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Factors influencing the biomass and distribution of sago pondweed, *Stuckenia pectinata* in a temporarily open/ closed estuary, Zandvlei, Cape Town, South Africa

By

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Declaration

I, Kyle Piers Maurer, declare that the contents of this dissertation/thesis represent my own unaided work, and that the dissertation/thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

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Abstract

Stuckenia pectinata (Börner, 1912) offers both advantages and disadvantages to the biota and user groups of Zandvlei Estuary, Cape Town. It is therefore imperative that *S. pectinata* is managed so that it provides ecosystem services without growing to levels where it negatively impacts user groups. This study aimed to understand factors influencing *S. pectinata* biomass and distribution in Zandvlei Estuary in order to provide conservation authorities with informed *S. pectinata* management options. *S. pectinata* biomass and distribution, and system physico- chemical parameters and nutrient characteristics were assessed monthly between November 2016 and November 2017. Samples were collected in the main body of the estuary, in the Marina da Gama canals and in three influent rivers. Elevated salinity was found to negatively influence *S. pectinata* biomass within the lower reaches. Nutrients were thought to influence seasonal variations in *S. pectinata* biomass. The distribution of sediment grain size was suspected to influence variations in *S. pectinata* biomass within the main body of the estuary. The results add to conservation authorities' understanding of the influence of environmental characteristics on *S. pectinata* biomass and distribution allowing more effective anticipation of changes in *S. pectinata* biomass and distribution thus preventing extremes in its growth. The knowledge acquired will assist conservation authorities in refining the *S. pectinata* harvesting protocol thereby allowing the macrophyte to be maintained more effectively.

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1. Introduction

Estuaries form the interface between the world's fresh and marine waters with an estuary's properties being defined by this interaction (Branch and Branch, 1981; Schlacher and Wooldridge, 1996; Allanson and Baird, 1999). Estuaries are among the most biologically productive ecosystems on earth and are consequently of high ecological and economic value (Barbier *et al*. 2011; Sheaves *et al*. 2014). The productivity, aesthetic nature and the calm water environments provided by estuaries mean that these ecosystems are very vulnerable to development (C.A.P.E., 2013; Sheaves *et al*. 2014).

Due to the anthropogenic degradation of many estuaries and potential impacts of climate change in the future it is vital to acquire knowledge on the complex functioning of estuaries (Mabaso, 2002; Whitfield and Bate, 2007). By gaining this understanding many estuaries can be spared from being degraded beyond repair whilst being managed effectively despite pressures arising from variability in climatic conditions (Mabaso, 2002; Whitfield and Bate, 2007).

The temporarily open/ closed Zandvlei Estuary is located on the North West shore of False Bay, 20 km south of Cape Town (34°06'21" S; 18°28'36" E) and falls within the cool temperate biogeographic zone (Quick and Harding, 1994; Whitfield and Baliwe, 2013). The main body of the estuary is 2.6 km long and 0.5 km wide at its widest point with the mean water level varying between 0.7–1.3 m (Quick and Harding, 1994; C.A.P.E., 2013). Zandvlei Estuary's main influent rivers are the Westlake River, Keysers River and the Sand River (Muhl *et al*. 2003; C.A.P.E., 2013). Rainfall in the 92 km^2 catchment occurs predominantly in winter from May to September and summers are hot and dry (Morant and Grindley, 1982; Hutchings *et al*. 2016). The mouth of Zandvlei Estuary is artificially opened and closed by the manipulation of a sand bar in order to maintain the water level for recreational activities, prevent flooding of houses in Marina da Gama and allow the estuary to be flushed by the sea (Quick and Harding, 1994; C.A.P.E., 2013).

Zandvlei Estuary is an important recreational space for Cape Town residents (Quick and Harding, 1994; C.A.P.E., 2013). Recreational activities include various types of boating as well as picnicking, birdwatching, hiking/ walking and fishing (C.A.P.E., 2013)**.** During peak holiday periods the system can host some two to three thousand visitors a day with the recreational value of the estuary being estimated at between one and five million rand per year (C.A.P.E., 2013). In addition to recreational users, home owners of Marina da Gama (a housing development located on a canal system joined to the eastern boundary of the estuary) have a vested interest in the health of the estuary as their homes and aesthetic value of their residential area depend on it. Furthermore, Zandvlei Estuary is highly valuable in terms of biodiversity and conservation (C.A.P.E., 2013). As described by Morant and Grindley (1982), Zandvlei Estuary has a diversity of fauna and flora and is the only estuary of significance as a fish nursery on the False Bay coastline. The estuary forms part of the Greater Zandvlei Estuary Nature Reserve (GZENR) further emphasising its natural value (C.A.P.E., 2013).

Stuckenia pectinata (Börner, 1912) is a submerged**,** rooted macrophyte with a nearly cosmopolitan distribution (Madsen and Adams, 1988; Kantrud, 1990; Quick and Harding, 1994). *S. pectinata* is indigenous to Zandvlei Estuary and for many years the estuary and Marina da Gama canals have been dominated by the macrophyte (Harding, 1994; C.A.P.E., 2013). *S. pectinata* has an important role in the ecology of Zandvlei Estuary acting as a nutrient sink, reducing sediment resuspension by

wind, waves and fish, oxygenating the water column and affording shelter to various invertebrate and fish species inhabiting the estuary (Morant and Grindley, 1982; Harding, 1994; C.A.P.E., 2013). Therefore, not only does the presence of *S. pectinata* contribute to the maintenance of estuarine health, but recreational users and home owners also benefit through improved water quality and visual appeal of the system. Morant and Grindley (1982) stated that the sound management of *S. pectinata* is possibly the most critical factor in the maintenance of Zandvlei Estuary for human activity and as a healthy natural system.

On the contrary, high nutrient concentrations present in the system may cause *S. pectinata* to reach nuisance levels (C.A.P.E., 2013). Under such conditions *S. pectinata* can form dense vegetation mats which can reduce light penetration, impede recreational activities and decrease current flow and therefore cause stagnation (C.A.P.E., 2013). When these dense mats break down nutrients are released back into the estuary and low dissolved oxygen conditions can develop in the bottom waters (C.A.P.E., 2013). Furthermore, undesirable odours are produced which can negatively affect the value of properties in the vicinity (C.A.P.E., 2013). These result in negative effects on the estuarine ecosystem, recreational users and home owners. The macrophyte has consequently been managed since 1976 using a mechanical harvester (C.A.P.E., 2013).

Stuckenia pectinata offers both advantages and disadvantages to the biota and user groups of Zandvlei Estuary. It is therefore imperative that *S. pectinata* is managed so that it remains at a biomass that allows it to provide its ecosystem services without growing to levels where it causes undesired impacts on user groups. Harding (1994) reported that the sudden collapse of the *S. pectinata* population at Zandvlei Estuary during 1991 occurred because no regular *S. pectinata* biomass monitoring was carried out and no data on the biomass or physiological condition of *S. pectinata* at Zandvlei Estuary were available. This study aimed to understand factors driving *S. pectinata* biomass and distribution at Zandvlei Estuary in order to assist management authorities in making informed decisions regarding *S. pectinata* management thereby contributing to overall estuarine functioning.

The main objectives of the study were to:

1. Quantify biomass and distribution of *Stuckenia pectinata* at Zandvlei Estuary
    I. To determine spatial (across sampling stations) and temporal (across seasons) trends in biomass and distribution of *S. pectinata*.
2. Quantify physico- chemical and nutrient conditions of Zandvlei Estuary
    I. To determine spatial (across sampling stations) and temporal (across seasons) trends in physico- chemical and nutrient conditions.
3. Quantify the influence of physico- chemical as well as nutrient conditions on biomass and distribution of *Stuckenia pectinata* at Zandvlei Estuary
    I. To determine spatial (across sampling stations) and temporal (across seasons) relationships between physico- chemical as well as nutrient conditions and the biomass and distribution of *S. pectinata*.

2. Literature review

2.1 South African estuaries

South African estuaries can be defined as partially enclosed coastal bodies of water that either permanently or temporarily connect rivers to the sea (Day, 1980; Allanson and Baird, 1999). There are approximately 250 functional estuaries in South Africa which cover an area of approximately 600 km^2 (Whitfield and Bate, 2007; Whitfield et al. 2008). South Africa's estuaries can be found in three biogeographic regions, namely the cool temperate region found between the Orange River on the west coast and the Krom Estuary on the Cape Peninsula; a warm temperate region between the Silwermyn Estuary in False Bay and the Mendu Estuary in the Eastern Cape; and a subtropical region between the Mbashe Estuary in the Eastern Cape and the Kosi Estuary in KwaZulu- Natal (Turpie et $al.$ 2000). South Africa's estuaries are micro tidal, having a spring tidal range of 1.8 – 2.0 meters (m) and a neap tidal range of 0.6 – 0.8m (Kaselowski and Adams, 2013).

According to Whitfield and Bate (2007), differences in climate, catchment geology and topography have resulted in a number of estuarine types in South Africa. These include permanently open estuaries (POEs), temporarily open/ closed estuaries (TOCEs), river mouths, estuarine lakes and estuarine bays (Whitfield, 1992; Whitfield and Bate, 2007). However, the two main estuarine types in South Africa are POEs and TOCEs (Whitfield and Bate, 2007).

Permanently open estuaries usually have large catchments with high runoff resulting in open mouth conditions year round (Whitfield and Bate, 2007). Conversely, TOCEs are characterised by a sandbar across the estuary mouth which severs its connection to the ocean (Kaselowski and Adams, 2013). TOCEs are the most common estuary type constituting 71% of South Africa's estuaries (Kaselowski and Adams, 2013). Small catchments, seasonal precipitation, limited tidal prisms during open mouth conditions and a surf zone capable of transporting significant quantities of sediment into and across the mouths of estuaries are responsible for TOCEs being the most widespread estuary type in South Africa (Whitfield and Bate, 2007). The cool temperate region has approximately 7 TOCEs, the warm temperate region approximately 86 and the subtropical region approximately 90 TOCEs (Whitfield, 2000).

TOCEs can display different mouth states including open, semi- closed and closed mouth state (Snow and Taljaard, 2007). Certain estuaries may exhibit all three mouth states at different times and others only open mouth and closed mouth state (Whitfield and Bate, 2007). The mouth status of TOCEs is controlled by a number of factors. When river inflow increases a TOCE fills up and the sandbar is breached leaving the estuary in an open mouth state. The main forces that trigger and prolong the open mouth state are river inflow and tidal water exchange (Whitfield and Bate, 2007). Wave energy, sediment availability and reduced river inflow are responsible for closing the mouth of TOCEs (Whitfield et $al.$ 2012; Kaselowski and Adams, 2013).

Macrophytes play an essential role in South African estuaries particularly TOCEs (Whitfield and Bate 2007). Macrophytes inhabit estuaries as submerged plants such as $Stuckenia$ $pectinata$ as well as emergent and floating plants (Whitfield and Bate 2007; Whitfield et $al.$ 2012). Fringing plants found on the border of estuaries including salt marshes, reeds, sedges and mangroves are also

macrophytes (Whitfield and Bate 2007; Whitfield *et al.* 2012). TOCEs with high water transparency, high concentrations of nutrients in the sediment, low current velocities as well as stable sediment and salinity levels are dominated by submerged macrophytes, reeds and sedges which thrive in these conditions (Whitfield and Bate 2007; Whitfield *et al.* 2012).

When an estuary mouth is closed stable physico- chemical conditions are present which encourage the growth of submerged macrophytes (Riddin and Adams, 2008). However, Riddin and Adams (2008) witnessed how an estuary can empty completely during the open mouth state causing submerged macrophytes to die off due to desiccation and exposure. Importantly, this loss will also affect the biota dependant on submerged macrophytes for food and shelter (Riddin and Adams, 2008).

2.2 Zandvlei Estuary

2.2.1 Physical description

Zandvlei Estuary is located on the North West shore of False Bay, 20 km south of Cape Town (34°06'21"S; 18°28'36"E) and falls within the cool temperate biogeographic zone (Quick and Harding, 1994; Whitfield and Baliwe, 2013). The system has been classified as a temporarily open/ closed estuary (Whitfield and Baliwe, 2013). Zandvlei Estuary is the only estuary of significance on the False Bay coastline making up about 80% of the estuarine area of False Bay (Morant and Grindley, 1982; Brown and Magoba, 2009). The estuary includes a wetland which covers 60 hectares (ha), the main body covering 56 ha, Marina da Gama canals 31 ha and an outlet channel of 9 ha (C.A.P.E., 2013). The main body of the estuary is 2.6 km long and 0.5 km wide at its widest point (Quick and Harding, 1994). Water levels vary between 0.7- 1.3 m in the main body and are deepest in the Marina da Gama canals at 2 m (Morant and Grindley, 1982; Quick and Harding, 1994; C.A.P.E., 2013). The estuary volume was estimated at 1.3×10^6 m^3 with the average hydraulic residence time calculated to be approximately 0.065 years (Harding, 1994; Thornton *et al.* 1995). CSIR (2015) mentioned that mud was the dominant sediment type at 71% of sampling stations within the main body and canals. Fine grained sand was dominant at the remaining sampling stations (CSIR, 2015).

The Zandvlei Estuary catchment lies entirely within the borders of the City of Cape Town (C.A.P.E., 2013). The catchment is made up of an area of approximately 92 km^2 or 9,655 ha (Hutchings *et al.* 2016). Land-use activities in the estuary's catchment vary from industry to housing, agriculture, forestry and conservation (Muhl *et al.* 2003; C.A.P.E., 2013). Rainfall in the catchment occurs predominantly in winter from May to September and summers are hot and dry (Morant and Grindley, 1982).

2.2.2 Hydrodynamics

Zandvlei Estuary's main influent rivers/ streams include the Westlake River, Keysers River and the Sand River (which includes the Diep River, Langvlei River and the Little Princess Vlei Stream) (Muhl *et al.* 2003; C.A.P.E., 2013). The Westlake and Keysers rivers join, pass through the Westlake Wetlands and enter Zandvlei Estuary in its north- western corner (Hutchings *et al.* 2016). The Sand and Langevlei rivers join and enter the system in its north- eastern corner via concrete canals (Hutchings *et al.* 2016). According to Harding (1994), estimated mean inflows to the estuary were 22×10^{62} m^3

per annum between 1983 and 1987 of which the Keysers, Sand and Westlake rivers supplied 45%, 43% and 12% respectively. Thornton *et al* (1995) stated that tidal inflows were approximately 3.1 X 10^6 m^3 per annum.

Artificial modifications: Attempts to control the amount of water in Zandvlei Estuary date back to 1866 when the system was shut off and drained so that it could be used for farming purposes (Hutchings *et al.* 2016). When winter rains commenced the plan failed and subsequent manipulations to the system concentrated on keeping water levels constant for recreational activities and avoiding flooding in Marina da Gama (C.A.P.E., 2013). In the 1950s the outlet channel was canalised followed by the construction of a rubble weir near the mouth (Hutchings *et al.* 2016). Other modifications included concreting the estuary shores to form steep embankments, construction of a railway line which separated the Westlake wetlands from the rest of the estuary, building of the Royal Road Bridge over the outlet channel, development of the Marina da Gama housing complex and general urbanisation around the estuary and catchment (Muhl *et al.* 2003; C.A.P.E., 2013). The aforementioned modifications have affected the quantity and quality of water and sediment moving into the system from both rivers and sea (C.A.P.E., 2013).

Mouth manipulation plan: The mouth manipulation plan for Zandvlei Estuary makes use of a rubble weir in the outlet channel together with the artificial manipulation of a sand bar across the estuary mouth (Quick and Harding, 1994; C.A.P.E, 2013). During the wet winter months the estuary mouth (and therefore the sand bar) is kept open to prevent flooding of houses in Marina da Gama but also to allow marine migrant fish into and out of the system (C.A.P.E., 2013). In contrast, during the dry summer months the sand bar is kept closed to maintain the water level for recreational activities (C.A.P.E., 2013). The mouth remains closed except for when there is a high spring tide which happens on five to six occasions every summer (C.A.P.E., 2013). In this case the mouth is artificially opened using a bulldozer to allow the estuary to be flushed by the sea and increase salinity, improve circulation and allow marine migrant fish into and out of the system (C.A.P.E., 2013).

2.2.3 Recreation and conservation value

Despite Zandvlei Estuary's history it remains highly valued for its natural attributes and as an area of regional importance for recreational activities (Gibbs *et al.* 2011). Recreational activities include various types of boating as well as picnicking, birdwatching, hiking/ walking and fishing (Gibbs *et al.* 2011). In terms of conservation, Zandvlei Nature Reserve was established in 1977 by the Cape Town City Council (C.A.P.E., 2013). Subsequent to this the borders of the nature reserve were expanded in 2000 from 22ha to 204ha and in 2006 the reserve became the Greater Zandvlei Estuary Nature Reserve (GZENR) (C.A.P.E., 2013).

Zandvlei Estuary offers a variety of habitats such as reed beds, salt marsh, sand banks and open water (Hutchings *et al.* 2016). The dominant terrestrial vegetation types surrounding the system are Cape Flats Dune Strandveld found on the low lying areas and Cape Peninsula Granite Fynbos found on the higher lying areas (Gibbs *et al.* 2011). Eighteen species of reptiles and amphibians, 40 fish, 173 birds (88 were water birds), 21 mammal and 440 plant species have been recorded in and around Zandvlei Estuary (Gibbs *et al.* 2011; Hutchings *et al.* 2016). The GZENR also conserves a number of IUCN red listed species (Hutchings *et al.* 2016).

Furthermore, Zandvlei Estuary has been described as the only estuary of real significance as a fish nursery on the False Bay coastline (Harding, 1994). This is a vital function as fish feed the many piscivorous birds of Zandvlei Estuary and surrounds (Thornton *et al.* 1995). When fish mature and leave the estuary they support the fishing industry in False Bay (Thornton *et al.* 1995).

2.2.4 Physico- chemical characteristics of Zandvlei Estuary

It is important to quantify an estuary's physico- chemical properties as they strongly influence estuarine ecology (Kaselowski, 2012). Furthermore, the overall health of an estuary can be understood by evaluating physico- chemical characteristics in conjunction with biological indicators (Kaselowski, 2012).

Temperature: The majority of aquatic organisms have a specific temperature range at which optimal growth, reproduction and general health occur (Whitfield, 1992). Long term temperature changes can affect the overall distribution and abundance of estuarine organisms (Ohrel and Register, 2006).

Zandvlei Estuary shows similar temperature values throughout, including when moving from the estuary mouth to the estuary head as well as from shallow waters to deep waters (Morant and Grindley, 1982; Hutchings *et al.* 2016). The presence of thermal stratification is rare as a result of the shallow depth of the estuary and the high winds in the area which cause mixing (Morant and Grindley, 1982). Haskins (2013) found that temperature rises as the summer season progresses but declines marginally when the mouth is open and cold seawater enters the system.

Salinity: According to Ohrel and Register (2006), salinity is the most important parameter that controls the habitat preference of the biota of an estuary. The majority of estuarine biota occurs within specific salinity tolerance ranges and variations in these ranges will directly affect estuarine organisms' distribution, life history cycles and physiological function (Muhl *et al.* 2003; Riddin and Adams, 2008). Harding (1994) mentioned that a continual decrease in salinity followed by exaggerated phytoplankton growth and a concomitant decrease in light penetration would result in the complete removal of *Stuckenia pectinata* from Zandvlei Estuary.

Monthly sampling at Zandvlei Estuary conducted by the City of Cape Town provided information on long term temporal changes in salinity (Hutchings *et al.* 2016). Salinity was fairly constant during the 1970s and then slowly decreased from a mean of 10 ppt to 5 ppt between 1980 and the early 1990s due to the height of the weir being increased (Hutchings *et al.* 2016). An increase to between 9 and 11 ppt was recorded between 2002 and 2010 due to the weir height being decreased (Hutchings *et al.* 2016). In terms of seasonal variations, between 1978 and 2003 salinity levels during winter remained relatively constant most likely as a result of mixing and dilution with fresh water from influent rivers (Muhl *et al.* 2003). During summer however, lower freshwater inflows and high evaporation rates resulted in higher salinity recordings (Muhl *et al.* 2003). Spatial variations in salinity were elucidated through the findings of a citizen science monitoring programme (Hutchings *et al.* 2016). Salinity was witnessed to fluctuate between 5 and 15 ppt near the head of the estuary, 5 and 20 ppt in the middle reaches and 5 and 32 ppt near the mouth (Hutchings *et al.* 2016).

pH: The pH of water is very important in evaluating water quality and also has a key influence on the survival of estuarine biota (Novotny and Olem, 1994; Ohrel and Register, 2006). When pH drops below 5 or increases above 9 many species become stressed (Ohrel and Register, 2006). Increased

pH creates more suitable conditions for algal blooms and increased aquatic weed growth and is therefore a concern in estuaries that experience nutrient enrichment (Mabaso, 2002).

According to Morant and Grindley (1982), Zandvlei Estuary exhibits wide pH ranges. Additionally, the estuary itself generally shows higher alkalinity than the rivers feeding into it (Morant and Grindley, 1982). In contrast, Hutchings *et al* (2016) commented that the system's pH values appeared to be relatively homogenous across the estuary and were within acceptable ranges.

Dissolved Oxygen: Dissolved oxygen is essential to the survival of aquatic biota and is an accurate indicator of estuarine health (Head, 1970; Ohrel and Register, 2006). If dissolved oxygen levels remain below 3 mg/L for an extended period of time, estuarine biota can become adversely affected which in turn would decrease the productivity and ultimately the ecological health of the estuary (Ohrel and Register, 2006; Snow and Taljaard, 2007).

Dissolved oxygen values at the surface of Zandvlei Estuary have been found to be similar over the entire system whilst bottom readings of zero, indicating anoxic conditions, have been recorded in both the main body of the estuary and in the Marina da Gama canals (Morant and Grindley, 1982). Hutchings *et al* (2016) added that dissolved oxygen values at the surface from the 1970s and 2000s were of an acceptable level. However, the limited data from the bottom waters indicate very low dissolved oxygen levels (Hutchings *et al.* 2016). According to Morant and Grindley (1982), dissolved oxygen readings were distinctively lower after *S. pectinata* had been mechanically harvested in the canals.

Water Transparency: Secchi depth at Zandvlei Estuary was shown to range from 0.2 – 1.8 m with an average of 0.7 m for the entire system (Morant and Grindley, 1982). Harding (1994) found that Secchi depth increased as one moved away from the head of the estuary and was lowest during winter rains and highest during summer. Mean Secchi depth was 0.54 m with a range of 0.09 – 1.2 m (Harding, 1994).

Depth: Haskins (2013) commented that when the mouth of Zandvlei Estuary opens water depth decreases but then gradually increases after the mouth has closed due to the inflow from rivers (Haskins, 2013).

Wind: The wind patterns at Zandvlei Estuary are a critical physical factor that influences estuarine functioning (Morant and Grindley, 1982). The main body of the estuary is usually well mixed**,** however conditions in the Marina da Gama canals are often calm with very little mixing due to the canals being aligned perpendicular to the predominant winds (Morant and Grindley, 1982; Harding, 1994). The calm conditions can lead to salinity stratification and subsequent anoxic conditions building up below the halocline (Morant and Grindley, 1982).

2.2.5 Physico- chemical characteristics- management targets

Salinity: Zandvlei Estuary management sets salinity targets for surface and bottom waters in the outlet channel (extends upstream to a point parallel to the downstream end of the marina) and main body of the estuary for both summer and winter (C.A.P.E., 2013). The current salinity targets for the main body are in winter, between 5 ppt for surface waters and 7ppt for bottom waters and in summer, 10 ppt throughout the water column (C.A.P.E., 2013). For the outlet channel in winter,

salinity must be between 6 ppt for surface waters and 18 ppt for bottom waters and in summer, between 11 ppt for surface waters and 13 ppt for bottom waters (C.A.P.E., 2013).

Dissolved oxygen: C.A.P.E. (2013) stated that the Water Quality Index project created guidelines which advised that dissolved oxygen values ranging from 6 – 8 mg/L were desired for the system (C.A.P.E., 2013). It has been proposed by C.A.P.E. (2013) that these values be used as targets for Zandvlei estuary.

2.2.6 Nutrient characteristics of Zandvlei Estuary

The concentration of dissolved inorganic nitrogen (DIN) in an estuary is of great importance as a result of its ability to stimulate the growth of aquatic plants and algae (Howarth and Marino 2006). DIN concentrations lower than 0.5 mg/L reduce the possibility of eutrophication and the presence of nuisance plants and algae (DWAF, 1996). When DIN concentrations are higher than 2.5 mg/L oxygen demand increases and this results in decreased dissolved oxygen levels (DWAF, 1996). Dissolved inorganic phosphorus (DIP) is a significant limiting nutrient to plant and algal growth and is known as the key nutrient influencing the extent of eutrophication in aquatic systems (DWAF, 1996). Estuaries with naturally low nutrient levels (oligotrophic) that are unmodified rarely display DIP concentrations exceeding 0.005 mg/L (DWAF, 1996). Concentrations higher than 0.025 mg/L are regarded as eutrophic (DWAF, 1996). The input of unnaturally high levels of nutrients into an estuary, whether DIN or DIP, often triggers prolific primary production which often results in hypoxic conditions that can be detrimental to estuarine life (Scharler *et al.* 1997; De Villiers and Thiart 2007).

Zandvlei Estuary is considered to be a eutrophic system (Morant and Grindley, 1982; Harding 1994; C.A.P.E., 2013). Furness (1979) recorded nitrogen and phosphorus concentrations in the estuary of between 1 and 2 mg/L and 0.01 and 0.3 mg/L respectively (Morant and Grindley, 1982). Nitrogen and phosphorus concentrations in the influent rivers were considerably higher ranging from 6 to 7 mg/L for nitrogen and 1 to 2 mg/L for phosphorus (Morant and Grindley, 1982). Harding (1994) found that the highest nitrogen and phosphorus levels in the estuary were recorded in the northern section of the system where rivers flow into the system. Harding (1994) recorded mean annual total nitrogen and phosphorus concentrations to be 1.79 and 0.18 mg/L respectively between 1978 and 1991. Furthermore, Harding (1994) estimated flow weighted mean annual concentrations of total nitrogen and phosphorus in the influent rivers to be 2.50 and 0.12 mg/L respectively for the same thirteen year period. These concentrations represent mean annual loads to the estuary of 55 tonnes for nitrogen and 2.6 tonnes for phosphorus (Harding, 1994). Harding (1994) compared the study's findings to nutrient levels in other South African estuaries and found that Zandvlei Estuary's nitrogen and phosphorus concentrations were high in comparison. Quick and Harding (1994) commented that there were no apparent seasonal changes in the concentrations of nitrogen and phosphorus at Zandvlei Estuary.

According to C.A.P.E. (2013), a gradual increase in total phosphorus and orthophosphate was reported in the middle to upper region of Zandvlei Estuary between 1978 and 2012. The total phosphorus concentrations reported suggest that Zandvlei Estuary can be classified into Category D (a large deviation from natural conditions) of the Water Quality Index estuary threshold levels (C.A.P.E., 2013). Hutchings *et al* (2016) commented that total nitrogen and phosphorus displayed a

slight reduction between 2000 and 2009, more often being indicative of mesotrophic conditions than eutrophic conditions.

The high levels of nutrients at Zandvlei Estuary have negative implications on the system and include decreased water quality (and associated problems) and fuelling the growth of *Stuckenia pectinata*, reed beds, alien aquatic plants and phytoplankton (C.A.P.E., 2013). The causes of nutrient loading at Zandvlei Estuary are diverse and include runoff from urban areas, industrial waste, fertilizers and pesticides from agriculture/ viticulture as well as domestic gardens and effluent from overflows of blocked sewers, pump stations and informal ablutions (Quick and Harding, 1994; C.A.P.E., 2013).

2.3 *Stuckenia pectinata*

2.3.1 Monitoring and management

Knowledge of what macrophytes were and are present in an estuary under natural conditions is very important from a management perspective (Whitfield and Bate, 2007). Estuarine managers also need an understanding of the life cycles and seasonality of the dominant macrophyte species, for example time of flowering, time of seed set and time to maximum biomass (Whitfield and Bate, 2007). This knowledge provides managers with the ability to predict what macrophyte species will occur at any time and the ability to understand whether changes taking place are due to natural variability or not (Whitfield and Bate, 2007). This knowledge will also aid in making sound management decisions such as the timing and frequency of artificial breaching (Whitfield and Bate, 2007). Furthermore, knowledge of the growth requirements and tolerance ranges (for example salinity, light and water level variations) of the most abundant macrophytes are imperative (Whitfield and Bate, 2007). When there is a change in a particular environmental variable this knowledge will give estuarine managers the ability to predict the associated change in macrophyte species composition, biomass and distribution (Whitfield and Bate, 2007).

According to Whitfield and Bate (2007), changes in the diversity of plant communities are indicative of an estuary under threat, for example the disappearance of *Stuckenia pectinata* due to increased salinity as a result of excessive fresh water abstraction in the catchment. Thus by monitoring the biomass and distribution of macrophytes in estuaries potential ecosystem threats can be recognised early and recovery actions put in place before the entire system is affected.

Morant and Grindley (1982) stated that the sound management of *S. pectinata* is possibly the most critical factor in the maintenance of Zandvlei Estuary as a healthy natural system as well as for human activity. If *S. pectinata* is completely removed from the system it will most likely be replaced by fast growing phytoplankton species which would reduce water transparency and therefore light penetration and in turn prevent the re-establishment of submerged macrophytes (Morant and Grindley, 1982).

The sudden collapse of the *S. pectinata* population at Zandvlei Estuary during 1991 was discussed by Harding (1994). The collapse was hardly noticed until high chlorophyll *a* levels were recorded as a result of phytoplankton presence (Harding, 1994). According to Harding (1994), the collapse occurred because no regular *S. pectinata* biomass monitoring was carried out and no data on the biomass or physiological condition of *S. pectinata* at Zandvlei Estuary were available.

2.3.2 Distribution, classification, identification and reproduction

Stuckenia pectinata is a submerged angiosperm with a nearly cosmopolitan distribution, ranging from the subtropics to the subarctic (Madsen and Adams, 1988; Kantrud, 1990). *S. pectinata* is found in North and South America, Europe, Australia, Africa and Asia where it can survive altitudes from sea level to almost 4900 m above sea level (Madsen and Adams, 1988; Kantrud, 1990). The macrophyte generally occurs in areas where water is constantly available or absent for periods no longer than 3 months. Here *S. pectinata* frequently grows in dense monotypic stands but can also occur together with other submersed and emergent macrophytes (Kantrud, 1990).

Stuckenia pectinata's former scientific name was *Potamogeton pectinatus* assigned by Linnaeus in his *Species Plantarum* of 1753 (Kantrud, 1990). There were approximately 100 species belonging to the genus *Potamogeton* (family *Potamogetonaceae*) around the world until the genus was split up (Kantrud, 1990; Preston, 1995). *Potamogeton* now includes broad leaved species such as *P. natans*, *P. perfoliatus* and *P. alpinus* (Preston, 1995)*.* Furthermore, the subgenus *Coleogeton* that contained *P. pectinata* (as well as *P. filiformis* and *P. vaginatus*) became a separate genus known as *Stuckenia* (Lindqvist *et al.* 2006). This resulted in the name change from *Potamogeton pectinatus* to *Stuckenia pectinata*. Throughout the current study the macrophyte has been referred to as *Stuckenia pectinata* even when discussing previous research which used the name *Potamogeton pectinatus*.

According to Kantrud (1990), the three species comprising the former subgenus *Coleogeton* (now genus *Stuckenia*) are characterised by all leaves being linear or setaceous and divided their full length by cross partitions. *S. pectinata* can be differentiated from the other two species in the genus by having sharp tipped or gradually pointed leaves and leaf sheaths that are narrow but free at the tips (Kantrud, 1990).

Stuckenia pectinata uses different reproductive strategies depending on habitat and environmental stress (Kantrud, 1990). Reproductive strategies include asexual/ vegetative propagules in the form of tubers/ turions and sexual propagules in the form of seeds/ drupelets (Madsen and Adams, 1988; Kantrud, 1990). Asexual tubers allow the plant to survive short term unfavourable conditions (winter season) and aid in dispersal but only over short distances (Madsen and Adams, 1988; Kantrud, 1990). In contrast to tubers, seeds give *S. pectinata* the ability to stay dormant (e.g. during a drought or periods of very high salinity) for long periods of time (years) and aid in dispersal over long distances in particular when carried in the stomachs of birds (Madsen and Adams, 1988; Kantrud, 1990).

2.3.3 Factors influencing the biomass and distribution of *Stuckenia pectinata*

2.3.3.1 Physico- chemical factors

Depth: Wersal *et al* (2006) investigated environmental factors affecting biomass and distribution of *Stuckenia pectinata* at the Heron Lake system in the USA. Depth was shown to have no significant effect on *S. pectinata* biomass. According to Wersal *et al* (2006), depth alone probably does not have an effect on *S. pectinata* biomass but depth can influence other factors such as light availability which do. A critical level of light is required for photosynthesis in all aquatic plants (Wersal *et al.* 2006). At greater depths the critical light level may not be reached and biomass can be reduced as a result of decreased photosynthetic activity (Wersal *et al.* 2006). Insufficient light can therefore

restrict aquatic plants such as *S. pectinata* to grow at shallower depths (Wersal *et al.* 2006). However, at shallower depths *S. pectinata* is then exposed to other limiting forces such as wave action, sediment texture and associated low water transparency (Wersal *et al.* 2006).

Light availability and water transparency: Light availability is a very important environmental factor limiting *S. pectinata* biomass (Wersal *et al.* 2006). Water with low transparency reduces light availability and has a negative impact on *S. pectinata* biomass. Water bodies with shallow depth, loose sediment, poor sediment texture (high concentration of sand), few submersed plants and a long fetch are affected by regular sediment resuspension as a result of wind and wave action and therefore have low water transparency (Wersal *et al.* 2006). In the study by Wersal *et al* (2006) light availability to *S. pectinata* during the time of early growth was reduced and consequently *S. pectinata* biomass decreased (Wersal *et al.* 2006). Wersal *et al* (2006) commented that the most important time for sufficient light availability is during the early growth phase (between germination and when leaves are photosynthetically active). As discussed by Kantrud (1990), who conducted a review paper on *S. pectinata*, decreased light availability to *S. pectinata* is also caused directly and indirectly by a number of other factors including suspended organic and inorganic particles as well as phytoplankton and the shading effects of filamentous algae or epiphytes. *S. pectinata* does not usually grow in waters with a Secchi depth less than 0.2 m (Kantrud, 1990).

Barko *et al* (1986) studied the management of submersed aquatic vegetation with particular emphasis on the influence of environmental factors. Barko *et al* (1986) mentioned that deep water pondweed species exhibited greater photosynthetic ability in comparison to shallow water species. The findings suggest that pondweed species occurring at greater depths had increased tolerance for growing in low light conditions (Barko *et al.* 1986). Furthermore, variations in the specific leaf area of pondweed species have been shown to be influential in determining their maximum depth of occurrence (Barko *et al.* 1986). Therefore, a species success in low light conditions can be affected by morphological adaptations that improve the capture of light (Barko *et al.* 1986).

Sediment type/ texture: Poor sediment texture (high percentage of sand) and high wave action have been noted to limit *S. pectinata* biomass in shallow water bodies (Wersal *et al.* 2006). A negative correlation was found between the percentage of sand in sediment and the presence of *S. pectinata* shoots (Wersal *et al.* 2006). Macrophytes such as *S. pectinata* that grow in sediment consisting of a high percentage of sand are more vulnerable to uprooting by wave action which results in reduced biomass levels (Wersal *et al.* 2006). In contrast, Kantrud (1990) stated that *S. pectinata* is not influenced by sediment type. Instead, *S. pectinata* biomass and distribution is influenced by wave action and fetch which both affect water transparency and sediment texture (Kantrud, 1990). Moreover, propagules of *S. pectinata* are tolerant of disturbed bottom sediments with rhizomes being able to solidify them (Kantrud, 1990).

Wave action and water movement: Wave action and water movement can affect *S. pectinata* biomass directly by uprooting in fine textured substrates or indirectly by re- suspending sediment and therefore decreasing water transparency (increasing turbidity) (Kantrud, 1990). However, according to Kantrud (1990), *S. pectinata* can be tolerant of water movement and may possibly benefit due to increased nutrient inflow and a decline in macrophyte competitors.

Temperature: According to Wersal *et al* (2006), water temperature has an effect on plant performance in particular photosynthetic rates. Increased water temperature increases the biomass of submerged macrophytes such as *S. pectinata* (Wersal *et al.* 2006). The increase in biomass with increased water temperature can be as a result of increased tuber germination and shoot elongation particularly in the early growing season as witnessed by Wersal *et al* (2006). However, both high (>25 °C) and low temperatures have the opposite effect, decreasing *S. pectinata* biomass as a result of reduced photosynthetic rates as well as reduced propagule germination and shoot elongation in the case of high temperatures (Wersal *et al.* 2006). Moreover, water temperature "has a regulatory effect on phenology and resource allocation to propagules" (Wersal *et al.* 2006). This has been seen when more energy is diverted to aboveground biomass of *S. pectinata* during warmer water temperatures (Wersal *et al.* 2006).

Salinity: Stuckenia pectinata has an optimal salinity range of 5 – 14 g/l (Kantrud, 1990). When salinity is above this range in coastal areas *S. pectinata* is often outcompeted by microalgae and *Ruppia* dominated communities (Kantrud, 1990). According to Kantrud (1990), *S. pectinata* appears to be tolerant of gradual salinity changes that are within its range of tolerance (Kantrud, 1990). Furthermore, the macrophyte frequently demonstrates considerable change in annual biomass at water bodies where salinity levels are increased via evaporation and decreased by rainfall (Kantrud, 1990).

pH: *Stuckenia pectinata* occurs in alkaline waters with a pH range of 7.0 – 9.0. The plant avoids acidic waters (but not acidic soils) having never been recorded at a pH value below 6.3. In contrast, the macrophyte will photosynthesise at > pH 10.5 and has been documented to occur in waters with pH of up to 10.7 (Kantrud, 1990).

2.3.3.2 Nutrient factors

Nitrogen: Elevated levels of nitrogen irrespective of form or source appear to have an influence on *Stuckenia pectinata* (Kantrud, 1990). However, in aquatic ecosystems where nitrogen concentrations are low *S. pectinata* has a great ability to take up nitrogen and compete for it (Kantrud, 1990). Therefore, according to Kantrud (1990), the biomass and distribution of *S. pectinata* are not likely to be limited by the availability of nitrogen.

Phosphorus: Stuckenia pectinata has the ability to absorb large quantities of phosphorus from the water column via roots and shoots (Kantrud, 1990). In contrast, the plant struggles to absorb phosphorus from the sediment (Kantrud, 1990). In ecosystems where phosphorus levels are low *S. pectinata* is less competitive with other angiosperms (Kantrud, 1990). The plant shows an affinity for waters high in phosphorus but under such conditions is often negatively affected by turbidity caused by phytoplankton (Kantrud, 1990). This could reduce *S. pectinata* growth substantially in deeper waters of temperate climates where the plant has to regrow from turions after winter (Kantrud, 1990). Kantrud (1990) added that the influence of phosphorus may be linked to other aspects of water chemistry.

Calcium and magnesium: Even though submersed macrophytes have the ability to mobilise Calcium (Ca) from sediment, *S. pectinata* was found to be unable to grow in the absence of Ca in solution in one particular study and in solutions low in Ca in another study (Barko *et al.* 1986). As a result of Ca's apparent involvement in bicarbonate utilisation during photosynthesis, Ca may be required in open

water by many macrophyte species (Barko *et al.* 1986). According to Barko *et al* (1986), the decreased growth of *S. pectinata* in solutions free of magnesium (Mg) indicates that Mg might also be needed in open water by certain submersed macrophyte species.

2.3.3.3 Biotic factors

Macrophyte: *Stuckenia pectinata* is commonly found together with a number of submerged and emergent angiosperms and macroalgae (Kantrud, 1990). In stressed conditions or those high in ionic content and pH, *S. pectinata* has the tendency to grow in discrete beds (Kantrud, 1990). The plant has the ability to exchange dominance with other species both seasonally and annually in a single water body (Kantrud, 1990). *S. pectinata* has a competitive advantage as a result of its phenoplasticity, leaf morphology, pollution tolerance and ability to quickly take over unoccupied habitats (Kantrud, 1990). In contrast, the macrophyte is at a disadvantage in acidic, mineral poor and hypersaline conditions as well as in water bodies where water level variations occur and where non rooted species or species with large floating or semi-erect leaves dominate (Kantrud, 1990). Moreover, in nearshore zones that experience organic and mineral matter deposits *S. pectinata* is often replaced by emergent plants (Kantrud, 1990).

Algal: Stuckenia pectinata grows together with several periphytic and planktonic algae (Kantrud, 1990). Kantrud (1990) mentioned that the biomass of *S. pectinata* can be reduced as a result of shading by periphyton particularly in sheltered water bodies with low depth. However, some epiphytes might help *S. pectinata* assimilate phosphorus (Kantrud, 1990). Kantrud (1990) added that phytoplankton often reduce *S. pectinata* biomass considerably as a result of decreased water transparency.

Invertebrates, fish and birds: Direct consumption of *S. pectinata* by invertebrates is relatively unimportant however a few species have been noted to significantly decrease the biomass of *S. pectinata* (Kantrud, 1990). In addition, only a few species of fish consume large quantities of *S. pectinata* (Kantrud, 1990). Young plants particularly those in soft sediments can be negatively affected by bottom feeders such as the common carp (Kantrud, 1990). Older plants are less at risk because they can reproduce from underground tubers that are not affected by carp (Kantrud, 1990). According to Kantrud (1990), the very high reproductive ability of *S. pectinata* combined with the fact that some of its propagules occur underground, and therefore out of the reach of birds, it is unlikely that birds are an important factor limiting *S. pectinata* biomass. Weisner *et al* (1997) carried out experiments to understand the effects of waterfowl grazing on macrophyte biomass. In contrast to Kantrud (1990), the results obtained by Weisner *et al* (1997) demonstrated that *S. pectinata* growth was decreased as a result of waterfowl grazing.

2.4 *Stuckenia pectinata* at Zandvlei Estuary

2.4.1 Introduction

For many years Zandvlei Estuary and the Marina da Gama canals have been dominated by *Stuckenia pectinata* (Harding, 1994). *S. pectinata* occurs mainly in the middle reaches of Zandvlei Estuary, most importantly the area off the western shore of Park Island, offshore of the Imperial Yacht Club and in the Marina da Gama canals (Harding, 1994). According to Harding (1994), the growth and distribution of *S. pectinata* are affected by water depth and the depth to which light can penetrate

the water column. In addition, *S. pectinata* has been found to have a salinity tolerance of between 5 and 20 ppt and in order to maintain its ecological advantage over other macrophytes and phytoplankton in Zandvlei Estuary, salinity levels should fall between 5 and 10 ppt (Harding, 1994; C.A.P.E., 2013). Thornton *et al* (1995) reported that annual yields of *S. pectinata* did not show any considerable variation between 1983 and 1988. There was however a clear seasonality in *S. pectinata* growth with maximum biomass being attained in late summer between January and April (Thornton *et al.* 1995). Total yields per year (harvested biomass plus standing crop) were estimated to be between 120 and 450g/ m^2 dry biomass in the main body of the estuary and between 280 and 690 g/ m^2 dry biomass in the Marina da Gama canals (Thornton *et al.* 1995).

Stuckenia pectinata is indigenous to Zandvlei Estuary and plays an important role in the functioning of the system (Quick and Harding, 1994; C.A.P.E., 2013). *S. pectinata* serves as a habitat for a number of organisms including invertebrates and juvenile fish (Quick and Harding, 1994; C.A.P.E., 2013). According to Harding (1994), Muir (1974) stated that the majority of fauna at Zandvlei Estuary were associated with *S. pectinata* as well as macroalgal species. *S. pectinata* oxygenates the water column and acts as a nutrient sink by absorbing nutrients from the water and sediment, thereby reducing the effects of nutrient loading (Morant and Grindley, 1982; C.A.P.E., 2013). Furthermore, *S. pectinata* increases water transparency by decreasing sediment resuspension caused by recreational activities, wind and fauna (Morant and Grindley, 1982; Quick and Harding, 1994).

In contrast, as a result of the high nutrient concentrations present at Zandvlei Estuary (as a result of a highly urbanised catchment) *S. pectinata* has the tendency to form dense mats which are a nuisance (C.A.P.E., 2013). Dense mats of *S. pectinata* reduce light penetration, intensify flooding, impede recreational activities (such as boating and fishing) and decrease current flow and therefore cause stagnation (Quick and Harding, 1994; C.A.P.E., 2013). When the dense mats start to break down nutrients are released back into the estuary and undesirable odours are produced which can negatively affect property values (C.A.P.E., 2013). According to Quick and Harding (1994), *S. pectinata* provides a surface for growth to nuisance algae including *Enteromorpha intestinalis* and *Cladophora* spp.

2.4.2 Mechanical control of *Stuckenia pectinata* at Zandvlei Estuary

As a result of *Stuckenia pectinata's* nuisance tendencies at Zandvlei Estuary, the macrophyte has been managed since 1976 using a mechanical harvester (C.A.P.E., 2013). According to Thornton *et al* (1995), mean annual removal of *S. pectinata* from the system was 224g/ m^2 dry biomass. Areas of the estuary used for recreation are kept clear of *S. pectinata* to a depth of 0.5 m in the Marina da Gama canals and as deep as possible in the main body of the system (C.A.P.E., 2013). Furthermore, there is a "pondweed reserve" making up 30% of the estuarine area (C.A.P.E., 2013). Only 20% of this reserve area can be harvested annually (C.A.P.E., 2013). Therefore, the aim of the "pondweed management plan" is to remove *S. pectinata* so that it does not become a nuisance but not to a level of removal where *S. pectinata's* ability to maintain good water quality at Zandvlei Estuary is impaired (Harding, 1994). Due to *S. pectinata's* ability to function as a nutrient sink, another benefit of its removal is that large quantities of nutrients are removed with it (Morant and Grindley, 1982).

Although mechanical harvesting of *S. pectinata* at Zandvlei Estuary has many benefits there are negatives as well (C.A.P.E., 2013). In the past excessive removal of the *S. pectinata* has resulted in collapses in the population (Quick and Harding, 1994). Population collapses can shift the system to a

phytoplankton dominated state which can have many negative effects on the system (Quick and Harding, 1994; C.A.P.E., 2013). Furthermore, mechanical harvesting at Zandvlei Estuary is expensive due to it being labour intensive, time consuming and the fact that the harvester constantly breaks down and then needs to be repaired (C.A.P.E., 2013). C.A.P.E. (2013) stated that "the current complement of one harvesting machine and a single driver/operator delivers less than half of the hours required to complete the schedule" (*S. pectinata* cutting schedule). An additional harvester and driver would solve this issue but a new harvester is a very expensive purchase (about 2.5 million rand) (C.A.P.E., 2013).

3. Research design and methodology

3.1 Study site

A detailed description of the study site is given in the literature review under the headings "Zandvlei Estuary" and "Physical description".
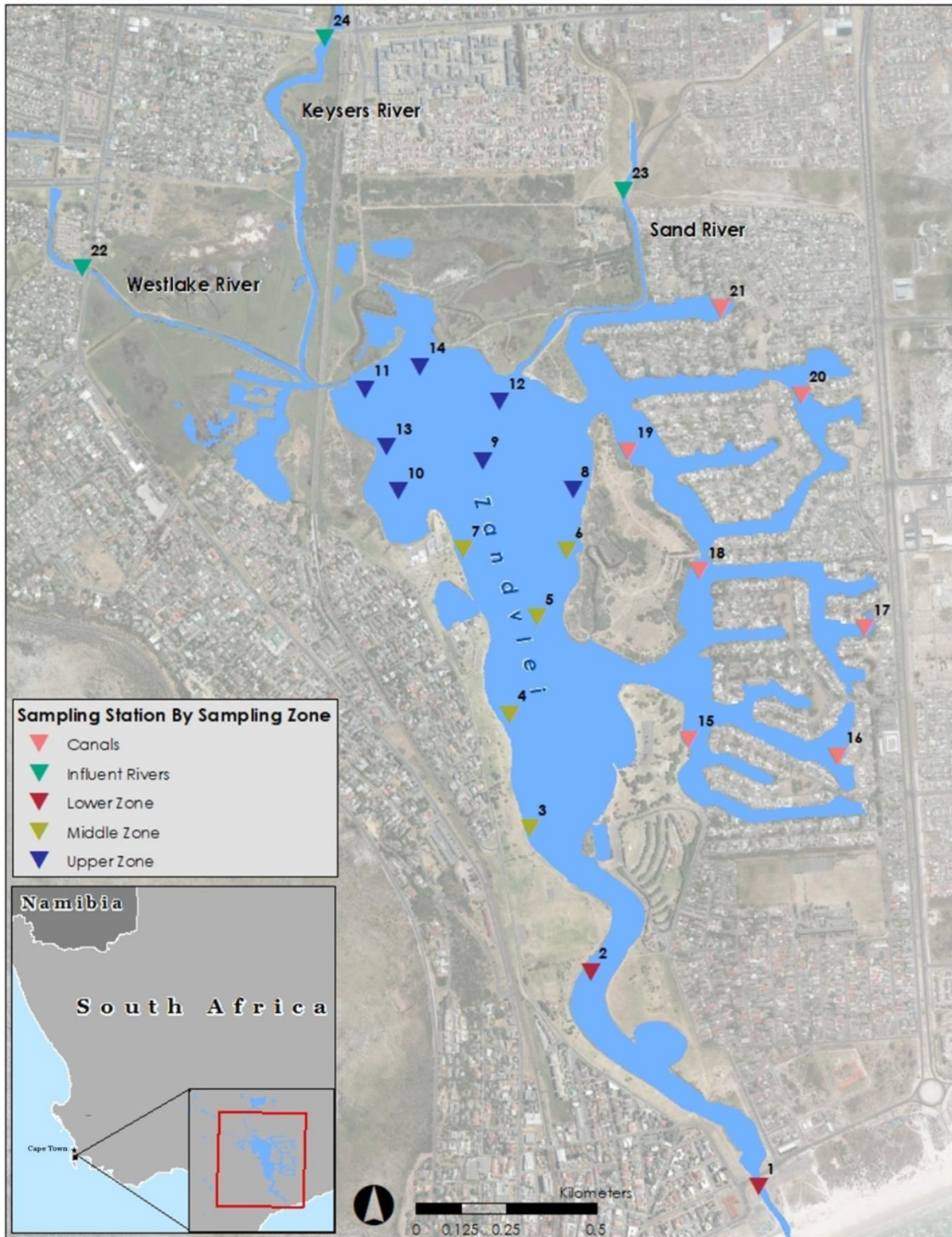

Figure 2: The study site including sampling stations 1 to 24 (Source: QGIS, 2019)

3.2 Sample collection

Stuckenia pectinata biomass and distribution, physico- chemical parameters and nutrient characteristics were assessed every month whilst sediment grain size composition was assessed once off. The study period commenced in November 2016 and concluded in November 2017 a thirteen month time frame in order to cover all seasons. Sampling was not conducted in September 2017 due to adverse weather conditions and therefore twelve sampling events were carried out. 31% of sampling events were conducted in spring, 23% in summer, 31% in autumn and 15% in winter. 57% of sampling events were carried out during open mouth conditions and 43% of sampling events during closed mouth conditions. Sampling was not conducted on specific tides, at specific times of the day nor at a specific number of days after opening/ closing of the mouth. For each sampling event the time of sampling at each sampling station, sampling date and mouth status was recorded. Environmental data including total monthly rainfall and maximum monthly air temperature, both during the sampling period and historically (1981 to 2010), was obtained from the South African Weather Service (SAWS Kirstenbosch weather station).

Samples were collected at the influent rivers, main body of the estuary and at the canals which form part of the Marina da Gama housing development. In total 24 stations were sampled (Figure 1). Stations 1 to 14 were located at the main body and stations 15 to 21 at the canals (Figure 1). Stations 22 to 24 were positioned at the influent rivers, Westlake, Keysers and Sand (Figure 1). An attempt was made to position the majority of sampling stations within the "pondweed reserve". This was done to avoid the effect of harvesting which would interfere with the natural growth patterns of *S. pectinata*. According to C.A.P.E. (2013), 20% of the "pondweed reserve" can be harvested annually and therefore harvesting could not be avoided completely. Furthermore, the majority of sampling stations were positioned to align with sampling stations used by the City of Cape Town's water quality monitoring programme. The data collected could therefore be compared with historical data to record temporal changes in the measured parameters.

Triplicate biomass samples (mass per unit area- g/m^2) of *S. pectinata* were taken at the 21 sampling stations within the main body and canals. Physico- chemical data including water depth (meters- m), temperature (degrees Celsius- °C), salinity (parts per thousand- ppt), pH, dissolved oxygen or DO (milligrams per litre- mg/L) and Secchi depth (percentage- %) were recorded at all 24 sampling stations. Water samples to be analysed for nutrients including nitrate + nitrite (micromolar- μM), nitrite (μM), nitrate (μM) and phosphate (μM) were taken at the main body, canals and influent rivers but only at 12 out of the 24 sampling stations. Single sediment samples were collected only at the 14 sampling stations within the main body.

Samples of *S. pectinata* for biomass estimates were collected above ground and below ground to a depth of at least 0.2 m into the sediment following the methods of Madsen (1993). In terms of physico- chemical parameters, if the water depth was less than or equal to 0.5 m only a surface reading would be taken. If, however the water depth was greater than 0.5 m but less than 2 m then both a bottom reading and a surface reading would be taken. If the water depth was 2 m or greater a bottom, middle and surface reading would be taken. Surface readings were taken at a depth of 0.1 m. In order to assess nutrient concentrations a single water sample was taken 0.1 m into the water column. Sediment samples were taken to a depth of 0.2 m into the sediment.

A PVC coring device with a cross sectional area of 0.018 m^2 (15.24 cm diameter) similar to the one designed and used by Madsen *et al* (2007) was employed to take above ground and below ground samples of *S. pectinata* for biomass estimates (Appendix: Figure 34, 37). This design was chosen as it samples biomass of submersed aquatic macrophytes in an effective manner (Madsen *et al.* 2007; Madsen and Wersal, 2012). As mentioned by Madsen *et al* (2007) the core sampler is lightweight and does not have valves or moving parts which make it simple to operate as well as construct, modify and repair. The design also allows research to be carried out quickly and therefore large amounts of data can be acquired (Madsen *et al.* 2007). Furthermore, the core sampling device demonstrated its ability to work appropriately *in situ* during trial sampling at Zandvlei Estuary.

A Secchi disk with a diameter of 0.2 m was used to measure water transparency and water depth. Temperature, salinity, pH and dissolved oxygen were measured using a YSI multimeter (professional plus model). Water samples for nutrient analysis were collected by hand using 250 ml plastic jars. To prevent contamination jars were rinsed three times with deionised water prior to sampling and three times with sample water *in situ*. The same PVC coring device used for biomass sampling was used to collect sediment samples. A boat was used to access sampling stations which were located with the use of a GPS and physical markers. A permit granting permission to sample within the GZENR was obtained from the reserve manager. In addition, an ethics clearance form was completed for the research conducted.

3.3 Sample processing and data preparation

Stuckenia pectinata biomass: After core samples were collected samples were appropriately processed. The method used was based on the methods outlined by Madsen (1993) and Madsen *et al* (2007). Core samples were rinsed through a 0.25 cm^2 mesh to separate plant biomass from sediment. Biomass obtained from the mesh was placed into sealable bags and stored in a cooler to prevent decomposition. At the laboratory plant biomass was separated into *S. pectinata* and other with other being discarded. *Stuckenia pectinata* biomass was washed to remove excess sediment and then weighed (Radwag four decimal place analytical balance) to obtain the wet mass (grams). Samples were dried at 60 °C for between 24 and 48 hours and then weighed to ascertain the dry mass (grams). Mass data was used to estimate biomass.

In order to calculate wet mass and dry mass per meter squared (m^2) the following calculations were performed. The cross sectional area of the core sampler was 0.018 m^2 and three core samples were taken at each sampling station. Therefore, the surface area of sediment sampled was 0.054 m^2. In order to convert 0.054 m^2 to 1m^2 multiplication by 18.5185 was required. Therefore, wet and dry mass results were multiplied by 18.5185 in order to obtain wet mass and dry mass per m^2.

Physico- chemical: No sample processing was required. The Secchi depth in meters was converted to a Secchi depth in percentage. Secchi depth (%) was determined by dividing the depth in meters by the Secchi depth in meters at the same sampling station. The answer was then multiplied by 100 to obtain a percentage. Therefore, a high Secchi depth (%) would signify high water transparency.

Nutrients: Water samples were stored in 250 ml jars on ice, in a cooler, in the dark. Water samples were transported to the laboratory and frozen (-20 °C) until analyses could commence. The described methods were used to minimise the consumption of nutrients by microorganisms (bacteria and algae) unavoidably collected with the sample. Nitrate + nitrite, nitrite, nitrate and

phosphate were analysed using standard chemical analyses (colourimetric methods) described by Bendschneider and Robinson (1952) and Strickland and Parsons (1968). Nutrient sample processing was carried out at the Oceanography Department laboratory at the University of Cape Town (UCT).

Sediment: Sediment samples were placed into sealable bags and transported to the laboratory. Here samples were dried at 60 °C for approximately 48 hours. Each sample was weighed to obtain the total sample mass (Radwag four decimal place analytical balance). Sediment samples were dry sieved using a stack of seven sieves (Kingtest 20cm diameter stainless steel sieves) to determine sediment grain size composition. Each sieve represented a sediment size class namely 1700 micrometre (μm) sieve (>1700 μm size class), 1180 μm sieve (1180 μm – 1700 μm size class), 500 μm sieve (500 μm – 1180 μm size class), 250 μm sieve (250 μm – 500 μm size class), 125 μm sieve (125 μm – 250 μm size class), 63 μm sieve (0.63 μm – 125 μm size class) and <63 μm sieve (<63 μm size class). The sieve stack was placed on top of a mechanical shaker and agitated for five minutes. The sediment retained on each sieve was carefully removed using a brush and then weighed to obtain the mass of sediment retained on each sieve. The mass of sediment retained on each sieve was divided by the total sample mass and then multiplied by 100 to produce a percentage sediment retained for each sieve/ size class.

3.4 Data analyses

Data was organised into columns so that analyses could be carried out. Each column represented one of the determinants sampled. Columns were also produced for sampling date, month, season, station, zone, surface/ bottom waters and mouth state so that sampled parameters could be analysed across these variables. In order to quantify spatial variations within the main body sampling stations 1 – 2 were grouped as the lower zone (closest to the estuary mouth), stations 3 – 7 as the middle zone and stations 8 – 14 as the upper zone (closest to the estuary head) (Figure 1). In order to understand spatial variations between the main body, canals and influent rivers sampling stations 1 – 14 were grouped as the main body, stations 15 – 21 as the canals and stations 22 – 24 as the influent rivers (Figure 1). In order to quantify temporal variations sampling events falling within the months of September, October and November were combined as spring, months December, January and February as summer, months March, April and May as autumn and months June, July and August as winter. Data was entered and organised in Microsoft excel 2010 and then imported into IBM SPSS Statistics 25.

Tables and graphs were created to illustrate spatial and temporal variations in the sampled parameters using IBM SPSS Statistics 25. Data was checked for normality using the Kolmogorov-Smirnov test and Shapiro- Wilk test in conjunction with reviewing the skewness and kurtosis values and histograms. Normality testing was conducted for each parameter sampled (physico- chemical, nutrient, sediment and biomass parameters) across sampling zones and sampling seasons. The data was found to be not normally distributed and therefore non parametric analyses were performed on the data.

Descriptive statistics were calculated for physico- chemical, nutrient, sediment and biomass parameters. A Mann- Whitney U test was performed to determine whether there were statistically significant differences (α= 0.05) between open mouth state and closed mouth state as well as between surface waters and bottom waters. Analyses were carried out on physico- chemical and nutrient parameters sampled. A Kruskal- Wallis H test was performed to determine whether there

were statistically significant differences (α= 0.05) between sampling zones as well as sampling seasons. Analyses were carried out on physico- chemical, nutrient, sediment and biomass parameters sampled. Following a statistically significant result post- hoc tests with pairwise comparisons using the Dunn- Bonferroni method were performed. Spearman rank- order correlation was performed to determine whether there were statistically significant relationships (α= 0.05) between sampled parameters (physico- chemical, nutrient, and sediment parameters) and *S. pectinata* biomass characteristics (wet mass, dry mass and tuber density) across sampling zones and sampling seasons. Statistical analyses were carried out using IBM SPSS Statistics 25.

4. Results

4.1 Environmental characteristics

Air temperature: Maximum air temperature was higher during the study period (22.05 °C) in comparison to historical data (21.47 °C) (Figure 2). When comparing seasons maximum air temperature was higher during the study period in comparison to historical data in spring (21.58 °C and 20.83 °C respectively), summer (25.87 °C and 25.00 °C respectively) and autumn (24.47 °C and 22.43 °C respectively) but not in winter (16.30 °C and 17.63 °C respectively) (Figure 2). The largest difference in maximum air temperature between the study period and historical data was noted during autumn (Figure 2).
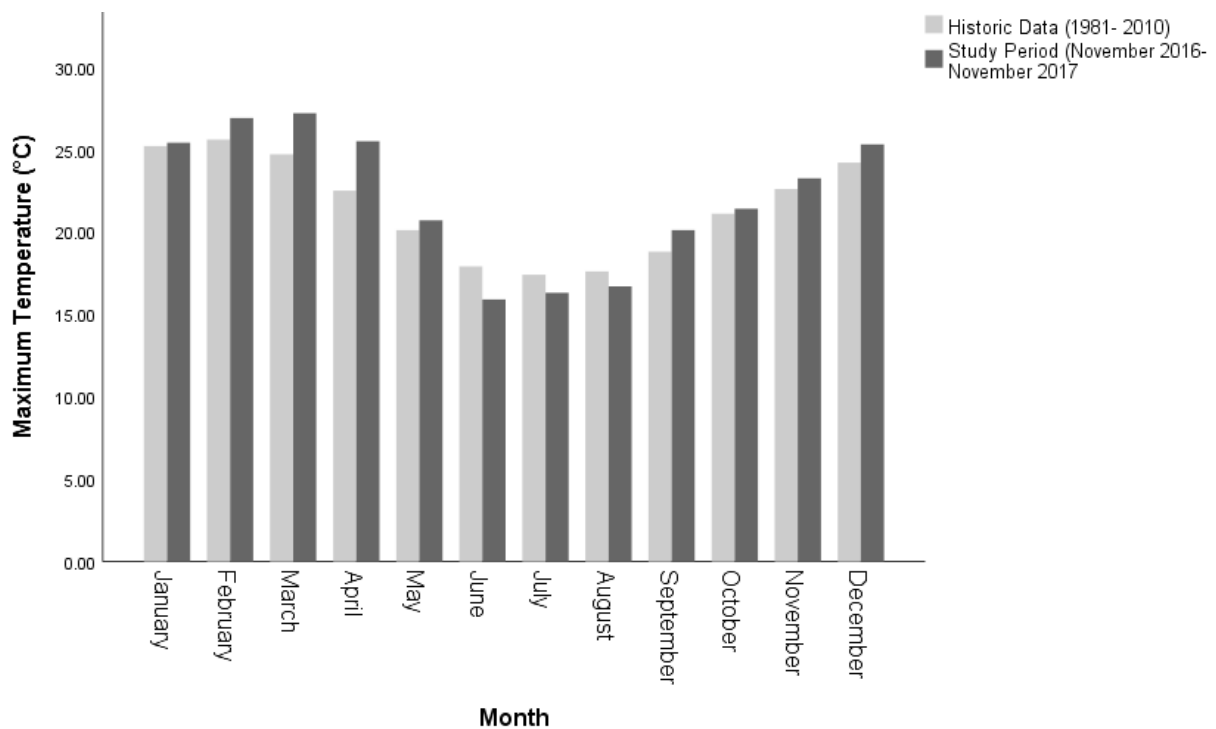
Figure 2: Maximum monthly temperature (°C) historically (1981 - 2010) and over the sampling period (November 2016 - November 2017)

Rainfall: Total rainfall was lower during the study period (1048.3 mm) in comparison to historical data (1399 mm) (Figure 3). When comparing seasons total rainfall was lower during the study period in comparison to historical data in autumn (35.07 mm and 106.00 mm respectively), winter (195.73 mm and 234.67 mm respectively) and spring (78.30 mm and 91.00 mm respectively) but not in summer (40.33 mm and 34.67 mm respectively) (Figure 3). The largest difference in total rainfall between the study period and historical data was observed during autumn (Figure 3).
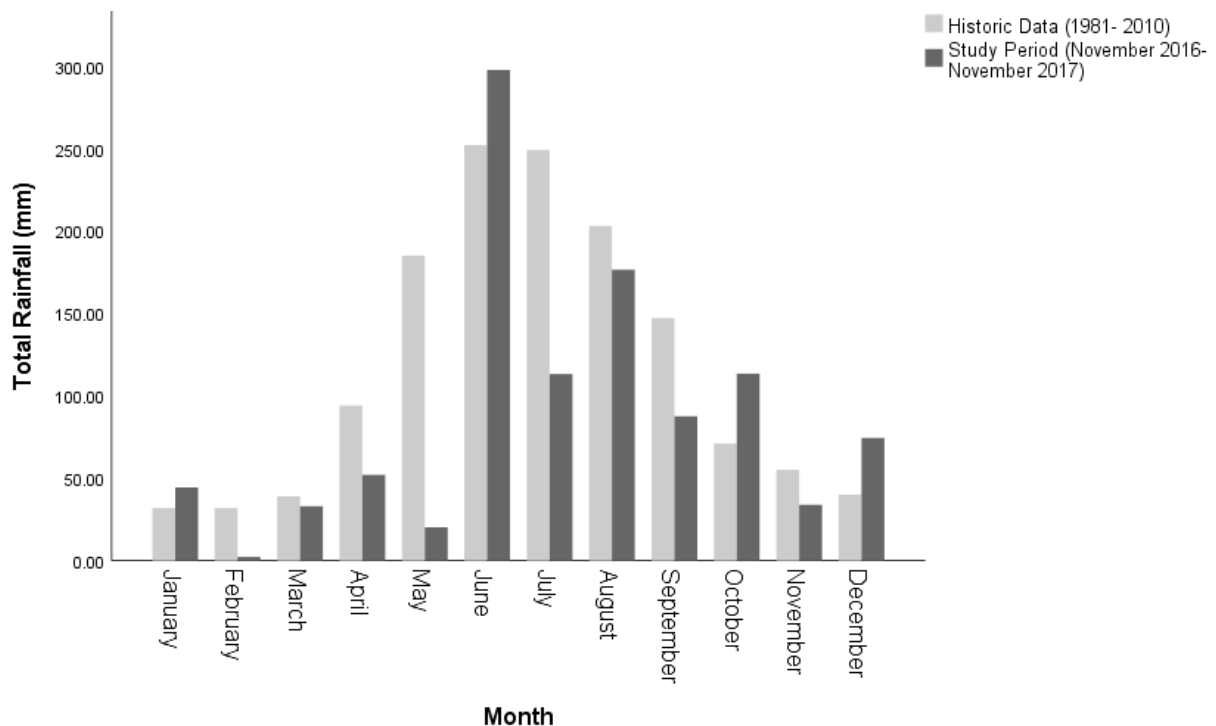
Figure 3: Total monthly rainfall (mm) historically (1981 - 2010) and over the sampling period (November 2016 - November 2017)

4.2 Physico- chemical characteristics

Descriptive statistics: A total of 523 measurements were taken for each parameter with the exceptions being Secchi depth and depth for which 241 measurements were taken (Table 1). A maximum value of 27.30 °C for temperature was measured during closed mouth state at the surface waters and a minimum value of 11.80 °C was recorded during open mouth state at the surface waters (Table 1). Maximum salinity was 34.38 ppt measured during open mouth state at the surface waters and minimum salinity was 0.23 ppt recorded during closed mouth state at the surface waters (Table 1). A maximum value for pH of 10.17 was measured during closed mouth state at the bottom waters and a minimum of 4.04 was recorded during closed mouth state at the surface waters (Table 1). Maximum dissolved oxygen was 24.60 mg/L recorded during open mouth state at the surface waters and minimum dissolved oxygen was 0.28 mg/L measured during open mouth state at the surface waters (Table 1). Secchi depth was found to have a minimum value of 9% recorded during open mouth state at the bottom waters (Table 1). Depth had a maximum value of 2.30 m measured during closed mouth state and a minimum of 0.30 m measured during open mouth state (Table 1). Median temperature was 20.20 °C, salinity 14.76 ppt, pH 8.44, dissolved oxygen 8.65 mg/L, Secchi depth 55.56% and depth 1.25 m (Table 1). Mean temperature was found to be 19.59 °C (SD= 3.26), salinity 14.40 ppt (SD= 5.56), pH 8.44 (SD= .58), dissolved oxygen 8.75 mg/L (SD= 4.36), Secchi depth 57.15% (SD= 30.55) and depth 1.31 m (SD= .34) (Table 1). Secchi depth displayed a considerably higher value for standard deviation when compared to the other recorded parameters (Table 1).

Table 1: Descriptive statistics for physico- chemical parameters

	Temperature (°C)	Salinity (ppt)	pH	Dissolved Oxygen (mg/L)	Depth (m)	Secchi Depth (%)
N	523	523	523	523	241	241
Minimum	11.80	.23	4.04	0.28	0.30	9.00
Maximum	27.30	34.38	10.17	24.60	2.30	100.00
Median	20.20	14.76	8.44	8.65	1.25	55.56
Mean	19.59	14.40	8.44	8.75	1.31	57.15
Standard Deviation	3.26	5.56	0.58	4.36	0.34	30.55

Mouth state comparison: Median dissolved oxygen was found to be 10.23 mg/L during open mouth state and 7.55 mg/L during closed mouth state and median depth 1.30 m and 1.13 m respectively (Table 2). Dissolved oxygen (U= 22055.5, Z= -6.59, p< .001) and depth (U= 4874, Z= -4.15, p< .001) were significantly higher during open mouth state in comparison to closed mouth state. Median temperature was calculated to be 17.50 °C during open mouth state and 21.60 °C during closed mouth state, median salinity 12.59 ppt and 17.63 ppt respectively, median pH 8.50 and 8.42 respectively and median Secchi depth 34.78% and 75.50% respectively (Table 2). Temperature (U= 15541.5, Z= -10.41, p< .001), salinity (U= 12877, Z= -11.97, p< .001) and Secchi depth (U= 3960, Z= -5.87, p< .001) were significantly higher during closed mouth state in comparison to open mouth state whilst pH was not significantly higher (U= 33013.5, Z= -.16, p= .872).

Table 2: Physico- chemical parameters (median values) across sampling zones including mouth state and surface/ bottom waters

		Lower		Middle		Upper		Canals		Influent Rivers	
		Open	Closed	Open	Closed	Open	Closed	Open	Closed	Open	Closed
Temperature (°C)	Surface	16.80	21.50	16.90	21.70	17.10	21.70	18.60	21.80	18.30	20.70
	Bottom	16.10	21.20	17.60	21.20	17.70	21.80	17.15	21.30	17.80	.
Salinity (ppt)	Surface	13.44	22.54	12.05	16.68	11.68	16.64	11.93	17.63	0.37	0.41
	Bottom	20.20	23.22	14.51	18.44	14.15	16.98	13.39	18.01	0.40	.
pH	Surface	8.58	7.73	8.63	8.48	8.62	8.45	8.67	8.57	7.71	8.10
	Bottom	8.01	7.62	8.14	8.29	8.40	8.40	8.42	8.46	7.29	.
Dissolved Oxygen (mg/L)	Surface	8.86	6.50	11.05	8.45	11.09	9.35	12.29	8.04	8.92	7.51
	Bottom	5.27	4.81	6.99	6.75	7.93	7.34	7.07	5.98	11.28	.
Secchi Depth (%)	Bottom	84.10	100.00	57.60	70.00	52.93	74.00	30.03	67.74	.	.
Depth (m)	Bottom	1.00	1.13	1.25	1.05	1.25	1.10	1.79	1.63	.	.

Surface and bottom waters comparison: Median temperature was found to be 20.20 °C at the surface waters and 20.30 °C at the bottom waters, median pH 8.55 and 8.35 respectively and median dissolved oxygen 10.07 mg/L and 6.76 mg/L respectively (Table 2). pH (U= 28934.5, Z= -2.96, p= .003)

and dissolved oxygen (*U*= 19496, *Z*= -8.43, *p*< .001) were significantly higher at the surface waters in comparison to the bottom waters whilst temperature was not significantly higher (*U*= 33111.5, *Z*= -.54, *p*= .591). Median salinity was calculated to be 13.38 ppt at the surface waters and 15.75 ppt at the bottom waters (Table 2). Salinity was significantly higher at the bottom waters in comparison to the surface waters (*U*= 22472.5, *Z*= -6.71, *p*< .001).

4.2.1 Spatial variations

Descriptive statistics: Maximum values for salinity decreased from the lower zone, through the middle zone to the upper zone and decreased further into the canals and influent rivers (Table 3). Minimum values for dissolved oxygen decreased from the lower zone, through the middle zone to the upper zone (Table 3). Maximum values for Secchi depth remained the same across the lower, middle and upper zones as well as the canals (Table 3). Maximum values for depth decreased from the lower zone, through the middle zone to the upper zone (Table 3).

Median temperature and dissolved oxygen increased from the lower zone, through the middle zone to the upper zone (Table 3). Median salinity decreased from the lower zone, through the middle zone to the upper zone and decreased further into the canals and influent rivers (Table 3). Median pH and depth increased from the lower zone, through the middle zone to the upper zone and increased further into the canals (Table 3). Median Secchi depth decreased from the lower zone, through the middle zone to the upper zone and decreased further into the canals (Table 3).

Table 3: Descriptive statistics for physico- chemical parameters across sampling zones

		Lower	Middle	Upper	Canals	Influent Rivers
Temperature (°C)	N	46	120	168	150	39
	Minimum	12.30	11.80	12.00	12.00	11.90
	Maximum	23.50	23.30	25.00	25.90	27.30
	Median	19.00	20.05	20.50	20.25	19.00
	Mean	18.81	19.17	19.79	19.97	19.43
	Standard Deviation	3.20	3.06	3.13	3.48	3.48
Salinity (ppt)	N	46	120	168	150	39
	Minimum	7.94	9.56	4.63	9.45	0.23
	Maximum	34.38	24.28	20.69	18.99	6.75
	Median	20.43	15.46	14.56	14.66	0.40
	Mean	21.26	15.56	14.70	14.60	0.69
	Standard Deviation	6.78	3.49	3.15	2.86	1.42
pH	N	46	120	168	150	39
	Minimum	7.08	7.49	7.00	6.93	4.04
	Maximum	9.35	9.96	9.76	10.17	9.55
	Median	7.96	8.37	8.50	8.54	7.96
	Mean	8.04	8.44	8.53	8.60	7.85
	Standard Deviation	0.58	0.51	0.40	0.51	0.97

Dissolved Oxygen (mg/L)	N	46	120	168	150	39
	Minimum	2.11	0.42	0.35	0.44	0.28
	Maximum	21.35	21.30	21.30	24.60	16.91
	Median	6.40	8.49	9.82	8.68	8.92
	Mean	7.00	8.50	9.34	8.94	8.34
	Standard Deviation	3.55	3.84	4.14	4.86	5.13
Secchi Depth (%)	N	23	60	83	75	0.00
	Minimum	20.80	18.57	16.43	9.00	.
	Maximum	100.00	100.00	100.00	100.00	.
	Median	100.00	63.28	58.33	40.54	.
	Mean	81.31	60.48	57.56	46.62	.
	Standard Deviation	31.60	29.35	27.62	29.90	.
Depth (m)	N	23	60	83	75	0.00
	Minimum	0.30	0.63	0.50	0.75	.
	Maximum	1.75	1.70	1.50	2.30	.
	Median	1.05	1.15	1.20	1.70	.
	Mean	1.06	1.16	1.16	1.69	.
	Standard Deviation	0.35	0.19	0.18	0.25	.

Main body, canals and influent rivers comparison: The lower, middle and upper zones were grouped together as the main body. Median temperature was highest at the main body (20.30 °C), lowest at the influent rivers (19.00 °C) and in between at the canals (20.25 °C) (Figure 4, Table 3). The differences in temperature across zones were not significantly different ($H(2)= 3.52$, $p= .172$).

Median salinity was highest at the main body (15.24 ppt), lowest at the influent rivers (0.40 ppt) and in between at the canals (14.66 ppt) (Figure 5, Table 3). The differences in salinity across zones were significantly different ($H(2)= 114.43$, $p< .001$). Post hoc tests found that the influent rivers differed significantly from the canals ($H(2)= 8.67$, $p< .001$) and the main body ($H(2)= -10.68$, $p< .001$). The canals showed no significant difference with the main body ($H(2)= -2.53$, $p= .068$).

Median pH was found to be highest at the canals (8.54), lowest at the influent rivers (7.96) and in between at the main body (8.42) (Table 3). The differences in pH across zones were significantly different ($H(2)= 37.21$, $p< .001$). Post hoc tests revealed that the influent rivers differed significantly from the main body ($H(2)= -3.96$, $p< .001$) and the canals ($H(2)= 5.83$, $p< .001$). The main body was significantly different from the canals ($H(2)= 3.86$, $p= .001$).
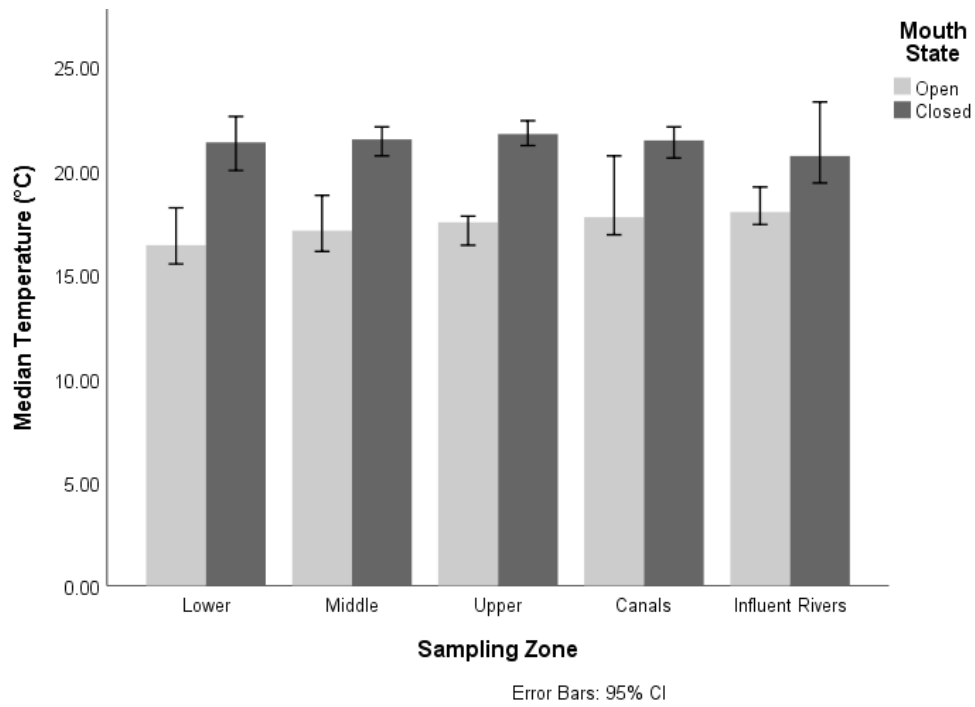
Figure 4: Median temperature (°C) across sampling zones including mouth state
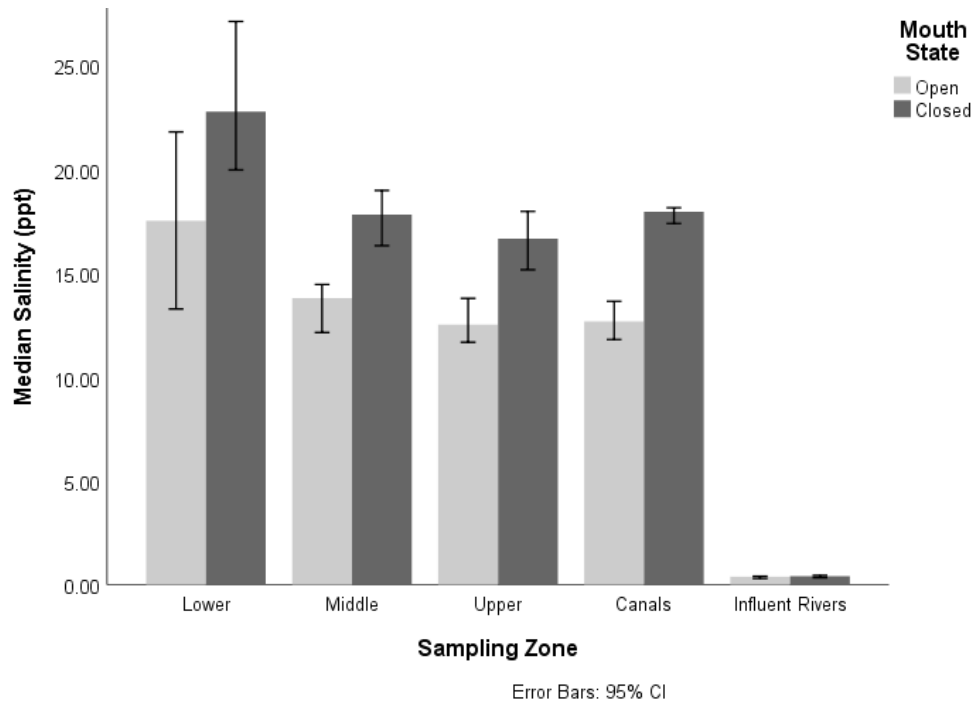
Figure 5: Median salinity (ppt) across sampling zones including mouth state

Median dissolved oxygen was highest at the influent rivers (8.92 mg/L), lowest at the main body (8.65 mg/L) and in between at the canals (8.68 mg/L) (Figure 6, Table 3). The differences in dissolved oxygen across zones were not significantly different ($H(2)= .48$, $p= .787$).
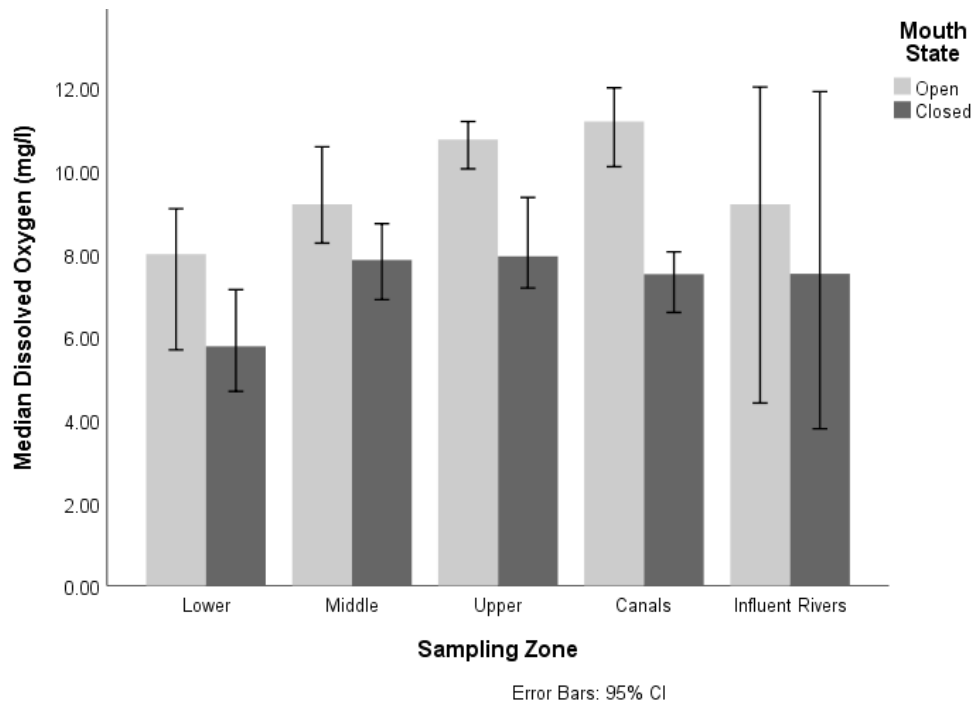
Figure 6: Median dissolved oxygen (mg/L) across sampling zones including mouth state

Median Secchi depth was significantly higher (U= 4356.50, Z= -3.74, p< .001) at the main body (65.40%) in comparison to the canals (40.54%) (Figure 7, Table 3).
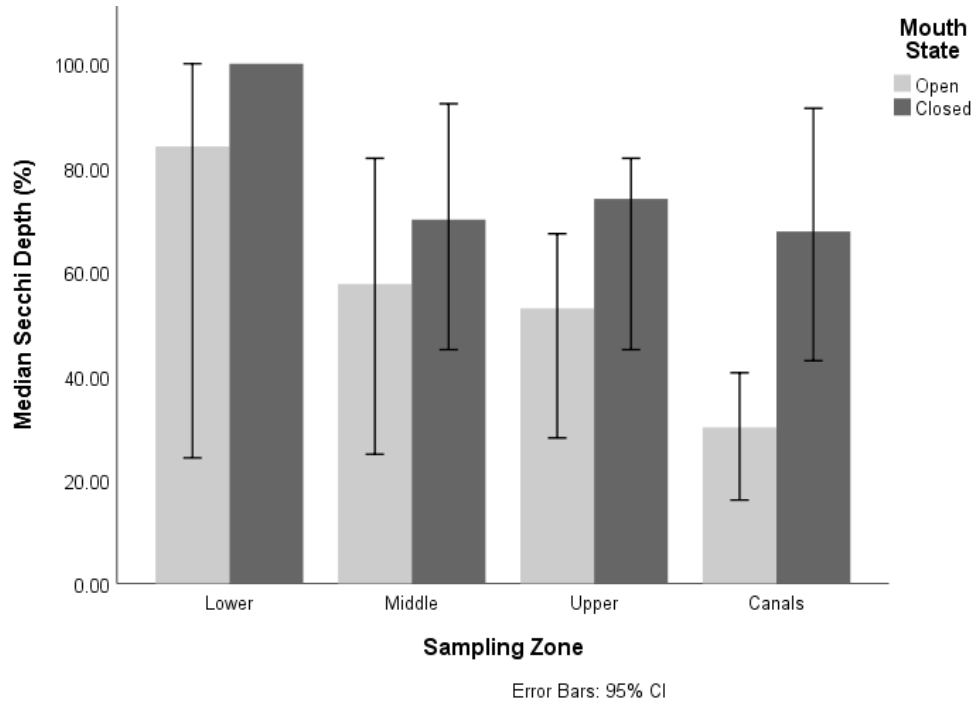
Figure 7: Median Secchi depth (%) across sampling zones including mouth state

Median depth was significantly higher (U= 688.50, Z= -11.06, $p<$ .001) at the canals (1.70 m) in comparison to the main body (1.15 m) (Figure 8, Table 3).
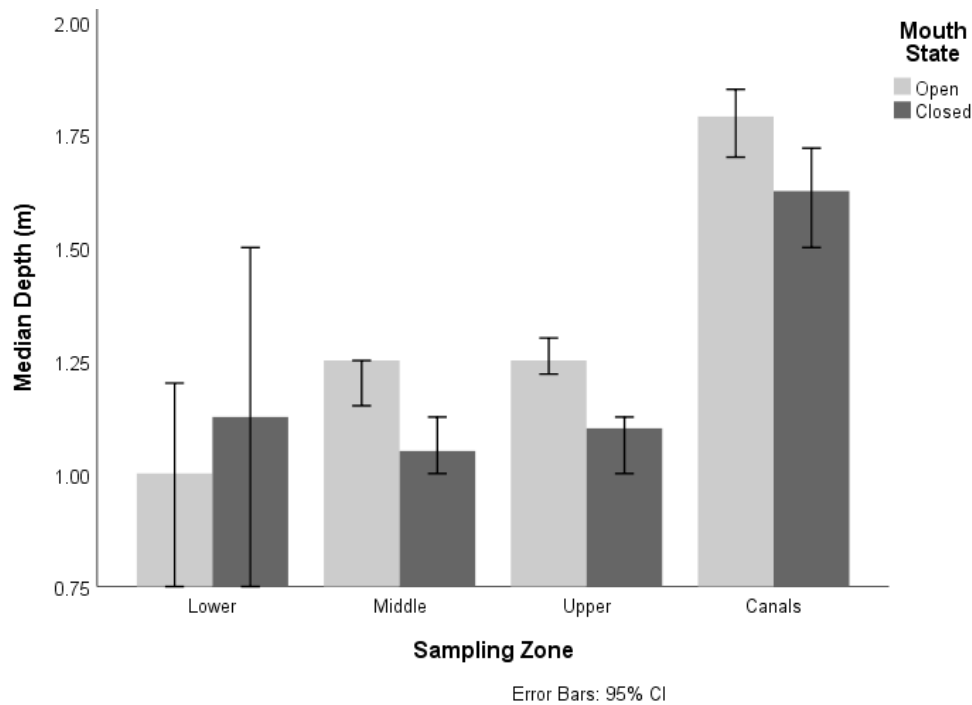
Figure 8: Median depth (m) across sampling zones including mouth state

Lower, middle and upper zone comparison: The main body was separated into lower, middle and upper zones. Median temperature increased from the lower zone (19.00 °C) through the middle zone (20.05 °C) to the upper zone (20.50 °C) (Figure 4, Table 3). The differences in temperature across zones were not significantly different (H(2)= 5.79, p= .055).

Median salinity decreased from the lower zone (20.43 ppt) through the middle zone (15.46 ppt) to the upper zone (14.56 ppt) (Figure 5, Table 3). The differences in salinity across zones were significantly different (H(2)= 41.52, $p<$ .001). Post hoc tests concluded that the upper zone did not differ significantly from the middle zone (H(2)= 1.79, p= .222) but did differ significantly from the lower zone (H(2)= 6.44, $p<$ .001). The middle zone was found to differ significantly from the lower zone (H(2)= 4.95, $p<$ .001).

Median pH increased from the lower zone (7.96) through the middle zone (8.37) to the upper zone (8.50) (Table 3). The differences in pH across zones were significantly different (H(2)= 29.22, $p<$ .001). Post hoc tests revealed that the lower zone differed significantly from the middle zone (H(2)= -3.47, p= .002) and upper zone (H(2)= -5.34, $p<$ .001). The middle zone differed significantly from the upper zone (H(2)= -2.40, p= .049).

Median dissolved oxygen increased from the lower zone (6.40 mg/L) through the middle zone (8.49 mg/L) to the upper zone (9.82 mg/L) (Figure 6, Table 3). The differences in dissolved oxygen across zones were significantly different (H(2)= 19.17, $p<$ .001). Post hoc tests found that the lower zone

differed significantly from the middle zone (H(2)= -2.71, p= .020) and upper zone (H(2)= -4.30, $p<$ .001). The middle zone showed no significant difference with the upper zone (H(2)= -2.06, p= .118).

Median Secchi depth decreased from the lower zone (100.00%) through the middle zone (63.28%) to the upper zone (58.33%) (Figure 7, Table 3). The differences in Secchi depth across zones were significantly different (H(2)= 13.36, p= .001). Post hoc tests concluded that the upper zone did not differ significantly from middle zone (H(2)= .66, p= 1.00) but did differ significantly from the lower zone (H(2)= 3.63, p= .001). The middle zone was significantly different from the lower zone (H(2)= 3.03, p= .007).

Median depth increased from the lower zone (1.05 m) through the middle zone (1.15 m) to the upper zone (1.20 m) (Figure 8, Table 3). The differences in depth across zones were not significantly different (H(2)= 3.86, p= .145).

4.2.2 Temporal variations

Descriptive statistics: Maximum temperature was highest for summer whilst minimum temperature was lowest for winter (Table 4). Maximum salinity was highest for spring and minimum salinity lowest for autumn (Table 4). Maximum pH was highest for autumn and minimum pH lowest for summer (Table 4). Maximum dissolved oxygen was highest for winter and minimum dissolved oxygen lowest for spring (Table 4). Maximum Secchi depth was equally highest for spring, summer and autumn whilst minimum Secchi depth was lowest for winter (Table 4). Maximum depth was highest for autumn and minimum depth lowest for spring (Table 4).

Median temperature was highest for summer and lowest for winter (Table 4). Median salinity was highest for autumn and lowest for winter (Table 4). Median pH was highest for winter and lowest for summer (Table 4). Median dissolved oxygen was highest for spring and lowest for autumn (Table 4). Median Secchi depth was highest for spring and lowest for winter (Table 4). Median depth was highest for winter and lowest for spring (Table 4).

Table 2: Descriptive statistics for physico- chemical parameters across sampling seasons

		Spring	Summer	Autumn	Winter
Temperature (°C)	N	161	91	180	91
	Minimum	15.20	20.30	14.20	11.80
	Maximum	25.90	27.30	26.60	18.90
	Median	21.10	22.40	19.90	14.70
	Mean	20.36	22.77	19.73	14.75
	Standard Deviation	2.62	1.41	2.29	1.47
Salinity (ppt)	N	161	91	180	91
	Minimum	0.24	0.26	0.23	0.24
	Maximum	34.38	23.22	31.92	29.20
	Median	12.72	14.96	18.08	11.19
	Mean	13.12	13.97	17.44	11.08

	Standard Deviation	5.49	4.94	5.07	4.19
pH	N	161	91	180	91
	Minimum	6.52	4.04	6.91	6.93
	Maximum	9.84	9.96	10.17	9.03
	Median	8.43	8.23	8.51	8.56
	Mean	8.47	8.27	8.52	8.38
	Standard Deviation	0.59	0.78	0.49	0.45
Dissolved Oxygen (mg/L)	N	161	91	180	91
	Minimum	0.28	1.97	.35	0.49
	Maximum	17.90	12.36	16.03	24.60
	Median	10.83	8.11	6.55	9.89
	Mean	10.59	8.15	6.64	10.30
	Standard Deviation	3.52	2.03	3.65	6.33
Secchi Depth (%)	N	74	41	84	42
	Minimum	30.06	23.33	12.23	9.00
	Maximum	100.00	100.00	100.00	92.00
	Median	77.16	77.14	44.73	19.62
	Mean	73.93	68.86	54.88	20.69
	Standard Deviation	20.50	28.16	29.50	12.67
Depth (m)	N	74	41	84	42
	Minimum	0.30	0.50	0.75	0.50
	Maximum	2.00	1.75	2.30	2.05
	Median	1.23	1.25	1.25	1.38
	Mean	1.27	1.21	1.32	1.46
	Standard Deviation	0.34	0.32	0.32	0.36

Season comparison: Median temperature was highest in summer (22.40 °C), lowest in winter (14.70 °C) and in between during spring (21.10 °C) and autumn (19.90 °C) (Figure 9, Table 4). The differences in temperature across seasons were significantly different ($H(3)= 270.72$, $p< .001$). Post hoc tests found that winter differed significantly from autumn ($H(3)= 10.42$, $p< .001$), spring ($H(3)= 12.05$, $p< .001$) and summer($H(3)= 16.05$, $p< .001$). Autumn did not differ significantly from spring ($H(3)= -2.21$, $p= .270$) but did differ significantly from summer ($H(3)= -8.08$, $p< .001$). Spring differed significantly from summer ($H(3)= -6.10$, $p< .001$).

Median salinity was highest in autumn (18.08 ppt), lowest in winter (11.19 ppt) and in-between during summer (14.96 ppt) and spring (12.72 ppt) (Figure 10, Table 4). The differences in salinity across seasons were significantly different ($H(3)= 213.26$, $p< .001$). Post hoc tests revealed that winter was significantly different from spring ($H(3)= 3.49$, $p= .005$), summer ($H(3)= 5.77$, $p< .001$) and autumn ($H(3)= 13.03$, $p< .001$). Spring was significantly different from summer ($H(3)= -3.04$, $p= .024$) and autumn ($H(3)= 11.24$, $p< .001$). Summer was significantly different from autumn ($H(3)= 6.38$, $p< .001$).
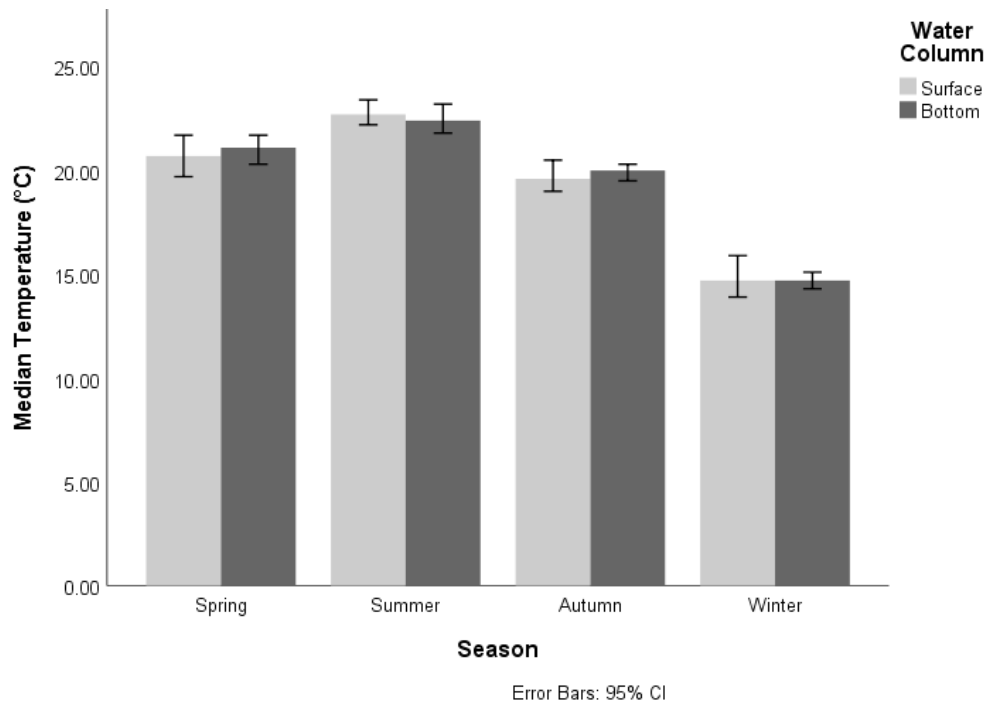
Figure 9: Median temperature (°C) across sampling seasons including surface/ bottom waters
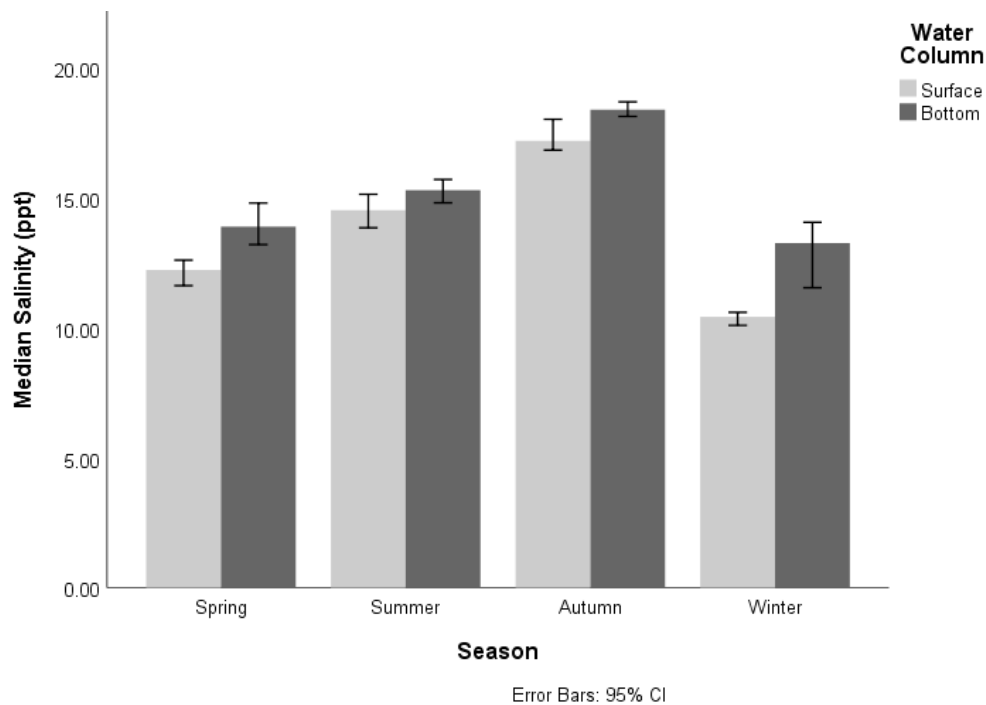
Figure 10: Median salinity (ppt) across sampling seasons including surface/ bottom waters

Median pH was highest in winter (8.56), lowest in summer (8.23) and in between during autumn (8.51) and spring (8.43) (Table 4). The differences in pH across seasons were significantly different ($H(3)= 21.66$, $p< .001$). Post hoc tests concluded that summer differed significantly from winter ($H(3)= -3.13$, $p= .018$), spring ($H(3)= 3.77$, $p= .002$) and autumn ($H(3)= 4.51$, $p< .001$). Winter did not

differ significantly from spring (*H*(3)= .23, *p*= 1.00) and autumn (*H*(3)= .91, *p*= 1.00). Spring did not differ significantly from autumn (*H*(3)= .80, *p*= 1.00).

Median dissolved oxygen was highest in spring (10.83 mg/L), lowest in autumn (6.55 mg/L) and in between during winter (9.89 mg/L) and summer (8.11 mg/L) (Figure 11, Table 4). The differences in dissolved oxygen across seasons were significantly different (*H*(3)= 93.85, *p*< .001). Post hoc tests found that autumn was not significantly different from summer (*H*(3)= -2.69, *p*= .071) but was significantly different from winter (*H*(3)= -5.39, *p*< .001) and spring (*H*(3)= -9.39, *p*< .001). Summer was not significantly different from winter (*H*(3)= -2.34, *p*= .195) but was significantly different from spring (*H*(3)= 5.13, *p*< .001). Winter was not significantly different from spring (*H*(3)= 2.49, *p*= .129).
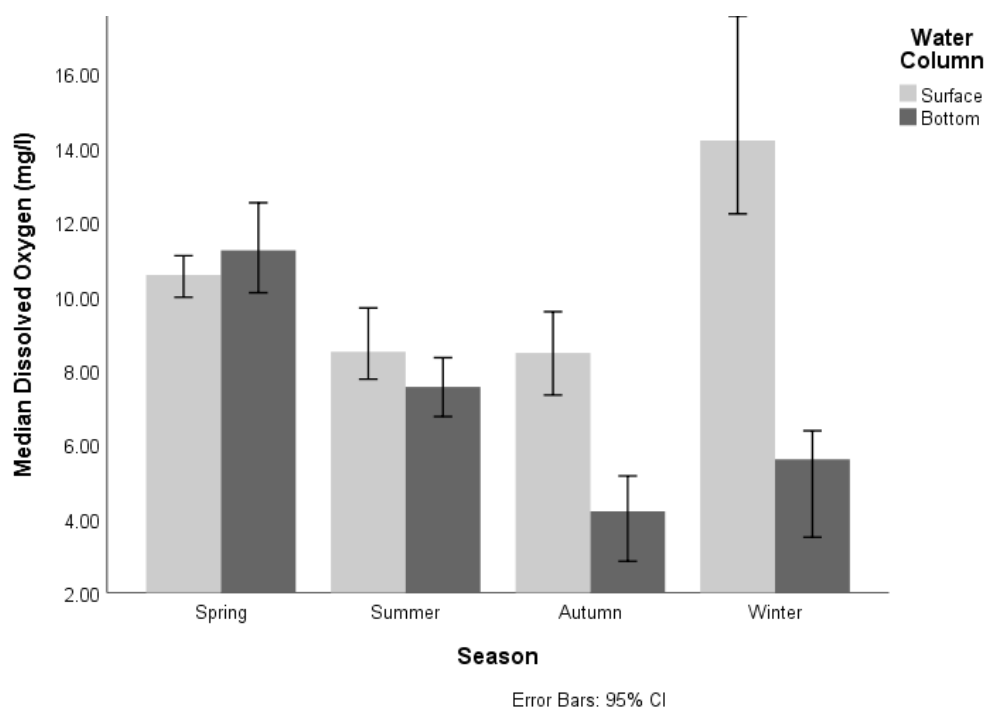
Figure 11: Median dissolved oxygen (mg/L) across sampling seasons including surface/ bottom waters

Median Secchi depth was highest in spring (77.16%), lowest in winter (19.62%) and in between in summer (77.14%) and autumn (44.73%) (Table 4). The differences in Secchi depth across seasons were significantly different (*H*(3)= 97.59, *p*< .001). Post hoc tests revealed that winter differed significantly from autumn (*H*(3)= 6.51, *p*< .001), summer (*H*(3)= 7.72, *p*< .001) and spring (*H*(3)= 9.42, *p*< .001). Autumn did not differ significantly from summer (*H*(3)= -2.43, *p*= .149) but did differ significantly from spring (*H*(3)= -3.70, *p*= .002). Summer did not differ significantly from spring (*H*(3)= .65, *p*= 1.00).

Median depth was highest in winter (1.38 m), lowest in spring (1.23 m) and in between during autumn (1.25 m) and summer (1.25 m) (Table 4). The differences in depth across seasons were significantly different (*H*(3)= 13.90, *p*= .003). Post hoc tests concluded that summer was not significantly different from spring (*H*(3)= .80, *p*= 1.00) and autumn (*H*(3)= 1.32, *p*= 1.00) but was significantly different from winter (*H*(3)= -3.44, *p*= .006). Spring was not significantly different from

autumn (*H*(3)= .60, *p*= 1.00) but was significantly different from winter (*H*(3)= -3.11, *p*= .019). Autumn was not significantly different from winter (*H*(3)= -2.67, *p*= .075).

4.3 Nutrient characteristics

Descriptive Statistics: A total of 141 measurements were taken for nitrate + nitrite, nitrite and phosphate with 117 measurements taken for nitrate (Table 5). Nitrate + nitrite displayed a maximum of 144.61 µM, nitrite 14.10 µM, nitrate 142.17 µM and phosphate 20.89 µM with maximum values being recorded during the open mouth state (Table 5). Minimum values for nutrient parameters studied were consistently low (Table 5). Median nitrate + nitrite was 1.58 µM, nitrite 0.65 µM, nitrate 1.12 µM and phosphate 2.58 µM (Table 5). Mean nitrate + nitrite was 11.85 µM (SD= 28.07), nitrite 1.00 µM (SD= 1.39), nitrate 13.26 µM (SD= 29.67) and phosphate 3.37 µM (SD= 3.14) (Table 5).

Table 5: Descriptive statistics for nutrient parameters

	Nitrate + Nitrite (µM)	Nitrite (µM)	Nitrate (µM)	Phosphate (µM)
N	141	141	117	141
Minimum	0.00	0.30	0.01	0.36
Maximum	144.61	14.10	142.17	20.89
Median	1.58	0.65	1.12	2.58
Mean	11.85	1.00	13.26	3.37
Standard Deviation	28.07	1.39	29.67	3.14

Mouth State comparison: Median nitrate + nitrite was 1.64 µM during open mouth state and 1.43 µM during closed mouth state, nitrite 0.75 µM and 0.59 µM respectively and nitrate 1.20 µM and 1.00 µM respectively. Nitrite (*U*= 1928, *Z*= -2.09, *p*= .036) was significantly higher during open mouth state in comparison to closed mouth state whilst nitrate + nitrite (*U*= 2287, *Z*= -.60, *p*= .551) and nitrate (*U*= 1409, *Z*= -1.57, *p*= .116) were not significantly higher. Median phosphate was 2.51 µM during open mouth state and 2.61 µM during closed mouth state with the differences between mouth state showing no significant difference (*U*= 2159, *Z*= -1.13, *p*= .258).

4.3.1 Spatial variations

Descriptive statistics: Maximum values for all nutrient parameters sampled were highest at the influent rivers with minimum values being similar across the main body, canals and influent rivers (Table 6). Median nitrate + nitrite, nitrate and phosphate were highest at the influent rivers and lowest at the canals (Table 6). Median nitrite increased from the main body, through the canals to the influent rivers (Table 6).

Table 6: Descriptive statistics for nutrient parameters across sampling zones

		Main Body	Canals	Influent Rivers
Nitrate + Nitrite (µM)	N	72	33	36
	Minimum	0.06	0.00	0.00
	Maximum	98.43	27.15	144.61
	Median	1.57	1.14	17.14
	Mean	3.39	2.26	37.56
	Standard Deviation	11.57	4.76	44.10
Nitrite (µM)	N	72	33	36
	Minimum	0.32	0.30	0.30
	Maximum	2.09	1.54	14.10
	Median	0.60	0.70	1.11
	Mean	0.69	0.71	1.88
	Standard Deviation	0.32	0.32	2.52
Nitrate (µM)	N	63	24	30
	Minimum	0.01	0.01	0.13
	Maximum	97.52	26.54	142.17
	Median	0.98	0.76	29.01
	Mean	3.13	2.23	43.33
	Standard Deviation	12.26	5.43	43.80
Phosphate (µM)	N	72	33	36
	Minimum	0.43	0.36	0.93
	Maximum	9.73	7.40	20.89
	Median	2.88	1.67	3.23
	Mean	2.98	2.01	5.39
	Standard Deviation	1.91	1.50	4.87

Main body, canals and influent rivers comparison: The lower, middle and upper zones were grouped together as the main body. Median nitrate + nitrite was highest at the influent rivers (17.14 µM), lowest at the canals (1.14 µM) and in between at the main body (1.57 µM) (Figure 12, Table 6). The differences in nitrate + nitrite across zones were significantly different ($H(2)= 18.59$, $p< .001$). Post hoc tests concluded that the influent rivers differed significantly from the canals ($H(2)= -4.17$, $p< .001$) and main body ($H(2)= 3.27$, $p= .006$). The main body was not significantly different from the canals ($H(2)= -1.60$, $p= .654$).

Median nitrite was highest at the influent rivers (1.11 µM), lowest at the main body (0.60 µM) and in between at the canals (0.70 µM) (Figure 13, Table 6). The differences in nitrite across zones were significantly different ($H(2)= 7.40$, $p= .025$). Post hoc tests found that the influent rivers showed no significant difference with the main body ($H(2)= 2.61$, $p= .054$) or canals ($H(2)= -2.1$, $p= .214$). The main body was not significantly different from the canals ($H(2)= .13$, $p= 1.00$).
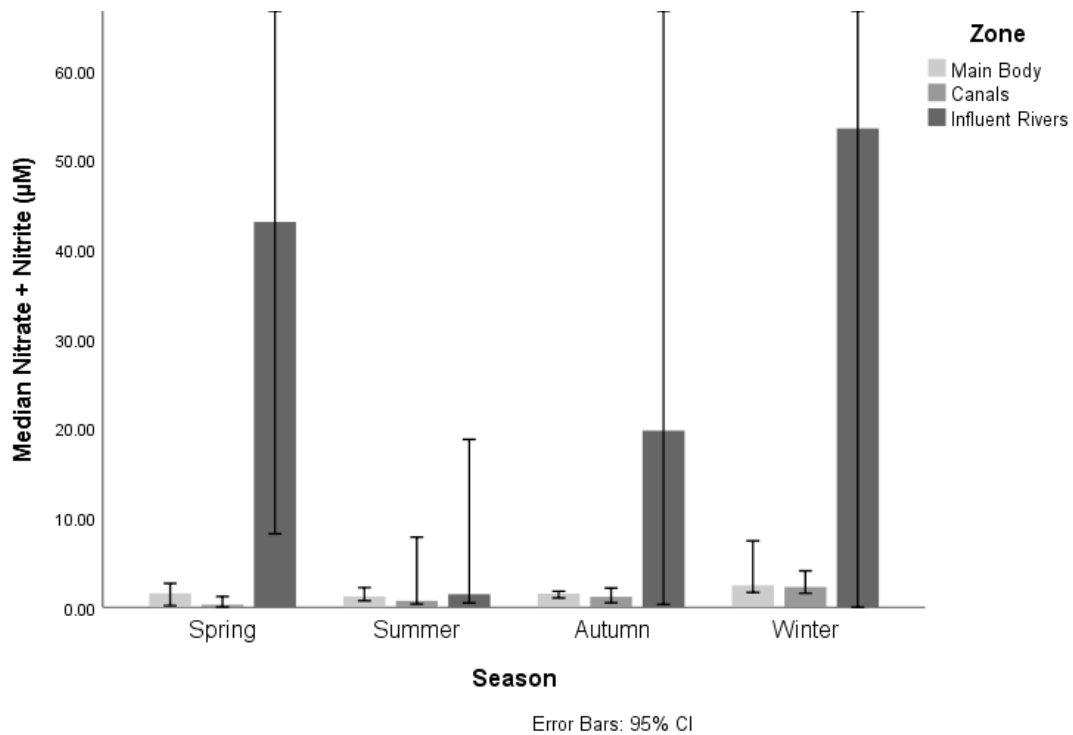
Figure 12: Median nitrate + nitrite (µM) across sampling zones including season
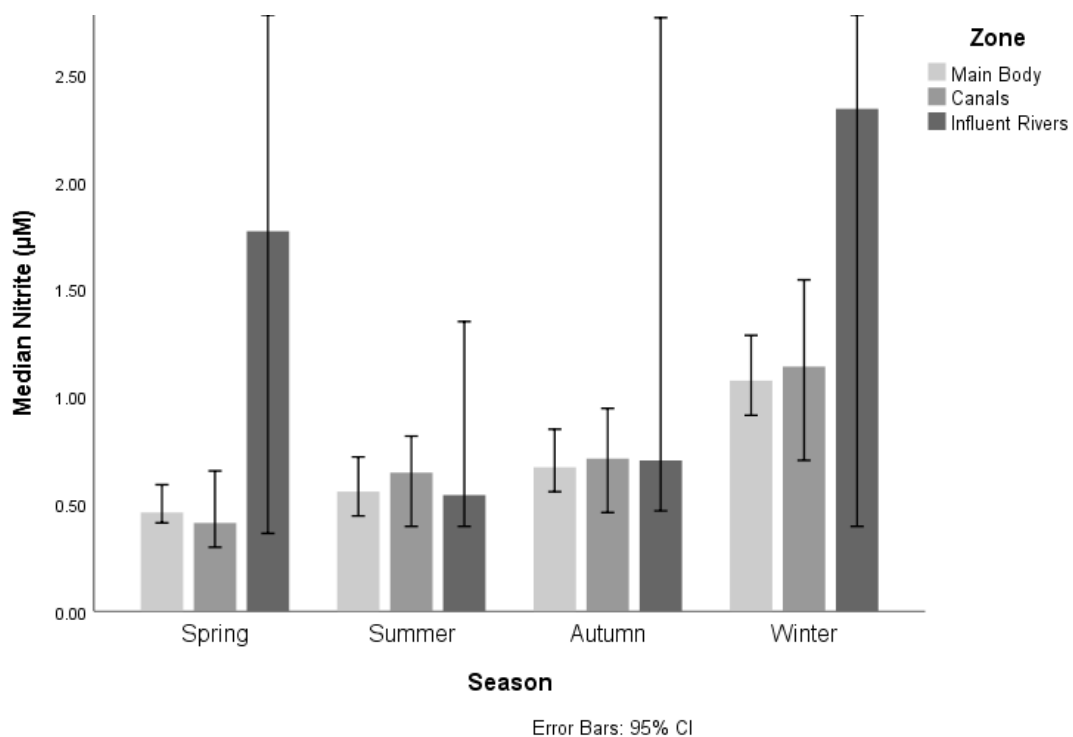
Figure 13: Median nitrite (µM) across sampling zones including season

Median nitrate was highest at the influent rivers (29.01 µM), lowest at the canals (0.76 µM) and in between at the main body (0.98 µM) (Figure 14, Table 6). The differences in nitrate across zones were significantly different ($H(2)= 32.02$, $p< .001$). Post hoc tests revealed that the influent rivers differed significantly from the canals ($H(2)= -4.99$, $p< .001$) and main body ($H(2)= 4.97$, $p< .001$). The main body was not significantly different from the canals ($H(2)= -1.11$, $p= 1.00$).
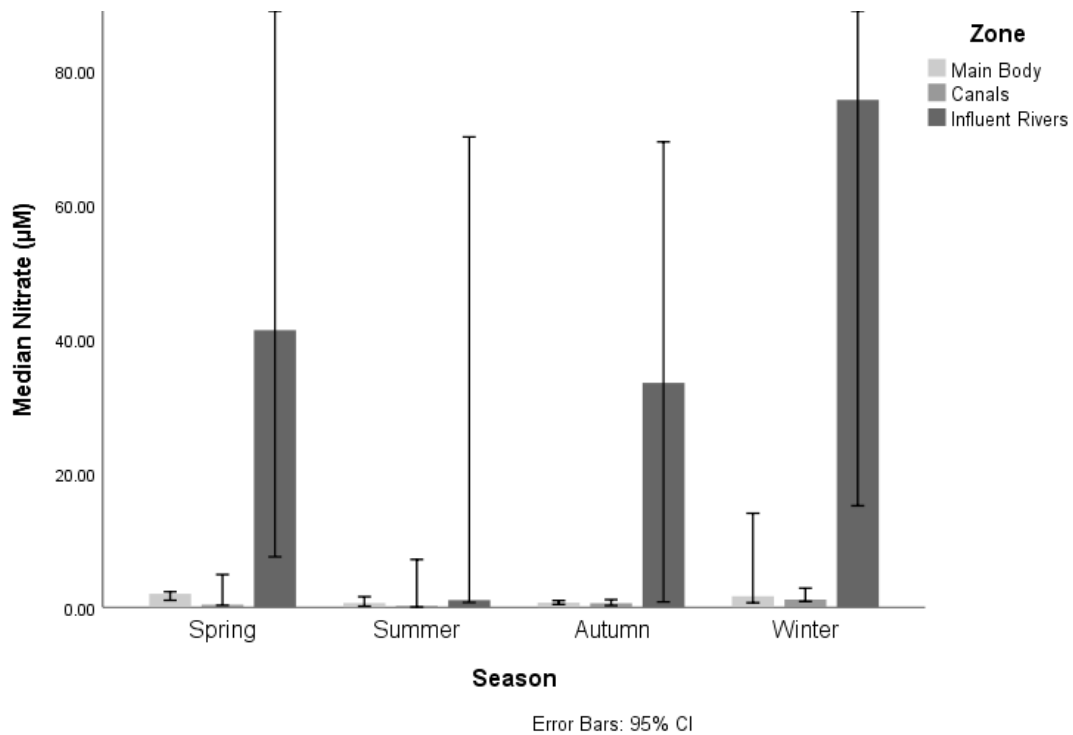
Figure 14: Median nitrate (µM) across sampling zones including season

Median phosphate was highest at the influent rivers (3.23 µM), lowest at the canals (1.67 µM) and in between at the main body (2.88 µM) (Figure 15, Table 6). The differences in phosphate across zones were significantly different ($H(2)= 17.14$, $p< .001$). Post hoc tests found that the influent rivers differed significantly from the canals ($H(2)= -4.14$, $p< .001$). The main body was not significantly different from the canals ($H(2)= -2.60$, $p= .056$) or influent rivers ($H(2)= 2.21$, $p= .163$).
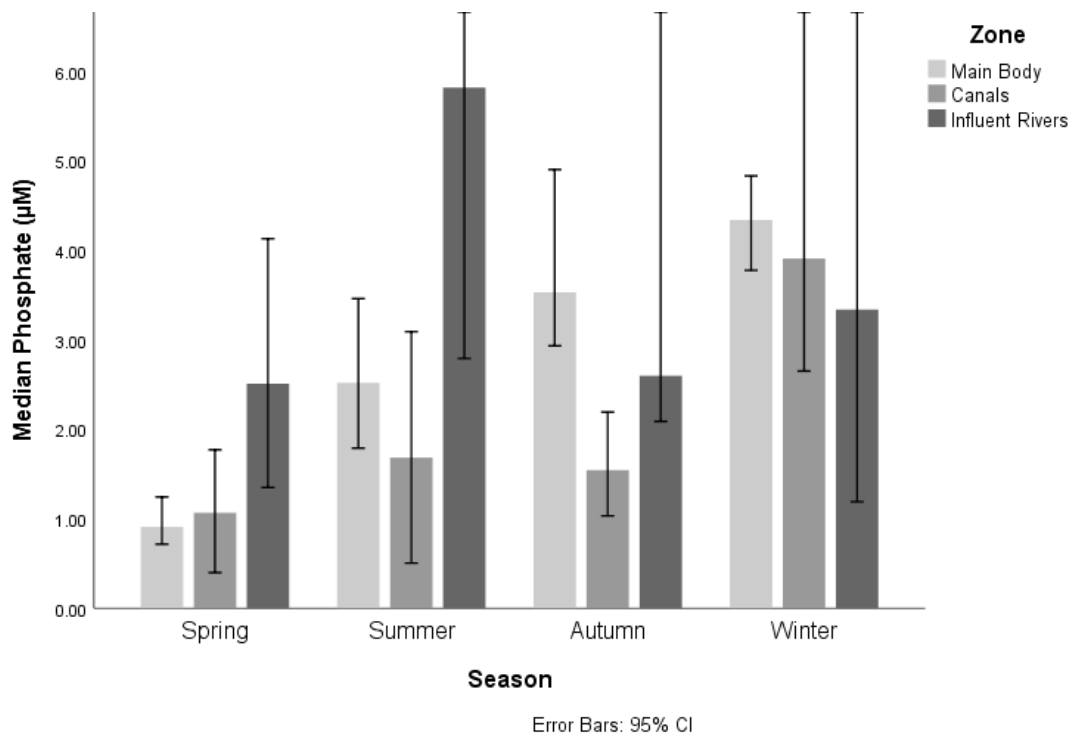
Figure 15: Median phosphate (µM) across sampling zones including season

Influent river comparison: Median nitrate + nitrite was highest at the Westlake River (56.14 µM), lowest at the Keysers River (4.21 µM) and in between at the Sand River (49.39 µM) (Figure 16). The differences in nitrate + nitrite across influent rivers were significantly different ($H(2)=6.02$, $p=.049$). Post hoc tests revealed that the Keysers River did not differ significantly from the Sand River ($H(2)=-1.77$, $p=.457$) or Westlake River ($H(2)=-2.35$, $p=.111$). The Sand River did not differ significantly from the Westlake River ($H(2)=-.58$, $p=1.00$).

Median nitrite was highest at the Sand River (2.83 µM), lowest at the Keysers River (0.50 µM) and in between at the Westlake River (1.68 µM) (Figure 16). The differences in nitrite across influent rivers were significantly different ($H(2)=12.31$, $p=.002$). Post hoc tests discovered that the Keysers River differed significantly from the Sand River ($H(2)=-3.51$, $p=.003$). The Westlake River did not differ significantly from the Keysers River ($H(2)=-1.73$, $p=.507$) or Sand River ($H(2)=1.78$, $p=.448$).

Median nitrate was highest at the Westlake River (71.11 µM), lowest at the Keysers River (6.93 µM) and in between at the Sand River (64.52 µM) (Figure 16). The differences in nitrate across influent rivers were significantly different ($H(2)=10.1$, $p=.006$). Post hoc tests found that the Keysers River differed significantly from the Westlake River ($H(2)=-3.1$, $p=.012$). The Sand River did not differ significantly from the Keysers River ($H(2)=-2.16$, $p=.185$) or the Westlake River ($H(2)=-.94$, $p=1.00$).

Median phosphate was highest at the Sand River (4.32 µM), lowest at the Westlake River (2.42 µM) and in between at the Keysers River (3.46 µM) (Figure 16). The differences in phosphate across influent rivers were not significantly different ($H(2)=2.38$, $p=.304$).
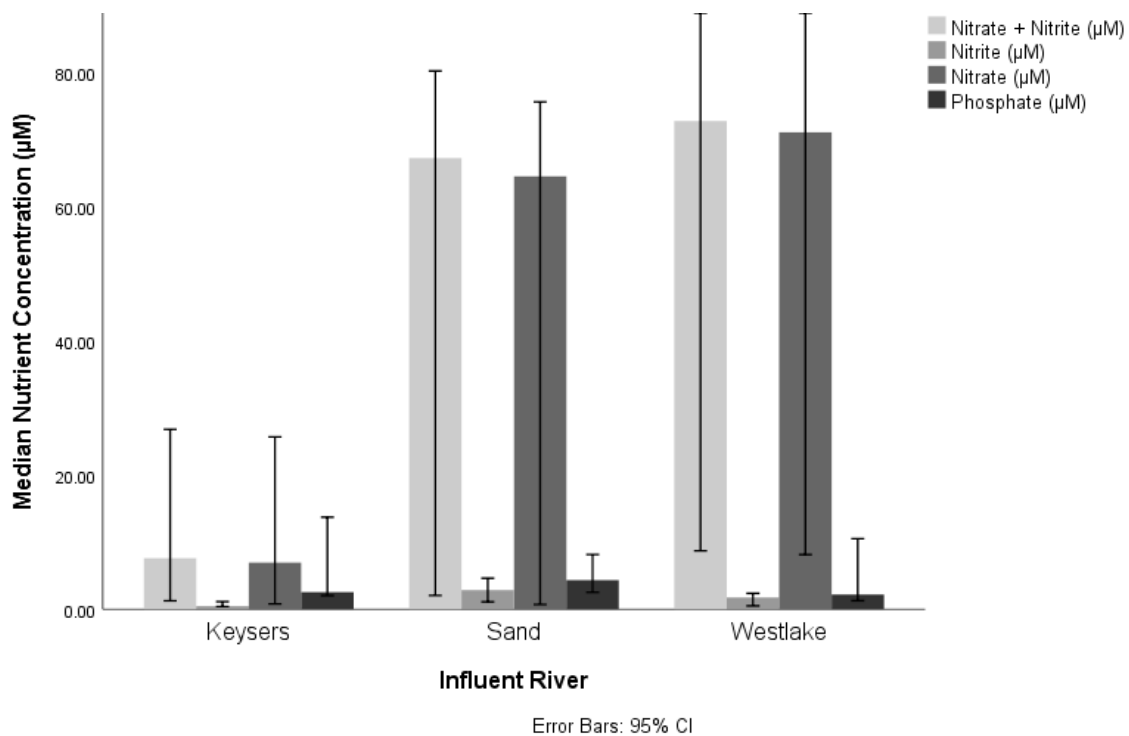
Figure 16: Nutrient parameters (median values- µM) across influent rivers

Descriptive statistics: Maximum nitrate + nitrite, nitrite, nitrate and phosphate were highest during winter (Table 7). Minimum values for nutrient parameters studied were comparable across seasons (Table 7). Median nitrate + nitrite, nitrite and phosphate were highest during winter whilst median nitrate was highest during spring (Table 7). Median nitrate + nitrite and nitrate were lowest during summer whilst median nitrite and phosphate were lowest during spring (Table 7).

Table 7: Descriptive statistics for nutrient parameters across sampling seasons

		Spring	Summer	Autumn	Winter
Nitrate + Nitrite (µM)	N	42	27	48	24
	Minimum	0.00	0.00	0.08	0.00
	Maximum	128.44	72.06	76.37	144.61
	Median	1.55	1.34	1.42	2.74
	Mean	12.58	5.00	9.20	23.57
	Standard Deviation	29.56	13.94	20.17	44.41
Nitrite (µM)	N	42	27	48	24
	Minimum	0.30	0.30	0.35	0.39
	Maximum	6.45	1.95	3.93	14.10
	Median	0.47	0.56	0.69	1.14
	Mean	0.85	0.65	0.88	1.90
	Standard Deviation	1.09	0.35	0.69	2.73
Nitrate (µM)	N	29	24	42	22
	Minimum	0.27	0.01	0.01	0.57
	Maximum	126.09	70.11	74.71	142.17
	Median	2.20	0.82	0.83	1.77
	Mean	17.12	4.91	9.56	24.33
	Standard Deviation	33.34	14.42	20.74	45.37
Phosphate (µM)	N	42	27	48	24
	Minimum	0.36	0.50	0.64	1.19
	Maximum	9.73	17.09	13.71	20.89
	Median	0.96	2.79	2.92	4.31
	Mean	1.63	4.04	3.74	4.92
	Standard Deviation	1.61	3.69	2.83	3.84

Season comparison: Median nitrate + nitrite was highest during winter (2.74 µM), lowest during summer (1.34 µM) and in between during spring (1.55 µM) and autumn (1.42 µM) (Figure 12, Table 7). The differences in nitrate + nitrite across seasons were significantly different ($H(3)= 10.68$, $p= .014$). Post hoc tests found that summer differed significantly from winter ($H(3)= -2.99$, $p= .028$) but did not differ significantly from spring ($H(3)= .65$, $p= 1.00$) or autumn ($H(3)= .69$, $p= 1.00$). Spring did

not differ significantly from autumn (H(3)= .032, p= 1.00) or winter (H(3)= -2.65, p= .08). Autumn did not differ significantly from winter (H(3)= -2.69, p= .072).

Median nitrite was highest during winter (1.14 µM), lowest during spring (0.47 µM) and in between during autumn (0.69 µM) and summer (0.56 µM) (Figure 13, Table 7). The differences in nitrite across seasons were significantly different (H(3)= 32.20, p< .001). Post hoc tests revealed that spring differed significantly from winter (H(3)= -5.36, p< .001) but did not differ significantly from summer (H(3)= -.47, p= 1.00) or autumn (H(3)= 2.51, p= .12). Summer differed significantly from winter (H(3)= -4.48, p< .001) but not from autumn (H(3)= 1.73, p= .835). Autumn differed significantly from winter (H(3)= -3.36, p= .008).

Median nitrate was highest during spring (2.20 µM), lowest during summer (0.82 µM) and in between during winter (1.77 µM) and autumn (0.83 µM) (Figure 14, Table 7). The differences in nitrate across seasons were significantly different (H(3)= 15.95, p= .001). Post hoc tests concluded that summer differed significantly from spring (H(3)= 2.90, p= .037) and winter (H(3)= -3.02, p= .025) but not from autumn (H(3)= .67, p= 1.00). Autumn did not differ significantly from spring (H(3)= -2.61, p= .091) or winter (H(3)= -2.74, p= .061). Spring did not differ significantly from winter (H(3)= -.325, p= 1.00).

Median phosphate was highest during winter (4.31 µM), lowest during spring (0.96 µM) and in between during autumn (2.92 µM) and summer (2.79 µM) (Figure 15, Table 7). The differences in phosphate across seasons were significantly different (H(3)= 45.26, p< .001). Post hoc tests discovered that spring differed significantly from summer (H(3)= -4.19, p< .001), autumn (H(3)= 5.02, p< .001) and winter (H(3)= -6.08, p< .001). Summer did not differ significantly from autumn (H(3)= .11, p= 1.00) or winter (H(3)= -1.86, p= .628). Autumn did not differ significantly from winter (H(3)= -1.98, p= .477).

4.4 Sediment characteristics

Descriptive statistics: For each of the seven sediment size classes 14 measurements (one from each sampling station) were taken of percentage sediment retained (hereon referred to as sediment retained) (Table 8). Sediment retained was lowest for the 1700 µm size class and highest for the 125 µm size class across all descriptive statistics reported (Table 8). Minimum sediment retained was 0.002% for the 1700 µm size class and maximum sediment retained was 69.99% for the 125 µm size class (Table 8). Median sediment retained was 0.22% for the 1700 µm size class, 1.59% for the 1180 µm size class, 11.13% for the 500 µm size class, 33.19% for the 250 µm size class, 39.71% for the 125 µm size class, 8.81% for the 63 µm size class and 1.83% for the <63 µm size class (Figure 17, Table 8). Mean sediment retained was 0.37% (SD= 0.45) for the 1700 µm size class and 41.80% (SD= 13.59) for the 125 µm size class (Table 8).
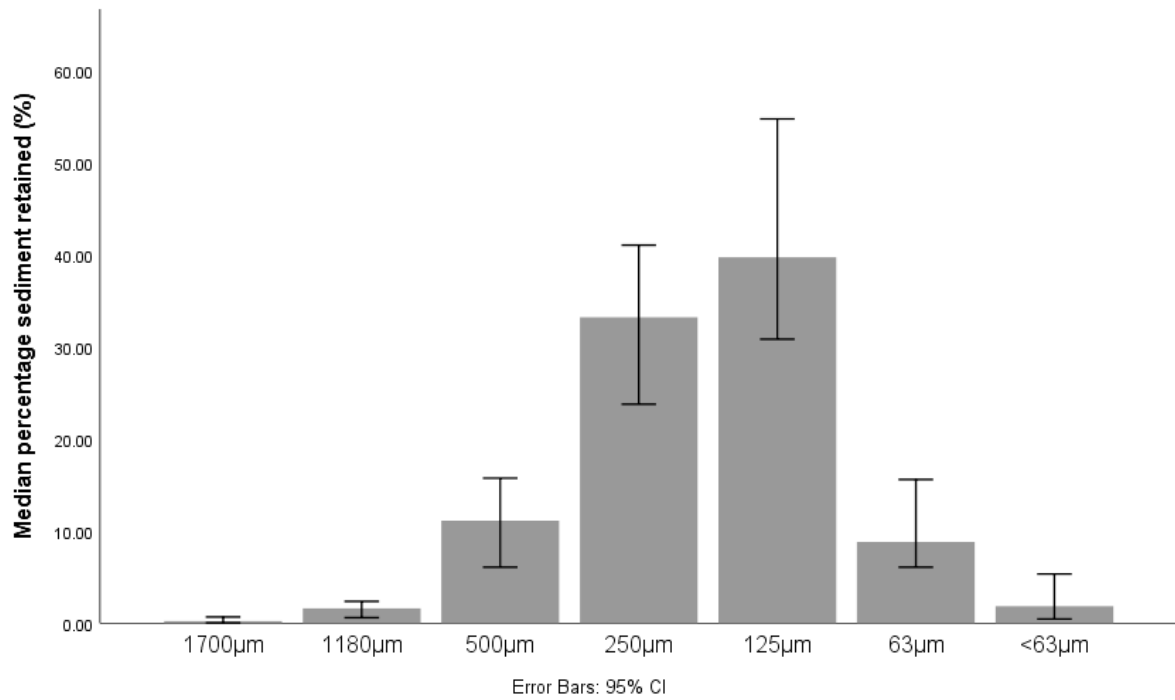
Figure 17: Median percentage sediment retained (%) across size classes

Table 8: Descriptive statistics for percentage sediment retained (%) across size classes

	1700 μm (%)	1180 μm (%)	500 μm (%)	250 μm (%)	125 μm (%)	63 μm (%)	<63 μm (%)
N	14	14	14	14	14	14	14
Minimum	0.002	.03	4.13	14.24	17.86	3.48	0.06
Maximum	1.28	9.60	30.03	45.12	69.99	17.13	7.38
Median	0.22	1.59	11.13	33.19	39.71	8.81	1.83
Mean	0.37	2.01	11.71	31.54	41.80	10.13	2.45
Standard Deviation	0.45	2.39	6.96	9.42	13.59	4.32	2.34

4.4.1 Spatial variations

Descriptive statistics across size classes: Median sediment retained at the lower zone was highest for the 125 μm size class and lowest for the <63 μm size class (Figure 18, Table 9). At the middle zone median sediment retained was highest for the 250 μm size class and lowest for the 1700 μm size class (Figure 18, Table 9). Median sediment retained at the upper zone was highest for the 125 μm size class and lowest for the 1700 μm size class (Figure 18, Table 9).

Descriptive statistics across zones: Median sediment retained was found to be highest at the lower zone and lowest at the middle zone for both the 1700 μm and 125 μm size classes (Figure 18, Table 9). For the 1180 μm and 500 μm size classes median sediment retained was highest at the lower zone and lowest at the upper zone (Figure 18, Table 9). The highest median sediment retained was

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measured at the middle zone and the lowest at the lower zone for the 250 μm size class (Figure 18, Table 9). For the 63 μm size class the upper zone had the highest median sediment retained and the middle zone the lowest (Figure 18, Table 9). For the <63 μm size class the upper zone had the highest median sediment retained and the lower zone the lowest (Figure 18, Table 9).

Table 9: Descriptive statistics for percentage sediment retained (%) across size classes and sampling zones

		Lower	Middle	Upper
1700 μm (%)	N	2	5	7
	Minimum	0.08	0.00	0.03
	Maximum	1.28	.33	1.28
	Median	0.68	0.03	0.43
	Mean	0.68	0.10	0.48
	Standard Deviation	0.85	0.14	0.44
1180 μm (%)	N	2	5	7
	Minimum	0.59	0.03	0.66
	Maximum	9.60	2.36	3.80
	Median	5.10	1.74	1.52
	Mean	5.10	1.21	1.69
	Standard Deviation	6.37	1.06	1.01
500 μm (%)	N	2	5	7
	Minimum	4.13	10.15	4.40
	Maximum	30.03	19.54	13.48
	Median	17.08	13.79	6.57
	Mean	17.08	14.33	8.30
	Standard Deviation	18.31	3.55	3.42
250 μm (%)	N	2	5	7
	Minimum	16.27	35.49	14.24
	Maximum	31.91	44.21	45.12
	Median	24.09	36.99	26.82
	Mean	24.09	38.70	28.55
	Standard Deviation	11.06	3.79	9.52
125 μm (%)	N	2	5	7
	Minimum	17.86	29.91	35.75
	Maximum	69.99	47.54	59.02
	Median	43.93	31.31	41.86
	Mean	43.93	36.04	45.30
	Standard Deviation	36.86	7.75	9.48
63 μm (%)	N	2	5	7
	Minimum	8.10	3.48	5.46
	Maximum	8.87	10.85	17.13

	Median	8.49	8.48	15.35
	Mean	8.49	8.12	12.03
	Standard Deviation	0.54	3.05	5.06
<63 µm (%)	N	2	5	7
	Minimum	0.06	0.45	0.32
	Maximum	1.22	2.67	7.38
	Median	0.64	1.08	2.95
	Mean	0.64	1.50	3.64
	Standard Deviation	0.82	1.05	2.75

For each of the sediment size classes there was no significant difference in sediment retained across the lower, middle and upper zones. The 1700 µm size class had a significance of (H(2)= 3.76, p= .153) across zones, 1180 µm (H(2)= .27, p= .873), 500 µm (H(2)= 4.12, p= .128), 250 µm (H(2)= 5.61, p= .061), 125 µm (H(2)= 2.16, p= .34), 63 µm (H(2)= 1.49, p= .474), and the <63 µm size class (H(2)= 3.02, p= .221).

When sediment retained was compared across each zone for each size class only the middle and upper zones differed significantly from each other for the 250 µm (U= 5.00, Z= -2.03, p= .042) and 500 µm (U= 3.00, Z= -2.36, p= .019) size classes.
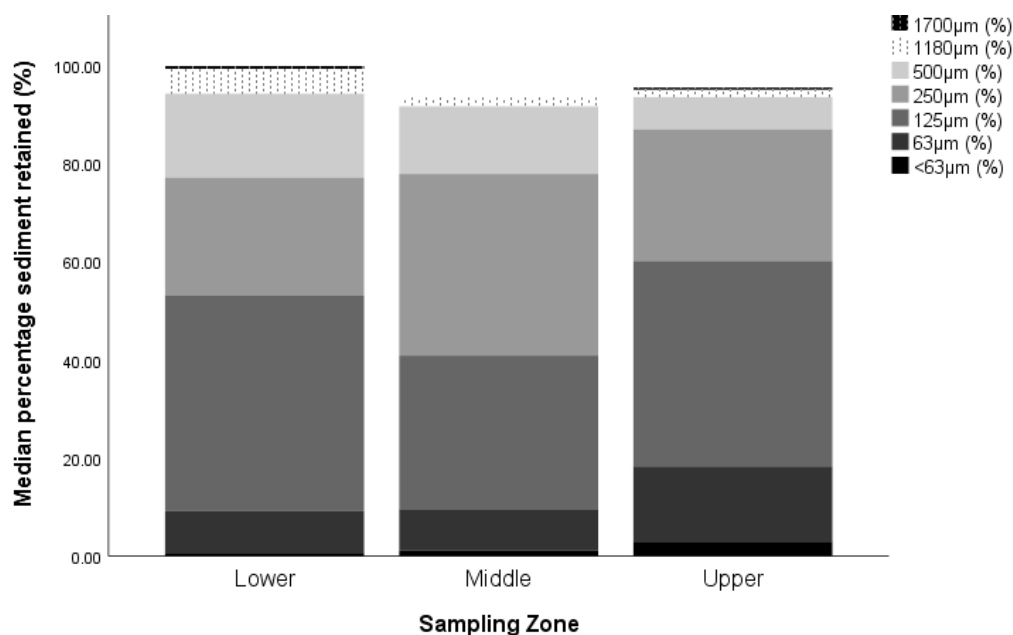
Figure 18: Median percentage sediment retained (%) across size classes and sampling zones

4.5 *Stuckenia pectinata* biomass and distribution characteristics

Descriptive statistics: A total of 243 samples were taken to be analysed for wet mass and dry mass. Of the 243 samples 209 were analysed for tuber density (Table 10). *S. pectinata* biomass was present in 62% of samples and *S. pectinata* tubers present in 37% of samples. Maximum wet mass was 2790.76 g/m^2, dry mass 377.57 g/m^2 and tuber density 1204 N/m^2 (Table 10). All three parameters displayed minimum values of zero (Table 10). Median wet mass was 17.56 g/m^2, dry mass 1.14 g/m^2 and tuber density 0 N/m^2 (Table 10). Mean wet mass was 149.75 g/m^2 (SD= 370.85), dry mass 17.69 g/m^2 (SD= 47.54) and tuber density 80 N/m^2 (SD= 196.79) (Table 10).

Table 10: Descriptive statistics for biomass parameters

	Wet mass (g/m²)	Dry mass (g/m²)	Tuber density (N/m²)
N	243	243	209
Minimum	0.00	0.00	0
Maximum	2790.76	377.57	1204
Median	17.56	1.14	0
Mean	149.75	17.69	80
Standard Deviation	370.85	47.54	197

Above/ below ground biomass: Samples containing both above and below ground biomass of *S. pectinata* had predominantly higher median/ mean wet mass and dry mass values as well as higher tuber densities in comparison to samples containing only above or only below ground biomass (Figure 19).

For wet mass, samples containing only below ground biomass did not differ significantly from samples containing only above ground biomass ($H(2)$= .01, p= 1.00) or samples containing both above and below ground biomass ($H(2)$= 1.99, p= .28). The wet mass of samples containing only above ground biomass differed significantly from samples containing both above and below ground biomass ($H(2)$= -3.11, p= .011). In terms of dry mass, samples containing only below ground biomass did not differ significantly from samples containing only above ground biomass ($H(2)$= -.76, p= 1.00) or from samples containing both above and below ground biomass ($H(2)$= 1.21, p= 1.00). The dry mass of samples containing only above ground biomass differed significantly from samples containing both above and below ground biomass ($H(2)$= -3.22, p= .008). For tuber density, samples containing only below ground biomass differed significantly from samples containing only above ground biomass ($H(2)$= -3.76, p= .001) but did not differ significantly from samples containing both above and below ground biomass ($H(2)$= -.23, p= 1.00). The tuber density of samples containing only above ground biomass differed significantly from samples containing both above and below ground biomass ($H(2)$= -6.46, p< .001).
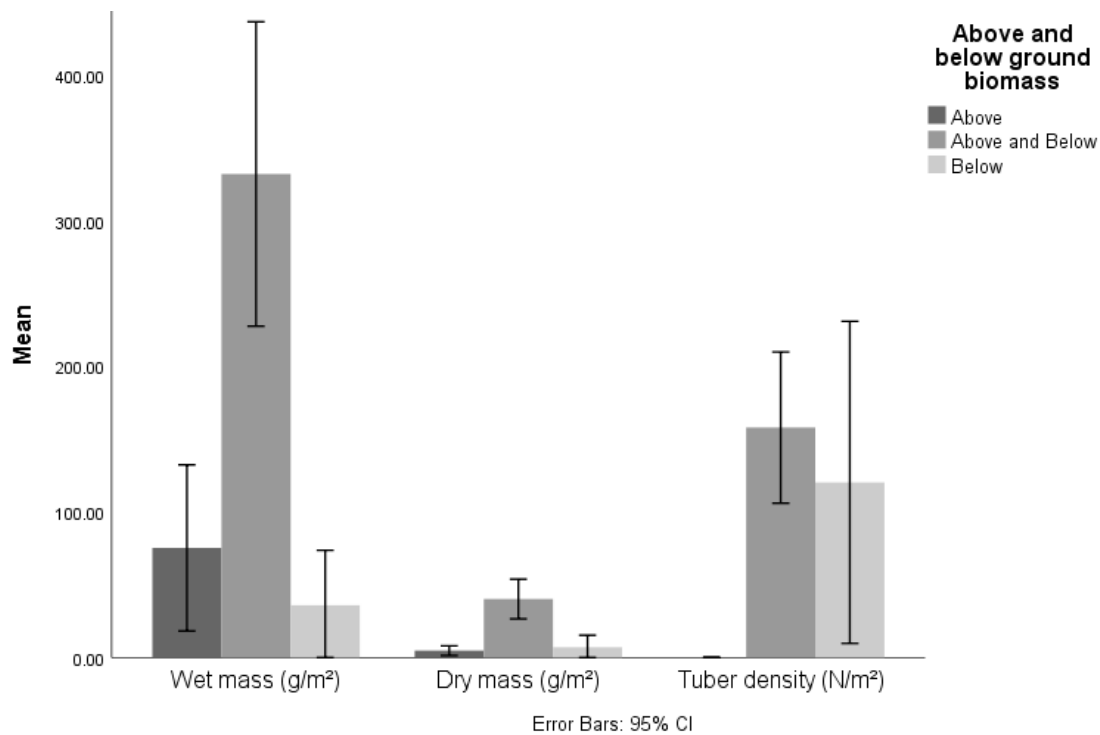
Figure 19: Above and below ground biomass comparison across mean wet mass (g/m^2), dry mass (g/m^2) and tuber density (N/m^2)

4.5.1 Spatial variations

Descriptive statistics: Percentage frequency of occurrence for wet mass and dry mass was similar between the canals (64%) and main body (61%). Percentage frequency of occurrence for wet mass and dry mass increased from the lower zone (0%), through the middle zone (57%) to the upper zone (82%). Percentage frequency of occurrence for tuber density was higher at the main body (42%) in comparison to the canals (28%). Percentage frequency of occurrence for tuber density increased from the lower zone (0%), through the middle zone (40%) to the upper zone (56%).

Maximum wet mass and dry mass increased from the lower zone, through the middle zone to the upper zone and increased further into the canals (Table 11). Mean wet mass increased from the lower zone, through the middle zone to the upper zone and increased further into the canals (Table 11). Maximum and mean tuber density decreased from the middle zone to the upper zone and decreased further into the canals (Table 11).

Table 11: Descriptive statistics for biomass parameters across sampling zones

		Lower	Middle	Upper	Canals
Wet mass (g/m²)	N	24	60	84	75
	Minimum	0.00	0.00	0.00	0.00
	Maximum	0.00	2042.58	2711.04	2790.76
	Median	0.00	8.95	34.28	19.87
	Mean	0.00	148.73	167.12	179.05
	Standard Deviation	0.00	333.63	364.05	451.53
Dry mass (g/m²)	N	24	60	84	75
	Minimum	0.00	0.00	0.00	0.00
	Maximum	0.00	174.12	261.51	377.57
	Median	0.00	1.01	2.05	0.85
	Mean	0.00	20.15	17.71	21.37
	Standard Deviation	0.00	43.09	38.60	64.18
Tuber density (N/m²)	N	20	50	70	69
	Minimum	0	0	0	0
	Maximum	0	1204	982	370
	Median	0	0	19	0
	Mean	0	122	121	30
	Standard Deviation	0	265	232	76

Main body and canals comparison: The lower, middle and upper zones were grouped together as the main body. Mean wet mass was 179.05 g/m² at the canals and 136.68 g/m² at the main body (Figure 20, Table 11). Wet mass was not significantly higher at the canals in comparison to the main body (U= 5990.50, Z= -.63, p= .53). Mean dry mass was 21.37 g/m² at the canals and 16.05 g/m² at the main body (Figure 20, Table 11). Dry mass was not significantly higher at the canals in comparison to the main body (U= 6196.50, Z= -.21, p= .833). Mean tuber density was 30 N/m² at the canals and 104 N/m² at the main body (Figure 20, Table 11). Tuber density was significantly higher at the main body in comparison to the canals (U= 3979.50, Z= -2.38, p= .017).

Lower, middle and upper zone comparison: The main body was separated into lower, middle and upper zones. Mean wet mass increased from the lower zone (0.00 g/m²), through the middle zone (148.73 g/m²) to the upper zone (167.12 g/m²) (Figure 20, Table 11). The differences in wet mass across zones were significantly different (H(2)= 37.51, p< .001). Post hoc tests concluded that the lower zone differed significantly from the middle (H(2)= -4.43, p< .001) and upper zones (H(2)= -6.12, p< .001). The middle zone did not differ significantly from the upper zone (H(2)= -2.05, p= .122).

Mean dry mass was highest at the middle zone (20.15 g/m²), lowest at the lower zone (0.00 g/m²) and in between at the upper zone (17.71 g/m²) (Figure 20, Table 11). The differences in dry mass across zones were significantly different (H(2)= 36.85, p< .001). Post hoc tests revealed that the

lower zone differed significantly from the middle ($H(2)$= -4.50, $p<$ .001) and upper zones ($H(2)$= -6.07, $p<$ .001). The middle zone did not differ significantly from the upper zone ($H(2)$= -1.88, p= .18).

Mean tuber density was highest at the middle zone (122 N/m^2), lowest at the lower zone (0 N/m^2) and in between at the upper zone (121 N/m^2) (Figure 20, Table 11). The differences in tuber density across zones were significantly different ($H(2)$= 16.61, $p<$ .001). Post hoc tests found that the lower zone differed significantly from the middle ($H(2)$= -3.11, p= .006) and upper zones ($H(2)$= -4.07, $p<$ .001). The middle zone did not differ significantly from the upper zone ($H(2)$= -1.13, p= .771).
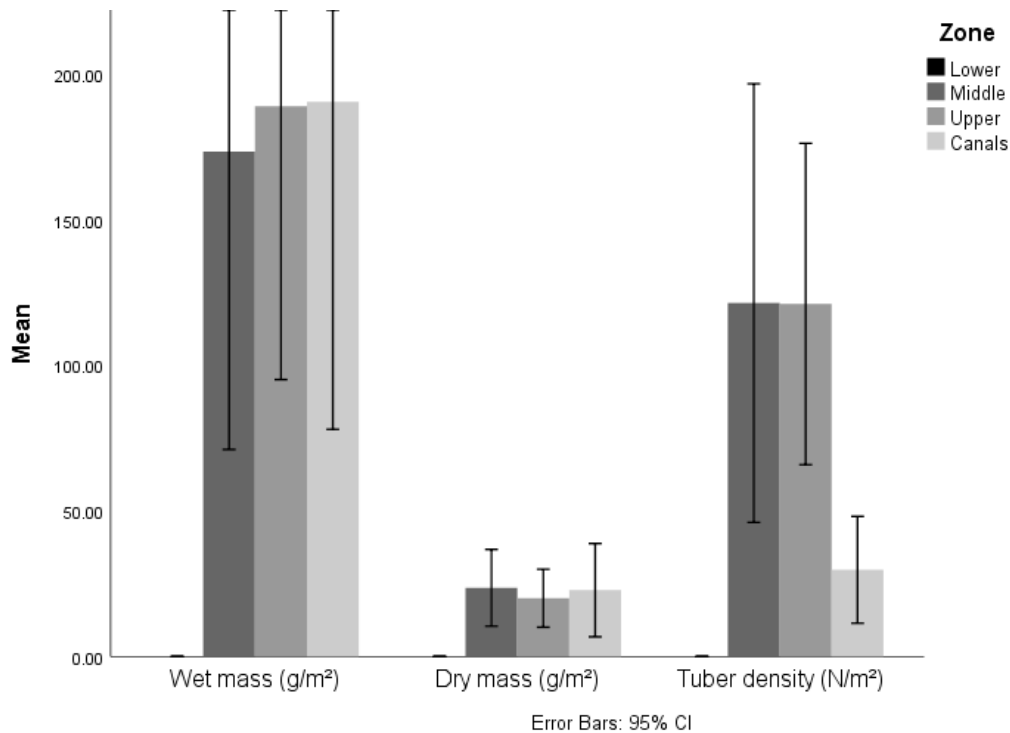
Figure 20: Mean wet mass (g/m^2), dry mass (g/m^2) and tuber density (N/m^2) across sampling zones

4.5.2 Temporal variations

Descriptive statistics: Percentage frequency of occurrence for wet mass and dry mass was highest in autumn (71%), lowest in summer (49%) and in between during spring (62%) and winter (57%). Percentage frequency of occurrence for tuber density was highest in autumn (40%), lowest in summer (25%) and in between during spring (38%) and winter (36%).

Maximum wet mass was highest in winter, maximum dry mass highest in autumn and maximum tuber density highest in spring (Table 12). Mean wet mass and dry mass were highest in winter and lowest in summer (Table 12). Mean tuber density was highest in spring and lowest in summer (Table 12).

Table 12: Descriptive statistics for biomass parameters across sampling seasons

		Spring	Summer	Autumn	Winter
Wet mass (g/m²)	N	76	41	84	42
	Minimum	0.00	0.00	0.00	0.00
	Maximum	2711.04	593.44	1415.37	2790.76
	Median	12.81	0.00	23.51	24.72
	Mean	203.91	61.88	113.54	209.96
	Standard Deviation	447.37	133.61	236.33	543.71
Dry mass (g/m²)	N	76	41	84	42
	Minimum	0.00	0.00	0.00	0.00
	Maximum	261.51	72.00	377.57	347.30
	Median	0.57	0.00	1.66	1.07
	Mean	23.45	5.39	14.04	26.58
	Standard Deviation	47.91	13.11	45.25	67.13
Tuber density (N/m²)	N	63	20	84	42
	Minimum	0	0	0	0
	Maximum	1204	241	778	889
	Median	0	0	0	0
	Mean	145	23	46	75
	Standard Deviation	294	59	111	169

Season comparison: Mean wet mass was highest in winter (209.96 g/m^2), lowest in summer (61.88 g/m^2) and in between during spring (203.91 g/m^2) and autumn (113.54 g/m^2) (Figure 21, Table 12). The differences in wet mass across seasons were not significantly different (H(3)= 4.20, p= .241).

Mean dry mass was highest in winter (26.58 g/m^2), lowest in summer (5.39 g/m^2) and in between during spring (23.45 g/m^2) and autumn (14.04 g/m^2) (Figure 22, Table 12). The differences in dry mass across seasons were not significantly different (H(3)= 5.47, p= .140).

Mean tuber density was highest in spring (145 N/m^2), lowest in summer (23 N/m^2) and in between during winter (75 N/m^2) and autumn (46 N/m^2) (Figure 23, Table 12). The differences in tuber density across seasons were not significantly different (H(3)= 2.18, p= .536).
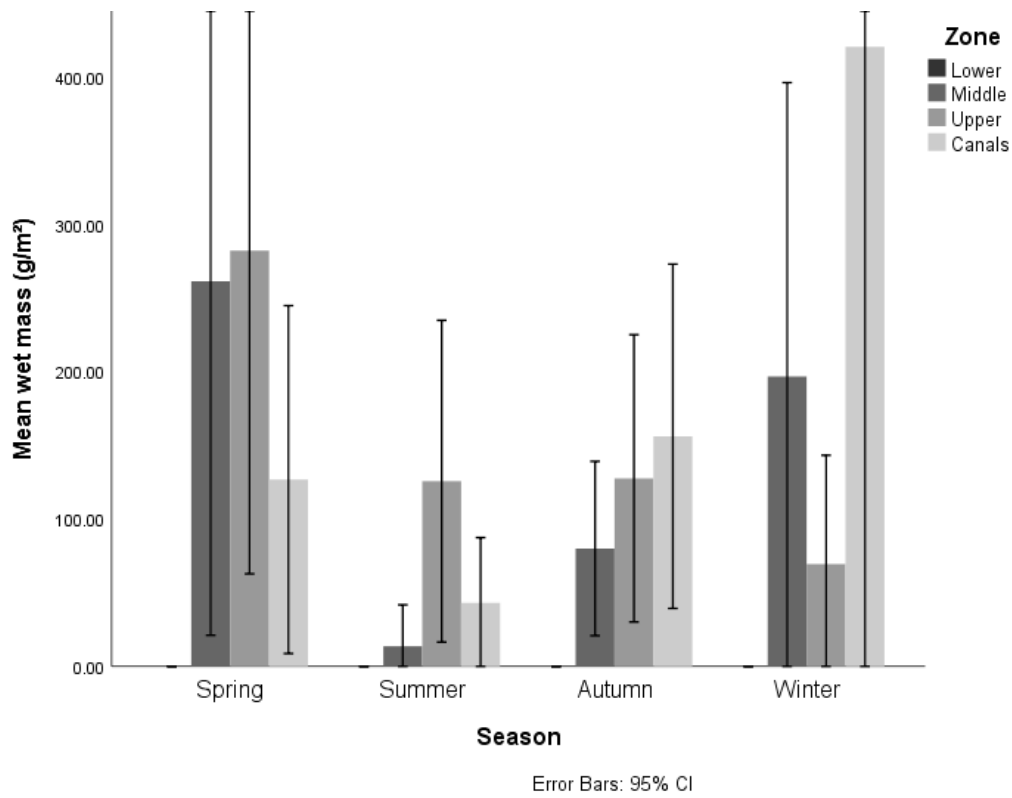
Figure 21: Mean wet mass (g/m^2) across sampling seasons including sampling zone
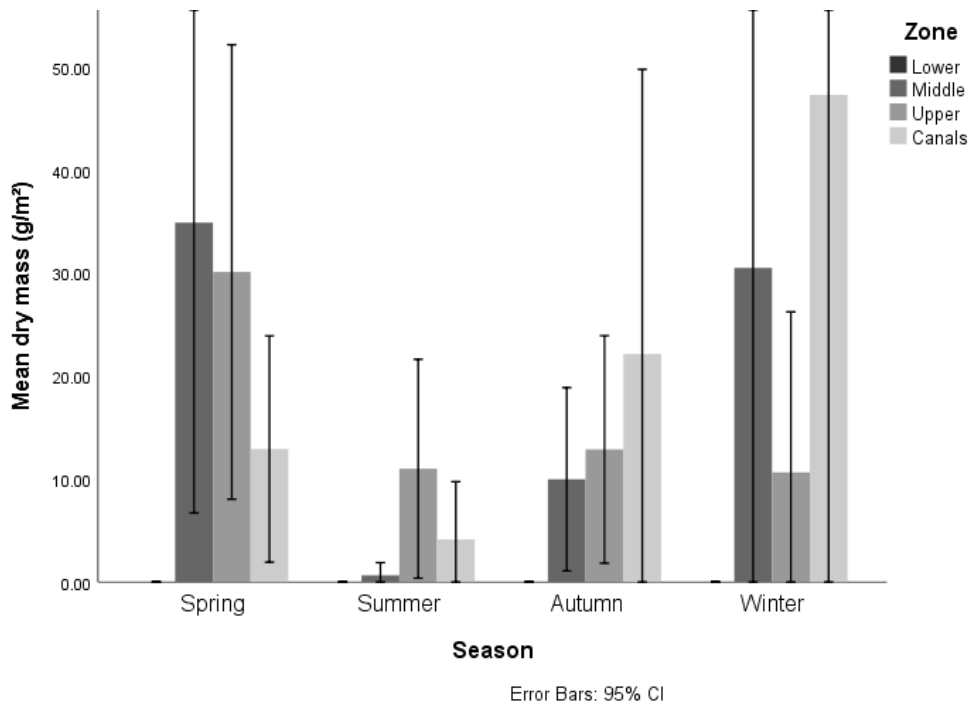
Figure 22: Mean dry mass (g/m^2) across sampling seasons including sampling zone
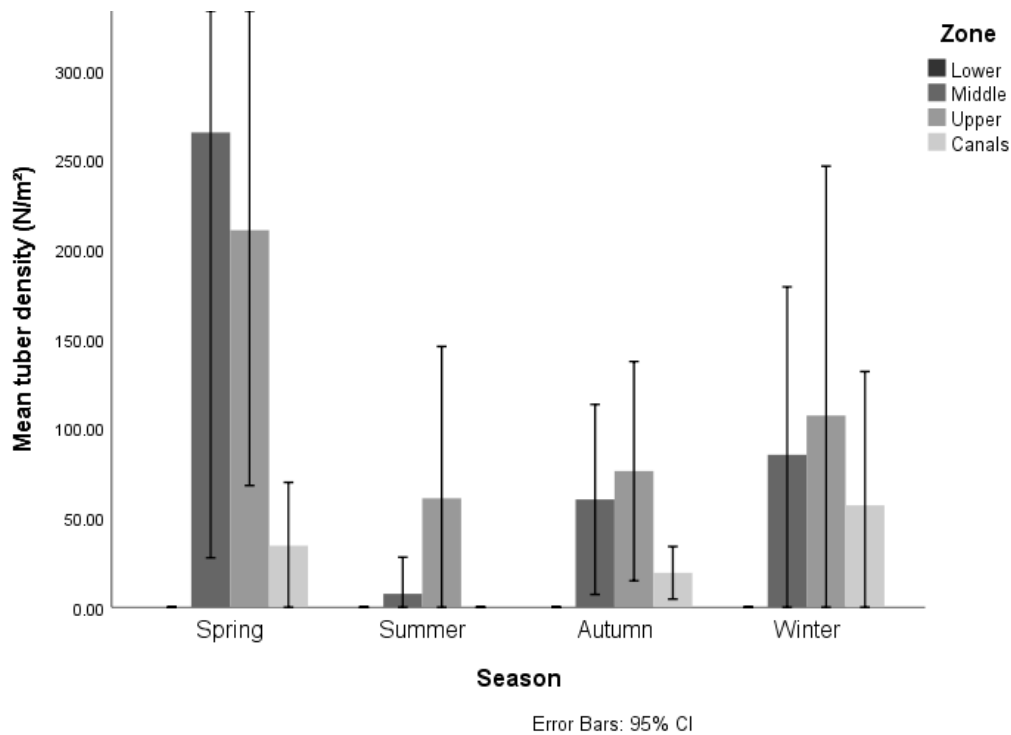
Figure 23: Mean tuber density (N/ m^2) across sampling seasons including sampling zone

4.6 Factors influencing the biomass and distribution of *Stuckenia pectinata*- correlations between *Stuckenia pectinata* biomass and other parameters studied

4.6.1 *Stuckenia pectinata* biomass and physico- chemical characteristics

Correlation analysis was conducted between all data for *Stuckenia pectinata* biomass parameters (wet mass, dry mass and tuber density) and physico- chemical parameters studied (temperature, salinity, pH, dissolved oxygen, Secchi depth and depth). Tuber density was significantly negatively correlated with depth (r(207)= -.171, p= .014) (Figure 24).

$$y = 1.97E2 - 87.29 * x$$

R^2 Linear = 0.023
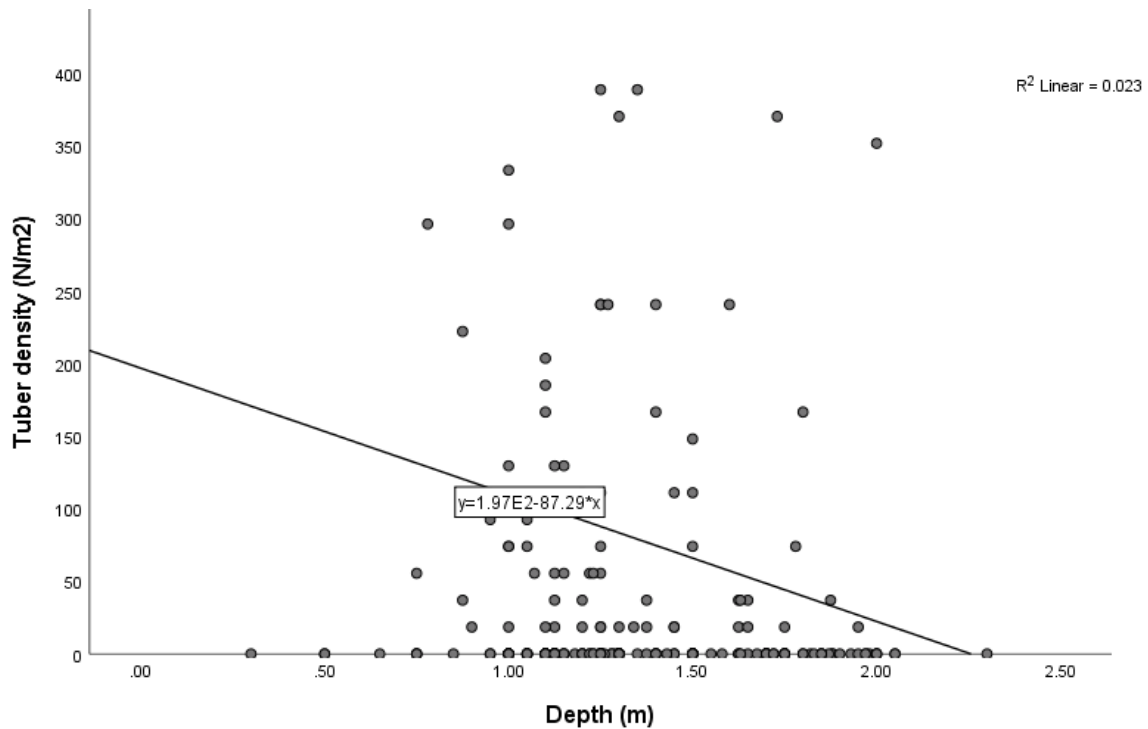
Figure 24: Scatter plot of tuber density (N/m^2) and depth (m)

Spatial variations

Main body and canals: The lower, middle and upper zones were combined as the main body. Correlation analysis was performed between *Stuckenia pectinata* biomass parameters and physico-chemical parameters sampled at the main body and canals. Wet mass was significantly negatively correlated with salinity ($r(168) = -.226$, $p = .003$) and Secchi depth ($r(166) = -.164$, $p = .035$) (Table 13) and significantly positively correlated with pH ($r(168) = .186$, $p = .016$) and dissolved oxygen ($r(168) = .179$, $p = .021$) at the main body (Table 13). Dry mass was significantly negatively correlated with salinity ($r(168) = -.204$, $p = .008$) (Figure 25, Table 13) and significantly positively correlated with pH ($r(168) = .175$, $p = .023$) and dissolved oxygen ($r(168) = .163$, $p = .034$) at the main body (Table 13). Tuber density was significantly negatively correlated with salinity at the main body ($r(140) = -.236$, $p = .005$) (Figure 26, Table 13). No significant correlations were found for the canals.

Table 13: Spearman's rank- order correlation between *Stuckenia pectinata* biomass parameters and physico-chemical parameters sampled at the main body. Significant results indicated in bold

		Wet mass (g/m²)	Dry mass (g/m²)	Tuber density (N/m^2)
Temperature (°C)	Correlation Coefficient	0.004	0.004	-0.020
	Sig. (2-tailed)	0.956	0.956	0.816
	N	168	168	140
Salinity (ppt)	Correlation Coefficient	**-0.226**[**]	**-0.204**[**]	**-0.236**[**]
	Sig. (2-tailed)	0.003	0.008	0.005
	N	168	168	140

50

pH	Correlation Coefficient	**0.186**[*]	**0.175**[*]	0.005
	Sig. (2-tailed)	0.016	0.023	0.957
	N	168	168	140
Dissolved oxygen (mg/L)	Correlation Coefficient	**0.179**[*]	**0.163**[*]	0.130
	Sig. (2-tailed)	0.021	0.034	0.126
	N	168	168	140
Secchi depth (%)	Correlation Coefficient	**-0.164**[*]	-0.151	-0.086
	Sig. (2-tailed)	0.035	0.052	0.315
	N	166	166	138
Depth (m)	Correlation Coefficient	0.011	0.005	-0.063
	Sig. (2-tailed)	0.884	0.945	0.466
	N	166	166	138
**Correlation is significant at the p< 0.01 level (2-tailed).				
*Correlation is significant at the P< 0.05 level (2-tailed).				

Figure 25: Scatter plot of dry mass (g/m^2) and salinity (ppt) sampled at the main body
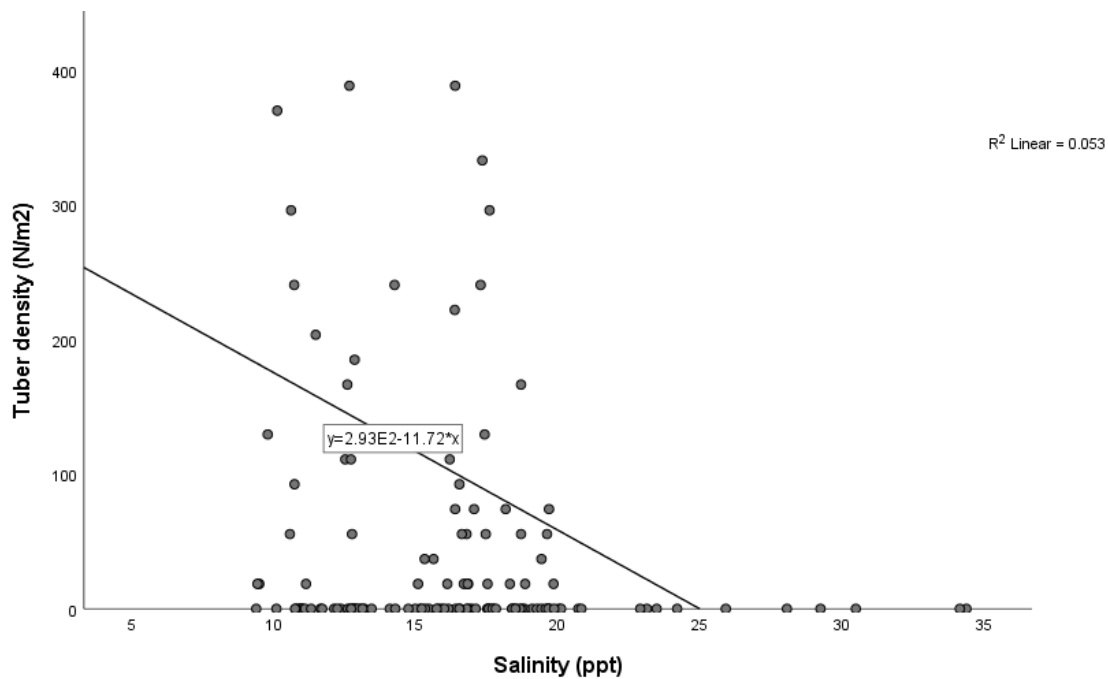
Figure 26: Scatter plot of tuber density (N/m^2) and salinity (ppt) sampled at the main body

Lower, middle and upper zone: Correlation analysis was carried out between *Stuckenia pectinata* biomass parameters and physico- chemical parameters recorded at the lower, middle and upper zones. Wet mass, dry mass and tuber density displayed values of zero at the lower zone and as a result, no correlations could be performed. Tuber density was significantly negatively correlated with salinity at the middle zone (r(50)= -.286, p= .044). Wet mass (r(83)= -.230, p= .037), dry mass (r(83)= -.241, p= .028) (Figure 27) and tuber density (r(69)= -.286, p= .017) were significantly negatively correlated with depth at the upper zone.
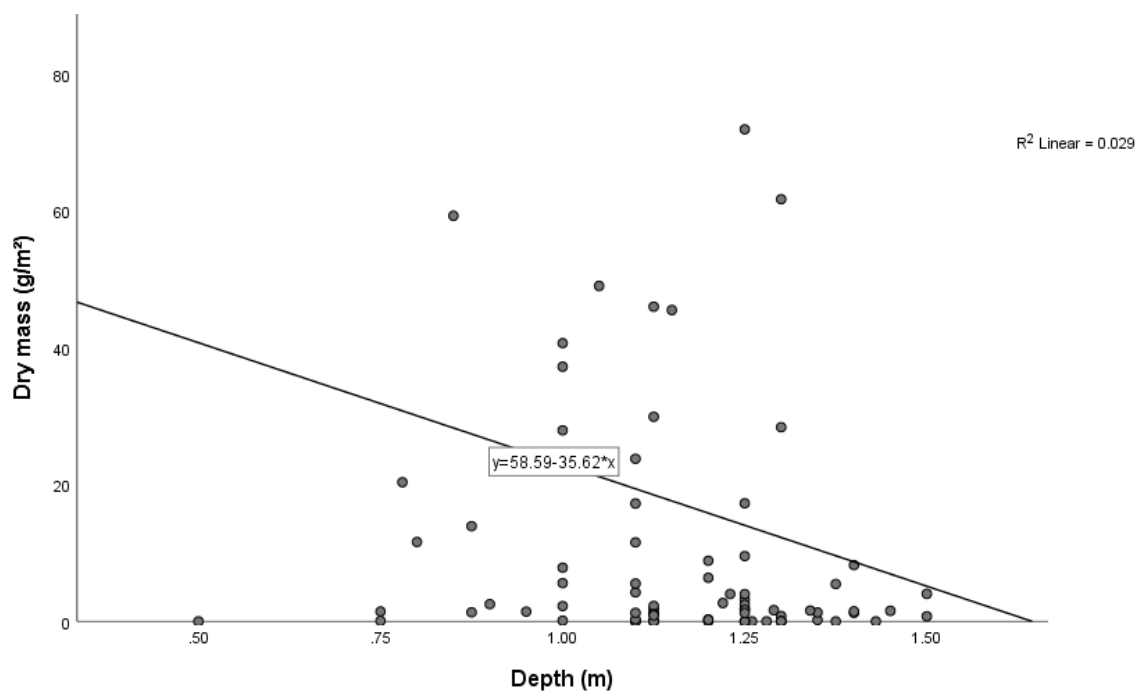
Figure 27: Scatter plot of dry mass (g/m^2) and depth (m) sampled at the upper zone

Temporal variations

Seasons: Correlation analysis was conducted between *Stuckenia pectinata* biomass parameters and physico- chemical parameters recorded during spring, summer, autumn and winter. Wet mass (r(41)= .416, p= .007), dry mass (r(41)= .428, p= .005) and tuber density (r(20)= .511, p= .021) were significantly positively correlated with dissolved oxygen during summer. Wet mass (r(84)= -.321, p= .003), dry mass (r(84)= -.340, p= .002) (Figure 28) and tuber density (r(84)= -.270, p= .013) were significantly negatively correlated with salinity during autumn. No significant correlations were recorded during spring or winter.
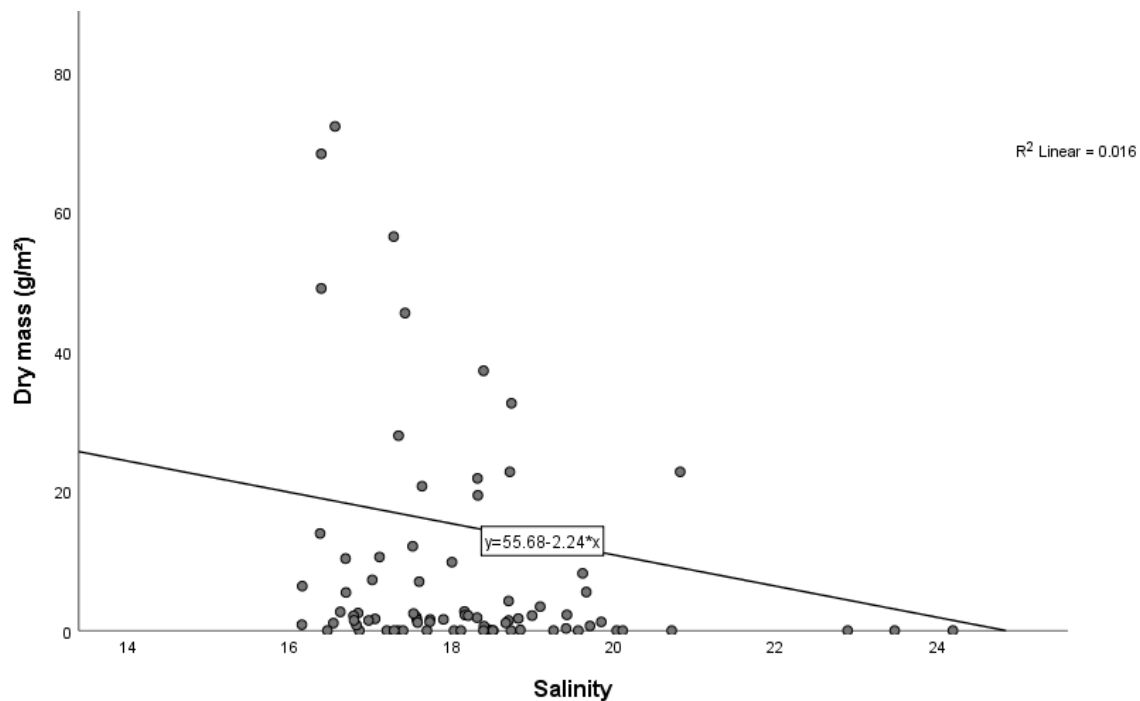
Figure 28: Scatter plot of dry mass (g/m^2) and salinity (ppt) sampled during autumn

One month, two months and three months prior: Correlation analysis was performed between *Stuckenia pectinata* biomass parameters and physico- chemical parameters sampled approximately one month, two months and three months prior (compared to when biomass parameters were sampled). Tuber density was significantly negatively correlated with salinity sampled one month prior (r(202)= -.140, p= .047). Wet mass (r(201)= .168, p= .017) and dry mass (r(201)= .165, p= .020) were significantly positively correlated with pH sampled two months prior. Tuber density was significantly negatively correlated with depth sampled two months prior (r(201)= -.142, p= .044). Wet mass (r(180)= .146, p= .050) and dry mass (r(180)= .149, p= .046) were significantly positively correlated with pH sampled three months prior.

4.6.2 *Stuckenia pectinata* biomass and nutrient characteristics

Correlation analysis was performed between all data for *Stuckenia pectinata* biomass determinants (wet mass, dry mass and tuber density) and nutrient determinants studied (nitrate + nitrite, nitrite, nitrate and phosphate). No significant correlations were observed.

Spatial variations

Main body and canals: Correlation analysis was performed between *Stuckenia pectinata* biomass determinants and nutrient determinants sampled at the main body and canals. Tuber density was significantly negatively correlated with nitrate + nitrite at the canals ($r(30)$= -.406, *p*= .026). No significant correlations were recorded for the main body.

Temporal variations

Correlation analysis was conducted between *Stuckenia pectinata* biomass determinants and nutrient determinants sampled during spring, summer, autumn and winter. No significant correlations were noted for any season.

One month, two months and three months prior: Correlation analysis was carried out between *Stuckenia pectinata* biomass parameters and nutrient parameters sampled approximately one month, two months and three months prior (compared to when biomass parameters were sampled). Tuber density was significantly positively correlated with nitrate + nitrite sampled one month prior ($r(87)$= .259, *p*= .016). No significant correlations were noted for two months and three months prior.

4.6.3 *Stuckenia pectinata* biomass and sediment characteristics

Correlation analysis was performed between all data for *Stuckenia pectinata* biomass parameters (wet mass, dry mass and tuber density) and sediment characteristics (percentage sediment retained across 1700 µm, 1180 µm, 500 µm, 250 µm, 125 µm, 63 µm and <63 µm size classes). Wet mass was found to have a significant positive relationship with percentage sediment retained (hereon referred to as sediment retained) for the 1180 µm ($r(168)$= .164, *p*= .034) and 250 µm ($r(168)$= .163, *p*= .035) size classes. Dry mass was also found to have a significant positive relationship with sediment retained for the 1180 µm ($r(168)$= .178, *p*= .021) and 250 µm ($r(168)$= .182, *p*= .018) size classes. Wet mass ($r(168)$= -.201, *p*= .009) (Figure 29) and dry mass ($r(168)$= -.187, *p*= .015) exhibited a significant negative relationship with sediment retained for the 500 µm size class. Tuber density displayed a significant positive relationship with sediment retained for the 250 µm size class ($r(140)$= .229, *p*= .007) (Figure 30).
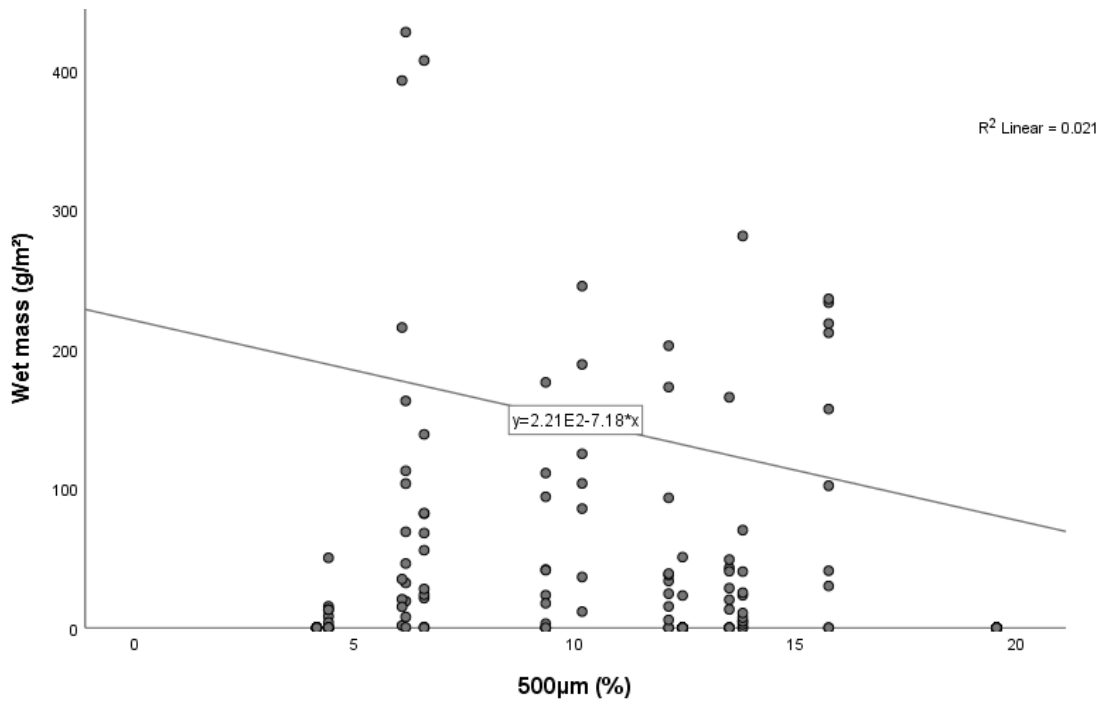
Figure 29: Scatter plot of wet mass (g/m^2) and percentage sediment retained (%) for the 500 μm size class
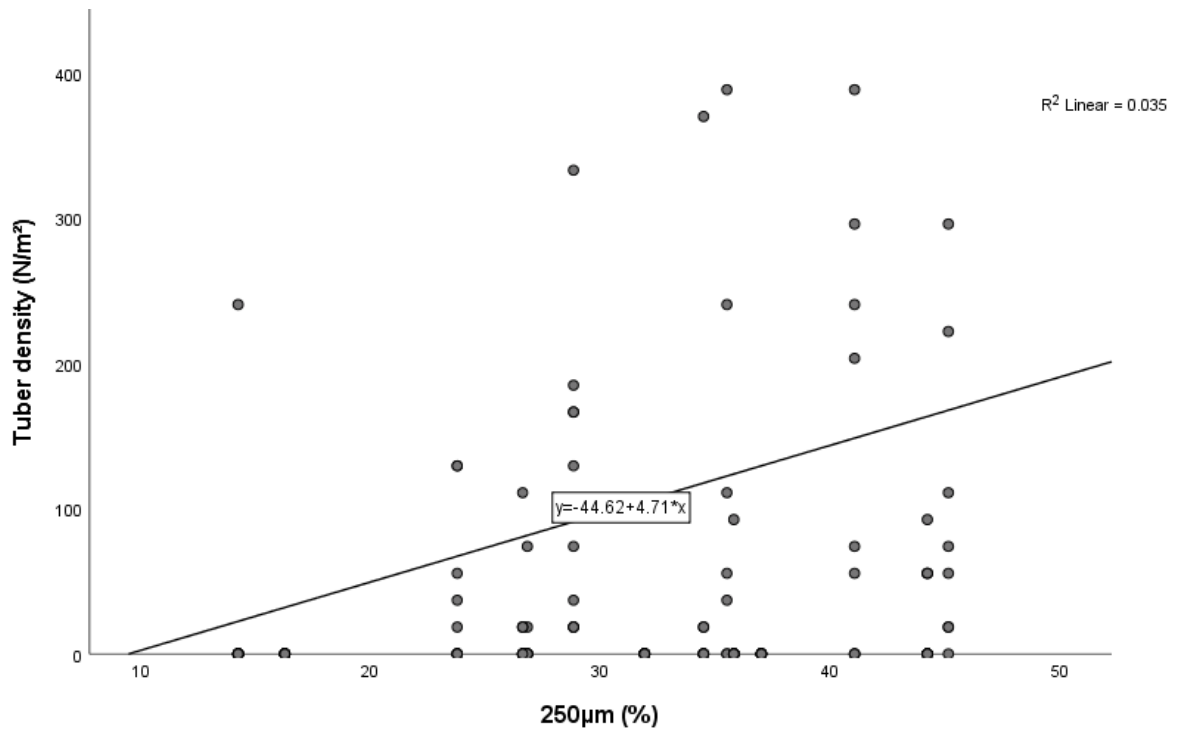
Figure 30: Scatter plot of tuber density (N/m^2) and percentage sediment retained (%) for the 250 μm size class

Spatial variations

Lower, middle and upper zone: Wet mass, dry mass and tuber density displayed values of zero at the lower zone and as a result, no correlations could be performed.

Correlation analysis was performed between *Stuckenia pectinata* biomass parameters and sediment characteristics recorded at the middle zone. Wet mass ($r(60)= .753$, $p= .000$), dry mass ($r(60)= .767$, $p= .000$) and tuber density ($r(50)= .619$, $p= .000$) (Figure 31) were significantly positively correlated with sediment retained for the 1700 µm size class. Wet mass ($r(60)= .720$, $p= .000$), dry mass ($r(60)= .743$, $p= .000$) and tuber density ($r(50)= .594$, $p= .000$) were significantly positively correlated with sediment retained for the 1180 µm size class. Wet mass ($r(60)= -.386$, $p= .002$), dry mass ($r(60)= -.360$, $p= .005$) and tuber density ($r(50)= -.298$, $p= .035$) were significantly negatively correlated with sediment retained for the 500 µm size class.
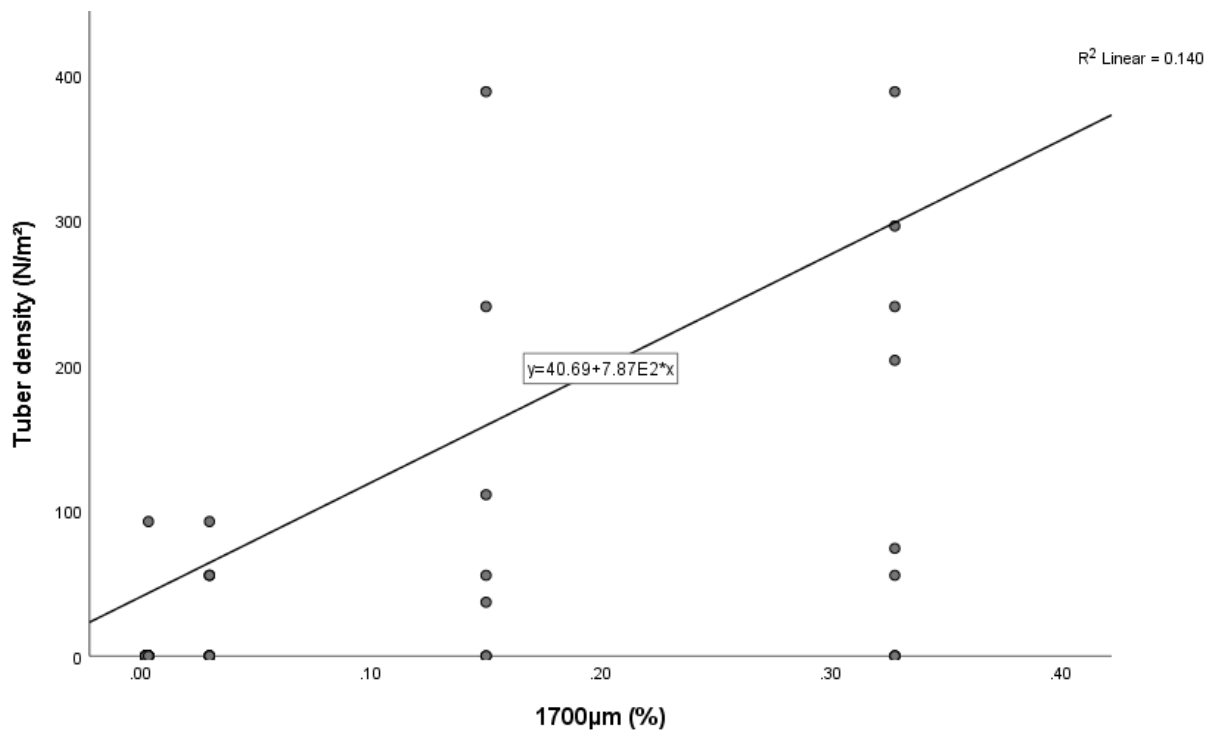
Figure 31: Scatter plot of tuber density (N/m^2) and percentage sediment retained (%) for the 1700 µm size class at the middle zone

Correlation analysis was conducted between *Stuckenia pectinata* biomass parameters and sediment characteristics sampled at the upper zone. Wet mass ($r(84)= -.370$, $p= .001$) and dry mass ($r(84)= -.347$, $p= .001$) were significantly negatively correlated with sediment retained for the 1700 µm size class (Table 14). Wet mass ($r(84)= -.391$, $p= .000$), dry mass ($r(84)= -.390$, $p= .000$) and tuber density ($r(70)= -.332$, $p= .005$) were significantly negatively correlated with sediment retained for the 1180 µm size class (Table 14). Wet mass ($r(84)= .344$, $p= .001$), dry mass ($r(84)= .344$, $p= .001$) (Figure 32) and tuber density ($r(70)= .434$, $p= .000$) were significantly positively correlated with sediment retained for the 250 µm size class (Table 14). Wet mass ($r(84)= -.355$, $p= .001$) (Figure 33), dry mass ($r(84)= -.351$, $p= .001$) and tuber density ($r(70)= -.235$, $p= .050$) were significantly negatively correlated with sediment retained for the 63 µm size class (Table 14). Wet mass ($r(84)= -.305$, $p=$

.005), dry mass ($r(84)= -.322$, $p= .003$) and tuber density ($r(70)= -.239$, $p= .047$) were significantly negatively correlated with sediment retained for the <63 μm size class (Table 14).

Table 14: Spearman's rank- order correlation between *Stuckenia pectinata* biomass parameters and percentage sediment retained across size classes at the upper zone. Significant results indicated in bold

		Wet mass (g/m²)	Dry mass (g/m²)	Tuber density (N/m²)
1700 μm (%)	Correlation Coefficient	**-0.370**[**]	**-0.347**[**]	-0.231
	Sig. (2-tailed)	0.001	0.001	0.054
	N	84	84	70
1180 μm (%)	Correlation Coefficient	**-0.391**[**]	**-0.390**[**]	**-0.332**[**]
	Sig. (2-tailed)	0.000	0.000	0.005
	N	84	84	70
500 μm (%)	Correlation Coefficient	-0.090	-0.093	0.131
	Sig. (2-tailed)	0.418	0.400	0.279
	N	84	84	70
250 μm (%)	Correlation Coefficient	**0.344**[**]	**0.344**[**]	**0.434**[**]
	Sig. (2-tailed)	0.001	0.001	0.000
	N	84	84	70
125 μm (%)	Correlation Coefficient	0.075	0.073	-0.185
	Sig. (2-tailed)	0.500	0.510	0.126
	N	84	84	70
63 μm (%)	Correlation Coefficient	**-0.355**[**]	**-0.351**[**]	**-0.235**[*]
	Sig. (2-tailed)	0.001	0.001	0.050
	N	84	84	70
<63 μm (%)	Correlation Coefficient	**-0.305**[**]	**-0.322**[**]	**-0.239**[*]
	Sig. (2-tailed)	0.005	0.003	0.047
	N	84	84	70
**Correlation is significant at the p< 0.01 level (2-tailed).				
*Correlation is significant at the p< 0.05 level (2-tailed).				

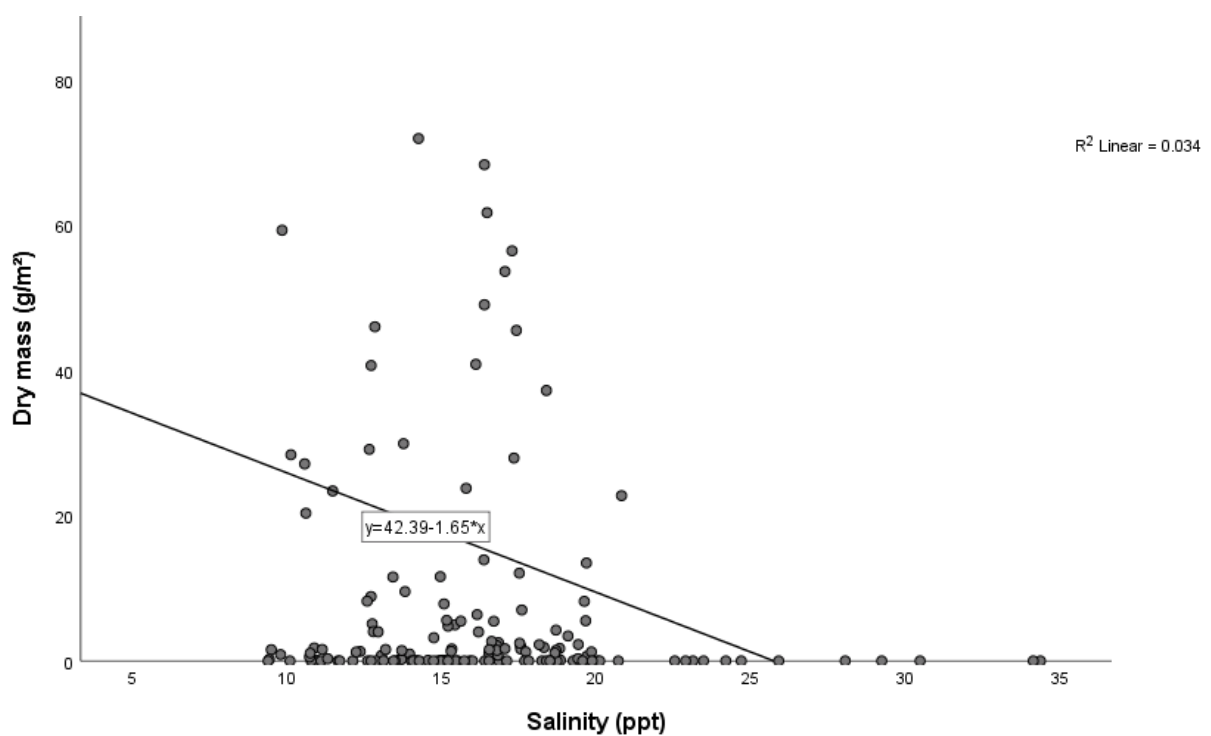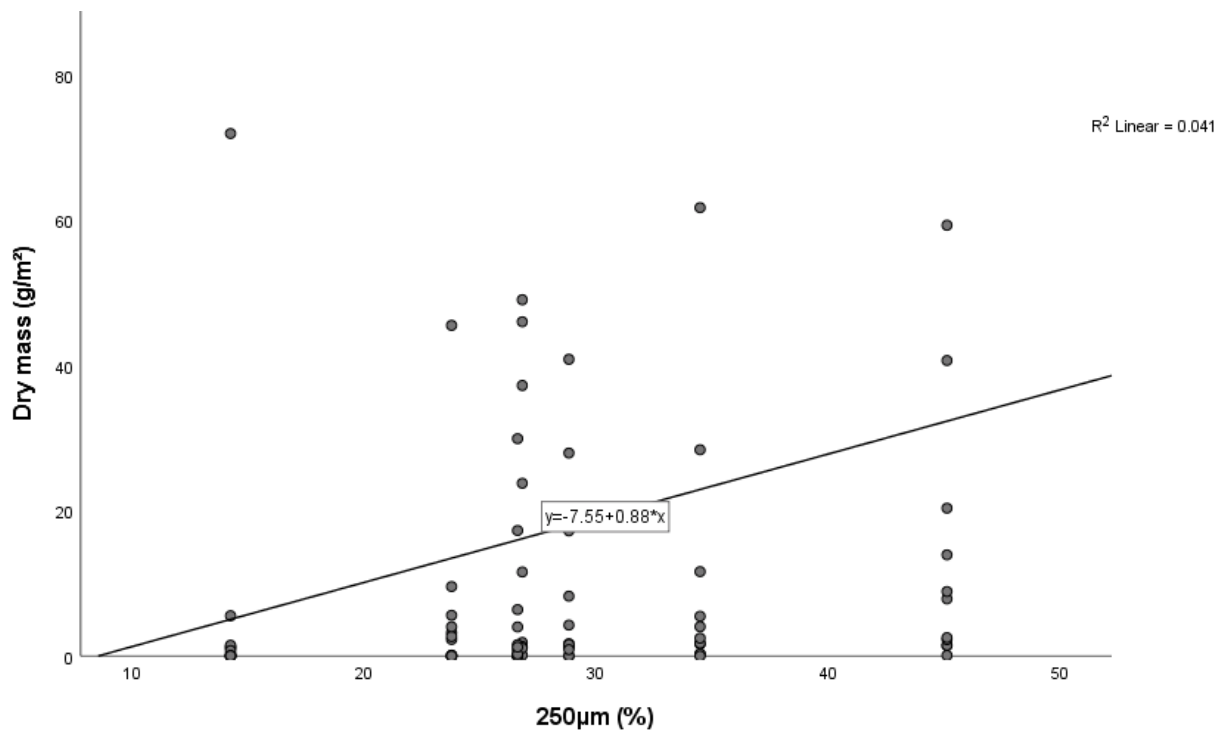**Figure 32: Scatter plot of dry mass (g/m^2) and percentage sediment retained (%) for the 250 μm size class at the upper zone**
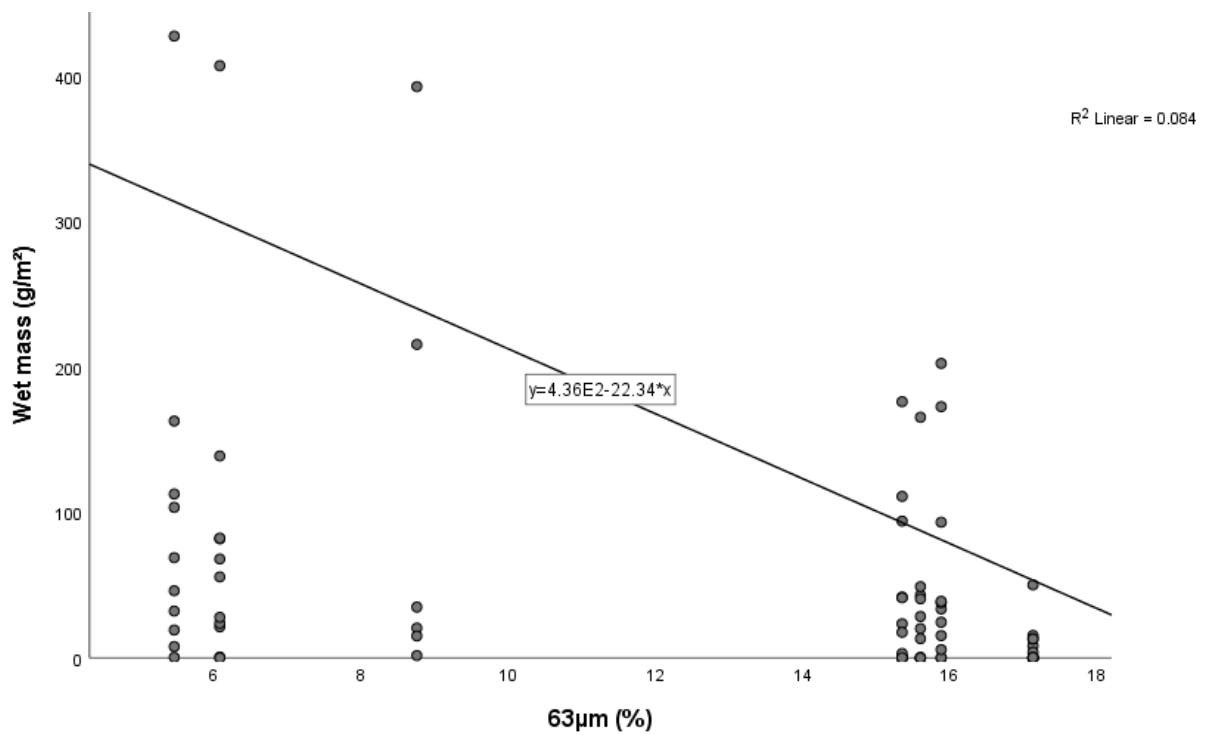
Figure 33: Scatter plot of wet mass (g/m^2) and percentage sediment retained (%) for the 63 μm size class at the upper zone

5. Discussion

5.1 Physico- chemical characteristics

The median for each determinant across the main body, canals and influent rivers was compared to previous research (mean values) from Zandvlei Estuary. Harding (1994) sampled several physico- chemical parameters across the entire Zandvlei Estuary, including the canals and three influent rivers between 1978 and 1991 (13 year period). In order to compare Harding (1994) results to the current study, a mean of Harding (1994) influent rivers (Sand, Keysers and Westlake), lake, outlet channel and marina data was calculated to produce a mean for the entire system for each physico- chemical parameter studied. From the calculations mean temperature was 17.77 °C, salinity 7.63 ppt, pH 8.07, dissolved oxygen 7.09 mg/L and Secchi depth 0.71 m (Harding, 1994).

Quick and Harding (1994) monitored a number of physico- chemical parameters at the main body and influent rivers of Zandvlei Estuary from 1992 to 1993. To be able to compare Quick and Harding (1994) data to the current study, a mean of Quick and Harding (1994) influent rivers (Sand, Keysers and Westlake) and Zandvlei data was calculated to produce a mean for the entire system for each physico- chemical parameter monitored. From the calculations mean temperature was 17.25 °C, salinity 3 ppt, pH 7.89 and Secchi depth 0.4 m (Quick and Harding, 1994).

Muhl *et al* (2003) analysed the estuary's salinity records for the period between 1978 and 2003 (25 year period) and found that mean salinity was 7 ppt. Salinity at Zandvlei Estuary averaged (mean) 6.8 ppt, Secchi depth 0.5 m and depth 1.14 m according to Thornton *et al* (1995), who studied the ecology and management of the system. Hutchings *et al* (2016), who conducted an impact assessment at the estuary, discussed how salinity levels in the 1970's were fairly constant but then decreased from a mean of 10 ppt to 5 ppt between 1980 and the early 1990's. Salinity values then increased from 2002 to 2010 to levels between 9 ppt and 11 ppt (Hutchings *et al.* 2016). Morant and Grindley (1982) analysed physico- chemical data from Zandvlei Estuary for the period from 1973 to 1982 and stated that mean Secchi depth was 0.7 m (for the "whole system").

After comparing results from the current study with the aforementioned literature the following trends were observed. Median salinity displayed increased values when compared to five other studies from Zandvlei Estuary (Harding, 1994; Quick and Harding, 1994; Thornton *et al.* 1995; Muhl *et al.* 2003; Hutchings *et al.* 2016). According C.A.P.E. (2013) and Hutchings *et al* (2016) since about 2000 salinity values within Zandvlei Estuary have increased. The increase was due to lowering the rubble weir and managing the mouth of the estuary in a manner that would increase seawater intrusion and therefore maintain higher salinity levels which the system requires in order to function more naturally (Cape, 2013; Hutchings *et al.* 2016).

Median Secchi depth was higher in comparison Quick and Harding (1994) whilst additional studies reviewed, also from Zandvlei Estuary, recorded values similar to those seen in the current study (Morant and Grindley, 1982; Harding, 1994). Median values for temperature, pH, dissolved oxygen and depth were comparable to several previous studies from the same system (Harding, 1994; Quick and Harding, 1994; Thornton *et al.* 1995).

Minimum and maximum values for sampled parameters from across the main body, canals and influent rivers were compared to previous research from Zandvlei Estuary. Harding (1994) found that minimum and maximum values for temperature were 8 °C and 26.7 °C respectively, salinity <1 ppt and 34 ppt respectively, pH 4.8 and 10.4 respectively, dissolved oxygen 0.2 mg/L and 17.9 mg/L respectvely and Secchi depth 0.09 m and 2.5 m respectively. According to Quick and Harding (1994), temperature displayed a minimum value of 10.5 °C and a maximum value of 22.9 °C, salinity <1 ppt and 14 ppt respectively, pH 6.5 and 9.00 respectively and Secchi depth 0.01 m and 1.05 m respectively. In addition, Morant and Grindley (1982) stated that minimum temperature was 11 °C and maximum temperature 31 °C, salinity 0.04 ppt and 26.20 ppt respectively, pH 5.8 and 9.2 respectively, dissolved oxygen 0 mg/L and 20 mg/L respectively and Secchi depth 0.2 m and 1.8 m respectively. Muhl *et al* (2003) found that minimum salinity was 0 ppt and maximum salinity 25 ppt.

The results from the current study were compared to the above mentioned literature and the following trends were apparent. Maximum salinity was higher in comparison to three previous studies from Zandvlei Estuary (Morant and Grindley, 1982; Quick and Harding, 1994; Muhl *et al.* 2003). This was most likely due to the lowering of the weir and changes to the mouth management strategy which promotes the ingress of greater volumes of saline water (C.A.P.E., 2013; Hutchings *et al.* 2016). Minimum pH was lower in comparison to two previous studies from Zandvlei estuary (Morant and Grindley, 1982; Quick and Harding, 1994) and maximum dissolved oxygen higher in comparison to two previous studies from the same system (Morant and Grindley, 1982; Harding, 1994). The remaining parameters were either similar to the results of past research from Zandvlei Estuary or showed no obvious trends.

Dissolved oxygen values below 3 mg/L are known to indicate hypoxic conditions (Snow and Taljaard, 2007; Kaselowski and Adams, 2013). In the current study 11.09% of readings (58 readings) fell below 3 mg/L. Hypoxic conditions can negatively affect estuarine biota if values remain at this level for extended periods of time (De Villiers and Thiart 2007; Kaselowski and Adams 2013). Morant and Grindley (1982) commented that anoxic bottom conditions in the main body of Zandvlei Estuary were most likely as a result of large quantities of organic matter building up on the bottom due to the winter die back of pondweed, *Stuckenia pectinata* and phytoplankton. Morant and Grindley (1982) added that dissolved oxygen readings were distinctively lower after *S. pectinata* had been mechanically harvested in the canals.

Mouth state comparison: Temperature was significantly higher during closed mouth state in comparison to open mouth state. In the study by C.A.P.E. (2013) two probes that recorded depth, temperature and salinity were positioned in the main body of the Zandvlei Estuary; one adjacent the yacht club (within the middle zone in this study) and the other near the mouth of the estuary (within the lower zone in this study). Data was collected for the period between September 2012 and January 2013 (C.A.P.E., 2013). Temperature data collected by C.A.P.E. (2013) demonstrated the same result as the current study whereby temperature was higher during closed mouth state in comparison to open mouth state. C.A.P.E. (2013) stated that the reason for the lower temperature values during open mouth state was as a result of the influx of cold seawater into the system.

Salinity was significantly higher during closed mouth state in comparison to open mouth state. Snow and Taljaard (2007) developed a conceptual model for water quality characteristics in temporarily open/closed estuaries. The authors compared the model to results from various temporarily

open/closed estuaries including the Diep Estuary (sampled in 1988 and 1989) and the Palmiet Estuary (sampled between 1986 and 2000) (Snow and Taljaard, 2007). According to Snow and Taljaard (2007), salinity in an estuary is affected by seawater intrusion, fresh water intrusion and evaporation. Under closed mouth conditions salinity levels would be influenced by fresh water intrusion, predominantly during winter and evaporation, predominantly during summer. Higher salinity levels during the closed mouth state at Zandvlei Estuary could be caused by evaporation due to elevated ambient air temperatures as well as reduced freshwater input. Data supplied by the South African Weather Service showed that the study period experienced higher maximum air temperatures and lower total rainfall in comparison to historic data (1981- 2010).

pH was not significantly different between open mouth and closed mouth state. Whitfield *et al* (2008) studied the influence of mouth state on the ecology of the East Kleinemonde Estuary in South Africa. In agreement with the findings of the current study, Whitfield *et al* (2008) stated that the East Kleinemonde Estuary did not show any considerable variation in pH between open mouth and closed mouth state. Snow and Taljaard (2007) commented that pH generally ranges between 7 – 8.5 in temporarily open/closed estuaries (this result was observed in the Diep and Palmiet Estuaries).

Dissolved oxygen was significantly higher during open mouth state in comparison to closed mouth state. The result is in agreement with the conceptual model for temporarily open/closed estuaries developed by Snow and Taljaard (2007) and the result found by Whitfield *et al* (2008). Under open mouth conditions temporarily open/ closed estuaries are generally sufficiently oxygenated (levels above 6 mg/L) (Snow and Taljaard, 2007; Whitfield *et al.* 2008). High oxygen levels are due to oxygenated seawater entering the system at the mouth and oxygenated freshwater entering at the head (Snow and Taljaard, 2007). The interaction between estuarine water and water entering an estuary from the sea and the influent rivers also helps break up stratification which can lead to low oxygen conditions at the bottom waters (Snow and Taljaard, 2007).

Interestingly, a higher percentage of readings that fell below 3 mg/L were recorded during open mouth state (60.35%) in comparison to closed mouth state (39.65%). A possible explanation could be linked to dissolved oxygen conditions in the canals. The canals are a protected environment both in terms of wind mixing and water circulation (Morant and Grindley, 1982; C.A.P.E., 2013). Therefore, low dissolved oxygen levels, particularly at the bottom waters of the canals could have persisted during open mouth conditions.

Secchi depth was significantly higher during closed mouth state in comparison to open mouth state. According to Snow and Taljaard (2007), river water can have low transparency due to the state of the catchment. As a result, river water flowing into an estuary can lower the water transparency of the system (Snow and Taljaard, 2007). During periods of high rainfall and therefore high river inflow, the mouth of Zandvlei Estuary is artificially opened providing a possible reason why Secchi depth/ transparency would be lower during open mouth state. Kaselowski (2012) studied the physico-chemical and microalgal characteristics of the Goukamma Estuary in South Africa. Significantly higher Secchi depth recordings were noted during closed mouth state in comparison to open mouth state (Kaselowski, 2012).

Depth was significantly higher during open mouth state in comparison to closed mouth state. In contrast, research conducted by C.A.P.E. (2013) demonstrated that the depth of Zandvlei Estuary

was higher when the mouth was closed. C.A.P.E. (2013) explained that when the mouth is closed, water levels build up in the estuary due to the inflow of freshwater from influent rivers. In agreement with C.A.P.E. (2013), Kaselowski (2012) found that depth was higher during closed mouth state at the Goukamma Estuary. A possible explanation for depth being higher during open mouth state in the current study could be due to anthropogenic modifications to the system which have forced the mouth to be artificially opened and closed. Artificial breaching results in a shallow breach and therefore there is not a sustained connection between sea and estuary (C.A.P.E, 2013). Seawater moves into the estuary on a high spring tide and as the tide recedes the newly entered seawater is trapped in the estuary due to the shallowness of the mouth and the presence of a rubble weir (C.A.P.E., 2013). In the current study the system would still be considered in an open mouth state but the water level has risen due to the input of sea water.

Surface and bottom waters comparison: Temperature was not significantly different between the surface and bottom waters. By looking at the similarity in median values and the lack of statistical significance one can assume that temperature was relatively homogenous between surface and bottom waters. Morant and Grindley (1982) found that mean temperature was similar between surface and bottom waters due to the shallowness of Zandvlei Estuary and the wind induced mixing that occurs in the system. Davies and Stewart (1984) analysed temperature, salinity and oxygen data from two canals within Marina da Gama between March and December 1983. The authors mentioned that no significant temperature differences were recorded through the water column.

Salinity was significantly higher at the bottom waters in comparison to the surface waters. Harding (1994) found a comparable result whereby bottom waters exhibited 5 ppt higher mean salinity in comparison to surface waters at Zandvlei Estuary. Harding (1994) stated that differences between surface and bottom waters were most obvious after the artificial opening of the estuary mouth which resulted in denser seawater moving into the estuary underneath (at the bottom waters) the outflowing fresh water (at the surface waters). According to Davies and Stewart (1984), differences in salinity through the water column were clear and varied between 5% and 17% in the canals.

pH was significantly higher at the surface waters in comparison to the bottom waters. Morant and Grindley (1982) commented that wide pH ranges were present at Zandvlei Estuary. pH differences in the system could be caused by several factors including seawater intrusion during open mouth state, freshwater inflow from rivers and stormwater drains as well as the photosynthetic activity of aquatic macrophytes and phytoplankton (Morant and Grindley, 1982).

Dissolved oxygen was significantly higher at the surface waters in comparison to the bottom waters. Furthermore, 10.34% of readings below 3 mg/L were noted at the surface waters and 89.66% at the bottom waters. Very low values for dissolved oxygen (as low as 0 mg/L) have been recorded at the bottom waters in Zandvlei Estuary (Morant and Grindley, 1982; Hutchings *et al.* 2016). Morant and Grindley (1982) mentioned that low dissolved oxygen values at the bottom waters were due to large quantities of organic matter collecting on the bottom and subsequently being broken down by bacteria with a concomitant removal of oxygen. Examples include the die back of *Stuckenia pectinata* and phytoplankton in winter as well as when *S. pectinata* has been harvested in the canals. Another reason could be due to the orientation of the canals so that the canals are protected from wind. The calm conditions result in salinity stratification which in turn causes anoxic conditions to build up below the halocline (Morant and Grindley, 1982). Furthermore according to Davies and

Stewart (1984), oxygen stratification was obvious particularly over winter in the canals with differences of up to 110% saturation.

5.1.1 Spatial variations

Main body, canals and influent rivers comparison: The lower, middle and upper zones were grouped together as the main body. Results from the current study were compared to research done by Harding (1994) who made use of 11 sampling sites. Stations 1 to 5 in the study by Harding (1994) were combined and compared to the main body in the current study, stations 6 to 8 were combined and compared to the canals and stations A, B and C were combined and compared to the influent rivers. Mean values were used by Harding (1994) and median values by the current study.

Median temperature was higher at the main body (20.30 °C and 17.78 °C respectively), canals (20.25 °C and 18.13 °C respectively) and influent rivers (19.00 °C and 17.63 °C respectively) when compared with the findings of Harding (1994). Higher maximum air temperatures were recorded during the study period in comparison to previous years (1981- 2010) which could explain why temperature was higher during the current study in comparison to Harding (1994) results. Median temperature was highest at the main body, lowest at the influent rivers and in between at the canals with the differences across zones being not significantly different. Harding (1994) also found mean temperature to be lowest at the influent rivers but in contrast found mean temperature to be highest at the canals and in between at the main body.

Median salinity was higher at the main body (15.24 ppt and 8.00 ppt respectively) and canals (14.66 ppt and 7.00 ppt respectively) when compared to the data from Harding (1994). Increased salinity compared to previous years is most likely due to the current mouth management protocol as mentioned previously (Cape, 2013; Hutchings *et al.* 2016). Median salinity was highest at the main body, lowest at the influent rivers and in between at the canals with the differences across zones being significantly different. Harding (1994) also observed higher salinity at the main body in comparison to the canals. Similarly Kaselowski (2012) commented that salinity was significantly negatively correlated with distance from the mouth at the Goukamma Estuary. Higher salinity at the main body is most likely due to seawater input under open mouth conditions (Morant and Grindley, 1982).

Median pH was lower at the main body (8.42 and 8.46 respectively) and canals (8.54 and 8.67 respectively) but higher at the influent rivers (7.96 and 7.6 respectively) when compared to the research by Harding (1994). Median pH was highest at the canals, lowest at the influent rivers and in between at the main body with the differences across zones being significantly different. The same trend was noted by Harding (1994). According to Snow and Taljaard (2007), the temporarily open/ closed Diep Estuary displayed lower pH values when freshwater input to the estuary was high. Therefore lower pH measurements at the influent rivers could be due to the influent rivers being very low in salinity (almost freshwater).

Median dissolved oxygen was higher at the main body (8.65 mg/L and 7.92 mg/L respectively), canals (8.68 mg/L and 8.53 mg/L respectively) and influent rivers (8.92 mg/L and 6.03 mg/L respectively) when compared to the study by Harding (1994). Median dissolved oxygen was highest

at the influent rivers, lowest at the main body and in between at the canals with the differences across zones being not significantly different. Furthermore, 48.28% of readings that fell below 3 mg/L were recorded at the main body, 39.65% at the canals and 12.07% at the influent rivers. In contrast, Harding (1994) found mean dissolved oxygen to be highest at the canals, lowest at the influent rivers and in between at the main body. Morant and Grindley (1982) mentioned that dissolved oxygen levels were lower at the influent rivers when compared to the "estuary". Furthermore, Kaselowski (2012) stated that dissolved oxygen was negatively correlated with distance from the mouth at the Goukamma Estuary.

Median Secchi depth was higher at the main body (0.75 m and 0.65 m respectively) and lower at the canals (0.69m and 0.79m respectively), when compared to research done by Harding (1994). In the current study median Secchi depth was significantly higher at the main body in comparison to the canals. In contrast, Harding (1994) found mean Secchi depth to be highest at the canals and lowest at the main body. However, in agreement with the current study, Kaselowski (2012) found that transparency was significantly negatively correlated with distance from the mouth at the Goukamma Estuary.

Median depth was significantly higher at the canals in comparison to the main body. Morant and Grindley (1982) noted the same result whereby the depth of the canals was greater than that of the main body. The main body generally shows shallower depths than the canals as a result of the bathymetry of the system according to C.A.P.E. (2013).

Lower, middle and upper zone comparison: The main body was separated into lower, middle and upper zones. Results from the current study were compared to research done by Harding (1994). Sampling station 1 from Harding's (1994) study was compared to the upper zone in the current study, station 2 and 3 were combined and compared to the middle zone and station 4 and 5 were combined and compared to the lower zone. Mean values were used by Harding (1994) and median values by the current study.

Median temperature was higher at the lower zone (19.00 °C and 17.80 °C respectively), middle zone (20.05 °C and 17.75 °C respectively) and upper zone (20.50 °C and 17.80 °C respectively) when compared to the research by Harding (1994). The sampling period was found to experience higher maximum air temperatures in comparison to previous years (1981- 2010). This could provide a reasoning for higher temperatures during the current study in comparison to Harding (1994) findings. Median temperature increased from the lower zone through the middle zone to the upper zone with the differences across zones being not significantly different. No trend was found for mean temperature across zones in Harding's (1994) data. Snow and Taljaard (2007) discussed how during the open mouth state, a longitudinal temperature gradient can sometimes develop in temporarily open/closed estuaries, with the lowest values being noted at the estuary mouth increasing towards the estuary head (as was seen in the Palmiet Estuary). Furthermore, Kaselowski (2012) found that temperature was positively correlated with distance from the mouth but only for the closed mouth state at the Goukamma Estuary. However, the lack of statistical significance found in the current study indicates that there was not much difference between zones, probably due to wind mixing and water circulation. Hutchings *et al* (2016) stated that temperature was mostly uniform across Zandvlei Estuary.

Median salinity was higher at the lower zone (20.43 ppt and 10.00 ppt respectively), middle zone (15.46 ppt and 7.00 ppt respectively) and upper zone (14.56 ppt and 6.00 ppt respectively) when compared to the results from Harding (1994). Higher salinity values in the current study compared to previous research is most likely due to changes in the mouth management protocol which allows for the more frequent ingress of greater volumes of seawater (Cape, 2013; Hutchings *et al.* 2016). Median salinity decreased from the lower zone through the middle zone to the upper zone with the differences across zones being significantly different. The same trend was found in the study by Harding (1994) for mean salinity across zones. Morant and Grindley (1982) and Hutchings *et al* (2016) studies' based at Zandvlei Estuary as well as Kaselowski (2012) at the Goukamma Estuary all noted highest salinity levels at the mouth of the estuary decreasing when moving towards the head. Higher salinity at the mouth is as a result of saline water moving into the system from the sea whilst lower salinity at the head is caused by freshwater intrusion from influent rivers (Morant and Grindley 1982; Snow and Taljaard, 2007). Muhl *et al* (2003) added that when weather conditions had been clear with no rain for an extended period the difference between salinity at the mouth and the head of Zandvlei Estuary was greater than when there had been rain. The sampling period experienced lower total rainfall in comparison historic data (1981- 2010). Reduced rainfall during the sampling period could have heightened salinity differences between mouth and head.

Median pH was lower at the lower zone (7.96 and 8.30 respectively) and middle zone (8.37 and 8.60 respectively) but equal to at the upper zone (8.50 and 8.50 respectively) when compared to the findings of Harding (1994). Median pH increased from the lower zone through the middle zone to the upper zone with the differences across zones being significantly different. No trend was found for mean pH across zones in Harding's (1994) data. Hutchings *et al* (2016) noted that pH was mostly uniform across Zandvlei Estuary. Contrastingly, Kaselowski (2012) commented that pH was negatively correlated with distance from mouth at the Goukamma Estuary. In support of Kaselowski (2012) findings, Snow and Taljaard (2007) mentioned that high saltwater inflow increases pH and high freshwater inflow lowers pH. A possible explanation for the current study's differing finding is that photosynthetic activity of aquatic macrophytes and phytoplankton was having an effect on pH at Zandvlei Estuary at the time of sampling. According to Morant and Grindley (1982), when aquatic plants photosynthesise they remove carbon from the water which can raise pH levels in the water.

Median dissolved oxygen was lower at the lower zone (6.40 mg/L and 7.05 mg/L respectively) and middle zone (8.49 mg/L and 8.55 mg/L respectively) but higher at the upper zone (9.82 mg/L and 8.4 mg/L) when compared to the results of Harding (1994). Median dissolved oxygen increased from the lower zone through the middle zone to the upper zone with the differences across zones being significantly different. No trend was found for mean dissolved oxygen across zones in Harding's (1994) data. Kaselowski (2012) stated that dissolved oxygen was negatively correlated with distance from the mouth at the Goukamma Estuary, a contrasting result to the findings of the current study.

Interestingly, in the current study, 14.29% of readings that fell below 3 mg/L were recorded at the lower zone, 32.14% at the middle zone and 53.57% at the upper zone. The influent rivers were found to have high concentrations of oxygen (8.92 mg/L) that were higher than levels found in the canals and main body. Perhaps oxygenated water from the influent rivers raised dissolved oxygen levels at the upper zone but only at the surface waters whilst the bottom waters remained low in oxygen.

Median Secchi depth was higher at the lower zone (1.05 m and 0.89 m respectively), middle zone (0.73m and 0.59m respectively) and upper zone (0.7m and 0.53m respectively) when compared to the findings of Harding (1994). Median Secchi depth decreased from the lower zone through the middle zone to the upper zone with the differences across zones being significantly different. Both Morant and Grindley (1982) and Harding (1994) found the same result whereby mean Secchi depth decreased from the lower zone through the middle zone to the upper zone. At the Goukamma estuary, Kaselowski (2012) found that transparency was significantly negatively correlated with distance from the mouth, a comparable result to the current study. A possible reason for Secchi depth being higher at the mouth in comparison to the head is as a result of the influx of seawater at the mouth. Whitfield *et al* (2008) mentioned that seawater entering estuaries on the cool and warm temperate coasts of South Africa is generally low in turbidity (high transparency).

In the current study, median depth increased from the lower zone through the middle zone to the upper zone with the differences across zones being not significantly different. A conceivable reasoning could be due to the bathymetry of Zandvlei Estuary which displays shallow depths close to the mouth getting deeper towards the middle and upper reaches (C.A.P.E., 2013). In addition, the lower reaches of the system have been gradually shallowing in past years (C.A.P.E., 2013). Shallowing of the lower reaches is due to the constant input of marine sediment under open mouth conditions which is then trapped behind a rubble weir (C.A.P.E., 2013).

5.1.2 Temporal variations

Season comparison: Median temperature was highest in summer, lowest in winter and in between during spring and autumn. The differences in temperature across seasons were significantly different. Harding (1994) noted that temperature at Zandvlei Estuary was highest during January/ February (summer) and lowest during June/ July (winter). Between September 2012 and January 2013, two probes set up in the main body of Zandvlei Estuary recorded salinity, depth and temperature (Haskins, 2013). Both probes recorded highest temperature readings in summer. Therefore, it appears that water temperature at Zandvlei Estuary tracks seasonal variations in atmospheric temperature, which is in agreement with the conceptual model for temporarily open/ closed estuaries proposed by Snow and Taljaard (2007). Similarly, a seasonal link between atmospheric and estuarine temperatures was noted by Kaselowski (2012) at the Goukamma estuary as well as Froneman (2002), who studied seasonal changes in several parameters at the temporarily opened/ closed Kasouga Estuary in South Africa.

According to Snow and Taljaard (2007), when estuaries are in the open mouth state, the influx of cold seawater can lower temperatures in an estuary, particularly at the lower and middle reaches. In the current study during winter 100% of sampling events were conducted during open mouth conditions. Therefore, in addition to atmospheric temperatures, the influx of cold seawater could have decreased water temperatures during winter at Zandvlei Estuary.

Median salinity was highest in autumn, lowest in winter and in between during summer and spring. The differences in salinity across seasons were significantly different. Both Thornton *et al* (1995) and Harding (1994) stated that salinity at Zandvlei Estuary was lowest during winter and highest during summer (December/ January). According to Muhl *et al* (2003), salinity at Zandvlei Estuary decreases

in winter with high rainfall and cool temperatures and increases in summer with low rainfall and warm temperatures.

Interestingly, median salinity was higher in autumn in comparison to summer in the current study. In autumn 75% of sampling events were conducted during closed mouth state. According to Snow and Taljaard (2007), salinity levels in a temporarily open/ closed estuary during closed mouth state, can rise sometimes to hypersaline levels. Froneman (2002) mentioned that during a period of low freshwater input and high evaporation rates, salinity reached 37 ppt in the Kasouga Estuary. Therefore, a possible explanation for high salinity during autumn could be due to warm and dry summer- like conditions lingering longer into the year (into autumn). The study period experienced higher maximum air temperatures and lower total rainfall in comparison to previous years (1981-2010). Furthermore, autumn was the season with the greatest difference in maximum air temperature and total rainfall between the study period and historic data (1981- 2010). Lower rainfall and higher temperatures (causing higher evaporation rates) would therefore have been affecting the system for an extended period of time, thereby raising salinity to levels higher than those observed in summer.

Moreover, Muhl *et al* (2003) noted that salinity was higher in autumn than in spring due to a "lag effect" in salinity. Muhl *et al* (2003) explained that during autumn rainfall is absorbed into the dry ground (after summer) before it can flow via rivers into an estuary and influence salinity. However, in spring even though precipitation is low the ground is saturated (after winter). Therefore, rainfall runs straight into the rivers without soaking into the ground and salinity is decreased in the estuary (Muhl *et al.* 2003).

Median pH was highest in winter, lowest in summer and in between during autumn and spring. The differences in pH across seasons were significantly different. In contrast, Harding (1994) noted that pH levels peaked during summer whilst Morant and Grindley (1982) observed pH values to be highest during late spring and early summer. However, an increase in photosynthetic activity of estuarine flora, for example macrophytes, has been documented to raise pH through the removal of carbon dioxide from the water column (Morant and Grindley, 1982; Harding, 1994). Perhaps an increase or decrease in photosynthetic activity influenced pH during the sampling period.

In the current study during winter 100% of sampling events were conducted during open mouth conditions. According to Snow and Taljaard (2007), pH in an estuary is influenced by fresh as well as saline water influx. When freshwater input is high, pH is usually lowered whereas when seawater input is high, pH is usually raised. Increased seawater input could have raised pH levels in winter at Zandvlei Estuary.

Median dissolved oxygen was highest in spring, lowest in autumn and in between during winter and summer. The differences in dissolved oxygen across seasons were significantly different. Furthermore, 13.79% of dissolved oxygen readings that fell below 3 mg/L were recorded during spring, 1.73% during summer, 62.07% during autumn and 22.41% during winter. Contrastingly, Harding (1994) stated that dissolved oxygen was highest during winter and lowest during summer at Zandvlei estuary. According to Snow and Taljaard (2007), during the open mouth state temporarily open/ closed estuaries are expected to display high dissolved oxygen levels as a result of good water exchange due to tidal flushing and river input. In the current study 75% of sampling events in spring

were carried out during open mouth conditions. Perhaps tidal flushing influenced the high dissolved oxygen levels seen in spring.

In addition, macrophytes such as *Stuckenia pectinata* are known to oxygenate the water column through photosynthetic activity (Morant and Grindley, 1982; Davies and Stewart, 1984). Morant and Grindley (1982) stated that photosynthetic activity was highest at Zandvlei Estuary during late spring and early summer, which could explain why dissolved oxygen was highest in spring. When macrophytes die back during senescence, low oxygen conditions can become apparent due to the decomposition process removing oxygen from the water column (Morant and Grindley, 1982; Davies and Stewart, 1984; Snow and Taljaard, 2007). Dissolved oxygen levels can drop further, in particular at the bottom waters, during calm weather conditions when the water column becomes stratified and a halocline develops (Morant and Grindley, 1982). The presence or absence of any of the before mentioned factors could have caused the temporal variations witnessed in the current study.

Median Secchi depth was highest in spring, lowest in winter and in between during summer and autumn. The differences in Secchi depth across seasons were significantly different. Whitfield *et al* (2008) stated that strong river inflow with a concomitant increase in turbulence can result in raised turbidity levels in an estuary. Zandvlei Estuary falls within a winter rainfall region whilst summers are warm and dry (Muhl *et al.* 2003). Therefore, a possible reason for low Secchi depth measurements during winter could be due to strong flows of high turbidity riverine water entering Zandvlei Estuary.

Harding (1994) found that water transparency was usually highest in summer at the lower reaches of Zandvlei Estuary. Harding (1994) result is comparable to the current study's findings as the Secchi depth in summer was only marginally lower than the Secchi depth in spring.

Median depth was highest in winter, lowest in spring and in between during autumn and summer. The differences in depth across seasons were significantly different. Zandvlei Estuary experiences high rainfall and low atmospheric temperatures in winter, but in summer, low rainfall and high atmospheric temperatures prevail (Muhl *et al.* 2003). Therefore, greater depth recordings over winter could be due to high rainfall whilst lower depth recordings during summer could be as a result of low rainfall and high evaporation rates. A further explanation for depth being higher during winter could be due to anthropogenic modifications to the system which have forced the mouth to be artificially opened and closed. Artificial breaching results in a shallow breach and therefore there is not a sustained connection between sea and estuary (C.A.P.E, 2013). Seawater moves into the estuary on a high spring tide and as the tide recedes the newly entered seawater is trapped in the estuary due to the shallowness of the mouth and the presence of a rubble weir (C.A.P.E., 2013).

Physico- chemical targets: Targets were outlined by C.A.P.E. (2013) for salinity and dissolved oxygen at Zandvlei Estuary. In order to find out whether the current study's data confirmed the targets, the lower zone in the current study was compared to the "outlet channel" in the study by (C.A.P.E., 2013) and the middle and upper zones in the current study were combined and compared to the "main body" in the study by (C.A.P.E., 2013).

For the "main body" of the estuary, the current study's results confirmed the winter salinity targets of 5 ppt (surface) and 7 ppt (bottom) with values of 10.50 ppt (surface) and 13.22 ppt (bottom) as well as the summer target of 10 ppt (throughout the water column) with a value of 14.84 ppt

(throughout the water column). For the "outlet channel", the current study's findings confirmed the winter target of 6 ppt (surface) with a value of 10.27 ppt (surface) but not the winter target of 18 ppt (bottom) with a value of 17.03 ppt (bottom). Interestingly, salinity at the bottom waters was higher than 18 ppt in all other seasons. For the outlet channel, the current study's data confirmed the summer targets of 11 ppt (surface) and 13 ppt (bottom) with values of 20.48 ppt (surface) and 21.71 ppt (bottom). C.A.P.E. (2013) set a target for dissolved oxygen of 6 to 8 mg/L for the entire estuary. The current study's results exceeded the target with a value of 8.65 mg/L for the entire estuary. The median depth for the entire estuary was found to be 1.25 m which is sufficient for recreational activities to be practically possible, allows the pondweed harvester to operate effectively and does not place the houses of Marina da Gama in danger.

5.2 Nutrient characteristics

Maximum and mean values for the entire system were calculated from nutrient results reported by Morant and Grindley (1982), Harding (1994) and Quick and Harding (1994) and compared to the current study's findings. Results of previous research were in mg/L and the current study in µM and therefore a conversion was required. From the calculations maximum nitrate + nitrite was 28.06 µM, maximum nitrite 4.76 µM and maximum nitrate 23.30 µM in the study by Morant and Grindley (1982). Mean soluble reactive phosphorus (SRP) was 0.63 µM in the study by Harding (1994) and mean reactive phosphorus (dissolved) 0.25 µM in the study by Quick and Harding (1994).

There was a paucity of comparable data from Zandvlei Estuary for the entire system. With the limited data all nutrient values were higher in the current study in comparison to those noted by Harding (1994), Quick and Harding (1994) and Morant and Grindley (1982). Elevated nutrient levels in the current study compared to previous research could be due to increasing urbanization of the borders of Zandvlei Estuary and its catchment. According to Harding (1994), raised nitrate and phosphate levels recorded at Zandvlei Estuary between the late 1970's and early 1990's were typical of a water body positioned in or near to an urbanised area.

Mouth State comparison: Nitrite was significantly higher during open mouth state in comparison to closed mouth state whilst nitrate + nitrite and nitrate were not significantly different. Total oxidised nitrogen (includes nitrate and nitrite) was significantly different between mouth states at the Goukamma Estuary with concentrations being higher during open mouth state (Kaselowski, 2012).

High riverine input usually results in an estuary mouth breaching. At Zandvlei Estuary the mouth will be artificially breached when high rainfall occurs or is anticipated. Nutrient levels in an estuary are usually higher during the open mouth state due to increased riverine and marine water inflow (Snow and Taljaard, 2007; Kaselowski, 2012). Rivers bring in nutrients from the catchment and seawater (in particular recently upwelled seawater) is known to contribute to nutrient levels in an estuary (Snow and Taljaard, 2007). Contrastingly, during closed mouth state, nutrient concentrations are expected to be lower due to decreased inflow from riverine and marine sources and therefore a decreased input of nutrients (Snow and Taljaard, 2007; Kaselowski, 2012). According to Kaselowski (2012), elevated nutrient levels during open mouth state in comparison to closed mouth state has been documented in several other studies. The before mentioned reasoning's could explain why all nitrogen containing nutrients were higher during open mouth state in comparison to closed mouth

state in the current study. Moreover, during closed mouth state, the residence time of estuarine water is increased and this provides an opportunity for primary producers to uptake the recently introduced nutrients (Snow and Taljaard, 2007). The increased uptake of nutrients would decrease nutrient levels during closed mouth state (Snow and Taljaard, 2007).

Phosphate was not significantly different between open mouth and closed mouth state. Similarly, Kaselowski (2012) found that soluble reactive phosphorus (SRP) was not significantly different between mouth states at the Goukamma Estuary.

All nutrient parameters studied with the exception of Nitrite displayed no significant difference between open mouth and closed mouth state. There are a number of artificial sources of nutrients affecting Zandvlei Estuary, both in the catchment and at the borders of the system (C.A.P.E, 2013). Artificial sources of nutrients include runoff from urbanised areas such as agricultural land and domestic gardens, stormwater drains, industrial waste and overflows from blocked sewers and informal ablutions (C.A.P.E., 2013; Haskins, 2016).

Perhaps the artificial input of nutrients coincided with low riverine inflow and breaching of the mouth was not necessary. Therefore, the system was in the closed mouth state but exhibited elevated nutrient levels similar to those recorded during open mouth conditions. Snow and Taljaard (2007) added that estuaries affected by artificial influences will not always follow the trends outlined by the conceptual model for temporarily open/ closed estuaries developed by Snow and Taljaard (2007).

5.2.1 Spatial variations

Main body, canals and influent rivers comparison: The lower, middle and upper zones were grouped together as the main body. Maximum and mean values for the main body, canals and influent rivers were calculated from the nutrient results reported by Morant and Grindley (1982), Harding (1994) and Quick and Harding (1994) and compared to the current study's maximum and median values. Results of previous research were in mg/L and the current study in µM and therefore a conversion was required.

Maximum nitrate + nitrite was higher at the main body (98.43 µM and 24.11 µM respectively), canals (27.15 µM and 8.36 µM respectively) and influent rivers (144.61 µM and 46.38 µM) when compared to the study by Morant and Grindley (1982). Maximum nitrate + nitrite was highest at the influent rivers, lowest at the canals and in between at the main body. The same trend was found in Morant and Grindley (1982) data. Median nitrate + nitrite was highest at the influent rivers, lowest at the canals and in between at the main body with the differences across zones being significantly different. The same trend was found in Harding (1994) data. In contrast, there was no significant correlation between total oxidised nitrogen levels (includes nitrate and nitrite) and distance from the mouth at the Goukamma Estuary (Kaselowski, 2012).

Maximum nitrite was lower at the main body (2.09 µM and 6.41 µM respectively) and canals (1.54 µM and 4.89 µM respectively) but higher at the influent rivers (14.10 µM and 2.46 µM respectively) when compared to Morant and Grindley (1982). Maximum nitrite was highest at the influent rivers,

lowest at the canals and in between at the main body. The same trend was not found in Morant and Grindley (1982) data.

Maximum nitrate was higher at the main body (97.52 µM and 17.70 µM respectively), canals (26.54 µM and 3.47 µM respectively) and influent rivers (142.17 µM and 43.92 µM respectively) when compared to Morant and Grindley (1982). Maximum nitrate was highest at the influent rivers, lowest at the canals and in between at the main body. The same trend was found in Morant and Grindley (1982) data. In addition, Morant and Grindley (1982) stated that total Kjeldahl nitrogen (TKN) levels were higher at the influent rivers compared to the main body ("Vlei") of Zandvlei Estuary.

Median phosphate was higher at the main body (2.88 µM and 0.14 µM respectively), canals (1.67 µM and 0.05 µM respectively) and influent rivers (3.23 µM and 0.28 µM respectively) when compared to Harding (1994) soluble reactive phosphorus (SRP) data. Median phosphate was higher at the main body (2.88 µM and 0.12 µM respectively) and influent rivers (3.23 µM and 0.30 µM respectively) when compared to Quick and Harding (1994) reactive phosphorus (dissolved) data. Median phosphate was highest at the influent rivers, lowest at the canals and in between at the main body with the differences across zones being significantly different. The same trend was found in Harding (1994) soluble reactive phosphorus (SRP) data. Higher phosphorus at the influent rivers was also noted in Quick and Harding (1994) reactive phosphorus (dissolved) data. In addition, total phosphorus was highest at the influent rivers, lowest at the canals and in between at the main body for mean total phosphorus in the study by Harding (1994) and for maximum total phosphorus in the study by Morant and Grindley (1982). Both Morant and Grindley (1982) and Quick and Harding (1994) found mean total phosphorus to be higher at the influent rivers in comparison to the main body of the system. Furthermore, Kaselowski (2012) found that soluble reactive phosphorus levels at the Goukamma Estuary increased significantly with increasing distance from the mouth but only during open mouth conditions. Mabaso (2002) studied the physico- chemical and macrobenthic characteristics of the Mlalazi Estuary in South Africa and found that soluble reactive phosphorus and total phosphate decreased from the upper reaches towards the mouth.

Nutrient determinants were compared to the before mentioned studies from Zandvlei Estuary. The current study's maximum and median values were higher in comparison to previous research for all nutrients monitored across all zones, with the only exception being maximum nitrite at the main body and canals. Elevated nutrient levels in the current study compared to previous research could be due to the catchment and surrounds of the estuary becoming progressively more urbanised. Urbanization could have resulted in an increased frequency and intensity of nutrient loading. Harding (1994) commented that increases in nitrates and phosphates recorded at Zandvlei Estuary between the late 1970's and early 1990's were characteristic of a water body positioned in or near to an urbanised area.

The current study found maximum and median nutrient concentrations to be highest at the influent rivers and lowest at the canals. The literature reviewed from Zandvlei Estuary was almost always in agreement with the before mentioned trend. There are a number of nutrient sources affecting Zandvlei Estuary, particularly in the catchment (C.A.P.E, 2013). The influent rivers drain the catchment and therefore it is expected that the majority of nutrients entering Zandvlei Estuary do so

via the influent rivers. Estuaries receive nutrients predominantly from external sources (allocthonous), mainly from influent rivers (Snow and Taljaard, 2007). Mabaso (2002) stated that higher nutrient concentrations at the upper reaches of the Mlalazi estuary were an indication that nutrients were being transported into the estuary via influent rivers (Mabaso, 2002).

C.A.P.E. (2013) compiled an estuary management plan for Zandvlei Estuary and speculated that phosphorus levels would be higher at the canals as a result of the breakdown of organic matter including pondweed, *Stuckenia pectinata* (C.A.P.E., 2013). Interestingly, the canals regularly displayed the lowest nutrient concentrations when compared to the main body and influent rivers, both in the current study's findings and those of previous literature. Perhaps there were other factors at play that caused nutrient levels to be lower at the canals. According to Snow and Taljaard (2007), a low nutrient concentration in an estuary can be as a result of the rapid uptake of that nutrient by primary producers.

Influent river comparison: Nutrient concentrations were highest at the influent rivers and therefore the influent rivers were most likely a very important source of nutrients to the estuary itself. As a result, it was deemed valuable to find out which of the influent rivers contributed most to nutrient input.

Morant and Grindley (1982) found maximum nitrite to be highest at the Sand River, lowest at the Westlake River and in between at the Keysers River. Mean annual total nitrogen was highest at the Sand River, lowest at the Westlake River and in between at the Keysers River according to Thornton *et al* (1995). Harding (1994) found that nitrate + nitrite was highest at the Sand River, lowest at the Keysers River and in between at the Westlake River. Furthermore, mean nitrate levels were two to four times greater at the Sand River in comparsion to the Keysers and Westlake Rivers (Harding, 1994). Morant and Grindley (1982) recorded maximum nitrate to be highest at the Sand River, lowest at the Keysers River and in between at the Westlake River.

Previous research therefore found nitrogen- related determinants to be highest at the Sand River and lowest at either the Westlake or Keysers Rivers. In agreement with the results of previous research, the current study found median nitrite to be highest at the Sand River and lowest at the Keysers River. Contrastingly, median nitrate + nitrite and median nitrate were highest at the Westlake River and lowest at the Keysers River.

Haskins (2016) studied nutrient levels within Zandvlei Estuary and the influent rivers. According to Haskins (2016), water quality within the Westlake River has been decreasing since approximately 2000 with a more obvious decrease occurring since 2008. Haskins (2016) finding could explain why certain nutrient parameters (nitrate + nitrite and nitrate) were highest at the Westlake River in the current study.

Harding (1994) noted that total phosphorus, total soluble phosphorus, and soluble reactive phosphorus were highest at the Westlake River, lowest at the Keysers River and in between at the Sand River. Total phosphorus was highest at the Westlake River, lowest at the Keysers River and in between at the Sand River according to Morant and Grindley (1982). Moreover, Thornton *et al* (1995) found slightly higher mean annual total phosphorus values at the Westlake River in comparison to the Sand and Keysers Rivers. According to Quick and Harding (1994), mean total

phosphorus as well as mean reactive phosphorus were highest at the Sand River, lowest at the Keysers River and in between at the Westlake River.

Previous research therefore found phosphorus- related parameters to display highest concentrations predominantly at the Westlake River and lowest concentrations at the Keysers River. The before mentioned finding was in contrast to the results of the current study which recorded median phosphate to be highest at the Sand River and lowest at the Westlake River.

5.2.2 Temporal variations

Season comparison: Median nitrate + nitrite, nitrite and phosphate were highest during winter whilst median nitrate was highest during spring. Median nitrate + nitrite and nitrate were lowest in summer whilst median nitrite and phosphate were lowest during spring. In agreement with the current study's findings, Morant and Grindley (1982) mentioned that nutrient levels rise during winter at Zandvlei Estuary. Harding (1994) added that nutrient input to Zandvlei Estuary occurs mainly between April and September which would include all winter months. However, according to a summary of Harding (1994) data by Quick and Harding (1994), no clear seasonal variations could be observed for nitrogen and phosphorus at Zandvlei Estuary.

Kaselowski (2012) noted that soluble reactive phosphorus (SRP) was significantly different between months with both the highest and lowest readings being recorded in winter at the Goukamma Estuary. Total oxidised nitrogen (includes nitrate and nitrite) at the Goukamma Estuary was significantly different between months with the highest recordings being witnessed in winter and the lowest recordings in spring (Kaselowski, 2012).

Mabaso (2002) stated that nitrate and nitrite levels were highest during winter and autumn in the Mlalazi Estuary. In contrast, orthophosphate and total phosphate levels were highest during spring and summer (Mabaso, 2002). The Mlalazi Estuary falls within the subtropical biogeographic region and experiences numerous high rainfall events in summer (Mabaso, 2002). High rainfall increases run off from agricultural areas and rural settlements which are potential sources of nutrient loading to estuaries (Mabaso, 2002).

Zandvlei Estuary is part of the cool temperate biogeographic zone and receives winter rainfall (Muhl *et al.* 2003; Whitfield and Baliwe, 2013). As mentioned by Mabaso (2002), rainfall increases run off from an estuary's surroundings and catchment, thereby facilitating the movement of nutrients into an estuary. Most of an estuary's nutrients come from outside the system, particularly from the catchment via river inflow (Snow and Taljaard, 2007). Therefore, seasonal rainfall patterns could provide an explanation for the higher nutrient levels recorded during winter at Zandvlei Estuary.

Moreover, in winter 100% of sampling events were conducted during open mouth conditions. Seawater input under open mouth conditions is known to contribute to nutrient levels in an estuary (Snow and Taljaard, 2007). Therefore, not only could the nutrient concentration in Zandvlei Estuary be influenced by river inflow but also by inflowing seawater at the mouth.

5.3 *Stuckenia pectinata* biomass and distribution characteristics

Stuckenia pectinata biomass was present in 62% of samples at Zandvlei Estuary. *S. pectinata* had a percentage frequency of occurrence of 50.2% at Heron Lake in the USA (Case and Madsen, 2004). At the same system, Wersal *et al* (2006) found percentage frequency of occurrence to be 77.60% and 76.30%. Therefore, the current study's results were comparable to those from Case and Madsen (2004) and Wersal *et al* (2006).

Thornton *et al* (1995) stated that estimates of total annual yield of *S. pectinata* from Zandvlei Estuary were comparable to other systems in the same region. However, when compared to Swartvlei Estuary, another temporarily open/ closed South African estuary (annual yields of 2506 g/m^2 dry mass per year), annual yields of *S. pectinata* were far lower at Zandvlei Estuary (Thornton *et al.* 1995). The current study did not look at total annual yield. However, a similar result was found for maximum dry biomass which was far lower at Zandvlei Estuary (377.57 g/m^2) in comparison to Swartvlei Estuary (1950 g/m^2) (Howard- Williams, 1978). Thornton *et al* (1995) mentioned that possible reasons for lower biomass levels at Zandvlei Estuary in comparison to Swartvlei Estuary were due to a more extreme temperature regime, reduced light penetration, more turbulent conditions (wave action caused by wind) and sediment less favourable to the growth of *S. pectinata*.

Kantrud (1990) summarised maximum biomass (g/m^2 dry mass) of *S. pectinata* from sixty two studies from across the globe. Kantrud (1990) found maximum dry biomass to range from <5 g/m^2 – 1988 g/m^2 with a calculated average of 388 g/m^2 from the sixty two studies. Madsen and Adams (1988) summarised maximum biomass (g/m^2 dry mass) of *S. pectinata* from twenty studies from around the world. Maximum dry biomass was observed to vary between 5 g/m^2 and 1952 g/m^2 with a calculated average from the twenty studies of 368 g/m^2 (Madsen and Adams, 1988). Maximum dry biomass was 377.57 g/m^2 in the current study and was therefore comparable to the average maximum biomass from the several previous studies reviewed by Madsen and Adams (1988) and Kantrud (1990). The highest biomass values found by Kantrud (1990) were however far higher than those sampled in the current study. Kantrud (1990) found the highest *S. pectinata* biomass levels (>1500 g/m^2 dry mass) to be recorded in Africa and included the studies by Zaky (1960) (1988 g/m^2), Aleem and Samaan (1969b) (<1568 g/m^2) and Howard- Williams (1978) (1952 g/m^2). Dry Biomass values over 1500 g/m^2 for any submerged macrophyte have been considered as exceptionally high and not the norm according to Casagranda and Boudouresque (2007).

To provide perspective, in the current study the maximum dry biomass value of 377.57 g/m^2 was the single highest biomass value found during the study period. The value was neither a spatial or temporal average nor a representation of the maximum biomass over the entire system. Mean biomass values were substantially lower in comparison to maximum biomass values in the current study.

Mean dry biomass in the current study was 17.69 g/m^2 and therefore biomass levels were comparable to those noted at Swartvlei Estuary only after the collapse in *S. pectinata* over the 1979 winter. Above ground dry biomass levels at Swartvlei Estuary were 8 g/m^2 in January 1980, 80 g/m^2 in January 1981 and 0.3 g/m^2 in January 1982 (Whitfield, 1984). Mean dry biomass data was not available for a healthy *S. pectinata* population at Swartvlei Estuary. Looking at maximum dry biomass values recorded by Howard- Williams (1978) it is expected that mean dry biomass at Swartvlei

Estuary would be far higher than mean dry biomass recorded at Zandvlei Estuary. Weisser *et al* (1992) studied the dynamics of submerged macrophytes in the Wilderness lakes, South Africa. Mean dry biomass of *S. pectinata* in 1982 was 109 g/m^2 at Eilandvlei and 750 g/m^2 at Langvlei (Weisser *et al.* 1992). In summary, mean dry biomass levels in the current study were substantially lower than those documented in other South African systems.

Kantrud (1990) summarised tuber density (N/m^2) of *S. pectinata* from twenty seven studies from around the world. Kantrud (1990) found tuber density to vary between 8 N/m^2 and 4909 N/m^2 with a calculated average from the twenty seven studies of 831 N/m^2. The current studies maximum tuber density of 1204 N/m^2 was therefore higher than the average tuber density from the twenty seven studies reviewed by Kantrud (1990). In the current study the maximum tuber density of 1204 N/m^2 was the single highest tuber density value noted during the study period. The value was neither a spatial or temporal average nor a representation of the maximum tuber density over the entire system. Mean tuber density was substantially lower in comparison to maximum tuber density in the current study.

Mean tuber density was 80 N/m^2. At the Heron Lake system in the USA, mean tuber density ranged from 23 N/m^2 – 105 N/m^2 (Case and Madsen, 2004; Wersal *et al.* 2006). Therefore, mean tuber density was comparable to the findings of Case and Madsen (2004) and Wersal *et al* (2006).

Mean dry mass and tuber density displayed high standard deviations (47.54 g/m^2 and 197 N/m^2 respectively). Variability in the data was seen by large differences between mean and maximum values for dry mass and tuber density. High standard deviations highlight the variable and patchy distribution of *S. pectinata* at Zandvlei Estuary. There were areas of moderately high biomass and there were also many areas where biomass was low or non-existent which caused mean biomass to be low for the entire system.

Furthermore, the results for dry mass were lower in comparison to previous studies whereas results for tuber density were more comparable. The finding may indicate that above ground biomass was under sampled. The design for the core sampler used in the current study was drawn up by Madsen *et al* (2007). The design has been documented to be very effective at sampling macrophyte biomass, in particular underground biomass including tubers (Madsen and Wersal, 2012). The core sampler did not sample emergent above ground biomass as successfully though according to Madsen and Wersal (2012). Madsen *et al* (2007) added that the effectiveness of the design was reduced when sampling in sandy sediments in comparison to silt and clay sediments.

5.3.1 Spatial variations

Main body and canals comparison: There was a lack of quantitative data on how *Stuckenia pectinata* biomass varied spatially at Zandvlei Estuary. Thornton *et al* (1995) commented that estimates of total annual yield of *S. pectinata* were higher at the canals than at the main body of Zandvlei Estuary. The current study found a similar trend whereby mean wet mass and dry mass were higher at the canals in comparison to the main body but not significantly so.

Wave action has been found to have a number of negative impacts on *S. pectinata* (Van Wijk, 1988; Kantrud, 1990; Whitfield *et al.* 2008). Wave action impacts *S. pectinata* directly through physical damage and uprooting (Kantrud, 1990; Case and Madsen, 2004; Whitfield *et al.* 2008). Wave action

causes sediment resuspension, therefore increasing turbidity and decreasing light availability, a very important parameter influencing *S. pectinata* biomass and distribution (Kantrud, 1990; Whitfield *et al.* 2008). Without a critical level of light submerged macrophytes such as *S. pectinata* cannot photosynthesise (Case and Madsen, 2004).

Furthermore, high wave action causes particle sorting and is therefore often associated with coarser sediments that are not favourable to the growth of submerged macrophytes (Case and Madsen, 2004). Macrophytes that grow in sediments made up of a high proportion of sand are more at risk of uprooting (Case and Madsen, 2004). Moreover, sediments comprising a high proportion of sand are generally lower in nutrients in comparison to finer sediments such as silt and clay (Case and Madsen, 2004). Case and Madsen (2004) found a negative correlation between the presence of *S. pectinata* shoots and the amount of sand in the sediment. At the main body sediment retained for the 500 μm size class was significantly negatively correlated with both wet mass and dry mass on two occasions. Sediment retained for the 500 μm size class would relate to coarse grained sand (0.5mm to 1mm) on the Wentworth scale (CSIR, 2015).

According to Morant and Grindley (1982), one of the most influential parameters at Zandvlei Estuary and especially at the canals, are wind patterns. The predominant winds are from the north in winter and the south in summer (Morant and Grindley, 1982). The canals have been constructed so that they align perpendicular to the predominant winds (Morant and Grindley, 1982). Therefore, conditions in the canals are often calm with very little associated wave action and turbulence in the water column (Morant and Grindley, 1982). In contrast, the main body lies parallel to predominant winds and therefore is exposed to wind and associated wave action and mixing (Morant and Grindley, 1982). Moreover, the main body was found to be shallower than the canals both in the current study and historically (Morant and Grindley, 1982). Shallower depths are known to exacerbate the negative effects of wave action on submerged macrophytes such as *S. pectinata* (Case and Madsen, 2004; Wersal *et al.* 2006). Therefore, the more wind and wave exposed nature of the main body could have caused *S. pectinata* biomass to be lower there in comparison to the canals which experience less wind and associated wave action.

Interestingly, mean tuber density was significantly higher at the main body in comparison to the canals. According to Kantrud (1990), below ground biomass of *S. pectinata*, which incorporates tubers, can vary between 4% and 78% of total plant biomass. The ratio of above and below ground biomass for *S. pectinata* depends on a number of environmental factors (Van Wijk, 1988; Kantrud, 1990). Kantrud (1990) stated that a higher percentage of total biomass of *S. pectinata* was allocated to above ground biomass when *S. pectinata* grew in soft sediment in sheltered areas in comparison to sand and gravel bottoms in exposed areas. In the current study sediment retained for the 1700 μm size class, which relates to very coarse grained sand (1.0 – 2.00 mm) and gravel (>2.0 mm) on the Wentworth scale, was significantly positively correlated with tuber density on one occasion at the main body (CSIR, 2015). The before mentioned findings could explain why tuber density, which contributes to belowground biomass, was higher at the wind and wave influenced main body in comparison to the more protected canals.

Madsen and Adams (1988) found underground biomass of *S. pectinata* to be higher in comparison to other studies. The authors speculated that *S. pectinata* adapted to high current speeds by allocating more biomass to underground structures (Madsen and Adams, 1988). Perhaps higher current speeds

in the more exposed main body resulted in *S. pectinata* producing more tubers there in comparison to the more sheltered canals.

Depth was significantly negatively correlated with tuber density on three occasions. It could be possible that the shallower depths of the main body provided conditions which promoted the growth of tubers. Whilst areas of lower depth are more susceptible to the negative effects of wave action, these areas can also experience greater light availability (Wersal *et al.* 2006). Increased light availability has been documented to allow *S. pectinata* to divert more energy to the production of tubers (Wersal *et al.* 2006).

Lower, middle and upper zone comparison: According to Morant and Grindley (1982), in terms of the main body of Zandvlei Estuary, *S. pectinata* occurred most frequently in the middle reaches particularly off the western shoreline of Park Island as well as offshore from the Imperial Yacht Club. Similarly, in the current study mean dry mass and mean tuber density were highest at the middle zone. Mean wet mass, dry mass and tuber density were lowest at the lower zone. For wet mass, dry mass and tuber density the lower zone differed significantly from both the middle and upper zones. The middle and upper zones were not significantly different from each other. The before mentioned findings indicate that the middle and upper zones were similar in terms of *S. pectinata* biomass but differed from the lower zone in which *S. pectinata* was never recorded.

Salinity is an important factor regulating the biomass and distribution of *S. pectinata* (Quick and Harding, 1994). Whilst increased salinities at Zandvlei Estuary have been noted to provide *S. pectinata* with an advantage over phytoplankton, salinity can still be a limiting factor to *S. pectinata* growth (Quick and Harding, 1994). Howard- Williams and Liptrot (1980) stated that *S. pectinata* was never found in areas were salinity reached 35 ppt ($^0/_{00}$) in the Swartvlei Estuary. *S. pectinata* has been found to have a salinity tolerance ranging between 5 and 20 ppt (C.A.P.E., 2013). Howard-Williams and Liptrot (1980) stated that Ward (1976) found 19 ppt ($^0/_{00}$) to be the highest salinity *S. pectinata* could endure for long time periods at the St Lucia Estuary in South Africa. At Swartvlei Estuary, salinity levels during 1976 averaged 16 ppt ($^0/_{00}$) for many months and no negative effects were observed on the standing stock of *S. pectinata* (Howard- Williams and Liptrot, 1980). However, in the Netherlands Verhoeven and van Vierssen (1978) commented that the maximum salinity tolerated by *S. pectinata* was 15 ppt ($^0/_{00}$) (Howard- Williams and Liptrot, 1980). Whitfield *et al* (2008) stated that *S. pectinata* favoured lower levels of salinity between 5 and 15 ppt. According to Kantrud (1990), *S. pectinata* had an optimal salinity range of 5 – 14 g/L (Kantrud, 1990). When salinity was between 13- 20 g/L in coastal areas, *S. pectinata* was often outcompeted by algae and *Ruppia* dominated communities (Kantrud, 1990). In light of the information presented in several previous studies, *S. pectinata* appears (particularly in South African systems) to be tolerant of salinities between 5 ppt and 20 ppt. However, at the higher end of this range *S. pectinata* may be outcompeted by other macrophytes. *S. pectinata* does not seem to tolerate salinity values over 20 ppt.

Salinity was significantly negatively correlated with both wet and dry mass on two occasions and with tuber density on four occasions. In the current study median salinity was 20.43 ppt at the lower zone, 15.46 ppt at the middle zone and 14.56 ppt at the upper zone. It is suspected that higher salinities experienced at the lower zone contributed to the complete exclusion of *S. pectinata* from

this region. Therefore, the *S. pectinata* population at Zandvlei Estuary is assumed to exhibit an upper salinity range approaching 20 ppt. Salinity levels during the study period did not fall below 10 ppt for a consistent period of time and therefore it is unlikely that *S. pectinata* was limited by low salinity. S. *pectinata* was found at moderately high biomass levels within both the middle and upper zones where salinity was lower. Interestingly, at the canals no significant negative correlations were found between *S. pectinata* biomass parameters and salinity, probably due to the narrower salinity range found in the canals.

Sediment retained for the 1700 µm and 1180 µm size classes was highest at the lower zone and lowest at the middle and upper zones. The 1700 µm size class relates to very coarse sand and gravel and the 1180 µm to very coarse sand on the Wentworth scale (CSIR, 2015). Sediment retained for the 63 µm and <63 µm size classes was highest at the upper zone and lowest at the middle and lower zones. The 63 µm size class relates to very fine grained sand and the <63 µm size class to mud on the Wentworth scale (CSIR, 2015). Therefore, the coarsest sediment sampled was most prominent at the lower zone and the finest sediment at the upper zone. Sediments comprising a high proportion of sand are generally lower in nutrients in comparison to finer sediments such as silt and clay (Case and Madsen, 2004). Madsen *et al* (2008) found a positive correlation between the presence of *S. pectinata* and the proportion of clay in the sediment at Swan Lake in the USA. Moreover, macrophytes that grew in sediments made up of a high proportion of sand were more at risk of uprooting (Case and Madsen, 2004). Case and Madsen (2004) found a negative correlation between the presence of *S. pectinata* shoots and the amount of sand in the sediment. Therefore, the distribution of sediment grain size at Zandvlei Estuary could have influenced the higher *S. pectinata* biomass levels recorded at the middle and upper zones in comparison to the lower zone.

However, the correlations carried out in the current study were in direct contrast to the findings of previous literature. Sediment retained for the 1700 µm size class was significantly positively correlated with tuber density on one occasion at the main body. Furthermore, sediment retained for both the 63 µm and <63 µm size classes was significantly negatively correlated with wet mass, dry mass and tuber density on one occasion at the main body.

Sediment retained for the 250 µm size class was significantly positively correlated with wet mass, dry mass and tuber density on two occasions. The 250 µm size class relates to medium grained sand on the Wentworth scale (CSIR, 2015). Sediment retained for the 250 µm size class was highest at the middle zone. At the main body, mean dry mass and tuber density were also highest at the middle zone. The before mentioned finding could suggest that *S. pectinata* had a preference for growing in medium grained sands at Zandvlei Estuary.

The influent rivers were found to have the highest nutrient levels anywhere in the system. The influent rivers enter Zandvlei Estuary at the upper zone and therefore it is suspected that the middle and upper zones would have higher nutrient levels in comparison to the lower zone. Increased nutrient levels could have contributed to the higher biomass levels recorded at the middle and upper zones in comparison to the lower zone.

The growth of *S. pectinata* and other macrophytes in the main channel of the Swartvlei Estuary was limited due to current speeds being above 1 m/s (Howard-Williams and Liptrot, 1980). Perhaps the lower zone at Zandvlei Estuary was exposed to higher current speeds due to the proximity of the

mouth and the associated inflowing and outflowing water. The turbulence created may have prevented the establishment of *S. pectinata* and thereby contributed to the exclusion of *S. pectinata* from the lower zone.

5.3.2 Temporal variations

Thornton *et al* (1995) stated that annual biomass produced by *Stuckenia pectinata* was similar between 1983 and 1988 at Zandvlei Estuary. *S. pectinata* did however display an obvious seasonal biomass trend with maximum biomass being noted in late summer between January and April (Thornton *et al.* 1995). Furthermore, Howard- Williams (1978) discussed the temporal variations in *S. pectinata* growth at the Swartvlei Estuary. According to Howard- Williams (1978), developing *S. pectinata* shoots became apparent in late winter and early spring (September to October) with maximum biomass being obtained in late summer and early autumn (March to April). *S. pectinata* would then die back in early to mid- winter (June to July) (Howard- Williams, 1978). In a polluted stream (Badfish Creek) in the USA, *S. pectinata* shoots started growing in spring and reached peak biomass in summer (Madsen and Adams, 1988). High production of tubers became apparent when the senescence period began at the end of summer (Madsen and Adams, 1988). Winter biomass was very low with underground structures, in particular tubers, making up the majority of total plant biomass (Madsen and Adams, 1988).

Therefore there was a shared seasonal trend in *S. pectinata* biomass between South African and international literature with highest biomass observed in summer and lowest biomass in winter. The results from the current study were not in agreement with those recorded in previous research. Mean wet mass and dry mass were highest in winter, lowest in summer and in between in spring and autumn. Mean tuber density was highest in spring, lowest in summer and in between in winter and autumn. The differences in wet mass, dry mass and tuber density across seasons were not significantly different indicating that *S. pectinata* biomass was relatively similar across seasons. The lack of significant difference between seasons made it difficult to identify meaningful trends. Moreover, the current studies contrasting seasonal biomass trend made it difficult to find supporting literature to explain the current study's findings. The observed seasonal biomass trend could have been influenced by rainfall and temperature dynamics during the study period. Data supplied by the South African Weather Service showed that the study period experienced higher maximum air temperatures and lower total rainfall in comparison to historic data (1981- 2010).

Nutrients are well known to be an important factor influencing the biomass and distribution of macrophytes including *S. pectinata* (Van Wijk, 1988; Kantrud, 1990; Whitfield and Bate, 2007). According to Kantrud (1990), *S. pectinata* is highly effective at taking up and concentrating major nutrients, micro nutrients and trace elements. The proliferation of *S. pectinata* over the years at Zandvlei Estuary is thought to be caused by nutrient loading (Whitfield *et al.* 2008; C.A.P.E., 2013).

In the current study both mean wet mass and dry mass were highest during winter with median nitrate + nitrite, nitrite and phosphate also highest in winter. Mean tuber density was highest in spring with median nitrate also highest in spring. Therefore, the seasons with the highest biomass levels (winter and to a lesser extent, spring) were also the seasons with the highest nutrient recordings (winter and to a lesser extent, spring). As a result, the nutrient regime at Zandvlei Estuary may have influenced certain seasonal variations in *S. pectinata* biomass observed during the study period.

Correlation analysis however did not support the argument that nutrients positively influenced *S. pectinata* biomass during certain seasons. Nitrite, nitrate and phosphate were never found to correlate significantly with wet mass, dry mass or tuber density. Nitrate + nitrite was never significantly correlated with either wet mass or dry mass. Nitrate + nitrite was significantly negatively correlated with tuber density on one occasion and significantly positively correlated with tuber density on one occasion.

The seasonal trend in *S. pectinata* biomass was in contrast to the findings of previous literature, both in a South African and International context. There may have been factors oustside the scope of the current study which influenced the documented seasonal variations in *S. pectinata* biomass. Over and above the parameters discussed previously, *S. pectinata* biomass may have been influenced by light availability, growth and subsequent shading from phytoplankton, epiphytes and multicellular algae, herbivorous grazing by waterfowl and fish, nutrient levels within the sediment and mechanical harvesting (Van Wijk, 1988; Kantrud, 1990; Thornton *et al.* 1995; Case and Madsen, 2004).

5.4 Factors influencing the biomass and distribution of *Stuckenia pectinata*- correlations between *Stuckenia pectinata* biomass and other parameters studied

5.4.1 *Stuckenia pectinata* biomass and physico- chemical characteristics

Temperature did not correlate significantly with wet mass, dry mass or tuber density. In contrast, the majority of previous literature found temperature to display a positive relationship with *Stuckenia pectinata* biomass. Increased temperature was found to raise biomass levels and seed production of *S. pectinata* according to Kantrud (1990). Wersal *et al* (2006) found that temperature exhibited a strong positive relationship with seasonal biomass of S*. pectinata*. Furthermore, low temperatures were found to negatively influence *S. pectinata* survival (Van Wijk, 1988).

Salinity was significantly negatively correlated with both wet and dry mass on two occasions and with tuber density on four occasions. Previous literature showed variable results indicating positive and negative relationships or no relationship at all. Riddin and Adams (2008) found no correlation between submerged macrophyte cover and salinity. At Zandvlei Estuary, increased salinity seemed to favour the growth of *S. pectinata* over phytoplankton (Quick and Harding, 1994). However, Menendez and Comin (1989) mentioned that *S. pectinata* benefited from periods of lower salinity caused by freshwater input. Macrophytes including *S. pectinata* live within a specific tolerance range for salinity (Whitfield *et al.* 2008). The negative correlation between salinity and *S. pectinata* biomass may have been due to *S. pectinata* experiencing salinity levels above its tolerance range.

pH was significantly positively correlated with both wet and dry mass on three occasions. pH was not significantly correlated with tuber density. *S. pectinata* occurs in alkaline waters with a pH range of 7.0 – 9.0 but has been documented to photosynthesise at pH >10.5 (Kantrud, 1990). Median pH in the current study was well within the before mentioned range and therefore it is assumed that *S. pectinata* was not limited by pH in the current study. Instead, it is thought that positive correlations observed between pH and *S. pectinata* biomass were as a result of the macrophyte's influence on pH. According to Morant and Grindley (1982), pH can be influenced by the photosynthetic activity of

aquatic macrophytes and phytoplankton. When plants photosynthesise they remove carbon from the water which can raise pH levels (Morant and Grindley, 1982).

Dissolved oxygen was significantly positively correlated with both wet mass and dry mass on two occasions and with tuber density on one occasion. According to Snow and Taljaard (2007), dissolved oxygen levels above 6 mg/L indicate that an estuary is sufficiently oxygenated. It is thought that *S. pectinata* was not limited by dissolved oxygen in the current study. Rather, as with pH, it is thought that positive correlations between dissolved oxygen and *S. pectinata* biomass were due to the macrophyte's influence on dissolved oxygen. Macrophytes such as *S. pectinata* are known to oxygenate the water column through photosynthetic activity (Morant and Grindley, 1982; Davies and Stewart, 1984). Furthermore, when macrophytes die back during senescence, low oxygen conditions can become apparent due to the decomposition process removing oxygen from the water column (Morant and Grindley, 1982; Davies and Stewart, 1984; Snow and Taljaard, 2007).

Secchi depth is an indicator of water transparency and turbidity. Secchi depth was significantly negatively correlated with wet mass on one occasion. Secchi depth was not significantly correlated with dry mass or tuber density. Similarly, Riddin and Adams (2008) found no correlation between submerged macrophyte cover and turbidity. According to Wersal *et al* (2006), water transparency doesn't influence *S. pectinata* biomass directly but it does influence other parameters such as light availability which do (Wersal *et al.* 2006). Water with low transparency reduces light availability which has a negative impact on *S. pectinata* biomass through lowered photosynthetic activity (Wersal *et al.* 2006). This would indicate a positive correlation between water transparency and *S. pectinata* biomass. The negative correlation between Secchi depth and *S. pectinata* biomass is therefore surprising.

Depth was significantly negatively correlated with both wet mass and dry mass on one occasion and with tuber density on three occasions. According to Quick and Harding (1994), lower water depths seemed to favour the growth of *S. pectinata* over phytoplankton at Zandvlei Estuary. Kantrud (1990) mentioned that no relationship was found between tuber density and depth in one particular study reviewed. Wersal *et al* (2006) noted that depth had no significant influence on *S. pectinata* biomass (Wersal *et al.* 2006). According to Wersal *et al* (2006), depth alone was not likely to influence *S. pectinata* biomass but depth could influence other factors such as light availability which do. A critical level of light is required for photosynthesis in all aquatic plants (Wersal *et al.* 2006). At greater depths the critical light level may not be obtained and biomass can be reduced as a result of decreased photosynthetic activity (Wersal *et al.* 2006). The negative correlation between depth and *S. pectinata* biomass was therefore justifiable but it is unlikely that depth alone influenced *S. pectinata* biomass.

5.4.2 *Stuckenia pectinata* biomass and nutrient characteristics

With the exception of one negative and one positive correlation with tuber density, no significant correlations were found between *Stuckenia pectinata* biomass (wet mass, dry mass and tuber density) and nutrient parameters sampled. Nutrients have been widely documented to have an important positive relationship with *S. pectinata* biomass (Van Wijk, 1988; Kantrud, 1990; Quick and Harding, 1994). Nutrient loading has been long regarded as the reason for high levels of *S. pectinata*

biomass at Zandvlei Estuary (Whitfield *et al.* 2008; C.A.P.E., 2013). However, the current studies finding of a lack of significance between nutrients and *S. pectinata* biomass is still plausible. According to Madsen and Adams (1988), during eutrophic conditions when nutrient levels are high, the ability of macrophytes to uptake the excess nutrients may be exceeded. In certain systems macrophytes are not nitrogen and phosphorus limited and therefore increases in nutrients will not have an impact on macrophyte growth (Madsen and Adams, 1988). Madsen and Adams (1988) mentioned that many calcareous streams display persistently high macrophyte biomass levels regardless of variations in nutrient input. Ozimek *et al* (1986) sampled the densest areas of *S. pectinata* within a Polish lake. Even though the system was eutrophic, total dry biomass was found to be low at 43.6 g/m^2 (Ozimek *et al.* 1986). Moreover, when nitrogen concentrations were low, Kantrud (1990) found that *S. pectinata* had a great ability to take up nitrogen and compete for it. Therefore, the biomass and distribution of *S. pectinata* was not likely to be limited by the availability of nitrogen according to Kantrud (1990).

5.4.3 *Stuckenia pectinata* biomass and sediment characteristics

The current study found many conflicting positive and negative correlations between *Stuckenia pectinata* biomass (wet mass, dry mass and tuber density) and sediment characteristics. As a result, clear trends were difficult to find. The general consensus amongst previous literature was that coarse sediments were associated with lower *S. pectinata* biomass and fine sediments with higher *S. pectinata* biomass. Case and Madsen (2004) found a negative correlation between the presence of *S. pectinata* shoots and the amount of sand in the sediment. Madsen *et al* (2008) found a positive correlation between the presence of *S. pectinata* and the proportion of clay (fine sediment) in the sediment. In the current study many of the correlations carried out were in direct contrast to the findings of previous literature. Sediment retained for the 1700 μm size class, relating to very coarse-grained sand and gravel, was significantly positively correlated with tuber density (CSIR, 2015). Furthermore, sediment retained for both the 63 μm and <63 μm size classes, relating to very fine grained sand and mud, was significantly negatively correlated with wet mass, dry mass and tuber density (CSIR, 2015). Not all correlations were in opposition to previous literature. Sediment retained for the 500 μm size class, relating to coarse grained sand, was significantly negatively correlated with wet mass, dry mass and tuber density. In addition, sediment retained for the 250 μm size class, relating to medium grained sand, was significantly positively correlated with wet mass, dry mass and tuber density on two occasions (CSIR, 2015). Therefore, *S. pectinata* may have favoured growing in medium grained sands at Zandvlei Estuary. Similar findings were not found in the literature reviewed.

6. Conclusion and recommendations

Important drivers of *Stuckenia pectinata* biomass and distribution, both spatially and temporally at Zandvlei Estuary were identified in this study. Elevated salinity negatively influenced *S. pectinata* biomass within the lower reaches. Nutrients were thought to influence seasonal variations in *S. pectinata* biomass. The distribution of sediment grain size was suspected to influence variations in *S. pectinata* biomass within the main body. Wave action and associated effects, caused by the wind regime, were thought to negatively influence *S. pectinata* biomass within the main body.

Salinity, Secchi depth and depth displayed a negative relationship with *S. pectinata* biomass whilst pH and dissolved oxygen displayed a positive relationship. Surprisingly, temperature and nutrient parameters had no relationship with *S. pectinata* biomass. Conflicting positive and negative relationships were recorded between *S. pectinata* biomass and sediment characteristics and as a result clear trends were difficult to extract. Furthermore, certain results were not in agreement with trends found in previous studies from Zandvlei Estuary as well as other systems. Lower rainfall and higher temperatures experienced during the sampling period could present an explanation.

Future studies at Zandvlei Estuary should consider conducting a point intercept survey to quantify *S. pectinata* distribution as outlined by Wersal *et al*. (2006). *S. pectinata* biomass sampling should be carried out in areas known to have dense stands of *S. pectinata* rather than areas of patchy coverage. This could give an improved understanding of how biomass varies temporally and should reduce some of the variability in the biomass data**,** thereby helping to elucidate significant factors influencing the biomass of *S. pectinata*. A future study may benefit from looking at light availability, mechanical harvesting, phytoplankton abundance and nutrient concentrations within the sediment. The use of flow gauges at the mouth and influent rivers would be important.

The current study produced field based, year- long, whole system data of *S. pectinata* biomass and distribution as well as an analysis of factors influencing the macrophyte including physico- chemical and nutrient characteristics. The results add to conservation authorities' understanding of the influence of environmental characteristics on *S. pectinata* biomass and distribution allowing more effective anticipation of changes in *S. pectinata* biomass and distribution thus preventing extremes in its growth. The knowledge acquired will assist conservation authorities in refining the *S. pectinata* harvesting protocol thereby allowing the macrophyte to be maintained more effectively. To expand on the knowledge acquired from the current study it is imperative that continued monitoring takes place to facilitate improved management of *S. pectinata*. A healthy standing stock of *S. pectinata* is a critically important factor ensuring that conditions at Zandvlei Estuary benefit both the human and biological components of the system.

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8. Appendix

Figure 34: Preparing to take a core sample (Photo by Cherry Giljam, July 2017)

Figure 35: Using a core sampler to obtain sediment and *Stuckenia pectinata* biomass samples (Photo by Cherry Giljam, July 2017)

Figure 36: Patches of *Stuckenia pectinata* at the upper reaches of Zandvlei Estuary (Photo by Kyle Maurer, November 2017)

Figure 37: *Stuckenia pectinata* with a covering of epiphytic algae at the middle reaches of Zandvlei Estuary (Photo by Kyle Maurer, November 2017)