breaching event to occur naturally and void sedimentation, possibly as a consequence of freshwater abstractions (Van Niekerk et al. 2020).

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Chapter 3: Spatio-temporal variations in zooplankton community structure in Lake St Lucia during a shift to a freshwater state

ABSTRACT

Shallow estuarine ecosystems are prone to global climate change and anthropogenic activities. Africa's largest estuarine lake, the St Lucia Estuary has experienced periodic dry and wet cycles dependent on climate patterns. Historically, the estuary relied on freshwater input from the Mfolozi River to alleviate droughts, but the canalisation of the Mfolozi swamplands resulted in high silt input and led to the artificial closure of the St Lucia-Mfolozi link in 1952. Freshwater deprivation has subsequently exacerbated droughts and threatened system integrity, with the drought phase in 2015/2016 resulting in up to 80 % desiccation of the lake surface area. However, the reconnection of the St Lucia-Mfolozi link in 2016/2017, combined with increased rainfall resulted in the system shifting from largely dry and hypersaline, to predominantly freshwater. Given the importance of zooplankton as indicators of change in aquatic ecosystems, this study aimed to investigate the system-wide impacts of the phase shift by monitoring the zooplankton community at 5 representative sites from quarterly surveys from February 2015 to November 2017. Salinities decreased throughout the estuary from 2017 onwards however, the reversed salinity gradient persisted with a maximum salinity of 36 recorded in the upper reaches. There was a shift in the zooplankton community with resident taxa being largely replaced by freshwater taxa, such as cyclopoids, rotifers, and cladocerans. The cyclopoid copepod *Oithona brevicornis* and the calanoid copepod *Acartiella natalensis* were virtually absent during the wet state and the mysid *Mesopodopsis africana* was restricted to the upper reaches which served as a refuge from the lower salinity areas. *Pseudodiaptomus stuhlmanni* was the only estuarine resident to persist throughout the study, although densities declined. This prolonged wet phase could forcibly exclude estuarine resident zooplankton. In addition, there is still the concern of siltation as a mouth breaching event has not yet been initiated. Further long-term monitoring is needed to understand the ecosystem responses which can similarly occur in other estuarine lake systems globally.

Keywords: Regime shift, transition, freshwater, zooplankton, estuary

3.1. INTRODUCTION

Estuaries are important productive ecosystems, serving as a habitat and providing food resources for a diverse range of flora and fauna (Wetz et al. 2014). Estuarine ecosystems are dynamic areas that face numerous natural stresses including extreme weather conditions such as floods and droughts (Taylor 2006, Cyrus et al. 2011). In addition, anthropogenic activities affect estuaries

through hydrodynamic alterations such as water abstraction, pollution, and inflow of silt-laden water due to land-use changes (Whitfield and Taylor 2009, Carrasco and Perissinotto 2015). Climate change will also have an influence on estuarine ecosystems through the alteration of rainfall patterns, changes in sea levels, and an increase in temperatures (Glamore et al. 2016, Masson-Delmotte et al. 2018). These factors alone or synergistically may affect the ecological integrity of estuarine systems (Coops and Hosper 2002, Coops et al. 2003, Masson-Delmotte et al. 2018).

Temporarily closed estuaries (TCE's) are systems closed off from the sea due to the development of a sand berm depending on water level fluctuations (Whitfield et al. 2012, Adams et al. 2016, Van Niekerk et al. 2020). TCE's remain closed by a sand bar during low freshwater input (Anandraj et al. 2008). The escalation in water abstractions from human populations (Schlacher and Wooldridge 1996, Mbandzi et al. 2018) may therefore prolong the duration of mouth closure, increasing residence time and hindering the role of an estuary as a nursery site for juveniles of marine breeding fish (Whitfield et al. 2013, Tweedley et al. 2019). The resilience of shallow estuarine systems is tested when exposed to changes in water fluctuation levels (Wallsten and Forsgren 1989, Coops et al. 2003), intense weather events (Hamilton and Mitchell 1988), and natural shifts (Scheffer and Jeppeson 2007). These changes in environmental conditions can exceed the threshold of shallow lakes and cause the system to shift beyond the 'transition' point to a new state (Chang et al. 2017). Shallow lakes are therefore prone to shifting to alternate states in response to the changing hydrological conditions (Scheffer and Jeppeson 2007). Extreme changes in hydrological conditions, most importantly between dry and wet conditions, can be associated with shifts in species diversity and abundance over short to long term time scales (Threlkeld 1982, Coops et al. 2003, Chang et al. 2017).

The St Lucia estuarine lake is a World Heritage Site and is sanctioned as a Ramsar Wetland of International Importance (Carrasco et al. 2010, Perissinotto et al. 2013, Whitfield et al. 2013). The estuary serves as an essential habitat for numerous fauna and flora (Begg 1978) and is an important nursery site for marine fish during open mouth conditions (Cyrus et al. 2010). The system experiences periodic wet and dry cycles which are determined by both climatic patterns (Carrasco et al. 2010, Gordon et al. 2016, Nunes et al. 2017) and anthropogenic alterations (Perissinotto et al. 2013, Nunes et al. 2017). Anthropogenic alterations that have occurred in the estuary include water abstractions as well as catchment and mouth manipulation (Whitfield and Taylor 2009, Nunes et al. 2017).

The St Lucia Estuary historically relied on the Mfolozi River as the main freshwater source during dry spells (Whitfield et al. 2013). However, the Mfolozi River was artificially diverted away from

the mouth of St Lucia estuarine lake in 1952 to prevent excessive silt input as a result of the Mfolozi swamplands being canalized for agricultural purposes (Begg 1978, Whitfield and Taylor 2009, Carrasco et al. 2013, Naidoo 2015). The estuarine lake is already shallow (Carrasco et al. 2010, Carrasco and Perissinotto 2015), so further sediment deposition could reduce habitat for planktonic biota (Kirk 1991, Shields et al. 1998, Levine et al. 2005, Lawson et al. 2007, Thrush et al. 2004, Jones et al. 2015) and a number of negative effects have been associated with increased turbidity e.g. decreased primary production due to reduced light availability, body lacerations and the smothering of some fauna and flora (Kirk and Gilbert 1990, Dejen et al. 2004, Thrush et al. 2004, Carrasco et al. 2007, Carrasco et al. 2013, Jones 2015). So, while the diversion of the Mfolozi River spared the St Lucia Estuary of the excessive silt input, droughts following the diversion were exacerbated by deprivation of freshwater supply from the Mfolozi River (Taylor et al. 2006, Cyrus et al. 2010, Whitfield et al. 2013). Droughts were characterised by large scale biodiversity loss, habitat fragmentation (Pillay and Perissinotto 2008, Naidoo 2015), hypersalinity, and desiccation in the northern reaches (Taylor et al. 2006, Cyrus et al. 2010, Carrasco et al. 2010, Cyrus et al. 2011, Whitfield et al. 2013).

Earlier attempts to increase freshwater input included the excavation of a back channel from the Mfolozi River to the Narrows in the 1960s (Whitfield et al. 2013), a link canal during the 1980's (Nunes et al. 2017), and a beach spillway during 2012 (Jones et al. 2016). The beach spillway allowed for the input of both freshwater and seawater when the Mfolozi mouth was open to the Indian Ocean but closed during low rainfall conditions (Whitfield and Baliwe 2014, Jones et al. 2016, Nunes et al. 2017). These past efforts were only able to alleviate drought conditions mainly in the lower reaches of the estuary. A full relinkage was needed to allow unimpeded freshwater into the estuary and to restore natural mouth functioning (Whitfield et al. 2013). The most recent attempt to allow for the full connection of the Mfolozi River to St Lucia was initiated during 2016 through a Global Environment Facility (GEF) funded project that brought about the dredging and removal of vegetation as well as spoilage from the eastern tip of the St Lucia island at the mouth (Fox and Mfeka 2017).

Just prior to this reconnection, the estuarine system experienced a severe drought (November 2015 to May 2016) that resulted in up to 80 % desiccation of the lake surface area. The combination of increased precipitation and freshwater input from the onset of restoration activities (August 2016) decreased salinities and increased water levels throughout the system. Though the St Lucia-Mfolozi link is essential to allow unimpeded freshwater into the estuary, excess silt input is still a concern, especially during high river flows from the Mfolozi River as there have been no measures put in place to reduce silt input from the Mfolozi River as yet (Whitfield et al. 2013).

Zooplankton form a vital link in the food web between primary producers and higher trophic levels (Hays et al. 2005, Bielecka and Boenhke 2014). Additionally, the short lifecycle and the high turnover rates of zooplankton make them useful indicators of alterations/changes in aquatic environments (Hays et al. 2005, Hooff and Peterson 2006). Dominant zooplankton in the St Lucia Estuary include the estuarine calanoid copepods *Acartiella natalensis*, *Pseudodiaptomus stuhlmanni*, the mysid *Mesopodopsis africana* and the resident cyclopoid *Oithona brevicornis* (Grindley 1982, Carrasco et al. 2010, Carrasco and Perissinotto 2015). The resident taxa of the St Lucia estuarine system have an essential role in the estuary (Carrasco et al. 2013) and changes in the assemblage would reflect changes in the environmental conditions of the estuarine system (Hays et al. 2005). Numerous studies have documented the effects of dry conditions (Taylor 2006, Pillay and Perissinotto 2008, Carrasco et al. 2010, Cyrus et al. 2010, Cyrus et al. 2011) on the estuarine system, but the current study reports on functioning during a transition to a wet phase, and also records changes associated with the restoration project. It is essential to understand the impact of the newly formed link on the estuary and its inhabitants. This study aimed to investigate the system-wide impacts of the phase shift by monitoring the zooplankton community at 5 representative sites within the system as it transitioned from a hypersaline state to a freshwater state from February 2015 to November 2017. It was firstly hypothesized that there would be spatial differences in the zooplankton community structure and abundance between sites along the estuary as the system transitioned from hypersaline conditions to a freshwater state. Secondly the zooplankton community of the pre-drought phase would differ from that of the wet phase as the St Lucia Estuary transitioned to a wet state. The current study will aid in understanding the impact of alternating stable states on zooplankton dynamics in a large shallow estuarine lake system in a subtropical estuary as the changes are driven by both climatic shifts and hydrological changes.

3.2. MATERIALS AND METHODS

3.2.1. Study site and sample collection

The St Lucia estuarine lake is located on the east coast of South Africa in the Northern part of KwaZulu Natal (Figure 3.1.1). When the system has a full coverage of water, it has a surface area of 350 km² and has a mean depth of 0.9 m (Begg 1978, Cyrus et al. 2010, Whitfield et al. 2013). The estuarine system occupies around 80 % of the estuarine area in KwaZulu-Natal (Begg 1978, Cyrus et al. 2010). Quarterly surveys were conducted seasonally at five representative sites (Figure 3.1.1): The Mouth, The Narrow's, Charter's Creek, Catalina Bay, and Lister's Point. Samples were at times collected from Dredger Harbour and Esengeni within the Narrow's, dependant on water levels, and accessibility by boat.

This study was conducted from February 2015 – November 2017 and covered 4 different hydrological phases which included a pre-drought phase (February 2015 to July 2015, Figure 3.1.2 a), a drought phase (November 2015 to May 2016, Figure 3.1.2 b), a transitional phase (August 2016 to January 2017, Figure 3.1.2 c) and a wet phase (April 2017 to November 2017, Figure 3.1.2 d). During the pre-drought phase (Figure 3.1.2 a), estuarine conditions were prevalent as all lake basins were connected with a strong reversed salinity gradient present. The drought phase (Figure 3.1.2 b) resulted in 80 % desiccation of the lake system which led to habitat fragmentation and hypersaline conditions in some areas. The transition phase (3.1.2 c) brought about the alleviation of drought conditions from August 2016 onwards, as increased precipitation and freshwater input from the onset of the rehabilitation project allowed for the lake basins to reconnect and salinities to decrease along the estuarine system. However, the further northern reaches took a longer time to reconnect as Lister's Point salinity only started to decrease from November 2016 onwards. During the wet phase (Figure 3.1.2 d), the entire estuarine system remained mainly fresh, but a slight reversed salinity gradient persisted. Also, the Mouth region had seawater intrusion from the beach spillway (May 2015) and marine overtopping as a result of equinox tides (November 2016) (Fox and Mfeka 2016). In the quarterly surveys, duplicate zooplankton samples, samples of phytoplankton as well as microphytobenthic biomass were collected and data was obtained on the physicochemical parameters.

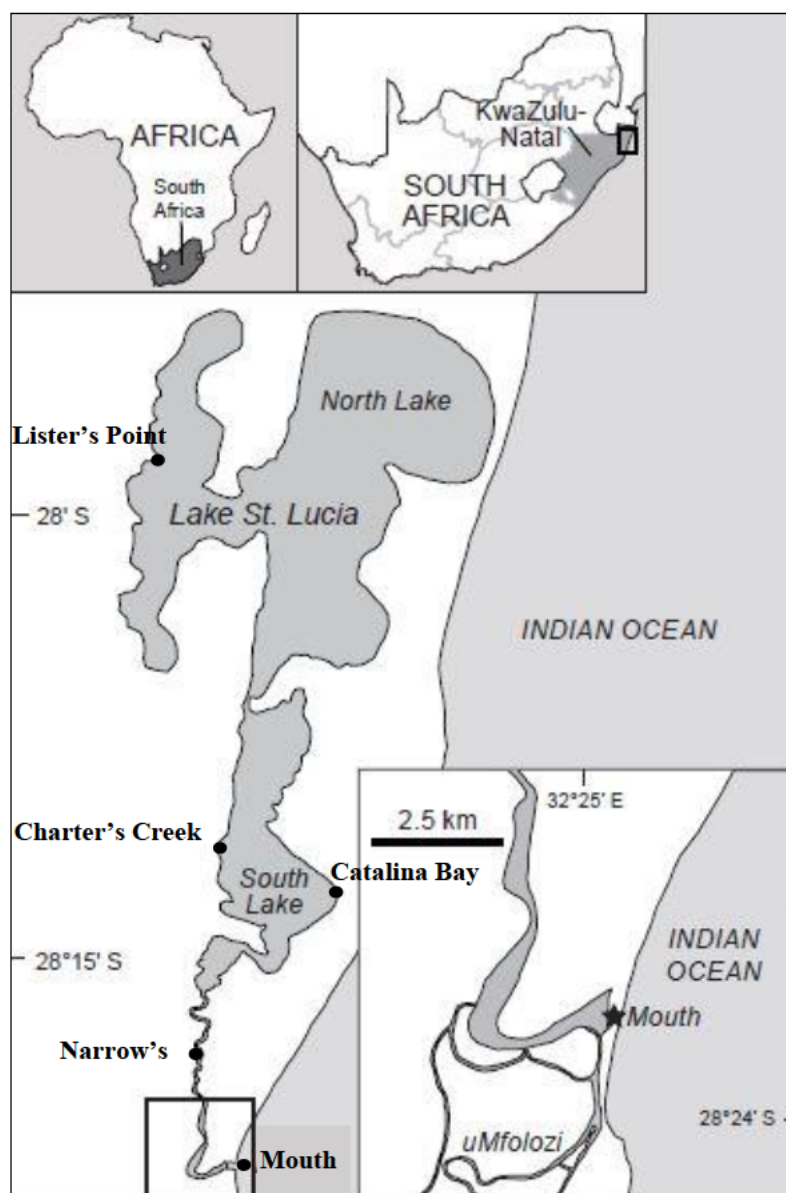


Figure 3.1.1: A map showing the five sampling sites at the St Lucia estuarine lake: The Mouth, The Narrow's, Charter's Creek, Catalina Bay and Lister's Point (Map adapted from Jones et al. 2020).

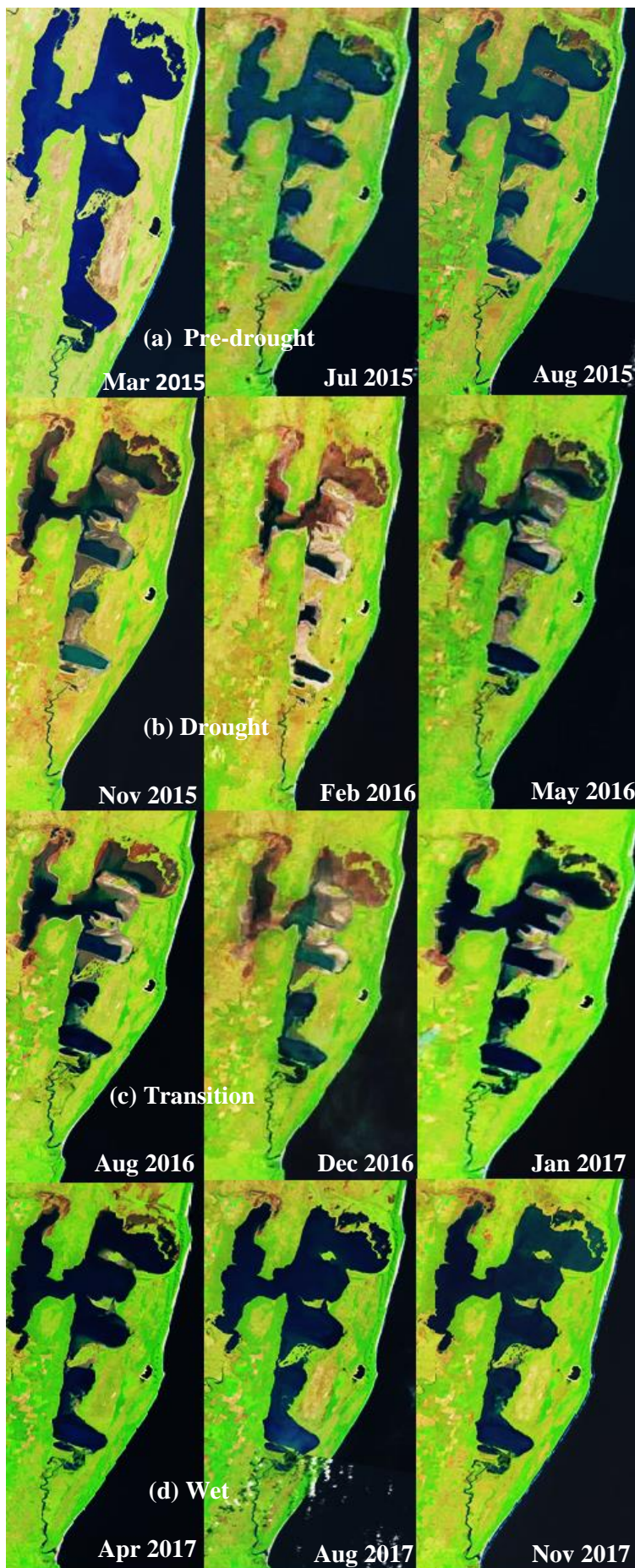


Figure 3.1.2: Available Landsat images of the different phases in the St Lucia estuarine lake over the three-year study period, a. Pre-drought phase: March 2015 to August 2015, b. Drought phase: November 2015 to May 2016, c. Transitional phase: August 2016 to January 2017, d. Wet phase: April 2017 to November 2017. (Landsat-7 ETM+ imagery courtesy of the United States Geological Survey).

3.2.2. Physico-chemical parameters

At each sampling site, a YSI 6600-V2 probe was used to measure the temperature ($^{\circ}\text{C}$), pH, salinity, dissolved oxygen concentration (mg l^{-1}), and turbidity (Nephelometric turbidity units, NTU) of the water. Occasionally on sampling trips, a turbidimeter (HACH2100Qis), as well as a hand refractometer (ATAGO S/Mill-E), was used to determine turbidity and salinity when the YSI probe was reporting inaccurate values for these parameters. At sites where depth was lower than 10 cm, the YSI probe was used horizontally, ensuring all measurements could be taken. Ezemvelo KZN Wildlife authority supplied the rainfall data. Dissolved inorganic nitrogen and phosphorus was determined by collecting subsurface water samples ($n=2$) which were sent to Nelson Mandela University (NMU) for subsequent analysis. Physico-chemical data could not be collected for both Charter's Creek and Catalina Bay during February 2016 as well as Listers Point in February, May and August 2016, due to dry conditions.

3.2.3. Microphytobenthos, phytoplankton and total suspended solids

Microphytobenthic samples were obtained with a Perspex twin corer (2 cm internal diameter). Quantitative samples ($n=3$) of the first centimetre of sediment were collected at each site and transferred into 100 ml polyethylene bottles containing 30 ml of 90 % acetone. The samples were then stored for 48 hours in a freezer for a cold-dark extraction of chlorophyll *a* (Nozais et al. 2001). The microphytobenthic biomass was finally determined fluorometrically (Turner Designs 10-AU non-Acidification system) and the biomass was expressed as $\text{mg chl } a \text{ m}^{-2}$. For the determination of phytoplankton biomass, duplicate estuarine water samples (150 – 250 ml) were collected for filtration through EconoFilt RGF filters ($1 \mu\text{m}$). The filters were thereafter placed into tubes containing 8 ml of 90% acetone for 48 hours to allow the cold extraction of chlorophyll *a*, and phaeopigments (Nozais et al. 2001). The biomass of phytoplankton was also determined with the use of a fluorometer and was expressed as $\text{mg chl } a \text{ m}^{-3}$.

Total suspended solids (mg l^{-1}) was obtained by firstly filtering between 150 ml and 250 ml of water collected nearshore at the sampling sites, through EconoFilt filters that were pre-combusted (420°C , 6 hours) and weighed with a Shimadzu AUW220D Uni Bloc balance (Carrasco et al. 2007, Jones et al. 2016). After filtration, the filters were dried in an oven (48 hours, 60°C) and weighed once again. The filters were then combusted (420°C , 6 hours) with a muffle furnace, thereafter the filters were weighed, and total suspended solids were determined as the difference between the weights of the dry and pre-combusted filters, taking into account the volume of water filtered (Carrasco et al. 2007, Jones et al. 2016).

3.2.4. Zooplankton

Zooplankton samples were collected during the daytime with the use of an epibenthic sled fitted with a 100 μm mesh. The collection method was used because of the shallow nature of the estuary as well as the diel migration habits of certain zooplankton taxa (Carrasco et al. 2010). The radius of the semi-circular net mouth was 18.5 m and the net had been mounted onto the sled whereby it was raised 7.5 cm above the ground as it was towed in the shallow areas at the sampling sites. The distance towed was multiplied by the area of the net mouth to calculate the volume of water filtered (≈ 1.43). Areas that were too shallow for the sled, 30 L – 100 L of water was filtered through a hand-held sieve (Carrasco et al. 2010). Zooplankton samples could not be collected at Charter's Creek as well as Catalina Bay (February 2016) and for Lister's Point (February 2016 to August 2016) due to dry conditions.

The zooplankton in the cod-end was transferred into 500 ml polyethylene bottles containing 5 % phloxine-stained formalin. Once the samples were in the laboratory, each sample was suspended in a beaker with a water solution of 0.6 -5 Litres, depending on the density of the zooplankton. With the use of a wooden rod, the sample was then stirred for the zooplankton to be suspended and 3 subsamples were taken at mid-depth using either a 10 ml or 20 ml plastic vial, which also depended on the density of the sample (Carrasco et al. 2010). From the subsamples, all zooplankton including benthic taxa that were unintentionally caught due to the hyperbenthic sampling method were counted and identified to the lowest possible taxonomic level under a dissecting microscope (40 \times), and taxa were further identified under a compound microscope (Nikon Eclipse E100, magnification:100 \times). Identifying of zooplankton was done with the use of identification guides (Day 1969, Griffiths 1976, Fernando 2002, Conway et al. 2003). The use of a 100 μm mesh would have underestimated the abundance of smaller zooplankton taxa. Also, as a result of the hyperbenthic sampling method, benthic taxa were included which would have overestimated taxonomic richness and abundance. After the zooplankton was counted, densities were calculated (ind. m^{-3}). It was ascertained that between the subsamples, the coefficient of variation was consistently less than 10 %.

3.2.5 Statistical analyses

Univariate statistical analyses were performed on STATISTICA version 13. 4 for Windows. Firstly, assumptions of normality were tested by using the One-sample Kolmogorov-Smirnov test and equal variances were determined by running a Levene's test. When assumptions were not met, the data was ranked (Conover and Iman 1976, 1981). A Two-way ANOVA was used to test if there were differences among the phases (pre-drought, drought, transition, and wet) and sites in total

zooplankton abundance and taxonomic richness. Tukey HSD post hoc tests were used to identify where the differences occurred between phases and sites. In addition, a One-Way Analysis of Variance (ANOVA) was used to test whether there were significant differences in the environmental parameters, phytoplankton as well as microphytobenthic biomass among the phases. Lastly, a Spearman's Rank correlation was used to find out whether the community parameters (abundance and taxonomic richness) correlated with the environmental variables.

Multivariate statistical analyses were performed on PRIMER version 6.0 (Clarke and Warwick 2001). The data had firstly been square root transformed to minimize the impact of the dominant species (Clarke and Warwick 2001). A Bray Curtis resemblance on the data was calculated thereafter cluster diagrams were obtained on each site to get a visual perspective of the phases on the community structure. Furthermore, a non-metric multidimensional scaling (MDS) plot was created to display the zooplankton assemblage among phases. PERMANOVA main test analysis was performed to test whether the phases, sites, or an interaction effect determined the community structure. PERMANOVA pairwise tests were used to determine where the differences occurred among phases and sites. SIMPER analysis was performed to reveal which species were responsible for the dissimilarities. BIOENV Spearman Rank Correlation determined which environmental variables were significantly involved in the structuring of the community overall. Additionally, a Distance-based Linear Model (DistLM) was produced to determine the proportion of variation in the zooplankton community structure explained by the main environmental parameters.

3.3. RESULTS

3.3.1. Physico-chemical parameters

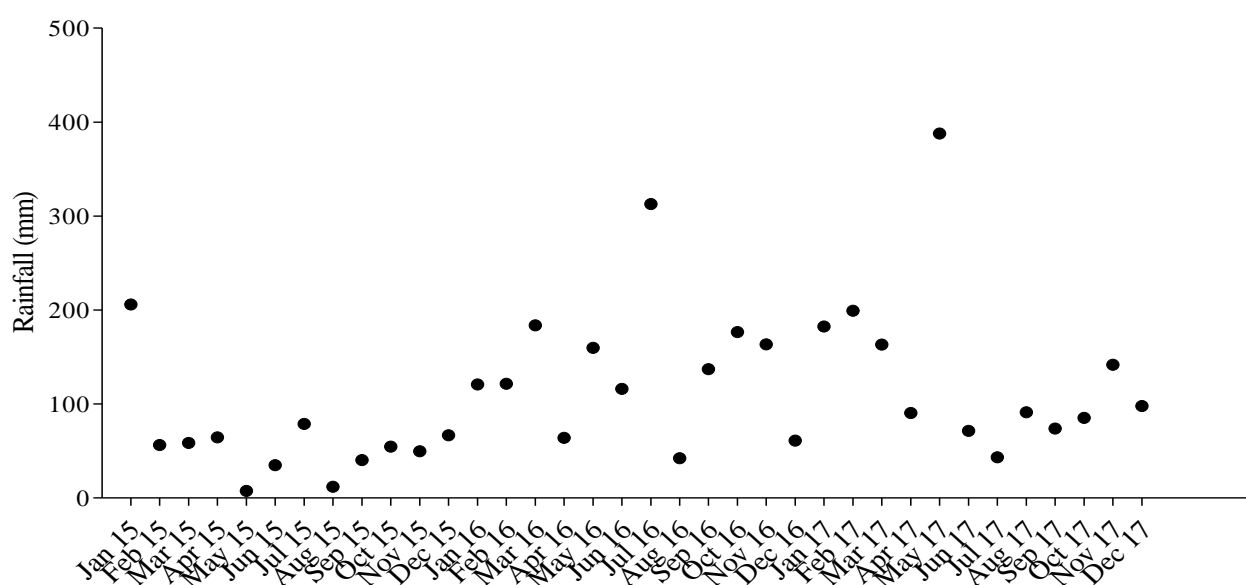
Rainfall in St Lucia was generally lower in 2015 compared to 2016 and 2017 (Figure 3.2, Table 3.1). The average monthly rainfall ranged from 12 mm (August 2015) to 387.8 mm (May 2017) (Figure 3.2, Table 3.1). Rainfall differed among phases ($F_{3,50} = 10.1$, $p < 0.05$), with the pre-drought phase being significantly lower than the transition and wet phases (Tukey post hoc test $p < 0.05$). Salinity levels ranged from 0.04 (November 2015 and May 2016) at the Narrow's to 121.5 at Lister's Point (November 2016) (Figure 3.3, Table 3.1). Salinity levels at the 5 sites during pre-drought conditions were slightly higher compared to the transitional and wet phase (Figure 3.3). Salinity differed between phases ($F_{3,50} = 5.01$, $p < 0.05$) with salinity during the wet phase being significantly lower than both the pre-drought and drought phases (Tukey post hoc test $p < 0.05$). Salinity levels started to decline from August 2016 (transitional phase) onwards at the Mouth, the Narrows, Charter's Creek, and Catalina Bay (Figure 3.3). Salinity at Lister's Point only started to decrease from November 2016 onwards (Figure 3.3). Even though salinities decreased throughout

the system during the transitional phase, a reversed salinity gradient did persist with the highest recorded at Lister's Point in January 2017 (36.31) and the remaining sites had salinities <14 throughout 2017 (Figure 3.3). During the study period, the Narrow's and the Mouth had lower salinities in comparison to the lakes, except for May 2015 at the Mouth, when seawater intrusion from the beach spillway resulted in higher salinities (35) as the Mfolozi River was open to the sea. Additionally, the Mouth had marine input from the Indian ocean as a result of equinox tides during November 2016 (Fox and Mfeka 2016). All other physico-chemical parameters showed no statistical differences among the phases (One-Way ANOVA, $p > 0.05$). Water temperatures generally remained seasonal with the higher temperatures occurring in summer and the lower temperatures in winter (Figure 3.3)

Dissolved oxygen concentration (DO) ranged from 2.3 mg l⁻¹ at the Narrow's (November 2016) to 10.43 mg l⁻¹ at Charter's Creek (November 2016) (Figure 3.3, Table 3.1). Overall, DO was higher during the wet phase compared to the pre-drought phase. pH levels ranged from 7.43 (The Narrow's, November 2016) to 9.9 (The Narrow's, November 2017) (Figure 3.3). Higher pH levels were generally recorded at Charter's Creek while lower pH levels were generally recorded at the Narrow's (Figure 3.3). Turbidity varied throughout the study but was generally higher at the Mouth and the Narrow's (Figure 3.3). There was a peak in turbidity during restoration activities and turbidity levels at all 5 sites increased by November 2017 (Figure 3.3).

Table 3.1: Physico-chemical parameter ranges during the four hydrological phases.

	Hydrological phases			
	Pre-drought	Drought	Transition	Wet
Rainfall (mm)	7.5 - 78.8	49.7 – 159.9	42.4 – 163.4	90.5 - 182.6
Temperature (°C)	16.02 - 30.36	20.68 - 33.07	19.52 – 28.32	19.77 - 34.61
Salinity	1.49- 58.25	0.04 - 111.01	0.51 - 121.5	0.34 - 36.31
Dissolved oxygen (mg l ⁻¹)	6.17 – 8.93	3.3 – 9.13	2.23 – 10.43	6.27 – 9.93
pH	8.08 – 8.8	7.74 -9.57	7.43 - 9.01	7.95 - 9.9
Turbidity (NTU)	0.33 - 398.33	6.3 – 207.6	0.8 – 1246.2	4.1 – 488.8

**Figure 3.2:** Average monthly rainfall for St Lucia from January 2015 to December 2017.

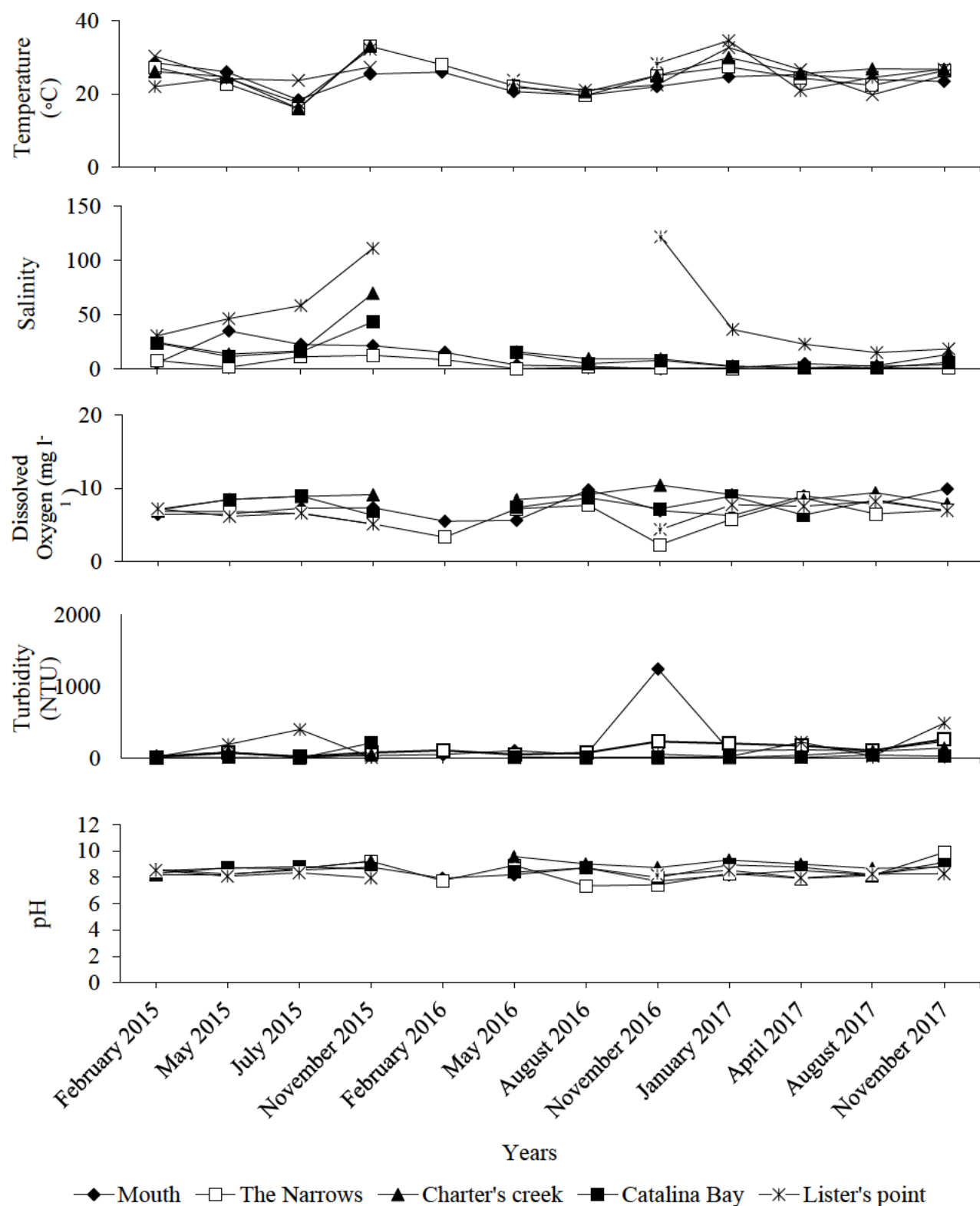


Figure 3.3: Physico-chemical variables obtained at the 5 sites from February 2015- November 2017 (Pre-drought phase: February 2015 to July 2015, Drought phase: November 2015 to May 2016, Transitional phase: August 2016 to January 2017, Wet phase: April 2017 to November 2017).

3.3.2. Dissolved inorganic nitrogen and phosphorous concentrations

Dissolved inorganic phosphorus (DIP) ranged from 0 to 2.37 μM (November 2016) at Lister's Point (Figure 3.4). DIP concentrations increased during the wet phase at all 5 sites (Figure 3.4). DIP differed between phases ($F_{3,50} = 23.7, p < 0.05$). DIP during the wet phase was significantly higher than the pre-drought and drought phases (Tukey post hoc test $p < 0.05$). Dissolved inorganic nitrogen (DIN) had a range of 0 to 96.99 μM (November 2017) at Charter's Creek (Figure 3.4). Generally, the higher concentrations of DIN occurred in the Narrow's and the Mouth region. DIN levels at all 5 sites increased markedly by November 2017 during the wet phase (Figure 3.4). DIN did not differ in between phases ($F_{3,50} = 0.66, p > 0.05$).

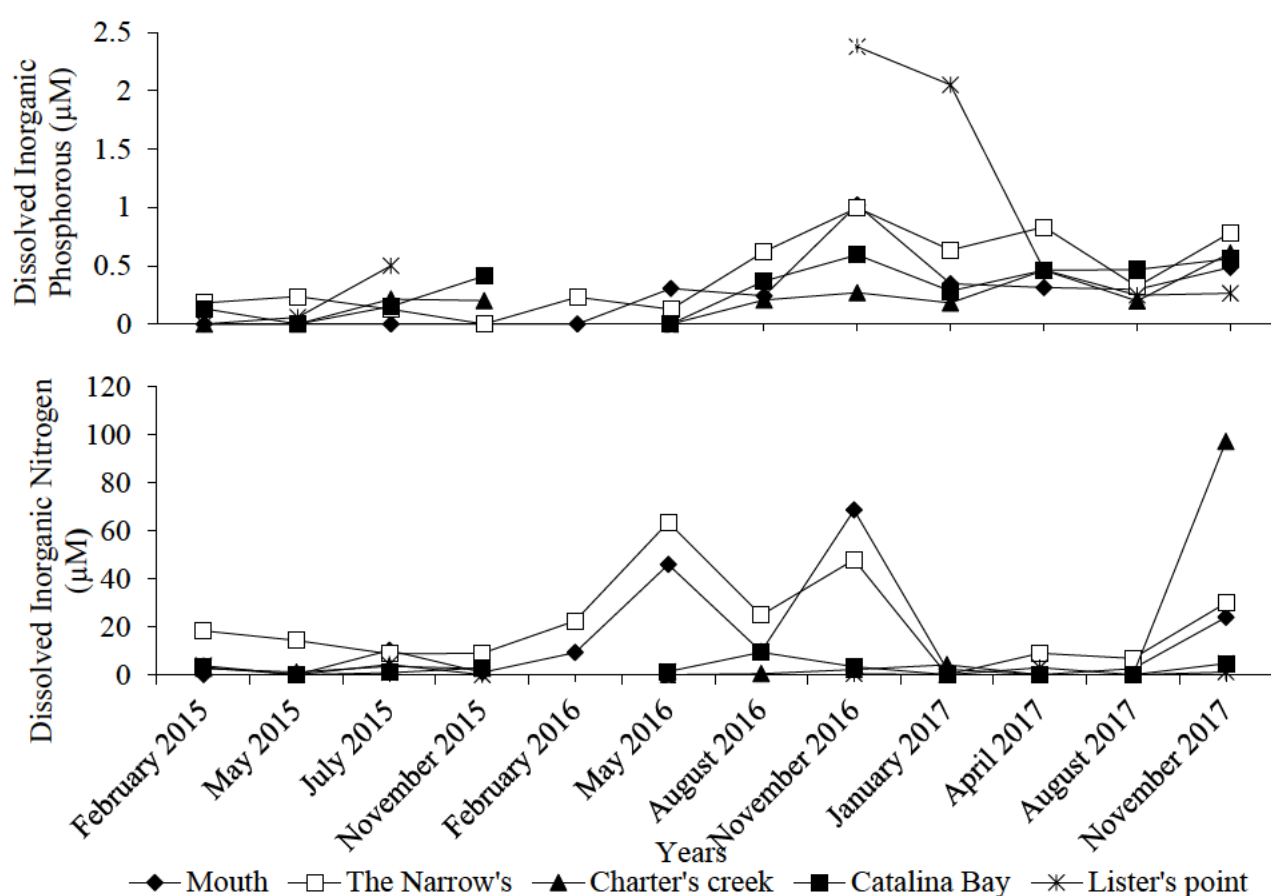


Figure 3.4: Dissolved inorganic nitrogen and phosphorous concentrations during the three-year study period at five sites (Pre-drought phase: February 2015 to July 2015, Drought phase: November 2015 to May 2016, Transitional phase: August 2016 to January 2017, Wet phase: April 2017 to November 2017).

3.3.3. Phytoplankton and microphytobenthic biomass

Phytoplankton biomass varied throughout the study period (Figure 3.5). Although there were no clear trends and no significant differences found ($F_{3,50} = 0.63, p > 0.05$) among phases, there were

peaks in phytoplankton biomass during May 2015 at all 5 sites (Figure 3.5). Phytoplankton biomass ranged from 0.81 (November 2017) to 267.56 mg m⁻³ (May 2015), with both values recorded at Lister's Point. The second highest phytoplankton biomass (August 2016, 197.48 mg m⁻³) (Figure 3.5) was recorded at the Narrows that occurred simultaneously with a drastic decline in DIN levels at the beginning of the transitional phase, thereafter phytoplankton biomass markedly decreased at the Narrows. Lister's Point phytoplankton biomass peaked during November 2016 (Figure 3.5) which coincided with lower DO levels (Figure 3.3) as well as a peak in DIP levels (Figure 3.4). Microphytobenthic biomass differed between phases ($F_{3,50} = 6.23$, $p < 0.05$), with the wet phase being significantly lower in comparison to the pre-drought and drought phases (Tukey post hoc test $p < 0.05$). (Figure 3.5). Microphytobenthic biomass (MPB) ranged from 4.30 mg m⁻² (Mouth, April 2017) to 612.21 mg m⁻² (Lister's Point, January 2017) (Figure 3.5). The peak in Lister's Point MPB biomass coincided with an increase in DIP levels during January 2017 (Figure 3.4).

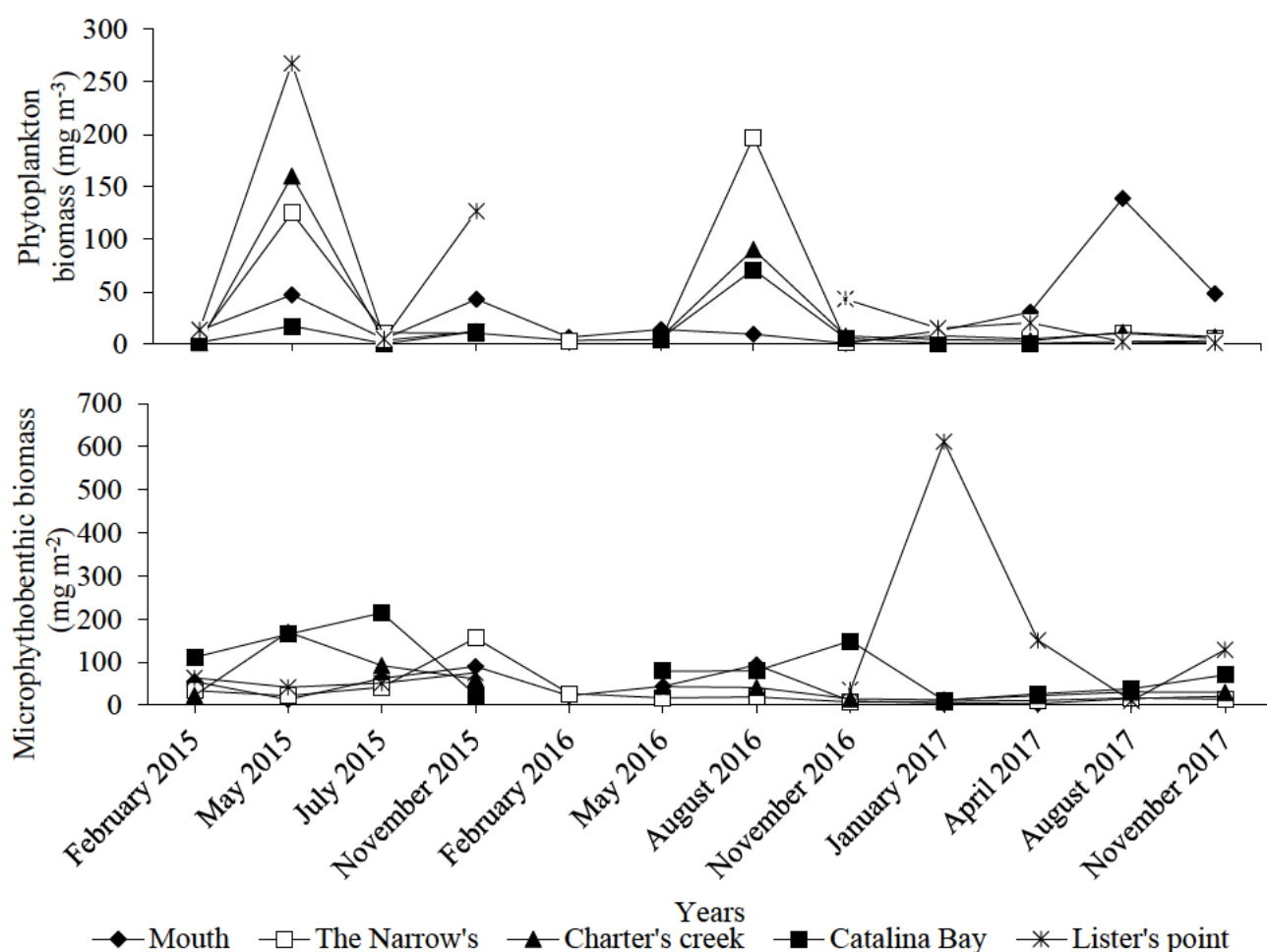


Figure 3.5: Phytoplankton and microphytobenthic biomass for the five sites over the three-year study period (Pre-drought phase: February 2015 to July 2015, Drought phase: November 2015 to May 2016, Transitional phase: August 2016 to January 2017, Wet phase: April 2017 to November 2017).

3.3.4. Total suspended solids

Overall Lister's Point had a higher concentration of total suspended solids (TSS), but peaks were also recorded in the Narrows (January 2017, 172.33 mg l⁻¹) as well as the Mouth during restoration activities (November 2016, 645.65 mg l⁻¹) (Figure 3.6). Total suspended solids did not have any significant differences ($F_{3,50} = 0.77, p > 0.05$) among phases.

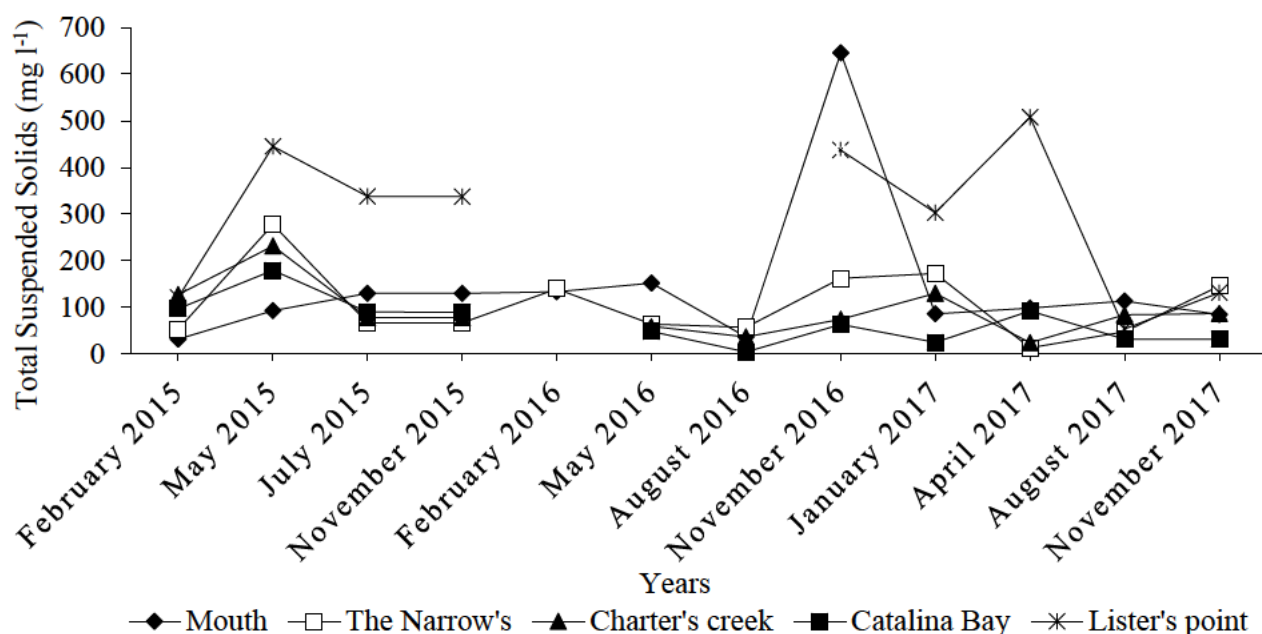


Figure 3.6: Total suspended solids for the five sites over the three-year study period (Pre-drought phase: February 2015 to July 2015, Drought phase: November 2015 to May 2016, Transitional phase: August 2016 to January 2017, Wet phase: April 2017 to November 2017).

3.3.5. Zooplankton abundance and taxonomic richness

Total recorded zooplankton abundance ranged from 327 ind. m⁻³ (Catalina Bay, April 2017) to 8×10^5 ind. m⁻³ (Mouth, May 2016) (Figure 3.7 a) during the study period. Abundance differed between sites ($F_{4,12} = 3.43, p < 0.05$) with abundance at the Narrows being significantly higher than that at Catalina Bay (Tukey post hoc test $p < 0.05$). Additionally, zooplankton abundance differed significantly between phases ($F_{3,12} = 3.23, p < 0.05$) with the zooplankton abundance during the drought phase differing with both the pre-drought and wet phase (Tukey post hoc test $p < 0.05$). Abundance during the drought phase was lower at Lister's Point and Charters Creek in comparison to the pre-drought and wet phase (Figure 3.7 a & b). At the beginning of the drought (November 2015) Catalina Bay had a markedly high abundance but abundance declined drastically with the onset of drought conditions (Figure 3.7 a & b).

Taxonomic richness ranged from 5 taxa (Catalina Bay, April 2017) to 46 taxa (Mouth, May 2015) (Figure 3.7 a). The latter occurred during a period of saltwater intrusion (May 2015) when the Mfolozi River was connected to the Indian Ocean via the beach spillway. Also, the second-highest richness of 41 taxa was recorded at the Mouth (November 2016) when marine overtopping combined with freshwater input from the Mfolozi River (Figure 3.7 a). Taxonomic richness differed between sites ($F_{4,12} = 5.09, p < 0.05$) but not phases ($F_{3,12} = 0.58, p > 0.05$). Taxonomic richness at the Narrows was significantly higher than that at Lister's Point and Charter's Creek (Tukey post hoc test $p < 0.05$).

Correlation analyses revealed zooplankton abundance exhibited significant correlations with dissolved oxygen concentrations ($r = -0.29, p < 0.01$) and DIN ($r = 0.39, p < 0.001$). Taxonomic richness was significantly correlated with salinity ($r = -0.28, p < 0.001$), and DIN ($r = 0.37, p < 0.001$).

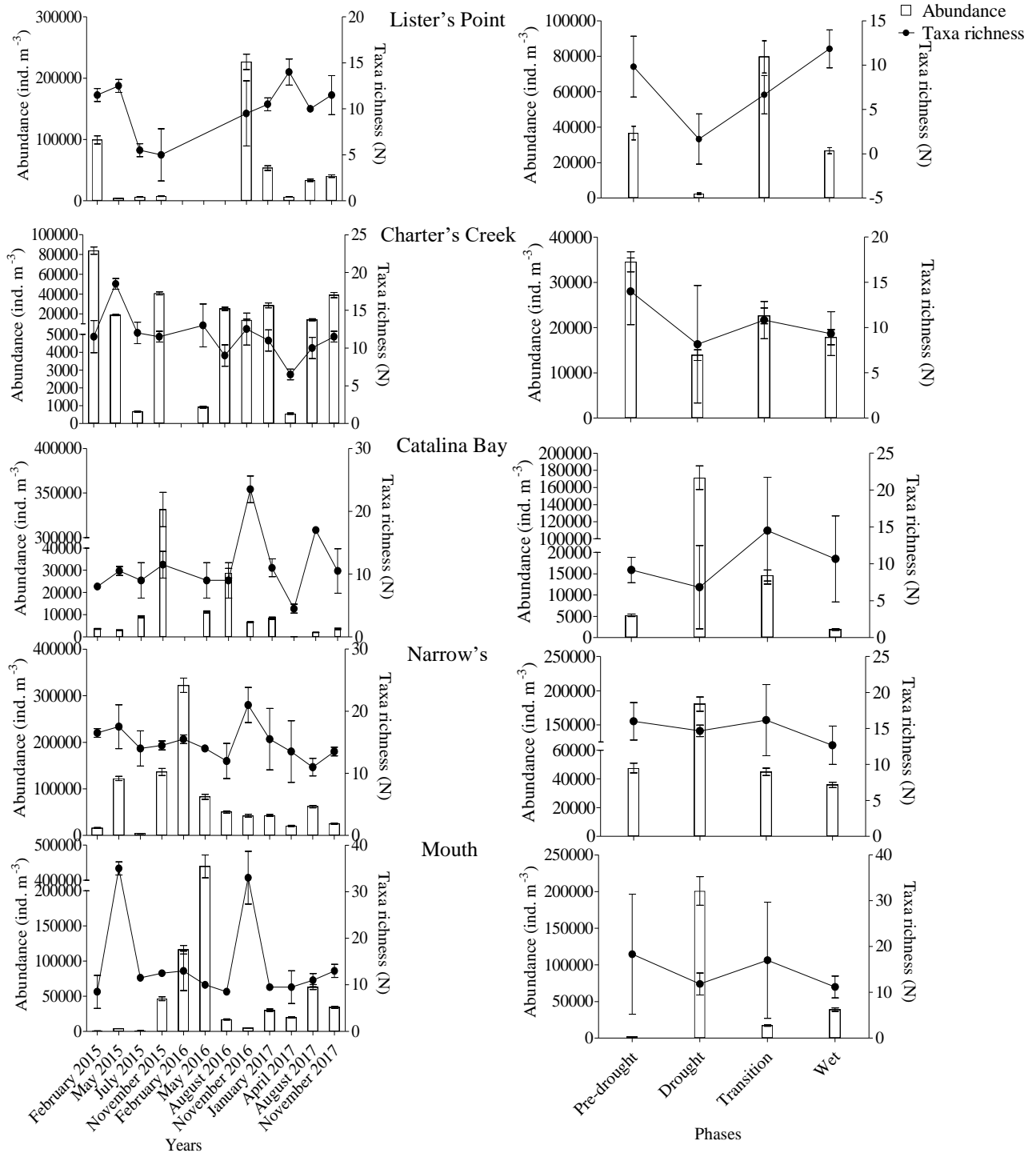


Figure 3.7: Average (\pm SD) zooplankton abundance (ind. m⁻³) and taxa richness (N) a. recorded over the three-year study period, b. of each hydrological phase (Pre-drought phase: February 2015 to July 2015, Drought phase: November 2015 to May 2016, Transitional phase: August 2016 to January 2017, Wet phase: April 2017 to November 2017).

3.3.6. Zooplankton community structure

In total, 118 taxa were recorded during the study period (Table 3.2). Benthic organisms were included in the taxa recorded due to the hyperbenthic sampling method. During the pre-drought conditions, all resident taxa of the estuary were present in high abundance at the five sites including the estuarine calanoid copepods *Pseudodiaptomus stuhlmanni*, *Acartiella natalensis*, the mysid *Mesopodopsis africana*, and the resident cyclopoid *Oithona brevicornis* (Table 3.2). Also, during the pre-drought conditions, there was an increase in marine taxa such as cirripede nauplii, harpacticoids *Euterpina acutifrons* as well as *Microsetella norvegica*, calanoid copepods *Temora* sp, *Paracalanus* spp., *Acartia danae*, etc. (Table 3.2) when there was seawater intrusion at the Mouth (May 2015). The community structure at Lister's Point during November 2016 (transitional phase) consisted mainly of halotolerant taxa including the cyclopoid copepod *Apocyclops cf. dengizicus*, the harpacticoid copepod *Cletocamptus confluentis* and the ciliate *Fabrea cf. salina* (Table 3.2). The community structure at both Charter's Creek and Catalina Bay consisted of numerous rotifer species during the transitional phase (Table 3.2).

There was a clear transition in the community structure across all the sites during the wet phase whereby resident taxa including the cyclopoid *O. brevicornis* and the estuarine calanoid copepod *A. natalensis* were virtually absent (Table 3.2). During the wet phase, the Mouth and the Narrows had mainly freshwater taxa including cyclopoids, rotifers, and cladocerans (Table 3.2). During the wet phase, *M. africana* was absent from both the Mouth as well as the Narrows community and only persisted at Charter's Creek, Lister's Point, and Catalina Bay in extremely low densities (Table 3.2). *Pseudodiaptomus stuhlmanni* was the only estuarine resident calanoid copepod present throughout the study at all 5 sites (Table 3.2).

Cluster analyses revealed distinct phase groupings at both the Mouth and the Narrows as these two sites had no estuarine taxa present during the wet phase (with the exception of *P. stuhlmanni*) and freshwater taxa were dominant (Figure 3.8). Cluster groupings for the lakes were less distinct as these sites were severely affected by the drought conditions. The lakes served as a refuge for another estuarine species, the mysid *M. africana* and freshwater taxa were not as prominent as in the lower reaches (Figure 3.8). There was a higher variability within the Lister's Point community due to the severe drought conditions. Although the community structure of Lister's Point had a high variability, the two samples from the wet phase (August and November 2017) grouped with a 45 % similarity (Figure 3.8). Also, there was a common outlier which was April 2017 that had <30 % similarity within the zooplankton assemblages at Catalina Bay and Charter's Creek (Figure 3.8).

Multidimensional scaling plots (MDS) revealed that the majority of the pre-drought zooplankton community had a 30 % similarity, with some overlap alongside the drought community (Figure 3.9). The drought phase community had a few overlaps with the transitional as well as the wet phase zooplankton assemblages (Figure 3.9). Also, there were a few outliers in the drought, transitional and wet phase communities (Figure 3.9). Overall, the drought community grouped together with a 30 % similarity, and both the transitional as well as the wet phase communities grouped together with a 30 % similarity (Figure 3.9).

PERMANOVA analysis revealed a significant difference in the community structure between sites (Pseudo- $F = 4.06$, $p < 0.001$) and phases (Pseudo- $F = 2.35$, $p < 0.001$). The zooplankton community of the pre-drought phase differed with the drought (pairwise tests, $p < 0.01$), transition and the wet phase (pairwise tests, $p < 0.001$). Additionally, the assemblage of the drought phase differed with the wet phase (pairwise tests, $p < 0.001$). The community structure of the Narrows differed with Catalina Bay (pairwise tests, $p < 0.001$), Lister's Point (pairwise tests, $p < 0.001$), Charter's Creek (pairwise tests, $p < 0.01$) and the Mouth (pairwise tests, $p < 0.01$). The Narrows had mainly freshwater taxa throughout the study compared to Charter's Creek, Catalina Bay and Lister's Point (Table 3.2). Furthermore, the community structure at the Mouth differed to the furthest site in the estuary which is Lister's Point (pairwise tests, $p < 0.01$).

SIMPER analysis revealed the highest dissimilarity (79.30 %) occurred between the pre-drought community and the wet phase community which were as a result of nine taxa contributing to the dissimilarities. The taxa included were copepod nauplii (13.60 %), cyclopoids (11.87 %), cladocerans (9.54 %), *O. brevicornis* (9.31 %), *P. stuhlmanni* (8.39 %), *A. natalensis* (7.95 %), rotifers (5.47 %), *M. africana* (0.62 %), and calanoid copepodites (0.75 %). Additionally, the drought phase differed (78.77 %) with the wet phase with ten taxa identified contributing to the dissimilarities. The taxa contributing to the dissimilarities between the drought and wet phase were the following: copepod nauplii (17.52 %), *P. stuhlmanni* (12.60 %), *A. natalensis* (6.38 %), *O. brevicornis* (6.10 %), calanoid copepodites (4.99 %), cyclopoids (7.49 %), rotifers (7.01 %), cladocerans (2.92 %) and the ciliate *Fabrea* cf. *salina* (2.58 %).

Table 3.2: Average abundance (ind. m⁻³) of zooplankton taxa identified from the 5 sites in the St Lucia estuarine lake from February 2015 to November 2017. (P) for Pre-drought, (D) drought, (T) Transition and (W) Wet. Unid.: unidentified.

	The Mouth				The Narrow's				Charter's Creek				Catalina Bay				Lister's Point			
	P	D	T	W	P	D	T	W	P	D	T	W	P	D	T	W	P	D	T	W
Foraminefera	R	-	-	-	R	R	-	-	-	A	-	-	R	P	R	-	R	P	P	R
Allogromids (Unid.)	R	R	R	-	-	-	-	-	-	R	P	-	-	-	-	-	-	-	-	-
<i>Fabrea cf. salina</i>	-	-	R	-	-	-	-	-	-	A	R	-	-	-	R	-	-	A	VA	-
CNIDARIA																				
Jelly polyp	R	-	-	-	R	R	R	R	R	-	-	-	-	-	-	R	-	-	-	R
Hydromedusae juveniles	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	R
<i>Moerisia inkermanica</i>	-	-	-	-	R	R	-	-	R	-	R	R	-	R	R	R	-	-	-	-
<i>Obelia</i> sp.	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ROTIFERA																				
<i>Brachionus</i> spp.	-	-	R	A	P	P	P	R	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brachionus calyciflorus</i>	-	-	R	VA	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brachionus cf. caudatus</i>	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brachionus cf. falcatus</i>	-	-	-	-	-	-	R	R	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brachionus patulus</i>	-	-	R	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brachionus cf. plicatilis</i>	-	VA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brachionus quadridentatus</i>	-	-	R	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brachionus rotundiformis</i>	-	-	-	-	P	P	P	-	-	R	R	-	-	-	R	R	-	-	VA	P
<i>Euchlanis</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
<i>Filinia</i> sp.	-	-	-	-	-	R	A	R	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lecane</i> spp.	-	-	-	-	-	-	P	-	-	-	-	-	-	-	P	R	-	-	-	-
<i>Lecane grandis</i>	-	R	R	-	-	-	P	-	-	R	A	-	-	R	P	-	-	-	-	-
<i>Mytilina</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
<i>Mytilina ventralis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
ANNELIDA																				
Polychaete larvae	R	R	P	R	R	A	R	-	A	-	P	-	P	R	R	-	A	A	P	R
Nereidae	R	-	-	-	-	-	-	-	-	-	-	-	R	-	-	R	-	-	-	-
Oligochaeta (Unid.)	R	-	R	-	-	-	R	-	-	-	-	R	-	-	R	R	-	-	-	-
Nematoda (Unid.)	R	R	P	P	-	-	P	R	R	R	P	P	P	A	P	R	R	-	A	R
Platyhelminthes																				
Turbellaria (Unid.)	-	R	R	-	-	-	-	-	-	P	R	R	-	-	-	R	-	-	P	R
ARTHROPODA																				
Branchiopoda																				
<i>Moina</i> spp.	-	-	R	A	A	-	P	P	P	-	-	-	-	-	-	R	-	-	-	-
<i>Ceriodaphnia</i> sp.	-	-	-	-	R	-	R	R	R	-	-	-	-	-	-	R	-	-	-	-
Chydoridae	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	R	-	-	-	-
<i>Diaphanosoma cf. excisum</i>	-	-	R	R	A	R	-	P	R	-	-	-	-	-	R	-	-	-	-	-
<i>Moina cf. micrura</i>	-	-	P	P	VA	R	A	A	P	-	-	-	R	-	-	-	-	-	-	R
<i>Moina cf. oryzae</i>	-	-	-	P	P	-	-	-	R	-	-	-	R	-	-	-	-	-	-	-
Malacostraca Decapoda																				
<i>Caridina</i> sp.	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Caridina africana</i>	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Palaemon concinnus</i>	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Palaemon debilis</i>	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Decapod juvenile (Unid.)	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caridean larvae (Unid.)	R	R	R	R	R	R	-	R	-	-	R	R	-	-	-	-	-	-	-	R
Megalopa	R	R	-	-	-	R	-	-	-	-	-	-	R	-	-	-	-	-	-	-
Zoeae	-	-	R	-	R	-	-	R	R	R	R	R	-	-	-	P	R	-	P	R
Mysida																				
<i>Mesopodopsis africana</i>	R	VA	R	-	R	R	R	-	R	R	R	R	-	R	-	R	R	-	-	R
Cumacea (Unid.)	-	R	-	-	-	-	-	-	R	R	-	-	R	-	-	-	R	-	-	-
Tanaidacea																				
<i>Halmyrapseudes cooperi</i>	R	P	-	R	R	R	R	R	R	P	-	R	R	R	R	-	-	-	-	R
Isopoda																				
Sphaeromatidae	-	-	-	-	R	-	-	R	-	-	-	-	-	-	-	R	-	-	-	-
Amphipoda																				
<i>Afrochiltonia capensis</i>	R	R	-	-	-	-	R	R	-	-	-	-	R	-	R	R	-	-	-	-

Table 3.2 cont.

	The Mouth				The Narrow's				Charter's Creek				Catalina Bay				Lister's Point			
	P	D	T	W	P	D	T	W	P	D	T	W	P	D	T	W	P	D	T	W
Amphithoidae	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Corophidae	R	R	-	-	R	R	R	R	-	-	-	-	-	-	-	-	-	-	-	-
<i>Corophium</i> sp.	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	R
<i>Corophium triaenonyx</i>	-	-	-	-	R	R	R	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Grandidierella</i> sp.	R	P	-	-	R	R	R	R	R	-	R	-	R	R	R	-	R	-	-	R
<i>Grandidierella bonnieroides</i>	R	R	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R
<i>Melita orgasmos</i>	-	-	-	-	R	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Orchestia</i> sp.	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Podocerospsis</i> sp.	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-
Stenothoidae	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Talitridae (Unid.)	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphipods (Unid.)	-	-	-	-	R	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maxillopoda																				
Cirripedia nauplii	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Copepoda																				
Nauplii	P	*VA	A	VA	A	VA	VA	A	A	A	VA	VA	P	VA	A	A	A	P	VA	A
Calanoida																				
<i>Acartiella natalensis</i>	P	VA	-	-	A	A	-	-	A	P	R	-	A	P	R	-	A	-	-	-
<i>Acartia danae</i>	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Nanocalanus minor</i>	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-
<i>Paracalanus</i> spp.	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudodiaptomus stuhlmanni</i>	P	A	A	A	VA	VA	A	A	A	A	P	A	A	*VA	P	P	P	-	A	A
<i>Temora</i> sp.	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Calanoid copepodites (Unid.)	R	P	-	-	A	VA	-	-	-	A	-	-	-	VA	-	-	-	-	-	-
Cyclopoida																				
<i>Apocyclops cf. dengizicus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-
Cyclopidae	P	R	P	A	R	R	A	A	P	R	P	R	-	R	-	R	-	-	P	-
<i>Mesocyclops</i> sp.	-	-	-	-	-	-	-	R	-	-	-	-	-	-	R	-	-	-	-	-
<i>Oithona brevicornis</i>	P	P	R	-	P	VA	R	-	VA	A	-	-	P	VA	-	-	VA	-	-	-
<i>Thermocyclops</i> sp.	-	-	-	-	R	-	R	P	-	-	-	-	-	-	-	-	-	-	-	-
Cyclopoid copepodites (Unid.)	R	R	A	A	P	P	A	A	-	P	-	-	-	R	R	R	P	P	-	R
<i>Corycaeus</i> sp.	R	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ergasilidae	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Farranula</i> sp.	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Harpacticoida																				
Ameiriidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-
<i>Clytemnestra</i> sp.	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cletodidae	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-	-	R	-	-	-
<i>Cletocamptus confluens</i>	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	A	-
Canthocamptidae	-	R	-	-	-	-	-	-	R	-	R	-	-	P	R	-	-	-	A	-
Darcythompsoniidae	-	-	R	-	-	-	-	R	-	-	-	-	-	-	P	-	-	-	-	-
Ectinosomatidae	R	R	R	-	-	R	-	-	R	-	P	-	-	-	R	R	R	-	-	R
<i>Euterpina acutifrons</i>	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Microsetella norvegica</i>	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Microsetella</i> sp.	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Miraciidae sp.	R	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Nitocra taylora</i>	-	-	R	R	R	-	R	R	R	-	-	-	R	P	P	P	-	-	-	-
<i>Porcellidium</i> sp.	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tegastidae	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Harpacticoids (Unid.)	R	P	R	R	-	P	R	-	R	-	P	P	-	P	P	R	-	P	P	R
Ostracoda (Unid.)	R	R	P	P	P	P	P	R	P	R	P	P	R	P	P	R	R	-	-	P
Insecta																				
Hymenoptera	R	R	-	-	-	R	-	-	-	R	-	R	R	-	R	-	R	-	P	-
Hemiptera	-	-	A	R	-	-	-	-	-	-	-	R	-	-	-	-	-	-	R	-
Corixidae	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diptera fly	-	-	R	-	-	-	R	-	-	-	-	-	-	-	-	-	R	P	-	-
Ephemoptera	-	-	P	-	-	-	R	-	-	-	-	R	-	-	-	-	-	-	-	-
Chironomid larvae	-	R	R	R	-	-	P	R	-	R	P	R	-	A	A	R	-	-	P	R
Chironomid egg	-	-	R	-	-	-	P	-	-	-	R	-	-	P	R	R	-	-	-	R
Hydrachnidia	-	-	-	-	-	-	R	R	-	-	-	-	R	P	-	-	-	-	-	-
Arachnida	-	R	R	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-
<i>Amurida</i> sp.	-	P	-	-	-	-	R	-	-	-	-	-	-	-	R	-	-	-	-	-
Coleoptera	R	R	R	R	-	-	R	-	R	-	-	-	-	-	R	-	-	-	-	-
Coleoptera pupa (different stages)	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odonata	R	-	-	R	-	-	-	-	-	-	R	-	-	-	R	R	-	-	-	-
Tipulidae	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 3.2 cont.

	The Mouth				The Narrow's				Charter's Creek				Catalina Bay				Lister's Point			
	P	D	T	W	P	D	T	W	P	D	T	W	P	D	T	W	P	D	T	W
Orthopteran	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-
Insect larvae (Unid.)	-	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-
MOLLUSCA																				
Gastropoda																				
Gastropod larvae	P	R	R	-	R	R	-	-	R	R	-	P	P	P	P	R	P	P	-	A
Bivalvia																				
Bivalve larvae	R	-	-	-	-	A	-	-	-	-	A	A	-	R	P	R	P	-	-	A
Cyphonautes larvae	R	P	-	-	R	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chaetognatha (Unid.)	R	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anura	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Osteichthyes																				
Fish egg	R	R	R	R	R	R	R	-	R	-	-	-	R	-	R	-	R	-	P	R
Fish larvae	R	R	R	R	R	R	-	R	R	-	R	R	R	-	-	R	-	-	-	R
<i>Oreochromis mossambicus</i>	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ambassis ambassis</i>	-	R	R	-	-	-	-	R	-	-	R	-	-	-	-	-	-	-	-	-
<i>Clarias garipinus</i>	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Glossogobius</i> sp.	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	Rare (R)	Present (P)	Abundant (A)	Very abundant (VA)	*Very abundant (*VA)
Density (ind. m ⁻³)	0-99	100-999	1000-9999	10000-100000	>100000

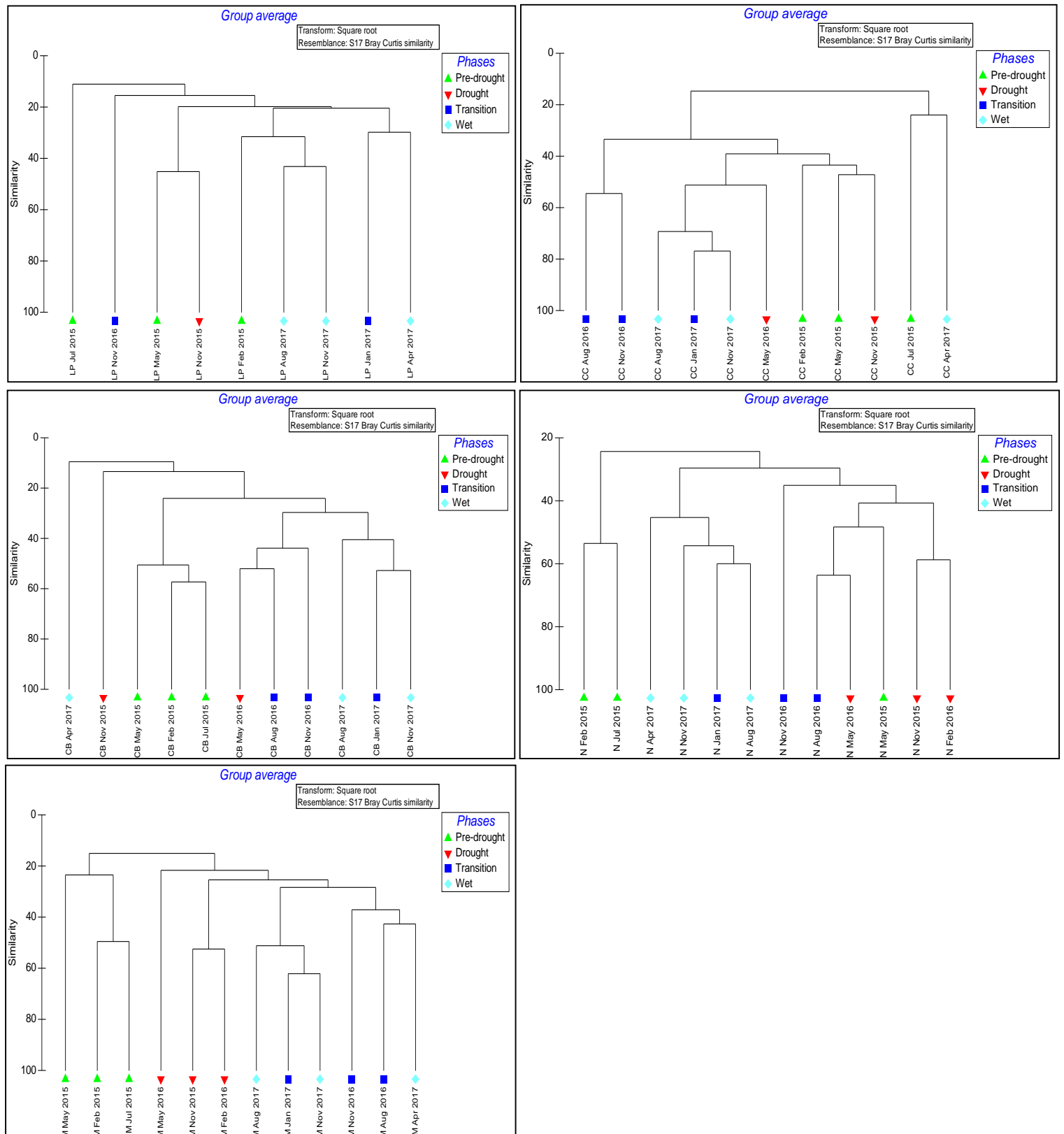


Figure 3.8: Cluster diagrams of the five sites showing the similarity in the zooplankton community structure (Charter's Creek-CC, Catalina Bay-CB, Lister's Point-LP, Mouth-M, and Narrow's-N).

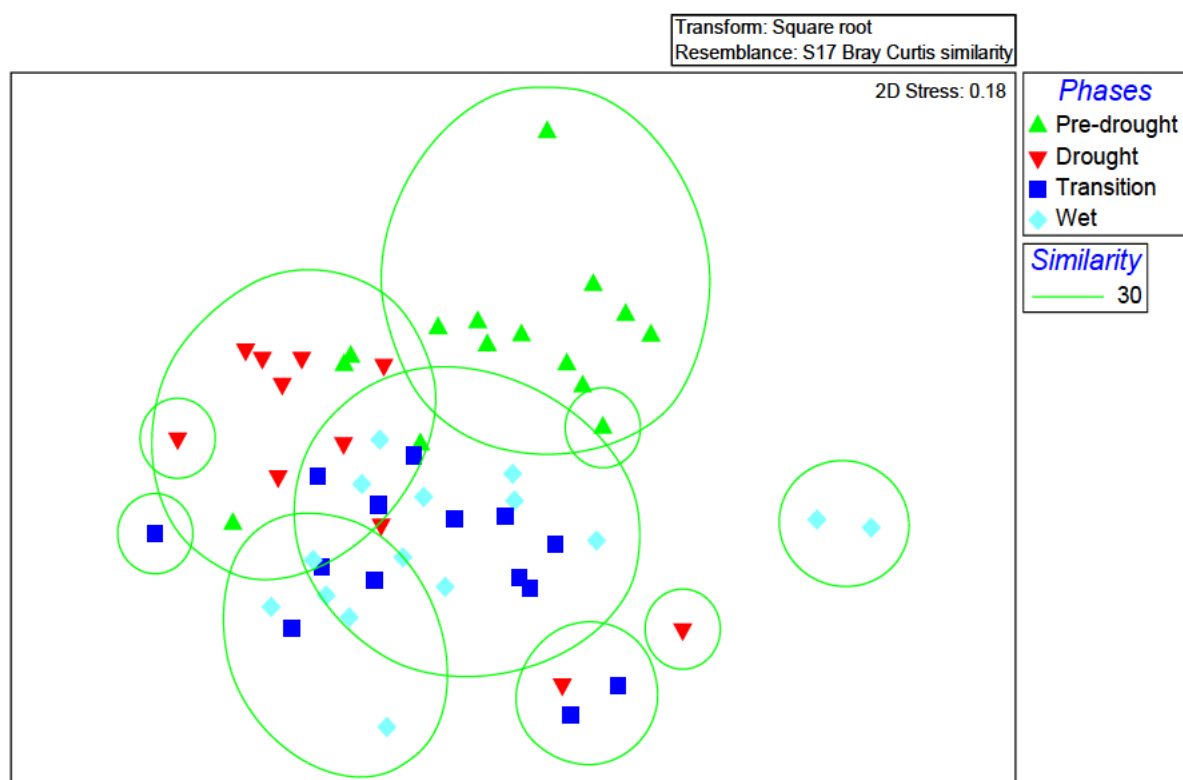


Figure 3.9: Multidimensional scaling plots showing the similarity in the zooplankton community structure amongst the phases (Pre-drought, drought, transition and wet).

The BIOENV analysis identified salinity and microphytobenthic biomass as the main determinants of the community structure ($R = 0.205$). Additionally, the DistLM model (Table 3.3) identified dissolved oxygen as another environmental factor affecting the zooplankton assemblage. Even though the environmental variables have a significant effect on the community structure, the model explains very little of the variation. The dbRDA plot (Figure 3.10), shows the first axis conveys 48.5 % of the fitted variability and 5.4 % of the variation (Salinity, MPB and DO).

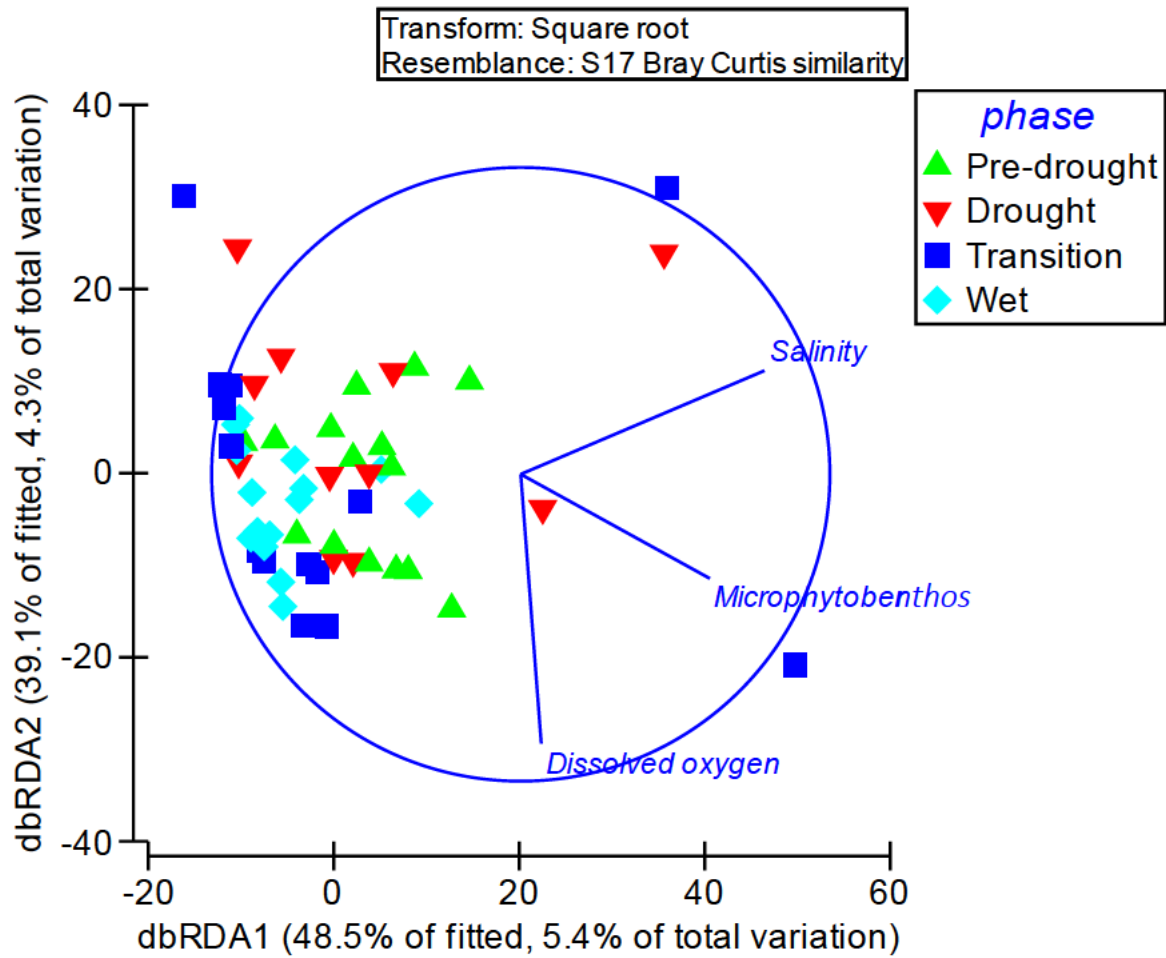


Figure 3.10: dbRDA model of the zooplankton community structure overlaid with the main environmental variables identified from BIOENV.

Table 3.3: DistLM (marginal tests) for variations in the zooplankton community structure explained by the main environmental variable.

Variable	Sum of squares (trace)	Pseudo-F	<i>P</i>	Proportion
Salinity	7268.6	2.5497	0.002	4.5899E-2
Microphytobenthos	5071.5	1.7535	0.029	3.32025E-2
Dissolved oxygen	5027.5	1.7378	0.037	3.1747E-2

3.4. DISCUSSION

Salinity levels are being altered drastically in estuarine systems as droughts and temporary hypersaline conditions are becoming more prevalent due to climate change and human alterations (Hossain et al. 2017, Breaux et al. 2019). Drought conditions will severely affect coastal

ecosystems in areas such as Africa, the USA and south-western Australia (Humphries et al. 2016, Hossain et al. 2017, Breaux et al. 2019). As temperatures rise, precipitation is expected to increase unevenly globally (Masson-Delmotte et al. 2018, Breaux et al. 2019, Tweedley et al. 2019). Climate models have predicted an increase in both frequency and magnitude of extreme weather events (IPCC 2014, Masson-Delmotte et al. 2018, Breaux et al. 2019). The occurrence of increased rainfall /droughts can affect the water level fluctuations (WLF's) in estuaries worldwide (Coops et al. 2003, Breaux et al. 2019). Shallow lakes are prone to shifting to alternate states in response to changing hydrological conditions (Coops et al. 2003, Chang et al. 2017). The St Lucia estuarine lake has experienced periodic shifts of dry and wet cycles, with the estuarine system experiencing extreme physico-chemical fluctuations (Carrasco et al. 2010, Perissinotto et al. 2013, Jones 2015, Tweedley et al. 2019).

This study period covered four different hydrological states that included a pre-drought phase (February 2015 to July 2015) where the majority of the system was covered in water and estuarine conditions were prevalent. The pre-drought phase was followed by a short periodic drought (November 2015 to May 2016) which was due to decreased freshwater input, less than average rainfall and increased evaporation rates that disconnected the lake basins. The drought phase lasted for half a year (November 2015 to July 2016) with 80 % of the lake surface area dried up and a maximum salinity of 111 recorded at Lister's Point (November 2015). The Mouth and the Narrow's were both protected from drought conditions due to the close proximity to the Mfolozi and Mpate River input (Jones et al. 2020). The increased precipitation coupled with the start of the restoration project (June 2016) initiated a transitional phase as increased freshwater input allowed for the relinkage of the lake basins and the alleviation of drought conditions. The increased freshwater input connected the Narrow's to the South Lake from August 2016 onwards, but the further northern reaches took a longer time to reconnect as water levels at Lister's Point only started to increase from November 2016. With increased freshwater input, from March 2017 onwards the entire system was fully covered with water which marked the start of the new wet phase (April 2017 to November 2017) in the St Lucia Estuary.

Salinities at all sites decreased markedly during the wet phase and water levels increased, however, siltation in the mouth area was prominent (Chapter 1). The sediment structure in the mouth area was composed primarily of silt, post restoration activities (Jones et al. 2020). During November 2016, increased precipitation coupled with restoration activities at the mouth brought about peaks in turbidity levels at the mouth region (1246 NTU) as increased freshwater input was allowed into the system. Also, heavy rainfall events during November 2016 (163 mm), January 2017 (182 mm) and November 2017(141 mm) coincided with high levels of total suspended solids mainly at the

Mouth, Narrow's, Charter's Creek and Lister's Point. The silt accumulating at the mouth region has thus far spread to the South Lake of the estuarine system (Jones et al. 2020). There was high spatial variability in the St Lucia estuarine system as each site varied vastly in terms of physico-chemical parameters during the 4 different hydrological states.

Temporal and spatial differences in zooplankton abundance are influenced by many factors including food availability and hydrological processes exporting as well as importing organisms (Costa et al. 2009). The input of freshwater in an estuarine system has an important impact on both the abundance and dispersal of zooplankton (Jerling and Cyrus 2016). During drought conditions, Catalina Bay, Charters Creek, and Lister's Point were severely affected as there was a drastic decline in zooplankton abundance due to reduced water levels and sometimes dry conditions as no zooplankton samples could be collected. The Mouth and the Narrows maintained higher abundance of zooplankton during the drought period since they are in close proximity to freshwater sources including the Mpate River and the link canal. Generally, Catalina Bay had lower zooplankton abundance than all the other sites which could be due to decreased food availability as lower phytoplankton biomasses were recorded at Catalina Bay (Sondergaard et al. 2007, Carrasco et al. 2010, Carrasco and Perissinotto 2015). Records of lower zooplankton abundance at Catalina Bay have also been recorded in previous studies (Carrasco and Perissinotto 2015).

Increased freshwater input has had a positive influence for zooplankton abundance, especially for the lake regions as the filling up of lake basins increases niche availability. Nutrient levels also increased during the wet phase, promoting primary production which is favourable for zooplankton (Sondergaard et al. 2007). The lower abundance of zooplankton recorded at the Narrow's during January 2017 and during the wet phase in comparison to the drought period could be due to the dilution effect as elevated water levels increases the volume of water resulting in zooplankton densities appearing lower (Urabe and Murano 1986). Jones et al. (2016) also reported lowest zooplankton abundance in the Narrows ($6.68 \times 10^4 \text{ ind. m}^{-3}$) during a flood event.

The peak in zooplankton abundance at the Narrows's during February 2016 (drought phase) could be due to the higher primary production in that region as the area is fertilised by hippopotamus dung (Taylor 2013, Mosepele et al. 2009, Carrasco and Perissinotto 2015). The dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorous (DIP) levels were generally higher at the Narrows compared to the other sites. The positive correlation between zooplankton abundance and dissolved inorganic nitrogen could be as a result of the combination from increased freshwater input and hippo dung stimulating primary production which is advantageous for zooplankton as they have increased food resources (Vieira et al. 2003, Carrasco and Perissinotto 2015). Zooplankton abundance (mainly in the lakes) increased in accordance with the increase in dissolved

inorganic nitrogen levels and lower salinities at all sites from November 2017. DIN levels at the Mouth region increased drastically in May 2016 which could be due to the increased freshwater input from the beach spillway leading from the Mfolozi River as the highest abundance of 8.79×10^5 ind. m^{-3} occurred, with copepod nauplii and the rotifer *B. plicatilis* dominating the assemblage.

In total, 118 taxa were recorded during the study period. Taxa richness differed spatially with northern sites (Lister's Point and Charter's Creek) having lower taxa richness compared to the lower reaches (Narrows) as there were harsher drought conditions experienced in the upper reaches, due to the distance from the main freshwater supply (Carrasco and Perissinotto 2012, 2015). Lister's Point in the northern reaches of the system experiences shallow and hypersaline conditions during drought periods (Carrasco and Perissinotto 2012, 2015). Lister's Point was completely dry from January 2016 to October 2016. Due to the high salinities that occurred during November 2016 at Lister's Point, halotolerant taxa were present including the cyclopoid *Apocyclops cf. dengizicus*, the ciliate *Fabrea cf. salina* and the harpacticoid *Cletocamptus confluens*. These taxa also formed a part of the halotolerant community recorded during hypersaline conditions in 2010 at Lister's Point and only disappeared when salinities were > 130 (Carrasco and Perissinotto 2012). Taxa richness was negatively correlated with salinity, indicating the negative effect of hypersalinity on taxa richness (Perissinotto et al. 2013). The Narrows maintained high taxa richness throughout the study with mainly freshwater species such as cladocerans, cyclopoids, and rotifers dominating. This could also explain the positive correlation between taxa richness and DIN levels since the Narrows maintained higher DIN levels throughout the study in comparison to the other sites.

The Mouth experienced seawater intrusion during May 2015 through the beach spillway which brought about the maximum richness of 46 taxa. The marine input introduced species similar to the open mouth conditions in 2007 (Carrasco et al. 2010), including the jellyfish *Obelia* sp., cyphonautes larvae, chaetognaths, marine harpacticoids *Euterpina acutifrons* and *Microsetella norvegica*., calanoid copepods *Acartia danae*, *Temora* sp., *Paracalanus* spp., the cyclopoids *Corycaeus* sp. and *Farranula* sp. The seawater also perforated through to the Narrows in May 2015 as a high abundance of cyphonautes larvae was recorded. Also, while the rehabilitation project was underway at the Mouth (November 2016), species richness increased as there was freshwater input from the Mfolozi River and overtopping of seawater from the Indian Ocean which increased taxa richness with both marine and freshwater taxa (41 species). During November 2016, there were also numerous freshwater taxa recorded including the rotifers *B. patulus*, *B. falcatus* as well as *L. grandis*., the harpacticoid Tegastidae (last recorded by Grindley 1982 in the Narrows), the shrimp *Caridina africana* and the freshwater Barbel catfish (*Clarias garipinus*). The Mouth and the Narrows had similar species richness as they are both in closer proximity to the Mfolozi River

than the rest of the lakes. Similarly, in the temperate Mondego Estuary (Portugal), the diversity was higher closer to the mouth region (Vieira et al. 2003, Marques et al. 2007, 2008). In the Mfolozi-Msunduzi system, it was found that taxa richness increased in combination with marine input and a reduced flow of freshwater input (Jerling and Cyrus 2016).

In this study, the shift to a wet state was accompanied by a shift in zooplankton community structure. During the wet phase, freshwater taxa mainly dominated at the Mouth, the Narrow's and Catalina Bay. Charter's Creek and Lister's Point also had freshwater taxa present during the wet phase but not as prominent as in the other sites. The estuarine resident zooplankton including *P. stuhmanni*, *M. africana*, *A. natalensis* and the resident cyclopoid *O. brevicornis* were dominant until the transitional phase, after which only *P. stuhmanni* persisted in all the sites. *Mesopodopsis africana* was present in the lakes during 2017, but in low densities.

Pseudodiaptomus stuhmanni is a dominant copepod in both the Mfolozi River and the St Lucia Estuary (Carrasco et al. 2010, Jerling et al. 2010, Jones et al. 2016). Through experimental studies, *P. stuhmanni* demonstrated its tolerance to high turbidity levels (Jones et al. 2015) and both freshwater conditions (<5), as well as hypersaline conditions (>70) (Grindley 1982, Jones et al. 2016). Although the abundance of *Pseudodiaptomus stuhmanni* declined during the transitional as well as for part of the wet phase, it still persisted throughout all four states, highlighting its ability to tolerate varying environmental conditions. The decline in densities could be due to lower salinity levels (Jones et al. 2016), increased competition from freshwater taxa (Jerling and Weerts 2018), increased predation as they are an important food source for zooplanktivorous fish (Dyer et al. 2015, Jones et al. 2015) or due to the dilution effect as it has been found that increased freshwater input could reduce populations of resident zooplankton taxa (Threlkard 1982).

Mesopodopsis africana was present only in the lake regions during the wet phase as the lakes had slightly higher salinity levels compared to the Mouth and the Narrows. *Mesopodopsis africana* is euryhaline as its salinity tolerance ranges from 2.55 up to 64 (Grindley 1982, Carrasco and Perissinotto 2011). The northern reaches may have served as a form of refuge for *M. africana* from the much lower saline areas but there had been a lag time before there was a connection of water to the lake basins. The lake basins were reconnected from August 2016 onwards, but salinities only started decreasing from November 2016 at Lister's Point. The low mysid densities recorded in the current study are within the range of those recorded during a transition phase in St Lucia from 2011 to 2013 (Carrasco and Perissinotto 2015). Similar low densities were also recorded at the Mfolozi River (Jerling and Weerts 2018) and at Richards Bay (Jerling 2008).

The estuarine calanoid copepod *Acartiella natalensis* and the resident cyclopoid *Oithona brevicornis* were absent from the community during the wet phase at all 5 sites. *Acartiella natalensis* can tolerate salinities ranging from fresh to 70 (Grindley 1982). *Acartiella natalensis* is endemic to estuaries locally where there are clear salinity gradients present and the successional patterns are determined by both temperature and salinity (Wooldridge 1999, Wooldridge and Melville-Smith 1979). In the Kromme Estuary (South Africa), *A. natalensis* was not recorded in the community structure during the controlled release of freshwater (Wooldridge and Callahan 2000). In the current study, *A. natalensis* was excluded due to both high salinity levels in the northern reaches and from increased freshwater input in the lower reaches. In response to the unfavourable salinity levels, *A. natalensis* may form resting eggs that sink to the bottom of the sediment and results in the formation of seed banks until conditions are favourable for hatching (Ianora and Santella 1991, Wooldridge and Callahan 2000, Brendonck and Meester 2003). Seed banks accumulate over years, forming biodiversity reserves (Brendonck and Meester 2003) and are essential for the survival and prevention of extinction of a wide variety of species (Brendonck and Meester 2003, Boero 1994, Hairston et al. 1996). In this study, resting eggs were recorded during drought conditions at Catalina Bay (MG, pers. observ.) suggesting that zooplankton unable to withstand the hypersaline conditions formed resting eggs and would only hatch once environmental conditions are favourable (Wooldridge and Callahan 2000).

Oithona brevicornis is a cyclopoid copepod that has been recorded in the dominant zooplankton community of the St Lucia Estuary since the 1970s (Grindley 1976, Jones et al. 2016). This cyclopoid mainly inhabits environments of salinity of five and higher (Grindley 1976, Jones et al. 2016), which suggests that their absence was possibly due to prevailing low salinities, competition with freshwater taxa or predation (Etilé et al. 2012). Similar findings were recorded in a tropical coastal lagoon (Grand-Lahou, Cote d'Ivoire) where *O. brevicornis* densities declined as salinity decreased below five (Etilé et al. 2012). During a transition period from a hypersaline to a wet state (2011 to 2013) in St Lucia, salinities remained below 20 at most sites but *O. brevicornis* persisted in high numbers (Carrasco and Perissinotto 2015).

In the current study, the Narrow's community structure differed mainly to the lake regions as freshwater taxa including rotifers, cladocerans and freshwater cyclopoids were prominent during all the phases from riverine input from both the Mpate and Mfolozi River. The cladoceran *Moina cf. micrura* occurred in high abundance in the Narrow's in this study and is known to also occur in the adjacent Mfolozi-Msunduzi system (Jerling and Cyrus 2016) explaining its presence in the Narrows, particularly after periods of high flow. In the Mossoro Estuary (Northern Brazil), there were similar salinity variations as in the wet phase in the current study from the mouth to the upper

reaches of the estuary where similar rotifer taxa were found including *Brachionus cf. caudatus*, *B. cf. plicatilis*, *B. cf. falcatus*, *Filinia* sp., *B. patulus* and *B. calyciflorus* (Silva et al. 2009). The genus *Brachionus* has been known to tolerate waters that are polluted (Pal et al. 2015, Sousa et al. 2008) therefore suggesting this genus was able to withstand the varying environmental conditions.

Prolonged mouth closure in the St Lucia Estuary has resulted in the lack of recruitment of estuarine associated marine fish species (Cyrus et al. 2020). During prolonged mouth closure, estuarine (*Ambassis ambassis*, *Glossogobius* spp. and *Gilchristella aestuarius*) and freshwater (*Oreochromis mossambicus* and *Pseudicrenilabrus philander*) fish dominate (Cyrus et al. 2020). Both estuarine and freshwater fish larvae were recorded in the plankton samples which could most likely be as a result of mouth state and salinity regime (Cyrus et al. 2020).

Salinity, predation and the availability of food (Toumi et al. 2005) are known to alter shifts in zooplankton community structure (Silva et al. 2009). In this study, salinity and microphytobenthic biomass (MPB) were identified as the determining factors of the zooplankton community structure. Microphytobenthic biomass occurs at the interface of water and sediment (Aberle-Malzahn 2004). Growth of microphytobenthic biomass depends on light availability (Aberle-Malzahn 2004), the substrate it grows on (Nunes et al. 2018) and occurs abundantly in systems where there is an increase of nutrients (Mangadze et al. 2017, Dalu et al. 2018). Therefore, the peak in microphytobenthic biomass during the transitional phase at Lister's Point (January 2017) was possibly as a result of increased dissolved inorganic phosphorous (DIP) levels from increased freshwater input alleviating drought conditions. Increased depth as a result of freshwater input could reduce the amount of light availability as depth increases which could limit MPB growth (Aberle-Malzahn 2004). Furthermore, the DistLM model identified dissolved oxygen concentration (DO) as an additional determinant of the zooplankton assemblage. Dissolved oxygen is an important determinant of zooplankton communities (Karpwicz et al. 2020). Variations in dissolved oxygen levels could interfere with their vertical distribution and physiological costs (Karpwicz et al. 2020).

Conclusion

Climatic changes coupled with the restoration project increased water levels within the St Lucia estuarine system. Water levels in shallow lakes are important as they determine both the functioning as well as the structure of these wetlands (Coops et al. 2003). Shifts in the biological community due to changes in hydrological regimes have been recorded in phytoplankton (Nicholls 2011), zooplankton (Meerhoff et al. 2007, Jeppesen et al. 2007) and fish communities (Cloern and Jassby 2012, Cyrus et al. 2020). The zooplankton community serves as an indicator of the changes

occurring within estuarine systems (Hays et al. 2005). This study documents the impact of the newly formed Mfolozi-St Lucia Link on the entire estuarine system. The phase shift resulted in the restructuring of the zooplankton assemblage of the St Lucia Estuary. The zooplankton assemblage during this prolonged wet phase is different from the previously documented transition to a wet phase (2011 – 2013) in the St Lucia estuarine system where resident taxa were still prominent (Carrasco and Perissinotto 2015). In the current study, there has been a transition from estuarine resident taxa to mainly freshwater taxa with the exception of the copepod *P. stuhlmanni* still present at all 5 sites and the mysid *M. africana* in the lake regions. Both hypotheses were supported as firstly there were spatial differences in the zooplankton community structure and abundance along the estuary. Secondly the zooplankton community of the pre-drought phase differed with that of the wet phase. The Global Environment Facility (GEF) funded project has been successful thus far in allowing freshwater input into the lake system but there has been insufficient water to allow for a breaching event of the mouth to allow the flushing out of the sediment. Silt loading still needs to be monitored as there are currently no measures put in place yet to reduce siltation into the estuary as the TSS levels had increased from the transitional phase onwards and turbidity increased at all 5 sites by November 2017 during the study period. The current wet phase has been considerably the most prolonged one thus far and is of concern as there could be the forced exclusion of the resident zooplankton taxa of the estuary. The results obtained in this study, can add on to existing knowledge of zooplankton communities during increased water level fluctuations in subtropical estuaries as they are essential indicators of the health of aquatic systems. Most importantly, the information obtained can assist St Lucia management in further decision making to allow for a successful long-term relinkage of the St Luca -Mfolozi link and for the long-term sustainability of this World Heritage Site.

3.5. Acknowledgments

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CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

Globally, climate change is expected to increase in the future as temperatures will rise (Masson-Delmotte et al. 2018) bringing about increased frequency and extremity of both drought and flood events (Humphries et al. 2016, Breaux 2019, Tweedley et al. 2019). Climate patterns and anthropogenic interferences such as water abstractions, dredging, irrigation and agricultural activities, to name a few, are major determinants of hydrological conditions in the St Lucia estuarine lake (Carrasco et al. 2010, Perissinotto et al. 2013). The St Lucia Estuary is a shallow estuarine system that experiences regular drought periods that have been exacerbated by mouth manipulation over the last century. While it is well known that the restored connection with the Mfolozi River is vital to ensure system functioning, the silt input that accompanies the Mfolozi input is of concern. The estuarine system underwent a short periodic drought (2015/2016) where 80 % of the lake system experienced desiccation. The full reconnection of the St Lucia-Mfolozi mouth (2016/2017), in combination with increased rainfall, has increased freshwater input to the St Lucia estuarine system. Numerous studies have documented the effects of dry conditions on the estuarine system (Taylor 2006, Pillay and Perissinotto 2008, Carrasco et al. 2010, Cyrus et al. 2010, Cyrus et al. 2011), but the transition from dry hypersaline to wet state provided the ideal opportunity to record spatial changes of the response of the zooplankton community structure as the estuary transitioned to a wet state with the estuarine system fully linked to the Mfolozi River.

The findings presented are important for assessing the impacts of different hydrological conditions in the estuary and to assess the impact of the Global Environment facility (GEF) funded restoration project that took place at the mouth of the St Lucia Estuary to restore the St Lucia-Mfolozi connection. The GEF funded rehabilitation project was a form of ecological engineering to restore the natural functioning of the estuary. Similar ecological engineering projects have been applied to estuarine systems in Australia, Europe, Asia and North America (Elliott et al. 2016). The manipulation of the Mfolozi/St Lucia estuarine system has been well recorded since 1932 (Elliott et al. 2016). Zooplankton have been used as indicators of restoration changes in lake ecosystems over many years (Perrow et al. 1999, Jeppeson et al. 2007, Kamaladasa and Jayatunga 2007, Kozak and Goldyn 2014, Rosińska et al. 2019, Bowszys et al. 2020). The current ecosystem monitoring study highlights the recovery of zooplankton communities after a short periodic drought, the response to the restoration project at the mouth and the response to a prolonged wet phase in the estuarine system. Understanding zooplankton responses to changing hydrological conditions due to climatic changes in combination with human alterations in the St Lucia Estuary is essential as it

will improve our understanding of changes in the zooplankton assemblages of the St Lucia system which can also occur in similar shallow estuarine lake ecosystems globally.

During past harsh drought conditions in the St Lucia Estuary, the lower reaches of the system were dominated by resident estuarine taxa including the estuarine calanoid copepods *Pseudodiaptomus stuhlmanni*, *Acartiella natalensis* and the mysid *Mesopodopsis africana* (Carrasco et al. 2010, Jerling et al. 2010). The beach spillway which was constructed in 2012 facilitated recruitment into the estuarine system from the Mfolozi River and the Indian Ocean during open mouth conditions but used to close under low rainfall conditions (Van Elden et al. 2014, Tweedley et al. 2019). In the current study, taxa richness increased at the mouth during May 2015 as a result of marine intrusion through the beach spillway as the Mfolozi River mouth was open to the sea. Post rehabilitation project at the mouth area, there was a transition in the zooplankton community to mainly freshwater taxa such as cladocerans, rotifers, and cyclopoid copepods as resident taxa were absent, except for *Pseudodiaptomus stuhlmanni* which persisted in low abundance. Both salinity and total suspended solids were determinants of the zooplankton assemblage. The onset of the rehabilitation project brought about decreased salinity levels and higher total suspended solids. While the decreased salinity to predominantly fresh conditions was likely responsible for the shift in zooplankton composition, increased siltation may have also played a contributing role. The peak in turbidity (1246 NTU) at the mouth area during restoration activities coincided with the disappearance of the mysid *M. africana* and the estuarine copepod *A. natalensis*. Experimental studies have revealed high turbidity levels (> 1000 NTU) could decrease the survivorship and could hinder the feeding ability of *A. natalensis* (Carrasco et al. 2013) and *M. africana* (Carrasco et al. 2007). Similarly, in a study looking at the impact of a flood event on the zooplankton community in the St Lucia Estuary along the Narrows, *A. natalensis* was absent from the community instantly while the population of *P. stuhlmanni* declined a month thereafter (Jones et al. 2016). The silt laden freshwater from the Mfolozi River has built up a 1 m layer of mud at the mouth which has limited habitat for planktonic biota. Results from the first chapter support the hypothesis that there was a difference in the zooplankton community composition before and after the restoration project.

Four different hydrological states were identified during the study period. Estuarine conditions were prevalent during the pre-drought phase as all the lake basins were connected and a strong reversed salinity gradient persisted in the estuarine system. The estuary experienced a severe short periodic drought phase which resulted in 80 % desiccation of the lake surface area and habitat fragmentation. A transitional phase occurred as a result of increased precipitation and freshwater input from the onset of restoration activities (August 2016) which alleviated drought conditions, reconnected the lake basins, and decreased salinities along the estuarine system. During the wet

phase, the entire estuarine system remained mainly fresh, but a slight reversed salinity gradient persisted. Both the Narrows and the Mouth are in closer proximity to the Mfolozi River in comparison to the lake regions thereby the lakes experienced harsher drought conditions which resulted in both zooplankton taxa richness and abundance being significantly higher at the Narrows. Zooplankton abundance (mainly in the lakes) increased in accordance with the increase in dissolved inorganic nitrogen levels and lower salinities at all sites from November 2017. The changes in salinity along the estuarine system characterised zooplankton communities at the different sites. Decreased salinities during the wet phase resulted in a shift in the zooplankton community with resident taxa being largely replaced by freshwater taxa, such as cyclopoids, rotifers, and cladocerans. The cyclopoid copepod *Oithona brevicornis* and the calanoid copepod *Acartiella natalensis* were virtually absent during the wet state and the mysid *Mesopodopsis africana* was restricted to the upper reaches which served as a refuge from the lower salinity areas. *Pseudodiaptomus stuhlmanni* was the only estuarine resident to persist throughout the study, although densities declined. Salinity was the main determinant of the spatial differences found in the zooplankton assemblages along the estuarine lake. Similarly, in the Nhlabane coastal estuarine lake, salinity was a factor influencing the zooplankton community structure as there was a shift from estuarine to freshwater zooplankton (Jerling and Cyrus 1998). In the current study, both hypotheses were supported as there were spatial differences in the zooplankton community structure and zooplankton composition, and abundance differed during the different hydrological states.

Both chapters in this study (Chapter 1 and 2) have reiterated the ability of the estuarine calanoid copepod *Pseudodiaptomus stuhlmanni* to be more tolerant of various environmental conditions than to its co-dominant resident taxa. *Pseudodiaptomus stuhlmanni* has proven highly tolerant of various environmental conditions (Jones 2018). *Pseudodiaptomus stuhlmanni* in the current study was able to tolerate a wide range of salinities and was resilient to high turbidity levels (1246 NTU). The tolerance of *P. stuhlmanni* to a wide range of salinities has been recorded by Grindley (1976) and their tolerance to varying turbidity levels has also been recorded by Jones et al. (2015). Though *P. stuhlmanni* densities declined during high turbidity levels and freshwater conditions, their continuous presence in the community structure throughout the study emphasizes the resilience of this species. Salinity has been a major determinant of the zooplankton assemblage both at the mouth area and throughout the estuarine system. It is evident from both studies that the increased freshwater input has restructured the zooplankton assemblage and affected zooplankton abundance along the estuary at each site. Freshwater zooplankton were prominent in the estuarine system during wet conditions, especially in the lower reaches as the lake regions had slightly higher

salinities. There has been a shift in the St Lucia estuarine system to a freshwater state which may result in the forced exclusion of the resident zooplankton taxa of the estuary. The wet state at the end of November 2017, showed an increase in zooplankton abundance.

Furthermore, increased siltation at the mouth has resulted in a 1 m layer of silt build up and has spread to the South Lake of the estuarine system (Jones et al. 2020). It is essential to understand the impacts of the newly formed St Lucia-Mfolozi link on the biota of the estuary including zooplankton as these organisms will be subjected to increased silt loading if there are no measures placed to reduce siltation. Siltation affects filter feeding organisms such as zooplankton and brings about the shallowing of affected areas which limits habitat for biota (Henley et al. 2000, Thrush et al. 2004). Aside from salinity as a determining factor, increased silt at the mouth area has been a determinant of the community structure (Chapter 1). Findings from this study can be used to compare to findings from other shallow estuarine lake systems that experience hydrological changes as a result of climate changes and anthropogenic interferences. Changes in zooplankton communities are essential in determining whether there has been a shift in an ecosystem (Chambord et al. 2016). There have been studies on the responses of zooplankton communities to nutrient loading and biomanipulation of lake ecosystems as a result of restoration projects, and the majority of these studies have been carried about in temperate ecosystems (Perrow et al. 1999, Kamaladasa and Jayatunga 2007, Kozak and Goldyn 2014, Rosińska et al. 2019, Bowszys et al. 2020), and in some warm lake ecosystems (Jeppeson et al. 2007). This study contributes to knowledge on (1) the impacts of the role of water level fluctuations in subtropical estuarine shallow lake ecosystems (Coops et al. 2003), (2) the effects of restoration efforts to restore natural processes (Coops et al. 2003, Jeppeson et al. 2005, Elliot et al. 2016), (3) the importance of spatial processes and the long term spatial variability in structuring zooplankton communities (Schallenberg et al. 2003, Chaparro et al. 2018) and most importantly (4) the information obtained can assist St Lucia management in further decision making and conservation planning to allow for a successful long-term relinkage of the St Luca -Mfolozi link and improved sustainability.

RECOMMENDATIONS FOR FUTURE RESEARCH

Studies have recorded changes in zooplankton community structure at the St Lucia Estuary during a drought period (Carrasco et al. 2010), through a transition to a wet phase (Carrasco and Perrissinotto 2015), during extreme hypersaline conditions in the northern reaches of the estuary (Carrasco and Perissinotto 2012) and post beach spillway (Van Elden et al. 2014). The full relinkage of the St Lucia-Mfolozi link at the mouth area has provided an opportunity to study the impacts of increased freshwater input to the estuarine system. The current study has provided

information on responses of zooplankton abundance and community structure during different hydrological conditions in the estuary and baseline information associated with the restoration activities and increased freshwater input. The recorded responses of zooplankton can be used to predict future changes in the St Lucia Estuary and determine the health of the estuarine system. The current wet phase in the St Lucia Estuary is the most prolonged one thus far, therefore zooplankton samples from the rest of the sites from 2018 onwards should be analysed to further determine whether there has been the forced exclusion of estuarine resident taxa and to gain further insight on the changes in physico-chemical parameters at different sites. Also, continued monitoring would determine if there is increased siltation in the estuary and whether it has an impact on the zooplankton assemblage. It is imperative to gain further understanding of changes in zooplankton community structure as well as abundance therefore modelling of long-term zooplankton data of the St Lucia Estuary would provide further information on zooplankton dynamics in the St Lucia estuarine lake.

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