Decadal shifts in macrobenthic community structure in a permanently open freshwater-deprived Eastern Cape Estuary

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Abstract

The decadal shifts in the macrobenthic community structure in the permanently open, freshwater-deprived Kariega Estuary along the southeastern coastline of South Africa were investigated between 2010 and 2022. The macrobenthic community structure was investigated at six stations in four distinct ecological zones: Zone I was made up of *Zostera capensis*, Zone II was made up of mud, Zone III was made up of *Spartina maritima*, and Zone IV was made up of *Sarcocornia perrenis* along the length of the estuary. The average abundance and biomass of macrobenthic organisms during the 2010 survey ranged from 16 to 504 ind/m^2 and from 0.03 to 245 g wwt/m^2, respectively. In 2022, the average abundance of macrobenthic organisms ranged from 6 to 216 ind/m^2. The average macrobenthos biomass was 2.60 to 93.40 g wwt/m^2. There were no significant differences in the estimates of the total macrobenthic abundance and biomass between the two surveys or the different ecological zones ($P > 0.05$ in all cases). Site-specific differences were, however, evident. During both surveys, the highest abundance and biomass values were recorded in the middle reach, corresponding to the region with the highest biomass of submerged macrophytes. Multidimensional scaling revealed a high degree of overlap in the macrobenthic community composition between the two surveys. The absence of any significant spatial or temporal patterns in the macrobenthic community structure along the length of the estuary can likely be related to the reduced freshwater inflow into the estuary, creating a homogenous marine-dominated system. Closer inspection of the macrobenthic community structure, however, revealed that there have been species-specific declines in the abundance of several species routinely collected for bait by subsistence fishers, including the mud prawn (*Upogebia africana*), pencil bait (*Solen cylindraceus*) and redworm (*Marphysa sanguina*). The decline of these species suggests increased exploitation of estuarine resources over the past decade, most likely in response to high levels of unemployment and poverty.

Keywords: Anthropogenic influence, Bait Harvesting, Exploitation, Kariega Estuary, Macrophyte.

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"In the name of Allah (God), the most kind, the most merciful."

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To the brave people of Palestine, we will continue to fight for you until our very last breath…

Table of Contents

List of Figures

List of Tables

List of Symbols/Abbreviations

MARiS - Marine and Antarctic Research Centre for Innovation and Sustainability

SOM - Sediment Organic Matte

Chapter 1

General introduction and literature review

1.1 Estuarine Systems

Estuaries are shallow, open and dynamic environments that represent transitional zones between freshwater and marine environments with unique ecosystems vital for maintaining global biodiversity (Sherman et al., 2009; Herman et al., 1999). They are typically classified based on the dynamic interaction between the river and sea, which creates a unique set of characteristics (Mabaso, 2002). They are commonly defined as ‘‘a semi-enclosed coastal body of water which is connected to the sea either permanently or periodically, has a salinity that is different from that of the adjacent open ocean due to freshwater inputs, and includes a characteristic biota” and being “transitional waters, a term which includes lagoons, rias, etc.” (Elliot & Whitfield, 2011 in Lonsdale et al., 2022). Estuaries serve as hubs for hydrological, biological and biogeochemical cycles, and their productivity rivals that of some of the most productive systems, such as tropical rainforests and coral reefs (Robins et al., 2016).

Estuaries provide various ecosystem services, including flood protection (Barbier, 2020), food provisioning, and recreational activities (Pinto et al., 2013). Coupled with the fact that they are highly productive systems, they are essential nursery areas and habitats for various vertebrates and invertebrates (Bloomfield & Gillanders, 2005). Additionally, they serve as important breeding and feeding grounds for terrestrial populations such as birds (Robins et al., 2016; de Villiers et al., 2009). These systems are regarded as among the most productive systems on the planet due mainly to the increased availability of nutrients derived from freshwater inflow that sustain high rates of primary productivity not only within the system but also within the coastal marine system, enhancing their suitability as foraging grounds or as a nesting and nursery ground for several species (Sherman et al., 2009; Turpie et al., 2002; Wallace & Whitfield, 1984).

Estuaries hold significant biological importance and act as nutrient traps, as the productivity of estuaries is derived from nutrients from the river and sea and the breakdown of vegetation found within the system, contributing to the prolific estuarine food web (de Villiers et al., 2009; Allanson & Baird, 1999). These systems also contain a multitude of emergent plants such as mangrove vegetation, seagrass beds and salt marshes, which increase detrital input that is then accumulated once broken down by bacteria and utilised by aquatic organisms within the estuary (de Villiers et al., 2009; Booth, 2007; Mabaso, 2002). The outflow of

nutrient-rich waters from estuaries also plays an essential role in promoting primary production in the nearshore marine environment (Vorwerk et al., 2008).

Due to the dynamics of estuaries and the fluctuations in physicochemical variables that characterise these systems, a select few species have adapted to live in estuaries; thus, diversity in estuaries is generally low (when compared with coastal and oceanic environments), supporting an abundant and functionally extensive but not diverse range of flora and fauna (de Villiers et al., 2009; Herman et al., 1999). Estuaries also support human activities like fishing, transport, tourism and recreation (Barbier, 2020; Pinto et al., 2013; Statham, 2012). Therefore, these factors also contribute to instability within these systems.

Estuarine systems pose several physiological constraints on the organisms that exist within them. With fluctuating physicochemical conditions driven by tidal cycles and variations in freshwater inflow, estuaries are known to have high biomass and densities of invertebrates, but generally low species diversity (Allanson & Baird, 1999). The increased availability of habitats, including submerged macrophytes, salt marshes, and sediment types, all contribute to maintaining biodiversity within these systems. Human-induced stressors such as global warming, freshwater abstraction, loss of habitat, and the overexploitation of renewable resources are likely to compromise these systems further, and thus, as aforementioned, few organisms are adapted to thrive within the estuarine system (Raffaelli et al., 2003; Lalli & Parsons, 1997).

1.1.1 What is macrobenthos

Benthos is the community of organisms that live on, in, or near the bottom of a sea, river, lake, or stream. Benthic organisms comprise several size classes, including microbenthos, meiobenthos and macrobenthos (Herman et al., 1999). The microbenthos is the smallest size class (< 32 µm) and includes bacteria and Protista (Maurya et al., 2020; Herman et al., 1999). The meiofauna range in size from > 32 µm to 1mm and are primarily dominated by Nematoda, Turbellaria, Copepoda, Foraminifera, and Ostracoda (Herman et al., 1999; Heip et al., 1995). Lastly, the macrofauna, the largest size class, are those organisms > 1 mm in size and include Polychaeta, Echinodermata, Mollusca and Crustaceans (Sinu, 2022; Herman et al., 1999; Lalli & Parsons, 1997). Macrobenthos are significantly larger than the sediment and can move

sediment when burrowing and feeding (Dong et al., 2021; Watling, 2019). These (macrobenthic) organisms choose to live in, on or near the surface of the sediment because this is where the most prominent food availability is found and because this sediment-water interface has the highest oxygen concentrations in shallow water ecosystems (Watling, 2019; Lalli & Parsons, 1997).

Macrobenthic organisms have sessile or sedentary lifestyles, dominating within soft sediments like sand and mud in or on the bottom sediment of aquatic systems and have a relatively long lifespan (Andersen & Pejrup, 2024; Dong et al., 2021; Watling, 2019; Henninger & Froneman, 2011). Macrobenthos are further categorised based on their life habit and size. Epibenthos (those organisms living on the sediment surface) and hyperbenthos (those living just above the sediment, but are closely associated with it) are used for mobile macrobenthic organisms that move freely between sediments and water interfaces, such as shrimps and copepods (Lalli & Parsons, 1997). They are then further categorised into infauna, organisms that burrow and dwell in the sediment, and epifauna, organisms that attach to hard substrates like rock surfaces or roots of vegetation like mangroves (Crump et al., 2022).

Traditionally, salinity and sediment composition characterise the geographical variability of macrobenthos along the estuarine gradient (Ysebaert et al., 2003). In shallow water ecosystems like estuaries, where benthic-pelagic coupling is heightened, the system's productivity is a major limiting factor to the distribution of macrobenthos (Herman et al., 1999). Researchers have also pointed out that dynamic factors like tidal action and static factors like sediment composition and organic content play a vital role in the community structure of macrobenthos in estuaries (Warwick et al., 1991; Warwick & Uncles, 1980). Further studies have also shown that hydrodynamic processes like wave action and currents are also imperative for transporting and distributing sediment and food particles and juvenile macrofauna, thus influencing their distribution within the estuarine system (Norkko et al., 2001; Snelgrove & Butman, 1995).

The interactions of the aforementioned variables, along with factors like food availability, predation, and organic content, have been proven to influence the structure of macrobenthic communities and patterns along the length of estuarine systems (Ysebaert et al., 2003; Herman et al., 2001).

1.1.2 Factors influencing the distribution of the macrobenthos

The spatial and temporal patterns in the distribution of macrofauna in estuaries have been demonstrated to be determined by both abiotic (Nebra et al., 2016; Njozela, 2013; Day et al., 2012; de Villiers et al., 2009) and biotic (Fromentin et al., 1997) factors, the relative importance of which demonstrates high spatial and temporal variability. Estuarine environments are often characterised by changes in co-occurring physical characteristics, of which geographical, hydrological, and meteorological conditions determine the scale of these changes (Nebra et al., 2016; Njozela, 2013; Day et al., 2012; de Villiers et al., 2009). These changes play an essential role in determining the spatial distribution of macrobenthos due to species-specific physiological and habitat requirements (Teske & Wooldridge, 2003; Mabaso, 2002).

Salinity gradients largely determine the spatial distribution and community structure of macrobenthos in estuaries (Shadrin et al., 2019; Thrush et al., 2013; Uwadiae, 2009; Teske & Wooldridge, 2003). However, although salinity is one of the primary limiting factors of macrobenthic abundance and diversity in estuaries, sediment composition also plays a critical role in shaping macrobenthic communities across estuarine systems (Teske & Wooldridge, 2003; Ysebaert et al., 2003; Herman et al., 2001). As an example, Teske and Wooldridge (2003) found that macrobenthos distributions in medium-sized temporarily open/closed estuaries along the south-east coast of South Africa were primarily determined by sediment, with sandy regions near the estuary mouths supporting distinct faunal groups compared to muddy upstream areas.

South Africa is a semi-arid country; water is a precious and scarce commodity. Rainfall is seasonal and erratic, so South African estuaries are prone to erratic flow and floods (de Villiers et al., 2009; Mabaso, 2002). Because most South African estuaries are considered micro-tidal (Allanson, 1992; Reddering & Rust, 1990), they are often subjected to extreme changes in physical conditions. Changes in salinity regimes within these systems are driven by hydrological events such as drought and floods. During periods of reduced freshwater inflow, such as prolonged droughts, a reverse salinity gradient may be recorded with hypersaline conditions persisting in the upper reaches of estuaries (Greenberg, 2012; de Villiers et al., 2009).

Aside from seasonal variations in estuarine water temperature driven by regional climatic regimes, freshwater inflow also influences the water temperature within the system (de Villiers et al., 2009). Thus, water temperatures in estuarine systems will fluctuate based on the volume of freshwater entering the system, the intensity of upwelling events, the magnitude of flooding, geographical location and meteorological conditions (de Villiers et al., 2009; Teske & Wooldridge, 2003; Day, 1980; Lockwood, 1976). As a result, macrobenthic organisms' abundance and distribution depend on these combined effects. To successfully occupy the estuarine habitat, these organisms need adaptations to withstand long and short-term changes in the system (de Villiers et al., 2009; Mabaso, 2002).

Estuaries can experience extreme and erratic changes in salinity for prolonged periods, ranging from hypersaline conditions during droughts to the absence of salinity gradients during extreme rainfall events. This means that macrobenthic organisms require a salinity tolerance (Nebra et al., 2016). Lack of freshwater inflow can often result in hypersaline conditions, be it because of anthropogenic influence or environmental disasters, resulting in low macrobenthic species diversity (de Villiers et al., 2009; Day, 1981). On the other hand, McLachlan and Grindley (1974) found that prolonged periods of freshwater inflow alter not only the individual organisms (by means of adaptation) but also the community structure by displacing species from their original localities within the system due to the abrasive force of flooding. Some studies have shown that short-term flooding can benefit some macrobenthic species, like the amphipod *Grandidierella lignorum* (de Villiers et al., 2009; McLachlan, 1974). However, little is known about its direct benefit to other macrobenthic species.

Submerged macrophytes also greatly influence macrobenthic diversity and abundance (Cheng et al., 2017; Henninger et al., 2009; Lloret & Marín, 2009). When comparing macrofaunal biomass and species richness to unvegetated zones, zones dominated by macrophytes have significantly higher levels of diversity and abundance. Higher species concentrations are supported by macrophytes' structural complexity, creating vital habitats, food sources, and predator protection (Henninger et al., 2009; Mattila et al., 2008; Whitfield, 1980). On the other hand, the absence of habitat and severe human interference from bait collecting is probably why places with little vegetation, especially those near the estuary mouth, have reduced macrofaunal variety and abundance (Henninger & Froneman, 2011).

1.1.3 Ecological importance of macrobenthos

Macrobenthic organisms can be seen as architects of ecological functioning as they play several crucial roles in the ecological functioning of aquatic ecosystems (Chowdhury et al., 2024; Wang et al., 2021). Gage (2001) summarised the direct and indirect effects and subsequent ecological importance of macrobenthos on the environment in which they are found, ranging from bioturbation to indicators of ecosystem health. Through their burrowing activities, macrobenthic organisms enhance habitat complexity and biodiversity (Thrush et al., 2013; Lalli & Parsons, 1997). The bio-suspension of sediments increases sediment mobility and openness, making it less compact (Wilson & Fleeger, 2012; Gage, 2001). Conversely, biodeposition creates sticky surfaces as the macrobenthic organisms secrete mucous (Wilson & Fleeger, 2012), which allows particles to become trapped, allowing for it to be readily available for suspension feeders to utilise (Li et al., 2022; Chen et al., 2009; Gage, 2001). These two processes work together to regulate sediment stability and erosion, which is vital for maintaining the structure of the benthos. Their subsequent role in bioturbation makes them ecosystem engineers (Herman et al., 2001).

The burrowing activities of macrobenthic organisms promote species coexistence and balance by preventing smaller, less dominant species from being outcompeted by larger, dominant ones (Gage, 2001). Thus, their role in the overall health and metabolism of marine ecosystems has been widely investigated in both shallow and deep-water marine ecosystems (Chowdhury et al., 2024; Li et al., 2022; Dong et al., 2021; Wang et al., 2021; Graf & Rosenberg, 1997; Somerfield et al., 1995).

Macrobenthos also contribute to the decomposition of benthic organic material, regulating the exchange of materials at the sediment-water interface and facilitating the self-purification of water bodies (Wang et al., 2021; Allanson & Baird, 1999). This accelerates nutrient recycling and sustains primary production in the water column, thereby driving energy flow through the pelagic food web. These processes fall under what is commonly known as benthopelagic coupling (Lam-Gordillo et al., 2020; Herman et al., 1999), meaning that there is a two-way exchange of matter and nutrients between the water column and the benthic habitat, which is vital for both the pelagic and benthic zones (Raffaelli et al., 2003).

Notwithstanding their role in structuring benthic communities and nutrient cycling, the macrobenthos also represent an important prey item for various invertebrates and vertebrates (de Villiers et al., 2009; Allanson & Baird, 1999). They are, therefore, critical in carbon and energy flow within aquatic systems. For example, spotted grunter (*Pomadasys commersonnii*) primarily feeds on the mud prawn (*Upogebia africana)* and sand prawn (*Callich*ir*us kraussi)* (de Villiers et al., 2009; Allanson & Baird, 1999). Aquatic birds have also been shown to feed on macrobenthic invertebrates, particularly within the littoral zones of shallow-water aquatic systems (Wilson & Fleeger, 2012; Dauvin & Desroy, 2005). Because of the critical ecological role they play in aquatic ecosystems; macrobenthos have been used in pollution monitoring surveys (Somerfield et al., 1995). Because of their distribution, sedentary lifestyle, and high fecundity, the macrobenthos is widely employed to monitor changes in ecological systems caused by disturbances, with some species more sensitive than others to physical disturbances (Dong et al., 2021). So much so that in recent years, indices using macrobenthos have been developed to evaluate the overall health of coastal ecosystems, far surpassing that of fish and zooplankton (Li et al., 2022; Wang et al., 2017).

1.1.4. Importance of estuarine systems in South Africa

The most widely accepted definition of a South African estuary is that of Day (1980): "a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of seawater with freshwater derived from land drainage". The South African coastline features around 290 estuaries and 42 micro-estuaries, which can broadly be separated into 22 ecosystem types and three micro-estuary types (Olisah & Adams, 2021; van Niekerk et al., 2020). Estuaries are typically focal points of tourism and recreation, and while they occupy less than 2% of the country's total terrain, they contribute approximately R4.2 billion to the national economy (Olisah & Adams, 2021; Turpie & Clark, 2007; Lamberth & Turpie, 2003).

Estuarine ecosystems in South Africa support many migratory bird species and other endemic species that depend on estuaries for survival (Henninger & Froneman, 2011; Turpie et al., 2002). The most imperative component of estuarine systems (concerning fisheries) is their provision of nursery grounds for juvenile fish and other migrating and recurring taxa (Sherman et al., 2009; Turpie et al., 2002). Of the 1500 species of fish recorded in South

African waters, ≈20% of these species have been recorded to utilise estuarine systems at some point during their life cycle (Sherman et al., 2009; Wallace & Whitfield, 1984). The importance of these systems as nursery and foraging grounds is thought to reflect increased food availability and the provision of refugia against predation in the form of submerged macrophyte beds (Booth, 2007; Kneib, 1987; Boesch & Turner, 1984).

Humans benefit from South African estuaries, not only from recreation and tourism but also through protection from natural disasters, providing food and sustaining small local subsistence fishing communities (Booi et al., 2022; Cooper et al., 2003). Land adjacent to estuaries has, in recent years, been a hotspot for holiday homes due to its aesthetics and, overall, has become a much sought-after location for human settlement (Booi et al., 2022; Matcher et al., 2018; Henninger & Froneman, 2011). Consequently, the negative impacts of anthropogenic influence on the health of estuarine systems in South Africa have increased in recent years (Henninger & Froneman, 2011).

1.2. Estuarine disturbances

Due to rapid urbanisation and human settlement, estuaries have been subjected to various anthropogenic activities, including tourism, transportation, pollution, and habitat loss and degradation (Naidoo et al., 2015; Sherman et al., 2009; Kennish, 2002). Indeed, estuaries are now among the most ecologically threatened ecosystems in South Africa due to freshwater abstraction, habitat loss and high levels of resource exploitation (Mahoney & Bishop, 2017; Kennish, 2002). The last two decades have documented a rapid increase and expansion of coastal development along South Africa's coastline, with much of the development focused on the lower reach of estuaries (Matcher et al., 2018). This expansion has resulted in the ecological degradation of many estuaries within the region (Henninger & Froneman, 2011; Peterson & Lowe, 2009; Bilkovic & Roggero, 2008). Moreover, due to high levels of unemployment and poverty within the sub-region, the exploitation of renewable resources by coastal communities and subsistence fishers has increased, and the adverse effects of human activities on estuarine ecosystem functioning are likely to be exacerbated by climate change (Matcher et al., 2018; James et al., 2013).

1.3. Study site – The Kariega Estuary

The Kariega Estuary is located in the Eastern Cape province of South Africa near the coastal town Kenton on Sea, approximately 120km from Gqberha (formerly Port Elizabeth) (Henninger & Froneman, 2011). The estuary is regarded as a freshwater-deprived system as a result of poor rainfall, small catchment size (690 km^2), coupled with the high levels of freshwater abstraction due to the construction of three dams upstream of the estuary along the Kariega River (Henninger & Froneman, 2011; Hodgson, 1987). Like many other estuaries within the region, the Kariega Estuary has a wide variety of habitats, including intertidal mudflats, salt marshes, and seagrass beds, which support a rich diversity of fauna and flora (Henninger & Froneman, 2011; Heyns & Froneman, 2010; Harrison et al., 2000; Hodgson, 1987). The availability of these habitats contributes to elevated biomass of fish and zooplankton, making the estuary an important foraging ground for several marine breeding fish species and seabirds. However, the estuary is subject to human pressures such as recreational boating and residential development. Stormwater drains lead directly into the system, the largest of which is at the mouth of the estuary (Jennings, 2006). Runoff from stormwater drains can often introduce high levels of nutrients such as nitrogen, iron, phosphorus and silicon, amongst other rate-limiting nutrients, which can boost phytoplankton growth. While some of the new biomass is recycled, excess production can sink to the seafloor, where microbial degradation causes anoxia that promotes the release of nutrients from sediments, triggering algal blooms, creating a positive feedback loop that drives ongoing eutrophication (Pinckney et al., 2001).

Moreover, due to adverse regional economic factors, the system has been subject to increased levels of resource utilisation primarily driven by the growth of the informal settlement resulting from urbanisation.

1.4. Problem Statement, Aims and objectives

The Eastern Cape province of South Africa has experienced a rapid expansion of coastal development, particularly in the vicinity of estuaries, over the past decade. Coupled with this, the high levels of unemployment and poverty have increased resource exploitation within these ecosystems (Nwabisa, 2018; Henninger & Froneman, 2011; Napier et al., 2009).

Estuarine systems are now regarded as the most threatened systems in South Africa but, surprisingly, the least protected (Morant & Quinn, 1999). The conservation and implementation of management strategies of these systems is critically dependent on our understanding of their ecological functioning over different spatial and temporal scales.

This study aims to describe the decadal shifts in macrobenthic community structure and distribution in selected habitats within the littoral zone along the length of the permanently open, freshwater-deprived Kariega Estuary on the southeastern coastline of South Africa in the Eastern Cape. More specifically, the study aims to determine:

1. The importance of physicochemical (salinity and temperature) variables in determining the macrobenthos distribution along the length of the estuary.
2. Examine the decadal shifts in macrobenthic community structure between 2010 and 2022.

Chapter 2

Materials and methods

2.1 Introduction

This study was conducted as a desktop study using data collected during 2022, which was then compared to a previous study conducted by Henninger & Froneman (2011). The data were gathered by qualified aquatic biologists from the Department of Zoology and Entomology, Rhodes University, as part of a long-term ongoing research program on the ecological status and health of the Kariega Estuary. Ethical clearance was unnecessary since no fieldwork or direct data collection was undertaken for this study. The use of pre-existing data allowed for a focused analysis of the decadal changes in the macrobenthic communities in the Kariega Estuary, drawing from the comprehensive and ethically sound fieldwork previously conducted by Henninger and Froneman (2011).

This research utilises a subset of the available data to assess changes in macrobenthic community structure at six stations along the length of the estuary between the 2010 and 2022 surveys in the permanently open Kariega Estuary (Figure 2.1). The variables analysed in this study include macrobenthic community structure and environmental factors such as sediment organic content, salinity, and water temperature. These variables were selected to provide insight into the biological communities and the physical conditions that may have contributed to shifts in the macrobenthic community structure s over a 12 year period.

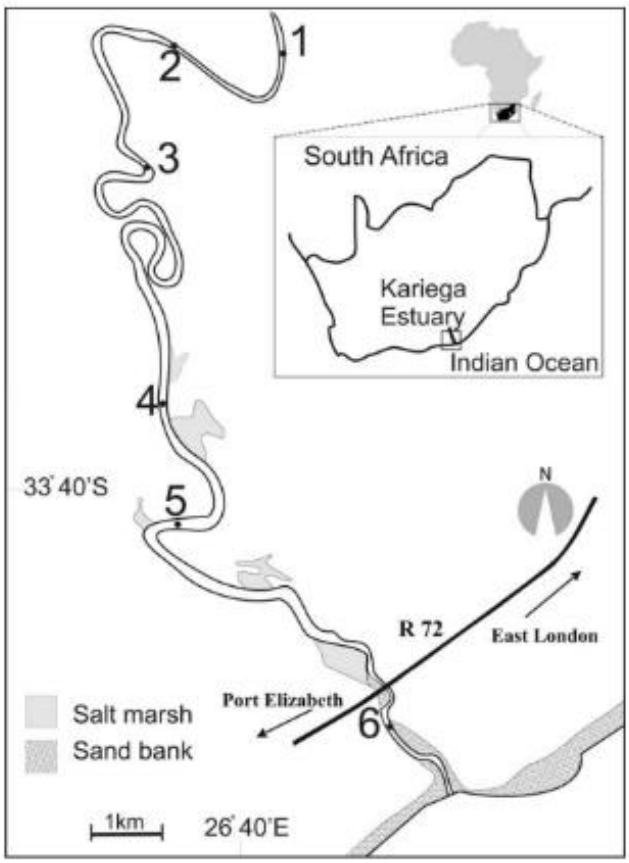

Figure 2.1 Localities of the six sampling stations utilised along the length of the Kariega estuary, Eastern Cape, South Africa (after Henninger & Froneman, 2011)

2.1.1 Study Site

The Kariega Estuary is a permanently open, homogenous, oligotrophic, marine-dominated system in the Eastern Cape province of South Africa (33° 40'32" S, 26°40' 34" E) (Henninger & Froneman, 2011; Jennings, 2006; Bate et al., 2002a). The estuary is approximately 120 km from Gqberha (previously Port Elizabeth) and is located within the warm, temperate biogeographic region along the southeastern coastline of South Africa (**Figure 2.2**) (Henninger & Froneman, 2011; Hodgson, 1987). The system is approximately 18 km in length with an average midstream depth of 2.5 to 3.5 meters (Henninger & Froneman, 2011; Bate et al., 2002a; Hodgson, 1987).

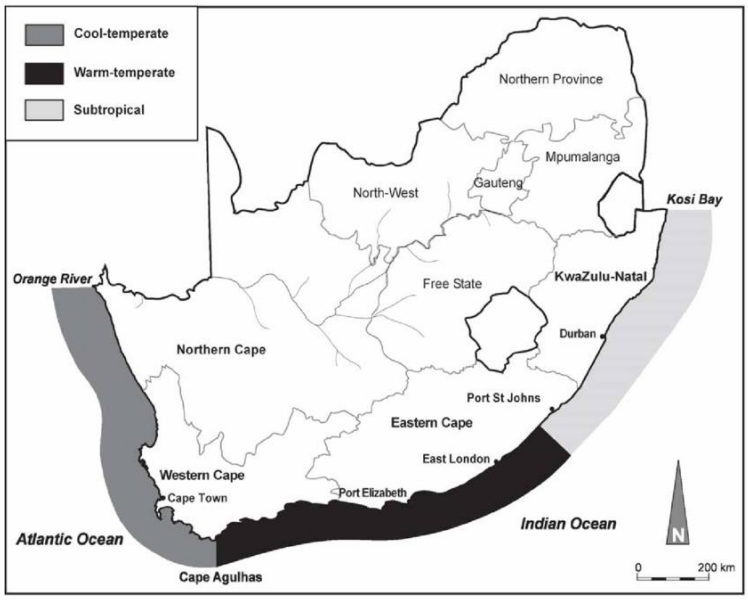

Figure 2.2 Biogeographic zones along the South African coastline, of which the Kariega Estuary, in the Eastern Cape, falls under the warm temperate biogeographic zone (Harrison, 2005).

The Kariega River has a catchment area of approximately 688-690 km^2, intensifying the system's marine dominance (Henninger & Froneman, 2011; Booth, 2007; Jennings, 2006). The estuary's upper reaches are characterised by a narrow upper channel ranging from 40 to 60 meters wide, which broadens to ≈100 meters in the middle and lower reaches of the estuary. The various sections are bordered by riparian vegetation, sandflats and salt marshes (Jennings, 2006).

The average freshwater inflow of the estuary is estimated at ≈ 2.5–35 × 10^6 m^3 per year, making it a tidally dominated system (Jennings, 2006; Henninger & Froneman, 2011). Consequently, the overall freshwater inflow is relatively low, and the spring tidal prism averages 1.9 × 10^6 m^3, resulting in a 106:1 ratio of tidal prism volume to river flow volume. The mean spring tidal range along the Eastern Cape coastline is 1.6m, and thus categorises the Kariega Estuary as a micro-tidal system because the mean tidal range is below the threshold of 2m (Warwick et al., 2018; Richardson et al., 2006; Paterson, 1999). The low freshwater inflow and strong scouring action of the tides, which outweighs the riverine inflow, have resulted in the mouth of the estuary (33°40'30.89" S, 26°40' 33.28" E) remaining permanently open (Jennings, 2006).

Several researchers have described the estuary as having a well-mixed water column throughout the tidal cycle and low turbidity (Jennings, 2006; Bate et al., 2002a; Froneman, 2000; Grange & Allanson, 1995). Like many other estuaries along the South African coastline, the Kariega Estuary was shaped by the drowning of a river valley due to rising sea levels, making it a classic example of a mature Ria-type estuary common in estuaries along the Eastern Cape, leading to the creation of these long, narrow inlets (Booth, 2007; Reddering & Rust, 1990).

2.1.2. Habitat types

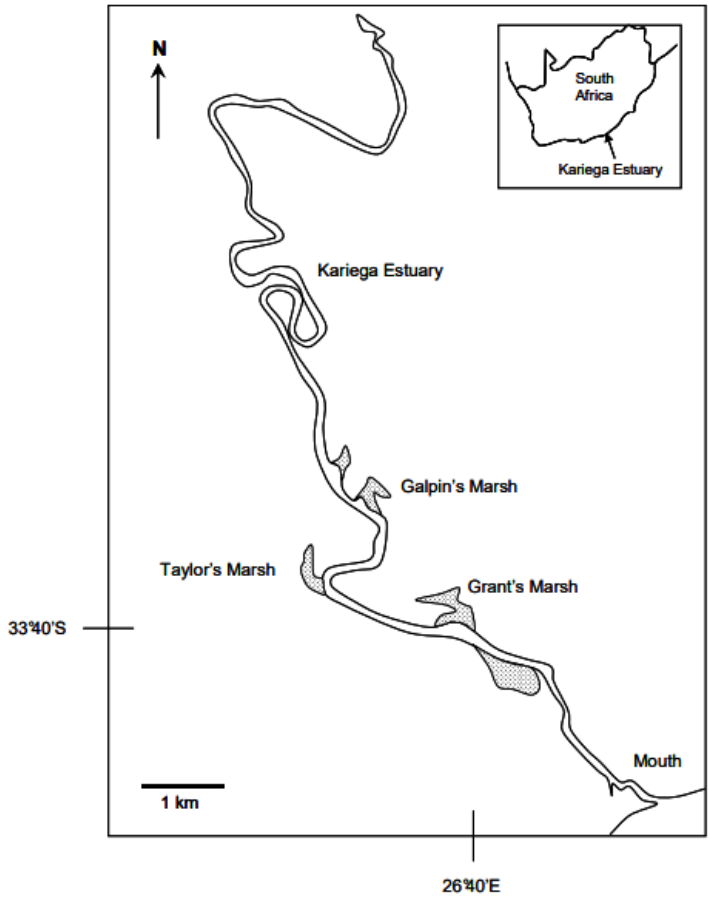

Figure 2.3 Map of the Kariega Estuary indicating the three main salt marshes, Taylor's Marsh. Galpin's Marsh and Grant's Marsh (after Booth, 2007).

Figure 2.3.1 The well-developed littoral zone of the freshwater-deprived, permanently open Kariega Estuary (captured by Froneman, 2024).

The estuary is regarded as a macrophyte-dominated system with extensive salt marsh communities and a well-developed littoral vegetation zone (Paterson & Whitfield, 1997). Due to the marine dominance of the system, the eelgrass, *Zostera capensis*, has been able to extend up the length of the system (Froneman, 2001; Paterson, 1999; Hodgson, 1987). The estuary comprises three main salt marshes: Taylor's Marsh, Grant's Marsh, and Galpin's Marsh (Figure 2.3) (Booth, 2007; Jennings, 2006; Paterson, 1999; Paterson & Whitfield, 1997). Closest to the mouth of the estuary is Grant's Marsh, made up of *Spartina maritima* and *Sarcocornia perennis*. Taylor's intertidal creek adjacent to eelgrass beds is unvegetated and has an area of 3756 m^2. It constitutes three main branches that connect at a single opening of the estuary (Paterson & Whitfield, 2003). The creek is relatively narrow (average width = 8.0 m) and shallow (mean spring high tide depth = 74 cm) (Paterson & Whitfield, 2003). The closest eelgrass beds are found on the opposite banks of the channel (Booth, 2007; Paterson & Whitfield, 2003).

Taylor's Marsh is dominated by the macrophytes *Chenolea diffusa* and *S. perennis* and has a single unvegetated creek of 2608 m^2 with a single opening into the estuary (Booth, 2007; Paterson & Whitfield, 2003; Paterson, 1999). Taylor's Marsh is similar to that of Grant's Marsh in that it too is narrow (average width = 5.2 m) and shallow (mean spring high tide depth = 50 cm) (Paterson, 1999; Paterson & Whitfield, 2003). Galpin's Marsh is different to that of Grant and Taylor's Marsh in that forms part of an estuarine embayment rather than being in the central channel (Booth, 2007; Paterson & Whitfield, 2003). *Sarcocornia perennis* and *S. maritima* dominate the salt marsh with a few high marsh pools (Paterson, 1999; Paterson & Whitfield, 2003). The intertidal creek of Galpin's Marsh is wide (average width = 15.2 m) and has a mean spring high tide depth = 106 cm, covering an area of 3343 m^2 (Paterson, 1999; Paterson & Whitfield, 2003). The intertidal creek of Galpin's Marsh has patches of *Z. capensis* within its channel. Significant eelgrass beds are also found within the embayment (Paterson, 1999).

The salt marshes contribute to the exchange of carbon, nitrogen, and phosphorus within the system (Richoux & Froneman, 2007; Jennings, 2006). The salt marshes also represent critical foraging grounds for many wading birds. Due to the marine dominance of the estuary, the eelgrass *Z. capensis* is found along the entire length of the system (Henninger & Froneman, 2011; Hodgson, 1987). Additionally, the lower reach of the estuary is characterised by extensive mud flats on the east bank of the system, which are extensively used for bait collection (Claassens et al., 2022; Henninger & Froneman, 2011; Hodgson, 1987).

2.1.3. Sediment composition

According to Hodgson (1987), the sediment composition in the lower reach of the Kariega Estuary is primarily comprised of well-sorted marine sands. Further upstream, the coarse marine sediments are replaced by fine mud. The sediment on the sandflats of the estuary comprises a higher proportion of mud. Most of the estuary's banks are composed of soft sediment, interspersed with rocky outcrops along the water's edge (Hodgson, 1987). Furthermore, a study by Richardson et al., (2006) found that along the longitudinal gradient of the Kariega Estuary, sediment composition was distinct, with the mouth of the estuary

characterised by fine sand with little to no silt, the mid reaches of the estuary had the highest silt content and a relatively low coarse-sand content, and finally, the upper reaches had high levels of coarse material and some silt.

2.1.4. Water conditions

The Kariega Estuary is considered a marine-dominated, freshwater-deprived system (Froneman, 2001). The reduced freshwater inflow contributes to the estuary, generally demonstrating a reverse salinity gradient and low macronutrient concentrations (Henninger & Froneman, 2011). During periods of drought, the estuary's upper reaches may become hypersaline, with salinities > 40 (Booth, 2007; Paterson, 1999). Due to low freshwater inflow, salinities along the length of the estuary are typically close to that of seawater, with the highest salinities typically recorded in the upper reach of the system due to evaporation. Water temperatures within the system range from 13 to 26◦C and demonstrate a strong seasonal pattern, with the highest temperatures recorded in summer (Dec - Feb) and lowest in winter (June - August). Intermediate temperatures are recorded in spring and autumn (Van der Walt, 2019; Heyns & Froneman, 2010). Turbidity levels within the estuary are relatively low (>10 NTU), reflecting the reduced freshwater inflow into the system (Booth, 2007; Paterson, 1999).

Due to low freshwater input and the low nutrient status of the Kariega Estuary, total water column chlorophyll-a (Chl-a) concentrations are generally low (<2 µg l^{-1}) and dominated by small phytoplankton (<2.0um) (Froneman, 2001; Paterson, 1999). The unfavourable size structure of the phytoplankton and low Chl-a standing stock contributes to low zooplankton standing stocks (generally < 15 mg dwt m^{-3}), which numerically and by biomass are dominated by mesozooplankton comprising mainly copepods, crustaceans and mysids (Froneman, 2001).

2.1.5. Human and environmental pressures

The Kariega Estuary enters the sea adjacent to the coastal town of Kenton-on-Sea and the township of Ekuphumleni, which are located on the western bank of the system. Kenton-on-Sea is part of the Ndlambe Local Municipality in the Sarah Baartman District Municipality of

the Eastern Cape province of South Africa. The total population of Kenton-on-Sea and Ekuphumleni is estimated at ≈ 5500 individuals. Due to the proximity of the coastal development to the estuary, the lower reach of the system is characterised by significant development, including the construction of sea walls, stormwater outflow pipes and boat slipways. Subsistence and recreational fishers extensively use the extensive mud flats adjacent to the town for bait collection (sand prawn, pencil bait, and red bait) (Henninger et al., 2009; Jennings, 2006; Hodgson, 1987). Seasonally, the estuary is a popular holiday destination, contributing to disruptive recreational activities, including boating, fishing, bait collection, and water skiing (Henninger & Froneman, 2011). The upper reaches of the estuary are, however, largely inaccessible to the public as it forms part of the Kariega Park private nature reserve as well as agricultural and grazing livestock farms (on both banks in upper and middle reaches) (Henninger & Froneman, 2011; Jennings, 2006).

2.2. Sampling methodology

Hodgson (1987) identified four distinct ecological zones in the littoral zone along the length of the estuary. The lowest zone, Zone I, which was exposed at spring low tide, was characterised by the dwarf eelgrass, *Z. capensis*. A mud flat, lacking vegetation, represented Zone II. In Zone III, the dominant vegetation was *S. maritima,* and lastly, Zone IV comprised a belt of *S. perennis* (Henninger & Froneman, 2011; Hodgson, 1987). Henninger and Froneman (2011) noted that, with few exceptions, these zones were present along the entire length of the system. The two notable exceptions were the absence of macrophytes at the mouth of the estuary and the subtidal presence of *Z. capensis* at the head of the system (Henninger & Froneman, 2011). Six sites within the littoral zone of Kariega Estuary, ≈3 km apart, were sampled once off, extending from the upper weir, 18km from the mouth of the estuary to the river mouth, from March to June 2010 and again in March 2022. These sites coincide with those previously sampled by Hodgson (1987).

2.2.1. Physico-chemical variables

At each site, physicochemical variables, salinity (PSU), and temperature (◦C) in the water column adjacent to the sample site were recorded using an Aquaread Aquameter 200/ Aquaprobe 800 during high tide (Henninger & Froneman, 2011). Three replicate readings of each physicochemical reading were made at each site and on each sampling occasion.

2.2.2. Sediment organic matter (SOM)

Three sediment samples were collected at each site to assess the organic carbon content of the sediment. The percentage of carbon content was determined using the loss of mass on ignition method (Hodgson, 1987). Pre-weighed sediment samples were oven-dried at 60◦C for 24 hours, followed by ashing at 450◦C for 4 hours (Henninger & Froneman, 2011). The difference in weight between the initial and final weights was assumed to correspond to the carbon content of the sediment (Henninger & Froneman, 2011).

2.2.3. Abundance and biomass of the macrobenthos

Three replicate sediment samples were collected from each site in each zone using a modified Van Veen grab, each covering an area of 0.25 m^2 and taken to a depth of 40 cm. The samples were sieved on-site using a 1 mm mesh sieve. The methods followed are described by Hodgson (1987). Animals found within the sediment samples were preserved in 70% alcohol, stored in zip-lock bags, and later in the laboratory, where possible, identified to the lowest taxonomic level using the keys of Day (1969) and Branch et al. (1994). The specimens were dried using a paper towel and weighed using a Sartorius microbalance to obtain the wet weight. Abundance and biomass data were expressed as individuals per unit area (ind/m^2) or biomass (g wwt/m^2) per unit area (Henninger & Froneman, 2011), respectively. In those samples where vegetation was present, vegetation collected in the grab was bagged and transported to the laboratory, where it was washed and dried at 60°C until it reached a constant weight. Plant biomass was expressed as grams dwt per unit area (g dwt/m^2) (Henninger & Froneman, 2011).

2.3 Statistical analysis

Analyses in this study were conducted using a subset of environmental and biological data to explore spatial and temporal trends in the Kariega Estuary. The variables analysed included salinity, temperature, plant and animal biomass, organic content (sediment organic matter), and overall macrobenthic abundance. These parameters were selected for their ecological significance in estuarine systems and their potential influence on macrobenthic community dynamics. The statistical approach combined univariate and multivariate techniques to assess

diversity indices and community structure across four zones, comparing data from 2010 and 2022.

2.3.1 Univariate analysis

Univariate analyses were conducted to assess macrobenthic diversity using the Shannon-Wiener diversity index (H') and species richness (S) indices between the two survey years. One-way analysis of Variance (ANOVA) test was performed on the macrobenthic abundance and biomass, and macrophyte biomass data in R Studio (Version 4.3.3) to determine significant differences across zones and stations along the horizontal gradient between 2010 and 2022. Additionally, ANOVA and Tukey HSD post hoc tests were applied to identify pairwise differences between 2010 and 2022 using zones and stations as replicates for significant differences found in sediment organic content, dominant species, macrophyte biomass and macrobenthos abundance and biomass between the two surveys within zones and stations along the horizontal gradient.

Simpsons Diversity Index (D) and Equitability Index (E_D) were also calculated for species composition and community structure in the two surveys, utilising the same approach of marking the presence and absence of species at each station within the four distinct zones, as Henninger and Froneman (2011).

A Variance Inflation Factor (VIF) test was conducted to check multicollinearity between variables, and thereafter, multicollinear variables (VIF > 5) were removed (Thompson et al., 2017; Galvão & Araújo, 2009; Sarabia & Ortiz, 2009). Thereafter, a quasipoisson generalised linear model was used to assess significant relationships between selected environmental variables (distance from the mouth of the estuary, organic content, salinity, temperature and plant biomass) and the macrobenthic abundance data in R Studios (Version 4.2.2.).

2.3.2 Multivariate analysis

Multivariate analyses were employed to evaluate spatial and temporal pattern shifts in macrobenthic community structure in the four habitat types during the two surveys along the length of the estuary. Data was prepared in Microsoft Excel 2011 before being imported into

the statistical package PRIMER 7 (Primer-E Ltd). To minimise the influence of dominant species, abundance and environmental data were log(x+1) transformed as per the methods by Henninger & Froneman (2011). Resemblance matrices were constructed using the Bray-Curtis Similarity Distance for abundance data and Euclidean Distance for ecological data. The relationship between macrofauna biomass and abundance estimates and the chosen biological (macrophyte biomass and organic content) and physicochemical (temperature and salinity) variables was then examined using Spearman correlation analysis. Non-metric Multidimensional Scaling (MDS) was then utilised to visualise spatial patterns in community structure. Fixed pairwise Permutational Multivariate Analysis of Variance (PERMANOVA) was then conducted to test significant differences in community composition across zones and between years. Finally, SIMPER (Similarity Percentages) analysis was employed to identify the species contributing to the observed differences.

Chapter 3

Results

3.1. Physico-chemical and biological variables

Horizontal gradients in salinity and temperature were observed along the length of the estuary during both surveys (2010 and 2022) (**Table 3.1**). Water temperatures in 2010 ranged between 17.5 and 20.6°C, with the highest temperatures found in the upper reach and the lowest at the mouth of the system. Similarly, in 2022, water temperatures ranged between 19.5 and 24.3 °C, with the highest temperatures again recorded in the upper reach (**Table 3.1**). Water temperatures during the 2022 survey were significantly higher than those recorded in 2010 ($F_{1,5}$ = 0.035, P = 0.001).

A reverse salinity gradient along the length of the estuary was recorded during both surveys. Salinities ranged from 35 to 42 (PSU) in 2010 and between 35 and 37.5 (PSU) in 2022. During both surveys, the highest salinity values were recorded in the upper reaches and the lowest values in the mouth. Intermediate salinity values were recorded in the middle reach of the estuary during both surveys. Overall, the salinity values recorded in 2022 were significantly lower than those recorded in 2010 ($F_{1,5}$ = 9.232, P = 0.01) (**Table 3.1**).

Table 3.1 Ranges of the physicochemical variables at six stations along the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape in May 2010 and March 2022.

Station:	1	2	3	4	5	6
Distance from mouth (km):	18	16	12	9	5	1
Water temperature (°C)						
2010	19.7-19.8	20.2-20.3	19.7-19.8	19.8-20.6	18.9-19.3	17.5-17.7
2022	24.3	24	24.1	23.5	22.8	19.5
Salinity (PSU)						
2010	42.0	42.0	40.0-41.0	38.5	36.5	35.0
2022	37.5	36.5	36.0	35.5	35.0	35.0

3.1.1. Sediment organic matter (SOM) concentrations

Within the four ecological zones, the sediment organic matter (SOM) content ranged between 0.61 and 2.42% (mean 1.77 ± 0.16%) in Zone I; from 0.67 to 2.55% (mean = 1.31 ± 0.12%) in Zone II; from 0.81 to 7.53% (mean of 4.56 ± 0.40 %) in Zone III; and between 2.81and 12.18% (mean = 7.68 ± 0.72%) in Zone IV (**Table 3.2**) in 2010. In 2022, the SOM content ranged between 0.80 and 3.76% (mean 1.61 ± 0.22%) in Zone I and between 0.85 and 3.07% (mean = 1.63 ± 0.16%) in Zone II. Finally, in Zone III, the sediment organic content ranged from 0.94 to 4.02% (mean of 1.83 ± 0.20%) and from 0.98–3.07% (mean = 1.67 ± 0.19%) in Zone IV (**Table 3.2**).

Table 3.2 Minimum, maximum, and mean (± S.E.) percentage of SOM in four zones of the Kariega Estuary in May 2010 and March 2022.

	Minimum %	Maximum%	Mean % ± S.E. between stations
Zone I			
2010	0.61	2.42	1.77 ± 0.16
2022	0.80	3.76	1.61 ± 0.22
Zone II			
2010	0.67	2.55	1.35 ± 0.12
2022	0.86	3.07	1.63 ± 0.16
Zone III			
2010	0.81	7.53	4.56 ± 0.40
2022	0.94	4.02	1.83 ± 0.20
Zone IV			
2010	2.81	12.18	7.68 ± 0.72
2022	0.98	3.07	1.69 ± 0.19

Significant differences in mean SOM were found in two zones between the two survey years. The organic content of the sediment in Zone III, *S. maritima* ($F_{1,34}$ = 12.06, P = 0.001) and Zone IV, *S. perennis* ($_{1,34}$ = 31.32, P < 0.0001) in 2010 was significantly higher than the mean SOM in 2022 (**Figure 3.1**). No significant temporal differences in the SOM were found in Zone I and Zone II (P > 0.05 in both cases).

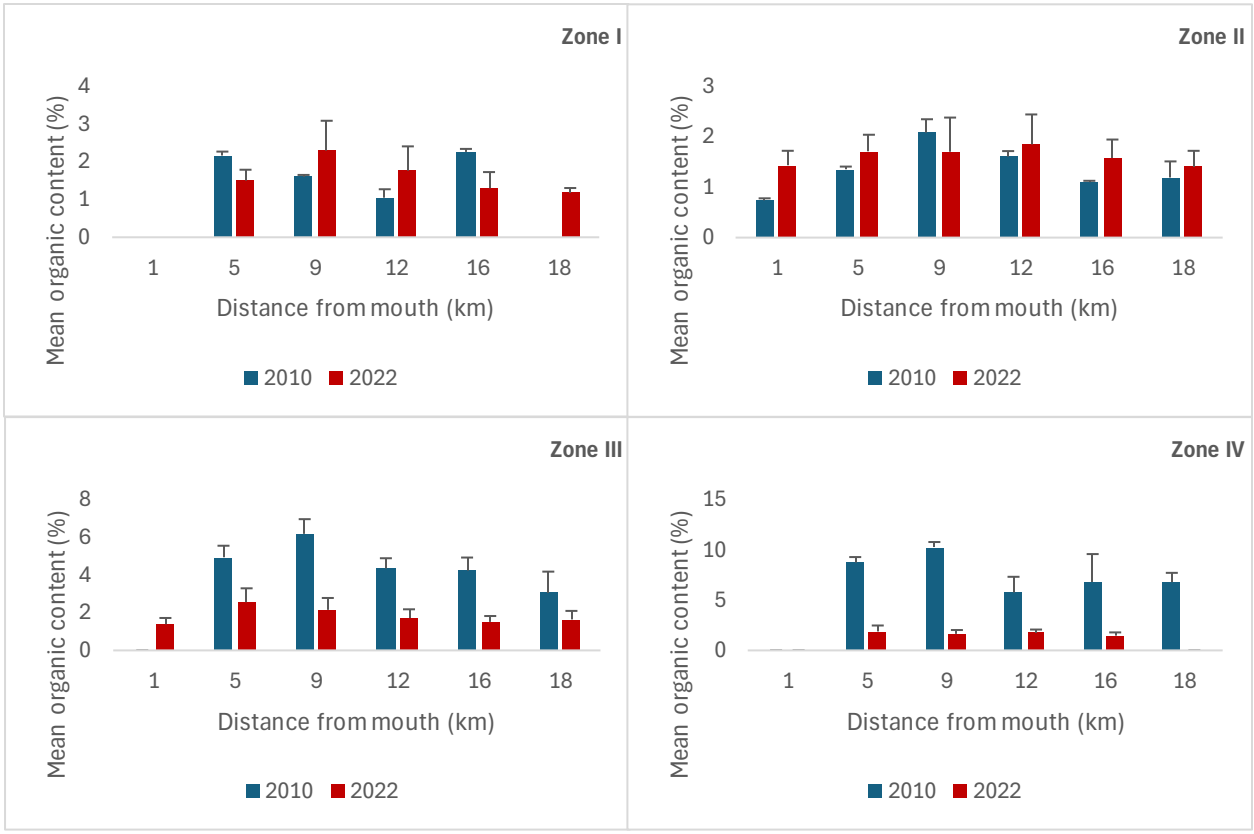

Figure 3.1 Mean (+ S.E.) sediment organic content (%) within the four zones of the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape between two surveys: 2010 and 2022. Key: Zone I = *Zostera*; Zone II = Mud; Zone III = *Spartina*; Zone IV = *Sarcocornia.*

The lowest mean SOM concentrations were recorded in Zone II during the 2010 survey, where values ranged between 0.68 and 2.55% (**Table 3.2**). During the 2022 survey, the lowest mean SOM was found in Zone I; here, it ranged between 0.85 and 3.07% (**Table 3.2**). The highest mean SOM were recorded in Zone IV for the 2010 survey, where it ranged between 2.81 and 12.18% (**Table 3.2**). The 2022 survey found the lowest mean SOM in Zone III, where concentrations ranged between 0.81 and 7.53% (**Table 3.2**).

Along the length of the estuary, the mean SOM content during 2010 was higher than that recorded in 2022. A notable exception was recorded at station 1, where the SOM content in 2022 was higher than in 2021. (**Figure 3.2**). Station 4, 9km from the mouth of the estuary, recorded the highest SOM content in both the 2010 and 2022 surveys. ANOVA and post hoc Tukey HSD testing revealed that organic content in sediment significantly differed between 2010 and 2022 at stations 2, 16km from the mouth ($F_{1,22} = 6.85$, $P = 0.015$), 4, 9km from the

mouth ($F_{1,22}$= 7.52, P = 0.012) and 5, 5km from the mouth ($F_{1,22}$ = 5.38, P = 0.030), where surveys conducted in 2010 had a higher percentage of SOM, as opposed to that of 2022.

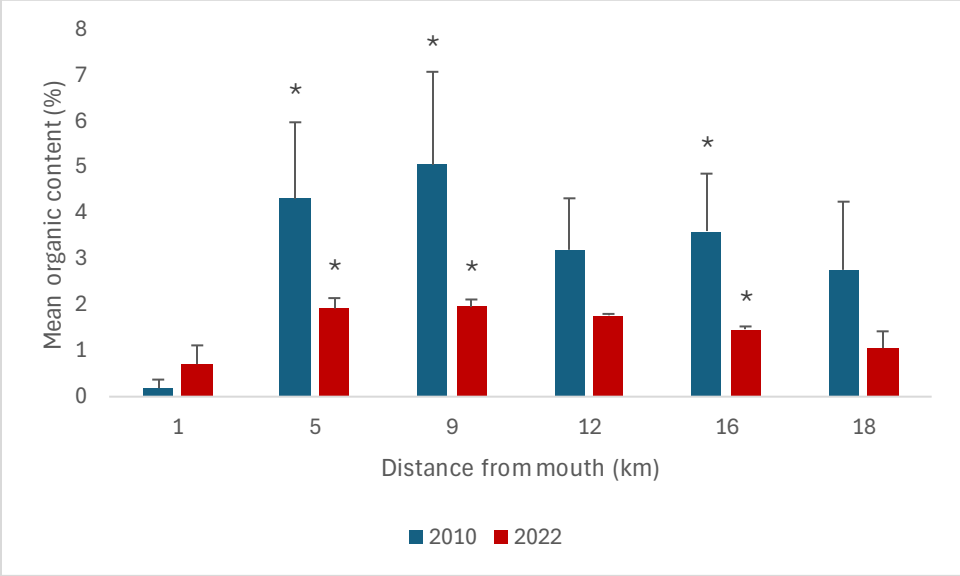

Figure 3.2 Mean (+S.E.) sediment organic content (%) along the length of the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape between two surveys: 2010 and 2022. Data points with an asterisk indicate significant differences between the surveys

3.1.2. Biomass of macrophytes

During the 2010 survey, macrophytes were absent from station 6, 1km from the mouth of the estuary (**Figure 3.3**). In 2022, macrophytes were present at all 6 stations. Across the horizontal gradient (length of the estuary) between the 2010 and 2022 surveys, station 5, 5 km from the mouth of the estuary, ANOVA and Tukey HSD post hoc testing revealed significant differences between the two surveys, wherein 2010 had a higher macrophyte biomass than 2022 ($F_{1,22}$= 4.382, P = 0.048) within that station. Station 5 also held the highest mean macrophyte biomass in 2010 (1129.33 g dwt/m^2), and station 3, 12km from the mouth of the estuary, had the highest mean macrophyte biomass in the 2022 survey (497.83 g dwt/m^2).

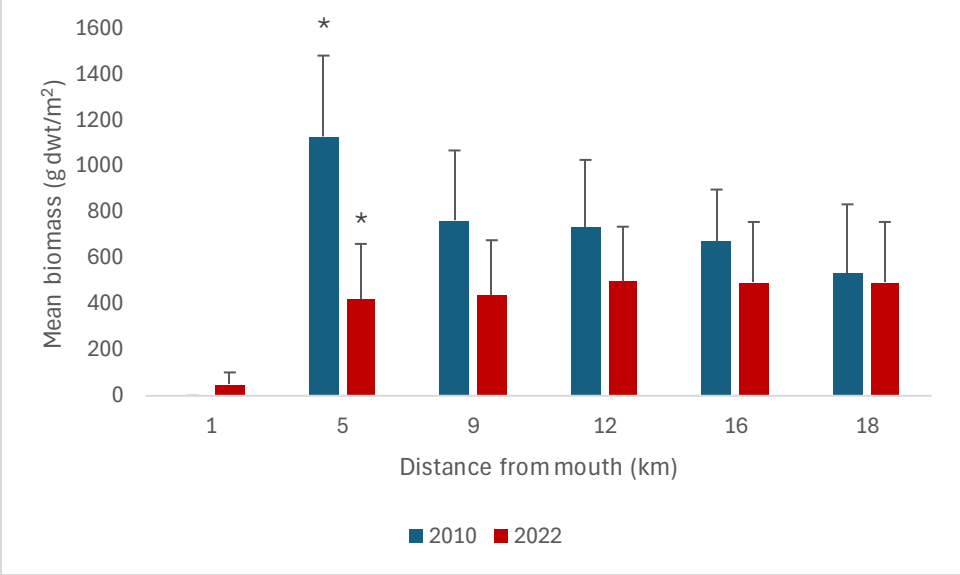

Figure 3.3 Mean (+S.E.) macrophyte biomass (g dwt/m^2) along the length of the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape between two surveys: 2010 and 2022. Data points with an asterisk indicate significant differences between the surveys

Within the three macrophyte-dominated zones of the estuarine system across all six sites, the biomass of *Z. capensis* ranged between 99.25 - 664.05 g dwt/m^2 (mean 184.51 ± 48.33 g dwt/m^2) in Zone I; the biomass of *S.maritima* ranged between 324.53 – 2869.49 g dwt/m^2 (mean 885.82 ± 158.63 g dwt/m^2) in Zone III, and the biomass of *S. perennis* between 817.01 – 1200.69 g dwt/m^2 (mean 844.66 ± 94.85 g dwt/m^2) in Zone IV, in 2010.

Similarly, in 2022, the biomass of *Z. capensis* ranged between 45.20 – 117.40 g dwt/m^2 (mean 72.28 ± 9.52 g dwt/m^2) in Zone I; the macrophyte biomass of *S. maritima* ranged between 104.00 – 616.00 g dwt/m^2 (mean 355.61 ± 36.81 g dwt/m^2) in Zone III, and the macrophyte biomass of *S. perennis* ranged between 506.00 – 1273.00 g dwt/m^2 (mean 612.50 ± 113.09 g dwt/m^2) in Zone IV.

The lowest mean macrophyte biomass was found in Zone I, *Z. capensis*, in both surveys, and the highest macrophyte biomass was found in Zone III, *S. maritima*, in 2010 and Zone IV, *S. perennis,* in 2022 (**Figure 3.3.1**). ANOVA and Tukey HSD post hoc testing revealed significant differences in macrophyte biomass between the two surveys in Zone I, *Zostera* ($F_{1,34}$= 5.192, P = 0.029) and Zone III, *Spartina* ($F_{1,34}$= 10.60, P = 0.003). Notable exceptions were recorded at station 6, at the mouth of the estuary, where, from the previous study by Henninger and Froneman (2011), it was identified as an outlier due to its lack of vegetation, which we see

specifically in zone I, III and IV. Additionally, Station 1, at the weir of the estuary, was further identified by Henninger and Froneman (2011), where *Z. capensis* was only found subtidally.

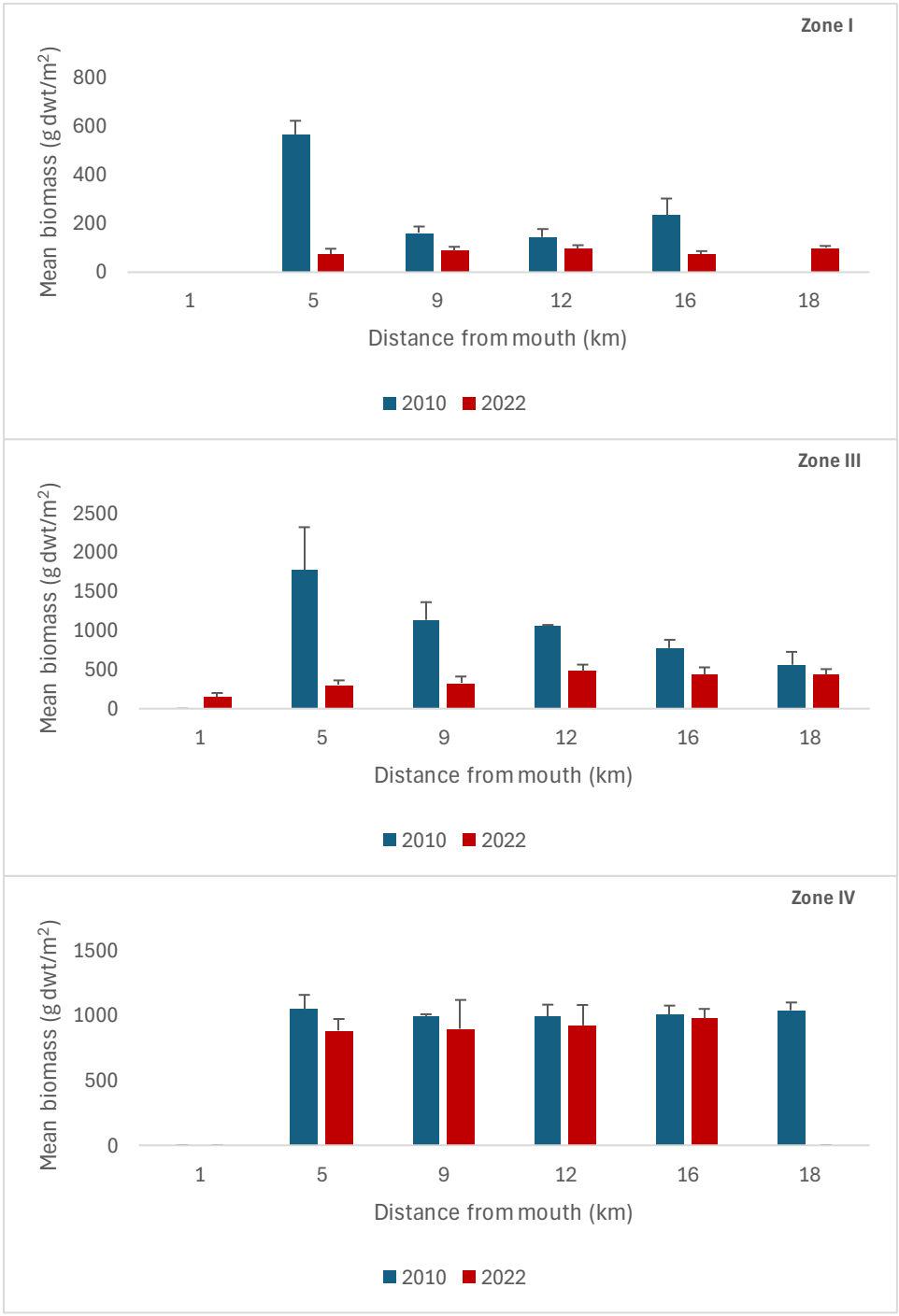

Figure 3.3.1 Mean (+ S.E.) macrophyte biomass (g dwt/m^2) across the horizontal gradient and within the three macrophyte dominant zones in the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape between two surveys: 2010 and 2022.

Key: Zone I = *Zostera*; Zone III = *Spartina*; Zone IV = *Sarcocornia*

3.1.3. **Abundance and biomass of macrobenthos**

The mean macrobenthos abundances ranged from 14 ± 14.4 to 110 ± 54.13 ind/m^2 in 2010 and from 33 ± 24.57 to 188 ± 73.85 ind/m^2 in 2022 (**Figure 3.4**). ANOVA and post hoc Tukey HSD test revealed no significant difference in the total macrofauna abundances between the two surveys ($P > 0.05$ in all cases).

Station 4, 9km from the mouth of the estuary, had the highest mean abundance of macrobenthos during the 2010 survey (110 ind/m^2). In 2022, the highest macrobenthic abundance was found at station 3, 12km from the mouth of the estuary (188 ind/m^2) (**Figure 3.4**).

Quasipoisson generalised linear modelling revealed several multicollinearities between variables in both years. Once collinear variables were removed, the model revealed that there was a significant relationship between the abundance of macrobenthos and salinity in 2010 ($P = 0.002$) and the abundance of macrobenthos and temperature in 2022 ($P = 0.044$) (see appendix for model outputs).

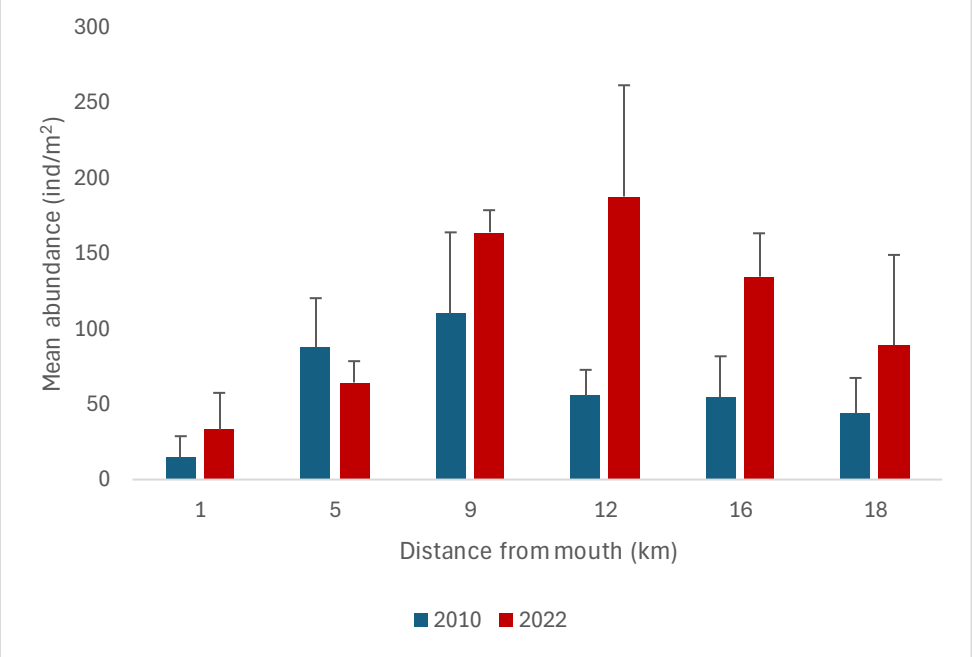

Figure 3.4. Mean (+S.E.) macrobenthic abundance (ind/m^2) along the horizontal gradient of the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape between two surveys: 2010 and 2022.

Within the four ecological zones, the mean macrobenthos abundances ranged from 18 ± 1.78 to 270± 109.82 ind/m^2 in 2010 and ranged from 30 ± 15.27 to 408 ± 36.17 ind/m^2 in 2022 (**Figure 3.5**).

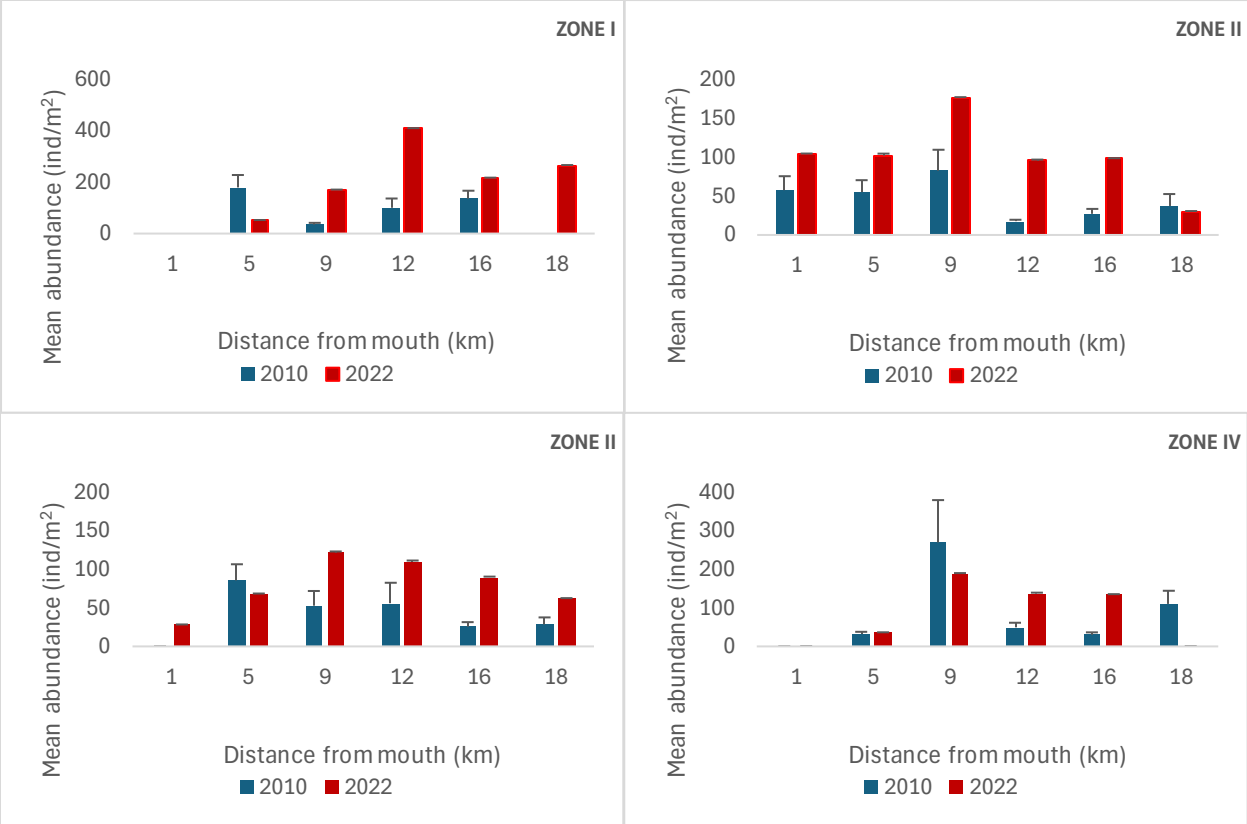

Figure 3.5. Mean (+ S.E.) macrobenthos abundance (ind/m^2) within the four zones of the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape between two surveys: 2010 and 2022. Key: Zone I = *Zostera*; Zone II = Mud; Zone III = *Spartina*; Zone IV = *Sarcocornia*

The lowest mean macrobenthos abundance was found in Zone III, *Spartina*, in 2010 (41 ind/m^2) and 2022 (80 ind/m^2). The highest mean macrobenthos abundance was found in Zone IV in 2010 (82 ind/m^2) and Zone I in 2022 (183 ind/m^2) (**Figure 3.5**). ANOVA and Tukey HSD post hoc test revealed significant differences in macrofauna abundance between the two surveys in Zone II, Mud ($F_{1,54}$ = 4.481, P = 0.038) and Zone III, *Spartina* ($F_{1,54}$ = 5.285, P = 0.025).

The mean macrobenthos biomass during 2010 ranged from 0.15 ± 0.150 to 56.72 ± 8.92 g wwt/m^2 and from 2.58 ± 1.49 to 33.14 ± 14.13 g wwt/m^2 in 2022 (**Figure 3.6**). Station 4, 9km from the mouth of the estuary, had the highest mean macrobenthic biomass of macrobenthos during the

2010 survey (56.72 g wwt/m^2). In 2022, the highest macrobenthic biomass (33.14 g wwt/m^2) was found that station 3, 12km from the mouth of the estuary (**Figure 3.6**).

ANOVA and post hoc Tukey HSD testing revealed that station 6, 1km from the mouth of the estuary ($F_{1,22} = 7.491$, $P = 0.012$), and station 4, 9km from the mouth of the estuary ($F_{1,22} = 4.364$, $P = 0.049$), were significantly different between the two surveys when assessing horizontal gradients.

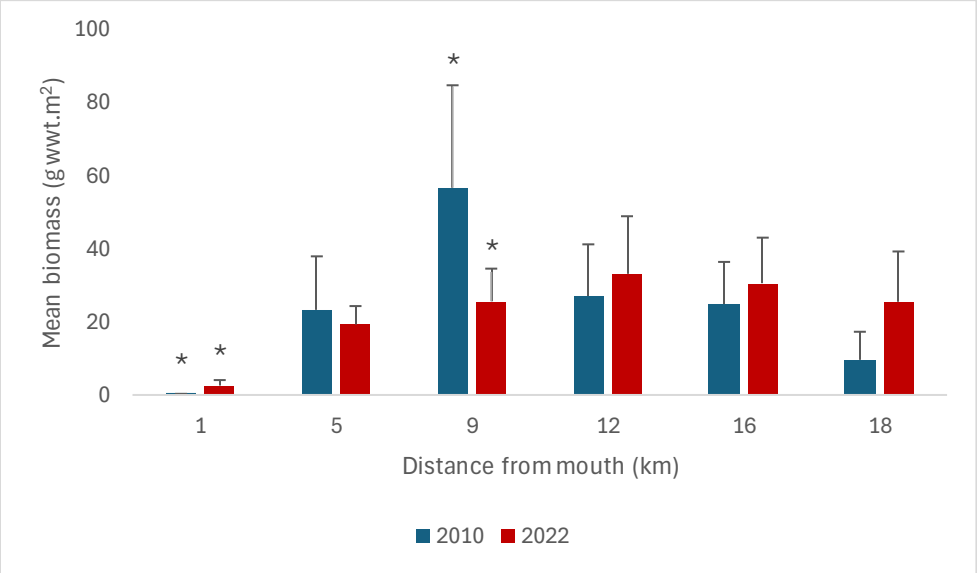

Figure 3.6 Mean (+S.E.) macrobenthic biomass (g wwt/m^2) along the horizontal gradient of the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape between two surveys: 2010 and 2022. Data points with an asterisk indicate significant differences between the surveys.

Within the four zones of the estuarine system, macrobenthos' mean biomass ranged from 0.60 ± 0.15 to 65.57 ± 21.79 g wwt.m^2 in 2010 and from 4.91 ± 1.236 to 80.13 ± 11.00 g wwt.m^2 in 2022 (**Figure 3.7**).

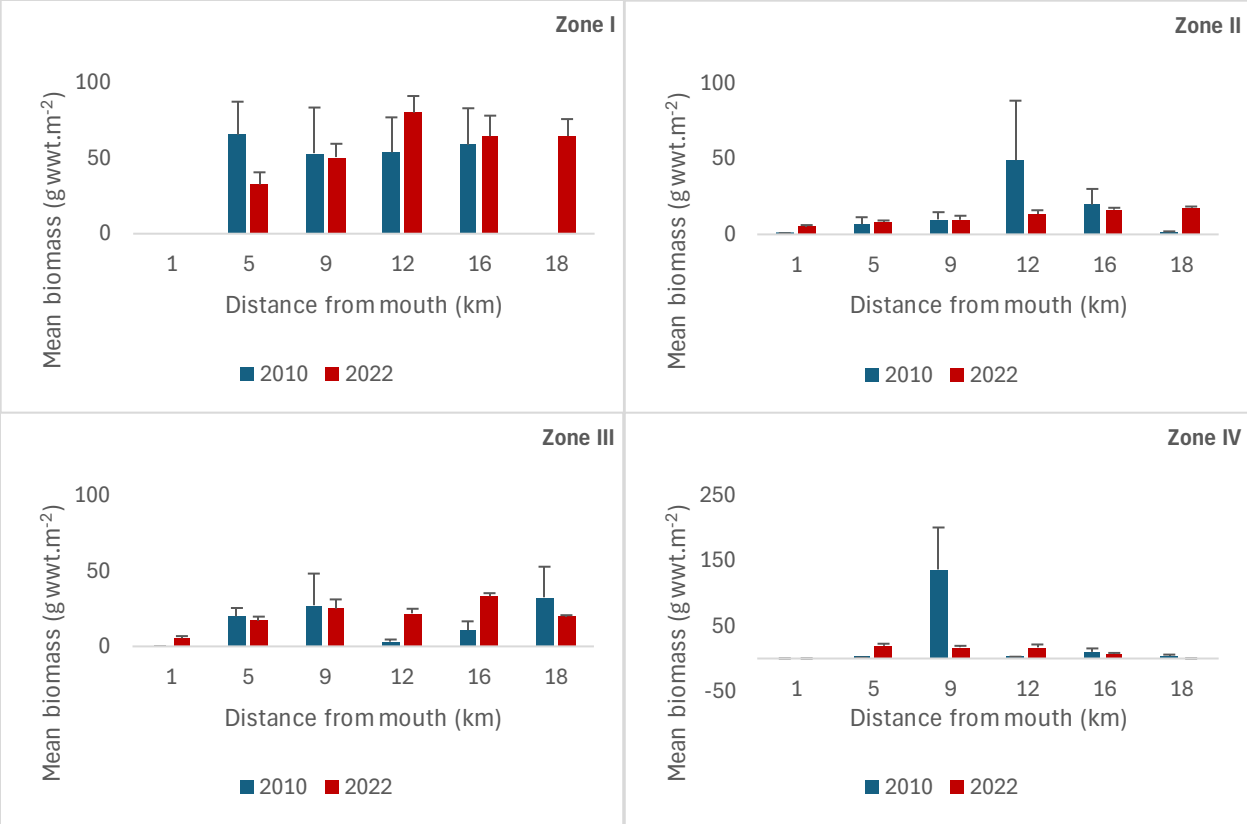

Figure 3.7 Mean (+ S.E.) macrobenthos biomass (g wwt/m^2) within the four zones of the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape between two surveys: 2010 and 2022. Key: Zone I = *Zostera*; Zone II = Mud; Zone III = *Spartina*; Zone IV = *Sarcocornia*

The lowest mean macrobenthos biomass was found in Zone II, Mud, in 2010 (14.58 g wwt/m^2) and Zone IV, Sarcocornia, in 2022 (10.32 g wwt/m^2). The highest mean macrobenthos biomass was found in Zone I, Zostera, in 2010 (38.61 g wwt/m^2) and again in 2022 (48.77 g wwt/m^2) (**Figure 3.7**). ANOVA and Tukey HSD post hoc testing revealed no significant differences in surveys between zones.

3.1.3.1. Zone I – *Zostera capensis*

In 2010, the mean macrobenthos abundances ranged from 35 ± 6.70 to 179 ± 48.34 ind/m^2 (**Figure 3.5**) and the biomass from 53 ± 30.19 to 66 ± 21.80 g wwt/m^2 (**Figure 3.7**). Fourteen

macrobenthic species were found within Zone I. Simpson's diversity index (D) values ranged from 2.58 to 3.77 (bearing in mind that a lower D value is more favourable), and the Simpson's equitability index (ED) values from 0.29 to 0.75 (**Table 3.5**). In 2022, the mean macrobenthos abundances ranged from 52 ± 0.68 to 408 ± 2.12 ind/m^2 (**Figure 3.5**). Total macrofaunal biomass ranged from 32.57 ± 8.08 to 80.13 ±11.00 g wwt/m^2 (**Figure 3.7**). Eighteen macrobenthic species were found in this zone. Simpson's diversity index (D) values ranged from 4.7 to 6.8, while Simpson's equitability index (ED) values ranged from 0.6 to 0.9 (**Table 3.7**). Mean species richness (S) in this zone was highest in 2022 (7.2), individuals (N) were highest in 2010 (1320), and the Shannon-Weiner Diversity Index (H') was highest in 2022 (1.57) (**Table 3.3**). ANOVA and Tukey HSD post hoc test revealed no significant overall differences in macrobenthos abundance between surveys in this zone. However, significant differences were found in the macrobenthic abundances between the 2010 and 2022 surveys at station 1 ($F_{1,54} = 8.421$, $P = 0.005$) (**Figure 3.5**). ANOVA and Tukey HSD post hoc testing further revealed no overall significant differences in macrobenthos biomass between surveys in this zone. By site, the total macrobenthic biomass at station 5 in 2010 was significantly higher than that recorded at the same station in 2022 ($F_{1,4} = 10.48$, $P = 0.032$) (**Figure 3.7**).

3.1.3.2. Zone II – Mud

In 2010, the mean abundances of macrofauna in Zone II ranged from 18 ± 1.78 to 93 ± 30.53 ind/m^2 **(Figure 3.5)** and the total l biomass from 0.60 ± 0.15 to 19.66 ± 10.42 g wwt/ m^2 **(Figure 3.7)**. Thirteen macrobenthic species were found in this zone. Simpson's diversity index (D) values ranged from 1.36 to 6.40, and Simpson's equitability index (ED) from 0.58 to 0.91 (**Table 3.5**). During 2022, the mean macrobenthos abundances within the corresponding ecological zone ranged from 30 ± 0.73 to 176 ± 1.20 ind/m^2 (**Figure 3.5**). Total macrofaunal biomass ranged from 4.91 ± 1.24 to 17.87 ± 0.578 g wwt/m^2 (**Figure 3.7**). Seventeen macrobenthic species were found in this zone. Simpson's diversity index (D) values ranged from 2.96 to 7.28, and Simpson's equitability index (ED) values from 0.60 to 0.99 (**Table 3.7**). Mean species richness (S) in this Zone was highest in 2022 (8), individuals (N) were highest in 2010 (322.6), and Shannon-Wiener Diversity index (H') was highest in 2022 (1.76) (**Table 3.3**). ANOVA and Tukey HSD post hoc testing

revealed significant differences in macrobenthos abundance between surveys in this zone ($F_{1,54}$ = 4.481, P = 0.038). However, no significant differences were found between stations within this zone (**Figure 3.5**). ANOVA and Tukey HSD post hoc testing further revealed no overall significant differences in macrobenthos biomass between surveys in this zone. However, statistically significant differences were found between Station 1, 18km from the mouth of the estuary ($F_{1,4}$ = 640.90, P < 0.0001), and Station 6, 1km from the mouth of the estuary ($F_{1,4}$ = 11.55, P = 0.027), where mean macrobenthos biomass was higher in 2022 in both stations (**Figure 3.7**).

3.1.3.3. Zone III – *Spartina maritima*

In 2010, the mean macrofauna abundances in Zone III ranged from 26± 5.44 to 86 ± 20.90 ind/m^2 **(Figure 3.5)**. Total macrofaunal biomass ranged from 3.15 ± 1.41 to 32.50 ± 20.24 g wwt/m^2 **(Figure 3.7)**. Nineteen invertebrate species were found in this zone, making it the most diverse zone in the littoral zone of the Kariega Estuary in 2010. Simpson's diversity index (D) ranged from 1.68 to 6.19, and Simpson's equitability index (ED) from 0.44 to 0.72 (**Table 3.5**).

In 2022, the mean macrobenthos abundances ranged from 28 ± 0.48 to 122 ± 1.15 ind/m^2 (**Figure 3.5**). Total macrofaunal biomass ranged from 5.4 ± 1.41 to 33.23 ± 1.99 g wwt/m^2 (**Figure 3.7**). Again, Zone III was identified as the most speciose of the four zones considered, with twenty-one macrobenthic species recorded. Simpson's diversity index (D) values ranged from 3.44 to 8.05, and Simpson's equitability index (ED) was from 0.52 to 0.89 (**Table 3.7**). Mean species richness (S) in this Zone was highest in 2022 (8.8), mean individuals (N) was highest in 2010 (453.3), and the Shannon-Wiener Diversity index (H') was highest in 2022 (1.88) (**Table 3.6**). ANOVA and Tukey HSD post hoc testing revealed overall significant differences in macrobenthos abundance between surveys in this zone ($F_{1,54}$ = 5.285, P = 0.025). Furthermore, significant differences were found between station 5, 5km from the mouth of the estuary ($F_{1,4}$ = 11.55, P = 0.027), where the mean macrobenthos abundance in 2010 was significantly higher than that recorded during 2022 (**Figure 3.5**).

ANOVA and Tukey HSD post hoc testing revealed no significant differences in macrobenthos biomass between surveys in this zone. However, significant differences were found between Station 2, 16km from the mouth of the estuary ($F_{1,4}$ = 29.62, P = 0.006), Station 3, 12km from the mouth of the estuary ($F_{1,4}$ = 26.33, P = 0.007), and Station 6, 1km from the mouth of the estuary ($F_{1,4}$ = 14.65, P = 0.019), where mean macrobenthos biomass was higher in 2022 in all stations (**Figure 3.7**).

3.1.3.4. Zone IV – *Sarcocornia perennis*

In Zone IV during 2010, the mean abundances of macrofauna ranged from 30 ± 6.22 to 270 ± 109.82 g/m^2 **(Figure 3.5)** and the biomass from 0.908 ± 0.281 to 136.50 ± 64.294 g wwt/m^2 **(Figure 3.7)**. Fourteen invertebrate species were recorded in Zone IV. Simpson's diversity index (D) ranged from 2.09 to 5.97, and Simpson's equitability index (ED) ranged from 0.57 to 0.87 (**Table 3.5**). In the corresponding zone, during 2022, the mean total macrobenthos abundances ranged from 36 ± 0.488 to 189 ± 1.31 ind/m^2 (**Figure 3.5**). Similarly, the total macrofaunal biomass ranged from 8.23 ± 0.27 to 19.37 ± 3.23 g wwt/m^2 (**Figure 3.7**). Twenty-one macrobenthic species were found in this zone. Simpson's diversity index (D) values ranged from 5.12 to 6.67, and Simpson's equitability index (ED) values from 0.47 to 1.03 (**Table 3.7**). Mean species richness (S) in this Zone was highest in 2022 (6.5), individuals (N) were highest in 2010 (648), and Shannon-Wiener Diversity index (H') was highest in 2022 (1.28) (**Table 3.3**). ANOVA and Tukey HSD post hoc testing revealed no significant temporal differences between surveys in the total macrobenthos abundance and biomass estimates (**Figure 3.5**). However, significant differences were found between survey years at station 1, 18km from the mouth of the estuary ($F_{1,4}$ = 20.16, P = 0.011), station 3, 12km from the mouth of the estuary ($F_{1,4}$ = 11.34, P = 0.028), station 4, 9km from the mouth of the estuary ($F_{1,4}$ = 11.86, P = 0.026), and station 5, 5km from the mouth of the estuary ($F_{1,4}$ = 32.89, P = 0.005) **(Figure 3.7)**.

Table 3.3 Comparison of mean species richness (S), individuals (N) and diversity (H') between 2010 and 2022 surveys in the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape.

	Mean species richness (S)	Mean Individuals (N)	Mean Diversity (H')
Zone I			
2010	5	1320	0.87
2022	7.2	185.2	1.57
Zone II			
2010	4.7	322.6	1.16
2022	8	101	1.76
Zone III			
2010	6	453.3	1.21
2022	8.8	80	1.88
Zone IV			
2010	4.2	648	1.01
2022	6.5	83	1.28

Two sample *t*-tests assuming equal variance were conducted and showed that there were significant differences across all indices between 2010 and 2022 ($p < 0.05$ in all cases). On average species diversity and richness increased but declines in mean individuals can be observed in each zone in 2022 (**Table 3.3**).

3.2. Species composition

Table 3.4 Distribution of the macrobenthic species found along the length of the freshwater-deprived permanently open Kariega Estuary in the Eastern Cape province of South Africa during a 2010 survey. Station 1 is identified as the estuary's upper reaches, and Station 6 is the mouth of the estuary, with + indicating a presence.

	Zone I						Zone II						Zone III						Zone IV					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Polychaeta																								
Dendronereis arborifera														+										
Glycera tridactyla			+	+																				
Lumbrineris tetraura					+		+							+										
Marphysa sanguinea		+	+	+	+					+	+		+		+	+	+			+				
Pectinaria capensis												+												
Crustacea																								
Amphipoda																								
Grandidierella chelata															+	+	+		+		+			
Isopoda																								
Apanthura sandalensis																	+							
Exosphaeroma hylocoetes																	+							
Ligia natalensis							+				+												+	
Pontogeloides latipes												+												
Tanaidacea																								
Apseudes digitalis		+			+																			
Anomura																								
Callichirus kraussi					+																			
Upogebia africana									+		+						+							
Brachyura																								
Cleistostoma edwardsii					+			+	+	+	+					+	+						+	
Cyclograpsus punctatus										+						+	+					+		
Dotilla fenestrata													+	+										

Table 3.4 (*continued*)

	Zone I						Zone II						Zone III						Zone IV					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Insecta																								
Carabid sp.														+		+							+	
Insect larva													+											
Tipulidae sp.					+														+	+	+			
Mollusca																								
Bivalvia																								
Arcuatula capensis		+	+		+				+	+			+	+	+	+	+		+	+	+			
Macoma litoralis		+	+	+	+		+	+	+				+				+			+				
Solen cylindraceus		+	+	+	+		+	+	+				+	+						+				
Gastropoda																								
Assiminea globulus														+		+			+	+		+		
Haminea alfredensis					+																			
Littorina scabra			+						+		+						+				+		+	
Nassarius kraussianus		+	+	+	+		+	+	+	+			+	+						+				
Natica gualteriana					+																			
Polychaeta																								
Onchidiid sp.																			+	+	+	+		

Table 3.5 Indication of species per zone and total number of species found in a 2010 survey amongst four zones of the permanently open Kariega Estuary in the Eastern Cape province of South Africa. *D* indicates Simpson's diversity index; E_D indicates Simpson's equitability index per station and zone.

	Zone I						Zone II						Zone III						Zone IV					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Total = 28 Spp	**14**						**12**						**17**						**14**					
D	3.34	2.58	3.77	3.52			3.31	3.27	6.4	3.22	2.19	1.36	5.04	5.65	1.68	3.49	6.19		2.86	5.97	3.22	2.09	3.46	
E_D	0.56	0.37	0.75	0.29			0.66	0.82	0.91	0.64	0.58	0.68	0.72	0.71	0.56	0.44	0.62		0.57	0.75	0.64	0.07	0.87	
Zone means *D*	3.30 ± 0.512						3.41 ± 1.640						4.41 ± 1.828						3.52 ± 1.463					
Zone means E_D	0.49 ± 0.206						0.72 ± 0.124						0.61 ± 0.116						0.71 ± 0.110					

Table 3.6 Distribution of the macrobenthic species found along the length of the freshwater-deprived permanently open Kariega Estuary in the Eastern Cape province of South Africa during the 2022 survey. Station 1 is identified as the estuary's upper reaches, and Station 6 is the mouth of the estuary, with + indicating a presence.

	Zone I						Zone II						Zone III						Zone IV					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Polychaeta																								
Dendronereis arborifera							+							+	+	+								
Glycera tridactyla			+	+																+				
Lumbrineris tetraura			+		+								+	+										
Marphysa sanguinea	+	+	+	+			+	+	+	+	+		+		+	+	+			+		+		
Pectinaria capensis							+																	
Crustacea																								
Amphipoda																								
Grandidierella chelata								+		+					+	+				+	+	+		
Isopoda																								
Apanthura sandalensis		+																		+	+			
Exosphaeroma hylocoetes	+	+		+			+	+			+	+				+	+						+	
Ligia natalensis							+	+	+	+	+											+	+	
Pontogeloides latipes							+	+				+				+								
Tanaidacea																								
Apseudes digitalis	+	+	+	+	+																			
Anomura																								
Callichiruskraussi					+																	+		
Upogebia africana								+	+				+	+			+	+		+	+			
Brachyura																								
Cleistostoma edwardsii	+			+			+		+	+	+		+			+	+					+	+	
Cyclograpsus punctatus									+	+							+				+	+		
Dotilla fenestrata									+				+	+	+									

Table 3.6 (*continued*)

	Zone I						Zone II						Zone III						Zone IV					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Insecta																								
Carabid sp.			+						+	+				+									+	
Insect larva													+											
Tipulidae sp.																				+				
Mollusca																								
Bivalvia																								
Arcuatula capensis	+	+	+						+				+	+	+	+	+	+			+	+		
Macoma litoralis	+	+	+	+	+		+	+	+	+			+				+			+		+		
Solen cylindraceus	+	+	+	+			+			+			+	+	+					+				
Gastropoda																								
Assiminea globulus	+												+	+	+	+					+	+		
Haminea alfredensis		+											+		+						+			
Littorina scabra			+				+				+						+	+		+		+	+	
Nassarius kraussianus	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+	+		+	+	+	+	
Natica gualteriana				+											+						+			
Polychaeta																								
Onchidiid sp.			+													+				+	+	+		

Table 3.7 Indication of species per zone and total number of species found during the 2022 survey amongst four zones of the permanently open Kariega Estuary in the Eastern Cape province of South Africa. *D* indicates Simpson's diversity index; E_D indicates Simpson's equitability index per station and zone.

	Zone I						Zone II						Zone III						Zone IV					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Total = 28 Spp			**18**						**17**						**21**						**21**			
D	6.8	5.7	7	6.8	4.7		6.67	6.93	7.28	4.7	3.5	2.96	7.56	7.57	4.70	5.93	8.05	3.44	5.12	5.53	6.67	6.18		
E_D	0.6	0.6	0.8	0.8	0.9		0.61	0.77	0.73	0.5	0.6	0.99	0.63	0.84	0.52	0.59	0.89	0.86	0.47	0.55	0.56	1.03		
Zone mean *D*	6.18 ± 0.973						5.34 ± 1.871						6.20 ± 1.850						5.87 ± 0.687					
Zone mean E_D	0.74 ± 0.126						0.70 ± 0.177						0.72 ± 0.152						0.65 ± 0.255					

3.3. Multidimensional scaling

The results of the non-metric Multidimensional Scaling (nMDS) analysis (**Figure 3.8**) illustrated, with some exceptions, a high degree of similarity in the community composition of the macrobenthos between the 2010 and 2022 surveys. Outliers were identified; these were Sar 4 (2010), Sar 5 (2010), and M6 (2010). At these stations, only 2-3 species were found as opposed to the other stations where the macrobenthic community comprised an average of 6 species. However, Sar 4 did have one of the highest numbers of total individuals, primarily *Onchidiid* sp. and *Assiminea globules*.

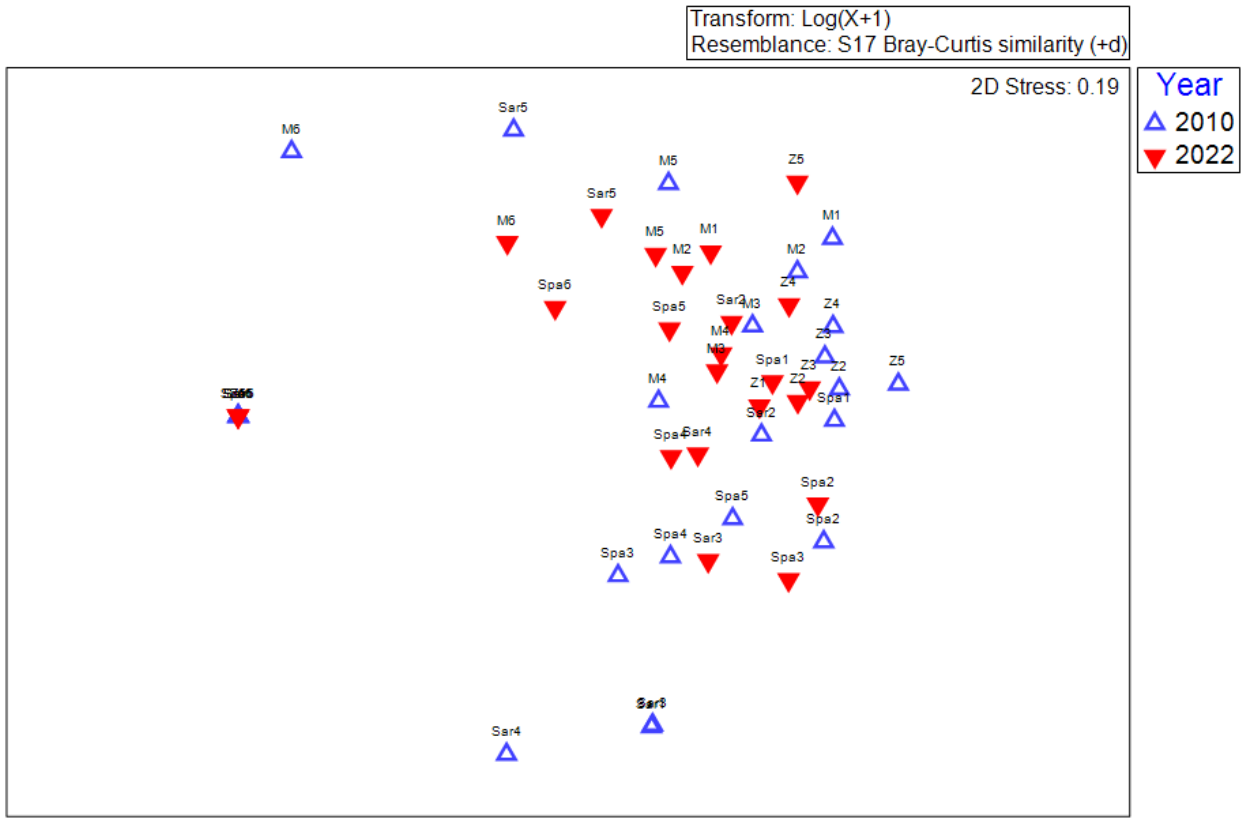

Figure 3.8 Multidimensional scaling of the macrofaunal community composition in stations 1-6 along the length of the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape of South Africa. Key: Z = *Zostera* Zone; M = Mud Zone; Spa = *Spartina* Zone; Sar = *Sarcocornia* Zone.

3.4. Community structure

The PERMANOVA pairwise tests assessing differences in community structure between 2010 and 2022 across four zones revealed no statistically significant changes over time ($P > 0.05$ in all cases. (**Table 3.8**).

Table 3.8. PERMANOVA results of the comparative analysis of community structure between 2010 and 2022 in the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape. Key: Zone I = *Zostera* Zone; Zone II = Mud Zone; Zone III = *Spartina* Zone; Zone IV = *Sarcocornia* Zone.

PERMANOVA Pairwise 2010 vs 2022				
	Average Distance	**T**	**P(perm)**	**perms**
Zone I	39.25	0.88	0.31	201
Zone II	38.93	1.02	0.44	405
Zone III	31.26	1.12	0.29	417
Zone IV	25.18	1.06	0.35	200

Table 3.9. SIMPER analysis indicating the upper 75% species composition from samples collected in 2010 from the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape.

Species	**Contributing %**	**Cumulative%**
Marphysa sanguinea	17.85	17.85
Solen cylindraceus	15.08	32.93
Nassarius kraussianus	14.44	47.37
Arcuatula capensis	12.47	59.84
Macoma litoralis	11.87	71.7
Cleistostoma edwardsii	7.64	79.35

Table 3.10. SIMPER analysis indicating the upper 75% species composition from samples collected in 2022 from the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape.

Species	Contributing %	Cumulative%
Nassarius kraussianus	31.63	31.63
Marphysa sanguinea	11.91	43.54
Macoma litoralis	8.33	51.87
Cleistostoma edwardsii	8.05	59.91
Arcuatula capensis	7.54	67.45
Exosphaeroma hylocoetes	5.97	73.42
Solen cylindraceus	4.55	77.97

Table 3.11 SIMPER analysis indicating the upper 70% species composition from samples collected 352 in 2010 and 2022 from the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape.

Species	2010 Av. Abund	2022 Av. Abund	Contributing%	Cumulative%
Marphysa sanguinea	1.74	1.25	8.95	8.95
Nassarius kraussianus	1.24	1.91	8.67	17.63
Macoma litoralis	1.25	0.97	6.78	24.41
Solen cylindraceus	1.37	0.72	6.77	31.18
Cleistostoma edwardsii	1.11	0.93	6.65	37.83
Arcuatula capensis	1.04	0.99	6.02	43.85
Assiminea globulus	0.8	0.48	5.24	49.09
Littorina scabra	0.68	0.58	4.88	53.97
***Onchidid* sp.**	0.76	0.29	4.37	58.35
Exosphaeroma hylocoetes	0.11	0.72	4.01	62.35
Grandidierella chelata	0.48	0.52	3.99	66.34
Upogebia africana	0.31	0.58	3.68	70.03
Pontogeloides latipes	0.3	0.28	3.48	73.51
Ligia natalensis	0.17	0.51	3.06	76.57

Between the two surveys, the species contributing most to dissimilarity were *M. sanguinea* (8.95%), *N.kraussianus* (8.67%), and *M.litoralis* (6.78%), reflecting shifts in their relative abundances between the two surveys (**Table 3.11**). Notably, *N.kraussianus* increased in abundance (from 1.24 in 2010 to 1.91 in 2022), while *M.sanguinea* (from 1.74 in 2010 to 1.25 in 2022) and *S.cylindraceus* (from 1.37 in 2010 to 0.72 in 2022) abundance declined.

3.5. Dominant species

Table 3.12 Minimum, maximum, and mean (± S.E.) of the numerically dominant macrobenthic species along the length of the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape during surveys conducted in 2010 and 2022

Species	Minimum	Maximum	Mean ± S.E.
Marphysa sanguinea			
2010	16	944	157 ± 59.7
2022	2	84	15 ± 4.41
Upogebia africana			
2010	16	96	6 ± 4.18
2022	2	18	4 ± 1.2
Cleistostoma edwardsii			
2010	16	1952	119 ± 83.6
2022	3	38	7 ± 2.06
Cyclograpsus punctatus			
2010	16	32	3 ± 1.66
2022	4	48	4 ± 2.08
Macoma litoralis			
2010	16	1024	74 ± 43.7
2022	2	56	7 ± 2.6
Solen cylindraceus			
2010	16	464	53 ± 21.1
2022	2	27	5 ± 1.53
Nassarius kraussianus			
2010	16	320	28 ± 15.8
2022	10	76	26 ± 3.9
Onchidid sp.			
2010	16	880	63 ± 39.3
2022	1	10	1 ± 0.49

A comparison of the abundance of various species between 2010 and 2022 revealed significant changes in the mean population densities across several taxa. *Marphysa sanguinea* mean abundances decreased from 157 ± 59.7 ind/m^2 in 2010 to 15 ± 4.41 ind/m^2 in 2022, with a corresponding decrease in both minimum and maximum densities (16–944 ind/m^2 in 2010 to 2–84 in 2022 ind/m^2) (**Table 3.12**). Mean abundances of the mud prawn*, Upogebia africana* ranged from 16 to 96 ind/m^2 (mean = 6 ± 4.18 ind/m^2) in 2010 and from 2 to 18 ind/m^2 (mean = 4 ± 1.2 ind/m^2) in 2022. (**Table 3.12**). Mean abundances of estuarine crab, *Cleistostoma edwardsii* declined, falling from 119 ± 83.6 ind/m^2 in 2010 to 7 ± 2.06 ind/m^2 in 2022. The range of individuals similarly contracted from 16–1952 ind/m^2 in 2010 to 3–38 ind/m^2 in 2022 (**Table 3.12**). By contrast, *Cyclograpsus punctatus* exhibited a minor increase in mean abundance, rising from 3 ± 1.66 ind/m^2 in 2010 to 4 ± 2.08 ind/m^2 in 2022, alongside a slight range expansion from 16–32 ind/m^2 in 2010 to 4–48 ind/m^2 in 2022 (**Table 3.12**).

Macoma litoralis abundances in 2010 ranged from 16 to 1024 ind/m2 (mean74 ± 43.7 ind/m^2) and from 2 to 56 ind/m^2 (mean = 7 ± 2.6 ind/m^2) in 2022 (**Table 3.12**). *Solen cylindraceus* abundances decreased from 53 ± 21.1 ind/m^2 (range 16–464 ind/m^2) in 2010 to 5 ± 1.53 ind/m^2 (range 2–27 ind/m^2) in 2022(**Table 3.12**). Abundances of the tick shell, *Nassarius kraussianus*, remained relatively stable between the two surveys, with a mean abundance of 28 ± 15.8 ind/m^2 in 2010 and 26 ± 3.9 ind/m^2 in 2022. (**Table 3.12**). Finally, *Onchidid* sp. also showed a decline, with mean abundance decreasing from 63 ± 39.3 ind/m^2 in 2010 to 1 ± 0.49 ind/m^2 in 2022 and its range contracting from 16–880 ind/m^2 to 1–10 ind/m^2 (**Table 3.12**).ANOVA and post hoc Tukey HSD test revealed that the mean abundances of *M. sanguinea* ($F_{1,46}$ = 5.681, *P* = 0.021) and *S. cylindraceus* ($F_{1,48}$ = 5.189, *P* = 0.027) in 2010 were significantly higher than those recorded in 2022. No significant temporal differences in the abundances of the remaining species were evident (P > 0.05) in all cases.

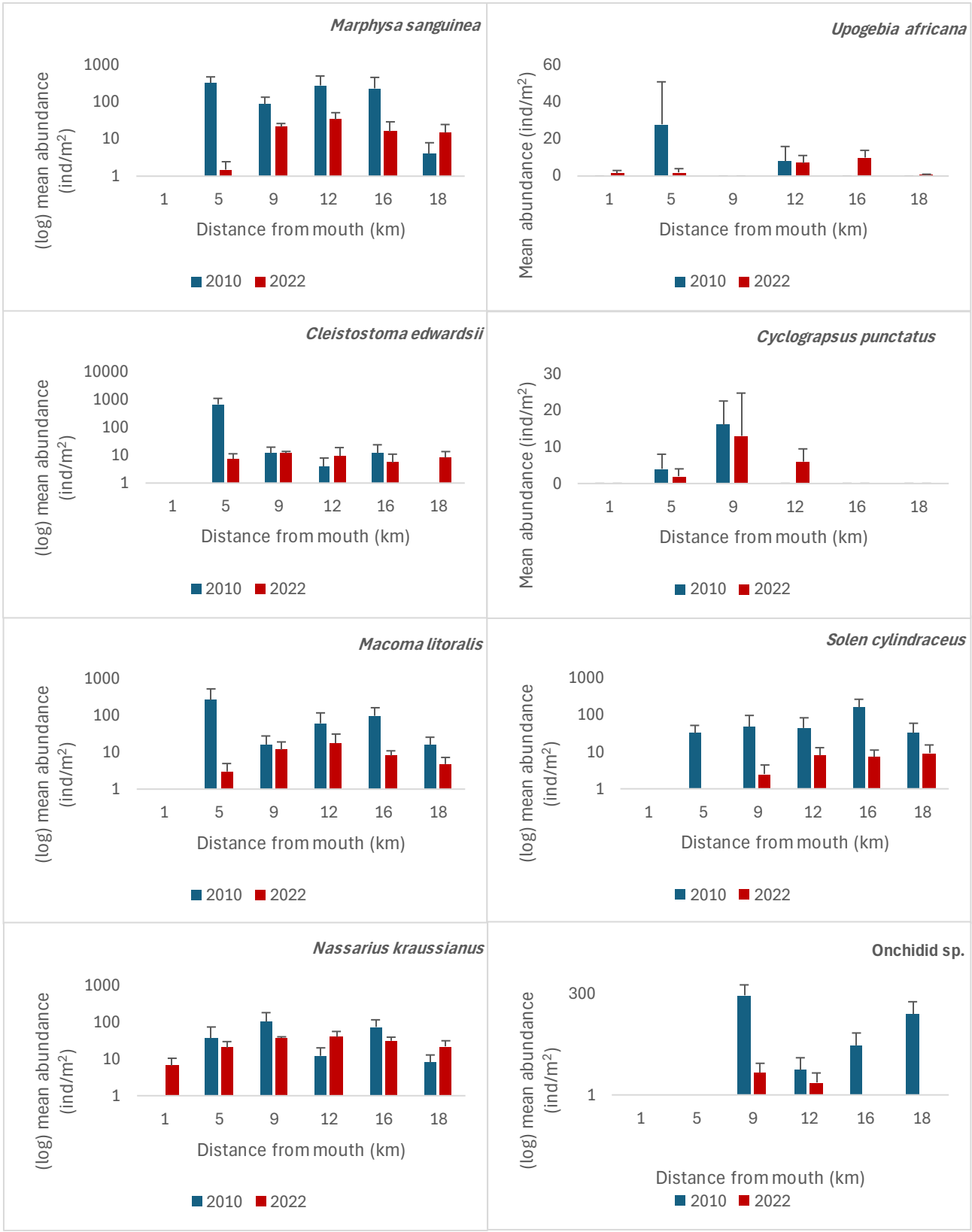

Figure 3.9 Distribution and abundance of the numerically dominant macrobenthic species along the length of the freshwater-deprived, permanently open Kariega Estuary in the Eastern Cape in 2010 and 2022. Note the difference in y-axis scales amongst species.

Chapter 4

Discussion

4. Introduction

Estuaries are essential feeding and nursing grounds for various invertebrates and vertebrates and represent biodiversity hotspots. (Sherman et al., 2009; Herman et al., 1999). Moreover, estuaries influence the nearshore marine environment by exporting organic matter and nutrients (Vorwerk & Froneman, 2009). These systems also provide essential goods and services and sustain the livelihoods of vulnerable coastal communities (Thrush et al., 2013; Henninger & Froneman, 2011; Huppert et al., 2003).

Both directly and indirectly, anthropogenic activities have dramatically affected the Kariega Estuary's system's functioning due to freshwater abstraction, overexploitation of renewable resources, pollution, and loss of habitats associated with coastal development. To understand the potential impacts of these activities on estuarine ecosystem functioning, we must understand the spatial and temporal patterns in the biology of these systems. This study focused on the long-term patterns in the macrobenthic community structure in the permanently open, saltwater-deprived Kariega Estuary in the Eastern Cape coastline of South Africa. Specifically, the study aimed to understand how selected environmental variables affect the macrobenthos' distribution and community structure and assess any decadal shifts in the macrobenthic community structure within the estuary. How these were addressed, and the findings thereof will be broken down in the subsections that follow.

4.1. Physiochemistry

In agreement with previous studies conducted in the Kariega Estuary (see for example: Froneman, 2000; Hodgson, 1987), reverse gradients in salinity and temperature were recorded along the length of the system during both surveys. The observed pattern can be attributed to the lack of freshwater inflow (Claassens et al., 2022; Van der Walt, 2019; Henninger & Froneman, 2011) due to the presence of impoundments along the Kariega River, a small catchment area (680-690km^2) and freshwater abstraction. According to Hodgson (1987), salinities within the estuary typically range from 35 to 40. During the 2010 survey, the Eastern Cape province of South Africa experienced a severe drought, contributing to a more marked salinity gradient than in 2022 (Henninger & Froneman, 2011). Indeed, hypersaline conditions were recorded in the upper reach of the system during 2012. By contrast, the

South African Weather Services classified 2022 as a wet year for the Eastern Cape, potentially contributing to the lower salinity. Studies have shown that reduced freshwater inflow adversely affects functioning and ecosystem health (Palmer et al., 2011; Benson, 1981). Inflow serves many purposes, including establishing and preserving low-salinity nurseries, sediment and nutrient transport, and assisting macrobenthic productivity (Palmer et al., 2011).

Several studies have shown that in conjunction with biological and regional scale processes, physicochemical variables like salinity interact and regulate the abundance, diversity, community structure, and productivity of the macrobenthos (Shank et al., 2009; Kim & Montagna, 2009; Russell et al., 2006; Montagna & Kalke, 1995). From the conducted quasipoisson generalised linear model, we found no significant effect of environmental variables (distance from the mouth, salinity, temperature and sediment organic content) on the abundance of macrobenthos. This is likely because, as aforementioned, complex interactions occur between abiotic (temperature, salinity, and habitat availability) and biotic (food availability, competition, predation and exploitation) variables that then influence the abundance of the macrobenthos (Ysebaert et al., 2003).

4.1.1. Sediment organic content

The total organic content of the sediment during 2010 ranged from 0.61% to 12.18% and from 0.80% to 3.76% in 2022. The estimates of organic content recorded during the surveys are in the range reported for permanently open estuaries within the same geographic region (Adeniji et al., 2017; Henninger et al., 2009; Orr, 2007; Hodgson, 1987). Sediment organic matter is derived from decaying plant matter, phytoplankton, marine algae, and zooplankton and is mixed with soil particles during erosion (Thalayappil et al., 2024). In the absence of freshwater inflow into the system, which contributes to low phytoplankton stocks, the organic content of the sediment is largely derived from the export of organic material from the extensive salt marshes and well-developed littoral vegetation within the system. Indeed, a previous stable isotope study conducted by Richoux and Froneman (2007) in the estuary highlighted the importance of salt marsh vegetation in the food web of the benthic and pelagic zones of the estuary. Previous research has found that weather events (rainfall and drought) can have cascading effects on the levels of organic matter available in estuaries

(Ducrotoy et al., 2019). In 2022, South Africa's summer rainfall areas experienced above-average rainfall due to the dominating La Nina event. Rainfall-runoff processes deplete organic matter from the marsh substrate in estuarine systems. This depletion is due to the preferential removal of organic matter, which is facilitated by its lower density (making it easier to mobilise) and raindrop impact (which helps to disperse it) (Torres et al., 2003).

Overall, there were no significant temporal differences in the estimates of the organic content of the sediment evident between the two surveys ($P < 0.05$ in both instances). However, site-specific differences were recorded in Zone III and Zone IV. These differences can likely be ascribed to the site-specific complexity of the beds, which would trap and accumulate organic matter derived from water columns and salt marshes.

4.2. Macrophytes

The total biomass of the macrophytes during the 2010 survey ranged from 99.25 to 2869.49 g dwt/m^2 and from 45.2 to 1273 g dwt/m^2 during 2022. The estimates of macrophyte biomass presented during this investigation are in the range reported for permanently open estuaries within the same biogeographic region during both years (Bezuidenhout, 2011; Hodgson, 1987; Adams et al., 1999). Macrophyte biomass was highest in the middle reaches of the estuary, which again coincides with an earlier study by Hodgson (1987) within the same system.

The macrophyte biomass and species composition in estuaries are determined by the complex interaction between physicochemical (temperature, nutrient, irradiance and salinity) and biological factors such as grazing and competition (Adams et al., 1999).The macrophyte biomass in *Zone I* and *Zone III* during the 2022 survey was significantly lower than in 2010. Since freshwater inflow is typically associated with a decrease in the biomass of macrophytes in estuaries, the reduced biomass of macrophytes during 2022 can potentially be attributed to the fact that it was classified as a wet year (Booth, 2007). The macrophytes' biomass changes between the two surveys will likely have far-reaching effects on the macrobenthic community structure.

Macrophytes are known to positively affect the diversity of macrobenthic species because they provide critical habitats for fish and invertebrate species (Njozela, 2013; Booth, 2007;

Bezuidenhout, 2011). They are also important for their contribution to the basis of the food web in the estuarine system, contributing to detrital output. They also provide refugia from predation and are surfaces used by epiphytic organisms grazed upon by macrobenthic invertebrates, thus providing additional input into the estuarine food web (Njozela, 2013; Henninger et al., 2009; Booth, 2007). Several studies have shown the importance of *Z. capensis* for utilisation by vertebrate and invertebrate species for foraging, nurseries, shelter, habitats and protection from predation (Human et al., 2015; Cyrus & Vivier, 2014; Wortmann et al., 1998; Barnabas, 1996; Adams & Bate, 1994; Talbot et al., 1990). Anthropogenic influences like coastal developments and habitat destruction likely cause the significant decline that we observe in *Z. capensis* (Adams, 2016) of which we have seen a significant increase in anthropogenic activity in 2022, which is a cause for concern. Previous studies have found that *Z. capensis* is extensively found along the middle and upper reaches of the estuarine system (Cowley & Daniel, 2001); however, in both surveys, *Z. capensis* has the lowest biomass in these stations and throughout the system.

Zostera capensis is a keystone species in the coastal environment. Hence, its decline could significantly impact ecosystem functioning and higher trophic levels. For instance, the limpet *Siphonaria compressa* is now one of the most endangered marine invertebrates in South Africa, as reported by Pillay et al. (2010) on the decline of *Z. capensis* in the Langebaan Lagoon and the corresponding decline in invertebrate species richness (Adams, 2016; Mead et al., 2013).

Spartina maritima is another highly productive submerged macrophyte species that has been studied, and it was found that the restoration of *S. maritima* beds has increased the biodiversity, density, species richness, and biomass of macrobenthic communities (Curado et al., 2014). The declines that we observed in *S. martima* in 2022 then pose a threat to macrobenthic communities. It had been shown in previous studies that those beds of restored *S. maritima* had the most different macrobenthic communities (Curado et al., 2014). *S. maritima* beds enhance the macroinvertebrate community, which is essential to the operation of these ecosystems—for instance, encouraging the decomposition of organic matter (Pozo & Colino, 1992). Moreover, it is a crucial trophic link between primary producers and consumers (fish, birds, etc.). (Sardá et al., 1995). The declines we observed in *S. maritima*

during 2022 have implications not only for the macrobenthic communities but also for the ecological functioning of the estuarine system, much like with *Z. capensis*.

The Kariega Estuary, as has been outlined, is an anthropogenically influenced system that has, in recent years, seen an influx in both formal and informal settlements. Although some stability remains in spatial patterns, the temporal shifts raise concerns about the long-term resilience of the system.

4.3. Abundance and biomass of macrobenthos

The average abundance of macrobenthic organisms during the 2010 survey ranged from 16 to 504 ind/m^2, and the biomass was between 0.03 and 245 g wwt/m^2, respectively. In 2022, the average abundance of macrobenthic organisms ranged from 6 to 216 ind/$m^{2,}$ and average macrobenthos biomass from 2.60 to 93.40 g wwt/m^2. Overall, there were no significant differences in the macrofauna abundance and biomass between the 2010 and 2022 surveys ($P > 0.05$ in both cases). The estimates of macrobenthic abundance and biomass recorded during the two surveys are in the lower range reported for freshwater-dominated estuaries within the same geographic region (see, for example, Hanekom & Russell, 2015; Teske & Wooldridge, 2001; Hanekom et al., 1988). The reduced estimates can likely be ascribed to the Kariega Estuary being regarded as an oligotrophic low-production system due to reduced levels of primary production resulting from limited freshwater inflow. It is worth noting that the estimates presented here are in the range reported for other coastal systems elsewhere in the world which are marine dominated (e.g. lagoons) (Chardy and Clavier, 1988; Mistri et al. 2001). Significant spatial differences in the abundance and biomass of the macrofauna were, however, recorded in Zone II and III between the two surveys. These results suggest that more in-depth studies of the various processes determining macrobenthos at different spatial scales are required. Overall, the abundance patterns in this study coincide with the findings of Hodgson (1987), where the highest macrobenthic abundances were recorded in the middle reaches of the estuarine system. The observed pattern likely reflects the importance of submerged macrophytes in providing the macrobenthos with a refugia predation (Cheng et al., 2017; Henninger et al., 2009; Lloret & Marín, 2009).

The species richness and diversity estimates recorded during the two surveys were lower than those reported for permanently open estuaries with freshwater inflow within the same biogeographic region. For example, Baird et al. (1986) recorded 122 macrobenthic species in the Swartkops River Estuary. The values are, however, in the range reported for the Kariega Estuary two decades prior to the current investigation (Hodgson, 1987). The reduced values reported for the Kariega Estuary can likely be ascribed to the marine dominance of the system, which contributes to the poor representation of freshwater and brackish water species (Hodgson, 1987). Notably, the species diversity in 2022, considered a wet year, was significantly higher than that recorded during the 2010 surveys.

Significance testing showed no significant difference in the horizontal pattern of macrobenthos abundance in the estuarine system between the 2010 and 2022 surveys, with the most incredible abundance found in the middle reaches of the estuary aligning with the first findings by Hodgson (1987). This means that spatially, there has been little change in the macrobenthic distribution of the estuarine system, but temporally, there is room for concern. While the overall abundance of species has remained relatively like that found in 2010, there have been some notable differences, specifically in community structure and dominant species found within the system.

4.4. Community structure

Results of the study indicate that the macrobenthic community structure within the estuary has remained largely consistent from 2010 to 2022. The spatial and temporal distribution of macrobenthos in estuaries has been linked to several variables, of which salinity and sediment type are considered the most important (Hodgson, 1987; Teske & Wooldridge, 2003). Freshwater and marine inflow are important in establishing both salinity gradients and sediment distribution in estuaries, which contribute to changes in habitat availability for selected species (Hofmeister et al., 2017; Bezuidenhout, 2011; Bate et al., 2002b). Given that the Kariega Estuary is regarded as a homogenous marine-dominated system, the absence of any horizontal gradient in the macrobenthic community composition is not unexpected. Again, this result is consistent with studies conducted elsewhere in the world where coastal systems, such as lagoon, are marine dominated (Chardy and Clavier, 1988; Mistri et al. 2001). At a local scale, variations in the macrobenthic community structure probably reflect the

complex interactions between a variety of abiotic (temperature, salinity and sediment type) and biotic (availability of refugia, food availability and biological interactions such as competition and predation) (Njozela, 2013; Bezuidenhout, 2011; Booth, 2007).

The quasipoisson generalised linear models found no significant effect of environmental variables (distance from the mouth, salinity, temperature and sediment organic content) on the abundance and biomass of macrobenthos in the Kariega Estuary during the present study. The absence of any significant relationships probably reflects the complex interaction between abiotic (temperature, salinity, and habitat availability) and biotic (food availability, competition, predation and exploitation) variables that ultimately influence the abundance and distribution of the macrobenthos in estuaries (Njozela, 2013; Ysebaert et al., 2003; Mabaso, 2002). It is worth noting that the highest macrobenthic abundances and biomass during both surveys were recorded in the middle reach of the system, coinciding with the highest submerged vegetation biomass. Submerged macrophytes are thought to provide benthic organisms with refugia against predation and are considered areas of increased food availability (Cheng et al., 2017; Human et al., 2015; Henninger et al., 2009; Lloret & Marín, 2009).

4.5. Dominant species

Despite the absence of any apparent temporal patterns in the overall macrobenthic community structure from 2012 to 2022, notable species-specific changes in their abundances were noted, particularly in the lower reach of the system (Figure 3.9). Densities of the mudprawn (*U. africana*), pencil bait (*S. cylindraceus*) and the common bait worm (*M.sanguinea*) have declined by between 4 and 81% over the past decade. The densities of these species are far below historical records (Henninger & Froneman, 2011; Teske & Wooldridge, 2003; A. Hodgson, 1987). For example, Hodgson (1987) recorded *U. africana* and *S. cylindraceus* densities in the Kariega Estuary of up to 600 ind m^{-2} and 400 ind m^{-2}, respectively. All three species are routinely collected for bait by subsistence and recreational fishers (Lewis & Karageorgopoulos, 2008; Jooste, 2003; Cretchley, 1996). The decline in abundance of the three prominent bait species suggests increased exploitation of resources in the estuary over the past decade. This can likely be attributed to reliance on renewable resources from the estuary due to high poverty levels and unemployment within the Eastern

Cape province of South Africa. Notably, the abundance of pencil bait attained the highest levels in the upper reach of the system, which is largely inaccessible to bait collectors (**Figure 3.9**). The decrease in the abundance of these species is likely to have far-reaching effects on estuarine ecosystem functioning. Pencil bait and sand prawn are important filtration species, removing silt particles and linking primary producers to higher trophic levels (Nel et al., 2013; Hwang et al., 2004; Gerritsen et al., 1994). Furthermore, many target bait species are the preferred prey of estuarine birds and fish (Jooste, 2003).

In addition to the bait species, several non-target species, including *Cleistostoma edwardsii* and *Macoma litoralis*, also demonstrated a decline in abundance over the past decade (**Figure 3.9; Table 3.12**). Studies conducted in a variety of estuaries along the South African coastline (Nel & Branch, 2014; Wynberg & Branch, 1994), and indeed, in other regions of the world, Watson et al., (2017) have shown that bait collection and destructive bait collection practices, e.g., digging, can have long-lasting adverse effects on non-target invertebrate species due to soil compaction and habitat loss, limiting recruitment opportunities (Nel & Branch, 2014)

In Langebaan Lagoon, Western Cape, Nel and Branch (2014) showed that the effects of trampling during the collection of *U. africana* and *Callichirus kraussi* had a more profound impact on the benthic biota of sandflats than the process of bait collection itself. Modifying habitats during bait collection can particularly have long-lasting effects on species that do not have dispersive larvae (Wynberg & Branch, 1994). It is also possible that the decline in non-target species can be attributed to the loss of so-called "promoter" species such as mud prawns and pencil bait. These species enhance sediment oxygenation, mineralization, and sediment composition, creating favourable habitats for other species to recruit (Reise, 2012; Hodgson et al., 2000)

Chapter 5

Conclusions

5.1. Overview

The findings presented in this research highlight the interplay between physicochemical factors, macrophyte biomass, and macrobenthic communities within the permanently open Kariega Estuary over a 12-year period. There were no apparent spatial changes, but temporal changes in the total macrobenthos abundance, biomass and species composition over the study period were shown. The low freshwater inflow, which contributes to the system being a homogenous marine-dominated system, likely contributes to these patterns. Total macrobenthic abundances during both surveys attained the highest levels in the middle reach of the estuary, coinciding with that region where maximum macrophyte biomass and cover were recorded. This highlights the need to implement management strategies to conserve submerged macrophyte beds within the system. There was strong evidence to suggest that the abundances of several benthic species routinely collected for bait, including *U. africana*, *S. cylindraceus*, and *M. sanguinea*, have declined over the past decades, particularly in the lower reach of the system. This study, however, is useful as an indicator for the assessment of other systems within the regions, to better understand the effects of prolonged anthropogenic influence on community structure and health of the coastal ecosystem. Urgent management interventions are necessary to monitor and limit the uncontrolled collection of bait species, particularly within the lower reach of the system.

5.1.1. Overall limitations of the study

While the present study provided insights into the decadal changes in the macrobenthic community structure within the estuary, the investigation was unable to identify the underlying causes of the observed patterns largely due to the absence of key physicochemical (sediment composition, dissolved oxygen concentrations) and biological (habitat complexity associated with the submerged macrophytes, competition and predation) data within the system.

5.1.2. Recommendations and further work

Future studies should focus on better understanding the various physicochemical and biological processes that account for site-specific changes in the macrobenthic community

structure within the estuary. Moreover, the long-term effects of bait collection on habitat modification and its impact on the macrobenthic community structure within the system should be investigated. More so since the exploitation of resources within estuaries is likely to accelerate due to increased urbanization and the ongoing adverse socio-economic conditions that persist within the Eastern Cape province of South Africa.

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Appendix

Chapter 4

Table A1. 2010 Generalised linear model output

Key: ORG- Organic Content, PLAB- Plant Biomass, SAL- Salinity, DIST- Distance from Mouth

```
Call:
glm(formula = ABUND ~ ORG + PLAB + SAL + DIST, family = quasipoisson(),
    data = AbundanceDataPrimer)

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) -3.813e+01  1.218e+01  -3.131  0.00551 **
ORG          1.161e-01  9.108e-02   1.275  0.21772
PLAB         9.772e-04  4.949e-04   1.975  0.06303 .
SAL          1.230e+00  3.343e-01   3.678  0.00160 **
DIST        -5.692e-02  3.984e-02  -1.429  0.16938
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasipoisson family taken to be 556.7906)

    Null deviance: 21720  on 23  degrees of freedom
Residual deviance: 11329  on 19  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 6
```

Table A2. 2022 Generalised linear model output

Key: ORG- Organic Content, PLAB- Plant Biomass, TEMP- Temperature, DIST- Distance from Mouth

```
Call:
glm(formula = ABUND ~ ORG + PLAB + SAL + TEMP, family = quasipoisson(),
    data = AbundanceDataPrimer)

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) -1.357e+01  6.965e+00  -1.949   0.0662 .
ORG          5.374e-01  3.538e-01   1.519   0.1453
PLAB        -6.104e-05  3.620e-04  -0.169   0.8679
SAL          4.309e-02  2.630e-01   0.164   0.8716
TEMP         6.348e-01  2.944e-01   2.156   0.0441 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasipoisson family taken to be 14.72005)

    Null deviance: 696.96  on 23  degrees of freedom
Residual deviance: 289.45  on 19  degrees of freedom
AIC: NA
```