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# **Diatom-Based Reconstruction of the Holocene Evolution of Lake St. Lucia, South Africa**

**By**

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Thesis submitted in fulfilment of the academic requirements for the degree of Master of Science

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## Declaration

I, Megan Gomes, declare that this thesis is my own, unaided work, except where referenced and otherwise acknowledged. This thesis is submitted in fulfilment of the requirements for the degree of Master of Science at the University of the Witwatersrand, Johannesburg. I have not submitted this work for examination at any other university.

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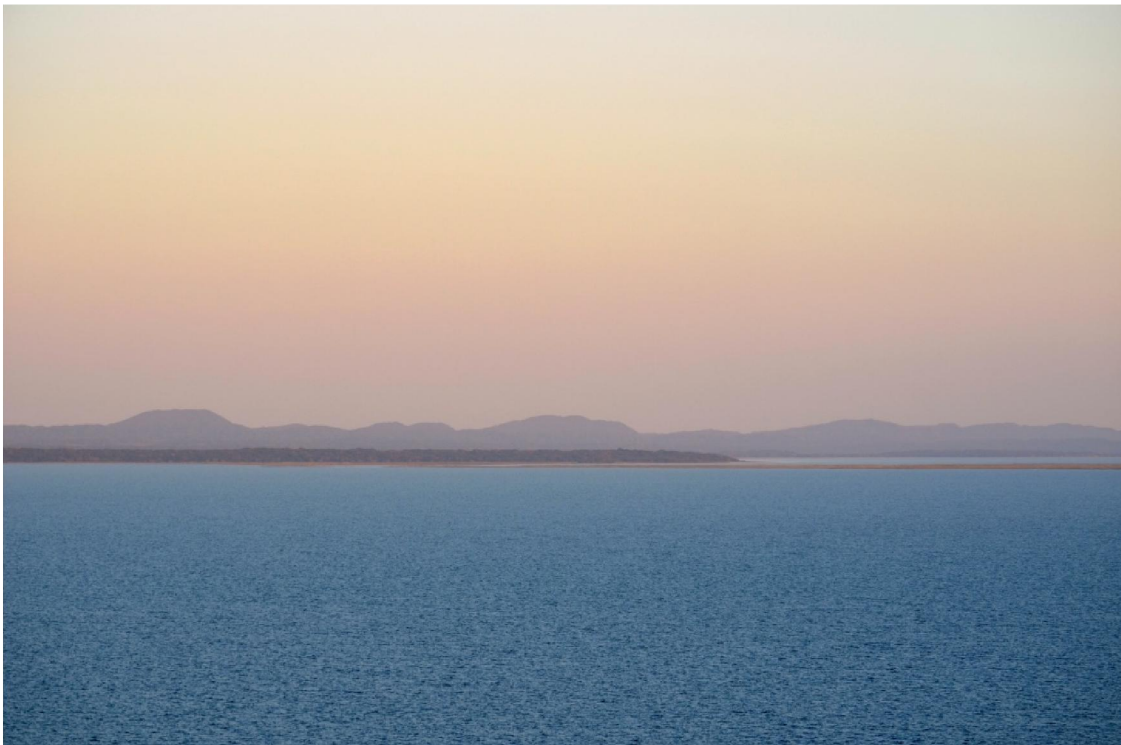
**Megan Gomes**

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**Date**



**False Bay, Lake St. Lucia, South Africa**



**North Lake, Lake St. Lucia, South Africa**

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## Abstract

Coastal waterbodies along the east coast of southern Africa evolved from fluvial origins that were slowly drowned by rising sea levels during the Holocene. The accumulation of sediment in these systems is relatively undisturbed, providing ideal sites from which longer term observations of palaeo-climatic variability over most of the Holocene period can be made. Lake St. Lucia, on the north coast of KwaZulu-Natal, is the largest estuarine lagoon in Africa and is widely regarded as one of the most important shallow water systems globally. Despite the importance of this system, little is currently known about the processes driving the long-term evolution of the lake. This study aimed to reconstruct the hydrological changes associated with the Holocene evolution of Lake St. Lucia using fossil diatoms. Analyses were performed on two sediment cores from the North Lake (15.6 m) and False Bay (15.9 m) basins of Lake St. Lucia. Age models, each based on eight radiocarbon dates, revealed continuous sedimentary records covering ~8300 cal. yr BP. A total of 150 samples were examined resulting in a total of 113 species recorded which were used to infer changes in environmental conditions based on their reported ecological preferences.

Changes in diatom assemblages document the evolution of Lake St. Lucia as it transitioned from an open estuary to a more confined lagoon, and finally to lacustrine conditions that prevail today. The establishment of estuarine conditions was initiated when rising sea-levels during the early Holocene stabilised near present day levels ~6500 cal. yr BP. The accumulation of fluvial sediment gradually filled the lagoon in response to rising sea levels and the development of a coastal barrier which led to the constriction of the tidal inlet at Leven Point. This was indicated by the decline in marine species and the increase in brackish and dilute species. The transition from open estuary to a more confined lagoon resulted from back-ponding behind an emergent coastal barrier at ~4600 cal. yr BP, inferred by the shift from benthic to planktonic species. Although, strong marine influences persisted, indicated by the increase in marine planktonics, likely associated with overwash events. The stabilisation of sea-levels and accretion of the coastal barrier resulted in the cessation of the final phase of lagoonal infilling between ~1600 and 1000 cal. yr BP, which led to reduced marine species. This led to the impoundment of the waterbody as it transitioned to lacustrine conditions, inferred from the increase of brackish and dilute species. This study highlights the value of diatom proxies in palaeoenvironmental reconstructions and provides new insight into the long-term processes that have driven the evolution of Lake St. Lucia during the Holocene. In particular, it provides new understanding regarding the role of Holocene climate and sea level changes in shaping the development of Lake St. Lucia. Such information is essential for the implementation of effective management strategies and predicting how the system will respond to future changes in climate.

Keywords

Diatoms, evolution, Holocene, Lake St. Lucia, sea-level changes

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## List of Acronyms

AMS: Accelerator Mass Spectrometry

CAB: Congo Air Boundary

~ cal. yr BP: calibrated AMS dates that are interpolated using the BACON model; years before present

CONISS: Constrained Incremental Sum of Squares

ITCZ: Inter-Tropical Convergence Zone

ka: thousand years

KZN: KwaZulu-Natal

LGM: Last Glacial Maximum

MSL: mean sea level

PCA: Principal Components Analysis

PC: Principal Component

rpm: revolutions per minute

SRZ: Summer Rainfall Zone

WRZ: Winter Rainfall Zone

YRZ: Year-round Rainfall Zone

yr BP: un-calibrated age-dates presented in publications

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## CHAPTER 1: INTRODUCTION

Natural climate variability and environmental change, as well as anthropogenic influences, shape and modify the ecological states of landscapes both spatially and temporally (Huntley, 1996). In order to understand the present ecological condition of a system and its response to existing environmental conditions, a greater understanding of the nature and magnitude of past climate changes over long temporal scales is necessary (Briner *et al.*, 2006; Jones *et al.*, 2009). In the absence of quantitative climate records, it becomes difficult to develop high resolution, robust climate models covering long-time periods, particularly in determining the resilience of a system to drought and extreme events. It is important to gain an understanding of how ecosystems developed in the past in response to changing environmental influences in order to understand how they may respond to future change; this information is vital for conservation policies and management strategies.

The majority of existing late Quaternary palaeoclimatic records has been developed in the middle to high latitudes in the Northern Hemisphere with a general paucity of data from the Southern Hemisphere (Holmgren *et al.*, 2012). Records of past climate variability in South Africa are relatively scarce but provide important, albeit incomplete information, on the environmental history of the region (Stager *et al.*, 2013). The majority of research in the reconstruction of past climates and environments in southern Africa focuses on the late Holocene and is sparsely distributed and spatially and temporally fragmented, due to limited sites with well-preserved fossil deposits and the discontinuous nature of archives (Neumann *et al.*, 2008; Stager *et al.*, 2013). In an effort to provide a more complete understanding of climate variability in southern Africa, there has been a focus on long-term, high-resolution palaeoenvironmental studies over the past two decades (e.g. Stager *et al.*, 1997, 2003; Gasse and Van Campo, 1998; Neumann *et al.*, 2010; Holmgren *et al.*, 2012; Chase *et al.*, 2013). Conceptual models have been developed over the course of the last 40 years to explain the climatic variations that have spanned across the subcontinent during the late Quaternary, although the use of climate models is still limited due to the paucity of information (Chase & Meadows, 2007). Access to traditional palaeoenvironmental archives, including peat deposits and ice cores, is limited in South Africa due to the arid climate, therefore, research has focused on other archives, such as hyrax middens (Chase *et al.*, 2010), speleothems (Holmgren *et al.*, 2003), wetland peat and baobab tree ring dating (Norström, 2008).

The presence of coastal lakes on the eastern coast of South Africa offers a good opportunity to examine past environmental change through the analysis of sediment archives (i.e. Finch & Hill, 2008; Neumann *et al.*, 2010, and Stager *et al.*, 2013). Lakes are excellent archives of environmental change as they respond to both natural and anthropogenic changes within their catchment and their sediments are often continuous and datable (Wolfe *et al.*, 2004). Changes within a lake that are related to environmental drivers can be rapid and are usually observed in the biological community. Therefore, by examining preserved microfossil

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assemblages it is possible to gain insight into environmental changes and their related causes (i.e. Stager *et al.*, 2013; Kirsten, 2014). Climate directly influences the hydrological budget of the lake, which ultimately has implications for the ecological and sedimentological characteristics of the system (Fritz *et al.*, 1999). A variety of biological proxies preserved in stratigraphic sequence in lacustrine sediments can be used to document these changes, including, pollen, fossil diatoms, foraminifera, ostracods, phytoliths, and chironomids (i.e. Wooller *et al.*, 2004; Finch & Hill, 2008; Stutz *et al.*, 2010; Strachen, 2013; Kirsten, 2014). Therefore, lacustrine sequences can be used in the reconstruction of environmental dynamics and examining changes in the underlying mechanisms driving the evolution of a system (Wolin & Duthie, 1999).

Fossil diatoms are particularly useful tools in reconstructions because they are abundant in most aquatic habitats and serve as good biological indicators of environmental change due to their ecological sensitivity; their rapid reproduction and short life-spans allow communities to respond rapidly to fluctuations in the environment (Stoermer & Smol, 1999). In coastal lakes diatoms have been successfully used to infer natural climate variability and fluctuations in salinity (Halfman *et al.*, 1992; Vos & de Wolf, 1993; Taylor *et al.*, 2006; Stager *et al.*, 2012, 2013) due to their species-specific salinity tolerances (Buzer & Sym, 1983). Lake St. Lucia, situated on the east coast of southern Africa, is the largest estuarine system in Africa and is listed as a wetland of international importance under the Ramsar Convention. Lake St. Lucia forms part of the iSimangaliso Wetland Park which was declared a World Heritage site in 1999 due to its high biodiversity. Owing to its elevated conservation status, Lake St. Lucia has become a major destination for eco-tourism and also serves as an important nursery area for estuarine-associated organisms (Taylor, 2006). Research has generally focused on the biology and short-term dynamics of the system (Cyrus and Blaber, 1987; Bate and Smailes, 2008; Perissinotto & Bate, 2010; Lawrie & Stretch, 2011). Despite these numerous studies, few have focused on the long-term development and hydrological evolution of Lake St. Lucia. This is particularly relevant today, as Lake St. Lucia faces increasing pressures associated with reduced freshwater flows, prolonged drought and sedimentation. In part, this has been driven by past ill-conceived management strategies that lacked an understanding of the long-term processes that govern change at a regional scale. This study was undertaken to examine the hydrological evolution of the system and its response to sea level variations and sedimentary processes, thereby building on our knowledge for effective management and conservation efforts. The study represents the first attempt to use diatom records to reconstruct the Holocene hydrological evolution of Lake St. Lucia.

## **1.1 Aims and Objectives**

The primary aim of this project is to utilise diatom fossils extracted from sedimentary archives to reconstruct the hydrological evolution of Lake St. Lucia. This work contributes to a larger multiproxy study,

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which aims to provide a greater understanding of past environmental change and the long-term evolution of Lake St. Lucia.

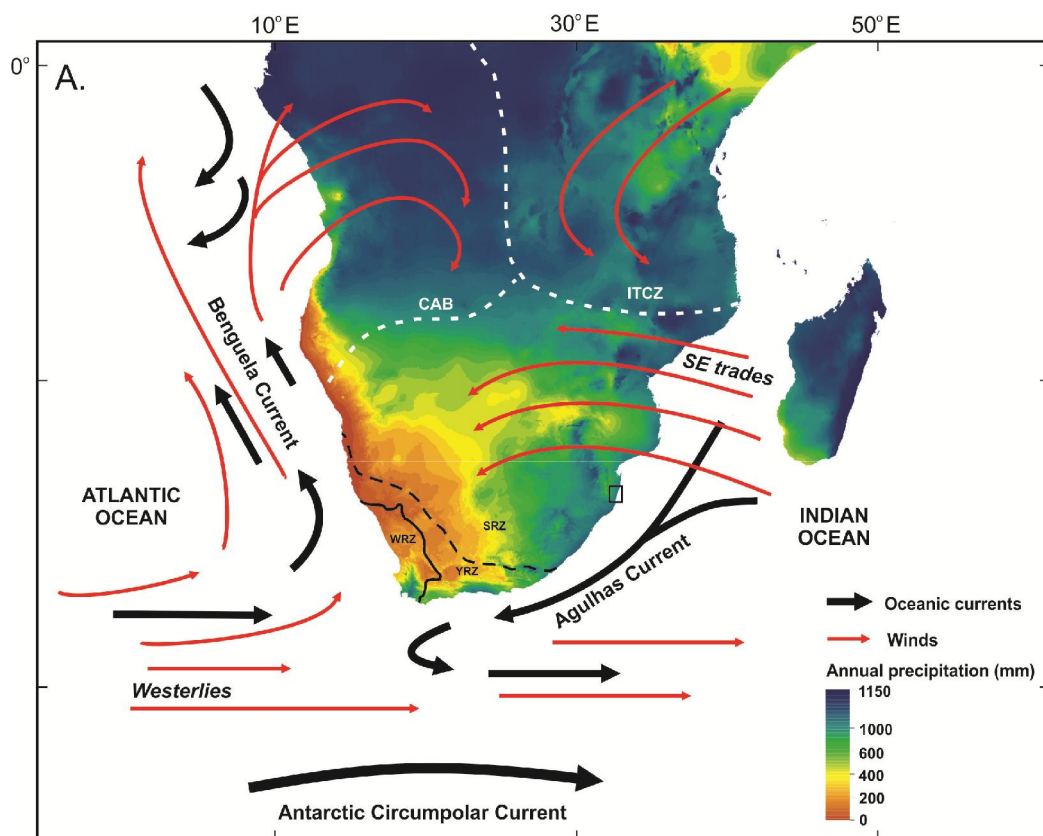
The main objectives of this study are to:

1. Identify the fossil diatom species in sediment cores from the North Lake and False Bay basins of Lake St. Lucia.
2. Temporally constrain changes in diatom proxies using radiocarbon derived chronologies.
3. Relate observed shifts in diatom community structure to changes in environmental conditions associated with the development of the St. Lucia system.
4. Determine the key underlying environmental drivers responsible for changes observed in the diatom community structure using PCA and cluster analysis.
5. Link the results from this study with previously published research to examine regional variations in sea level and climate.

## CHAPTER 2: REGIONAL SETTING

### 2.1 Climate Variability in southern Africa

Southern Africa is situated at the interface of the tropical, subtropical and temperate belts; which include shifts in the Intertropical Convergence Zone (ITCZ), the polar westerlies, tropical easterlies and the development and position of continental and oceanic anticyclones (Fig. 2.1) (Tyson *et al.*, 2002; Scott & Lee-Thorp, 2004; Chase and Meadows, 2007). Considerable changes in the amount and seasonality of precipitation across the subcontinent over the last glacial–interglacial cycle have been linked to the relative dominance of these systems (Chase & Meadows, 2007). The climate across this region is the result of the interplay between atmospheric, oceanographic and latitudinal influences gives rise to three rainfall regimes, namely the summer rainfall region (SRZ), the winter rainfall region (WRZ) and a year round rainfall regime (YRZ) (Tyson, 1999; Scott & Lee-Thorp, 2004; Chase & Meadows, 2007).



**Figure 2.1:** Map of southern Africa indicating the major oceanic (thick black arrows) and atmospheric (thin red arrows) circulation systems over southern Africa. Rainfall seasonality across the region is defined by the summer rainfall zone (SRZ), winter rainfall zone (WRZ) and the transitional year-round rainfall zone (YRZ). The following circulations are shown in their austral summer positions, namely the Congo Air Boundary (CAB) and Intertropical Convergence Zone (ITCZ) ([www.worldclim.org](http://www.worldclim.org)).

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During the last 50 000 years large-scale changes in climate in southern Africa have taken place along these three rainfall zones. The WRZ is isolated to the southwestern tip of Africa and quickly grades to extremely arid conditions toward the north; the YRZ extends eastward along the south coast, experiencing climatic phenomena linked to both temperate and tropical systems leading to progressively higher summer rainfall potential towards the east; and the SRZ expands into the semi-arid interior of the continent across the modern NE-SW rainfall gradient (Chase & Meadows, 2007; Fig. 2.1). The precipitation in the SRZ is associated with the southern edge of the ITCZ and eastward movement of thunderstorms, with most of the moisture originating over the southwestern Indian Ocean (Holmgren *et al.*, 2003). The summer rainfall in the region is responsible for 80% of the total annual precipitation over the country (Tyson, 1986). Conversely, frontal cyclonic systems embedded in the westerlies that form over the south Atlantic and Southern Ocean drive the precipitation in the WRZ (Stager *et al.*, 2012).

The coastline of South Africa is influenced by two ocean currents, namely the warm Agulhas Current, running along the east and south coast and the cold Benguela Current, flowing along the west coast (Fig. 2.1). Both currents serve as key components in the global ocean circulation and distribute both heat and moisture across the continent (Scott & Lee-Thorp, 2004). The greater Agulhas system is an integral part of the global ocean circulation and is particularly important to the east coast of South Africa (Gordon *et al.*, 1992). The Agulhas Current forms part of the southern Indian Ocean subtropical gyre and is driven by the pattern of wind stress curl between the southeast trade winds and the Southern Hemisphere westerlies (Beal *et al.*, 2011). It transports warm, salty water and flows parallel to the continental shelf as a narrow, fast boundary current in a southwesterly direction. The current then moves offshore south of the continent, before retroflecting back into the Indian Ocean as the eastward Agulhas return current, referred to as the Agulhas Retroflexion (Beal *et al.*, 2011). This loop sheds warm saline water as well as rings, eddies and filaments from the Indian Ocean into the Atlantic Ocean, which feeds the upper arm of the Atlantic Meridional Overturning Circulation (Beal *et al.*, 2011). The shedding of rings is controlled by the Indian Ocean Dipole and El Niño–Southern Oscillation events (Beal *et al.*, 2011). The Agulhas system influences storm development, storm tracks and the regional atmospheric circulation (Beal *et al.*, 2011). Furthermore, it is responsible for extreme rainfall events and the movement of tropical cyclones over southern Africa (Rouault *et al.*, 2002). The moderating effects of the oceans, particularly the warm Agulhas, and the semi-arid nature of the region suggest that moisture rather than temperature fluctuations has a greater influence on the region, at least during the Holocene (Scott & Lee-Thorp, 2004).

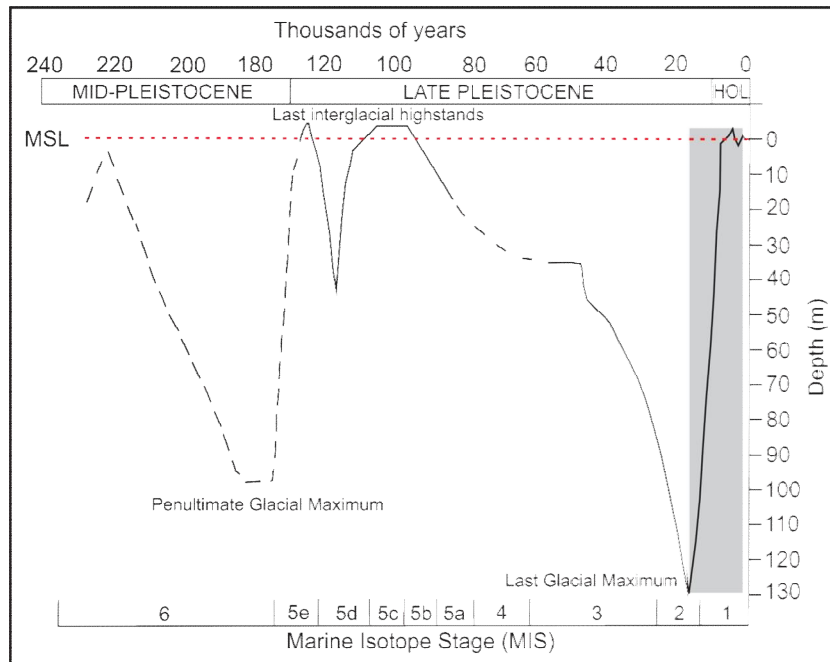
## **2.2 Quaternary Sea-Level History**

The extent and timing of sea level fluctuations is continually debated worldwide (Hendey & Volman, 1986). The South African coast and shelf comprises two trailing edge margins that were tectonically stable during

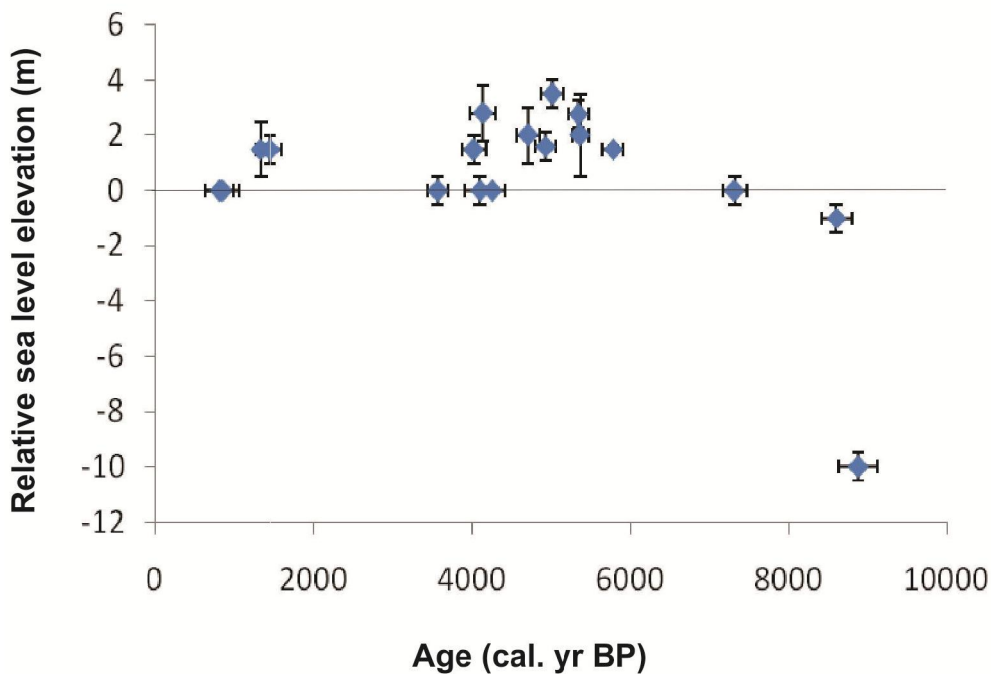
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the late Quaternary; thus, the region is well positioned for analyses into sea-level rise resulting from changes in thermal expansion of sea water and the extent of polar ice mass (Hendey & Volman, 1986; Ramsay & Cooper, 2002; Carr *et al.*, 2010). Locally, the coastal plain and adjacent continental shelf of KwaZulu-Natal signifies the emergence and submergence of the landscape which was influenced by relative sea-level changes (Ramsay, 1995). Evidence of past sea-level high-stands along the east coast of southern Africa originates from dating of geomorphological markers of palaeo-coastlines, including coastal dune complexes, wave-cut platforms, beachrocks, diamondiferous marine sediments and sites where marine sediments are exposed (cf. Martin, 1962; Maud, 1968; Hendey & Volman, 1986; Marker, 1987; Ramsay, 1995). Ramsay and Cooper (2002) synthesized a range of sea-level proxies from across the southern African coastline from which they constructed a late-Quaternary sea-level curve. There has, however, been extensive discussion surrounding the identification and dating of these markers (Ramsay & Cooper, 2002; Carr *et al.*, 2010). Furthermore, there are additional limitations to using geomorphological features as indicators of sea-level high-stands in that they reflect only discrete periods of extremes in sea-levels (Ramsay & Cooper, 2002). This has led to the increasing use of proxies within sediment profiles extracted from coastal sites to reconstruct sea-level changes, as they can track variations in sea level at a higher temporal resolution (Fitchett *et al.* *In press*).

According to Ramsay and Cooper (2002) sea-level dropped to  $-125$  m below mean sea-level (MSL) during a regression that occurred at approximately 25 ka (Fig. 2.2). This regression climaxed during the Last Glacial Maximum (LGM) which led to the scouring of river valleys on the Kwa-Zulu Natal continental shelf (Green, 2009). Amelioration in global temperatures following the LGM resulted in deglaciation and a rapid increase in sea levels, known as the Flandrian transgression. Sea-levels along the South African coastline rose at an average rate of 8 mm/year, reaching its contemporary level at  $\sim 8000$  cal. yr BP (Fig. 2.3). The sea-level then rose  $+1.5$  m above MSL at  $\sim 5000$  cal. yr BP and maintained this level until  $\sim 4000$  cal. yr BP. The mid-Holocene sea-level highstand persisted for a period of about 2500 years and at about 5000 cal. yr BP rising sea levels resulted in the deposition of beachrocks at an elevation of  $+2.75$  m along the KwaZulu-Natal coast (Ramsay, 1995). According to Ramsay and Cooper (2002) the Holocene transgression reached present sea level around 5500 cal. yr BP rising from 4800 – 3100 cal. yr BP before dropping again to present level between 2300 – 1600 cal. yr BP (Fig. 2.3). Evidence from Holocene beachrocks at Sodwana Bay indicated that sea-level dropped to  $-2$  m below MSL at  $\sim 3000$  cal. yr BP and subsequently rose to  $+1.5$  m above MSL at 1400 cal. yr BP, before reaching present levels at  $\sim 1000$  cal. yr BP (Fig. 2.3). The late Holocene marine transgression has been attributed to the combination of isostatic emergence and thermal expansion of sea water, with the later regressions coinciding with phases of global cooling (Ramsay & Cooper, 2002).



**Figure 2.2: Late Pleistocene sea-level curve for the east coast of South Africa. Note the rapid transgression during deglaciation in the late Pleistocene/early Holocene followed by slowing rates of sea-level fluctuations in the mid to late Holocene (redrawn after Ramsay & Cooper, 2002).**



**Figure 2.3: Holocene sea-level curve with calibrated ages for the east coast of South Africa based on beachrock and shell dating. Mean Seal Level (MSL=0). Note the highstand during the mid-Holocene followed by a regression in sea-level to present day (After Ramsay, 1995). Radiocarbon dates calibrated using SHCal13 (Hogg *et al.*, 2013).**

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## 2.3 Formation of coastal water bodies on the east coast

The geological evolution of the Maputaland coastal plain is complex and poorly understood mainly due to the lack of suitable dating material and widespread reworking of older sediments, which blanket most of the area (Wright *et al.*, 2000). Three large coastal water bodies (Lake St. Lucia, Lake Sibaya and Kosi Bay) occur along the eastern margin of the northern KwaZulu-Natal coastal plain, each of which has a markedly different contemporary morphology (Wright *et al.*, 2000). Their origins stem from several lowstands in sea level during the Quaternary (De Lecea *et al. In press*). The evolution of these coastal lakes involved the formation of incised valleys into Cretaceous and Palaeocene sedimentary sequences during cycles of marine regressions that were subsequently transgressively infilled (Cooper *et al.*, 2012). The sedimentation pattern of these infills represents the systems' evolution from fluvial through marine to lagoonal and lacustrine deposition (Cooper *et al.*, 2012). During the transgression, sand from the exposed continental shelf accumulated along the present coastline as an early Holocene dune barrier (Wright *et al.*, 2000). The confinement of incised valleys may often result in the exhumation of previous infilling linked to earlier sea level transgressions (De Lecea *et al. In press*). During interglacials when sea levels are higher than present, estuaries occupied a far greater area than currently and covered most of the extensive wetlands that adjoin the coastal water bodies (De Lecea *et al. In press*). Notable examples of this include Durban Bay (Mkhize, 2014), Maputo Bay (Green *et al.*, 2015) and the St. Lucia system (van Heerden, 1987), as evidenced by barnacles and corals found  $\pm 3$  m above MSL on a siltstone outcrop on the Munywana River, a tributary of the Mzinene River (Botha, 1997).

The site of the contemporary Lake St. Lucia occupies a Late Pleistocene lagoon (Hobday & Orme, 1974). The presence of a buried river valley, immediately offshore of the system, indicates that it was once connected to onshore drainage during the LGM (Green, 2009). A series of seismic stratigraphic studies revealed a complex network of bedrock-incised channels that extend to a depth of over forty meters below MSL into Cretaceous aged siltstones beneath the St. Lucia system (van Heerden, 1987). These incision patterns represent the substantial rejuvenation of rivers that are linked to stages of hinterland uplift during the Neogene (cf. Green, 2011). Coral-bearing fossiliferous limestones crop out along the western margins of False Bay, which indicate that this part of the St. Lucia system was once a sheltered marine embayment linked to the sea via Hells Gate (Cooper *et al.*, 2013). Open water conditions prevailed east of the peninsulas. Deposits along the western margins of False Bay comprise a succession of stacked shorelines that crop out at an elevation of 3-6 m above MSL providing evidence for multiple phases of oceanic connection to the east of the Nibela Peninsula, between the bluffs of Hell's Gate (Cooper *et al.*, 2013). These successions represent various sea level highstands ranging within a few metres of the contemporary sea level since the Late Cretaceous (Cooper *et al.*, 2013). A series of beach ridge and swale features mark the segmentation of the lagoon from a larger body of water, which was driven by wind fetch over the system

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causing the lake to segment. This rise in sea level and thus lake level led to the inundation of the lower Mfolozi River valley (Scott & Steenkamp, 1996) and could potentially be linked to the raised shore deposits at Lister's Point (Cooper *et al.*, 2013). The lake was sealed and separated from the ocean during stable sea levels at about the same elevation as present. The lake levels started to stabilise at ~ 600-900 yr BP consequently forming the foundation for the contemporary Lake St. Lucia complex (Botha *et al.*, 2013).

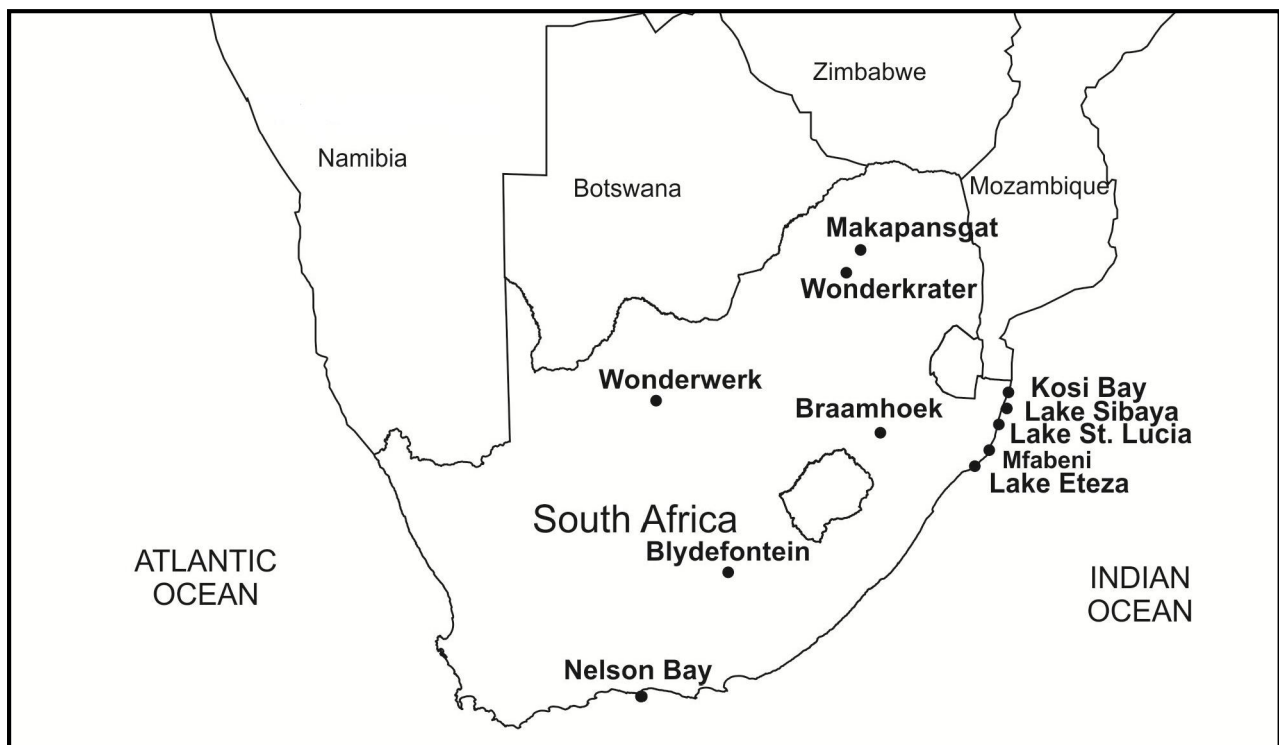
## 2.4 Palaeoclimate Records from South Africa

Climate variability in South Africa during the Holocene is both temporally and spatially fragmented; this is due to the paucity of appropriate study sites, with uninterrupted, undisturbed sediment profiles that contain preserved fossil proxies in sufficient concentrations to produce statistically significant analyses (Martin, 1968; Livingstone, 1975; Kristen *et al.*, 2007; Neumann *et al.*, 2008). Unlike much of Europe, where palaeoecological studies are comparatively more comprehensive due to the wealth of palaeoenvironmental archives, the climate in southern Africa is too arid to support the preservation of fossil pollen or aquatic microfossil proxies such as diatoms, ostracods and foraminifera (Livingstone, 1975; Scott, 1989; Chase & Meadows, 2007; Meadows, 2015). As a result, research has been restricted to wetlands in the more humid regions, and isolated springs in the interior (Scott, 1989; Neumann *et al.*, 2008; Meadows, 2015). However, the number of southern African palaeoenvironmental studies has grown as evidenced by the increase in papers published, sites explored, and proxies used (Meadows, 2007, 2015; Fig. 2.4). Previously, pollen was the most commonly used proxy for southern African palaeoenvironmental reconstructions, but more recently other proxies, such as isotopes, geochemistry and diatoms have been used (Chase & Meadows, 2007; Scott *et al.*, 2012). The use of various proxies facilitates a multi-proxy approach which has the potential to improve our understanding of the late Quaternary palaeoenvironmental and palaeoclimatic history of southern Africa.

Continuous debate persists regarding the extent to which Northern Hemisphere climate events have contemporaneous Southern Hemisphere equivalents (Holmgren *et al.*, 2003; Scott *et al.*, 2012; Truc *et al.*, 2013). There are several climate events that have been verified for the Northern Hemisphere, but remain unverified for southern Africa, these include the African Humid Period (Burrough & Thomas, 2013), the Younger Dryas (Peteet, 1995; Thackeray & Scott, 2006), the '8.2 kyr' event (Smith *et al.*, 2002), the Little Ice Age (Tyson *et al.*, 2000) and the '4.1 kyr' or '2.8 kyr' cold events (Mayewski *et al.*, 2004; Wanner *et al.*, 2015). Whether such events occurred in southern Africa and the specific environmental conditions potentially associated with them remains to a degree unresolved (Fitchett *et al. In press*). Conversely, the global records of the Holocene are comparatively more comprehensive, denoting four periods of rapid

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climate change occurring at 9 – 8 ka, 6 – 5 ka, 3.5 – 2.5 ka and the last 600 years; as well as two discrete climate events occurring between 4.2 – 3.8 ka and between 1.2 – 1.0 ka (Mayewski *et al.*, 2004).



**Figure 2.4: Distribution of southern African sites at which published palaeoenvironmental reconstructions have been undertaken which are discussed in text.**

Pollen sequences from Limpopo derived from the Wonderwerk Caves, Rietvlei and Tswaing Crater, all indicate rising temperatures between ca. 10 and 7.3 ka (Scott, 1993; Brook *et al.*, 2010; Fig. 2.4), with relative aridity predominant from 11 to 7.5 ka. Marine molluscs from Nelson’s Bay Cave, point to warmer sea surface temperatures (SST) at ca. 6800 cal. yr BP (Cohen & Tyson, 1995; Fig. 2.4). It is suggested that intensified westerlies and their associated frontal disturbances resulted in the increase in SST on the Agulhus Bank (Cohen & Tyson, 1995). Wetter and warmer conditions, leading to an enhancement in C3 vegetation density, are indicated from the stalagmite records in Makapansgat Valley between 6400 to 5100 cal. yr BP (Lee-Thorp *et al.*, 2001). Pollen records from Lake Eteza revealed an increase in precipitation and subsequent rise in the groundwater table from 6500 – 3600 cal. yr BP, before a prolonged dry period ensued in which grasses were prominent until 2000 cal. yr BP (Neumann *et al.*, 2010; Fig. 2.4). It is evident from various proxy data that there was a trend toward aridity across the subcontinent that began after 5000 cal. yr BP (Scott & Lee-Thorp, 2003; Chase *et al.*, 2010).

The longest, most complete record from the SRZ is derived from the stalagmite records from the Cold Air Cave (Tyson *et al.*, 2000; Fig. 2.4), indicated increased organic matter between 4300 and 3200 cal. yrs BP which supported dense vegetation, suggesting a period of variable warmth and moisture availability (Lee-

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Thorp *et al.*, 2001). Similarly, stalagmite records from Makapansgat Valley suggest a moist, warm period for the interior SRZ from 4300 to 3200 cal. yr BP (Lee-Thorp *et al.*, 2001). Thereafter, an increase in C4 grasses at 2100 cal. yr BP lead to decreased organic matter accumulation, which coincided with a cooler and more arid period between 3200 and 2100 cal. yrs BP (Lee-Thorp *et al.*, 2001). In addition, pollen in peat sediments from Mfabeni along the east coast suggests a cool, dry phase from ca. 3000 - 2500 cal. yrs BP (Finch & Hill, 2008). *Podocarpus* pollen fluctuations in lake and swamp deposits on the east coast, suggest extensive mesic forests during the mid-Holocene which began to diminish in size after 3100 cal. yr BP, mark a shift from moist to more arid conditions (Scott & Steenkamp, 1996). Charcoal records in the higher altitudes of the Drakensberg Mountains indicate wetter conditions at ca. 2400 cal. yr BP (Lee-Thorp *et al.*, 2001). *Podocarpus* pollen from lake and swamp deposits retreated northward to the Kosi Bay area by ca. 1300 cal. yr BP, suggesting increased aridity in the region (Mazus, 2000).

There is a general consensus that the climate of the last 2000 years in the SRZ was wetter with intermittent dry periods (Scott & Vogel, 2000). Numerous records based on pollen analysis have indicated a subhumid, moist environment (Scott *et al.*, 2005; Neumann *et al.*, 2010). At ca. 2000 cal. yr BP, a rise in forest, swamp, riverine, and mangrove-forest elements at Lake Eteza signify more moist coastal forest elements, before transforming to savanna conditions at 800 cal. yr BP (Neumann *et al.*, 2010). Evidence from the Braamhoek wetland indicated a shift from dry climate to subhumid conditions at 2500 cal. yr BP, prior to an increase in forest and grass elements at 1500 cal. yr BP (Norström *et al.*, 2009; Fig. 2.4). Subhumid conditions were prominent at Blydefontein between 2000 and 600 cal. yr BP, with a brief punctuated period of drier conditions occurring between 1300 and 1100 cal. yr BP (Scott *et al.*, 2005). The timing of the Medieval Climate Anomaly (MCA) is frequently placed between 1200 to 700 cal. yr BP (Chase *et al.*, 2009). Tyson and Lindesay (1992) present the MCA across the summer rainfall region as a period of enhanced wetter and warmer conditions, which peak between 1000 and 900 cal. yr BP. Changes in forest and swamp structures at Lake Eteza and Lake Sibaya temporally agrees with the beginning of the Little Ice Age (LIA) which was characterised by dry conditions until 250 cal. yr BP (Neumann *et al.*, 2008; Fig. 2.4). A drier, cooler climate implied by the decline in C4 grasses at Cold Air Cave, began at 1400 cal. yr BP and continued until the culmination of the LIA (Lee-Thorp *et al.*, 2001). In the Cold Air Cave  $\delta^{18}\text{O}$  record, values became more enriched between 770 and 615 cal. yr BP, correlating to the transition phase from the Medieval Climate Anomaly to the LIA (Holmgren *et al.*, 1999). A retreat in forest and swamp elements along the east coast at Lake Eteza and Lake Sibaya occurred at ca. 700 cal. yr BP indicating a period of cool and dry conditions which marked the beginning of the LIA (Holmgren *et al.*, 2003). Although, a generally cooler climate prevailed throughout the LIA, conditions were unstable (Tyson & Lindsey, 1992). According to Tyson and Lindesay (1992) the LIA appears to overlap with drier conditions in the SRZ, as a result of limited moisture transport due to weakened tropical easterly flow.

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## 2.5 Lakes as Indicators of Environmental Change

Palaeolimnology, a discipline in palaeoenvironmental studies, uses the sedimentation history of inland water systems to indirectly reconstruct past climate variability (Battarbee, 1999; Drebler *et al.*, 2011). The last two decades have witnessed the rapid development in palaeolimnological research, which has been recognised as an increasingly robust methodology for understanding contemporary lake dynamics (Battarbee, 1999). A lake's hydrological sensitivity is related to its catchment topography, local climate and its location (Anderson, 1995). Sediments that accumulate in climate-sensitive lakes can provide continuous records of palaeoclimate variations, often with high temporal resolution (Battarbee, 2000). Lake sediments comprise of a mixture of organic and inorganic material, which include deposition of plant and animal debris derived from within the lake, the lake's catchment, as well as inputs from rivers (Battarbee, 2000). Lake systems reflect the interplay between various factors that control moisture-balances in terms of the variation in hydrological inputs and outputs, which are represented by changes in lake levels, water chemistry and water column stratification (Verschuren, 2003). Inputs refer to moisture gains which are derived from precipitation, surface runoff, stream and groundwater inflow, whereas outputs indicate moisture losses through evaporation, groundwater recharge and stream outflow (Fritz *et al.*, 1999). Lake levels, however, are not solely influenced by surface water hydrology (i.e. open vs. closed basin) and can be dependent on climatic, biological and geological processes (Wolin & Duthie, 1999).

Chemical changes in the water body are driven by changes in hydrology and climate; thus, as the regional climate becomes drier and lakes transition from open basin to closed basin, salinity increases (Anderson, 1995). Closed basin lakes are especially sensitive to shifts in effective moisture, which may lead to changes in the concentration/dilution and ionic composition of dissolved salts in the basin (Fritz *et al.*, 2010). Fluctuations in the precipitation to evaporation ratio (P/E) influence environmental parameters, such as dilution of dissolved salts in lake systems (Gasse *et al.*, 1995). In particular, salinity levels depend on the quantity of both freshwater and marine inputs into a coastal system in conjunction with the relative amount of precipitation versus evaporation (Snoeijs, 1999). Therefore, salinity fluctuations in lakes can potentially be used as an indirect measure of changes in environmental and climatic conditions (Anderson, 1995). The relative influx of freshwater into the system is also influenced by flooding events that may cause dilution of lake chemistry, flush out the distinct biological communities, increase turbidity and disrupt the sediment profile and/or lead to scouring of the lake bed resulting in discontinuous palaeo-archives (Weilhoefer *et al.*, 2008).

Coastal lagoons are inland water bodies that are usually aligned parallel to the coast and separated from the ocean by a barrier; however they can connect to the ocean by one or more restricted inlets in which case they are shallow systems seldom exceeding a few meters (Phleger, 1969). These lagoons usually exhibit

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very high primary productivity which supports large fisheries, aquaculture, tourism and recreational activities, as well as intense agriculture in the surrounding catchments (Gilabert, 2001). Coastal lakes that have a contemporary link to the ocean via an intertidal transition zone may experience fluctuating salinities (Cooper *et al.*, 2010). The connection to the ocean allows for transport of marine sediments and species into the estuary and potentially further up into the coastal lake through tidal activity (Cooper *et al.*, 2010). For lake systems and waterbodies that experience some form of marine influence, the most common approach used to define salinity is the haline system, where generally accepted approximate limits are: freshwater <0.5 ‰, oligohaline 0.5–5 ‰, mesohaline 5–18 ‰, polyhaline 18–30 ‰, euhaline 30–40 ‰, hyperhaline >40 ‰ (Snoeijs & Weckström, 2010). In estuaries or coastal lakes, salinity is an important factor in species distribution as biota will respond to transitions between marine and freshwater conditions (Kirsten, 2014). In these transitional systems mixing of tidal waters and freshwater inputs may create vertical zonation across the estuary, where the estuary mouth experiences higher salinity compared to further up in the system (Saunders *et al.*, 2007). Salinity fluctuations will also affect the composition of the biological community which is in turn dependant on the species salt tolerances and their ability to adapt to changing environments (Snoeijs & Weckström, 2010). Therefore, an understanding of species distribution and composition across transitional zones makes it possible to reconstruct past environmental conditions, as well as indirectly infer changes in past sea level and climate (Snoeijs & Weckström, 2010).

### **2.5.1 Diatoms as Climate and Environmental Proxies**

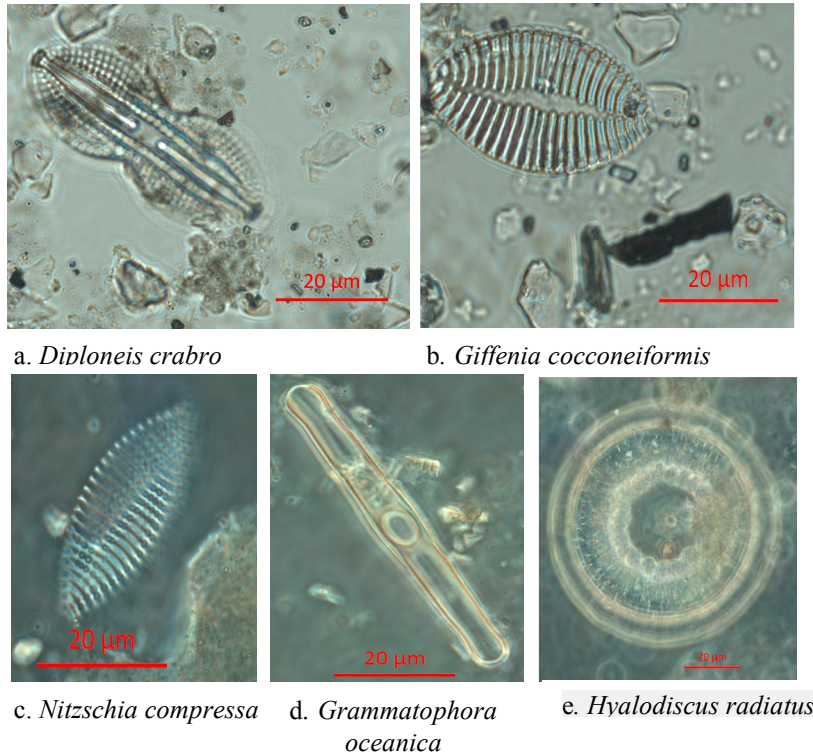
The use of these environmental proxies extracted from archives, requires certain assumptions to be made in order to understand the relationships between contemporary and past communities of those proxies (Fritz *et al.*, 1999). The method most commonly used is the Uniformitarian approach, which implies that the natural processes that operated in the past are the same processes that can be observed operating in the present; therefore, it is assumed that fossil organisms have the same biological and environmental requirements as their modern day counterparts (Lawrence, 1971; Reavie & Edlund, 2010; Meadows, 2012). Thus, by assuming the environmental conditions are the same for both the modern and fossil organisms, a snapshot of the environmental conditions during the time of deposition can be ascertained (Kirsten, 2014). However, caution must be taken when using the Principle of Uniformitarianism as it is assumed not proven and for very long time scales the uncertainty of this assumption increases as there is considerable risk of extinction of modern analogues (Roberts, 2014). Similar uncertainty, in using this approach, is recognised at shorter time scales - such as the late Holocene - owing to concerns of human disturbance to the environment resulting in the disturbance of past analogues (Meadows, 2012). However, the influence and extent of disruption of human activity on the environment does not affect all fossil proxies; nonetheless, one solution to this problem is to implement training sets that predate anthropogenic impacts (Juggins, 2013). Despite the

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limitations mentioned, the Uniformitarian approach remains the best available option to understand and link past and present conditions (Jackson, 2012; Knight & Harrison, 2014).

Diatoms are extremely powerful tools in identifying variations in climate and extreme events (Denys & de Wolf, 1999). Their ecological sensitivity has led to their increasing utilisation as biological indicator species reflecting changes in the environmental conditions (Wolin & Duthie, 1999; Hall & Smol, 2010). Diatoms are unicellular algae that belong to the phylum Heterokontophyta (Smol & Stoermer, 2010); they have characteristic features that aid in their identification, such as their opaline silica frustule which is composed of two valves (P-valve and R-valve) and several girdle bands (Stoermer & Smol, 1999). Diatoms can be identified based on two broad morphology classifications, namely centric and pennate groups (Battarbee *et al.*, 2001). Thereafter, identification to species level involves a more intricate analysis of the size and shape, as well as the existence of raphe, number of striae and sculpturing of the cell wall (Barber & Haworth, 1981; Battarbee *et al.*, 2001; Smol & Stoermer, 2010). Diatoms display species-specific physiological sensitivity to different ecological conditions, shown by the great variety in species composition of diatom assemblages (Stevenson, 1997). Diatoms are generally cosmopolitan in distribution and found in almost all aquatic environments (Stoermer & Smol, 1999). They are found in a range of habitats including marine, estuarine and shallow coastal systems to freshwater lakes and rivers (Hall & Smol, 1999), as well as subaerial habitats (Johansen, 2010). Their broad ecological range and high species diversity allows diatom communities to have specific habitat niches (Hall & Smol, 2010) and owing to their abundance, they are often the dominant constituent of the microalgal assemblage within the aquatic system (Sullivan, 1999). Each species also has a specific water chemistry tolerance range; thus, diatom communities are determined by the chemical, physical and biological parameters in their habitat (Hall & Smol, 1999). Light microscope photographs of a selection of diatoms commonly found in samples from this study are presented in Figure 2.5.

Diatom assemblages reflect the ecological conditions experienced during that period and thus in order for these microorganisms to thrive several environmental parameters are necessary, including the availability of light, carbon, silica and biolimiting nutrients (Stevenson, 1997). These ecological parameters have been organized into a hierarchical framework, such that higher-level factors, for instance climate and geology, can affect low-level factors, such as biolimiting nutrients (e.g. nitrogen, phosphorus, light) and stressors (i.e. pH, salinity, temperature, toxic substances) (Stevenson, 1997). Diatoms are sensitive to biotic and abiotic processes, however, they thrive after a disturbance owing to their rapid growth rates and immigration rates which ensures early colonization within a habitat, making them an ideal indicator of environmental change over varying spatial and temporal scales (Bradbury, 1999; Hall & Smol, 2010).



**Figure 2.5: Examples of a range of common diatom species from Lake St. Lucia under light microscope (1000x).**

Numerous studies have used diatoms for assessing both natural and anthropogenic influences on a system and evaluating whether measures should be taken to restore it to its original state (Hall & Smol, 2010). Diatom fossils are often well preserved in sediments owing to their resistant silica composition (Stoermer & Smol, 1999). The extent of frustule preservation may be important in reflecting the environmental conditions experienced during deposition, for instance degraded and fractured valves may indicate intertidal exposure or abrasion, whereas intact valves may indicate rapid burial with little disturbance in a low energy environment (Cooper, 1999a). The fossil deposits may reflect many years of sediment accumulation and combined with their niche specificity they are useful tools in palaeoclimate reconstructions. Therefore, by identifying fossils to species level and understanding their autecology, inferences can be made about changes in past climatic and environmental conditions, based on shifts in community structure (Bradbury, 1999, Denys & de Wolf, 1999; Stoermer & Smol, 2004). Nonetheless, there are some potential challenges in diatom analysis, such as the unpredictability of the diatom preservation in sediment deposits owing to mechanical erosion and disturbance of the chronological sequence of deposition as a result of mixing by tidal activity (Buzer & Sym, 1983).

### **2.5.2 Diatom Communities in Lakes**

The high preservation potential of fossils in lake sediments can provide continuous records of the palaeoecology of the region (Anderson, 1995; Battarbee, 2000). The life form of diatoms refers to the

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relative abundance of plankton and benthic species (Battarbee, 1986); whereby, planktonic diatoms are characterized as free floating, living in open lake water, whereas benthic diatoms are non-planktonic, living attached to submerged substrates in the littoral zone (Wolin & Duthie, 1999). Tycoplanktonic diatoms are commonly found in the benthic or near-shore community, but can be easily transported into the plankton (Wolin & Duthie, 1999). The plankton community thrives in open water or under turbid conditions which inhibits the growth of the benthic community (Wolin & Duthie, 1999). The approach most commonly used when inferring lake levels relies on the planktonic/benthic ratio of diatom species; for example, a dominance of planktonic diatoms indicates deeper water and an increase in the aphotic zone limiting benthic forms (Punning & Puusepp, 2007), whereas increases in benthic species suggests shallow conditions. Other factors, such as temperature and nutrient levels can also be attributed to fluctuations in the plankton/benthic ratio. Baars (1979) showed that a decrease in temperatures below 12 °C resulted in the reduction of planktonic species, while Reavie & Edlund (2010) showed that high nutrient levels and stagnant water resulted in plankton blooms. The plankton community can either be *in situ*, indicating that it originates within the lake or from elsewhere or allochthonous. Allochthonous species are usually transported either via tidal activity particularly in coastal areas or river inputs (Vos & De Wolf, 1993).

The benthic taxa can be classified according to the specific substrates they adapt to within the photic zone and are either attached permanently or are motile, these include species that inhabit the bottom of the lake floor (periphytic diatoms), attached to rocks/stones (epilithic diatoms), sand (epipsammic diatoms), fine sediments in the littoral zone (epipellic diatoms) and plants (epiphytic diatoms) (Hall & Smol, 2010). Another form of benthic diatoms are known as aerophilic diatoms that are able to survive in subaerial habitats during dry periods, with their species diversity depending on the availability of moisture in the environment (Spaulding *et al.*, 2010). Shifts within the benthic community may reflect changes within the hydrological regime or surrounding catchment (Reavie & Edlund, 2010). For example, the relative abundance of epiphytes may reflect a low energy environment with a submerged macrophyte community, which contributes to nutrient cycling, productivity, and stabilization of nearshore environments within the lake (Wolin, 1996; Cooper *et al.*, 2010; Reavie & Edlund, 2010). Benthic species are most abundant in clear, shallow waters (Bennion *et al.*, 2010); as these conditions provide a greater availability of habitats and oxygen concentrations are usually higher (Wolin & Stone, 2010). In comparison to the allochthonous taxa that occur in the plankton assemblages, benthic communities are deposited *in situ* (Reavie & Edlund, 2010).

### **2.5.3 Factors Influencing Diatom Assemblages**

Several factors determine the distribution of diatom taxa, namely salinity, light, temperature and water movements (Stevenson, 1997). Salinity is a reflection of the interplay between source waters and marine and freshwater inputs, and is recognised as the major factors influencing shifts in the biological community

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(Denys & de Wolf, 1999; Fritz *et al.*, 2010), such that salinity changes of 1 ‰ can completely alter the entire species composition within the water body (Snoeijs, 1999). Four groupings have been used to classify the biological community based on their salinity preferences, including dilute, brackish, marine-brackish and marine (Stager *et al.*, 2012; Kirsten, 2014). The dilute group encompasses species that would be considered freshwater and fresh-brackish and their dominance at a particular point in time can indicate periods of freshwater inputs into the system (Abrantes *et al.*, 2007). Changes in the ratio between freshwater and marine species are almost exclusively used when dealing with estuaries and coastal environments (Denys & de Wolf, 1999). Marine inputs into the system occur when a coastal water body has a direct connection to the ocean facilitating marine water exchanges; whereas, freshwater inputs are usually derived from rivers in the surrounding catchment (Denys & de Wolf, 1999). Other factors are also important in determining diatom assemblages, such as the water quality, changes in sediment substrate and tidal current transportation (Denys & de Wolf, 1999). Thus, shifts in diatom assemblages can indicate changes in ecological conditions through time, ultimately providing insights into the mechanisms driving variations in a system (Fritz *et al.*, 2010).

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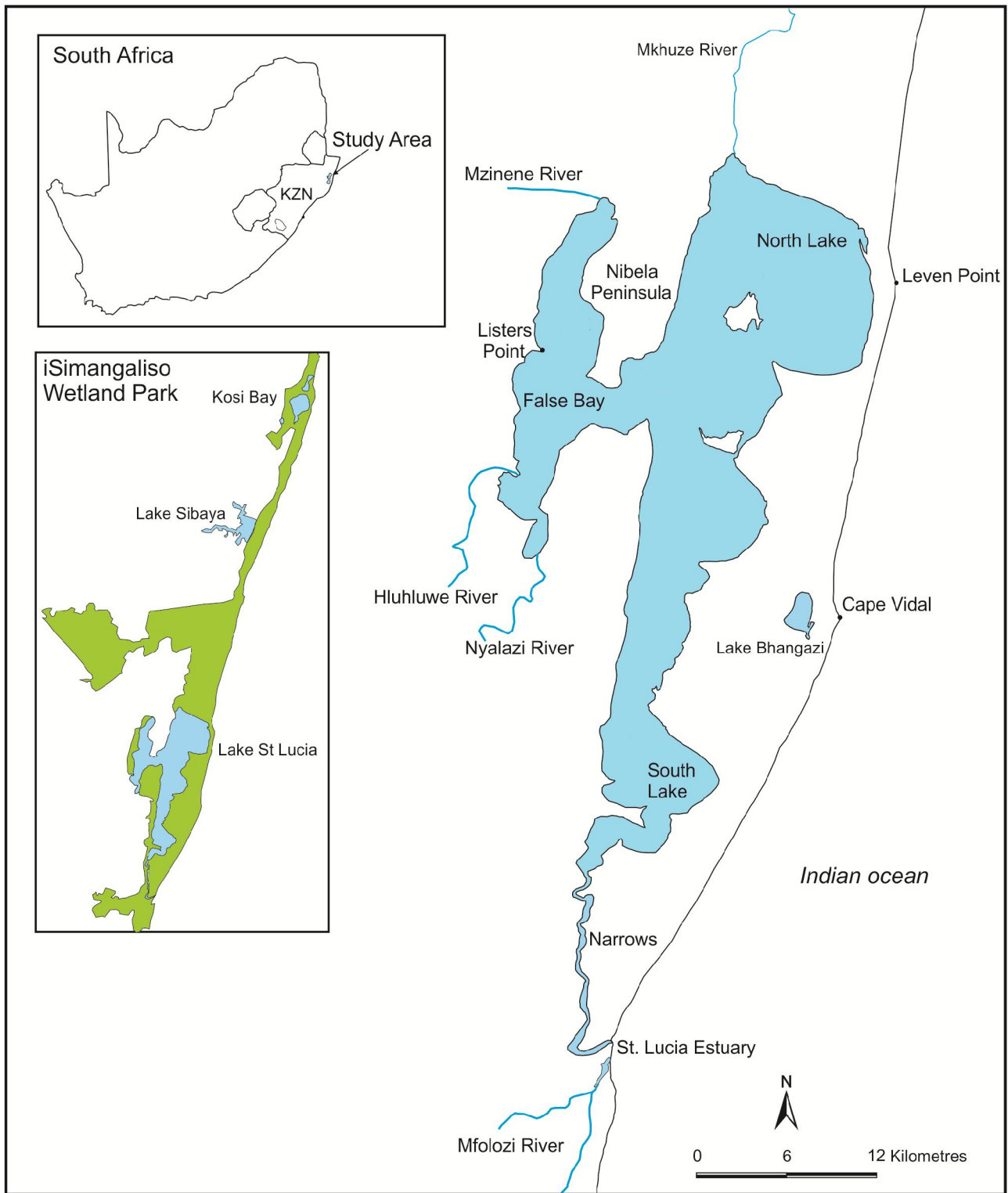
## CHAPTER 3: CONTEMPORARY ENVIRONMENTAL SETTING

### 3.1 Regional Environment

Lake St. Lucia is situated on the north-east coast of KwaZulu-Natal, South Africa (27° 52' S to 28°24' S and 32°21' E to 32°21' E; Fig. 3.1). Lake St. Lucia is a shallow estuarine system, attaining an average depth of ~1 m (Stretch *et al.*, 2013) and spans an area of approximately 350 km<sup>2</sup>, making it the largest coastal lagoon in Africa (Taylor *et al.*, 2006). The lake comprises three main depositional basins: False Bay, North Lake and South Lake. The former two basins are linked via an interconnecting strait known as Hell's Gate (Taylor *et al.*, 2006). A series of coastal plain dunes, known as the Eastern Shores, forms a boundary which separates the lake from the Indian Ocean (Wright *et al.*, 2000). These dunes form part of the main groundwater aquifer that discharges fresh water into the lake (Wright *et al.*, 2000). The present outlet in the south, a 21 km-long tidal channel called the Narrows, is the lake's only contemporary oceanic link (Wright, 1990). However, tidal effects only reach 14 km up the Narrows (Wright & Mason, 1993); thus marine influences do not affect North Lake and False Bay. The catchment area surrounding St. Lucia, which spans ~9000 km<sup>2</sup>, is drained by five freshwater rivers (Begg, 1978), although the two largest and most significant in terms of freshwater input the Mfolozi River in the south and the Mkhuze River which drains directly into the northern end of North Lake (Hutchison, 1976). The other three rivers, namely Hluhluwe, Nyalazi and Mzinene drain into False Bay (Fig. 3.1).

### 3.2 Regional Climate

The east coast of southern Africa experiences a humid, subtropical climate mainly due to onshore easterly atmospheric flow, as well as the warm Agulhas Current that leads to convective rainfall, high soil moisture and dense vegetation cover (DeJager & Schulze, 1977). Sea surface temperatures (SST) in the southwest Indian Ocean plays an important role in precipitation over northeastern KwaZulu-Natal. On a local scale, the average rainfall of St. Lucia varies on a yearly basis (Taylor *et al.*, 2006) with the estuary receiving ~ 1000 mm/year declining to ~ 625 mm/year at Listers Point (Van Heerden & Swart, 1986). The region experiences cyclical wet/dry patterns with a periodicity of 10 years (Tyson & Preston-Whyte, 2000). Cyclones that move through the Mozambique Channel can lead to severe flooding events, which dramatically modify the ecosystem (Hunter, 1988). Evaporation is an influential natural process in St. Lucia, and accounts for losses of up to 1200 mm/year, exceeding the annual average rainfall (Hutchison, 1976). The coastline is influenced by dominant northeasterly winds during the summer months and both north and south winds during the winter months (Porat & Botha, 2008). These coastal winds transport aeolian sediment which has formed the extensive dune complex that serves as a margin between the back-barrier system and the ocean (Porat & Botha, 2008).



**Figure 3.1: Location of Lake St. Lucia showing the main depositional basins (North Lake, False Bay and South Lake).**

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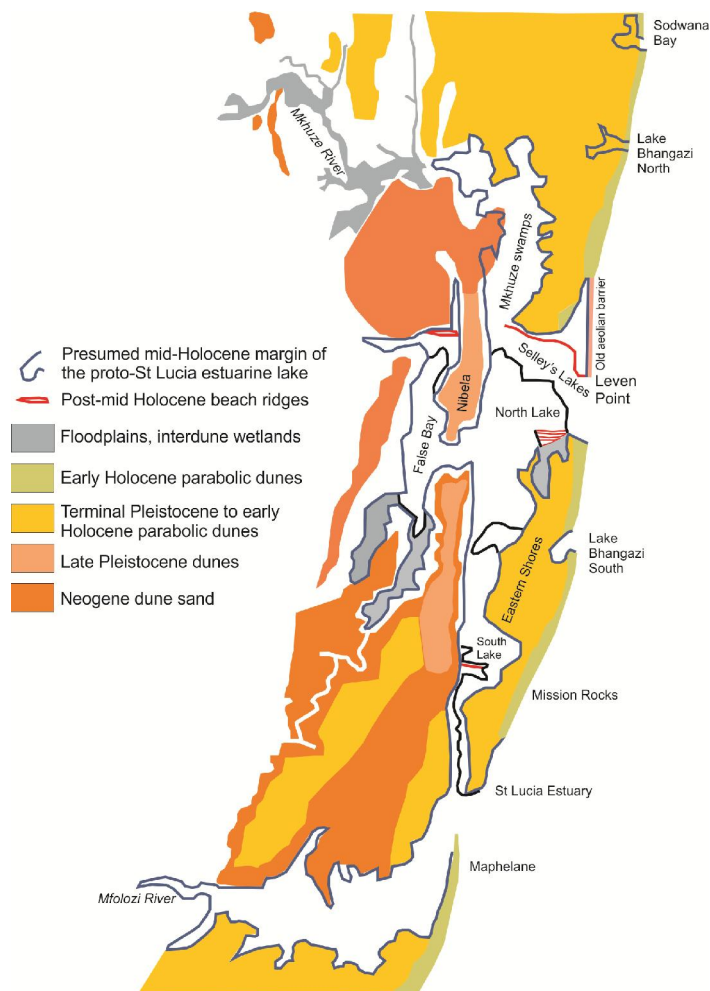
### 3.3 Geological History

The geological evolution of the southeast African coastal plain during the Cenozoic is complex and poorly understood. This is due to several factors including the lack of outcrop, scarcity of fossil remains and widespread mixing of older sand which forms a layer of reworked, unconsolidated, cover sands (Wright *et al.*, 2000). The complex geological evolution of the coastal plain, along with the lack of suitable dating material, renders it difficult to understand the geological history of this region (Wright *et al.*, 2000). However, the coastal water bodies located along the eastern coastal plain may provide insight into the evolution of this coastal margin. The evolution of the coastal plain and hinterland during the Quaternary Period (last 2.6 Ma) was initiated by denudational processes brought about by repetitive base-level changes as a result of glacio-eustatic sea level fluctuations which is related to climatic variability during the Pleistocene and Holocene (Botha *et al.*, 2013). The development of Lake St. Lucia during the Quaternary Period is preserved in Maputaland Group coastal lake, wetland and dune deposits (Botha *et al.*, 2013). In the catchments of the larger Mfolozi and Mkhuzi rivers and the smaller Hluhluwe, Nyalazi and Mzinene rivers that drain into Lake St. Lucia, the oldest rocks are the 3.2 Ga Kaapvaal craton granites and the overlying Pongola Supergroup sedimentary and volcanic units (~2.9 Ga) (Botha *et al.*, 2013). The Permo-Triassic Karoo Supergroup (~260 – 210 Ma), a sedimentary succession, nonconformably overlies the Pongola Supergroup (Botha *et al.*, 2013). The cliffs forming the linear western margins of the Nibela-Ndlozi Peninsulas and False Bay reveal fossiliferous Cretaceous siltstones which are capped by the calcareous, Mio-Pliocene Uloa Formation shell coquina and coarse-grain sandstone that were deposited in shallow marine and high energy beach and nearshore environments (Botha *et al.*, 2013).

The underlying geology of the western shoreline of St. Lucia is characterised by Cretaceous siltstone; whereas, the Eastern Shores comprise complex middle Pleistocene to Holocene aeolian dunes (Ramsay, 1995). The thick unconsolidated dune sand over the Maputaland coastal plain formed through long-term evolutionary processes, such as eroding catchments, littoral marine and terrestrial coastal plain and wetland environments (Botha *et al.*, 2013). These processes led to polyphase accretion representing periods of dune activity linked to climate variability over the past ~300 000 years (Botha *et al.*, 2013). The cyclical erosional history reveals that major rivers were responsible for the catchment-scale erosion pulses and subsequent sediment transport to the coast (Botha *et al.*, 2013). The vegetated dune barrier, known as the Eastern Shores, comprises of younger, less cemented aeolianite deposited at 64 ka (Porat & Botha, 2008). During the Last Interglacial sea level highstand, the coastal dune barrier series was breached and Lake St. Lucia and tributary valleys were inundated (Botha *et al.*, 2013). This led to the linear, western cliffs forming the ocean shoreline and False Bay forming a coastline embayment (Botha *et al.*, 2013).

### 3.4 Evolution of Lake St. Lucia

The evolution of the Lake St. Lucia basin has been driven by cyclical environmental changes over time scales spanning the Quaternary period (Botha *et al.*, 2013). The lake originated during the Mio-Pliocene low sea-level still stands, as a result of rivers scouring channels into Cretaceous and Palaeocene sedimentary sequences (Wright *et al.*, 2000), with subsequent infills during the Holocene transgression (Orme, 1973). Rivers incised deep valleys, up to 50 m, during the Last Glacial Maximum (LGM) when sea levels were ~120 m below present day. These valleys were slowly filled by a combination of marine, lagoonal and fluvial deposits in response to sea level transgression. Rising water levels back-flooded the Mfolozi and Mkhuze valleys resulting in the formation of proto-Lake St. Lucia that is estimated to have been 1165 km<sup>2</sup> (Orme, 1990; Fig. 3.2). Fluvial sediment accumulation led to the infilling of this system resulting in the transition of a deep water system to a shallow water lake (van Heerden, 1976).



**Figure 3.2: Proto St. Lucia estuarine lake configuration at ~6000 yr BP showing the marine link in the vicinity of Leven Point and the inundated Mkhuze and Mfolozi basins (redrawn after Botha *et al.*, 2013).**

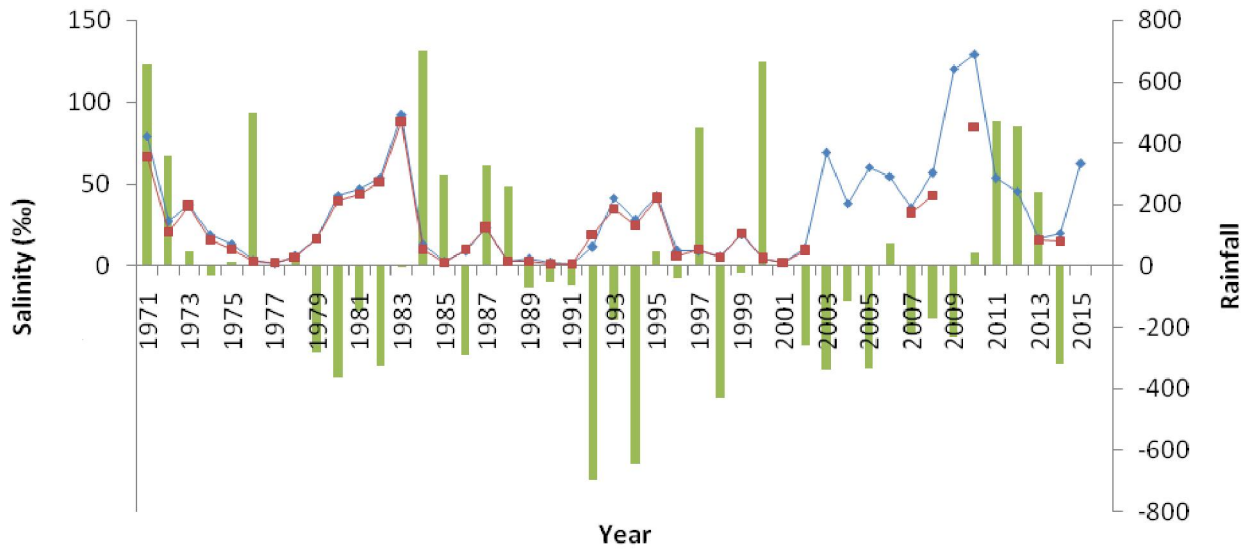
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The Eastern Shores region comprises of a series of sandy undulating dune complexes (3 – 10 km wide) that formed as a result of river and coastal erosion processes during Pleistocene glacial cycles (Taylor *et al.*, 2006). The present morphology of the eastern shoreline is the combination of two opposing forces, namely the beach ridge sets, which were raised by accretion and the promontories, a raised landmass declined abruptly to one side, which were formed by the erosive shorelines that created the embayed shore (Porat & Botha, 2008). In response to fluctuating sea levels and shifts in the confluence of the fluvial systems, the St. Lucia system has alternated between an open marine embayment or shallow lake environment during marine transgressions (highstands) and a subaerially exposed lowland incised by river channels during marine regressions (lowstands) (Wright *et al.*, 2000; Botha *et al.*, 2013).

### **3.5 Catchment Management**

Lake St. Lucia experiences naturally large fluctuations in physico-chemical parameters both temporally and spatially owing to climatic events, such as floods and droughts (Wright *et al.*, 2000). Major floods transform the physical nature of the system, such as the depth and sediment distribution; whereas, droughts influence the salinity and lake levels (Wright *et al.*, 2000; Bate and Taylor, 2008). The system is highly dynamic and will transition between fresh and hyper-saline states in response to rainfall and river flow and historical records indicate that the estuary mouth naturally opens and closes periodically (Taylor, 2011a). In general, the lake can shift between several ecological states over time, including fresh through to estuarine and marine to hypersaline, with marine-estuarine conditions being the dominant state (Taylor, 2011a, b). However, the system usually experiences a combination of these conditions. The annual average rainfall is ~1000 mm, but it has been recorded below 500 mm and above 3000 mm (Bate & Taylor, 2008). It is evident that since the early 1900s the lake has experienced below average rainfall lasting for periods of three years consecutively (KZN Wildlife; Fig. 3.3). Furthermore, in the recent past a combination of prolonged droughts, high evaporation rates and human-related decreases in freshwater inflow has seen reduced water levels and hypersaline conditions within the lake system (Taylor *et al.*, 2006, 2011a; Fig. 3.3).

The natural functioning of Lake St. Lucia has been drastically altered by human interventions over the past century (Whitfield & Taylor, 2009; Lawrie & Stretch, 2011). Significant anthropogenic impacts began in the early 20<sup>th</sup> century when large areas of the lower Mfolozi floodplain were converted into agricultural land (Grenfell *et al.*, 2009; Taylor, 2013). This subsequently led to the drainage of the Mfolozi swamps and partial canalization of the river which resulted in increased silt load and accumulation of sediment in the St. Lucia mouth (Whitfield *et al.*, 2006; Whitfield & Taylor, 2009).



**Figure 3.3: Variation in annual salinity recorded at North Lake (red) and False Bay (blue), and the annual deviation from median rainfall for St. Lucia town (green). A positive deviation indicates a relatively wet year whereas a negative deviation a dry year. A strong relationship between dry years and high lake salinity levels is evident (data source: KZN Wildlife).**

Historically, the St. Lucia system was connected to the Mfolozi River at the mouth and as a result of major floods, such as those associated with Tropical Cyclone Domoina, floodwater from the Mfolozi River overflowed into St. Lucia, greatly supplementing the water level of the latter system. However, prolonged droughts in the 1950s, resulted in the St. Lucia/Mfolozi mouth area being silted up and blocking the connection to the sea. In an attempt to prevent back-flooding of the Mfolozi floodplain, the river was artificially separated from St. Lucia by a canal (“Warner’s Drain”) that was dredged about 1.5 km south of the previous St. Lucia mouth forming a new Mfolozi mouth (Whitfield & Taylor, 2009; Taylor, 2013; Fig 3.5).



**Figure 3.5: The canalisation of the Mfolozi river was constructed to reduce flooding, but it led to an increase in water velocity and suspended sediment (photograph: Ezemvelo KZN Wildlife).**

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After the separation of the Mfolozi River, the St. Lucia inlet had a natural tendency to close and active management intervention was required to keep the mouth open. At the time, it was considered desirable to have a continuously open inlet to facilitate biological exchanges between estuary and sea. The decision to keep the inlets of the Mfolozi and St. Lucia systems separate while artificially maintaining an open St. Lucia mouth remained in place for the next 50 years. In 2002, the mouth was left to close following the onset of dry conditions. Coupled with persistent dry conditions, this led to the development of extreme hypersaline conditions within the lake and relinking the Mfolozi River with St. Lucia become a priority for management (Whitfield *et al.*, 2013). Recent droughts over the last 15 years have been particularly devastating, where 90% of the lake dried up in 2006 and 2016 (Fig. 3.4). This led to high salinity with the remaining water exceeding the salinity of the ocean in certain regions. This has major consequences on the ecological state and biodiversity of the lake. In 2012, a beach spillway was established to facilitate the relinking of the Mfolozi and St. Lucia systems.



**Figure 3.4:** Comparative satellite images of Lake St. Lucia taken in September 2014 (left) and February 2016 (right), illustrating the sensitivity of the system to changes in rainfall (data source: iSimangaliso Wetland Park Authority).

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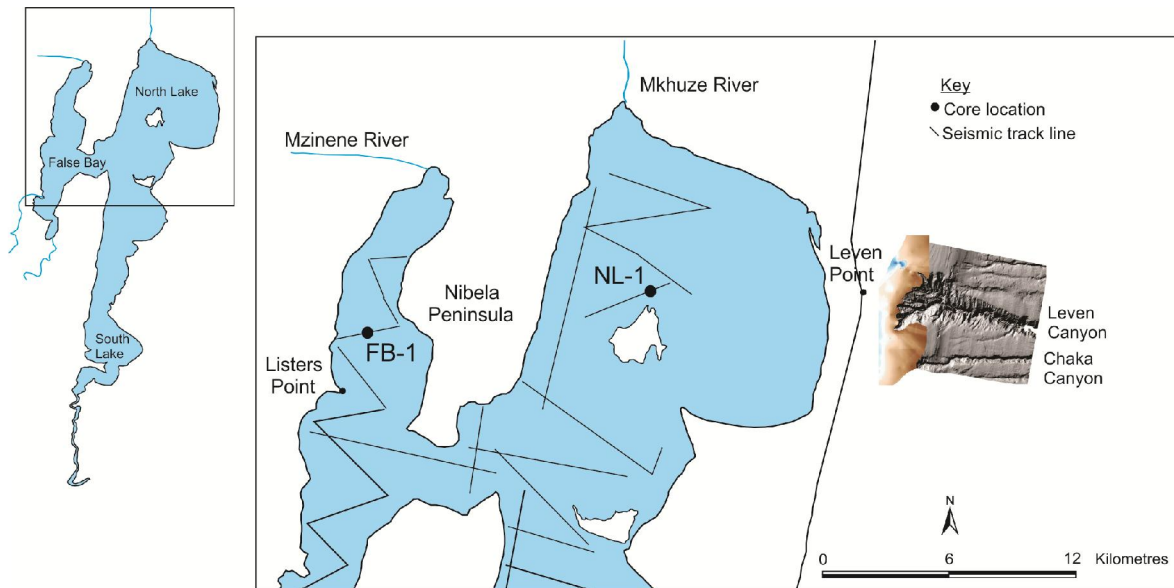
## CHAPTER 4: METHODS

### 4.1 Field Work

In 2014, a detailed seismic survey was conducted in order to examine the sedimentary infill of the major depocentres in Lake St. Lucia and identify suitable sites for coring (Fig. 4.1). An estimated 300 line kilometres of single-channel, high resolution seismic reflection data were collected from the three main lake basins, namely False Bay, North Lake and South Lake. This study focused on the two northern sub-basins, False Bay and North Lake, where sediment cores (NL-1, 15.63 m and FB-1, 15.91 m; Fig. 4.1) were extracted using a barge-mounted piston coring system and percussion drill (Fig. 4.2). Following retrieval, cores were sealed, labelled and transported to the laboratory at the University of the Witwatersrand for cold storage and analysis. Cores were split longitudinally and described using standard sedimentological procedures (Troels-Smith, 1955).

### 4.2 Radiocarbon Analysis and Age-Modelling

Eight samples from both NL-1 and FB-1 were selected for radiocarbon dating using accelerator mass spectrometry (AMS). Dating was performed on bulk sediment samples where possible, with intact shells used to date horizons with insufficient organic material. Analyses were carried out by Beta Analytic Inc., Florida, USA, following standard methods. Reported values were determined relative to NIST SRM-4990B and corrected for isotopic fractionation. Calendar calibrated ages were calculated using the Southern Hemisphere atmospheric curve SHCal13 (Hogg *et al.*, 2013). An age-depth model for each core was derived using the Bacon 2.2 source code and the R statistical software program (Blaauw & Christen, 2010). Generally, age-depth models assume that deposits accumulate at a constant rate between each dated level and that accumulation rates change abruptly at the dated depths (Blaauw & Christen, 2010). To avoid these assumptions Bacon uses Bayesian statistics to reconstruct accumulation histories for sediment deposits (Blaauw & Christen, 2010). The Bayesian accumulation uses radiocarbon dates and prior information, such as the sediment accumulation rates and its temporal variability (Blaauw & Christen, 2010). In Bacon, the core is divided into 5 cm thick vertical sections and then through millions of Markov Chain Monte Carlo iterations the accumulation rate is estimated in cm/year providing a more accurate sedimentation rate for each section (Blaauw & Christen, 2010). The estimated starting date for the surface section is then combined with these accumulation rates and used to construct age-depth models and provide a chronological framework for the sedimentation history. A reservoir correction was not performed due to the limited information regarding the marine reservoir effect on the east coast of southern Africa.



**Figure 4.1: Map displaying location of coring sites, in False Bay (FB-1) and North Lake (NL-1) and the seismic track lines used to identify core locations. The palaeo-inlet at Leven Point indicates a former connection to the ocean.**



**Figure 4.2: a) Barge and piston coring system used to extract sediment cores and b) inset of the dominantly clay rich core sediments.**

### 4.3 Diatom Analysis

For diatom analysis, cores were sub-sampled at 20 cm resolution, although only samples from every 40 cm interval were examined for diatoms. Subsamples of thickness of 1 cm<sup>3</sup> were collected using the water displacement method. A total of 76 samples were analysed from each core. Diatom fossils were isolated from sediments by chemically treating samples to remove any salts, organic matter and clays. A detailed procedure, adapted from Battarbee (1986), was followed to adequately extract the fossil diatoms and obtain

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representative microscope slides for analyses. The sediments were treated with 6 ml 10% Hydrochloric acid (HCl) to remove all carbonates. This involved placing the sediment in a beaker, adding 2 ml HCl and heating gently for 15 minutes while continuously swirling the contents. The volume of HCl added was increased until all carbonates were dissolved. The resulting residue was then diluted with distilled water and allowed to settle overnight. Excess supernatant liquid was removed with a pipette the next morning. The sample was washed in 20 ml 30% Hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) and gently heated in a water bath. This step was repeated several times to ensure complete removal of organic matter. Coarse detritus was removed by sieving the residue through a 0.5 mm screen. The remaining residue was centrifuged at a speed of 1400 rpm for four minutes and then washed with distilled water; this step was repeated several times. To remove clays and finer mineral material, the residue was suspended in deionised water for a period of eight hours, allowing diatoms to settle to the bottom before decanting the suspended clay. This was repeated multiple times until the solution remained clear after settling. The samples were then prepared as wet mounts to ensure an adequate removal of diluent material and a complete separation of frustules into their component valves.

Microscopic slides were prepared by pipetting three drops of diatom solution onto a clean cover slip and then diluting it with a few drops of distilled water. Once the solution had settled, it was placed on a hot plate at a low temperature (40 °C) to allow the water in the solution to slowly evaporate. The coverslip was then mounted onto a microscope slide using Pleurax (Refractive index = 1.73). A light microscope at a magnification of up to X1000, with an attached digital camera, was used for counting and identifying diatom species. In each sample, at least 300 - 500 diatom valves were counted to ensure that ecologically important taxa were represented and not masked by common species that occurred in abundance. Slides with less than 300 valves were excluded from analysis, which included 30 slides from both FB-1 and NL-1. Fragments were only counted if the valve centre was visible, thus preventing double counting. Identification of diatom species was based on type collections, keys and photographs in reference material (i.e. Taylor *et al.*, 2007). Each diatom frustule was measured and key features of the valve centre were observed and compared to the reference material. Ecological preferences based primarily on salinity affinities were then assigned to each species (c.f. Taylor *et al.*, 2007; Kirsten, 2014). Databases were consulted on to assist with ecological classifications ([www.algaebase.org](http://www.algaebase.org); [www.marinespecies.org](http://www.marinespecies.org); Guiry and Guiry, 2014; WoRMS Editorial Board, 2014).

#### **4.4 Statistical Analysis**

The diatom assemblages were analysed and displayed using the computer programme TILIA and the accompanying package TILIAGRAPH (Grimm, 1997). This programme plots percentage data against the y-axis of either depth and/or age with the inclusion of a secondary y-axis. The x-axis usually represents the

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species data which can be grouped according to species autecology (similar physiological and ecological requirements). TILIA was used to perform stratigraphically constrained cluster analysis by incremental sum of squares (CONISS) (Grimm, 1987, 1997). Stratigraphically constrained cluster analysis groups adjacent samples based on similarities and reveals relationships within and between zones (Grimm, 1987). A dendrogram was created and attached to the stratigraph in order to delineate zones according to the clusters. Furthermore, to ascertain how similar/dissimilar samples and sites were from each other and identify underlying environmental driving factors, principle component analysis (PCA) was used. The PCA identifies key environmental indicator species in the data and aids in the interpretation of the underlying driving mechanisms of the system (Mackay *et al.*, 2013). The PCA reduces the data and noise resulting in principal components that contain the important information. The factor loadings of the PCA indicate which species are relevant. Thus, factor loadings greater than 0.7 which explains 50% of the squared variance was considered to be significant. Statistical analyses were computed in the open-source statistical software programme R, using the VEGAN v2.3-0 package (Oksanen *et al.*, 2012).

## CHAPTER 5: RESULTS

### 5.1 NORTH LAKE

#### 5.1.1 Core Lithology

Core NL-1 comprises predominantly organic-rich clay units alternating with a number of thin horizons (0-0.05 m) containing abundant shell debris. This predominantly clayey sediment sequence is situated above a basal (16-12 m) sandy unit (Fig. 5.1). The basal section comprises medium to fine grained, deep brownish-orange quartz rich sand with thin (<1 cm) intermittent mud drapes (Fig. 5.1). The organic content at the base is typically low, increasing slightly towards the surface as indicated by gradual colour change from brownish-orange to a light grey (Fig. 5.1). An upward fining succession of sediment capped by a 10 cm thick dark, organic rich fine sandy bed with occasional interbedded organic matter horizons, such as root material and reworked shell debris occurs at 11 to 10 m. The remainder of the core is dominated by mostly clay sediments (dark grey to black and very rich in organic matter) with sparsely distributed fragmented shells. A 1 m thick silty unit occurs at 7 m. The top section of the core is capped by a thin (8 cm), fine grained, light grey, sandy unit.

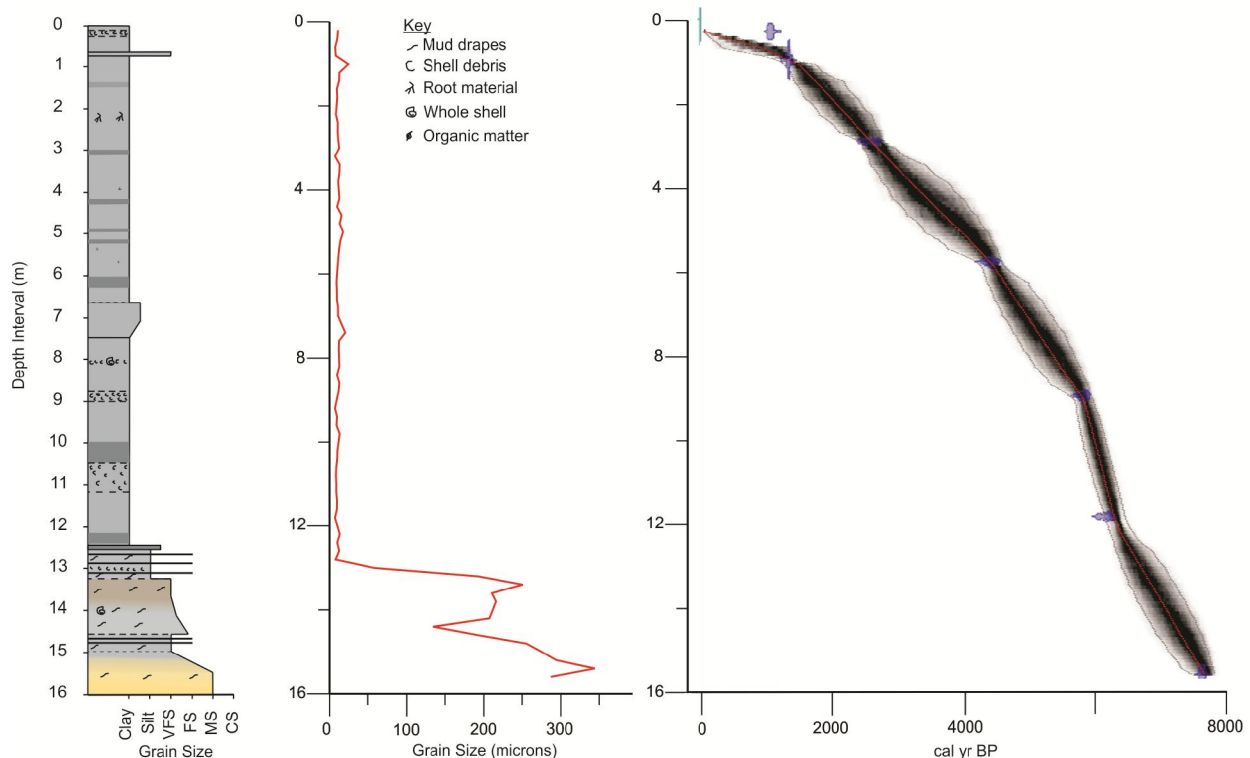


Figure 5.1: Lithostratigraphy of core NL-1 indicating variations in mean grain size (Benallack, 2014). Age-depth model calculated in Bacon 2.2 (Blaauw & Christen, 2010).

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### 5.1.2 Core Chronology

Eight bulk sediment samples were selected from NL-1 and submitted for radiocarbon analysis. Dates revealed a sedimentary record that spans the last ~7600 cal. yr BP (Table 1). An age reversal occurred at a depth of 1478 cm possibly related to sediment reworking. This date was excluded from the age depth model (Fig. 5.1). The sedimentation rates were variable with the base of the core showing relatively high accumulation rates (6 yr/cm), whereas the converse is true with recent surface sediments where low accumulation rates were observed (41 yr/cm) (Fig. 5.1). The average sedimentation rate covering the lacustrine infill (over the last 6000 yr) was ~5 yr/cm.

**Table 1: Radiocarbon ages for NL-1 calibrated to the Southern Hemisphere curve, SHCal13 (Hogg *et al.*, 2013).**

Lab code	Material	Depth (cm)	Conventional Age (C14)	Calibrated Age (cal yr BP)
Beta405603	Organic sediment	28.5	1170±30	957-1074 (99%)
Beta387868	Organic sediment	96	1430±30	1270-1352 (100%)
Beta386293	Organic sediment	290	2490±30	2358-2546 (57%) 2556- 2620 (16%) 2629- 2704 (25%)
Beta405604	Organic sediment	577	3980±30	4248-4275 (5%) 4280-4446 (84%) 4473-4515 (10%)
Beta386294	Organic sediment	897	5090±30	5664-5674 (1%) 5681-5686 (0.6%) 5710-5906 (97%)
Beta373289	Organic sediment	1185	5410±40	6004-6084 (25%) 6097-6279 (74%)
Beta405605	Shell	1478	7350±30	8024-8181 (100%)
Beta386295	Shell	1563	6830±30	7581-7679 (100%)

### 5.1.3 Stratigraphical Zonation

A total of 99 species were identified in core NL-1, which included 41 marine species, 4 marine-brackish species, 16 brackish species, 30 dilute species and 8 unknown species. The diatom assemblage was mostly dominated by marine species, although periods when brackish and freshwater species dominated were observed. Inferred changes in salinity and lake level were based on the identification of indicator groups. These groups were based on the life forms of the diatom species, for instance changes in salinity were inferred by dilute versus marine species; whereas, lake levels were inferred from the relative abundance of planktonic and benthic species. Dilute and marine species represent fresh and marine water sources, respectively, while planktonic and benthic species indicate deeper and shallow water levels, respectively. A list of all diatom species identified, along with their ecological preference based on published salinity

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tolerances can be found in Appendix 1. According to CONISS, the diatom assemblage can be divided into three zones; zone NL-A (~6200 – 4650 cal. yr BP; 901 – 641 cm), zone NL-B (~4650 – 4480 cal. yr BP; 641 – 597 cm) and zone NL-C (~4480 – 1130 cal. yr BP; 597 – 84 cm) (Fig. 5.2). Major periods of low fossil preservation were encountered at the base of the core (~6500 – 6200 cal. yr BP; 1244 – 1128 cm) and in the recent surface sediments (~1130 cal. yr BP to present; 84 – 0 cm) (Fig. 5.2).

Zone NL-A is defined by two minor periods of low preservation occurring at ~5800 – 5700 cal. yr BP (901 – 875 cm) and ~5530 – 5460 cal. yr BP (835 – 819 cm) (Fig. 5.2). Throughout zone NL-A, the marine species *Diploneis crabro*, and the two marine-brackish species, *Giffenia cocconeiformis* and *Nitzschia compressa* were persistently dominant particularly during the early stages. The marine species, *Surirella fastuosa*, complements the distribution of *D. crabro*, peaking at ~5990 cal. yr BP. The marine species, *D. crabro* and *Diploneis entomon* as well as *N. compressa* all simultaneously increased in abundance at ~5500 cal. yr BP. Thereafter, a greater proportional representation in the brackish taxa, *Achnanthes brevipes* occurs concurrently with *N. compressa* and *G. cocconeiformis*, as well as the marine species, *Amphora commutata* at ~5300 cal. yr BP. At ~5150 cal. yr BP *N. compressa* (18%), *G. cocconeiformis* (15%), and *D. crabro* (23%), peaked congruently. Thereafter, the former two marine-brackish species decreased in abundance while *D. crabro* further increased reaching a maximum of 34%. A peak in the fresh-brackish, *Cocconeis placentula* var. *euglypta* was observed toward the end of zone NL-A (~4670 cal. yr BP), reaching a maximum of 33%, which coincided with a decline in marine-brackish and marine species.

Marine and marine-brackish components remained prominent throughout zone NL-B (~4650 – 4480 cal. yr BP) (Fig. 5.2). In the early stages of zone NL-B at ~4650 cal. yr BP the fresh-brackish, *Epithemia adnata* and the marine, *Coscinodiscus wittianus*, peaked simultaneously. Thereafter, *N. compressa* and *M. moniliformis*, as well as *C. wittianus* and *H. radiatus* increase at ~4000 cal. yr BP. The latter species was dominant during this period reaching a maximum abundance of 34%.

The distribution of *N. compressa* and *G. cocconeiformis* fluctuated throughout zone NL-C with an average representation of ~5%; however, their abundance is diminished relative to zone NL-A. The two marine species, *H. radiatus* and *Paralia sulcata*, notably increased, reaching maximum relative abundances of 44% and 27% by ~3500 and 3300 cal. yr BP, respectively. The distribution of *D. crabro* and *C. wittianus* occurred consistently throughout zone NL-C, exhibiting a maximum abundance of 53% and 18% by ~3800 and 2600 cal. yr BP, respectively. In the early stages of zone NL-C, at ~4400 cal. yr BP, the fresh-brackish taxa, *Terpsinoe musica* (10%) and the two marine species *D. crabro* (14%) and *H. radiatus* (19%) peaked congruently. At ~3900 cal. yr BP, *T. musica* peaked in conjunction with *G. cocconeiformis* and *D. crabro*. Thereafter, *D. crabro* peaked drastically reaching a maximum of 54% at 3800 cal. yr BP, followed by an increase in *H. radiatus* (44%) at 3500 cal. yr BP. At ~3100 cal. yr BP, *H. radiatus* and *P. sulcata* increased

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concurrently, coinciding with the decrease in abundance in *D. crabro*. A further peak in *T. musica* at ~2600 cal. yr BP occurred along with an increase in *D. crabro* and *C. wittianus*. The two fresh-brackish species *T. musica* and *Stephanodiscus hantzchii* increased congruently at ~2550 cal. yr BP with frequent fluctuations in marine-brackish and marine species. The increase in the fresh-brackish species, *M. varians*, at ~2300 cal. yr BP coincided with the increase in *D. crabro* and *H. radiatus*. Thereafter, *M. varians* peaks at ~1800 cal. yr BP, reaching a maximum of 23%, which complimented the peak in *H. radiatus* and *P. sulcata*. Toward the end of zone NL-C (~1130 cal. yr BP) *N. compressa* and the two marine species, *C. wittianus* and *P. sulcata* peaked simultaneously. A major period of low preservation defined the top 80 cm of the core.

#### 5.1.4 Statistical Outputs

The key indicator species influencing patterns, as well as other underlying driving mechanisms of the data were identified using PCA. Species scores obtained from the PCA were used to identify potential environmental indicator species resulting in the inclusion of 16 species in the final PCA (Fig. 5.3). All species and scores are provided in Appendix 6. Two principal components were determined to be significant which explained 50.42% of the overall explained variance. Component one, explained 32.48% of the variance and had large positive loadings on *Achnanthes brevipes*, *Giffenia cocconeiformis* and *Nitzschia marginulata* (Fig. 5.4). The fresh-brackish, *Achnanthes brevipes* is reported to have a wide distribution in a range of water types, including marine and marsh environments, although it appears to be restricted to oligotrophic conditions (Guiry, 2016). Additionally, *A. brevipes* is relatively tolerant to desiccation from intertidal exposure, low water temperature and limited light penetration (Aleem, 1950; McIntire & Moore, 1977). The marine-brackish, *G. cocconeiformis* occurs in water with similar salinity to that of sea water (Kosugi, 1988; Guiry, 2016). The marine species, *N. marginulata*, occurs on benthic macrophytes (Cooper *et al.*, 1999b).

Component one has large negative loadings on *H. radiatus*, *P. sulcata* and *M. moniliformis* all of which are classified as marine (Fig. 5.4). *H. radiatus* occurs in the littoral zone (Hustedt & Aleem, 1951), while *P. sulcata* commonly occurs in planktonic and benthic microphyte communities in water with high fluctuating salinities (Zong, 1997). The epilithic species *M. moniliformis* occurs in the littoral zone (McIntire & Moore, 1977). The driving mechanisms of component one appears to be the salinity of the system as it shifts from an estuarine lake to a marine dominated system during periods of marine influences and reduced freshwater inputs.

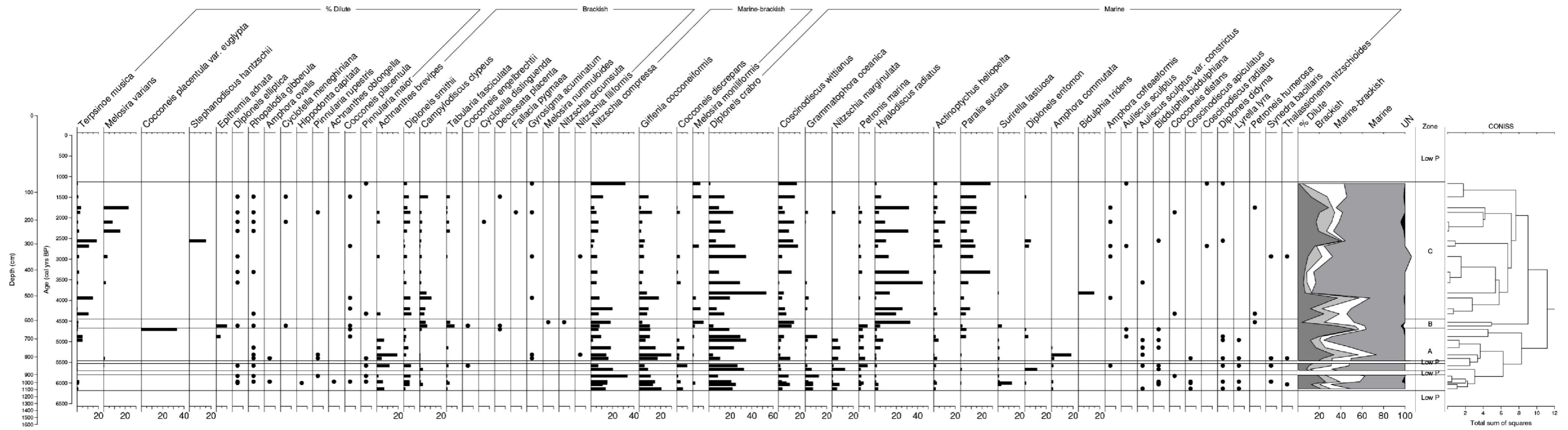
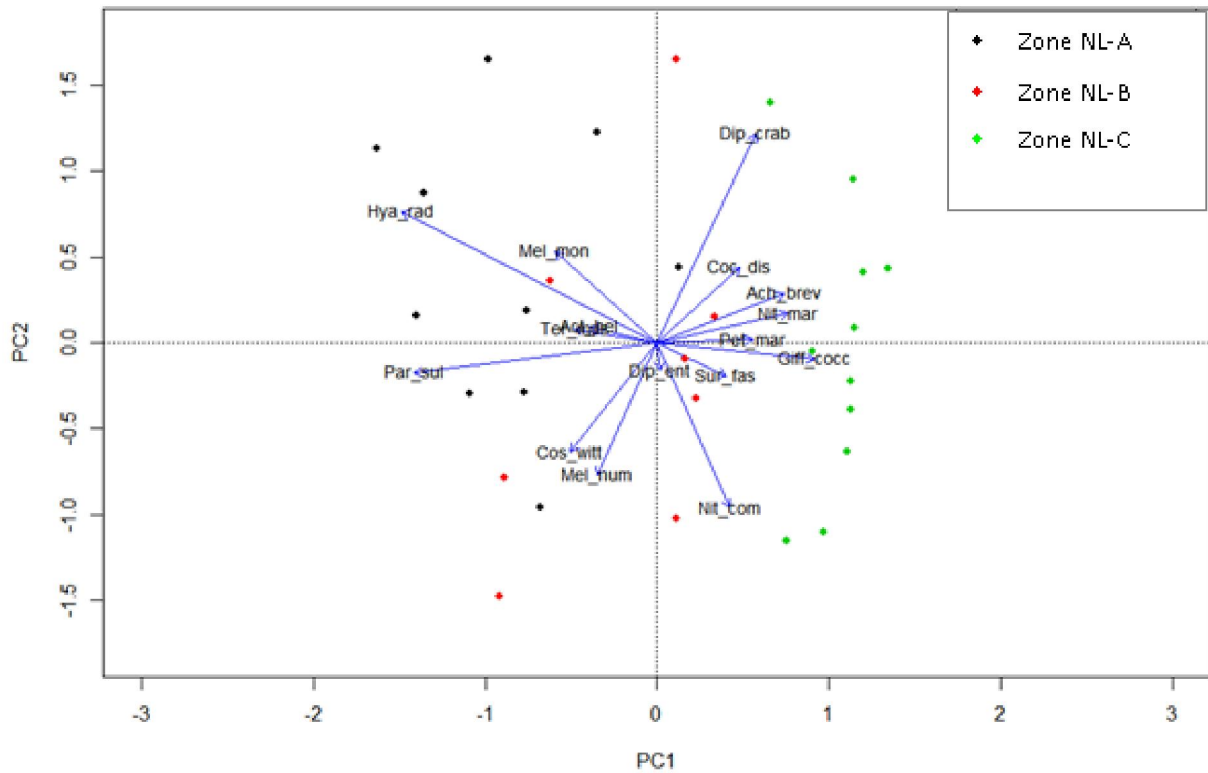
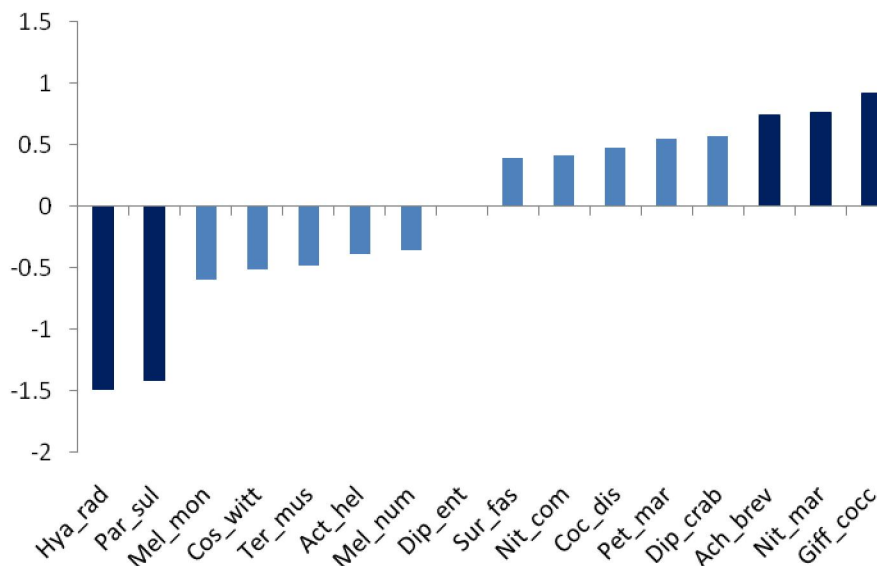


Figure 5.2: Relative percentage abundance of diatom species in core NL-1. Diatom species grouped into four salinity classes (% Dilute, % Brackish, % Marine-brackish and % Marine), with zones (NL-A, NL-B and NL-C) determined according to CONISS. Low P = low preservation zone.

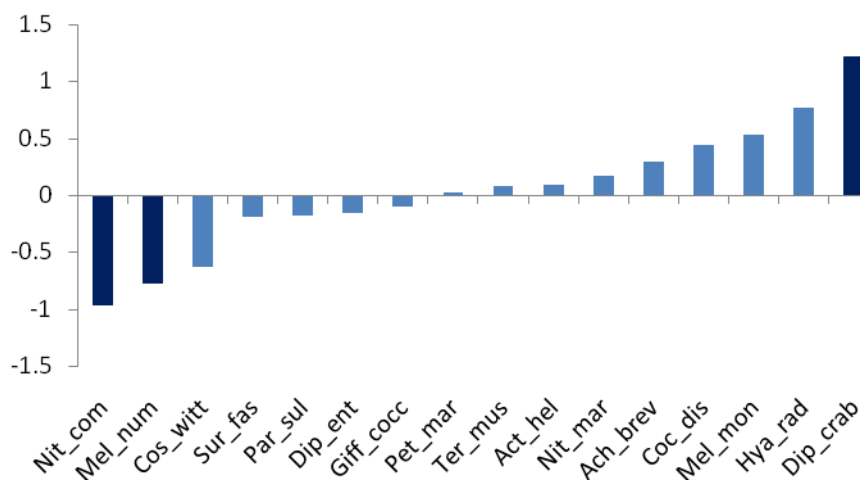


**Figure 5.3: Principal component analysis illustrating the relationship between species and samples at the NL site. Zones are constructed by CONISS in TILIA in which sample points are colour coded accordingly. Species names are noted: Mel\_num= *Melosira nummuloides*, Coc\_plac = *Cocconeis placentula*, Thal\_weis = *Thalassirosira weissflogii*, Epith\_sor = *Epithemia sorex*, Enc\_kram = *Encyonema krammeri*, Cos\_wit = *Coscinodiscus wittianus*, Nit\_comp = *Nitzschia compressa*, Cyc\_dis = *Cyclotella distinguenda*, Cyc\_men = *Cyclotella meneghiniana*, Mel\_mon = *Melosira moniliformis*, Par\_sul = *Paralia sulcata*, Act\_hel = *Actinoptychus heliopelta*, Dip\_cra = *Diploneis crabro*, Giff\_cocc = *Giffenia cocconeiformis*, Cam\_cly = *Campylodiscus clypeus*, Gram\_oce = *Grammatophora oceanica*.**



**Figure 5.4: Positive and negative factor loadings for principal component one for NL-1.**

Component two explained 17.94% of the variance (Fig. 5.5). Species with high positive loadings on the second component include *D. crabro* and to a lesser degree *H. radiatus* both of which are classified as marine. *D. crabro*, a cosmopolitan species, occurs in the near shore environments (Navarro, 1982) and found in the photic zone attached to submerged macrophytes (Niyomsilpchai *et al.*, 2009). The marine species, *H. radiatus*, occurs in the littoral zone near the river mouth where salinity is variable and usually high (Hustedt & Aleem, 1951). Species with high negative loadings on the second component include, *M. nummuloides*, *N. compressa* and to a lesser degree *C. wittianus* (Fig. 5.5). The brackish species, *M. nummuloides* thrives during periods of rapid salinity changes (McLean *et al.*, 1981; Rendall & Wilkinson, 1986). *N. compressa* is a marine-brackish epiphyte (Espinosa *et al.*, 2003). The marine species, *C. wittianus* is planktonic.



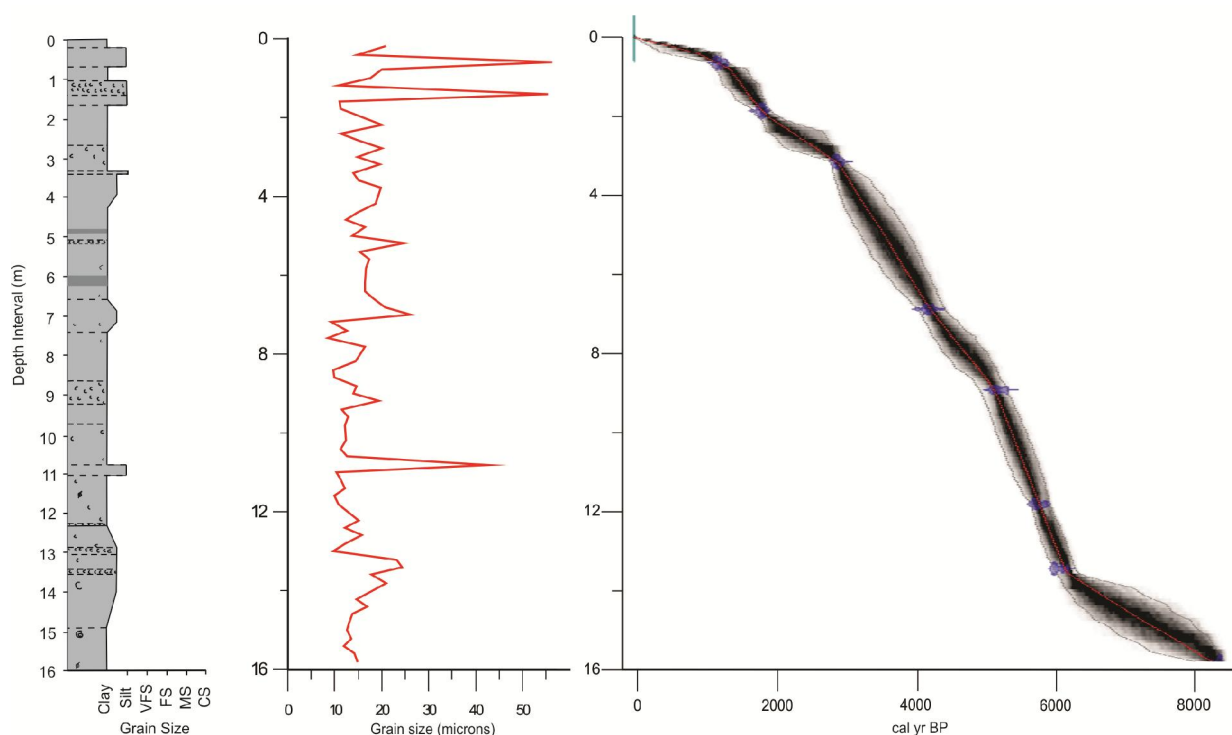
**Figure 5.5: Positive and negative factor loadings for principal component two for NL-1.**

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## 5.2 FALSE BAY

### 5.2.1 Core Lithology

The FB-1 core comprised predominantly of clayey sediment, ranging from dark brown (organic-rich) to very dark grey to black (very organic-rich), with a number of intermittent horizons of coarser grained sediment (Fig. 5.6). Two distinct horizons of very organic-rich clayey sediment occur at 6 m and 5 m. Occasional, unidentifiable fragments of shell and plant material as well as reworked shell debris are distributed throughout the core. In general, sediment grain size is variable throughout the core, with three distinct periods of noticeable increases at 0.5, 1.5 and 11 m.



**Figure 5.6: Lithostratigraphy of core FB-1 indicating variations in mean grain size (Benallack, 2014). Age-depth model calculated in Bacon 2.2 (Blaauw & Chirsten, 2010).**

### 5.2.2 Core Chronology

Eight bulk sediment samples were selected from the False Bay core for radiocarbon analysis. Dates revealed a stratigraphically consistent sediment record that spanned the last ~8300 cal. yr BP (Table 2). Sedimentation rates were variable with the base of the core showing relatively high accumulation rates (10 yr/cm), indicating rapid sediment deposition in a relatively short period of time; whereas the surface sediments show relatively low accumulation rates (20 yr/cm) (Fig. 5.6). The average sedimentation rate covering the lacustrine infill (over the last 6000 yr) was ~5 yr/cm.

**Table 2: Radiocarbon ages for FB-1 calibrated to the Southern Hemisphere curve, SHCal13 (Hogg *et al.*, 2013).**

Lab code	Material	Depth (cm)	Conventional Age (C14)	Calibrated Age (cal. yr BP)
Beta405600	Organic sediment	65	1280±30	1069-1189 (76%) 1210-1266 (23%)
Beta387867	Organic sediment	187	1870±30	1638-1640 (0.2%) 1701-1836 (99%) 1859-1861 (0.08%)
Beta386290	Organic sediment	316	2800±30	2775-2946 (100%)
Beta405601	Organic sediment	691	3830±30	3996-4037 (4%) 4077-4293 (95%)
Beta386291	Organic sediment	896	4570±30	5048-5199 (64%) 5211-5311 (35%)
Beta373287	Organic sediment	1186	5030±40	5606-5770 (76%) 5806-5891 (23%)
Beta405602	Shell	1350	5290±30	5921-6032 (63%) 6038-6120 (26%) 6148-6177 (10%)
Beta386292	Organic sediment	1591	7560±30	8208-8262 (13%) 8293-8403 (86%)

### 5.2.3 Stratigraphical Zonation

A total of 85 species were identified in FB-1, which included 30 marine species, 6 marine-brackish species, 18 brackish species, 25 dilute species and 6 unknown species. The diatom assemblage was mostly dominated by marine and marine-brackish species, although there were periods in which brackish species dominated. Indicator groups were identified using the same rationale as described for the NL-1 assemblage. A list of all diatom species identified, along with their ecological preference based on published salinity tolerances can be found in Appendix 1. The diatom assemblage can be divided into three zones according to CONISS; zone FB-A (~5600– 4580 cal. yr BP; 1115 – 778 cm), zone FB-B (~4300 – 3650 cal. yr BP; 719 – 539 cm) and zone FB-C (~3650 – 500 cal. yr BP; 539 – 25 cm) (Fig.5.7). Two major periods of low fossil diatom preservation were encountered at the base of the core (~6500 – 5640 cal. yr BP; 1406 – 1135 cm) and in recent surface sediments (~435 cal. yr BP to present; 22 – 0 cm).

The assemblage of zone FB-A was primarily dominated by marine to marine-brackish species (Fig. 5.7). Prior to the first period of low preservation the cosmopolitan marine species, *Diploneis crabro*, dominated between ~5550 – 5400 cal. yr BP (1090 – 1022 cm) reaching a maximum relative abundance of 30%. The marine-brackish species *Giffenia cocconeiformis* and the marine species *Surirella fastuosa* were subdominant representing 16% and 13%, respectively during this period. A period of low preservation

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occurred between 1090 and 1023 cm (~5550 – 5400 cal. yr BP). Thereafter, marine species, *D. crabro*, *Grammatophora oceanica* and *Amphora commutata*, and the two marine-brackish species, *G. cocconeiformis* and *Nitzschia compressa* peaked simultaneously at ~5300 cal. yr BP, before declining coincident with an increase in the marine species, *Coscinodiscus wittianus*, which peaked at 5200 cal. yr BP. A peak in *G. cocconeiformis*, *D. crabro* and *G. oceanica* is observed between ~4620 – 4580 cal. yr BP. Toward the end of zone FB-A there was a strong representation of *G. cocconeiformis* and *Paralia sulcata* peaking simultaneously at ~4500 cal. yr BP.

The transition between zone FB-A and FB-B was defined by a period of low preservation from ~4580 – 4300 cal. yr BP (778 – 717 cm). In zone FB-B a mixed assemblage was prevalent. The early stages of zone FB-B (~4300 cal. yr BP) was dominated by the marine-brackish species, *N. compressa* and the marine species, *Hyalodiscus radiatus*, reaching maximum relative abundances of 31% and 21%, respectively. Brackish species were present in low abundances during these early stages, including *Campylodiscus clypeus* and *Tabularia fasciculata*, representing 8% and 6%, respectively. Thereafter, the two dominant species, *H. radiatus* and *N. compressa*, decreased in percentage representation from 21% to 5% and 32% to 7%, respectively from ~4300 – 3600 cal. yr BP. Abundances in the brackish, *C. clypeus*, marine-brackish, *G. cocconeiformis* and marine species, *D. crabro* and *Actinoptychus heliopelta*, all peaked simultaneously between ~3750 – 3650 cal. yr BP (Fig. 5.7). Although, present in minor quantities typically reaching a maximum of 9% in zone FB-A, *C. clypeus* peaked to a maximum of 29% in zone FB-B at ~3800 cal. yr BP.

Zone FB-C showed high variability, with considerable marine and marine-brackish influences and intermittent intrusions of brackish species. The early stage of zone FB-C was defined by the dominance (30%) of the marine species, *H. radiatus*, at ~3600 cal. yr BP. A decline in *H. radiatus* was succeeded by the dilute species, *Thalassiosira weissflogii*, which reached a maximum of 28% at ~3400 cal. yr BP. This abrupt intrusion of *T. weissflogii* is noteworthy as it is commonly found in high nutrient conditions suggesting mixing of water sources of various salinities (Taylor *et al.*, 2007). The brackish taxon, *Diploneis smithii* and the two marine-brackish species, *G. cocconeiformis* and *N. compressa* corresponded with the distribution of *T. weissflogii*. Thereafter, *Melosira nummuloides* and *C. wittianus* peaked simultaneously at ~3200 cal. yr BP. The period ~3000 – 2400 cal. yr BP showed great variability in the biological community as well as frequent fluctuations in species abundance. Fluctuations in the marine species, *H. radiatus*, *C. wittianus*, *P. sulcata* and *M. moniliformis* appear out of phase with peaks in the marine-brackish species, *G. cocconeiformis* and *N. compressa*. At ~3000 cal. yr BP the marine-brackish taxa, *M. moniliformis* and the two marine species, *H. radiatus* and *P. sulcata* all peaked simultaneously before declining in abundance. *C. wittianus* and *D. crabro*, as well as, *G. cocconeiformis* and *N. compressa* all increased at ~2800 cal. yr BP. From ~2600 – 2300 cal. yr BP, the three marine species *D. crabro*, *C. wittianus* and *H. radiatus* and the three marine-brackish species *G. cocconeiformis* and *N. compressa* and *M. moniliformis* all appear to

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increase congruently. This trend continued throughout the rest of zone FB-C (Fig. 5.7). A notable peak in the brackish species, *C. clypeus* and *Cyclotella distinguenda* occurred at ~1750 cal. yr BP. Near the culmination of zone FB-C, two episodes of poor frustule preservation occurred at ~1300 – 1000 cal. yr BP and ~900 – 500 cal. yr BP. Prior to the first zone of low preservation at ~1300 cal. yr BP *N. compressa* and *C. wittianus* peaked simultaneously reaching a maximum of 38% and 23%, respectively. Subsequently, there was a period in which *N. compressa* and *G. cocconeiformis* and *C. wittianus* and *H. radiatus* were dominant at ~900 cal. yr BP. Thereafter, *H. radiatus* was dominant from ~900 - 500 cal. yr BP reaching a maximum of 30% at ~450 cal. yr BP. In general, zone FB-A was dominated by marine and marine-brackish species. The diatom assemblages of zone FB-B and FB-C were highly variable with considerable diversity in brackish, marine-brackish and marine species. This pronounced marine and marine-brackish influence continued throughout zone FB-C.

#### 5.2.4 Statistical Outputs

Principal component analysis (PCA) was conducted to identify the key indicator species influencing patterns within the dataset as well as to determine similarity/dissimilarity and underlying driving mechanisms between samples. Initially the PCA was constructed using species with an abundance of >5% throughout the core to determine the influential species, resulting in a total of 17 species in the final PCA. These key indicator species were used in the analysis to identify the underlying mechanisms driving their distribution (Fig. 5.8). All species and sites scores are provided in Appendix 7. According to the PCA, two principal component axes were identified as significant, with a combined contribution of 46.01%. Component one explained 23.32% of the variance and had large positive loadings on *M. nummuloides* and *N. compressa*, which are classed as brackish and marine-brackish, respectively (Fig. 5.9). *M. nummuloides* has optimal development in turbid, light-limited and nutrient-rich environments and can thrive during periods of sudden salinity changes (McLean *et al.*, 1981; Anderson *et al.*, 2015). *N. compressa* is a meso-halobous epiphyte, which thrives in salinities between 0.2 – 30‰ (Espinosa *et al.*, 2003).

Component one had large negative loadings on *Giffenia cocconeiformis* and *Diploneis crabro* (Fig. 5.9). The euhalobe species, *G. cocconeiformis*, usually occurs in marine water or water with similar concentration to that of sea water (35‰; Kosugi, 1988; Rashid, 2014). *Diploneis crabro* is a cosmopolitan marine species typically found attached to submerged macrophytes in the littoral zone (Navarro, 1982; Park *et al.*, 2012). The underlying factors driving component one appears to be an indication of the status of the system relative to amount of precipitation experienced. During periods of increased precipitation higher nutrient concentrations associated with fluvial inflow are expected. Conversely, the prevalence of *G. cocconeiformis* and *D. crabro* may indicate reduced precipitation.

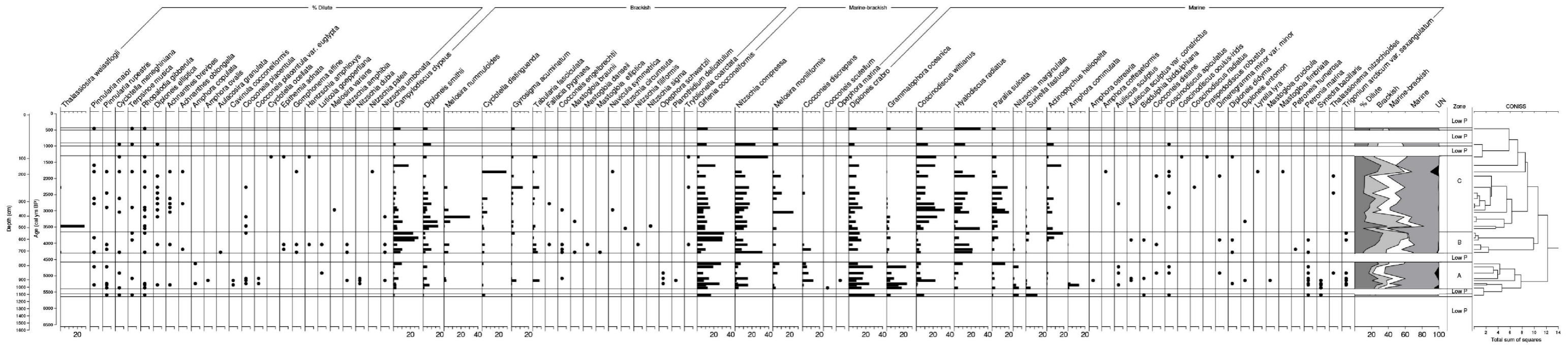
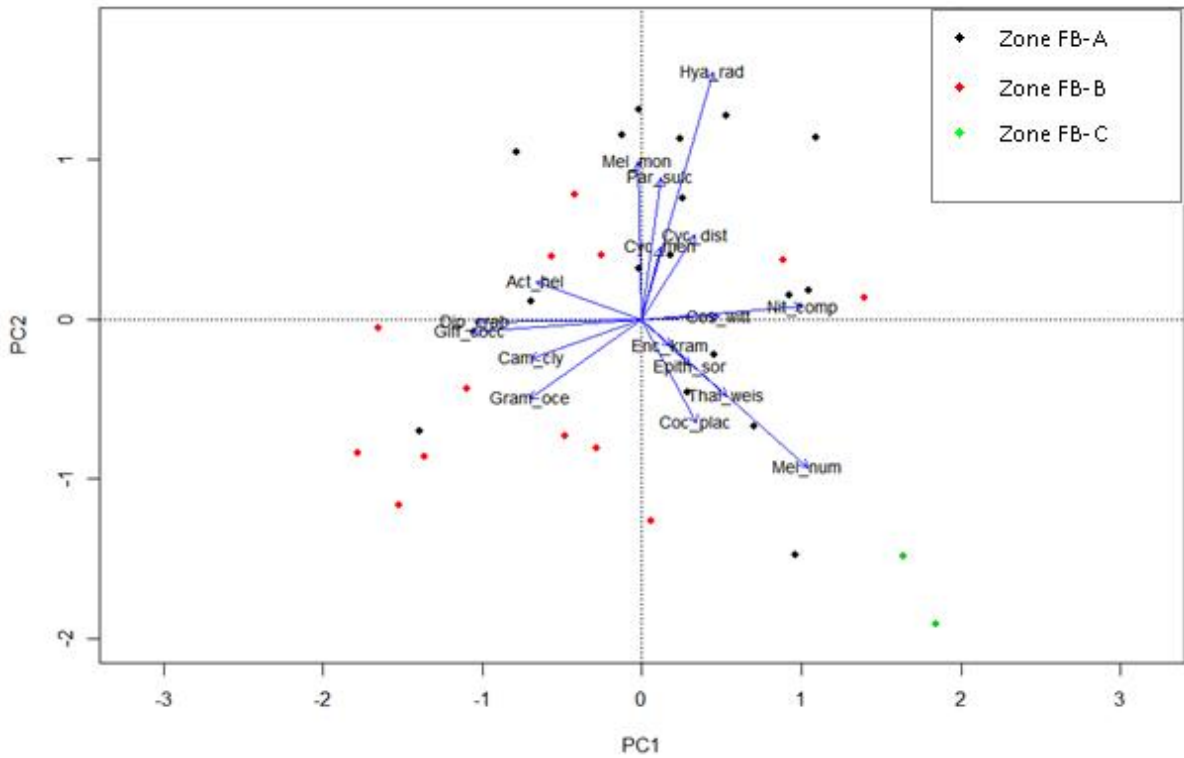
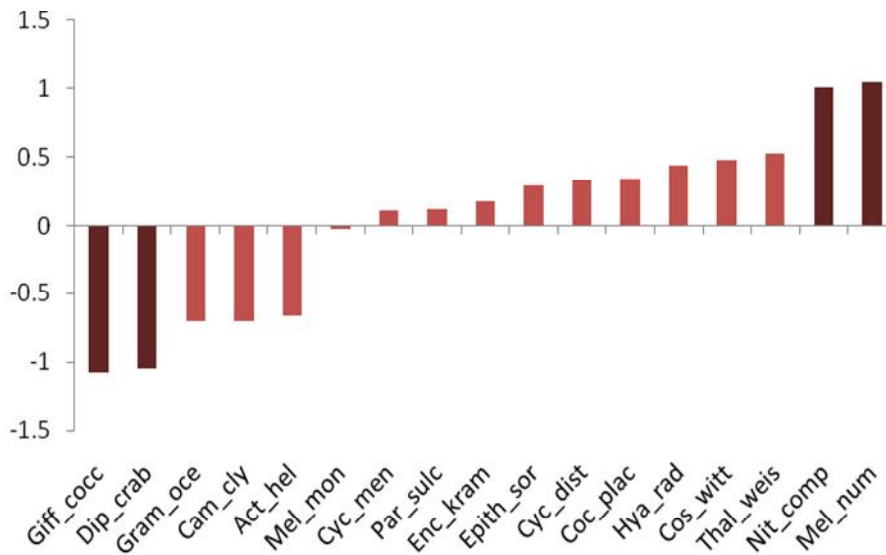


Figure 5.7: Relative percentage abundance of diatom species in core FB-1. Diatom species grouped into four salinity classes (% Dilute, % Brackish, % Marine-brackish and % Marine), with zones (FB-A, FB-B and FB-C) determined according to CONISS. Low P = low preservation zones.

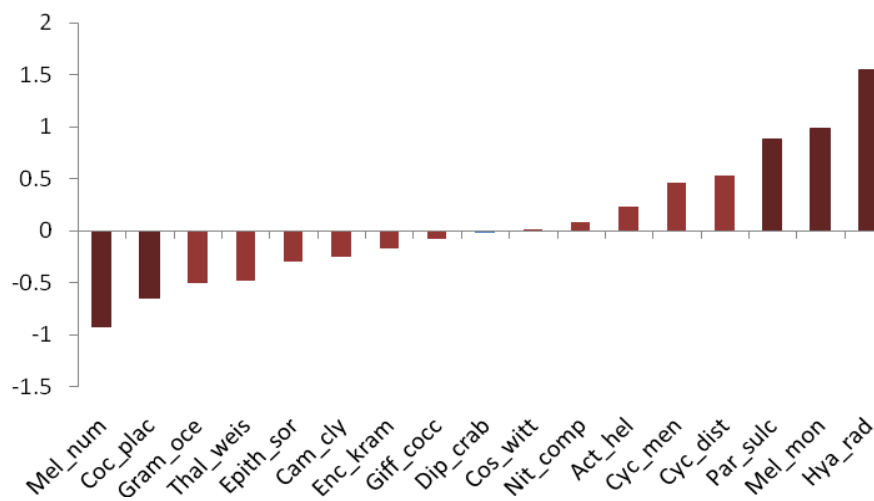


**Figure 5.8: The relationship between species and samples from FB-1 determined using PCA. Sample points are colour coded according to the three zones constructed by CONISS in TILIA. Species names are noted: Mel\_num = *Melosira nummuloides*, Coc\_plac = *Cocconeis placentula*, Thal\_weis = *Thalassiosira weissflogii*, Epith\_sor = *Epithemia sorex*, Enc\_kram = *Encyonema krameri*, Cos\_wit = *Coscinodiscus wittianus*, Nit\_comp = *Nitzschia compressa*, Cyc\_dis = *Cyclotella distinguenda*, Cyc\_men = *Cyclotella meneghiniana*, Mel\_mon = *Melosira moniliformis*, Par\_sul = *Paralia sulcata*, Act\_hel = *Actinoptychus heliopelta*, Dip\_cra = *Diploneis crabro*, Giff\_cocc = *Giffenia cocconeiformis*, Cam\_cly = *Campylodiscus clypeus*, Gram\_oce = *Grammatophora oceanica*.**



**Figure 5.9: Positive and negative factor loadings for principal component one for FB-1.**

Component two contributed 22.69% of the explained variance. Species with high positive loadings on the second component include the planktonic marine species *H. radiatus*, *M. moniliformis* and *P. sulcata* (Fig. 5.10). The marine species, *H. radiatus*, occurs in the littoral zone near river mouths where salinity is variable and usually high (Hustedt & Aleem, 1951; McIntire & Moore, 1977). The marine littoral species, *M. moniliformis*, is associated with non-living substrates other than sediments and requires periods of intertidal exposure to the air for maximum development (McIntire & Moore, 1977). *P. sulcata* is common in highly variable environments (McQuoida & Nordberg, 2003) and is widely found in both planktonic and benthic microphyte communities of temperate coastal waters. Furthermore, this species thrives in light-limited, nutrient-enriched environments and is considered a proxy of coastal upwelling (Zong, 1997).



**Figure 5.10: Positive and negative factor loadings for principal component two for FB-1.**

Species with high negative loadings on the second component are *C. placentula* and *M. nummuloides* which are both epiphytic and classed into fresh-brackish and brackish groups, respectively (Fig. 5.10). *C. placentula* is an epiphytic/epilithic, holoeuryhaline oligohalobous species that can tolerate salinities up to 30 ‰ (McIntire & Moore, 1977; Taylor *et al.*, 2007). *M. nummuloides* frequently occurs in brackish waters in the upper intertidal region and thrives in turbid, light-limited and nutrient-rich environments (McLean *et al.*, 1981; Anderson *et al.*, 2015). Furthermore, during periods of rapid salinity change, low oxygen saturation levels and/or organically polluted waters, *M. nummuloides* has the ability to dominate over other species (McLean *et al.*, 1981). Species with positive loadings include marine planktonic species that occur in highly variable environments, and can tolerate higher salinities and lower lake levels. On the other hand, negative loadings on fresh-brackish and brackish epiphytes suggest a macrophyte dominated community, nutrient rich environment with relatively deeper water levels. Thus, the second component may be representative of increased precipitation.

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## CHAPTER 6: DISCUSSION

### 6.1 Introduction

The east coast of southern Africa features several back-barrier coastal lakes comprising a series of incised valleys that formed during forced regressions and have subsequently been transgressively infilled. These coastal lakes have evolved differently in response to sea-level rise, mainly driven by sediment supply. Sedimentary records obtained from Lake St. Lucia cover the most recent transgressive infill and document the evolution of this system from its fluvial origins through to a classic back-barrier estuarine system, and finally to contemporary lacustrine conditions. In an attempt to reconstruct hydrological changes associated with the Holocene evolution of Lake St. Lucia, diatom species were classified according to their reported environmental preferences. This allowed the identification of indicator groups that could be used to infer changes in salinity (i.e. marine vs. fresh water species) and lake water level (i.e. planktonic vs. benthic species). Fossil diatom evidence obtained from the North Lake and False Bay records revealed three phases of lake development. Variations associated with these phases are discussed within the context of regional sea level change and climate variability.

### 6.2 Comparison with Modern Datasets

Interpretations of palaeo diatom assemblages are based on modern distributions and environmental affinities of diatoms in the region, thus it is important to relate the findings of dominant species from this study to the contemporary environment. A number of studies looking at modern diatom assemblages have been conducted at Lake St. Lucia (i.e. Cholnoky, 1963, 1968; Johnson, 1977; Gordon, 2008; Bate & Smailes, 2008; Nche-Fambo *et al.*, 2015). Cholnoky (1963, 1968) reported on an extensive taxonomic survey of St. Lucia's benthic diatoms, Johnson (1977) examined the system's phytoplankton population, while Gordon (2005) examined the epiphytes and Bate & Smailes (2008) and Nche-Fambo *et al.* (2015) examined the phytoplankton community composition and its resilience and variability under extreme environmental conditions. Appendix 3 provides a summary of the diatom genera common in these studies.

In this current study, *P. sulcata*, which is associated with upwelling events and common in water with high fluctuating salinities (Zong, 1997), was recorded in both FB-1 and NL-1 and was the only common species recorded from Cholnoky's (1963) work. The presence of *P. sulcata* was less common in Cholnoky's survey, presumably due to the limited marine influence today. Johnson (1977) reported the presence of quite a different suite of diatoms during the 1973 and 1974 studies, which were conducted shortly after a drought period when the system was hypersaline. The occurrence of two marine species and one brackish species during the Johnson (1977) sampling interval, including *Actinoptychus sp.*, *Pleurosigma delicatulum* and

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*Melosira nummuloides*, respectively suggests that these species are able to tolerate fluctuating salinities caused by high evaporation and low precipitation. In this study, these species occurred in very low abundances, except for *M. nummuloides* which was abundant in FB-1 at ~3200 cal. yr BP, suggesting high salinity fluctuations in the system during this time. Nche-Fambo *et al.* (2015) recorded 56 diatom genera in which the majority of the taxa were benthic. During their study the characteristic reverse salinity gradient was observed with hypersalinity furthest from the estuarine inlet. *Diploneis*, *Nitzschia* and *Navicula* are all common genera found at several sites across the lake (Cholnoky, 1968; Johnson, 1976; Nche-Fambo *et al.*, 2015). Representatives of these genera are present in this study, particularly *N. compressa* and *D. crabro* which were common throughout both NL-1 and FB-1, suggesting that these species have the ability to adapt to salinity fluctuations.

It would appear that the resilience of species in the lake system is dependent on the ability to tolerate high, fluctuating salinities, thus the most abundant diatom species were marine-brackish species that could persist in hypersaline conditions. The relative abundance of marine-brackish species, such as *N. compressa* and *G. cocconeiformis*, occurs consistently throughout the FB-1 and NL-1 cores, but decreases in relative abundance toward the top of the NL-1 core. Bate and Smailes, (2008) proposed that the various states of mouth closure and spatial variability were responsible for the differences in taxa recorded during different studies. Additionally, dissimilarities in the diatom communities between the sites may be due to diatoms being able to rapidly adapt to variability and thus vary over time (Perissinotto *et al.*, 2013), or due to a limited number of sampling sites or dates (Bate & Smailes, 2008; Nche-Fambo *et al.*, 2015). According to all the studies there was a high spatial and temporal variability in the abundance, composition and occurrence of diatom species. During low lake levels, segmentation of the main basins occurs (Fig. 3.4) producing a variety of habitats (estuary, South Lake, False Bay and North Lake). Diatom species will only occur in areas which satisfy their environmental preference. Therefore, salinity was identified as an important factor influencing the distribution and structure of the diatom assemblages in Lake St. Lucia.

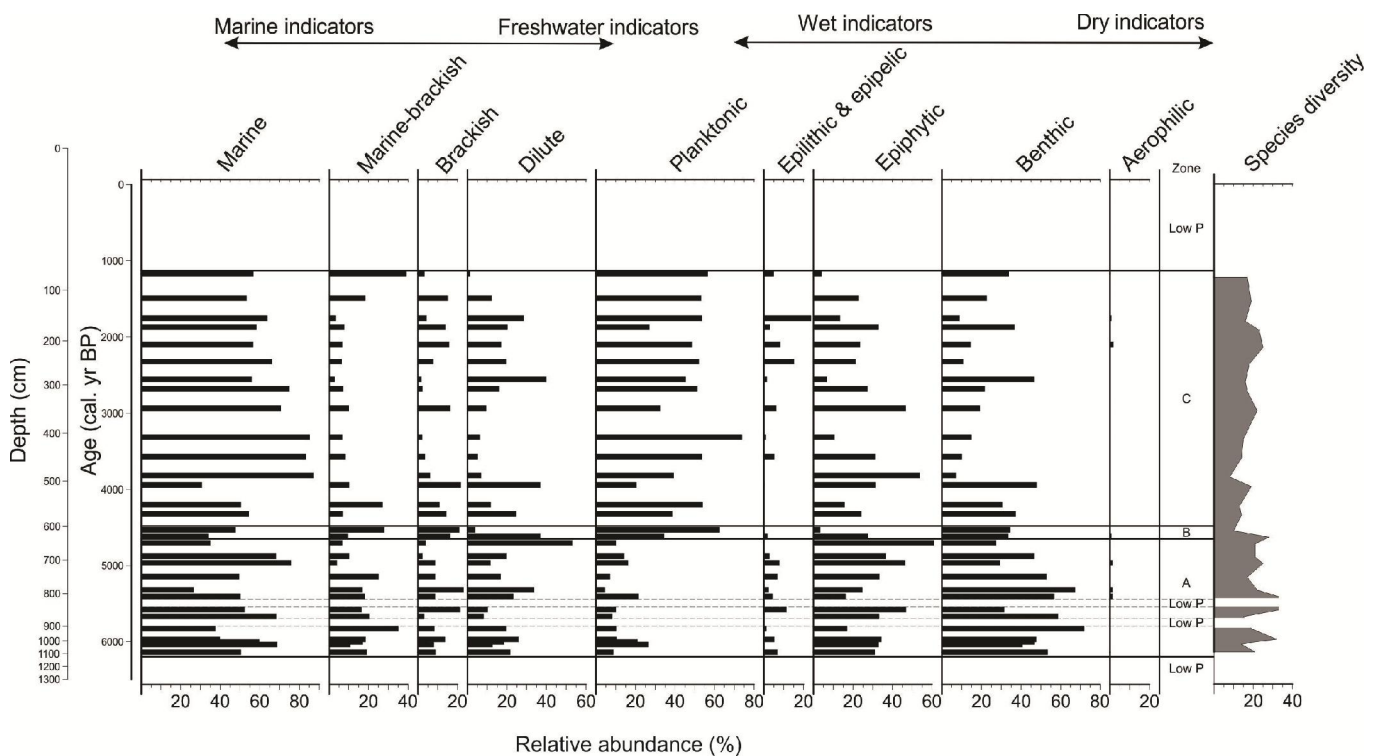
## **6.3 Palaeoenvironmental Reconstructions for NL-1 and FB-1**

### **6.3.1 North Lake Hydrological Development**

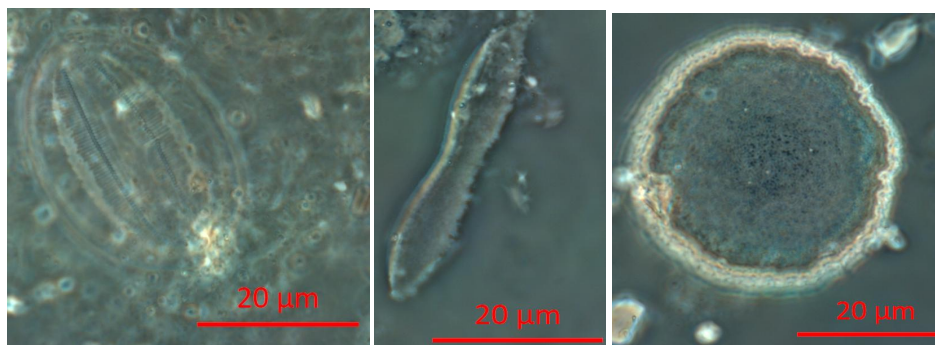
Zone-NL-A: ~6200 - 4400 cal. yr BP

The presence of coarse marine sands at the base of NL-1 provides evidence for strong marine influence prior to ~6200 cal. yr BP when there was a direct oceanic link through Leven Point. These sands are characterised by low diatom preservation and many fragmented frustules suggesting high energy conditions, likely

associated with tidal/wave action. Strong marine influences remain prevalent in the system from ~6200 to 4700 cal. yr BP, with periodic inputs of fresher water flushing the basin (Fig. 6.1). This would imply that North Lake was not solely dominated by seawater but had started transitioning into an estuarine system, while the dominance of marine-brackish and benthic taxa suggests the presence of a shallow water environment. Zones of low preservation (~5800 - 5700 cal. yr BP and ~5500 - 5300 cal. yr BP) suggest the presence of intermittent high energy conditions, likely linked to the penetration of tidal currents through Leven Point. The low preservation zones are characterised by fragmented diatom frustules as shown in Figure 6.2.



**Figure 6.1: Summary diagram for NL-1 indicating the classification of diatom species and their inferred environmental indicators.**



**Figure 6.2: Examples of fragmented diatom frustules that characterise the low preservation zones in North Lake (~840 cm; 5500 cal. yr BP and 890 cm; 5600 cal. yr BP). These are often not counted due to the uncertainty in correct identification.**

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Following the brief periods of low preservation, an increase in freshwater influences lead to less saline conditions, thereby creating a more favourable environment in which dilute and brackish species could persist from ~5300 to 5200 cal. yr BP. Toward the end of zone NL-A at ~4600 cal. yr BP, fresh water inputs increased drastically (Fig. 6.1). This suggests the presence of greater riverine influences coupled by a reduction in the marine influx, likely associated with constriction of the inlet at Leven Point. Shallow water environment provided a habitat niche for epiphytic and benthic species, from ~4000 to 3900 cal. yr BP, enabling the establishment of a swamp.

Zone-NL-B: ~4600 - 4480cal. yr BP

Zone NL-B marks a major transitional phase, where North Lake likely shifted from a shallow environment characterised by benthic and epiphytic species to a deep water basin dominated by planktonic species. The presence of a back-barrier system is inferred, likely driven by the ponding of water behind an emergent barrier at Leven Point. At ~4600 cal. yr BP, an increase in freshwater influences possibly led to mixing of various source waters and an environment characterised by salinity variability (Fig. 6.1). This likely led to a larger allochthonous component, resulting in higher species diversity. By ~4400 cal. yr BP marine and planktonic species increased pointing to a possible marine inundation episode.

Zone-NL-C: ~4480 - 1130 cal. yr BP

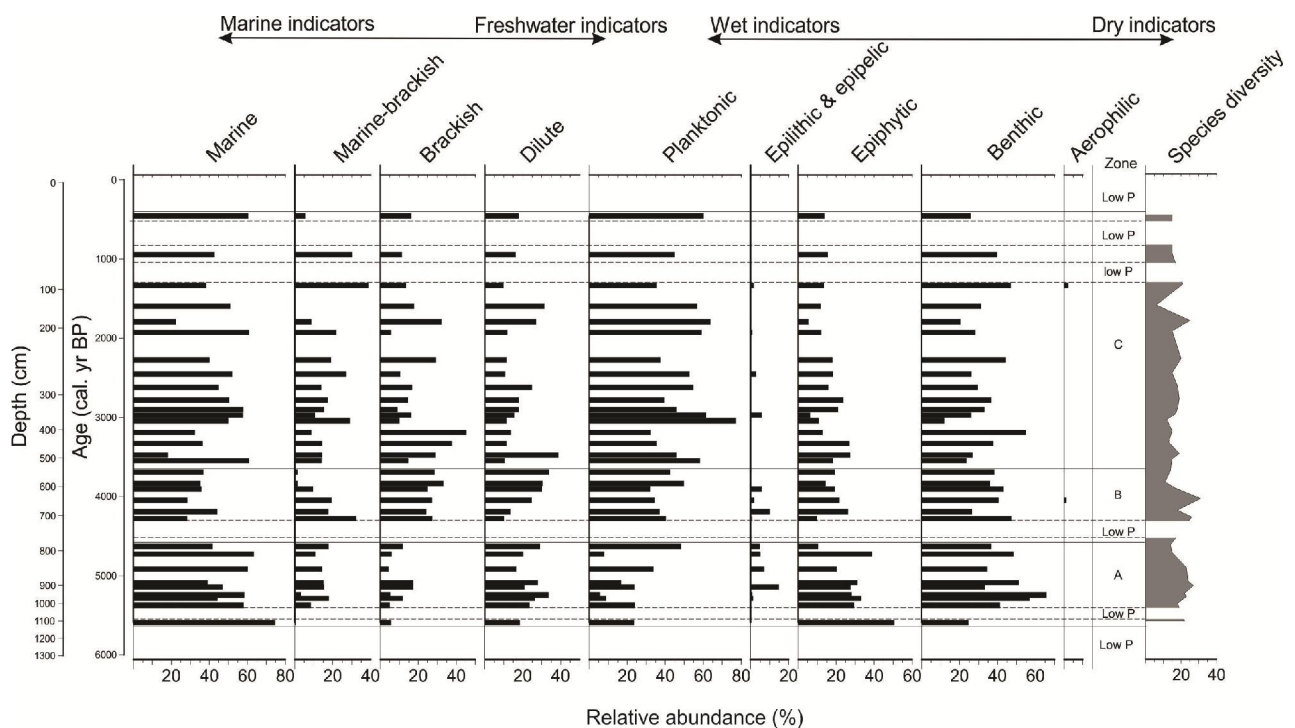
Strong marine influences persist until ~4300 cal. yr BP; however, freshwater influences provide a mixing environment in North Lake at ~3900 cal. yr BP, reducing the marine influxes (Fig. 6.1). A strong marine signal returns between ~3800 and 3300 cal. yr BP, before declining toward the culmination of the record at 1000 cal. yr BP, likely in response to coastal dune development and stabilisation at Leven Point. The high proportional representation of planktonics, mostly marine, supports the notion of episodic seawater intrusions into the lake basin, rather than a return to a fully marine environment. The relative increase in dilute species corresponds with increases in both epilithic/epipelics and epiphytes from ~2700 to 1800 cal. yr BP, indicating an increase in freshwater inputs, and the establishment of a submerged macrophyte community.

### **6.3.2 False Bay Hydrological Development**

Zone-FB-A: ~5,400 - 4580 cal. yr BP

The lack of marine sands at the base of FB-1 suggests the presence of relatively weak tidal currents in False Bay prior to ~6200 cal. yr BP. False Bay likely started accumulating fluvial sediment before North Lake owing to its relatively sheltered position behind the Nibela Peninsula. Since several rivers flow

into False Bay, the presence of fresh-brackish species throughout zone FB-A indicates the constant supply of riverine inputs/freshwater. The inflow of freshwater from the rivers draining into False Bay suggests a shallow estuarine environment was in effect prior to ~6500 cal. yr BP and occurring earlier than the development of estuarine conditions in North Lake at ~6500 cal. yr BP. The dominance of benthic and epiphytic species throughout zone FB-A, suggests a relatively shallow estuarine environment with a well-developed macrophyte community. Strong marine intrusions are evident in False Bay between ~4900 and 4700 cal. yr BP, before fresher conditions and possibly deeper water levels were established at ~4600 cal. yr BP. Several short-lived periods of low preservation from ~4500 to 4300 cal. yr BP, suggest intermittent high energy conditions, possibly associated with tidal currents (Fig. 6.3).



**Figure 6.3: Summary diagram for FB-1 indicating the classification of diatom species and their inferred environmental indicators.**

#### Zone-FB-B: ~4300 - 3600 cal. yr BP

An increase in freshwater influences throughout the zone, likely associated with the gradual transition from an open estuary to more confined lagoon, lead to a shift in the biological community from marine-brackish to brackish and dilute (Fig. 6.3). Increased freshwater inflow promoted a more variable environment, resulting in greater species diversity. An increase in planktonic species, typically ranging between 40 – 50%, coupled with a decrease in epiphytic species suggests the presence of a deeper water environment

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(Fig. 6.3). The fluctuations in epiphytes provide evidence of periods of wetland encroachment along the shores of False Bay.

Zone-FB-C: ~3600 - 500 cal. yr BP

A strong marine influence characterises much of this zone, although the persistence of dilute and brackish species, suggests mixing between fresh and marine water sources (Fig. 6.3). An increase in fluvial influence between ~3500 and 3200 cal. yr BP is inferred from substantial increases in *Thalassiosira weissflogii* at ~3400 cal. yr BP and *Melosira nummuloides* at ~3200 cal. yr BP. Strong marine influences return thereafter, between ~3100 and 2900 cal. yr BP, as marine planktonic species increase, before the increase in freshwater influences led to a well-mixed community at ~2600 cal. yr BP. The presence of benthics (~30%) and epiphytes (~20%) suggests that water levels were likely shallow during this period with an established wetland environment inferred. Higher water levels potentially linked to greater freshwater influences from ~1800 to 1500 cal. yr BP provided favourable habitats for freshwater and brackish planktonic species. This is possibly associated with increased precipitation that initiated the transition from estuarine to contemporary lacustrine conditions. While inferred lower water levels at ~1300 cal. yr BP potentially relates to a reduction in freshwater influences. Despite the low preservation of diatom species in the upper section of this zone, certain species were able to persist in low numbers, including *D. crabro*, *G. cocconeiformis*, *G. oceanic*, *H. radiatus*, *N. compressa* and *P. sulcata* (Appendix 4 and 5). The preservation of these species may be due to their more robust and heavily silicified structure, making them more resistant to degradation.

### 6.3.3 Between Core Comparisons

There is substantial overlap in diatom composition between the two sites, with only 28% of species occurring exclusively in NL-1 and 16% exclusively in FB-1 suggesting a well-mixed system. Great similarity in modern diatom assemblages between False Bay and North Lake was also noted by Bates & Smailes (2008). In the recent past (last 1000 years) differences in species diversity between False Bay and North Lake are more evident as is shown in the Chohnoky (1968) study where species richness was lower in False Bay compared to the other lake basins. This is likely due to the combination of the development of lacustrine conditions, the gradual shallowing of the basin as well as the higher salinity experienced by False Bay in comparison to North Lake. Although both sub-basins receive fluvial freshwater inputs, North Lake receives a greater volume during periods of drought due to the larger catchment drained by the Mkhuze River (Taylor *et al.*, 2006).

The differences in species diversity at the contemporary Lake St. Lucia would suggest that the salinity levels experienced in False Bay exceeds a critical threshold for many diatom species, therefore reducing the number of taxa which can persist at this site (Taylor *et al.*, 2006). Additionally, evaporite geochemical

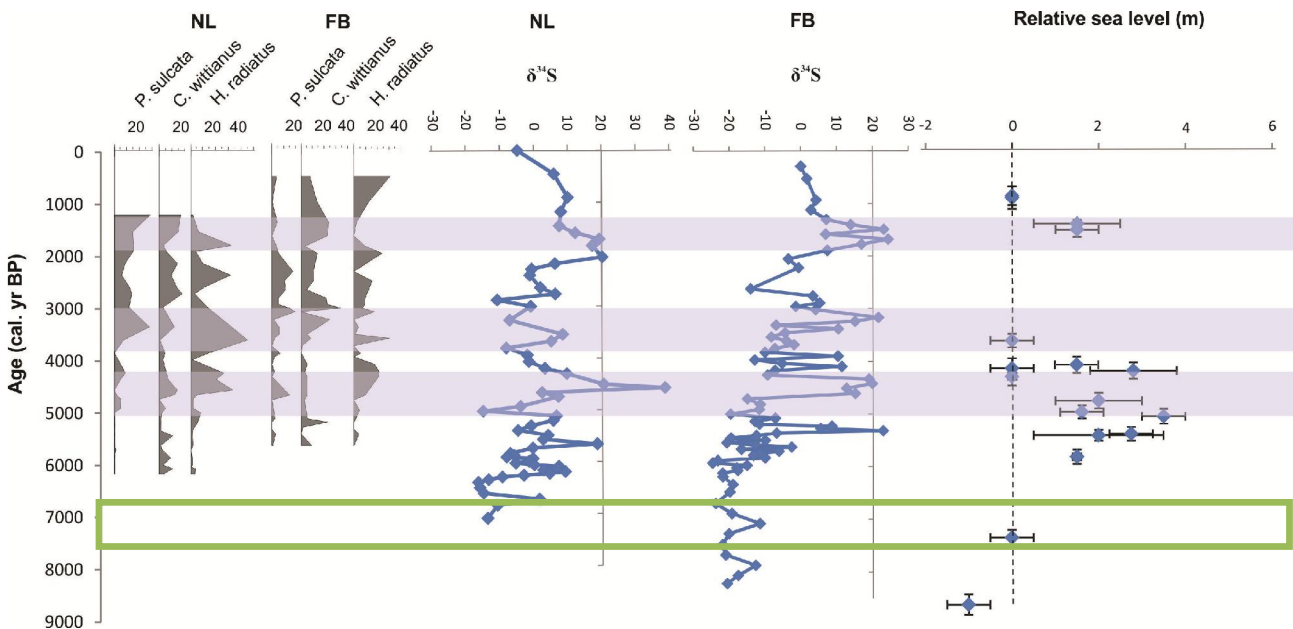
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evidence suggests that False Bay has experienced more severe/prolonged desiccation events in the past when compared to North Lake (Humphries *et al.*, 2015). Higher present day salinity levels are also frequently recorded in False Bay (Fig. 3.3). Fewer species are typically recorded with an increase in salinity since fewer species are able to osmoregulate and adapt to hypersaline environments (Williams, 1998; Pedros-Alio *et al.*, 2000; Barinova *et al.*, 2011). This is not the case in this study, where species diversity was similar between False Bay (18%) and North Lake (19%) (Figs. 6.1 and 6.3). It is possible that during the mid-Holocene period both systems experienced the same environmental mechanism over time. It is evident that both cores show low diatom preservation near the surface of the cores, this could be due to the development of hypersaline conditions restricting the persistence and preservation of species. It is apparent that North Lake and False Bay were dominated by marine influences ~5500 – 4600 cal. yr BP, indicating that shallow estuarine conditions prevailed at this time. Both sub-basins transitioned from an open estuarine system to a more confined deeper lagoonal system ~4600 cal. yr BP. A significant increase in marine influences is noticeable from ~4900 to 4700 cal. yr BP. Higher freshwater influences were observed at both sites at ~2000 cal. yr BP, indicating a well-mixed community likely associated with the establishment of lacustrine conditions.

#### **6.4 Sea level Influences on System Development**

The evolution of Lake St. Lucia is known to be strongly influenced by sea level variations and cyclical erosional pulses of sediment inputs, which are recorded in the transgressive sedimentary infills of submerged incised valleys underlying the lake system (Cooper *et al.*, 2012; Botha *et al.*, 2013). Along the eastern margin of the South Africa coastal plain the late Pleistocene-Holocene relic dune forms started to become established around 179 ka (Wright, 1999; Porat & Botha, 2008; Botha *et al.*, 2013). During the Last Interglacial sea level highstand, the coastal barrier dunes were breached and the St. Lucia estuary was subsequently inundated by the Indian Ocean (Botha *et al.*, 2013). This led to False Bay forming a coastline embayment with an open marine connection through the bluffs, where the corals *in situ* indicate circulation of marine water (Hobday, 1975; Wright *et al.*, 2000; Alverson *et al.*, 2003). The present barrier dune formed more recently from younger, less cemented aeolianite deposited ~64 ka (Porat & Botha, 2008). During most of the Late Pleistocene/Holocene transgression an open ocean connection was maintained at Leven Point. Closure of the mouth at Leven Point likely occurred in phases, with initial constriction being followed by several phases of dune building. This process is evident in the shift from benthic to planktonic species at ~4600 cal. yr BP, indicating the development of a back-barrier system. During early stages of dune development, overwash and marine exchange was likely still prevalent, evident by the increase in marine planktonic species from ~4600 to 4300 cal. yr BP. Dating of the coastal dune sands by Botha *et al.* (2013) suggests that the most recent phase of accretion occurred ~2000 yr BP.

Evidence of rising sea level along the east coast of southern Africa during the Holocene is preserved in submerged dune ridges and beachrock, which Ramsay & Cooper (2002) used to reconstruct sea level (Fig. 6.4). According to Ramsay and Cooper's (2002) sea-level rose at a rate of 8 mm/yr from the LGM to 8000 cal. yr BP, reaching its present level along the South African coastline at ~7300 cal. yr BP. Sea-level increased to +1.5 m above MSL at ~5800 cal. yr BP and continued to rise between 5300 to 4000 cal. yr BP, depositing a series of beachrocks at an elevation of +2.75 m. A mid-Holocene sea-level highstand is inferred at ~5000 cal. yr BP, where late Pleistocene aeolianites were wave-planned and potholes were incised at an elevation of +3.5 m (Ramsay, 1995; Fig. 6.4). This mid-Holocene sea-level highstand persisted for a period of ~2500 years, with the +3.5 m stillstand being the highest sea-level reached during the Holocene. Ramsay (1995) inferred lower sea levels between 3400 and 1600 cal. yr BP from a lack of preserved deposits on the coastline. A higher sea level (+1.5 m) is suggested at ~1400 cal. yr BP before stabilising around present day level ~800 cal. yr BP.



**Figure 6.4:** Relationship between variations in three marine planktonic species, sediment  $\delta^{34}\text{S}$  (Humphries, unpublished data), and reconstructed sea level (Ramsay, 1995). Development of estuarine conditions occurred earlier in False Bay compared to North Lake (green box). Note: Dates from Ramsay (1995) have been calibrated using SHCal13 and ocean water  $\delta^{34}\text{S} = \sim 20\text{‰}$ .

Variations in diatom assemblages from Lake St. Lucia show some correspondence with inferred changes in Holocene sea-level. The onset of estuarine conditions in North Lake occurred at ~6500 cal. yr BP, although it may have begun significantly earlier in False Bay owing to its more sheltered position (Fig. 6.4). This coincides with the timing of the Holocene sea level reaching contemporary levels. Significant increases in marine influences from ~4900 to 4700 cal. yr BP, temporally agrees with the onset of a mid-Holocene transgression when sea level was considered to have been +2 m above MSL (Ramsay, 1995; Fig. 6.4). This

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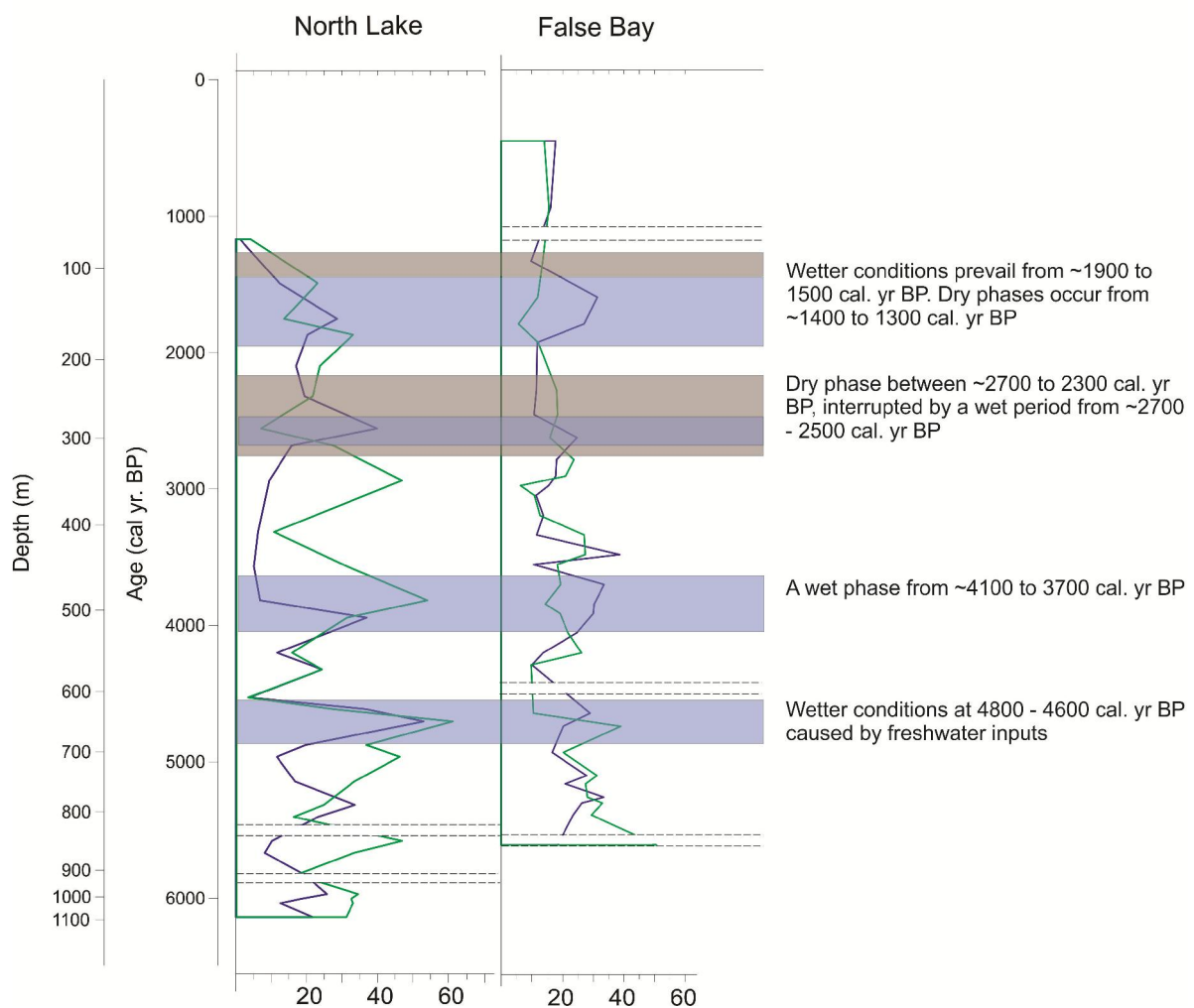
is supported by sediment  $\delta^{34}\text{S}$  data from NL-1 and FB-1, which show peaks that are characteristic of marine water ( $\delta^{34}\text{S} \sim 20\text{‰}$ ). Based on the shift from benthic to planktonic species and the reduction in marine taxa, back-ponding behind an emergent coastal barrier commenced  $\sim 4600$  cal. yr BP. This provides evidence for the early stages of dune development and initial phase of constriction at Leven Point that initiated the transition from open estuary to a more confined lagoon. This likely created tranquil conditions that favoured the accumulation of fluvial sediments from the surrounding catchments.

The decline in marine planktonic species and sulfur isotopes at  $\sim 3900$  cal. yr BP (Fig. 6.4), suggests increases in freshwater influences which are possibly fluvially dominated. In North Lake marine influences increased from  $\sim 3800$  to  $3300$  cal. yr BP, similarly in False Bay increases in marine influences occurred at  $\sim 3500$  and  $3000$  cal. yr BP (Fig. 6.4); this could be related to the washover associated with the mid-Holocene highstand that persisted for  $\sim 2500$  years, before reaching contemporary levels at  $\sim 3200$  cal. yr BP (Ramsay, 1995). The apparent offset between the two records suggest that inherent errors may have occurred when constructing the derived age models. The gradual decrease in marine influences and sulfur isotopes from  $\sim 2800$  to  $2500$  cal. yr BP suggests an increase in freshwater influences leading to mixing of fresh and marine waters (Fig. 6.4). Additionally, a possible marine regression between  $3400$  and  $1600$  cal. yr BP (Ramsay, 1995) could have also contributed to the reduced marine influences observed. Evidence of increased marine influences and sulfur isotopes are apparent between  $\sim 1800$  to  $1600$  cal. yr BP, possibly associated with the rise in sea level of  $+1.5$  m (Ramsay, 1995; Fig. 6.4). A gradual decline in marine species coupled with higher abundances in brackish and dilute species between  $\sim 1600$  -  $1000$  cal. yr BP, suggests a reduction in marine influence, likely associated with a shift towards lacustrine conditions as sea level started to stabilise around present day levels.

## 6.5 Regional Climate Dynamics

Substantial regional variations exist in the palaeoenvironmental records for southern Africa, influenced by the contemporary environment of the site, synoptic patterns, altitude and microclimates (Scott, 2002; Chase & Meadows, 2007). Increases in precipitation over KwaZulu-Natal have been linked to stronger atmospheric circulation on the southwestern Indian Ocean and increases in SST in the southern Mozambique Channel (Neumann *et al.*, 2010). It is of interest to assess whether regional Holocene climatic variations are expressed in the sedimentary records from Lake St. Lucia in an attempt to help understand the palaeoenvironmental history of southern Africa. The early to mid-Holocene developmental stages of the coastal dunes created a back-barrier system which initiated the transition from a shallow estuarine system to a deeper lagoonal system at  $\sim 4600$  cal. yr BP and a gradual expansion in the riparian vegetation. This period is punctuated by increases in freshwater supply, most notably from  $\sim 4800$  –  $4600$  cal. yr BP related to a

wetter phase (Fig. 6.5). This corresponds with a spread of forest taxa near Lake Eteza (Fig. 2.4) from 6500 – 3600 cal. yr BP (Neumann *et al.*, 2010). These wetter conditions have been linked to increased rainfall driven by elevated SST's and a higher sea level (Neumann *et al.*, 2010). Furthermore, according to Bard *et al.* (1997), elevated SST's in the Mozambique Channel between ~7000 – 4000 cal. yr BP, induced a southward penetration of the Agulhas current, leading to an increase in precipitation in coastal KwaZulu-Natal. Higher freshwater inputs from ~4100 to 3700 cal. yr BP, suggest wetter conditions likely linked to an increase in precipitation. This led to mixing of freshwater and marine waters, as well as the development of a well-established macrophyte community (Fig. 6.5). This is in agreement with a period of variable warmth and moisture availability between 4300 – 3200 cal. yr BP interpreted from a speleothem record at Cold Air Cave (Lee-Thorp *et al.*, 2001).



**Figure 6.5: Summary of inferred wet and dry phases for North Lake and False Bay. The relative abundance of dilute (blue) and epiphytic (green) species are used to indicate freshwater inputs and wetland expansion, respectively. Periods of low preservation are indicated by dotted lines.**

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A short-lived dry phase between ~2700 to 2300 cal. yr BP (Fig. 6.5), suggests lower precipitation leading to reduced riverine inputs into the basin. The decline in freshwater inputs negatively impacted the macrophyte community. Dry conditions are also inferred at Cold Air Cave from 3200 – 2100 cal. yr BP (Lee-Thorp *et al.*, 2001) and through the decline in most tree taxa at Lake Eteza between 3600 and 2500 cal. yr BP (Neumann *et al.*, 2010). Pollen analysis from Mfabeni Peatland also suggests the establishment of more open savanna/woodland vegetation along the east coast from 3000 – 2500 cal. yr BP (Finch & Hill, 2008). The decline in trees can be observed in a number of localities in KwaZulu-Natal since ~3100 cal. yr BP and therefore suggests a regional phenomenon that is strongly linked to aridification of the Late Holocene (Neumann *et al.*, 2010). These cooler, drier conditions were likely associated with a northward shift in westerlies caused by the equatorward expansion of the atmospheric circumpolar vortex (Holmgren *et al.*, 2003; Mayewski *et al.*, 2004). The expansion of the vortex led to a retreat of tropical circulations equatorward which resulted in the SRZ of South Africa becoming cooler and drier and the south-western WRZ of the subcontinent becoming wetter and cooler. This mechanism is thought to have controlled much of the changing climate patterns over southern Africa over long periods of time (Holmgren *et al.*, 2003).

A relatively wet phase interrupts the dry conditions from ~2700 to 2500 cal. yr BP (Fig. 6.5), as a slight increase in freshwater inputs from rivers enter St. Lucia. This is supported by pollen records from the Braamhoek wetland that shows a shift from a predominantly dry climate to subhumid, moist conditions at 2500 cal. yr BP (Norström *et al.*, 2009). The forcing mechanisms behind this variability is not fully understood, but some influence can be attributed to shifts in the circulation systems dominating the region, for instance the latitudinal movements of the ITCZ and the dynamics of the mid-latitude low pressure belts (Norström *et al.*, 2009). Relatively wetter or less evaporative conditions, interrupted by brief drier conditions, across the SRZ are evident during the last two millennia, this is supported by pollen analysis from Lake Eteza, Blydefontein Basin and Braamhoek wetland which indicates a subhumid, moist environment (Scott *et al.*, 2005; Lewis, 2008; Norström *et al.*, 2009; Neumann *et al.*, 2010). At St. Lucia increases in freshwater inputs from ~1900 to 1500 cal. yr BP (Fig. 6.5), also suggests wetter conditions likely associated with increased precipitation in the region. Enhanced moist conditions are supported by substantial increase in forest elements and extensive grass cover at 1500 cal. yr BP (Norström *et al.*, 2009); a rise in the P-E ratio at Lake Sibaya between 1710 and 1550 cal. yr BP (Stager *et al.*, 2013); an increase in siliceous microfossil preservation after 2000 cal. yrs BP at the Braamhoek wetland (Finne *et al.*, 2010) and pollen records from Lake Eteza from 2000 to 800 cal. yr BP, after which dry conditions prevailed (Neumann *et al.*, 2010). Additionally, late Pleistocene organic deposits used for the multi-proxy study from the Braamhoek wetland infer relatively wet climate conditions from 2500 to 500 cal. yr BP. Thereafter, a decline in freshwater influences suggests a short-lived period of drier conditions at St. Lucia from ~1400 to 1300 cal. yr BP (Fig. 6.5). This is in agreement with inferred lower lake levels at Lake Sibaya between 1550

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and 1160 cal. yr BP (Stager *et al.*, 2013) and a  $\delta^{18}\text{O}$  sequence from Cold Air Cave which indicates alternating cooler and drier conditions occurred from 1600 to 1100 cal. yr BP (Holmgren *et al.*, 1999). Additionally, *Podocarpus* pollen from lake and swamp deposits retreated northward to the Kosi Bay area by ca. 1300 cal. yr BP, suggesting increased aridity in the region (Mazus, 2000).

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## CHAPTER 7: CONCLUDING REMARKS AND RECOMMENDATIONS

This study has highlighted the use of diatom records in tracing hydrological changes in a coastal lake that developed in response to changes in Holocene sea level and climate. Analysis of cores extracted from the most recent sedimentary infill of Lake St. Lucia document the evolution of the system as it transitioned from an open estuary to a more confined lagoon, and finally to lacustrine conditions that prevail today. The establishment of estuarine conditions was initiated when rising sea-levels during the early Holocene stabilised near present day levels ~6500 cal. yr BP. Rising sea levels and development of a coastal barrier resulted in the constriction of the tidal inlet at Leven Point, promoting the accumulation of fluvial sediment which gradually began to fill the lagoon. Back-ponding behind an emergent coastal barrier at ~4600 cal. yr BP initiated the transition from open estuary to a more confined lagoon, although strong marine influences, likely associated with overwash events, persisted. The final phase of lagoonal infilling was curtailed between ~1600 and 1000 cal. yr BP in response to the stabilisation of sea-levels and accretion of the coastal barrier, eventually impounding the waterbody as it transitioned to lacustrine conditions.

This study highlights the value of diatom proxies in reconstructing the palaeoenvironmental history of a region. The work forms part of a larger multi-disciplinary project that aims to examine the long-term processes driving change at Lake St. Lucia and it provides an important dataset, which will be combined with other proxy analyses (pollen, foraminifera and geochemistry), to improve our understanding of the evolution of the system. Lake St. Lucia is a promising site for future studies, due to its relatively sheltered location and well-preserved sediments that have accumulated continuously since the mid-Holocene.

This study has started to provide new insight into the Holocene evolution of Lake St. Lucia and fills an important gap in our understanding of the long-term processes that have shaped the formation of the system. Understanding the influence of sea level rise and past changes in environmental conditions is of particular relevance in evaluating the system's response to predicted changes in climate, and drought events. Future projects should focus on applying a multi-proxy approach on several cores along the salinity gradient within the lake. This will provide a higher resolution study that will allow more precise inferences of the development of the system to be made, ultimately enhancing our understanding of the evolution of coastal systems on the east coast of southern Africa. Finally, an understanding of the long-term evolution and functioning of Lake St. Lucia is important in providing insight into how the system developed, how it used to function and predicting how it may respond in the future to changes in climate and water flow. This knowledge should ultimately underpin future management strategies for the St. Lucia ecosystem.

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# Appendices

**Appendix 1- Ecological affinities of diatom species from FB and NL; including salinity preference and life form.**

Species names	Salinity preference	Life form
<i>Achnanthes brevipes</i>	Fresh-brackish	Epiphytic
<i>Achnanthes oblongella</i>	Fresh-brackish	Benthic
<i>Actinocyclus circellus</i>	Unknown	Unknown
<i>Actinoptychus heliopelta</i>	Marine	Planktonic
<i>Amphora coffeaeformis</i>	Marine	Epiphytic
<i>Amphora commutata</i>	Marine	Benthic
<i>Amphora copulata</i>	Fresh-brackish	Epilithic & epipellic
<i>Amphora ostrearia</i>	Marine	Benthic
<i>Amphora ovalis</i>	Fresh-brackish	Epilithic & epipellic
<i>Aulacosira granulata</i>	Fresh	Planktonic
<i>Auliscua sculptus var. constrictus</i>	Marine	Benthic
<i>Auliscus sculptus</i>	Marine	Benthic
<i>Biddulphia biddulphiana</i>	Marine	Planktonic
<i>Campylodiscus clypeus</i>	Brackish	Planktonic
<i>Cavinula cocconeiformis</i>	Fresh	Benthic
<i>Cocconeis discrepans</i>	Marine-brackish	Epilithic & epipellic
<i>Cocconeis distans</i>	Marine	Benthic
<i>Cocconeis engelbrechtii</i>	Brackish	Benthic
<i>Cocconeis multiperforata</i>	Unknown	Unknown
<i>Cocconeis placentula</i>	Fresh-brackish	Epiphytic
<i>Cocconeis placentula var. euglypta</i>	Fresh-brackish	Epiphytic
<i>Cocconeis scutellum</i>	Marine-brackish	Epiphytic
<i>Coscinodiscus apiculatus</i>	Marine	Planktonic
<i>Coscinodiscus oculus-iridis</i>	Marine	Planktonic
<i>Coscinodiscus radiatus</i>	Marine	Planktonic
<i>Coscinodiscus wittianus</i>	Marine	Planktonic
<i>Craspedodiscus robustus</i>	Marine	Unknown
<i>Cyclotella distinguenda</i>	Brackish	Planktonic
<i>Cyclotella meneghiniana</i>	Fresh	Planktonic
<i>Cyclotella ocellata</i>	Fresh	Planktonic
<i>Dimeregramma minor var. minor</i>	Marine	Benthic
<i>Diploneis crabro</i>	Marine	Epiphytic
<i>Diploneis didyma</i>	Marine	Epilithic & epipellic
<i>Diploneis elliptica</i>	Fresh-brackish	Benthic
<i>Diploneis entomon</i>	Marine	Epiphytic
<i>Diploneis smithii</i>	Brackish	Epiphytic
<i>Diploneis suborbicularis</i>	Unknown	Unknown
<i>Epithemia adnata</i>	Fresh-brackish	Epiphytic
<i>Fallacia pygmaea</i>	Brackish	Epiphytic
<i>Giffenia cocconeiformis</i>	Marine-brackish	Benthic
<i>Gomphonema affine</i>	Fresh-brackish	Planktonic
<i>Grammatophora oceanica</i>	Marine	Benthic

<i>Gyrosigma acuminatum</i>	Brackish	Benthic
<i>Hantzschia amphioxys</i>	Fresh-brackish	Aerophilic
<i>Hyalodiscus radiatus</i>	Marine	Planktonic
<i>Luticola goeppertiana</i>	% Dilute	Benthic
<i>Lyrella lyra</i>	Marine	Benthic
<i>Mastogloia elliptica</i>	Brackish	Benthic
<i>Mastogloia braunii</i>	Brackish	Epiphytic
<i>Mastogloia crucicula</i>	Marine	Epiphytic
<i>Mastogloia danseii</i>	Brackish	Benthic
<i>Mastogloia fimbriata</i>	Marine	Epiphytic
<i>Mastogloia pumila</i>	Unknown	Unknown
<i>Melosira moniliformis</i>	Marine-brackish	Planktonic
<i>Melosira nummuloides</i>	Brackish	Benthic
<i>Melosira varians</i>	Fresh-brackish	Epilithic & epipelagic
<i>Navicula symmetrica</i>	Brackish	Benthic
<i>Nitzschia amphibia</i>	Fresh-brackish	Benthic
<i>Nitzschia circumscuta</i>	Brackish	Benthic
<i>Nitzschia compressa</i>	Marine-brackish	Benthic
<i>Nitzschia dubia</i>	Fresh-brackish	Benthic
<i>Nitzschia filiformis</i>	Brackish	Benthic
<i>Nitzschia marginulata</i>	Marine	Epiphytic
<i>Nitzschia palea</i>	Fresh-brackish	Epilithic & epipelagic
<i>Nitzschia sigma</i>	Brackish	Epiphytic
<i>Nitzschia umbonata</i>	Fresh-brackish	Benthic
<i>Opephora marina</i>	Marine-brackish	Benthic
<i>Opephora schwartzii</i>	Brackish	Benthic
<i>Paralia sulcata</i>	Marine	Planktonic
<i>Petrodictyon gemmoides</i>	Unknown	Unknown
<i>Petronis humerosa</i>	Marine	Benthic
<i>Petronis marina</i>	Marine	Benthic
<i>Pinnularia maior</i>	Fresh-brackish	Benthic
<i>Pinnularia rupestris</i>	Fresh-brackish	Benthic
<i>Plagiogramma salinarum</i>	Unknown	Unknown
<i>Planothidium delicatulum</i>	Brackish	Unknown
<i>Rhopalodia gibberula</i>	Fresh-brackish	Benthic
<i>Stephanodiscus hantzschii</i>	Fresh-brackish	Planktonic
<i>Surirella fastuosa</i>	Marine	Epiphytic
<i>Synedra bacillaris</i>	Marine	Planktonic
<i>Tabularia fasciculata</i>	Brackish	Epiphytic
<i>Terpsinoe musica</i>	Fresh-brackish	Benthic
<i>Thalassionema nitzschioides</i>	Marine	Planktonic
<i>Thalassiosira weissflogii</i>	Fresh-brackish	Planktonic
<i>Trigonium arcticum</i> var. <i>sexangulatum</i>	Marine	Epiphytic
<i>Tryblionella coarctata</i>	Brackish	Benthic

**Appendix 2- List of scientific names for diatom species with naming authority for both sites.**

<i>Achnanthes brevipes</i> Agardh var. <i>brevipes</i>	<i>Decussata placenta</i> (Ehrenberg) Lange-Bertalot & Metzeltin var. <i>placenta</i>	<i>Navicula symmetrica</i> Patrick
<i>Achnanthes danica</i> (Flögel) Grunow	<i>Diademoides luxuriosa</i> (Greville) Kemp & Paddock	<i>Nitzschia amphibia</i> Grunow f. <i>amphibia</i>
<i>Achnanthes oblongella</i> Oestrup	<i>Diatoma vulgare</i> Bory	<i>Nitzschia circumscuta</i> (J.W.Bailey) Grunow
<i>Actinocyclus circellus</i> Watkins	<i>Dimeregramma minor</i> (Gregory) Ralfs in Pritchard	<i>Nitzschia compressa</i> (J.W.Bailey) Boyer
<i>Actinocyclus heliopelta</i> Grunow in Van Heurck	<i>Diploneis crabro</i> Ehrenberg	<i>Nitzschia dissipata</i> (Kützing) Grunow var. <i>dissipata</i>
<i>Actinocyclus octonarius</i> Ehrenberg	<i>Diploneis didyma</i> (Ehrenberg) Cleve	<i>Nitzschia dubia</i> W.M.Smith
<i>Actinocyclus splendens</i> (Schadb.) Ralfs in Pritchard	<i>Diploneis elliptica</i> (Kützing) Cleve	<i>Nitzschia etoshensis</i> Cholnoky
<i>Amphora coffeaeformis</i> (Agardh) Kützing var. <i>coffeaeformis</i>	<i>Diploneis entomon</i> (Ehrenberg) Cleve	<i>Nitzschia filiformis</i> (W.M.Smith) Van Heurck var. <i>filiformis</i>
<i>Amphora commutata</i> Grunow	<i>Diploneis oblongella</i> (Naegeli) Cleve-Euler	<i>Nitzschia marginata</i> Hustedt
<i>Amphora copulata</i> (Kütz) Schoeman & Archibald	<i>Diploneis ovalis</i> (Hilse) Cleve	<i>Nitzschia palea</i> (Kützing) W.Smith
<i>Amphora ostrearia</i> Brébisson ex Kützing	<i>Diploneis smithii</i> (Brebisson) Cleve var. <i>smithii</i>	<i>Nitzschia sigma</i> (Kützing) W.M.Smith
<i>Amphora ovalis</i> (Kützing) Kützing var. <i>ovalis</i>	<i>Diploneis suborbicularis</i> (Gregory) Cleve var. <i>suborbicularis</i>	<i>Nitzschia umbonata</i> (Ehrenberg) Lange-Bertalot
<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen	<i>Encyonopsis krammeri</i> Reichardt	<i>Opephora marina</i> (Gregory) Petit
<i>Auliscus sculptus</i> (Wm.Smith) Ralfs in Pritchard	<i>Epithemia adnata</i> (Kützing) Brebisson	<i>Opephora schwartzii</i> (Grunow) Petit ex Pelletan
<i>Auliscus sculptus</i> var. <i>constrictus</i> (Wm.Smith) Ralfs in Pritchard	<i>Epithemia sorex</i> Kützing	<i>Paralia sulcata</i> (Ehrenberg) Cleve
<i>Biddulphia biddulphiana</i> (J.E.Smith) Boyer	<i>Fallacia florinae</i> (Moeller) Witkowski	<i>Petrodictyon gemma</i> (Ehrenberg) D.G. Mann
<i>Biddulphia rhombus</i> (Ehrenberg) W. Smith	<i>Fallacia pygmaea</i> (Kützing) Stickle & Mann ssp. <i>pygmaea</i> Lange-Bertalot	<i>Petronia humerosa</i> (Brebisson ex Wm. Smith) Stickle & Mann
<i>Biddulphia tridens</i> Ehrenberg	<i>Giffenia cocconeiformis</i> (Grunow) Round & Basson	<i>Petronia marina</i> (Ralfs) D.G. Mann in Round & al
<i>Campylodiscus clypeus</i> Ehrenberg	<i>Gomphonema affine</i> Kützing	<i>Pinnularia borealis</i> Ehrenberg var. <i>borealis</i>
<i>Cavinula cocconeiformis</i> (Gregory ex Greville) Mann & Stickle	<i>Gomphonema insigne</i> Gregory	<i>Pinnularia major</i> (Kützing) Rabenhorst
<i>Cocconeis costata</i> Gregory var. <i>costata</i>	<i>Grammatophora oceanica</i> Ehrenberg	<i>Pinnularia rupestris</i> Hantzsch in Rabenhorst
<i>Cocconeis discrepans</i> A.Schmidt	<i>Gyrosigma acuminatum</i> (Kützing) Rabenhorst	<i>Plagiogramma salinarum</i>
<i>Cocconeis distans</i> Gregory	<i>Hantzschia amphioxys</i> (Ehrenberg) Grunow	<i>Planothidium delicatulum</i> (Kütz.) Round & Bukhtiyarova
<i>Cocconeis engelbrechtii</i> Cholnoky	<i>Hippodonta capitata</i> (Ehrenberg) Lange-Bert. Metzeltin & Witkowski	<i>Rhopalodia gibberula</i> (Ehrenberg) O.Muller
<i>Cocconeis multiperforata</i>	<i>Hyalodiscus radiatus</i> (O'Meara) Grunow	<i>Stephanodiscus hantzschii</i> Grunow in Cl. & Grunow 1880
<i>Cocconeis placentula</i> Ehrenberg var. <i>placentula</i>	<i>Luticola goeppertiana</i> (Bleisch in Rabenhorst) D.G. Mann	<i>Stictodiscus novaezealandiae</i>
<i>Cocconeis placentula</i> Ehrenberg var. <i>euglypta</i> (Ehrenberg) Grunow	<i>Lyrella lyra</i> (Ehrenberg) Karayeva	<i>Surirella fastuosa</i> Ehrenberg
<i>Cocconeis scutellum</i> Ehrenberg var. <i>scutellum</i>	<i>Mastogloia elliptica</i> (C.A. Agardh) Cleve	<i>Synedra bacillaris</i> (Grunow) Hustedt
<i>Coscinodiscus apiculatus</i> Ehrenberg	<i>Mastogloia braunii</i> Grunow	<i>Tabularia fasciculata</i>
<i>Coscinodiscus oculus-iridis</i> Ehrenberg	<i>Mastogloia crucicula</i> (Grunow) Cleve var. <i>crucicula</i>	<i>Terpsinoe musica</i> Ehrenberg
<i>Coscinodiscus radiatus</i> Ehrenberg	<i>Mastogloia dansei</i> (Thwaites) Wm.Smith	<i>Thalassionema nitzschioides</i> (Grunow) Mereschkowsky
<i>Coscinodiscus wittianus</i>	<i>Mastogloia fimbriata</i> (Brightwell) Cleve	<i>Thalassiosira weissflogii</i> (Grunow) Fryxell & Hasle
<i>Craspedodiscus robustus</i>	<i>Mastogloia laterostrata</i> Hustedt	<i>Trachyneis aspera</i> (Ehrenberg) Cleve
<i>Cyclotella distinguenda</i> var. <i>distinguenda</i> Hustedt	<i>Mastogloia pumila</i> (Grunow) Cleve	<i>Triceratium favus</i> Ehrenberg
<i>Cyclotella meneghiniana</i> Kützing	<i>Melosira moniliformis</i> (O.F.Muller) Agardh v. <i>moniliformis</i>	<i>Trigonium arcticum</i> var. <i>sexangulatum</i>
<i>Cyclotella ocellata</i> Pantocsek	<i>Melosira nummuloides</i> (Dillwyn) C.A. Agardh	<i>Tryblionella coarctata</i> (Grunow in Cl. & Grunow) D.G. Mann
<i>Cymbella janischi</i> (A. Schmidt) De Toni	<i>Melosira varians</i> Agardh	
<i>Cymbella tumida</i> (Brebisson) Van Heurck	<i>Navicula radiosa</i> Kützing	

**Appendix 3- List of diatom genera from the St. Lucia system, including previous studies that recorded these diatom genera and the sites they were found at. PS- present study; BC- Brodies Crossing, LP- Listers Point,CC- Charters Creek, MT- Mouth, FB- False Bay and NL- North Lake.**

Genus	Other studies	Site
<i>Actinoptychus</i>	PS (Johnson, 1976; Nche-Fambo <i>et al.</i> , 2015)	CC, MT, FB, NL
<i>Amphora</i>	PS (Johnson, 1976; Bate and Smailes, 2008; Nche-Fambo <i>et al.</i> , 2015)	LP, CC, MT, FB, NL
<i>Auliscus</i>	(Johnson, 1976; Nche-Fambo <i>et al.</i> , 2015)	CC, FB, NL
<i>Campylodiscus</i>	PS (Nche-Fambo <i>et al.</i> , 2015)	CC, FB, NL
<i>Cerataulina</i>	(Nche-Fambo <i>et al.</i> , 2015)	CC
<i>Chaetoceros</i>	(Johnson, 1976; Nche-Fambo <i>et al.</i> , 2015)	LP
<i>Cocconies</i>	PS (Bate and Smailes, 2008; Cholnoky, 1968; Nche-Fambo <i>et al.</i> , 2015)	MT, FB, NL
<i>Craticula</i>	(Nche-Fambo <i>et al.</i> , 2015)	MT
<i>Cyclotella</i>	PS (Johnson, 1976; Nche-Fambo <i>et al.</i> , 2015)	CC, MT, FB, NL
<i>Diploneis</i>	PS (Cholnoky, 1968; Johnson, 1976; Bate and Smailes, 2008; Nche-Fambo <i>et al.</i> , 2015)	LP, CC, MT, FB, NL
<i>Encyonema</i>	(Bate and Smailes, 2008; Nche-Fambo <i>et al.</i> , 2015)	MT
<i>Entomoneis</i>	(Johnson, 1976; Nche-Fambo <i>et al.</i> , 2015)	LP, CC, MT
<i>Fragilaria</i>	(Cholnoky, 1968; Johnson, 1976; Nche-Fambo <i>et al.</i> , 2015)	CC, MT
<i>Gomphonema</i>	PS (Cholnoky, 1968; Nche-Fambo <i>et al.</i> , 2015)	LP,CC, FB, NL
<i>Gyrosigma</i>	PS (Cholnoky, 1968; Bate and Smailes, 2008; Nche-Fambo <i>et al.</i> , 2015)	LP,CC,MT, FB, NL
<i>Hantzschia</i>	PS (Nche-Fambo <i>et al.</i> , 2015)	CC, FB, NL
<i>Melosira</i>	PS (Cholnoky, 1968; Johnson, 1976; Nche-Fambo <i>et al.</i> , 2015)	CC,MT, FB, NL
<i>Navicula</i>	PS (Cholnoky, 1968; Johnson, 1976; Bate and Smailes, 2008; Nche-Fambo <i>et al.</i> , 2015)	LP,CC,MT, FB, NL
<i>Nitzschia</i>	PS (Cholnoky, 1968; Johnson, 1976; Bate and Smailes, 2008; Nche-Fambo <i>et al.</i> , 2015)	LP, CC,MT, FB, NL
<i>Odontella</i>	(Nche-Fambo <i>et al.</i> , 2015)	CC
<i>Paralia</i>	PS (Cholnoky, 1968; Nche-Fambo <i>et al.</i> , 2015)	BC, FB, NL
<i>Placoneis</i>	(Nche-Fambo <i>et al.</i> , 2015)	MT
<i>Plagiodiscus</i>	(Nche-Fambo <i>et al.</i> , 2015)	LP, CC
<i>Pleurosigma</i>	(Cholnoky, 1968; Johnson, 1976; Nche-Fambo <i>et al.</i> , 2015)	LP, CC, MT
<i>Rhopalodia</i>	PS (Bate and Smailes, 2008; Cholnoky, 1968; Nche-Fambo <i>et al.</i> , 2015)	MT, FB, NL
<i>Seminavis</i>	PS (Bate and Smailes, 2008; Nche-Fambo <i>et al.</i> , 2015)	LP, CC, MT
<i>Surirella</i>	PS (Johnson, 1976; Nche-Fambo <i>et al.</i> , 2015)	LP, CC, FB, NL
<i>Tryblionella</i>	PS (Nche-Fambo <i>et al.</i> , 2015)	CC, MT, FB, NL

**Appendix 4- Species that had low cell counts in the low preservation zones of FB.**

Sample name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Diploneis crabro</i>	0	0	0	1	0	0	0	0	1	0	0	0	0	0	2	0	0	2	1	0	0	0	0	0
<i>Diploneis smithii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coscinodiscus wittianus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0
<i>Hyalodiscus radiatus</i>	0	0	0	4	0	0	0	0	1	0	3	0	0	0	20	0	1	30	4	0	0	10	0	23
<i>Nitzschia compressa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	3	0	0	0	4	0	0
<i>Giffenia cocconeiformis</i>	0	0	0	3	0	0	0	0	1	0	2	1	0	0	0	0	0	6	5	0	0	3	0	0
<i>Campylodiscus clypeus</i>	0	0	0	0	0	0	0	0	1	0	1	1	0	0	2	0	1	8	1	0	0	0	0	0
<i>Paralia sulcata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0
<i>Actinoptychus heliopelta</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	10	1	0	0	0	0	0
<i>Terpsinoe musica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Grammatophora oceanica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
<i>Diploneis elliptica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Surirella fastuosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nitzschia marginulata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cocconeis discrepans</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cocconeis distans</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	108.5	748.5	1048.5	1088.5	1148.5	1188.5	1208.5	1248.5	1288.5	1308.5	1348.5	1368.5	1408.5	1448.5	1488.5	1508.5	1548.5	1588.5
23	0	0	9	0	0	1	5	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	6	0	0	5	15	0	0	0	0	0	0	0	0	0	0	0
1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

**Appendix 5- Species that had low cell counts in the low preservation zones of NL.**

Species name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	45.5
<i>Achnanthes brevipes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Actinoptychus heliopelta</i>	0	0	0	2	0	0	2	1	1	0	0	1	1	0	0	6	0	4	0	4	0	1	0	0	1	0	0
<i>amphora commutata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aulacoseira granulata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Auliscus sculptus</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	2	0	4	0	0	0	0	0	0	0	0
<i>Biddulphia biddulphiana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Campylodiscus clypeus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	6	1	1	0	4	0	2	0	2	0	0	0
<i>Cavinula cocconeiformis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cocconeis discrepans</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coscinodiscus apiculatus</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0
<i>Coscinodiscus apiculatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coscinodiscus radiatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Coscinodiscus wittianus</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	10	5	0	0	0	0	0	0	0
<i>Cyclotella distinguenda</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cyclotella meneghiniana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Diploneis crabro</i>	0	0	1	0	4	2	4	5	2	0	0	1	2	0	0	30	1	4	5	10	0	2	0	6	0	4	0
<i>Diploneis smithii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	
<i>Giffenia cocconeiformis</i>	0	0	0	0	1	0	4	5	2	0	0	2	0	0	0	10	2	3	3	10	0	0	0	2	0	3	0
<i>Grammatophora oceanica</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0
<i>Hippodonta capitata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hyalodiscus radiatus</i>	0	0	0	9	3	0	3	6	6	0	0	0	1	0	0	12	4	10	0	7	0	2	0	4	2	3	0
<i>Lyrella lyra</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Melosira nummuloides</i>	0	0	4	0	2	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
<i>Nitzschia compressa</i>	0	0	0	2	0	0	0	6	0	0	0	0	0	0	0	3	0	2	3	0	0	0	0	0	1	3	0
<i>Nitzschia littorea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>nitzschia marginulata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Paralia sulcata</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Pinnularia borealis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Pinnularia rupestris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Surirella fastuosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Synedra bacillaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tabularia fasciculata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0
<i>Terpsinoe musica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trachyneis aspera</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

888.5	948.5	1048.5	1068.5	1108.5	1148.5	1188.5	1208.5	1248.5	1288.5	1308.5	1348.5	1388.5	1408.5	1448.5	1488.5	1508.5	1548.5	1588.5
0	0	0	0	0	0	0	12	4	0	0	0	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	8	3	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	9	0	0	0	0	0	0	0	0	0	0	0
0	0	4	0	0	0	1	8	2	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	3	3	0	11	0	0	0	6	0	0	0	0	0	0	0
0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0
4	10	17	0	32	30	4	114	33	25	10	0	0	0	0	0	0	0	0
0	0	1	0	0	0	1	0	4	0	0	0	0	0	0	0	0	0	0
4	14	18	0	41	5	6	22	55	10	30	0	0	0	0	0	0	0	0
2	4	13	0	10	6	0	26	20	0	6	0	0	0	0	0	0	0	0

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0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
5	4	6	0	0	0	3	0	0	0	6	14	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	11	16	1	30	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	4	0	0	37	0	0	0	0	0	0	0
0	0	0	0	0	0	5	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0	0	0	0
0	0	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
0	1	2	0	0	0	0	17	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0

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**Appendix 6- Principle Component Analysis Output for NL.**

Importance of Components	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Eigenvalue	8.2852	4.5246	3.8391	2.85058	2.27993	2.1864	1.7879	1.59914	1.5102	1.13034
Proportion explained	0.2266	0.1237	0.105	0.07796	0.06236	0.0598	0.0489	0.04374	0.0413	0.03091
Cumulative proportion	0.2266	0.3503	0.4553	0.5333	0.59566	0.6554	0.7044	0.74809	0.7894	0.82031

Species scores	Species names	PC1	PC2	PC3	PC4	PC5	PC6
Achbrev	<i>Achnanthes brevipes</i>	-0.65122	0.021789	0.655442	-0.35599	0.249448	0.214685
Acthel	<i>Actinoptychus heliopelta</i>	0.27559	0.238051	-0.11543	-0.37345	0.204106	0.084025
Ampcom	<i>Amphora commutata</i>	-0.38499	-0.15053	0.348418	-0.13174	0.336683	0.127787
Bidbid	<i>Biddulphia biddulphiana</i>	-0.31581	0.030453	-0.15474	-0.08804	-0.13495	-0.06844
Bidtri	<i>Bidulphia tridens</i>	-0.01777	0.222099	-0.00545	0.262312	-0.16643	-0.12259
Camcly	<i>Campylodiscus clypeus</i>	0.20377	-0.02057	-0.24191	0.87411	0.324183	-0.05857
Cocdis	<i>Cocconeis discrepans</i>	-0.51011	0.122818	0.464278	-0.25671	-0.08016	-0.0883
Cospla	<i>Cocconeis placentula</i> <i>Cocconeis placentula</i>	-0.04285	-0.13958	-0.38731	0.218151	-0.00078	0.114066
Cocplaveug	<i>var. euglypta</i>	-0.06375	0.085046	-0.2028	0.217289	0.103399	0.433714
Coswit	<i>Coscinodiscus wittianus</i>	0.43058	-0.52631	-0.28063	-0.41775	-0.36167	-0.54653
Cydis	<i>Cyclotella distinguenda</i>	0.22443	-0.31745	0.328507	0.140391	-0.35224	0.507686
Cycmen	<i>Cyclotella meneghiniana</i>	0.21754	-0.39164	0.221263	0.210773	-0.34517	0.336333
Dipera	<i>Diploneis crabro</i>	-0.77134	1.286159	-0.34564	0.011257	-0.23735	-0.13247
Dipdid	<i>Diploneis didyma</i>	-0.13268	0.018355	-0.05888	-0.36055	-0.0057	0.040876
Dipent	<i>Diploneis entomon</i>	-0.09099	0.005273	-0.54803	-0.15018	-0.1794	0.096218
Dipsmi	<i>Diploneis smithii</i>	-0.05457	0.189193	-0.00492	-0.214	0.422846	0.003702
Epiadn	<i>Epithemia adnata</i>	-0.01767	-0.14473	-0.10509	0.102416	-0.17759	0.016484
Gifcoc	<i>Giffenia cocconeiformis</i> <i>Grammatophora</i>	-0.81255	-0.09991	-0.06931	0.42899	0.492405	0.061859
Gramoce	<i>oceanica</i>	-0.62605	0.040022	-0.21876	0.021384	0.032975	-0.06757
Gyroacu	<i>Gyrosigma acuminatum</i>	-0.07393	-0.11691	-0.03493	-0.03731	0.005468	-0.03908
Hyarad	<i>Hyalodiscus radiatus</i>	1.31263	0.640053	0.704025	0.261602	0.098116	-0.45007
Melnum	<i>Melosira nummuloides</i>	0.27061	-0.53296	-0.42769	-0.00799	0.181011	-0.36562
Melvar	<i>Melosira varians</i>	0.0963	-0.1344	0.059816	0.086637	0.030112	-0.20853
Melmon	<i>Mosira moniliformis</i>	0.56371	0.370655	0.530368	-0.2575	-0.08646	0.041644
Nitcir	<i>Nitzschia circumscuta</i>	0.0963	-0.1344	0.059816	0.086637	0.030112	-0.20853
Nitcom	<i>Nitzschia compressa</i>	-0.14835	-0.66932	0.114809	-0.38989	0.527981	-0.19439
Nitmar	<i>Nitzschia marginulata</i>	-0.66011	0.104897	0.156779	-0.1864	-0.08736	-0.15698
Parsul	<i>Paralia sulcata</i>	1.16935	0.195109	-0.51844	-0.3913	0.282566	0.497103
Petrgem	<i>Petrodictyon gemmoides</i>	0.10728	-0.18317	0.171495	0.098904	-0.19206	0.27361
Petmar	<i>Petronis marina</i>	-0.52649	-0.06514	-0.01925	-0.1558	-0.28586	0.078614
Rhopgib	<i>Rhopalodia gibberula</i> <i>Stephanodiscus</i>	-0.04784	-0.24808	0.337665	0.047075	-0.20457	0.253768
Stephhan	<i>hantzschii</i>	0.12652	0.03019	-0.16353	-0.13231	-0.06181	0.069871
Surfas	<i>Surirella fastuosa</i>	-0.35941	-0.19609	-0.08884	0.025045	-0.28362	-0.2054
Tabfas	<i>Tabularia fasciculata</i>	0.01514	-0.3422	0.163599	0.155248	-0.29735	-0.14982

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Termus	<i>Terpsinoe musica</i>	0.29989	0.195757	-0.47047	-0.30904	-0.11084	0.145761
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Site scores (weighted sums of species scores)						
	PC1	PC2	PC3	PC4	PC5	PC6
48.5	0.619077	-0.31645	0.63656	-0.3336	1.07733	-0.75744
88.5	1.225157	-1.63098	-0.95208	-2.3378	0.9908	0.08572
105.5	0.779675	-0.57243	-1.18818	0.2514	0.67598	-0.26653
148.5	1.651559	1.32023	1.06234	-0.9239	-0.26487	0.23442
188.5	1.164933	-1.989	1.86227	1.074	-2.08556	2.97113
208.5	0.874386	0.09027	0.66888	-0.7957	-0.3721	0.67161
248.5	1.434352	0.98153	0.94385	-0.2358	-0.29391	-0.6783
288.5	1.078023	0.25723	-1.39331	-1.1273	-0.52661	0.59532
308.5	0.646243	0.38955	-1.99113	-1.0177	-0.70431	0.21448
348.5	0.310849	1.36331	0.42772	-0.3428	-0.06445	0.30905
408.5	1.433375	0.52011	0.07729	-0.4289	0.06864	0.06934
448.5	0.888191	1.88895	0.91357	0.4338	0.16474	-0.47522
488.5	-0.1542	1.92772	-0.04733	2.2768	-1.44451	-1.06401
508.5	-0.32521	0.01802	-1.55725	1.0432	0.94256	0.38812
548.5	0.947756	-0.33754	-0.29017	0.6022	1.86952	-0.88566
588.5	-0.00184	0.51523	-0.5016	2.5582	1.99323	0.90725
608.5	1.299176	-1.81303	0.80693	1.1687	0.40622	-2.81307
628.5	0.142412	-1.76551	-0.15135	1.5144	-1.64756	-0.09586
648.5	-0.3673	0.48997	-1.16838	1.2518	0.5957	2.49869
688.5	-0.52683	0.37175	-1.53769	-0.6868	-0.37333	0.43238
708.5	-0.96818	1.38321	0.4118	-0.8476	-0.83516	-0.17665
748.5	-1.42405	0.09059	1.25364	-0.2625	0.03628	-0.42526
788.5	-1.21462	-1.08668	1.43218	-0.2051	2.42606	1.01994
808.5	-1.07635	-0.74545	0.95664	-0.6744	0.02999	-0.24089
848.5	-1.36263	0.49898	1.27854	-0.8458	-0.23602	0.45257
868.5	-1.29961	0.19127	-1.1972	-0.1144	-0.37954	0.01447
908.5	-0.84678	-1.29743	-0.56099	0.1442	-1.81545	-1.08091
988.5	-1.34834	-0.12434	0.47751	-0.4232	0.41765	0.16152
1008.5	-1.01437	-0.93369	-1.149	-0.5176	-0.75528	-0.60364
1028.5	-1.11742	0.11303	-0.31588	0.4538	-0.40531	-1.26054
1088.5	-1.44744	0.20162	0.79182	-0.6518	0.50926	-0.20203

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**Appendix 7- Principle Component Analysis Output for FB.**

Importance of Components	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Eigenvalue	7.4414	4.9791	3.9432	2.92137	2.36644	1.89377	1.55322	1.53044	1.21668	1.15097
Proportion explained	0.2162	0.1447	0.1146	0.08489	0.06877	0.05503	0.04513	0.04447	0.03536	0.03345
Cumulative proportion	0.2162	0.3609	0.4755	0.56041	0.62917	0.6842	0.72934	0.77381	0.80917	0.84261

Species scores	Species names	PC1	PC2	PC3	PC4	PC5	PC6
Achbrev	<i>Achnanthes brevipes</i>	0.05999	-0.06956	-0.19252	0.06905	0.144804	0.003833
Acthel	<i>Actinoptychus heliopelta</i>	-0.15377	-0.26136	0.98517	0.23011	-0.11192	-0.00059
Aulscul	<i>Auliscus sculptus</i>	-0.09787	-0.10013	-0.14577	-0.13272	-0.11514	-0.07178
Camcly	<i>Campylodiscus clypeus</i>	-0.46104	0.120098	0.85618	0.32861	0.476615	-0.21413
Cocdisc	<i>Cocconeis discrepans</i>	-0.12665	-0.10472	-0.36771	-0.5102	-0.17526	-0.32143
Cocmult	<i>Cocconeis multiperforata</i>	-0.13258	-0.08809	-0.1457	0.05437	0.007752	0.093165
Cocpla	<i>cocconeis placentula</i>	-0.14239	0.290577	-0.09387	-0.02917	-0.07174	0.082331
Coswit	<i>Coscinodiscus wittianus</i>	0.55839	0.975625	0.20538	-0.49389	-0.63241	-0.26937
Cyedis	<i>Cyclotella distinguenda</i>	0.46626	-0.29258	-0.33255	0.73521	-0.16591	-0.03121
Cycmen	<i>Cyclotella meneghiniana</i> <i>Dimeregramma minor</i> var. <i>minor</i>	0.19869	-0.50451	-0.35339	0.47568	-0.3505	0.005919
Dimmin		-0.02839	-0.13821	-0.04762	-0.11913	-0.18062	-0.06144
Dipcra	<i>Diploneis crabro</i>	-0.89337	-0.28405	0.0157	-0.583	-0.05226	0.207732
Dipdid	<i>Diploneis didyma</i>	-0.03933	0.069028	0.07664	0.11322	0.036283	-0.01183
Dipelli	<i>Diploneis elliptica</i>	0.30304	0.075516	-0.0181	-0.13757	-0.00658	0.05799
Dipsmi	<i>Diploneis smithii</i>	0.40768	0.338157	-0.06178	-0.31548	0.689976	0.173533
Gifcoc	<i>Giffenia cocconeiformis</i>	-0.75039	-0.10088	0.53463	-0.11695	0.172513	0.121421
Gramoce	<i>Grammatophora oceanica</i>	-0.93783	-0.12656	-0.75846	-0.15594	0.377535	-0.05795
Gyroacu	<i>Gyrosigma acuminatum</i>	0.10792	0.249688	0.10601	-0.20615	-0.21504	0.360582
Hyarad	<i>Hyalodiscus radiatus</i>	1.23014	-0.93707	0.20428	-0.33656	0.437665	-0.50255
Melmon	<i>Mosira moniliformis</i>	0.44714	-0.92087	-0.07258	-0.37659	-0.1619	0.281909
Melnum	<i>Melosira nummuloides</i>	0.26416	0.79049	-0.1359	0.02162	0.060853	-0.05236
Melvar	<i>Melosira varians</i>	0.07906	0.093341	0.04805	-0.02391	-0.04687	0.001173
Nitcom	<i>Nitzschia compressa</i>	0.94368	0.52096	-0.2689	0.01369	0.503052	0.194646
Nitmarg	<i>Nitzschia marginulata</i>	-0.38161	-0.11424	-0.45378	-0.04726	0.174852	0.033073
Parsul	<i>Paralia sulcata</i>	0.66544	-0.27791	0.31654	-0.11735	-0.12917	0.838088
Petgem	<i>Petrodictyon gemmoides</i>	0.12189	-0.0961	-0.13404	0.32383	-0.15255	-0.08464
Pinmai	<i>Pinnularia maior</i>	-0.11945	-0.00077	0.20884	0.08188	-0.11343	-0.20757
Rhogib	<i>Rhopalodia gibberula</i>	0.06616	0.012144	-0.2146	0.41089	-0.06012	0.009125
Surfas	<i>Surirella fastuosa</i>	-0.43554	0.100108	-0.1306	0.22567	-0.07956	0.230201
Synbac	<i>Synedra bacillaris</i>	-0.18669	-0.08759	-0.23424	0.07514	0.052143	0.101623
Tabfas	<i>Tabularia fasciculata</i>	0.36676	0.294411	-0.13887	0.19708	0.019742	-0.05472
Thalnit	<i>Thalassionema nitzchiodes</i>	0.08211	-0.17919	-0.07002	-0.27252	-0.1984	-0.02512
Thalwei	<i>Thalassiosira weissflogi</i>	0.10298	0.229513	-0.05449	0.16224	0.205001	0.363266

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Site scores (weighted sums of species scores)	PC1	PC2	PC3	PC4	PC5	PC6
22.5	0.08617	-1.25672	1.0225	-0.7634	0.22485	-0.77907
48.5	0.89403	-0.12185	0.6339	-0.60123	0.32324	-0.38222
88.5	1.18926	1.28568	-0.2432	0.5309	-0.54404	0.29705
148.5	-1.29942	0.50791	2.3242	0.57313	-1.8247	-1.6565
188.5	1.30527	-1.02909	-1.4354	3.46782	-1.63361	-0.90643
208.5	1.17548	-0.74379	-0.1369	-1.91057	-0.73336	0.06756
248.5	0.52878	1.15287	0.3653	-0.02032	-1.07533	2.73125
268.5	0.92626	-0.62551	0.1484	-1.75143	-0.16658	0.66175
288.5	0.93949	-1.00192	0.3409	0.5326	-0.33941	0.89949
308.5	0.66777	0.57441	0.2534	-0.7401	0.05092	0.0163
328.5	0.35138	0.40326	0.5579	-0.42338	-0.02665	-0.17108
348.5	1.0568	1.24773	0.6423	-0.31966	-0.62656	0.01568
368.5	1.00394	-2.39209	0.3309	0.50799	-0.23052	1.5891
408.5	0.10252	2.24791	-0.545	0.35757	-0.22844	-0.28638
448.5	0.26323	1.24838	0.2038	-0.62758	1.05397	0.37273
488.5	0.39954	1.17658	-0.3145	0.81846	1.21107	2.11622
508.5	0.73551	-0.87987	0.4911	-0.19219	0.82151	-0.92536
548.5	-1.65756	0.09393	1.9509	1.12981	0.10309	0.17891
588.5	-1.04277	-0.71797	1.7761	0.76921	1.44844	-0.00757
608.5	-1.06682	0.10653	1.4823	0.8872	0.27789	0.2027
648.5	1.05475	0.12035	-0.604	-0.07429	0.85006	-1.37036
688.5	0.12581	-0.36039	-0.2819	-0.87816	1.56587	-1.50044
708.5	1.27504	0.64513	-0.5419	1.42412	1.51217	-1.89057
788.5	0.04992	-0.88689	0.5162	-0.57319	-0.31318	0.53471
808.5	-1.7796	-0.27433	-1.5103	-1.25211	0.35732	-0.28904
848.5	-0.50509	-1.4088	-0.9365	-0.93967	-1.97341	-0.82569
888.5	-0.62198	0.65777	-0.3232	-0.36074	0.8322	0.42154
908.5	-0.65347	1.49908	-1.0299	-0.84405	-2.04676	-0.97505
948.5	-1.93627	0.03448	-0.7115	-0.05952	0.26382	0.1197
968.5	-0.8773	0.07404	-1.7491	0.30394	1.35251	0.07117
1008.5	-1.16102	-1.28067	-1.6489	0.68295	0.7457	1.0126
1108.5	-1.52966	-0.09613	-1.0278	0.34591	-1.23208	0.65731

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