THE PAST AND PRESENT LIMNOLOGY OF THE SOETENDALSVLEI WETLANDS, AGULHAS COAST, SOUTH AFRICA

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The Past and Present limnology of the Soetendalsvlei wetlands, Agulhas coast, South Africa

By

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DECLARATION

I, *Nuette Gordon*, student number *201312751*, hereby declare that the thesis for the degree of *Philosophiae Doctor* (Botany) is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.

Signature: ....

Date: 13 April 2012

Summary

As climatic conditions continue to change globally, there is a need to assess past environmental change in relation to changing water balance, temperature and sea-level. By understanding the extent of past environmental change, and how anthropogenic impacts have affected ecosystems, better and more accurate future predictions of change can be made. Through the use of the sedimentary record within coastal wetlands, geochemical, (organic content and stable isotopes) and biological (diatoms) proxies were utilised to determine; (i) the baseline water quality record for Soetendalsvlei, one of only a few coastal lakes in South Africa, (ii) the effect of agriculture and mouth manipulation of the Heuningnes Estuary on the microalgae ecology and (iii) the link between palaeo-salinity and trophic status on a regional basis between Soetendalsvlei and Groenvlei, situated 320 km apart. Present water quality and phytoplankton biomass and community structure were assessed for Soetendalsvlei and its associated wetlands, Voëlvlei and Waskraalsvlei to determine the current health of these systems and to obtain modern diatom analogues to be used in the palaeolimnological reconstruction of the coastal lake. Diatoms were not dominant during this study period. Chlorophytes and flagellates were the dominant phytoplankton groups throughout the different wetlands. With the exception of Voëlvlei, the wetlands were all in good health, although SRP concentrations were within the eutrophic to hypertrophic range and are cause for concern. In Voëlvlei, phytoplankton biomass was within the eutrophic range with chlorophyll *a* concentrations ranging between 20 – 400 ug.l^{-1} Cyanobacteria, a further indicator of eutrophic conditions, were dominant during the warmer summer periods. Rainfall and freshwater inflow had a significant effect on the biomass and composition of the phytoplankton and acted as a resetting mechanism for all the wetlands as water quality conditions improved thereafter. Comparisons of the water quality and phytoplankton community between the upper reaches of the Heuningnes Estuary and Soetendalsvlei, indicated that artificial breaching of the estuary mouth significantly impacted the connectivity between these two systems, with marine intrusion extending into the upper reaches, while freshwater conditions dominate in the coastal lake. Unfortunately for the palaeolimnological study diatom preservation was poor, however, geochemistry and stable isotope analyses did provide adequate evidence of marine transgression (~8000 yr BP and 4000-2000 yr BP) and regression events comparable to other South African sea-level models developed for the east and west coast. High organic matter content (i.e. higher trophic state) and estuarine POC (C_4 vegetation) were associated with periods of marine regression, i.e. increased freshwater, whereas marine transgression events were associated with low organic content and marine POC and DOC. This is comparable to studies conducted in Uruguay (South America) where palaeo-salinity was related to trophic status, i.e. increased freshwater input was associated with high nutrients. Comparisons of the palaeo-record with recorded historical occurrences of droughts and floods, also provided a means of assessing the sedimentary record and to infer anthropogenic impacts after 1850 AD. Overall it can be concluded that coastal lakes of both continents in the Southern Hemisphere displayed similar trophic responses to sea-level fluctuations during the Holocene. This adds valuable information to global sea-level change models.

Keywords: Palaeolimnology, coastal lake, diatoms, geochemistry, stable-isotopes, sea-level change

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Chapter 1

Introduction

Climate change has been occurring since the formation of the earth and has been driven mainly by geological processes, atmosphere-ocean-biosphere interactions, fluctuations in solar energy and the position of the earth relative to the sun (Oldfield and Alverson, 2002; Gasse *et al.,* 2008). With the advancement of industries and most notably the burning of fossil fuels, global climate change has been accelerated by the increase in the greenhouse effect (Clark *et al.*, undated; Nicholls *et al.*, 1999; Oldfield and Alverson, 2002). Within the terrestrial environments it is predicted that changes in rainfall patterns and increased ambient temperature will be the major causes for concern, while within the coastal and marine environments these climatic changes will be exacerbated by the additional impacts of increase in both sea-level and sea-surface temperatures (IPCC, 2007). Coastal systems across the world are already experiencing the effects of changing climatic conditions. These include increases in storm events, floods and rising sea-level (Nicholls *et al.*, 1999; Day *et al.,* 2008). As most human populations are situated within coastal areas (Nicholls *et al.*, 1999; Oldfield and Alverson, 2002), the impact of changing climate will have significant impacts on these communities. To aid in better management of our natural resources and to mitigate present climate changes, managers require the most current and up-to-date information about coastal systems, and an understanding of how climatic conditions may exert environmental changes. Long-term monitoring data provide such information, however, these are either insufficientt or unavailable in South Africa. Information is generally lacking or fragmentary for our 3000 km coastline. Palaeolimnology has been shown to be a reliable tool for determining baseline conditions for many aquatic systems worldwide (Garcia-Rodriguez *et al.*, 2010; Fisher *et al.*, 2011). The use of physical, chemical and biological markers or proxies, within the sedimentary record, has enabled scientists to infer past system productivity, catchment activities, climate and sea-level change, and anthropogenic impacts (Eastoe *et al.*, 2002; Oldfield and Alverson, 2002; Jinglu *et al.*, 2007; Leavitt *et al.*, 2009; Carr *et al.*, 2010;

Fisher *et al.*, 2011). By understanding the past effects of climate change on coastal environments, it would be possible to anticipate the effects of climate change on coastal systems, and therefore, better policies or mitigation approaches could be implemented.

The South African coastline is characterised by a very narrow continental shelf on the east coast, increasing in width towards the south, with a very wide Agulhas Bank at the most southern tip, narrowing again along the west coast. This changing coastline, together with the two major ocean currents (Agulhas and Benguela), significantly influences the current climate conditions within the different regions. It has been proposed by Baxter and Meadows (1999) and Cowling *et al.* (1999) that these changes existed throughout the Pleistocene and Holocene. The sea-level models for the South African east (Ramsay, 1995; Ramsay and Cooper, 2002) and west coasts (Miller *et al.*, 1995) indicate clear periods of high sea-level (marine transgression) and reduced sea-level (marine regression). Although these models postulate changing conditions along the coastline, they vary to certain degrees, thus highlighting the need for regional comparisons and further research. Soetendalsvlei is one of only a few coastal wetlands in South Africa and its current location at the most southern tip of South Africa, provides a unique opportunity to compare regional sea-level models for the South African coastline. Along this section of the coastline, the continental shelf is also at the widest, forming the Agulhas Bank that has been exposed during past marine regression events according to Tankard and Schweitzer (1974), Dingle and Rodgers (1972) and Tinley (1985). Bateman *et al.* (2004) investigated the palaeo-history of aeolianite deposits at Agulhas and the cordon dunes at Wilderness and showed that both regions along the southern Cape coastline experienced similar intergracial and glacial cycles in the past. However, although both regions experienced similar changes in the distant past, the recent past (i.e. Holocene) is less well understood, especially as their proximity and connectivity to the oceans varies. By investigating the palaeolimnology of Soetendalsvlei and Groenvlei, differences in the sea-level models for the east and west can be highlighted, providing information that can be incorporated into future climate change models.

The general objective of this study was to determine the extent of sea-level influence on the coastal lake Soetendalsvlei during the Holocene and to provide baseline information regarding climate change and anthropogenic impacts.

The specific objectives are listed below:

1. Determine the present water quality and phytoplankton community structure of Soetendalsvlei and associated wetlands, as modern analogues (Chapter 4 & 5),
2. Determine the past diatom community structure, identify Diatom Association Zones (DAZ) with the aid of ordination techniques, and infer palaeo-salinity changes linked with sea-level (Chapter 6),
3. Compare Soetendalsvlei with Groenvlei situated ~350 km away along the southern Cape coast as a regional comparative study (Chapter 7),
4. Investigate, as observed in South American lakes, whether there is an inverse relationship between palaeo-salinity and trophic status for South African lakes, to provide global information on Holocene evolution of coastal lagoons (Chapter 7).

With very limited research conducted within the Agulhas region, basic physical and chemical drivers of present wetland ecology and the effect these have on the phytoplankton community were investigated in Chapter 4 and published in the African Journal of Aquatic Sciences (2011, Issue 36(1), page 19–33). This region is characterised by high agricultural activities and the threat of eutrophication is high (Dallas *et al.,* 2006). A status assessment would not only provide baseline information to the wider research community and managers, but in terms of this thesis will also provide a timeline with specific characteristics used for inferring past conditions and the links between biological indicators and environmental conditions. The focus study area forms an important geographical location being situated at the most southernly tip of the African continent. This region is also falls within the Cape Floristic Region, rich in endemic fynbos species, being threatend by human impacts and changing climate conditions. Another major anthropogenic impact is the artificial breaching of the Heuningnes Estuary mouth during periods of closure and increased water level (related to freshwater inflow). The water quality and phytoplankton community was assessed for the Heuningnes Estuary in Chapter 5, to determine whether the two systems have similar characteristics at present and to provide some understanding of their interconnectivity over a seasonal period which represented different rainfall and therefore inflow conditions.

Chapter 6 investigated the palaeolimnological record for Soetendalsvlei and related the geochemistry (i.e. organic content, TN, TC, C:N ratios), stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and diatom species (i.e. palaeo-salinity) to marine transgression and regression events identified for the east and west coast of South Africa (Miller *et al.,* 1995; Ramsay, 1995; Ramsay and Cooper, 2002). Radiocarbon dating provided the chronological record for assessing these changes, while lead dating provided the timeframe for anthropogenic impacts over the last 150 years. Understanding the different time periods of change within the palaeo-record, will enable us to determine the effect of major anthropogenic impacts on the ecology of Soetendalsvlei, especially the period when argriculture and mouth manipulation started in the Heuningnes Estuary. Comparing the palaeo-record with the present physical-chemical characteristics and phytoplankton ecology will indicate the rate of change, as well as the direction of change, i.e. decrease or increase in diversity and health.

Palaeo-reconstructive research, based on diatoms and pollen, was completed by Martin (1959, 1962; 1968) at Groenvlei Lake which allowed a regional comparison of results (Chapter 7). This comparison will illustrate the overall regional change in coastal lake ecology during marine transgression and regression events, and will aid in the interpretation of sea-level change along the South African coastline. As inverse relationships between palaeo-salinity, as indicated by diatom species composition, and trophic status, as indicated by organic matter content, have been shown in South America (Uruguay), a biogeographical comparison with the South African data set was also included in Chapter 7 to contribute to the climate and sea-level models generated for the Southern Hemisphere.

Chapter 2

Literature Review

2.1 Wetland ecology

Wetlands comprise a number of different habitat types that form the transition zone between terrestrial and aquatic environments. Systems such as swamps, marshes, peatlands, shallow lakes, vleis, pans and floodplains (Ewart-Smith *et al.*, 2005) can all be classified as wetlands based on this one unifying factor, i.e. intermittent habitat between the dry and wet environments (Patten, 1990). According to SCOPE's classification, shallow lakes can be defined as "permanent or intermittent bodies of water, which may be saline, alkaline or fresh, where wind action or turbulent heat transfer (mainly in the tropics) permanently disturb the whole water mass causing high turbidity, unless the lake is highly vegetated" (Gopal *et al.*, 1990). Wetlands do not only fulfil ecological roles within the natural environment, but also provide goods and services utilized by humans (Bowd *et al.*, 2006; Dallas *et al.*, 2006; Jones *et al.*, 2000; Russell, 2009). Some of the uses of wetlands include the supply of water for drinking, irrigation and waste-water treatment (Jones *et al.*, 2000; Brantly *et al.*, 2008), the use of wetland sediment in mining (i.e. peat for fuel), enthobotanical uses of certain species (e.g. *Potamogeton* rhizomes consumed in India), and as building material (e.g. *Phragmites* as roofing, fencing) (Russell, 2009). Wetlands are also important wildlife sanctuaries, fish and invertebrate habitats, allowing for genetic diversity and biodiversity within regions (Löffer, 1990; Jones *et al.*, 2000; Russell, 2009), leading to the proclamation of a number of wetlands, including South African systems, as RAMSAR sites (Dallas *et al.*, 2006).

Each wetland has its own unique characteristics with specific physico-chemical processes and biological components (Jones *et al.*, 2000; Russell, 2009). This section looks at some of these characteristics that drive wetland ecology.

2.1.1 Physical processes

Numerous biological, chemical and physical processes drive wetland functioning and biodiversity (Jones *et al.*, 2000; Russell, 2009). One of the most notable physical processes is **water exchange** within these systems as wetlands are intimately linked to the hydrological cycle. Water exchange is clearly visible in wetlands as a change in water level, thereby regulating the overall available water surface area for primary producers and other wetland inhabitants. The balance between freshwater input through **precipitation** and loss through **evaporation** is generally responsible for changing water level, and can be linked to seasonal variation or climate change (Russell *et al.*, 2006). However, although their overall contribution may be limited, additional inflow (i.e. groundwater, stream and river inflow) and outflow (i.e. groundwater recharge, stream and river outflow) sources are also responsible for changing water levels (Davies and Botch, 1990; Duever, 1990).

Based on hydrological characteristics, wetlands can be defined as endorheic, lacustrine, palustrine and riverine (Jones *et al.*, 2000). Endorheic wetlands are closed basins with inflow, but no outflow; are seasonal or permanent and can vary in salinity and alkalinity. Lacustrine wetlands, such as Soetendalsvlei are large systems (>8ha, >2m depth) situated in depressions and can also be permanent or seasonal water bodies. Palustrine wetlands on the other hand are smaller systems (<8ha, < 2m depth) with emerging vegetation throughout the inundated land area and form at the boundaries of lacustrine or riverine systems (Jones *et al.*, 2000), while riverine systems form as channels associated with areas frequently flooded by river overflow and can be permanent or seasonal.

Not only are the input and outflow of water important drivers, but the **geomorphology** of the wetland itself will greatly affect its characteristics and functioning (Wagner and Zalewski, 2000). Closed systems will generally be more affected by precipitation, evaporation and groundwater recharge, showing less variation in water level compared to open systems greatly affected by the inflow and outflow of freshwater as well as groundwater recharge. The regional characteristics of the catchment area have great effects on the overall water level, with areas of low-gradient **topography** having low runoff into the wetlands and consequently high temporal variability (Duever, 1990). Not only will the overall amount of runoff be lower, but nutrients and material transported will also be less.

In most cases, regional **climate** is very important in maintaining wetland ecological function. Variations in precipitation, evaporation, drought cycles and seasonal variations are important variables in understanding wetland ecology (Davies and Botch, 1990; Russell *et al.*, 2006) and are responsible for the high temporal and spatial differences within and between wetlands (Jones *et al.*, 2000; Russell, 2009). Large changes and fluctuations in temperature and rainfall have substantial impacts on wetland characteristics and functioning (Brantly *et al.*, 2008). Other factors such as nutrient input, nutrient recycling and wind and water circulation further affect the biological components of these systems, thereby affecting their health and ecological role (Russell *et al.*, 2006; Brantly *et al.*, 2008). Consequently each wetland has its own unique microclimate based on its basin morphology, micro-relief and soil conditions (Davies and Botch, 1990).

Another important physical process that affects the overall characteristics and functioning of wetlands is sediment. Sediment transport to and from wetlands and sedimentation within the systems are depended on catchment characteristics, activities, flow rates and basin morphology (Sly, 1978). Bioturbation and sediment resuspension via organisms and/or wind and wave action are also important *in situ* processes that will affect biological components such as phytoplankton, submerged macrophytes and zooplankton and fish communities, in terms of available habitat, nutrient recycling and water column clarity (Wetzel, 1975; Csanady, 1978; Sly, 1978). The overall size and orientation of a wetland will also affect the overall impact that wind and wave action will have on sedimentary processes with significantly less effect in smaller systems than larger ones (Sly, 1978).

The sedimentary records of wetlands and lakes are generally considered as only a depository of catchment activities. However, they are also involved in several important wetland processes such as nutrient recycling, decomposition and pore-water fluids (Jones and Bowser, 1978). Sources of sediment in wetlands can be defined in three broad categories, namely allogenic (i.e. external origin), endogenic (i.e. internal origin) and authigenic. Of importance to the ecological function of wetlands are the interactions and processes between the surface sediment layers and the overlaying water column, i.e. **sediment-water interface**, which are affected by sediment particle size, porosity, pore fluid and bioturbation or resuspension (Blatt *et al.*, 1972; Robbins and Callender, 1975; Jones and Bowser, 1978; Sly, 1978).

The rate at which sediments are deposited is an important factor to consider for ecosystem health assessments and in interpreting any sediment-water interface processes. It will also aid in understanding the kinetics involved in transferring solutes between the sediment and water column. An effective means of measuring **sedimentation rates** is the use of lead-210 (^{210}Pb) dating or caesium – 137 (^{137}Cs) (Pennington *et al.*, 1973). By measuring the accumulation of these isotopes within the sediment layers, it is possible to accurately determine the amount of sediment that was deposited over a specific time interval.

2.1.2. Chemical processes

Nutrient input and **cycling** is vital in wetlands to sustain primary production and transfer of nitrogen, phosphorus and carbon between the biotic and abiotic components. Nutrients enter wetlands via the atmosphere, surface runoff, groundwater discharge, terrestrial litter and, to some extent, excreta from animals (Gopal and Masing, 1990), while being lost from these systems via atmospheric exchange, surface water outflows, groundwater recharge, as biological biomass, i.e. fish and bird biomass, and as respiratory loss, i.e. carbon lost as CO_2 and methane (Svensson, 1980). According to Lee *et al.* (1975), Richardson and Nichols (1985) and Richardson (1990) nutrients generally accumulate within wetlands during the growing season as plant and animal biomass, but are rapidly lost during the non-growing seasons and with the death of vegetation. In a study by Davies and Van Der Valk (1978) it was found that 35 – 75% of plant tissue phosphorus was released into the water column during vegetation death, while much smaller amounts of nitrogen were released. They argued that the lower levels of nitrogen in the water column were due to a large portion of the nitrogen being lost to the atmosphere through the process of denitrification.

There are three main storage compartments for nutrients within wetlands. The largest being the peat and litter that can contribute as much as 55% of the total nitrogen and phosphorus in the system. Unfortunately, most plants and animals cannot use the nitrogen and phosphorus in this form and the recycling of nutrients via microbial pathways is needed. Decomposition, denitrification and nitrogen fixation is facilitated by non-symbiotic, free-living micro-organisms such as cyanobacteria, photosynthetic bacteria and heterotrophic aerobic and anaerobic bacteria (Armentano and Verhoeven, 1990). The second compartment is within the vegetation itself. The amount of nutrients, stored within plants, depends greatly on the density and type of vegetation, and the age of the plants. This results in highly variable quantities of nutrients being stored throughout the year. The third and smallest compartment with the highest variability is the water column, being affected by the initial concentrations of nutrients within the inflow water (Verhoeven, 1986).

Phosphorus is generally considered a limiting nutrient within inland waters, while nitrogen is often limiting within the marine environment. Limiting nutrients in turn determine the maximum standing biomass of a system and Schindler (1977) found that phytoplankton growth was proportional to phosphorus concentrations within the water column. Phosphorus concentrations within the water column, or in dissolved state, are often a small portion, while the majority occurs in solid phase within the sediments, as precipitated with Ca, Al and Fe compounds (Stumm and Baccini, 1978). A dynamic equilibrium exists between the smaller, dissolved phosphorus concentrations and the larger, solid concentrations. However, under aerobic conditions phosphorus is often retained within the sediment. Under anaerobic conditions, on the other hand, phosphorus is released from the sediment into the water column. A sudden increase in phosphorus concentrations may at times seem to cause an apparent limitation in nitrogen or carbon. This is short lived however, as long-term processes such as CO_2 air-water interchange, denitrification and nitrogen fixation occur all the time. The ratio of nitrogen to phosphorus (N:P) within the water column is important to biological systems and primary production. A change in this ratio generally results in a shift in dominant algal species within a community (Janse van Vuuren *et al.*, 2005a,b; 2007). According to Stumm and Baccini (1978) at low N/P ratios, nitrogen-fixing cyanobacteria dominate, while at higher N/P ratios green algae are at an advantage. The N/P ratio also varies for different habitat types, with ocean water having a ratio of 15, where nitrogen is often limiting and phosphorus is precipitated with major cations. Within estuaries the N/P ratio can vary from 2 to 25 as denitrification is a common process within these systems and the input of nutrients from the catchment is highly variable. In inland waters the ratio also varies between 15 and 40 as wetlands and shallow lakes are greatly affected by agricultural return flow through which large amounts of bound nitrogen (fertilizers) are easily washed from the soil and into the watershed (Stumm and Baccini, 1978). Phytoplankton can also have N/P ratios ranging from 10 – 17, as different groups of microalgae have different nutrient uptake rates, based on surface area to volume ratio (Ferragut *et al.*, 2010), and nutrient requirements.

Factors that further affect the nutrient ratios in freshwater are photosynthesis, species composition of the algal community, nitrogen fixation, water column pH or alkalinity and nutrient concentrations from the catchment and that which is produced within the system itself. The residence time or renewal rate of water within the system, and turbulence or wind mixing of the sediment layers, further influence nutrient concentrations and ratios as settled (precipitated) nutrients are resuspended into the water column.

2.1.3. Biological processes (Phytoplankton Community)

According to Margalef (1978), Kruk *et al.* (2009) and Ferragut *et al.* (2010) phytoplankton community structure is a result of both form (size and density) and function (motility and behaviour). Organisms are adapted to different environmental conditions and thus the phytoplankton community will reflect those adaptations in terms of the dominance of a particular group of microalgae (Biggs and Thomsen, 1995; Kruk *et al.*, 2009; Pacheco *et al.*, 2010). Not only will resources (nutrient and light) be important in structuring the community (Jansen van Vuuren *et al.*, 2005a,b; 2007), but also turbulence, mixing and sedimentation (physical habitat variability), and grazing and competition (biological interactions; Biggs and Thomsen, 1995; Ferragut *et al.*, 2010; Pacheco *et al.*, 2010). For this reason not all phytoplankton communities are the same in terms of their structure and dominant microalgal groups. In San Fransico Bay, for example, diatoms contribute over 80% to the phytoplankton community, while dinoflagellates contribute 85% to the community in Patapsco River Estuary (Cloern & Dufford, 2005).

Phytoplankton biomass is greatly affected by nutrient concentrations (trophic status) and light conditions (Fathi and Flower, 2005; Jansen van Vuuren *et al.*, 2007; Ferragut *et al.*, 2010; Pacheco *et al.*, 2010). An increase in nutrients, i.e. eutrophication, can generally be associated with an increase in phytoplankton biomass, often resulting in an increase in water column turbidity that affects submerged macrophyte and the microalgal community itself (Asaeda *et al.,* 2001; Fontanarrosa *et al.*, 2010). Within Swartvlei Lake, South Africa, it was found that an increase in nutrients was responsible for an increase in phytoplankton biomass in early spring that negatively affected the submerged macrophyte community (Asaeda *et al.*, 2001) due to an increase in water column turbidity, i.e. reduce light conditions. It was also found that the longer the water retention time, the higher the phytoplankton biomass was. However, as nutrients become depleted, submerged macrophyte were favoured by the reduction in water column turbidity and increases in biomass. It is thus clear that nutrients have a profound impact on the structure of primary producers of aquatic systems.

Shifts in nutrient concentrations can also be associated with shifts in the phytoplankton primary producers, with rapidly growing, opportunistic species being favoured by increased nutrient levels (Biggs and Thomsen, 1995; Armitage and Fong, 2004; Jansen van Vuuren *et al.*, 2005a, b; 2007; Ferragut *et al.*, 2010; Pacheco *et al.*, 2010). Nutrient uptake rates of different species can greatly influence the phytoplankton community structure. Biggs and

Thomsen (1995) and McCormick (1996) described four groups of microalgae based on their adaptive strategies to exploit different nutrient concentrations and levels of disturbances, namely; competitors (C-strategist), stress-tolerant (S-strategist), disturbance-tolerant (C-S-Strategist) and ruderals (R-strategist). Kruk *et al.* (2009) on the other hand used morphologically based functional groups to classify phytoplankton into 7 groups, i.e. small with high surface to volume ratio; small flagellates with siliceous exoskeletal structures; large filamentous with aerotopes; medium lacking specialised traits; unicellular medium to large flagellates; non-flagellated with siliceous skeletons and large mucilaginous colonies. Each of the groups described by Biggs and Thomsen (1995), McCormick (1996) and Kruk *et al.* (2009) are based on adaptive strategies that include size class, growth forms and adherence forms (Ferragut *et al.*, 2010). Various stages of succession within the phytoplankton community as a whole will also affect the dominant groups present at any one time (Jansen van Vuuren *et al.*, 2007). Biggs and Thomsen (1995) stated that rudenals (R-strategists) are generally pioneer species that are adapted to colonise disturbed sites, where the overall phytoplankton abundance is low and hence little competition exists for resources, while nutrient concentrations are high. Cyanobacteria are generally classified as rudenals due to their relative large size providing grazing resistance and ability to exploit increased nutrient concentrations under low light conditions (Fong *et al.*, 1993; Armitage and Fong, 2004; Jansen van Vuuren *et al.*, 2007; Pacheco *et al.*, 2010). Stress-tolerant groups on the other hand will occur in advanced stages of succession within the phytoplankton community, generally indicative of resource availability (light and nutrient) and disturbance (Biggs and Thomsen, 1995; Ferragut *et al.*, 2010; Pacheco *et al.*, 2010). According to studies by Ferragut *et al.* (2010) true competitors (C-strategists) have the ability to exploit high concentrations of nutrients and are highly competitive in stable, eutrophic conditions. However, as these conditions do not occur for very long periods as resources are depleted or disturbances increase, disturbance-stress-tolerant species (C-S-strategists) will start to increase in abundance as they posses morphological adaptations that prevent their removal from suitable habitat, i.e. pennate diatoms with the ability to attached to substrata or motile flagellates, while their smaller size also ensure that they are better competitors in nutrient poor environments (Fong *et al.*, 1993; Armitage and Fong, 2004, Ferragut *et al.*, 2010; Pecheco *et al.*, 2010)

The ratio of nutrient elements to one another is also important in determining the structure of the phytoplankton community, especially N:Si, N:P, N:P and Si:N:P ratios (Armitage and Fong, 2004; Li *et al.*, 2007; Lopes *et al.*, 2007). The N:P ratio (Redfield ratio; 16:1) provides a measure of whether nitrogen or phosphorus is limiting the productivity of the system. Should nitrogen be the limiting factor, a slight increase in ammonia or total oxidised nitrogen (TOxN) (Horne and Goldman, 1972) will have a profound effect on the productivity and biomass of the community. The same holds for phosphorus limitation. According to Pinckey *et al.* (1998) and Jansen van Vuuren *et al.* (2005a,b; 2007) cyanobacteria are able to fix nitrogen and form blooms when phosphorus concentrations are high thus nitrogen is not always limiting. This is possible due to the fact that cyanobacteria can fix inorganic nitrogen (N_2) as they possess the necessary enzymes (Pickney *et al.*, 1998; Armitage and Fong, 2001).

According to Carrick and Lowe (2007) the ratio of N:P not only affects overall productivity but also the availability of Si, with higher N:P ratios generally associated with lower Si concentrations for diatom production (Jansen van Vuuren *et al.*, 2007). For diatoms the optimum molar ratio of nutrients is 106:16:16:1 for C:Si:N:P, illustrating the high importance of silica for diatom production. As dissolved silica is vital to the production of diatom frustules, a decrease in the availability will result in a reduction in diatom productivity and biomass (Fathi and Flower, 2005). At the same time, the rapid uptake of silica from the water column by diatoms will result in a reduction of silica concentrations and thus lead to a reduction in diatom productivity and biomass (Jansen van Vuuren *et al.*, 2007). According to Fathi and Flower (2005) this generally results in seasonal changes in the phytoplankton community structure with diatoms dominant during spring blooms. According to Li *et al.*, (2007) a high N:Si ratio is associated with eutrophication and an increase in noxious flagellate blooms, with a reduction in diatom biomass. A high P:Si ratio also generally results in a reduction in diatom biomass as silica becomes limiting, and an increase in non-siliceous algae, such as chlorophytes (Li *et al.*, 2007; Lopes *et al.*, 2007).

Phytoplankton communities are also structured via top-down mechanisms, such as grazing and resource competition (Armitage and Fong, 2004). According to Cloern and Dufford (2005) many consumers are selective feeders targeting taxa of a specific cell size or with specific biochemical properties. Organisms such as bivalves are less selective in the food sources as they are primarily ciliary filters that ingest a broad range of different size food particles. It is also believed that the trophic links between benthic filter-feeders and phytoplankton are much more efficient as few or almost no intermediary steps of transformation occur between the primary producers and consumers (Cloern & Dufford, 2005). Certain primary producers may also contain chemical compounds that deter consumers. *Gymnodinium catenatum,* as an example, produces metabolites inhibiting the feeding and growth of copepods (Carlsson *et al.*, 1994; Cloern & Dufford, 2005). Within the marine environment, top-down controls are the main regulatory factors in the phytoplankton community, while nutrients generally regulate microalgal biomass and community structure in freshwater systems.

Not all phytoplankton are simply photosynthesising organisms. Certain groups of microalgae also exhibit heterotrophy such as some flagellates (Sandgren, 1991; Pacheco *et al.*, 2010), dinoflagellates (e.g. *Dinophysis*) and cryptophytes (e.g. *Plagioselmis*). These are termed mixotrophic algae and have the ability to acquire energy from other primary producers allowing them to survive in conditions that would otherwise have been unsuitable, such as low nutrients or strongly light-limited conditions (Cloern & Dufford, 2005).

Various taxa within phytoplankton communities also have different life forms that can include planktonic, vegetative and benthic or suspended resting stages (Dale 2001; Cloern & Dufford, 2005). The different life forms are adaptations to nutrient depletion within the water column and disturbance (Biggs and Thomsen, 1995; Pacheco *et al.*, 2010) and the spores or cysts that generally form can remain dormant for extended periods of time until conditions becomes favourable for germination. Different taxa have different cues and periods of time before germination of the resting cells can occur. Some taxa, such as the dinoflagellate *Alexandrium tamarense* have a prolonged period of dormancy, while *Scrippsiella trochoidea* has a number of shorter periods (Montresor *et al.,* 1998).

2.2 Introduction to palaeolimnology

With changing climatic conditions, it has become vital to determine how much and to what effect human impacts have altered natural environments and their functioning (Oldfield and Alverson, 2002; Milecka *et al.*, 2011). It is important to differentiate between natural climate changes, which have been occurring since geological time, and anthropogenic impacts, most notably increased global warming and desertification. Environmental changes, whether natural or anthropogenic, differ globally and regionally and highlights the need for multiple studies at various temporal and spatial scales (Milecka *et al.*, 2011). However, a lack in long term instrumental records across the world has facilitated the need to develop precision chronologies from palaeo-environmental proxies (Gehrels *et al.*, 2005; Milecka *et al.*, 2011).

Sediments contain a range of physical, chemical and biological records of ecosystem responses to climate change (Eastoe *et al.*, 2002; Jinglu *et al.*, 2007; Leavitt *et al.*, 2009; Car *et al.*, 2010; Fisher *et al.*, 2011). Lake sediments are important palaeo-reconstructive tools as they act as archives of environmental and ecological responses to climate change (Jinglu *et al.*, 2007; Fisher *et al.*, 2011) as well as a means of testing and calibrating methods of palaeoclimatic reconstruction using proxy indicators in sediment records (Oldfield *et al.*, 1997). Through the response to changing water levels and changing water chemistry, lake sediments can provide information on the natural climatic variability of a region or the anthropogenic activities within that area (Milecka *et al.*, 2011). Biological components within the sediment further aid in the reconstruction of such variables through the use of transfer functions as the composition and abundance of species can be associated with certain environmental conditions (Gasse *et al.*, 1995; Battarbee *et al.*, 2000; Austin *et al.*, 2007). In recent times it has become evident that reconstructive research is needed on a regional and global scale in order to more accurately define climate variability and change occurring at present (Mackay *et al.*, 2005; Leavitt *et al.*, 2009; Milecka *et al.*, 2011). Regional information on climate change is not only needed to assess the global impacts of climate change (Milecka *et al.*, 2011), but also to assess the coastal response to changing sea-level (Leorri *et al.*, 2008).

2.2.1 Dating of material

To accurately reconstruct past environmental conditions it is important to determine the timeframe within which any changes have occurred (Labeyrie *et al.*, 2003). Numerous methods have been developed over the years to obtain chronologies for climate and sea-level changes. These include U/Th dating of coral samples and radiocarbon ($^{14}C/^{12}C$) dating of organic matter within the sediment (Labeyrie *et al.*, 2003). The use of radioactive isotopes to determine the age of samples is based either on the decay of radioactive nuclides or the built-up of daughter nuclides to attain equilibrium with its parent (Krishnaswani and Lal, 1978; Walker, 2005). For both these methods however, there are two assumptions made, namely that the flux of radionuclides to the sediment-water interfaces has remained fairly constant over time and that no migration of the nuclide over the period being dated has occurred. Ultimately it is assumed that the only change in the concentrations of nuclides within the sediment record is as result of radioactive decay and by measuring and comparing the concentrations of the ‘fossil’ isotope to modern sample, age can then be determined (Walker, 2005). Radiocarbon, or ^{14}C, is one of the most common radioactive isotopes used in palaeo-reconstructive studies.

Radiocarbon dating

Carbon, one of the most abundant elements on the planet, has three isotopes namely carbon-12 (^{12}C), carbon-13 (^{13}C) and carbon-14 (^{14}C), and occurs mainly as carbon dioxide in the atmosphere. Carbon-14 is produced in the atmosphere by the capture of thermal neutrons with nitrogen and is quickly oxidised to carbon dioxide ($^{14}CO_2$). $^{14}CO_2$ rapidly mixes with $^{12}CO_2$ in the atmosphere and enters the biological and chemical reactions of CO_2, i.e. airocean interchange and photosynthesis (Krishnaswani and Lal, 1978). All living organisms contain carbon-14 in equilibrium with that in the reservoir, i.e. atmosphere or ocean, until death when carbon-14 starts decaying. By measuring the ratio of carbon-12 to carbon-14, one is able to determine the age of a sample as the rate of decay of carbon-14 is well documented. The half-life of carbon-14 is 5730 years and thus this isotope is effective in dating samples of approximately 45 000 years (Walker, 2005). The carbon-14 activity, or concentration in the atmosphere, is taken as the present or modern concentration and corresponds to 0 years BP or 1950 AD. Radioactive decay is calculated using the following equation:

$$T\ (^{14}\text{C-years}) = (1/\lambda)\ \ln \frac{[^{14}\text{C} / {}^{12}\text{C}]_o}{[^{14}\text{C} / {}^{12}\text{C}]_t}$$

Where: λ = decay constant of ^{14}C

o = activity of sample when it formed

t = activity of sample measured at time T

Factors that affect the concentration of ^{14}C in the atmosphere and which have affected the calculation of sample age are:

1) the Bomb effect (de Vries, 1958), which states that the testing and detonation of nuclear bombs prior to 1950 has considerably affected the ^{14}C concentrations in the atmosphere and thus modern concentrations are measured in relation to 1950.
2) Seuss effect (Seuss, 1955), whereby a change in the ^{13}C and ^{14}C ratio of the atmosphere occurs due to the burning of fossil-fuel, thereby releasing large amounts of CO_2 that contain low concentrations of $^{13}CO_2$ and no $^{14}CO_2$.
3) Hard-water effect (Deevey *et al.*, 1954; Olsson, 1979), whereby older groundwater, containing dissolved inorganic carbon with lower ^{14}C concentrations enters lakes, resulting in apparent older radiocarbon dates.

Additional factors need to be considered in terms of dating samples from lakes. These include: the ^{14}C/^{12}C ratio of the inflowing water; CO_2 exchange between the lake water and atmosphere; water residence time within the lake and $^{14}C/^{12}C$ ratios of lake carbonates and organic carbon, which is generally less than that of terrestrial plants formed at the same time, resulting in apparent older ages (Krishnaswani and Lal, 1978).

Radiocarbon dates, however, need to be calibrated or corrected for the changes in the initial concentration of ^{14}C within the sample (Labeyrie *et al.*, 2002). Calibration also provides a calendar date that can be linked to events documented in the historical records and evident in the sedimentary record. Calibration can be done using tree ring measurements of coeval terrestrial vegetation or ‘floating calibrations’ can be obtained from the radiocarbon dating of macrofossils in laminated sediments (Labeyrie *et al.*, 2003).

Carbon Reservoir effect

Due to varying sources (i.e. CO_2, HCO_3) and reservoirs of carbon that are available for utilization by producers, the initial concentrations of ^{14}C differs between terrestrial, estuarine or aquatic environments (Stuiver and Braziunas, 1993). Concentrations of ^{14}C also change with the death of organisms as no active uptake is continued and disequilibrium is established with atmospheric concentrations (Eastoe *et al.*, 2002; Stuiver and Reimer, 1993). This is referred to as the carbon reservoir effect and mainly results in samples being dated at older ages due to depletion in ^{14}C concentrations compared to the atmosphere (Stuiver and Braziunas, 1993; Stuiver and Pearson, 1993; Stuiver and Reimer, 1993). Ocean surface water ^{14}C concentrations are also not the same worldwide with near-shore regions, prone to upwelling events, having lower ^{14}C concentrations and thus apparent older ages (Labeyrie *et al.*, 2003). This reservoir age (R-value) is calculated as the difference between the apparent older sample age and the true age of a coeval terrestrial plant (i.e. tree-ring age; Stuiver and Braziunas, 1993; Labeyrie et al, 2003). Once the R-value is known, the reservoir-corrected age is determined by subtracting the R-value from the laboratory age. The R-value is dependent on space and time. Eastoe *et al.* (2002) used coeval shells and charcoal from archaeological sites to determine the coastal R-value for samples.

Within the Northern Hemisphere the carbon reservoir has been calculated as approximately 400 years to a depth of 80 meters, within coastal areas, based on tree-ring measurements (Vogel *et al.*, 1993). This affects all recent samples in that they appear 400 years older than they really are. For the Southern Hemisphere, the same reservoir age was assumed, however an additional 40 years were included (Stuimer and Pearson, 1993; Vogel *et al.*, 1993). Factors that affect the reservoir effect are: 1) upwelling of deeper, older waters to the surface, 2) continental waters in coastal regions, 3) geometry of the various basins and 4) rocks or fossils that contribute to the non-active ^{14}C carbonates, thus lowering the ^{14}C values.

Organisms within each of these reservoirs will thus reflect the ^{14}C concentration of that particular reservoir (Geyh *et al.*, 1998; Stuiver *et al.*, 1998). However, ^{14}C concentrations within a specific reservoir may vary. According to Mook (1970) the ^{14}C of TDIC in surface water will be closely in equilibrium with the atmosphere, but may become depleted with depth. At the same time, TDIC may be biologically consumed and thus the ^{14}C values may vary further. It is thus important that factors such as water volume, lake surface area, sedimentation, and water column mixing are considered when determining the reservoir effect of a particular reservoir.

Lead dating

Lead – 210 (^{210}Pb) dating is generally used to date more recent samples, as ^{210}Pb has a half-life of only 22.3 years (Hohndorf, 1969). Lead-210 can enter lakes and aquatic habitats directly via precipitation from the atmosphere or through streams and rivers via soil weathering and groundwater discharge (Krishnaswani and Lal, 1978). Lead-210 is produced from the radioactive decay of ^{222}Rn, produced from ^{226}Ra in the earth's crust. As such it can also be formed within the lakes themselves through the radioactive decay of ^{226}Ra. The amount of *in situ* production of lead-210 in lakes depends largely on the concentration of ^{226}Ra in lake water, which is highly variable (Krishnaswani and Lal, 1978). As ^{226}Ra is formed in the crust, its concentration in stream and lake water is dependent on the weathering of bedrock. The nature of this bedrock, together with the chemical constitution of the stream or lake water, ultimately determines the initial concentration of Ra in lake water, thereby affecting the concentration of lead-210. Dissolved lead-210 is easily scavenged onto particles and deposited into the sedimentary layers of lakes. However, the deposition of lead is not always related to the radioactive decay of the parent (^{226}Ra) as there are numerous other inputs of lead-210 into lake water. The excess lead-210 is what sediment geochronology is based upon and can be defined by the following equation:

$$^{210}\mathrm{Pb}_{\mathrm{exc}} = {}^{210}\mathrm{Pb}_{\mathrm{tot}} - {}^{210}\mathrm{Pb}_{\mathrm{supp}}$$

Where: $\mathrm{Pb}_{\mathrm{exc}}$ = excess lead-210 in system
$\mathrm{Pb}_{\mathrm{tot}}$ = total lead-210 in system
$\mathrm{Pb}_{\mathrm{s\,upp}}$ = lead-210 in radioactive secular equilibrium with ^{226}Ra

Two main processes are also involved in modifying lead-210 concentrations within the sediment layers, namely bioturbation and physical disturbance such as wind mixing.

2.3 Type of proxies used for climatic reconstruction

There are a number of different proxies that can be used in the reconstruction of past environmental conditions within a region. These include: geomorphologic and sedimentary evidence such as Aeolian sediments and landforms, alluvial sediments, palaeo-lakes, caves, cave-deposits, periglacial landforms or deposits, relict shorelines, duricrust and palaeosols, as well as the isotopic composition of groundwater. Biological evidence generally includes microfossils, e.g. diatoms, foraminifera and pollen, and charcoal deposits, tree-rings, large mammal and micromammal fossils, marine shells as well as the stable isotope composition of bones. Each of these proxies have their own advantages and disadvantages. Which to use are determined by the objectives of the study, as well as the material available within the specific study area. Only those that are of relevance to this study are mentioned in this section.

2.3.1 Lithology (Sedimentology)

Sediment is constantly transported from sites of erosion to deposition. Riverine and floodplain deposits contain a large amount of information on the catchment through which the rivers and streams flow (Milecka *et al.*, 2011). These deposits are preserved as river terraces or buried channel ways and can provide information about the flow conditions at the time of deposition (Deacon and Lancaster, 1988). Information such as mineral composition, bedding features (varved or laminated), particle size, moisture and organic content can be obtained from sediments and are frequently used to differentiate various sedimentary sequences or lithological units within a single core (Last and Teller, 2002). A dominance of the larger particle sizes of the sediment core indicates periods of higher flow, with smaller particles remaining in the water column to be deposited further down the system where river flow decreases (Last and Teller, 2002). Very fine silt and mud deposits are generally indicative of depositional environments such as estuaries, lagoons and wetlands (Last and Teller, 2002). According to Magny *et al.* (2011) sediments deposited within lakes are generally also carbonate rich and fine, whereas coarser sand, rich in quartz, can be associated with runoff and/or wind-transport. Within the finer, carbonate rich lake sediments, the larger particular are made up of biochemical materials, mollusc and ostracod tests, and plant macro-remains. These have with specific morphotypes (i.e. plate-like, tube-like, oncolites, cauliflower-like forms) that can be used to compare to modern analogues, thereby determining lake water-level (i.e. high or low) (Magny *et al.*, 2011).

Colour of the sedimentary layers can further provide information about the catchment area as well as deposition. According to Magny *et al.* (2011) grey-coloured sediments can be associated with drier littoral areas. Dark mud may in turn indicate anaerobic conditions during deposition. Lighter coarse sediments may indicate more marine, sandy beach conditions. Palaeosols are regarded as very good regional chrono-stratigraphic markers for the identification of periods of stable environmental conditions. A carbonate-rich palaeosol is considered to be a good indicator of semi-arid to arid climatic conditions, while an organic rich layer indicates waterlogged conditions.

2.3.2 Organic Matter

Additional information about climate driven catchment processes can be obtained from the organic matter content from lake and wetland sediments (Schmidt *et al.*, 2004; Leavitt *et al.*, 2009). Both the sources of organic matter input and the productivity of a system can be distinguished (Meyers, 2003). Two main sources of organic matter in lakes and wetlands are firstly the remains of zooplankton, phytoplankton and bacteria, and secondly from the plants within the shallower environments. Organic matter can enter these systems via streams and rivers (allochthonous) or is produced within the system itself (autochthonous) (Hassan, 1997). Some of the most effective means for determining the sources of organic matter within sediment samples are to measure the total organic carbon (Meyers, 2003) and nitrogen content of the sample (Brenner *et al.*, 2006). Generally, terrestrial samples contain higher carbon (cellulose-rich), while aquatic vegetation (algae and bacteria) contains less carbon, but more nitrogen (protein-rich) (Meyers, 2003; Smith and Smith, 2006). As such, terrestrial samples generally have a higher C/N ratio varying between 20 and 80, whereas algae generally have a ratio of between 4 and 10 (Meyers, 2003; Brenner *et al.*, 2006). It is also generally assumed that small wetlands and lakes, with low nutrient concentrations and low inflow rates, are characterised by high C/N, terrestrial sediments, while larger, eutrophic systems are characterised by low C/N, algae dominated sediments (Brenner *et al.*, 2006).

Not only the bulk organic matter within sediment provides information about biological sources or the environmental conditions under which these sources occurred, but also the molecular composition of the organic matter can be useful. Hydrocarbons, esters and ketones, alcohols, sterols and fatty acids can all be analyses and used to infer past and present environmental conditions (Wilkes *et al.*, 1999; Meyers, 2003). Lipids, for instance, can be used as biomarkers that provide additional information to bulk organic matter. Sedimentation rates within wetlands and lakes are one of the most important factors that determine the preservation of lipids within the sedimentary record (Silliman *et al.,* 1996, Wilkes *et al.*, 1999). The ratio of unsaturated to saturated autochthonous fatty acids can also be used to indicate climatic changes (Kawamura and Ishiwatari, 1981), while the proportion of chlorines to total lipids in turn is a useful indicator of primary productivity (Wilkes *et al.,* 1999). Stable isotope signatures within the sedimentary sequence can also record the main contributors to the organic matter. Especially $\delta^{13}C$ and $\delta^{15}N$, and to a lesser extend $\delta\ ^{18}O$, are extensively used in palaeolimnological and palaeoecological reconstruction (Leng *et al.*, 2005; Jinglu *et al.*, 2007).

2.3.3 Stable Isotopes

Various studies have used stable isotopes in order to reconstruct past environmental conditions, as well as to understand the organic matter composition within sediments (Lamb *et al.*, 1999; Müller and Mathesius, 1999; Meyers, 2003; Leng *et al.*, 2005; Ng *et al.,* 2007; Guzzo *et al.,* 2011). The most used stable isotopes are oxygen, nitrogen and carbon. The ratio of these in relation to one another makes them ideally suited for palaeo-reconstructive studies. Based on the isotope composition of biogenic carbonates from sediment samples, it is possible to determine certain hydrological and climatic conditions that prevailed within lakes, as well as vegetative changes regulated in turn by climatic variation (Leng *et al.,* 2005). These conditions can include lake water level, warming and cooling events as well as productivity (Tevesz *et al.*, 1998).

The variations in the ratios of stable isotopes of different elements are due to isotopic fractionation during chemical reactions or physical processes (Pearson and Coplen 1978; Meyers, 2003). In most cases, one stable isotope of a particular element is lighter than another. During gaseous diffusion through a membrane, the lighter isotopes can move easier and more quickly than the heavier ones. In physical processes, such as evaporation or ultrafiltration, the heavier isotopes remain behind, thereby enriching the sample in that isotope. Chemically, heavier isotopes form bonds with lower vibrational frequency than lighter isotope bonds, which result in the heavier isotopes having a stronger bond that is not easily broken (Pearson and Coplen, 1978).

Oxygen

Oxygen has three stable isotopes, namely ^{16}O, ^{17}O and ^{18}O. Of these ^{16}O occurs 99.76% of the time, ^{17}O occurs 0.04% and ^{18}O occurs 0.20% (Pearson and Coplen, 1978). For palaeo-reconstructive studies the ratio of ^{18}O to ^{16}O is used. Within the natural environment the majority of bonds with oxygen are with ^{16}O, with some bonds of ^{18}O. Thus the natural isotopic species for water are both $H_2{}^{16}O$ and $H_2{}^{18}O$. In the case of water which occurs in various phases, i.e. solid (ice), liquid or vapour, the phase in which it is will be reflected in the isotopic ratio. The weaker bonds in $H_2{}^{16}O$ will result in easier and quicker conversion of liquid water into vapour. The remaining liquid water, however, will in turn be enriched with the heavier, stronger bonded $H_2{}^{18}O$. The isotopic ratio of oxygen can thus be used as an indicator of temperature, as temperature directly affects water phases (Leng *et al.*, 2005). According to Leng *et al.* (2005) $\delta\,^{18}O$ can also be used to reconstruct hydrological cycles and changes in precipitation. Dansgaard (1964) indeed showed that ^{18}O will increase by 0.7 ‰for every 1°C increase in mean temperature.

Calcium-carbonate ($CaCO_3$) acidification or precipitation can be linked and used for oxygen stable isotope studies, mainly because ^{16}O is used in the bonds. During precipitation from water, the weak ^{16}O bond in the carbonates is broken and replaced with the heavier ^{18}O. The calcium-carbonate thus becomes enriched in ^{18}O, while the water becomes depleted in ^{18}O and enriched in ^{16}O. According to Dansgaard (1964) water becomes depleted in ^{18}O at a rate of 0.24 $^{o}/_{oo}$ per 1°C temperature increase. The amount of change between isotopic ratios is thus dependent on temperature (Pearson and Coplen, 1978).

$$\tfrac{1}{3}\,CaC^{16}O_3 + H_2{}^{18}O \rightleftarrows \tfrac{1}{3}\,CaC^{18}O_3 + H_2{}^{16}O$$

Dansgaard (1964), Stuiver (1968) and Hendy and Wilson (1968) further showed that, based on the concentration of ^{18}O in a sample, temperature ranges can be determined, using the following equation:

$$\Delta^{18}O = {}^{18}O_{oc} + 0.70\Delta\,(t-t_{oc}) - 0.24\Delta\,t$$

However, for more recent samples, younger than 9000 years, the equation can be simplified to; $\Delta^{18}O = 0.46\Delta t$.

Nitrogen

Nitrogen stable isotopes are used to provide a measure of protein and can be used to indicate the trophic position of an organism, as enrichment in ^{15}N occurs higher up the food web (Guzzo *et al.*, 2011). Bulk organic matter can thus be identified as being dominated by producers, primary and secondary consumers and ultimately decomposers (i.e. bacteria). Nitrogen has two naturally occurring stable isotopes, namely ^{14}N and ^{15}N, occurring in a ratio of 272 ± 0.3 (Junk and Sven, 1958). Atmospheric nitrogen has a stable ratio of ^{15}N / ^{14}N and is also used as the standard in any nitrogen isotope study. Based on this stable ratio, $\delta^{15}N$ has a value of 0 ‰ for the atmosphere. Through the process of nitrification, atmospheric N_2 is available for utilization by terrestrial plants and thus the $\delta^{15}N$ values will by low. Within the aquatic environment, however, nitrogen is available for algae production in the form of dissolved NO_3^-, with a $\delta 1^5N$ value of 7 to 10 ‰ (Meyers, 2003), resulting in algae having a $\delta 1^5N$ value of ~8.5 ‰ (Meyers, 2003). The isotopic composition of any biological material is largely dependent on biological processes (i.e. cyanobacteria nitrification) and transformation of nitrogen, as well as catchment processes (i.e. agriculture) (Meyers, 2003). During nitrogen fixation, the lighter ^{14}N isotope is more readily taken up and utilized than the heavier ^{15}N. During denitrification by micro-organisms it is again the lighter ^{14}N that is preferred over the heavier ^{15}N, thereby enriching the sample in ^{15}N (Hassan, 1997). Due the various processes and intermediate products that occur within the nitrogen cycle it is very difficult to accurately determine the source of organic material within sedimentary layers based on ^{15}N / ^{14}N ratios. For this reason the combination of nitrogen isotopes and carbon isotopes are used.

Carbon

According to Meyers (2003) and Leng *et al.* (2005), the isotopic composition (carbon and nitrogen) of bulk organic material varies according to the different sources present within a specific environment. Carbon isotopes are generally used to differentiate between these sources as most living organisms consist of carbon. Plants mainly depend on atmospheric CO_2 as their source of carbon, while consumers rely on the carbon from their food sources. Aquatic plants also depend greatly on dissolved CO_2 as their carbon source. However, they will use bicarbonate (HCO_3^-) when dissolved CO_2 is depleted (Degens *et al.*, 1968; Falkowski 1991).

Carbon has three isotopes, namely ^{12}C (98.89 %), ^{13}C (1.11%) and the radioactive ^{14}C isotope. Atmospheric CO_2 has a ^{13}C isotopic value of approximately -7/-8 ‰ (Keeling *et al.,* 1995). Terrestrial plants, through CO_2 fixation, mainly fix ^{12}C via diffusion. As such, these plants will have a depleted concentration of ^{13}C within their tissue, compared to the atmosphere (Keeling *et al.*, 1995, Hassan, 1997). According to Pearson and Coplen (1978), Deines (1980), Hassan (1997) and Wilson *et al.* (2005a, b) C_3 plants generally have a ^{13}C value of -32 to -21 ‰, with C_4 plants having values ranging from -17 to -9 ‰. CAM plants, on the other hand, have a ^{13}C value ranging within the C_3 and C_4 values as these plants rely on both methods of carbon fixation during photosynthesis (Schleser, 1995).

Within aquatic environments carbon is mainly available as bicarbonate (HCO_3^-) and dissolved CO_2 (inorganic carbon), resulting in aquatic organisms having an isotopic value close to that of the source (Meyers, 2003; Wilson *et al.*, 2005a, b). According to Tevesz *et al.* (1998) the greater the CO_2 exchange, the lower the ^{13}C value for the total dissolved inorganic carbon (TDIC). Phytoplankton forms the primary carbon source within aquatic systems and mainly rely on dissolved CO_2, resulting in a ^{13}C value close to that of the atmosphere (Lamb *et al.*, 2006; Meyers, 2003), depending on the exchange rate between the water surface and the atmosphere.

It is important, however, to remember the role pH plays in the availability of dissolved CO_2 and bicarbonate in the water. More acidic waters (i.e. lower pH) generally have higher dissolved CO_2 concentrations than alkaline water, which has higher bicarbonate concentrations (Hutchinson, 1957). According to

Hassan (1997) in alkaline waters with a pH higher than 8.3, as much as 99% of the dissolved inorganic carbon is in the form of HCO_3^-.

Within marine environments less CO_2 is available and HCO_3^- is the main source of carbon. This results in higher ^{13}C values for marine algae ranging from -16 to -23 ‰ (Lamb *et al.*, 2006). Freshwater algae, however, are influenced by catchment activities and the primary producers within those environments. According to Schidlowski *et al.* (1983) and Chivas *et al.* (2001), freshwater algae within C_3 dominated environments, will have lower ^{13}C values, ranging between -26 to -30 ‰, while within C_4 dominated environments their ^{13}C values will be higher (i.e. < -16 ‰).

Within aquatic environments it is important to remember that not all carbon is autochthonous in source, but that many allochthonous sources also enter the system (Wilson *et al.*, 2005; Lamb *et al.*, 2006). This is predominantly true for particulate organic matter / carbon (POC) and dissolved organic matter/ carbon (DOC). Particulate organic matter consists of a variety of substances that include phytoplankton, zooplankton, terrestrial organic matter (i.e. debris) and anthropogenic sources (i.e. sewage) (Lamb *et al.*, 2006). According to Salomans and Mock (1981), Middelburg and Nieuwenhuizen (1998), Meyers (2003) and Wilson *et al.* (2005) freshwater phytoplankton and particulate terrestrial organics make up fluvial POC and have very similar ^{13}C values (i.e. -25 to -30 ‰). Again the dominant vegetation type within the catchment will affect the ^{13}C value of the sample, with C_3 vegetation in the catchment having lower ^{13}C values than C_4 vegetated catchments. According to Wilson *et al.* (2005) C_4 vegetation are characteristic of salt marsh areas within the coastal region and the ratio of C_3 to C_4 vegetation can be used as an indicator of sea-level fluctuation. Marine POC on the other hand, consists almost entirely of marine phytoplankton with very little organic matter input from terrestrial or anthropogenic sources, resulting in ^{13}C values ranging from -18 to -21 ‰ (Peters *et al.*, 1978; Middelburg and Nieuwenhuizen, 1998). Dissolved organic carbon (DOC) forms approximately 60% of the carbon within estuaries and rivers, and almost all of the carbon within the marine environment, except for the faction that consists of POC (Hedges *et al.*, 1997; Raymond and Bauer, 2001). Within freshwater environments DOC is mainly derived from phytoplankton and terrestrial organic matter and thus will have ^{13}C values reflecting these sources (i.e. -26 to -28 ‰). Within the marine environment, DOC is mainly derived from phytoplankton and thus has ^{13}C values between -22 and -25 ‰ (Peterson *et al.*, 1994). Although the ^{13}C values of DOC should reflect those of POC, bacteria decomposition is responsible for lower values. Bacteria are generally responsible for lowering the ^{13}C values within sediment and thus will lower the ^{13}C values of DOC accordingly (Cloern *et al.*, 2002).

According to Lamb *et al.* (2006) the use of stable isotopes to determine carbon sources within lagoons is beneficial as autochthonous organic matter makes up the bulk of the sedimentary organic carbon within these systems and narrows the potential sources of carbon. Under eutrophic conditions however, when phytoplankton is the primary carbon source, it is not so easy to determine the carbon source based on stable isotopes. This is because phytoplankton relies both on dissolved CO_2 as well as bicarbonate as its source of carbon, resulting in a variety of ^{13}C values. Instances where a broad overlap exists in the ^{13}C isotopic composition between the sources of bulk organic, the use of C/N ratios in conjunction with ^{13}C values is recommended (Leng *et al.*, 2005; Lamb *et al.*, 2006).

Carbon isotopes are not only used to determine past environmental conditions, but can also be used to determine present photosynthesis, respiration and decay of primary producers (Stuiver 1968, 1970; Ng *et al.*, 2007), and can be applied to both primary producers and primary consumers (Ng *et al.*, 2007). The ^{13}C values of molluscs, for example, are also affected by their food source, i.e. algae, and will have values not in equilibrium with their surrounding environment, but rather with their food source.

Carbon/Nitrogen Ratio

The organic carbon to nitrogen ratio has been extensively used to differentiate between marine and terrestrial sources of organic matter in sediment samples across the world (Thornton and McManus, 1994; Müller and Mathesius, 1999; Leng *et al.*, 2005; Lamb *et al.*, 2006). According to Fontugne and Jouanneau

(1987) and Müller and Mathesius (1999) sediment samples rich in nitrogen and ^{13}C isotopes have organic matter originating in the marine environment. While stable isotope concentrations indicate whether a sample is of marine or terrestrial origin, the carbon to nitrogen ratio provides a measure of the protein content of the sample. Generally, samples with higher protein content originate from animal or bacteria matter, while samples lower in protein originate from plants and algae (Müller, 1975). Carbon to nitrogen ratios can thus be used to differentiate between aquatic and terrestrial sources of organic matter as well as between plant, algae and animal sources. Müller (1975) states that animals have a higher protein content than plants, while marine algae have a higher protein content than higher plants (generally containing less than 20% protein). Thus the ratio of carbon to nitrogen will be lower in samples containing animal matter than in marine algae, which in turn will be lower than higher plants. Bordoviskiy (1965) found that planktonic organisms had a C/N ratio of 4 – 7, while Redfield *et al.* (1963) found that zooplankton and phytoplankton have ratios of 5 - 6. Bordovskiy (1965) also found that benthic organisms and bacteria, on the other hand, had lower C/N ratios, varying between 4.1 and 4.2 due to their higher protein and subsequent nitrogen content, while Abbott *et al.* (2000) found ratios of between 6 and 13 indicative of modern submerged aquatic vegetation. Due to the varying amounts of protein (1-10%) in the different species of higher plants, the ratio of C/N can vary between 20 and 200 (Hedges *et al.,* 1986; Nakai, 1986; Müller and Mathesius, 1999, and Abbott *et al.*, 2000). Therefore, stable carbon isotopes are used in conjunction with C/N ratios to identify the various sources of organic matter in sediment samples (Schimmelmann and Tegner, 1991; Müller and Mathesius, 1999).

Decomposition of bulk sediment organic carbon needs to be considered in the interpretation of results obtained from stable isotope analyses (Lehnmann *et al.* 2002). Melillo *et al.* (1989), White and Howes (1994), Lehnmann *et al.* (2002), Wang *et al.* (2003) and Wilson *et al.* (2005a, b) showed that the C/N ratio varies greatly during the different processes of decomposition. According to Melillo *et al.* (1989) and White and Howes (1994) decomposition can be divided into three processes, namely 1) leaching of soluble compounds, 2) microbial activity and 3) a refractory phase. During the leaching phase, nitrogen is more readily lost and there is an increase in the C/N ratio of the bulk organic matter. During microbial activity, on the other hand, nitrogen fixation is responsible for an increase in total nitrogen (Lehnmann *et al.*, 2002) and thus a decrease in the C/N ratio. During the refractory phase, substances such as lignin remain in the sediment and are slowly decomposed. During this phase the C/N ratio stabilises as carbon and nitrogen are being lost at a similar rate.

2.3.4 Microfossils

Pollen

Fossil pollen analyses, which falls under the broad decipline of palynology, of sediments are used worldwide to reconstruct past vegetation changes that are linked to climate change (i.e. precipitation and temperature) (Scott, 1999; Fontana, 2005; Zhao *et al.* 2006) as well as sea-level changes. Pollen generally preserves well within the sediment for thousands of years, with samples within the last 40,000 years being used to accurately reconstruct past environmental conditions (Coetzee, 1967; Martin, 1968; Deacon and Lancaster, 1988). Based on the botanical families within which pollen taxa fall, vegetation types can be inferred and from these climatic conditions, especially moisture and temperature, can be deduced. Poaceae for example are indicative of savanna or grassland vegetation and are associated with high summer rainfall (Scott, 1999), whereas Cyperaceae are characteristic of semi-aquatic habitats and indicate swamp, shallow lake or damp soil conditions, indicating wetter periods (Scott, 1999). Proteaceae and Ericaceae, both found within the Fynbos Biome of South Africa, are again used to reconstruct patterns of vegetation change linked to precipitation in arid and semi-arid regions of South Africa (Meadows *et al.*, 1995, 1999; Scott, 1999; Quick *et al.*, 2011). Mangrove (*Bruguiera* and *Rhizophora*) pollen has also been used in Australia (Woodroff *et al.*, 1985), Southeast Asia (Woodroff, 2000) and New Guinea (Ellison *et al.*, 2005) to indicate changes in sea-level.

Acid-waterlogged habitats such as peat bogs, vleis or wetlands are good environments for the preservation of pollen grains (Coetzee, 1967; Martin

1968; Deacon and Lancaster, 1988), as the sediments are relatively moist, preventing mechanical destruction (i.e. abrasion, oxidation or bacterial decomposition) of the pollen grains. Alkaline sediments, however, are very poor habitats for pollen preservation and most pollen is generally destroyed under these conditions.

According to Scott (1982) and Deacon and Lancaster (1988) different types of pollen will also be represented in different fractions within the sedimentary assemblage based on dispersal mechanism (wind, water or insect) and seasonal production (i.e. number of pollen grains produced). This can lead to inaccurate reconstruction of the palaeo-environment, with for example light, wind dispersed pollen being over-represented and insect pollinated species under-represented in the sample. It is thus important to study the modern pollen composition adjacent to any study area before any palaeo-interpretations are made (Scott 1982; Deacon and Lancaster, 1988).

Diatoms

Diatom species are very useful in palaeo-reconstructive studies as they occur in relatively diverse assemblages (Ryves *et al.*, 2009; Bere and Tundisi, 2011; Berthon *et al.*, 2011), with species being easily distinguished from one another by their unique morphological features (Stevenson and Pan, 1999). Diatoms form an abundant and diverse component of the microalgal community within aquatic systems, comprising a large portion of the total biomass of these communities (Kreis *et al.*, 1985, Hall and Smol, 1999; Ryves *et al.*, 2009; Bere and Tundisi, 2011). They have very short generation times and thus reproduce and respond rapidly to any changes in environmental conditions (Vinebrooke, 1996; Laing and Smol, 2003) in terms of both species composition and biomass (i.e. relative abundance) (Bere and Tundisi, 2011). They are found in almost all types of habitats (streams, lakes, wetlands and ephemeral aquatic habitats) which include freshwater, brackish and marine (Ryves *et al.*, 2009), and form the basis of the food web in most of these systems (Round, 1990; Lamberti, 1996; Stevenson and Pan, 1999). Diatom species and especially community structure have a narrow ecological preference, making them sensitive to environmental change and thus particularly suitable for inferring present and past environmental conditions (Tilman *et al.*, 1982; Hall and Smol, 1999; Mackay *et al.*, 2005; Saunders, 2010; Berthon *et al.*, 2011).

There are numerous methods of using diatoms as environmental indicators that include the use of the autecology of species and inference models as well as diversity indices. The first is through the understanding of the autecology of specific species, whereby it is possible to infer environmental conditions (Kolkwitz and Marsson, 1908, Stevenson and Pan, 1999). Within palaeolimnoloy the use of diatom-inference models (i.e. transfer functions) are extensive, whereby the species-environmental relationship that exists in modern analogues are used to infer past environmental conditions based on sub-fossil diatom assemblages (Reid, 2005; Saunders, 2010). Another method relies on the diversity of the assemblage and is generally used in monitoring of system health (Patrick and Strawbridge, 1963). Where species composition varies seasonally, species diversity is more stable and thus more indicative of a system’s health (Stevenson and Pan, 1999).

Diatoms can indicate a number of different environmental conditions (Saunders, 2010; Berthon *et al.*, 2011). Based on the life form of the diatoms present within a sample, i.e. benthic, epiphytic or planktonic, it is possible to infer water level changes that have occurred within a system (Wolin and Duthie, 1999; Laird *et al.*, 2010). Physical changes such as the stability of the water column, turbidity, salinity (Austin *et al.*, 2007; Garcia-Rodriguez *et al.*, 2010; Saunders, 2010) and thermal conditions (Laing and Smol, 2003) can also be inferred from diatoms, together with pH (i.e. acidification) and nutrient changes (i.e. eutrophication) (Garcia-Rodriguez *et al.*, 2002, 2004a, b; 2007; Reid, 2005). These are generally inferred from diatom indices, based on the species-specific responses to environmental conditions (Wolin and Duthie, 1999; Reid, 2005). Diatom species composition and their relationship to salinity have also been shown to indicate various levels of trophic status (i.e. oligo-, meso- and eutrophic) within coastal environments (Garcia-Rodriguez *et al.*, 2002, 2004a, b; 2007). The dominance of particular species, such as *Aulocoseira,* can also be used to indicate turbulent conditions, upwelling or wind-mixing of the water column. This is a heavy diatom which is dominant during turbulent conditions with high nutrient levels (Wolin and Duthie, 1999).

In order to accurately make these inferences, it is important to understand several aspects of diatom ecology, which includes the breakage and dissolution of diatom frustules during deposition (Ryves *et al.*, 2001, 2009). Should the frustules be partly dissolved, identification of the species may be compromised, while the complete dissolution may result in the entire removal of that species or assemblage from the sediment record (Flower, 1993; Battarbee *et al.*, 1999; 2004; Fritz *et al.*, 1999; Ryves *et al.*, 2001). According to Ryves *et al.* (2001, 2009) dissolution of biogenic silica (i.e. diatom frustules) is especially poor, but not limited to saline environments. Other factors also impacting the dissolution of biogenic silica include pH, temperature, ionic concentrations, surface area (i.e. frustules size) available for reactive processes and organic matter content within the sediment (Ryves *et al.*, 2001).

The deposition of diatoms is also important as certain species will remain longer in suspension before settling to the bottom than others (Mackay *et al.*, 2005). These are important factors to consider in order to accurately infer past conditions and to predict future changes.

Other problems associated with the use of diatoms in reconstructive research are:

1. The preservation and taphomony of the assemblages, i.e. mixing and transport of assemblages before deposition, whether the samples are spatially heterogeneous and how many of the species in the assemblage have been re-suspended from the sediments (Anderson, 1990; Anderson and Battarbee, 1994). These factors are important for the assumption that the assemblages in the deep sediments are true reflections of the composition of the living communities within the lake during deposition (Cameron, 1995; Battarbee *et al.*, 1999).
2. Salinity reconstruction. Although diatom assemblages may be found within samples, they may not be of that time interval and the inference

made on the presence of those species may thus be incorrect (Fritz *et al.*, 1999). Many of the taxa used in the reconstruction of salinity, generally have wide tolerance ranges to varying salinity and thus it is difficult to accurately infer specific salinity values based on such species. The number of specific species occurring at the high end of the salinity gradient is also small, resulting in low diversity and difficulty in reconstruction of past salinity conditions (Fritz *et al.*, 1999).

3. Climate reconstruction. Not all factors and variables are linearly related to lake level or the balance between precipitation and evaporation (*P* – *E*). Lakes can vary greatly in their response and sensitivity to changes in the hydrological balance. Ground water inflow, for example, may result in less variation in the water level of a lake, despite a large change in the *P* - *E* balance. Another example is lake salinity that may not always be a function of climate change, but a result of water flow through salt pans into the lake (Radle *et al.*, 1989, Fritz *et al.*, 1999).

Other

There are numerous other biological components within sediment that can be dated and used in palaeo-reconstructive work. **Charcoal** size and abundance can indicate terrestrial environments dominated by woody plants and subsequently vegetation changes linked to climate change (Figueiral and Mosbrugger, 2000), as well as the presence of human populations within the area (Edwards and Whittington, 2000). Scholtz (1986) showed that analyses of the anatomy of the charcoal fragments can be used to infer palaeo changes in the climate in terms of both rainfall and relative temperature. Charcoal also provides information on the occurrence of past fires (Carciallet *et al.*, 2001) and the effects of these on ecosystems (Edwards and Whittington, 2000; Tinner and Hu, 2003). **Dendrochronology** (tree-ring counting) is another method of establishing age as well as changes within the climate of a region (Deacon and Lancaster, 1988). Dendro-climatology provides information about the seasonal, annual and any unusual patterns in the growth of terrestrial vegetation that can be linked to rainfall and temperature variability.

Large **mammal** and **micro-faunal fossils** are also used to determine the past environmental conditions of an area. These fossils provide a means of dating the deposit through radiocarbon dating of the bone itself, as well as for relative dating taking the presence or absence of extinct genera and species as the apparent age of the sample (Deacon and Lancaster, 1988). Based on the relative abundance of various species within the sample, palaeo-environmental inferences can be made based on the modern habitat preferences of such species. The relationship between grazing and browsing animal remains also provides information about the vegetation at the time of deposition, with the dominance of grazers indicative of grassland or savanna-type vegetation associated with cooler periods and browsers indicative of warmer periods where shrubs dominated the vegetation (Klein 1983; Deacon and Lancaster, 1988). Whereas large mammal remains provide information about large scale vegetation changes, micro-faunal remains (i.e. small rodents, bats, lizards, snakes, frogs) provide information on more sensitive habitat specific changes. Often changes in the species composition of these samples occur before changes in the large mammal fossils are recorded (Avery, 1982; Deacon and Lancaster, 1988). Brain (1974) and Avery (1982) showed that, based on micro-mammal bones in owl pellet remains, it was possible to reconstruct past changes in temperature and rainfall.

Marine shells provide information about past environmental conditions, such as sea surface temperature and types of shorelines (i.e. rocky or sandy beaches). The isotopic composition of the shells provides means for establishing the temperature regimes present during deposition, i.e. oxygen isotopes (Leng *et al.*, 2005). However, only relatively recent shell deposits (> 125,000 years) are of use as older samples have been covered by sea water since the last glaciation period (Deacon and Lancaster, 1988). Shell middens are reminders of past human occupation within specific regions, which should also be considered in the interpretation of the data and during the inference of past climate and sea-level conditions.

2.4 Methods of reconstruction using diatoms

In order to reconstruct palaeo-environmental conditions based on past diatom assemblages, it is important to understand some aspects of present diatom ecology and distribution.

Generally, most diatom species are cosmopolitan, occurring throughout the world within various habitats. They can, however, be separated mainly on their affinity to specific salinity regimes (Garcia-Rodriguez *et al.*, 2002, 2004a, b; 2007; Ryves *et al.*, 2009). According to Williams (1981) and Fritz *et al.* (1999) diatoms species separate into freshwater and saline species along the 3 $g.l^{-1}$ concentration. Brackish species in turn can be separated on their affinity to more fresh (i.e. freshwater-brack) or more saline (i.e. brackish-marine) water. In addition to salinity, habitat type also separates diatom species, with different life forms occurring in different habitats, i.e. pennate forms occur mainly as benthic and epiphytic diatoms, while centric diatoms occur as phytoplankton within the water column (Ferragut *et al.*, 2010; Pacheco *et al.*, 2010). Understanding the relationship between diatom species or assemblages and responses to environmental factors allows for quantitative reconstruction of palaeo-environmental conditions (Leavitt *et al.*, 2009; Fisher *et al.*, 2011). Three of the methods most used are: 1) simple regression models, 2) ordination analyses and 3) weighted-averaging of the data (Wolin and Duthie, 1999).

2.4.1 Regression

Regression models generally focus on the linear relationship between present water-level and quality and present diatom assemblages. These models also focus on the life form ratios of the diatoms, i.e. plankton: littoral ratio (P/L) as an indicator of water level with higher phytoplankton abundance associated with increased water levels (Gasse *et al.*, 1989; 2008; Wolin and Duthie, 1999). Regression models are also generally well suited when considering Scheffer's concept (1998) of two alternative states for shallow lakes. The one state represents clear water conditions where transparency is high, resulting in benthic microalgal and macrophyte dominance. The second state represents turbid conditions and reduced transparency, which limits benthic production, favouring phytoplankton biomass production. Regression models indicate water level and clarity change and also changes in trophic states. Under oligotrophic conditions, the water column is generally clear and benthic diatoms occur in high numbers. Under eutrophic conditions however, phytoplankton species increase until blooms form, thereby reducing the photic zone within the water column and limiting benthic productivity and numbers (Irvine *et al.*, 1989).

2.4.2 Ordination analyses

Regression models rely on a linear relationship between specific environmental variables and diatom species, while ordination analyses relies on the relationship of diatoms species with a range of environmental variables. This allows groups of diatom species with similar tolerance ranges, and responses to fluctuating water quality, to be grouped together as indictors of environmental change. An advantage of using ordination analyses over regression is the redundancy of the data, thereby strengthening the inference made of environmental conditions based on the species present within a sample. Ordination analyses such as Canonical Correspondence Analyses (CCA) also enable any inference made between diatom species and environmental variable, e.g. conductivity, to be strengthened by a ‘goodness of fit’ measure (Austin *et al.*, 2007) thereby validating the observed effect of changing environmental conditions on the diatom species composition. CCA also identifies the minimum set of environmental variable that effect the diatom species composition (Denys, 2006), while Detrended Correspondence Analyses (DCA) can indicate whether the species distribution should be analysed along a linear or unimodal gradient (Denys, 2006).

2.4.3 Weighted-averaging

Based on the present occurrences of diatom species at specific environmental conditions, weighted-averaging determines the optima conditions under which each species would occur, as the frequency that each species occurs within present samples along the variable gradient (Stevenson *et al.*, 1989; Stevenson and Pan, 1999; Wolin and Duthie, 1999). Weighted-averaging is based on the unimodal relationships between species occurrence and environmental variables and not on a linear regression. It assumes that at a given environmental value, taxa that have an optimum closest to that value will be the most abundant species in the assemblage. It generally considers the occurrence of taxa in various lakes, called ‘the training set’, spanning a gradient in environmental variables, such as low to high salinity. The first step in the process determines the optimum environmental value at which taxa occur, based on the average of all the variable values in the training set (i.e. lakes) in which a specific taxon occurred, weighted by each taxon’s relative abundance. (Equation 1). This is termed the regression step.

$$U_k = \Sigma Y_{ik} X_i / \Sigma Y_{ik} \qquad \text{Equation 1}$$

Where: U_k = variable optimum for species k
Y_{ik} = abundance of species k at site i
X_i = value of variable at site i

The data obtained by this step are generally used to develop a diatom index. Currently there are three main diatom indices used for ecosystem health assessments and palaeo-reconstructive studies. The first is the British Columbian collection that is comprised of data collected in 219 lakes (Wilson *et al.*, 1996). The second is the northern Great Plains dataset, comprising data from over 100 lakes (Fritz *et al.*, 1991, 1993) and the third is the African collection, comprising 164 lakes and 282 diatom samples (Gasse *et al.*, 1995). There is also the European Diatom Database Initiative (EDDI), which incorporates samples from Europe, Africa and Asia (Battarbee *et al.*, 2000, 2005).

Once a diatom index or inference model has been developed, it is used in what is called ‘the calibration step’. During calibration, computed optima of the various taxa are used to infer environmental conditions that would be dominant within the system. Once again the assumption that diatom species with high relative abundance will have optima close to the values measured in the field is used. In order to determine the tolerance range of a species, the standard deviation of the weighted average is used.

To calculate the difference in the inferred and measured values of variables per species or taxon, the Root Mean Squared Error (RMSE) is used (Equation 2).

$$\mathrm{RMSE} = \{ [\Sigma (MD_i - ID_i)^2] / n - 1\}^{½} \qquad \text{Equation 2}$$

Where: MD_i = measured variable value for sample i
ID_i = inferred variable value for sample i

If the RMSE is low, there is little difference in the inferred and measured values of the environmental variables. Such diatom species are good indicators of environmental conditions and their presence within an assemblage ensures accurate reconstruction of past conditions. Two disadvantages of weighted-averaging, however, are that higher values are generally underestimated, while lower values are overestimated. Nevertheless, this method provides a high correlation between inferred and measured values with high r^2 values (i.e. $r^2 > 0.9$) (Wolin and Duthie, 1999).

To strengthen the calibration set, jack-knifing or bootstrapping can also be used to ‘re-sample’ the data entered into the computer. Bootstrapping is generally preferred as it allows for up to a 1000 cycles to be completed, thereby increasing the accuracy of the index (Fritz *et al.*, 1999).

2.5 Climate change and sea-level fluctuations during the Holocene

Climate change is a natural process that has continued to occur throughout the geological history of the earth (Oldfield and Alverson, 2002). Variability in atmospheric circulation is the main cause of climate change, however, changes in ice, ocean and continental processes also aid to the overall climate conditions, albeit on a slower temporal scale (Clark *et al.*, undated; Oldfield and Alverson, 2002). All of these factors in turn are mainly determined by seasonal or latitudinal solar radiation, which is affected by the earth's orbital parameters (Clark *et al.*, undated; Berger and Loutre, 1991; Oldfield and Alverson, 2002). Consequently, the earth's climate has changed considerably in the past, with glacial and interglacial periods dominating during the most recent past, i.e. Quaternary and Holocene.

Glacial cycles have been detected using magneto-stratigraphy as well as the changes in $\delta^{18}O$ isotopes in fossil *foraminifera*, which are used as a proxy for ice volume and temperature (Leng *et al.*, 2005). Chronologies of these events are then also determined using U/Th dating, radiocarbon dating, dendrochronology and laminated lacustrine sediments (Deacon and Lancaster, 1988).

2.5.1 Proxies for sea-level change

Numerous proxies are used to infer past regional sea-level change globally. Features such as aeolianite deposition, wavecut platforms and beachrock have been used as indicators of sea-level low stands (Ramsay, 1995; Ramsay and Cooper, 2002; Bateman *et al.*, 2004; Carr *et al.*, 2006). Biological indicators have also been applied (Laborel and Laborel-Deguen, 1995), mainly based on the spatial distribution of littoral fauna and flora on rocky shores (Ramsay, 1995; Ramsay and Cooper, 2002). **Biological zonation** at present follows a clear gradient from the supralittoral to sublittoral zones. Unique fauna and flora associated with each of these zones can thus be used to infer relative sea-level (Compton, 2001). The "**biological mean sea-level**" can thus be determined as the limit between the mid- and sublittoral zones, where there is an increase in species diversity. Sessile species, with generally narrow depth ranges close to this limit, are considered to be very good indicators of sea-level, e.g. barnacles and oyster beds (Kilburn and Rippey, 1982; Ramsay and Cooper, 2002). Salt-marsh species (Gehrels *et al.*, 2005) and associated *foraminifera* (Kemp et al., 2009; Leorri *et al.*, 2008), and mangrove pollen remains (Ellison, 2005) have also been used as indicators of sea-level changes due to their close association with tidal marine conditions. At the same time, organisms living at the "biological mean sea-level" are also responsible for processes resulting in either the breakdown or adding to of the rock substrata. **Bioerosion** or **bioconstruction**, i.e. tidal notches, burrows or perforations, or coral reefs, can be used as indicators of sea-level change (Ramsay, 1995). Biological indicators of sea-level can provide information about a) the direction of relative displacement (i.e. increase or decrease in sea-level), b) the vertical amplitude or by how much sea-level has changed, c) the complexity of sea-level change, d) how rapid the change was and e) the age when sea-level changed, if material is suitable for dating. The use of biological proxies, such as those mentioned above, is based on the assumption that the vertical difference between the upper limit of the fossil and modern proxy, indicate the change in sea-level. There are, however, a number of problems associated with the use of biological proxies as sea-level indicators. Firstly, sublittoral organisms are generally killed by emersion and their remains are transported upwards into the midlittoral zone. Secondly, in most instances small or frail organisms / skeletons are destroyed. Thirdly, erosion of structures such as reefs occur that can obscure the upper limits of these features and fourthly, the submergence of coastal areas is difficult to determine as the indictors will be rapidly destroyed by erosion (high water energy) or covered by new generations of individuals.

Other biological proxies include the vertical accretion or migration of salt marsh vegetation in coastal areas (Gehrels *et al.*, 2005; Day *et al.*, 2008). Salt marsh vegetation is generally associated with tidal fluctuation and present distribution of species occurs along a salinity and elevation gradient (Adams, 1994; Bornman *et al.*, 2002, 2008). The vegetated surface of salt marsh can be associated with the high tide mark throughout the middle and late

Holocene (Gehrels *et al.*, 2005; Day *et al.*, 2008). Sediment cores collected within vegetated salt-marsh can be radiocarbon dated and sea-level index points (SLIP) gathered that can be used in conjunction with the biostratigraphy of the salt-marsh sequence to provide a relatively complete and continuous record of sea-level change. However, the ability of salt marsh sediment to record changes in sea-level depends on the balance between sediment accretion and sea-level rise (Day *et al.*, 2008). Should sedimentation outpace sea-level rise, salt marsh surfaces increase in height relative to the tidal levels and a regression is recorded in the sedimentary record. Should sea-level rise outpace sediment accumulation rates, the salt marsh surface will be lower relative to tidal levels, and a transgression is recorded. It is also important to remember that auto-compaction continues constantly within the salt-marsh, where the sediment sequence is compacted under its own weight (Gehrels *et al.*, 2005; Day *et al.*, 2008).

2.5.2 Global climate change and sea-level fluctuations

To reconstruct global climate change is a daunting task and in most instances not realistic as different regions worldwide have and will continue to experience different climatic conditions. Global climate change is only really evident in events such as glacial and interglacial periods affected by geological processes (Oldfield and Alverson, 2002).

Based on a number of studies, utilizing the above mentioned proxies, together with micro-fossils as indicators of sea surface temperatures (SST), the Last Glacial Maximum (LGM) was determined to have occurred approximately 21,000 ± 2000 years BP (Labeyrie *et al.*, 2003; Mix *et al.*, 2002), with sea-levels of approximately 125m below MSL recorded on the Western Australia coast (Yokohama *et al.*, 2000). During this time period, most of the cooling occurred at the high latitudes, with small temperature changes in the tropical oceans (Labeyrie *et al.*, 2003), with temperatures in the Atlantic and Pacific oceans approximately 2º to 5ºC cooler than present (Yokohama *et al.*, 2000). Although climatic conditions were colder during the LGM, it was also drier (Labeyrie *et al.*, 2003) and consequently less productive (Pedersen *et al.*, 2002). The large glacial ice sheets also affected atmospheric circulation, especially in the northern hemisphere and played a critical role in structuring the regional climate change patterns world wide (Labeyrie *et al.*, 2003; Pedersen *et al.* 2002). With the termination of the LGM rapid melting occurred with approximately 54 x 10^6 km^3 of continental ice melting in ~10,000 years (Yokohoma *et al.*, 2000; Labeyrie *et al.*, 2003; Bateman *et al.*, 2004). According to ice-core data, the main cause of increased temperature was an increase in greenhouse gases (Layberie *et al.*, 2003). At ~19,000 yr BP sea-level started rising, with levels of ~20 m above present levels recorded during 14,200 – 13,800 yr BP (Labeyrie *et al.*, 2003). It is believed that the melting of ice sheets affected the thermocline circulation patterns as freshwater trapped in glaciers and ice sheets was rapidly released into the oceans. With the changing atmospheric circulation and freshwater anomaly, a second and third cooling event occurred, namely the Older Dryas in Europe and Younger Dryas globally. Following the Younger Dryas (~12,000 yr BP), temperatures continued to increase until the ~10,000 yr BP (Labeyrie *et al.*, 2003). According to Lambeck *et al.* (2002) temperature, moisture and ice sheet cover has remained fairly similar to present-day levels.

In the Southern Hemisphere the Younger Dryas was characterised by a cooling in SST (Cohen *et al.*, 1992), although conditions between 7,000 and 4,500 yr BP were still very arid in Asia and Africa (Gasse, 2002). It is generally accepted that both the Northern and Southern Hemispheres have experienced similar climatic histories, although on a temporal scale these changes occurred earlier in the Southern than in the Northern Hemisphere (Gasse *et al.*, 2008) by as much as 2,000 to 4,000 years (Labeyrie *et al.*, 2003). It is believed that the Southern Hemisphere is better buffered against major climatic change due to the large ocean regions. Thus temperature changes appear to be small within this hemisphere, although the effects of hydrological shifts (i.e. moisture) may be related to changing atmospheric circulation and were more pronounced in this region.

It is generally accepted that the Holocene started at the end of the last major pulse of glaciations, i.e. Younger Dryas. Overall, the Holocene is characterised by a relatively stable climate. In the tropical regions, however, there have been major changes in the hydrology, with wetter conditions in the late Holocene. Studies in Peru and northern China has shown that during the early to mid- Holocene conditions were much drier that in the late Holocene. Research in the northern deserts of Africa and in central Asia, however, has shown wetter conditions in the early and mid-Holocene, with drier conditions in the late Holocene. According to Vimeux *et al.* (2001) high latitudes are characterised by a decrease in temperature, while the low latitude oceans of the Southern Hemisphere is characterised by an increase in SST during the Holocene.

According to Bradley and Jones (1992) and Grove (2001) the Northern Hemisphere experienced another cooling event, the ‘Little Ice Age’ approximately 400 - 500 yr BP. During this period there was an expansion of glaciers and the redevelopment of ice caps. The ‘Little Ice Age’ was thus the coolest period of the Holocene between ~ A.D. 1250 and 1880. Evidence from a palaeosol, dated at A.D. 1264 – 1297 and located at the Knysna Estuary, South Africa, has also indicated a rapid fall in sea-level most likely due to glacial expansion and extension of the Antarctic ice sheet during the Little Ice Age (Marker, 1997).

2.5.3 South African climate change and sea-level fluctuations

South Africa, situated at the most southern tip of the African continent, is boarded on the east and south coasts by the warm Agulhas current following westwards, converging with the cold Benguela current at the Agulhas Bank. As such, climatic conditions inland have been greatly affected in the geological past by changes in the SST of these two major ocean current systems and thermocline and atmospheric circulation patterns, as moisture supply to the coastal inland areas were affected (Bateman *et al.*, 2004).

At present the west coast of South Africa, together with Namibia, is strongly influenced by the cold Benguela current that flows northwards along the shoreline. This region is characterised by numerous upwelling events and very low rainfall that occurs mainly during the winter months (i.e. southern

African winter rainfall zone (WRZ)). According to Gasse *et al.*, (2008) cold water reduces the flux of water vapour inland, while warmer water contributes to increased moisture and rainfall inland of the coastal belt. At the convergence of these two ocean currents, along the southern Cape coastline of South Africa and adjacent to the currently submerged Agulhas Plateau, the climate is characterised by year-round or bimodal rainfall patterns. According to Cowling *et al.* (1999) and Meadows and Baxter (1999) this difference in the present regional climate also existed during the Quaternary.

Gasse *et al.* (2008) stated that during the LGM the climate in the area adjacent to the Benguela upwelling region was cooler and wetter than at present. From pollen and charcoal evidence Baxter and Meadows (1999) in turn, showed that by the mid-Holocene the climate had become warmer as well as drier. Gasse *et al.* (2008) also indicated that during this period, the present bimodal rainfall area of the Cape Agulhas region had increased precipitation, resulting in an East - West precipitation gradient, opposite to the modern gradient, with higher winter rainfall received in the eastern areas. Their model indicates that 21,500 to 17,000 yr BP, the climate on the southern coastline of South Africa was mainly cold and dry, comparable to the termination of the LGM. Between 17,000 and 14,000 yr BP, a climatic optimum was reached with increased winter and summer rainfall. Subsequently, (14,000 and 10,000 yr BP) there was a reduction in rainfall with an increase in ambient temperature, to present day levels (Bateman *et al.*, 2004; Lambeck *et al.*, 2002)

On the western coastline, however, climatic conditions differed slightly. According to Scott and Woodborne (2007) material collected from Hyrax middens at Pakhuis Pass in the Cederberg region (Western Cape), indicate cold conditions with summer rainfall between 23,000 and 16,000 yr BP. During this time conditions fluctuated with moderate warming during 21,000 to 19,000 yr BP, an increase in moisture at approximately 19,000 yr BP, followed by a dry-spell, followed by another increase in moisture during 17,500 and 16,000 yr BP. Following this general cooler period, was a period of warming

(16,000 to 9,500 yr BP), with a gentle moisture increase at approximately 13,000 yr BP and a sharp increase in moisture between 10,000 – 9,500 yr BP.

It is believed that the strength of the Agulhas Current was the main influence on climatic conditions during the LGM as the current is responsible for the westwards movement of warm surface water plumes from the tropical Indian Ocean along the southern African coastline (Gasse *et al.*, 2008). During the LGM the Agulhas Current was weak, resulting in a reduction in the flux of heat and salt from the Indian Ocean, effecting thermocline circulation. According to Gasse *et al.* (2008) Benguela upwelling was also stronger during the LGM, thereby affecting the moisture in the adjacent terrestrial environment. This weaker Agulhas current, combined with a stronger Benguela upwelling regime, resulted in a greater difference in SST between the Mozambique Channel on the East coast and the Benguela current on the West coast, affecting the E-W moisture gradient of southern Africa. The weaker Agulhas current reduced thermocline circulation in this region that was re-activated between 20,000 and 17,000 yr BP (Gasse *et al.* 2008).

Although climatic conditions may have differed on a regional basis between the winter and bimodal rainfall zones, there seemed to have been some synchronicity in the climate history between these regions. According to research conducted by Bateman *et al.* (2004) aeolianite and barrier dunes from the Wilderness Lakes and Cape Agulhas regions showed similar depositional histories, with all being older than 60,000 years and being deposited in 5 phases. The aeolianites from both regions were carbonate rich containing *foraminifera* and marine shell fragments (Illenberger, 1996). According to Bateman *et al.* (2004) sea-level oscillations during the Late Quaternary could be responsible for the deposition of onshore carbonate rich sediment that appeared to have been deposited when sea-level was rapidly transgressing and regressing. Using present day topography and bathymetry data, Barrable *et al.* (2004) has shown that during the LGM lower sea-levels would have exposed the Agulhas Bank, resulting in the coastline extending approximately 80 km further south than present. With the subsequent increase in sea-level, this area of exposed coastal shelf would have been inundated rapidly, together with a rapid deposition of marine sediment in these areas (van Andel, 1989).

Sea-level during the LGM, or Marine Oxygen Isotope Stage 2, has generally been below present levels. According to Ramsay and Cooper (2002) submerged material dated in South Africa between 13,000 and 17,000 yr BP indicate a sea-level of -100 m below present levels. A maximum depth of -130 m below was recorded of the Cape St. Francis coastline (south coast) using red algal nodules (Vogel and Marais, 1971), while Pether (1994) inferred a sea-level of -102 to -90 m below present levels between 13,000 and 12,000 yr BP from relict molluscan assemblages on the southwest coast.

The continental shelf of southern Africa is situated very close to the shoreline on the eastern border. It extends further seaward towards the southern coastline and around Cape Point region forming the Agulhas Bank, where after it again moves closer to the coast on the western border. As such, changes in the major ocean current, namely Agulhas and Benguela currents, would have had significant impacts on these areas and the inland climates. According to van Andel (1989) sea-level during the late Pleistocene was much lower than present, extending to -130 m below the present level. The shallow Zululand shelf on the east coast of South Africa was exposed for most of the Quaternary. During this period weathering and eluviations transformed sediments into calcareous aeolinites and beachrocks (Ramsay 1991, 1994). With an increase in sea-level during the Holocene, these coastal features were submerged to form the base of modern coral reefs (Ramsay and Mason, 1990). According to Ramsay (1991) present beachrock formation occurs at an elevation of 10 – 20 cm above mean sea-level. Based on these beachrock formations, Ramsay (1995) reconstructed the sea-level fluctuations along the eastern coastline of South Africa. According to his model, sea-level rose rapidly between 9000 and 8000 yr BP, reaching its present level at approximately 6500 yr BP. At ~6000 yr BP, sea-level had further risen to +1.5 m above the mean sea-level (MSL), which was maintained until ~5080 yr BP. A further increase in sea-level occurred until 4650 yr BP to a level +2.75 m above MSL and to +3.5 m above MSL at 4480 yr BP. A sea-level highstand then occurred for approximately 2500 years, until 3880 yr BP when sea-level dropped to its present level. It remained at this level until 3360 yr BP. Ramsay (1995) could not find any reliable evidence of sea-level change for the period 3360 to 1610 yr BP, but it is believed that it was much lower than present levels, resulting in the subsequent submergence of these features. Based on the presence of submerged Holocene beachrocks at Sodwana Bay, sea-level could have been as low as -2 m below present during this time (Ramsay and Cooper, 2002). Evidence does exist, however, of an increase in sea-level to +1.5 m above present MSL at 1610 yr BP that decreased to present levels at approximately 900 yr BP (Siesser, 1974, Ramsay and Cooper, 2002).

Miller *et al.* (1995) developed a sea-level change model for the Western Cape coastline based on archaeological sites, indicating four major phases. Firstly, there was a period of marine transgression at approximately 6000 yr BP with sea levels +2 to 3 meters above present mean sea level. A significant regression period followed at approximately 4200 yr BP, with sea level dropping to present MSL. Sea level oscillation took place around 4000 yr BP, with a highstand of +2 m above MSL. Marine regression took place at 3500 yr BP to below present levels, with a minor transgression event at 1800 yr BP, where after sea level dropped to its present level (Miller *et al.*, 1995). Baxter and Meadows (1999) showed that Verlorenvlei, also on the south coast of South Africa, experienced marine transgression at 8000 yr BP, followed by a regression periods at 7200 yr BP, with a low-stand of -3 m below present MSL between 7200 and 6870 yr BP. At 6500 yr BP a period of very low sea level was recorded during which subaerial dunes were formed. Subsequently there was an increase in sea level to +1 to 2 m above MSL at approximately 6000 yr BP. A small regression period followed between 5200 – 4800 yr BP, with an increase again at 4340 yr BP. According to Baxter and Meadows (1999) sea level reached its highest levels during the Holocene at 4000 yr BP, reaching a level of +3 m aMSL. Sea level oscillated thereafter and decreased to present levels after approximately 3500 yr BP. According to Ramsay and Cooper (2002) the patterns of sea-level change on the western Cape coast correspond to that of the east coast, although it includes an additional peak at approximately 3800 yr BP (Jerardino, 1995).

A number of other studies within South Africa have also focused on the reconstruction of past sea-level changes, especially within the Holocene. Birch (1976) and Flemming (1977) showed that at Langebaan Lagoon sea-level peaked to +2 to 3 m above MSL at 6500 – 5000 BP and that the presence of fossil oyster beds proved that the water was warmer. Yates *et al.* (1986) obtained a +2 to 8 m sea-level high at Verlorenvlei during 3820 ± 50 BP by studying a buried cobble beach containing marine shell deposits. Martin (1968) showed a +1.5m sea-level at Groenvlei during 6870 ± 160 BP and 1905 ± 60 BP, looking at diatom species.

Studies in the Drakenberg region of the Eastern Cape, South Africa have indicated that eight climatic phases could be identified during the Holocene (Lewis, 2005). The first phase was characterised by dry conditions as evidenced from palynological research conducted by Coetzee (1967; Lewis, 2005). The early Holocene in turn was dominated by wetter conditions, while the mid-Holocene was characterised by a prolonged semi-arid phase. The late-Holocene, on the other hand was characterised by alternating periods of increased moisture and drier conditions (Lewis, 2005). According to Partridge *et al.* (1990) there was a significant increase in moisture from 5000 yr BP, although on a temporal scale the Western Cape, falling in the Winter Rainfall Zone (WRZ), only showed an increase in moisture content at approximately 3500 yr BP (Lewis, 2002).

Deacon and Lancaster (1988) showed that the Holocene climate and sea-level history of South Africa can be summarised as follows: 1) 10,000 – 7,000 BP the climate was warmer, but also drier, with a change in the vegetation from grasslands to scrubs and bush, 2) 7,000 – 4,000 BP temperatures were the highest with very low rainfall during the summers as indicated by stable oxygen isotopes of micro-mammals and charcoal analyses. Within the Cape regions, however, very warm and moist conditions dominated as indicated by pollen analyses, diatoms and oyster bed formations. During this period the sea-level along the Cape coasts was +1.5m higher than at present and 3) 4,000 – 0 BP temperatures decreased as indicated by pollen analyses and the increase in grass species, while sea-level decreased to its present level.

Table 1 Radiocarbon dates for sea-level indicators along the South African coastline 3 (After Ramsay and Cooper, 2002).

Sample	**Date (^{14}C yr BP)**	**Material**	**Elevation AMSL (m)**	**Location**	**Reference:**
East Coast of South Africa					
Pta-3597	9990 ± 30	Wood	-48	Mkomazi, KZN	Grobbler *et al.,* 1988
Pta-3570	8950 ± 30	Wood	-28	Mkomazi, KZN	Grobbler *et al.*, 1988
Pta-3622	8280 ± 80	Attached oysters	-18	Mkomazi, KZN	Grobbler *et al.*, 1988
Pta-3573	8140 ± 70	Attached oysters	-18	Mkomazi	Grobbler *et al.*, 1988
Pta-6190	8950 ± 80	Beachrock	-10	Kosi Bay	Ramsay, 1991
Pta-6248	6460 ± 80	Beachrock	0	Mabibi	Ramsay, 1991
Pta-6191	4650 ± 60	Beachrock	+2.75	Banga Nek	Ramsay, 1991
Pta-6252	4480 ± 70	Pothole fill	+3.5	Black Rock	Ramsay, 1991
Pta-6297	4350 ± 60	Shell in beachrock	+1.61	Black rock	Ramsay, 1991
Pta-5052	3780 ± 60	Coral in beachrock	0	Mabibi	Ramsay and Mason, 1990
Pta-6300	3740 ± 60	Shell in beachrock	+1.49	Black rock	Ramsay, 1991
Pta-6429	3360 ± 60	Beachrock	0	Sodwana Bay	Ramsay, 1991
Pta-4972	1610 ± 70	Coral in beachrock	+1.5	Kosi Bay	Ramsay, 1991
South coast of South Africa					
Pta-182	16990 ± 100	Calcareous algae	-130	Cape St. Francis	Vogel and Marais, 1971
Pta-265	14510 ± 120	Calcareous algae	-112	Cape St. Francis	Vogel and Marais, 1971
Pta-264	13670 ± 120	Calcareous algae	-115	Cape St. Francis	Vogel and Marais, 1971
Pta-185	12990 ± 100	Calcareous algae	-120	Cape St. Francis	Vogel and Marais, 1971
Pta-4317	5080 ± 70	Life position bivalve	+1.5	Keurbooms	Redding, 1988
Pta-4462	3880 ± 60	Life position bivalve	0	Keurbooms	Redding, 1988
West coast of South Africa					
Pta-955	13300 ± 100	Calcareous algae	-75.5	Orange river	Vogel and Marais, 1971
Pta-4705	4240 ± 60	Shell	+2	W. Cape	Miller *et al.*, 1995
Pta-4041	3820 ± 50	Shell	+2.8	W. Cape	Yates *et al.*, 1986
Pta-4311	1450 ± 50	Shell	+1.5	Verlorenvlei	Miller *et al.*, 1995

Chapter 3

Study Site

3.1 Locality

The wetlands selected for this study are situated in the Agulhas Plain, at the southern most tip of South Africa. This area falls within the Cape Floristic Region (CFR) and is rich in endemic plant species and overall biodiversity (Clever and Brown, 2005; Kraaij *et al.,* 2009). The Agulhas Biodiversity Initiative (ABI) was started through the efforts of the Cape Action Plan for the Environment and People (C.A.P.E; www.capeaction.org.za) and is one of three initiatives supported by the Global Environment Facility (GEF) (www.agulhasbiodiversity.co.za). One of the main objectives of the ABI is to protect freshwater ecosystems within the area through wetland rehabilitation and the development of conservancies (Clever and Brown, 2005). The Agulhas Plain has a unique low gradient topography from the Bredasdorp mountain range in the north-west to the Indian Ocean in the south-east (Figure 1). This low gradient has resulted in significant areas of wetland development within this region (Noble and Hemens, 1978; Kraaij *et al.*, 2009). According to Jones *et al.* (2000, as cited in Kraaij *et al.*, 2009) surface water within the Agulhas Plain wetlands can be seasonal or permanent. Of the numerous wetland types found within the Agulhas Plain, only six are permanent lacustrine systems, of which Soetendalsvlei, Voëlvlei and Waskraalsvlei are three. Due to the unique nature of these wetlands and the vital role they play in supporting the environments around them, their conservation importance is high (Kraaij *et al.,* 2009) and hence the interest in their ecological functioning, as well as the likely impacts both climate change and human disturbances has had and may have in the future.

The Agulhas region is characterised by a Mediterranean climate, with hot, dry summers and cold, wet winters (Kraaij *et al,* 2004; Cleaver and Brown, 2005) and thus falls within the Winter Rainfall Zone (WRZ) of South Africa (Lubke and Herting, 2001; Cleaver and Brown, 2005). The average annual rainfall for the region is 400 – 600 mm (Heydorn and Tinley, 1980). Maximum summer temperatures range from 21 to 26ºC during October to April, with winter temperatures ranging between 17 and 21ºC during May to September.

According to Blanchard (2004) 54% of the land cover within the Agulhas Plain region is natural vegetation of which ~3% is free from low density alien infestation. Of the remaining land cover approximately 30% is being cultivated, alternating between winter grain (i.e. cereal) farming and livestock pastures. Only ~1% of the land within this region has been developed for urban use, while for 15% of the area land use is unknown, consisting mainly of alien vegetation. A number of projects, such as the Working for Wetlands (www.wetlands.sanbi.org) and C.A.P.E. (www.capeaction.org.za) programmes have been implemented in this region to eradicate alien vegetation and rehabilitate wetland and fynbos areas.

As this region is one of the key wheat and cereal production areas of South Africa, agriculture is the main anthropogenic impact on these wetlands. Towards the east of the wetlands is the Heuningnes River and Estuary that flows into the Indian Ocean at the De Mond nature reserve. The Heuningnes Estuary was originally a temporarily open/closed estuary (TOCE), but due to back-flooding of agricultural lands during periods of mouth closure, current management policies ensure that the mouth is artificially breached and kept open for the majority of time (Bickerton, 1984). Consequently the Heuningnes Estuary is marine dominated at present with saline intrusion into the upper reaches of the river (Bickerton, 1984). Due to the high estuarine importance score of 83.1 (Turpie and Clark, 2007) for the Heuningnes River and Estuary, conservation and management efforts have been high, culminating in the development of an Estuarine Management Plan (EstMP) for the estuary (HilLand Associates, 2009). Some of the main concerns highlighted in the EstMP were the effect that rising sea-level will have on the salinity profile of the estuary and the catchment area, together with the effects of reduced rainfall and freshwater inflow on the salinity of both catchment water bodies and the estuary itself (HilLand Associates, 2009). The EstMP highlighted the potential additive impact of the artificial breaching of the estuary mouth, where back-flooding is reduced leading to drying out of previously inundated wetland systems and increasing saline conditions in those systems (HilLand Associates, 2009). It was recommended in the EstMP that the estuary and its associated wetlands (i.e. Soetendalsvlei) be monitored and that the various reaches be identified and maintained so as to ensure that an ecological corridor is maintained from the wetlands, along the river to the ocean and that the associated flora and fauna are protected (HilLand Associates, 2009). The EstMP stated that water quality, biota (including microalgae) and the exploitation of living resources (i.e. fish) should be monitored. Although monitoring of these aspects will aid in the current and future management of the Heuningnes and its associated wetlands, especially Soetendalsvlei, it does not provide information regarding how past management protocols have affected the systems. This study will thus provide some insight into how Soetendalsvlei has been affected by the artificial breaching of the estuary mouth, especially as very little data is available for any of the systems mentioned here (HilLand Associates, 2009).

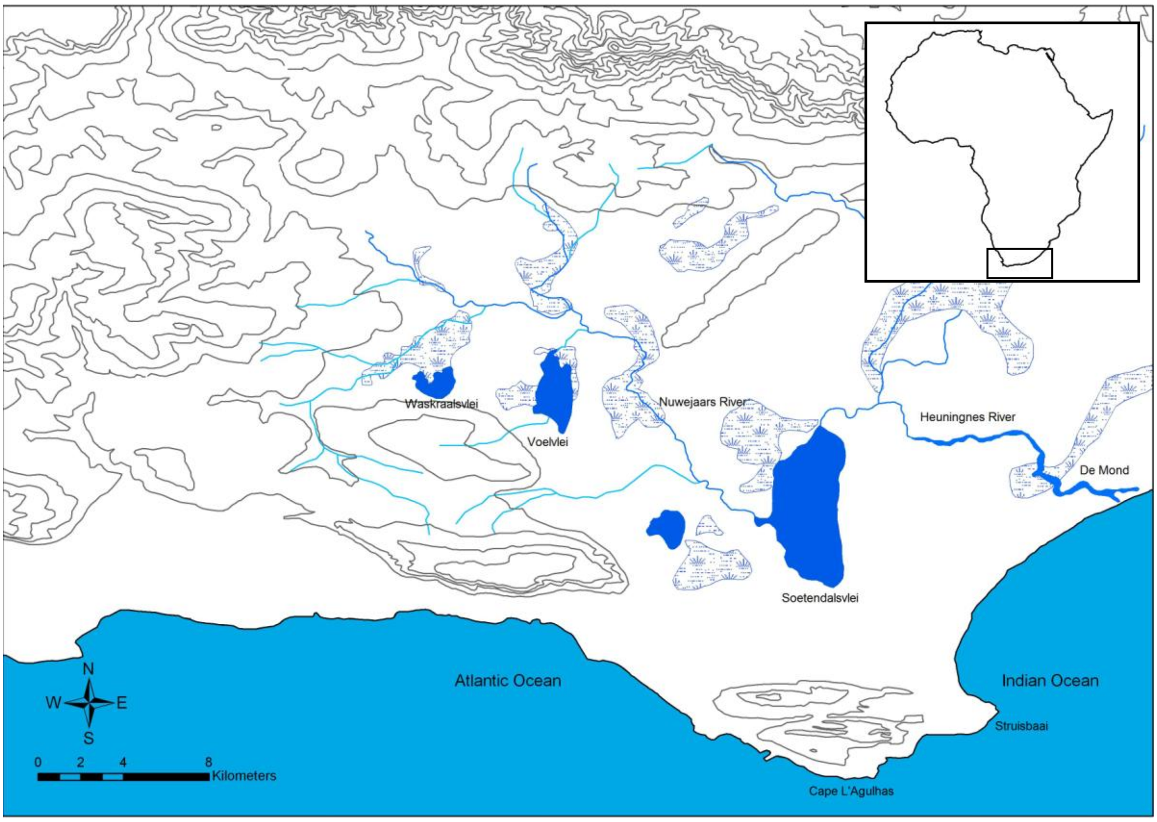


Figure 1 Study area with the three main wetlands as well as the Heuningnes River and estuary at De Mond.

3.2 Soetendalsvlei

Soetendalsvlei is a large, shallow coastal lake situated on the southern Cape coast within the Agulhas Plain region of South Africa. The lake or wetland has a water surface area of approximately 20 km^2 (Figure 1) and is 8 km long and 2.5 km wide (Noble and Hemens, 1978), with a mean water depth of 2 m, which can increase substantially during periods of high rainfall and freshwater inflow. Soetendalsvlei is moderately saline with electrical conductivity of between 300 and 700 mS/m, while the river water only reaches levels of approximately 230 – 280 mS/m during the dry seasons (January). It is estimated that groundwater entering Soetendalsvlei has an electrical conductivity of between 400 and 1000 mS/m, depending on seasonal rainfall and groundwater recharge (Toens *et al.*, 1998). Water entering the wetland is mainly alkaline and brackish due to river flow through limestone-bearing Strandveld sands and Bokkeveld shales (Noble and Hemens, 1978). A large reed bed, extending over the entire width of the wetland, separates Soetendalsvlei into a northern (hereafter referred to as Soetendalsvlei North) and southern (hereafter referred to as Soetendalsvlei South) section about half-way along the north/south axis (Plate 1 and 2, Figure 2). Due to the predominantly south-east winds that blow throughout the year in the region, reed growth mainly occurs on the western shore, with very few reeds occurring on the eastern shore.

The main anthropogenic influences on Soetendalsvlei are the agricultural practices on the eastern shore and freshwater abstraction from the Nuwejaars River. In addition, there is a lack of freshwater/ brackish exchange between Soetendalsvlei and the Heuningnes River and estuary, due to the mouth of the estuary being kept open artificially to prevent back-flooding of valuable agricultural lands and a weir construction at the convergence of the wetland and river (Plate 3).

Plate 1 Aerial photograph of Soetendalsvlei Lake with the Nuwejaars River entering mid-way on the western shore and the overflow weir at the most northern point of the Lake (image: Google Earth ®, 2006).

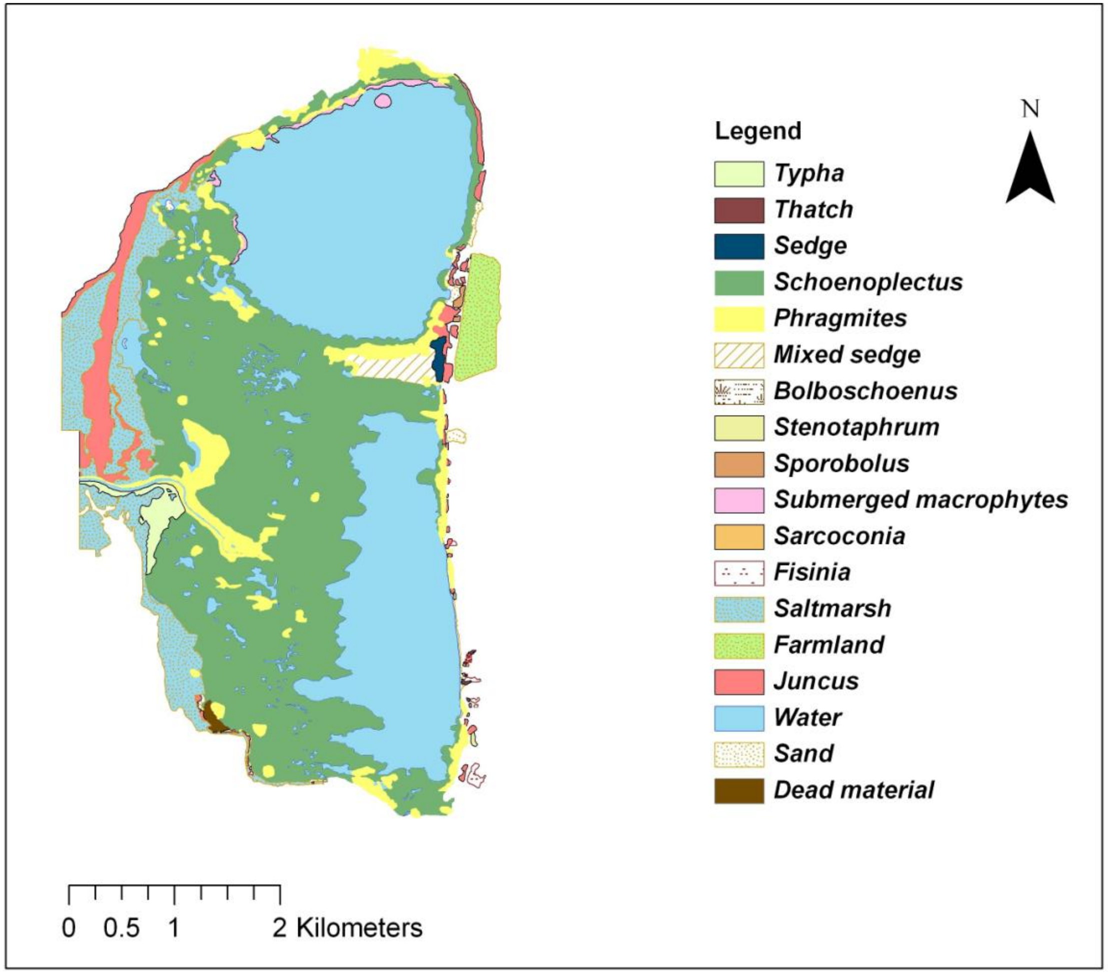


Figure 2 Vegetation map of Soetendalsvlei Lake, indicating the large reed bed extending across the lake, dividing it into a north and south section (Kotsedi, 2007).

(a)

(b)

Plate 2 (a) The southern section of the lake and (b) the large reed bed separating the Lake

(a)

(b)

Plate 3 (a) The northern section of Soetendalsvlei and (b) the weir at the convergence of Soetendalsvlei North and the Heuningnes River (August 2007).

3.3 Voëlvlei

Voëlvlei is situated towards the west of Soetendalsvlei along the Elim/Struisbaai road (Figure 1). It is approximately 2 km long and 2 km wide (Plates 4 and 5), with a mean water depth of 2 to 2.5 m. It is characterised by large reed beds on the northern and southern shores, but on the western and eastern shore no reeds were observed. This wetland holds a high number of resident bird species with 33 species recorded during 2005 by CapeNature (Clever and Brown, 2005). Its main source of freshwater comes from streams in the south and, during high rainfall, from the Nuwejaars River in the north. Voëlvlei has a unique hydrology as freshwater inflow from the Nuwejaars River occurs via the outflow channel during the high rainfall season. During periods of increased rainfall and flow in the Nuwejaars River, a reverse flow occurs in the outflow channel from Voëlvlei. Water flows via this channel into Voëlvlei, until the water level in the wetland has reached that of the river (U. Pratt, pers.comm.). Only once the wetland has essentially filled with river water, does the water flow onwards towards Soetendalsvlei. As soon as the river flow decreases and the water level drops, Voëlvlei again drains into the Nuwejaars River via the outflow / inflow channel. As a result of this hydrological feature, it is believed that water residence / retention time in this wetland is relatively long, leading to increased productivity and the high phytoplankton dominance (i.e. pea-colour).

Plate 4 Aerial photograph of Voëlvlei Lake with areas of salt marsh on the western and north-western shorelines behind stands of *Schoenoplectus* and *Phragmites* (image: Google Earth ®, 2006).

Plate 5 Voëlvlei Lake in the background with large reed beds along the shores and wheat fields in the front view.

3.4 Waskraalsvlei

Waskraalsvlei is situated further along the Elim/ Bredasdorp road, west from Voëlvlei (Figure 1). It lies within a depression flowing into the Nuwejaars River. It is the smallest of the wetlands, being approximately 1 km^2 (Plates 6, 7 and 8). It holds extensive reed beds along the northern, southern and western shore, but none on the very steep eastern shore. This wetland is characterised by clear water and dense submerged macrophyte beds. Surrounding the wetland are extensive areas of supratidal salt marsh species consisting of halophytes *Sarcocornia pillansia* and *Bassia diffusia*. During the high rainfall season, water inundates these areas (Plate 2.8).

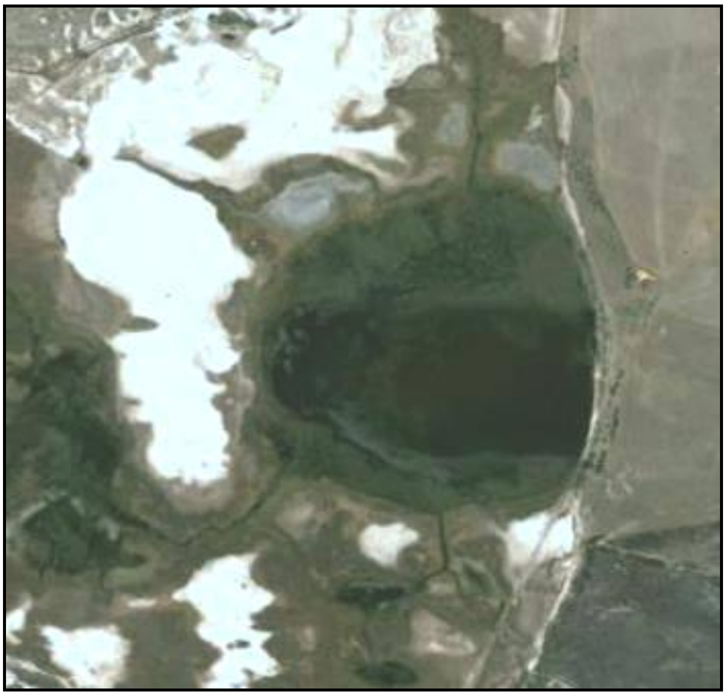


Plate 6 Aerial photograph of Waskraalsvlei indicating the large area of reeds along the shorelines as well as the large area of salt marsh towards the northern extremes of the wetland (image: Google Earth ®, 2006).

Plate 7 Waskraalsvlei indicating the large stands of *Phragmites australis* and *Schoenoplectus scirpoides* along the shoreline.

Plate 8 Waskraaslvlei during high rainfall (August 2007), indicating the extensive inundation of salt marsh areas.

3.5 Heuningnes River and Estuary

The Heuningnes Estuary is situated north-east of Stuisbaai, at the most southern tip of South Africa. The estuary is approximately 15 km long with large areas of salt marsh in the lower and middle reaches (Plate 9a), while large stands of *Phragmites australis* and *Schoenoplectus scirpoides* dominate the water channel in the upper reaches (Plate 9b). Historically the Heuningnes River and Estuary was connected to Soetendalsvlei Lake. At present, however, a weir (Plate 9c) prevents the free exchange of water between the Lake and the River and freshwater only enters the River during periods of very high rainfall and freshwater inflow into the lake, until water level is sufficient to overflow the weir. Freshwater thus mainly enters the system as rainfall, runoff and groundwater. The two main rivers that feed the Heuningnes River are the Nuwejaars River, via Soetendalsvlei, and the Kars River (Figure 11, Chapter 5, pg. 114). Very little urban development has occurred within the catchment area of the River and Estuary. Agriculture is the main anthropogenic impact in the region. River flow in the system is reduced by the Struisbaai / Bredasdorp Bridge in the upper reaches and a foot-bridge in the lower reaches of the estuary.

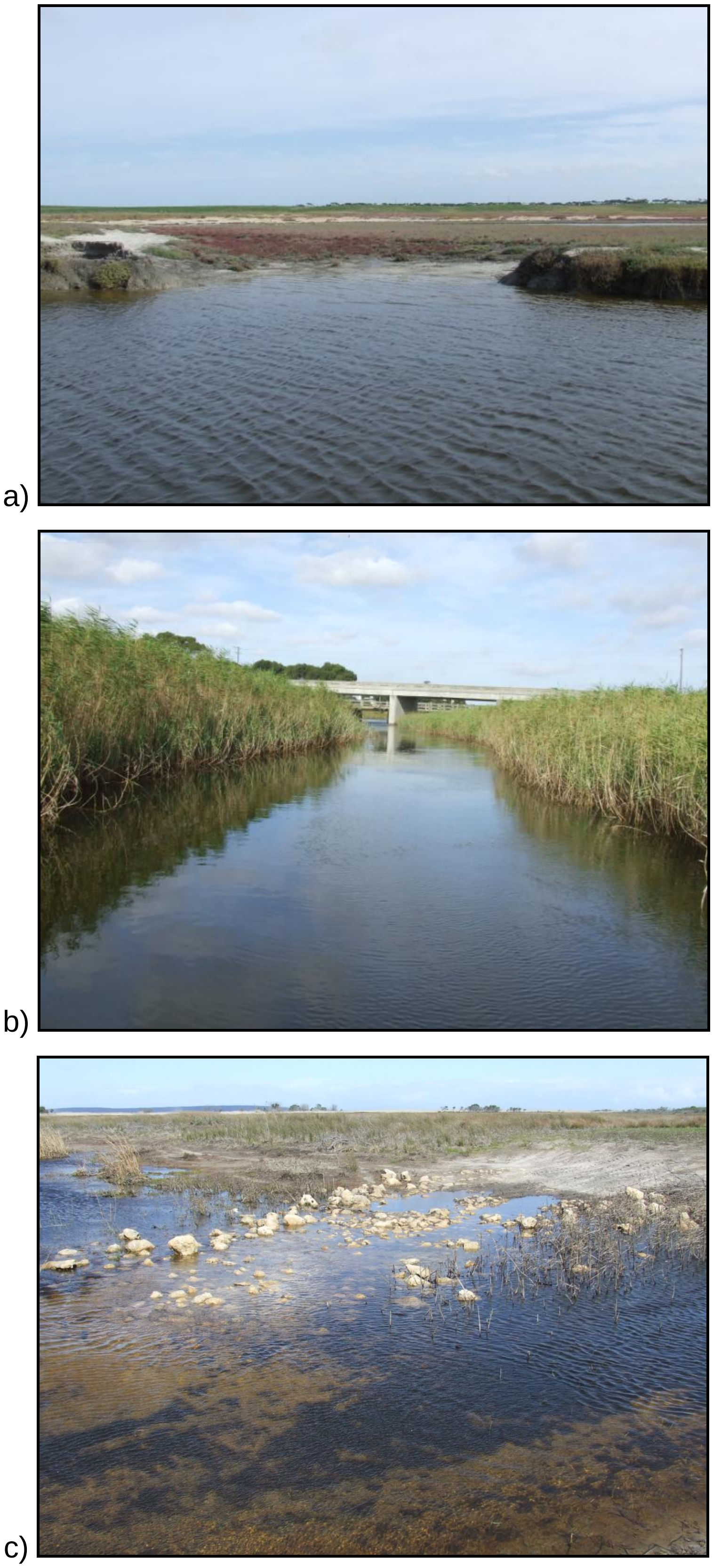


Plate 9 The middle to upper reaches of the Heuningnes Estuary; a) middle reaches with salt marsh areas; b) upper reaches with *Phragmites autralis* and *Schoenoplectus scirpoides*, and c) weir at the overflow from Soetendalsvlei Lake into the River and Estuary

3.6. Historical background

No clear history is available for the area. However, archaeological evidence of Later Stone Age populations is evident from numerous shell middens in the area. More recent historical evidence of human settlements is found at the Missionary station in Elim, where the church bell is date-stamped at 1764 (Bickerton, 1984). It would thus appear that humans have occupied this region for more than 300 years. Considering the present day agricultural activities and lack of urban develop, it can be presumed that historically agriculture was the main anthropogenic impact in this region. The construction of the Bredasdorp/ Struisbaai road across the Heuningnes River is another major impact on this system, especially with the construction of a drift across the river and later a bridge in 1976. Numerous other secondary roads and bridges across the Nuwejaars River may further have impacted the lake and downstream environments. Another major alteration that was made to the system was the stabilisation of the dune fields using European dune pioneer species, *Ammophila arenaria*, at the mouth of the Heuningnes Estuary by the Department of Forestry since 1930 (Lubke and Hertling, 2001). This was done to prevent the estuary mouth closing and the back-flooding of approximately 24,000 ha of valuable agricultural land (Bickerton, 1984; Lubke and Hertling, 2001) (See figure 3). At present the estuary mouth is still artificially opened during periods of increased freshwater inflow to prevent back-flooding, but since 1940 no back-flooding to the coastal lake and surrounding areas has occurred (Lubke and Hertling, 2001).

Although quantitative rainfall data are not available for this region, historical records from the farm Zoetendals vallei, indicate periods of prolonged drought in 1869, 1909 – 1910, 1926 to 1935 and 1970. Flood events occurred in 1871, 1880, 1902 – 1906, 1931, 1953 – 1956, 1964, 1966, 1975 and 1978 (Bickerton, 1984). More recently a major flood occurred in 2005 where water level was considerably higher, flooding vast areas of supratidal wetland and farm lands (personal communication with landowners).

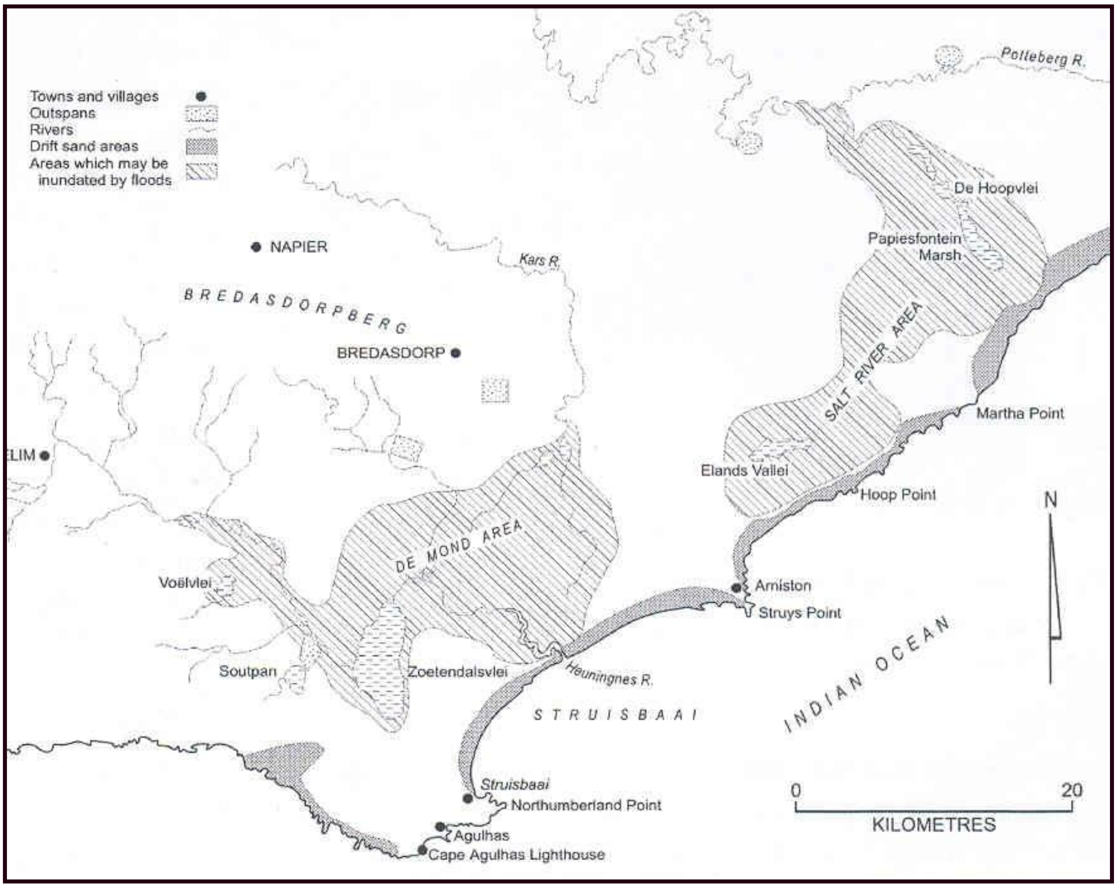


Figure 3 Areas of blackflooding in he Heuningnes Estuary catchment under closed mouth conditions (From Lubke and Hertling, 2001).

Chapter 4

Water Quality and Phytoplankton community structure of the Agulhas wetlands

4.1 Introduction

Wetlands play a valuable ecological function in reducing flooding effects, recharging groundwater and in the amelioration of water quality (Dallas *et al.*, 2006). They are also highly diverse, productive ecosystems (Cowan and Van Riet, 1998, Bowd *et al.*, 2006). They are important habitats for unique faunal and floral species biodiversity, leading to the proclamation of a number of wetlands as Ramsar sites of international importance. However, due to an increase in human population and a higher demand for freshwater, together with urbanisation and agricultural activities, most South African wetlands are degraded in terms of water quality and biodiversity.

To ensure the effective management of wetlands, it is essential to understand the ecological functioning of these systems in order to be able to mitigate negative impacts. Methods for quick, reliable and inexpensive means of assessing water quality are essential. As with most aquatic systems, wetlands have a number of interlinked trophic interactions that often lead to changes in water quality having a cascading effect on the system (DWAF, 1996; Ollis *et al.*, 2006). Existing water quality monitoring criteria for wetlands include assessing the chemical composition of the water, aquatic invertebrate composition (Bowd *et al.,* 2006, Ollis *et al.*, 2006), fish assemblages, vegetation and, more recently, the use of microalgae, most notably diatoms (Harding *et al.*, 2005; Ryder and Mascarenhas, 2007).

Physico-chemical measurements of the water column are only a snap-shot of the environmental conditions of a wetland at one specific time and place, while biological indicators have the advantage in that they are a response to long-term physico-chemical variables (Bate *et al.*, 2004). According to Barbour (1997), Karr and Chu (1997) and Sgro *et al.* (2006) biological indices provide a measure of the health of the system instead of a simple physico-chemical characterisation of the water. Two of the main problems associated with water quality management at present are the eutrophication of wetlands due to agricultural, urban and industrial inflow (Jansen van Vuuren and Pieterse, 2005a, b; Van Ginkel and Silberbauer, 2007) and the increase in salinity (Braune and Rogers, 1987). Eutrophication usually results in increased primary production and, most notably, the increase in nuisance taxa such as toxic cyanobacteria. Understanding the responses of such species, or even taxonomic algal groups, to changing environmental variables, is thus important as significant changes in the phytoplankton or algal community can lead to negative ecological and economic implications (Richardson *et al.,* 2001; Jansen van Vuuren and Pieterse, 2005a, b). Diatoms are considered reliable indicators of water quality because they are often numerically important autotrophic organisms at the base of the aquatic food chain, occurring in a variety of habitats ranging from freshwater to brackish to marine (Flower *et al.*, 1997). They respond to the chemical composition of the water, i.e. nutrients and pollution (Harding *et al.*, 2005) and to physical factors, i.e. hydrodynamics (Ryder and Mascarenhas, 2007), and thus can be used to determine the integrated conditions in aquatic environments.

An increase in nutrients, for example, is often correlated to an increase in primary productivity, but can also be related to the dominant producers. Numerous studies have indicated that the relationship between phytoplankton, microphytobenthos and submerged macrophytes is affected by nutrient concentrations within the water column (Malan and Day, 2002; Vadeboncoeur *et al.* 2001, 2003; Andersson and Brunberg 2006; Flöder *et al.* 2006). Under high nutrient conditions, phytoplankton biomass increases rapidly, thus negatively affecting both microphytobenthos and submerged macrophytes by limiting light availability to these communities (Asaeda *et al.* 2001). The interaction between phytoplankton and submerged macrophytes is very important in lake ecology as both compete for nutrients and light. A submerged macrophyte – phytoplankton model developed for Swartvlei, South Africa, indicated that an initial increase in phosphorus resulted in high phytoplankton biomass, with a concomitant increase in turbidity, thus limiting light availability to the submerged macrophytes (Howard-Williams and Liptrot, 1980; Vymazal, 1994). Once the phytoplankton blooms subsided, submerged macrophyte biomass increased because of the reduced phytoplankton nutrient uptake. Armitage and Fong (2004) also observed that increases in nutrients, whether from terrestrial or atmospheric input, natural or anthropogenic sources, led to high productivity of wetlands. At the same time, biological controls, such as competition and herbivory (Coelho *et al.*, 2007, Allan and Froneman, 2008) also affect the primary producers of the system. High nutrient input or eutrophication, may favour opportunistic species, thus changing the structure of the primary producer community. This shift will have cascading effects on the higher trophic communities, causing a further shift in the community structure (Allan and Froneman, 2008). Carrick and Lowe (2007) found that increases in both nitrogen and phosphorus within the water column would result in other elements such as silica becoming limiting, resulting in a shift from a microalgal community dominated by diatoms to communities dominated by non-siliceous algae, e.g. cyanobacteria.

This study focused on the Soetendalsvlei, Voëlvlei and Waskraalsvlei wetlands situated at the southern most tip of the African continent. The objective of this study was to assess the water quality of the three wetlands. Since very little research has been undertaken in the study area, the information reported here represents limnological baseline information to assist the system managers. It is hoped that the data collected in this study will aid in future freshwater management within this region in view of freshwater withdrawal practices. Since these wetlands fall within the Agulhas Plain and Cape Floristic Region, water quality information is important to ensure the future conservation of biodiversity.

Understanding the present water quality and ecological characteristics of the Agulhas Plain wetlands, will provide information regarding specific associations between microalgal taxa and environmental conditions. These associations in turn will provide some basis for inferring past environmental conditions, notably palaeo-salinity related to sea-level changes, that will be the focus of Chapter 6. It will also provide a measure of change over time and how anthropogenic and climate impacts have altered the systems.

Hypotheses tested in this Chapter were:

1. Due to agricultural return flow, phosphorus is not limiting within these systems and phytoplankton communities will be dominated by fast growing opportunistic species, leading to very high (>30 μgl^{-1}) chlorophyll a concentrations throughout the water column.
2. Cyanobacteria dominate the phytoplankton communities because of the low salinity and nutrient rich conditions.

4.2 Sampling stations

This study focussed on the three major Agulhas wetlands, namely Soetendalsvlei, Voëlvlei and Waskraalsvlei (Figure 4). A large reed bed, comprised of *Phragmites australis* and *Schoenoplectus scirpoides*, extended over the entire width of the wetland, separating Soetendalsvlei into a northern (hereafter referred to as Soetendalsvlei North) and southern (hereafter referred to as Soetendalsvlei South) section about half-way along the north/south axis.

Within each of the lake basins, five sampling stations were selected. Four of the stations were within 10 m of the shoreline, while the fifth station was in the middle of the water bodies. Due to the very large water surface area of Soetendalsvlei North, a sixth station was selected closer to the shoreline. GPS co-ordinates for each station were recorded and used to return to the same site during subsequent sampling trips.

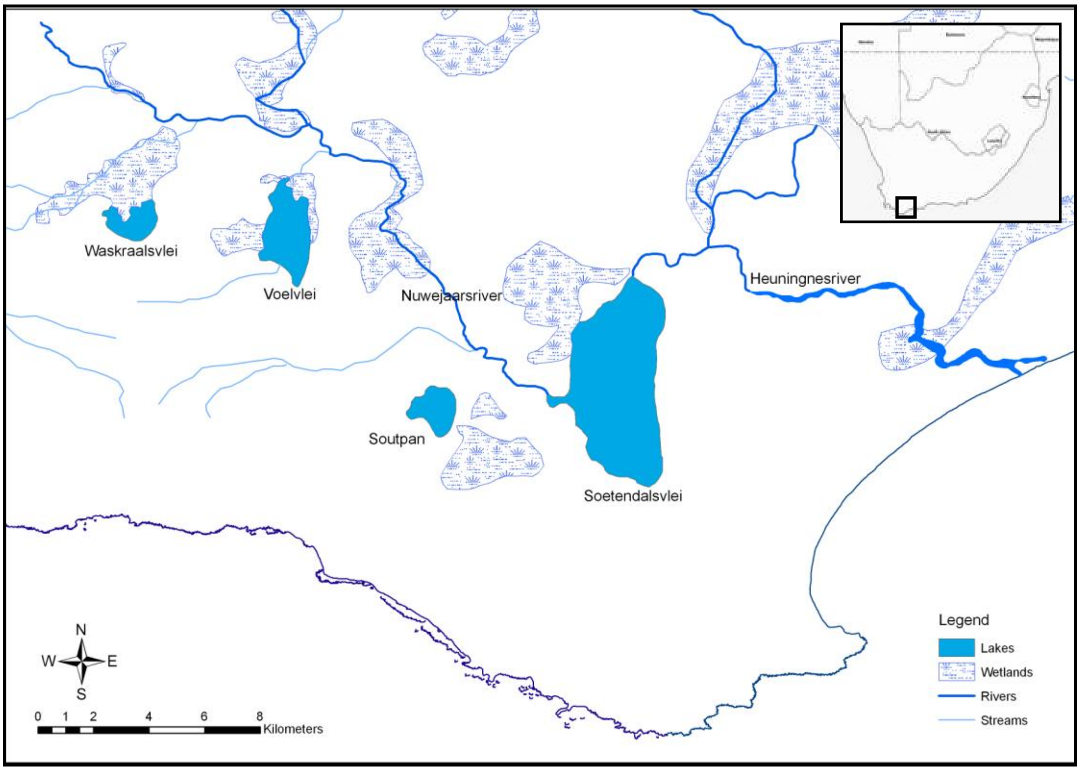


Figure 4 Study area map indicating the location of the three wetlands and the two main rivers (Nuwejaars and Heuningnes).

4.3 Materials and Methods

Four sampling sessions, at three month intervals, were undertaken during 2007, encompassing both wet and dry, and cold and warm climatic conditions within the region. Rainfall and wind data were obtained from the South African Weather Services stations at Bredasdorp and Struisbaai. Sampling of the flood events occurred after the main event, when water levels were still significantly higher, but water flow had been reduced. As GPS points were used to return to the same stations in subsequent sampling periods, sampling of the same points could occur irrelevant of water depth.

4.3.1 Physical parameters

Water column salinity (ppt), electrical conductivity (mScm^{-1}), temperature (°C), dissolved oxygen (% saturation) and pH were measured at each site at 0.5 m intervals with an YSI 6920 water logger (multiprobe).

4.3.2 Chemical parameters

Water samples for nutrient analyses were gravity filtered through Whatman glass-fibre GF/C filter paper and frozen until further analyses in the laboratory. Prior to freezing, 3 drops of mercuric chloride were added to preserve the samples. The water samples were collected at each site from the surface (10 cm) to the bottom (10 cm above sediment surface) of the water column at 0.5 m intervals. The samples were analysed for ammonium (NH_4^+), total oxidised nitrogen (TOxN), soluble reactive phosphorous (SRP) and silicate (Si) using standard nutrient kits from Merck, based on the methods of Strickland and Parsons (1972).

4.3.3 Phytoplankton biomass

Water samples were collected at the various stations from the surface (10 cm) to the bottom (10 cm above the sediment surface) of the water column every 0.5 m intervals. Due to the high turbidity of the water column, only 200 ml water could be gravity filtered though Whatman glass-fibre GF/C filters. The filter papers were placed in aluminium foil and frozen until further analyses in the laboratory. Laboratory analyses were usually completed within seven days from sample collection.

Once samples were unfrozen, chlorophyll *a* was extracted using 10 ml 95% (v/V) Ethanol overnight at 4°C in the dark. The absorbance of the extract was determined using an UV/vis spectrophotometer before and after acidification with 2 drops of 0.1N HCl. Chlorophyll *a* concentrations were calculated using the equation of Nusch (1980) modified by Hilmer (1990):

$$\text{Phytoplankton biomass } (\mu g \text{ Chl-}a \text{ } l^{-1}) = (E_{b665} - E_{a665}) \times 29.6 \times (v / (V \times L))$$

Where;

E_{b665} = Absorbency reading before acidification
E_{a665} = Absorbency reading after acidification
v = Volume of solvent used for extraction (ml)
V = Volume of sample filtered (l)
L = Path length of spectrophotometer cuvette (cm)
29.6 = a constant calculated from the maximum acid ratio (1.7) and the specific absorption coefficient of chl-*a* in ethanol (82 $g.l^{-1}$. $10mm^{-1}$)

4.3.4 Phytoplankton community structure

Water samples, for phytoplankton community counts, were collected at the same stations and depths as those for water quality analyses. The samples were preserved using 5% gluteraldehyde and kept in the dark until further analyses in the laboratory. Samples were stained using Rose Bengal solution and 60 ml were settled for 24 hours using Utermöhl (1958) settling chambers. Phytoplankton cells were counted using a Zeiss IM 35 inverted microscope at 630x magnification. A minimum of 200 cells was counted in each sample. Only the major taxonomic groups were differentiated during the counts.

4.3.5 Data analyses

Statistical and correlation analyses

One-way ANOVA (Tukey's Multiple Comparison Test) and Student's t-test were performed to relate all sampling stations and lake basins for significant differences using the programme Statistica © (Version 7, StatSoft, Inc., 2004). Pearson Product Moment Correlation analyses, with Monte Carlo Permutations (999) were also preformed to relate the major taxonomic algal groups to environmental variables.

Multivariate analyses

Multivariate analyses (ordination analyses) were performed on the environmental, phytoplankton chlorophyll *a* (biomass) and community structure data using the software package CANOCO for Windows (version 4.52, ter Braak 2003) to determine which environmental variables influenced phytoplankton chlorophyll *a* concentrations and taxonomic groups (microalgae relative abundance) within the various lake basins. Canonical Correspondence Analysis (CCA) was used, whereby the chlorophyll *a* and microalgae relative abundance data were constrained by the environmental variables. Monte Carlo permutations tests (999 permutations) were used to determine whether there were any significant relationships between the canonical axes and the environmental and chlorophyll *a* and microalgae relative abundance data. The results of the CCA's were plotted using CANODRAW (Version 4.52, ter Braak 2003). The arrows of these plots originate from the centre of the axes and represent the environmental variables.

The origin presents the mean value of the environmental variables, while the direction of the arrow represents the increase in the value of that particular variable. The length of the line indicates the importance of each variable. The position of the various chlorophyll *a* groups or microalgal groups to these environmental variables is an indication of the relationship of that chlorophyll *a* or microalgal groups to a particular variable and the closer it occurs to the variable, the stronger the relationship. Statistical results are displayed in a table below each CCA ordination diagram, indicating the relationship between the chlorophyll *a* or microalgae relative abundance (species) and environmental data, as well as the relationship between chlorophyll *a* or microalgae relative abundance data and the canonical axes.

4.4 Results

4.4.1 Rainfall

Rainfall measurements taken at Zoetendals Vallei farm and at Struisbaai since 1960 showed high winter rainfall (~ 60 mm) during April and June (Figure 5). The lowest rainfall was generally recorded during the summer months of November to February. During 2007 the lowest rainfall (10 mm) was recorded in January, while July exhibited the highest (~120 mm). During November 2007 a total of ~60 mm was recorded, which was considerably higher than that recorded for November in the preceding decades, which averaged approximately 30 mm.

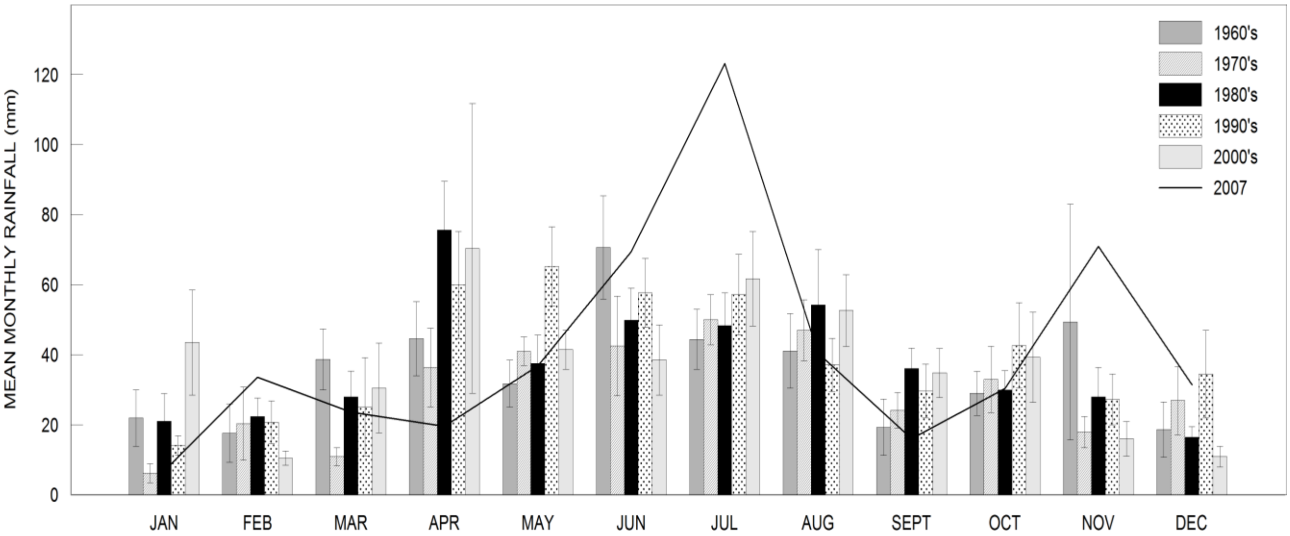


Figure 5 Mean monthly rainfall (mm) in increments of 10 years from 1960 until 2006, with 2007 rainfall plotted as the line graph.

4.4.2 Physical and chemical parameters

Measurements taken at the various sampling sites per lake basin showed no significant differences among the sites. Data were thus grouped together per depth for each of the wetlands and depth profiles were generated (Table 2).

Temperature

Temperature recordings indicated a clear seasonal change for all the wetlands and basins, with the highest temperatures (~22ºC) being recorded in February and the lowest in May 2007 (~12ºC, $p < 0.05$, $n = 207$). During February 2007 summer stratification was noted in Voëlvlei and Waskraalsvlei, with surface water temperatures significantly higher (22.1± 1.2ºC and 24.3 ±1.1ºC, respectively, $p < 0.05$, $n = 45$) than those in the bottom water (20.9 ±0.7ºC and 21.4 ±0.1ºC, respectively). For these two water basins, winter stratification in May and August 2007 was also observed, again with surface temperatures being significantly higher (12 to 13.5ºC and 13.1 to 13.8ºC, respectively) than bottom temperatures (11.4 to 12.8ºC and 12.5 to 12.7ºC, respectively, $p < 0.05$, $n = 45$). Winter stratification was also observed in Soetendalsvlei North in May 2007, with surface temperatures (12.2 ± 0.3ºC) significantly higher than bottom temperatures (11.9 ± 0.01ºC, $p < 0.05$, $n = 90$).

Electrical conductivity

As expected, electrical conductivity and salinity were strongly correlated ($r = 1.0$) and hence only conductivity will be reported on. For all the water basins the highest conductivities were recorded during late autumn/early winter (May 2007), ranging from 2.75 to 4.2 mS cm^{-1}. In Soetendalsvlei North the lowest conductivity (2.64 ± 0.001 mS cm^{-1}) was recorded during February 2007, with significant vertical differences observed only during November 2007 when conductivity was higher at the surface (2.8 ± 0.02 mS cm^{-1}) than at the bottom (2.74 ± 0.08 mS cm^{-1}, $p < 0.05$, $n = 90$). In Soetendalsvlei South, the lowest conductivity was recorded during November 2007 (2.1 ± 0.03 mS cm^{-1}) with no significant differences with water depth observed during any of the sampling periods. In Voëlvlei the lowest conductivity was recorded in August 2007 (2.2 ± 0.04 mS cm^{-1}) but, as in Soetendalsvlei South, no significant differences with water depth were observed during any of the sampling periods. Waskraalsvlei, similar to Voëlvlei, had its lowest conductivity during August 2007 (1.4 ± 0.01 mS cm^{-1}). However, significant differences with water depth were observed three times; during May when surface conductivity was higher than at the bottom (4.26 ± 0.01 mS cm^{-1} and 4.24 ± 0.01 mS cm^{-1}, respectively, $p < 0.05$, $n = 45$), during August when bottom conductivity was higher than at the surface (1.45 ± 0.03 mS cm^{-1} and 1.43 ± 0.03 mS cm^{-1}, respectively, $p < 0.05$, $n = 60$) and during November 2007 when surface conductivity was again higher than at the bottom (2.18 ± 0.004 mS cm^{-1} and 2.17 ± 0.003 mS cm^{-1}, respectively, $p < 0.05$, $n = 60$).

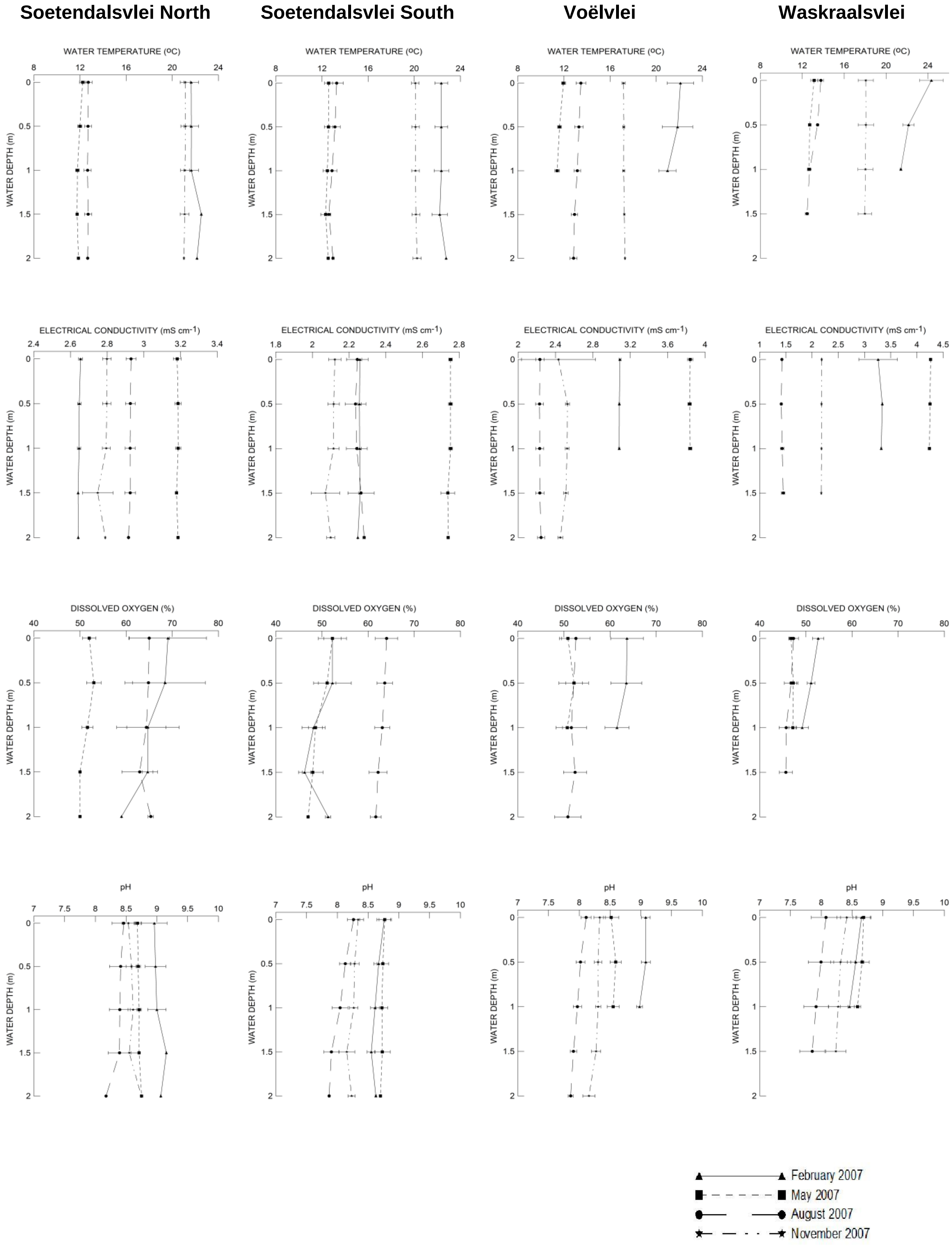
Dissolved oxygen saturation

Due to equipment failure during the November 2007 sampling, only data for February, May and August are presented. Dissolved oxygen saturation (%) varied greatly between the different wetlands and sampling periods. However, for most of the water basins, with the exception of Soetendalsvlei South, the highest saturation (49 to 69%) was recorded during February 2007. In Soetendalsvlei South, the highest saturation was recorded during August 2007, ranging from 61 to 64% throughout the water column. Although Soetendalsvlei South did not have its highest dissolved oxygen saturation during February 2007, as did the other water basins, significant differences were observed, with surface saturations higher than at the bottom (52.2 ± 3.0% and 46.2 ± 1.3%, respectively, $p < 0.05$, $n = 75$). Vertical differences in saturation in Soetendalsvlei South were also observed during May 2007, when the lowest saturation for this basin was recorded, with surface saturation being significantly higher than at the bottom (52.3 ± 1.9% and 47 ± 0 %, respectively, $p < 0.05$, $n = 75$). In Soetendalsvlei North the lowest saturation was also recorded in May 2007, again with surface saturation being significantly higher than at the bottom (52 ± 1.5% and 50 ± 0%, respectively, $p < 0.05$, $n = 90$). In Voëlvlei the lowest saturation was recorded during August 2007, when sub-surface (0.5 m) saturation (52.2 ± 1.8%) was significantly higher than both the surface and bottom saturations (50.8 ± 1.8% and 50.7 ± 1%, respectively, $p < 0.05$, $n = 45$). As in Voëlvlei, Waskraalsvlei also had its lowest saturation during August 2007, with surface saturation being significantly higher than at the bottom (47.3 ± 1.1% and 45.7 ± 1.4%, respectively, $p < 0.05$, $n = 60$). During February 2007, vertical differences were also observed in Waskraalsvlei, again with surface saturation being significantly higher than at the bottom (52.7 ± 1.2% and 49.2 ± 1.4%, respectively, $p < 0.05$, $n = 45$).

pH

The pH levels remained fairly alkaline (8 to 9) in all the wetlands and basins throughout the study period. Highest pH readings were recorded during February 2007 (8.4 to 9.1) for all of the water basins except Soetendalsvlei South, where highest readings were recorded during May (8.7 ± 0.1). Lowest readings were recorded during August 2007 for all the wetlands, ranging from 7.8 to 8.4. Vertical differences were observed for Soetendalsvlei South, Voëlvlei and Waskraalsvlei during February, August and November 2007, when surface readings were all significantly higher than bottom readings (Figure 3, $p < 0.05$). In Soetendalsvlei North, significant vertical differences were observed only during November 2007, when surface readings were lower than bottom readings (8.54 ± 0.1 and 8.75 ± 0.01, respectively, $p < 0.05$, $n = 90$). Although no significant vertical differences were evident in this water basin during the remaining sampling periods, the surface readings were generally higher than the bottom readings.

Table 2. Physical data collected at depth for the four lake basins over the four sampling periods (n = 10; horizontal bars = standard deviation).



4.4.3 Nutrients

Most of the nutrient data collected had no significant differences in concentration with depth, with the exception of ammonium concentrations in Soetendalsvlei North during November 2007, when surface concentrations were significantly higher (184 ± 227 µg l^{-1}), and silica concentrations in Soetendalsvlei South during August 2007, when silica concentrations were significantly lower (90 ± 2 µg l^{-1}). Results are thus discussed as mean concentrations per lake basin and sampling period (Figure 6).

Soetendalsvlei North

Ammonium concentrations were significantly higher during February and May (148.2 ± 7.5 µg l^{-1} and 147.7 ± 5.9 µg l^{-1}, respectively, $p<0.05$). TOxN concentrations, on the other hand, were highest during August (40.9 ± 0.6 µg l^{-1}) and lowest in May 2007 (24.9 ± 0.9 µg l^{-1}) with concentrations of 33.6 ± 0.7 µg l^{-1} being recorded during February and November 2007. SRP concentrations varied significantly between the sampling periods, with highest concentrations occurring in May and August (270.1 µg l^{-1} and 212.2 ± 0.2 µg l^{-1}, respectively, $p < 0.05$), while the lowest concentrations were recorded during November (5.0 ± 0.2 µg l^{-1}). Silica concentrations, however, were highest during February 2007 (559.2 ± 6.9 µg l^{-1}), where after they decreased significantly in May and August (231.9 ± 14.3 µg $l^{-1}$and 272.2 ± 15.7 µg l^{-1}, respectively, $p < 0.05$) and again in November (150.2 ± 6.4 µg l^{-1}).

Soetendalsvlei South

In Soetendalsvlei South, ammonium concentrations were similar to those recorded in Soetendalsvlei North, with the highest concentrations during February and May (166.2 ± 10.9 µg $l^{-1}$and 154 ± 2.2 µg l^{-1}, respectively). TOxN concentrations, however, were highest during May and August 2007 (89.2 ± 0.9 µg l^{-1} and 89.2 ± 2.0 µg l^{-1}, respectively) and lowest concentrations during February (25.2 ± 0.9 µg l^{-1}). SRP concentrations varied significantly between the different sampling periods. The highest concentrations were also measured during May and August (273.8 µg $l^{-1}$and 213.2 ± 0.1 µg l^{-1} respectively, $p < 0.05$). SRP concentrations were very similar to those measured in Soetendalsvlei North, with lowest concentrations measured in

November (5.7 ± 0.2 µg l^{-1}). Silica concentrations were significantly higher during August and November 2007 (887.5 ± 68.9 µg $l^{-1}$and 984.5 ± 6.6 µg l^{-1}, respectively, $p < 0.05$), and lowest concentrations during May (129.2 ± 3.1 µg l^{-1}).

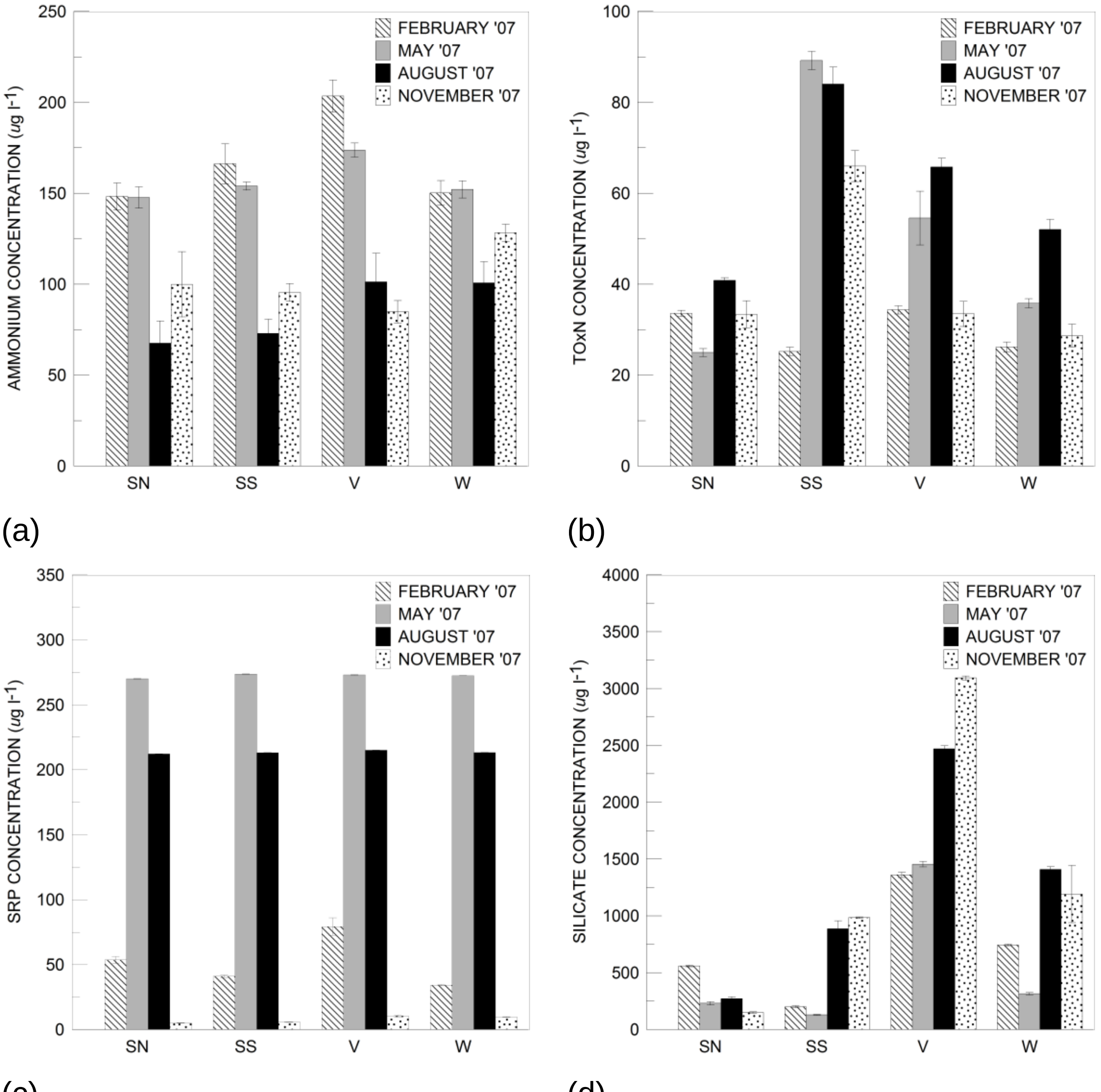
Voëlvlei

As in Soetendalsvlei North and South, Voëlvlei showed a similar pattern in ammonium concentrations, with the highest concentrations during February and May 2007 (203.5 ± 8.8 µg $l^{-1}$and 173.8 ± 3.9 µg l^{-1}, respectively) and the lowest concentrations (84.9 ± 6.2 µg l^{-1}) in November 2007. TOxN concentrations were significantly higher during May and August (54.5 ± 5.9 µg $l^{-1}$and 65.8 ± 1.9 µg l^{-1}, respectively, $p < 0.05$) than in February and November (34.3 ± 0.9 µg $l^{-1}$and 33.5 ± 2.8 µg l^{-1}, respectively). SRP concentrations were also similar to those of Soetendalsvlei North and South, with the highest concentrations during May and August (272.9 µg $l^{-1}$and 215.1 µg l^{-1}, respectively) and November 2007 having the lowest concentrations (10.4 ± 0.6 µg l^{-1}). Silica concentrations increased significantly from 1360.4 ± 22.7 µg l^{-1} during February to 3093.2 ± 17.6 µg l^{-1} during November 2007 ($p < 0.05$).

Waskraalsvlei

As in the other three wetland basins, Waskraalsvlei followed a similar pattern in ammonium concentration with the highest concentrations during February and May (150.2 ± 6.8 µg l^{-1} and 152.2 ± 4.7 µg l^{-1}, respectively). However, concentrations during November 2007 were significantly higher (128.3 ± 4.7 µg l^{-1}) than in August (100.7 ± 11.7 µg l^{-1}, $p < 0.05$). TOxN concentrations were significantly higher during May and August (35.8 ± 1.0 µg $l^{-1}$and 52.1 ± 2.2 µg l^{-1}, respectively, $p < 0.05$) than in February (26.2 ± 1.1 µg l^{-1}) and November (35.8 ± 1.0 µg l^{-1}). SRP concentrations were similar to those of the other wetland basins, again with the highest concentrations during May and August (272.5 µg $l^{-1}$and 213.3 µg l^{-1}, respectively) and the lowest during November (9.7 ± 0.3 µg l^{-1}). Silica concentrations varied significantly ($p < 0.05$) between the sampling periods with the highest concentrations being measured in August (1408.6 ± 23.9 µg l^{-1}), followed by those in November

(1192.1 ± 251.7 µg l^{-1}), February (743.4 ± 6.9 µg l^{-1}) and lastly May (315.7 ± 10.2 µg l^{-1}).



(a) (b) (c) (d)

Figure 6 Nutrient concentrations (µg.l^{-1}) for the different lake basins during the different sampling periods; (a) Ammonium, (b) Total Oxidised Nitrogen (TOxN), (c) Soluble Reactive Phosphorus (SRP) and (d) Silica.

4.4.4 Phytoplankton biomass

With the exception of Voëlvlei, phytoplankton biomass showed no significant differences with water depth. Voëlvlei had significantly higher chlorophyll *a* concentrations in the surface waters only during February 2007 (131.1 ± 54.9 $\mu g\ l^{-1}$, $p < 0.05$). Data were thus grouped together and results are presented as the overall phytoplankton biomass per wetland basin (Figure 7).

Voëlvlei showed significantly higher phytoplankton biomass, as indicated by chlorophyll *a* concentrations, during all sampling periods compared to the other wetlands, ranging from 428.2 ± 98.4 $\mu g\ l^{-1}$ in May 2007 ($p < 0.05$, $n = 42$,) to 17.03 ± 7.04 $\mu g\ l^{-1}$ in August 2007 (Figure 4). Waskraalsvlei, on the other hand, had significantly lower chlorophyll *a* concentrations ranging from 4.1 ± 1.8 $\mu g\ l^{-1}$ in May to 0.50 ± 0.6 $\mu g\ l^{-1}$ in August 2007 ($p < 0.05$, $n = 42$). All four wetlands followed a similar pattern with an increase in biomass from February to May 2007 followed by a significant decrease in August ($p < 0.05$, $n = 42$). However, Soetendalsvlei North and South showed a further significant decrease in November 2007 (4.6 ± 2.5 $\mu g\ l^{-1}$ and 4.2 ± 2.4 $\mu g\ l^{-1}$, respectively, $p < 0.05$, $n = 42$). Voëlvlei and Waskraalsvlei, on the other hand showed a significant increase in November 2007 (80.3 ± 25.1 $\mu g\ l^{-1}$ and 1.23 ± 1.1 $\mu g\ l^{-1}$, respectively, $p < 0.05$, $n = 42$). During August 2007 all the wetlands differed significantly from one another, whereas during the remaining three sampling periods only Voëlvlei had significantly different phytoplankton biomass.

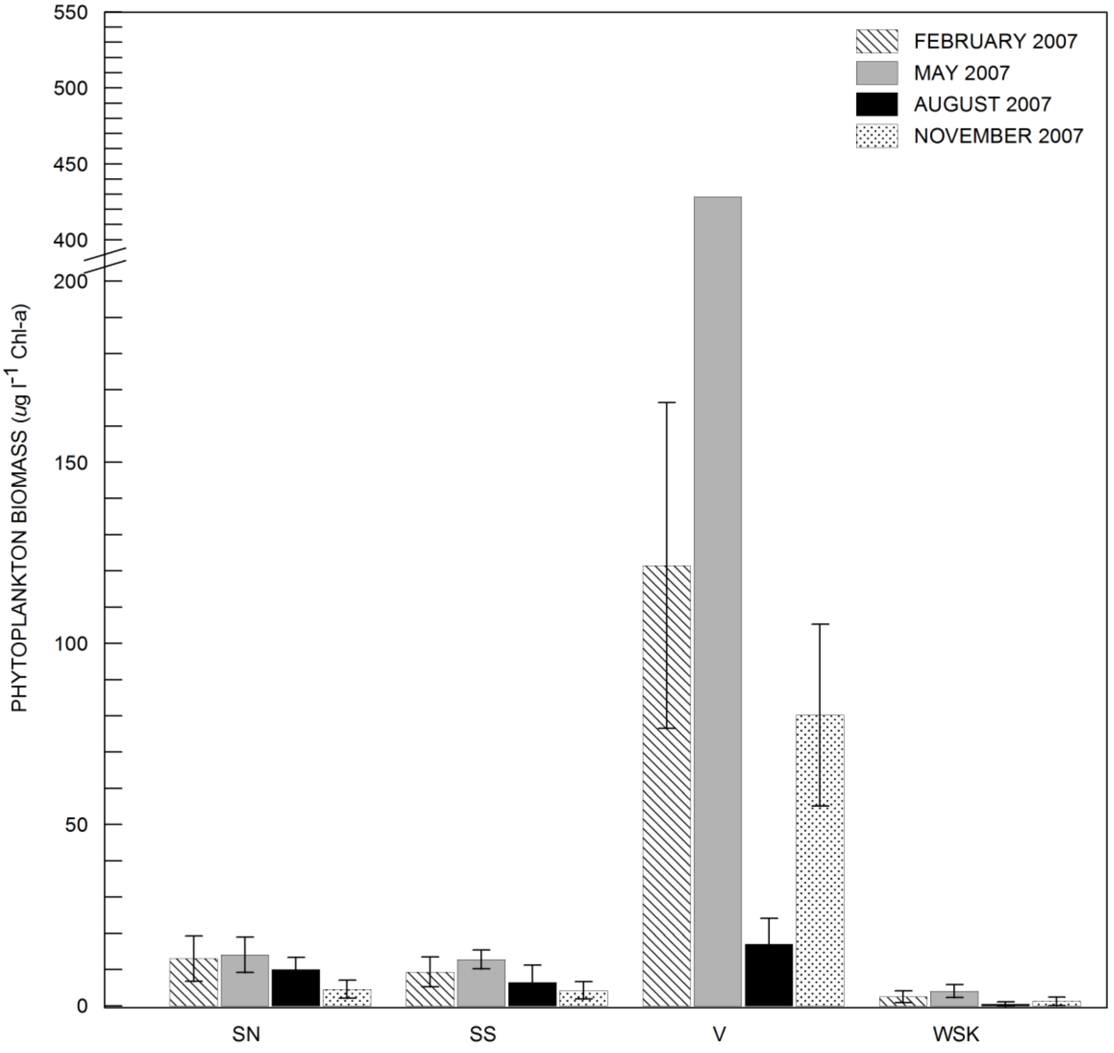


Figure 7 Phytoplankton biomass (µg Chl-*a*.l^{-1}) for the various lake basins measured during the four sampling periods (mean ± standard deviation).

4.4.5 Phytoplankton community structure

Five main microalgal groups were identified in this study, including diatoms (Bacillariophyceae), dinoflagellates (Dinophyceae), flagellates (Euglenophyceae), cyanobacteria (Cyanophyceae) and chlorophytes (green microalgae, Chlorophyceae). All other microalgae were grouped together with zooplankton as the 'other' group in the results (Figure 8).

Soetendalsvlei

Diatoms were initially dominant in Soetendalsvlei North during February 2007 (38 ± 3%, $p < 0.05$, $n = 20$) but were replaced by chlorophytes and flagellates during the subsequent sampling periods (65 ± 3% and 21 ± 3%, respectively, $p < 0.05$, $n = 20$). In Soetendalsvlei South, flagellates were the dominant microalgal group during all sampling periods, ranging from 86 ± 1% in May to 47 ± 3% in November 2007 ($p < 0.05$, $n = 18$). Diatoms accounted for 9 to 30% of the phytoplankton in Soetendalsvlei South, while chlorophytes contributed approximately 3 ± 1%. Both diatoms and chlorophytes increased in relative abundance in August 2007.

Voëlvlei

In Voëlvlei the relative abundance of cyanobacteria was significantly higher during late summer, i.e. February, and in early autumn, i.e. May 2007 (83 ± 8% and 99 ± 1%, respectively, $p < 0.05$, $n = 14$), but decreased considerably during August and November 2007 (<1% and 2 ± 0.5%, respectively, $p < 0.05$, $n = 14$). As cyanobacteria abundance decreased, chlorophytes increased significantly to 96 ± 1% and 93 ± 1% ($p < 0.05$, $n = 14$) during August and November, respectively. Diatoms accounted for only 5% of the phytoplankton community during February 2007, and then decreased until they reached values lower than 1%.

Waskraalsvlei

Flagellates were the dominant microalgal group in Waskraalsvlei in February, May and November 2007 (65%, 84% and 56%, respectively). During August 2007, however, chlorophytes became the most abundance group with an abundance of 66 ± 5% ($p < 0.05$, $n = 14$). Diatom abundance ranged from

12% in February and May to 7% in August, with an increase in November to 26% ($p < 0.05$, $n = 14$).

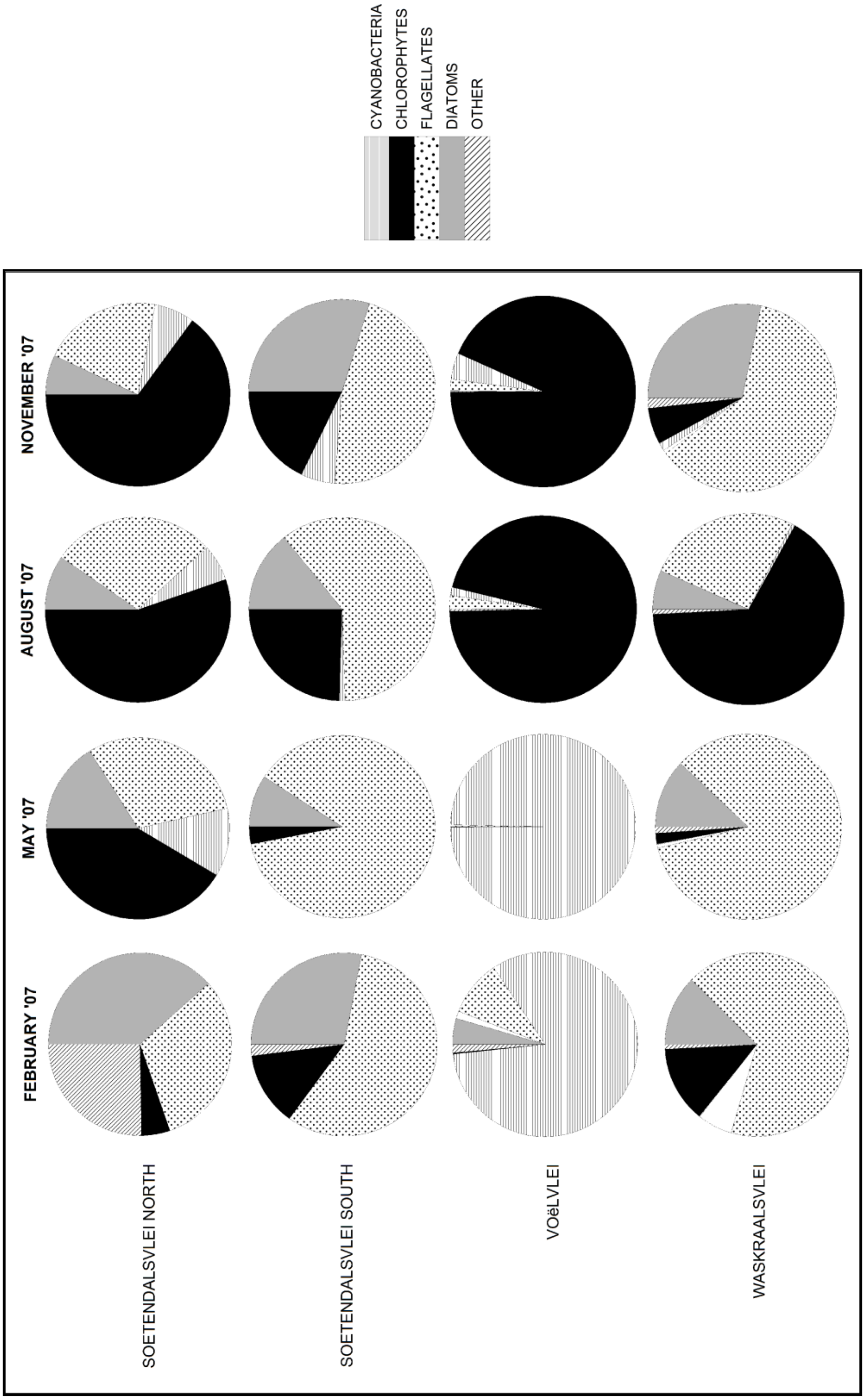


Figure 8 The phytoplankton functional groups and their change over time in relative abundance for the different lake basins.

4.4.6 Data analyses

Correlation analyses

Soetendalsvlei North

Correlation analyses for Soetendalsvlei North indicated that temperature (r = -0.83), pH (r = -0.84) and silica concentrations (r = -0.67) decreased significantly over time, while SRP concentrations increased (r = 0.70) (Table 3). Consequently, diatom relative abundance also decreased over time, while the presence of other micro-organisms increased (r = -0.78 and r = 0.77, respectively, $p < 0.05$, n = 64). Strong significant correlations were found between temperature and silica concentrations (r = 0.85), and consequently between temperature and diatom relative abundance (r = 0.74). Lower water temperature was significantly correlated with increased conductivity (r = -0.89) and SRP concentration (r = -0.98). In turn, conductivity correlated positively with SRP and negatively with silica concentrations (r = 0.96 and r = -0.80, respectively), while cyanobacteria relative abundance increased (r = 0.50) and diatom relative abundance decreased (r = -0.58). Higher dissolved oxygen saturation in turn was correlated with decreased SRP and increased silica concentrations (r = -0.63 and r = 0.58, respectively), consequently corresponding to increased diatom and decreased cyanobacteria relative abundance (r = 0.41 and r = -0.36, respectively). The pH levels showed similar correlations to those of dissolved oxygen, with decreased SRP (r = -0.61) and increased silica concentrations (r = 0.59) at higher alkalinities. Diatoms in turn increased in relative abundance (r = 0.54) at higher pH levels, while the other micro-organisms decreased (r = -0.65). Ammonium concentrations showed weak negative correlations with TOxN concentrations and with chlorophyte relative abundances (r = -0.41 and r = -0.38, respectively). TOxN concentrations, however, showed a positive correlation (r = 0.60) with increased relative abundance of other micro-organisms in this wetland, while SRP concentration correlated strongly with decreased diatom relative abundance (r = -0.69) and weakly with increased cyanobacteria and chlorophyte relative abundance (r = 0.47 and r = 0.31, respectively). SRP concentrations were strongly correlated with lower silica concentrations (r = -0.84). Silica correlated negatively with the relative abundance of cyanobacteria (r = -0.48) and chlorophytes (r = -0.44), and positively with diatom relative abundance (r = 0.73). Phytoplankton biomass (chlorophyll *a*) showed weak negative correlation with TOxN concentration (r = -0.38) and the relative abundance of other micro-organisms (r = -0.35).

Cyanobacteria, as well as chlorophyte relative abundances, corresponded with decreased relative abundances of both flagellates (r = -0.54 and r = -0.72, respectively) and diatoms (r = -0.39 and r = -0.77, respectively), which showed a weak correlation with each other (r = 0.32).

Soetendalsvlei South

Correlation analyses for Soetendalsvlei South (Table 4) indicated that temperature (r = -0.84) and pH (r = -0.75) decreased significantly over time, while dissolved oxygen (r = 0.77), TOxN (r = 0.73), SRP (r = 0.72) and silica concentrations (r = 0.67) increased. Cyanobacteria also increased over time (r = 0.56), while diatom relative abundance decreased (r = -0.51). Higher temperature in turn corresponded with lower TOxN and SRP concentrations (r = -0.85 and r = -0.97, respectively), while diatom relative abundance increased (r = 0.70). Higher conductivity correlated with increased SRP concentrations (r = 0.66) as well as with increased phytoplankton biomass (chlorophyll a; r = 0.53) and flagellate relative abundance (r = 0.79), while lower chlorophyte relative abundance was correlated with increased conductivity (r = -0.58). Dissolved oxygen saturation was strongly correlated with increased silica concentrations (r = 0.73) and high cyanobacteria relative abundance (r = 0.61), while corresponding negatively with pH levels (r = -0.76). The pH levels correlated with increased ammonium concentrations (r = 0.62) and lower silica concentrations (r = -0.64). Lower cyanobacteria relative abundance was also correlated within increased pH levels (r = -0.60) and ammonium concentrations (r = -0.50). Diatom relative abundance was correlated within decreased TOxN (r = -0.53) and SRP concentrations (r = -0.71) as well as lower flagellate relative abundance (r = -0.62). TOxN and SRP concentrations were strongly correlated (r = 0.82), while SRP concentrations were also correlated to increased flagellate relative abundance (r = 0.56). Silica concentrations, however, were correlated with increased chlorophyte relative abundance (r = 0.70), which was correlated with lower phytoplankton biomass (i.e. chlorophyll a; r = -0.56). Chlorophyte and flagellate relative abundance were also negatively correlated to each other (r = -0.78).

Voëlvlei

Correlation analyses for Voëlvlei (Table 5) indicated that conductivity (r = -0.62), pH (r = -0.75) and ammonium concentrations (r = -0.60) decreased over time, but that cyanobacteria relative abundance increased (r = 0.74). Conductivity correlated with increased pH levels (r = 0.59) and phytoplankton biomass (chlorophyll a; r = 0.87) and with decreased silica concentrations (r = -0.74) and cyanobacteria relative abundance (r = -0.66). Dissolved oxygen saturation was strongly correlated with lower SRP levels (r = -0.90) as well as with lower relative abundance of other micro-organisms (r = -0.57), while higher saturation levels were correlated with higher silica concentrations (r = 0.61) and cyanobacteria relative abundance (r = 0.64). pH levels increased with higher water temperature (r = 0.65), electrical conductivity (r = 0.9) and ammonium concentration (r = 0.50), but with lower silica concentrations (r = -0.67). Higher ammonium concentrations were also correlated with lower silica concentrations (r = -0.60), while increased TOxN concentrations were correlated with higher SRP concentrations (r = 0.53). SRP concentrations were strongly correlated with increased flagellate and other micro-organism relative abundances (r = 0.68 and r = 0.63, respectively) but with lower cyanobacteria relative abundance (r = -0.59). Lower silica concentrations were correlated to higher phytoplankton biomass (chlorophyll a; r = -0.57), while higher concentrations were correlated with increased cyanobacteria relative abundance (r = 0.78). Phytoplankton biomass (chlorophyll *a*) was correlated with increased relative abundance of cyanobacteria (r = 0.61) and a decrease in chlorophytes (r = -0.57).

Waskraalsvlei

Correlation analyses for Waskraalsvlei (Table 6) indicated that conductivity (r = -0.65) and phytoplankton biomass (chlorophyll a; r = -0.51) decreased over time, while dissolved oxygen (r = 0.66) and cyanobacteria relative abundance increased (r = 0.49). In Waskraalsvlei there were also significant correlations between physico-chemical variables (i.e., conductivity, pH and silica concentrations) and water depth, although most of these correlations were relatively weak ($r < 0.50$). Temperature showed significant correlation with decreased TOxN and SRP concentrations ($r = -0.51$ and $r = -0.84$, respectively), while electrical conductivity correlated with increased pH levels ($r = 0.79$), and higher phytoplankton biomass (chlorophyll a; $r = 0.75$) and flagellate abundance ($r = 0.61$). Higher conductivity was also correlated with lower silica concentrations ($r = -0.94$) and lower chlorophyte abundance ($r = -0.70$). Diatom relative abundance was correlated with increased dissolved oxygen saturation ($r = 0.73$), which in turn was correlated with decreased SRP concentrations ($r = -0.75$). Increased pH levels were correlated with decreased silica concentrations ($r = -0.77$) and chlorophyte abundance ($r = -0.79$) but with increased phytoplankton biomass (chlorophyll a; $r = 0.50$) and flagellate abundance ($r = 0.67$). TOxN concentrations were strongly correlated with high chlorophyte abundance ($r = 0.56$), while SRP concentrations showed weak correlation with high chlorophyte abundance ($r = 0.42$), and lower cyanobacteria ($r = -0.32$), diatom ($r = -0.47$) and other micro-organism abundances ($r = -0.35$). Silica concentrations, on the other hand, showed strong correlation with decreased phytoplankton biomass (chlorophyll a; $r = -0.70$) and flagellate abundance ($r = -0.65$) but with increased chlorophyte abundance ($r = 0.76$). Phytoplankton biomass (chlorophyll *a*) was significantly correlated with increased flagellate ($r = 0.45$) and decreased cyanobacteria and chlorophyte relative abundances ($r = -0.34$ and $r = -0.46$, respectively), with chlorophytes strongly correlated with lower flagellate abundance ($r = -0.67$).

Table 3. Pearson Product Moment Correlation Matrix for Soetendalsvlei North between environmental variables and the major taxonomic microalgal groups (n = 64, $p < 0.05$; (-) = non-significant correlations; EC = Electrical Conductivity; DO (%) = Dissolved oxygen saturation; NH_4^+ = Ammonia; TOxN = Total Oxidized Nitrogen; SRP = Soluble Reactive Phosphorus; Si = Silica; Phyto. Chl-a = Phytoplankton chlorophyll a).

	Depth	Date	Temperature	EC	Salinity	DO (%)	pH	NH_4^+	TOxN	SRP	Si	Phyto. Chl-a	Cyanobacteria	Chlorophytes	Flagellates	Diatoms	Other
Depth	1.00																
Date	-	1.00															
Temperature	-	-0.83	1.00														
EC	-	0.50	-0.89	1.00													
Salinity	-	0.51	-0.90	1.00	1.00												
DO (%)	-	-	0.52	-0.74	-0.73	1.00											
pH	-	-0.84	0.74	-0.43	-0.44	-	1.00										
NH_4^+	-	-0.51	-	-	-	-	0.32	1.00									
TOxN	-	0.40	-	-	-0.41	0.48	-0.37	-0.41	1.00								
SRP	-	0.70	-0.98	0.96	0.96	-0.63	-0.61	-	-	1.00							
Si	-	-0.67	0.85	-0.80	-0.80	0.58	0.59	-	-	-0.84	1.00						
Phyto. Chl-a	-	-0.26	-	-	-	-	-	-	-0.38	-	-	1.00					
Cyanobacteria	-	-	-0.42	0.50	0.50	-0.36	-	-	-	0.47	-0.48	-	1.00				
Chlorophytes	-	0.47	-0.35	-	-	-	-0.26	-0.38	-	0.31	-0.44	-	-	1.00			
Flagellates	-	-	-	-	-	-	-	-	-	-	-	-	-0.54	-0.72	1.00		
Diatoms	-	-0.78	0.74	-0.58	-0.59	0.41	0.54	0.39	-	-0.69	0.73	-	-0.39	-0.77	0.32	1.00	
Other	-	0.77	-0.42	-	-	-	-0.65	-0.46	0.60	0.25	-0.31	-0.35	-	0.26	-	-0.48	1.00

Table 4. Pearson Product Moment Correlation Matrix for Soetendalsvlei South between environmental variables and the major taxonomic microalgal groups (n = 54, $p < 0.05$; (-) = non-significant correlations; EC = Electrical Conductivity; DO (%) = Dissolved oxygen saturation; NH_4^+ = Ammonia; TOxN = Total Oxidized Nitrogen; SRP = Soluble Reactive Phosphorus; Si = Silica; Phyto. Chl-a = Phytoplankton chlorophyll a).

	Depth	Date	Temperature	EC	Salinity	DO (%)	pH	NH_4^+	TOxN	SRP	Si	Phyto. Chl-a	Cyanobacteria	Chlorophytes	Flagellates	Diatoms	Other
Depth	1.00																
Date	-	1.00															
Temperature	-	-0.84	1.00														
EC	-	-	-0.50	1.00													
Salinity	-	-	-0.52	1.00	1.00												
DO (%)	-	0.77	-0.38	-0.48	-0.46	1.00											
pH	-0.30	-0.75	0.35	0.54	0.52	-0.76	1.00										
NH_4^+	-	-0.55	0.35	-	-	-0.49	0.62	1.00									
TOxN	-	0.73	-0.85	0.39	0.41	0.36	-0.36	-	1.00								
SRP	-	0.72	-0.97	0.66	0.68	-	-	-	0.82	1.00							
Si	-	0.67	-0.34	-0.49	-0.47	0.73	-0.64	-0.36	0.38	-	1.00						
Phyto. Chl-a	-	-	-	0.53	0.52	-0.44	0.29	-	-	-	-0.44	1.00					
Cyanobacteria	-	0.56	-	-0.32	-0.30	0.61	-0.60	-0.50	-	-	0.32	-	1.00				
Chlorophytes	-	0.34	-	-0.58	-0.57	0.46	-0.46	-	-	-	0.70	-0.56	-	1.00			
Flagellates	-	-	-0.43	0.79	0.79	-	-	-	-	0.56	-0.49	0.41	-	-0.78	1.00		
Diatoms	-	-0.51	0.70	-0.47	-0.49	-	-	-	-0.53	-0.71	-	-	-	-	-0.62	1.00	
Other	-	-	0.37	-	-	-	-	-	-	-0.33	-	-	-	-	-	-	1.00

Table 5. Pearson Product Moment Correlation Matrix for Voëlvlei between environmental variables and the major taxonomic microalgal groups (n = 67, $p < 0.05$; (-) = non-significant correlations; EC = Electrical Conductivity; DO (%) = Dissolved oxygen saturation; NH_4^+ = Ammonia; TOxN = Total Oxidized Nitrogen; SRP = Soluble Reactive Phosphorus; Si = Silica; Phyto. Chl-a = Phytoplankton chlorophyll a).

	Depth	Date	Temperature	EC	Salinity	DO (%)	pH	NH_4^+	TOxN	SRP	Si	Phyto. Chl-a	Cyanobacteria	Chlorophytes	Flagellates	Diatoms	Other
Depth	1.00																
Date	-	1.00															
Temperature	-	-0.26	1.00														
EC	-	-0.62	-	1.00													
Salinity	-	-0.62	-	1.00	1.00												
DO (%)	-	0.56	0.52	-0.33	-0.33	1.00											
pH	-0.31	-0.75	0.64	0.59	0.58	-	1.00										
NH_4^+	-	-0.60	-	0.46	0.46	-	0.50	1.00									
TOxN	-	-	-0.49	-	-	-0.53	-0.48	-	1.00								
SRP	-	-0.36	-0.76	0.40	0.41	-0.91	-	-	0.53	1.00							
Si	-	0.95	-	-0.74	-0.74	0.61	-0.67	-0.60	-	-0.48	1.00						
Phyto. Chl-a	-	-0.39	-	0.87	0.88	-0.30	0.35	0.31	-	0.47	-0.57	1.00					
Cyanobacteria	-0.26	-0.84	0.24	0.80	0.80	-0.32	0.80	0.58	-0.26	0.25	-0.83	0.61	1.00				
Chlorophytes	0.26	0.92	-0.34	-0.78	-0.78	0.29	-0.89	-0.61	0.27	-	0.90	-0.57	-0.94	1.00			
Flagellates	-	-0.28	0.31	-	-	-	0.31	-	-	-	-0.25	-	-	-0.26	1.00		
Diatoms	-	-0.29	0.26	-	-	-	0.30	-	-	-	-0.29	-	-	-0.28	0.92	1.00	
Other	-	-0.34	0.29	-	-	-	0.34	-	-	-	-0.30	-	-	-0.29	0.89	0.82	1.00

Table 6. Pearson Product Moment Correlation Matrix for Waskraalsvlei between environmental variables and the major taxonomic microalgal groups (n = 67, $p < 0.05$; (-) = non-significant correlations; EC = Electrical Conductivity; DO (%) = Dissolved oxygen saturation; NH_4^+ = Ammonia; TOxN = Total Oxidized Nitrogen; SRP = Soluble Reactive Phosphorus; Si = Silica; Phyto. Chl-a = Phytoplankton chlorophyll a).

	Depth	Date	Temperature	EC	Salinity	DO (%)	pH	NH_4^+	TOxN	SRP	Si	Phyto. Chl-a	Cyanobacteria	Chlorophytes	Flagellates	Diatoms	Other
Depth	1.00																
Date	-	1.00															
Temperature	-	-0.33	1.00														
EC	-0.25	-0.65	-	1.00													
Salinity	-0.25	-0.65	-	1.00	1.00												
DO (%)	-	0.66	0.35	-	-	1.00											
pH	-0.42	-0.46	0.34	0.79	0.79	-	1.00										
NH_4^+	-	-0.29	-	0.37	0.36	-	0.48	1.00									
TOxN	-	-	-0.51	-0.42	-0.41	-0.26	-0.49	-	1.00								
SRP	-	-	-0.84	-	-	-0.75	-	-	0.42	1.00							
Si	0.27	0.44	-	-0.94	-0.94	-	-0.77	-0.26	0.42	-	1.00						
Phyto. Chl-a	-	-0.51	-	0.75	0.75	-0.24	0.50	-	-	0.26	-0.70	1.00					
Cyanobacteria	-	0.49	-	-0.30	-0.30	0.41	-	-	-	-0.32	-	-0.34	1.00				
Chlorophytes	0.29	-	-0.51	-0.70	-0.70	-0.40	-0.79	-0.25	0.56	0.42	0.76	-0.46	-	1.00			
Flagellates	-0.33	-	-	0.61	0.61	-	0.67	-	-0.26	-	-0.65	0.45	-	-0.67	1.00		
Diatoms	-	0.47	-	-	-	0.73	-	-	-	-0.47	-	-	-	-0.39	0.31	1.00	
Other	-	-0.32	0.53	0.25	0.25	-	0.40	-	-0.31	-0.35	-0.25	-	-	-0.36	0.34	-	1.00

Multivariate analyses

Summer sampling (February and November 2007)

Canonical correspondence analysis (CCA) for the February and November 2007 (Figure 9) sampling sessions indicate that the microalgal groups in Soetendalsvlei North and South and Waskraalsvlei were closely related to one another during February. Microalgal groups in all three lake basins were related to increased TOxN concentrations and lower silica concentrations and dissolved oxygen saturation. During November 2007, however, Waskraaslvlei was less related to Soetendalsvlei North and South, although all three wetlands still showed similar environmental correlations as in February 2007. Within Voëlvlei water quality and phytoplankton biomass were unrelated to the other wetlands during both February and November. During February 2007, phytoplankton biomass in Voëlvlei was closely related to increased salinity and electrical conductivity as well as increased concentrations of SRP and NH_4^+, and lower TOxN concentrations. In November 2007, on the other hand, phytoplankton biomass in Voëlvlei was related to increase silica concentrations and dissolved oxygen saturation, and lower concentrations of SRP and NH_4^+. For Soetendalsvlei North and South and Waskraalsvlei, all sites were closely related to the relative abundance of diatoms, flagellates and dinoflagellates, while Voëlvlei sites were related to cyanobacteria during February and chlorophyte relative abundance during November 2007.

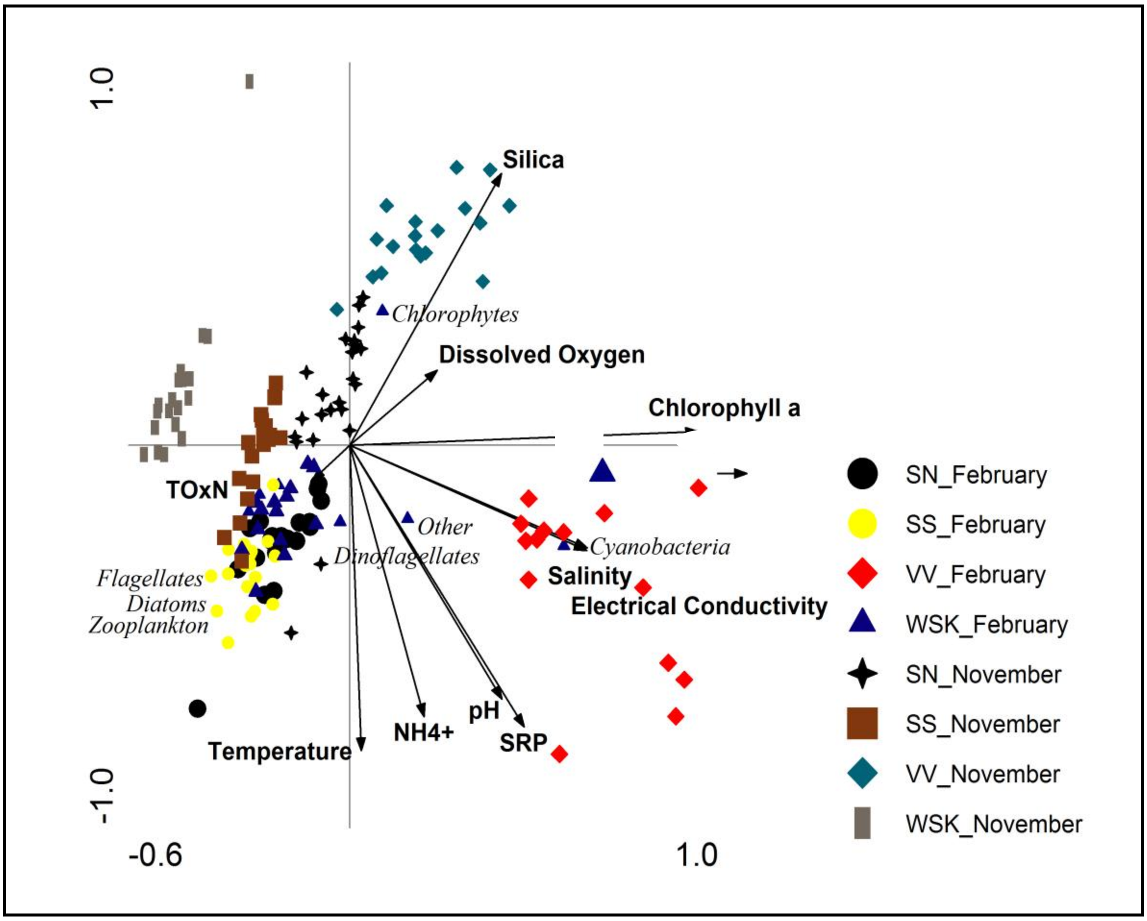


Figure 9 Canonical correspondence analysis (CCA) plot for the summer sampling periods, i.e. February and November 2007, indicating the relationship between environmental variables and the major taxonomic microalgal groups (NH4+ = Ammonium, SRP = Soluble Reactive Phosphorus, TOxN = Total Oxidised Nitrogen).

Table 7 Summary of the CCA for the summer periods, i.e. February and November 2007.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.602	0.417	0.074	0.011	1.701
Species-environment correlations	0.889	0.792	0.689	0.428	
Cumulative % variance:					
Of species data	35.4	59.9	64.3	64.9	
Of species-environment relation	54.0	91.3	98.0	99.0	
Sum of all eigenvalues					1.701
Sum of all canonical eigenvalues					1.116

Winter Sampling (May and August 2007)

Canonical correspondence analysis (CCA) for the winter sampling (Figure 10) indicated that, as for summer, microalgal groups in Soetendalsvlei North and South and Waskraaslvlei were closely related during May to one another as well as to increased dissolved oxygen saturation and TOxN concentrations. During August 2007, Soetendalsvlei North and South were also closely related to one another and again to increased dissolved oxygen saturation and TOxN concentrations. Waskraalsvlei, however, was slightly separated from the other two wetlands, and corresponded to increased TOxN concentrations and temperature and lower SRP concentrations and salinity and electrical conductivity. Voëlvlei was separated from the other three wetlands, corresponding with increased salinity and electrical conductivity as well as increased SRP concentrations and lower temperature and TOxN concentrations. During August, however, Voëlvlei corresponded with lower SRP concentrations and salinity and electrical conductivity.

Within Soetendalsvlei North and South and Waskraalsvlei, all sites were closely related to the relative abundance of diatoms, flagellates and dinoflagellates during both winter sampling periods. Within Voëlvlei, however, sites were related to high cyanobacteria relative abundance during May, and to high chlorophyte relative abundance during August 2007.

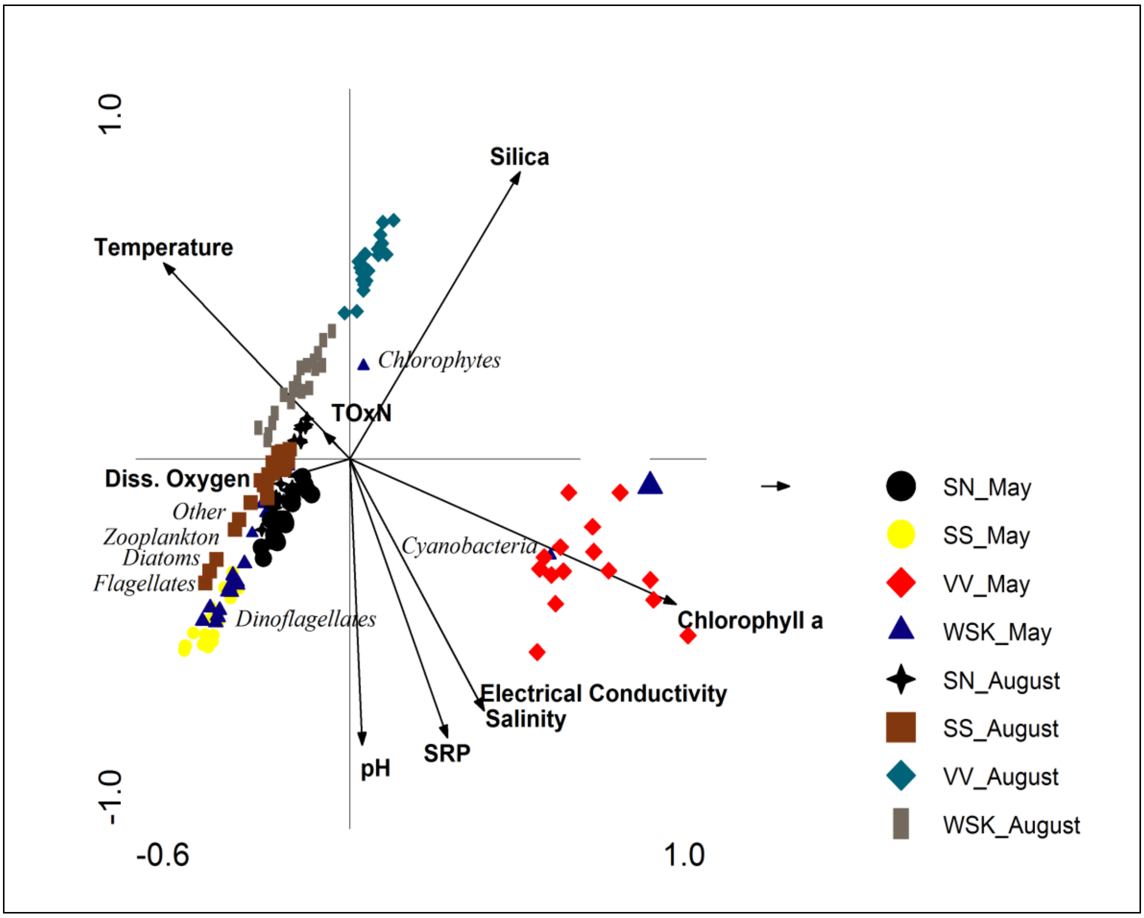


Figure 10 Canonical correspondence analysis (CCA) plot for the winter sampling periods, i.e. March and August 2007, indicating the relationship between environmental variables and the major taxonomic microalgal groups (NH4+ = Ammonium, SRP = Soluble Reactive Phosphorus).

Table 8 Summary of the CCA for the winter periods, i.e. March and August 2007.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.618	0.412	0.039	0.018	1.324
Species-environment correlations	0.956	0.933	0.678	0.603	
Cumulative % variance:					
Of species data	46.7	77.9	80.8	82.1	
Of species-environment relation	56.4	94.0	97.5	99.1	
Sum of all eigenvalues					1.324
Sum of all canonical eigenvalues					1.097

4.5. Discussion

The catchment area of the Agulhas Plain wetlands falls within the winter rainfall region of South Africa, which has its highest rainfall from April to June and lowest rainfall from November to February. During the study period the highest rainfall of approximately 65 mm was recorded in July 2007. This resulted in substantial areas of the Agulhas Plain being inundated with water, and all the study wetlands showed increases in water level. Clear seasonal differences could be observed in terms of the water temperature for the various wetlands, with temperatures in February and November significantly higher than those in May and August.

The wetlands were well oxygenated throughout the study period, with no anaerobic conditions being recorded during any of the sampling periods. Shallow lakes usually remain oxygenated throughout the year due to high wind action relative to depth, which ensures a well-mixed water column (Das *et al,.* 2008). High primary productivity rates could also be responsible for keeping the water column well oxygenated (Das *et al.,* 2008). The pH levels in all the wetlands were similar, with slightly-alkaline to alkaline conditions being recorded for most of the sampling periods. Only during periods of increased water inflow did the pH drop into the neutral range. This was most likely due to the increase in either return-flow through fynbos habitats, generally associated with the leaching of humic substances from the soil (Malan and Day, 2002), or due to the inundation of decomposing plant and algal material by high water levels, which would lower the pH of the water (Bernard *et al.,* 2004; Xiao-long *et al.,* 2007). According to Janse van Vuuren and Pieterse (2005a, b) and Das *et al.* (2008), photosynthetic activity within the water column can cause an increase in pH levels. This occurred in this study, as increased pH levels were recorded during periods of higher phytoplankton biomass (i.e. chlorophyll *a* concentrations).

Nutrient levels were generally low in all the wetlands, with the exception of SRP which ranged from 100 µg l^{-1} to 270 µg l^{-1}, falling within the upper eutrophic levels of the Department of Water Affairs and Forestry's target water quality range of < 5 µg l^{-1} for natural waters (DWAF, 1996). The high SRP concentrations are believed to result from winter die-back (Walmsley, 2000) of large areas of submerged and emergent macrophytes during mid-autumn, as well as from the high turbidity of these wetlands and the constant re-suspension of their sediments into the water column. Davies and Van Der Valk (1978) showed that 35 – 75% of the phosphorus in plant tissue can be rapidly released into the water column once death has occurred. A large proportion of phosphorus is also stored within the sediment as inorganic solid phosphorus (Malan and Day, 2002) bound to calcium, aluminium and iron oxides (Haggard and Soerens, 2006). During sediment disturbance phosphorus may become available within the water column, i.e. internal loading. Internal nutrient recycling of N and P between sediment and water column can be an important source of nutrients for primary production (Burger *et al.,* 2008). According to Smith (1983) and Burger *et al.* (2008) the greater the internal nutrient loading of a system, the more likely is the development of nuisance cyanobacteria blooms. According to Schallenberg and Burns (2003) and Das *et al.* (2008), the shallow depth of lakes such as Soetendalsvlei facilitates substantial sediment re-suspension, thereby increasing the availability of colloidal fractions of elements, e.g. phosphorus compounds, in the bottom layers of the water column. Increased river flow due to high rainfall further increases sediment re-suspension. Return-flow from poorly-managed agricultural lands could also increase the silt load of water entering a wetland, thereby affecting the overall concentrations of colloidal elements within the water column that are available for consumption by primary producers (Malan and Day, 2002). Phosphorus is considered a limiting factor in freshwater habitats (Malan and Day, 2002) and thus any change in its concentration could have significant effects on the productivity and community structure of the phytoplankton community (Froneman, 2002; 2006). Decreases in the concentration of nitrogen, especially NO_3, can also affect the concentration of SRP within the water column. As NO_3 concentration decreases, electron acceptors, vital for SRP absorption in the sediment, also decrease, resulting in enhanced rates of SRP release into the water column (Kleeberg and Kozerski, 1997; Burger *et al.,* 2008). For the wetlands in this study, the increased rainfall during July / August 2007 resulted in significant increases in river flow and freshwater inflow into the wetlands. This resulted in both increased silt input into the wetlands and the re-suspension of sediments into the water column which were most likely responsible for the significant increase in SRP concentration noted during this study. It is thus clear that phosphorus was not a limiting factor within the wetlands, which can be attributed to both agricultural practices and increased freshwater inflow during periods of rainfall.

Phytoplankton (chlorophyll *a*) production varied slightly between the wetlands, with the highest biomasses being recorded during February and May, and the lowest biomasses during November in Soetendalsvlei North and South, and during August in Voëlvlei and Waskraalsvlei. In Soetendalsvlei South, Voëlvlei and Waskraalsvlei, phytoplankton biomass could be correlated to increased conductivity, which occurred during May 2007. This corresponds well with the autumn bloom theory for phytoplankton, in which the increase in nutrients due to winter die-back of wetland vegetation results in a rapid, but short-lived, increase in phytoplankton production (Abrantes *et al.,* 2006). In the case of Voëlvlei and Waskraalsvlei, chlorophyll *a* also correlated significantly with SRP, and although Soetendalsvlei North and South did not show direct correlations between biomass and SRP, the dominant microalgal groups when biomass was high, did. In Soetendalsvlei North phytoplankton biomass was correlated with decreased TOxN concentrations, the result of TOxN uptake and utilisation by the microalgae (Abrantes *et al.* 2006). In Soetendalsvlei South, Voëlvlei and Waskraalsvlei phytoplankton biomass was also correlated with decreased Si concentrations, again indicating the uptake and utilisation of Si by siliceous microalgae, e.g. diatoms. For all the wetlands except Soetendalsvlei South, flagellates and diatoms co-occurred within the phytoplankton community. These two microalgal groups were dominant when chlorophyte relative abundance was low. However, in Voëlvlei cyanobacteria were the dominant microalgal group, and were replaced by chlorophytes during August 2007.

Shifts from diatom-dominated communities to chlorophyte and cyanobacteria domination within the various wetlands is most likely due to secondary limitation by silica as a result of the increase in phosphorus concentrations (Schelske *et al.,* 1986; Hecky and Kilham, 1988; Armitage and Fong, 2004; Carrick and Lowe, 2007) during the winter months. In all the wetlands, diatom relative abundance decreased as chlorophytes increased, which corresponded with increased phosphorus concentrations. According to Carrick and Lowe (2007), the timing and duration of phosphorus enrichment are important factors influencing the composition of phytoplankton communities. Nitrogen and phosphorus enrichment will thus result in an initial increase in growth rate and production of all major microalgal groups, but, at the same time, the demand for silica will increase until a limiting threshold is reached, leading to a decline in siliceous species (Carrick and Lowe, 2007; Janse van Vuuren *et al.,* 2007).

The dominance of chlorophytes in all the wetlands, especially in August 2007, was most likely due to their small size (high surface area: volume ratio) that ensures that chlorophytes can rapidly consume and utilise nutrients within the water column. However, according to Cloern and Dufford (2005), this advantage disappears during periods of high nutrient input, when larger, fast-responding algae dominate. Abrantes *et al.* (2006) also found that zooplankton grazing can have significant impacts on the biomass and diversity of phytoplankton within wetlands. Under high nutrient concentrations and light conditions there would be an increase in productivity of both small- and large-celled algae. However, an increase in a food source results in an increase in the community of consumers which prefer the smaller algae. Consequently the phytoplankton community becomes dominated by the larger, less palatable algae, such as cyanobacteria. There would thus be a succession from a chlorophyte-dominated community to a cyanobacteria-dominated community (Abrantes *et al.,* 2006). As the high rainfall event also occurs mainly during the winter rainfall season, the decrease in water temperature would favour chlorophytes over cyanobacteria (Ameryk *et al.,* 2005; Janse van Vuuren *et al.,* 2007; Allan and Froneman, 2008). Although the relative abundance of chlorophytes was highest during August 2007, overall phytoplankton biomass was the lowest during this period. During winter, phytoplankton production is generally low (Schumann *et al.,* 2005) due to a reduction in solar radiation available for photosynthesis (Abrantes *et al.,* 2006; Xiao-long *et al.,* 2007). The lower phytoplankton biomass recorded during August could also have been due to the 'dilution' effect of the increase in river flow into the wetlands (Das *et al.,* 2008), decreasing the chlorophyll *a* concentrations as the volume of water in the lakes and hydraulic flushing increased (Harding, 1992). According to Cloern and Dufford (2005) most phytoplankton communities are characterised by 'boom-bust' cycles of the larger-celled groups, while the smaller-celled algae remain fairly stable throughout. This could explain the high relative abundance of chlorophytes during the winter period in our study, when productivity of the larger algal groups was lowest.

The dominance of cyanobacteria within Voëlvlei indicates poor water quality (Janse van Vuuren *et al.,* 2007), which is most likely due to a prolonged water residence/retention time (Asaeda *et al.,* 2001). Because of its unique hydrology, Voëlvlei receives reverse flow from the Nuwejaars River via its outflow channel during flood periods. During periods of high freshwater input, water from the Nuwejaars River flows into Voëlvlei. Once this wetland has reached maximum levels, the excess water flows eastwards towards Soetendalsvlei (*personal communication with landowners*). Only when the water level within the Nuwejaars River has dropped will the wetland drain, through the same outflow channel, into the Nuwejaars River, this cause the long residence time. The July/August 2007 rainfall supported this water circulation mechanism, as the rapid input of freshwater resulted in a shift from cyanobacteria to chlorophytes. It is, however, not clear whether this succession from cyanobacteria to chlorophytes was due to the increased rainfall, or due to chlorophytes being more tolerant to lower water temperatures (Janse van Vuuren and Pieterse, 2005a, b; Janse van Vuuren *et al.,* 2007), or else due to a natural succession, as was found at Hartbeespoort Dam near Pretoria (van Ginkel and Silberbauer, 2007). High internal nutrient loading within Voëlvlei from the sediments could be another cause for its dominance of cyanobacteria during the summer periods when reduced freshwater inflow occurs. Harding (1992) showed that high productivity of cyanobacteria within Zeekoevlei occurred due to high internal nutrient loading during summer, when wind-induced mixing maintained the cells within the photic zone, thus maximising production. This seems to apply to Voëlvlei as well, where strong south-westerly winds could have an added affect on the very high levels of cyanobacteria production recorded in this wetland throughout the study. According to Harding (1992), Harding and Paxton (2001) and Janse van Vuuren and Pieterse (2005a, b), cyanobacteria can attain very high levels of production within shallow, nutrient-rich and warm lakes and wetlands, as was observed in Voëlvlei during February and May 2007.

The timing of increased freshwater inflow into the wetlands, especially Voëlvlei, appears to be very important in limiting the formation of nuisance cyanobacteria blooms. During the majority of the sampling periods, phytoplankton production was very high when cyanobacteria were the dominant microalgal group. Should increased rainfall and the subsequent increase in nutrient levels have occurred during the warmer summer periods, cyanobacteria might have been able to develop prolonged blooms, further decreasing the water quality of Voëlvlei and having severe impacts on other trophic levels of this wetland. At present it appears that the July / August 2007 rainfall event re-set the wetlands, improving their water quality, with the exception of SRP concentrations.

Overall, it would appear that the two main driving factors for the wetlands of the Agulhas Plain are freshwater inflow, which can be directly linked to rainfall and nutrient input, and wind-induced mixing of the water column. Phosphorus is also not limiting to production in any of the systems, resulting in the dominance of chlorophytes and cyanobacteria throughout.

4.6 Conclusion

Voëlvlei showed signs of eutrophication, mainly due to the presence of cyanobacteria such as *Anabaena* and *Trichomes* sp., which were associated with warmer water, pH levels of approximately 8 and high ammonium and SRP concentrations. This could potentially result in harmful algal blooms as well as anoxic conditions, which would have negative impacts on birds that use this wetland for foraging and shelter. Waskraalsvlei, on the other hand, had very low phytoplankton biomass, but was dominated by reeds and submerged macrophytes. Soetendalsvlei North and South lake showed some similarities in microalgal community structure and environmental variables. Reed growth and the lack of connection between its two sections may have detrimental effects on the system in the future. The lack of back-flooding of saline estuarine water into the lakes may further impact on both their physical and chemical environment, as well as on their phytoplankton community structure. This needs to be re-assessed in relation to the artificial breaching of the mouth of the Heuningnes Estuary.

Chapter 5

Water quality and phytoplankton community structure of the Heuningnes River and Estuary

5.1 Introduction

Estuaries are intrinsically important ecosystems as they provide a range of vital goods and services (Allanson, 2001; Armitage and Fong, 2004). They are highly productive systems acting as nursery grounds for mainly marine taxa and are responsible for the amelioration of water quality. Estuaries are characterised by the measurable dilution of sea water by freshwater, resulting in a gradient in salinity along the length of the estuary (Day, 1981). The South African coastline is characterised by different estuary types that include permanently open, temporarily open/closed (TOCE), river mouths, estuarine lakes and estuarine bays (Whitfield and Lubke, 1998). The formation of each of these estuary types are mainly determined by geomorphology, topography and river discharge (Allanson, 2001), and each type has specific physical characteristics that determine the chemical properties thereby affecting the overall ecological function of that particular system. According to Whitfield (1992) and Breen and McKenzie (2001) nearly 70% of South African estuaries are classified as temporarily open/closed systems (TOCE's), whereby the estuary is separated from the sea for extended periods of time by a sandbar or berm across the mouth of the estuary due to low freshwater inflow being insufficient to maintain an open connection (Allanson, 2001; Taljaard *et al.*, 2009a, b). Once adequate water levels are reached, the estuary will breach the berm and an open connection will be re-established, ensuring tidal exchange and the re-establishment of a longitudinal salinity gradient. Marine taxa will migrate into the estuary, generally for spawning purposes and juvenile taxa will move upstream.

The Heuningnes Estuary has historically been classified as a temporarily open/closed estuary, with extended periods of mouth closure influencing the physical and chemical characteristics of this system. But as stated earlier, due to backflooding of valuable agricultural land (~24,000 ha, figure 3, pg. 66.), the mouth is currently breached during periods of closure and high freshwater inflow. This will have severe effects on the chemical characteristics of this system as breaching of the mouth is not synchronised with seasonal freshwater inflow that would ensure a longitudinal salinity gradient, or that marine intrusion is limited during the dry, summer periods.

The conceptual model of Snow and Tajlaard (2007) for South African TOCE's describes three phases of mouth condition that affect the chemical characteristics of these systems. During the first phase, i.e. open, tidal exchange ensures a longitudinal and vertical salinity gradient throughout the estuary (Allanson, 2001; Taljaard *et al.,* 2009a, b), with nutrient input from both the marine and catchment area (Slinger *et al*., 1998; Snow and Taljaard, 2007). However, due to strong tidal action, the residence time for this phase is generally short, resulting in limited nutrient uptake and hence lower primary productivity throughout the system (Perissinotto *et al*., 2002). During the second phase, i.e. semi-closed, berm built-up is high enough to limit tidal exchange, but freshwater overtopping and marine overwash can occur at times. During this phase, nutrient input is mainly from the river inflow, with pulses of marine input associated with overwash events. Residence time is longer and primary productivity is increased. Due to limited marine water entering the system and continuous freshwater inflow, the estuary will become brackish and with high wind mixing, the water column will become homogenous. During the third phase, i.e. closed, berm build-up restricts any exchange of water (i.e. overwash or overtopping) and freshwater inflow is the main source of nutrients to the estuary. Residence time is longer and primary productivity increases until nutrient depletion occurs. Once water column nutrients have been depleted, biochemical and groundwater nutrient input will then determine primary production within these systems (Slinger *et al.,* 1998; Snow and Taljaard, 2007). Again the system will become homogenously fresh due to limited marine influence and continuous freshwater inflow. However, in systems where freshwater inflow is severely limited, reverse salinity gradients and hypersaline conditions can occur due to high evaporation rates, e.g. Lake St. Lucia, KwaZulu-Natal (Gordon *et al.,* 2008). In the case of the Heuningnes Estuary, reverse salinity gradients have been recorded in the past with salinities of ~50 ppt recorded in the upper reaches (Bickerton, 1984). The water quality of Heuningnes Estuary, however, is not only affected by the condition of its mouth, but also by the inflowing water from Soetendalsvlei Lake.

According to Allanson (2001) estuaries formed from barrier or estuarine lakes are influenced by the fact that river flow over the coastal plain is interrupted by these barrier lakes, which overflow into the estuary. In most instances the balance between freshwater inflow and water loss via evaporation is responsible for the chemical composition of the water column and subsequently the water flowing into the estuary. Should freshwater inflow exceed water loss, the lake is fresh, but should evaporative water loss exceed inflow, the lake may become hypersaline, e.g. St. Lucia (Allanson, 2001). In the case of Soetendalsvlei and the Heuningnes Estuary, water exchange is limited due to the construction of a weir at the overflow from the lake into the estuary. It is believed that limiting the back-flooding into the lake with estuarine water during closed mouth conditions, may have further altered the lake system to a freshwater system, thereby affecting the overall water quality of any overflow into the estuary. Since water quality, especially salinity (Bornman *et al.,* 2002; 2008; Pilkaityte *et al.,* 2004), affects the biota of both systems this could have severe effects on the overall ecological functioning of both systems and ultimately lead to loss in biodiversity. Since the estuary management plan (EMP) recommends that "*an ecological corridor is maintained along the river to ocean and that the associated flora and fauna are protected*" (HilLand Associates, 2008), it is vital to understand how these two systems compare at present, with the palaeolimnological study providing evidence of the past influence the estuary had on the water quality and phytoplankton community, prior to artificial breaching and agricultural impacts.

Phytoplankton productivity is important in estuaries as it takes place at the very lower level of the food web. Phytoplankton biomass and community structure is primarily regulated by nutrient concentrations and available light levels (Fathi and Flower, 2005), but also by grazing and resource competition between taxonomic groups and species (Armitage and Fong, 2004; Cloern &

Dufford, 2005). Sources of nutrients in estuaries include precipitation, freshwater inflow, salt marsh production and sediment porewater during resuspension (Lopes *et al.*, 2007). With an increase in nutrients, phytoplankton blooms generally develop, and may lead to changes in the water quality (i.e. pH and dissolved oxygen levels) of a particular system, and can have cascading effects within the food web (Armitage and Fong, 2004). It is generally accepted that coastal waters are nitrogen limited, while freshwater systems are phosphorus limited (Floder *et al.*, 2006; Lopes *et al.*, 2007). Within estuaries, it is however very difficult to establish whether nitrogen or phosphorus is the limiting nutrient due to the continuous inflow of freshwater inputs and marine intrusions. Consequently estuaries will show a shift in the phytoplankton biomass and community structure between the upper, middle and lower reaches due to varying nutrient concentrations and shifts in the ratios of nutrient elements to one another, i.e. N:P, N:Si and P:Si (Lopes *et al.*, 2007; Li *et al.*, 2007).

The aim of this study was to assess the present water quality and phytoplankton community structure of the Heuningnes Estuary and compare the findings with the conceptual model for South African TOCE's (Snow and Taljaard, 2007; Taljaard *et al.,* 2009a). The study will also aid in determining whether diatom taxa found in the sediment cores in the Soetendalsvlei come from marine or estuarine sources via the Heuningnes Estuary and River. An assessment of the similarities in water quality and phytoplankton community structure between the lake, river and estuary will also assist in determining the connectivity between the different systems, the effect of limited back-flooding on the coastal lake and the effect of the weir on the exchange of water between the two systems.

Hypotheses tested in this chapter were:

- During periods of mouth closure a reverse salinity gradient will be established within the estuary.
- Diatom taxa will contribute significantly to the microalgal community in terms of relative abundance (~50%).

- Marine diatom taxa will dominate the community due to the large tidal exchange within the estuary when the mouth is open.
- Freshwater diatom taxa will increase in relative abundance during the rainfall periods, i.e. August, due to increased freshwater inflow and water exchange between Soetendalsvlei and the estuary.
- Water quality parameters (salinity, pH, DO%, nutrients) and phytoplankton community structure between Soetendalsvlei and the Heuningnes River and Estuary are statistically similar, especially during periods of overflow from the coastal lake into the estuary.

5.2. Sampling stations

Three sampling stations were selected along the Heuningnes Estuary and River to represent the various estuarine reaches, i.e. lower, middle and upper reaches (Plate 14 Figure 11). The lower reach sampling station was situated in the middle of the channel opposite the CapeNature office buildings at the De Mond Nature reserve and upstream of the walk-bridge. The middle reach sampling station was situated approximately 7 km upstream at the start of the dense *Phragmites australis – Schoenoplectus scripoides* stand, but still where flood-plain salt marsh was present. The upper reach sampling station was located above the Bredasdorp / Struisbaai Bridge in a narrow channel with dense *P. australis* and *S. scirpoides* stands on both sides of the channel.

Plate 10 The lower reaches of the Heuningnes Estuary indicating the very high water levels attained during a period when the mouth was closed (August 2007).

Plate 11 Dune stabilization at the mouth of the Heuningnes Estuary using dried branches of *Acacia cyclops*.

Plate 12 Aerial photograph of the Heuiningnes Estuary in 1938 indicating a wide main channel and floodplain area.

Plate 13 Aerial photograph of the Heuningnes Estuary in 1980 indicating a much narrower main channel and the stabilised (vegetated) dune fields on the south-western section of the mouth.

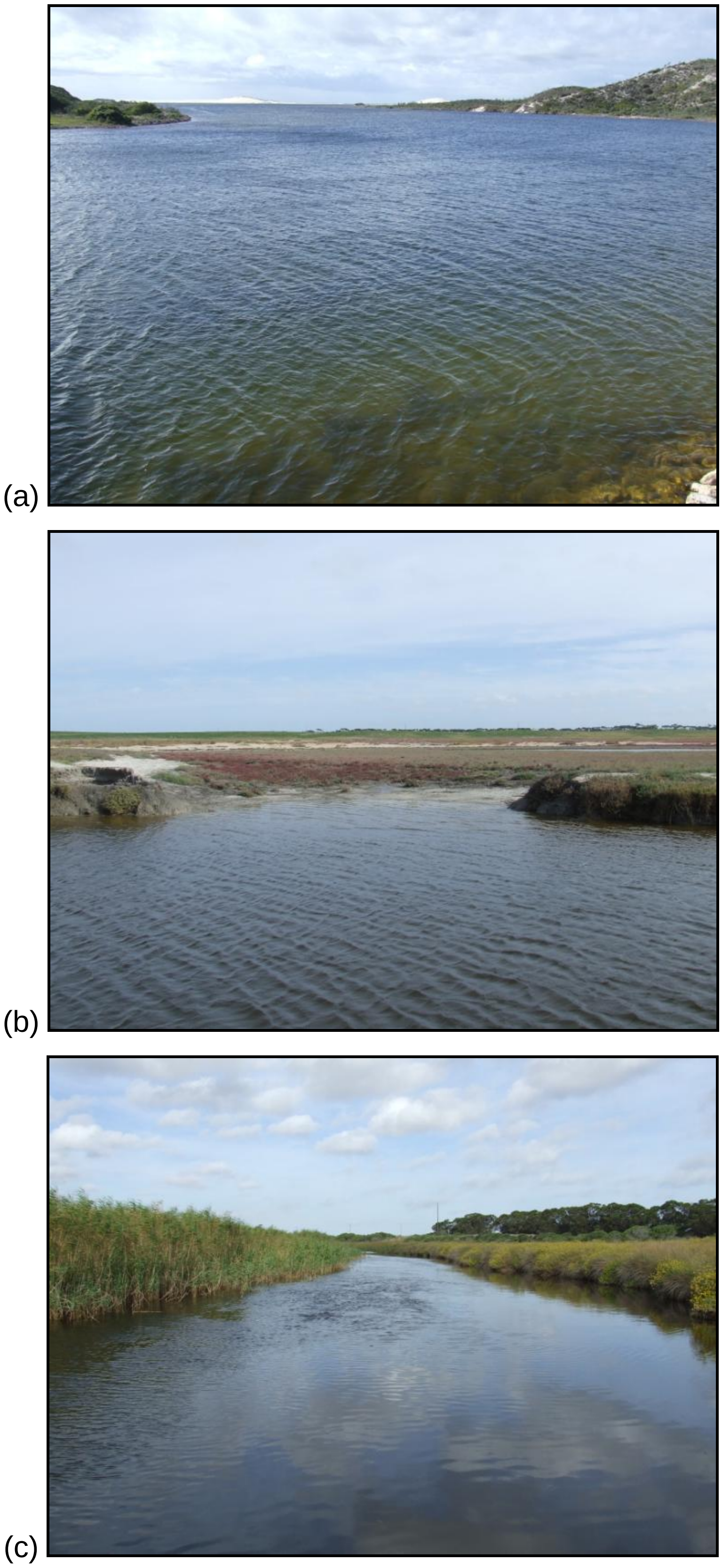


Plate 14 The various reaches of the Heuningnes Estuary; (a) Lower, (b) Middle and (c) Upper.

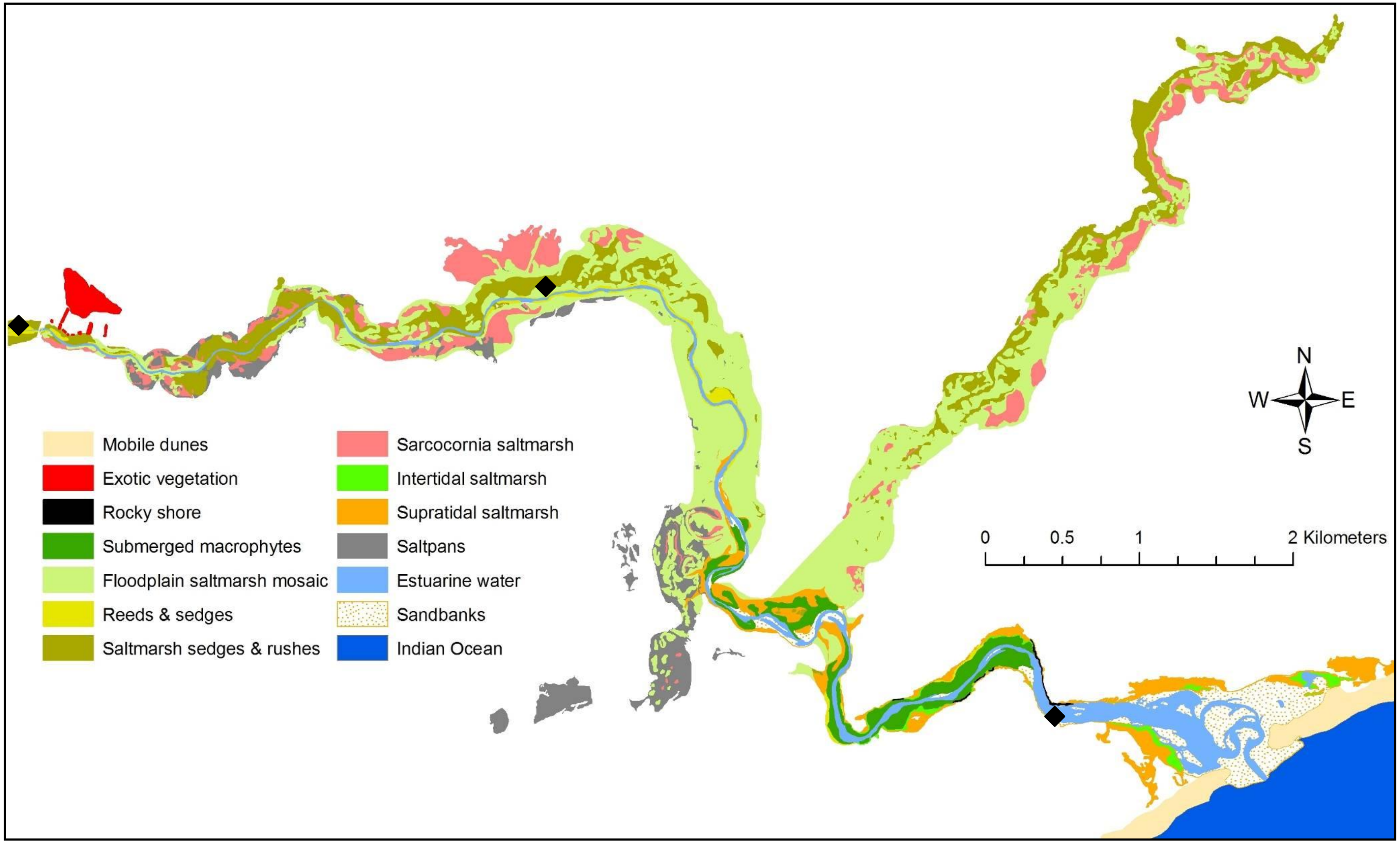


Figure 11 Vegetation map of the Heuningnes River and Estuary indicating the three sampling stations (♦) (with permission from Bornman, C.A.P.E. Estuaries Programme, 2007).

5.3 Materials and Methods

Sampling was undertaken in February, May, August and November 2007 to capture wet-dry and winter-summer cycles. Physical and chemical variables and phytoplankton biomass and community structure were analysed at each of the stations as reported in Section **4.3 Materials and Methods, Chapter 4, pg 65 -67.**

5.4 Results

The rainfall data presented in the preceding Chapter 4 (Figure 5, pg 75) will be referred to in this chapter with regard to the period of high freshwater inflow and increased water levels within the Heuningnes River and Estuary.

5.4.1 Physical and chemical parameters

Water Clarity

Water clarity as measured by Secchi disk (Figure 12) at the different sampling stations during the different periods, indicated clear water during open mouth, marine conditions (i.e. February and May 2007) throughout the estuary, while during the period of mouth closure when freshwater inflow was high (i.e. August 2007), water clarity decreased substantially, especially in the upper reaches (~25%). Subsequently however, a reverse gradient in clarity throughout the estuary was observed in November 2007, with lowest clarity in the lower reaches (~25%). The middle reaches showed greatest variability during the different sampling periods, with lowest water clarity measured in November 2007 at ~50%.

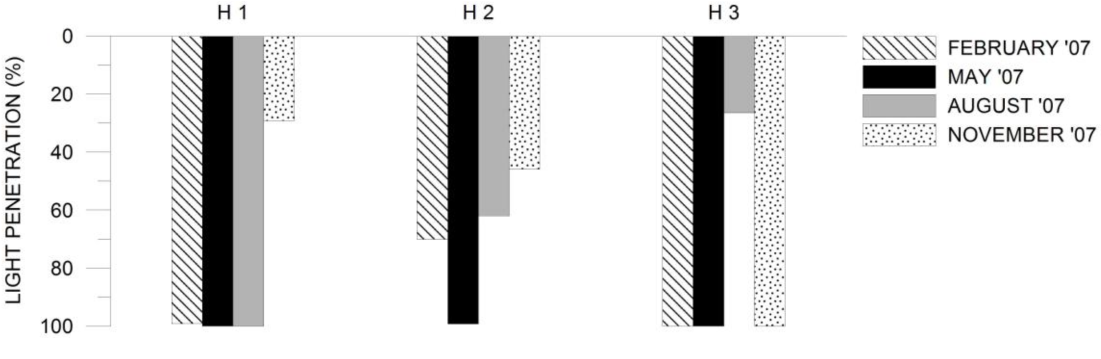


Figure 12 Light penetration (%) as measured by Secchi depth for the different reaches during the different sampling periods.

Temperature

There was a clear seasonal pattern in the water temperature (Figure 13) of the Heuningnes Estuary with mean summer temperatures of 25.5 ± 0.1°C and 18.3 ± 0.1°C (February and November, respectively) significantly higher than the mean winter temperatures of 15.3 ± 0.2°C and 14.9 ± 0.1°C measured in May and August, respectively ($n = 27$, $p < 0.001$). During open mouth conditions with strong marine influence, longitudinal gradients were observed with higher temperatures recorded in the upper reaches during February (~26.4°C, $n = 9$, $p <0.001$), and in the lower reaches during May (~16.3°C, $n = 9$, $p <0.001$). Although not evident in February, vertical stratification was present in May, with significantly warmer bottom marine water throughout the estuary (~15.7°C, $n = 9$, $p< 0.001$). During closed mouth conditions with high freshwater inflow (i.e. August), highest temperature was recorded in the middle reaches (~15.2°C). When the mouth was breached in November, there was a uniform temperature profile of approximately 18.3°C along the length of the estuary.

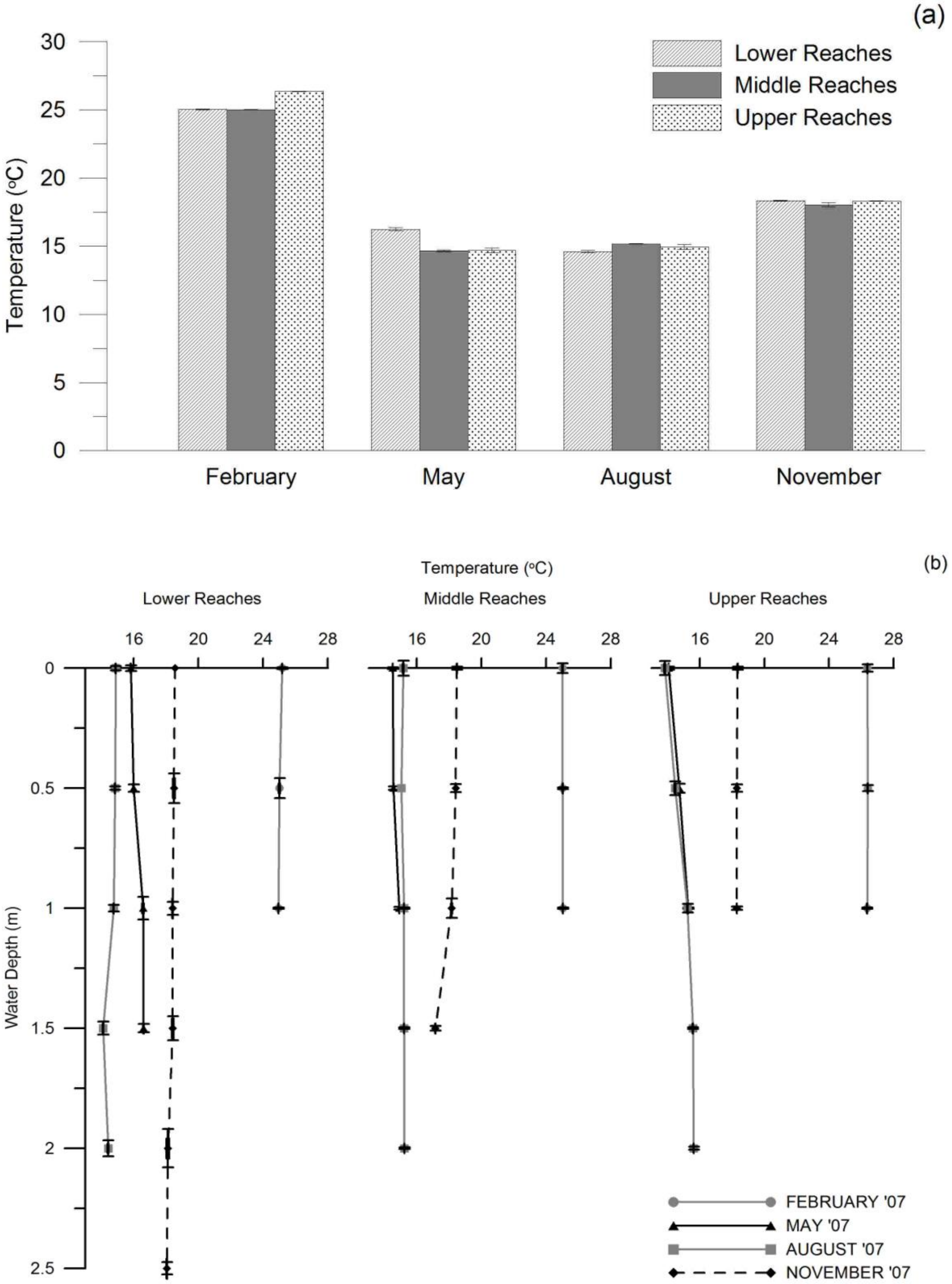


Figure 13 Water temperature (°C) for the Heuningnes Estuary during the various sampling periods; (a) the different reaches of the estuary and (b) different depths at the various reaches.

Electrical conductivity and Salinity

Water column electrical conductivity (EC) and salinity followed very similar patterns throughout the study period (Figure 14 and 15). During each of the sampling periods, longitudinal EC and salinity gradients were observed, with significantly higher values recorded in the lower reaches decreasing upstream. Although these gradients were observed throughout the study, the range of each gradient varied. During open mouth conditions, these gradients ranged from 54 $mS.cm^{-1}$ (36 ppt) to 53 $mS.cm^{-1}$ (35 ppt) to 34 $mS.cm^{-1}$ (22 ppt) during February, and from 56 $mS.cm^{-1}$ (37 ppt) to 43 $mS.cm^{-1}$ (28 ppt) to 31 $mS.cm^{-1}$ (19 ppt) during May. During closed mouth conditions (i.e. August), there was an overall reduction in EC and salinity throughout the system and the overall longitudinal gradient was much reduced ranging from 41 $mS.cm^{-1}$ (26 ppt) to 38 $mS.cm^{-1}$ (24 ppt) to 31 $mS.cm^{-1}$ (19 ppt) in the upper reaches. In response to the breaching of the mouth in November, there was a sharp decrease in EC and salinity in the upper and middle reaches, with increased marine influence in the lower reaches. Consequently the longitudinal gradient was strong ranging from 49 $mS.cm^{-1}$ (32 ppt) to 15 $mS.cm^{-1}$ (9 ppt) to 4 $mS.cm^{-1}$ (2 ppt) in the upper reaches. Vertical EC and salinity gradients were observed during the winter periods (i.e. May and August) where bottom water was significantly higher (34 – 47 $mS.cm^{-1}$ (21 – 31 ppt) and 41 – 43 $mS.cm^{-1}$ (26 – 28 ppt), respectively) than surface water (26 – 41 $mS.cm^{-1}$ (16 – 26 ppt) and 6 – 41 $mS.cm^{-1}$ (4 – 26 ppt) respectively; $n = 9$, $p < 0.001$).

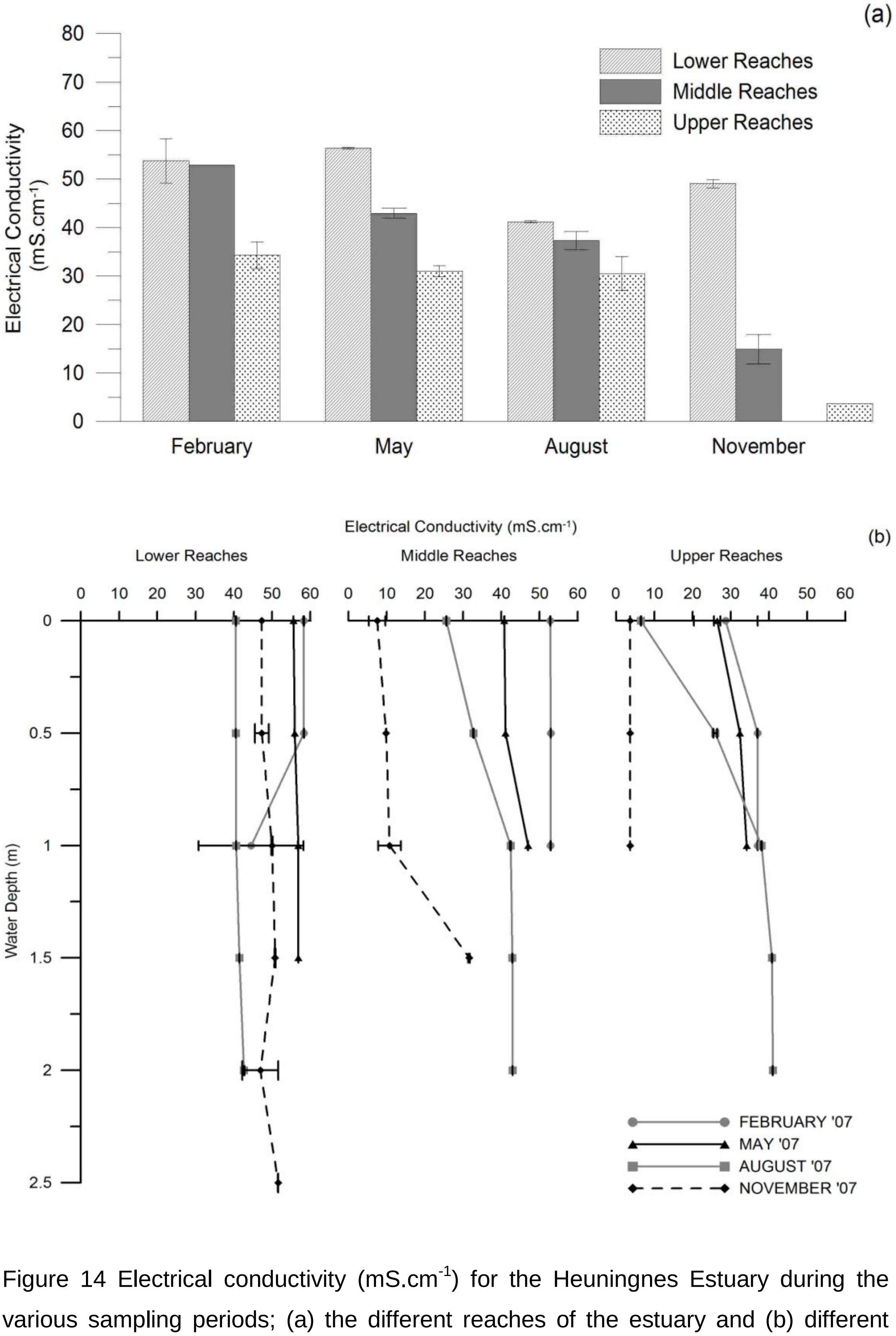


Figure 14 Electrical conductivity (mS.cm^{-1}) for the Heuningnes Estuary during the various sampling periods; (a) the different reaches of the estuary and (b) different depths at the various reaches.

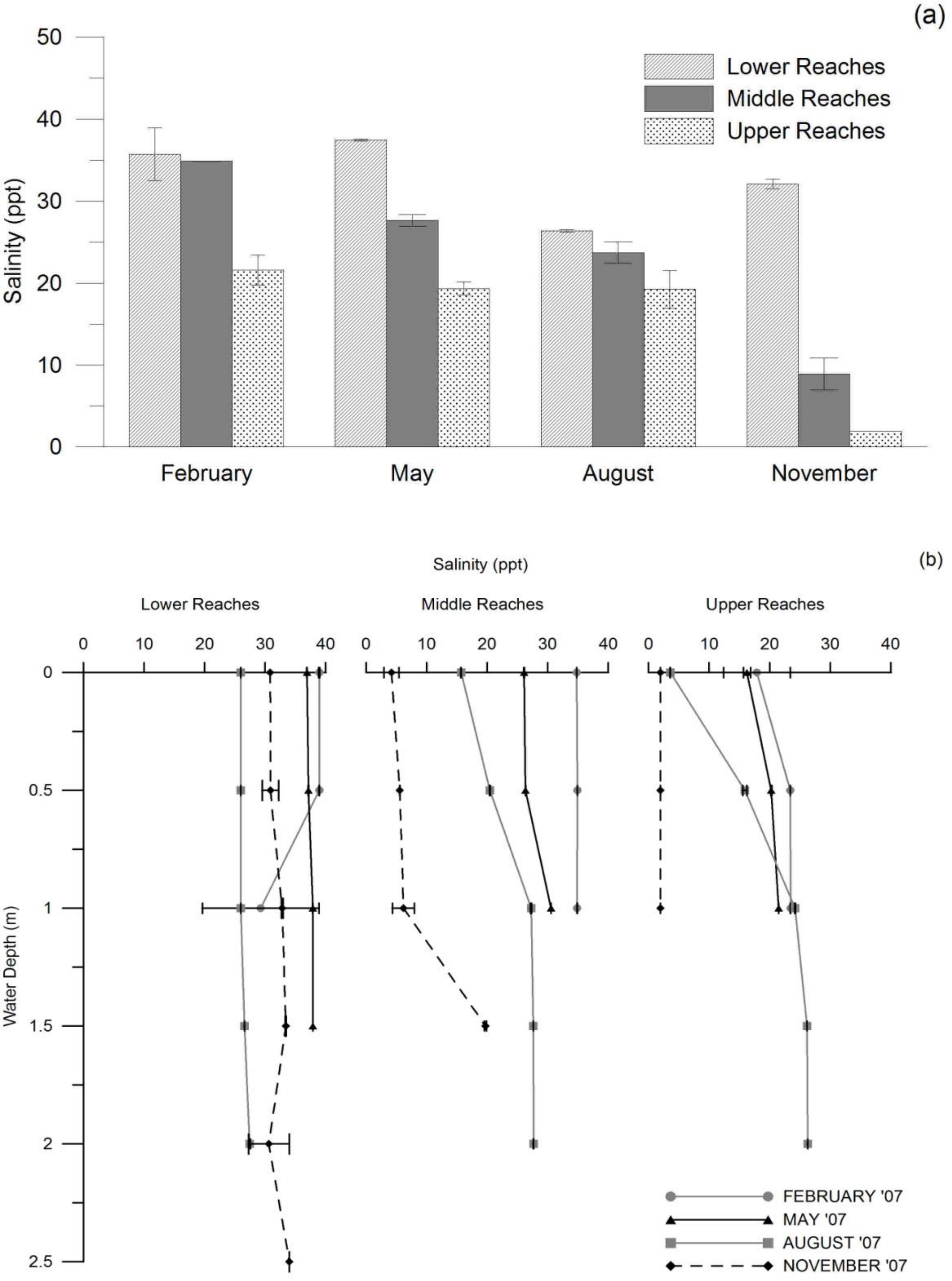


Figure 15 Water column salinity (ppt) for the Heuningnes Estuary during the various sampling periods; (a) the different reaches of the estuary and (b) different depths at the various reaches.

Dissolved Oxygen (% saturation)

Throughout the study period the estuary was well oxygenated and no anoxic conditions were detected (Figure 16). Overall dissolved oxygen saturation was the highest during November with a mean value of 84.5 ± 2.5 % ($n = 27$, $p < 0.001$). During February saturation levels were similar throughout the estuary (~ 39 %), while a longitudinal gradient was evident for the remaining sampling periods with higher saturation in the lower reaches (42, 41 and 98%, respectively) compared to the upper reaches (36, 30 and 63%, respectively, $n = 27$, $p < 0.001$).

Some vertical differences in saturation were observed during May, August and November. During May, oxygen saturation was significantly higher in the bottom waters at the lower (43%) and upper (39%) reaches of the estuary ($n = 27$, $p < 0.001$) During August and November, however bottom water oxygen saturation was significantly lower (28 – 41% and 62 – 96%, respectively) than the surface waters (37 – 45% and 64 – 100%, respectively).

pH

Overall pH throughout the estuary remained slightly alkaline (Figure 17), with highest levels recorded in February and November of 8.1 ± 0.02 ($n = 27$, $p < 0.001$). The lowest recorded levels were measured in August of 7.1 ± 0.05 ($n = 27$, $p < 0.001$). During February significantly higher pH levels were recorded in the middle reaches (8.0 ± 0.02) of the estuary, while during May and August a longitudinal gradient existed from the lower (8.0 ± 0.01 and 8.1 ± 0.01, respectively) to the upper reaches (7.9 ± 0.01 and 7.3 ± 0.06, respectively). During November, however, the system was well mixed with a mean pH level of 8.1 ± 0.02. Differences between surface and bottom water were observed during each of the sampling periods. During February surface water pH was lowest at the mouth (8.0 ± 0.07), while during May surface water pH was lowest at the mouth and middle reaches (7.9 ± 0.01). In August surface water pH was lowest in the middle reaches (7.5 ± 0.06) and highest in the upper reaches (7.8 ± 0.02), and in November surface water pH was lowest at the mouth (7.8 ± 0) and highest in the middle (8.1 ± 0.01) and upper (8.2 ± 0.01) reaches.

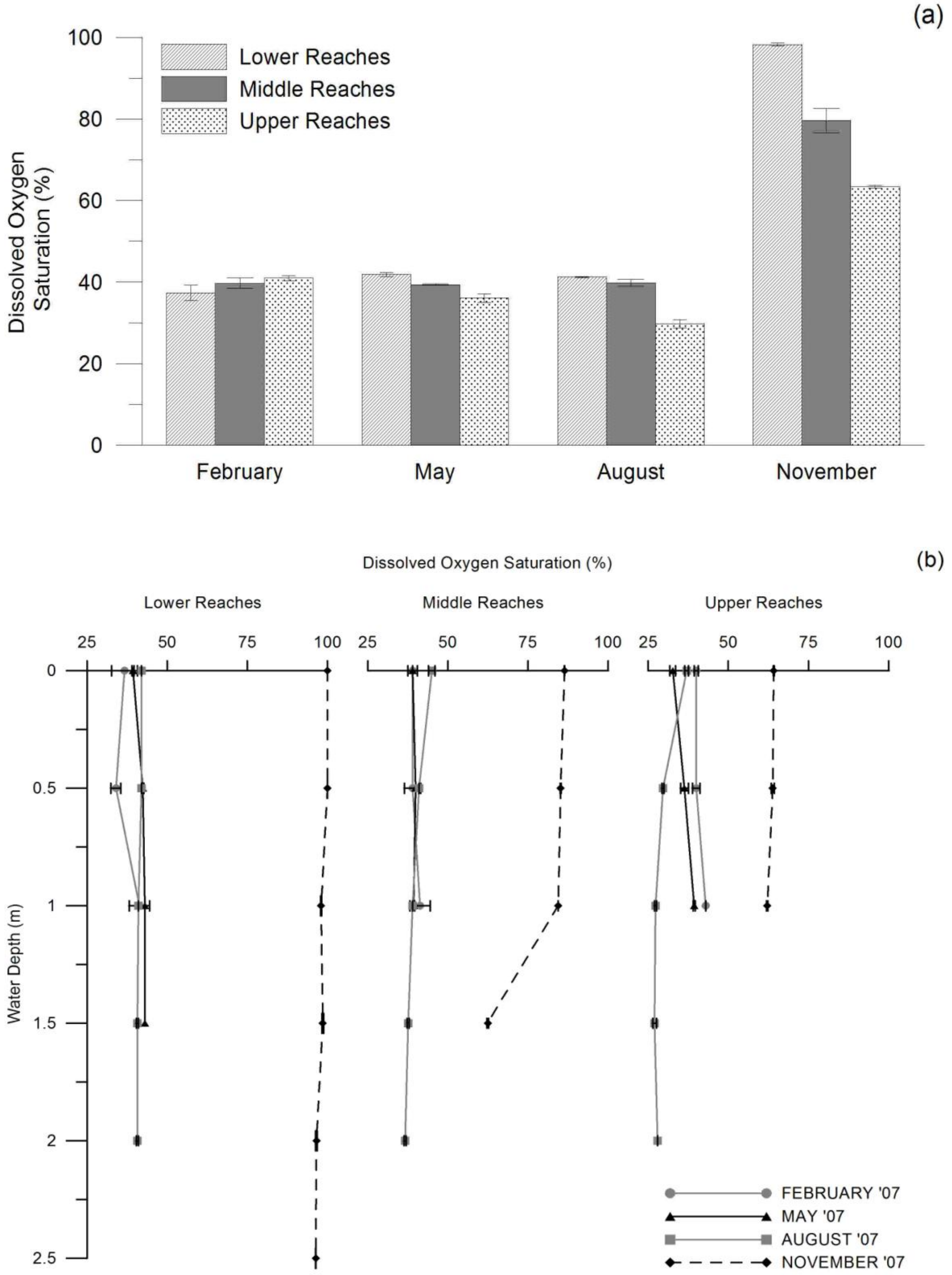


Figure 16 Dissolved oxygen saturation (%) for the Heuningnes Estuary during the various sampling periods; (a) the different reaches of the estuary and (b) different depths at the various reaches.

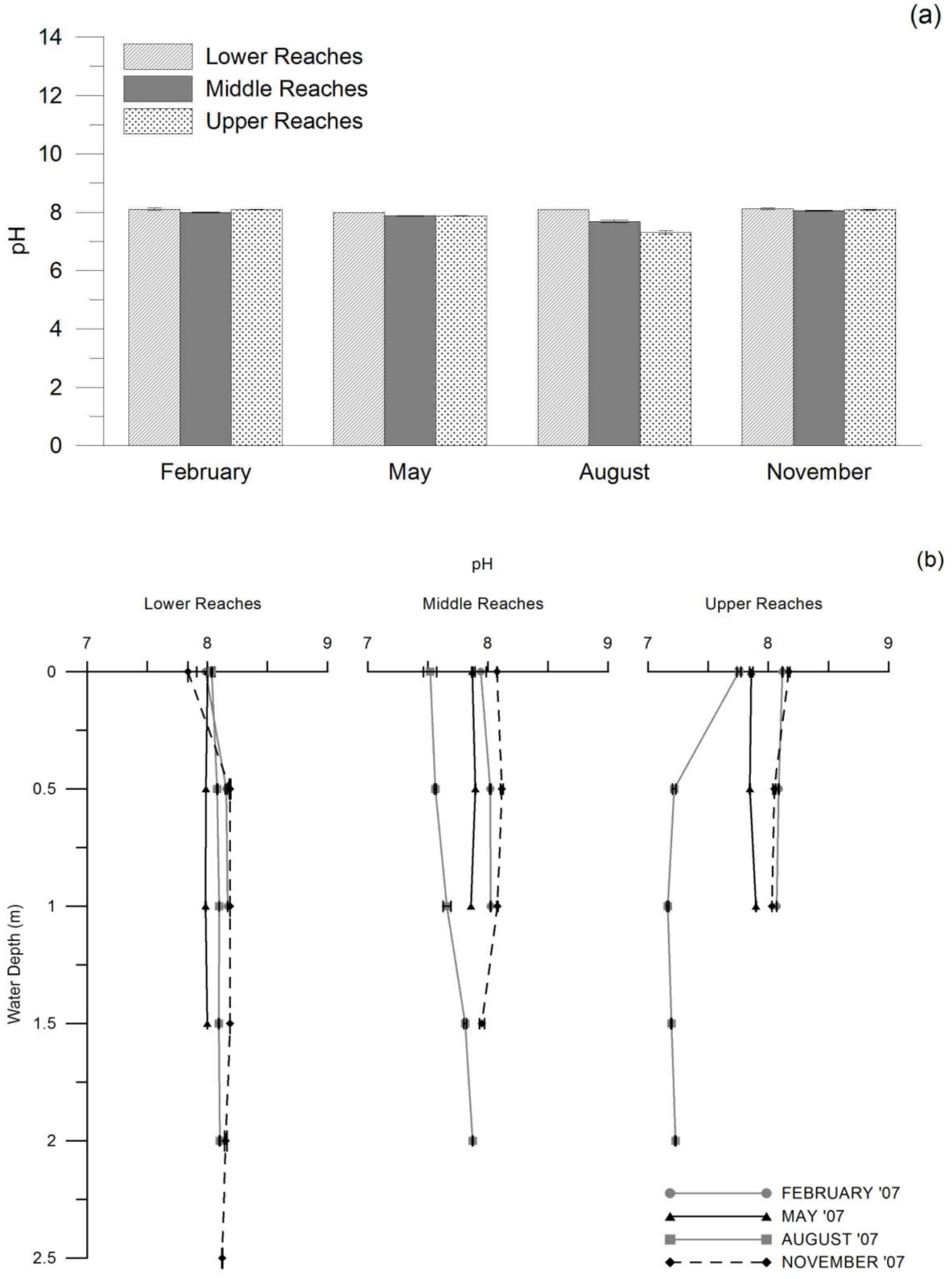


Figure 17 pH levels for the Heuningnes Estuary during the various sampling periods; (a) the different reaches of the estuary and (b) different depths at the various reaches.

5.4.2 Nutrients

Ammonium

Ammonium concentrations did not vary significantly with depth (Figure 18). During open mouth conditions with strong tidal exchange, concentrations were high. Highest concentrations were measured during May in the lower and middle reaches (661 ± 178 $\mu g.l^{-1}$ and 372 ± 100 $\mu g.l^{-1}$, respectively, $n = 18$, $p < 0.001$). During closed mouth conditions (i.e. August), concentrations were below detectable limits in both the lower and middle reaches, with very low recordings in the upper reaches (2.2 ± 1.9 $\mu g.l^{-1}$). Subsequent to the breaching of the estuary mouth, there was an increase in concentration throughout the estuary varying from 106 to 136 $\mu g.l^{-1}$ in the upper reaches.

Total Oxidized Nitrogen (TOxN)

Mean overall total oxidized nitrogen (TOxN) concentrations (Figure 19) were highest in May (33 ± 5 $\mu g.l^{-1}$), especially in the lower reaches (47 ± 11 $\mu g.l^{-1}$). Concentrations decreased with closed mouth conditions in August to 30 ± 1 $\mu g.l^{-1}$, which decreased even further in November to 20 ± 3 $\mu g.l^{-1}$. The only vertical differences in concentrations were also observed in May in the lower reaches, where bottom water had highest concentrations (79 ± 1 $\mu g.l^{-1}$).

Soluble Reactive Phosphorus (SRP)

Throughout the estuary, SRP concentrations remained fairly uniform during each of the sampling periods (Figure 20). Highest overall mean SRP concentrations were recorded in August (~212 $\mu g.l^{-1}$), closely followed by May (~204 $\mu g.l^{-1}$). Concentrations in February and November, however, were significantly lower (~29 $\mu g.l^{-1}$ and ~8 $\mu g.l^{-1}$, respectively, $n = 18$, $p < 0.001$). Vertical differences were only measured in May in the middle reaches with significantly higher concentrations in the bottom water (~273 $\mu g.l^{-1}$).

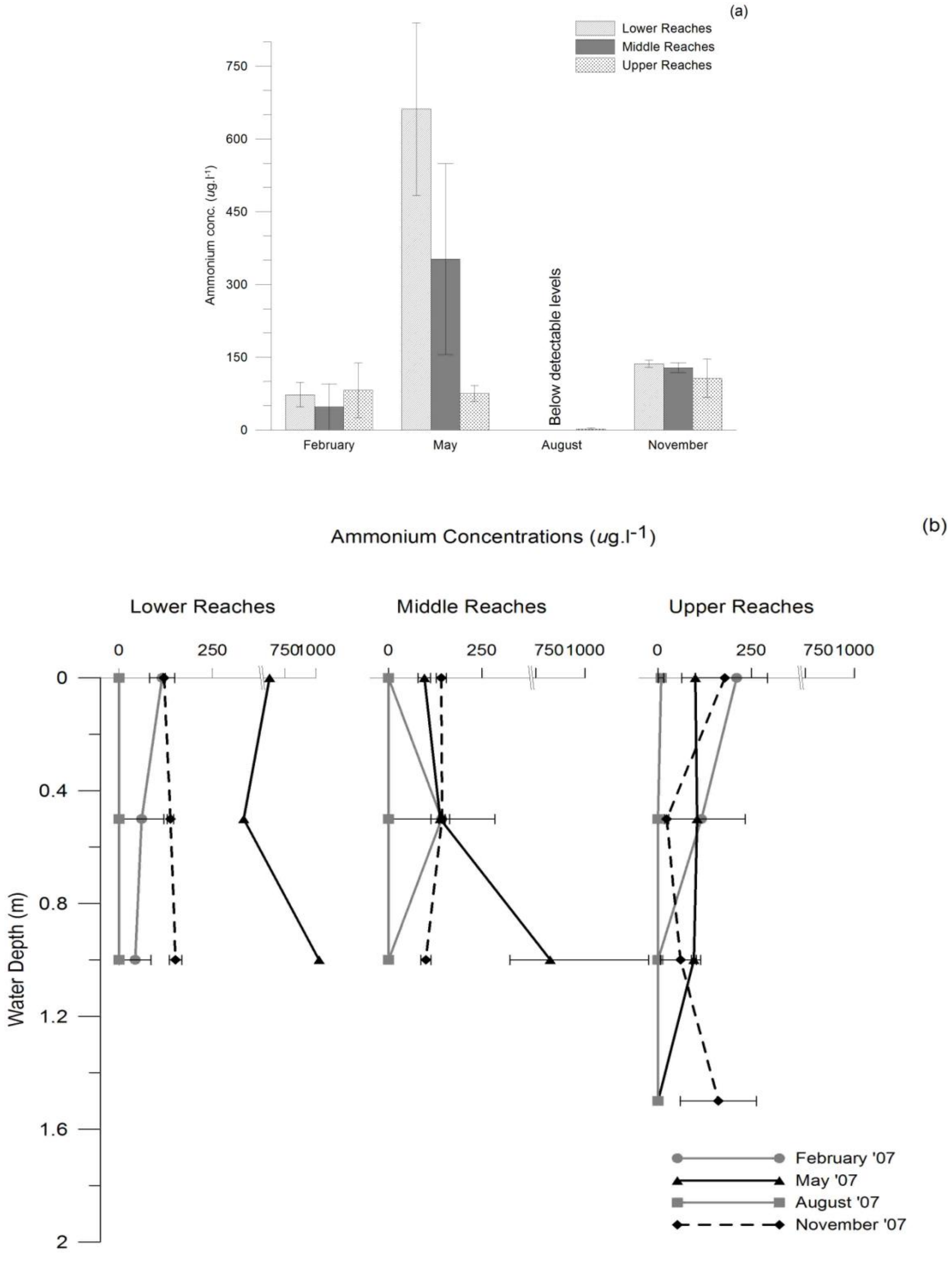


Figure 18 Ammonium concentrations (µg.l^{-1}) for the Heuningnes Estuary during the various sampling periods; (a) the different reaches of the estuary and (b) different depths at the various reaches.

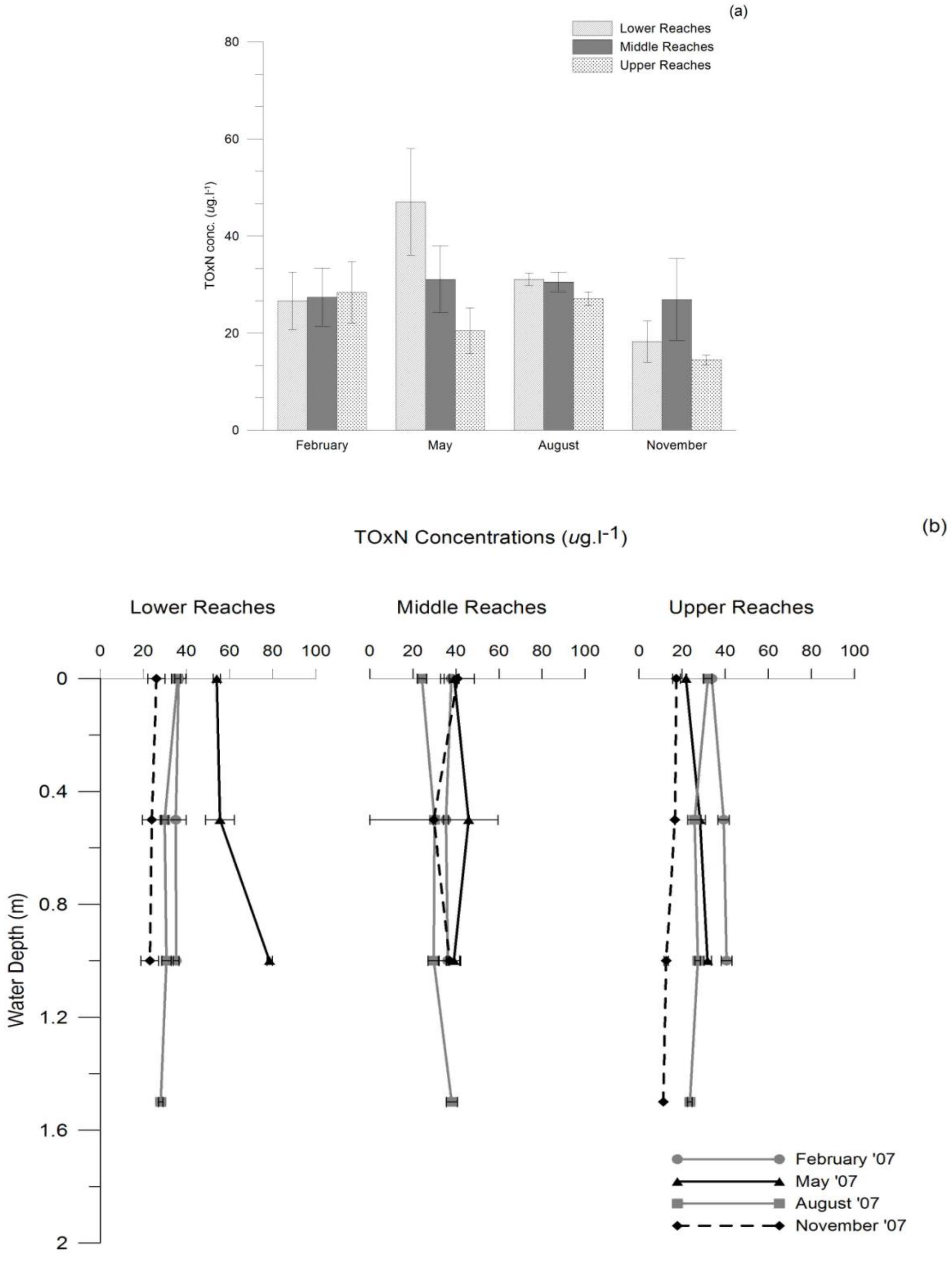


Figure 19 Mean Total Oxidized Nitrogen (TOxN) concentrations (μg.l^{-1}) for the Heuningnes Estuary during the various sampling periods; (a) the different reaches of the estuary and (b) different depths at the various reaches.

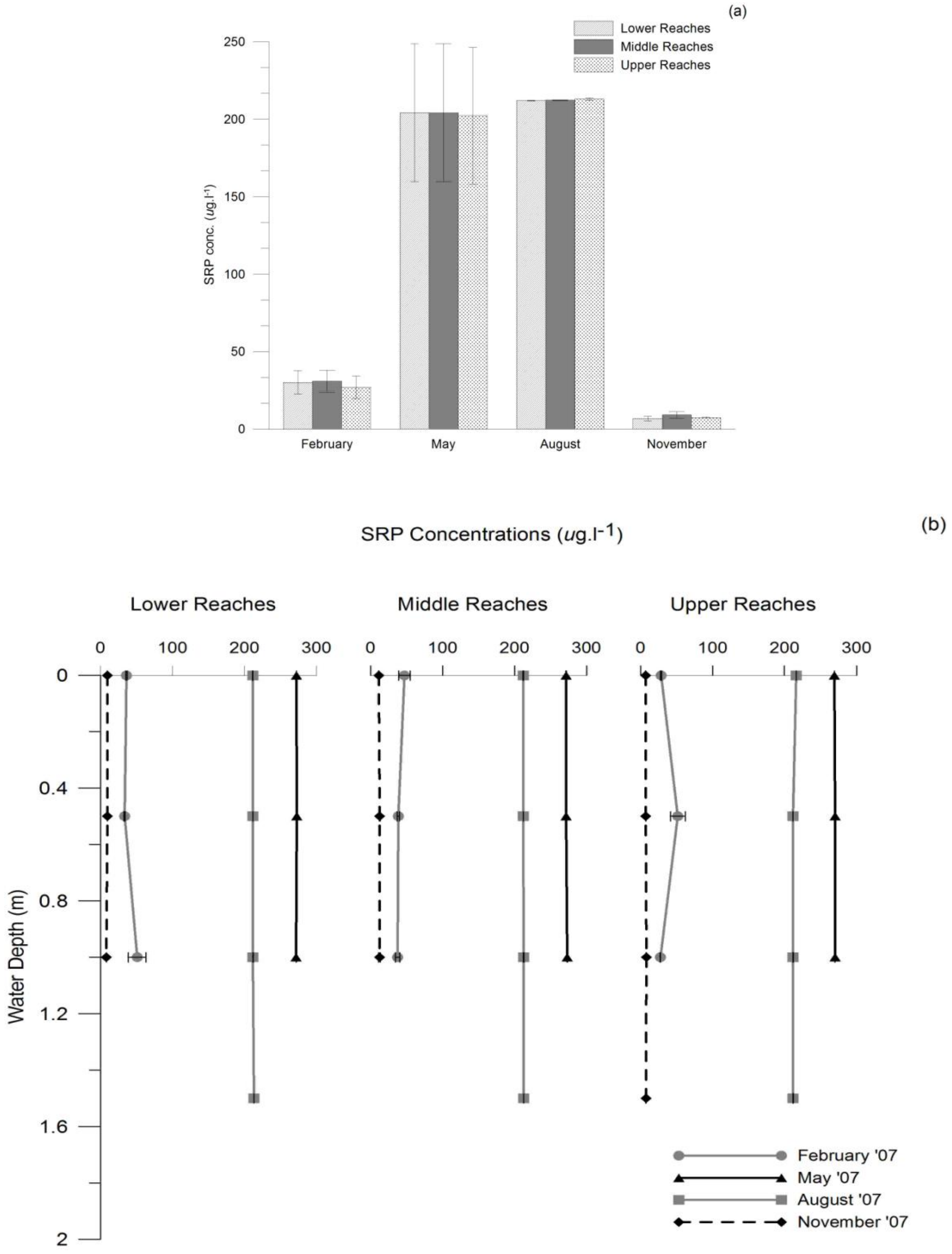


Figure 20 Mean Soluble Reactive Phosphorus (SRP) concentrations (µg.l^{-1}) for the Heuningnes Estuary during the various sampling periods; (a) for the different reaches of the estuary and (b) different depths at the various reaches.

Silica

Silica concentrations (Figure 21) were very high throughout the study with highest levels measured in February (871 ± 9 $\mu g.l^{-1}$), decreasing in May (644 ± 74 $\mu g.l^{-1}$), August (630 ± 109 $\mu g.l^{-1}$), and November (583 ± 69 $\mu g.l^{-1}$). Highest concentrations throughout the study periods were recorded in the upper and middle reaches ranging from 810 $\mu g.l^{-1}$ to 1294 $\mu g.l^{-1}$, while concentrations in the lower reaches remained fairly constant between ~275 $\mu g.l^{-1}$ to ~ 350 $\mu g.l^{-1}$. Vertical differences in concentrations were measured in May, when bottom water in the upper reaches were highest (~ 607 $\mu g.l^{-1}$), and in August when surface water concentrations were highest in the middle and upper reaches (~ 1295 $\mu g.l^{-1}$ and ~ 2096 $\mu g.l^{-1}$, respectively; $n = 18$, $p < 0.001$).

5.4.3 Phytoplankton biomass

Phytoplankton biomass (Figure 22) varied greatly between the different sampling periods but differences were not significant. Highest mean biomass was measured in August (3.5 ± 0.8 $\mu g.l^{-1}$), followed by May (2.2 ± 0.3 $\mu g.l^{-1}$), February (1.8 ± 0.2 $\mu g.l^{-1}$) and November (1.7 ± 0.3 $\mu g.l^{-1}$). With the exception of August, all the other sampling periods were characterised by high phytoplankton chlorophyll *a* in the middle reaches. During February there was a significant increase to reach values of 2.6 ± 0.3 $\mu g.l^{-1}$, while in May and November it was not significant, but still relatively high (2.8 ± 0.7 $\mu g.l^{-1}$and 2.8 ± 0.7 $\mu g.l^{-1}$, respectively). During August, however, significantly higher concentrations were recorded in the upper reaches (6.7 ± 2.1 $\mu g.l^{-1}$) than in the middle (1.8 ± 0.6 $\mu g.l^{-1}$) and lower reaches (1.9 ± 0.4 $\mu g.l^{-1}$). In addition, during August, the upper reaches showed a significant differences in chlorophyll *a* concentration between different depths, i.e. surface (11.7 ± 1.1 $\mu g.l^{-1}$) higher than bottom levels (0.8 ± 0.6 $\mu g.l^{-1}$).

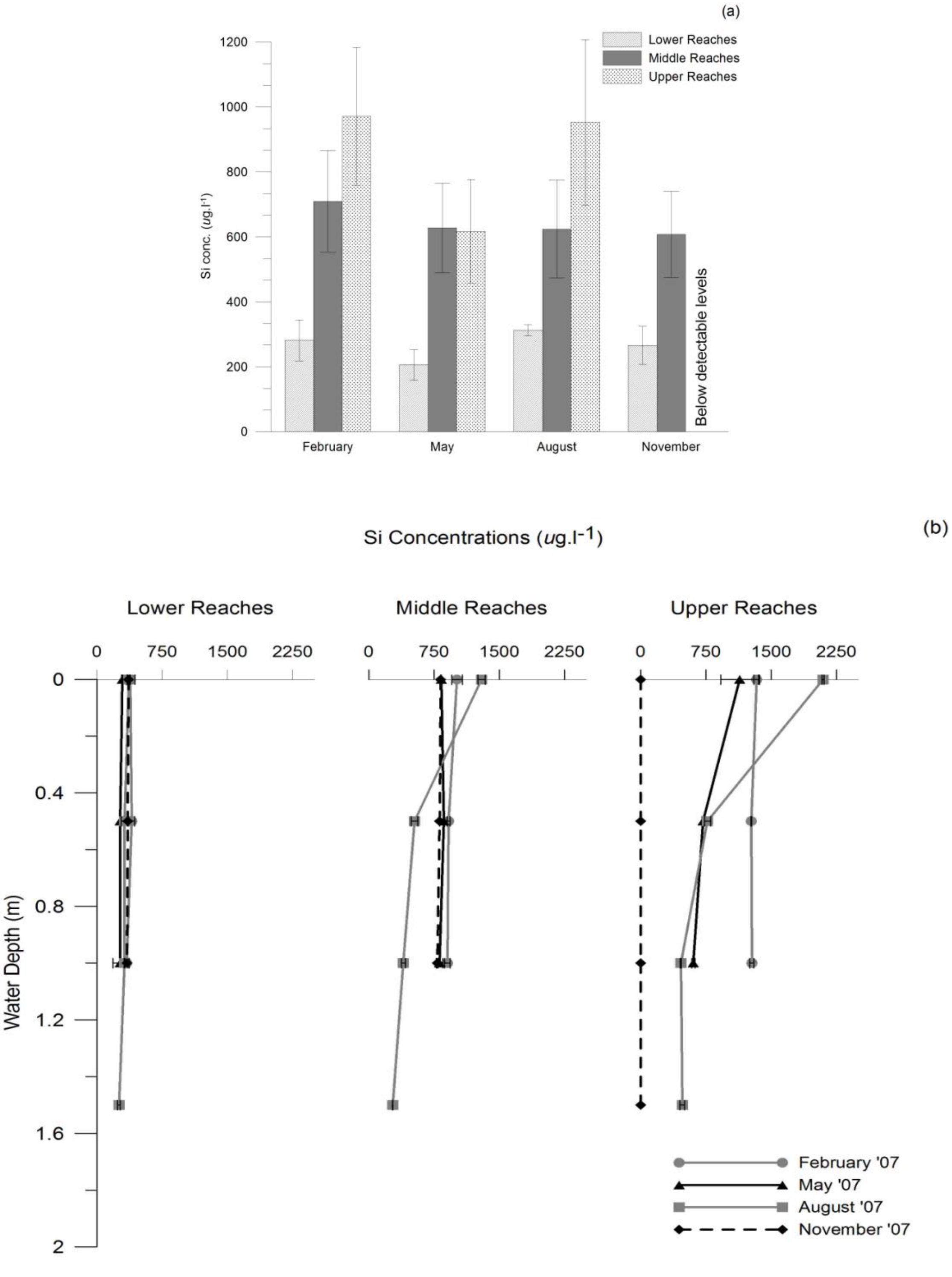


Figure 21 Mean silica (Si) concentrations (μg.l^{-1}) for the Heuningnes Estuary during the various sampling periods; (a) for the different reaches of the estuary and (b) different depths at the various reaches.

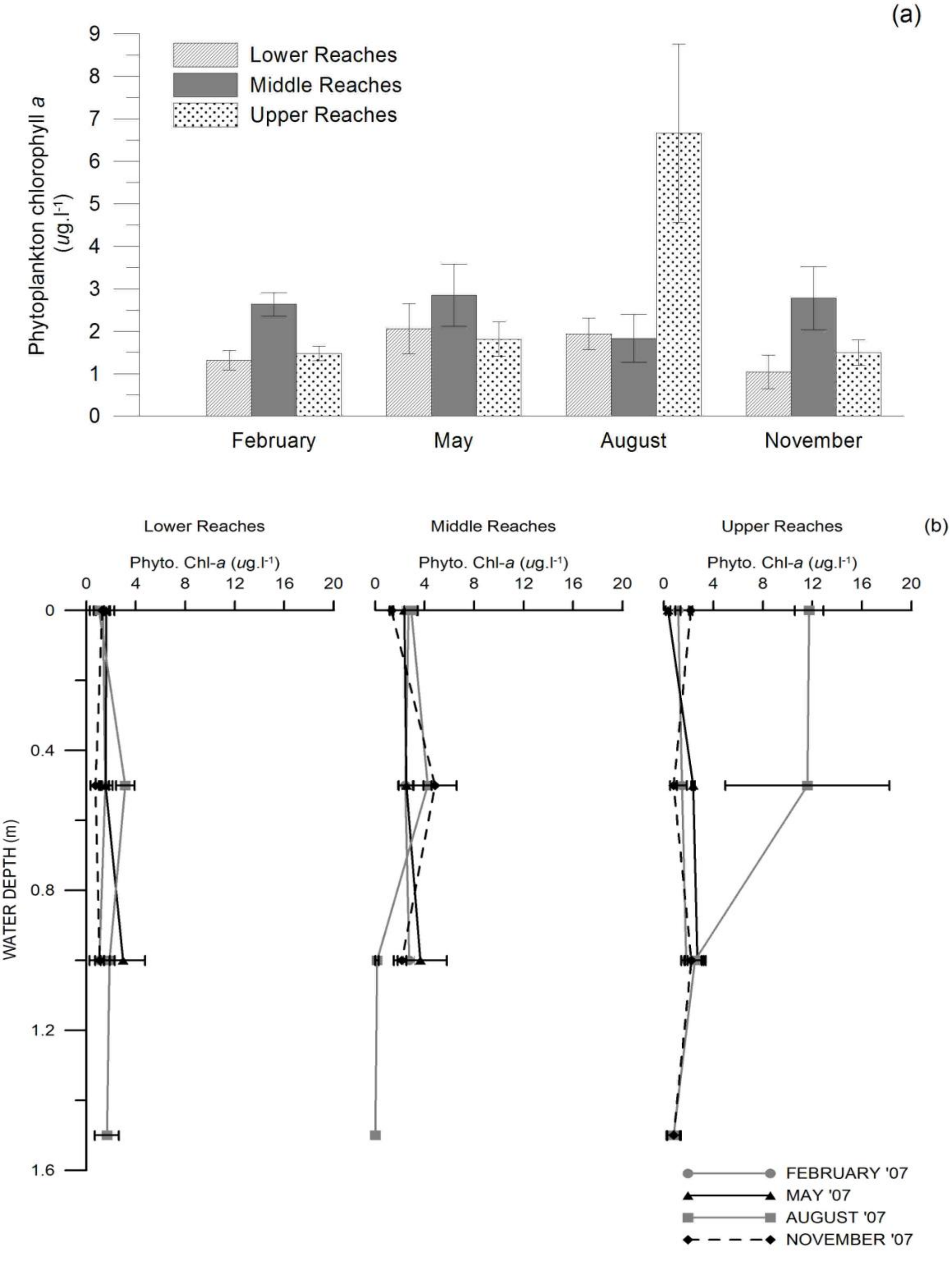


Figure 22 Phytoplankton biomass (chlorophyll *a*) concentrations (µg.l^{-1}) for the Heuningnes Estuary during the various sampling periods; (a) the different reaches of the estuary and (b) different depths at the various reaches.

5.4.4 Phytoplankton Community Structure

During periods of open mouth conditions with low flow and strong tidal exchange (i.e. February and May 2007) there was no significant difference in the phytoplankton community structure along the estuary (Figure 23). Chlorophytes accounted for the bulk of the community during the summer period and flagellates dominated during the autumn/winter period. The relative abundance of the diatoms was low throughout the estuary during February, while in May a significant decrease was recorded from the lower (22 ± 2 % and relative abundance) to the upper reaches (4.5 ± 1 % relative abundance; $n = 3$, $p < 0.05$). During closed mouth conditions with high freshwater inflow into the estuary and reduced tidal exchange (i.e. August 2007) the phytoplankton community was dominated by flagellates (54 – 76% relative abundance) throughout the estuary. Chlorophyte relative abundance in turn showed greatest variability between the sites, with highest numbers recorded in the middle reaches (37 ± 11% relative abundance). Diatom relative abundance was again low (~3% relative abundance) throughout the estuary. With the breaching of the estuary mouth in November 2007 and the subsequent re-establishment of a tidal regime, the phytoplankton community was dominated by flagellates in the lower reaches (70 ± 7 % relative abundance) that decreased significantly upstream (33.5 ± 1.5 %, relative abundance; $n = 3$, $p < 0.001$). Chlorophytes on the other hand had increased in relative abundance from the lower to the middle reaches (22 ± 6.5 % and 32.5 ± 11 % relative abundance, respectively), where after none were encountered in the upper reaches. Diatom relative abundance increased from the lower (7.3 ± 0.6 % relative abundance) to the upper reaches (63.5 ± 1.5 % relative abundance; $n = 3$, $p < 0.001$).

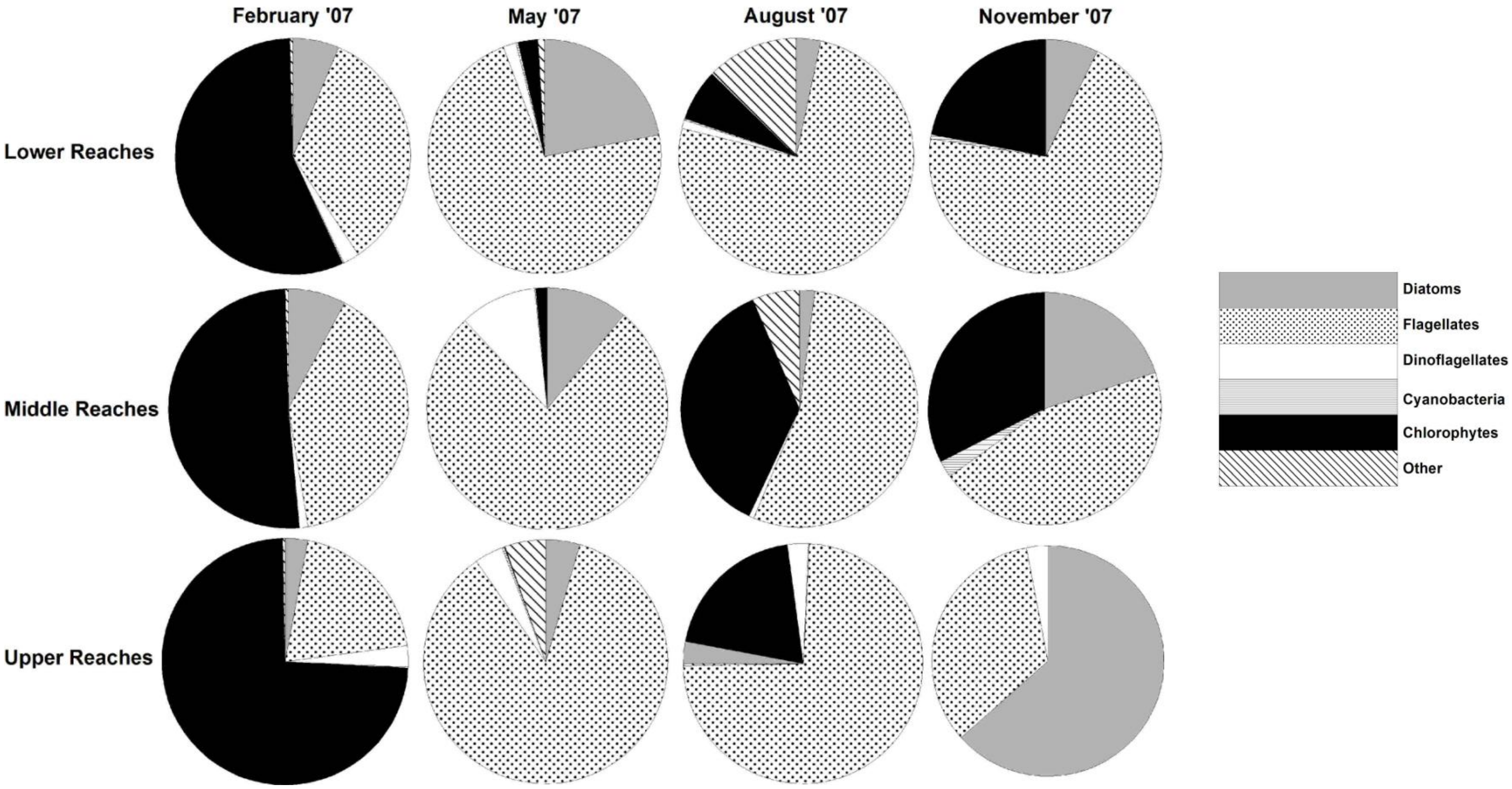


Figure 23 The major taxonomic groups comprising the phytoplankton communities at the different sampling stations in the Heuningnes Estuary during the different sampling periods.

5.4.5 Data analyses

Correlations Analyses

Significant correlations between physico-chemical variables, nutrients and phytoplankton biomass and taxonomic group composition indicated no clear trends or patterns. Data were split into the summer (February and November) and winter (May and August 2007) periods (Table 9) to differentiate between wet-dry and cold-hot conditions during the different sampling sessions. Full correlation matrices for each of the sampling periods are available in Appendix B.

Phytoplankton biomass (chlorophyll *a* concentrations) was highest in August 2007 and correlated with colder water ($r = -0.82$, $p < 0.05$) and lower salinity levels ($r = -0.85$, $p < 0.05$), but did not correlate with any of the major taxonomic groups during this period. Flagellates, the dominant group during August, also did not correlate to any of the environmental variables or nutrient groups. During periods of marine intrusion due to open mouth conditions (February and May 2007), low phytoplankton biomass (i.e. chlorophyll a concentrations) was recorded. Again no significant correlations could be observed between biomass and taxonomic groups. Diatom abundance did however, show significant correlations with higher salinity during May and February 2007 corresponding to open mouth marine conditions throughout the estuary. In addition during May 2007, diatom relative abundance could also be correlated to increased NH_4^+, TOxN and SRP concentrations ($r = 0.92$, $r = 0.82$, $r = 0.72$, $p<0.05$, respectively). During November 2007, however, the reverse was observed with diatom relative abundance significantly correlated to lower salinity levels ($r = -0.73$, $p<0.5$), as well as lower dissolved oxygen saturation levels ($r = -0.95$, $p<0.05$). Chlorophyte abundance on the other hand, was associated with increased water temperature ($r = 0.9$, $p<0.05$) and lower salinity levels ($r = -0.90$, $p<0.05$) during late summer open mouth conditions (February 2007), and with increased TOxN, SRP and Si concentrations ($r = 0.74$, $r = 0.70$ and $r = 0.77$, $p < 0.05$, respectively) during early summer open mouth conditions (November 2007).

Table 9 Summary of the Pearson Product Moment correlation analyses performed for all the (a) physical variables and (b) nutrients, and phytoplankton taxonomic groups, including phytoplankton biomass (chlorophyll *a*) during the various sampling periods (r values, (-) indicates negative correlations, $p < 0.05$).

(a)	Temperature (^{o}C)				Electrical Conductivity ($mS.cm^{-1}$)				Salinity (PSU)				Dissolved Oxygen (%)				pH			
	Summer		Winter		Summer		Winter		Summer		Winter		Summer		Winter		Summer		Winter	
	Febr	Nov	May	Aug	Febr	Nov	May	Aug	Febr	Nov	May	Aug	Febr	Nov	May	Aug	Febr	Nov	May	Aug
Chlorophyll-a				-0.82				-0.85				-0.85					-0.70			
Diatoms			0.81		0.71	-0.73	0.90		0.70	-0.72	0.91			-0.95					0.73	
Flagellates	-0.91				0.88	0.90	-0.82		0.88	0.90	-0.81			0.81	-0.89					
Dinoflagellates														-0.92						
Cyanobacteria																				
Chlorophytes	0.90				-0.90				-0.90											

(b)	Ammonium ($mg.l^{-1}$)				Total Oxidised Nitrogen ($mg.l^{-1}$)				Soluble Reactive Phosphorus ($mg.l^{-1}$)				Silica ($mg.l^{-1}$)			
	Summer		Winter		Summer		Winter		Summer		Winter		Summer		Winter	
	Febr	Nov	May	Aug	Febr	Nov	May	Aug	Febr	Nov	May	Aug	Febr	Nov	May	Aug
Chlorophyll-a																0.69
Diatoms			0.92				0.82				0.72				-0.74	
Flagellates							-0.72				-0.93					
Dinoflagellates						-0.80				-0.71				-0.83		
Cyanobacteria						0.75		0.66						0.72		
Chlorophytes						0.74				0.70				0.77		

Ordination analyses

Canonical correspondence analyses (CCA) for the physical and chemical variables indicated that the sampling stations of the Heuningnes Estuary (Sites 1-3) could be separated into clear estuarine reaches (Figure 24a), and also separated temporally, i.e. based on sampling periods. Summer data sets, i.e. February and November, were similar to one another and indicated clear gradients from the lower reaches (i.e. H1) to the upper reaches (i.e. H3). Winter sampling periods, i.e. May and August, were also closely associated, although the reaches during May showed some overlap in terms of environmental conditions.

CCA between the phytoplankton community and environmental variables (Figure 24b) indicated that during summer (i.e. February and November), the communities were associated with above average water temperature. During February the community was mainly dominated by Chlorophytes associated with very high water temperatures, while in November diatoms and cyanobacteria could be associated with higher ammonium, dissolved oxygen saturation and pH levels, and lower nutrient levels. Winter communities (i.e. May and August) were associated with higher salinity and nutrient levels, both being dominated by flagellates.

Table 10 Summary of the CCA for the Heuningnes Estuary.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.275	0.194	0.020	0.009	0.657
Species-environment correlations	0.898	0.935	0.687	0.546	
Cumulative percentage variance:					
Of species data	41.8	71.4	74.4	75.7	
Of species-environment relation	54.4	92.9	96.7	98.5	
Sum of all eigenvalues					0.657
Sum of all canonical eigenvalues					0.505

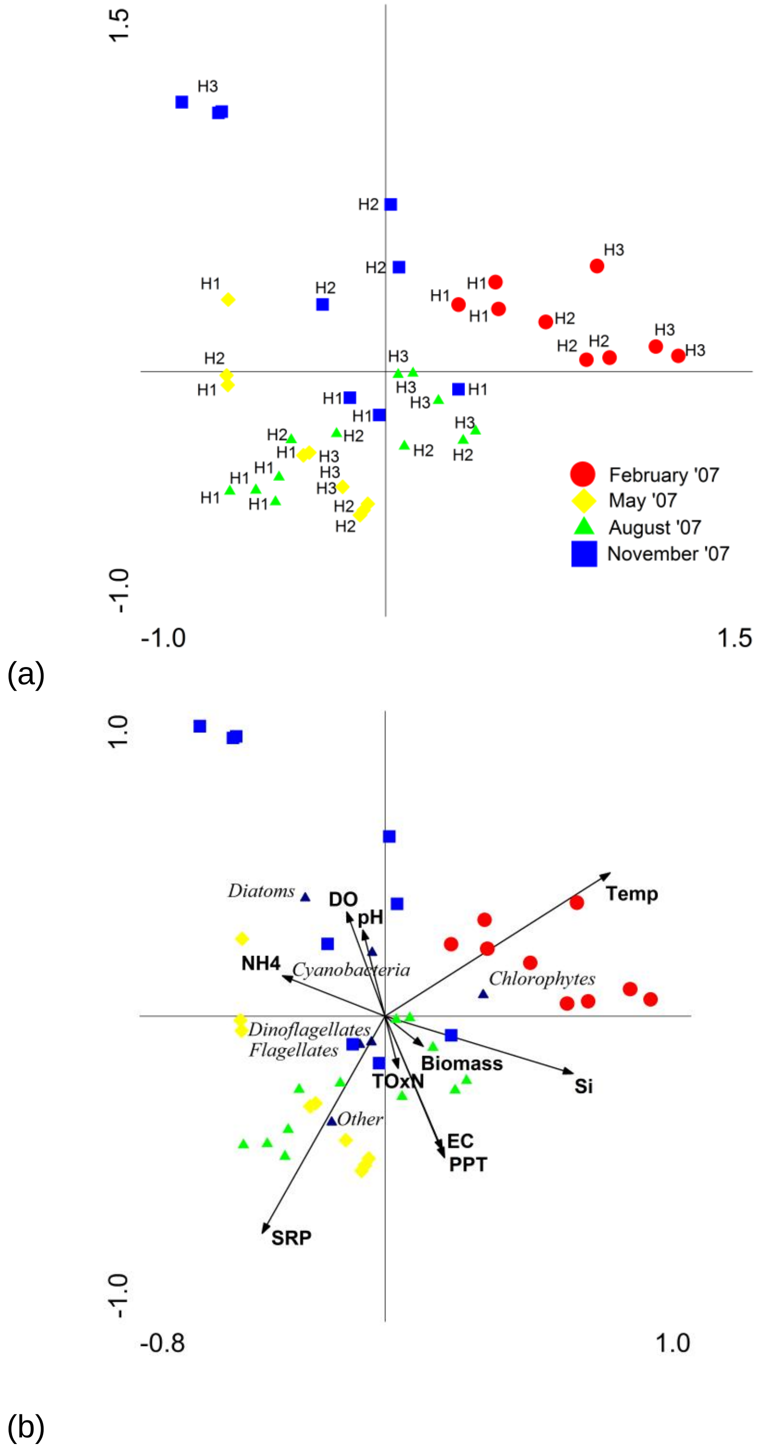


Figure 24 Canonical Correspondence Analyses (CCA) indicating (a) spatial correlation between sampling stations and (b) between phytoplankton groups and environmental variables during all the sampling periods.

5.4.6 Comparison between Soetendalsvlei and the Heuningnes River and Estuary (upper reaches)

In order to determine whether there were any similarities between Soetendalsvlei and the upper reaches of the Heuningnes Estuary, analyses of variance (One-way ANOVA's) were performed for physical, chemical and phytoplankton taxonomic group data (Table 11). Results indicate that temperature, electrical conductivity and salinity were generally higher in the upper reaches of the Heuningnes Estuary than in the Lake. Dissolved oxygen saturation on the other hand was lower throughout the study period within the River. pH levels were also significantly lower in the upper reaches. Nutrients were generally not significantly different between the Lake and the upper reaches of the estuary, with the exception of silicate concentrations within the River, which were higher during February, May and August (1294 ± 16 $\mu g.l^{-1}$; 822 ± 117 $\mu g.l^{-1}$ and 952 ± 254 $\mu g.l^{-1}$, respectively; $n = 6$, $p < 0.01$). Phytoplankton taxonomic group comparisons showed that diatom relative abundance was generally lower in the upper reaches than in the Lake, except during November when the upper reaches showed higher values (63 ± 1.5%; $n = 3$, $p < 0.001$). Flagellate relative abundance was only significantly higher in the upper reaches during May (86 ± 3.1%; $n = 3$, $p < 0.001$). Chlorophyte relative abundance was significantly higher in the upper reaches during February (74 ± 4%) and August (30 ± 5%), and lower during May and November (<1%; $n = 3$, $p < 0.001$). Dinoflagellate relative abundance was significantly higher in the upper reaches during February, May and November, but not during August ($n =3$, $p < 0.001$). Cyanobacteria relative abindance were only significantly higher in the Lake during November (7 ± 5%; $n = 3$, $p < 0.001$).

Table 11 Significant differences ($p < 0.05$) between physical, chemical and phytoplankton functional groups for Soetendalsvlei and the upper reaches of the Heuningnes Estuary (H / L = Higher / Lower recordings in the Heuningnes Estuary; (-) = not significant)

	Temperature	Conductivity (incl. Salinity)	Dissolved Oxygen	pH	Ammonium	Total Oxidised Nitrogen	Soluble Reactive	Silicate	Diatoms	Flagellates	Chlorophytes	Dinoflagellates	Cyanobacteria
February	H	H	L	L				H	L		H	H	
May	H	H	L	L				H	L	H	L	H	
August	H	H	L	L				H	L		H		
November	L		n/a*	L					H		L	H	L

* no data available for Soetendalsvlei during November sampling due to equipment malfunction

5.5 Discussion

In many South Africa estuaries prolonged periods of mouth closure and a continuous increase in freshwater inflow results in the flooding of large areas of urban and agricultural lands (Adams *et al.*, 1999). This has necessitated the artificial breaching of estuary mouths to prevent loss of property and to lower water levels. In the case of the Heuningnes Estuary, an estimated 24,000 ha of prime agricultural land will be inundated with saline water due to closed mouth conditions and continuous freshwater inflow (Bickerton, 1984). However, the risk of desertification and salinisation of the wetlands associated with the Heuningnes Estuary has highlighted the need to re-assess this strategy as back-flooding of the catchment area may be needed to reduce salt accumulation in the wetlands as well as to maintain an ecological corridor along the river to the ocean (HilLand Associates, 2009).

Breaching the estuary mouth during periods of reduced freshwater inflow may also result in marine intrusion upstream and according to Schumann *et al.* (1999) hypersaline conditions are common in the upper reaches of a number of South African estuaries, as tidal influence is large and freshwater inflow limited. In the

Heuningnes River and estuary reverse salinity gradients have been recorded in the past of up to 50 ppt above the Bredasdorp / Struisbaai bridge (Bickerton 1984), mainly due to the reduced water exchange between Soetendalsvlei Lake and the Heuningnes Estuary as a result of the weir. Although the mouth of the estuary was open for the majority of this study and saline intrusion into the upper reaches of the estuary were encountered, no reverse salinity gradient was observed. However these may occur in the future due to unfavourable climate conditions such as drought (Bickerton, 1984). It is advised that the artificial breaching of the estuary mouth should be timed to coincide with increased freshwater inflow, such as occurred during the August 2007 sampling period, to ensure that marine intrusion into the upper reaches is limited. This would prevent hypersaline conditions forming due to high evaporation rates.

The results from this study correspond well with the conceptual model for TOCE's proposed by Snow and Taljaard (2007) and Taljaard *et al.* (2009a) with longitudinal salinity gradients present during periods of open mouth conditions, being replaced by lower salinity profiles during closed conditions when freshwater inflow is high. The Heuningnes Estuary did not exhibit true homogenous mixing, but salinity was lowered in the middle to lower reaches by the high freshwater inflow. The subsequent breaching of the mouth and flushing of the system resulted in significantly lower salinity levels in the upper and middle reaches during November. This highlights the importance of synchronising mouth breaching with natural periods of high freshwater inflow to ensure scouring of the estuary and flushing of the water column. With the breaching event, tidal exchange was re-established as evident by the increase in salinity in the lower reaches. Similar results were obtained in previous assessments of the Heuningnes Estuary by Mehl (1973) and the Estuarine and Coastal Research Unit (ERCU; 1983 in Bickerton, 1984) of the Council for Scientific and Industrial Research (CSIR). In Mehl (1973) it was found that the Heuningnes Estuary exhibited marine conditions from October to May (i.e. dry season) and that a reverse salinity gradient of approximately 50 ppt in the upper reaches established under open mouth conditions. With the increase in freshwater inflow in the rainy season (i.e. June - August), however, overflow from the lake occurred and salinities were reduced throughout the system (< 5 ppt). ECRU (1983 in Bickerton, 1984) also found that strong outflow from Soetendalsvlei into the estuary, significantly lowered the salinity of the estuary to 2 ppt at the Bredasdorp / Struibaai Bridge and 8 ppt in the lower reaches. However, in 1973 – 1974, the mouth was closed and high salinities (i.e. < 40 ppt) were recorded throughout the estuary year-round, indicating the potential for hypersaline conditions to develop within the system. Unlike these previous observations, overflow from Soetendalsvlei did not appear to have a significant effect on the water quality of the estuary, with salinity in the upper reaches remaining brackish (~22 ppt) during August even though rainfall was high. Nevertheless the subsequent breaching of the mouth and flushing of the estuary lowered salinity throughout the water column in November, with a strong marine influence in the lower reaches. It thus appear that a delay in the effect of overflow into the estuary occurs, which could have significant effects on the overall trophic interactions of the ecosystem as breeding and spawning cues (Whitfield *et al*., 2009) may be influenced by this delay in salinity changes.

Difficulty arises with determining whether present estuarine ecological functioning has changed substantially from that which would have occurred naturally, as this area is characterised by high variability in rainfall as recored in the historical data from Zoetendasvallei farm since the 19th century. It can be argued that the present artificial breaching of the estuary mouth decreases water residence time within the estuary, thereby affecting overall system productivity, as well as the dominant primary producers. According to Snow and Taljaar (2007) phytoplankton biomass increases substaintally with increased residence time due to a lack of tidal flushing. Microalgae remain for longer in the estuary and can exploit highter nutrient levels during these periods. However, as nutrients are depleted, phytoplankton production and biomass will in turn be limited. In the Heuningnes Estuary, however the residence time is greatly reduced due to the artificial breaching of the mouth. Dominant microalgal biomass and community composition is also affected by abiotic (including residence time) and biotic variables (Costa *et al.,* 2011; Shen *et al.,* 2011). Longer residence time with less turbulent mixing, would favour motile taxa, especially flagellates, which can exploit the higher irradiance in the surface waters (Snow, 2007 and Hall and Paerl, 2011, while diatoms, which are influenced by buoyancy and hence turbulent mixing (Hall and Paerl, 2011; Nunes, 2011), would be at a disadvantage during such periods. During closed mouth conditions, marine influence is also limited and hence salinity profiles within the estuary would be affected. According to Turpie (2004) changing salinity gradients would greatly influence the community structure, biomass and productivity of the phytoplaknton community, thereby decreasing system biodiversity and resilience.

Patterns similar to that described in the conceptual model for TOCEs (Snow and Taljaard, 2007; Taljaard *et al.,* 2009a) influenced nutrient concentrations i.e. there was a marine and freshwater influence when the mouth was open which was replaced by a freshwater influence during closed mouth conditions. The very high nutrient concentrations recorded during May could be related to marine input as both NH_4^+ and TOxN were highest in the lower reaches. Slinger and Taljaard (1994) also observed that higher NH_3-N levels were related to marine input in the Great Brak Estuary. The very high NH_4^+ levels recorded in this study is considerably higher that those recorded in the Great Brak (Slinger and Taljaard, 1994), Keurbooms (Taljaard *et al.,* 2009a) and East Kleinemonde (Taljaard *et al*., 2009b) estuaries and could be due to either marine upwelling introducting nutrient rich bottom water into the estuary or the seasonal die-back of estuarine vegetation. The seasonal senescence of large stands of emergent macrophytes and salt marsh vegetation as noted in this study and the subsequent microbial decomposition of dead material would release nutrients into the water column (Kinney and Roman, 1998; Aseada *et al*., 2002; Windham and Meyerson, 2003). High SRP concentrations during May could be related to this die-back of vegetation, while the August high level could be related to high freshwater inflow and turbulent mixing whereby sediment is re-suspended and phosphorus is released into the water column (Mihaljević *et al*, 2010). Both these periods showed extremely high SRP concentrations in comparison to other TOCE's such as Keurbooms and East Kleinemonde with concentrations between 5 and 32 µg.l^{-1} (Taljaard *et al.,* 2009a, b). It needs to be noted that although recorded nutrient levels may be low, the assimilation of said nutrients by phytoplankton and other primary producers could be responsible for the lower levels recorded (Meyerson *et al*., 1999; Popovich *et al*., 2008). Dissolution of biogenic silica can effect the overall concentrations of silica (Si) measured within the water column and the overall amount available for siliceous algal (diatom) production. Lopes *et al.* (2007) indicated that freshwater inflow is responsible for silica input into estuaries. Slinger and Taljaard (1994) recorded silica concentrations similar to those measured during August that also indicate freshwater input of silica into estuaries in the range of 1500 to 2100 µg.l^{-1}. High water column silica concentrations can in turn be associated with non-siliceous algae such as flagellates and chlorophytes (Lopes *et al.,* 2007), as observed in the upper reaches of the Heuningnes Estuary. The assimilation of silica into diatom biomass, would explain the lower concentrations measured throughout the estuary during November when diatom relative abundance was the highest recorded during this study (10 to 65%).

Phytoplankton biomass (chlorophyll *a*) was low throughout the estuary and sampling period, but responded to freshwater inflow into the estuary as evident by the high biomass recorded during the August rainfall period. According to Adams *et al.* (1999) and Taljaard (2011) high rainfall events and the subsequent high runoff are generally responsible for a sudden increase in phytoplankton biomass in estuaries due to the increase in allochthonous materials. Phytoplankon biomass is comparable to that recorded in the Great Brak Estuary by Slinger and Taljaard (1994), but less than what was recorded more recently by Nunes (2011), again highlighting the inherent variability that characterises South African TOCEs. Based on the low phytoplankton chlorophyll *a* concentrations (< 10 µg.l^{-1}) measured in this study, it would appear that the Heuningnes Estuary is in a healthy state. It should however, be noted that large stands of emergent macrophytes (i.e. *Phragmites australis* and *Scoenoplectus scripoides*) along the estuary could be responsible for the rapid uptake of nutrients and the subsequent amelioration of water quality (Ozimek and Renman, 1995; Brix, 1999; Hardej and Ozimek, 2002).

The phytoplankton community was dominated by non-siliceous algae, namely flagellates and chlorophytes, alternating in relative abundance during the different sampling periods. Although nutrient concentrations could not be directly correlated to phytoplankton biomass, the relative abundance of the flagellates increased in response to higher TOxN and SRP concentrations. It can be argued that the flagellate community is well established within the estuary and that with the strong tidal exchange and marine intrusion, they were transported into the upper reaches, where they exploited any increase in nutrients associated with freshwater seepage / inflow. The high relative abundance of flagellates in the upper reaches during August support this assumption. According to Chisholm (1992) and Cloern and Dufford (2005) phytoplankton communities in oligotrophic waters are generally dominated by flagellates as the small cell size results in a high surface area to volume ratio. This ensures a competitive advantage to organisms of this size in that they can take up and utilize nutrient in systems that have very low concentrations (Chisholm, 1992; Cloern & Dufford, 2005). The ability to be mobile and remain within the photic zone could also explain the dominance of flagellates during periods when water clarity was reduced due to increase freshwater inflow and associated sediment re-suspension (i.e. August)(Hall and Paerl, 2011). Similar observations where made in the Great Brak Estuary, South Africa, with flagellate dominance attributed to their ability for diel vertical migration during closed mouth conditions (Snow, 2007; Nunes, 2011). The relative abundance of the chlorophytes was correlated with lower salinity during February (marine intrusion) and with increased nutrients during November (freshwater inflow). Again small cell size and the ability to rapidly exploit any increase in nutrients may explain their dominance during these periods. It would however, appear that flagellates have a competitive advantage over the chlorophytes due to their mobility and ability to remain within the photic zone for longer.

With high nutrient concentrations however, larger celled organisms such as diatoms can become dominant and develop blooms (Cloern & Dufford, 2005). According to Malone (1992) and Duarte *et al.* (2000) it is not only the increased growth of larger phytoplankton that contribute to their dominance, but also the consumption of the small cells by fast-responding consumers that amplify large-cell production. Diatom relative abundance showed a significant increase with increased TOxN and SRP concentrations. The apparent inverse relationship between flagellate and diatom relative abundance could indicate interspecific competition, where diatoms may have the ability of luxury consumption, enabling them to exploit any increase in nutrients within the system. Diatom relative abundance showed significant change over time, but they were only the dominant group in the phytoplankton community in November. The hypothesis that diatoms would contribute >50% to the overall phytoplankton community was not accepted. The competitive advantage of chlorophytes and flagellates could account for this apparent lack in dominance. Short residence time due to strong tidal exchange during open mouth conditions would also remove diatoms from the estuary. Consequently the relative abundance of diatoms were highest at the mouth of the estuary during these periods, indicating either that they were transported downstream during the ebb tide or that those diatoms were of marine origin. Unfortunately poor diatom preservation did not allow for the identification of taxa to species level and therefore the hypotheses stating that the marine and freshwater species would alternatively dominant the diatom community could not be tested. However, during low freshwater inflow conditions, diatom relative abundance could be associated with marine conditions, even though freshwater nutrient input did significantly affect relative abundance as observed after the August heavy rainfall and inflow. This change in correlations between diatoms and the physico-chemical variables indicate the importance of nutrient sources in determining the phytoplankton community structure. During periods of low flow, the marine environment is the primary source of nutrients, found in the bottom water of the estuary. During the high rainfall periods, however, river input is the major source of nutrient to the estuary, located in the less saline surface waters (Allanson, 2001). According to research conducted in the San Francisco Bay area, diatoms dominate the phytoplankton community during periods of increased nutrient concentrations (Cloern & Dufford, 2005). There are several reasons to explain the ability of diatoms to exploit higher nutrient conditions; 1) their higher growth rate than other taxa which enables them to divide and reproduce faster, 2) they can uptake nitrogen much faster under nitrate-rich conditions than other taxa, 3) they have higher growth efficiency at lower light intensities, 4) when dissolved CO_2 becomes depleted, diatoms can utilize bicarbonates for photosynthesis, 6) their silica cell wall provides resistance against grazing and 7) due to their large cell size they remain within the photic zone for longer periods before sinking to the bottom of the water column (Hobson, 1988; Dugdale & Wilkerson, 1992; Smayda, 1997; Goldman & McGillicuddy, 2003; Hamm *et al.*, 2003; Cloern & Dufford, 2005).

Comparisons with Soetendalsvlei Lake indicated that few physical variables were similar between the lake and the upper reaches of the estuary. One would expect similarity between the two systems as freshwater overflow occurs from the lake into the estuary as occurs in the Swartvlei Lake and estuary (Allanson, 2001). This is a clear indication that the weir has impacted on the water exchange between these two systems. Studies on the Nhlabane Lake and estuary system on the KwaZulu-Natal coast of South Africa, showed that nutrient levels within the estuary were considerably lower than that of the river due to the construction of a weir (Riddin, 1999). Similarly the weir in this case, restricts the water flow from the lake into the estuary and, resulted in significantly different salinity levels and only once the estuary was breached and flushing occurred did the levels in the upper reaches show a resemblance to that of the lake. As evident from this study, considerable freshwater inflow had to occur to reduce salinity throughout the estuary, with levels in the upper reaches not changing by much prior to breaching. Consequently, it could be argued that under natural conditions with back-flooding occurring, the lake would have received saline water during closed mouth periods. This would have meant that when overflow did occur at the end of the rainfall season, the salinity range of the lake would have been substantially higher than present and that the water flowing into the estuary may indeed have showed similar levels to that presently recorded. As already stated the artificial breaching of the estuary mouth during periods of limited freshwater flow such as droughts, would severely increase salinity throughout the estuary. This would entail that during closed mouth conditions, the amount of freshwater required to reduce the salinity profile within the estuary would increase substantially. Together with increased water level and the threat of back-flooding, the likely inundation of surrounding areas with saline water is high, increasing the risk of salinisation and loss of habitat and biodiversity.

5.6 Conclusion

The Heuningnes Estuary at present still maintains a salinity gradient, even under conditions of extreme low freshwater inflow and an open mouth. Hypersaline conditions may establish under very low flow together with increased freshwater abstraction within the catchment. Hypersaline conditions have been reported historically but were not recorded in this study. Although the catchment area of the estuary is highly impacted by agriculture, no sign of cultural eutrophication is evident within the estuary. However, the large stands of emergent reeds may overshadow the increase in nutrient concentrations as nutrient uptake rates, by especially *Phragmites australis*, may be high (Human and Adams, 2011) Consequently the water quality of the estuary is good, with phytoplankton biomass remaining relatively low throughout the study period. The importance of freshwater inflow was highlighted when there was increased rainfall during August that saw a reduction in the salinity gradient of the estuary and a slight shift in the phytoplankton community structure. The flushing of the estuary by such high flow conditions is important to maintain water quality as well as for nutrient input into the adjacent coastal environments. The lack of similarity between Soetendalsvlei Lake and the upper reaches of the Heuningnes River and estuary is cause for concern as this would mean a loss of habitat continuity, especially as one of the aims of the Estuary Management Plan (HilLand Associates, 2009) is to maintain an ecological corridor along the river to the ocean that includes the associated wetlands and their fauna and flora.

Chapter 6

The palaeolimnological investigation of Soetendalsvlei: geochemistry and sub-fossil diatom distribution

6.1 Introduction

Palaeo-reconstructions can be used to infer the response of coastal systems to sea level changes (Stanley 1995; Leorri *et al.*, 2008), the natural climatic variability of a region or even assess the anthropogenic impacts on lakes (Smol, 2002; Bigler *et al.*, 2006; Saunders, 2010). Sediments contain a range of physical, chemical and biological records that can be used to determine long-term ecosystem responses to climate change (Battarbee *et al.*, 2000, Eastoe *et al.*, 2002; Cohen, 2003; Fritz, 2008).

Both biotic and abiotic proxies are used to reconstruct changes. Carbon isotopes ($\delta^{13}C$) are generally used to differentiate between sources of organic matter (Meyers, 2003; Pueyo *et al.,* 2011). In aquatic environments, carbon is mainly available as bicarbonate (HCO_3^-) and dissolved CO_2 (inorganic carbon) and thus aquatic organisms have isotopic values close to such a source (Degens *et al.*, 1968; Falkowski, 1991). Organic matter within aquatic environments consists of particulate organic carbon (POC) and dissolved organic carbon (DOC). In most instances DOC is derived from the microbial breakdown of POC (Hedges *et al.*, 1997; Raymond and Bauer, 2001), which consists of phytoplankton, zooplankton, terrestrial organic matter (i.e. debris) and anthropogenic sources (i.e. sewage) (Lamb *et al.,* 2006). Because aquatic vegetation and phytoplankton utilize both dissolved CO_2 and bicarbonate, $\delta^{13}C$ values may overlap, making interpretation of data difficult. It is then best to use $\delta\ ^{13}C$ values in conjunction with C/N ratios in order to determine the source of bulk organic carbon (Lamb *et al.*, 2006) and in particular the contribution of autochthonous and allochthonous sources (Leng *et al.*, 2005). By combining these two proxies, it is possible to determine whether the source of organic material in the sedimentary record is marine, estuarine or freshwater. In addition, it is possible to determine the relative contribution of fauna, bacteria, algae or higher plants to the sedimentary organic matter (Fontugne and Jouanneau, 1987; Schimmelmann and Tegner, 1991; Thornton and McManus, 1994; Müller and Mathesius, 1999, Wilson *et al.*, 2005a, b; Lamb *et al.*, 2006).

The composition and abundance of biological species can in turn be associated with specific environmental conditions and thus they can be used as environmental proxies (Gasse *et al.*, 1995; Battarbee, 2000; Austin *et al.*, 2007; Hassan *et al.,* 2009).

Diatom species are useful in palaeo-reconstructions as they occur in relatively diverse environments and species can be easily distinguished by their unique morphological features (Smol, 1985; Stevenson and Pan, 1999; Tingstad *et al.*, 2011). They form an abundant and diverse component of the microalgal community within aquatic systems, comprising a large portion of the total biomass (Hall and Smol, 1999; Stroemer and Smol, 1999; Pappas 2010). Diatoms have a very short generation time and thus they respond rapidly to any changes in environmental conditions (Saunders, 2010). They are found in almost all types of streams, lakes, wetlands and ephemeral aquatic habitats, and form the basis of the food web in most of these systems (Lamberti, 1996; Stevenson and Pan, 1999; Pappas, 2010; Tingstad *et al.,* 2011). Diatoms species generally have a narrow ecological preference making them sensitive to environmental change (Jones and Juggins, 1995; MacKay *et al.*, 2005; Saunders, 2010) and are thus particularly suitable for inferring present and past environmental conditions (Hall and Smol, 1999; Mackay *et al.*, 2005; Pappas 2010). A number of studies have indicated that diatom species composition can be successfully used to infer both present and palaeo-salinity within lakes (Kaoru *et al.*, 1997; Stroemer and Smol, 1999; Ng and Sin, 2003; Saunders, 2010).

The aim of this chapter was to infer Holocene changes in palaeo-salinity over the last 10,000 yr BP for Soetendalsvlei Lake, and to determine whether there was any relationship between trophic status and salinity changes of the lake. The recent effect of anthropogenic impacts and agricultural practices on the trophic development of the lake was also investigated.

Hypotheses tested were:

- Geochemistry (i.e. organic and carbonate content, stable isotopes and C:N ratios) and diatoms are good indicators of past sea-level change and marine influence in Soetendalsvlei Lake
- The sedimentary record provided evidence of marine influence during the Early Holocene in the bottom sections of the palaeo-cores, estuarine influence during the Mid Holocene and freshwater influence during the Late Holocene
- The sea-level (influence) model inferred from the palaeolimnology proxies for Soetendalsvlei Lake correspond well with other sea-level change models for the East and West Coast of South Africa

6.2 Sampling stations

Five sampling stations (Figure 25) within Soetendalsvlei were selected for the retrieval of sediment cores for palaeolimnogical investigation. Three of the sites were selected in the southern section of the lake, with two in the northern section. Sites were selected based on water depth and the likely position of sediment deposition. Unfortunately no bathymetry data are available for the lake that could be used to determine the best possible site for sediment accumulation. Cores were retrieved from a stable platform using a gravity piston corer. Cores were retrieved in one meter sections and once extracted from the stainless steel coring device, sealed and kept in the dark until opened in the laboratory.

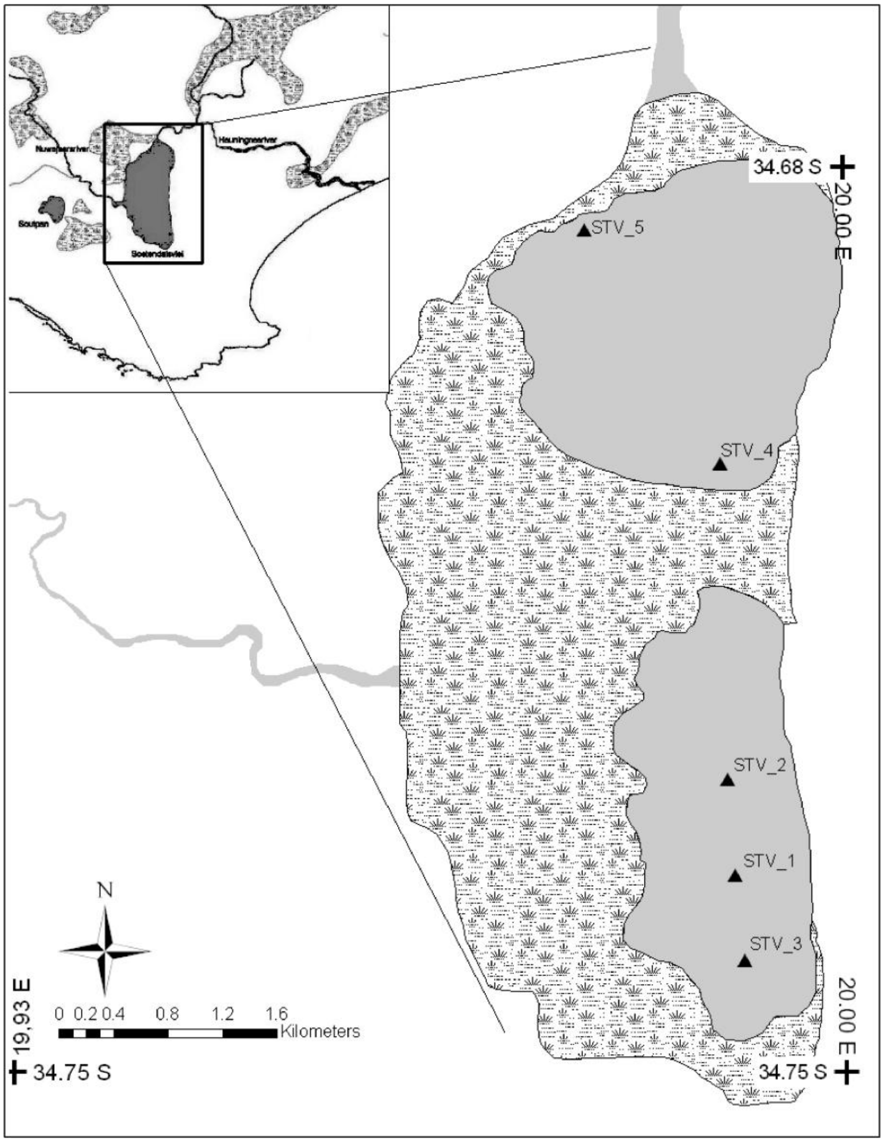


Figure 25 Sampling stations for the five different palaeo-cores collected in Soetendalsvlei Lake (STV_1 to 5 = Soetendalsvlei Core 1 to 5).

6.3 Materials and Methods

6.3.1 Coring

Sediment cores were retrieved using a 110 cm stainless-steel piston corer into which a black 75 mm internal diameter Perspex tube was placed to avoid extruding. Once the cores were collected, they were immediately sealed, labelled and brought to the laboratory, where the samples were longitudinally cut open. Photographs were taken of each core for reference purposes.

6.3.2 Sediment dating

Radiocarbon

Sediment dating was performed using the conventional radiocarbon (^{14}C) technique on the bulk sedimentary organic matter. AMS (Accelerated Mass Spectrometry) dating was also performed due to very low organic content within the sediments. The conventional radiocarbon dating was conducted by the Laboratorio Datacion ^{14}C, Montevideo, Uruguay. Samples were treated with dilute HCl in order to remove all inorganic carbon (i.e. carbonate). The bulk organic matter was converted into benzene and the radioactivity of this was measured using a Packard Tri-Carb 2560 TR/XL liquid scintillation spectrometer. The age of the sediment samples were expressed as uncalibrated conventional ^{14}C yr BP, corrected for isotopic fractionation by normalizing $\delta^{13}C$ values to -25‰. Quoted error (± 1σ) includes uncertainties in counting statistics. Radiocarbon ages were calibrated using the programme Calib Rev. 6.0 (Reimer *et al.,* 2009), corrected for isotopic fractionation by normalising $\delta^{13}C$ values to -25 ‰ and expressed as calibrated years AD (2σ). Samples were also sent for AMS dating to the Quaternary Dating Research Unit (QUADRU) at the CSIR, Pretoria, South Africa and sent to Groningen, Netherlands, for the final analysis.

Lead dating

Recent samples of the sediment core STV 3 were dated using the ^{210}Pb (excess) method (Appleby and Oldfield, 1992). The samples were cut every 2 cm for the top 32 cm. Samples were dried at 65°C for 48 hr, homogenised using a mortar and pestle and transferred to 50 ml plastic centrifuge tubes and sent to MyCore Scientific Inc., Canada, for dating. Radioactivity of the samples was measured using alpha spectrometry and the constant rate of supply (CRS) model (Appleby and Oldfield, 1978) was used to calculate the dates.

6.3.3 Sediment analyses

Lithology

Various lithological sections were identified based on sediment colour and texture as well as the presence of plant and mollusc shell remains. Samples were selected for organic matter, carbonate content and diatom species identification from each of the identified lithological units.

Organic and carbonate content

For organic and carbonate content, ca. 1 g of sediment were placed in crucibles and dried at 105°C for 24 hr. The weight loss on ignition method of Heiri *et al.* (2001) was used as a measure of organic matter and carbonate content (Tingstad *et al.,* 2011). Samples were ashed at 550°C for 4 hr, and at 950°C for 4 hr. Organic content was measured as the percentage weight loss after ashing at 550°C, while carbonate was measured as the weight loss after 950°C combustion multiplied by 1.36.

Stable isotopes

Samples collected for carbon and nitrogen stable isotope analyses were treated with 1N HCl to remove all inorganic carbon from the samples, rinsed with distilled water and dried at 85°C for 24 hr. After drying the samples were homogenized using a mortar and pestle. Samples were sent to the Stable Light Isotope Unit of the University of Cape Town, South Africa for further laboratory analyses.

6.3.4 Diatom species composition

Diatom samples were treated with sodium-pyrophosphate to deflocculate samples and remove clay. The samples were allowed to react with the sodium-pyrophosphate overnight, and then they were agitated to ensure complete sediment deflocculation. Distilled water was added to the sample and left overnight for the diatoms to settle. Samples were rinsed until no clay was observed in the supernatant. After the last decanting, 20 ml 35% HCl was added to the sample for 24 hr to remove all carbonate. The samples were rinsed four times with distilled water. Subsequently 20 ml of 30% H_2O_2 were added to the sample and allowed to stand for 24 hr to remove all organic material. The samples were boiled for 2 – 4 hr and rinsed with distilled water until the solution became clear. Samples were transferred to glass scintillation vials for storage. Permanent slides were made using 2 – 3 drops of sample that was air-dried onto glass cover slips. Slides were mounted using Entellan ®. A minimum of 300 valves were counted in each sample at 1000x magnification using a Zeiss Axionplan Light microscope. Using a camera attached to the microscope, images of the various diatom species were visualised using the image analyser software programme Image-Pro Express © (1993 version 4.5.1.3 for Windows 1998, Media Cybernetics Inc.). The relative abundance of each of the species was expressed as a percentage of the total number of cells counted.

Diatoms were identified to species level when possible using the nomenclature of Taylor *et al.* (2007), Metzeltin and Garcia-Rodriguez (2003), Metzeltin and Lange-Bertalot (2003), Lange-Bertalot (2001), Krammer and Lange-Bertalot (1991), Archibald (1983) and Husted (1976).

6.3.5 Statistical analyses

Ordination analyses were preformed for the diatom species and for the geochemical data using the program CANOCO for Windows (version 4.52, Ter Braak, 2003). Principal Component Analyses (PCA) were performed on all the data sets. The results of the PCA were plotted in two-dimensional graphs using CANODRAW (version 4.52, 2003). Sample-points that are similar are situated close to one another within the plot, while sample-points that are dissimilar will be located far apart.

6.4 Results

6.4.1 Chronology and sediment analyses

Conventional and calibrated radiocarbon dating indicated that the sediment cores were deposited during the early to mid Holocene (Table 12). Of the five collected cores in Soetendalsvlei Lake, core STV 3 proved to be the best representation of catchment activities as the organic matter in the other cores were too low to be accurately dated and diatom preservation was poor. Core STV 3 was 180 cm long and based on ordination analyses of the geochemistry (Figure 26) it was divided into five zones (Figure 27).

Table 12 Conventional, Calibrated, AMS and ^{210}Pb dates for core STV 3

Core Interval (cm)	**Age**	**Calibrated age ranges (2σ) BC**	**Lab number**	**Sedimentation Accumulation Rates (g.m^{-2}.yr^{-1})**
Lead dating (AD)				
0 – 2	2006	-	MyCore_81	-
2 – 4	2006	-	MyCore_82	-
4 – 6	2006	-	MyCore_83	-
6 – 8	2006 ± 0.03	-	MyCore_84	1064
8 – 10	2004 ± 0.46	-	MyCore_85	303
10 – 12	1993 ± 1.66	-	MyCore_86	217
12 – 14	1973 ± 5.7	-	MyCore_87	144
14 – 16	1916 ± 64	-	MyCore_88	136
Conventional ^{14}C (yr BP)				
46 – 58	2190 ± 60	390 - 94	URU 0492	
AMS (yr BP)				
90 – 95	6660 ± 40	5645 - 5511	Pta_C9058	
123 –126	7130 ± 40	6070 - 5974	Pta_C9059	

Lithological Zone Descriptions

Zone V, 160 - 140 cm, consisted of hard grey calcified sand with many shell fragments. This section displayed low organic content and total nitrogen levels, but high carbonate content (~20%). Due to the low total nitrogen and high total carbon content, C:N ratios were off the scale (i.e. >200). Zone IV, 140 – 125 cm, was dated at 7130 ± 40 yr BP and exhibited mainly grey clays, with very low organic (<5%) and carbonate content (<5%) and contained broken shell fragments. Stable carbon isotope values were approximately -24 ‰, but they increased to the upper section. C:N ratios were generally lower than 10, but also increased towards the top of the section, while $\delta\ ^{15}N$ values decreased. Zone III, 124 - 100 cm, consisted of a mixture of grey mud and sand with some bivalve shell fragments. This section displayed an organic content of approximately 7% and carbonate content of ~5%. Delta ^{13}C values ranged from -24 ‰ at 100 cm to -4 ‰ at 118 cm. This in turn resulted in the C:N ratios ranging from 10 at 100 cm to 40 at 118 cm. Zone II, 100 - 50 cm, was radiocarbon dated using the conventional method at 6660 ± 40 yr BP and consisted of a light grey mud-sand mixture with a layer of charcoal at 55 cm. This section was very similar in geochemistry to section IV (125 -140 cm), with slightly higher carbonate content (5 -10%) and $\delta^{13}C$ values of -24 ‰ and C:N ratios of 4.

The top zone I (i.e., 50 cm to the sediment surface), was an organic rich, muddy layer very rich in submerged macrophyte root material. Organic content was ~13 % and total nitrogen ranged from 0.02 ± 0.004 % to 0.18 ± 0.06 %. Carbonate content was low (1-3 %). Delta ^{13}C values ranged from -24 ‰ at 45 cm to -19 ‰ at the surface, resulting in C:N ratios ranging from 4 to 11 in this section. The top of this section was ^{210}Pb dated (Table 12) and indicated that the 16 cm layer was deposited in the last century (1916 ± 64 AD). Sediment accumulation rates were determined for the ^{210}Pb dated sections and indicated that during 2006, a large amount of sediment was deposited in the lake. Prior to 2006, a sedimentation rate of between 136 and 303 $g.m^{-2}.y^{-1}$ (Table 12) was observed. Conventional radiocarbon dating also indicated that sediments deposited at depth 46 – 58 cm were 2190 ± 60 yr BP.

The top ^{210}Pb dated 20cm of the core were further investigated to determine if any recent historically recorded events could be linked to the geochemistry of this section. The section dated at 1916 ± 64 AD corresponded to lower organic matter (<10%) and carbonate content (~2%), slightly enriched δ^{15}N values (1-2 ‰) and δ^{13}C values between -22 and -23 ‰. C:N ratios also varied between 10 and 11. The 1973 ± 6 AD section corresponded with increased organic matter (~13.5%) and lower carbonate content (~3%). δ^{13}C values were approximately -23 ‰ and C:N ratios varied between 10 and 11. The most recent section, dated at 2006 AD, corresponded with high organic matter (~12%), low carbonate content (~2%), δ^{13}C values ranging between -19 and -25 ‰ and subsequently C:N ratios of between 9 and 15.

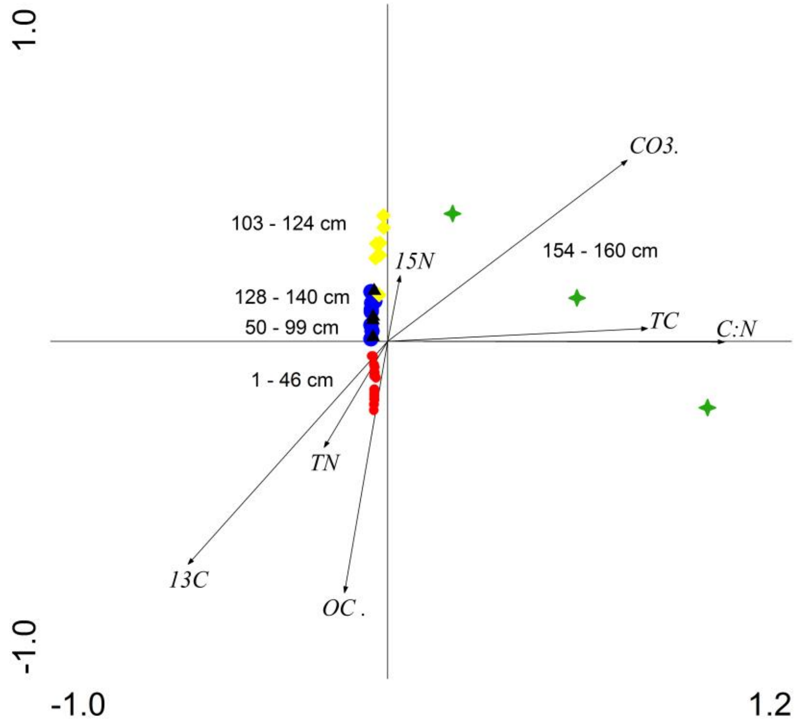


Figure 26 Principal Component Analysis (PCA) of geochemical data for core STV 3 (13C = δ^{13}C, 15N = δ^{15}N, OC = organic content, CO3 = carbonate content, TC = Total carbon content, TN = Total nitrogen content and C:N = C:N ratio)

Table 13 Summary of the PCA analyses for the geochemistry of palaeo-core STV 3

Axes	1	2	3	4	Total inertia
Eigenvalues					
Species-environment correlations	0.998	0.001	0.001	0.000	1.000
Cumulative % variance:					
Of species data	99.8	99.9	100.0	100.0	
Sum of all eigenvalues					1.000

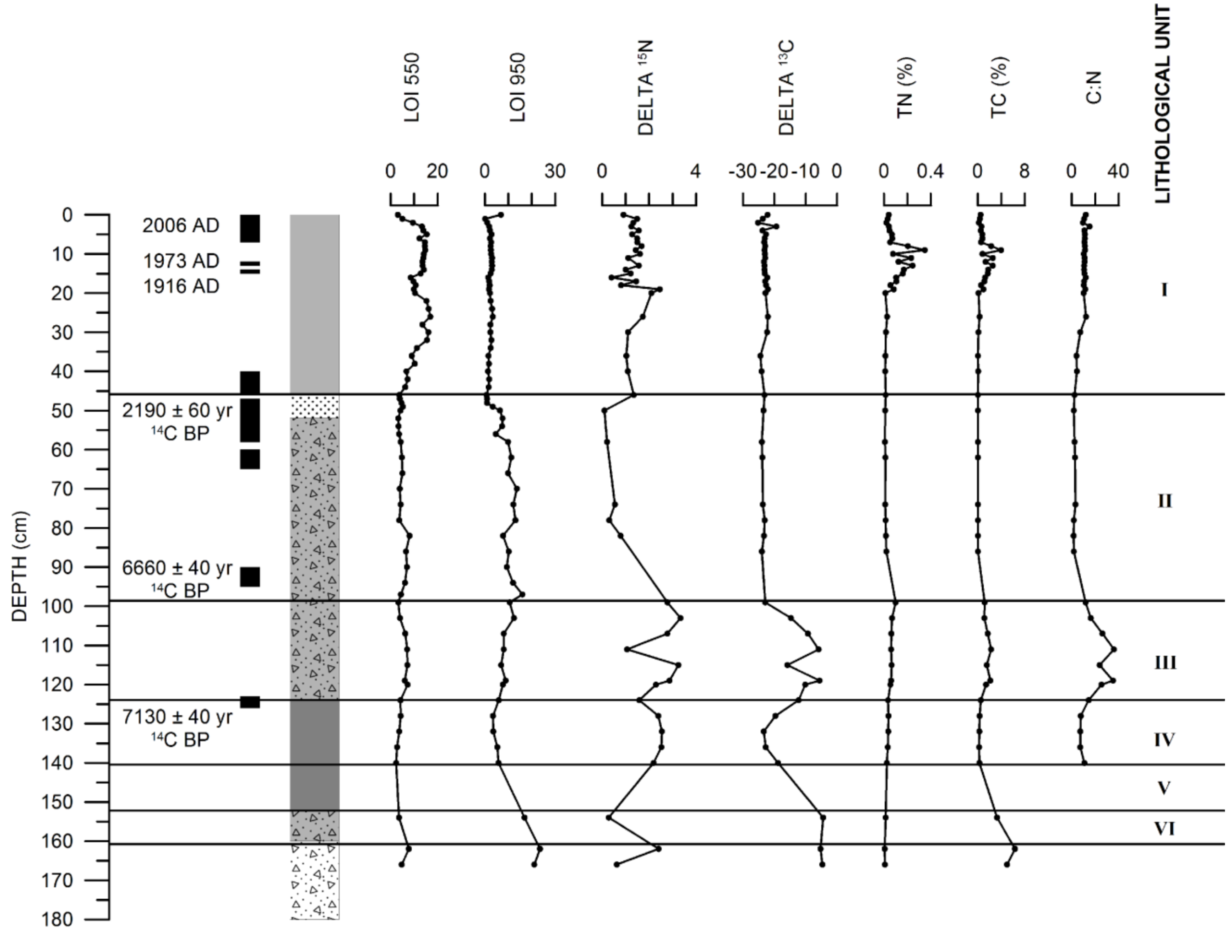


Figure 27 Summary diagram of all geochemical data for the entire Soetendalsvlei sediment core indicating the shift in organic (LOI 550) and carbonate (LOI 950) content, stable isotopes ($\delta^{13}C$ and $\delta^{15}N$), total nitrogen (TN%), total carbon (TC%) and C:N ratio

6.4.2 Diatom analyses

Diatoms were not well preserved throughout the sediment core, with frustules being very corroded or broken. Therefore it was not possible in all instances to identify all taxa to species level. A total of 51 diatom taxa were identified, but only species with a relative abundance higher than 2% in at least three samples were included in the analyses (Karst and Smol, 2000). Therefore only 28 diatom species were included in the ordination analyses (Figure 28).

Eight Diatom Assemblage Zones (DAZ) were identified based on ordination analyses of the 28 most abundant species (Figure 29). Below 154 cm no diatoms were recorded. The oldest assemblage, DAZ VIII, 154 - 130 cm, contained freshwater-brackish species such as *Cocconeis engelbrechtii* Cholnoky*, C. placentula* Ehrenberg*, Craticula acidoclinata* Lange-Bertalot and Metzeltin*, Rhopalodia operculata* (Agardh) Håkansson and *Melosira sp.* Agardh and *Nitzschia frustulum* (Kützing) Grunow*.* DAZ VII, 130- 120cm, was characterised by a decrease in *Melosira* sp. abundance and an increase in *N. frustulum* and *C. engelbrechtii* abundance, representing increased brackish conditions. Within DAZ VI, 120-110 cm, there was a decrease in abundance of brackish-marine taxa such as *M. elliptica*, *Cyclotella meneghiana* Kützing and *Tryblionella levidensis* W. Smith*,* while the abundance of *G. gracile* Ehrenberg and a *Navicula* species increased, indicating freshwater conditions. DAZ V, 107 - 100 cm, was characterised by freshwater species, namely *R. operculata* and some freshwater-brackish species including *C. engelbrechtii*, *C. meneghiniana* and *M. elliptica.* The basal section of DAZ IV, 99 - 70 cm, was almost sterile, except for a low number of *N. frustulum* valves. The section, 70 – 44 cm, however, contained a number of freshwater species, such as *C. meneghiana* and *Stephanodiscus aggassizensis* Håkansson and Kling. This section also showed an increase in the relative abundance of *C. engelbrechtii*, *C. placentula*, *F. investiens* and *S. aggassizensis* and *N. frustulum* at the transition between DAZ IV and III. DAZ III, 44 – 20 cm, exhibited freshwater-brackish species such as *C. engelbrechtii*, *C. placentula*, *M. elliptica* and *R. operculata*. DAZ II, 20 - 12 cm, was represented by an *Eunotia* sp. (Kützing) Grunow, *C. meneghiana*, *Navicula* sp., *Epithemia adnata* (Kützing) Brébisson, *Epithemia* sp. and *G. acidoclinatiforme*, thus indicating freshwater-brackish conditions. The top 8 cm of the sediment core (DAZ I) was characterised by freshwater-brackish species such as *N. frustulum*, *Melosira* sp., *G. gracile* and a *Navicula* sp.

The top 20 cm of the sediment core were investigated for human impacts that might have been captured in the sediment layer. Within the basal section of this layer, the relative abundance of the observed taxa was higher than after 1916 (Figure 29). The community was also dominated by benthic freshwater / brackish species, which also decreased in relative abundance by 1916. Within the section dated at 1973 ± 6 AD, the relative abundance of taxa were lower, and species such as *Eunotia* sp., *Melosira* sp. and *N. frustulum* were dominant. A shift from freshwater to freshwater / brackish taxa also occurred at this time. The most recent dated sediment section, i.e. 2006 AD, had a further reduction in the number of species recorded, although the relative abundance of plankton species increased. The basal sediment section was dominated by freshwater taxa, but towards the top, an increase in freshwater / brackish taxa was observed.

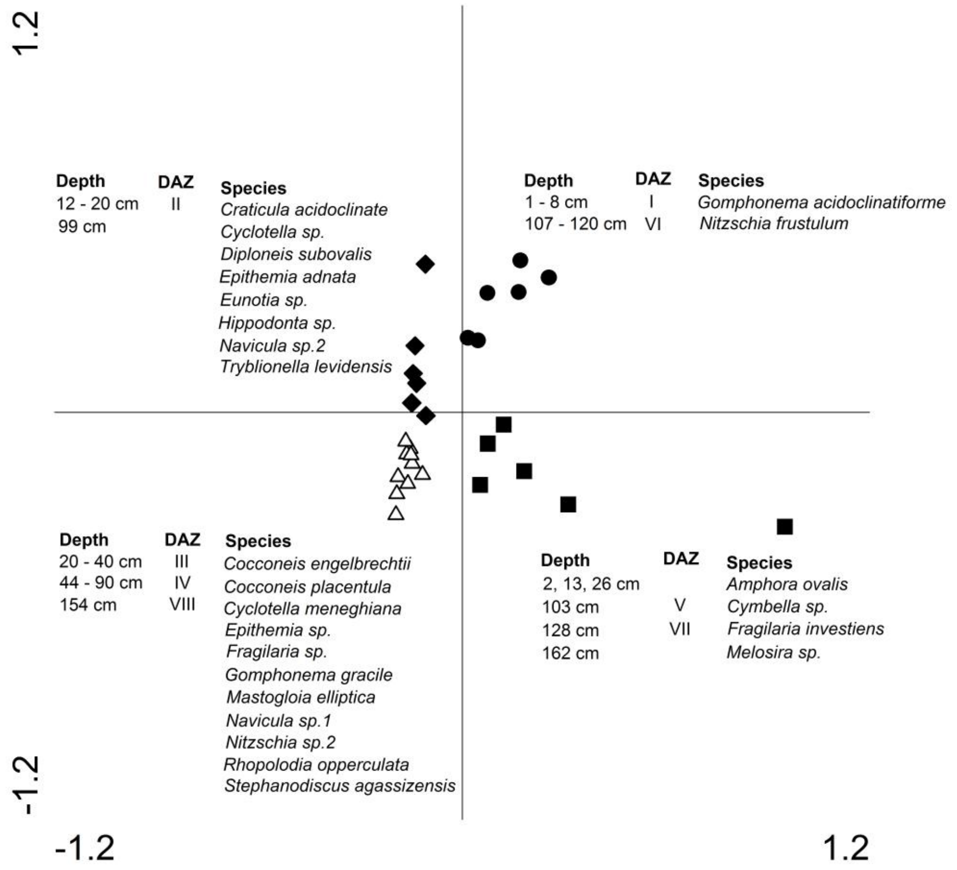


Figure 28 Principal Components Analysis (PCA) for diatom species indicating the various diatom assemblage zones (DAZ) and corresponding species.

Table 14 Summary of the PCA analyses for the sub-fossil diatoms of palaeo-core STV 3

Axes	1	2	3	4	Total inertia
Eigenvalues					
Species-environment correlations	0.410	0.244	0.095	0.058	1.000
Cumulative % variance:					
Of species data	41.0	65.4	74.9	80.8	
Sum of all eigenvalues					1.000

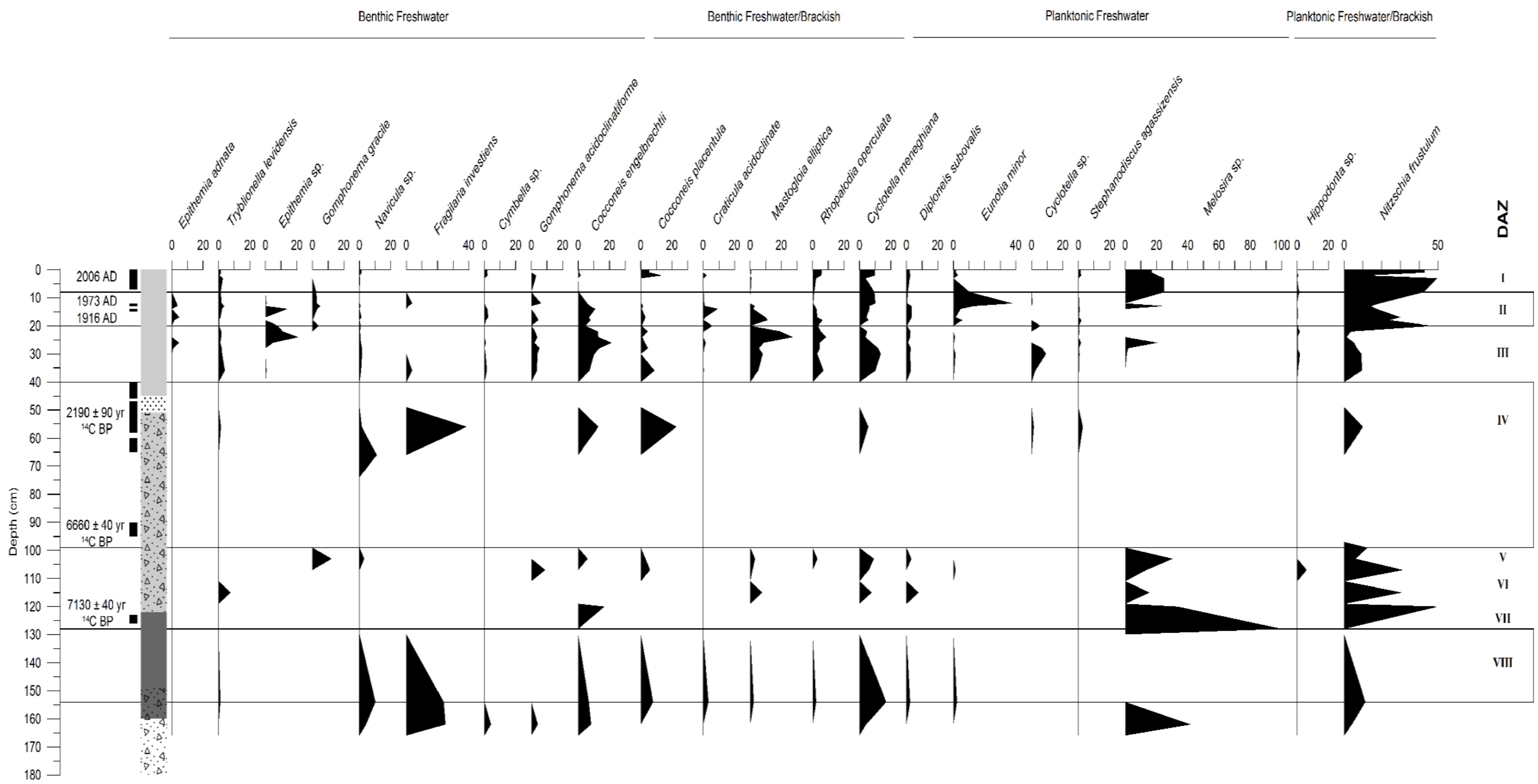


Figure 29 Stratigraphy of the dominant diatom species indicating the seven diatom assemblage zones (DAZ) throughout sediment core STV 3

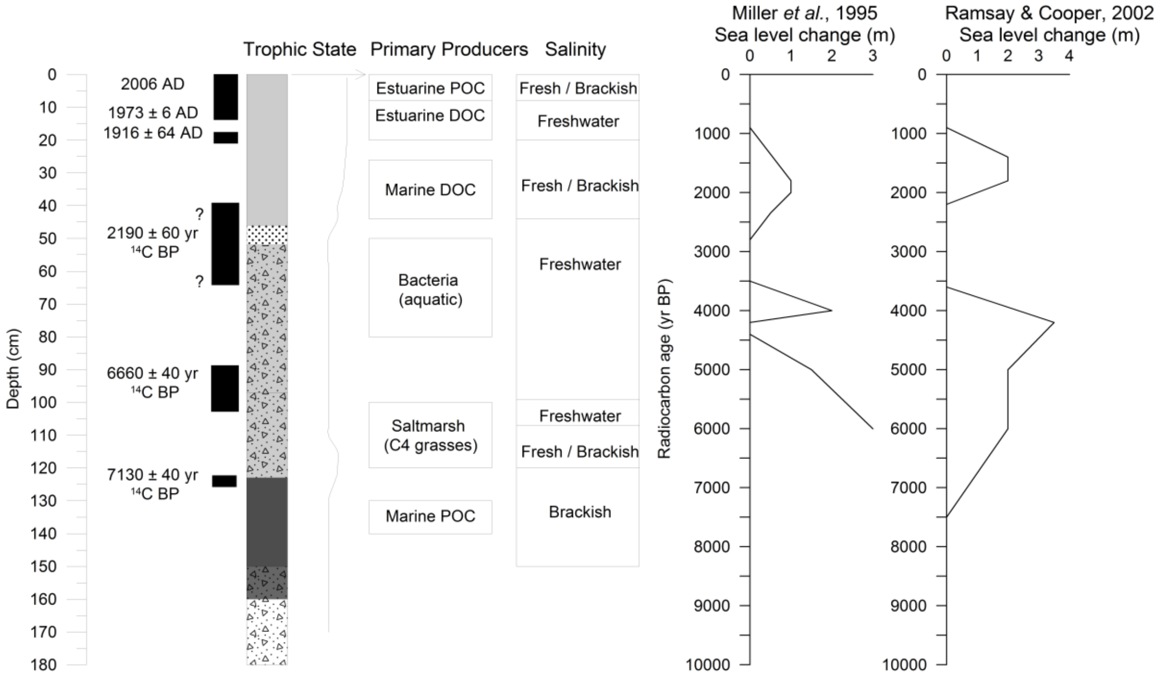


Figure 30 Summary stratigraph of the Soetendalsvlei sediment core (STV 3) compared with the sea-level change models of Miller *et al.* (1995) and Ramsay and Cooper (2002).

6.5 Discussion

Soetendalsvlei is situated near the convergence of the Agulhas and Benguela ocean currents at the Agulhas Bank. Previous research has indicated that the Agulhas Bank has experienced major marine transgression and regression events, significantly impacting inland environmental and climatic conditions (van Andel, 1989; Bateman *et al.*, 2004).

The data obtained in this study were used to infer palaeo-salinity and trophic status changes for Soetendalsvlei (Figure 30). From the model it is clear that Soetendalsvlei, presently separated approximately 15 km away from the Indian Ocean, did experience direct marine influence during the early to mid Holocene. Based on organic matter and carbonate content, with many bivalve shell remains, it is clear that during the early Holocene (> 7130 ± 40 yr BP) as well as between 6660 ± 40 and 2190 ± 60 yr BP the system contained marine derived organic matter. After the onset of Freshwater conditions, an increase in trophic status was observed between 7130 ± 40 and 6660 ± 40 to yr BP, but also after 2000 yr BP. The basic geochemistry of the core provided a measure of marine influence in the system which was supported by the stable isotope data.

According to Lamb *et al.* (2006) the use of $\delta^{13}C$ in conjunction with C:N ratios can indicate the various sources of organic matter within the sediment. Lamb *et al.* (2006) showed that organic matter derived from the marine environment would have higher $\delta^{13}C$ values, ranging from -16 to -25 ‰, than freshwater environments, ranging from -25 to -32 ‰. In turn the C:N ratios would differ between POC and DOC for both freshwater and marine environments, with C:N ratios for POC ranging between 5 and 10, and for DOC between 7 and 25. Terrestrial plants and aquatic vegetation that mainly depend on atmospheric CO_2, on the other hand would have higher C:N ratios as well as higher $\delta^{13}C$ values. The model of Lamb *et al.* (2006) was applied in this study and indicated that during periods of high carbonate content, the organic matter within that section of the sediment core, which had $\delta^{13}C$ values ranging from -23 to -21 ‰ and C:N ratios from 3.7 to 8.3, consisted of mainly marine particulate organic (i.e. algae and phytoplankton) and marine dissolved organic matter (Figure 6). The sections of the sediment core that displayed high organic content mainly contained estuarine particulate organic matter (top of the core), bacterial products (60 – 90 cm) and C_4 grasses, indicative of salt marsh vegetation. From the stable isotope data, it is clear that Soetendalsvlei experienced periods of marine dominance, followed by a period of brackish conditions with probably reduced water levels as salt marsh vegetation was dominant. Subsequently there was a period of increased water level, resulting in the inundation of the salt marsh vegetation and their subsequent decomposition, leading to the dominance of bacterial matter signals in the stable isotope analyses. At approximately 2000 yr BP, water level decreased with a concomitant increase in salinity. Stable isotope analyses indicated the presence of marine dissolved organic matter, which likely entered the system during periods of mouth closure of the

Heuningnes Estuary and back-flooding of estuarine water into Soetendalsvlei. At present the wetland is dominated by submerged and cosmopolitan emergent macrophyte beds, occurring in both freshwater and estuarine conditions (Kotsedi, 2007).

Diatom valves within the Soetendalsvlei sediment core were not well preserved as indicated by the sterile section between 70 and 95 cm. Poor preservation or the degradation of frustules is the result of either chemical (i.e. pH), mechanical (i.e. fluvial transport) or biological processes (i.e. silicate uptake during growth)(Saunders, 2010). Chemical degradation in this instance occurs mainly due to the high alkalinity (Flower, 1993; Chakrborty *et al.*, 2010) of the inflowing and interstitial water, which flows through limestone bearing sandstone. According to Fritz *et al.* (1991) and Ryves *et al.* (2001, 2009) diatom preservation is poor under saline conditions. Other factors that influence the dissolution of diatom silica frustules are pH and temperature (Flower, 1993), the initial concentration of silica in the water column and its saturation and diffusion equilibrium (Fritz *et al.*, 1991), the surface area to volume ratio of the diatom frustules (Fritz *et al.*, 1991; Ryves *et al.*, 2001, 2009; Saunders, 2010), species specific susceptibility to dissolution and rate of sediment accumulation (Flower, 1993). According to Ryves *et al.* (2001) large, robust species such as *Mastogloia elliptica*, *Cocconeis placentula*, *Cyclotella meneghiniana* and *Rhopalodia gibba*, are less susceptible to dissolution and may persist within the palaeo-record for longer periods of time. This may lead to inaccurate reconstructions of palaeo-salinity as most inference models use relative abundance of species as an indicator for environmental conditions (Ryves *et al.*, 2009). The sterile section of the sediment core (95 – 70 cm) observed in this study could be due to not only very high alkalinity, but also the result of dry conditions with a reduced water column within the wetland.

Diatom assemblages indicated marine/brackish conditions in the early Holocene (7130 ± 40 yr BP) with dominant species such as *Cocconeis engelbrechtii, C.*

placentula and *Mastogloia elliptica*. Following this period of strong marine influence, was a reduction in marine intrusion and increase freshwater input, with mainly freshwater/brackish taxa. During this period there was also a decrease in carbonate content, further illustrating the reduced influence of the marine environment in the lake. Subsequently by ~6000 yr BP, there was an increase in carbonate content, although the DAZ was dominated by freshwater/ brackish species. After ~6000 yr BP, a further increase in salinity, as indicated by the increase in carbonate content and decrease in trophic status, was observed. The most recent samples, i.e. after 2000 yr BP, indicate increase in trophic status together with a reduced marine influence, as suggested by the of low carbonate content. However, stable isotopes and C:N ratios indicate more estuarine conditions, which may be the result of inundation of salt marsh area adjacent to the lake (Lamb *et al.,* 2006). During periods of brackish conditions, the diatom assemblages were dominated by *Fragilaria investiens, Cyclotella meneghiana, Gomphonema gracile* and *Tryblionella levidensis*. The relationship between trophic status and salinity appears to be inverted with the exception of the most recent samples.

This conforms well to other palaeo-salinity and trophic status studies conducted in Uruguay that shows an inverse relationship between salinity and trophic status (Garcia-Rodriquez *et al.*, 2004a, 2004b, 2010; Bracco *et al.,* 2005; Inda *et al.*, 2006). Such a relationship would be a consequence of an increase in freshwater runoff and subsequent increase in nutrients and terrestrial organic matter input as well as increased erosion during marine regression periods i.e. lower salinity conditions (Garcia-Rodriguez *et al.*, 2004a).

This palaeo-salinity model agrees well with sea-level change models developed for the South African coastline (Figure 30). Understanding the regional impacts of past sea-level will aid in our understanding of climate change within the global context and what the likely future impacts of increased sea-level will mean for South Africa. The sea-level models developed for the South African coastline by

Ramsay (1995), Miller *et al.* (1995), Baxter and Meadows (1999) and Ramsay and Cooper (2002) indicate a level of -10 m below msl during the Early Holocene, Marine transgression then occurred to -1 m below msl at ~7800 yr BP and continued to increase to +2.75 m above msl at approximately 6500 yr BP. Marine regression took place with levels dropping to present mean sea level at ~4500 yr BP. This was followed by another transgression event until 4000 yr BP when maximum sea level of +3 m above msl was recorded. Sea-level dropped again to present levels at ~3500 yr BP and continued to drop to -2 m below msl at ~3000 yr BP. The last transgression event took place thereafter with sea-level reaching a high of +1.5 m above msl at approximately 1600 yr BP. Sea-level decreased again to present levels at ~900 yr BP and has been maintained since.

Although the various sea level change models for South Africa differ slightly, the major marine transgression and regression events follow similar temporal patterns. It is however difficult to determine an overall increase in sea-level for the entire coastline due to regional differences in topography and geomorphology for the different regions.

Studies in South America, i.e. Uruguay, have also indicated the important implications that changing sea-level has on salinity, in turn affecting the trophic status of coastal lakes. Garcia-Rodriguez *et al.* (2004a, b), Bracco *et al.* (2005) and Inda *et al.* (2006) showed that during periods of reduced marine influence (i.e. regression), the increase in freshwater can be linked to an increase in trophic status of the lakes, while an increase in sea-level and salinity are associated with lower trophic status.

The top 16 cm section of the sediment core was ^{210}Pb dated and provided a chronology within the last century for which historical information was available. The 16 cm depth was dated at 1916 ± 64 AD. From 1909- 1910 drought conditions were recorded for this region (Bickerton, 1984). Low sediment accumulation rates, low organic matter content and the dominance of DOC within the organic matter, correspond with low freshwater inflow conditions into the lake. The dominance of benthic freshwater / brackish diatom taxa further indicate low water levels, with increased salinity, mainly due to evaporative water loss and subsequent concentration of ions within the water column.

During the second ^{210}Pb-dated interval (1973 ± 6 AD), the system experienced a severe drought (i.e. from 1969 – 1972, Bickerton, 1984), when the lake dried up and salt crust formed. In 1973 the drought was interrupted and there was an increase in water level until 1976 when the mouth of the Heuningnes Estuary was artificially breached to prevent back-flooding of farmlands (Bickerton, 1984). The increase in estuarine organic matter during this period is believed to be a result of the death and senescence of lake vegetation due to low freshwater inflow. The slight enrichment in δ^{15}N values and TN also indicates an increase in microbial decomposition. Diatom analyses showed that the relative abundance of taxa such as *E. minor*, *Melosira* sp. and *N. frustulum* increased, mostly likely at the end of the drought period, when rainfall increased and subsequently freshwater inflow into the lake caused an increase in water level. A shift in diatom taxa from freshwater to freshwater / brackish appears to be the result of an increase water level due to freshwater inflow, thus inundating littoral salt marsh and the leaching of salts into the water.

Historical data for the most recent sediment section (2006) indicated that during 2005 a major flood occurred, with 225 – 325 mm of rainfall within 24 hours, inundating ~12,000 ha of surrounding farmland. This resulted in an extremely high sediment accumulation rate because of huge erosion (~1 kg m^{-2} y^{-1}). Organic matter input however did not increase substantially, remaining at ~12%. Stable isotope, however, did indicate a shift from freshwater POC and DOC, corresponding to increase freshwater inflow and terrestrial organic input, to estuarine / marine DOC and POC. Again the relative abundance of planktonic taxa increased due to the increase in freshwater inflow and lake water level. There was also a shift from mainly freshwater species to freshwater / brackish species as water level increased and littoral salt marsh areas were inundated. At present this condition prevails in the lake

6.6 Conclusion

The palaeo-reconstruction of salinity change of Soetendalsvlei Lake compares well with the sea-level change models developed for the west coast (Miller *et al.*, 1995; Baxter and Meadows, 1999) and the east coast (Ramsay 1995; Ramsay and Cooper, 2002). This study found that during the early to mid Holocene (~8000 yr BP and ~4000 to 2000 yr BP) marine intrusion occurred in Soetendalsvlei that may be associated with increased sea-level. At ~6000 yr BP and ~1800 yr BP, however, freshwater conditions prevailed, coinciding with marine regressions along the South African coastline. The data also indicate that during periods of increased marine influence, lake trophic status was lower and organic matter was dominated by marine POC and DOC, while during freshwater/brackish conditions there was an increase in trophic status with production being dominated by estuarine POC, i.e. vegetation. This study also provided a means of assessing the use of geochemistry and diatoms in reconstructing past environmental change by comparing data with known historical records of human impacts. The data did indicate the major drought and flood events of the last century. This study thus highlighted the importance of using multiple proxies in palaeo-reconstruction. Although there was poor preservation of diatoms, combining the limited diatom data with geochemical and stable isotope analyses ensured that trophic status, salinity and sources of organic matter could be determined and this aided in the overall understanding of the palaeolimnology of Soetendalsvlei.

Chapter 7

Palaeosalinity and trophic status relationships in coastal lakes: A regional comparison with Groenvlei Lake (Wilderness) and Uruguayan systems

7.1 Introduction

Present day climatic conditions vary and will continue to do so in the future due to varying degrees of influence by changing ice, ocean and continental processes. All of these factors are influenced by seasonal or latitudinal solar radiation affected by the earth's orbital parameters (Berger and Loutre, 1991). Consequently the earth's climate differs not only over time, but also on a spatial scale. Although different regions of the world have and are responding differently from one another to changing climatic conditions, global climate change affects each of these regions. To what extent each region is affected will be determined by that area's unique characteristics and the magnitude of climate change encountered. It thus stands to reason that different regions of the world, be it on a hemispherical, continental or regional scale will be affected by climate changes in a different way, even when the underlying mechanisms of change is similar. To develop accurate models of future climate change and to provide input for better management of global climate changes, models are needed on the regional scale that can be fed into continental or hemispherical models and ultimately into a global climate change model.

In South Africa, the east and south coast are influenced by the warm Agulhas current flowing westwards, converging with the cold Benguela current at the Agulhas Bank. Present climatic conditions vary geographically with the eastern seaboard characterised by hot, sub-tropical conditions, replaced by a Mediterranean climate on the southern and west coast. The southern coast can in turn be future divided into the summer and winter rainfall zones. According to Cowling *et al*. (1999), Meadows and Baxter (1999) and Bateman *et al*. (2004)

these difference were also present in the geological past as differences in the sea surface temperature (SST) of these two major ocean current systems ensured different moisture supplies to the coastal inland areas. Not only do climate conditions vary between the east and west coast of South Africa, sea-level models for these regions also differ in terms of timing and magnitude in rise or fall. Consequently any future climate change models need to take into account these regional difference and management protocols will have to the adjusted to accommodate these difference, i.e. what works on the east coast might not necessarily work on the west coast and *visa versa*. Anthropogenic impacts also vary regionally and can have significant impacts on the current ecological functioning of systems. This would need to be considered in the different management protocols.

The Wilderness Lakes are situated on the southern coast of South Africa and consist of five coastal lakes that include Groenvlei Lake, which have been the subject of detailed palaeoenvironmental studies (Martin, 1959; 1962; 1968; Illenberger, 1996; Meadows and Baxter, 1999). Martin (1959; 1962) retrieved a 650 cm long sediment core from Groenvlei Lake that extended to ~8000 yr BP, that was subjected to detailed diatom and pollen analyses. Martin (1962) was able to infer Holocene vegetation, climate and salinity changes from this core, indicating that during the early Holocene the Lake was freshwater dominated with a dry climate. By ~7000 yr BP, climate exhibited wetter conditions conducive to forest spread and peat formation. By ~6000 yr BP a marine system was established as a consequence of the maximum Holocene sea-level stand. Warmer climate conditions were inferred from the dominance of Chenopodiaceae and Restionaceae. After ~4000 yr BP a brackish lagoon was established because of sea-level decrease. By ~1900 yr BP a freshwater system and wet conditions, conducive to forest spread were observed. After ~1000 yr BP, there was evidence of a dry climate (Martin 1962). Although Martin (1959; 1962) presented a model of Holocene climatic and salinity change, he did not discuss the relationship between trophic state, palaeosalinity and sea-level fluctuations, nor did he address the composition or sources of organic matter within the sediment core.

Soetendalsvlei is situated approximately 500 km to the west of Groenvlei and ~15 km from the Indian Ocean. From the results in Chapter 6, it is clear that this lake has experienced marine intrusion during the early and mid Holocene as inferred from geochemical, stable isotope and diatom analyses. The palaeosalinity and trophic status of this lake also showed an inverse relationship with higher trophic conditions during periods of reduced salinity, as freshwater inflow increased nutrient and terrestrial organic matter input into the lake. The palaeosalinity of the lake could also be related to the major sea-level models for South Africa (Miller *et al.,* 1995; Ramsay, 1995; Baxter and Meadows, 1999; Ramsay and Cooper, 2002).

This chapter focussed the Holocene trophic state and palaeosalinity changes for Groenvlei Lake in relation to sea-level changes as well as the composition and source of organic matter into the lake in the past. These data are discussed in relation to the findings of the diatom and pollen analyses of Martin (1959; 1962). The results will be compared on a regional basis to that of Soetendalsvlei Lake (Chapter 6) and to similar studies undertaken in coastal systems of southern Uruguay, South America, located at a similar latitude (~ 33°S) (Garcia-Rodriguez *et al.,* 2001; 2002; 2004a;b; Garcia-Rodriguez and Witkowski, 2003; Bracco *et al.,* 2005; Inda *et al.,* 2006). Palaeolimnological methods were used to make biogeographic comparisons of the responses of subtropical coastal lakes in relation to Holocene sea-level changes.

Hypotheses tested were:

- An inverse relationship exists between trophic status and palaeo-salinity for Groenvlei lake based on organic matter content and diatom species composition, and

- Groenvlei and Soetendalsvlei lakes show similar palaeo-histories during the various stages of sea-level change along the southern Cape coast of South Africa.

7.2. Study area

Groenvlei Lake is one of a series of coastal aquatic systems on the south coast of Africa (Figure 31), where a successive line of dunes, known as the Wilderness cordon dunes, developed during the Late Quaternary. The dune formation consists of steep-sided ridges up to 207 m high separated by coastal lakes that formed during sea-level highstands of the Pleistocene interglacials (Illenberger, 1996). Because of the sea-level change history, there have been phases of dune-building followed by coastal erosion that led to the formation of sea-cliffs in the dune cordons. Groenvlei Lake is located in a depression, dated at 37,700 yr BP (Martin, 1962), that is 10 m AMSL and 3 km from the sea. The depression lies between two aeolianite ridges parallel to the coast.

The lake lacks outlets and is fed by rainfall, runoff and groundwater from the surrounding dunes (Martin, 1962). The water is hard due to calcium carbonate leaching from the surrounding dunes. The rate of leaching depends on climate, and is relatively rapid under warmer-temperature, with moderate to high rainfall conditions (600 – 900 $mm.y^{-1}$) that are commonly observed in the study area at present (Illenberger, 1996). The water column is well oxygenated, slightly saline, eutrophic, and well mixed because of the shallow water depth (maximum depth ~ 5m) and high wind intensities that characterize the area. Mean total dissolved solids (TDS) was 990 $mg.l^{-1}$, pH ~8.5, mean PO_4 ~ 0.11 $mg.l^{-1}$ (Martin, 1962) and Secchi depth was 1 m.

In Martin's work (1959, 1962) the sediment core was retrieved from the peat fen on the eastern section of the lake. During this palaeolimnological study, the sediment core was retrieved from the centre of the lake, thought to be the deepest section of the lake and hence best suited for sediment deposition.

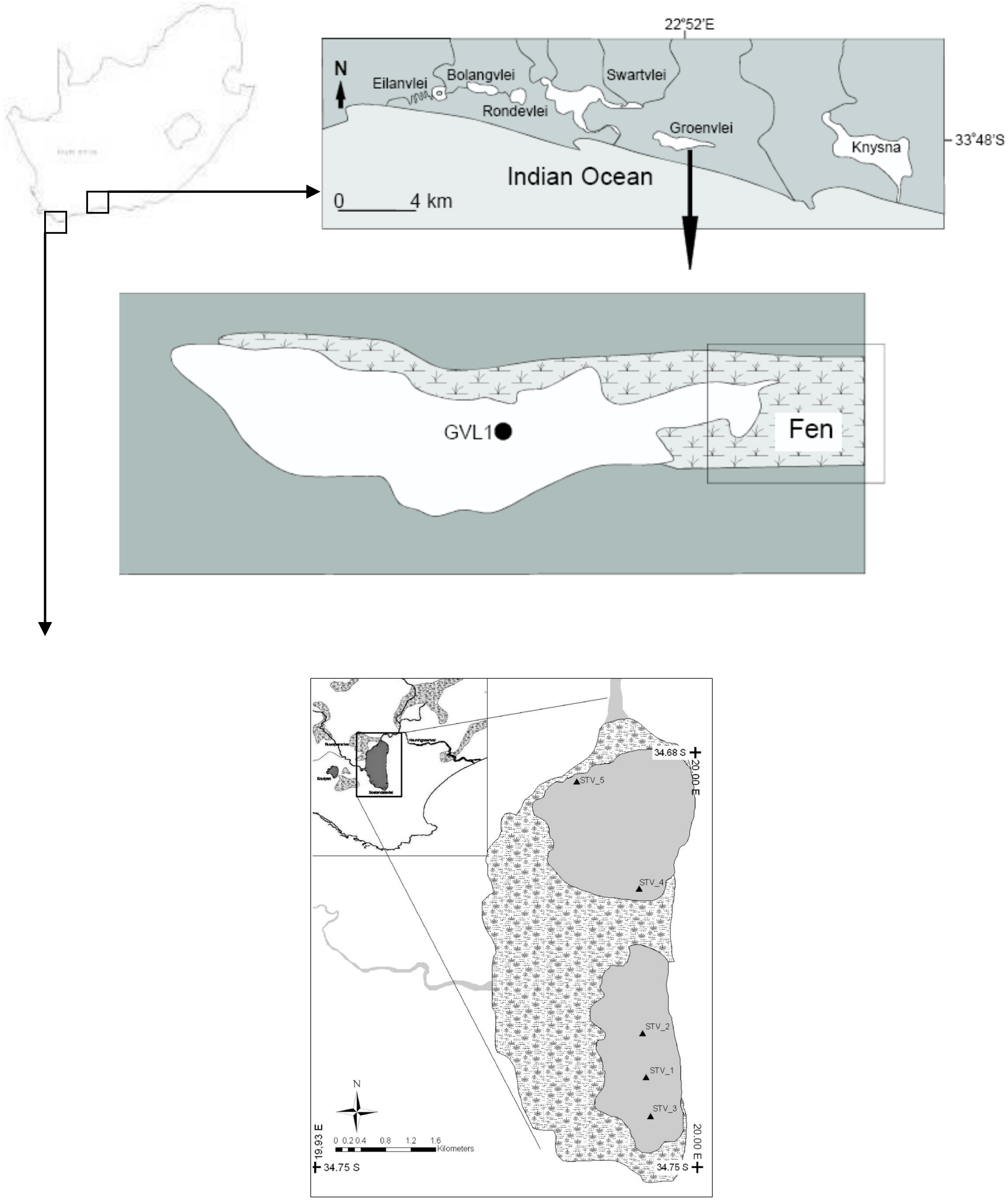


Figure 31 Soetendalsvlei with the various sampling stations and the Wilderness Lakes indicating the position of Groenvlei Lake. The frame on the right of Groenvlei Lake indicates the fen studied by Martin (1959; 1962)

7.3 Materials and Methods

7.3.1 Sampling

A 125 cm long core (GVL1) was taken in Groenvlei Lake in October 2005 with a 75 mm diameter piston corer (Figure 33). The sampling station was located at a site representing the maximum depth in the lake. After retrieval the core was immediately sealed and kept in the dark prior to laboratory analyses. A 180 cm long core (STV3) was taken in Soetendalsvlei Lake in May 2006 with the same corer used to collect the Groenvlei Lake core. The core was also immediately sealed and analysed in the laboratory.

7.3.2. Dating

Sediment age was determined by conventional ^{14}C in four intervals on bulk sedimentary organic matter and shells of *Modiola capensis* Krauss for the core GVL1. Sediment age for core STV3 was determined by both the conventional ^{14}C and AMS method on bulk sedimentary organic matter at six intervals. ^{210}Pb dating was also performed for the upper section of core STV3 (Chapter 6).

7.3.3 Lithology and thin sections

Lithological units were described based on changes in sediment colour / texture and conservation of biogenic material. Texture was determined by simply touching a small amount of sediment in each lithological unit with the fingers.

7.3.4 Sediment analyses

For the measurement of organic and carbonate content, ca. 1 g of sediment were placed in crucibles and dried at 105°C for 24 hr. The weight loss on ignition method of Heiri *et al.,* (2001) was used as a measure of organic matter and carbonate content (Tingstad *et al.,* 2011). Samples were ashed at 550°C for 8 hr, and at 950°C for 4 hr. Organic content was measured as the percentage weight loss after ashing at 550°, while carbonate was measured as the weight loss after 950°C combustion multiplied by 1.36.

Samples, collected from core GVL1, for total carbon and total nitrogen were sent to the South African Bureau of Standards (SABS). Samples were dried in the oven at 105°C for 24 hours, and the sediment was then homogenized and pressed as a pellet. Nutrient content was determined with a CHN analyzer.

For core STV3, samples collected for stable carbon and nitrogen isotope analyses were treated with 1N HCl to remove all inorganic carbon from the samples, rinsed with distilled water and dried at 85°C for 24 hr. After drying the samples were homogenized using a mortar and pestle. Samples were sent to the Stable Light Isotope Unit of the University of Cape Town, South Africa for further laboratory analyses.

7.3.5 Diatom analyses

Samples for diatom identification were treated with 35% HCl for 24 hours to eliminate carbonates, and then rinsed four times with distilled water. Next, 10 ml of 30% H_2O_2 were added to eliminate organic matter, where after the samples were boiled for 2 – 4 hours and rinsed five times with distilled water. Permanent slides were mounted in Entallen© for counting and identification. A minimum of 300 valves were counted in each sample at 1000x magnification using a Zeiss Axionplan Light microscope. Using a camera attached to the microscope, images of the various diatom species were visualised using the image analyser software programme Image-Pro Express © (1993 version 4.5.1.3 for Windows 1998, Media Cybernetics Inc.). The relative abundance of each of the species was expressed as a percentage of the total number of cells counted. Diatoms were identified to species level when possible using the nomenclature of Metzeltin *et al.* (2005), Taylor *et al.* (2007), Metzeltin and Garcia-Rodriguez (2003), Metzeltin and Lange-Bertalot (2002), Lange-Bertalot (2001), Krammer and Lange-Bertalot (1991), Archibald (1983), Husted (1976).

7.3.6 Statistical analyses

Ordination analyses were performed for the diatom species and for the geochemical data using the program CANOCO for Windows (version 4.52, Ter Braak, 2003). Principal Component Analyses (PCA) were performed on all the data sets. The results of the PCA were plotted in two-dimensional graphs using CANODRAW (version 4.52, 2003). Sample-points that are similar are situated close to one another within the plot, while sample-points that are dissimilar will be located far apart.

7.4 Results

Only the results for Groenvlei core, GVL 1, will be presented here. Complete descriptions and results of the Soetendalsvlei core, STV3, are presented in Chapter 6.

7.4.1 Chronology and lithology

Groenvlei core, GVL1

The basal section of the core was dated at ~6150 yr BP (Figure 32). Lithological unit VIII was dated at the bottom (95 – 110 cm) and top (74 – 92 cm), yielding ages of 5790 and 5630 yr BP, respectively. The age of the 35 – 45 cm section was ~ 3800 yr BP.

Core GVL1 was subdivided into ten lithological units (Figure 32). Unit X consisted of brown sand/silt sediments with entire/articulated shells of the marine/brackish mollusc *Modiola capensis*. Unit IX was dominated by dark brown silt sediments without shells. Unit VIII was similar to Unit X, but sediments exhibited a grey colour and higher content of shells. In Unit XII, the sediment was light brown in colour and a lower content of shells was found. Unit VI was similar to Unit VII in sediment composition, but was a darker colour. Unit V exhibited a light brown colour and contained no shells. Unit X, IV, III and II were also dominated by silt clay sediments, but they differed in sediment colour (Unit IV and II dark brown, and Unit III light brown). Unit I was similar to Unit V, however, freshwater mollusc shells and macrophyte remains were recorded.

7.4.2 Sediment analyses

Groenvlei core, GVL1

The basal section of the core exhibited relatively low values of organic matter and total nitrogen, but towards unit IX an increasing trend was observed (Figure 32). However, total carbon content showed a slight decreasing trend towards the base of unit IX, but then increased towards the upper section of this unit. C:N ratios decreased from 32 in the base of the core, to 15 in unit IX, but then showed an increasing trend until the upper section of unit V. From unit V towards the core surface C:N ratios generally decreased. In unit VIII, organic matter, total carbon and total nitrogen decreased. From unit VIII to VII, a further increasing trend in organic matter, total carbon and total nitrogen was detected. Above unit VII, the geochemical variables remained fairly constant through unit II, except for the peak in organic matter content at 57 cm (Figure 32). From unit II to the top of the core, an increase in total nitrogen and a decrease in total carbon were recorded. Organic matter content showed values similar to those observed in unit V, except at the basal section of unit I, where lower organic matter content was measured.

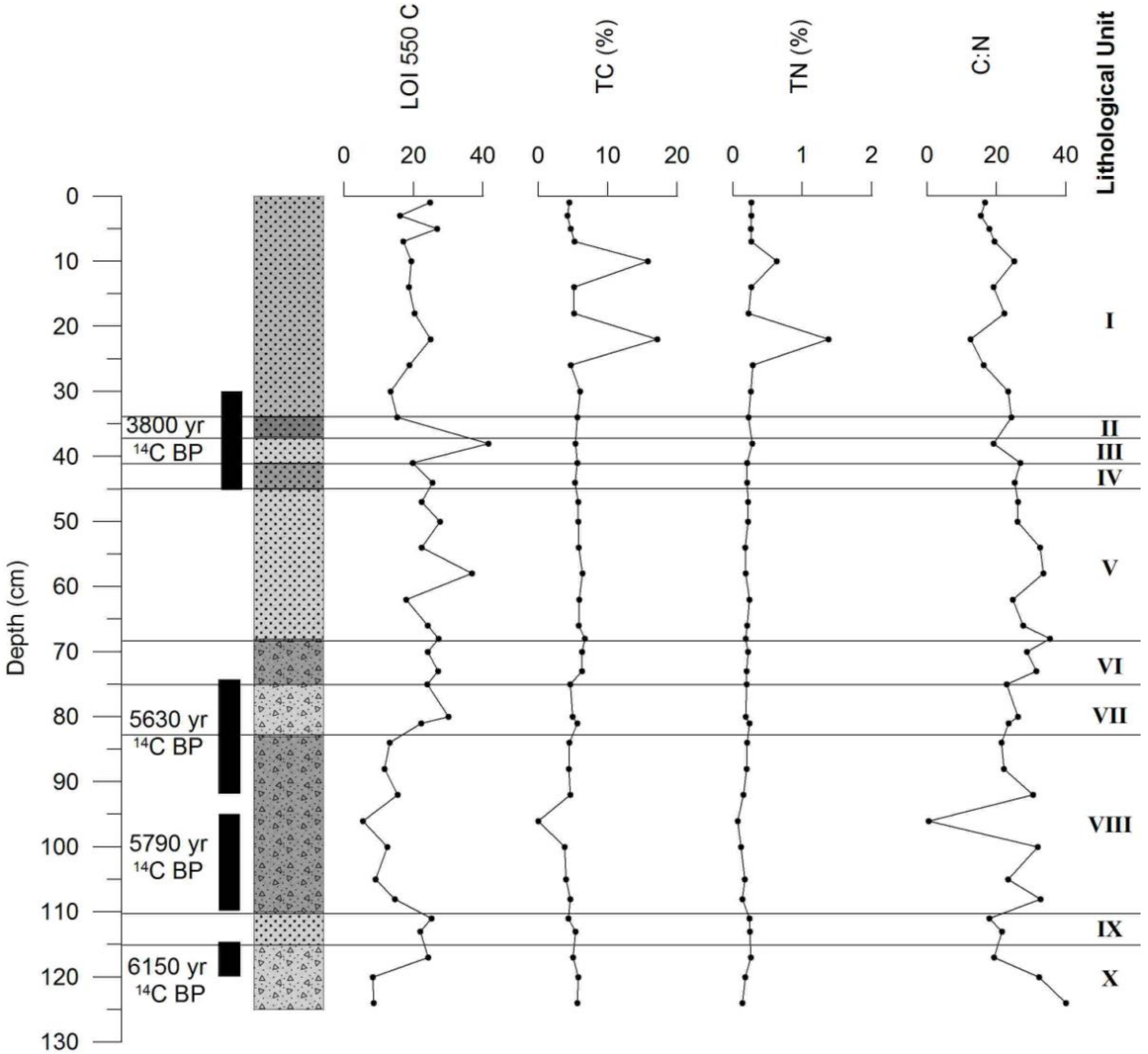


Figure 32 Geochemistry and C:N ratios for Groenvlei lake core (GVL1) (LOI = organic matter, TC = total carbon, TN = total nitrogen)

7.4.3 Diatoms analyses

Groenvlei core, GVL1

Martin (1959) investigated diatom slides obtained from a 650 cm long, 8000 yr old sediment core. His sediment record is much longer that that of core GVL1, and thus, the diatom analysis of Martin's paper have a much better resolution than ours. We thus compared our observations to the diatom data presented by Martin (1959) and added a few taxonomic amendments because Martin's identification was done following outdated keys.

Martin (1959) identified eight Diatom Assemblage Zones (DAZ, Figure 33). Zone F1 and F2 were dominated by oligohaline taxa, and zones P1 and P2, contained just a few diatoms. We have no record of the above mentioned zones in our sediment cores. Sections M1, M2 and L1 consisted of euhaline diatoms and corresponded to lithological units X through VI in our sediment core. Three varieties of *Paralia sulcata* were dominant in this section. Martin (1959) reported these species as *Melosira sulcata* (typical, var.1 and var.2), which have now been assigned to the genus *Paralia*. The three varieties, in order of relative abundance are *P. sulcata* var. *biseriata*, *radiata*, and *coronata*. Co-dominant species in this section were also euhalobous indicators: *Actinoptychus splendens*, *Actinoptychus janischii*, *Amphitetras antediluviana* [*Triceratium antediluvianum* in Martin (1959)], *Biddulphia pulchella*, *Triceratium favus* and *Grammatophora oceanica*.

In zone L2 (Figure 33), Martin (1959) reported low concentrations of mesohaline diatoms and *Campylodiscus clypeus*, *Epithemia adnata* [*E*. *zebra* in Martin (1959)], *E. turgida*, *Navicula crytocephala* and *Surirella straitula* were dominant. He also observed *Cocconeis clandestine* as one of the most abundant species in this interval. This species, however, was misidentified by Martin, as Cholnoky (1955) has described it earlier as *Cocconeis engelbrechtii* nov. spec. (see Archibald 1983, Plate 10, 161 – 167). This section can be stratigraphically correlated to lithological units V through II of core GVL1 (Figure 33), where a low concentration of diatoms was observed as well. In section F2 (lithological unit I in core GVL1), oligohaline diatom species dominated and are represented by *Epithemia adnata* and *E. turgida, Rhopalodia gibba*, and *Cocconeis engelbrechtii*. Other less abundance species were *Cymbella cymbiformis*, *Anomoeneis sphaerophora* and *Mastogloia elliptica*, *M. smithii* and *Campylodiscus clypeus* was still present in this section. In addition this was the only zone of the core where chrysophyte cysts, though rare, were observed.

Soetendalsvlei core, STV3

The diatom analyses in Chapter 6 indicated eight diatom association zones based on the ordination of the 28 most abundant and persistent species within the palaeo-core STV 3. Table 15 provided a summary of both Groenvlei and Soetendalsvlei diatom species and the different sections of the two cores that these were dominant in. Cosmopolitan species such as *Cocconeis englebrechtti, Epithemia adnata, Mastogloia elliptica* and *Rhopalodia gibba* were present at both these lakes and generally indicated oligohaline to mesohaline conditions (Table 15). Within Soetendalsvlei, no clear euhaline (marine) conditions were encountered as was the case in the bottom section of the Groenvlei core.

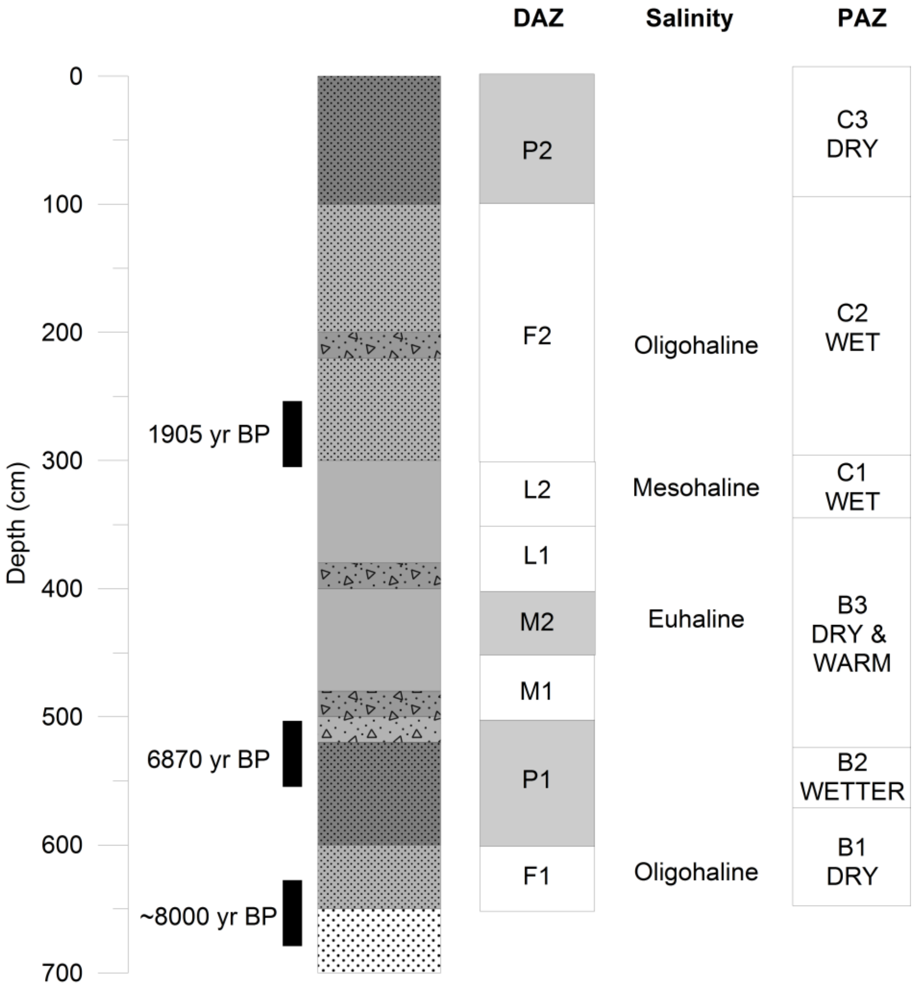


Figure 33 Lithology, Diatom Association zones (DAZ) and Pollen Association Zones (PAZ) determined by Martin (1959; 1962). Palaeosalinity and climatic change are indicated as inferred by Martin’s research.

Table 15 Diatoms species and inferred salinity ranges for both the Groenvlei and Soetendalsvlei palaeo-cores.

DAZ	Depth	Age (yr ^{14}C BP)	Diatoms	Salinity
Groenvlei				
I	0 – 40cm	< 3800	*Anomeoneis sphaerophora* *Cocconeis engelbrecthii* *Cymbella cymbiformis* *Epithemia adnata* *Epithemia turgida* *Mastogloia elliptica* *Mastogloia smithii* *Rhopalodia gibba*	Oligohaline
II	40 – 68cm	> 3800	*Campylodiscus clypeus* *Cocconeis engelbrecthii* *Epithemia adnata* *Epithemia turgida* *Navicula crytocephata* *Surirella striatula*	Mesohaline
III	70 – 125cm	~ 4000 -6150	*Actinoptychus janischii* *Actinoptychus spiendens* *Amphitetras antedluvlana* *Biddulphia putchella* *Grammatophora oceanica* *Paralia sulcuta* *Tricentratium favus*	Euhaline
Soetendalsvlei				
I	0 – 10 cm	< 1916 AD	*Gomphonema acidoclinatiforme* *Nitschia frustulum*	Oligohaline
II	10 – 20 cm	< 2000	*Cracticula acidoclinate* *Cyclotella* sp. *Diploneis subovalis* *Epithemia adnata* *Eunotia* sp. *Hippodonta* sp *Navicula* sp. *Trybionella levidensis*	Oligohaline
III IV VIII	20 – 40 cm 44 – 70 cm 130 – 154 cm	< 2200 2190 ± 60 ~ 8000	*Cocconeis engelbrecthii* *Cocconeis placentula* *Cyclotella meneghiana* *Epithemia* sp. *Fragilaria investiens* *Mastogloia elliptica* *Rhopalodia gibba* *Stephanodiscus aggassizensis*	Mesohaline Oligohaline Mesohaline
V VII	100 – 110 cm 120 – 130 cm	6660 ± 40 7130 ± 40	*Amphora ovalis* *Cymbella* sp. *Fragilaria investiens* *Melosira* sp.	Oligohaline Mesohaline

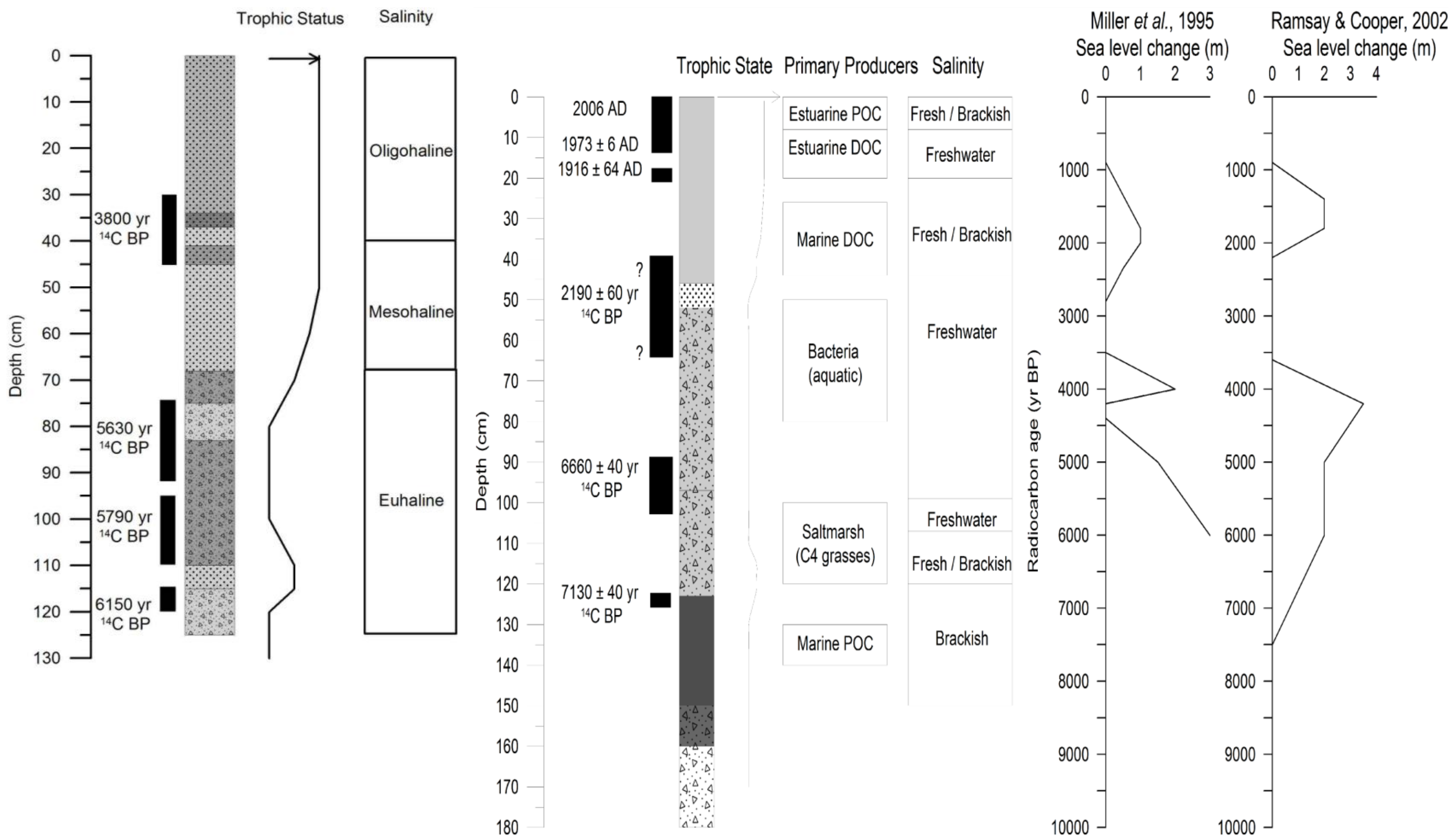


Figure 34 The relationship between trophic state changes, salinity levels and lithology of cores GVL1 (left) and STV3 (right), and the regional models of sea-level change

7.5 Discussion

The objectives of this study were to determine whether Holocene sea-level fluctuations along the southern coast of South Africa is comparable to the east and west coasts models developed by Ramsay and Cooper (2002) and Miller *et al.* (1995), respectively. The study also investigated the relationship between palaeosalinity and trophic status for Soetendalsvlei and Groenvlei lakes.

The Holocene sea level change model for the South African coast postulates that; (a) mean sea level was first overtaken at ~6500 yr BP, (b) it then rose to +2.75 m AMSL at ~6000 yr BP and maintained this level until ca. 5000 yr BP, (c) maximum Holocene sea-level was achieved at ~4000 yr BP (+3 m AMSL), (d) sea-level fell to present levels ca. 3500 yr BP, (e) between 3500 – 1600 yr BP sea-level was probably -2m below present MSL, (f) at ca. 1600 yr BP sea-level rose to +1.5 m AMSL and present MSL was attained at ca. 900 yr BP and has been maintained to the present (Miller *et al.,* 1995; Ramsay, 1995; Baxter and Meadows, 1999; Ramsay and Cooper, 2002).

The proximity of the lakes to the ocean most likely had an effect on the temporal scale and magnitude of sea-level rise or fall. Groenvlei Lake, currently situated approximately 3 km from the ocean, is separated from the ocean by a large coastal dune cordon. Soetendalsvlei Lake, on the other hand is situated approximately 15 km from the Indian Ocean. It is intermittently linked to the ocean via the Heuningnes River and estuary, a temporarily open/closed estuary. In terms of topography the two regions differ substantially from one another, with Groenvlei being surrounded by large, steep coastal dune fields, and Soetendalsvlei mainly situated in a very low gradient, large floodplain area surrounded by agricultural fields.

Nevertheless, both Groenvlei and Soetendalsvlei cores compared well with the sea-level models developed for the South African coastline, albeit there being a slight difference in temporal scales. The basal section of the Groenvlei Lake core, dated at >6150 yr BP, was deposited due to the Holocene marine transgression between 6000 and 7000 yr BP. Subsequently euhaline conditions dominated the system as evident from the lower five lithological units, corresponding to the elevated sea-level high-stand between 6000 and 5000 yr BP. This section of the core was dominated by euhaline diatoms, together with a high content of marine/brackish mollusc shells. During most of this stage, relatively low trophic state was observed (Figure 34), with significant external inputs of organic matter as supported by C:N ratios in the range of macrophytes, peat / shore vegetation and terrestrial plants (~25, Hassan, 1997; Kausal and Binford, 1999; Muller and Mathesius, 1999; Meyers and Lallier-Verges 1999; Lamb *et al.* 2006). The basal section of the Soetendalsvlei Lake core was dated younger at ~7000 yr BP. The presence of marine articulated and broken bivalve shell remains, combined with coarse sand and high carbonate content indicated that the system was influenced by marine intrusion during this first Holocene transgression (~6000 yr BP) when sea level rose to +2.75 m AMSL (Ramsay, 1995; Ramsay and Cooper, 2002).

Both the sea level models for the east (Ramsay, 1995; Ramsay and Cooper, 2002) and west (Miller *et al.,* 1995) coast of South Africa record the maximum sea level high-stand of approximately +3 m AMSL at ~4000 yr BP. Within Groenvlei Lake, however, there is no clear evidence of this high-stand, with the onset of a mesohaline state being observed between 5600 and 3800 yr BP (i.e. after the first Holocene regression, Figure 34). An increase in trophic state during this period was most probably a consequence of a decrease in sea-level and increased freshwater inflow, together with the formation of the dune cordon characteristic of the Wilderness region (Illenberger, 1996). During most of this mesohaline stage (lithological unit V), the palaeoenvironmental conditions were probably not conducive to diatom proliferation as we observed a very low diatom concentration in the slides. Martin (1959) argued that the low diatom concentrations might be due to dilution by rapid sedimentation and loss by alkaline corrosion. According to our data, the system might have been dominated by macrophytes and peat/ shore vegetation, with terrestrial input an important contributor as indicated by relatively high C:N ratios.

Within the Soetendalsvlei palaeo-core, there is also no record of the sea-level high-stand of +3 m AMSL at ~4000 yr BP. Instead, reduced marine influence and freshwater / brackish conditions prevailed between 5200 and 4200 yr BP as evident from the stable isotope data. As in the case of the Groenvlei palaeo-core, very few if any diatom valves were found within the sediment and it is believed that the lake may have dried up completely during this time. Stable isotope and geochemistry data indicated that freshwater conditions, with mainly bacterial activity, were dominant during this period. Following the sea-level high-stand at ~4000 yr BP, there was a strong marine regression with levels falling to below present mean sea-level between 3500 and 1600 yr BP (Ramsay and Cooper, 2002). In Groenvlei lake, this is evident from 38 cm depth (lithological unit II), where diatom concentrations increased sharply and oligohaline forms were dominant. *Epithemia adnata* and *E*. *turgida* were the most abundant species. A relatively high abundance of *Cocconeis engelbrechtii*, *Mastogloia elliptica, M. smithii* and *Rhopalodia gibba* was also observed, and *Campylodiscus clypeus* still persisted within the oligohaline stage. This was the only section of the core where chrysophyte cysts were also observed. According to Garcia-Rodriguez *et al.* (2010) changes in the abundance of chrysophyte cysts can be used to infer salinity trends within coastal regions, with an increase in concentrations under fresher conditions.

Soetendalsvlei exhibited the same trend in palaeo-salinity history during this period with mainly oligohaline taxa dominating the diatom communities, which included *Fragilaria investiens*, *C. meneghiana* and *Stephanodiscus aggassizensis.* There was also an increase in the relative abundance of *C. engelbrechtii*, *C. placentula* and *N. frustulum* in the upper centimetres of this layer.

The second marine transgression event that took place between 2000 and 1000 yr BP, with maximum high-stand at ~1600 yr BP, is not recorded in the Groenvlei Lake palaeo-core. Instead oligohaline conditions were recorded. It is believed that this continued decrease in salinity was probably a consequence of the separation of the water body from the sea during the late Holocene by the dune cordon (Illenberger 1996). According to our sediment record, isolation of Groenvlei Lake from the sea took place after 3800 yr BP. Martin (1959) however, established that the oligohaline stage was only established after 1900 yr BP. Therefore, it is likely that the record of core GVL1 exhibits a hiatus between 3800 and 1900 yr BP, or net sediment deposition was significantly lower than in the east fen of the lake (Figure 31). After the onset of an oligohaline system, no major changes in trophic state were observed as organic matter content was similar to that of the mesohaline stage. Only at 10 and 22 cm, where sharp increases in total carbon and total nitrogen were recorded, might the trophic state have been higher. A change in sediment organic matter composition from mainly macrophyte or terrestrial input (C:N ratio ~25) to microalgae (C:N ratio <15) could explain these isolated increases in trophic status. Higher diatom valve concentrations found during the slide examinations support this. In the east fen of the lake, Martin (1959) observed a peat layer and therefore, the establishment of a vegetated wetland in the east littoral of the lake. We have, however, no record of this last stage.

For Soetendalsvlei Lake, however, there does appear to be evidence of the second marine transgression event. Although the system did not experience a truly marine state, evidence suggests that it might have experienced tidal influence associated with an estuarine system. The diatom community was dominated by brackish/freshwater taxa such as *C. engelbrechtii*, *C. placentula*, *M. elliptica* and *R. operculata*, while estuarine particulate organic carbon (POC) and dissolved organic carbon (DOC) was the main source of organic matter during this period (Chapter 6). At present the lake is still characterised by estuarine DOC and POC, although there is no longer a connection between the lake and estuary. By comparing the geochemistry, stable isotopes and diatom data with historical data (i.e. personal records for the farm Zoetendalsvallei) it was found that drought and flood cycles, dominant in this region, influenced the hydrological cycle of the lake, thereby affecting the salinity of the lake and thus the structure of the biological community. Overall it was observed that with reduced salinity, there was an increase in trophic status, mainly due to the increase in freshwater inflow which resulted in increased nutrient input and productivity.

In conclusion; the development of Groenvlei Lake can be divided into three major stages (Figure 34). The first corresponded to a marine system that was caused by an early Holocene transgression. Dominance of the diatom *Paralia sulcata*, high abundances of the marine/brackish mollusc *Modiola capensis*, and the lower inferred Holocene trophic state of the system were observed during this stage. The second stage involved the transition to a mesohaline system attributed to the first Holocene regressive phase dated at ~4500 yr BP (Martin 1959). Concomitant increases in trophic state were observed and mollusc shells of *Modiola capensis* were no longer recorded. The last stage of the system is an oligohaline stage with similar trophic state to that observed for the mesohaline stage. The trophic state of Groenvlei Lake appears to have been moderated by sea-level changes, with higher trophic state during regressive episodes. The development of Soetendalsvlei Lake agrees well with that of Groenvlei Lake, although changes in palaeo-salinity may rather be as a result of marine intrusion via the estuary. Soetendalsvlei Lake is situated further from the coastline and as such would have been less affected by direct sea-level changes than Groenvlei Lake during the early Holocene. Overall both lakes show an inverse relationship between trophic state and palaeo-salinity.

Similar relations between tropic state and sea-level (i.e. palaeo-salinity) change have been observed in coastal systems in southern Uruguay, South America. Increases in trophic state associated with a regression episode were recorded after ~4000 yr BP. The Groenvlei Lake and Soetendalsvlei Lake data also show that after the first Holocene regressive phase, ~4000 yr BP, trophic state increased. Thus, both South African and South American coastal water bodies showed similar responses to sea-level change at similar times. Furthermore, a very similar Holocene diatom composition was observed in South Africa and South America. During the marine stage, *Paralia sulcata* was the dominant species. In the mesohaline stage, high relative abundance of diatom species common to both continents was observed (e.g. *Amphitetras antediluviana*, *Biddulphia pulchella*, *Campylodiscus clypeus*, *Surirella striatula*, *Triceratium favus*). During the oligohaline stage, *Epithemia adnata*, *E. turgida* and *Rhopalodia gibba* were dominant. Because the Holocene data collected for South Africa and South America suggest fairly similar / concomitant Holocene changes in trophic state and salinity, it is reasonable to suppose that Holocene coastal lagoons of other regions in the southern hemisphere, such as Australia and New Zealand, might have also exhibited parallel trophic state and salinity changes in response to sea-level variation.

Chapter 8

General Discussion and Conclusion

South Africa has an extensive coastline of approximately 3000 km. Due to the influence of two major ocean currents, present day climatic conditions vary from east to west. According to Cowling *et al*. (1999) and Meadows and Baxter (1999) these differences, most notably in rainfall and temperature, also existed during the Holocene. With the increase in awareness of global warming and increasing sea-level, numerous models have been developed (IPCC, 2007) to better predict how future climate change would affect the environment and human populations. For any predictive models to be accurate however, long-term instrumental data is vital, but in most regions of the world are sorely lacking. Palaeolimnological reconstruction of past environmental conditions, however, can address the degree to which systems have changed and pinpoint the likely causes of such conditions.

The aims of this study were to determine the Holocene sea-level influence on a South African coastal lake situated in an area that has historically been influenced by climate change and sea-level variations (Allanson, 2001). Once these data were available, the overall sea-level history was compared to that of Groenvlei Lake to check for temporal and spatial variability along the South African coastline. Results were also compared with studies undertaken in South America to add to an understanding of global change.

For the South African coastline and especially the south-western Cape region data regarding past climate change is mainly restricted to anthropological and aeolian evidence in isolated areas along the coast (i.e. De Kelders (Tankard and Schweitzer, 1974; Illenberger, 1996; Butzer, 2004; Avery *et al*., 2007) Boomplaas (Deacon *et al*., 1984); Blombos (Henshilwood *et al.,* 2002; Jacobs *et al.,* 2006), Klasies River (Deacon and Deacon, 1999) and the Agulhas Plain (Carr *et al.,* 2006)), some sea-level reconstructions along the east and west coast by Miller *et* *al.* (1995), Ramsay (1995) and Bateman *et al.* (2004), and a few climate reconstructive studies by Martin (1959, 1960), Meadows *et al.* (1995) and Meadows and Baxter (1999). Understanding the past ecology of Soetendalsvlei thus provided a measure for regional comparison, thereby strengthening the South African sea-level model and provided a measure of baseline information used to determine how much the system has been altered by both natural climate c3hange and anthropogenic impacts. Assessment of the palaeo-record of Soetendalsvlei indicated periods of marine transgression and regression which are in close agreement with the regional sea-level models of Miller *et al*. (1995), Ramsay (1995) and Ramsay and Cooper (2002) and provided long-term information on the trophic status of the system during the different stages. In South America, palaeo-salinity and trophic status of coastal lakes were shown to have an inverse relationship. Increased trophic status was associated with reduced marine influence, while lower trophic status was shown to be associated with an increase in marine influence and hence transgression events (Garcia-Rodriguez *et al*., 2004a, b, 2010). In this study of Soetendalsvlei and Groenvlei Lake, a similar inverse relationship between trophic status (i.e. bulk organic matter) and palaeo-salinity was observed. Stable isotope analyses further provided information on the sources of organic matter and in both instances higher freshwater inflow and associated nutrient input could be linked to higher productivity within these coastal lakes, and hence higher trophic status. The significant increase in organic content within the surface sediments of Soetendalsvlei, together with present elevated SRP concentrations, highlights the need for adequate management of agricultural return flow to prevent eutrophication within the system. Maintaining an open connection between the Soetendalsvlei and the Heuningnes River and Estuary is also considered vital in order to ensure that ecological functioning is maintained in both systems.

The study also highlighted the importance of using multiple proxies for palaeoecological reconstructions. Bulk organic matter content provided a good indicator of trophic status and together with $\delta^{13}C$ and C:N ratios made it possible to assess the various sources of the organic matter (Lamb *et al.,* 2006). Although diatom preservation was poor throughout the sediment core, taxa that could be identified were related to palaeo-salinity based on present day (i.e. modern) analogues (Kolkwitz and Marsson, 1908; Tilman *et al*., 1992; Gasse *et al*., 1995; Hall and Smol, 1999; Stevenson and Pan, 1999; Battarbee *et al*., 2000; Mackay *et al*., 2005; Austin *et al.,* 2007; Saunders, 2010).

Based on the correlation between the Holocene palaeo-record for Soetendalsvlei and regional sea-level models, it could be deduced that as the coastal lake is presently situated ~15 km away from the ocean, past marine influence occurred due to water exchange between the lake and the Heuningnes Estuary. Consequently, an open connection between these two systems would have ensured free water exchange and both systems would have experienced similar water quality (i.e. physical and chemical characteristics) and phytoplankton communities. Analyses of the top section of the sediment cores collected in Soetendalsvlei, indicated highly variable diatom communities and geochemistry. This high variability would indicate changing water quality conditions because of the alternating dominance of fresh and estuarine taxa as influenced by changing marine intrusion into the Heuningnes Estuary. Lead dating provided a time frame for these changes that could be related to major anthropogenic impacts, such as the stabilisation of the dune field at the estuary mouth in 1942 and the artificial breaching of the mouth during prolonged mouth closure and high water levels since the late 1950s (Bickerton, 1984). With the prevention of mouth closure, back-flooding of estuarine water into the lake has been limited and ultimately completed blocked, thereby creating a highly altered freshwater state within the coastal lake. Prior to 1972, the period when artificial breaching was re-instated, the coastal lake experienced estuarine conditions, but subsequently and at present freshwater conditions prevail (Chapter 4).

In Chapter 5, the present water quality and phytoplankton community of the Heuningnes River and Estuary were also investigated to determine whether the

Estuary and Soetendalsvlei (coastal lake) share any similarities in physical and chemical characteristics (i.e. water quality) or phytoplankton communities. As Soetendalsvlei acts as a barrier lake to the Heuningnes River and Estuary, it was expected that the water quality of the lake would have a significant influence on the River and Estuary, as observed for other similar systems, e.g. Swartvlei (Allanson, 2001). Swartvlei Estuary has the same mouth management protocol as the Heuningnes Estuary i.e. the mouth is opened when the water level is high to avoid back-flooding of residential areas. The results indicated that, firstly, the Heuningnes Estuary was marine dominated most of the time, with marine intrusion into the upper reaches that was only reduced during the winter rainfall period. Secondly, only during periods of very high freshwater inflow associated with winter rainfall, did salinity within the upper reaches of the estuary decrease to below 20 ppt. Similar results were obtained by Allanson (2001) for the Swartvlei Lake and Estuary, where salinity profiles within the estuary were reduced by as much as 50% due to overflow of brackish water from the Lake into the Estuary. According to Allanson (2001) the maintenance of a salinity gradient, although considerably reduced, is vital to ensure limited environmental stress on the biota. Although no clear similarities were observed between Soetendalsvlei and the Heuningnes River and Estuary, the influence of the lake on the estuary is nevertheless significant in terms of salinity, thereby affecting the phytoplankton community. During increased freshwater inflow as a result of winter rainfall, the salinity gradient was reduced and the phytoplankton community shifted from being dominated by chlorophytes to flagellates, which would have cascading effects on primary and secondary consumers within the estuary. During this increased freshwater inflow period, the mouth of the estuary was closed and in the process of being artificially breached. Consequently tidal exchange and marine influence was absent. Under open mouth conditions, a stronger salinity gradient might have been closer to the middle reaches of the estuary instead of in the upper reaches, as recorded in this study. The lack of similarities between Soetendalsvlei and the Heuningnes River and Estuary indicates the limited water exchange between the two systems and signifies the loss of connectivity and the development of two individual systems with very dissimilar characteristics and functioning. Should this continue to occur, the loss of biodiversity could be great, especially to aquatic invertebrates, fish and bird life that utilise both the estuary and coastal lake as reproductive and feeding areas (HilLand Associates, 2009).

Overall the results indicate that Soetendalsvlei Lake has become freshwater dominated as a result of the artificial breaching of the Heuningnes Estuary mouth preventing back-flooding of saline estuarine water into the lake, as well as the obstruction of free water exchange between these two system as a result of the Bredasdorp / Struisbaai road bridge and weir. Only brackish and marine conditions were observed in the palaeo-record, with no freshwater conditions recorded. This would indicate that the system has changed considerably during the most recent past (i.e. < 150 years) and could highlight the role that human impacts, most notably agriculture and freshwater abstraction has had on the system, together with the mouth manipulation.

It can be concluded that coastal lakes in South Africa did experience similar responses to sea-level fluctuations during the Holocene as was found for other southern Hemisphere systems (i.e. Uruguay). This study contributes valuable information to global sea-level change models. The change in Soetendalsvlei water quality, however, highlights the need for adequate management of such systems within South Africa and indeed other regions of the world to maintain ecological characteristics and functioning. Due to artificial breaching, both the Heungingnes Estuary and Soetendasvlei have been altered, with one becoming marine and the other freshwater dominated.

This study highlighted the importance of understanding the present limnological state to assess ecosystem functioning and to assess present water management decisions related to the overall characteristics and functionality of linked systems such as Soetendalsvlei and the Heuningnes Estuary. Although the limnological aspect of this study provided a snapshot of the current situation, it does not provide evidence on long-term changes such as whether the systems have changed due to natural climatic variation or as a result of anthropogenic impacts. Palaeolimnological techniques and the use of multiple proxies, made it possible to reconstruct environmental conditions to fill these knowledge gaps and provide assessments of baseline conditions. From this it was possible to determine the past environmental trajectories of change within these systems, thereby highlighting future concerns for management of Soetendalsvlei, its associated wetlands and the Heuningnes Estuary. Combining present limnology and palaeolimology thus allows for a much better and multiscale ecological understanding of ecosystem functioning and change during the Holocene.

Shortcomings of this study

The lack of proper diatom frustule preservation, as evident from broken and corroded valves, in both the present phytoplankton community as well as the sediment record reduces the accuracy and strength of the palaeo-reconstruction for Soetendalsvlei Lake. The section 70 – 100 cm for palaeo-core STV 3 appeared sterile in the diatom stratigraphy. Diatom species encountered and used to infer palaeo-salinity were generally cosmopolitan, e.g. *Melosira* sp., *Cocconeis placentula*, *C. engelbrechtii*, and *Nitzschia frustulum*. It is believed that these and the species that were encountered were either resistant to biogenic dissolution by high alkalinity or occurred in such high numbers that although dissolution did occur, enough frustules were present to still be represented in the sediment record (Battarbee *et al.,* 1999; 2005; Fritz *et al.,* 1999). In the first instance, this may mean that the palaeo-salinity reconstruction may have been under- or over-estimated. In the second instance, one can argue that the community would still have the same dominant species, with overall diatom numbers being higher, but relative abundance would be very similar to that measured with dissolution. It should, however, be acknowledged that diatom species with narrower tolerance ranges, which would have strengthened the reconstruction, could have been lost due to poor preservation.

It is believed that poor diatom preservation in Waskraalsvlei and Voëlvlei also resulted in no diatom frustules being observed in the sedimentary records. Both the systems, however, showed very different sedimentary records from Soetendalsvlei and although palaeo-sols were searched for, none were encountered. The present limnology study also indicated very different ecosystem characteristics and functioning in these wetland systems, and consequently the focus for the palaeolimnological reconstruction was only on Soetendalsvlei.

Future research needs

It is clear that poor diatom preservation was the biggest set-back to this study. It is thus recommended that future research addresses biogenic silica dissolution in South African estuaries and coastal lakes, especially alkaline system. Species-specific studies to determine diatom resistance to high alkalinity would also add to any future palaeo-environmental studies in this country. Specifically for the Soetendalsvlei Lake it is recommended that foraminifera and pollen studies are included to strengthen the Holocene climate reconstruction presented in this thesis.

Overall the findings in this thesis contributes to our understanding of coastal responses to changing climate and sea-level for South Africa, adding important information for future decision making in terms of resources management (i.e. freshwater abstraction) and agricultural practices (i.e. eutrophication). This work also represents one of two studies, know to the author, that utilised diatoms as palaeo-indicators for salinity in South African coastal systems and the first of its type for the Soetendalsvlei Lake system.

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